Examining the Thermal Performance of Two Eel River Snail Genera

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ABSTRACT

The Eel River, the third largest river in California, is an ecologically important watershed that has been the focus of restoration and management efforts over the past years. It is a major source of energy flow in the region along with a large source of regional biodiversity. Rising temperatures affect almost every aspect of stream communities, including trophic interactions and food webs, which can have profound implications for overall ecosystem health. Understanding the competitive potential of lower trophic level grazers, such as the native pulmonate snails *Helisoma sp.* and *Physella sp.*, in changing temperature regimes is critical in order to implement preventative management plans and to understand the possible trophic effects of climate change in this ecologically important area. The study conducted a series of controlled feeding trials over a temperature gradient from 14ºC to 30ºC on individuals of these two genera in order to construct thermal performance curves and determine the effects of temperature on feeding rate as a proxy for metabolic performance. Unlike *Physella, Helisoma* did not reach a thermal optimum before 30ºC, which implies that *Helisoma* may be a better competitor in higher temperature regimes. Along with this, both *Helisoma* and *Physella* also exhibited some degree of diel feeding behavior in this study.

KEYWORDS

INTRODUCTION

Experts predict that the effects of climate change regarding stream ecosystems are highly concerning for overall ecosystem health. Freshwater covers 0.8% of earth, but contains 6% of all species (Dudgeon et al. 2006). Streams are important biodiversity sources and avenues for energy flow among the various systems in a watershed (Nelson et al. 2008). And they are especially vulnerable to changing climate (Friberg et al. 2009). Stream ecosystems are subject to changing conditions throughout the watershed such as altered runoff regimes, rising temperatures, and vincreasingly dramatic temperature fluctuations (Alcamo et al. 2008, Palmer et al. 2008). Climate change also alters nutrient flow and cycling within stream ecosystems, which allows for increased opportunities of invasion by non-native species (Woodward et al. 2010). Therefore, altered physical characteristics of streams can change the ecological functioning and structure of biotic communities.

Rising temperatures affect almost every aspect of stream communities, including trophic interactions and food webs, which can have profound implications for overall ecosystem health. Water temperature and availability in stream systems (as they are often rain-fed or fed via glacial melting) are often totally climate dependent (Woodward et al. 2010). Food web alterations in streams due to climate change are the intersection of bottom-up and top-down ecological and trophic effects. These effects can change food web and performance of ecosystem services, as many ecosystem services temperature dependent (Spooner & Vaughn 2006). Bottom-up effects stem from the physical characteristics of streams, such as altered runoff and temperature regimes, which can alter primary production in the stream (Dodds 2006). Increased primary production can have profound effects on herbivory rates and energy flow within biotic communities, which can facilitate recruitment of non-desirable species (Brodie et al. 2005). Bottom-up effects can also result in favoring top-down trophic effects, as altered habitat can become more favorable to non-native species that are not predator limited, which can then either outcompete other species that are resource limited or predate upon them (Rahel and Olden 2008). Invasion by nonnative species can profoundly change the structure and functioning of ecological communities (Carpenter and Cottingham 1997). Favorable conditions provided by an organism's physical environment can give non-native species a competitive edge.

Successful competition within and among species requires careful energy budgeting by an organism. Energy budgets are balanced largely by metabolic performance. Most, if not all major members of stream communities are ectotherms, which are especially vulnerable to changes in temperature (Huey & Stevenson 1979, Huey & Bennett 1987). Climate change creates conditions that places physiological stress upon ectothermic organisms, and opens avenues for regime changes in relative native species abundances by creating conditions that favor certain species over others (Carpenter and Cottingham 1997, Rahel and Olden 2008). Physiological stress on organisms brought about by rising temperatures can cause organisms' metabolisms to rise, which results in having to allocate more energy to staying alive than other "non-essential" behaviors. This could mean more time is spent foraging for food rather than looking for mates and passing on genetic information, which lowers overall fitness. Stream habitats are by their nature fragmented, and many species are not able to disperse widely and become very adapted to certain temperature and flow regimes (Woodward et al. 2010). Often, environmental conditions change more swiftly than members of stream communities can adapt. Species that can perform more efficiently under temperature stress will, therefore, outcompete others. Gaining knowledge about the relative competitive performance of different native species in changing temperature conditions is important for future management of stream ecosystems.

The Eel River, the third largest river in California, is an ecologically important watershed and has been the intense focus of restoration and management efforts over the past years. It is a major source of energy flow in the region and is a large source of regional biodiversity (Ricketts 1999). Grazing snails are important first order consumers in stream ecosystems (Hawkins & Furnish 1987). There are two major genera of native snail, *Helisoma* and *Physella.* While these two genera of snail are both pulmonate snails and occur in relatively similar abundances in similar microhabitats under current Eel River conditions (personal observation, 2016), they exhibit slightly different life history strategies and feeding behaviors (Osenberg 1989, Chase et al. 2001). However, river temperatures are projected to warm with climate change. The effects on community structure and energy flow in stream systems caused by changes in relative herbivorous species abundance and composition is poorly understood (Byrnes et al. 2007). Differences in resource utilization, along with differences in palatability to different higher trophic organisms, could cause the competitive dominance of one genus over another to radically alter energy flow in stream communities (Hall et al. 2006). Understanding the competitive potential of native herbivores—in

changing conditions and temperature regimes is critical in order to implement preventative management plans and to understand the possible trophic effects of climate change in ecologically important areas.

Thermal performance curves are a convenient way of visualizing the effects of climate change and changing temperature regimes on performance traits of different taxonomic groups. Performance traits are defined as anything that can affect the relative fitness of an organism, such as respiration or metabolism (Schulte *et al.* 2011). Generally, a thermal performance curve is represented by an exponential rise in performance, until it reaches a peak known as the "thermal optimum" [T_{opt}] (Figure 1). Performance then abruptly drops off after T_{opt}, signaling a shutdown of physiological and biochemical processes due to stress. The "thermal optimum" usually represents high end of the thermal tolerance range of an organism. Thermal performance curves can be used to model responses of populations or species to climate change and compare the relative competitive potential of different groups of organisms.
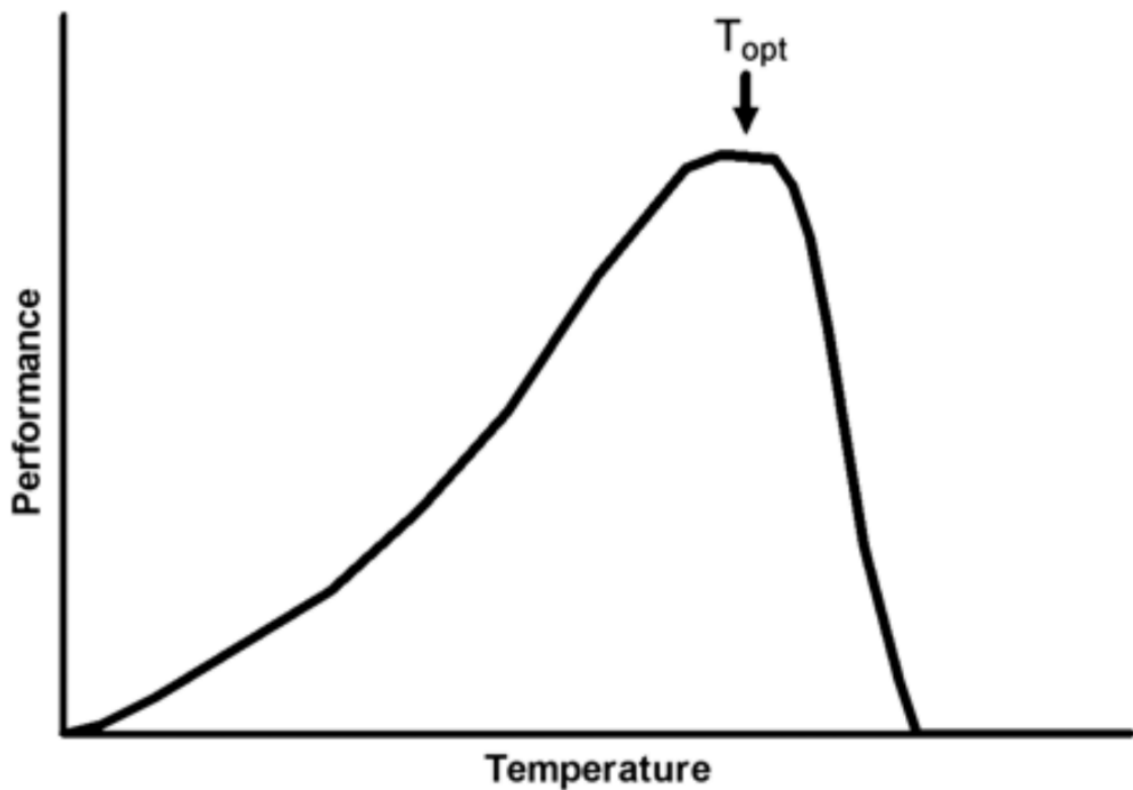

