LETTER

Tracking apex marine predator movements in a dynamic ocean

B. A. Block[1], I. D. Jonsen[2], S. J. Jorgensen[1], A. J. Winship[2], S. A. Shaffer[3], S. J. Bograd[4], E. L. Hazen[4], D. G. Foley[4], G. A. Breed[2,5], A.-L. Harrison[5], J. E. Ganong[1], A. Swithenbank[1], M. Castleton[1], H. Dewar[6], B. R. Mate[7], G. L. Shillinger[1], K. M. Schaefer[8], S. R. Benson[9], M. J. Weise[5], R. W. Henry[5] & D. P. Costa[5]

Pelagic marine predators face unprecedented challenges and uncertain futures. Overexploitation and climate variability impact the abundance and distribution of top predators in ocean ecosystems[1–4]. Improved understanding of ecological patterns, evolutionary constraints and ecosystem function is critical for preventing extinctions, loss of biodiversity and disruption of ecosystem services. Recent advances in electronic tagging techniques have provided the capacity to observe the movements and long-distance migrations of animals in relation to ocean processes across a range of ecological scales[5,6]. Tagging of Pacific Predators, a field programme of the Census of Marine Life, deployed 4,306 tags on 23 species in the North Pacific Ocean, resulting in a tracking data set of unprecedented scale and species diversity that covers 265,386 tracking days from 2000 to 2009. Here we report migration pathways, link ocean features to multispecies hotspots and illustrate niche partitioning within and among congener guilds. Our results indicate that the California Current large marine ecosystem and the North Pacific transition zone attract and retain a diverse assemblage of marine vertebrates. Within the California Current large marine ecosystem, several predator guilds seasonally undertake north–south migrations that may be driven by oceanic processes, species-specific thermal tolerances and shifts in prey distributions. We identify critical habitats across multinational boundaries and show that top predators exploit their environment in predictable ways, providing the foundation for spatial management of large marine ecosystems.

Large marine predators are important top consumers in marine ecosystems, and their depletion can have cascading effects on lower trophic levels in both coastal and open-ocean waters[3,7,8]. Although some taxa are protected internationally from direct harvest, intense overexploitation by high-seas fisheries and anthropogenic environmental change are threatening global marine biodiversity. The management and conservation of highly migratory marine predators depends on understanding how movements relate to ocean processes; however, the dynamic relationships among behaviour, physiology and oceanography over a range of temporal and spatial scales remains unclear[4,9,10].

Tagging of Pacific Predators (TOPP) examined the distribution of species that inhabit and migrate into the coastal upwelling region off the west coast of North America. Using simultaneous tag deployments, we tracked seven top-predator guilds (sharks, tunas, albatrosses, shearwaters, turtles, pinnipeds and rorqual whales) concurrently for nearly a decade. Habitat use, residency patterns and migration pathways to North American waters were previously unknown or poorly documented for most of these animals[5,6,11–13].

Deployments of 4,306 electronic tags yielded 1,791 individual animal tracks from 23 species, totalling 265,386 animal tracking days (Fig. 1 and Supplementary Tables 1–3). The tracking technologies used had different location precisions, and include ARGOS satellite tags ($n = 1,183$), archival and satellite transmitting tags ($n = 1,008$) and archival geolocation tags ($n = 2,115$); the latter two provide estimates of position based on sunrise and sunset times and sea surface temperature (SST). We used a state-space modelling approach[14] to estimate daily locations, and their uncertainty, from each track while accounting for the differing precisions of the tracking technologies.

