

Tidal migration patterns moderate thermal risk in the intertidal snail

Nucella ostrina

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Abstract

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Physical environmental characteristics place limits on when and where organisms can survive, thereby shaping distributions and abundances of species. A thermal performance curve is often used to describe the organism's performance along a thermal environmental gradient. Behavior can moderate temperatures experienced by an organism, increasing the time spent at optimal temperatures that confer high performance. Much of what is known about behavioral thermoregulation in ectotherms is based upon fast-moving animals, but organisms with relatively slow mobility, such as snails, may navigate their thermal environments on fundamentally different temporal or spatial scales. The intertidal zone has characteristics of both marine and terrestrial habitats, alternating between these two extremes multiple times per day. The timing of low tides has important consequences for the thermal environment; extreme temperatures depend on both aspect of the shoreline and the time during the day or night when the substrate is

exposed. The predictability of these tidal influences can be exploited by mobile animals living in the intertidal zone to access food resources during times of reduced thermal risk. I examined foraging and migration behavior of the intertidal snail *Nucella ostrina* in controlled field experiments and surveys of natural habitats, and estimated snail body temperatures from physical thermal mimics deployed in the field. I assayed snail performance across a range of temperatures and modeled the effect that behavior would have upon the temperatures snails experienced, performance under current conditions, and performance in a simulated future climate with 2°C increase. I found that snails migrate into high shore foraging areas for only 2-4 d per two-week tidal cycle, then retreat to locations lower on shore and in thermal refuges such as cracks. This periodic cycle of behavior, foraging on days with nighttime low tides that are reliably cool, is seen under both manipulated conditions and in natural populations. Furthermore, when given the choice between different substrate aspects, this species selects the cooler microhabitat. These temporal and spatial patterns of behavior lead to a reduction in the time spent at high temperatures (30°C and above). Snail performance declines above 30°C, taking several hours to recover from a 2 h duration of exposure to aerial temperature of 34°C and resulting in death for 75% of individuals at 35°C. Using a generalized model derived from observed snail behavior as a filter for temperatures experienced, I found that migratory behavior drastically decreases the exposure of *N. ostrina* to temperatures that cause reduced performance or death. Simulated climate change increases the frequency of high temperature events, but the benefit of migratory behavior is maintained. Selection of foraging time and location confers a thermal benefit to *N. ostrina*, reducing this snail's risk of exposure to detrimental temperatures that frequently occur in its habitat. Climate change is unlikely to directly affect this species as it simply is not present at times and in places where high temperatures occur, however, several

indirect effects should be considered. Slow animals may be thermoregulating on a different temporal or spatial scale than we are accustomed to examining for faster moving species.

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DEDICATION

To my grandparents, here and gone: Barbara, Bob, Dennis, Dorothy, Jack, Malcom, Nancy, Ruth J., Ruth M., & Wynn; for the wisdom you have shared with me.

Chapter 1. FORAGING BEHAVIOR MINIMIZES HEAT EXPOSURE IN A COMPLEX THERMAL LANDSCAPE

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Foraging behavior minimizes heat exposure in a complex thermal landscape

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ABSTRACT: Ectotherms use specialized behavior to balance amelioration of environmental temperature stress against the need to forage. The intertidal snail *Nucella ostrina* risks aerial exposure at low tide to feed on the barnacle *Balanus glandula*. We hypothesized that *N. ostrina* foraging behavior would be constrained by duration and timing of low tide exposure. We added snails to intertidal blocks on San Juan Island, Washington, USA, and forced them to choose between barnacles placed on the western or eastern face of each block, or to shelter and forgo foraging. Snail behavior and barnacle mortality were monitored daily for 8 wk during summer 2011. *N. ostrina* foraging peaked every 2 wk, when temperature was minimized by tidal cycling. Low tide timing determined which substrate orientation was coolest and coincided with the proportion of snails foraging on one substrate face or the other: snails foraged on the western faces on days with morning low tides and on eastern faces on days with afternoon low tides. Barnacle consumption rates mirrored this spatiotemporal foraging pattern. Our conceptual model predicted mobile organism presence and location: snails foraged during the days of the tidal cycle least likely to be hot and selected the coolest available surface when foraging. These results suggest that *N. ostrina* alters foraging behavior to minimize risk of exposure to high temperatures or other emersion stresses. Consequently, predation on barnacles varies over space and time. This spatiotemporal behavior may buffer warming air temperatures and should be considered in models of coastal population and community dynamics.

KEY WORDS: Thermoregulation · Intertidal ecology · Climate change · Tidal cycle · Predation · *Nucella* · Whelk

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INTRODUCTION

The impact of climate change on natural ecosystems is dictated by the relationship between organisms and their environments. A key assumption in many climate impact models is that ectothermic organisms, lacking the ability to metabolically regulate body temperature, will be susceptible to the most extreme environmental conditions (Fuller et al. 2010). However, behavior is critical in determining which environmental conditions an ectothermic organism actually experiences (Huey & Tewksbury

2009, Kearney et al. 2009). To make the link between potential temperature and resulting organismal distribution, we must know to what extent animals regulate their exposure to environmental conditions (Huey 1991, Chapperton & Seuront 2011).

Organisms that live in extreme habitats often have specialized behavioral and physiological strategies for surviving stressful environments (Rothschild & Mancinelli 2001). The relative successes of these strategies can have a large impact on community ecology as species are differentially affected and therefore the dynamics between species changes

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(O'Connor 2009, Yamane & Gilman 2009). The intertidal zone is a well-known example of a habitat with steep environmental gradients, where the transition from terrestrial to marine environment occurs in the space of a few meters (Doty 1946). Key emersion stressors, that generally co-occur, are air temperature (Wetthey 1983), solar radiation (Przeslawski et al. 2005), and desiccation (Helmuth 1998). Even when not in danger of lethal exposure, organisms can suffer sublethal effects of extreme environmental factors at the cost of growth, reproductive success, and other components of fitness (Hand & Hardewig 1996). Organisms that live in this transition zone use a combination of strategies to cope with emersion stress, including: (1) physiological, such as the heat shock response (Somero 2002); (2) morphological, such as the specialized structure of cell walls and body plans which foster desiccation resistance and tolerance in algae (Bell 1995); or (3) behavioral, as in the minimization of aerial exposure by limpets when they forage within range of a protective 'home' indentation in the rock (Wolcott 1973).

Exposure regulation strategies must be balanced against energetic needs. For example, one important behavioral strategy used by ectotherms to self-regulate is to seek refuge from high temperature by moving to protected areas when not actively foraging (Cowles & Bogert 1944). In the intertidal, mobile consumers commonly seek food higher on shore where competition is relatively low and prey are more abundant (Connell 1961a, b, 1970), and take refuge at lower shore levels, in cracks in the rock, or beneath sheltering organisms (Spight 1982, Garrity 1984, Johnson et al. 1998). Whereas many mobile consumers such as crabs or fish can move in a matter of seconds to avoid unfavorable conditions, responses by slow-moving animals like gastropods or echinoderms may take hours. When foraging on shore, slow-moving animals risk exposure to emersion stress unless they time their movements carefully. Poor timing can increase risk of exposure to lethally and/or sublethally stressful conditions.

The duration of aerial emersion experienced by an animal during low tide depends on the magnitude and duration of the tide as well as the shore height of the organism and the relative wave height (Harley & Helmuth 2003). Periods of maximum (spring) and minimum (neap) tidal exchange alternate approximately weekly, yielding a 2 wk cycle. The timing of low tide progresses by approximately 50 min each day. The risk of emersion stress cycles with the tides. For example, the highest organismal body temperatures occur during spring tides that coincide with

midday aerial exposure (Helmuth et al. 2002), whereas cool organismal temperatures occur if aerial exposure occurs at night. Mesocosm studies have shown strong temporal patterns in foraging of *Nucella ostrina* that followed the biweekly tidal cycle, with snails feeding continuously for 2 to 4 d when low tides occurred during cool early morning hours (Carrington & Kull 2011, Vaughn et al. 2014). One goal of this study is to determine whether these cyclical patterns of foraging also occur under natural tides in the field.

Animals may also reduce emersion stress by selecting less stressful microhabitats. In particular, locations that differ in solar aspect may differ not only in UV radiation, but also in temperature and relative humidity under the same tidal conditions (Miller et al. 2009, Helmuth & Hofmann 2001, Denny & Gaylord 2010). In this study, we focused on temperature as a tractable representation of these correlated factors. The location and timing of highest temperature change throughout the tidal cycle (Fig. 1). When low tide occurs in the morning, eastern faces of substrates are exposed to solar warming, whereas western faces are shaded, remaining cooler and moister. When the low tide occurs around midday, east and west faces receive about the same solar irradiance. When low tides occur during afternoon, western faces are most exposed to solar irradiance, warming, and drying. Fine-scale exposure gradients are therefore established on intertidal shores by the daily progression of the timing of the lower low tide. If an animal exhibited a preference for foraging in certain microclimates, we would expect to see a shift in the proportion of the population foraging on one side or the other as the low tide timing progressed through the lunar cycle (Fig. 1).

We chose a common mobile predator that lives on shorelines of the Northeast Pacific Ocean: the whelk *N. ostrina*. The genus is known for its impact on habitat-forming barnacles and mussels (Connell 1961a, b). *N. ostrina* preys upon the acorn barnacle *Balanus glandula* by drilling through the opercular ligament and ingesting the contents, commonly taking from 3 to 24 h per barnacle (Emlen 1966, S. E. Gilman & E. Carrington, unpubl. data). As the dominant *B. glandula* zone in the Northeast Pacific is aerially exposed for 5 to 21 h d⁻¹, even when *N. ostrina* begins foraging at high tide, it will likely be exposed to aerial conditions at some point in the foraging process. As low-tide substrate temperatures commonly exceed known lethal limits (LD₅₀) for some populations of *N. ostrina* (LD₅₀ = 34°C for 80 min at 100% relative humidity or for ~250 min at 0% relative humidity,

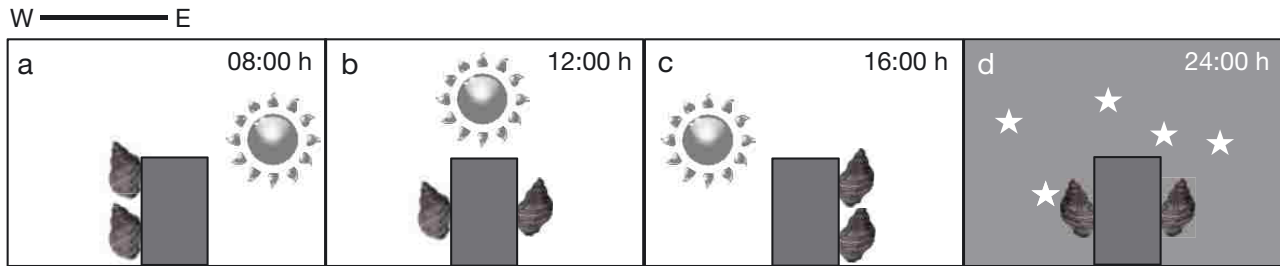


Fig. 1. Conceptual model of how interactions between tide timing and solar radiation influence microclimate and behavior of a mobile predator. Timing of low tide determines solar radiation received by surfaces of different orientations, which in turn determines emersion stress risk. In each panel, a central block represents habitat with prey available only on surfaces facing directly east (right) and directly west (left). Panels show predictions for when low tide occurs (a) in the morning, (b) at midday, (c) in the afternoon, and (d) at night. Snails are predicted to forage on the side more sheltered from direct solar radiation: west and east for morning and afternoon tides, respectively. When the risk on both faces is equal, when low tide occurs at solar noon or at night, snails may be found on either side

Bertness & Schneider 1976), we predicted that snails would avoid the hottest temperatures and show a preference for foraging on the cooler surface.

We hypothesized that: (1) snails would follow a predictable biweekly pattern of increased foraging during periods of cool temperatures and reduced aerial exposure, occurring during neap tide weeks for our study season and location; (2) snails would preferentially forage in cooler microclimates, shifting foraging from the west to the east to follow tidally created shifts in surface warming; and (3) as a result of these choices, snails would experience a cooler subset of the range of habitat temperatures encountered by their barnacle prey. To experimentally test these hypotheses, we corralled *N. ostrina* on artificial rocky outcrops in the intertidal and observed daily foraging.

MATERIALS AND METHODS

Study species

Nucella ostrina Gould, 1852 is a muricid gastropod ranging from Yakutat, Alaska, to Point Conception, California (Vermeij et al. 1990), with a typical vertical range of 0.6 to 1.9 m above mean lower low water (MLLW) at our study locale, San Juan Island, Washington ('SJI,' Connell 1970). *N. ostrina* was collected from Cedar Rock Preserve, Shaw Island (48° 33' N, 122° 57' W), Washington, and Friday Harbor Laboratories (FHL) Preserve, SJI, Washington (48° 32' N, 123° 00' W). Snails of 15.2 to 26.9 mm in length, with no difference in mean size across all experimental plots (1-way ANOVA, $F_{4,140} = 0.034$, $p = 0.998$), were housed in aquaria and allowed to self-regulate aerial exposure by crawling up and down aquaria walls. Post collection snails were fed *Balanus glandula* ad

libitum for 0.5 to 6 wk prior to being transferred to experimental plots. Initial surveys were conducted after a 2 wk adjustment period. Each *N. ostrina* was tagged with a vinyl cloth wire marker (20 × 5 mm, Smart Sign) affixed with cyanoacrylate to its shell. These tags allowed identification in refuges without disrupting snail behavior. New snails were sporadically introduced throughout the experiment when densities dropped below the minimum of 5 individuals per plot.

Experimental set-up

Feeding preference experiments were conducted on a south-facing gravel beach at FHL. Concrete slab islands (Fast-Setting Mix no. 1004, Quikrete) were used to mimic the natural bench habitat of *N. ostrina* while constraining the variability in topography. Five square islands (0.76 × 0.76 × 0.10 m) were aligned at +0.95 m above MLLW, separated from each other by 0.5 m (Figs. S1–S3 in the Supplement at www.int-res.com/articles/suppl/m518p165_supp.pdf). A standard cinder block (0.40 × 0.15 × 0.20 m) was placed in the center of each island, with the greatest surface areas facing east and west. Cobble spacers were used to create moist cool crack refuges beneath each block while enabling snails to move up the walls of the block. Each island was surrounded by a barrier of 15 cm high stainless wire mesh (73.6% open area, McMaster Carr) to deter *N. ostrina* escape. The mesh did not shade the block faces during hours of sunlight exposure.

Barnacle (*B. glandula*) bait shells were created from mussels *Mytilus trossulus* (collected from Argyle Pier, SJI, 48° 31' N, 123° 00' W) with barnacle epibionts. Mussels were shucked and drilled to facilitate attachment to the cinder block. Barnacle prey

(*B. glandula*) were placed ad libitum at +1.25 m (± 0.03 m) tidal elevation on both the eastern and western faces of each block. Barnacles placed on each face ranged from 8 to 35 individuals, with opercular sizes from 2 to 8 mm. Barnacle bait was exchanged when fewer than 8 living barnacles remained on a block face, except when snails were actively feeding on that face.

Substrate temperature and tidal cycle

Temperatures of the eastern and western faces of each block were recorded at 2 min intervals by one Hobo Tidbit v. 2 datalogger (Onset Computer) per face, adjacent to barnacle prey. Dataloggers were correlated to block temperature, measured by a thermocouple ($y = 1.02x$, $R^2 = 0.78$, $n = 126$ samples ranging from 34 to 47°C; data not shown). We assume block temperature is the primary driver of snail temperature, as has been shown for limpets (Denny & Harley 2006). However, datalogger temperatures likely overestimate snail body temperatures because live snails cool through evaporation. Observed tidal elevations (NOAA station #9449880, Friday Harbor) were used to distinguish exposed (low-tide) temperatures. Mean daily maximum temperatures and net daily difference between maximum face temperatures were averaged per block across 4 complete lunar tidal cycles (56 d).

Temporal foraging behavior

Foraging surveys were conducted opportunistically during daytime low tide, except for 4 done at night when plots were completely submerged by day. Individual snails were recorded as foraging if they were on the same block face as the bait. Most 'foraging' snails were on barnacles (Fig. S4 in the Supplement at www.int-res.com/articles/suppl/m518p165_supp.pdf); we chose to include those nearby on block faces because those individuals (<15%) were also exposed to higher emersion stress risk. Dead barnacles were counted daily on each face to assess the number newly consumed by snails. Snail consumption was evidenced by a barnacle test that was completely intact, but lacking tissue inside. Barnacles on faces with actively foraging snails were skipped so as not to disturb behavior. They were assessed on the following day and missing values for daily barnacle consumption were estimated by linear interpolation between known values.

Snails occasionally escaped the plots; most were found within 1 d and returned to their enclosure. Foraging behavior and barnacle consumption were standardized to the total number of *N. ostrina* present in each plot each day. Plots were removed from analysis on days when fewer than 5 *N. ostrina* were found.

Periodicity in foraging behavior and barnacle consumption was examined using autocorrelation (ACF) and cross-correlation (CCF) analyses, with significance assigned to correlation coefficients outside the 95% confidence intervals. These analyses were conducted with SPSS v.19 (IBM).

Microclimate temperature and behavior

Based on the relative length of aerial exposure before and after solar noon, we predicted *N. ostrina* presence on either the eastern or western face of each block. Trees on either side of the beach shaded the plots for approximately 2 h immediately after sunrise and 2 h immediately before sunset. We calculated the proportion of time blocks were exposed from the NOAA observed tides and used the total minutes of aerial exposure in the afternoon subtracted from aerial exposure in the morning to predict the location of foraging snails. Specifically, we tested for an association between the relative number of minutes of aerial exposure in the afternoon and the proportion of foraging snails found on the west face of each block using logistic regression in SAS Proc GLIMMIX (SAS v9.3, SAS Institute). Block and snail identity were included as random effects.

We compared the maximum daily temperatures of all substrate faces to the subset of maximum substrate temperatures on the days and locations of snail foraging to determine whether behavior was shifting snail exposure towards cooler temperatures.

