Characterizing the effects of heat stress on the survival and behavior of two New England *Crepidula fornicata* populations

Abby Castle[1], Masha Osipovich[1], Eric Piros[1]
[1] *Boston University Marine Program, Boston, MA, 02215*

Abstract
Marine invertebrates make up the majority of ocean life, and perform functions that are necessary to the wellbeing of marine ecosystems. *Crepidula fornicata,* the Atlantic Slippersnail, is a model organism for the study of gastropods and other marine invertebrates. Widely distributed along the Atlantic coast and invasive to Europe, *C. fornicata* is capable of establishing itself in a wide variety of habitats. *Crepidula fornicata* are generally resistant to thermal stress, which has played no small role in their ability to invade non-native European waters. Anthropogenic climate change threatens to wipe out or displace less versatile organisms, opening new niches for *C. fornicata* to continue to spread. While *C. fornicata* are widely studied, less research has been done into variation in thermal resistance across different populations. Using *C.fornicata* collected from intertidal areas in Newport, RI and Beverly, MA, we analyzed the movement, feeding rates, and survival of two populations under increasing temperature and control conditions. We found that there was no significant difference in movement, feeding rates, or survivorship between the two populations. These results show that between two native *C.fornicata* populations, population background does not impact thermal resilience. This may indicate that it is possible for *C. fornicata* individuals to survive in locations different from their native area, as well as in locations warmer than usual.

Introduction

Climate change has had a great impact on marine ecosystems, and will continue to cause changes within the oceans. Within coastal ecosystems, the effects of climate change may occur quicker than in terrestrial ecosystems due to the combination of the proximity of the human populations and accelerating climate change (Cloern et al. 2016). Models have been run that reveal that under high emission scenarios, marine biomass could decrease by 2100, showing how important it is to mitigate the effects of anthropogenic climate change (Bryndum-Buchholz et al. 2018). Understanding how marine species react to climate change is crucial to determining how to go about creating management plans to protect the ecosystems. Some species, particularly marine invertebrates, are actually resilient to the effects of ocean warming, which could point to changing ocean biodiversity (Clark et al. 2016).

Marine invertebrates comprise over 92% of life in the ocean and perform crucial ecosystem functions such as water filtration, nutrient cycling, and habitat engineering (Chen, 2021). Larvae of these organisms can be sensitive to both ocean warming and acidification, in addition to other stressors such as pollution (O'Connor, 2007). On the other hand, some marine invertebrate species actually have quicker larval growth in warmer temperatures (Chen, 2021). The

intertidal nearshore ecosystems where many marine invertebrates live experience daily pH, salinity, and temperature fluctuations, making them a very stressful environment to survive due to receding tides causing quick changes to these variables (Diederich & Pechenik, 2013). Studies have shown that these fluctuations may become exacerbated under climate change (Helmuth et al. 2011, Wethey & Woodin, 2006). Determining how marine organisms will adapt to climate change is essential for understanding the future of marine ecosystems.

One of the most common marine invertebrates in the New England region is the mollusk *Crepidula fornicata. Crepidula fornicata* live in these intertidal areas, and a study by Bashevkin & Pechenik (2015) found that high temperatures caused young *C. fornicata* to grow quicker than at the cooler temperatures studied. Thus, warmer temperatures could allow *C. fornicata* to outcompete other species and become more prevalent as temperatures increase. As *C. fornicata* are invasive and highly fecund, being able to outcompete other species will allow them to spread across even more of the ocean than they already have (Pechenik et al. 2017). Thus, certain intertidal organisms such as *C. fornicata* are extremely robust and able to survive in a wide range of conditions. *Crepidula fornicata* has substantially expanded its range away from the northwest Atlantic and west coast of Europe as an invasive species (Hayer, et al, 2019). The species exhibits relative resilience to changes in pH, and this may explain its success in invading other environments (Viard 2006). Diederich & Pechenik (2013) determined that intertidal *C. fornicata* individuals could reach body temperatures of 42°C, and subtidal individuals survived in temperatures up to 37°C. This difference between intertidal and subtidal shows that even populations from different species could potentially react differently to changing environments. It is important to continue to study these species to understand how they will react to heat stress due to rising temperatures from climate change, as the results could show what may happen with other species, or could point to further expansion of the invasive *C. fornicata.*

