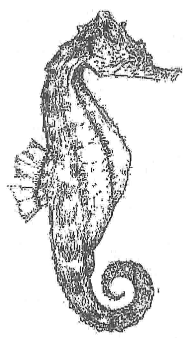
Sladek Nowlis, J, and A Friedlander. 2005. Marine reserve function and design for fisheries management. Pp. 280-301 in *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity* (EA Norse, LB Crowder, eds.). Island Press, Washington, DC (USA).

Marine Conservation Biology

THE SCIENCE OF MAINTAINING THE SEA'S BIODIVERSITY



Edited by Elliott A. Norse
and Larry B. Crowder

Foreword by Michael E. Soulé

Marine Conservation Biology Institute

ISLANDPRESS

WASHINGTON • COVELO • LONDON

COVER IMAGE: Steller's sea cow (*Hydrodamalis gigas*), a giantic North Pacific sirenian, in its kelp forest ecosystem (extinct 1798). © 2005 Ray Troll, www.trollart.com

Seahorse © 2004 Jamie Kelley

The authors and editors have made good faith efforts to secure permission to reprint the following figure, and have been unsuccessful in doing so. If the copyright holders will contact the publisher, any necessary corrections can be made to future printings.

Figure 12.2, page 200, from Sainsbury, J.C. (1996). *Commercial Fishing Methods: An Introduction to Vessels and Gears*. 3rd ed. Fishing New Books, Oxford (UK)

Library of Congress Cataloging-in-Publication Data

Marine conservation biology : the science of maintaining the sea's biodiversity / edited by Elliot A. Norse and Larry B. Crowder ; foreword by Michael E. Soulé
p. cm.
Includes bibliographical references and index.
ISBN 1-55963-661-0 (cloth : alk. paper)—
ISBN 1-55963-662-9 (pbk. : alk. paper)
1. Marine biological diversity conservation.
I. Norse, Elliot A. II. Crowder, Larry B. III. Title.

QH91.8.B6M37 2005
333.95'616—dc22 2004029346

British Cataloguing-in-Publication data available.

Printed on recycled, acid-free paper

Design by BookMatters, Berkeley

Manufactured in the United States of America
10 9 8 7 6 5 4 3 2 1

17 Marine Reserve Function and Design for Fisheries Management

Joshua Sladek Nowlis and Alan Friedlander

Marine reserves—areas permanently protected from fishing and other major human impacts—are especially controversial in fisheries management despite their use by some cultures for centuries (e.g., Johannes 1978; McEvoy 1986) and the use of less permanent closures by Western fisheries management for decades (e.g., Beverton and Holt 1957; Swarztrauber 1972). Reserves have fundamentally different outcomes than other fishery management tools. They reallocate fishing effort in space and protect populations, habitats, and ecosystems within their borders. As a result, they provide a spatial refuge for the ecological systems they contain. They also provide a powerful buffer against overfishing (Figure 17.1) (NRC 2001). Without reserves, heavier fishing pressure results in a higher proportion of the total population being caught, until it eventually balances at low population abundance from the difficulty of catching sparse fish. However, if managers create large and effective reserves, a substantial fraction of the population is off limits to fishing, thus making it virtually impossible to achieve high fishing mortality rates (the proportion of the population killed by fishing per unit time). If people fish harder, the reserve contains a greater total fraction of the population, thus effectively controlling fishing mortality rates.

Many other management tools—including size limits, gear limits, quota systems on effort or total catch, and even temporary closures—are used frequently but do not create a refuge for populations, habitats, and ecosystems, nor do they reallocate fishing effort across space. The failure of these more conventional management tools is apparent in the status of fished populations around the world. In 2000, it was estimated that three-quarters of major world fisheries were fished to or beyond their maximum capacity (FAO 2000), including reductions in large predatory fish populations to as little as one-tenth of their historic abundance (Myers and Worm 2003). Fished populations in the United States fared as badly despite the expenditure of substantial management resources (Sladek Nowlis and Bollermann 2002). Several challenges contribute to these management failures, including excessive fishing capacity (FAO 2000), environments degraded by fishing and other activities (Watling and Norse 1998), and management systems that require far more information than is available (NRC 1998; PDT 1990; Sladek Nowlis and Bollermann 2002). Marine reserves can make substantial contributions toward addressing some of these challenges, but they are not a panacea. For example, reserves do not necessarily address fishing capacity problems, although they can contribute by providing alternative employment opportunities (e.g., McClanahan and Kaunda-Arara 1996; Russ and Alcala 1999). They are also not necessarily the best way to protect popula-

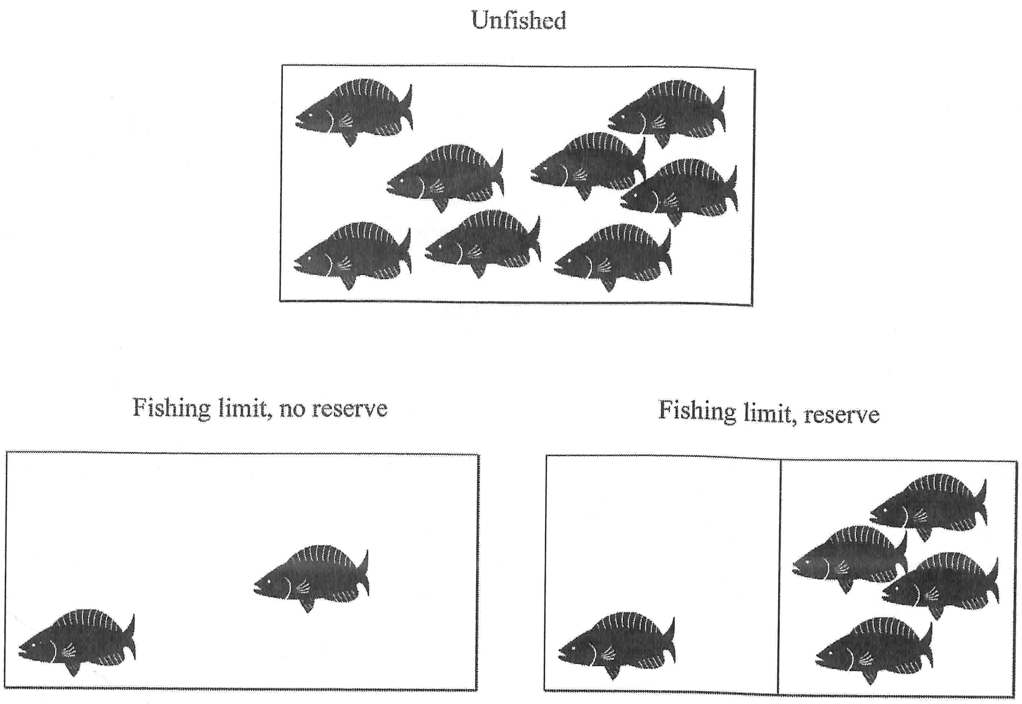


FIGURE 17.1. Marine reserves can reduce fishing mortality rates. Without reserves, fishing is ultimately limited by sparse fish, when even small catches take a substantial fraction of the population. With reserves, when catches are limited by sparse fish outside the reserve, the population inside constitutes a substantial amount of the total population. As a result, catches only take a small fraction of the total population, keeping fishing mortality rates low.

tions of highly mobile species (Bohnsack 1996; Sladek Nowlis and Bollermann 2002; but see Norse et al., Chapter 18).

Concern over fishing activity often drives marine reserve efforts. Unlike many other human threats (e.g., non–point-source pollution, global warming), fishing takes place at specific locations and can be effectively regulated spatially. At the same time, fishing is nearly ubiquitous, taking place in virtually every marine habitat (Vitousek et al. 1997). Consequently, reserve creation is bound to displace some fishers and have short-term negative consequences, at least for them. This potential for displacement motivates fishing communities and industries to become substantially involved in the designation of marine reserves. Their involvement can be an asset to the resulting reserve or reserve network because they play an important role in the enforceability and social acceptability of reserves (NRC 2001; PDT 1990; Proulx 1998; Sladek Nowlis and Friedlander 2004a). As long as the fishing considerations include long-term sustainability, there is likely to be substantial common ground with conservation interests (Appeldoorn and Recksiek 2000).

Benefits, Limitations, and Costs

Designing and evaluating the success of management choices is always easier if goals and objectives are specified (Ballantine 1997; Sladek Nowlis 2004a). This section discusses some major goals of fisheries management and the degree to which marine reserves are likely to satisfy them. Other nonfishery goals are discussed elsewhere in this volume (Roberts, Chapter 16) but might play an important role in the designation of marine reserves and broader marine zoning efforts.

