THE EFFECTS OF ENVIRONMENTAL CONDITIONS ON MARINE FEEDING INTERACTIONS

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ABSTRACT

Food webs and feeding interactions are an integral facet in the structuring and stability of ecosystems, especially in light of environmental instability and anthropogenic perturbations. Therefore, research linking environmental factors to feeding interactions is valuable. Previous research has confidently established predator-prey size as a determinant for food web structuring while many other studies have looked at environmental effects on predator-prey size. Although various environmental predictors of marine predator-prey size have already been determined (including depth, salinity, primary production, and oxygen availability), less is known concerning the direct effect of environmental factors on food webs on a global scale, and in particular, those of marine ecosystems. In this study, we hope outline what environmental factors impact the structure of food webs and feeding interactions by analyzing global wide data set detailing the predator-prey interactions of marine systems. Increasing our understanding of how the environment impacts feeding interaction structure will allow us to better predict ecosystem stability and trajectory and allow us to better prepare for rapid changes in climate.

INTRODUCTION

Food webs and feeding interactions are an integral facet in the structuring and stability of ecosystems, especially in light of environmental instability (i.e. climate change) (May 1972) and anthropogenic perturbations. Therefore, research linking environmental factors to feeding interactions is valuable.

The food web is a crucial ecological concept that describes the feeding relationships (interactions) in ecological communities. It allows for the investigation of various ecological phenomena and how they impact species relationships, such as predator-prey interactions (Hui, 2012). Food webs depict the variety of interactions between species and can be used to categorically organize the type of feeding interactions that occur. Categorically defining the interactions between species is important as they are a major determinant of the productivity, dynamics and the overall stability in marine ecosystems (Soares *et al.* 2018). Some common feeding strategies marine predators employ include piscivorous (i.e. fish-based diet), predacious (i.e. egg and invertebrate based diet), and planktivorous (i.e. phyto- and zooplankton based diet) interactions (Barnes et al. 2008). Although it is thought that change in environmental conditions can have an affect on marine predator-prey dynamics, there is a lack of marine food web studies on a global scale (Young *et al*. 2015).

Previous research has confidently established predator-prey size as a determinant for food web structuring (Emmerson and Raffaelli 2004), while many other studies have looked at environmental effects on predator-prey size. Furthermore, studies investigating the temperature-size rule (Atkinson and Sibly 1997) and climate fluctuations on animal mass (Lurgi, López, and Montoya 2012) provide strong motivation for finding direct links between the environment and feeding interactions. Various environmental predictors of marine predator-prey size have already been determined. For example, depth, salinity, primary production, and oxygen availability have all been found to impact the predator-prey sizes (Smith and Brown 2002; Berge et al. 1995; Clark and Flynn 2000; Dobashi, Iida, and Takemoto 2018). Considering the established mechanisms linking the environment and predator-prey body size and predator-prey body size and food webs, we hope these same mechanisms will be reflected in the structure of feeding interactions.

To look at the relationship between the environment and feeding interaction structure, we analyzed a dataset detailing predator-prey body sizes in marine food webs compiled by Barnes et al. (Barnes et al. 2008). Prior analysis of this dataset claims that few environmental factors, including temperature, are significant predictors of body size. Although this claim is controversial (Gibert and DeLong 2014), many other environmental predictors were also published including depth, primary production, temperature, and latitude; opening doors for varied sorts analysis. By increasing our understanding of how the environment impacts feeding interaction structure will allow us to better predict ecosystem stability and trajectory and allow us to better prepare for rapid changes in climate (Chamberlain, Bronstein, and Rudgers 2014).

Research Questions

To better understand how environmental factors impact feeding interaction structure in marine communities, we asked:

1. How are feeding interactions distributed on a global scale? What are the dominant feeding interactions at sampled geographic locations?
2. Do environmental factors predict the structure of feeding interactions? Which environmental factors are the best predictors?

