

Global distribution and conservation of marine mammals

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We identified 20 global key conservation sites for all marine (123) and freshwater (6) mammal species based on their geographic ranges. We created geographic range maps for all 129 species and a Geographic Information System database for a 46,184 1° x 1° grid-cells, ~10,000-km². Patterns of species richness, endemism, and risk were variable among all species and species groups. Interestingly, marine mammal species richness was correlated strongly with areas of human impact across the oceans. Key conservation sites in the global geographic grid were determined either by their species richness or by their irreplaceability or uniqueness, because of the presence of endemic species. Nine key conservation sites, comprising the 2.5% of the grid cells with the highest species richness, were found, mostly in temperate latitudes, and hold 84% of marine mammal species. In addition, we identified 11 irreplaceable key conservation sites, six of which were found in freshwater bodies and five in marine regions. These key conservation sites represent critical areas of conservation value at a global level and can serve as a first step for adopting global strategies with explicit geographic conservation targets for Marine Protected Areas.

biodiversity | conservation priorities | political endemism

The current loss of biological diversity is one of the most severe global environmental problems and probably is the only one that is truly irreversible. Recent studies show that anthropogenic factors are causing increasing rates of extinctions of both populations and species (1–3). Despite their immense value, marine ecosystems are deteriorating rapidly, especially because of habitat degradation, overexploitation, introduction of exotic species, pollution (including noise), acidification, and climate disruption (4, 5), in part because roughly 60% of the world's human population lives within 100 km of a coast, and 20% of ecosystems adjacent to oceans have been highly modified (6, 7). Because of those anthropogenic environmental changes, many species of marine animals have undergone local, regional, or global extinctions (8). Marine mammals provide some of the best-known cases of population and species extinction through over-exploitation. Many species have experienced severe population depletion, and at least three [Caribbean monk seal (*Monachus tropicalis*), Atlantic gray whale (*Eschrichtius robustus*), and the Steller's sea cow (*Hydrodamalis gigas*)] became extinct because of hunting for their fur, blubber, and meat during the 19th and 20th centuries. The most recent extinction, caused by several human activities including illegal hunting for meat and body parts used in traditional medicine, is the baiji (*Lipotes vexillifer*) from the Yangtze River in China, which was declared extinct in 2008 (9).

Understanding geographical variation in species richness and other large-scale patterns can be especially valuable for the establishment of global conservation priorities (10–13). Those patterns, for example, allow assessment of what would be required to preserve all species in a given taxon and to determine critical sites for their conservation (14–16). Given that the distribution patterns of species richness usually are not closely related to those of endemism and extinction risk, conservation actions to minimize global species extinction necessarily involve a combined evaluation of patterns of richness, endemism, and endangerment (17, 18). Global distribution patterns have been

determined for different vertebrate groups such as birds, amphibians, fish, and terrestrial mammals (19–22), but such large-scale analyses are lacking for marine/freshwater mammals (23).

Here we present a global analysis of distribution patterns for 129 marine mammals, focusing on the following goals: (i) describing their geographic ranges; (ii) assessing patterns of species richness and composition; and (iii) determining key conservation sites as a basis for understanding global conservation needs. We created a database with the geographic distribution of all 129 species of pinnipeds, cetaceans, sirenians, two species of otters, and the polar bear (24). We followed Reeves et al. (24) and Wilson and Reeder (25) for the basic taxonomic arrangement (*SI Appendix*). It is important to emphasize, however, that the taxonomy of many marine mammals is still confused. The oceans are the last remaining places where large, charismatic species doubtless remain to be described; new species have been found in the last 20 y. For example, *Mesoplodon perini* (a 4-m beaked whale) (26) and *Orcaella heinsolmi* (the 2-m Australian snubfin dolphin) (27) were scientifically described recently. The taxonomic position of many species is controversial and likely to change radically in the future when more data are available. For example, recent studies suggest that there are several species of orcas (28, 29), Bryde's whales (30), and Blue whales (31, 32). The taxonomy of dolphins also is complex. For example, some consider the Amazonian Tucuxi dolphin (*Sotalia fluviatilis*) to be two species (33, 34). Obviously, as taxonomic knowledge improves, one would expect changes in the overall distribution patterns we describe. We defined endemic species as those whose distribution is limited to a single country (political endemism), and the conservation status of all species follows that given by the International Union for the Conservation of Nature (*SI Appendix*) (35).

