Effects of Low Tide Conditions on Susceptibility to Herbivory for *Saccharina sessilis*

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Blinks/NSF REU Research Fellowship 2013
Summer 2013

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Keywords: *Saccharina sessilis*, *Katharina tunicata, Idotea wosnesenskii*, *Lacuna*, herbivory, wind desiccation

Abstract

Conditions in the intertidal zone differ at high and low tide. One potential low-tide stressor is wind, which can cause desiccation. Algae, unable to escape stressful conditions, accumulate damage over repeated low tides. We investigated whether damage from desiccation alters susceptibility to herbivory in the low intertidal canopy-forming kelp *Saccharina sessilis*. We assessed overall herbivory risk in the field by counting *S. sessilis* and three major consumers (the chiton *Katharina tunicata*, the isopod *Idotea wosnesenskii*, and the snail *Lacuna* spp.) in 0.25m^2 quadrats. We assessed the effects of desiccation on herbivory in the laboratory. We collected *S. sessilis* blades and cut two 25cm^2 samples from each. For 90 minutes once a day for three days, one sample from the pair experienced a "no-wind" simulated low tide while the other member of the pair experienced a "windy" low tide with airflow of 1 m/s. Before and after each low tide we measured area, wet weight, and the amount of visible damage on the kelp. After the third day, we placed paired kelp samples into a container either with or without herbivores. We conducted separate trials with *K. tunicata* and *I. wosnesenskii*. Once ~50% of the *S. sessilis* tissue in a herbivore container was consumed, we terminated the trial for a pair of herbivore and non-herbivore containers. Trials lasted 1 to 5 days. Our results showed that herbivore distribution in the field was patchy, and preference for damaged vs. undamaged tissue differed between herbivores. Overall, susceptibility to herbivory likely varies among individuals in the field due to differences in low-tide damage and the varying abundance of herbivores with different preferences.

Introduction

Organisms in the intertidal zone are submerged under seawater at high tide, and are exposed to terrestrial conditions at low tide. In the state of Washington, which has a mixed semi-diurnal tidal cycle, organisms in the low intertidal zone experience low tide only once per day. The environment is extremely different at low tide and high tide. At low tide, the intertidal zone is exposed to full strength sunlight, and therefore to intense UV radiation and higher temperatures than that of seawater, and organisms are vulnerable to wind desiccation among other things. On the other hand, when the tide is high and the intertidal zone is submerged under water, organisms are protected from the sun and wind, and experience the constant temperature of the seawater.

Many intertidal organisms can escape these stressful low tide conditions by remaining in shady refugia. Unlike mobile intertidal organisms, macroalgae are secured onto a rocky substrate in the intertidal zone. Since these algae do not have the ability to move to escape the stressful abiotic low tide conditions, they may dry out and accumulate damage. When these photosynthetic organisms are exposed to high light levels at low tide, photoinhibition can occur, causing damage to the photosynthetic systems (Raven and Hurd 2012). Researchers studying *C. peregrina*, a southern California intertidal macroalga, found that a combination of increased light and wind stresses resulted in a decreased net rate of photosynthesis (Matta and Chapman 1995). Exposure to multiple simultaneous low tide abiotic conditions can put substantial physiological stress on seaweeds in the intertidal zone.

Saccharina sessilis is a brown macroalga found in lower intertidal zones on the Pacific coast of North America from Alaska to California (Abbott and Hollenberg 1976) that has a life span of at least 2 years. This kelp is a dominant species in the low intertidal zone (Dayton 1975) and is known for providing canopy cover for other organisms, such as the chiton *Katharina tunicata* (Burnaford 2004). It has multiple blades which vary in size and are attached to a single holdfast. These blades vary in physical appearance in relation to the intensity of wave action they encounter (Armstrong 1987). Among the organisms that can be found in association with these blades are mesograzers, such as the isopod *Idotea wosnesenskii* and marine snails in the genus *Lacuna* (Van Alstyne et al. 2001). Mesograzers are invertebrates whose food is also their shelter (Van Alstyne et al. 2001). In addition, many macrograzers consume the alga: one of these documented macrograzers is the black leather chiton *Katharina tunicata* (Burnaford 2004).

In this study we asked the question: When *S. sessilis* tissue becomes damaged from repeated low tide exposure, is it just as susceptible to herbivory as undamaged *S. sessilis* tissue? We specifically investigated the effects of damage due to desiccation (by wind) on *S.sessilis*'s susceptibility to herbivory. We predicted that herbivores would prefer undamaged blade tissue because we hypothesized that damage may alter nutrient content or availability.

Methods

Study Site and Study Organisms

Field Studies

This study was conducted at Pile Point (48°28.9'N, 123°05.7"W) on San Juan Island, WA. The tidal cycle is mixed semi-diurnal, meaning that the low intertidal zone is exposed to terrestrial conditions once a day. In the summer, the low intertidal zone is uncovered during the morning and afternoon, exposing organisms to terrestrial temperatures which can be much higher than that of the seawater (Burnaford 2004).

Field Surveys

To assess the potential for herbivory on *S. sessilis* in the intertidal zone, I quantified the number of *K. tunicata*, *I. wosnesenskii*, *Lacuna* spp. and *S. sessilis* in three transects, each 10 meters in length, on different rocky benches in the low intertidal zone at Pile Point. All three transects were in the *Saccharina* zone, but they varied slightly in tidal height (and therefore in the amount of emersion time on any given low tide). On each transect, I surveyed ten randomly placed 0.25m^2 square quadrats.

