Title: Global latitudinal and bathymetric gradients in body size among cartilaginous fishes (Gnathostomata: Chondrichthyes)

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Running head: Bergmann's rule in sharks, rays, and chimaera

Abstract:

Understanding the macroecological rules governing body size variation across environmental gradients has long been a central focus of biology for centuries. Bergmann's rule – the tendency for animals to reach larger body sizes in colder environments – has been studied in endotherms but with mixed support. However, phylogenetically informed tests of this rule in ectotherms remain scarce, and there is very limited evidence at higher taxonomic scales. Here, we provide robust evidence for Bergmann's rule in Chondrichthyes (sharks, rays, and chimaera), a predominantly ectothermic clade, using a phylogenetically informed dataset of over 900 species extracted from existing databases and primary literature. We show that chondrichthyans tend to mature at larger sizes and also reach larger maximum body sizes at higher latitudes and in deeper habitats – a pattern that is consistent with Bergmann's rule. We suggest that increased survivorship in these environments may promote evolutionary shifts toward greater resource allocation to growth and larger body sizes. This work fills a critical gap in testing Bergmann's rule among ectotherms in a phylogenetic context, demonstrating the potential for environmental gradients to shape the evolution of body size in marine vertebrates.

Keywords: Life history, Sharks, Bergmann's rule, Temperature-size rule, Ectotherm, Evolution

Introduction:

Macroecological rules linking body size to ecological/environmental gradients have long been proposed (Allen, 1877; Bergmann, 1847; Blackburn et al., 1999; Carotenuto et al., 2015; Cooper and Purvis, 2010; Gloger, 1833; Smith and Brown, 2002; Van Valen, 1973), owing to the fundamental importance of body size in determining organisms' thermal and ecological niches (Blanckenhorn, 2000; Peters, 1986; Schmidt-Neilsen, 1984). Examples include Allen's rule (in which species inhabiting colder climates have smaller extremities), Foster's rule (in which insular populations evolve distinct body sizes relative to mainland counterparts) and Gloger's rule (in which endotherms in warm/humid environments exhibit darker pigmentation than those in cool/dry environments) (Allen, 1877; Gloger, 1833; Van Valen, 1973). Testing these hypothesised relationships between body size and the environment in different clades can improve our understanding of macroevolutionary processes by uncovering links between trait variation and putative selective pressures (Gardner et al., 2011; Nagel and Schluter, 1998; Zamora-Camacho et al., 2014). Furthermore, testing macroecological rules can provide insight into the drivers of community composition, the trophic structuring of ecosystems (Woodward et al., 2005), and species conservation (Gaston and Blackburn, 1996).

The best-known of these macroecological hypotheses is Bergmann's rule, which posits that endothermic animals tend to be larger in colder, high-latitude environments (Bergmann, 1847; Blackburn et al., 1999). Several selective and mechanistic explanations for Bergmann's rule have been proposed, the most popular of which relate to heat conservation strategies (Pincheira-Donoso et al., 2008). Specifically, it has been suggested that larger body size may reduce heat loss to the environment (Fernández-Torres et al., 2018), and that thermal constraints may act on cellular growth (Angilletta et al., 2004). There is abundant theoretical and empirical evidence for Bergmann's rule at the intraspecific level in mammals and birds, suggesting that populations at higher elevations or latitudes tend to be larger in body size (Oskyrko et al., 2026; Torres-Romero et al., 2016; Salewski and Watt, 2017). Initial studies additionally claimed support for Bergmann's rule among most ectothermic species (Lindsey, 1966; Ray, 1960); although, more recent studies suggest that most ectotherms do not follow the rule (Ashton and Feldman, 2003; Oskyrko et al., 2026; Pincheira-Donoso et al., 2008). However, our understanding of Bergmann's rule is incomplete, and interpretations are complicated by methodological issues. These include a failure to account for evolutionary relationships (e.g., Belk and Houston, 2002; Fernández-Torres et al., 2018; Lin and Costello, 2023; Olson et al., 2009), sparse within-clade sampling (e.g., Ashton and Feldman, 2003; Olalla-Tárraga et al., 2006), and confusion regarding the definition of the rule altogether (Watt et al., 2010). Importantly, most existing studies focus on intraspecific trends in body size (Gohli and Voje, 2016), despite Bergmann initially proposing his rule to apply between closely related species (Blackburn et al., 1999). Indeed, among the few interspecific studies of Bergmann's rule to use comparative phylogenetic methods, support for the rule is inconsistent (Troyer et al., 2022, but see also Wilson et al., 2024), even within endothermic lineages such as mammals (Gohli and Voje, 2016). Most recently, Oskyrko et al. (2026) found no evidence of Bergmann's rule in terrestrial vertebrates but did not consider aquatic taxa. To date, only Troyer et al. (2022) have investigated the validity of Bergmann's rule at the interspecific level (as originally proposed) in a major aquatic radiation using a comparative phylogenetic framework. However, Troyer et al (2022) focused on tetraodontiform fishes only (a small proportion of the total ecological and morphological diversity of fishes), and a deep-time manifestation of Bergmann's rule. Consequently, the extent to which their results could apply more broadly across aquatic vertebrate diversity in contemporary ecosystems remains uncertain. This taxonomic knowledge gap fundamentally constrains our understanding of environmental gradients in body size within marine environments.

Chondrichthyes (sharks, rays, and chimaeras) present a powerful case study for testing latitudinal body size gradients among marine ectotherms. Chondrichthyes is a speciose, ancient radiation, representing a critical piece of vertebrate biodiversity that fulfils several key ecological functions (Dedman et al., 2024). Not only do chondrichthyans exhibit extreme variation in body sizes (~0.2 to >21 m), but they are found globally across a wide range of marine and freshwater ecosystems (Ebert et al., 2021). Consequently, Chondrichthyes satisfies each of the criteria proposed by Pincheira-Donoso et al. (2008), who argued that future tests of Bergmann's rule should focus on taxa belonging to monophyletic clades that exhibit substantial variation in body size and occur across a broad geographical area, encompassing a wide range of environmental conditions. Few ectothermic vertebrate clades of comparable size and ecological variation to Chondrichthyes exist, meaning cartilaginous fishes may be uniquely suited for interspecific studies of Bergmann's rule.

