

1                   **The political biogeography of migratory marine predators**

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## **The political biogeography of migratory marine predators**

**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<sup>1</sup>. Migratory species are thus exposed to a variety of threats<sup>2</sup> 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*)<sup>3</sup>, Pacific bluefin tuna (*Thunnus orientalis*)<sup>4</sup>, and some sharks<sup>5</sup> and seabirds<sup>6</sup>. Under current management frameworks, migratory species have received varying levels of protection and many gaps remain<sup>7-10</sup>. National rights over marine resources are delineated by Exclusive Economic Zones (EEZs) which include waters out to 200 nautical miles from a country's

70 shoreline<sup>11</sup>. Areas beyond national jurisdiction, the ‘high seas’, are legally recognized as a global  
71 commons. Regional Fisheries Management Organizations (RFMOs) are the primary multi-  
72 jurisdictional mechanism for managing transboundary and high seas fish stocks<sup>12</sup>. In a joint  
73 management structure with member states, conservation and management rules are adopted by  
74 the RFMO while enforcement of these measures falls to individual countries. As such, individual  
75 nations are responsible for fishing and non-fishing related threats within their EEZs and, through  
76 their high seas fleets and flag vessels, share responsibility beyond their EEZs. To recover  
77 populations and to prevent declines of healthy populations, improved management and effective  
78 international cooperation and governance<sup>7</sup> are urgently needed. Key information needs at all  
79 levels include quantitative measures to indicate who has management jurisdiction over migratory  
80 species across their range and at different times during their migratory cycle, including for  
81 breeding, foraging, and migrating. Here we use biologging data to provide this information. We  
82 show how the migratory cycles of populations of 14 species relate to geopolitical boundaries of  
83 the Pacific Ocean using a subset of a large tracking dataset collected between 2000-2009 by the  
84 Tagging of Pacific Predators project (TOPP)<sup>1</sup> For each species of tuna (Pacific bluefin,  
85 yellowfin, *Thunnus albacares*; albacore, *Thunnus alalunga*); shark (blue, *Prionace glauca*,  
86 shortfin mako, *Isurus oxyrinchus*; white, *Carcharodon carcharias*; salmon, *Lamna ditropis*),  
87 pinniped (northern elephant seal, *Mirounga angustirostris*; California sea lion, *Zalophus*  
88 *californianus*), seabird (Laysan albatross, *Phoebastria immutabilis*; black-footed albatross,  
89 *Phoebastria nigripes*; sooty shearwater, *Puffinus griseus*), sea turtle (leatherback), and cetacean  
90 (blue whale, *Balaenoptera musculus*) we asked: 1) Which EEZs were visited? 2) What  
91 proportion of time was spent in each EEZ and the high seas? 3) When during their migratory  
92 cycle were animals within each EEZ or the high seas?

93 **Results and Discussion**

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

103 While these simple statistics provide insight into overall occurrence, they may be biased by  
104 effects of deployment location and sampling imbalances common to electronic tracking datasets.  
105 We addressed biases due to variability in sample size during the year (Supplementary Table 1,  
106 Supplementary Fig. 5), deployment dates (Supplementary Fig. 6), and track durations  
107 (Supplementary Figs. 7-8) using multinomial generalized additive models<sup>13,14</sup>. We predicted  
108 seasonal patterns of occurrence within specific countries and the high seas for multiple taxa (Fig.  
109 2), breeding populations (Fig. 3 and Supplementary Fig. 1), life history stages (Supplementary  
110 Fig. 2), and years (Supplementary Figs. 3-4). California sea lions and Yellowfin tuna were not  
111 modeled because greater than 90% of locations were within a single EEZ (Supplementary Table  
112 3). From model predictions we also estimated the percentage of an annual cycle spent in EEZs or  
113 in the high seas (Table 1). The TOPP project was unprecedented in producing a large multi-  
114 species, multi-year simultaneous animal movement dataset at an ocean-basin scale. Nonetheless,  
115 many datasets are not fully representative at the species level within the Pacific Ocean. TOPP

116 focused primarily on North American populations and many species datasets are age or sex-  
117 biased. For example, this study includes results from female salmon sharks in the eastern North  
118 Pacific, but not males from the western North Pacific. It includes female Northern elephant seals  
119 from Mexican and American rookeries, but not males. Additionally, some species in this study  
120 include few individuals relative to population size (for example, Sooty Shearwaters). Our results  
121 therefore describe only the specific geographic subsets of populations and life history stages  
122 studied by TOPP (see Methods, Supplementary Information and <sup>1</sup> for full dataset details and  
123 deployment locations).

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

126 ***When during the year are marine predators present within countries' waters?***

127 Marine predators cue on shifts of habitats and prey, which in turn concentrate individuals in  
128 specific regions during defined time periods<sup>1</sup>. Consequently, residency within each EEZ is not  
129 equally probable throughout the year (Fig. 2). It may be highly punctuated in time, for example  
130 the central Pacific island migration corridor of fast-moving sooty shearwaters<sup>15</sup> (Fig. 2). Or, a  
131 single EEZ may constitute half or more of yearly residency, for example, salmon sharks in  
132 Alaska and Pacific bluefin tuna in Mexico (Table 1). Some populations in this study remained  
133 almost entirely within the EEZs in which tag deployments occurred, making management more  
134 straightforward. For example, California sea lions from the U.S. breeding population remained  
135 within U.S. waters except during years of anomalous oceanographic conditions<sup>16</sup> when they  
136 ventured to the high seas (Supplementary Table 2). Some life history stages not represented in  
137 our dataset also remain in one or two EEZs, for example juvenile white sharks in the eastern  
138 north Pacific remain in USA and Mexican EEZs<sup>17</sup>.