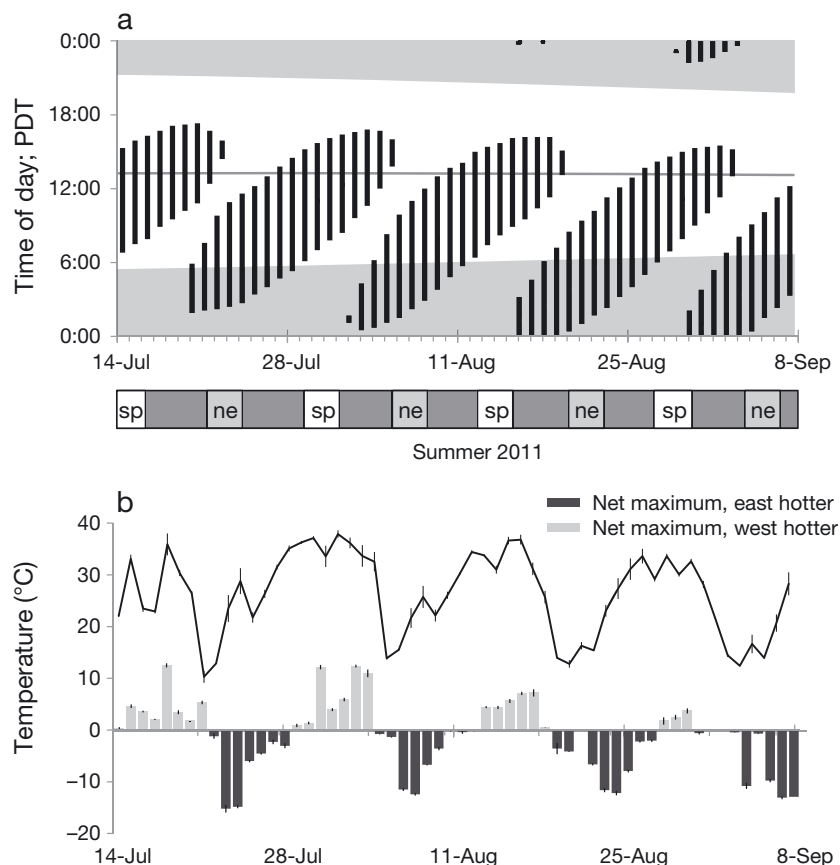
RESULTS

Substrate temperature and tidal cycle

Averaged across both faces, cinder block face temperature fluctuated periodically with the lunar tidal cycle (Fig. 2). The highest maximum temperatures occurred when the blocks were exposed to long low tides in the middle of the day (spring tides and transitions), whereas cooler maximum temperatures occurred when low tides were during the night, early

Fig. 2. Tidally driven temporal and spatial variation in temperature in intertidal microhabitats. (a) Vertical black bars: daily timing and duration of low tide aerial exposure at +1.25 m tidal elevation. Shaded areas: night; horizontal line: solar noon. The bar below shows the phases of the lunar tidal cycle as spring (sp, unshaded), neap (ne, lightly shaded), or transition between the two (darkly shaded). Note that spring tides have long periods of daytime exposure, whereas neap tides have primarily nighttime exposure. PDT: Pacific Daylight Time. (b) Black line: Daily mean maximum substrate temperature averaged over both eastern and western faces. Note temperatures are highest when aerial tidal exposure has longer midday intervals (spring tides). The bar graph below shows the mean difference between the mean maximum temperatures of eastern and western faces. Bars represent days with higher temperatures on the (dark grey) east and (light grey) west. Peak temperatures differ little between the 2 faces when tidal exposure is at night or midday.

Whiskers represent SEM, $n = 5$ blocks



morning, or for only brief periods during midday (neap tides).

The daily progression of the tides through the lunar cycle led to temperature differences between eastern and western substrate surfaces. Generally, periods of higher maximum temperatures on the east were followed by higher temperatures on the west a few days later. This shift corresponded to the gradual transition of low tide from morning to afternoon (Fig. 2). When averaged over the whole experiment, mean daily maximum temperatures were not significantly different between the faces (paired $t = 1.403$, $p = 0.255$); however, as predicted, there were significant differences during specific tidal phases (Fig. 2b, Table S1 in the Supplement at www.int-res.com/articles/suppl/m518p165_supp.pdf). On average, eastern faces were 3.7°C warmer during neap tides (paired $t = 8.015$, $p = 0.004$) and 8.3°C warmer during neap-to-spring transitions (paired $t = 5.988$, $p = 0.009$), while western faces were 4.8°C warmer during spring-to-neap transitions (paired $t = -3.451$, $p = 0.041$). During spring tides both surfaces were relatively hot (>30°C) and did not differ significantly (paired $t = -1.529$, $p = 0.224$). The highest mean daily maximum substrate temperature (32.6°C) occurred on western faces during spring tides, when afternoon

low tide exposure was greatest (Fig. 2b, Table S1 in the Supplement).

Temporal foraging patterns

The mean proportion of *Nucella ostrina* foraging each day varied substantially, from 0 to 0.50 (Fig. 3a). Prevalence of foraging varied with day of the tidal cycle (1-way ANOVA, $F_{3,12} = 6.672$, $p = 0.007$): foraging peaked during neap tides and spring-to-neap transitions, but was rare during spring tides and neap-to-spring transitions (Tukey's HSD, $\alpha = 0.05$; Table S1 in the Supplement). Both peaks and troughs of foraging occurred at regular 14 d intervals (significant autocorrelation coefficient = 0.464, Fig. 4a). Barnacle consumption matched snail foraging behavior (Fig. 3b) and trended towards a similar 14 d cycle, with a significant negative correlation after 7 d (autocorrelation coefficient = -0.251, Fig. 4a). Cross-correlation analysis of the proportion of snails foraging to barnacle consumption per snail showed the greatest significance at a lag of 0 to 1 d (cross-correlation coefficient = 0.550 to 0.592; Fig. 4b), indicating that barnacles were eaten within 1 d of observed snail foraging bouts.

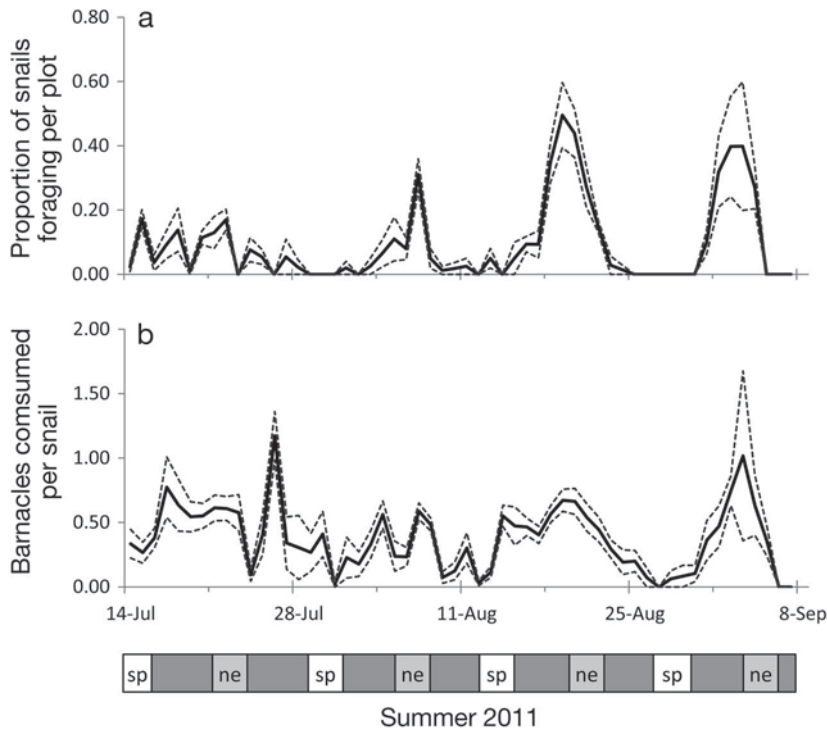


Fig. 3. Summary of temporal patterns in *Nucella ostrina* foraging. (a) Solid line: mean proportion of snails foraging for all plots; dashed lines: \pm SEM. The bar below shows the phases of the lunar tidal cycle as spring (sp, unshaded), neap (ne, lightly shaded), or transition between the two (darkly shaded). Note that periods of high and low foraging alternate weekly; highest foraging occurs during the neap tides. (b) Solid line: mean number of barnacles consumed per snail since previous day; dashed lines: \pm SEM. Note that pattern of peaks and troughs aligns with snail foraging behavior

Microclimate temperature and behavior

More snails foraged when low-tide temperatures were cool on both faces (neap tides), with very few snails observed foraging on hot days (Figs. 2b & 3a). Mean daily maximum temperature varied periodically with the tidal cycle (significant autocorrelation coefficient = 0.449 at 14 d lag, Fig. 4a) and was negatively correlated with the total proportion of snails foraging (significant cross-correlation coefficient = -0.481 to -0.673 at 0 to 1 d lag; Fig. 4b). The proportion of snails foraging on east versus west faces did not differ when averaged over the duration of the experiment ($t = -0.682$, $p = 0.506$) or tidal phase (Table S1 in the Supplement), but trends toward short-term preferences for east or west faces on certain days of the tidal cycle were evident (Fig. 5). Logistic regression revealed, as predicted, that the probability that a foraging snail would be found on the west side of block was greatest when the majority of the low tide exposure occurred in the morning ($F_{1,177} = 4.16$, $p = 0.043$). For every 10 min of increase in morning tide, there was a 2.9% increase in the odds ratio of a snail being on the west side (versus the east).

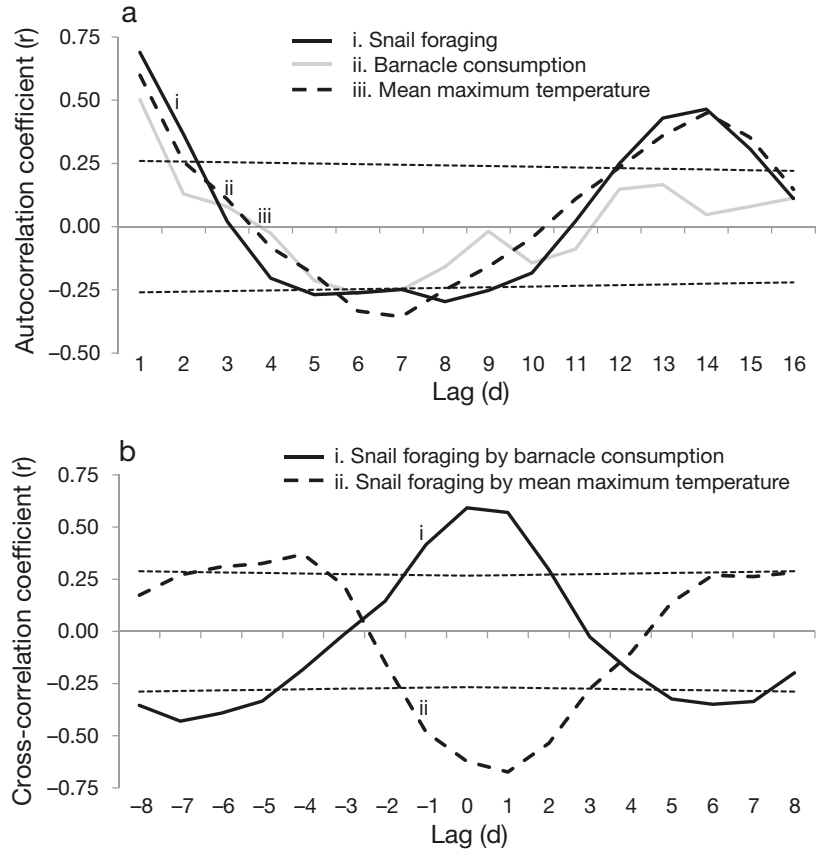
Snails foraged on only a subset of days and substrate faces, therefore experiencing only a subset of the possible emersion conditions. During periods when no snails foraged, the mean maximum daily

substrate temperature was $30.9^{\circ}\text{C} \pm 6.02$ SD; whereas during peak foraging times ($>25\%$ of snails foraging) the temperature was only $17.3^{\circ}\text{C} \pm 5.31$ SD. Snails were present for only some of the maximum substrate temperatures experienced by their barnacle prey (Fig. 6). Selectively choosing microhabitat increased the likelihood a snail foraged below its likely lethal limit (e.g. 34°C and up, Bertness & Schneider 1976); on 11 d, substrate temperatures were above 34°C on one side of the block, but not the other. Snails were exposed to a higher proportion of cooler maximum substrate temperatures ($\leq 34^{\circ}\text{C}$) and a lower proportion of temperatures above 34°C when they restricted foraging to certain days of the lunar tidal cycle ($\chi_1^2 = 8.10$, $p = 0.004$). The effect was even more striking when snails chose both restricted days and the cooler of the 2 substrate faces ($\chi_1^2 = 10.61$, $p = 0.001$).

DISCUSSION

Snails are small, slow-moving ectotherms that need hours to react to environmental changes. Snail decisions to be active or take refuge must thus anticipate whether environmental conditions on a given low tide might reach stressful levels. If they are caught high on shore during a long daytime low tide, they may suffer from heat, desiccation, and UV stress

Fig. 4. Time series analyses of *Nucella ostrina* foraging. Correlation coefficient (r) versus lag number (d). Horizontal dashed lines: 95% confidence interval for all correlations. (a) Autocorrelation coefficients of (i) proportion of *N. ostrina* foraging, (ii) *Balanus glandula* consumed per snail, and (iii) mean daily maximum temperature, showing a significant 2 wk periodicity in snail foraging behavior and mean daily maximum temperature, and a trend towards a 2 wk periodicity in barnacle mortality due to consumption. (b) Cross-correlation coefficients of proportion of *N. ostrina* foraging by (i) *B. glandula* consumed per snail, and (ii) mean daily maximum temperature, showing that snail foraging and barnacle consumption cycle within 1 d of one another, while snail foraging and temperature are negatively correlated, or are out of phase by approximately 7 d



before they can reach an adequate refuge. Tide cycles are the most predictable driver of temperature and humidity in the intertidal zone (Mislán et al. 2009). On predictably high risk days of the tide cycle, snails should therefore avoid high shore activity and either forage lower or stay in refuges. Careful selection of microclimate when foraging high on shore can further buffer the risk of extreme emersion stress. We found both temporal and spatial preferences for foraging in *Nucella ostrina* that are consistent with

emersion risk avoidance. In this study, we measured temperature as one of many correlated emersion stresses.

Biweekly foraging excursions of *N. ostrina* populations peaked on days when lower low tides were in the early morning hours and barnacle prey were submerged during the warmest times of day (neap tides). Barnacle mortality was highest at the same time as snail foraging, supporting our assumption that snails present on block faces were engaged in barnacle

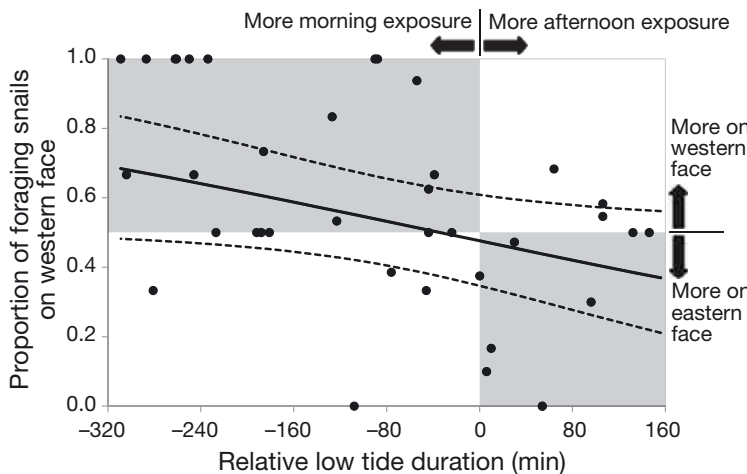


Fig. 5. Microclimate and foraging location with tidal shifts. Proportion of all foraging *Nucella ostrina* found on the western block face versus relative duration of afternoon low tide. Proportions below 0.5 denote a majority of snails on the eastern faces, whereas those above 0.5 represent a majority on the western faces. Relative low tide duration is the total time (min) of afternoon low tide minus the total time of morning low tide. A zero indicates that low tide exposure was equally distributed between morning and afternoon. Solid line: Best significant model fit; dashed lines: upper and lower 95% confidence intervals. Shading denotes expected cooler substrate orientation for given tidal exposure: west during morning low tides, east during afternoon low tides. In general, snails were found on the predictably cooler face during low tide

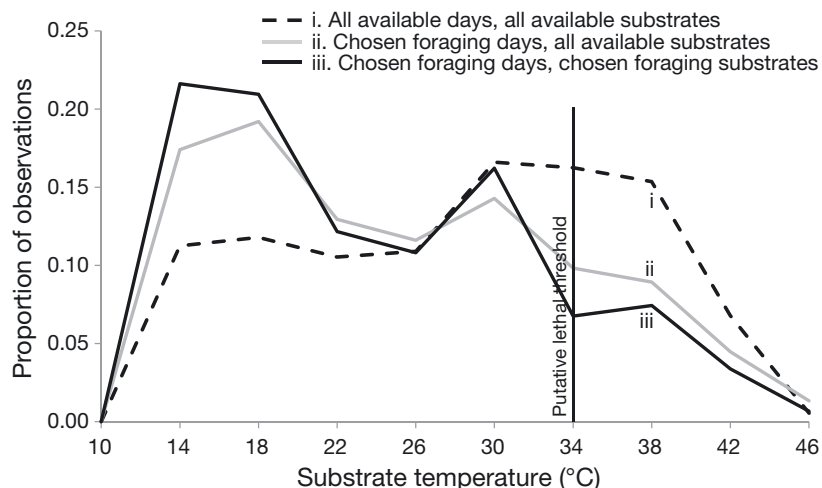


Fig. 6. Distribution of temperatures *Nucella ostrina* experiences for different foraging scenarios. (i) Proportion of daily maximum temperatures ($N = 56$ d) pooled from eastern and western block faces, (ii) subset of the pooled temperatures for days when snails chose to forage on either eastern or western block faces, and (iii) subset of the pooled temperatures for days and faces when and where snails chose to forage. Horizontal axis values represent upper bounds of each temperature bin. Snail behavior of preferring cooler days and faces increased the proportion of time spent below 26°C and reduced the proportion of time spent above the putative lethal limit for pro-longed exposure, 34°C, marked by the vertical line

consumption. Increased foraging activity during these periods of reliably cool temperatures effectively minimized thermal risk. This temporal pattern of activity relative to tidal conditions was previously described in *N. ostrina* in laboratory mesocosm studies (Carrington & Kull 2011, Vaughn et al. 2014), but this is the first field-based experiment. A similar pattern was observed in field studies of an Atlantic congener, *N. lapillus*, though it was dependent upon wave action (Burrows & Hughes 1989), and in an Australian muricid, *Morula marginalba* (Moran 1985). Natural populations of *N. ostrina* also decrease foraging during spring tides (Spight 1982, H. A. Hayford unpubl. data).

We observed shifts in *N. ostrina* foraging between eastern and western surfaces that matched our prediction that snails would forage preferentially on cooler surfaces. Thus snails have the ability to regulate thermal exposure on small spatial scales (Miller et al. 2009, Denny et al. 2011). The hottest overall substrate temperatures occurred during the afternoon low tides when western faces were directly exposed to the sun. This led to predictable shifts in snail foraging to the cooler eastern surface. Similar behavioral use of microclimates have been reported in other marine and terrestrial species, as differences in solar heating throughout the day create east and west microclimates potentially useful to thermoregulating ectotherms (Huey et al. 1989, Pringle et al. 2003, Harley 2008). This study is unique in its ability to predict spatial and temporal shifts in both predator behavior and predation rates from the biweekly tidal cycle. Risk avoidance mirroring temporal tidal cycling suggests that snails are responding to a tidal cue. Possible cues include sensitivity to water pressure, moonlight, and/or changes in temperature or desiccation (García-March et al. 2008, Chabot & Watson 2010).

Barnacle distribution was controlled in our experiment by placing equal numbers on eastern and western faces, thus emphasizing snail responses to abiotic factors. We recognize that natural barnacle distributions are unlikely to be homogenous (Lathlean et al. 2013), possibly with increased abundances on substrates with lower emersion stress. Barnacle distribution is determined by settlement preference and post-settlement survival, therefore barnacles can only respond to microclimate differences maintained over relatively long periods of time (mo, yr). In our 8 wk study, we observed no difference in temperature between eastern and western faces. In contrast, snail choices are made on the relatively short time-scale of tidal cycle (d). We therefore predict the influence of barnacle distribution on spatiotemporal patterns of snail foraging to be minimal.

