

Convergence of marine megafauna movement patterns in coastal and open oceans

A. M. M. Sequeira^{a,b,1,2}, J. P. Rodríguez^{c,1}, V. M. Eguíluz^c, R. Harcourt^d, M. Hindell^e, D. W. Sims^{f,g,h}, C. M. Duarte^{a,i}, D. P. Costa^j, J. Fernández-Gracia^c, L. C. Ferreira^k, G. C. Hays^l, M. R. Heupel^m, M. G. Meekan^k, A. Aven^{n,o}, F. Bailleul^p, A. M. M. Baylis^{q,r}, M. L. Berumen^j, C. D. Braun^{s,t}, J. Burns^u, M. J. Caley^{v,w}, R. Campbell^x, R. H. Carmichael^{n,o}, E. Clua^y, L. D. Einoder^{p,z}, Ari Friedlaender^j, M. E. Goebel^{aa}, S. D. Goldsworthy^p, C. Guinet^{bb}, J. Gunn^m, D. Hamer^{p,cc}, N. Hammerschlag^{dd}, M. Hammill^{ee}, L. A. Hütkstädt^j, N. E. Humphries^f, M.-A. Lea^{e,ff}, A. Lowther^{p,gg}, A. Mackay^p, E. McHuron^j, J. McKenzie^{p,hh}, L. McLeay^p, C. R. McMahon^{d,e,ii}, K. Mengersen^{v,w}, M. M. C. Muelbert^{e,ij}, A. M. Pagano^{kk}, B. Page^{p,ll}, N. Queiroz^{r,mm}, P. W. Robinson^j, S. A. Shafferⁿⁿ, M. Shivji^{oo}, G. B. Skomal^{pp}, S. R. Thorold^t, S. Villegas-Amtmann^j, M. Weise^{qq}, R. Wells^{rr}, B. Wetherbee^{ss}, A. Wiebkin^{p,ll}, B. Wienecke^{ss}, and M. Thums^k

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The extent of increasing anthropogenic impacts on large marine vertebrates partly depends on the animals' movement patterns. Effective conservation requires identification of the key drivers of movement including intrinsic properties and extrinsic constraints associated with the dynamic nature of the environments the animals inhabit. However, the relative importance of intrinsic versus extrinsic factors remains elusive. We analyze a global dataset of ~2.8 million locations from >2,600 tracked individuals across 50 marine vertebrates evolutionarily separated by millions of years and using different locomotion modes (fly, swim, walk/paddle). Strikingly, movement patterns show a remarkable convergence, being strongly conserved across species and independent of body length and mass, despite these traits ranging over 10 orders of magnitude among the species studied. This represents a fundamental difference between marine and terrestrial vertebrates not previously identified, likely linked to the reduced costs of locomotion in water. Movement patterns were primarily explained by the interaction between species-specific traits and the habitat(s) they move through, resulting in complex movement patterns when moving close to coasts compared with more predictable patterns when moving in open oceans. This distinct difference may be associated with greater complexity within coastal microhabitats, highlighting a critical role of preferred habitat in shaping marine vertebrate global movements. Efforts to develop understanding of the characteristics of vertebrate movement should consider the habitat(s) through which they move to identify how movement patterns will alter with forecasted severe ocean changes, such as reduced Arctic sea ice cover, sea level rise, and declining oxygen content.

global satellite tracking | probability density function | root-mean-square | turning angles | displacements

Unifying theoretical frameworks that explain general principles of animal life-history (1), optimal foraging (2, 3), and metabolic scaling in organisms (4, 5) facilitate the interpretation of data and the generation of testable hypotheses. Animal movement accounts for most of the energy budgets of vertebrates because it underpins critical components of their behavior, such as feeding and mating. Following the challenge posed by Aristotle millennia ago in *De Motu Animalium* (*On the Movement of Animals*) (6), efforts have been made to develop a unifying framework to study movement (7). ["Now we must consider in general the common reason for moving with any movement whatever (for some animals move by flying, some by swimming, some by stepping, some in other comparable ways)." (ref. 6, p. 24)] Such efforts have provided clarification that the primary challenge for understanding animal movement lies in the identification of the key external factors, internal states, and the motion and navigation capabilities influencing movement (7). It is also known that animal movement patterns are underpinned by common principles, such as "optimal" resource exploitation by predators ("optimality paradigm"; refs. 2, 3, 8, and 9) or the use of more efficient search trajectories