139 Among the six taxa of marine predators studied, some co-occurred seasonally within the same  
140 EEZs (Fig. 2). Tunas, sharks, and whales occurred within U.S. waters from July to December;  
141 female elephant seals, albatrosses, and leatherback turtles ranged throughout the high seas from  
142 April to November; and Laysan albatrosses and sooty shearwaters visited Russian waters from  
143 July through October. There are examples of similar patterns from other stocks and populations  
144 in the Pacific. White shark data modeled here represent individuals migrating between the U.S.  
145 EEZ (Central California) and the high seas. A second group of northeastern Pacific white sharks  
146 shows near identical phenology in migrations between the high seas and Guadalupe Island,  
147 Mexico<sup>18</sup>. By identifying seasonal patterns of co-occurrence across guilds, species, and  
148 populations, our results can help managers maximize their efforts across a range of migratory  
149 taxa. For example, dynamic and ecosystem-based management approaches require a synthetic  
150 understanding of the migratory cycles of multiple species. Our results also could help identify  
151 when and where to focus management efforts focused on human interactions, for example to  
152 help maximize bycatch mitigation efforts in places where currently there is a lack of observer  
153 coverage and enforcement.

154 ***Which countries should be cooperating, either directly, or through established international***  
155 ***bodies and frameworks?***

156 We identified the set of countries visited by each species (Fig 1., Supplementary Tables 1-2) and  
157 predicted when during the year animals moved among countries or into the high seas according  
158 to their cycles of breeding, foraging, and migration (Fig. 2-3, Supplementary Figs. 1-4).

159 Understanding the political biogeography of leatherback turtles in the Pacific Ocean is especially  
160 important as they are highly threatened<sup>19</sup> and their management is jurisdictionally complex.

161 During this study, leatherback turtles in the Pacific Ocean moved through 32 countries and the



162 high seas. Globally, seven leatherback turtle subpopulations are recognized and all are  
163 considered vulnerable to extinction. However, the western Pacific and eastern Pacific  
164 subpopulations we studied are critically endangered with estimates of a 96% population decline  
165 by 2040<sup>19</sup>. We compared Eastern (Fig. 2) and Western Pacific leatherbacks (Fig. 3), and breeding  
166 populations of Western Pacific leatherbacks (Fig. 3). In the Western Pacific, turtles that breed in  
167 the austral winter pass through Asian and Central Pacific EEZs; turtles that breed in the austral  
168 summer migrate to EEZs of the South Pacific (Fig. 3). We show that political biogeography is  
169 linked to population structure and breeding phenology for this species and our results thus  
170 provide the ability to link observed locations of human interactions to specific leatherback turtle  
171 breeding populations. To save leatherback turtles from extinction in the Pacific Ocean, a multi-  
172 lateral, cooperative approach is the only way forward, often stemming from private, local, or  
173 regional collaborations that provide a first step in cooperative research and conservation.  
174 Examples of such international coordination include the Inter-American Tropical Tuna  
175 Commission, the Commission for the Conservation of Antarctic Marine Living Resources, the  
176 Northern Fur Sea Treaty, and the Agreement on the Conservation of Albatrosses and Petrels. Our  
177 results could be a key ingredient in a holistic conservation strategy<sup>20</sup> that integrates protections  
178 throughout the pan-Pacific leatherback life cycle including: optimizing reproductive success on  
179 nesting beaches (e.g. beach protection, monitoring, and enforcement, conservation payments to  
180 local communities), and preventing deaths due to incidental catch by fisheries within EEZs (e.g.  
181 tailored approaches to scale of fishery and socio-economic context, adoption of gear-technology-  
182 handling standards to reduce incidental catch and increase probability of post-release survival,  
183 incentive-based mechanisms, use rights, time-area-closures) and in the high seas (e.g. expanding

184 pan-Pacific policy actions, increasing and enforcing observer coverage, adoption of gear-  
185 technology-handling standards, etc.)<sup>21</sup>.

186

187 ***How important are the high seas to marine predator populations?***

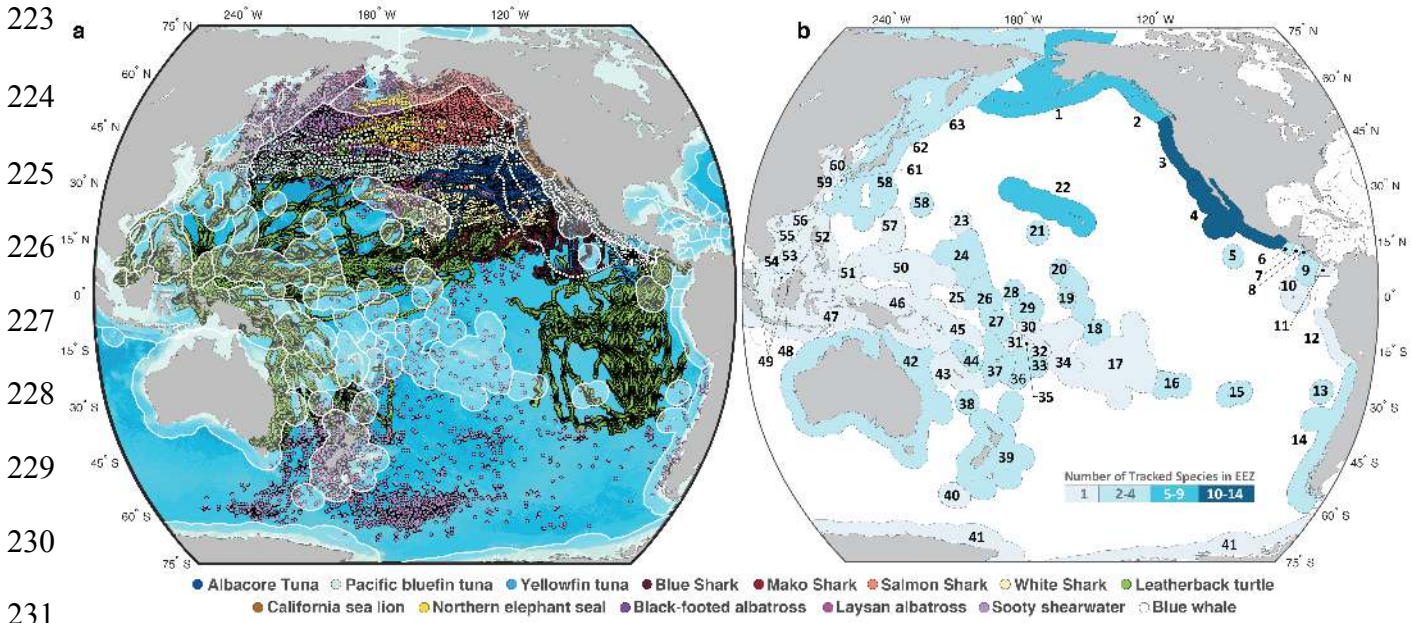
188 The high seas are one of the world's last global commons<sup>22</sup> and are among the least protected  
189 places on Earth<sup>23</sup>. Despite recent progress, many RFMOs have not ensured that all fish stocks  
190 under their mandates are fished sustainably<sup>9</sup> and/or have not suitably protected non-target species  
191 such as seabirds, sharks, turtles, and marine mammals<sup>10</sup>. Many approaches have been suggested  
192 or used to improve the sustainability of high seas fisheries, including: rights-based management,  
193 adopting and enforcing best practice gear technology standards, increasing observer coverage,  
194 time/area restrictions, protected areas, vessel monitoring, increasing and sharing scientific  
195 research, market and trade-based mechanisms, and the adoption of a new international legal  
196 instrument.<sup>7,10</sup> To implement many of these suggestions, quantitative measures of high seas use  
197 are needed.

