

Relating marine predator body mass and trophic position: A global approach

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Abstract

Predators play a critical role in maintaining food web stability. They regulate overpopulation of intermediate consumers, reduce pressure on primary producers through top-down control, and maintain species diversity. Understanding their energy consumption demands within a community is therefore critical to understanding marine ecosystem stability. Predator body mass is a widely accepted means of addressing this issue, as it can quantify a predator's trophic position. However, most studies rely on a few species of predator and low sample size, preventing an in-depth analysis of predator mass and trophic interactions. Using metadata from Barnes et al. (2008), we investigate this issue by modelling how a predator's lifestage, the mass of their prey, feeding preferences, and the productivity of their environment influence their body mass. We find that a predator's mass varies considerably over its lifetime, corresponding with changes in feeding preference, but that the average mass of predators in a habitat cannot be predicted by the productivity of the lowest trophic level. Overall, this suggests that using a predator's behaviour is a more effective means of predicting its body mass, and may be used to identify food webs most vulnerable to trophic degradation due to overharvesting of predators.

Introduction

Establishing the structure of marine food webs is notoriously difficult. They encompass complex interactions between benthic, pelagic, and surface habitats home to a plethora of primary producers, invertebrates, and vertebrates (Bascompte, Melián, & Sala, 2005). In these systems, predators play a critical role in maintaining food web stability by preventing overpopulation of intermediate consumers, reinforcing primary producer populations, and applying selective pressures that maintain species diversity (Atwood & Hammill, 2018). Investigating the factors influencing a predator's energy consumption within a community is therefore critical to understanding how we can maintain the stability of marine ecosystems under threat from anthropogenic disturbance.

Energetic demands can vary dramatically by the taxon of predator due to differences in ecology, evolutionary history, and habitat. Nonetheless, body mass, rather than taxonomic identity, is considered the preferred indicator of trophic position (Jennings, Pinnegar, Polunin, & Boon, 2001). This is largely due to ontogenetic effects on predator mass and feeding preferences, inhibiting a generalization of any one species' trophic position. In fact, over a predator's lifetime, its mass can increase over six orders of magnitude (Barnes, Maxwell, Reuman, & Jennings, 2010). This has consequences on habitat preferences and the predator's ability to catch larger prey. For example, small, juvenile squid shift toward piscivory as they grow (Hunsicker & Essington, 2006). This leads to increased pressure on fish populations in winter, when squid have developed into formidable predators.

Despite the clear significance of predicting predator mass in a food web context, the majority of dietary studies have occurred on a select number of commercially relevant species encompassing a small range of predator masses. This has made it difficult to elucidate a broader relationship between marine predator mass and trophic web interactions. Our research aimed to investigate how predator mass is related to its trophic position by using a more expansive data set, compiled by Barnes et al. (2008). The metadata includes 34,931 observations from 24 marine predator studies. It spans 27 geographic locations ranging from coastal to sea floor to open ocean habitats. It provides key characteristics such as the size and age of marine predators, their feeding preferences, and the mass and taxon of their prey. Environmental conditions including mean primary productivity (MPP), mean annual temperature, and depth are also included, making it suitable for investigations of how predator mass can be predicted.

Aspects such as life stage, feeding preference, and energy in the ecosystem were expected to affect predator mass. We hypothesized that predators from habitats with lower MPP would have a lower body mass due to less energy being available. We also expected that younger life stages would have lower mass than older life stages, as the young of a species are smaller than mature

individuals. Additionally, we expected that planktivorous predators would have lower mass than piscivorous or predacious predators, given that smaller species likely eat smaller prey due to size constraints. Expanding on this hypothesis, we expected an interaction between life stage and feeding preferences, such that younger, planktivorous predators would be smaller than older, piscivorous/predacious predators.

Methods

Data description and cleaning

The original metadata from Barnes et al. (2008) contained studies that collected predators through varying means, including commercial landings, sportfishing tournaments, purse-seine landings, and handgear landings. Furthermore, predator and prey mass estimate strategies varied by study. Using the authors' variable descriptions, we filtered the data to keep only predator observations obtained through direct measurements or the use of species/genus/family length-to-mass regressions. Each level of the quality index is defined in Table 1. We only used prey whose mass was estimated via general shape, as this was the most consistent estimation strategy across studies. We focused on ectothermic vertebrate predators and removed cephalopods as there were only 184 cephalopod observations from a single paper, and including them would influence our ability to distinguish the relative importance of geography, taxon, and sampling strategy on predator mass. Our final data was condensed into 18,383 observations.

Correlation analysis

In order to assess the potential role of environmental variables in contributing to differences in predator mass globally, we initially considered MPP, depth, and mean annual temperature. We generated correlograms to visualize correlation matrices, which assessed the Pearson's correlation coefficient between each pair and demonstrated the distributions. We found correlations between all pairs ($p < 0.001$) (Figure 1). To avoid confounding interpretations, we decided to only use MPP as it was the most biologically relevant to our analysis of trophic levels.