Hypotheses

In response to our research questions, we hypothesize that:

1. Feeding interactions will be incongruently distributed on a global scale.
2. Environmental factors will predict the structure of feeding interactions to a statistically significant degree ($p > 0.05$)

METHODS

Data Set

The analyses were based on a published set of data collected by Barnes *et al* (2008). It is a broad spectrum review of predator-prey data taken from published literature concerning predator-prey interactions. The data comprises of 34931 predation events from 27 geographic locations ranging from 66° N and 66°S for 93 types of predators. The columns of importance for our purposes included predator identity, prey identity, geographic location (with specific habitat description, latitude, longitude), mean sea surface temperature, mean primary productivity, depth, and type of feeding interaction. The data set described five types of feeding interactions: piscivorous, predacious, insectivorous, planktivorous, and predacious-piscivorous. The publication defines a piscivorous diet as one consisting of fish, and a predacious diet as one consisting of eggs and invertebrates (Barnes *et al*. 2008).

Distribution of Feeding Interactions and PCA

Various R packages were utilized to visualize and analyze the data in R (R Core Team, 2018). *maps* and *ggmap* (Kahle and Wickham, 2013) were used to visualize the distribution of geographic locations on the world map. *scatterpie* (Guangchuang, 2018) was used to draw and plot pie charts representing the distribution of feeding interactions per geographic location on the world map.

Principal component analysis was executed using the principal() function from *psych* (Revelle, 2018) and the built in R function prcomp() to identify the feeding interactions that best summarized the variation in feeding specialization. PCA was performed using five factors (nfactors = 5) representing the five feeding interactions with rotation set to varimax to maximize factor loadings under the assumption that the components are orthogonal (i.e. that there are no inter-correlations between components) (Brown, 2009). The loadings were visualized with *ggbiplot* (Vincent, 2011).

Environmental Effects on Feeding Interaction Structure

The ratio of predacious interactions to piscivorous interactions was calculated for each niche and plotted against each environmental factor individually. Only predacious and piscivorous interactions were included in the following analyses due to their dominance of the data set. Two further niches were excluded after both were deemed non-representative since they only included observations of a single species. The four environmental factors (Depth, Mean primary production, Mean temperature and latitude) were used to create a linear model of the data. We ran model selection on a number of different models containing different combinations of environmental factors using AICc to determine the best model to use. AICc was used since the number of observations over the number of parameters was less than 40. The AICc calculation showed that the model that used primary production and latitude as predictors while excluding depth and temperature was the best fitting model for our data. We performed a Type 3 anova from the car package on the selected model to identify significant predictors.

RESULTS

Distribution of Feeding Interactions and Principal Component Analysis (PCA)

The pie charts showed displays the distribution of feeding interactions at each of 25 unique geographic locations (two geographic locations were pruned for having less that ten observations) (Figure 1). Most geographic locations were dominated by either predacious or piscivorous feeding interactions ($\text{predacious}_{>50\%}$ = 11/25; $\text{piscivorous}_{>50\%}$ = 11/25), accounting for the majority of the overall variation in feeding interaction. Out of 34,931 rows, predacious and piscivorous interactions accounted for 33,169 (94.96%) of them. This predacious and piscivorous dominated variation was reflected in the PCA, with both feeding interactions loading exclusively onto the first component (Table 1).

Both Kaiser criterion and the Scree plot suggested a four-component solution (SS loadings = 1.71, 1.25, 1.03, 1.01, and 0 for the first five components respectively with varimax rotation; Table 1), with the first four components being cumulatively responsible for nearly all the variation in feeding interaction. A circle graphed on the plot delineates 68% of the global variation in feeding interaction. The first component explaining 37.3% of the variation in feeding interaction (Figure 2) mainly discriminated between predacious and piscivorous feeding interactions with both inversely loading onto the first component (Varimax: predacious = 0.97, piscivorous = -0.87; Table 1). The second component explaining 23.9% of the variation in feeding interaction mainly discriminates between planktivorous and insectivorous feeding interactions (Figure 2).

We continued analysis only on the predacious and piscivorous feeding interactions since they accounted for the majority of the variation in feeding interaction and were the most frequently observed feeding interactions (94.96% of observations).

Environmental Effects on Feeding Interaction

The results of the Anova on the optimized model determined that certain environmental conditions do affect the primary feeding style within a niche. Primary production seems to be the most significant single predictor within the final model, and depth, mean temperature and distance from the equator seem to be individually non-significant. The interaction of primary production and distance from the equator also appears significant, although distance from the equator alone is not expected to explain much variation.