Enhancing Catches

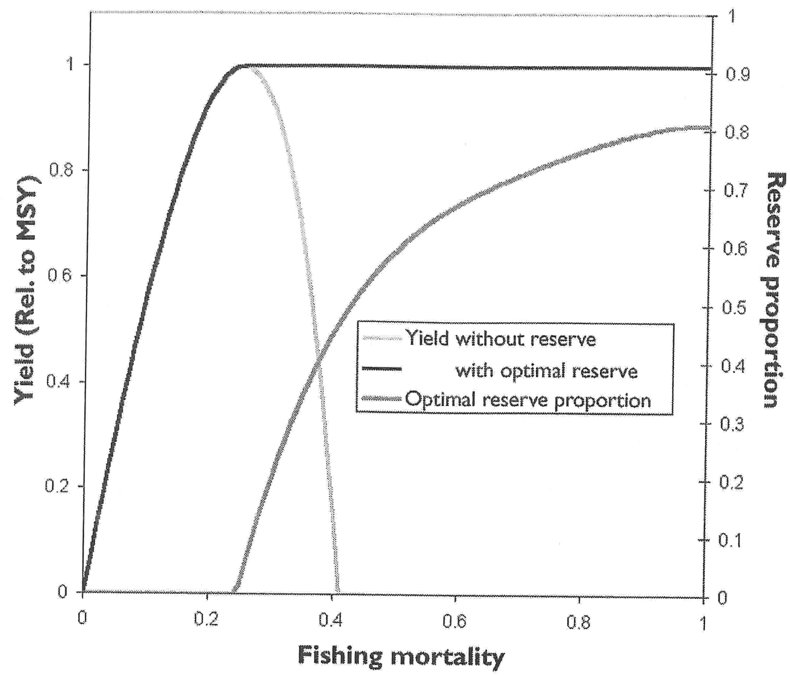
Catching more fish is an obvious potential goal of fisheries management. However, few managers now focus their efforts on immediately enhancing catches. Instead, managers tend to focus on rebuilding overfished fisheries, and hope that catches are enhanced in the future by a successful rebuilding plan. The capacity of marine reserves to rebuild overfished fisheries and thereby enhance catches is well supported by theory (Figure 17.2a) (Beverton and Holt 1957; DeMartini 1993; Polacheck 1990; Sladek Nowlis and Roberts 1999) and what empirical evidence exists (discussed in later sections). Studies predicted only substantial fishery enhancements, though, for fisheries on species whose adults generally stayed within reserve boundaries and whose eggs and larvae dispersed widely enough to make a substantial contribution to fishing areas (Sladek Nowlis and Roberts 1999). Studies of movement and dispersal capacities indicate that these conditions are quite common but not at all universal. Studies with more detailed socioeconomic attributes suggest that benefits might be even rarer than the biologically focused models indicate but are still most likely to produce benefits in overfished fisheries (Smith and Wilen 2003).

What reserves offer that other management tools cannot is an ability to control fishing rates in a manner that is relatively easy to enforce (PDT 1990; Sladek Nowlis and Friedlander 2004a) and requires relatively little scientific information (Sladek Nowlis and Bollermann 2002). In fact, Johannes (1998) identified marine reserves as a fundamental tool for what he termed "dataless" management. Reserves are an attractive option for regions without existing capacity for fisheries management for these reasons and because they can be designed and implemented on a local level (Castilla and Fernández 1998; Russ and Alcala 1999).

Marine reserves have the often-unrecognized potential to play similar roles in places with developed fishery management systems. Reserves can make a tremendous difference for the many "unknown" species in regions with existing management capacity (e.g., three-fourths of all fisheries managed by the US government; data compiled from NMFS 2002). They can also help with controlling bycatch, the incidental killing of fish not brought into port. Fishery managers in countries with fishery management capacity typically focus on how much fish is brought into port, using rough, inaccurate, or no estimates of how many additional fish were killed through bycatch. Reserves can reduce the impact of bycatch by providing a refuge for vulnerable species that otherwise might be depleted (PDT 1990). However, we should not necessarily expect reserves to enhance catches of fisheries with adequate existing controls or for fisheries that target highly mobile species. These situations are the exception, not the rule.

The openness and dynamic nature of marine environments make it extremely difficult to prove fisheries enhancements statistically because of the difficulty of separating reserve effects from other changes that might have occurred (PDT 1990; Sladek Nowlis and Friedlander 2004b). For example, if catches increase in an area after reserve creation, it does not rule out the possibility that a more productive set of marine conditions developed. To make these distinctions, statistical analyses require replication of reserve and nonreserve systems. Even if one were to navigate political systems successfully and create independent reserve or reserve networks in several regions while leaving several other regions without reserves, the comparison across regions experiencing different natural and human impacts would tend to confound the statistical results. These confounding influences make it nearly impossible to provide scientific proof that marine reserves enhance fisheries (Sladek Nowlis and Friedlander 2004b).

This is not a compelling reason to reject marine reserves, though, because the same challenges make it nearly impossible to prove the capacity of any other fishery management tool to enhance catches. For other tools, we believe they work if they are supported by a logical theory and if practical experience suggests they promote better long-term sustainable fishing. Marine reserves are supported by this sort of evidence as well a.



b.

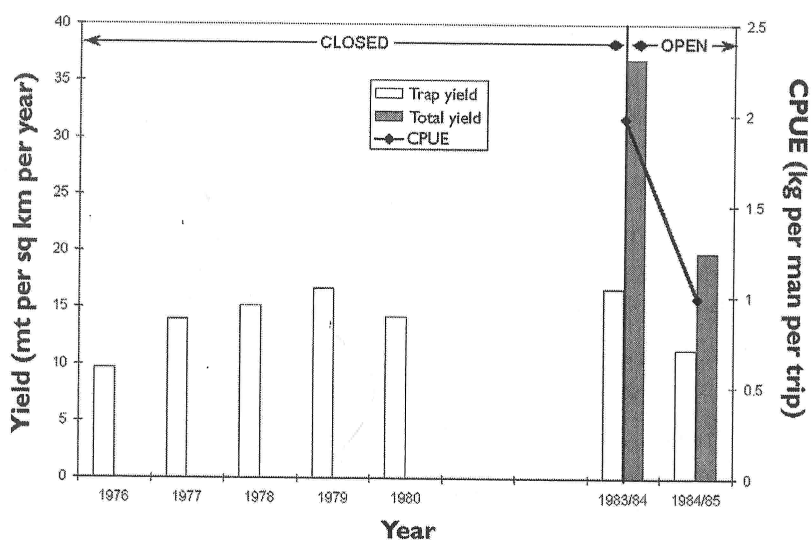


FIGURE 17.2. Marine reserves can provide catch enhancements. 17.2a: Reserves can enhance catches for overfished fisheries and achieve catches equal to maximum yields from fisheries managed perfectly using conventional management tools (data from Sladek Nowlis and Roberts 1999). 17.2b: Total catches and catch per unit effort (CPUE) dropped when a marine reserve on Sumilon Island, Philippines, was reopened to fishing in 1984 (data from Alcala and Russ 1990).

as any other fishery management technique in use today (Sladek Nowlis and Friedlander 2004b).

Two of the most widely cited studies examining marine reserves' effects on fisheries come from Apo and Sumilon Islands in the central Philippines (Russ and Alcala 1999). At Apo Island, Russ and Alcala (1996) found evidence of catch enhancements from a reserve encompassing 10 percent of coastal waters. They demonstrated increased abundance of adult fishes near the reserve border, and all the fishermen they interviewed believed their catch had at least doubled since the reserve was created nine years prior to the study. Even more convincing evidence came from Sumilon Island, where political reversals created, eliminated, created, and eliminated again a marine reserve encompassing approximately 25 percent of the island. Ten years after its creation, a local ordinance permitted fishing in the reserve, in conflict with national law that prohibited it, and fishing recommenced. Over the next two years, despite the increased fishing area and, at least initially, greater amounts of fish available from inside the former marine reserve, both total catch and catch per unit effort declined to half of their previous values (Figure 17.2b). This evidence strongly suggests that the reserve had contributed to higher sustained catches. The entire island was closed to fishing in the late 1980s, accompanied by a buildup of fish biomass. Since 1992, the area has been fished despite the national law, and fish biomass has declined.

Roberts and colleagues (2001) demonstrated similar effects from a reserve that encompassed about 35 percent of the southwestern management area on the Caribbean island of St. Lucia. Total catches and catch per unit effort had increased five years after reserve creation, as had the abundance of fishes in both the reserve and adjacent fished areas. These increases came despite a 35 percent reduction in fishing grounds and consistent effort levels. McClanahan and Kaunda-Arara (1996) also showed a dramatic doubling of catch per unit effort following the closure of over 60 percent of the fishing grounds around Mombasa, Kenya, after only two years. Though catches had not yet exceeded prereserve levels, they were close—an impressive result coming only two years after fishing grounds were reduced to 40 percent of their former size.

Other studies have identified contributions from marine reserves to surrounding fishing grounds but lacked the capacity to test whether overall catches had increased. In the Exuma Cays, Bahamas, populations of the Nassau grouper (*Epinephelus striatus*) within 5 kilometers of a reserve border were observed to be more similar to sites inside the park than those more than 5 kilometers away (Sluka et al. 1997). Johnson and colleagues (1999) demonstrated that, in addition to a buildup of biomass within a reserve off Cape Canaveral, Florida (USA), some fish moved in and out of the reserve, called the spillover effect. Consequently, a number of world record trophy fish were caught in the vicinity of the reserve (Roberts et al. 2001). In sum, the field evidence, when combined with strong theoretical support, indicates that marine reserves can enhance fish catches effectively. This scientific evidence matches or exceeds the support for any other fishery management tool (Sladek Nowlis and Friedlander 2004b).

