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**The effects of added nutrients on the growth and consumption of ulvoid algae by
*Strongylocentrotus droebachiensis***

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REU 2006

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HONORS THESIS

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Abstract

Macroalgal blooms are occurring more frequently worldwide. In particular, ulvoid algal species are creating harsh living conditions for several intertidal species of plants and animals. It is not understood yet why this is taking place but a large amount of effort has been allocated to projects for this very purpose. There are several hypotheses as to why ulvoid algae has increased in the last few decades. Eutrophication is a likely cause for the blooms that may be aided by the fact that ulvoids produce compounds that have been found to be feeding deterrents to certain herbivores such as the green sea urchin. In this study, several feeding experiments were carried out in the field looking at the relative palatability to sea urchins, growth rates, and chemical makeup of a few different algal species (green, red, and kelp) with and without added nutrients. While nutrients were not found to play any part in increasing growth or consumption, it was clear through these experiments that urchins prefer *Ulva lactuca* to *Ulvaria obscura* and *Chondracanthus exasperatus* (a red algae) to ulvoids in general. Interesting results were found in the chemical aspect of this study as well. DMSP levels were higher in the absence of added nutrients and urchins preferred algal species with higher carbon to nitrogen ratios giving more evidence to the fact that chemical defenses are present in ulvoids. This data will aid scientists in better understanding macroalgal blooms and creates many new questions for further research.

Introduction

The occurrence and intensity of harmful algal blooms is increasing around the globe. While there are hypotheses as to why this is happening the exact cause is unknown (Horner et al. 1997; Valiela et al. 1997). A great amount is known about the characteristics of microalgal blooms. They form the commonly known red tides that can cause paralytic shellfish poisoning, amnesiac shellfish poisoning, domoic acid poisoning, and so on (Horner et al. 1997). However, macroalgal blooms have also been found to release toxic compounds and have the potential to be a serious nuisance for both humans and marine organisms (Nelson et al. 2003).

Ulvoid algal blooms, which are also known as green tides, have been observed to create anoxic conditions, cause fish and invertebrate kills, displace seagrass beds by reducing shoot densities, inhibit larval development in barnacles, crabs, and flounder, reduce *Fucus gardneri* zygote germination, and be generally detrimental to marine

communities and the surrounding areas (Nelson and Lee 2001; McGlathery 2001; Magre 1974; Johnson and Welsh 1985; Johnson 1980; Nelson et al. 2003; Cataldo and Van Alstyne 2005; Van Alstyne et al. 2006). The main contributor to the increase in macroalgal blooms is thought to be eutrophication or “nutrient-enrichment” but removal of grazers has also been mentioned as a possible factor in macroalgal blooms (Valiela et al. 1997; Raffaelli et al. 1998; McGlathery 2001).

Ulvoid algae are able to withstand high temperatures, desiccation, and salinity changes and grow rapidly when conditions are optimal (Rafaelli et al. 1998). In addition to these characteristics, ulvoids have been found to produce compounds that act as chemical defenses against herbivores. In *Ulva* spp. dimethylsulfoniopropionate (DMSP) is an activated defense that breaks down to produce DMS and acrylic acid. These chemicals make individuals less preferable to green sea urchins than algae that do not produce DMSP, such as kelp (Van Alstyne et al. 2001; Van Alstyne and Houser 2003). *Ulvaria obscura* produces dopamine and is even less palatable to urchins than other ulvoids (Van Alstyne et al. 2006).

In order to predict where ulvoid macroalgal blooms will occur and prevent them from causing problems in marine communities world-wide, more knowledge of their physical and chemical characteristics, toxin producing properties, and the effects of nutrients, light, and herbivores on the blooms is required. I investigated the effects of added nutrients on the growth, chemistry, and consumption by sea urchins of *Ulva lactuca* and *Ulvaria obscura*, by setting up field experiments in which herbivores and nutrients were controlled. Plants generally have lower nitrogen concentrations than herbivores so herbivore diets are believed to be nitrogen limited (Mattson 1980). If the

nutrients added in this experiment are sequestered by the algae, the herbivores should preferentially consume the algae with the higher nitrogen content.

Most previous studies have been carried out in the laboratory so I conducted my experiments in the natural conditions of the field in hopes of gaining a better understanding of the effects of herbivores and nutrient enhancements on these macroalgal blooms. I tested three hypotheses: 1) that added nutrients would cause an increase in algal growth and urchin consumption of algae, 2) that urchins would prefer *U. lactuca* to *U. obscura* and kelp and red algae to any ulvoid algae, and 3) that carbon and nitrogen content and DMSP and dopamine production would also increase with the addition of nutrients and herbivores.

