Title: Ship collision risk threatens whales across the world's oceans

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Abstract: Following the near-complete cessation of commercial whaling, ship collisions have emerged as a primary threat to large whales, yet knowledge of collision risk is lacking across most of the world's oceans. We compiled a dataset of 435,000 whale locations to generate global distribution models for four globally-ranging species. We then combined >35 billion positions from 176,000 ships to produce a global estimate of whale-ship collision risk. Shipping occurred across 92% of whale ranges and <7% of risk hotspots contained management strategies to reduce collisions. Full coverage of hotspots could be achieved by expanding management over only 2.6% of the ocean's surface. These inferences support the continued recovery of large whales against the backdrop of a rapidly growing shipping industry.

Main Text:

Marine shipping is a massive and growing industry that presents a variety of threats to the ocean environment. With an estimated 90% of all traded goods traveling by sea in an increasingly globalized economy (*1*), shipping traffic has increased >4-fold since 1992 and is expected to grow even further in the coming decades, as maritime trade volume is projected to triple by 2050 (*2*, *3*). Some of the negative impacts that marine shipping has on ocean ecosystems include accelerating climate change (i.e. maritime shipping produces 2.89% of the world's anthropogenic greenhouse gas emissions, on par with the global airline industry (*4*)), causing chemical and noise pollution (*5*), spreading invasive species (*6*), and causing behavioral disturbance for marine life (*7*). One of shipping's most pernicious impacts is direct collisions with wildlife (*8*).

Collisions with ships (i.e., ship-strikes) are a major source of mortality for whales across the planet (*8*, *9*). Large whales play critical roles in marine ecosystems, including top-down and bottom-up forcing of marine food webs, cycling and transferring nutrients, and provisioning of detrital energy to deep sea species (*10*, *11*). They are also culturally, spiritually, and economically important for people around the world (*12–14*). These species are highly vulnerable, with most populations of large whales at a fraction of their historical abundances following the industrial whaling era (*15*). Ship-strikes are now a serious threat to whales, causing higher rates of mortality than are legally permissible from anthropogenic sources for some populations (*16*), contributing to the decline of critically endangered species (*17*), and occurring in all oceans (*9*, *18*). However, whale-ship collisions largely go unobserved and unreported, even in areas of high potential risk (*18*, *19*). Interventions to reduce whale-ship collisions, including reducing vessel speeds and changing vessel routings (*20*), depend on an accurate understanding of patterns in ship-strike risk. Despite a growing number of regional studies [e.g. (*16*, *21–24*)], the spatial distribution of ship-strike risk remains undescribed across the majority of the world's oceans, which is a critical impediment to scaling up effective solutions. Understanding the spatial dynamics of this problem at the global scale – at which both the shipping industry operates and whales migrate and inhabit the oceans – is essential, as transboundary and multinational efforts will be needed to mitigate this threat.

Robust global characterization of ship-strike risk to whales is now possible due to two recent technological advances. First, the increasing volume and accessibility of Automatic Identification System (AIS) data have made it possible to generate high-resolution maps of the global spatial footprint of marine shipping (*25*) and quantify exposure to vessels at locations where species are observed [e.g., (*26*, *27*)]. Second, advances in species distribution modeling allow for the integration of diverse data types and sources, supporting predictive species distribution modeling across larger geographic scales (*28*). This makes it possible to characterize whale distributions globally, which has until now proven difficult due to challenges in collecting and integrating data across remote and dynamic pelagic habitats, but is essential for understanding collision risk.

Here we present a global assessment of ship-strike risk to large whales, drawing from 435,370 records of whale locations from hundreds of datasets (Figs. S1-S5) and AIS vessel location data for 175,960 large vessels. We first developed global integrated species distribution models for four globally-ranging whale species among the most at-risk from ship-strikes yet for whom risk is unknown across large extents of their ranges (*9*): blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), and sperm whales (*Physeter macrocephalus*) (Fig. 1A, Fig. S6-S13, Movies S1-S4, Table S1). We then combined whale distributions with shipping-traffic AIS data (Fig. 1B) to calculate ship-strike risk (Fig. 2), identify risk hotspots for each species (Fig. 3), evaluate coverage of current ship-strike management efforts, and quantify how risk changes across jurisdictional and protection boundaries (i.e., exclusive economic zones and marine protected areas; Fig. 4). This work draws attention to the pervasive scale of ship-strike risk and exposure to other shipping-related impacts such as noise pollution, and provides a forward-looking roadmap to support the continued recovery of the great whales.

Global patterns of ship-strike risk to whales

We find that whales are at risk of ship-strikes across the world's oceans, with 91.5% of all grid cells within focal species' ranges containing large vessel activity (Fig. 1B&C, Fig. 2). Within each of the blue, humpback, and sperm whale ranges (defined by the International Union for the Conservation of Nature), large vessels traveled the equivalent of over 4,600 times the distance to the moon and back each year, and within the smaller range of fin whales, vessels traveled more than 2,600 times that distance. We calculated the extent of the ocean that has risk levels equivalent to or higher than our estimate of risk in the California Current Ecosystem, an exceptionally well-studied region where ship-strike mortality rates for three of our focal species are estimated to greatly exceed the legal removal limits (*16*, *29*). Over 15% of the area of the world's oceans has risk levels equivalent to this region (Fig. 1C, Fig. S14), demonstrating that ship-strike risk is a major threat capable of producing high rates of whale mortality across all oceans.

All ocean regions contained substantial ship-strike risk to each species (Fig. 2, Fig. S15). Hotspots, defined as grid cells with the top 1% of ship-strike risk, occurred in all regions besides the Southern Ocean (Fig. 3, Figs. S16-S18). Hotspots were mostly concentrated around continental coastlines (Fig. 3, Fig. S16), but high levels of risk were also found in some open ocean areas (e.g., the Azores) for blue, fin, and sperm whales (Fig 1C, Fig 2, Fig. S16). This highlights that while coastal regions have received the most study, ship-strike risk is high anywhere shipping routes intersect with key habitat or migratory corridors (*30*) and is not limited to coastlines. The Indian Ocean, western North Pacific Ocean, and Mediterranean contained the highest percentages of risk hotspots across all species (21.6%, 14.5%, and 13.3%, respectively), with high levels of risk also found in regions in the eastern North Pacific Ocean, North and South Atlantic Oceans, South Pacific Ocean, and the South China and Eastern Archipelagic Seas (Fig. 2, Fig. S18). The Arctic Ocean contained a very small percentage of hotspots (0.56%), and the Southern Ocean was the only region that did not contain any ship-strike hotspots due to low levels of shipping despite high whale space-use (Fig. 1C, Fig. 2, Fig. S17).

Some hotspots were shared across multiple species, with 19.8% of hotspots impacting two species, 4.69% impacting three, and 0.09% impacting all four (Fig. 3A). Multispecies hotspots were distributed along coastlines of all continents except Antarctica, with most occurring in the North Pacific Ocean. A substantial number of multispecies hotspots also occurred in the Indian, western South Pacific, eastern North Atlantic, and South Atlantic Oceans (Fig. 3). This highlights the value in considering a multispecies approach to ship-strike risk mitigation, as multispecies risk hotspots represent areas where mitigation measures based on reduced speed could be most effective and measures based on changing ship routings may need to take distribution of multiple species into account.

The International Whaling Commission (IWC), the intergovernmental organization charged with whale conservation and management, has compiled a list of high-ship-strike-risk areas based on previous local- and regional-scale analyses (Fig. S19) (*9*). These areas are evident in our global ship-strike risk estimates, including Sri Lanka and the eastern North Pacific for blue whales, Panama and the Arabian Sea for humpback whales, the Canary Islands for sperm whales, and Mediterranean areas for fin and sperm whales (Fig. 2, Fig. 3, Fig. S16). Our analysis also identifies regions of high ship-strike risk that have received less recognition and study, including the Azores, multiple regions along the South American coastline (e.g., the coasts of Brazil, Chile, Peru, and Ecuador), and the coast of southern Africa (e.g., the coasts of Namibia, South Africa, Mozambique, and Madagascar, Fig. 2, Fig. S16). These knowledge gaps reflect the need for additional regional studies examining whale ship-strikes, particularly in the Global South. Downscaled regional whale models populated more strongly by locally-collected data will be essential for interrogating patterns of risk at higher resolutions and informing localized mitigation efforts in these understudied regions [e.g. (*31*)].

Our analysis underscores the importance of preserving areas with high whale space use but low shipping traffic, which were identified at high latitudes in the Arctic and Southern Oceans (Fig. 1C, Fig. S20). High-whale, low-shipping areas can be considered relative spatial refugia for whales from collision risk, noise pollution, and other detrimental impacts of the shipping industry (*5*). However, it is important to note that whales are not completely free from the impacts of shipping even in these waters, as ship-strikes have been reported in both regions (*18*). Climate change will also alter these dynamics at northern latitudes due to changes in whale distributions and shipping traffic. Declining sea ice in the Arctic is expected to open new trade routes and increase vessel traffic, which combined with projected northward shifts in whale distributions driven by the same reductions in sea ice extent alongside whales tracking preferred sea surface temperatures, will likely result in higher rates of whale-ship collisions (*32*, *33*). Polar waters will also experience climate change-driven ecosystem changes that will likely be detrimental to many whale species and may compound the threats posed by shipping and ship-strikes (*34*, *35*).

Our analysis additionally predicts high ship-strike risk off the coasts of China, Japan, and the Republic of Korea. Our dataset included limited whale sightings and research effort from these regions (Fig. S1-S5) with contemporary space-use patterns of our focal species in those areas remaining unclear (though see (*36*, *37*) for fin and humpback whales). However, whaling records indicate that these regions were used historically by these species, suggesting that they may be suitable habitat that is currently unutilized by some species due to the legacy of intense whaling pressure (*38*, *39*). If whale populations continue to recover, populations may increase in areas of historical whale importance – thus, regions with high levels of shipping traffic and high predicted ship-strike risk, yet limited contemporary whale sightings, remain important areas to monitor pending continued recovery.

Most ship-strike risk hotspots do not have mitigation measures in place

The majority of predicted ship-strike hotspots, even defined conservatively as the top 1% of ship-strike risk (Table S2), lack any current management efforts aimed at reducing collisions. Reducing vessel speeds, which has been shown to reduce the probability that whale-ship collisions will occur as well as the lethality of vessel strikes (*40*), and routing vessels to avoid important whale habitat are the primary proposed ship-strike mitigation methods (*20*, *41*). The World Shipping Council collated existing ship-strike management measures across the globe (*42*). We digitized vessel speed reduction zones (including voluntary or mandatory zones that were spatially static and had a specific speed limit) and routing measures (including voluntary or mandatory area closures aimed at preventing ship-strikes) to evaluate whether hotspots intersected a ship-strike management measure (Fig. S21). We found that virtually no ship-strike risk hotspots were protected by mandatory measures (Fig. 3, Fig. S22; 0.54% of hotspots for blue whales, 0.27% for humpback whales, and 0% for fin and sperm whales). When voluntary measures were also considered, fewer than 7% of hotspots contained any management intervention for each species: 4.05% of hotspots for blue whales, 4.25% for fin whales, 4.52% for humpback whales, and 6.67% for sperm whales. Calculating the area of hotspots that currently lack any management efforts (either mandatory or voluntary) reveals that implementing vessel speed reduction zones over an additional 2.60% of the ocean's surface would be sufficient to reduce risk in all ship-strike risk hotspots, and expanding only over 0.58% would reduce risk in all multispecies hotspots (Fig. S21B&C). While mandatory management measures are uncommon, they are likely more effective at reducing whale mortalities than voluntary programs (*43*), so expanding mandatory measures may be particularly impactful and should be considered an important piece of management portfolios.

Regional levels of hotspot protection varied substantially, and there were often mismatches between predicted risk hotspots and areas with management measures (Fig. 3I). The highest rates of regional protection were in the eastern North Pacific Ocean, with 44.1%, 41.4%, and 27.5% of humpback, blue, and fin whale hotspots protected, and the Mediterranean region exhibited the highest regional protection rate for sperm whales (17.7%). With the exception of a high regional protection rate for the very few blue whale hotspots in the western North Atlantic, all other regions exhibited very low regional protection rates (Fig. 3I). For example, the Indian Ocean contained the majority of ship-strike hotspots for blue whales, but <1% overlapped with a management measure. Similarly, several regions contained relatively high proportions of species' hotspots but none that intersected with any management measures, including the Indian Ocean, eastern South Atlantic, and South Pacific for fin whales, the western North Pacific for humpback whales, and the North Atlantic for sperm whales. These results reflect the fact that there are entire regions that lack any ship-strike-related management efforts for the species considered here, such as the South American coastlines and the coast of southern Africa (Fig. 3A,F,G). This highlights the widespread opportunities for expanding ship-strike mitigation programs, which can confer important co-benefits beyond whales. For example, slow-speed measures result in reduced air pollution (which negatively impacts human health and is often high around ports, (*44*)), greenhouse gas emissions (*45*), and underwater noise pollution (*46*). Implementing vessel speed reduction programs can thus be a win-win-win for marine species, the climate, and public health (*41*).

The international nature of the shipping industry as well as the cosmopolitan nature of whale migrations and space use pose challenges for implementing mitigation efforts. However, risk was higher within exclusive economic zones compared to the high seas (Fig. 4A) and exclusive economic zones contained nearly all risk hotspots (98.1% of blue whale hotspots, 95.8% for fin whales, 100% for humpback whales, 97.6% for sperm whales). Within exclusive economic zones, countries have exclusive jurisdiction over marine resources and can propose changes in vessel operations, including speed reductions and routing changes, to the International Maritime Organization (*20*). Thus, this result indicates that ship-strike risk could largely be addressed with national proposals and resulting regulation rather than through international mandates necessary for high seas conservation. In addition, the majority of marine protected areas do not currently include any ship-strike management measures (*42*) and risk was higher within compared to outside marine protected areas for most regions (Fig. S23) – indicating that including speed restrictions could be a pathway for marine protected areas that contain risk hotspots to more fully meet mandates to protect biodiversity and marine resources. Because all large whales are transboundary species, international coordination across neighboring countries that share adjacent ship-strike hotspots is essential to effectively protect whale populations across their migratory routes and ensure that management in one area does not lead to unintended spillover of shipping traffic to other sensitive areas (*47*, *48*).

Conclusions

Whales experience high ship-strike risk across large extents of the world's oceans – and the majority of high-risk areas lack management efforts aimed at mitigating this issue. Ship-strike management measures, such as vessel speed reductions and changes in vessel routings, must be urgently expanded to conserve and recover the great whales. This is especially important in the many regions that have received less research attention and lack ship-strike management efforts, including regions along the South American coastlines and the coast of southern Africa, and for whale populations that are struggling to recover, such as Arabian Sea humpback whales. Our study highlights that expanding management efforts over only an additional 2.6% of the ocean would protect the highest-risk areas, and could largely be accomplished through changing regulations within pre-existing management boundaries. Moving forward, there is also an urgent need to expand and support country-led long-term monitoring of shipping lanes to improve ship-strike reporting (*18*, *19*), implement effective enforcement of management measures, and ensure management efforts are adaptive to future changes in whale and shipping distributions.

Our study opens several new doors for understanding threats to highly-mobile species on our changing planet. First, the shipping industry is the largest source of anthropogenic ocean noise, which negatively impacts whales through behavioral disruption, alteration of communication, and increased stress (*5*, *49*). While underwater noise propagation is a complex process that depends on bathymetry and other factors, in quantifying whale-ship overlap, our analysis also sheds light on areas where whales are likely to be exposed to higher levels of noise pollution. As vessels typically emit less noise when traveling at slower speeds, vessel speed reductions can often reduce both ship-strike risk and noise pollution (*41*, *46*). Additionally, our species distribution models can be used to quantify large whale exposure to other important anthropogenic threats, including entanglement with fishing gear (*50*), and predict how cetacean distributions and in turn ship-strike risk will shift with climate change. Global leaders have committed to protecting 30% of the ocean by 2030; broad-scale information on the distribution of whales and their threats is particularly timely to ensure these new protected areas are effectively placed to conserve whales. Finally, beyond the great whales, our predictive framework for integrating disparate data types to support large-scale modeling provides a roadmap for additional applications to evaluate other marine species that are threatened by the impacts of marine shipping, such as smaller cetaceans, sharks, sea turtles, and other marine mammals (*5*, *8*, *49*), thus paving the way for identifying multispecies and multitaxa hotspots. The increasing availability of biologging data makes it possible to synthesize species space-use patterns across larger geographic scales, which can shed light on species exposure to threats and inform mitigation efforts across wider extents of our planet.

