Original Article

The ghosts of competition past: body size, trophic ecology, diversity and distribution of global shark and pinniped species

Steven H. Ferguson[*1], Jeff W. Higdon[2], Ross F. Tallman[1], Aaron T. Fisk[3], Nigel E. Hussey[3]

[1] Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB, Canada, R3T 2N6
[2] Higdon Wildlife Consulting, 912 Ashburn Street, Winnipeg, MB, Canada, R3G 3C9
[3] Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada, N9B 3P4

Abstract

    Pinnipeds (Carnivora: Mammalia) and sharks (Elasmobranchii: Chondrichthyes) are both widely distributed marine top predators that occupy similar ecological niches. We examined global species diversity patterns of sharks (294 species) and pinnipeds (34 species) as a function of latitude. We then used body size and trophic position (TP) to test which relationship best described the global distributional pattern of species richness between the two clades: (1) pinniped as predator, (2) pinniped as competitor, or (3) pinniped as prey. Ecological relationships between the two species groups were diverse with some larger sharks actively consuming pinnipeds and some smaller shark species eaten by pinnipeds. Most sharks (81%) overlaped with pinnipeds for TP (3.3-4.3), however most sharks are smaller than pinnipeds (62% less than 128 cm maximum length), and only 8% of sharks (24) are longer than the largest pinniped. Latitudinal variation of sharks and pinnipeds indicated that species richness of pinnipeds was bimodally higher at temperate latitudes and lowest at equatorial latitudes between +40 and -40, the geographic region where shark species richness was greatest. A comparison of the three trophic models indicated that the predation model (sharks eat pinnipeds) best fit the distributional pattern. Oceanic regions that supported progressively more than 20 shark species resulted in progressively fewer pinniped species. Results suggest that sharks may exclude pinnipeds from much of the warmer oceanic waters through direct predation. However, an alternate hypothesis that differing thermal adaptations of the two clades may explain the observed distributional pattern is not refuted by our results. We discuss conservation implications associated with ocean warming assuming shark species distribution will expand to higher latitudes, likely at the expense of pinnipeds. [JMATE. 2014;7(1):23-39]

Keywords: Competitive exclusion, latitude, predation, seals, trophic position

Introduction

    Species of different taxonomic groups can co-occur in similar habitats but may differ significantly in competitive adaptations including morphology, life history, and behavior (35,65,66). Competition has been speculated to occur at cellular, individual, population, species, and clade levels through species sorting (5,12, 32,41,44,51). A possible example of competition at the species or clade level would be between sharks (Elasmobranchii: Chondrichthyes) and pinnipeds (Carnivora: Mammalia) (10). Mammals, as endothermic organisms, can occupy broader fundamental climate niches than ectothermic vertebrates or plants because they are able to buffer variation in climate (30). Thus, fundamental niche of mammals is likely wide and less subject to physiological constraints (18). The majority of sharks are ectothermic (exception family Lamnidae, heterothermic) while pinnipeds are endothermic and therefore it would be expected that mammals are better adapted to colder waters associated with high latitudes. Sharks have a long evolutionary history with evidence for temperature-dependent habitat preferences and more recent adaptation to high-latitude environments (19). Pinnipeds likely evolved in high-latitude environments and subsequently evolved adaptations to warmer environments (29,64). Sharks evolved adaptations to estuarine, coastal and pelagic environments (7,11,48). In contrast, pinnipeds have a much more recent evolutionary history (17) and yet display a similar diversity of habitat associations including estuarine coastal and pelagic (64). Interactions between the two taxonomic groups include predation by sharks on pinnipeds (39,50), pinnipeds on sharks (1,16), and evidence of competition for the same food sources (2,59). However, little consideration has been given to clade interactions and whether competitive exclusion occurs or whether past competition (ghosts) are responsible for the current distribution (10,14). Have the two taxonomic groups radiated to occupy all marine habitats or does one group competitively exclude the other?

    Previous research indicated that pinnipeds are largely relegated to high-latitude environments

JMATE

compared to the relatively warm-water habitats of sharks (10). Here we explore spatial patterns to see whether they are consistent with a possible competitive mechanism by first comparing latitudinal species diversity of sharks and pinnipeds to test whether their global distribution differs. Next we use trophic position (TP) and body size (length) to define whether indirect (competition for the same food) or direct (predation by sharks on pinnipeds and pinnipeds on sharks) interactions best fit the global pattern. Latitude is a robust habitat surrogate since it represents a number of environmental gradients that change relatively consistently from equator to pole, including temperature, primary productivity, seasonality and predictability (3,23,24,33). Finally, we consider how shark and pinniped global patterns in species diversity relates to conservation under a scenario of warming global ocean temperatures.

Materials and Methods

Data: We collected TP, body size, and range data on globally distributed shark species from the online version of Fishbase from data collected between December 2009 and March 2010 (28). We used the long-est of five length measures that are available in FishBase. Not all measures were available for all species and no species had more than three length variables (n = 135). Two variables were available for 140 species, and 19 species had only a single length variable. Maximum reported total length for females was available for 99 species, and this value was used for 63 species (longest length reported). Most species (288 of 294) had data for maximum reported length for male or unsexed specimens, and we used this value for 223 species. An additional six species had equal values for both of these variables, that is, both measures were the same, and this was the length value used. Commonly attained total length for male or unsexed specimens was available for 82 species but was only used for one species. Commonly attained total length for female specimens was only available for two species and was not used for any species, as it was not the longest value available. Standard length of male or unsexed specimens was reported for a single species only, and this was the length value used as it was the only one with data. Both

female and male/unsexed total length was available for 94 species, and the two measures were significantly correlated (r = 0.95, n = 94, P < 0.0001). Maximum total length (male/unsexed) and commonly attained total length (male/unsexed) was available for 83 species and the two measures were again highly correlated (r = 0.95, n = 83, P < 0.0001). Elasmobranch taxonomy is in a state of constant flux, with > 1,100 species currently recognized (21). We examined sharks only in the "superorder" Selachimorpha (8 orders of sharks), and excluded the superorder Batoidea with greater than 500 described species (3 orders; 17 families; eg skates, rays). A total of 495 shark species are currently recognized compared to 494 included in FishBase (21,28).

For pinnipeds, data were compiled from a variety of sources including Bininda-Emonds & Gittleman for body length, Pauly *et al.,* for TP, and Higdon and IUCN for global distribution and are detailed in subsequent sections (4,18,38,42). Length data available from Bininda-Emonds and Gittleman includes both male and female standard length in addition to the species average values which we used (4). All measures are highly correlated. For females and males, r = 0.82, n = 34 including the two *Pusa* species which were excluded from latitudinal analyses, P < 0.0001. Correlations between species averages and the male or female length values were even stronger, with r = 0.97 and r = 0.94, respectively. Some pinniped species are highly sexually dimorphic, but using male values instead of species averages would have had no significant influence on our classification. For example, if we used male length, the minimum length would be 129.3 cm, instead of 127.7 using the species average (minimum female standard length was 120 cm). Our data files are available upon request to the authors.

Trophic relations: Sharks were classed as pinniped-predators, pinniped-prey, or pinniped-competitors (with some overlap) based on TP and body size (length). For diet characterization, Cortés (15) included 17 shark species with marine mammal remains recorded in their diets, with a calculated minimum TP of 4.16. Nine of the 17 species overlapped with pinniped TP (range 3.3-4.3, (61)), and the other eight were higher than the maximum pinniped TP value (4.3). Using a TP cutoff of 4.3 (> than maximum

pinniped TP) would underestimate the number of pinniped-predators. We used 4.16 as the TP cutoff to identify pinniped-predators but also examined the effect of a less conservative threshold by comparing results with a TP value of 4.0 which was the mean pinniped TP, as the cutoff. TP assessments for sharks and pinnipeds likely are underestimated based on coarse scale grouping of prey items and associated bias in the TP calculation, but values derived from Pauly *et al.,* and Cortés for both taxonomic clades were used based on their standardized calculation and current availability of estimates for all species (15,35,61).

