

**A Comparison of Laboratory Feeding Rates with *in situ*  
Capture of Drift Algae by the Red Urchin  
*Strongylocentrotus franciscanus***

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Defended November 1, 2012

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## Abstract

The red sea urchin (*Strongylocentrotus franciscanus*) is a common subtidal herbivore throughout the northeast Pacific. In the San Juan Archipelago, Washington, red urchins are subject to little predation pressure and generally exposed and sedentary. Recent research has shown that subtidal red urchins feed primarily on detached drift algae, abundant at all subtidal depths surveyed in the San Juans. Here, I investigated whether field observations of urchin drift capture were consistent with red urchin feeding rates in the laboratory and feeding preferences shown in other studies. Feeding rates were quantified for captive red urchins; from most to least rapidly consumed (g/hr), 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<sup>2</sup> permanent transect at a depth of 18 m. We identified, blotted, and massed the “stolen” algae to compare proportions 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 this site, availability of an alga is more important in determining its proportion in captured drift than is urchin preference. However, comparing proportions of each specific alga between time frames revealed some tentative trends of selectivity. The most statistically and ecologically significant of these were kelps of the genus *Agarum*, which constituted a much smaller proportion of total mass when urchins were given six days to collect drift, indicating that urchins 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, often in the form of drift algae, for primary production. In the case of the San Juan Archipelago, a temperate environment full of deep channels and strong currents, drifting macrophytes- algae that grow from the seafloor such as kelps- 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 regionally, the transport of drifting macrophytes may be controlled by an interplay of environmental factors, the finer-scale influence of the organisms that interact with this drift via preferential selection, consumption, and digestion has been overlooked.

Worldwide, sea urchins are major constituents of 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 detached and drifting algae, known as detritus, that sink into deep water. Due to urchins' abundance and high capacity to both capture and consume detrital algae (Britton-Simmons, et al. 2009), these animals 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, a technique that can identify an animal's food sources by analyzing its tissues, 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). Urchins, therefore, contribute to this energy source by accelerating the degradation of 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 digestive efficiency (Vadas, 1977; Larson, et al. 1980; Väitilingon, 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, if any, studies have attempted to observe preferences for detrital algae in the wild. In this study, I assess the viability of inferring urchin detritus preference using observational data by collecting 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 laboratory feeding trials with the red sea urchin (*Strongylocentrotus franciscanus*), namely feeding rates, which, in conjunction with data from previous studies that compare many of the same algae in terms of urchin

selectivity, digestive efficiency, and caloric content (Vadas, 1977; Larson, et al. 1980), will allow me to infer trends in feeding preference.

### Background

The scarcity of research concerning spatial subsidies from kelp forests may seem to insinuate that they are a minor ecological phenomenon, but globally, the magnitude of drift exported from kelp forests may actually be comparable to the size of kelp forests themselves. Recent discoveries in the Galapagos Islands by Graham, et al. (2007) revealed kelp beds thriving in deep tropical waters. This presents the possibility for thousands of undiscovered kelp beds in environments closer to the equator and further offshore than previously thought possible. If we include these hypothesized regions of kelp production, depicted in red in panel 1, the estimate for the global carbon reservoir in standing kelp is as high as 20 billion kilograms of carbon (Reed & Brzezinski, 2009). However, using the same model, the corresponding high-end estimate for the net primary productivity- essentially, total plant growth- of kelp beds across the globe is nearly twice that number annually- 39 billion  $\text{kgC yr}^{-1}$ . By dividing these figures, we can calculate an average turnover rate of nearly  $2 \text{ yr}^{-1}$  and by subtracting, if we ignore the effects of algae harvests by factors such as herbivory and industry, we find that the global magnitude of the drift kelp subsidy can be estimated at roughly 19 billion  $\text{kgC}$ - a quantity comparable to that of all the oceans' standing kelp forests.

This realization that the primary productivity available for deep subtidal ecosystems may be near in size to that for kelp bed ecosystems is currently transforming our understanding of kelp ecology. There may be millions of locations on the world's

continental slopes where assemblages of animals thrive on algal subsidies transported from shallow waters. These ecosystems are presumably vulnerable to fluctuations in the availability of these subsidies and are likely declining in association with the global loss of kelp forests in recent history (Leighton, 1966; Foreman, 1997; Edgar 1997; Estes, et al. 1998; Steneck, et al. 2002). Estimating the condition of these poorly understood ecosystems exemplifies a recurring conundrum within modern conservation biology- the difficulty of predicting the future for a population without any baseline reference of its past levels. Because any quantitative data on deep subtidal communities is extremely scarce in scientific literature and because most observations of kelp population declines are proximately associated with grazing pressure from urchins, enhancing our understanding of urchin grazing behavior may provide an alternative approach to advancing the field. Thus, this study aims to bring new insight to the interactions between coastal and subtidal environments by studying how urchins' influence on spatial algae subsidies may persist long after the removal of kelp stands along the coasts of an environment where urchins are particularly important, ecologically.

The Northeast Pacific waters of British Columbia and Washington are currently at the cutting edge of discoveries in subtidal ecology and spatial subsidies. Lying between these states is a sea named for the indigenous Salish tribes that first inhabited it. The San Juan Archipelago rises from the heart of the Salish Sea; at the junction of Puget Sound, the Georgia strait, and the strait of Juan de Fuca (Panel 2). Previous research in the San Juans has used ROV (remotely operated vehicle) footage to show drift algae and red urchins (*Strongylocentrotus franciscanus*) to be common at depths ranging from 30 to 170 meters (Britton-Simmons, et al. 2012) and inferred from *in situ* feeding observations

and gut content analyses that drift algae is, in fact, the main food source of subtidal red urchins (Britton-Simmons, et al. 2009). Proportions, by mass, of these algae were dominated by kelps (order Laminariales), yet the question remains whether drift capture by urchins reflects patterns in abundance of algae or if preference is a factor in determining these species proportions, which subsequently determine the proportions that subsidize subtidal communities down-current.