Figures 4 through 7 show the ratio of predacious interactions to piscivorous interactions as a function of each environmental condition independently. Each plot includes a regression line and r^2 value for that individual condition. Individual Regression Some general trends are visible in the plots, but they are not significant enough to be conclusive and the r^2 values are very low. None of the individual environmental conditions fit the data very well and no one factor explained more than 6% of the variation within the data set.

The final, optimized model containing both mean primary production and distance from the equator had an r^2 of 0.4734 and an adjusted r^2 2 of 0.3746. This does not explain all the variation in the data, although it does explain a meaningful proportion. The Type 3 Anova showed a significant effect of mean primary production in each niche ($p = 0.00272$, $f = 12.5317$), and a significant interaction of mean primary production and distance from the equator ($p = 0.003667$, $f = 11.5537$).

DISCUSSION

Distribution of Feeding Interactions

Data was sampled from 27 geographic locations. We combined data from similar locations resulting in 25 locations overall. 44% of the locations were predacious dominant while 44% were piscivorous dominant. The prevalence of predacious and piscivorous feeding interactions is likely due to sampling bias; predacious and piscivorous predators accounted for almost 94.96% of the data set. Furthermore, most geographic locations were coastal and clustered at ~40N.

PCA Interpretation

The Principal Component Analysis revealed that predacious and piscivorous feeding interactions accounted for nearly 37.3% of the variation in feeding interaction. The second component explaining 23.9% of the variation indicated that planktivorous and insectivorous feeding interactions were also factors. The plot showed two main groupings reflecting the first and second components. These two groups were linear, meaning that most predators displayed the behaviour of two feeding interactions only. Few points did not fall within a linear grouping meaning there was little representation of predators that displayed three or more feeding interactions simultaneously. Predators that displayed only predacious or only piscivorous interactions loaded almost exclusively onto component one (Figure ___) indicating that not only was there little variation in type of feeding interaction, but also in the diversity of interactions displayed per predator.

The Overrepresentation of Predacious and Piscivorous Feeding Interactions

As mentioned, predacious and piscivorous feeding interactions strongly dominated the dataset. Although this is almost certainly due to sampling bias, previous research indicates that ecological communities tend to be dominated by few select feeding interactions and many weak interactions (Wootton and Emmerson 2005) which supports the distribution of feeding interactions in Barnes et al (2008). Similar skew in interactions is also seen at the population level in both marine and terrestrial ecosystems (Paine 1966; Fagan and Hurd 1994). Although this relationship might not hold past the population level, it is regardless an important realization as such variation is an indicator of ecosystem stability (Allesina and Tang 2012).

Environmental Effects on Feeding Interaction Structure

Primary production was the most significant single predictor within the final model. The remaining factors including depth, mean temperature, and distance from the equator seemed to be non-significant on an individual basis, although the interaction of primary production and distance from the equator did appear significant. The primary production/latitude interaction effect is likely created by other environmental factors that co-vary with distance from the equator. The combination of the low R^2 and significant interaction of latitude suggests that there are other environmental factors that were not measured in the data set that explain more of the variation in the data. This result suggests that primary production is a factor worthy of future study, and that future investigations should be made to determine what co-varying factors caused the significant impact of latitude.

Some environmental factors that have already been shown to significantly impact feeding interactions at the local level include light levels, habitat structure, temperature, and water clarity (Pawar, Dell, and Savage 2012; Gilbert et al. 2014; Byers, Holmes, and Malek 2017; Wissel, Boeing, and Ramcharan 2003), all of which are not measured or reflected in the Barnes et al. (2008) dataset. Although much of the environmental conditions measured and compiled in Barnes et al. (2008) did not significantly predict global feeding interaction structure, it does reinforce that there are underlying ecological mechanisms directly structuring the composition of marine food webs.

