EFFECTS OF HEATWAVES ON KEY ECOLOGICAL PROCESSES STRUCTURING EARLY SUCCESSIONAL TIDEPPOOL COMMUNITIES

by

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Abstract

With climate change, we are seeing an increase in mean temperatures globally. Perhaps of greater concern, however, is the associated increase in the frequency, magnitude, and duration of heat wave events. Through mass die offs, coral bleaching, and species range expansions and contractions, heatwaves have had large impacts on marine ecosystem and their function. While we have an understanding of how communities have been altered by naturally occurring heatwaves, we have little understanding of what factors are important in determining the response of a system to extreme heat events. In order to better predict the response of marine ecosystems to extreme heat events we must understand how extreme temperatures interact with key ecological processes. The goal of this thesis was to determine how heatwaves, in conjunction with key ecological processes, such as herbivory and dominant foundation species, alter community composition and function. I tested this using artificial tidepools in Burrard Inlet, British Columbia as a study system and manipulated temperature in situ through the design of a novel temperature manipulation system: the SAUTE. In chapter 2, I test how regular heat events of different intensities and herbivore density affect community composition through a 2-month field manipulation. My results demonstrate that tidepool communities in the Pacific Northwest may not be impacted directly by regular increases in maximum daily temperatures by 2-4°C throughout the summer, but that indirect effects through the loss of herbivore grazers could have impacts on community composition. In chapter 3, I ask how a late summer, longer duration heatwave influences community composition in tidepools and if this effect is dependent on the dominant foundation species present. The data that I present suggests that, though there were few direct impacts the heatwave on tidepool assemblages, the dominant foundation species was an important determinant of community composition and diversity. While I only observed a slight
decrease in the abundance of foundation species with heating, if extreme heat events modify ecological processes, such as herbivory, that create and allow different habitat types to persist, then they could have large indirect effects on tidepool communities.
Lay Summary

Heatwaves, which are becoming more common, can alter ecosystems through mass mortality events and changes in the interactions between organisms. It is therefore crucial to better understand their impacts on ecosystems. I sought to understand how heatwaves may impact species living in tidepools in Vancouver, British Columbia and whether these impacts would be altered by consumers or the identity of the dominant species present within a tidepool. I found that heatwaves may have little impact tidepool dwelling species but could trigger a loss of herbivore consumers from the system. I also found that the dominant space holding species had a large influence on tidepool diversity but did not modulate the response tidepool communities to heatwaves. The loss of consumers due to heatwaves could therefore play a large role in determining the dominant species present in tidepools and ultimately the diversity of species in the system.
Preface

This thesis is original, unpublished work. I conceived data chapters 2 and 3 in collaboration with Chris Harley. The SAUTE system was a refinement of a heating method originally designed by Graham Brownlee. I conducted the field manipulations, collected and analyzed the data, and wrote the manuscripts. Chris Harley aided with designing and naming the SAUTE system, interpreting the results, and editing the manuscripts.
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“When I was One,
I had just begun.
When I was Two,
I was nearly new.
When I was Three
I was hardly me.
When I was Four,
I was not much more.
When I was Five, I was just alive.
But now I am Six, I’m as clever as clever,
So I think I’ll be six now for ever and ever.”

— A.A. Milne, Now We Are Six
Dedication

In memory of my grandmother and best friend, Genevieve Gwendolyn Konecny. I wouldn’t be where I am today without you.

“GO WEST MY GIRL” – Hugs, Nana
1 Introduction

As anthropogenic pressures increase climatic variability and accelerate rates of environmental change, the role of ecology has expanded from one of understanding past and present species assemblages, to one of also predicting future assemblages and their capacity to sustain ecosystem services. Over the past few decades we have seen increases in global mean air temperatures, increases in mean sea surface temperatures, and decreases in surface ocean pH, (Bindoff et al., 2019). Further, extreme heat events are predicted to increase in frequency, duration, and intensity. As we face unprecedented rates of environmental change, we have seen, and will continue to see, modifications in species distributions and abundances as organisms respond to altered environmental temperatures (Brierley & Kingsford, 2009). Beyond the direct effects of warming, ecological interactions (e.g. herbivory, predation, competition, facilitation, etc.) have the potential to modify and modulate the response of communities to high temperatures. For example, the presence of grazers in the intertidal zone can increase biological diversity and reduce negative effects of warming (Kordas et al., 2017). Habitat-forming species, such as barnacles and mussels, also have the potential to buffer against thermal stress in the intertidal zone through the creation of microhabitat (Jurgens & Gaylord, 2018; Leonard, 2000). While some changes due to warming may be trivial, others will have substantial consequences for biodiversity and ecosystem function (Grimm et al., 2013). The magnitude of ongoing ecological change and predicted increases in climatic extremes moving forward, necessitate an increased understanding of climate change impacts on organisms, communities, and ecosystems in order to identify critical areas and increase resilience.
1.1 The intertidal zone

One of the harshest environments on earth is the intertidal zone, the interface between land and sea. Intertidal organisms can experience high levels of hydrodynamic stress from waves (Helmuth & Denny, 2003), desiccation (Connell, 1961b), and changes in body temperature of 30°C over a period of hours when the tide recedes (Elvin & Gonor, 1979). As a result, the intertidal zone is a great indicator system (a multispecies-system that will respond first to change acting as an early-warning system and used to assess the condition of an ecosystem) that can be used to assess the ecological impacts of environmental change on species distributions, interactions, and ecological processes (Mieszkowska, 2009). Further, the roles of abiotic stress and biological interactions in determining species distributions have long been studied in the intertidal, providing a solid base of knowledge on which we can build to better understand the potential impacts of climate change on ecological communities.

1.1.1 General effects of temperature

The Earth’s average temperature has increased, and will continue to increase, due to anthropogenic climate change. Since temperature affects all levels of biological organization (Angilletta et al., 2002), changes in average temperature will have impacts at a variety of scales, especially in ectotherms where body temperature is strongly determined by environmental temperature. For example, in the intertidal zone temperature has been shown to affect organism metabolism (Iles, 2014), feeding rate (Sanford, 1999), reproduction (Buschmann et al., 2004; Desai et al., 2006), and growth (Chomsky et al., 2004; Watt & Aiken, 2003). Temperature also has the potential to alter species distributions at a local and geographic scale when organisms are limited by temperature and not by other biological or physical factors (Helmuth, Mieszkowska, et al., 2006). However, species distribution patterns are often correlated with extreme, and not
mean environmental temperatures, as organisms experience fluctuating temperatures that can reach well above or below the environmental mean (Fey & Vasseur, 2016). As a result, ecological forecasting based on mean changes in temperature may not be particularly informative. As extreme heat events become more common (Meehl & Tebaldi, 2004), it is important to better understand the role of extreme temperatures in shaping species distributions.

1.1.2 Thermal extremes and heatwaves

Heatwaves, which are roughly defined as discrete prolonged periods of anomalously warm temperatures (Pezza et al., 2012), are projected to increase in frequency, intensity, and duration (Meehl & Tebaldi, 2004). While specific guidelines exist to define heatwaves, the thresholds and characteristics used to define these extreme events differ slightly depending on whether the event is an atmospheric or marine heatwave. Recently, atmospheric heatwaves have been defined as events lasting for at least three consecutive days where daily temperatures exceed the calendar day 90th percentile based on a historical baseline period (Perkins & Alexander, 2013). Marine heatwaves on the other hand, have been defined as anomalously warm events lasting for five or more days (due to the naturally longer time scales of ocean variability), with water temperatures warmer than the 90th percentile based on a 30-year historical baseline period (Hobday et al., 2018). Atmospheric heatwaves have caused mass die-offs in mussels (Petes et al., 2007; Makoto Tsuchiya, 1983), limpets (Harley, 2008) and turf algae (Harley & Paine, 2009) on rocky shores, while marine heatwaves have had large impacts on the abundance and distribution of shallow-subtidal organisms such as corals (Hughes et al., 2017), and kelp (Wernberg et al., 2016), causing shifts in coastal community composition. Heatwaves can happen independently in the atmosphere and in the ocean, or they can happen simultaneously which is especially important for residents of the intertidal zone, as they are exposed to both water and air temperatures daily.
As a result, coinciding atmospheric and marine heatwaves could have compounding effects on intertidal organisms. Further, as these extreme events increase in frequency and intensity, they will have negative impacts especially where summer mid-day low tides exist (Helmuth, Broitman, et al., 2006). While organisms may be able to survive a single low tide at extreme temperatures, consecutive days of exposure could have cumulative lethal effects (Denny et al., 2006) in the absence of a mechanisms to reduce body temperature such as behavioural thermoregulation (Sears et al., 2016).

1.2 Biotic interactions

The intertidal zone is full of complex biological interactions that can modulate species distribution and abundances, such as competition for space (Connell, 1961b). Consumers can have a large role in structuring intertidal communities. They can reduce diversity and abundances of organisms at high levels of consumption and reduce settlement through increased disturbance (Dayton, 1971). On the other hand, consumers can increase diversity through the removal of otherwise competitively dominant species (Lubchenco, 1978). Positive, facilitative interactions also play an important role in determining the distribution of species in the intertidal zone (Bertness & Callaway, 1994). In physically stressful environments, foundation species like barnacles and mussels, can ameliorate conditions by increasing habitat complexity and creating a more favourable settlement surface (Bertness et al., 1999). Foundation species can also play an important role in local nutrient levels (Pfister, 2007), water filtration (Dolmer, 2000) and create refuge from predation and physical stress (Stachowicz, 2001). Depending on the species present in an assemblage and their capacity to tolerate high temperatures, extreme heat events could cause losses in herbivores and foundation species, having consequences on community composition and stability.
1.3 Interaction between biological and physical drivers

In addition to direct effects, heatwaves could have large indirect effects on intertidal communities through the alteration of species interactions and ecological processes. While extreme temperatures can have direct negative impacts on organisms, interspecific variation in the thermal sensitivity of organisms can alter the strength of interactions through changes in per capita effects (temperature changes the strength of an individual’s interaction) or density effects (temperature changes number of individuals in populations; Kordas et al., 2011). These changes could alter species interactions allowing more thermal tolerant species to outcompete less thermal tolerant species that could otherwise have a competitive advantage. This has been demonstrated in turf-algae and consumers with warming. In the gastropod herbivore, *Turbo undulates*, grazing rates are highest at 19.31°C and declined substantially by 24 °C whereas the turf-algae that they consume has an optimal growth rate at 23.45°C (Mertens et al., 2015). This mismatch in performance across temperatures creates a thermal refuge for the turf-algae at high temperatures in this system where *T. undulates* is unable to persist. Further, in the rocky intertidal, when limpet grazers were excluded, warming reduced the abundance of habitat forming species (compared to under ambient conditions), the abundance of consumers (snails, amphipods, isopods), and caused a shift towards a lower-diversity algal dominated system (Kordas et al., 2017). When limpet grazers were present, they facilitated the survival of habitat modifying barnacles which facilitated the presence of a consumer guild under warmed conditions. This demonstrates how warming can allow more thermally tolerant species such as mat-forming algae to outcompete habitat forming species in the absence of grazers and how the direct effects of warming (decreases in the abundance of consumers and foundation species) can
have important consequences for community diversity and function. Warming has also been shown to have indirect effects on invasive species through the alteration of invaded community composition. While warming is positively correlated with population growth rates in the invasive bryozoan, *Membranipora membranacea*, warming has been linked to decreased growth rates in kelp (Denley et al., 2019). Further, the effects of climate change on *M. membranacea* have been shown to be dependent on kelp community composition with lower bryozoan population growth rates in communities with only one of the three prominent kelp species present in the system. This demonstrates that while warming has a positive effect on the invasive bryozoan, it also has an indirect negative effect on the invader through an alteration of community composition in the invaded kelp community. Since biological interactions are an important determinant of ecological community structure and composition, the sensitivity of key species (herbivores, foundation species) to heatwaves is of particular importance as changes in their per capita and density effects could have large impacts at the community level.

### 1.4 Thesis overview and research questions

Naturally occurring heatwaves can negatively impact organisms, communities, and ecosystems with their effects ranging from mass mortalities, to disease outbreak, and species range shifts (Oliver et al., 2019). While we know that these extreme events have the ability to drive changes at the ecosystem level, we have little understanding of the mechanisms by which these changes occur, and how they interact with the local ecological context. We can begin to answer these questions through in-situ field manipulative experiments. In my first data chapter, I ask how the intensity of extreme heat events influences tidepool assemblages and if the effect of heatwaves is dependent on herbivore density. Through a 2-month field manipulation, I test how heat events of different intensities and herbivore density affect community composition. In my second data
chapter, I ask how a late summer, longer duration heatwave influences community composition in tidepools and if there is an interaction between heating and dominant foundation species. I also measured whether community function and productivity were altered by these factors. I found that in tidepools, community structure is strongly determined by interspecific interactions and the abundance of key species (herbivores or foundation species), but the direct effects of realistic heatwaves were minor. Through assessment of both the direct, and indirect effects of extreme heat events on the tidepool assemblages, we can begin to understand and predict which systems or ecological interactions may be the most vulnerable to climate change to increase their resilience moving forward.
2 Herbivory, but not experimental warming, dictates tidepool community structure

2.1 Introduction

Temperature is a key driver of all biological systems and influences a range of processes from enzyme reaction rates to community interactions. As a result, understanding the influence of temperature on biological processes is an important step in predicting how organisms, communities, and ecosystems will respond to climate change (Deutsch et al., 2008). While average global temperatures are predicted to increase by 1.5-4 °C (depending on the emission scenario; IPCC, 2014) by 2100, perhaps of greater importance, are the predicted changes in climatic extremes. Extreme heat events have increased, and will continue to increase, in frequency and severity throughout the 21st century. While we have some understanding of how organisms will respond to mean increases in temperature, we have little understanding of how extreme temperatures and thermal variability will shape ecological communities.

