

Drivers and hotspots of extinction risk in marine mammals

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The world's oceans are undergoing profound changes as a result of human activities. However, the consequences of escalating human impacts on marine mammal biodiversity remain poorly understood. The International Union for the Conservation of Nature (IUCN) identifies 25% of marine mammals as at risk of extinction, but the conservation status of nearly 40% of marine mammals remains unknown due to insufficient data. Predictive models of extinction risk are crucial to informing present and future conservation needs, yet such models have not been developed for marine mammals. In this paper, we: (i) used powerful machine-learning and spatial-modeling approaches to understand the intrinsic and extrinsic drivers of marine mammal extinction risk; (ii) used this information to predict risk across all marine mammals, including IUCN "Data Deficient" species; and (iii) conducted a spatially explicit assessment of these results to understand how risk is distributed across the world's oceans. Rate of offspring production was the most important predictor of risk. Additional predictors included taxonomic group, small geographic range area, and small social group size. Although the interaction of both intrinsic and extrinsic variables was important in predicting risk, overall, intrinsic traits were more important than extrinsic variables. In addition to the 32 species already on the IUCN Red List, our model identified 15 more species, suggesting that 37% of all marine mammals are at risk of extinction. Most at-risk species occur in coastal areas and in productive regions of the high seas. We identify 13 global hotspots of risk and show how they overlap with human impacts and Marine Protected Areas.

International Union for the Conservation of Nature Red List | threatened and endangered species | life history | random forest models

Oceans occupy 71% of the earth's surface and harbor much of its biodiversity. Despite the vast expanse of the oceans, no area remains unaffected by humans (1). Human activities are polluting, warming, and acidifying the oceans, melting sea ice, overharvesting fisheries, and altering entire food webs (1–4). Fisheries bycatch causes deaths of more than 650,000 marine mammals each year (5). Overfishing has depleted food supplies by reducing fish populations by 50–90%, and industrial-scale krill harvesting will likely further deplete food resources (6–8). In addition, polar oceans are warming at rates twice as fast as the global average (3); this has already altered whale migrations, reduced benthic prey populations, and caused declines in seals and polar bears (*Ursus maritimus*) whose lifestyles are dependent on sea ice (9). The International Union for the Conservation of Nature (IUCN) Red List currently classifies 25% (32 of 128 species) of marine mammals as threatened with extinction. Examination of the threats on the basis of the Red List shows that nearly half of all species are threatened by two or more human impacts, with pollution being the most pervasive, followed by fishing, invasive species, development, hunting, and climate change (Fig. S1).

However, our understanding of which marine mammals are most at risk remains poor because many species are difficult to study, changes in their populations can be hard to detect, and their natural histories have not been well documented (10–12).

Indeed, the conservation status of about 40% of marine mammal species has not been categorized by the Red List, mostly because of insufficient information (i.e., "Data Deficient" species), and with ever-increasing human impacts on the oceans, many more species likely will become threatened in the near future. Predictive, spatially explicit models that can identify which species are most likely to be at risk are urgently needed to address the rapid changes impacting marine mammal biodiversity (13, 14). Such quantitative models have been developed for terrestrial mammals (14–17) and for some marine species (16, 18), but are lacking for marine mammals as a whole at the global scale.

Here, we provide a predictive, spatially explicit assessment of global marine mammal extinction risk. We combined spatial analyses with a powerful machine-learning technique and an ecoinformatic database to determine (i) which marine mammal species are at greatest risk; (ii) why they are threatened; and (iii) where risk is greatest globally. Because extinction results from the combination of species' attributes, geographic settings, and human threats, we developed a predictive model of extinction that considers the important interactions between intrinsic species' traits and extrinsic environmental variables, including spatially explicit human impacts on the world's oceans (1). Using this information, we then identified major geographic hotspots of extinction risk and showed how these regions overlap with human activities to inform marine conservation.

We compiled a species-level database for 125 extant marine mammals, including cetaceans, pinnipeds, sirenians, polar bears, and two species of otters. Our database consisted of two kinds of predictor variables: (i) intrinsic biological traits (adult body mass, geographic range size, life-history traits, social group size, trophic group, habitat, foraging location, taxonomic order, diet breadth, and migratory behavior) and (ii) extrinsic environmental variables [mean annual net primary production (ANPP) (19) and mean human impact index (1)] within each species' geographic range (*SI Materials and Methods*). For the intrinsic life-history variables, we included traits that determine the speed of life history (20, 21). Specifically, we used the components of mass-specific production, p , where $p = (m_w/m_A) \cdot l \cdot n$, where m_A is adult body mass, m_w is offspring weaning mass, l is litter size, and n is number of births per year (22). We then used a dichotomous response variable to represent extinction risk: species classified as Vulnerable, Endangered, Critically Endangered, or Extinct by the IUCN were considered "threatened"; species classified as Near Threatened or of Least Concern were considered "non-threatened" (23).

We quantified relationships between predictor variables and extinction risk using a random forest model of 500 classification

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trees (24, 25). This is a powerful machine learning technique that combines the predictions of multiple independent decision tree models into a robust composite model with high predictive accuracy (24, 26, 27). Decision trees are able to disentangle complex ecological phenomena, such as extinction risk, by identifying nonlinear, context-dependent interactions among multiple, correlated predictor variables (13, 24). Moreover, these models are non-parametric techniques that provide viable alternatives to phylogenetic contrasts (28). To assess the role of phylogeny, we included taxonomic group in our models. We used the random forest model to estimate the relative importance of each predictor variable and to predict threat status for each species, including Data Deficient species. We provide further details of methodology in *Materials and Methods* and in *SI Materials and Methods*, and a list of species predicted to be at risk in *Table S1*.

Results and Discussion

Our random forest model classified species on the Red List with 92% accuracy (Cohen's kappa = 0.8, $P < 0.0001$; see *Table S2* for all goodness-of-fit metrics). Our model identified 27 of the 32 species currently recognized as Vulnerable or Endangered on the Red List plus an additional 15 species (*Table S2*). Of the latter 15, 2 are currently listed as Least Concern and the remaining 13 are Data Deficient on the Red List. Summing the 27 species that were both predicted by our model and on the Red List, the 5 species on the Red List but not predicted by our model, and the 15 species predicted by our model but not on the Red List gives a total of 47 species, or 37% of extant marine mammals, likely to be at risk of extinction.

