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THE IMPACT OF TRANSPLANTED SEA URCHINS
ON ALIEN AND NATIVE FLORA

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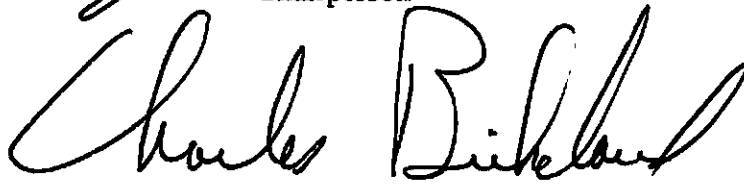
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The impact of transplanted sea urchins on alien and native flora

Abstract

After fish, urchins are the most conspicuous herbivores on coral reefs in Hawai'i, as elsewhere. In Kane'ohe Bay, O'ahu, the native urchin *Tripneustes gratilla* is present in small numbers, but is easily transplanted to patch reefs with high algal cover. Because it readily consumes several of the invasive algae in the bay, it has been proposed as a biological control agent for these algae. To determine its usefulness as a control of invasive algae and to examine its impact on the native benthic invertebrate and algal communities, urchins were placed in 1m² cages on the reef flat in varying densities and the substrate composition was monitored over time. After three months, high densities of urchins (6 urchins m⁻²) were able to significantly reduce high cover of *Gracilaria salicornia* and the medium density of urchins (3 urchins m⁻²) were able to further reduce and control the invasive alga in sites where it had previously been brought down manually. Background herbivory by fishes was not able to reduce or control *G. salicornia*, even in sites where the algal cover had been reduced manually first. Fish, but not urchins, seem to have an effect on the community composition of native turf algae. On reefs where invasive algae competes with corals, transplanting urchins to that coral-algal interface holds promise for controlling and reducing algal cover, especially in cases where algal biomass is physically reduced first.

Introduction

Whether or not it is the only contributing factor, top-down control of algal growth plays an undeniable role in structuring reef communities. This fact can be demonstrated several ways.

Studies have compared algal growth under different herbivore pressures inside and outside of areas protected from fishing pressure. For example, Hay (1984) showed that patterns of herbivory differed in regions where fishing pressure was high and urchins were the primary herbivores, and in areas where fishing pressure was low and fish were

the primary herbivores and urchins were only abundant in deeper waters. Shears and Babcock (2002) found significant differences in the benthic cover of fleshy algae in- and outside marine reserves in New Zealand. They found that within the reserves there were lower densities of herbivorous urchins and more macroalgae-dominated habitats, than there were outside the reserves where the lobsters and fish that prey on urchins were subjected to fishing pressure.

Several studies have shown that grazing fishes can alter succession on reefs often by slowing or halting the process via selective feeding (Hixon and Brostoff 1996, Smith 2003). Often, one key species is responsible for controlling the composition of the algal community. Hixon and Brostoff's work (1996) focused on turf community composition in damselfish territories and Tuya et al. (2004) demonstrated that the density of the urchin *Diadema antillarum* has a strong negative correlation with the percent cover of macroalgae in the Canary Islands. The importance of key herbivorous species was highlighted by the changes that were observed in the Caribbean during the 1980s and 1990s.

The importance of top-down control of algae can be demonstrated in the phase-shift from coral-dominated to algal-dominated reefs in the Caribbean Sea that was exacerbated by the mass mortality of the herbivorous urchin, *Diadema antillarum* (Morrison 1988, Ostrander et al. 2000). Although the die-off was not the only cause of the phase-shift, that event seemed to push the already stressed system into a new algal-dominated phase. A new algal-dominated regime is seen as a negative change because 1) it is considered to be associated with anthropogenic impacts on the ecosystem by overfishing (Hughes 1994, Hughes et al. 1999) and/or input of nutrients (Lapointe 1997 and 1999) in combination with natural phenomena such as bleaching and disease, and 2) the decrease in habitat complexity may support fewer species, leading to an decrease in overall diversity (Done 1992, Hughes 1996).

One of the lessons of the poor status of reefs in the Caribbean is that less obvious organisms, such as urchins, are vital members of the reef community. To understand the processes that influence the balance of coral and algal dominance on coral reefs, we must

gain a better understanding of the role of the herbivores other than fish, for example urchins.

To mitigate the harmful effects of major ecosystem shifts such as the coral-algal phase-shift that occurred in the Caribbean, all the trophic interactions of a reef ought to be taken into consideration. In Hawai'i, reefs throughout the main island chain are becoming invaded by native and non-native algae, causing habitat loss, localized diversity loss and economic loss (Smith et al. 2004). Lessons can be learned from research around the world and then applied locally to direct research and to mitigate the negative effects of these invasive algae.

Overfishing and “fishing down the food chain” (focusing efforts on smaller, and usually herbivorous, fish because larger apex predators have declined significantly) are problems facing many reefs throughout the world (Hay 1984, Morrison 1988, Pauly et al. 1998, Carreiro-Silva and McClanahan 2001). Even without those anthropogenic factors, a shift to algal dominance can occur. Friedlander and DeMartini (2002) showed that, while the main Hawaiian Islands have been heavily fished of apex predators, the herbivorous fish populations are similar to those in the protected northwestern Hawaiian Islands, but at a slightly lower biomass. In Kane'ohe Bay itself, the main extractive activities are recreational fisheries that focus on carnivores, such as octopus and jacks (Carangidae) with herbivorous fish (such as scarids) accounting for less than 5% of catch using active gear (Everson and Friedlander 2004). This recreational fishery is assumed to be small in scale, however even the authors of that paper admit that it can be difficult to obtain precise data on the quantity and exact type of catch in such an unregulated fishery.

Whether or not fishing activity is decreasing herbivorous fishes enough to be a cause of the algal abundance, Hawai'i has the added problem of non-native algae. Three introduced red algal species (*Gracilaria salicornia*, the *Kappaphycus/Euchuema* spp. complex and *Acanthophora spicifera*) and a native green algal species (*Dictyosphaeria cavernosa*) have become invasive within Kane'ohe Bay in O'ahu (Stimson et al. 2001, Smith et al. 2002, Smith 2003, Smith et al. 2004, Conklin and Smith 2005). Several species of herbivorous fishes are ubiquitous in the bay, yet these algae flourish. Current work suggests that the fish show strong preferences in food choice and do not consume

much *G. salicornia*, *Kappaphycus/ Euchuema* spp. and *D. cavernosa* though they will consume *A. spicifera* (Stimson et al. 2001, Smith 2003, Conklin and Smith 2005). There is much concern over the persistence of these invasive species and their potential for spread. Information is needed about the ability of other herbivores to contribute to the control of these invasive species.

Sea urchins are prominent members of the coral reef community. They are generally herbivores, but are often overlooked as such because their biomass seems small compared to herbivorous fishes, many species inhabit crevices and underhangs and usually consume only turf algae and their consumption rates on macroscopic algae have not been studied (Birkeland 1989). This is true of most species of urchin in Kane'ohē Bay, except for the collector urchin, *Tripneustes gratilla*.

Tripneustes gratilla is a generalist herbivore found across the Indo-Pacific and in the Red Sea (Ogden et al. 1989, Dafni 1992, Lawrence and Agatsuma 2001, Lessios et al. 2003). It is found on all the main Hawaiian islands and at numerous sites around the island of O'ahu. However, a comparison of its current distribution on O'ahu (personal observation) to that described by Ebert (1982) suggests that its recruitment is patchy, because it is not found in the same locations all the time. This is supported by work done by Dafni and Tobol (1986/1987) who described spotty recruitment of the subspecies *T. gratilla elatensis* in the Red Sea. The success of this type of recruitment can be related to an ability to utilize many different habitat types, including sand and seagrass beds, lagoons, reefs and intertidal zones (see Lawrence and Agatsuma 2001 for a review). As compared with fish, the limited movement capabilities of this urchin probably restricts it to the patch reef on which it recruited, as urchins have been observed to move across the area of a patch reef on the order of about one meter per day, but not travel down the reef slope (personal observation). This is in contrast to fish that can move from one patch reef to another on the order of tens of meters per day. Because of their greater mobility, fish are evidently able to show a greater degree of selectivity in their feeding, whereas urchins, with their more limited mobility, consume what is available in the immediate vicinity and display less strong preferences. A true generalist herbivore, *T. gratilla*

consumes a wide variety of marine plants, from turf algae to sea grasses and macroscopic algae (Ogden et al. 1989, Lawrence and Agatsuma 2001, personal observation).

Previous studies have focused on *T. gratilla* feeding preferences and movement patterns (Stimson et al. in review and Stimson unpublished data). Those studies have found that *T. gratilla* show some preferences for *Kappaphycus/Euchuema* spp., *Padina sanctae-crucis* (Phaeophyta) and, to a lesser extent, *Gracilaria salicornia*. Both *Kappaphycus/Euchuema* spp. and *G. salicornia* are invasive species and it would appear that this urchin species, in terms of consumption of alien algal species, complements the grazing performed by herbivorous fishes that prefer *Acanthophora spicifera*. These results arose from studies of *T. gratilla* in the lab. Conklin and Smith (2005) showed that the urchins would readily consume *Kappaphycus/Euchuema* spp. in small enclosures in the field, but pointed out that the study did not investigate the effects of heavy herbivory on the algal community as a whole. In that study, the density of urchins was 1/ 0.25 m², and impact may vary with density. Preliminary experiments on urchins grazing on *G. salicornia* suggested that urchins could reduce the benthic cover of this invasive alga on Coconut Island in a region of the reef where it occurs in high abundance and is close association with corals. Removal of urchins once algal cover had been reduced led to a slow but steady recovery of the alga, prompting concern over the low impact that herbivorous fish have on controlling *G. salicornia*, even when its biomass was reduced.

Urchins have been proposed as a possible means of biological control of invasive macroalgae in Kane'ohe Bay, O'ahu (Smith 2003, Stimson et al. in review). Both studies showed that *T. gratilla* readily consume the non-native macroalgae found in Kane'ohe Bay, as well as several of the native algal species found there. It is necessary to verify that the behavior of the urchins in the field is comparable to their behavior in the lab and that the urchins use different species of algae in a similar manner, so that these findings can be extrapolated to predict urchin behavior on a reef. It is also important to examine the relative impacts of urchins and fish, when both are present in the same habitat. Because the preliminary study suggested that at least one species of invasive algae (*G. salicornia*) will re-grow and possibly reinvade a reef if urchins are removed, it should be determined whether some fraction of the urchins added to bring macroalgae under control

will have to be left on a reef to prevent algal regrowth. In Stimson et al. (in review) the urchins chose macroalgae over substrate covered in turf algae, suggesting that urchins will consume macroscopic algae first, and only consume turf algae when nothing else is present. However, that hypothesis has yet to be examined more closely. If urchins must be added to a reef to control invasive macroalgae, the impact that the urchins have on the algal community- in the absence of invasive algae- is unknown.

