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Evolutionary diversification in the marine realm: a global case study with marine mammals

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Abstract

Speciation is thought to be predominantly driven by the geographical separation of populations of the ancestral species. Yet, in the marine realm, there is substantial biological diversity despite a lack of pronounced geographical barriers. Here, we investigate this paradox by considering the biogeography of marine mammals: cetaceans (whales and dolphins) and pinnipeds (seals and sea lions). We test for associations between past evolutionary diversification and current geographical distributions, after accounting for the potential effects of current environmental conditions. In general, cetacean lineages are widely dispersed and show few signs of geographically driven speciation, albeit with some notable exceptions. Pinnipeds, by contrast, show a more mixed pattern, with true seals (phocids) tending to be dispersed, whereas eared seals (otariids) are more geographically clustered. Both cetaceans and pinnipeds show strong evidence for environmental clustering of their phylogenetic lineages in relation to factors such as sea temperature, the extent of sea ice, and nitrate concentrations. Overall, current marine mammal biogeography is not indicative of geographical speciation mechanisms, with environmental factors being more important determinants of current taxonomic distributions. However, geographical isolation appears to have played a role in some important taxa, with evidence from the fossil record showing good support for these cases.

Highlights

- Marine mammals are an excellent case study for the role of geographically-driven diversification within open environments.
- Evidence for geographically-driven speciation in cetaceans and pinnipeds is limited, albeit with some notable exceptions.
- Whereas cetaceans show a trend from ancient geographical dispersion towards more recent geographically-driven diversification, the opposite is true of pinnipeds.
- Contemporary environmental factors play an important role, with deep lineages among both groups clustering within specific environmental conditions.
- Environmental structuring may either be a consequence of environmentally-driven speciation, or, alternatively, may indicate that post-speciation range shifts have largely erased signatures of geographically-driven diversification in marine mammals.

Keywords: barriers, biogeography, dispersal, ecology, evolution, oceanic, phylo-beta diversity, phylogenetic diversity

Introduction

“Since the ecology of marine organisms is fundamentally different from that of such typical land animals as mammals, birds, land snails, and butterflies, one might expect modes of speciation in the oceans that differ completely from the typical geographic speciation of land animals.” (Mayr 1954)

Assessing the importance of geographical isolation as a driver of speciation is often challenging. The vast open expanse of the marine realm is a classic example (Palumbi 1992). Compared to terrestrial environments, high population connectivity within marine systems is thought to limit geographical separation, reducing opportunities for allopatric divergence (Palumbi 1992, Bierne et al. 2003). Nevertheless, life in the oceans is

notably diverse, creating what has been coined the “marine speciation paradox” (Bierne et al. 2003). Some studies have highlighted the role of ecological factors in driving marine diversification (e.g., Momigliano et al. 2017). Beyond specific case studies, however, the extent to which geography drives speciation in the marine realm currently remains unclear.

Tests for the role of geographical isolation within open environments are confounded by post-speciation, environmentally-driven range shifts. Such distributional changes could erase speciation-related geographical patterns (Losos and Glor 2003); given that diversification typically occurs across hundreds of thousands to millions of years (Hedges et al. 2015), whereas environmental change can be far more rapid (Petit et al. 1999). As a result, assessments of geographically-driven diversification have been “frustratingly inconclusive” (Fitzpatrick et al. 2009). To avoid this pitfall, environmental variability needs to be explicitly considered when assessing biogeographical evidence for the geography of speciation.

Here, we use a combination of current species distributions and phylogenetic data to test for allopatric diversification in the two major groups of marine mammals – cetaceans and pinnipeds – after first accounting for environmental variation. Marine mammals are an excellent case study, owing to the existence of comprehensive phylogenies (e.g., Steeman et al. 2009, Higdon et al. 2007, McGowen et al. 2009), distributional data (IUCN 2016) and a relatively abundant fossil record (Marx et al. 2016, Berta et al. 2018). In addition, cetaceans and pinnipeds provide a useful comparison because of their fundamentally different reproductive strategies, with the former being fully aquatic, while the latter must return to land or ice to breed.

Both allopatric divergence (Steeman et al. 2009) and adaptive radiation (Slater et al. 2010, Marx and Uhen 2010) have been proposed as primary drivers of extant cetacean diversity. Pinniped diversification is typically discussed in an allopatric context (Deméré et al. 2003), even though much diversification appears to have occurred within, rather than between, marine regions (Fulton and Strobeck 2010). A signature of geographical diversification within either group would suggest that dispersal limitations in the ocean can indeed drive speciation.

Material and Methods

We tested biogeographical associations with diversification within a phylo-beta diversity framework, as introduced by Graham and Fine (2008) and employed in a variety of subsequent studies (Fine and Kembel 2011, Peixoto et al. 2014, Carlucci et al. 2017). We measured spatial phylogenetic turnover – the change in composition of evolutionary lineages from one location to the next – across assemblages in 2,559 global grid cells for cetaceans and pinnipeds as a whole, as well as for all of their subclades.

Data sources

Comprehensive species-level phylogenies were obtained from Higdon et al. (2007) and McGowen et al. (2009). For Cetacea, several alternative phylogenies were available (e.g., Steeman et al. 2009, Slater et al. 2010). Of these, we selected McGowen et al. (2009) because of its comprehensive taxon sampling. *Neophocaena asiaeorientalis*, *Orcaella heinsohni*, *Sousa teuszii*, and *Zalophus wollebaeki* were manually added to the phylogenies as sister species to their congeners. Freshwater and landlocked species, including the cetaceans *Inia geoffrensis*, *Lipotes vexillifer*, *Platanista* spp. and *Sotalia fluviatilis*, and the pinnipeds *Pusa caspica* and *P. sibirica*, were removed. The final dataset comprised 82 cetacean and 31 pinniped species.

