Effect of increased aerial temperature on sex specific foraging behavior in *Nucella ostrina*

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Global climate change impacts, including increasing frequency of extreme climatic events and elevated aerial and aquatic temperatures, are predicted to substantially affect organisms, ecosystems, and ecological communities. Species interactions' are fundamental drivers of ecosystem and community dynamics. Comprehensive climate change assessments demand consideration of both the role of species' interactions in communities, and modulation of body temperature and thus thermal stress impacts via organism morphology and mobility. Sharp environmental stress gradients and a gradient of emersion time make the rocky intertidal a model system for studying the effects of climate change on communities. In this study we manipulated low-tide aerial temperature to test the predicted effects of climate change on the interactions between a motile predator, the gastropod *Nucella ostrina,* and its sessile prey, the barnacle *Balanus glandula*. *Nucella ostrina*, exhibits periodicity in foraging on *Balanus glandula*, with maximum foraging occurring during periods of nighttime exposure. Subjecting *Nucella* to chronic and acute aerial temperature manipulations did not alter the timing or magnitude of a previously documented foraging bout, though asynchrony in the feeding of males and females was observed. Movement of *Nucella* away from food during low tide exceeded initiation of feeding independent of aerial temperature, suggesting behavioral refuge. Sex specific trends in movement may be the effect of different energetic costs for production of eggs and sperm. These results suggest thermal stress affects male and female *Nucella* differently, but does not disrupt the tide-specific timing of foraging bouts.

KEY WORDS: *Nucella ostrina*, *Balanus glandula*, species' interactions, rocky intertidal, zonation, foraging behavior, aerial temperature, ecosystem, periodicity

Introduction

Global climate change is predicted to appreciably impact many ecosystems. Predictions range from increased atmospheric carbon dioxide (CO_2) to elevated aerial and aquatic temperatures (Intergovernmental Panel on Climate Change 2001). Ecosystems are built upon several levels of organization, ranging from organisms to populations. Various interactions mediate ecosystem dynamics including competition, commensalism, mutualism, and predation, all of which are both key for ecosystem function and vulnerable to climate change. For example, decreased integrity of larval shells of the mussel *Mytilus californianus* under climate change scenario based elevated CO_2 conditions, suggests increased vulnerability of settled juveniles to predation by crushing and drilling predators (Gaylord *et al*. 2011). Correct predictions of climate impacts demand both an understanding of physical changes, and how these abiotic fluctuations alter the complex biological organizations driving ecosystems.

Temperature is a physical stressor ecologically relevant to marine organisms across multiple scales—from variability within one tidal cycle, to seasonal and latitudinal temperature variation. A mixed semidiurnal tidal regime is characteristic of the Pacific Northwest and consists of two high and two low tides of unequal amplitude within one tidal cycle (Hickey and Banas 2003). Previous experiments have used an unrealistic tidal cycle (Yee and Murray 2004), ignoring the potential importance of tides on foraging behavior and physiology. Though both water temperature and local climate play a role in influencing the patterns of heat stress during aerial exposure (Sanford 1999), region-specific variation in the timing and duration of low tides is a chief factor in driving variability in these patterns (Helmuth *et al*, 2002, Yamane and Gilman 2009). In particular, a twice monthly diminishing and increasing tidal range, neap and spring tides respectively, explain varying aerial exposure on a latitudinal gradient. Spring tides, when the lowest low tidal heights take place, happen midday in the northernmost latitudes along the Pacific coast, but at night at southernmost latitudes during spring and summer months. Specifically, in the Pacific Northwest from March to September spring tides occur midday when aerial temperature can be as much as 30°C above water temperatures, while from September to March when aerial temperatures are lower, exposure occurs during mid-night. Thus intertidal organisms along the Pacific Northwest coast are likely to be subjected to climate-dependent aerial thermal stress (Helmuth *et al*. 2002).

The rocky intertidal is characterized by steep environmental gradients; organisms inhabiting this land-sea interface are often living close to their thermal tolerance. The upper limits of organisms on rocky shores are regulated by temperature, while competition determines the lower limits of intertidal biota (Connell 1970, Helmuth and Hofmann 2001, Somero 2002). Sharp environmental stress gradients make the intertidal an ideal system for investigating the sensitivity of organisms and communities to climate change. Thermal stress has a wide variety of impacts on intertidal organisms, including effects on abundance, distribution, zonation, and performance (Helmuth *et al*. 2005, Parmesan 2006). Zonation, a vertical gradient of emersion time, is responsible for both aquatic and terrestrial habitats located within meters of one another (Harley and Helmuth 2003). Physical conditions are closely associated with distribution within the intertidal, and thus when faced with abiotic stress organisms to which they cannot adapt are forced to shift their ranges (Harley *et al*. 2006).

Physiological responses of organisms to predicted increases in global temperature have been a focus of previous studies, however there is less empirical data on possible indirect consequences of climate change for communities. Both organism physiological response, and how this response influences species interactions are chief factors when determining the impacts of climate change on communities (Harley *et al*. 2006). Abiotic stress, anthropogenic or natural, has a differential effect on individual organisms, thus interaction strength amongst species will be altered by climate change. Prediction and mediation of future impacts of climate change on ecosystems must evaluate organism to community level impacts. As we move towards increased understanding of how global climate change impacts ecosystems, we must recognize the importance of species' interactions in modulating organism range, fitness, and community structure (Gilman *et al*. 2010).

