Marine Reserves as a Tool for Ecosystem-Based Management: The Potential Importance of Megafauna

SASCHA K. HOOKER AND LEAH R. GERBER

Marine predators attract significant attention in ocean conservation planning and are therefore often used politically to promote reserve designation. We discuss whether their ecology and life history can help provide a rigorous ecological foundation for marine reserve design. In general, we find that reserves can benefit marine megafauna, and that megafauna can help establish target areas and boundaries for ecosystem reserves. However, the spatial nature of the interplay between potential threats and predator life histories requires careful consideration for the establishment of effective reserves. Modeling tools such as demographic sensitivity analysis will aid in establishing protection for different life stages and distributional ranges. The need for pelagic marine reserves is becoming increasingly apparent, and it is in this venue that marine predators may be most effectively used as indicator species of underlying prey distribution and ecosystem processes.

Keywords: marine predators, conservation, marine reserves, indicator species, modeling

> The seas are by no means dead, but they are unquestionably less alive than they were when humanity discovered them.
>
> —Leatherwood and Reeves (1983)

The state of the global oceans is rapidly deteriorating, with dire consequences for marine species (Jackson et al. 2001). Historically, most conservation efforts have focused on terrestrial systems, but it is becoming increasingly apparent that conservation efforts are urgently required for the oceans as well (Myers et al. 1997, Casey and Myers 1998). Recently, significant attention has been given to the establishment of marine reserves (Boersma and Parrish 1999, Mangel 2000), with most of the focus of research directed at economically valuable (i.e., mid–trophic level) species (Rowley 1994). Some of the lessons learned from these reserves have now been widely accepted (e.g., bigger is better, and dispersal matters; NCEAS 2001). However, one of the most interesting questions to emerge from the initial exploration of marine reserve design theory is the significance of life-history characteristics. Here we review issues concerning the ecology of higher predators and their relevance for the design and selection of marine reserves.

The grouping of higher marine predators describes ocean megafauna, including a variety of taxa: cetaceans, pinnipeds, sea otters, polar bears, seabirds, sharks, cephalopods, and predatory fish. Our primary expertise is in marine mammal ecology, and so most of our review focuses on the ecology and conservation of this group. Nevertheless, many aspects of these species' ecology, life history, and demography apply to other marine predators as well, allowing us to propose certain generalities that apply to all marine predators. There is currently a trend toward the advocation and establishment of marine sanctuaries based on their marine megafauna, and particularly their mammal or bird fauna (table 1). However, systematic theory on how to select, design, and monitor these reserves is lacking, and their efficacy in protecting marine predators is not clear. We discuss two issues here: (1) the potential for marine reserves to protect marine predators, and (2) the question of whether these species can serve as ecological indicators, demonstrating where and how to target and design marine reserves. This article is loosely based on

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Table 1. Examples of marine conservation areas established on the basis of their marine mammal and marine bird fauna.

Country/region	Type of reserve	Year	Geographic area	Faunal basis for establishment
International	Whale sanctuary, International Whaling Commission	1994	Southern Ocean	Baleen whales and sperm whale (for recovery from historical human exploitation)
Europe	European candidate special area of conservation	1996	Moray Firth, United Kingdom	Bottlenose dolphin
Europe (France, Monaco, and Italy)	International sanctuary for Mediterranean cetaceans	1999	Ligurian Sea, Mediterranean	Fin, sperm, Cuvier's beaked, and long-finned pilot whales; Risso's, striped, bottlenose, and short-beaked common dolphins
Germany	National park	1999	Wadden Sea, Germany	Harbor porpoise
Australia	Marine national park	1996	Great Australian Bight, southern Australia	Southern right whale, Australian sea lion (breeding colonies)
Australia	Conservation park	1954	Seal Bay, Kangaroo Island, South Australia	Australian sea lion, New Zealand fur seal
Australia	Marine park	1999	Macquarie Island, Subantarctic	Subantarctic fur seals, Antarctic tern, fairy prion, grey and blue petrels, and black-browed and wandering albatrosses (foraging grounds)
New Zealand	Marine mammal sanctuary	1988	Banks Peninsula, South Island	Hector's dolphin
Mexico	Biosphere reserve	1993	Upper Gulf of California	Vaquita
Argentina	Whale sanctuary (marine provincial park)	1974	Golfo San Jose, Peninsula Valdes	Southern right whale
Brazil	Ecological reserve	1983	Lobos Island	South American sea lion and fur seal
Dominican Republic	National humpback whale sanctuary	1986	Silver Bank	Humpback whale
Canada	Marine national park	1990	Saguenay–St. Lawrence, Quebec	Beluga whale
Canada	Pilot marine protected area	1999	The Gully, eastern Canada	Northern bottlenose whale
United States	Special reservation (US Department of the Treasury)	1869	Pribiloff Islands (St. Paul and St. George)	Northern fur seal (regulating commercial hunt)
United States	Fish cultural and forest reserve (Forest Reserves Act)	1892	Afognak Island, Alaska	Seals, walrus, and sea otters
United States	Año Nuevo State Park	1971	Año Nuevo, California	Northern elephant seals
United States	National marine sanctuaries	1980	Channel Islands, California	Several marine mammal and bird species
United States	National marine sanctuary	1992	Hawaiian Islands	Humpback whale

Source: Reeves 2000.

discussion generated by a symposium that we hosted at the annual meeting of the Society for Conservation Biology in 2001, which focused on case studies and modeling approaches in the design of marine reserves for marine megafauna.

Marine reserves

To date, conservation work has generally employed a triage approach: Species receive protection only after it has been demonstrated that there is a pressing need for such protection. Many of the conservation efforts around the world, therefore, focus on threatened or rare species (Soulé and Orians 2001). This focus has driven much of the legislation on conservation, which often lists species as a mechanism to initiate efforts to protect them (see, e.g., the Endangered Species Act and the Marine Mammal Protection Act in the United States). However, there has been an increasing emphasis on the need to use ecosystems, communities, and assemblages, rather than single species, as the basis for conservation. Reserves have the potential to take this type of holistic approach (rather than traditional single-species recovery models), providing protection both to the species of concern and to the entire ecosystem.

