

Biogeography and conservation of the pinnipeds (Carnivora:
Mammalia)

by

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Abstract

This thesis examines the biogeography of world pinnipeds, a unique group of marine mammals that have adapted to marine foraging while maintaining terrestrial (land or ice) habitat links. Comparative analyses of species range sizes controlled for phylogenetic relationships using a multi-gene supertree with divergence dates estimated using fossil calibrations. Adaptations to aquatic mating and especially sea ice parturition have influenced range size distribution, and ranges are larger than those of terrestrially mating and/or pupping species. Small range size is endangering for many taxa, and at risk pinnipeds are mainly terrestrial species with small ranges. Ancestral state reconstructions suggest that pinnipeds had a long association with sea ice, an adaptation that would have allowed early seals to expand into novel habitats and increase their distribution. Range sizes exhibit a strong Rapoport effect (positive relationship between range size and latitude) at the global scale, even after controlling for phylogeny and body size allometry. A latitudinal gradient in species diversity cannot explain the Rapoport effect for global pinniped ranges, as diversity is highest at mid-latitudes in both hemispheres. These regions are characterized by marginal ice zones and variable climates, supporting a mix of pagophilic and temperate species. The climatic variability hypothesis also did not explain the Rapoport effect. Variability is bimodal, and annual sea surface temperature (SST) variability does explain diversity patterns. Range size has a significant negative relationship with annual mean SST, and the largest ranges are found in areas with low mean SST. Temperature responses are possibly related to thermoregulation, sea ice availability, and ecological relationships with other large marine predators. These results agree with other studies and suggest that ocean temperature, and not productivity, drives

marine species richness patterns. Future research needs include studies of physiological tolerances, interactions with sharks as predators and competitors, and the role of climate and sea ice in speciation and evolution. A better understanding of distribution and diversity patterns, and the role of the environment in shaping these patterns, will improve conservation efforts, and studies on the role of SST and sea ice are particularly important given current warming trends and declines in ice extent.

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Table of Contents

Abstract	ii
Acknowledgements	iv
List of Tables	ix
List of Figures	x
Chapter 1: Introduction: Evolutionary biogeography, macroecology, and world pinnipeds	1
Introduction	1
Pinniped taxonomy and phylogeny, evolution and conservation status	1
Pinniped evolutionary biogeography	3
Biogeography and extinction risk	4
Evolutionary ecology and phylogenetic comparative methods	5
Thesis outline	6
References	9
Chapter 2: Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset	16
Abstract	16
Introduction	18
Methods	20
DNA sequence data	20
Phylogeny reconstruction and supertree analysis	22
Divergence date estimations	26

Results and Discussion	29
General structure of the supertree	29
Origins of major pinniped groups	32
Otariidae	34
Phylogeny	34
Divergence dates	37
Phocidae	39
Phylogeny	39
Divergence dates	42
Conclusions	45
References	48
Chapter 3: Aquatic mating, sea ice parturition, and the evolution of geographic range size in world pinnipeds	66
Abstract	66
Introduction	67
Methods	68
Results	72
Habitat adaptations, range size distributions, and extinction risk	72
Phylogenetically-informed analyses	74
Ancestral state reconstructions	75
Discussion	76
Habitat, dispersal, and range size evolution	76

Ancestral state reconstructions and the evolution of habitat adaptations	77
Pinniped evolutionary biogeography	82
Implications for pinniped conservation	83
Summary and conclusions	84
References	87
Chapter 4: Latitudinal variation in the geographic range size of world pinnipeds: body size, phylogeny, and the Rapoport effect	99
Abstract	99
Introduction	101
Methods	102
Results	105
Conventional (i.e., non-phylogenetically informed) analysis	105
Phylogenetically-informed analysis	106
Discussion	107
References	113
Chapter 5: Influence of climate variability on geographic range size and species diversity of world pinnipeds	122
Abstract	122
Introduction	124
Methods	125
Results	129

Description of data	129
Phylogeny and body size	130
Range size and climate	130
Species diversity and climate	131
Discussion	132
Why temperature?	133
Why not variability?	135
Implications and conclusions	137
References	139
Chapter 6: Summary, conclusions, and directions for further research	153
Introduction	153
Key findings and future research directions	153
Pinniped phylogeny	153
Pinniped taxonomy	155
Sea ice adaptations and range size evolution	156
Aquatic mating and sea ice parturition, speciation and pinniped historic biogeography	157
Latitudinal variation in pinniped range size	158
Climatic influences on pinniped species diversity and range size	160
Conclusion	162
References	164

List of Tables

Table 2.1. Indented taxonomy listing 34 pinniped taxa included in analyses.	56
Table 2.2. Genetic sequences used with their inferred models of evolution.	57
Table 2.3. Fossil calibrations used to anchor molecular date estimates.	59
Table 2.4. Divergence dates based on median relative molecular and/or one fossil date analyzed using relDate method.	60
Table 2.5. Divergence dates using Bayesian relaxed molecular clock.	62
Table 3.1. Range size related to family/clade and breeding habitat.	92
Table 3.2. Conventional and phylogenetically-informed ANOVAs and ANCOVAs of range size for mating and pupping habitats.	93
Table 4.1. Single regressions, conventional and phylogenetically-informed, testing Rapoport effect in world pinnipeds.	117
Table 4.2. Comparison of general linear models for a Rapoport effect on pinniped range size.	118
Table 5.1. Randomization tests for significance of phylogenetic signal.	144
Table 5.2. Ordinary least-squares and phylogenetic generalized least squares (PGLS) regressions of climate variability and range size.	145
Table 5.3. Species diversity and climatic variability.	146
Table 6.1. Revised otariid taxonomy from the first official list recognized by the Society for Marine Mammalogy, compared with taxonomy used here.	168

List of Figures

Figure 1.1. Distribution of risk categories among three pinniped families.	12
Figure 1.2. Biogeographic patterns of species diversity and extinction risk.	13
Figure 1.3. Risk of extinction as a function of geographic range size.	14
Figure 1.4. Comparison of conventional and phylogenetic methods.	15
Figure 2.1. Molecular supertree of the world's extant pinnipeds based on 50 maximum likelihood gene trees.	63
Figure 2.2. Molecular supertree of the world's extant pinnipeds based on 12 maximum likelihood gene trees.	64
Figure 2.3. Likelihood-based analyses of the molecular supermatrix of 50 gene trees.	65
Figure 3.1. Geographic range sizes of world pinnipeds.	94
Figure 3.2. Reconstructed ancestral states for mating substrate (water or land) and pupping substrate (ice or land).	96
Figure 3.3. Maximum-parsimony (MP) reconstruction of ancestral states for geographic range size.	98
Figure 4.1. Species diversity patterns of world pinnipeds (number of species per 5° latitudinal bin).	119

Figure 4.2. Latitudinal variation in geographic range size (the Rapoport effect) and body size (Bergmann's Rule).	120
Figure 5.1. Climate data used, showing global and latitudinal variation.	147
Figure 5.2. Relationships between climate and geographic range size.	148
Figure 5.3. Relationship between species diversity and climate.	150
Figure 5.4. Latitudinal variation in species diversity, range size, and climate.	152

Electronic Supplementary Material

Electronic Appendix 1. List of world pinniped species, with IUCN status, population size and trend, and distribution summary (Table A1.1).

Electronic Appendix 2. Genetic data for supertree/supermatix analyses, Chapter 2 (Table A2.1)

Electronic Appendix 3. Additional analyses for Chapter 4 (Tables A3.1 - A3.4, Figure A3.1)

- Rapoport effect tested using the Stevens' and midpoint methods

- Phylogenetic signal and branch length fit for independent contrasts

- The species-as-data method using maximum latitude

- References

Electronic Appendix 4. Supplementary analyses and data for Chapter 5, climatic variability hypothesis (Tables A4.1 - A4.4, Figure A4.1)

- Branch lengths and branch length fit for phylogenetic comparative analysis

- Testing the climatic variability hypothesis using latitude bins

- Pinniped climatic data summary

- References

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Permission from co-authors to include published material

As a co-author, we do hereby provide Jeffrey Wayde Higdon with permission to include the following journal article as a chapter in his PhD thesis.

Higdon, J.W., O.R.P. Bininda-Emonds, R.M.D. Beck, and S.H. Ferguson. 2007.

Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset. *BMC Evolutionary Biology* 7:216.

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Thesis format and manuscript claims

This thesis is presented in a manuscript format. Chapters 2, 3, 4, and 5 are written in manuscript style containing an Abstract, Introduction, Methods, Results and Discussion, with electronic supplementary material for three manuscripts (Chapters 2, 4, 5). Chapter 1 introduces the overall theme of the thesis and Chapter 6 synthesizes the major findings of the four manuscripts and provides direction for future research.

Chapter 2: **Higdon, J.W.**, O.R.P. Bininda-Emonds, R.M.D. Beck, and S.H. Ferguson. 2007. *Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset*. BMC Evolutionary Biology 7:216 (includes thesis Electronic Appendix A2). Jeff Higdon conceived of and coordinated the study, collected fossil data, assisted with analyses and wrote the manuscript with the guidance of the co-authors. OB-E collected data and conducted the supertree, supermatrix, and dating analyses. RB conducted the multidivtime analyses and helped draft the manuscript. All authors participated in the design of the study and helped draft the manuscript.

Chapter 3: **Higdon, J.W.**, and S.H. Ferguson. *Aquatic mating, sea ice parturition, and the evolution of geographic range size in world pinnipeds*. This manuscript in revision for submission to an evolutionary ecology journal (to be determined). Jeff Higdon collected range size data, conducted analyses, and wrote the manuscript, all with the participation and guidance of the co-author.

Chapter 4: **Higdon, J.W.**, and S.H. Ferguson. *Latitudinal variation in the geographic range size of world pinnipeds (Carnivora: Mammalia): body size, phylogeny, and the Rapoport effect*. This manuscript (and thesis Electronic Appendix A3) was accepted (pending revisions) by *Ecography* on 10 October 2010. Jeff Higdon conducted analyses and wrote the manuscript, with the participation and guidance of the co-author.

Chapter 5: **Higdon, J.W.**, and S.H. Ferguson. *Influence of climate variability on geographic range size and species diversity of world pinnipeds*. This manuscript (and thesis Electronic Appendix A4) is being revised for re-submission to *Journal of Biogeography*. Jeff Higdon conducted analyses and wrote the manuscript, with the participation and guidance of the co-author.

1. Evolutionary biogeography, macroecology, and world pinnipeds

Introduction

Species distribution patterns have long been of interest to ecologists and biologists (e.g., Wallace 1876), and the patterns are fundamental to much ecological theory (MacArthur 1972). Biogeography, the study of the spatiotemporal distribution of biodiversity, aims to determine species range patterns and the factors that influence these patterns (Brown 2000). An understanding of how and why species occur in some areas, but not in others, is critical to systematic conservation planning (Margules and Pressy 2000). Species distribution patterns can often be explained through a combination of historical factors (speciation, extinction, glaciations, etc.), in combination with geographic constraints and available energy supplies (Brown and Maurer 1989; Gaston 2003). Macroecology aims to explain patterns of abundance, distribution and diversity and particularly how climate, and climate changes, influence these patterns (Brown 2000; Gaston and Blackburn 2000). This thesis tests macroecological theories on distribution and diversity patterns using world pinnipeds (Carnivora (“Pinnipedia”), Mammalia).

Pinniped taxonomy and phylogeny, evolution and conservation status

The pinnipeds are a monophyletic group of semi-aquatic carnivores most closely related to either ursids or mustelids. Modern pinnipeds include 34-36 species (Rice 1998), with some taxonomic debate (see Electronic Appendix A1), in three extant families (plus one extinct). Over 50 fossil species have been described (Deméré et al. 2003). The family Otariidae contains 14-16 species of fur seal and sea lion (or “eared”

seals), depending on whether the three *Zalophus* taxa are treated as full species (three full species accepted by IUCN 2010). The Otariidae was traditionally divided into two monophyletic subfamilies (Arctocephalinae, nine species of fur seals; Otariinae, 5-7 species of sea lions) (e.g., King 1983). There is abundant evidence, both genetic (e.g., Davis et al. 2004; Delisle and Strobeck 2005) and morphological (Brunner 2003), of the need for revision (see Chapter 2). The family Phocidae (“true” or earless seals) contains 19 species, in two subfamilies – Phocinae (“northern phocids”, 10 species) and Monachinae (nine “southern phocids”). Phocids differ substantially from otariids in morphology, life-history, ecology, and behaviour (Reidman 1990). The family Odobenidae includes one extant species of walrus (*Odobenus rosmarus*), although the fossil record is diverse (Deméré et al. 2003). Otariidae and Odobenidae are aligned in the superfamily Otarioidea Gill, 1866, and phocids with the extinct family Desmatophocidae in the superfamily Phocoidea Smirnov, 1908.

Pinnipeds are arctoid carnivores (the infraorder Arctoidea, Flower 1869), closely related to the terrestrial carnivore families Ursidae (bears) and Mustelidae (weasels and allies). In the 1960s and 1970s many authorities supported a scenario of diphyletic origin (e.g., Reppening et al. 1979), where otariids and walruses evolved from an ursid ancestor and phocids from a mustelid ancestor. Virtually all recent studies have confirmed that pinnipeds are monophyletic (e.g., Davis et al. 2004; Delisle and Strobeck 2005; Arnason et al. 2006; Fulton and Strobeck 2006, 2010a). Pinnipeds last shared a common ancestor with other arctoid carnivores > 25 million years ago (mya) (Deméré et al. 2003; Chapter 2). Arctoid carnivore diversification occurred rapidly, and resolving relationships using both genetic and morphological methods has been difficult.

The IUCN Red List is widely recognized as the most objective, comprehensive and scientifically relevant listing of global extinction risk (Lamoreux et al. 2003). IUCN (2010) recognizes 36 pinniped species (i.e., treating the three *Zalophus* taxa as distinct species). Two species (*Z. japonicus*, Otariidae; *Monachus tropicalis*, Phocidae) are recently extinct, and 10 more are at risk (IUCN status ranks of “Critically Endangered” [two phocids], “Endangered” [four otariids and one phocid], and “Vulnerable” [two otariids and one phocid]) (Figure 1.1). Otariids are generally at greater risk of extinction than phocids (7/16 versus 5/19 extinct or at risk, also see Ferguson and Higdon 2006). Three species are ranked as “Data Deficient”, the walrus and two phocids. All depend on sea ice habitats in the Northern Hemisphere, and there is concern regarding the effects of recent and ongoing climate change, particularly sea ice declines (Laidre et al. 2008). Furthermore, data deficient species are often at risk (Purvis et al. 2000).

Pinniped evolutionary biogeography

Early hypotheses for pinniped origin, dispersal and diversification generally followed a narrative approach based on dispersalist (i.e., centre of origin) theory (reviewed by Deméré et al. 2003). Davies (1958a, b) presented the first thorough review of pinniped biogeography, and used evidence from fossils, geology and current distributions to support the Arctic Ocean as the centre of origin. Reppening et al. (1979) suggested that otariids evolved from an ursid ancestor in the North Pacific and phocids from a mustelid ancestor in the North Atlantic (assuming a diphyletic origin). In recent decades authors have been using phylogenetic relationships to develop testable hypotheses on pinniped evolutionary biogeography (e.g., Árnason et al. 2006; Fulton and Strobeck 2010b).

Deméré et al. (2003) used morphological relationships and > 50 fossil taxa and suggested an eastern North Pacific origin. However a recent fossil discovery in the Canadian Arctic (Rybczynski et al. 2009) lends support to Davies' (1958a, b) hypothesis of an Arctic origin (see Chapter 3).

Biogeography and extinction risk

Species geographic range size is closely tied to extinction risk (Gaston 1998). Small range size is a distinguishing characteristic of many imperiled species and is linked to small population size, also a significant predictor of extinction risk (Fisher and Owens 2004). Species with small range sizes are more susceptible to anthropogenic disturbance and habitat degradation (Baquero and Tellería 2001; Midgley et al. 2002), while widely distributed species are more likely to adapt and survive during climate shifts (Bennett 1997). Species risk is often non-randomly distributed, and certain areas (often tropical regions) contain a disproportionate number of endangered mammals (Gaston 2003). Each pinniped species was assigned to the biogeographic regions of Deméré et al. (2003) based on published distribution maps, including pre-exploitation distributions where applicable (see Chapter 3). Nine oceanic biogeographic regions are recognized, with Lake Baikal added (range for the continentally-restricted *Pusa sibirica*), for 10 regions in total. One additional species (*Pusa caspica*) is limited to the Caspian Sea, which is included in the Mid-Atlantic Ocean region (Deméré et al. 2003).

Species diversity per region ranges from 13 (including one historic) in the South Pacific Ocean region to one species in Lake Baikal (Figure 1.2). Pinnipeds are generally most abundant at mid-latitudes in both hemispheres, and diversity is lowest near the

Equator (Kelly 2001; see Chapters 4, 5). At risk species occur in most regions, including the Arctic, Pacific, Atlantic and Indian oceans. The three Data Deficient species are found at high latitudes in the Northern Hemisphere, in the Arctic, Atlantic, and Pacific oceans, and all depend on sea ice. Geographic range size, measured as the number of biogeographic regions, ranges from 1-4 in pinnipeds (using pre-exploitation distributions where applicable). At risk tend to have smaller ranges (Figure 1.3), with both extinct species and 8/10 at risk species limited to one region.

Evolutionary ecology and phylogenetic comparative methods

Species-level comparisons are valuable tools for determining life-history, behavioural and/or physiological differences among species that influence biogeography, habitat use, and extinction risk. For comparative analyses to be accurate and informed they must incorporate phylogenetic information. Conventional statistical analyses treat all data points (i.e., species) as independent, but species are not independent from each other due to shared ancestry, and comparative studies need to explicitly account for phylogenetic relationships. Phylogenetic comparative methods (PCMs) use information on these evolutionary relationships (phylogenetic trees) to compare species (Harvey and Pagel 1991). Conventional statistics, treating each species as independent, assume a star phylogeny, where all species descend from a common node and all branches are equal in length (Figure 1.4a). In comparison, PCMs adjust species values using a hypothesis of phylogenetic relationships (Figure 1.4b) and are necessary for studies on evolutionary ecology.

Various techniques allow analyses of character evolution across phylogenies (ancestral state reconstructions) (Pagel 1999; Lewis 2001), tests for correlated evolution in characters (Pagel 1994; Martins and Garland 1991), and to determine whether a trait contains phylogenetic signal (the tendency for related species to resemble each other) (Blomberg et al. 2003). Other methods allow the testing of ecological theories in an evolutionary framework by incorporating (or controlling for) similarities arising from common descent. Many conventional statistical tests have analogous methods that control for phylogeny, for example, see Garland et al. (1993) for ANOVA and ANCOVA methods, and Felsenstein (1985), Grafen (1989) and Garland et al. (1992) for phylogenetically independent contrasts and other generalized least-squares models.

Thesis outline

A better understanding of pinniped evolutionary biogeography and range size evolution will be instructive in establishing research and conservation priorities. Biogeographic research can help elucidate spatial processes that have determined, maintained and altered marine distributions (Briggs 2003), and this knowledge becomes increasingly valuable in the face of climate change and increased anthropogenic impacts. Biogeographic studies can assist marine conservation by improving knowledge of biogeographic distributions and the processes affecting them (Lourie and Vincent 2004). This thesis examines global-scale patterns in pinniped biogeography and macroecology and is comprised of six chapters, including this introduction (Chapter 1). Species-level comparative analyses require an accurate phylogeny, so a complete species-level pinniped phylogeny (using the taxonomy of Wilson and Reeder 1993, n = 34 species)

was created using genetic sequence data (GenBank) and supertree construction methods (Chapter 2, Higdon et al. 2007). The tree topology was then used as the phylogenetic hypothesis for all comparative analyses of biogeographic patterns.

Pinnipeds show remarkable variation in mating systems and reproductive biology, and there are fundamental life-history differences among families. The influence of different mating systems on pinniped life-history and reproductive biology has received considerable study (reviewed by Ferguson 2006), although the biogeographic implications of these adaptations have received little attention. In Chapter 3, I examine the influence of different habitat adaptations on range size evolution in pinnipeds. Species ranges (pre commercial exploitation where applicable) were mapped using GIS and compared by mating system using both conventional and phylogenetically-informed methods that controlled for body size allometry. Reconstructions of ancestral states indicate a long association with sea ice, and this has played a major role in the evolutionary ecology of the group.

Latitudinal variation in species range sizes has received considerable study (Gaston 2003), and a positive relationship between range size and latitude has been identified in a number of species groups (the Rapoport's effect, Stevens 1989). Species diversity tends to be highest at low latitudes (tropical regions), and this gradient is often used to explain the Rapoport effect. Many previous tests of latitudinal variation in range size have failed to control for two important factors, phylogeny and body size (Cruz et al. 2005; Read 2003). Body size often increases with latitude ("Bergmann's Rule) and therefore tends to have a positive relationship with range size. Pinnipeds are a

monophyletic group with a reasonably well-defined phylogeny, accurate range maps, and a wide distribution, and are thus an ideal species group for testing these ecological “rules”. I use independent contrasts (Felsenstein 1985; Garland et al. 1992) to control for phylogeny, and include body size as an explanatory variable in linear models (Chapter 4).

Stevens (1989) proposed the climatic variability hypothesis as another possible explanation of the Rapoport effect (also see Letcher and Harvey 1994; Fernandez and Vrba 2005). The hypothesis proposes that species at high latitudes are adapted to more variable climates, and can therefore exist in a wider range of environmental conditions and have larger geographic ranges. In Chapter 5, I use global sea surface temperatures to examine the influence of climatic conditions on pinniped range size and species diversity patterns. Finally, a summary of results and conclusions is presented in Chapter 6, in addition to directions for further study.

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Figure 1.1. Distribution of risk categories (IUCN 2010) among three pinniped families: Odobenidae (walrus), Otariidae (fur seals and sea lions), and Phocidae (true or earless seals). “At risk” includes status ranks “Critically Endangered”, “Endangered” and “Vulnerable”, and “Lower risk” contains the IUCN categories “Near Threatened” and “Least Concern”.

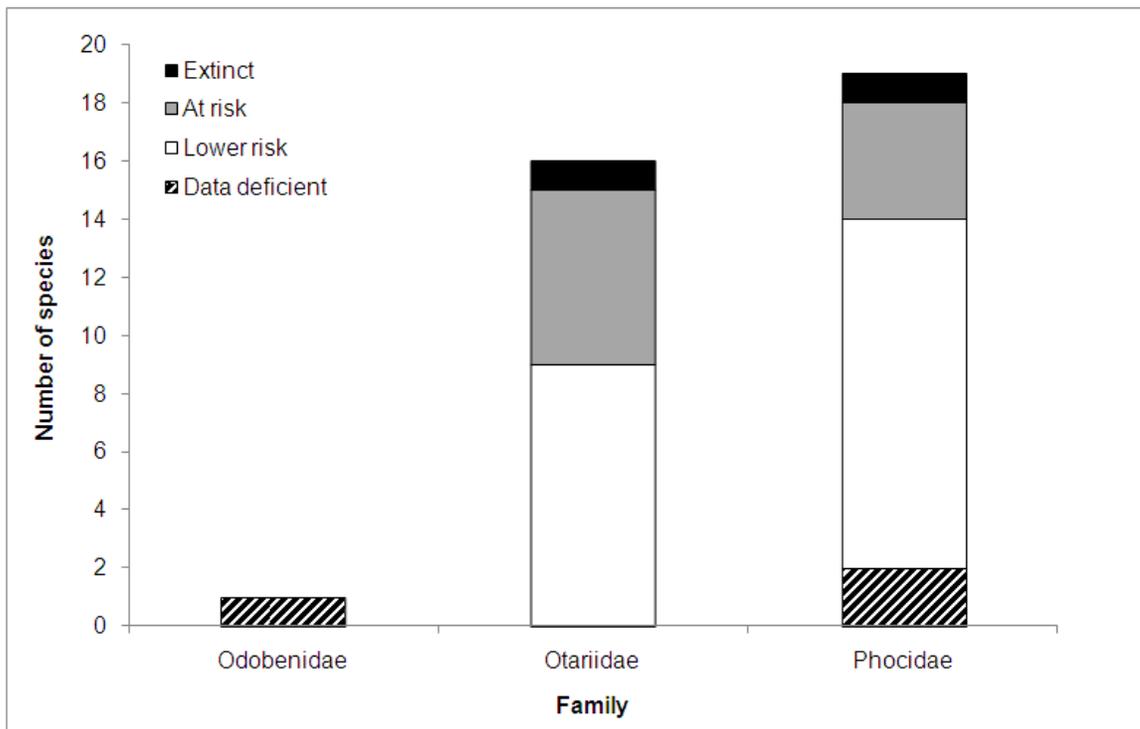


Figure 1.2. Biogeographic patterns of pinniped species diversity and extinction risk. Risk category “At risk” includes the IUCN (2010) status ranks “Critically Endangered”, “Endangered” and “Vulnerable”, and “Lower risk” contains the IUCN categories “Near Threatened” and “Least Concern”. Biogeographic regions from Deméré et al. (2003).

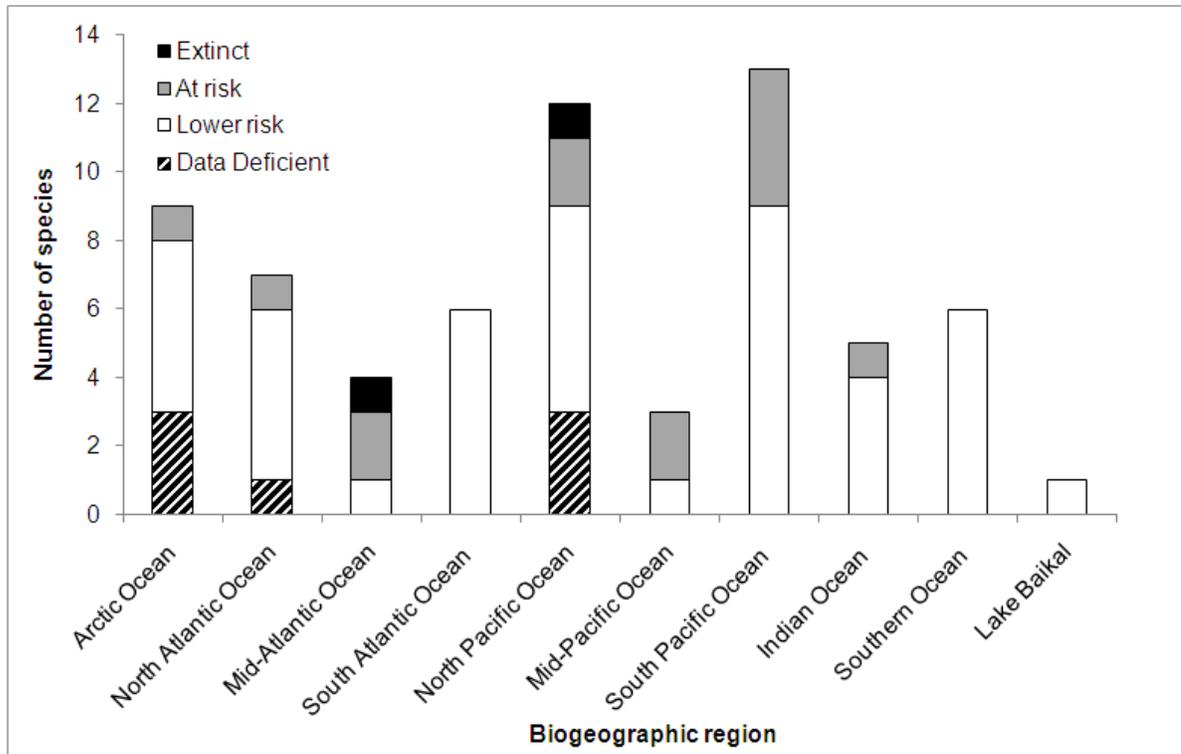
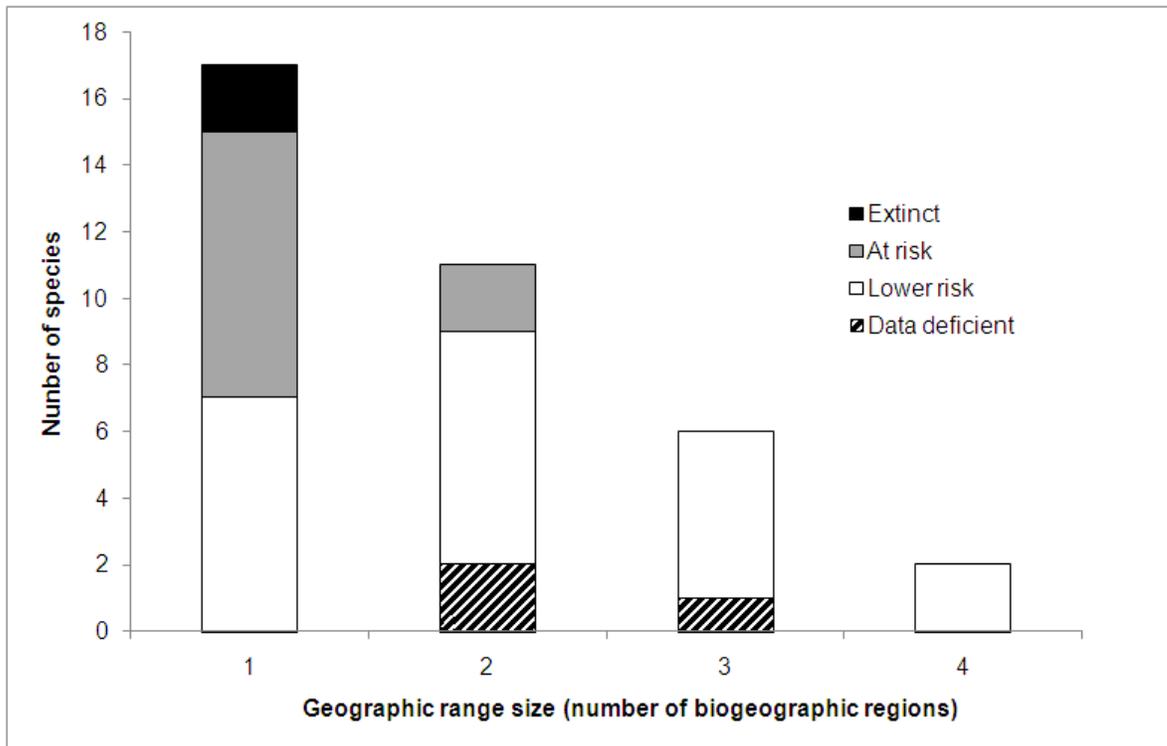


Figure 1.3. Risk of extinction among world pinnipeds ($n = 36$) as a function of geographic range size. Risk category “At risk” includes IUCN (2010) status ranks “Critically Endangered”, “Endangered” and “Vulnerable”, and “Lower risk” contains the categories “Near Threatened” and “Least Concern”. Range size measured using pre-exploitation distributions (see Chapter 2) and biogeographic regions from Deméré et al. (2003).