198 Our results provide measures of the time multiple populations spend within the high seas at a  
199 basin-wide scale (Table 1 and Fig. 2). For example, Pacific bluefin tuna tracked during their  
200 trans-Pacific migration (n=12, Supplementary Fig. 2), and seabirds, leatherback turtles, white  
201 sharks, and northern elephant seals spent between 45-75% of the year in the high seas (Table 1).  
202 Attention to high seas management issues is increasing. The United Nations General Assembly  
203 in 2015 resolved to develop an international legally binding instrument for the conservation and  
204 sustainable use of marine biodiversity of the high seas<sup>24</sup>. This process will advance in 2018 to  
205 full negotiation. The knowledge we present of how and when animals use the high seas is a  
206 critical contribution to these next steps to sustain marine biodiversity and is a complement to

207 new satellite services (for example, AIS, maritime Automated Identification System made  
208 publicly available through Global Fishing Watch<sup>25</sup>) that can be used to increase the transparency  
209 of high seas fishing.

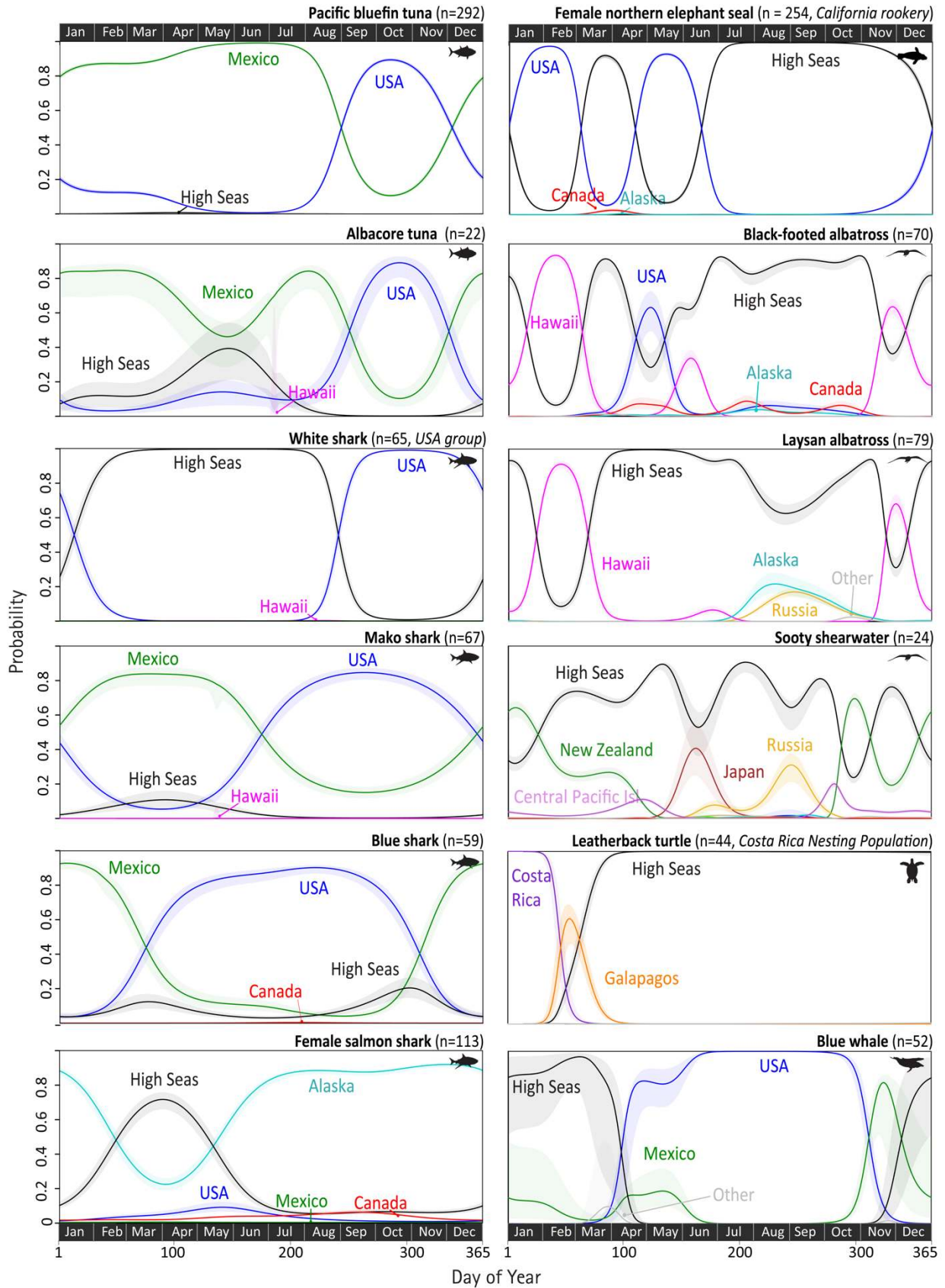
## 210 ***Conclusions***

211 Our analysis of tracking data collected from Pacific predators describes seasonal patterns  
212 of national and international management jurisdiction over migratory species. Actions to protect  
213 marine migratory species are needed throughout their range, including on the high seas. Multiple  
214 international conventions and agreements<sup>11,12,26</sup> seek to promote cooperation within and beyond  
215 national jurisdictions for managing migratory species. Nevertheless, scaled-up international  
