

**Diving Deeper: Investigating the Influence of Trophic Position and Body Size on Shark  
Metabolic Rate**

Group 1: Emma Booth (1149027), Annika Laurin (1183145), Samantha Mok (1126756),

Kayla Perez (1175585), Farah Sadoon (1302190)

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Department of Integrative Biology

*Link to final paper in Github Readme*

# **Diving Deeper: Investigating the Influence of Trophic Position and Body Size on Shark Metabolic Rate**

## **1.0 Introduction**

As biodiversity declines due to anthropogenic climate change, understanding how species loss causes cascading effects on ecosystem functions, services, and resources becomes increasingly critical (Cardinale et al., 2012). Marine ecosystems are particularly vulnerable to these impacts due to their inherent complexity. Vertical stratification, temperature and salinity gradients, and nutrient cycling are just a few of the interacting factors that shape marine organisms' functional specificity and their ecosystems' stability (Duffy et al., 2001, Graham & Nash, 2013). These dynamics are further compounded by the roles of predators, whose presence or absence can create cascading effects throughout the food web (Estes et al., 1998, Henderson et al., 2024). Apex and meso-predator sharks, in particular, are essential to marine ecosystems, regulating populations at lower trophic levels and maintaining ecological balance (Henderson et al., 2024). The removal of these predators can disrupt this balance, leading to top-down trophic cascades that alter ecosystem structure and function (Henderson et al., 2024). Despite extensive research on the ecological importance of apex predators, significant gaps remain in understanding the physiological traits that underpin their roles.

Existing literature has largely focused on morphological and behavioural traits to explain predator-prey dynamics, yet physiological traits such as metabolic rate (MR) are equally important to understanding trophic interactions. MR is considered the fundamental biological rate as it describes the rate of energy uptake, transformation and allocation within organisms. The metabolic theory of ecology (MTE) emphasizes that MR can predict the pace of population interactions, including those between predators and prey, as individual metabolic rates dictate rates of consumption and population growth (Brown et al., 2004).

Body size is one of the most critical factors influencing MR, where MR and body size have an allometric relationship. However, other environmental considerations such as temperature, oxygen availability, and nutrient availability also play a role in establishing MR (Brown et al., 2004, Bouyoucos et al., 2019, Lear et al., 2017, Ste-Marie et al., 2020). As such, studying the relationships between MR, body size, and trophic position is critical for understanding energy dynamics and the stability of food-webs, particularly within benthic and pelagic ecosystems, where sharks serve as key apex and meso-predators.

Apex and meso-predator sharks provide an ideal model for this investigation because their diversity in size, behaviour, and ecological roles offers a unique opportunity to test the relationships between MR, body size, and trophic position. This study investigates two primary hypotheses: the "ecology hypothesis," which posits that variation in metabolic rates is associated with ecological roles, such as diet and lifestyle, and the "body size hypothesis," which suggests that metabolic rates are primarily determined by body size, irrespective of ecological role. Furthermore, we predict that: (1) MR will be positively associated with trophic position, as the energetic demands of a predatory lifestyle require greater resource consumption; or (2) MR will scale with body size as described by MTE, and will have no associations with trophic position. These hypotheses will be tested using data from apex and meso-predator sharks to better understand their physiological contributions to trophic dynamics.

Understanding how physiological traits influence trophic position has significant implications for marine conservation. Ecosystem models often struggle to capture the complexity of trophic interactions, particularly in the face of anthropogenic stressors such as climate change, habitat destruction, and overfishing. By incorporating MR and body size into these models, this study aims to provide a more intricate perspective on predator-prey dynamics. Ultimately, this research contributes to a deeper understanding of the functional

roles of apex and meso-predators by shedding light on the mechanisms driving trophic cascades and their broader ecological implications.

## **2.0 Methods**

### **2.1 Data preparation**

The necessary libraries for data manipulation, analysis, and visualization were loaded. The raw dataset, *FULL\_Rmax\_LHT\_MR\_ms.csv*, was imported, and unnecessary columns, including *TeleostOrElasmo*, *MROriginLocation*, *MRCitation*, and *DFtype*, were removed. Column names were standardized to snake case. The cleaned dataset was merged with trophic position data from the online database FishBase using the *scientific\_name* column. Rows with missing values (NA) were removed, and numerical columns were converted to their appropriate data types for further analysis.

