

COMPARING MARINE AND TERRESTRIAL ECOSYSTEMS: IMPLICATIONS FOR THE DESIGN OF COASTAL MARINE RESERVES

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Abstract. Concepts and theory for the design and application of terrestrial reserves is based on our understanding of environmental, ecological, and evolutionary processes responsible for biological diversity and sustainability of terrestrial ecosystems and how humans have influenced these processes. How well this terrestrial-based theory can be applied toward the design and application of reserves in the coastal marine environment depends, in part, on the degree of similarity between these systems. Several marked differences in ecological and evolutionary processes exist between marine and terrestrial ecosystems as ramifications of fundamental differences in their physical environments (i.e., the relative prevalence of air and water) and contemporary patterns of human impacts. Most notably, the great extent and rate of dispersal of nutrients, materials, holoplanktonic organisms, and reproductive propagules of benthic organisms expand scales of connectivity among near-shore communities and ecosystems. Consequently, the “openness” of marine populations, communities, and ecosystems probably has marked influences on their spatial, genetic, and trophic structures and dynamics in ways experienced by only some terrestrial species. Such differences appear to be particularly significant for the kinds of organisms most exploited and targeted for protection in coastal marine ecosystems (fishes and macroinvertebrates). These and other differences imply some unique design criteria and application of reserves in the marine environment. In explaining the implications of these differences for marine reserve design and application, we identify many of the environmental and ecological processes and design criteria necessary for consideration in the development of the analytical approaches developed elsewhere in this Special Issue.

Key words: fisheries; marine conservation; marine protected areas; marine reserves; reserve network design.

INTRODUCTION

Reserve design theory has been developed primarily with terrestrial systems and species in mind, and most applications of reserve design theory have also been terrestrial (Soulé and Terborgh 1999). Currently, <1% of the marine realm is protected within reserves, in contrast to almost 6% in terrestrial systems (Groombridge 1992). However, there is growing interest by resource managers, policy makers, and academics in the potential for reserves in coastal marine ecosystems to both enhance the conservation of marine biodiversity and contribute to the management of fisheries. The overarching goal of terrestrial reserves has been to

maintain biological diversity. This has resulted in two strategic objectives for reserve network design: to efficiently include the full spectrum of regional-scale biodiversity within a system of protected areas, and to ensure the long-term persistence of biological diversity in a changing world (Soulé and Terborgh 1999). These strategic objectives—representation and persistence—seem equally appropriate for marine reserve networks. However, the relevance of terrestrial-based approaches in determining specific design criteria and prioritizing sites for conservation to effectively meet these objectives in marine systems requires an understanding of both the nature and degree of differences between marine and terrestrial systems. These potentially include differences in ecological, genetic, and evolutionary patterns and processes, the nature and scale of contemporary threatening processes, and the way we manage biotic resources on land and in the sea.

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TABLE 1. Key differences between terrestrial and marine ecosystems with respect to environmental and ecological features and the patterns and consequences of human impacts.

Feature	Terrestrial ecosystems	Marine ecosystems
Environmental		
Prevalence of aquatic medium	less	greater
Dimensions of species distribution	two-dimensional	three-dimensional
Scale of chemical and material transport	smaller	greater
“Openness” of local environment (i.e., rates of import and export)	less	greater
Ecological		
Phyletic diversity (α and β)	less	greater
Life-history traits		
Per capita fecundity of invertebrates and small vertebrates	lower	higher
Per capita fecundity of mammals	low	low
Difference in dispersal between life stages	less	greater
Importance of pollination syndromes	great	minimal
Rate of response to environmental variability	lower	faster
Sensitivity to large-scale environmental variability	lower	higher
Population structure		
Spatial scale of propagule transport	smaller	greater
Spatial structure of populations	less open	more open
Reliance on external sources of recruitment	lower	higher
Likelihood of local self replenishment	high	low
Sensitivity to habitat fragmentation	greater	less
Sensitivity to smaller scale perturbations	greater	less
Temporal response to large-scale events	slower (centuries)	higher (decades)
Trophic		
Lateral transport of energy	low (few planktivores)	high (many planktivores)
Turnover of primary producers	slow (many perennials)	high (few perennials)
Reliance of carnivores on external input of prey	lower	higher
Prey populations influenced by external input of predators	lower	higher
Pronounced ontogenetic shifts of vertebrates	rare	very common
Genetic		
Effective population size	smaller	larger
Spatial scale of gene flow	smaller	larger
Interpopulation genetic diversity	higher	lower
Types and relative importance of contemporary human threats		
Habitat destruction	widespread	spatially focused (e.g., estuaries, coral reefs)
Loss of biogenic habitat structure	widespread (e.g., deforestation)	spatially focused (e.g., estuaries, coral reefs)
Trophic levels threatened or exploited	lower (primary producers)	higher (predators)
Degree of domestication	higher	lower

Our purpose here is to provide an overview of some fundamental similarities and differences between terrestrial and marine ecosystems with the aim of understanding their implications for reserve network design in marine systems. To provide a context for the comparison, we begin with a brief review of key differences between marine and terrestrial ecosystems. We then go on to discuss the relevance and implications of these differences for designing representative systems of reserves aimed at contributing to both the persistence of marine biodiversity and protecting exploited species. Because many exploited species in marine ecosystems have profound influences on the communities they inhabit, these are mutually inclusive goals. For clarity,

the comparisons and their implications we raise are summarized in Tables 1 and 2, respectively. A rigorous analysis of the similarities and differences between marine and terrestrial ecosystems is clearly beyond the scope of this article. Our intentions are to highlight some of the perceived and largely supported differences asserted in the literature, provide references to direct the reader to the evidence upon which these assertions are based, and focus more on their implications for reserve design and application. There are, of course, numerous exceptions to almost any comparison (e.g., the relative “openness” of populations and communities) over such a tremendous variety of organisms and environments encompassed by terrestrial and

TABLE 2. Implications of relative differences between terrestrial and marine ecosystems for the objectives and design of reserve networks.

Feature	Terrestrial ecosystems	Marine ecosystems
Reserve objectives		
Spatial focus for protection	within reserves	within and outside reserves
Emphasis on propagule export	little	great
State of knowledge		
Taxonomic identification	good	poor
Patterns of species distribution and abundance	good	poor to moderate
Geographic patterns of marine ecosystem diversity	good	poor
Design criteria		
Movement (connectivity) corridors		
Importance of connectivity	less	greater
Type	primarily habitat based	primarily current based
Importance of habitat corridors	greater	lower
Human managed	great	little
Constancy/predictability	high	low
Protection of nonreserve populations	less critical	very critical
Reserve size		
Sufficient for local replenishment (single reserve)	smaller	larger
Habitat diversity necessary for resource requirements	smaller	larger
Reserve location		
Sensitivity to biogeographic transitions	less	greater
Importance of import-export processes (i.e., winds, currents)	less	great

coastal marine ecosystems. Nonetheless, the implications of several key differences identified in the literature suggest that the theoretical foundation for the design of marine reserves requires approaches that consider the uniqueness of coastal marine ecosystems.