Global distributional data were based on the IUCN Red List of Threatened Species™ (IUCN 2016) and matched to the species list provided by the Society for Marine Mammalogy (2016). Species not recognised on this list were excluded. Species distributions can also be derived from computer models based on environmental data. We avoided these data sources and instead relied on expert-derived range maps to avoid analytical circularity, as we included environmental data in our subsequent analyses (see ‘Environmental distance’ below).

We amended our distributional data according to the latest taxonomic information from the Society for Marine Mammalogy. Thus, the distribution of *Arctocephalus townsendi*, which is listed as a species by the IUCN but as a subspecies of *A. philippii* by the Society for Marine Mammalogy, was added to that of *A. philippii*. Similarly, the distribution of *Delphinus capensis* was added to that of *D. delphis*.

Distributional data were mapped and divided into grid cells based on an equal-area world grid in Behrmann projection, with cells equalling 148,953 km² and approximately equivalent to 4° latitude and longitude. This grid cell size is a compromise between data resolution and computational requirements and is suitable for testing global patterns.

Global current environmental data such as depth, surface temperature (mean, maximum, minimum and range), salinity, photosynthetically active radiation (PAR), primary productivity, nitrate concentration, surface current, ice cover (annual mean), and distance to land were obtained from Basher et al. (2018). As these data were provided at 5 arc-minute scale, we converted them to match our species distributions by taking the median of all the values found within a given grid cell.

Phylo-beta diversity: phylogenetic turnover

There are several beta diversity and phylo-beta diversity metrics quantifying different aspects of variation in species assemblage composition (Baselga 2010). Here, we were solely interested in spatial phylogenetic turnover among pairs of assemblages within grid cells, which was measured via the phylosim metric ($p\beta_{sim}$) as recommended for biogeographical studies (Holt et al. 2013, Daru et al. 2017, Kreft and Jetz 2010):

$$phylosim = 1 - \frac{a}{\min(b, c) + a}$$

Where a is the number of evolutionary lineages shared between two locations, and b and c the number of evolutionary lineages unique to each location.

Branch lengths were not included since our study focused purely on diversification and not subsequent divergence. Phylosim metrics were calculated separately for cetacean and pinniped assemblages, based on all pairwise comparisons of global grid cells. Major patterns were then summarised via Principal Coordinates Analysis (PCoA) and mapped by colouring grid cells according to their location in ordination space (as defined by the two major principal coordinates). To do so, we employed the hue, colour, luminance (HCL) colour scheme, which improves human perception of colour differences relative to red, green, blue (RGB) colour space (Zeileis et al. 2009). Ordination results were also mapped on to the original phylogenies by determining the mean colour in PCoA ordination space across the grid cells where the descendants of a particular phylogenetic branch occur.

Geographical & Environmental distances

We calculated geographical and environmental distances between all possible pairwise grid cell combinations. To account for correlations between variables, we reduced the environmental dataset of Basher et al. (2018) via Principal Components Analysis (Hotelling 1933). The two most relevant principal components (PCs) were then selected separately for cetaceans and pinnipeds, as follows:

1. All PCs contributing less than 8% of the overall variation were removed; we chose this threshold because if all of the PCs were equally important, each would account for roughly 8% of the total variation.
2. For each of the remaining PCs, we calculated pairwise environmental distances between grid cells and correlated them with marine mammal phylogenetic turnover.
3. Finally, we selected the two PCs showing the strongest correlation in terms of absolute Pearson correlation coefficients and used the ordination space defined by them to calculate pairwise Euclidean environmental distances between all grid cells.

Correlating phylogenetic turnover and explanatory variables

We tested for associations between phylogenetic turnover, geographical distance, and environmental distance using partial correlations, with the association between phylogenetic turnover and geographical distance being conditioned on the environmental distance matrix (Fisher 1924). We structured our analysis to provide a test of stated hypotheses in response to earlier criticisms which regarded biogeographical approaches

as merely “a narrative addition to phylogenetic studies” (Crisp et al. 2011). Specifically, we tested whether:

1. Current spatial biogeographical patterns are more correlated with geographical distance than expected by chance, after accounting for the effect of current environmental variation; if so, this would suggest geographically-driven diversification.
2. Current spatial biogeographical patterns are more correlated with current environmental variation than expected by chance, after accounting for the effect of geographical distance; if so, this would confirm that environmental variability influences the distribution of marine mammal clades.
3. Pinnipeds show stronger geographical clustering than cetaceans, as predicted by their need to breed outside of the water.

A key advantage of this assemblage-level approach is that it considers global diversification patterns within a geographical context, facilitating the identification of clades with significant geographical associations and of potential barriers to dispersal. It therefore provides a full overview of the extent to which evolutionary history is geographically structured and creates a framework for testing specific biogeographical hypotheses.

Since both the distributional data and the phylogenies are non-random, there is a risk that any correlations between them may be spurious. For example, species turnover across grid cells inevitably leads to some level of phylogenetic turnover, even if there is no real link between geographical distance and evolutionary relationships. To gauge statistical significance, we therefore tested our partial correlations against 1000 iterations of a null model which randomised the species names within our phylogenies and range data (both for the full analyses and for each subclade) but maintained their phylogenetic topology and geographical structure.

