MARINE CONSERVATION

Global tracking of marine megafauna space use reveals how to achieve conservation targets

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The recent Kunming-Montreal Global Biodiversity Framework (GBF) sets ambitious goals but no clear pathway for how zero loss of important biodiversity areas and halting human-induced extinction of threatened species will be achieved. We assembled a multi-taxa tracking dataset (11 million geopositions from 15,845 tracked individuals across 121 species) to provide a global assessment of space use of highly mobile marine megafauna, showing that 63% of the area that they cover is used 80% of the time as important migratory corridors or residence areas. The GBF 30% threshold (Target 3) will be insufficient for marine megafauna's effective conservation, leaving important areas exposed to major anthropogenic threats. Coupling area protection with mitigation strategies (e.g., fishing regulation, wildlife-traffic separation) will be essential to reach international goals and conserve biodiversity.

Together with the recently finalized United Nations High Seas Treaty (*1*, *2*), the Kunming-Montreal Global Biodiversity Framework (GBF) (*3*, *4*) seeks to protect, conserve, and manage at least 30% of oceans. This is a necessary step to support halting the loss of marine biodiversity (GBF Target 3), which has been particularly acute for large marine species (*5*–*7*). These include several iconic large marine vertebrates that have been driven to extinction by overexploitation [e.g., the Steller's sea cow (*Hydrodamalis gigas*), the great auk (*Pinguinus impennis*), and the Japanese sea lion (*Zalophus japonicus*)], and many others currently showing precipitous declines in abundance [e.g., the hawksbill turtle (*Eretmochelys imbricata*), shortfin mako shark (*Isurus oxyrinchus*), and North Atlantic right whale (*Eubalaena glacialis*)]. These mobile and highly migratory marine vertebrates, hereafter marine megafauna, can act as ecosystem and climate sentinels (*8*) (being good surrogates for other biodiversity) and hold key functional roles that assist in structuring and maintaining ecosystems (*9*–*11*). However, close to a third of species across marine megafauna taxa are now threatened with extinction (*5*, *12*–*18*).

Certain characteristics of marine megafauna, such as *K*-selected life-history traits, place them at priority for systematic conservation planning [i.e., high vulnerability and high irreplaceability (*19*)] and make the "effective conservation" outlined in GBF Target 3 urgently needed. Many also migrate thousands of kilometers crossing multiple exclusive economic zones (EEZs) and areas beyond national jurisdictions (ABNJs), presenting a challenge for area-based conservation approaches (*20*). Notably, such approaches are traditionally based on known geographical ranges reflecting historically known boundaries (*18*) or static maps of occurrence (*21*). However, devising a management plan that effectively conserves migratory species within Ecologically and Biologically Significant Areas (*22*) requires an understanding of how the species use space. Particularly, detecting important marine megafauna areas used for key life-history events, such as breeding or feeding and migratory behaviors, henceforth IMMegAs [to use a term similar to those recognized by the International Union for the Conservation of Nature (IUCN), such as IMMA (Important Marine Mammal Areas) or ISRA (Important Shark and Ray Areas)] is only tractable using telemetry data (*20*, *23*–*27*). Despite the challenges associated with collating such data at global scale (*28*), the detection of global IMMegAs is essential to understanding marine megafauna conservation needs to inform global treaties and should therefore be prioritized for creating the network of marine protected areas (MPAs) aimed by GBF (i.e., the planned increase to 30% of area protection).

Using telemetry data to understand global space use by marine megafauna

We assembled a telemetry dataset unparalleled in size and scope [as the result of a global effort initiated by the MegaMove project (*29*)] by accepting voluntary contributions of tracking data of highly mobile marine vertebrates—here referred to as marine megafauna, despite some (particularly flying birds) being under the 45-kg threshold (*10*). Our dataset encompasses more than three decades of tracked movements (1985 to 2018) from 15,845 individuals across 121 species, which after curation (*30*), resulted in 12,794 individual tracks from 111 species, covering 71.7% of the area of the world's oceans (Fig. 1). Species include flying birds (hereafter birds), cetaceans (mostly whales but also dolphins), fishes (mostly sharks), penguins, polar bears (*Ursus maritimus*), seals, sirenians (i.e., dugongs and manatees), and turtles. See fig. S1 for latitudinal and longitudinal coverage of the dataset, and tables S1 to S3, respectively, for lists of species tracked, tracking data details, and species-specific information. According to global assessments by the IUCN (*18*), of the 111 species considered, ~70% have decreasing (54 species) or unknown (23 species) population trends, and more than 50% (58 species) have a threatened conservation status of Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) (table S4). Five main regions exhibited the highest effective number of tracked species [as calculated based on the Shannon entropy (*31*)]: the central Indian Ocean, northeast Pacific, Atlantic northeast and northwest, and around Mozambique and South Africa. A few other locations empirically known as having high animal occurrence also showed a high number of species (fig. S2). Areas where more tracking data could be made available include southeast Asia, north of Europe (e.g., Spitsbergen and Greenland), Australia, central Pacific Ocean, and western Africa (particularly the southwest Atlantic and Gulf of Guinea) (Fig. 1 and fig. S2).