Spatial analysis

We visualized each site by predator mass and MPP to assess the potential relationship between the energy in the ecosystem and effect on predator mass (Figure 2). Given the wide distribution of our data, we also assessed if sites were correlated in space using Moran's I as an indicator of spatial autocorrelation. Sites that were closer together were not more similar in terms of standardized MPP ($p = 0.25$) but had more similar mean predator mass per site ($p < 0.001$). To

resolve this, geographic location was addressed in model selection to account for spatial autocorrelation in predator mass.

Linear Mixed Effects Model Selection

We performed linear mixed effects model selection to assess the importance of energy in a system and a predator's behaviour in predicting their body mass. We used MPP as a proxy for energy available in the food web. In terms of predator life stage, we assessed the larval, juvenile and adult stages on predator mass. We also considered feeding preferences including planktivorous (feeding on phytoplankton and zooplankton), piscivorous (feeding on fish), and predacious (feeding on eggs, invertebrates, and sometimes fish). Finally, prey mass and the interaction of life stage and feeding interaction were included as additional indicators of trophic position.

To meet model assumptions, predator mass was log10-transformed for a more normal distribution. The explanatory variables MPP and prey mass were standardized by subtracting each observation from the mean and dividing by the standard deviation. This was to ensure that estimated coefficients were on the same scale, enabling comparison of effect size. We accounted for variation in predator characteristics caused by sampling strategy, year of sampling, and distance between sites by using the “geographic location” variable — unique to each study in the metadata — as a random effect. We also included the predator's species as a random effect as we were more interested in general trends. Predator quality was included as a fixed effect as there were only four levels and variance could not be properly estimated as a random effect. Using the saturated model, we followed Akaike's Information Criterion (AIC, $n/k > 40$) to compare potential models.

Results

The top two models (within 2 AIC) were the model with no MPP and the saturated model (Table 2). We considered averaging the models, but the only noticeable difference between them was the presence of MPP in the saturated model, where it was a statistically insignificant predictor ($p > 0.05$). Therefore, we decided to use the model with the lowest AIC that did not include MPP.

Our final linear mixed effect model included predator lifestage, feeding preference, the interaction between life stage and feeding interaction, prey mass, and predator mass quality as predictors of predator mass (Table 3).

The comparison between juvenile and adult life stages and its effect on predator mass was non-significant with a slope estimate of 3.48 ($p = 0.840$), however, the comparison between

larval and adult life stages had a statistically significant negative relationship with a slope estimate of -0.07 ($p < 0.001$) (Table 3). Median predator mass is lower for larval than adult predators (Figure 4).

The model revealed two significant relationships between predator mass and feeding preference. The first was a significant negative relationship between planktivory and predator mass, in comparison to piscivory, with a slope estimate of -3.87 ($p < 0.001$) (Table 3). Additionally, there was a significant positive relationship between predacious feeding type and predator mass in comparison to that of piscivorous, wherein this relationship had a slope estimate of 0.09 ($p = 0.007$) (Table 3). Planktivorous predators have the lowest median predator mass, and predacious predators have the greatest (Figure 5).

Prey mass as a predictor of predator mass rendered a positive and significant relationship with a slope estimate of 0.08 ($p = 0.032$) (Table 3). However, the pattern appears to be mainly driven by a few over-represented populations (Figure 6), notably predators from the Atlantic Ocean and French Polynesia. Nonetheless, there is higher variation in predator mass at lower values of prey mass.

The quality of predator mass measurements had an impact on estimates of predator mass. Levels 2 and 3 rendered a positive and significant relationship with predator mass, with slope estimates of 0.08 and 0.28, respectively, in addition to p -values of < 0.001 (Table 3).

Finally, we assessed the interaction between predator life stage and feeding preference. The interaction of larva life stage and planktivorous feeding interaction was significant ($p < 0.001$) with a slope estimate of -5.61 (Table 3). This indicates that when planktivorous, the predator mass at the larval life stage is significantly lower than at the adult life stage, and the difference in mass between larva and adults is larger, compared to when piscivorous. The interaction of juvenile life stage and predacious feeding interaction was also significant ($p < 0.001$), with a slope estimate of -0.39 (Table 3). Thus, when predacious the predator mass at the juvenile life stage is significantly lower than at the adult life stage, and the difference in mass between juveniles and adults is larger than when piscivorous (Figure 7).

Discussion

Overall, our model supports our hypothesis that predator feeding preferences and lifestage have considerable effects on their body mass. However, it fails to demonstrate the theoretical importance of the lowest trophic level — the primary producers — in influencing the mass of predators at higher trophic levels. While previous research stresses the potential of trophic upsurge to fuel predators (Tanentzap et al. 2014), these effects may be translating in terms of

greater predator population, rather than average mass. Without access to population data, we cannot assess the influence of MPP properly. Furthermore, habitat suitability may be inhibiting the maximum size predators can achieve despite an abundance of energy, introducing variation in response to MPP among sites. For example, habitats with high structural complexity can decrease the likelihood of a predator encountering its prey by providing shelter to avoid detection or attack (Campanella, Auster, Taylor, & Muñoz, 2019). In this sense, a predator does not have access to all the potential energy in the ecosystem. Finally, external inputs of energy from terrestrial systems, such as organic debris, can considerably increase populations of benthic invertebrates, and consequently small fish. This may promote growth of predacious and piscivorous fish, who are not necessarily relying on primary production for energy, and may be reflected in the observed large predator masses at low MPP values. Terrestrial input is particularly relevant for our coastal and estuarine locations (Figure 3), where the most variation in body mass was also observed.