In decreasing order of importance, the primary predictors of risk identified by our random forest model were body mass at weaning, number of births per year, taxonomic group, geographic range area, and social group size (*Fig. 1* and *Fig. S2*). The first two predictors, mean body mass at weaning and number of births per year, highlight the influence of life history. Because all marine mammals except polar bears give birth to only one offspring per reproductive cycle, size of offspring at weaning multiplied by the frequency of breeding gives productivity, or rate of biomass production via reproduction (22). So, together, these two variables index the speed of life history and are the primary determinants of r_{max} , the maximum or intrinsic rate of population increase and the capacity for species to recover from reduced populations after threats have been removed. Rate of population increase after depletion is important to marine conservation (29–31). For example, baleen whales have fast life histories for their body size, and several species, including humpbacks and gray whales (*Megaptera novaeangliae* and *Eschrichtius robustus*), have shown strong recoveries following the international ban on commercial whaling (4, 30). Other taxa, including sea otters (*Enhydra lutris*) and northern elephant seals (*Mirounga angustirostris*), have increased exponentially after protection (30). The latter had been reduced to 20–30 individuals by 1900, and despite very low genetic diversity, elephant seals increased at an estimated 8.3% per year to a population of ~170,000 today (23, 32). These results imply that when species with high productivities fail to rebound rapidly after protection, they have not achieved the near-maximal rates of population growth expected on the basis of their life histories. This suggests that the original environmental threats have not been alleviated or that new threats, such as climate change, have arisen to inhibit recovery (e.g., 33). Similar issues apply to species

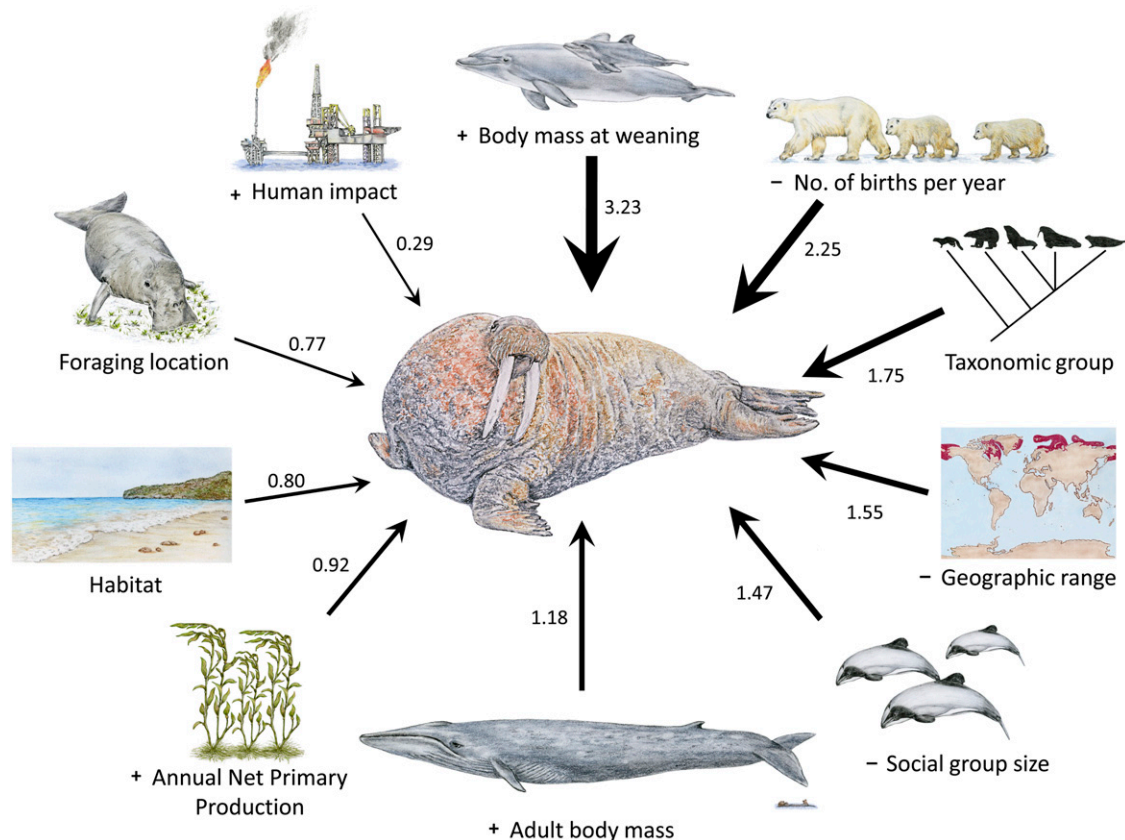


Fig. 1. Relative importance, in rank order, of intrinsic and extrinsic predictors of marine mammal extinction risk. Numerical values of importance for each predictor variable were calculated as the decrease in classification accuracy after predictor removal in a random forest of 500 trees. Model accuracy was 92% (Cohen's kappa = 0.8, $P < 0.0001$; *Table S2* and *Fig. S2*). "+" or "-" indicates the direction of correlation for the continuous variables. Drawings are by Sharyn N. Davidson.

with low productivities, but more time may be required to assess whether failure to recover after protection is due to intrinsic life-history characteristics or extrinsic environmental factors.

At the high-risk end of the spectrum were species with low rates of production and so with slow life histories. These species often belonged to specific taxa (orders, families, and genera), suggesting constraints of intrinsic traits inherited from common ancestors and therefore related to phylogeny. Interestingly, slow speed of life history also has been shown to be a strong predictor of risk in ungulates and terrestrial carnivores (34). Sirenians (Order Sirenia: manatees and dugongs) are a good example of marine mammals at the high-risk end of the spectrum. They have low productivities and are the only herbivorous marine mammals. All five extant species in the order are at risk (23), and the giant Steller's sea cow (*Hydrodamalis gigas*) was hunted to extinction within a few decades after discovery by Europeans. Most toothed whales also have low production rates, but they have large geographic ranges and often form large social groups, which helps offset risk. Pinnipeds, on the other hand, have relatively high rates of production; however, walrus (*Odobenus rosmarus*) and eared seals (Otariidae) generally have slower rates than true seals (Phocidae), which can make them more vulnerable. Nevertheless, some true seals, such as monk seals (*Monachus* spp.), are critically endangered due to high human impacts within their small geographic ranges (5). So, although speed of life history is the most important predictor of extinction risk overall, decision tree analyses emphasize that there are multiple pathways to extinction, and risk usually cannot be attributed to a single intrinsic or extrinsic variable (16) (Fig. 1).

Other intrinsic traits, including small geographic range area and small social group size, were also important predictors, consistent with traits identified for terrestrial mammals in general (16) (Fig. 1 and Fig. S3). Small geographic range is a robust predictor of risk across many vertebrate groups (16, 34–36), and this includes species whose ranges have contracted significantly due to human impacts (16, 37). In marine mammals, social group size may reduce risk because of the advantages of sociality in reducing predation and enhancing foraging. The endangered, endemic Galápagos fur seal (*Arctocephalus galapagoensis*) (5, 23) is a good example; it has one of the smallest ranges of all marine mammals and a small social group size. Extrinsic environmental variables were generally poorer predictors than were intrinsic traits, perhaps in part because they are indirect and affect extinction by interacting with life history and other biological traits and in part because environmental variables were obtained from global databases that may be too coarse-grained to capture localized human threats.

Our analysis predicted that 13, or about one-third, of all Data Deficient species may be at risk of extinction. One of these is the boto (Amazon River dolphin; *Inia geoffrensis*). It and other river dolphins are especially vulnerable because they have not only slow life histories, but also small social group sizes and extremely small geographic ranges. Although our analysis was not able to evaluate extrinsic predictors for river dolphins (see *Materials and Methods*), they do face intense human pressures from pollution, fishing, and damming (e.g., by Brazil's recently approved Belo Monte hydroelectric dam, which will be the third largest in the world). The walrus is another Data Deficient species predicted to be at risk. It is threatened by ocean warming, which is reducing sea ice used for breeding, feeding, and resting and leading to increased shipping traffic, pollution, and development (38). Several Data Deficient beaked whales (Ziphiidae) and other whale and dolphin species were also predicted to be at risk. In fact, none of the beaked whales have a designated conservation status under the Red List (23). They are elusive, deep-sea mammals that occur in low abundances and depend on critical habitat like isolated deep-sea canyons (39). Because of their deep-diving behavior, they appear to be especially vulnerable to decompression sickness triggered by naval sonar (39).