There were several goals of this study. The first was to determine the relationship between urchin density and rate of decrease of macroalgae. The next was to determine the relationship between urchin density and prevention of macroalgal (re-) invasion of reef substrate. Furthermore, it was important to determine the level of impact herbivorous fish have on the invasive alga and this was accomplished by comparing its reinvasion potential in the presence and absence of all herbivory. Finally, this study examined the impact of urchins on the benthic communities of invertebrates and algae in Kane'ohe Bay, O'ahu. The objective of these studies was elucidate the role of *T. gratilla* in structuring the reef flat communities, as well as provide information on the practicality of using this native herbivore for the biological control of non-native invasive macroalgae.

Methods

Study Site

Experiments were conducted at the Hawai'i Institute of Marine Biology (HIMB), on the reef flat of Coconut Island in Kane'ohe Bay, O'ahu at the northern end of the island (N 21° 26' 9.08", W 157° 47' 13.22"). The alga of interest, *Gracilaria salicornia*, is generally found in highest abundance on the reef flat from the shore to about 10-20 m. from the reef crest. The outer 10-20 m. of the reef flat is dominated by the dense growth of *Porites compressa* and *Monitpora capitata*. The experiments were performed just shoreward of this coral platform, a zone where *G. salicornia* is abundant and in competition with corals but also exposed to grazing pressure by herbivorous fishes. Previous studies have shown that *Tripneustes gratilla* transplanted into this zone tend to

remain in this zone (Stimson et al. in review). Not only was *G. salicornia* found in great abundance here, but it was nearly the only macroalga found in this region. Occasionally, the native *Dictyosphaeria cavernosa*, *Rosenvingeia intricata* (Phaeophyta) and a particularly bushy *Centroceras* sp. (Rhodophyta) were found in the study site.

Urchins used in the experiments were collected from sites along the Sampan Channel and brought back to HIMB for use in the studies. Urchins ranged in size from 6 to 9 cm in diameter. Sexual maturity of these urchins is reached when the urchins are about 6 cm in diameter (Juinio-Meñez et al. 1998); all urchins used were mature adults.

Clearing Rate Experiment

Wire mesh pens were constructed on the reef flat to measure the rate at which *Tripneustes gratilla* could clear macroalgae from an area of high algal cover.

Eight open-topped pens were erected in the zone of high *Gracilaria salicornia* cover described in the previous section approximately 1 – 6 m shoreward of the coral platform. Pieces of rocks covered in *G. salicornia* mats were added to the pens, along with a few coral heads, to create habitat representative of nearby areas of reef, highly infested with *G. salicornia*. Pens were constructed of chicken wire and were 1 m² by 45 cm tall. The large mesh size (2.5 cm x 3.5 cm) and open tops allowed herbivorous fishes (principally acanthurids and juvenile scarids) to move through the and over the walls of the pens and graze, but kept the urchins inside. Therefore, all pens were exposed to the same background level of herbivory, with the treatments varying in the number of urchins present. The average size of scarids was around 7cm TL, so the smaller individuals were able to pass through the sides, but most of the larger individuals and the acanthurids could only enter through the tops.

The clearing rate experiment consisted of four treatments which were replicated twice in each of two seasons. The treatments were: control (no urchins present), low density (1 urchin), medium density (3 urchins) and high density (6 urchins). The medium density treatment is comparable to Smith's (2003) study, in which she used 1 urchin per ¼ m² pen to examine their impact on *Kappaphycus/ Euchuema* spp. cover. The pens were checked every week to make sure they were still sound, to check for escaped

urchins and reestablish nominal densities. Percent cover was measured every two weeks. Percent cover was estimated by recording substrate directly under each of the 25 points of a $\frac{1}{4}$ m² quadrat placed in each corner of the pen, thereby representing the entire 1 m² area. The change in cover for each category (*G. salicornia*, coral, sand, and limestone) was tracked over time for each pen. Data were collected for 3 months. Data were analyzed by comparing the rates at which cover of *G. salicornia* and other benthic categories' cover changed under the different treatments. Comparisons of rate of change in *G. salicornia* cover under different treatments were performed, using an ANOVA. A regression analysis was used to examine rate of change versus urchin density, with the expectation that algal cover would decrease faster with increasing urchin density. (Unless otherwise noted, all statistical analyses were performed using the software Minitab v.14.)

The experiment was run twice, once from August to November of 2004 and again from May to August of 2005. This allowed for four replicates for each treatment, balancing limitations on space and resources with the need to allow for comparison of feeding rates between the two seasons.

The main purpose of this experiment was to determine how fast urchins at a range of densities could clear an area of an invasive alga (in this case *G. salicornia*). Measures of the wet weight-to-surface area ratio and the growth rate of the alga make it possible to convert measures of the cover of *G. salicornia* into biomass estimates and to compare consumption rate of the urchins to the growth rate of the alga.

Maintenance Experiment

This experiment made use of the same type of pen as the Clearing Rate Experiment. It was designed to examine how well the urchins could keep an area clear of invasive algae once algal biomass and cover had been reduced.

In this test, almost all of the biomass of invasive macroscopic algae was removed from the pens. This was done manually first, and then by placing several urchins in the pens to consume as much of the algae as possible (though in only a few days, *Tripneustes gratilla* seem to be unable to remove the most basal attachment points of the thalli). The

treatments for this test were control (urchin density 0 m^{-2}), low density (1 m^{-2}) and medium density (3 m^{-2}), with four replicates for each treatment. The high density of urchins (6 urchins m^{-2}) used in the Clearing Experiment was considered impractical to maintain, given that the urchins will escape the cages when macroscopic algae gets scarce (personal observation). Again, percent cover was estimated every two weeks, focusing on the following categories: *Gracilaria salicornia*, coral, turf algae, crustose algae, sand, and other macroscopic algae. The experiment was run for four months from mid-March 2005 to early July 2005. At the end of the experiment, the turf algae community was sampled to look for differences in diversity between the treatments (see Benthic Communities section). The cover data were analyzed by comparing the rates at which *G. salicornia* cover changed under the different treatments, using an ANOVA and a regression analysis of change in cover versus urchin density. *A priori* expectations were that the presence of urchins would prevent the algae from returning and that 3 urchins m^{-2} would be more effective at this than 1 urchin m^{-2} .

The purpose of this experiment was to study how density of urchins impacts the return of invasive algae versus corals or non-invasive algae.

Herbivorous Fish Exclusion Experiment

The preliminary study showed that little *Gracilaria salicornia* recovery occurred after intensive urchin herbivory. This may have been because the urchins brought the *G. salicornia* levels down low enough that the fish grazing could prevent algal recovery.

To test this hypothesis, eight 1 m^2 plots were created, but without the pens described above. They were cleared of *G. salicornia* by hand and then by adding a high density of urchins for a short period of time. One half of each plot covered with a cage of $\frac{1}{2} \text{ in} \times \frac{1}{2} \text{ in}$ hardware mesh, to protect it from all herbivory. Hixon and Brostoff (1996) showed that this size mesh is effective at excluding fish, but does not decrease light levels or water flow enough to negatively impact algal growth within the cage.

The plots were surveyed for percent cover of coral, limestone, sand, *G. salicornia*, and other macroscopic algae. These plots were monitored for three months (from May 2005 to August 2005) and the rate of change of the different substrata was recorded. The

turf communities were sampled in the caged and uncaged portions of each plot to examine the difference in species composition with and without the pressure of herbivory.

The data were analyzed by comparing the rates at which *G. salicornia* cover changed under the different treatments, using a two-sample t-test with the *a priori* expectation that the rates would be higher for the plots protected from herbivory. Turf communities were also assessed at the end of this experiment (see section on Benthic Communities).

The purpose of this study was to examine the impact of fish grazing on cleared reef and whether the slow algal recovery observed in preliminary experiments was due to fish grazing. This, combined with the Maintenance Experiment, would help determine whether urchins were needed to keep invasive algae under control, or whether they could be removed after they had cleared a reef of invasive algae.

Algal Growth

The change in weight of pieces of *Gracilaria salicornia* mats were measured in the presence and absence of herbivorous fish to examine the growth rate and background level of herbivory on the alga. Because of this low-level herbivory, *G. salicornia* thalli become thick mats with intertwined branches and rather than separate, distinct thalli.

Growth was measured as an increase in wet weight over a two week period. Ten pieces of algae were selected and weighed, with an average starting weight of 202.51 +/- 38.58 g (mean +/- 1SD) and were approximately 25 cm long x 10 cm in diameter. Each piece was wrapped loosely in a coil of insulated wire (to avoid exposing potentially toxic copper wire to grazers). The coil was attached to a base and either caged using ½ in x ½ in mesh on all sides (protected from herbivory) or uncaged (exposed to herbivores). The samples were placed on the reef near the study site to measure the growth rates of the alga in the same environment as the other experiments. The change in weight was measured after 2 weeks. Data were collected in four trials: January, May, June and August 2005. A General Linear Model (GLM) ANOVA was used to compare the effects of treatment, month, and the interaction between the two.

This experiment provided growth data for mats of *G. salicornia* such as those used in the Clearing and Maintenance experiments. Previous studies (Stimson et al 2001, E. Conklin, personal communication) have used small thalli, which give more precise measures of growth rate, but it was considered important in this study to use large, thick mats whose morphology more closely resembles that of *G. salicornia* in the field.

Seasonal Consumption Rate

Consumption rates of adult *Tripneustes gratilla* on *Gracilaria salicornia* were obtained from experiments performed from 2003 through 2005 and were compiled to examine the seasonality of feeding rates. All data were collected using urchins in individual aquaria, each with its own air and water from a common source at the outdoors labs at HIMB. The urchins used were adults, 6 - 9 cm in diameter, the same size as those used in all other tests. These data provided an average consumption rate for *T. gratilla* on *G. salicornia*, and also permitted an exploration of any seasonal changes in the consumption rate.