## 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 weighted, perforated buckets with grating at the bottom to separate urchins from the negatively buoyant feces. Lids with large holes were attached with strings tied across to allow intake of new water while still preventing urchins from escaping. Fresh thalli of the species *Nereocystis luetkeana*, *Saccharina* sp., *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 and divided by duration of the trial. All urchins were returned to the wild after trials were conducted.

### **Observational Analysis of Drift Capture**

To compare the detrital algae captured by urchins over short and long time frames as well as in both spring and neap tides, SCUBA 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 and number of fragments for each algal taxon, as well as each quantity averaged per urchin.

## Results

Over 21 varieties of algae were identified in drift collected from urchins, which contributed vastly different proportions to the total mass (Figure 1). Proportions of total fragments recovered showed a more even distribution across taxa and phyla (Figure 2). The vast majority (>90% by mass) of drift algae collected from urchins during both time frames were found to be Phaeophytes or brown algae, particularly the abundant and massive kelps (Laminariales). 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 3). However, analyzing proportions of each particular alga captured during different time frames suggested that urchins may selectively retain and let go of different taxa. *Agarum spp.* represented an average proportion by mass over four times higher after a one day capture period than after a six-day period (Figure 4,  $p=.0562$ ,  $t=2.3608$ ,  $df=6$ ), implying urchin selectivity against this particular alga. Because most

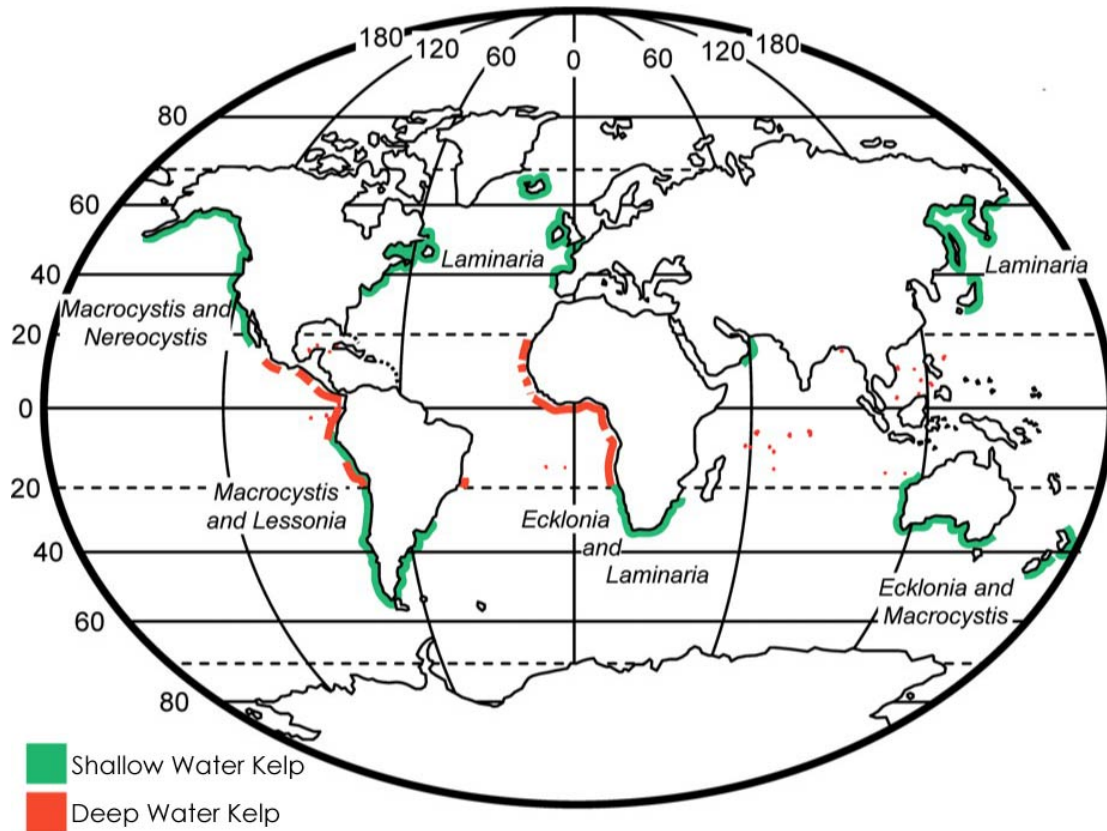


algae were light and insignificant by proportion of total mass, each was also compared between time frames in terms of raw mass. By this standard, *Plocamium spp.* showed the reverse trend, with over five times higher average mass captured during the six-day time frame (Figure 5,  $p=.0761$ ,  $t = 2.2312$ ,  $df=5$ ).