Figure 1. *Simple thermal performance curve.* An example of a thermal performance curve provided by Shulte *et al.* (2011). Note the relative exponential increase on the left side of the curve, and then the sharp drop off after the "thermal optimum" [T_{opt}].

With this study, I attempt to investigate the possible trophic effects of rising temperature in the Eel River by examining the competitive potential of the two native genera of snail, *Helisoma* and *Physella.* To do this, I ask these questions: What are the performance curves of the feeding rates of the three snail species in different temperatures? Does either of these snail genera perform more efficiently in stressful conditions than the others? What would this imply about community structure and trophic flow in the context of climate change? In this paper, I attempt to use physiological concepts to answer an ecological question, in hopes to create a framework to better predict the biotic effects of climate change on aquatic ecosystems.

METHODS

Study system and snail collection

The Eel River, the third largest river in California, is an ecologically important watershed that has been the intense focus of restoration and management efforts over the past years (Ricketts 1999, Higgins 2013). The Eel River flows from south to north. The river and its tributaries are entirely rain fed, so it is subject to extreme seasonal temperature variation (Higgins 2013). In late September 2016, I collected snails from two sites in the South Fork of the Eel River. One site was farther south and upstream from a site called Fox Creek in Mendocino County, CA (39°39'21.04"N, 123°38'0.19"W), and the other was near the mouth of the river at Fernbridge, Humboldt County, CA (40°36'53.30"N, 124°12'10.54"W) (Figure 1).

Both sites were areas of low river flow and less than half a meter deep. The river at Fernbridge had mostly a sandy bottom with some rocks and cobbles and a high amount of algae vegetation. At Fox Creek the substrate was mainly cobbles with only some algae growing on the bottom. At each site I noted location, weather, ambient air temperature, water temperature, and the location of snails in river as snails collected, along with species of snail. I collected and stored the snails in insulated containers and monitored during transport to lab, where they were then stored at room temperature in a mixture of water collected from river and spring water. Both genera of snail were left to acclimate for ten days before the experiment in order to in effect "erase" their thermal history and mitigate differences that may arise in between snails from different sites.
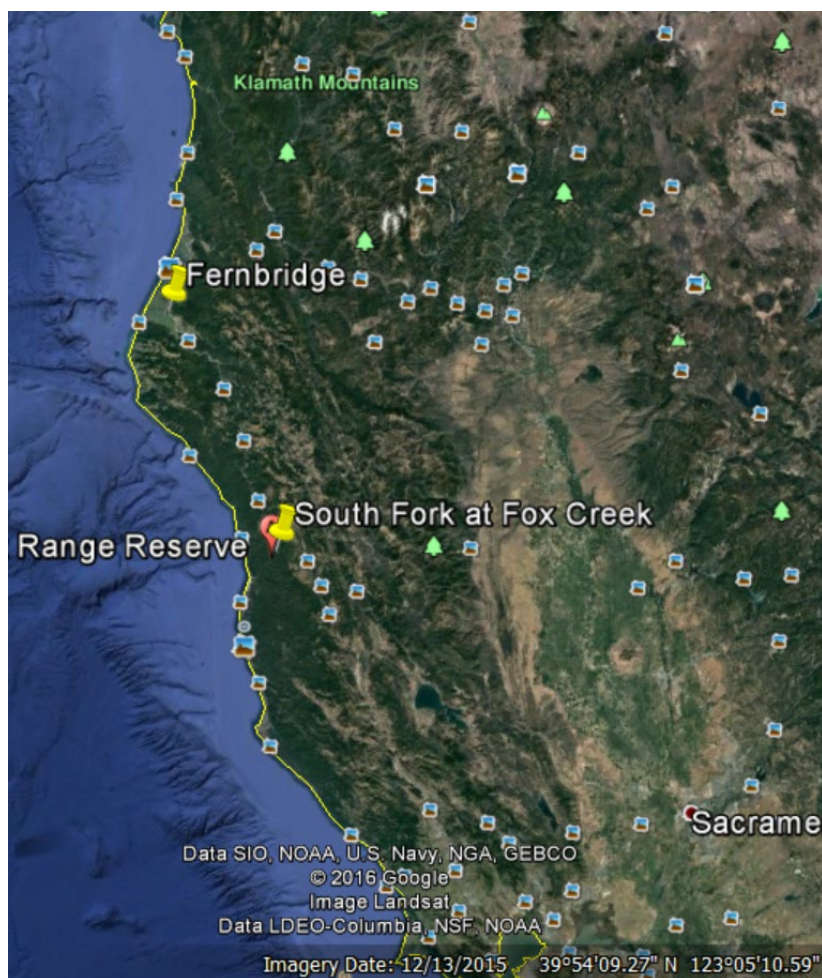
Figure 2. *Map of study sites in Northern California.* The Fox Creek site was located at 39°39'21.04"N, 123°38'0.19"W on the Angelo Range Reserve in Mendocino County, CA. The Fernbridge site was located at 40°36'53.30"N, 124°12'10.54"W near Fortuna, CA in Humboldt County.

Feeding Trials

I conducted a series of controlled feeding trials to determine the effects of temperature on feeding rate after the acclimation period, I gave each snail a unique number based on genus and collection site and kept them in a marked container so I could track the progress of each individual snail. The storage containers were discrete with no water flow, so no snails shared water while they were being stored. I conducted trials using seventy-three snails, 34 individuals of *Helisoma* and 39 individuals of *Physella*. For each feeding trial, I fed each snail one Omega One algae pellet, which was weighed dry the night before the trial. To examine the full effects of temperature on the physiology of these snails, I conducted the trials over a wide range of five temperatures, starting

with 14ºC, at the lowest temperature, then 18 ºC, 22ºC, 26 ºC, and ending with 30 ºC as my highest experimental temperature. I chose this temperature ramp due to average temperatures in the Eel ranging from 15-24ºC, and I wanted to cover the full range of seasonal temperature variation in the river along with projected higher temperatures that may come about due to climate change (Higgins 2013). The snails were starved for at least 24 hours before the four hour trials to make sure the snails ate during the time period. Feeding trials were conducted over the course of ten days, with trials commencing every other day and each snail receiving each temperature treatment.