Probably the most fundamental difference between terrestrial and marine systems is the prevalence of the aquatic medium in which all marine organisms live. The properties of water have profound effects on the physical and biological characteristics of marine systems (Denny 1993). For instance, the transport of materials and organisms by the convective forces of ocean waves and currents extends the spatial scale of many processes, so that marine systems tend to be more "open" (i.e., greater magnitudes and higher rates of import and export) than their terrestrial counterparts. Related to this is the overwhelming prevalence of animal species whose relatively sedentary benthic adults produce early life stages (e.g., spores, eggs, larvae) that can potentially disperse great distances in the plankton (Strathman 1990, Leis 1991, Hay and Steinberg 1992). For example, the review by Shanks et al. (2003) of dispersal distances of benthic marine animals suggests a modal dispersal distance of <1 km for some sessile taxa (corals, tunicates, bryozoans) and another mode far exceeding 20 km, typical of broadcast-spawning mollusks, crustaceans, and fishes.

This decoupling of local offspring production from the subsequent recruitment of young to a parental population is in marked contrast to the more limited dis-

persal of offspring of many terrestrial animals, especially vertebrates (Wasser and Jones 1983, Turchin 1998, Lena et al. 2000). Comprehensive syntheses of dispersal estimates of terrestrial vertebrates are difficult to find. The most comprehensive syntheses we encountered were tabulated by Turchin (1998: Tables 7.1 and 7.2). Recalculating his dispersal diffusion coefficients (D) to estimate median linear dispersal distances (we calculated the 25th quartile of the distribution of $[4 \times D]^{-2}$, which we assumed to be normally distributed), mean dispersal distances for mammals and birds were 1.6 and 17 km/yr, respectively.

Although such estimates provide only gross approximations for both marine and terrestrial animals, such dispersal distances relative to adult dispersal exemplifies the marked contrast in decoupling of local production from local recruitment in these systems. The contrast appears less between marine macroalgae and terrestrial plants, where the dominant perception for both has been very limited dispersal (Howe and Smallwood 1982, Santelices 1990; references in Kot et al. 1996, Clark et al. 1998, 1999) but a growing body of evidence suggests longer distance dispersal is also important (van den Hoek 1987, Reed et al. 1988, Cain et al. 2000). This difference in the relative dispersal of life stages, has profound effects on population structure and the spatial scale over which isolated adult populations interact.

A related difference is that marine species with pelagically dispersed propagules appear to experience

higher gene flow, have larger effective population sizes, and develop less genetic structure relative to terrestrial species (Neigel 1997*b*). Yet another implication of physical differences involves the capacity of species to respond spatially to environmental change. Habitat corridors are often advocated in terrestrial reserve networks, in part to maintain potential for migration or range shifts in response to climate change (e.g., Rosenberg et al. 1997, Hill et al. 1999, Parmesan et al. 1999). Marine organisms with pelagic life stages have greater potential for long-distance dispersal across habitat discontinuities, and thus habitat corridors may be less important for many marine organisms, although mobile benthic species may be more sensitive to habitat fragmentation (e.g., Acosta 1999). Even marine mammals and, to a lesser extent, birds, tend to be more mobile than their terrestrial counterparts (e.g., inter-polar migrations of Arctic Terns and Shearwaters, the biannual migrations of northern elephant seals; Bowen and Siniff 1999, Le Boeuf et al. 2000).

Another fundamental difference is the trophic status of species contemporarily targeted by human exploitation—mostly plants on land and almost exclusively animals (many of which are higher level predators) in the sea. And finally, many exploited species on land have been greatly altered by selection for domesticated forms, whereas in the sea we still exploit mostly wild stocks. One critical implication of these differences is that export or supply of individuals from protected to exploited populations outside reserves is often an explicit objective of marine reserves but is less often a targeted feature of reserves in terrestrial systems. A stark example of this mind set for terrestrial systems is the reintroduction of the wolf into Yellowstone National Park (USA) and the uproar over the “spill-over” of those animals beyond the “reserve” boundaries.

At a minimum, designing effective and efficient reserve networks requires knowledge of how species and ecosystems are distributed (i.e., biodiversity patterns), knowledge of the processes that maintain these patterns at small and large scales, and knowledge of the threatening processes that diminish biodiversity at any level, including population or species endangerment or extinction. In the following sections we consider the differences between marine and terrestrial systems mentioned above, and the implications of these differences for reserve network design.

BIODIVERSITY PATTERNS IN THE SEA AND ON LAND

Approaches to ensuring comprehensive representation of biological diversity in terrestrial reserves have focused primarily on contemporary patterns of distribution and abundance. In terrestrial systems, reserve selection methods such as gap analysis (Scott et al. 1993) and related approaches (e.g., Noss 1992, Forest Ecosystem Management Assessment Team [FEMAT] 1993, Dinerstein et al. 1995, Davis et al. 1996, 1999,

Noss et al. 1997, Olson and Dinerstein 1998) are used to identify efficient reserve networks that represent all or most biodiversity at the ecosystem or landscape level. These approaches integrate spatially explicit data on vegetation cover (or other measures of biodiversity) and land management to prioritize potential sites for conservation. These spatial analyses are becoming increasingly sophisticated, and when coupled with heuristic or linear programming algorithms, can identify nearly optimal reserve networks, as long as the necessary data are available. Only recently have similar analytical approaches been applied to marine systems (e.g., Beck and Odaya 2001, Leslie et al. 2003). Moreover, the necessary data (habitat maps, habitat–diversity relationships, spatial patterns of diversity) at the spatial scale applicable to reserve design are far less organized and available for most coastal marine environments than for many terrestrial environments, perhaps with the exception of the eastern and southern coasts of the United States (National Research Council [NRC] 1995, Gray 1997*a* and other contributions in Ormond et al. 1997).

Some levels of taxonomic diversity may be higher in the sea than on land (Gray 1997*b*). For example, all but one of the 35 extant animal phyla are found in the sea and almost half of these are exclusively marine, while other algal and animal phyla are primarily marine (Norse 1993, Snelgrove 1999). Yet despite this great diversity, geographic patterns of marine biodiversity and ecosystem diversity are poorly described (Norse 1993, NRC 1995, Gray 1997*b*). Thus, there are few comprehensive marine classifications analogous to those developed for terrestrial ecosystems (e.g., Kuchler 1964, Udvardy 1975, Bailey 1994) that might serve as the basis for prioritization of marine conservation sites at any scale. Moreover, Marquet et al. 1993 have pointed out how an important third dimension (vertically through the water column) in marine systems contributes to the complexity of understanding how species distributions and diversity scale with area.