The lack of better distributional data precludes more sophisticated analysis, such as modeling standard habitat suitability, to predict ranges of the majority of marine mammal species on very large scales (36). Any comprehensive consideration of the distribution of cetaceans is hampered by the uneven sighting effort; range maps therefore must be interpreted with caution. To date, descriptive statistical techniques have been used to explore cetacean-habitat relationships for selected species in specific areas. There are fewer studies that examine patterns of species richness and geographic ranges using computationally intensive statistic modeling techniques. The development of models to test specific hypotheses about the ecological processes determining cetacean distributions has just begun (37). Marine spatial planning is clearly a way forward, particularly for the high seas, where nonspatial monitoring is difficult and where data gaps obstruct conventional management approaches (38).

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To make the data from different species as compatible as possible, we used the same source of distribution information for all species. Despite the limitations in present knowledge, it is imperative to evaluate and implement conservation measures in ways that attempt to compensate for the uncertainties. Spatial modeling incorporates data on the environment to generate a spatial prediction of relative density based on the preference for habitats defined by combinations of environmental covariates. The areas identified for the candidate Marine Protected Areas (MPAs) thus provide a good description of distribution available, as informed by features of the habitat that are shown to be important (39). Terrestrial mammal conservation faces similar uncertainties (40, 41), but significant progress has been made in identifying conservation sites critical for species richness, endemism, and endangerment, using data similar to those used in our study. Such knowledge has contributed to the steps that have been taken to protect many species (2, 15–18).

Results and Discussion

Marine mammals are a polyphyletic group that comprises 129 species grouped in three orders, Cetacea, Sirenia, and Carnivora (Table 1). The smallest marine mammal is the sea otter (1.15 m, 4.5 kg), and the biggest is the blue whale (30 m, 190 tons). Marine mammals show very complex, heterogeneous distributions throughout the oceans and also are found in a few freshwater lakes and rivers. The average geographic range for all species is 52 million km² (Fig. 1A). The most widely distributed species, with ranges exceeding 350 million km², are Bryde's (*Balaenoptera edeni*) and humpback (*Megaptera novaeangliae*) baleen whales. The marine species with the most restricted range is the vaquita (42) (*Phocoena sinus*), a porpoise species endemic to 4 000 km² in the upper northern Gulf of California, Mexico. However, most of the species with very restricted ranges, such as the Baikal seal (*Pusa sibirica*), are freshwater species endemic to lakes. They probably have relict distributions, remnants of much larger ranges in geologic times (24). Both endemic and restricted-range species have high priority for conservation because they usually are more vulnerable to anthropogenic impacts (2, 10).

In terms of richness, the analysis of our 46,184-cell, ~10,000-km² global geographic quadrant grid (*Methods*) showed that the number of species per cell varied from 1 to 38, with an average of 17 species, across vast regions of the oceans. Interestingly, latitudinal gradients of species richness of marine and land mammals are very different. Marine mammals have undergone considerable anatomical modifications during their evolution. The unique characteristics of the marine ecosystems have resulted in the many different physiological and ecological responses that marine mammals have experienced. These modifications undoubtedly have resulted in energetic constraints. One of several complex structures of the marine environment is a more-or-less unpredictable, patchy distribution of food over large spatial and temporal scales; this patchy distribution almost certainly has contributed to the evolution of marine mammal energetics, especially through its effect upon energy storage and expenditure strategies. Species richness of land mammals increases sharply from temperate latitudes toward the equator. In contrast, species richness in marine mammals has a more northerly temperate

component, showing a higher concentration of species (24 species average) between 30° N and 40° S (Figs. 1B and 2A). Other factors contributing to this pattern in marine mammals remain to be evaluated; nevertheless, the results of our richness-distribution patterns are consistent with other approaches analyzing marine mammal distribution patterns (36, 43).

Regions especially rich in marine species (Fig. 2A) were found along the coasts of North and South America, Africa, Asia, and Australia. Such patterns apparently are correlated with ocean currents and their dynamics, especially with nutrient flows connected to upwellings. For example, along the Pacific coast of the American continent, the highest species richness was found along the California, Baja California, and Peruvian coasts, where large upwelling systems maintain very productive fish communities (44). Interestingly, among higher taxa, patterns of species distribution in marine mammals differed strongly (Fig. 3A–C). Pinniped (seal and sea lion) species richness was concentrated at the poles, especially near Antarctica, whereas Mysticetes (baleen whales) exhibited high species richness at 30° S latitude, and Odontocetes (toothed whales) were concentrated near tropical coasts. There also was variation in distribution at the family level within and among orders; for example, the two families in Sirenia had contrasting distributions: The Trichechidae (manatees) were found exclusively in the North and South Atlantic, whereas the Dugongidae (dugong) were restricted to the North Pacific and Indo-Pacific.