Mitigating the negative environmental impacts of marine shipping is essential for the coming decades (*3*). Changes in ocean ecosystems caused by the loss of historic whale populations have been hard to reverse. Ship-strike risk is a ubiquitous yet solvable conservation challenge for large whales, and our results can provide a foundation for expanded management measures to protect these ocean giants.

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Supplementary Materials

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Materials and Methods

Figs. S1 to S23

Tables S1 to S2

References (*52–104*)

Movies S1 to S4

Data S1

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Figure 1. Spatial overlap between whales and shipping traffic. A) Average annual whale space use across blue, fin, humpback, and sperm whales. B) Global marine shipping traffic for large (>300GT) vessels, from Automatic Identification System (AIS) data from 2017-2022. The shipping traffic index weights shipping density by vessel speed on a log-scale, standardized between 0 and 1. C) Bivariate map showing the intensity of both whale space use and shipping traffic in each 1˚x1˚ grid cell.

Figure 2. Predicted global ship-strike risk at the species-level for blue, fin, humpback, and sperm whales. Ship-strike risk is the product of the shipping traffic index and the modeled whale space use index for each species. We predicted ship-strike risk across each species' range defined by the International Union for the Conservation of Nature (IUCN) with areas outside a species' range shown in white.

Figure 3. Ship-strike risk hotspots for large whales. A) The spatial overlap of ship-strike hotspots across blue, fin, humpback, and sperm whales. Hotspots were defined as the top 1% of ship-strike risk for each species. Boxes show the locations of zoomed-in panels B-H showing hotspots and management zones for B) the west coast of North America, C) the Northern Indian Ocean, D) the Mediterranean region, E) the coast of East Asia, F) the east coast of South America, G) the coast of Southern Africa, and H) the east coast of Australia. I) Regional percentages of hotspot protection (i.e., the number of hotspots that contained any management measure, either voluntary or mandatory, divided by the number of hotspots in that region) versus the percentage of total global hotspots in each region. There were no hotspots in the Southern Ocean for any species.

Figure 4. Mean predicted ship-strike risk by species within Exclusive Economic Zones (EEZs) compared to the high seas. Error bars are 95% confidence intervals and asterisks indicate significant differences ($p < 0.001$).

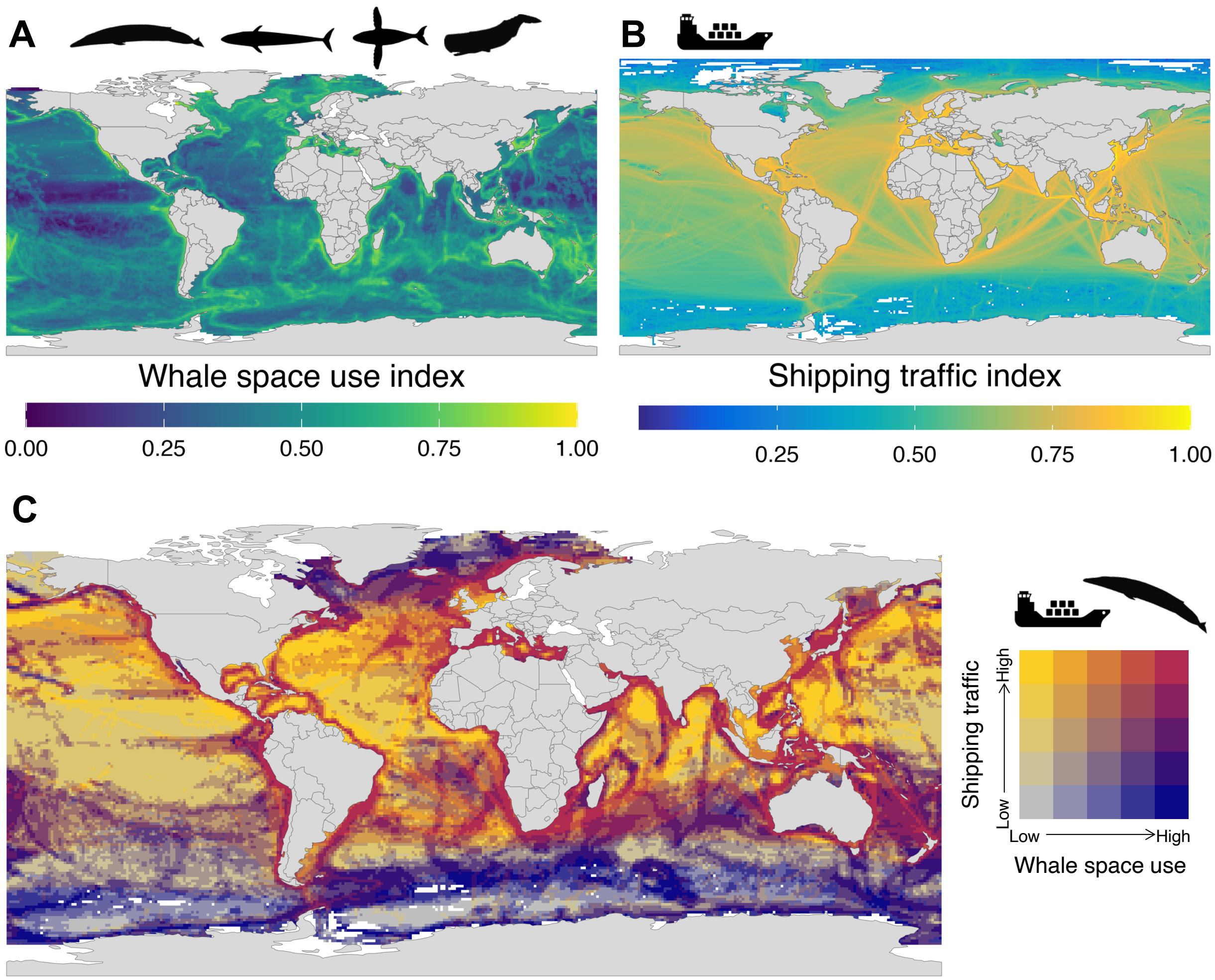

Figure 1. Spatial overlap between whales and shipping traffic. A) Average annual whale space use across blue, fin, humpback, and sperm whales. B) Global marine shipping traffic for large (>300GT) vessels, from Automatic Identification System (AIS) data from 2017-2022. The shipping traffic index weights shipping density by vessel speed on a log-scale, standardized between 0 and 1. C) Bivariate map showing the intensity of both whale space use and shipping traffic in each 1˚x1˚ grid cell.

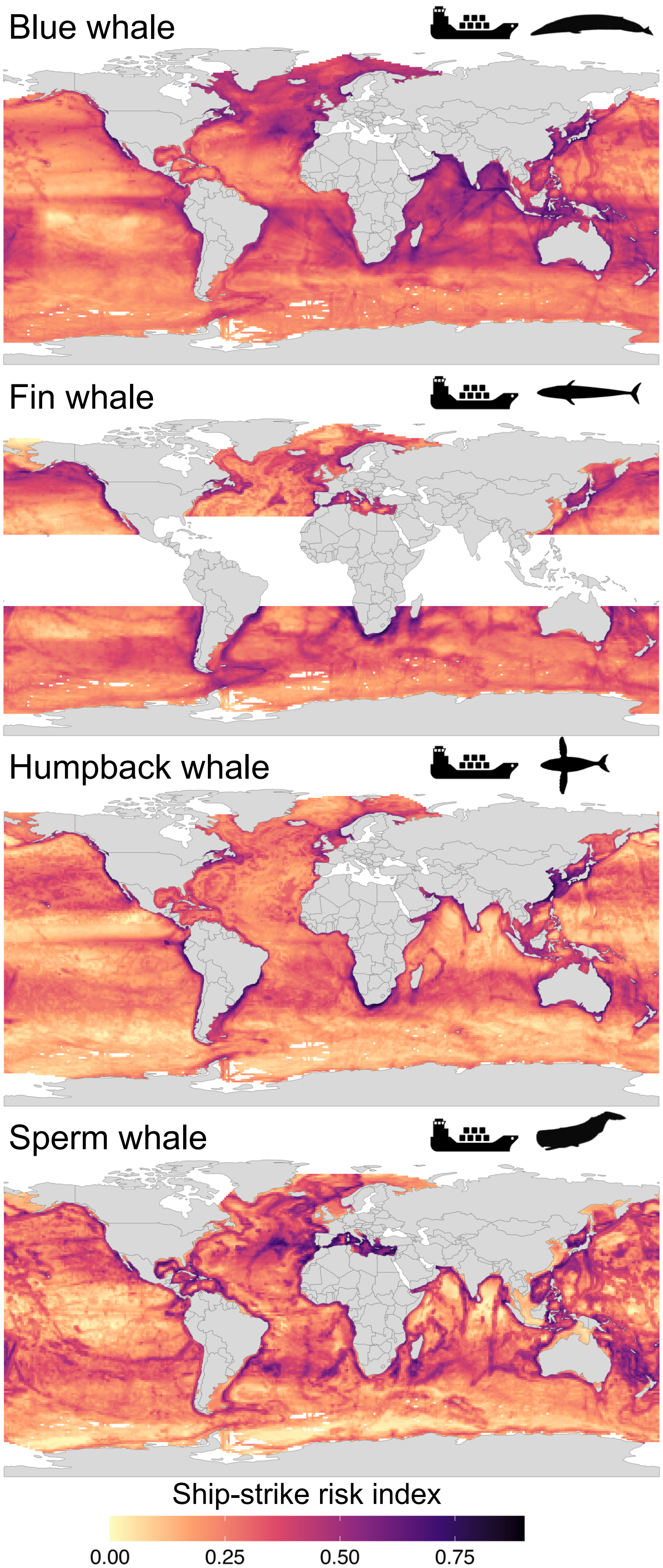
Blue whale
Fin whale
Humpback whale
Sperm whale
Ship-strike risk index
0.00
0.25
0.50
0.75

Figure 2. Predicted global ship-strike risk at the species-level for blue, fin, humpback, and sperm whales. Ship-strike risk is the product of the shipping traffic index and the modeled whale space use index for each species. We predicted ship-strike risk across each species' range defined by the International Union for the Conservation of Nature (IUCN) with areas outside a species' range shown in white.

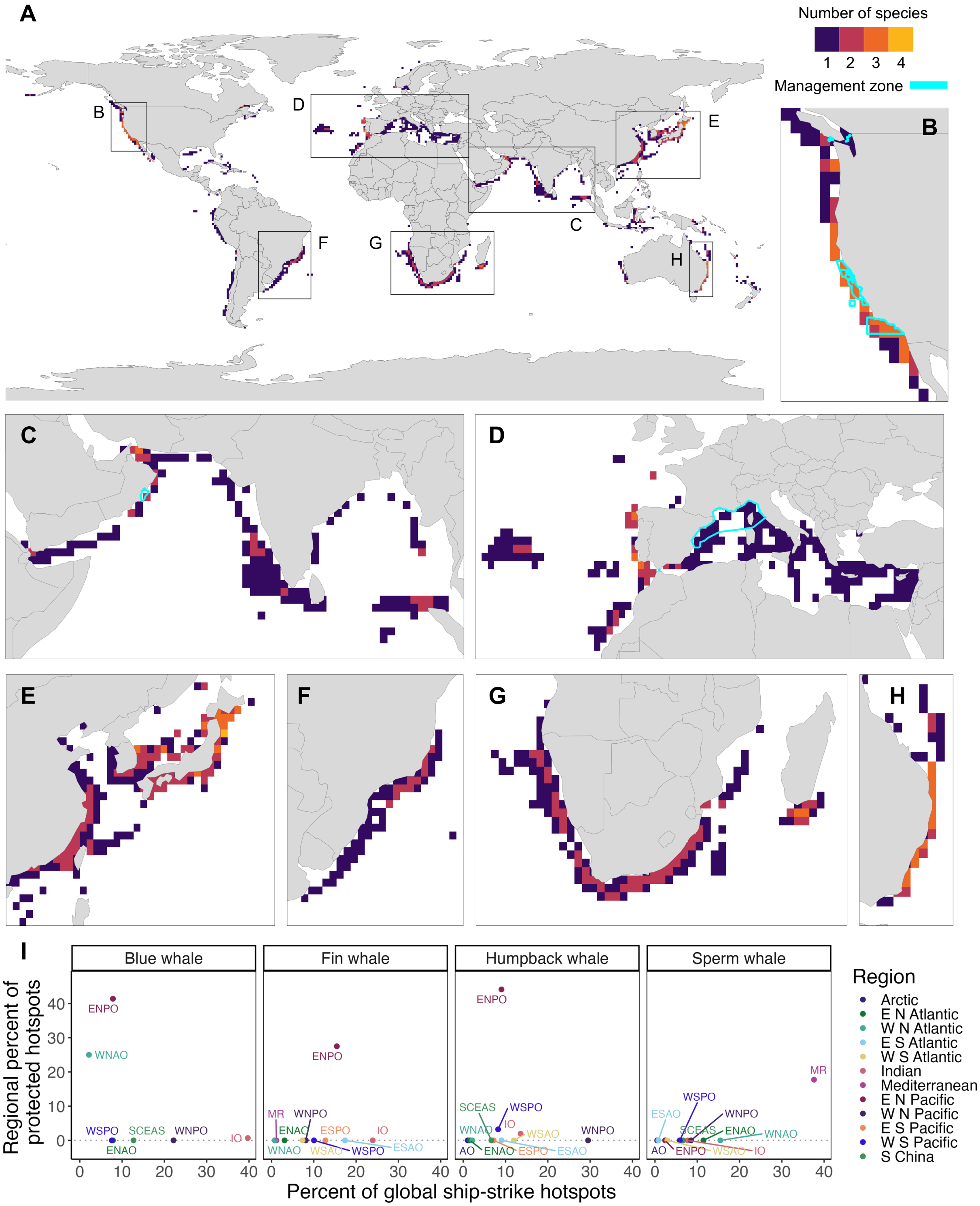

Figure 3. Ship-strike risk hotspots for large whales. A) The spatial overlap of ship-strike hotspots across blue, fin, humpback, and sperm whales. Hotspots were defined as the top 1% of ship-strike risk for each species. Boxes show the locations of zoomed-in panels B-H showing hotspots and management zones for B) the west coast of North America, C) the Northern Indian

Ocean, D) the Mediterranean region, E) the coast of East Asia, F) the east coast of South America, G) the coast of Southern Africa, and H) the east coast of Australia. I) Regional percentages of hotspot protection (i.e., the number of hotspots that contained any management measure, either voluntary or mandatory, divided by the number of hotspots in that region) versus the percentage of total global hotspots in each region. There were no hotspots in the Southern Ocean for any species.

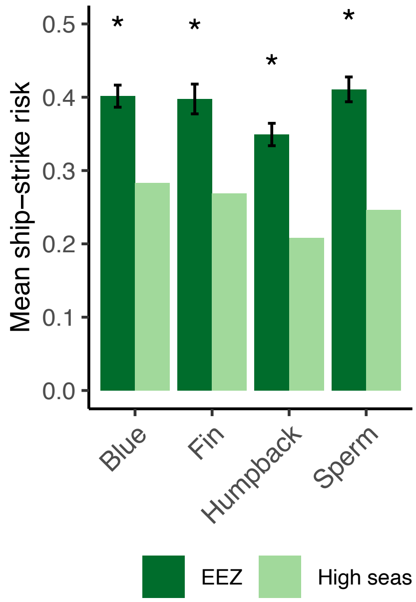

Figure 4. Mean predicted ship-strike risk by species within Exclusive Economic Zones (EEZs) compared to the high seas. Error bars are 95% confidence intervals and asterisks indicate significant differences ($p < 0.001$).

