

**Effects of Intertidal Algal Canopies on the Marine Gastropod *Lottia scutum***

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## **Introduction**

The intertidal zone is an area submerged by seawater during high tide and exposed to air during low tide. In the west coast, tides occur in a mixed semi-diurnal pattern, meaning that there are two high tides and two low tides per day. The low intertidal is exposed once a day, but the high intertidal is exposed more than once. Therefore, the high intertidal zone is exposed for longer periods than the low intertidal. During the summertime in the San Juan Islands (WA), one of the two low tides occurs during the middle of the day (Figure 1).

Aquatic conditions during the high tide are different from terrestrial conditions during the low tide. For example, during the high tide, intertidal animals are completely submerged under cold seawater. In contrast, low tides subject intertidal animals to increased temperatures, aerial exposure, and desiccation risks. Because temperatures can be high during the day in the summer, the mid-day low tide is likely to be the most stressful for intertidal animals. Specifically, temperatures drastically increase as a result of direct sun exposure when the tide falls. A previous study found that canopy-forming algae can reduce low tide exposure by providing a sheltered and shaded microhabitat during the low tide (Burnaford, 2004).

Exposure to high temperatures is a low tide risk that can cause intertidal animals to experience heat stress, which has been shown to affect physiological function. For example, a previous study found that temperature changes can directly affect intertidal

organisms' cardiac functioning and oxygen intake (Bjelde and Todgham 2013). Typically, limpet species that are found high in the intertidal zone can tolerate greater exposure to higher temperatures than lower-shore limpet species (Ricketts et al 1985). However, studies have shown that even higher-shore limpet species such as *Lottia digitalis* can have reduced physiological function as a result of high temperatures (Bjelde and Todgham 2013). Because lower-shore limpet species are exposed for shorter periods, it is likely that exposure to direct sunlight during the low tide can have a big effect on these species than on higher-shore limpet species.

Other risks during the low tide include exposure to visual predators such as birds. Since birds are visual predators, limpets are especially susceptible to bird predation once the water level recedes and limpets are exposed. By actively feeding on limpets during the low tide, oystercatchers can significantly decrease limpet abundance in an intertidal area (Lindberg et al. 1987). However, if limpets remain under algal canopies, they may remain hidden from visual bird predators during the low tide and avoid predation.

Once limpet populations are submerged at high tide, they are exposed to aquatic predators such as sea stars. Many limpets have escape responses that are induced when faced with a sea star (Ricketts et al 1985). One such behavior entails limpets quickly moving away from a sea star predator when threatened (Bros, 1986). However, previous evidence has shown that after exposure to a warm temperature low tide, the limpet species *L. scutum* loses the ability to escape a sea star when they encounter a predator immediately upon being re-immersed (Burnaford and Gomez, 2012).

For our investigation, we used the limpet *Lottia scutum* as our study organism. *L. scutum* is found in the mid to low intertidal zone and is mostly immobile during daytime low tides (Ricketts et al 1985). On the west side of the San Juan Islands, a common predator for *L. scutum* during the high tide is the sea star *Leptasterias hexactis*. Common predators for *L. scutum* during the low tide are black oystercatchers and crows (J. Burnaford, personal observation). Because canopy-forming algae can provide shaded microhabitats in which temperatures can be cooler than in open habitats (Figure 2), we evaluated the potential for interaction between algal canopies and limpet predation using two dominant algal species at our study site, *Saccharina sessilis* and *Fucus distichus*. *Fucus distichus* is a mid intertidal alga and *S. sessilis* is a low intertidal alga and their distributions overlap at the lower edge of the *F. distichus* zone and upper edge of the *S. sessilis* zone.

In this study, we investigated how intertidal algal canopies affect susceptibility of limpets to predation and also how the temperature experienced by limpets at low tide affects limpet susceptibility to predation at high tide. Specifically, we studied the effects of habitat amelioration by *Saccharina sessilis* and *Fucus distichus* on *L. scutum* populations. We hypothesized that in the *F. distichus* zone (during the low tide), predation would be high in open areas (because limpets in these areas are visible to foraging bird predators), and that predation would be low under the *F. distichus* canopy (because limpets would be hidden from bird predators during low tide exposure). Secondly, we hypothesized that in the *S. sessilis* zone, predation would be higher under the canopy (because sea stars commonly reside under the canopy to avoid stress from the low tide (Burnaford, 2001)

than in open areas during the high tide. Additionally, we investigated how long it takes *L. scutum* to recover from heat stress and regain their escape responses after low tide exposure. We predicted that limpets exposed to cooler low tides (simulating conditions under a shaded algal canopy) would recover their escape responses faster than limpets exposed to warm low tides (simulating conditions in open sun-exposed intertidal areas).

## **Materials and Methods**

### *Field studies of predation susceptibility*

Field studies were conducted at Pile Point on the west side of San Juan Island Washington, 48° 28.9' N, 123° 05.7' W. Our study organism *L. scutum*, inhabits the mid to low intertidal zone (Ricketts et al 1985). One of the dominant algal canopies occupying the intertidal zone is *S. sessilis*, which is found primarily in the lower intertidal zone. Another dominant algal canopy is *F. distichus*, which occupies the mid- intertidal zone.

