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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 declines is a failure of 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 dataset to show how the movements and migratory phenology of 1,648 individuals representing 14 species—from leatherback turtles to white sharks—relate to 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 time[1]. Migratory species are thus exposed to a variety of threats[2] 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 turtles (*Dermochelys coriacea)*[3], Pacific bluefin tuna (*Thunnus orientalis)*[4], and some sharks[5] and seabirds[6]. 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 shoreline[11]. 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 stocks[12]. In a joint management structure with member states, conservation and management rules are adopted by the RFMO 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 governance[7] 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 dataset collected between 2000-2009 by the Tagging of Pacific Predators project (TOPP)[1] For each species of tuna (Pacific bluefin, 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), 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, Supplementary Table 2). Some species (Pacific bluefin tuna, leatherback 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 United States (23%); 71% of all locations were within the boundaries of an EEZ (Supplementary Table 3).

While these simple statistics provide insight into overall occurrence, they may be biased by effects of deployment location and sampling imbalances common to electronic tracking datasets. 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. 7-8) using multinomial generalized additive models[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. 3-4). California sea lions and Yellowfin tuna were not modeled because greater than 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 multi-species, multi-year simultaneous animal movement dataset at an ocean-basin scale. Nonetheless, many datasets are not fully representative at the species level within the Pacific Ocean. TOPP focused primarily on North American populations and many species datasets 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). Our results therefore describe only the specific geographic subsets of populations and life history stages studied by TOPP (see Methods, Supplementary Information and [1] for full dataset 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.

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 periods[1]. 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 corridor of fast-moving sooty shearwaters[15] (Fig. 2). Or, 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 tag deployments occurred, making management more straightforward. For example, California sea lions from the U.S. breeding population remained within U.S. waters except during years of anomalous oceanographic conditions[16] when they ventured to the high seas (Supplementary Table 2). Some life history stages not represented in our dataset also remain in one or two EEZs, for example juvenile white sharks in the eastern north Pacific remain in USA and Mexican EEZs[17].

Among the six taxa of marine predators studied, some co-occurred seasonally within the same EEZs (Fig. 2). Tunas, sharks, and whales occurred within U.S. waters from July to December; female elephant seals, albatrosses, and leatherback turtles ranged throughout the high seas from April to November; and Laysan albatrosses and sooty shearwaters visited Russian waters from July through October. There are examples of similar patterns from other stocks and populations in the Pacific. White shark data modeled here represent individuals migrating between the U.S. 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, Mexico[18]. 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 also could help identify when and where to focus management efforts focused on human interactions, for example to help maximize bycatch 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., Supplementary Tables 1-2) and predicted when during the year animals moved among countries or into the high seas according to their cycles of breeding, foraging, and migration (Fig. 2-3, Supplementary Figs. 1-4).

Understanding the political biogeography of leatherback turtles in the Pacific Ocean is especially important as they are highly threatened[19] and their management is jurisdictionally complex. During this study, leatherback turtles in the Pacific Ocean moved through 32 countries and the high seas. Globally, seven leatherback 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 2040[19]. We compared Eastern (Fig. 2) and Western Pacific leatherbacks (Fig. 3), and 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 and our results thus provide the ability to link observed locations of human interactions to specific leatherback turtle breeding populations. To save leatherback turtles from extinction in the Pacific Ocean, a multi-lateral, 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 Sea Treaty, and the Agreement on the Conservation of Albatrosses and Petrels. Our results could be a key ingredient in a holistic conservation strategy[20] that integrates protections throughout the pan-Pacific leatherback life cycle including: optimizing reproductive success on nesting beaches (e.g. beach protection, monitoring, and enforcement, conservation payments to local communities), and preventing deaths due to incidental catch by fisheries within EEZs (e.g. tailored approaches to scale of fishery and socio-economic context, adoption of gear-technology-handling standards to reduce incidental catch and increase probability of post-release survival, incentive-based mechanisms, use rights, time-area-closures) and in the high seas (e.g. expanding pan-Pacific policy actions, increasing and enforcing observer coverage, adoption of gear-technology-handling standards, etc.)[21].

How important are the high seas to marine predator populations?

