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The Impact of Tidal Elevation and Climate Change on the Growth and Performance of Balanus glandula

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The Impact of Anthropogenic Climate Change and Tidal Elevation on the Growth and Performance of *Balanus glandula*

A Thesis Presented by

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Abstract

Tidal elevation affects the survival, growth, and performance of intertidal organisms because it regulates their exposure to heat, waves, food availability, and a variety of other abiotic factors. While previous research has explored the relationship between temperature and the performance of the barnacle *Balanus glandula*, there are unanswered questions about how tidal elevation affects *B. glandula* performance and growth. I compared the growth of *B. glandula* at three tidal elevations in Friday Harbor, Washington, and estimated the metabolic cost of emersion at each tidal elevation using a cost equation gained from thermal performance curves and average daily maximum temperatures. I also modeled climate change by adding 2°C to the average daily maximum temperatures at each shore height. I hypothesized that growth would decrease as tidal elevation increased as a result of increased heat stress. I also hypothesized that performance would decrease as tidal elevation increased, and that an increase in average daily maximum temperatures would most greatly affect high tidal elevations. I found that low tidal elevations had the highest growth. Energetic cost and aerial temperature were the highest at mid and high tidal elevations. Under the 2°C increase in temperature, energetic cost decreased with tidal elevation. These results are consistent with previous findings showing that *B. glandula a*t higher tidal elevations had higher energetic demand. Further research is necessary to determine how growth and performance are correlated in *B. glandula* and how other factors such as food availability, optimal size, and reproduction affect their success.

Introduction

As global anthropogenic climate change progresses, heightened climate patterns are expected to threaten organisms in a variety of habitats and locations. In coastal areas, increased aquatic temperatures and aerial temperatures as well as high storm frequency, wind velocity, and a variety of other abiotic factors are expected to affect and threaten intertidal organisms (Helmuth et. al, 2002). The intertidal zone, or the area of the shore between low and high tide, is defined by changing conditions, as tidal variation causes heat stress, desiccation, and high wave intensity. These changing conditions provide both benefits and challenges for intertidal organisms (Helmuth et. al, 2002). Within the intertidal zone, location on the shore greatly determines the abiotic factors that an organism will experience. In many intertidal organisms, vertical zonation, or the distribution of an organism within the intertidal zone, is determined by their tolerance to the aforementioned abiotic factors (Connell, 1970). The body temperatures of intertidal organisms can dramatically increase during emersion, and stress responses are often increased (Helmuth et. al, 2002).

Thermal performance curves measure the relationship between temperature and fitness by analyzing a variety of factors including aerial respiration. They show how ectotherms perform at ranging temperatures, and include a minimum critical temperature, an optimal temperature, and a critical maximum temperature (Miller, 2012). Anthropogenic climate change is predicted to have an increasing impact on intertidal organisms as both aquatic and aerial temperatures rise, and weather patterns become more severe (Helmuth et. al, 2002). Thermal performance curves will change based on an organism's tolerance, as well as how close they are already living to their physical limit.

While mobile species can move in response to abiotic and biotic factors, sessile organisms such as the barnacle *Balanus glandula* are forced to experience stressors that come with the tides, sun, and the presence of other organisms. *B. glandula* is a high-shore intertidal barnacle that ranges from Baja, California to the Aleutian Islands of Alaska and is found on rocks, hard-shelled organisms, piers, and other hard surfaces in middle to high intertidal zones of bays (Image 1). While they can live up to ten years, *B. glandula* are susceptible to predation by snails and other gastropods, and as filter feeders, they prey on phytoplankton (Connell, 1970).

Image 1. *Balanus glandula.* Photo: Dave Cowles, 2005

Previous research on *B. glandula* growth shows that barnacles have an energetic optimal size (Sebens, 2002). Additionally, Gilman and Rognstad (2018) analyzed the effect of food supply on *B. glandula* growth and found that growth declined with shore height. Unanswered questions lie in how heat stress and emersion cause tidal elevation to affect *B. glandula* growth. While previous research has explored the relationship between aerial temperature and energetic cost of emersion (Ober et. al, 2019), there are still additional unanswered questions about the relationship between tidal elevation and cost. Further, the effects of warming aerial temperatures on *B. glandula* performance are unknown.

