

Trends in Marine Traits Across Latitudinal Gradients & Depth Classes

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Abstract

Species interactions and traits are expected to be structured over space and time by many different natural phenomena. Abiotic factors can structure species traits, with Bergmann's rule predicting larger species in cold environments, while higher species richness is expected at warmer temperatures. Using a data set with marine species traits and geographic factor data, we explored the expectations of Bergmann's rule, higher equatorial diversity, and how other environmental gradients shape ecosystems. We found no evidence for classical Bergmann's rule, with species mass greatest around the median temperature values. Equatorial species richness was not found to be higher than in temperate regions, going against accepted literature. However, both of these results are confounded by oversampling in the Northeastern United States, which created a dataset that routinely violated statistical assumptions, nullifying these results. We found significant results for depth class and temperature structuring individual size across hemispheres, but with no clear trends globally. Finally we found significant results structuring age class, with larval species found between 1000 and 3500 m depth, while adults are found above 1000 m.

Introduction

A cursory glimpse of the flora and fauna of the world immediately illustrates that species traits vary across geographic location. This simple observation has been the subject of ecological work by those who are unsatisfied with the mere observation of variation and seek to understand why. Despite being the subject of intense discussion for hundreds of years, research on trait variation across geographic location is still ongoing, with few definitive results as of yet. A substantial body of ecological work focuses on the traits and abundances of species across spatial gradients (Lamanna et al. 2014;), with the intention of making sense of the complicated web of species distribution. We seek to add to this body of work by examining how various abiotic factors affect the physical traits and spatial distribution of marine fauna using a comprehensive sample from the world's oceans. We will focus on Bergmann's rule, a zoological law which describes how species change across temperature gradients (Teplitsky and Millien 2014).

Bergmann's rule posits that species of larger size are found at colder temperatures, with the opposite holding true for warmer temperatures (Teplitsky and Millien 2014). The rule was proposed for mammals and birds, the only two groups of endothermic organisms. In conjunction with Bergmann's rule, it is possible that higher latitudes should show larger species, as the average temperature becomes colder as distance from the equator increases. An accepted rationale for this apparent trend is that larger species minimize their surface area to volume ratio to stay warm and that smaller animals do the inverse to stay cool (Teplitsky and Millien 2014). Recent work has suggested that Bergmann's rule may hold true for not just mammals but also fish in the ocean (Torres et al. 2018).

In addition to having species of smaller size, equatorial ecosystems are usually more species rich (Brown 2013). The mechanism causing this is still unknown, and it remains a contentious point of debate in the literature. Some suggest that because tropical land masses have been warmer for longer, there has been more time for speciation (Fischer 1960). Another theory posits wetter and warmer environments can support more primary productivity, and allow more consumer species to share the ample resources (Hutchinson 1959). Irrespective of the forces behind it, higher species richness at tropical latitudes is expected in marine species (Brown 2013), and is worthwhile to test for.

In aquatic systems, depth is an intrinsic factor which may describe trends in species size and distribution. Previous studies show that less species diversity is present in the deep ocean, but found no clear trends on how depth predicted species size (Smith & Brown 2002). Furthermore, Smith & Brown (2002) showed that closely related species can differ in size in opposite directions across different depths. This study was conducted on very few species and offers no explanation for these trends. The lack of understanding of the effect of depth on body size make it a prime target for further study.

The results of the analyses of Bergmann's rule and species richness across latitudinal gradient led us to want to investigate a third possible trend in the data: the potential for depth to structure life history traits. The dataset contains values for the species lifestage, with species being categorised as larval, juvenile, and adult. Fish species often spend different life stages in different locations, with Salmon being a classic example of this across a spatial gradient. In the case of depth gradients, Mayor et al. (2014) showed that the larval stage of species is often found at lower depths than the adult stage. Given this, we used the dataset to investigate if depth structured lifestage.

We investigated the marine traits dataset published by Barnes et al. (2008) in *Ecology*. From this dataset, we have chosen to investigate marine species sizes and abundances across depth, latitude (as a proxy of temperature), and temperature itself. This allows us to investigate Bergmann's rule, where species richness is greatest, and the effect of depth on life history traits. We hypothesised that Bergmann's Rule would predict marine organism sizes across temperature gradients, that taxonomic diversity is highest around the equator, and that depth would structure life history traits such as life stage.

Methods

Data Description

The dataset published by Barnes et al. (2008) is a summary dataset which uses data pulled from many individual marine surveys. It is chiefly concerned with measures of body mass and length of predator and prey species, while also recording data on abiotic factors such as location (*Fig. 1*), depth, and mean annual temperature. The data is highly coastal, reflecting that most sampling is based out of ports, which is substantially cheaper than having a ship sail for long periods away from the shore. However, we chose to ignore this, largely because most marine life is concentrated close to coastal regions anyways (Tittensor et al. 2010). The data appeared to be fairly robust and though not collected specifically for the analyses described in our introduction, its sheer size led us to believe that it may present results for our questions of interest.