Surface Area vs. Mass of *Gracilaria salicornia*

Most studies of urchin consumption rate measure consumption in terms of weight of algae consumed per unit time. However the field experiments in this study examined the change in cover of *Gracilaria salicornia* due to grazing. In order to estimate the consumption of urchins in the field in terms of weight, it was necessary to determine the relationship between cover (area) and mass of the mats of *G. salicornia*.

In the field, mats of *G. salicornia* of varying sizes were chosen and planar area was measured for each. The area of each mat was estimated using point-intercept estimates of percent cover. The mass of the alga was determined by removing the biomass, spinning it to remove excess water, and then obtaining wet weight. Mass was regressed on percent cover in an analysis that forced the regression line through the origin. The equation obtained from the regression describing this relationship allows for a calculation of the mass removed per unit time by an urchin in the course of clearing an

area of *G. salicornia*. To look for potential seasonal variation in mass versus area, data were taken at several times during the year, in January, May, June, July and August 2005.

Benthic Communities

As the invasive macroalgae was cleared from an area, the inorganic substrate, invertebrates and other algae became exposed. Increases in abundance of members of the invertebrate community developed with each successive bi-weekly substrate measurement of cover. Changes in the turf algae were less easy to assess, because the algae are difficult to identify to species in the field.

Samples of turf algae were collected from each plot- each pen at the end of the Maintenance Experiment and each caged and uncaged site from Herbivore Exclusion experiments. A $\frac{1}{4}$ m² quadrat, with strings making 25 cm² divisions was placed haphazardly in the plot being sampled and samples were taken using forceps to scrape the turf algae from under the first 10 intersections with turf algae. The sample for each intersection was bagged separately because the proportion of intersections containing a given alga was used as a measure of its relative abundance. The samples were examined microscopically to identify the algae to the lowest taxonomic level possible (family, genus or species). This generated a taxon list for each plot, gave the number of taxa present and gave the relative abundance of each taxon. Overall diversity of the plots was assessed by comparing the Shannon-Wiener measure of diversity (H') within and among all treatments to investigate whether the level of herbivory impacted the diversity of the turf community. The similarity of the community composition within and among treatments was assessed using the multivariate analysis software, Primer. Multivariate analyses used were Bray-Curtis similarity matrices, non-parametric multi-dimensional scaling (MDS) cluster models, dendrograms, Analysis of Similarities (ANOSIM), and Similarity Percentages (SIMPER).

No survey was made of the algal community before the various experiments began, and the biomass of the algae present was not measured, but this study was meant to serve as a primary survey of turf algal complexity under varying levels of herbivory.

Results

Clearing Rate

A high density of urchins (i.e., six urchins per square meter) was required to significantly reduce the cover of invasive macroalgae in the three month experimental periods (Figure 1). Starting conditions were similar for all plots, with over 50% cover of *G. salicornia*, although the cover was slightly lower at the start of the summer period. By the end of the experiment, the cover in the Control and Low and Medium density cages was the same or higher than it was at the beginning, but in the High density cages, cover dropped to about 30% or lower.

The slopes of the relationships shown in Figure 1 were calculated and these slope values, called rate of change in invasive macroalgal cover, were significantly different among treatments by a factorial ANOVA (Table 1). There was a strong ($r^2 = 0.974$) inverse relationship between the rate at which *G. salicornia* cover changed and urchin density: low densities of urchins allowed for an increase in cover, whereas high densities showed a greater decrease (Figure 2). There was neither an effect of season nor one due to an interaction between treatment and season (see Table 1). *A priori* contrasts revealed a significant difference between the rate of change in *G. salicornia* cover in the control treatment and the treatments containing urchins, and between the high treatment and the low and medium treatments. There was no significant difference between the low and medium treatments; $\alpha=0.05$ was used for all contrast calculations.

Maintenance

The Maintenance experiment showed that >1 urchin m^{-2} was required to suppress algal regrowth. This was apparent in a plot of the change in *Gracilaria salicornia* cover versus urchin density (Figure 3). An initial decrease can be seen for all treatments, but cover quickly increased in Control cages. In the Low-density cages, cover seemed to decrease slightly but apparently increased during the second half of the experiment, bringing the cover back up to original levels. In the Medium-density cages, *G. salicornia* dropped below 10% cover and never increased throughout the experiment.

Values of the rate of change in *G. salicornia* cover were computed for the data in Figure 3 by square root transformation of percent cover values followed by the calculation of slope of the relationships among the transformed data for percent cover versus time. These rate-of-change values were then compared by a one-way ANOVA (Table 2) which showed a significant difference in the rate of change among the treatments ($p < 0.001$). *A priori* tests showed that the rate of change in *G. salicornia* cover in Control cages was significantly higher than the rates in the two treatments containing urchins, and that the rate of change in the medium density treatment was significantly lower than the rate in the low density treatment (all contrasts used $\alpha = 0.05$). Urchin density had no significant impact on the rate of change in coral cover or turf cover, but it did significantly change the amount of sand that was uncovered ($p = 0.005$) with higher urchin density uncovering more sand than lower densities.

There was a significant negative regression between the rate of change in *G. salicornia* cover and urchin density (Figure 4). Urchin density accounted for approximately 75% of the variation in the rates observed in all the plots.

It was assumed that the density of urchins would remain the same over the course of the experiment, however urchins did escape the pens sometimes and, even more rarely, extra urchins entered the pens. Densities were corrected on a weekly basis and any change in density was recorded at these times. The actual density in the pens was calculated as the average of the initial and final densities over the course of the week and then obtaining an average weekly density. Reanalysis of the data in Figure 4 using the actual density instead of the nominal density did not change the results of the initial analysis using the nominal density. Furthermore, a regression of actual density versus clearing rate showed no better fit than when the nominal density was used.

Herbivorous Fish Exclusion Experiment

Grazing by herbivorous fishes alone was not sufficient to prevent *Gracilaria salicornia* from regrowing in cleared areas (Figure 5). This experiment was conducted concurrently with the Maintenance Experiment and during the same period, one or more

urchins per square meter could prevent algal regrowth (see Figure 4). In those areas where herbivorous fishes were prevented from grazing, the invasive alga recovered and covered up to 50% of the area after three months, whereas *G. salicornia* in those areas exposed to herbivory by fishes did not recover as well (Figure 5). There was a significant difference ($p=0.001$) between the rate of change in *G. salicornia* cover (slope of the percent cover values versus time) in open plots and those that were caged off from all herbivory (Table 3). The plots open to herbivory saw an increase in *G. salicornia* cover at an average rate of 0.054 (+/-0.078) % change/week, while those protected from herbivory saw a greater rate of increase at 0.32 (+/-0.15) % change/week.

The cages and control areas in this experiment varied slightly in their position on the reef flat and this had an influence on the rate of change in algal cover seen in Figure 5. The outer reef flat is a raised platform approximately 45 cm higher than the level of the sand on the more shoreward parts of the reef flat. The cages and control areas were just shoreward of the platform. Cages closer to the platform appeared to have a higher rate of algal recovery than cages further from the platform, but this relationship was not significant by a regression analysis (Figure 6). Regression analysis showed that Uncaged areas closer to the platform had a significantly lower rate of recovery than uncaged areas further from the platform.

Algal Growth

Caged and uncaged mats of *Gracilaria salicornia* showed no significant difference in growth rates over a two-week period. Mats of *G. salicornia* that were caged and protected from herbivory grew an average of 0.0204 +/- 0.0040 g/g/day (mean +/- 1SD). Those exposed to herbivory by fish grew an average of 0.0121 +/-0.0027 g/g/day. A two-sample t-test showed that there was no statistical difference between the growth rates of the samples in the two treatments ($df= 32, p=0.083$).

An attempt was made to determine whether there was any seasonality to the growth rate of *G. salicornia*. No pattern, beyond a slight peak in the summer between May and August, could be detected from the growth rates of the mats in the field. Data

on the growth rate of branches in the lab compiled between 1995 and 2005 (J. Stimson, unpub.) did not show a clear seasonal pattern (see Figures 7 and 8).

Seasonal Consumption Rate

The average consumption rate of *Tripneustes gratilla* on *Gracilaria salicornia* in laboratory aquaria was 10.16 +/-7.63 g/urchin/day (n=171). Consumption rate was highest in the winter (data from February-March) and lowest in the late summer (August-September) and Autumn (November). See Table 4 for data.

Surface Area vs. Mass of *G. salicornia*

A straight line with the equation $\text{Mass (kg)} = 11.694 * \text{Area (m}^2\text{)}$ best describes the relationship between the mass of a *Gracilaria salicornia* mat and its planar area (Figure 9). The regression fits the data well ($r^2 = 0.906$) and is significant ($p < 0.001$, $n=43$).

Comparing this relationship with the average consumption rate of *T. gratilla* on *G. salicornia*, one can estimate the amount of time it would take a certain density of urchins to clear an area. This calculation assumes that growth is insignificant relative to consumption rate and that the urchins would stay in an area even if the macroalgal abundance were low. Given these assumptions, six urchins would be predicted to completely clear one square meter of algae in a little over six months. Whether it would be realistic to believe that they would stay in the area and completely clear that area of algae is debatable.

Benthic Communities

Urchin addition treatments did not cause a decrease in coral cover in any of the experiments: Clearing (ANOVA of range of urchin densities, $p=0.54$ $df = 15$), Maintenance (ANOVA of range of urchin densities, $p=0.97$ $df=11$) and Herbivore Exclusion (t-test comparing caged and uncaged plots, $p=0.22$ $df=10$). However, in the Clearing experiment control and low-density treatments there was a trend towards a decrease in coral cover as *G. salicornia* overgrew the coral heads, as can be observed on

many of the reefs in Kane'ohē Bay. It was not possible to detect any growth or recovery by coral in experimental units with increased herbivory.

Urchin addition did not decrease the overall turf algae community diversity (Table 5, $p=0.55$). The same was true of all analyses to determine whether the communities under one treatment were more similar to one another than they were to communities under different treatments (MDS, ANOSIM and Dendrogram comparisons). A list of the taxa found in the Maintenance Experiment pens can be found in Appendix A.