2: Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset

Abstract

Phylogenetic comparative methods are often improved by complete phylogenies with meaningful branch lengths (e.g., divergence dates). This chapter presents a dated molecular supertree for all 34 world pinniped species derived from a weighted matrix representation with parsimony (MRP) supertree analysis of 50 gene trees, each determined under a maximum likelihood (ML) framework. Divergence times were determined by mapping the same sequence data (plus two additional genes) on the supertree topology and calibrating the ML branch lengths against a range of fossil calibrations. Sensitivity of the supertree topology was tested in two ways: 1) a second supertree with all mtDNA genes combined into a single source tree, and 2) likelihood-based supermatrix analyses. Divergence dates were also calculated using a Bayesian relaxed molecular clock with rate autocorrelation to test the sensitivity of the supertree results further. The resulting phylogenies all agreed broadly with recent molecular studies, in particular supporting the monophyly of Phocidae, Otariidae, and the two phocid subfamilies, as well as an Odobenidae + Otariidae sister relationship; areas of disagreement were limited to four more poorly supported regions. Neither the supertree nor supermatrix analyses supported the monophyly of the two traditional otariid subfamilies, supporting suggestions for the need for taxonomic revision in this group. Phocid relationships were similar to other recent studies and deeper branches were generally well-resolved. *Halichoerus grypus* was nested within a paraphyletic *Pusa*,

although relationships within Phocina tend to be poorly supported. Divergence date estimates for the supertree were in good agreement with other studies and the available fossil record; however, the Bayesian relaxed molecular clock divergence date estimates were significantly older. These results join other recent studies and highlight the need for a re-evaluation of pinniped taxonomy, especially as regards the subfamilial classification of otariids and the generic nomenclature of Phocina. Even with the recent publication of new sequence data, the available genetic sequence information for several species, particularly those in *Arctocephalus*, remains very limited, especially for nuclear markers. Resolution of parts of the tree will probably remain difficult, even with additional data, due to apparent rapid radiations. This study addresses the lack of a recent pinniped phylogeny that includes all species and robust divergence dates for all nodes, and will prove useful for comparative and macroevolutionary studies of this group of carnivores.

Introduction

The pinnipeds are a monophyletic group of aquatic carnivores most closely related to either mustelids or ursids. The three monophyletic families – Phocidae (earless or true seals), Otariidae (sea lions and fur seals), and Odobenidae (one extant species of walrus) last shared a common ancestor within arctoid carnivores > 25 million years ago (mya) (Berta and Adam 2001; Deméré et al. 2003). Some morphological studies (Wozencraft 1989; Bininda-Emonds and Russell 1996) and virtually all molecular studies (e.g., Vrana et al. 1994; Arnason et al. 1995; Lento et al. 1995; Ledje and Arnason 1996a, b; Arnason et al. 2002, 2006; Davis et al. 2004; Delisle and Strobeck 2005; Flynn et al. 2005; Fulton and Strobeck 2006) support a link between otariids and odobenids (Otarioidea). Several morphologists prefer a phocid-odobenid clade (e.g. Wyss 1987; Wyss and Flynn 1993; Berta and Wyss; Deméré et al. 2003).

There are 34 extant species of pinniped, including *Monachus tropicalis* (which is widely believed to have gone extinct recently) and treating *Zalophus* as being monotypic (*Z. californianus*) (Table 2.1). The family Phocidae contains 19 species in two subfamilies: Monachinae or "southern" hemisphere seals (nine species comprising Antarctic, elephant, and monk seals) and Phocinae or "northern" hemisphere seals (10 species that inhabit the Arctic and sub-Arctic) (Rice 1998). Some authors have questioned the monophyly of Monachinae (Repenning and Ray 1977; de Muizon 1982; Wyss 1988), although recent studies have shown this subfamily to be monophyletic (Bininda-Emonds and Russell 1996; Bininda-Emonds et al. 1999; Davis et al. 2004; Fyler et al. 2005; Arnason et al. 2006; Fulton and Strobeck 2006). The monophyly of Phocinae has not been questioned since being established by King (1966); however, there remains

considerable debate over inter-group relationships, especially within Phocina (reviewed by Davis et al. 2004; Palo and Väinölä 2006). The family Otariidae contains 14 extant species that have been divided traditionally into the subfamilies Arctocephalinae (fur seals) and Otariinae (sea lions) (e.g. Reidman 1990; Reynolds et al. 1999). Early suggestions that this subfamilial classification might be incorrect (e.g. Reppenning and Tedford 1977) have received increasing support from recent molecular analyses (Wynen et al. 2001; Brunner 2000, 2003; Delisle and Strobeck 2005; Arnason et al. 2006; Fulton and Strobeck 2006). Taken together with a number of reports of both interspecific and intergeneric hybrids within Otariidae (e.g. Rice 1998; Goldsworthy et al. 1999; Brunner 2002), a reassessment of otariid taxonomy based on additional phylogenetic evidence is needed. Brunner (2003) provides an extensive review of the history of otariid classification. Finally, Odobenidae today comprises only the single species of walrus, *Odobenus rosmarus*.

Several recent genetic studies (Wynen et al. 2001; Davis et al. 2004; Delisle and Strobeck 2005; Fyler et al. 2005; Arnason et al. 2006; Fulton and Strobeck 2006; Palo and Väinölä 2006) have advanced our knowledge of relationships within Pinnipedia considerably. Unfortunately, many of these (the exceptions being Fyler et al. 2005; Arnason et al. 2006; Palo and Väinölä 2006) did not include divergence-date estimates as required for some types of macroevolutionary studies and phylogenetic comparative analyses. In addition, none included all species. The only study to include divergence-date estimates for all extant pinnipeds was that of Bininda-Emonds et al. (1999) as a part of a larger carnivore supertree. This tree has been used extensively in comparative studies of carnivores in general (e.g., Bininda-Emonds et al. 2001; Diniz-Filho and Tôrres 2002;

Ferguson and Larivière 2002, 2004; Larivière and Ferguson 2002, 2003; Nunn et al. 2003; Cardillo et al. 2004) and pinnipeds in particular (e.g., Bininda-Emonds and Gittleman 2000; Lindenfors et al. 2002; Schulz and Bowen 2005; Ferguson 2006; Ferguson and Higdon 2006). Despite this popularity of use, it remains that the carnivore supertree is nearly a decade old and might no longer reflect current phylogenetic opinion.

The objective of this study is to address the lack of a recent phylogenetic study that includes all extant pinniped species and to provide date estimates for all nodes. To accomplish this task, the supertree method matrix representation with parsimony (MRP, Baum 1992; Ragan 1992) was used to derive a complete phylogeny of the group from 50 gene trees (with mtDNA markers analyzed either individually or combined as a single source tree), with corresponding maximum likelihood (ML) and Bayesian (BI) analyses of the concatenated supermatrix serving as a form of topological sensitivity analysis in a global congruence framework (Lapointe et al. 1999). Divergence dates within the supertree topology were estimated using 52 genes calibrated with eight robust fossil dates using two different methods. Together, the use of a larger data set focussed exclusively on the pinnipeds should yield both a more accurate topology and divergence dates than those present in the global carnivore supertree of Bininda-Emonds et al. (1999).

Methods

DNA sequence data

The use of large, multigene data sets provides the numerous informative changes required for correct inferences, and may also help to raise weak phylogenetic signals above the noise level (Bull et al. 1993). In addition, the best topologies are often resolved

when estimates are based on a combination of mitochondrial and nuclear DNA. With these points in mind, GenBank was mined for all available pinniped DNA sequence data to infer a phylogeny based on the largest data set possible. All sequence data were downloaded on January 30, 2006 and mined using the Perl script GenBankStrip v2.0 (Bininda-Emonds 2007) to retain only those genes that had been sequenced for at least three pinniped species and were longer than 200 bp (except for tRNA genes, which had to be longer than 50 bp). For the 52 genes meeting these criteria (see Table 2.2), matching sequences for exemplars from Canidae (either *Canis lupus* or, on one occasion, *C. latrans*) and/or Ursidae (usually *Ursus arctos*, but also *U. americanus* or *U. maritimus* as needed) were downloaded for outgroup analysis.

Sequences in each data set were aligned using ClustalW (Thompson et al. 1994) or with transAlign (Bininda-Emonds 2005) in combination with ClustalW for the protein-coding sequences, and improved manually where needed. Thereafter, each aligned data set was passed through the Perl script seqCleaner v1.0.2 (Bininda-Emonds 2007) to standardize the species names, to eliminate inferior sequences (i.e., those with >5% Ns), and to ensure that all sequences overlapped pairwise by at least 100 bps (or 25 bps for the tRNA genes). Note that although species names were standardized according to Wilson and Reeder (1993) for the analyses, those used in the text for Phocini follow the currently accepted International Commission of Zoological Nomenclature (ICZN) taxonomy, which recognizes the five genera *Halichoerus*, *Histiophoca*, *Pagophilus*, *Phoca*, and *Pusa*.

The final data set of 52 genes (Table 2.2) comprises 26 818 bps in total, or an average of 515.7 bp per gene (range = 68-1980 bps). On average, each gene was sampled

for 11.2 species (range = 3-35); however, only an average of 5.5 species per nuclear gene were available for study. Two genes, *LYZ* and exon 29 of *APOB*, contained fewer than three pinniped species and, as such, were uninformative for resolving pinniped interrelationships. They were still retained to determine times of divergence. Accession numbers for all sequences used in the final data set are provided in Appendix A2 (electronic supplementary material).

The final data set was dominated by mitochondrial genes, which forms a single locus due to its common inheritance and general lack of recombination. As such, it must be kept in mind that all the resulting topologies (be they derived in a supertree or supermatrix framework) and divergence times could be biased by any peculiarities related to mitochondrial sequence data (e.g., introgression or linkage) or simply the disproportionately large amount of mitochondrial data. However, the data set represents the “current systematic database” for pinnipeds and so the best possible current data source for which to infer their phylogenetic relationships. To assess the impact of this potential source of bias, a second supertree analysis was performed where all mtDNA genes were combined to form a single source tree (yielding 12 source trees in total). Nevertheless, the collection of additional nuclear markers is desperately needed for this group.

The final data set used for the phylogenetic analyses, together with the supertree and supermatrix trees is freely available from TreeBASE (Sanderson et al. 1994; study accession number S1911, matrix accession numbers M3516-M3518).

Phylogeny reconstruction and supertree analysis

The general approach used to infer the phylogeny of the pinnipeds involved a divide-and-conquer strategy in which individual gene trees were determined using the best possible methodology for each and then combined as a supertree. Compared to a simultaneous analysis of the multigene "supermatrix", this procedure has been argued to potentially account better for the differential models of evolution that might be present (Daubin et al. 2001) and, for extremely large matrices, looks to be a faster analytical method without any appreciable loss of accuracy (Bininda-Emonds and Stamatakis 2006). Although the use of mixed models is possible in both maximum likelihood (ML, Felsenstein 1981) and Bayesian frameworks, the accuracy of the resulting tree, at least in a Bayesian framework, has recently been called into question (Mossel and Vigoda 2005), especially when reasonable levels of conflict exist between the different data partitions (Kubatko and Degnan 2007). Furthermore, Jeffroy et al. (2006) have also recently argued that trees derived from multigene, phylogenomic data sets should be treated more cautiously than those from single-gene analyses given that the systematic biases inherent to phylogeny reconstruction become more apparent with larger data sets. Nevertheless, in light of the fierce criticism that the supertree approach has attracted (e.g., Gatesy et al. 2002, 2004; but see Bininda-Emonds 2004; Bininda-Emonds et al. 2003), ML and Bayesian inference (BI) analyses of the concatenated supermatrix was also conducted to help identify especially problematic regions of the pinniped tree as part of a global congruence framework (Lapointe et al. 1999) and to add to the growing body of studies comparing phylogenetic inference under these two frameworks (e.g., Guindon and Gsacuel 2003; Fulton and Strobeck 2006).

For the supertree analyses, PHYML (Guindon and Gsacuel 2003) was used to determine the ML tree for each of the 50 phylogenetically informative genes after determining their optimal model of evolution according to either AIC or AICc (as appropriate, the latter being a version of the AIC corrected for small sample sizes) using MrAIC (Nylander 2004) and PHYML (Guindon and Gsacuel 2003) (Table 2.2). The 50 gene trees were then used to build a weighted supertree of the group using matrix representation with parsimony (MRP, Baum 1992; Ragan 1992). In so doing, it is assumed that each gene tree forms an independent unit in the preferred supertree, something that is admittedly debatable for the mitochondrial genes and especially the very small tRNA genes. In the absence of any robust linkage information, this assumption seemed more justifiable and objective than the defining of gene partitions based on assumed linkage or for purely practical considerations (e.g., concatenating all the tRNA genes because of their small size). Nonetheless, the sensitivity of these assumptions was assessed using the second supertree in which all mtDNA genes formed a single source tree.

All gene trees were encoded for the MRP analysis using semi-rooted coding (Bininda-Emonds et al. 2005), whereby only those trees with either a canid and/or ursid outgroup taxon and where the pinnipeds were reconstructed as being monophyletic were held to be rooted. Furthermore, the individual MRP characters, which correspond to a particular node on a gene tree, were weighted according to the bootstrap frequency (Felsenstein 1985) of that node, as determined using PHYML and based on 1000 replicates. This procedure has been demonstrated to increase the accuracy of MRP supertree construction in simulation (Bininda-Emonds and Sanderson 2001). The

weighted parsimony analysis of the resulting MRP matrix was accomplished using a branch-and-bound search in PAUP* v4.0b10 (Swofford 2002), with Canidae and Ursidae being specified as a paraphyletic outgroup. *Monachus tropicalis*, for which no molecular data exist, was added to the supertree manually as the sister species of *M. schauinslandii* (following Bininda-Emonds and Russell 1996; Bininda-Emonds et al. 1999).

Support for both supertrees and the relationships in them were quantified with the supertree-specific rQS index (Bininda-Emonds 2003; Price et al. 2005), which compares the topology of the supertree to that of each of the source trees contributing to it. As such, it is preferable to such conventional, character-based support measures such as Bremer support (Bremer 1988) and the bootstrap, which are invalid in this context given that MRP characters for a given source tree are non-independent. Values for rQS range from +1 to -1, with the two values indicating that a given node is directly supported or directly contradicted by all source trees, respectively. The rQS value for the entire tree is simply the average of all the nodal rQS values. Previous applications of the rQS index show that it often tends to negative values (Bininda-Emonds 2003; Price et al. 2005; Beck et al. 2006), indicating that more conflict than agreement generally exists among a set of source trees for a given node. As such, positive values of rQS can be taken to indicate good support in the sense that more source trees support the relationship than contradict it.

The individual gene data sets were also concatenated to form a single supermatrix that was analyzed using both partitioned ML and BI methods. ML analyses used RAxML VI-HPC v2.2.3 (Stamatakis 2006a). A GTR + G model was assumed for the data using the CAT approximation of the gamma distribution, with the model parameters being

allowed to vary independently for each gene. CAT is both a fast approximation of the gamma model (due to its lower computational and memory costs) and one that appears to yield better log likelihood scores even when calculated under a real gamma model (Stamatakis 2006b), and therefore is ideally suited to large, computationally intensive data matrices such as mine. The ML tree was taken to be the optimal tree over 100 replicates, for which nodal support was estimated using the bootstrap with 1000 replicates and search parameters matching those for the optimality search.

BI used MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003), with the individual models specified for each individual gene matching the optimal model determined in the gene-tree analyses as closely as possible. Otherwise, flat priors were used in all cases. Searches employed a MCMC algorithm of two separate runs, each with four chains that were run for 10 000 000 generations and with the first 5 000 000 generations being discarded as burn-in. Trees were sampled every 5000 generations to derive the final BI tree and estimates of the posterior probabilities.

Divergence date estimations

Following Bininda-Emonds et al. (Bininda-Emonds et al. 2007), divergence times on the supertree only were determined using a combination of fossil calibration points and molecular dates under the assumption of a local molecular clock (see Purvis 1995). As a first step, the optimal model of evolution for all 52 genes was (re)determined using an AIC in ModelTEST v3.6 (Posada and Crandall 1998) in combination with PAUP*, with the appropriately pruned supertree topology being used as the reference tree in place of the default NJ tree. This combination was used here in place of the previous MrAIC /

PHYML combination largely because it can be used to test for the applicability of a molecular clock (through PAUP*) using a likelihood-ratio test. The small taxonomic distribution meant that all but six genes (*CYPIA1*, *MT-ND4*, *MT-ND5*, *MT-RNR2*, *OB*, and *MT-TQ*) evolved according to a molecular clock.

Thereafter, PAUP* was used to fit the sequence data for each gene to the (pruned) supertree topology under the optimal model in a ML framework. In line with Purvis' (1995) local-clock model, the relative branch lengths for each gene tree relative to the topology of the supertree were determined using the Perl script relDate v2.2.1 (Bininda-Emonds 2007). Only the gene trees for the clock-like genes were considered to be rooted and relative branch lengths were calculated with respect to ancestral nodes only (and not also with respect to daughter nodes).

Divergence times were then determined by calibrating the relative branch lengths for each gene tree using a set of fossil dates (Table 2.3). For a given node, the initial divergence date was taken to be the maximum of 1) the median of all fossil plus molecular estimates and 2) the fossil estimate. In this way, the fossil estimate acts as a minimum age constraint that can overrule the molecular estimates. Upper and lower bounds on any given date estimates took the form of the 95% confidence interval derived from all individual gene and/or fossil estimates for that node. Although error in the branch-length estimation for the individual gene trees can also contribute to uncertainty in the final date estimates (Graur and Martin 2004), it is likely to be less important than the variation present between the different genes themselves. Together with uncertainties in the fossil dates, it cannot be excluded that the confidence intervals are underestimates of the true values.

Finally, the Perl script chronoGrapher v1.3.3 (Bininda-Emonds 2007) was used to correct for any negative branch lengths and simultaneously to derive a divergence-time estimate for the single node lacking an initial estimate (that linking *Monachus schauinslandi* and *M. tropicalis*). The date for this latter node was interpolated from the dates of up to five of its ancestral nodes based on the relative number of species descended from each node, assuming a constant birth model (see Bininda-Emonds et al. 2007).

More details regarding this dating procedure, including its strengths and weaknesses with respect to other relaxed molecular clock methods (recently reviewed in Renner 2005) can be found in Bininda-Emonds et al. (2007).

The Bayesian relaxed molecular clock method implemented by multidivtime (Thorne et al. 1998; Kishino et al. 2001) was also used to calculate divergence dates from the supermatrix data fitted to the preferred supertree topology. General methodology followed Rutschman (2005), with maximum likelihood parameters estimated using PAML version 3.15 (Yang 1997). Due to incomplete overlap of sequences between taxa the analysis was conducted on the concatenated matrix using a single F84 + gamma model. The root prior rttm (the mean of the prior distribution for the time from the ingroup root to the tips; in other words, the age of the ursid-pinniped split) was specified as 19.5 mya, with the remaining constraints the same as in the supertree dating analysis (Table 2.3). Other multidivtime parameters were calculated following the recommendations of Rutschmann (2005): rtrate (mean of prior distribution for the rate at the root node) = $X / rttm$, where X is the median amount of evolution from the root to tips; rratesd (standard deviation of rtrate) = $0.5 \times rtrate$; brownmean (mean of the prior

distribution for the autocorrelation parameter, $\nu = 1 / \text{rttm}$; brownsd (standard deviation of brownmean) = brownmean. Three independent multidivtime analyses were run for 1×10^6 cycles, with samples taken every 100 cycles after a burn-in period of 1×10^5 cycles. The dates presented here are mean values for the three runs. The multidivtime analyses were then repeated using only the mitochondrial genes to investigate whether the inclusion of nuclear genes greatly altered the estimated divergence dates.

Results and Discussion

General structure of the supertree

The preferred hypothesis of pinniped evolution is that derived from the molecular supertree with all genes analyzed individually (Figure 2.1). It agrees broadly with other recent studies (e.g., Bininda-Emonds et al. 1999; Wynen et al. 2001; Arnason et al. 2002, 2006; Davis et al. 2004; Delisle and Strobeck 2005; Flynn et al. 2005; Fyler et al. 2005; Fulton and Strobeck 2006; Palo and Väinölä 2006). In particular, the monophyly of each of Pinnipedia, Otarioidea, Phocidae, Otariidae, and the two phocid subfamilies was supported. Many of these nodes are among the most strongly supported in the supertree. The high level of congruence across numerous studies using different data sources and methodologies would suggest that higher-level pinniped relationships are well resolved. Many relationships closer to the tips of the tree, particularly those within each of *Arctocephalus* and Phocina, remain contentious.

Support values within the supertree (Table 2.4) were generally much higher than values typically reported for the supertree-specific support measure rQS (see Bininda-Emonds 2003; Price et al. 2005), with an average rQS value (\pm SD) across the tree of

0.234 ± 0.214. As such, most nodes are directly supported by a majority of the 50 source trees containing all the relevant taxa. The only exception is the node comprising *Halichoerus grypus*, *Pusa caspica* and *Pusa sibirica*, which has a slightly negative rQS value (-0.040). Even so, all more inclusive nodes possess positive rQS values, indicating that the conflict has more to do with the exact placement of *Halichoerus* within *Pusa* rather than the placement of it within this genus *per se*.

Alternative analyses of the molecular data set (supertree analysis with all mtDNA forming a single source tree or ML or BI analyses of the combined supermatrix; Figures 2.2 and 2.3, respectively) yield topologies that agree broadly with that in Figure 2.1. The rQs support measure across the supertree (0.18 ± 0.11) again showed that most nodes are directly supported by a majority of the 12 source trees containing all the relevant taxa. In all cases, the changes occur in parts of the tree with noticeably weaker support and/or branch lengths, indicating general regions of uncertainty: 1) *Neophoca cinerea* nests deeper within otariids, either as the sister taxon to *Phocarctos hookeri* (ML) or to the clade comprising the genera *Arctocephalus*, *Otaria*, and *Phocarctos* (BI), or forms the sister taxon to *Callorhinus ursinus* (supertree); 2) the formation of a sister-group relationship between *Otaria byronia* and *Arctocephalus pusillus*, which were previously adjacent to one another (all analyses); 3) the clades (*Arctocephalus townsendii* + *A. phillippi*) and (*A. gazella* + *A. tropicalis*) trade places (all analyses); and 4) changes to the internal relationships of Phocina, either with *Halichoerus grypus* and *Pusa caspica* being pulled basally with respect to the remainder of the group, with *Halichoerus* forming the sister group to the remaining species (ML), or with *Pusa hispida* and the clade of *Histriophoca fasciata* and *Pagophilus groenlandicus* nesting deeper within the group

(BI), or with *Pusa hispida* moving inside *P. sibirica* and with a polytomy at the base of Phocini (supertree).

In the supertree, nodes 1 and 2 (see Figure 2.1) represent the divergences of the canid and ursid lineages, respectively, and nodes 3 to 35 represent the various pinniped divergences. The total sample size (molecular and fossil date estimates) underlying the divergence times for each node ranged from 0 (node 35 – the split between *Monachus schauinslandi* and *M. tropicalis*, where the date was interpolated using a constant birth model) to 27 (Table 2.4). Over half (19) of the pinniped nodes were dated using at least 12 separate estimates. The remaining 14 nodes were dated by five or fewer estimates. Ten of these 14 nodes relate to otariid relationships, and seven concern *Arctocephalus* species. Divergences within the *Pusa* + *Halichoerus* clade were also dated by a comparatively small number of estimates. No obvious relationship existed between the variability in a date estimate (given by the coefficient of variation, CV) and the number of estimates it was derived from ($R^2 = 0.02$, $P = 0.4849$, $df = 26$).

The inferred relDate dates for the supertree topology (see Methods) are also significantly correlated with those for comparable nodes (which are restricted largely to Phocidae) in the two major studies to estimate divergence times within pinnipeds, those of Bininda-Emonds et al. (1999) ($R^2 = 0.52$, $P = 0.004$) and Arnason et al. (2006) ($R^2 = 0.958$, $P < 0.0001$) ($df = 12$ in both cases using ln-transformed values). Dates did not differ significantly from those of Bininda-Emonds et al. (1999) (paired- t of ln-transformed values = -1.36, $P = 0.197$; $df = 13$), but they were significantly more recent than those of Arnason et al. (2006) (paired- t of ln-transformed values = -9.82, $P < 0.0001$; $df = 13$), probably reflecting their use of a only single and more distant

calibration point (the caniform-feliform split at 52 mya) as well as topological differences between the trees and different methodologies used to derive the dates.

Both sets of multidivtime divergence dates (Table 2.5) are significantly different from the relDate divergence dates (paired-*t* of ln-transformed values = -11.39, $P < 0.0001$; $df = 32$, for relDate versus multidivtime all genes; paired-*t* of ln-transformed values = -4.53, $P < 0.0001$; $df = 32$, for relDate versus multidivtime mtDNA only). The supertree (relDate) divergence dates underestimate the multidivtime dates from all genes and mtDNA genes by 88% and 51% on average, respectively. With respect to confidence intervals (CIs), only 9 and 7 (of 33) of the relDate dates fall into the range provided by the multidivtime CIs for mtDNA or all genes, respectively. Conversely, only 3 and 4 (of 33) dates for all genes and mtDNA only, respectively, fall within the CIs of the relDate dates. It is also important to note that the two sets of multidivtime dates themselves are also significantly different from one another (paired-*t* of ln-transformed values = 2.36, $P = 0.02$; $df = 32$). In the following sections, both sets of divergence dates (i.e., the relDate and multidivtime dates) are compared with those from the fossil record and other studies.

Origins of major pinniped groups

The split between ursids and pinnipeds is estimated to be 35.7 ± 2.63 (= mean \pm SE) mya (relDate, Table 2.4; the multidivtime dates for this node were similar (Table 2.5)), although this should not be taken to imply that ursids are the closest living relatives of pinnipeds among arctoid carnivores. Early pinnipeds (pinnipedimorphs) are held to have originated in the North Pacific during the late Oligocene (34-24 mya) Wyss 1988; Berta and Sumich 1999; Deméré et al. 2003; Schulz and Bowen 2005, but see Arnason et

al. 2006, who speculate on an origin on the southern shores of North America), which is consistent with my estimate. Thereafter, a substantial lag is apparent, with the basal pinniped split between Phocidae and Otarioidea occurring some 12 million years later at 23.0 ± 1.36 mya (Table 2.4) (ca. 26 mya with multidivtime, Table 2.5). Both values are more recent than the 28.1 mya and 33.0 mya estimates obtained by Bininda-Emonds et al. (1999) and Arnason et al. (2006), respectively.

Odobenidae includes a single extant species and at least 20 fossil species in 14 genera (Deméré et al. 2003), with the most basal taxa known from the late early Miocene (ca. 21-16 mya). Deméré et al. (2003) suggest that odobenoids first evolved in the North Pacific region sometime before 18 mya (late early Miocene), and this analysis indicates the upper bound to be 20.7 mya. The multidivtime dates were similar at ca. 21 mya. Both values are substantially older than the 14.2 mya estimate obtained by Bininda-Emonds et al. (1999), but younger than the 26.0 mya estimate of Arnason et al. (2006).

Modern fur seals and sea lions are thought to have evolved from the ancestral family Enaliarctidae ca. 11 mya (Repenning 1976; Repenning et al. 1979; Miyazaki et al. 1995), with these results showing that the diversification of the crown group occurred shortly thereafter at 8.2 ± 2.09 mya (the dates estimated using multidivtime were again older, ca. 11 mya). Arnason et al. (2006) consider the late Oligocene Enaliarctinae (Mitchell and Tedford 1973) to be the oldest otarioid lineage so far described (25-27 mya; Berta 1991), but Deméré et al. (2003) consider this group to be early pinnipedimorphs that originated before the evolution of the modern crown-group pinnipeds.

The first phocid fossils date from the middle Miocene (ca. 16-14 mya) (but see Koretsky and Sanders 1997, 2002) in the North Atlantic (Barnes et al. 1985), although some authors (e.g., Costa 1993; Bininda-Emonds and Russell 1996; Deméré et al. 2003) have speculated over a North Pacific origin. Koretsky and Sanders (1997, 2002) recently described the “Oligocene seal” from the late Oligocene (ca. 28 mya) in South Carolina as the oldest known true seal, a fossil that predates my estimate for the basal-most split in all pinnipeds. Because this new description was based on a very small sample (two partial femora), and because Deméré et al. (2003) noted that its stratigraphic provenience may be in question, I instead used 23 mya as a conservative fossil calibration point for the split between Phocidae and Otarioidea. Obviously, acceptance of the “Oligocene seal” as the oldest known phocid (and therefore crown-group pinniped) would cause all divergence times within the pinnipeds to be older than those reported.