Deviations from the null model demonstrate unexpected associations between the phylogenetic and distributional data. The strength of these associations was expressed using Standardised Effect Sizes (SES), which subtract the mean of the 1000 random correlation coefficients from the observed correlation coefficient, and then divide the result by the standard deviation of the random correlation coefficients. Correlations that were either higher or lower than 95% of null model correlations were interpreted as statistically significant, as follows:

- Significant positive correlation: larger geographical distances are associated with larger phylogenetic turnover (after accounting for species turnover and environmental distances), indicating **geographical phylogenetic clustering** and, thus, potential evolutionary divergence driven by geographical isolation.
- Significant lack of correlation: no association between geographical distances and phylogenetic turnover (after accounting for species turnover and environmental distances), indicating **geographical phylogenetic dispersion** and no evidence for

evolutionary divergence driven by geographic isolation.

There is no theoretical basis to expect negative correlations. Note that ‘clustering’ and ‘dispersion’ here refer to patterns within the geographical range of each focal (sub) clade, rather than across the entire marine realm.

In addition to the main analysis described above, we also ran the reverse test for associations between phylogenetic turnover and environmental distance, after controlling for geographical distance (using partial correlations conditioned on the geographical distance matrix). In this case, significant positive correlations between phylogenetic turnover and environmental distance suggest specific environmental preferences for evolutionary lineages, whereas a significant lack of correlation would indicate that taxa are dispersed across a wider range of environmental conditions than random expectations. Again, ‘clustering’ and ‘dispersion’ here refer to patterns within the range of environmental conditions experienced by the focal clade.

Results

Geographical patterns of marine mammal phylogenetic turnover

Cetaceans

Overall phylogenetic turnover is not associated with geographic distance (Fig. 1ai, $partial\ r = 0.23$, $SES = -2.09$, $P = 0.028$; see Supplementary File S1 for full results). Cetacean lineages are significantly dispersed throughout the world’s oceans, albeit with the major axis of variation separating a circumtropical region from two polar areas (Fig. 2a,c & e).

In total, 40 subclades show stronger geographical clustering than mean random expectations, with seven of these being statistically significant (Fig. 1ai). Geographical phylogenetic clustering is pronounced in the clade comprising Lissodelphininae *sensu* LeDuc et al. (1999) and its sister species *Lagenorhynchus albirostris* (node 29, $partial\ r = 0.63$, $SES = 6.60$, $P < 0.001$), as well as the clade comprising monodontids + porpoises (node 39, $partial\ r = 0.66$, $SES = 6.03$, $P < 0.001$). Despite not being statistically significant, geographical phylogenetic clustering within right whales (Balaenidae) is also notable ($partial\ r = 0.67$, $SES = 2.23$, $P = 0.104$). No species pairs returned a significant result for geographical clustering despite several pairs returning high empirical correlation values, e.g., Node 28 *O. brevirostris* + *O. heinsohni* ($partial\ r = 0.71$, $SES = 1.38$, $P = 0.362$), Node 20 *Sousa chinensis* + *S. teuszii* ($partial\ r = 0.56$, $SES = 1.01$, $P = 0.416$), Node 65 *Hyperoodon ampullatus* + *H. planifrons* ($partial\ r = 0.82$, $SES = 1.89$, $P = 0.176$).

Of the remaining 40 subclades, five are significantly more dispersed than null expectations, including delphinidans, delphinoids, and the clades formed by the two basal nodes within delphinids (Fig. 2ai). In general, geographical dispersion tends to be stronger than null expectations among the major subclades, whereas smaller clades either conform to null expectations

(e.g., balaenopterids and delphinines) or show evidence of geographical clustering.

Pinnipeds

Overall pinniped phylogenetic turnover is positively associated with geographical distance, but not significantly beyond random expectations (Fig. 1bi, $partial\ r = 0.54$, $SES = 1.85$, $P = 0.080$). Nevertheless, spatial patterns are stronger than within cetaceans (Figs. 1 & 2). Thirteen of the 29 pinniped subclades show stronger spatial correlations than mean random expectations, with three of these associations being statistically significant (Fig. 1bi).

Geographical clustering is strongest in otariids ($partial\ r = 0.75$, $SES = 2.43$, $P = 0.010$), and it is also evident in subclades within this family (Figs. 1bi). Globally, otariid phylogenetic turnover is predominantly latitudinal (Fig. 2b, d & f). Thus, three of the four most basal species – northern fur seals (*Callorhinus ursinus*), California sea lions (*Zalophus californianus*), and Steller sea lions (*Eumetopias jubatus*) – occur in the Northern Pacific, whereas all remaining species have more southerly distributions. The only exception is the Guadalupe fur seal (*Arctocephalus philippii townsendi*), which overlaps with the southern limit of the California sea lion. Within the Southern Ocean, the clade comprising *Arctocephalus gazella* and *A. tropicalis* is geographically dispersed (Node 12, $partial\ r = 0.00$, $SES = -1.92$, $P = 0.032$).

Phylogenetic turnover within true seals (Phocidae) is not significantly correlated with geographical distance, neither for the family overall ($partial\ r = 0.68$, $SES = 1.96$, $P = 0.050$; Fig. 1bi), nor most of its subclades. The two major phocid subfamilies are split on a north/south basis, with monachines distributed throughout Antarctica and across the equator into the Mediterranean and North East Pacific, whereas phocines occupy Arctic and northern temperate regions (Fig. 2b, d & f). Within these two lineages, there is no strong evidence for geographical phylogenetic clustering, except for monk seals (Node 31, *Monachus monachus* & *Neomonachus schauinslandi*, $partial\ r = 0.99$, $SES = 1.12$, $P = 0.010$). There is, however, evidence for significant geographical dispersion in the Antarctic circumpolar lobodontines ($partial\ r = 0.00$, $SES = -2.38$, $P = 0.020$).

