



Seasonal changes in the thermal regime and gastropod tolerance to temperature and desiccation stress in the rocky intertidal zone in Southeast Alaska



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ABSTRACT

Low tide emersion of intertidal fauna in the inside passage from Puget Sound, WA to Skagway, AK produces more extreme emersion temperatures than on the outer continental coastline because the timing of low tides increases the potential for summer high temperatures and winter low temperatures. This study documents seasonal changes in water/aerial temperatures at different tidal heights in 2007–2008 and the summer of 2015 and reports the high emersion temperature (5 h) and desiccation tolerance of three species of rocky shore gastropods. Vertical transects of probes were deployed at Bridget Cove at +5.0 m (above the tidal range), +3.5, +2.5 m, +1.5 m and 0 m. Two additional probes were partially buried at +1.5 m; burial ameliorated freezing temperatures. Duration of emersion increased with intertidal height and was of longer duration at +3.5 m during Neap tides and at +1.5 and 0 m during Spring tides. Monthly measures of temperature were: average temperature, monthly maximum, average daily monthly maximum, average daily monthly minimum, and monthly minimum. Monthly maximum air temperature increased with tidal height. Winter average daily monthly minimum fell below 0 °C at the +3.5, +2.5, and +1.5 m tidal heights for the aerially exposed probes. The number of days when emersion temperature fell below 0 °C increased with intertidal height as did the number of hours per day. High temperature emersion tolerance of *Nucella lamellosa*, *Nucella lima* and *Littorina sitkana* varied directly with their intertidal range but their desiccation tolerance did not suggesting that desiccation is not an abiotic stressor in this temperate rain forest intertidal zone. The LT₅₀ temperature (5 h) was considerably above recorded monthly maximum temperatures in the vertical range of *N. lamellosa* and *L. sitkana* but the LT₅₀ of *N. lima* was very near the maximum monthly temperature at +2.5 m.

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1. Introduction

Rocky intertidal zonation of species is frequently determined by tolerance of emersion temperature and desiccation at the upper end of the species range (Connell, 1970, 1972; Menge and Sutherland, 1987) and by biotic interactions at the lower end of the species range (Paine, 1966, 1969).

The latitudinal and vertical patterning of species distributions in the intertidal zone commonly reflects gradients or discontinuities in environmental temperatures with an emphasis on emersion temperatures (Somero, 2002, 2005).

Modifying factors such as regional differences in the timing of low tides can overwhelm large-scale climatic gradients. The thermal emersion regime on the outer Pacific coast of the continental United States is ameliorated because Spring low tides occur at night in the summer

and during the day in the winter. In contrast, the timing of Spring low tide emersions in the inside passage from Puget Sound, WA north to Skagway, AK produces more extreme emersion temperatures because low Spring tides occur during the day in the summer and at night in the winter. Emersion temperatures at the mid tide level on the continental US coast have been documented by Helmuth et al. (2002, 2006a, 2006b). Helmuth et al. (2006b) also reported mid-tidal emersion data for two locations at the southern end of the inside passage on San Juan Island, WA and noted significantly more freezing events at those locations than occurred on the outer coast. Stickle et al. (2011, 2015) recorded ambient temperatures for 16 months with probes located at five rocky intertidal heights at a location near the north end of the inside passage and focused on freezing events. These freezing events were significantly colder than at Cattle Point and Collins Cove on San Juan Island, WA (Helmuth et al., 2006b). The number of days when emersion temperature fell below 0 °C increased with intertidal height as did the number of hours per day when the emersion temperature was <0 °C (Stickle et al., 2015).

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A number of studies have documented the effects of emersion temperature on the acute and chronic performance of rocky intertidal fauna throughout their latitudinal and intertidal thermal zones on the continental Pacific coast of the United States. Among the physiological traits related to intertidal vertical zonation are thermal tolerance, heart function, mitochondrial respiration, membrane fluidity, action potential generation, protein synthesis, heat-shock protein expression and protein thermal stability (Somero, 2002). It is important to link patterns and mechanisms of physiological adaptation to global climate change (Somero, 2012). Earlier studies have either investigated the thermal responses of congeneric species as a function of their intertidal zonation or their latitudinal distribution for: *Tegula* spp.—Tomanek and Somero (1999), field/lab, Tomanek (2002) field/lab; *Haliotis* spp.—Dahlhoff and Somero (1993) field/lab; *Nucella canaliculata* (Sorte and Hofmann, 2004) field; *Nucella ostrina*—Dalhoff et al. (2001) field; *Petrolisthes* spp. (Stillman and Somero, 1996, lab and Stillman and Somero, 1999, lab); *Mytilus californianus* (Roberts et al., 1997) and *Mytilus galloprovincialis* and *Mytilus trossulus* (Schneider, 2008) lab.