However, applying models developed for terrestrial systems to the marine environment is not straightforward. Terrestrial and marine systems are quite different ecologically in terms of spatial structure, scale, and trophic structure (Soulé and Orians 2001). The difficulty of placing boundaries around ecosystems is exacerbated in the marine environment, where borders are dynamic and fluid. The pelagic marine environment is vast in scale, and marine reserve areas consequently often need to be larger than their terrestrial equivalents. There are also differences between basic ecological structures in marine and terrestrial environments, most notably dynamism and connectedness (Link 2002). The spatial discreteness of terrestrial ecosystems, which allows straightforward identification of habitats to protect, is not evident in the majority of oceanic ecosystems, which may be transient in space and time.

Most conservation initiatives are driven by economic opportunities and constraints. In terrestrial settings, the hunting and, more recently, tourism industries have often spurred conservation initiatives; in the marine environment, the majority of economic pressure has come from failing fisheries. Thus, most work on marine conservation issues, and recently most evaluation of marine reserves, has been concerned with fishery recovery (NRC 2001). A recent review of models pertaining to marine reserves (Gerber et al. 2003) showed that none explicitly addressed reserves for top predators, few included explicit movement, and there was little focus on extinction risk or multispecies interactions.

In spite of the lack of a solid theoretical foundation, large ocean megafauna—marine mammals and birds—are often used to direct conservation efforts (table 1, figure 1). Yet these initiatives often have little ecological basis and are driven by public affection toward charismatic species. That said, marine mammals are relatively vulnerable to extinction. Of the approximately 120 currently recognized marine mammal species, 4 species or significant populations have gone extinct, 11 are thought to be in imminent peril of extinction, 17 are thought to be of significant concern with respect to extinction, and 8 were once thought to be at risk of extinction but are now recovering (table 2; VanBlaricom et al. 2000).

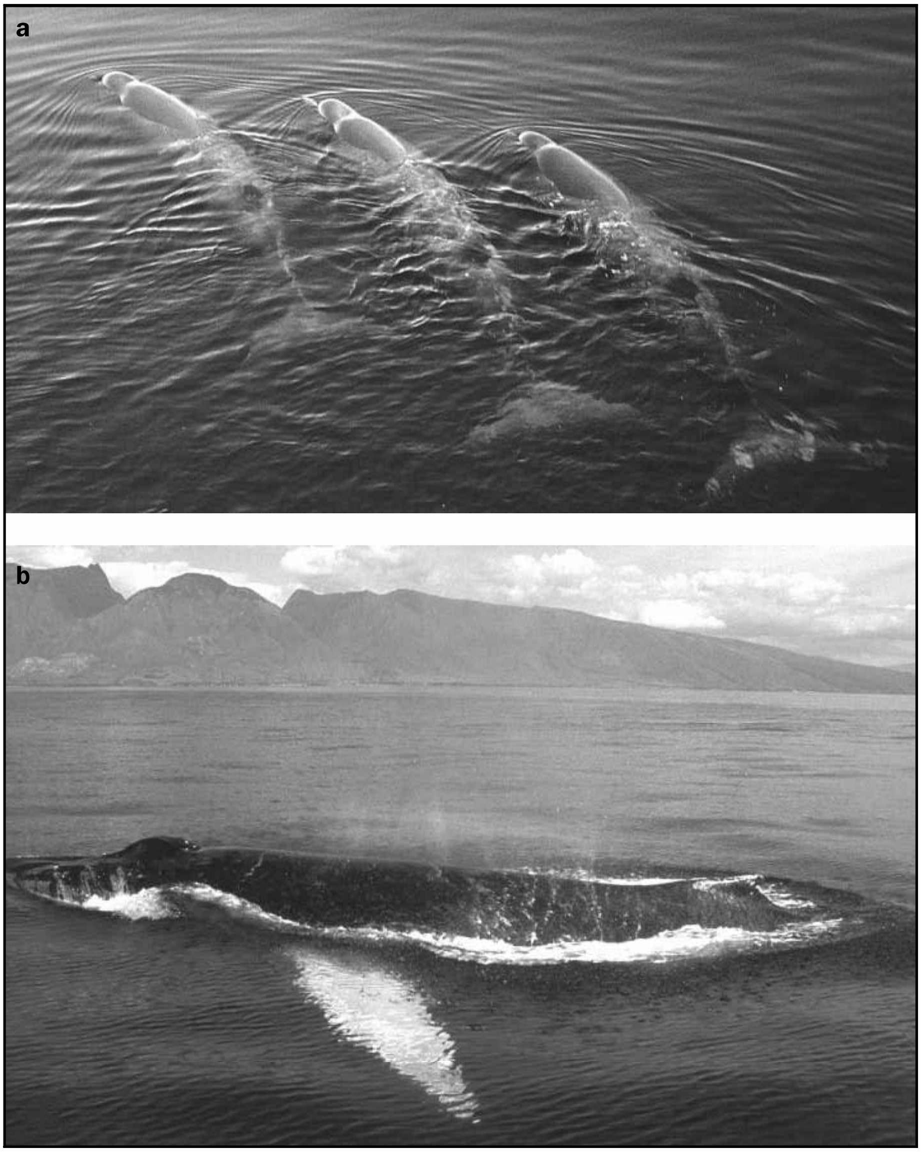

Figure 1. (a) Bottlenose whales in the Gully, eastern Canada. The Gully has been designated a pilot marine protected area, largely because of the northern bottlenose whales found there. These whales often spend periods of time resting at the surface between foraging dives. Threats to these and other cetaceans in this region include ship strikes, noise pollution from exploitation and exploration, and interactions with longline fisheries. Photograph: Hal Whitehead laboratory. (b) Humpback whales in Hawaii. The Hawaiian Islands Humpback Whale National Marine Sanctuary was established to protect breeding humpback whales. In general, threats are low in this area, although a growing whale-watching industry and acoustic testing nearby may be causes for concern. Photograph: Robin W. Baird.

Definitions and goals

We define a marine protected area as a geographic area designated for protection. This may include a broad area with limited management restrictions (e.g., prohibiting some activities such as seismic exploration) but may also encompass smaller "marine reserve areas"—zones designated as closed to extraction (NRC 2001). In this article, we focus on the degree to which the spatial nature of marine protected areas can promote recovery and enhance protection from the threats that marine predators face. The question of whether marine reserves will provide protection and will prohibit the activities that threaten these predators or their ecosystems is a key issue. A major criticism of marine reserves generally, and particularly several of those established for marine mammals, is that they represent "paper parks" that provide a false sense of conservation achievement (Duffus and Dearden 1995). This criticism stems from the lack of regulation and policing or wardening for such reserves or sanctuaries (Hooker et al. 1999).