Life stage

The observation that larval predators have a lower mass than adults (Table 3, Figure 4) was expected, as it coincides with the natural progression of organisms throughout their life. Most marine organisms, fish in particular, follow a specific order of development from fertilized egg to adult, where they increase in mass, overall size and strength, and transition from planktonic to predatory (Margules, 1989). It is nonetheless interesting that this trend was consistent across a wide geographic area and 91 predator species, as it supports our assumptions that a predator's lifestage and mass are more biologically relevant predictors of predator interactions than their taxonomic identity (Scharf, Juanes, & Rountree, 2000). Interestingly, the juvenile life stage did not have a significant relationship with predator mass, likely due to incredible variation in the growth rates across species. Additionally, within a single species, mean juvenile mass varies much more than larval mass, depending on climatic conditions and their stage along a seasonal migration (Power et al. 2007).

Feeding preference

There were two significant and complementary relationships regarding predator feeding preference and mass (Table 3). Planktivorous predators have a lower mass than piscivorous predators, and predacious predators have a greater mass than piscivorous predators (Figure 5). Various researchers have attempted to characterize the relationship between predator mass and prey consumption, and numerous studies have identified a relationship between larger predator mass, and a consumption of a greater range of prey (Barnes et al. 2008), thus reinforcing the relationship that predacious predators, of which consume a range of prey types, have greater mass than piscivorous and planktivorous predators. Moreover, many marine predators are

characterised as transiently planktivorous (Jackson & Lenz 2016), or more specifically zooplanktivorous, when they are in their larval stage of life, which is evident to correspond to lower predator mass, as per our model.

Predator mass quality

The difference in predator mass estimates among quality levels suggests potential systematic bias in our interpretation of predator mass. The positive significant relationship between level 3 and predator mass compared to level 1 (Table 3), implies an exaggeration or a positive skew in the determination of predator mass values as a result of the family regression. Given that most studies used multiple strategies to estimate predator mass, this likely did not have strong effects on the interpretation of our model.

Prey mass

The positive relationship between prey and predator mass (Table 3) appears to vary in magnitude by geographic location (Figure 6). The greater variation in predator mass at lower prey masses suggests that the predator-prey relationship is stronger when predator and prey are larger. While the over-representation of certain habitats prevents us from making this generalization on a global scale, positive lines of best fit occur across studies. This relationship is expected given that smaller predators are only able to consume a narrow repertoire of prey due to gape size or mobility constraints, while larger predators can consume more diverse prey ranging in mass and width (Scharf, Juanes, & Rountree, 2000). These results are reinforced by the finding that predacious predators, which consume a wider variety of fish, eggs, and invertebrates had a greater mass than piscivorous and planktivorous predators, which have more restricted feeding behaviour. This has implications for food web stability. Notably, food webs are usually more robust when predators are larger than their prey, as it minimizes the chance that new predators invade and outcompete current predatory species (Tucker and Rogers, 2014).

Interaction between predator life stage and feeding preference

The significant interaction between juvenile life stage and predacious feeding aligns with our expectation that smaller and younger predators would eat smaller prey due to size constraints. We found the difference between juvenile and adult predator mass to be greater when the predator is predacious in comparison to when the predator is piscivorous. These results can be explained by predator traits such as gape size, mobility, and strength, which can affect the size and variety of prey that a predator can feed on (Scharf, Juanes, & Rountree, 2000; Schmitz 2017). These traits may vary between different predator species, but can also vary based on predator ontogeny. Characteristics such as gape size are better developed in adults than juveniles,

meaning predacious predators are better able to consume a wider range of prey as they grow older, and will thus display a greater body mass (Scharf, Juanes, & Rountree, 2000). Piscivorous predators on the other hand, are defined as eating primarily fish, hence their prey selection is limited even into adulthood. Having better developed traits such as gape size may not provide as great an advantage to a piscivorous adult predator as to a predacious adult predator.

Conclusion

Our study was limited largely due to a lack of environmental information. Notably, only one depth, MPP, and temperature value were assigned per study, making it difficult to investigate effects on predators. Additionally, the only information on the amount of energy available in the trophic web was MPP. We also did not have information on the season during which sampling occurred, which influences the food available to predators, their feeding preferences, and consequently their size. Nonetheless, we had considerable evidence that suggested a predator's life stage, feeding preferences, and the mass of prey they target are strong predictors of their mass, while MPP is not. Our results support previous findings that predator mass is a useful way of disentangling complicated marine food webs. Furthermore, they suggest that using a predator's behaviour is an effective means of predicting its body mass, and may be used to identify food webs most vulnerable to trophic degradation given the overharvesting of predators.