Political endemic species [i.e., species found in only one country, a restriction that may increase their vulnerability (2)] included seven species; the Baikal seal (*Pusa sibirica*), the Australian sea lion (*Neophoca cinerea*), the Galapagos fur seal (*Arctocephalus galapagoensis*), the Galapagos sea lion (*Zalophus wollebaeki*), the New Zealand dolphin (*Cephalorhynchus hectori*), the Hawaiian monk seal (*Monachus schauinslandi*), and the vaquita (*Phocoena sinus*) (45). Seven species, among them the New Zealand sea lion (*Phocartos hookeri*) and the Australian Snubfin dolphin (*Orcaella heinsohni*), had restricted ranges. In terms of extinction risk, 10% of all marine mammals are considered vulnerable, 11% endangered, and 3% critically endangered (*SI Appendix*). Species at risk were found throughout the oceans but were concentrated at higher latitudes, especially near the Aleutian Islands and the Kamchatka Peninsula, where extensive exploitation of whales and seals occurred in the past (Fig. 4).

To assess the conservation challenges to marine mammals, we determined the area (i.e., the number of cells) required to incorporate different percentages (i.e., 10%, 15%, 20%, and 25%) of the geographic ranges of all species, using the Marxan optimization algorithm (*Methods*). Conserving at least 10% of all of the species' geographic range required ca. 45 million km² (5,700 grid cells), roughly equivalent to 12% of the world's ocean area (e.g., two times the extent of the Southern Ocean). This study provides grounds for future assessment of an area-explicit conservation parameter for marine mammals. The "target" of 10% was used so this work would be comparable to our previous papers on terrestrial mammals (15, 46); it also is one of the targets suggested by the Convention on Biological Diversity (47). This Convention has called for networks of protected areas, which, in addition to other conservation measures, are necessary components of sustainable use (39). Targeting 15%, 20%, and 25% of each marine mammal's distribution range considerably increased the area required to meet the targets (Fig. 5). Clearly, protecting larger targets must incorporate, by necessity, other conservation mechanisms in addition to reserves or MPA's (48, 49).

Our next step was to identify key conservation sites representing all marine mammal species in a geographically explicit way. We selected those sites using the grid cells with the greatest diversity followed by "irreplaceable" cells (i.e., cells with species represented nowhere else), using the Marxan optimization algorithm (*Methods*). We evaluated the representation of all marine mammal species in 1%, 2.5%, 5%, 7.5%, and 10% of the grid cells (Table 1). We chose 2.5% because these grid cells in-

Table 1. Variation in the number of cells and the area covered by different targets to select top-priority cells for marine mammal conservation

% Grid cells	# Grid cells evaluated	Extension (km ²)	Total species richness
1	462	4,620,000	91 (71%)
2.5	1,155	11,550,000	108 (84%)
5	2,309	23,090,000	127 (98%)
7.5	3,464	38,104,000	129 (100%)

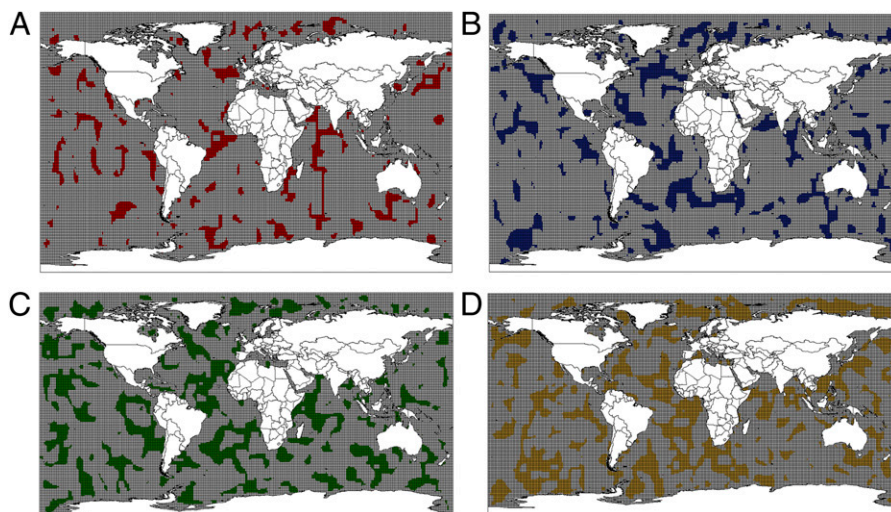


Fig. 5. Conservation targets covering (A) 10%, (B) 15%, (C) 20%, and (D) 25% of the marine mammal distributions using the Marxan optimization algorithm to optimize the number of grid cells and its geographic location.

