Spring 4-18-2024

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Recommended Citation

Woelber, Jacob, "Metabolic Scaling of Aquatic Macroinvertebrates" (2024). *Honors Thesis*. 345.
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METABOLIC SCALING OF AQUATIC MACROINVERTEBRATES

by

Jacob Woelber

A Thesis Submitted in Partial Fulfillment
Of the Requirements for the
University Honors Program

Department of Biology
The University of South Dakota
May 2024

The members of the Honors Thesis Committee appointed

to examine the thesis of Jacob Woelber

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ABSTRACT

Metabolic Scaling of Aquatic Macroinvertebrates

Jacob Woelber

Director: Jeff Wesner, Ph D.

The common assumption in regard to metabolic rate scaling with body size is the 3/4 law, which predicts a scaling exponent of 0.75 between log metabolic rate and log body size. Supporting evidence exists for this theory on a large, general scale. However, factors such as temperature, predation, and environment can cause the scaling exponent to deviate from 0.75. This paper takes a closer look at the effects of temperature and predation on metabolic rates via oxygen consumption in freshwater macroinvertebrate populations. To do this, 24 tanks were filled with water to allow natural populations of macroinvertebrates (predominantly Chironomidae) to colonize. The tanks were randomly heated, heated with a fish living in the tank, unheated with a fish, or neither. Benthic macroinvertebrates were sampled and sorted into individual vials. The decrease in dissolved oxygen content was then measured over 30 minutes. The results suggest a metabolic scaling more in the ranges of 0.4 and 0.5 across treatments, substantially lower than the 0.75 predicted by theory. An interaction between temperature and predation was also observed. Increased temperatures caused the scaling exponent to increase in the absence of fish but decrease in the presence of fish. These findings indicate not only a strong deviation from 0.75, but also provide insight on how environmental changes will shape ecosystem dynamics in the future.

KEYWORDS: Metabolic scaling, macroinvertebrates, fish, temperature, predation

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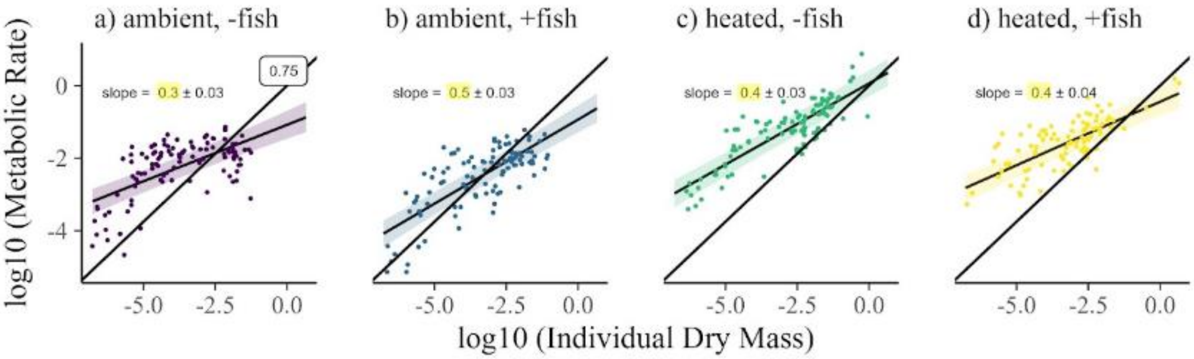

Figure 1: Comparison of the metabolic scaling of the individual treatments compared to the 0.75 line predicted by theory. Each data point represents a single macroinvertebrate.