("random" paradigm; refs. 10–12). Overall, animal movement patterns have been attributed to extrinsic factors, including the dynamic nature of the environments they inhabit and constrained by intrinsic properties (13–19), including allometric and metabolic scaling with day or home range and locomotion speed, particularly for terrestrial animals (4, 15, 20–23). However, the relative importance of extrinsic versus intrinsic properties in determining the observed patterns of movement of free-ranging animals remains ambiguous. To effectively partition the relative contributions of extrinsic versus intrinsic factors and effectively investigate whether a unifying framework exists irrespective of location, scale of movement, and stage or phase, a large-scale comparison across multiple species is needed (24, 25).

Rapid technological developments in animal-attached electronic tags (telemetry/biologging) have generated large tracking datasets across an array of marine vertebrates, now available for

Significance

Understanding the key drivers of animal movement is crucial to assist in mitigating adverse impacts of anthropogenic activities on marine megafauna. We found that movement patterns of marine megafauna are mostly independent of their evolutionary histories, differing significantly from patterns for terrestrial animals. We detected a remarkable convergence in the distribution of speed and turning angles across organisms ranging from whales to turtles (epitome for the slowest animals on land but not at sea). Marine megafauna show a prevalence of movement patterns dominated by search behavior in coastal habitats compared with more directed, ballistic movement patterns when the animals move across the open ocean. The habitats through which they move will therefore need to be considered for effective conservation.

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¹A.M.M.S. and J.P.R. contributed equally to this work.

²To whom correspondence should be addressed. Email: ana.sequeira@uwa.edu.au.

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analysis of displacements (d_{RMS}) scaled with time as a power law ($d_{RMS} \sim T^\mu$) with exponents (μ) mostly above the value of 0.5 (commonly associated with Brownian motion) (Fig. 1*B*), indicating that most individuals moved superdiffusively—that is, faster than expected in a normal diffusion process. Using predetermined time windows of 1 d, we compared the probability density functions (PDFs) of the observed displacements for each individual using a dimensionless coefficient of PDF spread (CS), defined as the ratio between the second moment (average square displacement) and the square of the first moment (square of the average displacement). Our CS can be used for comparison across all individuals irrespective of scale and provides an estimate of the spread of the resulting PDF normalized by the square of the average displacement (Fig. 2*A*). Generally, $CS \gg 1$ indicates wide distributions with heavy tails, such as a power law or lognormal. Lower values generally highlight a narrower range of displacements identified in the tracked movement resulting in a smaller spread of the PDFs. Our CS results show high variability among individuals within and among species (Fig. 2*B* and *SI Appendix, Table S4*), revealing substantial within-species variability in movement patterns, with increasing mean coefficient of variation from 22.94%, 38.10%, and 40.37% for species grouped within low, mixed, and high coastal affinity, respectively (Fig. 2*B*). Lower CS values generally represented simpler, more linear paths, while higher values represented more varied, complex movement patterns (Fig. 2*A*).