Using properties of the movement detected in the tracking dataset, including speed, direction, and movement coherence (*30*) (figs. S12 and S13), we identified IMMegAs based on key behaviors reflected in residency or migratory (including nomadic or dispersive) behavior. We did this by using an approach (*30*) able to evaluate these behaviors collectively across multiple tracks without relying on interpolation across highly variable sampling intervals. This is not possible with the traditionally used state-space models that are typically designed to detect behavioral states on single tracks after interpolating position estimates [e.g., (*32*)].

We then assessed how much of the IMMegAs occurred within existing MPAs (including marine parks) (*33*) or exclusive economic zones [EEZs; (*34*)] (shown in fig. S3). We used an optimization algorithm to estimate what configuration of the area covered by our tracking dataset would yield the best selection for setting protected areas for marine megafauna, giving priority to grid cells that are used for both residency and migratory behaviors across multiple taxa (*30*). For comparison, we repeated this procedure after developing statistical models to predict areas likely to be used for residency or migration for each taxon within the areas covered by our tracking dataset (*30*). For data used as input for the models, see Table 2. After this modeling procedure, we considered the priority grid cells as those resulting in highest probabilities (i.e., >0.5 and closest to 1) of being an important area across all taxa.

Finally, we assessed the extent to which the GBF's planned increase to 30% in area protection could assist with reducing impacts from marine megafauna's exposure to anthropogenic threats with a global footprint (*35*), such as fishing (*36*–*38*), shipping (*39*–*41*), warming