To determine how microhabitat (under an algal canopy or on open rock) affects the susceptibility of limpets to predation we attached limpets to a piece of fishing line tied to a fixed anchor set to the rock. We glued a 9cm-10cm piece of fishing line (Power Pro Braid, 15lb test, Innovative Textiles, INC) to the posterior end of the limpet shell with superglue (Gorilla, The Gorilla Glue Company Cincinnati, OH or KDS nail glue, KDS Professional Nail Products, Sacramento CA). The anchor was a stainless steel screw set

into a wall anchor embedded in the rock. The limpet could move freely around the screw within the radius of the fishing line.

Attachment points (screws) were set in pairs. Each pair consisted of one screw under an algal canopy (either *Sacharrina sessilis* or *Fucus distichus*) and one screw on open rock. The distance between screws within a pair ranged from 35-67cm. The closest screws in neighboring pairs 1m to 8.2m apart. Two blocks of 5 *S. sessilis*/ open rock pairs and 5 *F. distichus*/open rock pairs were set up at the study site.

For tethers set under the *S. sessilis* canopy, the distance to the edge of the canopy ranged from 6cm-20cm. For tethers set under the *F. distichus* canopy, the distance to the edge of the canopy ranged from 3cm-25cm. Distances between the open microhabitat screws and the nearest canopy edge were also measured in order assess whether limpets attached to open microhabitats had access to shade. For open tethers in the *S. sessilis* zone, the distance to the edge of the canopy ranged from 11cm-40cm. For open tethers in the *F. distichus* zone, the distance to the edge of the canopy ranged from 12cm-31cm. Although limpets that were tethered in canopy habitat could occasionally move to an area that was not covered by canopy, limpets that were tethered in open habitats could not move under an algal canopy.

All limpets were collected at Pile Point and were within the size range of 19-25mm. Prior to attachment, limpet shell damage was carefully recorded. Tether locations were checked daily during the low tide (for 14 days total). If a limpet was found alive, the

location of the limpet was recorded (under canopy, in shaded crevice, or open rock). Limpets that were dead or missing were replaced on the same day. For limpets that were found dead, predator type was determined by recording shell damage (if any) as well as the condition of the limpet tissue (if any). Limpet shells found severely crushed were categorized as crab predation. Limpet shells that were highly chipped at the edges with some tissue left were categorized as bird predation. Limpets that were found clean of tissue with no new shell damage could have been from either sea stars or sea anemones. However we only categorized limpets under the sea anemone category if limpet shells (still attached to string) were found inside sea anemones (Table 1). We also noted the presence of any anemones within the radius of the tether. We also had an unknown category in which cause of death could not be determined (limpet tissue and shell was found in varying conditions and categorized in 3 types, Table 1). Lastly, we had a heat stress category in which dead limpets found undamaged (tissue and shell) were determined to have died from heat stress (Table 1).

*Laboratory studies of the effect of low tide temperature on the high tide escape response of L. scutum*

To test how long it takes limpets to recover their escape responses after low tide exposure, we conducted a laboratory experiment. Limpets were collected from the intertidal zone at Pile Point and the Friday Harbor Laboratory Beach. Limpets were carefully removed from the rock surface and transported to the laboratory. Limpets were maintained in flow-through seawater tables at ambient water temperature in flow-through

plastic containers. Limpets were supplied *ad libitum* with blades of the kelp *Nereocystis leutkeana*. *L. hexactis* were collected from the same locations and were maintained in individual flow-through containers in a separate tank from the limpets. *L. hexactis* were fed one limpet every two days.

Our experiment involved two different low tide conditions: cool and warm. In each, limpets were individually placed on ceramic tiles (4.6 x 4.6cm) while still in seawater tanks. Limpets were allowed to attach to the tiles for several minutes before tiles were removed from the tank for the low tide treatment. For all trials, we tested animals in sets of 5 limpets (5 limpets = 1 block: total sample size = 10 blocks/ treatment). In the cool temperature low tide simulation, we placed limpets (on tiles) on top of the lab bench for 1 hour. Temperature during cool low tide simulations was recorded every five minutes using a tidbit data logger (UTBI-001 Tidbit v2 Temp Logger) placed next to the limpets. Mean temperature over the 10 trials = 21°C, range 19.0°-23.8°. A Kestrel 4500 Pocket Weather Meter (Nielsen-Kellerman, Boothwyn, PA), placed next to the limpets, recorded relative humidity every 20 seconds (mean RH= 59.8%, range= 52.4-66.7%).

For the warm low tide treatment, limpets (on tiles) were placed in a temperature-controlled wind tunnel (owned by the Carrington Lab). Tiles were placed in predetermined positions on a rock slab located inside the tunnel's chamber. To minimize limpet mortality from heat stress, the duration of the warm low tide treatment was kept at 30 min. Temperatures were maintained through the use of heat lamps located above the tunnel. Temperatures were recorded every 5 minutes using the same Tidbit data loggers

as in the cool low tide treatment (1 logger placed next to each limpet; mean temp 33.9°C; range 30.0°C- 36.3°C). Relative humidity was also recorded every 20 seconds using the Kestrel 4500 Pocket Weather Meter (mean RH= 53.6%; range= 46.6-64%).