These results were expected for a number of reasons. Temperate macroalgae is believed to be nitrogen limited (McGlathery et al 1992). Assuming that the ulvoid algae used in this experiment were also nitrogen limited, added nutrients would be expected to cause increased growth. Increased urchin consumption of algae due to added nutrients was also expected because herbivores are also often nitrogen limited (Mattson 1980). Laboratory experiments have shown that sea urchins prefer *U. lactuca* to *U. obscura* and kelp and red algae to ulvoid algae so similar results were expected in a field setting (Van Alstyne et al. 2001; Van Alstyne and Houser 2003; Van Alstyne et al. 2006). Populations of green algae in tropical environments with high herbivore density have been shown to produce higher levels of chemical defenses and are thus more resistant to herbivores than algae growing in areas of lower herbivore density (Duffy and Hay 1990, Paul and Van Alstyne 1988). Thus, it was expected that the ulvoid algae chemical defense production would increase in the presence of herbivores.

Materials and Methods

Study Site – The west end of Penn Cove, Whidbey Island, WA was chosen for this study. Penn Cove is a protected bay that is fed from the east by the waters of Skagit Bay. It has a substratum of small, gravel-sized rocks and a high mussel density. During the end of July and beginning of August, when this study was being conducted, large mats of ulvoid green algae were present. A small inlet off the north side of the Cove creates a marshy, wetland habitat. It was straight southward, from this inlet, into the Cove that these experiments were conducted. Water visibility was bad every time the experiments were put out and taken in. Water temperature ranged from about 10°C to 14°C while both sets of experiments were in the field with a salinity ranging from about 26 ppt to 30 ppt.

Float Preparation – No-choice and Multiple-choice feeding experiments took place in 600 ml polyethylene bottles with holes drilled in them to allow for water flow. To anchor the bottles, 10-0.3m x 0.3m x 5cm cement blocks were fitted with 2 eye hooks (1” diameter) each using a plastic wall anchor on opposite corners of the block. The blocks were spray painted orange for increased visibility underwater. The blocks were placed in the west end of Penn Cove, Whidbey Island, WA (48°14’N, 122°44’W) ~2m apart along a line perpendicular to shore far enough out so they were always submerged under at least ~1m of water. Twenty small floats were each tied to a ~2m piece of nylon rope attached to a carabiner. A ½ inch loop was tied in the rope ~0.3m above the carabiner and 0.6m below the float. Bottles containing algae, nutrients, and urchins were cable tied to the loop in the rope and attached to the blocks with the carabiner.

Organisms – Algae were collected from Penn Cove, Lovric’s Marina on Guemes Channel in Anacortes, WA, and the Skyline Marina in Anacortes, WA using snorkel or

SCUBA. *Ulva lactuca* and *U. prolifera* were collected from Penn Cove, *U. obscura* and *C. exasperatus* were collected from Lovric's Marina, and *S. latissima* was collected off a dock at the Skyline Marina. Several large pieces (~0.3m²) of each species; enough to use a different plant for each replicate; were placed in plastic Ziploc bags and transported on ice back to the Shannon Point Marine Center in Anacortes, WA for identification. The algae were cut into ~7 cm squares, weighed, and placed in the numbered polyethylene bottles in a sea water table over night. The no-choice experiments spent an extra night in the sea water table with nutrients and sea urchins already added due to bad visibility at Penn Cove that prevented the blocks from being found.

Green sea urchins were collected at Penn Cove immediately before placing the experiments in the field, with the exception of the no-choice experiments as explained above. The diameters of the urchins were measured with calipers and were placed in bottles that were then attached to the cement blocks.

Nutrient Preparation – Nutrient packets were made using 1 x 1mm fiberglass mesh, Osmocote slow-release plant fertilizer, and hot melt glue. Small pieces of mesh were folded in half and glued on 2 sides to make pouches. Exactly 1.60 grams of 19-6-12 Osmocote fertilizer granules, as calculated using Karina Nielsen's doctorate thesis (1998) on the effects of nutrients in tidepools and the size of the polyethylene bottles, were then poured into each pouch and sealed with hot melt glue.