The tracking data show that the California Current large marine ecosystem (CCLME; Supplementary Fig. 1) is an important habitat (Figs 2–4) for tunas (Pacific bluefin, *Thunnus orientalis*; yellowfin, *Thunnus albacares*; albacore, *Thunnus alalunga*), sharks (shortfin mako, *Isurus oxyrinchus*; white, *Carcharodon carcharias*; salmon, *Lamna ditropis*; blue, *Prionace glauca*; common thresher, *Alopias vulpinus*), cetaceans (blue whale, *Balaenoptera musculus*), pinnipeds (northern elephant seal, *Mirounga angustirostris*; California sea lion, *Zalophus californianus*), seabirds (Laysan albatross, *Phoebastria immutabilis*; black-footed albatross, *Phoebastria nigripes*; sooty shearwater, *Puffinus griseus*) and sea turtles (leatherback, *Dermochelys coriacea*; loggerhead, *Caretta caretta*). Annual migratory periodicity was evident in the movements of many tagged animals that showed fidelity to the cool, nutrient-rich waters of the CCLME (Figs 2 and 3). Extended residency within the CCLME was revealed by examining tracks that spanned multiple seasons, using a behavioural switching state-space model[14]. Numerous species (leatherback sea turtles, black-footed albatrosses, sooty shearwaters, bluefin tunas and salmon sharks; Fig. 2b) had a strong attraction to the CCLME and undertook long migrations ($>2,000$ km) from the western, central or south Pacific basin. Some species (bluefin and yellowfin tunas; mako, white and salmon sharks; blue whales; male elephant seals; and leatherback sea turtles; Fig. 3a and Supplementary Fig. 2) undertook a seasonally recurring north–south migration in the North Pacific and within the CCLME. Other taxa undertook movements between near-shore and offshore waters, with a residency period within the CCLME or the Gulf of Alaska, followed by an offshore migration that ranged into the North Pacific transition zone (NPTZ) (female elephant seals, salmon sharks and Laysan albatrosses), the subtropical gyre and north equatorial current (blue and mako sharks and leatherback sea turtles), or the 'Café' region of the eastern Pacific and the Hawaiian Islands (white sharks; albacore tunas, *Thunnus alalunga*; and black-footed albatrosses). The mechanisms and cues underlying fidelity to seasonally modulated migration pathways are not entirely known, but may represent a capacity to discriminate among areas of seasonal significance for foraging or reproduction.

The quarterly predator density in relation to the median satellite-derived SST measurements within the CCLME (Fig. 3b and Supplementary Fig. 3) suggests that seasonal warming (quarter three) along the Baja California peninsula may trigger northward movements of predator populations. Increased metabolic expenditures in ectotherms

