

Marine Predator and Prey Interactions

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Abstract

Interactions are pivotal to the functioning of marine ecosystems globally. Ecosystem functioning can be examined by studying the trophic complexity of communities locally. However, it is unclear how geography, specifically latitude influences trophic complexity. Here we show that there is an unclear relationship between trophic complexity and latitude. We came to this result by showing that trophic connectance and species richness varied with latitude in marine ecosystems. These findings give a spatial and temporal baseline of trophic complexity that can be compared to future data under anthropogenic climate change.

Introduction

Marine ecosystems have been under threat for centuries due to anthropogenic influences, and are rapidly deteriorating (Worm, 2013). Despite this global threat, marine ecosystems are relatively poorly understood and sensitive to many of the challenges they are currently facing, including warming, acidification, and eutrophication (Halpern *et al.*, 2007). Recent research suggests that trophic complexity can bring stability to marine ecosystems and assist ecosystems in resisting invasion by non-native species (Heesterbeek *et al.*, 2007). Understanding how ecological and anthropogenic factors influence complexity is critical to maintaining biodiversity in marine ecosystems.

Research on food web complexity has resulted in numerous laws and models that describe the relationship between ecosystem components. The link-species scaling (LSS) law predicts that species richness is inversely proportional to the connectance (number of links/species²), and that there are two predator-prey interactions per species in a given food web (Cohen and Briand, 1984; Cohen and Newman, 1985). Contrary to the LSS law, the constant connectance pattern predicts that the number of predator-prey interactions increases with the number of species in a community (Martinez, 1991). Although there is a general dispute over the exact link between food web complexity (ie. the level of connectance, number of links, etc.) and species richness, it is clear that there is a positive relationship between species richness and food web complexity. Since marine species richness gradients are influenced by latitude (Grady *et al.*, 2019; McRae *et al.*, 2017) and body size (Peters, 1983), it is important to examine how these factors influence food web complexity, given the important role complexity plays in ecosystem stability and maintenance (Heesterbeek *et al.*, 2007).

In marine community ecology, concern has been voiced over the need to utilize an individual-level approach when studying trophic interactions instead of the species-level or community-level view that has been common historically (Nakazawa, 2017). Trophic interactions at the individual level allows for examination of how the trophic interactions change through life stages of organisms within the community. Organism trophic level and mass have a quadratic relationship and are related to the gape of the organism (Segura *et al.*, 2015). This suggests that the gape of the organism may also constrains the size of their prey. However, gape can be difficult to discern so organism mass is usually the study unit of choice.

Ontogenetic shifts have previously been studied in sharks, however, how the predator-prey mass relationship changes through life stages is unclear (Lotifora, 2009). A greater understanding of how the predator-prey mass relationship changes with life-history stage can help us understand how interspecific interactions change ontogenetically. Other research suggests that the strength of trophic interactions can be dependent on organism mass and can help us understand how to maintain critical marine ecosystem complexity which is required for marine ecosystems to thrive (Emmerson and Raffaelli, 2004).

As patterns of species richness across communities change with latitudes, so do the size of the individual animals. Bergmann's rule (Bergmann, 1847), arguably the best-known and most widely studied ecogeographical rule, states that body size tends to increase as we move towards higher latitudes. However, this rule has been widely criticized and several studies have refuted it (Giest, 1986; Adams, 2007). In addition, while Bergmann's rule has been heavily studied in mammals and terrestrial species, data involving ectothermic marine species is still lacking.

This study will investigate how predator-prey interactions change with size and latitude at both the individual and community level. This approach will allow us to get a holistic view of the factors that can influence food web complexity, and ultimately predict resilience in ecosystem stability.

Methods - Data Description

A dataset was compiled from 29 data sources, covering 25 marine locations, collected between 1967 and 2006, over a broad range of conditions. The original data were compiled by Barnes *et al.* (2008) who standardized the predator and prey length and mass data, and calculated any missing values. If species was recorded, the regression used was based on species mass-to-length information from primary sources. Genus, family, and general shape regressions were used, respectively, if none of the more specific prior classifications were available from the original records. These mass values were checked against the calculated mass of a sphere with a diameter equal to the length. Each of the 34,931 final

records contains predator and prey scientific and common names, taxa, length and mass (with conversion information), type of feeding interaction, life stage, location (latitude, longitude, habitat description, and geographic location), and environmental data (mean annual temperature, SD annual temperature, mean annual precipitation, SD annual precipitation).

Methods - Data Analysis

To investigate the relationship between predator mass and the respective prey mass, we first cleaned the data set by removing N/A values for lifestage, and log-transformed the mass data. Life stage data were available for the following categories: adult, Adult, larva, postlarva, juvenile, postlarva/juvenile, larva/juvenile. The “Adult” category was merged with the “adult” category as they represent the same life stage. The postlarva, postlarva/juvenile, and larva/juvenile life stages were removed, as they contained only 105, 856, and 650 data points, respectively. In addition, the double categorization would pose problems for result interpretation, so they were removed. We then compared predator size to the corresponding prey size and examined how predator mass and predator lifestage influenced prey mass using a general linear mixed model (GLMM).

The R package ‘foodweb’ (Perdomo, 2015) was used to analyze food web complexity for the 25 geographic locations in the dataset. As required by the package, a binary predator-prey matrix was created for each site, where the species of column n corresponds to the species of row n , with 0 representing no predation interaction and 1 representing the column species preying on the row species (Supplemental Table 1). This format allows for cannibalism and cross-predation (ie species that both predate on each other) to be accounted for. The `analyse.list()` function was then used to calculate standard food web complexity metrics for each geographic location. These included: number of links (L) in a food web, the species richness (SR) of each location, and the connectance (C) of each site. Connectance is calculated as the total number of links divided by the species richness squared (the total number of possible links in a given food web) to account for the inherent increase in number of links that occurs as species richness increases. Food webs of specific locations were then created using the `plotweb()` function in the ‘foodweb’ package (Figure 6). A Shapiro-Wilk test was conducted to test for normality of the data. Linear models were then fit to test the assumptions of the link-species scaling law and the constant connectance pattern. The relationship between food web complexity and latitude was also tested using linear models.

