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OCEANS AT RISK

Research Priorities in Marine Conservation Biology

Mark A. Hixon, P. Dee Boersma,
Malcolm L. Hunter Jr., Fiorenza Micheli, Elliott A. Norse,
Hugh P. Possingham, and Paul V. R. Snelgrove

In the end, we will conserve only what we love.
We will love only what we understand.
—Baba Dioum, Senegalese naturalist and poet

The marine environment encompasses a broad array of ecosystems, ranging from spectacular coral reefs and kelp forests to coastal mangroves, seagrass beds, and salt marshes; to expansive deep-sea plains interspersed with trenches, seamounts, ridges, and hydrothermal vents; to the vast open water column up to thousands of meters deep. Although the oceans cover 70.8 percent of the earth's surface, we know little about the three levels of biodiversity in the sea: genetic, species, and ecosystem (Norse 1993; NRC 1995; McAllister 1996; Ormond et al. 1997). However, we do know that marine biodiversity is extremely valuable to humankind, accounting for over 60 percent of the economic value of the biosphere (Costanza et al. 1997). Sea life provides five basic services to humans (Norse 1993; Daily 1997; Costanza 1999; Moberg and Folke 1999):

- *Ecosystem services.* Examples range from the global "biological pump" that sequesters atmospheric carbon dioxide and transports carbon to the deep sea, to the regional role of coral reefs and salt marshes in moderating coastal erosion.
- *Food.* About 20 percent of the animal protein consumed by humans comes from marine fisheries.
- *Medicines.* Marine organisms are increasingly found to contain biomedically active compounds, including antitumor agents.
- *Minerals and chemicals.* Examples include abiotic resources (fossil fuels, manganese, table salt, etc.), as well as chemicals derived from organisms (such as alginate from seaweeds and chitin from crustaceans, both used in a broad variety of food, medical, and technological applications).
- *Recreation and ecotourism.* Marine life, especially the charismatic megafauna of the seas (marine mammals, etc.), has inspired humankind since time immemorial. Recreational use of coral reefs supports many regional economies.

Despite their immense value, marine ecosystems are deteriorating rapidly due to human activities, especially physical alteration of habitat, overexploitation, species introductions, global climate change, and marine pollution (reviews by GESAMP 1990; Norse 1993; NRC 1995; Peterson and Estes 2000; Steneck and Carlton 2000). The most threatened systems are coastal, especially wetlands (including estuaries, salt marshes, and mangroves), coral reefs, and communities associated with the seafloor of the continental shelves.

Unfortunately, because detailed exploration of the oceans is a recent endeavor, we have little knowledge of what species are being lost (Irish and Norse 1996). It is nonetheless becoming increasingly clear that human-induced extinction in the sea is a sad and threatening reality (Carlton et al. 1991; Carlton 1993; Norse 1993; Vermeij 1993; Culotta 1994; Vincent and Hall 1996; Malakoff 1997; Casey and Myers 1998; Carlton et al. 1999; Roberts and Hawkins 1999). To date, it has been documented that only four marine snails, five seabirds, and three marine mammals have gone extinct in recent history due to human activities, but these cases are undoubtedly the mere tip of the iceberg of ongoing marine extinctions. Conservative estimates suggest that over 50,000 species of coral-reef organisms have already been lost (Carlton et al. 1999).

The goals of this chapter are twofold. First, we provide a brief review of the major differences between marine and terrestrial systems relevant to conservation biology, emphasizing the present limits of our knowledge. Second, we propose nine broad scientific research priorities in marine conservation biology, emphasizing six of these as particularly urgent. These priorities were derived from the literature, from canvassing experts (the thirty-five respondents listed in the acknowledgments), and from the workshop participants. Our list extends related research priorities previously proposed by Grassle et al. (1991) (table 7.1) and by the NRC (1995) (table 7.2), as well as the general research thrust described in the Sustainable Biosphere Initiative (Lubchenco et al. 1991). The focus is on natural science rather than socioeconomic issues, although the latter are also crucially important (e.g., Myers and Kent 1998; Costanza et al. 1999; chapter 10). Additionally, we focus more on urgent empirical priorities than on theoretical research questions, even though theory clearly has a role in all conservation efforts.

Addressing research priorities in marine conservation biology will require a broadly based interdisciplinary approach, including oceanography, toxicology, physiology, genetics, paleontology, taxonomy, systematics, and ecology.

TABLE 7.1. Research Questions Regarding Marine Biodiversity Previously Reported by Grassle et al. (1991).

1. Is the spectrum of environmental variation in marine and terrestrial ecosystems fundamentally different?
2. Are biogeographic patterns of biodiversity and ecosystem function determined by a combination of environmental patterns (i.e., are single-factor theories not viable)?
3. Are offshore primary production and nutrient cycling dominated by pelagic processes that determine biogeographic differences in biodiversity?
4. Do increases in environmental heterogeneity in space and time, including disturbance, increase biodiversity, especially in the coastal zones?
5. Do keystone species play a more important role in marine than in terrestrial ecosystems, and is that role more important in the lower latitudes?
6. Do species introductions have major consequences for marine ecosystem function?
7. Are extinctions less likely to occur in marine than in terrestrial systems?
8. Are increases in airborne and waterborne pollutants (including terrestrially derived disease species) and/or overfishing currently resulting in widespread changes in marine systems?
9. Have marine ecosystems and organisms developed less robust internal processes to respond to the low-magnitude short-term variations, and would this result in a reduced ability to respond to large-scale environmental changes?
10. Is redundancy of genes and species necessary for the long-term survival of marine ecosystems?
11. Is there greater genetic variation at the molecular level within species in marine environments than in terrestrial ones?