After a low tide treatment, predation trials were conducted under high-tide conditions in ambient temperature flowing seawater. A plastic container with two mesh windows was placed in the seawater tank to serve as an experimental arena (Gladware Deep Dish Containers, 20x15x10cm). Timed thirty-second trials started when a limpet (on a tile) was placed in contact with an individual *L. hexactis* predator. Limpet behavior was recorded every 5 seconds in four response categories: not moving, turning shell, moving in the opposite direction from predator and clamping down in place.

After the completion of a low tide trial (1 hour for cool low tide, 30 min for warm low tide) 4 out of 5 limpets from the block were re-submerged in a flowing ambient temperature seawater tank to begin their high-tide recovery. The 5<sup>th</sup> limpet was immediately placed in the experimental arena and exposed to the sea star predator. Subsequently, every 10 minutes, one limpet was removed from the high-tide recovery tank and placed into a predation trial with a sea star. Thus after each low tide exposure, we measured one limpet after 0 min recovery, one after 10 min recovery, one after 20 min, one after 30 min, and one after 40 min.

Control limpets were not exposed to any type of low tide simulation and were continuously maintained in a seawater tank. Before each low-tide block was exposed to a

predator, one control limpet was individually placed on one ceramic tile (4.6 x 4.6cm) and given time to settle. After all 5 treated limpets from the low tide block were exposed to a sea star in a predation trial, one control limpet was subjected to a sea star predation trial. Our final sample size was 20 control limpets.

### *Statistical Analysis*

To analyze the differences of predation (for attached limpets) between canopy vs. open microhabitats for both *S. sessilis* and *F. distichus* zones, we used a Chi- Square test. In order to assess a difference of first response in predation trials between both warm and cool treatment types we utilized the Wilcoxon Sum Rank test. We also used the Wilcoxon Sum Rank test to determine a difference in the proportion of time that limpets spent moving for both the cool and warm treated blocks.

## **Results**

### *Field studies of predation susceptibility*

Analyzing predation in the *Saccharina sessilis* zone, there was no significant difference in the proportion of the total limpets eaten between open and canopy habitats (chi-square test  $\chi^2=1.14$ ,  $p>0.05$ ; N = 104 total limpets in the open of which 17 were eaten N=94 total limpets attached under the canopy of which 22 were eaten; Figure 3). However,

there was a significant difference in the proportion of total limpets eaten between open and canopy *F. distichus* habitats (chi-square test  $\chi^2 = 4.3$   $p < 0.05$ ;  $N = 114$  total limpets in the open of which 4 were eaten;  $N = 111$  total limpets attached under the canopy of which 13 were eaten; Figure 3).

Cause of death for limpets attached to open vs. canopy pairs included sea star predation, bird predation, crab predation, limpets dead from heat stress, and an unknown category (cause of death could not be determined). Tethered empty limpet shells were found inside sea anemones (*Anthopleura*) but cause of death was probably due to other unknown causes. The dead limpets likely drifted into neighboring anemones at high tide. In the *S. sessilis* zone most of the mortality appeared to be caused by sea stars while in the *F. distichus* zone the canopy appeared to reduce predation risk from bird predators during low tide but overall mortality was higher under the *Fucus* canopy than in the open (Figure 4).

*Laboratory studies of the effect of low tide temperature on the high tide escape responses of L. scutum*

Most of the control limpets that were not exposed to a low tide simulation showed escape responses in the 30-second predation trials ( $N = 20$  control limpets; Figure 5). Control limpets moved on average 60% of the time in predation trials (Figure 6). Low tide temperature affected the ability of limpets to escape from sea star predators (Wilcoxon Rank Sum Test:  $Z = 2.99$ ,  $p = 0.0028$ , Figure. 7). After cool low tides, limpets exhibited

escape behavior (moving or turning) after 0 or 10 minutes of recovery. After warm low tides, most limpets exposed to predators after 0 and 10 minutes of high tide did not exhibit escape responses, but limpets given longer to recover did attempt to escape.

With  $\leq 20$  min of recovery, individuals in Cool Low Tide treatments spent more time moving to avoid the predator than limpets in Warm Low Tide treatments (N = 10 limpets / recovery time category, Wilcoxon Rank Sum tests within each time category: all  $p < 0.015$ , Figure 8). With  $> 20$  minutes to recover, there was no effect of low tide temperature on the amount of time limpets spent moving in predator trials (N = 10 limpets / recovery time category, Wilcoxon Rank Sum tests within each time category: both  $p > 0.17$ , Figure 8). Cooler temperature treated limpets showed escape responses at every recovery time category with limpets spending at least 36% of the time moving in trials. In contrast, the longest time that the warm low tide treatment blocks spent moving was 33%.

We also compared escape response type (moving opposite direction vs. turning shell) between warm and cool low tide treatments (N= 10/ treatment type). Limpets in the cool low tide treatment spent a higher proportion of time moving in the opposite direction than just turning shell in every time category (Figure 9). For limpets in the warm low tide treatment, only turning shell was recorded in the 0 min time category. The highest proportion of time spent moving in the opposite direction of *L. hexactis* was recorded in the 30 min time category (Figure 10).