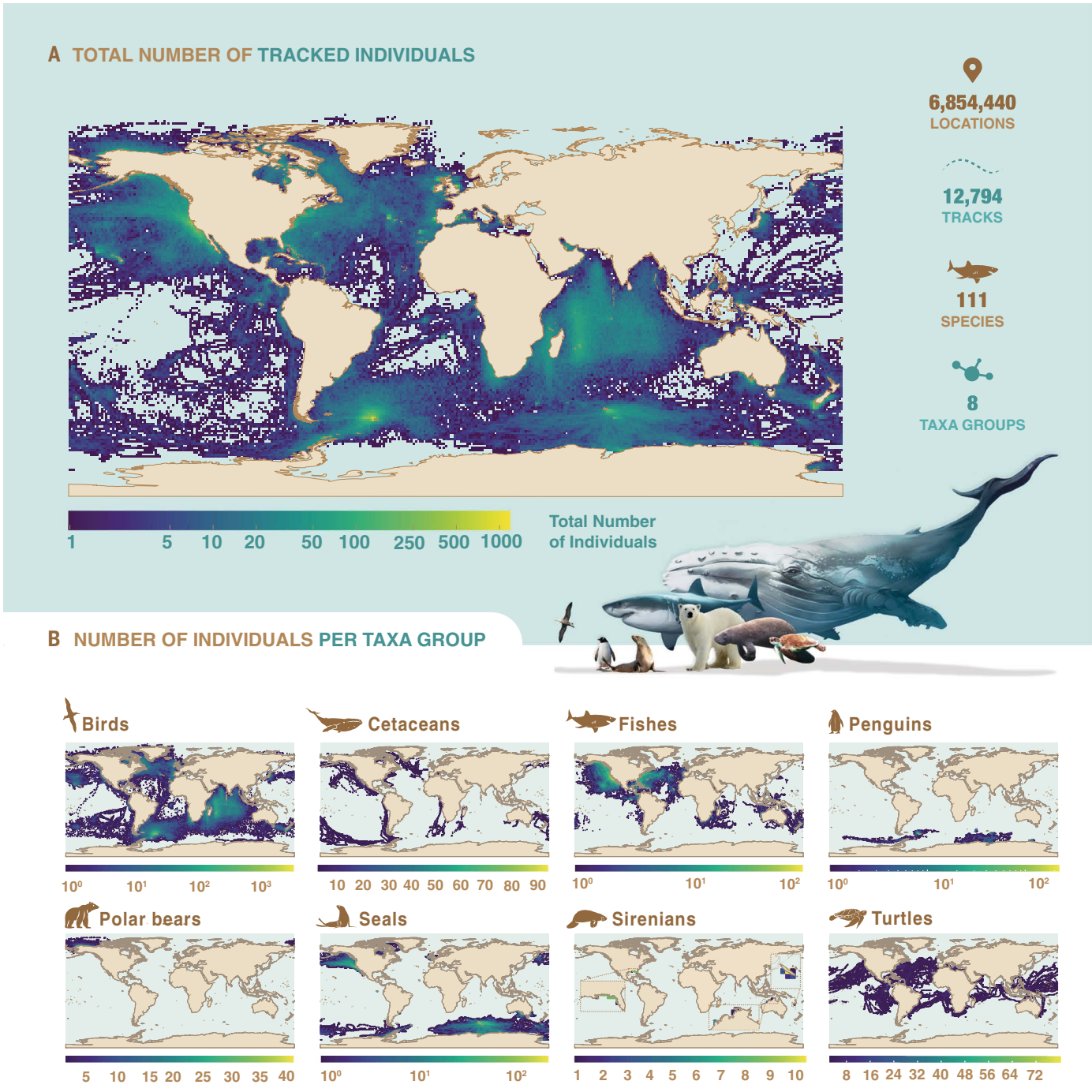

Fig. 1. Tracked movements of marine megafauna at the global scale. (**A**) Map of the total number of 12,794 individual track locations in the global dataset at 1° resolution showing the global coverage of 71.7% of the global ocean. (**B**) Maps per taxon showing the number of distinct individual track locations within each 1° grid cell. From top left to bottom right, maps per taxon show 6324 individual tracks for 39 species of flying birds; 749 for cetaceans, including 11 whales and 3 delphinid species; 1760 for fishes, including 23 shark species, 2 manta rays, and 1 ocean sunfish; 1324 for 6 species of penguins; 65 for polar bears; 1698 for 16 species of seals; 28 for sirenians, including dugongs and West Indian manatees; and 846 for all 7 sea turtles. The latitudinal and longitudinal coverage of tracked data is displayed in fig. S1. For reference, the first position obtained for each tracked individual (i.e., representing tagging locations), as well as captured and expected global biodiversity, is given in fig. S2. Maps showing the spatial extent of space use per species at 1° resolution can be seen in the data repository.

(*42*–*45*), plastic (*46*, *47*), and noise pollution (*48*, *49*). We identified these as threats on the basis of the IUCN Threats Classification Scheme (TCS) v3.3 (*50*, *51*) complemented with information from existing literature (*12*, *52*–*54*) and expert knowledge (fig. S4, and see table S4 for details). We then obtained available global threat data for fishing intensity (*55*), shipping density (*56*), plastic density (*46*, *57*), and warming (*58*, *59*) and considered noise to be ubiquitous [based on (*60*)], as no noise dataset is currently available at the resolution needed for a global analyses [but see, e.g., (*61*)].

Known biases (*23*, *62*, *63*) associated with uneven sampling and with tagging individuals in known aggregations or colonies were reduced in our analyses as far as possible by using multiple tagging sites for each species and, where applicable, by normalizing data to allow for direct comparisons across species and taxa. From specific tests to

assess the influence of (i) tagging location bias, (ii) temporal resolution of tracking data (i.e., including only one location per individual per day, in addition to all locations detected), and (iii) spatial resolution (i.e., repeating all procedures at 0.5°, 1°, and 2° grid cells), we found that these potential confounding factors had negligible effects on our main conclusions (figs. S5 to S8). Finally, randomization of tracks confirmed that animals are selectively using space for important behaviors (fig. S14).

Detected ecologically important areas for marine megafauna and extent of existing threats

We found that, on average, 66.1% of the total area covered by our tracking data was used as migratory corridors (50%) or residencies (44.8%) (Fig. 2A), with ~29% used for both behaviors (*30*); noting that for sirenians, data were insufficient to detect migratory behaviors (fig. S9). Animals spent on average 90% of their tracked time (estimated using one position per day) within areas where we detected these behaviors (Fig. 2B). Most of this time (~80%) was spent in areas used for residency (or both residency and migration) (fig. S10), with considerable overlap across both behaviors.

On average, only 7.5% of the entire area covered by our tracking dataset occurred inside MPAs (which currently cover ~8% of the global ocean), with ~5% corresponding to areas of detected residency or migratory behaviors (Fig. 2). Similarly, animals spent a greater amount of time outside, than inside, MPAs (on average >85%). The time spent inside MPAs corresponded, on average, to 13.6% of all time animals spent displaying residency or migratory behaviors (ranging between 0.3% for polar bears and 23.9% for penguins) (Fig. 2). The results indicate limited opportunity for meaningful conservation of marine megafauna within the current extent of global MPAs, which were mainly designed to protect specific habitats rather than threatened mobile marine megafauna. However, conservation efforts could be considerably improved in the future by specifically including IMMegAs in new MPA placement.