The goals of establishing a marine protected area are several: conservation of biodiversity (minimizing extinction risk), ecosystem protection, reestablishment of ecosystem integrity, and enhancement of the size and productivity of harvested fish or invertebrate populations to help support fisheries outside the reserve. The ranking of these goals will depend on the societal and economic pressures for a given region. Here, for the most part, we focus on the impact of reserves on higher predators, although we also consider multispecies and multipurpose reserves in terms of whether fishery enhancement is possible in conjunction with conservation of higher predators.

Table 2. Marine mammal species, subspecies, and populations that are extinct, at risk of extinction, or recovering from near-extinct status.

Status	Species (population)	Latin name
Extinct (4)	Steller's sea cow	*Hydrodamalis gigas*
	Caribbean monk seal	*Monachus tropicalis*
	Japanese sea lion	*Zalophus japonicus*
	Gray whale (North Atlantic)	*Eschrichtius robustus*
In imminent peril of extinction (11)	Baiji	*Lipotes vexillifer*
	Vaquita	*Phocoena sinus*
	Indian river dolphin (Indus river)	*Platanista gangetica*
	Mediterranean monk seal	*Monachus monachus*
	Gray whale (western North Pacific)	*Eschrichtius robustus*
	Right whale (eastern North Pacific)	*Balaena glacialis*
	Right whale (North Atlantic)	*Balaena glacialis*
	Bowhead whale (Davis Strait, Hudson Bay, Spitsbergen, Barents Sea, and Sea of Okhotsk)	*Balaena mysticetus*
	Beluga whale (Gulf of Alaska)	*Delphinapterus leucas*
	Beluga whale (Gulf of St. Lawrence)	*Delphinapterus leucas*
	Ringed seal (Lake Saimaa)	*Pusa hispida saimensis*
Of significant concern (17)	Blue whale	*Balaenoptera musculus*
	Hawaiian monk seal	*Monachus schauinslandi*
	Ringed seal (Baltic Sea)	*Pusa hispida botnica*
	Ringed seal (Lake Ladoga)	*Pusa hispida ladogensis*
	Harbor seal (western North Pacific)	*Phoca vitulina stejnegeri*
	Steller's sea lion (western North Pacific)	*Eumetopias jubatus*
	Australian sea lion	*Neophoca cinerea*
	Hooker's sea lion	*Phocarctos hookeri*
	Guadalupe fur seal	*Arctocephalus townsendi*
	Juan Fernandez fur seal	*Arctocephalus philippii*
	Walrus (Atlantic)	*Odobenus rosmarus rosmarus*
	Walrus (Laptev Sea)	*Odobenus rosmarus laptevi*
	Amazonian manatee	*Trichechus inunguis*
	West African manatee	*Trichechus senegalensis*
	West Indian manatee	*Trichechus manatus*
	Sea otter (California)	*Enhydra lutris nereis*
	Marine otter	*Lutra felina*
Once thought to be faced with extinction but now recovering (8)	Bowhead whale (western Arctic)	*Balaena mysticetus*
	Humpback whale	*Megaptera novaeangliae*
	Gray whale (eastern North Pacific)	*Eschrichtius robustus*
	Northern elephant seal	*Mirounga angustirostris*
	Galapagos fur seal	*Arctocephalus galapagoensis*
	Subantarctic fur seal	*Arctocephalus tropicalis*
	Antarctic fur seal	*Arctocephalus gazella*
	Sea otter (North Pacific and Russian coastal waters)	*Enhydra lutris kenyoni*

Source: VanBlaricom et al. 2000.

Marine predators and marine reserves

Threats to marine predators may take several forms (box 1, figure 2; Richardson et al. 1995, Simmonds and Hutchinson 1996, Coe and Rogers 1997). Physical threats may include strikes from ships or entanglement by fisheries, often leading to the death of individual animals. Acoustic or environmental impacts may be more insidious. Seismic exploration, military exercises, shipping, or drilling may have far-reaching acoustic impacts that cause species to leave an area, to become temporarily unable to forage, or even to sustain physical damage. Similarly, pollution, dumping, and oil spills may increase the risk of extinction by increasing mortality. Ingestion of plastic debris, oil contamination, and pollutants may have an incremental effect on animals throughout their lives, ultimately resulting in immunosuppression or reproductive failure. Potentially irreparable ecosystem changes caused by competition for resources may radically alter ecosystem structure, resulting in dramatic shifts in population demographics (e.g., the Southern Ocean; May 1979), and habitat disturbance or destruction can result in spatial shifts to distribution or migration routes due to loss of cultural memory. Many of these threats may be mitigated by spatial protection.

In protecting a specific population, the optimal protected area would encompass that population's year-round distribution (Reeves 2000). However, for many marine predators, the year-round distribution of a population may span entire ocean basins. The question therefore becomes whether limited spatial protection in specific parts of a species' range is worthwhile. In some cases, when only a portion of a wide-ranging predator population may use a protected area, there may be the potential for recolonization of overexploited

Box 1. Threats to higher predators and to the ecosystem

Direct threats

Direct threats are those that cause mortality of top predators.

Fishery bycatch. Several seabird and cetacean species are killed in fisheries around the world. The establishment of reserves can mitigate these population-level impacts and reduce exposure at an individual level.

Direct killing. In some places, seabird, cetacean, and pinniped species are still the focus of directed hunts.

Ship strikes. In certain areas there are increased risks of ship strikes. For instance, in the Bay of Fundy, in the northeastern United States, ship traffic en route to Boston presents a large threat to northern right whales.

Indirect threats

Rather than causing immediate death, these insidious threats may cause accumulating harm over longer time scales.

Overexploitation of lower trophic levels. By removing lower trophic levels from the food chain, nutritional stress may be imposed on upper trophic predators, causing switching of prey, offspring desertion, and, in extreme cases, starvation.

Habitat degradation. This may take a variety of forms:

- *Acoustic pollution.* This can cause potential immediate damage to soft tissues in the case of high-intensity sounds, or behavioral avoidance of an area in the case of lower-intensity sounds.
- *Chemical pollution.* This can affect all levels of the food chain but becomes bioaccumulated at increasing trophic levels. Among higher predators, it can cause immunosuppression and potential reproductive failure.
- *Marine debris.* Animals may become entangled in discarded rope and nets, or materials such as plastic bags may be ingested.
- *Physical habitat destruction.* Some trawling methods cause long-lasting damage to the sea floor, which may take decades to recover to its previous physical structure. Similarly, because pinnipeds and seabirds rely on terrestrial sites for breeding, they may also be susceptible to habitat degradation and disturbance (e.g., invasive vegetation, introduced predators, light pollution).