Body length (see Data above) was also considered in identifying pinniped-predator sharks. A large number of shark species have high TP values (≥ 4.0) despite being small in physical size. For example, Saldanha catshark (*Apristurus saldanha*) has a maximum length of 88 cm and a TP of 4.24. If length were ignored, this shark species would be classified as a pinniped-predator, despite being 30-40 cm shorter than the shortest pinniped species. Of the 17 sharks with marine mammal diet contributions listed by Cortés, species range in length from 120 cm to 750 cm maximum length (15). The shortest species, Portuguese dogfish (*Centroscymnus coelolepis*), feeds mainly on fish including other sharks and cephalopods, but also gastropods and cetacean meat on occasion (13). They are not known as a predator of pinnipeds, and are more likely a scavenger of cetacean carcasses. If Portuguese dogfish is excluded as a pinniped-predator, the next smallest species with a marine mammal component to the diet is 200 cm and is the Australian blacktip shark, *Carcharhinus tilstoni*. This is the same as the median length for pinniped species (200 cm, mean 211 cm) (4). We therefore used 200 cm minimum length as a factor in classifying sharks as possible pinniped-predators in combination with the TP requirements noted above.

TP for 32 pinniped species ranged from a minimum of 3.3 (Crabeater seal, *Lobodon carcinophagus*) to a maximum of 4.3 (both Elephant seals, *Mirounga* species) (61). Pinniped-competitor sharks were all those species that overlapped with pinnipeds in TP (3.3-4.3), regardless of length (overlapping with pinniped-predators, as some sharks could be both). Standard adult length (average of both sexes) of pinnipeds ranged from 127.7 cm (Ringed seal,

Pusa hispida) to 372.5 cm (Northern elephant seal, *Mirounga angustirostris*) (4). We classed sharks with a maximum length ≤ 100 cm as pinniped-prey and this also overlapped with the pinniped-competitor category.

Latitudinal distribution: For each shark species, FishBase provides a link to AquaMaps, including the point data used to produce the predictive maps (28,45). AquaMaps uses point data from OBIS-SEAMAP and GBIF (37, 49). The FishBase database also contains a link to point data, and also provides locations from OBIS and GBIF, in addition to other record locations specific to the FishBase database. We extracted maximum and minimum latitude, and the total number of point locations, from both data sets, for all 494 shark species. Pinniped distributions are better known than for most shark species, with established distribution maps (polygons) versus the point data available for sharks. A number of sources provide distribution maps (38). Recently, the IUCN produced a GIS dataset (ESRI ArcView shapefile) of global mammal ranges that contains distributional polygons for 34 extant pinniped species (42). We digitized the ranges for two recently extinct pinnipeds – Japanese sea lion (*Zalaphus japonicus*) and Caribbean monk seal (*Monachus tropicalis*) based on available historic information and included them in the analyses (63). Both species are extinct due to human persecution, and we assumed that both would still exist in their native range had such over-exploitation not occurred. Two pinniped species the Baikal seal (*Pusa sibirica*) and Caspian seal (*P. caspica*) are restricted to inland lakes/seas, where no sharks are present, and were therefore removed from the analyses (n = 34 pinnipeds total). For each pinniped species we calculated the maximum northern and southern latitudes of their range polygons. Each species (sharks and pinnipeds) was assigned to 5° degree latitude bands (n = 36) to plot latitudinal patterns in species richness.

Testing for competition: Latitudinal variation in shark and pinniped species diversity was examined via regression analysis. Analyses using latitudinal bands can be problematic due to statistical non-independence of band values because each species often contributes to more than one latitude band (31). If not addressed with

the proper analyses methods, this spatial pseudoreplication increases Type I error rates and produces artificially small p-values. The band data are spatially autocorrelated, and we therefore examined latitudinal diversity patterns using generalized least-squares (GLS) regressions with an autoregressive first-order process (gls function in R package 'nlme') (62). The standard linear model is of the form: $y = X*\beta + e$, where y is the response variable; X is the explanatory variable; β is the regression coefficient to estimate; and e is the error term. The generalized-least-squares (GLS) estimator of $\beta = b_{GLS} = (X'\Sigma^{-1}X)^{-1}X'\Sigma^{-1}y$, with covariance matrix $V(b_{GLS}) = (X'\Sigma^{-1}X)^{-1}$ and a first-order auto-regressive process, AR(1), defined as $\varepsilon t = \varphi\varepsilon_{t-1} + v_s$. The random shocks v_s are assumed to be Gaussian white noise and the covariance of two errors depends only upon their separation in s space (27). The models assessed the best fit relationships among the three shark-pinniped groupings: shark predation on pinnipeds, pinniped predation on sharks and competitive interactions.

Results

Trophic relations: Among all 294 shark species, overall length ranged from 20 to 2,000 cm and TP ranged from 3.06 to 4.6. Box-whisker plots of body length and TP summarize differences between sharks and pinnipeds (Figure 1). Body length and TP are both highly variable in sharks. Some orders, for example the Heterodontiformes and Pristiophoriformes, show little variation in total length, while the Carcharhiniformes, Lamniformes and Squaliformes show large variation. This variation in body length observed by order equated to larger variation in TP as would be expected. Pinnipeds show similarly large variation in TP, but are generally more similar in body length. Pinnipeds overlap, in both size (length) and TP, with members of all eight shark orders. Standard adult length (average of both sexes) of pinnipeds ranges from a minimum of 127.7 cm to a maximum of 372.5 cm. Mean average body length (n = 32) is 210.7 cm, close to the median value of 200.3 cm. Mean TP for pinnipeds was 3.97, with the median again similar (4.0). There were nine species with TP < 4 and 23 species with TP ≥ 4.

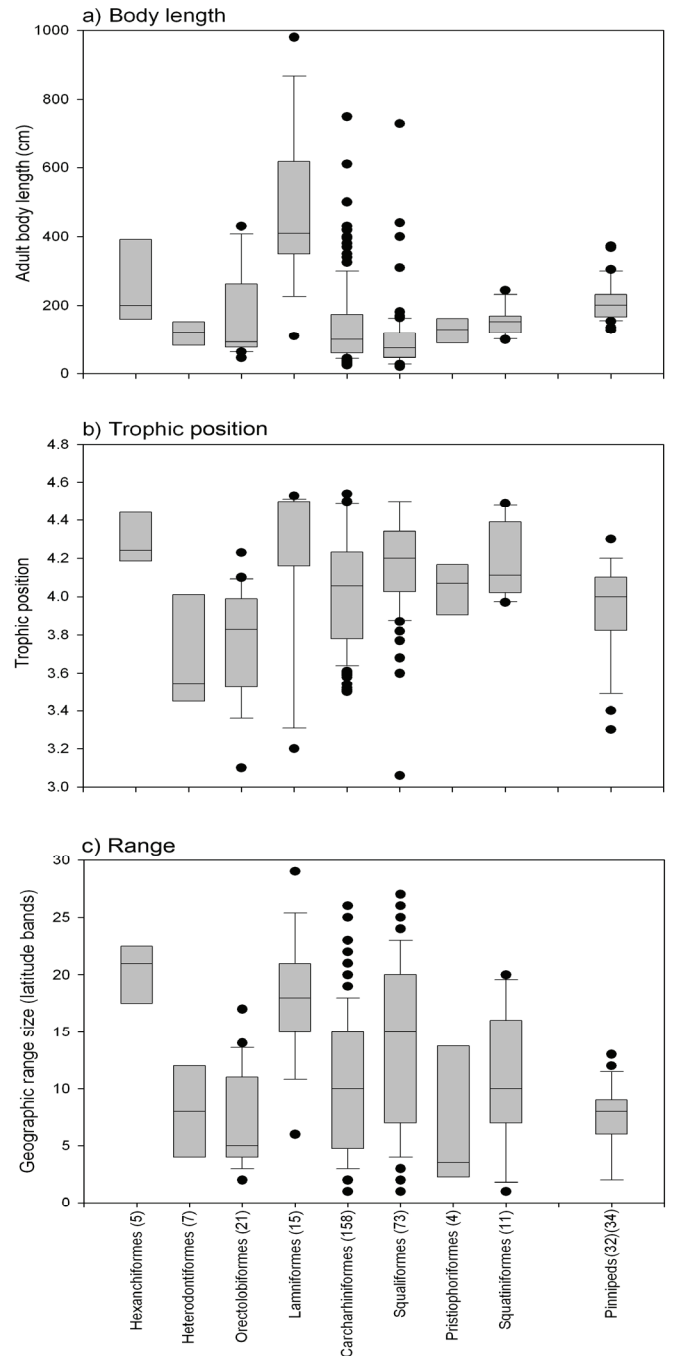We found correlations between TP and body size

Figure 1: Box-whisker plots summarizing (a) body length; (b) trophic position; (c) geographic range size of shark orders and pinnipeds. The lower boundary of the box indicates the 25th percentile, the line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. Whiskers above and below the box indicate the 90th and 10th percentiles, points are outliers. Body length plot excludes one 2000 cm long shark outlier (Lamniformes). Order of shark groups (orders) follows that of the Catalog of Fishes (21). Pinniped N = 32 for trophic position and length, n = 34 for range size (varying data available from original sources).

across all sharks combined, but no correlations within orders with the exception of Carcharhiniformes. TP and body size were correlated for all pinnipeds minus three that primarily consume invertebrates (molluscs, krill) using 2-tailed test looking for positive or negative values (Table 1).