Model fits from boosted regression trees (BRTs; ref. 33) to the resulting CSs for all individuals showed that species group and coastal affinity had the highest relative importance (74.0% and 21.5%, respectively) and identified an interaction (size = 36.0) between these two variables (*SI Appendix, Fig. S2*). This interaction highlights that the different movement patterns in the coastal and open ocean are not uniquely a species-specific trait and partly accounts for the high variability in movement patterns among individuals within species (Fig. 2 and *SI Appendix, Fig. S2*). Moreover, life-history traits, such as breeding and foraging strategies, as well as allometric traits, such as body mass and length, were not shown to greatly influence CS and were mostly removed during the simplification procedure in the BRTs. Based on our modeling results, CS increases with greater coastal affinity (Fig. 2*B*), indicating a

larger range of displacements observed when individuals move mostly through coastal areas (i.e., including small and very large displacements). An association between coastal affinity and the d_{RMS} exponent (with 0.5–1.0 indicating normal random to superdiffusive, more directed, ballistic motion) was also detected. Higher d_{RMS} exponents were found for all displacements taking place in the open ocean, where depths ≥ 150 m (d_{RMS} exponent = $0.791 - 0.112 \times \text{ocean}$, where *ocean* is “open ocean” or “coastal ocean”, $P < 0.001$ for the linear model) (Fig. 3). This result is congruent with simple, extensive, and directed movements in that habitat. It is also supported by the finding of prevailing frequency of angles of 0° —that is, more directed, forward movement patterns in open ocean (depths ≥ 150 m), and less directed patterns for displacements in the coastal ocean (depths < 150 m) with higher frequency of lateral and backward angles (Fig. 3 and *SI Appendix, Fig. S3*).

The Kolmogorov–Smirnov analysis of the distances between the cumulative distributions of displacements for each species pair was used to compute a dendrogram that resulted in two main clusters above and below California sea lions (a species with mixed coastal affinity). The split of clusters was consistent with a split between species moving in coastal and open oceans (i.e., high and low coastal affinities as shown in the color scale for Fig. 4*A*). The resulting dendrogram was unrelated to phylogeny, such that closely related species were no more similar in their displacement patterns than were distantly related ones. This result further reinforces that habitat structure is an important driver of the movement patterns among marine megafauna and reiterates that differences are not fully dependent on intrinsic traits.

Discussion

Our integrated, multispecies study revealed that differences in movement patterns of large marine vertebrates are primarily defined by the species to which they belong (74% relative influence) but underpinned by a strong interaction with the habitat through which the animals move (open or coastal ocean; 21% relative influence). This interaction partly accounts for the large variability in movement patterns among individuals of the same species (Fig. 2 and *SI Appendix, Fig. S6*) and is likely related to a combination of directed- and resident-type movements that can occur over the

