A COMPARISON OF TEMPERATURE AND SALINITY CONDITIONS ON THE EAST AND WEST COASTS OF VANCOUVER ISLAND: IMPLICATIONS FOR INTERTIDAL INVERTEBRATE POPULATION PERSISTENCE IN THE FACE OF CLIMATE CHANGE

by

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ABSTRACT

Climate change is altering the physical and chemical conditions of ocean habitats, including changes to seawater temperature, pH and salinity. Such changes to ocean conditions have the potential to impact marine organisms by altering population abundance or by driving evolutionary change in adaptive traits. The rate at which these abiotic conditions change is important, as this may determine whether populations adapt or are extirpated. Given the significant effects of temperature and salinity on the physiology and performance of marine animals, knowledge of temporal trends and the extent of spatial variations in these conditions is essential to understand the selective pressures that have influenced the evolution of extant populations and to make predictions regarding their persistence in the face of climate change. Therefore, to improve our understanding of the regional climate conditions on the southern coast of Vancouver Island, I have (1) characterized the long-term trends in sea surface temperature (SST) and salinity (SSS) experienced by coastal marine animals during the most stressful time of year, and (2) documented variation between east and west coasts of Vancouver Island in terms of SST, SSS, and intertidal rock surface temperature during low-tide emersion. I then examined the effects of the distinct local climate conditions on east and west coasts on the tolerance thresholds of populations on each coast. Using a series of common garden experiments, the tolerance thresholds of populations of four benthic intertidal invertebrates (*Littorina scutulata, Littorina sitkana, Balanus glandula* and *Nucella* lamellosa) were determined for (1) elevated temperature during low tide emersion, (2) elevated water temperature, and (3) low salinity.

This study found that over an 82 y period, from 1935 to 2016, summertime SST on both coasts increased by 0.67– 0.78 °C (i.e. 0.82 – 0.97 °C per century). Trends in salinity differed between coasts: east coast salinity increased by 3.9 PSU while west coast salinity decreased by 0.64 PSU. Although long-term SST trends are the same on both coasts, east coast waters are on average 4.3 °C warmer, and salinity is 7.8 PSU lower, than on the west coast. Rock temperature in the mid and upper intertidal zone during daytime low tides is 3.9

– 4.2 °C warmer on the east coast. Populations of marine organisms inhabiting the coasts of Vancouver Island have therefore been experiencing long-term changes in abiotic stress as well as persistent spatial variation in climate-related conditions during the most stressful months of the year.

Laboratory experiments revealed three important findings regarding population tolerance thresholds to SST, SSS and emersion temperature among marine invertebrate species. Firstly, substantial differences in tolerance to increased SST and emersion temperature conditions were discovered between species, secondly, similar tolerances to the abiotic parameters existed between east and west coast populations of species, and finally, acute exposure to increased SST and emersion temperature or decreased SSS conditions is not an immediate threat to the populations studied. Overall, it appears that populations are living well within their tolerance limits and their present-day tolerances are well-suited to withstand the predicted changes in ocean conditions.

Keywords: Northeast Pacific; acute environmental stress; climate change; climate change variability; population persistence

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DEDICATION

This thesis is dedicated to my family and close friends for their continued support and motivation for all things near and dear to me. Thank you- Robert, Alesia, and Kyle Iwabuchi as well as Jolene Orkusz and Paul Antonelli.

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CHAPTER 1: General Introduction

Climate change is altering the physical and chemical conditions of ocean habitats around the world, including changes to seawater temperature, pH, and salinity (Harley et al. 2006, Hoegh-Guldberg & Bruno 2010, IPCC 2014). Furthermore, alterations in air temperature due to climate change are compounding the effects of altered ocean conditions within marine intertidal habitats (the area of shoreline exposed during low tide and submerged during high tide), which causes them to be considered a particularly vulnerable ecosystem to the effects of climate change (Harley et al. 2006, Helmuth et al. 2013). The combined effects of changing aquatic and terrestrial conditions may expose coastal marine animals to climate conditions that have never been experienced in the course of the evolutionary history of a species (Hoegh-Guldberg & Bruno 2010), and the rates of these changes might outpace the ability of a species to adapt over time (Chevin et al. 2010). Ultimately, species can respond to changing climate conditions in one of three ways: persistence, migration or extirpation (Aitken et al. 2008, Sorte et al. 2010, Valladares et al. 2014). To persist within a given region in the future, a species must either already possess broad physiological tolerance that will allow it to survive, grow and reproduce under new conditions, or evolve increased tolerance thresholds rapidly enough to keep up with the changing conditions (Chevin et al. 2010). Should enough intertidal species be unable to tolerate alterations in climate conditions, marine community assemblages may become altered and productivity of intertidal ecosystems in turn could suffer. Furthermore, consequences may extend to humans as ecological goods and services (i.e. habitat/refugia, food production, nutrient cycling, culture, recreation etc.) experience decline (Costanza et al. 1997) along with important economic resources tied to the marine intertidal, including fisheries and aquaculture.

The cascading effects of alterations to intertidal species abundance and distribution (i.e. reduced ecosystem health, declines in economic/ ecosystem goods and services etc.) is cause for concern. Attempting to understand and predict the responses of a species to future climate conditions may help mitigate unfavorable outcomes. Predicting future species responses to climate change, however, requires a solid understanding of the rates at which relevant climate parameters (i.e. sea surface temperature (SST), and sea surface salinity (SSS) in the case of intertidal animals) are changing at a local scale that is relevant to the populations of interest (Monaco & Helmuth 2011). Given that regional differences in SST and SSS are influenced by local and regional weather systems, or by pinpoint sources such as localized freshwater input from major rivers, seasonal snow and/or ice melt (IPCC 2014), global or broad oceanic trends do not accurately reflect the conditions experienced by populations of marine organisms within a given geographical region. It is therefore important that trends in SST and SSS be documented separately for each region of interest, and to determine the extent of variation within a region. In the context of climate change projections, this is particularly important for those months when these conditions are most stressful for marine animals. Should significant long-term, prevailing differences exist between regions, there may be potential for evolutionary divergence among populations of intertidal animals, which in turn may have consequences for how each population responds to changing climate conditions.

Accurate predictions of species responses to climate change will also depend, in part, on understanding the extent of physiological variability among populations of the species, as tolerance thresholds may vary among populations as a result of local adaptation (O'Neill et al. 2008, Yampolsky et al. 2014). Given that climate conditions, such as air and sea surface temperature as well as SSS, differ across temporal (e.g. seasons, ENSO events, and interdecadal ocean oscillations) and spatial scales (e.g. latitudinal, regional, local), it is important to consider how local climate conditions (past and present), have shaped the present-day physiological tolerances among different populations (Monaco & Helmuth 2011). Several studies have explored the relationship between present-day local climate conditions and tolerance thresholds in intertidal marine invertebrate populations across spatial scales, from small-scale microhabitats (Harley & Helmuth 2003), to mid-scale latitudinal gradients (Helmuth et al. 2002, Kuo & Sanford 2009, Zippay & Hofmann 2010, Kelly et al. 2012), and even across global scales (Compton et al. 2007, Morley et al. 2016). However, intraspecific variation in tolerance thresholds, specifically variation among populations, is not well understood, likely due to the logistic challenges of such studies: assessments of the link between interpopulation variation and local environmental conditions are most effective when (1) specimens are collected from two or more populations that are distant enough to have limited gene flow and to experience distinct climates, (2) all studied populations are located at a same latitude to avoid confounding latitudinal effects (Bernardo

1996, Levitan 2000) and (3) specimens from all populations are tested at the same time in a common garden setting using similar methodology (Byrne 2012).

Coastal areas surrounding Vancouver Island, British Columbia, Canada, provide ideal conditions for studying the effects of climate conditions on interpopulation variation in tolerance thresholds of intertidal marine invertebrate species (Fig. 1.1). This region of the Northeast Pacific is of particular interest because the southern coast of the island supports all of the aforementioned requirements to make meaningful comparisons of tolerance thresholds between populations across similar latitudes. Populations of intertidal invertebrate species that inhabit the east and west coasts of Southern Vancouver Island are far enough from each other to favor genetic isolation, even among the planktonic dispersing bivalve species *Panopea abrupta* (Miller et al. 2006), while being within a driving distance that allows for same-day sampling from all locations. In addition, there is some evidence that east and west coasts of the island also likely experienced long-term differences in climate conditions (Thomson 1981).

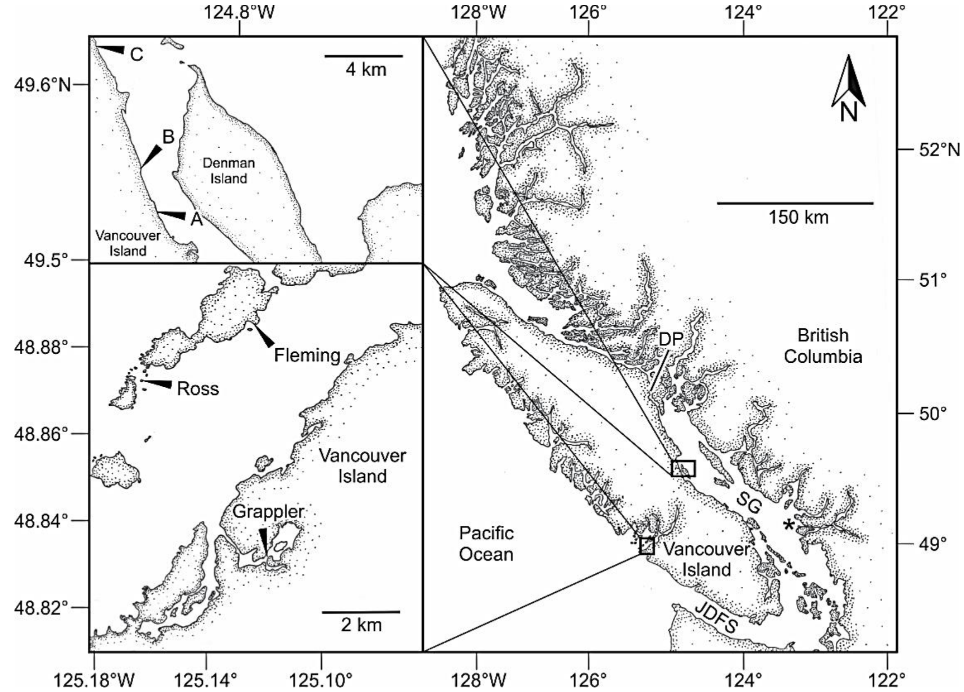

Figure 1. 1. Vancouver Island, British Columbia, Canada (right) with intertidal field sites (n = 6) located on east (top left) and west (bottom left) coasts. JDFS= Juan de Fuca Strait, SG = Strait of Georgia, DP = Discovery Passage. * denotes Fraser River estuary.

The coastal waters along Southern Vancouver Island are influenced by abiotic conditions that vary substantively due to differences in physiography on the east and west coasts. The east coast of the island is separated from the mainland of British Columbia by a 28 km wide oceanic strait known as the Strait of Georgia, a 200-km long basin with a mean depth of 155 m. The Pacific Ocean enters this strait via turbulent water passages on the northern (Discovery Passage) and southern (Juan de Fuca Strait) tips of the island (Davenne & Masson 2001). Surface water properties in this region are known to fluctuate due to the many rivers which empty into the strait (particularly the Fraser River) (Fig. 1.1). These fluctuations in salinity occur seasonally, and are at their peak during May and June, a time which coincides with the spring snow melt (Tully & Dodimead 1957). Sea-surface temperatures in this region peak in late summer (July and August), when cloud cover is minimal and the sun's potential to heat both water and air is maximized (Tully & Dodimead 1957). The physiography of the west coast of Vancouver Island differs from that of the island's east coast in several ways which affect water properties such as SST and SSS. The Pacific waters in contact with the west coast originate from an upwelling domain, a region where deeper, colder, and more saline waters rise to the surface due to northwesterly winds. Because of this phenomenon, summertime sea surface salinities may be between 0.1-0.3 PSU higher than ocean waters outside the zone of upwelling, with peak salinities occurring from July – August. SST along the west coast are also affected by the upwelling through the mixing of deeper, colder waters with warmer surface waters; peaks in west coast SST occur during the month of August (Thomson 1981). Cloud cover and fog are prevalent along the west, with coastal areas experiencing as much as 70% cloud cover in July, and fog lasting an average of 15 days in August (Thomson 1981). Such conditions may affect SST by reducing the amount of solar energy available to heat the surface waters of this region (Tully & Dodimead 1957).

By the year 2100, the entire North Pacific Region is projected to experience substantial changes in climate, including average SST increases as high as 5 – 6 °C (Sanderson et al. 2011) and reductions in salinity ≥0.5 PSU (Plattner et al. 2001). For intertidal benthic marine invertebrates, these changes are compounded by alterations in terrestrial conditions, such as the warming of average annual air temperatures between 1.7 ºC to 4.5 ºC by the year 2100 (White et al. 2016). Although such predictions in SST, SSS and air temperature represent broad regional (North Pacific Region) rates of climate change, variation within these rates may exist at the local level (i.e. east versus west coast of southern Vancouver Island). To fully understand how populations of intertidal animals inhabiting southern Vancouver Island will respond (persist, migrate or extirpation) to future changes in local climate conditions, it is important to explore how past climate regimes may have influenced the development of interpopulation variation in tolerance to specific abiotic conditions that differ persistently between regions. The knowledge of (1) past and present-day trends to changing local climate conditions (e.g. east versus west coast) and (2) how these local climate conditions have affected the interpopulation variation in tolerance will provide more detailed information to policy makers implementing strategies to help mitigate the effects of global climate change along British Columbia's coastline.

Given the significant effects of temperature and salinity on the physiology and performance of marine species, knowledge of temporal trends in these conditions and of the extent of their spatial variation are essential to understand the selective pressures that have influenced the evolution of extant populations and to make predictions regarding their persistence in the face of climate change (Monaco & Helmuth 2011, Sorte et al. 2011). The purpose of Chapter 2 is to document local trends in climate-related abiotic conditions experienced by coastal marine species on the southern coast of British Columbia and to compare the conditions prevailing on the east and west coasts of Vancouver Island. Chapter 2 specifically examines variation in SST and SSS along the coasts of Vancouver Island, focusing on the most physiologically stressful time of year for coastal marine species. Summertime (July & August) SST's impose the warmest and most stressful conditions of the year on either coast, while SSS is at its lowest and most stressful during June & July on the east coast and January & February on the west coast. Historical SST and SSS data were obtained from light stations established along Vancouver Island by the Department of Fisheries and Oceans (DFO). The specific goals of the study were to (1) determine climate change trends on both coasts in terms of (1.1) sea surface temperature and (1.2) salinity over an 82 y period and to (2) determine the extent to which both coasts differ in terms of (2.1) sea surface temperature (2.2) sea surface salinity and (2.3) daytime intertidal rock surface temperatures.

Once long-term trends in climate conditions for the southern coast of Vancouver Island were determined (Chapter 2), their influence on the evolution of tolerance thresholds within local populations were explored. Chapter 3 examines whether the selective pressures imposed by persistent differences in SST and SSS regimes on either coast may have promoted the development of distinct physiological tolerances within east and west coast populations. Should physiological tolerance to temperature and salinity be evolutionarily responsive, then it was predicted that populations on the east coast should have higher tolerance thresholds to elevated temperature and reduced salinity than west coast populations of the same species. Specifically, this chapter examined whether the east and west coast populations differ in terms of tolerance to (1) elevated air temperature, (2) elevated water temperature, and (3) low salinity. Four species of benthic invertebrates common to each coast were studied for this chapter: the marine snails *Littorina scutulata*, *Littorina sitkana,* and *Nucella lamellosa*, as well as the barnacle *Balanus glandula* (Fig. 1.2).

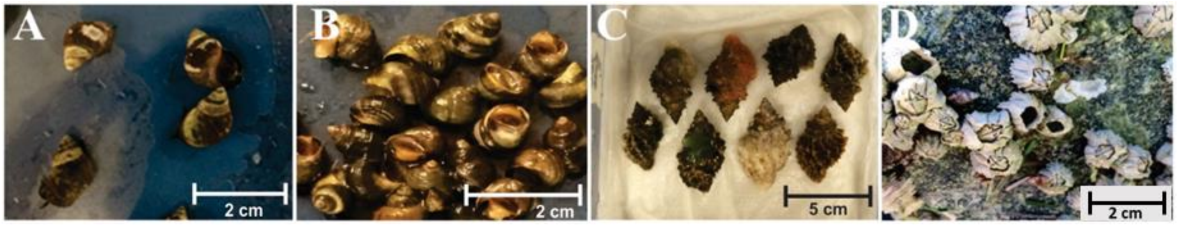

Figure 1.2. Study species of intertidal benthic marine invertebrates common to east and west coast Vancouver Island, Canada. A) *Littorina scutulata*, B) *Littoirna sitkana*, C) *Nucella lamellosa* and D) *Balanus glandula.* Photos by B. Iwabuchi.

To test the tolerances of east and west coast populations, samples of individuals from three sites on each coast were brought to the Bamfield Marine Sciences Centre (BMSC), where they were subjected to common garden experiments under laboratory conditions. Tolerance thresholds were measured, and these were then compared between populations to determine the extent of variation in tolerance. If interpopulation variation in tolerance thresholds exists between populations of coasts on southern Vancouver Island there could be implications for intertidal benthic invertebrate species responses to future climate conditions in the Northeast Pacific region.

In chapter 4, broad-scale implications of the results of chapters 2 and 3 will be reviewed separately and also in relation to one another. In this concluding chapter, the relevance of all the findings will be explored in the context of: (a) management and policy surrounding the mitigation of climate change effects on the coastal marine environment of Vancouver Island and (b) proposed future studies.

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CHAPTER 2: Long-term trends and regional variability in extreme temperature and salinity conditions experienced by coastal marine organisms on Vancouver Island, Canada[1]

INTRODUCTION

Climate change is altering the physical and chemical conditions of ocean habitats around the world, including changes to seawater temperature, pH, and salinity (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010, IPCC 2014). Such changes to ocean conditions have the potential to impact marine organisms by altering population abundance (Hawkins et al. 2008) or by driving evolutionary change in adaptive traits (Reusch 2014). Of particular importance is the rate at which these conditions change, as this may determine whether populations adapt or are extirpated. Temperature and salinity can have significant effects on the physiology and performance of marine organisms (Newell and Branch 1980, Doroudi et al. 1999, Dahlhoff et al. 2002, Portner and Langenbuch 2005, Portner and Kunst 2007, Byrne 2011), especially during the time of year when these parameters reach the most extreme levels. Given these effects, knowledge of these abiotic conditions at various temporal scales (i.e. ranging from long-term climate trends to short-term weather fluctuations) and the extent of their spatial variation are essential for understanding the selective pressures that have influenced the evolution of extant populations and to make predictions regarding their persistence in the face of climate change (Sorte et al. 2011, Monaco and Helmuth 2011).

Sea surface temperature (SST) and sea surface salinity (SSS) are changing over time in most regions of the planet, and present trends in SST and SSS are predicted to continue throughout the remainder of the 21st century (IPCC 2014). Average global SST has been changing at a rate of 1.1°C per century, based on measurements between 1971 – 2010 (IPCC 2014). However, the rate of change in SST is not identical among regions of the planet, and in the case of SSS even the direction of long-term trends differs among regions. Over a 50 y period from 1950 – 2008, certain regions experienced ocean water freshening by as much as 0.2 PSU while other regions became more saline by as much as 0.2 PSU, and others yet have experienced no significant change (Durack and Wijffels 2010, IPCC 2014). Geographic

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[1] A version of this chapter has been published by the Bulletin of Marine Science: Iwabuchi BL & Gosselin LA (2019) Long-term trends and regional variability in sea surface temperature, salinity and rock surface temperature on Vancouver Island, Canada. Bulletin of Marine Science 95: 337- 354 https://doi.org/10.5343/bms.2018.0051

differences in SST and SSS trends result from localized weather systems, such as wind and precipitation patterns, or from pinpoint sources such as localized freshwater input from major rivers, seasonal snow and/or ice melt, and rainfall (IPCC 2014). Consequently, global trends are not an accurate way to assess past, present, or future conditions experienced by populations of marine organisms within a restricted region, such as the rocky intertidal ecosystems of the Northeast Pacific. It is therefore important that trends in SST and SSS be documented separately for each area of interest, thereby accounting for spatial differences in these trends, in addition to determining the extent of variation occurring among geographical areas. In addition, broad averages in temperature or salinity, such as annual or even seasonal (four month) averages, do not inform of the stressful conditions experienced by marine organisms, because temperature and salinity conditions experienced during most of the year cause little or no stress. Only the most extreme conditions, occurring during relatively brief periods of the year (e.g. temperatures during the warmest part of the summer), are stressful to these organisms; it is only during those brief periods that temperature and salinity act as intense selective pressures and cause mortality that influences population abundance and distribution.