216 collaboration and effective governance are essential. While our results demonstrate the  
217 jurisdictional complexity of managing some critically endangered highly migratory species like  
218 Pacific leatherback turtles, they also demonstrate that for some species or populations,  
219 agreements between just a few countries could help reverse declines. Our approach capitalizes on  
220 what biologging technologies do best<sup>27</sup>: provide continuous movement data on individual  
221 animals who spend most of their lives away from direct scientific observation. This information  
222 can<sup>28-30</sup> and should be used to inform management.

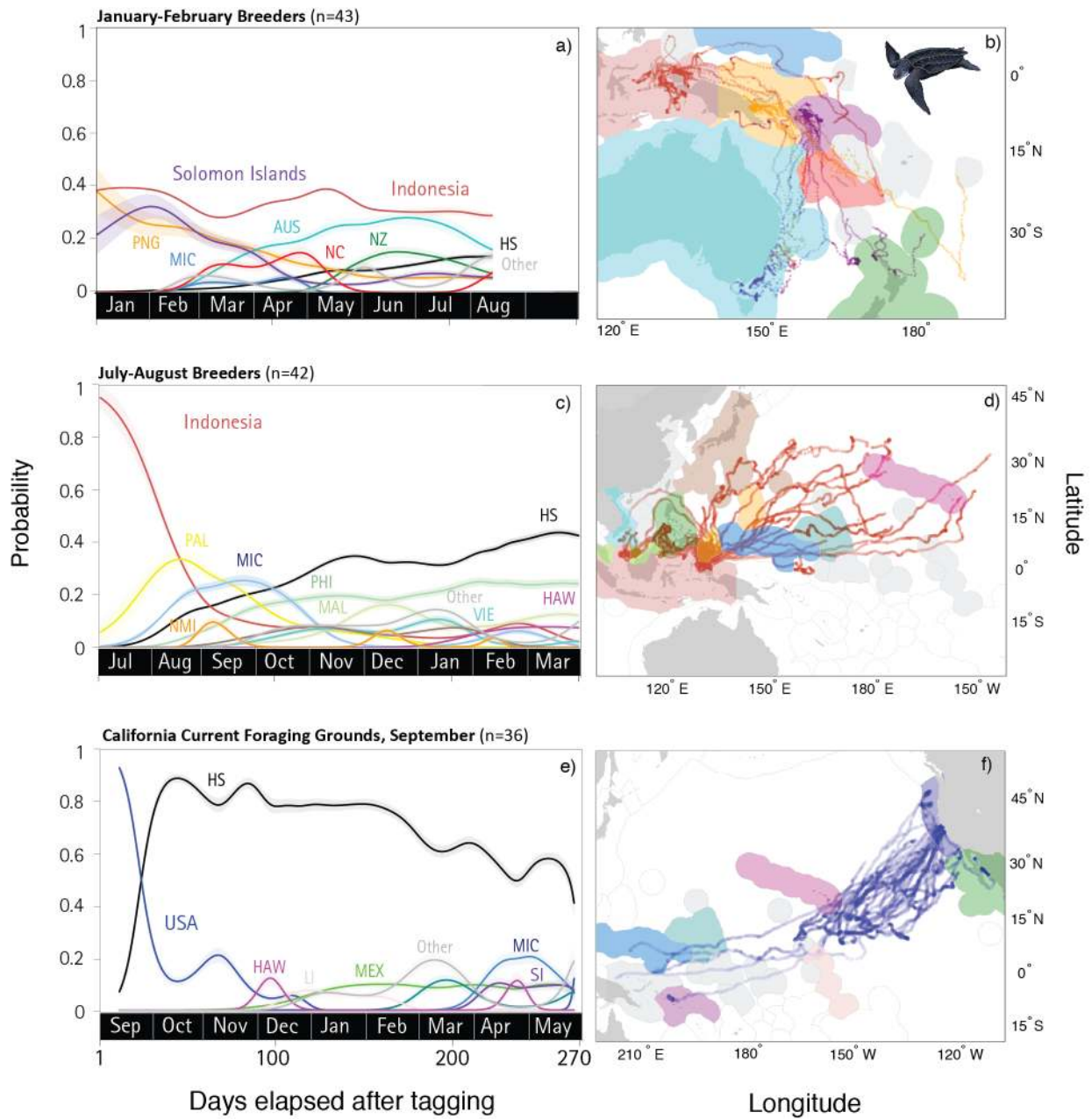


**Fig. 1. Daily locations of marine predators electronically tracked within EEZs and the high seas of the Pacific Ocean. (a)** State space modeled daily locations of 14 marine predator species electronically tracked 2000-2009 in EEZs (transparent overlay) and the high seas (ocean water falling outside transparent overlay). Modified from<sup>1</sup>. **(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

246 Fiji; 38 Norfolk Island (AUS); 39 New Zealand; 40 Macquarie Island (AUS); 41 Antarctica; 42  
247 Australia; 43 New Caledonia (France); 44 Vanuatu; 45 Solomon Islands; 46 Papua New Guinea;  
248 47 Indonesia; 48 Brunei; 49 Malaysia; 50 Micronesia; 51 Palau; 52 Philippines; 53 Spratly Islands  
249 (Disputed); 54 Viet Nam; 55 Paracel Islands (Disputed); 56 Taiwan; 57 Northern Mariana Islands  
250 and Guam (USA); 58 Japan; 59 China; 60 South Korea; 61 Japan-Korea Joint Development Zone;  
251 62 Southern Kuriles (Disputed); 63 Russia.