Environmental variation associated with marine mammal turnover

Cetaceans

The first and third principal components derived from the environmental data showed the strongest correlations with cetacean phylogenetic turnover ($r = 0.76$ & 0.19 , respectively), and were therefore used for further analysis (figure 3a & c). Eigenvectors indicate that PC1, which explains 44% of the total environmental variance, is positively associated with sea surface temperature and negatively associated with extent of sea ice and with nitrate concentrations. PC3, which explains 12% of the total environmental variance, is positively associated with extent of sea ice,

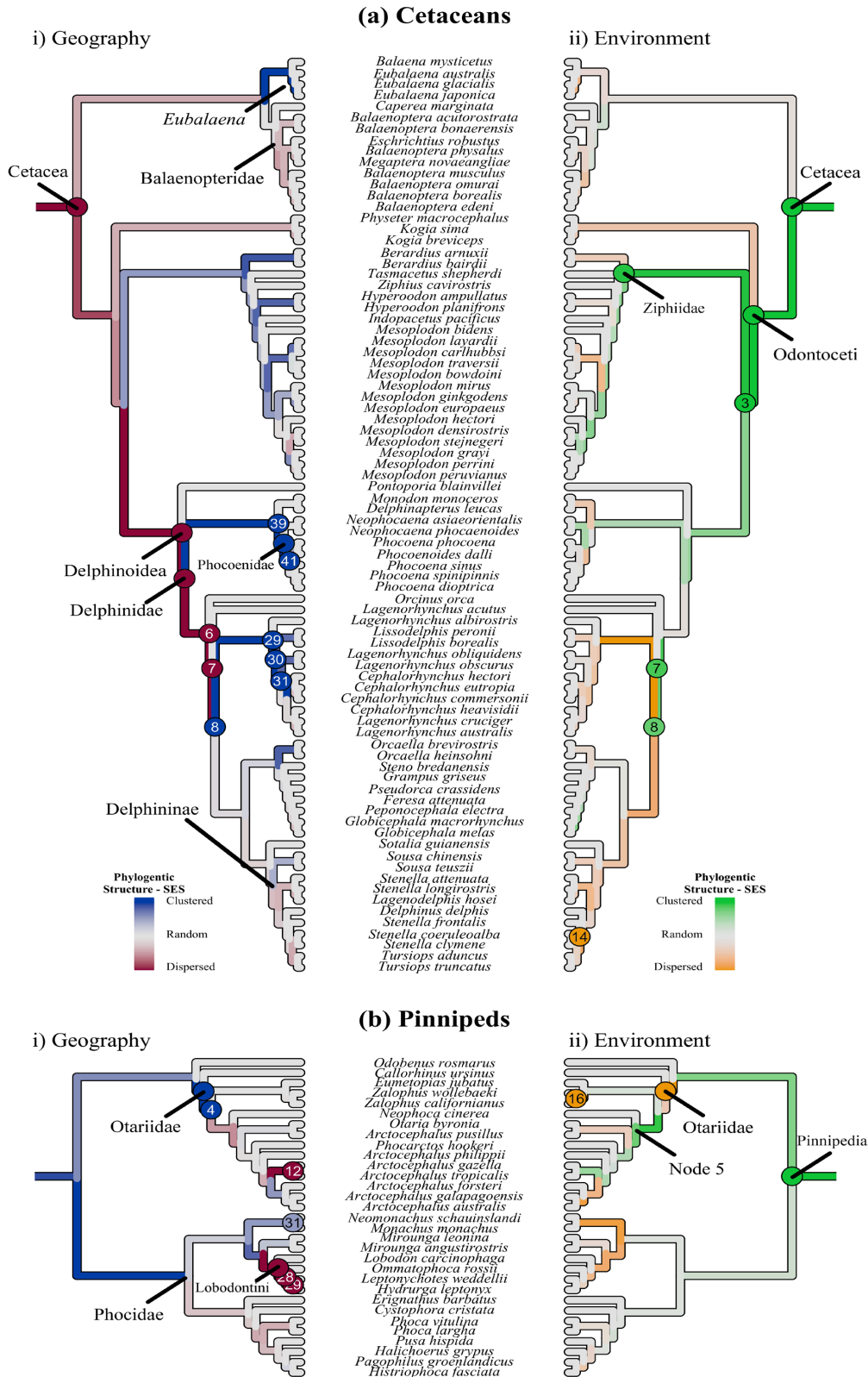


Figure 1. Geographical and environmental structuring of phylogenetic lineages for (a) cetaceans and (b) pinnipeds. Clustering indicates associations with specific geographical areas or environmental conditions, whereas dispersion signifies lineages that are broadly geographical or environmentally distributed. Colours indicate the strength of deviation from random expectations, measured as Standardised Effect Sizes (SES). Colours are scaled to maximum absolute SES values of 1.96. (see Supplementary Material for actual SES values). Nodes that significantly deviate from random expectations are highlighted with circles and labelled with taxon names, or node numbers for unnamed taxa (see also Figs S2 & S3). Other taxa and nodes highlighted in the main text are labelled with their names or numbers only.

