MARINE CONSERVATION

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

All authors with their affiliations appear at the end of this paper.

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

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

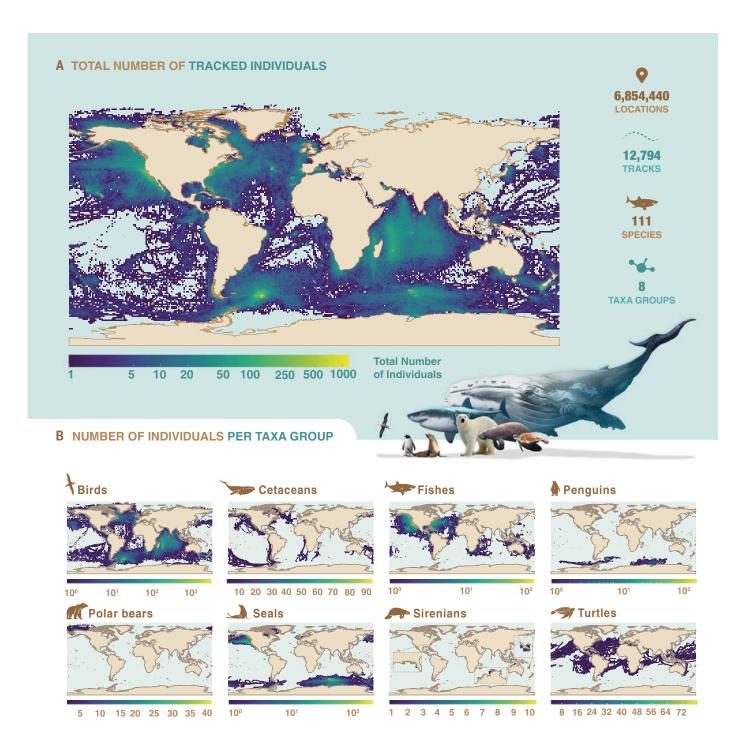


Fig. 1. Tracked movements of marine megafauna at the global scale. (A) Map of the total number of 12,794 individual track locations in the global dataset at 1° resolution showing the global coverage of 71.7% of the global ocean. (B) Maps per taxon showing the number of distinct individual track locations 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).

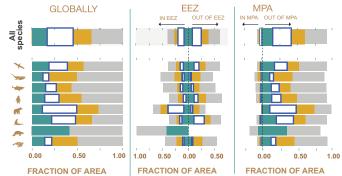
Detected ecologically important areas for marine megafauna and extent of existing threats

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.

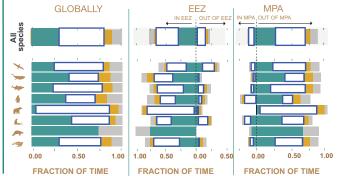
On average, only 7.5% of the entire area covered by our tracking dataset occurred inside MPAs (which currently cover ~8% of the global ocean), with ~5% corresponding to areas of detected residency or migratory behaviors (Fig. 2). Similarly, animals spent a greater amount of time outside, than inside, 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.

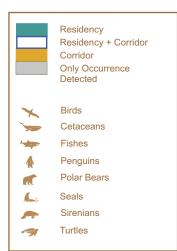
All space use and identified residency and migratory behaviors occurred with a ~40/60% split, respectively, between EEZs and the high seas, respectively (which, also respectively, cover 41.3 and 58.7% of the oceans) (Fig. 2). A similar split of space use between EEZ and high seas was obtained across 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

A FRACTION OF AREA USED IN EACH BEHAVIOUR



B FRACTION OF TIME SPENT IN EACH BEHAVIOUR





C GLOBAL MAP OF DETECTED MIGRATORY CORRIDORS & RESIDENCY BEHAVIOUR

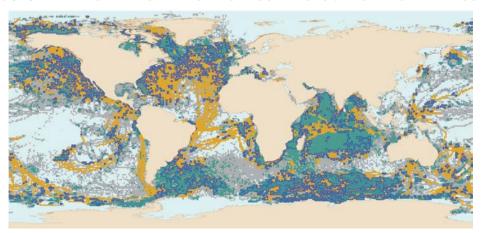


Fig. 2. Global space use of marine megafauna and time spent in different behaviors. Fractions of area (A) and time (B) used by animals globally (left plots), within and outside exclusive economic zones (EEZs) (middle plots), and within and outside existing marine protected areas (MPAs) (right plots), 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.

(flying)	Cetaceans Fishes Pengui		Penguins	Polar bear	Seals	Sirenians	Turtles	
Climate								
Decreased survival	UV damage	Habitat shift Reduc		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 ham- merhead 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 sur- vival 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 temper- atures (90)	
Plastic								
Ingestion	Ingestion	on Ingestion In		_	Entanglement	Ingestion	Ingestion	
Death of shearwa- ter 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 entan- glement in marine debris (95)	Death of West Indian manatees from ingestion of plastic debris (96)	50% probability of mortality when tur- tles 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 con- comitantly 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 colli- sions (102)	Decreased surviva 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 man- atees 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).