In this paper, I investigated the effect of tidal elevation on the growth of *B. glandula* over a one year period divided into two, 6 month intervals. I also studied how tidal elevation impacts average daily maximum temperatures, and used this data to estimate energetic cost using a cost equation drawn from aerial respiration thermal performance curves. Finally, I modeled climate change by adding 2℃ to average daily maximum temperatures at each shore height to study the effect of warming aerial temperatures on the metabolic cost of *B. glandula.*

Investigating the effect of climate change on species' performance is imperative to estimating the thermal stress that organisms will experience. This research aims to inform further research on the thermal tolerance of *B. glandula* by estimating metabolic cost of emersion at varying tidal elevations. *B. glandula* are foundation species that provide habitats for other intertidal organisms and are food sources for many gastropods (Connell, 1970). Thus, it is important to know if their populations will be severely altered by climate change, and to identify how and when their performance will be affected.

I hypothesize that the growth rate of *B. glandula* will decrease as tidal elevation increases as a result of increased emersion and increased heat stress at high tidal elevations. Further, I predict that the smallest *B. glandula* will have the highest change in length because they are further from their physical size limit than larger barnacles. I additionally hypothesize that *B. glandula* at low tidal elevations will experience lower temperatures because they are immersed for a longer period of time, while barnacles at upper elevations will experience higher temperatures because they are exposed to aerial conditions more frequently. Because the abiotic stresses of emersion are known to cause debilitating effects such as desiccation and heat stress on intertidal organisms, I hypothesize that cost will increase with tidal elevation. Finally, I hypothesize that cost will increase as tidal elevation increases when 2℃ is added to average daily maximum temperatures, because *B. glandula* at higher shore heights will experience increased aerial temperatures for a longer period of time than barnacles at low elevations.

Methods

Data Collection and Measurements

This study investigated *B. glandula* growth and performance at three tidal elevations: 1.20, 1.55, and 1.99 meters above MLLW in Friday Harbor, Washington (Image 2). The highest barnacles at this site were located 2 - 2.1 m above MLLW height, so this study accounted for most barnacle heights present. To measure growth, eleven 12" x 12" square quadrats at each tidal elevation were previously established and photographed using a PentaxK50 camera in February 2018, August 2018, and May 2019 (three, 6 months intervals over one year) (Image 3). At each timepoint, *B. glandula* were counted and labeled using ImageJ, and their operculum diameters were measured to the nearest 0.01 mm. After the 6 month period, barnacles that were still present were recorded and measured, and barnacles that were not measurable were marked either dead, absent, or covered. Blurry barnacles or barnacles at awkward angles were not measured for measurement consistency.

Image 2. Data collection site in Friday Harbor, WA at low tide (Photo: Gordon Ober, 2019).

Image 3. Sample of a 12” by 12” quadrat (Photo: Gordon Ober, 2019).

Data Analysis and Statistical Calculations

All statistical analyses were run in RStudio version 1.3.1093. An analysis of covariance (ANCOVA) was used to determine the effect of growth rate on tidal elevation with size as a covariant. The slopes at each elevation were tested and found to be not significantly different, so the interaction term was pooled. A Shapiro Test demonstrated that the data did not have a normal distribution of growth or initial length for either time point, but I determined that the ANCOVA test was robust to non-normal data and thus proceeded with my statistical analysis. One outlier was excluded from the first time point because the growth was less than -1 mm. All data was log-transformed when running statistical analyses, and all log-transformed data met the assumption of equal variances among the groups.