Science
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Supplementary Materials for

Ship collision risk threatens whales across the world's oceans

Anna C. Nisi, Heather Welch, Stephanie Brodie, Callie Leiphardt, Rachel Rhodes, Elliott L. Hazen, Jessica V. Redfern, Trevor A. Branch, Andre S. Barreto, John Calambokidis, Tyler Clavelle, Lauren Dares, Asha de Vos, Shane Gero, Jennifer A. Jackson, Robert D. Kenney, David Kroodsma, Russell Leaper, Douglas J. McCauley, Sue E. Moore, Ekaterina Ovsyanikova, Simone Panigada, Chloe V. Robinson, Tim White, Jono Wilson, Briana Abrahms

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This PDF file includes:

- Materials and Methods
- Figs. S1 to S23
- Tables S1 to S2
- Captions for Movies S1 to S4
- Captions for Data S1

Other Supplementary Materials for this manuscript include the following:

- Movies S1 to S4
- Data S1

Materials and Methods

Whale species distribution modeling

Whale location data

We first assessed data availability for all thirteen species of great whales, including all baleen whales and sperm whales, by collating downloadable location data (from the Global Biodiversity Information Facility, Ocean Biodiversity Information System, Spatial Ecological Analysis of Megavertebrate Populations, MoveBank, Pacific Islands Ocean Observing System, Australian Antarctic Data Center, California Department of Fish and Wildlife, and Southwest Fisheries Science Center Surveys), and acquiring additional data to fill geographic gaps (including data from the International Whaling Commission (IWC), the North Atlantic Right Whale Consortium, Ocean Wise Conservation Association (*52*), Heritage Expeditions, Sistema de Apoio ao Monitoramento de Mamíferos Marinhos (SIMMAM), and Southern Ocean Whale and Ecosystem Research Programme; see Supplementary Data S1 for a full list of dataset citations). We identified four globally-ranging species that the IWC recognizes as being significantly threatened by ship-strikes and that had sufficient location data to conduct global analyses (*9*, *53*): blue whales, fin whales, humpback whales, and sperm whales. Locations that were recorded between 1960-01-01 and 2020-12-31 were included in the analysis (Figs. S1-S5).

North Atlantic right whales (*Eubalaena glacialis)* are also threatened by collisions with vessels, and ship-strikes, alongside fishing gear entanglement, have driven a population decline resulting in this species being considered Critically Endangered (*17*, *54*). This species has been the subject of intensive monitoring (e.g., (*55–57*)) and species distribution models already exist for this species over most of its occupied range (*58*, *59*). As our objective is to quantify ship-strike risk for globally-ranging species for whom risk was unknown across large extents of their ranges, we did not include North Atlantic right whales in our analysis.

Integrated Species Distribution Modeling

Integrated species distribution models are an analytical approach to integrate location data from multiple data types and sources (*28*). In brief, integrated species distribution models are state-space models that allow for different data types to be described with different observation models while contributing to the same ecological process model, which is generally an inhomogeneous point process model (*28*, *60*). This approach enhances model performance and accuracy compared to traditional species distribution models that are fit to a single data type and facilitates modeling distributions over larger geographic scales (*28*, *61*). We used Bayesian hierarchical modeling to fit integrated species distribution models incorporating four different data types – survey data (presence-absence), opportunistic sightings (presence-only), tagging data (presence-only), and whaling records (presence-only) – into models relating whale space use to environmental conditions (see *Spatial covariates and model terms* below for information on covariates and model specification). We used the Integrated Nested Laplace Approximation to fit integrated species distribution models using *INLA* and *inlabru* packages in R version 4.2.2 (*62*, *63*).

Absence and background data

For each presence location, we sampled one absence or background location. For surveys (presence-absence), absences were randomly sub-sampled along survey tracklines. For presence-only data types characterized by high sampling bias (opportunistic sightings and whaling records), we used a target-group approach to generate background locations to account for sampling bias (*64*, *65*). Target group sampling is a method of choosing background data with the same bias as presence data through estimating areas with non-zero detection probability from presence data of similar species, and is effective at reducing sampling bias in species distribution models (*64*, *66*). For opportunistic sightings, target group sampling was done by fitting 100km-radius buffers around each recorded presence for all thirteen species of great whales and taking the union of those spatial buffers as in (*65*), which represented the area under observation. We then drew background locations for each species from this buffered region. This approach has been shown to out-perform uniform background sampling (*65*). For tagging data (presence-only), we first subsampled tracks by selecting one location per day per individual (*31*, *67*). We generated background locations by fitting minimum convex polygons around all recorded locations for each species in each tagging dataset, and randomly sampled an equivalent number of background locations as presence locations (*68*). We included whaling records for blue and fin whales, as these species lacked sufficient data from other sources, and used the target group sampling approach to generate background locations. Regions over which background locations were generated and survey tracklines are shown in Figures S2-S5.

Regional definitions

We modeled blue, fin, and humpback whale sub-populations separately to account for the regional patterns of population structure evident in genetic analyses and subspecies classifications (*69*). For each species, we generated background locations separately by region to ensure a 1:1 ratio of presence to background locations within each region. For blue whales, 5 sub-populations were defined for the North Pacific, North Atlantic, eastern South Pacific, Antarctic, and Indian Ocean-Western Pacific, following (*70*). Note that a recent analysis suggests that the eastern South Pacific population interbreeds with eastern North Pacific populations, and accordingly characterizes all eastern Pacific blue whales as one Evolutionarily Significant Unit (ESU) (*71*). However, there is genetic divergence between eastern South Pacific and eastern North Pacific populations, which the analysis identifies as two distinct conservation units within the higher-level ESU. Both humpback and fin whales exhibit genetic differentiation between the North Pacific, North Atlantic, and Southern Hemisphere (*72–74*), so these three regional sub-populations were applied for both species. The Southern Hemisphere region extends to 5˚N to account for the oceanographic equator being north of the geographical equator in the Tropical Surface Water mass (*73*, *75*). In contrast to the other species, sperm whales do not exhibit nuclear genetic differentiation across ocean basins due to male dispersal and migration (*76*). As such, sperm whales were modeled as a single, global population [*sensu* (*77*)].

Spatial covariates and model terms

We extracted data on environmental conditions that have been shown to be important drivers of whale space use [e.g., (*24*, *31*, *77*)]. Covariate data were downloaded from Copernicus Marine Environment Monitoring Service (CMEMS) Global Ocean Physics Reanalysis (*78*), CMEMS Global Ocean Biogeochemistry Hindcast (*79*), and ETOPO1 Global Relief Model (*80*). Covariates included bathymetry (m), rugosity (a proxy for seabed complexity calculated as standard deviation of bathymetry; m), sea surface temperature (SST; °C), the standard deviation of sea surface temperature (a proxy for frontal activity; °C), net primary production (mg m^{-3} day^{-1}), mixed layer depth (m), and sea level anomaly (m). Covariate data were at 0.25°x0.25° spatial resolution, and dynamic covariates were at monthly mean temporal resolution. To minimize missing covariate values around the coasts, we smoothed covariate data by 1.25 degrees (i.e., each quarter degree pixel was re-calculated as the spatial mean of all pixels within a 1.25 degree surrounding square). Contemporaneous dynamic covariate data were available for all covariates from 1993-01-01 to 2021-01-01. Whale locations recorded in this window were matched with monthly contemporaneous ocean conditions in that grid cell, and locations recorded before 1993 were matched with long-term monthly average ocean conditions in that grid cell (i.e., climatological; monthly means of 1990-2020 for SST and mixed layer depth; 1993-2020 for sea level anomaly; and 1992-2020 for primary productivity).

We included smooth terms for environmental covariates to allow species-environment relationships to be nonlinear, and estimated these relationships using stochastic partial differential equation models with one-dimensional meshes that included ten knots (*81*).

Model validation

We used out-of-sample validation to evaluate each model using a random 80:20% training:testing split (Table S1) (*82*) . We used Area Under the receiver operating characteristic Curve (AUC) and True Skill Statistic (TSS) to evaluate model performance for the testing set, which are both commonly used to evaluate species distribution models (*83*). The AUC represents the true positive rate (sensitivity) versus false positive rate (1 – specificity). AUC ranges from 0 to 1, with values >0.5 indicating better performance than random and values >0.75 considered effective for use in conservation planning (*84*). The TSS score is calculated as the sum of sensitivity and specificity minus 1 and ranges from -1 to 1, with values >0 indicating better performance than random (*85*, *86*). We also consulted with experts on each whale species to ensure the biological realism of the resulting spatial predictions (*68*, *87*).

Model prediction

For each species, we predicted whale distributions (predicted probability of species occurrence) across each species range defined by the International Union for Conservation of Nature (IUCN; *88–91*), and refer readers to (*92*) for additional range maps. As models included dynamic covariates at the monthly temporal resolution, we predicted monthly whale distributions based on mean conditions for each climatological month (n=12). Our objective was to characterize broad-scale global patterns of ship-strike risk without introducing false precision, so we aggregated predictions to 1˚ resolution for final whale distribution maps (Figs. S6-S9) (*26*, *93*). We calculated the whale space-use index (w_j) in each grid cell j for each species by averaging predicted probability of occurrence in that grid cell across months and then scaling between 0-1 to develop a static metric of whale space use from which to calculate ship-strike risk.

Vessel data

Vessels broadcast Automatic Identification System (AIS) signals for navigational safety, and these signals are relayed by satellites and terrestrial receivers to nearby vessels. In recent years, AIS has evolved into a valuable scientific and managerial tool for quantifying vessel traffic in space and time (*25*). We used newly-available global AIS data for vessels to map global shipping traffic between 2017 and 2022. AIS data were sourced from Spire and Orbcomm and processed by Global Fishing Watch to determine vessel type and size (*25*, *94*). Spire's satellites were launched in 2017, so we only use AIS data starting in 2017 in order to ensure more complete coverage (*93*). We interpolated AIS data by connecting consecutive locations for each vessel and regularized tracks to one location for each vessel every five minutes. We calculated vessel speed for each location as the speed between that location and the vessel's previous location. We restricted our analysis to non-fishing vessels >300GT, as larger vessels have stricter AIS requirements and are more likely to lethally strike whales. The International Maritime Organization (IMO) requires AIS transmission by all vessels >500GT and vessels >300GT that are traveling internationally, and AIS usage declines as vessel size decreases (*95*). Larger vessels also pose a greater threat to whales based on probability of collision and lethality of collision (*40*, *96*, *97*). We excluded fishing vessels because previous analyses have shown considerable gaps in the AIS record for fishing vessels compared to non-fishing vessels (*93*, *98*).

To calculate speed-weighted vessel density in each 0.25˚x0.25˚ grid cell, we used an additive approach that reduces bias in shipping density and probability of lethal collision calculations (*16*, *99*). The probability that a collision between a vessel and a whale is lethal increases with faster vessel speeds (*40*):

$$p_{\,lethal\,collision,i} = \frac{1}{1 + exp-(-1.905 + 0.217 * speed_i)} \qquad \text{Equation 1}$$

We calculated $p_{lethal\,collision,\,i}$ for each vessel location i, based on the speed of the vessel between that location and its previous location.

Next, we calculated speed-weighted vessel distance traveled for each vessel location by multiplying the $p_{lethal\,collision,\,i}$ and the distance (d_i) between location i and location i-1 (*99*). We then calculated speed-weighted vessel density (D_j) by summing speed-weighted distance traveled values for each vessel location in each grid cell j:

$$D_j = \sum_{i=1}^{N} (p_{lethal\,collision,i} * d_i) \qquad \text{Equation 2}$$

where N is the number of vessel locations within the grid cell j. We log-transformed speed-weighted vessel density and rescaled between 0 and 1 (*100*).

Quantifying ship-strike risk

We multiplied the speed-weighted vessel density (D_j) and each species' space-use index (w_j) to yield our ship-strike risk index (R_j) in each grid cell j at 1˚x1˚ resolution (*99*):

$$R_j = w_j * D_j \qquad \text{Equation 3}$$

We identified ship-strike hotspots as areas with greater than or equal to the 99th percentile of risk from the static maps for each species (i.e., grid cells in the top 1% of risk). We conducted a sensitivity analysis, considering 90, 95, 99, and 99.5 percentile cutoffs to evaluate the sensitivity of our hotspot analysis to choice in cutoff value (Table S2, Fig. S16). We overlaid risk hotspots for each species to identify areas that present high collision risk to multiple species.

Summarizing ship-strike risk by region and management status

Shipping calculations

We calculated the number of 1˚x1˚ grid cells within species IUCN-defined ranges that did not contain any large vessel traffic during each year. We also calculated the total distance traveled by vessels in each species IUCN-defined range each year.

Comparison with risk in the California Current Ecosystem

The California Current Ecosystem is a well-studied region in which rates of mortality from ship-strikes have been calculated for blue, fin, and humpback whales and have been found to be between 2-(humpback) to 8-(blue whale) times higher than the legal limit for anthropogenic mortality (*16*, *29*). We calculated the mean ship-strike risk across all species in the California Current Ecosystem and identified grid cells that had equivalent or higher predicted risk.

Ship-strike risk across regions

We quantified how ship-strike risk varied across ocean regions, exclusive economic zones, and marine protected areas. For ocean regions, we used regional definitions for global oceans and seas from (*101*). We accessed exclusive economic zone boundaries from (*102*) and the single polygon designating the high seas from (*103*). We extracted the mean predicted ship-strike risk for each species in each exclusive economic zone as well as the high seas polygon. We then used a *t*-test to determine whether the difference between predicted risk within each exclusive economic zone and mean value in the high seas was significantly different from zero. Similarly, we evaluated whether predicted ship-strike risk differed within and outside of marine protected areas. We split up this analysis by ocean region because marine protected area coverage varies across regions. We accessed marine protected area polygons from (*104*). For each ocean region, we calculated the difference in ship-strike risk within each marine protected area compared to the mean ship-strike risk outside of marine protected areas for that region, and used *t*-tests to evaluate whether the difference was significantly different from zero.

Management status of ship-strike risk hotspots

We characterized the management status of ship-strike risk hotspots. The World Shipping Council (WSC) compiled governmental measures aimed at reducing ship-strike risk to whales into a report (*42*). From this report, we digitized spatially-static measures (i.e., zones that cover the same area across years, rather than spatially-dynamic or mobile areas triggered by the detection of a target species), including vessel speed reduction and area closures (i.e., areas to be avoided) aimed at protecting whales from shipping. We excluded spatially-dynamic zones because they do not represent areas that are permanently protected year-to-year, and no spatially-dynamic zones were aimed at protecting any of our four focal species. For vessel speed reduction zones, we considered areas with a stated speed limit (e.g., 10 knots rather than a directive such as "use caution"). We considered both voluntary and mandatory measures, and year-round and seasonal measures. Moving shipping lanes has also been successfully implemented in some areas (*20*), however because we are looking at current management strategies in the time these hotspots were identified (shipping data from 2017-2022), past movement of shipping lanes would be reflected in AIS data. We considered a hotspot "managed" if it overlapped to any degree with a management area. We calculated the percentage of hotspots that were protected overall and by species. We calculated the total area of hotspots that lack any management, and compared that to the area of the global oceans.

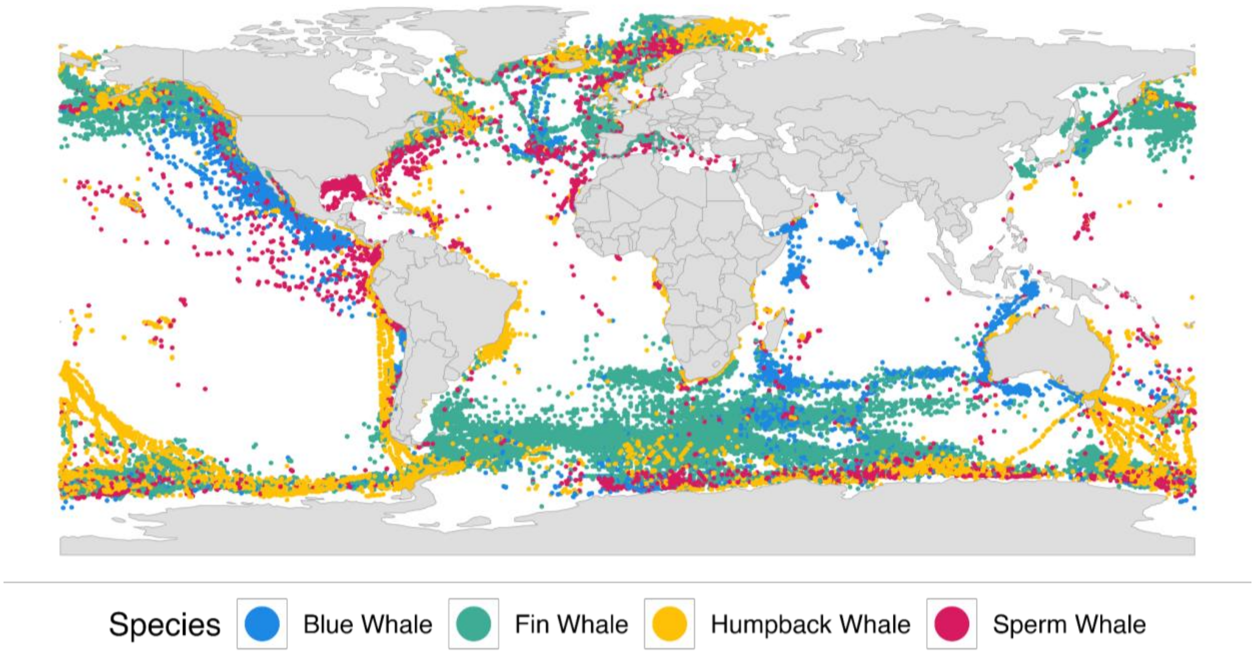

Figure S1. Whale location data. Location data for blue, fin, humpback, and sperm whales from 1960-2020.

