

The political biogeography of migratory marine predators

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During their migrations, marine predators experience varying levels of protection and face many threats as they travel through multiple countries' jurisdictions and across ocean basins. Some populations are declining rapidly. Contributing to such declines is a failure of some international agreements to ensure effective cooperation by the stakeholders responsible for managing species throughout their ranges, including in the high seas, a global commons. Here we use biologging data from marine predators to provide quantitative measures with great potential to inform local, national and international management efforts in the Pacific Ocean. We synthesized a large tracking data set to show how the movements and migratory phenology of 1,648 individuals representing 14 species—from leatherback turtles to white sharks—relate to the geopolitical boundaries of the Pacific Ocean throughout species' annual cycles. Cumulatively, these species visited 86% of Pacific Ocean countries and some spent three-quarters of their annual cycles in the high seas. With our results, we offer answers to questions posed when designing international strategies for managing migratory species.

Marine migrations can span ocean basins and are dynamic in space and time¹. Migratory species are thus exposed to a variety of threats² as they travel through multiple countries' jurisdictions and the open ocean. As a result, numerous migratory marine species from diverse taxa have experienced recent drastic population declines including leatherback sea turtles (*Dermochelys coriacea*)³, Pacific bluefin tuna (*Thunnus orientalis*)⁴, and some sharks⁵ and seabirds⁶. Under current management frameworks, migratory species have received varying levels of protection and many gaps remain^{7–10}. National rights over marine resources are delineated by exclusive economic zones (EEZs), which include waters out to 200 nautical miles from a country's shoreline¹¹. Areas beyond national jurisdiction, the 'high seas', are legally recognized as a global commons. Regional fisheries management organizations (RFMOs) are the primary multi-jurisdictional mechanism for managing transboundary and high seas fish stocks¹². In a joint management structure with member states, conservation and management rules are adopted by the RFMOs while enforcement of these measures falls to individual

countries. As such, individual nations are responsible for fishing and non-fishing-related threats within their EEZs and, through their high seas fleets and flag vessels, share responsibility beyond their EEZs. To recover populations and to prevent declines of healthy populations, improved management and effective international cooperation and governance⁷ are urgently needed. Key information needs at all levels include quantitative measures to indicate who has management jurisdiction over migratory species across their range and at different times during their migratory cycle, including for breeding, foraging and migrating. Here we use biologging data to provide this information. We show how the migratory cycles of populations of 14 species relate to geopolitical boundaries of the Pacific Ocean using a subset of a large tracking data set collected between 2000 and 2009 by the Tagging of Pacific Predators (TOPP) project¹. For each species of tuna (Pacific bluefin tuna, yellowfin *Thunnus albacares*, albacore *Thunnus alalunga*); shark (blue *Prionace glauca*, shortfin mako *Isurus oxyrinchus*, white *Carcharodon carcharias* and salmon *Lamna ditropis*); pinniped (northern elephant seal *Mirounga angustirostris*,

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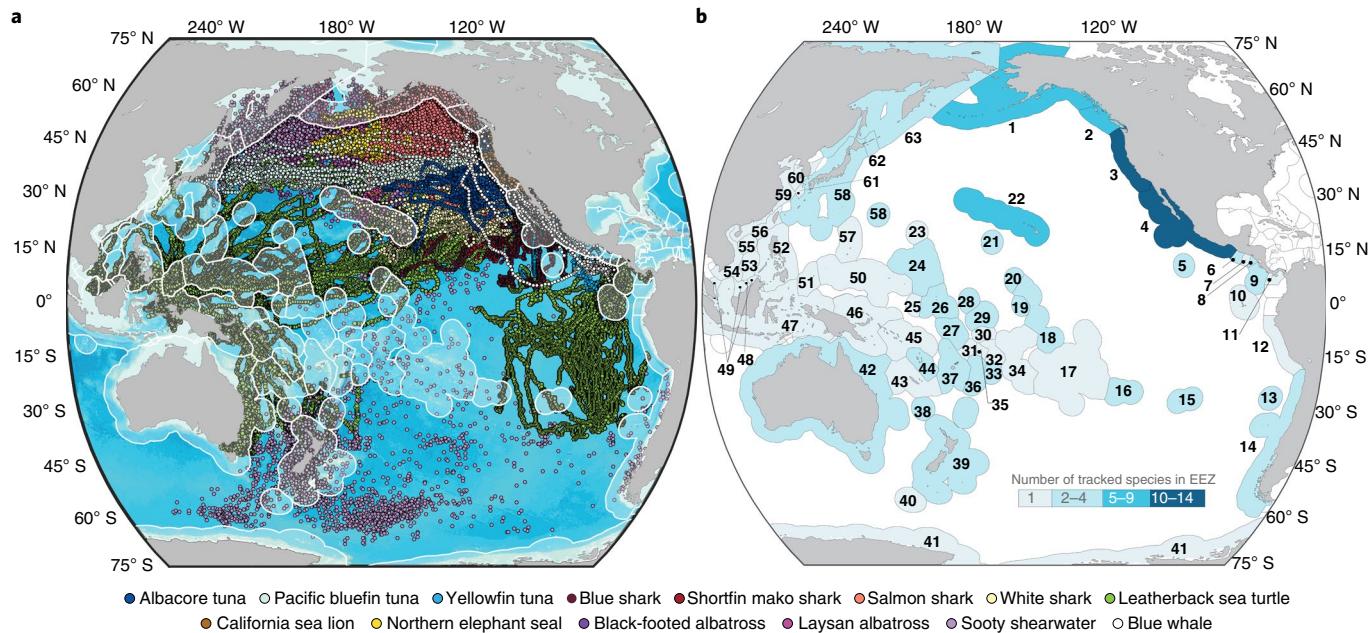