The present study thus examines trends over time in SST and SSS, measured during the most stressful time of year, for one region of the Pacific Ocean, as well as variation in these conditions within the region. Specifically, SST and SSS properties were documented within the coastal areas surrounding Vancouver Island, located in the Northeast Pacific. The Northeast Pacific, extending from Oregon to Alaska, is an area of particular interest due to its high primary productivity, high coastal biomass, and high species diversity (Simard 1995). The east and west coasts of Vancouver Island are nevertheless subjected to very different oceanic conditions; the east coast is sheltered within the Strait of Georgia, a 200 km long basin with a mean depth of 155 m that separates it from Canada’s mainland (Davenne and Masson 2001), while the west coast of the island is in direct contact with the open waters of the Pacific Ocean (Fig. 2.1). Such differences in physiography suggest the physical and chemical properties of seawater are likely to differ substantively between the east and west coasts of the island (Tully and Dodimead 1957, Thomson 1981). Furthermore, long-term studies, ranging from 13 to 79 y (between 1935 and 2014), have reported the existence of seasonal and annual variation in SST and SSS along the coast of Vancouver Island, as well as seasonal changes in the degree of ocean water mixing and fresh water input (Pickard and McLeod 1953, Cummins and Masson 2014, White et al. 2016). Although previous studies have documented trends in annual average SST and SSS along the coast of Vancouver Island (Freeland 1990 & 2013, Freeland et al. 1997, Masson and Cummins 2007, Cummins and Masson 2014, White et al. 2016), none have focused on time periods or conditions that are most critical to marine organisms. This knowledge gap may be filled by examining SST and SSS trends during months when these parameters are likely to impose stressful conditions on coastal marine organisms (i.e. high SST and low SSS conditions). Interestingly, intertidal assemblages differ conspicuously between the two coasts in terms of species composition; several invertebrate species that are highly abundant on the west coast are absent or in low abundance on the east coast, such as the snail *Nucella ostrina*, the mussel *Mytilus trossulus,* and the seastar *Pisaster ochraceus* (Gosselin and Iwabuchi, pers. obs.). In addition, there is evidence of genetic segregation between east and west coast populations of some benthic invertebrates with dispersing planktonic larvae, suggesting restricted gene flow between coasts and the potential for local adaptation (Miller et al. 2006).

The present study therefore examines variation in SST and SSS along the coasts of Vancouver Island, focusing on the most physiologically stressful time of year for coastal marine organisms. The study was made possible by a set of monitoring stations along the coastline of Vancouver Island, which are part of the British Columbia Shore Station Oceanographic Program (BCSOP). Most of the stations are lighthouses and have been monitoring seawater conditions daily for over 80 y using relatively unchanged sampling methods which have been used by several other studies (Masson and Cummins 2007; Freeland 2013; Cummins and Masson 2014). The unique physiography of Vancouver Island, coupled with long-term records of SST and SSS conditions, makes this area an ideal natural laboratory to study the conditions faced by populations of organisms inhabiting different geographic locations of this region, particularly in light of current concerns regarding climate change impacts on marine organisms (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010, Monaco and Helmuth 2011). The specific goals of this study were (1) to characterize long-term trends in SST and SSS conditions experienced by coastal marine organisms during the most stressful time of year around Vancouver Island, and (2) to assess the extent of variation between east and west coasts of Vancouver Island in terms of SST, SSS, and daytime rock surface temperatures in the intertidal zone at low tide during the most stressful time of year.

METHODS

Sea surface temperature and salinity

Study sites

Data on SST and SSS were obtained from four monitoring stations, located on the east and west coasts of Vancouver Island, that participate in the BCSOP, two being located on the east coast and two located on the west coast (Fig. 2.1, Table 2.1). Monitoring stations were chosen primarily based on availability of continuous SST and SSS datasets between 1935 – 2016. Both Departure Bay and Amphitrite Point monitoring stations are within close proximity to civilization on their respective coasts, while the remaining two monitoring stations, Entrance Island and Kains Island, are located in more remote areas. Aside from the BC Ferries' terminal being located in Departure Bay, there are no other features of note (i.e. industries, freshwater input, etc.) near the other monitoring stations. At each monitoring station, daily surface temperature and salinity were recorded within one hour of the daytime high tide, at a depth of 1 m, over the 82 y period from 1935 to 2016 (Hollister and Sandnes 1972). SST and SSS data were obtained from the Government of Canada website (http://dfo-mpo.gc.ca/science/data-donnees/lightstations-phares/index-eng.html).

Study design

Sea surface temperature

To quantify trends in peak summertime SST and to compare SST conditions between the east and west coasts of Vancouver Island, data analysis focused on measurements recorded during the months of July and August, the time of year when ocean surface temperature is highest on both coasts (Pickard and McLeod 1953)(Fig. 2.2 A) and thus most stressful for marine organisms. Average summertime SST values for each monitoring station were attained in three steps: (1) obtaining monthly average SST values for July and August from the database (based on daily measurements) for each monitoring station; (2) for each station, combining the July and August monthly averages into a single average for the two months for each of the 82 y, hereafter referred to as the two-month average SST; and (3) a coastal two-month average SST was calculated for each coast by averaging the summertime SST from east coast monitoring stations (Departure Bay (DB) and Entrance Island (EI)), and the same for west coast monitoring stations (Amphitrite Point (AP) and Kains Island (KI)).

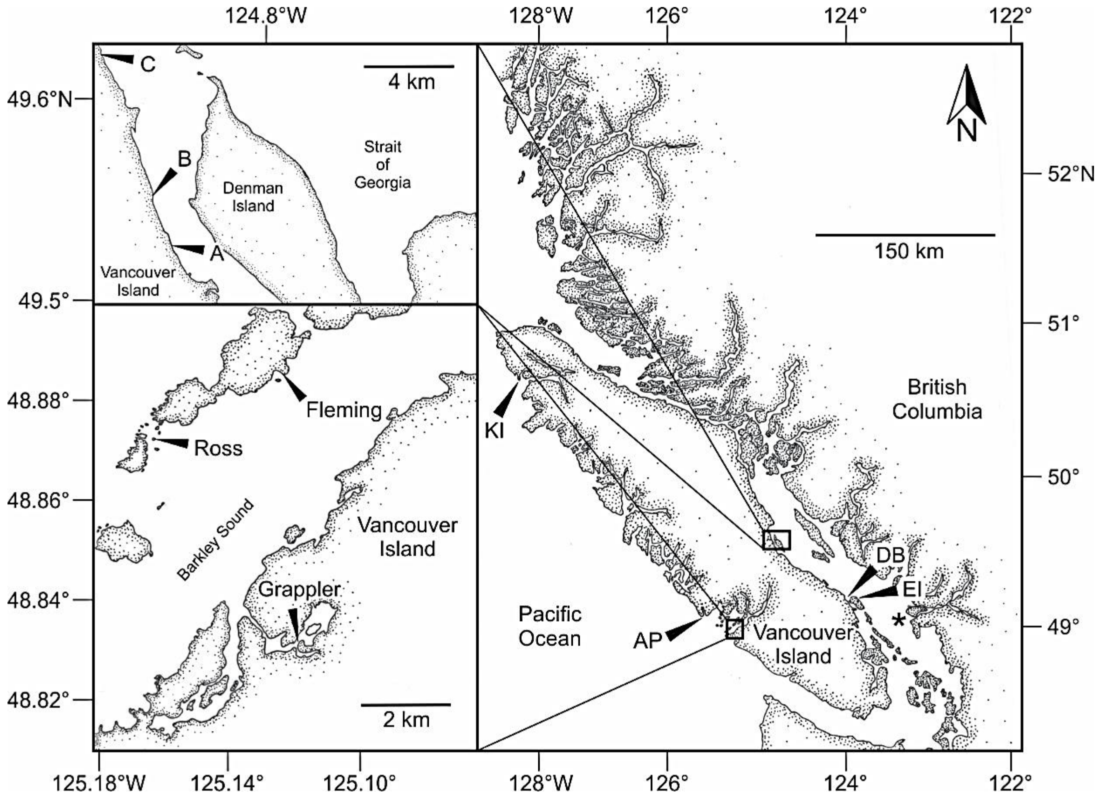

Figure 2.1. (Right) Locations of monitoring stations on the east and west coasts of Vancouver Island, British Columbia, Canada, from which SST and SSS data were obtained, including Amphitrite Point (AP), Kains Island (KI), Departure Bay (DB), and Entrance Island (EI). * denotes Fraser River estuary. (Left) Insets of field sites (A, B, C, Grappler, Ross, Fleming) at which intertidal rock surface temperature was recorded on the east (top left) and west coasts (bottom left) of Vancouver Island, British Columbia, Canada.

Table 2.1. Coordinates of monitoring stations from which SST and SSS data was obtained.

Monitoring station	Latitude (N)	Longitude (W)
WEST		
Amphitrite Point	48° 55.272'	125° 32.468'
Kains Island	50° 26.559'	128° 01.998'
EAST		
Departure Bay	49° 11.738'	123° 57.355'
Entrance Island	49° 12.539'	123° 48.564'

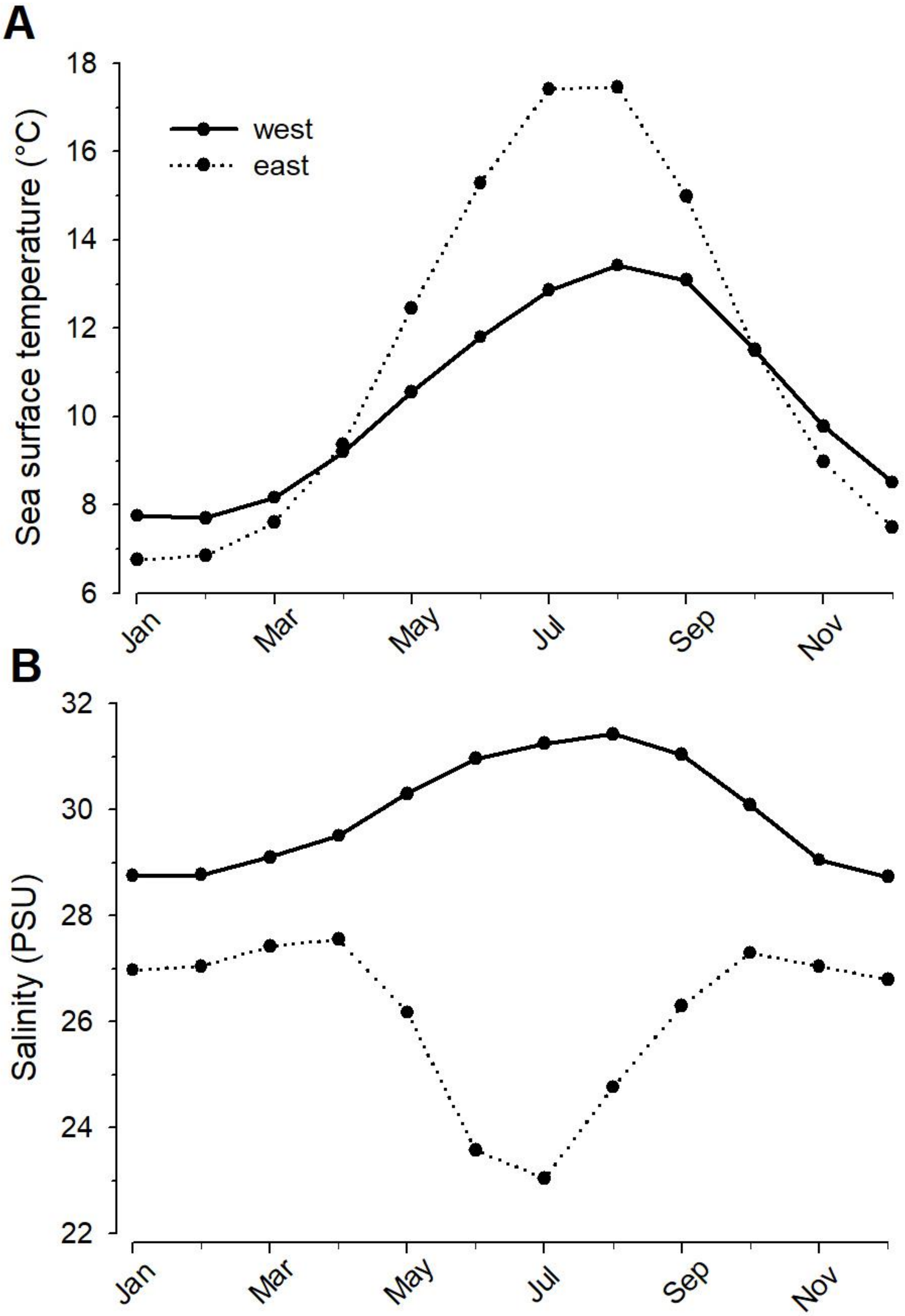

Figure 2.2. Monthly mean values of (A) sea surface temperature and (B) sea surface salinity on east (dotted line) and west (solid line) coast Vancouver Island, recorded by BCSOP monitoring stations (n = 2 per coast) from 1935 – 2016.

We also identified annual extremes in SST conditions for each coast as follows: (1) extracting the three highest daily SSTs throughout July and August for each monitoring station; (2) combining these SST extremes into a single average for each of the 82 y at each monitoring station, termed extreme SST; and (3) extreme SSTs from east coast monitoring stations (DP and EI) were averaged, and the same was repeated for the west coast stations (AP and KI). The two-month average SST and the extreme SST values for each year were then used to determine regional climate change trends in SST and to compare east and west coasts.

Sea surface salinity

To quantify trends in SSS and to compare the salinity of seawater along the east and west coasts of Vancouver Island, a similar approach to that described for SST was used. Here also, data analysis focused on the months of highest stress for marine organisms (i.e. times of reduced salinity conditions); SSS is at its lowest during June and July on the east coast and between November and February on the west coast (Pickard and McLeod 1953) (Fig. 2.2B). For the purposes of this study, SSS measurements were therefore analyzed in June and July for the east coast, and January and February for the west coast. East and west coast extreme SSS values were obtained using the same approach as for extreme SST, except that the lowest salinities were used to calculate extreme SSS conditions.

Daytime intertidal rock surface temperature data

Study sites

To determine temperature conditions experienced by intertidal animals at low tide during the summer on east and west coasts of Vancouver Island, temperature probes were placed in the intertidal zone at three sites on each coast during the months of July and August of 2015 and 2016, as described below. West coast sites were located within Barkley Sound, whereas east coast sites were located in the Strait of Georgia between Fanny Bay and Royston (Fig. 2.1). All six sites were selected based on the following criteria: occurring at similar latitudes, consisting of rocky substrata, and experiencing low to moderate wave action as evidenced by the presence of *Nucella lamellosa*, an intertidal gastropod that does not colonize wave-exposed habitats (Kitching 1976). East and west coast sites nevertheless differed to some extent in substratum, being dominated by boulders on the east coast and by bedrock on the west coast, and by tidal amplitude (Table 2.2).

Table 2.2. Coordinates and characteristics of the intertidal zone at each east and west coast site on Vancouver Island, British Columbia, Canada.

Site	Latitude (N)	Longitude (W)	Substrate	Max tidal height (m)
WEST COAST				
Fleming Island	48° 53.07'	125° 07.40'	bedrock & boulders	3.9
Ross Islets	48° 52.33'	125° 09.72'	bedrock & boulders	3.9
Grappler Inlet	48° 49.91'	125° 07.10'	bedrock & gravel	3.9
EAST COAST				
Site A	49° 32.26'	124° 51.55'	boulders & gravel	5.2
Site B	49° 33.50'	124° 52.30'	boulders & mud	5.2
Site C	49° 36.84'	124° 54.15'	boulders & gravel	5.2

[*] Maximum tidal height refers to the highest high tide recorded in the summer (April – Sept.) of 2015 and 2016 as per DFO chart datum.

Study design

Recording intertidal rock surface temperature

To determine the thermal characteristics of rock surfaces during low tide at east and west coast sites, Thermochron® iButton temperature loggers (model DS1921G-F5) were deployed at two tidal heights at each site: 1.5 m and 2.25 m. These heights were chosen to be representative of high intertidal (2.25 m) and mid-intertidal (1.5 m) shore levels. At each tidal height, three temperature loggers were deployed at 12 – 15 m intervals, totalling 36 loggers simultaneously recording rock surface temperatures (3 temperature loggers × 2 tidal heights × 3 sites × 2 coasts). Loggers recorded temperature over the course of a 50 d period in 2015 and again in 2016, lasting from 1 July to 19 August. All temperature loggers were encased in marine grade silicone and placed in mesh bags, which were then attached to vertical, north-facing surfaces of bedrock or boulders. In 2015, temperature loggers were deployed in grey window-screen pouches (Fig. 2.3A). Due to some damaged pouches and lost or malfunctioning temperature loggers in 2015, thicker black Vexar® netting was used to protect all temperature loggers in 2016 (Fig. 2.3B). Temperature loggers were set to record the surrounding temperature at 15 min intervals, and data were downloaded on a bi-weekly basis.

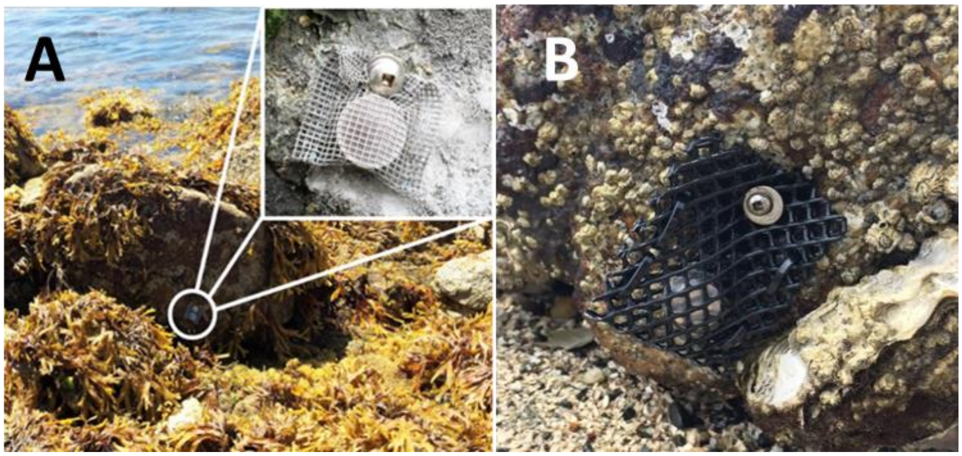

Figure 2.3 Temperature logger installation in intertidal zone, showing (A) the mesh screen bags used in 2015, and (B) the Vexar® bags used in 2016.

Calculation of intertidal rock surface temperature

To characterize the warmest temperatures experienced by intertidal organisms during low tide emersion, data analysis focussed exclusively on daytime temperatures (i.e. recorded between the hours of 8 am and 8 pm) when tides were lower than the height of the temperature logger (1.5 m or 2.25 m), as determined by consulting tide prediction charts for the towns of Bamfield (west coast) and Comox (east coast) (www.tides.gc.ca). To exclude temperature readings that could have been affected by waves splashing above the tideline, an hour of data, just prior to the time of immersion and an additional hour immediately after the time of emersion of the temperature loggers, was also excluded from the analysis. Intertidal rock surface temperatures for each tidal height at each site were then averaged across temperature loggers. Three metrics were extracted from the above datasets to determine thermal characteristics at the 1.5 m and 2.25 m heights for each site: (1) absolute highest temperature, which reports the single highest temperature recorded during the 50 d period; (2) average highest daily temperature, determined by averaging the highest reported temperature per day among the 50 d of the monitoring period, and (3) cumulative hours above temperature threshold, calculated as the cumulative number of hours when temperatures were above a predetermined temperature (27 °C at 1.5 m, and 30 °C at 2.25 m). These temperature thresholds were selected based on thermal tolerances of four intertidal invertebrates occurring at all six east and west coast sites: two marine gastropods (*Littorina scutulata* and *Littorina sitkana*) and a barnacle (*Balanus glandula*) that inhabit the upper intertidal zone (Kozloff 1974, Rudy and Rudy 1983), and a gastropod (*Nucella lamellosa*) found at low and mid-intertidal heights (Bertness and Schneider 1976). In a separate study (Chapter 3), it was determined that *N. lamellosa* could not survive temperatures above 27 °C for prolonged periods, while the three species colonizing higher tidal heights experienced mortality when exposed to temperatures above 30 °C for prolonged periods. The values obtained at all sites for each of the three metrics were then averaged for a given coast to determine the thermal characteristics at each intertidal height for 2015 and 2016.

In addition to the above daytime rock surface temperature metrics, short-term variation in rock surface temperature fluctuations, using all measurements recorded during day and night, is also presented for one sample location on each coast: Fleming Island on the west coast, and Site B on the east coast. All rock surface temperatures recorded at 15 min intervals from 8 June to 6 August 2016 were plotted.

Statistical analysis

Prior to all analysis for SST, SSS, and rock surface temperature parameters, each dataset was tested for normality using the Shapiro-Wilk test, and for homogeneity of variance using the Flinger-Killeen test. No data transformations were performed unless otherwise stated below. Furthermore, SST and SSS data used for regression analysis of long-term trends were tested for serial correlation using the Durbin-Watson test, which revealed no serial correlation in any of the data. All statistical analyses were performed using R statistical software (version 3.2.3) (R Core Team 2015).