Additionally, investigations of Bergmann's rule among chondrichthyans could substantially improve our understanding of body size evolution more broadly in the clade. Bergmann's rule has not yet been tested in this clade besides isolated studies considering single species (e.g., Leyton and Chiaramonte, 2024; Shimada et al., 2023), even though latitude and water depth are known correlates of other aspects of chondrichthyan morphology, such as neurocranium shape (Gayford et al., 2024) and pectoral fin shape (Sternes et al., 2024). Body size is also known to correlate with trophic ecology, thermal physiology, and reproductive mode, such that mesothermic, filter-feeding, and viviparous species are generally larger in size (Mull et al., 2024; Pimiento et al., 2019), but these do not fully explain the observed diversity of body sizes (Cachera and Le Loc'h, 2017).

Here, we use a comparative phylogenetic approach to test for Bergmann's rule at the interspecific level across a comprehensive dataset of over 900 chondrichthyan species, including both Elasmobranchii (sharks and rays) and Holocephali (Chimaeras). Specifically, we test for significant relationships between body size and several metrics of latitude and water depth. Higher latitudes and greater water depths are associated with lower temperatures, and if Bergmann's rule is valid in cartilaginous fishes, we expect positive relationships between body size and these environmental variables. We also test the relationship between body size and trophic level to corroborate the findings of previous studies that have used smaller datasets (e.g., Pimiento et al., 2019). Our approach addresses key limitations of previous work by considering multiple evolutionary models, two size metrics (maximum size and size at maturity), and an unprecedented taxonomic sample grounded in a robust phylogenetic framework.

Methodology

Data Collection

Previous evolutionary studies of body size variation in chondrichthyans have used maximum total length and disc width as proxies for body size (Marion et al., 2024; Mull et al., 2024; Pimiento et al., 2019). For species subject to intense fishing pressure with indeterminate growth, maximum length or width may not represent the ideal metric to quantify body size, and for this reason we collected data for total length at sexual maturity (herein LSM; cm) in addition to maximum total length (herein MTL; cm). LSM also has the additional advantages of being less susceptible to potential anthropogenic selection and reporting biases. We obtained these data from FishBase (Froese and Pauly, 2010) for 271 and 948 species respectively, and manually cross-validated these data with reference guides (Ebert et al., 2021; Last et al., 2016) to avoid the inclusion of erroneous (impossible) values. Previous studies have combined total length and disc width in macroevolutionary analyses of body size due to the extreme morphological divergence of many batoids from the general shark body plan (Pimiento et al., 2019). However, as total length and disc width are not anatomically homologous or geometrically equivalent, they scale differently with body mass and are likely underlain by different evolutionary covariance structures. Consequently, for our main analyses, we used total length (MTL or LSM) only. However, disc width values were also collated for myliobatiform rays to facilitate sensitivity tests (see data analysis section) to examine whether use of total length or disc width measures would significantly influence our results.

To enable the testing of Bergmann's rule, the following ecological variables were gathered from FishBase: Maximum latitude (degrees), Minimum latitude (degrees), Maximum depth (m), Minimum depth (m), and Trophic level. Maximum latitude was calculated as the most poleward extent (furthest from the equator) of species' distributions, regardless of which hemisphere(s) they occupy. Minimum latitude was similarly calculated as the lowest latitude (closest to the equator) in which a species can be found. If species are found in both hemispheres with a distribution overlapping the equator, minimum latitude was set to zero. Sea surface and deep-water temperatures decline predictably with increasing absolute latitude, making the combination of poleward and equatorial extents a robust proxy for thermal regime at macroecological scales. A positive relationship between body size and trophic level is expected on the basis of previous studies (Pimiento et al., 2019), and positive relationships between body size and maximum latitude, maximum depth or minimum depth would be expected if Bergmann's rule is valid in Chondrichthyes. Conversely, negative relationships between body size and minimum latitude would provide evidence against

Bergmann’s rule, indicating that species found in shallower, tropical environments tend to be smaller. These relationships could also be confounded by relationships between water depth, latitude, and other environmental variables such as oxygen concentration and productivity.

We downloaded the full set of 10,000 molecular, time-calibrated phylogenetic trees from Stein et al. (2018), which include 10 fossil calibration points. A series of pruned tree sets (two sets of 10,000 trees per body size metric – one corresponding to maximum total length and another corresponding to total length at sexual maturity) were produced in the R package phytools (Revell, 2024), dropping taxa for which either the respective body size or ecological variables (trophic level, minimum latitude, maximum latitude, minimum depth, and maximum depth) were unavailable (Table S1). We then inferred a maximum clade credibility (MCC) tree (Figure 1) for each of these tree sets using the R package ape (Paradis and Schliep, 2019). This MCC tree was used for maximum likelihood estimates of phylogenetic signal (see below) as inbuilt permutation tests account for uncertainty in signal estimates. However, for all other analyses a Bayesian approach was used to better account for phylogenetic uncertainty (see below).