For all the plots in the Herbivore Exclusion experiment there were twenty taxa identified (Appendix B). In a comparison (t-test) of the Shannon-Weiner indices of diversity, the plots protected from herbivory were significantly more diverse ($p=0.009$, $df = 11$) than those exposed to herbivory (Table 6). ANOSIM analyses indicate that the community composition of plots under the two treatments were significantly different from one another ($p=0.002$), as one might expect from the difference in diversity. However, there is no one taxon responsible for this difference. For example, of the twenty taxa found in the Herbivore Exclusion plots, six accounted for 50% of the difference between the treatments and the contribution of three more brought the cumulative difference to over 66%; none stood out as contributing particularly more to the difference than any other of these nine taxa (Table 7). MDS cluster analyses show that the caged plots are similar to one another in composition and that several of the uncaged plots are similar to the caged plots, while others are less similar to the caged plots (Figure 10). The uncaged plots that do not cluster with the other plots were all less than 2 m from the edge of the reef platform, whereas the four uncaged plots that plotted closest to the caged plots were all more than 3 m from the platform, indicating a rapid lessening of herbivory with increasing distance from the coral platform.

Discussion

The purpose of these studies was to determine the density of the sea urchin *Tripneustes gratilla* that would be necessary to reduce the cover of a chronic infestation

of *Gracilaria salicornia* and what density would be necessary to maintain a low level of the alga in the region of patch reefs where it competes with corals. It has already been determined that the urchins would consume *G. salicornia* (Stimson et al. in review) and could clear a delineated area of *Kappaphycus/ Euchuema* spp. (Conklin and Smith 2005), so field experiments using a range of densities were expected to yield information about the urchin's ability to clear and control *G. salicornia*.

A reef with a high starting cover of *G. salicornia* requires transplanting a high number of urchins needed to establish the high density of urchins needed to completely clear the region of the invasive alga. The high density of urchins (6 m^{-2}) created a rate of change that was significantly less than zero (the 95% confidence interval of the rates of change under the high density does not include zero) indicating a significant decrease in algal cover over time. However, this method of removing algal biomass is impractical due to the need for a very large number of urchins, even for a small area. In a three-month period, 6 urchins m^{-2} were able to reduce the cover of *G. salicornia* from ~60% to ~20%. This was similar to findings that 4 urchins m^{-2} reducing the *Kappaphycus/ Euchuema* spp. from 62% to 16% - from 9.3 to 2.4 kg wet weight in terms of biomass- in a five-month period (Conklin and Smith 2005). A lower density of urchins may be able to clear a high biomass of *G. salicornia* if given more time, perhaps as little as four or five months, total. While Figure 1 does not show a clear pattern of decrease in *G. salicornia* cover for a density of 3 urchins m^{-2} , a decrease was noticed in the thickness of the algal cover in this treatment. The high density treatment with 6 urchins m^{-2} (Fig. 1) showed an initial period of little decline in algal cover before reaching a turning point when the cover began to decrease steadily. At the end of the experiment, the pens with 3 urchins m^{-2} were closer in appearance to that turning point in the high density treatment. This is presumably due to the fact that the urchins were decreasing the thickness of the mat, but not yet influencing cover.

A high density of urchins is required to clear a heavily infested area of algae because of the mat morphology of *G. salicornia* which can reach 5-10 cm in depth (Smith et al. 2004). These mats can vary from 5.19 kg m^{-2} (wet weight) on the southern shore of O'ahu (Smith et al. 2004) to as much as 11 kg m^{-2} in Kane'ohu Bay (this study, see Figure

9). This is comparable to the biomass of *Kappaphycus/ Euchuema* spp. in Kane'ohe Bay, which can reach 15 kg m⁻² or more (Conklin and Smith 2005). These values can be compared with data from other studies, when converted to dry weights using equations from Larned (1997) and are comparable to the biomass of other invasive algae (Table 8). In several of the other cases (Marinho-Soriano et al. 2002, Lapointe et al. 2004) the highest biomass measures were associated with incredibly high nutrient inputs. Clearly, the biomass of invasive algae in Kane'ohe Bay is high. This biomass is often the result of stands of a single species or species complex without particularly high measures of nutrient input; Stimson et al (2001) reported nutrient concentrations of <1µM in Kane'ohe Bay, versus values of 1.25µM DIN in areas receiving land-based nutrient input in Lapointe et al. (2004) and the nutrients associated with shrimp aquaculture (Marinho-Soriano et al. 2002).

In the Maintenance Experiment, we can see that a density of 3 urchins m⁻² was able to bring an already low cover of *G. salicornia* even lower (Figure 3). The rate of change in algal cover under that treatment was significantly less than zero (95% confidence interval did not include zero), suggesting that that density is more than sufficient for suppressing algal recovery. The rate of change in algal cover for pens with 1 urchin m⁻² was not significantly different from zero and there seemed to be an increase in algal cover towards the end of the experiment, during the warmest time of the year. This suggests that while this density may suppress algal recovery for a time, especially during colder winter months when algal growth may be slowest, it will not be sufficient for complete suppression. This seems to be due to the fact that, given this large an area, an urchin could not keep up with the fastest summer algal growth rate, however these studies did not detect a significant difference in seasonal growth rates.

As noted above, it can take urchins months to eat through a *G. salicornia* mat enough to expose the benthos below the mat. The urchins can be found on top of the alga, and eat through the mat. However, they can also move underneath it and consume it from the base or feed on the underside of the thallus while upside-down, often removing or weakening its attachment points (personal observation). This can lead to the mats becoming dislodged and moving around or across the reef. The pens used in

this experiment trapped any mats that became freed from the substratum, however, on a reef, this biomass would be transported elsewhere, decreasing the localized cover of *G. salicornia* faster than the data suggest. Crescent-shaped traps have been set up on the reef flat of Coconut Island to intercept mats that are being transported by tradewind-driven currents. Preliminary studies show that about 56.9 g of *G. salicornia* is caught per day per meter of trap width near where the field experiments took place (Stimson unpublished data). This can decrease the local biomass of algae on the windward sides of reefs much faster than the consumption rate of the urchins, however the rate of transport seems to vary greatly and the impact of algae in the area to which it is exported is not fully understood.

The Herbivorous Fish Exclusion Experiment was performed to determine whether, once an area had been cleared of *G. salicornia*, the fish could then keep it clear of the alga. Williams et al. (2001) suggested that the reason that herbivorous fish were not controlling macroalgal abundance in the Caribbean was that the cover was too high, but that if one decreased the cover, then natural fish populations would be able to prevent regrowth. In preliminary experiments, urchins were placed in long pens, allowed to clear the area of *G. salicornia* and then removed from the pens. While the cover was not surveyed carefully, it appeared that the algae did not recover quickly and the possibility of herbivorous fish having a role in algal suppression was interesting (Figure 11). In the Herbivorous Fish Exclusion experiment, we could see a positive relationship between the rate of increase in algal cover in areas open to fish grazing and the distance to the coral platform (Figure 6). Data show that there is no difference in the growth rate of *G. salicornia* branches across the reef- from the crest shoreward (E. Conklin, personal communication). The alga can be found starting just shoreward of the coral platform, with cover being highest there (the region in which the field experiments described in this paper took place) and becoming more patchy moving towards the shore. Stimson et al. (2001) showed that grazing on the most preferred invasive alga (*Acanthophora spicifera*) decreased from the crest shoreward. Given that *G. salicornia* was also consumed somewhat by herbivorous fish, the trend observed for the open plots (dashed line in Figure 6) may be attributed to decreasing grazing pressure by fish with increasing

distance from the coral platform. Herbivorous fish abundance on the reef (Figure 12) decreases from the crest to over the coral platform and increases slightly at the end of the platform, finally decreasing shoreward from there. This supports the suggestion that the trend may be caused by herbivory by fish. The ultimate cause of the decrease in fish abundance from the coral platform shoreward cannot be elucidated by these data.

Tripneustes gratilla seems to be the best option for the biological control of invasive algae in Kane'ohe Bay, Hawai'i. It readily consumes the invasive species, but concerns about urchins degrading the reef infrastructure (Mills et al. 2000, Carreiro-Silva and McClanahan 2001) seem to not pertain to this species because when macroscopic algae are present, it bites off the thallus without scraping the substratum (Birkeland 1989). In fact, it was observed that as the cover of invasive algae decreased, the urchins could be found on the smaller patches of *G. salicornia* and not on turf- or crustose algae-covered limestone. Also, Ogden et al. (1989) noted that when *T. gratilla* were present on calcareous pavement, they consumed sand and its associated microflora, unlike *Echinometra mathaei*, whose fecal pellets contained well-digested crustose coralline algae.

An interesting implication arising from these studies comes from the observation that as urchins remove *G. salicornia*, the overall grazeable area (macroscopic and turf algae) decreases. This is due to the fact that much of the mat of *G. salicornia* is over sand, as it uses a small area for attachment. This may impact the relevance of fish in the recovery of a more natural reef habitat, because herbivorous fish may avoid a region with little food. While fish may not be the most effective herbivores for controlling the invasive alga, they do seem to exert some effect on *G. salicornia* and their use of the habitat needs to be better understood.

The impact of urchin grazing on the turf algae communities appears to be minimal. The communities that flourished under the different treatments were composed of filamentous red, green and brown algae and cyanobacteria. There was no time component to this experiment, so I could not detect a change in community composition over time. However, the presence of all the filamentous algae, and rareness of thick filaments and bladed algae and of crusts and mats is different from any of the treatments

in Hixon and Brostoff's (1996) experiments. Specifically, the presence of red filamentous algae, a category that was notable in its absence outside of damselfish territories where the community was subjected to heaving fish grazing pressure, suggests that the pens excluded some fish. Even so, the filamentous red algae that can reach the greatest stature, namely *Ceramium* spp. and *Centroceras* spp., were only ever abundant in the Herbivorous Fish Exclusion experiment cages, where they were protected from all herbivory. In fact, in that experiment, the abundance of *Cermaiium* spp. contributed most to the overall differences in turf community composition (Table 9). Still, the average dissimilarity between those two treatments was 37.97 %, so the communities under the two treatments were more similar than they were different. If these experiments were to take place in a region of higher fish abundance (i.e. closer to the reef crest) perhaps the caged and uncaged turf communities might more closely resemble the communities that developed in Hixon and Brostoff's (1996) "caged" and "outside territories" treatments.

The urchins used in these experiments averaged about 7.5 cm in test diameter, a common size for urchins found naturally in the field. Consumption rate is dependant on urchin size (Figure 13) and this has implications for efforts to enrich populations using aquaculture or wild juvenile urchins, as the smaller sized individuals will have less of an impact on invasive algae on the reef.