Insuring against Uncertainty

Insurance against uncertainty would be desirable for the long-term prospects of most fishing fleets. Most fisheries, even those that are actively managed and well studied, are prone to crashing because management reference points have a high likelihood of being off by 50 percent or more (NRC 1998). The most effective way to counter uncertainty is responsiveness. When fishery management systems respond rapidly to evidence of fish declines by reducing fishing rates decisively, fisheries are much less likely to collapse even if information is wrong or unavailable (Figure 17.3) (Sladek Nowlis and Bollermann 2002). This responsiveness is best achieved by protecting a set amount of fish from fishing through marine reserves, size limits, or abundance-based quota-setting systems. By protecting a set amount of fish, and thereby providing responsiveness, marine reserves have shown strong potential to protect stocks from collapse in

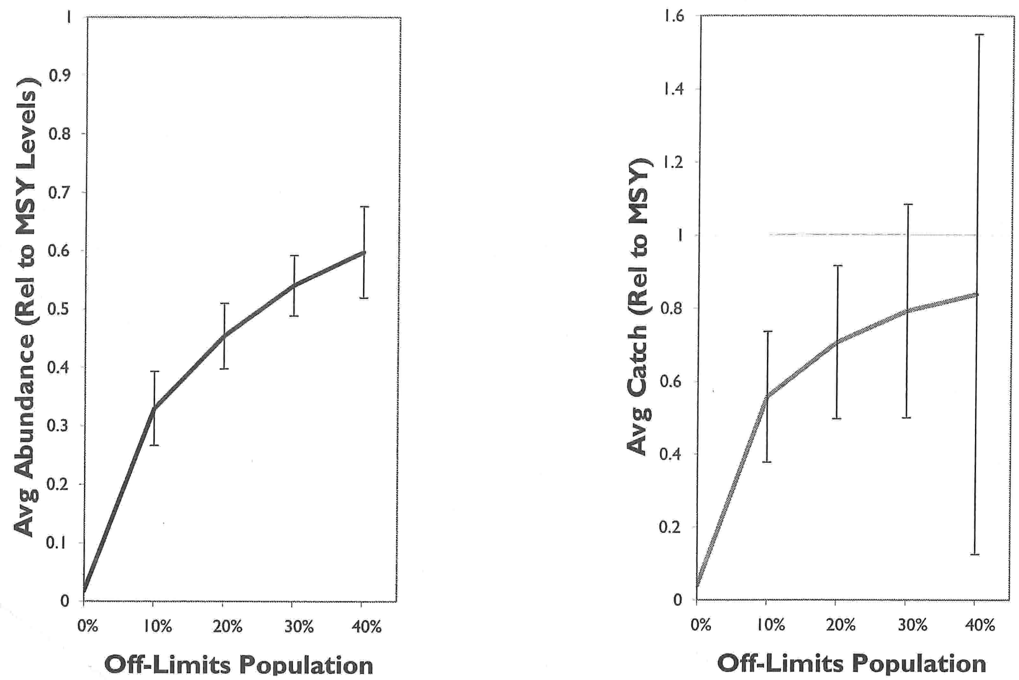


FIGURE 17.3. Marine reserves can provide insurance against management mistakes. Management systems were more robust to 50% errors in two key parameter estimates and a moderately variable and unpredictable environment when part of the fish population was off-limits to all fishing. Without an off-limits population, this scenario led to a crash in abundance (a) and the productivity (b) of the fishery. Both increased with increasing size of the off-limits population such that average abundance was 60% of the maximally productive level and average catches were 80% of maximum possible levels when 40% of the population was off-limits, despite the management errors described above (data from Sladek Nowlis and Bollermann 2002). Error bars represent one standard deviation.

varying and uncertain environments (Lauck et al. 1998; Mangel 1998; Sladek Nowlis and Bollermann 2002). In contrast, common fishery management techniques—such as setting constant catch limits regardless of current abundance or even as a constant fraction of current abundance—lack resiliency in the face of uncertainties (Sladek Nowlis 2004a).

Most species and virtually every habitat have the potential to be insured through the use of marine reserves. For some highly mobile species, size limits or responsive quota systems might provide better insurance. For the rest, reserves have advantages over the other responsive techniques in that they require less information, are implemented more easily, and apply more universally to multispecies fisheries (PDT 1990; Ricker 1958).

Traditional practices by indigenous people provide evidence of the value of setting aside a healthy amount of fish and managing responsively as an insurance policy. Pacific Islanders relied on strict and proactive fishery management systems, including frequent creation of closed areas (Johannes 1978). The traditional system in Hawaii (pre-1800) emphasized social and cultural controls on fishing with a code of conduct that was strictly enforced. Fishery management systems were not based on overall catch quotas. Instead, they identified the specific times and places that fishing could occur so as not to disrupt basic processes and habitats of important food resources (Friedlander et al. 2002; Poepoe et al. 2003). Similarly, indigenous groups in northern California relied on strict religion-based fishery management systems that ensured numerous salmon would reach tributaries and reproduce, even if that meant hardship for some people (McEvoy 1986). These systems sustained highly productive fisheries for centuries, even by modern standards, despite a complete lack of formal scientific data, highlighting the value of setting aside unfished portions of populations.

Today, some fishery managers have begun to move toward quota policies that utilize reserved populations. Groundfish in the US North Pacific are managed under a system that reduces fishing rates when some fished populations drop below target abundances, but only provides limited insurance because fishing does not end until a population reaches 2 percent of its unfished abundance, and only the best-studied populations are managed this way (NPFMC 1998). Groundfish along the US West Coast are managed with a system that recommends ending fishing when a population reaches 10 percent of its unfished abundance (PFMC 1998). However, this policy is optional and managers have consistently provided a catch quota—as a way of avoiding discarded bycatch at sea—on populations that have dropped to levels as low as 2 to 4 percent of their unfished abundance. Most recently, the State of California has proposed a plan that would end fishing if a population dropped below 20 percent of its unfished abundance (CDFG 2002), but no species yet qualify for management under this plan. We have a long way to go to ensure the future of fish populations, fishing communities, and marine ecosystems across the globe. Large reserve networks are certain to play a central role in providing this insurance in the future.

Preserving Desirable Traits

Selective fishing can affect a number of population characteristics—size and age composition, sex ratio, genetic makeup, and large-scale behavioral phenomena like spawning aggregations (PDT 1990). Numerous species of fish aggregate to spawn in both tropical (Johannes 1978; Johannes et al. 1999; Sadovy 1996) and temperate (Cushing 1995) marine environments. Because spawning aggregations are often predictable in space and time, they leave fish highly vulnerable to fishing. Several grouper and snapper species have been greatly depleted throughout the world, largely due to extreme exploitation of spawning aggregations. Despite the ecological importance and vulnerability of spawning aggregations, few have been closed to fishing.

Because selective fishing usually removes individuals with desirable fishery traits, those that remain can pass on less preferred characteristics (Law and Stokes, Chapter 14) and confound future fishing efforts. Closures can help to protect aggregating behaviors and other desirable traits. Due to the loss of a Nassau grouper (*Epinephelus striatus*) spawning aggregation and evidence of decline of another grouper species, red hind (*E. guttatus*), a seasonal closure was implemented at a spawning aggregation site in the US Virgin Islands in 1990 (Beets and Friedlander 1992). The closure was based on data that demonstrated a decline in catch per unit effort and average length for red hind (Figure 17.4), and a low number of males landed (Beets and Friedlander 1999). Since red hind change sex from female to male, the loss of large individuals—primarily males—in the population potentially could result in reduced productivity due to sperm limitation (Sadovy 1996). Moreover, larger fish were desirable to catch, so the loss of large males and decreased average size represented a decline in desirable fishery traits.

An evaluation of the red hind spawning aggregation within this closed area after more than a decade suggested a large increase in average size of fish (Fig. 17.4) and a great improvement in the sex ratio, with many large males in the sample (Beets and Friedlander 1999). Moreover, fishers reported increased red hind landings throughout the region. The protection of the spawning aggregation for red hind has apparently reversed the previous declining trend in desirable fishery traits.

Maintaining System Productivity

Can marine reserves protect habitats from destructive fishing practices? The key issue is whether marine reserves concentrate fishing effort in remaining fishing grounds and, if so, whether this leads to a net gain or loss in habitat quality. In some cases, fishing effort de-

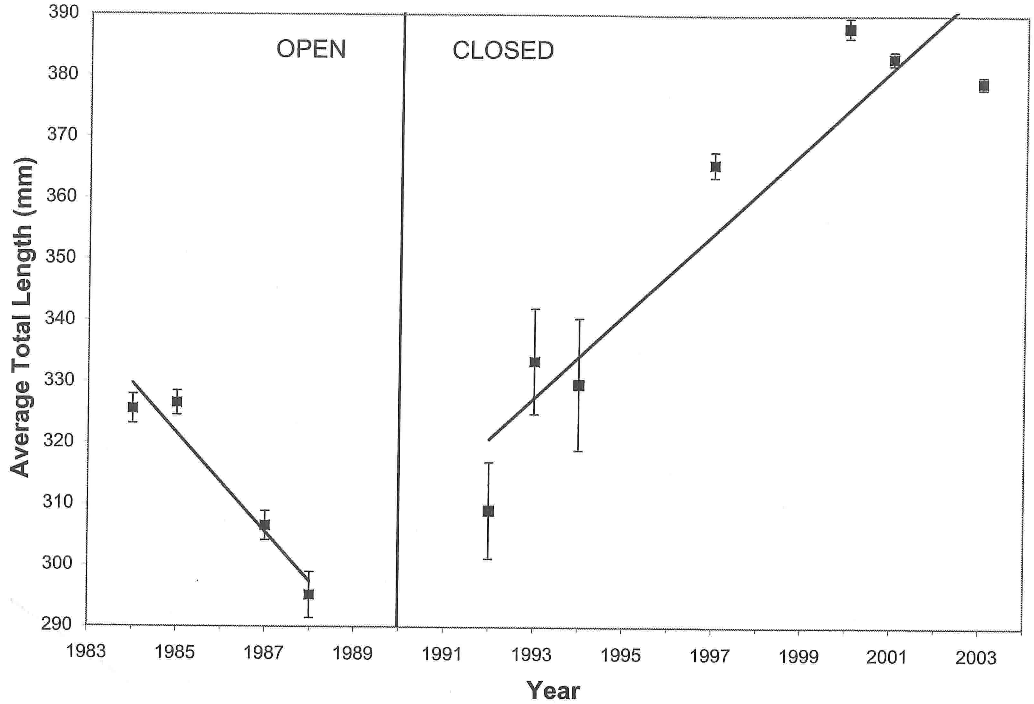


FIGURE 17.4. Marine reserves can protect desirable fish stock traits. Average total length frequency data for red hind, St. Thomas, US Virgin Islands, from fishery landings, 1984–1994 and spawning aggregation investigations, 1997–2003 (data from Beets and Friedlander 1992, 1999; Nemeth 2004; Whiteman et al., in press). The spawning aggregation site was closed to fishing seasonally starting in 1990 and year-round starting in 1998. Error bars represent one standard error of the mean, and lines indicate significant regressions ($R^2 = 0.8698$ and 0.9321, respectively). Data from 1986 were excluded because of incompatible methods.

creases in response to reserves (e.g., McClanahan and Kaunda-Arara 1996). In these cases, it is fairly clear that habitats have received protection. Even when fishing effort is reallocated and concentrated as a result of reserve creation, marine reserves can reduce habitat impacts if either of two conditions is met.