Organismal responses to environmental change range from behavioral to physiological, and are often interconnected. Temperature, which is predicted to increase under climate change models, plays a critical role in driving predator and prey behavior (Burnaford 2004). However, the impact of elevated temperature on foraging behavior, consumption rates, and predator-prey interactions is an area less studied, and studies present differing results (Sanford 1999, Pincebourde *et al*. 2008). Determining the effects of climate on predator and prey body temperature, and foraging activities of predators is necessary. Previous studies have correlated environmental variables to organism response or performance, using habitat temperature as a loose measure of body temperature (Burrows & Hughes 1989). However, recent studies have shown the importance of linking body temperature, not solely environmental temperature, to predator performance and physiological rate processes (Gilman et al. 2006, Helmuth 1998, Denny and Harley 2006).

Two intertidal organisms that are prominent along the Pacific Northwest coastline are: *Nucella ostrina*, an intertidal predatory whelk and its primary prey source, the sessile, suspension-feeding barnacle *Balanus glandula.* Located within the mid-intertidal, these organisms are subject to higher levels of environmental stress than conspecifics with lower ranges (Dahlhoff *et al*. 2001). *Nucella ostrina* are fundamental in regulating the distribution and abundance of their barnacle prey (Connell 1970). Previous studies have linked *Nucella* foraging behavior with weather and the tidal cycle (Hughes *et al*. 1992, Palmer 2000), finding that during hot periods of aerial exposure foraging is reduced (Burrows and Hughes 1989, Dahlhoff *et al*. 2001, Yamane and Gilman 2009). A previous experiment (Carrington *et al*., unpubl) documented a 2-week pattern in foraging behavior that correlated with the spring and neap tides. This pattern included a 3-day bout of increased foraging activity following the transition from spring to neap tides, a period during the cycle where temperatures are reliably cooler due to nighttime aerial exposure, accompanied by decreased exposure times—a strategic interlude to investigate recurring acute temperature stress. These previous study suggest the importance and possible interacting effects of increased aerial temperature and exposure, and tides on the interactions between *N. ostrina* and *B. glandula.*

In this study we investigated the effect of increased aerial temperatures on the foraging behavior of the intertidal gastropod *Nucella ostrina*. The snail *N. ostrina*, and their prey *Balanus glandula* were maintained within a controlled tidal mesocosm system. Groups of snails of opposite sex were placed together in separate cages located in larger experimental tanks within the system. Three treatments manipulated aerial temperature on different scales of temperature variability. These treatments, which included a chronic high temperature, acute high temperature, and a low temperature (control) treatment, allowed us to specifically address key predictions of climate change including the effects of increased aerial temperature (chronic treatment) and an increase in the frequency and intensity of extreme climatic events such as heat waves (Jentsch *et al*. 2007) (acute treatment) on organisms. For our acute treatment we chose to briefly but sharply increase aerial temperature at a previously observed three-day period of feeding during the neap tide cycle (Carrington *et al*., unpubl). We hypothesized that chronic or acute elevated aerial temperature would result in 1) increased foraging activity as the snails attempt to keep up with the greater metabolic demand associated with increased body temperature or 2) decreased foraging activity as a means to avoid thermal stress or 3) no change in foraging activity. Snails experiencing chronically high temperature may have time to adjust to higher temperatures, while acute stress may be more disruptive to foraging behavior in the long run. In addition, for the acute treatment, in which snails were exposed to short bursts of elevated aerial temperature during the first few days of neap tide, we hypothesized that snails would alter their 2-week pattern in foraging behavior to feed during a different period in the tidal cycle. Lastly, we hypothesized that thermal stress affects males and females. Possible differences between the sexes could be related to female and male reproductive physiology with different energetic requirements for the production of eggs and sperm.

Materials and Methods

Organism collection, preparation, and storage

This experiment was executed at University of Washington's Friday Harbor Laboratories (FHL), located on San Juan Island, Washington. *Nucella ostrina*, formerly included in *N. emarginata* (Marko *et al*. 2003), were collected from Deadman Bay (48-30'44" N, 123-08'43" W). Barnacles, *Balanus glandula,* were collected on mussel shells, *Mytilus trossulus*, from the pier at Argyle Lagoon (48° 31'N, 123° 01' W), an FHL-managed reserve on the island. In order to minimize the effect of predator or prey size on our measured responses, *Nucella ostrina* and *Balanus glandula* were selected from a narrow size range. *B. glandula* were between 2-4 mm in opercular diameter, within the preferred prey size for *N. ostrina*. To maximize the growth rate of *N. ostrina* we chose individual whelks whose shells measured between18-20 mm in length (measured along the longest axis, from the tip of the spire to the base *sensu* Palmer 1983).

Dead *B. glandula* and those outside our selected size range were removed from the mussel shells. The mussels were then shucked to separate the valves and the barnacle covered valves were adhered to circular thin Plexiglas discs (7 cm diameter). One or two valves were attached with cyanoacrylate glue to each disc strategically to attain a standardized total number of barnacles per disc between 50 and 60. Each disc was replaced approximately every 10 days so that food was available *ad libitum* to the predatory snails.

N. ostrina were sexed based on a technique conveyed in a personal communication with A. R. Palmer. The sex of each adult *Nucella ostrina* was determined by submerging individual snails in filtered seawater in a small tray aperture side up. In an attempt to right itself a snail extends it's foot during which time the penis (if present) is visible just behind the right tentacle (Figure 3). Both males and females can develop a penis, however if the penis is longer than the right tentacle, it is a male (A. R. Palmer, *pers. comm.*, Hargis 1957). Immediately upon determining the sex of an individual snail we attached a small numbered tag with cyanoacrylate glue. The unique tags allowed us to monitor the foraging behavior of individual snails.