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Appendix

Table 1. Definition of predator mass measurement qualities, according to the Ecological Society of America

Predator quality of length-mass conversion	Variable definition
1	Species regression
2	Genus regression
3	Family regression

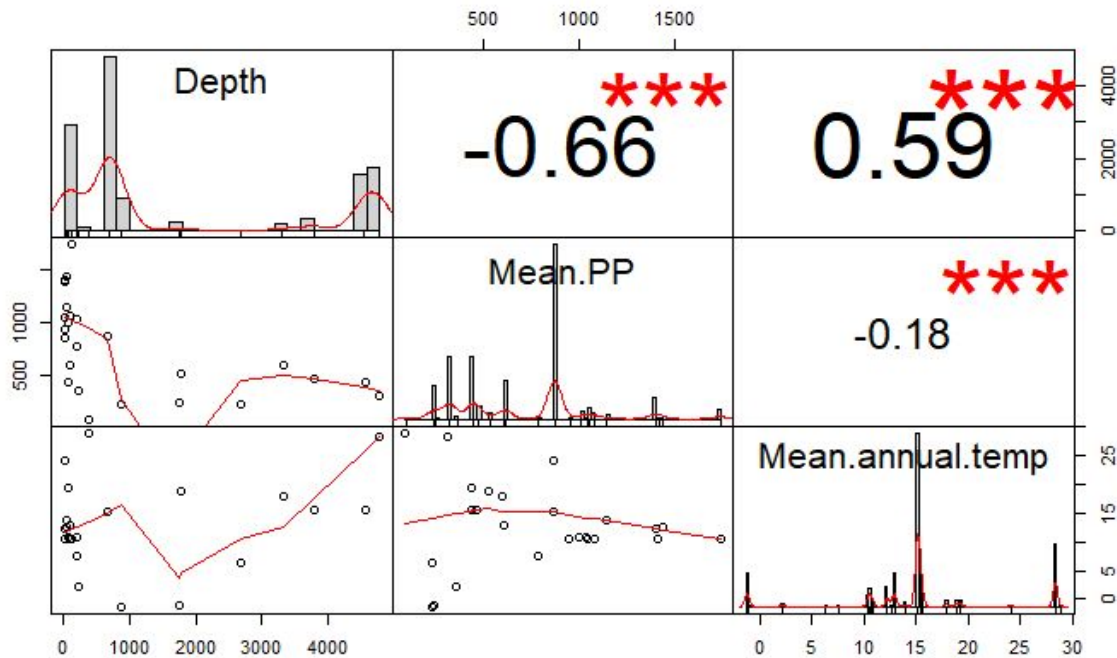


Figure 1. Correlogram of Pearson correlation coefficients between all pairings of depth, mean primary productivity, and mean annual temperature

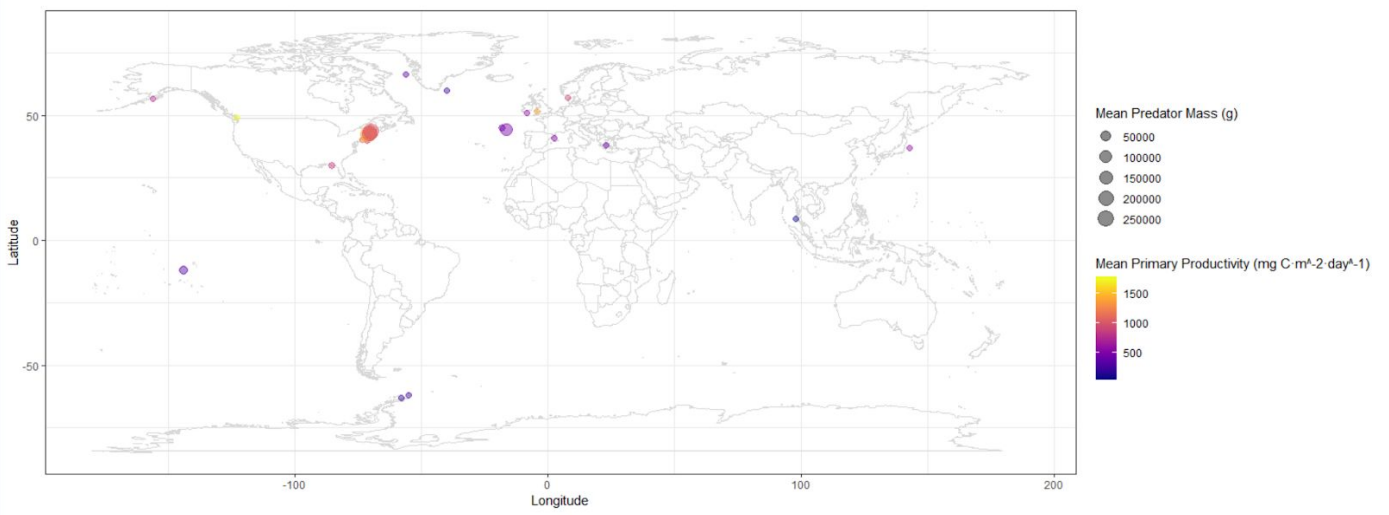


Figure 2. Mean primary productivity and predator mass across geographic locations