First, marine reserves can lead to overall habitat protection if reserves preferentially encompass vulnerable habitats. A deep-water coral bank, for example, is far more vulnerable to impacts from bottom fishing gear than a sandy area without living or nonliving habitat structures. If a reserve displaces effort from the coral bank to sand, it will provide overall habitat protection.

The second condition is more complicated. Marine reserves can lead to overall habitat protection if concentrated fishing effort does less cumulative damage than more widespread, but less intense, fishing. This boils down to a question of whether fishing activity does more damage to an area the first time or on subsequent efforts, and the answer lies in the recovery time of the system involved. If recovery is quick, then concentrated fishing effort is more likely to overwhelm that recovery, making reserves less likely to protect habitat. Alternatively, if recovery is slow, the first fishing effort is likely to do more damage than subsequent fishing on an already damaged system. Since habitat features are often nonliving and shaped by geology, or are slow-growing living organisms, habitats are likely to recover slowly from fishing practices that cause physical damage. Consequently, we should expect that reserves provide overall habitat

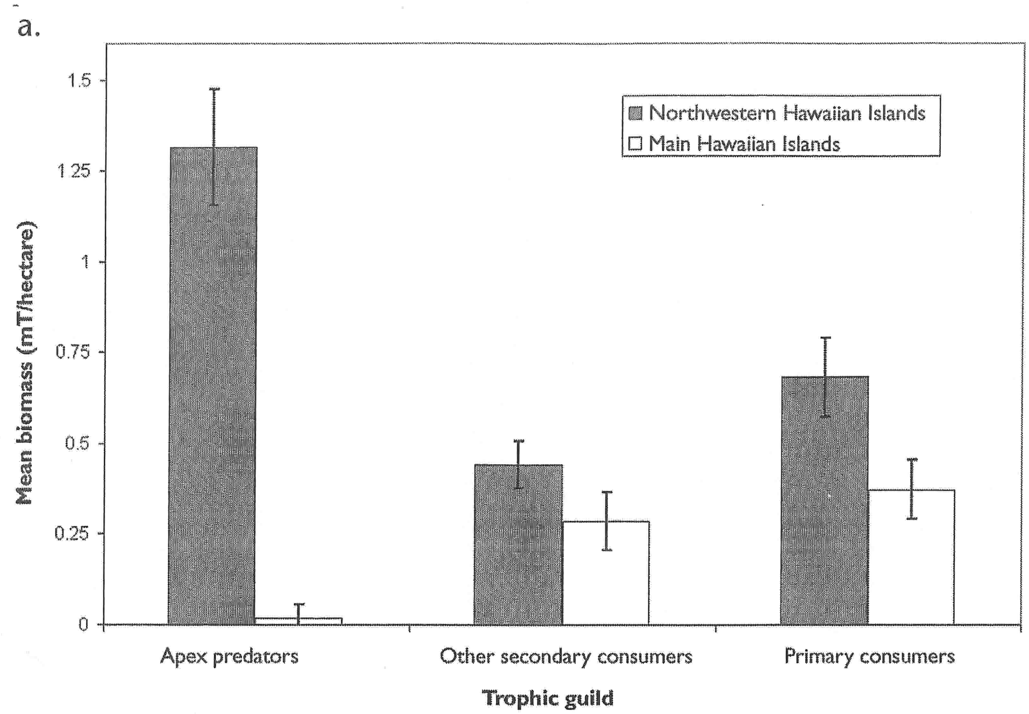


FIGURE 17.5. Marine reserves conserve natural ecosystem balances and system productivity. 17.5a (above): Lightly fished areas in the Northwestern Hawaiian Islands contain greater biomass of all trophic guilds than sites in the main Hawaiian Islands (data from Friedlander and DeMartini 2002). The difference is especially large for apex predators, which account for the majority of all biomass in the Northwestern Hawaiian Islands. 17.5b and 17.5c (right): A small marine reserve in the Channel Islands, California, maintained greater abundance of sea urchin predators than nearby fished areas. These have kept white and purple sea urchins in check within the reserve though they have exploded in fished areas, wiping out the kelp that sustains kelp forest ecosystems (data from Sladek Nowlis, in press).

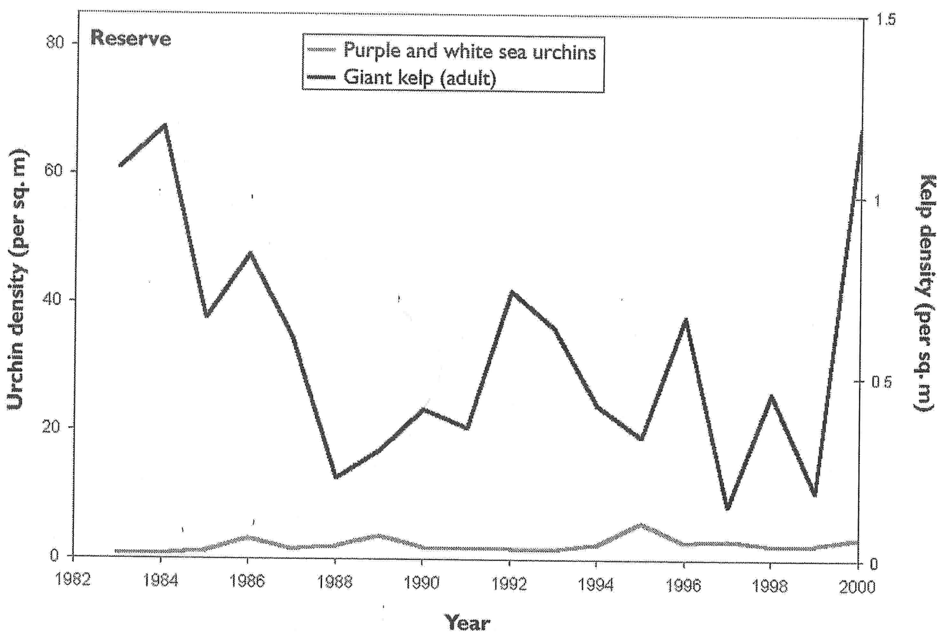
protection more often than not as long as the areas encompassed have not been damaged beyond recoverability and represent more vulnerable habitats.

System productivity can also be reduced by fishing activity through the disruption of species interactions (Jackson et al. 2001). For example, fish assemblages in the Northwestern Hawaiian Islands—a remote area that experiences only limited fishing activity—are dominated by large apex predators, such as sharks and jacks, which likely have a profound impact on the structure of the entire coral reef ecosystem (Figure 17.5a) (Friedlander and DeMartini 2002). This trophic dynamic is in sharp contrast to fish assemblages in the heavily fished main Hawaiian Islands and throughout tropical coral reef ecosystems where herbivores make up the majority of the reef fish biomass.

The result of these population changes can have severe consequences for marine ecosystems (Jackson et al. 2001). In the Channel Islands, California (USA), fishing has caused ecosystem-wide degradation by reducing the numbers of the two major sea urchin predators, California spiny lobster (*Panulirus interruptus*) and sheephead wrasse (*Semicossyphus pulcher*) (Sladek Nowlis 2004b). These changes have led to a cascading effect of urchin explosions and, ultimately, kelp loss (Figure 17.5b), whereas sites within a small marine reserve have maintained a more natural balance (Figure 17.5c). Results from the Northwestern Hawaiian Is-b.


Fishing Area
Purple and white sea urchins
Giant kelp (adult)
Urchin density (per sq. m)
Kelp density (per sq. m)
Year
0
20
40
60
80
0
0.5
1
1.5
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000

c.


Reserve
Purple and white sea urchins
Giant kelp (adult)
Urchin density (per sq. m)
Kelp density (per sq. m)
Year
0
20
40
60
80
0
0.5
1
1.5
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000

lands and Channel Islands demonstrate that reserves can conserve thriving natural ecosystems within their borders even when fishing activity has wreaked havoc outside. Since ecosystems, like habitat structures, are generally slow to recover from fishing impacts, reserves are likely to produce net ecosystem benefits even if they concentrate fishing efforts.

Providing Unfished Reference Areas

As stated earlier, distinguishing between natural and fishery-related changes in marine systems is difficult, which dramatically limits a manager's ability to explain past events and predict future ones. These challenges can range from identifying natural shifts in species abundance to determining natural mortality rates, an essential parameter in fishery management models. Unfished or lightly fished areas have been useful for gathering natural history information and improving management systems (PDT 1990). For example, Polovina (1994) used minimally disturbed areas to implicate the climate, rather than fishing, in the decline of Hawaiian lobsters (*Panulirus* spp.) In fact, the best information available on the impacts of fishing activity on marine populations, habitats, and ecosystems has come through comparison of closed or lightly fished areas to heavily fished areas.