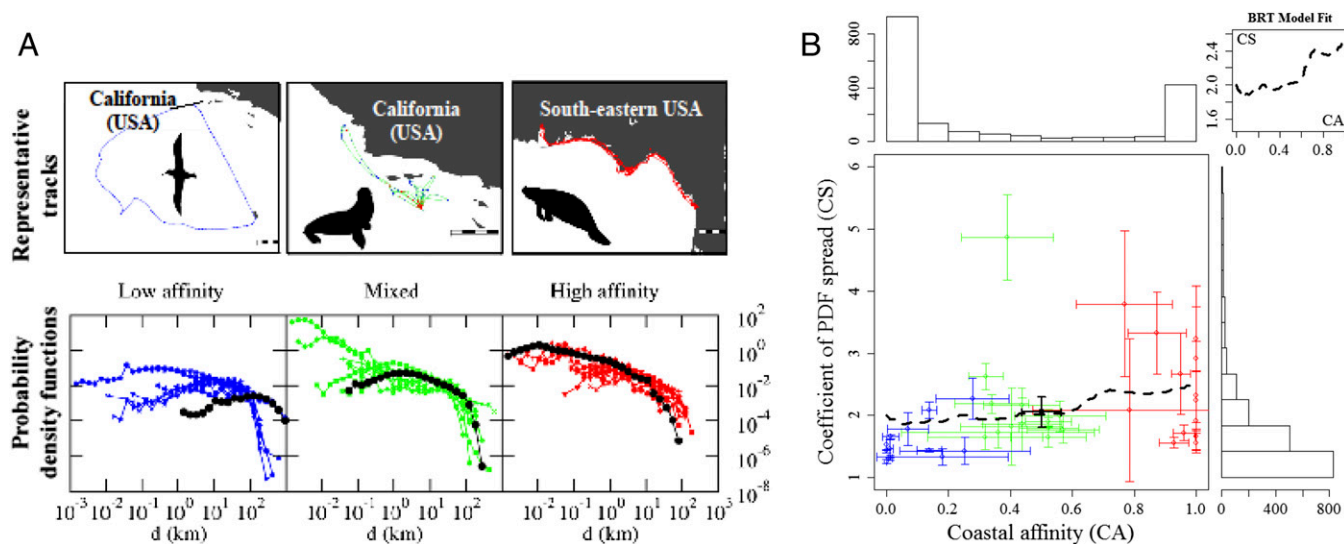


Fig. 2. Results of the analysis of displacements. (*A*) PDF of displacements (d , km) at the species level with 1-d time windows for species with low (mean < 0.3 ; *Left*), mixed (*Center*), and high (mean > 0.7 ; *Right*) coastal affinity (*Bottom*), and example tracks for each group (*Top*; black and white scale bars represent 100 km; black dotted lines: PDF for the example track shown). (*B*) Relationship between coefficient of PDF spread (CS) and coastal affinity (CA) obtained from the BRTs (dashed black line; also shown in the *Top Right Inset*). To the top and right are histograms of CA and CS, respectively. Outlier green point: western gulls ($0 \leq CA \leq 1$; *SI Appendix, Table S4*). Average coefficients of variation: 22.94%, 38.10%, and 40.37% for CS, and 243.55%, 85.93%, and 11.48% for CA for low (blue), mixed (green), and high (red) CA species, respectively. Solid black: mean \pm SD among all species with a coefficient of variation of 37.20% for CS and 39.51% CA.

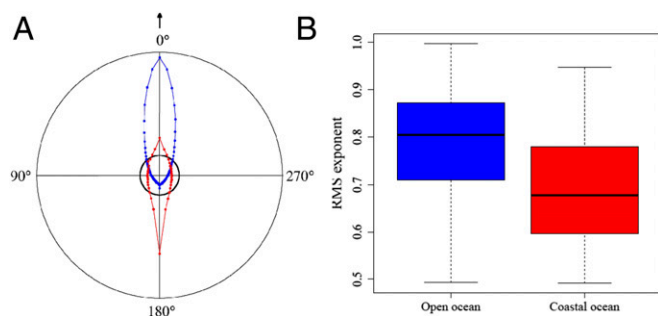


Fig. 3. Comparison of movement patterns in open and coastal oceans. The classification into open or coastal was based on the depth at which the displacements occurred with depth ≤ 150 m classified as coastal ocean. (A) Distribution of turning angles (arrow points to 0°) in open (blue) and coastal oceans (red). The circular plot reveals high frequency of 0° angles in open ocean and a large number of angles between 90° and 270° angles (peaking at 180°; i.e., returns) in coastal oceans. Black inner circle: uniform distribution of angles. (B) Boxplot of d_{RMS} exponents (μ) for individuals showing coastal affinity below (blue) and above (red) 0.5 ($\mu = 0.784 - 0.085 \times \text{coastal ocean}$; $P < 0.001$).

course of an individual's track in association with different behaviors (e.g., transiting and foraging, resting, breeding) (34). Here, we used an analysis of displacements with no prior assumptions for the movement patterns observed and show that coastal and open ocean habitats directly influence the horizontal movement patterns of marine megafauna potentially in association with habitat complexity and related prey availability. The patterns we found emerged consistently across a diverse array of marine vertebrates and locomotion modes, confirming that habitat structure is a powerful driver of