This study had two objectives, (1) document the thermal regime of rocky intertidal fauna from a location at the north end of the inside passage of Southeast Alaska and (2) document the recent aerial thermal history and temperature and desiccation tolerance of three species of rocky intertidal gastropods; high intertidal *Littorina sitkana*, mid-intertidal *Nucella lima*, and low intertidal *Nucella lamellosa*.

2. Materials and methods

2.1. Seasonal change in thermal conditions

Two vertical transects of ProV2 Hobo temperature probes covered with protective sleeves were deployed at Bridget Cove (Transect 1: MHHW (+5 m)—N58.62970 W134.94151; Zero tide—N58.62947 W134.94332; Transect 2: MHHW—N58.62921 W134.94206; Zero tide—N58.62903 W134.94309) along Lynn Canal, AK as described in Stickle et al. (2011). The two transects were separated by 40 m and transect 1 had a shallower slope than transect 2. Probes were deployed at +5.0 m (above the usual tidal range), +3.5 m (transect 1 only) the upper (+2.5 m) and lower (+1.5 m) edges of the mid intertidal range of *M. trossulus* and *N. lima*, and the zero tide level (0 m). Two additional probes were partially buried at the lower edge of the mid intertidal range (+1.5 m), one in tightly packed particulate material (transect 1) and the other in loosely packed particulate material (transect 2) to reflect the density of particulate material around burrowed fauna. The transect 1 zero tide level probe was tampered with and lost prior to the June 2008 data download, the last data collection was April 4.

The hours of emersion for all spring and neap tide dates were computed based on the NOAA/CO-OPS observed water levels at the Juneau Harmonic station (58.2983°N 134.0150°W; mixed semidiurnal tidal pattern), which was the closest available Harmonic station to Bridget Cove. The CO-OPS Data Retrieval API was used to obtain the hourly water levels across all dates of the study period, with MLLW as the 0 tide level. The water levels for the spring and neap tide dates were extracted from these data. The spring and neap tide events were determined by the dates of the primary moon phases, obtained via the data services of the Astronomical Application Department of the U.S. Naval Observatory. Finally, for each spring and neap tide event, the number of hours of emersion at each intertidal height was computed as the number of hours the water level was below that height with two emersion events per lunar day. Welch's correction of the t-test was used to compare Neap and Spring tide events at each tidal height with significant differences between means given at the $p < 0.05$ level.

Five monthly temperature measures of the records were extracted from the data set as described by Helmuth et al. (2006b). The average monthly temperature is the average of all temperatures during the month. The daily maximum and minimum are the highest and lowest

temperature recorded in a day: The average daily maximum and minimum is the average of all daily maxima and minima recorded during the month and is a measure of chronic temperature exposure. Maximum and Minimum data are emersion data in both this and the Helmuth et al. (2006b) paper.

The transect data panels in Fig. 1 were constructed using a script written in Python 3.4 with the support of multiple third-party modules. For each probe, the temperature records were read in by the script, and methods from the Matplotlib and NumPy modules were used to plot those records in a stacked bar chart (Hunter, 2007). In the bar charts, each month has three stacked bars representing temperature ranges. The solid black bar shows the range from the monthly minimum to the average daily minimum temperature. The solid white bar shows the range from the average daily minimum to the average daily maximum, and finally the white bar with diagonal hatch marks shows the range from the average daily monthly maximum to the monthly maximum temperature. The average monthly temperatures were plotted as a line overlaying the bars.

2.2. 2015 emersion temperature

Probes for transect 1 were redeployed at the same positions during May–August 2015. The maximum monthly, daily average monthly maximum, and average monthly temperature at each intertidal height from May through August 2015 was recorded for comparison with the determination of maximum 5 h aerial emersion temperature and desiccation tolerance of the three species of intertidal gastropods. Emersion temperatures were recorded from the first temperature at least 1 °C above the surface seawater temperature. Summer meltwater from the Eagle and Herbert Glaciers creates a freshwater lens system that stratifies the surface seawater temperature at Sunshine and Bridget Coves (Stickle and Denoux, 1976). Likewise the Neap and Spring tide \pm one day emersion temperatures were calculated from May 1 through August 31, 2015. Probes bounding the vertical distribution of *L. sitkana* were +3.5 and +1.5 m, for *N. lima* were +2.5 and +1.5 m, and for *N. lamellosa* was below 0 M +1.5 m.