In order to investigate whether Bergmann’s Rule could be observed in this data set, only species from the predator column were used, while the prey column was discarded due to the lack of specific species. The latitude column came in the sexagesimal degree (degree, minute, second) format and was converted into a numeric format in order to be analyzed in R. The absolute value was taken to avoid

negative latitudes. The first model compared mean mass of species, grouped by life stage and latitude, using a linear regression. The second model involved using only species that were sampled at more than one latitude. The mass of these six species were compared at different latitudes and a linear regression was used. A new data frame was created for simplicity and included the six species, as well as latitude and mass data. In order to avoid selecting all Atlantic cod from different life stages, all adult “Atlantic cod” were renamed “Atlantic cod adult” and used in the data frame.

Results

The Shapiro-Wilk test was performed on the log-transformed predator and prey mass data for each lifestage. The data failed these tests of normality ($p \leq 4.381e-15$). Despite failing the tests of normality we went ahead with the analyses. A general linear model was created to examine the effect of predator mass on prey mass with no random effects (Figure 1). It was significant with a p -value $< 2.2e-16$. This result shows that larger predators generally eat larger prey, and vice-versa. A general linear model was created to examine the interaction between predator mass and predator lifestage on prey mass (Figure 2). It was significant with a p -value $< 2.2e-16$. A GLMM was created which incorporated site as a random effect. This model is saturated and is unable to calculate a p -value. Despite this, it is clear there is a significant interaction between the life stage of the predator and the mass of the predator which influences the mass of the prey.

To examine what biological causes could be driving this interaction, the association between predator lifestage and the type of dietary interaction was examined using a Chi-squared test. We found a significant non-random association of certain feeding interactions among the different life stages ($X^2 = 14077$, $df = 6$, p -value $< 2.2e-16$) (Supp Figure 1).

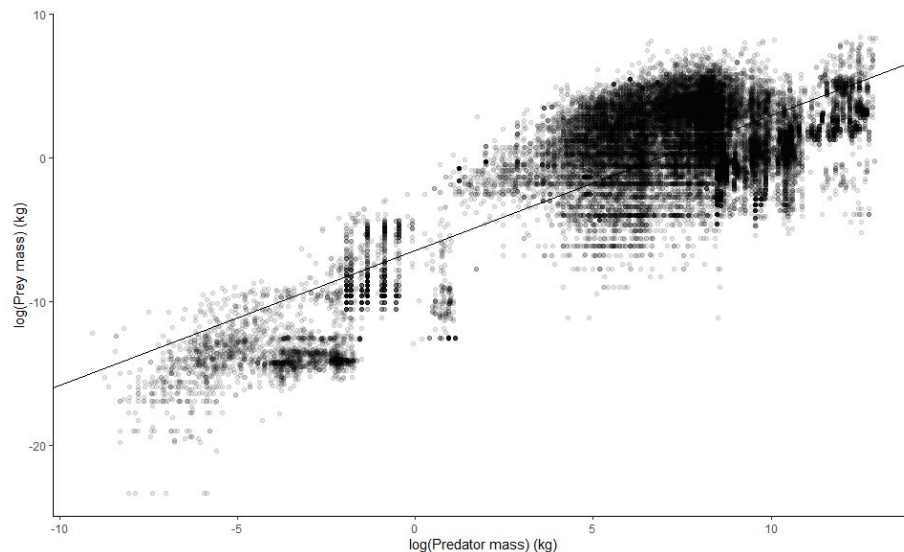


Figure 1. A scatter plot of the relationship between predator mass and prey mass exhibiting a significant positive relationship ($R^2 = 0.6098$, $p < 2.2e-16$). Note that both axes are log-transformed.

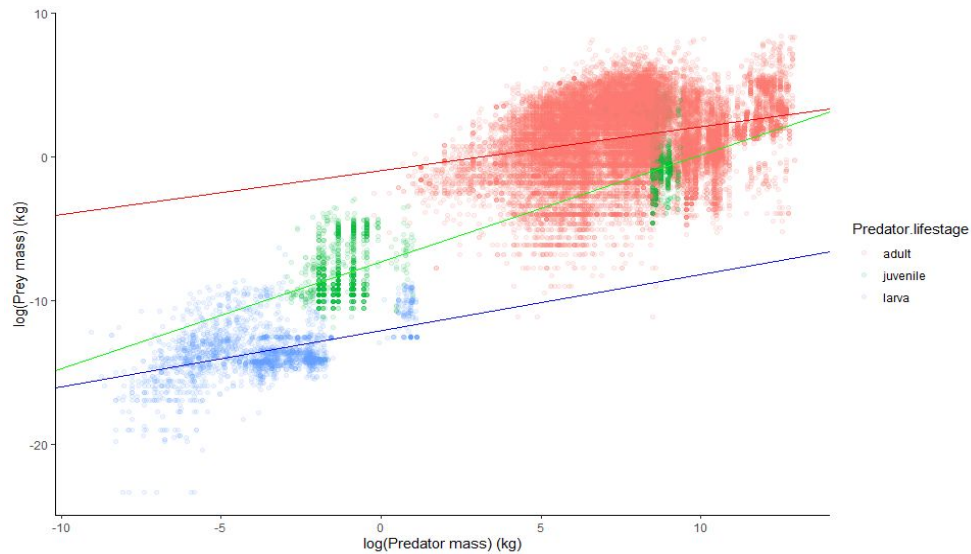


Figure 2. A scatter plot of the relationship between predator mass and prey mass when grouped by the life stage of the predator, exhibiting a significant positive relationship. Adults are coloured red, juveniles are coloured green, and larva are coloured blue. The diagonal lines represent the slope of the relationship between predator mass and prey mass (adult $R^2 = 0.07551$, juvenile $R^2 = 0.8562$, larva $R^2 = 0.1852$; interaction $p < 2.2e-16$). Note that both axes are log-transformed.