Source: F. Grassle, P. Lasserre, A. D. McIntyre, and G. C. Ray, "Marine Biodiversity and Ecosystem Function: A Proposal for an International Programme of Research." *Biology International* 23 (Special Issue, 1991): 1–19.

TABLE 7.2. Research Questions Regarding Marine Conservation Biology Previously Reported by the National Research Council (1995).

Natural Variation in Biodiversity Pattern and Why Biodiversity Matters

1. How do genetic, species, and ecosystem diversity vary in space and time at different regional scales and within habitats within those regions? Examples of specific research questions are:
   - To what extent does the maintenance of local biodiversity (genetic or species) depend on linkages between distant populations, the dispersal between them, and the availability of suitable habitat?
   - How does genetic diversity within a species influence reproduction and population growth or susceptibility to epidemic disease?
   - To what extent do changes in biodiversity at one site within a region—or between regions—affect the biodiversity at another site or in another region?
   - What specific characteristics of a habitat directly or indirectly influence genetic and species diversity? For example, are there parallels in the origin and maintenance of coral reef and deep-sea biodiversity?
2. What is the functional significance of biodiversity at the genetic, species, and ecosystem levels? Are species within a functional group interchangeable? What might be learned from comparing and contrasting systems in terms of the functional significance of biodiversity? (For example, are there parallels between the ecological significance of microbial diversity as coral reef symbionts [zooxanthellae] and as open-ocean primary producers [picoplankton]?)
3. To what extent does the diversity of a community determine (a) "stability," (b) productivity, (c) resistance to invasion or disease, and (d) ability to recover from natural and human impacts? Equally important, how do these factors interact? Do high-diversity systems have higher or lower production than systems whose diversity has been impaired? What is the role of biological invasions in altering system production or energy flow?
4. How good are the estimates of genetic, species, and ecosystem biodiversity, and how do the limitations (i.e., understanding of the scale of error) influence an understanding of biodiversity patterns and of ecosystem structure and function?

Human Impact on Processes Responsible for Biodiversity Change

1. What are the direct impacts on biodiversity of human-altered systems? That is, what is the variation in biodiversity over spatial and temporal scales relevant to the critical environmental issues? Examples of specific research questions are:
   - How do human influences on biodiversity differ from those caused by natural processes?
   - To what extent do human effects alter the probability of ecosystem collapse in different systems?
   - To what extent are particular changes in biodiversity due to human activities reversible?
   - Given the often direct impacts on certain target species within a region, are species within functional groups interchangeable within a system?
   - How does the addition or loss of species due to human activities affect community structure and resilience?
2. What are the indirect impacts on biodiversity of human-altered systems? Examples of specific research questions are:
   - What characteristics of species enhance susceptibility or provide immunity to precipitous declines?
   - In what types of habitats are alternative ecological communities stable?
   - Are threshold processes involved in precipitous declines (and the persistence of those declines) in biodiversity, and ultimately, in the risk of extinction of individual species?
   - Does genetic or species diversity provide a buffer against irreversible or massive perturbations?
   - What are the long-term effects of species replacements (e.g., exotic species) on ecosystem function?

Source: National Research Council, *Understanding Marine Biodiversity: A Research Agenda for the Nation* (Washington, D.C.: National Academy Press, 1995).

Given the scope of challenges in conserving sea life, we cite key publications to facilitate entry into the marine biodiversity and conservation literature. For recent accounts in the popular press regarding the plight of the seas, we suggest Marx (1999), Thorne-Miller (1999), and Woodard (2000).

Differences between Marine and Terrestrial Conservation Biology

There are substantial ecological differences between the sea and the land (reviews by Steele 1974, 1985; Norse 1993; Cohen 1994; May 1994; NRC 1995; Field et al. 1998), several of which pose contrasts regarding challenges in conservation research:

- *Oceans are huge and difficult to study.* Relative to that of air, the high density of seawater provides greater buoyancy and support for organisms, thereby distributing planktonic (drifting) and nektonic (swimming) sea life over a vast three-dimensional environment. Assuming that the terrestrial biosphere effectively averages 50 m thick, Childress (1983) estimates that the oceans constitute approximately 99.5 percent of the volume of the biosphere (21.0 percent less than 1,000 m deep and 78.5 percent greater than 1,000 m deep). Averaging some 4,000 m in depth and very difficult to access by humans, the abyssal plain is the largest continuous environment on the earth, accounting for about 42 percent of the area of the oceans and about 30 percent of the planet.

Marine biodiversity is high but largely unknown. As the probable original source of life on the earth, the sea has a greater diversity of animal phyla (fifteen phyla are solely marine vs. one solely terrestrial) than the land (Norse 1993; NRC 1995). Newly discovered marine ecosystems have revealed a variety of taxa previously unknown to science. For example, over twenty new families, one hundred new genera, and two hundred new species (with high endemism) have been discovered on and near deep-sea hydrothermal vents (Tunnicliffe 1991; Van Dover 2000). Hundreds of newly discovered species of invertebrates and fishes are described annually (WCMC 1992).