Experimental Design – For the No-choice Experiment, 2 species of ulvoid algae were used: *U. lactuca* and *U. obscura*. The algae were placed in a bottle either with or without nutrients and either with or without herbivores in a factorial design: a control with neither nutrients nor herbivores, a treatment with nutrients, a treatment with herbivores, and a

treatment with both nutrients and herbivores (N=5 per treatment). Three bottles were cable tied to each float, 2 floats were attached to each block, and treatments with and without added nutrients put on alternate blocks.

A Multiple-choice Experiment was also conducted in which urchins were offered *U. lactuca*, *C. exasperatus*, and *S. latissima* at the same time (N=5 per treatment). Two bottles were cable tied to each float, two floats were attached to each block, and nutrient treatments were again kept separate from no nutrient treatments. All experiments were left in the field for a total of 4 days at which point they were retrieved and transported on ice back to the lab for analysis. The No-choice Experiment was put in place at 9:00am on July 22, 2006 and was taken out on July 26, 2006 at 11:30am. The Multiple-choice Experiment was started on August 2, 2006 at 10:00am and ended on August 6, 2006 at 9:00am.

Data Collection – Algae were weighed upon arrival at the lab and, if at least 0.1g of the alga was left after urchin consumption, it was prepared for several chemical analyses. Any bottles, in which the final weight was zero, were excluded from the analyses. To measure tissue DMSP concentrations, a ~0.1g piece of each ulvoid algae was dried, weighed, and placed in a gas-tight vial in 4ml 4N NaOH for 24 hours after which 10µl of headspace gas was injected into an SRI Gas Chromatograph according to the methods described by Van Alstyne et al. (2001). Four standard additions of 500, 250, 125, and 50µg DMSP to equal volumes of NaOH were used for calibration.

To determine the concentration of dopamine in *U. obscura*, high performance liquid chromatography (HPLC) was used following the methods outlined by Van Alstyne et al. (2006). HPLC is used for the isolation, identification, and quantification of

specified compounds. For this study, approximately 0.1 g pieces of *U. obscura* were soaked in 10 ml of MeOH for 3 weeks at -70°C. These extracts were filtered through GF/A glass fiber filters and a 0.22 µm filter. The Waters HPLC method was used in which 10 µl of the extract was injected to determine dopamine concentrations. The electrochemical detector was too sensitive for this experiment so the photodiode array detector at a wavelength of 279.4 nm was used instead.

An EA 1112 Elemental Analyzer was used to determine carbon and nitrogen content of the algae. About 0.1g of each alga from each bottle were dried, ground into a fine powder, and ~5-10mg of the powder was put in tin capsules that were then folded up to eliminate any air in the samples prior to the analysis. Atropine was used as a standard.

All of the data were compiled and analyzed with SPSS. Univariate and multivariate analyses of variance were carried out to test for between-subjects effects. Pearson's correlations were run to test the effect of increased nutrients on DMSP concentration. A Tukey test was also used to examine chemical differences among the three algal species: *U. lactuca*, *C. exasperatus*, and *S. latissima*.

Results

No-choice Experiment – A significant species by herbivore interaction effect occurred because herbivores consumed 52.5% more *Ulva lactuca* than *Ulvaria obscura* (Fig. 1, $P < 0.05$, $F_{1,18} = 5.588$). *U. lactuca* grew 11.4% more than *U. obscura* in the absence of herbivores (Fig. 1).

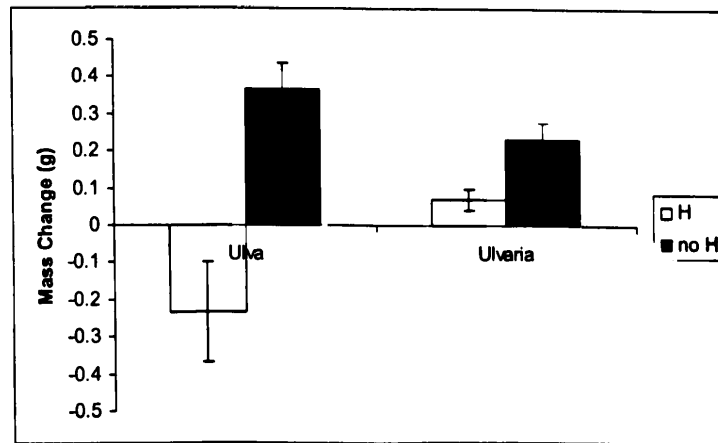


Figure 1. Mean (± 1 SE) algal mass difference for each ulvoid in the presence and absence of sea urchins (H, no H). Mass difference was calculated by subtracting initial weight from final. ($P < 0.05$, $F_{1,18} = 5.588$)

There was no effect of nutrients on either the growth or consumption of the ulvoid algae.