Crepidula fornicata for this study were taken from locations in Newport, RI, and Beverly, MA to look into the differences between different populations. Although only a short physical distance apart, geographic features of the Gulf of Maine lead to differences between these two sites (Bigelow, 1933) Sea surface temperatures in the Gulf of Maine are influenced by the warm waters of the Gulf Stream which flow in from the south and the cold waters of the Labrador Current which enter from the north. Warm water from the Gulf Stream has a difficult time penetrating the north shores of Cape Cod. Because of this, temperatures on the south shore are not only significantly warmer, but also more seasonally variable (Bigelow, 1933). Populations from this south shore are expected to be more resilient to heat stress than their northern neighbors. What's more, anthropogenic climate change has shifted the Gulf Stream over the last few decades. The Gulf Stream is moving northward, rapidly heating all waters in the Gulf of Maine. However, the greatest rates of warming have been taking place in the

Scotian shelf region, near the northern end of the Gulf of Maine (Seidov, 2021). These warm water currents are expected to infiltrate Massachusetts Bay. A better understanding of differences in resilience between latitudinally different populations of *C. fornicata* could prove a useful tool in determining the impact of continued Gulf Stream migration.

In this study, *C. fornicata* from two different locations in New England were studied to test differences in response to heat stress between populations. We hypothesize that there will be a difference in survival and feeding and movement behavior between the heat stressed and the control tanks, as well as a difference in these metrics between the Beverly and Newport populations under heat stress. We also hypothesize, based on what we know about the currents in the Gulf of Maine, that the *C. fornicata* from the Newport population will have higher survival rates. Additionally, we hypothesize that as temperature increases, there will be increased movement of the snails before eventually declining as the temperature reaches the most extreme being tested, which is 33℃.

Materials and Methods

Collection and setup

Crepidula fornicata were collected from Beverly, MA (42.546715, -70.863762) and Newport, RI (41.574386, -71.287369) on October 9th, 2022, and October 11th, 2022, respectively (Figure 1). They were brought to the Boston University Marine Program lab in Boston, MA where they were maintained at 22°C for 12 days until the experiment began. Stacks of *C. fornicata* shells were carefully separated by hand, and each individual *C. fornicata* was placed on its own petri dish and its shell was dried with a washcloth for marking. The length and width of each *C. fornicata* was measured with a digital caliper. Organisms smaller than 5mm were categorized as juveniles and were not used for the experiment. *Crepidula fornicata* were then marked with nail polish to differentiate which population the snail came from. Each marked individual was then photographed using a LimoStudio tabletop light box and an iPhone 12 mini camera. *Crepidula fornicata* were randomly assigned into either a control or heat treatment, for a total of 21 individuals from each population in each condition. Each experiment consisted of three tanks, and each tank held 7 Beverly and 7 Newport individuals. Only single *Crepidula* were used, including individuals attached to an empty shell or rock. Any snails that were attached to other living snails or multiples on one rock were removed from the experiment. After sorting, petri dishes were weighed down by flat glass marbles to prevent the dishes from flipping over in their tanks.