Otariidae

Phylogeny

The supertree resolved *Callorhinus ursinus* as sister to all remaining otariids (as is now generally accepted, Bininda-Emonds et al. 1999; Wynen et al. 2001; Delisle and Strobeck 2005; Flynn et al. 2005; Arnason et al. 2006), with neither the sea lions nor *Arctocephalus* forming clades. The five sea lion genera were generally positioned basally to the various *Arctocephalus* species. The exception was *Phocarcos* (and possibly *Otaria* in the supermatrix analyses), which nested within *Arctocephalus*. Wynen et al. (2001) also reconstructed *Neophoca* as being the next otariid species to diverge (contra the supermatrix results) and found *Zalophus* + *Eumetopias* to form the sister clade to the

remaining forms (*Arctocephalus*, *Otaria* and *Phocarcotos*). These results add to the already large body of evidence, both molecular and morphological, that subfamilial descriptions in Otariidae, traditionally based on the single character of presence or absence of underfur, are incorrect (Repenning et al. 1971; Lento et al. 1995; Berta and Sumich 1999; Brunner 2000, 2003; Wynen et al. 2001; Delisle and Strobeck 2005; Arnason et al. 2006; Fulton and Strobeck 2006). Resolution of most of the more inclusive otariid clades remains problematic (Wynen et al. 2001; Arnason et al. 2006; Fulton and Strobeck 2006), especially the relationships among the various *Arctocephalus* species, and the placements of the *A. australis* + *A. forsteri* + *A. galapagoensis* and *A. philippii* + *A. townsendi* clades in particular. The likelihood-based supermatrix analyses reinforce the generally weak or conflicting phylogenetic signal in the data set for otariids, with both suggesting a novel, more nested position for *Neophoca* (although the inferred location differs between the analyses).

The supertree resolved *A. forsteri* as the sister to *A. australis* + *A. galapagoensis*, with all three as sister to an *A. gazella* + *A. tropicalis* clade, an arrangement with relatively moderate support (Table 2.4). Wynen et al. (2001) found a similar result, placing *A. gazella* as sister to the *A. australis* + *A. forsteri* + *A. galapagoensis* clade, but placed *A. tropicalis* as sister to *A. pusillus* on a more basal branch separate from other arctocephaline species. These results also support a polyphyletic *Arctocephalus*, but with *A. pusillus* as the separate lineage. The separation of *A. pusillus* from other *Arctocephalus* species (and possible pairing with *Otaria* as found in both the supermatrix analyses and the combined mtDNA supertree) is perhaps not unexpected in hindsight, given that this species has long been considered as having an “enigmatic taxonomic position” due to its

similarity to sea lions in size, skull morphology, and behaviour (Stirling and Warneke 1971; Trillmich and Majluf 1981; Goldsworthy et al. 1997).

Several authors (Wynen et al. 2001; Brunner 2003) have recently questioned the status of *A. philippii* and *A. townsendi* as separate species (also see King 1954; Scheffer 1958). Brunner (2003) went so far as to suggest that both taxa be removed from *Arctocephalus* to form subspecies in the previously described genus *Arctophoca* (*Arctophoca philippii philippii* and *A. p. townsendi*, Sivertsen 1954). These results are equivocal on this latter issue, given that these two taxa do form part of the main clade of *Arctocephalus*, but as sister to the remaining species. The two taxa, however, are indicated to have diverged from one another earlier (0.3 mya; relDate date) than another pair of undisputed *Arctocephalus* species (namely *A. gazella* and *A. tropicalis* at 0.1 mya), a potential argument in favour of them retaining separate species status (regardless of the generic appellation).

The close genetic relationship found between *A. australis*, *A. forsteri* and *A. galapagoensis* (also Wynen et al. 2001) is also congruent with the morphometric results of Brunner (2003), who suggested that *A. galapagoensis* be considered a subspecies of *A. australis* (as per King 1954; Goldsworthy et al. 1997). Again, the relatively long divergence time between these two taxa (0.7 mya; relDate date) could argue against this arrangement.

Ultimately, relationships within *Arctocephalus* remain poorly resolved with little agreement between different studies or, as shown in this study, even different analyses of the same base data set. This situation will likely remain at least until additional genes for these taxa are sequenced. It should be noted that the relationships and divergence times

within *Arctocephalus* presented here are based on the only genetic marker available at the time data were extracted from GenBank (*MT-CYB* sequences, Wynen et al. 2001).

Additional genetic sequences for these species are desperately required (but see Arnason et al. 2006; Fulton and Strobeck 2006).

Divergence dates

The only recent studies to estimate divergence dates for otariids are those of Bininda-Emonds et al. (1999) and Arnason et al. (2006). Here, estimates are compared to those two studies and the available fossil record, which is unfortunately limited. The relDate estimate of 8.2 ± 2.09 mya for the root of the otariid crown-group is younger than other recent estimates (Bininda-Emonds et al. 1999; Arnason et al. 2006). The multidivtime dates (ca. 11-12 mya) agree well with Bininda-Emonds et al. (1999), but are still younger than that estimated by Arnason et al. (2006). Thereafter, a series of rapid divergences are inferred to have occurred. The origin of *Neophoca* was estimated at 6.1 mya based on *MT-CYB* only (ca. 10 mya using multidivtime), followed by the initial radiation of the remaining species at 5.2 ± 1.09 mya (ca. 9 mya using multidivtime), and the origins of *Otaria* at 4.5 ± 0.21 mya and *Arctocephalus pusillus* at 4.3 mya (the latter, again, based only on *MT-CYB*; both divergences ca. 7 mya in the multidivtime analyses).

The oldest known record for the southern hemisphere otariids is established by *Hydrarctos lomasiensis* from the late Pliocene or early Pleistocene (< 3.4 mya, de Muizon 1978; de Muizon and De Vries 1985). Fossils from California and Japan suggest that sea lions did not diversify until ca. 3 mya (Kim et al. 1975; Repenning et al. 1979; Miyazaki et al. 1995); however, only the late Pleistocene occurrences (< 0.8 mya) of

Otaria bryonia (Drehmer and Ribeiro 1998) and *Neophoca palatine* (King 1983) are considered reliable at present (Deméré et al. 2003). The date for the origin of the lineage leading to *Otaria* as a whole is naturally much older than this and almost three times older than that in Bininda-Emonds et al. (1999) (which places *Otaria* in a very different position). Arnason et al. (2006) estimated an older divergence time, but also based on a different phylogeny. *Phocarctos* is inferred to have split from the remaining *Arctocephalus* species 3.4 ± 0.34 mya. Finally, the divergence between *Eumetopias* and *Zalophus* was dated as 4.5 ± 0.37 mya, which is considerably older than the earliest known fossils (Pleistocene, 1.64-0.79 mya, Miyazaki et al. 1995), but younger than the 8 mya estimate of Arnason et al. (2006) (which is still older than the multidivtime estimate of ca. 6 mya).

The results similarly indicate a rapid radiation within *Arctocephalus*, with many species originating within the past 1 million years (both dating methods, Tables 2.4, 2.5). Overall, the date estimates showed reasonable levels of variation (relDate median CV of 27.5), although some were highly variable. For example, the split between the clades *A. gazella* + *A. tropicalis* and *A. australis* + *A. forsteri* + *A. galapagoensis* had a final date estimate of 3.1 mya but a large SE (3.43 my) and 95% confidence intervals on the input date (-2.76-10.68 mya), possibly reflecting weak signal in this area of the tree (see sensitivity analyses). Arctocephaline species are known in the fossil record only from poorly documented records of *A. pusillus* and *A. townsendi* from the Pleistocene (< 0.8 mya) (Repenning and Tedford 1977). The origin of *Arctocephalus* + *Phocarctos hookeri* was estimated here using *MT-CYB* data at 4.3 mya, which is younger than other recent estimates based on different topologies (Bininda-Emonds et al. 1999; Arnason et al.

2006). Although these results lend support to previous suggestions (Wynen et al. 2001; Deméré et al. 2003) that both sea lions and *Arctocephalus* underwent recent periods of rapid radiation, all the evidence to date tend to be based on a small dataset for most species.

Phocidae

Phylogeny

Compared to otariids, phocid relationships are generally much more agreed upon. The traditional and well-accepted phocid subfamilies Monachinae and Phocinae were both recovered as monophyletic in the supertree and supermatrix analyses (also see Bininda-Emonds and Russell 1996; Bininda-Emonds et al. 1999; Davis et al. 2004; Delisle and Strobeck 2005; Flynn et al. 2005; Arnason et al. 2006; Fulton and Strobeck 2006; Palo and Väinölä 2006). *Erignathus barbatus* was sister to the remaining northern phocids, followed by *Cystophora cristata*. The next branch of the tree separated *Pagophilus groenlandicus* and *Histriophoca fasciata* (= Histriophocina) as the sister group to the remaining taxa (but note the differences in the alternative supertree and the BI supermatrix). Most recent studies (Bininda-Emonds et al. 1999; Davis et al. 2004; Delisle and Strobeck 2005; Flynn et al. 2005; Arnason et al. 2006; Fulton and Strobeck 2006; Palo and Väinölä 2006) have found support for this arrangement among the early branches (i.e., involving the lineages *Erignathus*, *Cystophora*, and Histriophocina). Of the six *Pusa*, *Phoca*, and *Halichoerus* species (= Phocina), in the preferred tree *Pusa hispida* was found to be sister to the remaining species in which *Phoca vitulina* + *Phoca largha* formed the sister clade to (*Pusa sibirica* + (*Halichoerus* + *Pusa caspica*)) (again

note the alternative arrangements in Figures 2.2 and 2.3, indicating poor signal in this part of the pinniped phylogeny). The sister-group relationship between *Phoca vitulina* and *P. largha* recovered here in all analyses is consistent among and well supported in numerous studies based on diverse data types (Bininda-Emonds and Russell 1996; Bininda-Emonds et al. 1999; Davis et al. 2004; Delisle and Strobeck 2005; Flynn et al. 2005; Arnason et al. 2006; Fulton and Strobeck 2006; Palo and Väinölä 2006), and reflects early suggestions that the latter species represents a subspecies of the former (Scheffer 1958; Burns 1970).

Arguably the biggest outstanding problem in phocid phylogeny concerns the placement of *Halichoerus* within Phocina, and there have been long-standing suggestions (e.g., McLaren 1975) for taxonomic revision of these taxa. Both Davis et al. (2004) and Delisle and Strobeck (2005) found the strongest support for *Halichoerus* as sister to *Pusa*, with both being sister to *Phoca*. Both studies also included only *Pusa hispida* as an exemplar for *Pusa*. Fulton and Strobeck (2006) also recovered a similar result, but did not include *Pusa sibirica*. Four recent studies have included all three *Pusa* species (Bininda-Emonds and Russell 1996; Bininda-Emonds et al. 1999; Arnason et al. 2006; Palo and Väinölä 2006). Bininda-Emonds and Russell (1996) recovered *Halichoerus* as sister to *Erignathus* + *Histiophocina* + the remaining Phocina using morphological data. Bininda-Emonds et al. (1999) resolved an unresolved *Pusa* as sister to the two *Phoca* species in their supertree, with *Halichoerus* being sister to this clade. The molecular results of Arnason et al. (2006) and Palo and Väinölä (2006) were similar to those recovered here, indicating weak support for a *P. caspica* + *H. grypus* clade, and for a basal position for *P. hispida* within Phocina. Although the precise interrelationships of the species differ

slightly, these results support the suggestions of these other recent studies that both *Halichoerus* and *Pusa* be included within a redefined *Phoca*, possibly as subgenera. In fact, Arnason et al. (1995) suggested recently that the scientific name for the grey seal be *Phoca grypa*. This solution also works in light of the continuing uncertainty concerning interrelationships within Phocina (compare Figures 2.1, 2.2, and 2.3 and these with the references above), especially the increasing number of suggestions that *Pusa* might be paraphyletic (except if it were to be retained as a subgenus).

It is also noteworthy that all the relevant divergences within Phocina apparently occurred in a very short time frame (also see Arnason et al. 2006; Palo and Väinölä 2006), which might make resolution within this group difficult to obtain even with additional markers. By contrast, there were no negative branch lengths in this part of the supertree (although nodes 23 and 24 in Figure 2.1 were held to be simultaneous initially), indicating relatively good agreement among the sequence data. Also, except for node 25, all the rQS values in this part of the (preferred) tree are >0, again indicating more agreement than conflict among the set of gene trees (note the rQs values in Figure 2.2, the only negative value in the alternative supertree concerns the sister-group relations of the two *Histiophocina* species).

Within Monachinae, all analyses recovered a monophyletic *Monachus* as sister to Miroungini + Lobodontini. Relationships within *Monachus* and *Mirounga* recovered here are consistent among and well supported in numerous studies (Bininda-Emonds and Russell 1996; Bininda-Emonds et al. 1999; Davis et al. 2004; Delisle and Strobeck 2005; Flynn et al. 2005; Arnason et al. 2006; Fulton and Strobeck 2006; Palo and Väinölä 2006, but see Wyss 1988 regarding *Monachus*). Relationships within Lobodontini have

traditionally been contentious, although recent studies (Davis et al. 2004; Delisle and Strobeck 2005; Flynn et al. 2005; Arnason, et al. 2006; Fulton and Strobeck 2006) all support the sister relationship between *Leptonychotes* and *Hydrurga* recovered here (contra Bininda-Emonds and Russell 1996; Bininda-Emonds et al. 1999). The positions of *Ommatophoca* and *Lobodon* relative to each other and to the *Leptonychotes* + *Hydrurga* clade remain problematic. Many recent studies (Davis et al. 2004; Delisle and Strobeck 2005; Arnason, et al. 2006; Fulton and Strobeck 2006) found the strongest support for an (*Ommatophoca*, (*Lobodon*, (*Leptonychotes* + *Hydrurga*))) relationship. These results differed and, similar to Fyler et al. (2005), supported *Lobodon* as being sister to the remaining species. The supermatrix analyses indicated the identical sets of relationships for Monachinae.

Divergence dates

The fossil record suggests that the divergence of the two phocid subfamilies occurred sometime prior to the middle Miocene (> 14.6 mya) (Ray 1977) and 16 mya was used here as a minimum age constraint for the corresponding node (also see Bininda-Emonds et al. 1999). Similarly, Fyler et al. (2005) used 15 and 17 mya as calibration points from which to estimate divergence dates in Monachinae. The corresponding molecular estimate of Arnason et al. (2006) at 22 mya is older still and in better agreement with the multidivtime dates. The initial divergence in phocines (i.e., the lineage leading to *Erignathus*) was dated at 13.0 ± 0.90 mya, which is slightly younger than other estimates (Bininda-Emonds et al. 1999; Fyler et al. 2005; Arnason et al. 2006; Palo and Väinölä 2006) (the multidivtime dates are again older, ca. 19 mya). The relDate

dates for the origins of *Cystophora* (8.0 ± 0.42 mya) and *Histriophoca* + *Pagophilus* (6.4 ± 0.40 mya) are considerably younger than the corresponding estimates from Bininda-Emonds et al. (1999) (which are in closer agreement with the multidivtime dates), but considerably older than the available fossil evidence. Deméré et al. (2003) suggested that these basal phocines originated in the Arctic during the Pleistocene and represent the products of a glacioeustatic-forced allopatric speciation event. Arnason et al. (2006) estimated a considerably older date (12 mya) for the divergence of *Cystophora*, again in agreement with both Bininda-Emonds et al. (1999) and the multidivtime results, but a comparable 7 mya estimate for the origin of Histiophocina.

The genus *Phoca* arose 2.4 ± 0.62 mya (using relDate; multidivtime dates ca. 5-6 mya), with both extant species diverging from one another 1.1 ± 0.18 mya. These two nodes were well sampled, with 18 and 12 molecular estimates, respectively. The suggested recent separation and evolution of the two *Phoca* species (using both dating methods) is in general agreement with other studies (Scheffer 1958; Burns 1970; Bininda-Emonds et al. 1999; Arnason et al. 1996, 2006). *Pusa sibirica* arose 2.1 ± 0.21 mya, and *Halichoerus grypus* and *Pusa caspica* diverged immediately thereafter at 2.0 ± 0.14 mya; the divergence estimates for these last two nodes were each dated by only three genes apiece, and both are considerably older in the multidivtime analyses. Bininda-Emonds et al. (1999), by contrast, estimated the origin of *Halichoerus* to be 7.1 mya, although this was based on a different topology, with *Halichoerus* in a more basal position. They also dated a *Pusa* polytomy to 2.8 mya, whereas I estimate here (using relDate) that the three genera *Phoca*, *Halichoerus*, and *Pusa* all arose over a short time span ranging from 2.2 to 1.1 mya (2-6 mya using multidivtime). Palo and Väinölä (2006)

similarly estimated that the radiation of the five main Phocini mtDNA lineages occurred ca. 2.5-3.1 mya, whereas Arnason et al. (2006) estimated that the basal Phocina radiations occurred at 4.5 mya. Sasaki et al. (2003) derived considerably younger estimates for divergences within *Pusa*, although their calibration was based on an incorrect estimate of the general mammalian substitution rate (Palo and Väinölä 2006). In addition, the sister-group relationships on which their dates are based conflict with these results and those of other recent studies (Arnason et al. 2006; Palo and Väinölä 2006). Regardless of the precise relationships upon which the dates are based, the general consensus is that the diversification within Phocina was both rapid and relatively recent, which agrees with biogeographic evidence suggesting that the evolution of the *Halichoerus-Pusa-Phoca* complex likely occurred in the Greenland Sea/Barents Sea portion of the Arctic (Deméré et al. 2003), and was possibly related to the closing of the Panama Canal 3.2-2.8 mya, which resulted in the freezing over of the Arctic Ocean (Miya and Nishida 1997; Haug and Tiedemann 1998; Mercer and Roth 2003).

Among the southern phocids, most nodes (with the obvious exception of the *Monachus schauinslandi* and *M. tropicalis* split) were well sampled, with 12-21 date estimates each. The lineage leading to *Monachus* split from the remaining species 11.3 ± 0.60 mya, which is slightly younger than other recent estimates (Bininda-Emonds et al. 1999; Fyler et al. 2005) (and these other estimates are themselves slightly younger than the multidivtime dates). The relDate estimate of the origin of the lineage leading to *M. monachus* (9.9 ± 0.28 mya) is considerably older than the 4.8 mya estimate of Bininda-Emonds et al. (1999), but in good accord with those of Fyler et al. (2005) and Arnason et al. (2006). The multidivtime dates for this node are again older, ca. 15-16 mya. The split

between *M. schauinslandi* and *M. tropicalis* was interpolated to be 4.9 mya, compared to 2.8 mya estimate from Bininda-Emonds et al. (1999) (also based on interpolation from a pure-birth model).

These results indicate that the *Mirounga* lineage split from the lobodontine seals 10.0 ± 0.65 mya (ca. 15-16 mya using multidivtime), which accords well with recent genetic studies (Bininda-Emonds et al. 1999; Fyler et al. 2005; Arnason et al. 2006) and with fossil evidence indicating that the oldest fossils of southern lobodontines are from the late Miocene (6.7-5.2 mya) (de Muizon and De Vries 1985) and suggesting that the divergence occurred sometime before 11 mya (Ray 1976; Deméré et al. 2003). The relDate date for the split between the two *Mirounga* species (2.3 ± 0.85 mya) was slightly younger than that in other recent studies (Bininda-Emonds et al. 1999; Fyler et al. 2005; Arnason et al. 2006) (which were all in general agreement with the multidivtime results), but considerably older than the 0.8 mya estimate of Slade et al. (1998).

Among the four lobodontine seals, *Lobodon* diverged first at 7.1 ± 0.34 mya, followed shortly thereafter by *Ommatophoca* at 6.8 ± 0.26 mya, and finally by *Hydrurga* + *Leptonychotes* at 4.3 ± 0.55 mya. The time of origin of the lineage leading to *Lobodon* is younger than the date estimated by Fyler et al. (2005), but older than that of Arnason et al. (2006) (who also resolved a different topology). Both it and time of origin of the lineage leading to *Ommatophoca* correspond well to the dates of Bininda-Emonds et al. (1999). The divergence dates determined using multidivtime were again considerably older (Table 2.5).

Conclusions

These results add to the growing list of studies that highlight the need for a re-evaluation of pinniped taxonomy, with revisions being required for both otariids (with respect to subfamilial classification and the genus *Arctocephalus*) and phocids (within Phocina, especially as regards *Halichoerus* and *Pusa*), ideally based on additional and especially nuclear genetic markers. The divergence-date estimates herein indicate rapid radiations in both families, particularly the southern hemisphere fur seals (*Arctocephalus*) and the northern phocids (Phocina), a fact which might account for the historical difficulties in assessing the phylogenetic relationships within each group. The historically unusual, but increasingly suggested nesting of *Halichoerus* within *Pusa* (see also Arnason et al. 1995, 2006; Fulton and Strobeck 2006; Palo and Väinölä 2006) highlights both the utility of large molecular datasets with numerous genes and the value of including all relevant species in phylogenetic analysis (see also Bininda-Emonds and Russell 1996). Increased genetic sampling throughout the group will be the best approach to further improving our understanding of pinniped phylogenetics. For example, at the time data were collected, only *MT-CYB* had been sequenced for most otariid species and only a small number of genes were available for several *Pusa* species, although additional sequences have since been provided (Arnason et al. 2006; Fulton and Strobeck 2006). That being said, the problem areas within Phocina and *Arctocephalus* that were identified by both supertree and supermatrix analyses might prove resistant to resolution even with increased sampling should the apparent rapid branching in these parts of the tree be real.

Phylogenetic comparative methods have become the standard way for comparing aspects of the biology of a group of species while avoiding statistical problems associated with species not being independent due to their shared evolutionary history (Harvey and

Pagel 1991). Phylogenetic analyses are improved with appropriate reconstruction of ancestral nodes using divergence-date information (Garland et al. 1999; Polly 2001), and estimates of divergence dates provide conservation biology with a powerful tool in assessing vulnerability to conservation problems and comparative analysis of extinction risk (Fisher and Owens 2004; Isaac et al. 2007). These results will allow the use of phylogenetic comparative methods with a robust estimate of pinniped phylogeny and divergence times that includes all species.

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Table 2.1. Indented taxonomy listing the 34 pinniped taxa (including the extinct *Monachus tropicalis*) included in the analyses († indicates extinct species).

Pinnipedia		
Odobenidae		Walruses
	<i>Odobenus rosmarus</i>	Walrus
Otariidae		Sea lions and fur seals
Callorhinae		
	<i>Callorhinus ursinus</i>	Northern Fur Seal
Arctocephalinae / Otariinae		
	<i>Arctocephalus townsendi</i>	Guadalupe Fur Seal
	<i>Arctocephalus philippii</i>	Juan Fernandez Fur Seal
	<i>Arctocephalus galapagoensis</i>	Galapagos Fur Seal
	<i>Arctocephalus australis</i>	South American Fur Seal
	<i>Arctocephalus tropicalis</i>	Subantarctic Fur Seal
	<i>Arctocephalus gazella</i>	Antarctic Fur Seal
	<i>Arctocephalus forsteri</i>	New Zealand Fur Seal
	<i>Arctocephalus pusillus</i>	South African Fur Seal
	<i>Zalophus californianus</i>	California Sea Lion
	<i>Phocartos hookeri</i>	Hooker's Sea Lion
	<i>Neophoca cinerea</i>	Australian Sea Lion
	<i>Otaria byronia</i>	Southern Sea Lion
	<i>Eumetopias jubatus</i>	Northern Sea Lion
Phocidae		True seals
Monachinae		“Southern” true seals
Monachini		Monk seals
	<i>Monachus schauinslandi</i>	Hawaiian Monk Seal
	<i>Monachus tropicalis</i> †	Caribbean Monk Seal
	<i>Monachus monachus</i>	Mediterranean Monk Seal
Miroungini		Elephant seals
	<i>Mirounga angustirostris</i>	Northern Elephant Seal
	<i>Mirounga leonina</i>	Southern Elephant Seal
Lobodontini		Antarctic seals
	<i>Lobodon carcinophagus</i>	Crabeater Seal
	<i>Leptonychotes weddellii</i>	Weddell Seal
	<i>Hydrurga leptonyx</i>	Leopard Seal
	<i>Ommatophoca rossii</i>	Ross Seal
Phocinae (northern true seals)		Northern true seals
Erignathini		<no common name>
	<i>Erignathus barbatus</i>	Bearded Seal
Cystophorini		<no common name>
	<i>Cystophora cristata</i>	Hooded Seal
Phocini		<no common name>
Histriophocina		<no common name>
	<i>Histriophoca fasciata</i>	Ribbon Seal
	<i>Pagophilus groenlandicus</i>	Harp Seal
Phocina		<no common name>
	<i>Phoca largha</i>	Largha Seal
	<i>Phoca vitulina</i>	Harbor Seal
	<i>Pusa hispida</i>	Ringed Seal
	<i>Pusa sibirica</i>	Baikal Seal
	<i>Pusa caspica</i>	Caspian Seal
	<i>Halichoerus grypus</i>	Grey Seal

Table 2.2. Genetic sequences used in this study with their inferred models of evolution. Gene symbols follow Wain et al. (2002).

Gene	Number of taxa	Number of bps	Phylogeny estimation				Fitting to supertree topology				Clock In L	Chi-squared	df	LRT P-value	Clock?
			Model selected ¹	Nonclock In L	Model selected	Nonclock In L	Model selected	Nonclock In L							
<i>ALDOA</i>	7	120	K80 *	228.5901	K80	228.5901	228.98093	0.78166	5	0.9782	yes				
<i>ALDOC</i>	7	129	K3P *	213.1006	K81+I	216.4168	218.7521	4.6706	5	0.4574	yes				
<i>APOB</i> (editing region)	5	175	TVM *	317.7049	TVM+G	317.3427	319.90041	5.1154	3	0.1635	yes				
<i>APOB</i> (exon 26)	6	963	HKY	1701.6729	HKY	1701.673	1705.76283	8.1797	4	0.08521	yes				
<i>APOB</i> (exon 29) ²	3	621	n/a	n/a	TVM+G	1380.1937	1381.96031	3.5332	1	0.06015	yes				
<i>CYP1A1</i>	5	1560	HKY	2641.2015	HKY+I	2913.9797	3546.2776	1264.6	3	0	yes				
<i>CYP1A2</i>	5	1539	TVM+G	2859.5616	TVM+I	2861.4082	2863.05456	3.2927	3	0.3487	yes				
<i>H2AFZ</i>	7	52	TrNef *	95.5468	TrNef	97.6302	99.00264	2.7449	5	0.7392	yes				
<i>HLA-DOA</i>	5	399	HKY *	598.9182	HKY	598.9182	599.15301	0.46962	3	0.9255	yes				
<i>LEP</i>	5	504	GTR *	1110.6539	GTR	1110.6539	1126.3367	31.366	3	7.12E-07	yes				
<i>LYZ^b</i>	3	447	n/a	n/a	K80	677.5543	677.71442	0.32024	1	0.5715	yes				
<i>MHC-DQA1</i>	7	162	TVMef *	393.3731	TVMef	393.7065	395.79033	4.1677	5	0.5255	yes				
<i>MHC-DQA2</i>	7	230	HKY+G *	455.7005	HKY+I	458.4345	460.01745	3.1659	5	0.6744	yes				
<i>MHC-DQB1</i>	5	141	K3Puf+G *	307.2022	TVM+I	306.0257	306.25311	0.45482	3	0.9287	yes				
<i>MT-ATP6</i>	22	681	GTR+I+G *	4821.8578	TVM+I+G	4823.9243	4837.61057	27.373	20	0.1251	yes				
<i>MT-ATP8</i>	22	204	HKY+I+G *	1598.4148	TVM+I+G	1597.1221	1609.01567	23.787	20	0.2518	yes				
<i>MT-COI</i>	25	1545	GTR+I+G *	10168.6228	TVM+I+G	10171.9424	10194.06882	44.253	23	0.004901	yes				
<i>MT-CO2</i>	25	687	HKY+I+G *	4427.0054	HKY+I+G	4428.0015	4446.36885	36.735	23	0.03465	yes				
<i>MT-CO3</i>	22	784	HKY+I+G *	4896.904	TVM+I+G	4893.5391	4909.02367	30.969	20	0.0556	yes				
<i>MT-CYB</i>	35	1140	TrN+I+G *	8835.9098	GTR+I+G	8836.9434	8872.23839	70.59	33	0.0001522	yes				
<i>MT-ND1</i>	22	957	HKY+I+G *	5866.8206	TVM+I+G	5863.5283	5882.62305	38.19	20	0.008394	yes				
<i>MT-ND2</i>	24	1044	TrN+I+G *	7689.7091	TIM+I+G	7698.3613	7720.88041	45.038	22	0.002625	yes				
<i>MT-ND3</i>	22	350	HKY+G *	2365.8095	TVM+I+G	2363.5559	2374.43717	21.763	20	0.3535	yes				
<i>MT-ND4</i>	21	1378	GTR+I+G *	9587.3198	TVM+I+G	9586.7549	9609.42621	45.343	19	0.0006135	yes				
<i>MT-ND4L</i>	22	300	HKY+I+G *	1900.4839	HKY+I+G	1897.8574	1909.16103	22.607	20	0.3085	yes				
<i>MT-ND5</i>	22	1836	GTR+I+G *	13444.3742	TVM+I+G	13450.124	13482.66844	65.089	20	1.13E-06	yes				

Gene	Number of taxa	Number of bps	Phylogeny estimation		Fitting to supertree topology		Clock In L	Chi-squared	df	LRT P-value	Clock?
			Model selected ¹	Nonclock In L	Model selected	Nonclock In L					
<i>MT-ND6</i>	13	528	HKY+I+G *	2457.8525	HKY+I+G	2457.8848	2466.38674	17.004	11	0.1078	yes
<i>MT-RNR1</i>	18	984	GTR+G *	4033.2182	GTR+I+G	4033.6277	4047.13902	27.023	16	0.04123	yes
<i>MT-RNR2</i>	14	1608	GTR+I+G	5722.1966	GTR+I+G	5710.8447	5730.04437	38.399	12	0.0001321	
<i>MT-TA</i>	7	69	HKY+G *	193.586	HKY+G	192.1818	197.11463	9.8657	5	0.07913	yes
<i>MT-TC</i>	7	69	K80+G *	190.9928	K80+G	190.9817	192.76403	3.5647	5	0.6136	yes
<i>MT-TD</i>	7	68	HKY+G *	177.8663	HKY+G	177.7805	178.50213	1.4433	5	0.9195	yes
<i>MT-TE</i>	9	72	HKY+G *	205.1879	HKY+I	204.3486	208.84935	9.0015	7	0.2525	yes
<i>MT-TF</i>	7	72	TrNef *	201.267	TrN+G	197.1401	202.84986	11.42	5	0.04366	yes
<i>MT-TG</i>	7	72	TrNef+G *	269.0899	HKY+G	267.3327	271.41557	8.1657	5	0.1473	yes
<i>MT-TH</i>	7	69	HKY+G *	201.8982	HKY+G	203.5126	205.11176	3.1983	5	0.6694	yes
<i>MT-TI</i>	7	71	HKY+G *	141.7316	HKY+I	142.4105	145.12331	5.4256	5	0.3662	yes
<i>MT-TK</i>	7	70	HKY+G *	219.0096	HKY+G	221.4528	228.78366	14.662	5	0.01191	yes
<i>MT-TM</i>	7	71	K80+G *	140.5878	TrNef+I+G	135.8801	145.67015	19.58	5	0.001498	yes
<i>MT-TN</i>	7	73	K80+G *	204.0605	HKY+I	201.8885	205.49416	7.2113	5	0.2054	yes
<i>MT-TP</i>	8	68	HKY+G *	200.9591	HKY+G	202.8423	204.98693	4.2893	6	0.6376	yes
<i>MT-TQ</i>	7	76	HKY+G *	202.9076	TrN+G	203.4861	222.92371	38.875	5	2.52E-07	
<i>MT-TR</i>	8	71	HKY+G *	197.8915	K81uf+G	196.7379	201.8366	10.197	6	0.1166	yes
<i>MT-TT</i>	9	74	K80+G *	226.9842	HKY+I	224.7003	230.34978	11.299	7	0.1261	yes
<i>MT-TV</i>	8	76	K80+G *	231.1146	HKY+G	230.1562	233.04494	5.7775	6	0.4486	yes
<i>MT-TW</i>	7	68	K80+I+G *	215.6285	HKY+I+G	211.9622	218.25694	12.589	5	0.02755	yes
<i>MT-TY</i>	7	70	K80+G *	225.9578	HKY+I	222.7287	230.7563	16.055	5	0.006689	yes
<i>MXI</i>	4	1980	TrN+G	3887.1331	TrN+G	3887.1331	3892.79094	11.316	2	0.003489	yes
<i>RAG1</i>	5	741	HKY+G	1713.0793	TVM+I	1709.8627	1712.53176	5.3381	3	0.1486	yes
<i>RHO</i>	5	1077	HKY+I+G	2055.8504	HKY+I	2056.0244	2056.56021	1.0716	3	0.7839	yes
<i>SERPINA7</i>	7	442	TrNef *	869.6311	TrNef	869.631	870.82096	2.3799	5	0.7945	yes
<i>SRY</i>	21	231	HKY *	488.8158	HKY	488.3143	494.82962	13.031	19	0.837	yes
TOTAL		26818									

¹ Models followed by an asterisk were determined using AICc; all others were determined using AIC.