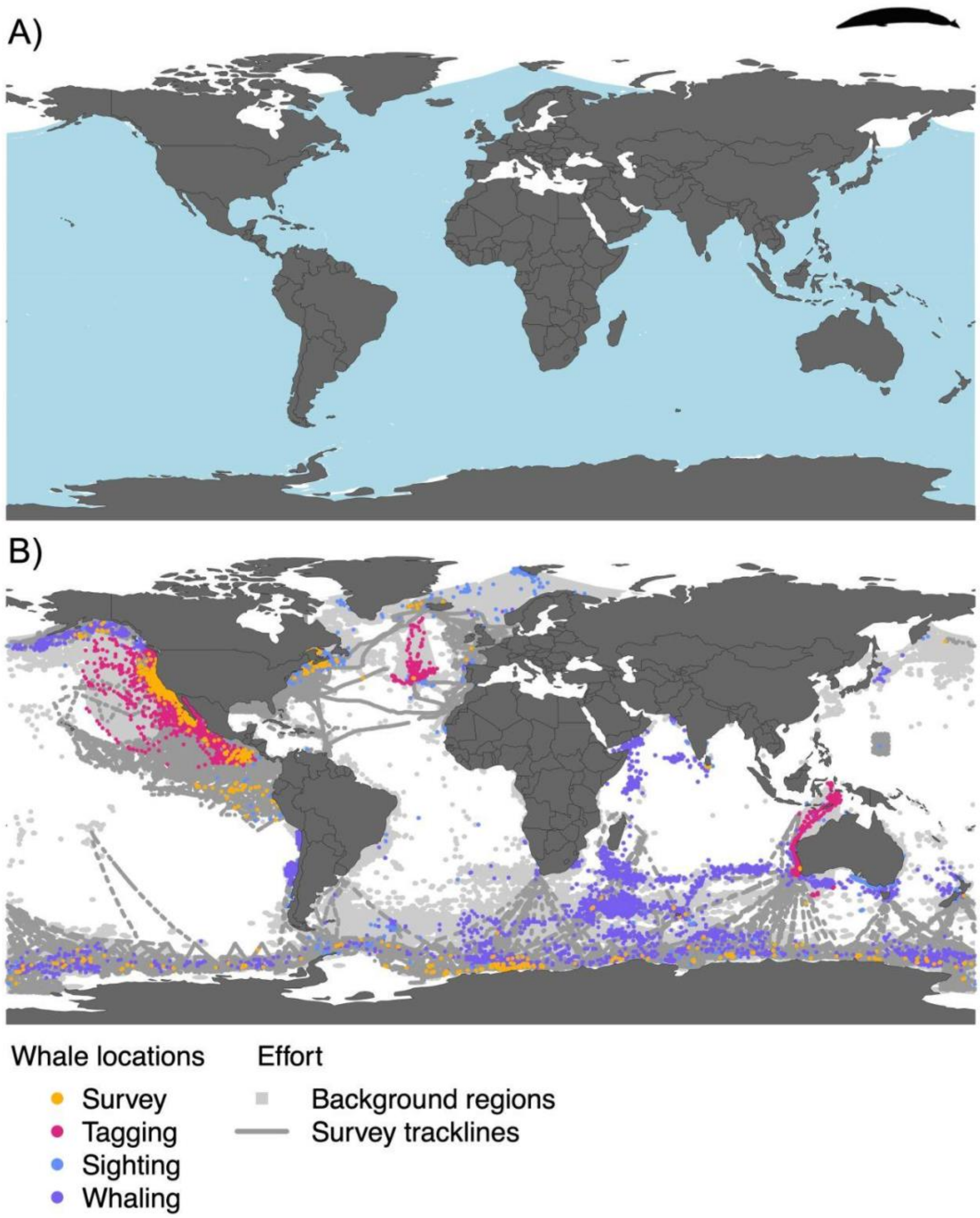

Figure S2. Blue whale range and location data. A) Blue whale range map as defined by the International Union for Conservation of Nature (IUCN). B) Blue whale locations and effort data. Blue whale locations are color-coded by data type. Survey tracklines are shown in dark gray. The light gray shaded region indicates the area over which background points were generated for presence-only data types (see Materials and Methods).

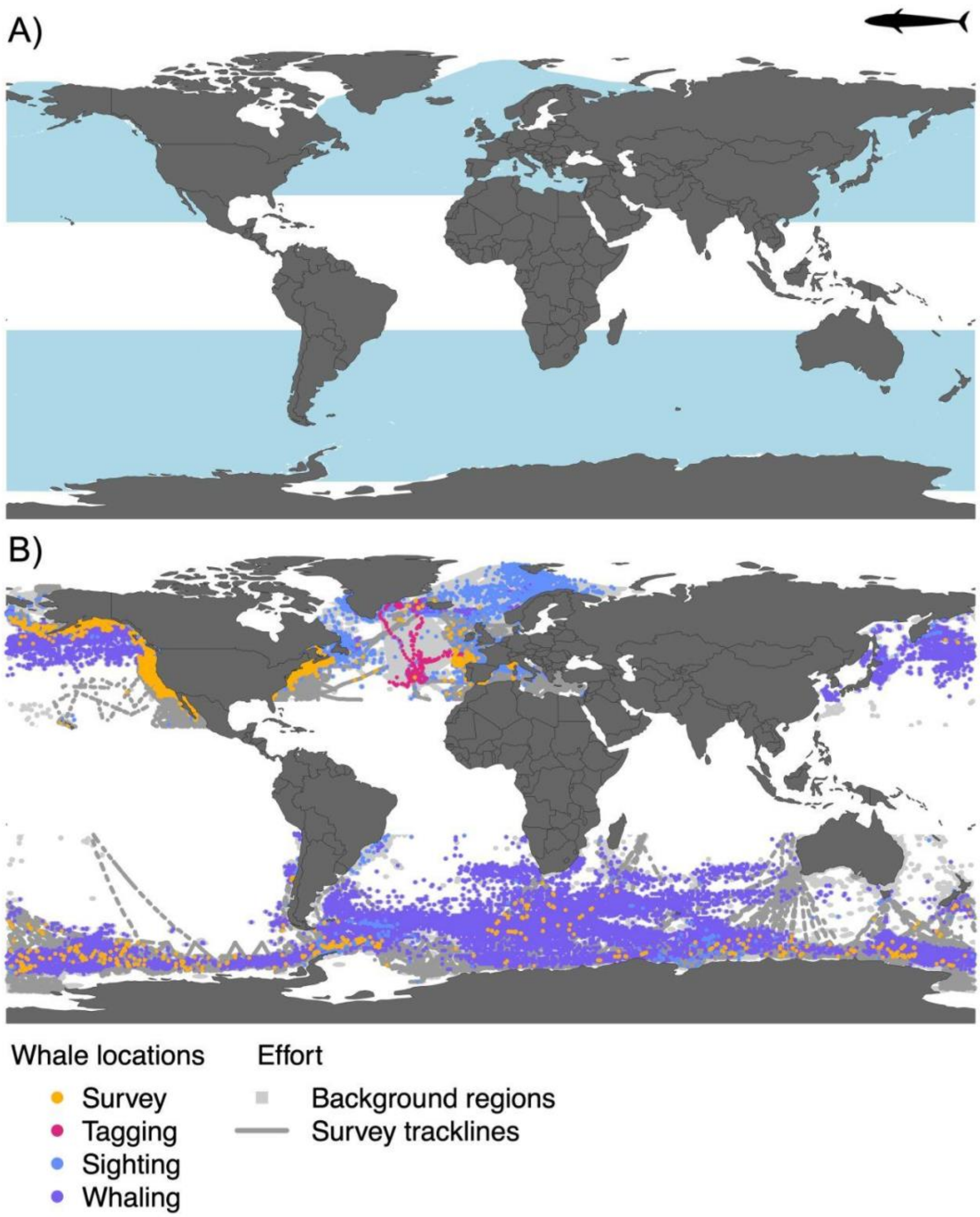

Figure S3. Fin whale range and location data. A) Fin whale range map as defined by the International Union for Conservation of Nature (IUCN). B) Fin whale locations and effort data. Fin whale locations are color-coded by data type. Survey tracklines are shown in dark gray. The light gray shaded region indicates the area over which background points were generated for presence-only data types (see Materials and Methods).

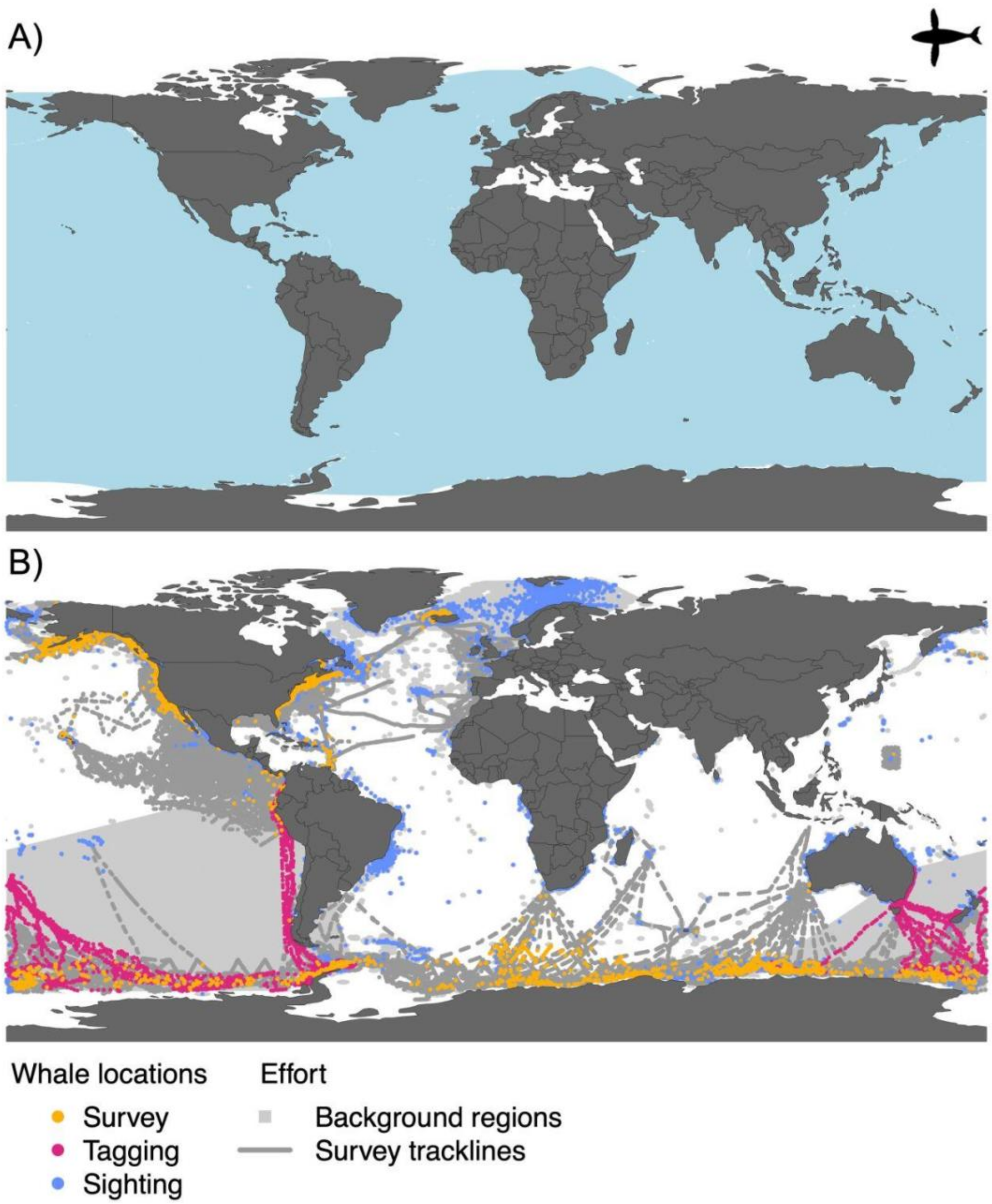

Figure S4. Humpback whale range and location data. A) Humpback whale range map as defined by the International Union for Conservation of Nature (IUCN). B) Humpback whale locations and effort data. Humpback whale locations are color-coded by data type. Survey tracklines are shown in dark gray. The light gray shaded region indicates the area over which background points were generated for presence-only data types (see Materials and Methods).

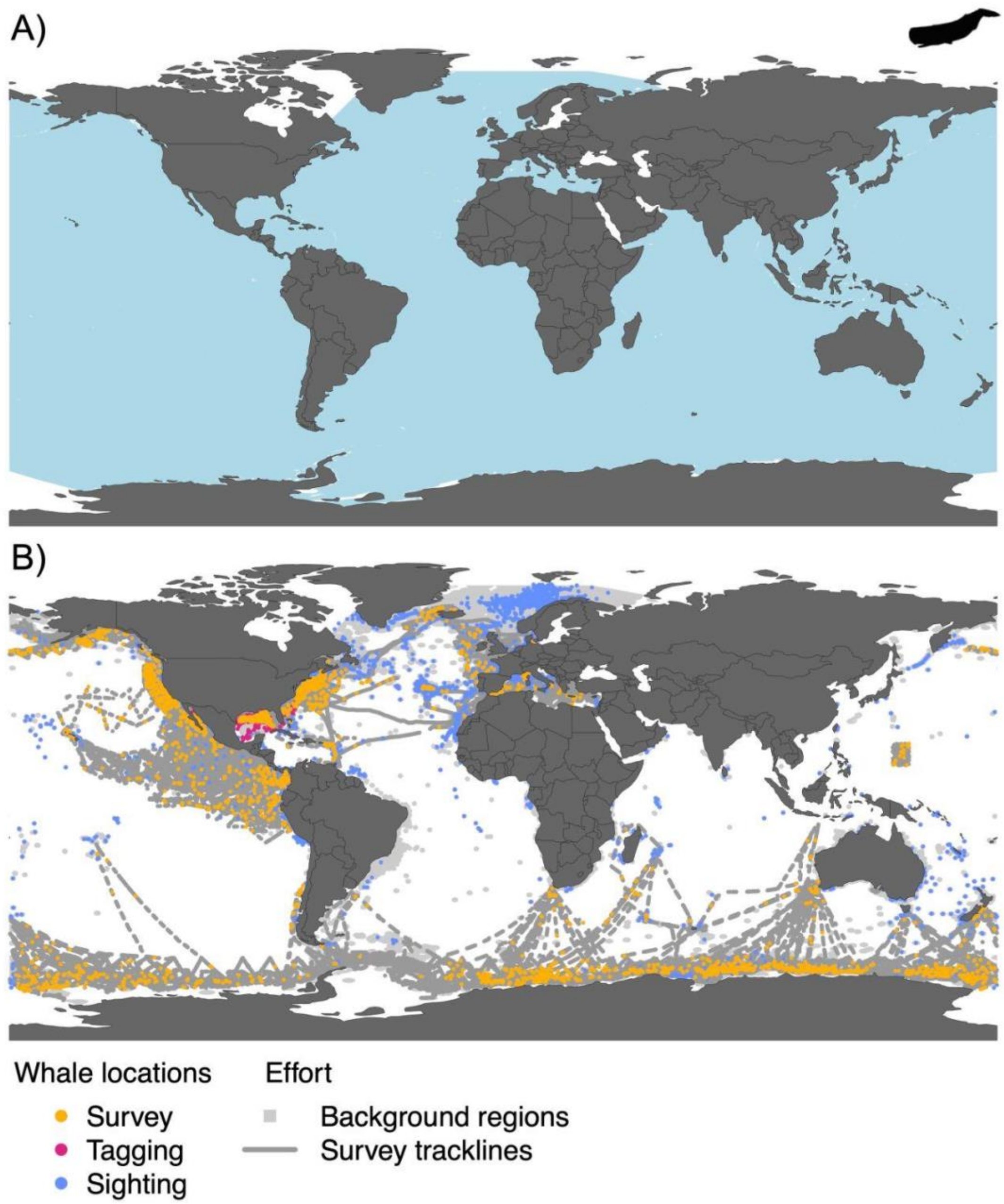

Figure S5. Sperm whale range and location data. A) Sperm whale range map as defined by the International Union for Conservation of Nature (IUCN). B) Sperm whale locations and effort data. Sperm whale locations are color-coded by data type. Survey tracklines are shown in dark gray. The light gray shaded region indicates the area over which background points were generated for presence-only data types (see Materials and Methods).