Predation by *N. ostrina* on *Balanus glandula* varied in both space and time. Tidal dynamics predicted locations and time periods when interaction strength was intensified. In a scenario of global warming, these results suggest behavioral thermoregulation may give this predator an initial thermal advantage over its sessile prey, but decreased thermal risk comes at a cost: decreased feeding. Foraging peaks could become even more infrequent, with feeding occurring only when risk is at an absolute minimum (fewer days per tidal cycle). These consequences are likely to be exacerbated by the increased metabolic demands that accompany increased temperature: snails can reduce foraging to decrease heat exposure or increase foraging to compensate for increased metabolic demands, but in either case may suffer lower growth, reproductive success, and/or survival, as resources in survivors are allocated to cellular repair. Thus *B. glandula* may experience a release from predation pressure if air temperatures warm

(Menge et al. 2002, Yamane & Gilman 2009, Pincebourde et al. 2012). These temporal fluctuations of interaction strength could shape future communities; quantification may be critical to the goal of predicting functional response to environmental change (Wootton & Emmerson 2005, Gilman et al. 2010).

These effects may be seen at other trophic levels. Our conceptual model assumes *N. ostrina* alters foraging activity primarily to avoid exposure to risky temperatures. However, *N. ostrina* and *B. glandula* are not the only species in this complex coastal food web; *N. ostrina* must also avoid predation. During the experiment we saw signs of predation by the red rock crab *Cancer productus* (Zipser & Vermeij 1978). Predation on *N. ostrina* peaked approximately every 13 d, 2 to 3 d after peak snail foraging, just before the start of the spring tide (Fig. S5 in the Supplement at www.int-res.com/articles/suppl/m518p165_supp.pdf). It is possible that the crab predator follows the snail prey's movement and/or that predation risk is the impetus for snail migration (Yamada & Boulding 1996). However, crab movement is also consistent with our hypothesis that the mobile predator minimizes its aerial exposure. *C. productus* is nocturnal and forages underwater. Therefore, the ideal conditions for vertical migration onshore are likely to be different from those of *N. ostrina*: crab activity should be highest on nights with long tidal immersion. These periods coincide with low tides occurring just before the spring tide series. Crab predation risk cannot explain the shift seen in snail preference for east versus west microclimates; crabs had equal access to both block faces and were foraging primarily when the plots were immersed in cool, benign water.

We were able to test the effect of emersion stress on snail foraging behavior in a natural setting because of the midday low tides in the San Juan Islands during the summer months. We would predict the same pattern of biweekly foraging during the winter months, when low tides occur in the night, but for slightly different reasons. Water, with its high specific heat capacity, is far more resistant to thermal change than air and immersion in water therefore serves as an effective thermal insulator for intertidal organisms. When aerial temperatures dip below freezing, mobile organisms should minimize their time in air. In the winter in the San Juan Islands, this means minimizing exposure to air at night and we would expect to see selection of the same part of the lunar cycle to avoid freezing stress. In other regions of the world, we would also expect to see this pattern of minimizing daytime aerial exposure during summertime low tides. In locations such as California,

however, where spring low tides occur in the pre-dawn hours in summer, only eastern faces would be exposed to sunlight during low tide emersion. We would therefore expect to see more foragers on western than eastern faces, with minimal migration from one face to another.

Our observed shifts in the spatiotemporal pattern of *N. ostrina* foraging demonstrate the importance of selecting not only the right time to forage, but also the right place. For intertidal snails, the most appropriate selection criteria shift over the course of the lunar cycle. These findings have important implications for the design of population surveys, as foraging snails are easily visible compared to those in refuges. Many mobile organisms are bounded by the same principles of resource acquisition versus refuge (Connell 1961a, b, Huey et al. 1977, Stevenson 1985), and are therefore likely to make precisely timed migrations. Censuses, if not properly designed, may incorrectly yield apparent differences in abundance that are, in fact, due to periodic foraging behavior—especially if the sites differ in orientation.

Our results support behavior as an important factor for predicting distribution and predation pressure based upon temperature, important goals of both ecologists and physiologists (Huey 1991, Menge et al. 2002, Kearney et al. 2010). Although individuals may exhibit complex behavior, close examination of the population's spatiotemporal distribution yield predictable patterns of foraging that can be used in mechanistic models to predict changes in distribution and abundance with climate change.

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Chapter 2. RADIO TRACKING DETECTS THERMOREGULATION AT A SNAIL'S PACE

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2.1 ABSTRACT

The dynamic ebb and flood of tides makes the marine intertidal zone a habitat with temperatures that fluctuate rapidly in both space and time. This is problematic for slow intertidal organisms that cannot move at the speed of the fluctuations. The timing of low tides determines which days of a two-week tidal cycle may reach extreme temperatures, controlling microclimate to a greater degree than weather patterns. When low tides occur midday, temperatures can exceed critical thermal maxima for many species. Although high shore areas experience the greatest environmental extremes, they often harbor untapped food resources. The periodicity of tides creates a predictable cycle, and we hypothesize that marine ectothermic animals can use it to obtain food in risky areas while minimizing exposure to thermal extremes. We used a two-part approach to characterize a natural habitat at times that are traditionally understudied and assess un-caged behavior of the snail, *Nucella ostrina*. We used radio tracking to detect the presence/absence of snails in high shore feeding areas continuously for 14 weeks and used physical thermal mimics to approximate snail body temperature in those high shore areas. Snails were absent when extreme low tides occurred at times of high solar irradiance (midday). Comparing the subset of temperatures snails experienced to all available temperatures in the environment showed that snails spent a disproportionate amount of time at 10-12°C and were absent at temperatures greater than 31°C. These patterns matched previous experimental findings, demonstrating that migrating behavior effectively moderates snail experience of environmental temperature in nature.

Summary statement: Intertidal snails tracked with radio frequency identification (RFID) tags regulated their foraging bouts spatiotemporally such that they avoided hot, dry areas.

2.2 INTRODUCTION

Much of what we know about animal behavior is limited in scope because experiments and observations are: (1) conducted in altered environments, such as zoos, aquariums, and laboratories; (2) conducted in natural settings, but only during the times and at the places where humans can readily observe; or (3) limited by dangers to humans, presented either by the animals themselves or by the pressures of their physical environment. As a consequence, understanding is biased towards behaviors exhibited in the presence of humans or at times we find convenient to observe (Chapman, 2000). The relatively rare studies that use remote tracking often find novel behaviors, changing the way we interpret an animal's role in its ecosystem. Examples of recent breakthroughs include predation by alligators in the southeast United States (Nifong et al., 2014), the thermoregulatory function of ocean sunfish floating in shallow surface waters (Nakamura et al., 2015), and the impact of house cats on reptile and other wildlife populations (Loyd et al., 2013).

The behavioral use of habitat to moderate body temperature determines the ecological performance of an animal (Huey 1991), and therefore the temporal and spatial scales at which a species will be affected by climate change (Deutsch et al., 2008, Kearney et al., 2009, Woods et al., 2015). Heterogeneous habitats offer a greater range of options than thermally homogenous areas, but complexity of habitat does not imply adequate utilization—an animal may not move between microclimates and will be subjected only to local conditions. Patterns of utilization could have profound effects on thermal experience (Kearney et al., 2009, Buckley et al., 2013, Lathlean, 2014, Sunday et al., 2014). Species with complex behaviors may be able to exploit

microclimates and withstand temperature variability at a lesser fitness cost than species that do not (Sears et al., 2011, Woods et al., 2015).

In the marine intertidal zone, tidal cycling creates thermal complexity across relatively short spatial and temporal scales, exerting more control on small-scale conditions than any climatic factor and creating a variety of microhabitats (Mislán et al. 2009). When tides are low, receding water levels leave the intertidal zone exposed to solar radiation. Low tide aerial exposure varies seasonally and geographically, occurring at different times of day. Aerial exposure during midday exposes intertidal organisms to higher temperatures than they experience when low tide occurs at other times of day (Helmuth et al., 2002, Hayford et al., 2015). Warm, dry, sunny periods are great conditions for coastal scientists, but these weather conditions are also the most likely to be stressful to marine intertidal organisms and may change their behavior drastically (for example, Muñoz et al., 2005, Chapperon and Seuront, 2011a). Yet the vast majority of intertidal ecological studies are conducted during low tide when observers can access the shoreline without wave hazards. While a few are done at high tide, the ability of snorkelers/divers to accurately see animal activity is also disrupted by wave action and algal cover. Darkness may further inhibit the accuracy of surveying small organisms. This leaves a large portion of any given day, let alone year, open to extrapolation and speculation that may not be accurate.

Intertidal zones have a gradient of thermal and desiccation stress: higher shore elevations are exposed to air for longer than lower elevations and therefore are more likely to reach temperature and humidity extremes. Mobile predators in the intertidal zone must choose between food sources high on shore in exposed areas where competition is limited to the most physiologically robust species (Connell, 1970), or refuges in cracks and lower on shore that may be the first food

stocks depleted (Johnson et al., 1998). The horizontal distance between high and low intertidal elevations can be several meters in a lot of systems, varying with place-based tidal regime and slope of the substrate. Additionally, many organisms are constrained by potential water loss and only move when submerged at high tide or across wet substrates. Fast organisms move into new foraging areas with a flooding tide and retreat with the receding tide (Yamada & Boulding, 1996, Holsman et al., 2006). For example, small shore crabs can run over ground up to 1.4 m s^{-1} (Martinez 2001). The much slower locomotion and feeding of slow animals suggests they must adopt a different mechanism of balancing foraging with risk avoidance. *Nucella ostrina* [Gould, 1852] is a predatory snail common to intertidal shore throughout the Northeast Pacific. The process of crawling (1.3 cm min^{-1} , data not shown), selecting, drilling, and ingesting a prey item ($5.3 \pm 0.37 \text{ h}$ for drilling and ingesting an average sized barnacle) can exceed 24 h and typically takes longer than the duration of a high tide (John M. Emlen, Time, energy and risk in two species of carnivorous gastropods, PhD thesis, University of Washington, 1966).

Slow intertidal animals can take advantage of both food and thermal refuge if they are selective in their foraging timing. Risk is reduced on days when low tides are timed such that most aerial exposure is at night or early in the morning (Hayford et al., 2015). We therefore predict that slow mobile organisms are most active in the high shore region on those days of the tidal cycle. This prediction was supported in experimental tests using caged snails in the laboratory and field (Vaughn et al., 2014 and Hayford et al., 2015, respectively); snails move into exposed areas in the high intertidal during days of the two week long tidal cycle when thermal and desiccation risk were reliably low, and foraged for multiple consecutive days before retreating to thermal refuges. Snails selected days of the tidal cycle when foraging areas were subject to reduced sun exposure, which enabled both feeding on high shore resources and

avoidance of high temperatures most likely to be stressful. However, these manipulated conditions offered a dichotomous choice of food or refuge, and so only provide suggestive evidence of how snails behave in more heterogeneous natural habitats. Furthermore, previous experiments placed food and refuge within a few cm of one another, when a more realistic scenario is separation by several meters in natural habitats.

We followed snail behavior to assess how snails use their habitat in nature and whether behavior moderated the thermal environment experienced within the wide range of natural habitat heterogeneity. Typically near 2 cm in length, *N. ostrina* is too small to carry a traditional temperature logger. We instead took a two-part approach to surveying snail behavior and estimating operative body temperature of this small mobile animal: a combination of tracking *N. ostrina* with radio frequency identification (RFID) tags and approximating temperature with thermal mimics—physical models used to approximate the body temperature of live organisms. We hypothesized that uncaged snails in their natural habitats would: (1) match field mesocosm studies by exhibiting a periodicity to their foraging behavior, increasing presence in exposed, high shore areas for 2-3 d of the tidal cycle before retreating to refuges and lower shore elevations; and (2) selectively use exposed high shore areas to reduce the range of environmental temperatures experienced.

2.3 MATERIALS & METHODS

Overview

We explored the behavior of free-range intertidal snails through two different uses of radio frequency identification (RFID) tags: (1) proximate tracking—detecting tags using a hand-held device, locating the same individuals on subsequent days of low tide field surveys; and (2)

continuous remote tracking—detecting tags in one exposed, high shore location, determining snail presence or absence throughout both high and low tides. We used tidal water levels (NOAA station #9449880, www.tidesandcurrents.noaa.gov) to assess the relationship between snail behavior and day of tidal cycle. We compared the subset of temperatures taken when *N. ostrina* was present to the full range of potential operative temperatures to evaluate thermoregulation of the environment.

Field surveys & RFID tracking by hand

Surveys of snail counts in discrete locations were conducted at multiple locations on the University of Washington Friday Harbor Laboratories Research Preserve (FHL, 48°33' N, 123°00' W). Data were collected daily over a 2 wk lunar tidal cycle, August 6, 2012 to August 19, 2012. Previous observations indicate this is a season when fluctuations in both substrate temperature and snail density are large (data not shown). Three intertidal sites, separated from one another by approximately 100 m alongshore distance, were selected for their relatively steep rock faces. We chose this semi-vertical substrate because it decreased the horizontal distance that an animal would have to travel to move up or down in tidal elevation, enabling us to detect vertical movements from one day to the next. Each site consisted of a rectangular swath stretching 1 m alongshore and perpendicular to shore from 1.0 m above mean lower low water (MLLW) to 2.25 m above MLLW. Each site was divided into two adjacent plots of vertical tidal elevations: below 1.5 m (low shore) and 1.5 m or above (high shore). Epoxy markers (#788, Z-spar Coatings, Kop-Coat, Inc., Rockaway, New Jersey, USA) were used to semi-permanently mark plots. Plot areas varied with rock slope. Snails were counted daily in each plot and totals

divided by estimated plot area to calculate density. The total count of snails in each plot was determined daily and averaged across all three plots.

RFID tags enabled individuals to be detected even when they were in thermal refuges with low visibility. We assessed solar exposure level of tagged animals by noting whether or not they were in refuges such as cracks or under algal canopy, microhabitats known to be cooler on this shoreline (Gilman et al. 2015). RFID tags were affixed to the shells of *N. ostrina* naturally occupying chosen survey sites. Only individuals 2 cm or greater in shell length were tagged (Fig. 1). Snails were collected during a low tide period, had a tag affixed to the dorsal region of the shell with z-spar marine epoxy, and returned. A total of 23 snails were tagged with RFID: 6-10 individuals at each site. To compare survey efficiency to traditional visual methods, we marked 20 snails with numbered wire tags (WireMarkerBooks.com, Brooklyn, New York, USA). Each plot and its surrounding area, representing approximately 20 m², were scanned for the presence of radio or visual tags. Tag searches were conducted during low tides, using a handheld tag reader with an attached wand antenna (APR 350 with AEA 580, Agrident GmbH, Barsinghausen, Germany).

Changes in distributions of snails throughout a two week tidal cycle were assessed by Generalized Linear Mixed Modeling (GLMM, Table 1). GLMM allowed us to calculate probability with spatially and temporally correlated data and incorporate a binomial distribution of error terms to account for a binary response variable (Bolker et al. 2009). In each test we compared our hypothesized model to a null model that included only an intercept and random factor and used Chi-square Goodness of Fit test to determine whether our model fit our data better than the null, as in Lowe et al. (2015). We tested two different response variables as a function of fixed factor day of tidal cycle and random factor survey site; first, snail use of

habitat, either in refuge or exposed, and second, snail elevation, high (≥ 1.5 m) or low (< 1.5 m), on shore. Fitted models were checked for overdispersion.

Continuous remote tracking

Higher temporal resolution of snail behavior was monitored using antennas mounted to intertidal rock at two elevations in one location (Fig. 2). Antennas encircled high shore areas with barnacle prey present, but few topographical or biological thermal refuges. These areas were termed “exposed” in reference to their lack of protection from solar radiation. Antennas scanned for RFID tag signals continuously, recording tag detections to a data logger when a snail crossed into the range of the antenna (typically 1-15 cm, depending on tag angle).

Antennas were constructed of stranded tin-copper wire, 0.8 mm diameter (20 AWG, Newark element14, Chicago, Illinois, USA), turned in 5 consecutive oblong loops of 15 cm by 1.1 m (inductance 50 μ H). Antennas were then wrapped in electrical tape to protect from abrasion against the substrate and installed at 1.5 m and 2.0 m above mean lower low water (MLLW) with marine epoxy (Splashzone Epoxy #788, Z-spar Coatings, Kop-Coat, Inc., Rockaway, New Jersey, USA). Snails could crawl over the wire as well as under in some locations. Snail tags were within 1 cm of antenna loop when snails were crossing, however read range variability affected whether or not snails in the center of the loop were continually detected.

Antenna tuner boards (Slim Tuning Capacitors, Oregon RFID, Portland, Oregon, USA) were waterproofed using modified methods of Bond et al. (2007, see supplemental information for details, Appendix B). In the field, tuner boards were bolted to the rock (Supplemental Fig. B.1). Shielded twinaxial cables ran from tuner boards 10 m upshore, secured with cable ties to a series of stainless steel eyebolts sunk into the rock, to a data logger (Multi-Antenna HDX Reader,

Oregon RFID, Portland, Oregon, USA) housed onshore and connected to AC power. The data logger was set to a scan rate of 0.95 Hz (50 ms charge period and 1000 ms listen period). Data files were accessed using the open source terminal emulator, Putty (www.putty.org).

Sixty-three *N. ostrina* individuals were tagged over the 4 mo prior to the beginning of the remote detection study and another 5 tags were added throughout the survey period as new snails were found in survey regions, for a total of 68 individuals. Tagged individuals in the study area decreased over time, presumably due to snails moving out of the survey area or to death.

Antennas scanned for tags continuously from August 15, 2013 to November 23, 2013 (14 wk). Gaps in detections of a tag could have been due to snail movement changing the orientation of the tag in relation to the antenna, within the antenna loop but out of antenna read range, or completely out of the high shore area. Snails were presumed to be continuously occupying areas adjacent to antennas when the duration of time between subsequent detections for a given tag was less than 24 h. This value was chosen to overestimate the range of temperatures that snails might experience when present in high shore areas, a conservative approach to evaluating snail behavior in thermal extremes. To verify that snails were absent from sun-exposed high shore areas when there were no detections, we conducted daily surveys using a hand scanner and antenna (as above) from August 19, 2013 to September 21, 2013 (4.5 wk). We found only one incident of false negative: four undetected snails were in the antenna area on August 20, 2013.

Thermal consequences of movements

Physical thermal models were constructed to closely approximate body temperature of *N. ostrina* in its environment, following the design of Gilman et al. (2015). Thermal models were created from the shells of deceased *N. ostrina* (length 2.0-2.5 cm), with one end of a

thermocouple embedded at the apical end of the shell and filled with Two Ton Epoxy (Devcon, Danvers, Massachusetts, USA). Thermal models were wired to a multiplexer (25T and CR1000, Campbell Sci, Logan, Utah, USA) logging temperature every 15 min. Thermocouple wires were secured with wire clips and screws drilled into the rock. Thermal models were affixed to the substrate with Z-spar marine epoxy in unshaded portions of the south-facing rock, adjacent to each antenna (Fig. 2). The relationship between midday aerial exposure due to low tide and daily maximum temperature was evaluated by linear regression.

We hypothesized that snail movement reduced the range of temperatures experienced relative to continual occupation of high shore areas. Physical thermal models adjacent to each antenna were used to approximate the body temperature *N. ostrina* would experience if present in that location. A relevant subset of these temperatures was extracted to estimate the temperature experienced by any snail (T_s) migrating through these locations. We compared the subset of migrating snails, T_s , to environmental temperatures (T_e) by resampling from the full pool of measured T_e values, a technique similar to bootstrapping. A sample size equivalent to the subset T_s ($n = 2,343$) was randomly drawn from the full data set T_e ($n = 19,200$) without replacement. The maximum and minimum values of the random draw were calculated for 10,000 iterations. The range of values of T_e was considered to be significantly larger than that of T_s if the 95% CI for the maximum and minimum of resampled T_e values exceeded the maximum and minimum of observed T_s .