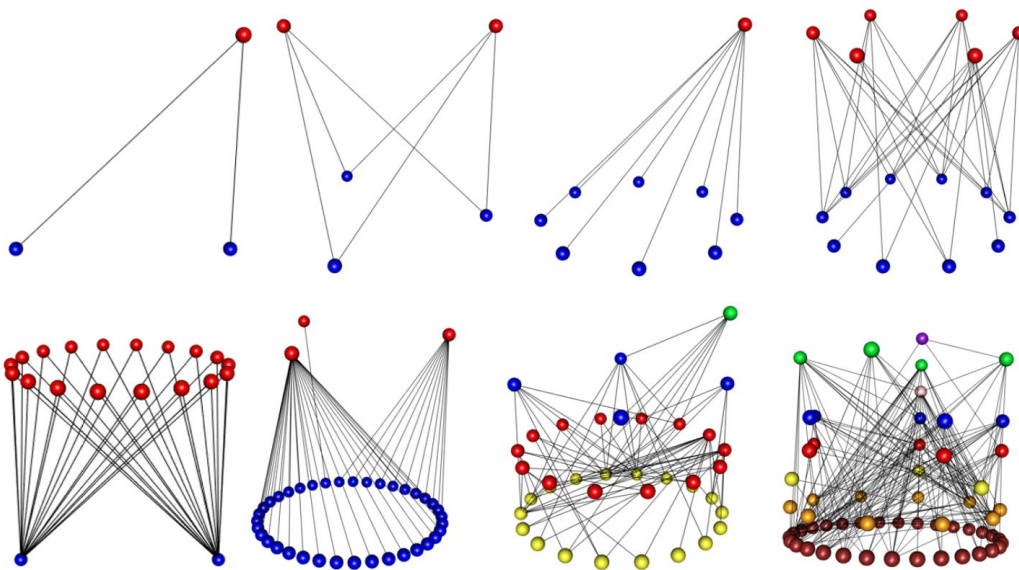


Figure 3. Food web plots as generated by the 'foodweb' package for **3.a** Mid Atlantic, **3.b** West Greenland, **3.c** Stellwagen Bank, Gulf of Maine, New England, **3.d** Catalan Sea, **3.e**, Atlantic Ocean, **3.f**

Bay of Biscay, **3.g** Strait of Georgia, **3.h** Celtic Sea. Coloured nodes represent species, with each colour corresponding to a trophic level. Lines between nodes represent predation of the lower positioned species by the higher positioned species.

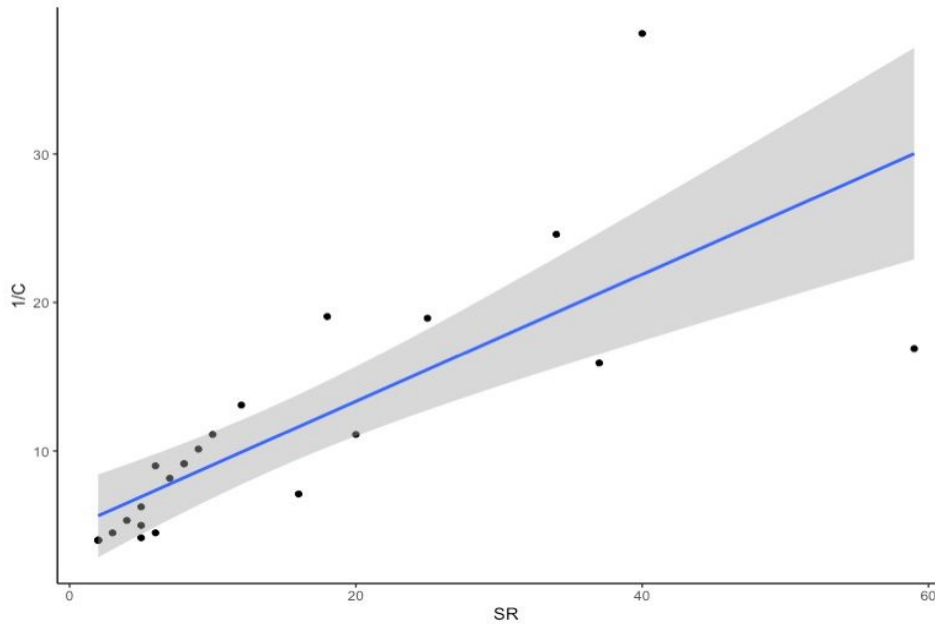


Figure 4. Species richness for each site graphed against the inverse connectance. Connectance is calculated as the number of links in each food web divided by the number of species squared.