Saccharina sessilis adults and juveniles were counted in each plot. Individuals were classified as juveniles if they had only a single undivided blade off a small holdfast. Holdfasts with no blades were excluded from the counts as our study focused on herbivory on blade tissue. Within each plot, I counted the number of *I. wosnesenskii* and *K. tunicata*. The number of *Lacuna* snails was counted on 2 randomly selected adult *S.*

sessilis individuals in each quadrat. In cases when there was only one *S. sessilis* individual in a quadrat, the number of *Lacuna* snails was counted on that individual. If there were no *S. sessilis* individuals, then *Lacuna* snails were not counted at all.

To quantify low tide conditions, ambient temperature and light levels were recorded during field surveys with HOBO® Pendant DataLoggers. Measurements were taken on unshaded rocky benches above the water level every 5 minutes during low tide for 6 consecutive days. Pendants recorded temperature in °C with an accuracy of ±0.53°C and light levels in (lumens/ft^2). Wind speed was recorded every 20 seconds during field surveys using a Kestrel 4500 Pocket Weather Tracker placed in the *Saccharina* zone.

During the field surveys, ambient temperature in the intertidal zone ranged from 10.7°C to 37.7°C, ambient light levels ranged from 400 lumens/ft^2 to 22,528 lumens/ft^2. The ambient wind speed ranged from 0 m/s to 3.1 m/s.

Laboratory Studies

Laboratory herbivory experiments were conducted at the University of Washington Friday Harbor Laboratories, Friday Harbor, WA (48° 32.7' N, 123° 00.6' W). *Saccharina sessilis* and *Katharina tunicata* used in the feeding experiments were collected from the low intertidal zone in Pile Point, San Juan Island, WA (Figure 1). All collections at Pile Point were made on rocky benches that were isolated from the field study locations. *Idotea wosnesenskii* used in feeding experiments were collected at Cattle Point, San Juan Island, WA. After collection, all experimental animals and kelp were kept in flow-through containers submerged in ambient temperature flowing seawater

tanks at Friday Harbor Laboratories. *Saccharina sessilis* was held in outdoor tanks no more than 3 days after collection before being used in experiments. Animals were held for 2 hours to 24 days before being used in experiments. During the holding period, animals were fed *Nereocystis luetkeana* collected from the Friday Harbor Laboratories dock. Food was provided *ad libitum*. Each individual was only used once in an experiment.

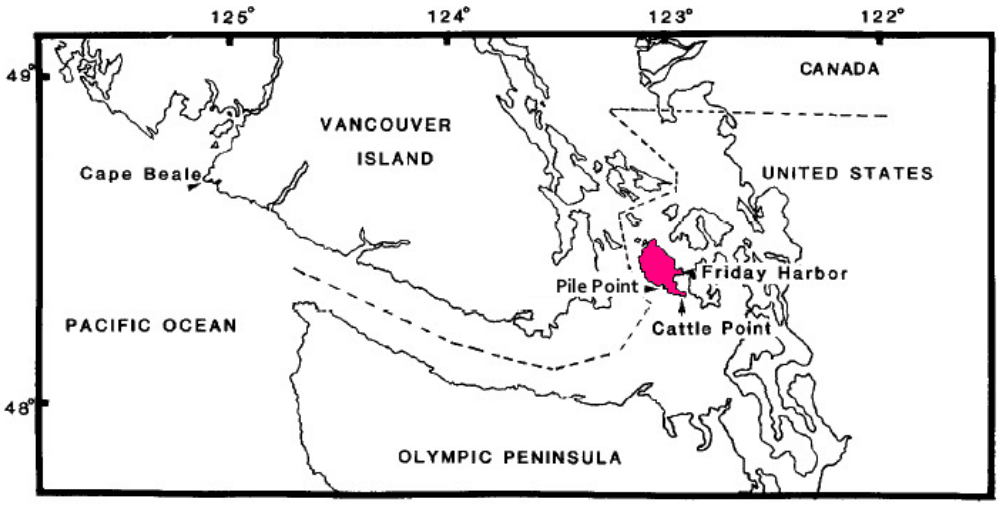

Figure 1. Map of study site and collection sites (modified from Armstrong 1987), with San Juan Island shaded in.

Laboratory Feeding Preference Assays

Algal Preparation

To determine whether damaged *S. sessilis* was just as susceptible to herbivory as undamaged *S. sessilis* individuals, we cut two pieces of algae from each *S. sessilis* individual (to control for any physiological and chemical variation among individuals).

The paired samples from a single blade were cut so that the members of each pair had similar morphology (flat vs. bullate) but different pairs had a variety of morphologies.

Algal samples were squares ranging from 23.5 to 28.6 cm^2 in area with a mean wet weight of 2.48g (± 0.39 SD). Wet weights were taken after we removed excess seawater from the surface of the blades by blotting with a damp paper towel. Repeated measurements on individual samples (n=5 samples, measured 2-5 times) showed that wet weight measurements were repeatable to an accuracy of ± 0.06g. Samples were allowed to heal from 11.5 to 38.5 hours between cutting and use in an experiment.

At the start of the experiment, each pair of samples experienced three consecutive days of simulated low tides. One sample from the pair was put under a fan (stress treatment) while the other sample from the pair was put on the lab countertop (no stress treatment) for the same amount of time. We conducted preliminary trials to evaluate the rate of water loss over a two-hour period (Figure 2). Subsequently we conducted one trial with treatments with a low tide simulation that lasted for 60 minutes and three trials which had a low tide simulation that lasted for 90 minutes. The time between these simulated low tides for a set of samples was, on average, 23.7 hours. During low tide simulations, all samples were next to a window on a flat surface. Temperature and light levels were recorded every 2 or 5 minutes using HOBO® Pendant DataLoggers or a TidbiT v2 DataLogger, and wind speed was recorded every 20 seconds or 2 minutes using a Kestrel 4500 Pocket Weather Tracker (Table 1). Before and after each low tide exposure, I measured wet mass (g), % damage (point-contact method), and area (cm^2) of kelp samples.