Global coupled climate models (separate atmosphere, ocean, sea ice, and land component models which interact through a flux-coupler) indicate that there will be an increase in the magnitude and frequency of warm days and nights and a decrease in the number of cold days and nights through the 21st century. Overall, this will cause an increase in mean temperatures (Seneviratne et al., 2012; Vincent et al., 2018). With predicted increases in the frequency, magnitude, and duration of extreme heat events (Meehl & Tebaldi, 2004), however, temperatures will also become more variable. Due to the nonlinearity of species responses across temperature (Denny, 2017; Martin & Huey, 2008) during these extreme heat events, even slight changes in
temperature can have large impacts on performance (Vasseur et al., 2014). At low temperatures, warming can benefit organisms through increased activity rates and efficiency of physiological processes. At high temperatures, beyond the thermal optimum of an organism, however, warming results in more time spent at or above dangerously high temperatures, which can negatively alter energy allocation and induce physiological stress. As extreme temperatures become more frequent, there is an increased likelihood that organismal body temperatures will exceed thermal optima with consequent negative impacts on performance and potentially irreversible damage. This could lead to shifts in community structure and composition as cold adapted species are replaced by warm adapted, or more thermotolerant, species (Arafeh-Dalmau et al., 2019).

Climate warming has been associated with changes in species distributions, abundances, and range limits in response to climate change (Doney et al., 2012). However, it is unclear what role thermal extremes have played in producing these patterns and to what extent ecosystems will be altered by an increased frequency of extreme temperature events (Thompson et al., 2013). Depending on the performance and tolerance of organisms, extreme temperatures have the potential to impact community structure directly through reduced survival and species richness. In the rocky intertidal, moderate warming by approximately 2°C caused a decrease in the abundance of limpet herbivores and barnacles, thereby reducing richness and altering community structure (Kordas et al., 2015). While 2°C of warming did not necessarily generate extreme temperatures daily, it likely caused temperatures to exceed the lethal limits of some organisms on days where they otherwise would have remained below this threshold. Extreme temperatures also have the ability to alter communities indirectly through mismatches in producer-consumer relationships (Mertens et al., 2015) and modifications in the strength of competitive interactions.
Herbivores have been shown to increase the capacity of ecological communities to resist warming through the facilitation of foundation species; in the absence of herbivores, warming altered competitive interactions, decreasing barnacle abundance and ultimately decreasing community stability (Kordas et al., 2017). Because some species are more sensitive to thermal effects than others, and because indirect effects are common in ecological interaction webs, both the direct and indirect effects of warming on ecological communities are important to consider when investigating the potential impacts of heatwaves on marine assemblages.

In this chapter, I examine how extreme heat events of different intensities and grazing pressure impact community composition in marine tidepools. Tidepools are habitats within the intertidal that are rich in biodiversity and host complex food webs (Firth et al., 2013; Mendonça et al., 2018; Anna Metaxas & Scheibling, 1996). Like the intertidal zone, abiotic stress plays a large role in structuring tidepool communities. During low-tide, pools remain isolated from the ocean and tidepool water temperature is strongly correlated with air temperature (Morris & Taylor, 1983) causing community composition to vary with shore height and exhibit seasonality in some cases (Bertocci et al., 2011; Rubal et al., 2011; Underwood & Jernakoff, 1984). Increases in summertime temperatures, and more frequent extreme heat events, will therefore likely impact the performance and survival organisms, especially since many intertidal organisms are living near their upper thermal limits. Grazers also play an important role in structuring tidepool communities. They have been shown to increase diversity by inhibiting competitively dominant species (Lubchenco, 1978) and to free up primary space for the settlement of other species (Dethier, 1982). At high levels of grazing, however, herbivores can reduce settlement through disturbance leading to decreases in diversity and species abundances (Dayton, 1971). Further,
herbivory is a temperature dependant ecological process and therefore the strength of producer-consumer interactions can vary with temperature. Herbivore-plant interaction strength can increase with temperature as consumption increases at a greater rate than primary production with temperature (O’Connor, 2009). At high temperatures, however, consumers can exhibit metabolic depression, decreasing rates of consumption (Mertens et al., 2015), and prolonged exposure to extreme temperatures can result in mortality (Leung et al., 2017). The temperature dependence of herbivory and herbivore performance is therefore important to consider as mismatches in producer-consumer interactions could impact marine food webs and alter community structure (O’Connor et al., 2009; Ullah et al., 2018).

In this study, I heated replicate artificial tidepools, in-situ, to varying intensities (+2°C, +4°C), during low tide 2-3 days a week, for a period of two months. While heating by +2°C and +4°C on top of ambient temperatures does not inherently generate extreme temperatures, it increases the likelihood of an extreme heat event occurring throughout the thermal manipulation period. Temperature treatments were selected to represent realistic changes in temperature that we might expect in the future (IPCC, 2014). With warming alone, I predicted that community structure would be altered through a decrease in the abundance and richness of species as well as a decrease in the evenness of their composition. Many intertidal organisms live just below their upper thermal limits and therefore some species may fare poorly or be excluded from warmed communities while others may be resistant and able to take advantage of less competition for resources. To understand how increases in temperature may interact with herbivory, I created two limpet density treatments; one treatment with a high density of Lottia pelta, and one control treatment with no manipulation of limpet density. I predicted that warming and herbivory would interact to control community structure, although the nature of this interaction would depend on
the relationship between grazers and species richness under ambient conditions (Figure 2.1). If grazing by limpets increases the settlement of other organisms through the reduction of microalgae (Figure 2.1a), then we would expect the addition of herbivores to increase invertebrate species abundances, richness, and evenness, increasing overall community diversity. Conversely, if herbivores reduce settlement through disturbance (Figure 2.1b), then we would expect species abundances, richness, and evenness to be lower with the addition of herbivores, decreasing diversity. On rocky shores, facilitation by herbivores has shown to buffer communities against warming through the increased recruitment of habitat-forming species which alter the thermal environment, providing refuge and reducing physiological stress on herbivores. However, since whole communities are submerged (including grazers) in tidepools, habitat forming species provide less of a thermal refuge for consumers. With warming, I therefore expected the performance of mobile grazers to decrease due to an alteration in the allocation of energy away from consumption and towards maintaining basic metabolic processes for survival (Menge et al., 2002). As a result, we would expect the effect of herbivory (whether positive, or negative) to weaken with increasing temperatures to a point where at high temperatures, communities in both herbivore density treatments would have similar levels of diversity due to the inhibition of herbivore activity.
2.2 Methods

2.2.1 Study site

This experiment was conducted in Burrard Inlet, British Columbia. Burrard Inlet is a protected body of water connected to the Salish Sea, characterized by seasonal variability in sea surface temperature and salinity (Held & Harley, 2009; Thomson, 1981). Tides in Burrard inlet are mixed semidiurnal with lower low tides occurring near mid-day in the summer. As a result, intertidal organisms in this area are regularly exposed to high temperatures during the summer.

The north end of Dunbar Street (49.273378 N, 123.184121 W; Figure 2.2) was selected as a field site for this experiment as it experiences low levels of wave-exposure thereby reducing the risk of dislodgement due to log disturbance. In addition, the presence of a large, flat, and nearly horizontal bedrock shelf located in the mid-high intertidal provides an ideal location to install replicate artificial tidepools.
2.2.2 Experimental manipulation - temperature and herbivory

This experiment was conducted using a novel heating system, the Seaside Array for Understanding Thermal Effects (SAUTE). Replicate artificial tidepools were installed in the intertidal (N=48) in late June 2018 and were left in the field for 3 weeks prior to manipulation (June 19 – July 11, 2018) to allow for recruitment and colonization in the tidepools. Tidepool seawater temperature was manipulated 2-3 days/week for seven weeks (July-August 2018) and herbivore density manipulations were maintained over the entire seven-week experiment. Artificial tidepools were arranged in a randomized block design with three temperature treatments (ambient, +2°C, +4°C) crossed with two herbivore treatments (ambient limpet density, high limpet density) represented in each block. Tidepool blocks were installed at a shore height of approximately 2.5m above Canadian chart datum and cages were placed in two rows parallel to shore.

Each tidepool was constructed by securing a 10.5 x 11 cm (diameter x height) plastic jar (ULINE Ltd., Milton, ON, Canada) into a 15.25 x 17.15 cm (diameter x height) PVC (polyvinyl chloride;
schedule SDR35) cap using quick setting cement (QUICKRETE®, Abbotsford, BC, Canada). SeaGoin’ marine epoxy putty (Permalite Plastics Corp, Compton, CA, US) was set inside the bottom of each plastic jar and coarse salt was pressed into the surface of the epoxy before it set following the methods of Kordas et al. (2015). Once the epoxy was dry, the salt was rinsed away using warm water leaving a roughened settlement surface. This concentric pool design was constructed such that the outer pool (PVC cap) acted as a temperature bath for the inner, experimental pool (plastic jar; Figure 2.3a). A frosted microscope slide was placed inside each tidepool, vertically along the wall, to act as a standardized settlement surface for the measurement of microalgal chlorophyll-a content at the end of the experiment. Data loggers (Thermochron ibutton, Maxim Integrated, San Jose, CA, USA) were installed in 12 tidepools (2 per treatment) to record continuous, high-resolution temperature data throughout the entire duration of the experiment. Data logging rate was set to one observation per hour. Cages (71 x 30.5 x 13 cm) were built from PVC coated garden fencing with a mesh size of 5cm x 10cm (Peak Products, Richmond, BC, Canada) in order to secure the tidepools onto the bedrock. The mesh size of the cages was large enough to allow for the immigration and emigration of most mobile species present at the field site but likely excluded larger organisms such as sea stars, fish and avian predators during low tide. Cages were built with a lid so that the tidepools could be easily accessed throughout the experiment with minimal disturbance (Figure 2.3b). The cages were attached to the substrate using screw eyes (anchored into the bedrock) and cable ties and remained in the intertidal for the entire course of the experiment.

Artificial tidepools were heated using a propane powered turkey fryer. Heatwaves were simulated weekly and pools were heated to two intensities (+2°C, ambient +4°C) in addition to an unmanipulated control treatment. Water was heated in a large pot and irrigation lines (0.64 cm
internal diameter) were run from the water filled pot into the outer pool of each of the heated treatment pools (Figure 2.3c). A flow control valve was placed at the end of each irrigation line in order to control the flow rate of heated water and thus the tidepool temperature. The irrigation lines were siphoned at the beginning of each heating period to begin the passive movement of water from the heating pot to the tidepools. The volume of water in the heating pot was maintained at a constant level by a gravity-fed supply from a bucket (~ 40 L) which served as a header tank. Temperature was recorded in all experimental pools at the beginning of each heating period and measured every subsequent hour using a thermocouple (Oakton Temp-100). These additional measurements of temperature were made as not all pools had embedded data loggers and real-time measurements allowed for adjustments to the flow rate of the water lines where required to achieve the desired temperature treatments. Tidepools were heated for four hours total on each heating day, or until the pools became immersed. Four hours was chosen based on the amount of time that tidepools would typically be exposed to high temperatures during mid-day summer low-tides. Once the tide came back in, the irrigation lines, turkey fryer, propane tank, and buckets were removed, and the tidepools were left in place.

Herbivore pressure was manipulated by adding limpets, *Lottia pelta*, to half of the tidepools of each thermal treatment level. A density of three added limpets was maintained in the high herbivore density treatment and none were added to the control tidepools. Limpets were marked with Bee tags (The Bee Works) in order to differentiate them from limpets that naturally recruited into the pools. Limpet survival was assessed weekly (one day after heating) and dead or missing tagged limpets (i.e. not recruits), were replaced with new individuals to maintain the high-density treatments. Limpet replacements were not recorded initially and therefore there is no data for the first two weeks of the manipulation.
Figure 2.3 Components of the SAUTE (Seaside Array for Understanding Thermal Effects) system. (a) Double-walled artificial tidepool showing the experimental (central) and jacketed (outer) sections, with a microscope slide for biofilm secured with an alligator clip at the top of the image; (b) block of six tidepools in cage secured onto the bedrock; (c) SAUTE system set-up in the intertidal during a day of thermal manipulations, showing the header tank and propane supply (right), the turkey fryer (center), and the black irrigation lines supplying heated water to the experimental blocks where the water lines are further split into the jacketed layer surrounding individual pools according to their assigned treatment.
2.2.3 Data collection

After seven weeks of manipulations, microscope slides were removed from the pools and transported back to the lab on ice and in the dark. Chlorophyll-a was extracted by steeping each entire slide in 90% acetone at 4°C for 24 hours (methods adapted from Arar & Collins, 1997). After 24-hours, the chl-a concentration was measured for each tidepool on a fluorometer (Turner Designs Trilogy; access provided by MI O’Connor). The fluorescence of three subsamples was measured and the average was used to calculate the mean concentration of chlorophyll-a for each slide. The concentration was then standardized by the volume of acetone used and microscope slide area. At the end of the experiment, artificial tidepools were capped in the field during low tide and transported back to the lab. Tidepools were destructively sampled, contents were divided into three size fractions (<50 um, 50-300 um, >300 um), and preserved in 70% ethanol until they were processed. Invertebrate density (mussels, limpets, amphipods, anemones, snails, crabs, etc.) was measured in each tidepool.

2.2.4 Statistical analysis

To verify that the average daily maximum tidepool temperatures were different between heating intensity treatments but similar within treatments, a linear mixed-effect model (ez package; Lawrence, 2016) was used with heating intensity and limpet density as between-subject effects, date as a within-subject effect, and tidepool ID as an identifier. In order to visualize differences in the treatments through time, average daily maximum water temperature (n=8 per treatment combination on days that pools were heated) was calculated and plotted alongside average control pool temperature from a subset of pools (continuous hourly measurements, combined herbivore density treatments, n=4), daily air temperature range for Vancouver International Airport (Environment and Climate Change Canada, 2019), and tide height data for Vancouver.
Harbour (Canadian Hydrographic Service, 2019). To compare the average post-heatwave abundance of experimentally added limpets in each pool between heating intensity treatments throughout the experiment, a linear mixed-effects model (ez package; Lawrence, 2016) was used with heating intensity as a between-subject effect, date as a within-subject effect, and tidepool ID as an identifier. To determine which heating treatments had significant differences in average limpet abundance post-heating, I used a Tukey HSD post-hoc test.