In a comparison of sharks and pinnipeds we observed size and diet overlap with a proportion of sharks that overlap with pinnipeds for length and TP. Most sharks (n=237, 81%) overlap with pinnipeds for TP (3.3-4.3). Some (n=53, 18%) have a higher TP, only 4 species have a lower TP (< 3.3) than any pinniped species. Despite the overlap in TP, most sharks are smaller (shorter) than pinnipeds (<128 cm maximum length) (n=181, 62%). Nearly one third (n = 89, 30%) overlap in length and only 8% of sharks (n=24) are longer than the largest pinnipeds (total length > 373 cm).

Due to a lack of field data, we inferred sharks as pinniped-predators, pinniped-competitors, or pinniped-prey based on the combined metrics of TP and total length. Using TP ≥ 4.16 and total length ≥ 200 cm as thresholds, we classified 45 sharks as pinniped-predators, including all marine mammal eating sharks identified by Cortés (n = 16), excluding Portuguese dogfish (*C. coelolepis)* (28). This included 18 sharks that were also classed as pinniped-competitors. As a test of sensitivity, we also used a TP cutoff of 4.0 (mean and median pinniped TP) that resulted in 51 sharks being classified as pinniped-predators (including 24 pinniped-competitors). A total of 228 shark species were classified as pinniped-competitors, and 141 classified as pinniped-prey (with overlap for 124 species in both categories). If pinniped-prey were classified as those smaller than 128 cm instead (minimum pinniped adult length), an additional 40 shark species would be considered pinniped-prey. Table 2 summarizes the number of classified sharks by order and family.

Based on our definitions, there were 22 shark species that were unclassified including Portuguese dogfish, *C. coelolepis*. Generally the unclassified shark species were between 100 and 200 cm, and thus not classed as prey (> 100 cm), while their TP was too low or too high to be classed as pinniped-competitors (< 3.3 or > 4.3). The unclassified sharks were spread among 11 families in six orders, including two families (Stegostomatidae [order Orectolobiformes] and

Group	n	r	P
All sharks	294	0.21	< 0.001
Hexanchiformes	5	0.46	0.44
Heterodontiformes	7	-0.40	0.37
Orectolobiformes	21	0.023	0.92
Lamniformes	15	-0.35	0.21
Carcharhiniformes	158	0.39	< 0.001
Squaliformes	73	0.19	0.11
Pristiophoriformes	4	0.91	0.09
Squatiniformes	11	-0.52	0.11
All pinnipeds	31	0.19	0.31
Pinnipeds excluding three species that mainly consume invertebrates (TP 3.3-3.4)	28	0.62	< 0.001

Table 1: Correlations between total length and trophic position (TP) for sharks and pinnipeds.

Cetorhinidae [order Lamniformes]) with only one species each. Nine of the 22 are > 100 cm but < 128 cm, the minimum pinniped length (and would be included as pinniped-prey using an alternative cutoff, above). Another 11 are 130 to 175 cm, these generally have high TP, 4.31 to 4.5, except for one with TP = 3.06. One large species is included, the Basking shark (*Cetorhinus maximus*), is 980 cm long but TP = 3.2, and therefore lower than pinniped minimum. There are two other filter-feeders that eat zooplankton, the Megamouth shark, (*Megachasma pelagios*), (TP = 3.38) and the Whale shark (*Rhincodon typus)* (TP = 3.55). Both were classed as pinniped-competitors because their TP overlapped with the three pinnipeds with the lowest TP scores (3.3-3.4) that are planktonic or benthic foraging. These are the Crabeater seal (*Lobodon carcinophagus*), Walrus (*Odobenus rosmarus*) and Bearded seal (*Erignathus barbatus*) that are all limited to high latitudes in both hemispheres where sharks are unlikely to be abundant. We nonetheless retained these two species as potential pinniped-competitors.

Latitudinal distribution: The shark distribution dataset contained 303 species with at least 10 location points (range 10-24, 515 points, mean = 577, median = 73,

Order	Family (n w/ data)	Predators	Competitors	Prey	Unclassified[*]
Hexanchiformes	Hexanchidae (4)	2	3	0	
	Chlamydoselachidae (1)	1	1	0	
Heterodontiformes	Heterodontidae (7)	0	6	2	1
Orectolobiformes	Rhincodontidae (1)	0	1	0	
	Parascylliidae (3)	0	3	3	
	Brachaeluridae (2)	0	2	1	
	Orectolobidae (4)	1	4	2	
	Hemiscylliidae (8)	0	8	6	
	Stegostomatidae (1)	0	0	0	1
	Ginglymostomatidae (2)	0	2	0	
Lamniformes	Odontaspididae (3)	3	1	0	
	Mitsukurinidae (1)	0	1	0	
	Pseudocarchariidae (1)	0	1	0	
	Lamnidae (5)	5	0	0	
	Megachasmidae (1)	0	1	0	
	Cetorhinidae (1)	0	0	0	1
	Alopiidae (3)	3	0	0	
Carcharhiniformes	Scyliorhinidae (69)	0	62	64	2
	Proscylliidae (4)	0	4	3	
	Pseudotriakidae (2)	1	1	0	
	Leptochariidae (1)	0	1	1	
	Triakidae (26)	0	23	5	2
	Hemigaleidae (4)	1	3	1	1
	Carcharhinidae (44)	21	30	6	3
	Sphyrnidae (8)	3	5	0	
Squaliformes	Dalatiidae (51)	2	41	37	5
	Centrophoridae (11)	0	7	4	2
	Squalidae (9)	0	5	4	2
	Echinorhinidae (2)	2	0	0	
Pristiophoriformes	Pristiophoridae (4)	0	4	1	
Squatiniformes	Squatinidae (11)	0	8	1	2
Total	294	45	228	141	22

*Unclassified shark species (incl. Portuguese dogfish, *Centroscymnus coelolepis*) occurred due to their size (100 and 200 cm), and thus not classed as prey (> 100 cm), while their TP was too high or too low to be classed as pinniped-competitors (< 3.3 or > 4.3).