² *LYZ* and *APOB* (exon 29) were not used to construct the supertree

Table 2.3. Fossil calibrations used to anchor molecular date estimates. All dates (in millions of years ago) also represent minimum age constraints.

Divergence	Date	Source(s)	Node
Canids from arctoid carnivores	43.5	McKenna and Bell 1997	1
Pinniped and ursid split	19.5	Wyss and Flynn 1993	2
Split between Phocidae and Otariidae + Odobenidae	23	Deméré et al. 2003	3
Odobenoids first evolved	18	Deméré et al. 2003	4
Monachinae-Phocinae split	16	Repenning et al. 1979; de Muizon 1982; Berta and Adam 2001	18
Split between <i>Monachus</i> and other southern phocids	8	de Muizon 1982; de Muizon and De Vries 1985	28
Split between <i>Mirounga</i> + <i>Lobodontini</i>	7	de Muizon 1982; de Muizon and De Vries 1985	29
Origin of <i>Callorhinus</i>	6	Miyazaki et al. 1995	5

Table 2.4. Divergence dates for the world's pinnipeds based on the median of up to 52 relative molecular and/or one fossil date analyzed using the relDate method. Node numbers correspond to Figure 2.1. Dates and 95% confidence intervals are in millions of years ago, with the latter applying to the input dates only. Fossil dates correspond to those listed in Table 2.3 and act as constraints on the minimum divergence time for the node in question. Support values for each node, as measured by rQS (Bininda-Emonds 2003; Price et al. 2005) are also provided.

Node	rQS	Input date	Corrected date (SE)	Confidence Interval		Number of date estimates		
				Lower	Upper	Total	Molecular	Fossil
1	n/a	43.35	43.4			1	0	1
2	n/a	35.7	35.7 (2.63)	30.56	40.85	14	13	1
3	0.60	23	23 (1.36)	20.33	25.67	27	26	1
4	0.12	18	18 (1.40)	15.25	20.75	16	15	1
5	0.42	8.22	8.2 (2.09)	4.12	12.32	5	4	1
6	0.36	6.11	6.1			1	1	0
7	0.36	5.15	5.2 (1.09)	3.01	7.30	16	16	0
8	0.12	4.36	4.5 (0.21)	3.95	4.77	12	12	0
9	0.20	4.36	4.3			1	1	0
10	0.20	3.21	3.4 (0.34)	2.55	3.88	2	2	0
11	0.20	2.46	3.2			1	1	0
12	0.20	3.96	3.1(3.43)	-2.76	10.68	3	3	0
13	0.20	1.05	1.1 (0.25)	0.55	1.55	12	12	0
14	0.02	0.74	0.7			1	1	0
15	0.02	0.13	0.1			1	1	0
16	0.02	0.32	0.3			1	1	0
17	0.06	4.52	4.5 (0.37)	3.79	5.24	5	5	0
18	0.50	16	16 (0.93)	14.18	17.82	23	22	1
19	0.36	12.96	13 (0.90)	11.20	14.72	12	12	0
20	0.42	7.97	8 (0.42)	7.15	8.78	12	12	0
21	0.26	6.4	6.4 (0.40)	5.62	7.18	13	13	0
22	0.38	2.29	2.4 (0.23)	1.84	2.73	12	12	0
23	0.10	2.2	2.2 (0.62)	0.99	3.41	18	18	0
24	-0.04	2.2	2.1 (0.21)	1.79	2.61	3	3	0
25	0.00	1.99	2 (0.14)	1.71	2.27	3	3	0
26	0.12	1.07	1.1 (0.18)	0.71	1.43	12	12	0
27	0.02	4.34	4.3 (0.51)	3.35	5.33	5	5	0
28	0.22	11.33	11.3 (0.60)	10.16	12.51	15	14	1
29	0.18	9.97	10 (0.65)	8.69	11.25	21	20	1
30	0.30	7.07	7.1 (0.34)	6.41	7.73	16	16	0
31	0.06	6.81	6.8 (0.26)	6.29	7.32	17	17	0
32	0.34	4.32	4.3 (0.55)	3.24	5.39	21	21	0
33	0.32	2.28	2.3 (0.85)	0.61	3.96	21	21	0
34	0.08	9.95	9.9 (0.28)	9.40	10.49	12	12	0
35	n/a	4.9 ¹	4.9			0	0	0

¹ Interpolated date assuming a constant birth model (see Methods)

Table 2.5. Divergence dates calculated using Bayesian relaxed molecular clock method implemented by multidivtime (Thorne et al. 1998; Kishino et al. 2001) for all genes combined and for mtDNA genes only, each fitted to the preferred supertree topology (Figure 2.1).

Node	MultiDivTime dates (rttm=1.95; bigtime=4.335)							
	All genes				mtDNA genes only			
	Point estimate	1 SD	95% CI (lower)	95% CI (upper)	Point estimate	1 SD	95% CI (lower)	95% CI (upper)
1								
2	35.27	3.53	29.91	42.52	36.34	3.39	30.61	42.74
3	26.67	2.64	23.15	32.44	26.73	2.36	23.28	31.86
4	21.67	2.27	18.47	26.77	21.16	2.01	18.29	25.77
5	11.91	1.98	8.18	16.05	10.72	1.84	7.45	14.66
6	9.98	1.86	6.58	13.94	9.27	1.71	6.29	12.98
7	9.16	1.76	6.00	12.89	8.72	1.64	5.87	12.25
8	7.35	1.54	4.67	10.68	6.86	1.39	4.50	9.96
9	7.07	1.50	4.46	10.32	6.58	1.36	4.29	9.59
10	5.98	1.43	3.54	9.11	5.56	1.29	3.41	8.43
11	4.87	1.21	2.86	7.58	4.58	1.08	2.81	6.99
12	4.63	1.17	2.69	7.26	4.34	1.05	2.64	6.68
13	2.02	0.63	1.07	3.51	1.91	0.54	1.09	3.21
14	0.95	0.55	0.11	2.24	0.90	0.51	0.11	2.07
15	0.50	0.40	0.03	1.51	0.02	0.02	0.00	0.07
16	0.79	0.59	0.07	2.32	0.70	0.49	0.06	1.96
17	6.57	1.50	3.98	9.83	6.10	1.37	3.81	9.14
18	22.22	2.33	18.95	27.40	21.37	2.00	18.56	26.01
19	19.89	2.21	16.57	24.84	18.63	1.85	16.15	22.98
20	14.45	1.93	11.21	18.72	12.53	1.62	9.87	16.21
21	12.68	1.85	9.51	16.75	10.93	1.56	8.33	14.44
22	6.86	1.48	4.37	10.15	4.48	1.04	2.85	6.90
23	6.47	1.41	4.10	9.62	4.05	0.95	2.56	6.26
24	6.06	1.36	3.78	9.12	3.77	0.91	2.36	5.89
25	5.46	1.29	3.33	8.35	3.31	0.83	2.03	5.26
26	2.11	0.56	1.23	3.40	1.75	0.46	1.04	2.82
27	8.34	1.66	5.45	11.93	7.40	1.41	5.01	10.53
28	18.16	2.23	14.54	23.15	16.80	1.92	13.76	21.21
29	16.54	2.19	12.82	21.45	15.05	1.87	11.97	19.30
30	13.43	2.09	9.78	18.05	11.91	1.75	8.96	15.82
31	12.92	2.07	9.30	17.51	11.41	1.72	8.52	15.29
32	8.93	1.77	5.84	12.86	7.47	1.40	5.14	10.63
33	4.64	1.49	2.47	8.24	3.45	0.97	2.07	5.82
34	16.25	2.22	12.44	21.17	14.98	1.91	11.81	19.27
35	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Figure 2.1. Molecular supertree of the world's extant pinnipeds (plus one recently extinct *Monachus* species) based on a weighted matrix representation with parsimony analysis of 50 maximum likelihood gene trees. Node numbers correspond to divergence dates in Table 2.4. Branch lengths correspond to time with the scale bar indicating one million years. Boxed subset provides additional detail on branching order for two parts of the supertree where divergences occurred over a short timeframe.

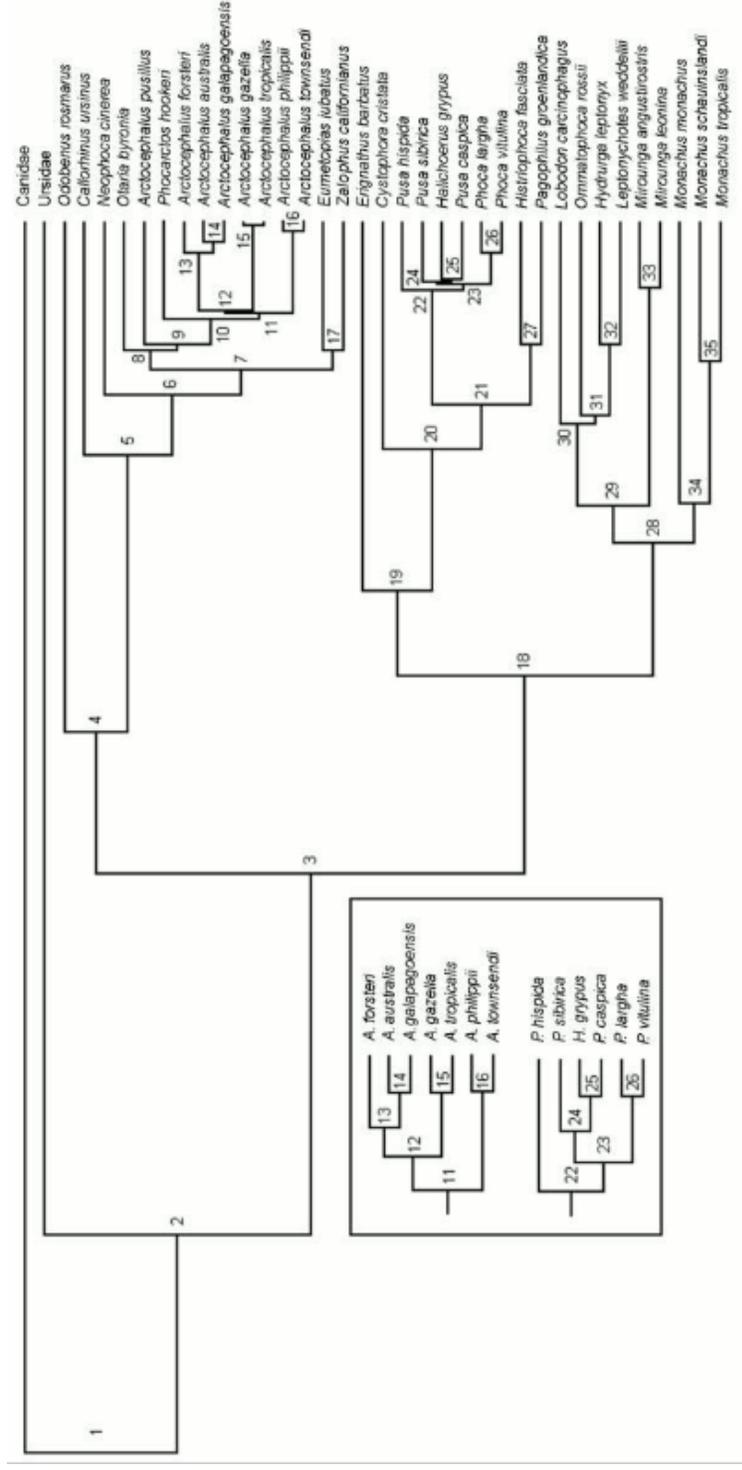
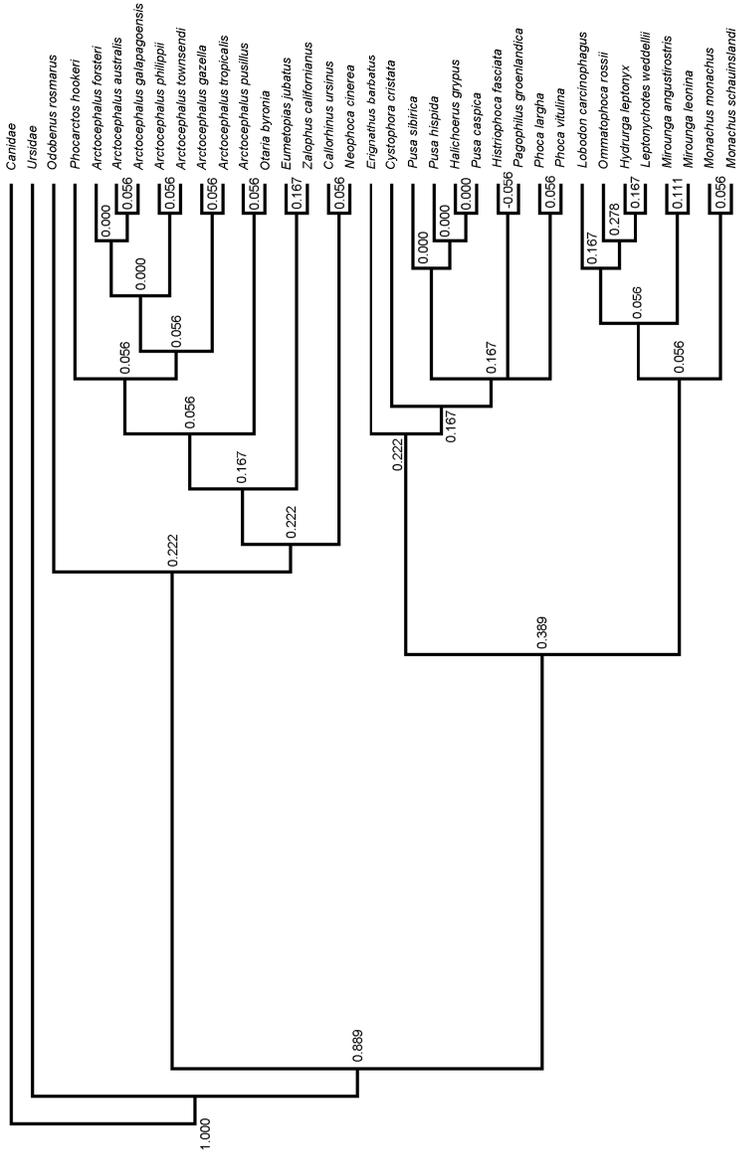


Figure 2.2. Molecular supertree of the world's extant pinnipeds (excluding the recently extinct *Monachus tropicalis*) based on a weighted matrix representation with parsimony analysis of 12 maximum likelihood gene trees, where all mtDNA genes were combined to form a single source tree. Support values for each node, as measured by rQS (Bininda-Emonds 2003; Price et al. 2005) are also provided.



3. Aquatic mating, sea ice parturition, and the evolution of geographic range size in world pinnipeds

Abstract

Knowledge of biogeographic range size patterns and extinction risk is needed for effective conservation. This study examined range sizes of world pinnipeds, a widely distributed group of marine mammals that evolved from a terrestrial ancestor to use a mix of terrestrial, sea ice, and aquatic habitats. I hypothesized that breeding adaptations to sea ice and aquatic habitats facilitated range expansion, and examined range size distributions as a function of habitat. Significant differences were found between mating and parturition substrates, with larger ranges for ice-pupping versus land-pupping species and aquatic versus terrestrially-mating species. Range-size distributions for species with sea ice-parturition and aquatic-mating were significantly left-skewed, characteristic of higher dispersal capabilities. Comparative methods that controlled for phylogeny and body-size allometry indicated that adaptations to aquatic mating and particularly sea ice parturition led to increased range sizes. Ancestral state reconstructions suggested early adaptations to sea ice and aquatic mating that arose with the initial evolution of pinnipeds. At risk species have significantly smaller range sizes and include mostly terrestrial breeders. Most current threats to pinnipeds are anthropogenic, but there is concern that sea ice declines will result in range contractions and increased extinction risk for pagophilic species.

Keywords: aquatic mating, biogeography, conservation, dispersal, distribution, extinction, evolution, parturition, phylogeny, sea ice, seals, terrestrial mating

Introduction

Many fundamental questions in biogeography and conservation biology are related to geographic range size patterns, and an understanding of these patterns is central to studies on the effects of climate and environmental change (Brown 2000; Gaston and Blackburn 2000). Range size also has a significant influence on extinction risk in extant species (McKinney 1997; Purvis et al. 2000) and species persistence throughout the fossil record (Jablonski 2008). Here I examine the evolution of species range sizes in world pinnipeds (Carnivora: Mammalia) as a function of life-history adaptations to different breeding environments and climates, and discuss the biogeographic and conservation implications of these patterns. Pinnipeds have a wide global distribution in a range of marine, estuarine and freshwater habitats. The group evolved from a terrestrial arctoid ancestor and have retained certain terrestrial traits while adapting to an aquatic lifestyle, foraging in the marine environment but remaining tied to solid habitat substrates (land or ice) for reproduction (Stirling 1983; Deméré et al. 2003). Conservation challenges in the sea are fundamentally different than on land (Norse and Crowder 2005), and pinnipeds, with their use of both marine and terrestrial environments, are a particularly interesting group for biogeographic study.

There are three extant pinniped families – Phocidae (earless or true seals, 19 species including one recently extinct), Otariidae (fur seals and sea lions, 14 species treating *Zalophus* as monotypic, Higdon et al. 2007), and Odobenidae (walrus, *Odobenus rosmarus*). Variation in breeding habitat has influenced the evolution of mating systems and the different families show significant variation (Bartholomew 1970; Stirling 1983). Otariids are among the most sexually dimorphic mammals, with gregarious breeding

females at land-based rookeries and a mating system characterized as extreme polygyny. In contrast, most phocids (and the walrus) copulate in the water, give birth on sea ice, and exhibit moderate polygyny, with breeding females more sparsely distributed. Variations on these general patterns include some phocids that mate and/or give birth on land. The influence of breeding habitat on pinniped mating systems and life-history variation has been well-researched (reviewed by Ferguson 2006); however, less attention has been paid to the biogeographic implications of adaptations to aquatic mating and sea ice parturition.

I hypothesized that adaptations for aquatic mating and sea ice parturition facilitated range expansion into novel habitats by removing the requirement for suitable terrestrial rookeries, and predicted that aquatic-mating and/or ice-pupping species would have larger geographic ranges than terrestrially breeding species, and that the effect would be most pronounced for sea ice parturition. Statistical properties of world pinniped ranges, such as skew and fit to lognormal, were used to determine range size structure relative to habitat. In particular I searched for significant left-skew as this typically characterizes species with greater dispersal capability (Macpherson 2003). Species' range sizes were compared based on mating and parturition habitats using conventional and phylogenetically-informed statistics, and ancestral state reconstructions were used to infer evolutionary adaptations to the different habitats. Relationships between habitat, range size and extinction risk (IUCN 2010) are used to discuss pinniped conservation in light of increasing anthropogenic impacts and changing climate.

Methods

Geographic ranges (area of occupancy, Gaston 1991) of world pinnipeds were digitized (ArcView 3.3) based on range maps in Riedman (1990), Jefferson et al. (1993), Perrin et al. (2002) and Nowak (2003). Range size was measured in square kilometers using a world cylindrical equal-area projection. Ranges included historic pre-exploitation range where applicable (e.g., all three *Monachus* monk seals) to remove the effects of recent human-induced range contractions (Murray and Dickman 2000; Gaston et al. 2005). Two taxa are recently extinct due to anthropogenic causes (Caribbean monk seal, *M. tropicalis*; Japanese sea lion, *Zalophus [californianus] japonicus*), and most species have suffered population declines from historic over-exploitation. Both extinct taxa were included, using the best available information on historic range. Ranges include known areas where species have been extirpated, but do not account for possible historic changes in distribution that were not directly related to anthropogenic disturbance. Ranges are the total recorded distribution of a species with no measure of seasonal variation, and for species with disjunct ranges the total range was summed. While range size is measured to the nearest square kilometre, they should not be considered accurate to this level of precision.

I first examined general patterns of the range size distribution to see how they compared to those identified for many other species groups (Gaston 2003). Two species (both aquatic mating and ice pupping phocids) are restricted to inland waters (*Pusa caspica* in the Caspian Sea, *P. sibirica* in Lake Baikal, Russia). These ‘continental endemics’ were removed from analyses of range size trends (Gaston 2003). I created normal probability plots of log-transformed range sizes, measured their skewness, and tested for departure from lognormal using Shapiro-Wilks tests. These summary statistics

provide information on relative dispersal capabilities (Macpherson 2003). I examined differences in range size between different clades (family, superfamily) and different breeding environments. Breeding was divided into two events: 'mating' is the act of copulation and occurs either in water or on land, and 'pupping' is parturition and suckling which occurs on ice or land, with data from Riedman (1990), Stirling and Thomas (2003) and Van Parjis (2003).

Some species use a combination of habitats for mating and parturition, and these were scored based on the dominant habitat category as used by most individuals. Among phocids, both *Mirounga* and *Halichoerus* typically mate on land, but a small percentage of copulations occur in water (Boness et al. 1993; Le Boeuf 1991). Elephant seals (*M. leonina*) also occasionally haul out, and have even mated, on ice (Siniff et al. 2008). Some populations/individuals of *Halichoerus* and *Phoca vitulina* pup on ice (Jüssi et al. 2008; Kovacs and Lydersen 2008; Van Parjis 2003). Otariids will occasionally copulate in shallow water near rookeries (Riedman 1990), although this is not truly aquatic mating because males still require the mechanical support provided by solid ground (Cassini 1999). All of these species were scored as terrestrial mating and/or pupping, as appropriate.

Range size is a significant predictor of extinction risk (McKinney 1997; Purvis et al. 2000), and IUCN (2010) global status ranks were used to examine relationships for pinnipeds. IUCN (2010) considers 36 pinniped species (i.e, three *Zalophus* taxa as separate species), with two extinct (*M. tropicalis* and *Z. [c.] californianus*) and 10 at risk (status ranks Critically Endangered to Vulnerable, including *Z. [c.] wollebaeki*, considered a subspecies of the Least Concern *Z. californianus* here). Geographic range

size variation was compared for at risk versus secure (Least Concern and Near Threatened ranks) species (*Zalaphus taxa*, *M. tropicalis*, three Data Deficient species, and both endemics excluded) (ANOVA).

Phylogenetically-informed analyses were conducted using a molecular supertree topology (Higdon et al. 2007) and equal (or constant) (all = 1) branch lengths (a speciation model of evolution, Martins and Garland 1991). Branch length fit diagnostics (Garland et al. 1992; Midford et al. 2008) and MSE calculations (Blomberg et al. 2003) were used to ensure the suitability of equal branch lengths. The Blomberg et al. (2003) PHYSIG_LL.M MatLab script (1000 permutations) was used to measure phylogenetic signal (the tendency for related species to resemble each other) in the range size and body mass data. Geographic range size is often positively related to body size (Gaston 2003) (see Results). I regressed range size (\log_{10}) against average adult body mass (average of adult male and adult female mass in \log_{10} grams, Ferguson and Higdon 2006) and used residuals to control for body size allometry.

Conventional and phylogenetically-informed ANOVAs and ANCOVAs were used to examine variation in range size between binary habitats, using the PDAP software package (Garland et al. 1993, 2004) and 5000 simulated data sets. Phylogenetically-informed ANOVAs are performed by simulating trait evolution on a phylogenetic tree to obtain null distributions of F statistics, allow one to test hypotheses with critical values that account for non-independence due to the specified tree topology, branch lengths, and model of character evolution (Garland et al. 1993). Pagel's (1994) correlation test, in the correl package (Midford and Maddison 2006) of MESQUITE 2.5 (Maddison and Maddison 2008a), was used to test for correlated evolution between mating and birthing

habitats. The method tests for independent or correlated evolution of two binary characters based on likelihood values for a particular combination of tree and character states (Midford and Maddison 2006).

Ancestral states for mating and pupping habitat and geographic range were reconstructed with constant branch lengths and no outgroup (i.e., root node representing the most recent common ancestor [MRCA] of crown-group pinnipeds and not early pinnipedimorphs). The ancstates module (Maddison and Maddison 2008b) for MESQUITE 2.5 was used to estimate ancestral states of habitat (discrete variables) using maximum parsimony (MP) and maximum likelihood (ML). I also used MP to reconstruct ancestral states for geographic range size (log-transformed continuous variable).

Ancestral states for range size were not reconstructed using ML as this technique is not suitable for continuous data (Maddison and Maddison 2008b). Reconstructions are presented for all 34 species, but reconstructed states with both continental endemics removed were similar.

Results

Habitat adaptations, range size distributions, and extinction risk

The histogram of range sizes was strongly right-skewed (skewness = 2.25), with most species (62%) found in the smallest range-size class (Figure 3.1a). Two-thirds (n = 22, including both continental endemics) of species have a range size less than 10% of the range size of the most wide-ranging species (*Mirounga leonina*). Phocid ranges (n = 17, excluding two endemics) are generally larger than otarioid (n = 15, superfamily Otarioidea = Otariidae + Odobenidae) or otariid (n = 14) ranges (Table 3.1). The walrus

has one of the largest ranges among the otarioids, but the pattern did not change significantly when it was excluded. While larger, phocid ranges were lognormally distributed, similar to those for otariids and otarioids (and as for all pinnipeds as a group, Figure 3.1b). There were similar range size differences for habitat comparisons, with species that mate aquatically and/or pup on sea ice having large ranges compared to terrestrial species (Table 3.1, Figure 3.1c). Eight of the ten largest ranges are found in aquatic mating and ice breeding species (seven phocids and walrus), but the largest range of all is found in *M. leonina* (Phocidae), which is the most sexually dimorphic pinniped and mates and pups on land with an ‘otariid’ mating system. Unlike the comparison for families (and superfamilies), ranges for aquatic mating and ice pupping species were significantly skewed, compared to lognormal for terrestrial mating/pupping species.

Mating and parturition habitat can be combined into three different groups – aquatic mating and sea ice pupping (water-ice), aquatic mating and terrestrial pupping (water-land), and terrestrial mating and pupping (land-land) (no terrestrially-mating species pup on ice). No otariids mate aquatically or use ice as a pupping substrate, with the walrus being the only otarioid that does, whereas the majority of phocids mate aquatically (15/17) and pup on ice (11/17) (plus both endemics). Phocidae, however, does include all three combinations (two species mate and give birth on land, five mate aquatically but give birth on land). Comparing range size distribution among the three groups (Table 3.1) suggests that sea ice adaptations have had a greater impact on range sizes than aquatic mating.

