A comparison of laboratory feeding rates with *in situ* capture of drift algae by the red urchin *Strongylocentrotus franciscanus*

Spencer Roberts[1,2]

REU Blinks Fellowship, Summer 2012

[1]Friday Harbor Laboratories, University of Washington, Friday Harbor, WA 98250
[2]Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO 80309

Contact Information:
Spencer Roberts
Ecology and Evolutionary Biology Department
University of Colorado at Boulder
Boulder, CO 80309
spencer.roberts@colorado.edu

Keywords: urchin, *Stongylocentrotus franciscanus*, spatial subsidy, feeding preference, drift kelp, Point Caution

The red sea urchin (*Strongylocentrotus franciscanus*) is a common subtidal herbivore throughout the northeast Pacific. In the San Juan Archipelago (SJA), Washington, red urchins are subject to little predation pressure and are generally exposed and sedentary. Recent research has shown that detached drift algae are common and abundant at all subtidal depths surveyed (>150 m) in the SJA. Here, we investigated whether red urchin feeding rates observed in the laboratory were consistent with field observations of drift capture. Feeding rates were quantified for captive red urchins; from most to least rapidly consumed (grams per hour), these were: *Nereocystis luetkeana, Mazzaella splendens, Saccharina sp., Agarum fimbriatum,* and *Ulva sp.* In the field using SCUBA, we repeatedly collected all algae captured by urchins at one-day and six-day intervals within a 25 m^2 permanent transect at a depth of 18 m. We identified, blotted, and massed the 'stolen' algae to compare taxonomic composition and mass captured over different time frames, assuming that drift held after a longer time period would more closely reflect urchin preference. Results indicate that at least at this site, availability of particular algae is more important in determining overall drift capture rates than is urchin preference. However, captured *Agarum* constituted a smaller proportion of total algal mass when urchins were given six days to collect drift, indicating that they are likely discarding this alga. This result is consistent with current and previous lab preference studies and suggests that the large quantity of *Agarum* drift into deep water is a low-quality subsidy, at least for urchins.

Introduction

Deep subtidal environments represent some of the least understood marine ecosystems on Earth. In the absence of major photosynthetic activity, these systems must rely on spatial subsidies for primary production. In the case of the San Juan Archipelago, a temperate environment full of deep channels and strong currents, drifting macrophytes appear to be a major constituent of the base of deep subtidal foodwebs (Britton-Simmons, et. al, 2012). As demonstrated in other locations, the distribution of this drift can be influenced by a multitude of factors, including, but not limited to seafloor topography, current systems, storm activity, and seasonal patterns (Ebeling et. al, 1985; Vetter & Dayton 1999; Vanderklift & Wernberg 2008). However, while the transport of macrophyte detritus may be controlled by an interplay of abiotic factors regionally, the finer-scale influence of the biota that interact with this drift via preferential selection, consumption, and digestion has been overlooked.

Worldwide, sea urchins are major constituents of deep subtidal regions (Choat & Schiel, 1982; Peckol & Searles, 1984; Pérez-Matus, et. al, 2006; Bonaviri, et. al, 2011), and therefore are likely to be important herbivores on the detrital algae that sink into deep water. Due to their abundance and high capacity to both capture and consume detrital algae (Britton-Simmons, et. al, 2009), they may also play an important role in governing the food available to other grazers on the seafloor in such environments, a phenomenon observed in shallower habitats (Vance, 1979). In addition, while urchins may limit available food for local grazers, the innate inefficiency of their digestive systems may actually provide nutritionally valuable food in the form of particulate feces for suspension-feeders down-current. Multiple stable isotope analysis has indicated drift kelp to be the main form of sustenance for many marine filter-feeders, even in intertidal zones with abundant phytoplankton production (Bustamante & Branch 1996; Fredriksen 2003), and urchins contribute to this process by accelerating the degradation of the drift. Locally, the detritus of the San Juan Channel has been demonstrated as highly diverse in its origins (Britton-Simmons, et. al, 2012), but the hypothesis that sea urchin feces comprises an important part of the detrital diet of nearby filter-feeders is poorly tested. Therefore, understanding urchin feeding preference is important to the ecology of both shallow (Paine & Vadas, 1969; Harrold & Reed, 1985) and deeper waters.