Days when precipitation occurred were recorded from a Weather Source database for precipitation at Lena Point north of Juneau, AK (58.3867°N; 134.766°W: <https://Weathersource.com>). Lena Point is 26.5 km south of the collecting site at Sunshine Cove and 27 km south of the probe site at Bridget Cove.

2.3. Snail collection and maintenance

The three species of gastropods were collected during late July through early August 2015 at Sunshine Cove, 0.5 km south of Bridget Cove and returned to a seawater table at the University of and Southeast and moved and to after Southeast maintained at 8.5–9.8 °C and 30 PSU. Snails were used for thermal and desiccation studies within one week of collection.

2.4. Desiccation tolerance

Snails of each species were placed into a desiccator filled with Drierite and the desiccator was sealed with Silicone Grease. Ten individuals of each species were removed from the desiccator every 24 h and placed aperture up in a Pyrex dish filled with 30 PSU seawater at 8.5–10 °C for 1 h. Snail activity was assessed as follows:

1.0—snail was righted and foot attached to the dish,

0.5—foot was irritable and extended from the aperture

0.0—foot was not irritable to the touch and the snail was deemed dead after 1 h.

The desiccation experiment was continued until all 10 snails assayed for that day had an activity score of 0.0. Lt_{50} values in days of desiccation were determined by the method of PoloPlus v. 2.0 (LeOr Software Company; Petaluma, CA) and desiccation tolerance differences between

the species were determined by non-overlap of 95% confidence intervals.

2.5. High temperature emersion tolerance

Snails of each species were subjected to 5 h emersion exposures in a recirculating water bath in 250 ml screw top centrifuge bottles at a series of 4–5 emersion temperatures. A 5 h emersion temperature was chosen since it represents an average emersion period at the mid tidal level. The duration of freezing emersion of *N. lamellosa* at 2 and 5 h and *L. sitkana* at 5 and 10 h had no effect on LT_{50} of these snails at this collection site (Stickle et al., 2015). The number of snails of all species exposed at all experimental temperatures was 15. Emersion temperatures were determined to be the asymptote temperature (within 1 °C

of the final temperature) with a Hobo ProV2 probe that read the emersion bottle temperature once per minute as was done in freeze tolerance studies on the same species of snails (Stickle et al., 2011; Stickle et al., 2015). The time from introduction of the bottle into the water bath until the bottle reached the asymptote temperature varied from 18 to 78 min out of the 300 min (5 h) emersion exposure accounting for 6–26% of the exposure time. Snail activity was determined as in the desiccation tolerance experiments. LT_{50} temperatures were determined by the Spearman Karber test (Silverstone, 1957) of data from each species. The treatments used with this analysis require one 0% mortality temperature, two partial percent mortality temperatures and one 100% mortality emersion temperature. Emersion tolerance differences between the species of snails were determined by non-overlap of 95% confidence intervals.