Birds

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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	Карра	Model	k	wAIC	pcdev	 Карра
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

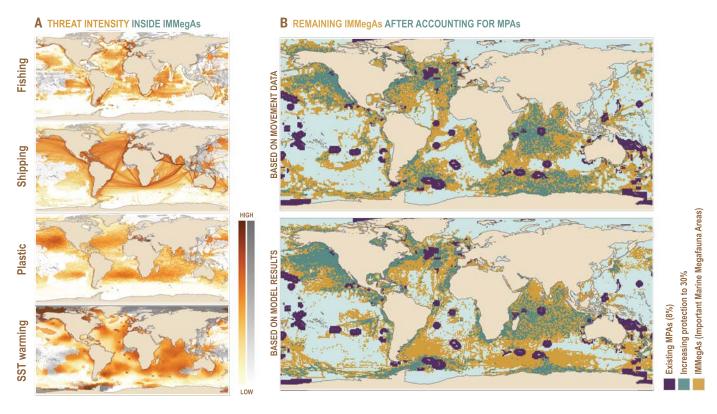


Fig. 3. Increase in area protection to 30% will leave ~60% of IMMegAs exposed to major anthropogenic threats. (A) Maps depicting average threat intensities for major anthropogenic threats with a global footprint: (from top to bottom) fishing, shipping, plastic pollution, and sea surface temperature (SST) 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

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 humaninduced 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 spatiotemporal 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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ACKNOWLEDGMENTS

This research contributes to the MegaMove project endorsed by the UN Decade of Ocean Science (megamove.org). We thank M. Heupel for early discussions, L. Londoño for early assistance with formatting data, K. Goetz for earlier involvement, and all involved in fieldwork and data collection; see full details in supplementary acknowledgments. We thank Global Fishing Watch and the Global Shark Movement Project for making data available. Ethics and permits information are fully detailed in the supplementary materials. This study has been conducted using EU Copernicus Marine Service Information (https://doi.org/10.48670/ moi-00021 and https://doi.org/10.48670/moi-00019); NASA Ocean Biology Distributed Active Archive Center (OB.DAAC) data (https://oceandata.sci.gsfc.nasa.gov/opendap/ SeaWiFS/L3SMI/ and https://oceandata.sci.gsfc.nasa.gov/opendap/MODISA/L3SMI/ contents.html); and the European Centre for Medium-Range Weather Forecasts ERA-Interim Reanalysis product (https://www.ecmwf.int/en/forecasts/dataset/ecmwf-reanalysisinterim). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government. Funding: A.M.M.S. was funded by a 2020 Fellowship in Marine Conservation by the Pew Charitable Trusts, and ARC DP DP210103091, and through support provided by the Jock Clough Marine Foundation and three other anonymous donors. G.C.H. acknowledges funding from the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science (BPMS-2017-4). D.P.C. was funded by ONR and SERDP grant RC20-C2-1284. D.W.S. acknowledges funding from ERC-2019-ADG 883583 OCEAN DEOXYFISH and NERC NE/R00997X/1. V.M.E. acknowledges funding from MCIN/ AEI/10.13039/501100011033 (PID2020-114324GB-C22). S.A. was supported by Ministerio de Educación, Cultura y Deporte (Spain) [FPU15/01823]. Satellite transmission fees were funded by Universitat Politècnica de València. Tag acquisitions were supported by Universitat Politécnica de València, Asociación Chelonia and Centro de Recuperación de Animales Marinos (CRAM). A.S.A. acknowledges funding granted by the National Geographic Society Conservation Trust (no. C314-15), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES (BJT/A049-2013), and Fundação para a Ciência e Tecnologia - FCT (CEEIND/02566/2021, UIDP/04292/2020, and LA/P/0069/2020). N.P.A.B. was funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPa) under grant no. 482557/2011-7. R.D.A. was funded by the North Pacific Research Board and NOAA Fisheries with additional support from Texas A&M University and the Alaska SeaLife Center. M. Antonopoulou acknowledges seed funding for this work provided by the Emirates Nature -World Wild Fund for Nature office in the UAE and by the numerous private sponsors, listed here in alphabetical order: 7Days, Abu Dhabi Urban Planning Council, Bridgestone, CASP, College of the North Atlantic, Qatar, Deutsche Bank, Dubai Electricity & Water Authority, Dubai Festival City, Emirates Palace, Environment & Protected Areas Authority, Sharjah, Environment Agency-Abu Dhabi, Fairmont, Géant, Gulftainer, HSBC, Intercontinental, Dubai Festival City, Jebel Ali Golf Resort & Spa, Jumeirah Etihad Towers, Linklaters, Momentum Logistics, Mubadala, Murjan Marinas, Nokia, Sheikha Salama bint Hamdan Al Nahyan Foundation, The Club, TimeOut Dubai, and the Young Presidents Organisation. J.A.A. was funded by a scholarship from the Comisión Nacional de Investigación Científica y Tecnológica (CONICYT),