Both *N. ostrina* and *B. glandula* were maintained in a flow-through seawater system at Friday Harbor Laboratories prior to use in the experiment. *N. ostrina* were kept in the lab for 7 days prior to assignment to one of the treatments, and B. glandula were collected weekly. The experiment took place for 25 days (from July 11, 2011 to August 5, 2011).

Tank setup

The experiments were conducted in an outdoor tidal mesocosm, consisting of 7 identical 120 x 60 cm clear acrylic tanks, each simulating the local tidal regime. Tidal submersion and emersion times were based on the summer tidal cycle experienced by *Nucella ostrina* on San Juan Island (WWW Tide and Current Predictor). Each tank held three experimental cages (PetKeeper Acrylic Tanks, 11 ¾ x 7 ¾ x 8", PETCO), one for each of the three thermal treatments. Cage positions within each tidal tank were randomized at the start of the experiment. At high tide, seawater was continuously flowing between the treatment cages and within each experimental tank (Figures 1, 2). At low tide, water flow was restricted between treatment cages, though low seawater flow was maintained within each individual cage. Each cage included a separate water inflow and the flow of incoming seawater was kept constant throughout the experiments so that water flowed across the bottom of each cage even during low tide periods.

Two of the walls of the cages were cut (10 ½ x 25 ½ cm) and covered with fine window mesh and functioned as separate drains in each cage to prevent exchange of heated water from one cage to another. Gravel was collected along with the *Nucella* at Deadman Bay, and rinsed with freshwater to remove organic materials. This gravel was placed in each cage, reaching to approximately the lower lip of each mesh-covered window. Terra cotta pots (4.5” dia., 6” height) were placed upside down on top of an inverted terracotta drip plate. The Plexiglas discs with mussel shells covered in *B. glandula* were attached with hot melt glue to the bottom of each terra cotta pot, and individual temperature probes were attached to each pot so that the probe was level with the plastic disc with the barnacle prey. The placement of the temperature probe directly next to the barnacle prey allowed us to measure and manipulate air temperature experienced by a foraging snail. Refuge areas for the whelks consisted of ~2 inch lengths of ¾ inch PCV pipe pieces of ~6 cm length, adhered directly above the substrate to the two ends of each cage. A woven steel lid covered each cage.

Temperature treatments

The tanks were programmed to simulate the local tidal regime. Tides were produced manually for the first two days, and electronically programmed for the rest of the experiment. Temperature was controlled via heat lamps (100 Watt Nocturnal Infrared Heat Lamps, Zoo Med Laboratories) mounted over each individual cage, and controlled by temperature probes with an accuracy of ±5 °F (True Temp Digital Heat Controller). The lamps emitted a small amount of red light, a wavelength which marine snails are unable to visualize (Cronin 1986).

We manipulated aerial temperature only during exposure at low tide. Each tank contained six *N.ostrina*, three males and three females. The snails were exposed to one of three temperature treatments: chronic, acute and low. In the chronic treatment the aerial temperature was increased from 20°C by 2°C over four days to a maximum of 28°C. In the acute thermal treatment, aerial temperature was raised from 20 °C to 28°C and returned to 20°C within a three-day period. Lastly, in a low thermal treatment aerial temperature was maintained at 20 °C throughout the experiment. Though *N. ostrina* normally experience mid-day low tides only during spring tides, we chose to aerially stress the snails during all low tides (i.e., during both spring and neap tides) in order to best test the rigidity of a two-week cycle in foraging behavior (*sensu* Carrington et al., unpublished data) under acute temperature stress.

Data collection and analysis

For each individual snail initial measurements were taken of shell length and width, as well as shell, tissue, and an estimated body weight (buoyant weight (shell weight) – damp weight (shell weight + tissue weight)). Shell length and width were measured using digital calipers (Neiko Stainless Steel Digital Caliper), and were accurate to 0.01 mm. These morphological measures were used to determine any pre-experiment differences in the size of male and female snails. Foraging activity, egg capsule production, and survival were monitored three times daily; at the beginning, middle and end of each low tide. Snail locations were recorded as either: feeding, on barnacle platform but not feeding, tank bottom, tank wall, tank wall above high tide line, or not visible. For most statistical analyses, snails were simply grouped as feeding or not feeding. Egg capsules were removed daily, when present, and numbers recorded.

Analyses were performed in JMP 8 (SAS Institute), Sigma Stat (Jandel Scientific, San Rafael, CA) and Excel. Changes in the percent of foraging snails in each treatment were compared using repeated measures multivariate analysis of variance (MANOVA) (JMP, ver. 8.0) with treatment (low, acute and chronic) and sex (male or female) as the main effects and time (days) as the repeated measure. One-way analysis of variance (ANOVA) calculated differences among treatments in barnacle consumption. Student t-tests compared differences in mean percent foraging of males and females in each treatment.

Results

Temperature, sex, and *Nucella ostrina* foraging behavior

Temperature did not affect *Nucella ostrina* foraging behavior. Aerial temperature differences in acute, chronic, and low temperature treatments had no significant effects on previous observed periodicity in *Nucella* foraging (p =0.32, Figure 4).