While many studies conducted in laboratory settings have shown correlations between urchin feeding preference and season, dietary history, or assimilation efficiency (Vadas, 1977; Larson, et. al, 1980; Vaïtilingon, et. al, 2003; Lyons & Scheibling, 2006), the removal of kelp stands by urchins in the field appears to show no such preference hierarchy (Schiel, 1982). However, few studies have attempted to observe preferences for different detrital algae in the wild. In this study, I assess the viability of inferring urchin detrital preference using observational data by collecting detrital algae selected from the drift by urchins in a given area. The constituents of the captured drift are then compared between long and short time frames during which the urchins selected detritus. I will then compare these data to those obtained from feeding trials with the red sea urchin (*Strongylocentrotus franciscanus*), namely feeding rates and nutritional values quantified by comparing the caloric and fatty acid content of different algal diets and the respective urchin feces.

Methods

Feeding Rates on Various Algae

Red sea urchins (*Strongylocentrotus franciscanus*) were collected from Neck Point off Shaw Island, Washington, USA. After a sufficient feeding period on treatment diets (3 days) to ensure previous gut contents were cleared, trials began. Urchins were held in perforated buckets with weights and grating at the bottom to separate urchins from the negatively buoyant feces. Lids with large holes were attached with string tied across to allow intake of new water while still preventing urchins from escaping. Fresh thalli of the species *Nereocystis luetkeana, Agarum fimbriatum, Ulva sp.,* and *Mazzaella splendens* were each fed to at least three urchins, who were given between 61 and 78 hours to feed. To calculate feeding rate, mass of each thallus was measured both before and after trials. All urchins were returned to the wild after trials were conducted.

Observational Analysis of Feeding Preference

To compare the detrital algae captured by urchins over short and long time frames as well as in both spring and neap tides, dives were conducted regularly at one site over four weeks during summer. A permanent transect was established at Point Caution off San Juan Island, ranging from approximately 30 feet to 65 feet of depth. Each week, one dive was conducted after a hiatus of six days, followed by a dive roughly 24 hours later when the tidal slack provided a safe current.

On each dive, urchins in the area were counted and all algal pieces held in the spines of urchins were collected and carefully brought to the surface. In the laboratory, algae were separated and identified to genus. Fragments present in each genus were counted and all algae were blotted and massed. From these data, we inferred mass, fragments, and mass per fragment of each algal taxon, as well as captured algal mass per urchin and fragments per urchin of each taxon.

Results

The vast majority of proportion by mass of drift algae collected from urchins was found to be Phaeophyta, particularly the abundant and massive kelps (Figure 1). The mass of drift captured per urchin after one day was consistently about half the mass of that captured per urchin after six days (Figure 2, p=.0693, t=2.3059, df=5). Analyzing particular species of drift algae captured during different time frames suggested that urchins may selectively retain and let go of different species. *Agarum fimbriatum* was present in higher proportion by mass after a one day capture period than after a six day period (Figure 3, p=.0562, t=2.3608, df=6). *Plocamium spp.* showed a reverse trend, with higher average mass captured during the six-day time frame (Figure 4, p=.0761, t = 2.2312, df=5).

In laboratory trials, feeding rates, measured in grams per hour, show variability between the treatment diets, but overall, urchins consumed the 5 species at different rates (Figure 5, one-way ANOVA, p<.001, df=35). Pairwise comparisons showed that *Nereocystis luetkeana* was consumed faster than all other algae than *Mazzaella splendens,* which was consumed faster than all algae than *N. luetkeana* and *Saccharina spp.* (Figure 4, p<.001, df=35). A consistent downward trend was observed in the number of urchins present at the transect ever since pilot data recording began (Figure 6) and the average mass captured per urchin also decreased steadily over the course of the four weeks of the study (Figure 1).

Discussion

Drift algae captured by red urchins in the shallow subtidal zone were heavily dominated by brown algae (Phaeophyta); this probably reflects the large biomass of these species in local waters (Van Blaricom & Chambers, 2003). This suggests that, at this location, urchin drift capture is largely determined by availability of algae, rather than urchin feeding preference. However, the fact that drift captured per urchin in one day was consistently about half of that captured over the previous six days implies that urchins do not accumulate algal mass linearly with respect to time, but that their rate of capture slows after the first day, which supports the hypothesis of urchins discarding algae (Vanderklift & Kendrick, 2005).

To further support this hypothesis, the proportion of total captured mass represented by *Agarum spp.* was quite different between the two time frames. This trend suggests that this alga, which has been demonstrated as both less preferable and less nutritious to urchins when compared to other algae (Vadas, 1977; Larson, et. al, 1980), is typically captured from the current and subsequently discarded somewhere between the first and sixth day. My laboratory feeding rate data further supports that *Agarum spp.* are a non-preferred food source for urchins.