Data Cleaning

As the dataset had been published in *Ecology*, it was quite clean from the outstart, containing only a few minor errors. To start, the column names contained spaces, which were replaced with underscores using the R function `gsub`. Following that, some column values contained capitalised and uncapitalised

versions of the same value, such as adult and Adult. This was easily fixed by again using gsub to replace capitalised with uncapitalised data. For measurements of length and mass, the dataset contained multiple units, which we wanted to correct to only one unit measure. To fix this, we mutated the measurement columns with conversion factors based on the unit type (for instance to convert from g to mg a conversion factor of 1000 was used). Finally, latitude and longitude were originally presented in degree minutes format, which presented substantial difficulties because this format does not plot easily. Ultimately, a function was found that could remove the degree symbol and convert the minutes to decimal degrees and add the the two chunks together. To continue accounting for hemisphere, we used grepl to mutate new columns with values of 1 for east and north and values of -1 to. After removing the N, S, E, W, signifiers from the latitude and longitude we were able to multiply these column back to the new decimal degrees values to ensure that we maintained directionality of the data. At this point the data was clean and ready to be used for our analyses.

Data Analysis

We created initial plots and linear models of prey and predator mass over latitude, to determine our starting point. A principal components analysis was done to identify other correlated traits of interest to guide further tests. To address our initial hypothesis, we used linear regression to test whether or not Latitude and mean annual temperature could predict body size, using both mass as well as length as a response variable. We also repeated these tests using mean estimates for predator length at each latitudinal location. In addition, we repeated this type of linear model, removing a number of biased samples, and regressing the length of predators against a suite of variables including depth, latitude, longitude, geographic location and mean annual temperature. .

Then, we separated the dataset into Northern and Southern hemisphere, to see if trends changed when examining each hemisphere independently. We ran linear models to test the predictive power of mean annual temperature, latitude, and depth on predator length (a measure of predator size) in each hemisphere separately. We ran models with combinations of these factors on the southern hemisphere, where single factor models showed promise: an ANOVA model of hemisphere and depth (Ocean layer) predicting predator length, and an ANOVA model of hemisphere and mean annual temperature predicting predator length. We additionally examined a series of additive models to determine which abiotic factors were influencing sizes of predators and prey.

To test our hypothesis regarding equatorial diversity, the number of unique species of prey and predators were grouped by latitude in both hemispheres separately, which acts as a count of species richness over space. Plots and linear models were run for these data.

Finally, to test the effect of depth on structuring life stage, we ran a simple one-way ANOVA. Assumptions of normality and equality of variance were made by plotting the residuals and running a Bartlett's test respectively.

Results

Preliminary tests using predator and prey masses over latitude (which is classically related to temperature) were significant results ($p < 0.001$) but very low R squared, suggesting it was the sheer amount of data points at 40 degrees latitude that made it significant (*Figure 2*). Due to very abnormal plots testing normality and variance, this significance result is likely not valid. We went on to do a principal components analysis to find more correlated variables to test (*Table 1*). This model found that

our continuous variables could be collected into three groups: prey length, prey mass and predator mass were all correlated, then mean annual temperature, depth, and a negatively correlated longitude. And finally the third group was longitude, latitude, and predator total length.

Our initial results indicated that while mean annual temperature had some effect on the mean length of predators (*Figure 3*), it was not in a direction that supported our hypothesis surrounding Bergmann's rule. This was confirmed again with the linear model that removed the largest values, again showing no discernable trend supporting Bergmann's rule.

We found that Ocean layer, mean annual temperature, and hemisphere structure predator size, but with no clear global trends. (*Figure 5 & 6*) Shows that predators at all ocean depths in the northern hemisphere are approximately the same size. In the Southern hemisphere, predators in very deep water are the largest while those in shallower water are smaller than other Northern hemisphere fish and the deeper southern hemisphere predators ($p < 0.001$). The ANOVA found that both Hemisphere and Ocean layer were significant predictors of predator size as well as the interaction between the two. Meaning that not only does the depth layer in which predators are found determine their size by hemisphere ($p < 0.001$) but the way in which depth impacts size depends on which hemisphere the predator is found in. Mean annual temperature as well as hemisphere and their interaction were also significant predictors of predator length (*Figure 6*).

The data suggests that predators vary in size depending on what hemisphere they are found in ($p < 0.01$), what temperature they are found at ($p < 0.001$) and that the way hemisphere predicts predator size depends on what temperature the predator is found in ($p < 0.001$). This suggests that though Bergmann's rule is not found, temperature does still have a strong influence on structuring where species live. Furthermore, the ocean layer in which a predator is found predicts its length as does the mean annual temperature of the area on its own. These three factors and their interactions have significant effects in structuring predator size, though they afford us no overall trends, suggesting that abiotic factors may structure populations, but not in any consistent manner. The two preceding ANOVAs violated the assumption of homoscedasticity of variance as well, so interpretations of significance levels should be done with caution, however the trends are visually evident nonetheless.