The maximum daily average temperature was recorded with temperature loggers at three sites per tidal elevation. I compared the effect of tidal elevation on the average daily temperature, and ran an ANOVA and a Tukey’s HSD test to determine significance. To measure performance, thermal performance curves were used from a previous study on the cost of emersion for *B. glandula* (Ober et. al, 2019). This study estimated the metabolic cost of emersion for *B. glandula* by measuring respiration rates using a fluorometric O_2 system. They graphed thermal performance curves based on aquatic and aerial respiration rates and additionally estimated the metabolic cost of low tide exposure in an equation:

$$\mathrm{Cost}_{\mathrm{mol}} = ce^{-E/kT}$$

In this equation, c is the normalization constant 0.518, E is the activation energy 0.294 eV, K is the Boltzmann's constant $8.623*10^{-5}$ eVK^{-1}, and T is the temperature in Kelvins. This equation is based on an average barnacle size of 5.15 mm. Micromoles of O_2 were converted to Joules using a conversion factor of 0.457. The energetic cost of emersion was calculated using Ober et. al's equation (2019), and the cost at each tidal elevation was graphed and analysed using an ANOVA and a Tukey's HSD test. Finally, the effect of a 2℃ increase in aerial temperature was determined by adding 2℃ to the temperature variable in the cost equation, and the climate change model was compared against the 2018/2019 data.

Results

Tidal Elevation and *B. glandula* growth

For February 2018 - August 2018, there were no significant differences in growth among the three elevations (ANCOVA, df =2, F=1.614, p=0.2008). However, there was a significant negative relationship between initial size and growth (ANCOVA, df=1, F=59.67, p<0.001). At an initial length of 3.3 mm, growth was approximately 50% greater at low tidal elevations than at mid and upper elevations. While the relationship between tidal elevation and growth was not significant, the data showed a trend that *B. glandula* at low tidal elevations had the highest growth, while middle and upper elevations had lower growth.

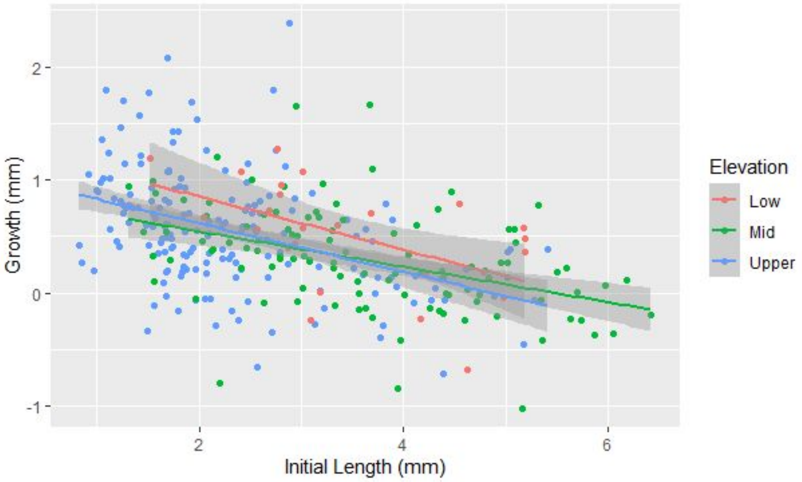

Figure 1. The effect of initial size and tidal elevation on the growth of *B. glandula*, February 2018 - August 2019.

August 2018 - March 2019 data showed a similar significant negative relationship between growth and initial size (ANCOVA, df=1, F=65.65, p<0.001). The relationship between tidal elevation and growth was not significant, but trends showed that *B. glandula* at low tidal elevations had higher growth than those at mid and upper shore heights (ANCOVA, df=2, F=0.6906, p=0.5022). At an average size of 3.0 mm, low tidal elevations had 20% greater growth than mid and high tidal elevations. Although this trend was not significant, low tidal elevation showed the highest growth, while mid and upper had decreased growth. Again, there was a significant negative relationship between initial size and *B. glandula* growth.