Fig. 1 | Daily locations of marine predators electronically tracked within EEZs and the high seas of the Pacific Ocean. **a**, State-space-modelled daily locations of 14 marine predator species electronically tracked (2000–2009) in EEZs (transparent overlay) and the high seas (ocean water falling outside the transparent overlay). Adapted with permission from ref.¹, Springer Nature Ltd. **b**, Key to visited EEZs. EEZ boundaries from the VLIZ Maritime Boundaries Geodatabase (2016); some are disputed. Refer to official records for all claimants and alternative geographies. 1, Alaska (USA); 2, Canada; 3, USA; 4, Mexico; 5, Clipperton Island (France); 6, Guatemala; 7, El Salvador; 8, Nicaragua; 9, Costa Rica; 10, Galapagos Islands (Ecuador); 11, Panama; 12, Peru; 13, Desventuradas Islands (Chile); 14, Chile (includes Juan Fernández Islands); 15, Easter Island (Chile); 16, Pitcairn Islands (UK); 17, French Polynesia (France); 18, Line Islands Group (Kiribati); 19, Jarvis Island (USA); 20, Palmyra Atoll (USA); 21, Johnston Atoll (USA); 22, Hawaii (USA); 23, Wake Island (Wake Island); 24, Marshall Islands; 25, Nauru; 26, Kiribati; 27, Tuvalu; 28, Howland and Baker Islands (USA); 29, Phoenix Islands Group (Kiribati); 30, Tokelau (New Zealand); 31, Wallis and Futuna (France); 32, American Samoa (USA); 33, Niue (New Zealand); 34, Cook Islands (New Zealand); 35, Samoa; 36, Tonga; 37, Fiji; 38, Norfolk Island (Australia); 39, New Zealand; 40, Macquarie Island (Australia); 41, Antarctica; 42, Australia; 43, New Caledonia (France); 44, Vanuatu; 45, Solomon Islands; 46, Papua New Guinea; 47, Indonesia; 48, Brunei; 49, Malaysia; 50, Micronesia; 51, Palau; 52, Philippines; 53, Spratly Islands (disputed); 54, Vietnam; 55, Paracel Islands (disputed); 56, Taiwan/Chinese Taipei; 57, Northern Mariana Islands and Guam (USA); 58, Japan; 59, China; 60, South Korea; 61, Japan-Korea Joint Development Zone; 62, Southern Kuriles (disputed); 63, Russia.

California sea lion *Zalophus californianus*); seabird (Laysan albatross *Phoebastria immutabilis*, black-footed albatross *Phoebastria nigripes*, sooty shearwater *Puffinus griseus*); leatherback sea turtle; and cetacean (blue whale *Balaenoptera musculus*), we asked: (1) Which EEZs were visited? (2) What proportion of time was spent in each EEZ and the high seas? (3) When, during their migratory cycle, were animals within each EEZ or the high seas?

Results and discussion

Individual animals ($n=1,648$) representing 265,881 tracking days (Supplementary Table 1) visited 63 Pacific Ocean EEZs (Fig. 1) under the jurisdiction of 37 countries. (Some sovereignties are disputed; disjunct EEZs for a given country were treated separately. See Supplementary Table 2.) Some species (Pacific bluefin tuna, leatherback sea turtle, sooty shearwater, Laysan albatross) travelled across the Pacific and all species entered numerous jurisdictions. The high seas were visited by 48% ($n=797$) of individuals. Tag deployments occurred primarily in the eastern Pacific Ocean and over 83% of daily locations were either in Mexico (31%), the high seas (29%) or the USA (23%); 71% of all locations were within the boundaries of an EEZ (Supplementary Table 3).

While these simple statistics provide an insight into overall occurrence, they may be biased by effects of deployment location and sampling imbalances common to electronic tracking data sets. We addressed biases due to variability in sample size during the year (Supplementary Table 1, Supplementary Fig. 5), deployment dates (Supplementary Fig. 6) and track durations (Supplementary

Figs. 7 and 8) using multinomial generalized additive models (GAMs)^{13,14}. We predicted seasonal patterns of occurrence within specific countries and the high seas for multiple taxa (Fig. 2), breeding populations (Fig. 3 and Supplementary Fig. 1), life history stages (Supplementary Fig. 2) and years (Supplementary Figs. 3 and 4). California sea lions and yellowfin tuna were not modelled because >90% of locations were within a single EEZ (Supplementary Table 3). From model predictions we also estimated the percentage of an annual cycle spent in EEZs or in the high seas (Table 1). The TOPP project was unprecedented in producing a large multispecies, multi-year simultaneous animal movement data set at an ocean basin scale. Nonetheless, many data sets are not fully representative at the species level within the Pacific Ocean. TOPP focused primarily on North American populations and many species data sets are age- or sex-biased. For example, this study includes results from female salmon sharks in the eastern North Pacific, but not males from the western North Pacific. It includes female northern elephant seals from Mexican and American rookeries, but not males. Additionally, some species in this study include few individuals relative to population size (for example, sooty shearwaters). Therefore, our results describe only the specific geographical subsets of populations and life history stages studied by the TOPP project (see Methods, Supplementary Information and Block et al.¹ for full data set details and deployment locations).

Using our results, we offer examples of scientific answers to key questions posed when designing international strategies for managing migratory marine species.