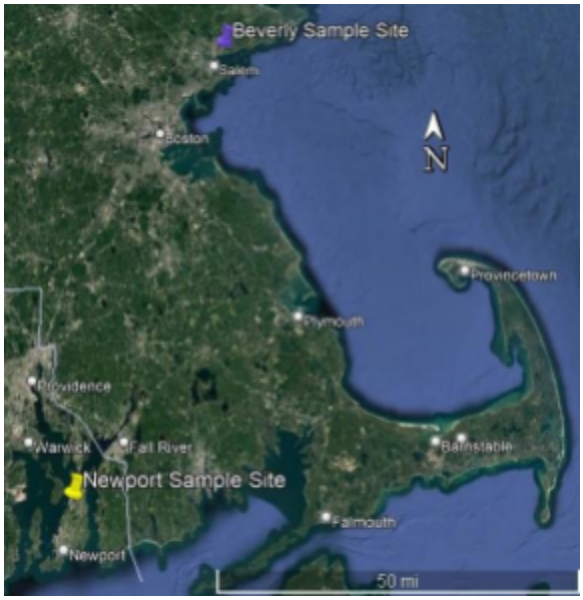

Figure 1. Map of *Crepidula fornicata* collection sites. Location of C.fornicata population collection sites on a satellite image map. The Beverly, MA population was located at 42.546715, -70.863762 and the Newport, RI population was located at 41.574386, -71.287369.

Tank maintenance and feeding

Water temperatures and salinities in each experimental tank were measured three times daily, at approximately 10 AM, noon, and 4 PM. In the first two days of the experiment the quality was only measured twice a day, with the noontime measurements being added on day 3 of the experiment. Temperatures were measured using a standard glass thermometer. The thermometer was left in each tank to acclimate for one minute before the reading was recorded. Salinity was measured for each tank using a Bulk Reef Supply refractometer, which was wiped off between each measurement. The salinity was maintained at approximately 33-34 ppt (Figure 2).

Crepidula were fed daily except for the final experimental day when individual feeding trials were performed (day 14). All the individuals from each tank were moved into different feeding tanks with just enough saltwater to cover the individuals fully. Each tank was kept separated to prevent any mix up, and all three tanks of one treatment were fed at the same time. 1 mL of Shellfish Diet 1800 was put into 200 mL of water in a flask and mixed, before being added to the three tanks with snails. *C.fornicata* were left to feed for 30 minutes, before being returned to their respective tanks. Each feeding container was rinsed with RO DI water, and the feeding was repeated for the other treatment.

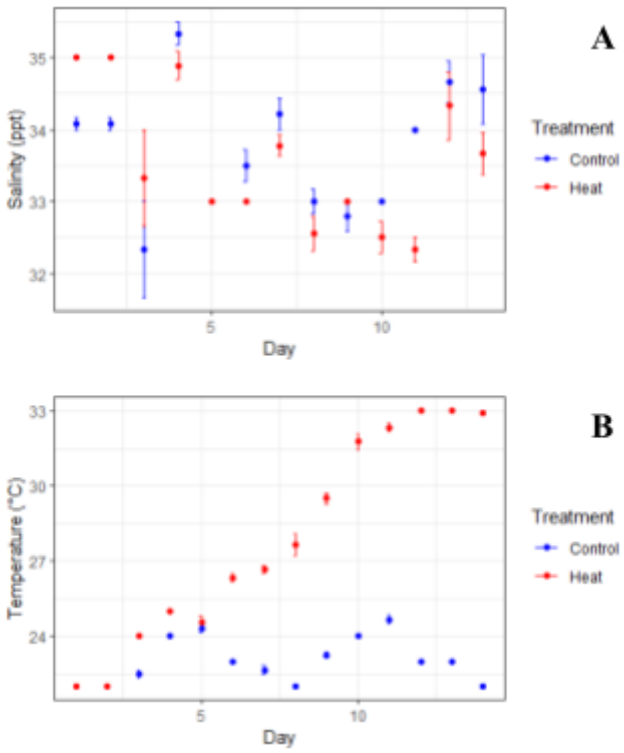

Figure 2. Water quality measurements. A. Salinity levels were kept at approximately 33-34 ppt, though an error at the beginning of the experiment caused levels to drop a bit.

B. Water temperatures over the experimental period. The control was kept at 22°C, whereas the heat experiment was ramped up to 33°C and then plateaued around day 12. The experimental temperatures had spikes around days 4-5 and 11 due to increased room temperatures in the tank room.