### **2.2 Transformations**

Performed Shapiro-Wilk tests to assess the normality of columns containing MR, body mass, and trophic position data. To achieve normality, applied fourth-root transformations to the MR and body mass variables, followed by standardizing the transformed data using z-scores. Created histograms of MR, body mass, and trophic position for both raw and transformed data to visually evaluate distributions. Identified outliers in the standardized fourth-root-transformed variables using the interquartile range (IQR) method.

### **2.3 Ordinary Least Squares (OLS) Modelling**

A simple linear regression was performed to examine the relationships between standardized whole-organism MR and standardized trophic position, standardized whole-organism MR and standardized body mass, and standardized trophic position and standardized body mass. A multiple linear regression was conducted to evaluate the combined effects of standardized trophic position and standardized body mass on standardized whole-organism MR. Residuals from the multiple regression model were

extracted for analysis and visualization. Scatter plots of residuals against standardized trophic position and standardized body mass were created to identify potential patterns and deviations. A diagnostic plot of fitted values versus residuals was generated to assess model assumptions and overall fit.

## 2.4 Phylogenetic Tree

Loaded the full teleost chronogram and the chondro subset phylogenetic tree from the Gravel et al., 2024 dataset. Species names in the phylogenetic tree were updated to correct the nomenclature and match the dataset created in section 2.2. Species names were extracted from both the dataset and the phylogenetic tree, and a comparison was made to identify any mismatches between the two datasets. The phylogenetic tree was then pruned to include only the species present in the dataset.

## 2.5 Phylogenetic Least Squares (PGLS) Modelling

Reordered the dataset to align with the order of tree tips by filtering for species present in both the tree and dataset, then arranging the rows according to the sequence of tree tips. Verified the root edge length of the pruned tree and corrected it by setting the value to 0. Fitted three PGLS models: one predicting whole-organism MR using both trophic position and body mass, another using only trophic position, and a third using only body mass. Performed a model comparison to identify the best models based on delta AIC values.

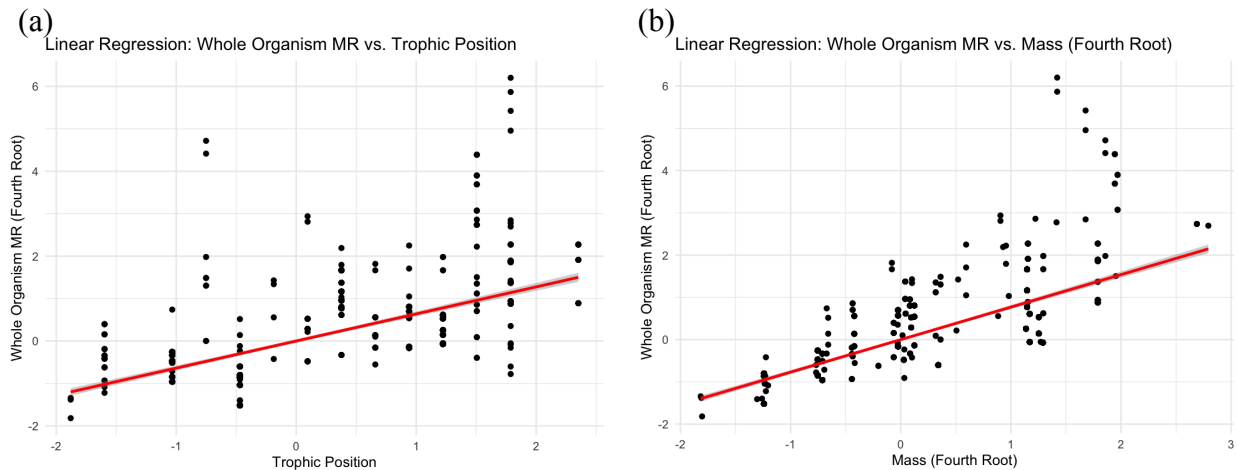
## 2.6 Trait Mapping

Calculated the phylogenetic signal for average whole-organism MR using the lambda method. Grouped the dataset by species and calculated the mean values for standardized whole-organism MR, trophic position, and body mass. Created 3 phylogenetic trees with the traits MR, trophic position, and body mass respectively.