Limitations

There are several key limitations to this study. There were many thousands of observations in the data set, but since those took place in only 25 distinct locations there are only 25 distinct observations of environmental conditions and 25 estimates of the predacious-piscivorous ratio. Several of these observations are obviously biased outliers that cannot be used in the analysis, such as the Greenland observation which includes just 49 observations (compared to several thousand in most of the other niches) of a single planktivorous species. Once all of the extremely biased or outlying samples are pruned, only 20 data points remain, which provides too little power to make strong conclusions. Additionally, many of those remaining 20 data points could be biased or non-representative of the actual niche, which would bias the results of our model. The data does not perfectly conform to all the assumptions of linear models, so the results of our model may not be perfectly accurate. This is reflected in the literature, as some studies have resulted in different or sometimes opposite conclusions to ones suggested by this data (Gibert and DeLong 2014). Increasing the accuracy of the model would require more representative data that better conforms to the expectations of statistical models. Finally, only four valuable environmental conditions were measured (Depth, Temperature, Mean Primary Production and Latitude), which were not enough environmental conditions to explain the observed variation in dominant feeding style. More environmental conditions are required to construct a model that explain all the variation observed in the data.

Future Directions

The next steps would be to gather more representative samples and measure more environmental conditions. Researchers could return to the niches sampled in the original data set and gather unbiased and representative samples of the feeding styles within each niche to ensure accuracy in the analysis. At the same time, measurements of additional environmental factors could be taken. There are numerous environmental conditions not measured by the study that could influence feeding interactions, such as light, oxygen, pollution or fishing intensity. Researchers could also take new observations of feeding styles and environmental conditions in other niches around the world to increase the number of data points and by extension increase the power of the analysis. A greater number of highly representative samples containing measurements of numerous environmental conditions

CONCLUSION

Understanding the structure of food webs and feeding interactions is a vital aspect of overall ecosystem structure and stability. By understanding how environmental factors impact variation in food webs, we can better predict consequences in ecosystem dynamics in reaction to environmental fluctuations, and as a result improve conservation strategies and policy. Although various environmental and ecological conditions have been shown to significantly impact food web and feeding interaction structure at the local level, how these factors interact with systems on a global scale remains elusive. Our study showed that while primary production (both alone and while interacting with latitude) significantly explained a portion of the variation in feeding interaction, it was a relatively small portion overall, with no other measured environmental conditions contributing to a significant degree. While virtually no other signal was found, the discovery of primary production as a significant predictor is a start to answering our question. Future research may reliably discover better predictors potentially allowing for an improved understanding of how ecosystems are structured in general.

FIGURES AND TABLES

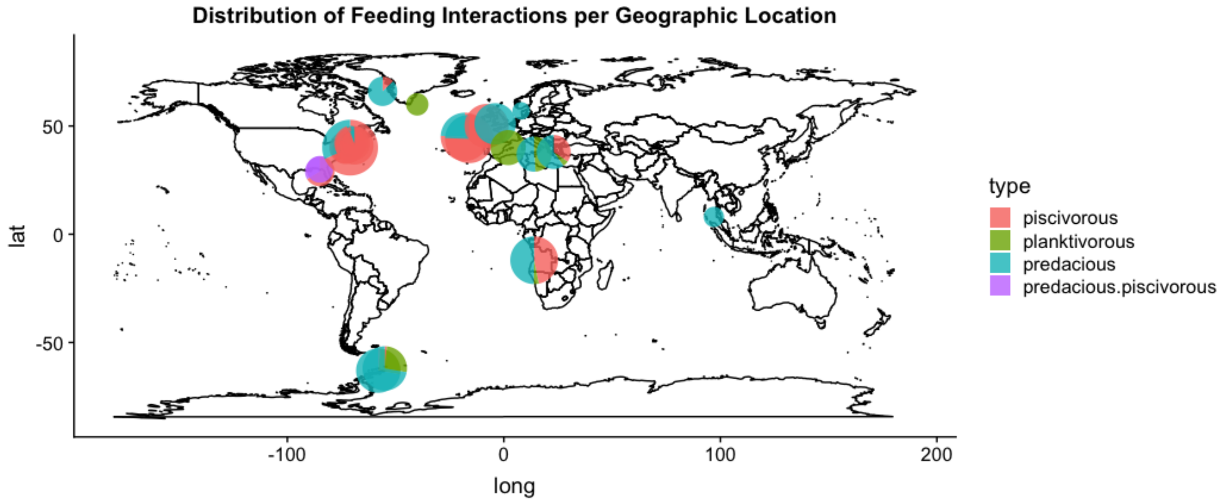

Figure 1. Distribution of feeding interactions per geographic location. Pie charts represent the proportion of feeding interactions observed at each location. Size of pie chart is log scaled to the number of observations made at each location multiplied by one and one third ($\log_n * 1.33$). The figure shows predacious and piscivorous are the dominant feeding interactions globally.