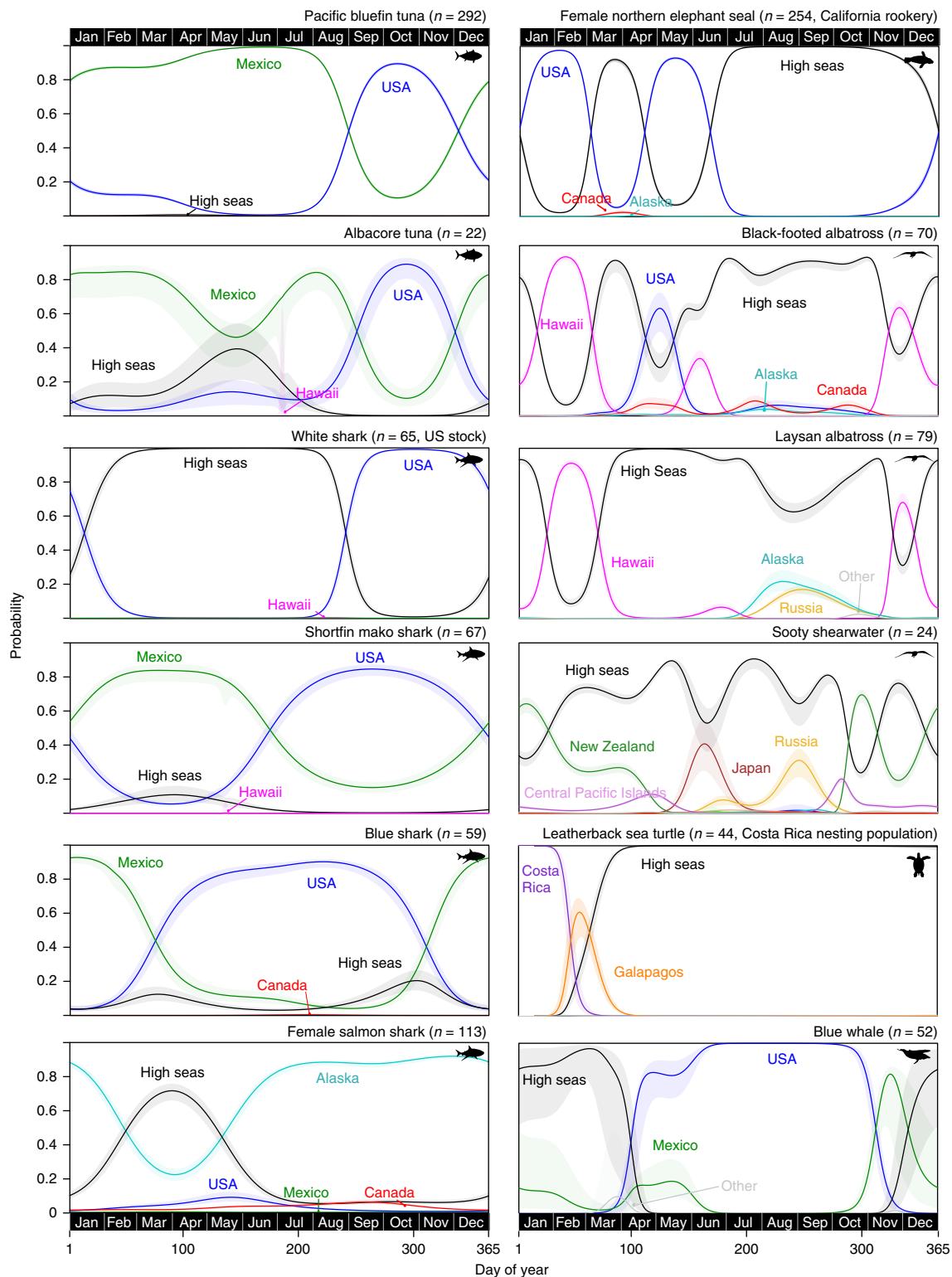


Fig. 2 | Seasonal probability of marine predator occurrence in Pacific Ocean EEZs and the high seas from electronic tracking. The lines represent the estimated effect of day of year on the probability of a randomly selected individual from the tracked population occurring in each region. The shading represents the interquartile range of estimates simulated from the posterior distribution of the model parameters. The total sample size for each population is represented by n ; tracking duration varied among individuals (see Methods). Model details: see Methods and Supplementary Table 4. Leatherback sea turtles have a multi-year migratory cycle; estimates begin on 21 January and continue through the first year of this cycle following breeding/tag deployment.

When, during the year, are marine predators present within countries' waters? Marine predators cue on shifts of habitats and prey, which in turn concentrate individuals in specific regions during

defined time periods¹. Consequently, residency within each EEZ is not equally probable throughout the year (Fig. 2). It may be highly punctuated in time, for example, the central Pacific island migration

