Convergence of marine megafauna movement patterns in coastal and open oceans

Ana M. M. Sequeira[1], Jorge Rodríguez[2], Victor Eguíluz[2], Robert Harcourt[3], Mark Hindell[4], David Sims[5], Carlos Duarte[6], Daniel Costa[7], J. Fernández-Gracia[2], Luciana Ferreira[8], Graeme Hays[9], Michelle Heupel[8], Mark Meekan[8], Allen Aven[10], Fred Bailleul[11], Alastair Baylis[12], Michael Berumen[13], Camrin Braun[14], Jennifer Burns[15], Julian Caley[16], Richard Campbell[17], Ruth Carmichael[10], Eric Clua[18], Luke Einoder[11], Ari Friedlaender[19], Mike Goebel[20], Simon Goldsworthy[21], Christophe Guinet[22], John Gunn[8], Derek Hamer[11], Neil Hammerschlag[23], Mike Hammill[24], Luis Huckstadt[25], Nicolas Humphries[5], Mary-Anne Lea[4], Andrew Lowther[11], Alice Mackay[11], Elizabeth McHuron[7], Jane McKenzie[11], Lachlan McLeay[11], Clive McMahon[26], Kerrie Mengersen[27], Monica Muelbert[28], Anthony Pagano[29], Bradley Page[11], Queiroz Nuno[30], Patrick Robinson[31], Scott Shaffer[32], Mahmood Shivji[33], Gregory Skomal[34], Simon Thorrold[14], Stella Villegas-Amtmann[7], Michael Weise[35], Randall Wells[36], Bradley Wetherbee[37], Annelise Wiebkin[11], Barbara Wienecke[38], Michele Thums[39]

[1]The University of Western Australia, [2]IFISC (CSIC-UIB), [3]Macquarie University, [4]University of Tasmania, [5]Marine Biological Association of the UK, [6]King Abdullah University of Science and Technology, [7]University of California, Santa Cruz, [8]Australian Institute of Marine Science, [9]Deakin University, [10]Dauphin Island Sea Lab, [11]South Australian Research and Development Institute, [12]South Atlantic Environmental Research Institute, [13]King Abdullah University of Science and Tecnology, [14]Woods Hole Oceanographic Institution, [15]University of Alaska, [16]Queensland University of Technology, [17]Department of Parks and Wildlife, [18]Ecole Pratique des Hautes Etudes, [19]University of California Santa Cruz, [20]NOAA Fisheries Service, [21]SARDI Aquatic Sciences, [22]CNRS-Université de La Rochelle, [23]University of Miami, Rosenstiel School of Marine & Atmospheric Science, [24]DFO, [25]University of California at Santa Cruz, [26]Macquarie University and University of Tasmania, [27]Queensland University of Technology (QUT), [28]Universidade Federal do Rio Grande, [29]U.S. Geological Survey, Alaska Science Center, [30]CIBIO, University of Porto, [31]Center for Ocean Health, Institute of Marine Sciences, Long Marine Laboratory, University of California, [32]San Jose State University, [33]Guy Harvey Research Institute, [34]Massachusetts Division of Marine Fisheries, [35]Office of Naval Research, [36]Chicago Zoological Society, [37]University of Rhode Island, [38]Department of the Environment, [39]Australian Institute of Marine Sciences

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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 analyse a global dataset of $\sim$ 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 to more predictable patterns when moving in open oceans. This distinct difference may be associated with greater complexity within coastal micro-habitats, 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

Introduction

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 behaviour, such as feeding and mating. Following the challenge posed by Aristotle millennia ago[1] in *De Motu Animalium* (On the Movement of Animals) (6), efforts have been made to develop a unifying framework to study movement (7). 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 capacities influencing movement (7). It is also known that animal movement patterns are underpinned by common principles, such as 'optimal' resource exploitation by