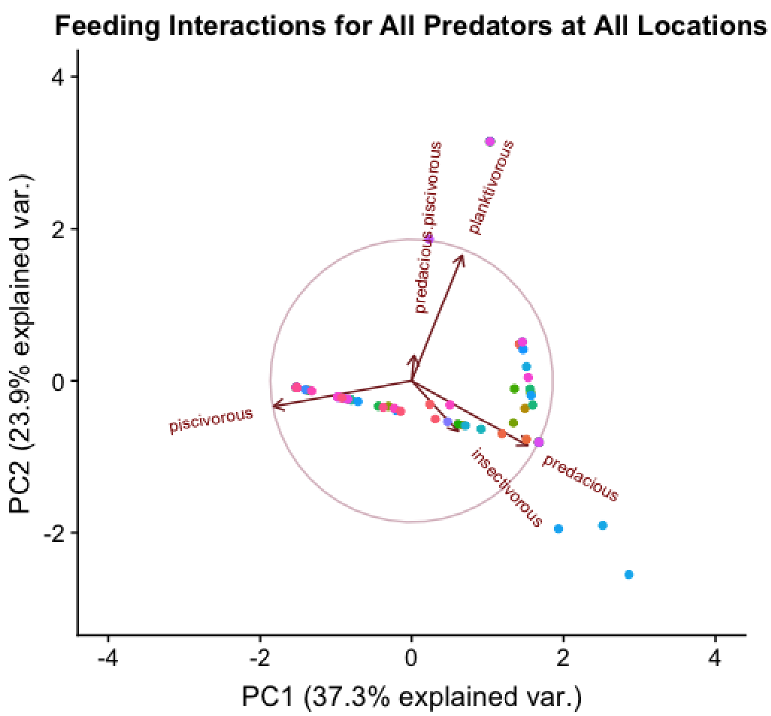

Figure 2. PCA of proportions of displayed feeding interactions per predator. The PCA indicates that component one discriminates between predacious and piscivorous feeding interactions and accounts for 37.3% of the variation. Rotation set to varimax.