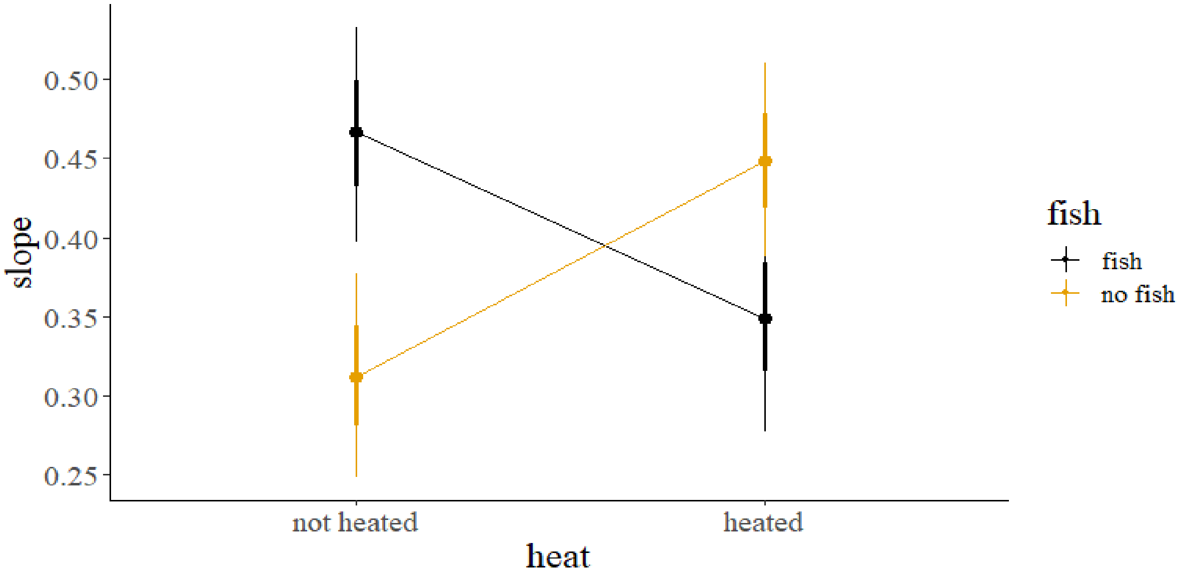

Figure 2: Comparison of the scaling exponents derived from each treatment. Lines for visual connection between treatments and do not represent data points.

Introduction

Larger organisms have higher metabolic rates than smaller organisms due to higher energetic requirements (Kleiber 1961). However, the increase in metabolic rate with body mass is not a one-to-one relationship. Instead, larger organisms have more efficient metabolic systems, leading to scaling that is often closer to a 3/4 power law (Banavar et al 2014). The 3/4 power law is a widely used metric for metabolic scaling. Metabolic scaling relates the quantitative properties of respiration rate to body mass using the equation ($R=aM^b$), where R represents respiration rate, M represents body mass, a is a constant, and b is the power scaling exponent (3/4) (Glazier 2005). Gaining its origins through studies performed on terrestrial mammals, the 3/4 power law has now been used in experiments on everything from unicellular microorganisms to elephants (Calder 1984, Niklas 1994, Thommen et al 2019, West & Brown 2005). The scaling exponent of 0.75 fits a substantial number of multicellular endotherms (West & Brown 2005). However, its ability to accurately estimate metabolic scaling across all organisms has come under question (Glazier et al 2011, Gjoni et al 2020). One such counter example exists in the realm of freshwater aquatic macroinvertebrates.

Aquatic macroinvertebrates are omnipresent in freshwater environments (Lancaster & Downes 2013). In their larval stage, they reside in the water. As adults, they emerge and interact with the surrounding terrestrial environment, meaning they take part in at least two ecosystems over the course of their existence. Their involvement in multiple ecosystems makes them an important marker for ecosystem function. Aquatic macroinvertebrates are useful for estimating ecosystem function thanks to their diversity and responsiveness to environmental stressors (Aazami et al 2019).

Ecological factors, such as temperature and predation, affect the metabolic rates of individuals in ecosystems, including freshwater macroinvertebrate-dominated ecosystems (Glazier et al 2011). For example, a rise in temperature will increase the metabolism of ectotherms (Glazier et al 2020, Bruno et al 2015, Gjoni et al 2020, Rotvit & Jacobsen 2013). However, studies of temperature effects are typically conducted on a single species and leave out species interactions like predation. Unlike the effect of temperature, predation can affect certain body sizes more than others, due to size-selective predation (Glazier et al 2011). For example, a fish may see larger macroinvertebrates and target them first, leaving the smaller macroinvertebrates and the larger macroinvertebrates that exhibit predator avoidance behaviors (Gjoni et al 2020). Both Abjornsson et al (2004) and Glazier et al (2011) have found that macroinvertebrates will change their behavior in response to the presence of a predator in their environment. The macroinvertebrates sense predators ("smelling" the predator) and respond by restricting movement and seeking sheltered spots. Glazier et al (2011) found that these behavioral responses correlate with lower metabolic rates in the body sizes experiencing the highest predatory pressure. This skews the metabolic scaling away from the 3/4 scaling (Glazier et al. 2011). Furthermore, temperature and predation interact with each other when both are present variables. The body sizes experiencing the most predatory pressure experience a compound effect when a rise in temperature occurs (Glazier et al 2020).