The high seas are one of the world's last global commons[22] and are among the least protected places on Earth[23]. Despite recent progress, many RFMOs have not ensured that all fish stocks under their mandates are fished sustainably[9] and/or have not suitably protected non-target species such as seabirds, sharks, turtles, and marine mammals[10]. 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), and seabirds, leatherback turtles, white sharks, and northern elephant seals spent between 45-75% 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 seas[24]. 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, AIS, maritime Automated Identification System made publicly available through Global Fishing Watch[25]) that can be used to increase the transparency of high seas fishing.

Conclusions

Our analysis of tracking data collected from Pacific 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 turtles, they also demonstrate that for some species or populations, agreements between just a few countries could help reverse declines. Our approach capitalizes on what biologging technologies do best[27]: 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.

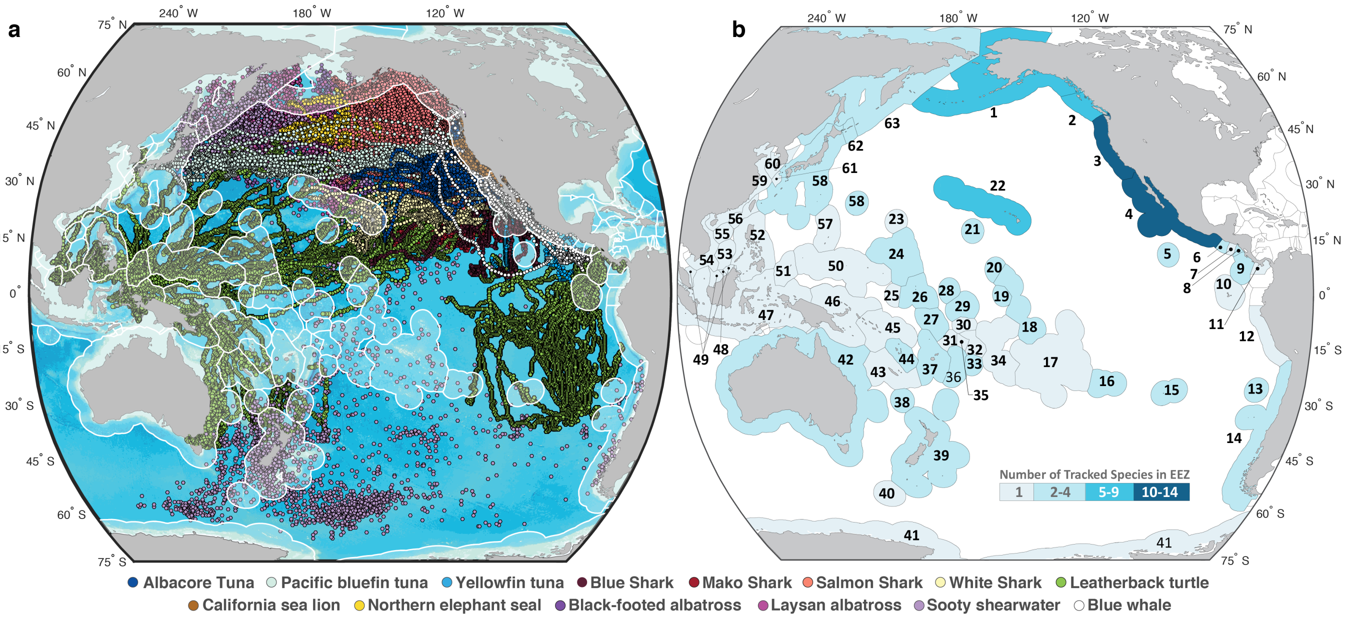
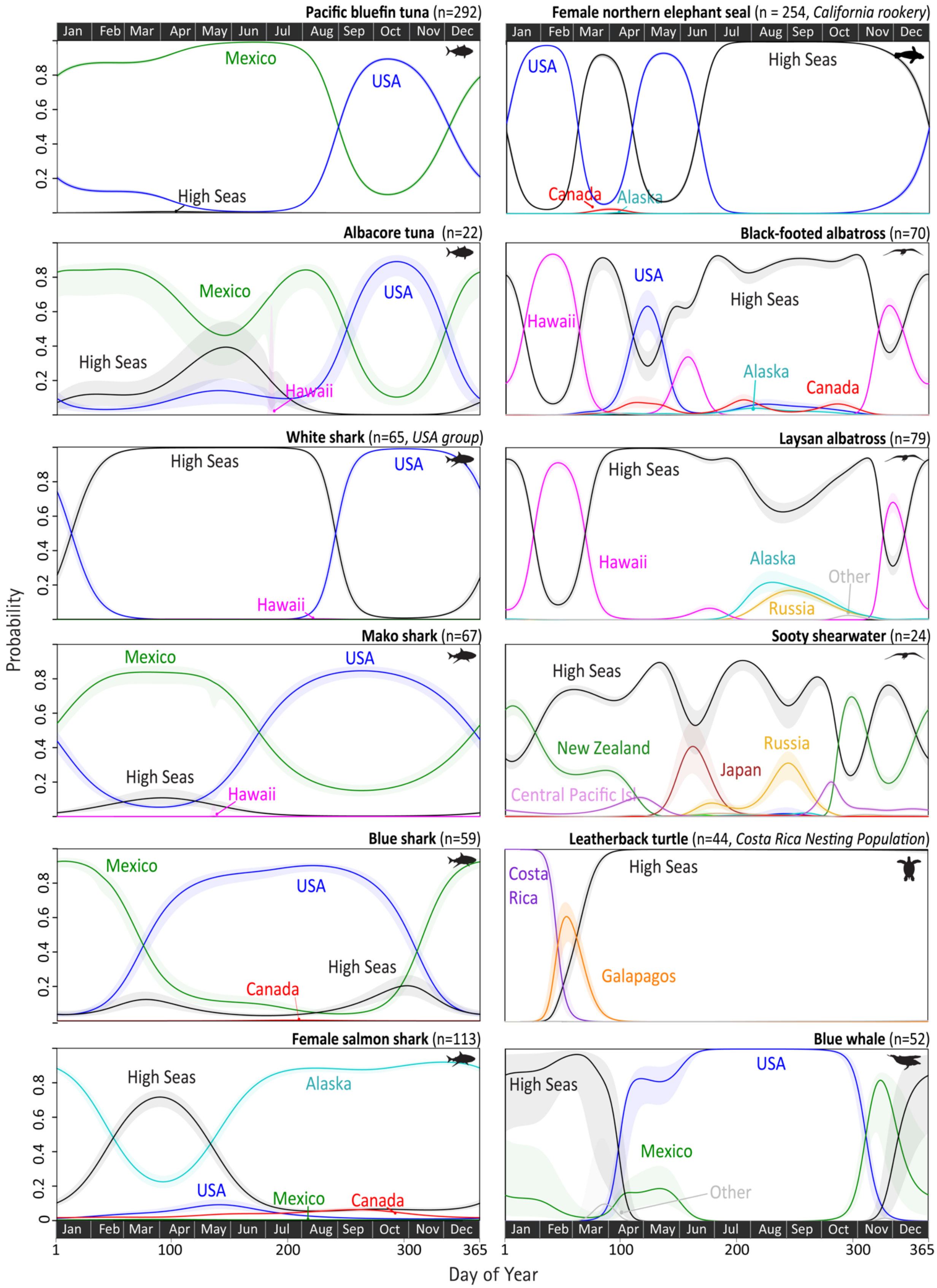