The immense volume of the oceans, combined with the small size of most marine plankton, offers particular challenges in documenting and understanding the diversity of tiny marine organisms. Entire species groups, such as the prochlorophyte picoplankton, have been discovered only recently (Chisholm et al. 1988; Olson et al. 1990). Undiscovered marine microorganisms may comprise at least thirty-four phyla and eighty-three classes (Corliss 1994).

As a consequence of the huge size, the variety of life and habitats, and the inaccessibility of the oceans, estimates of species diversity in the sea are very rough (reviews by WCMC 1992; Norse 1993; NRC 1995). Grassle and Maciolek (1992) estimate that ten million macroscopic animal species inhabit the deep sea. Snelgrove et al. (1997) report that there are some one hundred thousand species described from marine sediments in general, and perhaps one hundred million undescribed species. Reaka-Kudla (1997) estimates that up to nine million species, including about 30 percent of marine fish species (Roberts et al. 2000), inhabit coral reefs. Accounting for less than 1 percent of the ocean surface, coral reefs can be considered the tropical rain forests of the seas in terms of both high biodiversity and threatened status, with 50–70 percent of reefs under direct threat from human activities (Wilkinson 1999).

Genetic diversity among and within marine species is also high, including many cryptic and sibling species, but is very poorly understood (Palumbi 1992, 1994; Knowlton 1993; Avise 1998). The genetic diversity of marine viruses is particularly immense, with typically fifteen to forty visibly distinct genome sizes in a given sample of seawater, including high spatial and temporal variation (Fuhrman 1999). Genetic diversity of marine bacteria is also huge (Giovannoni et al. 1990). Given that less than 15 percent of the approximately 1.7–1.8 million described species worldwide are marine (WCMC 1992; May 1994), we are sorely in need of a comprehensive assessment of marine species richness and biodiversity. However, immediate conservation action to conserve this diversity is needed before we can afford the time for such an assessment.

- *Marine food webs are extremely complex.* The small size of marine phytoplankton strongly influences the structure of oceanic food webs. Most of the primary production in the sea is consumed by herbivores, unlike the situation on land, where most plant material dies and enters the decomposer food web (detritus nonetheless being the major food input to the deep sea). Indeed, the turnover of phytoplankton can be so high that there can be inverted pyramids of biomass, in which the standing crop of herbivorous zooplankton actually exceeds that of the phytoplankton. Thus, "ecological efficiency," the percentage of energy stored in one trophic level (say, plants) that becomes incorporated in the next higher trophic level (say, herbivores), tends to be greater in the sea than on land (about 20 percent vs. about 10 percent). This fact, combined with the virtual absence of size constraints in marine animals due to the support provided by water, results in marine food webs often having more trophic levels than those on land. Moreover, the relative morphological and evolutionary complexity of marine life results in many cases of omnivory (organisms that consume more than one trophic level below them) and mixotrophy (organisms that both photosynthesize and consume other organisms). These phenomena multiply the number of trophic linkages in marine food webs, creating ecologically complex communities. This complexity, including a variety of direct and indirect interactions, offers challenges in understanding, managing, and conserving marine life at the scale of entire ecosystems (see chapter 3).
- *Oceanic currents transport both larvae and pollutants.* The common reproductive mode of multicellular organisms in the sea (with the exception of sharks, marine mammals, and a few other groups) is broadcast spawning of small gametes, with dispersal occurring during a pelagic (open-water) larval stage. Especially in species that are associated with the seafloor as adults (benthos and demersal fishes), this life history pattern may result in local populations that are largely demographically and genetically open, linked by larval dispersal (a population of populations typically called a metapopulation). However, at some larger spatial scale, all marine populations are reproductively closed (Jones et al. 1999; Swearer et al. 1999). Poorly known is the extent of larval retention within local populations as well as the level of connectivity among populations (Cowen et al. 2000), both of which have important ramifications for conservation of marine species. Larval dispersal may in fact

reduce the risk of extinction in some marine organisms. However, this hypothesis has not been adequately tested, and severe declines in populations of large predatory fishes due to overfishing suggest that reliance on this hypothesis is dangerous. In fact, increasing recognition of large numbers of sibling species in the oceans suggests that there may be substantial subdivision of species and populations (Knowlton 1993). Patterns of larval dispersal between spatially isolated local populations may result in genetically identifiable subpopulations or "stocks" delineated by ocean circulation patterns. At the same time, larval transport creates fluid boundaries between oceanic ecosystems and biogeographic regions. Consequently, geographical ranges of species tend to be larger in the sea than on land (reviews by Norse 1993; NRC 1995; Ormond et al. 1997). The spatial scales of resulting "large marine ecosystems" (Sherman et al. 1990) are typically greater than those of political boundaries, creating management problems for straddling fish stocks and highly migratory fishery species.

Finally, oceanic currents transport chemicals as well as organisms, so that it may be more difficult to contain the spread of both pollutants and exotic species in the sea vs. on land (excluding atmospheric dispersal). The oceans are biogeochemical sinks located downstream from land. Coastal marine ecosystems, particularly near the mouths of major rivers, receive tremendous inputs of terrestrially generated pollutants, especially via agricultural runoff.