Sex significantly affected foraging behavior in the acute temperature treatment (p = 0.008, Figure 5) however no significant affect of sex was found in the chronic treatment (p = 0.43, Figure 6) or the low treatment (p = 0.72, Figure 7). When considering all treatments, the affect of temperature treatments over time was marginally significant (p =0.058).

Barnacle consumption

There were no significant differences in barnacle consumption by *Nucella* during week one of the study across the acute, chronic, and low temperature treatments (p=0.85). In week two there were also no significant differences in barnacle consumption among the three treatments (p=0.65).

Nucella low tide behavior

Movement was observed during low tide in 30% of the 334 snails observed feeding during this period. Across acute, chronic, and low temperature treatments movement off of the feeding platform dominated (Figure 8). Both males and females tended to move off, rather than move onto the foraging platforms, however there was no significant differences among movement in males and females (p=0.23, Figure 9). However, males were more likely to move off of the foraging platform than were females, and females were more likely to move onto the platform than males (Figure 9).

Discussion

No effect of temperature treatments, independently or collectively, in modifying behavior of *Nucella ostrina* was one of the outcomes we hypothesized. Many factors could be responsible for driving periodicity in Nucella foraging behavior, and leading to bouts of foraging occurring during the neap tidal cycles characterized by nighttime aerial exposure, and thus reliably cool conditions in the Pacific Northwest. Nucella may be cueing into one or more of many variables present within their specific microhabitats in the mid-intertidal. Potential variables these whelks could be cueing into include: visible predation, light, or changes in water pressure corresponding with daily or weekly periodicity in the rising and falling of the water. Alternately, changes in biotic composition of the water column may change with incoming or outgoing tidal cycle, and be cuing foraging. Current trends indicate feeding is picking up suggesting neap tide will herald another foraging bout. However, this experiment is to be continued for an additional neap and spring tidal cycle, during which the timing, magnitude, or duration of the feeding bout may change.

Our hypothesis that male and female foraging behavior is differentially affected by thermal stress is supported in our acute treatment, but not as evident at chronic and low temperatures. In all treatments, however, synchronicity in Nucella foraging among males and females was not present. This asynchronicity in male and female foraging behavior was most pronounced in the acute treatment, and drove the marginal significance across all treatments. Over time, males and females in all treatments seem to be synchronizing their foraging behavior, possibly as a result of behavioral aggregation amongst conspecifics. Should synchronicity in foraging be evident, treatment effects may become apparent.

Barnacle consumption did not prove to be an indicator of trends in foraging among different treatments that our behavioral data could have missed

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References

Burnaford JL. (2004). "Habitat modification and refuge from sublethal stress drive a marine plant-herbivore association". Ecology 85:2837–49

Burrows, M.T., Hughes, R.N. (1989). "Natural foraging of the dogwhelk, *Nucella lapillus* (Linnaeus): the weather and whether to feed". Journal of Molluscan Studies 55:285–295

Connell, J. H. (1970). "A predator-prey system in the marine intertidal region I. Balanus glandula and several predatory species of Thais." Ecological Monographs 40(1): 49-78

Cronin, T. W (1986)."Photoreception in marine invertebrates." American Zoologist. 26: 403-415

Dahlhoff, E. P., B. A. Buckley, and B. A. Menge. (2001). "Physiology of the rocky intertidal predator Nucella ostrina along an environmental stress gradient". Ecology, 822816-2829

Denny, M. W. and Harley, C. D. G. (2006). "Hot limpets: predicting body temperature in a conductance-mediated thermal system". Journal of Experimental Biology 209,2409 -2419

Dethier MN, Williams SL, Freeman A (2005). "Seaweeds under stress: manipulated stress and herbivory affect critical life-history functions." Ecological Monographs 75:403–418

Gaylord, B., Hill, T. M., Sanford, E., Lenz, E. A., Jacobs, L. A., Sato, K. N., Russell, A. D. and Hettinger, A. (2011). "Functional impacts of ocean acidification in an ecologically critical foundation species". Journal of Experimental Biology. 214, 2586-2594

Gilman S.E., Urban M.C., Tewksbury J., Gilchrist G.W. & Holt R.D. (2010).“A framework for community interactions under climate change”. Trends in Ecology and Evolution, 25:325–331.

Gilman S.E., Wethey D.S., Helmuth, B. (2006). “Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales”. Proceedings of the National Academy of Science USA 103:9560–9565

Harley, C.D.G., Helmuth, B.S.T. (2003). “Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation”. Limnology and Oceanography, 48, 1498–1508

Harley, C. D. G., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L.F. Rodriguez, L. Tomanek and S. L. Williams. (2006). “The impacts of climate change in costal marine systems”. Ecology Letters 9: 228-241

Helmuth, B.S.T. (1998) “Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate”. Ecological Monographs 68:51–74

Helmuth, B., E. Carrington, et al. (2005). "Biophysics, physiological ecology, and climate change: does mechanism matter?" Annual Review of Physiology 67: 177-201.

Helmuth, B. S. T. and G. E. Hofmann. 2001. “Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone”. Biological Bulletin 201(3): 374-384.

Helmuth, B., Harley, C.D.G., Halpin, P.M., O’Donnell, M., Hofmann, G.E. & Blanchette, C.A. (2002). “Climate change and latitudinal patterns of intertidal thermal stress”. Science, 298, 1015–1017

Hickey, B.M., Banas, N.S., 2003. “Oceanography of the Pacific Northwest coastal ocean and estuaries with application to coastal ecosystems”. Estuaries 26 (48), 1010–1031.