A significant effect of the sea urchins was found, however, on the algal weight difference (Table 1, $P < 0.01$, $F_{1,18} = 17.885$). No interaction effects were seen involving nutrients but there was a significant interaction between algal species and sea urchins (Table 1, $P < 0.05$, $F_{1,18} = 5.588$).

Table 1. Tests of between-subjects effects. Dependent variable = difference in algal weight.

Source	Type III Sum of Squares	df	Mean Square	F	Significance
Species	0.036	1	0.036	0.759	0.395
Nutrients	0.003	1	0.003	0.060	0.809
Herbivores	0.858	1	0.858	17.885	0.001
Species x Nutrients	0.003	1	0.003	0.061	0.807
Species x Herbivores	0.268	1	0.268	5.588	0.030
Nutrients x Herbivores	0.000	1	0.000	0.008	0.930
Species x Nutrients x Herbivores	0.002	1	0.002	0.043	0.837

There was a positive correlation between nitrogen and DMSP content and between carbon and DMSP content across all treatments in *U. lactuca* (Fig. 2 & 3, $P < 0.01$). A significant correlation between these elements and DMSP content was not seen in *U. obscura* but the average percent nitrogen of algal dry mass was 4.44% and the average percent carbon of algal dry mass was 34.64%.

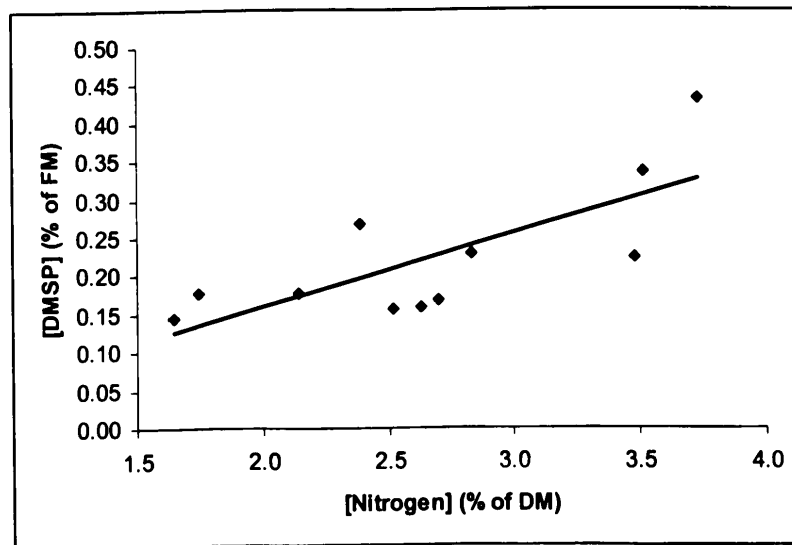


Figure 2. Correlation between percent nitrogen content and percent DMSP content for *U. lactuca*. ($P < 0.01$, correlation coefficient = 0.74).

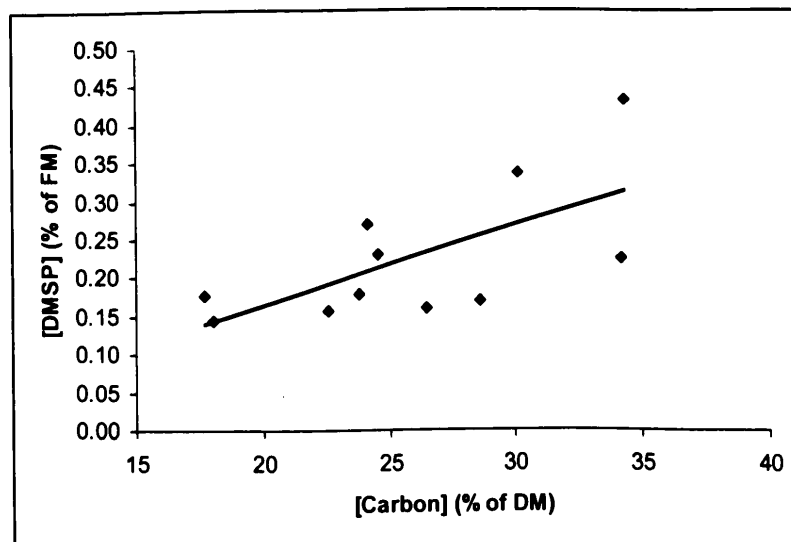


Figure 3. Correlation between percent carbon content and percent DMSP content for *U. lactuca*. ($P < 0.01$, correlation coefficient = 0.65).