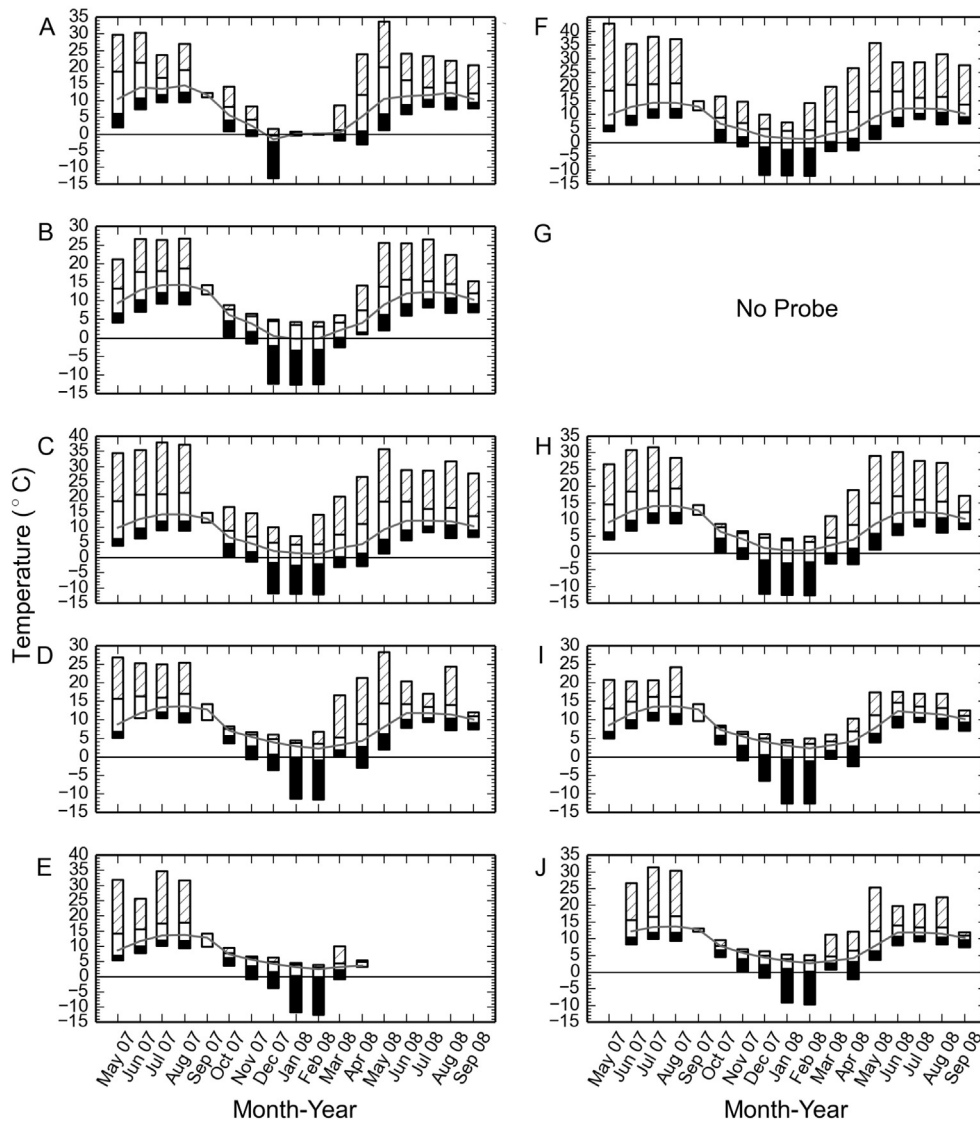


Fig. 1. Temperature measurements were recorded every 5 min along two transects of the rocky intertidal zone at Bridget Cove Alaska between May 2007 and September 2008. Probes were deployed at +5 m (A, F), the upper (+2.5 m; C, H) and lower edges (+1.5 m; D, I) of the mid intertidal range of *Mytilus trossulus* and *Nucella lima*, and the zero tide level (E, J). One additional probe was deployed in transect 1 in the middle of the high intertidal zone (+3.5 m; B). Temperature data for transect 1 are shown in the left hand vertical bank of panels (A–E) and Transect 2 is shown in the right hand bank (F–J). Four mathematical measures of the temperature records were the monthly maximum which is the highest daily maximum recorded during the month, upper end of the hatched bar in each month; the average daily maximum which is the average of all daily maxima recorded during the month, lower end of the hatched bar for each month; the average daily minimum was the average lowest temperature recorded for each day in a month, upper end of the black bar for each month; and the monthly minimum is the lowest daily minimum recorded during the month, lower end of the black bar for each month. The average monthly temperature is shown by the line which connects the monthly bars.

Table 1

Hours of emersion for all spring and neap tide dates plus and minus 1 day at 0, 1.5, 2.5, 3.5 and 5 m tidal heights based on the Juneau Harmonic Station during our study duration in 2007–2008. All emersion times are based on still tidal heights (no wave modification). Data are given as $h \pm \text{SEM}$ (n = number of Neap or Spring tide events) and t-test of difference between Neap and spring tide emersion events at each tidal height.

Tidal datum (m)	Neap tide \pm 1 day (n)	Spring tide \pm 1 day (n)	t-test ($p < 0.05$)
5	23.700 \pm 0.001(35)	21.408 \pm 0.001(36)	Yes
3.5	17.870 \pm 0.001(35)	14.867 \pm 0.001(36)	Yes
2.5	11.002 \pm 0.001(35)	11.703 \pm 0.001(36)	Yes
1.5	5.053 \pm 0.001(35)	8.123 \pm 0.001(36)	Yes
0	0.048 \pm 0.000 (4)	2.602 \pm 0.000 (36)	Yes

3. Results

3.1. Emersion times as a function of neap and spring tides

The average tidal data for the Juneau station were: MLLW = – 1.030 m; MTL = 3.612 m; and MHHW = 6.001 m. Emersion times increased as a function of intertidal height during Neap and Spring tides (Table 1). Emersion times were higher in the upper region of the intertidal zone (+5 and +3.5 m) during Neap tides because the low high tide did not rise as high during Neap tides. Conversely, emersion times were longer at +2.5 m, +1.5 m and 0 m levels during Spring tides. Significant differences between Neap and Spring tide emersions existed at all tidal levels and were biologically significant at +5, +3.5, +1.5, and 0 m tidal levels. These calculations were based on a flat sea surface so wave activity would decrease emersion time at all intertidal heights.