Statistical tests were performed in R v. 3.1.3 (R Core Team, Vienna Austria, 2015) with package lme4 (Bates et al. 2015).

2.4 RESULTS

Field surveys & RFID tracking by hand

We found radio tags to be an order of magnitude more efficient for relocating an organism than the traditional method of marking with a visual tag. Of an initial 20 visual tags and 23 RFID tags, 27 visual and 253 RFID detections were cumulatively made within the same search time. Not all detected RFID tags could be visually located. RFID tags allowed us to assess the habitat of individual snails by enabling us to find a greater number in cracks, thus better characterizing refuge use. Sixteen of the 23 tags (70%) were detected at least once following initial tagging.

There was a greater number of *Nucella ostrina* in exposed high shore areas on certain days of the two week tidal cycle, apparently the result of both snails moving from out of adjacent refuge areas and moving up shore (Fig. 3). Snails were not evenly distributed in exposed and refuge areas (Table 1). Although refuges, such as cracks and algal canopies, were used throughout the two week survey, the snail count in exposed areas greatly increased on days 3-5 of the tidal cycle (Fig. 3A). Increased use of exposed areas coincided with the shortest duration of midday aerial exposure (for exposure at 1.5 m, $R^2 = 0.84$, $P < 0.001$, Fig. 3).

The highest mean counts of *Nucella ostrina* were seen when midday low tide was minimized while the lowest values were seen during long periods of midday low tide, although this trend was not statistically significant at the $\alpha = 0.05$ level ($P = 0.084$, Table 1, Fig. 3B). Density fluctuation was most obvious in high shore areas. While snail numbers in the <1.5 m plot were relatively consistent over a biweekly tidal cycle, increases in total density were largely driven by increases in the high shore plot (≥ 1.5 m). Importantly, the greatest density of snails in the highest shore regions (1.5 m and above) was observed during the three days predicted to be

foraging peaks by the tidal conditions (Hayford et al. 2015)—those days with the shortest duration of midday aerial exposure (Fig. 3C).

Continuous remote tracking

We received a total of 811 tag detections for *N. ostrina* during the course of antenna deployment, representing 23 different tags or a 34% recapture of the 67 tags deployed. Twenty-one tags were detected more than 1 wk and 15 were detected more than 4 wk after tagging. Over the 14 wk survey period (97 d), *N. ostrina* ventured into the 1.5 m exposed region frequently (on 50 days) and into the 2.0 m exposed region on rare occasions (4 d). Snails ventured into exposed high shore areas on days of the tidal cycle that had reduced periods of midday (within 3 h of solar noon) aerial exposure and reduced T_{\max} (Fig. 4).

Snails did not make brief excursions into high shore areas at high tide. We observed only two incidences of an individual moving from the 1.5 m into the 2.0 m area and retreating within the course of a high tide. Each organism spent less than 2 hours at the 2.0 m elevation.

Thermal consequences of movements

Duration of aerial exposure due to low tides had a strong influence on daily T_{\max} of thermal mimics ($R^2 = 0.446$, $p < 0.001$, Fig. 5).

Snails were disproportionately present in high shore areas when those areas were seawater temperature, and minimized time spent at higher or lower temperatures. Although on some days thermal model temperatures neared 38°C, snails were not present in the adjacent antenna locations on these days (Fig. 6). These detection absences in our continuous monitoring were confirmed with visual surveys. Snails were never detected in high shore areas above 30.75°C,

whereas the mean maximum temperature of 10,000 resamples of environmental temperature (T_e) was 36.17°C (95% CI 36.15-36.19). Similarly, snails spent no time below 3.90°C, but the mean minimum of resampled T_e was 0.10°C (95% CI 0.10-0.11).

2.5 DISCUSSION

Nucella ostrina restricted foraging bouts in risky areas to days of the tidal cycle when aerial exposure risk was minimized. Snails moved into these sun-exposed, high shore areas, but were selective in their timing. This confirms that the same behavioral patterns that we had observed in manipulative experiments (Vaughn et al., 2014, Hayford et al., 2015) also occur in un-caged, natural settings, and furthers the observations of natural snail movements by Spight (1982). This behavior effectively minimized exposure to low tide conditions and the associated potential stresses.

The periodicity of snail behavior shows us that surveys of *N. ostrina* local distribution and abundance on exposed intertidal shores are very likely to yield inaccurately low numbers on all of the days of the tidal cycle except the cool, dark tides—those that occur at night or in the early morning and are traditionally least likely to be sampled by researchers. Thus there is a discrepancy between conditions that are preferential for human observations and those that are preferential for organisms attempting to thrive in a dynamic habitat. It is important to keep this behavioral difference in mind when designing and interpreting field surveys to avoid human bias to the evaluation. While this point is obvious in some animals, such as nocturnal species (Jaburg & Guisan 2001), this study shows it may apply to many cases where microclimate periodicity is less apparent.

Snails use two types of refuges to avoid exposed high shore areas during periods of stressful conditions: microclimates such as cracks in the rock and retreats lower on shore. The RFID method of tracking allowed us to better investigate the use of refuges; individual snails can be found in locations where visual search is difficult and may prevent identification of visual markers. Tagged snails were regularly detected deeper in cracks than we could find by visual searching alone. Importantly, we were able to locate and identify organisms without interfering with their location and behavior. While tags may inhibit the ability of snails to fit into the smallest cracks, we did not observe any other interference with their natural behavior.

Small scale habitat variability can determine evolutionary trajectories of animal populations (Dowd et al., 2015). This may be of elevated importance for slow organisms. Organisms can benefit from heterogeneity in environments where they can move to avoid stressful temperatures or thermoregulate digestive efficiency (Coggan et al., 2011, Caillon et al., 2014, Lathlean, 2014). The range of motion of a snail is limited to a few meters per day and to submerged or moistened rock. If there is a high abundance of refuges created by microtopography, the energy expended to travel from thermal refuge to food and back could be greatly reduced. Similarly, a steep substrate slope, with abrupt changes in tidal water levels compared to a shallow slope, could enable movements between low and high shore areas for slow-moving animals. We would therefore predict to see a greater abundance of *N. ostrina* or other slow mobile intertidal invertebrates on substrates with higher heterogeneity (Gosselin and Bourget, 1989, Chapperon and Seuront, 2011b) and greater interaction strength between mobile predators and their sessile prey in thermally variable areas.

Though we measured temperature, this parameter often covaries with other stressors such as humidity, UV, and salinity (Wolcott, 1973, Helmuth and Hofmann, 2001, Denny and Gaylord,

2010). It is unknown which, if any, of these correlated variables is the most important driver of snail response. We suspect that the risk of these multiple stressors contributed to the development of avoidance of long daytime low tides. In fact, artificially warming low tide periods did not deter foraging behavior (Vaughn et al. 2014); suggesting that temperature alone is not the driving factor. Whichever factors are drivers, it is clear that all are exacerbated by longer daytime aerial exposure. Perhaps tidal cycling gives snails a periodic environmental cue with stress-avoidance benefits.

Thermoregulation in slow-moving animals may be achieved over longer timescales than for fast-moving animals, and may depend on environmental cues that recur at known intervals rather than in response to continuous temperature sensing. We observed an avoidance of high shore areas by *N. ostrina* on days that reached thermal extremes, but not a clear selection of an optimal temperature. We presume the disproportionate amount of time spent at 9-12°C is coincident with snails targeting high shore areas when those regions are submerged in seawater, although a more precise understanding of *N. ostrina* performance across temperatures is needed to evaluate possible benefits of this temperature selection (Hertz et al., 1993). Commonly, physiological ecology has shown behavioral thermoregulation in ectotherms to be based on optimizing conditions, with organisms preferentially selecting temperatures approaching maximum performance (Martin and Huey 2008). This paradigm comes predominantly from work on quickly-moving animals such as reptiles (Huey and Bennett, 1987, Angilletta et al., 2002) and insects (e.g., Coggan et al. 2011). Conditions that change rapidly require rapid movement if an animal is going to take advantage of abiotic shifts. Optimization may be physically impossible if the speed of an animal does not allow it to travel at a scale that is spatiotemporally beneficial. Repeated evidence that *N. ostrina* behavior is reducing risk of exposure to extreme conditions

(Carrington and Kull, 2011, Vaughn et al. 2013, Hayford et al., 2015) suggests that risk avoidance, not optimization, may be the primary factor determining performance for slow intertidal invertebrates.

Increases in temperature due to climate changes are unlikely to directly negatively affect *N. ostrina*—it simply isn't present in the times and places where temperatures are extreme and it effectively avoids temperatures near its lethal threshold. On the whole, this snail experiences moderate temperatures well within its tolerable range. Overall increases in temperature could increase the metabolic requirements of this predator and lead to elevated predation during times that are low risk for overexposure. This may cause increased predation pressure on barnacles in pulses of feeding that occur during tides favorable for snails, leading to a potential shift in timing and magnitude of interaction strength between snails and their barnacle prey. This example, and other ways in which spatiotemporal variability of temperature affects species interactions, should be focal in studies addressing the impact of climate change on intertidal communities as variability may influence ecological release and fitness benefits of population shifts (Gilman et al., 2010, Buckley et al., 2013).

Using remote sampling, we were able to track snail movements during high tide when the intertidal habitat was covered with seawater, in contrast to traditional field methods which are limited to low tide observations. We learned that, unlike some Crustaceans (Naylor et al., 1971, Chabot et al., 2004), *N. ostrina* does not generally migrate into and out of high shore areas during the course of one high tide. Over the 14 wk period of observation there were only two incidents of an individual crawling onshore with the incoming tide and retreating within 2 h when the tide receded. While food may have been consumed during this journey, it could not have been a large amount due to the slow rate of consumption in this animal (mean 5.3 h, John

M. Emlen, Time, energy and risk in two species of carnivorous gastropods, PhD thesis, University of Washington, 1966). Therefore, all substantive prey consumption was conducted during periods of time where the predatory snail was exposed to low tide aerial stresses for at least a portion of the foraging bout.

Our two-part approach to estimating operative temperature—radio tracking and physical thermal mimic—may be a good choice for organisms that are too small for traditional telemetry. While estimates of organismal temperature are limited to the relatively small proportion of time that organism is present in targeted areas, this method does allow us to identify the upper bounds of what a small organism experiences. Temperature extremes can provide us with a more accurate prediction of organismal stress and performance than average temperature experienced (Kingsolver et al., 2015b). Temperatures may fluctuate above critical thermal limits while mean temperature remains within an organism's operating range (Rezende et al., 2014, Camacho et al., 2015).

Here we confirm that snails in natural populations follow predictable changes in the tidal cycle, taking advantage of high shore food sources during times of low risk of exposure to damaging temperatures and associated aerial stresses. Reference to the biweekly tidal cycle is critical to designing accurate surveys to estimate snail densities. Using continuous tracking we found that observations limited to low tide in fact give a comprehensive snapshot of snail behavior. Our evidence supports prior conclusions (Vaughn et al. 2013, Hayford et al. 2015) that *N. ostrina* selectively forages in places and at times that minimize aerial exposure and decrease the risk of exposure to lethal microclimate conditions. The behavior of this species may or may not maximize time spent at its thermal optimum. This slow-moving species in a highly fluctuating habitat may thermoregulate using different strategies than those traditionally

observed in other organisms. This ability to thermoregulate may significantly alter the way we think this and similar species will respond to climate change.

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Competing interests

No competing interests declared.

Author contributions

HAH, MJO, and EC conceived of the methods. HAH and MJO developed the techniques. EC provided financial and equipment support. HAH carried out construction, collected and analyzed data. HAH, MJO, and EC wrote the paper.

2.6 TABLES

Table 2.1 Summary of linear model statistics

Generalized linear mixed modeling (GLMM) with a binomial distribution of error terms was used to assess snail distribution in refuge versus exposed habitats and distribution above or below 1.5 m shore elevation.

<u>Response</u>	<u>Model</u>	<u>Error</u>	<u>AIC</u>	<u>χ^2</u>	<u>df</u>	<u>P</u>
Snail	1: habitat ~ day + (1 site)	binomial	944.1			
habitat	2: habitat ~ 1 + (1 site)	binomial	1107.1			
				189.0	13	<0.001
Snail	1: elevation ~ day + (1 site)	binomial	1112.1			
elevation	2: elevation ~ 1 + (1 site)	binomial	1106.5			
				20.5	13	0.084

2.7 FIGURES

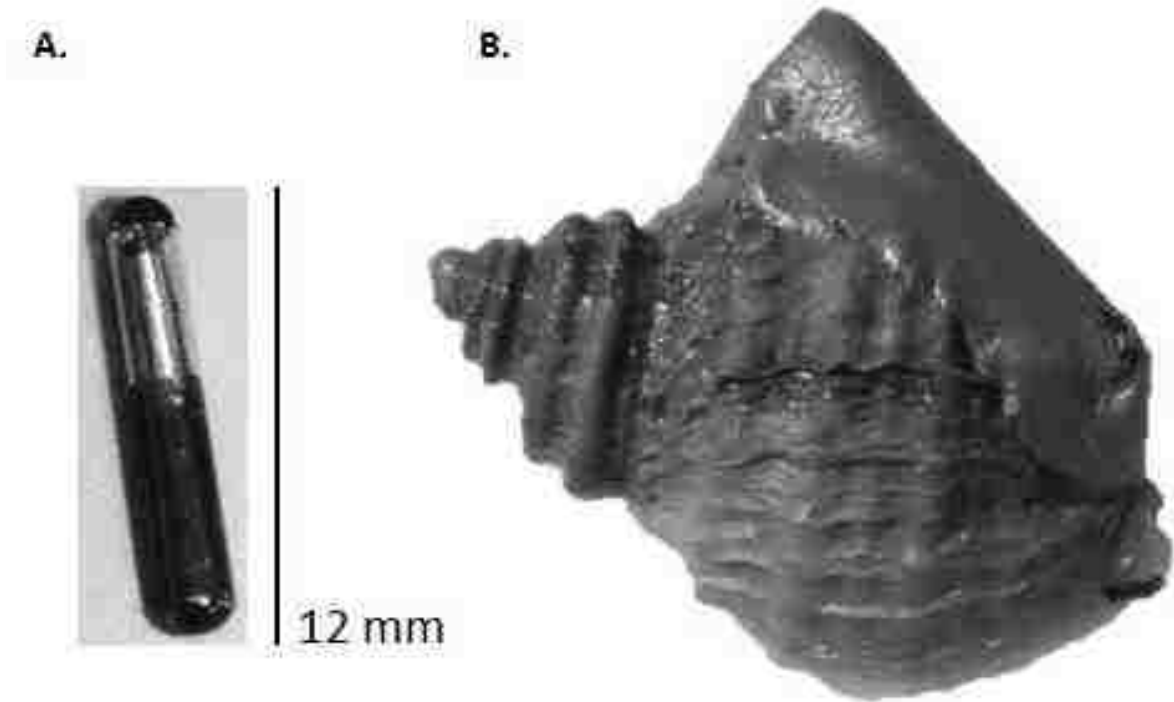


Figure 2.1 Radio frequency identification (RFID) tag and *Nucella ostrina*

(A) RFID tag, 12 mm x 2.12 mm; (B) tag encased in epoxy and affixed to the dorsal shell of *N. ostrina*.

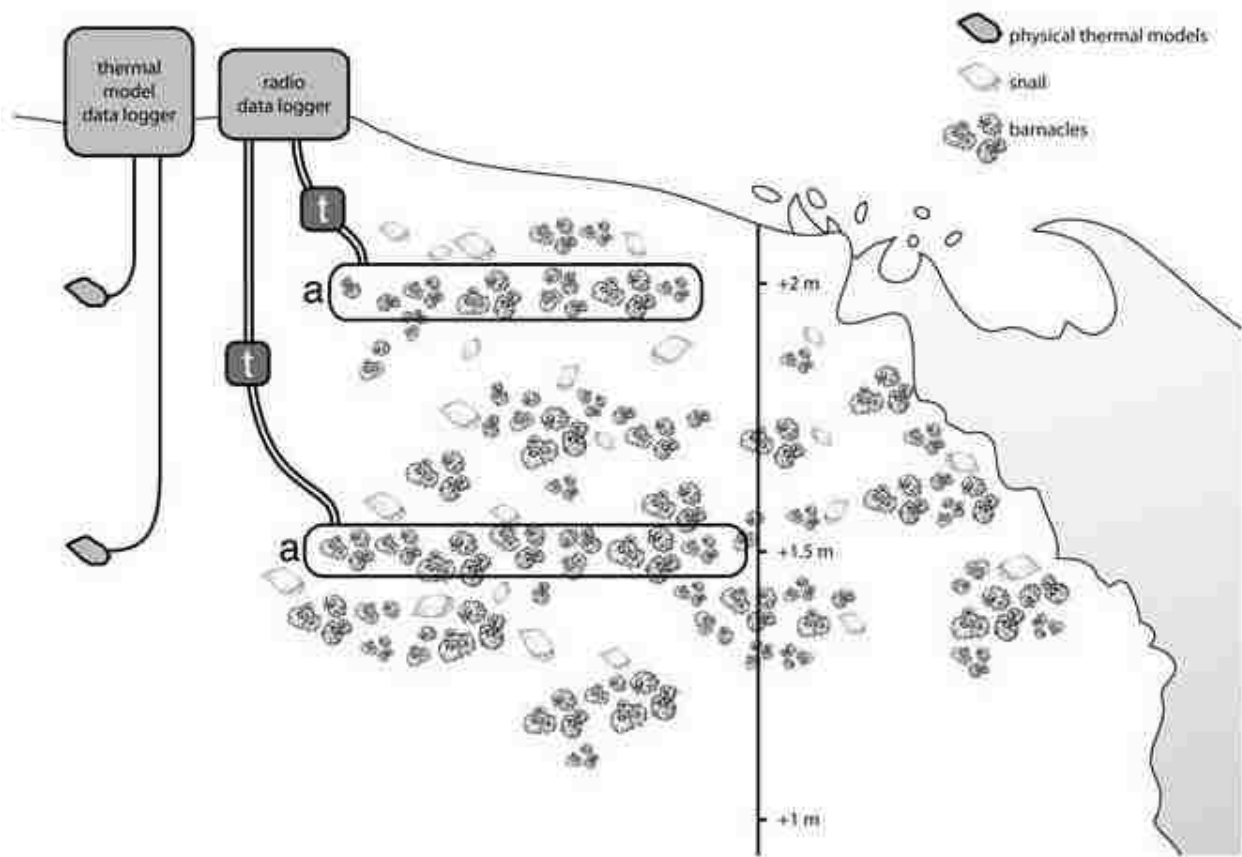


Figure 2.2 Schematic of radio antennas and physical thermal models mounted to the intertidal shoreline

Movement and temperature of the snail, *Nucella ostrina*, as it preyed upon the barnacle, *Balanus glandula*, was monitored using a two-part system: (1) radio frequency identification (RFID), consisting of RFID-tagged snails, antenna wire loops (a), antenna tuners (t), shielded wire (double line), and radio data logger; (2) temperature, consisting of thermocouple wires (fine line), physical thermal models, and thermal model data logger. Systems were placed adjacent to each other at two tidal elevations, 1.5 and 2.0 m. In the late summer and autumn, low shore barnacles had been consumed and available prey density was highest in high shore regions.

