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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 LT_{50} temperature (5 h) was considerably above recorded monthly maximum temperatures in the vertical range of *N. lamellosa* and *L. sitkana* but the LT_{50} of *N. lima* was very near the maximum monthly temperature at +2.5 m.

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 Unites 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 y

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 ± 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 and move 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 (LeOra Software Company; Petaluma, CA) and desiccation tolerance differences between