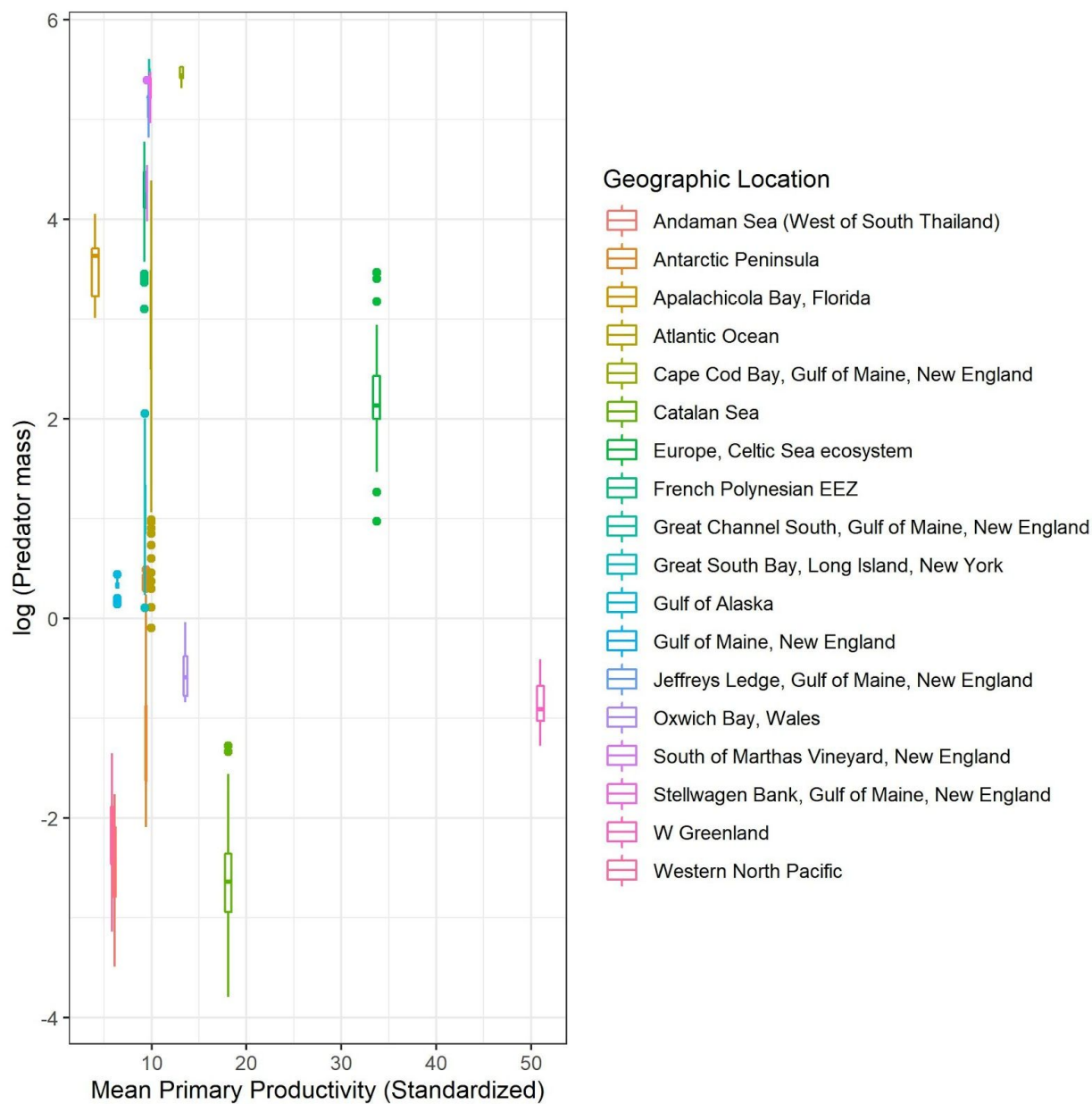


Figure 3. Standardized mean primary productivity against the log-10 of predator mass, coloured by sampling site

Table 2. AIC scores from the candidate models used in model selection

Model	df	AIC
mixed_model_saturated	14	15117.49
mixed_model_interactions_no_PP	13	15116.68
mixed_model_interactions_no_preymass	14	15866.04
mixed_model_no_interactions	12	15169.28
mixed_model_no_interactions_no_PP	10	15171.87
mixed_model_no_interactions_no_lifestage	10	15192.12
mixed_model_no_interactions_no_feeding	10	15196.57
mixed_model_no_interactions_no_preymass	11	15941.52