To test for changes in community structure (excluding microalgal cover) due to heating intensity and herbivore density treatments, I used the manyglm function with a negative binomial distribution in the mvabund package (Wang et al., 2020). This function was used as it has higher power than traditional multivariate approaches such as PERMANOVA and ANOSIM and accounts for a mean-variance relationship in the data. This method fits a separate GLM to each species and uses resampling to test for significance at the community level. Model terms were tested for significance using a likelihood ratio test and Monte Carlo resampling with 999, with an “adjusted” p.uni argument, taking in to account multiple testing and the correlation between species abundances. Cage ID was used as a blocking variable to allow for cage resampling (abundances are assumed to be independent across cages and not within cages). To test for differences in the multivariate homogeneity of groups dispersions, or beta diversity, between treatments I used the betadisper function in the vegan package (Oksanen et al., 2019) which uses the PERMDISP (Anderson et al., 2006) procedure. A Bray-Curtis dissimilarity matrix was calculated from the community data and Non-metric multidimensional scaling (NMDS) was used to visualize the effect of treatments on tidepool communities. A linear mixed-effect model was used to test the effects of heating intensity and herbivore density on chl-a content with cage included as a random effect. In order to account for variability in chl-a content due to differences
in limpet survival between pools, the mean post-heatwave abundance of experimentally added limpets was calculated and used as a continuous variable in the model. Linear mixed-effect models were used to test for the effects of heating intensity and limpet density on species richness, Shannon diversity and Pielou’s evenness with cage included as a random effect in both models. Diagnostic plots of the residuals were used to assess the fit of each model. All analyses were carried out using R statistical software v3.6.1 (R Core Team, 2019).

2.3 Results

2.3.1 Thermal manipulations

Temperatures in July and August of 2018 were typical of recent summers in Vancouver, BC, although daily maximum temperatures did exceed the 90th percentile of average daily max temperatures, calculated over a 30-year period (1987-2017), for five consecutive days (August 6-10, 2018; Figure 2.4). Tidepools were heated at low tide for a total of 19 days over the course of the approximately 50-day experiment (Figure 2.5). On days that tidepools were heated, average daily maximum water temperatures were significantly higher in the high (average max. temp. ± SE; 30.7 ± 0.2°C) and medium (28.0 ± 0.2°C) heating intensity treatments than control tidepools (25.5 ± 0.2°C ; Figure 2.6; Table 2.1). Date had a significant effect on tidepool temperature and there was a significant date by temperature treatment interaction where the degree of heating varied across manipulation days. Daily weather conditions likely had an impact on the efficacy of temperature treatments with factors such as wind speed decreasing the overall heat transfer from the system to the pools. There were no significant differences in tidepool temperature between limpet density treatments and no significant interactions between any other predictor variables.
Figure 2.4 Average daily maximum temperatures for the summer of 2018 (solid black line), and the average daily maximum temperature (solid grey line) and 90th percentile of average daily maximum temperatures calculated from the past 30 years (grey dashed line).

Figure 2.5 Average maximum daily tidepool temperature by treatment (points, n=8 per treatment combination per heating day, error bars represent mean ± SE.), control pool water temperature (n=4 with limpet density treatments.
combined, black line), daily air temperature range (grey ribbon), and tide height data (blue shading represents time that the tidepools were submerged, yellow shading highlights 10:00-16:00 which is typically the hottest part of the day) during the field manipulation.

**Figure 2.6** Temperature profile for July 24, 2018 by treatment. Tidepools were exposed by the retreating tide at 06:15 and experimental heating was initiated at 08:30. Curves are fit using Loess regression smoothing and shading represents 95% confidence intervals.

### 2.3.2 Limpet responses to heating

Heating intensity did have a significant effect on the abundance of experimentally added limpets with significantly higher survivorship in the ambient and medium intensity treatments post heating than in the high heat intensity treatment (Figure 2.7; Table 2.2). There was a significant effect of date on post-heating limpet abundance. The degree of mortality of experimentally added limpets varied by heatwave, with especially high mortality in the high heat intensity treatments on August 9, 2018, when the highest temperatures of the summer were reached in the high heat treatment pools. The overall contribution of naturally recruiting limpets to grazing pressure was
low, with recruits (1-4 individuals) present in only 35% of tidepools at the final timepoint and ranging in size from 0.3-1.1 cm compared to the experimentally added limpets measuring 1.5 – 2.8 cm.

Figure 2.7 Average post heat event abundance of experimentally added limpets by temperature treatment from July 26-Aug. 26, 2018. Error bars represent mean ± SE.

Table 2.1 Linear mixed-effect model for a) average daily maximum water temperature during heating manipulation between treatments. N=48 temperature records (8 replicates per treatment combination, 19 days of heating). (*) indicates a significant effect.

<table>
<thead>
<tr>
<th>Source</th>
<th>DFn</th>
<th>DFd</th>
<th>F value</th>
<th>p-value</th>
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</thead>
<tbody>
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<td>2</td>
<td>42</td>
<td>234.7510</td>
<td>&lt;0.001*</td>
<td>0.7258</td>
</tr>
<tr>
<td>date (d)</td>
<td>18</td>
<td>756</td>
<td>364.1289</td>
<td>&lt;0.001*</td>
<td>0.8687</td>
</tr>
<tr>
<td>h*l</td>
<td>2</td>
<td>42</td>
<td>0.1636</td>
<td>0.8496</td>
<td>0.0018</td>
</tr>
<tr>
<td>h*d</td>
<td>36</td>
<td>756</td>
<td>6.5492</td>
<td>&lt;0.001*</td>
<td>0.1923</td>
</tr>
<tr>
<td>l*d</td>
<td>18</td>
<td>756</td>
<td>0.9099</td>
<td>0.5665</td>
<td>0.0163</td>
</tr>
<tr>
<td>h * l *d</td>
<td>36</td>
<td>756</td>
<td>0.5113</td>
<td>0.9927</td>
<td>0.0182</td>
</tr>
</tbody>
</table>

Table 2.2 Average abundance of experimentally added limpets following simulated heatwaves and Tukey post-hoc pairwise comparisons. N=24 temperature records (8 replicate records per treatment, 5 days of heating). (*) indicates a significant effect.
### 2.3.3 Taxa-specific responses

In this study, tidepool communities were made up of nine core taxa representing four phyla; Crustacea, Cnidaria, Molluscsa, and Chrysophyta. Chlorophyll-a content differed between herbivore density treatments, but this effect was to a degree dependent on heating intensity (Figure 2.8; Table 2.3a). Average chlorophyll-a content per slide was strongly decreased by the experimental addition of limpets, although this effect was slightly more pronounced in the high temperature treatment and less so in the medium and control temperature treatments with a significant interaction between heating intensity and limpet density. There was no main effect of heating treatment on chlorophyll-a content. Average barnacle (*Balanus glandula*) abundance did not differ between heating intensity treatments but was significantly higher in the increased herbivore density treatments (Fig. 2.9 a; Table 2.3 b). There was no effect of heating intensity or limpet density on the abundance of amphipods, mussels (*Mytilus trossulus*), limpets, littorine snails (*Littorina scutulata*), anemones (*Diadumene lineata*), hermit crabs, shore crabs (*Hemigrapsus oregonensis*), or isopods in tidepools (Figure 2.9 a-i; Table 2.3b).
Figure 2.8 Chlorophyll-a content standardized per unit area (ug/cm²) measured as a proxy for microalgal cover in response to heating and average post-heating abundance of experimentally added herbivores (shading represents 95% confidence intervals).
Figure 2.9 Taxa-specific responses to heating and herbivore density treatments: (a) *B. glandula*, (b) amphipod, (c) *M. trossulus*, (d) limpet, (e) *L. scutulata*, (f) *D. lineata*, (g) *H. oregonensis*, (h) hermit crab and (i) isopod abundance per tidepool.

Table 2.3 Effect of heating intensity and limpet density on a) chlorophyll-a content, and b) invertebrate taxa abundances. (*) indicates a significant effect.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>DF</th>
<th>DenDF</th>
<th>F Value</th>
<th>Pr(&gt;F)</th>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a) Chlorophyll-a (LME)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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</table>
### b) Single species effects (ManyGLM)

<table>
<thead>
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<th>Taxa</th>
<th>Source</th>
<th>Deviance</th>
<th>p-value</th>
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<tr>
<td><em>B. glandula</em></td>
<td>heating intensity (h)</td>
<td>0.645</td>
<td>0.977</td>
</tr>
<tr>
<td></td>
<td>limpet density (l)</td>
<td>18.096</td>
<td>0.001 *</td>
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<tr>
<td></td>
<td>h x l</td>
<td>1.245</td>
<td>0.968</td>
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<tr>
<td>Amphipods</td>
<td>heating intensity (h)</td>
<td>0.055</td>
<td>0.985</td>
</tr>
<tr>
<td></td>
<td>limpet density (l)</td>
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<td>0.987</td>
</tr>
<tr>
<td></td>
<td>h x l</td>
<td>0.031</td>
<td>0.989</td>
</tr>
<tr>
<td><em>M. trossulus</em></td>
<td>heating intensity (h)</td>
<td>2.707</td>
<td>0.895</td>
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<tr>
<td></td>
<td>limpet density (l)</td>
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<tr>
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<td>h x l</td>
<td>0.607</td>
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<tr>
<td>Limpets (naturally recruited)</td>
<td>heating intensity (h)</td>
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<td></td>
<td>limpet density (l)</td>
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<td>h x l</td>
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<td><em>L. scutulata</em></td>
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<td></td>
<td>h x l</td>
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<tr>
<td><em>D. lineata</em></td>
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<td>limpet density (l)</td>
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<td></td>
<td>h x l</td>
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<td><em>H. oregonensis</em></td>
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<td></td>
<td>limpet density (l)</td>
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<td></td>
<td>h x l</td>
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<td>Hermit crab</td>
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<td></td>
<td>h x l</td>
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</tr>
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### 2.3.4 Community responses

Increased heatwave intensity had no effect on community structure within tidepools (Table 2.4a; Figure 2.10) or on the variability of community structure within heating intensity treatments (Table 2.4b). Increased herbivore pressure did alter tidepool community structure (Table 2.4a;...
Figure 2.10) but not the variability within limpet density treatments (Table 2.4c). There was no interaction between heating intensity and herbivore pressure on community structure (Table 2.4a). Species richness and Pielou’s evenness were unrelated to heating intensity but were significantly lower with increased limpet density (Figure 2.11 a,c; Table 2.5 a,c). Heating intensity and limpet density did not have a significant effect on the Shannon diversity index in tidepools (Figure 2.11b; Table 2.5b). There was no interactive effect between heating intensity and limpet density on average species richness, Shannon diversity, or Pielou’s evenness.

**Figure 2.10** NMDS plot of tidepool communities following experimental manipulations based on a Bray-Curtis dissimilarity matrix with a Wisconsin double standardization ($N = 48$; Stress = 0.21). The centroid of each treatment combination is indicated by the solid symbols.

**Table 2.4** Effect of heating intensity and limpet density on a) differences in structure and b), c) variability in community assemblage, at the end of the experimental manipulation. (*) indicates a significant effect.
### a) Community structure (ManyGLM)

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<td>limpet density (l)</td>
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<td>h x l</td>
<td>42</td>
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### b) Community variability – Heating Intensity (PERMDISP)

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<td>0.6015</td>
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### c) Community variability – Limpet Density (PERMDISP)

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---

**Figure 2.11** Effects of field-based experimental warming and herbivore density on (a) average species richness, (b) Shannon diversity Index and (c) Pielou evenness, after seven weeks of experimental manipulation.

**Table 2.5** Effects of heating intensity and limpet density on (a) Shannon’s diversity Index and (b) species richness and (c) Pielou’s evenness. (*) indicates a significant effect.

### a) Species richness (LME)

#### Fixed

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<thead>
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2.4 Discussion

With climate change, mean air temperatures are predicted to increase. Further, there will be an increase in the frequency and magnitude of warm days and nights and a decrease in cold days and nights. Importantly, heatwaves not only have direct negative consequences on performance and survival but can have indirect consequences mediated by alterations in species interactions. Understanding how increased summer temperatures will impact community structure in conjunction with key ecological processes such as herbivory is therefore an important step towards understanding how ecosystems will respond to climate change.

Herbivore density manipulations were successful with a greater abundance of limpets in the increased limpet density treatments than in the ambient limpet density treatments throughout the manipulation. Naturally recruiting gastropod herbivores (limpets and littorines) were rare overall
While there were decreases in limpet abundances post-heating, individuals were replaced after each heating event to maintain high levels of herbivory in the high limpet density treatments.

Based on previous studies on interactions between temperature and herbivory, I predicted that increased tidepool temperatures would alter organismal performance and species interactions. However, in this study heating intensity did not have a significant effect on any community level responses (community structure, community variability, Shannon diversity, average species richness, or Pielou’s evenness). Overall there were no changes in the species present or their abundances in the heated vs ambient tidepools or in the β-diversity within temperature treatments. In contrast to the general absence of temperature effects, herbivore manipulations significantly altered species richness and Pielou’s evenness, with richness increasing and evenness decreasing significantly with increasing limpet density. No other community-level metrics or invertebrate species abundances were impacted by limpet density manipulations.