To understand the interactions of these ecological factors (predation and temperature), I conducted a mesocosm experiment with freshwater macroinvertebrates and fish. As higher temperatures correlate with higher individual metabolic rates, I predicted that the metabolic rates of individuals exposed to predation would increase less than the rates of those experiencing less predatory pressure, causing metabolic scaling to become shallower in the presence of predator.

Methods

Study Site

Data was collected at the University of South Dakota's Experimental Aquatic Research Site, Vermillion, SD. The site consists of 24 fiberglass tanks (1136 L). The tanks were filled with 714 L of water over a mix of cobble and sand for substrate in May of 2023. Water levels were monitored and maintained over the course of the experiment. Each tank had an overflow spout and a magnetic drive water pump (Danner Supreme Aqua-Mag). Local populations of macroinvertebrates colonized the tanks via oviposition before data collection occurred in late June. AQQA Aquarium 800W Heaters (AQQA Inc.) were placed in half of the tanks and set to ~5 degrees C above ambient nighttime temperatures. Temperature data were taken daily in the middle of the water column using a YSI Pro-Series DSS (YSI Inc., Yellow Springs, OH, USA). Heaters were adjusted to maintain a temperature of ~5 degrees C above ambient. Fish (*Lepomis cyanellus*) were gathered from a local pond with a seine net and set free in half of the tanks (one fish per tank). The four treatment groups included ambient temperatures with fish, ambient temperatures without fish, heated with fish, and heated without fish.

Sampling

Metabolic measurements occurred 30 days after treatments were started. A Hess sampler (0.032 m^2, 500 um collection mesh) was used to sample benthic macroinvertebrates following the methods of Henry & Wesner (2018).

Macroinvertebrates from the sediment were sorted and placed in containers with filtered water from their corresponding treatment and held without food for 24 hours to empty their guts. After 24 hours, they were separated into individual glass vials with 20 mL of oxygenated, filtered water. Nine vials with a macroinvertebrate and one without (to correct for oxygen changes not due to respiration) were used for each run of measurements. Two O2 readings were taken an hour apart with each vial using a Fibox 4 oxygen sensor (Presens, Regensburg, Germany). The macroinvertebrates were then photographed (lengths measured using ImageJ) before being dried and measured on a microbalance. Oxygen consumption was estimated using the following equation.

$$R_{O_2} = \frac{(P_E - P_C)S \times A \times V}{t}$$

P_E and P_C represent partial pressures of oxygen in the experimental environment (20 mL vials) and control, respectively, *S* is the solubility coefficient of oxygen in water, *A* is the volume of 1 mol O_2 at standard temperature and pressure, *V* is the volume of water in the vials, and *t* is the time of incubation.

To ensure accurate results, preliminary testing was performed to see how long it would take for a visible drop in dissolved oxygen content to occur. This determined the 60-minute time span between measurements. During the experiment, macroinvertebrates were kept in water that corresponded to their respective treatment.

Statistical Modeling

To quantify metabolic scaling, I fit a linear mixed model with a response variable of log10 metabolic rate. The predictor variables were log10 individual dry mass, heat, fish, and their interactions. The tanks were included as a random effect. I fit these models in R version 4.4.0 (R Core Team 2024) using the brms package (Burkner 2017), which estimated posteriors using rstan (Stan Development Team 2024). Posteriors were estimated with four chains with 2000 iterations each and the first 1000 iterations of each chain were discarded as warm up. I used an informative prior of Normal(0.75, 0.2) (mean, sd) for the coefficient of log10 dry mass. The intercept was set at Normal(0, 0.2). All other fixed effects were Normal(0, 1).

Results

Out of 414 collected macroinvertebrates, ~90% were from Chironomidae, ~8% from Odonata, and ~2% from Ceratopogonidae. Chironomids were the most abundant, ranging from 80 to 97% across treatments. Odonata made up 16% of individuals in the heated+fish treatment, but less than 8% in all other treatments. Metabolic scaling in all treatments differed from the 0.75 line predicted by theory. The scaling exponents also showed a clear interaction between predator and temperature treatments (Figures 1 and 2). Under ambient temperatures, treatments with no fish had the lowest scaling exponent (0.3 ± 0.03, posterior mean ± SD), whereas treatments with fish had the highest scaling exponent (0.5 ± 0.03). The average metabolic rate was also ~70% lower in ambient treatments compared to heated treatments (Figure 1). However, this dynamic flipped in the heated tanks, with tanks containing fish showing lower scaling exponents on average compared to those without fish (Figure 2).