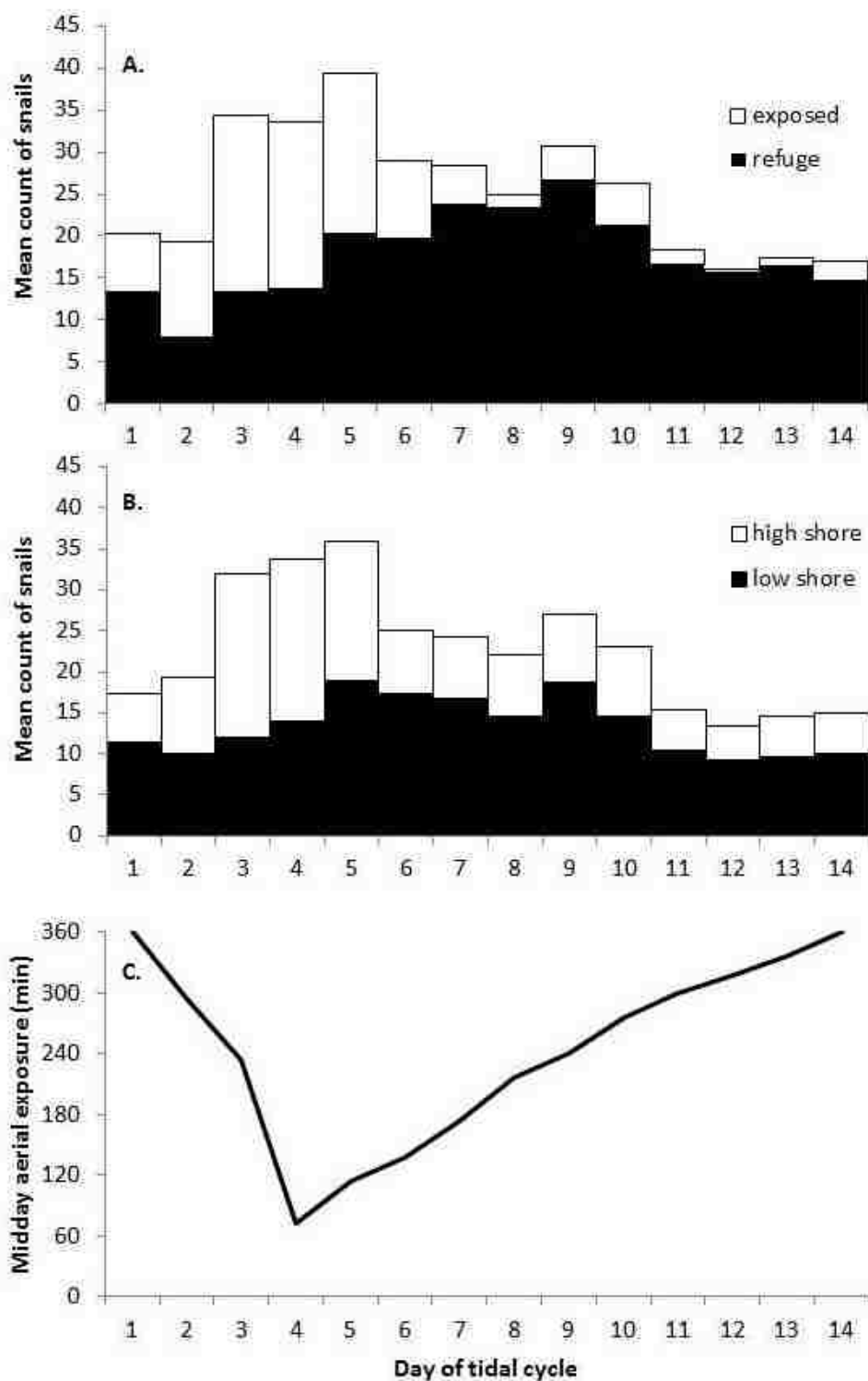


Figure 2.3 Daily distribution of snails over two-week tidal cycle in August 2012

Nucella ostrina present at three intertidal sites on the FHL Preserve over a 14 d tidal cycle, beginning August 6, 2012. At each site a 1 m horizontal band was surveyed from 1 m above mean lower low water (MLLW) to 2.25 m above MLLW. Less extreme low tides (neap) occurred day 3-5 of the tidal cycle; extreme maxima and minima (spring) tides day 12-14. **(A)** Mean count of individual snails found at sites or in the surrounding 20 m² search area in refuge habitat, defined as shaded by algae or by depth in a crack (black), versus present in fully air-exposed locations (white). **(B)** Mean count of snails found from 1 m to 1.5 m above MLLW (low shore, black), and from 1.5 m to 2.25 m (high shore, gray). Note that the increases in overall density days 3-5 are driven by increases in density high on shore. **(C)** Duration of midday aerial exposure due to low tide (min), defined as low tides occurring within 3 h of solar noon, for each elevation. Midday aerial exposure is minimal day 2-6 and maximal day 12-14.

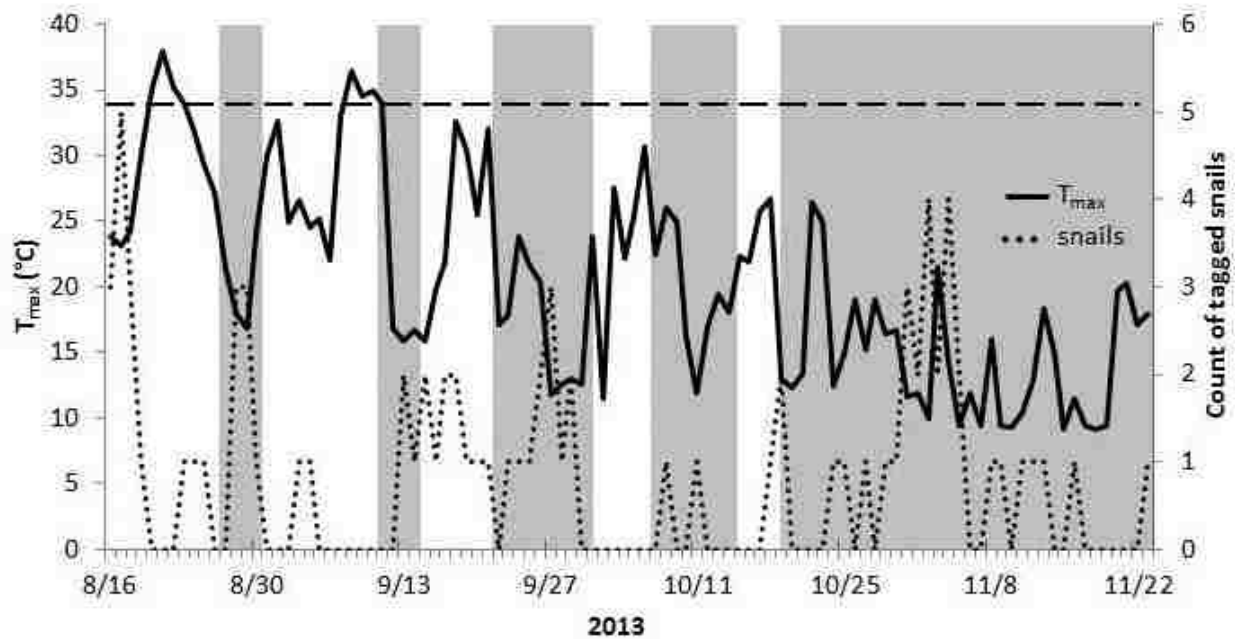


Figure 2.4 Snails absent on days with at high maximum temperatures in autumn 2013

Maximum daily temperature of physical thermal model in high shore zone (solid line) and count of tagged snails found in high shore areas (dotted line) over 14 wk sampling period from August to November 2013. Dashed line marks LT_{50} of *Nucella ostrina*, 34°C , based on Bertness and Schneider (1976). Days with fewer than 180 min of midday aerial exposure (low tides occurring within 3 h of solar noon), representing days with reduced thermal risk, are shaded in gray.

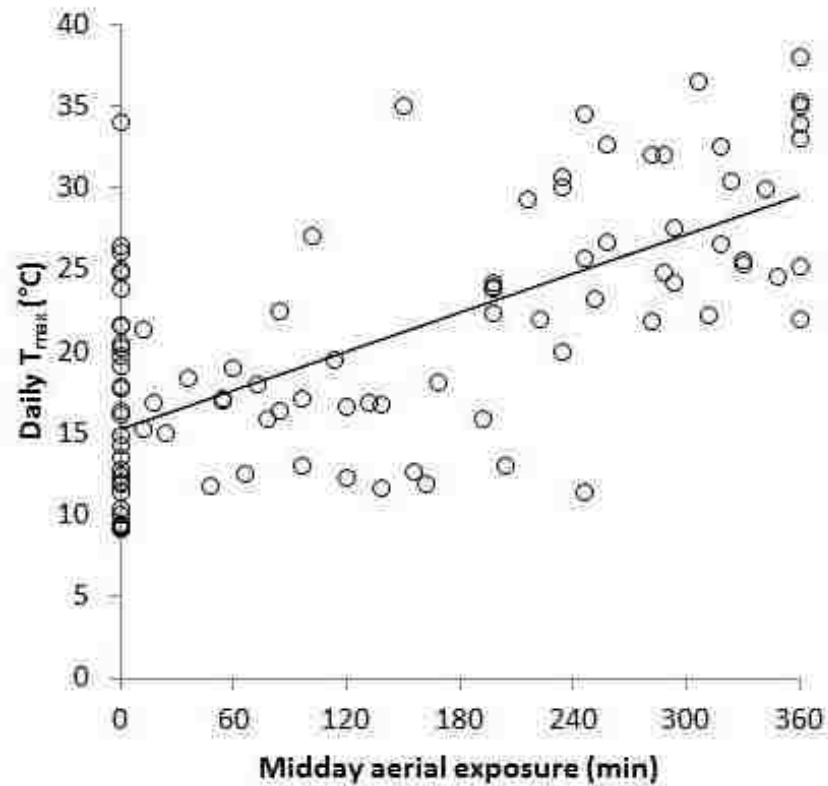


Figure 2.5 Timing and duration of aerial exposure at low tide regulates daily maximum temperature

Daily maximum temperature as a function of duration of midday aerial exposure due to low tide, defined as low tides occurring at solar noon \pm 3 h, over 14 wk sampling period from August to November 2013 (97 d). Solid line shows linear fit, $R_2 = 0.446$, $p < 0.001$.

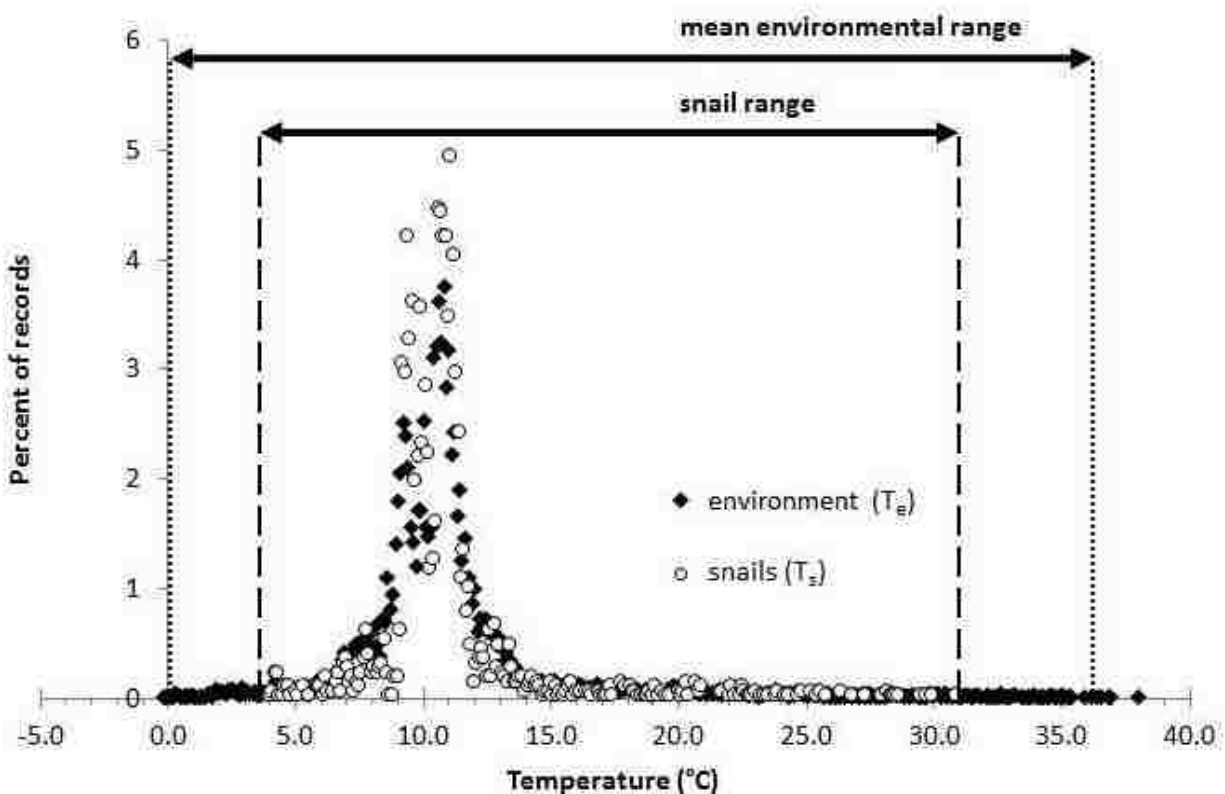


Figure 2.6 Temperature experienced by snails

Distribution of environmental temperatures measured every 15 min over 14 wk sampling period from August to November 2013 by physical thermal models (T_e , black markers, $n = 19,200$) compared to the subset of temperatures experienced by snails (T_s , white markers, $n = 2,343$).

Dashed lines mark the breadth of temperatures experienced by snails (26.9°C). Dotted lines mark the mean minimum (0.10°C) and maximum (36.17°C) temperatures of 10,000 resamples of environmental data. Snails experience a disproportionate amount of time at water temperature ($9\text{--}12^\circ\text{C}$).

Chapter 3. PERFORMANCE BENEFITS OF SLOW MIGRATORY BEHAVIOR IN A PREDICTABLY DYNAMIC HABITAT

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3.1 ABSTRACT

Ecological outcomes of climate change are predicted based on temperatures with spatial and temporal fluctuations. The patterns of these fluctuations not only influence organisms experiencing them, but may be used by organisms to thermoregulate if the patterns are predictable. In the marine intertidal zone, tidal cycling creates large but predictable temperature fluctuations on a two-week cycle. Temperatures are highest at high shore elevations and on days with long durations of midday low tides. The intertidal snail *Nucella ostrina* forages on barnacles high on shore on days with short durations of midday low tide (cooler) and retreats into refuges in cracks or lower on shore on days with long midday low tides (hotter). We assayed thermal performance of *N. ostrina* using righting behavior following aerial exposure to different temperatures. We found that performance of this species drops dramatically after a 2 h exposure above 30°C and the death rate is high at 35°C. We used the migration of *N. ostrina* between sun-exposed foraging areas and refuges to model the environment the snail actually experiences during spring and summer low tide exposure to air. We found snail migratory behavior led to a 60% or greater reduction in days of risky temperatures experienced by the snail. This behavioral filter of environment greatly reduced the proportion of time *N. ostrina* was exposed to thermally risky temperatures, including those predicted with global climate change. This snail is unlikely to be directly affected by increasing temperatures in the near future because it simply isn't present in times and places where those temperatures reduce performance. However, indirect effects, such as thermoregulatory behavior inhibiting evolutionary adaptation or the differential exposure and response between the snail predator and its barnacle prey, are likely to detrimentally affect this species.

3.2 INTRODUCTION

Increasing temperature due to climate change will alter the distributions of organisms in space and time, potentially changing latitudinal and altitudinal ranges (Sunday et al. 2011, Ettinger et al. 2011, respectively), phenology (Edwards & Richardson 2004), altering metabolic energy budgets (Dillon et al. 2010), available oxygen (Deutsch et al. 2015), and creating no-analog communities (Williams & Jackson 2007) or changing dynamics of existing communities (Harley 2013). The IPCC prediction of 1.5-2.5°C increase in global mean surface temperature by 2100 (RCP4.5 and RCP6.0, Pauchuri et al. 2014) does not describe the predicted spatial and temporal patterns of temperature variability. The scale of these patterns is critical to predicting the effect they will have on organisms. Furthermore, behavior can moderate an organism's experience of increasing temperature (Kearney et al. 2009, Sunday et al. 2014), especially if that organism uses available microhabitats to its benefit.

The ability of an organism to thrive in its environment is often considered in terms of performance along an environmental gradient, such as temperature (Huey & Stevenson 1979, Huey 1991). Even small-scale differences in microhabitat can lead to different thermal performance levels in animals (Lima et al. 2016). Determining performance values for field conditions can be used to create mechanistic models of climate change effects (Buckley et al. 2010).

Predicting how patchy fluctuations will influence the performance of species pushed to their limits is a challenge. One approach is to look to species that currently live in habitats with large fluctuations of environmental conditions, such as the intertidal zone on the edge of both marine and terrestrial habitats. The high intertidal is exposed to air daily at low tide, whereas the low intertidal may only be uncovered on rare occasions. We often think of this region as having steep

environmental gradients such as temperature, humidity, salinity, and UV, but these are not static. Tidal cycling yields spatiotemporal variation in these gradients that also fluctuate over the two-week tidal cycle (Denny et al. 2004), and is the most important driver of microclimate variability (Mislán et al. 2009). Among other strategies, organisms that live in this zone may have specialized behavior that assists them in navigating fluctuating stress. Their behavioral filter may fundamentally change the thermal environment they experience (Chappon & Seuront 2011a,b).

Often resources are distributed unevenly throughout the intertidal zone. Resources in the highest tidal elevations, such as algae and barnacles that can serve as food for other species, are only available to those mobile animals that can withstand the harsh physical conditions that occur there. Barnacles have a higher thermal tolerance than their snail, crab, and sea star predators (Bertness & Schneider 1976, Pincebourde et al. 2008, Gilman et al. 2015), but those predators may be able to feed upon barnacles if they choose the right times to travel to the high intertidal. Mobile animals in the intertidal move through tidal elevations on timescales that differ among species. Fast organisms, for example crabs (Yamada & Boulding 1996) and sea stars (Robles et al. 1995) are known to move among thermal microhabitats at a rate comparable to the tide or to the rate of temperature change in those habitats. Similarly, refuge habitats such as cracks in the rock and underneath algal canopy can provide shelter for mobile predators, but food resources in these locations are typically the first depleted (Johnson et al. 1998, Bertness et al. 1999).

At an average speed of 1.3 cm min^{-1} (data not shown), the snail *Nucella ostrina* is not a fast organism and cannot track rapid changes in thermal conditions. Instead, *N. ostrina* times its migrations to high shore foraging areas with the two-week tidal cycle, selecting the days that minimize aerial exposure at low tide during high solar radiation (daylight hours; Carrington &

Kull 2011, Vaughn et al. 2014, Hayford et al. 2015, Hayford et al. *unpublished manuscript*). This behavior can be modeled as several days in which snails forage in high shore areas, 2-4 d at high intensity, followed by retreat to refuges and low shore areas for the remainder of the two-week tidal cycle (Fig. 1). This results in a reduced risk of a snail being subjected to stressful or lethal temperatures. The extent to which this species' behavior plays a role in its response to climate change is unknown.

We sought to explore the benefit of tidally-driven migrations to *N. ostrina* performance and of the added risk imposed by temperature increases due to climate change. We hypothesized that the migratory behavior of snails would confer a thermal performance benefit to contemporary populations as well as decrease the likelihood that future temperature increases would be directly detrimental to this species.