Chlorophyll-a content was reduced with high limpet density but, the magnitude of this effect was dependant on the level of warming with a greater decrease in the high heat intensity treatment. Interestingly, chlorophyll was the only response variable for which the magnitude of the herbivore effect depended on temperature or vice versa (i.e., the temperature x herbivore interaction was significant).

The absence of thermal effects on species abundances and community composition was unexpected as many biological and ecological processes are known to be temperature dependent. Previous studies have shown that warming can alter community structure and species richness (Gruner et al., 2017; Kordas et al., 2015; Smale & Wernberg, 2012) but the magnitude and
directions of change can be contingent on the local species composition. On Salt Spring Island, BC, Canada, field-based passive warming of settlement plates by an average of 2°C in the intertidal caused a reduction in invertebrate diversity and change in community structure, with herbivores being rare or absent on warmed plates, and a reduction in the abundance of habitat forming species such as barnacles (Kordas et al., 2015). Further, a shallow sub-tidal warming experiment showed altered community structure on heated (approx. + 2°C) settlement plates compared to control plates, however, the direction of change in mean species richness differed between experimental sites. This suggests that changes in community structure with warming are dependent on the local community assemblage (Smale & Wernberg, 2012).

Organisms living in Burrard Inlet frequently experience high temperatures during the summer (Thomson, 1981) and are likely adapted to living at extreme temperatures during low tide. Although the summer of 2018 was one of the warmest summers that Vancouver, BC has experienced recently, it was not the warmest summer that organisms in this area have experienced. For example, in 2004, mean and maximum air temperatures for July and August (19.5°C and 29.8°C respectively) were higher (by 0.8°C and 0.7°C respectively; Environment and Climate Change Canada, 2019). Further, while heated tidepools were significantly warmer than controls (during the manipulation), and the magnitude of warming (+ 4.0°C ) was greater than magnitudes of warming that have caused ecological effects (+ 2.0°C), overall, they did not reach temperatures as high as other studies (mean maximum temperature of 40.9°C on plates in Kordas et al. study compared to 35.5°C here) or temperatures that they would experience in other intertidal microhabitats. Most organisms recorded in tidepools in this study, can also be found outside of tidepools on emergent rock or at higher elevations in the intertidal where their body temperatures can get much warmer during summertime low tides. As a result, they are
likely adapted to more extreme temperatures than they would experience in a tidepool, even with aggressive levels of warming. *B. glandula*, for example, has a $CT_{\text{max}}$ (critical thermal maximum) of approximately $44\pm1^\circ C$ (CK unpublished data) in air which is $10^\circ C$ higher than the maximum tidepool temperatures used in this study. This suggests that in tidepools, organisms like barnacles that live both in and out of tidepools have a large thermal safety margin between their $CT_{\text{max}}$ and the maximum habitat temperatures that they would experience. As a result, with warming tidepools in Burrard Inlet will likely continue to act as a thermal refuge during extreme events. Another factor that could be important to consider is the successional stage of the system. This experiment tested the influence of increased heating intensity on early successional stages of tidepool communities; however, it is possible that late-successional stages could be more vulnerable to warming. In marine fouling communities, heat-wave resistance has been shown to decrease with age such that juvenile assemblages are more resistant to experimental warming than adult communities (Sorte et al., 2010). It is possible that late-successional communities would be differentially impacted by an increased intensity of extreme heat events.

In this study, the greatest changes in community structure were association with increased levels of herbivore pressure. Chlorophyll-a content decreased in the high herbivore density treatments compared to ambient conditions, however it decreased to a greater degree in the high heat intensity treatment than in other temperature treatments. This could be due to an increase in the metabolic demands of herbivores at elevated temperatures. Warming has been shown to increase the strength of herbivore plant interactions (Carr et al., 2018; O’Connor, 2009) and in the lab, a simulated heat event has been shown to increase consumption rates of turf-algae by gastropod herbivores (Ghedini et al., 2015). Follow-up work is required to determine the mechanism behind the observed pattern in this study. In low densities, diatoms can act as a settlement cue for
barnacles increasing recruitment (Le Tourneux & Bourget, 1988), however in high densities, diatoms can impede barnacle settlement and recruitment through competition for space (Connell, 1961a; Luckens, 1975). Changes in microalgal cover could therefore have large impacts on recruitment and the development of early successional communities.

In this study I used an increased density of herbivores to simulate increased grazing pressure. Although we might expect the metabolic demands of herbivores to increase with temperature, thus causing an increase in grazing pressure, extreme temperatures can also reduce herbivore performance (Miller et al., 2015) and have lethal effects (Harley, 2008; Williams & Morritt, 1995), ultimately decreasing the efficiency of energy transfer and biomass of primary consumers in the system (Ullah et al., 2018). In this study, I found that there was high mortality in experimentally added limpets in the high heat intensity treatment, especially when temperature was manipulated on top of a naturally occurring extreme heat event. Previous studies have estimated the CTmax of *L. pelta* to be 34°C in air (Miller et al., 2015) and lethal temperatures to be 34-35°C in water (Wolcott, 1973). This indicates that the larger, experimentally added herbivores were likely unable to cope with the most extreme temperatures (35-39°C) and reached a physiological threshold. It is also possible that some limpet mortality was due to cumulative stress effects compounded over multiple simulated heat events. At the beginning of the summer there were increasing levels of post-heatwave limpet mortality with heating intensity but by the end of the summer there were low levels of mortality in the control and high heat intensity treatments and high levels of mortality in the medium heat intensity treatment. Individuals in the control temperature treatments would experience low levels of thermal stress over the course of the summer, but individuals in the high temperature treatments would also likely have low cumulative stress effects on average as limpets were replaced more frequently than in other
treatments, and almost entirely after the die-off which occurred approximately half-way through the experiment. As a result, by the end of the experiment, limpets in the medium heat intensity treatment may have had the highest cumulative levels of heat stress. Although limpet density was maintained throughout this experiment by replacing dead individuals after each heat event, without replacement the added limpets would have become absent early on in the high heat intensity treatment, rendering that treatment similar to the ambient limpet density, high heat intensity treatment. My results suggest that gastropod herbivores are less robust to warming than sessile marine invertebrates and primary producers. Consequently, it is likely that we will see a reduction in the abundance of dominant herbivore species as the intensity of extreme heat events increases, highlighting an important potential indirect effect of warming on community composition. This is significant as herbivores have been shown to buffer communities against warming (Kordas et al., 2017). In the absence of herbivores, warming had a greater negative impact on community structure than when herbivores were present. Herbivore exclusions caused a decreased abundance of barnacles and sessile invertebrates and shifted communities towards a diatom dominated state. Due to the geographic isolation of the Salish Sea relative to sources of warmer adapted genotypes or species (see e.g., Helmuth et al. 2002, Helmuth et al. 2006), it is unlikely that we will see replacement of herbivores with warm adapted species in the near term. This could in turn cause important habitat-forming species (e.g., barnacles) to be outcompeted by algae, reducing community diversity.

In addition to grazer manipulations, I was able to achieve two different levels of heating in this study with significantly greater maximum and mean daily water temperatures in medium (+2.5°C, +2.0°C respectively) and high (+5.0°C, +4.0°C respectively) heat intensity treatments relative to the controls. The degree of heating was found to be dependent on the day of the
manipulation. This can likely be attributed to variation in environmental conditions such as air temperature, wind speed, wind direction, and precipitation which would affect the efficiency of heat transfer through the system. This in-situ heating technique maintains natural patterns of thermal variability and it can be scaled to effectively heat relatively large organisms (compared to previous in-situ heating methods) or organisms that aren’t necessarily in complete contact with the substratum but immersed in the tidepool (macroalgae, mobile crustaceans, plankton, etc.). Since the tidepools were open, organisms were free to move in and out of pools throughout the course of the experiment. While many organisms found in the tidepools were sessile or slow moving it isn’t possible to know exactly how much heating mobile organisms (i.e. amphipods, shore crabs, etc.) experienced over the two-month experiment. Nevertheless, this study provides a method that can be used in the future to explore questions surrounding warming and global change in the field.

In summary, I found that increased water temperature during low tide had little effect on community structure and composition in tidepools, but that herbivore pressure altered species richness, microalgal cover, and barnacle abundance. While an increase in mean air temperatures by 2-4°C may not directly impact community composition in mid intertidal pools in Burrard Inlet, it has the potential to alter these communities indirectly through changes in the abundances of large herbivore grazers, such as limpets, that may have lower lethal limits than sessile invertebrates and microalgae. When investigating the response of ecological communities to global anthropogenic stressors it is important to consider local interspecific interactions such as herbivory, which may or may not modify the effects of climate change and can in some cases heavily outweigh them.
3 Biogenic habitat effects outweigh heatwave impacts on tidepool assemblages

3.1 Introduction

Understanding and predicting the response of ecosystems to climate change is perhaps one of the greatest challenges for scientists in the 21st century. While ecosystems naturally experience a great deal of variability, anthropogenic global change is driving increases in environmental extremes (Oliver, 2019). Increases in mean temperature have the potential to affect organismal physiology, species interactions, and ecosystems function, but we have little understanding of how changes in the frequency and duration of extreme temperature events will impact these processes. While organisms experience some degree of thermal variability in their environment, large or prolonged increases in temperature can have consequences on ecosystem function and stability (Smale et al., 2019). Increases in the frequency and intensity of thermal extremes that accompany increases in mean temperature thereby challenge our predictive capabilities and ability to manage, mitigate, or adapt to the ecological consequences of extreme climatic events due to the non-linear relationship between temperature and organismal performance (Vasseur et al., 2014; Vázquez et al., 2017).

Rising global temperatures have increased the frequency and duration of anomalously warm temperature events, referred to as heatwaves, over the past century (Oliver et al., 2018). As heatwaves become more common and gain attention, standardized approaches have been developed for defining and tracking atmospheric and marine heatwaves (Perkins and Alexander 2013; Oliver et al. 2018; Schlegel & Smit, 2018). Atmospheric heatwaves are events lasting for
at least three consecutive days where daily temperatures exceed the calendar day 90\textsuperscript{th} percentile based on a historical baseline period (Perkins & Alexander, 2013), while marine heatwaves are events lasting for five or more days with water temperatures warmer than the 90\textsuperscript{th} percentile based on a 30-year historical baseline period (Hobday et al., 2018). Though gradual increases in mean habitat temperatures can impact organisms, communities, and ecosystems, acute extreme temperature events can have disproportionately large ecological impacts (Gaines & Denny, 1993). Naturally occurring heatwaves have caused mass mortalities, species range shifts, and the closure of fisheries (Oliver et al., 2018). Heatwave impacts and their severity, however, are dependent on characteristics such as the duration and magnitude of the heat event, mean environmental temperature and the background variability of the environment. Even prior to modern global warming, temperate systems experienced higher levels of thermal variability than tropical systems. As a consequence, heatwaves of the same intensity are predicted to have larger impacts in tropical systems than in a temperate system (Janzen, 1967; Vasseur et al., 2014). Hobday et al. (2018) propose that a maximum heatwave intensity of 5°C in a temperate ocean is approximately equivalent to a maximum heatwave intensity of 2°C in a less variable tropical ocean in terms of the sensitivity of biological systems. While scientists predict that temperate systems will be more robust to extreme temperature events, it remains unclear how intertidal communities (Tewksbury et al., 2008), which experience high levels of environmental variability, will respond to increasingly severe heatwaves.

The biological impacts of heatwaves are also highly dependent on the species present in the system, their ecological function, and their thermal tolerance limits. One way that heatwaves can impact communities is through the loss of habitat forming species (Wernberg et al., 2016).
Habitat forming species influence community composition through two primary pathways: 1) the creation of physical structure and habitat, and 2) the buffering of temperature through the provision of cool microhabitat. Habitat forming species influence diversity through increased environmental heterogeneity, larval retention, altered habitat temperatures and refuge from predation (Bertness & Callaway, 1994). The role of habitat forming species in intertidal systems is especially important due to the already high levels of abiotic stress (Leonard, 2000). By buffering abiotic conditions, they allow species to live in areas where they otherwise would not be able to survive. Habitat forming species could therefore increase community stability under stressful conditions, such as a heatwave, but if pushed beyond their physiological limits, their loss could have cascading impacts on community structure and diversity.

Tidepools are an important habitat within the intertidal. They retain water during low tide creating a favourable environment for organisms, minimizing stress due to desiccation, and harbouring high levels of diversity and complex interactions. While many temperate species living in tidepools have positive thermal safety margins (Critical thermal maximum ($CT_{max}$) > maximum environmental temperature $T_{e,max}$), with a 3°C increase in maximum temperatures, thermal safety margins become negative for many species (Vinagre et al., 2019). This suggests that in the absence of acclimatization or adaptation, tidepool organisms may not be able to tolerate more frequent and severe heatwaves. This is especially important as increasingly intense heatwaves could have lethal effects on habitat forming species which play an important role in structuring tidepool communities through increased habitat complexity (Sueiro et al., 2011). On the other hand, differences in the composition of tidepool assemblages and among-species
variation in the thermal tolerance of habitat forming species could allow some communities to persist in the face of extreme temperatures.