Using the at-risk species identified by our model and the Red List, we created maps showing the global distribution and hotspots of risk (Figs. 2–4). Hotspots were defined as cells with six or more at-risk species, corresponding to the top 2% of geographic grid cells (totaling about 12,950,000 km²). Globally, the marine grid cells contained from 0 to 11 at-risk marine mammal species (Fig. 2); cells with 6 or more at-risk species represent the 75th percentile of at-risk marine mammal richness. We then mapped marine mammal species richness (Fig. S4A), marine productivity (ANPP) (19) (Fig. S4B), human impacts (1) (Figs. 3 and 4), and Marine Protected Areas (MPAs) (40) (Fig. 4D) to relate the geographic distribution of risk predicted by our model to the distributions of marine mammal species, extrinsic environmental factors included in our model, and protected areas. We determined the correlations between risk and species richness and ANPP, and calculated mean and range of the human impact index (1) within each risk hotspot in ArcGIS v9.3 (Fig. S5). We also overlapped our hotspots with the geographic distributions of total human impacts (1), specific human impacts (including commercial fishing, shipping, pollution, and sea-surface temperature anomalies indicating recent climate change) (1), and MPAs (40) (Figs. 3 and 4; Fig. S6).

Not surprisingly, there was broad agreement in the geographic distribution of species on the Red List and those that our model predicted to be at risk. Importantly, however, our model identified additional high-risk areas in the Indo-Pacific, around South

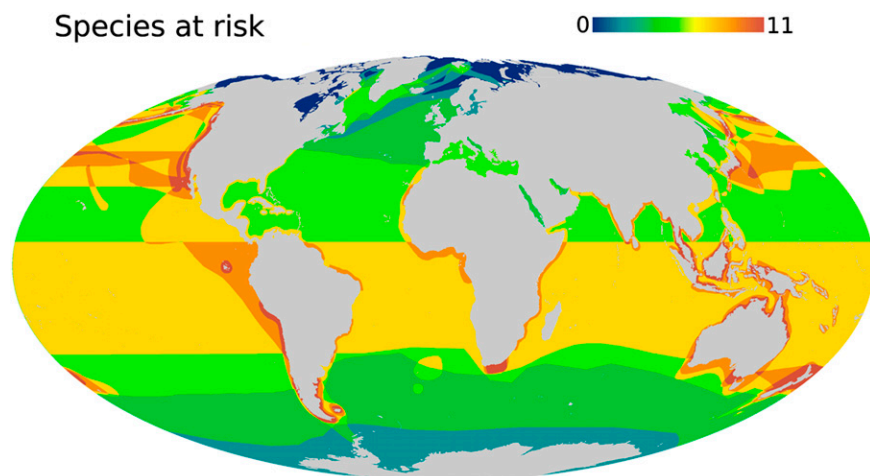


Fig. 2. Global distribution of marine mammal species at risk (model-predicted plus IUCN Red List species).

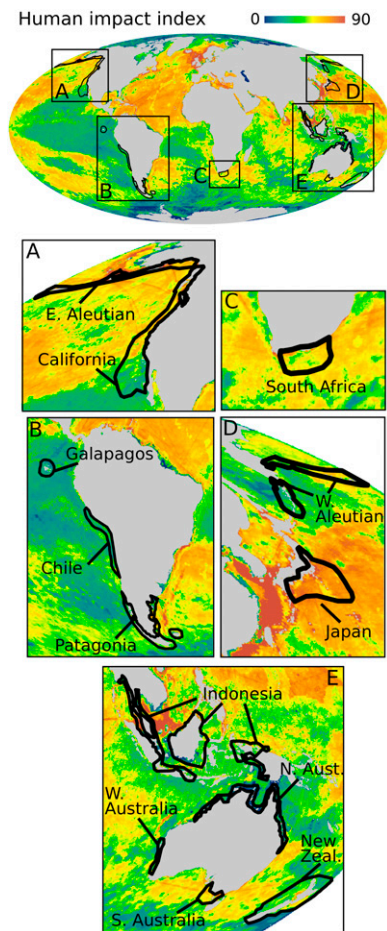


Fig. 3. Global hotspots of marine mammal species extinction risk, overlaid with human impact on the world's oceans (1). Hotspots show the top 2% of geographic grid cells for at-risk species (model-predicted plus IUCN Red List species). Panels A–E provide a magnified view of hotspots.

Africa, New Zealand, and Patagonia, and along the western coasts of South America and central Africa (Fig. 2) that are not currently recognized (12). In general, the spatial distribution of risk correlated strongly with that of marine mammal species richness ($r = 0.58$, $n = 50,927$, $P < 0.0001$) and, to a lesser extent, with net primary productivity ($r = 0.18$, $n = 50,927$, $P < 0.0001$) (Fig. S4). Most at-risk species and all 13 hotspots were distributed along coastlines (Figs. 2 and 3). Coastal areas with cold currents and upwelling are highly productive and support large populations and diverse species of marine mammals (12). However, most coastal areas also experience high levels of human impact (1), and our random forest model indicated that species that live, forage, or breed along coasts are at higher risk. Consequently, other coastal regions, in addition to the specific hotspots identified here, should be considered as high priority areas for conservation. Some regions of the open ocean, such as the North Pacific Transition Zone, also warrant protection because they are highly productive, have high abundance and species diversity of large predators (including marine mammals), and have been heavily impacted by human activities (41, 42).

Our analysis showed that 74% of marine mammal species experience high levels of human impact [impact index >60 (1)] within their geographic ranges (Fig. S7). These reflect the cumulative effects of many factors, including fishing, shipping, pollution, sea-surface temperature change, ocean acidification, invasive species, oil rigs, and human population density (1). However, levels of human impact varied spatially across most species' geographic ranges and even within hotspots (Fig. 3 and Fig. S5). Localized

human impacts were extremely high in the Indonesian, Japanese, Californian, and northern Australian hotspots (Fig. 3 and Fig. S5).

Overfishing and bycatch are among the leading anthropogenic threats to marine mammals worldwide (5) and were particularly high in the hotspots of the eastern Aleutian Islands and Patagonia, and especially in the Indonesian hotspot in the biologically rich Indo-Pacific (Fig. 4A). Shipping and pollution are widespread throughout the Northern Hemisphere (1) and impact marine mammals through direct ship strikes, noise (e.g., ship, military, and industrial activities), and other forms of pollution (e.g., oil spills, chemical wastes, entanglement in abandoned fishing gear, ingestion of plastic debris) (43). These impacts are especially high in the Californian and Japanese hotspots, where there are major human population centers and shipping routes (Fig. 4B) (1). Climate and oceanographic changes are widespread and escalating throughout the world's oceans (1, 3) and figure importantly in some of the higher latitude hotspots (e.g., western and eastern Aleutian Islands, Japan, and South Australia) where temperature changes have been more dramatic (Fig. 4C). The prospect of a warming ocean is especially serious for marine mammals, such as polar bears, walrus, and several species of seals, which occur at high latitudes and depend on sea ice for feeding, breeding, and/or resting (38).