A concern over the use of *T. gratilla* for biological control of invasive alien algae, such as *G. salicornia*, is whether the urchins will stay where the effect of their grazing will do the most good, i.e. where macroalgae and coral are found in competition. Even at about 10% *G. salicornia* cover, urchins could be found on the remaining algae, but when the cover dropped much further, an increasing proportion of the urchins tended to escape the pens, for example in the Maintenance Experiment. This suggests that, without the pens, urchins may move out of an area with too little algae, the localized densities may fall and control of algae may no longer be effective. The long-term effects of this remain to be seen. The experiments described here did not investigate the time frame in which nearly 0% *G. salicornia* cover might return to cover of ~20% (the starting conditions for the Maintenance Experiment). While movement is a concern, it is worth noting that the urchins seem to remain on the reef flat and are rarely found to move across the coral- and

turf-covered platform and down the slopes of a patch reef (personal observation), suggesting that they will not leave a patch reef onto which they have been transplanted. Alien invasive algae tend to be found on the reef flat (Stimson et al. 2001) so, the tendency of urchins to remain in that portion of the reef suggests that they may exert effective long-term control of the algae. However this remains to be shown

The purpose of biological control of invasive species should be to improve and restore the function of the ecosystem. As Secord (2003) points out, biological control often focuses on host specificity so that maximal effects will be seen on the pest with minimal side-effects on other organisms. While these experiments showed that urchins do not have an impact on turf algal diversity and community composition, there were no native macroscopic algae for the urchins to impact. There does not seem to be much information about the macroscopic algae that might have inhabited this region before *G. salicornia* was introduced. Common native macrophytes in Kane'ohe Bay include *Dictyosphaeria cavernosa*, *Dictyota* spp., *Padina* spp., *Rosenvingea intricata* (seasonally available during the spring and summer), *Sargassum* spp., and *Turbinaria ornata*. Soegiarto (1973) reported finding the macroalgae *Acanthopora spicifera*, *D. cavernosa*, *Hypnea* sp. and *Polysiphonia* sp. on the Coconut Island reef in abundances high enough to be included in visual surveys and of those, only *D. cavernosa* is definitely a native species, though *Hypnea* sp. and *Polysiphonia* sp. may be as well. Feeding preference tests have shown that *T. gratilla* readily consume *D. cavernosa*, *P. sanctae-crucis*, *R. intricate*, *Sargassum* spp., and *Ulva* spp. (Stimson et al. in review and unpublished materials). They have also been seen in the field on *T. ornata* and *Dictyota* spp. (pers obs.).

The experiments were too short in duration to elucidate any changes in coral cover and potential reef recovery. These urchins are not specialists to begin with (Stimson et al. in review), so their impact on other macroscopic algae is a concern, especially in light of the possibility of recruitment of native algae in a previously invaded area. Little is known about the longer-term effects of transplanting urchins onto a reef for the purpose of restoring ecosystem diversity and function.

Recommendations

From a feasibility standpoint, it would be impractical to use *Tripneustes gratilla* to remove algae from a heavily infested reef. From the work of Conklin and Smith (2005) and from this research, it would take at least four urchins per square meter to effectively consume all the *Kappaphycus* spp. or *Gracilaria salicornia* from such a reef and in several months. For example, a small patch reef in Kane'ohe Bay might have a reef flat with a radius of 15 m, which would make the area of the flat a little over 700 m². A density of 4 urchins m⁻² would require over 2800 urchins and if invasive algae represented 100% cover those urchins might remove the algae in about four months. Neither the number of urchins needed for such a task, nor the time frame required for this biological control method are practical. However, a lower density of urchins is effective at controlling already reduced algal cover and preventing reinvasion, at least of *G. salicornia*. From Figure 4, we would expect that a density of about 2 urchins m⁻² would be effective at repressing algal recovery after an initial removal of the majority of algal biomass. An even lower density may be able to impede the recovery during most of the year, however concerns remain about the efficacy of this density during the late summer. In their efforts to investigate the control of the invasive alga *Caulerpa taxifolia* in the Mediterranean, Thibaut and Meinesz (2000) show that seasonality in the efficacy of biological control is not an uncommon issue and perhaps efforts can be concentrated during periods of low algal abundance and/or growth rates.

The data collected in this study suggest that the urchins would need to be left in place on the reefs and could not be removed once the algal cover was brought down, as we have shown that fish are not effective at controlling *G. salicornia*. This demonstrates the need for long-term monitoring. However, given that invasive species are rarely eradicated and are more often mitigated or controlled, this should not come as a surprise. We cannot rely on the natural density of urchins around the island of O'ahu to control invasive algae. The distribution of this species is very patchy and survey attempts in many sites could only record the number of urchins noted in a timed swim, so the density was not measurable. Where there were enough urchins present for transect surveys,

surveys of urchin density around the island of O'ahu showed an average density of (\pm 1SD) 0.128 \pm 0.103 individuals m^{-2} (C. Hunter, unpublished data).

There are some potential negative side effects of using *T. gratilla* for biological control and these possible risks need to be addressed. First, there is some concern over fragmentation of *G. salicornia* due to urchin behavior (i.e., during feeding) because this alga is known for its vegetative propagation via fragmentation (Smith et al. 2002). On the one hand, fragments of *G. salicornia* that pass through the urchin's gut are not viable (Stimson, unpublished data). On the other hand, urchins do cause mats of the *G. salicornia* to break off and the transportation of these mats to other locations may further the spread of the alga.

It is also important to examine the effects of this urchin on coral recruitment and recovery. While *T. gratilla* evidently prefers fleshy algae, it does occasionally, inadvertently scrape the surface and may scrape off or damage coral recruits. Long-term studies are needed to show whether or not the presence of *T. gratilla* can increase coral recovery, because the three-month time frame of these experiments was not sufficient to show significant change.

Important issues in the recovery of patch reef habitats in Kane'ohe Bay still remain to be examined. As a native species, *T. gratilla* has the potential to suppress non-native invasive algae, without inviting the problems associated with the introduction of yet another organism to provide biological control (see Louda and Stiling 2004 for an overview). When considering the implementation of a program that includes transplanting *T. gratilla* to reefs in Kane'ohe Bay, one sociological issue must be addressed, human consumption of the urchin. There are no data on the number of urchins taken by humans in Hawai'i, but anecdotal evidence (from communication with many people and from Ogden et al. 1989) suggest that this is a popular food item. As with any successful conservation effort, there needs to be proper public education to ensure the persistence of the urchins on the reefs, to the extent that their natural mortality permits.

On the basis of this study, this animal holds the potential to function as a biological control agent that could supplement the grazing of herbivorous fishes. Its classification as a biocontrol agent should not hold the same negative connotations as

many examples from land as it is a native species. This study, and related studies over the past few years (Conklin and Smith 2005, Stimson et al. in review), have shown that despite being uncommon in the bay, it survives well on the reefs to which it was introduced and has grown on diets consisting mainly or entirely of non-native invasive algae. On highly invaded reefs, the physical removal of most of the algal biomass, followed by the addition of *T. gratilla*, holds promise for effective suppression of the spread of invasive algae and the possible return of ecosystem diversity in Kane'ohē Bay, O'ahu.

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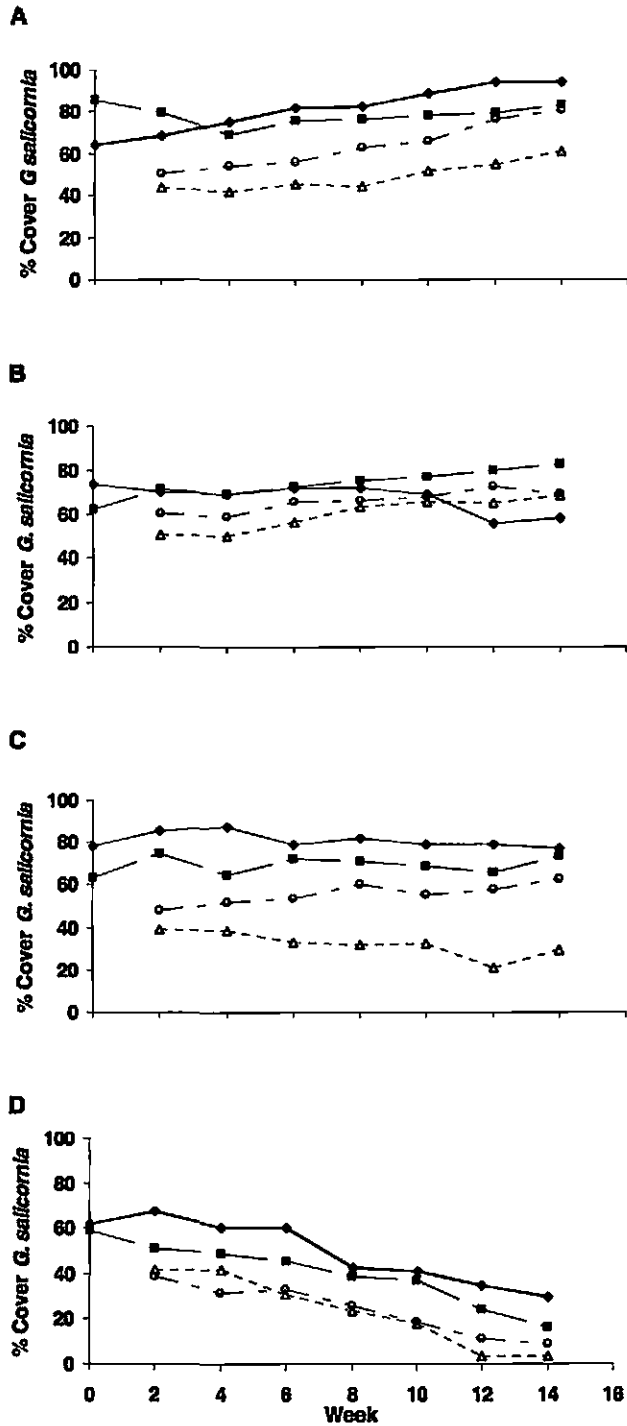


Figure 1: Response of *G. salicornia* (in percent cover) to increasing urchin densities over the course of the Clearing Experiment. A. Control cages with 0 urchins/m² B. Low-density cages with 1 urchin/m² C. Medium-density cages with 3 urchins/m² D. High-density cages with 6 urchins/m². (Separate symbols used for each replicate; closed symbols denote the Fall/Winter plots and open symbols denote the Summer plots.)