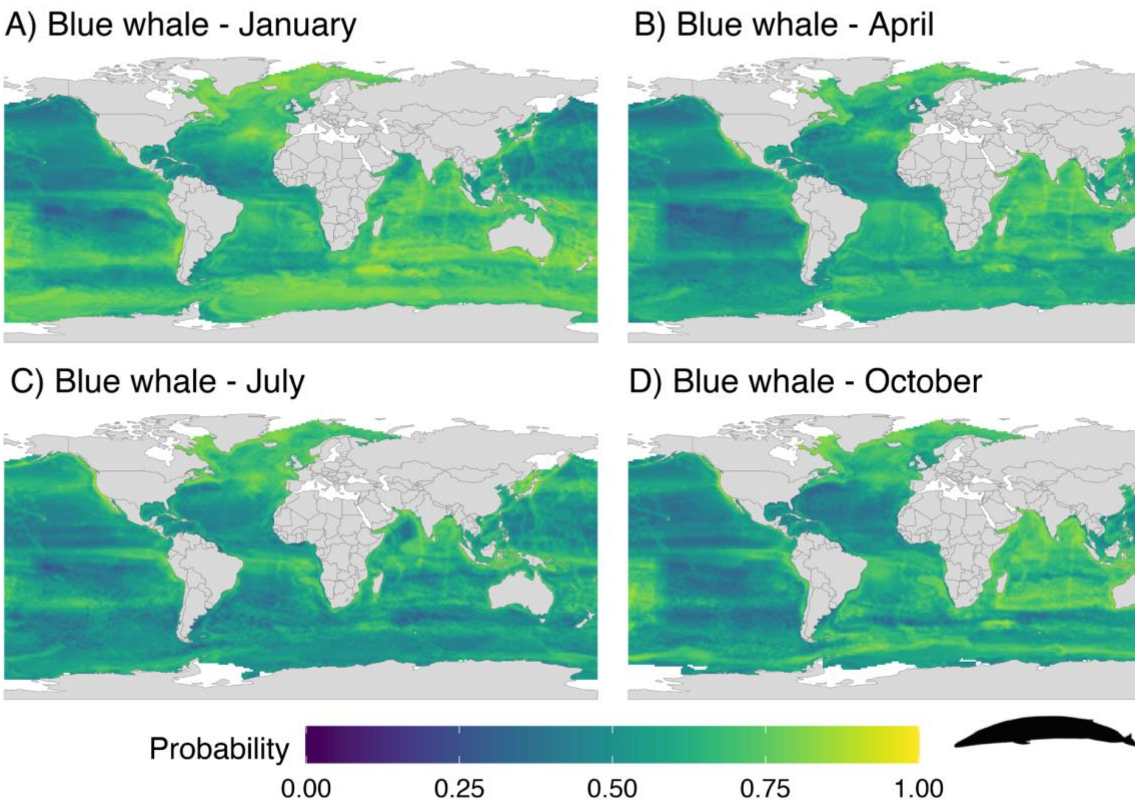

Figure S6. Blue whale distribution in January, April, July, and October. Probability of blue whale occurrence for climatological mean conditions from 1993-2020 in January, April, July, and October from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined blue whale range.

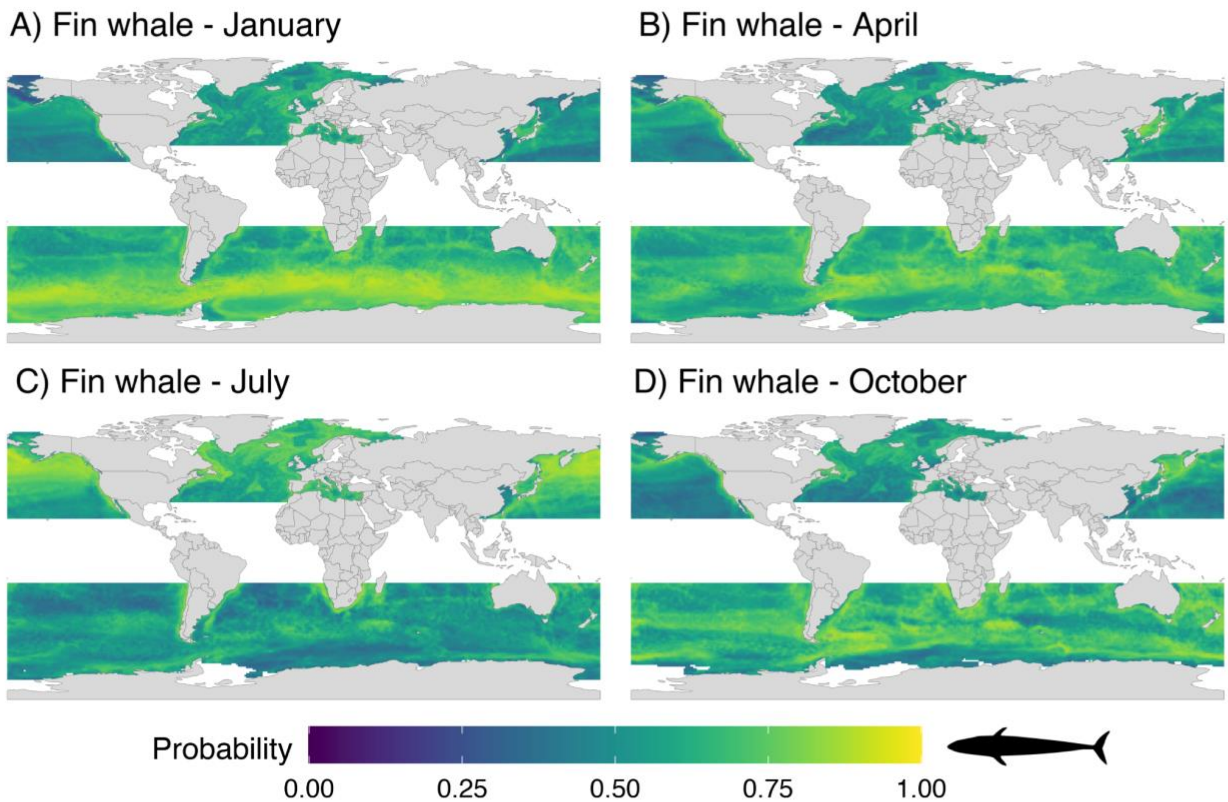

Figure S7. Fin whale distribution in January, April, July, and October. Probability of fin whale occurrence for climatological mean conditions from 1993-2020 in January, April, July, and October from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined fin whale range.

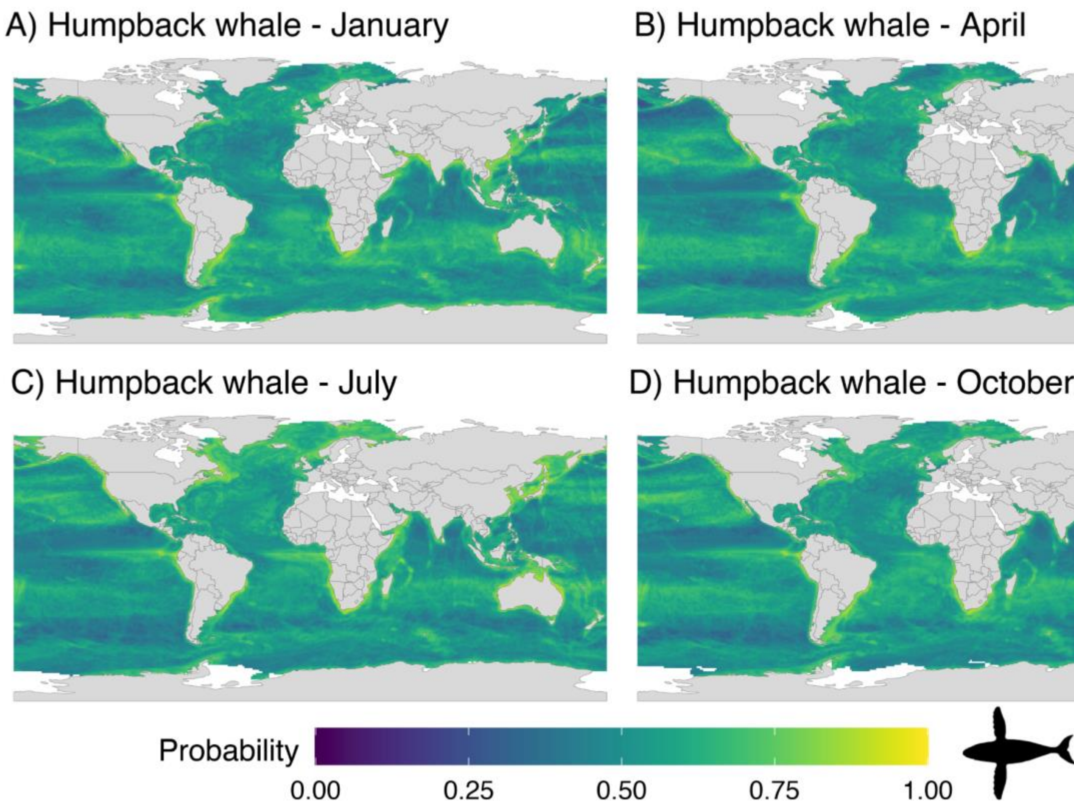

Figure S8. Humpback whale distribution in January, April, July, and October. Probability of humpback whale occurrence for climatological mean conditions from 1993-2020 in January, April, July, and October from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined humpback whale range.

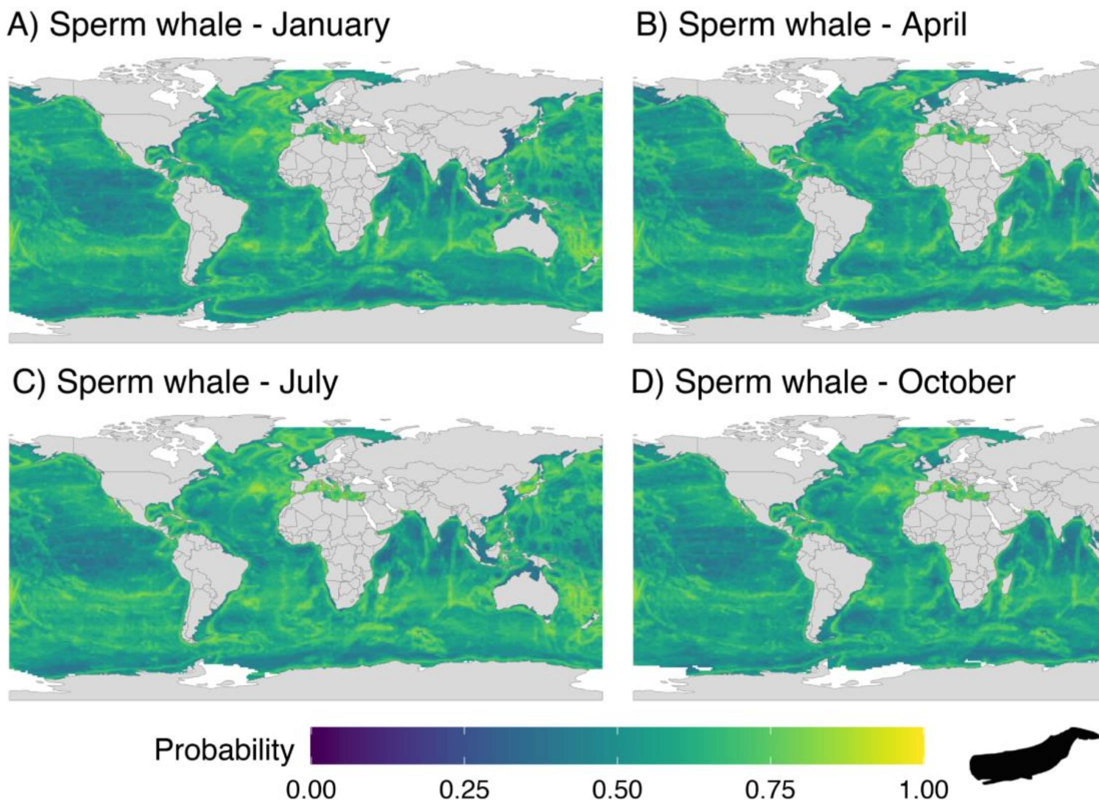

Figure S9. Sperm whale distribution in January, April, July, and October. Probability of sperm whale occurrence for climatological mean conditions from 1993-2020 in January, April, July, and October from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined sperm whale range.

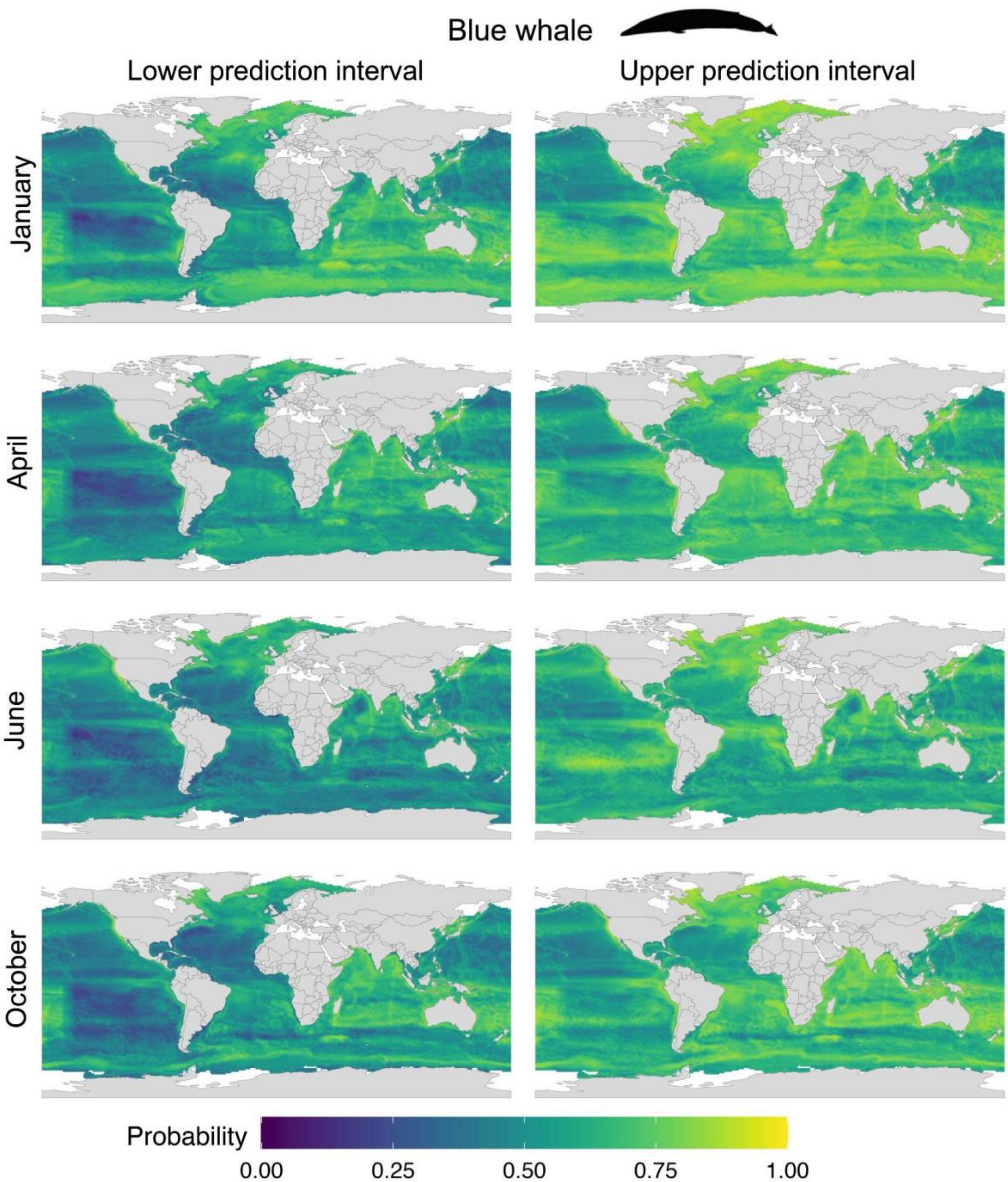

Figure S10. Upper and lower prediction intervals for blue whale distribution. Upper and lower bounds of 95% prediction intervals of probability of blue whale occurrence for climatological mean conditions from 1993-2020 in January, April, July, and October from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined blue whale range.