Due to the amount of snails in my sample and the size of my water bath, I split the snails in into two equal groups, a morning (AM) and an afternoon (PM) group. I performed trials at different temperatures in different random orders in order to account for possible ramping effects due to physiological stress. Snails that were put through trials in the morning were always tested in the morning, and the same with those in the afternoon. I did not administer temperatures in a continuous ramp so I could account for the effects of stress at high temperatures, because individuals who were exposed to the high temperatures earlier may behave differently in later trials. Temperatures were administered using a water bath and a temperature controller. After setting the water bath to the appropriate temperature, I put each snail into a marked petri dish filled with appropriate temperature water, which were then stacked in beakers and placed in the water bath. Snails were left to acclimate for half an hour before given a pre-weighed pellet, and then left for four hours to eat. After four hours, I took out the snails and let them recover, and collected the remaining food. I then placed the food in the drying oven at 60ºC for 24 hours. Once the water in the bath was changed after the morning group trials were conducted, and then the second group was put into acclimation and the procedure repeated at a different temperature. After 24 hours and the food remnants were dried, they were weighed and their weights recorded. Once all of the trials were completed, the snails were weighed both in and out of shells so I could normalize the amount of food they ate by their biomass.

Data Analysis

In order to examine the effects of temperature on feeding rate, I constructed performance curves comparing the amount of food eaten to temperature for each snail based on the amount of food they ate in each trial, with the amount of food they ate normalized by body weight by dividing

the amount of food eaten by each snail by their biomass. This data was square root transformed in order to fit the normality requirements needed for parametric statistical tests. I used R to construct a single curve for each snail species using a LOESS method from the data provided by each individual snail at each temperature point. I then used a mixed effects model and a repeated measures ANOVA to compare the numerical differences in the amount of food eaten at each temperature point to compare the shapes of each curve for differences. The shape of each curve has implications for overall performance efficiency along with the raw numerical data. This sort of analysis allows me to see differences in non-linear regression data. I ran a separate analysis for each species, and also ran analyses to check for differences due to site origin and the time of day individual snails were fed.

RESULTS

Comparison of genus performance curves

Different ambient water temperatures resulted in different feeding rates. Generally, feeding rates increased significantly ($p<0.05$) as temperatures increased in both genera of snail. *Helisoma* overall ate less at lower temperatures and more at higher temperatures than *Physella*. *Helisoma's* performance curve exhibited a more linear trend than *Physella,* and did not experience a peak in performance within the experimental temperature range. After performing a LOESS analysis, the overall performance curves for each species were not significantly different from each other in a numerical context. The 95% confidence intervals of the data curves overlap significantly at almost every temperature point except 30ºC (Figure 3). *Physella* did exhibit significantly lower feeding rates than *Helisoma* at the highest experimental temperature. While the majority of the numerical averages of feeding rates at each temperature point did not differ significantly from each other, the shapes of the performance curves were different.

Physella

Over the experimental 14ᶜC – 30ºC temperature gradient, individuals of *Physella* ate between 0.2237 +/- 0.08503 grams of food per gram of biomass over four hours (at 14ºC) and 0.4007 +/-

0.1691 grams of food per gram of biomass over four hours (at 30ºC). From 14ºC to 22ºC, *Physella* feeding rates increased slightly from 0.2237 +/- 0.08503 g food/g biomass/4hrs at 14ºC, to 0.2317 +/- 0.1109 g food/g biomass/4hrs at 18ºC, to 0.2387 +/- 0.08274 g food/g biomass/4hr at 22ºC (Figure 4). However, these values did not differ significantly. From 22ºC to 26ºC, there was a significant ($p < 0.05$) uptick from 0.2387 +/- 0.08274 g food/g biomass/4hr to 0.3572 +/- 0.07794 g food/g biomass/4hr. After this, there was no significant increase in feeding rate between 26ºC and 30ºC. There is a peak in *Physella* feeding rate between 26ºC and 30ºC, which may signal that the thermal optimum for this genus may be in between these two temperature points (Figure 4).
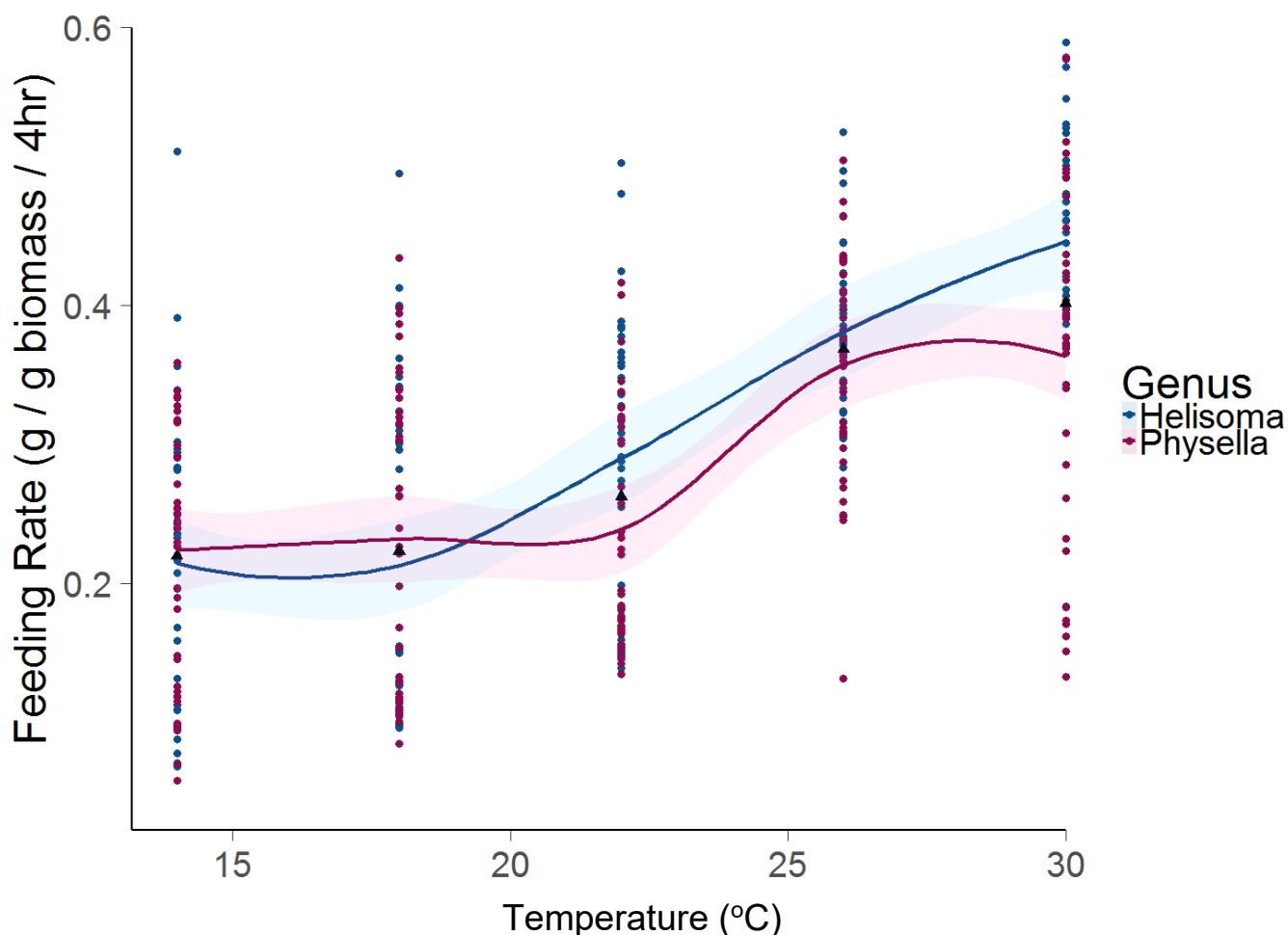