## Discussion

### *Field Studies on Predation Susceptibility Hypothesis*

We had initially hypothesized that limpets would have a higher susceptibility to predation in open exposed areas than under the *F. distichus* canopy during the low tide. The data show that *F. distichus* may be obstructing intertidal bird predators from finding *L. scutum* hidden under the canopy. Comparing bird predation between canopy zones, results indicated that bird predation was lower in the *S. sessilis* zone than in the *F. distichus* zone. This could be a pattern that relates to the length of time that the *S. sessilis* zone is exposed. Specifically because the lower intertidal (location of *S. sessilis* canopy) is exposed for a shorter period than the mid intertidal (location of *F. distichus* canopy), birds would have less time to forage in the *S. sessilis* zone. Though there was no significant difference in the amount of predation on tethered limpets between open vs. canopy microhabitats in the *S. sessilis* zone, results indicated high proportions of limpets eaten by sea stars in both open vs. canopy microhabitats. Feeding in the *S. sessilis* zone could be more convenient than feeding in the *F. distichus* zone for sea stars because they are submerged underwater for longer periods and exposure time during the low tide is reduced. This could explain why sea star predation was higher in the *S. sessilis* zone.

Dead limpets found in conditions in which predator type could not be determined were subcategorized under 3 types (Table 1). Some of the limpets dead from unknown causes could have potentially landed on neighboring sea anemones during the high tide.

Specifically, sea anemones could have consumed the remaining tissue on limpet shells after limpets had already been killed by other mechanisms and then released the shell back to the environment. One tethered pair in the *S. sessilis* zone had sea anemones within range of the attached limpet. However in the *F. distichus* zone, 7 tethered pairs (open vs. canopy) had sea anemones within range of attached limpets with empty limpet shells found inside *Anthopleura* only under the *F. distichus* canopy.

We also found a few limpets dead from heat stress in the *F. distichus* and in the *S. sessilis* zone. Five percent of limpets attached in *S. sessilis* open microhabitats died from what we perceived to be heat stress. In the *F. distichus* zone, we assigned and 11% of the deaths under the *F. distichus* canopy and 20% of the deaths in the open to heat stress. The fact that the *F. distichus* zone (located in the mid-intertidal) is exposed longer than the *S. sessilis* canopy (located in the low-intertidal zone) may explain why the highest incidence of death by heat stress occurred in the *F. distichus* zone.

*Laboratory studies of the effect of low tide temperature on the high tide escape responses of L. scutum*

We found that 85% of control limpets that were not exposed to a low tide showed escape responses in a predator encounter and moved at least 60% of the time in predation trials. Therefore, we can ascertain that most limpets unstressed by low tide conditions have uninhibited escape responses and can escape a sea star in a predation encounter. However, limpets exposed to low tide treatments showed delayed and reduced escape

responses when exposed to a sea star predator. Given less than or 20 min of recovery time at high tide, limpets exposed to a cool low tide (simulating refuge under an algal canopy) spent more time moving to avoid the predator than limpets exposed to a warm low tide (simulating conditions on an open rock microhabitat) treatments. These results indicate that limpet escape responses are still severely delayed and reduced from heat stress within the first 20 minutes after high tide submersion. However, if given more than 20 minutes to recover, we found that there was no effect of low tide temperature on the amount of time limpets spent moving in predator trials. These results indicate that *L. scutum* can fully recover from the effects of low tide conditions if they have at least 20 minutes of recovery at high tide.

Overall, our results suggest that algal canopies can affect limpet susceptibility to predation during the low tide and the high tide. Specifically, the shaded refuge that algal canopies provide during the low tide keeps limpets in cooler temperatures and hides them from visual predators. By remaining in cooler temperature areas during the low tide, limpets also avoid heat stress from direct sun exposure. Therefore, unstressed limpets could avoid sea star predation during the high tide. Realizing how intertidal associations between species are connected can be important in understanding the extent of species interdependence during stressful conditions.

### *Future Studies*

Future studies should investigate the exact cause of death for the limpets in the categories classified as 'unknown' in this study. Methods for this future study could involve placing video recording devices next to attached limpets in the field. For the lab portion of this project, future studies should focus on narrowing down the limpet escape response recovery time. Since this project focused on limpet escape response recovery within 10-minute time categories, a future investigation could reduce the time that limpets are allowed to recover their escape responses to 5 minutes in order to narrow down on the length of time that it takes stressed limpets to recover escape responses.