3.3 MATERIALS & METHODS

Summary

Nucella ostrina Gould, 1852, is a common intertidal gastropod from Yakutat, Alaska to Point Conception, California (Palmer et al. 1990). In our study region, San Juan Island (SJI), WA, *N. ostrina* occupies tidal elevations from 0.6 m to 1.9 m above mean lower low water (MLLW, Connell 1970). Even the low end of this tidal range is exposed to air an average 25 days per month during our survey years (2013-2015, calculated from NOAA station #9449880, www.tidesandcurrents.noaa.gov), meaning that this species is regularly exposed to air during periods of low tide.

We integrated physiological, behavioral, and environmental data collected over the past five years for *N. ostrina* and created a conceptual model to predict the relative performance benefit of its migratory behavior. In order to estimate thermal performance of *N. ostrina* in its natural habitat, we conducted lab trials of ecological performance across temperatures. We used this performance assessment combined with conceptual models of snail behavior derived from past studies to filter two years of measured thermal mimic temperatures. We contrasted this to a hypothetical snail that did not migrate, but remained relatively stationary in air-exposed, high shore regions. We then added 2°C to all temperatures, representing a future climate scenario, and predicted the resulting additional stress placed on migratory versus stationary snails.

Ecological performance across temperatures: righting behavior

We collected *N. ostrina* from Cattle Pt., SJI in June 2014. Individuals were weighed, measured, affixed with a small number tag, and housed in aquaria with running sea water prior to performance experiments. Experiments were conducted in July and August 2014 at Friday Harbor Laboratories (FHL).

Ecological performance of *N. ostrina* as a function of temperature was assessed as time to recover an upright posture following an aerial immersion period. We took this whole-body approach to quantifying snail performance because it measured a survival skill relevant to this species; *N. ostrina* releases its grip on the substrate at high temperature and low humidity (Hayford *unpublished data*) and can be swept off the substrate by wave action. The snail must be able to right itself and reattach to the rock or it will be washed away from the high intertidal zone, facing numerous deeper-dwelling competitors and predators.

Snails were given an aerial immersion stress that mimicked a low tide for 2 h. Individuals were sorted into treatment groups ($n = 12$) of mean shell length $21.3 \text{ mm} \pm 1.90 \text{ SD}$. Each individual was placed at the bottom of a 50 mL conical vial on a small piece of plastic mesh forming a stage with open circulation. 3 ml of seawater was added to the bottom of each conical vial below the plastic mesh stage to maintain the relative humidity near 100%. We kept humidity high to conservatively estimate stressful temperatures in the field, without including the often correlated stress of desiccation. The conical vial was placed in a recirculating water bath at ambient temperature ($20\text{-}23^\circ\text{C}$) which was then ramped to desired treatment temperature. Ramping rate was adjusted in order to hold the duration of aerial emersion consistent. Following immersion, each snail was removed from the vial and placed upside down in a small chamber with flowing seawater.

Full recovery was achieved when the snail righted itself and reattached to the substrate. A time lapse camera (Garden Watch Cam, Brinno, Inc., Taipei, Taiwan) captured images at 1 min intervals, tracking snail behavior for 24 h. Snails unable to right within this period were noted and checked repeatedly over subsequent days until it could be determined if they were living or dead. Twelve individuals were used at each temperature. Each individual was tested at only one temperature (no repeated measures). Temperatures ranged from 5°C to 20°C in 5°C intervals, plus 12.5°C , and 2.5°C intervals from 20°C to 37.5°C . We determined the upper lethal limit as the lowest temperature trial in which no snails survived. Once an upper lethal limit was established, an additional test at 34°C was performed to determine range of the lethal temperature of 50% of individuals (LT_{50}).

Based on the critical temperature range identified after 2 h aerial exposure, similar trials were repeated using 1 h aerial exposure at 34, 35, and 36°C. The difference in recovery time between 2 h and 1 h duration of exposure was assessed for 34°C by two-sample t-test.

Temperature of thermal mimics

Estimates of *Nucella ostrina* body temperatures in its microhabitat were made by mounting physical thermal mimics in the field at Friday Harbor Laboratories Preserve on San Juan Island (SJI), Washington (48°32' N 123°00' W). Each mimic was constructed by inserting a thermocouple into an epoxy-filled shell following the methods of Gilman et al. (2015), and mounted to the intertidal substrate on a south-facing slope in a high shore area 1.5 m above mean lower low water (MLLW). Mimic temperatures were sampled by a data logger (25T and CR1000, Campbell Sci, Logan, Utah, USA) every 15 minutes for nearly 26 months.

We censused two continuous years (August 2, 2013 to September 30, 2015) of temperatures of thermal mimics in the high intertidal (1.5 m above MLLW) to determine the season, frequency, and duration of high temperature events occurring at or above a threshold temperature. Specifically, we queried the data for the onset of a chosen threshold temperature (30°C, for example), and then counted the number of subsequently logged temperatures at or above that threshold, producing a duration of time for each high temperature event. The frequency of a given duration length was calculated for threshold temperatures 30, 35, and 40°C. Only during spring and summer months did mimic temperatures reach 30°C for durations over 1 h and a total of 5 h or longer. We therefore removed data recorded from October through March and used complete spring and summer seasons (April through September) of 2014 and 2015 for all further analyses.

Behavioral filter of environmental temperatures & climate change risk

We took the minimum time required to recover (right and reattach to the substrate) and assigned it a value of 100%, or the maximum performance level for the measured trait. The time required to recover from each other temperature treatment was divided by this maximum value to calculate a relative performance level. We calculated the frequency of high risk temperatures occurring continuously for 2 h or more throughout the spring/summer seasons of 2014 and 2015. This distribution of temperatures was used to estimate the relative performance level for *N. ostrina*.

We used behavioral patterns identified in several previous studies of *N. ostrina* during the summer months on SJI to filter snail behavior across a two-week tidal cycle (Supplementary Table C.1). In each study, we compared a standardized mean count of *N. ostrina* in foraging areas per day to the duration of midday aerial exposure (4 h before to 4 h after approximate solar noon, 12:00 PST). Days with the longest midday aerial exposures were identified as least likely to observe snail foraging. We pooled the data from all five studies into two categories of tide type: 7 d of longest duration of exposure versus all other days. We determined that the 7 d of longest midday low tide exposure had fewer number of snails present in high shore areas than the other 7 d of the two-week tidal cycle ($t = 5.83$, $df = 156.28$, $P < 0.001$, Supplementary Fig. C.1).

We analyzed temperature data from 2014 and 2015 to compare the relative performance of a stationary snail remaining in exposed high shore areas to a snail with migrations throughout the two week tidal cycle. Refuge temperatures (1.4 m above MLLW) were measured by a thermal mimic from June through August 2015 and regressed to nearby exposed thermal mimic at 1.5 m ($R^2 = 0.880$, $P < 0.001$, Fig. 2). This relationship ($y = 0.5763x + 5.0302$) was used to estimate refuge temperatures from 2014 and April-May 2015. Due to the distribution of data, refuge

temperatures are likely overestimated at the highest end of the exposed temperature range. This will not affect the overall trend because refuges were always cooler when exposed temperatures were above 30°C, but may inflate the difference in some cases. We calculated the number of days per year at or above the threshold for *N. ostrina* where performance begins to decline (above 30°C) from the physical thermal mimic statically exposed in the high shore area. We hypothetically moved snails from exposed high shore areas during the 7 d of the tidal cycle when we predicted them to be in refuges and replaced these portions of the time series with estimated refuge temperatures. We again ran our model on this modified time series to determine the number of days above 30°C experienced by a snail migrating between exposed and refuge habitats (Fig. 1).

Based on the range of IPCC projections of global temperature increase by the year 2100 (Pachauri et al. 2014), we added 2°C to the time series of snail temperature for both stationary and migrating models and reran the analyses described above.

Analyses were made using Matlab v.R2009a (The MathWorks, Inc. Natick, Massachusetts, USA) and R v.3.1.3 (R Core Team, Vienna, Austria) with packages plyr (Wickham 2011), and ggplot2 (Wickham 2009).

3.4 RESULTS

Ecological performance across temperatures: righting behavior

Nucella ostrina did not immediately right and reattach to the substrate upon submersion following a simulated low tide. Commonly, a recovering snail would stretch its muscular foot out

of its shell in several directions for a number of minutes before attempting to right itself. The decrease in snail performance at elevated temperatures was sharp (Fig. 3A). All snails recovered within an hour (mean 14 min) at 30°C, while at 32.5°C, 11 out of 12 individuals recovered within 24 h and the mean recovery duration of those successful increased to 107 min. Regardless of recovery duration, all snails survived the emersion exposure and eventually resumed normal behavior at treatments up to 34°C (Fig. 3B). At 35°C, nine out of 12 individuals died during or following the emersion treatment. At 37.5°C all 12 individuals died. These numbers are comparable to those found by Bertness & Schneider (1976), $LT_{50} = 34$ after 4 h exposure.

As predicted, snails exposed to high temperatures for shorter durations of time performed better than their counterparts exposed to longer durations (Fig. 4). Snails recovered from exposure to 34°C for 1 h 206.6 min faster than exposure to 34°C for 2 h (two-sample t-test, $t = -2.69$, $df = 8.60$, $P = 0.026$). Nine of 12 individuals died after 2 h exposed to 35°C, while not a single death occurred in the 1 h exposure to 35°C.

Temperature of thermal mimics

Based on our laboratory observations, we chose 30°C as the tipping point above which temperatures reduced the performance of *N. ostrina*. Intertidal temperatures exceeded 30°C 184 times in 2 yr. On 124 occasions the temperature remained above 30°C for an hour or more, with one event exceeding 6 h duration (Fig. 5). We chose 35°C as a lethal temperature, because 75% of individuals perished after 2 h exposed to this aerial temperature in our performance assays. Although instances of reaching 40°C were relatively rare, on four occasions it remained above 40°C for more than 2 h.

Behavioral filter of environmental temperatures & climate change risk

The aerial temperatures in high shore intertidal environments are predominantly below 30°C, which corresponds to a near-maximum relative performance for *N. ostrina* (Fig.3). However, over the course of two summer seasons 28 d of 358 d (7.8%) had 35°C temperatures for durations of 2 h or longer (Fig. 5).

Behavior predicted in our model resulted in a reduction of 99 d of exposure per year (61.5%) to temperatures 30°C or greater and a reduction of 57 d (82.6%) to temperatures 35°C or greater (Table 1). Migrating snails experienced a lower frequency of all risky temperatures, compared to stationary snails (Fig. 6). This was particularly notable where migration decreased by 92.9% the frequency of lethal temperatures experienced.

A predicted 2°C increase across all temperatures resulted in a gain of 22 d of risky temperatures 30°C or greater per year (13.7%) and 35 d of lethal temperatures 35°C or greater (50.7%) in high intertidal areas. The modeled snail migrating behavior reduced this to a gain of 12 d of risky temperatures and 16 d of lethal temperatures (Table 1). The benefit of migration in a hotter world was reduced when considering only risky, non-lethal temperatures (below 35°C), but was comparable to the benefit seen today when considering lethal temperatures; migration reduced exposure to 35°C and greater by 91.5% (Fig. 6).

3.5 DISCUSSION

Nucella ostrina functions successfully in a wide range of environmental temperatures, recovering in minutes from exposure to temperatures ranging nearly 30°C. However, once

temperatures climb above 30°C, performance of this snail deteriorates rapidly. The intertidal shores it inhabits are subject to lethal or risky temperatures in half the months of the year at durations that can disrupt *N. ostrina* physiology. Behavioral modification of thermal environment, achieved by carefully timed migrations between sun-exposed and refuge locations, reduces the chance that the snail will ever experience threatening temperatures. Not only does snail avoidance of foraging on risky days help them to avoid lethal temperatures, it helps them to avoid high temperatures that lead to even slightly reduced performance.

This migratory behavior expands the fundamental niche into places that otherwise would have appeared too hot. The realized niche of *N. ostrina* includes spaces that would be overlooked by a simpler biogeographic model (Parmesan et al. 2005). Temperature variability across tidal elevation and microhabitat is an important characteristic of the intertidal that creates opportunities for small organisms (Gilman et al. 2015). While we knew how those habitats are used by *N. ostrina* over space and time (Spight 1982, Carrington & Kull 2011, Vaughn et al. 2014, Hayford et al. 2015, Hayford et al. *unpublished manuscript*), this study introduces evaluation of the performance consequences of thermoregulation.

The duration of a high temperature event directly increases the performance risk of that event (Rezende et al. 2014). Although climate change estimates only added a few days with temperatures over 30°C, both the number of days exceeding lethal temperature (35°C) and the number of days with 2 h or longer durations of these high temperatures increased by several weeks. This suggests there are a large number of days when stationary snails are currently experiencing temperatures just under the lethal threshold; without migratory behavior, perhaps this species would be nearing a tipping point. Although our study area in the San Juan Islands has among the hottest intertidal zones on the U.S. West Coast due to the midday timing of

extreme low tides during the spring and summer months (Helmuth 2002), this site is near the middle of the species' range. Differences in temperature due to tidal timing or latitude could lead to very different consequences if *N. ostrina* exhibits the same behavior in other locations.

Temperature increases due to climate change will affect *N. ostrina*, but perhaps not directly. While increased temperatures will yield a greater number of days that could potentially expose snails to lethal conditions, the snails simply aren't present in the highest risk areas on those days. In fact, a 2°C increase is far less dangerous than a change in behavior that eliminates migration between refuge and foraging areas. In this manner, thermoregulation can buffer species from temperature increases due to climate change (Kearney et al. 2009). Increasing the number of hot days when this avoidance behavior is needed could lead to a greater temporal patchiness of predation pressure on barnacles (O'Connor 2009, Sorte & White 2013) and the spatial scales of microclimate and substrate heterogeneity become increasingly important (Sears et al. 2011, Marshall et al. 2013).

Increases of the moderate temperatures that snails generally experience could be beneficial if food assimilation and growth rates increase (Brett 1971, Sanford 2002, Kingsolver & Huey 2008). While we do not know the optimal temperature for *N. ostrina*, this species' slow movement, coarse behavior, and highly fluctuating environment, may prevent taking advantage of higher temperatures that would otherwise be energetically beneficial (Yamane & Gilman 2009, Miller et al. 2015). Note that our performance metric of righting and reattaching to the substrate is only one of many biological processes that *N. ostrina* must carry out to be successful in its habitat. Other key processes may yield different threshold temperatures (Huey & Kingsolver 1989), but we expect those differences to be minor compared to the range of temperatures experienced in the intertidal zone. Moreover, our understanding of temperature

effects on performance is largely based on prolonged exposure to static temperatures. Intertidal organisms are subjected to substrate temperatures that regularly vary 30°C in a single day. This regime of variability may have profound effects that are not accurately characterized by performance response to steady thermal conditions (Benedetti Cecchi et al. 2006, Niehaus et al. 2012, Dowd et al. 2015, Hong & Shurin 2015).

Understanding the different ways in which predators and their prey are affected by increasing temperature is critical to predicting climate change effects (Kordas et al. 2011, Dell et al. 2014). Responses that differ between coupled predators and prey could lead to a shift in the relationship between population sizes (Broitman et al. 2009). The thermal tolerance of *N. ostrina*'s barnacle prey, *Balanus glandula*, is significantly higher than that of *N. ostrina* (40°C for LT₅₀ after 4 h exposure, Gilman et al. 2015), yet sessile barnacles will be continuously subjected to thermal increases in the high intertidal. This is particularly risky for newly settled juvenile barnacles (Gosselin & Jones 2010). The inability of settled barnacles to migrate away from high shore regions on the hottest days may lead to slower growth, reduced lifetime fecundity, higher mortality and reduced population sizes. This would have an indirect adverse effect on the snail which could, in turn, have cascading effects between other species in the community. As a predator, *N. ostrina* can have a large effect on competitors and prey species (Navarrete & Menge 1996). For example, in the absence of the sea star, *N. ostrina* is the primary predator on *B. glandula*, shifting the barnacle population to a less-preferred species by the end of the summer (Dayton 1971).

Thermoregulation may provide strong benefit species in the short term, but behavioral buffering of environmental change may slow the rate of adaptation (Kingsolver & Buckley 2015, Hao et al. 2015). Once temperatures increase beyond a threshold, species using thermoregulation

may not have the genetic scope to withstand ambient temperatures through physiological and morphological mechanisms alone (Somero 2010). If there is no selection for tolerance of higher maximum temperatures, when refuge temperatures have increased to detrimental levels entire populations of *N. ostrina* could go extinct.

Overall, this study shows careful selection of foraging day and location dramatically reduces the thermal risk experienced by *N. ostrina*. Avoidance of hot high shore areas on days with long midday exposure to sun and air protects this species from experiencing decreased ecological performance. Due to its slow and cyclical migratory behavior, future increases in habitat temperature due to climate warming are unlikely to push this snail beyond its performance threshold.

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3.6 TABLES

Table 3.1 Effect of snail behavior and potential temperature increase on number of thermally stressful days experienced by snails in spring and summer pooled over two years (n = 358).

Stationary indicates a snail foraging continually in the high intertidal (1.5 m above MLLW), whereas migrating indicates a snail shuttling from a high intertidal foraging area to a refuge crack (1.4 m above MLLW) on the 7 d of the two-week tidal cycle when midday aerial exposure is longest. Percent of all days shown in parentheses.