Marine animal species are often more genetically diverse than their terrestrial counterparts (Ward et al. 1994, Gray 1997*a*), although this diversity tends to be less structured spatially or geographically. For marine animal species with open populations, gene flow is usually assumed to be higher than for most terrestrial species (Crisp 1978, Burton 1983, Hedgecock 1986, Utter and Ryman 1993, Neigel 1997*b*). High gene flow may explain why marine animals with pelagic life stages typically exhibit little interpopulation genetic divergence (Gyllenstein 1985, Hedgecock 1986, Burton 1998). Observations of more pronounced interpopulation divergence in species that lack pelagic life stages (Burton 1983, Hellberg 1996) are consistent with the view that pelagic dispersal maintains genetic homogeneity.

In addition to gene flow, other factors should be considered that may also reduce genetic divergence among marine populations. Observed levels of genetic divergence among populations represent a dynamic balance between gene flow and other processes, most importantly genetic drift and natural selection (Neigel 1997a). Thus, even low levels of gene flow may lead to genetic uniformity if genetic drift and natural selection are also relatively weak. High levels of genetic polymorphism in marine populations are indicative of populations with large effective sizes (N_e), and consequently little genetic drift. If genetic drift is weak, even moderate levels of gene flow should be able to prevent interpopulation differentiation. In this light, it is interesting to note that slight, but statistically significant, genetic differentiation has been observed on both macrogeographic (Buroker 1983, Kordos and Burton 1993, McMillen-Jackson et al. 1994) and microgeographic (Johnson and Black 1982, David et al. 1997) scales for marine animals with pelagic larvae. These differences suggest that marine populations do not always behave as large, panmictic populations.

Although the processes that shape genetic variation in marine animal species are not fully understood, the general pattern of high levels of intraspecific genetic diversity without pronounced spatial or geographic structure is well documented. This pattern reflects fundamental differences between marine and terrestrial animal species in the spatial scales of population and evolutionary processes. The implications of these differences are discussed in *Scale and variability of physical and ecological processes: Managing populations to meet multiple objectives*.

SCALE AND VARIABILITY OF PHYSICAL AND ECOLOGICAL PROCESSES

Life histories, dispersal, and population structure

Some principal life-history characteristics that distinguish many marine animals from those that live on land are direct consequences of evolution in an aquatic medium: the prevalence of external fertilization and the production of large numbers of extremely small, well-dispersed offspring (relative to the parent). These have profound implications for marine vs. terrestrial reserves. First, because the offspring of most marine species are small (and most are pelagic), they are more vulnerable to physical influences than terrestrial young, and thus experience wide fluctuations in survival. This leads to dramatic differences in the strength of recruitment from year to year, independent of the size of the local adult population (Hjort 1914, Doherty and Williams 1988). Thus, the results of local protection by marine reserves may be less predictable and more difficult to detect both locally and regionally in the short term.

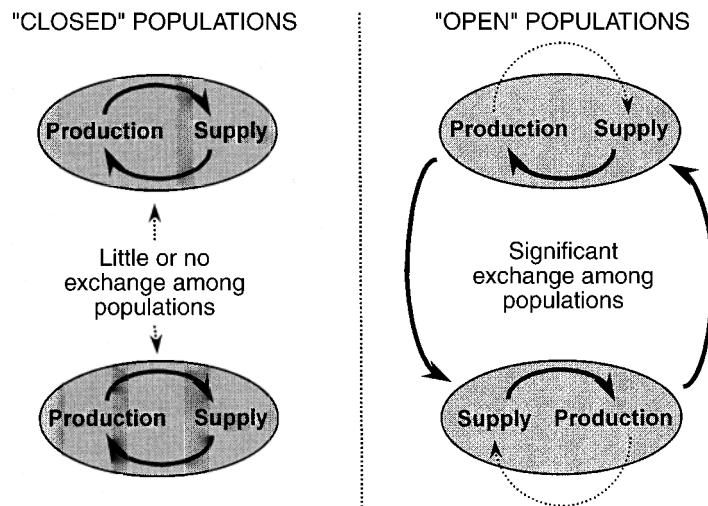
Second, because densities of marine fishes often fluctuate tremendously from year to year, the behavior and

life history of individuals is often phenotypically plastic relative to population density (Warner 1991). For example, shifts in social structure and mating systems corresponding with changes in density have been documented in many species of marine reef fishes (Thresher 1984, Warner 1991). For reef fishes, as density increases, social systems often shift from male mate monopolization to more equitable mating. This would magnify an increase in effective population size well beyond that expected from simple increases in abundance. Thus, marine reserves may act to increase the genetic diversity of component populations well beyond the levels expected from models based on terrestrial reserves.

Equally, for more sedentary species, exploitation or other adverse affects outside reserves can reduce population densities to such a point that finding a mate becomes difficult or fertilization rates are reduced (Levitan and Petersen 1995). These Allee effects are likely to be common in sedentary marine species, and thus increased densities of exploited species within reserves may be particularly valuable in fostering population recovery. External fertilization also contributes to aggregative spawning behavior of mobile species, often at discrete permanent locations, which would also be critical areas to protect.

Another fundamental implication of the relatively small egg-size characteristic of marine organisms is that it lessens the difference in size between female and male gametes relative to the same difference in terrestrial organisms. This, and the fact that fertilization is often external, reduces the anatomical differences between males and females. Very often, marine animals are hermaphroditic or capable of changing sex as a matter of normal life history, and this is a major feature distinguishing marine and terrestrial fauna (Warner 1978). For plants and algae, differences in gamete size and adult morphology are not as extreme between sexes. The extensive presence of sequential hermaphrodites among marine fishes can have immediate consequences relative to vulnerability to fishing, and thus to the protection from exploitation that reserves provide. In a sequential hermaphrodite, one sex is found among larger and older individuals, while the other sex is smaller and younger. Fisheries concentrate on the largest individuals within a population, and thus heavy exploitation can be quite sex specific. For protogynous hermaphrodites (those that change from female to male), the shortage of males may be compensated for by increased activity of the remaining males, or by social control of sex change. In the case of social control, the age and size of sex change diminishes as large males are removed. However, for protandrous species (where males change to females), the effects of fishing can be dramatic, with severe reductions in spawning potential as the large females are removed. Again, this suggests marked responses of marine species with such

FIG. 1. Comparison of two conceptual models of population replenishment. Ovals represent spatially isolated adult populations. Solid and dashed arrows represent proportionately strong and weak relationships, respectively, between propagule production and subsequent supply of offspring to a population. Many populations are best represented somewhere along the continuum between these two extreme scenarios.



attributes to the protection afforded them within reserves.

The fact that young are relatively small in marine organisms has a corollary in high fecundity. One commonly asserted implication of this high fecundity is that even very small populations of marine species with high fecundity have the potential for rapid population growth. For vertebrates, this high fecundity and high dispersal potential suggests a much greater resilience for fish populations relative to terrestrial vertebrates. Two consequences of this perceived greater resilience of marine vertebrates are that fisheries often fail before species are driven to extinction and even severely exploited species have the opportunity to recover when protected. With respect to reserve design, this suggests that as long as there is some retention of local production, even quite small marine reserves have the potential to protect populations within them and enhance population recovery beyond their boundaries (see Halpern 2003). However, recent evidence of the very slow recovery of exploited marine fishes suggests that this perceived greater resilience of marine populations may be overestimated (Hutchings 2000). All this suggests that, while small marine reserves may be effective, the strength of these effects in both protecting populations within and outside reserves increases with reserve size.