Ten pinniped taxa are at risk: four aquatic-mating phocids (two pagophilic species, including the endemic *P. caspica*), and six terrestrially-breeding otariids

(including *Z. [c.] wollebaeki*) (IUCN 2010). There are significant differences in range sizes for at risk species ($n = 8$) and secure species ($n = 19$) (ANOVA: $F(1, 25) = 4.668$, $P = 0.041$), and range sizes for secure species are on average nearly five times larger (Table 3.1) (excluding species as noted in Methods, and pre-exploitation distribution). Five pagophilic phocids have relatively small ranges: hooded (*Cystophora cristata*), spotted (*Phoca largha*) and ribbon (*Histriophoca fasciata*) seals and both continental endemics. Two are at risk (*P. caspica*; *C. cristata*, recently upgraded from Least Concern to Vulnerable, Kovacs 2008), and another two (*H. fasciata* and *P. largha*) are Data Deficient (IUCN 2010) (the pagophilic walrus is similarly ranked).

Phylogenetically-informed analyses

The Blomberg et al. (2003) test indicated significant phylogenetic signal in both geographic range size ($K = 0.537$, $P < 0.05$) and average adult body mass (\log_{10} grams) ($K = 1.016$, $P < 0.001$). The two are also significantly and positively related ($n = 32$, $R^2 = 0.161$, $F(1, 30) = 5.741$, $\beta = 0.723$, $P = 0.023$), and regression residuals ($K = 0.3751$, $P < 0.05$) were therefore used to control for body size allometry in ANOVAs and ANCOVAs. Both conventional and phylogenetically-informed ANOVAs indicated significant habitat-related differences in residual range size (Table 3.2). Pagel's (1994) test indicated a significant correlation ($P = 0.012$) between the evolution of mating and birthing habitat adaptations, and ANCOVA models again indicated that pupping habitat adaptations (i.e., sea ice parturition) had a much greater impact on the evolution of large range sizes than mating habitat (Table 3.2).

Ancestral state reconstructions

For ML reconstruction of ancestral states of mating and pupping habitat (Figure 3.2) the one-rate Mk1 model was significantly ($P < 0.05$) better than the asymmetrical two-rate model. The reconstruction of mating environment suggested that aquatic mating was the most likely ancestral state (probability 0.95, $P < 0.05$, estimated rate = 0.0533, negative log-likelihood = 12.5907). All node reconstructions were significantly supported ($P < 0.05$), and MP reconstruction also unequivocally returned aquatic mating as the ancestral state (three steps for most parsimonious solution, no equivocal nodes). Results were the same (all still significant) when both aquatic-mating endemics were excluded.

Reconstructions for birthing habitat were much less certain, but ice was the reconstructed ancestral substrate (probability 0.65, $P > 0.05$, estimated rate = 0.0967, negative log-likelihood = 16.6222). Under MP (five steps) the ancestral state was equivocal for the root node plus four others (Figure 3.2). For three, ML probabilities were higher for ice, but all non-significant ($P > 0.05$): the pinniped most recent common ancestor (MRCA) as noted above, the otarioid MRCA (0.63), and the phocid MRCA (0.67). The two other equivocal nodes had highest ML support for terrestrial pupping (non-significant): the MRCA for the southern phocids (0.65) and the MRCA for the Mirounga-Lobodontini clade (0.62). Results are similar for these nodes (i.e., still uncertain) if ancestral states are reconstructed on trees pruned to exclude both continental endemics or with otarioids or phocids only.

Reconstructed ancestral states (MP) for geographic range size ($\log_{10} \text{ km}^2$) are shown in Figure 3.3 (squared length for reconstruction = 8.1267). The reconstructed range size for the root node (MRCA of crown-group pinnipeds) was relatively large

(greater than the range of 23 extant species). Among otariids, only two species (*Callorhinus ursinus* and *Arctocephalus gazella*) have ranges larger than the reconstructed root value (plus walrus, i.e., 3/15 otarioids). Eight of 19 extant phocids have a large range in relation to the reconstructed MRCA. Seven of these species mate aquatically and pup on sea ice, with the terrestrially mating *M. leonina* (largest range of all extant species) the only exception. Speciation events resulted in both increases and decreases in range sizes (Figure 3.3), although the positive associations between habitat adaptations and larger ranges was maintained throughout the evolution of the group (Mann-Whitney U-tests – mating habitat: $U_A = 828$, $Z = -3.39$, $P \leq 0.001$; pupping habitat (including five equivocal nodes): $U_A = 255$, $Z = 3.69$, $P = \leq 0.001$; equivocal nodes excluded: $U_A = 216$, $Z = 3.53$, $P \leq 0.001$).

Discussion

Habitat, dispersal, and range size evolution

Left-skewed distributions of log-transformed range sizes are characteristic of taxa with higher dispersal capabilities that occupy larger ranges, while lognormal distributions are predominant for taxa which are less capable of dispersal and occupy smaller range areas (Macpherson 2003). As a group, and among families/superfamilies, pinniped range size distribution is lognormal; however, the habitat comparisons allow examination of relative dispersal capabilities. Ranges for ice pupping and aquatic-mating species are significantly left skewed, whereas those of the terrestrial species remain lognormal. Otariids (and some phocids) with restrictions to suitable land habitats for mating and/or parturition generally have reduced geographic ranges in relation to aquatic mating and ice

pupping phocids. Furthermore, range sizes are smaller for species at greater risk of extinction.

Relationships between habitat adaptations and geographic range size are maintained after controlling for phylogenetic relationships, body size allometry, and co-evolutionary relationships between aquatic mating and sea ice parturition and range size. Mating and pupping habitat adaptations are correlated, but sea ice parturition had a greater effect on range expansions – aquatic-mating phocids that pup on ice have much larger ranges than those that pup on land. Aquatic mating alone would provide little dispersal benefit if females were forced to return to limited terrestrial rookeries to give birth. Life-history adaptations (e.g., high-fat milk, short lactation periods) (Bartholomew 1970; Burns 1970) to novel and unpredictable sea-ice environments would have favoured habitat specialization and dispersal into new areas, and possibly facilitated speciation (c.f. Coyne and Orr 2004; Dieckmann et al. 2004).

Many endangered pinnipeds have suffered range contractions, and the differences in range size between at risk species and those currently deemed secure are even more pronounced than shown here (i.e., because pre-exploitation ranges were used). Small range size is a consistent predictor of species persistence at multiple temporal scales (Purvis et al. 2000; Jablonski 2008), and often correlates with small population size, habitat specificity and intolerance to climatic and environmental variation (Stevens 1989; McKinney 1997). All of these factors, coupled with large body size (Cardillo et al. 2005), may contribute to an increased level of background risk for these species, with extinction probability increased through adverse anthropogenic effects.

Range maps are often imprecise (Gaston 2003), which can lead to bias and uncertainty in biogeographic studies. In contrast, pinniped ranges are well documented compared to most marine species groups, and the pinniped range size data are accurate for species-level comparisons at a global scale. Both endemic phocids are aquatic mating/ice pupping species, and their inclusion has a significant effect on the ANOVA for mating habitat (no significant difference, results not shown but available on request). For pupping habitat, the significant differences are maintained even when these species are included.

Ancestral state reconstructions and the evolution of habitat adaptations

Both ML and MP reconstructions strongly support aquatic mating as the ancestral state for crown-group pinnipeds. This is opposite to the generally hypothesized evolutionary pathway (e.g., Bonner 1984), i.e., ancestral evolution of a harem-based terrestrial mating system followed by aquatic mating adaptations. Early pinnipedimorphs evolved from a terrestrial arctoid ancestor, and the earliest stem “pinnipeds” were terrestrial. Reconstructions suggest that aquatic mating was a very early adaptation that occurred with the lineage leading to all modern species, and these initial adaptations may have been a major driving force in early pinniped evolution. Three transitions to terrestrial mating were reconstructed, first with the otariid MRCA, which was also characterized by a possible (but uncertain) shift from ice to land for parturition and a reconstructed contraction in geographic range. The other two transitions to terrestrial mating (origin of *Halichoerus* and *Mirounga*) resulted in increased range sizes.

Reconstructions for parturition habitat are less certain. The ancestral state for the pinniped MRCA was equivocal, but ice received the most ML-support. Modern pinnipeds originated during the Oligocene (Deméré et al. 2003; Higdon et al. 2007), corresponding with a major climatic episode at the Eocene–Oligocene transition ca. 33.5 mya when the global climate shifted from a ‘greenhouse’ to an ‘icehouse’ world (Zachos et al. 2001; Liu et al. 2009). While uncertain, sea ice adaptations likely influenced early pinniped divergences. The possibility of early adaptation to sea ice is intriguing as it is contrary to general interpretations of terrestrial pupping as ancestral, even for phocids (e.g. Bonner 1984).

The common ancestor to the northern phocids (ca. 13 mya, Higdon et al. 2007) was reconstructed as ice-adapted, with high support (ML probability 0.97, $P < 0.05$), and with a range expansion relative to the parent node. Sea ice parturition has been regarded as the most parsimonious ancestral condition of the Phocinae (Perry et al. 1995), and it may have evolved even earlier in the modern pinniped lineage (also see Fulton and Strobeck 2010a). Significant perennial ice cover in the Northern Hemisphere started 14–13 mya (Darby 2008; Krylov et al. 2008), and adaptations to ice habitats would have allowed ancestral northern phocids to expand into new areas with increasing ice cover. The presence and extent of sea ice has significantly varied throughout geologic time (Lear et al. 2004) and likely played a substantial role in phocid speciation events (Davies 1958a, b; Déméré et al. 2003). Two reconstructed transitions from ice to terrestrial parturition occurred among the northern phocids, with the origin of *H. grypus* and *Phoca vitulina* (both also occasionally pup on ice).

Phylogenetic uncertainty with respect to the placement of *Halichoerus* should be noted. The supertree (Higdon et al. 2007) nested *H. grypus* within a paraphyletic *Pusa*, but Fulton and Strobeck (2010b) recently used a large dataset including 15 nuclear genes and recovered strong support for a monophyletic *Pusa*. Accurate placement of *Halichoerus* is of particular interest given the reconstructed transitions to terrestrial mating and parturition for most individuals, coupled with the population-level variation in habitat substrates. This temperate North Atlantic species is the most flexible pinniped in terms of habitat (Kovacs and Lydersen 2008) and is the only species that gives birth at terrestrial colonies and on both pack-ice and fast-ice (but mostly terrestrial, as scored here). There is concern for some ice-breeding populations (Jüssi et al. 2008), but Kovacs and Lydersen (2008) predict a continued overall population increase and range expansion in coming decades. In fact, *Halichoerus* may expand northward and compete with endemic Arctic species (Moore and Huntington 2008), although Ferguson and Higdon (2006) considered *Halichoerus* life-history traits and environmental conditions as suggestive of a vulnerable species and recommended a cautious management approach. Given this ambiguity, *Halichoerus* may represent an important model species for predicting climate change impacts on phocids. Phylogenetic uncertainty among otariid relationships (Higdon et al. 2007) is likely less of a bias given that all species use terrestrial habitats.

Reconstructed pupping habitat for the southern phocid MRCA was also uncertain, but a switch from ice to land receives the most ML support (probability 0.65), with an accompanying decrease in range size. Despite the uncertainty, a shift in parturition habitat must have occurred among southern phocids given the differences among extant

species and the well-accepted relationships among clades. Assuming early adaptations to sea ice, southern dispersal events would have resulted in a secondary adaptation to terrestrial habitats in ice free zones. The monk seals (*Monachus*) adapted to terrestrial parturition while maintaining the ancestral aquatic mating strategy. The ML reconstruction for the *Mirounga*-Lobodontini MRCA was terrestrial parturition (again uncertain), which transitioned to sea ice parturition ($P < 0.05$) with the origin of the lobodontines. The life-history of the two elephant seals (*Mirounga*) evolved into an otariid-type strategy, with harem-based terrestrial mating and terrestrial pupping (and significant sexual size dimorphism). A re-affinity with ice occurred with the origin of the southern lobodontines in the early to mid-Miocene (Deméré et al. 2003; Higdon et al. 2007). This period was characterized by long-term cooling and glacial expansion (Holbourn et al. 2007), corresponding with an increase in geographic range size.

The reconstructions suggest that pinniped speciation events have occurred with shifts between different habitat types, but provide no indication of possible transitions that may have occurred within species. The distributions of pagophilic pinnipeds have shifted in the past with changing climatic conditions (Déméré et al. 2003; Harrington 2008), and some species have possibly shifted between ice and land as parturition substrates. For example, walrus fossils are closely linked to Holocene sea ice conditions (Dyke et al. 1999) and show extensive southern migrations at times of intensified glaciations (Harrington 2008). Atlantic walruses (*O. r. rosmarus*) historically occurred in areas with only seasonal or no predictable sea ice coverage (Gulf of St. Lawrence and Sable Island in eastern Canada, Iceland, and Norway), and may adapt to changing sea ice regimes more easily than pagophilic phocids (Kovacs and Lydersen 2008).

Pinniped evolutionary biogeography

A North Pacific origin for pinnipeds is generally accepted based on the occurrence of the earliest known fossils (Repenning et al. 1979; Deméré et al. 2003). A recent fossil discovery (*Puijila darwini*) from the early Miocene (Rybczynski et al. 2009) suggests the Arctic Basin as a centre for early pinniped evolution (also see Matthew 1939; Davies 1958a; Fulton and Strobeck 2010a). This hypothesis may gain support from our reconstructions that indicate the common ancestor to both modern groups evolved in ice covered regions. The Otarioidea-Phocidae split occurred ca. 23 mya and the walrus-otariid split ca. 15-21 mya (Higdon et al. 2007; Fulton and Strobeck 2010a), when episodic northern ice sheets existed (DeConto et al. 2008). Early adaptations to expanding polar conditions may have facilitated speciation, dispersal and range expansion, and biogeographic models (e.g., Ree and Smith 2008) could be used to test the hypothesis of Arctic evolution.

Otariid biogeographic hypotheses generally include dispersal from the Northern to Southern hemispheres through the eastern Pacific, with the North Pacific as the centre of evolution (Repenning et al. 1979; Deméré et al. 2003). The lineage may have adapted to terrestrial habitats after southward movement away from polar environments. Many Southern Hemisphere otariids, particularly *Arctocephalus*, arose via rapid and recent radiations (Higdon et al. 2007). Subpopulations of ancestral species may have colonized remote breeding sites, where terrestrial mating and the associated requirement for limited suitable rookeries led to isolation and speciation and small range sizes (Deméré et al. 2003).

Implications for pinniped conservation

Almost all pinniped species were negatively impacted by commercial over-exploitation and are in various stages of recovery (IUCN 2010). Mating behaviour can influence extinction risk (Bessa-Gomes et al. 2003; Sæther et al. 2004), but anthropogenic impacts are often just as significant (Cardillo et al. 2004). Most direct threats to pinnipeds are anthropogenic in nature (IUCN 2010). All otariids are land breeders (mating and pupping), and suitable sites are few and patchily distributed, leading to a heterogeneous distribution. The abundance of suitable breeding sites limits range size (Harwood 2001; Deméré et al. 2003), and otariid species may be more susceptible to direct human impacts given their high relative density in limited sites (Riedman 1990). Restricted distributions are a conservation concern for a number of otariids (e.g., *A. galapagoensis*, Aurioles and Trillmich 2008; *Neophoca cinerea*, Goldsworthy and Gales 2008; *Phocarctos hookeri*, Gales 2008). Several terrestrially-pupping phocids are also at risk – both extant *Monachus* (monk seal) species are Critically Endangered (IUCN 2010), and a third species (*M. tropicalis*) is extinct due to human exploitation. Both extant species have suffered range contractions and extensive population declines, and all major threats are anthropogenic (Aguilar and Lowry 2008; Lowry and Aguilar 2008). There are concerns about the loss of terrestrial habitat due to rising sea levels (e.g., Baker et al. 2006), but mitigation of anthropogenic impacts is clearly the more immediate conservation priority.

Ice-adapted pinnipeds generally have larger geographic ranges, and the most widely distributed pagophilic species are at present considered to be at a low risk of

extinction (IUCN 2010). The high-latitude sea-ice habitats critical to these species are currently experiencing significant environmental change (IPCC 2007), and a number of recent studies predicted negative impacts on pagophilic pinnipeds (e.g., Jüssi et al. 2008; Kovacs and Lydersen 2008; Laidre et al. 2008, Siniff et al. 2008). Pinniped ranges have shifted in response to past climatic changes (e.g., Harrington 2008), and with declining sea ice, pagophilic species will need to respond through shifting distributions and/or behavioural adaptations. As mobile species, pinnipeds could theoretically track changes in distribution of optimum habitats. Niche tracking may have allowed early pagophilic phocids to maintain stable selective environments (Eldredge 1999; Gould 2002), and extant species may be able to mediate climatic changes by following shifting climatic zones (Barnosky 2005). Dispersal capabilities, as they relate to the limitations imposed by habitat requirements, will be a significant factor in pinniped adaptations to changing climate regimes. In a rapidly changing environment, behavioural plasticity could also facilitate adaptive shifts (Robinson and Dukas 1999) (e.g., past phocid shifts in parturition habitat). This will require that the rate of environmental change not exceed the pace of behavioural responses (Ackerly et al. 2010), and this is a critical question concerning pagophilic phocids (e.g., *C. cristata*, *Pagophilus groenlandicus*; Kovacs and Lydersen 2008).

Summary and conclusions

Terrestrially-adapted pinnipeds generally have smaller geographic range sizes than species that mate aquatically or use sea ice as a parturition substrate, with differences most pronounced for parturition habitat. Adaptations to aquatic and sea ice

environments removed the requirement for suitable terrestrial habitats for critical life-history processes, leading to improved dispersal capability across evolutionary timescales. However, ancestral state reconstructions also indicated that adaptations to non-terrestrial habitats occurred with the evolution of the modern pinniped lineage and terrestrial (harem-based) reproduction evolved secondarily. While reconstructions for parturition habitat were uncertain, a long-term association with ice has likely been a driving factor in phocid evolution and speciation. Secondary adaptations to terrestrial habitats possibly arose with the origin of the otariids, with habitat restrictions resulting in isolation and speciation.

Pinnipeds at risk of extinction (IUCN 2010) also tend to have smaller ranges, even prior to human over-exploitation, and most endangered species mate and/or pup on land. Only two pagophilic species are currently at risk, although three more are Data Deficient (IUCN 2010). Anthropogenic risks are most significant, but declines in sea ice have led to concern about the future of a number of ice-adapted species (e.g., Laidre et al 2008; Siniff et al 2008). High-latitude pinnipeds are adapted to fluctuating environments and can tolerate significant climatic variability (Ferguson and Higdon 2006; Laidre et al. 2008). Pagophilic species have survived repeated periods of cooling or warming over evolutionary timescales (Harington 2008), although the accelerated rate of change may be unusual and pose unique challenges to species-level adaptations (MacDonald 2010). There is concern that long-term unidirectional changes, as opposed to large-scale inter-annual variation, will present a challenge to species' responses, particularly when coupled with increasing anthropogenic impacts (Ackerly et al. 2010). Reductions in sea ice habitat may result in geographic range contractions and increased

extinction risk. Efficient conservation requires knowledge about species responses to climate change (Godley 2009), and a better understanding of the role of climate variation on pinniped speciation and biogeography will assist with predicting impacts and prioritizing conservation activities.

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Table 3.1. Comparisons of range size (km², extent of occurrence and including historic pre-exploitation range where applicable) related to pinniped family/clade and mating and pupping environments. Skewness and Shapiro-Wilks test statistic provide a measure of departure from a lognormal distribution (* = significant skew, P ≤ 0.05). Results are shown for mating and pupping habitat separately and also combined into three different combinations of mating-pupping substrate (with aquatic mating-ice pupping equal to ice pupping, i.e., all pagophilic species mate aquatically). Species status based on ranks from IUCN (2010) (see text) and excludes recently extinct taxa, Data Deficient species, and *Zalophus* taxa (taxonomic uncertainty). Two continental endemics (*Pusa caspica* and *P. sibirica*, aquatic mating phocids that pup on ice) are excluded from all summaries.

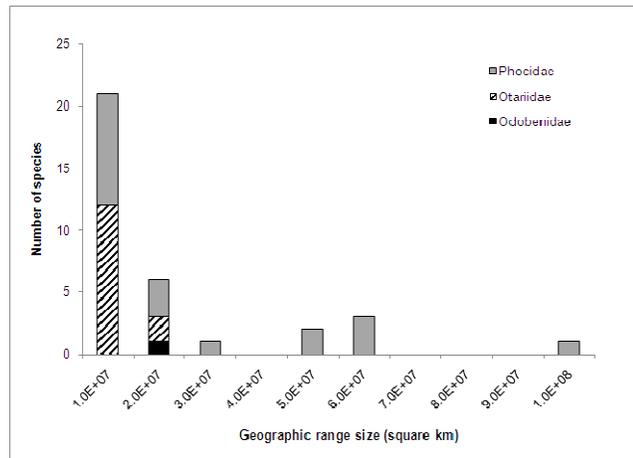
Group (n)	Mean range size (million km ²)	Median range size (million km ²)	Skewness	Shapiro-Wilks
All species (32)	17.5	7.5	-0.449	0.967 ^{NS}
Phocids (17)	28.1	12.2	-0.627	0.942 ^{NS}
Otarioids (15)	4.5	3	-0.682	0.930 ^{NS}
Otariids (14)	4.6	2.5	-0.709	0.928 ^{NS}
Sea ice pupping (11)	32.3	25.6	-0.421	0.874*
Terrestrial pupping (21)	9.8	3.5	-0.091	0.970 ^{NS}
Aquatic mating (15)	25.1	18.3	-1.102	0.895*
Terrestrial mating (17)	10.8	3.5	-0.032	0.960 ^{NS}
Aquatic mating/ice pupping (11)	32.3	25.6	-0.421	0.874*
Aquatic mating/land pupping (4)	5.4	4.6	-0.996	NA
Land mating and pupping (17)	10.8	3.5	-0.032	0.960 ^{NS}
At risk species (8)	5.2	3.9	-0.618	0.914 ^{NS}
Not at risk species (19)	25.3	12.2	-0.651	0.948 ^{NS}

Table 3.2. Conventional and phylogenetically-informed ANOVAs and ANCOVAs to examine variation in pinniped range size for different mating and pupping habitats. Residual range size used to control for body size allometry, and two continental endemics (both aquatic mating/ice-pupping phocids) excluded.

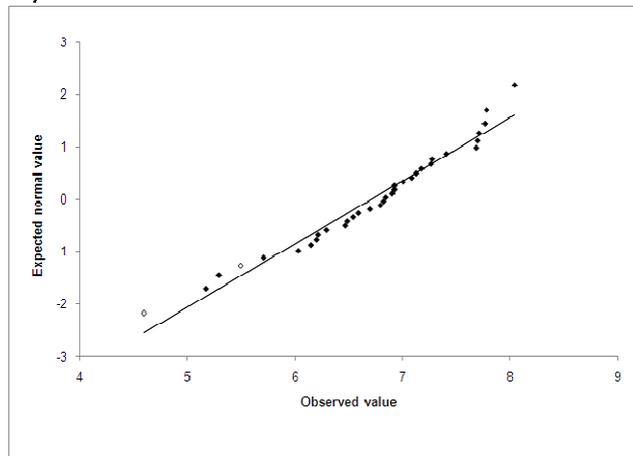
Variable	Test	Source of variation	Sum of Squares	df	Mean Square	F-ratio	Conventional		Phylogenetically-informed	
							Critical value	P	Critical value	P
Mating habitat	ANOVA	Among groups	2.890	1	2.890	8.600	4.171	0.006	4.254	0.007
		Within groups	10.083	30	0.336					
		Total	12.973	31	0.418					
Pupping habitat	ANCOVA	Main effect	0.000	1	<0.001	<0.001	4.183	0.989	4.188	0.989
		Covariate (Pupping)	1.949	1	1.949	6.951	4.183	0.013	4.116	0.012
		Explained	4.840	2	2.420	8.628	3.328	0.001	3.381	0.001
		Error	8.134	29	0.280					
		Total	12.973	31	0.418					
Mating habitat	ANOVA	Among groups	4.840	1	4.840	17.851	4.171	<0.001	4.180	<0.001
		Within groups	8.134	30	0.271					
		Total	12.973	31	0.418					
Pupping habitat	ANCOVA	Main effect	1.949	1	1.949	6.951	4.183	0.013	4.214	0.014
		Covariate (Mating)	0.000	1	<0.001	<0.001	4.183	0.989	4.322	0.989
		Explained	4.840	2	2.420	8.628	3.328	0.001	3.371	0.001
		Error	8.134	29	0.280					
		Total	12.973	31	0.418					

Figure 3.1. Geographic range sizes of world pinnipeds: (a) distribution of untransformed range size for all species ($n = 34$) separated by family; (b) normal probability plot for log-transformed range sizes; (c) distribution of untransformed range size for pinnipeds based on mating and pupping habitat. Two continental endemics (aquatic mating and ice pupping phocids) have small ranges, occurring in the smallest range size bin (a, c), and are identified by open circles in 1(b).

a)



b)



c)

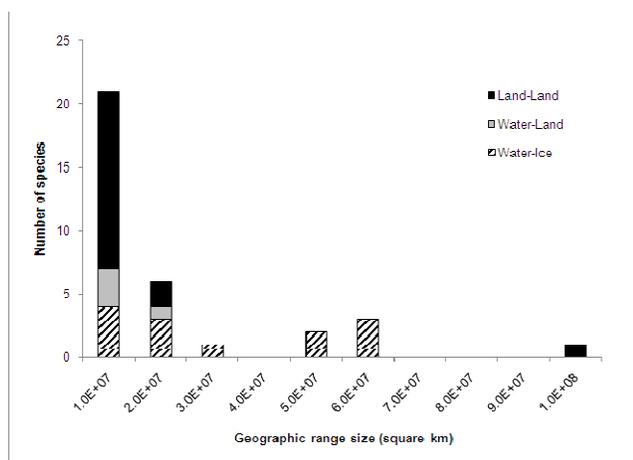
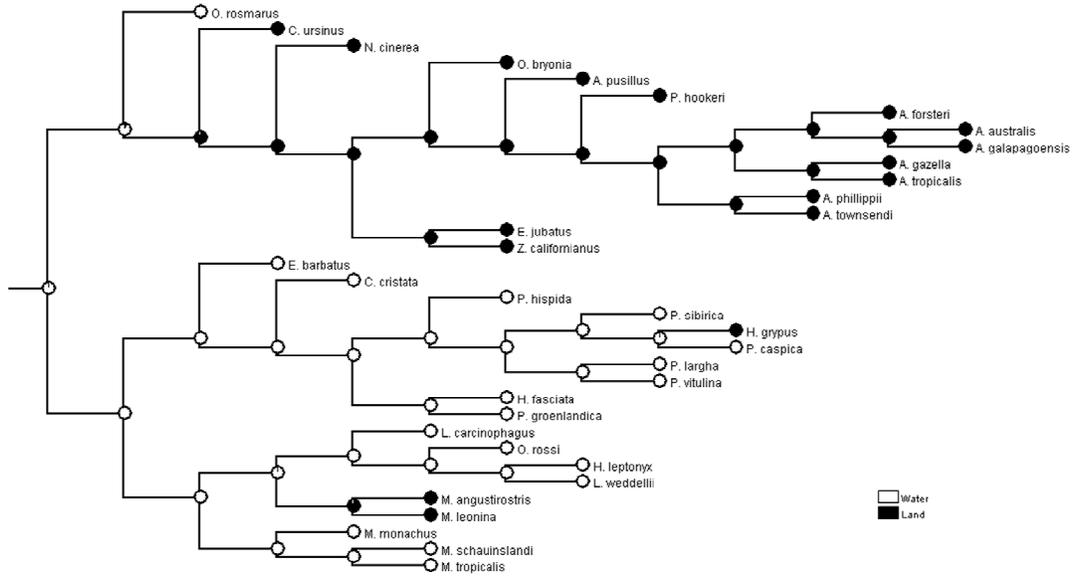


Figure 3.2. Top: Reconstructed ancestral states for mating habitat (water or land), both endemic species included. Nodes show proportional probability for each of the two states, as estimated using maximum likelihood (ML). Maximum parsimony (MP) reconstructions produced similar results, with no equivocal nodes. Bottom: Reconstructed ancestral states for parturition habitat (ice or land). Nodes again show probability for each of the two states, as estimated using ML, and nodes inside square boxes were equivocal (i.e., ice or land) under MP reconstruction. All reconstructions using equal branch lengths (all = 1).