Overall, compared to that of its terrestrial counterpart, the science of marine conservation biology is in its infancy for three related reasons: (1) the relative size and inaccessibility of the seas (e.g., SCUBA and research submersibles have been widely used by biologists only since the 1970s); (2) the relatively scant funding of marine conservation (e.g., in FY 1999, the U.S. National Parks Service received US$1.7 billion in funding, whereas the U.S. National Marine Sanctuary Program received US$14.3 million); and (3) the relatively sparse literature on this subject (e.g., until recently, terrestrial papers in *Conservation Biology* outnumbered marine papers thirteen to one). Scant funding and sparse literature may be a consequence of the general focus of marine science on issues other than conservation biology. All told, only 0.25 percent of the oceans are afforded some level of conservation protection, compared to over 5 percent of the land (McAllister 1996).

Research Priorities in Marine Conservation Biology

Given our general lack of detailed knowledge relevant to marine conservation biology, research priorities for the next decade (indeed, the next century) include the nature of marine biodiversity, the threats to that biodiversity, and

the tools for conserving life in the sea. Nine research priorities are discussed in sequence below and listed with specific priority actions in box 7.1.

Understanding the Nature of Marine Biodiversity

It is difficult to conserve something that is unknown. The key questions underlying this section are: What are we trying to conserve, and how does it function? As is true on land, substantial efforts at documenting marine biodiversity at the level of ecosystems, species, and genes are important. There is also an urgent need for long-term monitoring of marine ecosystems at multiple spatial scales (e.g., CARICOMP in the Caribbean, Ogden and Gladfelter 1986). (Note, however, that biodiversity assessment and monitoring are not necessarily related, as the latter can focus on only a few indicator species.) Marine taxonomy and systematics must also be revitalized (Winston 1992; Feldmann and Manning 1992; Vecchione and Collette 1996). Less formal but equally important, local cultural knowledge can be a major source of information on marine species and their ecology, as exemplified by Johannes's (1981) studies of Pacific coral reef fishes and fisheries.

However, while immediate estimation of undescribed species richness is an important tool, pursuing long-term monitoring and alpha taxonomy should not delay resolution of urgent conservation issues. Therefore, we advocate a major initiative to organize the spatial and temporal information on marine biodiversity that is already available, constructing databases that will be of immediate use for conservation efforts. Geographic information systems (GIS) mapping patterns of marine habitats and biodiversity will be especially valuable for the establishment of substantial networks of no-take marine reserves. At the same time, we see the importance of intensive ecological studies of several key marine ecosystems. We thus propose three research priorities concerning the nature of marine biodiversity:

- *Map the distribution of and threats to biodiversity (ecosystems, species, genes).* Cataloging the distribution of marine life among ecosystem types is the traditional realm of marine biogeography (Briggs 1974). However, conservation efforts require detailed geographic information systems that overlay different aspects of biodiversity (as well as threats) at nested spatial scales, including species-area relationships (Johnston 1998). This endeavor is the focus of seascape ecology (Bartlett and Carter 1991; Ray 1991; Jones and Andrew 1992). GIS assessments of species richness are already being developed and are proving effective for some taxa, such as coral reef fishes (Roberts et al. 2000). An important issue is whether habitat-generating species (such as corals, large seaweeds) and visually dominant groups (such as fishes, large invertebrates) can provide accurate indices of total diversity within highly species-rich communities or those that are otherwise difficult to study (Ward et al. 1999).

We emphasize that much of the needed mapping will require not new research but assembly of existing data. Related research is required to determine the most effective ways to map marine habitats and associated biodiversity. Some approaches may be biophysically based, while others may be based on actual species composition at different locations. For select groups of organisms, indirect mapping tools can be ground-truthed by detailed field assessments.

Regarding genetic diversity, marine conservation genetics is in its infancy (Knowlton 1993; Palumbi 1992, 1994; Avise 1998). Expanded use of modern molecular methods will provide insight on population genetics, identify cryptic and sibling species, elucidate levels of endemism, and generate novel measures of genetic biodiversity. Of course, such analyses take time that we can ill afford, so immediate conservation action remains a higher priority than detailed assessments of genetic diversity.

GIS assessments should also incorporate ecosystem diversity, including coastal zones integrated with associated terrestrial systems (Ray and Hayden 1992; Ray 1996). Overall, these tools will identify regions of high species richness and high endemism, spawning and nursery habitats, migration routes, unique or special environments (such as hydrothermal vents), and particularly sensitive ecosystems. Overlying data on the nature, intensity, and urgency of threats to these regions will enable policy makers and managers to choose and rank areas for immediate conservation efforts, as well as identify sites for long-term study and monitoring.

- *Document temporal changes in biodiversity (ecosystems, species) over historical and geological time scales.* Because long-term knowledge of marine communities is lacking for most systems, the status of marine ecosystems and especially our perceptions of their pre-impact baseline conditions are both shifting rapidly (Pauly 1995; Sheppard 1995; Jackson 1997; Dayton et al. 1998; Steneck and Carlton 2000). Increasing evidence suggests that human impacts on marine ecosystems occurred long before the latter half of the twentieth century (reviews by Pauly 1995; Steneck and Carlton 2000). Examples have been documented in Alaska (Simenstad et al. 1978), the Caribbean (Jackson 1997), California (Dayton et al. 1998), the Gulf of Maine (Steneck and Carlton 2000), and elsewhere (Aronson 1990). Continued examination of historical accounts, as well as intensified monitoring, will provide better estimates of recent changes in marine communities and patterns of biodiversity. Over longer time scales, the fossil record can provide insight on the relative stability of species assemblages (e.g., Sepkoski 1992; Jackson 1995). Further exploration of existing community-level paleontological data will provide estimates of background rates of extinction in the sea. Such baselines will provide a basis of comparison for modern trends that may help to convince governments of the urgency of marine conservation issues.