## 3.0 Results:

### 3.1 OLS

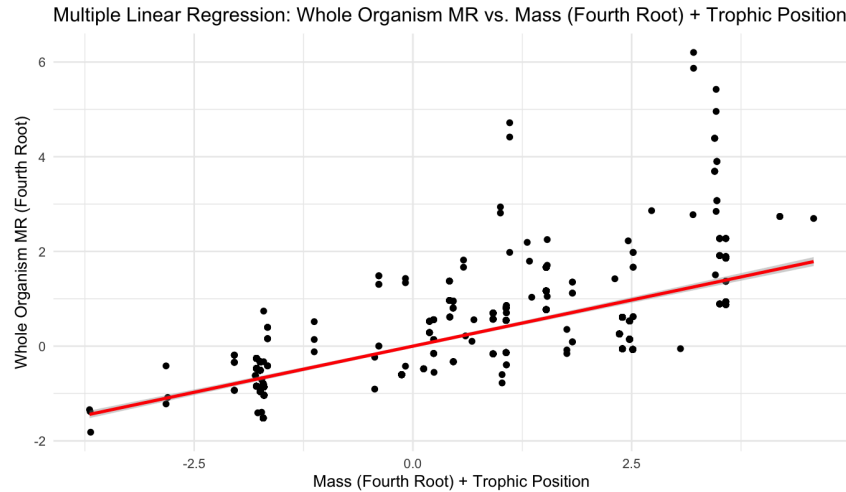
Our first linear regression model examined the relationship between MR and trophic position, which revealed a significantly positive relationship (slope = 0.638, p-value <  $2 \times 10^{-16}$ ), explaining 40.7% of the variance in MR ( $R^2 = 0.407$ ) with a residual standard error (RSE) of 0.7703. This indicates that when trophic position is considered as the only explanatory variable, it is a strong predictor for MR.



**Fig 1. Linear regression models examining predictors of metabolic rate:** (a) Trophic position showed a significant positive relationship with MR (slope = 0.638,  $p < 2 \times 10^{-16}$ ), explaining 40.7% of the variance ( $R^2 = 0.407$ ) with an RSE of 0.7703. (b) Body mass showed a stronger positive relationship (slope = 0.769,  $p < 2 \times 10^{-16}$ ), explaining 59.2% of the variance ( $R^2 = 0.592$ ) with a lower RSE of 0.6392.

In comparison, the results from our MR vs. body mass showed a significantly stronger positive relationship (slope = 0.769, p-value <  $2 \times 10^{-16}$ ) that explained a higher proportion of variance in MR ( $R^2 = 0.592$ ) with a lower RSE of 0.6392. Therefore, these results propose that the body mass model is a better fit when compared to the trophic position-only model.

When both variables were included in a multiple linear regression model, body mass remained the dominant predictor (slope = 0.727, p-value <  $2 \times 10^{-16}$ ), while the trophic position was weak and non-significant (slope = 0.053,  $p = 0.072$ ). This model explained 59.3% of variance in MR ( $R^2 = 0.593$ ) with an RSE of 0.6386, which only slightly differed from the body mass-only model.

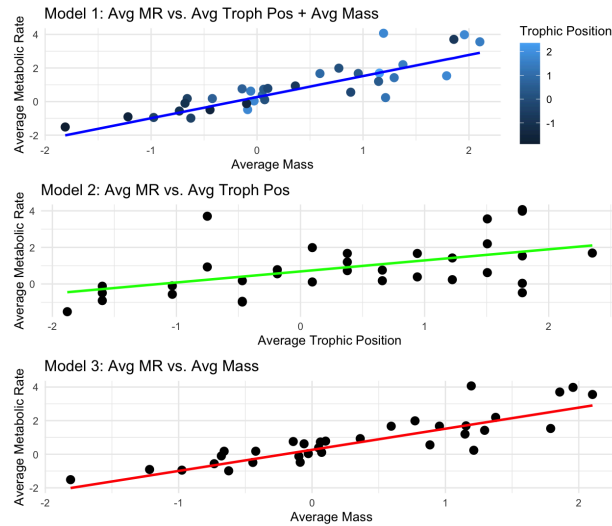


**Fig 2. Multiple linear regression model examining predictors of metabolic rate:** Body mass was the dominant predictor (slope = 0.727,  $p < 2 \times 10^{-16}$ ), while trophic position was non-significant (slope = 0.053,  $p = 0.072$ ). The model explained 59.3% of the variance in MR ( $R^2 = 0.593$ ) with an RSE of 0.6386.

These findings suggest that trophic position has minimal influence when body mass is accounted for in the model. The residuals of the combined model were also evenly distributed around zero (702 positive, 629 negative values) with no patterns, confirming the validity of the model.