Global effects

Global effects, such as climate change, will have consequences for higher predators and their marine ecosystems. These threats require mitigation at a global level.

subpopulations because of migration from this viable subpopulation (i.e., source–sink dynamics). However, even when this is not the case, the establishment of areas in which these threats are reduced or removed can only be beneficial, since several of the threats faced by marine mammals are site specific and others have cumulative effects (box 1). Even if a predator used the protected area for only a portion of its life span, this would reduce the frequency with which each individual was exposed to certain impacts and diminish the overall cumulative impact of other threats.

Modeling approaches can be usefully applied to the question of when and how to protect different life stages and distributional ranges to promote population protection. The annual cycle of many higher predators consists of discrete foraging and breeding portions. Thus, both foraging and breeding habitat and the migratory route should be considered (figure 3). Demographic rates may differ with the annual cycle or with specific habitats, and consideration of these variations may help to prioritize potential reserve sites. Similarly, the vulnerability of the population may be habitat and stage specific. For example, evidence of depressed breeding success due to local food limitation or disturbance at breeding sites would suggest that enhancement of the breeding population (e.g., by enhancing reproductive success or breeding population size) would be of most value. Thus, when this is the case, reserves should be established around breeding areas to protect important food resources during the breeding season along with the breeding individuals themselves. Conversely, evidence of food limitation or population-level threats during foraging would suggest that protected areas need to be established at sea, away from breeding colonies. Likewise, if migrating individuals become spatially concentrated at particular ocean areas or near particular features, where they could be especially vulnerable to threats such as ship strikes or bycatch, then establishing reserves in these areas would be warranted.

The current criteria used to select reserves for marine mammals have primarily involved the identification of breeding areas and have only occasionally taken account of foraging or migration habitats (table 1). Among pinnipeds, seabirds, and turtles, breeding and pupping or nesting takes place at terrestrial sites, where breeding animals are frequently highly aggregated. Part of the impetus for selection of such sites is likely to have come from their ability to encompass high spatial aggregations of individuals in a relatively small protected area, rather than from a thorough consideration of spatial and demographic threats. Future research should couple quantitative approaches to predict reserve efficacy with field studies of habitat use (i.e., the importance of foraging, migration, and breeding habitats). On a global scale, an examination of the threats faced by these animals (box 1) suggests that it is likely to be during foraging that most individuals are at risk, and it is here that research attention needs to be directed.

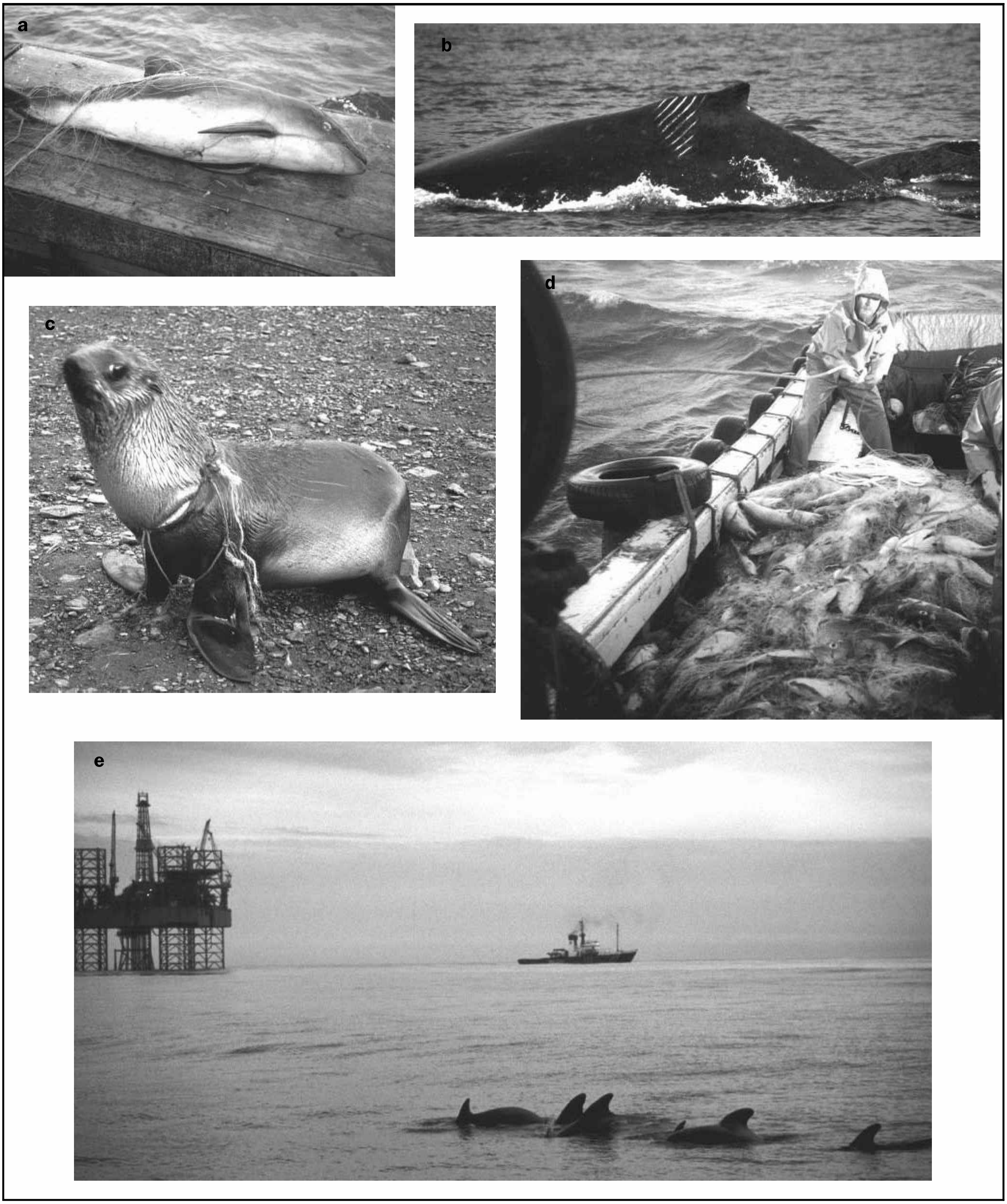

Figure 2. Threats to marine mammal species may be direct, including (a) fishery bycatch (harbor porpoise caught accidentally in a fishery; photograph: Nigel Godden, Sea Mammal Research Unit) or (b) ship strikes (propeller wound in right whale; photograph: Robin W. Baird), or indirect, including (c) debris (Antarctic fur seal entangled in discarded fishing gear; photograph: Sascha Hooker), (d) reduction in prey because of fisheries (photograph: Dave Sanderson, Sea Mammal Research Unit), or (e) oil and gas activity (pilot whales swimming beside rig, eastern Canada; photograph: Robin W. Baird).