In *U. lactuca*, there was more DMSP in the absence of herbivores than in the presence of herbivores (Fig. 4, $P < 0.01$, $F_{1,16} = 8.901$). No difference in DMSP production was seen between herbivore treatments in *U. obscura* ($P > 0.05$). In both *U. lactuca* and *U. obscura* a higher percentage of DMSP was seen in treatments without nutrients (Fig. 5, $P < 0.05$, $F_{1,16} = 5.998$).

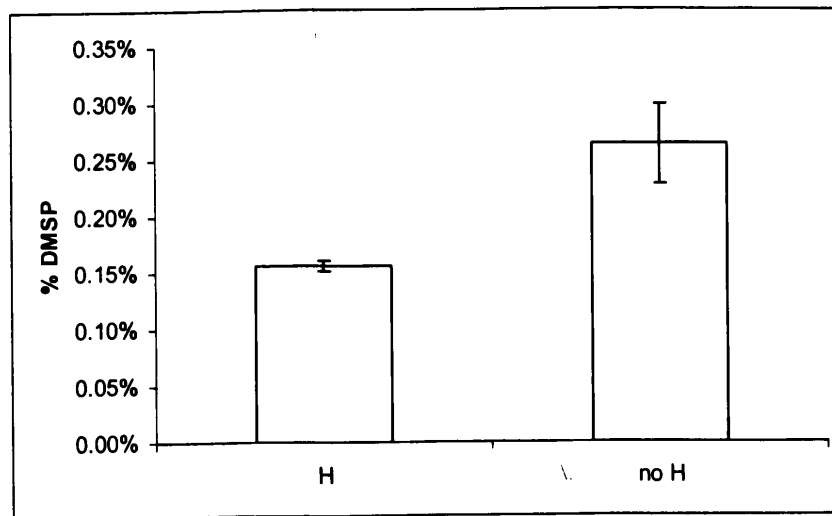


Figure 4. Mean percent DMSP (\pm 1SE) in *U. lactuca* in the presence (H) and absence (no H) of sea urchins ($P < 0.01$, $F_{1,16} = 8.901$).