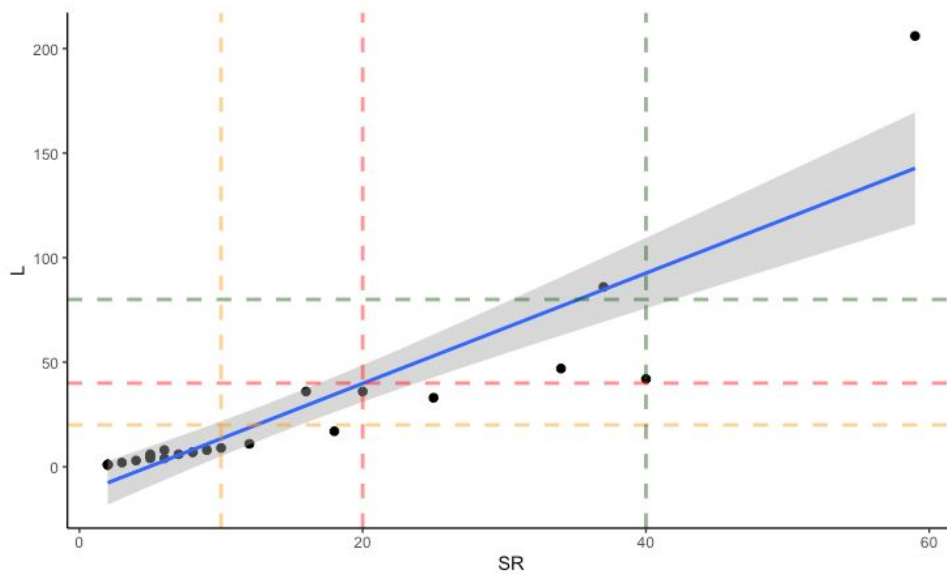


Figure 5. Species richness of each site graphed against the number of links in the food web. Intersecting coloured lines show expectations outlined by the link-species scaling law, which predicts 2 predator-prey interactions per species in a food web.

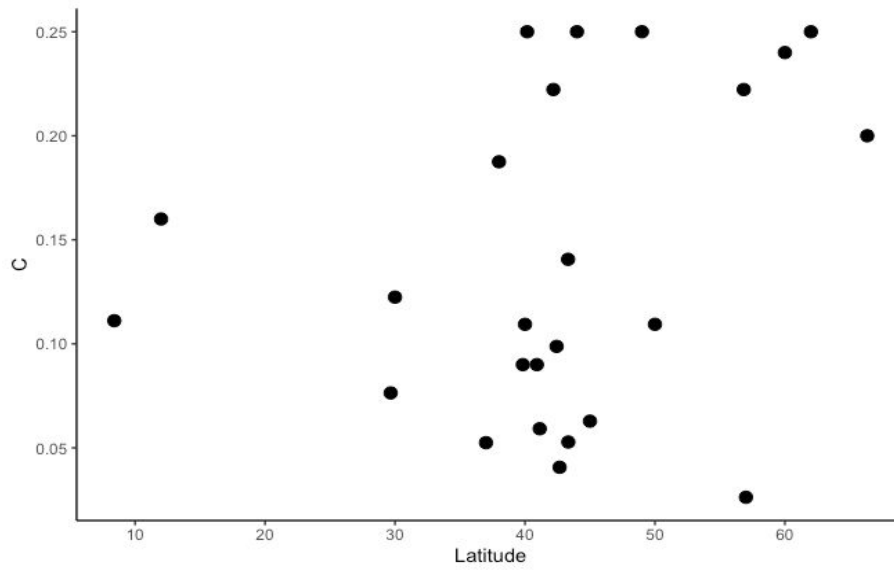


Figure 6. Latitude versus connectance for each geographical location in the study.

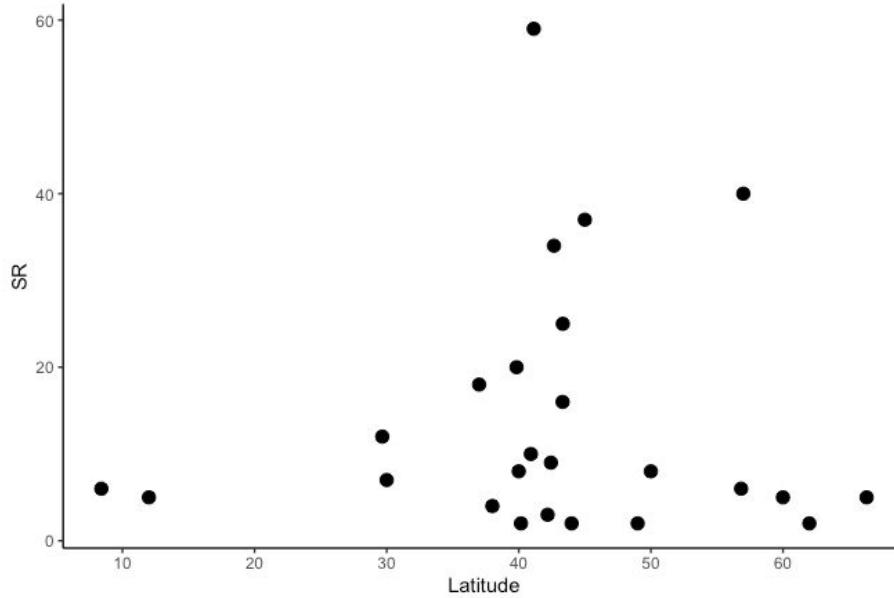


Figure 7. Latitude versus species richness for each geographical location in the study.

All the calculated food web complexity metrics of links, connectance, and species richness failed the Shapiro Wilks test for normality with $p < 0.05$, $p = 0.02$, and $p < 0.05$, respectively. The dataset

found support for the first assumption of the LSS law (Figure 4), where the species richness is significantly proportional to the inverse of connectance, as calculated by a linear model ($t_{1,23} = 5.902$; $p < 0.05$). The second assumption of the LSS law, which predicts that there are 2 predator-prey interactions per species in a food web, was also supported (Figure 5), according to the linear model (Estimate = 2.6; $t_{1,23} = 9.678$; $p < 0.05$). These results counter the predictions of the constant connectance patterns that suggests that the number of predator-prey interactions per species increases as the species richness of an ecosystem increases.