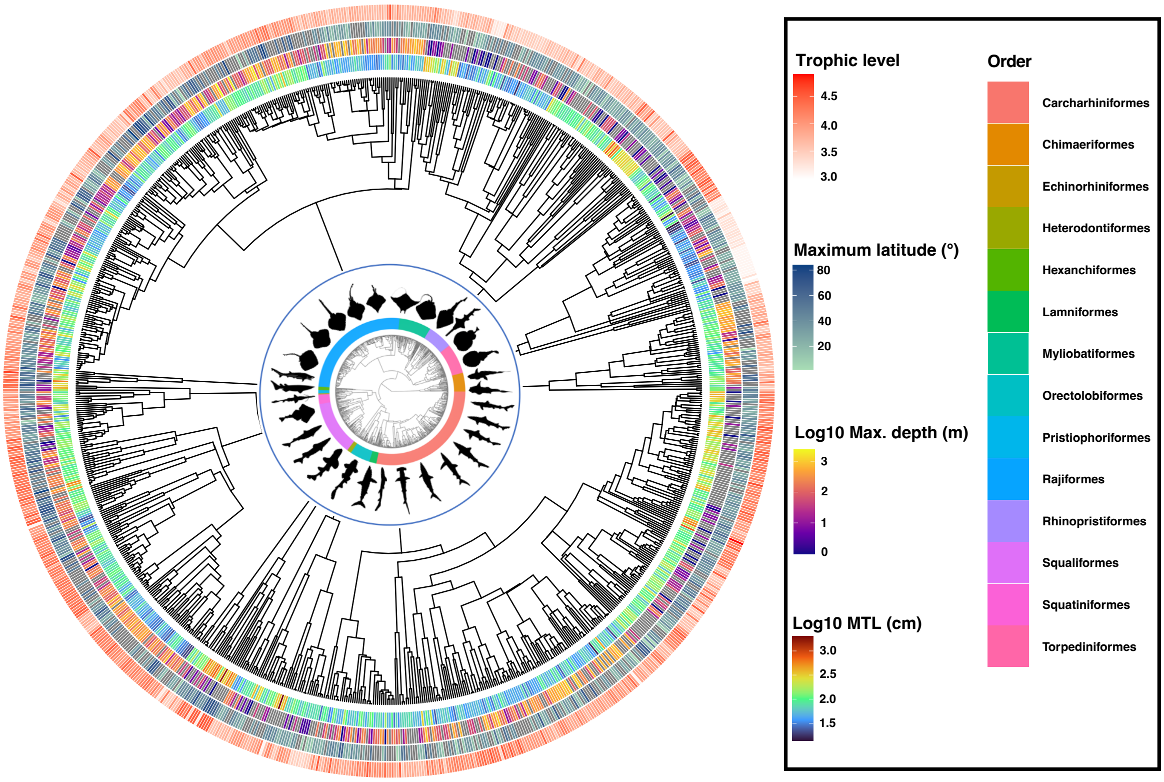

Figure 1: Time-scaled molecular MCC phylogeny demonstrating the taxonomic, morphological, and ecological diversity of the dataset. The MCC tree was compiled from the original set of phylogenies presented by Stein et al. (2018) as outlined in the methodology.

Data analysis

Prior to all data analyses, both measures of body size and depth were log10 transformed. A constant of one was added to all Minimum Depth values prior to log transformation, due to the presence of zero values in the dataset, which cannot be log10 transformed.

Phylogenetic signal

To understand the evolution of morphological traits such as body size, it is necessary to examine patterns of phylogenetic signal (Münkemüller et al., 2012). This signal describes the tendency of closely related species to resemble each other more than species drawn randomly from the same phylogeny and can be important in selecting appropriate downstream statistical methods for macroevolutionary analyses (Münkmüller et al., 2012). To model phylogenetic we calculated Blomberg's K (Blomberg et al., 2003) for both MTL and LSM in the R package phytools (Revell, 2024). We evaluated the statistical significance of observed K values by randomising body size data across tips of our phylogeny and calculating K in 10000 simulations for each of MTL and LSM, subsequently calculating the p value of our observed K values in light of this prior distribution of expected K values. We calculated Pagel's Lambda as an additional measure of phylogenetic signal for both MTL and LSM in the package phytools (Revell, 2024). To test whether observed values of lambda differ from the null expectations of zero, we performed likelihood ratio tests.

Phylogenetic generalised least squares (PGLS)

To test the expectations of Bergmann's rule (positive relationships between body size and measures of latitude/depth) while accounting for shared ancestry, we performed phylogenetic generalised least squares (PGLS) analyses using the package *phylolm* (Ho et al, 2016). As previous studies have found evidence of evolutionary relationships between body size and trophic level in elasmobranchs (Pimiento et al., 2019) we also examined whether such signal was present across our expanded dataset.

We tested ten distinct relationships, each comprising one measure of body size as a response variable—either maximum total length (MTL) or length at sexual maturity (LSM)—and a single environmental variable as a predictor (maximum depth, minimum depth, maximum latitude, minimum latitude, or trophic level). Phylogenetic uncertainty was incorporated by fitting each model across a randomly selected posterior sample of 100 trees from the original set of 10,000, pruned to match the taxa in each dataset. Positive relationships between body size and depth/latitude (characterised by positive posterior mean slope estimates, with 95% credible intervals that do not overlap with zero) would indicate support for Bergmann's rule.

Previous studies of chondrichthyan trait evolution have found support for different evolutionary covariance structures, depending on the traits in question and the size/composition of the dataset (e.g., Gayford et al., 2025a; Pimiento et al., 2019; Torralba Sáez et al., 2024). As these different covariance structures can exert significant influence on perceived relationships between traits (e.g., Hunt et al., 2015), it is important to utilise the most appropriate phylogenetically-informed model. Consequently, to determine the most appropriate covariance structure from which to base interpretations of relationships between body size and ecological variables (depth, latitude, and trophic level) we repeated our analyses across a range of different covariance structures.

Specifically, for each relationship, we fit multiple PGLS models incorporating Brownian motion (BM), Ornstein–Uhlenbeck with fixed root (OUfixedRoot), early burst (EB), and Pagel's lambda (λ) covariance structures. An OLS model, without any phylogenetic covariance structure, was also fit for comparative purposes. For each relationship, the fit of these five PGLS models was assessed using the corrected Akaike Information Criterion (AICc), and the best-supported model for each relationship was identified across the posterior tree sample. The best supported model is defined as the model with the lowest AICc score, with a ΔAICc value of at least 2 from the model associated with the second lowest AICc score. Regression slopes and intercepts were summarised as posterior means with 95% credible intervals derived from the tree-wise distribution of parameter estimates. Posterior p-values were calculated as the median p-value across trees, and multiple comparisons were accounted for using a Benjamini–Hochberg false discovery rate correction. All subsequent inferences about the magnitude and direction of correlations between size and ecological variables (depth, latitude, and trophic level) will be based on the best supported model.