The risk hotspots cover only 1.7% of the global oceans, but they include at least parts of the geographic ranges of 88 (70%) marine mammal species. These hotspots do not capture all regions and habitats in need of protection, however, because high levels of human impact threaten populations and species of marine mammals well beyond the hotspots. For example, the vaquita (*Phocoena sinus*), perhaps the single most endangered marine mammal species, is threatened by localized artisanal fishing activity in inadequately protected areas in the Gulf of California (5, 44). Ship strikes also are the primary threat to the world's remaining ~ 350 North Atlantic right whales (*Eubalaena glacialis*), whose geographic range overlaps with intensive shipping activity (45) (Fig. 4B). Climate change is likely to have wide-ranging, disruptive impacts on many species throughout the world's oceans, but these are only beginning to be understood (38, 46). Nevertheless, the distribution of hotspots of at-risk species in relation to human impacts provides information that can be used to manage key areas for marine mammal protection.

Importantly, the hotspots of risk overlap little with current Marine Protected Areas (Fig. 4D and Fig. S6). International efforts are underway to increase MPAs from 0.7% of the world's oceans currently to 10% by 2020 (39, 47). The magnitude and geographic distribution of extinction risk that we identify here is key to informing this process. Although previous studies have identified global patterns of marine diversity and current Red List status (12, 48–50), our study builds on this work not only by mapping the 32 species currently on the Red List, but also by adding the additional 15 species predicted to be at risk by our model. In addition, our maps (Figs. 2–4) provide insights into the geographic overlap of risk, human impacts, and protected areas across the world's oceans. Our results, coupled with previous studies, provide an important basis for specific conservation actions. Still needed, however, are more and better biological data, especially on migratory routes, and the location of feeding, calving/pupping, and breeding grounds to protect the geographic areas and networks of critical habitats on which highly mobile marine animals and other taxa depend (41, 51).

Conclusions

We show that the most important predictor of extinction risk is speed of life history because this captures the capacity of a species to rebound from human impacts. Our model also shows that intrinsic traits are more important predictors of risk than extrinsic factors because they are measures of the inherent susceptibility to human impacts and ability to recover from them. Therefore, our analysis emphasizes the importance of understanding the basic biology and ecology of marine mammals to assess the correlates and causes of extinction and to implement science-based

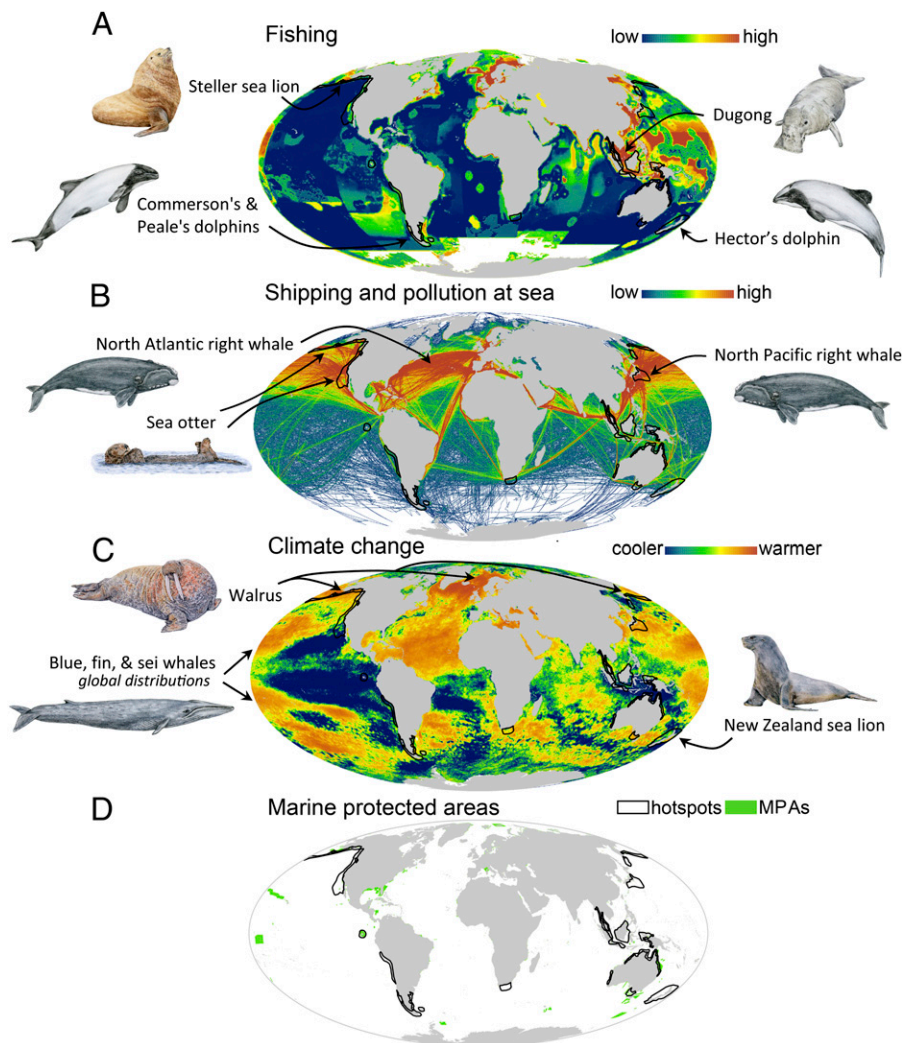


Fig. 4. Global hotspots of marine mammal species extinction risk, overlaid with the geographic distributions of the leading human impacts (1) on marine mammals and with Marine Protected Areas (MPAs) (39). (A) Fishing intensity. (B) Ship traffic and pollution. (C) Sea-surface temperature change: 1985–2005. (D) World distribution of MPAs (see also Fig. S6 for magnified view of D). Hotspots show the top 2% of geographic grid cells for at-risk species (model-predicted plus IUCN Red List species). Maps A, B, and C show examples of species predicted to be at risk by our model that occur within the hotspots, or other highly impacted regions, and whose populations are threatened by fishing, shipping, pollution, or climate change. Drawings are by Sharyn N. Davidson.

conservation. Unfortunately, such basic information remains poorly known for most species, and not just for those considered Data Deficient, but new technologies are beginning to provide new and better data on both the biology of marine mammals and the ecology of the oceans (51). Incorporating this key information into scientifically sound, well-informed management of local and regional ecosystems has the potential to mitigate the threats facing many species. In addition, however, because of the large magnitude and spatial scale of anthropogenic impacts and the wide ranges of many species, conservation of marine mammals will require unprecedented global effort and political will. There is little time to avoid widespread declines and extinctions of marine mammals with large attendant ecological, economic, social, and political consequences.

Materials and Methods

Database. Our database consisted of 125 (of 128) marine mammals for which sufficient species' trait data were available. We collected data on intrinsic predictor variables: adult body mass, body mass at weaning, number of births per year, number of offspring per reproductive bout, geographic range size, social group size, trophic group, habitat (coastal, oceanic), foraging location (continental shelf, continental slope, epipelagic, mesopelagic/bathypelagic zones), taxonomic order, diet breadth (generalist, specialist), and migratory behavior. We also gathered data on extrinsic variables: mean ANPP (19) and mean human impact index (1) within each species' geographic range. Our geographic range area data were from Geographic Information System maps used in Pompa et al. (12), which were based on Reeves et al. (52). We used a dichotomous response variable to represent extinction risk: species

classified as Vulnerable, Endangered, Critically Endangered, or Extinct by the IUCN were considered "threatened", and species classified as Near Threatened or Least Concern were considered "non-threatened" (23).