Climate change trends on the south coast of British Columbia

Sea surface temperature and salinity

The relationship between the two-month average values (SST and SSS) and time (year) was analyzed by regression analysis for the east and west coasts of Vancouver Island separately, to determine if SST has been changing over the 82 y period on either coast; for each coast, a single regression analysis, combining the data from the two monitoring stations, was carried out. Next, to determine if SST and SSS were changing at a similar rate on the two coasts, the slopes of the regression lines were compared between coasts using an analysis of covariance (ANCOVA). To determine if extremes in SST and SSS have been changing over the 82 y period on either coast and to establish if rates of change were similar among coasts, the annual extreme SST and SSS values were analyzed using the same approach as described above for average values.

Comparisons of east and west coast climate-related conditions

Sea surface temperature and salinity

For SST, the analyses described above of rates of change over time in the two-month average values and in the extreme values found no significant difference between east and west coasts. Consequently, further analysis was carried out to determine if SST and SSS conditions differ between the two coasts; the intercepts of these regressions were compared between coasts by ANCOVA, using time as a covariate. In the case of SSS, however, given that the rate of change in the two-month average values as well as in the extreme SSS values differed significantly between coasts, comparisons of intercepts for SSS between coasts were not possible (Underwood 1981).

Daytime intertidal rock surface temperature

The three metrics used to quantify thermal characteristics of intertidal rock surfaces at low tide were compared between the two coasts using separate random complete block ANOVAs for each tidal height, with year as a blocking variable. A Bonferroni correction was applied for multiple analyses of a same dataset. A square-root transformation was required for cumulative hours above the threshold temperature at 2.25 m to correct for non-homogeneity of variance; no other transformation was required for the other metrics.

RESULTS

Climate change trends on the south coast of British Columbia

Sea surface temperature

Despite substantial year-to-year variation, there was a significant trend of increasing two-month average SST over time on both coasts of Vancouver Island (Fig. 2.4A), as determined by linear regression analysis (Table 2.3). SST increased by 0.67 – 0.78 °C over the 82 y period, corresponding to a rate between 0.82 (95 % CI 0.17 to 1.47) and 0.97 (95 % CI 0.40 to 1.54) °C per century. The slopes of the relationship between two-month average SST and time did not differ significantly between coasts (ANCOVA: $F_{1,161}$ = 0.0301, p = 0.862), indicating a similar rate of change on both coasts.

Extreme SST reached a maximum of 23.25 °C on the east coast and 16.78 °C on the west coast. Extreme SST values also increased significantly over time on the east and west coasts (Fig. 2.4B), as determined by linear regression analysis (Table 2.3). Over the 82 y period, extreme SST conditions increased by 0.66 – 0.92 °C, corresponding to a rate of 0.81 (95 % CI 0.13 to 1.48) – 1.13 (95 % CI 0.22 to 2.04) °C per century. Once again, the slopes of the relationship between SST and time did not differ significantly between coasts (ANCOVA: $F_{1, 150}$ = 0.3211, p = 0.572), indicating that both coasts are undergoing a similar rate of change.

Sea surface salinity

The two-month average SSS values changed significantly over the 82 y period on the west coast of Vancouver Island, but not on the east coast (Table 2.4 and Fig. 2.5A). Along the west coast, SSS during the January and February period has decreased by 0.64 PSU over the 82 y period, which is consistent with a rate of - 0.79 (95 % CI -1.44 to -0.14) PSU per century. The slopes of the relationship between salinity and time differed significantly between coasts (ANCOVA: $F_{1, 161}$ = 6.987, p = 0.009).

SSS extremes (i.e. lowest SSS reported during the two-month period) increased significantly on the east coast of Vancouver Island, but not on the west coast (Table 2.4 and Fig. 2.5B), as determined by linear regression analysis. Over the 82 y period, east coast extreme SSS increased by 3.92 PSU, which corresponds to a 4.84 (95 % CI 2.56 to 7.12) PSU increase per century. The slopes of the relationship between extreme SSS and time differed significantly between the east and west coasts (ANCOVA: $F_{1, 161}$ = 9.1958, p = 0.003).

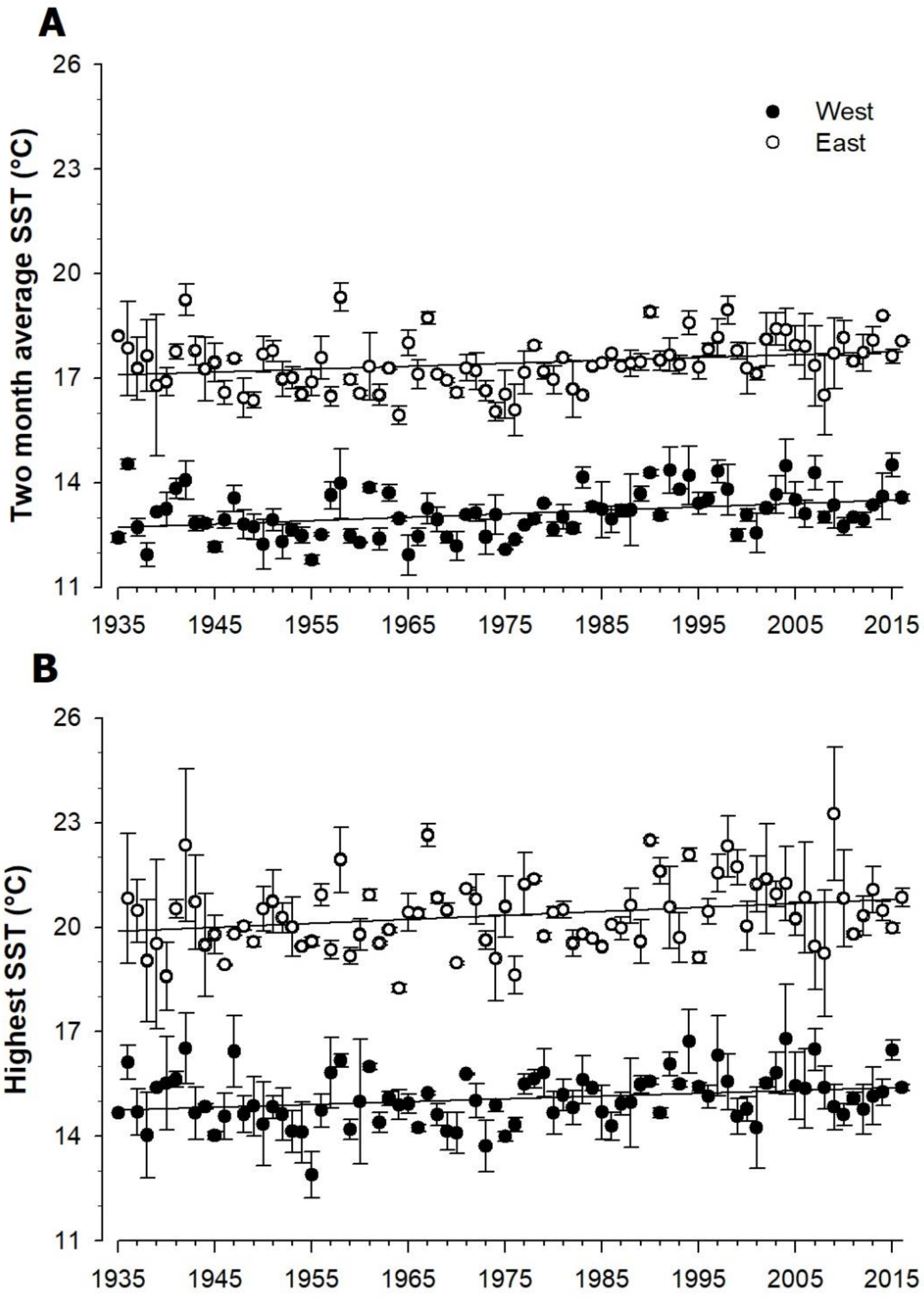

Figure 2.4. Summertime sea surface temperature (SST) conditions on east and west coast Vancouver Island, recorded by BCSOP monitoring stations (n = 2 per coast) from 1935 to 2016. (A) Summertime (July and August) SST on east and west coasts. (B) Highest annual SST conditions reported for east and west coasts. In these graphs, each value represents an average of data from the two monitoring stations per coast, and error bars represent standard deviation.

Table 2.3. Relationship between summertime (July – August) sea surface temperature (°C) and time (year) on the east and west coasts of Vancouver Island from 1935 to 2016; n=82 y for each coast. CI = confidence interval.

Coast	Equation	R^2	p	Trend ± 95% CI °C/century
TWO-MONTH AVERAGE SST				
East	SST = 17.11 + 0.00821×(year – 1935)	0.0724	0.015	0.82 ± 0.65
West	SST = 12.73 + 0.00967×(year – 1935)	0.1256	0.001	0.97 ± 0.57
WARMEST SST OF THE YEAR				
East	SST = 19.89 + 0.0113×(year – 1935)	0.0714	0.014	1.13 ± 0.91
West	SST = 14.80 + 0.0081×(year – 1935)	0.06	0.02	0.81 ± 0.68

Comparisons of east and west coast climate-related conditions

Sea surface temperature

The intercepts of regression lines of the relationships between SST and time differed significantly between coasts of Vancouver Island for the two-month average SST (ANCOVA: $F_{1, 161} = 1687.389$, $p < 0.001$) (Fig. 2.4A) as well as for extreme SST values (ANCOVA: $F_{1, 160} = 1553.580$, $p < 0.001$) (Fig. 2.4B). Over the 82 y, the two-month average SST on the east coast was 4.34 (SD 0.73) °C warmer than on the west coast, and extreme SST was 5.21 (SD 1.04) °C warmer on the east coast.

Sea surface salinity

Given that east and west coast trends were not parallel for either two-month average SSS or extreme SSS, it was not possible to compare corrected mean salinity conditions between coasts using ANCOVA. Observations of plotted SSS data (Fig. 2.5), however, reveals that there is little to no overlap over the entire 82 y period between east and west coast two-month average SSS or extreme SSS conditions, east coast SSS values being consistently lower than on the west coast. Over the last 10 y (2007 – 2016) the east coast was an average of 5.43 (SD 1.70) PSU lower than the west coast in terms of the two-month average SSS (Fig. 2.5A), and an average of 8.72 (SD 2.23) PSU lower in terms of extreme SSS conditions (Fig. 2.5B). It was also noted that the two-month average salinity varied significantly more from year to year on the east coast than on the west coast (Flinger-Killeen test: χ^2 (2, n = 82) = 47.294, $p < 0.001$).

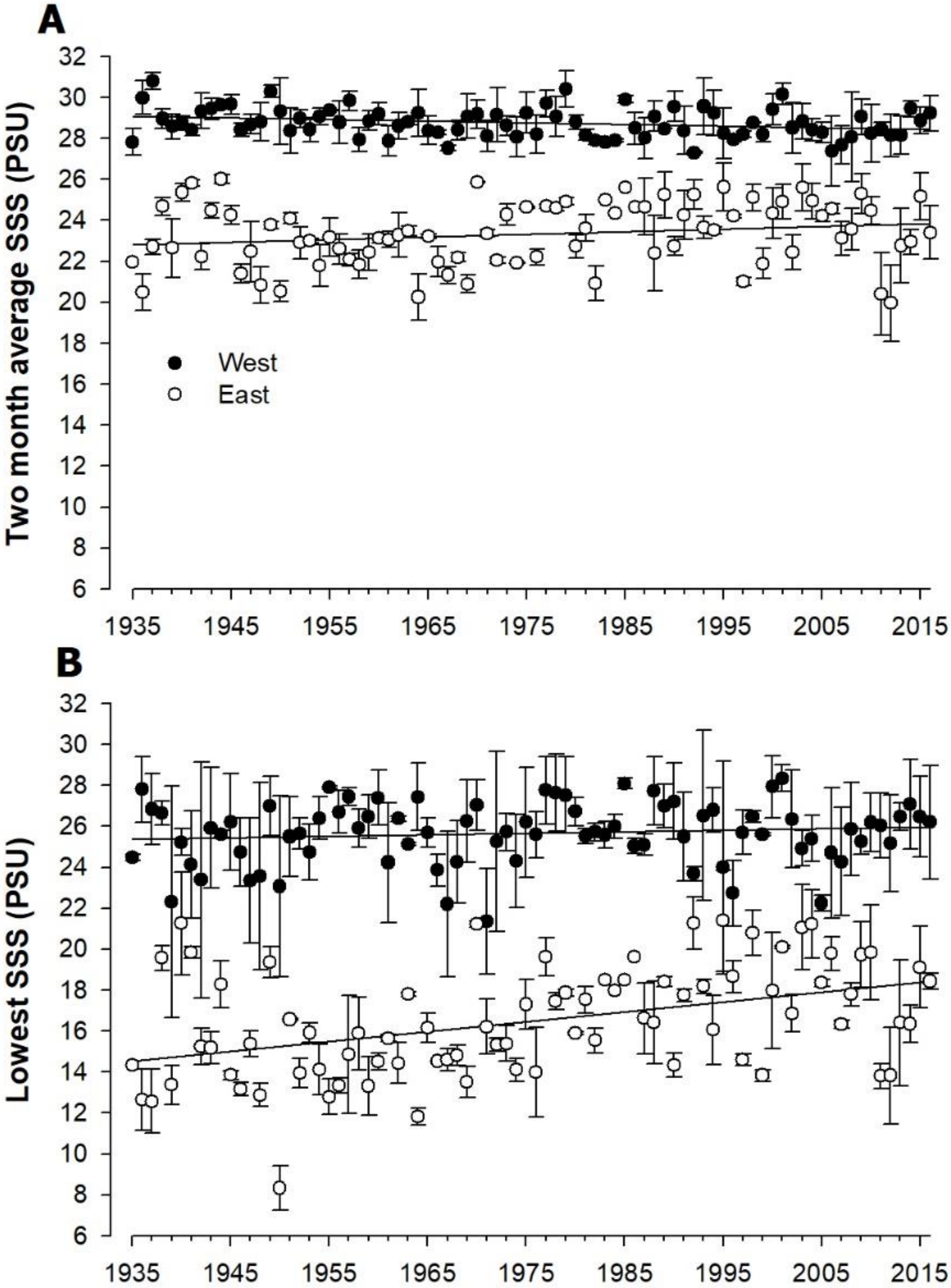

Figure 2.5. Sea surface salinity (SSS) conditions on east and west coast Vancouver Island, recorded by BCSOP monitoring stations (n = 2 per coast) from 1935 to 2016. (A) SSS conditions during the least saline months of the year for east coast (June and July) west coast (January and February). (B) Lowest annual SSS conditions reported for east and west coasts. In these graphs, each value represents an average of data from the two monitoring stations per coast.

Table 2.4. Relationship between sea surface salinity (PSU) and time during the least saline months of the year on the east (June – July) and west (January – February) coasts of Vancouver Island from 1935 to 2016; n=82 y for each coast. CI = confidence interval.

Coast	Equation	R^2	p	Trend ± 95% CI PSU/century
TWO-MONTH AVERAGE SSS				
East	SSS = 21.95 – 0.0127×(year – 1935)	0.0385	0.0773	Not significant
West	SSS = 27.83 – 0.0079×(year – 1935)	0.0690	0.0171	-0.79 ± 0.65
LOWEST SSS OF THE YEAR				
East	SSS = 14.55 + 0.0484×(year – 1935)	0.1821	< 0.0001	4.84 ± 2.28
West	SSS = 24.48 + 0.007 ×(year – 1935)	0.0141	0.288	Not significant

Weather-related trends on the south coast of British Columbia

Daytime intertidal rock surface temperature

To test for differences between coasts in absolute maximum rock surface temperature and in average highest daily temperature during daytime low tides, a Bonferroni correction was applied to the significance threshold (α) to control for type I errors. Using the corrected α of 0.025, absolute maximum temperature (Fig. 2.6 A, B) did not differ significantly between coasts, whether at tidal heights of 1.5 m (Blocked ANOVA: $F_{1, 8} = 1.546$, $p = 0.249$) or 2.25 m (Blocked ANOVA: $F_{1, 8} = 5.458$, $p = 0.047$). However, differences between coasts in average highest daily temperature (Fig. 2.6 C, D) were highly significant at tidal heights of 1.5 m (Blocked ANOVA: $F_{1, 8} = 36.9$, $p < 0.001$) and 2.25 m (Blocked ANOVA: $F_{1, 8} = 27.4$, $p < 0.001$). The average highest daily temperature at the intertidal height of 1.5 m was 3.93 (SD 1.54) °C warmer on the east coast than on the west coast, and at 2.25 m the temperature was 4.22 (SD 1.13) °C warmer on the east coast (Fig. 2.6 C, D). Finally, although the cumulative amount of time that rock surface temperature exceeded the threshold seemed to be slightly higher on the east coast than on the west coast (Fig. 2.6 E, F), the difference was not significant at 1.5 m (ANOVA: $F_{1, 8} = 0.105$, $p = 0.755$) or at 2.25 m (ANOVA: $F_{1, 8} = 4.444$, $p = 0.068$), mainly due to substantial variation among sites within a same coast.

Raw data for rock surface temperature reveals considerable variation over short time periods at sites on both coasts (Fig. 2.7), with temperatures rising rapidly after the tidal emersion, especially on warm sunny days. The lower temperatures in Fig. 2.7 represent submersion temperature, further demonstrating the cooler seawater temperatures on the west coast.

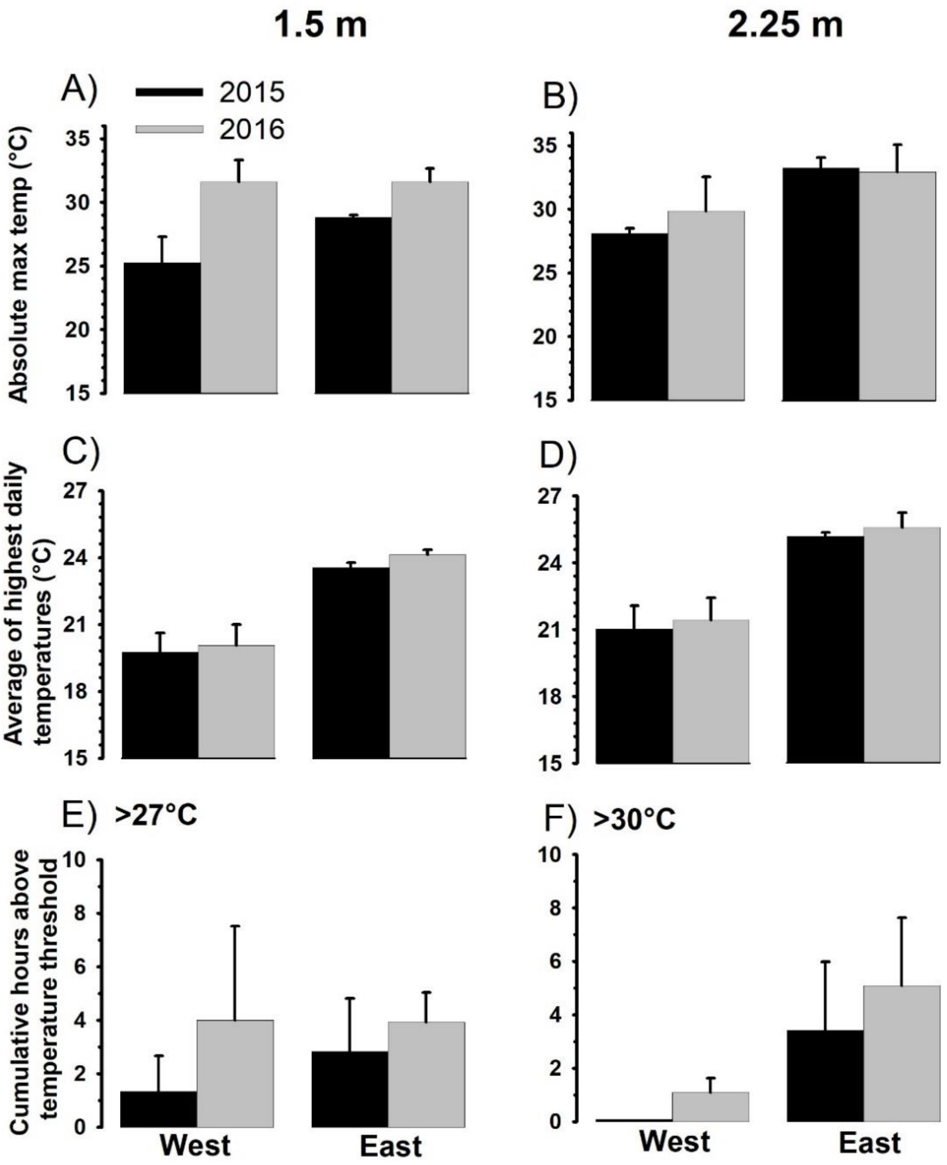

Figure 2.6. Summertime (1 July to 19 August, 2015 and 2016) climate-related abiotic conditions experienced at 1.5 m and 2.25 m intertidal heights on the east and west coasts (n= 3 sites per coast) of Vancouver Island. (A, B) Maximum temperature recorded in both 2015 and 2016 on both the east and west coast. (C, D) The average of highest daily temperatures on both east and west coast. (E) Cumulative number of hours with temperatures exceeding 27°C, at 1.5 m intertidal height. (F) Cumulative number of hours with temperatures exceeding 30°C, at 2.25 m intertidal height. Bars represent averages among the three sites per coast; data from the three sensors per site (for a given tidal height) were averaged, then these averages were pooled among the three sites of a given coast to obtain an average per coast. Error bars represent standard errors.