Fig. 1. Daily locations of marine predators electronically tracked within EEZs and the high seas of the Pacific Ocean. (**a**) State space modeled daily locations of 14 marine predator species electronically tracked 2000-2009 in EEZs (transparent overlay) and the high seas (ocean water falling outside transparent overlay). Modified from[1]. (**b**) Key to visited EEZs. EEZ boundaries from VLIZ Maritime Boundaries Geodatabase (2016); some are disputed. Refer to official record for all claimants and alternative geographies. 1 Alaska (USA); 2 Canada; 3 United States of America; 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 Fernandez Islands); 15 Easter Island (Chile); 16 Pitcairn (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 (USA); 24 Marshall Islands; 25 Nauru; 26 Kiribati; 27 Tuvalu; 28 Howland Island and Baker Island (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 (AUS); 39 New Zealand; 40 Macquarie Island (AUS); 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 Viet Nam; 55 Paracel Islands (Disputed); 56 Taiwan; 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.



Pacific bluefin tuna (n=292)
Mexico
USA
High Seas
Female northern elephant seal (n = 254, California rookery)
USA
High Seas
Canada
Alaska
Albacore tuna (n=22)
Mexico
USA
High Seas
Hawaii
Black-footed albatross (n=70)
Hawaii
USA
High Seas
Alaska
Canada
White shark (n=65, USA group)
High Seas
USA
Hawaii
Laysan albatross (n=79)
High Seas
Hawaii
Alaska
Other
Russia
Mako shark (n=67)
Mexico
USA
High Seas
Hawaii
Sooty shearwater (n=24)
High Seas
New Zealand
Russia
Japan
Central Pacific Isl.
Blue shark (n=59)
Mexico
USA
High Seas
Canada
Leatherback turtle (n=44, Costa Rica Nesting Population)
Costa Rica
High Seas
Galapagos
Female salmon shark (n=113)
High Seas
Alaska
USA
Mexico
Canada
Blue whale (n=52)
USA
High Seas
Mexico
Other
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Probability
0 0.2 0.4 0.6 0.8
Day of Year
1 100 200 300 365