Concerning the influence of urchin feeding preference on spatial macrophyte subsidies, selective drift capture may imply that drift algae available to deeper or down-current urchins is less diverse and/or less desirable. Perhaps future studies could employ a flume or a consistent unidirectional current in the field to compare drift captured by up-current versus down-current urchins and further test this hypothesis. However, future studies that aim to recover algae from urchins would ideally be longer-term, which means that less invasive techniques would be required to mitigate the observed effect of handling the animals. Also implicit is the hypothesis that selective drift capture creates more valuable suspended urchin feces down-current. One possible way to address this question could be biomarker analyses on suspension feeders near versus far from urchin assemblages.

Feeding rates obtained from trials are consistent with results from other studies and preference hierarchies they have calculated (Vadas, 1977; Larson, et. al, 1980). *Nereocystis luetkeana* was consumed at a significantly higher rate than all algae besides *Mazzaellea splendens*. The low feeding rate, and inferably, low preference for *Agarum fimbriatum* seems to be consistent with the field data, suggesting another supporting argument for the hypothesis of drift discard.

Overall, the variability of both total and per urchin mass of drift captured suggests that, at this site, drift-catching behavior is governed more importantly by the availability of drifting macrophytes than preferences for specific algae. However, because determining the actual proportions of algae in the drift is highly difficult logistically, our interpretations of availability are constrained to what we observe urchins having captured and surveys of local seaweed populations. Nonetheless, the data obtained from this study implies that while urchins may possess an evolutionary mechanism to seek out nutritionally valuable food sources, they may not often have the ability to choose in nature. Interestingly, the urchins in deep subtidal areas where algae has come to rest in mats on the seafloor may have more food choice than those in sites such as Point Caution, where urchins must capture passing drift, which is subject to vary with seasons and disturbances (Ebeling, 1985; Gibbert et. al, 2003). The results of this study suggest that urchins may have a significant effect on the drifting macrophytes that subsidize deep subtidal ecosystems, especially considering that we have only examined one site during one month of the year. Urchin preferences for drift algae in other locations and environments have the potential to have both much stronger and much weaker effects on spatial macrophyte subsidies. As research progresses and methods are refined, drift collection could become a useful technique for observing urchin feeding preferences in nature.