Heat challenge experimental design

A total combined number of 42 *C. fornicata* individuals from the Beverly and Newport populations were divided into two separate temperature treatments, with each treatment divided into three tanks (Figure 3). Seven *C. fornicata* from each population were randomly assigned to each tank. Both systems started at a temperature of 22 °C, which was the target temperature of the control temperature treatment group. In the heat treatment system, the temperature was ramped up by 1°C daily up to 33°C by day 12 with a water heater, which was maintained through the end of the experimental period (Figure 2). A 1℃ margin of error in the accuracy of the heater was expected, usually 1℃ colder than the target temperature. If measured temperatures were found to be beneath the target temperature the following morning, the heater was adjusted throughout the day in order to reach the intended temperatures, before having the target temperature increased again during the evening. The control treatment system was not heated but did not have a water chiller. Due to issues with building heating and cooling systems as a result of unseasonably warm outside temperatures, the temperature of the room where the tanks were housed had variable fluctuation. This impacted the maintenance of the water temperature for both experimental groups, more so the control due to the room being several degrees warmer than 22°C at some points.

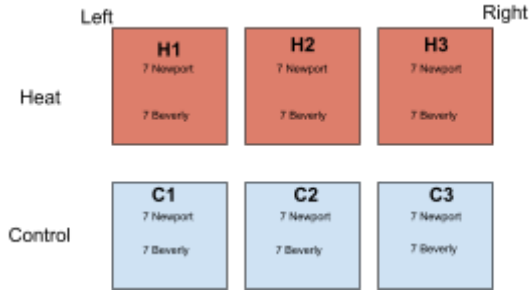

Figure 3. Experimental Setup. 42 *Crepidula fornicata* from Beverly, MA, and 42 *Crepidula fornicata* from Newport, RI were evenly distributed across the 6 tanks, as shown in the figure. All surviving heat experiment snails were used for feeding trials (6 from Beverly and 6 from Newport), as well as 12 of the 22 surviving control snails (6 from Beverly and 6 from Newport).

Survival and behavior

Survivorship was recorded twice daily, at approximately 10 AM and 4 PM. Each individual was checked to see if it was alive by first testing if the individual was attached to either the petri dish or to their empty shell or rock. If the snail was not attached, they were gently poked to check for movement. If it was determined that the *C. fornicata* individual was dead, it was recorded and removed from the system. Movement behavior was also measured twice daily, at 10 AM and 4 PM, and was classified in a binary construct of whether an individual moved from their petri dish or not. Any snails that moved were then moved back to their petri dish.

Feeding Trials

Individual feeding trials using *Dunaliella salina* algal cultures were performed on *C. fornicata* from control and heat challenge conditions on the final day (day 14) of the experiment. For each temperature treatment, six individuals from each population and treatment were selected for the feeding trial. These 24 individuals were placed into 50mL glass jars in their respective temperature conditions with 25 mL of seawater and 25 mL of algal culture. 1 mL aliquots were taken from each jar prior to adding organisms and placed into 1.5 mL tubes. *Crepidula fornicata* were allowed to feed for 30 minutes and a final 1mL sample from each solution was taken at the end of the feeding period. Algal cells from each sample were counted on a hemocytometer using a standard light microscope at 10x magnification. 1 uL of each sample was placed on the hemocytometer and the number of cells in the center grid (1 mm^2) was counted. These counts were conducted three times for each sample to quantify the average concentration of cells in each solution. Algal concentrations before and after the feeding period were calculated by multiplying the average count by 1000 to get the total number of cells in 1mL and then multiplying by 25 to get the number of cells in the 50 mL jar solution. In order to calculate feeding rates, the final concentration was subtracted from the initial concentration, and the resulting value was divided by the initial concentration.

Statistical analysis

All statistical analysis and visualization was done in Rstudio using R version 4.2.2. The difference between the survival proportions of the Beverly and Newport populations under heat stress treatment was calculated with a two-tailed hypothesis Z-score calculation. A two sample t-test was used to compare movement between the heat-stressed Beverly and Newport populations. For the individual feeding trials we used a two-way ANOVA to determine if there was any significance between the independent variables and the dependent variable, the feeding rate. All plots were created using RStudio.