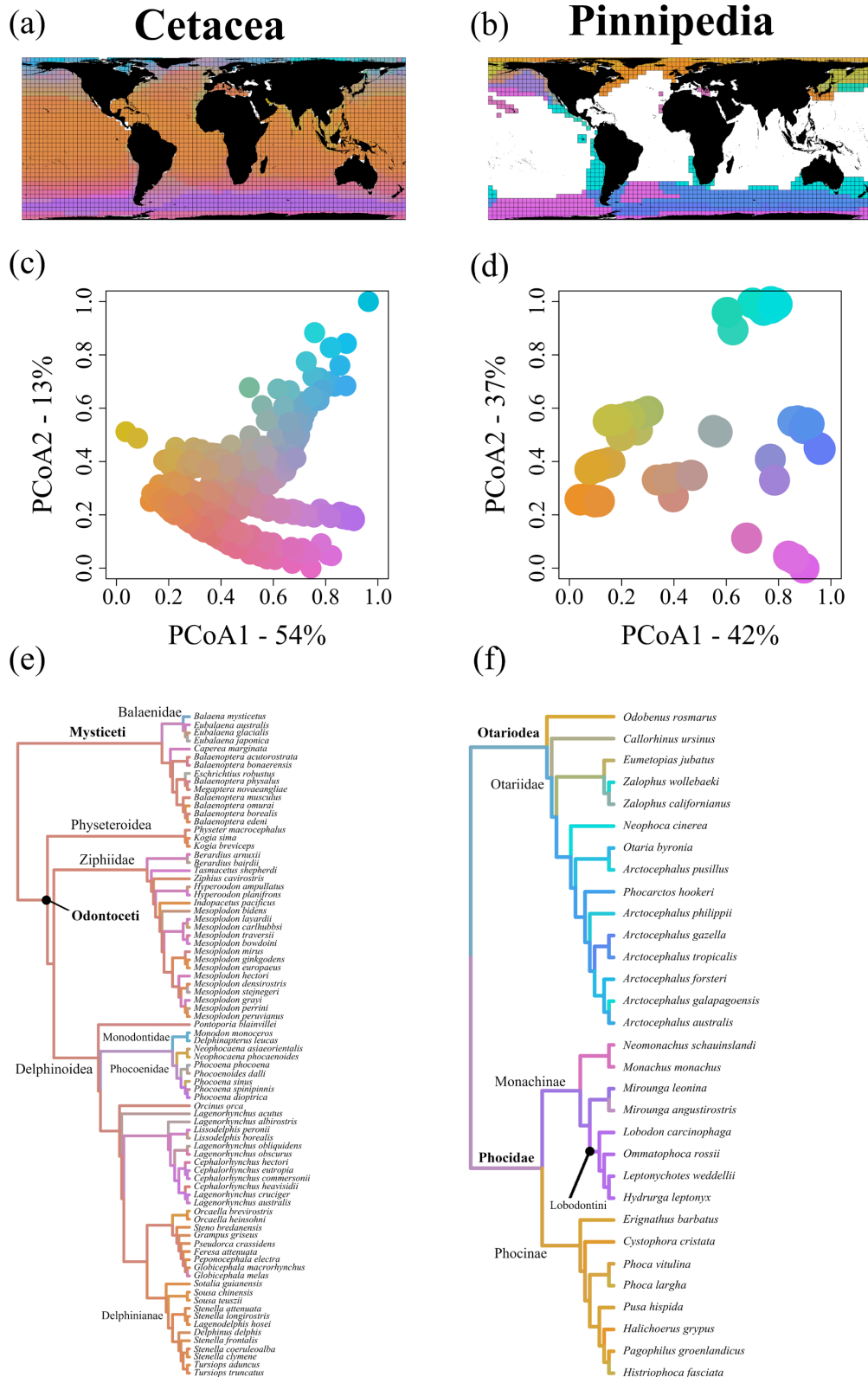


Figure 2. Phylogenetic turnover among cetaceans (a,c & e) and pinnipeds (b, d & f). Maps (a & b) show global grid cells in Behrmann projection, coloured according to the ordinations plots shown in (c) and (d), which in turn show major axes of variation of phylogenetic turnover. Points in ordination spaces are coloured according to a two-dimensional colour scheme, which allows closely located points to have similar colours. Percentage values on axis labels reflect the amount of total variation explained. Phylogenetic branches (e & f) show the average colour of all grid cells occupied by their descendant species. Three grid cells, located in the Red Sea and Arabian Gulf, were removed from the cetacean ordination because their assemblages showed extreme values for PC1, which greatly reduced colour variation for the remaining grid cells.