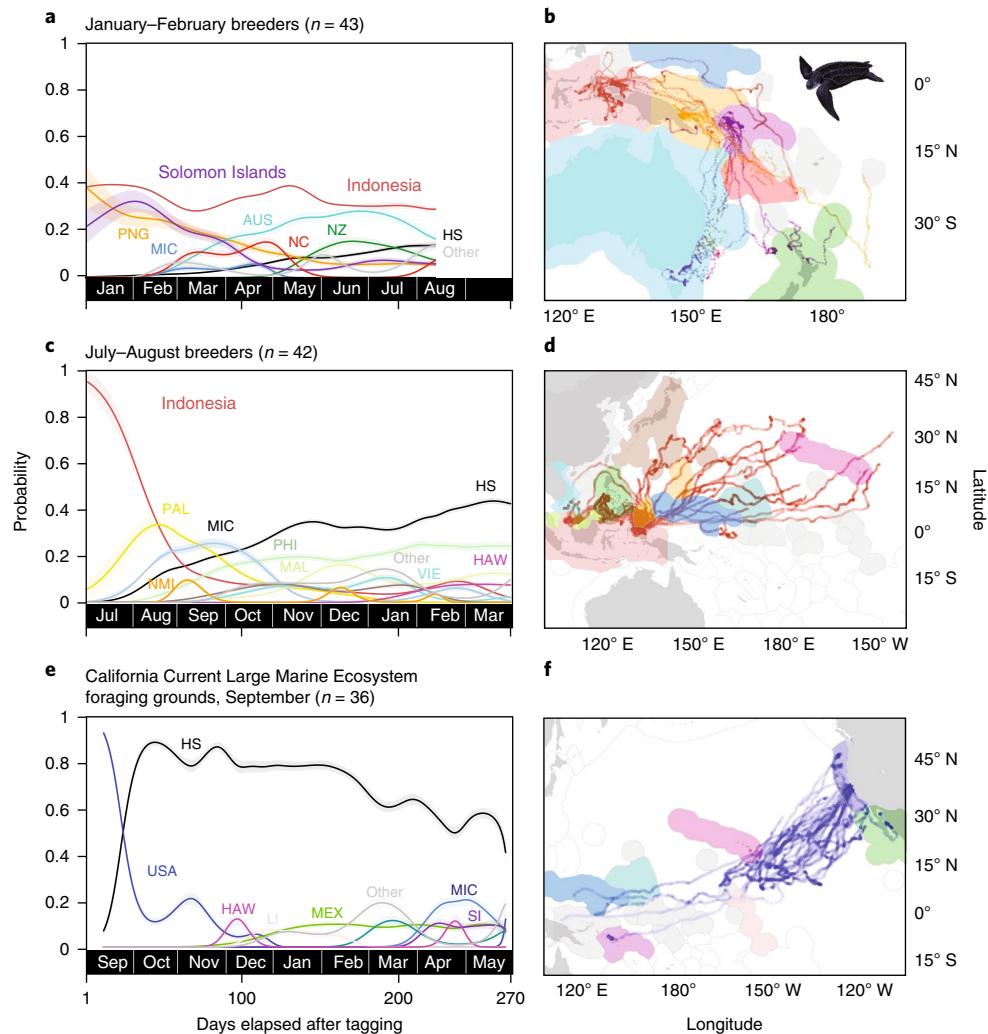


Fig. 3 | Population differences in western Pacific leatherback sea turtle use of EEZs and the high seas. **a,c,e.** Probability of turtle occurrence in EEZs and the high seas during the 7–9 months following tag deployment. Tags were deployed during the breeding period (**a-d**) or on foraging grounds (**e,f**). The lines represent the estimated effect of days elapsed after tag deployment on the probability of a randomly selected individual from the tracked population occurring in each region. The shading represents the interquartile range of estimates simulated from the posterior distribution of the model parameters. Sample size and longevity of tags dictated the number of days elapsed since tagging (7–9 months) considered in the models. Model details: see Methods and Supplementary Table 4. **b,d,f.** State-space-modelled daily locations of individuals electronically tracked from each population (the location colours correspond to the EEZ where the tags were deployed) and EEZ boundaries (the colours correspond to the facing panel). **a,b.** Austral summer breeding populations tagged during breeding in Indonesia, the Solomon Islands and Papua New Guinea. **c,d.** Austral winter breeding population tagged during breeding in Indonesia. **e,f.** Foraging population in the California Current Large Marine Ecosystem. EEZ and high seas codes: AUS, Australia; HAW, Hawaii; HS, high seas; LI, Line Islands; MAL, Malaysia; MEX, Mexico; MIC, Micronesia; NC, New Caledonia; NZ, New Zealand; NMI, Northern Mariana Islands; PAL, Palau; PHI, Philippines; PNG, Papua New Guinea; SI, Solomon Islands; VIE, Vietnam.

corridor of fast-moving sooty shearwaters¹⁵ (Fig. 2). Alternatively, a single EEZ may constitute half or more of yearly residency, for example, salmon sharks in Alaska and Pacific bluefin tuna in Mexico (Table 1). Some populations in this study remained almost entirely within the EEZs in which the tag deployments occurred, making management more straightforward. For example, California sea lions from the US breeding population remained within US waters except during years of anomalous oceanographic conditions¹⁶ when they ventured to the high seas (Supplementary Table 2). Some life history stages not represented in our data set also remain in one or two EEZs, for example, juvenile white sharks in the eastern North Pacific remain in the USA and Mexican EEZs¹⁷.

Among the six taxa of marine predators studied, some co-occurred seasonally within the same EEZs (Fig. 2). Tunas, sharks and whales occurred within US waters from July to December;

female elephant seals, albatrosses and leatherback sea turtles ranged throughout the high seas from April to November; and Laysan albatrosses and sooty shearwaters visited Russian waters from July to October. There are examples of similar patterns from other stocks and populations in the Pacific. The white shark data modelled here represent individuals migrating between the US EEZ (Central California) and the high seas. A second group of northeastern Pacific white sharks shows near identical phenology in migrations between the high seas and Guadalupe Island, Mexico¹⁸. By identifying seasonal patterns of co-occurrence across guilds, species and populations, our results can help managers maximize their efforts across a range of migratory taxa. For example, dynamic and ecosystem-based management approaches require a synthetic understanding of the migratory cycles of multiple species. Our results could also help identify

Table 1 | Percentage of the year marine predators are estimated to spend within Pacific Ocean EEZs and the high seas

	PBT	PBT (TP)	AT	WS	MS	BS	SS	NELE	BFAL	LAAL	SOSH	LET (CR)	BLWH
High seas	0.2	44.9	12.2	62.5	3.7	0.8	23.7	66.6	66.7	74.5	65.9	78.2	30.3
USA	28.7	25.7	27.6	37.4	46.8	55.9	3.2	33.1	7.7	<1			55.8
Mexico	71.1	28.3	60.2	<1	49.5	35.7	<1			<1			13.2
Alaska							70.0	0.1	1.0	4.5	<1		
Canada							<1	3.1	0.3	2.7			
Hawaii	<1		<1	<1	<1				21.6	17.5			
Russia										3.2	4.2		
Central Pacific islands											3.8		
Japan	<1	1.1									4.0		
New Zealand											20.7		
Costa Rica												17.8	
Galapagos												3.7	
Other	<1	<1				<1			<1	<1	<1	<1	<1

Percentages were estimated from the model results presented in Fig. 2 and Supplementary Fig. 2 (PBT, TP) using electronic tagging data. Model details: see Methods and Supplementary Table 4. Species codes: PBT, Pacific bluefin tuna (all individuals); PBT (TP), trans-Pacific migrants (see Supplementary Fig. 2); AT, albacore tuna; WS, white shark; MS, shortfin mako shark; BS, blue shark; SS, salmon shark; NELE, (female) northern elephant seal; BFAL, black-footed albatross; LAAL, Laysan albatross; SOSH, sooty shearwater; LET (CR), leatherback sea turtle from Costa Rica; BLWH, blue whale. Percentages may not total 100 due to rounding. Leatherback sea turtles have a multi-year migratory cycle; estimates are for the first year of this cycle following breeding/tag deployment. Uncertainty in these estimates and estimates for additional data subsets are presented in Supplementary Table 5.

when and where to focus management efforts focused on human interactions, for example, to help maximize by-catch mitigation efforts in places where currently there is a lack of observer coverage and enforcement.

Which countries should be cooperating, either directly or through established international bodies and frameworks? We identified the set of countries visited by each species (Fig. 1 and Supplementary Tables 1 and 2) and predicted when, during the year, animals moved among countries or into the high seas according to their cycles of breeding, foraging and migration (Figs. 2 and 3, Supplementary Figs. 1–4).