Managing populations to meet multiple objectives

The more limited dispersal of many terrestrial species, in conjunction with large-scale habitat destruction in many terrestrial systems, have traditionally focused terrestrial reserve design efforts on the single objective of protecting habitat and species within reserves (Soulé and Sanjayan 1998, Soulé and Terborgh 1999). With some exceptions (e.g., migratory waterfowl and insects), few terrestrial reserves are designed with the explicit intent to not only sustain target populations within reserves, but also to maximize export of indi-

viduals from reserves in order to sustain populations or to sustain or increase exploitation rates outside reserves. In contrast, the high fecundity and dispersal potential of marine species suggest that populations protected within reserves have the potential to sustain exploited populations outside reserves (Carr and Reed 1993, Botsford et al. 1994, Hastings and Botsford 1999), and maximizing export from reserve to exploited areas is often an explicit objective in marine systems.

Most species of conservation concern in terrestrial environments have simple life histories involving direct development (e.g., plants and most vertebrates), in which offspring do not disperse far from parental populations (with the exception of some birds, spiders, and insects). This limited dispersal of offspring provides direct feedback between adult fecundity, offspring production, and subsequent growth of a local population. Theoretically, such "closed" populations, given sufficient resources and genetic variability, can be self-sustaining, with limited exchange of individuals between populations (Fig. 1). In contrast, commercial fisheries target marine vertebrates (fishes) and many invertebrates (echinoderms, crustaceans, molluscs), most of which produce large numbers of young that can be dispersed long distances in the pelagic environment. The great dispersal potential of many invertebrates and vertebrates, particularly exploited species, can effectively decouple local offspring production from replenishment of that parental population (Roughgarden et al. 1988, Caley et al. 1996). For such "open" populations, larvae are likely to be dispersed from local parental populations to replenish distant populations, leaving parental populations reliant on the replenishment of larvae produced elsewhere, by other populations (Fig. 1). Of course, the relative openness of populations is a function of spatial scale (at sufficiently large scales, all populations are closed) and the pro-

cesses that contribute to the relative dispersal of life stages vary markedly in space and time (e.g., wind and water currents) and among species.

This apparent open population structure has two fundamental consequences for the design of marine reserves. First, sustainability of local protected populations requires one of three conditions: (1) reserves must be large enough to encompass dispersal distances so that protected populations within reserves are self sustaining, or (2) protected areas must be linked by dispersal (i.e., networked), thereby replenishing one another, or (3) reproductive output of unprotected populations must be sufficient to sustain protected populations. Thus, larval dispersal has a profound influence on the minimum size of self-sustaining protected communities. The rate of dispersal into unsuitable or sink habitats (e.g., areas with extremely high fishing mortality) influences the minimum size of a spatially isolated reserve that can support a stable population (i.e., critical patch size). With random dispersal, lethal surroundings outside reserves, and low rates of population increase, the critical reserve size is much larger than the average individual dispersal distance (Kierstead and Slobodkin 1953). High intrinsic rates of increase, more benign surroundings outside reserves, and habitat selection behavior of dispersing individuals tend to decrease critical reserve size (Okubo 1980, Pease et al. 1989, Soulé and Terborgh 1999). Thus, in the absence of knowledge about individual protected areas that are too small to encompass dispersal (i.e., self-sustaining), protected populations may require connectivity via larval dispersal. To the extent that protected areas are neither locally self sustaining nor linked, management practices must insure some minimum level of sustainability (including larval production and habitat protection) of unprotected populations (Carr and Reed 1993).

How well a species' or community's geographic range or area of occupancy reflects the area of a perturbation necessary to endanger it, depends on many factors. Most critical are spatial and temporal variability in the contribution of populations to the overall maintenance of a species range. If populations distributed throughout a vast species range are largely dependent on one or a few source populations within a small portion of that range, the entire range is as susceptible to smaller scale perturbations (that impact source populations) as species with much smaller ranges. In contrast, if populations throughout a species' range contribute similarly to maintenance of that range, the greater the spatial extent of a species range, the larger the environmental perturbation necessary to drive that species to extinction. Identifying such spatial structure is fundamental to the distribution of a system of reserves (Carr and Reed 1993, Botsford et al. 1994, Allison et al. 1998, Roberts 1997). Spatial patterns in the distribution of genetic variation may provide some insights into the uniformity and scale of dispersal pro-

cesses in marine populations. Even slight differentiation among populations, as described in a previous section (*Biodiversity patterns in the sea and on land*), suggests limited dispersal. In more extreme cases, a sharp genetic "break" within the range of a species implies a complete barrier to dispersal (Reeb and Avise 1990, Barber et al. 2000).

Because of general relationships between the duration propagules exist in the pelagic environment, their dispersal distance, and a species' geographic range (Jablonski 1986, Scheltema 1986, 1988), the perceived greater dispersal potential and homogeneity of marine environments have led some to argue that the geographic range and areas of occupancy of marine species are greater than taxonomically similar terrestrial species (Hockey and Branch 1994). This suggests that marine species with long distance dispersal (propagules or adults) are less vulnerable to smaller scale perturbations. Reserves distributed over these larger ranges may spread the risk of whole-scale extinction, buffering them from more frequent, smaller scale perturbations that would otherwise eliminate more spatially restricted species or communities. However, some marine species are not characterized by long distance dispersal and propagules may be locally retained by currents and behavioral mechanisms (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000). Also, there are examples of species ranges maintained by larval replenishment from source populations within a restricted portion of a species range (e.g., Cowen 1985). Additionally, many of the arguments for greater geographic ranges of marine species or communities are based on latitudinal ranges, "neglecting" longitudinal width and overall area of occupancy. Because reserves are presently focused on nearshore communities, the longitudinal extent of these communities is highly constrained to the width of continental shelves, depth ranges, or the very narrow intertidal region. Moreover, the greater resolution of newer genetic tools (e.g., microsatellites) have discovered marked genetic differentiation in populations once thought to be homogeneous. Thus, drawing from terrestrial reserve design, marine reserves designed to sustain biodiversity will likely have to be numerous and distributed broadly in order to increase the likelihood of protecting small populations, key source populations, and genetic variability across a species range.