Random Forest Modeling. Following the modeling approach used in Davidson et al. (16), we tested for quantitative relationships between predictor variables and extinction risk using the randomForest package in R version 1.10.1 (24, 25, 53). For our main random forest model (Fig. 1), we included only those species that occur in the marine environment. Species found solely in rivers or lakes were excluded from the model because we were unable to obtain extrinsic data on ANPP and human impacts that were comparable to those of the marine system (1, 19). However, to provide predictions of threat status for freshwater species as well, we ran a separate random forest model that included only the intrinsic variables for all species (freshwater and marine) to predict risk for marine mammals occurring in river and lake environments. The intrinsic variables included were the same as those in the main model (Fig. 1); only the extrinsic variables of ANPP and human impact were excluded from this intrinsic model. To predict risk for Data Deficient species (Table S1), we used the main random forest model to predict risk for marine species and the intrinsic model for freshwater species. The intrinsic model was comparable in accuracy to the main model because the extrinsic variables were not especially strong predictors of risk. Variables that did not improve accuracy were not included in the final models, and differences in importance between predictors were quantified with pairwise two-tailed z-tests ($\alpha = 0.05$) (53).

Spatial Analyses. We used ESRI's ArcGIS v9.3 to calculate spatial statistics for the two extrinsic variables used in the main random forest model, ANPP (19) and human impact (1), within the geographic range of each species. We

used the zonal statistics tool to overlay each species' range on top of the extrinsic variable raster dataset and counted pixels that fell within each range. We then used this tool to calculate mean values of ANPP and human impact experienced by each marine mammal species.

Our map of species at risk was created by overlapping geographic ranges of marine mammal species identified as at risk by our model and those on the Red List, and then by counting how many of these species were found in each spatial grid cell (Fig. 2). Hotspots were defined as grid cells ≥ 75 th percentile of at-risk species, which corresponds to about 2% of all geographic grid cells (Figs. 3 and 4). Hotspot cutoff values near 2% have been used widely in both marine and terrestrial conservation studies (12, 54, 55). Note that marine mammals occurring in rivers and lakes were not included in our risk maps because the extrinsic data for the marine and freshwater environments are not comparable. Also, included in our maps were five species not predicted by our main model, but listed by the IUCN as Vulnerable (i.e., at risk) (Table S1).

We created maps on the geographic distribution of species richness, environmental variables, and MPAs to understand how they relate to the distribution of risk. Our map of species richness was similar to those produced elsewhere (especially ref. 12) and was created by overlapping the geographic ranges of all marine mammal species and counting how many

species occur in each spatial grid cell. Our map of ANPP was based on Oregon State University's map of ocean productivity (19), and our maps of human impacts were obtained from Halpern et al. (1). We measured correlation of risk with richness and ANPP and used the zonal statistics tool to calculate the mean human impact index (1) within each hotspot (Fig. 55). Note that data on commercial fishing are based on 2008 values (1) (Fig. 4A). Because fishing impacts are highly variable over time and space, the map showing global distribution of fishing impacts may not accurately reflect present or future impacts and should be interpreted cautiously (Fig. 4A).

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Supporting Information

Davidson et al. 10.1073/pnas.1121469109

SI Materials and Methods

Database. We compiled a database for 125 extant marine mammal species (out of 128) for which we had sufficient trait data. Our database included the following intrinsic predictor variables: adult body mass, body mass at weaning, number of births per year, number of offspring per reproductive bout, geographic range size, social group size, trophic group (herbivore, carnivore, omnivore), habitat (coastal, oceanic), foraging location (continental shelf, continental slope, epipelagic, mesopelagic/bathypelagic zones), taxonomic group [(i) otters (*Mustelidae*) and polar bears (*Ursidae: Ursus maritimus*), (ii) baleen whales (*Mysticeti*), (iii) toothed whales (*Odontoceti*), (iv) eared seals (*Otariidae*) and walrus (*Odobenidae: Odobenus rosmarus*), (v) true seals (*Phocidae*), and (vi) sea cows (*Sirenia*)]; diet breadth (generalist, specialist), and migratory behavior (migratory or not) (1–22). We also gathered data on the following extrinsic variables: mean annual net primary production (ANPP) (23) for the year 2006 and mean human impact index (24) within each species' geographic range. For life-history traits, our model included traits that comprise the rate of mean mass-specific production at the species level, p , a key measure of the speed of life history, where $p = (m_w/m_A) \cdot l \cdot n$, where m_A is adult body mass, m_w is offspring weaning mass, l is litter size, and n is number of births per year (25). We used a dichotomous response variable to represent extinction risk: species classified as Vulnerable, Endangered, Critically Endangered, or Extinct by the International Union for the Conservation of Nature (IUCN) Red List were considered “threatened,” and Near Threatened and Least Concern species were considered “non-threatened” (1).

The IUCN lists threatened (Vulnerable or higher) mammal species under four criteria (11): (i) criterion A—species listed because of recent population declines; (ii) criterion B—species listed simply because of limited geographic occurrence, regardless of population status; (iii) criterion C—species listed because of low abundance (2,500 individuals) resulting from ongoing population declines; and (iv) criterion D—species listed because of extremely low abundance (250 individuals). To avoid potential circularity in models evaluating extinction risk, similar studies have excluded threatened species listed under criterion B because of their restricted geographic ranges (26–28). In this paper, there was no need to exclude species listed under criterion B because none of the marine mammals listed as threatened were listed solely under this criterion. Some studies have restricted their analysis of threatened species to those listed only under criterion A (i.e., they have excluded species under criteria B, C, and D) (29–31). We included species listed under criteria C and D because we used the area of historic geographic range in our models (*ca.* past 100 y) (12, 32), and we did not include data on population density (geographic range and population density are the two key components of species abundance). By doing so, our models avoid any potential circularity with IUCN listing criteria.

Our Modeling Approach. Following methods used by Davidson et al. (27), we used the randomForest package in R version 1.10.1 to build random forest models of 500 classification trees and test for quantitative relationships between predictor variables and extinction risk (33–35). The models provided predictions of marine mammal species threat status (Table S1) and determined the relative importance of predictor variables. For our main random forest model (Fig. 1), we included only those species that occur in the marine environment. Species found solely in

rivers or lakes were excluded from the model because we were unable to obtain extrinsic data on ANPP and human impacts that were comparable with those of the marine system (24, 36).

However, to provide predictions of threat status for freshwater species as well, we ran a separate random forest model with only intrinsic variables for all species (freshwater and marine) to predict risk in freshwater species. The intrinsic variables included were the same as those in the main model (Fig. 1), only the extrinsic variables of ANPP and human impact were excluded from this intrinsic model. We also predicted risk for Data Deficient species (Table S1). To do this, we used the main random forest model to predict risk in Data Deficient marine species and used the intrinsic model to predict risk in Data Deficient freshwater species. The intrinsic model was comparable in accuracy to the main model because the extrinsic variables were not especially strong predictors of risk.