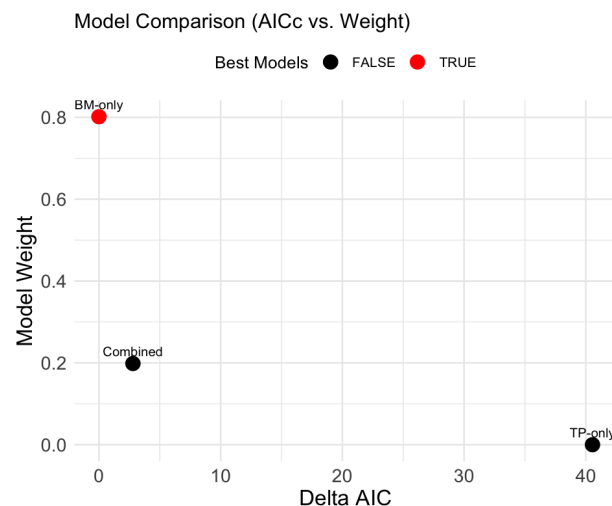
### 3.2 PGLS

In order to account for phylogenetic relationships among species, we utilized a PGLS model to assess the relationship between variables MR, trophic position, and body mass. In the combined model (trophic position + body mass) body mass remained a significant predictor ( $\beta = 1.253$ ,  $p\text{-value} < 0.001$ ), while trophic position did not show a significant effect ( $\beta = 0.0036$ ,  $p\text{-value} = 0.9752$ ). The model explained 79.5% of the variance in MR and had a strong phylogenetic signal of 0.814 meaning that metabolic rates were highly conserved in closely related species.



**Fig 3. PGLS models examining MR, trophic position, and body mass:** (Model 1) The combined model showed body mass as a significant predictor ( $\beta = 1.253$ ,  $p < 0.001$ ) and trophic position as non-significant ( $\beta = 0.0036$ ,  $p = 0.9752$ ), explaining 79.5% of the variance in MR with a phylogenetic signal of 0.814. (Model 2) The trophic position-only model had a non-significant effect ( $\beta = 0.604$ ,  $p = 0.9752$ ). (Model 3) The body mass-only model explained a similar proportion of variance in MR, with body mass as the strong predictor.

The body mass-only model showed to have the lowest AIC value ( $AIC = 73.03$ ) and explained a similar proportion of variance as the combined model. Body mass persisted as a strong predictor for MR; however, the trophic position-only model showed a much poorer fit with a high AIC value ( $AIC = 113.58$ ) and a non-significant effect ( $\beta = 0.604$ ,  $p = 0.9752$ ).