All space use and identified residency and migratory behaviors occurred with a ~40/60% split, respectively, between EEZs and the high seas, respectively (which, also respectively, cover 41.3 and 58.7% of the oceans) (Fig. 2). A similar split of space use between EEZ and high seas was obtained across each taxon, with clear exceptions for sirenians and polar bears (for which most movements occurred inside EEZs). Despite this pattern of space use slightly biased toward the high seas, most time (on average 74.1%, of which 67.1% corresponded to detected migration or residency) was spent inside, rather than outside, EEZs, and ranged from 61.5% for flying birds to 90.2% for cetaceans (Fig. 2). Although protection of high seas IMMegAs is urgently needed, the large proportion of time that animals spend conducting important behaviors within EEZs suggests that an initial focus on enhancing protection

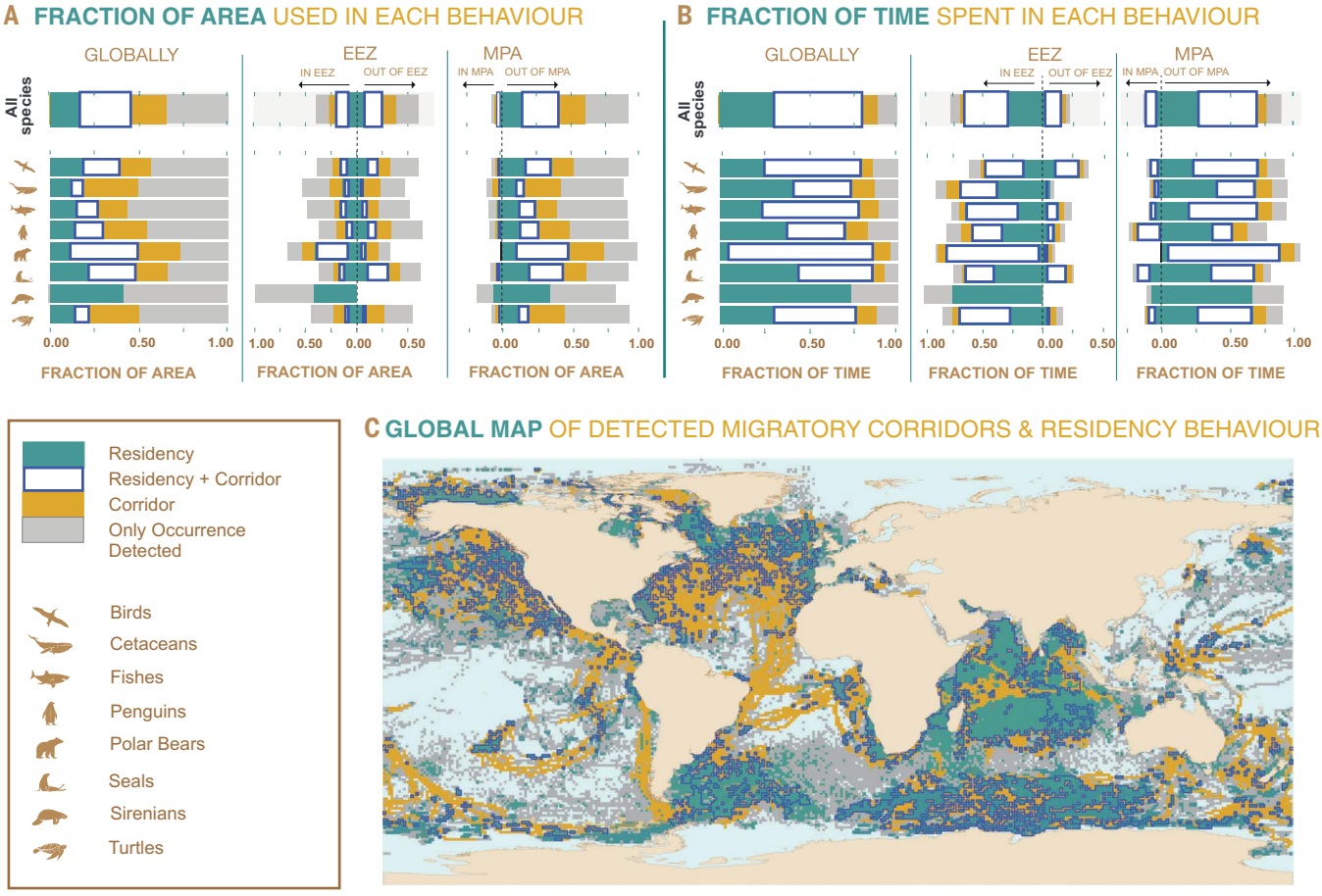

Fig. 2. Global space use of marine megafauna and time spent in different behaviors. Fractions of area (**A**) and time (**B**) used by animals globally (left plots), within and outside exclusive economic zones (EEZs) (middle plots), and within and outside existing marine protected areas (MPAs) (right plots), showing how much of the movements corresponded to detected migratory corridors or residency. Results are shown across all species together (top bar) and for each taxon (as displayed in the legend). For each taxon, the light gray portion in the bars indicates movement where no behaviors were detected. Species in each taxon group include flying birds (listed as birds), cetaceans (mostly whales but also dolphins), fishes (mostly sharks), penguins, polar bears (*Ursus maritimus*), seals, sirenians (i.e., dugongs and manatees), and turtles. (**C**) Map of detected migratory corridors, residence areas, and both corridors and residencies across taxa. Gray indicates grid cells where tracking data were available but no specific behavior was identified for any taxon. Light blue areas depict regions where we did not have tracking data. Maps of detected behaviors per taxon can be seen in fig. S9.

Table 1. Evidence of impacts from overlap of marine megafauna with anthropogenic threats. Examples of the range of impacts derived from the overlap of marine megafauna with anthropogenic threats such as climate warming, plastic pollution, shipping, noise pollution, and fishing. SST, sea surface temperature; UV, ultraviolet.

Birds (flying)	Cetaceans	Fishes	Penguins	Polar bear	Seals	Sirenians	Turtles
Climate							
Decreased survival	**UV damage**	**Habitat shift**	**Reduced prey**	**Habitat contraction**	**Habitat shift**	**Reduced food**	**Sex bias**