Mating habitat



Parturition habitat

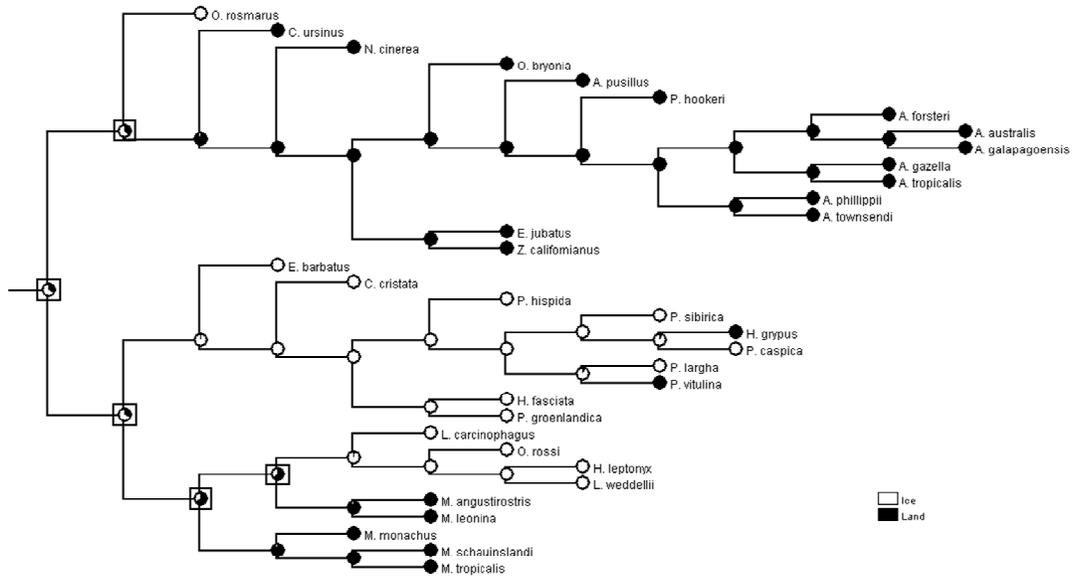
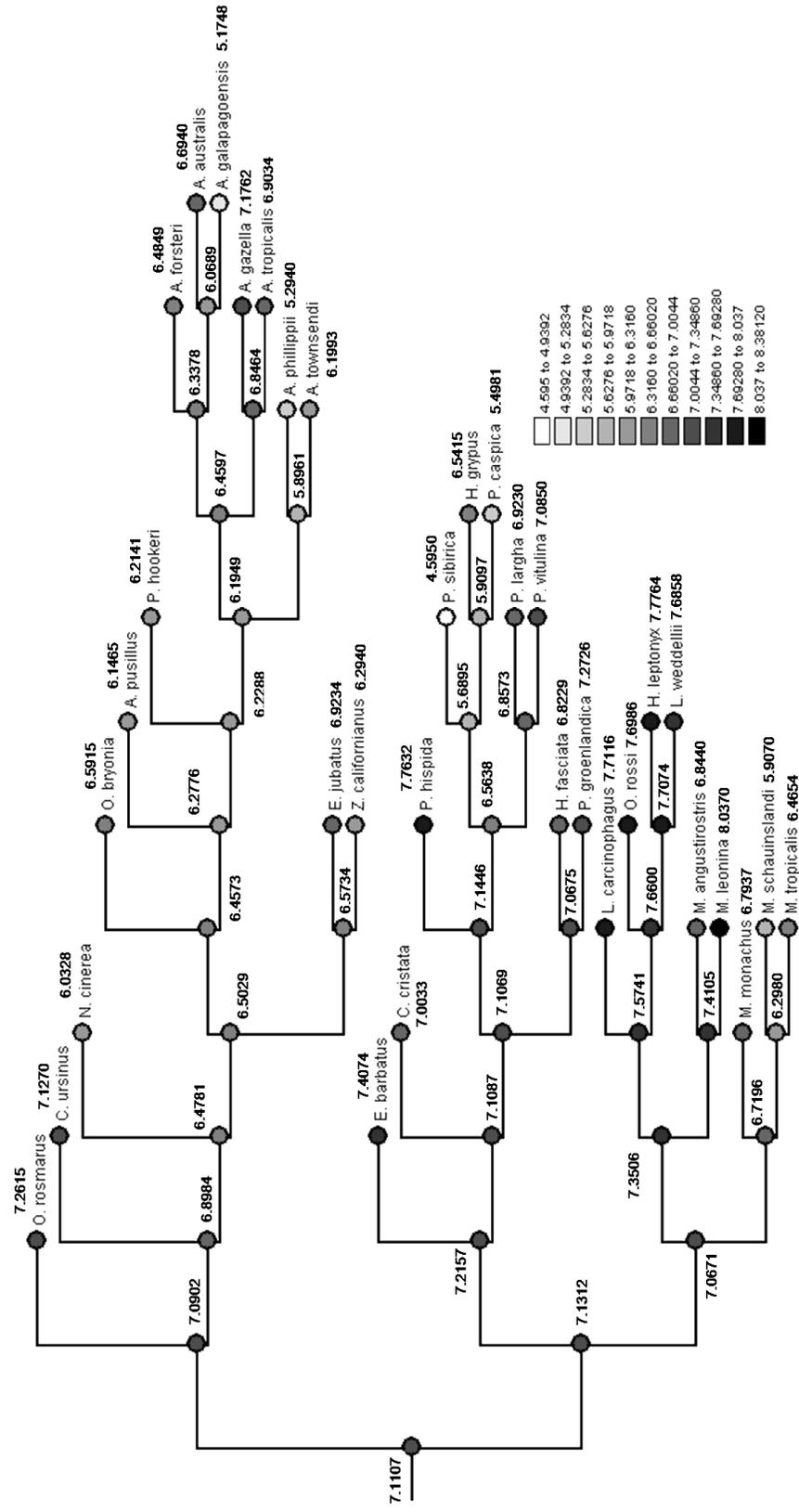


Figure 3.3. Maximum-parsimony (MP) reconstruction of ancestral states for geographic range size ($\log_{10}\text{-km}^2$) (equal branch lengths, all = 1). Values are reconstructed range size for internal nodes, and pre-exploitation range size data (see text) for species nodes.



4. Latitudinal variation in the geographic range size of world pinnipeds (Carnivora: Mammalia): body size, phylogeny, and the Rapoport effect

Abstract

A better understanding of species range sizes, distribution patterns and range limits is central to informed and efficient conservation at global scales. Several general ecological patterns have been identified, although none is consistent across all tested taxa or spatial scales. Species richness is often highest at low latitudes, a trend often used to explain a related pattern, the Rapoport effect, of species geographic ranges being larger at high latitudes. Body size also often increases with latitude (Bergmann's rule) and, thus, has a positive relationship with geographic range size. I used world pinnipeds (a monophyletic group of seals, sea lions and fur seals, and the walrus; $n = 34$ species) to examine latitudinal variation in species diversity, range size, and body size using phylogenetically-independent contrasts. Both conventional and phylogenetically-informed analyses indicated strong support for the Rapoport effect, as range sizes are largest at higher latitudes. There is significant phylogenetic signal in body size, and a positive relationship with latitude is supported using conventional analyses only. Species diversity is lowest in the tropics, and relationships between diversity and range size therefore cannot explain the Rapoport pattern in pinnipeds. Previous studies have suggested that the Rapoport effect does not apply to marine taxa, but there is a significant pattern for pinnipeds, a widely-distributed group of marine aquatic carnivores. Species richness is highest in mid-

latitude regions characterized by variable climatic conditions (e.g., marginal sea-ice zones), and thus climatic variability may be a significant explanation of pinniped range size variation.

Keywords: body size, climate, distribution, seals, species diversity

Introduction

Consideration of latitudinal patterns in species diversity and geographic distributions are central to many important questions in macroecology and conservation biology (Gaston and Blackburn 2000; Gaston 2003). A number of different “rules” have been proposed to describe biogeographic patterns in species richness and range size (Willig et al. 2003). Two common tendencies are for species richness to decrease at high latitudes, and the related pattern of increased geographic range sizes at high latitudes (Stevens 1989). The latitudinal diversity gradient is often considered a universal feature of the spatial variation in biodiversity and has been identified in many taxa at many different spatial scales (Hillebrand 2004; Ruggiero and Wrenkrait 2007; but see Arita et al. 2005 regarding scale sensitivity). The positive association between latitude and geographic range size (or latitudinal extent, as originally proposed), known as Rapoport’s rule and defined by Stevens 1989 as an explanation of the gradient in species richness, has been contentious.

In recent years Rapoport’s rule has received significant attention, and much criticism (reviewed by Arita et al. 2005; Ruggiero and Wrenkrait 2007). Many studies have supported it, but there are numerous exceptions and the generality of it as a “rule” has been questioned (Gaston et al. 1998; Blackburn and Gaston 1996). Comparisons among different studies are made difficult by varying ways in which species range is defined, different techniques for measuring range size, and different statistical methods for assessing correlations between range size and latitude (Ruggiero and Wrenkrait 2007). Given these questions around the generality of the pattern, I follow Blackburn and Gaston (1996) and use the term Rapoport effect rather than “rule”.

Previous studies have also been criticized for ignoring several important confounding factors, particularly effects of body size and phylogeny (Gaston et al. 1998; Cowlshaw and Hacker 1998; Read 2003; Cruz et al. 2005). Body size tends to increase with latitude, often defined as Bergmann's Rule (but see Watt et al. 2010). Body size is also often positively associated with range size (Gaston and Blackburn 1996a, b), and can therefore bias the Rapoport effect (Reed 2003). Also, tests of relationships between latitude, body size, and geographic range have to control for phylogenetic relationships (Read 2003; Cruz et al. 2005).

Pinnipeds (seals, sea lions and fur seals, and the walrus; Carnivora, Mammalia) are a monophyletic group with an extensive latitudinal distribution, well-known geographic ranges, and generally well-accepted phylogenetic relationships, and are thus an ideal group for testing these patterns (Cruz et al. 2005). Pinnipeds are semi-aquatic (generally marine) mammals that are found throughout world oceans at a range of latitudes, ranging from the poles to the tropics. There is a general lack of global analyses (but see Gaston et al. 2005; Orme et al. 2006 for examples), and analyses at this scale are important (Gaston 2003). I examine latitudinal trends in geographic range size and body size of world pinniped species, using several different methods, including independent contrasts (Felsenstein 1985; Garland et al. 1992) to examine relationships while controlling for common ancestry.

Methods

Species ranges ($\log\text{-km}^2$) were the area of occupancy (Gaston 1991) of species historic (i.e., pre-commercial exploitation) distributions (Chapter 3). Ranges were

digitized in ArcView 3.3 (cylindrical equal area projection) using maps in Jefferson et al. (1993), Riedman (1990), Nowak (2003), and Perrin et al. (2002). I determined the midpoint and maximum (northern or southern) latitude for each species using the digitized range maps. Latitudinal patterns in geographic range size were analyzed using both the species-as-data method (the primary analysis – see Discussion) and the Stevens and modified midpoint method (Stevens 1989; Rohde et al. 1993) (electronic supplementary material, Appendix A3). I included 34 pinniped species (following the phylogeny of Higdon et al. 2007 (Chapter 2), treating *Zalophus* as one species with three subspecies). Species diversity was plotted as a function of latitude by dividing the globe into 36 5° latitude bins and summing all species whose range fell within that bin.

For the across-species method, I compared geographic range size using both the latitudinal midpoint and maximum (northern or southern) latitude of each species range. Results of both conventional and phylogenetically-informed statistics are presented, as recommended by Garland et al. (1999). Female mass data (Ferguson and Higdon 2006) were used to examine interactions between body size, range size, and latitude. I examined direct linear relationships between mass and range size and the interaction between mass and latitude (i.e., Bergmann's Rule).

I first examined the behaviour of each (conventional) predictor variable separately using single regressions, and then examined all variables together using general linear models (GLM). Seven different GLMs, containing from one to three variables, were used to examine all possible variable combinations and test for relationships between the three different mechanisms simultaneously. Model selection was guided by AIC_c scores (Akaike 1974) with Δ_i AIC_c values < 2.0 used to indicate models with substantial

statistical support and values < 3.0 indicating moderate support (Burnham and Anderson 2002). Correlation coefficients and initial GLM modeling indicated significant multicollinearity between the two latitude measures (tolerance < 0.2), so two sets of models were assessed, one using midpoint latitude and one using maximum latitude as a candidate predictor variable (see Appendix A3 for results using maximum latitude). Variables were centered by subtracting the mean from each value to reduce multicollinearity for interaction terms (Grafen and Hails 2002).

Species data are non-independent due to their common ancestry and shared phylogenetic constraints (Harvey and Pagel 1991). Phylogenetically-informed analyses using the species-as-data method used the molecular supertree of Higdson et al. (2007). All phylogenetically-informed results are presented using constant (or equal) branch lengths (all = 1, a speciation model of evolution; Martins and Garland 1991). Two different sets of estimated divergence dates (in millions of years) (Higdson et al. 2007) were also examined, but diagnostic tests (Garland et al. 1992; Blomberg et al. 2003) indicated that constant branch lengths were most suitable (Appendix A3).

I controlled for species relatedness by using phylogenetically independent contrasts (PIC) (Felsenstein 1985) as implemented in the PDAP:PDTREE (Midford et al., 2008) module of MESQUITE version 2.6 (Maddison and Maddison 2009). By definition, the Rapoport effect at a global scale is a quadratic relationship (positive and negative latitude values). This creates a problem with the use of PIC as the method is designed to detect linear relationships (Felsenstein 1985; Garland et al. 1992) and can fail to detect evolutionary correlations when the relationship between two traits is nonlinear (Quader et al. 2004). Simple data transformations are effective in many cases (Garland et al. 1992),

but not for quadratic relationships. Absolute values of latitude were therefore used to maintain a linear relationship for PIC, but results for quadratic relationships for conventional analyses are also presented.

Results

Pinnipeds are widely distributed, occurring at all latitudes. Species diversity follows a bimodal distribution, with distinct peaks at mid-latitudes in both hemispheres (Figure 4.1). Species diversity is highest in the Northern Hemisphere, and higher in Arctic and sub-Arctic than Antarctic regions. Compared to otariid species, phocid species are more diverse at high latitudes in both hemispheres, and among phocids the number of species is greater in the Northern hemisphere. Conversely, otariid species diversity is greater at mid-latitudes in the Southern Hemisphere.

Conventional (i.e., non-phylogenetically informed) analysis

Conventional tests using the species-as-data method indicates strong support for the Rapoport effect (Figure 4.2a) for both midpoint and maximum latitude (Table 4.1 for midpoint latitude, see Appendix A3 for tests using maximum latitude). There is a clear trend of increasing range size towards the poles and the smallest ranges are found closest to the Equator. *Pusa sibirica*, which is restricted to Lake Baikal in Russia, appears as a significant outlier at ca. 53° N. When absolute values of midpoint are used instead to create a linear trend as required for PIC (see below) a significant relationship between range size and latitude still exists (Figure 4.2b, Table 4.1). Single linear regressions also indicated a significant positive relationship for increasing range size with increasing body

size (female mass), in addition to a significant interaction between latitude and body mass (i.e., Bergmann's Rule, Table 4.1). The Rapoport effect is also strongly supported using the Stevens and midpoint methods (Appendix A3, Table A3.1). There was no significant relationship between species diversity and geographic range size per latitude bin (linear regressions of \log_{10} -transformed data, $n = 36$; median range size: $R^2 = 0.007$, $F(1, 34) = 0.237$, $p = 0.629$; mean range size: $R^2 = 0.005$, $F(1, 34) = 0.166$, $p = 0.686$).

The best-fitting conventional GLM for midpoint latitude included one variable, a positive interaction between body size and latitude (i.e., Bergmann's Rule) (Table 4.2). One additional model with substantial support ($\Delta_i \text{AIC}_c < 2$) also included a negative relationship with latitude (but $p > 0.10$). Two other models had moderate statistical support (Table 4.2) (see Table A2.4 for maximum latitude, with similar results). Conventional analyses indicate that interactions between latitude and body size is the most parsimonious explanation of latitudinal variation in pinniped range size.

Phylogenetically-informed analysis

All phylogenetically-informed analyses were conducted using constant (equal, all = 1) branch lengths (see Appendix A3, Table A3.2). Phylogenetically-informed single linear regressions are similar to conventional regressions for latitude (Table 4.1), but female mass and the interaction between mass and latitude are no longer significant after phylogenetic controls (there was also a significant phylogenetic signal for the female mass variable, Table A2.3). The Rapoport effect is still strongly supported, but Bergmann's Rule (as commonly defined) is not supported using phylogenetically-informed methods.

Three of the seven phylogenetically-informed GLMs had at least moderate statistical support ($\Delta_i \text{AIC}_c < 3$) (Table 4.2). The most parsimonious model included only one variable, a significant positive association between range size and latitude. The other two supported models also included a significant relationship with latitude, and one each of the other two variables, although both were non-significant ($p > 0.10$). Results using maximum latitude were nearly identical (Table A2.4). Thus, after controlling for phylogeny I find a significant positive relationship between latitude and geographic range size, supporting the Rapoport effect in world pinnipeds (Figure 4.2c). A positive relationship between latitude and body size (i.e., Bergmann's rule), however, is no longer supported with phylogenetically-informed analyses.

Discussion

World pinniped ranges show strong support for the Rapoport effect, with a significant positive relationship between latitude and range size. This pattern holds using both the Stevens'/midpoint methods and the species-as-data method. Furthermore, the Rapoport effect is still supported using the species-as-data method after controlling for the effects of both body size and phylogeny. I consider this approach as the primary method, as it offers a number of advantages and eliminates some of the statistical issues related to band methods (Appendix A3). Species-as-data approaches also tend to support the Rapoport effect across a variety of spatial scales and taxon groups (Ruggiero and Werenkraut 2007). Studies that use individual species as independent data points (i.e., phylogenetically-uninformed) generally indicate a positive relationship, although the pattern tends to be weaker than those assessed using latitude bands.

When phylogenetically-informed methods are used (i.e., the proper approach for comparative analyses), relationships tend to be still positive overall, but with reduced significance (reviewed by Gaston et al. 1998; Ruggiero and Werenkraut 2007). Many previous studies either did not include body size, or examined relationships with body size using conventional statistics only (e.g., Pagel et al. 1991; Blackburn and Gaston 1996a). Gaston and Blackburn (1996b) did examine interactions between mass and latitude while controlling for phylogeny for waterfowl (Anseriformes) ranges, and also found no interaction between the two using phylogenetic comparative methods (also see Taylor and Gotelli 1994). The similarity between conventional and phylogenetically-informed results in many studies may be biased by not including body size, which tends to exhibit significant phylogenetic signal (Blomberg et al. 2003).

The Rapoport pattern for pinnipeds occurs at the global scale, and trends are similar for both hemispheres. This is in contrast to many studies that have suggested that the Rapoport effect is a regional phenomenon, most prevalent at high latitudes in the Northern Hemisphere (Rhode 1996, 1999; Gaston et al. 1998; but see Cardillo 2002). The relationship between latitude and range size is often not significant in the Southern Hemisphere (Gaston et al. 1998; Reed 2003; Hernández et al. 2005). For many species groups there is a significant lack of knowledge of Southern Hemisphere taxa compared to those in the Northern Hemisphere (Remsen and Cardiff 1990), and this may have influenced past studies that failed to find a Rapoport effect south of the Equator (Fortes and Absalão 2004). Pinniped ranges, in contrast, are generally well known, including the Southern Hemisphere, and the global Rapoport effect is supported.

Most studies in the marine environment have failed to find any significant range size patterns with either latitude or depth (Haedrich and Merrett 1988; Rhode 1996; Rohde et al. 1993; Roy et al. 1994; Smith and Gaines 2003; but see Stevens 1996; Santelices and Marquet 1998; Fortes and Absalão 2004 for exceptions). These results have led some authors to claim that the Rapoport effect is not present in marine systems (Rohde et al. 1993; Roy et al. 1994), and a recent meta-analysis indicated that patterns tend to be weaker in oceans versus terrestrial habitats (Ruggiero and Werenkraut 2007). These results indicate a strong Rapoport effect for pinnipeds, a widely distributed group of marine carnivores with some degree of a terrestrial link. Latitudinal trends tend to be stronger in terrestrial systems, and this terrestrial habitat requirement of pinnipeds may help explain the strength of the patterns compared to exclusively marine species groups.

Several studies (Rohde et al. 1993; Roy et al. 1994; Willig et al. 2003) have found a latitudinal gradient in species diversity among marine taxa, despite not supporting the Rapoport effect, which underscores the need for caution in inferring links (Smith and Gaines 2003). My results are opposite; with a strong Rapoport effect but no link to species diversity patterns, which for pinnipeds is lowest in the tropics. For pinnipeds, the latitudinal gradient in range size is not explained by a latitudinal gradient in diversity. Pinniped species diversity is highest at mid latitudes in both hemispheres, in regions that correspond to marginal ice zones (Kelly 2001) and variable climates. A number of phocid species are pagophilic (ice-adapted) and use sea-ice (rather than terrestrial sites) as a platform for pupping. Mid-latitudes support both pagophilic and temperate species, leading to higher species diversity. Geographic range sizes are larger in ice-pupping and aquatic mating species than in terrestrial species (Chapter 2). Adaptations to sea ice

habitats would have improved dispersal capabilities by removing a necessary tie to land, resulting in larger ranges. These ice-covered seas occur at higher latitudes, and adaptations to sea ice parturition and associated range expansion provide some explanation for the strong Rapoport effect in world pinnipeds.

The positive relationship between latitude and pinniped body size (“Bergmann’s Rule”) is not supported using phylogenetic independent contrasts. Body size in pinnipeds exhibits significant phylogenetic signal (also see Ferguson 2006; Chapter 3), but range size does not. This trend has been identified in various other species groups (Brown 1995; Gittleman et al. 1996; Gaston and Blackburn 1997; Diniz-Filho and Tôrres 2002), suggesting that ecological traits such as range size are more labile than biological traits (also see Blomberg et al. 2003). Neither a positive relationship between body mass and range size nor an interaction between mass and latitude can explain the Rapoport effect in pinnipeds.

I used female mass to examine relationships between body size, geographic range size and latitude. Some pinnipeds, particularly those with terrestrial harem-based mating systems (all otariids and some phocids), are extremely sexually dimorphic (Ferguson 2006). There is a significant positive relationship between male body size and degree of sexual size dimorphism (i.e., Rensch’s Rule, Rensch 1960) in pinnipeds (Alexander et al. 1979; Abouheif and Fairbairn 1997; Linderfors et al. 2002). Relationships between mass (both sexes), sexual selection on harem size and sexual size dimorphism, and the geographic variation in suitable terrestrial breeding sites (Linderfors et al. 2002; Ferguson 2006), coupled with the significant phylogenetic signal in body size, could explain the lack of support for Bergmann’s rule using phylogenetically-informed analyses. The

number of pagophilic phocid species with no significant sexual size dimorphism is greater at higher latitudes, whereas otariids predominate at moderate latitudes, particularly in the Southern Hemisphere. Also, phocid species in more temperate regions (e.g., *Mirounga*) tend to utilize a terrestrial harem-based mating system (Ferguson 2006). The geographic limitations imposed by terrestrial habitat dependence (Chapter 3) also provide an explanation of the Rapoport effect. Further research on the influence of body size, sexual size dimorphism and mating system on range size would be instructive.

Analyses of range size patterns often exclude endemic species (i.e., island endemics in a terrestrial sense) and species that have suffered substantial range contractions due to human activities (Gaston 2003). These analyses used all pinniped species, including two endemic species (*Pusa sibirica* and *P. caspica*, both restricted to inland seas/lakes) and a number that have suffered range contractions. Historic distributions were used to mitigate the negative effects of human-induced range contractions (Murray and Dickman 2000; Gaston et al. 2005). If both endemics are removed from the analyses the Rapoport effect is still supported using all the different methods, and statistical patterns are in fact even stronger.

In conclusion, pinniped range size patterns show a strong and consistent Rapoport effect at a global scale. The strength of the pattern could not be explained by latitudinal patterns in species diversity or positive relationships between body size and range size, although further research on sexual selection, sexual size dimorphism and mating system may be informative. Sea ice habitats have been critical to pinniped species dispersal and evolutionary biogeography (Davies 1958a, b; Fulton and Strobeck 2010; Chapter 3). Species diversity is highest in mid-latitude regions and marginal ice zones, and these

areas are characterized by significant temporal variability in energy and productivity (Kelly 2001). Climatic conditions may play a key role in pinniped distribution and geographic range sizes, and a test of the climatic variability hypothesis (Stevens 1989) will be an important step in studying the geographic distribution of world pinnipeds. This hypothesis predicts that species in more variable climates are adapted to a wider range of climatic conditions, and this greater tolerance allows for larger ranges. Increased understanding of relationships between climate, distribution and diversity will assist in predicting the impacts of climatic changes on species distribution (e.g., Laidre et al. 2008).

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Table 4.1. Single regressions (quadratic and linear), both conventional (n = 34) and phylogenetically-informed (n = 33). Dependent variable is \log_{10} range size in km^2 , with absolute values for midpoint latitude square-root transformed for linear regressions, and actual values cube-root transformed for quadratic regressions (see text). Phylogenetically-informed tests used independent contrasts calculated using constant branch lengths (see Electronic Appendix A3).

Regression	Variable	Conventional			Phylogenetically-informed				
		R ²	F (df)	β	P	R ²	F (df)	β	P
Quadratic	Latitude	0.41	10.63 (2, 31)	0.015	0.0003	NA			
	Mass	0.188	6.735 (2,31)	0.047	0.0393	NA			
Linear	Latitude	0.349	18.666 (1, 32)	0.318	< 0.0001	0.292	13.191 (1, 32)	0.314	0.001
	Mass	0.207	9.617 (1, 32)	0.105	0.004	0.065	2.226 (1, 32)	0.629	0.145
	Latitude*Mass	0.420	24.909 (1, 32)	0.158	< 0.0001	0.062	2.128 (1, 32)	0.936	0.154

Table 4.2. Comparison of general linear models for a Rapoport effect on pinniped range size (34 world species). Only models with moderate or substantial support are presented (Δ_i AICc < 3). Models tested range size variation against midpoint latitude (see Methods) and were analyzed using both raw data (conventional statistics) and standardized phylogenetically-independent contrasts to control for phylogeny. Blanks in the “variables” fields indicate variables not included in the model, “*” indicates the variable was included and significant at $p \leq 0.05$, “ ≤ 0.10 ” indicates included variables that were significant at a reduced $p \leq 0.10$, and “NS” indicates included variables that were not significant ($p > 0.10$).

Method	Variable(s)												
	LAT		MASS		LAT*MASS		F	d.f.	R ²	P	AIC _c	Δ_i AIC _c	w
	P	β	P	β	P	β							
Conventional (n = 34)													
	NS	-0.172			*	0.060	24.919	1, 32	0.420	0.0001	-30.391	0.000	0.442
				*	0.088	12.511	2, 31	0.411	0.0001	0.0001	-28.516	1.875	0.173
			NS	0.187	*	0.054	12.310	2, 31	0.407	0.0001	-28.271	2.120	0.153
	*	0.258	<0.10	0.569		11.831	2, 31	0.396	0.0001	0.0001	-27.682	2.709	0.114
PIC (n = 33)													
	*	0.314				13.191	1, 32	0.292	0.001	0.001	-55.509	0.000	0.539
	*	0.297	NS	0.216		6.603	2, 31	0.276	0.004	0.004	-53.555	1.954	0.203
	*	0.302			NS	0.201	6.466	2, 31	0.272	0.004	-53.347	2.162	0.183

Figure 4.1. Species diversity patterns of world pinnipeds, measured as number of species (n = 34) found in each 5° latitudinal bin.