Hughes R.N., Burrows M.T., Rogers S.E.B. (1992). “Ontogenic changes in foraging behaviour of the dogwhelk Nucella lapillus (L.)”. Journal of Experimental Marine Biology and Ecology 155:199–212

IPCC (Intergovernmental Panel on Climate Change) (2001) Climate change 2001: the scientific basis. In: McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS (eds) Cambridge University Press, Cambridge

Jentsch, A., Kreyling, J., Beierkuhnlein, C. (2007). “A new generation of climate-change experiments: events, not trends”. Frontiers in Ecology and the Environment 5:365–374

Marko, P. B., A. R. Palmer, et al. (2003). "Resurrection of Nucella ostrina (Gould, 1852), lectotype designation for N-emarginata (Deshayes, 1839), and molecular genetic evidence of Pleistocene speciation." Veliger 46(1): 77-85

Palmer, A. R. (1983). "Growth rate as a measure of food value in thaidid gastropods assumptions and implications for prey morphology and distribution”. Journal of Experimental Marine Biology and Ecology 73(2): 95-124

Palmer, J. D. (2000). “The clocks controlling the tide-associated rhythms of intertidal animals”. Bio Essays 22:32-37

Parmesan, C (2006)” Ecological and evolutionary responses to recent climate change”. Annual Review of Ecology, Evolution, and Systematics, 37, 637–669

Pincebourde S, Sanford E, Helmuth B. (2008). “Body temperature during low tide alters the feeding performance of a top intertidal predator”. Limnology and Oceanography 53:1562-1573

Sanford, E. (1999). "Regulation of keystone predation by small changes in ocean temperature." Science (Washington D.C.) 283(5410): 2095-2097

Somero, G. N. 2002. “Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living”. Integrative Composition Biology 42:780-789

Yamane, L. and Gilman, S. E. (2009). “Opposite responses by an intertidal predator to increasing aquatic and aerial temperatures.” Marine Ecology Progress Series 393, 27-36.

Yee, E.H. & Murray, S.N. (2004) “Effects of temperature on activity, food consumption rates, and gut passage times of seaweed-eating Tegula species (Trochidae) from California. Marine Biology, 145, 895–903.

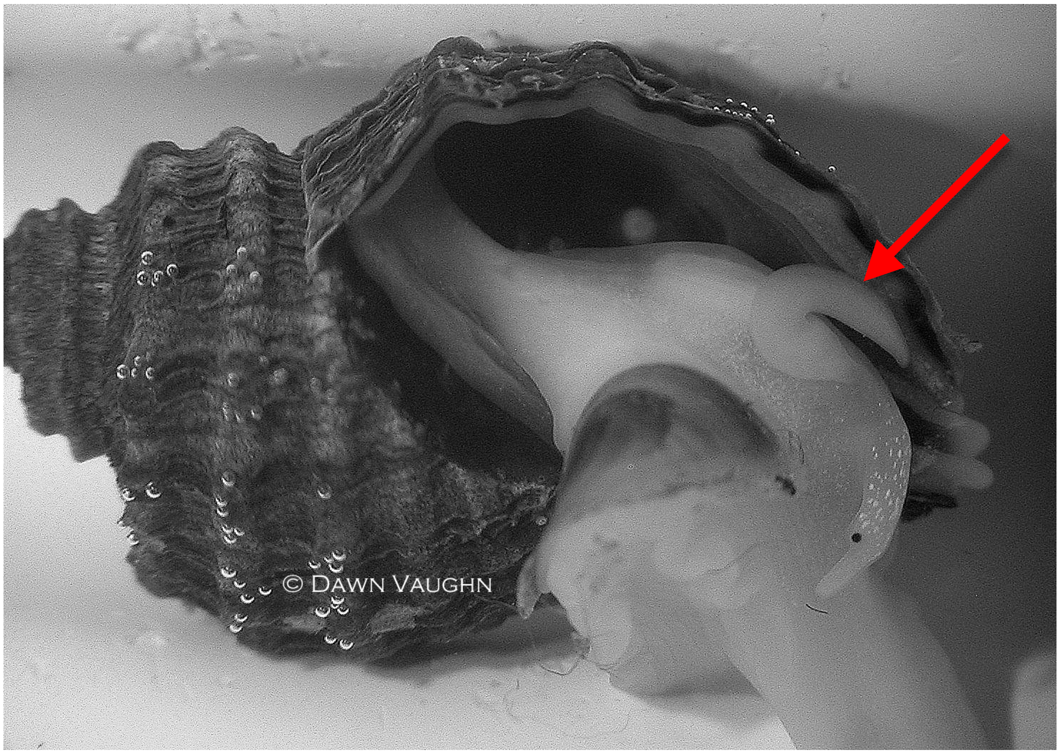

Figure 1. *Nucella ostrina, male. The penis can be observed below the right tentacle, resting against the inner surface of the aperture (indicated by arrow). This organ is absent in females. Image: Dawn Vaughn.*