Table 2: Breakdown of sharks classified as pinniped-predator, pinniped-prey or pinniped-competitors, by order and family.
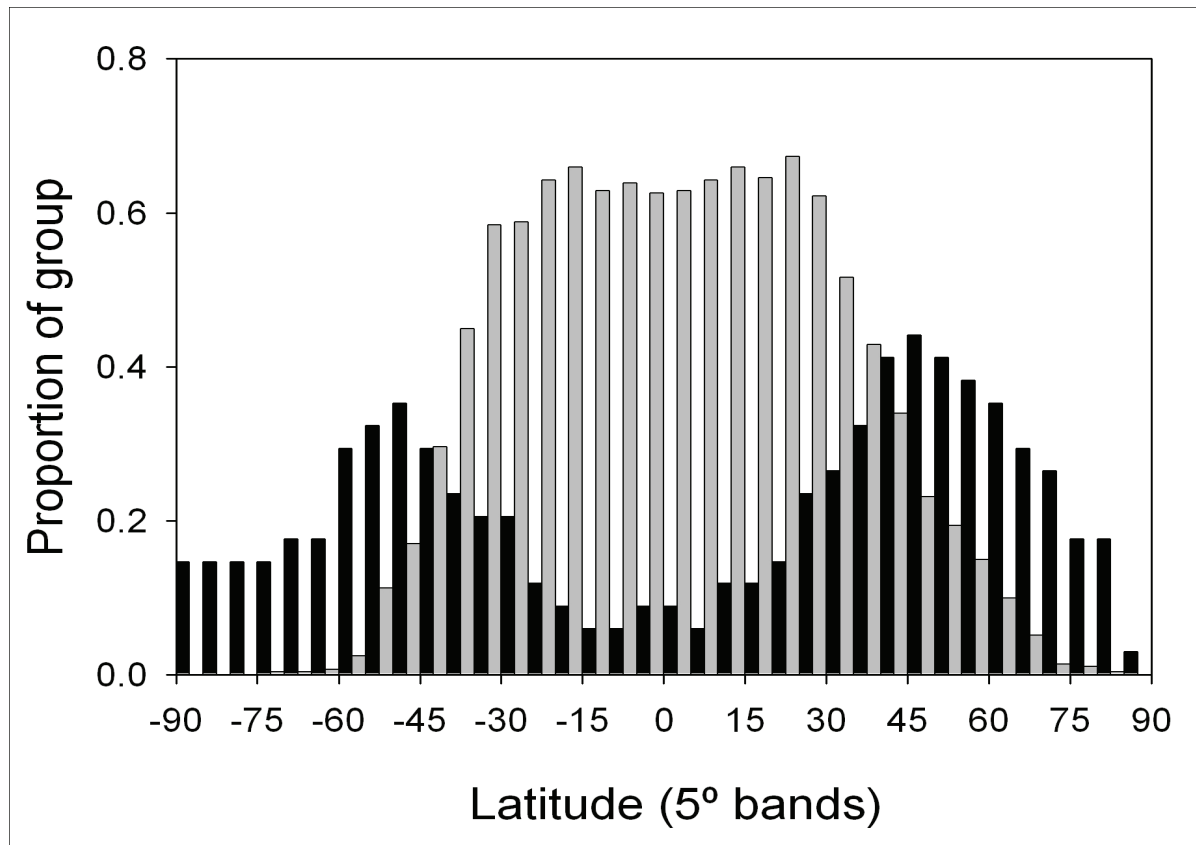
Figure 2: Latitudinal variation in species richness of sharks (gray bars, n = 294) and pinnipeds (black bars, n = 34) (36 5° latitude bands). The y-axis shows the percentage of the total examined species (294 sharks, 34 pinnipeds) in each group that occur in the 5° latitude band.

5-95th percentile range 12-2, 458). This distribution dataset was pruned to include only species with length data and TP available on FishBase, resulting in a final shark data set of 294, or 60% of the total recognized species. Coverage per shark family ranged from 32% to 100% and included 31 families (range 1-146 species per family) in eight orders (2-270 species per order). We measured total latitudinal extent (Figure 1c) using whichever data set included the largest number of locations (usually FishBase, 290 species; see Supplementary Material). There was still a significant relationship between total extent and the number of location points (linear regression on $\log_{10}$ data, n = 303, R^2 = 0.19, F(1, 301) = 70.84, p < 0.0001). Species are included from all eight orders (ranging from 50% to 94% of the species per order) (Appendix 3).

Latitudinal variation in species richness of sharks and pinnipeds was largely reversed with pinnipeds dominating at high latitudes and sharks dominating at low latitudes (Figure 2). Pinniped species richness distribution was bimodal with peaks at temperate latitudes, whereas shark species richness was normally distributed with a peak within +40 and -40° latitude, the area with few pinniped species.

Testing for competition: To explore spatial patterns and test whether they are consistent with a possible trophic explanation for the observed pattern, we investigated the relationship of richness per latitudinal band after dividing the sharks into pinniped-predator, pinniped-competitor, and pinniped-prey groupings. We tested both methods of classifying sharks as predators but found no qualitative difference in results; therefore we report only on pinniped-predators defined as sharks greater than 200 cm in length and having a TP > 4.16. Plots of shark species richness versus pinniped species richness were fit to all shark species and three shark groupings using a second-order polynomial relationship (Figure 3). A
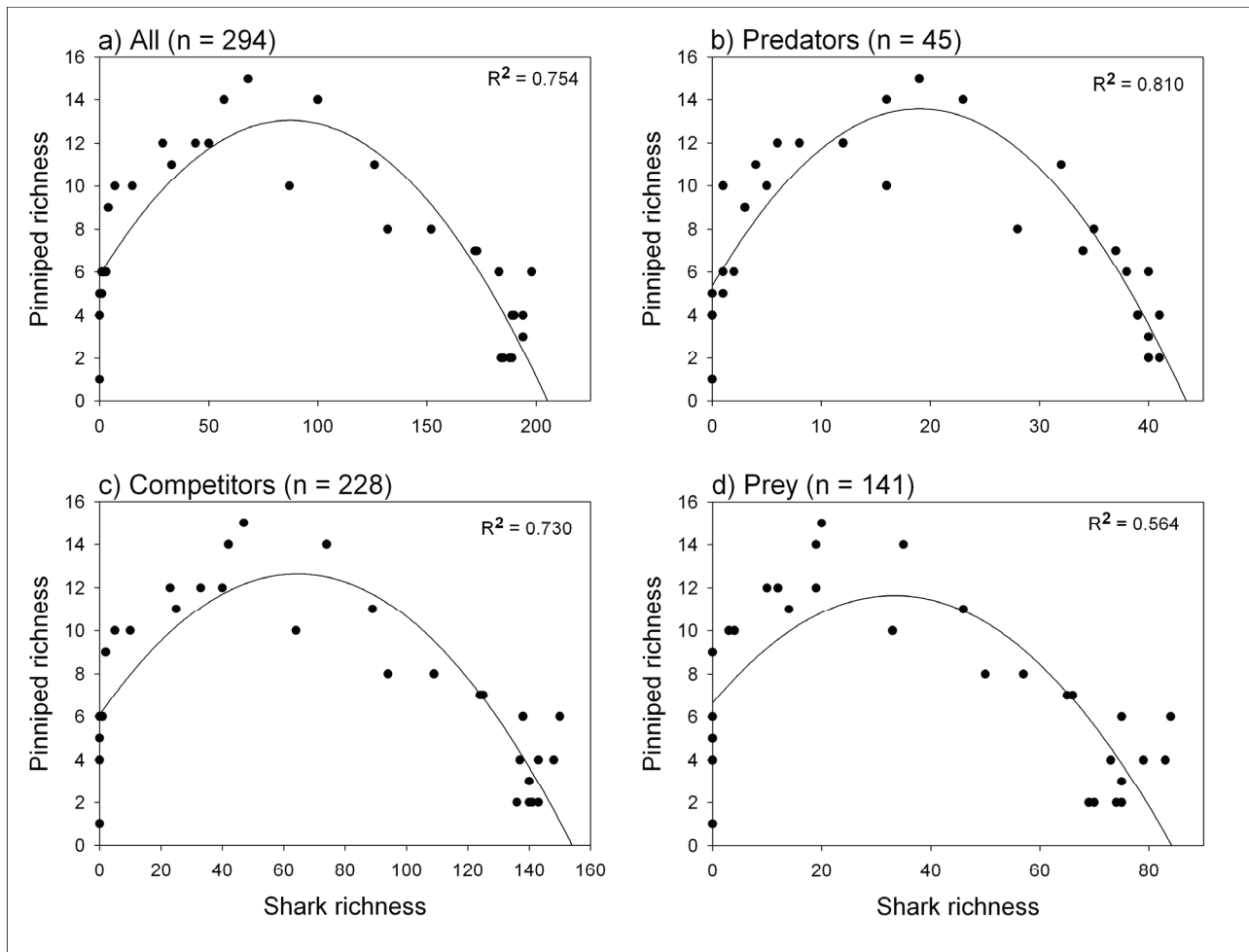
Figure 3: Plots of shark species richness (n=294) versus pinniped species richness (n=34) per 5° latitude band (n = 36) (2-order polynomial lines of best fit) according to (a) all sharks, (b) sharks classified as pinniped-predators (conservative classification), (c) as pinniped-competitors, and (d) pinniped-prey.

significant serial auto correlation existed in the different classifications of shark and pinniped species richness per latitude band (smallest first-order correlation coefficient AR(1) = 0.960). Autoregressive first-order models indicated a positive autocorrelation among error terms using first order autocorrelation and Durbin-Watson statistics. Mixed effects models with an autoregressive first-order process to control for the non-independence indicated significant relationships for all sharks and the pinniped-predator classification, but not for pinniped-competitors or pinniped-prey (Table 3). The relationship is nonlinear with: (1) some latitudinal bands having few shark and pinniped species, (2) as the number of shark species increases we initially see an increase in pinniped species until the species richness of sharks exceeds 20 species, after which (3) a negative relationship occurs

with fewer and fewer pinniped species occurring as shark diversity increases.