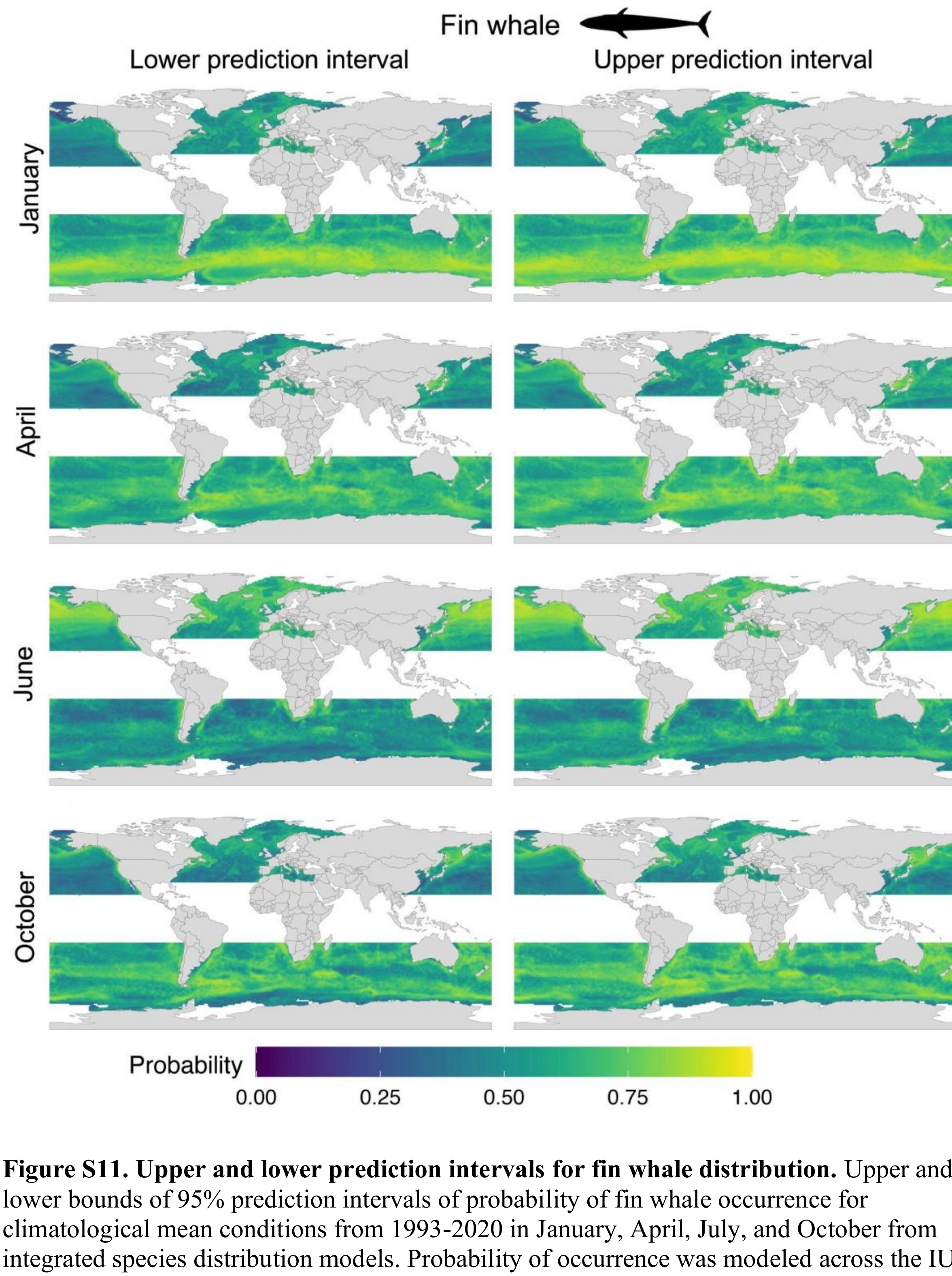

Figure S11. Upper and lower prediction intervals for fin whale distribution. Upper and lower bounds of 95% prediction intervals of probability of fin whale occurrence for climatological mean conditions from 1993-2020 in January, April, July, and October from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined fin whale range.

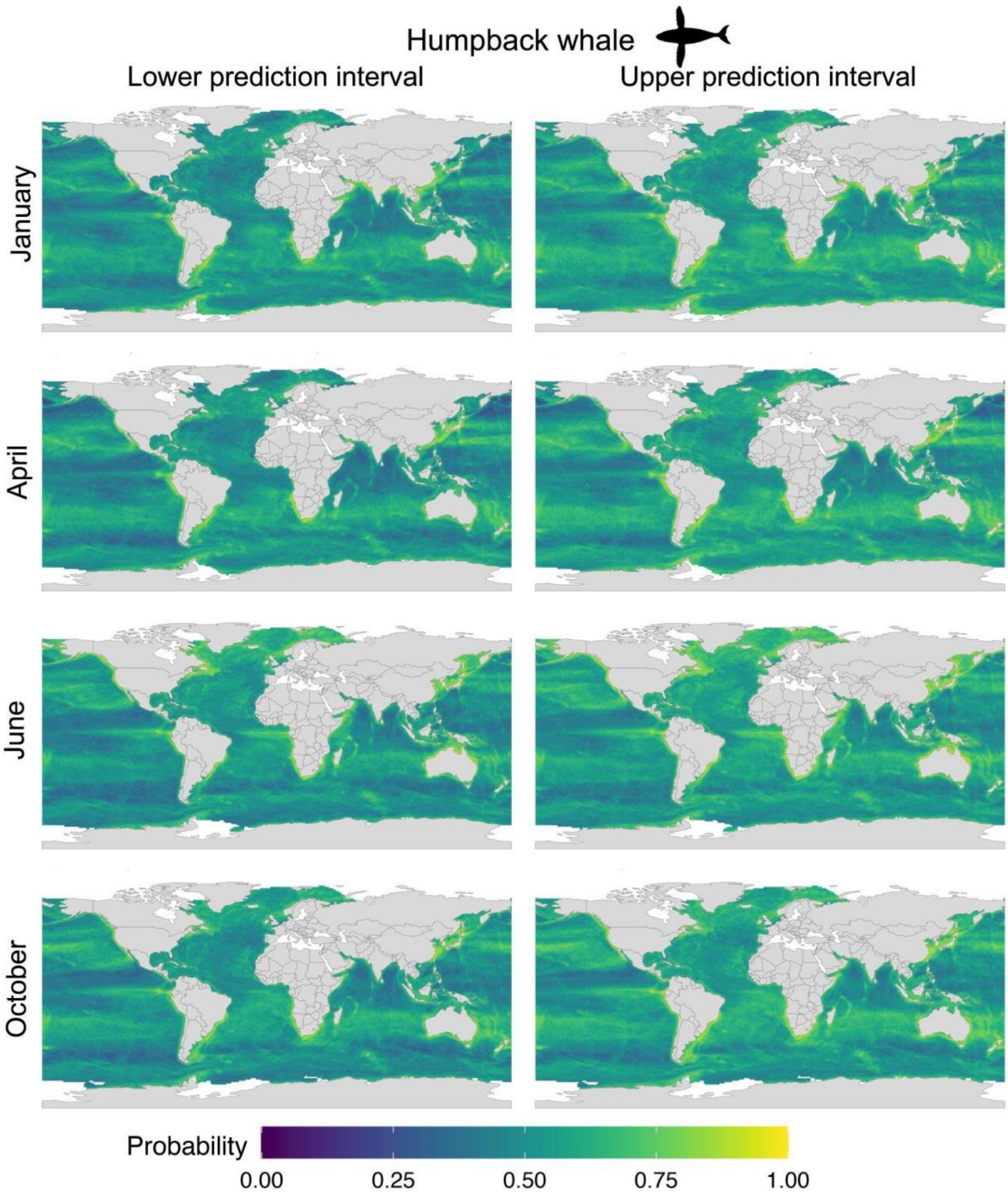

Figure S12. Upper and lower prediction intervals for humpback whale distribution. Upper and lower bounds of 95% prediction intervals of probability of humpback whale occurrence for climatological mean conditions from 1993-2020 in January, April, July, and October from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined humpback whale range.

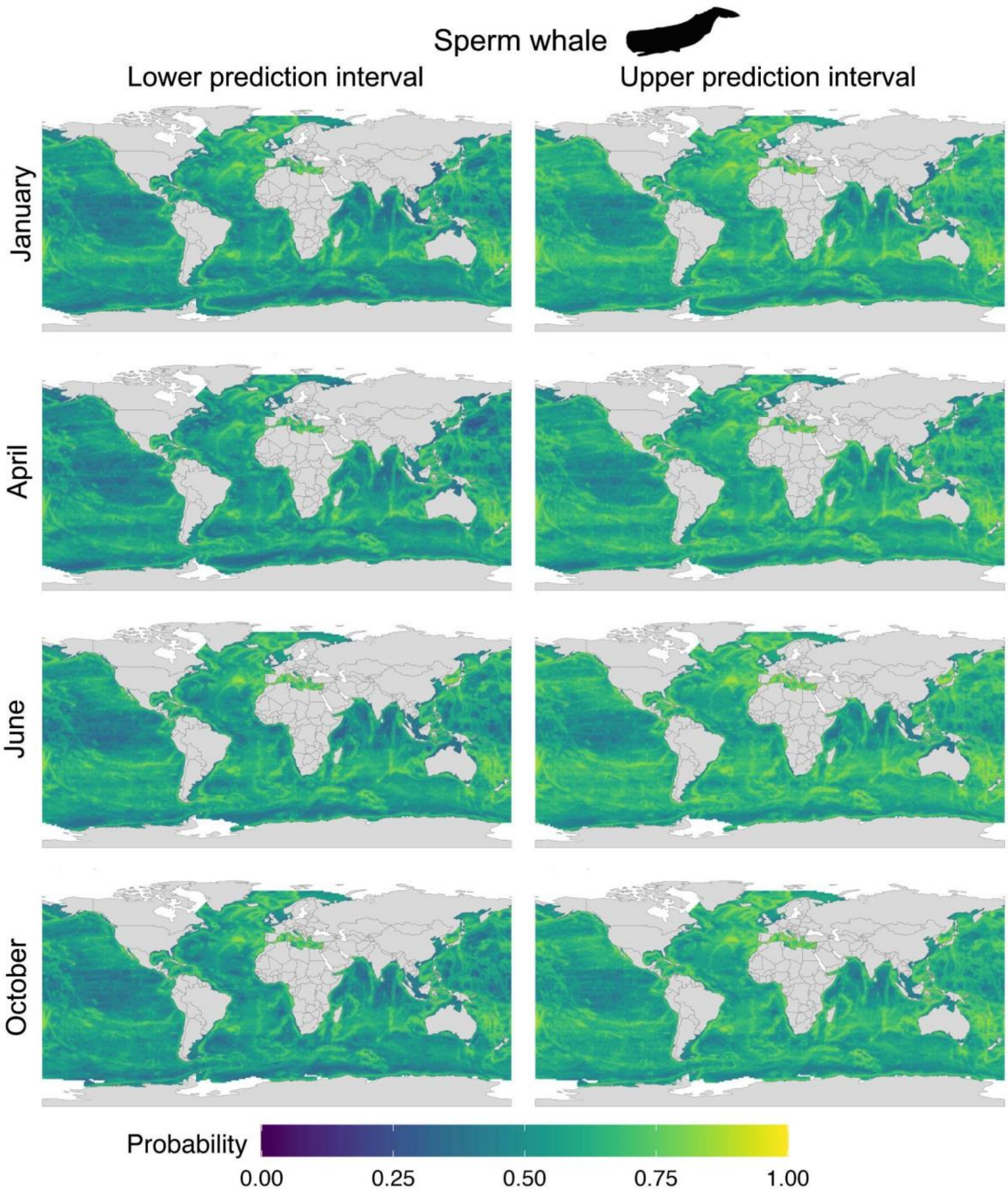

Figure S13. Upper and lower prediction intervals for sperm whale distribution. Upper and lower bounds of 95% prediction intervals of probability of sperm whale occurrence for climatological mean conditions from 1993-2020 in January, April, July, and October from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined sperm whale range.

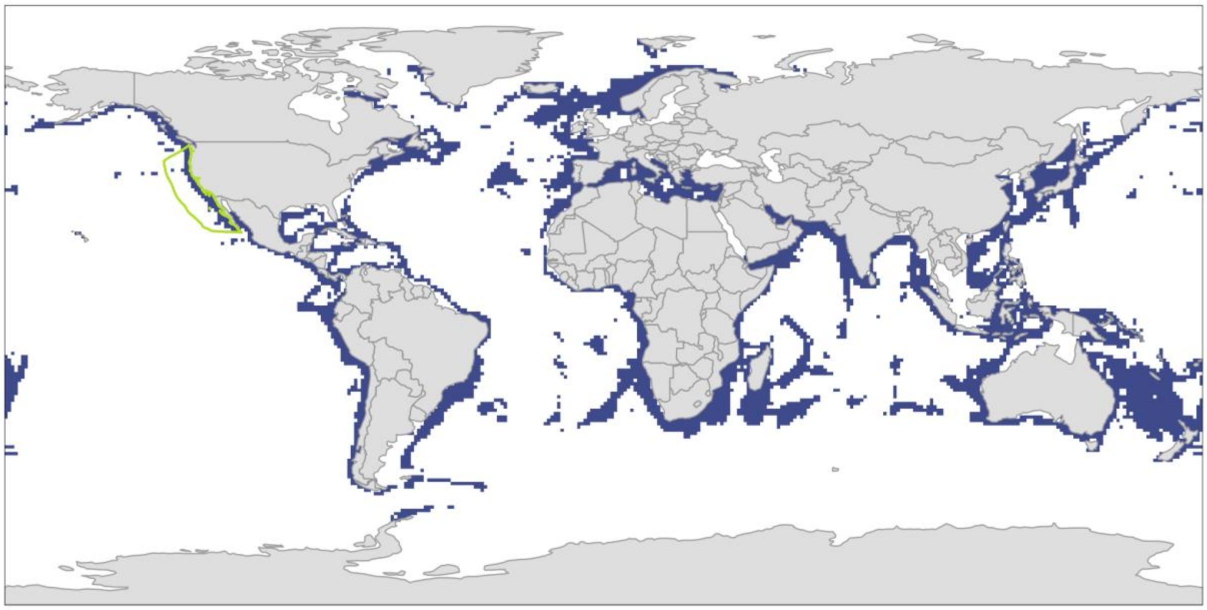

Figure S14. Areas of equivalent risk to the California Current Ecosystem. Areas of equivalent or higher predicted ship-strike risk than mean ship-strike risk across all species in the California Current Ecosystem (shown in green outline, with mean predicted risk value of 0.397).