- *Explore the ecological mechanisms driving population dynamics, structuring communities, and affecting biodiversity in several key ecosystems.* Despite advances in our knowledge of rocky intertidal communities and other reasonably well-studied systems, we know little of basic population and community ecology as they relate to marine conservation biology. Certainly, such information will come only with time and substantial effort, but this knowledge is crucial for understanding what naturally regulates marine populations and maintains species diversity. We advocate intensive ecological study of several ecologically important and representative systems, including: (1) small open-ocean fishes and krill, which constitute the major trophic links between plankton and high-seas fishery species; (2) coastal bottom-oriented fishes (and the seafloor communities of which they are a part), which are often severely overexploited and their habitats physically altered by trawling (see below); and (3) coral reefs, the most species-rich and among the most threatened of all marine ecosystems (see above).

At the population level, increasing use of genetic methods (Avise 1998), otolith (fish ear-stone) microchemistry (Swearer et al. 1999), larval tagging (Jones et al. 1999), and physical oceanography (Cowen et al. 2000) will answer questions regarding population connectivity, metapopulation structure, and stock boundaries. These issues are particularly important for designing and implementing marine protected areas (see below). The mechanisms driving and regulating population fluctuations in the sea are also largely unknown, although hypotheses abound (Rothschild 1986; Sale 1991; Cushing 1995; Caley et al. 1996). Increasing use of controlled field experiments, especially at larger spatial scales, will be especially informative, but not always possible (Hixon and Webster 2001). Central topics in community ecology relevant to conservation include the roles of habitat complexity, disturbance and succession, webs of direct and indirect interactions, and diversity-stability and diversity-function relationships (conceptual reviews by Huston 1994; Pickett et al. 1998).

Ultimately, such knowledge will allow us to answer crucial questions regarding extinction and conservation in the sea. Is our knowledge of terrestrial species relevant for conserving marine species (reviews by WCMC 1992; Carlton et al. 1999; Roberts and Hawkins 1999)? Does larval dispersal render marine species less prone to extinction than terrestrial species (Grassle et al. 1991)? What are minimal viable population sizes (review by Soulé 1987)—from both a demographic and a genetic perspective—in marine species with relatively open vs. closed populations? How (if at all) does the Allee effect (a decreasing population growth rate at low population sizes, reviewed by Courchamp et al. 1999) operate in the sea? Are increases in population sizes of protected marine species hastening the decline of other threatened species, such as sea otters contributing to the demise of white abalone in California (Tegner et al. 1996) or orcas causing the decline in sea otters off Alaska (Estes et al. 1998)?

Understanding the Threats to Marine Biodiversity

The ultimate threat to biodiversity in the sea, as on land, is human overpopulation and overconsumption spurred by technological developments, global commerce, ignorance, greed, and inadequate conservation programs. Proximally, there are five major categories of human-induced threats in the oceans (general reviews by GESAMP 1990; Norse 1993; NRC 1995; Botsford et al. 1997; Peterson and Estes 2000; Steneck and Carlton 2000):

- *Physical alteration of habitat.* Marine habitats are physically degraded by (1) coastal development (including mariculture practices that destroy or alter estuaries, salt marshes, and mangroves), dredging, shoreline erosion, and resulting sedimentation; (2) ocean mining and seafloor drilling; and (3) destructive fishing practices, including bottom trawling and dynamite fishing.
- *Overexploitation.* Widespread overfishing of the seas has resulted in stock collapses and alterations of population and community structure.
- *Species introductions.* Transported across the seas attached to ship hulls or contained in ballast water, introduced exotic species have potential competitive, predatory, and biological-disturbance impacts on native species and communities.
- *Marine pollution.* Located downstream from land, the sea carries the burden of human-generated excess nutrients via runoff of sewage and fertilizers (as well as atmospheric deposition of nitrogenous compounds), petroleum spills, halogenated hydrocarbons (pesticides, PCBs, dioxins, etc.), heavy metals, radioactive waste, plastics, etc.
- *Global climate change.* Global warming is altering oceanic currents and patterns of marine productivity, is associated with increasing coral bleaching, and threatens coastal marine ecosystems via sea level rise, while stratospheric ozone depletion is increasing UV-B penetration in the sea, with documented negative effects on marine organisms.