The importance of geographic range in determining the area over which reserves should be distributed is also influenced by how variable long-term environmental conditions are and how well species can track changes in the spatial distribution of environmental conditions over time. A species with a small range capable of shifting its distribution and tracking changing environmental conditions may be more resilient to large-scale, long-term changes than a species with a broad but inflexible geographic range. However, inte-

grating this knowledge into reserve design requires that we can reliably identify the life history and environmental factors that influence the degree of flexibility in ranges. Archaeological, paleontological, and long-term records of nearshore assemblages suggests that species distributions have shifted markedly in response to long term, large-scale, environmental conditions (Hubbs 1948, McCall 1986, Barry et al. 1995, Roy et al. 1995), and that these changes are occurring over time scales meaningful to management strategies (100–1000 yr range; Valentine and Mead 1960). Based on pelagic ecosystems, Steele (1991) suggests that population abundance and geographic ranges of marine species respond to physical processes on the order of decades, while comparable changes in terrestrial systems occurs over centuries. One suggested reason for the difference in response times is that primary producers in terrestrial systems are large, long-lived species (trees) whereas primary producers in marine systems are small and short lived (phytoplankton; Steele 1991). This contrast may be as applicable to nearshore systems where even the large macroalgae have shorter life spans than many terrestrial plants. This suggested reliance of species on shifting distributions in response to climatic changes implies that spacing marine reserves over large areas to accommodate such shifts is critical to their long-term efficacy. Moreover, because some geographic range shifts have involved changes in depth distribution (Roy et al. 1995), and the depth distributions of many extant species change with latitude, reserves that extend onshore–offshore encompassing a wide range of depths may best accommodate longer term distributional shifts in response to climatic change. The importance of habitat-based corridors for providing species protection as their distributions shift may not be as important for species dispersed long distances in the plankton, but important to the many marine species with short distance dispersal (Roberts and Hawkins 1999).

Productivity, trophic structure, and patterns of human exploitation

A growing understanding of trophic interactions is beginning to influence thinking about the design of marine reserves and protected areas. Studies of rocky shores (Paine 1966, Hockey and Branch 1984, Menge et al. 1994), kelp forests (Estes and Palmisano 1974, Cowen 1983), tropical reefs (Hughes 1994, Hixon 1997, Hixon and Carr 1997, Pennings 1997), as well as freshwater habitats (Carpenter and Kitchell 1993, Power et al. 1996, McPeck 1998), deserts (Brown and Davidson 1977, Brown et al. 1986, Heske et al. 1994), tropical forests (Crockett and Eisenberg 1986, Terborgh et al. 1997), and other terrestrial habitats (Krebs et al. 1995) demonstrate or suggest the importance of apex predators and trophic cascades in community structure (Pace et al. 1999). Top-down interactions and trophic

cascades remain largely unstudied and unappreciated by open-ocean ecologists. Concern for the potential cascading effects caused by the loss of top predators, especially keystone predators (sensu Power et al. 1996), is one reason for their popular designation as focal species in the design of terrestrial reserves aimed at protecting biodiversity (Miller et al. 1999).

The frequently demonstrated importance of apex predators in maintaining community structure and biodiversity has had direct implications for the size of terrestrial reserves. Because apex predators in terrestrial systems commonly occur at relatively low densities and exhibit large home ranges, reserves must be large—large enough to encompass predator home ranges and maintain viable populations (Soulé and Terborgh 1999). The significance of reserve size was emphasized in a recent analysis of mammalian carnivores in terrestrial reserves, showing that the probability of extinction was more strongly related to home range than it was to population density (Woodroffe and Ginsberg 1998). Similar rationale holds for the many marine predators that exhibit large scale movement patterns whether seasonally or over their lifetime, shifting among habitats and depths in response to ontogenetic transitions in resource requirements.

Fundamental differences between terrestrial and marine ecosystems in rates of productivity and trophic structure emphasized in previous comparisons have been based primarily on pelagic systems (Steele 1985, 1991). Our focus on nearshore (coastal) marine systems, where the likelihood of reserve establishment and management is greater, suggests some of these differences may not be so pronounced (Dayton and Tegner 1984). For example, Steele (1991) pointed out the striking difference between marine and terrestrial systems in lifespan and rate of turnover of primary producers relative to higher trophic levels (phytoplankton vs. forests—hours to millennia, almost seven orders of magnitude!). Nearshore, in addition to phytoplankton, macroalgae are also important primary producers and have lifespans more comparable to terrestrial annuals and short-lived perennials. Nonetheless, the longevity of annual or perennial macroalgae, especially larger species (e.g., kelps) that contribute importantly to production and the physical structure of reef habitats (Duggins et al. 1989), appears substantially less than that of many of the large, structure-forming species of most terrestrial plant communities (Dayton and Tegner 1984, Dayton et al. 1984, 1999).

Another critical difference between marine and terrestrial systems is the relative extent of lateral transport of energy, materials, and individual organisms in and out of communities. Lateral transport includes both the passive movement of material by water or air currents or the more active movement of mobile individuals in and out of a community. Though lateral transport augments local primary and secondary production in ter-

restrial communities (e.g., Polis et al. 1997, Scott et al. 1999), the rate and magnitude is almost trivial compared to marine communities bathed in a constant influx of primary producers (phytoplankton), herbivores, and primary carnivores (zooplankton). This tremendous augmentation, both in terms of turnover rate and overall biomass, to local sources of primary production (algae, corals) contributes to marked differences in the distribution of biomass among trophic levels and key characteristics of each level (i.e., the prevalence and disproportionate biomass of filter feeding herbivores and secondary carnivores; Duggins et al. 1989).

Pronounced differences in dispersal modes and the "openness" of populations among trophic levels has critical implications for the design of marine reserves. One case involves closed populations of predators with limited dispersal potential that are reliant upon open prey populations replenished by pelagically dispersed larvae. This concern seems primarily relevant to apex megacarnivores, including sea otters and live-bearing or brooding fishes, whose young have short, if any, pelagic duration and whose prey (e.g., sea urchins, abalone) are exploited by humans (Bustamante et al. 1995, Estes and Duggins 1995, Watt et al. 2000). Success of reserves designed to sustain such predators will depend on the sustained influx (i.e., replenishment) of prey populations. This again dictates that such prey populations are linked across a system of reserves networked by pelagic dispersal or the sustainability of parental populations (larval sources) outside of reserves. Conversely, if reserves are not sufficiently large or connected to sustain open populations of keystone predators, closed populations of prey species protected within reserves may experience dramatic changes in relative abundance, jeopardizing the integrity of protected ecosystems.

"Bottom-up" and "top-down" processes are well documented in coastal marine ecosystems (Menge 1992, Pinnegar et al. 2000, Estes and Peterson 2000). Because of the prevalence of both local and lateral transport of primary production (and primary consumers), "bottom up" effects in coastal marine systems are manifested not only by local primary production, but also the import of phyto- and zooplankters, and the spores and larvae of early life stages of lower trophic levels. Moreover, evidence is growing for interactions among pelagic food availability, larval condition, and recruitment success, underscoring again the fact that reserves do not function in isolation from the surrounding matrix (Connell 1961, Menge 1992, Menge et al. 1997). Such links between nearby pelagic conditions and these external sources of input have further implications for the location of marine reserves. Reserves located such that they receive input of water rich in larvae and phytoplankton may experience more consistent recruitment than those that do not. Macroalgae and corals, like terrestrial plants, are both critical sources

of production and biogenic habitat structure. The limited dispersal potential of many macroalgae (Santelices 1990) and corals imply that such closed populations, like many terrestrial plants, must be self sustaining. Thus, like their terrestrial counterparts, marine reserves must be sufficiently large to assure local sustainability and reduce edge effects.