Chile, and acknowledges the Chilean Antarctic Institute, which funded the field campaign. GLS tags were provided by the British Antarctic Survey (BAS). G.A. acknowledges The Rufford Foundation. I.A. was funded by the Basque Government and the European Data Collection Programme. M. Auger-Méthé acknowledges the Canadian Research Chairs Program. R.W.B acknowledges the US Navy (Pacific Fleet, Atlantic Fleet, Living Marine Resources and Office of Naval Research) and the NMFS (Pacific Islands Fisheries Science Center and Southwest Fisheries Science Center). A. Barnett acknowledges the Save Our Seas Foundation, Holsworth Wildlife Research Endowment, Winifred Violet Scott Charitable Trust and the Slattery Family Trust. E.J. Belda acknowledges that satellite transmission fees were supported by personal research funds made available by the Universitat Politècnica de València. Tags acquisition was funded by Ministerio de Agricultura y Medio Ambiente (16MNSV006); Ministerio de Economía, Industria y Competitividad (CGL2011-30413); Fundación CRAM, Fundación Hombre y Territorio. J. Tomás was supported by project Prometeoll (Generalitat Valenciana) and project INDICIT (EU). Funding for the transmitters came from the JM Kaplan Foundation award to the World Wildlife Fund (WWF) Canada, and from several European institutions: the Spanish International Cooperation Agency (AECI Projects A/2991/05 and A/5641/06), the Spanish Ministry of Education and Sciences (CGL2006-02936-BOS and CGL2011-30413) and the General Foundation of the University of Valencia. The project also received funding from the European Union (Marie Curie grant nos. FP6 and FP7). A. Bennison was funded by the Irish Research Council (Project ID: GOIPG/2016/503). S.R.B. acknowledges financial support and personnel provided by NMFS (Southwest Fisheries Science Center, Southwest Region, Pacific Islands Region, and Office of Protected Resources), and the Tagging of Pacific Predators (TOPP) program of the Census of Marine Life. R.B. received funding from The Wildlife Conservation Society, The Roe Foundation Inc., NABU/Shark Tracker, The National Geographic Society Explorations Council, and The Eppley Foundation. S.E.C. acknowledges funding from the International Governance Strategy of Fisheries and Oceans Canada. H.A.C. acknowledges Australia Zoo. V.G.C. was funded by the Buenos Aires Zoo, Wildlife Conservation Society, Fondo para la Conservación Ambiental from Banco Galicia, the Cleveland Metropark Zoo-Scott Neotropical Fund, the Inter-American Institute for Global Change Research (IAI) CRN 2076 sponsored by the US National Science Foundation (NSF) grant GEO-0452325, and the Agencia Nacional de Promoción Científica y Tecnológica FONCyT PICT 2013-2099 Prestamo BID. R.H.C. was funded in part by the Dauphin Island Sea Lab, University of South Alabama, Alabama Division of Wildlife and Freshwater Fisheries under traditional Section 6 of the US Fish and Wildlife Service, the Northern Gulf Institute, Mobile Bay National Estuary Program, and the Seamen's Foundation. G.C. was supported by a Macquarie University Research Excellence Scholarship. J. Charrassin acknowledges that the Weddell seals tagging study in Dumont d'Urville by LOCEAN laboratory was supported by the Program Terre-Océan-Surface Continentale-Atmosphère from Centre National d'Etudes Spatiales (TOSCA-CNES), and the Australian Animal Tracking and Monitoring System (AATAMS), a facility of Integrated Marine Observing System (IMOS). The Institut Paul Émile Victor (IPÉV) programs 109 and 394, Terres Australes et Antarctiques Françaises (TAAF), and the Australian Antarctic Division provided logistical support. A. Chiaradia acknowledges funding provided by the Australian Government Research Training Program, Australian Research Council (Linkage Project; LP140100404), Monash University, Phillip Island Nature Parks, Institut Pluridisciplinaire Hubert Curien, ANR-2010-BLAN-1728-01, Australian Conservation Foundation, The Penguin Foundation, Parks Victoria, Centre d'Etudes Biologiques de Chizé and La Rochelle Université, Holsworth Wildlife Research Trust, and Coastcare Australia. C.C. was supported by the New Caledonian Dugong Technical Committee under the 2010-2015 Dugong Action Plan in New Caledonia. E.E.G.C. was supported by the Coral Reef Initiative for the South Pacific (CRISP) mostly funded by the Agence Française de Développement (AFD). R.C. acknowledges the New Zealand Ministry for Primary Industries – BRAG; Pew Charitable Trusts; Southern Ocean Research Partnership – International Whaling Commission; Australian Antarctic Division; University of Auckland; Institut de Recherche pour le Développement, France; Conservation International; Blue Planet Marine; Opération Cétacés, New Caledonia; National Marine Mammal Laboratory - NOAA; and the Scientific Committee for Antarctic Research (SCAR), UK. M.L.C. was funded by a Pew Fellowship Award in Marine Conservation and acknowledges European project FEDER Biodiversité. E. Cuevas-Flores acknowledges the Mexican National Council for Science and Technology - Mexican Ministry of Environment and Natural Resources (project 107770, CAMP-2005-C01-046), the National Fish and Wildlife Foundation (2006-0091-005), Alliance WWF- Carlos Slim Fund, Chelonia, Inc., Satellite Tracking and Analysis Tool (STAT). S. Diamant was supported by the PADI Foundation and IDEA WILD. K.L.D. acknowledges funding support from the University of New Hampshire Marine Program, Large Pelagics Research Center, NOAA grants (NAO4NMF4550391 and NA10NMF4720028), National Fish and Wildlife Foundation (2008-0076-000), and the Cape Cod Commercial Fishermen's Alliance. A.D.M.D. was funded by the Georgia Aquarium, UKG Darwin Initiative St Helena Government, T.K.D. was funded by the UCC Strategic Research Fund, L.L.D. acknowledges funding provided by the North Carolina Renewable Ocean Energy Program, administered by the Coastal Studies Institute (East Carolina University Outer Banks Campus). M.V.E. warmly thanks the Indonesian Ministry of Environment and Forestry and Ministry of Marine Affairs and Fisheries, the Cenderawasih Bay National Park Authority, the Raja Ampat MPA Management Authority, and the people and government of Raja Ampat, Milne Bay, West Papua, Bali, East Kalimantan and Nusa Tenggara Timor provinces (especially those from Desa Labuhan Jambu and Desa Kwatisore) for their sponsorship and support, as well the following donors who financially supported our tagging: the Sunbridge Foundation, SEA Aquarium Singapore, MAC3 Impact Philanthropies, and the Wolcott Henry Foundation, the owners and guests of the MV True North, Asia Coating Enterprise, M.E. Mali, D. Roozen, A. and S. Wong, E. Tan, S. Argyropolous, D. Arnall, A. Hasan, R. Mambrasar, S. Heinrichs, S. Lewis. I. Syakurachman, M. Brooks, P. Rorke-Levy, and S. Neiman. N.E. acknowledges the Dutch Caribbean Nature Alliance. C.F. acknowledges that sooty tern tracking in Seychelles was funded by the Percy Sladen Foundation, James Cadbury, Robert Gaines-Cooper, Kang Nee, Amanda O'Keefe, Colin & Fiona Short, and Brian & Margaret Jasper. Funding was provided by DFO (Emerging Fisheries), Government of Nunavut, Nunavut Wildlife Research Trust Fund, Nunavut General Monitoring Program, Nunavut Wildlife Management Board (no. 3-09-04), Ocean Tracking Network, University of Windsor, University of Manitoba, ArcticNet Centre of Excellence, Natural Sciences and Engineering Research Council Canadian, Federal Program Office of International,