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. Pairwise comparisons showed that *Nereocystis luetkeana* was consumed faster than all other algae, except *Mazzaella splendens*, which was consumed faster than all algae besides *N. luetkeana* and *Saccharina sp.* (Figure 6, one-way ANOVA,  $p<.001$ ,  $df=35$ ). The fact that after one day, urchins accumulated an average of about half the mass that they do over six days (Figure 7,  $p=.0693$ ,  $t=2.3059$ ,  $df=5$ ) implies that they do not accumulate algal mass linearly with respect to time and that selection at maximum drift capacity may optimize foraging. Downward trends were observed in the average mass captured per urchin over the course of the four weeks of the study (Figure 7) and the number of urchins present at the transect since pilot data recording began (Figure 8). These are most likely artifacts of the disturbance caused by divers.

Panels

## Global Location of Kelp Forests



Panel 1. Global distribution of kelp forest ecosystems with potential areas for tropical kelp beds shown in red. Figure published by Santelices in 2007.



## Figures

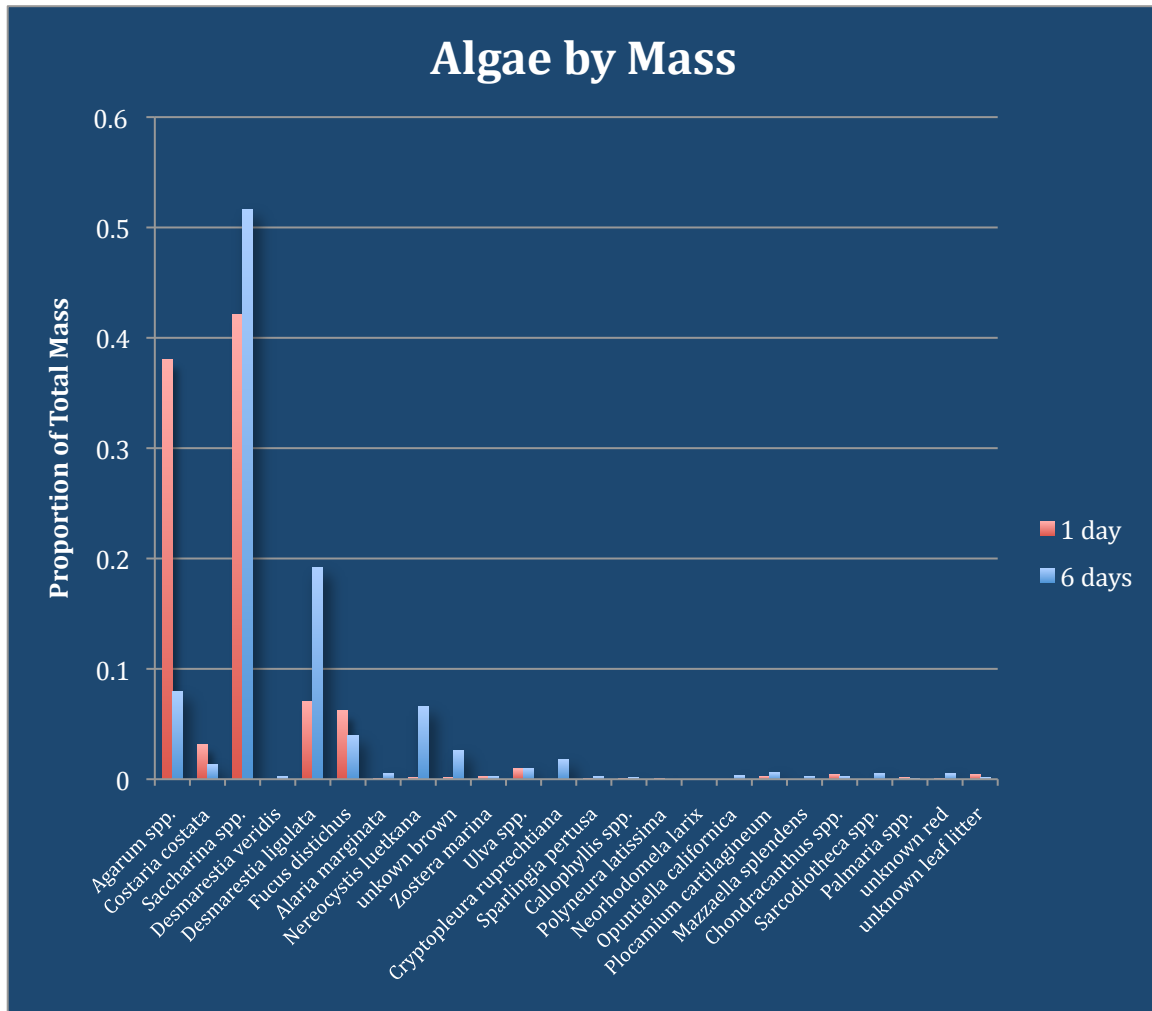


Figure 1. Proportions of total mass represented by each algal taxon identified in urchin drift capture compared at one-day versus six-day intervals.