Affected survival and population growth rate of black-browed albatross juveniles with SST changes (*83*)	Increased skin lesions on whale related with increased UV irradiance (*84*)	Reduced counts of Scalloped hammerhead sharks *Sphyrna lewini* associated with rise in SST (*85*)	Decreased population size for penguin prey species with climate change (*86*)	Contraction of polar bear's habitat in the Arctic linked to long-term sea ice loss (*87*)	Decreased survival of southern elephant seal due to effects of sea ice dynamics on access to foraging (*88*)	Reduced dugong density by ~70% due to seagrass die-off triggered by an extreme heat wave (*89*)	Female-biased turtle populations linked to warming temperatures (*90*)
Plastic							
Ingestion	**Ingestion**	**Ingestion**	**Ingestion**	–	**Entanglement**	**Ingestion**	**Ingestion**
Death of shearwater and northern gannet due to plastic ingestion (*91*)	Stranded sperm whale stomachs with large amounts of plastic debris (*92*)	Threatened filter-feeding elasmobranchs by microplastic (*93*)	Plastic ingestion may have caused death (*94*)		Mortality of fur seals due to entanglement in marine debris (*95*)	Death of West Indian manatees from ingestion of plastic debris (*96*)	50% probability of mortality when turtles ingest pieces of plastic (*97*)
Shipping							
Habitat loss	**Ship strike**	**Ship strike**	**Noise effects**	**Ship strike**	**Propeller strike**	**Ship strike**	**Ship strike**
Habitat loss for common Eider's avoiding shipping traffic (*98*)	Increased ship strikes with humpback whales in shipping lanes (*39*)	Mortality of whale sharks correlated with risk of collision with ships (*41*)	Population collapse concomitantly with increase in noise (*99*)	Increased vulnerability of polar bears to vessel strike (*100*)	Propeller strikes affect harbor seals (*101*)	Death of manatees due to boat collisions (*102*)	Decreased survival of green turtles due to boat strikes (*103*)
Noise							
–	**Behav. change**	–	–	**Disturbance**	**Physical damage**	**Behav. change**	–
	Change in humpback whales foraging activity due to ship noise (*104*)			Disturbance of maternal dens due to seismic surveys (*105*)	Temporary hearing loss of gray and harbor seals around the British Isles (*106*)	Reduced foraging habitat for manatees due to boat noise (*107*)	
Fishing							
By-catch	**By-catch**	**Mortality**	**Reduced prey**	–	**Entanglement**	**Entanglement**	**By-catch**
High bycatch of seabirds in longline fisheries (*38*)	Higher rates of dolphin bycatch in a trawl fishery (*108*)	Greater mortality of pelagic sharks where sharks have higher exposure to longline fisheries (*23*)	Decreased population size of prey species with increased fishing of Antarctic Krill (*86*)		Increased entanglement of Cape fur seals associated with fishing (*109*)	Manatee mortalities from entanglement in fishing gear (*110*)	High levels of turtle bycatch in fishing gear hotspots (*37*)

within jurisdictions could provide the fastest benefits for marine megafauna conservation, particularly because implementation may be easier.