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[1]Stanford University, Biology Department, Hopkins Marine Station, Pacific Grove, California 93950, USA. [2]Dalhousie University, Department of Biology, Halifax, Nova Scotia B3H 4J1, Canada. [3]San Jose State University, Department of Biological Sciences, San Jose, California 95192, USA. [4]NOAA Southwest Fisheries Science Center, Environmental Research Division, Pacific Grove, California 93950, USA. [5]University of California, Santa Cruz, Department of Ecology & Evolutionary Biology, Long Marine Laboratory, Santa Cruz, California 95060, USA. [6]NOAA Southwest Fisheries Science Center, Fisheries Research Division, La Jolla, California 92037, USA. [7]Oregon State University, Hatfield Marine Science Center, Newport, Oregon 97365, USA. [8]Inter-American Tropical Tuna Commission, La Jolla, California 92037, USA. [9]NOAA Southwest Fisheries Science Center, Protected Resources Division, La Jolla, California 92037, USA.
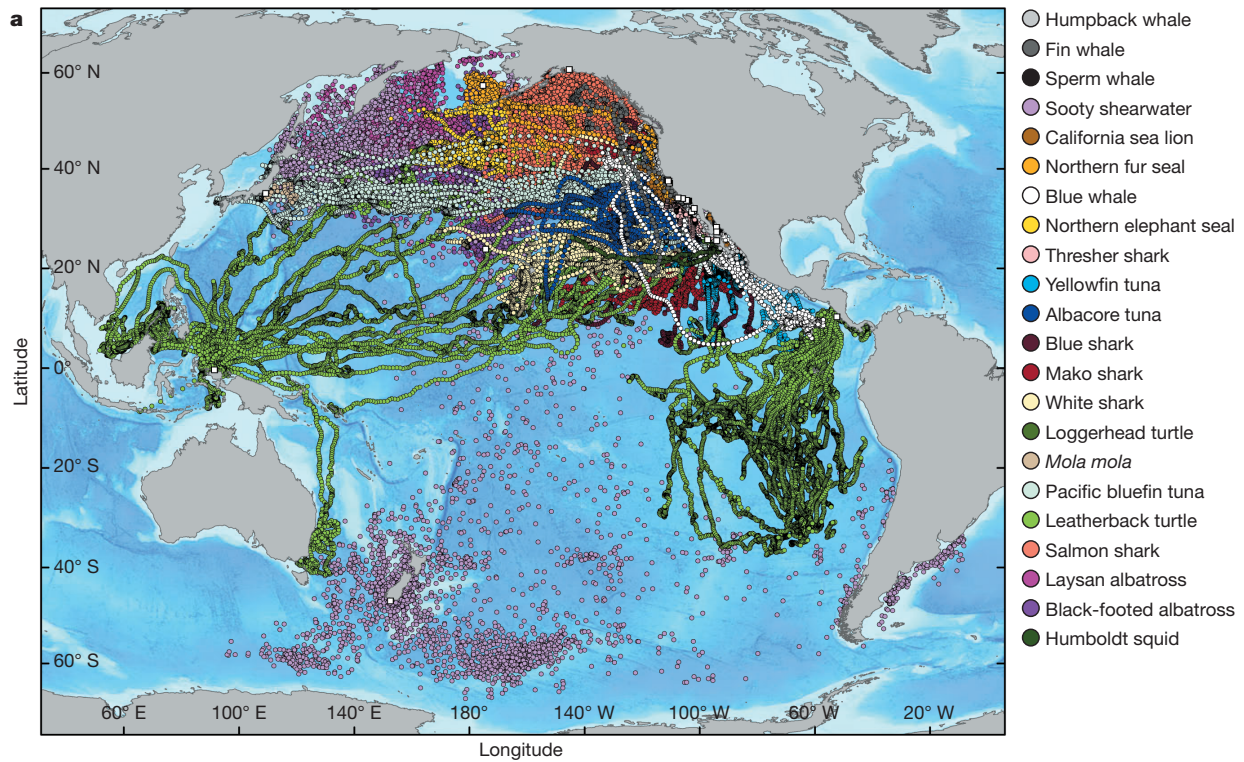
Figure 1 | All TOPP species state space position estimates and distribution from electronic tagging. a, Daily mean position estimates (circles) and annual median deployment locations (white squares) of all tagged species. **b,** Daily mean position estimates of the major TOPP guilds (from left): tunas (yellowfin, bluefin and albacore), pinnipeds (northern elephant seals, California sea lions and northern fur seals), sharks (salmon, white, blue, common thresher and mako), seabirds (Laysan and black-footed albatrosses and sooty shearwaters), sea turtles (leatherback and loggerhead) and cetaceans (blue, fin, sperm and humpback whales).

as the ocean warms, subsurface hypoxia[15] and declines in primary productivity (Fig. 3b and Supplementary Fig. 3g) all potentially decrease the suitability of this habitat. In the northern waters of the CCLME (Fig. 3b and Supplementary Fig. 3a–d), cooler temperatures (9–11 °C), particularly during the spring upwelling season, limit cardiac function[13,16] in many fishes and sharks, reducing their capacity to exploit these environs. Predators were observed moving south into warmer water despite regions of persistent productivity in the north (Fig. 3b). A similar relationship may hold for endotherms, such as seabirds, pinnipeds and whales, but the linkage is indirect as the physiological constraints are largely on their prey.