Connectance did not decrease with increasing latitude as originally predicted (Figure 6), but rather showed no significant relationship in any direction ($t_{1,23} = 1.424$; $p = 0.168$). The original assumption that species richness decreased with increasing latitude, which formed the basis of the previous prediction, was not supported by this data set (Figure 7; $t_{1,23} = 0.252$; $p = 0.8$).

To investigate Bergmann's Rule, the log-transformed mean mass for each predator species was plotted against their latitude measurement (Figure 8). A linear regression was performed for each life stage to investigate the relationship between latitude and mass. Only the larva life stage showed a positive relationship, but was not significant, while the remaining life stages observed a negative relationship. The juvenile life stage had a significant p value $< 5.6e-3$ (Supplemental Table 2).

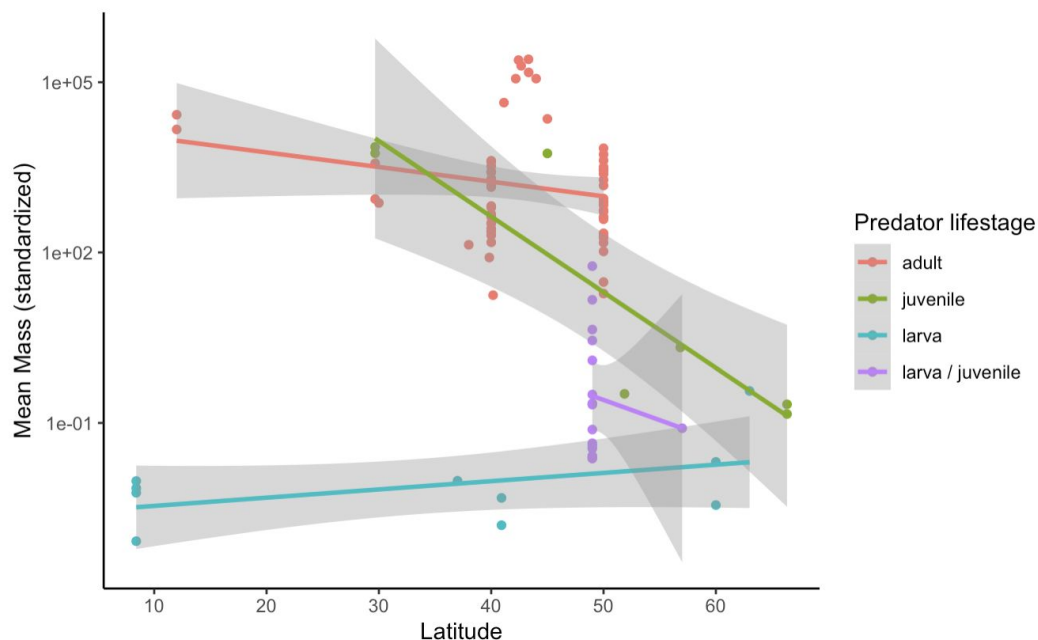


Figure 8. Mean mass (standardized) of predator species at each latitude sampled, grouped by life stage. Mean mass axis was log-transformed. Significant negative relationship of species in juvenile life stage (p value $< 5.6e-3$).

The log-transformed mass for individual predator species was plotted against their latitude (Supp Figure 3). Since observations among these species are clustered due to non-independence, separate linear regressions were run for each species (Figure 9). Significant positive relationships were seen for Atlantic bluefin tuna (*Thunnus thynnus*) (p value < 5.0e-06) and John dory (*Zeus faber*) (p value < 2.1e-8) (Supplemental Table 3).

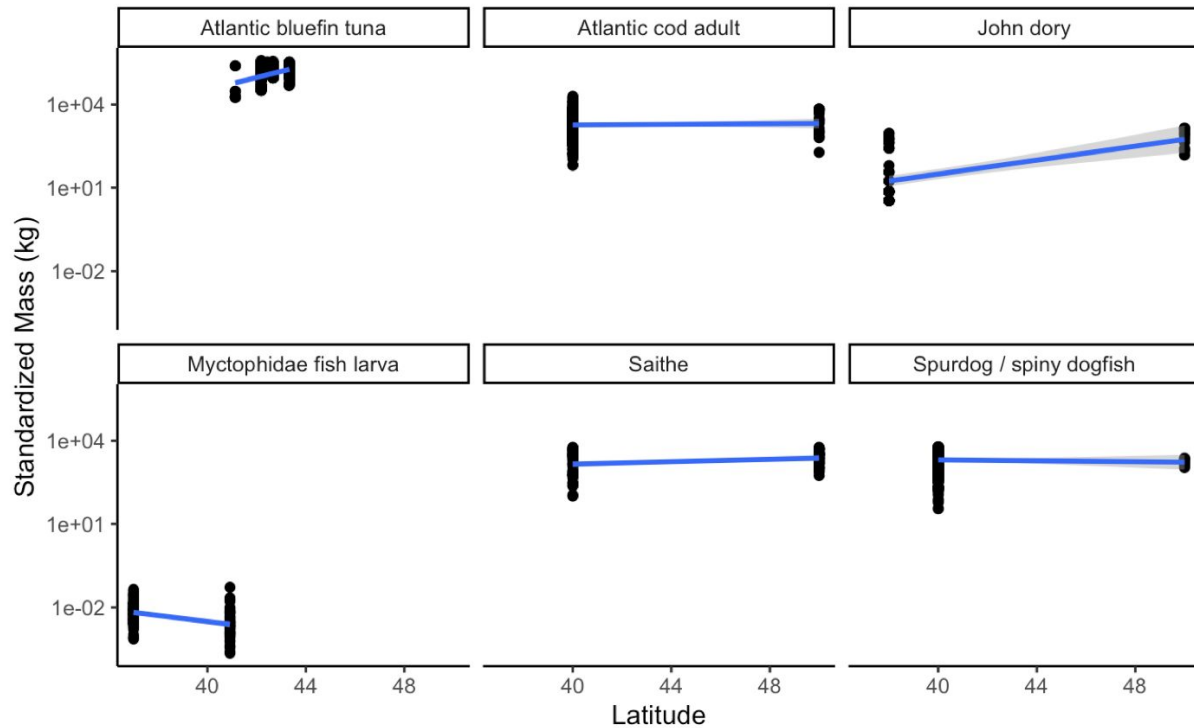


Figure 9. Mass (standardized) of predator species observed at each latitude. Mass axis was log-transformed.