Our second question concerned taxonomic diversity across latitudinal gradients, and we found some significant results but probably not due to real ecological trends. For this we plotted in north and south hemispheres separately, for latitude effect on prey and predator species richness. Both the prey and predators in the northern hemisphere had a significant effect of latitude ($p < 0.01$), and R squared values of 0.5, which is quite high. In the northern hemisphere, the correlation is positive (*Figure 7*), and we see the most richness at the 40 latitudinal lines. This goes against the expected trend of seeing higher species richness around the equator, and is likely due to biased sampling. In the southern hemisphere, the results were not significant ($p > 0.05$), likely due to there being only three latitudes sampled.

To address our third question, the group investigated how depth may structure marine traits, with one proving to be of interest: life stage. The three major life stages in this data set are larval, juvenile, and adult, with our group hypothesising that there would be differences in the depths these groups resided. ANOVA results for depth structuring life stage were significant ($F < 1127$, $df = 6$, $p < 0.001$). We ran a Tukey HSD test to determine the individual groups that differed and found a value of $p < 0.001$ between all combinations of groups. *Figure 8* is not a direct plot of the ANOVA, but rather is designed to make it easy to see where each age class, and here we see that larva tend to live from depths of 1000 to 3500m, an area which is not inhabited by any other life stage. Finally, we had to check the ANOVA assumptions. In this

case, the assumption of normality was met, while the assumption of equality of variances was not (Bartlett's test $p < 0.001$), which limits our ability to apply the results. However, *Figure 8* is still useful as a visual indicator of the trends.

Discussion

Assigning laws to how the natural world works is common in ecology, yet should be backed by rigorous testing and data. We attempted to test three such ecological rules using marine species, and hypothesized that they would follow Bergmann's rule, be more species rich at the equator, and have traits otherwise structured by their environment. Using linear models, plot visualizations, and other techniques, we found no support for our Bergmann hypothesis, no support for increased equatorial diversity, and some support that other geographic factors may structure species traits. Much of our data was confounded by uneven sampling and factors that we could not adjust for. So, the question becomes why we did or did not see the anticipated trends.

When examining predator and prey traits, like mass and length, over temperature and latitudes we did not find the trends expected. Instead of larger organisms being found in colder temperatures and latitudes, we see that large animals are often grouped around middle temperatures, which coincides with 40 degrees North (*Figure 2*). This is due to sampling bias, as previously described. Then, separating by hemisphere, we observe a potential inverse-Bergmann's Rule in the South, with the smallest organisms at the coldest temperatures (*Figure 6*). The inverse of this rule (smaller bodies at colder temperatures) was suggested to be applicable to ectotherms like fish by Mousseau (1996). Ectothermic body size is usually directly correlated with how much time they have to grow, which tends to be shorter in cooler climates and lead to smaller organisms (Mousseau 1996). In different reviews of Bergmann's rule, it was suggested that predators follow the law more closely, since their body size is linked to the prey's body sizes (McNab 1971), however we did not see strong evidence of this occurring either (*Figure 2*) despite predator and prey size being correlated in the PCA (*Table 1*). In recent years, new evidence suggests invasive fish species have been altering the expected latitudinal trends of Bergmann's rule, since invasive fish are increasing the median sizes (Blanchet et al. 2010). This effect was more significant in the southern hemisphere of the ocean, and interacted with temperature, which *is* similar to the significant result and interaction we had in *Figure 6*. The south hemisphere was less affected by sampling biases, and so we may be seeing the combined effects from the work of Mousseau (1996) and Blanchet (2010) at work.

In attempting to determine what other factors might be structuring our data, we initially hypothesized that depth could potentially be driving the distribution of size in our data. While it is a commonly observed biological fact that different life stages of marine pelagic fish inhabit different depths (Young et al. 2012), there is less evidence to show that depth is correlated with size. However some work has showed that in fact mesopelagic fish (fish inhabiting the second most shallow depth class) are some of the largest, particularly in open ocean environments (Irigoien et al. 2014). Given this, we posited that we might see larger individuals in our data (when controlling for lifestage) in some of the more shallow ocean layers. However, we did not see any results that supported this in our data, which could be explained by the fact that most of our observations come from coastal regions, and not the open ocean.

In thinking about how temperature could structure body size in this marine system, it is important to remember the caveats of context when thinking about why our data do not match our hypotheses with respect to temperature or latitude. While Bergmann's rule has been shown in some marine fishes

(Fernández-Torres et al. 2018), our data include a much wider range of taxa, and the nature of marine environments predispose Bergmann's rule to be less applicable in this system. For instance, currents which shift over the course of the calendar year obscure mean annual temperature measurements, and, unless matched perfectly, can lead to inaccurate conclusions surrounding the matching of fish taxa to temperature depending on the sampling time/location. Also, depth may be a confounding factor when looking at mean annual temperature, as temperatures were not sampled from different depth classes. In addition, one would obviously expect ectothermic organisms to behave differently than endothermic organisms. Furthermore, varying migration patterns and timing could confound any measurement of patterns suggesting Bergmann's rule, as many marine fish species have wide ranges and migrate across hemispheres every year. While there are clear rules that do exist and can be used to identify structure in marine ecosystems, mean annual temperature and depth do not appear to structure body size in our data.