All these threats are important. We see global climate change as one of the most dangerous threats to marine biodiversity, but due to its universal nature, we defer to the chapter on that topic (chapter 9). Therefore, we advocate focused research priorities within each of the four remaining categories of threats. Despite this separation of impacts into distinct categories, it is important to keep in mind that anthropogenic threats to marine biodiversity are ubiquitous, cumulative, and synergistic, as exemplified by the sorry states of the Baltic Sea (Elmgren 1989), the Black Sea (Zaitsev 1992), and the Caribbean Sea (Hughes 1994). The four remaining categories of threats are as follows:

- *Document how physical alteration and fragmentation of habitats affect seafloor ecosystems.* Seafloor habitats are structured physically by geological and oceanographic processes (resulting in different seafloor types, such as sand vs. rock), and biologically by biogenic habitat builders (species such as mangroves, salt marsh grasses, seagrasses, seaweeds, and corals that create living space for other species), as well as by agents of biological disturbance (such as stingrays digging for buried prey and infaunal clams turning over sediments).

  Degradation and outright destruction of the physical structure of habitat is the most direct negative impact of humanity on the seas. Studies to date indicate that nearshore marine populations and communities are negatively affected by human-induced coastal erosion and sedimentation, artificial beach nourishment, and dredging (reviews by Nelson 1993; Maragos et al. 1996; Peterson et al. 2000). About half of all mangroves are already lost, increasingly due to construction of mariculture ponds, mostly for shrimp and prawn production (Fortes 1988; Kaly and Jones 1998). Offshore, where we have fewer data, trawl and dredge fisheries are clearly degrading crucial seafloor environments and communities (reviews by Jones 1992; Dayton et al. 1995; Watling and Norse 1998; Auster and Langton 1999). Between 1976 and 1991, Georges Bank off New England was trawled and dredged an average of 200 to 400 percent of its area annually. In impoverished developing nations, both demand and greed have led to degradation of coral reefs via dynamite, cyanide, and bleach fishing, all devastating forms of Malthusian overfishing (Pauly 1988). This tragedy is exacerbated by a developing "live fish" restaurant and aquarium trade (Johannes and Riepen 1995).

We need more accurate information on the extent of these impacts, the effects they have on biodiversity over different spatial and temporal scales, and how reversible they are. How much more marine habitat—including salt marshes, mangroves, coral reefs, seagrass beds, and kelp forests—can be lost without the substantial loss of associated species? If human impacts are ameliorated, how long will it take these ecosystems to recover (if they ever can)? Regarding habitat fragmentation, we need more information on population dynamics and movements of bottom-living fish and invertebrates among patches of seafloor habitat created by human activities (Butman et al. 1995; Irlandi and Crawford 1997; Micheli and Peterson 1999).

- *Document how overfishing alters marine food webs.* Compared to terrestrial systems, food extracted by humans from the sea comprises wild (rather than domestic) species at high (rather than low) trophic levels (Pauly et al. 1998). There is increasing evidence that the seas are severely overfished (e.g., Dayton et al. 1995; Pauly and Christensen 1995; Safina 1995; Botsford et al. 1997; FAO 1997; Jennings and Kaiser 1998; Pauly et al. 1998; Hall 1999; NRC 1999). The general question is: What are the direct (i.e., demographic and genetic) and indirect (i.e., community and ecosystem) ecological impacts of fishing on marine populations and communities? Direct effects have been the conceptual realm of fishery science, and we have no intention of presumptuously setting research priorities for fisheries management agencies. We are encouraged by ongoing fisheries research designed to predict sustainable levels of exploitation more realistically by increasing the accuracy of stock assessments (NRC 1998). Also encouraging is a trend for fisheries scientists to examine deeper questions regarding the effects of exploitation on both the demography (e.g., Musick, Berkeley, et al. 2000; Musick, Burgess, et al. 2000; Coleman et al. 2000; Parker et al. 2000) and the genetics (e.g., Ryman 1991; Smith et al. 1991) of targeted species.

  However, the indirect effects of overfishing on entire marine communities are still seldom addressed due to the historical single-species focus of fishery biology and general lack of funding. Importantly, fished species are parts of larger systems, so altering their abundance often has ramifications for the entire system. Decreases in population sizes of both targeted and bycatch species can result in "biomass dominance shifts," due to alterations of competitive and predatory interactions (e.g., May et al. 1979; Fogarty and Murawski 1998). In extreme cases, such shifts can lead to systems switching between "alternate stable states" (e.g., Simenstad et al. 1978; Estes et al. 1998). An area of special concern is bycatch, which is the capture of nontargeted species by fisheries, and which accounts for about a quarter of the entire marine catch (reviews by Alverson et al. 1994; Hall 1996; Crowder and Murawski 1998). Most bycatch is discarded at sea, which provides a supplemental food source for seabirds, sharks, crabs, and other scavengers, with unknown community-wide consequences. These and other indirect effects of overfishing are examined in detail in chapter 3, but few are well documented and all clearly pose important research priorities.

- *Document how species introductions affect native species and alter community structure.* The largely inadvertent translocation of marine species, both as sessile adults attached to ship hulls and as larvae carried in ballast water, is increasingly well documented, but the ecological impacts of most introduced exotics are poorly known (reviews by Carlton 1985, 1999; Carlton and Geller 1993; Ruiz et al. 1997, 1999). Unfortunately, in many systems we do not always know which species are truly native vs. introduced vs. cryptogenic (of unknown history; Carlton 1996). Indeed, more than one thousand common intertidal and subtidal species may have been introduced by ships worldwide between 1500 and 1800 (Carlton 1999), and an estimated three thousand species are in transit daily in the ballast water of ships (Carlton and Geller 1993). Mariculture programs may introduce not only cultured species, but also their close associates and their diseases (Naylor et al. 2000). The rate at which marine diseases are spread by human activities and especially the consequences (such as the Caribbean-wide pandemic affecting long-spined urchins in the early 1980s; Lessios 1988) are areas of special concern (Harvell et al. 1999).