Table 3. Model output

<i>Predictors</i>	logpredmass		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	3.46	2.79 – 4.13	<0.001
Predator.lifestage [juvenile]	0.12	-1.01 – 1.25	0.840
Predator.lifestage [larva]	-0.07	-0.09 – -0.05	<0.001
Type.of.feeding.interaction [planktivorous]	-3.87	-5.52 – -2.21	<0.001
Type.of.feeding.interaction [predacious]	0.09	0.02 – 0.15	0.007
Prey.mass	0.08	0.01 – 0.16	0.032
Predator.quality.of.length.mass.conversion [2]	0.00	0.00 – 0.00	<0.001
Predator.quality.of.length.mass.conversion [3]	0.28	0.16 – 0.39	<0.001
Predator.lifestage [larva] * Type.of.feeding.interaction [planktivorous]	-5.61	-6.79 – -4.44	<0.001
Predator.lifestage [juvenile] * Type.of.feeding.interaction [predacious]	-0.39	-0.50 – -0.28	<0.001
Random Effects			
σ^2	0.13		
τ_{00} Predator.common.name	0.25		
τ_{00} Geographic.location	0.76		
ICC	0.89		
N Predator.common.name	45		
N Geographic.location	18		
Observations	18383		
Marginal R^2 / Conditional R^2	0.721 / 0.968		

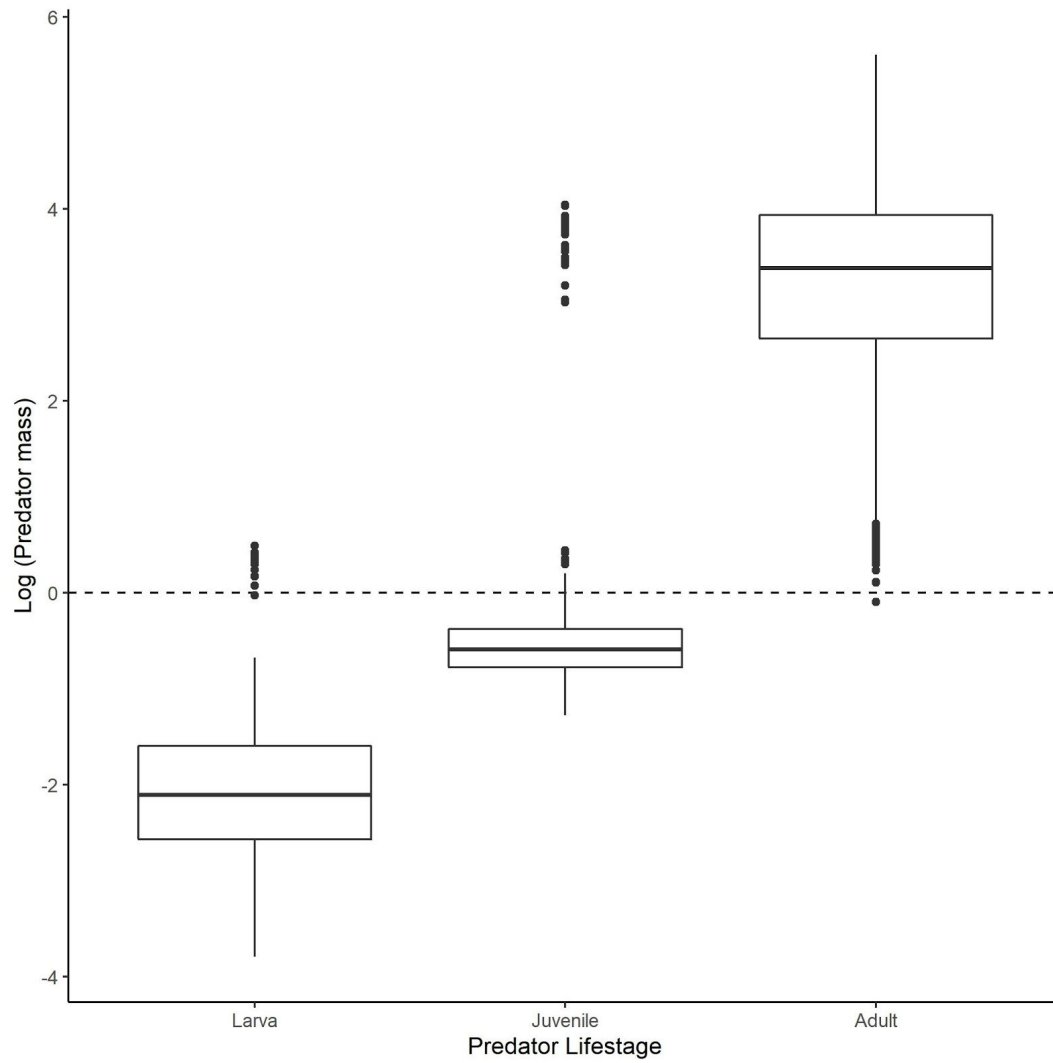


Figure 4. Log10-transformed predator mass across three categories of predator life stage: larva, juvenile, and adult