Herbivore Trials

After three days of repeated low tide simulations, kelp samples were used in herbivore feeding assays. All experiments were carried out in outdoor flow-through seawater tanks at Friday Harbor Laboratories. Each pair of stressed and not stressed samples (originating from the same *S. sessilis* individual,) was placed into a single container. We used GladWare® Containers (20cm x 14.5cm x 9cm for trials with *Katharina*; and 10cm x 14.5cm x 7cm for trials with *Idotea*) that were modified with windows covered with 1 mm mesh screening to allow water flow. Smaller containers with windows on 3 sides were used for trials with *Idotea*. The larger containers with an additional mesh panel on the 4th side (1.9cm square mesh, Deer-X ® Deer Fencing) were used for *Katharina* trials. Paired *S. sessilis* samples were sewn with a needle and fishing line to the container windows on opposite sides to keep pieces from moving around the container and ensure that we could identify treatments at the end of the herbivory trial (small markings on the outside of the container identified which piece belonged to each treatment).

We carried out four herbivory trials: two with the chiton *Katharina tunicata* and two with the isopod *Idotea wosnesenskii*. *K. tunicata* individuals ranged in length from 61.3 mm to 119.4 mm. Overall mean length of the *K. tunicata* used was 83.2 mm (±15.7 mm SD). *Katharina* were divided into four size classes and one individual was randomly selected from each size class for each container so that the herbivore populations were similar across containers. For most replicates, there were 4 *Katharina* per container; one replicate had only 3 individuals but this replicate included the largest *Katharina*

individual collected. Prior to the start of the herbivory trials, we starved the *Katharina* for 39-41 hours.

I. wosnesenskii individuals ranged in length from 15.0 mm to 38.6 mm, with a mean length of 25.1 mm (±5.4 mm SD). Again, herbivores were divided into 4 size classes and for each container one (trial 1) or two (trial 2) individuals were randomly selected from each size class for each container. After 5 days we added a 5^{th} individual to each of the containers in trial 1. Prior to the start of herbivory trials, we starved *Idotea* for 69 hours (trial 1) or 53 hours (trial 2).

Each herbivory trial consisted of 10 containers: 5 with herbivores, and 5 without herbivores. Pairs of containers were randomly distributed among 3 outdoor tanks. Containers were checked several times a day. When approximately 50% of the tissue (by area) in a herbivore container had disappeared, we removed the herbivore container and its matched 'no-herbivore' container from the tank. We measured the wet mass (g) and the area (cm^2) of the remaining tissue in both containers. *K. tunicata* trials took minimally 18 hours for the first pair of containers to be removed and maximally 4.75 days for the last to be removed. Herbivory rates in the first *I. wosnesenskii* trial were very low, and all replicates were terminated after 12 days. The second *I. wosnesenskii* trial ran for 2.5 days before the first pair of containers was removed and 5.6 days until the last containers were removed.

Data Analysis

All statistical analyses were conducted using JMP v.9 or JMP v.10 statistical software (SAS Institute, Cary, NC). Data used in parametric tests were tested to

determine whether they met test assumptions. The assumption of normality was tested with a Sharpio-Wilk W test comparing data to a continuous normal distribution. The assumption of equal variances among groups was tested using Levene's test. Raw data were used if they met parametric test assumptions (p values > 0.05 for both test statistics). If data did not meet both test assumptions, they were transformed, or if we could not find a transformation that met test assumptions, we used a non-parametric test.

To determine whether the abundance of *S. sessilis*, *K. tunicata*, *I. wosnesenskii*, and *Lacuna* snails differed among our field transects, we used one-way ANOVAs for each species. To determine if there were any differences in temperature, light levels, or wind speed between the stress and no-stress low tide simulation conditions, we used paired t-tests. We used paired t–tests to also determine if there were any differences in biomass loss (by weight or by area) and final % cover of healthy tissue between the stress and no stress *S. sessilis* samples that were under the fan for 90 minutes.

For the herbivory trials, we calculated the percent mass and area loss during the trial for each individual container. We followed Van Alstyne et al. 2001 to evaluate the amount of tissue lost to herbivory in the herbivore containers. We calculated the difference in mass (Final – Initial) for individual stressed and not stressed *S. sessilis* samples in herbivore and no-herbivore containers. We then subtracted the change in mass for the not-stressed sample and subtracted it from the change in mass of the stressed sample generating a value for each container. We compared these values between paired herbivore and non-herbivore containers using Wilcoxon Rank Sum tests. After data analysis showed no differences between the two *Katharina* trials, we combined the two trials for analysis (resulting in a single analysis using all 10 replicate pairs of containers).

However, because of the differences in methodology between the two *Idotea* trials, we analyzed the two trials separately for that herbivore.

To calculate the amount of area lost during the herbivory trials, the perimeter of each *S. sessilis* sample was traced onto Rite-in-the-Rain Copier paper (before and after the herbivore trials). Traces were scanned and analyzed using a contour tracing method in ImageJ 1.45s (Java 1.6.0_20). We determined area loss or gain by comparing the total area of each sample before and after the herbivory trial.