Figures

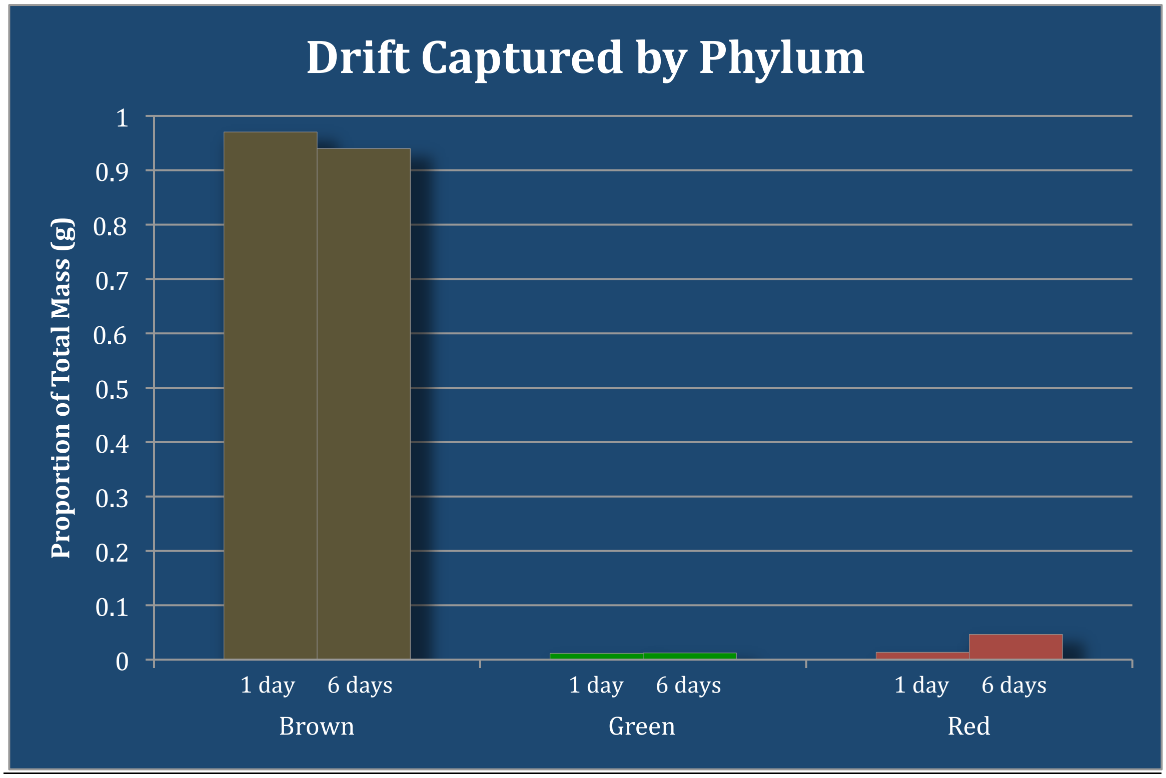

Figure 1. Bars represent the average proportion of total mass captured by urchins divided by phylum after one day versus six days. It is clear that over 90% was identified as brown

algae (Phaeophyta). It appears that there may be some selectivity preferring red algae, but due to their much lower mass, this number is insignificant in terms of proportion of mass.

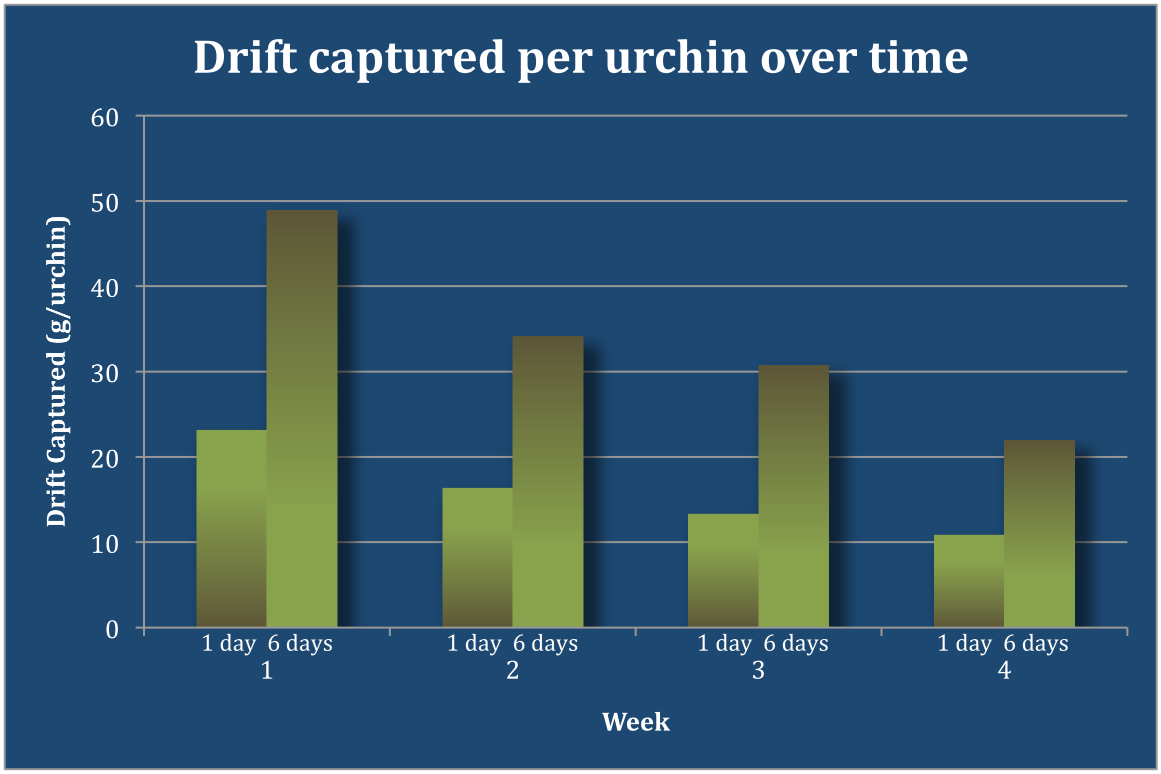

Figure 2. This graph shows the average mass of drift algae captured per urchin on each dive. The fact that after one day, urchins have accumulated half the mass that they do over six days (p=.0693, t=2.3059, df=5) implies that they do not accumulate algal mass linearly with respect to time. Also clear is the consistent downward trend, which can likely be attributed to the handling effect on the animals.