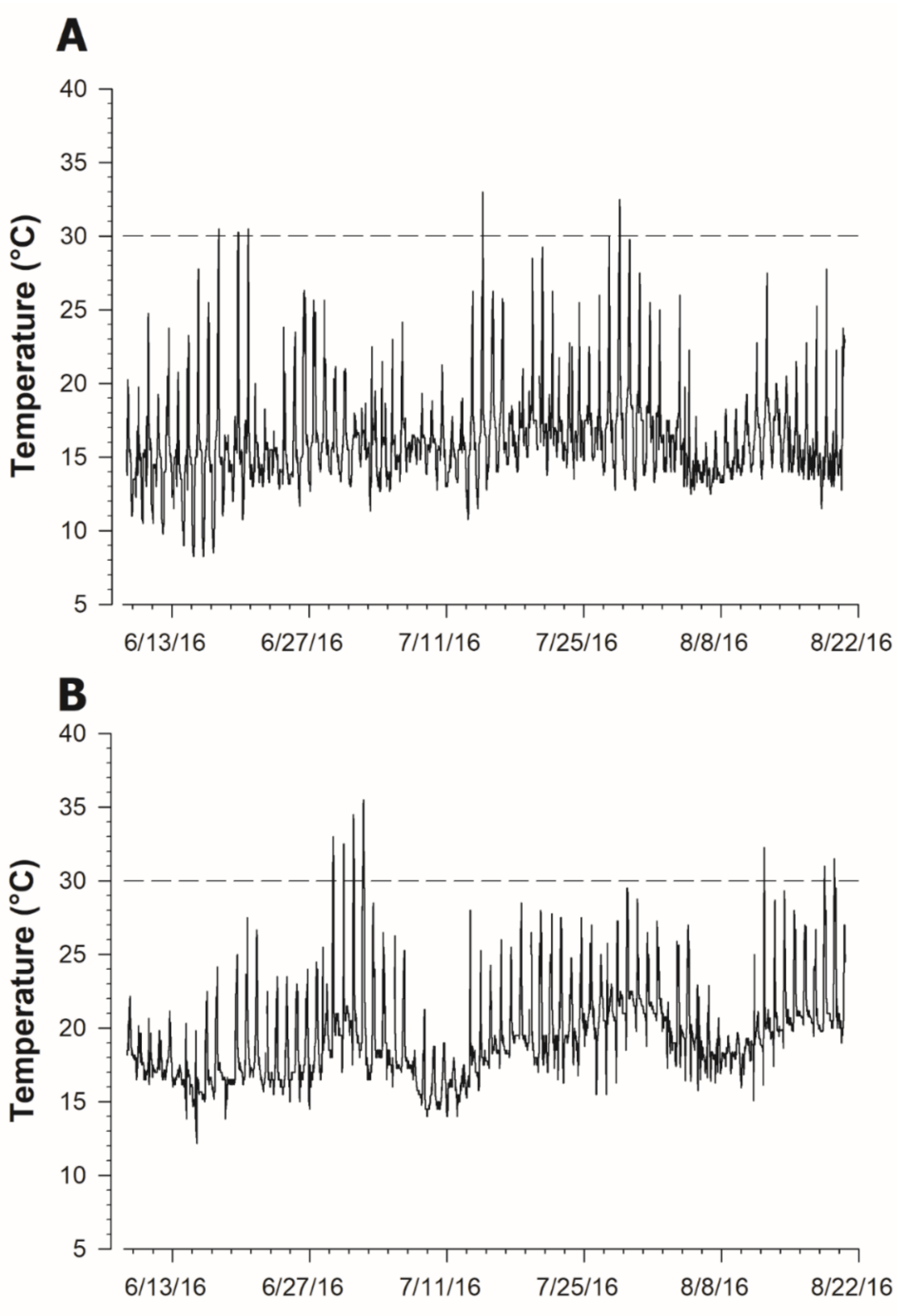

Figure 2.7. Intertidal rock surface temperature variability at 2.25 m, obtained from temperature probes (n = 3 per coast) monitoring from 8 July – 20 August 2016. (A) West coast intertidal rock surface temperature on Fleming Island. (B) East coast intertidal rock surface temperature at Site B (see Fig. 2.1).

DISCUSSION

Climate change trends on the south coast of British Columbia

Current and predicted trends in sea surface temperature

Over at least the last eight decades, marine organisms inhabiting the coastal waters of Vancouver Island have been experiencing gradual increases in SST during the critical July and August summer months when temperature stress is greatest. Summer SST has increased by 0.67 – 0.78 °C between 1935 - 2016, corresponding to a rate of 0.82 – 0.97 °C per century, and the warmest SST reached each year has also increased by 0.66 – 0.92 °C from 1935 - 2016, corresponding to a rate of 0.81 – 1.13 °C per century. These trends in summertime SST are slightly higher than the 0.52 – 0.75 °C increase per century reported by Freeland (2013) using full-year average SST data from the west coast of Vancouver Island. Our July – August values are lower than the predicted increases in global SST (1.1 °C per century, IPCC 2014), but are consistent with two other studies that examined full-year average SST for the period 1935 – 2014, reporting a broad range of increasing SST trends of 0.6 – 1.4 °C per century (White et al. 2016), and 0.89 (SD 0.62) °C per century (Cummins and Masson 2014).

At the current rate of change, by the year 2100 populations of marine organisms living in coastal waters of Vancouver Island will experience extreme summertime SST conditions that are 0.77 – 1.07 °C warmer than during the period 1986 – 2005. By comparison, Collins et al. (2013) predicted that average global SST would increase by 0.5 – 1.8 °C by the year 2100 relative to 1986 – 2005 average SST.

Current and predicted trends in sea surface salinity

The trends in two-month SSS conditions, at the time of year when SSS are lowest, differed between the east and west coasts of Vancouver Island. On the west coast, two-month average SSS conditions decreased by 0.64 PSU from 1935 – 2016, corresponding to a decrease of 0.79 PSU per century, whereas no significant change over time was found for the east coast. The west coast freshening trend is consistent with studies examining year-round average SSS on the west coast between 1935 – 2013, which have reported decreasing trends ranging from 0.47 PSU (Cummins and Masson 2014) to 1.00 PSU (Freeland 2013) per century. The increasing trend in two-month average SSS on the east coast was almost significant (p = 0.077), and changes in extreme SSS were significant; extreme SSS events on the east coast have been getting less extreme, and thus less stressful to marine organisms, increasing at a rate of 4.84 PSU per century.

The trend of increasing values for extreme SSS conditions on the east coast contrasts with the IPCC's broad-scale predictions for the North Pacific region of decreasing SSS (IPCC 2014), revealing that broad-scale assessments may not be representative of local-scale changes in SSS conditions. The increasing trend in extreme SSS on the east coast also contrasts with the report by Cummins and Mason (2014) of an absence of detectable SSS trend in the Strait of Georgia based on year-round average SSS from the same monitoring stations, further confirming that year-round averages are poor indicators of the most stressful conditions experienced by coastal marine organisms. This discrepancy between full-year averages (Cummins and Mason 2014) and our summertime values for the east coast may be due to decreasing peak summer outflow from the Fraser River, the dominant source of freshwater to the southern Strait of Georgia. Finally, the present study's findings of increasing summertime SSS on the east coast contrast with the results of other research reporting SSS freshening trends throughout the North Pacific. A possible explanation for the discrepancy between the present study's findings and those of studies strictly reporting decreases in SSS over time in the North Pacific may include: (1) seasonal differences, as the other studies used datasets encompassing all months of the year, whereas the present study focused on months when salinity is lowest, and (2) differences in local salinity regimes and processes, such as those associated with estuarine-like areas (Strait of Georgia) versus oceanic areas (Barkley Sound) (Pickard and McLeod 1953) being misrepresented by averaging data from both locations or by representing SSS data from one locale only.

Comparisons of east and west coast climate-related conditions

Sea surface temperature

Populations of coastal marine organisms on the east and west coasts of Vancouver Island experience very different levels of stressful temperature and salinity conditions. Over the 82 y period, July and August SSTs were on average 4.34 °C warmer on the east coast than on the west coast, the single greatest two-month difference between coasts being 6.13 °C in the summer of 1965. It is also notable that the coldest July and August average temperature on the east coast (15.91 °C, in 1964) did not overlap with the warmest July and August average temperature on the west coast (14.52 °C, in 1936 and 2015). The warmest SST per year (extreme SST) on the east coast was on average 5.20 °C warmer than on the west coast; the single greatest difference between coasts being 8.41 °C in 2009. Once again, there was no overlap between the lowest of the extreme SST conditions of the east coast (18.34 °C, in 1964) and the highest extreme SST of the west coast (16.82 °C, in 2004). In addition, the parallel trajectories of summertime SST on both coasts, for two-month average SST and for extreme SST, throughout the 82 y period suggest the differences in SST conditions have been a long-term, persistent feature of the region.

These long-term differences in SST between coasts are the result of several factors, including the amounts of solar radiation reaching the sea surface in each region, and the levels of ocean mixing in each region. The east coast of the island experiences minimal cloud cover during the summer months of July and August, maximizing the sun's potential to heat both water and air (Tully and Dodimead 1957). In contrast, the west coast can experience as much as 70% cloud cover in July and fog lasting an average of 15 d in August (Thomson 1981). Such conditions may affect SST by reducing the amount of solar energy available to heat the surface waters of the west coast (Tully and Dodimead 1957). In addition, the two coasts also differ in terms of the degree of coastal upwelling, a process that brings deep, cold, high salinity water to the surface. The west coast of Vancouver Island experiences active upwelling, particularly during summer months (Pickard and McLeod 1953, Thomson 1981, Cummins and Masson 2014), whereas the east coast does not experience significant upwelling during any time of the year.

Sea surface salinity

East and west coast populations of marine organisms on Vancouver Island have experienced distinct levels of salinity stress during the periods of lowest salinity on each coast. Two-month average SSS conditions throughout the 82 y study period were on average 5.44 PSU higher on the west coast, the lowest salinity conditions of the west coast (27.32 PSU, in 1992) never overlapping with the highest salinities of the east coast (26.00 PSU, in 1994). It is not clear, however, whether this pattern will persist into the future, given the converging trajectories of SSS on the two coasts, in terms of two-month average SSS and also extreme SSS.

The overall pattern of salinity minima consistently being lower and more variable on the east coast than on the west coast is likely the result of the physiography of the region. Seasonal variability in SSS within the Strait of Georgia is directly correlated to freshwater output from the Fraser River (Cummins and Masson 2014), as this output varies from year to year largely depending on the amount of stored precipitation (i.e. snow and ice) within the drainage basin of the river. The lower variability and higher salinity experienced along the west coast are linked to greater oceanic mixing resulting from spring upwelling winds (Pickard and McLeod 1953) as well as considerably smaller drainage basins, collecting rainfall and transferring to the ocean, than in the Strait of Georgia (Cummins and Masson 2014).

Comparisons of east and west coast weather-related conditions

Intertidal rock surface temperature

The intertidal zone of Vancouver Island experiences wide fluctuations in rock surface temperature during the summer; on some days in 2015 and 2016, rock temperatures varied by more than 20 °C over a 12 h tide cycle. Such short-term fluctuations help to reveal the selective pressures imposed on marine organisms and help explain their subsequent tolerance to these conditions (Monaco and Helmuth 2011). In addition, during daytime low tide exposure, the rocky intertidal environment of the east coast of Vancouver Island is more thermally stressful during the summer than at a similar latitude on the west coast. East coast shores were substantially warmer during low tide emersion than on the west coast in terms of average highest daily temperature, with a difference of 3.80 – 4.07 °C at an intertidal height of 1.5 m, and a difference of 4.15 – 4.16 °C at 2.25 m. Intertidal organisms on the east coast therefore experience warmer temperatures during low tide emersion and also during high tide immersion than west coast organisms. The warmer low tide intertidal temperatures on the east coast are likely attributable to a combination of the warmer SST and air temperatures, and the greater solar radiation, on the east side of Vancouver Island during summer months (Pickard and McLeod 1953).

Implications for coastal organisms

The intertidal and subtidal habitats of Vancouver Island are colonized by several species of marine animals and algae that inhabit the east as well as the west coasts; populations on these two coasts experience distinct summertime SST and salinity conditions, and these differences appear to have persisted over a prolonged period that probably far exceeds a century, and likely much longer. Such long-term exposure to distinct climate conditions has implications for the ecology and evolution of populations of benthic marine invertebrates (Helmuth et al. 2006). The observed differences in SST and SSS between east and west coasts during the most stressful time of the year constitute selective environments that likely favor different physiological tolerance thresholds among local populations of marine organisms. If an organism's degree of physiological tolerance of temperature and salinity can evolve relatively rapidly in response to local conditions, and the amount of gene flow between coasts is modest, then we predict that populations on the east coast should have higher tolerance thresholds to elevated temperature and reduced salinity than west coast populations of the same species.

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CHAPTER 3: Implications of acute temperature and salinity tolerance thresholds for the persistence of marine invertebrate populations experiencing climate change

INTRODUCTION

Current and predicted changes in seawater temperature, air temperature, and seawater salinity are significant climate change-related threats to many marine invertebrates (Byrne 2012, Wernberg et al. 2012), creating conditions that have the potential to cause alterations in species abundance and distribution (Hawkins et al. 2008). Average global sea surface temperature (SST) has been increasing at a rate of 1.1°C per century (IPCC 2014), and is projected to increase by 0.5-1.8 °C by the year 2100 relative to 1986-2005. In turn, sea surface salinity (SSS) trends vary among regions, with certain regions having experienced ocean water freshening by as much as 0.2 PSU from 1950 – 2008, while other regions became more saline by as much as 0.2 PSU and others yet experienced no significant change (Durack & Wijffels 2010, IPCC 2014). It is predicted that SSS will become less saline in high latitude regions that currently have low SSS, and more saline in subtropical regions with high SSS (Collins et al. 2013).

Rates of change in global SST and SSS vary by region (IPCC 2014), such that populations and communities may experience localized trends in climate-related conditions. One region in which local trends in SST and SSS are well defined is the coast of Vancouver Island, Canada. Since 1935, yearly SSS minima have increased on the east coast of Vancouver Island, while no significant change in SSS minima were detected on the west coast (Chapter 2). SST along the same coasts, however, is increasing; during summertime, when SST is highest and most stressful for coastal marine animals, SST has been increasing at a rate of 0.82-0.97 °C per century (Chapter 2). Given these changing environmental conditions, for populations to persist in their present-day range they must either (1) already have broad enough tolerances to function under future environmental conditions, or (2) evolve increased tolerance thresholds rapidly enough to keep pace with the changing conditions (Clarke 2003). Neither of these options, however, are well understood for coastal marine animals, constraining our ability to predict how populations will respond to future changes in climate conditions.

In the context of predicting the effects of future climate change on marine populations, it is informative to understand how past climate-related conditions have shaped present-day tolerance thresholds. In particular, the responsiveness of populations to altered climate conditions can be indirectly assessed by examining the extent to which present-day tolerance thresholds have diverged among populations of given species in response to existing spatial variation in climate conditions. The relationship between local climate conditions and tolerance thresholds in intertidal invertebrates has been studied across spatial scales, from small-scale microhabitats (Harley & Helmuth 2003), to mid-scale latitudinal gradients (Helmuth et al. 2002, Kuo & Sanford 2009, Zippay & Hofmann 2010, Kelly et al. 2012), and even across global scales (Compton et al. 2007, Morley et al. 2016). Nevertheless, intraspecific variation in tolerance thresholds, specifically variation among populations of a given species, remains poorly understood, likely due to the logistic challenges of such studies. Assessments of the link between interpopulation variation and local environmental conditions are most effective when (1) specimens are collected from two or more populations that are distant enough to have limited gene flow and to experience distinct climates, (2) all studied populations are located at a same latitude to avoid confounding latitudinal effects (Bernardo 1996, Gosselin et al. 2019) and (3) tolerance thresholds of all populations are tested at the same time in a common garden setting using similar methodology (Byrne 2012).

The southern region of Vancouver Island in British Columbia, Canada, provides an ideal setting to study the relationship between present-day tolerance thresholds of intertidal invertebrate populations and local environmental conditions. Populations on east and west coasts of the island have experienced persistent regional differences in SST and SSS, with east coast surface waters being on average 4.3 °C warmer and 7.8 PSU lower during the most stressful months than on the west coast (Chapter 2). Rock surface temperature in the intertidal zone during summertime low tides is also 3.9 - 4.2 °C warmer on the east coast than on the west coast (Chapter 2). In addition, populations of marine animals on the east and west coasts are separated by dispersal distances >350 km around the south of the island; restricted gene flow between east and west coasts is further suggested by genetic differentiation between east and west coast populations of the bivalve *Panopea abrupta*, a species with dispersing planktonic larvae (Miller et al. 2006). For researchers, however, travel distances by road across the island are only ~150 km, allowing the sampling of intertidal animals from both coasts and their return to a common laboratory within a few hours. Furthermore, the coastal waters of the Northeast Pacific are of particular interest due to their high primary productivity, high coastal biomass, and high species diversity (Croom et al. 1995) which may be threatened by changing climate conditions.

If tolerance thresholds of intertidal species evolve rapidly in response to local SST, SSS, and temperature during low tide emersion, then the persistent and substantial differences in these conditions between the east and west coasts of Vancouver Island, coupled with dispersal distances that restrict genetic mixing of populations, would be expected to have promoted divergence in tolerance thresholds between populations of these two coasts. We therefore hypothesized that east coast populations of marine species should currently exhibit greater tolerance to elevated temperature and to reduced salinity than west coast populations. To test this hypothesis, we examined four species of intertidal invertebrates that have substantial populations on both coasts of Vancouver Island: the marine snails *Nucella lamellosa*, *Littorina scutulata* and *Littorina sitkana,* and the barnacle *Balanus glandula*. As in many benthic invertebrate species, generation time in three of these species is relatively short, with individuals starting to reproduce after only 1 y in *L. sitkana* (Reid 1996), *L. scutulata* (Chow 1987), and *B. glandula* (Barnes & Barnes 1956), providing opportunity for rapid evolutionary responses to selective pressures. *N. lamellosa* have a longer generation time, reportedly reaching maturity at 3-4 y of age (Spight 1975, Marko 2004). Additionally, these species differ in terms of dispersal abilities, and thus possibly in gene flow: *L. scutulata* and *B. glandula* have dispersing planktonic larvae, whereas *L. sitkana* and *N. lamellosa* have benthic direct-developing larvae (Strathmann 1987). Dispersal ability is of particular interest for studies of interpopulation variation, as local adaptation is expected to occur most often in species with limited dispersal capability (Scheltema 1971, Endler 1977, Foden et al. 2013).

Determining the tolerance thresholds of local populations that have been exposed to different climate conditions for extended periods of time will help us to understand how intertidal species may respond to future changes in climate conditions. Persistence of coastal populations of marine animals in the face of climate change will depend on their overcoming three main types of challenges: (1) occasional acute exposure to extreme levels of stressors, (2) chronic exposure to elevated levels of stressors and (3) indirect effects caused by the impacts of the stressors on other parts of the community. The focus of the present study is on the first of these challenges, as acute stress is likely the most immediate concern for intertidal animals experiencing changing climate conditions. This study therefore aimed to (1) determine the extent to which populations of intertidal invertebrates, exposed to different degrees of acute temperature and salinity stress over many generations, have diverged in their physiological tolerance to these stresses, and also (2) to determine if present-day tolerance thresholds of intertidal invertebrates are likely to be overwhelmed in the near future by acute temperature and salinity extremes that are predicted for these coasts. Using a series of common garden experiments, the study specifically compared populations inhabiting the east and west coasts of Vancouver Island to elevated temperature during low tide emersion, elevated water temperature, and low salinity. In addition, the study included species with direct-development as well as species with planktonic larval development, providing insight into the influence of dispersal ability on local adaptation to temperature and salinity conditions

MATERIALS AND METHODS

Study sites and animals

Intertidal invertebrates were sampled from six sites along the coast of Vancouver Island, British Columbia, Canada. Three sites were located along the west coast of the island, within Barkley Sound, and three sites were located on the east coast in the Strait of Georgia between Fanny Bay and Royston (Fig. 3.1). All six sites were selected based on the following criteria: occurring at similar latitudes, consisting of rocky substrata, and experiencing low to moderate wave action. The latter criterion was confirmed by direct observations and by the presence of *Nucella lamellosa*, an intertidal gastropod that does not colonize wave-exposed habitats (Kitching 1976). East and west coast sites nevertheless differed somewhat in substratum, being dominated by boulders on the east coast and by bedrock on the west coast, and by tidal amplitude, tides reaching a maximum height of 5.2 m at east coast sites and 3.9 m at west coast sites (Table 3.1).