Tracking data typically were acquired for less than one year; however, for some taxa (tunas, turtles and sharks) multiyear tracks were obtained (maximum of 1,380 days, for salmon sharks; Supplementary Table 1 and Supplementary Fig. 4). To account for abbreviated tracks and for variation in sample size among taxa, we applied time weighting and species normalization schemes before examining multispecies density patterns (Supplementary Methods). The relative spatial density of large marine predators indicates that high-use areas in the northeastern Pacific occur both on the high seas (NPTZ; Fig. 4a and Supplementary Fig. 1) and within the exclusive economic zones of North America (CCLME; Fig. 4b). These observed patterns differ markedly from those expected
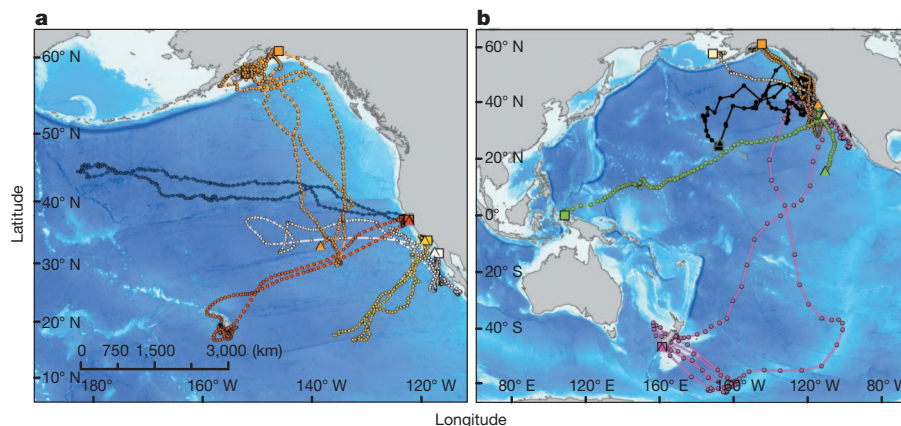
Figure 2 | Fidelity and attraction to the CCLME. a, Examples of pelagic predators released and electronically tracked in the CCLME that show fidelity to deployment locations and the CCLME. We show the release locations (square), pop-up satellite end point locations (triangle) and daily mean positions (circles) of the following species: yellowfin tuna (yellow), bluefin tuna (white), white shark (red), elephant seal (blue) and salmon shark (orange). **b,** Individual tracks of pelagic animals released >2,000 km away from the CCLME that are indicative of cross-basin or ecosystem attraction to, and temporary residency within, the eastern North Pacific. Symbols are as in **a**, for leatherback sea turtles (green), sooty shearwaters (pink), fur seals (pale yellow), black-footed albatrosses (black) and salmon sharks (orange).
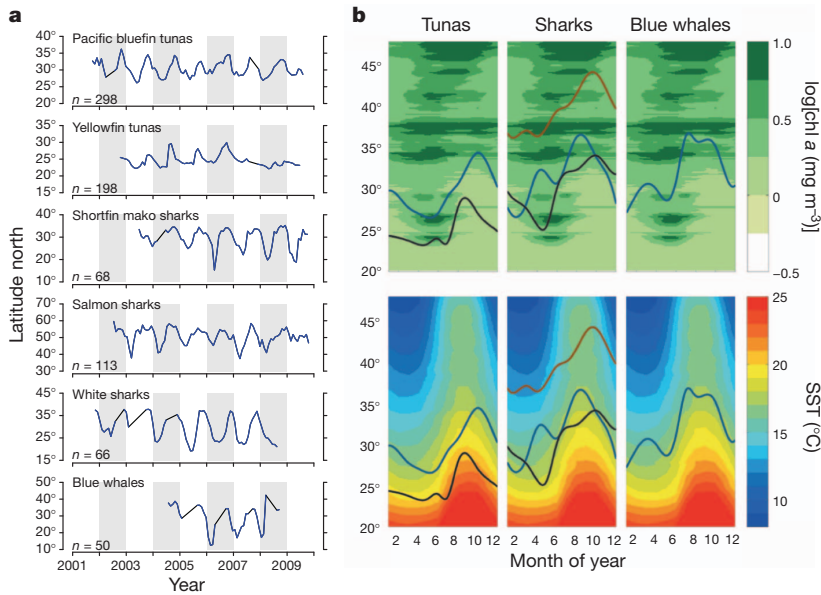
Figure 3 | Latitudinal migration cycles and seasonal climatologies within the CCLME. **a**, Monthly mean latitudes of predators residing within or migrating to the CCLME. Black line segments denote gaps where no data were available. Sample sizes indicate the numbers of individual tracks contributing to the time series. **b**, Seasonal climatologies in the California Current for tunas (Pacific bluefin, blue; yellowfin, black), sharks (salmon shark, brown; shortfin mako, black; white shark, blue) and blue whales relative to median chlorophyll *a* densities and SST values between 2000 and 2009.

under a null model of random diffusion from tag deployment locations (Supplementary Fig. 5 and Supplementary Methods), confirming that the observed density patterns are not driven by the tag deployment locations.