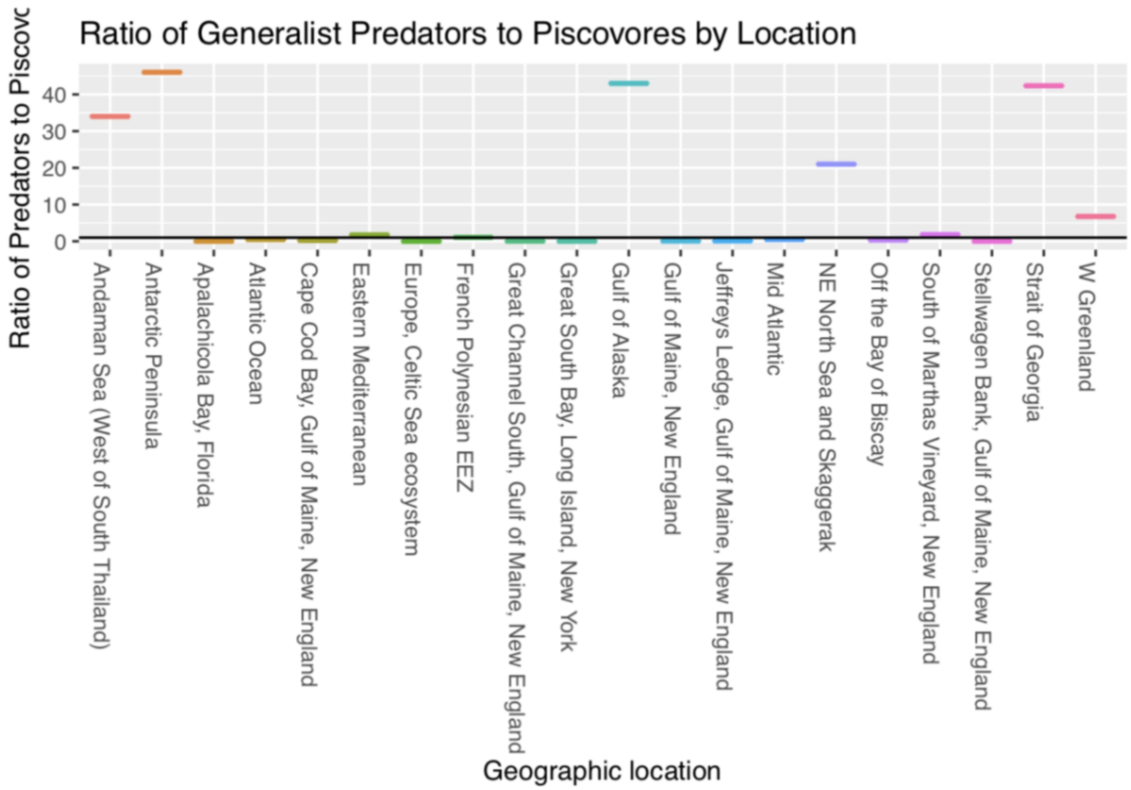

Figure 3. Ratio of predacious interactions to piscivorous interactions by niche

Figure 3 shows the ratio of observed predacious interactions to piscivorous interactions within each niche. There are an equal number of primarily predacious and primarily piscivorous niches, and there does not appear to be any strong geographic trend.

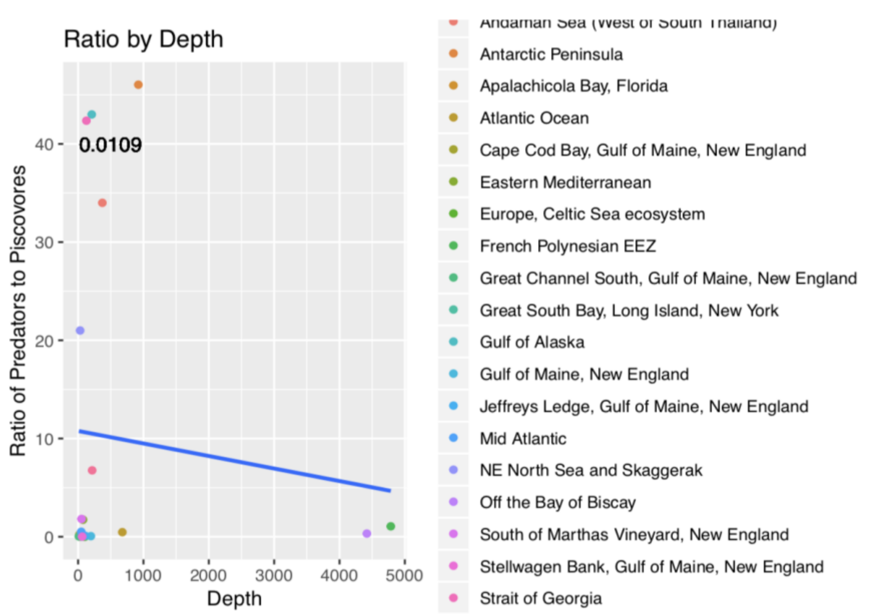

Figure 4. Ratio of predacious interactions to piscivorous interactions in each niche by Depth. Includes a simple linear regression line and the r^2 value.