Keystone roles have been attributed to seastars, reef fish, shore birds, sea otters, and humans, to list the better known examples (Paine 1966, Cowen 1983, Hockey and Branch 1984, Kvitek et al. 1992, Estes and Duggins 1995, Navarette and Menge 1996, Lindberg et al. 1998). Marine communities with such strong top-down effects are not immune to external natural and anthropogenic events (Pinnegar et al. 2000). One recent example is the decline in sea otters, a keystone predator in kelp forests along the Aleutian Islands, which corresponded with increased occurrences of killer whales inshore. This decline in sea otters, attributed to predation by killer whales, resulted in predictable and marked responses of lower trophic levels (Estes et al. 1999). The increased occurrence of killer whales inshore is thought to be caused by declines in their major prey offshore, sea lions, which in turn may be related to declines in their prey, commercially exploited fishes. Another critical implication is that reserves of insufficient area to encompass movements of keystone species may increase their vulnerability to exploitation and jeopardize their effects on the structure of protected communities. Similarly, sustainable populations of keystone predators with dispersive larvae, as is the case for most fishes, will require mechanisms of larval retention, e.g., pelagic "corridors" between reserves, or management strategies that maintain sufficient spawning sources in the matrix of populations outside reserves.

Strategies for connectivity

Connectivity is an important consideration in reserve network design. However, the needs for connectivity differ between land and sea. On land, connectivity among reserves is needed because of large-scale habitat destruction in the surrounding matrix. Habitat destruction is clearly also of concern in the sea, but its effects may be less problematic for issues of dispersal. In the sea, the need for connectivity stems from the openness of populations. Hence, dispersal in the context of terrestrial reserves has been emphasized more in terms of connectivity between reserves: the linking of reserves via habitat "corridors" to protect and enhance the exchange of individuals among a network of reserves (Dobson et al. 1999, Perault and Lomolino 2000). By design, such corridors are created or demarcated across a landscape, and once designated are static features of a habitat or network design. "Corridors" of connectivity in marine systems can be similar in design if intended to protect the movement of the benthic stages

of mobile species among essential habitats (e.g., Acosta 1999). However, connectivity in marine systems also involves the movement of pelagic propagules independent of benthic habitat features. Corridors of larval dispersal involve water currents that must be identified, but that cannot be created and are not static. Thus, design of marine corridors requires the description of current patterns and their variability, as well as knowledge of how behavioral and biophysical attributes of propagules influence the distance and direction of dispersal (Cowen 1985, Blot et al. 1990, Palumbi 1995, Planes et al. 2000). Moreover, in the context of fisheries reserves, there is clear value in identifying corridors between reserves and exploited populations, not just between reserves, as has been the focus in terrestrial systems.

Like many freshwater species, the complex life histories and indeterminate growth of many marine species often translates into dramatic ontogenetic shifts in food and habitat requirements. Again, examples are most evident between vertebrates, which exhibit less dramatic dietary and habitat shifts in terrestrial systems (e.g., birds, reptiles, mammals) than do marine fish that often settle in shallower "nursery" habitats, feeding at lower trophic levels (plankton), eventually migrating to entirely different adult habitat as top carnivores (Love et al. 1991). Such strong ontogenetic differences have several implications for reserve design. Marine reserves might have to encompass a greater habitat diversity to insure that all requisite habitats and associated resources over the life of an individual are included. This in turn implies that marine reserves might need to be larger, to include greater habitat diversity, or might need more care in locating adult reserves near nursery habitats to ensure replenishment and sustainability of protected communities (Carr and Reed 1993).

Maintaining potential for adaptation and response to environmental change

In the early 1980s, the role of population genetics in the conservation of terrestrial wildlife populations became firmly established (e.g., Frankel and Soulé 1981). This coincided with a shift in emphasis from the implications of island biogeography for reserve design to the management of small populations (Simberloff 1988). Thus, the primary concerns of conservation genetics have been the loss of genetic variation in small populations and the negative effects of this loss. It has been argued that, for small wildlife populations, genetic effects are less likely to be the ultimate cause of extinction than are stochastic fluctuations in reproductive success or environmental conditions (Lande 1988; but for an alternative view, see Soulé and Mills 1998).

The avoidance of inbreeding is believed to be a major component of mate choice for terrestrial plants and animals species (Charlesworth and Charlesworth

1987). In closed populations, with low rates of immigration and emigration, relatedness and spatial proximity are likely to be correlated, and as a result, inbreeding would occur without mechanisms to prevent it. The effects of inbreeding are assumed to be deleterious, although inbreeding depression is difficult to measure in natural populations. In the colonial tunicate with limited larval dispersal, *Botryllus schlosseri*, inbreeding is reduced by a gametic incompatibility system that follows the same genetic rules as the sporophytic incompatibility systems of flowering plants (Schofield et al. 1982). This incompatibility system prevents mating between colonies that are members of the same clone, and reduces mating between related colonies that may be nearby as a consequence of extremely limited larval dispersal (Grosberg 1987).

In open marine populations, inbreeding is unlikely to occur because the probability of encounters between related adults is presumed to be diminished greatly by dispersal of planktonic offspring. This has both positive and negative implications for marine species protected in reserves. Population genetic studies of marine organisms suggest that the "small-population paradigm" is inappropriate for the conservation of marine species with pelagic life stages; we would expect that inbreeding would not be a problem to contend with in designing reserves for the many species characterized by open populations. Small populations contained in small reserves linked to external populations by larval dispersal may not be as vulnerable to inbreeding effects as similar sized terrestrial populations. However these studies point to other concerns that may be of considerable importance. We also would not expect to find that inbreeding avoidance mechanisms have evolved in species with open populations. Furthermore, in the absence of inbreeding, open populations may accumulate high proportions of deleterious recessive alleles (Haldane 1937). We can therefore predict that if populations of these species were suddenly closed (i.e., if protected populations did not receive sufficient gene flow from external populations), mating between related individuals would occur and severe inbreeding depression could result. This concern emphasizes again the importance of guaranteeing sufficient larval exchange among networked protected populations and unprotected populations.