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## Literature Cited

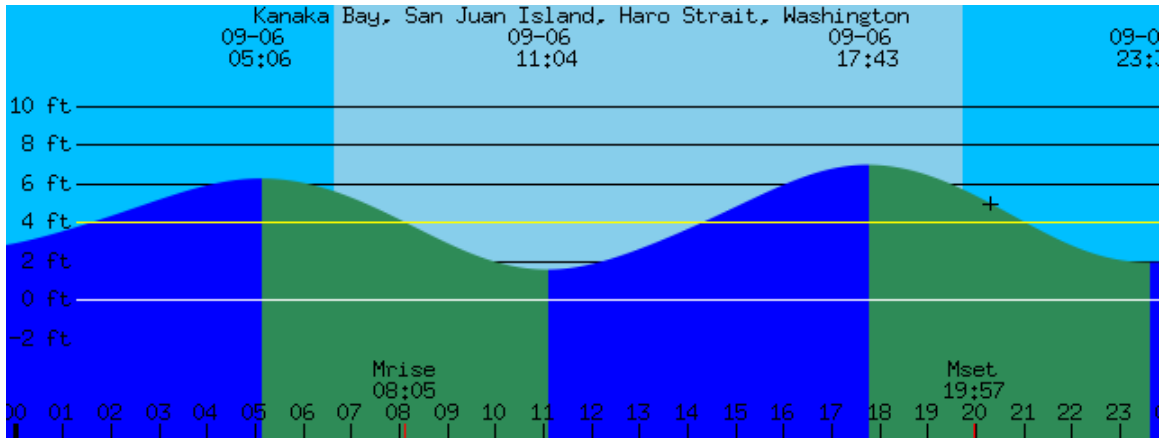
- Bjelde, B.E and Todgham, A.E. 2013. Thermal physiology of the fingered limpet *Lottia digitalis* under emersion and immersion. The Journal of Experimental Biology [Internet]. 2013 [cited 2013 Aug 9]. 216:2858-2869. Available from <http://jeb.biologists.org/lookup/doi/10.1242/jeb.084178>
- Bros, W.E 1986. Mortality of the limpets, *Collisella pelta* (Rathke) and *Notoacmea scutum* (Rathke), as a function of predation from the seastar, *Pisaster ochraceus* (Brant). Bulletin of Marine Science. 39(1): 92-101
- Burnaford, J.L. 2001. Evaluating the relative roles of positive and negative interactions in communities: shade, herbivory and physiological stress in the rocky intertidal zone. Dissertation, Oregon State University, Corvallis, OR.
- Burnaford, J. L. 2004. Habitat modification and refuge from sublethal stress drive a marine plant-herbivore association. Ecology. 85(10): 2837-2849
- Gomez, M. and Burnaford, J.L. 2012. Effects of heat stress on predation risk for intertidal molluscs. Poster presented at the SACNAS meeting, Seattle, WA.
- Lindberg, D.R., Warheit, K.I., and Estes, J.A. 1987. Prey preference and seasonal predation by oystercatchers on limpets at San Nicolas Island, California, USA. Marine Ecology Progress Series 39: 105-113
- Miller, L.P. Harley C.D.G., and Denny, M.W. 2009. The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. Functional Ecology 23: 756-767

Ricketts, E.F and Calvin, J. 1985. *Between Pacific Tides*, 5<sup>th</sup> ed. Stanford University Press. Stanford CA, pp. 680.

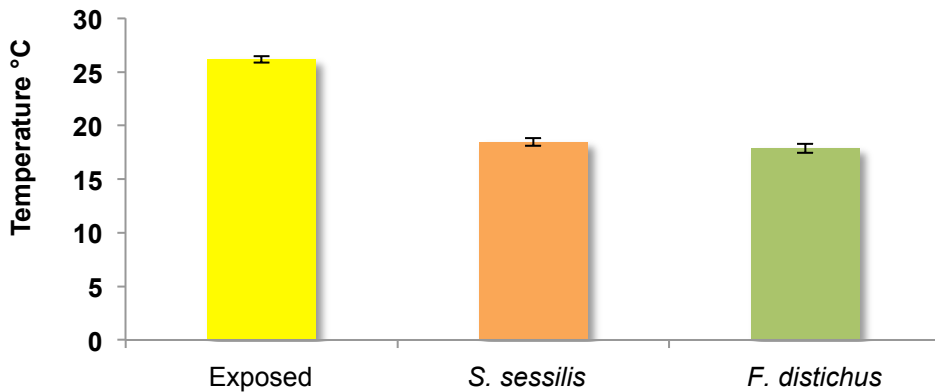
**Table 1.** Cause of death for limpets attached in canopy vs. open microhabitats.

Mortality was categorized by damage on shell as well as the condition of the remaining tissue (if any). Horizontal rows represent the potential cause of death; vertical columns represent the number of limpets attached at each microhabitat (canopy vs. open).

	Zone: <i>S. sessilis</i> Canopy	Zone: <i>S. sessilis</i> : Open	Zone: <i>F. distichus</i> Canopy	Zone: <i>F. distichus</i> Open
<b><u>Possible Sea star predation:</u></b> Limpet tissue: no tissue Shell: undamaged shell	<u>10</u>	<u>11</u>	<u>6</u>	<u>0</u>
<b><u>Observed Sea star Predation</u></b> Limpet found being preyed upon by sea star	<u>8</u>	<u>2</u>	<u>0</u>	<u>1</u>
<b><u>Possible Bird Predation</u></b> Limpet tissue: Some tissue Shell: Chipped at edges	<u>1</u>	<u>2</u>	<u>2</u>	<u>3</u>
<b><u>Possible Crab Predation</u></b> Limpet Tissue: None Shell: Crushed; small piece left	<u>0</u>	<u>2</u>	<u>0</u>	<u>0</u>
<b><u>Unknown Predation Type 1</u></b> Limpet tissue: No head; small part of foot Shell: no damage	<u>1</u>	<u>0</u>	<u>4</u>	<u>0</u>
<b><u>Unknown Predation Type 2</u></b> Limpet tissue: part of tissue Shell: no damage	<u>0</u>	<u>0</u>	<u>1</u>	<u>0</u>
<b><u>Unknown Predation Type 3</u></b> Limpet tissue: tissue around inner rim Shell: no damage	<u>2</u>	<u>0</u>	<u>0</u>	<u>0</u>
<b><u>Found In Anthopleura</u></b> Limpet tissue: some around rim Shell: no damage	<u>0</u>	<u>0</u>	<u>3</u>	<u>0</u>
<b><u>Possible Heat Stressed Limpet</u></b> Limpet tissue: whole limpet found Shell: no damage	<u>0</u>	<u>1</u>	<u>2</u>	<u>1</u>



**Figure 1. Predicted tidal cycle over 24 hours for Kanaka Bay, San Juan Island, WA Summer 2013.** Y-axis: tidal level in ft. X-axis: time (hours). Blue blocks show rising tides; green blocks show falling tides. Figure shows two high tides and two low tides per day.