Results

Field Studies

The mean number of adult *S. sessilis* per $0.25m^2$ quadrat did not differ significantly across the three transects (ANOVA on ln-transformed data, N=10 quadrats / transect, 3 transects, F=1.43, P=0.26, Figure 3), although abundance did vary slightly among the transects. The mean number of *K. tunicata* per $0.25m^2$ differed across the three transects (Kruskal-Wallis test on ln-transformed data, $\chi^2 = 19.52$, $p < 0.0001$ Figure 4A). The mean number of *I. wosnesenskii* per $0.25m^2$ was different across the three transects (Kruskal-Wallis test on ln-transformed data, $\chi^2 = 10.68$, $p = 0.005$ Figure 4B). The number of *Lacuna* snails per quadrat were estimated by taking the average number of *Lacuna* from on the two *S. sessilis* individuals in a quadrat and multiplying that by the number of *S. sessilis* adults in that quadrat. The estimated mean number of *Lacuna* per quadrat was then calculated for each transect. Based off these estimates we saw that the

abundance of *Lacuna* did not differ significantly across transects (ANOVA, N=10, F=1.40, P=0.27, Figure 4C).

Effect of desiccation on kelp blade tissue

After the third consecutive day of low tide simulations, stressed samples differed from unstressed samples in a number of metrics. The weight of each sample type dropped after low tide and recovery differed between treatments. The not stressed samples were able to recover, on average, 96.9 to 99.0% of their weight after each low tide simulation, whereas the stressed samples recovered, on average, 84.0% of their weight after the first low tide and gradually recovered less after each subsequent low tide. At the end of the three days of low tide treatments and recovery periods, stressed samples lost, on average, 26.9% of their weight, and not stressed samples lost, on average, 3.1% of their weight; the two sample types differed in their post-repeated low tide weights (Paired t-test on LN-Transformed data, N=30 pairs, T= 9.8, P<0.0001, Figure 5). Stressed samples also showed more visible damage than unstressed samples: stressed samples percent brown decreased 49.2%, whereas the not stressed samples percent brown decreased by 0.4% by the end of the three low tide simulations (Paired t-test, N=30 pairs, T=16.75, P<0.0001, Figure 6A). Lastly, stressed samples got smaller after repeated low tide exposure. After the end of the repeated low tide simulations, stressed samples on average, had 20.0% less of their area and the not stressed samples actually gained on average, 1.2% of their area by the end of the repeated low tide simulation (Paired t-test, N=30 pairs, T=14.96, P<0.0001, Figure 6B).

Herbivore Trials

Katharina tunicata consumed significantly more stressed *S. sessilis* tissue than not stressed tissue (Wilcoxon Sign Rank Test on raw data, N=10 pairs, S=19.5, P=0.049, Figure 7A). For both of their trials, the amount of stressed *S. sessilis* tissue *Idotea wosnesenskii* consumed was not different from the amount of not stressed tissue consumed (Trial 1: Wilcoxon Sign Rank test on raw data, N=5 pairs, S=0.813, P=0.406, Figure 7B; Trial 2: Wilcoxon Sign Rank test on raw data, N=5 pairs, S=0.5, P=1.00, Figure 7B).

Discussion

The effects of low tide stressors on *Saccharina sessilis* are poorly understood. This study showed that repeated exposure to wind causes *S. sessilis* blades to shrink. Applying this concept to *S. sessilis* in the low intertidal zone during low tide means that the canopy that *S. sessilis* provides also has the potential to shrink after repeated exposure to winds of even low speeds and short duration (e.g. 1.0 m/s for 90 minutes). Smaller algal canopies lead to less space for intertidal organisms, like *Katharina tunicata*, to escape stressful low tide conditions. This may intensify competition for space, which could alter intra- and inter-species interactions in the intertidal zone.

In this study, we also found that *K. tunicata* favored damaged tissue over undamaged *S. sessilis* tissue—an unexpected finding—and that *I. wosnesenskii* had no preference between damaged and undamaged tissue. Therefore, some herbivores of *S. sessilis* have a preference for damaged tissue while others do not. Past research has found

that *S. sessilis* produces polyphenolic compounds in both adult and juvenile tissue (Van Alstyne et al. 1999). Polyphenolic compounds are known act as herbivore deterrents in algae (Van Alstyne et al. 1999, Ragan and Glombitza 1986; Steinberg 1992). This brings up the question of whether the concentration of these compounds is altered after the tissue accumulates damage. In addition, I observed that damaged *S. sessilis* tissue was easier to tear than undamaged tissue. We do not know the mechanism behind the demonstrated preference of *K. tunicata* for damaged *S. sessilis* tissue; chemical or mechanical differences—or both—between damaged and undamaged tissue may be factors. In contrast, *I. wosnesenskii* did not have a preference for damage or undamaged tissue. Previous research has showed that marine isopods *P. reticulata* and *P. rubra* do not have digestive fluids that react to phenolic compounds (Tugwell and Branch 1992). In addition, tissue toughness may not be factor in *I. wosnesenskii* food choice because of their mandible mouthparts. Unlike radula teeth that have to be continually replaced because of wearing (Runham 1962), these isopod mandibles are never replaced (Hassall 1977).

Our data show that susceptibility to herbivory for *Saccharina sessilis* depends on many factors, including the amount of damage it experiences during low tide and the differences among the feeding preferences of its herbivores. In order to evaluate the potential for herbivory on an individual we have to consider not only the abundance of herbivores around an *S. sessilis* individual, but also the identity of the herbivores, the amount of damage that kelp individual has experienced, the way the herbivores feed mechanically and the rate that they feed. Future studies should investigate the levels of polyphenolic compounds in damaged *S. sessilis* tissue in comparison to those in

undamaged tissue. Additionally, studies should also look at potential incentives there may be in the two types of tissue for herbivores, for example, the amount of nitrogen content.