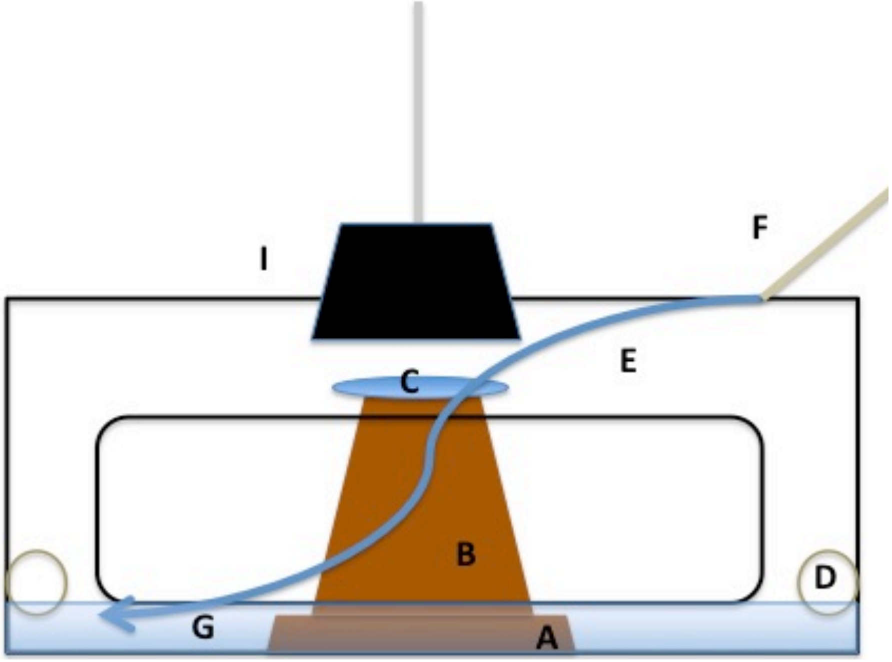

Figure 2. *Individual cage, side view.*

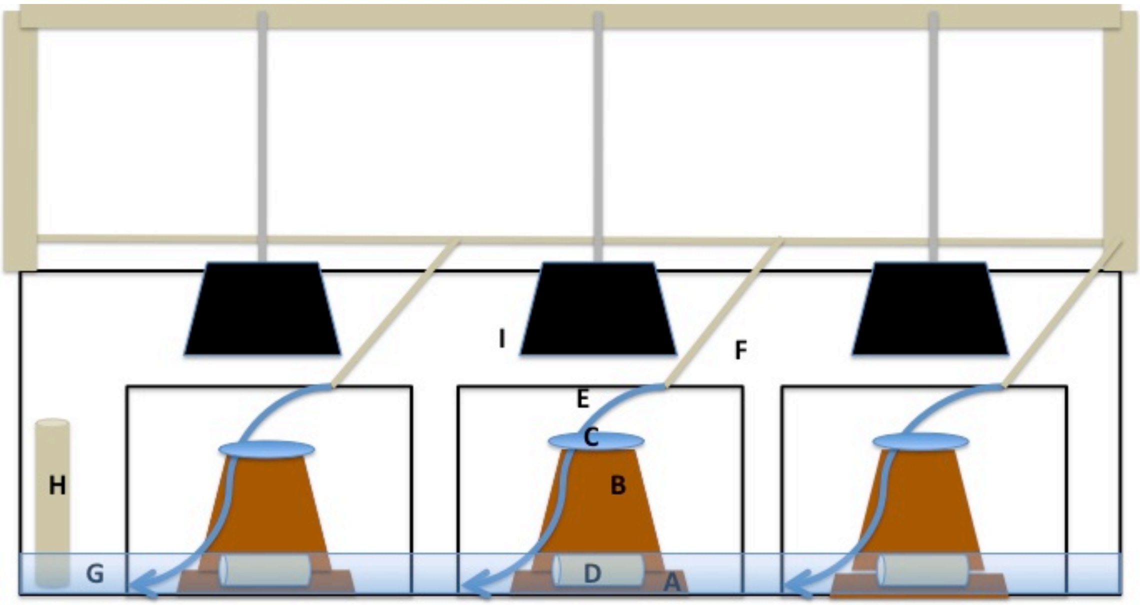

Figure 3. *Experimental tank, side view. A, Terracotta drip plate; B, Terracotta pot; C, Plexiglas barnacle plate; D, PVC refuge; E, flexible plastic tubing; F, PCV water delivery spout; G, continuously flowing water as viewed at low tide; H, PVC standpipe controlling water height. Adjacent to "H" is a second standpipe regulating low tide height; I, heat lamp.*