Polar Year (MD-112), Northern Scientific Training Program (Canadian Polar Commission), Polar Continental Shelf Project, W. Garfield Weston Award for Northern Research, and the Molson Foundation. F.F. acknowledges the Bertarelli Foundation. S.F. acknowledges financial and logistical support provided by Megaptera, its members and friends, the Greenland Institute of Natural Resources, Axa Research Fund, Exagone, Sea Blue Safari, Mikkels Vaerksted, Fondation Nature et Decouverte and the National Geographic Society Waitt Grant Program. A.S.F. was funded by the Antarctic Wildlife Research Fund (ANT-0823101), NSF Office of Polar Programs (OPP) ANT-0823101, 1250208, and 1440435, IWC, and Southern Ocean Research Partnership awards. C. Garrigue was funded by New Caledonian Government, Ministère de la Transition Ecologique et Solidaire, WWF for Nature France, Greenpeace International, and Fondation d'Entreprise Total and Opération cétacés NC. B.J.G. acknowledges the Natural Environment Research Council (NERC), Darwin Initiative, Marine Turtle Conservation Fund (USFWS, US Department of the Interior). S.D.G. acknowledges the Australian Marine Mammal Centre, Fisheries Research and Development (PN 2005/031), Integrated Marine Observing System (IMOS), DEW, Professional Association of Diving Instructors (PADI) Project Advancing Wellness and Resilience in Education (AWARE), Australian Bird Environment Foundation, Holdsworth Wildlife Research Endowment, Sea World Research and Rescue Foundation Inc., Nature Foundation of South Australia, South Australian Department for Environment and Heritage Wildlife Conservation Fund, Australian Geographic Society, Norman Wettenhall Foundation, Wildlife Conservation Fund of South Australia, South Australian Research and Development Institute (SARDI) Women's Bursary 2005, MA Ingram Trust, and Lirabenda Fund (Field Naturalist Society). T.L.G. acknowledges the Save Our Seas Foundation, Swiss Shark Foundation, Watermen Project. Staff and volunteers at Bimini Biological Field Station Foundation. K.C.H. acknowledges funds provided by NERC and the Department for Business, Energy and Industrial Strategy. N.H. acknowledges support by The Batchelor Foundation, Disney Conservation Fund, Wells Fargo, Guy Harvey Ocean Foundation, Oceana, Oracle, and the West Coast Inland Navigation District. R.H. acknowledges funding provided by the Ministry for Business, Innovation and Employment Endeavour Fund C01 1710: "RAMPing-up protection of the Ross Sea," by NZARI (NZ Antarctic Research Institute) and Fisheries New Zealand (respectively), with Regina Eisert as CI, and tags and some field personnel funded by IMOS. The IMOS deployments in Prydz Bay were supported logistically by the Australian Antarctic Division through the Australian Antarctic Science Grant Scheme (ÁAS Projects 2794 and 4329). Work was partially funded by an Australian Research Council Linkage Grant to R.H. and David Slip (LP110200603). C.E.H. acknowledges the Earthwatch Institute, David and Lucile Packard Foundation, Wallace Research Foundation, PADI Foundation, and the Arizona-Sonora Desert Museum. Funding was also provided by the Secretaría de Educación y Posgrado - Instituto Politécnico Nacional (projects: SIP20141052; SIP20151561; SIP20161935) and the NGO Investigacion, Capacitacion y Soluciones Ambientales y Sociales A.C. C.E.H. received a Masters degree bursary from the University of Exeter and the European Social Fund and would like to thank Consejo Nacional de Ciencia y Tecnología (Mexico) for support through a PhD scholarship. L.A. Huckstadt was funded under NSF OPP grants ANT-0110687, 0840375, 0533332 and 0838937, the National Undersea Research Program, and the National Oceanographic Partnership through the Office of Naval Research (ONR). N.E. Hussey acknowledges funding from the National Sciences and Engineering Research Council of Canada. C.H. acknowledges support from the Nature Foundation SA Inc., Save Our Seas Foundation, Neiser Foundation, Humane Society International, and Mohamed bin Zayed species conservation fund. R.W.H.I. acknowledges TOPP funding (ONR, NSF, Moore, Sloan, and Packard Foundation) and US EPA GRO fellowship. A.A.K. also acknowledges the following management/advisory affiliations/paid consulting activities as part of the Top Predator Scientific Working Group of South Africa (Department of Forestry, Fisheries, and the Environment); the Global Shark Movement Project; Shark Spotters NPO (executive committee); South African Whale Disentanglement network (executive committee). D.M.P.J. acknowledges funding from the National Marine Aquarium (UK) and National Geographic. M.J. was supported by the Science Foundation Ireland Centre for Marine Renewable Energy Research (MaREI 12/RC/2302) and fieldwork supported by the Petroleum Infrastructure Programme (IS13/08) and FishKOSM project funded by the Department of Agriculture, Fisheries and the Marine (15/S/744). F.O.L. acknowledges The Pew Charitable Trusts (PEW) Ocean Science Division and Global Shark Conservation Campaign and Fundação Apolônio Salles de Desenvolvimento Educacional (FADURPE). P.H.L. thanks CENPES/PETROBRAS (Centro de Pesquisas da PETROBRAS) for supporting the 'Mamíferos e Quelônios Marinhos Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, PhD scholarship to T.Z.S., process number 141361/2010-7. J.L. thanks the Founder of the Save Our Seas Foundation for funding and providing all facilities for his work. G.L. was funded in part by US Fleet Forces Command and managed by Naval Facilities engineering Command Atlantic as part of the US Navy's marine species monitoring program. Additional funding was provided by the National Marine Fisheries Grant to States Program (grant NA09NMF4720033) and by private donations managed by the Virginia Aquarium & Marine Science Foundation. P.L. acknowledges the Italian Consiglio Nazionale delle Ricerche (CNR) and Ministry of Research, University of Pisa, Swedish Natural Science Research Council, NERC, the Darwin Initiative, Italian Space Agency and Accademia Nazionale dei Lincei. The work at Ascension Island was financed by grants from the Swedish Research Council and the Crafoord Foundation to S.Å. B.C.L.M. acknowledges the Secretaria da Comissão Interministerial para os Recursos do Mar (SECIRM/Brazilian Navy) and CNPq provided grant (no. 405460/2012-0) for logistics and equipment through Pró-Arquipélago/Oceanic Islands Program. The Grupo Fundação Boticário de Proteção à Natureza (0760/2007.2), Save Our Seas Foundation (66/2008) and CNPq (478070/2008-0, 482557/2011-7), provided grants for the satellite tags. A.I.M., S.D.G. and R.H. acknowledge that satellite tagging of Southern Right Whales in the Great Australian Bight, Australia was funded by a grant from the Department of the Environment Australian Marine Mammal Center, with in kind support from the South Australian Research and Development Institute (Aquatic Sciences), Blue Planet Marine, Macquarie University and Flinders University. They would like to acknowledge the support provided by M. Double and V. Andrews-Goff at the Australian Marine Mammal Centre, and all those who participated in fieldwork, M.L. Mallory acknowledges Environment Canada, Natural Resources Canada, Greenland Institute of Nature, Molson Foundation, Natural Sciences and Engineering Research Council of Canada, Canadian Wildlife Federation, and Acadia University. J.C.M. acknowledges