movement patterns. Species with movements that occurred mostly in coastal environments displayed a greater variety of displacement lengths (indicated by the generally higher CS; Fig. 2 and *SI Appendix, Fig. S6*), regardless of the intrinsic factors related to each species. In contrast, species moving mostly off-shelf in deep, oceanic habitat conformed to a relatively narrower range of displacements, which indicated less variability in displacement lengths (generally larger). We suggest that this difference in behavior between on- and off-shelf movements is related to habitat complexity, with open water habitats off the continental shelves being comparatively less complex (i.e., more homogeneous physical habitat) despite their highly dynamic nature. Open ocean species tend to use oceanographic features, such as fronts, eddies, and currents, as foraging and movement cues (e.g., ref. 35). This difference may explain the convergence of movement behaviors characterized by more directed movement with generally higher d_{RMS} exponents among species when moving off the continental shelf. In contrast, animals moving over the shelf and in the coastal ocean experience a much wider variety of structurally complex habitats (e.g., reef, seagrass) that support a diverse suite of varying resources (e.g., prey, refuges) and threats (e.g., predators, human disturbance), stimulating more complex movement patterns and covering a larger range of displacements (Fig. 2 and *SI Appendix, Fig. S6*). This complex mix of features provides a rich and diverse array of opportunities for foraging, breeding, and other behaviors (36). Previous studies of movement have also revealed different patterns exhibited by marine fish and foraging albatrosses in a manner consistent with prey distribution between coastal shelf and oceanic areas (37, 38).

Our results reveal a remarkable convergence in movement patterns among a large range of marine vertebrates, departing from those reported for terrestrial animals in that the patterns we detected were independent of body length and mass (despite these