However, there are limits to the value of some reserves as reference areas. Marine reserves in the main Hawaiian Islands sustain substantially more fish than sites that receive partial or no site-specific protection from fishing (Figure 17.6). Thus it might be tempting to view the marine reserves as indicators of what fish populations would look like in the absence of fishing. However, if these marine reserves are compared to sites in the remote, lightly fished, and expansive Northwestern Hawaiian Islands, a different picture emerges. Despite limitations on coral reef fish productivity in the Northwestern Hawaiian Islands due to northerly latitudes and restricted habitat structure, sites there contained significantly more fish than marine reserves in the main Hawaiian Islands (see Figure 17.6) (Friedlander and DeMartini 2002; Friedlander et al. 2003a). The difference is explained primarily by the virtual absence of large predators in the main Hawaiian Islands due to fishing. Consequently, the marine reserves in the main Hawaiian Islands have some limits on their value as reference areas. They are helpful in demonstrating that fishing drives down fish abundance, understanding the impacts of human activities other than fishing, and perhaps even giving a glimpse of something approximating unfished abundance for many species other than top predators. However, these Hawaiian marine reserves do not produce ecosystems unimpacted from fishing because they are too small (collectively encompassing 0.3 percent of Hawaiian state waters; Gulko et al. 2000) and the fishing impacts surrounding them are too large. Even if they were large and fishing impacts were light, we should not necessarily expect reserves to contain unfished abundance levels for highly mobile species.

Limitations Due to Fish Movement

Marine reserves work best for species with sedentary adult and mobile but partially retained egg and larval stages. The degree to which marine reserves leak eggs, larvae, and adults is a function not only of the biology of the species but also of the reserve design (Carr and Reed 1993). There are important implications for the leakiness of reproduction from marine reserves. A leaky reserve can provide eggs and larvae to sustain fished areas. Therefore, from a fisheries perspective, this leakiness is generally a good thing. However, if insufficient amounts of eggs and larvae are retained within the reserve or reserve network, all population-level benefits can be compromised. Most marine species have the potential to both retain eggs and larvae within reserves and provide long-distance–dispersing larvae to outside areas. Larval durations vary tremendously, from hours to months, with an equally broad range for potential dispersal distances (Shanks et al. 2003; Palumbi and Hedgecock, Chapter 3). Over a period of a month or two, larvae have the potential to move throughout a region by drifting with surface currents (Roberts 1997). However, larval behavior, inshore turbulence, and diffusion can all result in a substantial amount of local retention of eggs and larvae (Cowen et al. 2000). Recent

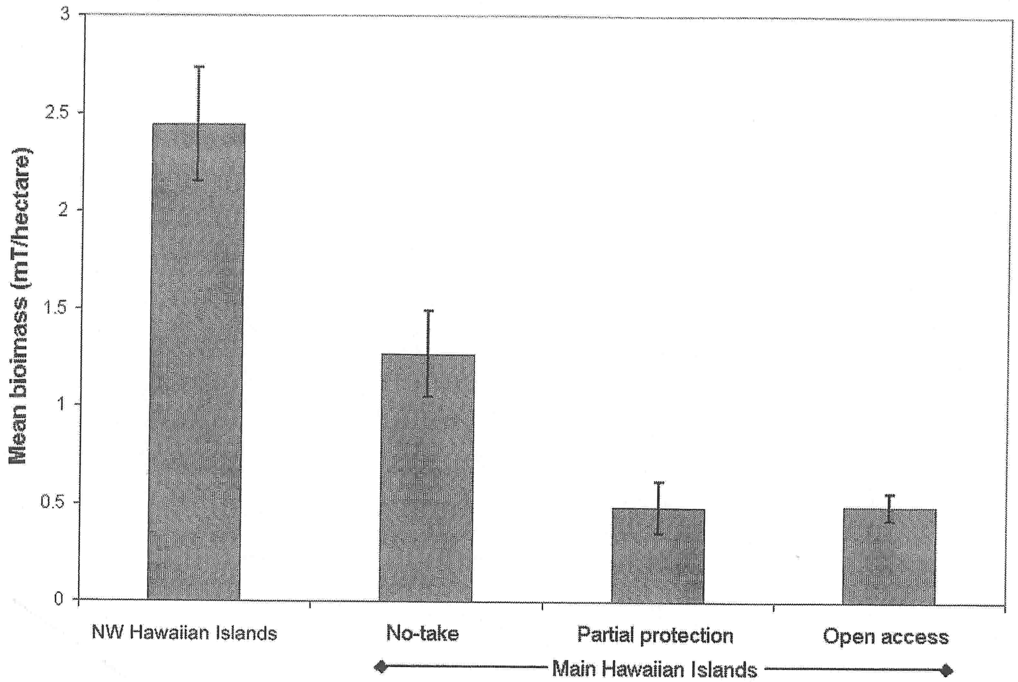


FIGURE 17.6. The size of marine reserves limits their effectiveness as reference areas. Main Hawaiian marine reserves have significantly higher fish biomass than partially protected or open access areas (data from Friedlander and DeMartini 2002; Friedlander et al., 2003a). However, even these small reserves do not measure up to the much larger, lightly fished Northwestern Hawaiian Islands, demonstrating that small, sparse reserves will not necessarily reestablish pristine populations.

field studies of fishes with high larval dispersal potential have indicated that many individuals spend their larval period in close proximity to where they were produced (Jones et al. 1999; Swearer et al. 1999) although a few may disperse far away. This mixed strategy should come as no surprise, as it has been shown to be highly effective ecologically and evolutionarily (Cohen and Levin 1987).

Regarding adults, retention and population growth rates provide the engine to power all population-level benefits. Therefore, from a fisheries perspective, leakiness of adults—known as the spillover effect—is generally a bad thing (Sladek Nowlis and Roberts 1999). Fortunately, most species are fairly sedentary as adults. Many species live attached to the bottom in their adult phase, including many marine plants and invertebrates, while other species of fishes and invertebrates maintain small home ranges for their adult lives. Emerging evidence about fish movement suggests that even fish with the potential to swim long distances might stay in the same area for long periods of time, as shown in Table 17.1 (e.g., Attwood and Bennett 1994; Holland et al. 1996). In support of this notion is the fact that most populations studied in marine reserves responded positively to protection, even though many of the reserves were small (Halpern 2003). Few species are highly mobile, but these are often targets of fishing efforts.

For these species, spillover does have the potential to provide trophy-fishing opportunities (Roberts et al. 2001) and also mitigates against costs associated with marine reserves. Moreover, reserves have the capacity to reduce overall fishing rates on these species by making them off limits for limited time periods (Guénette et al. 2000). Finally, marine reserves do offer the opportunity to protect vulnerable stages or habitats for these species, including spawning aggregations and juvenile nursery areas (NRC 2001).

TABLE 17.1. Low Movement Tendencies Despite Long-Distance Dispersal Abilities

Distance from Release	*Number*	*Percent of Total*
Galjoen[a]		
0–5 km	828	82.1
25–75 km	57	5.6
75–125 km	39	3.9
125–175 km	24	2.4
175–225 km	26	2.6
225–275 km	10	1.0
275–325 km	10	1.0
325–1025 km	14	1.4
Total	1008	
Blue Trevally[b]		
0–0.5 km	72	75.5
0.5–1 km	3	3.2
1–2 km	10	10.6
2–3 km	5	5.3
3–75 km	5	5.3
Total	95	

[a] Movement of tagged galjoen (*Coracinus capensis*) in South Africa (data from Attwood and Bennett 1994). Most stayed within 5 km of the release site despite a potential to move over 1000 km.
[b] Movement of tagged blue trevally (*Caranx melampygus*) on Oahu, Hawaii (data from Holland et al. 1996). Most stayed within 0.5 km of the release site despite a potential to move tens of kilometers.

Nevertheless, marine reserves do have limitations, particularly for species that range widely as adults. For these species, we will need additional management measures to complement reserves (Bohnsack 1996). Though some have criticized reserves for banning fishing on such species, given their potential lack of effectiveness there are two very good reasons for doing so: enforcement and unfished reference areas. These issues will be discussed later with respect to regulations and the design of marine reserves.

Costs

Despite their many beneficial traits, reserves do not come free. Short-term catch reductions should be expected with the establishment of new marine reserves, just as they should with any new management restriction. The degree of reduction is determined by the extent of the reserve or reserve network, the present value of the areas it encompasses as fishing grounds, and the extent to which adults are retained within the reserve. Larger, more valuable, and less leaky reserves have the highest costs associated with them. However, these reserves also fuel the greatest benefits.

Sladek Nowlis and Roberts (1997) examined the costs associated with reserves on overfished fisheries where reserves retained adults but leaked larvae. They found catch reductions would be temporary for overfished fisheries if reserves were designed effectively. The duration of these costs, as measured in terms of the time until catches exceeded prereserve levels, depended upon the degree to which the fishery was overfished, with fisheries in poorest condition recovering most quickly. Phasing reserves in over a period of several years reduced the magnitude of short-term costs but also delayed the recovery. Adult movement in and out of reserves would have similar effects of reducing costs but delaying benefits.