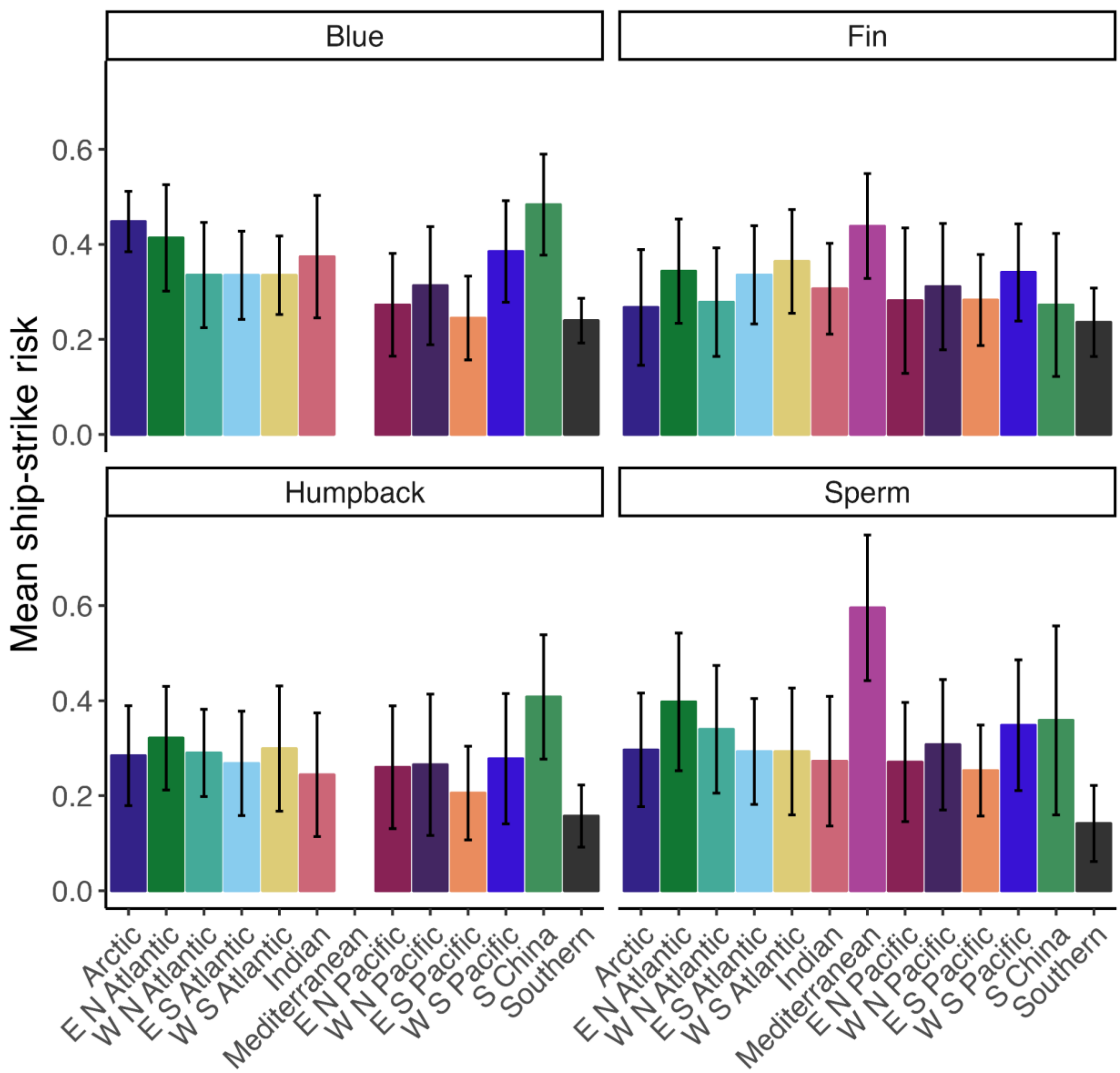

Figure S15. Mean ship-strike risk across global oceans and seas for each species. Error bars are ± 1 standard deviation. The International Union for the Conservation of Nature (IUCN) blue whale and humpback whale range maps do not include the Mediterranean so ship-strike risk was not calculated for that region.

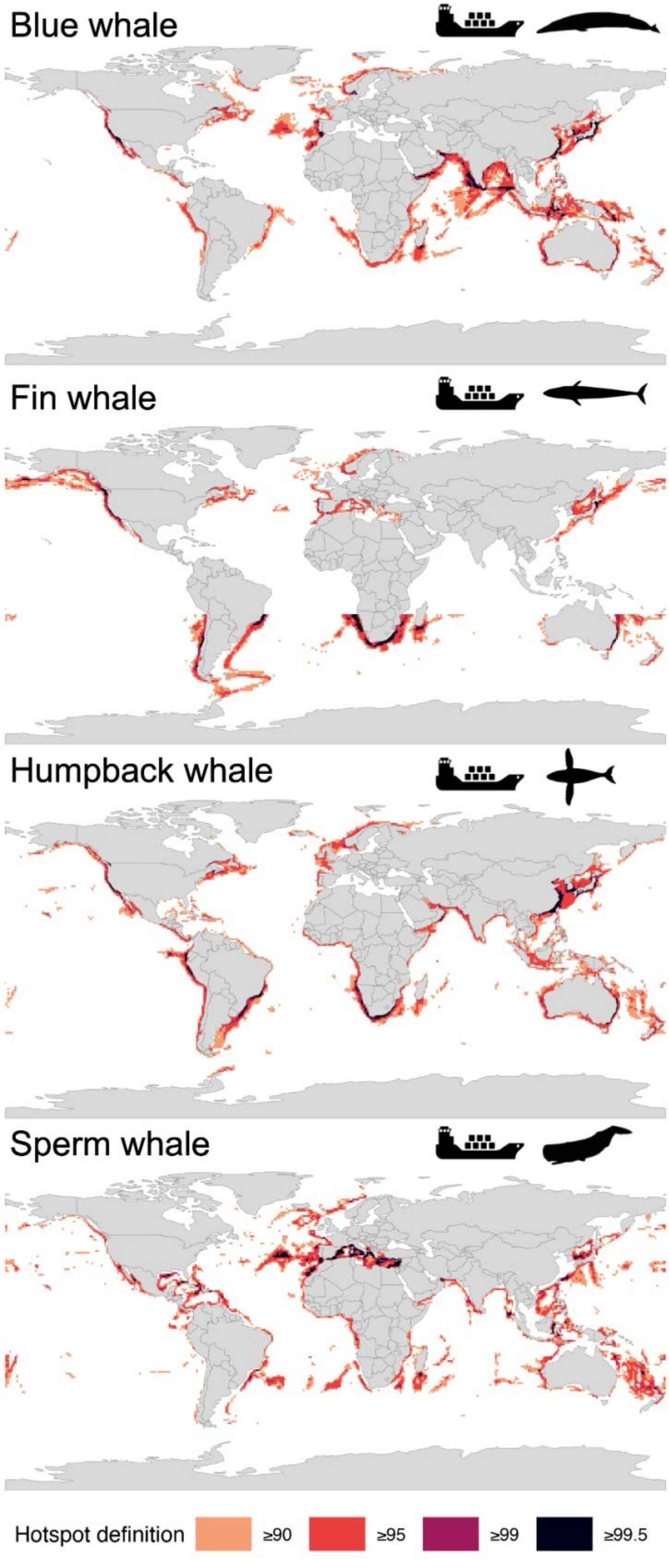
Blue whale
Fin whale
Humpback whale
Sperm whale
Hotspot definition
≥90
≥95
≥99
≥99.5

Figure S16. Ship-strike risk hotspots for blue, fin, sperm, and humpback whales defined using different percentile cutoffs (90%, 95%, 99%, and 99.5% of predicted ship-strike risk for each species). In the main text, hotspots are defined using the 99th percentile cutoff – i.e., grid cells in the top 1% of risk for each species.

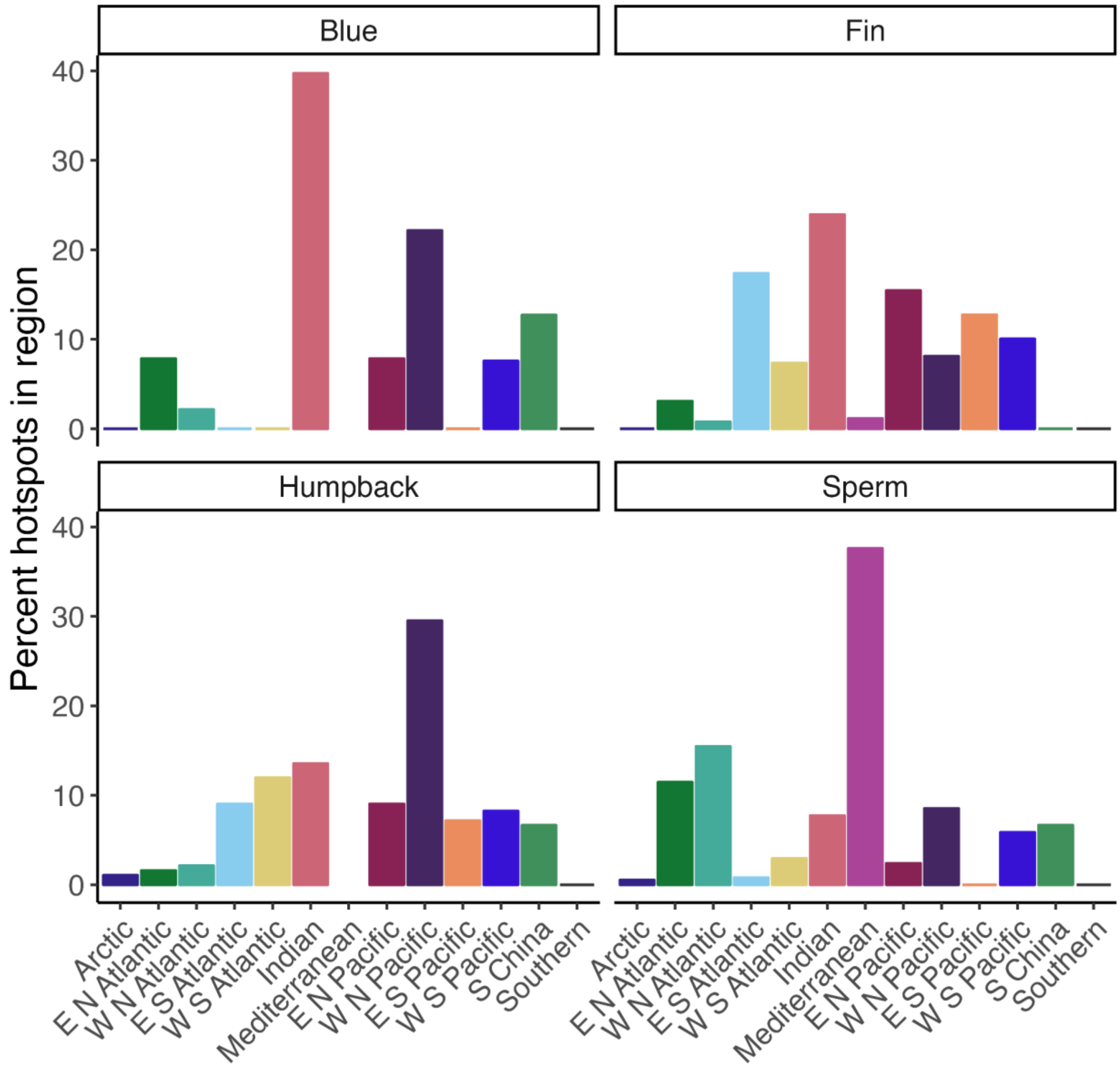

Figure S17. Distribution of hotspots across global oceans and seas for each species. Percent of global ship-strike risk hotspots (defined as top 1% of global ship-strike risk for each species) in each region.

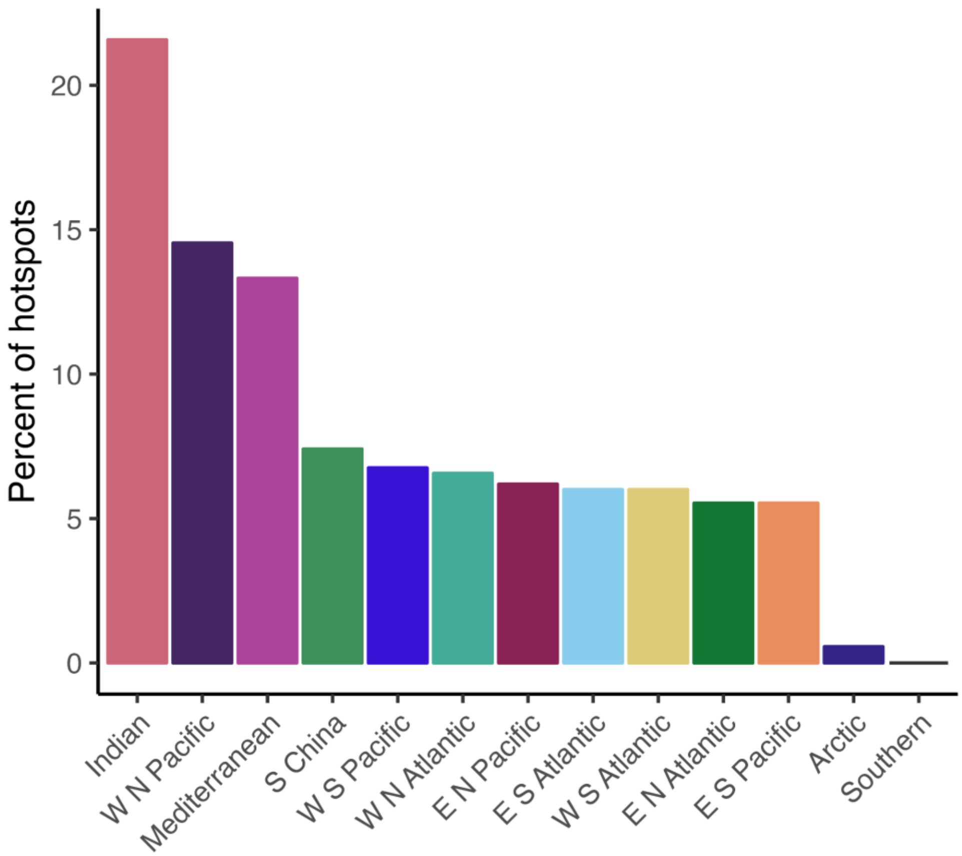

Figure S18. Distribution of hotspots across global oceans and seas. Percent of global ship-strike risk hotspots (defined as top 1% of global ship-strike risk for any species) in each region.

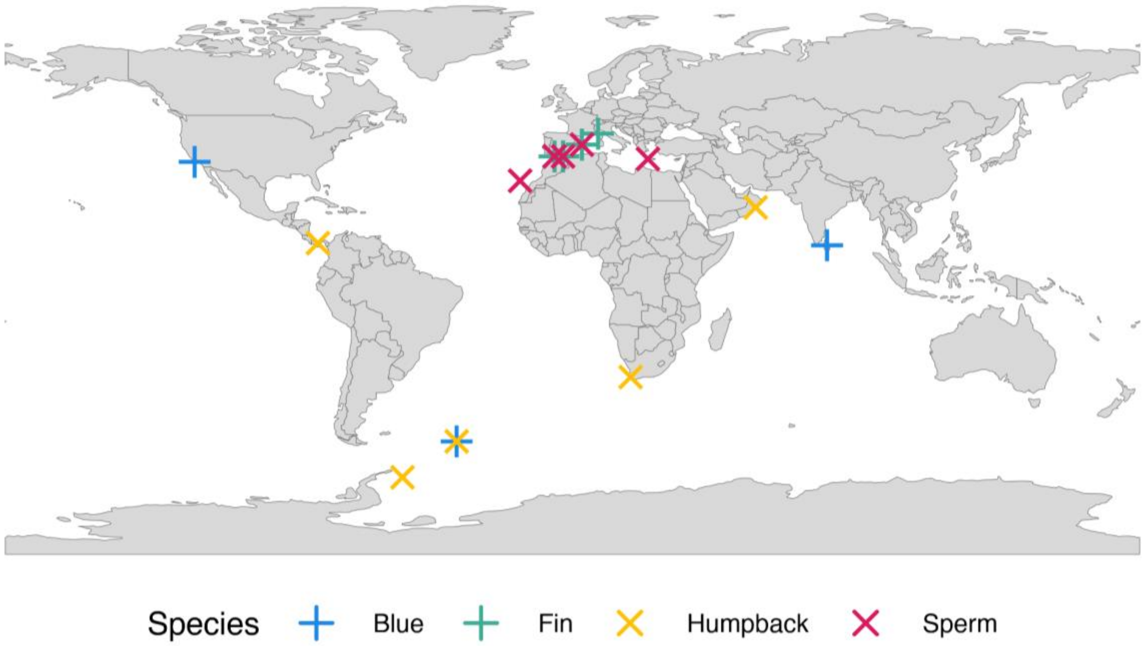

Figure S19. Locations of recognized high-risk areas for blue, fin, humpback, and sperm whales designated by the International Whaling Commission (*9*). Symbol shapes differ across species to allow shared high-risk areas to be visible (e.g., three regions in the Mediterranean are recognized as high risk for both fin and sperm whales).