In this study, I test how an experimental late summer multiday heatwave impacts community structure and function in intertidal tidepools and if this effect is dependent on the dominant foundation species present (mussels, barnacles, or mat-forming diatoms). I test these questions through the in situ manipulation of water temperature and dominant foundation species in replicate artificial tidepools. Post-manipulation, I counted species abundances, measured whole community clearance rate, and measured community net O$_2$ production and O$_2$ consumption (through light and dark measurements O$_2$ measurements). I predicted that warming would alter community structure (number of species present and their relative abundances) and function (water clearance rate, productivity) in heated pools, directly through the decreased performance and survival of individuals or through the evasion of heated pools, and indirectly through a decrease in the abundance of habitat forming foundation species which facilitate the presence of other species. Further, I predicted that tidepools with more thermotolerant foundation species would be less impacted by heatwaves as there would be fewer cascading impacts on associated or dependant species. I predicted that communities dominated by *M. trossulus* would be most vulnerable to heatwaves as their upper thermal tolerance limit (LT$_{50}$ = 38.3) is lower than that of adult *B. glandula* (LT$_{50}$ = 42.8; Hamilton, 2017). The upper thermal tolerance of marine benthic diatoms are species specific, but the diatom assemblage found in high-shore pools is expected to be more thermal tolerant than barnacles or mussels, as diatoms can dominate even very warm pools in the high-intertidal zone from which macro-invertebrates are absent (Metaxas et al., 1994). Under ambient conditions, I predicted that mussel and barnacle dominated communities would support a greater number of species than diatom dominated communities due to their high
structural complexity (Barnes, 2000; M Tsuchiya & Nishihira, 1986). I predicted that community clearance rates would be higher in mussel dominated communities compared to barnacle dominated communities as previous studies have shown the clearance rate of mussels to be significantly greater than barnacles (Lesser et al., 1992). I predicted that both mussel and barnacle dominated communities would have higher clearance rates compared to diatom dominated communities due to a greater abundance of filter-feeders. Further, I predicted that mussel and barnacle dominated pools would support a greater biomass than diatom dominated pools and therefore have higher levels of O$_2$ consumption. Contrastingly, I predicted that productivity would be highest in the diatom dominated pools both due to a high percent cover of microalgae and a lower abundance of invertebrates than mussel and barnacle dominated communities. Following heating, I predicted that community structure, average species richness, evenness, and diversity would decrease as some organisms and species would be lost from warmed communities. I predicted that communities would have overall reduced clearance rates and rates of O$_2$ consumption due to a decreased performance and/or the loss of individuals. I predicted that rates of O$_2$ production (photosynthesis) would either remain unchanged or increase with warming. Overall, I predicted that there would be an increase in net productivity due to reduced rates of O$_2$ consumption and unchanged or increased rates of O$_2$ production. I predicted that there would be an interaction between heating and dominant foundation species, whereby mussel dominated communities would see the greatest changes in community structure and function post-heating, followed by barnacle and diatom dominated communities due to their respective thermal tolerances as dominant habitat-forming species.
3.2 Methods

3.2.1 Study Site

This experiment was conducted on a representative intertidal sandstone bench in Burrard Inlet, British Columbia (49.273378 N, 123.184121 W). This site, at the end of Dunbar Street in Vancouver, is dominated by a mix of barnacles, mussels, rockweed, and microalgae on the mid-shore, with larger predators such as *Pisaster ochraceus* and *Nucella lamellosa* restricted to the low shore (see Covernton & Harley, 2020; Kay et al., 2019; Konecny & Harley, 2019 for further details of this site). Burrard Inlet is a protected body of water connected to the Salish Sea, and experiences large seasonal fluctuations in sea surface temperature and salinity (Held & Harley, 2009; Thomson, 1981). The tidal range in Burrard inlet is approximately 5 m. Tides are mixed semidiurnal with lower low tides occurring during the day from April through August and therefore intertidal organisms in this area are regularly exposed to high temperatures during the summer. The study site experiences low levels of wave-exposure due to a marina and breakwater immediately to the west, and therefore the risk of dislodgement due to waves and log disturbance is minimal.

3.2.2 Experimental manipulation – dominant species and temperature

This experiment was conducted using the SAUTE (Seaside Array for Understanding Thermal Effects) system. Replicate artificial tidepools were installed in the intertidal (N=42) on April 15, 2019 and were left in the field prior to thermal manipulations (July 30 – August 5, 2019) to allow for recruitment and colonization in the tidepools. Tidepool seawater temperature was manipulated for six days out of a seven-day period (July 30 – Aug. 1; Aug. 3- Aug. 5). No manipulation was conducted on August 2nd due to the risk of thunderstorms. Dominant
foundation species were also manipulated throughout the duration of the summer prior to thermal manipulations in order to create barnacle, mussel, and diatom dominated tidepools. Temperature treatments (ambient, +4°C) were crossed with three dominant habitat types (barnacles, mussels, diatoms). Tidepools were installed at a shore height of approximately 2.5m above Canadian chart datum and cages were placed side-by-side, in one row, parallel to shore (see Figure 3.1).

Each tidepool was constructed by securing a 1L plastic jar (ULINE Ltd., Milton, ON, Canada) into a 6” diameter PVC cap using quick setting cement (QUICKRETE ®, Abbotsford, BC, Canada). SeaGoin’ marine epoxy putty (Permalite Plastics Corp, Compton, CA, US) was set inside the bottom of each plastic jar and coarse salt was pressed into the surface of the epoxy. Once the epoxy was dry, the salt was dissolved using warm water leaving a roughened settlement surface. The pools were constructed using this double pool design so that the outer pool (PVC cap) could act as a water bath for the inner pool. Cages (71cm x 30.5cm x 13cm) were built from PVC coated garden fencing with a mesh size of 5cm x 10cm (Peak Products, Richmond, BC, Canada) in order to secure the tidepools onto the bedrock. Cages were built with a lid so that the
tidepools could be easily accessed throughout the experiment with minimal disturbance. The cages were attached to the substrate using stainless steel screw eyes (anchored into the bedrock) and cable ties and remained in situ for the entire course of the experiment. ibutton data loggers (Thermochron, Maxim Integrated, San Jose, CA, US) were initially installed in 12 tidepools (2 per treatment combination) using SeaGoin’ marine epoxy putty to record tidepool temperature at 1-hour intervals. To increase replication and the resolution of thermal data, an ibutton was placed in each tidepool (N= 42) on May 30, 2019 and set to record temperature at 15-minute intervals. Data loggers were hung above each tidepool and secured to the top of the cage using a cable tie.

After one month of recruitment, some tidepools naturally had a high abundance of barnacles while the others were diatom dominated. Half of the diatom dominated pools were haphazardly selected and diatoms were removed using a toothbrush. I added approximately 150-200 mussels (under 1cm in length; field-collected from a nearby mussel bed) to the pools. The mussels attached to the pools naturally using their byssal threads and spread out to eventually cover the tidepool walls. The remaining 14 pools were left as diatom dominated pools with barnacles being present in some cases but overall in low abundances. Artificial tidepools were then re-arranged in a randomized block design with each combination of temperature and foundation species present within each cage.

Artificial tidepools were heated using the SAUTE (a propane powered turkey fryer heat exchanger) in order to simulate a late summer multiday heatwave. Water was heated in a large pot and irrigation lines were run from the water filled pot into the outer pool of each of the heated treatment pools. A flow control valve was placed at the end of each irrigation line in order to control the flow rate of the water and thus tidepool temperature. The irrigation lines were siphoned at the beginning of each heating period to begin the passive movement of water from
the heating pot to the tidepools. Water in the heating pot was replenished throughout the entire heating period in order to keep water flowing through the water lines at all times. An additional bucket of water was used as a header tank “upstream” of the hot water pot to help ensure that the heating pot remained full. Temperature was recorded in all experimental pools at the beginning of each heating period using a thermocouple (Oakton Temp-100) and measured every subsequent hour. Adjustments to the flow rate of the water lines were made as required to achieve desired temperatures across treatments. Tidepools were heated for four hours total on each of the six heating days. Four hours was chosen based on the amount of time that tidepools would typically be exposed to high temperatures during mid-day summer low-tides. Once the tide came back in, the irrigation lines, turkey fryer, propane tank, and buckets were removed, and the tidepools were left in place.

![Figure 3.1](image)

**Figure 3.1** The SAUTE system set up at Dunbar Street during the late July/early August simulated heatwave (a). One block of replicates with showing the iButton temperature loggers suspended in each pool (b).

### 3.2.3 Data collection

*Dissolved oxygen measurements*
In order to measure relative oxygen production and respiration between treatments, I measured dissolved oxygen (DO) at two time points: 1) one hour after exposure during a night time low-tide (4:30 am August 6, 2019) and 2) one hour after exposure during the subsequent day time low-tide (3:00 pm August 6, 2019). Reference pools (n=3) containing only seawater were also established and were exposed for the same duration and measured in the same way to get an estimate of background DO due to biological activity in the seawater. For each sampling period, after the pools had been exposed for an hour, I filled a 250 ml borosilicate glass bottle with water from each tidepool ensuring that there were no air bubbles in the samples. I stored the samples in the dark and brought them back to the lab immediately after sampling for analysis. Samples were analyzed using a FOXY oxygen sensor (Ocean Optics; access provided by MI O'Connor). The sensor was calibrated using a two-point calibration of 100% DO (seawater aerated for 10 minutes) and 0% DO (seawater + sodium sulfite) measured at the same salinity and temperature as the collected samples. The sensor was calibrated before use during each sampling period and all samples were analyzed within 3 hours of collection.

Community clearance rate

To measure if the tidepool community’s ability to filter water was altered, I measured community clearance rates. During low-tide August 7, 2019 I added 40 ml of Thalassiosira sp. phytoplankton concentrate (~ 8 million cells/mL; cells 8-20 μm; Brightwell Aquatics, PhytoGold-M) to each tidepool in the field. Each pool was stirred, and an initial sample (1.5 mL) was taken. After 15 minutes (determined based on pilot trials as an adequate amount of time to deplete a measurable number of cells), a second sample was collected from each pool. Samples were brought back to the lab and frozen until analysis. A hemocytometer was used to count the cells in each sample. A minimum of 100 cells were counted per sample and based on the number
of squares counted, the concentration of cells per ml was calculated. I then calculated the clearance rate as the proportion of cells cleared per minute.

*Tidepool census*

After community clearance rates were measured, water was siphoned out of the tidepools and they were brought back to the lab. Percent cover of algae was estimated in a standardized area on four sides of each tidepool, to account for differences that could exist between sides. The number of living barnacles were counted in each tidepool. I destructively sampled each tidepool and preserved all content larger than 1mm in 70% Ethanol. Samples were sorted and organisms were counted and identified to the lowest taxonomic unit possible.

### 3.2.4 Statistical analysis

To ensure that the average daily maximum tidepool temperatures were different between temperature treatments but similar within treatments, repeated measures ANOVA was used with temperature and dominant foundation species as between group factors and date as a within group factor. In order to visualize temperature differences in the treatments, average water temperature by treatment combination (n=7) was calculated and plotted alongside observed tide height data for Vancouver Harbour, (Canadian Hydrographic Service, 2019). An ANOVA was used to test the effect of temperature treatment and foundation species on clearance rate. Analysis of Variance was used to test the effect of temperature treatment and foundation species on DO, and to test the effect of temperature treatment on the abundance of foundation species. Where the main effect of foundation species was significant in the ANOVA analyses, a Tukey HSD post hoc test was conducted using the *emmeans* package (Lenth, 2020) to determine which contrasts were significant. To test for changes in community structure due to temperature
treatment and foundation species treatments, I used the *manyglm* function with a negative binomial distribution in the *mvabund* package (Wang et al., 2020). This function was used as it has higher power than traditional multivariate approaches, accounting for a mean-variance relationship, and fitting a separate GLM to each species to test for significance at the community level. This method fits a separate GLM to each species and uses resampling to test for significance at the community level. Model terms were tested for significance using a likelihood ratio test and Monte Carlo resampling with 999, with an “adjusted” p.uni argument, taking into account multiple testing and the correlation between species abundances. Cage ID was used as a blocking variable to allow for cage resampling (abundances are assumed to be independent across cages and not within cages). To test for differences in the multivariate homogeneity of groups dispersions, or beta diversity, between temperature and foundation species treatments, I used the *betadisper* function in the *vegan* package (Oksanen et al., 2019) which uses the PERMDISP (Anderson et al., 2006) procedure. A Bray-Curtis dissimilarity matrix was calculated from the community data and a Non-metric multidimensional scaling (NMDS) was used to visualize the tidepool communities by treatment groups. ANOVA was used to test for the effects of temperature treatment and foundation species on average species richness, Pielou evenness, and Shannon diversity. A Tukey HSD post hoc test was conducted using the *emmeans* package to determine which contrasts were significant where the main effect of foundation species was significant. The manipulated habitat forming species (barnacles, adult mussels larger than 2cm, and microalgae) were excluded from all community-level analyses. I conducted separate analyses to test for the effect of temperature treatment on the abundance/cover of each habitat forming species. ANOVA was used to test the effects of temperature treatment on the abundance of barnacles and the percent cover of diatoms. A non-parametric Kruskal-Wallis test was used to test the effect of temperature on the abundance of mussels as the residuals were non-
normally distributed when running an ANOVA. All analyses were carried out using R statistical software v3.6.1 (R Core Team, 2019).

3.3 Results

During the month prior to the simulated heatwave, daily maximum tidepool temperatures remained similar between temperature treatments (mean +/- SD; Control: 23.0 +/- 2.9°C; Heated: 23.0 +/- 2.9°C; Reference source not found.). Foundation species manipulations had a significant effect on daily maximum temperature, with mussel (mean +/- SE; 22.7 +/- 2.8°C) dominated pools being marginally cooler than barnacle (23.2 +/- 2.91°C), and diatom dominated pools (23.3 +/- 3.0°C; Reference source not found.). This temperature difference could be due to the protrusion of mussels above the surface of the water, potentially increasing evaporative cooling in mussel dominated pools. The exact mechanism behind this pattern remains unknown. There was a significant effect of date on tidepool temperature as well as a significant interaction between the main effects of foundation species and date. During the simulated heatwave, tidepool temperature was significantly higher in the heated treatments (mean +/- SE; 31.9 +/- 0.3°C) compared to the controls (26.1 +/- 0.2°C; Figure 3.2b, Table 3.2). There was a significant interaction between tidepool temperature and date, indicating that the magnitude of experimental heating varied by day. However, heating was consistent across habitat types with no significant effect of foundation species on temperature.