Maintenance of genetic diversity of protected populations also raises the question of just how open marine populations really are. It is somewhat surprising that any genetic differentiation has been observed among populations of marine species with pelagic larvae, because high levels of gene flow should reduce genetic differentiation to undetectable levels (Wright 1965). One scenario that could account for both the temporal variance in allele frequencies and the high levels of genetic variation observed in marine populations is for a few populations to act as sources of

propagules for themselves and for downstream populations (Kordos and Burton 1993, Hedgecock 1994). Genetic variation would be maintained within the source populations, and variation in the contributions of source populations to downstream sink populations could drive temporal variation. If such source-sink relationships exist, they are clearly of great importance in the management of populations (Pulliam 1988). A second concern is that, for some marine species, estimates of effective population size (N_e) are surprisingly low compared to the census population size (N_c ; Hedgecock 1994, Neigel 1997b). While these estimates may be subject to alternative interpretations, they do reflect an essential difference between marine species with pelagic life stages and traditional wildlife species. The low estimates of N_e for marine species imply a high variance in one or more processes that are related to reproduction and recruitment. This suggests a greater degree of demographic unpredictability than is typically assumed for terrestrial wildlife populations.

Physical and ecological processes influence the performance of a reserve over ecological time scales (<100 yr), and may also determine the likelihood that a reserve system protects species and communities in the face of longer-term climatic changes (>100 yr). Steele (1985, 1991, 1998) has discussed how marine populations and communities respond rapidly to (and hence are more temporally coupled with) changes in their physical environment over ecological time scales. This responsiveness is manifested in dramatic changes in pelagic and benthic communities during regime shifts on the order of one to several decades (Roemmich and McGowan 1995, Hayward 1997, Holbrook et al. 1997, Francis et al. 1998, McGowan et al. 1998). Though such regime shifts are driven by atmospheric processes, biotic responses to decadal regime shifts have been argued to be far more dramatic in marine systems compared to terrestrial systems (Steele 1991, 1998). Thus, regime shifts on the order of decades need to be considered in regards to the persistence and design of marine reserves. Areas of biogeographic transitions may be particularly sensitive. The likely consequence is marked changes in community structure within a reserve and such changes would have to be accounted for when assessing the response of communities to protection by reserves. The broader implication is to distribute reserves across latitudes such that reserves afford protection to communities as they shift spatially in response to climatic regimes. Though it might be difficult for species with short-distance dispersal to do this, species that produce planktonic propagules that disperse long distances may be more successful at responding to such large-scale perturbations than many of their terrestrial counterparts. Again, this may be particularly important for exploited species, many of which produce pelagically dispersed propagules.

THREATENING PROCESSES

The primary threats to both marine and terrestrial systems are anthropogenic. Habitat destruction (including habitat loss, degradation and fragmentation), overexploitation, and introduced species are the main causes of biodiversity loss and extinction risk in terrestrial systems. Although, historically, overexploitation and introduced species were probably more important in terrestrial systems, particularly on islands, terrestrial species arguably are currently most threatened by habitat loss (Wilcove 1998). Habitat destruction (including fragmentation) contributes to the imperilment of three quarters of the threatened mammals of Australasia and the Americas and of more than half of the world's endangered birds (Groombridge 1992, Soulé and Sanjayan 1998). Thus, a major focus of terrestrial reserves is on mitigating habitat loss, with a particular focus on minimizing fragmentation. However, hunting and international trade in wildlife products contribute significantly to the extinction risk of more than half of the threatened mammals in Australasia and the Americas and more than one third of the world's threatened birds (Groombridge 1992), and have caused local extinctions of many mammals and birds in forested ecosystems, even in areas where habitat is largely intact (Redford 1992, Lande 1999). Indeed, in tropical regions of Africa and Latin America the thriving bush meat trade now rivals deforestation as the primary threat to many types of biodiversity (Robinson et al. 1999).

Nevertheless, a great many marine species, although also influenced markedly by habitat destruction in coastal environments, are presently influenced to a far greater extent by direct overexploitation relative to most terrestrial ecosystems. Globally, the combination of fish and other marine taxa provide a larger source of animal protein to the human diet than any single domesticated species (e.g., chicken, cattle; Norse 1993), and about half of the fisheries in Europe and the USA are now classified as overexploited (Food and Agricultural Organization [FAO] 1999). In contrast, most land-based food now comes from domesticated plants and animals. A second important characteristic of this exploitation in the sea is that it targets species of higher trophic levels than on land. In the sea, losses of top carnivores, and any cascading ramifications of their removal to the integrity of ecosystems, are more likely to be managed by controlling fishing activities (Fogarty and Murawski 1998, Pauly et al. 1998). Thirdly, the act of exploiting wild stocks in the sea (e.g., trawling, dynamiting) has insidious detrimental effects on benthic communities, habitat, and other resources required to sustain exploited species (Dayton et al. 1995, Lenihan and Peterson 1998, Wolff 2000). This relatively greater role of direct exploitation in the sea and the many indirect and associated impacts to coastal marine environments emphasizes the greater role of

reserves as mechanisms to manage and sustain fisheries (Bohnsack 1998, Hastings and Botsford 1999, Murray et al. 1999). In this context, given the importance of populations within reserves as sources to replenish exploited populations outside reserves, theory focused on processes that determine rates of larval and mobile adult export is particularly important to marine reserves.

Habitat destruction also occurs in marine systems, especially in more enclosed estuaries and embayments, but also in open coast unconsolidated habitats and coral reefs (Auster et al. 1996, Watling and Norse 1998, Freese et al. 1999, Edgar et al. 2000). Historically, however, habitat destruction has probably been much less problematic along the open coast than on land. One obvious reason for this is that human structures (buildings, roads, homes, etc.—the vehicles of more permanent habitat destruction) occur mostly on land. A less obvious reason stems from differences between land and sea in the generation time of autotrophs, and in the interplay between autotrophs and their physical environments. In terrestrial systems, long-lived plants form an important component of habitat. When these plants are disturbed by human activities (logging, fires, roads, etc.), their long generation times mandate very slow recovery. Furthermore, terrestrial plants interact in complex but important ways with various physical dimensions of terrestrial habitats. For instance, rain-forest trees sometimes hold a large fraction of certain limiting nutrients, terrestrial canopies greatly modify wind and sunlight on the forest floor, and disturbances such as fires often alter plant successional dynamics in ways that prevent recovery to the predisturbed state (thus creating alternate stable states, *sensu* Lewontin 1969 and Sutherland 1974). Although kelp forests and seagrass meadows display some similarities to the slower recovery rates characteristic of many terrestrial plants, they are generally less extreme. The vast majority of marine plants and algae have the capacity for faster recovery following even extreme disturbance events (e.g., Reed et al. 1998). Furthermore, marine autotrophs (kelps, phytoplankton, microbes) do not seem to hold a significant fraction of limiting nutrients in the sea. For these reasons, with the important exception of wetlands and seagrass habitats, habitat destruction via altered plant assemblages has been of less concern at sea than it has on land.