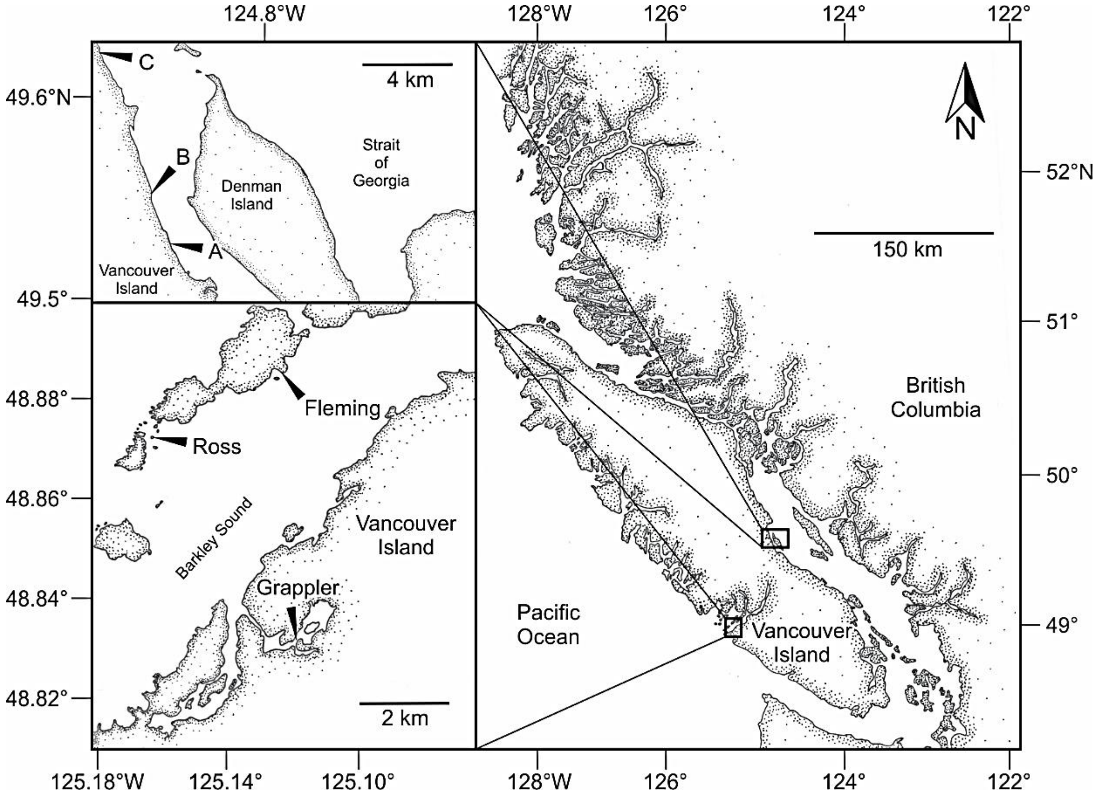

Figure 3.1. Field sites at which intertidal rock surface temperature was recorded on the east (top left) and west (bottom left) coasts of Vancouver Island, British Columbia, Canada (right).

Table 3.1. Coordinates and characteristics of the intertidal zone at each east and west coast site on Vancouver Island, British Columbia, Canada. Maximum tidal height refers to the highest high tide recorded in the summer (April – Sept.) of 2015 and 2016 as per chart datum.

Site	Latitude (N)	Longitude (W)	Substrate	Max. tidal height (m)
West coast				
Fleming Island	48° 53.07'	125° 07.40'	bedrock & boulders	3.9
Ross Islets	48° 52.33'	125° 09.72'	bedrock & boulders	3.9
Grappler Inlet	48° 49.91'	125° 07.10'	bedrock & gravel	3.9
East coast				
Site A	49° 32.26'	124° 51.55'	boulders & gravel	5.2
Site B	49° 33.50'	124° 52.30'	boulders & mud	5.2
Site C	49° 36.84'	124° 54.15'	boulders & gravel	5.2

Adults of four species of rocky intertidal invertebrates were examined: the snails *N. lamellosa*, *L. sitkana*, and *L. scutulata*, and the barnacle *B. glandula*. These species were selected based on the following criteria: (1) the presence of a large number of individuals of the species at all study sites, and (2) ease of specimen collection and transport for common garden experiments. In addition to experiments determining tolerance thresholds, the upper limit of intertidal distribution of each species was also assessed. At each site, three 5 m long by 0.5 m wide, vertical transects were carefully surveyed within the intertidal zone at low tide; the vertical height relative to chart datum of the highest-living individual of each species was then measured. For each species, the vertical heights of the highest individuals were averaged among the three transects per site, and then among the three sites per coast.

Field collection and acclimation of animals

All common garden experiments in this study were carried out at the Bamfield Marine Sciences Centre (BMSC), on the west coast of Vancouver Island. Given the travel distances between study sites and BMSC, it was not quite possible to collect animals from all six sites on a same day. For a given trial, collections at east and west coast sites were therefore carried out on two consecutive days. Animals were collected on East coast sites were accessed by road and travel time to bring animals from the field to BMSC was 2.0-6.5 h. West coast sites were accessed by boat, and travel time to BMSC was approximately 2.5 h. While some east coast animals experienced a longer transportation time than west coast animals, the duration of emersion experienced by all animals was within the timeframe of a low tide emersion period. In all cases, care was taken to minimize stress to the animals during transport from the field to BMSC. Heat stress on the trip from east coast sites to BMSC was prevented by placing animals in a cooler containing bags of seawater (11 – 14 °C) as well as ice packs covered by towels; temperature within the cooler always remained below 17 °C during transportation, as monitored by Thermochron® iButton temperature loggers (model DS1921G-F5) placed within the cooler. On the west coast, potential heat stress was minimized by the shorter travel duration and by keeping animals in shaded conditions. Individuals of each snail species (*L. sitkana, L. scutulata* and *N. lamellosa*) and small rocks with at least 10 individuals of *B. glandula* were collected throughout each site on days when the daytime low tide dropped below 1.5 m.

Upon arrival at BMSC, healthy adults of *N. lamellosa*, *L. sitkana,* and *L. scutulata* were distributed among experimental cages, one species per cage. To ensure all cages of a given species contained a similar size range of animals, an equal number of small, medium, and large adults were placed in each cage. Experimental cages consisted of plastic containers that were 2.54 cm wide and 3.10 cm in diameter (for species *L. sitkana* and *L. scutulata*) and 15.56 cm wide by 15.56 cm long by 8.57 cm tall (for *N. lamellosa*), with screened walls allowing free movement of water through the cage. Each rock containing *B. glandula* was labelled according to site and replicate number using an oil-based paint marker (Fig. 3.2A). Ten adult barnacles of a similar size were haphazardly selected on each rock and labelled with a small dot on one of their lateral plates (Fig. 3.2B). Finally, all animals were acclimated for 48-72 h in trays containing aerated seawater filtered to 200 µm, and held between 15.0-17.5 °C and 30 – 32 PSU (Fig. 3.3) before starting the tolerance experiments. During all circumstances where animals were submerged in seawater (i.e. acclimation, water temperature and salinity tolerance experiments), *N. lamellosa* were held in tanks that were isolated from *L. sitkana, L. scutulata* and *B. glandula,* preventing the exchange of odours and thus stress associated with the proximity of a predator and its prey (Fig. 3.3).

Tolerance experiments

Three experiments were performed to compare tolerance thresholds between east and west coast populations of the four study species. These experiments tested population tolerance thresholds to (1) elevated ambient temperature during low tide emersion, (2) elevated water temperature when immersed, and (3) decreased salinity when immersed.

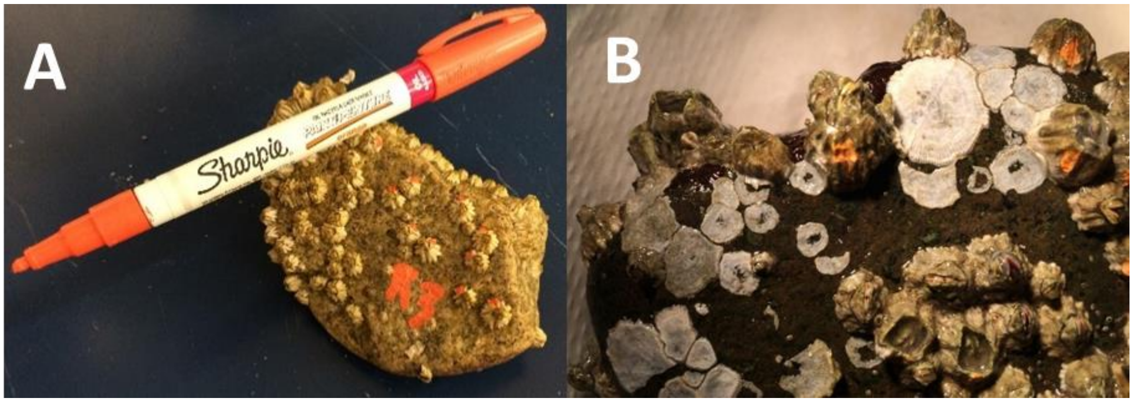

Figure 3.2. Labelled rocks containing *Balanus glandula.* The labels identified (A) the collection site and replicate number, and (B) marked barnacle individuals.

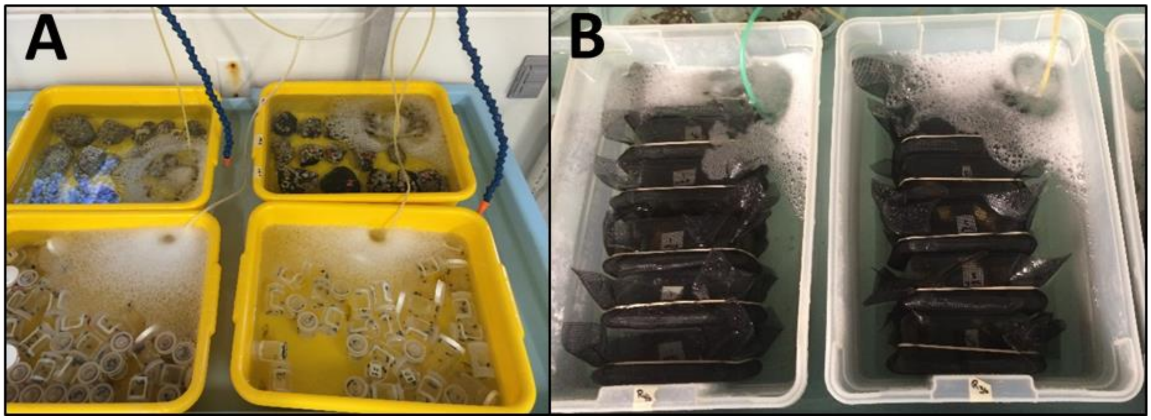

Figure 3.3. Acclimation tanks containing (A) *B. glandula*, *L. sitkana, L. scutulata,* and (B) *N. lamellosa.*

<u>Emersion temperature tolerance</u>

To determine temperature tolerance thresholds during emersion for east and west coast populations, groups of individuals were subjected to a series of species-specific temperature treatments (Table 3.2). *L. sitkana* and *L. scutulata* were collected from the six study sites on 28 and 29 July 2015; *N. lamellosa* and *B. glandula* were collected on 13 and 14 August 2015.

Immediately before starting each trial of the emersion temperature experiment, cages (or rocks, in the case of *B. glandula*) were removed from acclimation tanks, and residual water was blot-dried from both the animals and cages. Next, the replicate cages (*N. lamellosa*, *L. sitkana*, *L. scutulata*) or rocks (*B. glandula*) were placed in either air-tight plastic bags (Fig. 3.4A) or containers (Fig. 3.4B). Each bag or container held three 4 x 4 cm paper towels saturated with seawater to maintain elevated humidity and thus minimize desiccation stress throughout the experiment; relative humidity remained in the 80-98 % range in these bags and containers, as monitored by iButton® model DS1923 humidity loggers. The bags and containers were then transferred into temperature-controlled incubators, pre-set to the desired temperature treatment, for a 12 h duration.

Table 3.2. Summary of emersion temperature tolerance experimental design for each of the four species. For this experiment, separate groups of animals were placed in each of the temperature treatments, and temperature treatments for a given species were carried out simultaneously.

Species	Number of study sites	Replicate cages per site	Number of individuals per cage	Emersion temperature treatments (°C)	Total number of individuals used in experiment
Nucella lamellosa	6	3	8	25, 28, 30, 32	576
Littorina scutulata	6	5	10	36, 38, 40, 42, 45	1500
Littorina sitkana	6	5	10	36, 38, 40, 42, 45	1500
Balanus glandula	6	5	10	37, 42, 45	900

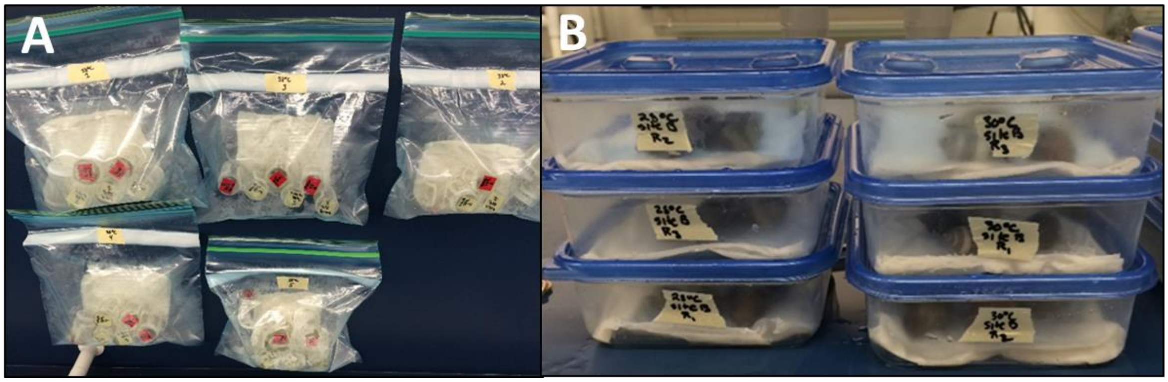

Figure 3.4. Distribution of replicate cages within air-tight experimental bags/containers for a single emersion temperature tolerance treatment: (A) bags used for *L. sitkana*, *L. scutulata* and *B. glandula* and (B) plastic containers used for *N. lamellosa*

After the 12 h treatment, cages or rocks were submerged in filtered and aerated seawater at 17 °C for a 12 h recovery period. Animals were then checked for mortality using species-specific procedures involving the inspection of inactive organisms for movement responses via gentle probing or timed seawater immersion; details of the procedure are listed in Appendix A. The temperature treatments used in this experiment were chosen based on preliminary trials with each species to ensure mortality outcomes ranging from 0% to 100%. The binomial mortality data (i.e. alive or dead) was used to calculate the temperature lethal to 50% of individuals (LT_{50}) for each site and species using general linear model (GLM) analysis in R statistical software (R Core Team 2015); the LT_{50} values calculated for each of the three sites of a same coast were then averaged to represent the population average thermal tolerance.

Water temperature tolerance

Animals used in water temperature tolerance experiments were collected from east and west coast sites on 3 and 4 August 2016, respectively. Following acclimation, cages were distributed amongst aerated experimental tanks (Fig. 3.5A & B) containing 30 – 32 PSU, 200 µm filtered seawater pre-heated to a desired temperature treatment.

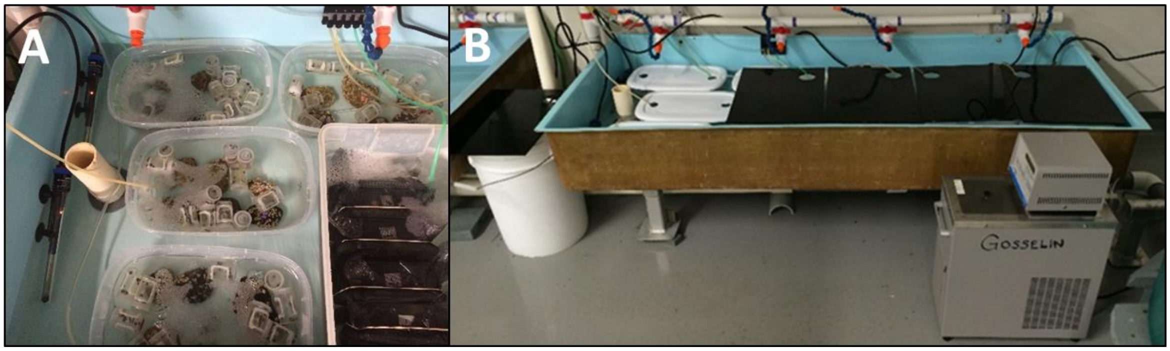

Figure 3.5. Water temperature tolerance experimental tank design. (A) Distribution of replicate cages among experimental tanks within a heated water bath. (B) Complete experimental set-up with white-lidded tanks containing *L. sitkana*, *L. scutulata* and *B. glandula*, and black-lidded tanks containing *N. lamellosa*.

Preliminary water temperature tolerance experiments revealed that all species survived temperatures up to 24 °C. To gradually acclimate animals to this minimum temperature level, they were exposed to a 1 °C increase in seawater temperature per day until 24 °C was reached; details of the procedure are listed in Appendix B. To determine water temperature tolerances of east and west coast populations of each species, animals from each site were exposed to progressively warmer temperatures, starting at 25 °C and then increasing at 3 °C intervals (Table 3.3), with one exception: in the last *N. lamellosa* temperature treatment there was a malfunction of the heater units resulting in a temperature increase of only 1 °C from 28 °C to 29 °C (Table 3.3). Animals were exposed to a given temperature treatment for 36 h, followed by an 8 h recovery period at 17 °C, and then a 4 h mortality check (Appendix A) at room temperature (~20 °C). Surviving animals were then placed in the next warmer temperature treatment (Table 3.3). Water temperature treatments for each species ceased when all animals had died. The temperature at death (TAD) of each animal in the experiment was then used to calculate the average TAD for each species, for each site.

Table 3.3. Summary of water temperature experimental design for each of the four species. For this experiment, all animals of a given species experienced all of the temperature treatments (except for those dying before reaching the warmest temperature), and temperature treatments were carried out sequentially starting with the lowest temperature.

Species	Number of study sites	Replicate cages per site	Number of individuals per cage	Total number of individuals used in experiment	Water temperature treatments (°C)
Nucella lamellosa	6	4	7	168	25, 28, 29
Littorina scutulata	6	4	10	240	24, 28, 31, 34
Littorina sitkana	6	4	10	240	25, 28, 31, 34
Balanus glandula	6	4	10	240	25, 28, 31, 34

Salinity tolerance

East and west coast animals were collected on 22 and 23 June 2016, respectively. After acclimation, cages of animals were distributed into aerated experimental tanks. All seawater used in the experiment, including salinity treatments and recovery periods, was filtered to 200 µm and held at 17 – 19 °C. Reduced salinities in this experiment were obtained by mixing filtered seawater with deionized water. To determine salinity tolerances of east and west coast populations, animals were exposed to 12 progressively decreasing salinity treatments, starting at 25 PSU, then decreasing to 20 PSU, and from then on decreasing at 2 PSU intervals (Table 3.4). Within each treatment, animals were exposed to a given salinity for 33 h, followed by a 12 h recovery period at 30 PSU, and then monitored for mortality over a 3 h period at room temperature (~ 20 °C). Surviving animals were then placed in the next reduced salinity treatment. The salinity at death (SAD) of each animal in the experiment was then used to calculate the average SAD for each species, for each site.

Table 3.4. Summary of salinity experimental design for each of the four species. For this experiment, all animals of a given species experienced all of the salinity treatments (except for those dying before reaching the lowest salinity), and salinity treatments were carried out sequentially starting with the highest salinity.

Species	Number of study sites	Replicate cages per site	Number of individuals per cage	Total number of individuals used in experiment	Salinity treatments (PSU)
Nucella lamellosa	6	4	5	120	25, 20, 18, 16, 14, 12, 10, 8, 6, 4, 2
Littorina scutulata	6	5	10	300	25, 20, 18, 16, 14, 12, 10, 8, 6, 4, 2, 0
Littorina sitkana	6	5	10	300	25, 20, 18, 16, 14, 12, 10, 8, 6, 4, 2, 0
Balanus glandula	6	5	10	300	25, 20, 18, 16, 14, 12, 10, 8, 6, 4, 2

Present-day tolerance thresholds relative to predicted future conditions

Determining if extreme levels of acute temperature and salinity stress are likely to overwhelm the present-day tolerance thresholds of intertidal populations in the near future was explored in two steps. In the first step, present-day tolerance thresholds to temperature and salinity were compared to the most stressful SST, SSS and emersion temperature conditions recorded on each coast. Extreme summertime (July and August) SST conditions were defined as the highest SST reported from 2006-2016 for both coasts. Extreme SSS conditions were defined by the lowest SSS reported from 2006-2016, which on the east coast occurs in June and July, and on the west coast occurs in January and February (Chapter 2). Extreme emersion temperatures were defined by the highest intertidal rock surface temperatures recorded at 1.5 m and 2.25 m tidal heights during daytime low tides in the summers (July and August) of 2015 – 2016 (Chapter 2). Then, to assess whether the persistence of these populations might be in jeopardy in the near future by the predicted increases in extreme summertime temperatures, the next step consisted of calculating the year at which extreme SST and emersion temperature would reach levels matching the present-day tolerance thresholds of each population. These calculations assumed recent rates of change in extreme SST and in emersion temperature would continue into the future and considered only the effects of exposure to occasional acute temperature stress on these intertidal animals. This was accomplished by extrapolating forward based on present-day extreme levels and known rates of change for each parameter, to estimate the year when extremes of each parameter would reach the present-day tolerance threshold of each population. For SST, the rate of change for each coast, reported in Chapter 2, was based on long-term (1935-2016) datasets from coastal lighthouse monitoring stations. In contrast, no long-term dataset exists for intertidal rock surface temperature in this region, so there was no direct way of quantifying rates of change to predict future levels of intertidal substratum temperature. Predictions of future trends in air temperature on these same coasts, however, has been reported (White et al. 2016); these trends in air temperature were used to predict future substratum temperature. While air temperature and intertidal substratum temperature are often quite different at any given time (Judge et al. 2018), the prediction of long-term rate of change in air temperature was nevertheless used here as a rough estimator of long-term rate of change in low tide substratum temperature.