Discussion

We have provided correlative evidence that the shark clade has competitively excluded the pinniped clade from much of the world's marine waters. Shark species richness was opposite pinnipeds with pinnipeds dominating at high latitudes and sharks dominating at low latitudes. Of the various shark groups, sharks classified as predators of pinnipeds were the only group with a significant spatial relationship between shark and pinniped richness by latitude. Here, the pattern was curvilinear with fewer shark predators in areas with very few pinnipeds in equatorial regions. The distribution of pinnipeds is noticeably bimodal with few species

Shark classification	β	SE	t	P	RSE	Correl	AR(1)
Predators* (n = 45)	2.341	0.635	3.688	< 0.001	1.787	-0.264	0.9396
Competitors (n = 228)	0.977	0.831	1.176	0.248	2.315	-0.269	0.9382
Prey (n = 141)	1.014	0.860	1.179	0.247	2.222	-0.309	0.9279
All sharks (n = 294)	2.489	0.636	3.912	< 0.001	2.082	-0.199	0.9554

Shark predators of pinnipeds defined as having body length > 200 cm and trophic position (TP) > 4.16 (n = 45). A second classification of predators as TP > 4.0 (n = 51) was also used but results are not shown.

Table 3. Generalized least squares (GLS) regression fit by maximum likelihood models and with an autoregressive first-order process (AR(1)), comparing pinniped (n = 34) and shark (various classifications) diversity (log10 number of species per latitudinal band) across latitude (5-degree latitude bands, n = 36). Zero-values changed to 0.001 prior to log-10 transformation. For all models, df = 36 total, 34 residual. Regression analysis indicates that predation model is the best fit compared to competitor and prey models.

distributed in low-latitude warm waters, the areas where sharks thrive. Most pinnipeds occur in high-latitude regions with relatively few shark predators and most shark predators occur in temperate water areas. The divergence occurred in latitudinal regions with greater than 20 shark species.

Our distributional results are descriptive. However, we consider the likely mechanism of the distribution pattern to be superior predatory adaptations of sharks and inferior pinniped adaptations to minimize this predation risk. Most sharks (62%) are smaller than pinnipeds and only 8% of sharks are longer than the largest pinnipeds. Marine trophic dynamics are gape-limited and sharks have a larger gape than pinnipeds relative to body size as an adaptation to engulfing or biting large prey such as pinnipeds, particularly small-bodied juveniles (36).

The observed pattern found in pinnipeds is not evident for other endothermic animals such as cetaceans that have been shown to display greater biodiversity at warmer sea surface temperatures (71). Cetaceans are more evolved swimmers than pinnipeds with greater speed and include species such as Killer whales (*Orcinus orca)* that regularly eat large sharks (26). In contrast, seals are slower swimmers and generally smaller than cetaceans. Also, endothermic pursuit-diving sea birds that are smaller than pinnipeds and cetaceans also show a similar geographic distribution pattern as pinnipeds suggesting that their world distribution could also be limited by shark diversity (9, 10). The differences

associated with diving birds and pinnipeds versus cetaceans suggests that it is the evolved morphological ability to escape sharks using their size/speed or defend using 'weaponry/armor' that is an important factor in determining the outcome of higher-level competition selection.

Many pinnipeds are locked into land-use because of the evolutionary pre-condition that necessitates a need for land breeding, particularly among otariid seals (46). During their time on land, pinnipeds mate, give birth, and care for their dependent young while lactating (6). Land sites are chosen that have few terrestrial predators. However, during the period of learning to use water, seal pups are at a considerable disadvantage to marine predators, such as sharks and killer whales (8,43). Evidence of shark predation on seal pups is mostly reported in temperate waters in agreement with the shark-pinniped species richness trend (57,58). Future research on the evolutionary origins of pinnipeds relative to geography such as ocean temperature and sea ice distribution may assist in understanding the ghosts of competition past (14).

The evolutionary time scale of sharks (neoselachians – sharks, skates and rays) of ~420 million years (55) considerably predates the first occurrence of pinnipeds at ~50 million years (17). This long evolutionary history likely enabled sharks to evolve superior predatory skills and to diversify to occupy a broad range of niches within the marine realm prior to the occurrence and diversification of pinnipeds. The

radiation of modern day extant sharks occurred in the early Jurassic, with most species considered to be small bodied and oviparous in reproductive mode. Diversification increased rapidly through the early/middle Jurassic, while extinction rate was low with peak diversification occurring in the Taorcian, coincidental with sea level rise (47,55,67). Sea level rise created extensive shallow marine and epicontinental environments and was the precursor event for selection over evolutionary time favoring larger body size, later age at maturity, and ability to colonize broader habitat types including the deep ocean (34). Much of the distribution patterns of modern day sharks reflect this geologic phase, with highest species diversity occurring at intermediate latitudes, on upper continental slopes, along coastlines and near submerged features (53). Predation on seals by sharks is postulated from the fossil record during the Eocene (17). Sharks consequently gained an evolutionary advantage over pinnipeds in terms of niche, predatory skill, adaptability and habitat occurrence; through 'opportunistic' radiation events and possible evolution of novel body plans (47).

Heterothermic (endothermic and ectothermic) sharks include only a few species within the lamnids, the Great white (*Carcharodon cacharias*), Shortfin and Longfin mako (*Isurus oxyrinchus* and *I. paucus*) and the Salmon shark (*Lamna ditropis*). These represent large, fast swimming, agile species that occur in both sub-tropical and temperate waters and are known to occasionally predate on pinnipeds with the white shark considered to be a specialized seal hunter (57). Interestingly, the lamnids represent one of the more recent shark groups in evolutionary history, first occurring in the Miocene and thought to have evolved from *Isurus* sp. in the Eocene (21), coincidental with the occurrence of Pinnipedia. These heterothermic sharks may have specifically evolved heat exchange systems, the *rete mirabile*, to exploit latitudes where pinniped diversification occurred. Notably these species that overlap in latitudinal range are all large bodied animals with serrated teeth design and gape size capable of predating and handling seal prey. In polar waters, few shark species occur and are dominated by one family, Somniosidae, that is known to feed on seals although little is known about actual predator-prey interactions (25,72). The Greenland shark (*Somniosus*

microcephalus), Pacific sleeper shark (*Somniosus pacificus*) and Antarctic sleeper shark (*Somniosus antarcticus*) are all very large bodied species that do not possess heat exchange systems but have physiologically adapted to cold water environments through increased lipid levels, thick skin layer, high urea content and likely very low metabolic rates (54). Thus, sharks of the Lamnidae and Somniosidae have consequently evolved adaptations that support predation on seals through independent evolutionary trajectories.

Considerable research has described sharks as predators of pinnipeds including a summary by Cortés of diet composition and TP for 149 species of shark within eight orders and 23 families (15). Marine mammal prey (0.1 to 35.5%) was included in the standard diet composition of 18 species in five families of four orders: a) Carcharhiniformes (11 species, 10 in family Carcharhinidae); b) Hexanchiformes (2); c) Lamniformes (2), and d) Squaliformes (3). Marine mammal prey was a minor component of the diet of most of the 18 sharks (< 1% for seven species, < 5% for 12 species). TPs from Cortés are significantly (t-test: t = 6.707, df = 37, P < 0.001) higher for mammal-eating sharks (n=18; mean 4.26, range 4.2-4.7) compared to those with no recorded mammal diet (n=131; mean 3.98, range 3.1-4.4) (15).

However, we recognize the limitations of our assumptions. For example, the coarse metrics used to delineate shark species as possible pinniped predators overlooks the likelihood that most of the sharks with higher TP may not typically eat pinnipeds. The presence of remains of prey in the stomachs of a predator species does not provide information on the intensity of predation interactions, the dynamics of trophic energy flow or the population-dynamic effects (60). Although, we have considered the overlap in trophic position as evidence for potential interspecific competition, we encourage future research to more explicitly explore the nature of species interactions between sharks and pinnipeds and their differential use of the water column. Field data is limited but given that these sharks eat higher order and likely larger prey does at least provide clues into the possibility that they are capable of predation on pinnipeds and that there may be ghosts of past evolutionary processes at play in the background (14). Other trophic considerations that were not included

are sharks and pinnipeds that feed on lower trophic food sources such as krill (see above on planktonivores as pinniped-competitors) and potential interactions associated with common predators of both groups, such as Killer whales, humans and other sharks. Also, the current distributions provided by Fish Base are likely to be modified by human pressures (direct hunting and elimination of food resources) and may not reflect the ranges in which the sharks naturally occurred.