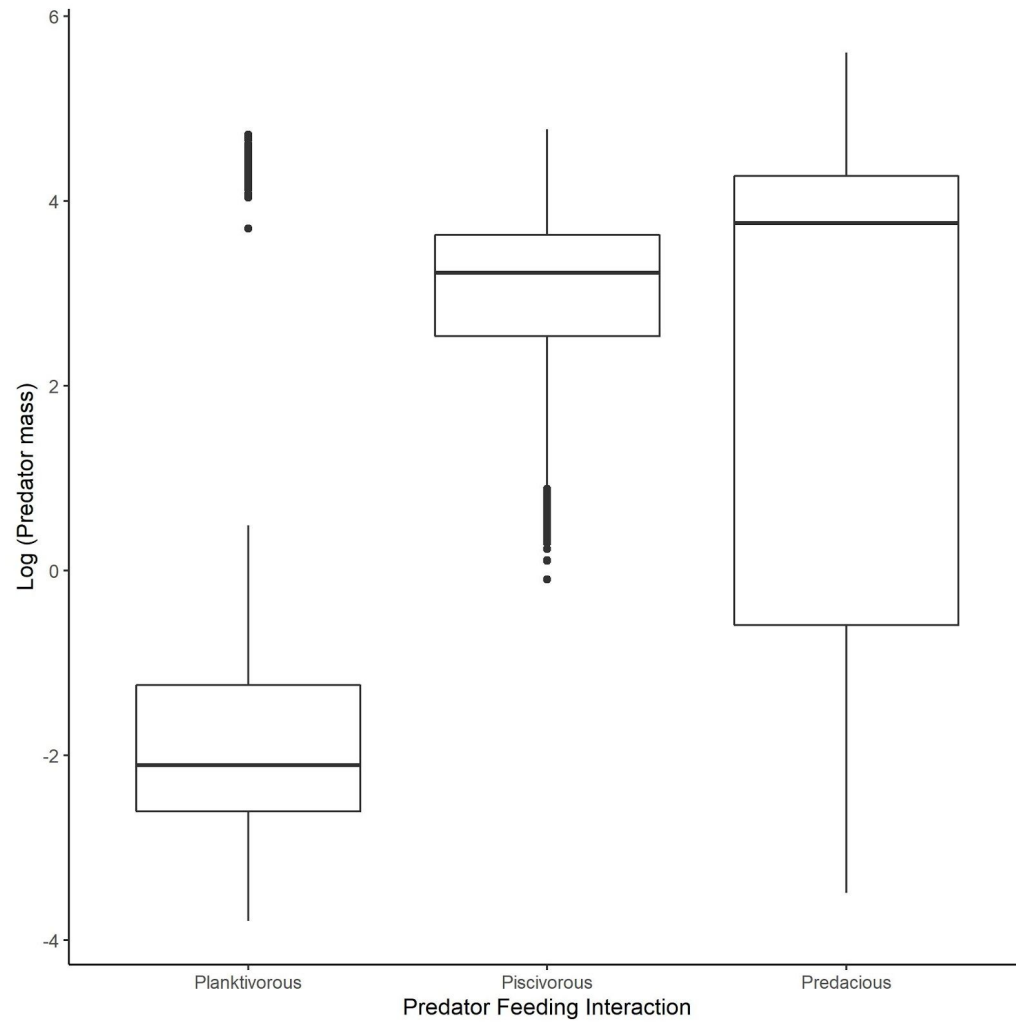


Figure 5. Log10-transformed predator mass across three types of predator feeding interactions: planktivorous, piscivorous, and predacious