The substantial diversity in body form exhibited by extant chondrichthyans (Ebert et al., 2021; Gayford et al., 2025b; Last et al., 2016) means that the use of any single metric of body size is likely to introduce uncertainty into macroevolutionary analyses. This is particularly relevant in the case of myliobatiform batoids, where the extreme dorsoventral flattening of the body, specialisation of the tail, and fusion of the head, pectoral fins, and anterior body may significantly alter relationships between total length, width, and body mass (Last et al., 2016). To address the potential influence of body form diversity on global latitudinal and bathymetric trends in body size, we first re-ran PGLS models (using the best-fit covariance structure) using DW values for myliobatiform rays instead of MTL values. Subsequently, we re-ran PGLS models (using the best fit covariance structure) for all 10 relationships (MTL and LSM) separately for each order for which over 20 species were present in the dataset (Carcharhiniformes, Chimaeriformes, Myliobatiformes, Orectolobiformes, Rajiformes, Rhinopristiformes, Squaliformes, Squatiniformes, and Torpediniformes). The remaining orders (Lamniformes, Pristiophoriformes, Echinorhiniformes, Heterodontiformes and Hexanchiformes) were excluded as their sample size was insufficient to achieve reliable regression results.

Correlated trait evolution in BayesTraits

All comparative phylogenetic methods make assumptions about underlying evolutionary processes, and each has different pitfalls and limitations (Symonds and Blomberg, 2014). For this reason, in addition to PGLS, we tested for trait correlations in a Bayesian phylogenetic framework using the program BayesTraits (Pagel and Meade, 2007). Unlike the PGLS models described above, the BayesTraits analysis used here assumed a Brownian Motion covariance matrix (BayesTraits does not provide the option to perform correlation analyses with other covariance structures) and incorporates phylogenetic uncertainty by using the full set of 10,000 original phylogenetic trees as opposed to an MCC tree (Pagel and Meade, 2007). In the Continuous module of BayesTraits, we tested each of the possible trait correlations described in the previous section by fitting a dependent model (allowing correlation between the two traits) and an independent model (which forces the correlation between traits to be zero). For each model, we performed 5 reversible jump Markov chain Monte Carlo (MCMC) runs for 5,000,000 iterations each, with a burn-in of 20%. We visualised trace and density plots and single chain diagnostics to ensure convergence among chains. We applied a steppingstone sampler to each run to calculate the harmonic mean of the marginal log likelihood of each model, sampling every 100 iterations after a burn-in of 1000 iterations. These parameters were chosen after performing preliminary analyses to evaluate convergence, and after reviewing usage of the Continuous BayesTraits module in related literature (e.g., Jung and Lee, 2012; Mitchell et al., 2018). Marginal log likelihood values for each 5 runs of the MCMC chain were averaged (which had very little effect on results given the convergence between chains) to provide a single value for each dependent and independent model. Subsequently, we calculated the log-Bayes Factor (BF) for each potential trait correlation. A log-BF value greater than 2 provides some evidence for correlation, values greater than 5 provide strong evidence for correlation and values greater than 10 provide very strong evidence for correlation (Pagel and Meade, 2007). Given that multiple BayesTraits analyses were conducted, we interpret only log Bayes factors ≥ 5 as providing strong support for an association. Notably, unlike PGLS, this approach does not provide information regarding the direction of any identified correlation (Pagel and Meade, 2007).

Results

Phylogenetic signal

We found that both MTL (maximum total length) and LSM (length at sexual maturity) have low K_{mult} values (Figure S1). However, in both cases, values were still significantly higher than expected due to chance alone (Figure S1; $K_{MTL}=0.04$, $K_{LSM}=0.21$, $p<0.001$). Similarly, whilst values for Pagel's lambda were lower than 1 in both cases ($\lambda_{MTL} = 0.85, \lambda_{LSM} = 0.88$), likelihood ratio tests indicating that these are significantly higher than 0 ($p<0.001$; Figure S2). Cumulatively, these results indicate relatively strong phylogenetic signal underlying body size (both MTL and LSM) in chondrichthyans. This suggests, in turn, that closely related species generally exhibit similar body sizes.

Phylogenetic generalised least squares (PGLS)

Model comparisons across a posterior sample of 100 trees consistently identified Pagel's λ models as the best-fitting evolutionary model for all relationships (Table 1). Across all body size–ecology relationships, OU, BM, and EB models were poorly supported, often showing markedly higher AICc values, whereas OLS models received intermediate support (Table 1). These results suggest that evolutionary changes in body size are not adequately captured by simple Brownian or early burst models, and that accounting for phylogenetic covariance via λ provides a substantially better fit. Full model output including posterior mean slopes and evolutionary model parameters for all models can be found in the supplementary materials (Table S1).

Table 1: Relative support for evolutionary models of body size in cartilaginous fishes (Chondrichthyes). Mean corrected Akaike Information Criterion (AICc) values are shown for each model across a posterior sample of 100 phylogenetic trees. Models tested include ordinary least squares (OLS), Brownian motion (BM), Ornstein-Uhlenbeck with fixed root (OUfixedRoot), Pagel's λ (lambda), and early burst (EB).

Lower AICc values indicate better model fit. For each ecological relationship (e.g., maximum depth, latitude, trophic level), the best-supported model is highlighted in bold.