project funding and equipment provided by NOAA, NMFS Southwest Fisheries Science Center, and the National Fish and Wildlife Foundation. D.M. acknowledges the BBVA Foundation ("Ayudas Fundación BBVA a Equipos de Investigación Científica 2016"), Spanish Government (grant "Juan de la Cierva-Formación" FJCI-2014-20064), Fundación Reina Sofía (LIBERA 2017), and NOAA. A.M. acknowledges the Doñana Biological Station (EBD-CSIC), Consejería de Medio Ambiente y Ordenación del Territorio (CMAOT) of Junta de Andalucía, the Andalusian Marine Énvironment Management Center (CEGMA) and the NGO Equinac M. Marcoux was funded by the DFO Nunavut Implementation Fund and the Strategic Program for Ecosystem-Based Research and Advice. Narwhal tagging efforts were supported from the World Wildlife Fund and the Nunavut Wildlife Management Board. L.M. was principally supported through the Australian Government's Fisheries Research and Development Corporation (FRDC) Grants Scheme (PN 2005/031), co-funded by the South Australian Sardine Fishery. We also thank the Nature Foundation South Australia for financial assistance that supported the purchase of GPS units. G.M. was principally supported by Xunta de Galicia, Spain, throught Isabel Barreto Programme (2009–2012) and FCT grants (PTDC/ MARBIO/4458/2012; IF/01611/2013; NORTE-01-0145-FÉDER-000031). M.M.C.M. acknowledges the MEOP-BR (Marine Mammals Exploring the Oceans Pole to Pole; Brazil), an International Polar Year (IPY) program funded by the Brazilian Science, Technology and Innovation Ministry through the Brazilian National Research Council (CNPq, grant no. 520196/2006-6). M.A.C.N. acknowledges the petrel tracking program and Malcolm Nicoll were supported by NERC (grant NE/H5081500) with insitu support from MWF and NPCS. W.J.N. was supported by a Fulbright Fellowship and a Marshall Fellowship during the period field research in Baja California was conducted. B.M.N. and S.D.R. acknowledges the many supporters, funders, donors and volunteers of ECOCEAN Inc. B.P. received a Commonwealth Scientific and Industrial Research Organisation (CSIRO) Marine Research scholarship. E.O. acknowledges funding provided by NOAA NMFS, the Institute of Marine Research in Norway, the Nordic Council of Ministers, and FCT (grants: SFRH/BD/32520/2006 and SFRH/ BPD/29841/2006). S. Oppel acknowledges that work on Ascension Island was partly funded by a Darwin Grant (19026) to Ascension Island Government and the University of Exeter (A.C.B. and B.J.G.), managed on-island by N.W. and S.B.W.. The king eider study was funded by the Coastal Marine Institute (University of Alaska, Fairbanks), Minerals Management Service, US Geological Survey (Outer Continental Shelf Program), and Canadian Wildlife Service. Further financial and technical support was provided by the Sea Duck Joint Venture, USFWS, North Slope Borough, ConocoPhillips Alaska Inc., Inuvialuit Wildlife Management Advisory Council, WWF, BP Exploration Alaska, Polar Continental Shelf Project, US Geological Survey Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology (University of Alaska Fairbanks), and German Academic Exchange Service. The work on St Helena was partly funded by Enterprise St Helena and the Seabird Group. The David and Lucile Packard Foundation, Darwin Plus: Overseas Territories Environment and Climate Fund, the Sir Peter Scott Commemorative Expedition to the Pitcairn Islands, generous donors, and the Royal Society for the Protection of Birds (RSPB) helped to fund our research. A.M.P. acknowledges the US Geological Survey (USGS) Ecosystems and Climate and Land Use Change Mission Areas, the USGS Changing Arctic Ecosystems Initiative, and the Bureau of Land Management for primary funding. Additional support was provided through a National Science Foundation grant to the University of Wyoming; the United States Fish and Wildlife Service, Marine Mammals Management and the Arctic National Wildlife Refuge; Environment and Climate Change Canada; the North Slope Borough, Department of Wildlife Management; the Polar Continental Shelf Project; Polar Bears International; the University of California, Santa Cruz; the San Diego Zoo Wildlife Alliance; and the University of Alberta. V.H.P. acknowledges EU INTERREG project FAME: The Future of the Atlantic Marine Environment (2009-1/089) and by LIFE+Berlenga (LIFE13 NAT/PT/000458). Strategic program of Marine and Environmental Sciences Centre (MARE), financed by FCT (MARE – UID MAR/04292/2013). LIFE Project Marine Important Bird Areas (2004–2008) by the EU INTERREG Project FAME: The Future of the Atlantic Environment (2010-2012) founded by the EU. D.M. Palacios and B.M. acknowledge support provided by the TOPP program of the Census of Marine Life, the US Minerals Management Service, the US ONR (Grants 9610608, 0010085, 0310861, N0014-02-1-0885, NO-176A, and NO0014-09-1-0453), NSF, the Alfred P. Sloan Foundation, the Moore Foundation, the Packard Foundation, the National Geographic Society, the IWC (with funds provided by Exxon Neftegas Limited and Sakhalin Energy Investment Company), the National Research Foundation of South Africa (GUN no. 2047517), NOAA through the Northeast Consortium, based at the University of New Hampshire (grant no. NA16FL1324), the International Association of Oil and Gas Producers "Sound and Marine Life Joint Industry Programme," and private donors to the Oregon State University Endowed Marine Mammal Institute. L.R.P. was funded by the Save Our Seas Foundation and supported by the Manta Trust, the University of Western Australia, and the Australian Institute of Marine Science. Field work was supported by the SOSF-D'Arros Research Centre. N.J.P. was funded by Emirates Nature - WWF and multiple supporting agencies. M.P. acknowledges that New Zealand funding was provided by MBIE Endeavour Fund C01X1710 (Ross-RAMP), NIWA SSIF (Coasts & Ocean Centre, program 4) and NIWA Strategic CAPEX. L.P. and M. Lopez Mendilaharsu were funded by the Convention of Migratory Species, WWF as part of the Trans-Atlantic Leatherback Conservation Initiative, and Peoples Trust for Endangered Species, UK. The Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior (CAPES) provided a grant to M. Lopez Mendilaharsu. N.Q. acknowledges CEECIND/02857/2018; PTDC/MAR/100345/2008 and COMPETE FCOMP-01-0124-FEDER-010580; PTDC/BIA/28855/2017 - COMPETE 1094 POCI-01-0145-FEDER-028855 F.R.C. acknowledges the transitory norm contract at the University of Coimbra (DL57/2016/ CP1370/CT90) and the projects UIDB/04292/2020, UIDP/04292/2020, granted to MARE, and LA/P/0069/2020, granted to the Associate Laboratory ARNET, financed by the Foundation for Science and Technology (FCT; Portugal). J.A.R. acknowledges EU INTERREG project FAME (Future of the Atlantic Marine Environment), Fundação para a Ciência e Tecnologia (FCT; SFRH/BPD/63825/2009 and SFRH/BPD/85024/2012), EU project LIFE09 NAT/PT/000041 and by EU INTERREG project FAME 2009-1/089, as well as co-sponsorship by FCT and the European Social Fund (POPH, EU) through post-doctoral grants SFRH/ BPD/95372/2013SFRH/BPD/85024/2012 and the strategic program of MARE (UID/ MAR/04292/2013 and UID/MAR/04292/2020), and LIFE project "Safe Islands for Seabirds" (LIFE07 NAT/P/000649). A.J. Read acknowledges the US Navy (Atlantic Fleet Forces