To identify what areas could be prioritized for protection, we used an optimization algorithm (figs. S15 and S16) to select a total of 30% of the 71.7% area covered by our tracking dataset (i.e., 21.3% of the global ocean; Fig. 3). We did this because our tracking dataset does not cover the entire ocean, and also to allow for later additions of new protected areas if other IMMegAs are identified once new tracking data are available. The optimization algorithm aims to highlight which areas could provide higher representativeness of IMMegAs, but also to indicate where the additional protected areas could be complementary to existing MPAs [sensu (*19*)], which currently fail to represent marine megafauna space use (*25*) (Fig. 3). Our results show that 30% area protection allows coverage of only less than half of the IMMegAs that we discovered (41.6 and 38.8%, respectively, based on data and model predictions; fig. S17), leaving ~60% unprotected (58.4%, and 61.2% based on data and model predictions, respectively) (Fig. 3).

Our complemented IUCN Threats Classification Scheme (*50*, *51*) (table S4) showed that commercial fishing and climate change affect more than 80% of the species included in our dataset (fig. S4). Shipping has impacts on species across all taxa, including all turtles, sirenians, polar bears, and most species of cetaceans considered, plus five birds, four fishes, five seals, and one penguin. Plastic pollution is a threat for all turtles and seals [but not yet listed on IUCN for leopard seals (*Hydrurga leptonyx*)], most cetaceans, and ~35% of birds. Some fishes are also listed as potentially being affected by this threat, including two manta rays and five sharks. Noise is listed as affecting all cetaceans, some seals, both sirenians, and also the polar bear, but for the latter this is likely due to potential disturbance of maternal dens on land.

Overlaying the identified (and predicted) areas used by marine megafauna for migration or residency behaviors at a global scale with each of the major global anthropogenic threats considered here (fig. S11), we found that >96% of IMMegAs are exposed to plastic pollution, shipping, and warming, and ~75% to fishing. This exposure includes overlaps within the areas of highest pressure observed for most threats—for example, in the North Atlantic, where we detected important areas for birds, cetaceans, fishes, and turtles (Fig. 2 and fig. S9).

Table 2. Summary of the logistic modeling inputs and results per taxon. Results of the generalized linear models relating the probability of a grid cell to be used as residence or for migratory behaviors with the set of environmental variables included in each model. Shown are the results for the highest ranked model according to the weight of the Akaike's information criteria (*wAIC*), as well as the number of parameters (*k*), the percentage of deviance explained (*pcdev*), and *Kappa*. Bold indicates the models not used to estimate the important marine megafauna areas (IMMegAs) derived from our modeling predictions (as presented in Fig. 3 and fig. S11). Species in each taxon group include flying birds (listed as birds), cetaceans (mostly whales but also dolphins), fishes (mostly sharks), penguins, polar bears (*Ursus maritimus*), seals, sirenians (i.e., dugongs and manatees), and turtles.

Taxon	Input			Results									
	Number of grid cells with:			Residence behavior					Migratory behavior				
	Presence	Residency	Migration	Model	*k*	*wAIC*	*pcdev*	*Kappa*	Model	*k*	*wAIC*	*pcdev*	*Kappa*
Birds	35,875	13,448	9,128	2	19	1.000	4.13	0.22	2	19	1.000	11.19	0.33
Cetaceans	4,397	1,501	1,758	2	19	1.000	16.52	0.44	2	19	0.980	12.62	0.29
Fishes	15,648	4,346	4,252	2	19	1.000	14.44	0.38	2	19	1.000	12.56	0.30
Penguins	1,385	446	452	1	17	1.000	13.62	0.4	2	19	1.000	40.16	0.56
Polar bear	1,124	451	803	2	14	0.995	24.78	0.33	2	14	1.000	27.78	0.48
Seals	11,358	5,510	7,175	2	19	1.000	3.12	0.22	2	19	1.000	14.91	0.30
Sirenians	114	27	0	–	–	–	–	–	–	–	–	–	–
Turtles	10,360	3,462	3,370	3	7	1.000	7.71	0.28	**2**	**19**	**1.000**	**5.18**	**0.17**