253 **Fig. 2. Seasonal probability of marine predator occurrence in Pacific Ocean EEZs and the**  
254 **high seas from electronic tracking.** Lines represent the estimated effect of day of the year on the  
255 probability of a randomly selected individual from the tracked population occurring in each region.  
256 Shading represents the inter-quartile range of estimates simulated from the posterior distribution of the  
257 model parameters. Total sample size for each population is represented by n; tracking duration varied  
258 among individuals (see Methods). Model details: Methods and Supplementary Table 4. Leatherback  
259 turtles have a multi-year migratory cycle; estimates begin on January 21 and continue through the first  
260 year of this cycle following breeding/tag deployment.  
261



263

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



267 grounds (**E-F**). Lines represent the estimated effect of days elapsed after tag deployment on the  
268 probability of a randomly selected individual from the tracked population occurring in each region.  
269 Shading represents the inter-quartile range of estimates simulated from the posterior distribution of the  
270 model parameters. Sample size and longevity of tags dictated the number of days elapsed since tagging  
271 (7-9 months) considered in the models. Model details: Methods and Supplementary Table 4. (**B, D, F**)  
272 State space modeled daily locations of individuals electronically tracked from each population (colors  
273 correspond to EEZ where tags were deployed) and EEZ boundaries (colors correspond to facing panel).  
274 (**A-B**) Austral summer breeding populations tagged during breeding in Indonesia, Solomon Islands, and  
275 Papua New Guinea (**C-D**) Austral winter breeding population tagged during breeding in Indonesia, (**E-**  
276 **F**) Foraging population in California Current Large Marine Ecosystem.

277



**Other** <1 <1 <1 <1 <1 <1 <1 <1

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292 **Methods:**

293 **1. Data summary and availability**

294 From 2000 to 2009, researchers with the Tagging of Pacific Predators (TOPP) project deployed  
295 4,306 electronic tags which provided 1,791 individual animal tracks from populations of 23  
296 species in the Pacific Ocean<sup>1</sup>. Animal research was conducted in accordance with institutional  
297 animal care and use protocols from Stanford University and the University of California, for  
298 endangered species in accordance with guidance from the U.S. Endangered Species Act and for  
299 marine mammals in accordance with the U.S. Marine Mammal Protection Act.

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

304 We used a subset of this TOPP dataset; only species tracked over multiple years were  
305 included. The dataset we analyzed included 14 species, 1,648 individuals and 265,881 modeled  
306 daily locations (Supplementary Table 1). Yearly sampling effort varied (Supplementary Table 1).  
307 Tags were deployed within the boundaries of eight EEZs (Supplementary Tables 2-3). For full  
308 deployment details:<sup>1</sup>. There are multiple populations in the Pacific Ocean of many species  
309 considered here---we refer only to the specific populations and life history stages in the TOPP  
310 dataset<sup>1</sup>.

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

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

315 *Pinnipeds and seabirds:* Distributions of deployment dates and track durations reflected  
316 these species' life histories. To capture the full annual cycle of land-breeding and moulting  
317 species, tags were deployed multiple times in a given year (northern elephant seals, prior to the  
318 short post-breeding and long post-moult migrations; seabirds: prior to the short breeding and  
319 long post-breeding migrations). Typically, unique sets of individuals were tracked during each  
320 migration although some seals were tracked during both migrations in a given year, or during the  
321 same migration in multiple years. California sea lions were predominantly tagged while nursing  
322 pups to facilitate tag recovery; most individuals were tracked only during the breeding period. In  
323 general, tag failure was rare and tags were recovered upon recapture of the animals. Pinnipeds  
324 included in this analysis were females and all pinnipeds and seabirds were adults.

325 *Tunas, sharks, whales:* For these species, deployment timing varied among years partially  
326 because of reasons unrelated to species' life history (sampling design considerations or cruise  
327 availability). Primary tagging months were: Pacific bluefin tuna, January, March, July-  
328 September, November-December; yellowfin tuna, February, August, October-December;  
329 shortfin mako shark June-August, November; blue shark, January-February, June-August,  
330 October-December; salmon shark, July-August; and white shark, January and December.  
331 Because of a higher frequency of tag failure and the difficulty of targeted recapture, the  
332 distributions of track durations for these species (Supplementary Fig. 7) were a function of tag  
333 attrition and harvest recapture. In general, these datasets contained a high number of individuals  
334 tracked for less than a year. Salmon shark was an exception with 16 individuals tracked for at  
335 least two years (Supplementary Fig. 7). Salmon sharks studied were all females; white sharks

336 were large adults and subadults; Pacific bluefin tuna, albacore tuna, shortfin mako shark, and  
337 blue sharks were largely juveniles

338 *Leatherback turtles:* Leatherback turtles have a multi-year migratory cycle and all tags  
339 experienced attrition before recording the full multi-year migration. The eastern Pacific and  
340 western Pacific subpopulations of leatherback turtles were considered separately in this study.  
341 Tags on eastern Pacific leatherbacks were deployed in January during the nesting period<sup>33</sup>.  
342 Tracking of the western Pacific subpopulation included both summer (Indonesia) and winter  
343 breeders (Indonesia, Papua New Guinea, Solomon Islands), and animals captured while foraging  
344 in the California Current. Tag deployment thus occurred in three different pulses (see <sup>34</sup> for more  
345 detail on the multi-year migratory cycles of Western Pacific leatherbacks and their population  
346 dynamics among breeding rookeries). All turtles included here were breeding adults.