Statistical analysis

All statistical analyses of data from emersion temperature, water temperature, and salinity experiments, as well as upper limits of intertidal distribution, were completed using R Statistical software (R Core Team 2015). In each case, data was tested for normality using the Shapiro-Wilk test and for homogeneity of variance using the Flinger-Killeen test. The tolerance thresholds of east and west coast populations to elevated emersion temperature were compared using a general linear mixed model (GLMM) with a binomial distribution (i.e. alive or dead) for each species. In this model, both temperature and coast were designated fixed effects, while site was random. To determine if there were differences in tolerance thresholds to elevated water temperature or reduced salinity between east and west coast populations of a species, TAD and SAD were compared between populations using mixed model nested analysis of variance (ANOVA). In both analyses, coast was treated as a fixed effect whereas site was classified as a random effect and was nested within coast. Finally, to determine the interspecific relationships between upper limit of intertidal distribution and tolerance thresholds (i.e. emersion LT_{50}, TAD, SAD), Pearson correlation analyses were performed for each species using the Hmisc package in R.

RESULTS

Tolerance experiments

Emersion temperature tolerance

Intraspecific variation in emersion temperature tolerance was detected in two of the four species; emersion temperature tolerance thresholds differed significantly between east and west coast populations of *N. lamellosa* and *B. glandula*, but not in *L. sitkana* and *L. scutulata* (Table 3.5). In the two species with significant intraspecific variation, east coast populations were more tolerant of elevated emersion temperature than west coast populations; this same trend was also apparent in *L. sitkana* but was not significant (Table 3.5). For *N. lamellosa*, the LT_{50} of the east coast population was 1.4 °C higher than that of the west coast population; in *B. glandula*, the LT_{50} of the east coast population was 1.5°C higher than that of the west coast population (Fig. 3.6).

Interspecific variation in emersion temperature tolerance was significantly related to the upper limit of intertidal distribution of these species (Table 3.6). This was primarily due to the low intertidal species (*N. lamellosa)* displaying a considerably (8.7 – 11.3 °C) lower tolerance to emersion temperature than the upper intertidal species (*L. sitkana, L. scutulata, B. glandula)* (Fig. 3.7A). No species survived emersion temperatures greater than 42 °C (Fig. 3.6).

Table 3.5. Results of general linear mixed model (GLMM) with binomial distribution analyzing the effect of location (i.e. east or west coast) on mortality of invertebrate populations in response to emersion temperature treatments. Shown are the estimated coefficients, standard errors (SE), and statistical significance for the explanatory variables.

	Estimate	SE	Pr(>|z|)
***N. lamellosa*[a]**			
Intercept	57.801	5.526	< 0.001
Temperature	-1.919	0.184	< 0.001
West coast	-2.293	0.429	< 0.001
***L. scutulata*[b]**			
Intercept	51.969	2.863	< 0.001
Temperature	-1.335	0.072	< 0.001
West coast	0.632	0.712	0.374
***L. sitkana*[c]**			
Intercept	56.982	3.292	< 0.001
Temperature	-1.389	0.079	< 0.001
West coast	-1.323	0.880	0.133
***B. glandula*[d]**			
Intercept	47.928	3.745	< 0.001
Temperature	-1.135	0.088	< 0.001
West coast	-1.953	0.324	< 0.001

[a] 8 animals x 3 replicates x 4 treatments
[b] 10 animals x 5 replicates x 5 treatments
[c] 10 animals x 5 replicates x 5 treatments
[d] 10 animals x 5 replicates x 3 treatments

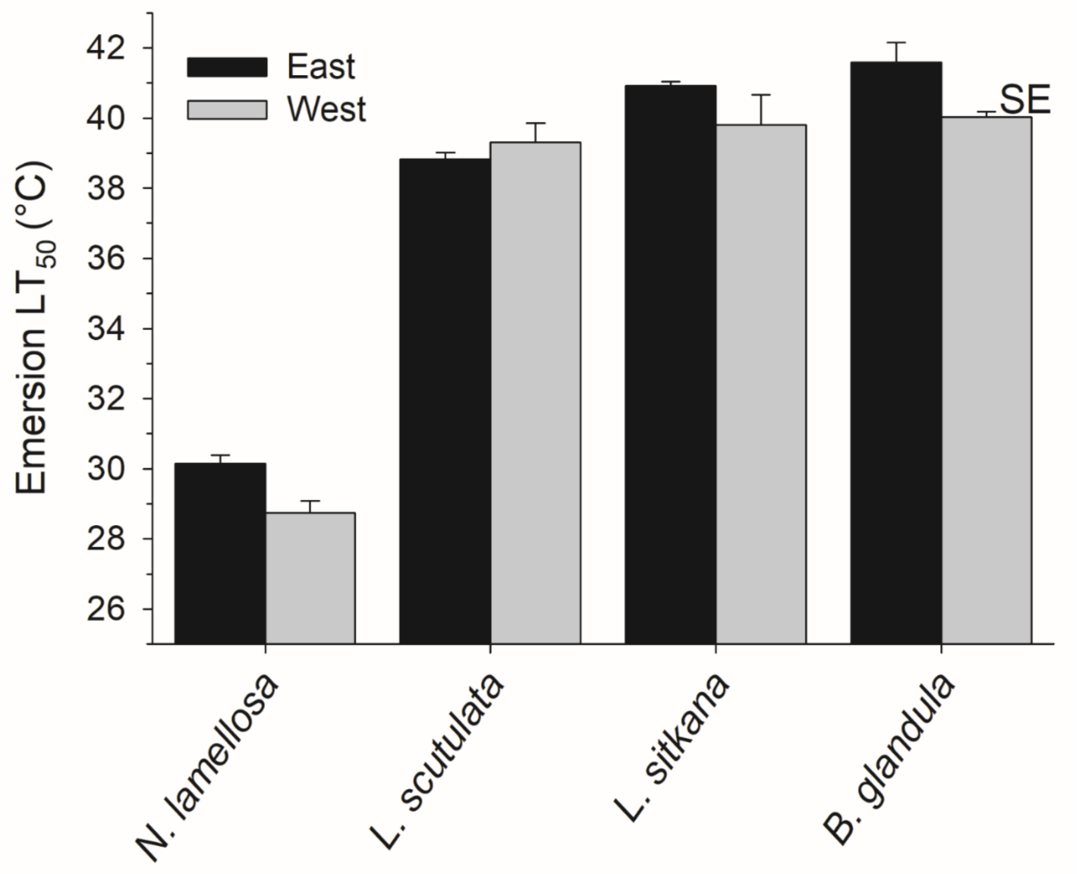

Figure 3.6. Emersion temperature causing 50% mortality (LT_{50}) for the east and west coast populations of four intertidal species.

Table 3.6. Pearson correlation analyses of the relationship between upper limit of intertidal distribution of east and west coast populations and tolerance thresholds to elevated emersion and sea surface temperatures and to reduced salinity (n=4).

	East		West	
Parameter	r	p	r	p
Emersion LT_{50}	0.9546	0.0454	0.9871	0.0130
Water temperature at death	0.9953	0.0045	0.9915	0.0085
Salinity at death	-0.8315	0.1685	-0.9327	0.0673

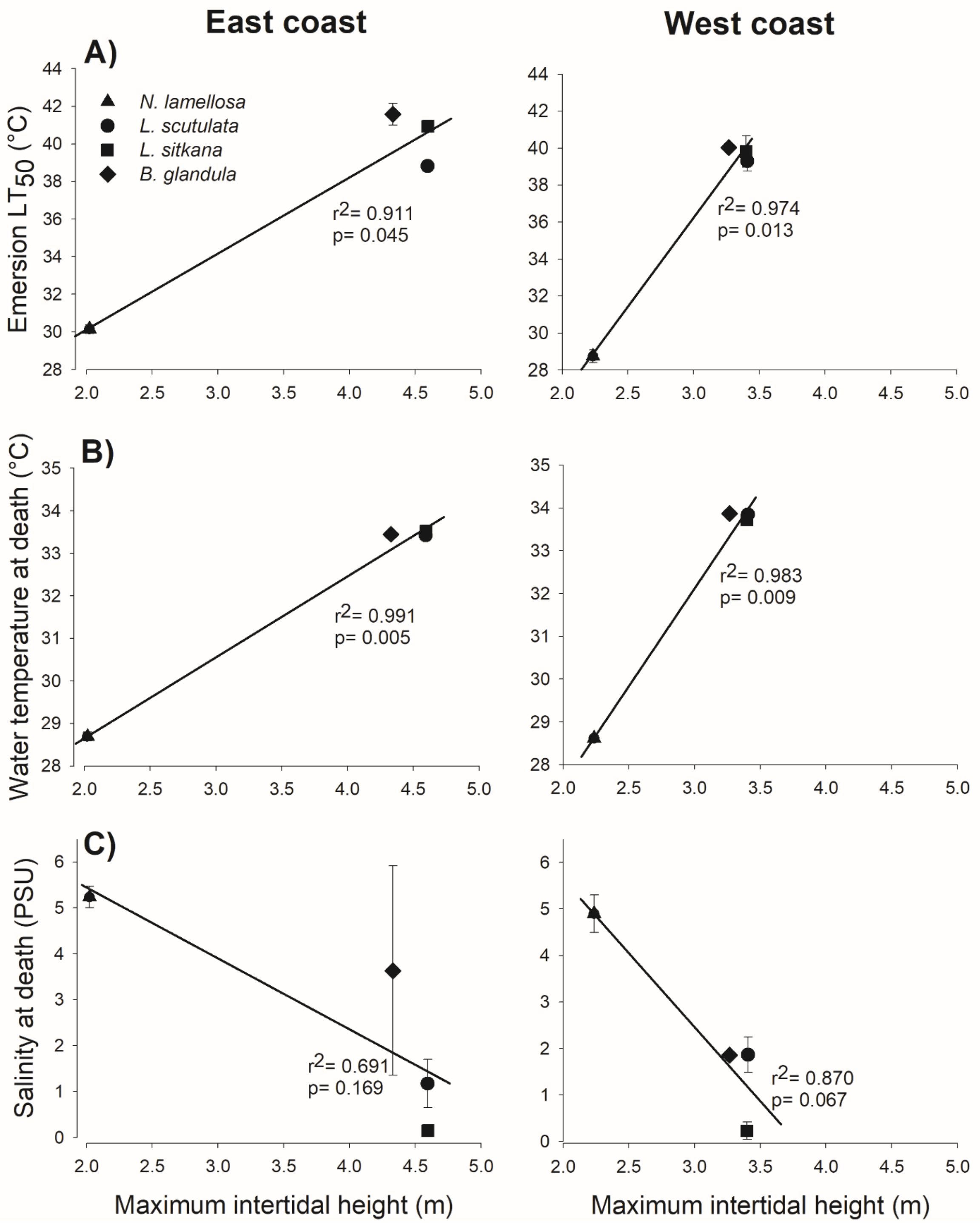

Figure 3.7. Interspecific relationship between upper limit of intertidal distribution and tolerance thresholds to A) elevated emersion temperature, B) elevated water temperature, and C) low salinity conditions. East and west coast populations of the four species were analyzed separately.

Water temperature tolerance

Intraspecific variation in water temperature tolerance (TAD) was detected in two species. Water temperature tolerance differed significantly between east and west coast populations of *B. glandula* (Nested ANOVA: $F_{1, 4} = 9.97$, $p = 0.034$) and *L. scutulata* (Nested ANOVA: $F_{1, 4} = 9.30$, $p = 0.045$), with west coast populations displaying higher tolerance thresholds to elevated water temperature than east coast populations by 0.4 °C in both species (Fig. 3.8). No significant difference in water temperature tolerance between east and west coast populations of *N. lamellosa* (Nested ANOVA: $F_{1, 4} = 0.39$, $p = 0.566$) or *L. sitkana* (Nested ANOVA: $F_{1, 4} = 2.69$, $p = 0.177$) was present.

Interspecific variation in water temperature tolerance was also significantly related to the upper limit of intertidal distribution of these species on both coasts (Table 3.6). Here again, the trend was mainly due to *N. lamellosa* being substantially less tolerant and distributed lower in the intertidal zone than the three other species (Fig. 3.7B). The TAD of *N. lamellosa* was 4.8 – 5.2 °C lower than in the other species (Fig. 3.8). Overall, water temperature tolerance did not exceed 34 °C for any of the species.

Salinity tolerance

Intraspecific variation in salinity tolerance (SAD), between east and west coast populations, was not detected in *N. lamellosa* (Nested ANOVA: $F_{1, 4} = 0.510$, $p = 0.524$), *L. scutulata* (Nested ANOVA: $F_{1, 4}= 1.14$, $p = 0.351$), *L. sitkana* (Nested ANOVA: $F_{1, 4}= 0.175$, $p = 0.714$), or *B. glandula* (Nested ANOVA: $F_{1, 4}= 0.604$, $p = 0.518$). Interspecific variation in tolerance to reduced salinity conditions was extensive, with *N. lamellosa* being substantially less tolerant than the other three species (Fig. 3.7C); SAD in *N. lamellosa* was 1.6 – 5.1 PSU higher than in the other species (Fig 3.9). Interspecific variation in SAD, however, was not quite significantly related to the upper limit of intertidal distribution (Table 3.6).

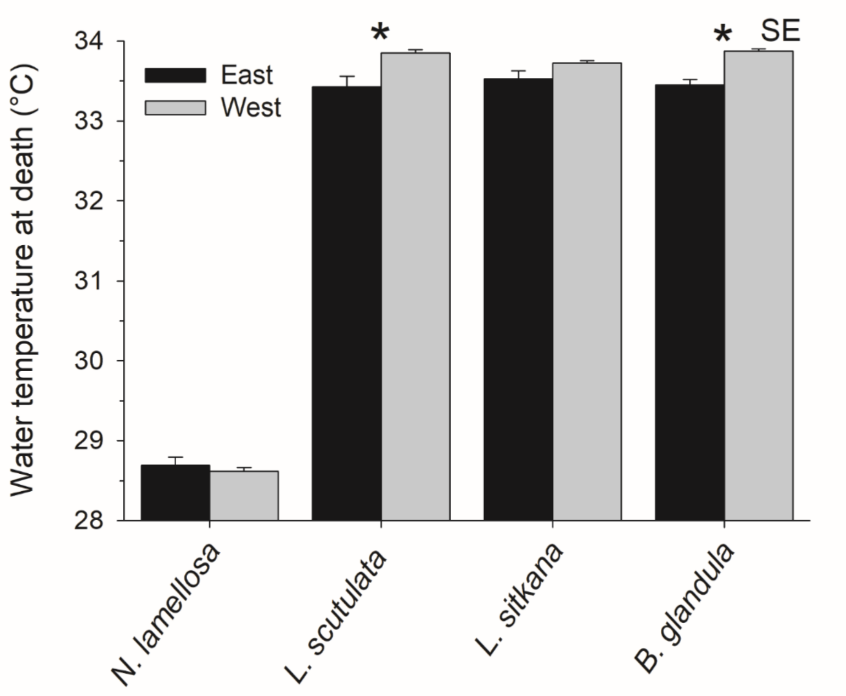

Figure 3.8. Immersion temperature tolerance (water temperature at death) for east and west coast populations of four intertidal invertebrate species on Vancouver Island (n = 3 sites per coast). * indicates a significant difference between populations.

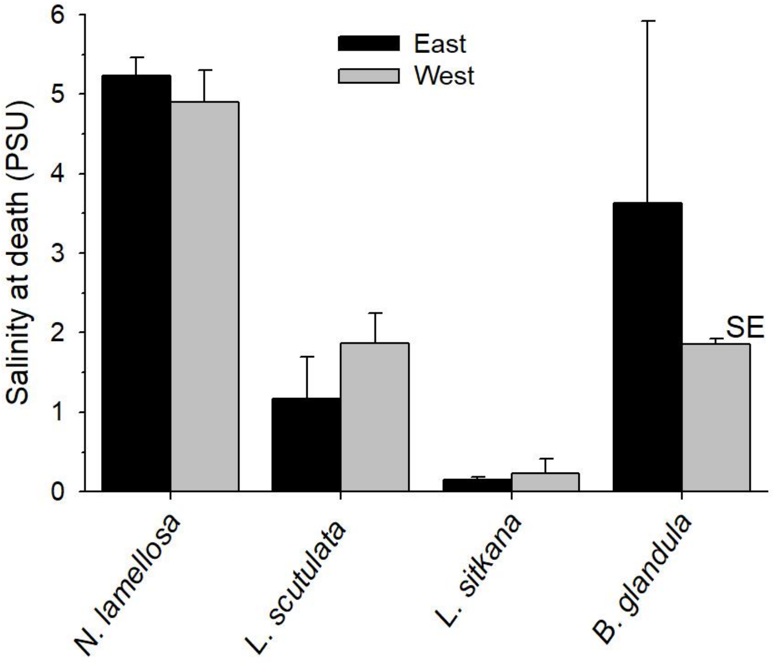

Figure 3.9. Salinity at death (SAD) for east and west coast populations of four intertidal invertebrate species on Vancouver Island (n = 3 sites per coast).

Present-day tolerance thresholds relative to predicted future conditions

For the three upper intertidal species examined herein, emersion LT_{50} values for east and west coast populations were substantially higher than the warmest emersion temperature recorded at 2.25 m on the respective coast (Fig. 3.10a, b). The temperature tolerance thresholds of east coast populations of upper intertidal species were 5.6 – 8.3 °C higher than the highest rock surface temperature recorded on the east coast, while west coast temperature tolerances were 9.5 – 10.2 °C higher than the warmest rock surface temperature recorded on that coast. In contrast, east and west coast populations of the low intertidal species *N. lamellosa* had emersion LT_{50} values that were 1.4 and 2.8 °C lower, respectively, than present-day highest substratum temperatures reported at 1.5 m on either coast (Fig. 3.10a, b). Finally, if substratum temperature were to continue to increase at the same rate as summertime air temperature (i.e. 0.8 °C per century on the east coast and 1.1 °C per century on the west coast, Whyte et al. 2016), then future predicted maximum emersion temperatures would not match present-day LT_{50} values of populations of the three upper intertidal species for several hundred years on the east and west coasts (Fig. 3.10c). No such calculations were made for *N. lamellosa*, as emersion temperature tolerances of this species are already exceeded by present-day maximum rock surface temperatures at 1.5 m.