Results

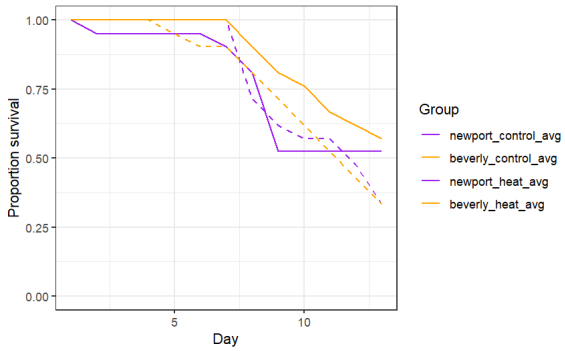

Figure 4. Mortality of Crepidula across treatment groups and populations over the experimental period. Daily proportion of surviving individuals by population and temperature treatment. Both heat treatment groups had the same final proportion of surviving individuals.

There was mortality observed across the experimental period in both *Crepidula* populations and in both heat and control treatments (Figure 4). In the control treatment, 52% of the Newport population individuals and 57% of the Beverly

population individuals survived. In the heat treatment, the same proportion of individuals (29%) from each population survived. Between the two temperature groups alone, 23 out of 42 individuals in the control system survived while only 12 out of 42 individuals in the heat system survived to the end of the experiment. These treatment population proportions were compared using a standard two-tailed hypothesis Z score calculation to see if the null hypothesis - no difference between these two proportions - could be rejected. The value of z was determined to be 2.43 and the p value as 0.015. The result is significant at $p < 0.05$. This means that there was a significant difference between the percent survival of control and heat treatment groups. There was no significant difference in the proportion of survival between the Newport and Beverly control populations within each temperature condition. However, the Newport control temperature individuals experienced mortality earlier than other groups.

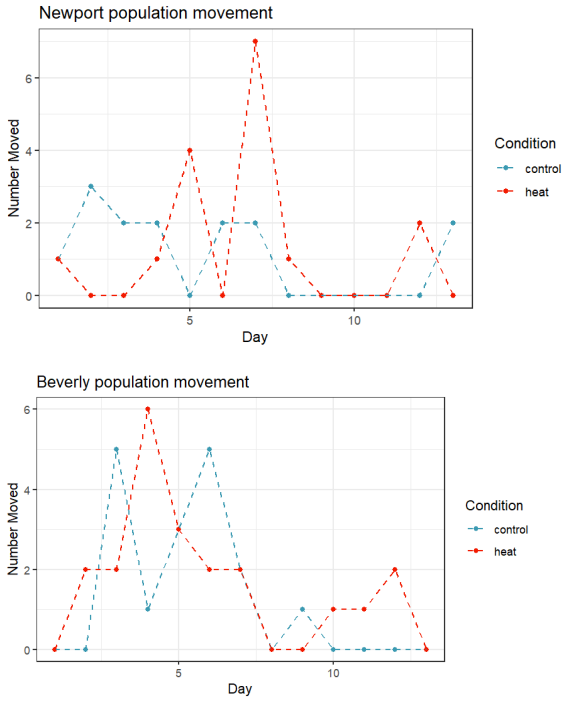

Figure 5. *Crepidula* movement behavior over the experimental period. Daily number of moved Crepidula individuals per population and experimental treatment.

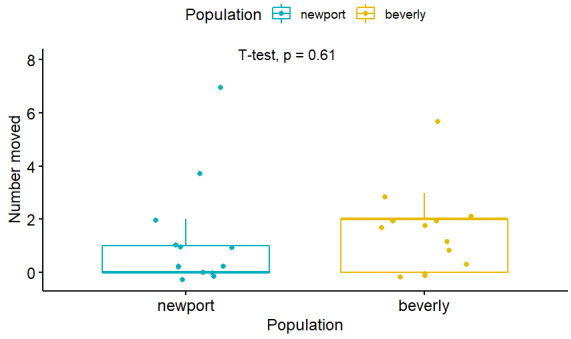

Figure 6. Amount of *Crepidula* moved under heat stress in two populations over the experimental period. There was no significant difference between average movement over the experimental period between the Beverly and Newport populations under heat stress(T test, $p > 0.05$).