Significance

Understanding the key drivers of animal movement is crucial to assist 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 the well-known 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 shows a prevalence of movement patterns dominated by search behaviour on coastal habitats compared to 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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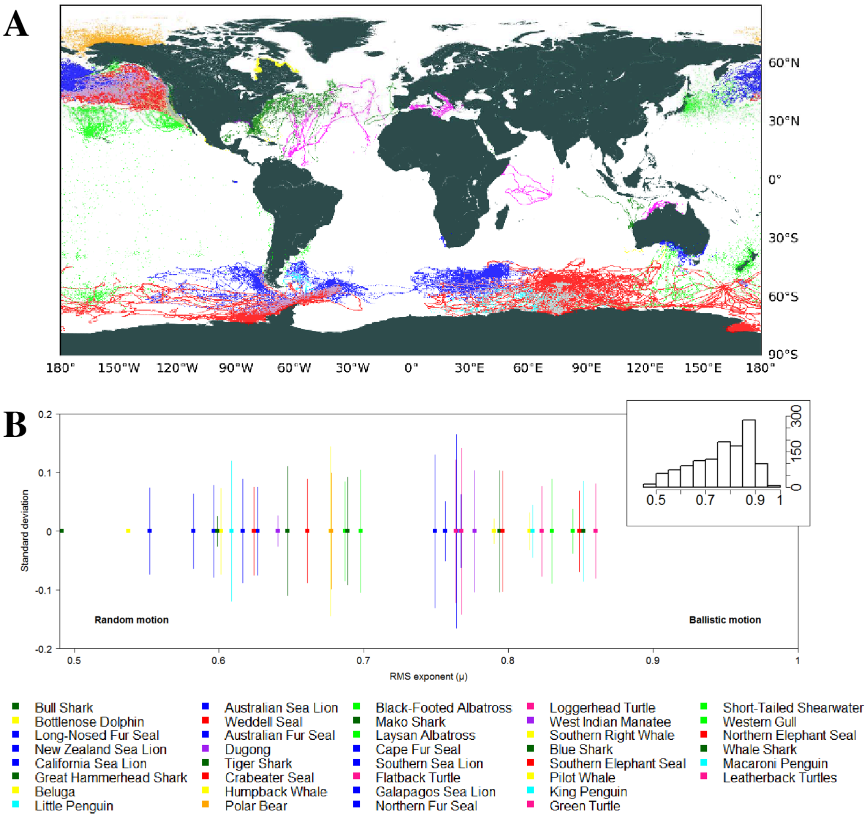

Fig. 1. Representation of the global satellite tracking dataset and scaling properties for all species analysed.(A) Global map with trajectories obtained by satellite tracking for all 50 species. (B) The scaling exponents (μ) obtained from the root-mean-square (d_{RMS}) analysis of displacements for all species analysed (squares indicate mean values, and bars show the standard deviation). Histogram in inset shows the number of individuals for the range of scaling exponents. Long-nosed fur seal: common name for the South Australian population of New Zealand fur seal. Colours represent each of the nine guilds with data: cetaceans (yellow), eared seals (blue), flying birds (green), penguins (cyan), polar bears (orange), sharks (dark green), sirenians (purple), true seals (red), and turtles (pink).