The CCLME is a highly retentive area for many species tagged there, and is an attractive area for animals undergoing long migrations from the western and central North Pacific and the Gulf of Alaska (Figs 2 and 4a, b). Pacific bluefin and yellowfin tunas spent significantly more time in the CCLME than expected on the basis of null model simulations (Supplementary Fig. 6). Several species (tunas, white, mako and salmon sharks, leatherback sea turtles and blue whales) had substantial residency periods within, or were return migrants to, the CCLME, according to behavioural inferences from a switching state-space model[14] (Fig. 4c). Additionally, all species tagged outside the CCLME spent significantly more time on average in the CCLME than expected on the basis of null model simulations (Supplementary Fig. 6). Representatives from several guilds exhibited cross-basin migrations (>2,000 km) into the CCLME from the western (leatherback sea turtles and bluefin tunas), central (black-footed albatrosses and salmon sharks) and south Pacific basins (sooty shearwaters; Fig. 2b). The retention within and attraction to the CCLME is consistent with the high productivity of this region, which supports large biomasses of krill, sardines, anchovies, salmon, groundfish and squid that provide a predictable forage base for top predators[2,17]. The NPTZ is another important region, serving as an east–west migration corridor (Fig. 4a) and foraging region for elephant seals, salmon and blue sharks (Fig. 4c), Laysan and black-footed albatrosses, and bluefin tunas (Fig. 1). This is a complex region encompassing an abrupt north-to-south transition between sub-Arctic and subtropical water masses with dynamic frontal regions[18].

To investigate which aspects of the biophysical environment putatively attract these predators, we explored both presence/absence and relative habitat use with generalized additive mixed models[19]. We examined the collective response of 16 marine predator species to environmental covariates (Supplementary Fig. 7 and Supplementary Methods). In the binary presence/absence model, predator incidence showed a strong positive relationship with SST across a broad temperature range that peaked near 15 °C (Supplementary Fig. 7a). Tagged animals occupied a small portion of cool, nutrient-rich water in coastal regions and northern latitudes in preference to the broadly available warm oligotrophic waters in lower latitudes (Supplementary Fig. 3). Relative density models showed a strong positive relationship between density and chlorophyll *a* suggesting that the suite of tagged species preferentially occupy regions of high productivity (Supplementary Fig. 7c). The observed patterns of predator distribution in this study may be indicative of trade-offs between access to areas of higher productivity

and physiological thermal tolerances, either directly by the predators or indirectly by their lower-trophic-level prey.

To examine how closely related taxa partition marine resources, we compared thermal preferences from *in situ*, tag-based SST measurements for sympatrically occurring species within three guilds (albatrosses, tunas and sharks). Differences in habitat use evident among congeneric species illustrate how more-recently divergent species partition the oceanic environment (Fig. 5). During the June–November post-breeding phase, black-footed albatrosses were associated with a broader range of higher SSTs primarily in the eastern Pacific, whereas Laysan albatrosses were associated with a narrower range of lower SSTs in the western and central North Pacific (Fig. 5a and Supplementary Table 9). Bluefin tunas ranged farther north in the colder waters of the CCLME, whereas yellowfin tunas occupied warmer waters in the southern CCLME (Fig. 5b and Supplementary Table 10). These differences are consistent with physiological specializations in bluefin tuna cardiac performance[16]. The lamnid sharks had a more complex separation of habitats. Salmon sharks, with their cold-tolerant cardiac physiology[13], occupied the cooler, sub-Arctic waters in the North Pacific. Most salmon sharks, but not all, migrated seasonally into the warmer NPTZ and CCLME waters (Fig. 5c and Supplementary Table 11). White sharks overlapped with salmon sharks in the near-shore CCLME but also migrated into warmer, offshore waters of the subtropical gyre[12] and the Hawaiian Islands (Fig. 5c and Supplementary Table 11). Shortfin mako sharks were distributed throughout the CCLME and into the subtropical gyre but occupied a thermal range intermediate between the two modes of the white shark range (Fig. 5c and Supplementary Table 11).