There were differences in the amount of daily individual movement between treatment groups and populations. The Newport population individuals in the heat treatment had the highest amount of movement out of any group in the experimental period. Within each population, more individuals in the heat stress group moved than in the control group. Over the experimental period, in the Newport population, there were a total of 16 instances of movement in heat treatment individuals and 13 total instances in the control treatment, while in the Beverly population, there were 21 instances of movement in the heat treatment and 12 in the control (Figure 5). The amount of daily movement from each population was observed to be variable. There was no significant difference ($p = 0.61$) in average total movement over the experimental period between the Beverly and Newport individuals in the heat stress condition (Figure 6).

Location and treatment condition does not affect Crepidula fornicata feeding rates

A two-way ANOVA test determined that there was no significant difference between feeding rates and location ($p = 0.796$) as well as feeding rates and treatment conditions ($p = 0.721$). Beverly heat and control snails, as well as Newport control had a wider range of feeding rates (Figure 7).

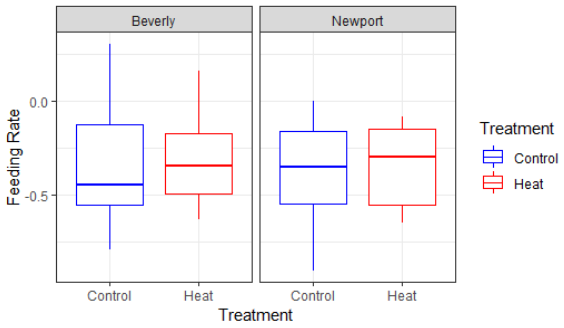

Figure 7. Feeding rates of *Crepidula fornicata.* Feeding rates separated by location and treatment. Neither location (P=0.721) nor treatment (P=0.796) were statistically significant, and snails did not eat more or less depending on where they were from or what treatment they were in.

Discussion

The goal of this study was to see whether two geographically different populations of *C. fornicata* would respond differently to thermal stress. *Crepidula fornicata* are incredibly resistant to thermal stress in both subtidal and intertidal populations (Diderich & Pechenik, 2013), at nearly all stages of life (Bashkevin & Pechenik, 2015), at increased CO2 levels (Noisette et al, 2015), and even after being acclimated to winter temperatures (Pechenik et al, 2020). *Crepidula* species have been found to display changes in behavior based on temperature, however, with *C. fornicata* displaying much greater propensity for movement than the similar *C. plana* (Alter et al, 2020). This encouraged an investigation into the effects of geography on *C. fornicata* behavior. However, little difference was found between the two populations.

No significance in differences in mortality between populations

In the heated tanks, both populations of snails had 6 survivors at the end of the experimental period. There was a significant difference between mortality between the control and heat treatment. It's possible that a difference would emerge at greater thermal stress levels, as *C. fornicata* has been found to withstand temperatures as high as 37°C in previous studies (Diderich & Pechenik, 2013, Pechenik et al*.,* 2020). It is also possible that a longer experimental period would have given different results, as some snails in the experimental tank displayed signs of being close to death when the final tally was taken, with one individual even dying in the middle of the final feeding trial. Further survival analysis, such as a Cox hazards proportion model, can be performed to more accurately determine the amount of influence population or temperature has on mortality.

Mortality was high in both tanks, over 70% for the heat treatment and nearly 50% for the control. Rapid changes in temperature may have worsened the effects, caused by both the imprecision of heating instruments and ambient factors outside of our control. A malfunction in the heating system of the laboratory building caused greatly increased temperatures during day 4 and 5 of the experiment, and on day 8 a new heater had to be added to the tank because the previous one was failing to meet target temperatures. The new heater rapidly increased the temperature of the tank 2-3°C in the span of a few hours whereas otherwise heating had only occurred at a rate of 1°C per day. Temperature shock may have also occurred during daily feedings as snails were transferred into temporary feeding tanks not acclimated to the conditions of the experiment.