Random forest metrics. Predictor importance was measured by the decrease in classification accuracy resulting from removal of the focal variable from the model (35, 37). Pairwise z -tests on the mean importance of each predictor across all 500 trees were used to identify significant differences between predictors. We quantified overall model accuracy using the percentage of species correctly classified, specificity (percentage of non-threatened species correctly classified), and sensitivity (percentage of threatened species correctly classified) (33) (Table S2). We also used Cohen's kappa statistic [function kappa2 in R package irr (38)] to measure the agreement between predicted and actual categorizations while correcting for agreement due to chance (33, 39) (Table S2). Misclassification costs (false positives and false negatives) were equally weighted in our models.

Predictive accuracy of random forest models. Our modeling is based on the best species-level information currently available, but basic ecological knowledge of marine mammals remains sparse. The random forest model helps overcome this limitation by interpolating missing values, allowing for the inclusion of all species in the analysis. Random forest models, which combine the predictions of many independent decision-tree models into a robust composite model, have among the highest predictive accuracies of current machine-learning techniques, and machine-learning approaches in general are proving to have greater predictive accuracies than linear modeling approaches (33, 39–44).

Phylogenetic relationships. Although extinction risk often is not phylogenetically random, and species traits are the product of shared evolutionary history, decision tree models identify the observed relationships between predictors and extinction risk and are not designed to test evolutionary hypotheses (40, 45, 46). Decision trees, including random forest models, are non-parametric techniques that are viable alternatives to linear models with phylogenetic contrasts (40, 46, 47). Nevertheless, to capture the importance of phylogeny, we included taxonomic group as a variable in our random forest models.

Spatial Analyses. We obtained the extrinsic variables of ANPP of the world's oceans from Oregon State University (23), and human impact data from Halpern et al. (24). The ANPP dataset was at a spatial resolution of one-twelfth decimal degree in an equidistant cylindrical projection, whereas the human impact dataset had ~1-km resolution in the World Geodetic System 1984 Mollweide projection.

We used ESRI's ArcGIS v9.3 to calculate spatial statistics for these two extrinsic variables within the geographic range of each species. Before we applied the “zonal statistics” tool, we first

re-projected all data to a cylindrical equal area projection to prevent the distortion of the “area” property, which is critical to zonal statistics. The zonal statistics tool overlays the species range on top of the raster dataset, counts all pixels that fall into the range, and then calculates a statistical summary including minimum, maximum, range, mean, and standard deviation. Using this tool, we calculated mean values of ANPP and human impact index for each marine mammal species. These variables were used in the main random forest model.

Our map of species at risk was created by overlapping geographic ranges of marine mammal species identified as at risk by our model and those on the Red List and then by counting how many of these species were found in each spatial grid cell (Fig. 2). Note that freshwater species were not included in our maps. There were several species not predicted by our main model to be at risk, but are listed by the IUCN as Vulnerable (i.e., at risk) (Table S1). To best reflect the global geographic distribution of marine mammal species at risk, we present those species that our model predicted to be at risk, in addition to the several species that are listed by the IUCN as at risk but were not predicted to be by our model.

We created additional maps on the geographic distribution of species richness, environmental variables, and Marine Protected Areas (MPAs) to understand how they relate to the distribution of risk. The map of species richness was similar to those produced elsewhere (48, and especially ref. 49) and was created by overlapping all marine mammal species’ ranges and counting how many species were found in each spatial grid cell, whereas the map of ANPP was based on ref. 23 (Fig. S4). We used a Pearson’s correlation analysis to evaluate the relationship of risk with rich-

ness and ANPP. So that all raster datasets would be in the same projection and spatial resolution for the correlation analysis, each dataset was reprojected into cylindrical equal area projection, and the risk and richness datasets were resampled to match the lowest resolution grid, the ANPP dataset.

Next, on the basis of the species-level risk predictions from our main model along with the Red List, we created maps showing the global hotspots of marine mammal extinction risk (Figs. 3 and 4). Hotspots were defined as the top 2% of geographic grid cells containing the most at-risk species (areas containing six or more at-risk species). Globally, marine grid cells contained from 0 to 11 at-risk marine mammal species; cells with six or more at-risk species represent the 75th percentile of at-risk marine mammal richness. Hotspot cutoff values near 2% have been used previously in both marine and terrestrial conservation studies (49–51).

Mean human impact index (24) was then calculated within each hotspot in ArcGIS v9.3 (Fig. S5). Data on specific impacts of humans within risk hotspots also were gathered from Halpern et al. (24). These included commercial fishing (cumulative impact of five different types of commercial fishing, sum with equal weighting for each fishing type), shipping and pollution at sea, and recent sea-surface temperature anomalies reflecting observed climate changes. Data on commercial fishing were based on 2008 data (24) (Fig. 4A). Because fishing impacts are highly variable over time and space, the map showing global distribution of fishing impacts may not be representative of present or future impacts and should be interpreted with this in mind (Fig. 4A). Data on MPAs were obtained from the World Database on Marine Protected Areas (52) (Fig. 4D).

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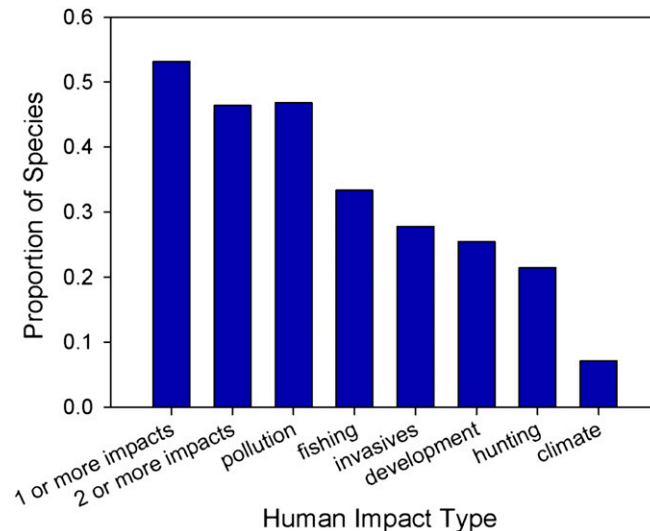


Fig. S1. Proportion of marine mammal species affected by the primary human impacts on the world's oceans, based on the IUCN Red List's Global Mammal Assessment 2008.