347

## 348 **2. Location Classification**

349 Global EEZ boundaries were obtained as shapefiles from the VLIZ Maritime Boundaries  
350 Geodatabase (v.8, 2014). Some EEZ boundaries between countries are disputed; full details of  
351 boundary delineation are available (VLIZ: <http://www.vliz.be/vmcdcddata/marbound/>). Shapefiles  
352 were converted to polygon vectors using the MATLAB mapping toolbox (The MathWorks Inc.,  
353 R2015b). We developed a custom script based upon MATLAB's "inpolygon" function to  
354 classify each location as present or absent (binary, ones and zeros) in each EEZ of the Pacific  
355 basin. We classified locations on an EEZ boundary as inside the EEZ (and thus, those few  
356 locations located exactly on the boundary/edge of two EEZs would be classified as within two  
357 EEZs). If a location was neither on land nor in an EEZ, we classified it as a high seas location.

358 Disjunct EEZs for a given country were treated separately. For example, Hawaii and Alaska  
359 were each treated as unique to the mainland USA EEZ.

360

### 361 ***3. EEZ and High Seas Occurrence and models of seasonal use***

362

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

377 We therefore took a modeling approach to better estimate seasonal EEZ and high seas  
378 occurrence for the tagged population given the effects of individual variability in track duration  
379 and tagging location and date. The presence of an individual from the tagged sample in each  
380 EEZ or the high seas was modeled with a generalized additive model<sup>14</sup>, specifically a

381 multinomial logistic regression<sup>13</sup>. For species predicted to have an annual migratory cycle (all  
382 species except leatherback turtles), a cyclic effect was used for day of the year enforcing  
383 continuity in the estimated probabilities from year to year. Individual identity was treated as a  
384 random intercept effect to account for differences in behavior and sample size throughout the  
385 year among tagged individuals. Both day-of-year and individual effects were allowed to vary  
386 across EEZs and the high seas. The multinomial model structure ensured that the probabilities of  
387 presence in EEZs and the high seas summed to 1 for any given day of the year for any given  
388 individual. Models were fitted using the ‘mgcv’ package<sup>14</sup> in R (R Development Core Team  
389 2016). The ordering of categories in the model formulation (i.e., EEZs and the high seas) can  
390 somewhat affect the fit of the multinomial models used (see R package mgcv reference manual,  
391 GAM multinomial logistic regression, for more detail<sup>36</sup>), typically (in our case) by inflating  
392 uncertainty estimates when EEZs with few observed locations are ordered first. For consistency  
393 we ordered the categories for each model from the highest to lowest numbers of 'observed'  
394 locations.

395 For each species, the formulation of the models depended upon species life history and  
396 dataset quality (Supplementary Table 4). Models were not developed for species who spent most  
397 of their time within a single EEZ (yellowfin tuna; California sea lion). Yearly models were  
398 considered for species with balanced datasets over multiple years (Supplementary Tables 1 and  
399 4): female northern elephant seals (Supplementary Fig. 3) and salmon shark (Supplementary Fig.  
400 4).

401 For some species, there was enough information to separately model life history stages or  
402 breeding populations. Separate models were fitted for female northern elephant seals from U.S.  
403 and Mexican breeding populations (Supplementary Fig. 1). Two model groups were also



404 constructed for Pacific bluefin tuna. Group 1 included all PBT individuals. The second PBT  
405 model group included only those tuna that undertook trans-Pacific migrations (n=12,  
406 Supplementary Fig. 2).

407 For western Pacific leatherbacks, we modeled each breeding population and the  
408 California foraging population separately due to the multi-modality of tag deployments and our  
409 interest in differences in EEZ use by the different populations. In order to compare EEZ  
410 occurrence in the months following breeding (regardless of whether breeding occurred in  
411 summer or winter), and in the months following tag deployment in the California foraging  
412 grounds, the number of days elapsed following tag deployment was the fixed effect (rather than  
413 day of year, Supplementary Table 4). Therefore, the model was related to a life history event,  
414 estimating EEZ and high seas occurrence during the migration following this event, rather than  
415 to the calendar year.

416

#### 417 ***4. Model predictions and uncertainty***

418 From fitted models we predicted the probability that a randomly selected individual from the  
419 tracked population would occur in an EEZ or in the high seas on each day of the year. Use of  
420 EEZs by tagged western Pacific leatherback turtles was estimated only for the 7.5-9 months  
421 following tag deployment, due to the impacts of tag attrition on data availability after this time.  
422 EEZs with few occurrences were grouped together into an “Other” category. For Sooty  
423 Shearwaters, island EEZs falling within the Central Pacific were also grouped together,  
424 representing their migration corridor<sup>15</sup>. Population-level predictions were derived by setting the  
425 random intercept effect of individual in the model to zero. We estimated the proportion of the

426 year spent in each EEZ or in the high seas for each tracked population by summing the  
427 population-level predicted daily probabilities over the course of a year and dividing by 365.  
428 Models also provided predictions of the probabilities of specific tagged individuals occurring in  
429 EEZs or the high seas on each day of the year. These probabilities were sometimes highly  
430 variable among tagged individuals of a species/population (Supplementary Fig. 9). In some  
431 cases, non-negligible numbers of individuals of a species visited an EEZ during a year (as an  
432 annual summary), but the mean population response on any given day of year may not represent  
433 this. For example, 20% of individual white sharks tracked in this study (Supplementary Table 1)  
434 visited Hawaii and 6% of all locations were in Hawaii (Supplementary Table 2), but the mean  
435 population response on any day of year was near 0 (Fig. 2, Table 1). A similar pattern was  
436 observed for elephant seals in Canada (Supplementary Fig. 9). Because the models estimate a  
437 population response on a given day of year, a substantial proportion of individuals would need to  
438 visit the EEZ at the same time to be represented in the population response. Summaries of  
439 individual use of EEZs and the high seas (Supplementary Table 1), therefore provide information  
440 that may be of use to managers in addition to model results, keeping in mind caveats due to  
441 variability in tracking duration discussed in Methods sections 1 and 5.