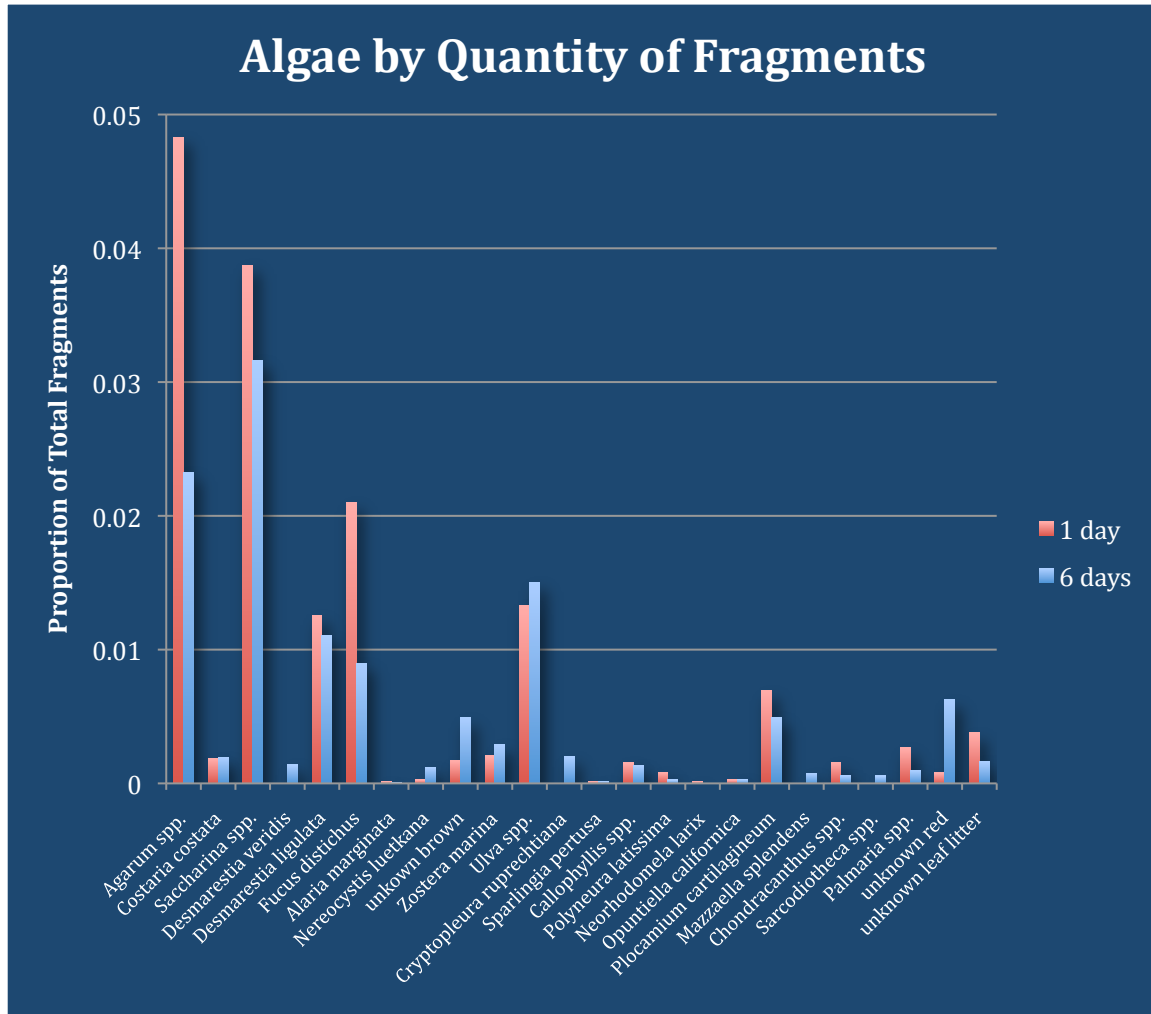


Figure 2. Proportions of total fragments represented by each algal taxon identified in urchin drift capture compared at one-day versus six-day intervals.



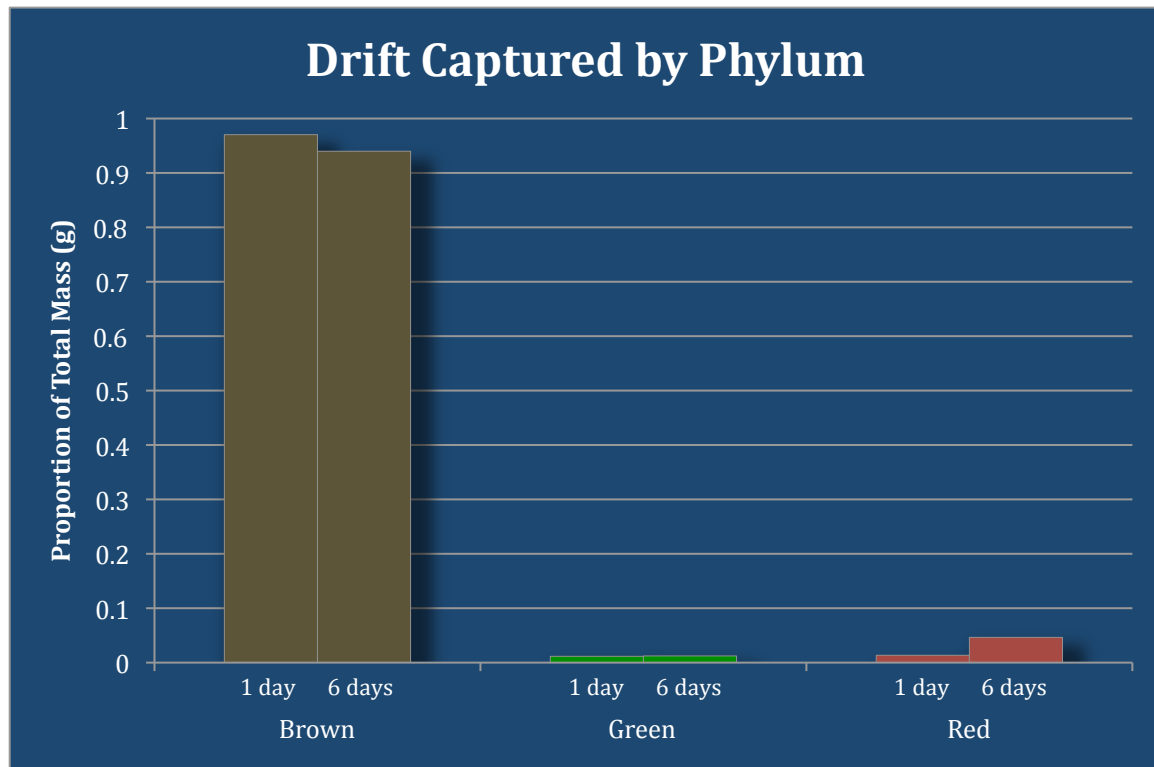


Figure 3. Bars represent the average proportion of total mass captured by urchins separated by phylum after one day versus six days.