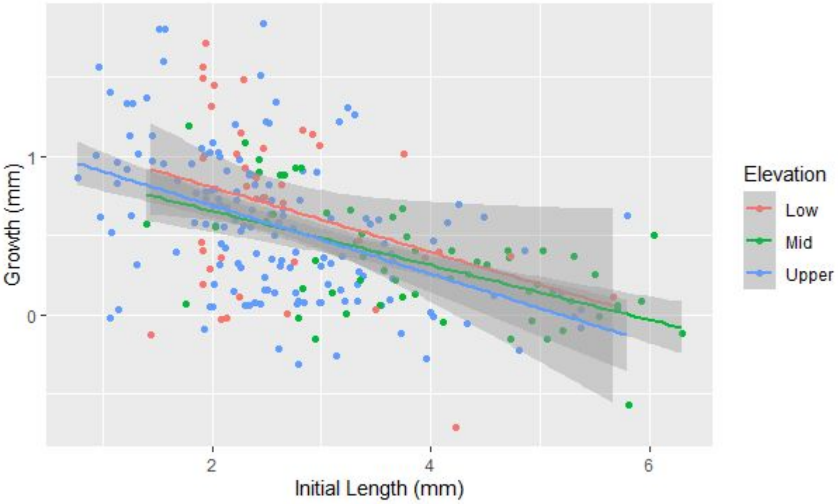

Figure 2. The effect of initial size and tidal elevation on the growth of *B. glandula*, August 2018 - March 2019.

Climate Change and the Energetic Cost of Rising Temperatures

Low tidal elevations had the lowest temperatures, while mid and upper tidal elevations had higher temperatures (Figure 3) (TukeyHSD, Feb 2018 - Aug 2018: low-high p<0.001, mid-upper p<0.001, mid-low p<0.001. Aug 2018 - Mar 2019: mid-low p=0.00, upper-low p=0.00, upper-mid p=0.186). Statistics account for autocorrelation using the previous day's temperature as a covariate. For the first time point, there was a significant difference between all tidal elevations (ANCOVA, df=2, F=6.25, p=0.00206). The second time point showed a significant trend between the elevations, with significant differences between low and mid and low and upper, but not between mid and upper (ANCOVA, df=2, F=2.76, p=0.0638).

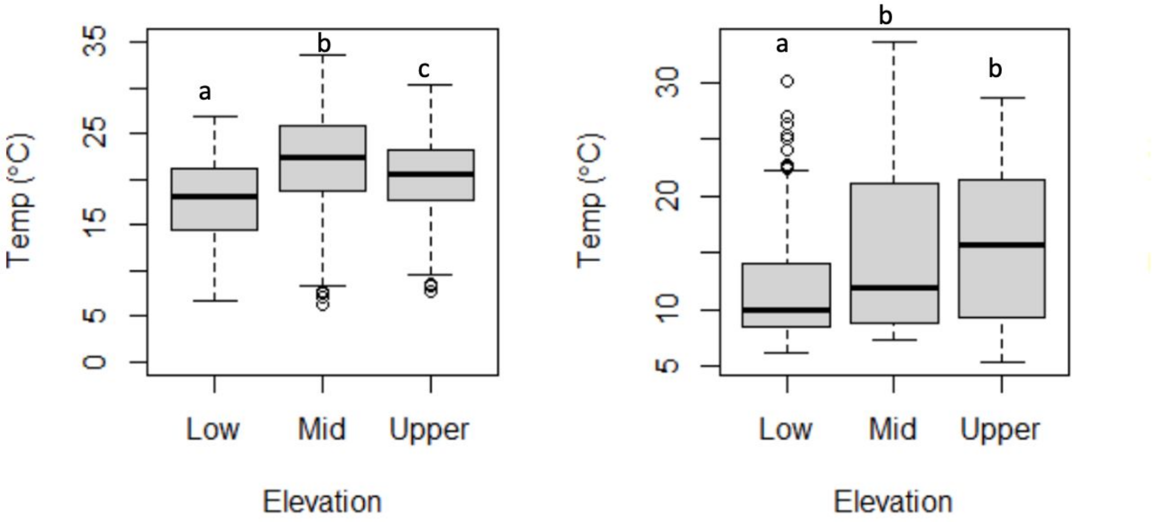

Figure 3. The effect of tidal elevation on the mean daily temperature in Friday Harbor, WA. February 2018-August 2018 (left) and August 2018 - March 2019 (right).

After converting the temperature data into energetic cost using the calculated cost equation, I found similar patterns in the data (statistics excluded because they were identical to the temperature data). The first time point showed slightly increased costs, which is likely a result of higher temperatures in the summer than in the winter (Figure 4). The lowest costs are seen in the low tidal elevations, while mid and upper elevations show heightened metabolic costs.