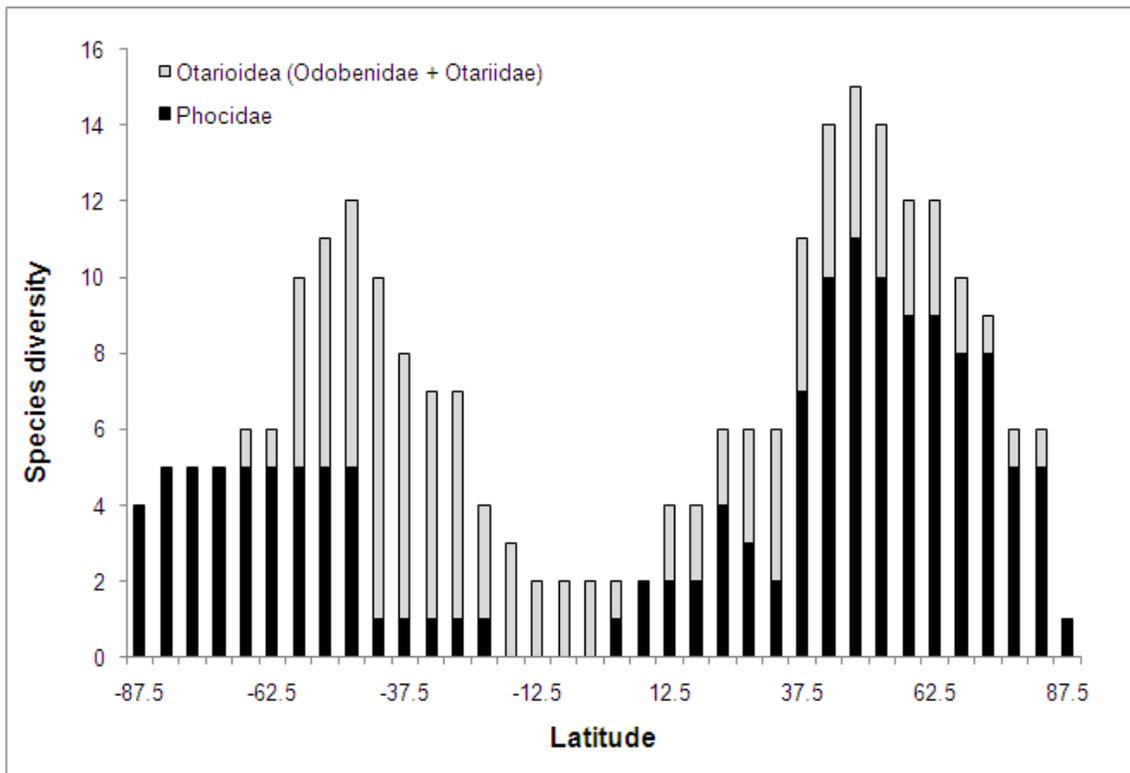
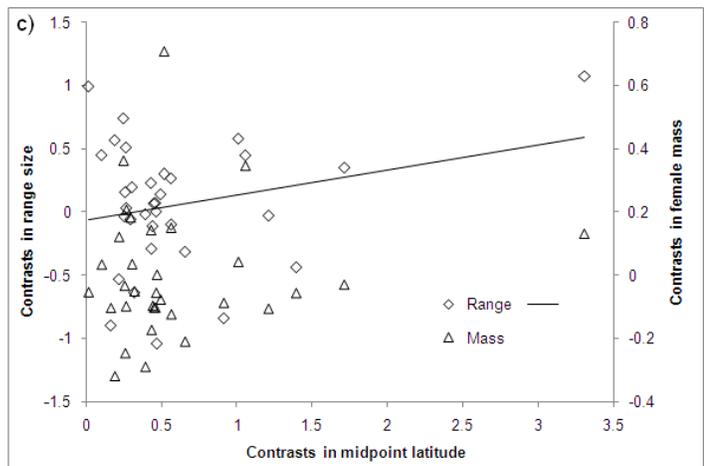
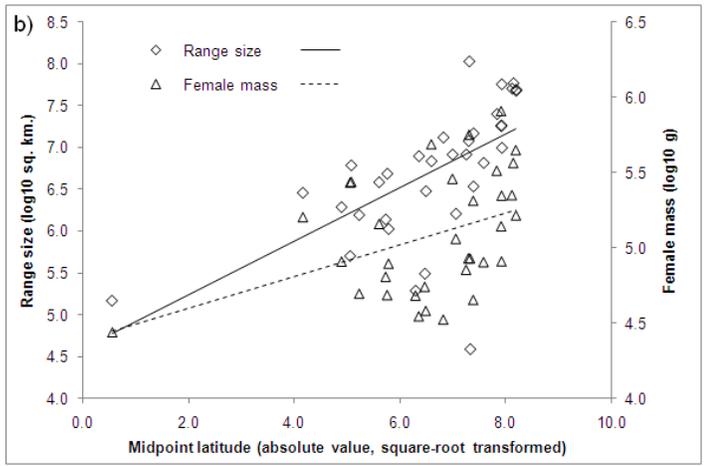
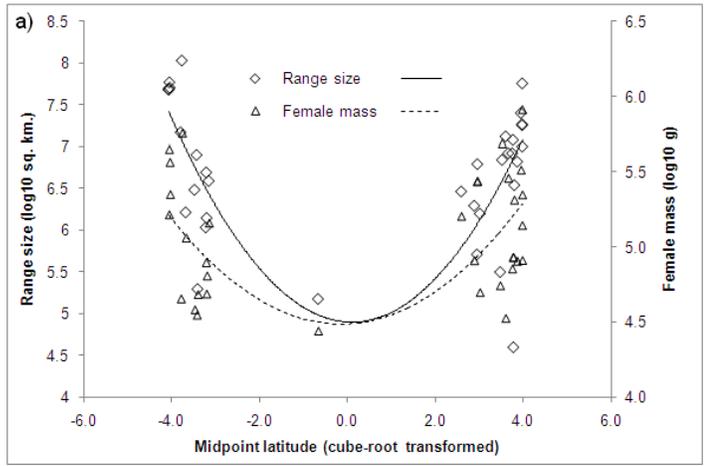


Figure 4.2. Latitudinal variation in geographic range size (the Rapoport effect) and body size (Bergmann's Rule) in world pinnipeds, using latitudinal midpoint of species range:

a) at the global scale both patterns are quadratic, range size ($\log_{10} \text{ km}^2$) and female mass ($\log_{10} \text{ g}$) plotted against latitude (cube-root transformed), with quadratic lines of best fit;

b) the same two variables plotted against absolute value of latitude (square-root transformed) to produce a linear trend as required for phylogenetically-independent contrasts (see text), best-fit linear trend line indicates that relationship between latitude and range size is maintained across both hemispheres; c) scatterplot of phylogenetically independent contrasts to control for common ancestry, with contrasts in latitude positimized for presentation as recommended by Garland et al. (1992).



5. Influence of climate variability on geographic range size and species diversity of world pinnipeds

Abstract

Climatic conditions have a strong influence on distribution and richness patterns. I tested the climatic variability hypothesis (CVH) as an explanation of range size variation in world pinnipeds using a global sea surface temperature (SST) data set. The CVH assumes that species at higher latitudes experience greater climatic variability, increasing their tolerance range and thereby increasing range size. I also tested for a climatic explanation to latitudinal patterns in species diversity. Three measures of SST were included: average (objectively-analyzed mean annual SST), intra-annual variation (standard deviation of mean annual SST), and inter-annual variation (standard error of the statistically-analyzed mean SST over multiple years). Climate variables were summarized across pinniped species ranges and comparative analyses controlled for both body size and phylogeny. The CVH was not supported as SST variation could not explain the Rapoport effect. Mean annual SST was a significant predictor of range sizes, and was also the only variable that followed a consistent global latitudinal gradient. Temperature variation did explain trends in pinniped diversity, which also had a significant quadratic relationship with mean annual SST. Responses to SST gradients are likely related to thermoregulation, sea ice availability, and ecological interactions including predation. Pinnipeds use marine and terrestrial habitats, and air temperature may also play a large role in distribution patterns. Increasing temperatures may have a significant influence on

pinniped range sizes and distribution patterns, and further research on responses to environmental variation is necessary for informed predictions of effects.

Keywords: climatic variability hypothesis (CVH), latitude, allometry, climate change, thermoregulation, seals, sea ice, distribution, predation

Introduction

Knowledge of species distribution and diversity patterns is required for efficient biodiversity conservation. A number of general trends and patterns in species diversity and geographic range size have been identified (Gaston and Blackburn 2000; Gaston 2003). Across most species groups, diversity is highest in low-latitude tropical regions (Stevens, 1989), and geographic range size tends to increase with latitude. Stevens (1989) named this trend Rapoport's Rule and linked it with diversity patterns (i.e., more species leads to smaller geographic range sizes). Neither pattern is consistent across all taxa and spatial scales, and both have received considerable criticism (Gaston et al. 1998). I acknowledge this debate and use the term "Rapoport effect" (Blackburn and Gaston 1996).

One explanation for the latitudinal gradient in range size is the climatic variability hypothesis (CVH) (Stevens 1989), which states that animals at higher latitudes experience greater temporal variability in climatic conditions, which increases their tolerance range, allowing them to become more widely distributed (see Gaston and Chown 1999 for a historical review). The CVH has important implications for the study of both species richness and range size patterns (Gaston et al. 1998). The CVH has been supported in studies on African mammals (Cowlshaw and Hacker 1997; Harcourt 2000; Fernández and Vrba 2005). Letcher and Harvey (1994) found a positive association between range size and annual temperature range among Palearctic mammals (but not with two other measures of climate variability). Range size variation in New World birds is mostly a result of biogeographic structure (Blackburn and Gaston 1996), and Roy et al. (1994) similarly suggested that latitudinal range size in molluscs was mainly influenced

by major oceanographic barriers and not temperature variability. Overall, direct evidence to test the CVH in the marine environment is scarce (Gaston et al, 1998; Spicer and Gaston 1999; but see Compton et al., 2007).

Global macroecological patterns are different in terrestrial versus marine environments, but it has been suggested that common mechanisms occur (Schipper et al. 2008). Most biogeographic research has concentrated on terrestrial species, and Rapoport patterns tend to be weaker in marine systems (Ruggiero and Werenkraut 2007). The geographic range sizes of world pinnipeds, however, a monophyletic group of widely-distributed marine mammals, strongly support the Rapoport effect at the global-scale, even after controlling for the effects of body size and phylogeny (Chapter 4). Pinnipeds show remarkable variation in life-history and mating systems, and many species pup on sea ice. These adaptations to sea ice habitats have facilitated range expansion, and pagophilic species have larger geographic ranges than those that use terrestrial rookeries for parturition (Chapter 3). Species diversity is lowest in the tropics and highest at mid-latitude regions with marginal ice cover and variable climates (Kelly 2001). Adaptations to variable climates (and wide thermal tolerances) may thus be a significant factor in range size and species diversity variation. I test the CVH using world pinniped ranges and a global climate dataset, and predict a positive relationship between climatic variability and both geographic range size and species diversity.

Methods

I used published range maps of world pinniped ranges as discussed in Chapters 3 and 4. Maps were historic distributions and included ranges occupied prior to human

exploitation, to remove the effects of recent anthropogenic disturbance. I assumed that climatic conditions remain similar enough that species would still occur in areas where they were extirpated within the past several centuries. Historic range sizes are highly correlated ($r = 0.988$, $n = 31$) with recent ranges as mapped by IUCN (2010), with the biggest differences occurring for species that have suffered recent range contractions (e.g., *Odobenus rosmarus*, *Monachus monachus*). One species, *Pusa sibirica* (Baikal Seal), was excluded from the analyses due to missing climate data (see below), for a total of 35 species.

Sea surface temperature (SST) data were collected from the World Ocean Atlas 2005 (WOA05) (Locarnini et al. 2006). The World Ocean Atlas 2005 is a global climatology (all-data regardless of year of observation) of objectively analyzed and interpolated in situ oceanographic data fields on a 1-degree latitude-longitude grid (41,456 ocean data points) at standard depth levels, including the surface, and available for different temporal compositing periods (annual, seasonal, monthly). Data were available for all world oceans and the Mediterranean and Caspian seas, but not for the Baikal Sea. Data were imported into ArcView 3.3 (ESRI Inc., Redlands, CA, USA) for analyses and extraction of data within pinniped species range polygons. Species range size was measured as the number of one degree grid cells. Three different climate variables were used to represent climate and climate variability (both inter- and intra-annual variation). Mean annual SST (meanSST) was measured as the mean of the monthly objectively analyzed mean values, for a general measure of “typical” SST. The standard deviation of the mean monthly SST (sdSST) was calculated as a measure of intra-annual temperature seasonality (Naya et al. 2008). Finally, the standard error of the

statistical mean temperature was measured across multiple years of data (seSST), a measure of inter-annual (between year) variation (Ferguson and Messier 1996). These data are measured values only (versus interpolated values used to calculate objectively-analyzed mean SST), and some cells have no data, particularly in ice-covered regions, leading to smaller overall sample sizes within species ranges. One additional climate variable (annual range of SST, difference between the warmest month and coldest month, objectively-analyzed values) was initially examined but was strongly correlated with sdSST across all cells ($r = 0.995$, $P < 0.001$), and I therefore included only sdSST as a measure of within-year climate variation.

By definition, the CVH requires a latitudinal gradient in climate variability (Gaston et al. 1998). I first looked for a global gradient with correlations between latitude (absolute values, square-root transformed) and the three climate variables (ln-transformed, with a constant of 2 added to mean annual SST due to negative values) for both all points ($n = 41,456$) and for median values in each 5° lat band ($n = 36$, but no climate data for the band with midpoint 87.5° South) (and reduced sample sizes for seSST as noted above). I also used pairwise correlations to examine global-scale spatial correlations between cells for the different climate variables.

The CVH was tested using both species as data and latitude-band methods (same methods used to test the Rapoport effect, Chapter 4). For bin-methods, I used 5° latitude bins and employed both the Stevens (1989) and midpoint (Rhode et al., 1993) methods (Electronic Appendix A4). Latitude bands were also used to examine relationships between climatic factors and species diversity. For the species-as-data method, I extracted the relevant cells for each pinniped range and each climate variable and

calculated summary statistics. The median of the range of cells was used as the species-level data point for comparison, with the 25th and 75th percentiles as a measure of overall spatial variation in each range (Appendix A4). I also examined correlations between climate variables using species' median values.

To be reliable and informative, comparative studies must incorporate the effects of phylogenetic similarities in closely-related species (Harvey and Pagel 1991). I controlled for phylogeny using phylogenetic generalized least squares (PGLS) regressions and the supertree topology of Higdon et al. (2007) (Chapter 2), but present both conventional and phylogenetically-informed results as recommended by Garland et al. (1999). The REGRESSIONv2.m Matlab code (Lavin et al. 2008) was used to conduct regression analyses using both ordinary (i.e., non-phylogenetic) least-squares (OLS) and PGLS methods. An information-theoretic approach (Burnham and Anderson 2002) was used to guide model selection. Seven different models were examined using all variable combinations (1-3 variables per model), with model support based on AIC_c and Akaike weights. No interaction terms were included, as initial analyses indicated no significant interactions.

The molecular supertree topology (Higdon et al., 2007) included 34 species, treating the *Zalophus* sea lion complex as a single species with three subspecies (c.f. Wilson and Reeder, 1993). Higdon et al. (2007) used sequence data from one *Zalophus* taxon only (*Z. californianus*, California sea lion), and therefore only considered a single species in the phylogeny. The species status of the three taxa is still in debate, although recent genetic studies suggest that the three should be separate species (Sakahira and Niimi 2007; Wolf et al. 2007). The three taxa are found at different latitudes, with

varying climatic conditions, and the phylogeny was therefore modified to include three separate species (following Wolf et al. 2007, see Appendix A4).

Three sets of branch lengths (divergence dates) were originally examined – constant (equal) branch lengths (all = 1) in addition to two sets of estimated dates (Higdon et al. 2007). Further details on branch lengths assigned to the two additional *Zalophus* taxa are presented in the Appendix A4. Diagnostic correlations (Garland et al. 1992) indicated that only constant branch lengths had a suitable fit to the tip data for all the variables (Table A3.1), and all phylogenetically-informed analyses were therefore conducted using equal branch lengths only. The PHYSIG_LL.m Matlab code (Blomberg et al. 2003) was used to measure phylogenetic signal in the variables and as a further confirmation of branch length suitability and tree fit. Body size has a significant positive relationship with range size (Chapter 3), so female mass (\log_{10} g) was regressed against range size, using mass data from Ferguson and Higdon (2006) updated with *Z. wollebaeki* from IUCN (2010). Mass for *Z. japonicus* was estimated by comparing limited adult length data to length-mass relationships for the other two *Zalophus* species (using data summarized in IUCN 2010). All OLS and PGLS models used regression residuals to control for body size allometry in range sizes.

Results

Description of data

Annual mean SST ranges from high-latitude areas with a mean temperature below freezing (e.g., Arctic Ocean, with multi-year ice cover) to warm tropical waters that average nearly 30° C year-round (Figure 5.1). The warmest regions are also the least

variable, and climate variability (both inter- and intra-annual) is highest at mid-latitudes in both hemispheres (but more pronounced in the Northern Hemisphere than Southern). For all ocean data points ($n = 41,456$), there was a strong negative correlation between latitude and meanSST ($r = -0.830$, $P < 0.01$) and a weak positive correlation with seSST ($r = 0.233$, $P < 0.01$, $n = 35,970$), but no correlation with sdSST ($r = -0.094$, $P < 0.01$). Trends were similar using latitude bins ($n = 35$): meanSST: $r = -0.846$, $P < 0.001$; sdSST: $r = -0.079$, $P = 0.652$; seSST: $r = -0.032$, $P = 0.857$, $n = 34$). Spatial correlations between the three climate variables (all ocean data, $n = 41,456$) were all significant ($P < 0.05$) but weak (r from -0.210 to 0.131). For species median values, there was a significant correlation between meanSST and sdSST ($r = 0.476$, $P = 0.002$) but not between meanSST and seSST ($r = -0.212$, $P = 0.111$) or sdSST and seSST ($r = 0.210$, $P = 0.123$).

Phylogeny and body size

Significant ($P \leq 0.05$) phylogenetic signal was indicated for annual mean SST, geographic range size, and female mass (Table 5.1), but not for the other two climatic variables. Body size (female mass) is positively related to range size ($n = 35$, $R^2 = 0.224$, $F(1, 33) = 10.821$, $\beta = 0.981$, $P = 0.002$), and residuals were therefore used to control for body size allometry. Signal was reduced, but still significant, for residual range size (Table 5.1). For most variables a star phylogeny (i.e., conventional analysis) has a lower MSE than the phylogenetic tree. Results of both conventional (OLS) and phylogenetically-informed (PGLS) regressions are presented.

Range size and climate

Three (of seven) regression models of climatic effects on species range size received significant support (based on Δ_i AIC_c). Conventional and phylogenetically-informed results were similar, as the same three models were supported using both OLS and PGLS methods (trends were less extreme using PGLS regressions but still significant). All three models included a significant negative relationship between residual range size and meanSST (Table 5.2). The best model included meanSST only (OLS and PGLS), and the other two supported models each contained a non-significant negative relationship with one of the other variables. Temperature, but not temperature variability, has a significant effect on pinniped range size. Species ranges are not significantly larger in more variable temperatures, but rather are largest in areas with lower annual temperatures (Figure 5.2). Results were similar for latitude-band methods and again indicated a significant relationship with only temperature and not inter- or intra-annual temperature variability (Figure A3.1, Table A3.2).

Species diversity and climate

Two GLMs of climatic influences on pinniped species diversity had strong statistical support (AIC_c \leq 2) (Table 5.3). Both included a significant effect ($P \leq 0.05$) for meanSST² (a quadratic fit) plus a significant linear relationship with sdSST (Figure 5.3). One model included inter-annual variability but at $P > 0.10$. Temperature (mean annual SST) has a significant effect on pinniped species diversity, with diversity highest at moderate temperatures. Unlike patterns for geographic range size, however, intra-annual climatic variability (sdSST) also influences species diversity patterns (Figure 5.4).

Discussion

Pinnipeds exhibit a strong Rapoport effect, with a significant positive relationship between latitude and range size in both hemispheres, although the pattern cannot be explained by species diversity patterns (Chapter 4). Contrary to predictions, climate variability also failed to explain the Rapoport effect, and species in more variable climates (inter- and intra-annual variation in SST) do not occupy larger geographic ranges. There is also no significant latitudinal gradient in either sdSST or seSST, and both have a bimodal distribution with peaks at mid-latitudes in both hemispheres. Temperature (annual mean SST) does have a significant negative relationship with range size, and also exhibits a consistent latitudinal gradient across the globe. Results were similar for species-as-data methods and latitude-band methods (Appendix A4). The results of phylogenetically-informed statistics were similar to conventional analysis, which is not surprising as there is typically little phylogenetic signal in ecogeographical traits compared to life history traits (Chapter 4, plus references therein). Nonetheless, PCMs are required given the strong phylogenetic signal in body size, which also has a positive relationship with range size. Among the climate variables, only annual mean SST had significant signal, likely related to distributional patterns of the different pinniped families (i.e., phocids in Arctic and Antarctic areas with cold temperatures).

Temperature variability (sdSST) does have a significant positive relationship with species diversity (across 5° latitudinal bands), and this prediction was therefore supported. Diversity per latitude band also had a significant quadratic relationship with meanSST. Pinniped diversity is highest at latitudes with moderate mean SST and high monthly variation. Stevens (1989) argued that latitudinal gradients in geographical range

size and species richness may be directly connected, and proposed that the greater ecological flexibility of high-latitude organisms allows them to exist in ephemeral populations at lower latitudes, which leads to an increase in species richness in those regions. This could explain the high diversity of pinnipeds in marginal ice zones in both hemispheres, as these regions support a mix of pagophilic (ice-adapted) and terrestrially-mating species.

Why temperature?

The CVH requires both an appropriate gradient in climatic variability and a matching cline in the physiological tolerances of species, likely in thermal tolerances (Gaston et al. 1998). In the marine realm, temperature oscillations are less in polar and tropical than in temperate areas (leading to a bimodal distribution), the reverse of air temperatures, which increase at high latitudes, particularly in the Northern Hemisphere (Gaston and Chown 1999; Pörtner 2004). I tested for a gradient in climate variability (which wasn't supported at the global scale), but did not examine thermal tolerances. Despite its obvious importance as a mechanism for range size variation, the role of thermal tolerances across large latitudinal gradients has seldom been assessed (Spicer and Gaston 1999).

Among mammals, pinnipeds are unique in that they feed in the marine environment and reproduce on ice or land, and thus have a spatiotemporal separation of feeding and lactation (Bartholomew 1970). This amphibious nature has resulted in a range of physiological adaptations to life in two significantly different environments, and as a group pinnipeds show remarkable variation in life history, ecological and

physiological traits (Costa 1993; Boness and Bowen 1996). For endothermic animals, maintaining thermal balance is especially challenging when in water (Hind and Gurney 1997; Williams and Worthy 2002). The high thermal conductivity and heat capacity of water versus air promotes elevated rates of heat loss through conductive and convective pathways (Dejours 1987). Pinnipeds are exposed to a wide range of environmental conditions and variable temperatures, in conditions ranging from below freezing (polar habitats and at depth) to tropical, and species must also tolerate large amounts of thermal radiation when hauled out (Wartzok 1991; Costa 1993). Thick blubber layers (and fur) allow pinnipeds to retain heat in the ocean, but may promote overheating on land (Reijnders et al. 1993; Castellini 2008; Crocker and Costa 2008).

I used SST in these analyses, but with pinniped adaptations to cold water, air temperatures and possible thermoregulatory difficulties in warm climates may also provide an explanation of species richness and range size patterns. Research on upper thermal limits in air (e.g., Langman et al. 1996) would be instructive, providing information for predictions of future distributional changes with warming. Pinnipeds evolved in high latitude environments in the North Pacific or Arctic (Deméré et al. 2003; Rybczynsk et al. 2009) and are best adapted to cold conditions (Ferguson and Higdon 2006). The most parsimonious explanation for the significance of SST may relate to the presence of sea ice at higher latitudes: sea ice adaptations have resulted in larger ranges (Chapter 3), and colder ocean temperatures are required for sea ice formation.

Endothermic (seabirds and marine mammals) marine predators are most abundant at higher latitudes, with ectothermic (sharks, tuna, etc.) predators occupying top positions in tropical waters. Optimal performance temperatures in active animals tend to be close to

their upper thermal limits (Angilletta et al. 2002), and Cairns et al. (2008) proposed that temperature-dependent predation success (TPS) could explain global patterns in marine vertebrate diversity and distribution. Pinnipeds and pursuit-diving seabirds are most abundant in areas with summer SST cooler than the mid-teens to low 20s ($^{\circ}\text{C}$) (see Figure 5.3 for a similar trend with annual mean SST), and their near absence in tropical regions may in part be due to TPS, both as predators and prey. Warm water increases the difficulty of capturing fish prey and while increasing pinniped vulnerability to predation by large sharks (Cairns et al. 2008). Shark predation can be a significant limiting factor on pinniped populations (e.g., Lucas and Stobo 2000; Bertilsson-Friedman 2006), and the distribution of sharks, as predators, prey, and competitors, may have a significant impact on pinniped distributions. Further research on the biogeography of both species groups will be instructive and may assist in disentangling temperature effects related to physiology and thermoregulation from those related to community structure and ecological interactions.

Why not variability?

Among mammals, Letcher and Harvey (1994) reported that latitude is a better predictor of Palearctic mammal range sizes than temperature variability, similar to my results. Latitude also explains more variance in global-scale patterns of small mammals' metabolic rates (Rezende et al. 2004) and digestive tract efficiency (Naya et al. 2008) than climatic variables. One proposed explanation is that latitude is correlated with other ecologically relevant factors, such as day length and environmental productivity (Rezende et al. 2004). Temperature variability is not well related to latitude, with distinct

peaks at mid-latitudes in both hemispheres (Stevens 1989 found a similar pattern from terrestrial systems, but with peaks at higher latitude). At the global scale there is no consistent latitudinal gradient in SST variability, an implicit requirement for the CVH. Both intra- and inter-annual variability peak around 45° latitude in both hemispheres, although the peak is most pronounced in the Northern Hemisphere. The Northern Hemisphere peak in pinniped species diversity at this latitude also corresponds to areas with the most productive global fisheries (Gelchu and Pauly 2007). The relationship between energy availability (productivity) and species richness (the species-energy relationship) is a well documented macroecological phenomenon (Bonn et al. 2004), and ocean productivity may be a significant predictor of pinniped species diversity.

Schipper et al. (2008) presented marine mammal diversity patterns which featured strong latitudinal peaks in species richness around 40° in both hemispheres, suggesting that cetacean diversity patterns are similar to those of pinnipeds. The authors suggested that hotspots of marine mammal richness are associated with peaks of marine primary productivity that occur at those latitudes (Field et al. 1998). In contrast, however, a number of empirical studies have revealed SST, and not productivity, as the major factor driving species richness patterns for marine vertebrate predators (tuna and billfish, cetaceans) (Worm et al. 2005; Boyce et al. 2008; Whitehead et al. 2008, 2010). These results suggest that global increases in SST (e.g., IPCC 2007) will have a greater impact on diversity patterns of marine predators than changes in marine productivity (also see Cairns et al. 2008; Worm and Lotze 2009). Further empirical studies on pinnipeds are warranted, as different physiological traits and thermal adaptations (compared to cetaceans) may result in different responses to current and future predicted SST and

productivity conditions. As noted, air temperatures may play a significant role in pinniped distribution, a factor which would be expected to be less significant for cetaceans and large predatory fish.

Implications and conclusions

Species distributions are affected by large-scale climatic fluctuations at a variety of temporal scales (Stenseth et al. 2002; Walther et al. 2002), and environmental variability can have a considerable impact on top predator life history and demography (Isaac 2009). Pinniped range sizes respond strongly to annual mean SST (and also to annual variation in SST for species diversity). Species are adapted to cold conditions (Ferguson and Higdon 2006; Cairns et al. 2008), and sea ice adaptations in particular have resulted in large distributions (Chapter 3). Variable mid-latitude environments support a mix of temperate and polar species, leading to high diversity.

Pinnipeds are sensitive to temperature limits and may suffer range contractions as temperatures increase (in both water and air) (Reijnders et al. 1993; Cairns et al. 2008). Contractions in range size will influence species diversity patterns, and the most species-rich areas may shift. Poleward shifts in temperate species could result in increased competition with Arctic and Antarctic species (phocids and the walrus) as these species suffer their own range reductions due to declining sea ice availability. Climate-induced range contractions will most likely increase a species' risk of extinction (Isaac 2009; Thomas et al. 2004), and marine mammals with restricted geographic distributions and/or temperature tolerances are predicted to be particularly negatively affected by climatic changes (Learmonth et al. 2006). Large scale research on clinal patterns in physiological

traits (macrophysiology, Chown et al. 2004) is expected to be important for understanding species' distributions in the marine environment (Osovitz and Hofmann 2007). Climatic niche models (e.g., Elith and Leathwick 2009) can be combined with climate projection data to improve predictions of pinniped responses to warming climate (Buckley 2007; Wake et al. 2009).

The CVH was not supported as an explanation of the latitudinal gradient in pinniped geographic range, although annual SST variability does have a positive relationship with species richness. Temperature, but not temperature variability, appears to be the most limiting factor in pinniped distribution patterns (also see Cairns et al. 2008; Whitehead et al. 2008, 2010). Temperature-related range size and diversity patterns in pinnipeds are likely a function of sea ice formation (Chapter 3), thermoregulatory effects (Castellini 2008; Crocker and Costa 2008), and ecological interactions with ectothermic fish as predators and prey (Cairns et al. 2008). Additional research on the effects of air and water temperatures, spatiotemporal patterns of productivity, and interactions with other marine top predators on pinniped distribution will provide a better understanding of conservation needs and provide guidance to predictions of future changes. Climatic factors influence distributions and range sizes but also life history and ecological processes (e.g., Twiss et al. 2007). A better understanding of the complex interactions between latitudinal range, climatic seasonality and breeding systems (Millien et al. 2006; Isaac et al. 2009) is also required to improve conservation of pinnipeds (and other marine top predators) in a rapidly changing environment.

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Table 5.1. Statistics for randomization tests for significance of phylogenetic signal for geographic range size, female body mass, residual range size controlling for body size allometry, and climatic variables as calculated with the Matlab program PHYSIG_LL.m (Blomberg *et al.*, 2003). The phylogenetic tree is from Chapter 2 and constant branch lengths (all = 1) were used. Significant results for the randomization test of the mean squared error (MSE; lower values indicate better fit of tree to data) on the phylogenetic tree indicate the presence of phylogenetic signal for a trait. K-statistics indicate the amount of phylogenetic signal relative to a Brownian motion expectation (Blomberg *et al.*, 2003).

Trait	Expected		Observed				log maximum		
	MSE0/MSE	2.501	MSE0/MSE	K	MSE	MSE _{star}	P	likelihood	likelihood _{star}
Ann. mean SST	2.501	1.425	0.567	0.150	0.210	0.000	0.000	-15.9439	-21.8227
SD ann. mean	2.501	0.918	0.367	0.062	0.053	0.058	0.058	-0.4394	2.4079
Inter-ann. SE	2.501	0.576	0.230	0.076	0.041	0.945	0.945	-3.9388	6.6514
Geog. range size	2.501	1.133	0.453	0.573	0.604	0.005	0.005	-39.4067	-40.3403
Female mass	2.501	1.692	0.677	0.131	0.155	0.000	0.000	-13.5840	-16.5287
Residual range size	2.501	0.964	0.385	0.474	0.455	0.016	0.016	-36.0832	-35.3772

Table 5.2. Comparison of ordinary (non-phylogenetic) least-squares (OLS) and phylogenetic generalized least squares (PGLS) regressions of climate variability and geographic range size. Only models with significant statistical support ($\Delta_i AIC_c \leq 2$) are presented (15 different models total). Dependent variable is residual range size (controlling for body size). Blank fields for variables indicate those not included in the model. Regression coefficients shown for included variables, significance (** < 0.001, * < 0.01, or not significant) based on t-statistics.

Regression type	Variable(s) in model (β)			F	d.f.	R ²	P	AIC _c	$\Delta_i AIC_c$	w
	Ann. mean SST	SD ann. mean	Inter-ann. SE							
OLS	-1.038**			32.509	1, 33	0.481	< 0.001	53.530	0.000	0.550
	-0.963**		-0.337 ^{NS}	15.779	2, 32	0.465	< 0.001	55.395	1.865	0.221
	-0.966**	-0.303 ^{NS}		16.287	2, 32	0.473	< 0.001	55.515	1.985	0.167
PGLS	-0.990**			14.827	1, 33	0.310	< 0.01	65.952	0.000	0.483
	-1.023**		-0.341 ^{NS}	16.344	2, 32	0.328	< 0.01	67.579	1.627	0.214
	-0.833*	-0.440 ^{NS}		8.091	2, 32	0.328	< 0.01	67.610	1.657	0.211

Table 5.3. Species diversity versus climatic variability (5° latitude bins), with meanSST included as both linear and quadratic terms (see Figure 5.3).