Relationship	**AIC$_C$ (OLS)**	**AIC$_C$ (BM)**	**AIC$_C$ (OU)**	**AIC$_C$ (λ)**	**AIC$_C$ (EB)**
MTL~Minimum Depth	-154.63438	674.140978	143.900813	**-241.62878**	676.140978
LSM~Minimum Depth	67.6488171	70.3566033	48.0818615	**33.8753921**	72.3566033
MTL~Maximum Depth	-163.50156	1035.36914	470.407641	**-276.52691**	1037.36914
LSM~Maximum Depth	23.033738	106.775441	52.4162407	**-19.149175**	108.775441
MTL~Minimum Latitude	-38.240237	801.576205	368.241754	**-106.81676**	803.576205
LSM~Minimum Latitude	60.2965702	124.187447	71.6388841	**21.0487418**	126.187447
MTL~Maximum Latitude	-241.84683	527.10741	177.62098	**-313.78894**	529.10741
LSM_Maximum Latitude	16.1403264	55.601807	16.8277972	**-23.516649**	57.601807
MTL~Trophic Level	-163.29272	1081.94656	400.925107	**-313.60493**	1083.94656
LSM~Trophic Level	27.7202578	90.5553584	36.3134864	**-20.24114**	92.5553584

Our PGLS regressions reveal that MTL and LSM broadly exhibit similar latitudinal and bathymetric gradients, largely consistent with Bergmann's rule (Table 2). We found that maximum depth, maximum latitude, and trophic level correlate significantly with both MTL and LSM; whereas, minimum depth only correlated significantly with MTL (Table 2), and minimum latitude did not correlate significantly with either body size metric. The coefficients of these regression models indicate that body size (MTL, LSM, or both) increases with maximum depth and maximum latitude, consistent with Bergmann's rule (Figure 2) Both size measures also increase with trophic level (Figure 2). Consistent with our previous estimates of phylogenetic signal, mean values of Pagel's λ calculated across our posterior sample varied from 0.838 to 0.946 (Table 2).

Table 2: Posterior PGLS parameter estimates for the best-supported evolutionary model (Pagel's λ) for each body size–ecology relationship. For each model, we report the mean slope and intercept of the relationship, their standard errors (SE) and 95% credible intervals (CI), the mean evolutionary rate (σ^2), mean estimated phylogenetic signal (λ), and median posterior p-values before and after Benjamini–Hochberg false discovery rate correction. For sample sizes of each PGLS model, and 95% credible intervals for all parameters, please see Table S1.

Relationship	Slope	SE	Slope CI	Intercept	Intercept CI	σ^2	λ	P (posterior)	p(FDR corrected)
MTL_trophic	**0.276**	**0.028**	**0.261 - 0.290**	**0.955**	**0.901 - 1.009**	**3.83E-06**	**0.838**	**1.62E-21**	**8.12E-21**
LSM_trophic	**0.238**	**0.045**	**0.216- 0.259**	**0.984**	**0.908 - 1.060**	**5.74E-06**	**0.946**	**2.50E-07**	**3.57E-07**
MTL_depmin	**-0.111**	**0.013**	**-0.118 - -0.106**	**2.173**	**2.157 - 2.189**	**3.59E-06**	**0.848**	**6.26E-18**	**1.56E-17**
LSM_depmin	-0.042	0.030	-0.055 - -0.029	1.970	1.944 - 1.995	5.78E-06	0.923	0.17234801	0.19953897
MTL_depmax	**0.178**	**0.019**	**0.167- 0.188**	**1.549**	**1.516 - 1.584**	**4.00E-06**	**0.851**	**1.88E-19**	**6.26E-19**
LSM_depmax	**0.169**	**0.030**	**0.150 - 0.187**	**1.457**	**1.407 - 1.503**	**4.98E-06**	**0.919**	**7.84E-08**	**1.31E-07**
MTL_latmin	0.001	0.001	0.001- 0.001	2.017	1.998 - 2.031	4.57E-06	0.859	0.17958508	0.19953897
LSM_latmin	0.002	0.002	0.001 - 0.003	1.873	1.837 - 1.890	6.07E-06	0.931	0.24631149	0.24631149
MTL_latmax	**0.008**	**0.001**	**0.007- 0.008**	**1.712**	**1.692 - 1.730**	**3.38E-06**	**0.862**	**4.92E-47**	**4.92E-46**
LSM_latmax	**0.008**	**0.001**	**0.007 - 0.009**	**1.511**	**1.472 - 1.565**	**5.21E-06**	**0.941**	**2.34E-11**	**4.68E-11**