Understanding the political biogeography of leatherback sea turtles in the Pacific Ocean is especially important because they are highly threatened¹⁹ and their management is jurisdictionally complex. During this study, leatherback sea turtles in the Pacific Ocean moved through 32 countries and the high seas. Globally, seven leatherback sea turtle subpopulations are recognized and all are considered vulnerable to extinction. However, the western Pacific and eastern Pacific subpopulations we studied are critically endangered with estimates of a 96% population decline by 2040¹⁹. We compared eastern (Fig. 2) and western Pacific leatherbacks (Fig. 3), and multiple breeding populations of western Pacific leatherbacks (Fig. 3). In the western Pacific, turtles that breed in the austral winter pass through Asian and central Pacific EEZs; turtles that breed in the austral summer migrate to EEZs of the South Pacific (Fig. 3). We show that political biogeography is linked to population structure and breeding phenology for this species; thus, our results provide the ability to link observed locations of human interactions to specific leatherback sea turtle breeding populations. To save leatherback turtles from extinction in the Pacific Ocean, a multilateral, cooperative approach is the only way forward, often stemming from private, local or regional collaborations that provide a first step in cooperative research and conservation. Examples of such international coordination include the Inter-American Tropical Tuna Commission, the Commission for the Conservation of Antarctic Marine Living Resources, the Northern Fur Seal Treaty and the Agreement on the Conservation of Albatrosses and Petrels. Our

results could be a key ingredient in a holistic conservation strategy²⁰ that integrates protections throughout the pan-Pacific leatherback life cycle including: optimizing reproductive success on nesting beaches (for example, beach protection, monitoring and enforcement, conservation payments to local communities), and preventing deaths due to incidental catch by fisheries within EEZs (for example, tailored approaches to scale of fishery and socio-economic context, adoption of gear technology handling standards to reduce incidental catch and increase the probability of post-release survival, incentive-based mechanisms, use rights, time/area closures) and in the high seas (for example, expanding pan-Pacific policy actions, increasing and enforcing observer coverage, adopting gear technology handling standards, and so on)²¹.

How important are the high seas to marine predator populations? The high seas are one of the world's last global commons²² and are among the least protected places on Earth²³. Despite recent progress, many RFMOs have not ensured that all fish stocks under their mandates are fished sustainably⁹ and/or have not suitably protected non-target species such as seabirds, sharks, turtles and marine mammals¹⁰. Many approaches have been suggested or used to improve the sustainability of high seas fisheries, including: rights-based management; adopting and enforcing best practice gear technology standards; increasing observer coverage; time/area restrictions; protected areas; vessel monitoring; increasing and sharing scientific research; market and trade-based mechanisms; and the adoption of a new international legal instrument^{7,10}. To implement many of these suggestions, quantitative measures of high seas use are needed.

Our results provide measures of the time multiple populations spend within the high seas at a basin-wide scale (Table 1 and Fig. 2). For example, Pacific bluefin tuna tracked during their trans-Pacific migration ($n=12$, Supplementary Fig. 2), seabirds, leatherback sea turtles, white sharks and northern elephant seals spent between 45 and 75% of the year in the high seas (Table 1). Attention to high seas management issues is increasing. The United Nations General Assembly in 2015 resolved to develop an international legally binding instrument for the conservation and sustainable use of marine

biodiversity of the high seas²⁴. This process will advance in 2018 to full negotiation. The knowledge we present of how and when animals use the high seas is a critical contribution to these next steps to sustain marine biodiversity and is a complement to new satellite services (for example, maritime automated identification system data made publicly available through Global Fishing Watch²⁵) that can be used to increase the transparency of high seas fishing.

Conclusions

Our analysis of tracking data collected from Pacific Ocean predators describes seasonal patterns of national and international management jurisdiction over migratory species. Actions to protect marine migratory species are needed throughout their range, including on the high seas. Multiple international conventions and agreements^{11,12,26} seek to promote cooperation within and beyond national jurisdictions for managing migratory species. Nevertheless, scaled-up international collaboration and effective governance are essential. While our results demonstrate the jurisdictional complexity of managing some critically endangered, highly migratory species like Pacific leatherback sea turtles, they also demonstrate that for some species or populations, agreements among just a few countries could help reverse declines. Our approach capitalizes on what biologging technologies do best²⁷: provide continuous movement data on individual animals who spend most of their lives away from direct scientific observation. This information can^{28–30} and should be used to inform management.

Methods

Data summary and availability. From 2000 to 2009, researchers with the TOPP project deployed 4,306 electronic tags that provided 1,791 individual animal tracks from populations of 23 species in the Pacific Ocean¹. Animal research was conducted in accordance with the institutional animal care and use protocols of Stanford University and the University of California, in accordance with guidance from the US Endangered Species Act for endangered species, and the US Marine Mammal Protection Act for marine mammals.

A Bayesian state-space model³¹ was fitted to the tag data to derive regular, daily mean estimates of locations at sea while accounting for tag observation error³². The state-space model also provided estimates of the uncertainty in the location estimates. This modelled TOPP data set is archived in the [US Animal Tracking Network Data Assembly Center](#).

We used a subset of this TOPP data set; only species tracked over multiple years were included. The data set we analysed included 14 species, 1,648 individuals and 265,881 modelled daily locations (Supplementary Table 1). Yearly sampling efforts varied (Supplementary Table 1). Tags were deployed within the boundaries of eight EEZs (Supplementary Tables 2–3). For full deployment details, see Block et al.¹. There are multiple populations in the Pacific Ocean of many species considered here—we refer only to the specific populations and life history stages in the TOPP data set¹.

Variability in deployment date and track duration. The timing of tag deployments was multimodal for some species (Supplementary Fig. 6) and track duration varied among individuals (Supplementary Fig. 7). This variability in a tracking data set can affect spatio-temporal analyses when deployment dates and track duration are unrelated to the life history of species.

- Pinnipeds and seabirds. Distributions of deployment dates and track durations reflected the life histories of these species. To capture the full annual cycle of land-breeding and moulting species, tags were deployed multiple times in a given year (northern elephant seals, before the short post-breeding and long post-moult migrations; seabirds, before the short breeding and long post-breeding migrations). Typically, unique sets of individuals were tracked during each migration, although some seals were tracked during both migrations in a given year or during the same migration in multiple years. California sea lions were predominantly tagged while nursing pups to facilitate tag recovery; most individuals were tracked only during the breeding period. In general, tag failure was rare and tags were recovered on recapture of the animals. Pinnipeds included in this analysis were females and all pinnipeds and seabirds were adults.
- Tunas, sharks and whales. For these species, deployment timing varied among years partially because of reasons unrelated to the life history of species (sampling design considerations or cruise availability). The primary tagging months were: Pacific bluefin tuna, January, March, July–September, November–December; yellowfin tuna, February, August, October–December; shortfin mako shark, June–August, November; blue shark, January–February, June–August, October–December; salmon shark, July–August; and white shark, January and December. Because of a higher frequency of tag failure and the difficulty of

targeted recapture, the distributions of track durations for these species (Supplementary Fig. 7) were a function of tag attrition and harvest recapture. In general, these data sets contained a high number of individuals tracked for less than a year. Salmon sharks were an exception with 16 individuals tracked for at least 2 years (Supplementary Fig. 7). The salmon sharks studied were all females; white sharks were large adults and subadults; Pacific bluefin tuna, albacore tuna, shortfin mako shark and blue sharks were largely juveniles.