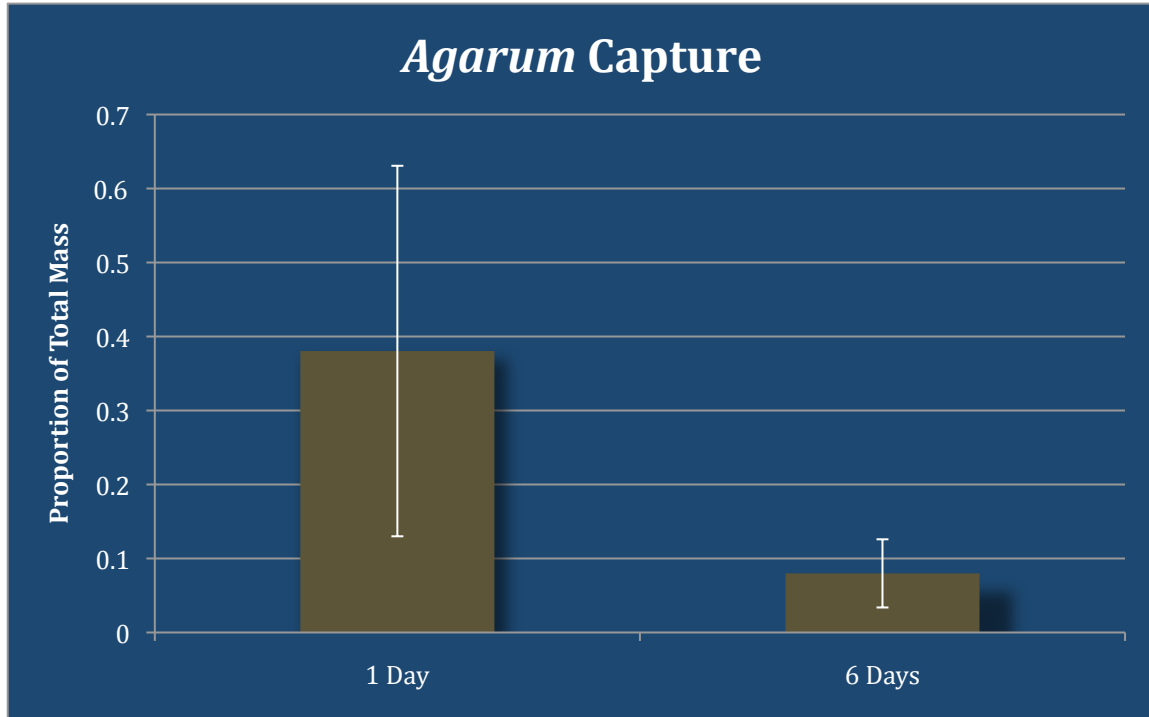


Figure 4. Average proportion of total mass represented by kelps of the genus *Agarum* compared at one-day versus six-day intervals ( $p=.0562$ ,  $t=2.3608$ ,  $df=6$ ). Bars represent standard deviations.