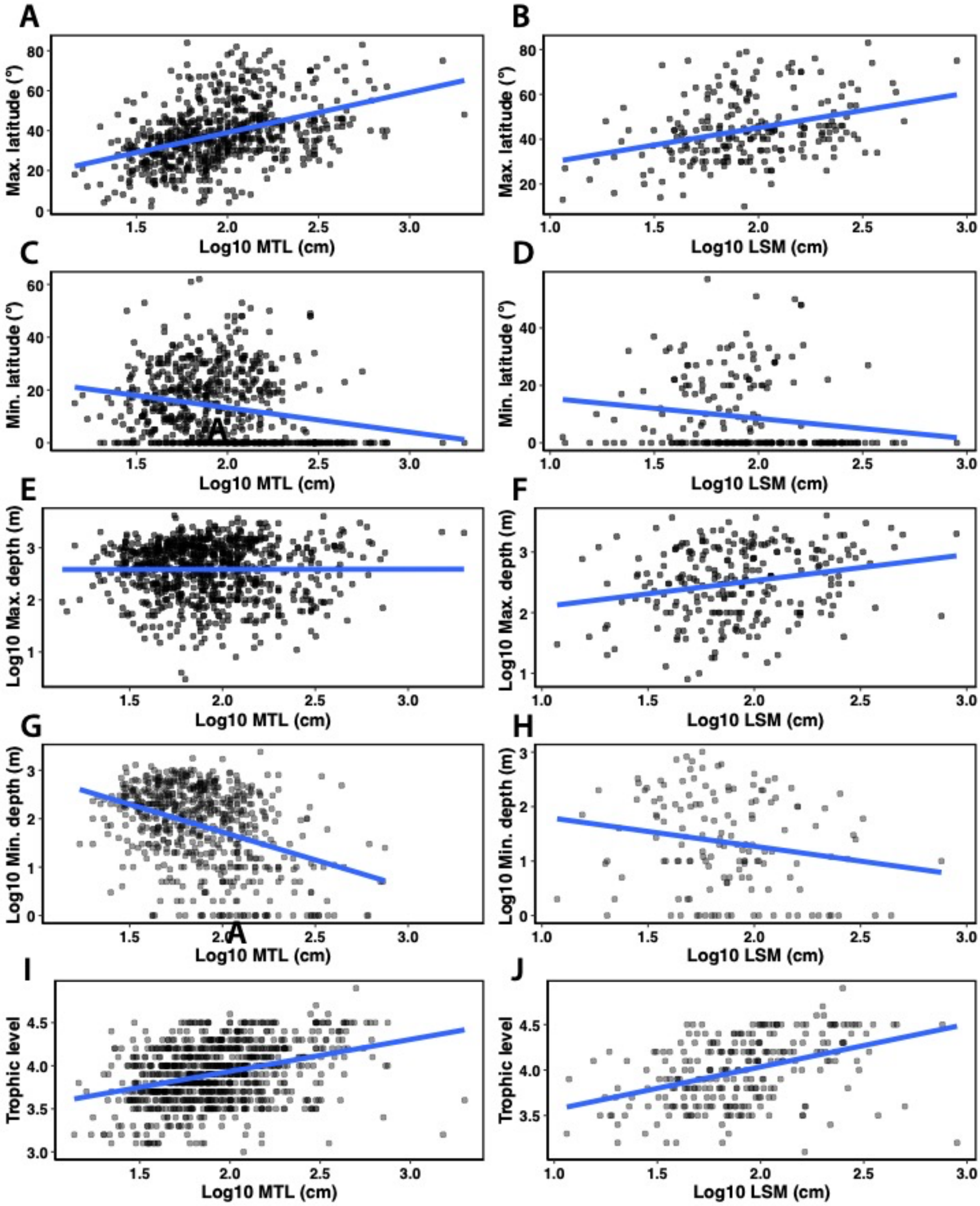

Figure 2: Relationships between ecological variables and measures of body size, as recovered in PGLS analyses. Note that these plots do not take into account the phylogenetic covariance structures incorporated into the regression models.

Use of disc width (DW) values instead of MTL values for myliobatiform rays did not have any statistically significant or qualitative impact on the relationship between body size and trophic level, maximum depth, maximum latitude, minimum depth, or minimum latitude (Table S2).

Similarly, PGLS regressions fit independently for each chondrichthyan order comprising at least 20 species in our dataset indicate that the global latitudinal and bathymetric gradients in MTL and LSM hold across the majority of extant chondrichthyan diversity, despite substantial variety in body form (Figure 3; Figure S3). The positive relationship found between body size (both MTL and LSM) and trophic level is consistent across all orders, as is the positive relationship between body size and maximum latitude (Figure 3; Table S3). A positive relationship between body size and depth is observed in all orders apart from Rhinopristiformes and Squatiniformes, both of which are overwhelming shallow-water taxa (Figure 3; Table S3). The negative relationship observed between body size and minimum latitude was consistent across all orders other than Rhinopristiformes, whereas the relationship between body size and minimum depth was highly variable (Figure S3; Table S3), underscoring the non-significance of this relationship when applied to the total dataset (Table 2).

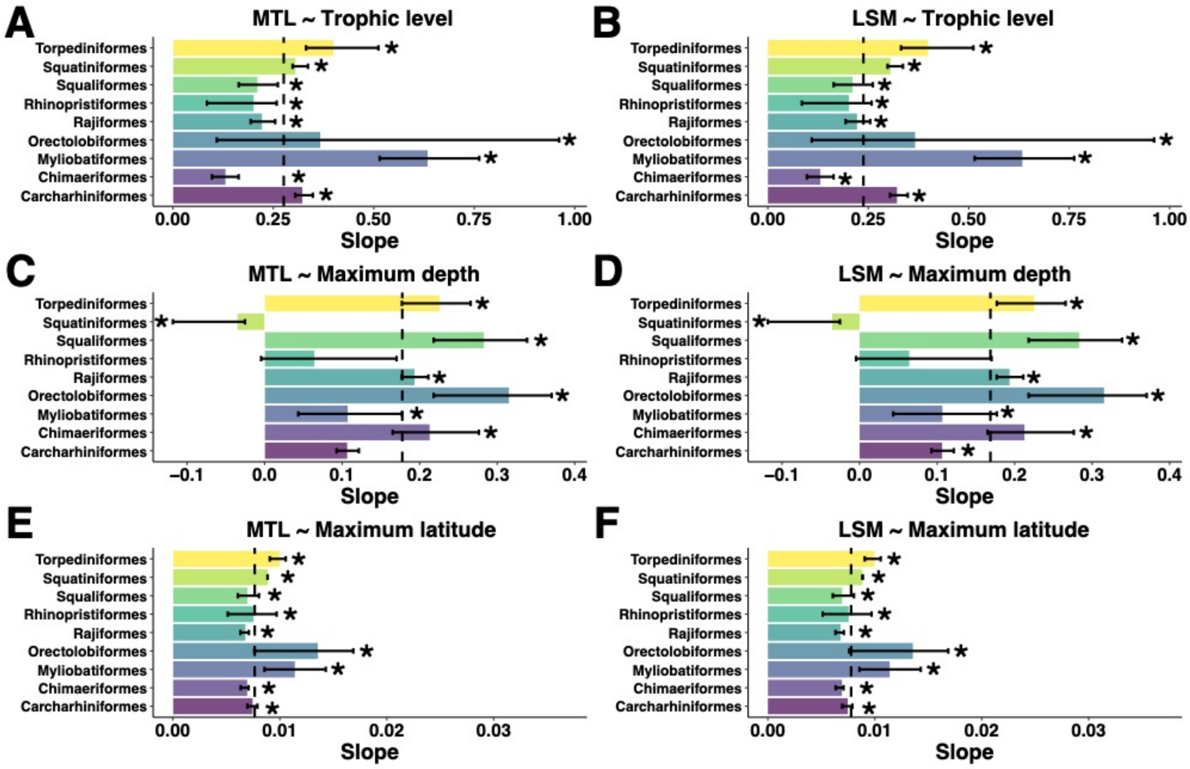

Figure 3: Posterior mean slope estimates from PGLS analyses for each relationship between body size and trophic level (A,B), maximum depth (C,D), and maximum latitude (E,F). Stars indicate a statistically significant relationship, in which the 95% credible interval (represented here by error bars) for the slope estimate does not overlap with zero. Horizontal dashed lines indicate the magnitude of the relationship when using the full dataset across all orders, as presented in Table 2. Slope estimates for all examined trait combinations are presented in supplementary Figure S3.