442         Uncertainty in model predictions was characterized by simulating a sample of estimates  
443 from the posterior distribution of the model parameters<sup>14</sup>. The posterior distribution was assumed  
444 to be multivariate normal with means equal to the parameter estimates and variances/covariances  
445 from the estimated covariance matrix. The estimated uncertainty generally reflected sample size  
446 across species/populations and throughout the year for individual species/populations  
447 demonstrating the usefulness of the model in accounting for sample size. For example, compare  
448 uncertainty and sample sizes in northern elephant seal yearly models to results for the full

449 population. Uncertainty in the proportion of the year spent in each EEZ and in the high seas was  
450 estimated by calculating these proportions for each parameter set from the posterior sample and  
451 characterizing the distribution of proportions across the sample.

452         The estimates of uncertainty presented here are likely underestimates of the true  
453 uncertainty in the effect of day of the year on the occurrence of tagged animals in EEZs and the  
454 high seas. Although individual identity was included as a model effect, sequential correlation in  
455 the model residuals for an individual could have remained, in which case the true uncertainty in  
456 the day-of-year effect would be greater. Also, the presence data that the models were fitted to  
457 were themselves derived from state-space model location estimates with associated positional  
458 uncertainty <sup>1</sup> that was not accounted for here. Nevertheless, the estimates of uncertainty  
459 presented here provide an upper bound on the confidence that should be placed in the estimated  
460 effects of day of year on the occurrence of the tagged populations in EEZs and the high seas.

461

462         **5. Additional considerations: Effects of tag deployment location and variability in**  
463         **deployment data and track duration on probability estimates**

464 Statistical summaries of time spent in EEZs from electronic tracking data are influenced by the  
465 distribution of track durations and deployment dates and locations. Early in a track, individuals  
466 have a high likelihood of being located within the deployment EEZ because tags were deployed  
467 there. As time passes, individuals have the ability to disperse from the release location and the  
468 proportion of time spent within the deployment EEZ should level to a more biologically  
469 representative proportion unaffected by the initial tag deployment event. Therefore, an  
470 interaction between deployment location and track duration has the potential to bias estimates of

471 EEZ use in favor of the EEZ in which tags were deployed when a large proportion of the tracked  
472 population has short-duration tracks.

473 We explored the effects of track duration and timing of tag deployment in the TOPP  
474 dataset by calculating the running proportion of time spent by each individual within primary  
475 EEZs and the high seas according to the relative day along each individual's track (i.e. days  
476 elapsed since deployment) and according to the month in which the tag was deployed  
477 (Supplementary Fig. 8). For example, most tags were deployed on Pacific bluefin tuna in March,  
478 July-August, and November-December within the Mexican EEZ<sup>1</sup>. Individuals tracked for less  
479 than 30 days spent 80-100% of their time within Mexico. Individuals tracked for greater than a  
480 year, spent 50% of their time in Mexico (Supplementary Fig. 8) with little change in this  
481 proportion as track length increased beyond a year. Tuna released in Mexico in November spent  
482 a higher proportion of their time in Mexico in the few months after being tagged than those  
483 tagged in July (Supplementary Fig. 8).

484 We attempted to account for this effect of track duration and tag deployment location in  
485 the models by exploring the use of a day-of-track term. Ideally such a term would capture the  
486 higher probability of being in the tagging EEZ at the beginning of a track and the effect would  
487 diminish during a track. Some of the models we explored partially captured the expected day-of-  
488 track effect, but the predicted effects did not diminish monotonically over time and often  
489 exhibited non-intuitive patterns later in a track. For example, the Pacific bluefin tuna model  
490 exhibited an expected decrease in the predicted probability of being in the Mexico EEZ (the  
491 deployment EEZ) during the early part of a track, but the predicted probability increased later in  
492 the track and exhibited non-intuitive patterns for some days of the year (Supplementary Fig. 10).

493 These results suggested that the combination of data and model structure used was unable to  
494 capture the expected effect of track duration, so these models were not considered further.

495 Tag deployment location is an experimental design feature of a tracking dataset that can  
496 bias interpretation of space use for the tracked population. In this paper, it might have imposed  
497 an upward bias on estimates of probability of occurrence in EEZs in which tags were deployed,  
498 especially when combined with a dataset subject to a high amount of tag attrition (i.e. “short”  
499 tracks). For datasets in which many individuals were tracked for multiple years (i.e. salmon  
500 sharks), we expect a minimal effect of this bias for the tracked population.

501 **References:**

- 502 1. Block, B. A. et al. Tracking apex marine predator movements in a dynamic ocean. *Nature*  
503 475, 86–90 (2011).
- 504 2. Halpern, B. S. et al. A Global Map of Human Impact on Marine Ecosystems. *Science*  
505 319, 948–952 (2008).
- 506 3. Tapilatu, R. F. et al. Long-term decline of the western Pacific leatherback, *Dermochelys*  
507 *coriacea*: a globally important sea turtle population. *Ecosphere* 4, art25–15 (2013).
- 508 4. ISC (International Scientific Committee for Tuna and Tuna-Like Species in the North  
509 Pacific Ocean). Pacific bluefin tuna stock assessment. 1–140 (2016).
- 510 5. Dulvy, N. K. et al. Extinction risk and conservation of the world’s sharks and rays. *eLife*  
511 3, 1001–34 (2014).
- 512 6. Croxall, J. P. et al. Seabird conservation status, threats and priority actions: a global  
513 assessment. *Bird Conservation International* 22, 1–34 (2012).
- 514 7. Lascelles, B. et al. Migratory marine species: their status, threats and conservation  
515 management needs. *Aquatic Conserv: Mar. Freshw. Ecosyst.* 24, 111–127 (2014).
- 516 8. Mora, C. et al. Management Effectiveness of the World's Marine Fisheries. *PLoS Biol* 7,  
517 e1000131–11 (2009).
- 518 9. Cullis-Suzuki, S. & Pauly, D. Failing the high seas: A global evaluation of regional  
519 fisheries management organizations. *Marine Policy* 34, 1036–1042 (2010).
- 520 10. Gilman, E., Passfield, K. & Nakamura, K. Performance of regional fisheries management  
521 organizations: ecosystem-based governance of bycatch and discards. *Fish and Fisheries*  
522 15, 327–351 (2013).