Our second hypothesis which addressed taxonomic diversity over latitudinal space was not supported by our dataset (*Figure 7*). In a paper by Cardillo (2012), they describe the importance of life history traits in determining fish species richness at the equator, which we did not find correlated. Additionally, they pointed out the importance of phylogenies in influencing the results, with many false positives being attributed to neglecting to incorporate the phylogeny. While we had general taxonomic data, building a phylogeny was outside the scope of this course, and may not have added much of interest since the results were not significant. An additional important thing to note, is that the trend does not have to be symmetrical across hemispheres. A paper on marine copepod diversity found that the Northern hemisphere diversity peaked at subtropical latitudes, while the Southern hemisphere diversity plateaus and does not decrease as dramatically at higher latitudes (Rombouts et al. 2009) While they still found temperature was a significant factor in determining species richness, this inequality may only worsen the issues that our sampling bias bring with them. Overall, there were not enough latitudes represented in the southern hemisphere of our dataset to accurately see diversity trends, even if there were many data points at each latitude.

The results of our ANOVA are interesting in that they tell us that species do tend to spend their different life stages at different depths. It is clear that larva tend to inhabit 1000 to 3500 m depth while the vast majority of adult species live above the 1000 m depth marker. This data is supported by previous research by Young et al. (2012) which found larvae tend to reside deeper than the corresponding adults of the species. The question that this raises is why this difference might be occurring. Although we cannot determine why based on this dataset, we can speculate why this may be occurring based on previous research on marine depth zones. Within the ocean, there is only enough sunlight for photosynthesis in the top 200 m, with zero light penetration below 1000 m depth, leading to the term 'aphotic zone' (NOAA, 2018). All ecosystems are structured by the presence of primary producers, and this is no exception here. The majority of the organic chemical energy in the ocean is in the top 200 m, meaning that the energy to support the largest organisms is present here. This energy can filter up the trophic levels effectively, helping to support large animals (D'Alelio 2016). In the aphotic zone, most consumers rely on detritus sinking from above, as there are no zooplankton to consume in this area (Mayor et al. 2014). Energy input by detritus is substantially lower than energy input by autotrophs, and so we see an area which cannot support large animals (D'Alelio 2016). For the larva the benefit is twofold, they are able to subsist on the low energy provided by detritus while also escaping predation. These larval benefits are two likely reasons why we see 1000 to 3500 m depth as the main region of larvae inhabitants.

The greatest challenge encountered during the course of this analysis was that of unequal sampling. A vast majority of the data was collected in the northern hemisphere and heavily over-represented between 40 and 50 degrees of latitude. This not only created a massive skew, destroying predictive power of models, but also caused many models to violate key assumptions, rendering their p-values meaningless. This problem of skewed sampling is by no means unique to this dataset, but rather a large problem in ecology as a whole. Places with more research funding are better studied, but not necessarily, or even likely to be, representative of other areas around the world (Schmidt-Lebuhn et al. 2012). With this, datasets being used to explain spatial trends of species should be evenly sampled across the space parameter of interest. This reason for this is twofold: balance allows for more comprehensive data to demonstrate trends across space and balance ensures the models used to test them do not violate assumptions which would undermine their credibility.

Conclusion

We set out to examine Bergmann's rule, equatorial taxonomic diversity, and how other geographic factors like depth structure species traits. We found possible evidence for reverse Bergmann's rule in the southern hemisphere, no expected trends in taxonomic diversity, and that depth and temperature were important variables in structuring species life stages and size. Many of the problems with this dataset are inherent because it was not sampled with the intention of testing these ideas. A more thorough test of the rules we aimed to test would require a dataset which had been sampled more proportionally across latitudes, without the large skew seen here.

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Tables

Table 1. Results table of a principal components analysis. Three natural groups were formed from our continuous data. The first group was between prey length and mass with predator mass. The second grouping was mean annual temperature, depth, and a negatively correlated longitude. The third group was longitude, latitude, and predator total length.

	item	RC2	RC1	RC3	h2	u2	com
Prey_length	3	0.86			0.78	0.22	1.1
Prey_mass	4	0.80			0.65	0.35	1.0
Predator_mass	2	0.59			0.38	0.62	1.2
Mean_annual_temp	8		0.91		0.90	0.10	1.2
Depth	7		0.78		0.64	0.36	1.1
Longitude	6		-0.58	0.42	0.52	0.48	1.9
Latitude	5			0.80	0.70	0.30	1.2
Predator_total_length	1			0.61	0.38	0.62	1.1

	RC2	RC1	RC3
SS loadings	1.80	1.80	1.36
Proportion Var	0.22	0.22	0.17
Cumulative Var	0.22	0.45	0.62
Proportion Explained	0.36	0.36	0.27
Cumulative Proportion	0.36	0.73	1.00

Mean item complexity = 1.2

Test of the hypothesis that 3 components are sufficient.