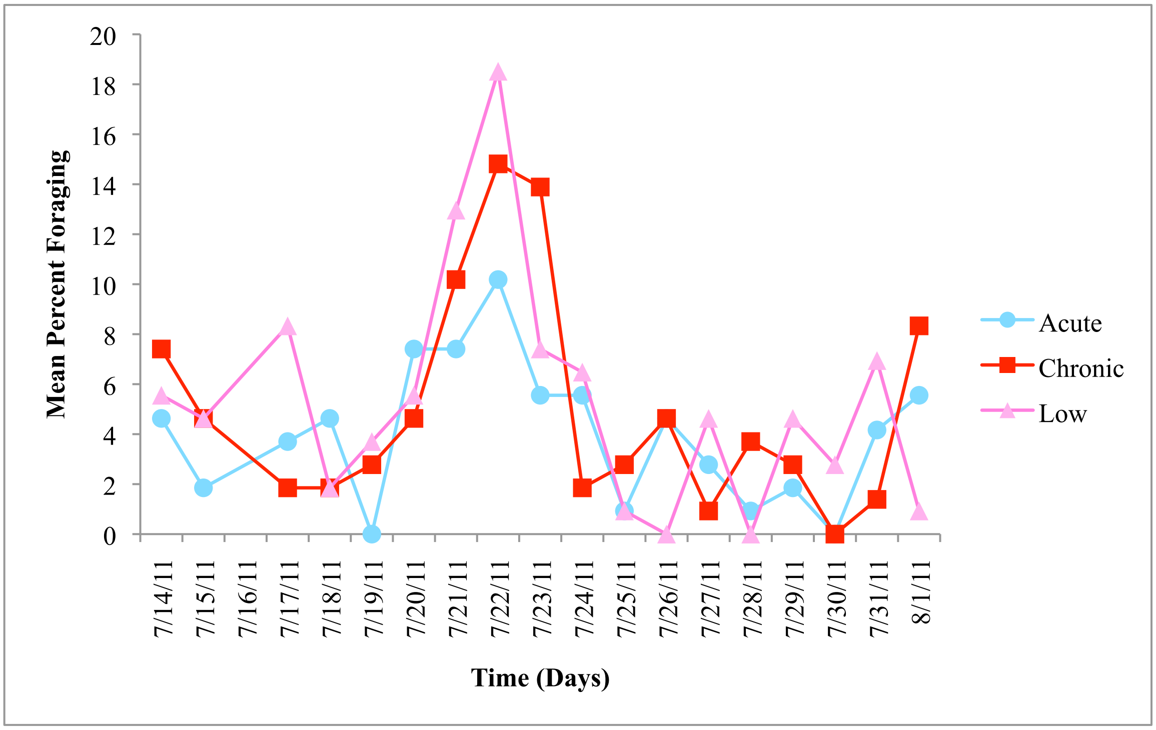

Figure 4. *Mean percent foraging of Nucella ostrina in temperature treatments (acute, chronic, and low) over time (daily measurements over two weeks). No significances were found among treatments (p = 0. 32).*

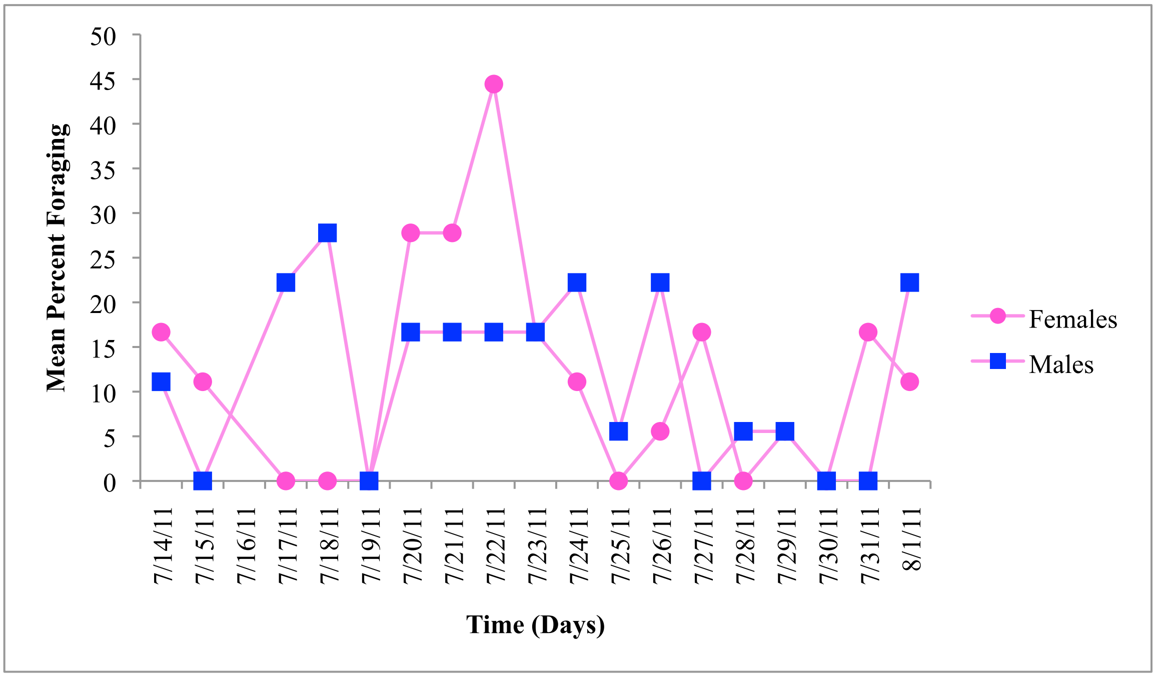

Figure 5. *Mean percent foraging of Nucella ostrina males and females in the acute temperature treatment over time (daily measurements over two weeks). Significant differences were found among mean feeding of males and females in the acute treatment (p =0.008).*