Alternative explanations to the observed distributional pattern include the distribution of oceanic primary productivity and physiological differences between the two clades. Among marine environments, temperate latitudes, especially areas of upwelling, support the highest productivity (56) and therefore, tend to support higher abundance of large predators than tropical latitudes (69). Pinnipeds as endotherms are adapted to maintain high metabolism with a large caloric intake that is provided by temperate latitude marine environments. Thus, pinniped latitudinal distribution may be a direct result of adaptations to feed in areas with the greatest abundance of food resources that generally occurs in temperate areas. Ectothermic sharks are limited in their distribution due to thermal constraints associated with their physiology. The exceptions are heterothermic lamnids, well-known active predators of pinnipeds. Lamnids, because they can take advantage of temperate waters, also appear to have one of the greatest ranges in distribution (Appendix 2). As a result, temperate upwelling areas would be beneficial for both sharks and pinnipeds to occupy. Therefore, an alternative untested explanation for the observed distribution reflects thermal constraints rather than competitive exclusion or predation risk. Future research should investigate the lamnid, somniosid, and White shark distribution relative to seal abundance and primary productivity (68).

There are conservation implications of our distribution results. An expanding range for the shark clade towards the poles with warming ocean temperature may prove problematic for pinnipeds. Many of the pinnipeds that inhabit temperate marine environments are at an evolutionary risk of extinction due to warming waters (22). Here, seals make their home around islands that are observing more shark predation. For example, Grey seals (*Halichoerus grypus)* on Sable Island, Nova Scotia, Canada (52). Predictions are for the world's

oceans to continue to warm which would suggest high-latitude areas would become better shark habitat and poorer environments for pinnipeds. With the accelerated climate change occurring at higher latitudes, research into global biogeographic patterns of ecosystem structure will assist in predicting latitudinal shifts in species distribution (70). Understanding climate-related changes in species distribution has conservation implications and can influence human activities, including commercial fisheries. Thus, there is a need to shift some of the current attention on climate-change impacts on marine predators that emphasizes changes at species-level ecological scales towards interspecific effects at global community scales since interspecific competition has the potential to alter populations, communities and the evolution of trophic interactions.

References

1. Allen SJ, Huveneers C. First record of an Australian fur seal (*Arctocephalus pusillus doriferus*) feeding on wobbegong shark (*Orectolobus ornatus*). *Proceedings Linnean Society New South Wales* 126:95-97. 2005.
2. Askin N, Belanger M, Wittnich C. Competitive feeding behavior interaction between a dogfish shark (*Squalus acanthias*) and a pinniped (*Phoca vitulina*). *Journal of Marine Animals and Their Ecology* 5:6-8. 2012.
3. Bertram DF, Harfenist A, Hedd A. Seabird nestling diets reflect latitudinal temperature-dependent variation in availability of key zooplankton prey populations. *Marine Ecology Progress Series* 393:199-210. 2009.
4. Bininda-Emonds ORP, Gittleman JL. Are pinnipeds functionally different from fissiped carnivores? The importance of phylogenetic comparative analyses.

Evolution 54:1011-1023. 2000.

5. Bolnick DI, Ingram T, Strutz WE, Snowberg LK, Lau OL, Paul JS. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society B* 1689: 1789-1797. 2010.

6. Bonnes DJ, Bowen WD. The evolution of maternal care in pinnipeds. *Bioscience* 46:645-654. 1996.

7. Brett CE, Walker SE. Predators and predation in Paleozoic marine environments. *Paleontological Society Papers* 8:93-118. 2002.

8. Brodie P, Beck B. Predation by sharks of the gray seal (*Halichoerus grypus*) in eastern Canada. *Canadian Journal Fisheries & Aquaculture* 40:267-271. 1983.

9. Brooke ML. The food consumption of the world's seabirds. *Biology Letters* 271 (Suppl 4):S246–S248. 2004.

10. Cairns DK, Gaston V, Huettmann F. Endothermy, ectothermy and the global structure of marine vertebrate communities. *Marine Ecology Progress Series* 35:239-250. 2008.

11. Camhi M, Fowler SL, Musick JA, Bräutigam A, Fordham SV. *Sharks and their Relatives – Ecology and Conservation*. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. 1998.

12. Clark, J.S. Individuals and the variation needed for high species diversity in forest trees. *Science* 327: 1129-1132. 2010.

13. Compagno LVJ. Hexanchiformes to lamniformes. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. *FAO 492 Fisheries Synopsis* 125:1–249. 1984.

14. Connell JH. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138. 1980.

15. Cortés E. Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science* 56:707-717. 1999.

16. Deagle BE, Kirkwood R, Jarman SJ. Analysis of Australian fur seal diet by pyrosequencing prey DNA in faeces. *Molecular Ecology* 18:2022-2038. 2009.

17. Diedrich C. The world's oldest fossil seal record.

Natural Science 3:914-920. 2011.

18. Dormann CF, Gruber B, Winter M, Herrmann D. Evolution of climate niches in European mammals? *Biological Letters* 6:229-232. 2010.

19. Eastman JT, Grande L. Evolution of the Antarctic fish fauna with emphasis on the recent notothenioids. In: *Origins and Evolution of the Antarctic Biota*, Geological Society Special Publication 47 (ed. J. A. Crame), pp. 241–252. London: Geological Society of London. 1989.

20. Ehret DJ, McFadden BJ, Jones DS, Devires TJ, Foster DA, Salas-Gismondi R. Origin of the white shark Carcharodon (Lamniformes: Lamnidae) based on recalibration of the upper neogene pisco formation of Peru. *Palaeontology* 55:1139-1153. 2012.

21. Eschmeyer WN (ed.). Catalogue of Fishes electronic version (19 February 2010). http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp. 2010.

22. Ferguson SH, Higdon JW. How seals divide up the world: environment, life-history, and conservation. *Oecologia* 150:318-329. 2006.

23. Ferguson SH, Messier F. Ecological implications of a latitudinal gradient in inter-annual climatic variability: a test using fractal and chaos theories. *Ecography* 19:282-292. 1996.

24. Ferguson SH, McLoughlin PD. Effect of energy availability, seasonality, and geographic range on brown bear life-history. *Ecography* 23:193–200. 2000.

25. Fisk AT, Tittlemier SA, Pranschke JL, Norstrom RJ. Using anthropogenic contaminants and stable isotopes to assess the feeding ecology of Greenland sharks. *Ecology* 83:2162-2172. 2002.

26. Ford JKB, Ellis GM, Matkin CO, Wetklo MH, Barrett-Lennard LG, Withler RE. Shark predation and tooth wear in a population of northeastern Pacific killer whales. *Aquatic Biology* 11:213–224. 2011.

27. Fox J, Weisberg S. Time-Series Regression and Generalized Least Squares in R, an Appendix to *An R Companion to Applied Regression*, Second Edition. Sage Publications, New York, NY. 472 p. 2010.

28. Froese R, Pauly D (eds). FishBase. World Wide

Web electronic publication. www.fishbase.org, versions April 2009 and January 2010. 2010.

29. Fulton TL, Strobeck C. Multiple fossil calibrations, nuclear loci and mitochondrial genomes provide new insight into biogeography and divergence timing for true seals (Phocidae, Pinnipedia).
Journal of Biogeography 37:814-829. 2010.

30. Gaston KJ. *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford, UK. 2003.

31. Gaston KJ, Blackburn TM, Spicer JI. Rapoport's rule: time for an epitaph?
Trends in Ecology and Evolution 13:70-74. 1998.

32. Gould SJ. Trends as changes in variance: a new slant on progress and directionality in evolution.
Journal of Paleontology 62:319-329. 1988.

33. Grimaldi S, Partonen T, Haukka J, Aromaa A, Lönnqvist J. Seasonal vegetative and affective symptoms in the Finnish general population: testing the dual vulnerability and latitude effect hypotheses.
Nord Journal Psychiatry 63:397–404. 2009.

34. Grogan ED, Lund R. The origin and relationships of early chondrichthyes. In: *Biology of Sharks and Their Relatives* (eds Carrier, JC, Musick, JA & Heithaus, MR). CRC press, Boca Raton, FL, pp. 3–31. 2004.

35. Gurevitch J, Morrow LL, Wallace A, Walsh JS. A meta-analysis of competition in field experiments.
American Naturalist 140: 539–572. 1992.

36. Hairston NG Jr., Hairston NG Sr. Cause-Effect Relationships in Energy Flow, Trophic Structure, and Interspecific Interactions.
American Naturalist 142:379-411. 1993.