The root mean square of the residuals (RMSR) is 0.13

Figures

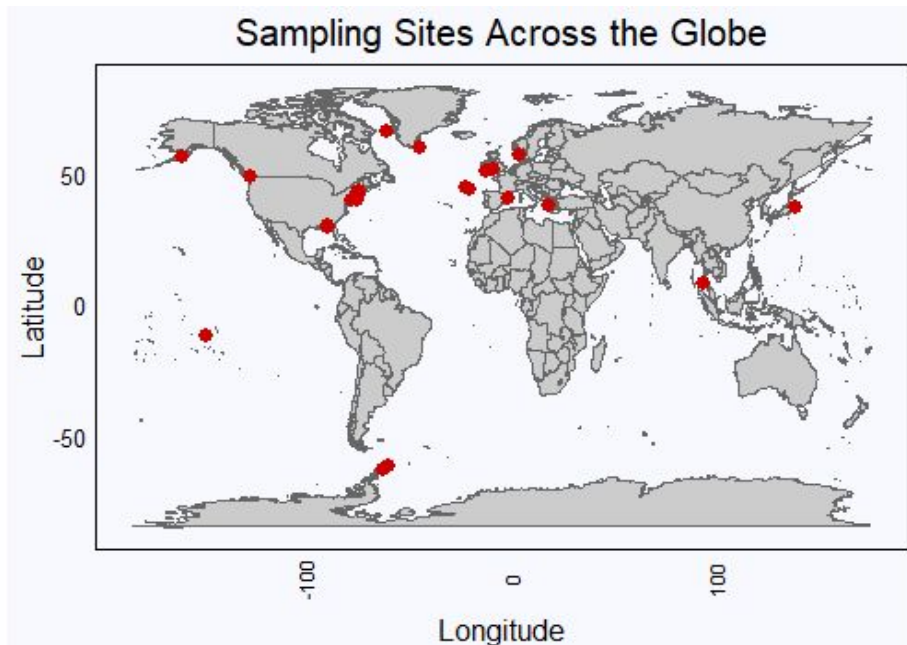


Figure 1. Sampling sites across the world. Red points indicate the sampling sites that were included in this paper, spanning almost pole to pole and across all longitudes. Mostly coastal in nature, these sites represent a single sampling site from an original study that was then included in this dataset.

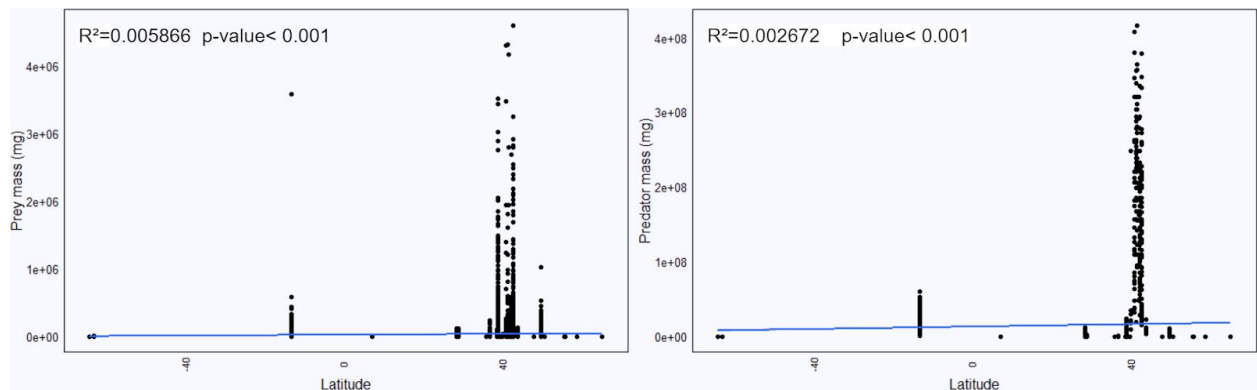


Figure 2. Species mass versus latitude. The relationship between prey and predator mass (mg) over latitude. Linear models were run and found significant results but very low R squared, suggesting it was the sheer amount of data points at 40 degrees latitude that made it significant.