3.2. Seasonal tracking of average monthly temperatures

Daily and monthly variation in the amplitude of emersion temperatures was much more extreme than the variation in the average monthly ambient temperature due to seasonal variation in air temperatures (Fig. 1). Monthly maximum temperature tended to increase with the tidal height of the Hobo probes and varied with the probe placement relative to vegetative cover and aspect relative to solar illumination. The average daily minimum temperatures exhibited more variability by probe intertidal position during the winter, was inversely related with intertidal height and is indicative of chronic cold temperature stress (Fig. 1). Average monthly minimum temperatures occurred at night during spring tides in both the summer and winter months.

The number of days when emersion temperature fell below 0 °C increased with intertidal height as did the number of hours per day when the emersion temperature was <0 °C (Table 2). The Hobo probes were exposed to 45 days of air temperatures below 0 °C at +2.5 m and 82 days at +3.5 m. The temperature recordings at +5 m was only <0 °C for 53 days due to the presence of snow cover at this supratidal height for significant time periods during winter. The average daily minimum temperature fell below 0 °C at the +5, +3.5, +2.5, +1.5, and 0 m tidal heights during probe emersions between December 2007 and February 2008. The average daily minimum during winter was

Table 2

Days when emersion temperature was <0 °C and hours per day (Mean \pm SEM (n) when the temperature was <0 °C (at Bridget Cove, AK in 2007–2008 for Transect 1 (T1) and Transect 2 (T2). 1.5 m buried (T1 = tightly packed) (T2 = loosely packed). X = no data.

Probe height (m)	Days <0° – T1	Days <0° T2	h < 0 °C (T1)	h < 0 °C (T2)
5	54	38	15.44 \pm 1.24(54)	14.41 \pm 1.53(23)
3.5	82	x	10.49 \pm 1.24(54)	X
2.5	84	92	6.14 \pm 0.46(84)	7.41 \pm 0.54(92)
1.5	40	44	3.17 \pm 0.35(40)	2.65 \pm 0.30(44)
1.5 Buried	9	42	3.35 \pm 0.85(9)	2.67 \pm 0.34(44)
0	38	23	2.47 \pm 0.27(38)	2.34 \pm 0.42(23)

higher, never <0 °C, for the tightly packed buried probe (transect 1 at the +1.5 m tide level) between December and February compared with an average minimum temperature of –0.49 °C in January and –0.94 °C in February for the loosely packed probe (transect 2). There was no difference in the minimum temperature of the loosely packed and emersed probes in transect 2 during the winter nor in either buried probe relative to emersed probes at +1.5 m during the summer.

The average daily maximum temperature varied directly with the intertidal height of the probe to a greater extent during May–August of both years than during the winter, and is indicative of chronic stress to intertidal biota (Fig. 1). Monthly average maximum temperatures peaked in May and June of both years and dropped in July and August; this observation is potentially correlated with an increase in rainy weather later in the summer. Weather data on precipitation from May through August of 2007 and 2008 did not reveal a seasonal pattern in precipitation as a surrogate for cloud cover.

The seasonal variability in the average daily maximum temperature is affected by the long photophase during the summer months and long scotophase during the winter. The average daily maximum temperatures of the buried probes at +1.5 m were significantly lower than that of the exposed probes during the summer.

3.3. Extreme temperature emersion exposure in 2007 and 2008

Biota from Bridget Cove Alaska are exposed to freezing emersion temperature gradients which increase in frequency and duration during tidal cycles as a function of intertidal height (Table 1). Monthly minima were lowest from November 2007 through March 2008 (Fig. 1) and are indicative of acute temperature stress associated with emersion freezing.

Only the +5 m probe of transect 2 recorded multiple events >30 °C, 35 °C, and 40 °C for 2.5 h during May through August in both 2007 and 2008. The +5 m probes were above the upshore distribution of *L. sitkana* (+3.5 m). Most of the 2.5 h exposures to temperatures >30 °C, 35 °C, and 40 °C occurred in May and June of 2007 and 2008. The only other probe to record emersion temperatures >30 °C for 2.5 h was the 2.5 m probe of transect 1; 3 times in May 2007.