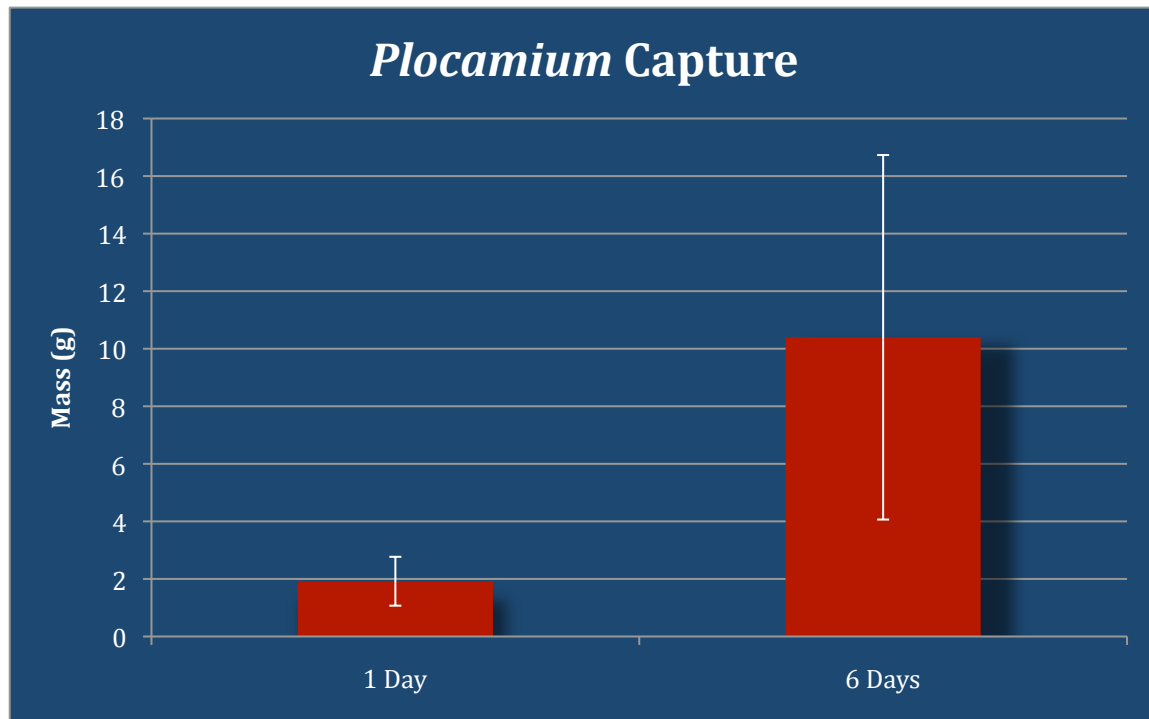


Figure 5. Average mass represented by *Plocamium spp.* compared at one-day versus six-day intervals ( $p=.0761$ ,  $t = 2.2312$ ,  $df=5$ ). Bars represent standard deviations.



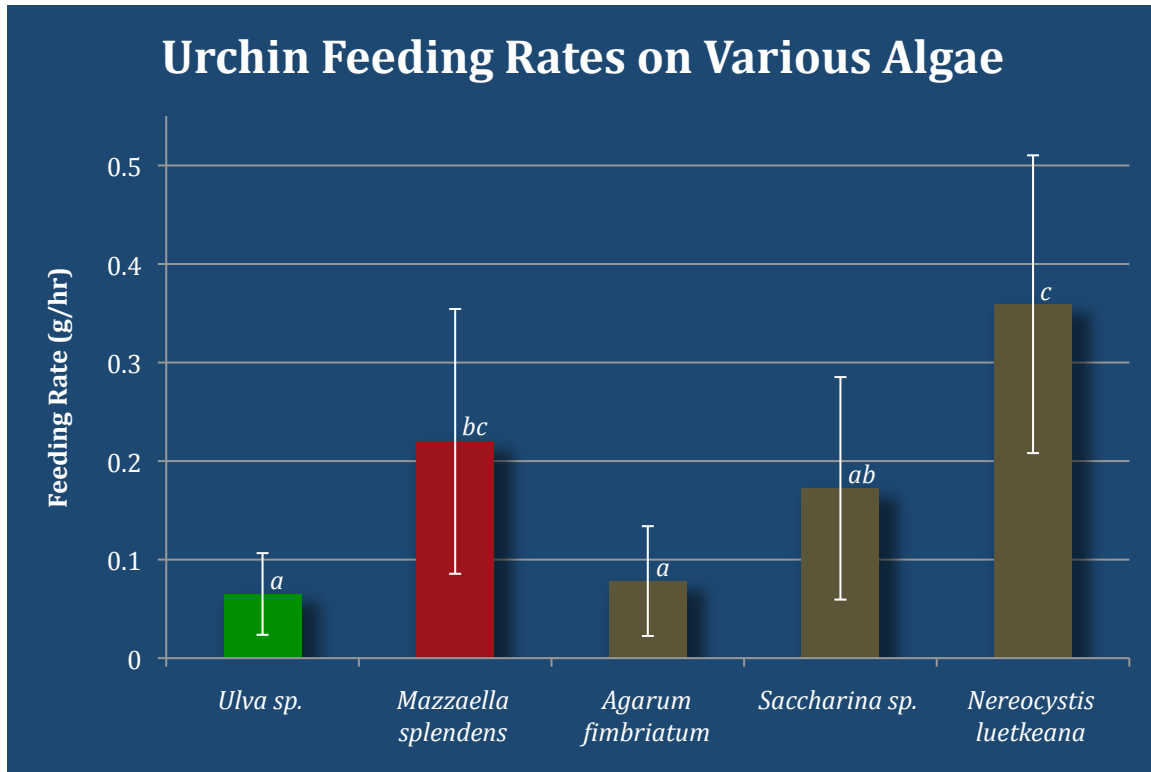


Figure 6. Feeding rates for *Strongylocentrotus franciscanus* on different algal treatment diets. Colors represent colloquial names for algal phyla (green, red, and brown). Columns that do not share a letter have statistically different means. Again, bars represent standard deviation from each mean (one-way ANOVA,  $p < .001$ ,  $df=35$ ).