Variable(s) in model (β)		F	d.f.	R^2	P	AIC_c	$\Delta_i AIC_c$	w
meanSST	meanSST ²							
	sdSST							
	seSSTie							
0.242	-0.156**	40.737	3, 31	0.778	<0.001	-74.208	0.000	0.507
0.178	-0.135*	32.514	4, 30	0.788	<0.001	-74.151	0.057	0.493

Figure 5.1. Climate data used in this study, showing global and latitudinal variation. Top: mean objectively analyzed annual SST, middle: standard deviation of mean annual SST (inter-annual variation), bottom: standard error of statistically analyzed annual mean SST (intra-annual variation).

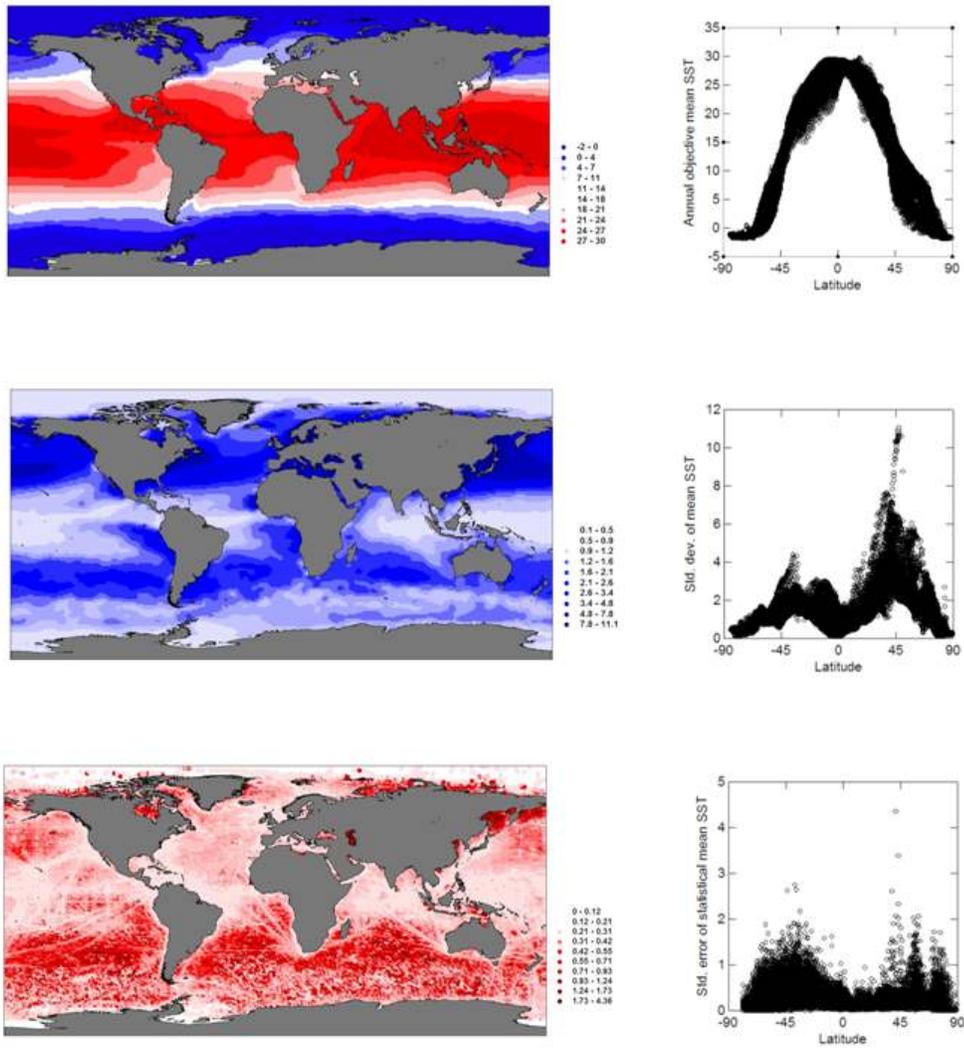


Figure 5.2. Scatterplots of relationships between climate variables and geographic range size in world pinnipeds (using species-as-data approach, with no controlling for phylogeny). Range size is residual of regression against female mass to control for body size allometry. Top: mean objectively analyzed annual SST (meanSST), middle: standard deviation of mean annual SST (inter-annual variation) (sdSST), bottom: standard error of statistically analyzed annual mean SST (intra-annual variation) (seSST).

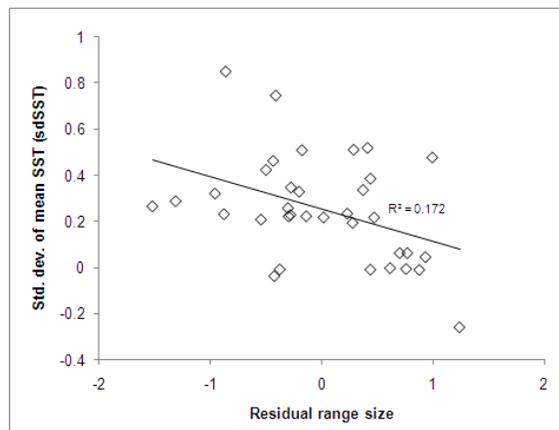
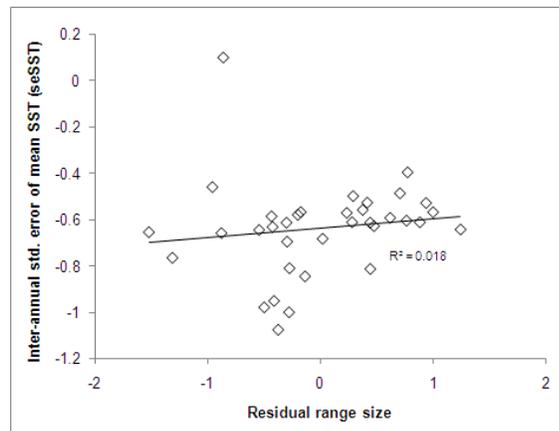
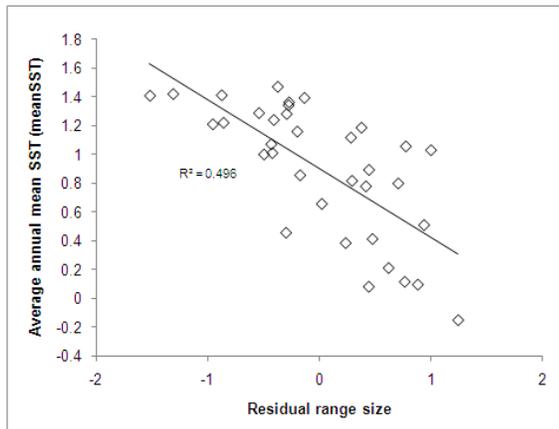


Figure 5.3. Scatterplots of relationship between pinniped species diversity and median climate values per 5° latitude bin. Top: mean objectively analyzed annual SST (meanSST), middle: standard deviation of mean annual SST (inter-annual variation) (sdSST), bottom: standard error of statistically analyzed annual mean SST (intra-annual variation) (seSST).

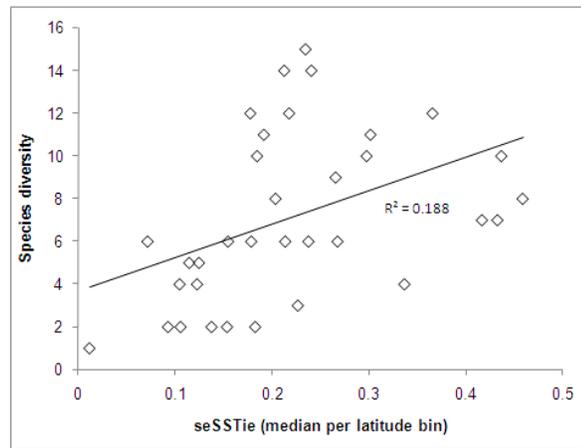
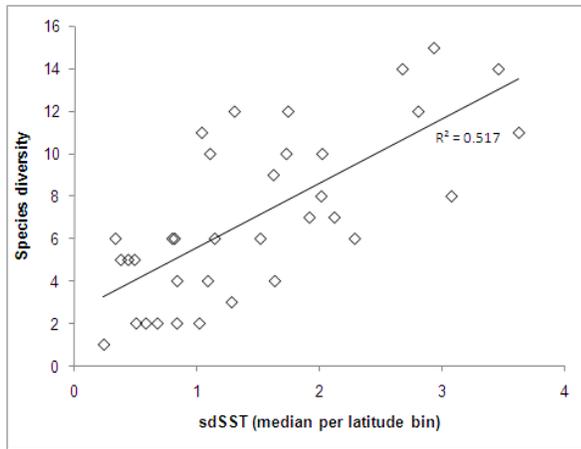
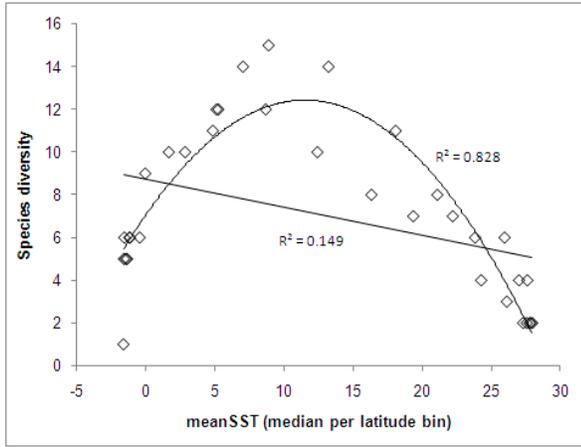
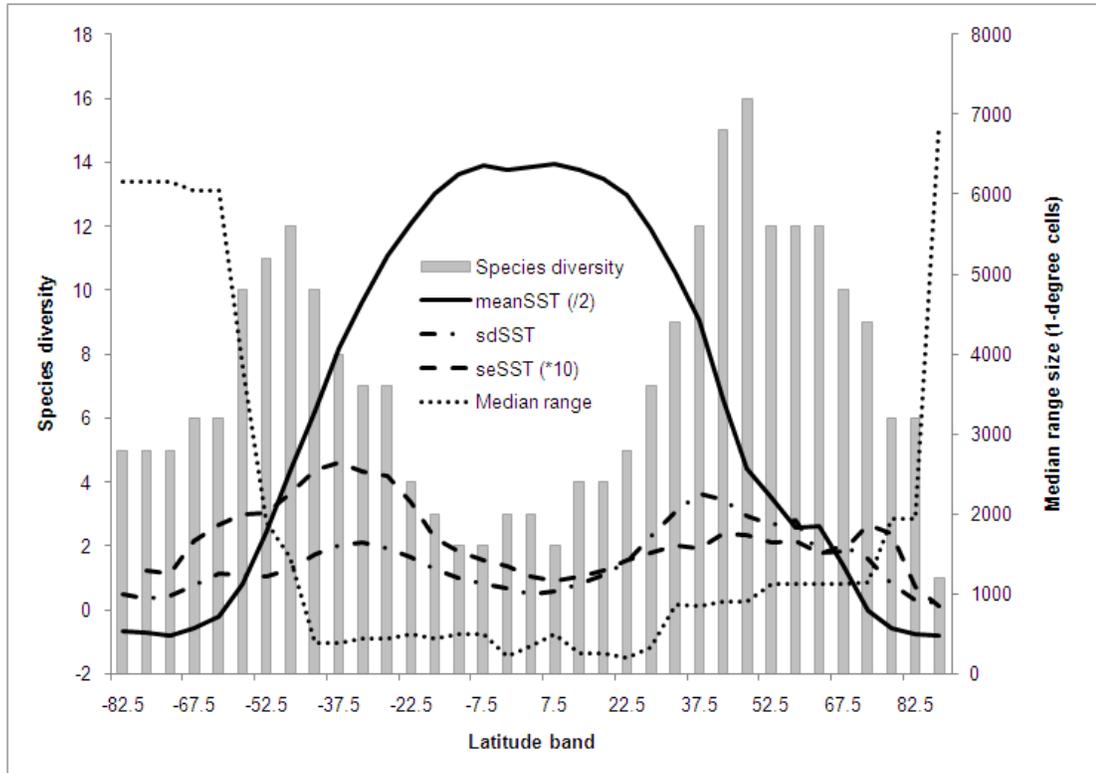


Figure 5.4. Latitudinal variation in species diversity, median range size, and climate variables (median values per 5° latitude band).



6. Summary, conclusions, and directions for further research

Introduction

A better understanding of global-scale biogeographic processes is necessary for improved conservation and management, particularly with current environmental changes associated with shifting climate patterns and increased anthropogenic impact (Margules and Pressy 2000). This thesis used species-level comparative analyses to examine latitudinal patterns in geographic range size and species diversity of world pinnipeds (Carnivora: Mammalia), a monophyletic group of marine mammals with an extensive global distribution. These results provide important information on pinniped phylogeny and evolution and on the factors influencing global distribution, and are summarized below along with directions for further study.

Key findings and future research directions

Pinniped phylogeny

Accurate phylogenies are essential for effective conservation research, and ecologists and biologists are increasingly recognizing the need for PCM techniques in comparative analyses (Fisher and Owens 2004). Supertree and supermatrix construction methods were used with genetic sequence data (GenBank) to build a complete species-level phylogeny with dated branch lengths (Chapter 2). All the resulting phylogenies

were in broad agreement with other recent molecular studies and supported the monophyly of the pinniped families Otariidae and Phocidae, both phocid subfamilies, and an Odobenidae + Otariidae sister relationship. The main areas of disagreement between the different analyses, and with other studies, occurred in four poorly-supported regions of the topology. Divergence dates as estimated with fossil calibrations were in agreement with other studies (plus a more recent phocid analysis by Fulton and Strobeck 2010a) and the available fossil record.

Additional sequence data have since (post-2007) become available, but are still limited, particularly for southern fur seals (*Arctocephalus*) and especially for nuclear genetic markers. Even with additional data, resolution of parts of the tree will likely remain difficult given the apparent rapid radiations (also see Fulton and Strobeck 2010a). Among phocids, relationships within Phocina were poorly supported, and *Halichoerus* was nested within a paraphyletic *Pusa*. Fulton and Strobeck (2010b) used a large dataset including 15 nuclear genes, and provided the first molecular support for Phocina relationships that are consistent with morphology (Burns and Fay 1970), including a monophyletic *Pusa*. Accurate placement of *Halichoerus* is of particular interest given the evolutionary transitions in habitat types and significant variability in habitat use (Chapter 3). There is also uncertainty among otariid relationships, but additional data have added little resolution (Dasmahapatra et al. 2009; Yonezawa et al. 2009).

Slight changes to tree topology tend to have little quantitative effect on PCM results (Ferguson 2006), although an accurate phylogeny is necessary for studies on historic biogeography (e.g., Chapter 3). Deméré et al. (2003) reviewed fossil taxa,

although an extensive and thorough re-analyses of the pinniped fossil record would be instructive given the recent findings in the Canadian Arctic (Rybczynski et al. 2009). Morphological data from extant and extinct taxa could be combined with genetic and stratigraphic data, and similar total-evidence studies have provided important information on cetacean evolution (e.g., Messenger and McGuire 1998; Geisler and Uhen 2005; O'Leary and Gatesy 2008). Accurate phylogenetic information is also essential for informed conservation research. With limited funds and increasing impacts, prioritization of conservation efforts is becoming increasingly necessary, and measures based on phylogenetic diversity (Faith 2008) provide an effective method, provided phylogenies are accurate. Accurate branch lengths estimates (divergence dates) are also necessary for studies on pinniped historical demography (e.g., Hoffman et al. 2009; Pinsky et al. 2010), which provide important information for effective species conservation.

Pinniped taxonomy

The supertree results also have implications for taxonomic revision of the pinnipeds. A number of studies, both morphologic and genetic (reviewed in Chapter 2), have suggested the need for revision of otariid taxonomy. The Society for Marine Mammalogy (SMM) recently established a Committee on Taxonomy to produce the first official SMM list of species and subspecies (Committee on Taxonomy 2009). The Committee followed the classification and scientific names of Rice (1998) with adjustments to reflect recent research. All 19 phocid species were recognized and accepted, but the species-level taxonomy of otariids was modified significantly. Otariid revisions are summarized in Table 6.1, with 12 species (including one extinct) recognized

(Committee on Taxonomy 2009) versus the 14-16 species traditionally recognized. The Committee followed Brunner (2004) (a morphological analysis) for otariid revisions, but even among the members consensus on some issues was not possible (Committee on Taxonomy 2009), particularly for cases in which genetic support is lacking. Further research on otariid relationships is clearly required (as is further study on some relationships in both phocid subfamilies).

Sea ice adaptations and range size evolution

Pinnipeds are unique among mammals in that they utilize marine habitats for feeding and terrestrial (land or ice) habitats for parturition, and this dichotomy had a significant influence on life-history evolution (reviewed in Chapters 3-5). Chapter 3 examined the influence of sea ice parturition and aquatic-mating adaptations on pinniped range size evolution while controlling for body size allometry and phylogeny. Both mating and parturition adaptations influenced range size evolution, with aquatic mating and ice pupping species having larger ranges. Sea ice adaptations had the biggest impact on range size expansion, allowing early pinnipeds to reduce their ties to terrestrial sites, which increased dispersal into novel habitats. Distributions of terrestrially-breeding species are limited by the availability of suitable terrestrial rookeries (Ferguson 2006).

Range size also has a significant influence on extinction risk (McKinney 1997), and at risk pinnipeds, which are mostly terrestrial breeders, have significantly smaller range sizes. Current threats to pinnipeds are mainly anthropogenic, but there is concern regarding sea ice declines resulting in range contractions and increasing extinction risk for pagophilic species (Isaac 2009). In the past, phocids have transitioned between

parturition habitats, and similar shifts could happen again in the future (although anthropogenic impacts are also greater now than at any time in the past). Some pagophilic species may be able to adapt to suitable terrestrial sites, and an analysis of life-history variation as it relates to different habitat types (land, pack ice, fast ice) may assist in predictions of species' adaptability. Distributions have shifted in response to past climatic conditions, and an assessment of the availability of suitable terrestrial sites, assuming species can adapt to them, would be instructive. Pagophilic species in the North Atlantic may be in a better position to adapt to loss of sea ice habitats than those in the North Pacific and the Antarctic because there would be no competition with terrestrially-mating otariids for limited habitats.

Aquatic mating and sea ice parturition, speciation and pinniped historic biogeography

Both maximum likelihood (ML) and maximum parsimony (MP) reconstruction methods strongly support aquatic mating as the ancestral state, evolving with the most recent common ancestor (MRCA) of crown-group pinnipeds (Chapter 3). Adaptations to aquatic mating may have been a major driving force in early pinniped evolution. Reconstructions for parturition habitat were less certain, but sea ice was reconstructed as the ancestral habitat for the pinniped MRCA. Modern pinnipeds originated ca. 33.5 mya at a time corresponding with a major global climatic shift from a 'greenhouse' to an 'icehouse' world (Zachos et al. 2001; Liu et al. 2009). Early adaptations to expanding polar conditions may have facilitated speciation, dispersal and range expansion, and likelihood-based biogeographic models (e.g., Ree et al. 2005; Ree and Smith 2008) could be used to study pinniped evolutionary biogeography in greater detail.

Latitudinal variation in pinniped range size

High-latitude pagophilic species have larger geographic range sizes, and as a group pinnipeds show strong support for the Rapoport effect (positive relationship between latitude and range size, Stevens 1989) (Chapter 4). A global-scale Rapoport effect is supported after controlling for body size allometry and phylogenetic relationships. Using conventional statistics a positive relationship between body size and latitude (Bergmann's Rule) is supported. Body size also exhibits significant phylogenetic signal, and Bergmann's Rule was no longer supported after phylogenetic corrections. The Rapoport effect was also supported using latitude-band methods. Several authors have suggested that the Rapoport effect is not present in the ocean (Rohde et al. 1993; Roy et al. 1994), but it is strongly supported for world pinniped ranges.

Several different explanations have been proposed for the Rapoport effect. One is the trend for species diversity to be highest in low latitude tropical areas, which Stevens (1989) hypothesized would result in smaller range sizes. A negative relationship between latitude and species diversity does exist for many species groups, in both marine and terrestrial ecosystems, but there are also exceptions (Gaston 2003). Pinnipeds provide one of these exceptions, and richness is lowest in tropical latitudes. Species diversity has a bimodal distribution, with peaks at mid-latitudes in both hemispheres, and cannot explain the global-scale Rapoport effect for pinniped ranges. Several other explanations for increasing range sizes at higher latitudes have been proposed, including the climatic variability hypothesis (Stevens 1989) tested in Chapter 5. Other factors that may

influence pinniped geographic range sizes include species evolutionary age (Webb and Gaston 2000) and constraints imposed by coastline geography (Brown et al. 1996).

The bimodal distribution of pinniped species diversity, with mid-latitude peaks in each hemisphere, suggests possible mid-domain effects operating both north and south of tropical waters. This refers to the phenomenon of increasing overlap in species ranges towards the centre of a domain due to geometric constraints on range size distributions, producing a peak in richness towards the center of the domain (Colwell and Lees 2000, also see Colwell and Hurtt 1994; Willig and Lyons 1998). These models have been controversial, as some studies found evidence for a mid-domain effect in latitudinal gradients in species richness (e.g., Lees and Colwell 2007; Rahbek et al. 2007; Dunn et al. 2007), and other report little to no correspondence between predicted and observed latitudinal patterns (Hawkins and Diniz-Filho 2002; Kerr et al. 2006; Currie and Kerr 2007). These differences highlight both the pitfalls associated with assuming that species groups fit general patterns and the importance of empirical tests using the group(s) of conservation interest.

Evolutionary relationships between speciation and range size are also of interest. Two studies have examined associations between diversification rate and mean range size between clades. Gaston and Blackburn (1997) used North American birds and found no significant association, but Cardillo et al. (2003) found a significant positive association for Australian mammals, with faster diversification within a clade leading to larger geographical ranges. Higher dispersal capabilities (e.g., birds versus non-volant Australian mammals) may allow some species groups to more easily avoid environmental

disturbances and reduce extinction threats, leading to increased diversification rates and larger ranges in more diverse clades. Cardillo et al. (2003) suggested that further studies compare the effect of geographic range size on diversification rate between taxa which differ in their dispersal abilities. A comparison of speciation rate of phocids and otariids or ice-adapted versus terrestrial species would be of interest given the differences in population-level dispersal imposed by mating system (Chapter 3).

Climatic influences on pinniped species diversity and range size

The climatic variability hypothesis (CVH) (Stevens 1989) was tested as an explanation for the Rapoport effect and latitudinal patterns in species diversity. The hypothesis postulates that species at higher latitudes experience greater temporal variability in climatic conditions, which they evolve adaptations to, increasing their tolerance range and leading to larger range sizes. The CVH was not supported as an explanation of the Rapoport effect. Mean annual SST was a significant predictor of range sizes, and this was also the only climate variable that followed a consistent latitudinal gradient at the global-scale. Temperature variation did explain latitudinal patterns in pinniped diversity, which also had a significant quadratic relationship with mean annual SST. The CVH requires a gradient in climatic variability, but there is no consistent global gradient in inter- or intra-annual variation in SST, with peaks at mid-latitudes in both hemispheres. High temperature, but not temperature variability, appears to be the most important limiting factor in pinniped distribution patterns. Temperature-related range size and diversity patterns in pinnipeds are likely a function of sea ice formation (Chapter 3),

thermoregulatory effects (Castellini 2008), and ecological interactions with ectothermic fish (Cairns et al. 2008).

The CVH implicitly requires a latitudinal cline in the physiological tolerances of species, likely in thermal tolerances (Gaston et al. 1998; Chown et al. 2004). I tested for a gradient in climate variability, but did not examine thermal tolerances. Pinnipeds use a combination of marine and terrestrial habitats, and are likely influenced by temperatures in both environments. Thick blubber layers allow pinnipeds to retain heat in the ocean, but may promote overheating on land (Castellini 2008). Research on clinal patterns in upper thermal limits in air and water would provide critical information for predictions of future distributional changes with warming. Cairns et al. (2008) proposed that temperature-dependent predation success could explain global patterns in marine vertebrate diversity and distribution. Pinnipeds are most abundant in areas with cooler summer temperatures, and their near absence in tropical regions may in part be due to competitive and predation interactions with ectothermic and partially endothermic predators like sharks. Predation can be a significant limiting factor for pinniped populations (Riedman 1990), and the distribution of sharks may have a significant impact on pinniped distribution patterns.

Stevens (1989) proposed that the greater ecological flexibility of high-latitude organisms allows them to exist in ephemeral populations at lower latitudes, leading to an increase in species richness in those regions. This could explain the high diversity of pinnipeds in marginal ice zones in both hemispheres, as these regions support a mix of pagophilic and terrestrially-mating species. Temperature is the major factor driving

marine richness patterns (see Chapter 5), and global increases in SST (e.g., IPCC 2007) could have a significant impact on diversity patterns. Improved understanding of past responses to climatic variation (e.g., Harrington 1998) will benefit predictions of response to future changes.

Conclusion

This thesis examined global distribution and diversity patterns of world pinniped species (Carnivora (“Pinnipedia”), Mammalia), and provided important information on latitudinal trends in range size, body size and species diversity. Macroecological studies are important for explaining global-scale distribution and diversity patterns, and provide important information on how climate influences these patterns (Brown 2000; Gaston and Blackburn 2000). Environmental conditions play a significant role in shaping species’ distributions, life-history, and extinction risk (Isaac 2009), and a better understanding of these relationships will improve conservation efforts, particularly given the rapid climatic changes and increasing anthropogenic impacts species currently face. Information on range size distributions and species richness patterns is critical to effective conservation planning (reserve design, area closures, etc.). It will be important for conservationists to examine highly diverse regions at mid-latitudes to protect the highest number of species, but care must be taken to ensure consideration of changing patterns.

Pinnipeds are adapted to cold conditions (Ferguson and Higdon 2006), and sea ice adaptations have resulted in large ranges (Chapter 3). Variable mid-latitude environments

support a mix of temperate and polar species, leading to high diversity. The sea-ice habitats critical to these species are currently experiencing significant environmental change, and declines in sea ice have led to concern about the future of a number of ice-adapted species (e.g., Laidre et al. 2008). The most parsimonious explanation for the significance of SST may relate to the presence of sea ice at higher latitudes: sea ice adaptations have resulted in larger ranges, and colder ocean temperatures are required for sea ice formation. Warming temperatures and declines in sea ice extent are likely to cause range contractions, and increased extinction risk, for at least some pagophilic species. With declining sea ice, these species will need to respond through shifting distributions and/or behavioural adaptations. A better understanding of the role of past climatic and sea ice trends on pinniped evolutionary biogeography will assist with predictions of response to environmental change. Species are sensitive to temperature limits and some may suffer range contractions as temperatures increase, likely increasing extinction risk.

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Table 6.1. Revised otariid taxonomy from the first official list recognized by the Society for Marine Mammalogy (Committee on Taxonomy 2009), compared with the (more traditional) taxonomy used here.

Species	Subspecies	This thesis
<i>Arctocephalus pusillus</i> (Schreber, 1775)	<i>A. p. pusillus</i> (Schreber, 1775) <i>A. p. doriferus</i> Wood Jones, 1925	<i>A. pusillus</i>
<i>Arctocephalus gazella</i> (Peters, 1875)		<i>A. gazella</i>
<i>Arctocephalus tropicalis</i> (Gray, 1872)		<i>A. tropicalis</i>
<i>Arctocephalus australis</i> (Zimmerman, 1783)	<i>A. a. australis</i> (Zimmermann, 1783) <i>A. a. forsteri</i> (Lesson, 1828) <i>A. a. galapagoensis</i> Heller, 1904 <i>A. a. gracilis</i> Nehring, 1887	<i>A. australis</i> <i>A. forsteri</i> <i>A. galapagoensis</i>
<i>Arctophoca philippii</i> (Peters, 1866)	<i>A. p. philippii</i> Peters, 1866 <i>A. p. townsendi</i> (Merriam, 1897)	<i>Arctocephalus philippii</i> <i>Arctocephalus townsendi</i>
<i>Callorhinus ursinus</i> (Linnaeus, 1758)		<i>Callorhinus ursinus</i>
<i>Zalophus japonicus</i> (Peters, 1866) (extinct)		<i>Zalophus japonicus</i> ¹
<i>Zalophus californianus</i> (Lesson, 1828)	<i>Z. c. californianus</i> (Lesson, 1828) <i>Z. c. wollebaeki</i> Sivertsen, 1953	<i>Zalophus californianus</i> ¹ <i>Zalophus wollebaeki</i> ¹
<i>Eumetopias jubatus</i> (Schreber, 1776)	<i>E. j. jubatus</i> (Schreber, 1776) <i>E. j. monteriensis</i> (Gray, 1859)	<i>Eumetopias jubatus</i>
<i>Neophoca cinerea</i> (Peron, 1816)		<i>Neophoca cinerea</i>
<i>Phocarcos hookeri</i> (Gray, 1844)		<i>Phocarcos hookeri</i>
<i>Otaria byronia</i> (Blainville, 1820)		<i>Otaria byronia</i>

¹ Only one taxon (*Z. californianus*) included in the supertree/supermatrix analyses (Chapter 2), based on data availability from GenBank, but updated to recognize three species (following Wolf et al. 2007) in Chapter 5.

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