Acknowledgements

I would like to thank my mentors Jennifer Burnaford and Scottie Henderson for all their guidance, support, and enthusiasm during the study. I would also like to thank my lab partners Jafaeth Gomez and Vy Nguyen for their assistance during the study. I would like to acknowledge the Ragen Family for allowing me to conduct this research on their property. I would like to thank Dianna Padilla for her help in identifying *Lacuna* snails. I would like to acknowledge Alan Cairns, Cassandra Donatelli, Rachel Pound, and Samantha Chavez for their technical help. I would like to thank the Friday Harbor Labs Staff and Blinks/NSF REU Program for making it possible for me to do the research. This research was conducted under the NSF grant number: DBI 1262239.

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Tables and Figures

Table 1. Mean (± standard error) low tide conditions over all low tide simulations

	Treatment Type	
	Stress	**No Stress**
Temperature (°C)	22.2 (± 0.05)	21.8 (± 0.05)
Light (Lum/ft^2)*	89.4 (± 2.11)	101.1 (± 3.88)
Wind Speed (m/s)*	1.0 (± 0.002)	0.0 (± 0)

*Conditions significantly different between treatments (Paired t-test, $p<0.05$)

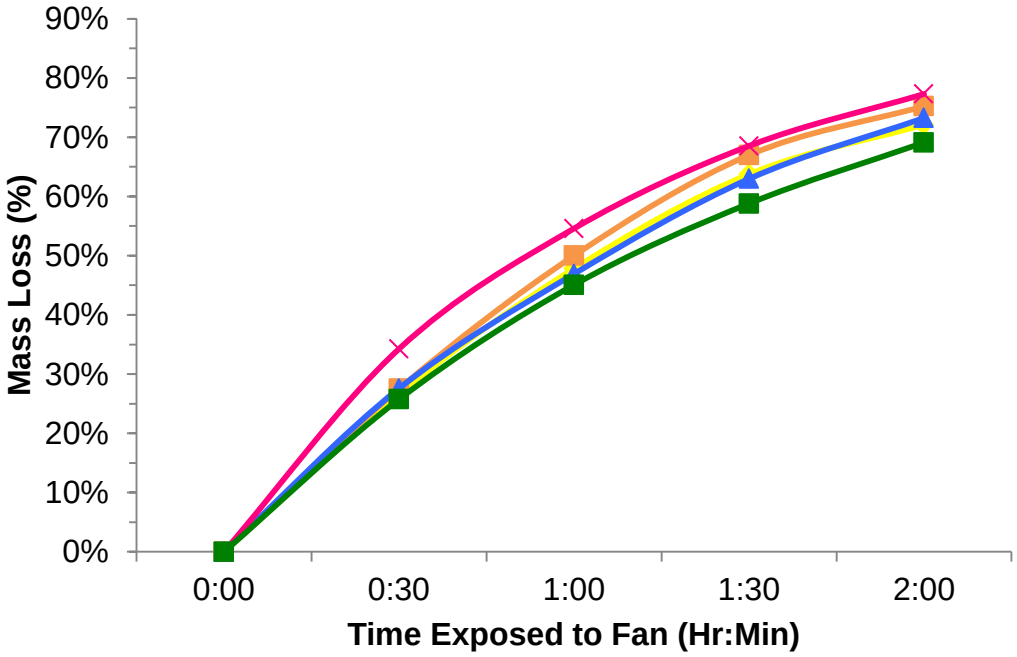

Figure 2. Effect of desiccation treatment on wet mass loss of *S. sessilis* samples. Preliminary data showing desiccation rate of *S. sessilis* 25cm^2 tissue samples (N = 5 samples) exposed to a fan for 2 hours. Each line indicates an individual sample.

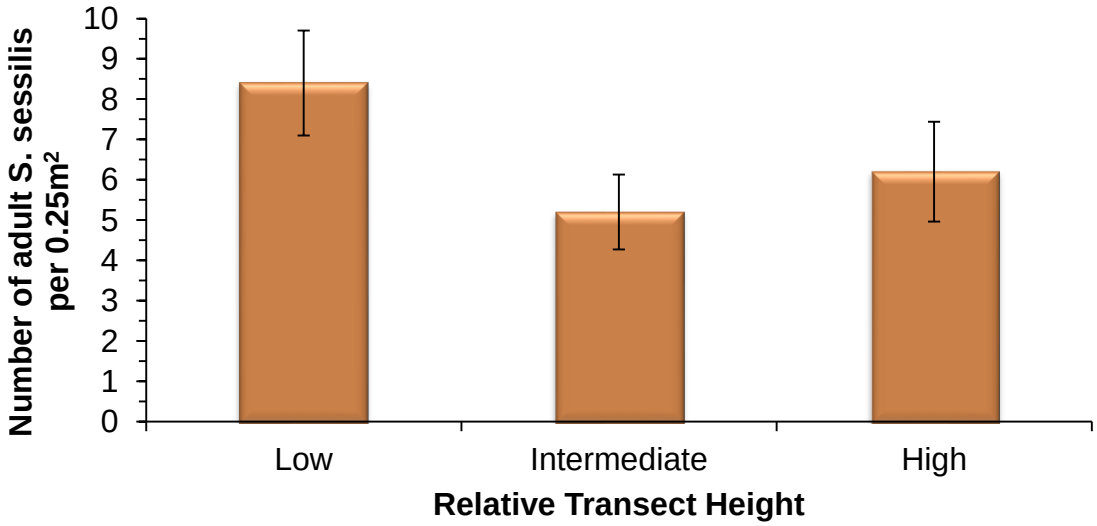

Figure 3. Abundance of *S. sessilis* adults in three transects. The number of individuals was counted in 10 0.25m^2 quadrats / transect. Data are mean ± standard error. Each transect is labeled according to relative tidal height.