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

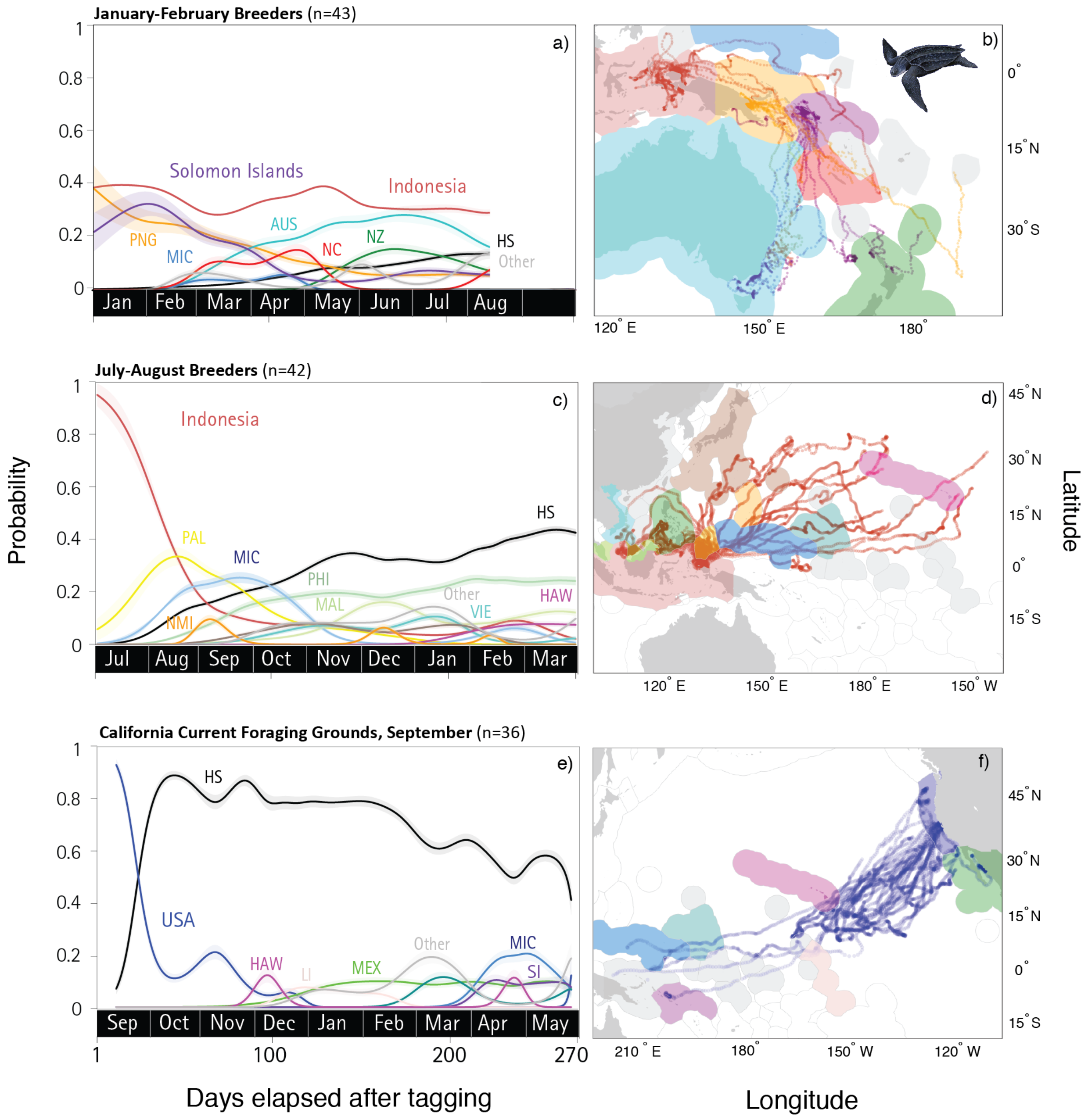


Fig. 3. Population differences in Western Pacific leatherback turtle use of EEZs and the high seas. (**A**, **C**, **E**) Probability of turtle occurrence in EEZs and the high seas during the 7-9 months following tag deployment. Tags were deployed during the breeding period (**A-D**), or on foraging

grounds (**E**-**F**). 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. Shading represents the inter-quartile 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: Methods and Supplementary Table 4. (**B**, **D**, **F**) State space modeled daily locations of individuals electronically tracked from each population (colors correspond to EEZ where tags were deployed) and EEZ boundaries (colors correspond to facing panel). (**A**-**B**) Austral summer breeding populations tagged during breeding in Indonesia, Solomon Islands, and Papua New Guinea (**C**-**D**) Austral winter breeding population tagged during breeding in Indonesia, (**E**-**F**) Foraging population in California Current Large Marine Ecosystem.

Table 1: Percentage of the year marine predators are estimated to spend within Pacific Ocean EEZs and the high seas. Percentages were estimated from model results presented in Fig. 2 and Supplementary Fig. 2 (PBT, TP) using electronic tagging data. Model details: 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, 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 turtle from Costa Rica; BLWH, blue whale. Percentages may not total 100 due to rounding. Leatherback 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.

	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 Pac. Isl.											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

Methods:

1. Data summary and availability

From 2000 to 2009, researchers with the Tagging of Pacific Predators (TOPP) project deployed 4,306 electronic tags which provided 1,791 individual animal tracks from populations of 23 species in the Pacific Ocean[1]. Animal research was conducted in accordance with institutional animal care and use protocols from Stanford University and the University of California, for endangered species in accordance with guidance from the U.S. Endangered Species Act and for marine mammals in accordance with the U.S. Marine Mammal Protection Act.

A Bayesian state-space model[31] was fitted to the tag data to derive regular, daily mean estimates of locations at sea while accounting for tag observation error[32]. The state-space model also provided estimates of the uncertainty in the location estimates. This modeled TOPP dataset is archived in the U.S. Animal Tracking Network Data Assembly Center.

We used a subset of this TOPP dataset; only species tracked over multiple years were included. The dataset we analyzed included 14 species, 1,648 individuals and 265,881 modeled daily locations (Supplementary Table 1). Yearly sampling effort varied (Supplementary Table 1). Tags were deployed within the boundaries of eight EEZs (Supplementary Tables 2-3). For full deployment details:[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 dataset[1].

Variability in deployment date and track duration: Timing of tag deployments was multi-modal for some species (Supplementary Fig. 6), and track duration varied among individuals

(Supplementary Fig. 7). This variability in a tracking dataset can affect spatio-temporal analyses when deployment dates and track duration are unrelated to species life history.

Pinnipeds and seabirds: Distributions of deployment dates and track durations reflected these species' life histories. To capture the full annual cycle of land-breeding and moulting species, tags were deployed multiple times in a given year (northern elephant seals, prior to the short post-breeding and long post-moult migrations; seabirds: prior to 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 upon recapture of the animals. Pinnipeds included in this analysis were females and all pinnipeds and seabirds were adults.