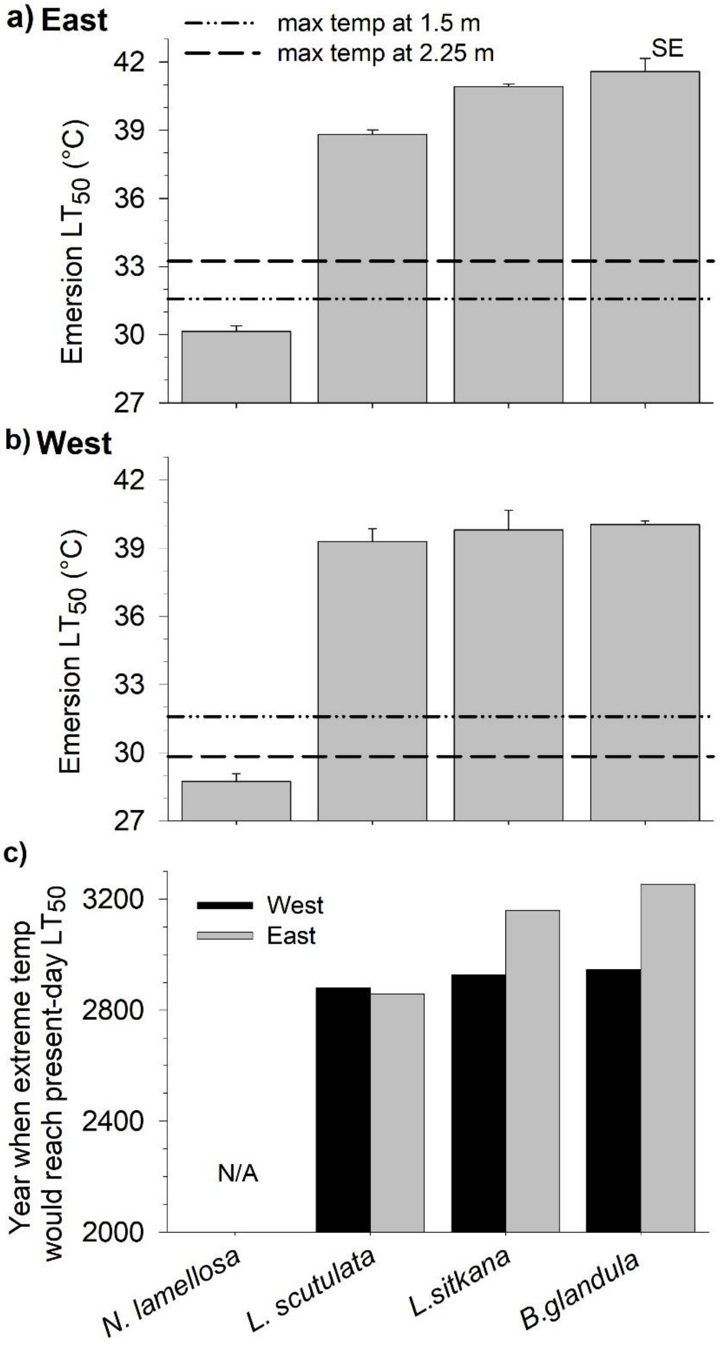

Figure 3.10. Emersion temperature tolerance (LT_{50}) of (a) east and (b) west coast populations of four marine invertebrate species (this study) relative to the maximum temperatures recorded at the field sites on each coast (Chapter 2); the dashed lines represent the single highest maximum summertime (July – August, 2015 and 2016) rock surface temperature at low tide per coast at 1.5 m and 2.25 m; (c) estimated year when extreme temperature conditions (Chapter 2) would reach present-day LT_{50} values for east and west coast populations of marine invertebrate species (excluding *N. lamellosa*), assuming that recent rates of change would continue into the future.

Present-day water temperature tolerances of east and west coast populations in all four species were considerably greater than the warmest extreme SST recorded on each coast in July and August from 2006-2016 (Fig. 3.11a, b). East coast populations displayed temperature tolerance thresholds that were 7.8 – 12.7 °C greater than the highest reported extreme SST on the east coast, and tolerance thresholds of west coast populations were 12.1 – 17.4 °C greater than the highest reported SST on that coast. Although maximum summertime SSTs are predicted to become progressively warmer in the future on both coasts of Vancouver Island, maximum SSTs are not expected to match present-day acute immersion temperature tolerance of either of the four species for several hundred years (Fig. 3.11c).

Populations of all four species were able to tolerate acute exposure to salinities substantially lower than the lowest SSS conditions recorded on either coast from 2006-2016 (Fig. 3.12a, b). Upper intertidal species were the most tolerant of low salinities, with present-day salinity tolerance thresholds of east coast populations enabling them to withstand salinity conditions 10.2-13.7 PSU lower than the single lowest SSS presently occurring on the east coast, and west coast populations tolerating acute exposure to salinity conditions 22.4 - 24.0 PSU lower than the single lowest SSS reported for that coast. Although not quite as tolerant of low salinities as the upper intertidal species, *N. lamellosa* could withstand acute exposure to SSS conditions 8.6 (east) and 19.4 (west) PSU lower than the lowest SSS conditions presently experienced on each respective coast (Fig. 3.12 a, b). Given the ongoing trend of increasing minimum SSS on the east coast and the absence of a trend on the west coast (i.e. no significant change in minimum SSS), the lowest SSS conditions predicted for Vancouver Island would not reach the present-day SSS tolerance thresholds of the populations studied herein for the foreseeable future.

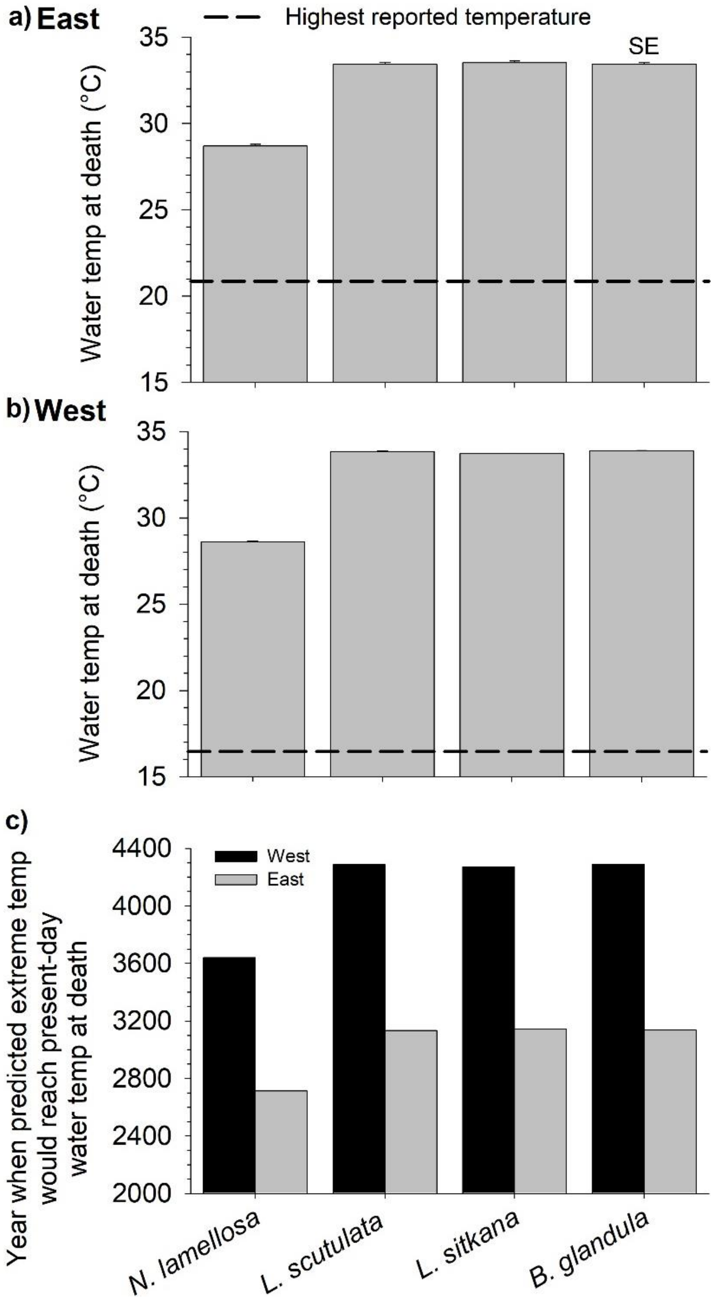

Figure 3.11. Immersion temperature tolerance (water temperature at death) of (a) east and (b) west coast invertebrate species (this study) relative to the maximum temperatures recorded by near-shore monitoring stations on each coast (n = 2 per coast)(Chapter 2); the dashed lines represent the single highest maximum summertime (July – August, 1935-2016) sea surface temperature recorded on each coast; (c) estimated year when extreme sea surface temperature conditions (Chapter 2) would reach the present-day water temperature at death for east and west coast populations of marine invertebrate species, assuming that recent changes would continue into the future.

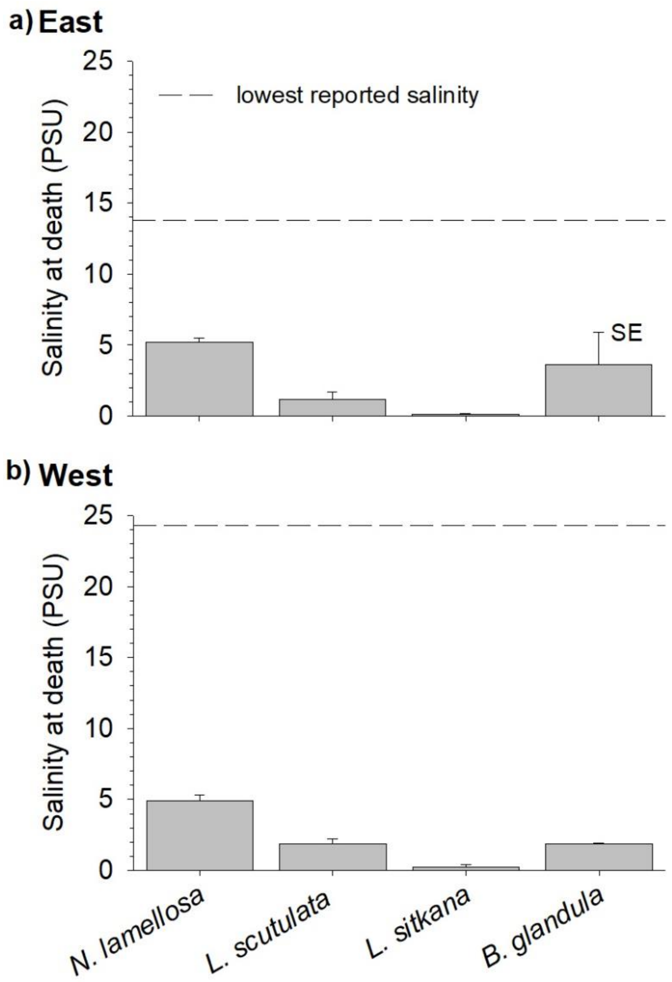

Figure 3.12. Salinity tolerance (salinity at death) of (a) east and (b) west coast populations of four marine invertebrate species (this study) relative to the lowest salinities recorded by near shore monitoring stations on each coast (n= 2 per coast)(Chapter 2); the dashed lines represent the single lowest sea surface salinity on the east between June and July, and the west between January and February between 2006 – 2016.

DISCUSSION

Extent of interpopulation variation tolerance thresholds

Populations of marine invertebrates living on the east and west coasts of Vancouver Island have been exposed to distinct SST and SSS conditions for at least as long as these parameters have been recorded (82 y), and probably for considerably longer (Chapter 2). Populations inhabiting these two coasts further experience different emersion temperatures, especially during summertime low tides (Chapter 2). East and west coast populations will have experienced these distinct environmental conditions over many generations, providing opportunity for evolutionary responses to local selective pressures (Kawecki 2008, Sanford & Kelly 2011). The age at first reproduction in most benthic invertebrates is 1 y or less (Gosselin & Qian 1997), providing opportunity for evolutionary changes to occur over only a few years. The species in this study begin reproducing at the age of 1 or 4 y, resulting in 25-100 generations per century. Yet, this study found limited evidence to suggest these populations have become locally adapted to the temperature and salinity conditions they have experienced.

The finding that best supported the local adaptation hypothesis was the difference between east and west coast populations in acute tolerance to elevated emersion temperatures in two species, *B. glandula* and *N. lamellosa*, with east coast populations of these species displaying higher emersion temperature tolerance than west coast populations. The higher tolerance thresholds of the east coast populations are consistent with the higher summertime (June-July) rock surface temperatures documented on this coast relative to the west coast. However, summertime rock surface temperatures at low tide were 4.2 °C warmer on the east coast (Chapter 2), whereas tolerance thresholds to elevated emersion temperatures were ≤ 1.5 °C higher in east coast populations of these species, suggesting only a partial divergence of tolerance thresholds. In addition, no divergence in emersion temperature tolerance was detected between east and west coast populations of the two other species, *L. sitkana* and *L. scutulata*. Consequently, emersion temperature tolerance in these four species provides modest support for the local adaptation hypothesis.

East coast populations of intertidal organisms also experience July and August seawater temperatures that are on average 5.2 °C warmer than on the west coast (Chapter 2). This historical difference in summer SST, however, did not lead to corresponding differences in tolerance of acute exposure to elevated water temperature. Tolerance thresholds to elevated seawater temperature differed between east and west coast populations only in two species, *B. glandula* and *L. scutulata*, and these differences were not consistent with summertime SST on those coasts; east coast populations of these two species were less tolerant of elevated SST than west coast populations.

Although SSS fluctuates seasonally on both coasts of Vancouver Island (Pickard & McLeod 1953), the SSS on the east coast drops substantially lower (5.2 PSU) than on the west coast each year (Chapter 2). Accordingly, it was expected that east coast populations of intertidal invertebrates would be more tolerant of reduced salinity than west coast populations of the same species. That, however, was not the case; east and west coast populations of each species had similar tolerance thresholds to low SSS. This lack of interpopulation differences contrasts with evidence of local adaptation in some invertebrate species, such as *L. sitkana* and *L. scutulata* in Washington and Oregon, in which differences among populations in tolerance to low salinity was attributed to differences in salinity regime among the study sites (Yamada 1989). Local adaptation in salinity tolerance has also been reported in the intertidal gastropods *L. sitkana* and *Littorina subrotunda* (Sokolova & Boulding 2004). The lack of divergence in salinity tolerance in the present study could be an indication that SSS is not the most important cause of salinity stress in these two populations. Rather, salinity tolerance may be determined mainly by exposure to heavy rainfall during low tide emersion, directly exposing these animals to freshwater for several hours (Dong et al. 2014). The large volume of seasonal rainfall experienced throughout the Pacific Northwest (Tully & Dodimead 1957, Thomson 1981) would cause frequent exposure of intertidal animals on both coasts of Vancouver Island to fully freshwater conditions at low tide, possibly causing them to develop similar salinity tolerance thresholds. Thus acute exposure to near-freshwater conditions when rainfall events occur during low tide may be a more relevant parameter to study than reduced SSS conditions, as future increases in precipitation are predicted for the North Pacific region (IPCC 2014).

Dispersal ability

This study included two species with dispersing planktonic larvae (*B. glandula, L. scutulata*) as well as two species with direct-development and thus limited dispersal capabilities (*N. lamellosa, L. sitkana*). Although it has been suggested that gene flow might be more restricted in direct-developing than in planktonic dispersing species (Yamada 1989), leading to greater interpopulation divergence in direct-developing species, there was no indication that larval dispersal ability influenced the extent of divergence in tolerance in the species studied herein. Population divergence in tolerance to elevated emersion temperature was similar in *N. lamellosa* (1.4 °C; direct-development) and *B. glandula* (1.5 °C; planktonic), and there was no divergence between east and west coast populations in the 2 other species. As for immersion temperature tolerance, divergence in tolerance thresholds only occurred in species with planktonic development. Finally, there was no evidence of divergence in tolerance to reduced salinity in either direct-developing or planktonic dispersing species. While these findings are inconsistent with the postulate that direct-developers have an increased potential for local adaptation relative to species with planktonic development (Endler 1977, Yamada 1989, Hellberg 1996, Chevin et al. 2010, Sanford & Kelly 2011), the present findings add to a growing body of evidence suggesting local adaptation is equally common in direct developers and planktonic dispersers (Sotka 2012). Rather, other environmental or organismal traits, such as exposure to strong and consistent environmental gradients (Linhardt & Grant 1996) or maternal effects (Sokolova & Boulding 2004), may have a greater ability to influence processes governing local adaptation in populations of benthic invertebrates.

Intertidal height

Tolerance to physiological stressors plays a pivotal role in dictating the upper zonation of intertidal animals (Broekhuysen 1940, Newell 1976, Newell & Branch 1980). As expected, the species in the present study that inhabit the upper intertidal zone possessed superior acute tolerance to elevated emersion temperature as well as elevated SST relative to the low intertidal species. The superior tolerance to elevated emersion temperature of upper intertidal species reflects, in part, their need to endure longer emersion periods than low intertidal animals (Newell 1976, Peterson 2013). Furthermore, upper intertidal species are typically found on open surfaces with little or no access to refugia (pers. obs.), directly experiencing the elevated temperature at low tide, whereas low intertidal species such as *N. lamellosa* are found almost exclusively under boulders or in crevices, where conditions are likely moister and cooler, thus avoiding the more extreme conditions prevalent on the nearby exposed rock surfaces (Garrity 1984).

Present-day tolerance thresholds relative to predicted future conditions

Temperature and salinity conditions are not equally stressful year-round to marine organisms; rather, stress induced by these factors peaks during a limited time of year when these factors reach extreme levels. On Vancouver Island, yearly minimum SSS has been increasing on the east coast for the last 82 y, thus becoming less stressful, while minimum SSS conditions on the west coast have not changed (Chapter 2). Over the same time scale, peak summertime SST has been increasing on both coasts and so is expected to become increasingly stressful in the future (Chapter 2). Furthermore, maximum summertime substratum temperature in the intertidal zone during low tide emersion is also expected to increase along both coasts into the future (Chapter 2). However, even if tolerance thresholds of these intertidal populations were to remain unchanged, the findings of this study suggest acute exposure to extreme levels of these abiotic factors are unlikely to overwhelm the present-day tolerance thresholds of populations in the near future (i.e. next few hundred years), should the rates of change in SST, SSS and substratum temperature in the future be similar to recent rates of change.

Present-day TAD and SAD values of all east and west coast populations were substantially greater than the warmest SST or SSS recently recorded on the respective coast, and emersion temperature tolerance thresholds of three of the four species were greater than the warmest emersion temperature on each coast. These findings reveal that present-day tolerance thresholds to elevated emersion and seawater temperatures and to low SSS are sufficient to allow populations to persist when experiencing acute exposure to all extreme heat and low salinity stresses presently occurring on both coasts. The only exception to this was *N. lamellosa*, in which emersion temperature tolerance was lower than present-day maximum rock surface temperatures. This would seem to suggest that *N. lamellosa* populations should not be able to persist at these sites; however, individual *N. lamellosa* position themselves in crevices or under rocks or algae during low tide (pers. obs.), where thermal stress during low tide emersion can be substantially lower than on nearby exposed rock surfaces (Garrity 1984). This would explain why *N. lamellosa* is almost exclusively found in cryptic microhabitats at low tide, and suggests the persistence of *N. lamellosa* at a given site is likely dependent on availability of these cryptic microhabitats. This finding also reveals that intertidal substratum temperature, present or future, is not an appropriate indicator of the stress levels experienced by *N. lamellosa* during low tide.

If future rates of change in extreme SST and emersion temperature are comparable to present rates of change in this region (Chapter 2), and considering only the effects of occasional acute exposure to extreme conditions, then we estimate present-day emersion and water temperature tolerance thresholds of these intertidal populations would exceed the highest predicted emersion and immersion temperatures for an extended period of time, likely several hundred years. So, despite the seemingly slow rate of evolution of acute tolerance thresholds reported herein, exposure to occasional acute temperature stress is not expected to be an immediate threat to the persistence of these populations. Interestingly, the estimated year at which acute temperature extremes would match present-day tolerance thresholds differs between the east and west coast populations of these four species. It is estimated that increases in maximum summertime emersion temperature will take longer to reach present-day emersion temperature tolerance thresholds of populations on the east coast than on the west coast, while the reverse is true for water temperature tolerance in these populations. For immersion temperature, this is due to the substantially less stressful conditions presently occurring on the west coast, which create conditions wherein west coast populations are living further from their tolerance thresholds compared to east coast populations. However, while present-day emersion temperature conditions are also less stressful on the west coast, it does not explain why increases in maximum summertime emersion temperature would take longer to reach present-day tolerance thresholds on the east coast. Rather, the higher emersion temperature tolerances found in some populations of east coast species may provide a partial explanation. Our predictions also suggest that increasing emersion temperature is likely to threaten the persistence of these populations sooner than acute stress from extreme levels of SST or SSS.

Implications for population persistence

The persistence of coastal populations of marine organisms faced with increasing abiotic stress will depend on overcoming three types of challenges: (1) occasional acute exposure to extreme levels of stressors, (2) chronic exposure to elevated levels of stressors, and (3) indirect effects caused by impacts of the stressors on other parts of the community. The present study examined the first of these challenges. Our study revealed that acute exposure to extreme levels of three climate parameters (elevated substratum temperature and SST, and reduced salinity) do not appear to be a threat to the persistence of these species on Vancouver Island in the near future. Salinity tolerance thresholds of the four study species are sufficient to survive present-day levels of SSS minima (this study), and the yearly extreme lows of SSS are predicted to stay the same or become less stressful in the future (Chapter 2). Extreme levels of elevated temperature, in terms of SST and substratum temperature during low-tide emersion, are expected to become more stressful in the future, but present temperature tolerance thresholds are high enough to exceed the extreme temperatures that are predicted for at least the next several hundred years.

The persistence of populations in a given region also depends on whether individuals can survive chronic (i.e. long-term) exposure to sublethal climate-related stressors, as even moderate levels of climate-related stress can affect organisms if they are subjected to these conditions for prolonged periods (Whiteley & Mackenzie 2016). Chronic exposure to elevated temperature can occur either through persistent exposure to elevated SST or, in intertidal organisms, from repeated exposure to several successive low tide periods with elevated substratum temperature, or a combination of these two circumstances. Exposure to increased temperature conditions for extended periods can negatively affect intertidal animals, such as causing decreased foraging activity and growth rate of the seastar *Pisaster ochraceus* (Pincebourde et al. 2008) and reducing the upper tolerance limits of intertidal and subtidal gastropods and arthropods (Nguyen et al. 2011, Sorte et al. 2011). As emersion temperature increases on the coasts of Vancouver Island, this parameter will likely impose increased levels of stress on populations well into the future. More work on chronic effects, especially with regards to heat stress, is needed, as the implications of chronic effects for the persistence of coastal invertebrate populations is underrepresented in the literature relative to studies focusing on marine vertebrates or terrestrial biota.