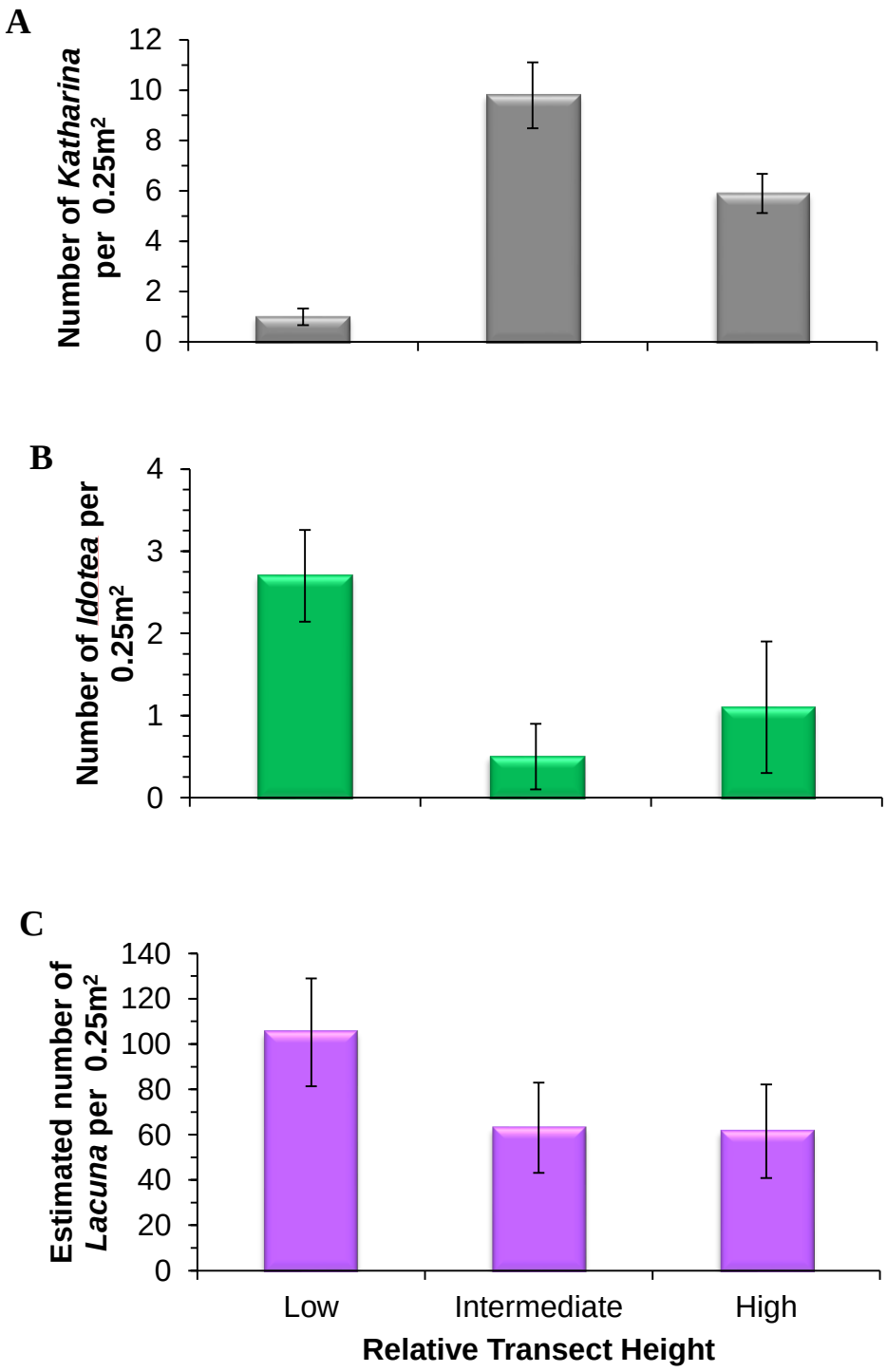

Figure 4. Abundance of *K. tunicata* (A), *I. wosnesenskii* (B), and *Lacuna* snails (C) in three transects. The number of individuals was counted in 10 0.25m^2 quadrats / transect. *Lacuna* counts were estimated. Data are mean ± standard error. Each transect is labeled according to relative tidal height.