37. Halpin PN, Read AJ, Fujioka E, Best BD, Donnelly B, Hazen LJ, et al. OBIS-SEAMAP: The world data center for marine mammal, sea bird and sea turtle distributions.
Oceanography 22:104–115. 2009.

38. Higdon JW. Biogeography and conservation of the pinnipeds (Carnivora: Mammalia). PhD Thesis, Department of Environment and Geography, University of Manitoba. Winnipeg, MB. 2011.

39. Hussey NE, McCann H, Cliff G, Dudley SFJ, Wintner SP, Fisk AT. Size-based analysis of the diet and trophic position of the white shark (*Carcharodon carcharias*) in South African waters. In *Global perspectives on the biology and life history of the great white shark* (ed. ML Domeier), CRC Press, Boca Raton, Fl., USA. 2011.

40. Hussey NE, MacNeil MA, McMeans BC, Olin JA, Dudley SFJ, Cliff G, et al. Rescaling the trophic structure of marine food webs.
Ecology Letters 17:239-250. 2014.

41. Hutchins DA, Witter AE, Butler A, Luther III GW. Competition among marine phytoplankton for different chelated iron species.
Nature 400:858-861. 2009.

42. IUCN. IUCN Red List of Threatened Species - Digital Distribution Maps of The IUCN Red List of Threatened Species Version 3. Version 2012.1. http://www.iucnredlist.org. 2012.

43. Jefferson TA, Stacey PF, Baird RW. A review of killer whale interactions with other marine mammals: predation to co-existence.
Mammal Review 21:151-180. 1991.

44. Johnson LA. Competitive interactions between cells: Death, growth, and geography.
Science 324:1679-1682. 2009.

45. Kaschner K, Rius-Barile J, Kesner-Reyes K, Garilao C, Kullander SO, Rees T, et al. AquaMaps: Predicted range maps for aquatic species. World wide web electronic publication, www.aquamaps.org, Version 08/2010. 2010.

46. Kovacs KM, Aguilar A, Aurioles D, Burkanov V, Compagna C, Gales N, et al. Global threats to pinnipeds.
Marine Mammal Science 28:414-436. 2012.

47. Kriwet J, Kiessling W, Klug S. Diversification trajectories and evolutionary life-history traits in early sharks and batoids. *Proceedings of the Royal Society B* 276:945-951. 2009.

48. Lam K, Tsui T, Nadano K, Randall DJ. Physiological adaptations of fishes to tropical intertidal environments.
Fish Physiology 21:501-581. 2005.

49. Lane MA. Copenhagen: Global Biodiversity Information Facility. GBIF Strategic and Operational Plans 2007–2011: From Prototype towards Full Operation. Online:

http://www.gbif.org/GBIF_org/GBIF_Documents/strategic_plans.pdf. 2007.

50. Leclerc L-ME, Lydersen C, Haug T, Bachmann L, Fisk AT, Kovacs KM. A missing piece in the Arctic food web puzzle? Stomach contents of Greenland sharks sampled in Svalbard, Norway. *Polar Biology* 35:1197-1208. 2012.

51. Lidgard S, Mckinney FK, Taylor PD. Competition, clade replacement, and a history of cyclostome and cheilostome bryozoan diversity. *Paleobiology* 19:352-371. 1993.

52. Lucas Z, Stobo WT. Shark-inflicted mortality on a population of harbour seals (Phoca vitulina) at Sable Island, Nova Scotia. *Journal of Zoology London* 252:414. 2006.

53. Lucifora LO, García VB, Worm B. Global Diversity Hotspots and Conservation Priorities for Sharks. *PLoS ONE* 6:e19356. 2011.

54. MacNeil MA, McMeans BC, Hussey N, Vecsei P, Svavarsson J, Kovacs KM, et al. Biology of the Greenland shark *Somiosus microcephalus* Bloch and Schneider, 1801. *Journal of Fisheries Biology* 80:991-1018. 2012.

55. Maisey JG, Naylor GJP, Ward DJ. Mesozoic elasmobranchs, neoselachian phylogeny and the rise of modern elasmobranch diversity. In *Mesozoic fishes 3—systematics, paleoenvironments and biodiversity* (eds G Arratia & A Tintori), pp. 17–56. Munich, Germany: Verlag Dr. Friedrich Pfeil. 2004.

56. Marañón E, Holligan PM, Barciela R, González N, Mouriño B, Pazó1 MJ, et al. Patterns of phytoplankton size structure and productivity in contrasting open-ocean environments. *Marine Ecological Progress Series* 216:43–56. 2001.

57. Martin RA, Hammerschlag N, Collier RS, Fallows C. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *Journal Marine Biology Association U.K.* 85:1121-1135. 2005.

58. McMeans BC, Arts MT, Lydersen C, Kovacs KM, Hop H, Falk-Petersen S, et al. The role of Greenland sharks (Somniosus microcephalus) in an Arctic ecosystem: assessed via stable isotopes and fatty acids. *Marine Biology* 160:1–16. 2013.

59. McMeans BC, Svavarsson J, Dennard S, Fisk AT.

Diet and resource use among Greenland sharks (*Somniosus microcephalus*) and teleosts sampled in Icelandic waters, using δ13C, δ15N, and mercury. *Canadian Journal Fisheries & Aquatic Science* 67:1428-1438. 2010.

60. Paine RT. Food web complexity and species diversity. *American Naturalist* 100:65-75. 1966.

61. Pauly D, Trites AW, Capuli E, Christensen V. Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* 55:467-481. 1998.

62. Pinheiro J, Bates D, DebRoy S, Sarka D, the R Core team. R package 'nlme', Linear and nonlinear mixed effects models, version 3.1-97. http://www.r-project.org/. 2010.

63. Reidman M. *The Pinnipeds: seals, sea lions, and walruses*. University of California Press, Berkley, Calif. 1990.

64. Rybczynski N, Dawson MR, Tedford RH. A semiaquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia. *Nature* 458:1021–1024. 2009.

65. Schluter D. Ecology and the origin of species. *Trends Ecology Evolution* 16, 372–380. 2001.

66. Schoener TW. Field experiments on interspecific competition. *American Naturalist* 122:240-285. 1983.

67. Sellwood BW, Valdes PJ. Mesozoic climates. In: *Deep-time perspectives on climate change: marrying the signal from computer models and biological proxies* (eds Williams H, Haywood AM, Gregory FJ, Schmidt DN), pp. 201–224. London, UK: The Geological Society, Special Publications. 2007.

68. Skomal GB, Chisholm J, Correia SJ. Implications of increasing pinniped populations on the diet and abundance of white sharks off the coast of Massachusetts. In: Domeier ML, editor. *Global Perspectives on the Biology and Life History of the White Shark*. CRC Press. 405–417. 2012.

69. Taggart SJ, Andrews AG, Mondragon J, Mathews EA. Co-occurrence of Pacific Sleeper Sharks *Somniosus pacificus* and Harbor Seals *Phoca vitulina* in Glacier Bay. *Alaska Fishery Research Bulletin* 11:113–117. 2005.

70. Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard

D, Vanden Berghe E, et al. Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098–1101. 2010.

71. Whitehead H, McGill B, Worm B. Diversity of deep-water cetaceans in relation to temperature: implications for ocean warming. *Ecology Letters* 11:1198–1207. 2008.

72. Yano K, Stevens JD, Compagno LJV. Distribution, reproduction and feeding of the Greenland shark *Somniosus* (*Somniosus*) *microcephalus*, with notes on two other sleeper sharks *Somniosus* (*Somniosus*) *pacificus* and *Somniosus* (*Somniosus*) *antarcticus*. *Journal Fisheries Biology* 70:374-390. 2007.

Additional Supporting Information may be found in the online version of this article:

Appendix 1 Distribution data
The AquaMaps (see Methods) database included point data (at least two locations) for 232 shark species (range 2-1,468 locations per species). There was a significant positive trend between total latitudinal extent (range size) and the number of locations (both $\log_{10}$-transformed) (linear regression, n = 232, R^2 = 0.250, F (1, 230) = 76.75, p < 0.0001). The FishBase (see Methods) database included 391 shark species with at least two locations (range 2-24,515). Of these, 13 species (2-4 locations per species) had zero latitude range (all point locations at same latitude) and were excluded from further analyses, for a total of 378 species initially retained. There was again a significant relationship between the number of point locations and the total latitudinal extent (n = 378, R^2 = 0.349, F (1, 376) = 201.23, p < 0.0001).