Discussion

Since the dataset was compiled from multiple sources, the base studies varied greatly in extent, which led to limitations in the analyses. The largest base study had $n=16,084$ (Scharf et al 2000) while the smallest base study had $n=4$ (Quero et al 2004). This poses problems for any analysis regarding abundance, as the more extensive studies will have a much greater weight. Any species present in the large studies will likewise receive greater weight. The clustered data also poses a challenge for any test of normality. In addition, data were not available at key latitudes. Only two studies were conducted between 29 degrees north and 61 degrees south. This key region encompasses all tropical environments. These two

studies looked at a combined 6 species with $n=34$ and $n=4011$. These studies also only looked at larva and adult tuna, which happen to be very large. This genus with physically large members is not representative of the real distribution of sizes in the tropics.

Preliminary analyses to observe whether species at different life stages conform to Bergmann's rule are faulty, as taxonomic orders need to be analyzed independently. When individual species were analyzed, only two species of seven showed a clear Bergmannian pattern (Figure 9). These findings concur with previous analyses involving Actinopterygii species (Fernandez-Torres *et al.*, 2018), which included other factors that may have affected body mass, such as sea surface temperature (SST) and net primary productivity (NPP). In contrast, analysis performed by Ashtone *et al.* (2000) involving species sampled over a wide geographic range, found no relationship between the tendency to conform to Bergmann's rule and body mass. In addition, Wilson (2009), analyzed two genera of Actinopterygii and while a correlation was found in the Syngnathus genus, none was observed for Hippocampus. Similarly, our results lack a relationship in Saithe (*Pollachius virens*) and adult Atlantic cod (*Gadus morhua*), and confirms that there may be different mechanisms that affect different taxonomic groups (Angiletta and Dunham, 2003), and we cannot generalize Bergmann's rule across all marine species.

Our results suggest that there is a significant positive relationship between predator mass and prey mass. However, this does not tell us anything more than large predators are more likely to eat large prey and small predators are more likely to eat small prey. When separated by life stage of the predator, the relationship between the size of predators and the size of the prey differed significantly between the different life stages. This was likely attributed to the differences in the feeding interactions of the life stages. We found that there was a non-random association between the life stage of the predator and the type of feeding interaction. Even though our results are based on a global compilation of many studies they can be used as a baseline in some of the well sampled ecosystems of predator and prey mass relationships and how they change ontogenetically. These baselines can also be used as a temporal snapshot to quantify predator-prey mass relationships and can be used to examine the effects of anthropogenic factors on marine biodiversity

In terms of food web analysis, our results supported the link-species scaling law as opposed to the constant connectance pattern hypothesis. The LSS law is often viewed as the widely accepted food web model (Gardner and Ashby, 1970; Pimm, 1982; May, 1983; May, 1988; Cohen and Newman 1985; Sugihara *et al.*, 1989; Cohen *et al.*, 1990), however other work that has found support for the constant connectance pattern instead (Martinez, 1992), cites low resolution data as the cause of misidentifying LSS (Martinez, 1988, 1991a, 1991b; Paine 1988; Lawton 1989). This uncertainty surrounding LSS also calls into question the validity of other hypotheses, such as the hyperbolic connectance pattern and the cascade

model, whose assumptions are based on LSS (Martinez, 1992). Given the many shortcomings of this data set as explored above, we do not believe that our findings provide clear concrete evidence for the LSS law, nor do they support the constant connectance hypothesis.