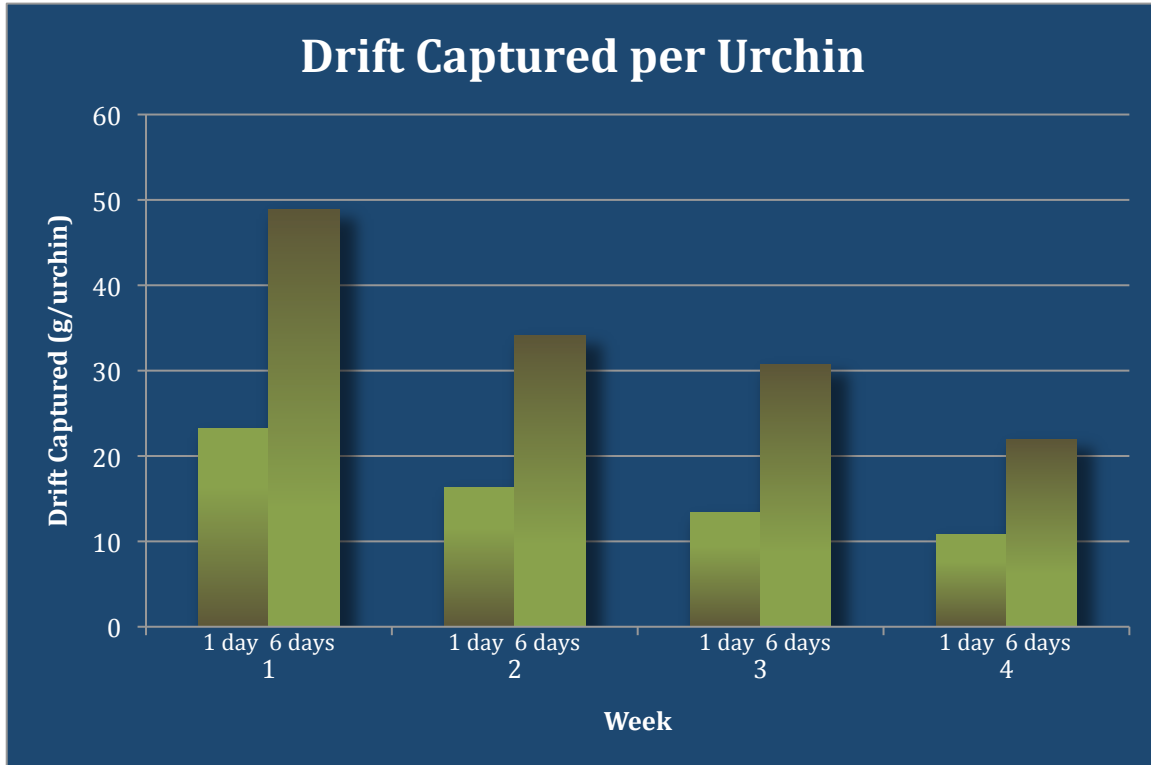


Figure 7. Average mass of drift algae captured per urchin on each dive over the four-week period.

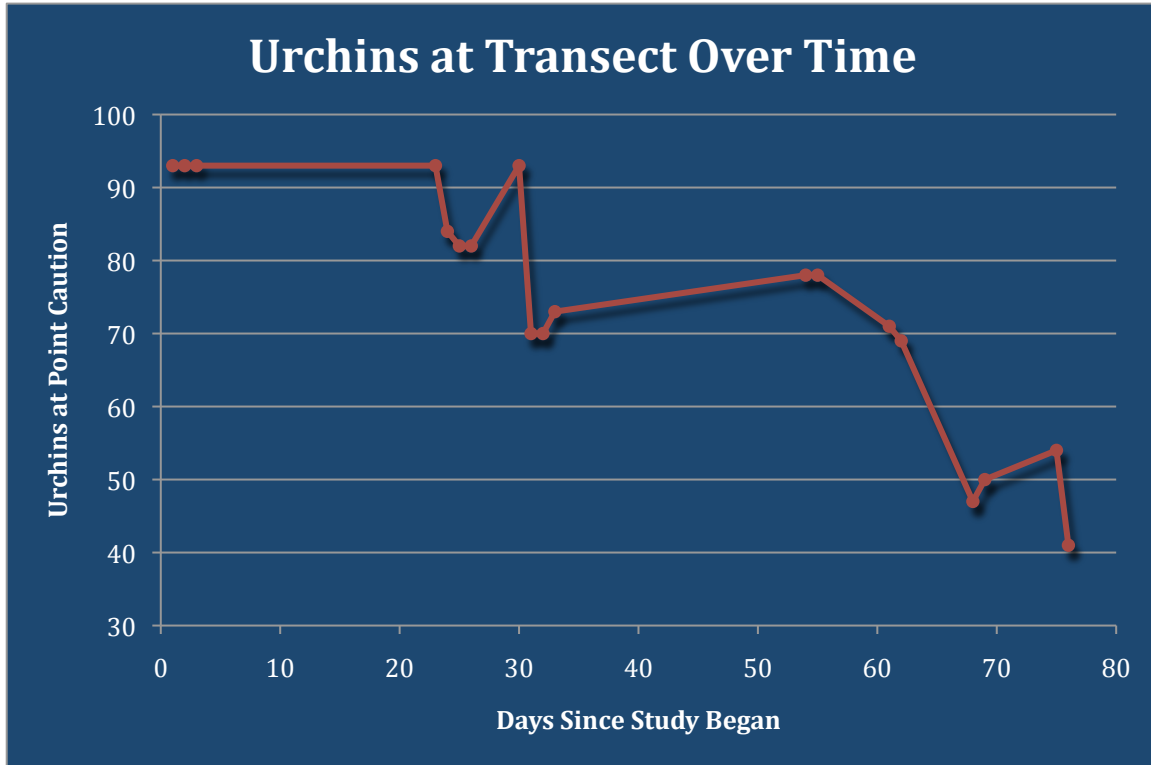


Figure 8. Urchins present at the study transect are plotted against the number of days since the pilot observations began. Each point represents an individual dive.

## Discussion

The fact that drift algae captured by red urchins in the shallow subtidal zone were heavily dominated by brown algae (Phaeophyta) probably reflects the large biomass of these species in local waters (Van Blaricom & Chambers, 2003). This finding suggests that, at this location, urchin drift capture is largely determined by availability of algae, rather than by 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).