  There is need for the geographic origin of marine species to be elucidated by paleontological data (the recent fossil record; e.g., Pandolfi and Minchin 1995; Pandolfi and Jackson 2001), anthropological information (such as human middens; e.g., Simenstad et al. 1978; Borque 1996), and genetic analyses (Avise 1998). Ultimately, there is need to understand the determinants of whether and how introduced species survive and spread in their new habitats, and whether a successfully invasive introduced species comes to dominate its new habitat via competition, predation, or biological disturbance. Of particular concern are the ecological impacts of genetically modified mariculture species, such as the effects of cultured salmon on wild stocks (Naylor et al. 2000).

- *Document how the increasing scale of human-induced eutrophication alters ecosystems.* Given that the oceans are downstream from land, there are numerous pollutants in the seas. These include excess nutrients via runoff of sewage and fertilizers (as well as atmospheric deposition of nitrogenous compounds), petroleum spills, halogenated hydrocarbons (pesticides, PCBs, dioxins, etc.), heavy metals, plastics (including abandoned fishing nets), and radioactive waste (GESAMP 1990; Kennish 1998; Sindermann 1996). GESAMP estimates that the sources of marine pollutants are runoff and land-based discharge (44 percent), atmospheric deposition (33 percent), maritime transportation (12 percent), ocean dumping (10 percent), and offshore oil production (1 percent). Most coastal pollutants are deposited directly from the land (runoff), whereas most open-ocean pollutants are deposited from the atmosphere.

While all these pollutants pose substantial threats, we believe that human-induced eutrophication of the seas is the most pressing problem and the highest research priority regarding marine pollution. Human activities now add at least as much fixed nitrogen to terrestrial ecosystems as do all natural sources combined (Schlesinger 1997; Vitousek et al. 1997), and the oceans receive this nitrogenous pollution from both coastal runoff and via atmospheric deposition. The resulting eutrophication induces macroalgal and microbial blooms, some of which are highly toxic (Hallegraeff 1993), produce expanding "dead zones" of decomposing primary producers (Turner and Rabalais 1994), and alter associated marine communities (Diaz and Rosenberg 1995; Burkholder 1998; Micheli 1999). Ample data show how individual sites respond to organic enrichment, but we are less able to predict the consequences of the increasing scale of eutrophication in terms of specific threats to marine species and general effects on ecosystem services.

Taking Action to Conserve Marine Biodiversity

We emphasize that, although we know relatively little about the nature of and threats to marine biodiversity, enough is known to justify immediate conservation action (Ludwig et al. 1993; Costanza et al. 1998). By the time we understand enough about the oceans to implement conservation policies that are strongly empirically based, it may well be too late (see also Johannes 1998). Scientific uncertainty (Ludwig et al. 1993) and the precautionary principle (Earll 1992) dictate that we take substantial conservation action now, preferably in the experimental context of true adaptive management (Walters and Hilborn 1978; Holling 1978). We see the implementation of marine protected areas as the most immediate and effective conservation action, and the development of marine restoration ecology as an important general priority:

- *Implement and evaluate networks of marine protected areas.* Given that less than 0.25 percent of the oceans are now offered some level of protection (McAllister 1996), the immediate implementation of a substantial network of no-take marine reserves is crucial (Murray et al. 1999). Protecting regions of the sea from all direct human impacts prevents physical alteration of habitat, overexploitation, and point-source pollution (but not global climate change or widespread pollution, and perhaps not species introductions). Such ecosystem-based management applies the precautionary principle by conserving entire systems that we do not fully understand (Earll 1992; Ludwig et al. 1993; Griffis and Kimball 1996; Agardy 1997; Murray et al. 1999; Palumbi 2001).

  The first step in implementing reserves is using available data to map regional patterns of habitat and biodiversity, then selecting initial sites for protection (Leslie et al. in press). Identification of both representative and crucial ecosystems for protection (both relatively pristine and degraded) requires detailed GIS assessments (see above). Once provisional networks of no-take marine reserves are in place, we can begin to learn how they function ecologically and, politics permitting, implement adaptive management in terms of evaluating and optimizing the number, size, and spacing of reserves. At present, the rule-of-thumb recommendation is that at least 20 percent of the oceans be protected such that all ecosystems are represented proportionally within no-take reserves (Murray et al. 1999). Currently, the only scientific basis for this percentage is that fishery biologists believe that at least 20 percent of a spawning stock must be conserved to ensure population viability (Bohnsack et al. manuscript). Of course, the siting of reserves is also crucial. For example, conservation of Pacific salmon and other species that migrate between fresh and saltwater will require integrated land-and-sea reserves (see Lichatowich et al. 2000).