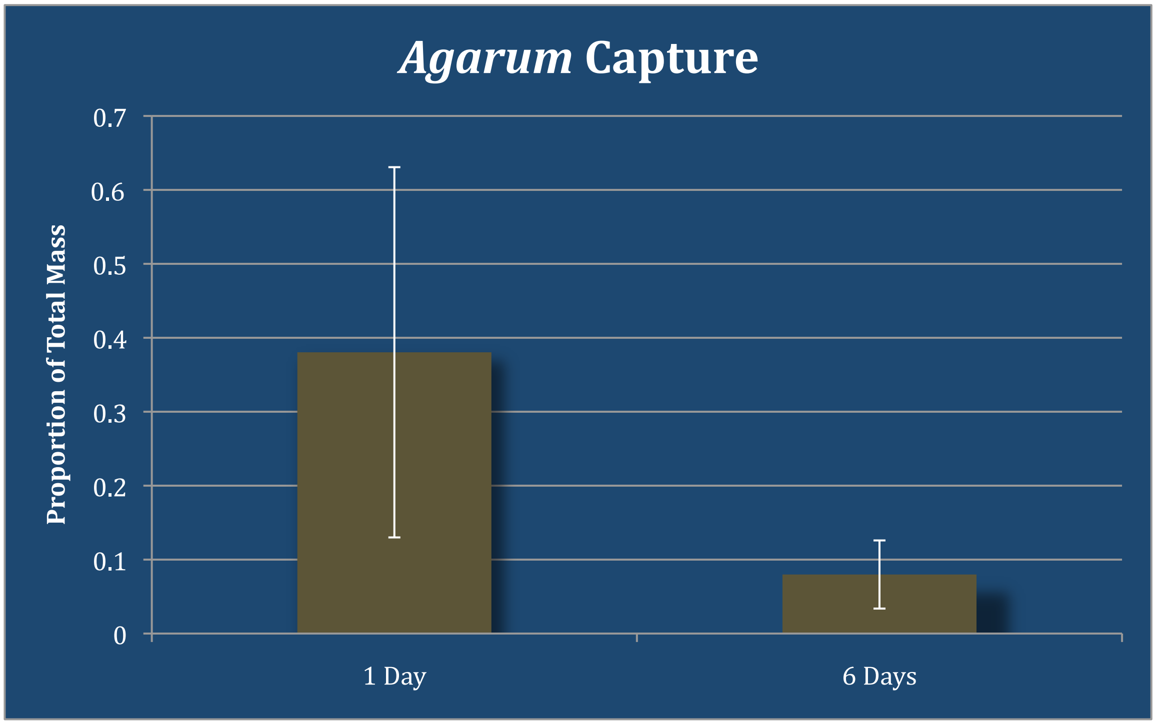

Figure 3. Depicted here is the average proportion of total mass represented by *Agarum spp.* compared at one-day versus six-day intervals. The difference seen here implies urchin selectivity against this particular alga (p=.0562, t=2.3608, df=6).