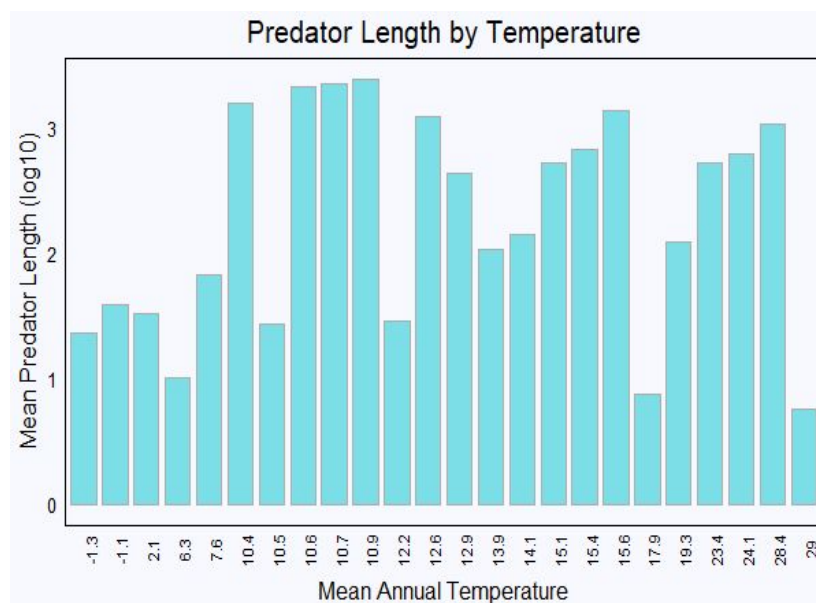


Figure 3. Predator length by mean annual temperature. The log-transformed mean predator length at each of the observed mean annual temperatures across our data. This confirms our result that there is no trend showing larger body sizes with colder temperatures

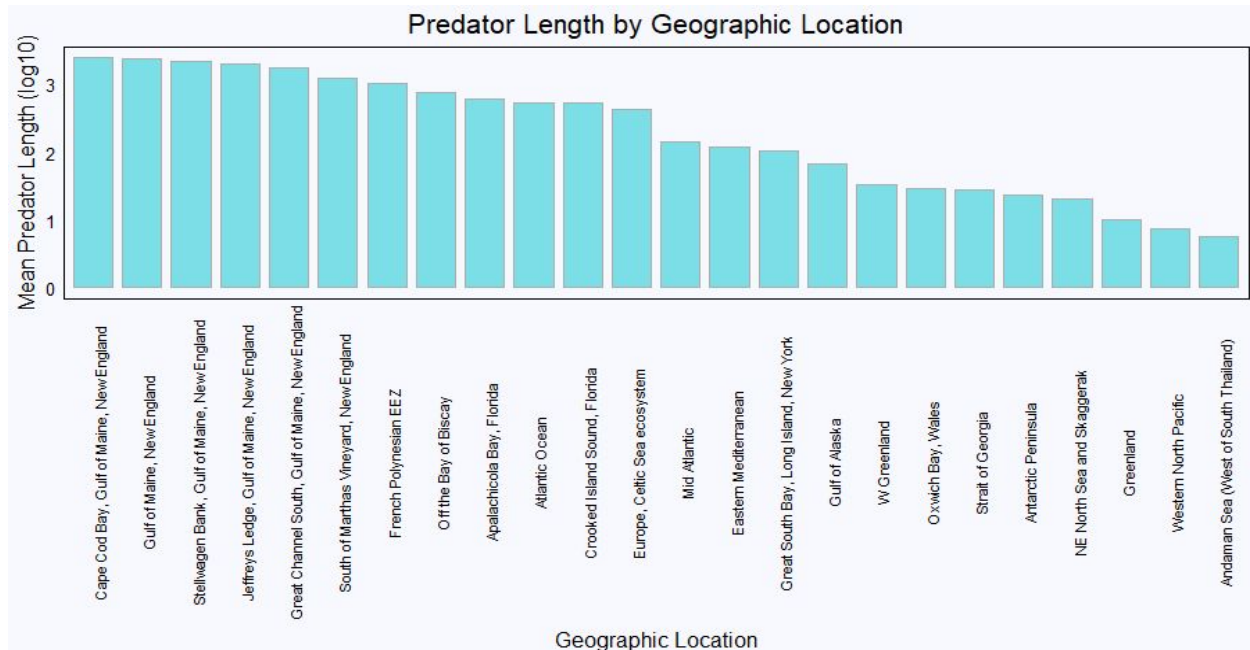


Figure 4. Predator length by geographic location. Here we can see that our size measurements were biased by a series of large means concentrated on the North-eastern seaboard of the United States. This plot prompted the removal of these values and the subsequent re-analysis of the data.