Command) for funding field work and analysis. A.F.R. acknowledges the TOTAL Foundation and TOTAL Muscat Branch. D.R. was supported by Save our Seas Foundation, Project Aware, Royal Geographical Society through (EXERCISE JURASSIC SHARK 2), A1 scuba, downtown aquarium, Azul Marino Restaurant, Palapas Ventana, WWF-telcel, PADI, National Geographic, and Cabo Expeditions. R.D.R. acknowledges funding from the Australian Research Council Linkage grant LP140100404 and the Holsworth Wildlife Research Endowment R.R.R. and P.J.N.B. acknowledges funding provided by the National Research Foundation Thuthuka (grant 76230) and South African National Antarctic programmes (grant nos. 93071 and 110722) through the Department of Science and Technology, Republic of South Africa, the Mohamed bin Zayed Species Conservation Fund (project no. 10251290) and the IWC Southern Ocean Research Partnership (IWC-SORP). F.G.R. acknowledges funding provided by the US Marine Mammal Commission under grant no. E4047335 and ONR grant N00014-08-1-1195, the E&P Sound and Marine Life Joint Industry Project of the International Association of Oil and Gas Producers. D.P.R. acknowledges the Oatar Ministry of Municipality and Environment (OMMOE) and Maersk Oil Research and Technology Centre (MORTC), and was supported by two small grants from the Save Our Seas Foundation. Many thanks to the Save Our Seas Foundation, Al Ghurair Foods and the Emirates Diving Association, Emirates Natural History Group and Le Meridien Al Aqah Beach Resort for providing financial support for individual satellite tags. P.W.R. acknowledges that northern elephant seal research was supported by the Moore, Packard, and Sloan Foundations with additional support from the Office of Naval Research and the E&P Sound and Marine Life Joint Industry Project of the International Association of Oil and Gas Producers, Exxon-Mobil and Shell oil. J.P.R. was supported by Juan de la Cierva Formacion program (Ref. FJC2019-040622-I) funded by MCIN/AEI/10.13039/501100011033. He also received additional funding from Sustainable Ocean Alliance for the Artificial Intelligence & Animal Movement (AIAM, ref. D017) project under the SOA Grants program. Funding from Vicenc Mut program of Govern de les Illes Balears. T.L.R. acknowledges the Australian Research Council Linkage Program, LP0989933; Antarctic Science Advisory Committee Program 1144, Sea World Research & Rescue Foundation Inc., Australian Research Council; and the Scott Foundation. C.A.R. and S.J.P. acknowledge two private trusts, Aqua-Firma, the Shark Foundation, Waterlust, Rufford Small Grant, and the PADI Foundation. Y.R. acknowledges the French Polar Institute Paul Emile Victor (IPEV), the WWF-UK, the PEW Foundation, the Centre National de la Recherche Scientifique (Programme Zone Atelier de Recherches sur l'Environnement Antarctique et Subantarctique, ZATA), the Agence Nationale pour la Recherche (ANR-2010-BLAN-1728-01), the Fondation Albert II de Monaco, and the Fondation des Treilles. P.M.S. was funded by New Zealand's Foundation for Research, Science & Technology under contracts CO1X0008 and CO1507. G. Schofield acknowledges Deakin University, Australia; Queen Mary University of London, UK; Swansea University, UK; National Marine Park of Zakynthos, Greece; AXA Research Fund, Boyd Lyon Sea Turtle Fund, British Chelonia Group, People's Trust for Endangered Species, Project Aware, and Thermadap. J.M.S. was funded by the Holsworth Wildlife Research Endowment. S.A.S. acknowledges TOPP funding (ONR, NSF, Moore, Sloan, and Packard Foundations). K.S. acknowledges funding received by the Centre for Ecological Sciences, Indian Institute of Science, Bangalore; the Indian Space Research Organisation/Indian Institute of Science, Bangalore Space Technology Cell; and the International Seafood Sustainability Foundation. G.L.S. acknowledges major funding from support of the TOPP program of the Census of Marine Life, and was supported by the Alfred P. Sloan Foundation, the Gordon and Betty Moore Foundation, the Packard Foundation, the National Oceanographic Partnership Program of ONR, the United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Program (via the United Nations Foundation and Global Conservation Fund of Conservation International), the Dr. Earl H. Myers and Ethel M. Myers Oceanographic and Marine Biology Trust, the sponsors of the 2007 Great Turtle Race, Earthwatch Institute and the National Aeronautics and Space Administration (NASA) through a grant provided by the Applied Sciences Program in the Earth Science Division. M.A. Silva and R.P. acknowledge funds provided by FCT through research grants TRACE-PTDC/MAR/74071/2006, IF/00943/2013/CP1199/CT0001, individual contracts/grants to MAS (FCT-IF/00943/2013) and RP (SFRH/BPD/108007/2015), and the strategic projects MARE (UID/MAR/04292/2019) and Okeanos (UIDB/05634/2020 and UIDP/05634/2020), co-funded by FEDER, COMPETE, QREN, POPH, FSE, and the Portuguese Ministry for Science and Education; the Regional Government of the Azores, FRCT, and the Operational Program AZORES 2020 through research grant MAPCET-M2.1.2/F/012/2011, project M1.1.A/REEQ.CIENTÍFICO UI&D/2021/010, and contracts to MAS and RP through Fund 01-0145-FEDER-000140 "MarAZ Researchers: Consolidate a body of researchers in Marine Sciences in the Azores" of the European Union. D.W.S. further acknowledges additional field research support provided by the Save Our Seas Foundation (grants 45, 87, 308) and the NERC Oceans 2025 Strategic Research Programme. G. Skomal acknowledges the Large Pelagics Research Center (grant 06-125), Federal Aid in Sport Fish Restoration, NSF (OCE-0825148), the John J. Sacco and Edith L. Sacco Charitable Foundation, the Atlantic White Shark Conservancy, the Massachusetts Environmental Trust, Discovery Communications, National Geographic, and the Woods Hole Oceanographic Institution. L.L.S. thanks G. Hays for contributing funds to purchase four Argos-GPS tags; the Oceanário de Lisboa for contributing funding to purchase two Argos-GPS tags.. Funding was provided by the FCT SFRH/BD/68717/ 2010. J.D. Stewart acknowledges the PADI Foundation (grant no. 7842), the New England Aguarium, MCAF, Carl F. Bucherer, the Punta Mita Foundation, David Connell, Mary O'Malley, Lupo Dion, CIMEC, and the Gulf of California Marine Program. A. Takahashi acknowledges funding provided by the North Pacific Research Board (contribution no. 1612-3), Japan Society for the Promotion of Science KAKENHI grant no. JP16H02705, and the Arctic Challenge for Sustainability program (JPMXD1300000000) of Japan Ministry of Education, Culture, Sports, Science and Technology. Work was supported by Grant-in-Aid for Scientific Research (20241001 and 24370016). JSPS research grants (19651100 and 19255001), and by a Grant-in-Aid for Scientific Research (Special Promotion) of the Ministry of Education, Culture, Sports, Science and Technology-Japan to Yamashina Institute for Ornithology. P.M.T. acknowledges funding provided by Marine Alliance for Science and Technology for Scotland, Beatrice Offshore Windfarm Ltd, Crown Estate, Highlands & Islands Enterprise, and Moray Firth Offshore Renewables Limited. J. Tomás thanks the European Union Marie Curie FP7 and the Spanish Ministry of Education and Sciences, and was also supported by project LIFE INTEMARES (LIFE18 NAT/IT/000103) F.V. acknowledges the Foundation for Science and