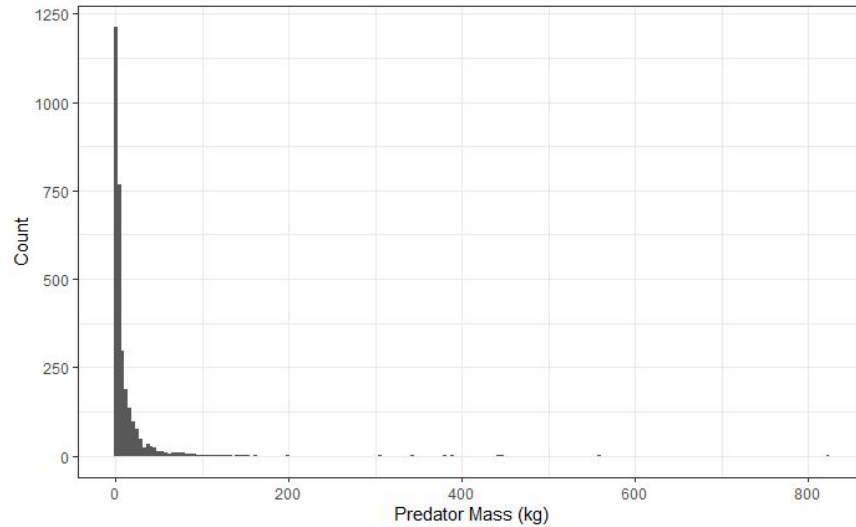


Figure 10. Histogram of predator masses

Our original hypothesis that food web complexity would decrease with latitude was based on the assumptions that: 1) Large predators consume large prey, 2) Larger animals are found at higher latitudes (as per Bergmann's rule), 3) there are fewer larger animals in the ocean than smaller ones (Figure 10), and 4) that species richness declines as latitude increases. Based on these assumptions, at higher latitudes there would be fewer, larger animals, resulting in less species rich communities. Therefore, since we observe a relationship between species richness and food web complexity (Figure 4; Figure 5), we would expect that food web complexity decreases with latitude. Our results did not show this relationship (Figure 6). The lack of relationship between food web complexity and latitude may have occurred due to our incorrect assumption of the validity in Bergmann's Rule for our dataset (Figure 8; Figure 9). Additionally, as discussed above, there are few studies in this dataset located at the low latitude tropics, which, combined with uneven sampling efforts between studies, is likely the reason we did not observe a decline in species richness with latitude (Figure 7), as is well established within the literature (Grady *et al.*, 2019; McRae *et al.*, 2017). Since we found a strong correlation between species richness and food web complexity (Figure 4; Figure 5), and species richness in marine communities declines with latitude (Figure 11; Grady *et al.*, 2019; McRae *et al.*, 2017), it is still possible that food web complexity decreases with latitude.

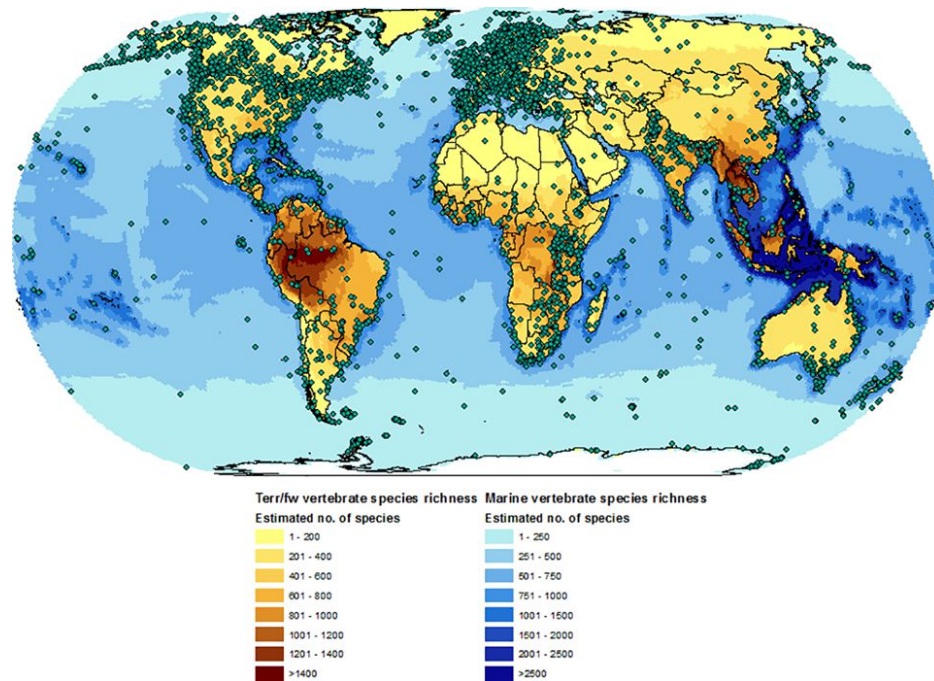
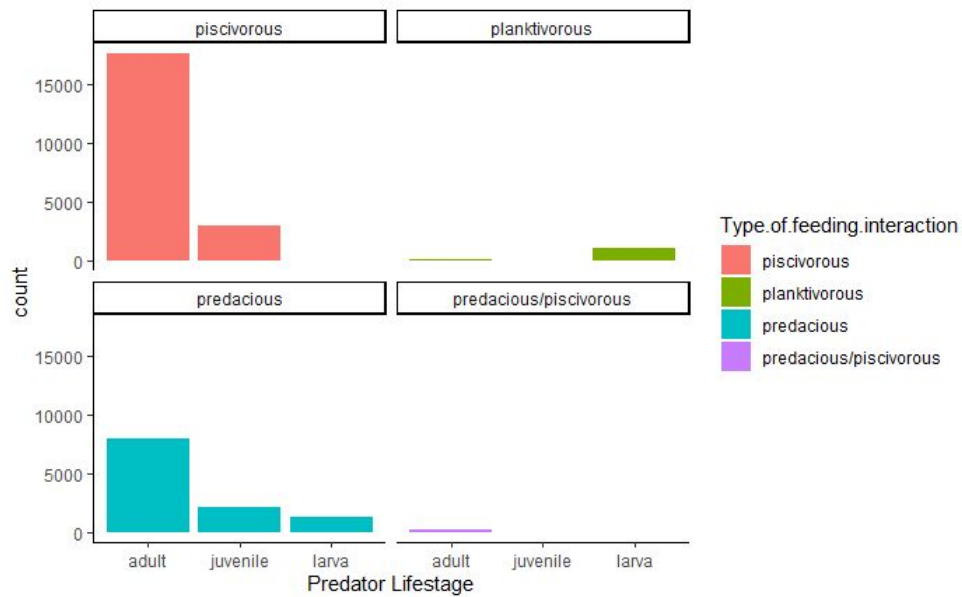


Figure 11: Map showing terrestrial and marine species richness (McRae *et al.* 2017), with the darker the blue, the more species rich marine environment