Tunas, sharks, whales: For these species, deployment timing varied among years partially because of reasons unrelated to species' life history (sampling design considerations or cruise availability). 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 datasets contained a high number of individuals tracked for less than a year. Salmon shark was an exception with 16 individuals tracked for at least two years (Supplementary Fig. 7). 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 turtles: Leatherback 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 turtles were considered separately in this study. Tags on eastern Pacific leatherbacks were deployed in January during the nesting period[33]. 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. Tag deployment thus occurred in three different pulses (see [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.

2. 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 (VLIZ: http://www.vliz.be/vmdcdata/marbound/). Shapefiles were converted to polygon vectors using the MATLAB mapping toolbox (The MathWorks Inc., R2015b). We developed a custom script based upon 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 (and 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.

3. 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 related literature (for example, see [35]). However, for our dataset 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 toward the EEZs in which tags were deployed (Supplementary Figs. 7-8); 2) deployment date affected 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 years. One solution is to remove from analysis individuals with abbreviated tracking durations (for example <30 days or <1 year). However, we felt there was value in retaining all available information to elucidate seasonal patterns of EEZ use.

We therefore took a modeling 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 modeled with a generalized additive model[14], specifically a multinomial logistic regression[13]. For species predicted to have an annual migratory cycle (all species except leatherback turtles), a cyclic effect was used for day of the year enforcing continuity in the estimated probabilities from year to year. Individual identity was treated as a random intercept effect to account for differences in behavior 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 summed to 1 for any given day of the year for any given individual. Models were fitted using the 'mgcv' package[14] in R (R Development Core Team 2016). The ordering of categories in the model formulation (i.e., EEZs and the high seas) can somewhat affect the fit of the multinomial models used (see R package mgcv reference manual, GAM multinomial logistic regression, for more detail [36]), 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 lowest numbers of 'observed' locations.

For each species, the formulation of the models depended upon species life history and dataset quality (Supplementary Table 4). Models were not developed for species who spent most of their time within a single EEZ (yellowfin tuna; California sea lion). Yearly models were considered for species with balanced datasets 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 U.S. and Mexican breeding populations (Supplementary Fig. 1). Two model groups were also constructed for Pacific bluefin tuna. Group 1 included all PBT individuals. The second PBT model group included only those tuna that undertook trans-Pacific migrations (n=12, Supplementary Fig. 2).

For western Pacific leatherbacks, we modeled each breeding population and the California foraging population separately due to the multi-modality of tag deployments and our interest in differences in EEZ use by the different populations. In order 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 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.

4. *Model predictions and uncertainty*

From 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 the year. Use of EEZs by tagged western Pacific leatherback turtles was estimated only for the 7.5-9 months following tag deployment, due to the impacts 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 corridor[15]. Population-level predictions were derived by setting the random intercept effect of 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 the 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, 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. Summaries of individual use of EEZs and the high seas (Supplementary Table 1), therefore provide information that may be of use to managers in addition to model results, keeping in mind caveats due to variability in tracking duration discussed in Methods sections 1 and 5.

Uncertainty in model predictions was characterized by simulating a sample of estimates from the posterior distribution of the model parameters[14]. 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 uncertainty and sample sizes in northern elephant seal yearly models to 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 the 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 uncertainty [1] 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.

5. 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 durations 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 have the ability to 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 favor 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 dataset 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 (i.e. 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 EEZ[1]. Individuals tracked for less than 30 days spent 80-100% of their time within Mexico. Individuals tracked for greater than a 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 higher 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 was unable to 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 dataset that can bias interpretation of space use for the tracked population. In this paper, 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 dataset subject to a high amount of tag attrition (i.e. “short” tracks). For datasets in which many individuals were tracked for multiple years (i.e. salmon sharks), we expect a minimal effect of this bias for the tracked population.

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End Notes

Supplementary Information is linked to the online version of the paper.

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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.

Data Availability Statement: The tracking data used are archived in the U.S. Animal Tracking Network Data Assembly Center. http://oceanview.pfeg.noaa.gov/ATN/

Code Availability Statement: Custom R scripts will be made available via GitHub upon publication in the political-biogeography project, and are also available upon request to the corresponding author.