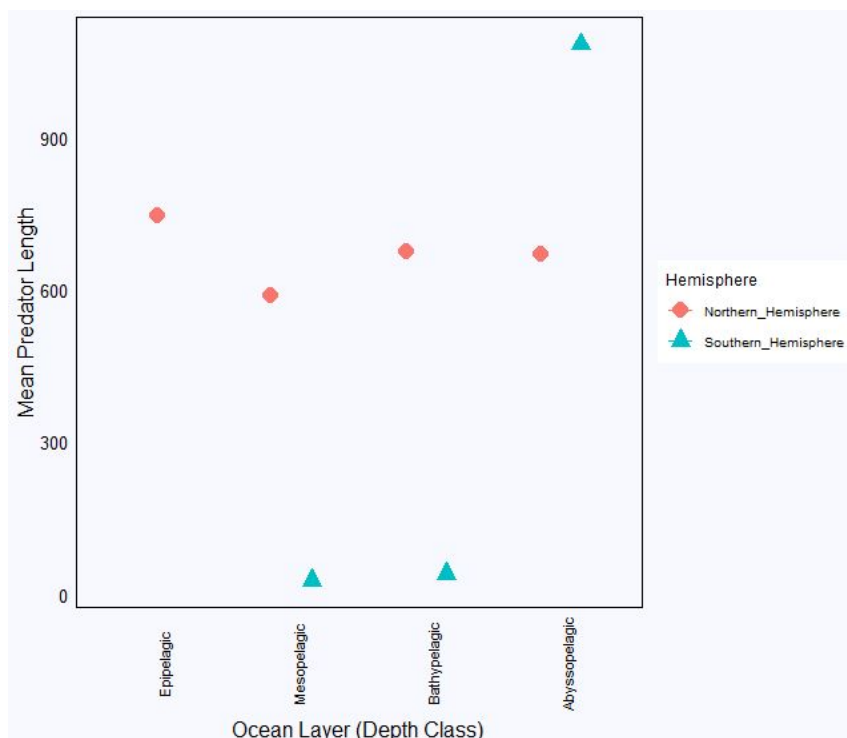


Figure 5. Mean Predator Length by Ocean Depth Class in each Hemisphere. An ANOVA of Ocean Layer where epipelagic = 0-200m, mesopelagic = 200-1000m, bathypelagic = 1000-4000m, abyssopelagic = 4000-6000m, $df = 2$, $p < 0.0001$.

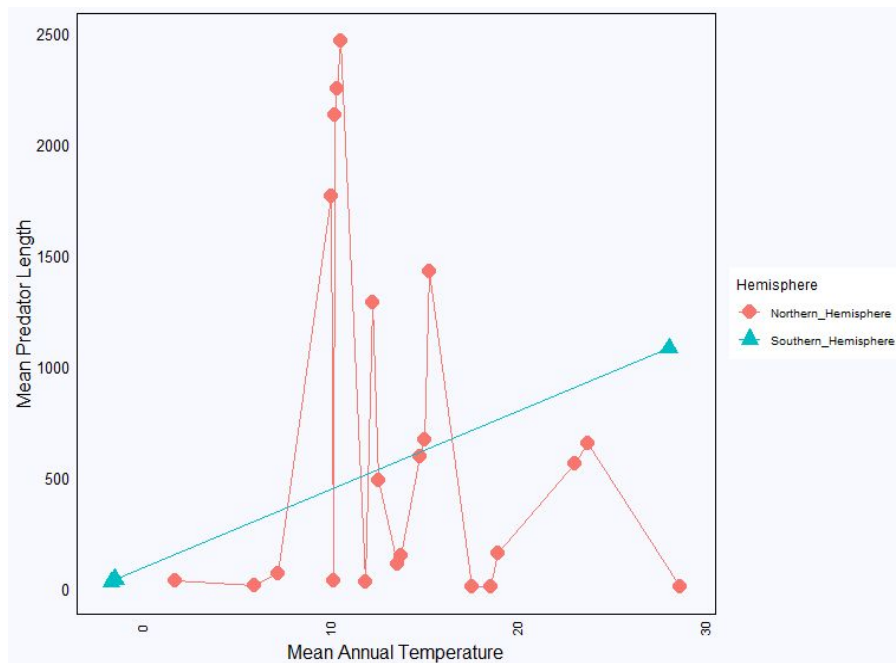


Figure 6. Mean Predator Length vs Mean Annual Temperature in each Hemisphere. An ANOVA of Mean annual temperature (°C) and Hemisphere predicting mean predator length (mm), $df=1$, $p<0.01$.