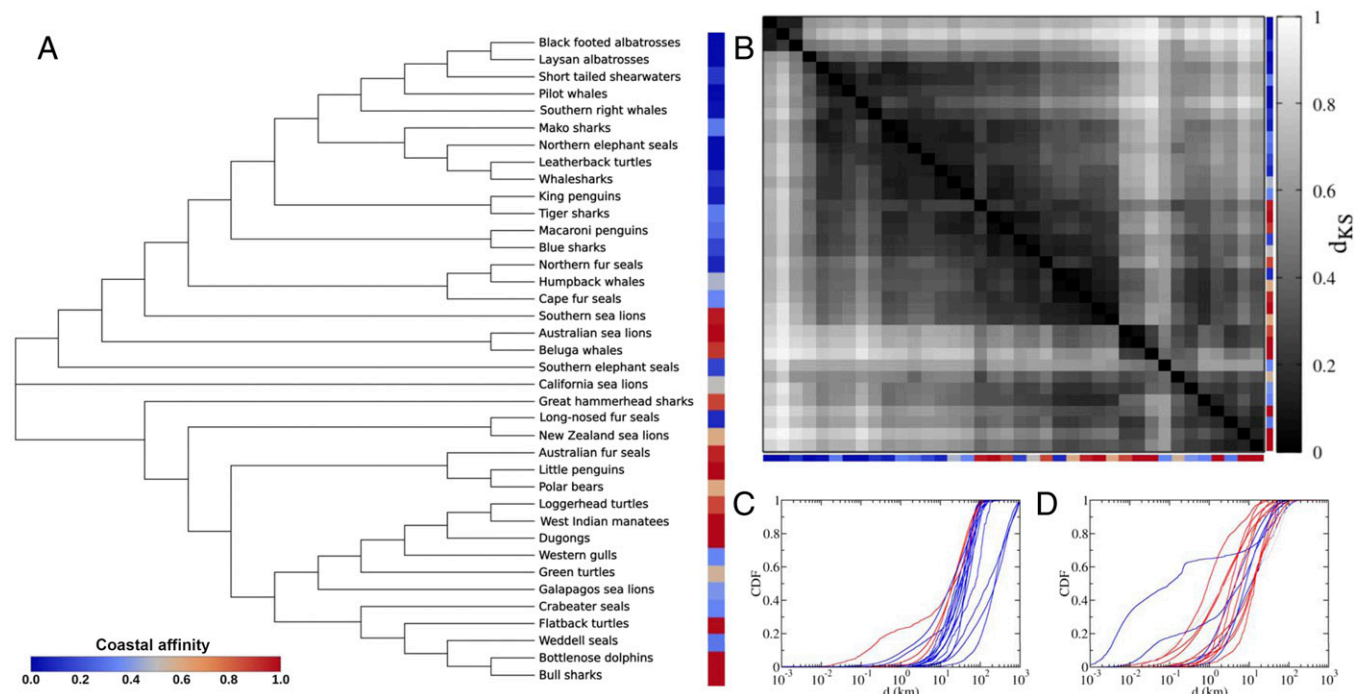


Fig. 4. Analysis of distances between the CDFs of displacements for each pair of species. The colors shown correspond to the classification of each species as having high (red) or low coastal affinity (blue) based on the proportion of their observed displacements occurring completely within coastal ocean for each individual of the same species (*SI Appendix, Table S4*). (A) Dendrogram obtained from the distance matrix derived from the Kolmogorov-Smirnov analysis showing two main branches (anchored by the line for California sea lions) broadly associated with low (<0.5 ; upper branch) and high (>0.5 , lower branch) coastal affinity. (B) Distance matrix (mirror image from diagonal) with darker colors indicating short distances (d_{KS}) between the species' CDFs. C and D show the CDF of displacements for species in the upper and lower branch of the dendrogram, respectively, highlighting distinct displacement regions (d in the x axis) for the curves relative to species occurring mostly on open and coastal oceans, respectively.

ranging 10 orders of magnitude among the species studied). By contrast, for a variety of terrestrial species, the DR is known to scale with body mass, following power laws with exponents around 0.25 (20, 21), with slight differences in the scaling for different taxonomic groups associated with diet types and foraging habitats (21). Our finding suggests that the fluid dynamics (air and water) of the ocean environment has lessened some of the physical constraints that operate on land—for example, the similarity between the density of seawater and animal bodies largely reduces the energetic costs of body mass displacement in the ocean compared with land (15). Also, the marine environment is a 3D foraging habitat, a factor that has also been found to decrease the scaling of DR for primates (which use the 3D habitat offered by forest canopies) in comparison with other terrestrial mammals (21). We found no significant phylogenetic differences in the components of movement analyzed here despite the evolutionary histories of these animals spanning millions of years from turtles to polar bears with evolutionary ages of ~ 157 million y and $\sim 150,000$ y, respectively.

Our comparative analysis of movement across this diverse group of marine megafauna contributes two key underpinnings to our understanding of their movements. First, internal factors that affect movement are species-specific and independent of the phylogenetic history or traits shared at higher taxonomic or functional groupings (such as family or taxa) and of life-history traits alone, such as breeding strategies. Second, we identified that the key external factor influencing movement of marine megafauna species is their interaction with coastal or open ocean habitats. This finding was corroborated by the dendrogram based on the Kolmogorov–Smirnov distances between the cumulative distribution functions (CDFs) of displacements for each pair of species (Fig. 4). As a consequence, there is a broad diversity of individual movement patterns, ranging from random searching patterns to more directed movement, largely in response to extrinsic forcing (i.e., depending on whether they occur in an offshore or coastal environment). Such differences of scale are consistent with differences in oceanographic processes and the related biophysical coupling (39). We highlight, however, that when available, the internal species-specific factors that may affect movement patterns should be included in future models to further assess how individual movement varies within species.

The study of the different movement behaviors of single species has mostly been framed within the random or optimality paradigms, but when applied in isolation, such theories fail to encompass all of the components associated with movement (7). We propose that a more encompassing framework for understanding animal movement, its connections with habitat, and the species-specific traits that influence it, would define how, where, and why animals move in three sequential levels of analysis. The first level would focus on how animals move by analyzing the characteristics of their displacements, for example, as we have done here using predetermined time windows to understand and describe the observed movement patterns. The second level would focus on quantifying the drivers of movement and specifically on where animals move, for example, by using models to estimate the relative importance of drivers throughout the range of habitats where movement occurs (e.g., open versus coastal oceans or microhabitats). If habitat information is not available, discretizing space into low and high occupancy areas can also be a practical method (40). The final level would focus on why animals move and involve hypothesis testing for specific behaviors as commonly undertaken using the random and the optimality paradigms (12). We expect that a unifying framework of animal movement would consist of the integration of these multiple assessments rather than on the results from specific single assessments completed in isolation. This hierarchical framework encompassing three levels of quantitative exploration to understand movement will provide a strong basis from which to predict potential changes in animal movement associated with forecasted severe environmental changes.