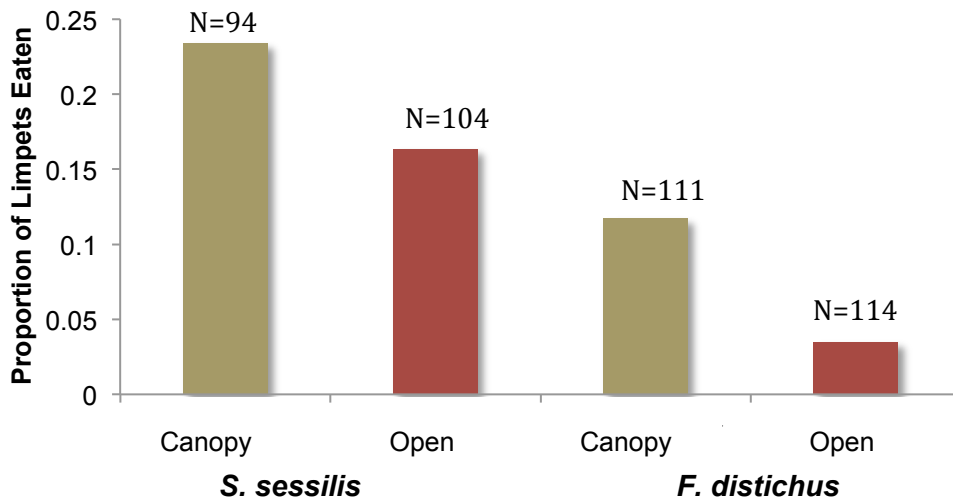


**Figure 2. Low tide temperature conditions in intertidal microhabitats.**

Data are mean ( $\pm$  SE) temperature over 6 low tides in summer 2013.

Dataloggers were placed in exposed (unshaded) areas or under the canopy of

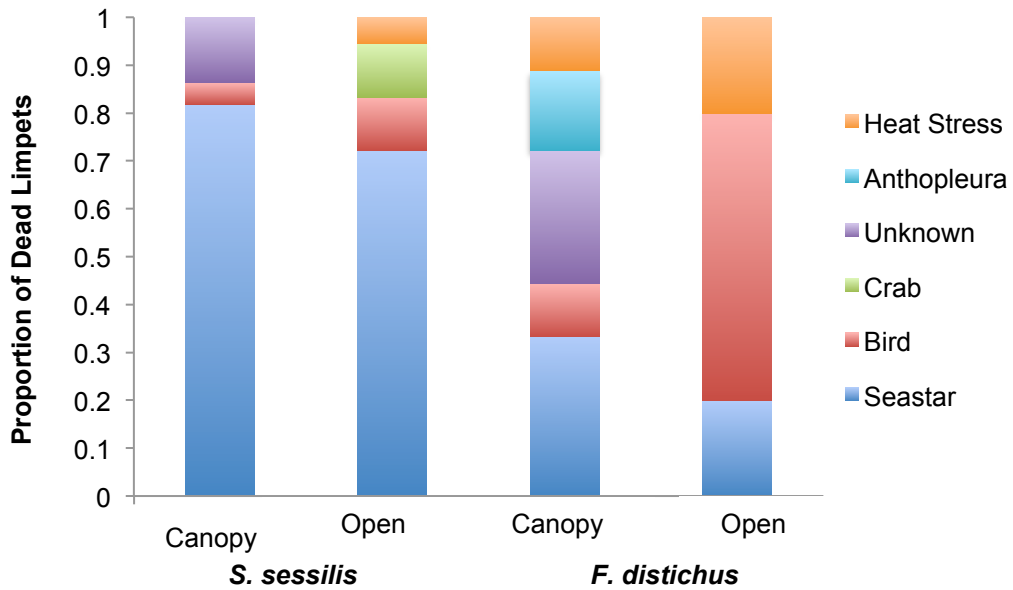
*S. sessilis* or *F. distichus*. Loggers recorded temperatures every 5 minutes.



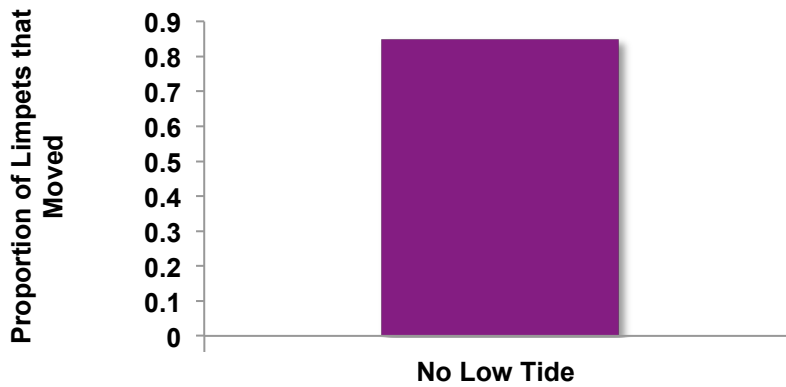
**Figure 3. Mortality of tethered limpets in open and canopy microhabitats.**

Numbers above bar = number of limpets tethered and recovered in that habitat type.