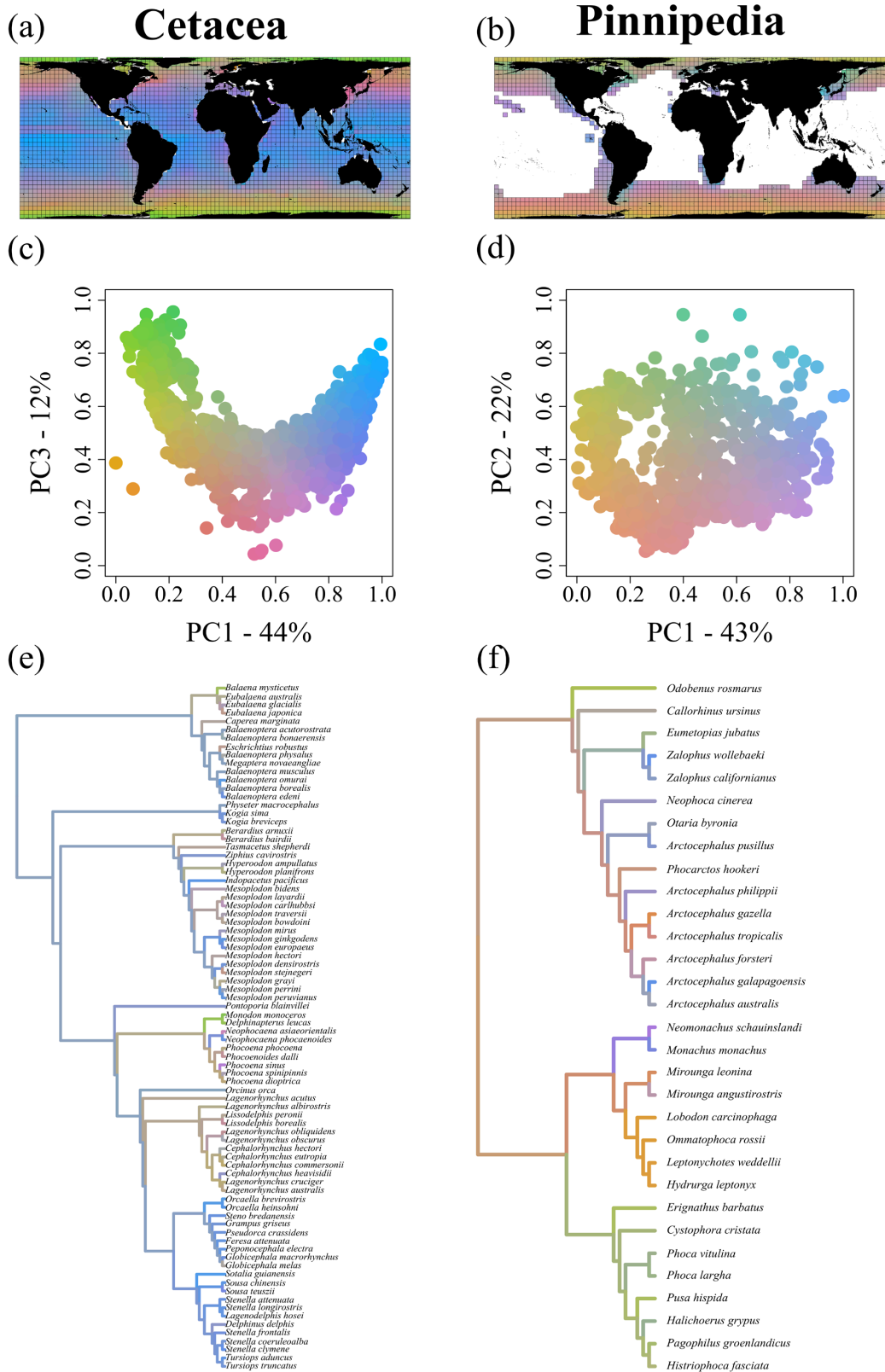


Figure 3. Environmental variation associated with cetacean (a, c, e) and pinniped (b, d, f) phylogenetic turnover. Maps (a & b) show global grid cells in Behrmann projection, coloured according to the ordinations shown in (c) and (d), which in turn show major axes of variation of environmental variation. Points in ordination spaces are coloured according to a two-dimensional colour scheme, which allows closely located points to have similar colours. Percentage values on axis labels reflect the amount of total variation explained. Branches of the phylogenetic trees (e & f) show the average colour of all grid cells occupied by their descendant species. Two grid cells in the Baltic Sea were removed from both ordinations because their low salinities resulted in extreme values that greatly reduced colour variation for the remaining grid cells.

and negatively associated with sea surface temperature range. Geographically, PC1 is negatively associated with latitude, whereas PC3 is positively associated with distance from temperate regions (Fig. 3a).

Overall, cetacean phylogenetic turnover is more strongly associated with environmental distances than random expectations (Fig. 1a_{ii}, *partial r* = 0.73, SES = 3.75, *P* < 0.001). Major subclades also show evidence of environmental phylogenetic clustering, with odontocetes being a clear example (Fig. 1a_{iii}, *partial r* = 0.72, SES = 2.98, *P* < 0.001).

Pinnipeds

Each of the first three principal components explained at least 8% of the total variance, with PC1 (explaining 43%) and PC2 (explaining 22%) showing the strongest correlations with pinniped phylogenetic turnover (*r* = 0.22 & 0.35, respectively). As with the cetacean analysis, PC1 is positively associated with sea surface temperature and negatively associated with the extent of sea ice and with nitrate concentration. By contrast, PC2 is positively associated with sea depth, and negatively associated with distance to land and surface current strength. Geographically, PC1 is negatively associated with latitude, and PC2 is negatively associated with distance from land (Fig. 3b & d).

Overall pinniped phylogenetic turnover is more strongly associated with environmental variation than random expectations (Fig. 1b_{ii}, *partial r* = 0.33, SES = 2.82, *P* = 0.008). There are no further statistically significant positive associations, but a clade of predominantly southern otariids comes close (node 5, Fig. 1b_{ii}; *partial r* = 0.46, SES = 1.88, *P* = 0.058). Two clades – otariids (*partial r* = 0.00, SES = -2.86, *P* = 0.004) and *Zalophus* (node 16, Fig. 2, *partial r* = -0.50, SES = -2.18, *P* = 0.046) – show evidence of significant environmental phylogenetic dispersion.

Discussion

The role of geographical isolation in marine mammal diversification

Generally, biogeographical patterns, as quantified by pairwise phylogenetic turnover distances across global grid cells, were not more correlated with geographical distance than expected by chance, and therefore present no overall signal of geographically-driven diversification. Nevertheless, standardised effect scores are consistent with the idea that pinnipeds are more geographically clustered than cetaceans, which in turn may reflect their fundamentally different reproductive strategy. Biogeographical patterns in both groups are significantly associated with current environmental factors, which could plausibly have erased geographical signatures of evolutionary diversification. Some clades, however, defy this trend and reveal evidence consistent with allopatric divergence.