Figure 3. Feeding rate (g food/ g biomass/4hr) vs temperature of both *Physella* and *Helisoma* -- Performance curve of both genera of snail depicting temperature versus the amount of food eaten at each temperature point (normalized as grams of food eaten per gram of biomass). Note that while these two curves are not numerically different, they are different in shape.
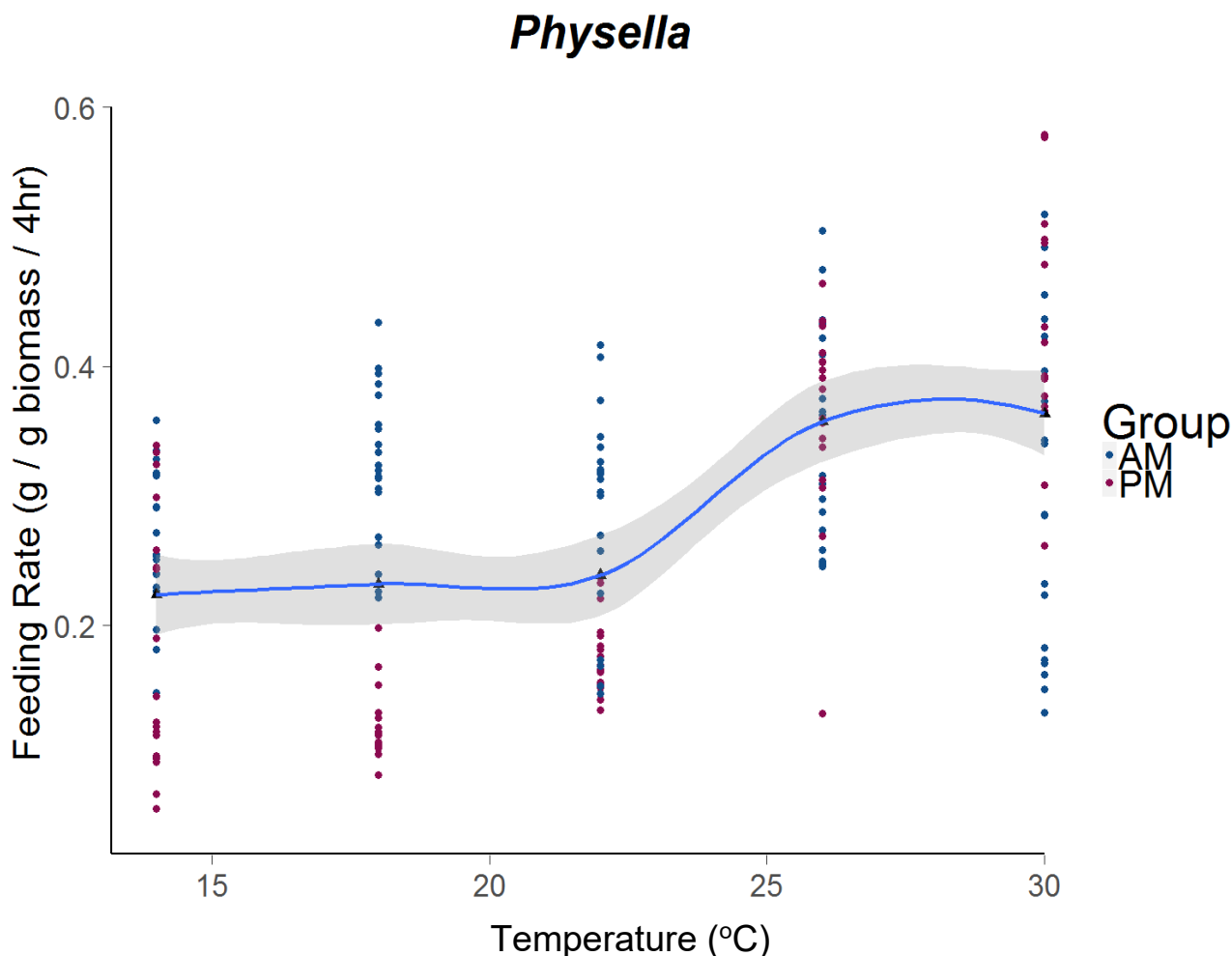
Physella

Figure 4. Feeding rate (g food/ g biomass/4hr) vs temperature (*Physella*) -- Performance curve of *Physella* depicting temperature versus the amount of food eaten at each temperature point (normalized as grams of food eaten per gram of biomass). *Physella* only ate significantly more food after the 22°C temperature point, after which it quickly peaked between 26°C and 30°C

Helisoma

Similar to *Physella, Helisoma* feeding rates responded significantly ($p < 0.001$) to changes in ambient water temperature. On average, snails ate between 0.2088 +/- 0.1113 grams of food per gram of biomass at 14°C and 0.4759 +/- 0.1207 grams of food per gram of biomass at 30°C. Overall, the shape of the performance curve for *Helisoma* is more linear than that of *Physella,* as the amount of food consumed per gram of biomass significantly increased at each increasing temperature point after 18°C (Figure 5). From 14°C to 18°C, feeding rates fluctuated but were relatively constant with no significant change, ranging from 0.2088 +/- 0.1113 g food/g biomass/4hrs at 14°C to 0.2070 +/- 0.1212 g food/g biomass/4hrs at 18°C. Rates then increased to

0.2897 +/- 0.1057 g food/g biomass/4hrs at 22°C, 0.3809 +/- 0.05953 g food/g biomass/4hrs at 26°C, and 0.4759 +/- 0.1207 g food/g biomass/4hrs at 30°C, with no signs of peaking within the experimental temperature range.