3.4. Extreme temperature emersion exposure in the summer of 2015

Summer maximum air temperature at 5 m height was over 40 °C from May through August 2015 (Table 3). This probe was only emersed 53 times out of 246 high tides over these 4 months and all but 7 of the immersion events occurred during the scotophase. Maximum probe temperature at 5 m can be considered indicative of the maximum air temperature at Bridget Cove. Maximum monthly temperatures peaked at all probe heights in May and June and were highest at the +1.5 m height. There was no relationship between intertidal height and maximum monthly or average daily monthly temperature. Aspect and macroalgal cover differences in probe position may have masked the intertidal height relationship with the monthly and average daily maximum temperatures. Average daily maximum temperature as a percentage of the maximum temperature each month at 5 m likely reveals a good relationship with rainfall events and cold freshwater outflow from the Eagle and Herbert rivers as the Eagle and Herbert

3.5. Desiccation tolerance

There was no significant difference in the desiccation tolerance of the low intertidal *N. lamellosa* (2.89; 2.47–3.31 days, 95% CI), the midtidal *N. lima* (2.17; 1.43–2.91 days), and the upper intertidal *L. sitkana* 2.97; 2.20–3.42 days). Desiccation tolerance of all three species was of short duration (Fig. 2A).

4. High temperature emersion tolerance

Thermal tolerance of the three species of intertidal gastropods varied directly with their intertidal distribution. Low intertidal *N. lamellosa* exhibited a 5 h emersion thermal tolerance of 29.63(29.46–29.80 °C, 95% CI), midtidal *N. lima* exhibited a thermal tolerance of 31.39(31.18–31.60 °C), and mid-upper intertidal *L. sitkana* exhibited a thermal tolerance of 41.51(40.59–42.44 °C; Fig. 2B). *L. sitkana* is clearly more eurythermal than either species of *Nucella*.

5. Discussion

This study extends our understanding of the thermal regime in the rocky intertidal zone of the Pacific coast of North America to the northern end of the inside passage where the timing of Spring low tides maximizes the effects of emersion temperature extremes. The study also documents variability in emersion temperatures throughout the vertical intertidal zone. Southeast Alaska lies in a temperate rain forest which ameliorates the number of sunny days during the photophase

of summer low tides. Bridget Cove and Sunshine Cove are also salinity stressed during the summer due to meltwater flowing north from the Eagle and Herbert rivers (Stickle and Denoux, 1976). A more complete understanding of the effects of emersion on rocky intertidal snails in the inside passage can be gained by conducting parallel studies to those at our site (Stickle et al., 2011, 2015 and this manuscript) at a more arid habitat at the southern end of the inside passage.

The duration of emersion increased with height in the intertidal zone as shown by hours of emersion during both neap and spring tides at the Juneau Harmonic station (Table 1). Monthly maximum temperature tended to increase with the tidal height of the Hobo probes and varied with the probe placement relative to vegetative cover and aspect relative to solar illumination. Days of freezing and hours per emersion during freezing air temperatures in the winter increased with intertidal height (Stickle et al., 2015).

Numerous tolerance and sub lethal stress studies from the rocky intertidal zone of the continental United States have been conducted in a setting that consists of a latitudinal mosaic of emersion temperatures rather than along a latitudinal emersion stress gradient that occurs along the inside passage of Washington, British Columbia and Southeast Alaska.

High temperature and desiccation tolerance tend to be correlated with the species vertical limits of upshore distribution on rocky shores (Newell, 1970, 1976; Wolcott, 1973; Underwood, 1979). High temperature emersion tolerance of the three species of snails, *N. lamellosa*, *N. lima*, and *L. sitkana* at Sunshine Cove, AK increases directly with their upshore distribution. In the few studies which gave measurements of prevailing ambient conditions and snail body temperatures in the field, body temperatures were usually well below the snail tolerance values determined in the laboratory (Underwood, 1979). Thermal tolerance of *N. lamellosa* at 0 m and *L. sitkana* at 3.5 m is well above the maximum temperatures recorded with the Hobo probes at our study site. Maximum monthly temperatures are above the 5 h LT₅₀ value for *N. lima* at +1.5 m but below its LT₅₀ at +2.5 m indicating that the aspect of snails and the probe relative to solar radiation has a major effect on the snails thermal regime. The percent of days when it rained in Juneau and the quantity of rainfall increased during the summer months which ameliorated thermal and desiccation stress on many days which would reduce sub-lethal stress on intertidal snails. Duration of exposure to high emersion temperature and desiccation as well as behavioral avoidance by crawling into crevices, onto the shady side of rocks and under rocks should be included in the suite of sub-lethal adaptations to elevated ambient temperatures (Hayford et al., 2015; Stickle et al., 2011).