Technology (FCT) for individual grants (CEECIND/03469/2017, CEECIND/03426/2020) and research funds under the project UIDB/05634/2020 and UIDP/05634/2020, and support of the Regional Government of the Azores through the initiative to support Research Centers of the University of the Azores and through the project M1.1.A/REEO.CIENTÍFICO UI&D/2021/010. M. Vedor was funded by Fundação para a Ciência e Tecnologia (FCT; PTDC/ ASP-PES/2503/2020). S.V. thanks the TOPP Program supported by the Sloan, Packard and Moore Foundations, as well as the ONR, the E&P Sound and Marine Life Joint Industry Project of the IAGOP (no. JIP 2207-23), UC MEXUS, CONACYT in Mexico and Instituto Politécnico Nacional (IPN) (Project SIP-2012006) of Mexico, NSF Office of Polar Programs and Center for Remote Sensing at University of California Santa Cruz for funding and logistic support. C.V. was funded by DREAL Bretagne, FEOGA Funds (EU), DREAL Basse Normandie, Région Poitou-Charente, La Compagnie du Vent, and the Parc naturel marin d'Iroise. S. Wanless was funded by the NERC Centre for Ecology & Hydrology. R.S.W. was funded by ONR and Dolphin Quest, Inc. S.D.W. acknowledges the Department of Environment and Natural Resources, Conservation Volunteers Australia, Tiwi Land Council, Natural Heritage Trust, Charles Darwin University, and the Australian Government. B.W. acknowledges the Australian Antarctic Division. N.E.W. acknowledges that tags were part of WWF-Australia's Flatback Whereabouts Project funded by WWF, Factorie, and Winnifred Violet Scott Trust, supported by the Gudjuda Aboriginal Reference Group. D.N.W. acknowledges the Volgenau Foundation, Mudge Foundation, BOEM, Stellwagen Bank National Marine Sanctuary, and the National Marine Sanctuary Foundation. F.C.W. was funded by the UK Natural Environment Research Council (NERC) through a University of Southampton INSPIRE DTP Studentship. L.J.W. acknowledges funding by the UK Department for Energy and Climate Change (DECC). J.C.X. acknowledges the strategic program of MARE (Marine and Environmental Sciences Centre), financed by the Foundation for Science and Technology (UIDB/04292/2020), through the grants Investigator FCT program (IF/00616/2013), PTDC/BIA-BDE/64539/2006 and SFRH/BPD/28879/2006. T.Y. was partially supported by the Japan Society for the Promotion of Science research grants (19651100, 19255001) and Grant-in-Aid for Scientific Research (Special Promotion) of the Ministry of Education, Culture, Sports, Science and Technology-Japan. D.J.Y. acknowledges funding provided by Polar Continental Shelf Program, Ocean Tracking Network, Fisheries and Oceans Canada, University of Windsor, Ontario Graduate Scholarships, W. Garfield Weston Foundation and Natural Science and Engineering Research Council of Canada. P.M.Z. acknowledges the United Nations Office for Project Services, GEF Humboldt for providing tags and funding for the expedition. J.M.A. was supported by project LIFE+ INDEMARES. Author contributions: All authors contributed to aspects of fieldwork, animal tagging, data collection, data formatting, and/or contribution of tools (full details provided in the supplementary text: "Supplementary Author Contributions"). Conceptualization: A.M.M.S., C.M.D., V.M.E., J.P.R., D.W.S., and G.C.H. Methodology: A.M.M.S. J.P.R., M. van der Mheen, S.A.M., M. Vedor, N.Q., L.M.A., H.J.C., M. VanCompernolle, L.R.P. with input from all authors Investigation: All authors Visualization: A.M.M.S., J.P.R., N.Q., H.J.C., and M. VanCompernolle Funding acquisition: A.M.M.S. Project administration: A.M.M.S., S.A.M. Writing – original draft: A.M.M.S., D.W.S., and G.C.H Writing – review & editing: All authors. Competing interests: The authors declare that they have no competing interests. Data and materials availability: All data, code, and materials needed to reproduce this analysis are available at Dryad (111). Data obtained from literature review are presented in supplementary materials. Sources of environmental data collated from online databases are described in supplementary materials. License information: Copyright @ 2025 the authors; exclusive licensee American Association for the Advancement of Science subject to: Ownership by the Commonwealth of Australia, © Commonwealth of Australia 2025, apart from any use as permitted under the Copyright Act 1968 (Cth); no claim to US government works. All other rights reserved by American Association for the Advancement of Science. https://www.science.org/about/science-licenses-journal-article-reuse.