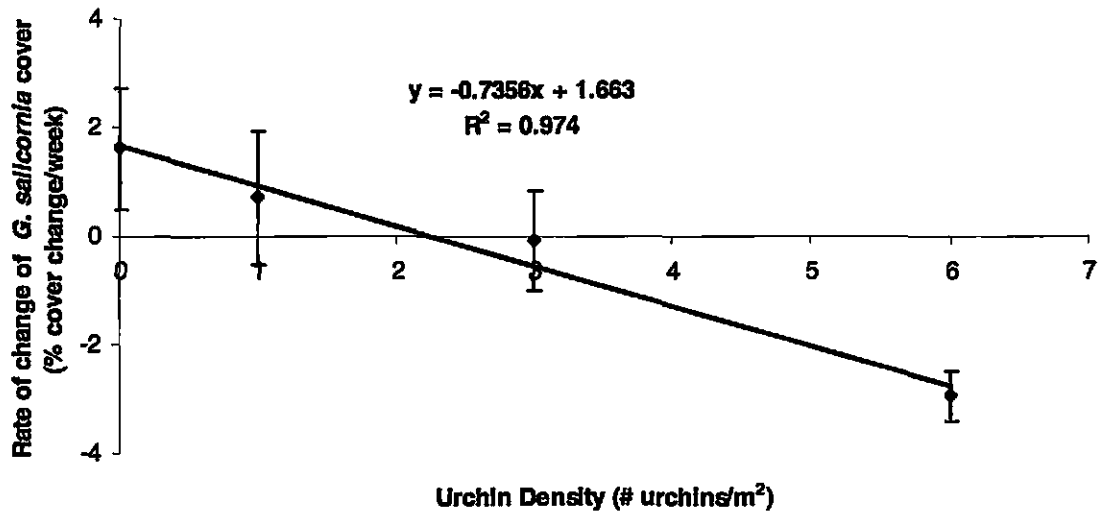


Figure 2: The rate of change of *G. salicornia* cover as a function of urchin density in the Clearing Experiment. Rate of change calculated using the slope of the best fit lines for the data presented in Figure 1. Positive y-values signify positive rate of change (increase) in *G. salicornia* cover and negative y-values are produced by a removal of *G. salicornia*, resulting in the decrease in the area it covered. Points indicate the average rate of change in the four replicate plots \pm 1 SD.

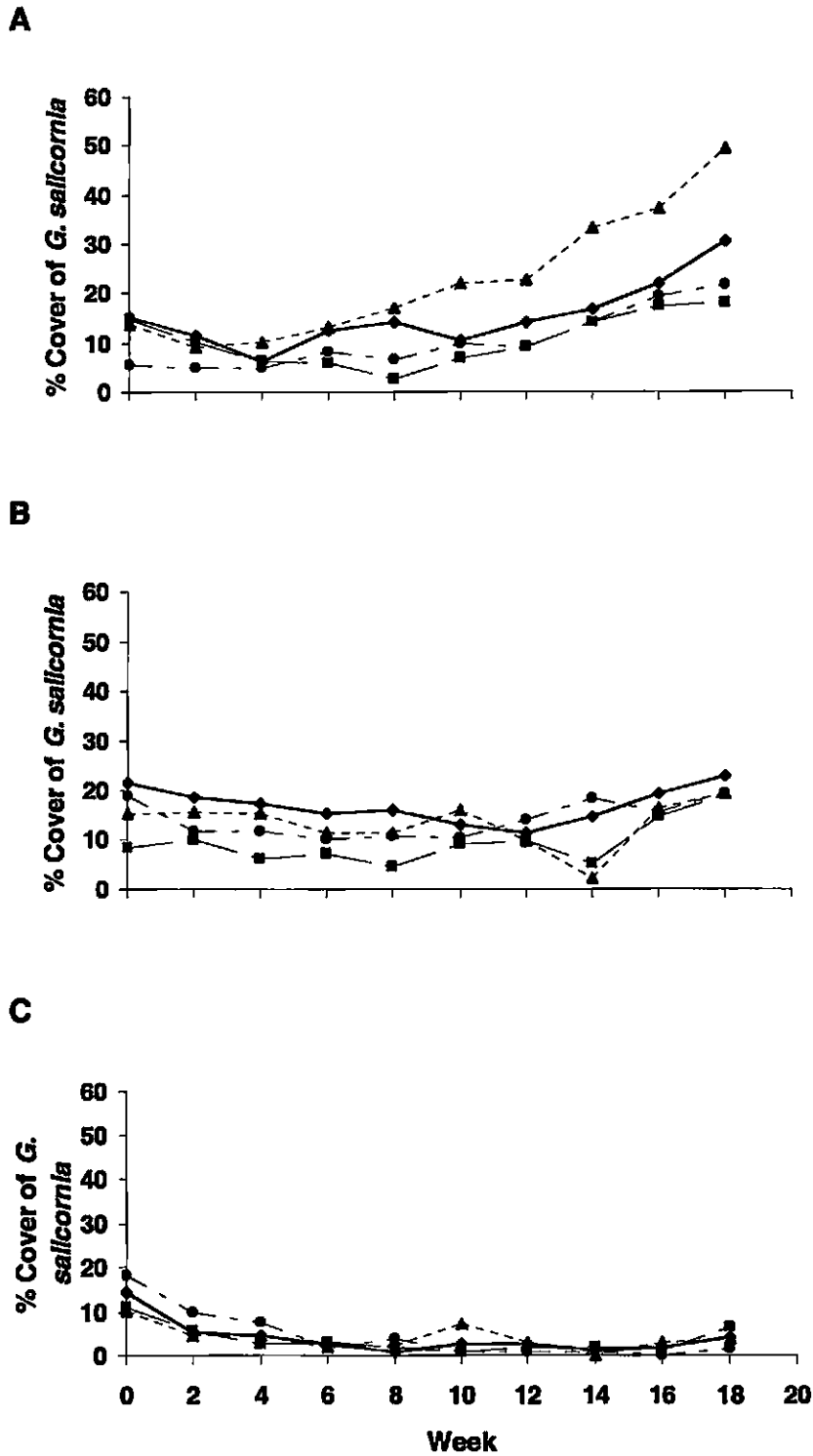


Figure 3: Response of *G. salicornia* (in percent cover) to increasing urchin density in Maintenance Experiment. A. Control cages contained no urchins. B. Low-density cages had 1 urchin/m². C. Medium density had 3 urchins/m². Different symbols represent the separate replicates for each treatment.

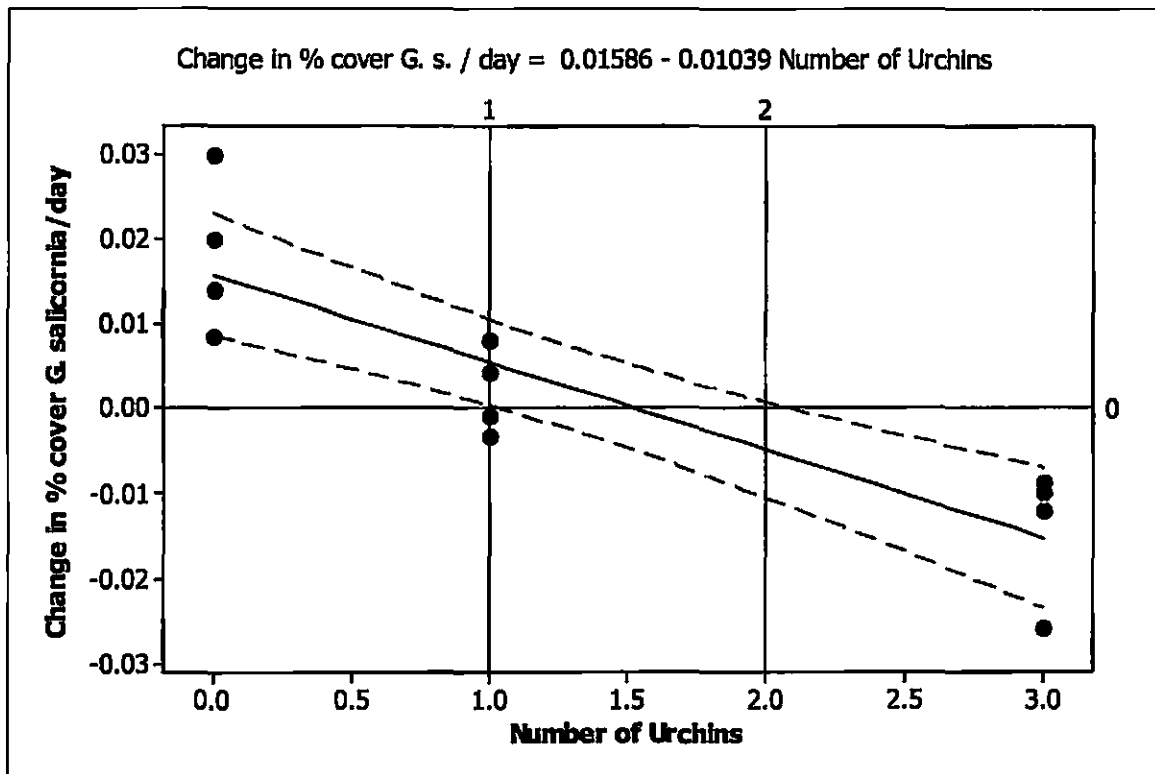


Figure 4: Increased urchin density leads to decrease in *G. salicornia* cover ($p < 0.001$, $r^2 = 0.77$). Regression is solid line; dashed lines represent 95% Confidence Interval.