Table 3.1 Effect of temperature (t), foundation species (f) and date (d) on daily maximum water temperature prior to temperature manipulations. (*) indicates a significant effect.

<table>
<thead>
<tr>
<th>Source</th>
<th>Df</th>
<th>Chisq</th>
<th>Pr(&gt;Chisq)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (t)</td>
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<td>0.2338</td>
<td>0.6288</td>
</tr>
<tr>
<td>Foundation species (f)</td>
<td>2</td>
<td>12.5933</td>
<td>0.0018 *</td>
</tr>
<tr>
<td>date (d)</td>
<td>30</td>
<td>24495.9717</td>
<td>&lt;0.0001 *</td>
</tr>
<tr>
<td>t*f</td>
<td>2</td>
<td>0.8457</td>
<td>0.6552</td>
</tr>
<tr>
<td>Contrast</td>
<td>Estimate</td>
<td>SE</td>
<td>Df</td>
</tr>
<tr>
<td>-------------------</td>
<td>----------</td>
<td>-----</td>
<td>----</td>
</tr>
<tr>
<td>Barnacle - Diatom</td>
<td>-0.135</td>
<td>0.202</td>
<td>36</td>
</tr>
<tr>
<td>Barnacle - Mussel</td>
<td>0.541</td>
<td>0.202</td>
<td>36</td>
</tr>
<tr>
<td>Diatom - Mussel</td>
<td>0.676</td>
<td>0.202</td>
<td>36</td>
</tr>
</tbody>
</table>
Figure 3.2 Mean tidepool temperature by temperature and foundation species treatment during (a) the entire summer, (b) the simulated heatwave period with the corresponding tide height (black line; blue shading indicate tidepools were submerged). Yellow shading highlights 10:00-16:00 which is typically the hottest part of the day. Mean tidepool temperatures by treatment combination and tide height throughout thermal manipulations on July 30 are shown in panel c). Shaded intervals around mean temperatures represents SD.
Table 3.2 Statistical results from repeated measures ANOVA of daily maximum water temperature on days that tidepool temperature was manipulated. The generalized eta-squared ($\eta^2_{G}$) value is a measure of effect size that provides comparability across between-subjects and within-subjects designs, (*) indicates a significant effect.

<table>
<thead>
<tr>
<th>Source</th>
<th>Unadjusted DF</th>
<th>F value</th>
<th>p value</th>
<th>$\eta^2_{G}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (t)</td>
<td>1</td>
<td>124.3381739</td>
<td>&lt; 0.0001 *</td>
<td>0.6856</td>
</tr>
<tr>
<td>Foundation species (f)</td>
<td>2</td>
<td>0.2170743</td>
<td>0.8059</td>
<td>0.0076</td>
</tr>
<tr>
<td>date (d)</td>
<td>5</td>
<td>9.5491410</td>
<td>&lt;0.0001 *</td>
<td>0.0953</td>
</tr>
<tr>
<td>t*f</td>
<td>2</td>
<td>1.8265380</td>
<td>0.1760</td>
<td>0.0602</td>
</tr>
<tr>
<td>t*d</td>
<td>5</td>
<td>30.7903897</td>
<td>&lt;0.0001 *</td>
<td>0.2536</td>
</tr>
<tr>
<td>f*d</td>
<td>10</td>
<td>0.1676281</td>
<td>0.9981</td>
<td>0.0036</td>
</tr>
<tr>
<td>t<em>f</em>d</td>
<td>10</td>
<td>0.9507284</td>
<td>0.4884</td>
<td>0.0206</td>
</tr>
</tbody>
</table>

3.3.1 Community responses

Post-heatwave, there were no significant differences in community clearance rate between heated and control pools, however, there was a significant effect of foundation species on clearance rate with mussels having a significantly higher clearance rate than barnacles (Figure 3.3, Table 3.3). The community clearance rate of the mussel- and barnacle-dominated tidepools did not differ from the diatom treatment. Dissolved oxygen concentrations ranged from 7-115 umol/L in the dark (proxy for respiration) and 52-589 umol/L in the light (proxy for net production). To provide context for these measurements the onset of hypoxia (20% saturation) would have occurred at 76 umol/L and saturation would have occurred at 351 umol/L. At the tidepool community level, there was a significant effect of foundation species on dissolved oxygen measured in the dark, but no difference between the pools that experienced the simulated heatwave and the control pools (Figure 3.4a, Table 3.4a). In the dark, mussel tidepools consumed more oxygen than diatom dominated pools, but neither treatment was significantly different from the barnacle dominated pools. In the light, there was a significant but independent effect of temperature treatment and foundation species on DO (Figure 3.4b, Table 3.4b): DO was higher in
the heated tidepools than the control pools, and higher in the mussel dominated pools compared to the barnacle dominated pools.

Figure 3.3 Tidepool clearance rate measured as the average proportion of *Thalassiosira* sp. cells cleared per minute.

Table 3.3 Effect of Temperature and foundation species manipulations on tidepool community clearance rate (average proportion of *Thalassiosira* sp. cells cleared per minute). (*) indicates a significant effect.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>F value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
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<tr>
<td>Temperature (t)</td>
<td>1</td>
<td>0.0000087</td>
<td>0.00000871</td>
<td>0.0504</td>
<td>0.82359</td>
</tr>
<tr>
<td>Foundation species (f)</td>
<td>2</td>
<td>0.0016095</td>
<td>0.00080475</td>
<td>4.6590</td>
<td>0.01587 *</td>
</tr>
<tr>
<td>t x f</td>
<td>2</td>
<td>0.0000073</td>
<td>0.00000364</td>
<td>0.0211</td>
<td>0.97915</td>
</tr>
<tr>
<td>Residuals</td>
<td>36</td>
<td>0.0062183</td>
<td>0.00017273</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Post hoc test – Foundation species (Tukey HSD)

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Estimate</th>
<th>SE</th>
<th>Df</th>
<th>z value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barnacle - Diatom</td>
<td>-0.00344</td>
<td>0.00497</td>
<td>36</td>
<td>-0.692</td>
<td>0.7699</td>
</tr>
<tr>
<td>Barnacle - Mussel</td>
<td>-0.01451</td>
<td>0.00497</td>
<td>36</td>
<td>-2.921</td>
<td>0.0161 *</td>
</tr>
<tr>
<td>Diatom - Mussel</td>
<td>-0.01107</td>
<td>0.00497</td>
<td>36</td>
<td>-2.229</td>
<td>0.0798</td>
</tr>
</tbody>
</table>
Figure 3.4 Dissolved oxygen (DO) in tidepools, one day after heating, measured in (a) the dark (respiration), and (b) in the light (production and respiration). Solid gray lines represent the mean DO in reference pools (n=3) containing only seawater, dashed lines represent SE of the mean.

Table 3.4 The effect of temperature treatment and foundation species on dissolved oxygen measured in the a) dark, and b) light. (*) indicates a significant effect.

### a) Dissolved Oxygen – Dark (ANOVA)

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>Mean Sq</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (t)</td>
<td>1</td>
<td>455.1</td>
<td>455.1</td>
<td>1.0321</td>
<td>0.3165</td>
</tr>
<tr>
<td>Foundation species (f)</td>
<td>2</td>
<td>7702.8</td>
<td>3851.4</td>
<td>8.7349</td>
<td>&lt; 0.0008*</td>
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<tr>
<td>t x f</td>
<td>2</td>
<td>974.8</td>
<td>487.4</td>
<td>1.1054</td>
<td>0.3421</td>
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<tr>
<td>Residuals</td>
<td>36</td>
<td>15873.1</td>
<td>440.9</td>
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</table>

**Post hoc test – Foundation species (Tukey HSD)**

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barnacle - Diatom</td>
<td>-19</td>
<td>7.94</td>
<td>-2.398</td>
<td>0.0554</td>
</tr>
<tr>
<td>Barnacle - Mussel</td>
<td>14</td>
<td>7.94</td>
<td>1.765</td>
<td>0.1957</td>
</tr>
<tr>
<td>Diatom - Mussel</td>
<td>33</td>
<td>7.94</td>
<td>4.164</td>
<td>0.0005*</td>
</tr>
</tbody>
</table>

### b) Dissolved Oxygen – Light (ANOVA)

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>Mean Sq</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (t)</td>
<td>1</td>
<td>196866</td>
<td>196866</td>
<td>7.5791</td>
<td>0.0092*</td>
</tr>
<tr>
<td>Foundation species (f)</td>
<td>2</td>
<td>368346</td>
<td>184173</td>
<td>7.0904</td>
<td>0.0025*</td>
</tr>
<tr>
<td>t x f</td>
<td>2</td>
<td>150089</td>
<td>75045</td>
<td>2.8891</td>
<td>0.0686</td>
</tr>
</tbody>
</table>
Tidepool communities were made up of 11 core taxa in addition to the 3 dominant foundation species (excluded from community-level analyses). I found that both the simulated heatwave and dominant foundation species had a significant effect on community structure but there was no interaction between factors (Table 3.5a, Figure 3.5). Temperature treatment and foundation species did not alter the variability of communities, the beta diversity, within treatments groups (Table 3.5 b,c). Temperature treatment had a significant effect on tidepool average species richness with decreased species richness in tidepools that experienced the simulated heatwave (Table 3.6a, Figure 3.6a). There was also a significant effect of foundation species on average species richness. The barnacle and mussel dominated treatments had higher richness than the diatom dominated communities however there was no significant difference in richness between the barnacle and mussel dominated treatments. There was no effect of temperature treatment on evenness however there was a significant effect of foundation species (Table 3.6b, Figure 3.6b). Diatom dominated communities had greater evenness of taxa between tidepools compared to barnacles however there were no significant differences in evenness between other treatment combinations. Overall there was no effect of temperature treatment or foundation species on Shannon diversity (Table 3.6c, Figure 3.6c).
Figure 3.5 NMDS plot of tidepool communities by dominant foundation species and temperature treatment following a simulated heatwave. Based on a Bray-Curtis dissimilarity matrix with Wisconsin double standardization ($N = 42$; Stress = 0.23). The centroid of each treatment combination is marked by solid symbols.

Table 3.5 Effect of temperature treatment and foundation species on a) differences in structure and b), c) variability in community assemblages, at the end of manipulations. (*) indicates a significant effect.

<table>
<thead>
<tr>
<th>Source</th>
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<th>Deviance</th>
<th>p-value</th>
<th>No. permutations</th>
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</thead>
<tbody>
<tr>
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<td>31.64</td>
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<tr>
<td>Foundation species (f)</td>
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<td>2</td>
<td>178.86</td>
<td>0.001</td>
<td>9999</td>
</tr>
<tr>
<td>t x f</td>
<td>36</td>
<td>2</td>
<td>10.82</td>
<td>0.985</td>
<td></td>
</tr>
</tbody>
</table>

b) Community variability – Temperature treatment (PERMDISP)

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>Mean Sq</th>
<th>F</th>
<th>Pr(&gt;F)</th>
<th>No. permutations</th>
</tr>
</thead>
<tbody>
<tr>
<td>groups</td>
<td>1</td>
<td>0.00758</td>
<td>0.0075821</td>
<td>0.3619</td>
<td>0.51</td>
<td>9999</td>
</tr>
<tr>
<td>residuals</td>
<td>40</td>
<td>0.83798</td>
<td>0.0209496</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

c) Community variability – Foundation species (PERMDISP)

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>Mean Sq</th>
<th>F</th>
<th>Pr(&gt;F)</th>
<th>No. permutations</th>
</tr>
</thead>
<tbody>
<tr>
<td>groups</td>
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<td>0.014491</td>
<td>0.8199</td>
<td>0.4479</td>
<td>9999</td>
</tr>
<tr>
<td>residuals</td>
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<td>0.68932</td>
<td>0.017675</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.6 (a) average species richness, (b) Pielou’s evenness, and (c) Shannon’s diversity index of tidepool invertebrate communities (algal cover excluded) by dominant foundation species and temperature treatment following the simulated heatwave.