Cetacea

Cetacean phylogenetic turnover, especially within the major subclades, tends to be geographically dispersed but environmentally clustered, suggesting a role for clade-specific environmental preferences and ecologically-driven diversification. However, some clades also show a strong geographical signal, hinting at the possibility of geographical isolation and allopatric speciation. Notable examples include lissodelphinines, porpoises, and – to a lesser degree – right whales.

Two possible interpretations of the overall Cetacean result are immediately apparent. Firstly, cetaceans may have generally diversified based on non-geographical processes. The strongest current evidence to support ecological divergence within Cetacea comes from Slater et al. (2010), who provided morphological and phylogenetic data supporting an adaptive radiation driven by the evolution of novel feeding strategies. Alternatively, post-speciation range shifts may have erased most of the evidence for geographically-driven diversification. This interpretation is consistent with the strong environmental signature within cetaceans, the time that has passed since initial diversification, and the fact that younger clades show stronger evidence of geographical clustering. Steeman et al. (2009) argued for allopatric diversification within cetaceans associated with oceanic restructuring, in particular for delphinids during the period between 13 and 4 Ma. Our results partially support this hypothesis, with strong geographical clustering evident in lissodelphinines, but not among other delphinids. If the passage of time has indeed erased signatures of geographical diversification across cetaceans, then the strong signal remaining in some clades is remarkable.

The strong geographical clustering of porpoises and lissodelphinines may be explained by their similar ecologies. Lissodelphinines are small-sized and often coastal, and at least some of them – notably, *Cephalorhynchus* – strikingly resemble porpoises in size and habitat choice (Read 2002, Galatius 2010). Both lineages seemingly achieved small size through paedomorphosis, possibly as an adaptation to localised yet highly productive and reliable coastal food sources (Galatius 2010). Small size is associated with higher rates of heat loss and a limited capacity for energy storage (Brodie 1975). As a result, small cetaceans are tied to productive environments, which in turn may reduce their dispersal ability and increase the potential for allopatric divergence (Fontaine et al. 2007).

Another factor that may have contributed to lissodelphinine and phocoenid diversification is dispersal across the usually impermeable tropics, resulting in antitropical species pairs within *Lissodelphis*, *Lagenorhynchus* (Banguera-Hinestroza et al. 2014) and porpoises (Fajardo-Mellor et al. 2006). An equatorial barrier presumably also explains the non-overlapping distributions of northern and southern right whales (*Eubalaena* spp.), as well as certain beaked whales (*Berardius* spp., *Hyperoodon* spp., and *Mesoplodon carlhubbsi* + *M. layardii*), all of which show stronger than expected geographical clustering. Likewise, separation by the tropics likely accounts for notable antitropical population structuring in humpback

(Jackson et al. 2014), fin (Archer et al. 2013), common minke (Pastene et al. 2007), and long-finned pilot whales (Davies 1963).

Finally, the geographical structuring of the clade comprising monodontids and porpoises may reflect the exclusively Arctic distribution of the former, which, however, appears to be a relatively recent (<5 Ma) phenomenon (Vélez-Juarbe and Pyenson 2012).

Pinnipedia

While overall phylogenetic turnover in pinnipeds is consistent with random expectations, it appears that – unlike with cetaceans – their initial diversification may have been influenced by geographical isolation. Both otariids and phocids are either significantly geographically clustered or close to it, as are pinnipeds as a whole. It is possible that the lack of statistical significance in this case reflects dilution of the signal through subsequent dispersal and/or alternative modes of diversification, as indicated by the lack of obvious clustering in most subclades.

Geographical divergence within otariids is supported by the fossil record: after originating in the North Pacific, possibly around 17–15 Ma (Boessenecker and Churchill 2015), the family only moved beyond this region during the late Miocene (7–6 Ma), in a major trans-equatorial dispersal that gave rise to a new Southern Hemisphere clade (Yonezawa et al. 2009, Churchill et al. 2014). Within this clade, two sister species – the Subantarctic fur seal *Arctocephalus tropicalis* and the Antarctic fur seal *A. gazella* – show evidence of significant geographical dispersion and partly overlapping distributions separated only by latitude. This situation coincides with a clear difference in breeding strategy, with Antarctic fur seals being characterised by a short lactation period fuelled by high foraging efforts, whereas Subantarctic fur seals employ a longer and less seasonal strategy (Bailleul et al. 2005).

Within phocids, there is a strong north/south basal split separating the phocine and monachine subfamilies. This pattern is, however, at least partially reflective of local extinctions, with the oldest representatives of both groups occurring together in the North Atlantic during the Early–Middle Miocene (Dewaele et al. 2017, Repenning et al. 1979). Significant evidence for clustering also exists within monk seals, even though its strength is likely to have been underestimated owing to the recent extinction of the Caribbean monk seal (*Neomonachus tropicalis*; here excluded owing to a lack of distributional data). Caribbean monk seals were closely related to Hawaiian monk seals and likely diverged from them via allopatric speciation after closure of the Panama Seaway (Scheel et al. 2014).

The strong geographical clustering of lobodontines and *Mirounga* (node 26) is likely driven solely by the antitropical distribution of the latter. This interpretation is consistent with fossil evidence for a Southern Hemisphere origin of elephant seals, based on a Late Pliocene specimen from New Zealand (Boessenecker and Churchill 2016). Otherwise, there is little evidence for allopatric divergence in either monachines or phocines. On the contrary, lobodontines, all of which

have a circumpolar Antarctic distribution, show evidence for phylogenetic dispersion, as well as clear ecological divergence. Whether this ecological variation arose before or after the diversification of the group is unresolved.