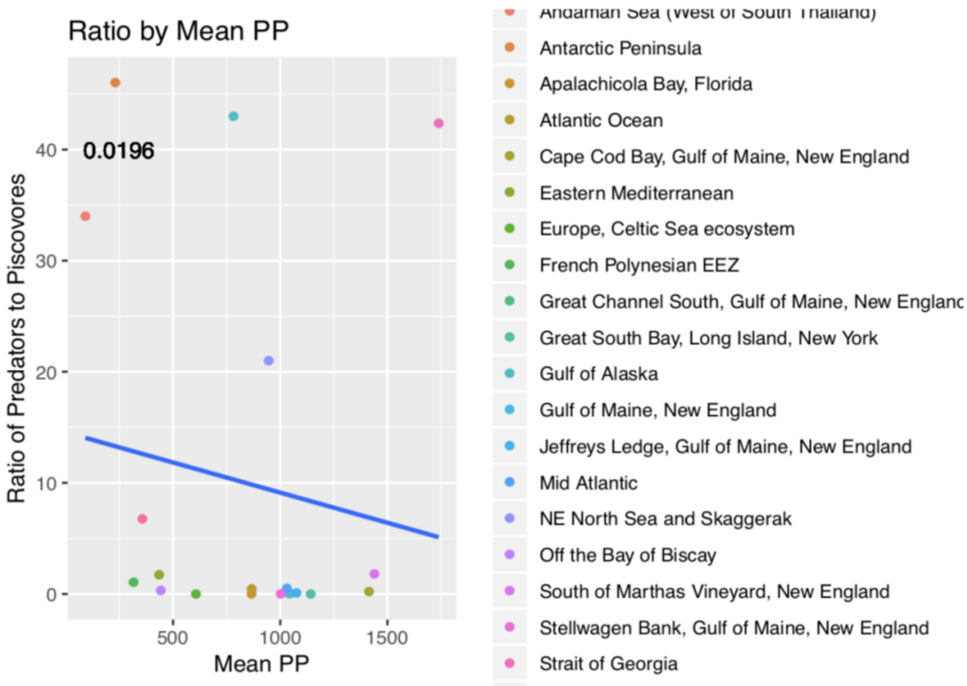

Figure 5. Ratio of predacious interactions to piscivorous interactions in each niche by Mean Primary Production. Includes a simple linear regression line and the r^2 value.

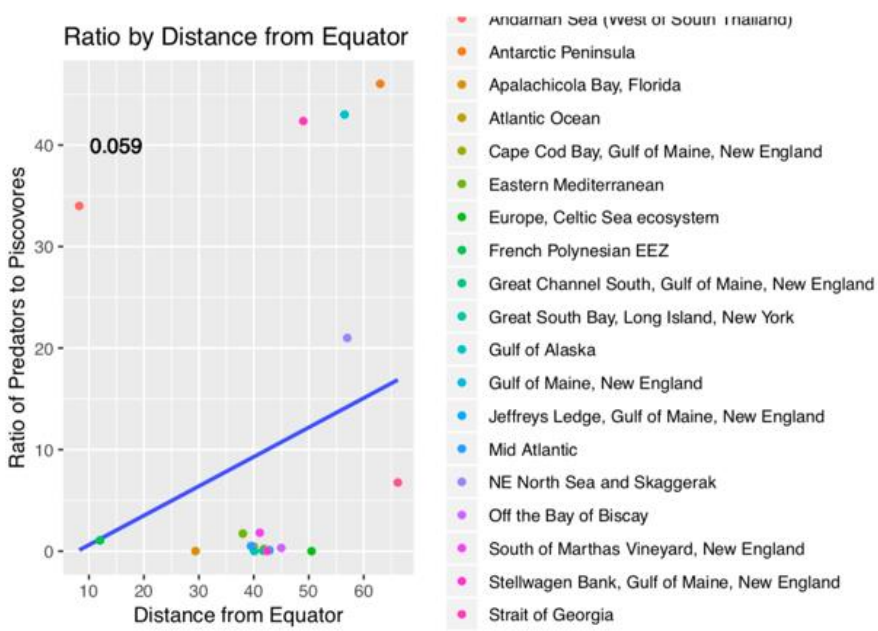

Figure 6. Ratio of predacious interactions to piscivorous interactions in each niche by Distance from the Equator. Includes a simple linear regression line and the r^2 value.