- Leatherback sea turtles. Leatherback sea turtles have a multi-year migratory cycle and all tags experienced attrition before recording the full multi-year migration. The eastern Pacific and western Pacific subpopulations of leatherback sea turtles were considered separately in this study. Tags on eastern Pacific leatherbacks were deployed in January during the nesting period³³. Tracking of the western Pacific subpopulation included both summer (Indonesia) and winter breeders (Indonesia, Papua New Guinea, Solomon Islands), and animals captured while foraging in the California Current. Thus, tag deployment occurred in three different pulses. (See Benson et al.³⁴ for more detail on the multi-year migratory cycles of western Pacific leatherbacks and their population dynamics among breeding rookeries.) All turtles included here were breeding adults.

Location classification. Global EEZ boundaries were obtained as shapefiles from the VLIZ Maritime Boundaries Geodatabase (v.8, 2014). Some EEZ boundaries between countries are disputed; full details of boundary delineation are available (Marine Regions, an integration of the VLIMAR Gazetteer and the VLIZ Maritime Boundaries Geodatabase: <http://www.vliz.be/vmdcdata/marbound/>). Shapefiles were converted to polygon vectors using the MATLAB mapping toolbox (The MathWorks, Inc., R2015b release). We developed a custom script based on MATLAB's 'inpolygon' function to classify each location as present or absent (binary, ones and zeros) in each EEZ of the Pacific basin. We classified locations on an EEZ boundary as inside the EEZ. Thus, those few locations located exactly on the boundary/edge of two EEZs would be classified as within two EEZs. If a location was neither on land nor in an EEZ, we classified it as a high seas location. Disjunct EEZs for a given country were treated separately. For example, Hawaii and Alaska were each treated as unique to the mainland USA EEZ.

EEZ and high seas occurrence and models of seasonal use. For each species we calculated the percentage of individuals (Supplementary Table 2) and the percentage of daily locations (Supplementary Table 3) spent in each EEZ and the high seas. We began our analysis exploring the proportion of time spent by individuals of each species in each EEZ and the high seas, a value most often reported in the related literature (for example, see Suryan et al.³⁵). However, for our data set these simple statistical summaries of EEZ use were biased in the following ways: (1) statistical summaries of individual EEZ use calculated from data sets with high tag attrition (and thus a high number of abbreviated tracks: tunas, sharks, whales and turtles) were biased towards the EEZs in which tags were deployed (Supplementary Figs. 7 and 8); (2) the deployment date affected the interpretation of EEZ use (Supplementary Figs. 6 and 8); and (3) yearly summaries were affected by variability in sample size (Supplementary Table 1 and Supplementary Fig. 5) and deployment dates (Supplementary Fig. 6) across the years. One solution is to remove from the analysis individuals with abbreviated tracking durations (for example, <30 days or <1 year). However, we felt that there was value in retaining all available information to elucidate seasonal patterns of EEZ use.

Therefore, we took a modelling approach to better estimate seasonal EEZ and high seas occurrence for the tagged population given the effects of individual variability in track duration and tagging location and date. The presence of an individual from the tagged sample in each EEZ or the high seas was modelled with a GAM¹⁴, specifically a multinomial logistic regression¹⁵. For species predicted to have an annual migratory cycle (that is, all species except leatherback sea turtles), a cyclic effect was used for the day of year, thereby enforcing continuity in the estimated probabilities from year to year. Individual identity was treated as a random intercept effect to account for differences in behaviour and sample size throughout the year among tagged individuals. Both day-of-year and individual effects were allowed to vary across EEZs and the high seas. The multinomial model structure ensured that the probabilities of presence in EEZs and the high seas added up to 1 for any given day of year for any given individual. Models were fitted using the 'mgcv' package¹⁴ in R (R Development Core Team, 2016). The ordering of categories in the model formulation (that is, EEZs and the high seas) can somewhat affect the fit of the multinomial models used (see the reference manual for the R package 'mgcv', GAM multinomial logistic regression; for more detail see Wood³⁶), typically (in our case) by inflating uncertainty estimates when EEZs with few observed locations are ordered first. For consistency, we ordered the categories for each model from the highest to the lowest numbers of 'observed' locations.

For each species, the formulation of the models depended on the life history of the species and data set quality (Supplementary Table 4). Models were not developed for species that spent most of their time within a single EEZ (yellowfin tuna, California sea lion). Yearly models were considered for species with balanced data sets over multiple years (Supplementary Tables 1 and 4): female northern elephant seals (Supplementary Fig. 3) and salmon shark (Supplementary Fig. 4).

For some species, there was enough information to separately model life history stages or breeding populations. Separate models were fitted for female northern elephant seals from the US and Mexican breeding populations (Supplementary Fig. 1). Two model groups were also constructed for Pacific bluefin tuna. Group 1 included all Pacific bluefin tuna individuals. The second Pacific bluefin tuna model group included only those tuna that undertook trans-Pacific migrations ($n=12$, Supplementary Fig. 2).

For western Pacific leatherbacks, we modelled each breeding population and the California foraging population separately due to the multimodality of tag deployments and our interest in the differences in EEZ use by the different populations. To compare EEZ occurrence in the months following breeding (regardless of whether breeding occurred in summer or winter), and in the months following tag deployment in the California foraging grounds, the number of days elapsed following tag deployment was the fixed effect (rather than the day of year, Supplementary Table 4). Therefore, the model was related to a life history event, estimating EEZ and high seas occurrence during the migration following this event, rather than to the calendar year.

Model predictions and uncertainty. From the fitted models we predicted the probability that a randomly selected individual from the tracked population would occur in an EEZ or in the high seas on each day of year. Use of EEZs by tagged western Pacific leatherback sea turtles was estimated only for the 7.5–9 months following tag deployment, due to the impact of tag attrition on data availability after this time. EEZs with few occurrences were grouped together into an 'Other' category. For sooty shearwaters, island EEZs falling within the central Pacific were also grouped together, representing their migration corridor¹⁵. Population-level predictions were derived by setting the random intercept effect of the individual in the model to zero. We estimated the proportion of the year spent in each EEZ or in the high seas for each tracked population by summing the population-level predicted daily probabilities over the course of a year and dividing by 365.