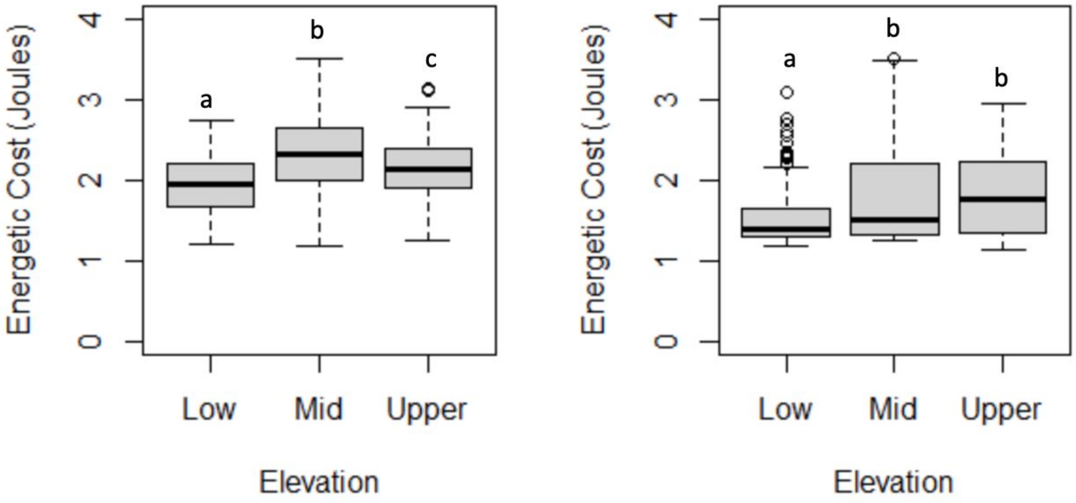

Figure 4. The effect of tidal elevation on the daily energetic cost of emersion (left: February 2018- August 2018, right: August 2018- March 2019.) Average barnacle size = 5.15 mm. Replicates are mean daily temperatures.

When climate change was simulated by adding a 2 ℃ increase in temperature, an increase in cost at all three tidal elevations was seen in both time points (Figure 5). February 2018 - August 2018 data showed that mid tidal elevations had a mean cost increase of 18% over low tidal elevations (Figure 5). High tidal elevations had a slightly decreased change in cost from the mid tidal elevation, but this difference was not significant. August 2018 - March 2019 data showed that absolute change in energetic cost increased as tidal elevation increased. Upper elevations had a mean cost that was 10% higher than that of low tidal elevations (Figure 5). Further, mean percent change in cost at all elevations ranged from 8.2%-8.4% for the first time point, and 8.4%-8.7% for the second time point.