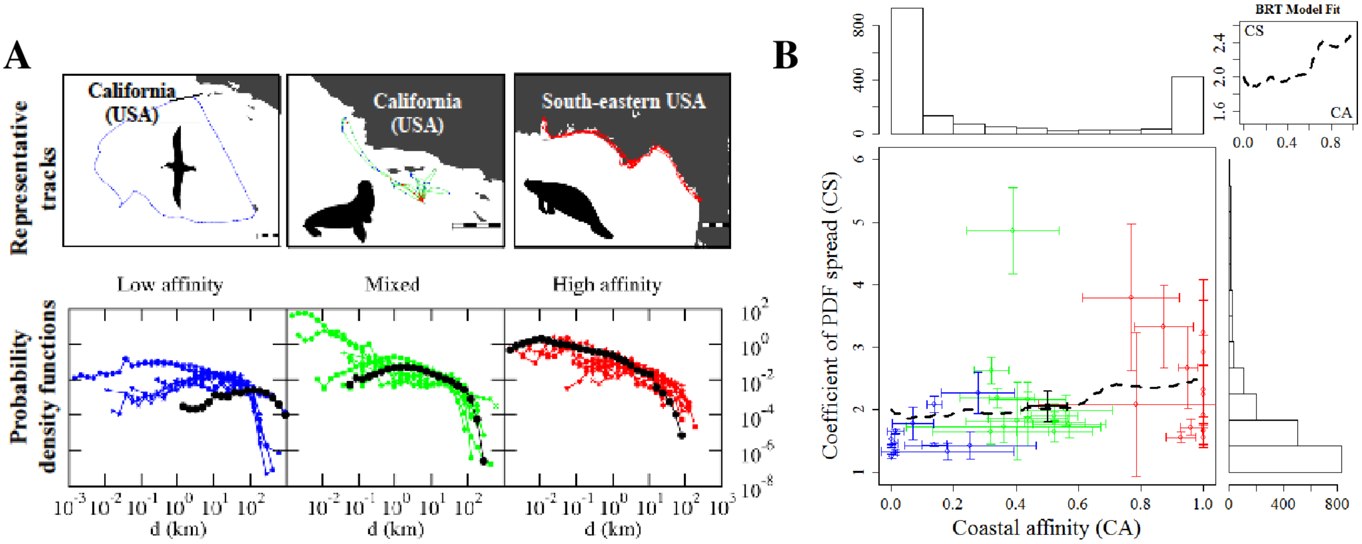

Fig. 2. Results of the analysis of displacements(A) Probability density function of displacements (d, km) at the species level with 1 day time windows for species with low (mean < 0.3; left), mixed (centre) and high (mean > 0.7, right) coastal affinity (bottom), and example tracks for each group (top; 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 boosted regression trees (BRT, 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 ($0 \le CA \le 1$; 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 ± sd among all species with coefficient of variation 37.20 % for CS and 39.51 % CA.

predators ('optimality paradigm'; 2, 3, 8, 9), or the use of more efficient search trajectories ('random' paradigm; 10, 11, 12). Overall, animal movement patterns have been attributed to 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), and constrained by extrinsic factors, including the dynamic nature of the environments they inhabit (24-26). 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

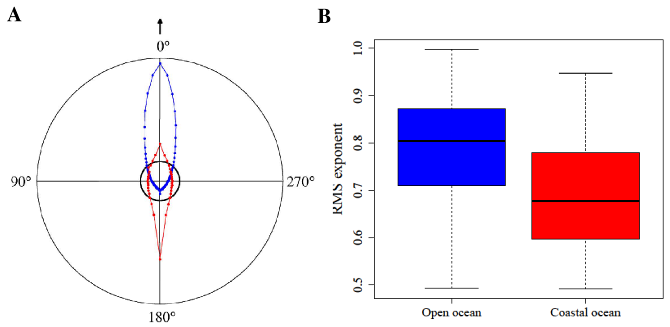

Fig. 3. Comparison of movement patterns in open and coastal oceans.The classification into open or coastal was based on the depth at which the displacements occurred with depth ≤ 150 m classified as coastal ocean. A) Distribution of turning angles (arrow points to 0°) in open (blue) and coastal oceans (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 ($\mu = 0.784 - 0.085$ *x coastal ocean* ; $p < 0.001$).

framework exists irrespective of location, scale of movement, and stage or phase, a large scale comparison across multiple species is needed (27, 28).

Rapid technological developments in animal-attached electronic tags (telemetry/biologging) have generated large tracking datasets across an array of marine vertebrates now available for multiple regions, temporal scales and habitats across the globe. Such large datasets provide the foundational information required to discover commonalities in movement patterns across species and environments and to assess the influence of a range of intrinsic and extrinsic factors. Because marine vertebrates have diverse life histories, and include all extant vertebrate classes except Amphibia, they provide an ideal group for the exploration of the underlying principles that might govern animal movement. Moreover, marine vertebrates range broadly in their movement patterns, from species with small home ranges (m to km) to highly migratory animals travelling hundreds to thousands of km while crossing entire ocean basins (24, 25, 29). For these reasons, answering questions about marine animal movement will have broad-reaching application to understanding movement in species from terrestrial vertebrates to aquatic invertebrates (30). Moreover, marine vertebrates include many threatened species that are particularly vulnerable to changing environments (*e.g.*, polar bears and penguins) (31) or to extractive anthropogenic activities (*e.g.*, whales, sharks and seals), as well as species with important economic value to human societies (32, 33). Hence, understanding how marine vertebrates move is critical to broadly understand mechanisms of animal movement, as well as, to assist development of effective conservation measures and predict the potential impacts of global change on populations.