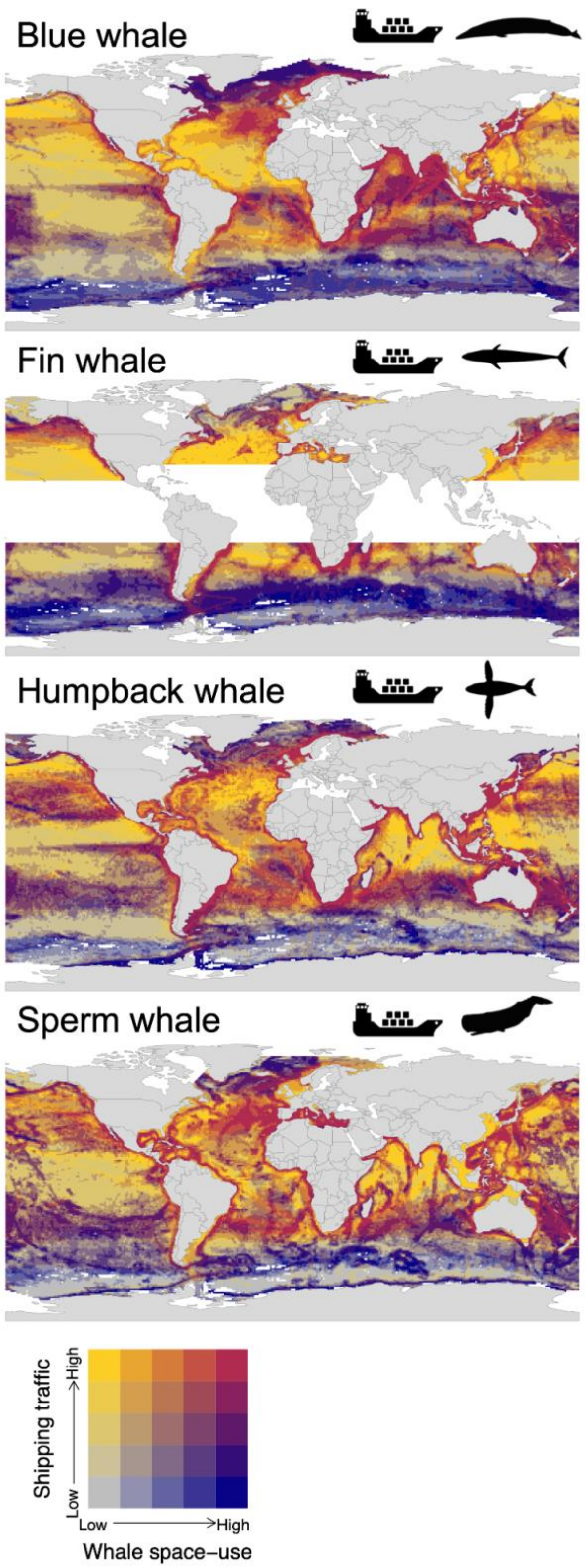

Figure S20. Whale space use and shipping traffic by species. Bivariate map showing the relative levels of whale space use and shipping traffic in each grid cell, both split into 5 quantiles.

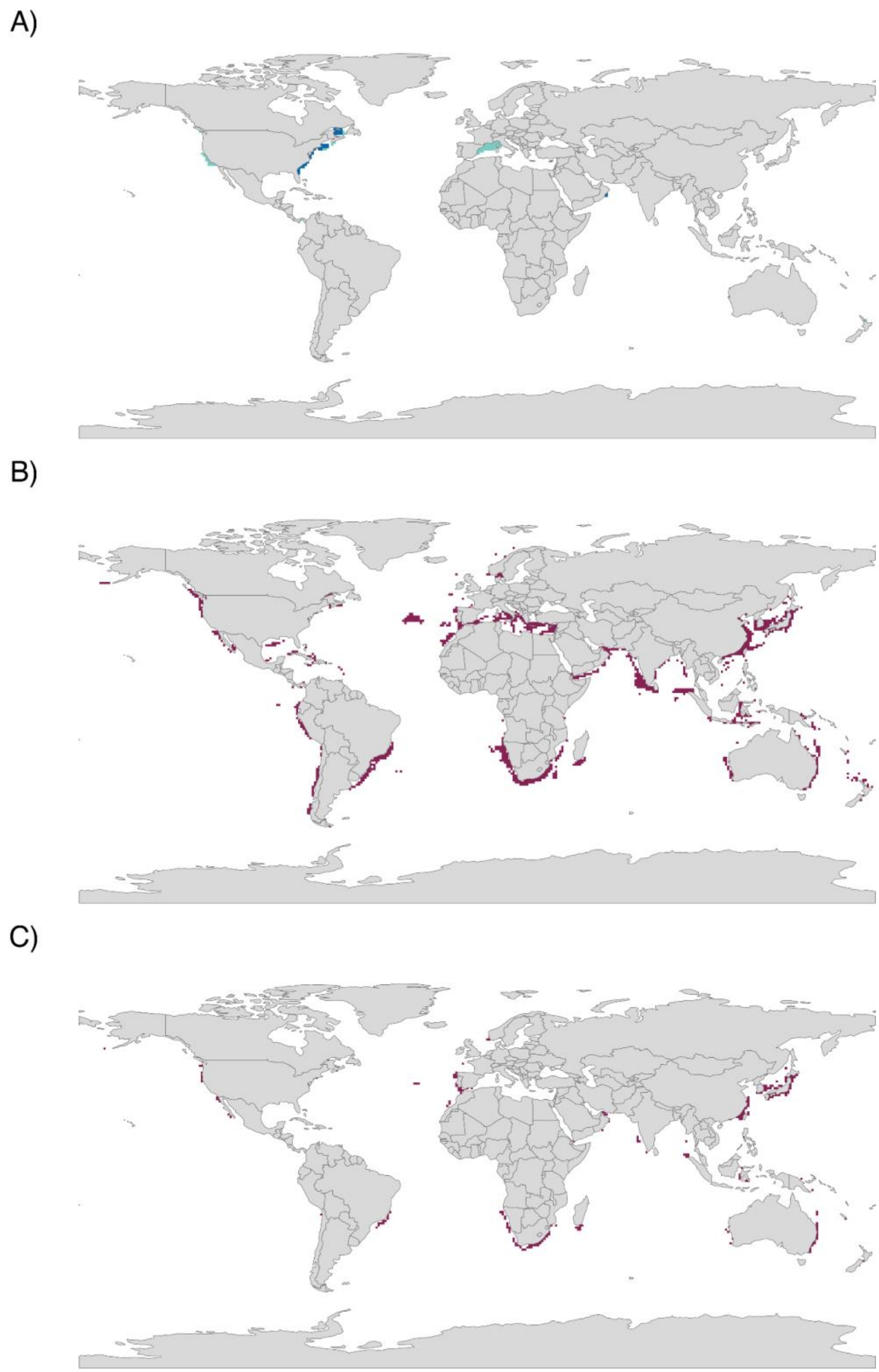

Figure S21. Maps of existing ship-strike management efforts and unmanaged ship-strike risk hotspots. Management zones were digitized from the World Shipping Council report (*42*), and include mandatory or voluntary measures that are spatially static and that either involve the closure of an area to vessels or vessel speed reduction that is associated with a specific speed limit. A) Mandatory (blue) and voluntary (teal) ship-strike management measures. Because many areas are very small, for ease of viewing this map shows management interventions on the 1˚ gridded resolution used for mapping ship-strike risk. B) Ship-strike risk hotspots for any species that do not overlap with an existing ship-strike management measure. C) Multi-species ship-strike risk hotspots (i.e., risk hotspots that are shared by ≥2 species) that do not overlap with an existing ship-strike management measure.

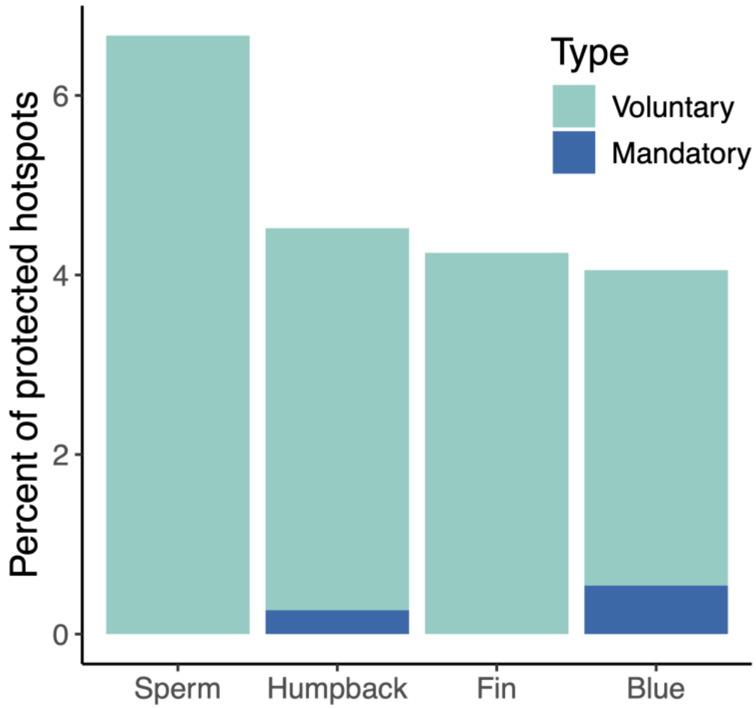

Fig. S22: Percentages of each species ship-strike risk hotspots that are protected by mandatory and voluntary management measures.

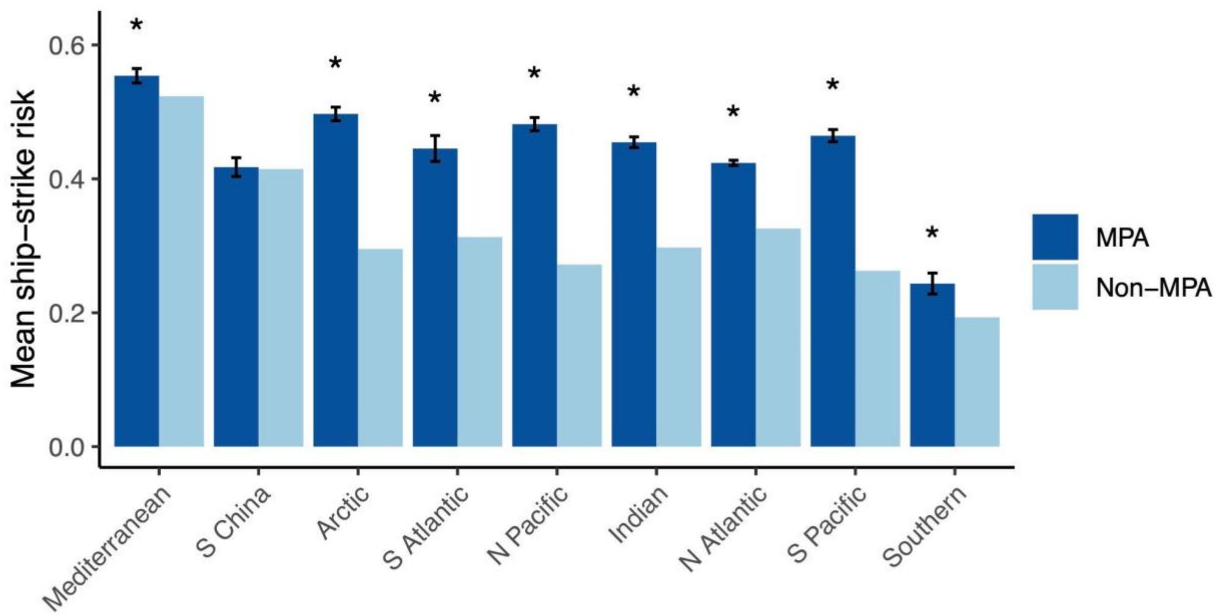

Figure S23: Ship-strike risk in Marine Protected Areas. Mean predicted ship-strike risk by region within MPAs compared to non-MPA areas. Error bars are 95% confidence intervals and asterisks indicate significant differences ($p < 0.001$).

Table S1. Model validation and sample sizes for whale species distribution models. Model validation metrics include the area under the receiver operating characteristic Curve (AUC) and the true skill statistic (TSS). Sample sizes indicate the number of presence locations. The total sample size is the total number of whale locations included in each model, and the Sightings through Whaling records columns are the number of locations within that data type.

		Model validation		Sample size				
Species	Region	AUC	TSS	Total	Sighting	Survey	Tagging	Whaling records
Blue whale	Antarctic	0.776	0.396	1824	93	310	0	1421
Blue whale	Eastern South Pacific	0.856	0.516	901	32	43	0	826
Blue whale	Indian Ocean-Western Pacific	0.853	0.546	6666	753	143	480	5290
Blue whale	North Pacific	0.908	0.688	13646	5466	851	6849	480
Blue whale	North Atlantic	0.838	0.517	1345	938	147	241	19
Fin whale	North Atlantic	0.765	0.405	41675	19521	10418	294	11442
Fin whale	North Pacific	0.882	0.617	20818	2330	1982	374	16132
Fin whale	Southern Hemisphere	0.875	0.624	27505	400	724	0	26381
Humpback whale	North Atlantic	0.907	0.66	43032	34655	8377	0	0
Humpback whale	North Pacific	0.954	0.77	59558	55375	4183	0	0
Humpback whale	Southern Hemisphere	0.85	0.581	33609	25331	3074	5204	0
Sperm whale	Global	0.808	0.465	23578	12705	7673	3200	0

Table S2. Sensitivity analysis for percentile cutoffs for risk hotspot definitions. Spatial distribution and management coverage of species hotspots defined using different percentile cutoffs (99.5%, 99% [used in the main analysis], 95%, and 90%). For each region, values are the percent of each species' hotspots defined by the focal cutoff value that fell within each ocean region. Dashes indicate regions that are not included in species' ranges as defined by the International Union for the Conservation of Nature (i.e., blue and humpback whale ranges do not include the Mediterranean Sea). For management type, values are the percent of each species' hotspots defined by the focal cutoff value that contained a mandatory management (Mandatory) or any management effort, either mandatory or voluntary (All).

		Region									Management type	
Species	Hotspot percentile	Arctic	Indian	Mediterranean	N Atlantic	N Pacific	S Atlantic	S China	S Pacific	Southern	Mandatory	All
Blue	99.5	0	32.97	-	7.03	38.92	0	12.97	8.11	0	0	5.41
Blue	99	0	39.73	-	10	30	0	12.7	7.57	0	0.54	4.05
Blue	95	3.35	38.2	-	13.58	17.48	3.9	11.26	12.23	0	0.54	1.95
Blue	90	6.41	36.93	-	15.56	12.91	6.06	8.74	13.37	0.03	0.54	1.3
Fin	99.5	0	25.38	1.54	0.77	22.31	31.54	0	18.46	0	0	6.15
Fin	99	0	23.94	1.16	3.86	23.55	24.71	0	22.78	0	0	4.25
Fin	95	2.24	14.31	7.27	10.83	29.54	17.71	0.23	16.32	1.55	0.54	4.41
Fin	90	3.21	12.49	6.73	11.79	28.73	17.75	0.43	16.74	2.13	0.54	3.05
Humpback	99.5	0.53	12.23	-	1.06	46.28	17.02	9.04	13.83	0	0.53	4.79
Humpback	99	1.06	13.56	-	3.72	38.56	21.01	6.65	15.43	0	0.27	4.52
Humpback	95	3.41	19.58	-	12.99	26.61	12.35	8.46	16.18	0.43	1.01	2.34
Humpback	90	4.18	20.41	-	15.25	21.5	11.5	9.37	17.03	0.77	0.69	1.49
Sperm	99.5	0.53	4.26	53.19	26.6	7.45	1.6	4.26	2.13	0	0	10.11

Sperm	99	0.53	7.73	37.6	26.93	10.93	3.73	6.67	5.87	0	0	6.67
Sperm	95	1.71	14.29	12.59	26.03	13.44	9.28	8.16	14.51	0	0	1.92
Sperm	90	1.84	17.2	7.28	24.25	17.55	9.26	6.86	15.76	0	0	1.28

Movie S1. Blue whale distribution across months of the year. Probability of blue whale occurrence for climatological mean conditions for each month from 1993-2020 from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined blue whale range.

Movie S2. Fin whale distribution across months of the year. Probability of fin whale occurrence for climatological mean conditions for each month from 1993-2020 from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined fin whale range.

Movie S3. Humpback whale distribution across months of the year. Probability of humpback whale occurrence for climatological mean conditions for each month from 1993-2020 from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined humpback whale range.

Movie S4. Sperm whale distribution across months of the year. Probability of sperm whale occurrence for climatological mean conditions for each month from 1993-2020 from integrated species distribution models. Probability of occurrence was modeled across the IUCN-defined sperm whale range.

Data S1. Citations for whale location datasets included in whale distribution modeling analysis.