- 523 11. United Nations General Assembly. United Nations Convention on the Law of the Sea. 1–  
524 202 (1982).
- 525 12. United Nations General Assembly. United Nations Conference on Straddling Fish Stocks  
526 and Highly Migratory Fish Stocks: Agreement for the Implementation of the Provisions  
527 of the United Nations Convention of the Law of the Sea of 10 December 1982, Relating  
528 to the Conservation and Management of Straddling Fish Stocks and Highly Migratory  
529 Fish Stocks. (1995).
- 530 13. Wood, S. N., Pya, N. & Säfken, B. Smoothing Parameter and Model Selection for  
531 General Smooth Models. *Journal of the American Statistical Association* 111, 1548–1575  
532 (2016).
- 533 14. Wood, S. N. *Generalized Additive Models*. (CRC Press, 2006).
- 534 15. Shaffer, S. A. et al. Migratory shearwaters integrate oceanic resources across the Pacific  
535 Ocean in an endless summer. *Proceedings of the National Academy of Sciences* 103,  
536 12799–12802 (2006).
- 537 16. Weise, M. J., Costa, D. P. & Kudela, R. M. Movement and diving behavior of male  
538 California sea lion (*Zalophus californianus*) during anomalous oceanographic conditions  
539 of 2005 compared to those of 2004. *Geophys. Res. Lett.* 33, L22S10 (2006).
- 540 17. Lyons, K. et al. The degree and result of gillnet fishery interactions with juvenile white  
541 sharks in southern California assessed by fishery-independent and -dependent methods.  
542 *Fisheries Research* 1–11 (2013). doi:10.1016/j.fishres.2013.07.009
- 543 18. Domeier, M. L. & Nasby-Lucas, N. Migration patterns of white sharks *Carcharodon*  
544 *carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific  
545 shared offshore foraging area. *Mar. Ecol. Prog. Ser.* 370, 221–237 (2008).

- 546 19. Wallace, B. P., Tiwari, M. & Girondot, M. *Dermochelys coriacea*. The IUCN Red List of  
547 Threatened Species e.T6494A43526147, (2013).
- 548 20. Dutton, P. H. & Squires, D. Reconciling Biodiversity with Fishing: A Holistic Strategy  
549 for Pacific Sea Turtle Recovery. *Ocean Development & International Law* 39, 200–222  
550 (2008).
- 551 21. Dutton, P. H. & Squires, D. in Conservation of Pacific Sea Turtles (eds. Dutton, P. H.,  
552 Squires, D. & Ahmed, M.) 1–23 (2011).
- 553 22. Russ, G. R. & Zeller, D. C. From *Mare Liberum* to *Mare Reservarum*. *Marine Policy* 27,  
554 75–78 (2003).
- 555 23. Lubchenco, J. & Grorud-Colvert, K. Making waves: The science and politics of ocean  
556 protection. *Science* 350, 382–383 (2015).
- 557 24. Cressey, D. Talks aim to tame marine Wild West: nations debate how to protect  
558 biodiversity in the high seas." 532, 18–19 (2016).
- 559 25. McCauley, D. J. et al. Ending hide and seek at sea. *Science* 351, 1148–1150 (2016).
- 560 26. Convention on the Conservation of Migratory Species of Wild Animals. (1979).
- 561 27. Hussey, N. E. et al. Aquatic animal telemetry: A panoramic window into the underwater  
562 world. *Science* 348, 1255642–1255642 (2015).
- 563 28. Burger, A. E. & Shaffer, S. A. Application of tracking and data-logging technology in  
564 research and conservation of seabirds. *The Auk* 125, 253–264 (2008).
- 565 29. Lascelles, B. G. et al. Applying global criteria to tracking data to define important areas  
566 for marine conservation. *Diversity Distrib.* 22, 422–431 (2016).
- 567 30. Ogburn, M. B. et al. Addressing Challenges in the Application of Animal Movement  
568 Ecology to Aquatic Conservation and Management. *Front. Mar. Sci.* 4, 155–7 (2017).



- 569 31. Jonsen, I. D., Flemming, J. M. & Myers, R. A. Robust state–space modeling of animal  
570 movement data. *Ecology* 86, 2874–2880 (2005).
- 571 32. Winship, A. J. et al. State-space framework for estimating measurement error from  
572 double-tagging telemetry experiments. *Methods in Ecology and Evolution* 3, 291–302  
573 (2011).
- 574 33. Shillinger, G. L. et al. Persistent Leatherback Turtle Migrations Present Opportunities for  
575 Conservation. *PLoS Biol* 6, e171–13 (2008).
- 576 34. Benson, S. R. et al. Large-scale movements and high-use areas of western Pacific  
577 leatherback turtles, *Dermochelys coriacea*. *Ecosphere* 2, art84–27 (2011).
- 578 35. Suryan, R. M. et al. Migratory routes of short-tailed albatrosses: Use of exclusive  
579 economic zones of North Pacific Rim countries and spatial overlap with commercial  
580 fisheries in Alaska. *Biological Conservation* 137, 450–460 (2007).
- 581 36. Wood, S. N. Package ‘mgcv’ reference manual: Mixed GAM computation vehicle with  
582 automatic smoothness estimation. 1–290 (2017).

583

584 **End Notes**

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

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