Sladek Nowlis (2000) also compared these costs to those associated with other management tools for rebuilding overfished fisheries (Figure 17.7). He showed that, in most circumstances, reserves could rebuild fisheries with fewer short-term costs than other management tools because the full range of fish sizes that developed inside reserves was a superior rebuilding engine to those provided by other tools, which were powered by fish that only grew slightly larger. The exception to this rule was a fishery that caught juveniles. In that case, reserves were less effective than size limits that protected fish until they had a chance to reproduce (Sladek Nowlis 2000). This result was consistent with other studies showing that avoiding the catch of juveniles can contribute substantially to sus-

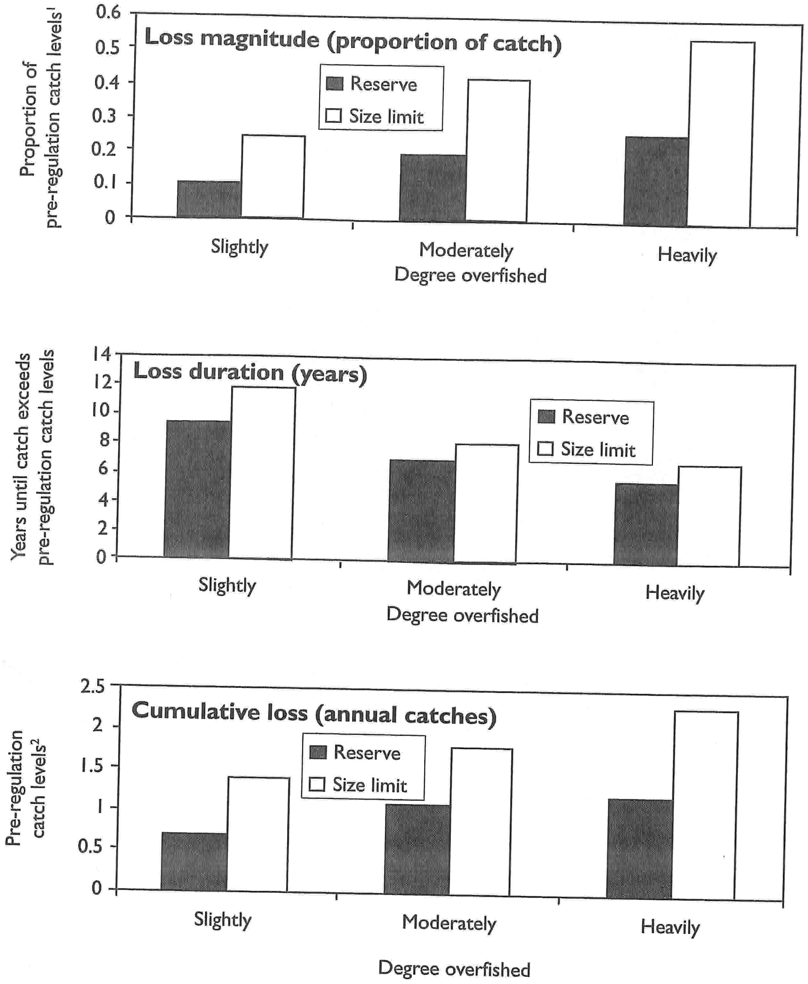


FIGURE 17.7. Marine reserves reduce short-term fishing opportunities less than other management tools. Regardless of the degree to which the red hind was overfished, models indicated that effectively designed marine reserves would cause shorter and less severe short-term losses than effectively designed size limits, resulting in fewer cumulative losses (data from Sladek Nowlis 2000).

[1] 1.0 represents a complete loss of all catch.

[2] 1.0 represents a fishery that lost a year's worth of status quo fish catch during the time it took for the fishery to rebuild to pre-regulation catch levels.

tainable and productive fisheries (Myers and Mertz 1998).

Design Principles

Because of their general utility for protecting populations, habitats, and ecosystems, marine reserves can satisfy a wide range of potential goals. Many of these goals relate to fisheries management, but many others relate to broader management of marine systems. We focus on the biological fishery management goals here—a more complete list and discussion of goals can be found elsewhere (e.g., Bohnsack 1996; PDT 1990; Roberts, Chapter 16). Ideally, a range of goals would be considered simultaneously in an effort to zone the sea to reduce conflict while providing greater protections (Norse, Chapter 25).

The input of people from coastal communities is

TABLE 17.2. Design Principles for Marine Reserves for Fisheries Management

Better	*Worse*
• 20–50 percent of the management area	• Less than 10 percent of the management area
• Straight-line boundaries with clearly defined navigational references	• Irregular boundaries
• Large enough to contain viable populations of species of interest	• Larger than dispersal distances of species targeted by fisheries
• Inclusive of all habitats with an emphasis on special habitats	• Noninclusive of all habitat types and an emphasis on poor-quality habitats
• Stakeholder approved	• Stakeholder opposed
• No fishing, no exceptions	• Exceptions that allow some fishing

This table summarizes better and worse design properties of marine reserve design as discussed in the text.

vital to maintaining public support for and long-term viability of marine reserves. Without this support, enforcement can be compromised greatly (Proulx 1998) and future political changes can lead to the dismantling of marine reserves (Russ and Alcala 1999). Traditional knowledge and local preferences should be focused using a set of general scientific design criteria, as shown in Table 17.2.

Extent of Reserve Network

Studies have shown that the optimal set-aside in reserves, expressed as a fraction of the total fishing area, depends on a variety of factors, including adult movement tendencies, individual growth rates, Allee effects (see Levitan and McGovern, Chapter 4), metapopulation dynamics, socioeconomic factors, and, most importantly, fishing pressure outside the reserve relative to the growth rate of the exploited stock (reviewed in Guénette et al. 1998). Since reserve design depends on so many factors, it is hard to generalize about the optimal design. In fact, Sladek Nowlis and Roberts (1999) demonstrated that the optimal reserve size to maximize catches differed among four species of a coral reef assemblage, assuming the same fishing rate applied to all species, as one might expect in an unselective fishery. The optimum reserve proportion for achieving maximum catches for these four species ranged from 0 to 80 percent, depending on the growth rates of the fish and fishing rates outside the reserve.

In order to ensure productive catches into the future, models have predicted that reserves might have to encompass over half the management area (Lauck et al. 1998; Mangel 1998). Generally, the amount of reserved fish need not exceed the amount necessary to sustain maximal yields (typically assumed to be 40 to 60 percent of unfished abundance). Consequently, a reserve designed to contain 40 to 60 percent of unfished abundance might be sufficient to ensure maximal catches into the future even if there are no other checks on fishing rates. For well-studied fisheries, insurance needs might only require a reserve encompassing 10 to 20 percent (Sladek Nowlis and Bollermann 2002).

The extents mentioned above, ranging from 0 to 80 percent of a management area, need to be scaled up to account for two critical factors. First, some ecosystems are more open than others, and the more open the system, the larger the reserve must be to achieve the same levels of population protection. Second, natural and human-caused catastrophes (e.g., hurricanes and oil spills) are likely to render some of the reserve network nonfunctional at any given time. Analyses of the frequency and extent of such catastrophes have indicated that reserves might need to be scaled up by a factor of 20 to 80 percent (Allison et al. 2003).

Size and Shape of Individual Reserves

A reserve network should be partitioned with two overriding forces in mind: human compliance and fish dispersal. Unless fishers comply with the reserve, it will not function. Compliance is greatly enhanced by involving fishing communities in the designation of marine reserve networks and by making the boundaries of reserves simple (Russ and Alcala 1999; Sladek Nowlis and Friedlander 2004a). Straight boundaries that run north–south or east–west are ideal, while complex shapes—like following a depth contour—are difficult to recognize or enforce. Simplified boundaries might be less necessary in areas where fishing boats can be equipped with vessel monitoring systems that give precise positioning information to fishers so they avoid crossing reserve boundaries and to enforcement agents to track compliance. Reserves that are partitioned into few relatively large areas also aid enforcement.

Dispersal, on the other hand, is aided by smaller reserves in some cases. For sedentary species, including many plants, invertebrates, and reef-associated fishes, reserves need not be large to keep adults in, and smaller reserves will promote the transport of productivity to fishing grounds, especially for species with limited dispersal ability. To protect or enhance catches of more mobile species, reserve units might need to be larger in order to keep adults in. Since no single reserve design fits all circumstances, it is up to managers to request scientific advice on how best to partition reserves based on dispersal attributes of the species of greatest interest to them.

Area Selection

If reserves are focused on specific fisheries, areas should be chosen from among habitats used by species in that fishery throughout their life cycles. If reserves are intended to achieve benefits for all fisheries in a region (e.g., providing insurance that no fisheries crash), areas should be chosen from among all habitat types. Once the set of habitat types are identified, reserves will be most effective if they encompass representative proportions of each (Ballantine 1997). Friedlander and colleagues (2003b) used a representative habitat–type approach in providing design criteria for a marine reserve network in the Seaflower Biosphere Reserve, Colombia. Their work included defining a list of habitat types, confirming their ecological relevance through fieldwork, and recommending the inclusion of all habitat types in the final marine reserve network design.

However, it can be valuable to include crucial or especially vulnerable habitat types more completely. Spawning aggregation sites are one example of a habitat type requiring additional representation because of the crucial role they play in the life cycle of some fishes, the vulnerability of fish populations while aggregated, and the potential for aggregations to indicate complex habitat that can be vulnerable to damage from certain fishing practices. It might also be valuable to encompass larger amounts of rare habitat types, especially if the rarity comes from prior human impacts. Mangrove lagoons are good choices for inclusion in marine reserves (Friedlander et al., 2003b) because they play a key role in the ecology of coral reef ecosystems (Ogden and Gladfelter 1983), have suffered from being the frequent target of coastal development, and are now often rare.

It could also be beneficial to focus marine reserve efforts on known ecological connections among habitat types (Appeldoorn et al. 2003). For example, connections among mangroves, seagrasses, and coral reefs serve to support a highly productive and diverse coral reef ecosystem in an otherwise nutrient-poor environment (Ogden and Gladfelter 1983). Choosing areas that are characterized by diverse habitats can foster these ecological connections and increase the capacity of even very small reserves to sustain productive populations within their borders (Appeldoorn et al. 1997). Finally, strategic decisions should be made with respect to degraded habitats. These habitats should be avoided if they show little potential for recovery in the short to medium term. However, degraded habitats can be excellent candidates for marine reserves if they show high potential for quick recovery. For example, an overfished area with intact habitat structure might serve well as a marine reserve because there is a greater chance such an area will gain political support. If these areas show a high potential for quick recovery, they will not only create effective marine reserves but might also help to build support for reserves when people see dramatic results within them.