Only two species with AquaMaps data have less than 10 point locations, compared to 80 from the FishBase data set. When these species are removed, the relationship between the number of locations and overall extent was not as strong but was still significant (n = 298, R^2 = 0.192, F(1, 296) = 70.363, p < 0.0001). To reduce biases in shark distribution knowledge we excluded all these species with < 10 locations. FishBase generally had more points per species (more points for 219 species, versus 13 for AquaMaps, in addition to another 146

species with location data in the FishBase set only). Latitudinal extents were also larger for the FishBase set. Both datasets provide locations from the same sources (GBIF, OBIS), and both latitudinal extent and the total number of location points (n = 230 species) were correlated in the two data sets (r = 0.85, p < 0.01 and r = 0.78, p < 0.01, respectively).

Appendix 2 Comparison of subgroup distributions
To compare subgroup patterns, we provide figures of the two major pinniped subgroups (phocids versus otariids together with walrus) (Top) and the distribution of lamnid sharks compared to other sharks (Bottom). Lamniformes is the order with the highest proportion of predators; 11 or 12 of 15 species, depending on classification; followed by Hexanchiformes, with 3 of 5 species classed as predators (both classifications). Three orders have no species classed as predators: Heterodontidae, Pristiophoriformes and Squatiniformes, and the remaining three orders have few species classed as predators (< 20%). Using ANOVAs, shark families differed in maximum length (F(7, 286) = 11.527, P < 0.001), trophic position (F (7, 286) = 8.595, P < 0.001) and global range (F(7, 286) = 8.177, P < 0.001). On average, Lamniformes (n = 15) are the largest (longest) of the eight shark families (mean length = 482.7 cm, standard deviation (SD) = 223.3 cm), followed by Hexanchiformes (n = 5, mean length = 260.4 cm, SD = 137.2 cm). Lamnids had the second highest average trophic position (mean = 4.26, SD = 0.42), slightly lower than Hexanchiformes (mean = 4.30, SD = 0.17). Lamnids also had the second greatest global range (n = 15, mean = 17.9 5 - degree latitude bands, SD = 5.2), again with Hexanchiformes having the greatest range (n = 5, mean = 20.2, SD = 5.2).
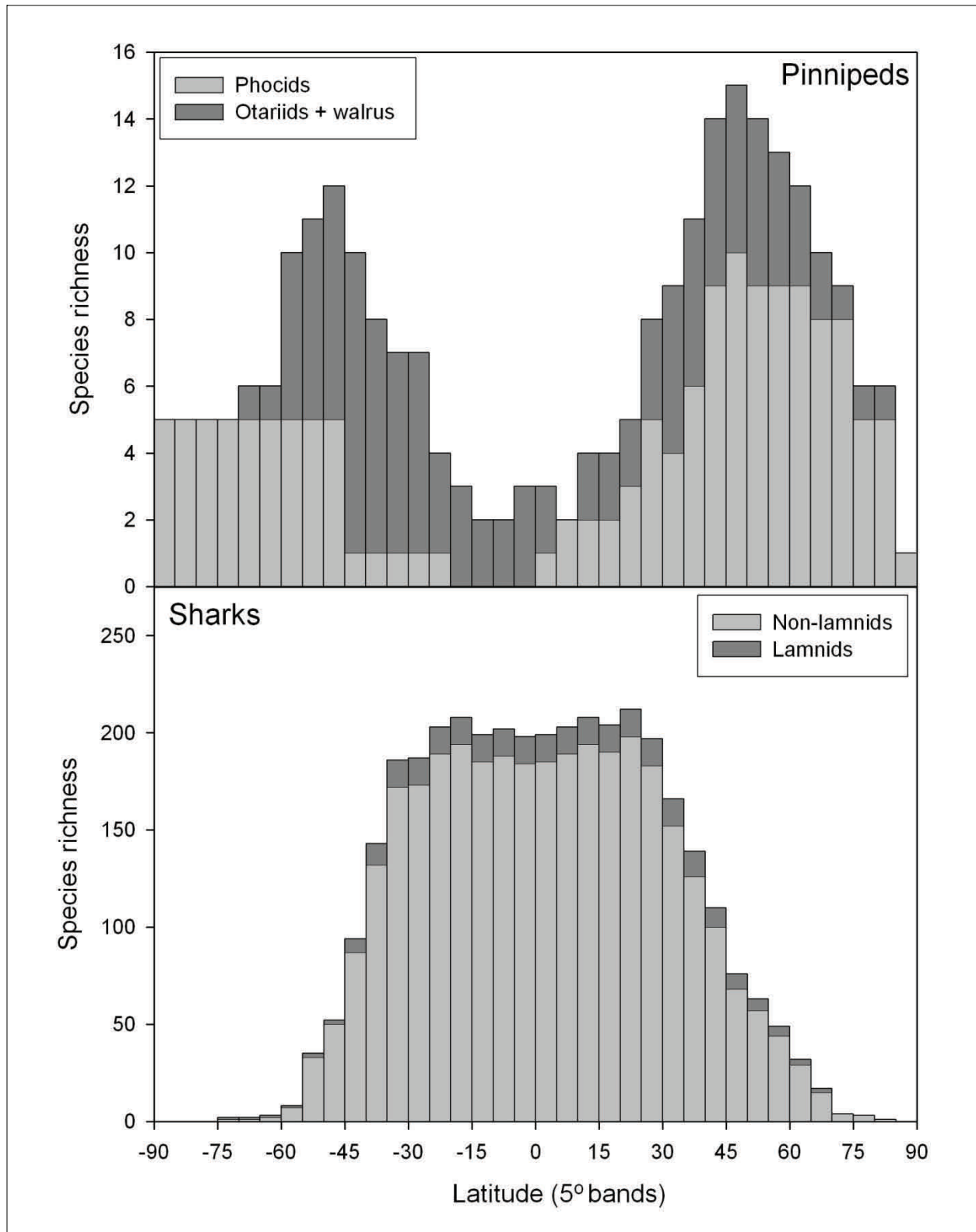
Appendix 3. Shark summary data (see Methods)

Order (n)	Family	No. with data		Length (cm) Minimum	Length (cm) Maximum		Trophic position Minimum	Trophic position Maximum
Hexanchiformes (6)	Hexanchidae (4)	4		140	482		4.16	4.6
	Chlamydoselachidae (2)	1		200			4.21	
Heterodontiformes (9)	Heterodontidae (9)	7		70	165		3.2	4.15
Orectolobiformes (41)	Rhincodontidae (1)	1		2000			3.55	
	Parascylliidae (8)	3		80	91		3.76	3.79
	Brachaeluridae (2)	2		76	122		3.5	3.85
	Orectolobidae (11)	4		63	320		3.91	4.23
	Hemiscylliidae (15)	8		46	121		3.36	4.06
	Stegostomatidae (1)	1		235			3.1	
	Ginglymostomatidae (3)	2		320	430		3.83	4.1
Lamniformes (16)	Odontaspididae (4)	3		320	410		4.16	4.5
	Mitsukurinidae (1)	1		617			4.14	
	Pseudocarchariidae (1)	1		110			4.21	
	Lamnidae (5)	5		305	792		4.5	4.53
	Megachasmidae (1)	1		549			3.38	
	Cetorhinidae (1)	1		980			3.2	
	Alopiidae (3)	3		383	760		4.5	
Carcharhiniformes (270)	Scyliorhinidae (146)	69		28	170		3.5	4.5
	Proscylliidae (7)	4		24	200		3.83	4.2
	Pseudotriakidae (2)	2		109	295		4.22	4.34
	Leptochariidae (1)	1		82			3.79	
	Triakidae (45)	26		58	220		3.5	4.5
	Hemigaleidae (8)	4		114	240		4.16	4.32
	Carcharhinidae (52)	44		69	750		3.8	4.54
	Sphyrnidae (9)	8		148	610		3.64	4.5
Squaliformes (124)	Dalatiidae (76)	51		20	730		3.06	4.5
	Centrophoridae (18)	11		79	164		4.06	4.5
	Squalidae (28)	9		71	160		3.97	4.5
	Echinorhinidae (2)	2		310	400		4.38	4.39
Pristiophoriformes (6)	Pristiophoridae (6)	4		80	170		3.88	4.17
Squatiniformes (22)	Squatinidae (22)	11		108	244		3.97	4.49
Total (494)		294						

39