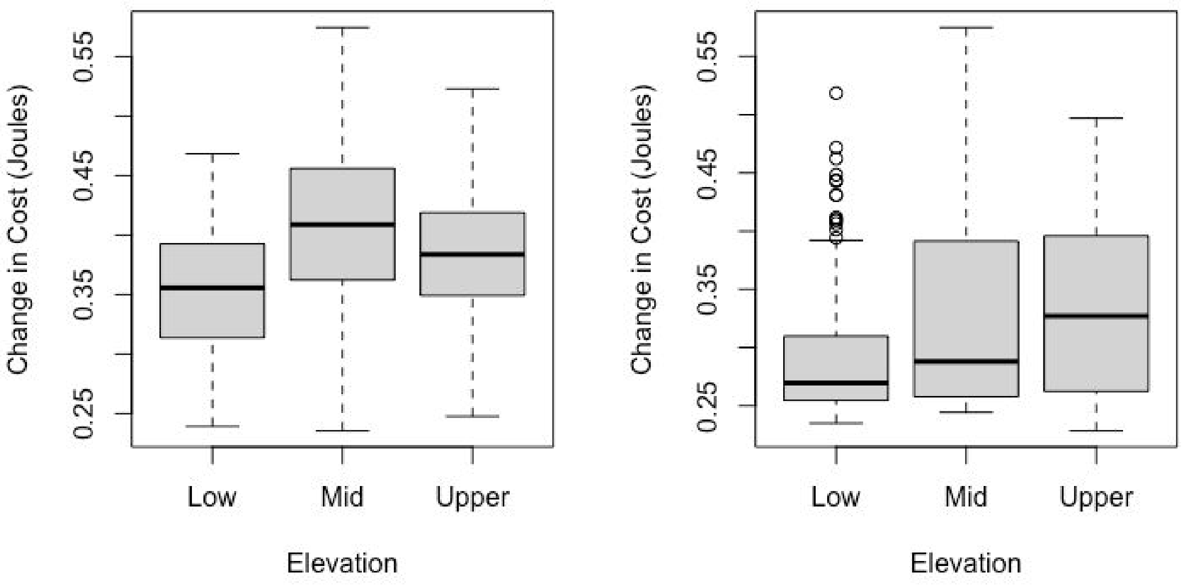

Figure 5. The median change in energetic cost (Joules) between 2018-2019 data and the effect of a 2 ℃ increase in temperature, February 2018 - August 2018 (left) and August 2018 - March 2019 (right).

Discussion

In this study, I investigated the effects of tidal elevation on *B. glandula* growth. I also studied how temperature, tidal elevation, and climate change affect *B. glandula* energetic cost. I hypothesized that *B. glandula* growth would increase as tidal elevation decreased as a result of increased heat stress at high tidal elevations. I also hypothesized that there would be a negative relationship between initial size and growth. Further, I hypothesized that *B. glandula* performance would decrease as tidal elevation increased as a result of increased emersion and exposure to aerial temperatures at high shore heights. Finally, I predicted that *B. glandula* cost would increase with shore height when 2℃ was added. I found that *B. glandula* at low tidal elevations experienced the highest growth, while barnacles at mid and upper tidal elevations had decreased growth. Energetic cost increased as tidal elevation increased, and an increased temperature of 2℃ affected mid and high tidal elevations the most drastically. Although I used a cost equation to obtain a calculated estimate of energetic cost, metabolic data showed the same trend that biological growth data did: *B. glandula* at high tidal elevations are most negatively affected by heat stress (Figures 1, 2, 5), and negative impacts will only intensify as global warming persists.

I found that growth decreased significantly as initial size increased, which is an indicator that larger barnacles are closer to their physiological size limit than smaller barnacles. Research on optimal size and energetics conducted by Sebens (2002) shows that organisms that are too small can not take advantage of all of the resources that are available, while organisms that are too large require more energy to be used on maintenance, instead of on reproduction. Thus, Sebens argues that there is an energetic optimal size, which is the mass that provides the greatest surplus of energy (Sebens, 2002). My data showed a linear trend in the relationship between initial size and growth. I also found that most barnacles with an initial size greater than 5.0 mm had 0 growth, which confirms that large barnacles are at their energetic optimal size. Sebens' model shows that when growth is 0, organisms are at their optimal size, and all energy is going towards reproduction. While my research did not include reproduction as a factor, it is possible that growth decreases as initial size increases because larger barnacles shift their energy to reproduction.

While growth did not differ significantly among shore heights, trends indicated that low tidal elevations had the highest growth, while mid and upper elevations had similar growths that were lower than the low tidal elevation (Figure 1 and 2). This supports my hypothesis that low tidal elevations will have the highest growth as a result of decreased heat stress and decreased emersion. Because the abiotic stresses of emersion are known to cause debilitating effects such as desiccation and heat stress on intertidal organisms, I predicted that *B. glandula* at low tidal elevations would experience the most success, while upper elevations would be more prone to the challenges of emersion. Gilman and Rognstad's research on the influence of shore height on *B. glandula* points out that survival at varying shore heights is likely not a result of heat stress, but that another factor is playing a role (Gilman and Rognstad, 2018). They also found that growth declined with shore height, which supports my results showing that low tidal elevations had the highest growth. Further research should investigate the relationship between tidal elevation and growth, but should control for external factors such as food availability, wave action, presence of predators, and juvenile settlement.