Table 3.6 Results of ANOVA analyses and accompanying post-hoc test results (where applicable) on the effect of temperature treatment and foundation species on (a) species richness and (b) Pielou’s evenness and (c) Shannon diversity. (*) indicates a significant effect.

a) Species Richness (ANOVA)

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>F Value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (t)</td>
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<td>9.524</td>
<td>9.5238</td>
<td>5.8537</td>
<td>0.02072 *</td>
</tr>
<tr>
<td>Foundation species (f)</td>
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<td>47.048</td>
<td>23.5238</td>
<td>14.4585</td>
<td>&lt; 0.0001 *</td>
</tr>
<tr>
<td>t x f</td>
<td>2</td>
<td>2.476</td>
<td>1.2381</td>
<td>0.7610</td>
<td>0.47458</td>
</tr>
<tr>
<td>Residuals</td>
<td>36</td>
<td>58.571</td>
<td>1.6270</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Post hoc test – Foundation species (Tukey HSD)

| Comparison             | Estimate | Std. Error | t value | Pr(>|t|) |
|------------------------|----------|------------|---------|---------|
| Barnacle - Diatom      | 2.57     | 0.482      | 5.334   | < 0.0001 *|
| Barnacle - Mussel      | 1.00     | 0.482      | 2.074   | 0.1095  |
| Diatom - Mussel        | -1.57    | 0.482      | -3.260  | 0.0067 *|

b) Pielou’s Evenness (ANOVA)

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>F Value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (t)</td>
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<td>0.04053</td>
<td>0.4307</td>
<td>0.51581</td>
</tr>
<tr>
<td>Foundation species (f)</td>
<td>2</td>
<td>0.6814</td>
<td>0.34069</td>
<td>3.6206</td>
<td>0.03692 *</td>
</tr>
<tr>
<td>t x f</td>
<td>2</td>
<td>0.1245</td>
<td>0.06226</td>
<td>0.6616</td>
<td>0.52218</td>
</tr>
<tr>
<td>Residuals</td>
<td>36</td>
<td>3.3875</td>
<td>0.09410</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Post hoc test – Foundation species (Tukey HSD)

| Comparison             | Estimate | Std. Error | t value | Pr(>|t|) |
|------------------------|----------|------------|---------|---------|
| Barnacle - Diatom      | -0.312   | 0.116      | -2.689  | 0.0284 *|
| Barnacle - Mussel      | -0.147   | 0.116      | -1.265  | 0.4238  |
| Diatom - Mussel        | 0.165    | 0.116      | 1.424   | 0.3393  |

b) Shannon Diversity (ANOVA)
3.3.2 **Taxon-specific responses**

There was a significant effect of temperature and habitat treatment on the abundance of the marine isopod, *Gnorimosphaeroma oregonense*. Isopods were more abundant in non-heated pools and either absent or present in very low abundances in heated tidepools (Figure 3.7a, Table 3.7). *G. oregonense* was also more abundant in mussel and barnacle dominated pools. There was a significant effect of foundation species on the abundance of amphipods, mussel recruits, ribbon worms, *Ulva*, polychaetes and shore crabs (Figure 3.7 b-g, Table 3.7). Amphipods, mussel recruits, ribbon worms, and *Ulva* were more abundant in the barnacle dominated pools while polychaetes and shore crabs were more abundant in mussel dominated pools. Limpets, littorine snails (*Littorina* spp.), clams, and hermit crabs were not significantly impacted by heating or foundation species identity and did not contribute to any structural differences at the community level; however, they were only present in low abundances (0-5 individuals/tidepool). There was no significant effect of temperature on the abundance any of the foundation species (barnacles, mussels, diatoms; Table 3.8, Figure 3.8) however, there was a marginally non-significant trend of fewer barnacles in heated tidepools compared to control pools.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>F Value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.04045</td>
<td>0.040452</td>
<td>1.8924</td>
<td>0.1774</td>
</tr>
<tr>
<td>Foundation species (f)</td>
<td>2</td>
<td>0.05121</td>
<td>0.025607</td>
<td>1.1979</td>
<td>0.3136</td>
</tr>
<tr>
<td>t x f</td>
<td>2</td>
<td>0.00299</td>
<td>0.001494</td>
<td>0.0699</td>
<td>0.9326</td>
</tr>
<tr>
<td>Residuals</td>
<td>36</td>
<td>0.76954</td>
<td>0.021376</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.7 Taxa contributing to differences in community structure between temperature and habitat treatments: (a) isopods, *Gnorimosphaeroma oregonense*, (b) amphipods, (c) mussel, *Mytilus trossulus* recruits, (d) ribbon worm, *Emplectonema gracile*, (e) *Ulva*, (f) polychaetes, and (g) shore crabs, *Hemigrapsus oregonensis*.

Table 3.7 Effect of temperature treatment and foundation species on taxon abundances. (*) indicates a significant effect.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Source</th>
<th>Deviance</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphipods</td>
<td>Temperature (t)</td>
<td>0.497</td>
<td>0.963</td>
</tr>
<tr>
<td></td>
<td>Foundation species (f)</td>
<td>14.444</td>
<td>0.007 *</td>
</tr>
<tr>
<td></td>
<td>t x f</td>
<td>0.034</td>
<td>1.000</td>
</tr>
<tr>
<td>Polychaetes</td>
<td>Temperature (t)</td>
<td>1.214</td>
<td>0.896</td>
</tr>
<tr>
<td></td>
<td>Foundation species (f)</td>
<td>22.18</td>
<td>0.001 *</td>
</tr>
<tr>
<td></td>
<td>t x f</td>
<td>3.175</td>
<td>0.942</td>
</tr>
<tr>
<td>Mussel recruits</td>
<td>Temperature (t)</td>
<td>1.412</td>
<td>0.896</td>
</tr>
<tr>
<td></td>
<td>Foundation species (f)</td>
<td>33.017</td>
<td>0.001 *</td>
</tr>
<tr>
<td></td>
<td>t x f</td>
<td>0.68</td>
<td>0.999</td>
</tr>
<tr>
<td>Ribbon worms</td>
<td>Temperature (t)</td>
<td>1.486</td>
<td>0.896</td>
</tr>
<tr>
<td></td>
<td>Foundation species (f)</td>
<td>31.44</td>
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</tr>
<tr>
<td></td>
<td>t x f</td>
<td>0.618</td>
<td>1.000</td>
</tr>
<tr>
<td>Shore crabs</td>
<td>Temperature (t)</td>
<td>0</td>
<td>0.996</td>
</tr>
<tr>
<td></td>
<td>Foundation species (f)</td>
<td>15.935</td>
<td>0.002 *</td>
</tr>
<tr>
<td></td>
<td>t x f</td>
<td>1.78</td>
<td>0.995</td>
</tr>
<tr>
<td><em>Ulva</em></td>
<td>Temperature (t)</td>
<td>0.171</td>
<td>0.987</td>
</tr>
<tr>
<td></td>
<td>Foundation species (f)</td>
<td>40.883</td>
<td>0.001 *</td>
</tr>
<tr>
<td></td>
<td>t x f</td>
<td>0.246</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>Temperature (t)</td>
<td>20.93</td>
<td>0.001 *</td>
</tr>
</tbody>
</table>
Isopod (Gnorimosphaeroma oregonense) Foundation species (f) 11.098 0.028 *
t x f 0.099 1.000

Littorines (Littorina scutulata)
Temperature (t) 0 0.996
Foundation species (f) 1.846 0.667
t x f 3.172 0.942

Limpets (Lottia paradigitalis)
Temperature (t) 1.045 0.896
Foundation species (f) 3.886 0.519
t x f 0.393 1.000

Clams
Temperature (t) 0.063 0.995
Foundation species (f) 0.12 0.953
t x f 0.102 1.000

Hermit Crabs
Temperature (t) 4.818 0.266
Foundation species (f) 4.007 0.519
t x f 0.526 1.000

Figure 3.8 Response of foundation species to the simulated heatwave; Abundance of (a) barnacles, (b) mussels, and percent cover of (c) Diatoms.

Table 3.8 Statistical results of analyses testing the effect of the simulated heatwave (temperature treatment) on each foundation species. (*) indicates a significant effect.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>Mean Sq</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Barnacle abundance (ANOVA)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
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<td>7132.6</td>
<td>7132.6</td>
<td>4.4642</td>
<td>0.05625</td>
</tr>
<tr>
<td>Residuals</td>
<td>12</td>
<td>19172.9</td>
<td>1597.7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a) Mussel abundance (Kruskal–Wallis)

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>Mean Sq</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
</table>
### 3.4 Discussion

Heatwaves have the potential to impact community diversity and function. While the effects of heatwaves could be dictated by pre-existing community composition, they could also have indirect effects on the community through the loss of habitat forming foundation species. I predicted that heatwaves would alter community structure and function in heated tidepools through a direct loss of species and/or a decrease in the number of individuals due to heat stress decreasing species richness, diversity, and evenness. In addition, I predicted that O\(_2\) production and consumption, and community clearance rate would decrease if the number of individuals and biomass in the community decrease in response to warming. Further, I predicted that community structure (species richness, diversity, evenness) and function (O\(_2\) consumption and production, filtration rate) would be influenced by the interaction between warming and the assemblage dominant where communities with thermotolerant foundation species might buffer the effects of warming on the community. I predicted that heatwaves would most negatively impact mussel dominated communities, followed by barnacle, and then finally diatom dominated communities based on the thermal tolerance of these habitat forming species. While heatwaves will have species-specific effects, impacts on habitat-forming foundation species could be of particular importance as even small decreases in the abundance of these species could have larger cascading effects on tidepool community structure and function.
In this study I found that while there were large community-level differences (i.e. species richness, evenness, species relative abundances) between foundation species treatments, there was little direct effect of heating on tidepool assemblages. Further, I did not find a significant effect of heating on the abundance of habitat forming foundation species. Overall, I found that there were greater differences in species richness between foundation species treatments than between heated and ambient treatments. Communities dominated by barnacles or mussels had greater species richness than diatom dominated communities, even with heating. In contrast, diatom dominated pools had higher community evenness than barnacle dominated pools while mussel dominated pools were not significantly different from either treatment. Further, mussel dominated communities had higher community clearance rates and higher O$_2$ production levels than other foundation species treatments. My results suggest that the dominant habitat-forming species present in this system (barnacles, mussels, diatoms) may be able to tolerate moderate late-summer heatwaves and that understanding the ecological processes or mechanisms that produce these different habitats, and how they could be altered by more intense and more frequent heatwaves, could be of greater importance.

I expected tidepool communities to have a decreased filtration rate post-heating due to a decrease in the abundance or performance of filter feeding invertebrates. I found no effect of the simulated heatwave, however, on clearance rate at the community level. The community census data support the contention that there was little heat-related mortality in dominant filter feeding taxa as I did not measure any significant decreases in the abundance of invertebrate foundation species (barnacles and adult mussels) or in the abundance of mussel recruits. While the average maximum daily temperature in the heated pools was 31.8 +/- 2.5 ºC (mean +/- sd), this is likely
below the lethal limits of the filter feeders present in these communities. For example, the CTmax of *B. glandula* in Burrard inlet is approximately 38.5°C while submerged (CK unpublished data). The CTmax of mussels is likely lower than the CTmax of barnacles as in air, the lethal limit of *M. trossulus* (38.3 °C) is 3.5 degrees lower than the lethal limit of *B. glandula* (42.8 °C; Hamilton, 2017). As a result, we would not expect changes in clearance rates due to changes in abundance. Another way which clearance rate could be altered is due to sub-lethal effects. One physiological response of intertidal ectotherms to extreme temperatures is the production and upregulation of heat-shock proteins which act to rescue damaged proteins and prevent irreversible protein damage (Berger & Emlet, 2007; Hofmann & Somero, 1995). The synthesis of these proteins has an associated fitness cost and therefore could impact organism performance (Krebs & Bettencourt, 1999). Since I measured community clearance rates one day after heating, it is not possible to say if organisms had decreased performance during heating, however, it seems that organisms were able to recover from any damage incurred due to the manipulated heatwave. It is also possible that organisms remained below thermally stressful temperatures. While the thermal tolerance of submersed intertidal organisms can be lower than when exposed to air (Huang et al., 2015; Hunt & Denny, 2008), maximum tidepool water temperatures are well below the maximum temperature that intertidal organisms would reach on emergent rock during the summer. As a result, they likely have a higher thermal safety margin in tidepool habitats and spend more time in a thermally benign environment.

Similarly, I saw no differences in O$_2$ consumption following a simulated heatwave. I expected that there may be change in O$_2$ consumption in heated communities due to either a decrease in abundance of organisms or a change in metabolism due to thermal stress. While I did see a decrease in the abundance of the isopod *Gnorimosphaeroma oregonense* in the heated treatment,
it appears that reductions in this species were not sufficient to drive a net change in O$_2$ consumption post heatwave at the community level. Mussel dominated pools consumed more O$_2$ than diatom dominated pools, with barnacle-dominated pools statistically intermediate. This follows the pattern that we would expect based on the abundance and size of organisms in the tidepools treatments. The mussel dominated pools have a high abundance of larger mussels in addition to an abundant invertebrate assemblage. The barnacle treatments also hosted an abundance of invertebrates but lacked large individuals. The diatom treatments had the lowest recorded abundances of invertebrates.

In contrast, the net production of O$_2$, used as a proxy for net community productivity (not a direct measurement of net primary productivity), increased post-heatwave in the heated pools. Some studies have found an increase in the photosynthesis of macroalgae during periods of warming (Davison et al., 1991; Sorte & Bracken, 2015), while responses in microalgae have shown to be species-specific (Salleh & McMinn, 2011). Since O$_2$ measurements were conducted post-warming in this study, I expected changes in productivity to be driven by changes in algal biomass and not photosynthetic activity. Although I didn’t find any differences in the cover of macro- or microalgae, it is possible that there were changes in the density or thickness of algal cover that I did not capture in the measurement of percent cover. The loss of small crustaceans (e.g., *G. oregonense*) could have decreased grazing pressure, leading to higher microalgal density in the heated pools; however, more work must be done to determine the mechanism behind this pattern. Mussel dominated tidepools also had higher net O$_2$ production than barnacle dominated pools. In tidepools, *Mytilus californianus* has been shown to increase the amount of inorganic nitrogen and phosphorus in tidepools through animal-excreted ammonium and can increase benthic microalgal abundance by 4-8 times compared to in the absence of mussels.
Tidepools dominated by *M. trossulus* may have had higher nutrient levels than other treatments causing an increase in the productivity of microalgae and therefore net O₂ production. While tidepools did reach hypoxic DO levels during the night and super-saturated DO levels during the day, this is not uncommon in tidepools (see Truchot & Duhamel-Jouve, 1980).

I found little effect of a simulated heatwave on community performance, but I did see a decrease in average species richness. This was driven by a significant decrease in the abundance of *G. oregonense*, a marine isopod distributed along the west coast of North America (Richardson, 1905), in heated pools. It is not possible to say whether the decrease in abundance of isopods was due to high levels of mortality or if they actively avoided the warmed habitats by moving out of the pools. In Head Lagoon, British Columbia, *G. oregonense* has been found in water temperatures ranging from 5-31ºC and have been observed crawling out of water in response to high water temperatures (Standing & Beatty, 1978). These observations suggest that the latter may explain the decrease in abundance of *G. oregonense* in warmed pools. Altered behaviour of *G. oregonense* could impact the turnover of nutrients in the system and energy flow to higher trophic levels. *G. oregonense* is an omnivore and also feeds on marine and terrestrial detritus (Zimmer et al., 2002). Further, it is an important prey species for fish (Howe et al., 2014). It is unclear however what role these marine isopods play in the flow of energy through the food web and therefore more work must be done to understand the magnitude of these potential impacts.