Models also provided predictions of the probabilities of specific tagged individuals occurring in EEZs or the high seas on each day of year. These probabilities were sometimes highly variable among tagged individuals of a species/population (Supplementary Fig. 9). In some cases, non-negligible numbers of individuals of a species visited an EEZ during a year (as an annual summary), but the mean population response on any given day of year may not represent this. For example, 20% of individual white sharks tracked in this study (Supplementary Table 1) visited Hawaii and 6% of all locations were in Hawaii (Supplementary Table 2), but the mean population response on any day of year was near 0 (Fig. 2 and Table 1). A similar pattern was observed for elephant seals in Canada (Supplementary Fig. 9). Because the models estimate a population response on a given day of year, a substantial proportion of individuals would need to visit the EEZ at the same time to be represented in the population response. Therefore, summaries of individual use of EEZs and the high seas (Supplementary Table 1) provide information that may be of use to managers in addition to model results, keeping in mind the caveats due to variability in tracking duration already discussed.

Uncertainty in model prediction was characterized by simulating a sample of estimates from the posterior distribution of the model parameters¹⁴. The posterior distribution was assumed to be multivariate normal with means equal to the parameter estimates and variances/covariances from the estimated covariance matrix. The estimated uncertainty generally reflected sample size across species/populations and throughout the year for individual species/populations demonstrating the usefulness of the model in accounting for sample size. For example, compare the uncertainty and sample sizes in the northern elephant seal yearly models to the results for the full population. Uncertainty in the proportion of the year spent in each EEZ and in the high seas was estimated by calculating these proportions for each parameter set from the posterior sample and characterizing the distribution of proportions across the sample.

The estimates of uncertainty presented here are likely underestimates of the true uncertainty in the effect of day of year on the occurrence of tagged animals in EEZs and the high seas. Although individual identity was included as a model effect, sequential correlation in the model residuals for an individual could have remained, in which case the true uncertainty in the day-of-year effect would be greater. Also, the presence data that the models were fitted to were themselves derived from state-space model location estimates with associated positional uncertainty¹ that was not accounted for here. Nevertheless, the estimates of uncertainty presented here provide an upper bound on the confidence that should be placed in the estimated effects of day of year on the occurrence of the tagged populations in EEZs and the high seas.

Additional considerations: effects of tag deployment location and variability in deployment data and track duration on probability estimates. Statistical summaries of time spent in EEZs from electronic tracking data are influenced by the distribution of track duration and deployment dates and locations. Early in a track, individuals have a high likelihood of being located within the deployment EEZ because tags were deployed there. As time passes, individuals can disperse from the release location and the proportion of time spent within the deployment

EEZ should level to a more biologically representative proportion unaffected by the initial tag deployment event. Therefore, an interaction between deployment location and track duration has the potential to bias estimates of EEZ use in favour of the EEZ in which tags were deployed when a large proportion of the tracked population has short-duration tracks.

We explored the effects of track duration and timing of tag deployment in the TOPP data set by calculating the running proportion of time spent by each individual within primary EEZs and the high seas according to the relative day along each individual's track (that is, days elapsed since deployment) and according to the month in which the tag was deployed (Supplementary Fig. 8). For example, most tags were deployed on Pacific bluefin tuna in March, July–August and November–December within the Mexican EEZ¹. Individuals tracked for <30 days spent 80–100% of their time within Mexico. Individuals tracked for >1 year, spent 50% of their time in Mexico (Supplementary Fig. 8) with little change in this proportion as track length increased beyond a year. Tuna released in Mexico in November spent a higher proportion of their time in Mexico in the few months after being tagged than those tagged in July (Supplementary Fig. 8).

We attempted to account for this effect of track duration and tag deployment location in the models by exploring the use of a day-of-track term. Ideally such a term would capture the highest probability of being in the tagging EEZ at the beginning of a track and the effect would diminish during a track. Some of the models we explored partially captured the expected day-of-track effect, but the predicted effects did not diminish monotonically over time and often exhibited non-intuitive patterns later in a track. For example, the Pacific bluefin tuna model exhibited an expected decrease in the predicted probability of being in the Mexico EEZ (the deployment EEZ) during the early part of a track, but the predicted probability increased later in the track and exhibited non-intuitive patterns for some days of the year (Supplementary Fig. 10). These results suggested that the combination of data and model structure used could not capture the expected effect of track duration, so these models were not considered further.

Tag deployment location is an experimental design feature of a tracking data set that can bias interpretation of space use for the tracked population. In this study, it might have imposed an upward bias on estimates of probability of occurrence in EEZs in which tags were deployed, especially when combined with a data set subject to a high amount of tag attrition (that is, 'short' tracks). For data sets in which many individuals were tracked for multiple years (that is, salmon sharks), we expect a minimal effect of this bias for the tracked population.

Code availability. Custom R scripts will be made available via GitHub (<https://github.com>) on publication in the political-biogeography project and are also available on request to the corresponding author.

Data availability. The tracking data used are archived in the US Animal Tracking Network Data Assembly Center (<https://atn.ioos.us>).

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Author contributions

This study was conceived by A.-L.H. The TOPP project was designed and coordinated by B.A.B., D.P.C. and S.J.B. B.A.B., A.B.C., H.D., S.J.J., S.K., K.M.S., G.L.S and K.C.W. designed the experiments and deployed the electronic tags on fish and sharks. S.R.B., P.H.D., G.L.S and B.A.B., designed the experiments and deployed the electronic tags on leatherback sea turtles. D.P.C., P.W.R., S.E.S. and B.R.M. designed the experiments and deployed the electronic tags on marine mammals. S.A.S. and M.A. designed the experiments and deployed the electronic tags on seabirds. Analyses were conducted by A.-L.H. and A.J.W. Figures were created by A.-L.H. The manuscript was drafted by A.-L.H. and edited by D.P.C., A.J.W., S.R.B., S.J.B., A.B.C., H.D., P.H.D, S.J.J., M.A., S.K., S.A.S., K.M.S., G.L.S., S.E.S., K.C.W. and B.A.B.

Competing interests

Kristina Gjerde is an unpaid member of the Sargasso Sea Project, Inc. Board, the Global Ocean Biodiversity Initiative Scientific Steering Committee, the Deep Ocean Stewardship Initiative Executive Board, the High Seas Alliance Steering Committee, and the Deep Ocean Observing Strategy Scientific Steering Committee.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41559-018-0646-8>.