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Hearn^{40,176}, Mads Peter Heide-Jørgensen¹⁷⁷, Leeann Henry¹⁰³, Robert William Henry III^{100,178,179}. Vicente Guzman Hernandez¹⁸⁰. Arturo E. Herrera¹⁸¹. Mark A. Hindell¹⁸², John C. Holdsworth¹⁸³, Bonnie J. Holmes¹⁸⁴, Lucy A. Howey^{185,186,187} Edgar Mauricio Hoyos Padilla^{188,189}, Luis A. Huckstadt^{100,126,157}, Robert E. Hueter^{92,147}, Paulo H. Lara¹⁹⁰, Nigel E. Hussey¹⁹¹, Charlie Huveneers¹³⁰, Kevin Hyland⁵³, Dylan T. Irion^{192,193}, David M. P. Jacoby¹⁹⁴, Audrey Jaeger¹⁹⁵, Mohammed Y. Jaidah⁴⁶, Mark Jessopp^{58,59}, Oliver J. D. Jewell^{2,196}, Ryan Johnson¹⁹⁷, Carl G. Jones^{198,199}, Ian D. Jonsen²⁰⁰, Lance K. B. Jordan¹⁸⁶, Salvador J. Jorgensen²⁰¹, Akiko Kato³⁴, James T. Ketchum^{40,188,202}, Alexander S. Kitaysky²⁰³, A. Peter Klimley^{40,204}, Alison A. Kock^{116,205}, Pieter Koen^{206,207}, Felipe Ladino Archila⁶⁵, Fernanda O. Lana^{66,208}, Jude V. Lane⁷¹, Matthieu Le Corre¹⁹⁵, Mary-Anne Lea^{182,209,210}, James Lea^{11,78}, Eliza H. K. Leat²¹¹, Olivia A. Lee²¹², J. 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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adl0239 Materials and Methods; Supplementary Acknowledgments; Supplementary Author Contributions; Figs. S1 to S17; References (112-135) Submitted 26 September 2023; accepted 9 April 2025

10.1126/science.adI0239