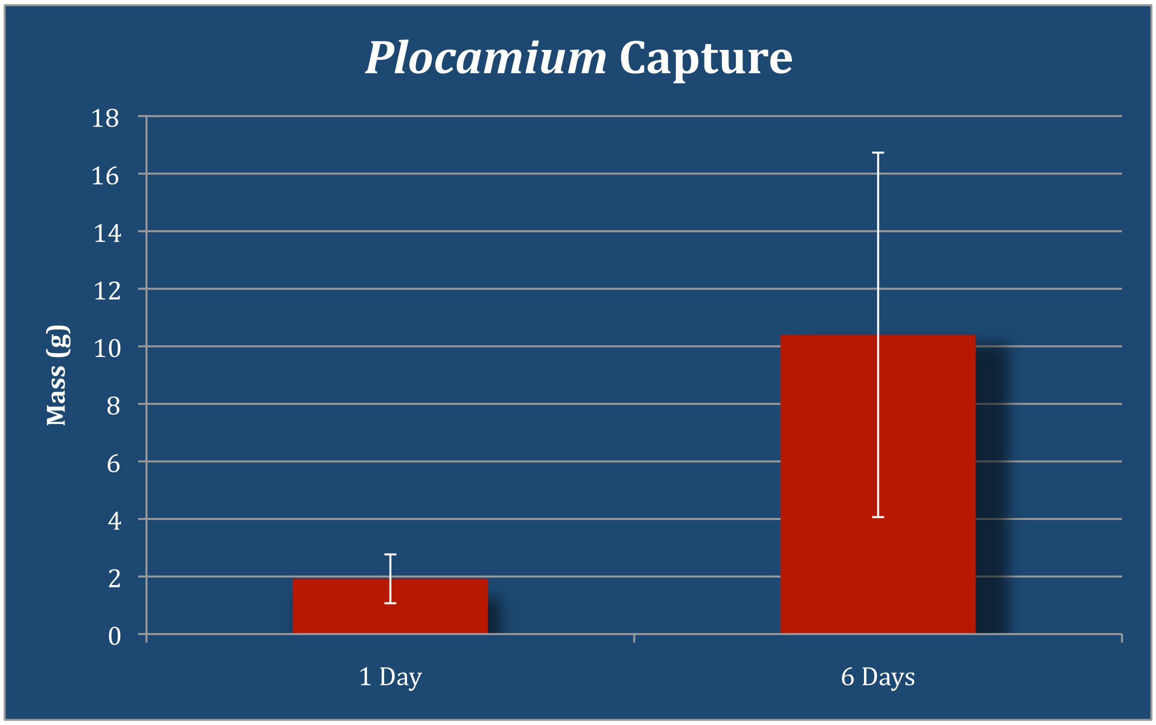

Figure 4. Because red algae were so insignificant by proportion of total mass, this graph analyzes the average mass represented by *Plocamium spp.* compared at one-day versus six-day intervals (p=.0761, t = 2.2312, df=5). It appears that this may be an alga that urchins select for.

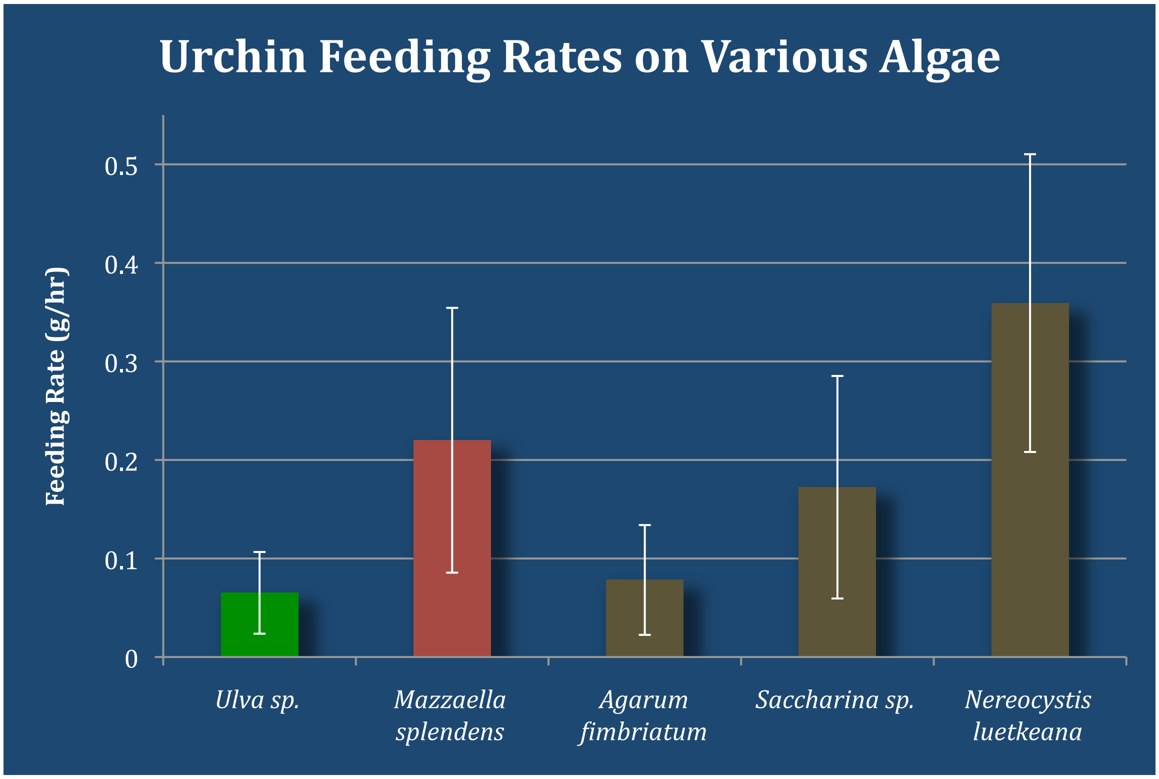

Figure 5. Represented here are feeding rates for *Strongylocentrotus franciscanus* on different algal treatments. Statistical analyses show that *Mazzaella splendens* and *Nereocystis luetkeana* were consumed at higher rates than the three other treatments (one-way ANOVA, p<.001, df=35).