However, growing evidence suggests that new and cumulative impacts to coastal marine environments are increasing markedly. In addition to impacts associated with fishing activities mentioned above, sedimentation and eutrophication have degraded highly productive estuarine and coral reef habitats (Turner and Rabalais 1994, Burkholder 1998, NRC 2000). Especially, the strong influence of terrestrial and riverine input on coastal ecosystems in gulfs, protected embayments and lagoons reflects concerns about connectivity among ad-

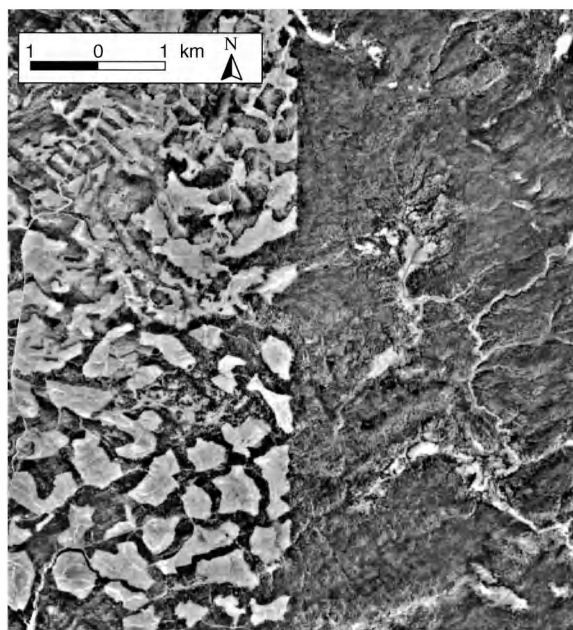


FIG. 2. Landsat photograph depicting the striking demarcation in terrestrial habitat alteration created by administrative and political boundaries. Pictured is a 14-km section of the western border of Yellowstone National Park and the adjacent Targhee National Forest to the west of the park.

jacent environments frequently expressed in the design of terrestrial reserve systems. Here, the design of marine reserves is more similar to terrestrial designs in that greater emphasis must be placed on controlling terrestrial and riverine inputs and coastal development (e.g., shoreline hardening).

ACCESS AND OWNERSHIP

Historically, both marine fisheries and terrestrial wildlife populations have been managed as open access, common-property, renewable resources. Inadequate regulation of user groups is a major cause of overexploitation and depletion of such resources (Ludwig et al. 1993, Walters and Maguire 1996, Myers et al. 1997). Human traditions of land ownership and settlement, and the resulting administrative and political boundaries, have literally painted a network of lines across the landscape of every major continent. Indeed, the imprints of these ownership lines, in the form of altered plant community composition and structure, are so distinct that they are clearly visible even from space, as evidenced by inspection of a Landsat image of the area around Yellowstone or Olympic National Parks (Fig. 2).

In principle, the design and management of reserves would be guided by science and would consider both ecological theory and biogeographic patterns (Soulé and Terborgh 1999). Historically, however, in terrestrial systems, both the design (or lack thereof) and management of reserves have been severely constrained by

administrative rather than by natural boundaries (e.g., Pickett and Ostfeld 1995). In part, this approach arose from a fragmented vision of natural resources in which managers viewed areas within a particular administrative designation (e.g., a national park or other public land) as islands, impervious to outside forces (NRC 1993). In the past decade, the focus of reserve network design and management in terrestrial systems has begun to shift away from administrative units or ownership status, towards designing sets of sites to conserve a range of biodiversity, including, not only species, but also ecosystem-level biodiversity and natural landscapes. Along with this growing recognition that biodiversity at the population and ecosystem levels could not effectively be maintained within relatively arbitrary administrative boundaries, new types of public-private ownership, or quasipublic institutions have expanded the potential options for achieving conservation to include complex partnerships or management agreements among multiple landowners or interests.

Of necessity, conservation strategies and techniques on land have developed in response to land ownership patterns. In the USA, although more than half of all land is privately owned, most terrestrial reserves have been created on public, not private, lands. Nevertheless, virtually all existing public land in the USA was previously owned by other nations and tribes, and was acquired through both purchase and conquest. Thus, in addition to constraining the size of reserves and their boundaries, land ownership patterns have created a complex set of constraints and opportunities for implementing reserves. For example, public subsidies and the lack of market pricing for some public resources can create disincentives for conservation, as when short-term "mining" of resources is favored over long-term sustainability. On the other hand, many important tools for financing terrestrial reserves, such as conservation easements, transferable development rights, extractive reserves, dedication, land exchange, or land banks, are all predicated on patterns of land ownership.

The fact that ownership boundaries in the sea are often less distinct than on land creates both opportunities and challenges for marine reserves. In principle, lack of clear ownership lines should facilitate the design of more ecologically effective reserve networks in marine than in terrestrial systems. However, while indistinct ownership patterns may facilitate the design of marine reserves, they may hinder their creation or designation, because of complex and difficult decisions about "who should decide" and "who should pay" for marine reserves. At present, management of marine resources is confounded both by a mix of jurisdictional entities (at least in the USA where local, state, regional fisheries council and federal fisheries jurisdictions overlap extensively) and by combinations of partially space-based (e.g., state and federal boundaries) and take-based (e.g., catch and size limits) regulations.

Thus, the coordination of jurisdictional entities will likely be a more formidable task in the design of coastal marine reserves. In addition, the range of legislative and financial tools and strategies for implementing reserves in terrestrial systems are largely nonexistent in the sea, and the creation of new sorts of tools will require both political and economic sophistication.

CONCLUSIONS

People with a diversity of interests (scientists, managers, conservationists, and those from industry) are rapidly moving toward the view that reserves will be necessary for sustainability of marine ecosystems and biodiversity from the local to global scale. Three essential questions (variables) in any design strategy are (1) how large must reserves be, (2) how many must there be, and (3) where should they be located? Our comparison between terrestrial and marine systems indicates that there is no single answer for all systems. Specific answers (i.e., design criteria) depend on relationships between the spatial and temporal scales of physical processes and the characteristics of species, populations, communities, and ecosystems. We have identified many fundamental differences between land and sea at each of these levels of ecological organization, determined in large part by differences in aerial and aquatic environments. While such differences imply distinct objectives and design criteria for reserves, we have also demonstrated many merits of reserves common to both marine and terrestrial systems. Though we have identified several fundamental ecological and environmental differences that underscore the need for new theory and models for designing marine reserves, two similarities are particularly noteworthy. One is the commonality of positive species-area relationships characteristic of many terrestrial and marine ecosystems. The underpinning of such relationships, common to both marine and terrestrial ecosystems, is the increase in species diversity concomitant with increasing habitat diversity as a function of area. This similarity stresses the importance of larger marine reserves that encompass a greater diversity of habitat types; habitat diversity that supports and protects both a greater diversity of species and the greater breadth of resource (habitat-based) requirements during the ontogeny of exploited marine species. Secondly, the effectiveness of terrestrial reserves have suffered dramatically from the lack of infrastructure that provides the means for diligent management and evaluation. Marine reserve programs must heed this invaluable lesson from their terrestrial counterpart. Less than 1% of the world's oceans are currently afforded reserve status. The challenge now is to incorporate the objectives and criteria distinct to coastal marine systems into the design and implementation of marine reserves. Much of the conceptual and theoretical considerations in this issue rec-

ognize these differences and have attempted to achieve this goal.

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