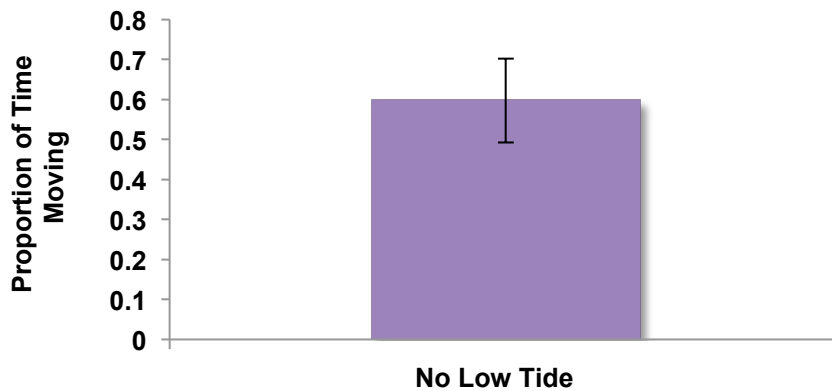
Limpets were checked daily during low tide for 14 days.



**Figure 4. Mortality categories for dead limpets.** Mortality categories based on observations of shells and tissue for recovered dead animals. Total number of dead limpets in each habitat type as in Table 1.

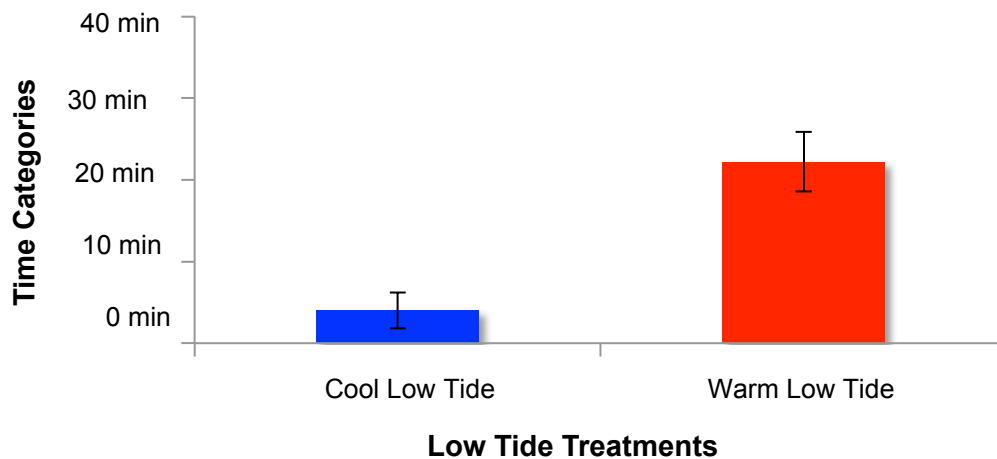


**Figure 5. Escape frequency in No Low Tide limpets.** Twenty limpets were exposed to sea star predators without exposure to simulated low tide conditions