Modeling approaches and the influence of life history

To date, marine reserves have been developed with little scientific basis to assess the effectiveness of various reserve designs and with few quantitative approaches to monitor these reserves. Models of marine reserves are relatively new in the literature; Gerber and colleagues (2003) reviewed 34 articles concerning marine reserve modeling, of which 32 were published after 1990. Based on these existing models of marine reserves, they reported that reserves will provide fewer benefits for species with greater adult rates of movement. However, few models have been developed explicitly for wide-ranging species. Those studies that have included migration and movement in reserve models show continued benefits even to highly mobile species (Apostolaki et al. 2002, Roberts and Sargant 2002); there is also empirical support for this (Gell and Roberts 2003).

While models of marine reserves are beginning to yield information on the necessary spatial configurations of reserves to allow populations with specific dispersal distances to persist, spatial configuration remains an aspect of reserve design in need of further analysis. Important directions for future modeling include the effects of particular forms of density dependence and multispecies interactions and the consideration of full life-stage models in reserve design. This additional modeling and analysis will improve prospects for a better understanding of the potential of marine reserves for conserving biodiversity.

The major difference between the modeling approaches we advocate for higher predators and those previously used for fisheries involves the explicit consideration of life-history strategies, with conservation goals operating over much larger spatial and temporal scales. The multispecies nature of most marine ecosystems also necessitates delicate structuring of conservation priorities between ecosystem levels. We propose that modeling tools such as demographic sensitivity analysis and multispecies models may be worth consideration to explore approaches for the conservation of higher marine predators.

One interesting facet of the debate on reserve design is that most reserves are quite small in area and represent only a small portion of the total range of species. At the same time, modeling work suggests that as movement rates increase, larger areas are needed for reserves to achieve benefits (Gell and Roberts 2003, Gerber et al. 2003). Whereas fish may disperse, and therefore an individual fish may move away from an area for the majority of its life, many higher predator species are relatively site faithful over time scales varying from annual (in the case of migratory species) to decadal (in the case of species following El Niño effects). Most of the models that have incorporated animal movement have taken little of this into account (Roberts and Sargant 2002). Few existing models have considered all life stages; thus, most have failed to acknowledge that wide-ranging marine species may have life-history stages that occur in very different habitats. Much of the theory developed for marine reserves has instead focused on issues of larval dispersal; very few studies have addressed the question, "For which types of species should reserves be most effective?" Demographic population models (e.g., Caswell 2001) are one promising approach to examining the potential efficacy of marine reserves that target particular life-history stages or their habitats.

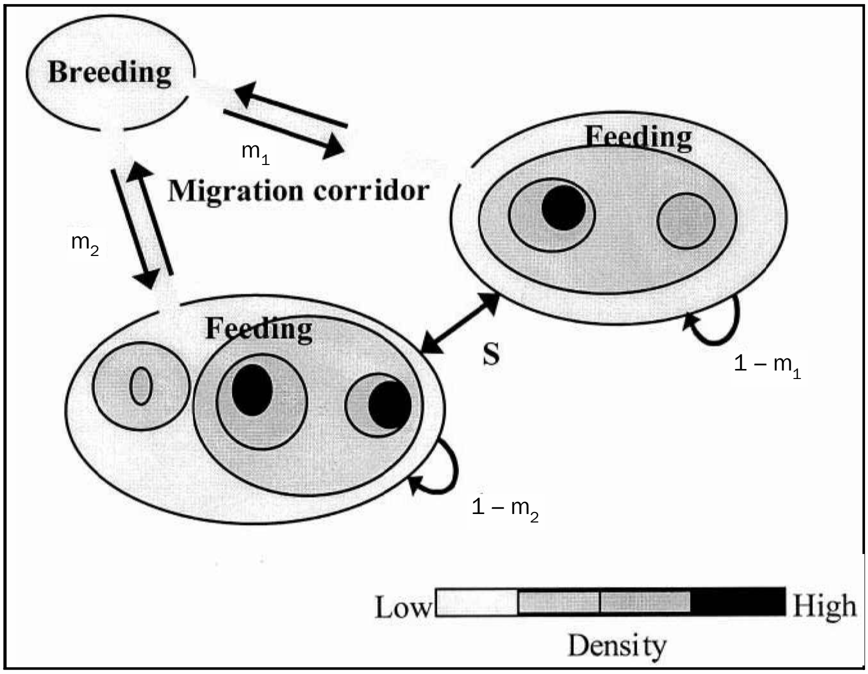

Figure 3. Life stages of some marine predators (e.g., baleen whales, pinnipeds, seabirds) are separated spatially into discrete feeding and breeding areas, with migration between them. Reserves can be placed in feeding, breeding, or migratory habitats. Abbreviations: m, migration rate (m_1 and m_2 indicate different rates for migration to each feeding area); S, mixing between feeding areas.

Demographic sensitivity analysis allows researchers to analyze how much a small change in a demographic rate (e.g., adult survival) would influence a population's potential for recovery. Further, such approaches rely on minimal data (e.g., survival and fecundity rates) and may allow researchers to predict the effects of various management actions. Alternative designs for marine protected areas should be treated as hypotheses and tested with models in advance (Heppell and Crowder 1998). Because life-history information is lacking for many marine populations, categorizing life histories according to their response to changes in stage-specific mortality may provide a useful framework for considering conservation options (Heppell et al. 2000a). For example, it is well established that fecundity will be more important than survival for shorter-lived species, such as many fish and invertebrates, whereas adult and juvenile survival elasticity will be important for long-lived species such as marine mammals, sea turtles, and seabirds (Heppell et al. 2000b, Saether and Bakke 2000).