Correlated trait evolution in BayesTraits

Log Bayes Factors (calculated on the basis of marginal log likelihood) for each of the possible trait correlations included in this study confirmed the importance of depth, latitude, and trophic level as predictors of body size (Table 3). The support for correlation with ecological was largely equivalent between MTL and LSM, matching our PGLS results qualitatively. Again, BayesTraits analysis suggests that LSM and minimum latitude are the only two variables to show no evidence of statistically significant correlation with a log Bayes Traits value <0, with limited evidence of significant correlation between LSM and minimum depth, and between MTL and minimum latitude (Table 3). Consequently, the results of our BayesTraits and PGLS analyses are fully concordant and support the presence of significant relationships between body size, maximum latitude, maximum water depth, and trophic level.

Table 3: Summary of BayesTraits models for correlation between two continuous traits. Log Bayes Factor values greater than 2 indicate some evidence for correlation, values greater than 5 indicate strong evidence for correlation, and values greater than 10 indicate very strong evidence for correlation.

Trait 1	Trait 2	Marginal log likelihood (correlated)	Marginal log likelihood (null)	Log Bayes Factor
MTL	Minimum Depth	-1265.3	-1296.1	30.8
LSM	Minimum Depth	-299.1	-300.5	2.7
MTL	Maximum Depth	-860.1	-884.2	24.1
LSM	Maximum Depth	-184.8	-193.5	17.3
MTL	Minimum Latitude	-3048.4	-3049.4	1.1
LSM	Minimum Latitude	-886.2	-886.2	-0.1
MTL	Maximum Latitude	-3031.5	-3152.3	120.7
LSM	Maximum Latitude	-913.00	-927.0	28.1
MTL	Trophic Level	-479.3	-508.7	29.5
LSM	Trophic Level	-94.0	-108.1	28.1

Discussion

The purpose of this study was to provide a comprehensive phylogenetically informed test of Bergmann's rule at the interspecific level (as originally proposed) in a speciose, ecologically and morphologically diverse aquatic clade. We found evidence of significant correlations between body size, maximum latitude, and maximum water depth that are consistent with Bergmann's rule (Figure 2; Table 2; Table 3), indicating that cartilaginous fishes are larger in colder environments. These relationships hold across distinct statistical approaches (Table 2; Table 3), regardless of whether disc width or total length is used to measure body size in batoids (Table S2) and across the majority of extant chondrichthyan orders (Figure 3; Table S3) despite substantial ecomorphological diversity.

At the interspecific level, conformity with Bergmann's rule is extremely rare among ectotherms (Gohli and Voje, 2016; Mousseau, 1997; Oskyrko et al., 2026; Pincheira-Donoso et al., 2008; Troyer et al., 2022). Moreover, it remains uncertain whether there is any theoretical support for the notion of Bergmann's rule in the absence of endothermy (Angilletta et al., 2003; Mousseau, 1997). Even in endotherms, support for Bergmann's rule is not universal, particularly at the interspecific level (Ashton et al., 2000; Gohli and Voje, 2016). It is intriguing, therefore, that both PGLS and BayesTraits analyses indicate significant positive correlations between body size (both MTL and LSM) and maximum latitude in Chondrichthyes, with the reverse trend observed between body size and minimum latitude (Figure 2; Figure 3; Table 2; Table 3). Increased body size is also significantly associated with increasing maximum water depth (Table 2; Table 3). These patterns are consistent with Bergmann's rule, as higher latitude and deeper marine environments will, on average, be colder than lower latitude and shallower marine environments. They are also consistent with recent work in bony fishes (Troyer et al., 2022), suggesting that Bergmann's rule may be a general phenomenon across aquatic ectothermic verterbates, although additional studies from other clades would be necessary to confirm this.

Explanations for Bergmann's rule in chondrichthyans

The classic explanation for Bergmann's rule, particularly favoured for endotherms, suggests that larger organisms have a lower surface area to volume ratio, reducing heat loss to the environment (Fernández-Torres et al., 2018). Whilst recent work indicates that surface area to volume ratio does indeed decrease with body size in sharks (Gayford et al., 2025c), reduction of heat loss is an unsatisfactory explanation given that the vast majority of chondrichthyans are ectothermic (Ebert et al., 2021; Pimiento et al., 2019). This explanation is also inconsistent with Bergmann's rule in Tetraodontiform fishes (Troyer et al., 2022), which are similarly ectothermic.

More recently, theoretical and empirical studies indicate that thermal constraints on cellular growth, or adaptive benefits of delayed/accelerated maturation in cold and warm environments, respectively, provide more viable explanations for temperature-size relationships in ectotherms. Whilst initially framed in the context of intraspecific relationships between temperature and size at maturity (Angilletta et al., 2004), these hypotheses are at least theoretically applicable to temperature-size relationships among species and other measurements of body size. Among the most popular of these hypotheses is that thermal constraints in cellular or gonadal growth rates result in larger size in colder environments (Angilletta et al., 2004; Van der Have and De Jong, 1996). However, in the case of Chondrichthyes, there is little evidence to suggest that shifts in ambient temperature substantially alter the rate of cellular growth either within or among species (Lear et al., 2017; Thomas et al., 2023). Alternatively, the compound interest hypothesis suggests that ectotherms in warmer environments mature at smaller sizes as this enables the completion of multiple generations within a single reproductive season (Partridge and French, 1996). Whilst our finding that maximum latitude is a better predictor of body size than minimum latitude (Table 2; Table 3) is not sufficient to reject the compound interest hypothesis, this explanation nevertheless appears unrealistic for chondrichthyans given their long generation times, making the completion of multiple generations within a single reproductive season impossible. Consequently, adaptive evolution toward small body size in warm environments and constraints on cellular growth rates are unlikely to explain Bergmann's rule in Chondrichthyes.