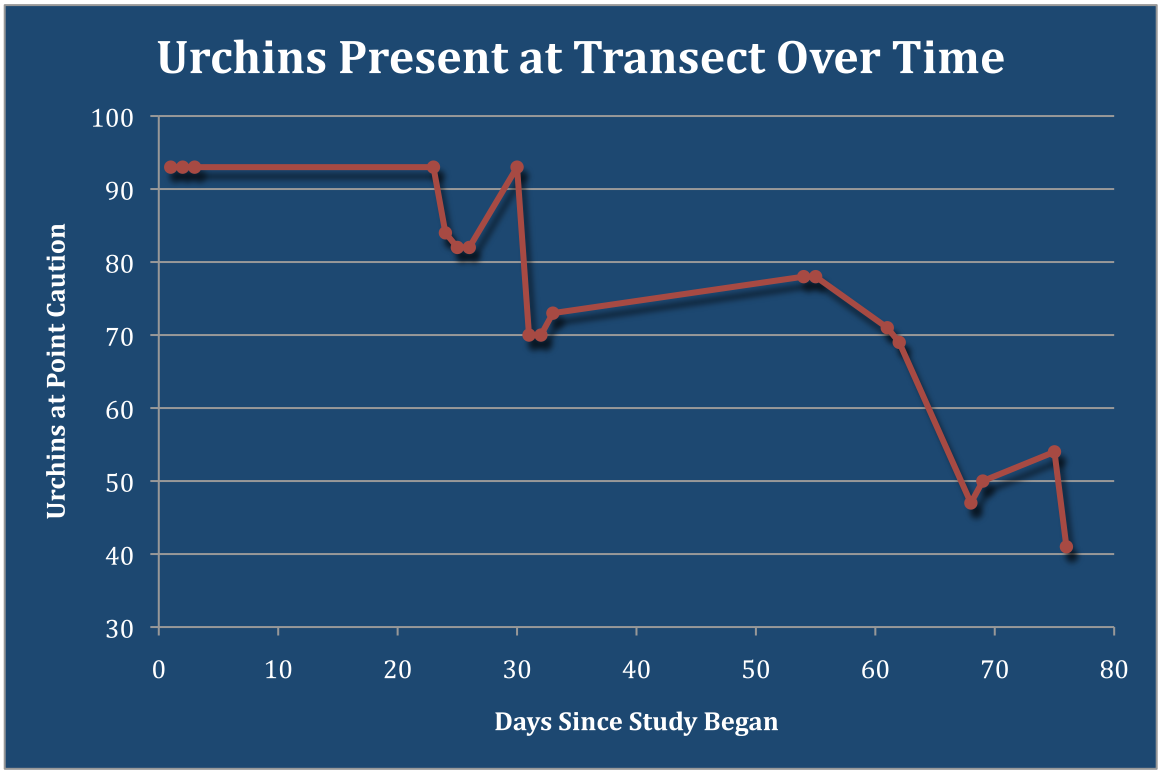

Figure 6. Urchins present at the transect are plotted against the number of days since the study began. Each point represents an individual dive. The data display a consistent decreasing trend with respect to time and number of dives.

Acknowledgements

For their endless support and help, I owe thanks to David Duggins, Megan Dethier, Aaron Galloway, Alex Lowe, Shelby Burgess, Wendel Raymond, Laura Watson, Sarah Weisner, Nat Clarke, Adam Summers, the National Science Foundation, Friday Harbor Laboratories, my summer 2012 REU cohort, and the all of the urchins who participated.

<u>References</u>

Bonaviri, C., T. Vega Fernández, G. Fanelli, F. Badalamenti, and P. Gianguzza. "Leading Role of the Sea Urchin *Arbacia Lixula* in Maintaining the Barren State in Southwestern Mediterranean." *Marine Biology* 158.11 (2011): 2505-13.

Britton-Simmons, Kevin H., G. Foley, and D. Okamoto. "Spatial Subsidy in the Subtidal Zone: Utilization of Drift Algae by a Deep Subtidal Sea Urchin." *Aquatic Biology* 5 (2009): 233-43.

Britton-Simmons, Kevin H., Alison L. Rhoades, Robert E. Pacunski, Aaron W. E. Galloway, Alexander T. Lowe, Elizabeth A. Sosik, Megan N. Dethier, and David O. Duggins. "Habitat and bathymetry influence the landscape-scale distribution and abundance of drift macrophytes and associated invertebrates." *Limnology and Oceanography* 57.1 (2012): 176-84.