Here, we synthesize movement data from the largest satellite telemetry dataset yet assembled at a global scale for large marine vertebrate species (termed “megafauna”), to quantify the relative importance of both extrinsic and intrinsic factors as drivers of movement and identify unifying patterns in marine megafauna movement. Our dataset includes species that fly, swim and walk/paddle, with distributional ranges varying across tropical, temperate, and polar regions, and comprising sharks, turtles, flying and swimming birds, true and eared seals, cetaceans, sirenians, and polar bears (Figure 1A). We analysed individual movement by characterizing horizontal displacements as the shortest great circle distances between two consecutive locations and the turning angles between them. We tested for differences in these attributes among taxonomic groups (taxa, family, species), allometric scaling (body length and mass), life history traits (*e.g.*, breeding and foraging strategies), energy requirements, as well as locomotion mode, region (polar, temperate, tropical) and coastal affinity, defined as the fraction of displacements within the 0 – 150 m depth range (here referred to as ‘coastal ocean’) (see Methods for details, and Tables S1-S3).

Results

The mean displacements *per* day (*d* in km/day; effective speed), referred to in the terrestrial animal movement literature as “day range” (21) or “daily movement range” (20), were mostly independent of body length and mass (Figure S1) both among species and within species groups. Exceptions include true seals (body length only) and turtles, but the latter is simply associated with the different mode of foraging of the largest turtle considered, the leatherback turtle, which constantly travels large distances in search of prey. The other turtle species included in the analysis tend to be neritic as adults, living most of their lives in shallow coastal waters where they move little. The root-mean-square analysis of displacements (d_{RMS}) scaled with time as a power law ($d_{\mathrm{RMS}} \sim T^{\mu}$) with exponents (μ) mostly above the value of 0.5 (commonly associated with Brownian motion) (Figure 1B), indicating that most individuals moved super-diffusively, *i.e.*, faster than expected in a normal diffusion process. Using pre-determined time-windows of one day, we compared the probability density functions (PDF) 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 (Figure 2A). 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 PDF. Our CS results show high variability among individuals within and among species (Figure 2B and 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 (Figure 2B). Lower CS values generally represented simpler, more linear paths while higher values represented more varied, complex movement patterns (Figure 2A).

Model fits from boosted regression trees (BRT; 34) to the resulting CS 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 (Figure 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 (Figure 2 and Figure 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 BRT. Based on our modelling results, CS increases with greater coastal affinity (Figure 2B) 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

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[1] *“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).”*