Species such as black-footed albatrosses, sooty shearwaters, leatherback sea turtles and salmon sharks have evolved migration or foraging strategies that entail long-distance journeys to productive foraging habitats within the CCLME and the NPTZ. Shearwaters[6] and leatherback sea turtles tagged in the south and western Pacific arrived in the central and northern portions of the CCLME each year, when SSTs were seasonally highest. These patterns indicate that resources within the CCLME and the NPTZ are valuable to species throughout the Pacific basin, highlighting the importance of maintaining ecological connectivity across hemispheres. It is likely that other areas of the Pacific, not extensively covered by our tagging efforts, are similarly important. For example, estimates of global marine species richness peak around Southeast Asia, and richness of primarily oceanic taxa peaks at latitude 30° (north or south) along boundary currents such as the Kuroshio in the western Pacific[20].

The concentration and residency of multiple predators at predictable locations in the Pacific reveals the importance of these regions as biological hotspots. Given the high density of tracked animals in these regions, predators may have an important top-down role in structuring
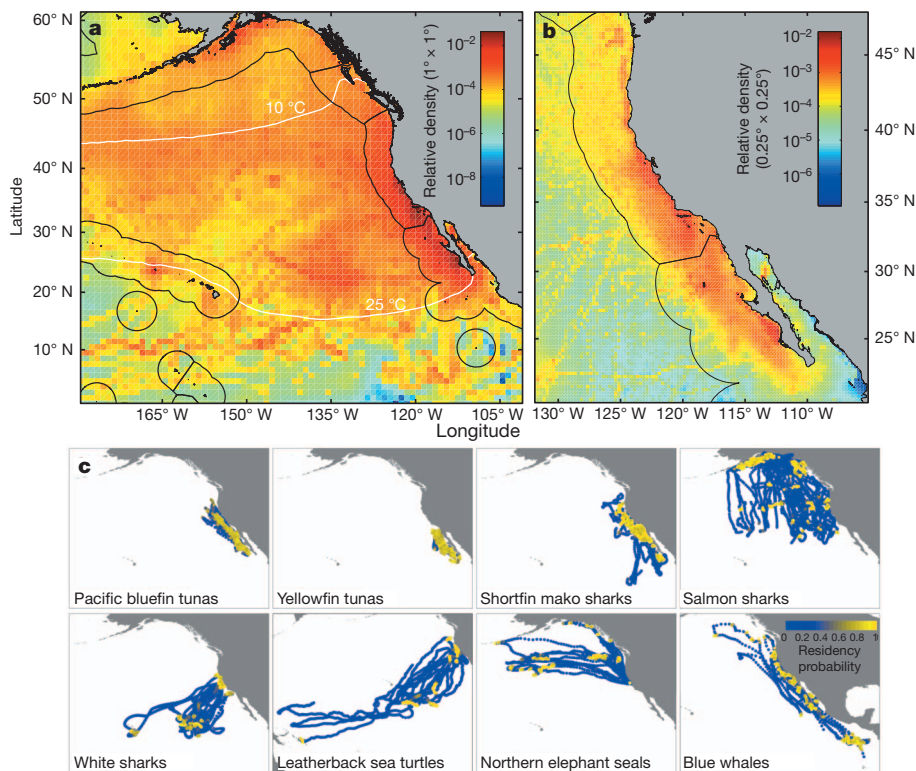
Figure 4 | Predator density maps and residency patterns. a, Density of large marine predators within the eastern North Pacific. Densities of the time-weighted and species-normalized position estimates of all tagged individuals were summed within $1° \times 1°$ grid cells. **b**, Density of large marine predators within the CCLME at a $0.25° \times 0.25°$ resolution. **c**, Patterns of resident (slow, area-restricted movements) versus transient (fast, directed movements) behaviours of predators that primarily occupied or migrated to the CCLME, estimated using a switching state-space model. The coloured points grading from blue to yellow display the posterior mean probability of the resident behaviour associated with each daily mean position estimate. Each panel displays residency patterns for ten individuals. Uncertainty in position estimates in **a** and **b** is included by calculating densities using all 2000 Markov chain Monte Carlo samples from the joint posterior distributions of the daily positions, rather than using only the posterior means. SST contours in **a** are denoted by solid white lines. Exclusive economic zones are delineated by solid black lines.