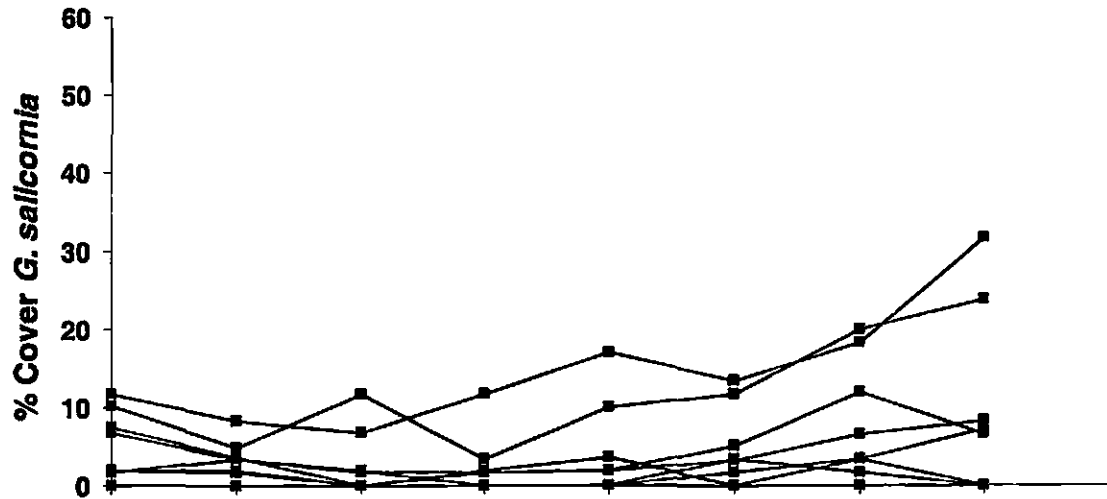
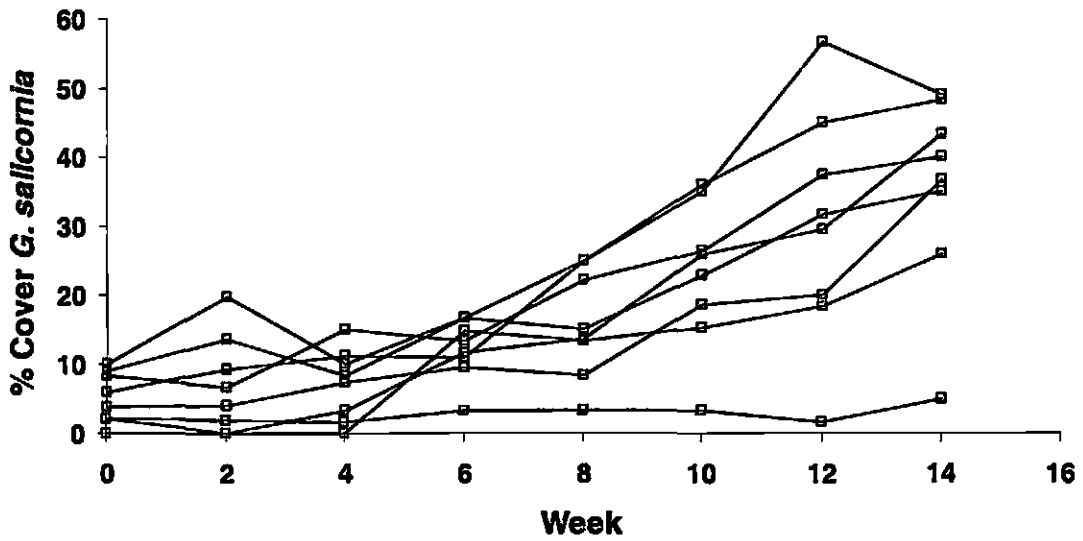
A**B**

Figure 5: The recovery of *G. salicornia* with (A) and without (B) herbivorous fish grazing pressure (in absence of urchins).

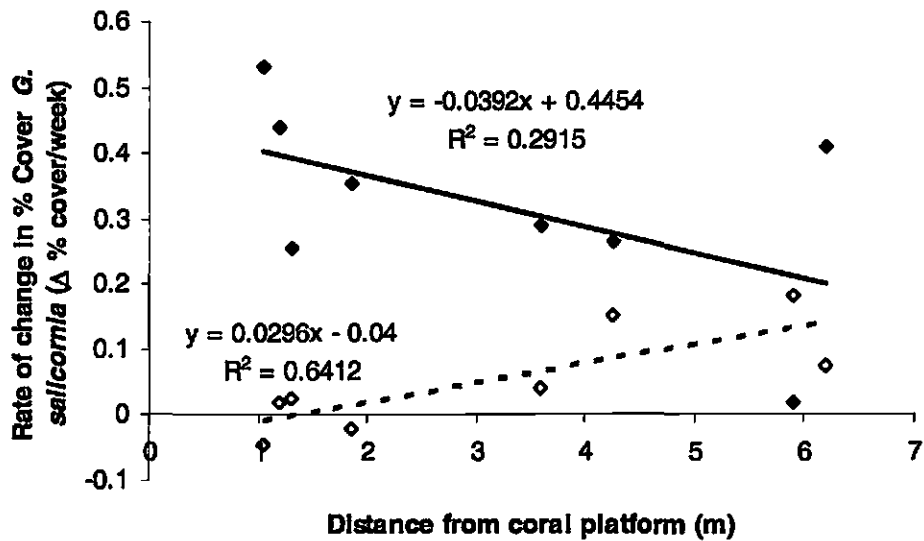


Figure 6: The effect of distance from the back edge of the reef (nearly 100% coral cover) on the rate of change in *G. salicornia* cover. Closed symbols are the caged plots (upper equation) and open symbols are the plots left open to fish grazing (lower equation).

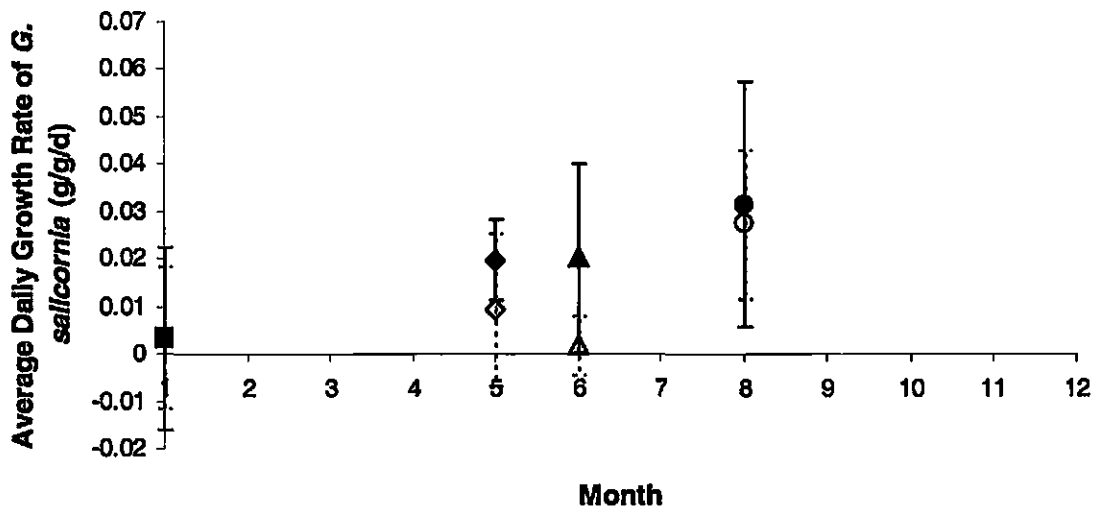


Figure 7: Growth rate of *G. salicornia* mats when protected from (Caged) and exposed to (Uncaged) herbivory in 2005. Average growth rate given by month and treatment ± 1 SD. (Symbols: \square - January, \diamond - May, Δ - June, \circ - August; closed symbols - Caged, open symbols - Uncaged)

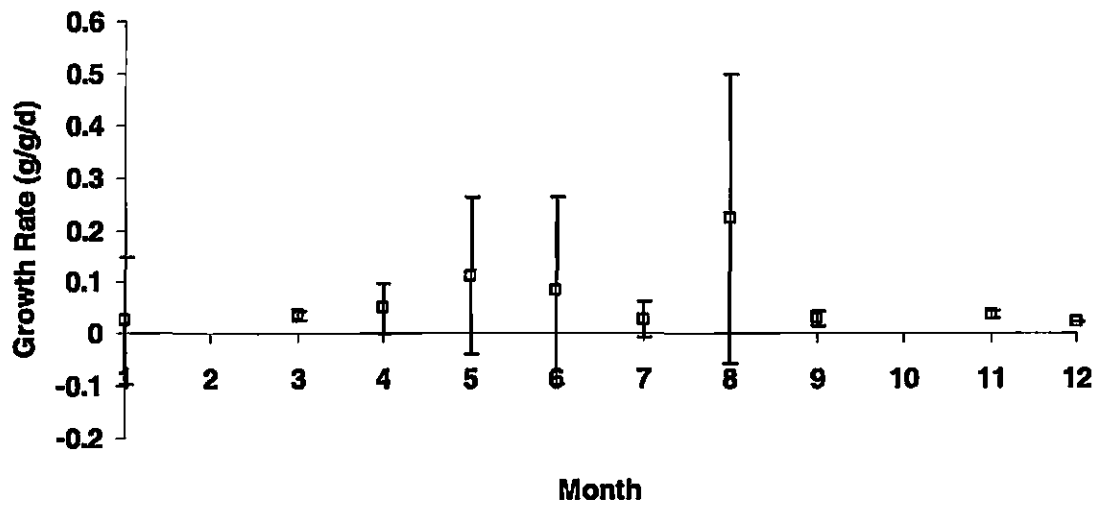


Figure 8: Seasonal growth rate of *G. salicornia* from all studies (this study and Stimson, unpublished data). Data from 1995, 1998, 2000, 2004 and 2005 combined. Values for x-axis are numerical representations of months (i.e. January = 1, February = 2, etc.).