Desiccation tolerance of these species of snails was not related to their intertidal distribution which may be influenced by the fact that this site is in the largest temperate rain forest in North America and all three species have life histories with crawl away juveniles emerging from egg capsules (Strathmann, 1987). Natural selection is likely not a selective factor increasing desiccation tolerance in the absence of increased desiccation stress. The percent of days when it rained in Juneau and the quantity of rainfall increased during the summer months would ameliorate desiccation stress. Previous studies at Monterey, CA demonstrated a correlation between vertical stratification of three species of gastropods (*Tegula funebralis*, *Littorina scutulata*, and *Littorina planaxis*) and their desiccation tolerance (Hewatt, 1937); at Point Arago, OR in *Calliostoma ligatum*, *Tegula funebralis*, and *L. scutulata* (Emerson, 1965); in north Wales in seven species of intertidal gastropods where an even more striking correlation existed between desiccation tolerance and their zone within crevices (Kensler, 1967). Finally, a direct relationship was observed between the rate of water loss of *Patella aspera* and *Patella vulgata* as well as the median lethal percent of water loss and the intertidal zonation of *P. vulgata* on the Isles of Cumbrae and Little Cumbrae in Great Britain (Spencer Davies, 1969) and the gastropod species at Point Arago, OR (Emerson, 1965). The conclusion of the study on *P. aspera* and *P. vulgata* was that the upper intertidal level of distribution

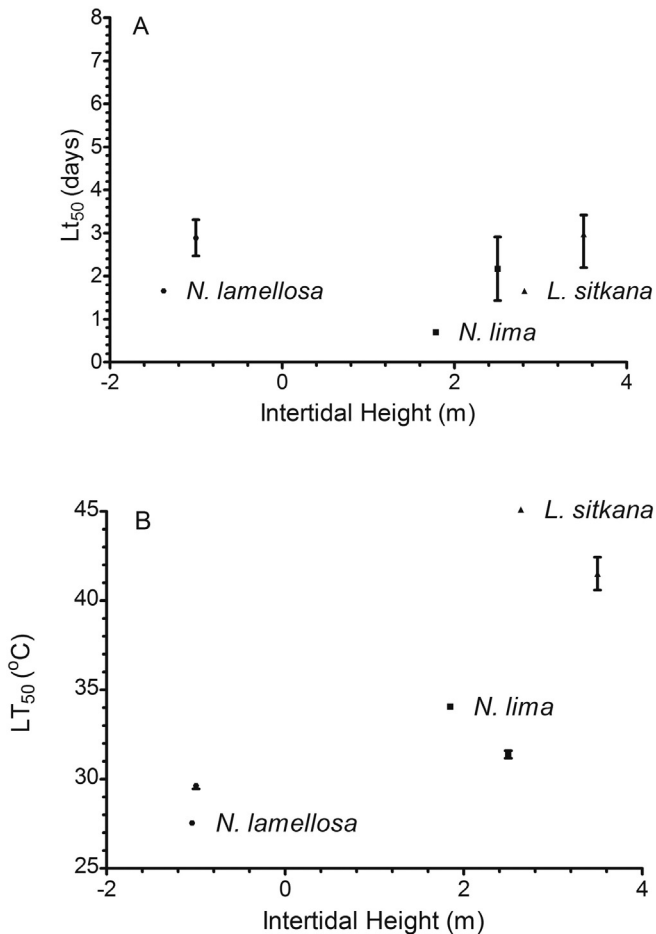


Fig. 2. Desiccation (A) and 5 h emersion temperature tolerance (B) of low intertidal *Nucella lamellosa*, mid intertidal *N. lima*, and high intertidal *Littorina sitkana*. Data are plotted as the average \pm 95% confidence interval in days. Significant differences between species are shown by non-overlap of 95% confidence ranges between species.

of these limpets may be set by an interplay between loss of water and the time required to regain water when the limpet is next immersed.

The three species of snails from Sunshine Cove Alaska were also exposed to a freezing emersion temperature gradient which increased in frequency and duration as a function of intertidal height. Freeze tolerance of the three species increased directly with their intertidal vertical range. The supercooling point of the three species also varied directly with their intertidal range. Freezing of the three species of gastropods does not occur during emersion until the snail's body temperature falls below the supercooling point after the exophthalmic release of heat. Seasonally adaptive synthesis of free amino acid compatible osmolytes, alanine, taurine and total FAA, in the winter also enhanced the freeze tolerance of all three species (Stickle et al., 2015). *N. lima* moved from rock surfaces to crevices, under rocks, or into particulate material in the winter (Stickle et al., 2011). Conduction and radiation of heat from rocks or interstitial material likely dampened the severity of exposure to freezing conditions (Stickle et al., 2015). Buried probe results from the + 1.5 m intertidal height in this study indicated that movement of *N. lima* into crevices, under boulders or into the sediment at the base of rocks in the winter ameliorated extreme freezing conditions at this site as documented by Stickle et al. (2011). Similar behaviors likely occur in *N. lamellosa* and *L. sitkana*.