  Evaluating and optimizing the effectiveness of existing marine reserve networks will require substantial research in several areas *after* reserves are already implemented in an experimental framework. First, knowledge of the level of connectivity of open populations via larval dispersal is essential for understanding whether populations within reserves replenish those outside (the "seeding effect"). Second, knowledge of the movement patterns of animals into and out of reserves is required to understand whether individuals that settle and grow within reserves eventually move to adjacent unprotected areas, thereby augmenting fisheries (the "spillover effect"). Documenting this phenomenon requires knowledge of home ranges, erratic movements, dispersal,

BOX 7.1. General Research Priorities and Specific Action Items in Marine Conservation Biology

Understanding the Nature of Marine Biodiversity

*1. Map the distribution of and threats to biodiversity (ecosystems, species, genes).
   - Use geographic information systems to assemble existing data.
   - Determine whether habitat-generating and visually dominant species can provide accurate indices of total biodiversity.
   - Identify regions of high species richness, crucial habitats, special environments, and sensitive ecosystems.
2. Document temporal changes in biodiversity (ecosystems, species) over historical and geological time scales.
   - Examine historical records to document recent changes in ecosystems and biodiversity.
   - Examine paleontological data to estimate background rates of extinction.
3. Explore the ecological mechanisms driving population dynamics, structuring communities, and affecting biodiversity in several key ecosystems.
   - Focus on understanding the ecology of small open-ocean fishes and krill, coastal bottom-oriented fishes, and coral reefs.
   - Determine population boundaries and connectivity, as well as natural mechanisms of population regulation.
   - Determine community-level mechanisms that naturally maintain biodiversity.

Understanding the Threats to Marine Biodiversity

*1. Document how physical alteration and fragmentation of habitats affect seafloor ecosystems.
   - Determine relationship between habitat loss and species loss.
   - Determine effects of habitat fragmentation on population viability.

*2. Document how overfishing alters marine food webs.
   - Document cascading effects of declining large vertebrates (predatory fishes, sea turtles, seabirds, and marine mammals) on ecosystem function and stability.
   - Explore effects of biomass dominance shifts on ecosystem function and stability.
   - Document effects of discarded bycatch on ecosystem function and stability.
*3. Document how species introductions affect native species and alter community structure.
   - Determine mechanisms by which introduced exotic species become established and displace native species.
   - Document impacts of exotic disease organisms introduced by human activities.
   - Document effects of genetically modified mariculture species on native species.
*4. Document how the increasing scale of human-induced eutrophication alters ecosystems.
   - Determine effects of algal blooms and resulting dead zones on biodiversity and ecosystems.

Taking Action to Conserve Marine Biodiversity

*1. Implement and evaluate networks of marine protected areas.
   - Implement adaptive management to evaluate and optimize siting, number, size, and spacing of reserves.
   - Document ecological changes inside vs. outside reserves and test whether and how populations inside reserves replenish those outside.
2. Develop the science of marine restoration ecology.
   - Develop methods to enhance recovery of degraded ecosystems.

Note: Asterisks denote the six highest priorities for the decade.

and migrations of mobile juveniles and adults, and thus innovations in tagging and telemetry. Third, simultaneous socioeconomic studies are necessary to document feedback between exploited marine populations and human society. Again, such knowledge should be used in the framework of adaptive management after immediate implementation of provisional reserves based on existing data.

- *Develop the science of marine restoration ecology.* Given the high level of degradation already suffered by many coastal ecosystems—especially estuarine salt marshes and mangroves, coral reefs, and seagrass beds—research on how to augment recovery of these systems will be useful if and when environmental assaults are ameliorated. The science of marine restoration ecology is in its infancy (Thayer 1992; NRC 1994) and focuses mostly on estuarine systems (Kennish 2000; Zedler 2000). Besides controlling deleterious inputs, case studies to date on enhancing recovery include cleanup following oil spills (Doerffer 1992; see also Paine et al. 1996; Peterson 2000), rehabilitation of mangroves (Day et al. 1999), and transplants of corals and seagrass (Rinkevich 1995; Bortone 2000). General issues and research priorities in restoration ecology are reviewed in chapter 11.

Conclusions

Because funding constraints often force prioritization of priorities, box 7.1 indicates what we believe to be the six most important research thrusts needed to conserve marine biodiversity. Importantly, so little is known about all aspects of marine biodiversity and its demise that precautionary action is needed immediately, even before new research initiatives (Ludwig et al. 1993; Costanza et al. 1998). The most prudent precautionary measure is to set aside areas of the oceans for protection from all direct human activities. Establishing substantial networks of no-take marine reserves in an adaptive management framework will allow us to separate the effects of direct and local human impacts (physical alteration of habitat, overexploitation, local species introductions, and point-source pollutants) from indirect and ubiquitous effects (wide-ranging species introductions, global climate change, widespread pollutants), as well as to examine experimentally the most effective size, shape, spacing, and location of reserves (Murray et al. 1999). Additional precautionary action would be to reverse the burden of proof (Dayton 1998), whereby the instigators of potentially deleterious activities would have to demonstrate that their proposed actions are not a threat (rather than the present situation in which environmental regulators have to document that a deleterious effect has occurred). Success of these measures will require environmental scientists to educate the public and policy makers concerning the importance of action despite scientific uncertainty. Fundamental change is needed regarding the role of the scientist-citizen in society so that scientific advocacy is no longer considered an oxymoron (Hixon 2000). Once precautionary policies are implemented, major research efforts are required to effect adaptive management and enlightened conservation efforts that balance the necessity of conserving life in the sea with society's need to exploit marine resources. The risks of continued research without immediate conservation action are too great to ignore.

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