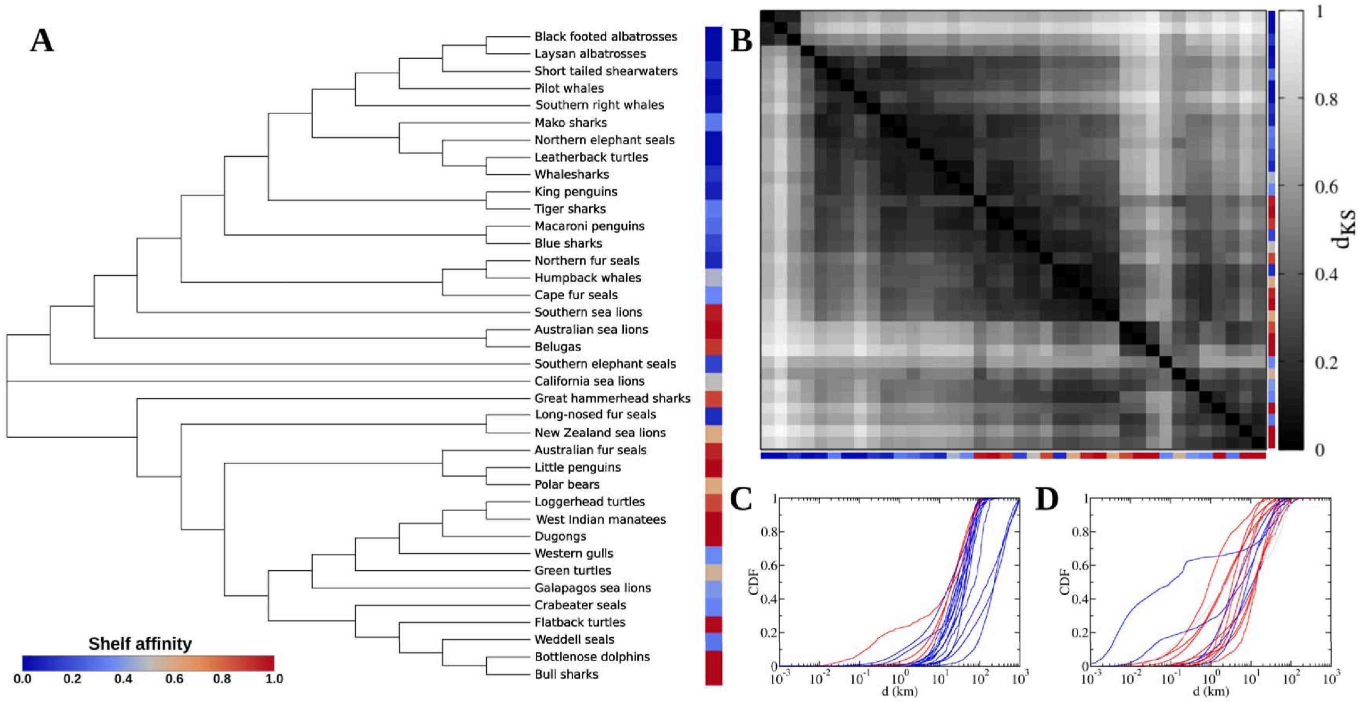

Fig. 4. Analysis of distances between the cumulative distribution functions of displacements for each pair of species.The colours shown correspond to the classification of each species as having high (red) or low coastal affinity (blue) based on the proportion of their observed displacements occurring completely within coastal ocean for each individual of the same species (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 colours indicating short distances (d_{KS}) between the species' cumulative distribution functions. C) and D) show the cumulative density functions (CDF) of displacements for species in the upper and lower branch of the dendrogram, respectively, highlighting distinct displacements regions ('d' in the *x*-axis) for the curves relative to species occurring mostly on open and coastal ocean, respectively.Supporting Information

the d_{RMS} exponent (with 0.5 to 1.0 indicating normal random to super diffusive, 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 $= 0.791 - 0.112\,x\ ocean$, where *ocean* = "open ocean" or "coastal ocean", $p < 0.001$for the linear model) (Figure 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°, *i.e.*, 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 (Figure 3 and Figure S3).

The Kolmogorov-Smirnov analysis of the distances between the cumulative distributions of displacements for each species pair was used to compute a dendrogram which 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 colour scale for Figure 4A). 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 re-iterates that differences are not fully dependent on intrinsic traits.

Discussion

Our integrated, multi-species study reveals 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 (Figure 2 and Figure S6), and is likely related to a combination of directed- and resident-type movements that can occur over the course of an individual's track in association with different behaviours (e.g., transiting and foraging, resting, breeding) (35). Here, we used an analysis of displacements with no prior assumptions for the movement patterns observed, and show, for the first time, 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; Figure 2 and Figure 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 behaviour 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., 36). This difference may explain the convergence of movement behaviours 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 (Figure 2 and Figure S6). This complex mix of features provides a rich and diverse array of opportunities for foraging, breeding and other behaviours (37). Previous studies of vertical 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 (26, 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 ranging 10 orders of magnitude among the species studied). By contrast, for a variety of terrestrial species, the day range (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 to land (15). Also, the marine environment is a three-dimensional foraging habitat, a factor which has also been found to decrease the scaling of day range for primates (which use the 3-D habitat offered by forest canopies) in comparison to other terrestrial mammals (21). We found no significant phylogenetic differences in the components of movement analysed here despite the evolutionary histories of these animals spanning millions of years from turtles to polar bears with evolutionary ages of $\sim$157 million and $\sim$150 thousand years, respectively.

Our comparative analysis of movement across this diverse group of marine megafauna contributes two key underpinnings to our understanding of its movements. First, internal factors that affect movement are species-specific and independent of 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 or central place foraging. 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 (CDF) of displacements for each pair of species (Figure 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 bio-physical 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 behaviours of single species has mostly been framed within the random or optimality paradigms, but when applied in isolation, such theories fail to encompass all 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 analysing 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 micro-habitats). 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 behaviours 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 palaeobiology 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 behavioural 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 behavioural 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 2557 individuals from 50 marine vertebrate species. Details given in SI Supporting 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 day) along an individual track. Details given in SI Supporting 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 given in SI Supporting Materials and Methods.

Boosted regression trees. We fitted Boosted Regression Trees models to the final set of 2303 individuals across 38 species and the 12 predictor variables (Tables S2-S4). Modelling details given in SI Supporting 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 day. We then used those distances to produce the dendrogram. Details given in SI Supporting Materials and Methods.

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