I found that temperature differed significantly between the low-upper and low-mid zones, but not between mid and upper (Figure 3). Low tidal elevations having the lowest temperatures supports my hypothesis, and is likely because low tidal elevations experience aerial temperatures less frequently than mid and upper. At the Friday Harbor data collection site, the rocky intertidal zone had an overhang at the upper tidal elevation, which is likely the cause of similar average daily temperatures at middle and high elevations (Image 2). The upper zone was likely shaded, and thus experienced less direct sunlight due to the different aspects of the substrate. While I hypothesized that aerial temperature would increase with shore height, I found that mid and high tidal elevations had very similar temperature and cost data, likely as a result of these microclimates. Because the cost equation was a calculated estimate that used a multiplier to determine metabolic cost, all cost results had the same relationship with tidal elevation that the temperature data had. When studying the metabolic cost of emersion for *B. glandula,* Gilman and Rognstad found that average daily temperatures were a poor indicator of emersion stress, and did not find significant differences in temperatures (Gilman and Rognstad, 2018). This was because barnacles that were high on the shore were exposed to the air for the hottest parts of the day, and going higher on the shore did not raise maximum temperatures, even though the time they were exposed to the air was increased. Their research was conducted in Southern California, which confirms that the geographical location as well as the topographical makeup of the site are important in determining the cost of heat stress. Further research could be conducted on how the shore type and protected shore areas are affected by heat stress and tidal elevation.

The relationship between energetic cost of emersion and tidal elevation has been studied in multiple other organisms and metrics. My data showed that temperature and energetic cost increased with tidal elevation. This trend supported my hypothesis, and further supported Ober et. al's findings that higher tidal elevations have higher energetic demand (Ober et al, 2019). Fly et. al found similar trends when investigating the effect of tidal elevation on energetic cost for *Pisaster ochraceous*. They found that sea stars at upper tidal elevations had increased costs of ≤ 35% over 0.5 m of tidal elevation (Fly et. al, 2012). However, they also found that slight variations in water temperature had a greater effect on energetic cost than large variations in aerial temperatures (Fly et. al, 2012). This suggests that different intertidal organisms respond differently to warming temperatures. Thus, my research on the cost of rising temperatures should be replicated on a variety of intertidal organisms in order to gain a bigger picture understanding of how climate change will affect a variety of organisms.

The cost of climate change has been widely studied, and it is well known that rising aerial temperatures will have devastating effects on organisms and their environments (Helmuth et. al, 2002). My data showed that a 2℃ increase in mean daily temperatures increased energetic cost by 8.4% - 8.8%. One limitation of this data is that cost data is adapted from Ober et. al's cost of emersion equation, which means that all cost information is a calculated estimate based on mean daily maximum temperatures and Ober et. al's analysis of thermal performance curves and O_2 consumption (Ober et. al, 2019). Because Ober et. al's research was a lab study, it will be important to replicate this type of research in the field, where types of substrate, storms, and other weather patterns are accounted for. Additionally, barnacles at different tidal elevations are likely acclimated to climate conditions at their respective tidal elevations, which could be one reason why respiration rates differ at varying tidal elevations. Further research in which *B. glandula* are actually exposed to increased aerial temperatures, in both field and lab settings, will be important in understanding the true cost of climate change.

Although my research does not investigate the relationship between growth and cost, similar patterns are shown in both sets of data: *B. glandula* growth decreases with shore height, and *B. glandula* energetic cost increases with shore height. Yin et. al (2017) investigated the relationship between aerial respiration, duration of air exposure, and oxidative damage in Manila Clams. They found that clams exposed to air for longer time periods had a decreased survival rate and increased oxidative damage (Yin et. al, 2017). While they did not account for tidal elevations, this study connects to my research because *B. glandula* at higher tidal elevations experience longer air exposure. It is possible that oxidative damage would limit growth in *B. glandula*, which is another explanation for why growth decreased with shore height. This would link both growth and cost as results of increased air exposure. Thus, further research on *B. glandula* investigating the relationship between oxidative damage and tidal elevation is necessary.