Discussion

The most important result in this experiment is predation and temperature effects interact to change the metabolic scaling of a population. These results go against the broad use of the 3/4 power law as an accurate predictor of metabolic scaling. Regarding the first conclusion, the effect of temperature on the metabolic rate of an individual is well understood: higher temperatures raise the metabolic rates of all individuals in an ecosystem, as seen in our results and literature. For example, Glazier et al. (2020) found that a 4 degree C increase in temperature caused a 3-fold increase in metabolic rates of amphipods. That is strikingly similar to our result, which found a 3-fold increase in metabolic rates of macroinvertebrates in response to a 5 degree C increase in temperature. Predation on its own can affect the metabolism and behavior of macroinvertebrates. Abjornsson et al (2004) found that amphipods increased their use of available cover to hide in response to the presence of predatory chemical cues. These behaviors correlate to lower metabolic rates than those experiencing predatory pressure (Glazier et al 2011).

Under ambient temperatures, the tanks with fish had steeper scaling exponents than those without fish. However, the opposite was observed in the heated tanks. Shallow scaling exponents imply higher metabolic rates in the smaller body sizes, lower metabolic rates in the larger body sizes, or a combination of both. Glazier et al (2011) suggested a combination of the two. They found that metabolic rates of small macroinvertebrates increased in response to predation threats in order to reach reproductive size faster. In contrast, metabolic rates of large macroinvertebrates decreased in response to predation as they limited movement to avoid predators. Abjornsson et al (2004) recorded a higher rate of sheltering behaviors when predatory cues were present, and Wisenden et al (2001) noted that these avoidance behaviors occurred more frequently with larger body sizes. The shallower scaling exponents seen in the heat + fish treatment from this experiment match these observations. The opposite effect observed in the ambient + fish treatment was also observed in an experiment by Glazier et al (2020).

Aside from the interactions between predatory pressure and temperature effects, all of the observed scaling exponents were much shallower than the theoretical values of 0.75 predicted by the 3/4 power law. The 3/4 power law is often used as the predicting coefficient for metazoans (Bruno et al 2015, Glazier et al 2020, Gjoni et al 2020). However, there is increasing evidence that challenges its universal use (Riisgård 1998). For example, Yvon-Durocher & Allen (2012) performed a similar experiment to ours looking at changes in metabolic scaling of ecosystems when exposed to temperature changes. Although they used 0.75 as a null exponent, their results showed a value closer to 0.4 much like the exponent values found in this experiment. On a species level, amphipods demonstrate a scaling exponent around 0.6 when in the presence of fish predators (Glazier et al 2011). The 3/4 power law cannot universally predict metabolic scaling, especially in smaller organisms such as macroinvertebrates.

These two conclusions are important because metabolic scaling is used as a predictor of the ecosystem function (Yvon-Durocher & Allen 2012). For example, assumptions of a fixed scaling rate have been used to predict temperature effects of consumer-resource interactions, ecosystem production, and effects of resource supply (Bruno et al 2015). It is vital to develop reliable methods of quantifying ecosystem health to help advocate for areas in need. These results challenge the ay ecologists predict metabolic scaling. Macroinvertebrates appear to fit a shallower metabolic scaling exponent than the 0.75 predicted by theory. Additionally, the diversity and complexity of the ecosystem (predator and prey relationships) further adds to the variation among their metabolisms.

In summary, the metabolic scaling at the community-level among macroinvertebrate species from distinctly different aquatic ecosystems is influenced by acclimation to temperature and fish cues in a combined manner. Our findings contribute to the increasing evidence that metabolic scaling is highly flexible, shaped by long-term evolutionary adaptations. They indicate that metabolic scaling is not solely dictated by internal body-design constraints, but also reacts to various abiotic and biotic environmental factors. An important takeaway is that research on how global warming impacts biological and ecological processes needs to be conducted within realistic ecological frameworks.

Acknowledgments

We thank Trevor Welch, Aria Smith, Mariah Block, and Staci Reynolds for help in the field and lab. This work was conducted under approved IACUC protocol #03-03-18-21. The work was supported by a National Science Foundation grant to Jeff Wesner (#2106067) and through the Nolop Endowment Funds in the Department of Biology.

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