The “common reason for moving” sought by Aristotle and many others since appears to be, at least for the vast group of marine megafauna, largely associated with the contrasting use of the coastal and open ocean habitats. The convergence of movement patterns across marine vertebrates separated by millions of years of evolution and using fundamentally different locomotion modes is remarkable. Given recurring changes in the extent and location of continental shelves over the millennia, the influence of habitat change on the evolution of species should not be underestimated (41–43). Indeed, the importance of understanding paleobiology in the conservation of terrestrial ecosystems was recently identified (44). The importance of habitat shaping the movement patterns of marine megafauna might also be associated with habitat-specific ecological roles of these large species and be key to identifying specific areas of behavioral interest. Our study suggests that efforts to understand marine megafauna movement through analysis of its evolutionary history may yield fewer advances than a focus on understanding the habitats through which animals move (e.g., movement phases in coastal versus open ocean). Such a shift in focus, together with the use of a more encompassing framework, will assist predicting the effects of changes already underway, for example, with the reduction in Arctic shelf areas (45) and predicted sea level rise during the next millennia (46, 47). The great behavioral plasticity of coastal marine vertebrates provides some hope of their higher resilience in a rapidly changing coastal marine environment.

Materials and Methods

Tracking Datasets. Our dataset spans three decades (1985–2015) and includes a total of 2,557 individuals from 50 marine vertebrate species. Details are given in *SI Appendix, SI Materials and Methods*.

Probabilistic Analysis of Displacements. We characterized movement patterns from the time-series of displacements recorded in the spatial trajectories of tagged animals. Displacements were measured as the shortest great circle distance between two locations separated by a predetermined time-window T (e.g., 1 d) along an individual track. Details are given in [SI Appendix, SI Materials and Methods](#).

Assessing Coastal Affinity. We considered coastal habitats to be those located in emerging and submerged lands within depths of 0–150 m and calculated coastal affinity as the fraction of observed displacements completely occurring within coastal habitats for each individual. Further details are given in *SI Appendix, SI Materials and Methods*.

BRTs. We fitted BRT models to the final set of 2,303 individuals across 38 species and the 12 predictor variables (*SI Appendix, Tables S2–S4*). Modeling details are given in *SI Appendix, SI Materials and Methods*.

Dendrogram of Movement. We calculated the Kolmogorov–Smirnov distance between the set of displacements for each species pair when using a time window of 1 d. We then used these distances to produce the dendrogram. Details are given in [SI Appendix, SI Materials and Methods](#).