Average species richness was greater in the barnacle and mussel dominated communities compared to the diatom dominated communities. This is not surprising as the importance of habitat-forming species in determining diversity has long been demonstrated (Bruno & Bertness,
The presence of mussels and barnacles in the tidepools increase the heterogeneity and structural complexity of the environment, creating habitat and providing refuge from predation. Barnacle dominated communities had greater abundances of amphipods, mussel recruits, ribbon worms, and macroalgae whereas mussel dominated communities had a greater abundance of polychaetes and shore crabs. Marine benthic diatoms can also increase habitat complexity, but they likely do so at a smaller scale than mussels and barnacles. As a result, the true richness of the diatom dominated communities was conceivably higher than the measured species richness but was underestimated in this study due to the exclusion of smaller organisms during sample processing (< 1mm). While diatom dominated pools had lower species richness and abundances compared to the pools dominated by barnacles or mussels, organisms were more evenly distributed within the diatom dominated pools. Overall, there was no difference in the Shannon-Wiener index between communities as more speciose communities had lower evenness in species abundances.

Naturally occurring heatwaves have caused significant shifts in community structure, decreasing biogenic habitat, biodiversity, and ecosystem health (Smale et al., 2019); however, there have been few in-situ community-level manipulations testing the effects of heatwaves on community structure. A set of *in situ* sub-tidal warming experiments were conducted in Australia with settlements plates heated by ~2°C for 3 weeks (Smale & Wernberg, 2012). At all sites warming caused a significant shift in community structure, however the community-level responses were contingent on the response of the assemblage dominants to warming. Though I did not see any large shifts in the abundance of primary space holders with a simulated heatwave, I did find that the dominant foundation species impacted community structure, species richness, and productivity. This suggests that if the foundation species had been vulnerable to warming
manipulations, they could have driven large changes in community function and composition. Another pattern that has been observed in other studies is the potential for biogenic habitat to buffer the effects of thermal stress on organisms and ecological communities. In the high intertidal zone, for example, seaweed canopies buffer thermal stress through the reduction of maximum daily rock temperatures by 5-10°C, increasing recruitment and survival of intertidal organisms (Bertness et al., 1999). On the other hand, in the lower intertidal zone where thermal stress is minimal, seaweed canopies have neutral or negative effects on recruitment, growth, and survival. Similarly, a passive warming experiment in the intertidal zone on Salt Spring Island, BC demonstrated that on heated plates, herbivores facilitated the presence of barnacles which facilitated the colonization of other mobile consumers that were otherwise absent in warmed communities (Kordas et al., 2017). In this study, I did not find an interaction between dominant foundation species and heating. One potential explanation for the lack of interaction is that biogenic habitat does not ameliorate thermal and/or desiccation stress in tidepools as it does on emergent substrata. In tidepools, although foundation species increase habitat complexity, they do not modify environmental stress, and therefore do not buffer communities from extreme heat events.

My study has demonstrated that a late summer multi-day heating event had little direct effect on tidepool communities despite the fact that temperatures in the heated pools exceeded any other temperatures experienced during the summer by approximately 5°C. This lack of a strong thermal effect contrasts sharply with the large impacts of foundation species on diversity and community function. Heating had the largest impact on the abundance of the mobile isopod, *G. oregonense*, but no consistent measurable impact on other mobile or sessile species in the assemblage. This suggests that factors that control the abundance of tidepool foundation species
could be of greater importance than heatwaves, at least of the duration and magnitude examined here. Thermal impacts on foundation species would occur at some point if temperatures rose high enough; the marginally non-significant decrease in barnacle abundance suggests that I may have been near this threshold in this experiment. Barnacle dominated treatments also had the largest abundance of mussel recruits and therefore, a decrease in this habitat could have cascading impacts on the community as tidepool communities continued through their successional development. Further, depending on spatio-temporal patters of barnacle and mussel recruitment, a decrease in barnacle abundance late in the summer could shift the community towards a diatom dominated community in the absence of sessile invertebrate recruitment.

My study highlights the importance of foundation species in tidepools in determining diversity and function and the potential indirect effects of changes in the small-scale distribution and abundances of foundation species. Future research should expand on what mechanisms act to create different habitats in tidepools and how those processes might be impacted by extreme heat events. Further, it would be of great interest to study these communities on a longer timescale to track the long-term responses of these communities to an extreme heat event. While many unknowns remain in understanding the impacts of heatwaves across scales and systems, my study suggests that tidepool communities, at least at earlier successional stages, may be relatively robust in the face of warming. However, more work must be done to understand how applicable this finding may be to other microhabitats within the intertidal and if my results apply more broadly beyond this study area.
4 Conclusion

4.1 Summary of results

Incorporating increased environmental variability into ecology is necessary as climate change carves a future of uncertainty. While theoretical models allow us to predict physiological changes in a thermally variable environment (Denny, 2017), few empirical tests of these models exist, especially under conditions that incorporate natural cycles of environmental variability and full complements of interacting species. In order to understand how increasingly variable environmental temperatures might impact ecosystems, we must test their potential direct and indirect effects on species and their interactions. In chapter 2, the data that I present demonstrates that tidepool communities in the Pacific Northwest may be not be impacted directly by regular increases in maximum daily temperatures by 2-4°C but that indirect effects through the loss of herbivore grazers could have impacts on community composition. The data that I present in chapter 3 also suggests that because there were few direct impacts of a late summer, multiday heatwave on tidepool assemblages, the loss invertebrate foundation species could have negative consequences for community composition and diversity. While I only observed a slight decrease in the abundance of barnacles, if extreme heat events modify the ecological processes that create and allow different habitat types to persist, then they could have large indirect effects on tidepool communities.

4.2 Effects of extreme heat events on tidepool communities

My thesis demonstrates that realistic increases in maximum daily temperatures (2-5°C) during low-tide in the summer may have little direct impact on tide-pool dwelling species in the Pacific Northwest. While I did not observe any changes in community composition during the first
summer of field manipulations due to heating, I did see changes between density treatments. Communities with grazers present had higher species richness and an increased abundance of barnacles, an important habitat-forming species. On the warmest days of heating manipulations, I also observed high levels of mortality in the experimentally added limpets, suggesting that they could be vulnerable to future extreme temperature events. The loss of grazers could cause increased competition between sessile invertebrates (barnacles) and microalgae (diatoms) resulting in a decrease in cover of the more structurally complex barnacles.

In chapter 3 I sought to understand the importance of foundation species in determining tidepool community composition function as well as test if there was a differential response of habitat forming species to an experimental heatwave. I found that while there was a direct impact of the heatwave on the abundance of one species (a common but not overwhelmingly abundant isopod), overall there was no difference in community performance or productivity due to heating. I found that barnacle and mussel dominated communities were higher in species richness than diatom dominated communities, and that mussel dominated communities had the highest clearance rate and the highest net primary productivity. These results suggest that sessile invertebrate habitat-forming species are important contributors to tidepool diversity. Although there was only a slight decrease in the abundance of barnacles due to heating, more intense and frequent heatwaves could alter the abundance of dominant foundation species directly, or indirectly through a decrease in herbivore pressure as I saw in chapter 2. This thesis contributes to the larger body of research that aims to better understand the relative importance of abiotic factors (including warming and extreme temperature events) vs biotic interactions in structuring communities. While abiotic and regional environmental factors have shown to be more important
than local species interactions in determining intertidal community structure at a large scale (Hacker et al., 2019), my results from chapters 2 and 3, add to a growing number of studies that have found stronger indirect effects of warming on communities through the modification of species interactions (Blake & Duffy, 2012; Lathlean et al., 2017; Ockendon et al., 2014).

4.3 Study limitations

As with all empirical field studies, my experimental manipulations of tidepool temperatures have their limitations and it is important to bear these in mind. While I monitored temperature every hour during heating, there was some degree of variability in treatment temperatures. Occasionally, irrigation lining would get clogged, causing a temperature drop in some pools while other pools remained at the target temperature. Further, on windy days, the experimental heating was less effective, and it was difficult to achieve the high heat intensity treatment temperatures. This variability means that tidepools were not necessarily held at the intended treatment temperatures for the entire four hours of heating. My analyses show that despite these drops in temperature, the treatments remained significantly different from each other, and treatment temperatures were greater than ambient water temperatures.

Another limitation of these studies is that the tidepools were constructed from a combination of roughened marine epoxy and PVC which differed from the walls of a natural tidepool. Larval settlement has been shown to be influenced by settlement surface microtopography, with rougher surfaces having a more turbulent boundary layer than smooth surfaces (Chase et al., 2016; Howell & Behrends, 2006). The roughness, or lack thereof, of the boundary layer will therefore favour certain taxa over others and influence overall community composition.
One drawback of having the tidepools installed in the field is that I was not able to control immigration and emigration of organisms in and out of the tidepools. It is possible that not all of the organisms in the tidepool at the final timepoint were subjected to the entire heating manipulation. This potentially underestimates the effects of a natural heatwave where organisms would be influenced over a larger geographic area, limiting the potential for rescue through immigration or dispersal from surrounding populations (Hanski, 1998). Further, these studies were conducted over relatively short time scales and did not incorporate the potential for tidepool species to acclimate or adapt to more intense heatwaves. There is evidence that temperate tidepool species can acclimate in response to extreme temperature events, increasing their upper lethal limits to resist future heat events (Vinagre et al., 2018). Following exposures to temperatures above mean habitat temperatures, the majority of temperate tidepool species had a higher upper thermal limit than those held at mean habitat temperatures. It is unclear what the adaptive potential of organisms may be to higher temperatures with such a great acclimation capacity in their upper lethal limits (Stillman, 2003). In addition, a difference in acclimation capacities between species, could further alter species interactions and assemblages.

Finally, these studies were conducted on early successional communities and in a relatively low-diversity system which both have implications for the generality of these results. The artificial tidepools were installed during the spring but were only given a few months to establish prior to the thermal manipulations. As a result, both studies were conducted on early successional communities. It would be worth repeating these manipulations in late-successional communities to see if similar patterns emerge or if successional stages are differentially impacted by extreme temperatures as this remains a relatively unexplored question (but see Smale et al., 2015; Sorte et al., 2010). Further, Burrard Inlet where the tidepools were installed, is a relatively species poor
area. This is due to the low levels of salinity in the summer (Held & Harley, 2009; Thomson, 1981) which act as an abiotic filter, limiting the number of species that can establish and sustain populations year-round. It is possible that I would see different results if I were to conduct a similar experiment in a higher salinity, and therefore higher diversity, system such as Salt Spring Island or Bamfield, BC. It is also possible that previous heatwave events could have acted as an abiotic filter (Keddy, 1992), reducing the number of species present at the study site, or at a larger spatial scale, in Burrard Inlet, BC, prior to thermal manipulations. Through filtering the species pool, previous heat events could have reduced the scope for communities to respond to subsequent heating events through the removal of the most sensitive taxa. The intertidal zone in Burrard Inlet is also regularly exposed to high and variable air temperatures in the summer (Thomson, 1981) which could act as a selective mechanism, promoting the persistence of warm-adapted species (Gutschick & BassiriRad, 2003).

### 4.4 Recommendations for future research

I have only melted the tip of the iceberg in this thesis, and while the above-mentioned limitations warrant further work, many questions remain with regards to how ecosystems will respond to extreme heat events. Heatwaves are often defined by characteristics such as their duration and intensity. While we know that these characteristics, along with heatwave timing and frequency, are important when considering the impacts of heatwaves on organisms and their physiology, we have little understanding of how these factors, and their interaction, will impact organisms and ecological processes. One study looked at disentangling the effects of heatwave magnitude, duration and timing on sessile invertebrate assemblages in a mesocosm study and found that there were no clear patterns across treatments (Smale et al., 2015). It would be of interest to investigate the role of recovery temperatures between heat events (during high tide) and cooling
degree-hours in modulating ecological responses to heatwaves. This will be of particular importance in understanding how marine and atmospheric heatwaves may interact in the future as both increase in severity.

Finally, it will be important to consider changes in species phenology, recruitment and succession with more frequent and intense heatwaves. Spatiotemporal variation in recruitment events in the intertidal influence succession and therefore assemblage structure. Previous studies have demonstrated that barnacle, mussel, and fucoid recruitment can vary over 3-4 orders of magnitude with variation in recruitment leading to either mussel beds of fucoid stands as alternative states (Petraitis & Dudgeon, 2015). Further, non-local processes such as availability of recruits and the timing of physical stress have shown to be of primary importance in determining assemblage structure on the shores of Hong-Kong (Hutchinson & Williams, 2001). The timing of extreme thermal conditions relative to recruitment events will therefore be important to consider when predicting the potential impacts on community structure, diversity and function.

Another topic that warrants further investigation is the potential for warm adapted species to replace cold adapted species that are lost due to warming, and whether these changes could maintain ecosystem function and diversity. There is evidence that in open systems with high connectivity, invasions of warm adapted species could help to buffer the effects of climate change on ecosystem structure and function (Zhang et al., 2017). In contrast, isolated systems and tropical systems lacking warmer-adapted species, will require evolutionary adaptation to maintain ecosystem diversity and function (Norberg et al., 2012).
Although I conclude asking likely more questions than I have answered, this thesis demonstrates the importance of understanding and maintaining the ecological processes that contribute to habitat heterogeneity and community diversity. Extreme heat events have the potential to shift, alter, and destroy the ecosystems on which we, and other species, depend. That said, in some systems such as the tidepools I have studied, the role of key species, whose abundance may only be weakly related to warming, can be of much greater importance in determining community structure and ecosystem function. By understanding the direct and indirect effects of heatwaves and other drivers of change, we can move towards a path of understanding and conserving biodiversity and ecosystem services for future generations.

“The process of gathering knowledge does not lead to knowing … An answer is invariably the parent of a great family of new questions”

- John Steinbeck
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