	2014-2015		Predicted 2100		Gain due to climate	
	temperatures		temperatures		change	
	≥ 30°C	≥ 35°C	≥ 30°C	≥ 35°C	≥ 30°C	≥ 35°C
Stationary snail	161 (45.0)	69 (19.3)	183 (51.1)	104 (29.1)	22 (6.1)	35 (9.8)
Migrating snail	62 (17.3)	12 (3.4)	74 (20.7)	28 (7.8)	12 (3.4)	16 (4.5)
Reduction due to migration	99 (27.7)	57 (15.9)	109 (20.3)	76 (21.2)		

3.7 FIGURES

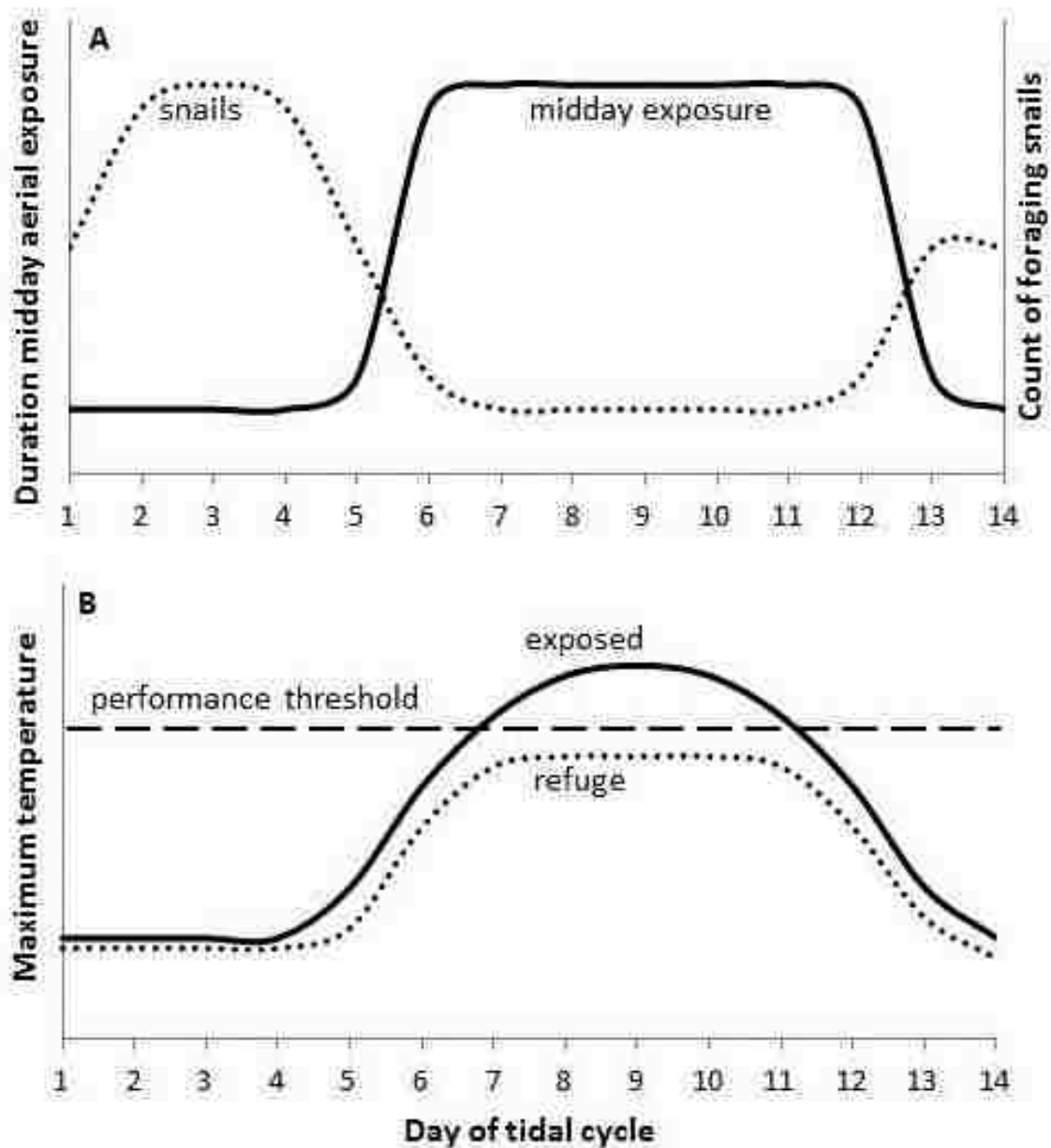


Figure 3.1 Conceptual model of tide, temperature, and snail behavior throughout a two-week tidal cycle

(A) Duration of midday aerial exposure due to low tide (solid) and foraging behavior of snails in sun-exposed high shore areas (dotted). Snail counts are lowest on days with the longest midday

exposure and highest on days with the shortest midday exposure. When snail counts are low in exposed areas, they have moved into refuge areas such as lower on shore or into cracks. **(B)** Maximum temperature of sun-exposed (solid) and refuge (dotted) habitats. Putative performance threshold (dashed) lies below maximum temperatures reached in exposed areas, indicating that refuge habitats would confer performance benefit on these days. Note that snails are not present in exposed areas on days that temperatures exceed performance threshold.

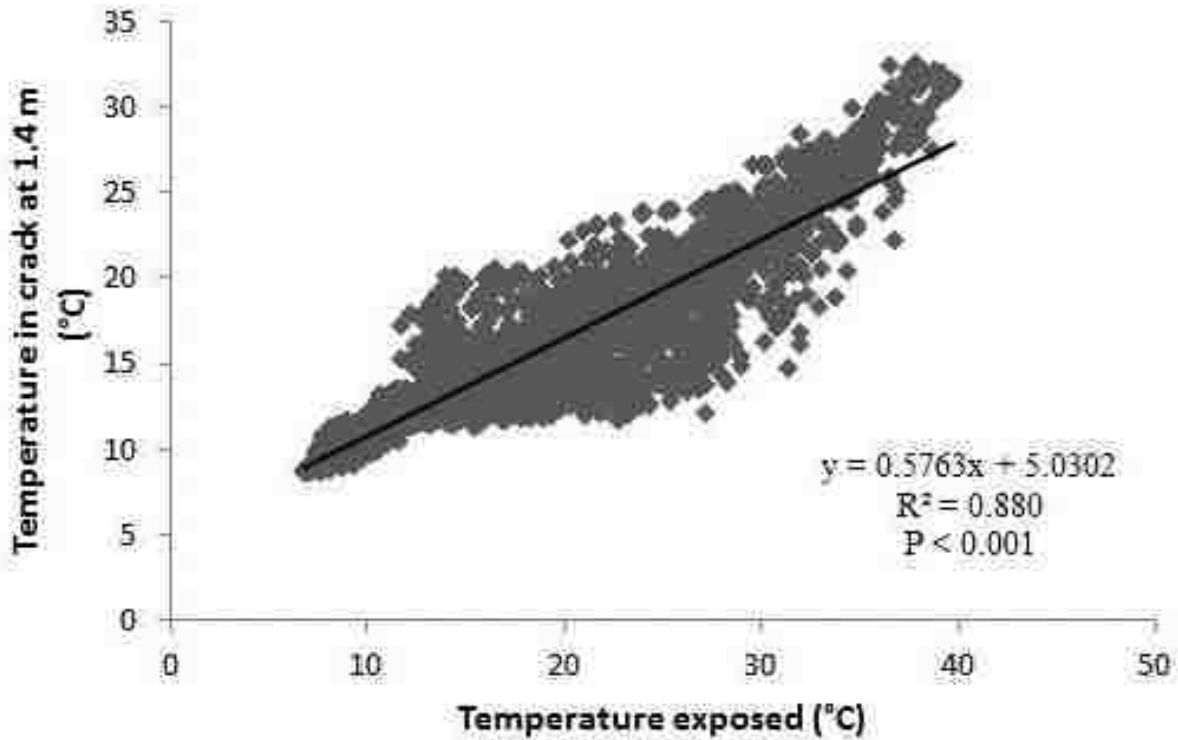


Figure 3.2 Relationship between physical thermal model in sun-exposed area at 1.5 m tidal elevation and physical thermal model in a refuge crack at 1.4 m tidal elevation

Line indicates fit of linear regression ($y = 0.5763x + 5.0302$, $R^2 = 0.880$, $P < 0.001$), used to estimate refuge temperature from sun-exposed temperature during 2014 and April-May 2015.

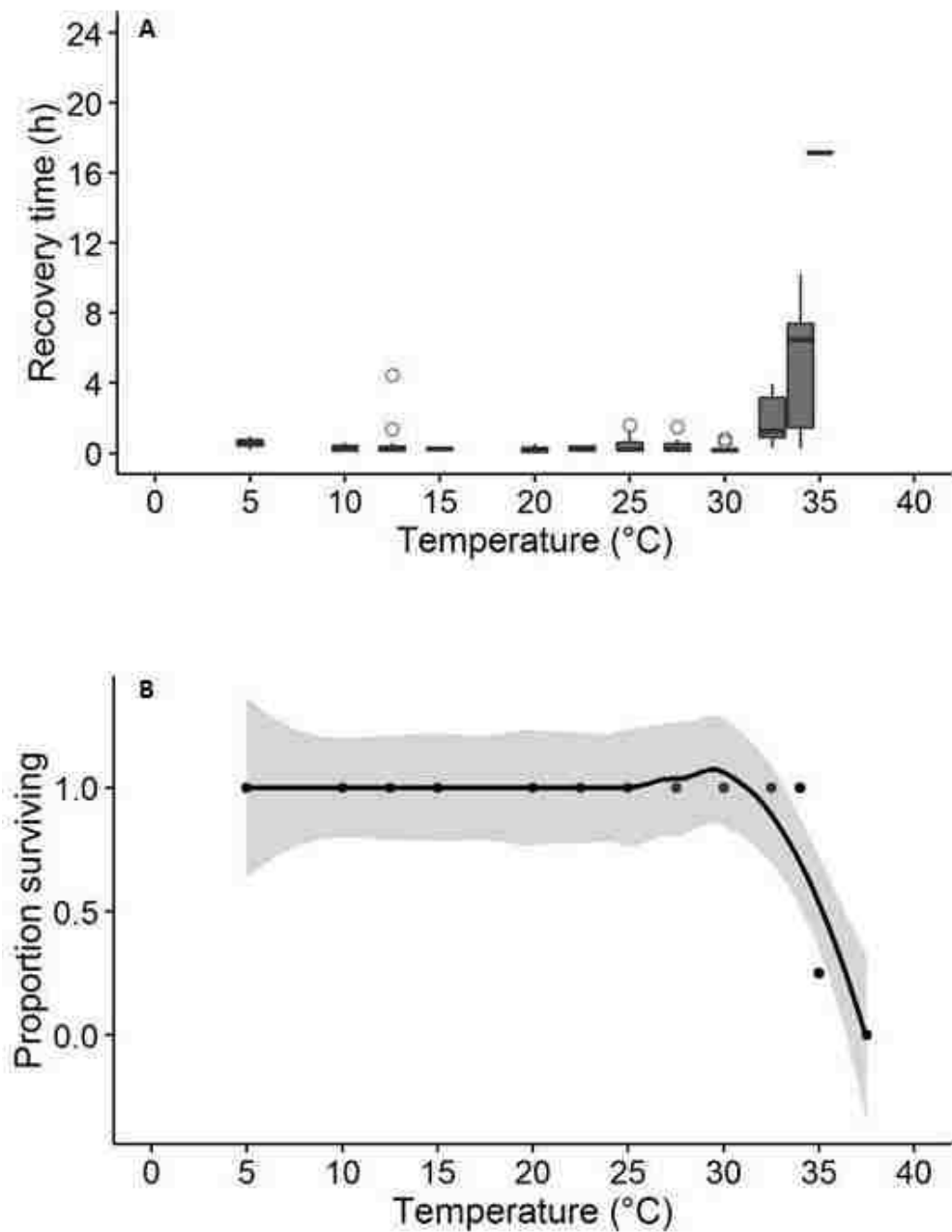


Figure 3.3 Recovery of *Nucella ostrina* when submerged in seawater following experimental exposure to simulated low tide

(A) Duration of time between submergence and recovery, defined as righting and reattaching to substrate. Box extends from 25% to 75% percentile with median (black bar), 95% confidence interval (whiskers), and outliers (circles) indicated. Only one individual recovered in treatment of

35°C, so only this value is represented. **(B)** Proportion of individuals that survived and resumed crawling within 48 hours. Curve depicts locally weighted regression and 95% confidence interval of the curve (shaded area). $N = 12$ for each treatment.

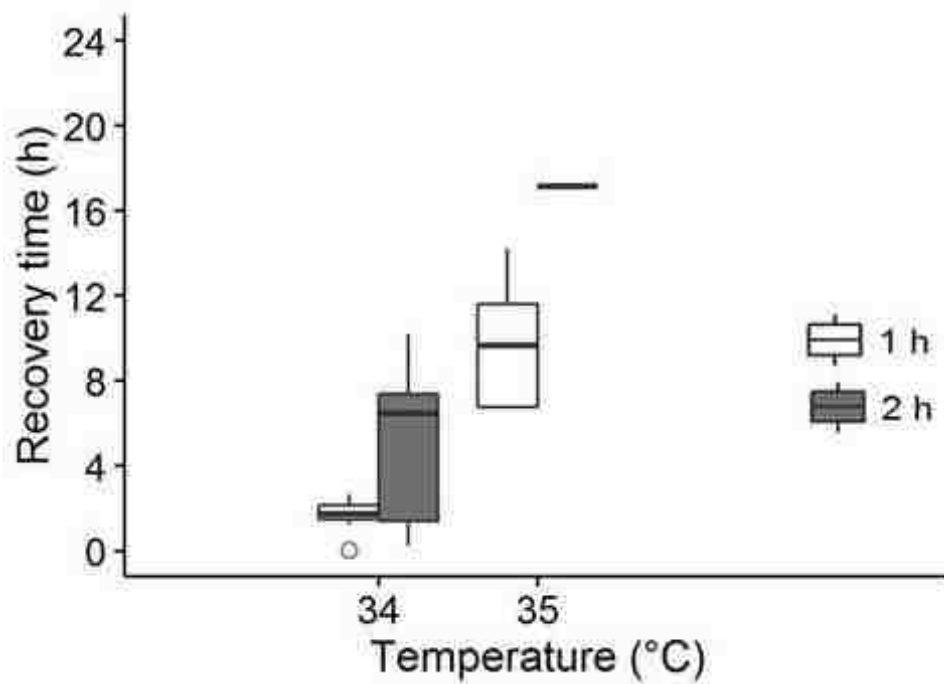


Figure 3.4 Comparison of recovery time for *Nucella ostrina* to right and reattach to substrate after different durations of simulated low tide, 1 h (white) and 2 h (gray)

Box extends from 25% to 75% percentile with median (black bar), 95% confidence interval (whiskers), and outliers (circles) indicated. Only one individual recovered in 2 h treatment at 35°C, so only this value is represented. Recovery was much faster after 1 h exposure than after 2 h and faster at 34°C than at 35°C in both exposure treatments.

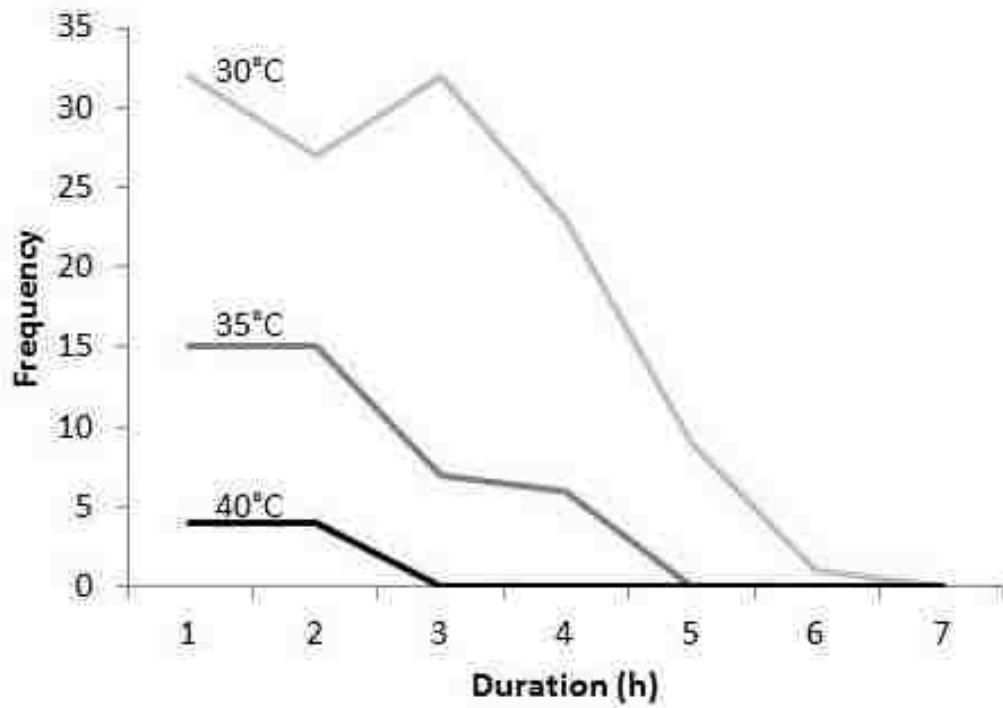


Figure 3.5 Frequency and duration of high temperature events in this high intertidal habitat, calculated from thermal mimic temperatures

Duration of events at or above 30°C (light gray), 35°C (dark gray), and 40°C (black), pooled from spring and summer of 2014 and 2015.

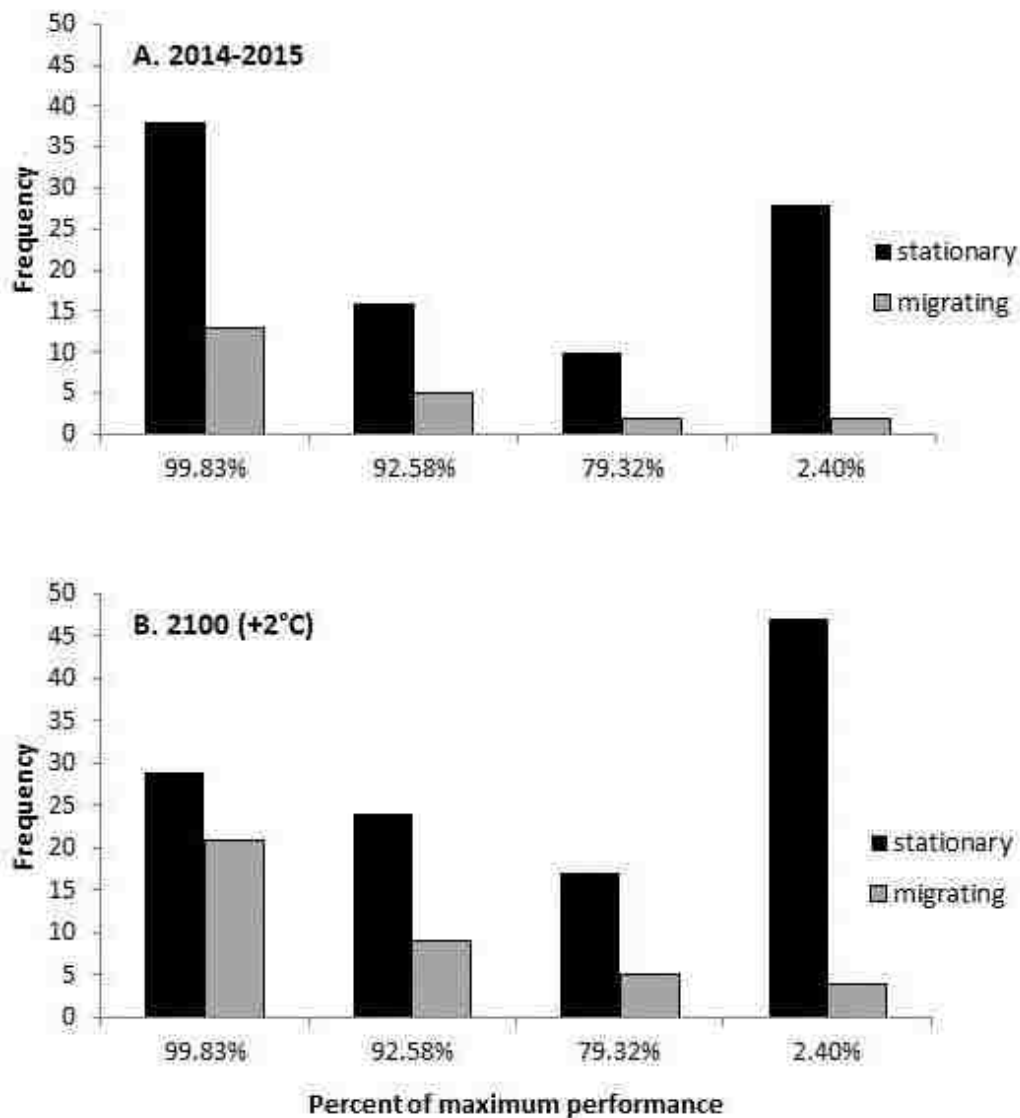


Figure 3.6 Effect of frequency of high temperature events on snail performance

Frequency of performance level based on the righting experiment and distribution of high temperature ($\geq 30^{\circ}\text{C}$) events for durations of 2 h or longer. **(A)** Based on thermal mimic temperatures from spring and summer of 2014 and 2015. **(B)** Based on thermal mimic temperatures with a 2°C increase as predicted by climate change for the year 2100. Note that a predicted 2°C temperature increase yields a much larger frequency of lethal or near-lethal (2.40% performance) events. Modeled snail behavior keeps these events close to today's frequency.