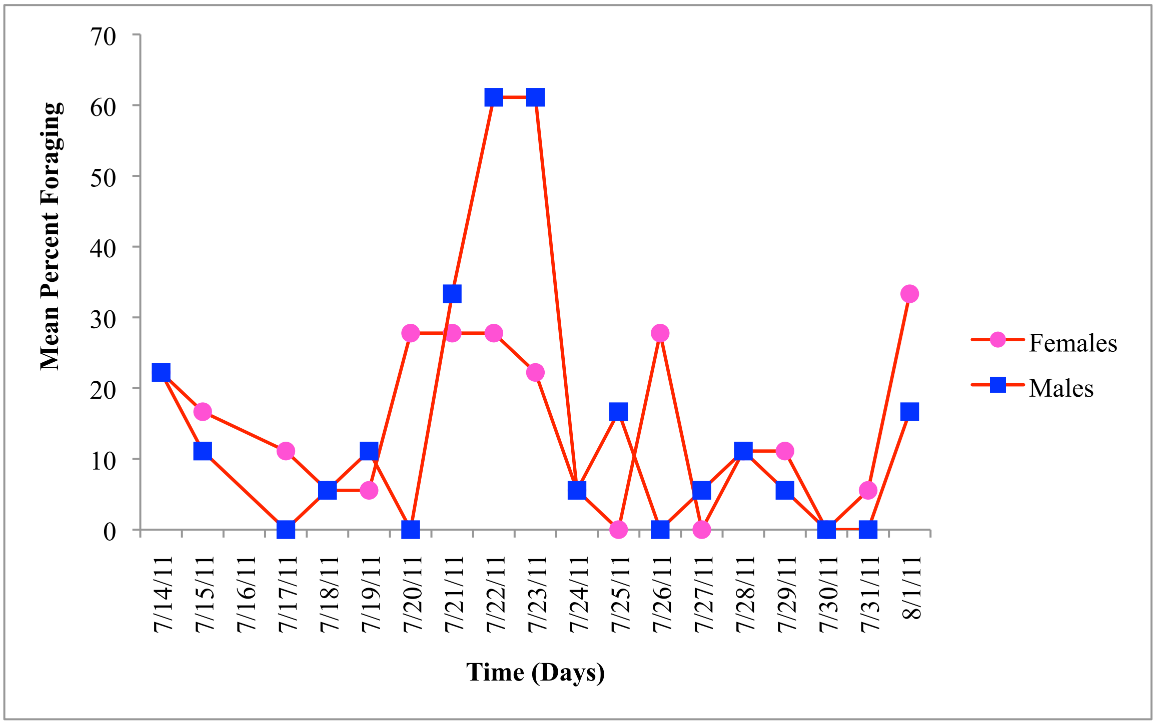

Figure 6. *Mean percent foraging of Nucella ostrina males and females in the chronic temperature treatment over time (daily measurements over two weeks). No significant*

differences were found among mean feeding of males and females in the acute treatment (p =0.43).

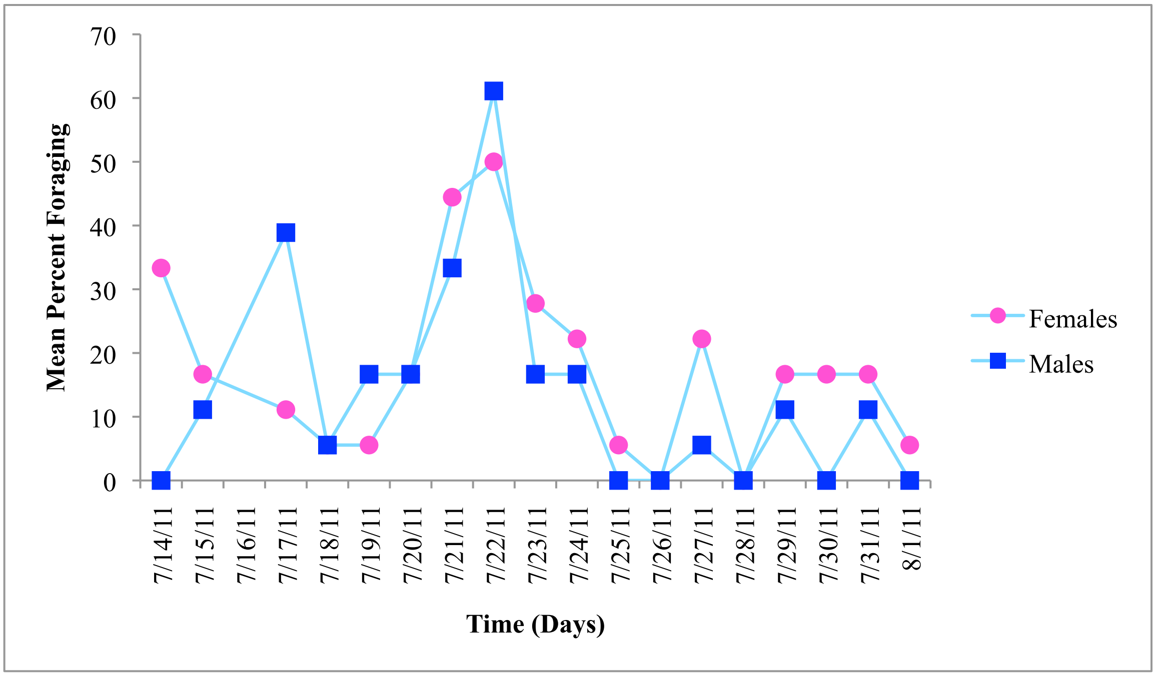

Figure 7. *Mean percent foraging of Nucella ostrina males and females in the low temperature treatment over time (daily measurements over two weeks). Significant differences were found among mean feeding of males and females in the low treatment (p =0.75).*

	Movement Off	**Movement On**
Acute	73.17%	26.83%
Chronic	69.57%	30.43%
Low	75%	25%

Figure 8. *Percent movement off versus movement onto the barnacle foraging platform out the total number of Nucella ostrina moving amongst the acute, chronic, and low treatments. Movement off exceeded movement on in all treatments.*

	Movement Off	**Movement On**
Males	82.69%	17.30%
Females	62.5%	37.5%

Figure 9. *Percent movement off versus movement onto the barnacle foraging platform out of the total number of Nucella ostrina moving amongst the acute, chronic, and low treatments. Movement off exceeded movement on in males and in females, while males were more likely to move off than females, and females were move likely to move on than males.*