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^aUWA Oceans Institute, Indian Ocean Marine Research Centre, University of Western Australia, Crawley, WA 6009, Australia; ^bSchool of Biological Sciences, University of Western Australia, Crawley, WA 6009, Australia; ^cInstituto de Física Interdisciplinar y Sistemas Complejos, Consejo Superior de Investigaciones Científicas–University of the Balearic Islands, E-07122 Palma de Mallorca, Spain; ^dDepartment of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia; ^eEcology and Biodiversity Centre, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7004, Australia; ^fMarine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, United Kingdom; ^gOcean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton SO14 3ZH, United Kingdom; ^hCentre for Biological Sciences, University of Southampton, Southampton SO17 1BJ, United Kingdom; ⁱRed Sea Research Center, King Abdullah University of Science and Technology, 23955-6900 Thuwal, Kingdom of Saudi Arabia; ^jDepartment of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95060; ^kAustralian Institute of Marine Science, Indian Ocean Marine Research Centre (M096), University of Western Australia, Crawley, WA 6009, Australia; ^lSchool of Life and Environmental Sciences, Deakin University, Warrnambool, VIC 3280, Australia; ^mAustralian Institute of Marine Science, Townsville, QLD 4810, Australia; ⁿUniversity Programs, Dauphin Island Sea Lab, Dauphin Island, AL 36528; ^oDepartment of Marine Sciences, University of South Alabama, Mobile, AL 36688; ^pSouth Australian Research and Development Institute, West Beach, SA 5024, Australia; ^qSouth Atlantic Environmental Research Institute, FIQQ1ZZ Stanley, Falkland Islands; ^rFalklands Conservation, FIQQ1ZZ Stanley, Falkland Islands; ^sJoint Program in Oceanography/Applied Ocean Science and Engineering, Massachusetts Institute of Technology–Woods Hole Oceanographic Institution, Cambridge, MA 02139; ^tBiology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543; ^uDepartment of Biological Sciences, University of Alaska, Anchorage, AK 99508; ^vSchool of Mathematical Sciences, Queensland University of Technology, Brisbane, QL 4000, Australia; ^wAustralian Research Council Centre of Excellence for Mathematical and Statistical Frontiers, Queensland University of Technology, Brisbane, QL 4000, Australia; ^xMarine Science Division, Department of Parks and Wildlife, Kensington, WA 6151, Australia; ^yParis Science Lettre, Laboratoire d'Excellence CORAIL, Centre de Recherche Insulaire et Observatoire de l'Environnement 3278, Ecole Pratique des Hautes Etudes, 66860 Perpignan, France; ^zResearch Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0810, Australia; ^{aa}Antarctic Ecosystem Research Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, CA 92037; ^{bb}Centre d'Études Biologiques de Chizé, UMR 7372 CNRS–Université de La Rochelle, 79360 Villiers-en-Bois, France; ^{cc}Depredation and By-Catch Mitigation Solutions (DBMS), Global Oceans, Hobart, Tasmania 7001, Australia; ^{dd}Rosenstiel School of Marine and Atmospheric Science, Abess Center for Ecosystem Science and Policy, University of Miami, Miami, FL 33149; ^{ee}Department of Fisheries and Oceans, Maurice Lamontagne Institute, Mont Joli, QC G5H3Z4, Canada; ^{ff}Alaska Ecosystems Program, National Marine Mammal Laboratory, National Oceanic and Atmospheric Administration Fisheries, Alaska Fisheries Science Center, Seattle, WA 98115; ^{gg}Research Department, Biodiversity Section, Norwegian Polar Institute, 9296 Tromsø, Norway; ^{hh}Science Group, Department of Environment, Water and Natural Resources, Adelaide, SA 5001, Australia; ⁱⁱSydney Institute of Marine Science, Mosman, NSW 2088, Australia; ^{jj}Instituto de Oceanografia, Universidade Federal do Rio Grande, Rio Grande, RS 96203-900, Brazil; ^{kk}Alaska Science Center, US Geological Survey, Anchorage, AK 99508; ^{ll}Biosecurity South Australia, Primary Industries and Regions South Australia, South Australia, Adelaide, SA 5001, Australia; ^{mm}Centro de Investigação em Biodiversidade e Recursos Genéticos (Research Centre in Biodiversity and Genetic Resources), Associate Laboratory, Universidade do Porto, 4485-668 Vairão, Portugal; ⁿⁿDepartment of Biological Sciences, San Jose State University, San Jose, CA 95192; ^{oo}Guy Harvey Research Institute, Halmos College of Natural Sciences & Oceanography, Nova Southeastern University, Dania Beach, FL 33004; ^{pp}Shark Research Program, Massachusetts Division of Marine Fisheries, New Bedford, MA 02740; ^{qq}Marine Mammal Program, Office of Naval Research, Arlington, VA 22203-1995; ^{rr}Sarasota Dolphin Research Program, Chicago Zoological Society, c/o Mote Marine Laboratory, Sarasota, FL 34236; and ^{ss}Australian Antarctic Division, Department of the Environment and Energy, Kingston, TAS 7052, Australia

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