Other potential stressors include a dip in salinity that occurred on day 3 due to an error in replacing the water reserves of the tank and stress caused by physical contact with team members. Individuals were physically removed from adjoined surfaces in order to be relocated to their petri dishes during the daily checks, as well as sharing direct contact with researchers during daily feedings as they were transferred to temporary feeding tanks and back. Snails were also briefly kept out of water during measurement and marking at the initial stages of the experiment, though the risk of desiccation was low. Damage to the shell was also possible due to the physical strain caused by the calipers used to measure specimen length.

No significance in movement across treatment or population

There were no significant differences in observed movement across populations within the heat treatment group, though both treatment groups saw less movement as time went on. It is possible that as individuals spent more time within the tank they became more acclimated to the surfaces of their petri dishes. Some individuals became attached to the glass weights used to hold down the petri dishes within the tanks instead of the dish. If individuals moved, they were picked up and moved back to their respective dish at the start of each day. This removal, often forceful, may have also impacted behavior. Movement was much lower than found in a

similar experiment from two years prior (Alter *et al*., 2020), never surpassing more than 7 individuals on any given day. Most days contained 2 or less movers.

In one example an individual relocated to a petri dish already inhabited by another, but we were unable to determine who was the original inhabitant and who had moved. In the event of a "swap" between two *Crepidula*, we would have no way of knowing which had moved, and so it's possible that movement was underestimated. Movement within petri dishes was also not recorded. One way to potentially measure individual movement in the future would be by recording an individual in a dish for a 24 hour period and use 3D tracking to measure movement in video footage to compare patterns in movement between populations and treatment groups.

No significance in differences in feeding

Feeding rates were similar across both treatment and population. Median feeding rates were slightly higher among *C. fornicata* from Beverly and among *C. fornicata* in the heat treatment, but were not determined to be statistically significant. This experiment did not replicate the results from Alter *et al*.(2020) which observed that *Crepidula* had higher rates of feeding at high temperatures, however their experimental ranges were between a control of 18°C and an experimental treatment of 26.6°C, which could indicate that temperatures effect on feeding rate plateaus somewhere in between 18°C and our control of 22°C. Pechenik *et al.* (2020) found that snails in heat stress are able to recover from lower feeding rates, showing their resilience to changing environments. Pechenik et al. (2015) also found that when the snails are allowed to attach to substrate, they have higher feeding rates. All snails in our feeding trial were placed rightside up in the jars, and the majority then attached, or were already attached to a rock or other empty shell. While no snails were placed upside down to determine if this was a factor that affected feeding rates, it could be a potential reasoning for no variation in feeding rates.

There were numerous difficulties during the feeding trial. The malfunction in the laboratory's heating system may have damaged the algal specimen being grown for the feeding trial, as initial concentrations were far lower than was anticipated. The feeding trial was only 30 minutes long due to the low initial concentrations, which may have also impacted the feeding rates of snails. With higher concentrations, the cell counts could have been done at 30, 40, and 60 minutes, which may have had different results and feeding rates. Since cells were scarce, they were difficult to count, increasing the chance of human error.

Conclusions & future directions of interest

Measurements between groups were subtle and statistically insignificant. This is not unsurprising, given the small difference in geographic location and previously observed thermal resilience of *Crepidula fornicata.* While the northern and southern shores of cape cod do experience sizable differences in thermal conditions, this variation is still much smaller than seasonal and intertidal variations in conditions that *C. fornicata* are acclimated to. 33°C is below the lethal range of conditions found in

previous studies of *C. fornicata* (Diderik & Pechenik, 2013, Pechenik et al., 2020), and the timeframe of the study is short at only two weeks. While thermoresistance is likely similar across most *Crepidula* in the Gulf of Maine, *C. fornicata* is an incredibly prolific species. Quantifying the expression of genes related to thermotolerance between the Newport and Beverly populations may reveal if these populations respond to heat stress differently on a cellular level. Differences in population response to heat stress may be more pronounced in populations across greater geographic distance, such as invasive *C. fornicata* populations in Europe and the Pacific.

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