Maximum and minimum monthly temperatures are rare events which can lead to intertidal zone organismal mortalities or acute sublethal stress responses. *M. trossulus* suffered near total mortality over a three week exposure to recorded air temperatures as low as -31°C in the rocky upper mid-intertidal zone at Kachemak Bay in south Central Alaska in January 1989 (Carroll and Highsmith, 1996). Emersion exposure to temperatures of $30\text{--}40^{\circ}\text{C}$ for 2.5 h have induced Hsp synthesis in laboratory experiments in three species of *Tegula* from Monterey California and the Gulf of California (Tomanek and Somero, 1999) and in the two temperate sister species. The Hsp response of *Tegula brunnea* and *Tegula montereyi* that occupy the subtidal and low-intertidal zone differ from that of the low- to mid-intertidal *Tegula funebralis* (and the subtropical mid-intertidal *Tegula rugosa* in (i) heat tolerance, (ii) the onset temperature of their main hsp, hsp70 (70 kDa), (iii) the temperature of maximal hsp70 synthesis, (iv) the upper temperature of hsp synthesis, and (v) the recovery from a thermal stress typical for the mid-intertidal zone. The results therefore confirm the importance of interspecific differences in the stress response for setting limits in a snail's thermal environment. Heat shock protein synthesis varies with high temperature stress as a function of intertidal height of intertidal congeneric species of snails in the genus *Tegula* (recently renamed *Chlorostoma* (Carlton, 2007)) and the heat shock protein response will likely affect biogeographical range shifts due to global climate change (Tomanek, 2008). Regional differences in the heat shock response of populations of *Chlorostoma funebralis* were upregulated in both regions with Hsp70s being upregulated more in the northern populations and southern populations showing greater upregulation of Hsp40s (Gleason and Burton, 2015).

Animals from stable, moderately variable, and highly variable thermal environments differ in their heat shock response. Some species living in stable thermal environments lack the heat shock response. Subtidal animals are characterized by moderately variable thermal environments, and their cells start synthesizing Hsps at seawater temperatures above the highest temperatures that they normally experience. In contrast, rocky intertidal animals that experience highly variable thermal conditions during emersion start synthesizing Hsps below the highest temperature to which they are exposed. These organisms experience thermal conditions in their environment that are close to the upper thermal limits to which they can defend themselves against cellular thermal injury by the heat shock response. Consequently, organisms with the narrowest and widest temperature tolerance ranges live closest to their thermal limits and possess a very limited ability to acclimate which suggests that they will be most affected by global climate change (Tomanek, 2008). Results from this study indicate that none of

the three species of gastropods are exposed to sublethal emersion temperature stress for a sufficient duration to trigger the syntheses of Hsps.

While larvae of sessile fauna settle in the rocky shore and are subject to emersion temperatures which impact them larvae, juveniles, and adults of mobile fauna utilize behavioral strategies to ameliorate minimum and maximum temperature exposure (Stickle et al., 2011; Hayford et al., 2015). During the summer the mid-tidal whelk *N. ostrina* on San Juan Island, WA foraged and preyed on the barnacle *Balanus glandula* during the days of the tidal cycle least likely to be hot and also selected the coolest available substrate surface relative to the time of tidal emersion during daylight hours (Hayford et al., 2015). Whereas many rapidly moving mobile consumers such as crabs and fish can move in a matter of seconds to avoid unfavorable conditions, responses by slow moving gastropods, chitons and echinoderms can take hours.

This study documented the seasonal changes that occur in seawater and emersion temperatures as a function of intertidal height at a northern site along the inside passage of Southeast Alaska. High temperature emersion tolerance of *N. lamellosa*, *N. lima* and *L. sitkana* varied directly with their intertidal range but their desiccation tolerance did not suggesting that desiccation is not an abiotic stressor in this temperate rain forest intertidal zone. Previous freeze tolerance studies at this site have revealed freeze tolerance adaptations of rocky intertidal gastropod species to exhibit a direct relationship with the upper end of their intertidal zonation. Studies are planned on the same or congeneric species to emersion temperature and desiccation at a companion site at the southern end of the inside passage which has arid weather patterns in the summer.

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