These insights from life-history theory can be used to predict a priori when marine reserves are likely to be most effective, and perturbation analysis can serve as an early step in reserve planning. Perturbation analysis is useful to show that different life-history characteristics will exhibit variable responses to changes in mortality. For example, across a representative range of marine life histories (e.g., urchin, haddock, sea lion), the change in population growth rate (λ) resulting from a decrease in adult mortality will be greatest for marine invertebrates and fish, and lowest for species with very low adult mortality rates (e.g., salmon will show a more striking response than sea lions). Results from demographic analysis suggest that adult survival rate and maximum life span are critically important in determining reserve efficacy. Standardized demographic analysis *(sensu* Caswell 2001) may be a useful first step to compare disparate conservation goals for marine reserve design for species with distinct life histories.

Multispecies and habitat-based models

Predictions of the effect of a reserve on a particular species may also vary depending on species interactions. Thus, a major challenge in marine reserve design is the incorporation of multispecies interactions and management objectives. Decades of experimental studies have shown dramatic effects of consumer–resource interactions on populations and communities (Soulé and Orians 2001). The relationship between marine predator distribution and areas of primary productivity has been observed for several species (McConnell et al. 1992, Jaquet and Whitehead 1996). Bottom-up effects of resources on consumers and top-down effects of consumers on other species in the community often include a suite of direct and indirect pathways of interaction (Bowen 1997). Predator–prey, competitive, and mutualistic interactions can cause unanticipated changes in community structure and nontarget effects of management interventions. Adding species interactions to predator–prey models to explore the effects of different reserve designs can generate complex responses to protection, changing not only the magnitude but also the direction of the species response. Previous perturbations and reduction in certain components of a food web relative to other components mean that management actions to restore the system may result in an oscillation that causes unforeseen consequences and, in the worst case, a complete ecosystem shift (Estes et al. 1998). In addition, population size and ecosystem effects may be linked with disease outbreak. In general, maintaining high trophic connectivity and preventing competitive release that leads to abnormally elevated population levels will decrease the levels and impact of disease (Lafferty and Gerber 2002).

Multipurpose reserves

Can enhancement of fisheries (e.g., increase in the size and productivity of harvested fish and invertebrate populations to help support fisheries outside reserves) be viable alongside reserves that maintain higher predator numbers? In California, marine reserves have been established to protect depleted and reintroduced sea otters. However, there is also an interest in the promotion of abalone populations, which have expanded in the absence of sea otters. Sea otters in Alaska have been shown to exert a profound effect on the structure of their marine community, encouraging kelp growth through predation on slow-moving herbivorous invertebrates (Estes and Palmisano 1974). Such cascading ecosystems are governed by the strength of the trophic link between otters and invertebrates relative to other factors, such as recruitment variability or natural disturbance, that affect biodiversity in kelp forests. With strong linkage, the presence of sea otters can provide a control on the herbivore population, enhancing the overall biodiversity of kelp forest ecosystems, increasing the amount of productivity and pathways through the food web, and promoting structural complexity in the ecosystem (Estes et al. 1998). In such cases, it would appear that sea otter presence within marine reserves is desirable.

However, recent empirical work has shown that the strength of sea otter predation on abalone was greater than the pressure of the fishery on abalone, so that there were fewer abalone in reserve areas containing sea otters than in fished areas with no sea otters present (Fanshawe et al. 2003). Thus, reserves that maintain ecosystem integrity and natural (unperturbed) levels of predation do not appear to be consistent with additional abalone harvesting. While this example suggests that there may be situations in which marine reserves cannot simultaneously protect multiple trophic levels, one approach to addressing this particular issue is to spatially separate areas into two single-use marine protected areas: one focusing on restoring ecosystem integrity and the other focusing on protecting the harvested stocks to enhance productivity (Fanshawe et al. 2003).

This conflict, like many conflicts between fisheries and conservation of higher predators, has arisen largely because of historical changes in the ecosystem (Jackson et al. 2001). Removal of sea otters caused increases in the population sizes of lower levels of the food web. Fanshawe and colleagues (2003) suggest that an incomplete ecosystem may provide greater value to human consumers than the restored system. However, in general, it is thought that increased food web complexity leads to greater ecosystem resilience, and a restored ecosystem would be preferred on this basis (Soulé and Orians 2001). The value of the fishery economically and sociologically must therefore be weighed against the risks associated with maintenance of the perturbed ecosystem.

Marine predators as indicator species

In terrestrial ecosystems, predator distribution can be used to establish criteria for reserve design (Soulé and Simberloff

1986), but the application of this concept to oceanic systems is relatively untested. Larger predators have been used as indicator (or focal) species, whose protection aids in protecting the more complex environments that they use (Simberloff 1998, Zacharias and Roff 2001). There are several variants on the meaning of *focal species,* and marine predators have been used to address most of these concepts (table 3). In general, although these concepts may be useful to drive conservation efforts, the majority are focused on achieving political support through publicity or are extensions of single-species conservation efforts (Simberloff 1998, Andelman and Fagan 2000). Of all these, the indicator-species approach appears to have the most potential to direct marine reserve selection (Zacharias and Roff 2001).

Another related approach is to identify biodiversity hotspots that are worthy of protection. These may be areas that are particularly rich in species, in rare species, in threatened species, or in some combination of these attributes (Reid 1998, Myers et al. 2000). In the marine environment, Roberts and colleagues (2002) found that centers of endemism among coral reef systems are major biodiversity hotspots. However, there is still much disagreement in the academic community over what constitutes biodiversity. Is species richness the answer, or are these simply locations in which several species overlap, possibly at the edges of their ranges (Price 2002)? We would suggest that, at least in the pelagic realm, a more appropriate definition of oceanic hotspots may be areas of increased productivity, in terms of the abundance of organisms within the area relative to other oceanic areas. The Gully, a submarine canyon offshore of eastern Canada, appears to be a hotspot for cetaceans, which show elevated abundances in the vicinity of this feature compared with the levels in surrounding regions (Hooker et al. 1999). Similarly, the Patagonian shelf has been demonstrated to be a rich feeding ground for several predator species in the south Atlantic (Croxall and Wood 2002).