Many marine species and populations [e.g., North Atlantic right whale (*Eubalaena glacialis*) and the Sei whale (*Balaenoptera borealis*)] are at the brink of extinction from overharvesting, pollution, bycatch, and exhaustion of prey-species populations (24, 25, 56–58), and their long-term survival depends on sound management that addresses the factors causing their decline. The baiji dolphin, once endemic to the Yang-Tze River in China, is a disturbing example of the plight of marine mammals impacted by human activities (9). The next candidate to become extinct if no solid conservation and management strategies are implemented is the Mexican vaquita. Endemic to the Gulf of Baja California, the species has been declining sharply for at least 2 decades; one fifth of the population is killed in gillnets every year, and there now are only an estimated 150–300 individuals (59). Indeed, more than 650,000 marine mammals die from entanglement in fishing nets each year (60), making bycatch the single largest cause of mortality for small cetaceans and pushing several species to the verge of extinction.

Conservation strategies also should take into account the possible impacts of anthropogenic climate disruption (61, 62) on the distribution of these mammals and its repercussions on the establishment of connective corridor systems between protected areas (61) and on management plans. Finally, management interventions must be evaluated critically with regard to ecological viability and benefits vs. costs (61).

By selecting the smallest area of reserves using an optimization algorithm, the opportunity conservation cost would be generally lower, but this approach will depend on the distribution of other potential economic activities (63). For instance, an evaluation of fisheries values could provide a feasible first cut at calculating those costs. Given the distribution patterns of marine mammals, the increasing pressures of human activities in the oceans, and the threat of climate disruption, the conservation of marine mammals is a daunting problem. Saving one or two populations of most species will not be enough (2) because of the role that such charismatic mammals play in the ecological dynamics of marine and freshwater ecosystems and in the provision of ecosystem services. As many scientists have emphasized in other forums, especially in connection with whaling (64), the complexity and scale of the problem requires an unprecedented international effort with the development of both new attitudes and institutions (65). The main objectives of selection criteria for MPAs are to identify potential MPAs for highly mobile and temporally variable pelagic species, including high-density areas, feeding or breeding grounds, and migratory routes; to provide a transparent and systematic approach to selection; and to help determine priorities for action (39).

Uncertainty will always be a factor in research on pelagic organisms and their environment. Empirical data point to dramatic

declines and changes in marine systems, and ongoing research continues to provide techniques to incorporate and contend with uncertainty. The challenge is to produce timely and scientifically defensible research based on available data to address this conservation crisis now (56). The future of marine mammals in particular and biodiversity in general will depend on the actions we take.

Methods

We compiled and digitized the geographic range maps from published sources for all 129 species and created a Geographic Information System database for 46,184 1° x 1° grid-cells, ~10,000-km². We then conducted a presence/absence analysis to determine the number of species in each grid cell and the number of cells in which each species was recorded. We created maps of global species richness, irreplaceable sites, endemism, and threatened species. Key conservation sites for species richness were determined either as the 2.5% of the cells with the highest species richness or as irreplaceable sites, defined as regions containing species not represented in any other part of the world (17, 18). Additionally, we used optimization algorithms, i.e., ResNet (66) and Marxan (67, 68–69), to determine the number of cells required to cover 10%, 15%, 20%, and 25% of the geographic ranges of all species and the area of the ocean covered by each percentage.

Marxan is software that delivers decision support for reserve system design intended to solve a particular class of reserve design problem in which the goal is to achieve some minimum representation of biodiversity features for the smallest possible cost. Given reasonably comprehensive data on species, habitats, and/or other relevant biodiversity features, Marxan aims to identify the reserve system (a combination of planning units) that will meet user-defined biodiversity targets for the minimum cost. In this particular case, Marxan selected planning units (here, grid cells) to meet the targets (10%, 15%, 20%, and 25% of the geographic ranges of all 129 species) and also considered the following factors. Each grid cell is assigned a “cost” depending on the target (e.g., area, number of species, threat), and Marxan minimizes the combined grid-cell cost of the conservation network, still selecting expensive grid cells if they are needed to meet the targets. This cost can be a measure of any aspect of the planning unit (25, 69, 70); in this case, it was species richness plus cells weighted for breeding/feeding ground or migratory route. We set Marxan to select adjacent planning units preferentially rather than a series of unconnected units, which would be less ecologically viable and more difficult to manage. Then Marxan identified a set of grid cells each time it was run: 100 runs generated 100 different grid-cell networks (67). Units that appeared in every network were considered irreplaceable, because they always would be needed to meet the targets, whereas other units could be swapped with similar units, and the targets still would be met. Fig. 5 was achieved using these methods.

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