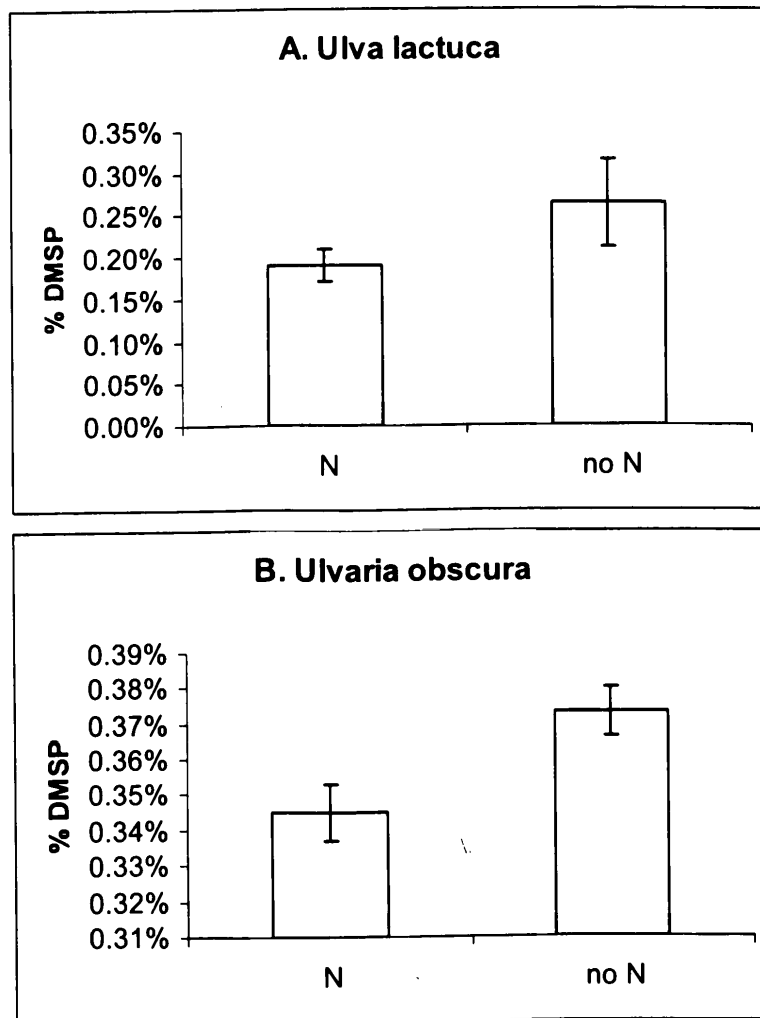


Figure 5. Mean percent DMSP (\pm 1SE) in *U. lactuca* and *U. obscura* in the presence (N) and absence (no N) of nutrients ($P < 0.05$, $F_{1,16} = 5.998$).

Neither herbivores nor nutrients had a significant effect on tissue dopamine concentrations ($P > 0.05$). The average dopamine concentration in *U. obscura* for this experiment was found to be $0.85 \mu\text{g}$ with a standard deviation of 0.29. This translates to dopamine at 0.83% (\pm 0.28) of the fresh mass of the algae.

Multiple-choice across algal species – The sea urchins ate significantly more *Chondracanthus exasperatus* than either *Saccharina latissima* or *Ulva lactuca* (Fig. 6, $P < 0.05$).

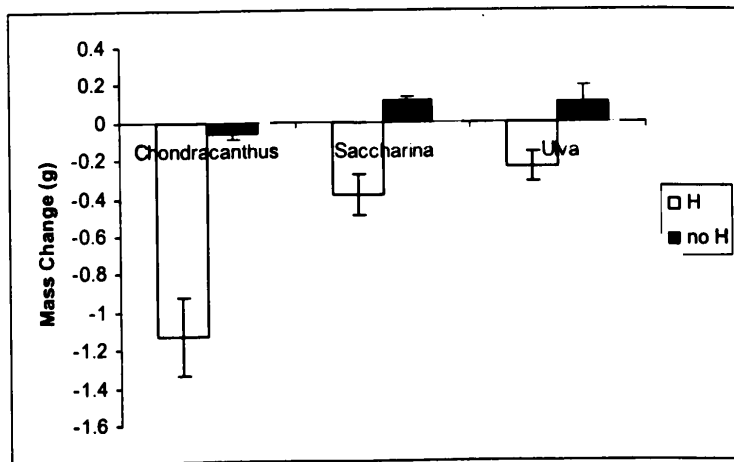


Figure 6. Average algal mass difference (\pm 1 SE) for each alga in the presence (H) and absence (no H) of sea urchins. Weight difference was calculated by subtracting initial weight from final. ($P < 0.05$).

Nitrogen content in *S. latissima* was significantly lower than that of *U. lactuca* (Fig. 7, $P < 0.05$, $F_{2,47} = 3.451$). Nitrogen content in *C. exasperatus* was not different from either of the other species ($P > 0.05$, $F_{2,47} = 1.244$). Carbon content in all three species was statistically the same but the carbon to nitrogen ratios in *S. latissima* and *C. exasperatus* were significantly higher than that of *U. lactuca* (Fig. 8, $P < 0.01$, $F_{2,47} = 11.639$).

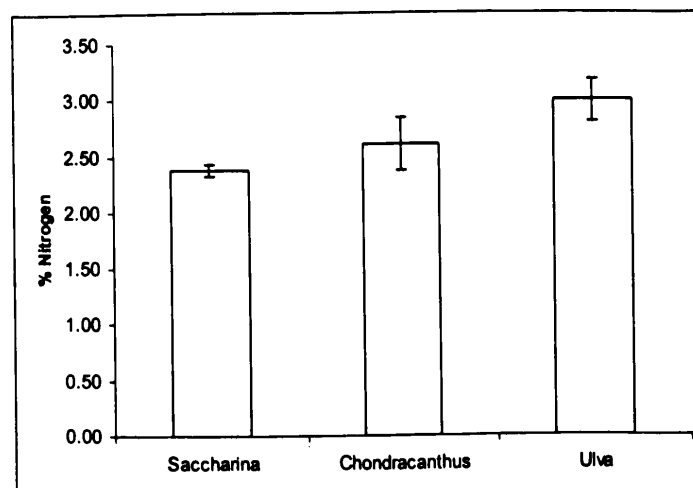


Figure 7. Mean percent nitrogen (\pm 1 SE) in each of the three algal species, all treatments combined. Significant difference between *S. latissima* and *U. lactuca* ($P < 0.05$, $F_{2,47} = 3.451$).