Intra-genus variation in performance

There was no significant difference in feeding rates in either genus of snail based on site origin (Figure 6). The 95% confidence intervals for each performance curve based on site origin overlap significantly with each other at every temperature point within both genera. However, both *Physella* and *Helisoma* exhibited significantly different (p<0.001) trends in feeding rates depending on the time of day in which they were fed.
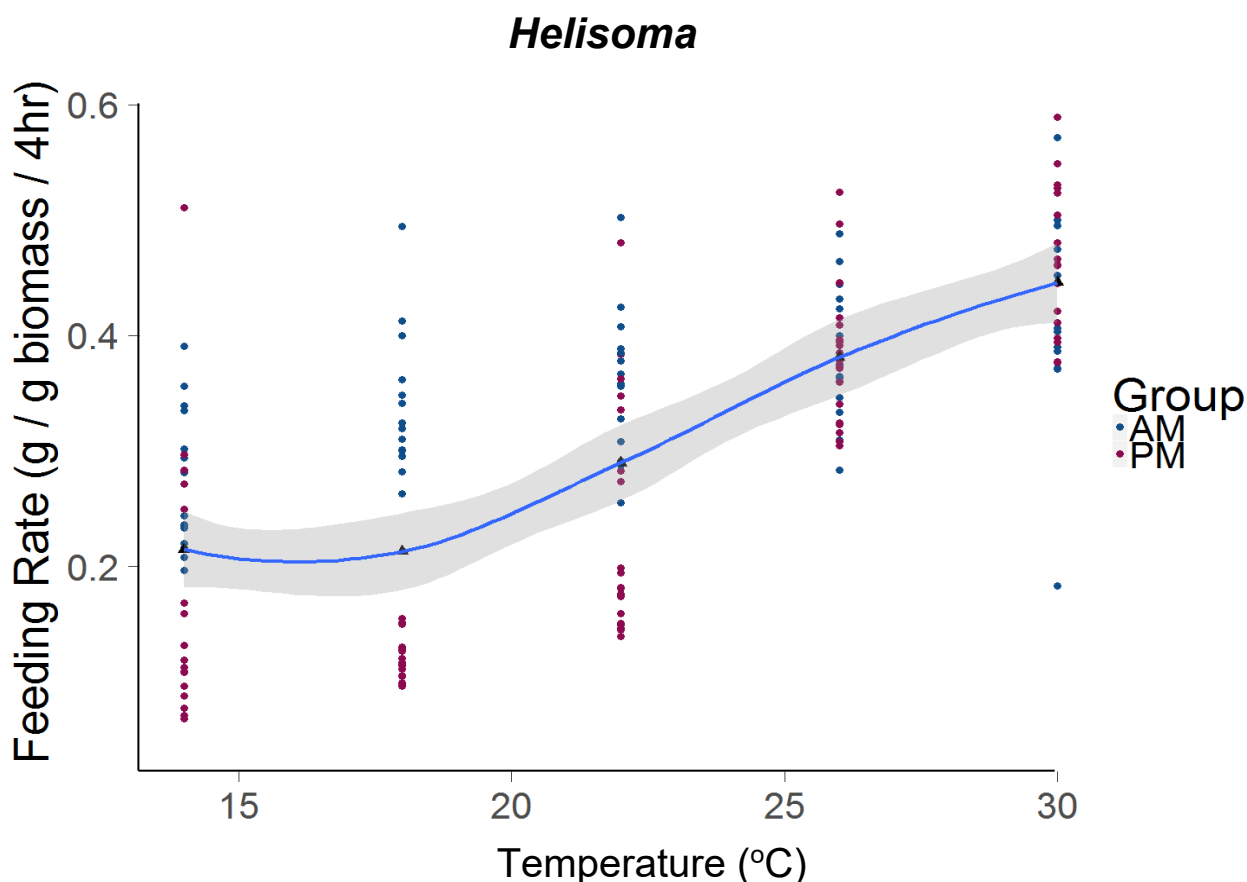

Figure 5. Feeding rate (g food/ g biomass/4hr) vs temperature (*Helisoma*) Performance curve of *Helisoma* depicting temperature versus the amount of food eaten at each temperature point (normalized as grams of food eaten per gram of biomass). *Helisoma* ate significantly more food at each tested temperature point after 18°C.
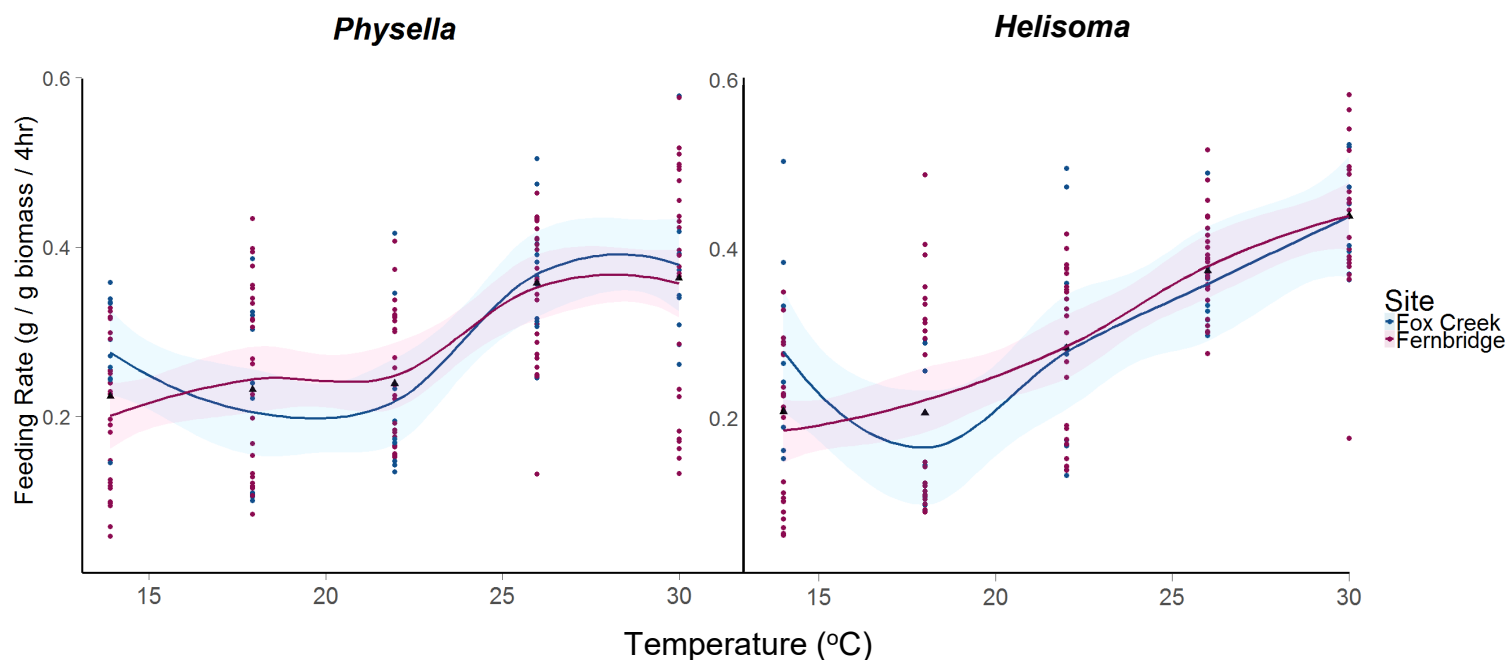
Figure 6. Feeding rate (g food/ g biomass/4hrs) vs temperature, separated by site origin – Performance did not differ significantly in both genera of snail based on collection site origin. There is a slight difference in feeding rates at 14ºC and 18ºC in *Helisoma* from Fox Creek compared to those from Fernbridge, but they do not differ significantly and could be explained by random variation.