Bustamante, Rodrigo H., and George M. Branch. "The Dependence of Intertidal Consumers on Kelp-derived Organic Matter on the West Coast of South Africa." *Journal of Experimental Marine Biology and Ecology* 196.1-2 (1996): 1-28.

Choat, J., and D. Schiel. "Patterns of Distribution and Abundance of Large Brown Algae and Invertebrate Herbivores in Subtidal Regions of Northern New Zealand." *Journal of Experimental Marine Biology and Ecology* 60.2-3 (1982): 129-62.

Ebeling, AW, DR Laur, and RJ Rowling. "Severe storm disturbances and reversal of community structure in a southern California kelp forest." *Marine Biology* 84.3 (1985): 287-294.

Fredriksen, S. "Food Web Studies in a Norwegian Kelp Forest Based on Stable Isotope (δ13C and δ15N) Analysis." *Marine Ecology Progress Series* 260 (2003): 71-81.

Harrold, Christopher, and Daniel C. Reed. "Food Availability, Sea Urchin Grazing, and Kelp Forest Community Structure." *Ecology* 66 (1985): 1160-69.

Larson, B. R., R. L. Vadas, and M. Keser. "Feeding and Nutritional Ecology of the Sea Urchin Strongylocentrotus Drobachiensis in Maine, USA." *Marine Biology* 59.1 (1980): 49-62.

Lyons, D., and R. Scheibling. "Effect of Dietary History and Algal Traits on Feeding Rate and Food Preference in the Green Sea Urchin *Strongylocentrotus Droebachiensis*." *Journal of Experimental Marine Biology and Ecology* 349.1 (2007): 194-204.

Paine, Robert T., and Robert L. Vadas. "The Effects of Grazing by Sea Urchins, *Strongylcentrotus Spp.*, on Benthic Algal Populations." *Limnology and Oceanography* 14.5 (1969): 710-19.

Peckol, P., and R. Searles. "Temporal and Spatial Patterns of Growth and Survival of Invertebrate and Algal Populations of a North Carolina Continental Shelf Community." *Estuarine, Coastal and Shelf Science* 18.2 (1984): 133-43.

Pérez-Matus, Alejandro, Lara A. Ferry-Graham, Alfredo Cea, and Julio A. Vásquez. "Community Structure of Temperate Reef Fishes in Kelp-dominated Subtidal Habitats of Northern Chile." *Marine and Freshwater Research* 58.12 (2007): 1069-85.

Schiel, David R. "Selective Feeding by the Echinoid, *Evechinus Chloroticus*, and the Removal of Plants from Subtidal Algal Stands in Northern New Zealand." *Oecologia* 54.3 (1982): 379-88.

Vadas, Robert L. "Preferential Feeding: An Optimization Strategy in Sea Urchins." *Ecological Monographs* 47.4 (1977): 337-71.

Vaïtilingon, D., R. Rasolofonirina, and M. Jangoux. "Feeding Preferences, Seasonal Gut Repletion Indices, and Diel Feeding Patterns of the Sea Urchin *Tripneustes Gratilla* (Echinodermata: Echinoidea) on a Coastal Habitat off Toliara (Madagascar)." *Marine Biology* 143.3 (2003): 451-58.

Van Blaricom, Glenn R., and Melinda D. Chambers. "Testing a Charismatic Paradigm: Consequences of a Growing Sea Otter Population for Nearshore Benthic

Communities along the South Shore of the Strait of Juan De Fuca." *Final Project Report: Marine Ecosystem Health Program* (2003)

Vance, Richard R. "Effects of Grazing by the Sea Urchin, *Centrostephanus Coronatus*, on Prey Community Composition." *Ecology* 60.3 (1979): 537-46.

Vanderklift, MA, and GA Kendrick. "Contrasting Influence of Sea Urchins on Attached and Drift Macroalgae." *Marine Ecology Progress Series* 299 (2005): 101-10.

Vanderklift, Mathew A., and Thomas Wernberg. "Detached Kelps from Distant Sources Are a Food Subsidy for Sea Urchins." *Oecologia* 157.2 (2008): 327-35.

Vetter, EW, and PK Dayton. "Organic Enrichment by Macrophyte Detritus, and Abundance Patterns of Megafaunal Populations in Submarine Canyons." *Marine Ecology Progress Series* 186 (1999): 137-48.