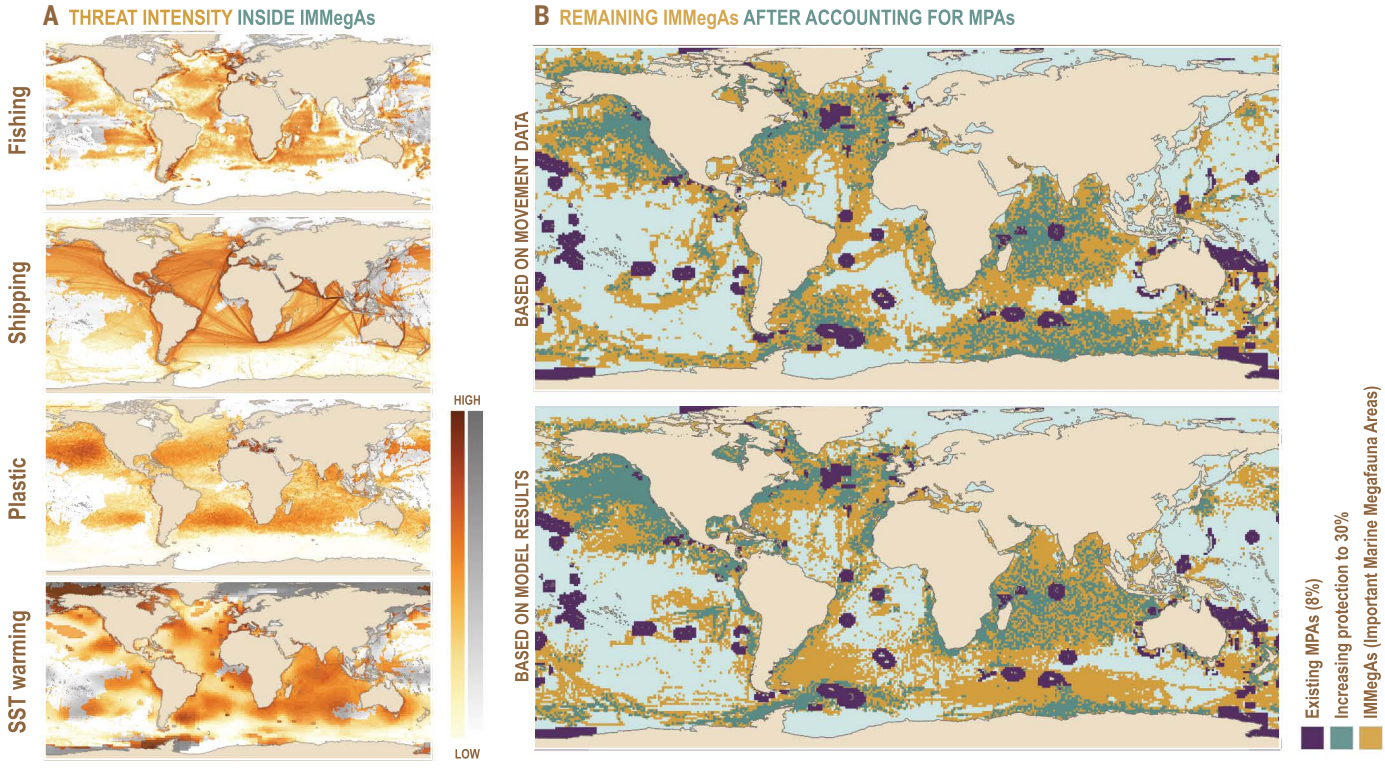

Fig. 3. Increase in area protection to 30% will leave ~60% of IMMegAs exposed to major anthropogenic threats. (**A**) Maps depicting average threat intensities for major anthropogenic threats with a global footprint: (from top to bottom) fishing, shipping, plastic pollution, and sea surface temperature (SST) warming. Displayed with an orange color palette are the threat intensities occurring inside IMMegAs, while a gray color palette is used to show the threat intensities outside IMMegAs. Note that we considered noise to be ubiquitous, as no noise dataset is currently available at the resolution needed for a global analyses. (**B**) Maps showing how much the increase in MPAs from the current 8% (purple) to 30% (green) would cover from our prioritization of IMMegAs detected from movement data (top map) and from our modeling predictions (bottom results). Note that coverage by MPAs only translates into protection from the anthropogenic threats considered if they are designated with the highest level of protection (i.e., with no activities allowed), and even then MPAs could only be effective for protection from fishing and shipping, leaving plastic and warming threats to continue to affect species. In addition to the increase in the current extent of MPAs, the introduction of mitigation strategies will assist in reducing the impact of existing threats and therefore the likelihood of human-induced extinctions.

Mitigation strategies will be needed in addition to the proposed increase in area protection to safeguard marine megafauna

Our results reveal that the 30% threshold is insufficient to encompass all IMMegAs globally (Fig. 3), leaving substantial conservation risks for marine megafauna. Considering the ubiquity of existing threats, which are pervasive in the IMMegAs that we detected (Fig. 3 and fig. S11), and the limited scope of the 30% GBF target for area protection, attaining the goal of zero loss of important biodiversity areas and halting human-induced mortality of threatened species seems unlikely (noting some management measures already in place for some species, table S5). Shipping and fishing can in part be alleviated by increasing MPAs [particularly if the highest level of protection is afforded (*64*)], which can also help reduce noise pollution. However, plastic pollution or climate change impacts will not be alleviated with the planned increase in area protection [even if MPAs can assist improving species resistance and resilience (*65*)]. Therefore, attaining the goal of zero loss of important biodiversity areas will need further action to mitigate anthropogenic pressures.