There is some evidence that the distribution and relative abundance of marine predators can be used as an indication of underlying prey distributions and ecosystem processes (Preen 1988, Tershy et al. 1991, Croll et al. 1998). In the Gully, although the underlying process driving this ecosystem is not well understood, top predators could be used to help derive boundaries for protection (Hooker et al. 1999, 2002). Although this area is relatively far offshore, the distribution of cetaceans is primarily governed by bathymetric features and so could be well defined by spatial boundaries. Such associations have not been found for other areas, and offshore environments are generally more dynamic, making it difficult to establish distinct spatial boundaries. However, establishing such boundaries may be a matter of directing research attention to oceanographic features that may show stability in space and time. Thus far, conservation in the pelagic realm has received little attention, although there have been suggestions that a system of open ocean reserves is needed (Mills and Carlton 1998).

The identification of foraging hotspots for predators (see figure 3) and the consideration of boundaries determined by oceanographic processes show potential as useful approaches in the pelagic arena. Hyrenbach and colleagues (2000) identified three types of oceanic hotspots: (1) static systems, which are determined by topographic features; (2) persistent hydrographic features, such as currents and frontal systems; and (3) ephemeral habitats, shaped by wind- or current-driven upwelling, eddies, and filaments. Of these, ephemeral habitats are by far the most difficult to map or protect. All three types of hotspots may be identified by analyzing the foraging distribution of higher predators (table 4). Thus, the overlaying maps of different marine predators' foraging habits, together with basic knowledge of their diet (e.g., piscivory or teuthophagy), broader ecosystems (e.g., upwelling dynamics), and habitat variability (e.g., persistence and spatial variation over annual and decadal cycles), should allow researchers to identify various hotspot features.

Networks of marine reserves

The choice of new areas to protect will necessarily be influenced by the types of areas that are already being protected. A good deal of research effort has been expended in assess-

Table 3. Focal species concepts, with examples from marine mammal fauna.

Type	Description	Example
Flagship	Charismatic species that serve as guarantors of broad-scale conservation, used politically to attract funding and support	Right whales or humpback whales (national marine sanctuaries, United States)
Keystone	Species that have a disproportionate effect relative to their abundance, underpinning the ecosystem	Sea otters
Umbrella	Wide-ranging species, the protection of whose habitat will encompass several other species within their ecosystem	Manatees, river dolphins
Composition indicators	Species whose presence or abundance is used to characterize a particular habitat or biological community	Northern bottlenose whales (pilot marine protected area, the Gully, Canada)
Condition indicators	Species that reflect ecosystem health or the levels of pollutants within the system	Arctic cetaceans

Source: Simberloff 1998, Zacharias and Roff 2001.

Table 4. Types of oceanic hotspots and examples of top predator distribution associated with them.

Type of hotspot	Location	Higher predator
Static systems	The Gully, Nova Scotia	Northern bottlenose distribution is driven by the bathymetry of the submarine canyon (Hooker et al. 1999).
	Hawaiian Islands National Marine Sanctuary	Humpback whale distribution in the breeding season is primarily defined by the shallow water region around the Hawaiian Islands.
Persistent hydrographic features	Bird Island, South Georgia	Antarctic fur seal and macaroni penguin distribution is found to the northwest of South Georgia, where there appears to be a persistent frontal system (Barlow et al. 2002).
Ephemeral habitats	Warm core ring, North Atlantic	Sperm whales are found primarily along the periphery of warm-core rings (Griffin 1999).

Note: Hotspot type is derived from Hyrenbach and colleagues (2000).

ing optimality in networks of protected areas. Explicit, quantitative methods of identifying priority areas for biodiversity are replacing the ad hoc procedures often used in the past to design networks of reserves. The concept of complementarity ensures that areas chosen for inclusion in a reserve network complement those already selected, reducing duplication of species in reserves and providing the most efficient network of protected areas. The network of reserves is identified based on uncorrelated habitat types or assemblages to provide a network of protected areas encompassing a high proportion of biodiversity. This concept is gaining support in terrestrial reserve network assessment (Howard et al. 1998, Reyers et al. 2000), but it could be applied equally well to marine systems. Furthermore, although in the past this method has relied on high-quality information on the spatial distribution of all species of concern, it appears that reserve selection based on data obtained with low sampling effort can be highly effective in the representation of species (Gaston and Rodrigues 2003). This is likely to have important consequences in the identification of marine mammal habitats, which are generally poorly known, but for which peaks of abundance are better documented.

Socioeconomic concerns also strongly influence the decisionmaking process for the establishment of networks of reserves. In the southern Gulf of California, multiple levels of information on biodiversity, ecological processes, and socioeconomic factors were used to establish a network of reserves that would cover a large proportion of habitat and reduce social conflict (Sala et al. 2002). A major benefit of the optimization technique used in creating this network is the ability to generate portfolios of solutions that can be presented to decisionmakers, who can evaluate the costs and benefits of different management options within relevant socioeconomic constraints.

Management case studies

Two political vehicles for protected area management are illustrated in boxes 2 and 3. In the European Union, a recent directive (Council Directive 92/43/EEC) has led to the need to establish special areas of conservation for species and habitats (box 2). Five marine mammal species require protection under this scheme. The ease of designating these areas reflects many of the issues we have discussed here. The protection of two sites encompassing large colonies of breeding grey seals and the protection of small, localized bottlenose dolphin populations have been fairly straightforward. However, more broadly distributed species without large breeding aggregations are more difficult to assess. For instance, harbor porpoises do not appear to show site fidelity, and the relationship between their foraging areas and local oceanography is unknown. Setting up a marine reserve for harbor porpoises would therefore require the zoning of large offshore areas, a prospect that is unlikely to be politically or economically palatable.

At a much larger scale, the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) has been established to protect the Southern Ocean (box 3). CCAMLR is heavily management driven, concerning itself primarily with catch quotas and fishery licensing. Nevertheless, one of its mandates is to ensure that the other ecosystem components of these fisheries are not adversely affected. Thus, the survival and growth rates of higher predators (pinnipeds and seabirds) are monitored and the fishery adjusted accordingly (Constable et al. 2000). Thus far, this legislation has not considered the possibility of using offshore reserves, although concerns over seabird bycatch may encourage such an approach in the near future.