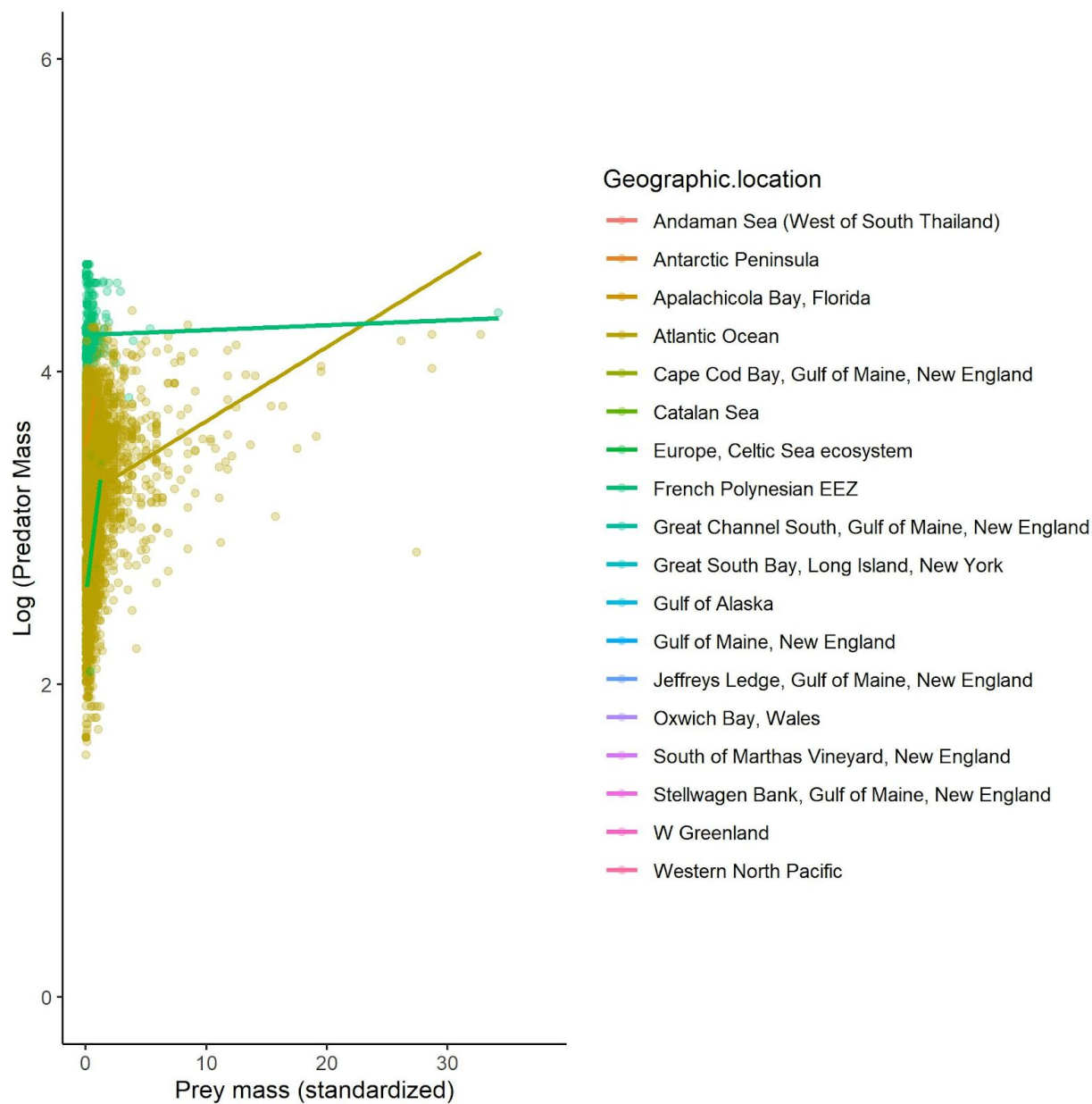


Figure 6. Scatter plot of log10-transformed predator mass vs. standardized prey mass, coloured by geographic location

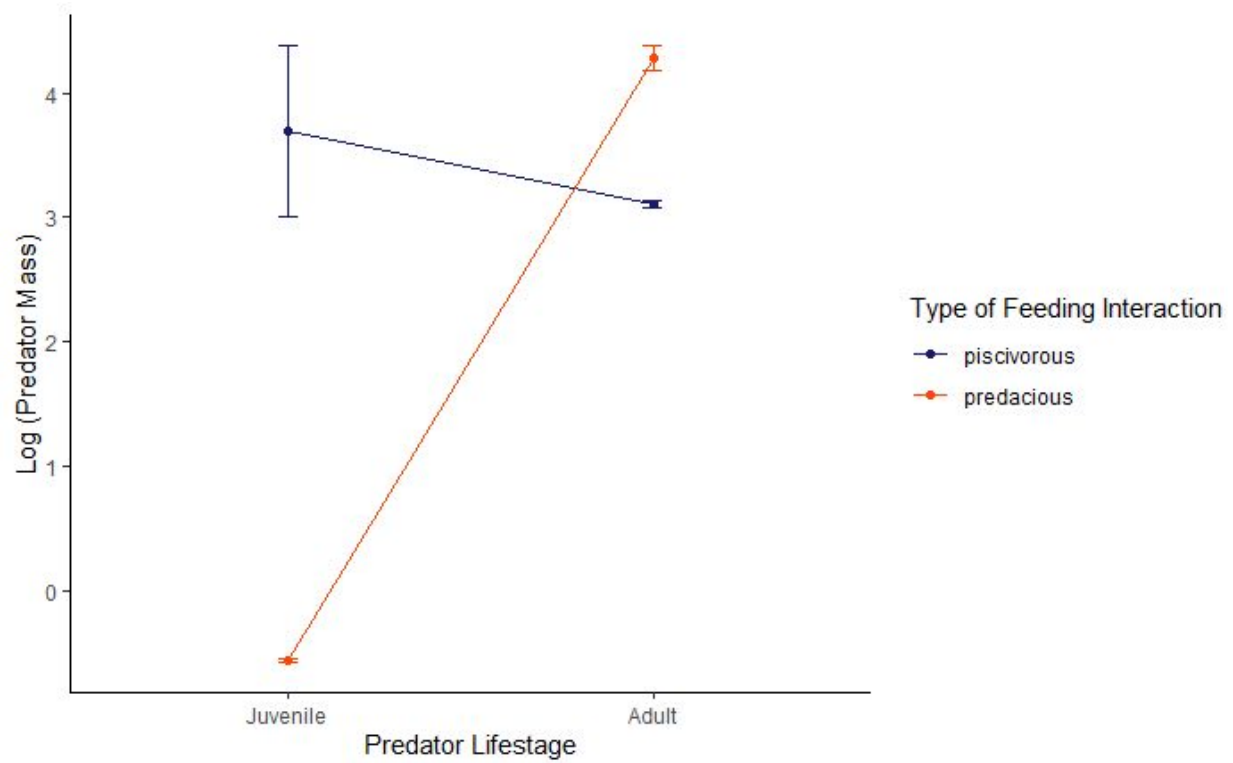


Figure 7. Log10-transformed predator mass across juvenile and adult life stages, in both piscivorous and predacious feeding interactions