Physella

In the *Physella* AM group, feeding rates tended to fluctuate without temperature exhibiting a significant effect at any temperature point relative to others (Figure 7). The AM group feeding rates ranged from 0.2593 +/- 0.05281 g food/g biomass/4hrs at 14ºC to 0.3431 +/- 0.1826 g food/g biomass/4hrs at 30ºC. High points in feeding rates in the AM occurred at 18ºC (0.3242+/- 0.05281 g food/g biomass/4hrs) and 26ºC (0.3506 +/- 0.07962 g food/g biomass/4hrs), while low points occurred at 14ºC, 22ºC (0.2910 +/- 0.06005 g food/g biomass/4hrs), and 30ºC. None of these values were significantly different from each other.

The PM group performance curve followed a more exponential trend, as feeding rates ranged from 0.1821 +/- 0.09741 g food/g biomass/4hrs at 14ºC to 0.4689 +/- 0.1245 g food/g biomass/4hrs at 30ºC. The shape of the PM curve reflects the composite curve in that feeding rates fluctuate but do not differ significantly from 14ºC, to 0.1238 +/- 0.02643 g food/g biomass/4hrs at 18ºC, to 0.1777 +/- 0.02902 g food/g biomass/4hrs at 22ºC. There is then a significant uptick to 0.3649 +- 0.07747 g food/g biomass/4hrs at 26ºC. The PM curve starts to peak as it approaches

30ºC, as there is no significant increase between feeding rates at 26ºC and 30ºC. *Physella* feeding rates differed significantly ($p < 0.05$) between morning and afternoon groups at 14ºC, 18ºC, and 22ºC, as they tended to eat more at these temperature points in the morning. Feeding rates did not significantly differ between feeding groups at 26ºC, but the AM group fed at significantly ($p < 0.001$) lower rates than the PM group at 30ºC.

Helisoma

In the *Helisoma* AM group, feeding rates tended to increase with temperature, but the effects of temperature were mitigated (Figure 8). The AM group feeding rates ranged from 0.2725 +/- 0.06088 g food/g biomass/4hrs at 14ºC to 0.4656 +/- 0.1596 g food/g biomass/4hrs at 30ºC.
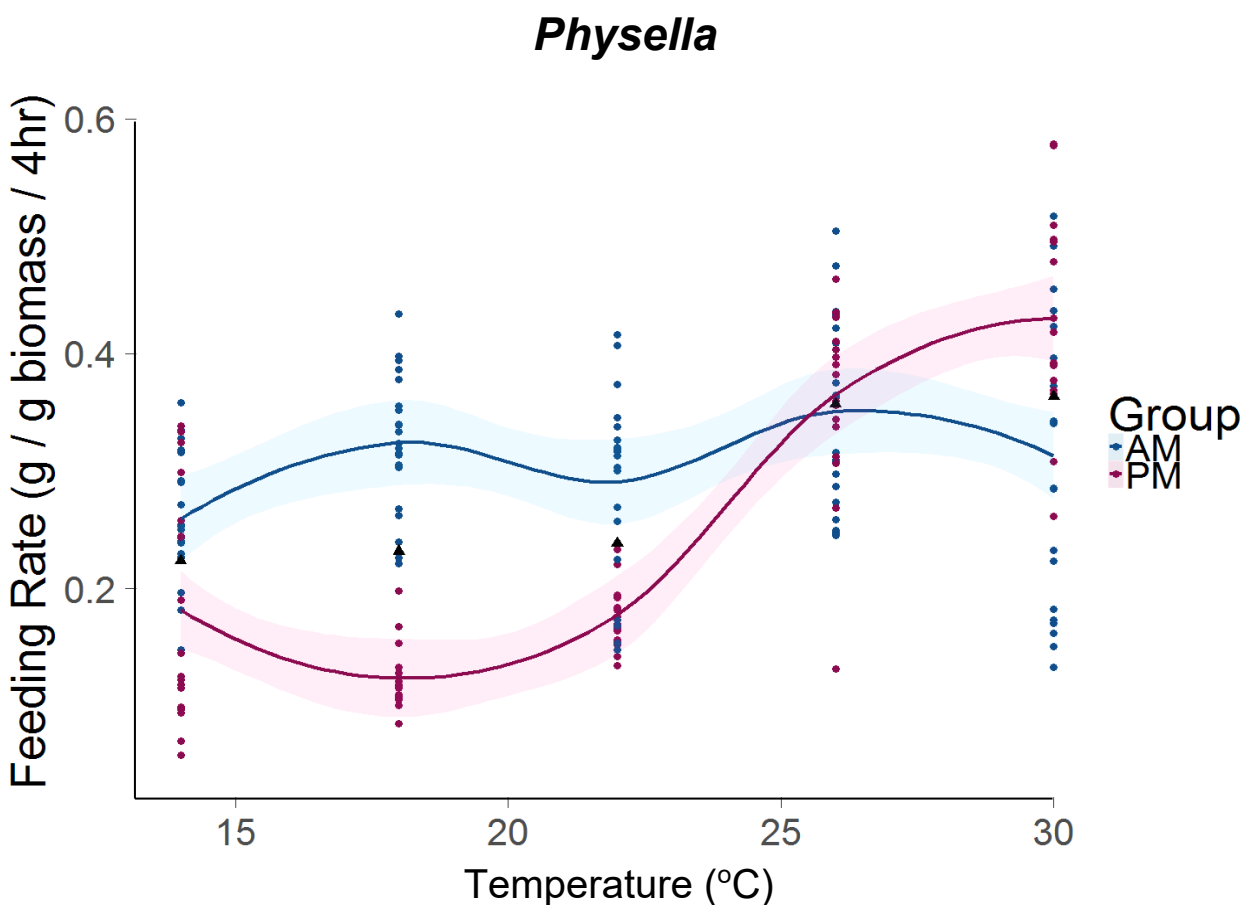

Figure 7. Feeding rate (g food/ g biomass/4hr) vs temperature, separated by feeding group (*Physella*) -- There is a clear separation of feeding behavior based on time of day *Physella* were fed. The AM group fluctuates, while the PM group responds linearly to temperature.

These were the only two temperature points at which feeding rates were significantly ($p < 0.001$) different. Like the composite curve, the *Helisoma* AM curve tended to increase linearly with temperature from 14°C to 0.3179 +/- 0.1031 g food/g biomass/4hrs at 18°C, to 0.3591 +/- 0.06171 g food/g biomass/4hrs at 22°C, to 0.3795 +/- 0.06098 g food/g biomass/4hrs at 26°, to 30°C with no sign of rates peaking throughout the experimental temperature range.