Conclusion

B. glandula experience a range of temperatures during emersion, and thus are adapted to experience a variety of weather patterns. However, tidal elevation determines how close these barnacles are to their physiological limits based on what they are already adapted to (Miller, 2012). I investigated the relationship between tidal elevation and growth, as well as the relationship between tidal elevation and energetic cost. I found that *B. glandula* at mid and upper tidal elevations have the least growth and the highest energetic cost. Further, the greatest increase in *B. glandula* energetic cost was found at mid and high tidal elevations. The knowledge that *B. glandula* at all tidal elevations will experience intensified heat stress as climate change progresses helps us identify the ecological impact of climate change, and additionally shows that more research is needed to explore the true cost of global warming on marine invertebrates. Global temperatures may increase by 1.5℃ by 2024 (World Meteorological Organization, 2020). If climate change continues at this rate, warming will increase by 2℃ in the next century (World Meteorological Organization, 2020). This study shows that efforts to slow the progression of climate change, as well as direct efforts towards the protection of marine invertebrates, is urgent. Climate change must be slowed-- not in a century, not in a decade, but now. Anthropogenic climate change will cause temperatures to rise and weather patterns to intensify, and immediate action is essential.

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References

Connell, J. H. (1970). A predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. *Ecological Monographs*, *40*(1), 49–78.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude.

Proceedings of the National Academy of Sciences, *105*(18), 6668–6672.

Gilman, S. E., & Rognstad, R. L. (2018a). Influence of food supply and shore height on the survival and growth of the barnacle Balanus glandula (Darwin). *Journal of Experimental Marine Biology and Ecology*, *498*, 32–38. https://doi.org/10.1016/j.jembe.2017.10.006

Gilman, S. E., & Rognstad, R. L. (2018b). Influence of food supply and shore height on the survival and growth of the barnacle Balanus glandula (Darwin). *Journal of Experimental Marine Biology and Ecology*, *498*, 32–38. https://doi.org/10.1016/j.jembe.2017.10.006

Gilman, S., Hayford, H., Craig, C., & Carrington, E. (2015). Body temperatures of an intertidal barnacle and two whelk predators in relation to shore height, solar aspect, and microhabitat. *Marine Ecology Progress Series*, *536*, 77–88. https://doi.org/10.3354/meps11418

Harley, C. D. G., & O'Riley, J. L. (2011). Non-linear density-dependent effects of an intertidal ecosystem engineer. *Oecologia*, *166*(2), 531–541. https://doi.org/10.1007/s00442-010-1864-1

Helmuth, B., Harley, C., Halpin, P., O'Donnell, M., Hofmann, GE., & Blanchette, C. (2002). Climate change and latitudinal patterns of intertidal thermal stress. *Science (Washington D C)*, *298*(5595), 1015–1017.

Kordas, R. L., Dudgeon, S., Storey, S., & Harley, C. D. G. (2015). Intertidal community responses to field-based experimental warming. *Oikos*, *124*(7), 888–898. https://doi.org/10.1111/oik.00806

Miller, N. A. & Stillman, J. H. (2012) Physiological Optima and Critical Limits. *Nature Education Knowledge* 3(10):1

Ober, G. T., Rognstad, R. L., & Gilman, S. E. (2019). The cost of emersion for the barnacle Balanus glandula. *Marine Ecology Progress Series*, *627*, 95–107. https://doi.org/10.3354/meps13058

Sebens, K. P. (2002). Energetic Constraints, Size Gradients, and Size Limits in Benthic Marine] Invertebrates. *Integrative and Comparative Biology*, *42*(4), 853–861. https://doi.org/10.1093/icb/42.4.853

Sinclair, B. J., Marshall, K. E., Sewell, M. A., Levesque, D. L., Willett, C. S., Slotsbo, S., Dong, Y. W., Harley, C. D. G., Marshall, D. J., Helmuth, B. S., & Huey, R. B. (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters*, *19*(11), 1372–1385. https://doi.org/10.1111/ele.12686

World Meteorological Organization. (2020). "New Climate Predictions Assess Global Temperatures in Coming Five Years," https://public.wmo.int/en/media/press-release/new-climate-predictions-assess-global-temperatures-coming-five-years.

Yin, Xuwang, Peng Chen, Hai Chen, Wen Jin, and Xiwu Yan. (2017). "Physiological Performance of the Intertidal Manila Clam (Ruditapes Philippinarum) to Long-Term Daily Rhythms of Air Exposure." *Scientific Reports* 7. https://doi.org/10.1038/srep41648.