The most plausible explanation for observed latitudinal and depth-mediated gradients in chondrichthyan body size is that increased size in colder and deeper environments provides some other adaptive benefit, besides heat conservation or changes to generation time. Whilst the underlying driver of the Bergmann's rule in tetraodontiform fishes has not yet been determined, this hypothesis is consistent with the fact that dramatic increases in body size in this clade were associated with decreasing oceanic temperatures (Troyer et al., 2022). According to resource allocation theory, large body sizes should be favoured where mortality is lower (Atkinson and Sibly, 1996; Kozlowski et al., 2004; Kozlowski, 1996; Roff, 2002; Stearns, 1992). In line with this theory, the biotic interactions hypothesis suggests that predation rates are lower in temperate than tropical environments (Schemske, 2009). Whilst there is mixed evidence for this hypothesis in marine environments (Ashton et al., 2022; Roesti et al., 2020), no study to date has explicitly addressed latitudinal gradients in predation pressure among chondrichthyans. In addition to predation, competition may influence levels of mortality in different environments. Generally speaking, tropical marine environments harbour more diverse/complex communities and greater intensity of clade competition (Pianka, 1966; Schemske et al., 2009). Consequently, shallow tropical ecosystems, with greater competition for resources and plausibly higher predation pressure, may correspond to higher mortality rates in tropical chondrichthyans, compared to those inhabiting deeper and more temperate environments.

Assuming this is the case, optimal resource allocation theory would favour the evolution of larger body sizes in these colder and higher latitude environments (Kozlowski et al., 2004), particularly in taxa with long generation times and relatively low fecundity such as chondrichthyans. Under such conditions, larger body sizes may prove particularly advantageous as they enable individuals to traverse a larger search area during foraging, which may help explain the poor correlation between body size and minimum latitude (Table 2; Table 3). Indeed, resource acquisition is thought to be the predominant constraint upon the evolution of large body size in marine megafauna (Ferrón et al., 2018; Goldbogen and Madsen, 2018; Pimiento et al., 2019). Consequently, we hypothesise that the validity of Bergmann's rule in Chondrichthyes may result from elevated rates of survivorship in species living at high depths and latitudes, favouring the evolution of increased body sizes through an adaptive shift in the allocation of resources. Although current data are insufficient to test this hypothesis directly, methods developed for other marine taxa could provide a pathway forward. For example, studies have quantified latitudinal and bathymetric gradients in predation pressure using wounds or injuries as proxies for predation events (Harper and Peck, 2016) and by integrating trophic, demographic, and behavioural data (Queirós et al., 2018). Applying similar approaches to cartilaginous fishes could yield valuable insights. However, due to the large number of chondrichthyan species, many of which are essentially unknown from a trophic and demographic perspective (Ebert et al., 2021), vast amounts of novel data would be needed to satisfactorily test the hypothesis of elevated survivorship at high depths and latitudes.

Future studies and limitations

Whilst the results of this study provide novel insight into body size evolution and Bergmann's rule, there are several limitations that must be acknowledged but could form the basis of future studies. Firstly, we used phylogenetic data from Stein et al. (2018), which resolved polytomies using a birth-death model. Consequently, macroevolutionary inferences may be influenced by model-estimated branch lengths. However, we mitigated this by accounting for phylogenetic uncertainty through implementation of Bayesian analyses.

Furthermore, shark and ray species are highly migratory (Mull et al., 2022), and consequently all observed relationships between body size and ecology/temperature (Table 2; Table 3) must be considered within this context. Similarly, habitat usage (both latitudinal and bathymetric) commonly varies seasonally, through ontogeny, and among discrete populations of individual chondrichthyan species (Andrzejaczek et al., 2022). In some cases, these discrete populations also differ in terms of body size. These factors likely explain the poor predictive performance of minimum latitude and minimum depth, as many species that predominantly inhabit deep water or high-latitude environments are nonetheless capable of entering warmer environments at times (Ebert et al., 2021). Unfortunately, spatiotemporal variation in ecology and body size cannot be accounted for using existing data. Technological advances pertaining to satellite tracking and related methodologies may overcome this limitation to some extent, but many additional studies including standardized maturity assessments will be required to improve our understanding of intraspecific variation in body size among chondrichthyans. Future studies should consider exploring the extent to which Bergmann's rule may vary among specific trophic, morphological, or ecological guilds, and how these trends may be affected by migratory capabilities.

Finally, our choice of ecological, morphological, and phylogenetic parameters could have influenced our results. Whilst PGLS models incorporating a Pagel's lamda covariance structure outperformed alternatives (Table 1), it is not possible to confirm with certainty that such a covariance structure perfectly captures models trait variation among species. Likewise, some chondrichthyan taxa exhibit idiosyncratic and highly specialized morphological or ecological characters, the inclusion of which could distort perceivecd relationships. This is particularly the case for large-bodied planktivorous taxa, and those with extreme axial adaptations such as thresher sharks (*Alopias* spp.) and sawfishes (Pristidae). However, the relatively depauperate nature of these clades means that any confounding effect is likely minimal.

Conclusions

Despite the intense interest in Bergmann's rule and associated macroecological hypotheses, this study represents one of the few phylogenetically broad tests of Bergmann's rule at the interspecific level in any major ectothermic clade, finding that chondrichthyans tend to comply with the rule. We do not provide any direct tests for the mechanism underlying compliance with Bergmann's rule in chondrichthyans, but elevated survivorship at high latitudes/depths is plausible, in contrast with most common explanations for the temperature-size rule. Future work quantifying predation and mortality rates across ecological gradients will be necessary to test this hypothesis. Nonetheless, cumulatively, this study provides robust evidence for a long-theorised macroecological ‘law’ and highlights the need to ground investigations of Bergmann’s rule in a phylogenetic framework.

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