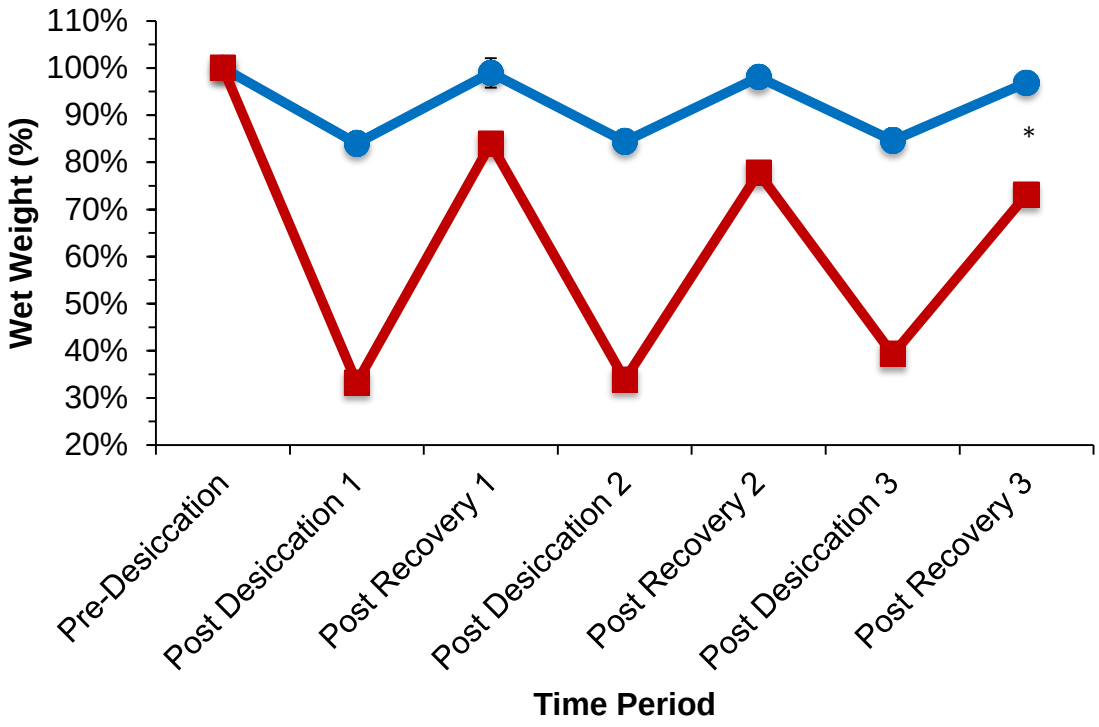

Figure 5. Wet weight of experimental kelp samples during pre-herbivory preparation period (N=30 pairs). Stressed samples (red line, square symbols) were exposed to desiccating low tide conditions for 90 minutes each day for three consecutive days. Unstressed samples (blue line, circle symbols) were exposed to non-desiccating low tide conditions for the same period of time. Samples were weighed before low tide treatments began (pre-desiccation weight) and subsequent weight measurements were scaled to this original weight (expressed as % pre-desiccation weight). Samples were weighed immediately after each low tide simulation (Post Desiccation), and after recovering in seawater for approximately 24 hours (Post Recovery). Data are means ± SE (in some cases symbols are large enough to obscure error bars). The asterisk represents the data that were used for statistical comparison of wet weights.