To reduce exposure of marine megafauna to existing threats and achieve the goals set out in the GBF, the introduction of additional forms of ocean management will be needed, including greater scrutiny of practices and additional direct management decisions with increased enforcement. For example, direct mortality can be reduced by applying fishing thresholds and enforcing standards in fishing operations (including modifications to gear) (*66*–*70*), and by developing wildlife-ship traffic separation schemes and slow-down areas (*71*, *72*) [e.g., to 2.16 knots (*73*)]. If applied in tandem with the increase in protected areas, such interventions will afford marine megafauna a much greater spatial protection from the major threats of industrialized fishing (*23*) and shipping (*41*) known to cause direct mortality (Table 1).

Our analyses show that animals use a large proportion of the high seas but spend the majority of their time within jurisdictions. This presents an opportunity for marine megafauna conservation because individual countries regulate and control most operations within their borders and are therefore able to implement mitigation measures to manage species that use their EEZs. Management of IMMegAs in the high seas, outside national jurisdictions, would benefit from better integration into the United Nations Convention for the Law of the Sea (UNCLOS) and should be considered in the ongoing process to better regulate biological resources in the high seas (*1*, *2*). For shipping threats specifically, International Maritime Organization regulations can reduce impacts and propel conservation success. For example, the double hull policy resulted in an average reduction of up to 62% in the size of oil spills (*74*). Engaging (and better regulating) the private sector is another timely way to advance conservation [e.g., (*75*)], as environmental damage is increasingly recognized as a threat to financial stability (*75*, *76*). Past management decisions, either involving the private sector [e.g., end of the whaling industry following the moratorium by the International Convention for Regulation on Whaling (*77*)] or by listing species on CITES [Convention on International Trade in Endangered Species (*78*)] have demonstrated success by leading to populations' recovery. However, the drivers of contrasting trajectories of similar populations or species (e.g., right whales increase in the Southern Ocean versus decrease in the North Atlantic) are not well understood and likely relate to different exposure to anthropogenic threats in the different regions.

Creating a larger network of MPAs will also greatly benefit from following a systematic conservation planning framework. Although our aim was to identify IMMegAs (rather than outlining what the final 30% of area protection should look like), we followed the initial necessary steps of that framework, including (i) using marine megafauna biodiversity data (as a surrogate for marine biodiversity); (ii) using the set targets from the GBF and UN High Seas Treaty as a goal; (iii) focusing on complementing existing MPAs; and (iv) selecting IMMegAs for potential inclusion as MPAs. We then provide a scenario for protection for up to 30% extension of MPAs to show that even if all areas selected for protection specifically included IMMegAs, the 30% protection would still be insufficient to reach set targets, and other mitigation measures will be needed. To follow a systematic conservation planning approach, the final selection of protected areas should also take into consideration aspects not considered here, such as ecosystems of high ecological importance or habitat types that are not yet well represented, as well as considerations of equity and principles of environmental justice (*79*). It is, however, likely that the final selection of areas for protection will end up being designed to minimize impacts to stakeholders (including the fishing, shipping, energy production, and tourism industries). Such a possible result further reinforces our conclusion that relying on the 30% area protection will be insufficient to reach the goal of zero loss of important biodiversity areas and halt human-induced mortality of threatened species, and that additional mitigation measures are needed before it is too late.

The work we provide here shows the power of assembling tracking datasets to answer pressing conservation concerns. The continued expansion of MegaMove through voluntary contributions will foster greater collaborations allowing researchers to fill data gaps and further reduce biases. Whereas our tracking data cover about 71% of ocean space, the tagging effort was neither random nor uniform in space and time, and 29% of the ocean space was not covered by our dataset (including the central and northwest Pacific ocean). We suggest that statistical models using existing tracking data as input could be used to develop refined global species distributions that take into account animal movements associated with short-term changes in environmental parameters to project the likelihood of encountering animals in areas underexplored by telemetry or bio-logging (*80*–*82*).

We also recognize that the available threat distribution data that we used here are incomplete and do not include, for example, illegal or artisanal fishing fleets, or discrimination across fishing gear (which affects species differently). This means that a more detailed spatio-temporal analysis of exposure to threats, as well as an assessment of the vulnerability of different species to specific threats, is required to quantify their potential impacts on species' life-history characteristics. Consideration of the phylogenetic diversity of marine megafauna by examining evolutionary drivers could also be relevant to improving spatial maps. Nevertheless, the IMMegAs that we have identified are key to informing the expansion of existing MPAs to reach the 30% target both within EEZs and in the High Seas.

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SUPPLEMENTARY MATERIALS

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