these ecosystems. The impact that the removal of top predators has had on the trophic dynamics of coastal and oceanic ecosystems is contentious[3,21]. For example, a failure to manage marine resources effectively in the Atlantic has led to a decline of pelagic species such as the Atlantic bluefin tuna[3] and the porbeagle shark[22], and has brought demersal fish, such as cod, to the brink of ecological extinction[23]. In the Pacific, commercial fisheries removed over 50 million tonnes of tunas and sharks from pelagic ecosystems between 1950 and 2004[21], resulting in significant declines in populations of large fish. Furthermore, unsustainable levels of fishery bycatch mortality has decimated populations of Pacific sea turtle (leatherback and loggerhead) and threatened some populations of albatross[24,25]. The impact of these top-predator biodiversity losses on ecosystem stability is unknown. Establishing the population baselines for top-predator populations and conserving remaining populations in regions such as the CCLME, and quantifying the ecosystem services they provide, remains an important management priority[26]. Our study provides a clearer understanding of where predators are concentrated in the North Pacific and which environmental parameters can be used to predict their occurrence.

Tracking data can be used to examine behaviours and distributions, inform population assessments and improve estimates of natural and fishery-induced mortality[27–29]. Despite their high monetary and conservation value, population assessments of many predators in this study are rare or non-existent. Long-term observations of predator movements provide information on the spatial extent of highly migratory populations and potential rates of exchange among them. High archival tag returns (Supplementary Table 1) for bluefin (56%) and yellowfin (39%) tunas indicate that high fishery-induced mortality currently occurs within the CCLME. The recovery of cetacean populations, such as blue whales, which are endangered, can be enhanced through the use of electronic tracking data to identify high-use areas and coordinate policy actions that mitigate anthropogenic risks[30] (for example ship strikes). Finally, an improved understanding of the horizontal and vertical spatiotemporal distribution of leatherback sea turtles and North Pacific albatrosses in relation to pelagic fisheries could better inform management protocols (for example time–area closures and gear mitigation) to reduce bycatch of these endangered and threatened species.
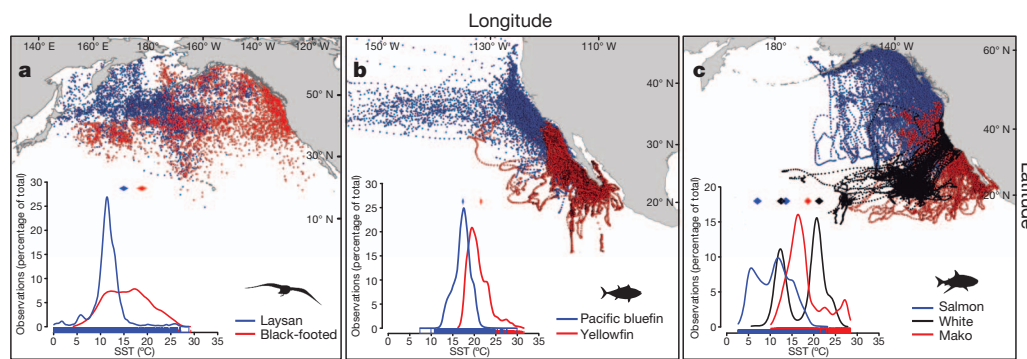
Figure 5 | Niche separation within three predator guilds. Spatial distribution and thermal habitat use (insets) across three guilds of sympatric species: Laysan and black-footed albatrosses ($n = 55$ individuals, 8,743 daily SSTs; **a**), Pacific bluefin and yellowfin tunas ($n = 376$ individuals, 75,177 daily SSTs; **b**), lamnid (salmon, mako and white) sharks ($n = 137$ individuals, 12,971 daily SSTs; **c**). SST profiles are daily means of tag-derived SSTs. Linear mixed-effects model estimates of mean ($\pm95\%$ confidence interval) SST for each species are displayed as diamonds at the top of each inset graph. The distribution of daily mean SSTs for each species is displayed along the x axes.