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Software and code

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Data collection

No software was used.

Data analysis

A description of the software and code has been included in the Methods. Computational analysis was performed using commercial/custom code written in Matlab R2015b and R and will be made publicly available (with open source MIT license) on GitHub prior to publication. We also used Package mgcv for R (mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation), developed by Simon Wood and available on CRAN (<https://cran.r-project.org/web/packages/mgcv/index.html>). Finally, Global EEZ boundaries were obtained as shapefiles from the VLIZ Maritime Boundaries Geodatabase (v.8, 2014, <http://www.vliz.be/vmdcdata/marbound/>).

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The tracking data used in this manuscript (and presented in Figure 1) are available from the U.S. Animal Tracking Network Data Assembly Center. <https://oceanview.pfeg.noaa.gov/ATN/>

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Study description

We predicted seasonal patterns of marine predator occurrence within countries and the high seas of the Pacific Ocean for 1,648 electronically-tracked individuals representing populations of 14 species. To do this, we took a hierarchical multinomial generalized additive modeling approach.

Research sample

The research we present leverages a decade-long field study of migratory marine animals in the Pacific Ocean, the Tagging of Pacific Predators (TOPP) Project of the Census of Marine Life (Block et al. 2011). At the initiation of the project 2000–2002, workshops composed of species experts considered species behavior, available pilot tracking studies, funding, and field logistics to determine the species, populations, and sample sizes to be targeted in the study. Sample size in this case represents not only the number of individuals, but also the number of years represented in the study to account for environmental variability, and the specific populations included to represent the species at the scale of the Pacific Ocean.

Block, B. A. et al. Tracking apex marine predator movements in a dynamic ocean. *Nature* 475, 86–90 (2011).

Taxa represented include:

Tuna (Pacific bluefin, *Thunnus orientalis*, yellowfin, *Thunnus albacares*; albacore, *Thunnus alalunga*);
 Shark (blue, *Prionace glauca*, shortfin mako, *Isurus oxyrinchus*; white, *Carcharodon carcharias*; salmon, *Lamna ditropis*)
 Pinniped (northern elephant seal, *Mirounga angustirostris*; California sea lion, *Zalophus californianus*),
 Seabird (Laysan albatross, *Phoebastria immutabilis*; black-footed albatross, *Phoebastria nigripes*; sooty shearwater, *Puffinus griseus*),
 Sea turtle (leatherback, *Dermochelys coriacea*)
 Cetacean (blue whale, *Balaenoptera musculus*)

Sampling strategy

For this study, sample size was determined by the data available to us from TOPP. Some species datasets were very large (northern elephant seal and Pacific bluefin tuna, nearly 300 individuals each). Others included representative breeding populations at the ocean basin scale (leatherback turtles). When possible, we explored the effect of inter-annual variability on observed patterns by modeling patterns over multiple years and determined that patterns were conserved across years. We have confidence that some datasets represent population patterns of space use. However, we make caveats related to non-representativeness of our results at the population and/or the species level clear in our manuscript.

Data collection

Data were collected *in situ* by electronic tracking devices deployed on wild marine animals. Further information is provided in Block et al. 2011 including geographic coordinates of capture locations, and citations of all papers detailing capture, handling, and tag deployment techniques for each species.

Timing and spatial scale

TOPP field studies ran from 2001 to 2009 in the Pacific Ocean. Details of collection periods for each species are provided in full detail in Supplementary Table 1 in this paper, and in Block et al. 2011, *Nature*.

Data exclusions

From the original TOPP dataset (Block et al. 2011, *Nature*) we excluded from analysis all species for which the majority of individuals were sampled for less than a year (northern fur seal, loggerhead turtle, thresher shark, humpback whale, fin whale).

Reproducibility

All results in the paper are drawn from the analysis of multiple animals and when possible, inter-annual, life history stage, and population-level comparisons were also made. Prior to publication we will prepare a worked example whereby readers can follow through custom R code to replicate our results with an electronic tracking dataset, including initial data exploration (dot plots and mapping), the geographic assignment of animal locations to EEZs or to the High Seas, the fitting of multinomial models to these data, the calculation of uncertainty (simulating a sample of estimates from the posterior distribution of the model parameters) and the plotting of results.

Randomization

In the original field study (Block et al. 2011), researchers attempted to select individuals at random from study populations for tag

Randomization

deployments and these individuals are assumed to be representative of their study population. However, some individuals were actively excluded from selection for the dual purposes of animal welfare and potential success of the study, for example, obviously unhealthy or underweight individuals. Some datasets were also age and/or sex biased and these situations are made clear in the Methods. For modeling purposes, animals were assigned to groups as detailed in the Methods based on previous knowledge of population structure (Northern elephant seal), breeding phenology (leatherback turtle), life history stage (Pacific bluefin tuna), or sex (Northern elephant seal and Salmon Shark).

Blinding

Blinding was not relevant to our study. See above Randomization discussion.

Did the study involve field work? Yes No

Reporting for specific materials, systems and methods

Materials & experimental systems

- | | |
|-------------------------------------|-----------------------------|
| n/a | Involved in the study |
| <input checked="" type="checkbox"/> | Unique biological materials |
| <input checked="" type="checkbox"/> | Antibodies |
| <input checked="" type="checkbox"/> | Eukaryotic cell lines |
| <input checked="" type="checkbox"/> | Palaeontology |
| <input type="checkbox"/> | Animals and other organisms |
| <input checked="" type="checkbox"/> | Human research participants |

Methods

- | | |
|-------------------------------------|------------------------|
| n/a | Involved in the study |
| <input checked="" type="checkbox"/> | ChIP-seq |
| <input checked="" type="checkbox"/> | Flow cytometry |
| <input checked="" type="checkbox"/> | MRI-based neuroimaging |

Animals and other organisms

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Laboratory animals

This study did not involve laboratory animals

Wild animals

This study leverages an existing dataset of wild animal movements. Summary details of the over 1,648 wild animals and 14 species incorporated in this study have been included in the Methods section of this manuscript. Full details regarding the original field study is provided in Block et al. 2011 including geographic coordinates of capture locations, and citations of all papers detailing capture, handling, and tag deployment techniques for each species.

Field-collected samples

This study did not involve samples collected from the field.