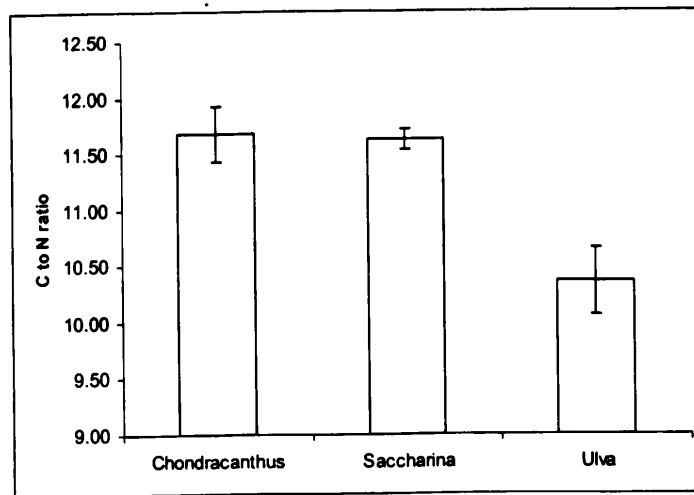


Figure 8. Mean carbon to nitrogen ratios (± 1 SE) in each of the three algal species all treatments combined. Significant difference between *C. exasperatus* and *U. lactuca* and *S. latissima* and *U. lactuca* ($P < 0.01$, $F_{2,47} = 11.639$).

No effect of nutrients was seen on either the growth or consumption of any of the algal species used in this experiment. No significant difference in DMSP content of *U. lactuca* was seen in herbivore versus no herbivore treatments or nutrient versus no nutrient treatments. The average DMSP concentration of *U. lactuca* in this experiment was found to be 0.38% (± 0.0009) of the dry mass of the algae.

Discussion

The algal species by herbivore interaction effect that was seen in this study demonstrates that the sea urchins preferred one algal species over the other. The sea urchins preferred *U. lactuca* over *U. obscura*. The dopamine produced by *U. obscura* as a feeding deterrent is the probable cause of this preference (Van Alstyne et al. 2006). In addition, urchins preferred *C. exasperatus* over *S. latissima* and *U. lactuca*. DMSP produced by *U. lactuca* can deter urchins from feeding on it (Van Alstyne et al. 2001; Van Alstyne and Houser 2003). But what causes the preference of the red algae over the kelp? Generally urchins prefer kelp to red algae (Van Alstyne and Houser 2003; Van

Alstyne et al. 2006). However, in the two previous studies, different species of red algae were used. Van Alstyne and Houser (2003) used *Polysiphonia hendryi*, which is known to produce DMSP at relatively high levels, and *Mazzaella splendens*, which produces another type of defense. In my study, *C. exasperatus* was used as the red algae species and does not produce chemical defenses. The production of DMSP by the red algae used previously could have deterred the herbivores making kelp the most palatable algae. Not only does *C. exasperatus* not produce DMSP, the kelps used in my experiment looked unhealthy, and a few individuals died, after being cut up. This added stress may have made the kelp less palatable than usual or the location from which it was collected (Skyline Marina) may have produced a less palatable kelp.

The lack of any interaction effects involving nutrients shows that there was no effect of added nutrients on the growth or consumption of ulvoid algae throughout this study. These results do not necessarily show that ulvoids do not grow more in eutrophic conditions or that urchins do not prefer algae with a higher nutrient content. The four days the experiments were in the field may have been too short to allow the algae adequate time to sequester the added nutrients and allocate them towards enhanced growth. This demonstrates that short impulses of nutrients may not have an effect on algal growth. Longer periods of increased nutrients inputs could yield different results in the form of a bloom or increased algal growth.