Most important, though, in selecting marine reserve locations is stakeholder involvement. Ideally, we should strive to convince local people, particularly fishers, to take enough ownership and propose reserve alternatives themselves. When achieved, this objective dramatically aids in compliance and enforcement and makes reserves resilient to shifting political winds. It is important that proposals meet basic scientific criteria but equally important to recognize that hundreds of potential reserve designs do so (Sladek Nowlis and Friedlander 2004a). Selecting among them is best left to local stakeholders if they are willing to take on this task and if a support system is available to provide feedback on and ultimately confirm their decision's scientific validity.

Regulations

Marine protected areas (MPAs)—areas with special protections, of which marine reserves are a subset—function best when regulations are easy to understand and enforce. Marine reserves have the potential to protect some species regardless of where they are established and to protect virtually all species if established in the right places. Nevertheless, reserve establishment inevitably brings up requests for exemptions for some sector of the fishing industry because that sector had less impact historically, has less impact today, or focuses on fish that pass through and are thus less likely to benefit from the reserve in the first place. Although a complete ban on fishing in an area might seem unfair, allowing exceptions is far more inequitable.

Exceptions cause two major problems. First, they create a substantial enforcement challenge. It is easier to enforce a fully protected reserve than more conventional management measures because one need not board a vessel and inspect equipment or catch to determine whether a violation has been committed. Partially protected areas eliminate this advantage. Studies in Hawaii indicate that partially protected areas fare no better than areas with no specific regulations, while fully protected marine reserves contain substantially more fish (see Figure 17.6). For example, Friedlander (2001) compared three marine protected areas that contained potentially productive fish habitat on the island of Oahu. He found that the fully protected Hanauma Bay had seven times more fish than two other sites with partial protection. Brock and Kamm (1993) found equally unimpressive results in a study of a rotational closure on Oahu, where fish abundance that built up during the closed years quickly disappeared when the area was reopened to all types of fishing. Similarly, though fishing northern abalone (*Haliotis kamtschatkana*) is prohibited throughout British Columbia, populations were found at higher densities in places with built-in enforcement (e.g., a military base) and in fully protected marine reserves than in areas where other forms of fishing were allowed (Wallace 1999).

The second problem with exceptions is that marine protected areas become less useful as reference points. If people are doing some fishing inside an area, we lose the ability to use it as a true unfished reference. In many cases, there will also be the potential for the allowable fishing activity to impact other fish in the system through bycatch or through ecological interactions.

Nevertheless, there might be value to having partially protected areas in addition to marine reserves. A comprehensive zoning process, including marine reserves and other forms of marine protected areas, is usually preferable to solely designating marine reserves. The broader zoning process allows a number of additional user conflicts to be addressed (e.g., commercial versus recreational fishing), while also providing buffers to protect marine reserves from inevitable edge effects (Norse, Chapter 25).

Conclusions

Despite decades of focused studies, we remain incapable of predicting the responses of marine systems to human perturbations. Fishery failures in developing countries (e.g., FAO 2000) might be explained by a lack of resources for management. The same explanation cannot account for the widespread failures in industrialized countries like the United States (e.g., NMFS 2002). In large part, the failure is attributable to management systems that require better information than is available, which opens up too much scientific wiggle room in politically charged processes. Simpler systems that leave a certain fraction of all populations off limits to extraction provide substantially greater long-term resiliency (Sladek Nowlis and Bollermann 2002), yet managers typically use management systems that rely heavily on target fishing mortality rates imprecisely determined from poor information, without building in a buffer against inescapable uncertainty.

Marine reserves can serve two fundamentally important roles in improving fishery management. By creating an off-limits population, marine reserves provide an invaluable reference area for managers. Similarly, reserves can serve as an effective buffer against uncertainty. Engineers build in safety margins against uncertainty to avoid catastrophes in projects ranging from the guidance system of a moon launch to the structural integrity of a bridge. Fishery managers urgently need this safety margin given the large gaps in our knowledge of complex marine ecosystems.

Marine reserves can play central roles in both precautionary and ecosystem-based management. Precautionary management should allow only levels of human activity known to be safe for the ecosystem and long-term prosperity of humans. By providing a safety buffer, marine reserves serve as precautionary management by mitigating against limitations in our knowledge. Impressively, this can be achieved without loss of long-term fishing opportunity (Sladek Nowlis and Roberts 1999; Sladek Nowlis and Bollermann 2002). Ecosystem-based management should take into account the complexities of marine ecosystems. This feat can be accomplished either by gaining a thorough understanding of complex marine ecosystems or by allowing ecosystems to thrive naturally in designated areas (Buck 1993). Even if a thorough understanding of marine ecosystems was possible—and there is no reason to believe that it is—it would take decades to achieve. Until that day, ecosystem-based management can be achieved best by acknowledging in management decisions the ecological phenomena we know, while allowing marine ecosystems to thrive naturally in designated marine reserves.

Acknowledgments

The authors are indebted to Elliott Norse and Larry Crowder for giving us the opportunity to contribute to this book, and for their tolerance of our many delays in getting them the chapter. We also sincerely thank Richard Appeldoorn and an anonymous reviewer for thoughtful comments on the manuscript. Finally, the writing of the manuscript was improved dramatically due to the editing efforts of Rebecca Sladek Nowlis. This work was supported in part by the University of Puerto Rico Sea Grant College Program.

Literature Cited

Alcala, A. and G.R. Russ (1990). A direct test of the effects of protective management on abundance and yield of tropical marine resources. *Journal du Conseil International pour l'Exploration de la Mer* 46: 40–47

Allison, G.W., S. Gaines, J. Lubchenco, and H. Possingham (2003). Ensuring persistence of marine reserves: Catastrophes require adopting an insurance factor. *Ecological Applications* 13(1) Supplement: S8–S24

Appeldoorn, R.S. and C.W. Recksiek (2000). Marine fisheries reserves versus marine parks: Unity disguised as conflict. *Proceedings of the Gulf and Caribbean Fisheries Institute* 51: 471–474

Appeldoorn, R.S., C.W. Recksiek, R.L. Hill, F.E. Pagan, and G.D. Dennis (1997). Marine protected areas and reef fish movements: The role of habitat in controlling ontogenetic migration. *Proceedings of the 8th International Coral Reef Symposium* 2: 1917–1922

Appeldoorn, R.S., A. Friedlander, J. Sladek Nowlis, P. Usseglio, and A. Mitchell-Chui (2003). Habitat connectivity in reef fish communities and marine reserve design in Old Providence–Santa Catalina, Colombia. *Gulf and Caribbean Research* 14(2): 61–78

Attwood, C.G. and B.A. Bennett (1994). Variation in dispersal of galjoen (*Coracinus capensis*) (Teleostei: Coracinidae) from a marine reserve. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1247–1257

Ballantine, W.J. (1997). Design principles for systems of "no-take" marine reserves. *Workshop on the Design and Monitoring of Marine Reserves, February 18–20.* Fisheries Centre, University of British Columbia, Vancouver, British Columbia (Canada)

Beets, J. and A. Friedlander (1992). Stock analysis and management strategies for red hind, *Epinephelus guttatus,* in the U.S. Virgin Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute* 42: 66–79

Beets, J. and A. Friedlander (1999). Evaluation of a conservation strategy: A spawning aggregation closure for grouper in the Virgin Islands. *Environmental Biology of Fishes* 55: 91–98

Beverton, R.J.H. and S.J. Holt (1957). *On the Dynamics of Exploited Fish Populations.* Chapman and Hall, New York (USA)

Bohnsack, J.A. (1996). Maintenance and recovery of reef fishery productivity. Pp. 283–313 in N.V.C. Polunin and C.M. Roberts, eds. *Reef Fisheries.* Chapman and Hall, London (UK)

Brock, R.E. and A.K.H. Kamm (1993). *Fishing and Its Impact on Coral Reef Fish Communities.* Report to Main Hawaiian Islands–Marine Resource Investigation, Division of Aquatic Resources, Department of Land and Natural Resources, Honolulu, Hawaii (USA)

Buck, E.H. (1993). *Marine Ecosystem Management.* Congressional Research Service, The Library of Congress, Washington, DC (USA)

California Department of Fish and Game (CDFG) (2002). *Nearshore Fishery Management Plan.* CDFG Marine Region, Sacramento, California (USA)

Carr, M.H. and D.C. Reed (1993). Conceptual issues relevant to marine harvest refuges: Examples from temperate reef fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2019–2028

Castilla, J.C. and M. Fernández (1998). Small-scale benthic fisheries in Chile: On co-management and sustainable use of benthic invertebrates. *Ecological Applications* 8: S124–S132

Cohen, D. and S.A. Levin (1987). The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. *Lecture Notes in Biomathematics* 71: 110–122

Cowen, R.K., K.M.M. Lwiza, S. Sponaugle, C.B. Paris, and D.B. Olson (2000). Connectivity of marine populations: open or closed? *Science* 287: 857–859

Cushing, D. (1995). *Population Production and Regulation in the Sea.* Cambridge University Press, Cambridge (UK)

DeMartini, E.D. (1993). Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin* 91: 414–427.