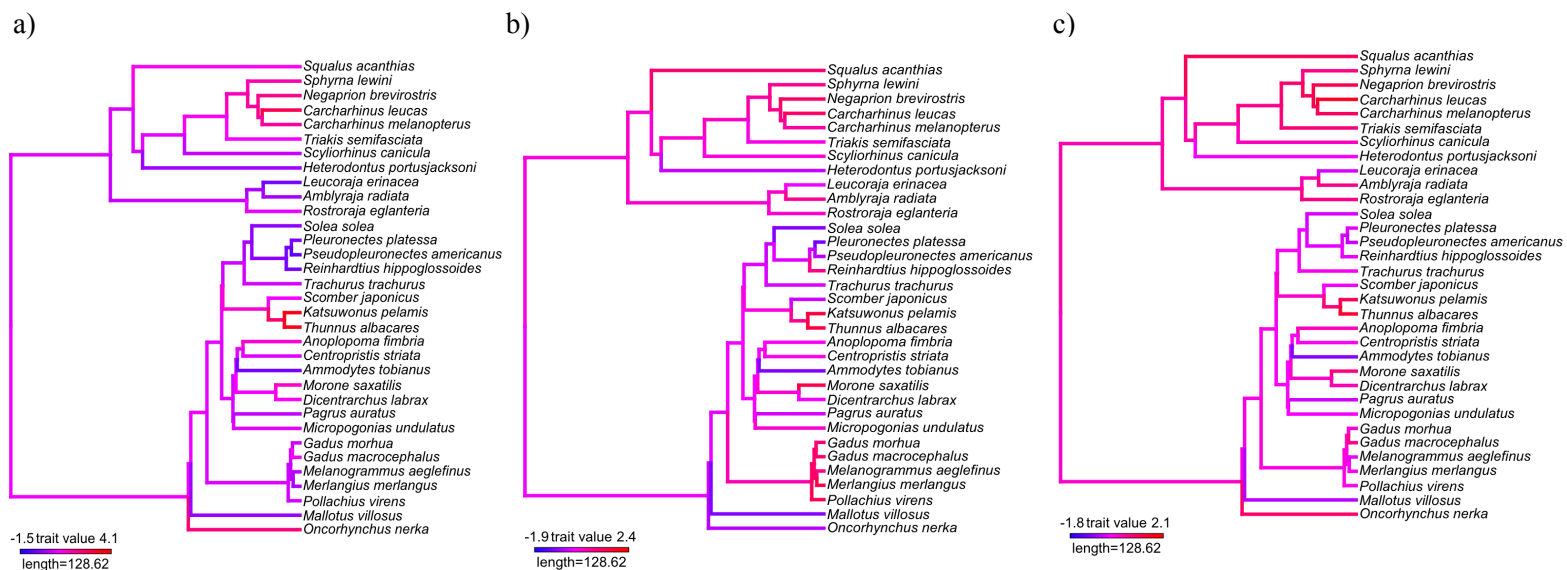




**Fig 4. Model comparison plot** comparing the fit of three models in terms of standardized MR predictability based on body mass (BM), trophic position (TP), or a combination of both variables. The x-axis represents the delta AIC (Akaike Information Criterion) which explains model performance relative to the best model. The y-axis represents the model weight, showing the relative likelihood of each model. Labels on each plotted point ("BM-only," "Combined," "TP-only") indicate the variable included in each model, with red points highlighting models within the  $\Delta AIC < 2$  threshold.

Our model selection then identified the body mass-only model as the best-supported model ( $\Delta AIC = 0$ ), which accounted for 80.2% of the model weight. The combined model was the second best model ( $\Delta AIC = 2.79$ , model weight = 19.8%) and trophic position performed the worst ( $\Delta AIC = 40.55$ ). In the model comparison plot, the body mass-only model was the only one to fall into the  $\Delta AIC < 2$  threshold (fig 4) indicating the dominant role of body mass in explaining MR variability across shark species.

### 3.3 Trait Mapping



**Fig 5. Trait mapping on phylogenetic tree examining MR, trophic position, and body mass:** (a) MR across phylogeny with branches coloured according to metabolic rate values. (b) trophic position across phylogeny, with branches coloured by trophic position values. (c) body mass across phylogeny with branches coloured by their respective mass values. All plots include a legend that depicts trait intensity throughout the phylogenetic tree.

Trait mapping revealed no clear pattern in the distribution of metabolic rates associated with ecological roles across species since some carnivorous and omnivorous species both had high metabolic rates, therefore our ecological hypothesis is not supported. In

contrast, body mass showed some correlation to MR since larger species like *Oncorhynchus nerka* exhibited higher metabolic rates. However, there are some exceptions such as small species like *Gadus morhua* having moderate rates indicating that other factors may play a role in determining metabolic rates.

Overall, our results strongly support the “Body Size” hypothesis demonstrating that body mass is the primary driver of metabolic rate across shark species, outperforming trophic position in terms of explaining variation. While trophic position was a strong predictive value when considered alone, its effect was minimal when body mass was included.

#### **4.0 Discussion:**

The relationship between body size and MR is a key component of the metabolic theory (Brown et al., 2004). Our research suggests that body size can be a strong predictor of MR in individuals, enhancing our understanding of marine metabolism (Brown et al., 2004). Typically, MR is measured in controlled laboratory settings where basal metabolic rate (BMR) is assessed when the organism is inactive (Brown et al., 2004). However, in natural environments, field metabolic rates (FMR) are typically higher than BMR, as organisms must allocate energy for activities like foraging, predator avoidance, physiological regulation, and other maintenance processes (Brown et al., 2004). This discrepancy between BMR and FMR is an important area of study, as it provides insights into energy expenditure, survival strategies, and ecological adaptations.

By understanding the relationship between trophic position and metabolic rates, we can better identify species that are sensitive to overfishing (Gravel et al., 2024). Since sharks often exhibit slow life histories characterized by slow growth, they are more sensitive to overfishing (Gravel et al., 2024). By better understanding the relationship between trophic

position, metabolisms and body size, our research can help identify where different species fall along a spectrum of sensitivity to population declines.

By examining how metabolism and life history traits, such as body size and trophic position, are connected, we can gain a deeper understanding of how species evolve in response to their environment (Gravel et al., 2024). This approach can also enhance our understanding of Elasmobranch evolution and shed light on how these species have survived for so long.

Key questions emerging from our research are focused on understanding how climate change may interact with marine populations. With rising global ocean temperatures, understanding how Elasmobranch metabolism responds to environmental changes can help predict shifts in their populations and ranges (Osgood et al., 2021).

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