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APPENDIX A: SUPPLEMENTARY MATERIAL FOR CHAPTER 1

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Foraging behavior minimizes heat exposure in a complex thermal landscape

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Supplementary materials



Fig. S1. Overview of experimental plots in the rocky intertidal zone. Artificial islands aligned at +0.95 m tidal elevation above mean lower low water (MLLW), on south-facing beach on San Juan Island, WA. View is looking west and offshore. East and west faces of each cinder block have a temperature logger (t) and transplanted snail bait (b). Snails roam freely on each island, deterred from leaving by the wire mesh cage



Fig. S2. Overhead view from south of one plot. Cinder block is aligned north–south on island so that long surfaces face east and west. Mesh cage is to deter movement of snails out of plot



Fig. S3. Side view from east of one plot. Cobble spacers (c) provide shaded crack refuge (r) approximately 25 mm in height beneath cinder block



Fig. S4. *Nucella ostrina* foraging on barnacle bait, *Balanus glandula*, transplanted on *Mytilus trossulus* shell, in an experimental plot

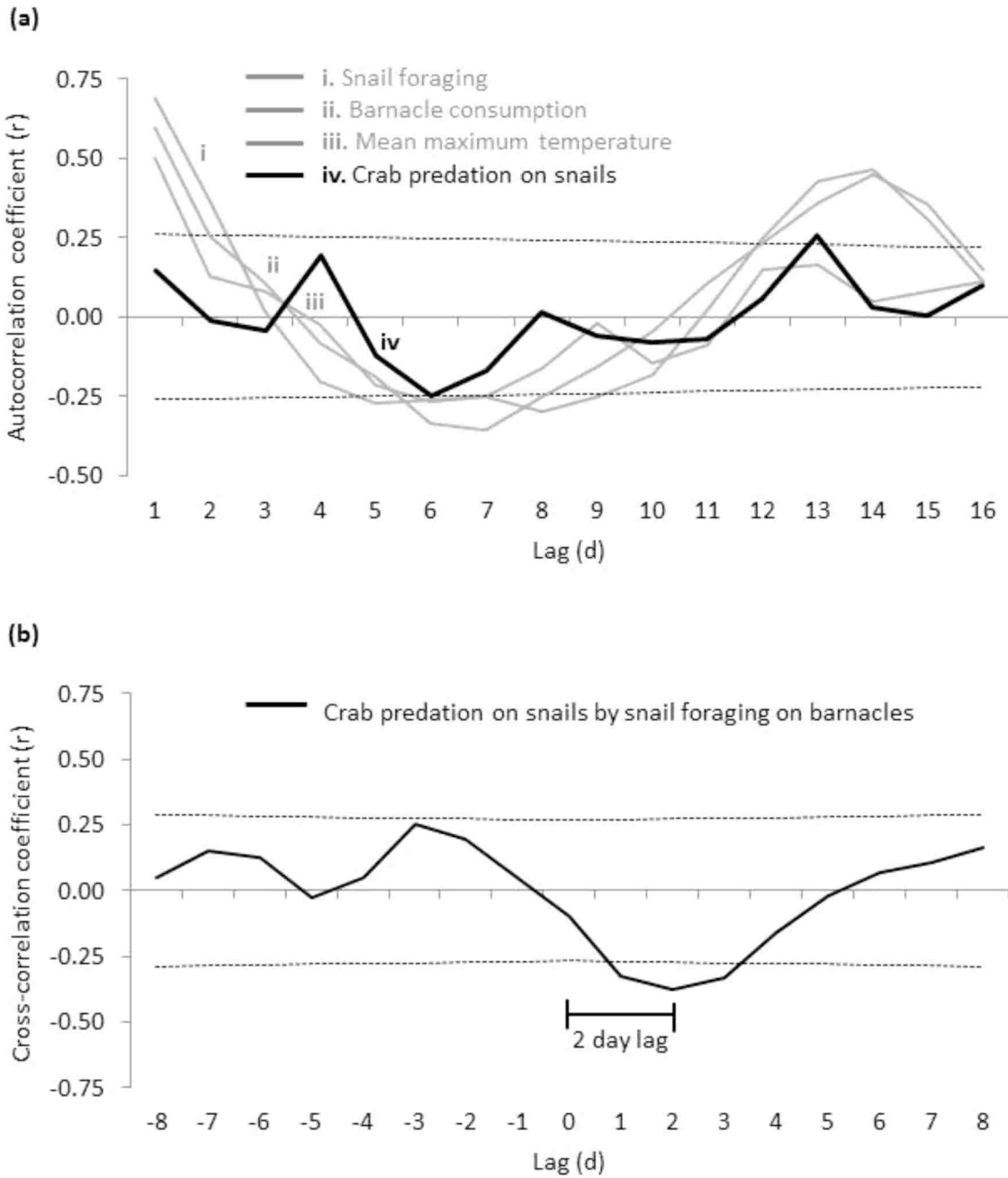


Fig. S5. Time series analyses of crab predation on snails. Correlation coefficient (r) versus lag number (d). Thin dotted lines mark 95% confidence interval for all correlations. (a) Autocorrelation coefficient of newly empty snail shells (crab predation) found per day (iv) superimposed over Fig. 4, autocorrelation of (i) proportion of *Nucella ostrina* foraging, (ii) *Balanus glandula* consumed per snail, and (iii) mean daily maximum temperature. Significant negative correlation of deaths seen at 6 d and positive correlation at 13 d. Note that crab predation trends towards matching the pattern of other tidally correlated metrics. (b) Cross-correlation coefficients of number of newly dead snails by proportion of *N. ostrina* foraging, showing that snail deaths and snail foraging are not occurring at the same time, but offset from one another by an average 2 d lag

Table S1. Summary of substrate temperature and snail foraging by tidal cycle. Temperature: Mean daily maximum temperature for eastern and western faces during spring, neap, and transition phases. The p-value is from a paired *t*-test of west versus east. Foraging: Mean proportion of all snails in experiment that foraged during given tidal phase and mean proportion of foraging snails present on the western or eastern face. Different superscript letters indicate that groups are significantly different at $\alpha = 0.05$ level (1-way ANOVA, Tukey's HSD). Note high levels of foraging occurring during neap and spring-to-neap transitions, and almost no foraging during other tidal phases. The p-value is from a paired *t*-test of west versus east. There is no net difference in maximum daily temperature or mean proportion foraging between the block faces. Unlike the mechanistic predictor of relative minutes of low tide in the morning versus the afternoon, categorical tidal phase is not an adequate predictor of foraging location; however, tidal phase does predict surface of maximum temperature. Despite lack of significant preference, note trend towards increased foraging on western face when temperature difference is maximized ($\Delta T = 8.4^\circ\text{C}$). For all, $N = 4$ lunar tidal cycles; $df = 3$

	Temperature ($^\circ\text{C}$)				Foraging			
	Mean daily max (SEM)				Mean proportion of total (SEM)	Mean proportion of foragers (SEM)		
	west	east	ΔT	p	whole plot	west	east	p
All phases	25.1 (1.67)	26.4 (0.75)	1.3	0.255	1.00	0.58 (0.04)	0.42 (0.04)	0.506
Spring	32.6 (2.01)	30.8 (1.54)	1.8	0.224	0.06 (0.05) ^a	0.58 (0.06)	0.42 (0.06)	0.330
Spring-to-neap	30.4 (3.64)	25.6 (2.26)	4.8	0.041	0.42 (0.21) ^b	0.49 (0.07)	0.51 (0.07)	0.478
Neap	14.6 (0.96)	18.2 (1.28)	3.7	0.004	0.43 (0.09) ^b	0.53 (0.06)	0.47 (0.06)	0.366
Neap-to-spring	22.8 (1.46)	31.1 (1.00)	8.3	0.009	0.09 (0.04) ^a	0.72 (0.14)	0.28 (0.14)	0.171

APPENDIX B: SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Additional methods

Waterproofing antenna tuner boards

Female waterproof mini-buccaneer connectors (Bulgin, Cambridge, England, UK) were soldered to tuner boards, providing a water-tight connection to sealed electronic components. Tuner boards were potted in electronics resin (Sealtronic 21AC, System Three, Auburn, Washington, USA) with female connectors protruding from resin to enable future connection to antenna and to logger.

Detection validation

Each antenna is capable of detecting only one tag signal at a time. Whereas in many applications the organism, such as a salmon, passes through the antenna read range within a matter of seconds, slow-moving benthic snails may spend several consecutive hours within read range of the antenna, essentially jamming the system. Limiting the density of tagged organisms in a given location therefore reduces the likelihood of interference between tags and of missing a detection due to presence of another organism.

Antennas were mounted in an aquarium tank with artificial tidal cycles matching those of the ambient natural tides. High tide was a full aquarium whereas low tide was created by draining to a short standpipe that stood approximately 5 cm above the bottom of the aquarium. Eight radio-tagged *Nucella ostrina* were observed by time lapse photography (Garden Watch Cam, Corp., City, State) at 3 min intervals. Different combinations of brightly colored plastic fragments (3 mm x 5 mm) were epoxied to the outside of each radio tag affixed to each snail shell to enable

visual identification. Visual crossings of antenna were compared to logged crossings for each tag.



Figure B.1 Photo of antenna components mounted to rocky intertidal shoreline

Wire loop antennas were mounted in each of two high shore tidal areas. Antennas were powered by adjacent tuners. Antenna tuners were secured to the rock using strips of Vexar® mesh bolted into rock with stainless steel hex nuts. Shielded wire connected antenna tuners to a data logger.

(See Fig. 2 in main text for schematic.)

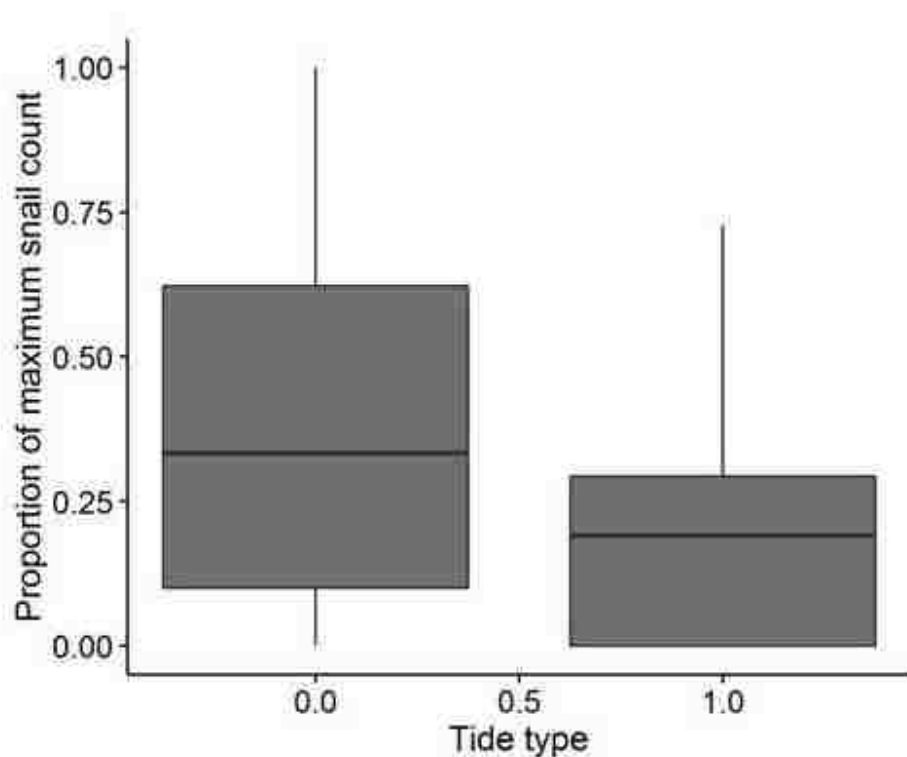
APPENDIX C: SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Supplementary Table C.1 Snail foraging behavior studies incorporated into conceptual model of snail presence varying with duration of midday aerial exposure

All five studies found a periodic snail foraging migration that correlated to the two-week tidal cycle; snails were absent from high shore foraging areas on days of the tidal cycle when midday low tides were of long duration. Based on the integrated finding of these studies, our model used shortest midday low tide duration to determine 7 d of each two-week tidal cycle when snails would be present in exposed foraging areas. The remaining 7 d they were modeled as in thermal refuges. Studies were conducted in both the laboratory and the field and lasted from 2-8 wk (one to four, two-week tidal cycles). Mesocosm studies were conducted in manipulated cages or aquaria that simulated snail habitats, whereas surveys tracked un-caged organisms in natural habitats. Experimental manipulations included location of food, timing of the simulated tidal cycle, or attachment of radio tags to the shell of the snail. See reference for data.

Date	Duration (wk)	Location Type		Manipulation	Reference
July-August 2010	5	field	mesocosm	food location	unpublished data (see Appendix C, Fig. C.2)
July-September 2011	8	field	mesocosm	food location	Hayford et al. 2015 <i>Marine Ecology Progress Series</i>
August 2012	2	field	survey	none	Hayford unpublished manuscript (see Chapter 2)
August-September 2012	8	lab	mesocosm	tidal cycling	unpublished data (see Appendix C, Fig. C.3)
August-September 2013	7	field	survey	radio tracking	Hayford unpublished manuscript (see Chapter 2)

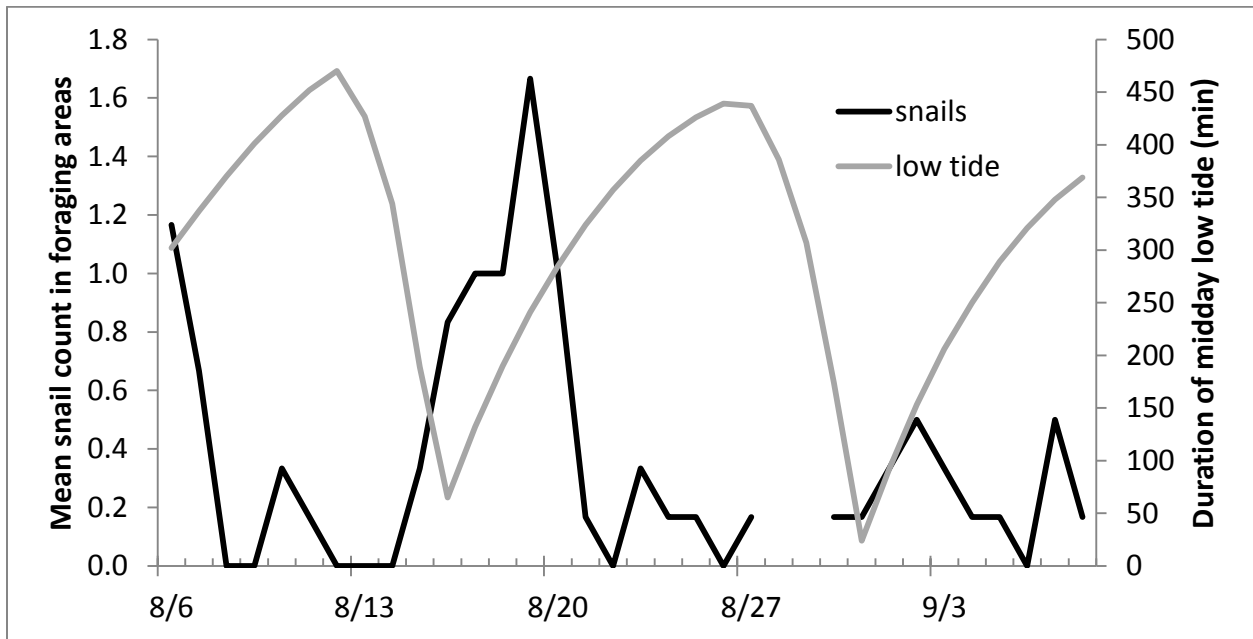
Supplementary Fig. A



Supplementary Figure C.1 Synthesis of previous snail foraging behavior studies for conceptual model

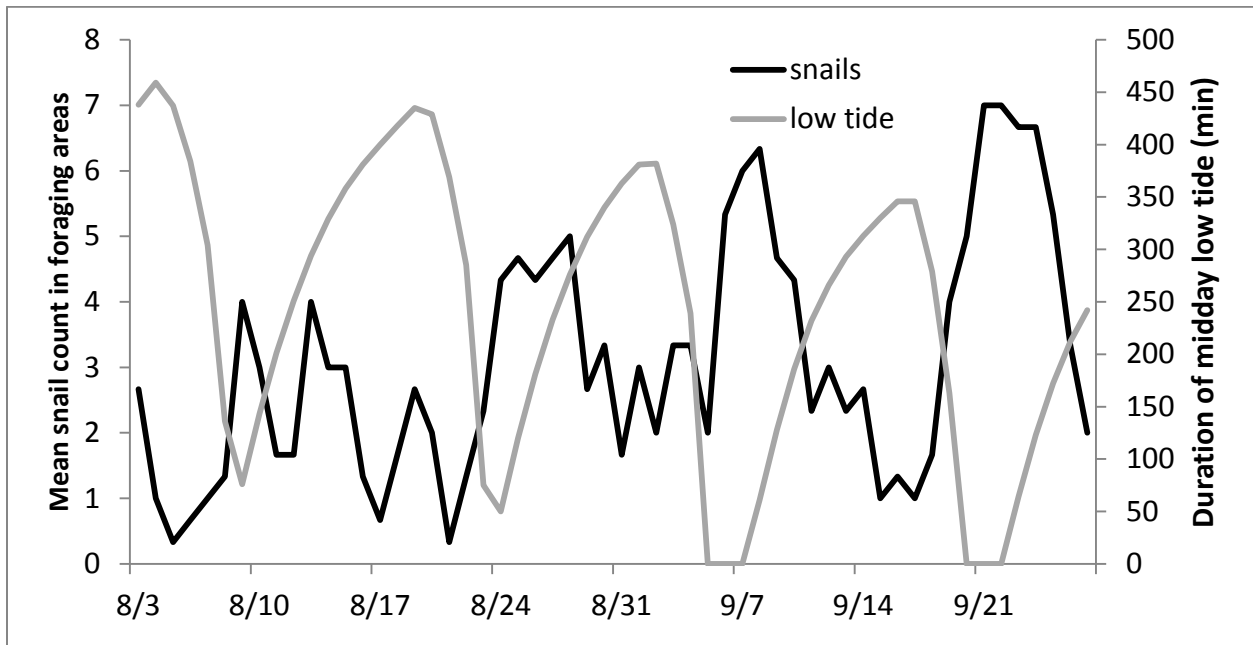
Proportion of the maximum snail count found in aerially exposed and/or high shore foraging areas on a given day as a function of tide type for that day. Tide type 0 represents the 7 d of a two-week tidal cycle with the shortest duration of midday low tide (within 4 h of noon) exposure to air. Tide type 1 represents the 7 d with the longest duration of midday low tide exposure.

Snails forage in exposed locations more frequently on days without long daytime aerial exposure. Behavior data are taken from five separate studies conducted 2010-2013. Proportion of maximum snail count for each study is used to standardize data from several different experimental designs.



Supplementary Figure C.2 Mean snail count in foraging areas in 4 wk field mesocosm experiment

Daily mean count of snails in foraging areas averaged across six replicate plots in the intertidal (black line) and daily duration of midday low tide within 4 h of noon (gray line), throughout 4 wk in late summer of 2010. Note that snail counts increase when the midday low tide duration decreases.



Supplementary Figure C.3 Mean snail count in foraging areas in 8 wk aquarium mesocosm experiment

Daily mean count of snails in foraging areas averaged across three replicate outdoor aquaria (black line) and daily duration of midday low tide within 4 h of noon (gray line), throughout 8 wk in summer of 2012. Note that snail counts increase when the simulated midday low tide duration decreases.

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