Monitoring and policing

One of the greatest limitations facing novel conservation initiatives is the difficulty involved in assessing their effectiveness at protecting target species. Once a reserve area or management strategy has been implemented, can researchers assess whether it has slowed the rate of decline of the target species? Most higher predators have long life spans, and consequently it is often several years before any changes in population growth or structure become apparent. A potentially promising method to investigate this is to look at shifts in age structure. Although these shifts will also take several years to observe, there is usually a transitory oscillation immediately

Box 2. Case study: The European Union's special areas of conservation

The recent European Council Directive 92/43/EEC, also known as the Habitats Directive, was passed to provide protection to 632 species and 56 habitat types within Europe. This legislation requires European countries to designate special areas of conservation (SACs). There are three main criteria for the designation of these areas:

- Each area must contain priority species that are rare in the country where the area is located.
- If possible, an area should be chosen to protect both specific species and specific habitats, not simply by drawing a box around species distribution but by identifying and incorporating habitat types around a species distribution.
- Within the European Union (EU), a high proportion of the entire population of the priority species should be conserved.

Fifty to ninety percent of the EU populations of most marine mammals are found within the United Kingdom (UK), placing a requirement on this country to develop plans for designating and implementing reserves for these species.

Five marine mammal species require protection:

- *Grey seal* (UK population approximately 130,000). Breeds in localized colonies on islands around Scotland. Primary threat is to breeding rather than foraging sites. Three to four SACs will encompass approximately 50% of the breeding population.
- *Bottlenose dolphin* (UK population approximately 300–500). Localized areas of distribution in the Moray Firth, Scotland, and Cardigan Bay, Wales. Each SAC encompasses a large portion of the distribution of a local population.
- *Harbor seal* (UK population approximately 50,000). Hauls out in diffuse groups at several locations; no large colonies. High haul-out densities along the west coast of Scotland, Shetland and Orkney, but would require a number of different sites to protect a significant portion of the population. Conflicts with inshore fishermen. Also vulnerable to occasional epidemics.
- *Mediterranean monk seal* (European population approximately 500). Population has suffered catastrophic collapses, leaving remnant groups of animals. Vulnerable to disturbance at haul-out and breeding sites. Protection of viable breeding habitat is encouraging recolonization; however, 2 areas in Portugal and 11 in Greece are probably protecting fewer than 100 individuals.
- *Harbor porpoises* (North Sea population approximately 340,000). Areas of high density offshore are dispersed and mobile; a vast protected area would be required to protect survival and reproduction. This has led to a stalemate in terms of reserve designation.

after the successful implementation of a management action, which may be observed using proxies for age structure (e.g., juvenile-to-adult ratios; Holmes and York 2003).

In addition to monitoring the progress of protected populations in the context of management goals (e.g., recovery from overexploitation), it is important to document levels of illegal take from hunting or fishing in protected areas. Unless there is strong community support for a particular marine protected area, there is likely to be some take within the area that may obscure detection of its protective effects or undermine those effects completely. Similarly, the policing of marine protected areas is extremely difficult, particularly within the highly dynamic pelagic system. The pirate fishery for Patagonian toothfish in the Southern Ocean is an example of this, occurring within the CCAMLR management system (Constable et al. 2000). This is where economics may provide the simplest answer—it will only be by controlling the market that such pirate fishing may become unsustainable.

Conclusion and future directions for research

Can new management tools such as marine reserves be useful for conserving marine megafauna? Although marine mammals and birds have traditionally been used as flagship species for conservation efforts, novel designs of marine protected areas guided by a consideration of these species' distribution and life history may greatly enhance the effectiveness of existing protective measures. We have discussed several issues that will play a role in developing such designs. Most important, assessment of the threats that will be mitigated by a reserve, and consideration of the anticipated management actions, should be incorporated at an early stage. Consideration of such threats in combination with distribution and life-history data will help to establish the size and placement of protected areas. In terms of modeling options, demographic sensitivity analysis may be relevant to the question of when and how to protect different life stages and distributional ranges to promote population protection. In particular, alternative designs for marine protected areas can be compared with demographic and ecological models before experimental reserves are established (Heppell and Crowder 1998). The impacts of reserves on species other than their targets are more difficult to predict, and future work is needed on the dynamics of interspecific interactions associated with the recovery of populations. However, in systems that have not suffered large-scale ecological perturbation, or systems in which reserves will serve to provide precautionary protection, this will not be an issue.

The use of marine predators as indicator species may provide a useful approach to the protection of productive ocean areas. Existing knowledge of areas that represent peaks of abundance for marine megafauna should enable establishment of networks of pelagic reserves based on distributional hotspots and complementary species protection (Reyers et al. 2000, Gaston and Rodrigues 2003). The final limiting factor for such reserves is more likely to be the political will and international cooperation necessary to achieve them.

Box 3. The Southern Ocean: Convention for the Conservation of Antarctic Marine Living Resources

In contrast to other multilateral fisheries conventions, the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR; *www.ccamlr.org)* not only is concerned with the regulation of fishing but also has a mandate to conserve the entire Antarctic marine ecosystem. CCAMLR was a pioneer in developing this ecosystem approach to the regulation of fisheries, considering the whole Southern Ocean as a suite of interlinked systems.

A conventional definition of an ecosystem is any unit that includes all of the organisms in a given area, interacting with the physical environment so that a flow of energy leads to clearly defined trophic structures, biotic diversity, and material cycles (i.e., exchange of materials between living and nonliving parts) within the system. An ecosystem approach does not concentrate solely on the species fished; it also seeks to minimize the risk that fisheries will adversely affect "dependent and related species," that is, species with which humans compete for food. However, regulating large and complex marine ecosystems is a task for which managers currently have neither sufficient knowledge nor adequate tools. Instead, CCAMLR's approach is to regulate human activities (e.g., fishing) proactively so that deleterious changes in the Antarctic ecosystems are avoided.

CCAMLR applies to all areas south of 60° S and to waters between that latitude and the Antarctic Convergence, the oceanographic boundary between the Southern Ocean and other global oceans. Its goals are

- to facilitate research into and comprehensive studies of Antarctic marine living resources and the Antarctic marine ecosystem
- to compile data on the status of and changes in populations of Antarctic marine living resources
- to ensure the acquisition of catch-and-effort statistics on harvested populations
- to identify conservation needs and analyze the effectiveness of conservation measures

However, the use of marine reserves for conserving marine megafauna will be of limited value without the backup of firm management guidelines. Scientists and managers need to become less accepting of having areas designated as sanctuaries without tangible protection. Of course, with any management restrictions, enforcement will be a problem, particularly on the high seas. For effective conservation, a change in public sentiment may be required, such that ocean users become more effective at policing themselves. Ultimately, conservation benefits in the ocean are likely to depend on greater vision on the part of scientists—and, most critically, of policymakers—in realizing the benefits of favoring long-term sustainability over short-term economic profit.

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