The PM group performance curve also followed a general linear/exponential trend, with feeding rates that ranged from 0.1585 +/- 0.1175 g food/g biomass/4hrs at 14°C to 0.4841 +/- 0.08311 g food/g biomass/4hrs at 30°C (Figure 8). The shape of the PM curve reflects the composite curve in that feeding rates fluctuate but do not differ significantly from the mean feeding rate at 14°C to 0.1194 +/- 0.01787 g food/g biomass/4hrs at 18°C. There is then a significant ($p < 0.05$) uptick to 0.2349 +/- 0.1018 g food/g biomass/4hrs at 22°C and at every temperature point
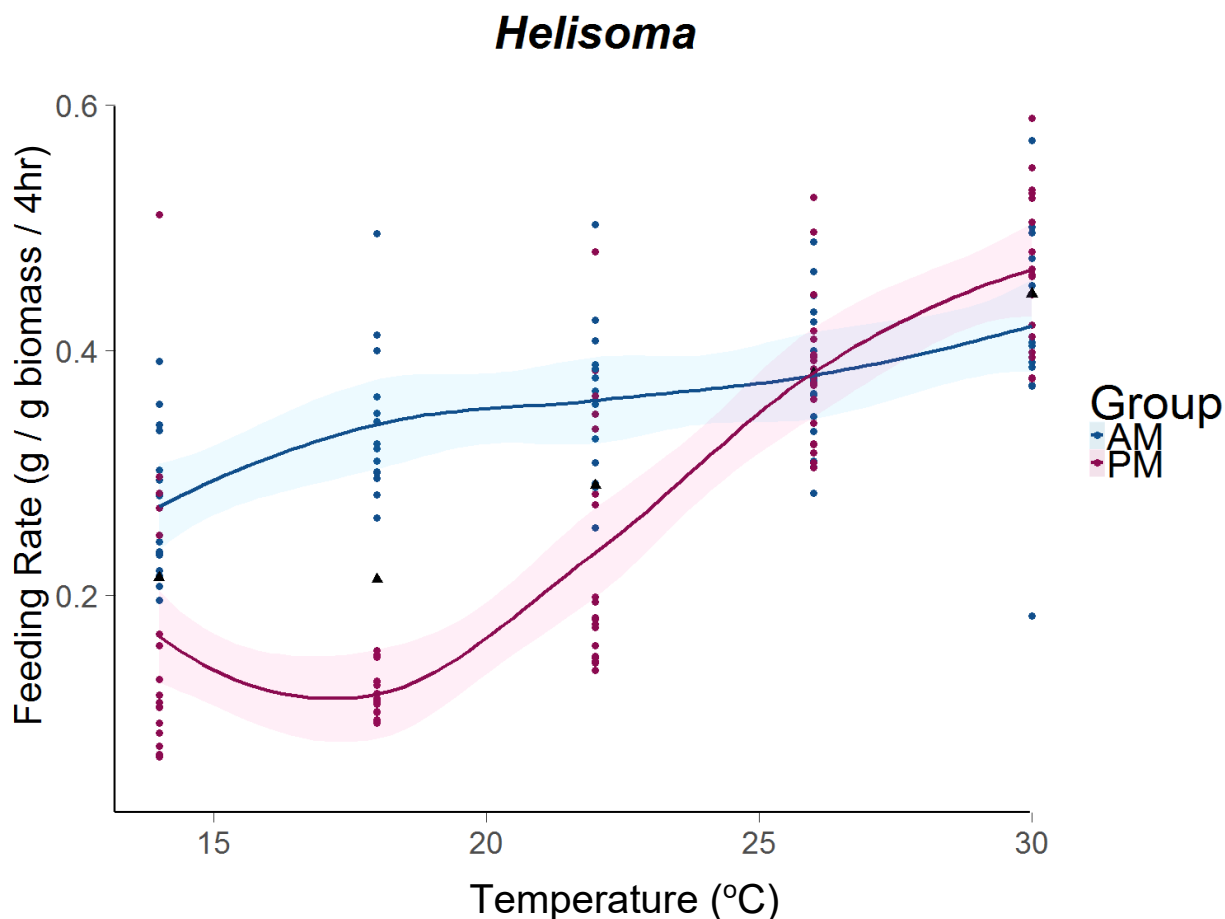

Figure 8. Feeding rate (g food/ g biomass/4hr) vs temperature, separated by feeding group (Helisoma) -- There is a clear separation of feeding behavior based on time of day *Helisoma* were fed. Both the AM and PM groups respond relatively linearly to temperature, but *Helisoma* in the AM eat more at lower temperatures than the PM group.

after that, to 0.3819 +/- 0.06002 g food/g biomass/4hrs at 26ºC and 0.4841 +/- 0.08311 g food/g biomass/4hrs at 30ºC. Like *Physella¸ Helisoma* feeding rates differed significantly ($p < 0.05$) between morning and afternoon groups at 14ºC, 18ºC, and 22ºC. Feeding rates did not significantly differ between groups at 26ºC or 30ºC.

DISCUSSION

Feeding rates changed in each species of snail as a result of changing temperatures. Overall, *Helisoma* responded more strongly to changing temperature, with feeding rate increasing exponentially in response to temperature at each point. Except for between 14 degrees Celsius and 18 degrees Celsius, *Helisoma* exhibited significantly higher feeding rates at each increasing temperature point, implying that its thermal optimum is above the experimental range. On the other hand, *Physella* reacted to increasing temperature less robustly, only experiencing a significant uptick in feeding rates between 22 degrees Celsius and 26 degrees Celsius before exhibiting a feeding rate peak in between 26 degrees Celsius and 30 degrees Celsius. Less obvious are the effects of diel foraging behavior, as both genus of snail exhibited significantly different performance curves based on whether they were fed in the morning or the afternoon. Overall, this data can be used to answer questions regarding the effects of temperature on metabolic performance in either of these species and their relative competitive potentials.

Diel foraging behavior

The time of day that each of the snail genera were fed did have a large difference in temperature response. Overall, snails of both species that were fed in the morning, particularly at lower temperatures, ate significantly more than snails fed in the afternoon at the same temperatures. *Helisoma* fed in the morning had a much weaker linear response to temperature than those fed in the afternoon, although they fed at significantly higher rates at high temperatures than at lower temperatures. *Physella*, however, ate a relatively constant amount in the morning regardless of temperature, while in the afternoon there was the expected exponential metabolic increase as an effect of temperature. This difference in response may be an effect of diel foraging

behavior, in which both *Physella* and *Helisoma* forage primarily in the morning while feeding in the afternoon is a direct response of metabolism to temperature.

  Physella feeding rates do not fluctuate significantly during the morning, so the effects of temperature may be highly reduced or disappear during optimal foraging time. *Helisoma*, on the other hand, had significant increases in feeding rate with temperature in both morning and afternoon groups. This may imply a higher temperature sensitivity in *Helisoma* versus *Physella*. Though like *Physella,* the effect of temperature on *Helisoma* feeding rate was reduced in the morning, as the slope of the AM curve is less steep than the PM curve. Reduced sensitivity to temperature in gastropods under certain conditions is not necessarily unheard of – some species of snail have been found to be able to regulate their resting metabolism if they are adapted to environments with regularly fluctuating temperature regimes (Marshall *et al.* 2011).

  Previous studies have also found that both *Physella* and *Helisoma* exhibit natural circadian rhythms, in which foraging tends to increase during the morning and early afternoon when peak photosynthesis rates occur (Lombardo et al. 2010, Kavaliers 2011). However, as a result of neurological impulses, both *Physella* and *Helisoma* will eat if they come into contact with what they perceive as food, which implies that they will forage in the afternoon given the chance (Kater 1974). So, both of these effects are important in discussing the overall effects temperature has on the feeding rates of both *Physella* and *Helisoma,.* Afternoon behavior in both genera also tend to reflect the behavior of the overall composite performance curve. So, pooled data by genus may still be a good metric by which to measure overall performance for these reasons.

  It also is worth noting that feeding rates were significantly lower for *Physella* at 30ºC in the morning than in the afternoon. While the feeding rates of *Helisoma* at this temperature tended to not be dependent on whether it was the AM or PM, there was a relatively large spread in the data for *Physella* at this temperature. The feeding rates of many individual *Physella* in the AM group dropped off at 30ºC, which may be signs of stress in these individuals (Sanford 1999, Peck *et al.* 2009). Because the temperature of Eel River water is completely dependent on ambient temperature, temperatures of 30ºC during the morning would be highly unusual (Higgins 2013). This perturbation may have disrupted *Physella*'s natural circadian rhythm. In any case, the response of the metabolism of each genus of snail to temperature may be different from one another, the effects of which may become more pronounced in the face of rising temperatures.