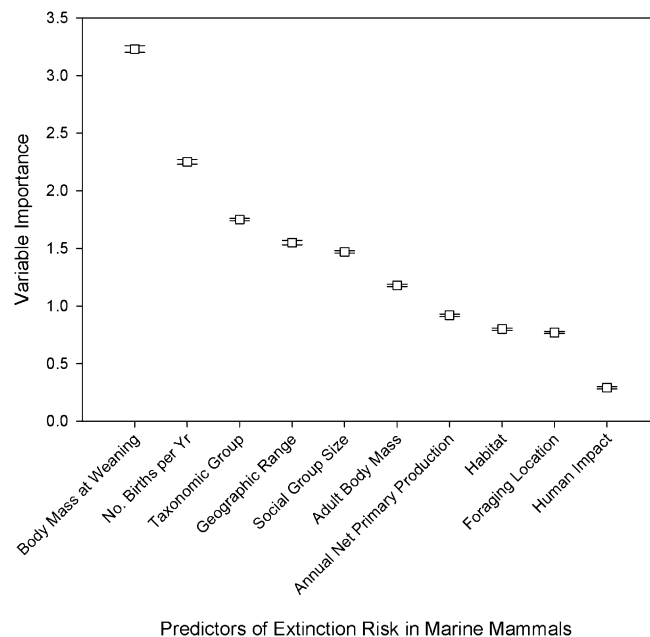


Fig. S2. Relative importance, in rank order, of intrinsic and extrinsic predictors of marine mammal extinction risk. Numerical values of importance for each predictor variable were calculated as the decrease in classification accuracy after predictor removal in a random forest of 500 trees. Variables that did not improve accuracy were not included in the final model. Differences in importance between predictors were quantified with pairwise two-tailed z-tests ($\alpha = 0.05$), and these indicated that each predictor was significantly more important than the one below it, except between "Habitat" and "Foraging Location."

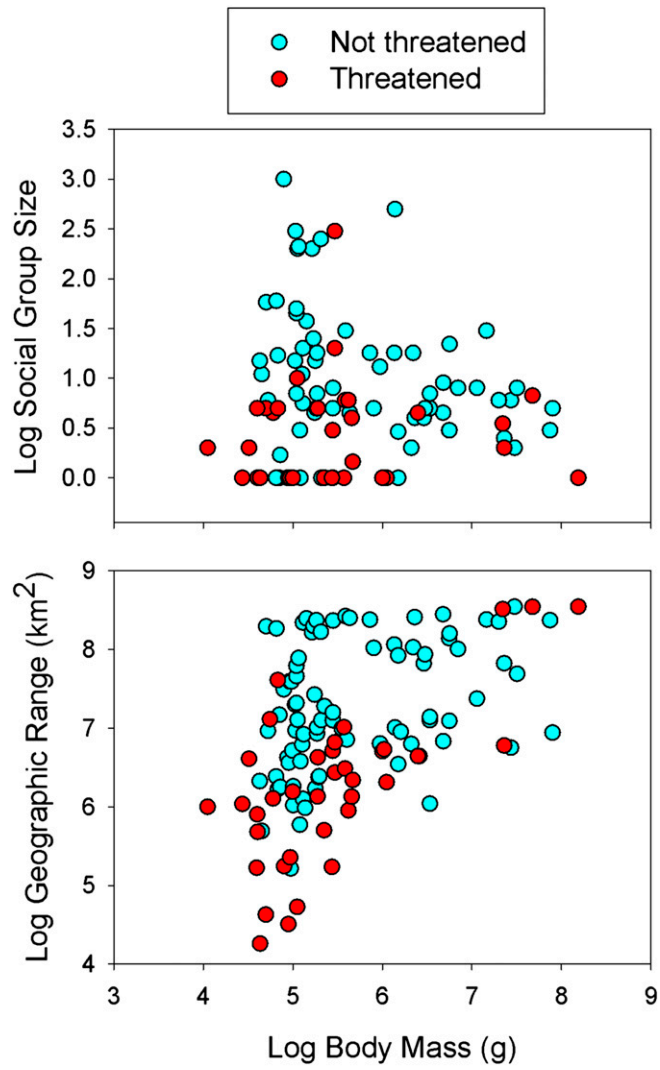


Fig. 53. Bivariate plots of geographic range and social group size as a function of body mass in marine mammals, showing that species with small geographic ranges and small social group sizes for their body size are most at risk.

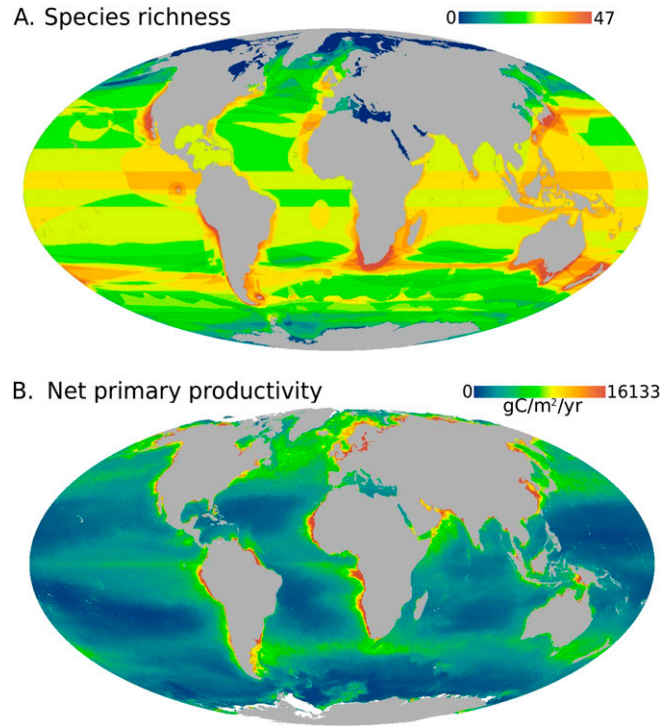


Fig. S4. Global distributions of (A) marine mammal species richness and (B) mean annual net primary productivity of the oceans (23).

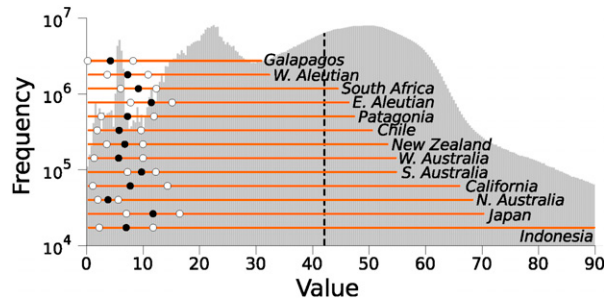


Fig. S5. Global distribution of human impact index on the world’s oceans (gray area; median value shown by black dashed line) (24), and the distribution of human impact index within identified hotspots of risk for marine mammals (horizontal orange lines). White circles show the 25th and 75th percentiles and black circles show median values of human impact within each hotspot.

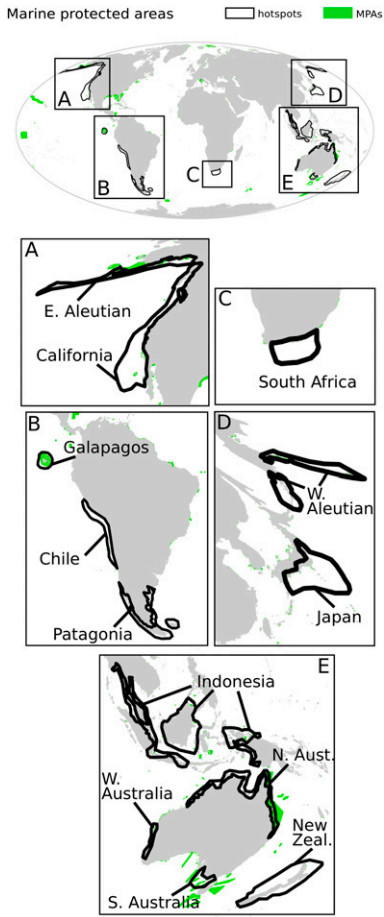


Fig. S6. Thirteen hotspots of marine mammal species extinction risk, overlaid with the world distribution of Marine Protected Areas (52). Hotspots show the top 2% of geographic grid cells for at-risk species (model predictions plus IUCN Red Listed species). Panels A–E provide a magnified view of hotspots and their relative location to MPAs.