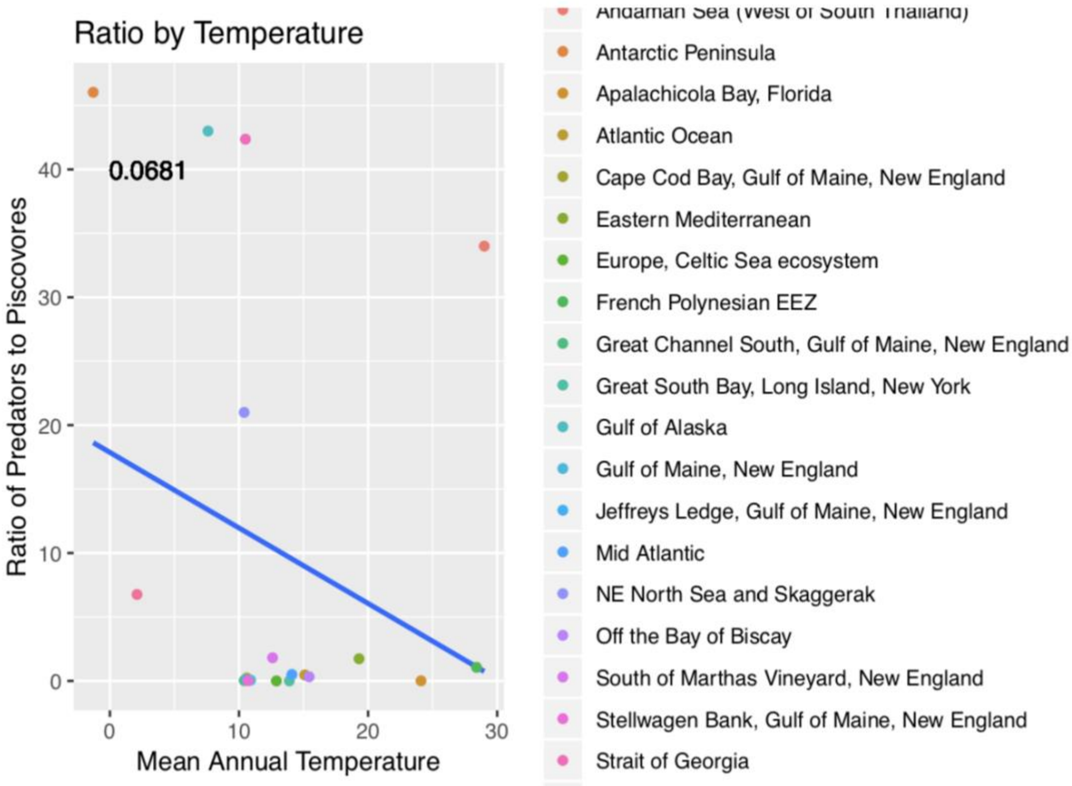

Figure 7. Ratio of predacious interactions to piscivorous interactions in each niche by Mean Annual Temperature. Includes a simple linear regression line and the r^2 value

Table 1. Output of the principal() function from psych package in R. Data shows loading of variables onto each component and the SS loadings of each component. The analysis included 5 factors reflecting each feeding interaction with rotation set to varimax (assuming orthogonality of components).

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Principal Components Analysis
Call: principal(r = pp.data.all, nfactors = 5, rotate = "varimax")
Standardized loadings (pattern matrix) based upon correlation matrix
                       item   RC1   RC2   RC3   RC4   RC5 h2       u2 com
predacious                4  0.97                          1 -6.7e-16 1.1
piscivorous               2 -0.87 -0.47                    1 -6.7e-16 1.6
planktivorous             3        1.00                    1 -1.3e-15 1.0
predacious.piscivorous    5              1.00              1 -1.3e-15 1.0
insectivorous             1                    1.00        1 -2.2e-16 1.0

                       RC1  RC2  RC3  RC4 RC5
SS loadings           1.71 1.25 1.03 1.01   0
Proportion Var        0.34 0.25 0.21 0.20   0
Cumulative Var        0.34 0.59 0.80 1.00   1
Proportion Explained  0.34 0.25 0.21 0.20   0
Cumulative Proportion 0.34 0.59 0.80 1.00   1

Mean item complexity =  1.2
Test of the hypothesis that 5 components are sufficient.

The root mean square of the residuals (RMSR) is  0
 with the empirical chi square  0  with prob <  NA

Fit based upon off diagonal values = 1
```

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