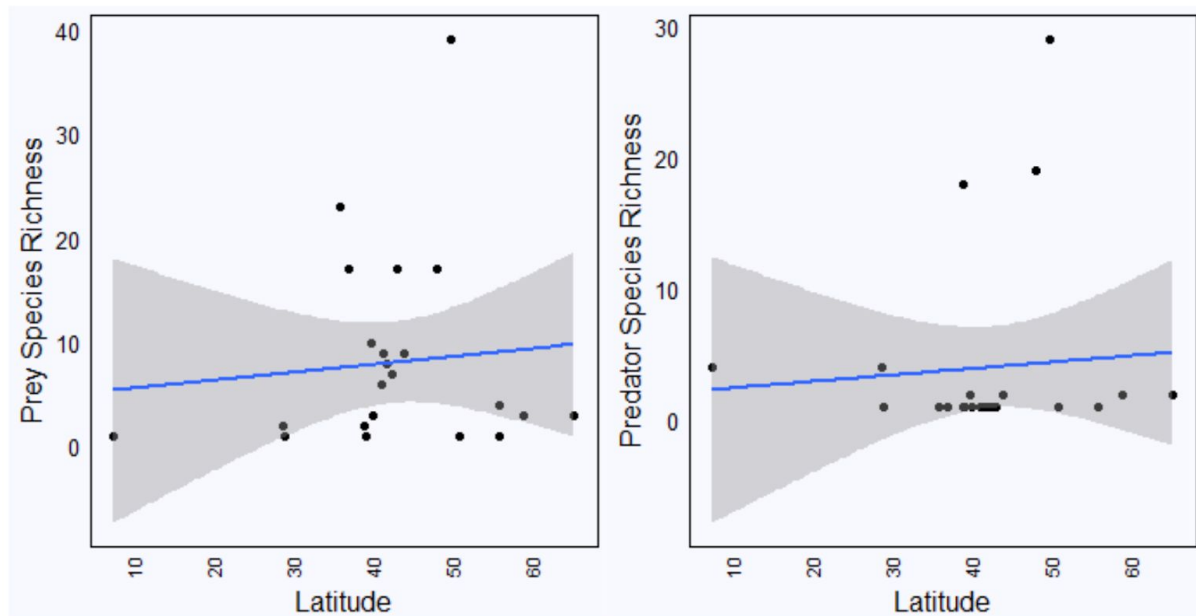


Figure 7. Species Richness vs. latitude in the Northern hemisphere. The number of unique species of predators and prey in the northern latitudes. Both linear models were significant at $p<0.01$, and had an R squared of 0.5. Southern hemisphere data was not significant. Data in the northern hemisphere was surprisingly normal when run with a `plot()` function.

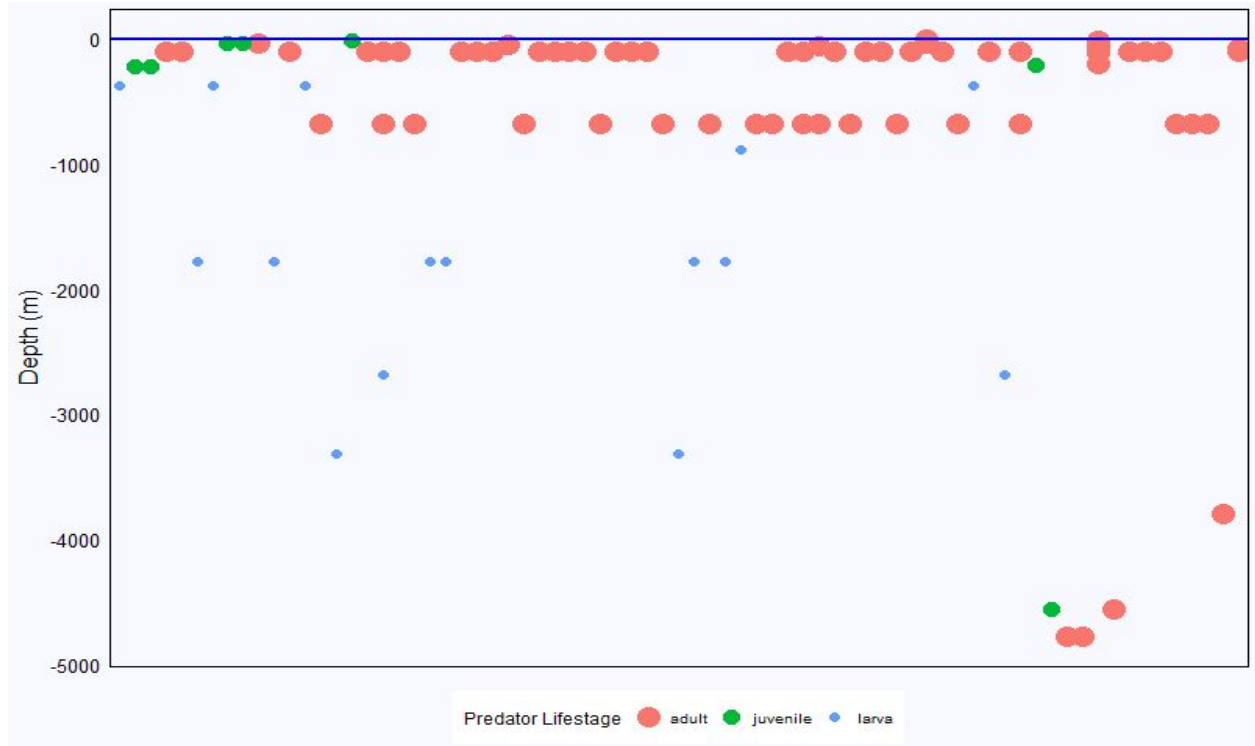


Figure 8. Depth of sampling vs. lifestage of predator found at that depth. The horizontal blue line represents the ocean surface at depth of 0 m. This plot only uses lifestage values of adult, juvenile, and larva, while excluding the others, which were undefined. This plot is a visualisation of the ANOVA for depth values being different across depth.