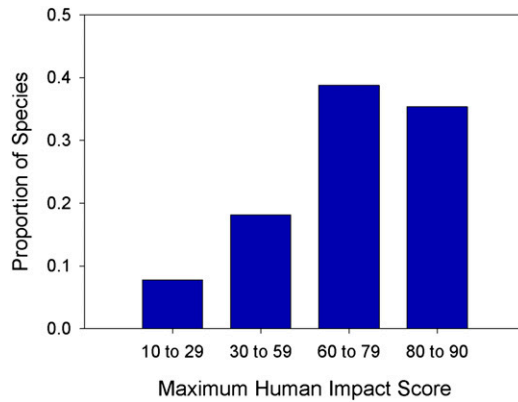


Fig. S7. Distribution of maximum human impact scores (24) within the geographic ranges of each marine mammal species.

Table S1. Species at risk and their associated IUCN Red List status

Order	Family	Common name (Latin binomial)	IUCN Red List
Cetacea	Iniidae	Baiji (<i>Lipotes vexillifer</i>)	CR
Carnivora	Phocidae	Mediterranean monk seal (<i>Monachus monachus</i>)	CR
Carnivora	Phocidae	Hawaiian monk seal (<i>Monachus schauinslandi</i>)	CR
Cetacea	Phocoenidae	Vaquita (<i>Phocoena sinus</i>)	CR
Cetacea	Balaenopteridae	Antarctic minke whale (<i>Balaenoptera bonaerensis</i>)	DD
Cetacea	Balaenopteridae	Bryde's whale (<i>Balaenoptera edeni</i>)	DD
Cetacea	Ziphiidae	Baird's beaked whale (<i>Berardius bairdii</i>)	DD
Cetacea	Delphinidae	Commerson's dolphin (<i>Cephalorhynchus commersonii</i>)	DD
Cetacea	Iniidae	Boto (<i>Inia geoffrensis</i>)	DD
Cetacea	Delphinidae	Peale's dolphin (<i>Lagenorhynchus australis</i>)	DD
Cetacea	Ziphiidae	Andrew's beaked whale (<i>Mesoplodon bowdoini</i>)	DD
Cetacea	Ziphiidae	Hubbs' beaked whale (<i>Mesoplodon carlhubbsi</i>)	DD
Cetacea	Ziphiidae	Hector's beaked whale (<i>Mesoplodon hectori</i>)	DD
Cetacea	Ziphiidae	Perrin's beaked whale (<i>Mesoplodon perrini</i>)	DD
Cetacea	Ziphiidae	Pygmy beaked whale (<i>Mesoplodon peruvianus</i>)	DD
Carnivora	Odobenidae	Walrus (<i>Odobenus rosmarus</i>)	DD
Cetacea	Ziphiidae	Shepherd's beaked whale (<i>Tasmacetus shepherdi</i>)	DD
Carnivora	Otariidae	Galápagos fur seal (<i>Arctocephalus galapagoensis</i>)	EN
Cetacea	Balaenopteridae	Sei whale (<i>Balaenoptera borealis</i>)	EN
Cetacea	Balaenopteridae	Blue whale (<i>Balaenoptera musculus</i>)	EN
Cetacea	Balaenopteridae	Fin whale (<i>Balaenoptera physalus</i>)	EN
Cetacea	Delphinidae	Hector's dolphin (<i>Cephalorhynchus hectori</i>)	EN
Carnivora	Mustelidae	Sea otter (<i>Enhydra lutris</i>)	EN
Cetacea	Balaenidae	North Pacific right whale (<i>Eubalaena japonica</i>)	EN
Carnivora	Otariidae	Steller sea lion (<i>Eumetopias jubatus</i>)	EN
Carnivora	Mustelidae	Marine otter (<i>Lontra felina</i>)	EN
Carnivora	Otariidae	Australian sea lion (<i>Neophoca cinerea</i>)	EN
Cetacea	Platanistidae	South Asian river dolphin (<i>Platanista gangetica</i>)	EN
Carnivora	Otariidae	Galápagos sea lion (<i>Zalophus wollebaeki</i>)	EN
Sirenia	Dugongidae	Steller's sea cow (<i>Hydrodamalis gigas</i>)	EX
Carnivora	Phocidae	Caribbean monk seal (<i>Monachus tropicalis</i>)	EX
Carnivora	Otariidae	Japanese sea lion (<i>Zalophus japonicus</i>)	EX
Carnivora	Phocidae	Northern elephant seal (<i>Mirounga angustirostris</i>)	LC
Carnivora	Phocidae	Baikal seal (<i>Pusa sibirica</i>)	LC
Carnivora	Otariidae	Northern fur seal (<i>Callorhinus ursinus</i>)*	VU
Carnivora	Phocidae	Hooded seal (<i>Cystophora cristata</i>)*	VU
Sirenia	Dugongidae	Dugong (<i>Dugong dugon</i>)	VU
Cetacea	Phocoenidae	Finless porpoise (<i>Neophocaena phocaenoides</i>)*	VU
Cetacea	Delphinidae	Irrawaddy dolphin (<i>Orcaella brevirostris</i>)*	VU
Carnivora	Otariidae	New Zealand sea lion (<i>Phocarctos hookeri</i>)	VU
Cetacea	Physeteridae	Sperm whale (<i>Physeter macrocephalus</i>)	VU
Cetacea	Iniidae	Franciscana (<i>Pontoporia blainvillei</i>)	VU
Cetacea	Delphinidae	Atlantic humpbacked dolphin (<i>Sousa teuszii</i>)	VU
Sirenia	Trichechidae	South American manatee (<i>Trichechus inunguis</i>)	VU
Sirenia	Trichechidae	West Indian manatee (<i>Trichechus manatus</i>)	VU
Sirenia	Trichechidae	West African manatee (<i>Trichechus senegalensis</i>)	VU
Carnivora	Ursidae	Polar bear (<i>Ursus maritimus</i>)*	VU

CR (Critically Endangered), DD (Data Deficient), EN (Endangered), EX (Extinct), LC (Least Concern), VU (Vulnerable) (1) are terms from the Global Mammal Assessment (2008).

*All species listed are predicted to be at risk according to our *main* model (or *intrinsic* model for freshwater species), except those with an asterisk.

1. IUCN (2001) *IUCN Red List of Threatened Species: Categories and Criteria (version 3.1)* (IUCN/SSC Red List Programme, Gland, Switzerland).

Table S2. Accuracy measures for the *main* random forest model predicting threat status in marine mammal species ($n = 116$)

Metric	Value (%)
PCC	91.67
Specificity	97.87
Sensitivity	80.00
Error rate	08.33
Cohen's kappa (P value)	0.803 (<0.0001)

"PCC" denotes percentage correctly classified. "Specificity" is the percentage of non-threatened species correctly classified. "Sensitivity" is the percentage of threatened species correctly classified. "Cohen's kappa" is a measure of the agreement between predictions and actual values, corrected for agreement due to chance alone; kappa was highly significant, indicating a very low probability that agreement can be attributed to chance.