Food and Agriculture Organization (FAO) (2000). *The State of World Fisheries and Aquaculture.* Food and Agriculture Organization of the United Nations, Rome (Italy)

Friedlander, A.M. (2001). Essential fish habitat and the effective design of marine reserves: Applications for marine ornamental fishes. *Aquarium Sciences and Conservation* 3: 135–150

Friedlander, A.M. and E.E. DeMartini (2002). Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: The effects of fishing down apex predators. *Marine Ecology Progress Series* 230: 253–264

Friedlander, A., K. Poepoe, K. Poepoe, K. Helm, P. Bartram, J. Maragos, and I. Abbott (2002). Application of Hawaiian traditions to community-based fishery management. *Proceedings of the 9th International Coral Reef Symposium* 2: 813–818

Friedlander, A.M., E.K. Brown, P.L. Jokiel. W.R. Smith, and K.S. Rodgers (2003a). Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22: 291–305

Friedlander, A., J. Sladek Nowlis, J.A. Sanchez, R. Appeldoorn, P. Usseglio, C. McCormick, S. Bejarano, and A. Mitchell-Chui (2003b). Designing effective marine protected areas in Seaflower Biosphere Reserve, Colombia, based on biological and sociological information. *Conservation Biology* 17: 1769–1784

Guénette, S., T. Lauck, and C. Clark (1998). Marine reserves: From Beverton and Holt to the present. *Reviews in Fish Biology and Fisheries* 8: 1–21

Guénette, S., T.J. Pitcher, and C.J. Walters (2000). The potential of marine reserves for the management of northern cod in Newfoundland. *Bulletin of Marine Science* 66: 831–852

Gulko, D., J. Maragos, A. Friedlander, C. Hunter, and R. Brainard (2000). Status of coral reef in the Hawaiian Archipelago. Pp. 219–238 in C. Wilkinson, ed. *Status of Coral Reefs of the World: 2000*. Australian Institute of Marine Science, Cape Ferguson, Queensland, and Dampier (Australia)

Halpern, B. (2003). The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications* 13(1) Supplement: S117–S137

Holland, K.N., C.G. Lowe, and B.M. Wetherbee (1996). Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. *Fisheries Research* 25: 279–292

Jackson J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Coke, J. Erlandson, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J.M. Pandolfi, C.H. Peterson, R.S. Steneck, M.J. Tegner, and R.R. Warner (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629–638

Johannes, R.E. (1978). Traditional marine conservation methods in Oceania and their demise. *Annual Reviews of Ecology Systematics* 9: 349–364

Johannes, R.E. (1998). The case for data-less marine resource management: Examples from tropical nearshore finfisheries. *Trends in Ecology and Evolution* 13: 243–246

Johannes, R.E., L. Squire, T. Graham, Y. Sadovy, and H. Renguul (1999). *Spawning Aggregations of Groupers (Serranidae) in Palau*. The Nature Conservancy Marine Conservation Research Series 1. Arlington, Virginia (USA)

Johnson, D.R., N.A. Funicelli, and J.A. Bohnsack (1999). Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. *North American Journal of Fisheries Management* 19: 436–453

Jones, G.P., M.J. Milicich, M.J. Emslie, and C. Lunow (1999). Self-recruitment in a coral reef fish population. *Nature* 402: 802–804

Lauck, T., C.W. Clark, M. Mangel, and G.R. Munro (1998). Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications* 8: S72–S78

Mangel, M. (1998). No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters* 1: 87–90

McClanahan, T.R. and B. Kaunda-Arara (1996). Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology* 10: 1187–1199

McEvoy, A.F. (1986). *The Fisherman's Problem: Ecology and Law in the California Fisheries 1850–1980*. Cambridge University Press, Cambridge (UK)

Myers, R.A. and G. Mertz (1998). The limits of exploitation: a precautionary approach. *Ecological Applications* 8: S165–S169

Myers, R.A. and B. Worm (2003). Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280–283

National Marine Fisheries Service (NMFS) (2002). *Towards Rebuilding America's Marine Fisheries: Annual Report to Congress on the Status of U.S. Fisheries—*

2001. U.S. Department of Commerce, Silver Spring, Maryland (USA)

National Research Council (NRC) (1998). *Improving Fish Stock Assessments*. National Academy Press, Washington, DC (USA)

National Research Council (NRC) (2001). *Marine Protected Areas: Tools for Sustaining Ocean Ecosystems*. National Academy Press, Washington, DC (USA)

Nemeth, R.S. (2004). Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. *Marine Ecology Progress Series* 286: 81–97

North Pacific Fishery Management Council (NPFMC) (1998). *Bering Sea/Aleutian Islands Groundfish Fishery Management Plan*. North Pacific Fishery Management Council, Anchorage, Alaska (USA)

Ogden, J.C. and E.H. Gladfelter, eds. (1983). *Coral Reefs, Seagrass Beds, and Mangroves: Their Interaction in the Coastal Zones of the Caribbean*. UNESCO Reports in Marine Science 23. Paris (France)

Pacific Fishery Management Council (PFMC) (1998). *Final Environmental Assessment/Regulatory Impact Review for Amendment 11 to the Pacific Coast Groundfish Fishery Management Plan*. Pacific Fishery Management Council, Portland, Oregon (USA)

Plan Development Team (PDT) (1990). *The Potential of Marine Fishery Reserves for Reef Fish Management in the U.S. Southern Atlantic*. U.S. Department of Commerce Technical Memorandum NMFS-SEFC-261

Poepoe, K.M., P.K. Bartram, and A.M. Friedlander (2003). The use of traditional Hawaiian knowledge in the contemporary management of marine resources. Pp. 328–339 in N. Haggan, C. Brignall, and L. Wood, eds. *Putting Fishers' Knowledge to Work*. University of British Columbia, Fisheries Centre Research Reports 11(1). British Columbia (Canada)

Polacheck, T. (1990). Year around closed areas as a management tool. *Natural Resource Modeling* 4: 327–353

Polovina, J.J. (1994). The case of the missing lobsters. *Natural History* 103: 50–59

Proulx, E. (1998). The role of law enforcement in the creation and management of marine reserves. Pp. 74–77 in M.M. Yoklavich, ed. *Marine Harvest Refugia for West Coast Rockfish: A Workshop*. U.S. Department of Commerce Technical Memorandum NOAA-TM-NMFS-SWFSC-255

Ricker, W.E. (1958). Maximum yields from fluctuating environments and mixed stocks. *Journal of the Fisheries Research Board of Canada* 15: 991–1006

Roberts C.M. (1997). Connectivity and management of Caribbean coral reefs. *Science* 278: 1454–1457

Roberts, C.M., J.A. Bohnsack, F. Gell, J.P. Hawkins, and R. Goodridge (2001). Effects of marine reserves on adjacent fisheries. *Science* 294: 1920–1923

Russ, G.R. and A.C. Alcala (1996). Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* 132: 1–9

Russ, G.R. and A.C. Alcala (1999). Management histories of Sumilon and Apo marine reserves, Philippines, and their influence on national marine resource policy. *Coral Reefs* 18: 307–319

Sadovy, Y.J. (1996). Reproduction of reef fishery species. Pp. 15–59 in N.V.C. Polunin and C.M. Roberts, eds. *Reef Fisheries*. Chapman and Hall, London (UK)

Shanks, A.L., B. Grantham, and M. Carr (2003). Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13(1) Supplement: S159–S169

Sladek Nowlis, J. (2000). Short- and long-term effects of three fishery-management tools on depleted fisheries. *Bulletin of Marine Science* 66: 651–662

Sladek Nowlis, J. (2004a). Performance indices that facilitate informed, value-driven decision making in fisheries management. *Bulletin of Marine Science* 74(3): 709–726

Sladek Nowlis, J. (2004b). California's Channel Islands and the U.S. West Coast. Pp. 237–267 in J. Sobel and C. Dahlgren, eds. *Marine Reserves: A Guide to Science, Design, and Use*. Island Press, Washington, DC (USA)

Sladek Nowlis, J. and B. Bollermann (2002). Methods for increasing the likelihood of restoring and maintaining productive fisheries. *Bulletin of Marine Science* 70: 715–731

Sladek Nowlis, J. and A. Friedlander (2004 a). Design and designation of marine reserves. Pp. 128–163 in J. Sobel and C. Dahlgren. *Marine Reserves: A Guide to Science, Design, and Use.* Island Press, Washington, DC (USA)

Sladek Nowlis, J. and A. Friedlander (2004 b). Research priorities and techniques. Pp. 187–233 in J. Sobel and C. Dahlgren. *Marine Reserves: A Guide to Science, Design, and Use.* Island Press, Washington, DC (USA)

Sladek Nowlis, J. and C.M. Roberts (1997). You can have your fish and eat it, too: Theoretical approaches to marine reserve design. *Proceedings of the 8th International Coral Reef Symposium* 2: 1907–1910

Sladek Nowlis, J. and C.M. Roberts (1999). Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin* 97: 604–616

Sluka, R., M. Chiappone, K.M. Sullivan, and R. Wright (1997). The benefits of a marine fishery reserve for Nassau grouper (*Epinephelus striatus*) in the central Bahamas. *Proceedings of the 8th International Coral Reef Symposium* 2: 1961–1964

Smith, M.D. and J.E. Wilen (2003). Economic impacts of marine reserves: The importance of spatial behavior. *Journal of Environmental Economics and Management* 46: 183–206

Swarztrauber, S. (1972). *The Three-Mile Limit of Territorial Seas.* Naval Institute Press, Annapolis, Maryland (USA)

Swearer, S.E., J.E. Caselle, D.W. Lea, and R.R. Warner (1999). Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402: 799–802

Vitousek, P.M., H.A. Mooney, J. Lubchenco, and J.M. Melillo (1997). Human domination of Earth's ecosystems. *Science* 277: 494–499

Wallace, S.S. (1999). Evaluating the effects of three forms of marine reserve on northern abalone populations in British Columbia, Canada. *Conservation Biology* 13: 882–887

Watling, L. and E.A. Norse (1998). Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conservation Biology* 12: 1180–1197

Whiteman, E.A., C.A. Jennings, R.S. Nemeth (In press). Sex structure and potential female fecundity in a red hind (*Epinephelus guttatus*) spawning aggregation: Applying ultrasonic imaging. *Journal of Fish Biology*