The decadal record of multitaxa electronic tagging generated by TOPP provides information on cross-border movements between US, Mexican and Canadian waters that has important implications for conservation and management efforts. This extensive data set serves as a baseline for monitoring and forecasting these seasonal patterns and assessing shifts in abundance among countries. Linking movements to ocean temperatures can help predict the potential ecosystem-level effects of climate variability. This baseline information could provide the foundation for launching a management scheme on a scale never before achieved for a pelagic eco-system. International policy vehicles such as a UNESCO Marine World Heritage designation could provide an effective approach to generating global interest and, in turn, funding to support ecosystem-based manage-ment efforts within the CCLME. Furthermore, if a conservation corridor was extended across the NPTZ, key ecological foraging hotspots and migratory corridors that link the eastern and western Pacific basins for transoceanic migrants could be sustainably managed. Without an aggressive effort to zone and effectively manage these resources, the pred-ator populations they support will decline and the biodiversity of this open-ocean wilderness will be irreplaceably lost.

METHODS SUMMARY

We used a Bayesian state-space model[14] to account for observation error among tag types and to obtain regular daily location and uncertainty estimates. Argos satellite errors were estimated previously[14]. Errors for archival geolocation and pop-up satellite archival tags were estimated from taxon-specific double-tagging experiments (Supplementary Methods) and captive sea pen studies. We used a behavioural switching state-space model[14] to infer patterns of residency versus transience from a subset of species' tracks that at least partly inhabited the CCLME.

Unnaturally abbreviated tracks were normalized by weighting each location estim-ate by the inverse of the number of individuals of that species that had location estimates for the same relative day of their track. We imposed a threshold relative day of track (85th percentile) above which locations received the same weight as on the threshold day. We normalized the data set by species to account for the over-representation of species with large sample sizes. The normalized and weighted tracks were summed within $1° \times 1°$ or $0.25° \times 0.25°$ grid cells to obtain relative densities of 16 predator species across the North Pacific and within the CCLME, respectively. The influence of the tag deployment locations on the spatial density pattern was assessed through null model simulations. The relative density of predator species in the $1° \times 1°$ grid cells was related to oceanographic variables using generalized additive mixed models[19], with season and year as random covariates. Satellite-derived chloro-phyll *a*, SST and sea surface height anomalies and variances, and wind stress curl, were summarized quarterly in each grid cell between June 2002 and June 2009. A two-model approach dealt with over-dispersion, non-normality and non-constant variance of the relative density data. We used a binary presence/absence habitat model with a logit link function to model the occurrence of predators within grid cells. All cells with non-zero density were log-transformed and fitted to environ-mental correlates to create a relative-use habitat model.

Further details of the methods are included in Supplementary Information.

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Author Contributions This synthesis study was initiated by B.A.B. and I.D.J. The TOPP project was designed and coordinated by B.A.B., D.P.C. and S.J.B. B.A.B., S.J.J., H.D. and K.M.S. designed experiments and deployed electronic tags on fish and sharks. D.P.C., S.A.S., R.W.H., M.J.W. and B.R.M. designed experiments and deployed electronic tags on marine mammals and birds. G.L.S., B.A.B. and S.R.B. designed experiments and deployed electronic tags on sea turtles. Tracking data were compiled by S.J.J., S.A.S., G.A.B., A.-L.H., B.A.B., G.L.S. and M.C. Data management was coordinated by A.S. and J.E.G. Oceanographic data were compiled by S.J.B., E.L.H. and D.G.F. Analyses were conducted by A.J.W., S.J.J., I.D.J., G.A.B, E.L.H., D.G.F., A.-L.H., J.E.G. and A.S. Figures were created by B.A.B., M.C., A.-L.H., I.D.J., S.J.J., A.J.W., J.E.G., A.S., E.L.H. and D.G.F. The manuscript was drafted by B.A.B. and edited by I.D.J., D.P.C., S.J.J., S.A.S., S.J.B., E.L.H., A.-L.H., A.J.W., H.D., G.L.S. and B.R.M.