In further support of this hypothesis, the proportion of total captured mass represented by *Agarum spp.* was quite different between the two time frames. When given six days, this kelp comprised less than ten percent, on average, of the mass captured by the urchins, whereas after only one day, it constituted an average near forty percent. The difference observed between these two means suggests that this locally abundant alga, which is both less preferable and less nutritious to urchins when compared to other algae (Vadas, 1977; Larson, et al. 1980), was being captured from the current and subsequently discarded somewhere between the first and sixth day. My laboratory feeding rate data further supports the contention that *Agarum fimbriatum* is 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 are 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 the hypothesis that urchins nearer the source of the subsidy obtain higher quality algae. However, future studies that aim to recover algae from urchins should ideally be longer-term, meaning 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, such as fatty acid or multiple stable isotope ratios, which would quantify the composition of suspension feeder tissues near versus far from urchin assemblages.

Feeding rates obtained from trials in the present study are consistent with results from other studies and preference hierarchies calculated therein (Vadas, 1977; Larson, et al. 1980). *Nereocystis luetkeana* was consumed at a significantly higher rate than all algae besides *Mazzaella splendens*. The low feeding rate measured, 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 also suggest that, at this site, drift-catching behavior is governed primarily by availability of drifting macrophytes, rather than preferences for specific algae. However, because determining the actual proportions of algae in the drift is highly difficult logistically, we cannot compare proportions captured to a control group and our interpretations of availability are constrained to what we observe urchins having captured and surveys of local seaweed populations. Nonetheless, the data observed in the drift collection study

suggest that while urchins may possess an evolutionary mechanism to seek out nutritionally valuable food sources, they may not often have the opportunity to choose in nature. Interestingly, urchins in deep subtidal areas where algae have 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 varies with seasons and disturbances, and other factors (Ebeling, 1985; Gibbert et al. 2003).

While it employs a novel technique for observing urchin feeding preference *in situ*, the present study and its results are generally concurrent with Schiel (1982) and unable to demonstrate a definitive instance of urchin feeding preference in the wild, despite the abundance of evidence for preference in studies with captive urchins (Vadas, 1977; Larson, et al. 1980; Väitilingon, et al. 2003; Lyons & Scheibling, 2006). This conclusion emphasizes the importance of testing experimentally substantiated theories in ecological settings. However, this is not to say that such preference patterns do not exist. My results suggest that urchins may have a significant effect on the proportions of drifting macrophytes that subsidize deep subtidal ecosystems that has yet to be quantified, 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 algae subsidies. Therefore, site replication, a longer time for observations (at least one year), less invasive methods of drift “stealing”, and if possible, a method of indiscriminately capturing drift algae as a control are four modifications to my research design that, if achieved, could very likely provide strong statistical evidence for the hypothesis of drift

selection by urchins. As research progresses and methods are refined, drift collection could become a useful technique for observing urchin feeding preferences in nature.

### Acknowledgements

For their endless support and assistance, 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, my University of Colorado honors committee, and the all of the urchins who participated.

## References

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, A. W., D. R. Laur, and R. J. Rowling. "Severe Storm Disturbances and Reversal of Community Structure in a Southern California Kelp Forest." *Marine Biology* 84.3 (1985): 287-294.

Edgar, G., J. Moverly, N. S. Barrett, D. Peters, and C. Reed. "The Conservation-related Benefits of a Systematic Marine Biological Sampling Programme: The Tasmanian Reef Bioregionalisation as a Case Study." *Biological Conservation* 79.2-3 (1997): 227-40.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. "Killer Whale Predation on Sea Otters Linking Oceanic and Nearshore Ecosystems." *Science* 282 (1998): 473-76.

Foreman, R. E. "Benthic Community Modification and Recovery following Intensive Grazing by *Strongylocentrotus droebachiensis*." *Helgoländer Wissenschaftliche Meeresuntersuchungen* 30.1-4 (1977): 468-84.

Fredriksen, S. "Food Web Studies in a Norwegian Kelp Forest Based on Stable Isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) Analysis." *Marine Ecology Progress Series* 260 (2003): 71-81.

Graham, M. H., B. P. Kinlan, L. D. Druehl, L. E. Garske, and S. Banks. "Deep-water Kelp Refugia as Potential Hotspots of Tropical Marine Diversity and Productivity." *Proceedings of the National Academy of Sciences* 104.42 (2007): 16576-6580.

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 droebachiensis* in Maine, USA." *Marine Biology* 59.1 (1980): 49-62.

Leighton, David L. "Studies of Food Preference in Algivorous Invertebrates of Southern California Kelp Beds." *Pacific Science* 20.1 (1966): 104-13.

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, *Strongylocentrotus 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.

Reed, Daniel C., and Mark A. Brzezinski. "Kelp Forests." *The Management of Natural Coastal Carbon Sinks*. Gland, Switzerland: IUCN, 2009. 31-38.

Santelices, Bernabé. "The Discovery of Kelp Forests in Deep-water Habitats of Tropical Regions." *Proceedings of the National Academy of Sciences* 104.49 (2007): 191.

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.

Steneck, Robert S., Michael H. Graham, Bruce J. Bourque, Debbie Corbett, Jon M. Erlandson, James A. Estes, and Mia J. Tegner. "Kelp Forest Ecosystems: Biodiversity, Stability, Resilience and Future." *Environmental Conservation* 29.4 (2002): 436-59.

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, M. A., and G. A. 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, E. W., and P. K. Dayton. "Organic Enrichment by Macrophyte Detritus, and Abundance Patterns of Megafaunal Populations in Submarine Canyons." *Marine Ecology Progress Series* 186 (1999): 137-48.