The algae used in this study may not have been nutrient limited, in which case any added nutrients would not have caused an increase in growth. Nitrogen is widely believed to be the limiting nutrient for macroalgal growth, however, for many species nitrogen is only limiting during certain parts of the year (Wheeler and Bjornsater 1992,

Naldi and Wheeler 1999). It has also been found that, for most algal species, the level below which nitrogen is limiting is generally about 2% nitrogen by dry weight (O'Brien and Wheeler 1987). In this study, the average nitrogen content in *U. lactuca* was just over two at 2.66% N while the nitrogen content in *U. obscura* was substantially higher at 4.44% N. These numbers could help explain why there was no effect of nutrients on algal growth. Algal species have also been found to accumulate nitrogen for times when these levels are low and nitrogen is the limiting factor (Naldi and Wheeler 1999). This could also serve as a possible explanation for the absence of an effect of nutrients on growth.

In *U. lactuca* with higher nitrogen and carbon content, greater DMSP levels were observed. Healthy plants may have more energy to use toward defense than unhealthy plants that must focus their energy solely on survival. This is consistent with the results of an experiment in which a positive correlation between DMSP and carbon concentrations was found (Van Alstyne et al. 2007). However, in this same experiment, there was no correlation of DMSP concentration with nitrogen concentration and in a second experiment no correlation was found at all (Van Alstyne et al. 2007). There is a large amount of spatial variation in the production of DMSP and several factors, such as salinity, water temperature, and nutrients may have an effect on it (Van Alstyne et al. 2007). Until more research on the matter is done it is difficult to say whether these correlations were seen because higher nitrogen and carbon content is really an indicator for higher DMSP production or if spatial and temporal variation is the explanation.

It was hypothesized that DMSP production by ulvoid algae would increase in the presence of herbivores as it does in many tropical systems, but this was not the case. In

U. lactuca in the No-choice Experiment, the opposite occurred. DMSP content was higher in the treatment without urchins than the treatment with urchins. The algae may have increased DMSP production in the initial stages of being introduced to urchins, but through the stress of being in the presence of urchins for an extended period of time and being transported back to the lab, released the DMSP. When analysis was done the algae would have given the appearance of having produced less DMSP.

Without added nutrients, the ulvoids produced more DMSP than they did with added nutrients. Spatial and temporal variation could again play a role in this result and the next set of ulvoid algae used in a similar experiment could provide different results. Another possibility is that the sea urchins used in the experiment and their wastes were a nitrogen source as well. Treatments that contained urchins but not nutrients could, in fact, have been receiving similar inputs. This was not focused on in this study and more research is necessary to determine the magnitude and significance of such an effect.

The nitrogen content in *U. lactuca* was higher than that of both *C. exasperatus* and *S. latissima*. The carbon to nitrogen ratio was much lower in *U. lactuca* than in either *C. exasperatus* or *S. latissima*. It is more efficient for herbivores to consume plants with more nitrogen and lower carbon to nitrogen ratios if nitrogen is the limiting nutrient for the herbivore, but the urchins in this study ate more of the algae with less nitrogen and higher carbon to nitrogen ratios. Herbivores typically contain much more nitrogen than plants do mainly because they use proteins as important building-blocks and excrete a large proportion of their nitrogen intake as waste (Mattson 1980). This makes nitrogen a limiting nutrient and despite differences among organisms in the daily requirement, all herbivores need nitrogen as a vital part of their diet (Mattson 1980). Because sea urchins

are herbivores and they ate the algae with less nitrogen in this study we can conclude that there is another important factor in *U. lactuca* that causes the urchins to avoid it. The chemistry of ulvoid green algae is such that DMSP may deter urchins from feeding on *U. lactuca* and cause them to feed less efficiently (Van Alstyne et al. 2001; Van Alstyne and Houser 2003).

As macroalgal blooms have begun to increase around the world many ideas about how to eradicate or lessen the problem have arisen. Natural consumers may be able to prevent blooms, lessen their intensity, or cause them to die out more quickly (Raffaelli et al. 1998). The fact that macroalgal blooms are ephemeral suggests that consumers may already be playing a role to a certain extent (Pregnall and Rudy 1985, Raffaelli et al. 1998). This brings us to question; if herbivores were transplanted in high quantities to areas of macroalgal blooms could they act as bio-control and help get rid of the problems caused by such blooms? Based on the results of this preliminary study urchins do not appear to be a good candidate. They will eat anything if they are hungry enough but if there are other choices around besides ulvoids they tend to avoid the ulvoids. Also, added nutrients do not increase grazing so any eutrophic conditions that helped start the bloom would not aid in its eradication by urchins. Of course, this is only an initial study and further research on algal growth and consumption rates are necessary to answer this question completely. This is an important area of research and any path found to finish the macroalgal bloom problems should be followed.

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