Inter-genus performance comparison

The performance curve of *Helisoma* suggests that this species has not yet hit peak performance and may outcompete *Physella* at higher temperatures. The LOESS curve constructed from the *Physella* feeding rate data, along with an ANOVA of a linear mixed effects model regarding the intra-species significance at each temperature point estimates a thermal optimum for this species between 26ºC and 30 ºC. Based on these performance curves, *Physella* may have somewhat of a competitive advantage at moderate temperatures, as it does not have a significant change in metabolic rate until after the twenty two degree threshold. *Helisoma* may need to forage more at these temperatures (14, 18, and 22ºC) and are thus more limited by food and resources (Peck *et al*. 2009).

Although feeding rates for *Physella* were significantly lower than *Helisoma* at the highest experimental temperature, this may not have been a sign of higher metabolic efficiency, but rather a stress response by *Physella* to the increased temperature. While *Physella* eats less overall at higher temperatures, this is implied to be a result of decreasing performance due to thermal stress rather than a measure of efficiency, because it occurs after the curve peak between 26 and 30ºC, *Physella*'s estimated thermal optimum. A major tenant of thermal biology is the concept that physiological performance tends to decrease sharply after the thermal optimum, as higher temperatures may cause a shutdown of important organismal and biochemical processes (Shulte 2011).

Phenotypic plasticity

Differences in collection site may have effects on the experimental feeding rates of these snails. *Physella* have been found to exhibit a high amount of phenotypic plasticity with regard to stream habitat (Crowl 1990). Phenotypic plasticity can result in different temperature responses within species, which cannot be erased by a ten day acclimation period since it has to do with the genetics of the home stream. Genetic dispersal in stream communities tends to be low, and pulmonate snails in particular can become highly adapted to the temperature regimes of their home streams (EPA 1973, Wood 1997, Woodward et al. 2010, Alexander & Wagoner 2016). After analysis, I found that there was no significant difference in feeding rate in response to temperature

that correlated with site origin in either species. Phenotypic plasticity may come into account in future climate change scenarios and the ability for these species to adjust with rising temperatures. Because of their high rate of adaptation, *Physella* in future scenarios may have some degree of higher thermal tolerance with an elevated potential to compete with *Helisoma* in future climate change scenarios.

Resource utilization

The effects of climate change on resource availability may be an important factor when assessing the competitive potential of these two genera of snail. *Physella* and *Helisoma* exhibit slightly different foraging behaviors and life history strategies (Osenberg 1989, Chase et al. 2001). Dominance of one genus of these snails over the other in overlapping ranges of thermal tolerance is usually determined by resource patchiness (Chase et al. 2001). *Physella* are highly mobile and tend to more effective grazers when algae is broadly distributed over a large area, while *Helisoma* are more efficient at foraging in highly patchy environments (Chase et al. 2001). The amount of algal patchiness in a river or stream system is usually controlled by disturbances in stream flow, such as flood or drought (Pringle *et al.* 1988, Matthaei 2003). In cases of drought, resources become less patchy and algal mats more continuous through the river (Lake 2000). Conversely, higher amounts of flow transports more sediment down the river and introduces a scouring effect, which can greatly affect how patchy algae becomes (Lake 2000).

The amount of precipitation to the Eel River under future climate change conditions could be the competitive tipping point for these two snail genera, especially if ambient water temperatures do not rise much farther above current average temperatures. *Physella* may be more metabolically efficient at moderate temperatures, though previous studies have shown that there tends to be little difference in metabolic or feeding efficiency among pulmonate snail taxa at current average ambient water temperatures (Barnese et al. 1990, Alexander & Wagoner 2016). Current climate forecasts for the area surrounding the Eel River predict increased winter precipitation in the future (Ghose 2015), which may impact the amount of patchiness of algal resources and favor feeding behaviors exhibited by *Helisoma.* And above the 26-30ºC threshold, *Helisoma* may prove to be the more advantageous competitor regardless of resource distribution as performance drops in *Physella* above these temperatures.

Limitations

Physella, and to some extent *Helisoma*, exhibit a high amount of phenotypic plasticity with regard to environmental factors in home streams. Although this study found no phenotypic variation with regard to thermal response as an effect of collection site, I would hesitate to apply these findings to these genera as a whole. Furthermore, my inability to identify these snails to the species level also complicates things, as there also may be some variation within genus due to species differences, and species composition of gastropod mollusks in the Eel River is poorly recorded. Collection of individuals from these two genera from more sites in the stream to compare to the individuals in this study, along with an analysis of the genetic makeup of the sampled populations, would be beneficial. Also, the overall pooled performance curves constructed for these two genera of snail only briefly take into account the complex response that time of day has on feeding rates in both species—this was an emergent result and was not originally factored into the initial experimental design. Further study into the diel foraging behavior of these two species should be taken into account when creating similar experiments on these two genera.

Further Directions

I originally incorporated a third species of snail, *Radix auricularia*, an exotic pulmonate snail that is invasive over a broad geographic range, into the design of this experiment. However, all of the collected *Radix* died during the acclimation period, and due to inclement weather I was unable to go back out into the field and collect more. Recreation of this experiment with the inclusion of *Radix* as a species of interest in order to examine the effects of climate change on its possible further invasion would be an important step in examining the effects of climate change in the Eel. Also, the relative effects of local salinity on the performance of these snails as well as *Radix* would be interesting to examine. *Radix* was only found near the mouth of the Eel River where it is slightly more estuarine. One current hypothesis regarding the mortality *Radix* in the lab is currently an insufficient amount of dissolved minerals in the acclimation water. Increasing temperatures, erosion, and sedimentation are all forecasted effects of climate change and can have significant effects on the mineral content of shallow streams like the Eel. Dissolved minerals are especially important for calcifying organisms.

Ecological Community Implications

Differences in community species composition of herbivores can affect the trophic energy flow of the river (Hall et al. 2006). Rivers are more or less linear systems, and changes in community composition upstream can affect areas downstream. Shifts in species dominance between *Physella* and *Helisoma* may significantly change herbivory rates, even if not directly competing with each other (Hall et al. 2006). Even if not direct competitors, differences in taxon abundance due to changes in ambient environmental conditions can affect energy flow through increased or decreased intraspecific competition and the differences in palatability of each species to higher order consumers (Byrnes et al. 2007). These two genera of snails are the only major constituents of the mollusk species in the Eel River and changes in one can have effects on the whole system. In effect, these results could be used to model what to expect in the face of rising temperatures in the Eel River.

The results of this study could form the foundation of a preliminary model of how these two genera respond to climate change. Both of these genera fairly wide-ranging throughout the northwestern United States and beyond, and are important low trophic level consumers. Managers need more high resolution trophic data, especially with regard to herbivory in aquatic systems, as altered energy flow is relatively understudied as a result of climate change. Streams are complex linear systems, and change in herbivory regimes in one area of the stream can have cascading effects regarding energy flow downstream (Palmer et al. 2008). Examining responses of lower order consumers in the face of climate change—the first step in introducing energy from primary productivity into the system—is a necessary factor in predicting future climate change scenarios.

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