Drivers of marine mammal biogeography

Our results suggest that geographical diversification has not played a major role in the shaping modern marine mammal biogeography, with environmental factors, including sea temperature, the extent of sea ice, and nitrate concentrations being more important. Nevertheless, at least some intriguing cases of geographical divergence do seem to exist. Three geographical barriers, in particular, appear to have influenced marine mammal biogeography: (i) the tropical waters of the equator (Davies 1963); (ii) the Isthmus of Panama, which closed the Central American Seaway during the Pliocene and thus prevented gene flow between the tropical Atlantic and Pacific (O’Dea et al. 2016); and (iii) the Bering Strait, which opened during the Pliocene and formed a new northern connection between the North Atlantic and the North Pacific (Marincovich and Gladenkov 2001, Marincovich 2000).

Whereas the Isthmus of Panama and the Bering Strait relate to obvious physical barriers to oceanic dispersal, the nature of the equatorial barrier is more subtle. Thus, the tropics have been interpreted as both a physical warm-water barrier affecting cold-adapted species (Davies 1963); and as a biotic barrier related to either the high number of resident ectothermic predators like sharks (Ferguson et al. 2014) or the relatively low availability of prey (Banguera-Hinestroza et al. 2014). These ideas explain how a lack of physical barriers need not preclude geographically-driven diversification: resources like upwelling zones and breeding grounds tend to be distributed in a patchy manner and separated by vast distances, plausibly hindering interactions between populations. Similar barriers may also exist outside the marine realm and may be specific to the ecology of particular clades.

The importance of the equatorial barrier to extant marine mammal biogeography is manifest in numerous antitropical species pairs, intraspecific antitropical population structuring, and the strong geographical phylogenetic clustering of otariids. Insights from the fossil record further support its significance, e.g. in the form of a short-lived Pleistocene northern hemisphere dispersal of the enigmatic pygmy right whale (Tsai et al. 2017), or the existence of antitropical species pairs among extinct ziphiids (Bianucci et al. 2016). The same, however, does not apply to the Isthmus of Panama. Although some species pairs (e.g., monk seals) likely relate to the existence of this barrier, overall, the effects of the closure of the Central American Seaway seem counterintuitive.

Fossil distributions suggest that the marine mammal assemblages of the North Atlantic and the North Pacific remained distinct during the Miocene, when the seaway between both was open (Peredo and Uhen 2016). Parallel patterns are seen in a diverse array of other marine

taxa (Lessios 2008), again suggesting that barriers to marine dispersal can exist in the open ocean. Marked differences in North Atlantic and the North Pacific marine mammal assemblages seemingly persisted into the Pliocene, but then gradually disappeared (Boessenecker 2013a, Boessenecker 2013b). Today, the differences between the two basins are minimal for cetacean taxa, even though the seaway between them is closed (Fig. 2).

We suggest that this striking pattern might once again relate to the isolating effects of the tropics. Thus, its location close to the equator may have made the Central American Seaway difficult to reach for most marine mammals, effectively keeping Atlantic and Pacific faunas separate. This situation only changed when an alternative dispersal route via the Arctic Ocean became available during the Pliocene. As the Bering Strait opened, faunal exchange between the North Atlantic and North Pacific accelerated (Peredo and Uhen 2016), resulting in large scale range-shifts that created the modern, evenly-distributed pattern.

Areas for future study

Whereas our study provides an overview of entire taxonomic clades, future work might focus on specific cases. For example, it is surprising that almost no species pair shows significant evidence of geographical clustering, even though some of them have clearly separate distributions. This suggests that it is rare for two randomly selected marine mammal species to have overlapping distributions, and therefore that geographical separation of sister species does not by itself imply allopatric speciation. In some cases, however, species pairs are separated by well-established geographical barriers. Where this is the case, testing the strength of such barriers may prove informative.

Explicit modelling of the equatorial barrier might suggest significant geographical clustering in antitropical species pairs like *Berardius* spp., *Hyperoodon* spp. and *Mirounga* spp. Likewise, deep-water channels within the Wallacea region may be responsible for the divergence of the Irrawaddy (*Orcaella brevirostris*) and Australian snubfin (*O. heinsohni*) dolphins (Beasley et al. 2005, Beasley et al. 2002), as well as the Indo-Pacific (*Sousa chinensis*) and Australian (*S. sahalensis*) humpback dolphins (Mendez et al. 2013, Jefferson and Rosenbaum 2014). Finally, *Sousa chinensis* and the Atlantic humpback dolphin (*S. teuszii*) may have diverged across the Benguela Current (do Amaral et al. 2018, Jefferson and Van Waerebeek 2004). Future studies may benefit from examining evidence for these specific geographical barriers across and within taxa, as opposed to our more general 'isolation by distance' approach.

Our results suggest that cetaceans and phocids did not, on the whole, diversify because of geographical isolation, implying that other diversification mechanisms may have been at play. Alternatively, original geographical signatures might have been erased by bouts of subsequent dispersal, with changeable barriers such as the tropics acting as environmentally-controlled 'on/off' switches. To investigate this further, we suggest analyses based

on data for both inter- and intraspecific divergence, focusing on data-rich taxa and testing the impact of time elapsed since divergence. It may be possible to integrate fossil data into such analyses whilst maintaining our systematic approach or, alternatively, to consider the impact of past environmental conditions on the geography of fossil data.

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Supplementary Materials

The following materials are available as part of the online article from <https://escholarship.org/uc/fb>
File S1. Full analytical results.

Figure S2. Cetacean phylogeny used within our analysis.

Figure S3. Pinniped phylogeny used within our analysis.

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