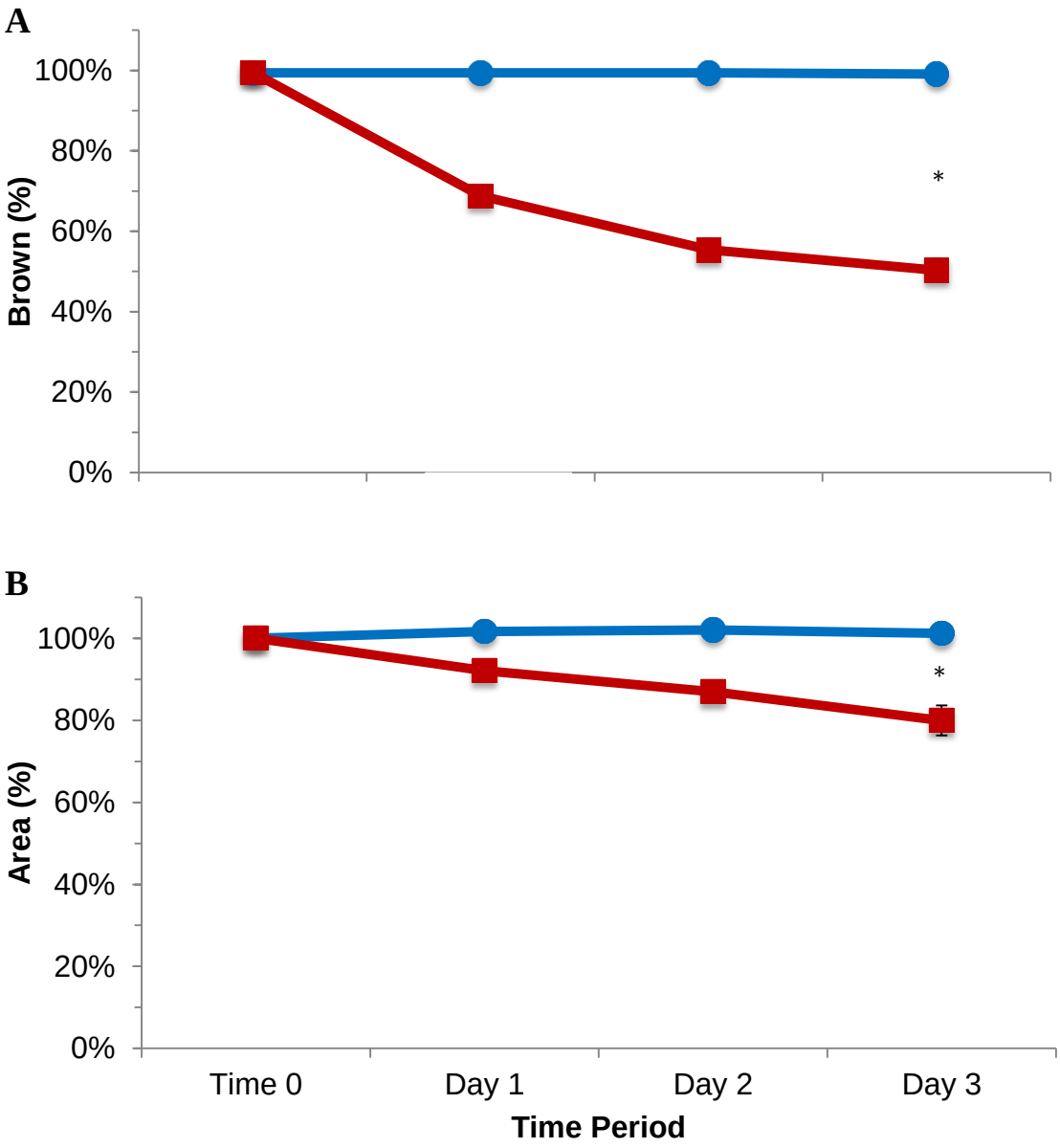

Figure 6. Percent of blade area which was visibly undamaged (A) and area (B) of experimental kelp samples during pre-herbivory preparation period (N=30 pairs). Stressed samples (red line, square symbols) were exposed to desiccating low tide conditions for 90 minutes each day for three consecutive days. Unstressed samples (blue line, circle symbols) were exposed to non-desiccating low tide conditions for the same period of time. Samples were surveyed and measured before low tide treatments began (Time 0) and subsequent surveys and measurements were scaled to their original metric (expressed as % pre-desiccation percent brown or area). Samples were surveyed and measured after recovering in seawater for approximately 24 hours (Day 1, 2 and 3). Data are means ± SE (in some cases symbols are large enough to obscure error bars). The asterisk represents the data that were used for statistical comparison of wet weights.

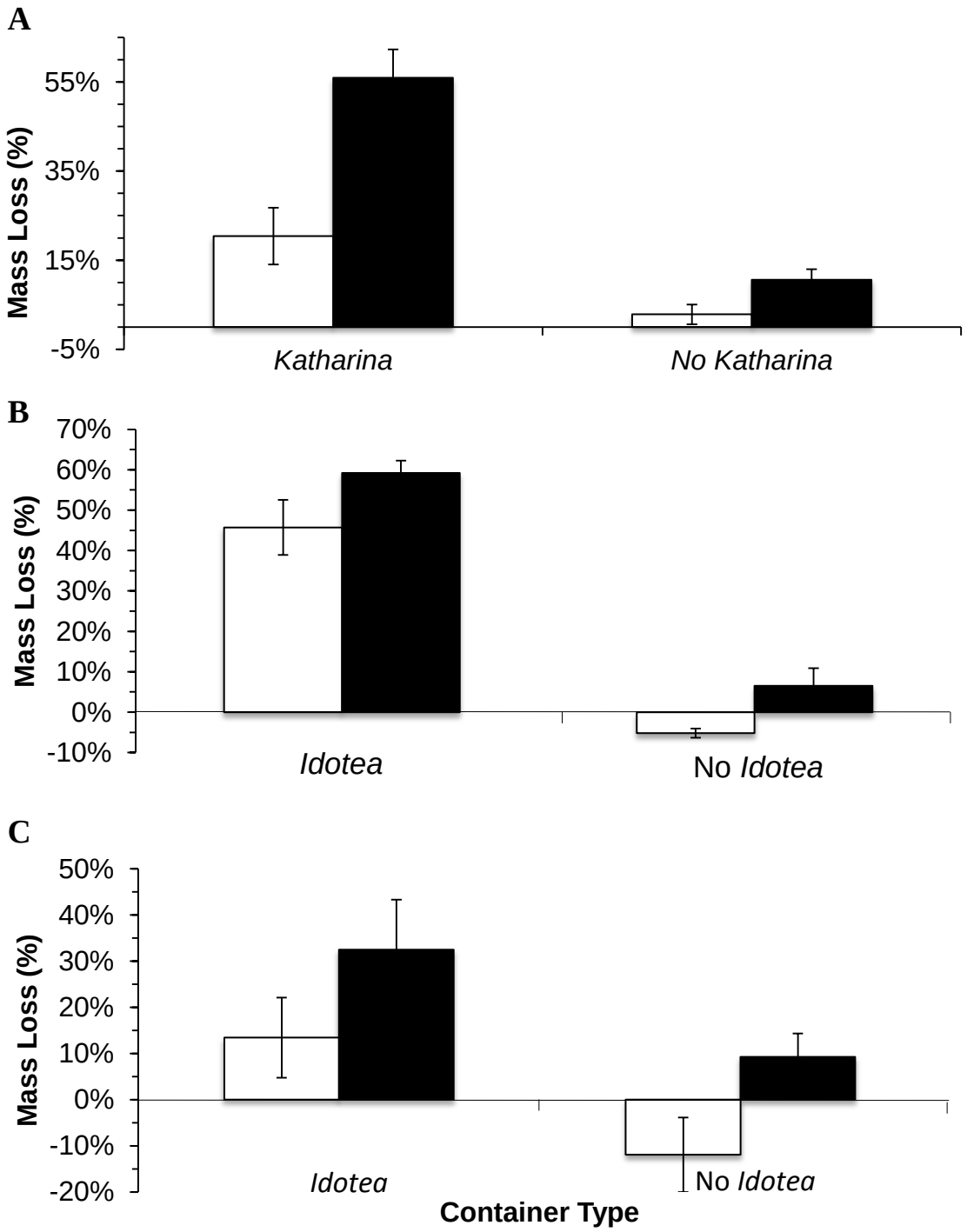

Figure 7. Mass loss of experimental kelp samples during herbivory trials. *Katharina* trials (A) consisted of 10 container pairs. *Idotea* trials (B and C) consisted of 5 container pairs each. Stressed samples (black bars) were exposed to desiccating low tide conditions for 90 (A, B) or 60 (C) minutes each day for three consecutive days before the start of herbivory trials. Unstressed samples (white bars) were exposed to non-desiccating low tide conditions for the same period of time. Samples were weighted immediately before and after the herbivory trial. Final weight measurements were scaled to the sample's original weight (expressed as % pre-herbivory weight). Data are means ± SE. Negative percent mass loss indicates growth.