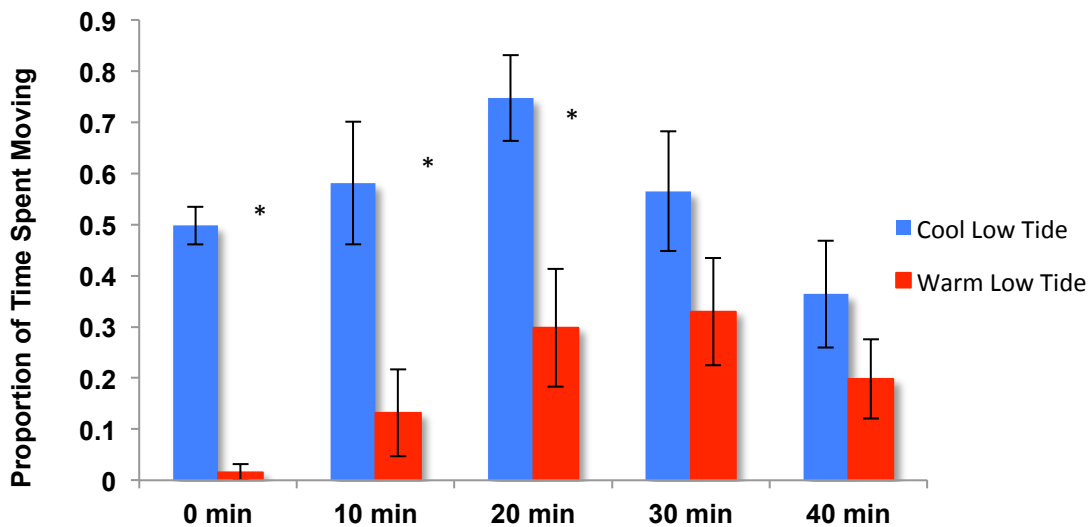


**Figure 6. Duration of escape response in No Low Tide limpets.**

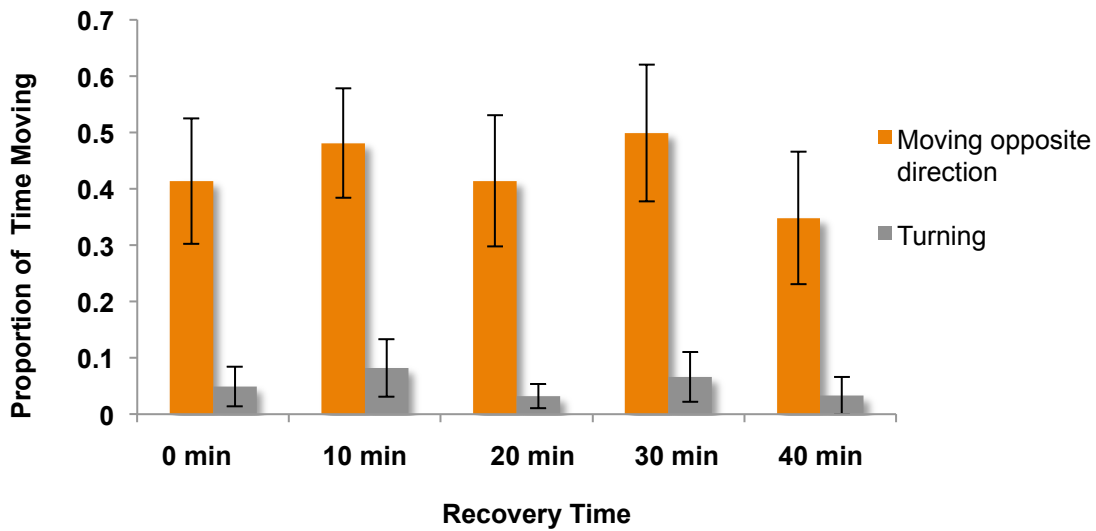
Mean ( $\pm$  SE) proportion of observation times that limpets in No Low Tide treatment were turning or running in 30-second predation trials. N = 20 limpets.



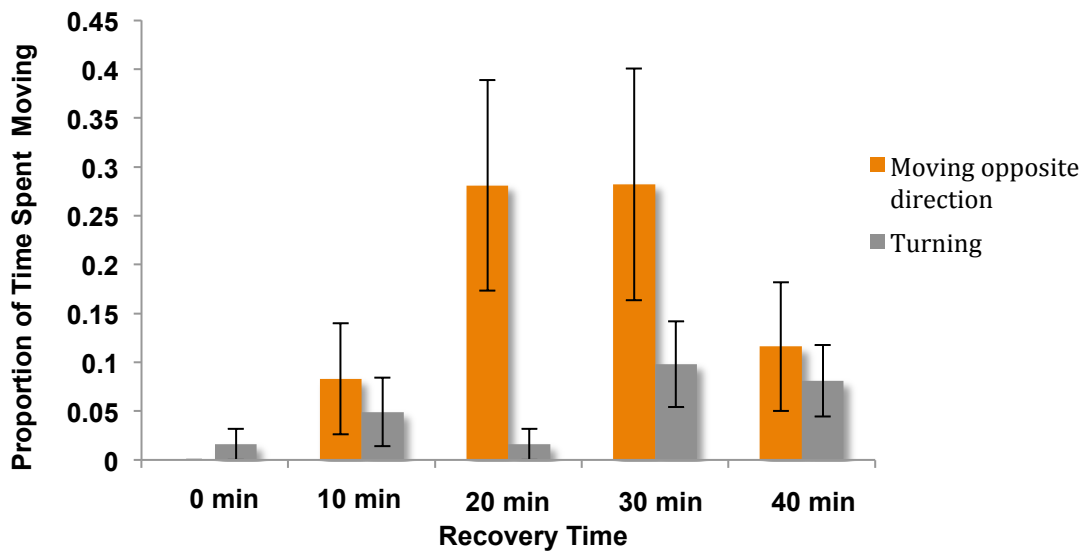
**Figure 7. Effect of low tide temperature on the timing of the escape response in predator trials.** Data are mean ( $\pm$  SE) response time (as categories) for the first limpet to move in each low tide treatment block (N = 10 blocks per temperature treatment).



**Figure 8. Effect of low tide temperature on the duration of the escape response in predator trials.** Data are mean ( $\pm$  SE) proportion of observations in which limpets in each category were turning or running. (N = 10 limpets / recovery time category / treatment). X-axis = time categories. Asterisks represent times at which there was a significant difference ( $p < 0.05$ ) between Cool and Warm Low Tide treatments.



**Figure 9. Components of the escape response in predator trials for cool low tide treatment limpets.** Mean ( $\pm$  SE) proportion of time that limpets from cool low tide blocks (N=10) spent in different behaviors in predation trials.



**Figure 10. Components of the escape response in predator trials for warm low tide treatment limpets.** Mean ( $\pm$  SE) proportion of time that limpets from warm low tide blocks (N=10) spent in different behaviors in predation trials.