Population persistence also depends on impacts of climate-related stressors on other parts of the community, which then have secondary effects on other species (Harley et al. 2006, Kordas et al. 2011). Although a population may be sufficiently tolerant of abiotic conditions to withstand climate conditions in a given area, the population may still be at risk from cascading community level changes that occur when less tolerant organisms are affected by changing climate conditions (Helmuth et al. 2013). These indirect effects of climate change have been demonstrated to negatively impact marine ecosystems in a variety of ways, including disruptions to food webs (Hoegh-Guldberg & Bruno 2010, Ainsworth et al. 2011, Johnson et al. 2011), increased predation pressure (Harley 2011), altered interactions with competing species (Hawkins et al. 2008, Kordas et al. 2011), changes to community composition (Southward et al. 1995, Sagarin et al. 1999) or increased prevalence of diseases (Harvell et al. 2002, Hoegh-Guldberg & Bruno 2010) and parasites (Poulin & Mouritsen 2006). Given the increases in SST and intertidal emersion temperature that are predicted for the east and west coasts of Vancouver Island (Chapter 2) it is likely that populations on both coasts will be at risk from indirect effects of changing abiotic conditions into the future. Although indirect effects could be major determinants of population persistence, there is presently limited knowledge regarding the effects of single indirect stressors on persistence of individuals, and indirect effects of combinations of climate stressors are even less well understood; this remains a major knowledge gap limiting our ability to predict the fate of populations faced with changing abiotic conditions.

Finally, the likelihood of persistence of coastal populations will be enhanced if they are capable of evolving increased tolerance thresholds (Somero 2010, Knight 2010). There are concerns, however, that evolutionary rates of change in tolerance thresholds may not be fast enough to keep pace with climate change (Henson et al. 2017). The present study revealed minimal divergence in tolerance thresholds between east and west coast populations, supporting the hypothesis that physiological tolerance evolves very slowly in these species. If a population has tolerance thresholds that are only slightly higher than the most stressful conditions in the inhabited region, then a slow rate of evolution in physiological tolerance could lead to extirpation of the population in the near future due to increasing SST and emersion temperature conditions. However, present-day tolerance thresholds of the populations examined herein would not match future extreme temperature conditions for several hundred years, suggesting that a slow rate of evolution in these traits might be sufficient for these populations to persist, assuming that recent rates of change continue into the future.

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CHAPTER 4: General Conclusion

Summary of results

Climate change is altering the physical and chemical conditions of ocean habitats around the world, including changes to seawater temperature, pH, and salinity (Harley et al. 2006, Hoegh-Guldberg & Bruno 2010, IPCC 2014). Such changes to ocean conditions have the potential to impact marine organisms by altering population abundance (Hawkins et al. 2008) or by driving evolutionary change in adaptive traits (Reusch 2014). Of particular importance is the rate at which these abiotic conditions change, as this may determine whether populations adapt or are extirpated. Given the significant effects of temperature and salinity on the physiology and performance of marine organisms, knowledge of temporal trends in these conditions and of the extent of their spatial variation is essential to understand the selective pressures that have influenced the evolution of extant populations and to make predictions regarding their persistence in the face of climate change (Sorte et al. 2011). Therefore, to improve our understanding of the regional climate conditions on the southern coast of Vancouver Island, I have (1) characterized the long-term trends in surface seawater temperature (SST) and salinity (SSS) experienced by coastal marine animals during the most stressful time of year, and (2) documented variation between east and west coasts of Vancouver Island in terms of SST, SSS, and intertidal rock surface temperature during low-tide emersion. The most important findings were: (1) extreme summertime (July-August) SST increased at a rate of 0.81 – 1.13 °C per century for east and west coast regions of the island, while extreme SSS, during the time of year when salinity is lowest, increased by 3.9 PSU on the east coast (June-July) and remained unchanged on the west coast (January-February); and (2) the east coast waters were on average 4.3 °C warmer in the summer, and salinity reached lows that were 7.8 PSU lower, than on the west coast, while summertime rock surface temperatures in the mid and upper intertidal zone during daytime low tides were an average of 3.9-4.2 °C warmer on the east coast. Next, I examined the effects of the distinct local climate conditions on east and west coasts on the tolerance thresholds of populations on each coast. Using a series of common garden experiments, the tolerance thresholds of east and west coast populations of four benthic intertidal invertebrates were determined for (1) elevated temperature during low tide emersion, (2) elevated water temperature, and (3) low salinity. The most important findings being: (1) substantial differences in tolerance to increased SST and emersion temperature conditions were found between species of intertidal invertebrates, (2) similar tolerances to the abiotic parameters tested were found between east and west coast populations of intertidal species, and (3) acute exposure to increased SST and emersion temperature or decreased SSS conditions is not an immediate threat to the survival of at least some species of intertidal benthic invertebrates that colonize both the east and west coasts of Vancouver Island

Relevance of findings to policy

The findings of this study are relevant to numerous areas of Canadian policy regarding climate change and climate change adaptation planning. Knowledge of distinct rates of SST and SSS change between coasts, along with the subtle differences in species tolerance thresholds to significant climate-induced stressors, may aid in the implementation of mitigation policies important to British Columbia's marine-related industries and marine ecosystem health.

Chapter 2 Implications: east and west coast climate conditions and rates of SST and SSS change

The results of this research support previous assessments that rocky intertidal habitats are highly heterogenous in terms of local-scale climate conditions (Helmuth et al. 2006). In the present study, the east and west coasts of Southern Vancouver Island were found to differ noticeably in terms of climate conditions (i.e. SST, SSS, and intertidal rock surface temperature), but also in terms of rates of change of these environmental conditions. These differences in present-day climate conditions and their rates of change have implications for policy on climate change mitigation and adaptive planning, particularly regarding predictions of changing coastal conditions and the responses of organisms to these changes. Unfortunately, many policy and regulation reviews do not account for the differences in environmental conditions that can occur over short distances within ecosystems and give limited or no consideration of the different requirements and tolerance thresholds of each species (Nowlan, 1999). Acknowledging differences in local climate conditions will allow for more accurate predictions regarding future climate conditions and species responses at relevant spatial scales, which may improve the future success of some of British Columbia's marine-related industries. For example, knowledge of differing SST and SSS trends on the east and west coasts of Vancouver Island has implications for the future success of aquaculture practices important to British Columbia’s economy.

This study found that SST conditions are increasing on both the east and west coasts of Vancouver Island, and while SST is increasing at a similar rate on both coasts, the differences in present day SST conditions will cause east coast populations of species to experience stressful SST conditions before populations of west coast species. The greater increase in SST conditions predicted for the east coast means that ocean water conditions may become less favourable to rearing marketable species, and also that the west coast may become more favorable than the east coast for aquaculture practices (Jose 2012); this is most likely for animal species unable to tolerate warmer SST conditions, such as salmon (Noakes et al. 2000, White et al. 2016) and certain bivalves (Jose 2012). Furthermore, there is an increased risk of disease associated with warmer seawater conditions (Harvell et al. 2002), which may make the cooler water of the west coast even more favorable for aquaculture practices than the east coast. Spatially accurate predictions of increases in SST conditions may also have implications for natural resources that are both culturally important, as well as economically relevant. At least three groups of First Nations occupy different coastlines of Vancouver Island; the Nuu-chah-nulth to the west, the Coast Salish to the southeast and the Kwakwaka’wakw to the northeast. The rates of change in climate conditions distinct to each coast has implications for the abundance and availability of culturally important marine animals (e.g. abalone, salmon and seals) and edible seaweeds (e.g. giant kelp) (Lemmen et al. 2016). Loss of these culturally important resources may impact the identity of local First Nations as well as their economic well-being. To help mitigate potential future losses in First Nations natural resources and capital, it is important to incorporate local rates of climate change into future policy and planning, as not all indigenous communities could be affected in the same ways.

This study also determined that distinct trends in minimum SSS conditions existed between the east and west coasts; SSS conditions remain unchanged on the west coast, while the east coast is becoming more saline. Interestingly, these trends are reversed when the 2-month average lowest SSSs were used in place of minimum SSS conditions; 2-mo average SSS conditions showed a freshening trend on the west coast, while no changes in 2-mo average SSS were found on the east coast. Implications exist for the trends of both SSS parameters (i.e. minimum SSS and 2-mo average SSS). Minimum SSS trends are most relevant to the persistence of populations of intertidal species as it is these conditions that are most likely to cause mortality of individuals. As such, trends in minimum SSS suggest that the SSS stress imposed on populations of species will either remain at their current level (west coast) or become less stressful (east coast) in the future. Therefore, policy makers and resource mangers will not need to plan for the potential effects of worsening SSS conditions on population persistence. However, policy makers and resource managers should still consider the 2-mo average trends in SSS, in which the combined effects of SST increase and SSS freshening present on the west coast may promote alterations in the stratification of coastal ocean water (White et al. 2016). The combined effects of increased SST and freshening SSS conditions on the west coast has implications for British Columbia's wild-harvest fisheries industry, as changes in these parameters may influence food availability (Roemmich & Mcgowan 1995, Capotondi et al. 2012) to economically important fish species (i.e. Pacific Salmon), causing alterations in fish stock abundance and distribution (White et al. 2016). To help limit the potential economic losses to the fisheries sector, knowledge of fine-scale alterations in SST and SSS conditions may allow for more accurate predictions of when fish stock declines may occur and where future fish stocks will likely relocate.

Chapter 3 Implications: east and west coast population tolerance thresholds

This study found substantial differences among the four species in tolerance thresholds to increased SST and emersion temperature conditions as well as to decreased SSS conditions. In cases of acute temperature stress (i.e. SST and emersion temperature), high intertidal species displayed an increased tolerance compared to low intertidal species. While in contrast, more robust tolerance to reduced SSS conditions were found in low intertidal species compared to high intertidal species. This finding suggests that as SST and emersion temperature conditions continue to rise around Vancouver Island, some intertidal species will be more susceptible to these changes than others (while minimum SSS conditions become less stressful, imposing little threat to any study species). Differences in tolerance to climate-induced temperature stress between species occupying different intertidal heights can ultimately result in spatially distinct patterns of species response, which may create a series of cascading changes (ex. colonization by invasive species (Harley et al. 2006), or changes to food webs or ecosystem complexity (Harley et al. 2006, Ainsworth et al. 2011)) that effect overall ecosystem health. By framing policy around the most vulnerable populations, ecosystem health around the whole of Vancouver Island can be maintained to its fullest extent by decreasing the instances of ecosystem degradation. Unfortunately, a current assessment by Canada's Adaptation Platform, named "Canada's Marine Coasts in a Changing Climate", fails to address any possible concerns regarding species inhabiting rocky intertidal habitats, rather focusing on those living in estuaries, beaches and mudflats (Lemmen et al. 2016). Furthermore, no consideration for differences in tolerance thresholds among species are present within the policy outlined in "Canada's Marine Coasts in a Changing Climate". It is therefore relevant that policymakers consider all coastal habitat types as well as potential differences in tolerance to climate-related stressors among populations of the same species to employ the most effective climate change planning and mitigation strategies.

This study also shows that for each species, populations on the two coasts had similar tolerance thresholds. These similar tolerance thresholds among populations to SST, SSS, and emersion temperature exist despite differences in local climate conditions. This finding suggests that despite prolonged exposure (> 81 y), individuals of benthic marine invertebrates have not been quick to adapt to the local conditions imposed upon them by the east and west coasts of Vancouver Island (Chapter 2). Therefore, as SST and emersion temperature conditions continue to become more stressful into the future, it is unlikely that the persistence of populations will be aided by timely evolution of greater temperature tolerance thresholds. In terms of policy planning and mitigation strategies, the existence of similar tolerances between populations suggests that effective strategies may be framed around species tolerances as whole, instead of focusing on how differences in local climate conditions may affect these populations. Based on the slow evolution of distinct tolerance thresholds among populations, policy makers should intervene if climate-related stressors become too great for the persistence of populations; waiting for species to develop increased physiological tolerance to new conditions may cause the unwanted migration or extirpation of vulnerable species.

Finally, this study found that acute exposure to increased SST and emersion temperature is not an immediate threat to the survival of at least some species of intertidal benthic invertebrates that colonize both the east and west coasts of Vancouver Island, despite the predicted increases in these conditions into the future (Chapter 2). Based on the assumption that current rates of temperature change will continue into the future and present-day tolerance thresholds of animals will not evolve, occasional exposure to these future temperature conditions are unlikely to directly affect the survival of three gastropod species (*N. lamellosa*, *L. sitkana* and *L. scutulata*) and common barnacle species *(B. glandula*) for several hundreds of years (Chapter 3). The effects of changes in acute SSS stress on the survival of these intertidal animals are of even less concern than temperature- related stressors, as acute SSS stress is predicted to decrease (east coast) or remain the same (west coast) into the future. However, in addition to responses to acute exposure to extreme levels of these abiotic conditions, the persistence of populations in a given region also depends on whether individuals can survive exposures to these conditions over longer periods of time (Whiteley & Mackenzie 2016), or survive the indirect effects associated with changing climate (i.e. increased predator abundance, competition with invasive species, increased disease prevalence, food source depletion, etc.) (Harley et al. 2006, Ainsworth et al. 2011). Populations may therefore be vulnerable to ongoing changes in abiotic conditions despite their tolerance of acute conditions. It is therefore important to also consider the effects of these other climate-related stressors when predicting if a population is likely to persist within a given region in the future. Overall these findings suggest that current policy and adaptative planning has time to focus on other climate-related stressors that may be of more immediate concern to future species survival than acute stress, such as community level effects or chronic stress conditions.

Conclusions

In conclusion, this study suggests that variations in local SST, SSS, and emersion temperature conditions on the east and west coasts of Southern Vancouver Island are present and are changing at different rates (Chapter 2). This study also demonstrated that differences among populations of intertidal species in tolerance to climate-related stressors are not always representative of the conditions in which they live (Chapter 3). Overall, these findings confirm a high degree of variability present within the rocky intertidal ecosystem, from both an abiotic (i.e. climate) and biotic (i.e. tolerance threshold) perspective. Current policy and adaptive planning have failed to account for variation in regional climate change trends, or differences among species in tolerance to climate-related stressors, rather implementing overarching policies, assuming the needs of all animals along the intertidal ecosystem are equal and rates of change are the same. To increase the potential effectiveness of climate change mitigation, it is recommended that policy makers (1) include adaptive planning measures that specifically incorporate rocky intertidal ecosystems and the climate-related stressors relevant to the survival of intertidal species, (2) account for spatial differences in rates of climate change around regions of British Columbia's coastline, and (3) recognize that not all intertidal species possess the same tolerance to climate-related stressors, nor are they necessarily locally adapted to the conditions where they live. By incorporating the latter knowledge into climate change mitigation policy, especially with regards to harvested populations or species at risk, the development of spatially relevant management practices may help mitigate potentially harmful shifts in marine ecosystem health and limit impacts to the human communities that depend on marine resources.

Directions for future study

Implementing effective climate change mitigation policy regarding the protection of British Columbia's rocky intertidal shores will be challenging due to the large degree of natural variation present in these ecosystems. As such, a comprehensive understanding of spatial variation in rates of climate conditions as well as variation among populations in tolerance to climate-related stressors will be exceedingly useful for understanding how climate change will affect the coastal ecosystems of Vancouver Island. The distinct rates of change in SST and SSS on the east and west coasts of southern Vancouver Island prompt the question of whether there are also distinct trends in these conditions on the coastlines of the northern regions of Vancouver Island and elsewhere along the coast of British Columbia. Future studies should determine the rates of change in SST and SSS conditions in those regions during the most physiologically stressful time of year for local animal populations in order to build a better picture of the variation in climate conditions present around Vancouver Island.

Given the substantial differences in tolerance to increased immersion and emersion temperatures between high and low intertidal species, future research may wish to investigate if the species most tolerant of temperature stress are also more tolerant to other climate-related stressors such as desiccation and reduced pH. Moreover, future studies should determine if population extirpation might result from medium or long-term exposure of organisms to elevated SST levels that are predicted for coastlines around Vancouver Island in the future. Finally, the effects of chronic exposure to reduced salinity stress on the persistence of populations of intertidal animas will also be of intertest as climate-related conditions change around Vancouver Island into the future. As SSS is not the most important cause of salinity stress in these populations another salinity stress should be studied; within the northeast Pacific region, instances of rainfall are expected to increase into the future (IPCC 2014), and as such future studies may wish to determine how chronic exposure to heavy rainfall during low tide emersion affects the survival of intertidal invertebrate species.

Future research dedicated to the above areas of study, will provide further insight to the types of climate-related stress most relevant to climate change policy surrounding the response of intertidal populations and communities to climate change. By elucidating the effects of specific climate-related stressors during the time of year when these stressors are at their most intense for intertidal animals, it is possible that more accurate predications of population persistence may be made in the future. Overall, the greater understanding of the effects of climate change on intertidal animals, the more informed policy makers and resource mangers may be about types of strategies that are most effective for the protection of various coastal habitats at spatially relevant scales.

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APPENDIX A: Health assessment of animals

The health of the snail *N. lamellosa* was determined by first observing their active state immediately after emersion. Those individuals adhered to the walls of the cage using their muscular foot were deemed healthy, while those that were unattached required further testing using a blunt probe to evoke a response (i.e. movement or retraction of muscular foot and/or siphon) after touching the muscular foot, siphon or operculum as appropriate. If no response was elicited via probe, fine-tipped tweezers were used to gently probe under the operculum. When no responses were prompted, the individual was reported as deceased and removed from the experiment.

Determining the health of *L. sitkana* and *L. scutulata* was similar to the procedures used with *N. lamellosa*; immediately after emersion those individuals who were attached to the walls of the cage using their muscular foot were deemed healthy, while those who were unattached required further testing. Unattached individuals were submersed into a shallow well of sea water for one min and monitored for responses (i.e. emergence from shell and/ or attachment of foot to dish), before using a blunt probe to determine their condition (Fig. A.1). If no responses occurred after the course of these two procedures the individual was deemed deceased and removed from the experiment.

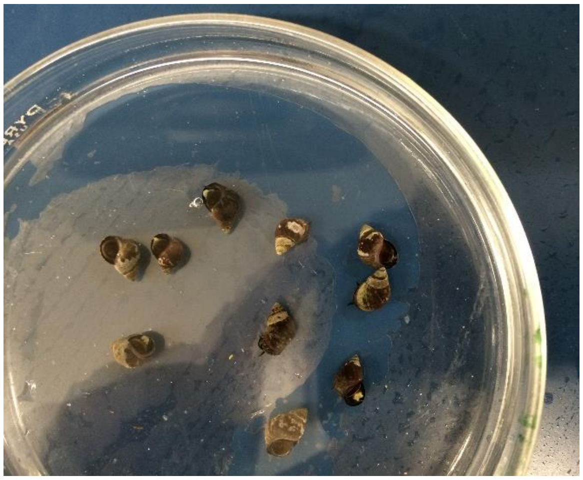

Figure A1. Mortality procedure for littorinid species involved submersion in full salinity ocean water to determine health as shown with *L. sitkana* above.

In the case of *B. glandula*, opercular plates were tapped or gently depressed using a fine-tipped probe to determine if an individual was alive and responsive. Deceased individuals were unable to hold their opercular plates in-situ and would be cleaned from the stone.

APPENDIX B: Preliminary water temperature tolerance experiments

Collections of animals were made from east and west coast sites on 17 July 2015, respectively (Table 1). All animals were acclimated for 48 h in trays containing aerated seawater filtered to 200 µm and held at 15.0-17.5 °C and 30 – 32 PSU. At the onset of preliminary water temperature tolerance experiments cages were removed from acclimation tanks, distributed into experimental amongst aerated experimental tanks, covered with lids and containing 30 – 32 PSU, 200 µ filtered seawater, pre-heated to a desired temperature treatment.

Table B.1. Preliminary water temperature tolerance experimental design summary per species

	Water temperature			
Species	Replicate cages per site (n = 6)	Number of individuals per cage	Total number of individuals used in experiment	Water temperature treatments (°C)
Nucella lamellosa	12	5	60	25, 33
Balanus glandula	12	10	120	25, 33, 40
Littorina sitkana	12	7	84	25, 33, 40
Littorina scutulata	12	7	84	25, 33, 40

To determine the range of water temperatures necessary to induce 0 – 100 % mortality within animals, they were immersed at a particular seawater temperature for 24 h, followed by a recovery period immersed in 30 – 32 PSU, 200 µ filtered seawater at 17 °C, and then examined during a 4 h mortality check wherein they were exposed to air temperature conditions between 20 – 22 °C (see appendix A). Surviving individuals were then placed in the next warmer temperature treatment (Table B.1.) for 24 h and was repeated until 100 % mortality was experienced.