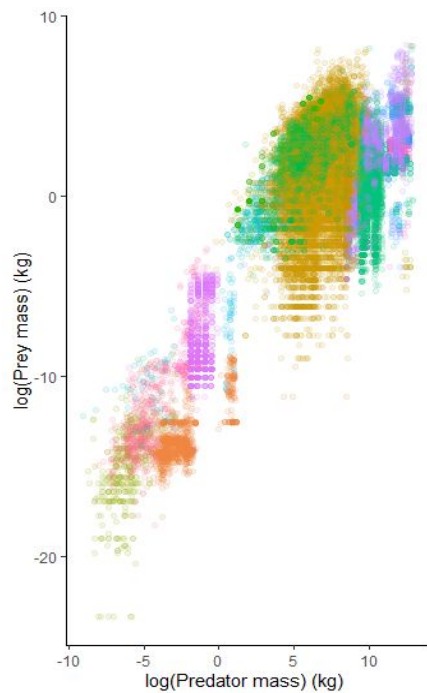
Conclusion

Only two species were found to conform to Bergmann's rule, however, this is expected due to the inability to generalize Bergmann's rule and implement on all taxa. There is a significant interaction between the life stage of the predator and the predator-prey mass relationship, with larger predators generally consuming large prey. Different predator life stages are significantly associated with different feeding strategies. Our results support the link species scaling law, but we did not find any significant relationship between latitude and food web complexity, as originally predicted. However, there are significant flaws in our dataset that prevent us from properly addressing our question, resulting in some ambiguity in the exact results of the patterns we were examining.

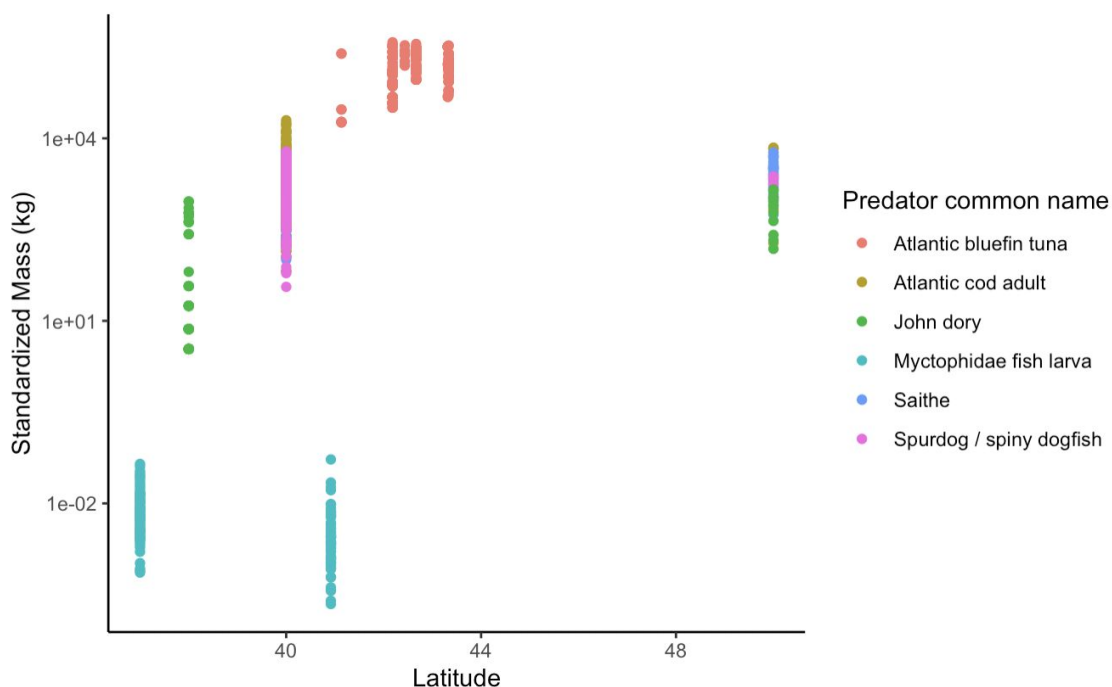
Appendix



Supplemental Figure 1. A bar plot of the frequency of different feeding interaction-predator lifestage relationships. Predator life stage is on the x-axis with the frequencies on the y-axis. Plots are grouped and coloured by the type of feeding interaction.



Supplemental Figure 2. A scatter plot of the relationship between predator mass and prey mass coloured by geographic location. Note that both axes are log-transformed.



Supplemental Figure 3. Mass (standardized) of predator species observed at each latitude. Mass axis was log-transformed.

Supplemental Table 1. Symmetrical binary predator-prey matrix created for survey site Apalachicola Bay, Florida. Rows and columns represent all species recorded in predator prey interactions, with the species in column 'n' corresponding to the species in row 'n'. Records of 0 annotate no predation interaction between the column and row species, while records of 1 annotate a predation event by the column species on the row species.

	Rhizoprionodon terraenovae	Carcharhinus limbatus	Carcharhinus isodon	Carcharhinus brevipinna	teleosts/molluscs /crustaceans	"fish unidentified
Rhizoprionodon terraenovae	0	0	0	0	0	0
Carcharhinus limbatus	0	0	0	0	0	0
Carcharhinus isodon	0	0	0	0	0	0
Carcharhinus brevipinna	0	0	0	0	0	0
teleosts/molluscs /crustaceans	1	0	0	0	0	0
"fish unidentified	0	1	1	1	0	0

Supplemental Table 2. Linear regression coefficients and significance values based on Figure 8. (*) denotes significant p values.

	Individuals sampled (n)	Estimate	P value
Adult	6487	-3.668620e+02	0.692424392
Juvenile	1282	-1.939653e+02	0.005660517 *
Larva	559	2.224247e-03	0.184733000
Larva / Juvenile	163	-6.703610e-01	0.732192171

Supplemental Table 3. Linear regression coefficients and significance values based on Figure 9. (*) denotes significant p values.

	Individuals sampled (n)	Estimate	P value
Atlantic bluefin tuna	318	4.427115e+04	5.024827e-06
Atlantic cod (adult)	413	2.283081e+01	7.111461e-01
John dory	71	4.987362e+01	2.102458e-08
Myctophidae fish larva	136	-1.303531e-03	7.126776e-04
Saithe	96	5.235059e+01	1.072582e-01
Spurdog	547	-7.199867e+01	2.065489e-01

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