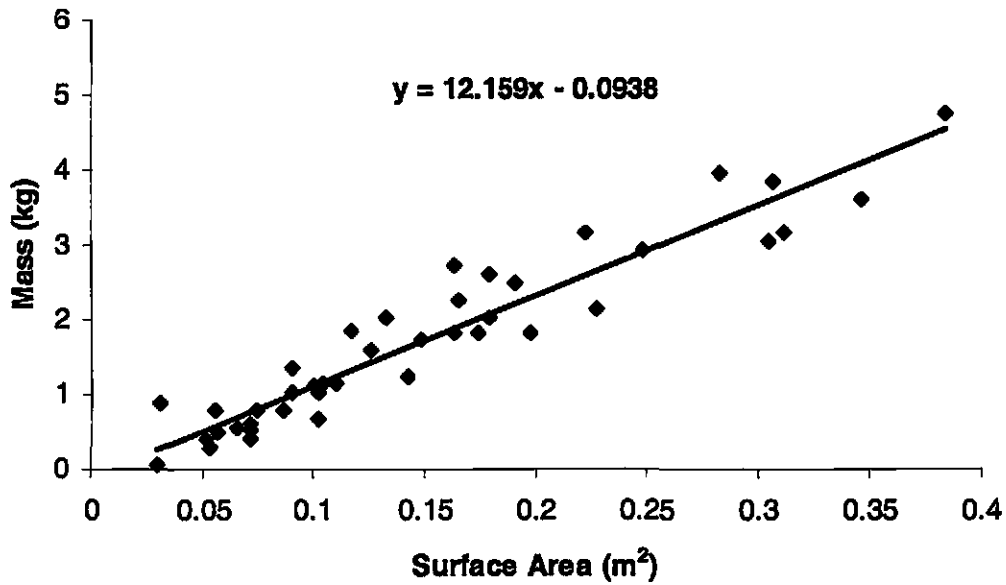


Figure 9: Correlation between the area of a *G. salicornia* mat and its mass in wet weight ($p=0.000$, $r^2=0.91$)

Turf Communities- Herbivorous Fish Exclusion Experiment

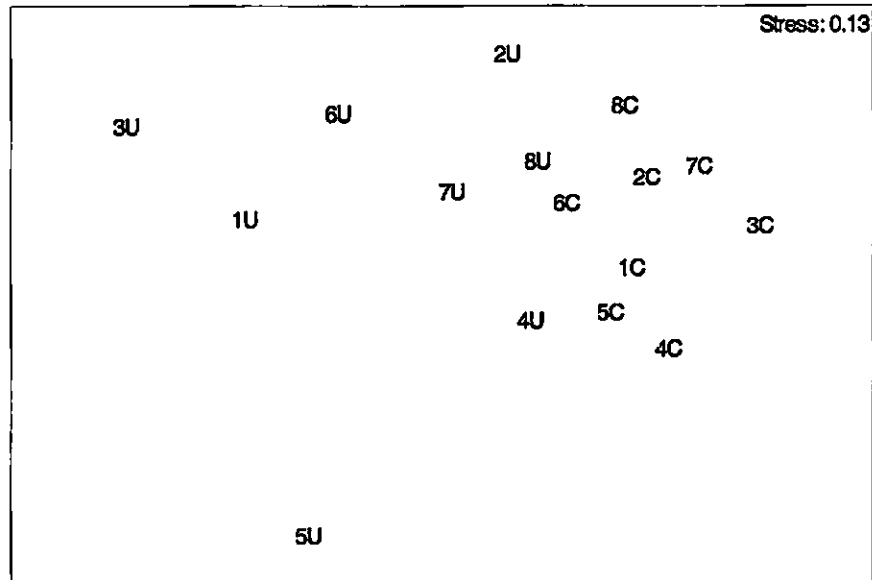


Figure 10: Non-parametric Multidimensional Scaling (MDS) diagram of the turf communities in replicate plots in the Herbivore Impact Experiment (C- Caged plots, U- Uncaged plots). The separation of the Caged and Uncaged communities is supported through 25 iterations of the algorithm. There are no units or scale to the axes; the points are placed in such a way as to fit the most similar communities closer to one another and the least similar ones further away from one another, with as little 'stress' possible.

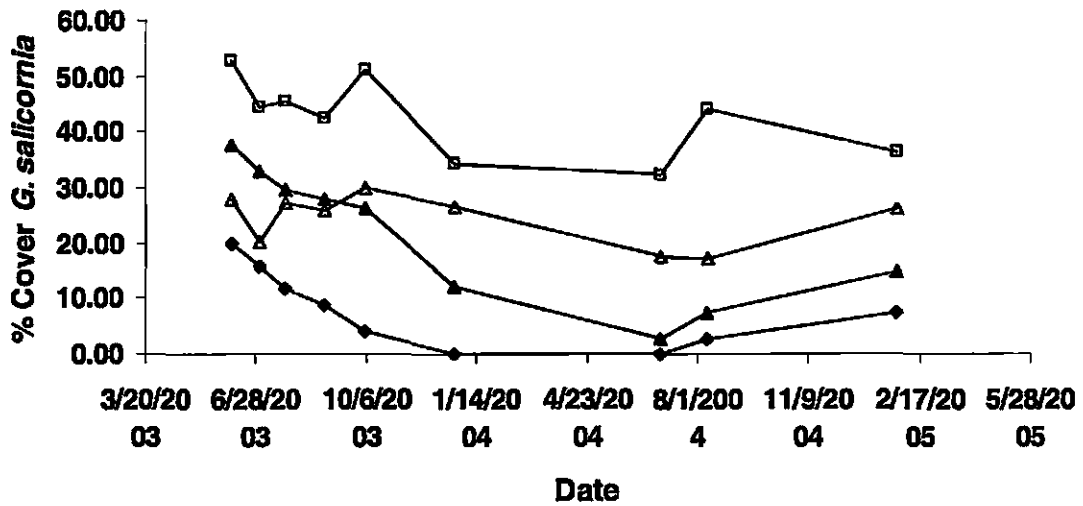


Figure 11: Preliminary Experiment: Area of *G. salicornia* in experimental pens. Open symbols indicate control pens with no urchins added, closed symbols indicate pens with urchins added at the beginning of the experiment. Urchins were removed in spring 2004.

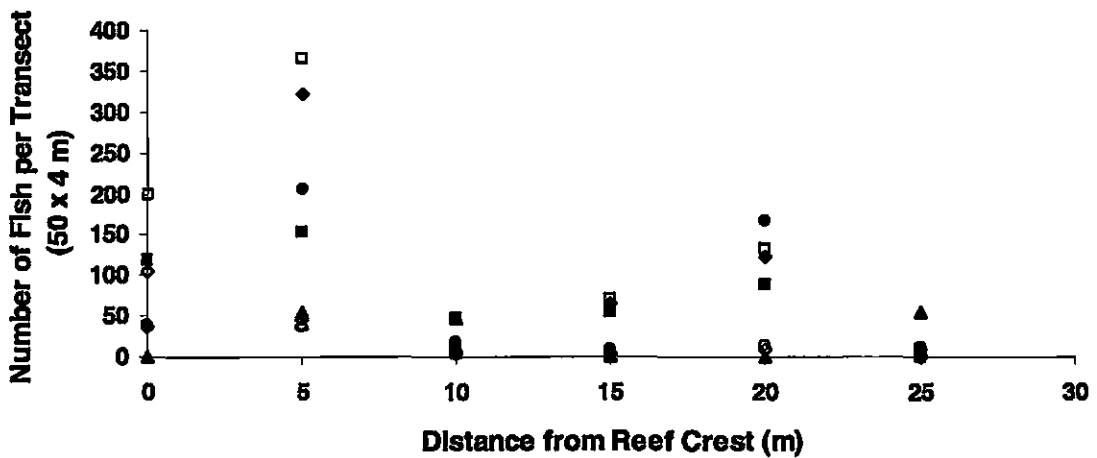


Figure 12: Abundance of herbivorous fish varies with distance from reef crest. The coral reef platform ends around 20 m from the crest. Closed symbols represent scarids and open symbols represent acanthurids. (Data collected in 2001 and used with permission from J. Stimson.)

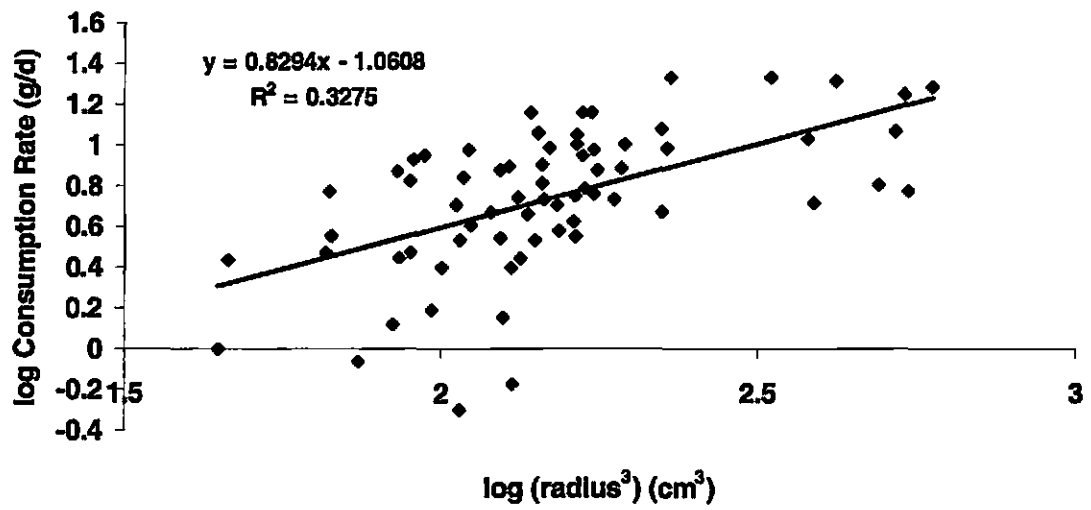


Figure 13: Positive relationship between log consumption rate of urchins and log size (cm³) of the urchins.

Table 1: Increasing density of urchins significantly decreases the cover of *G. salicornia* but there is no significant effect of time of year.

<u>Treatments</u>	<u>Number of pens</u>	<u>Mean (% change/week)</u>	<u>Standard Deviation</u>
0 urchins/m ²	4	3.22	2.24
1 urchin/m ²	4	1.42	2.44
3 urchins/m ²	4	-0.16	1.84
6 urchins/m ²	4	-5.90	0.96

<u>Source</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>p</u>
Treatment	3	62.32	13.62	0.002
Season	1	3.15	0.69	0.43
Interaction	3	2.00	0.44	0.73
Error	8	4.57		
Total	15			

Table 2: There was a significant difference in the square root- transformed rate of change in *G. salicornia* cover under the treatments of the Maintenance Experiment.

<u>Treatments</u>	<u>Number of pens</u>	<u>Mean (% change/week)</u>	<u>Standard Deviation</u>
0 urchins/m ²	4	0.018	0.0092
1 urchin/m ²	4	0.0021	0.0052
3 urchins/m ²	4	-0.014	0.0080

<u>Source</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>p</u>
Treatment	2	0.0010	17.83	0.00074
Error	9	5.85x10 ⁻⁵		
Total	11			

Table 3: Recovery of cropped *G. salicornia* when protected from herbivory versus when exposed to herbivores other than urchins.

<u>Treatment</u>	<u>Number of plots</u>	<u>Mean (% change/week)</u>	<u>Standard Deviation</u>
Caged	8	0.32	0.15
Uncaged	8	0.054	0.078

Difference = $\mu(\text{Caged}) - \mu(\text{Uncaged})$

t-test of difference (assuming unequal variance) = 0 (vs. not =): t-value = 4.37; p = 0.001 (df=10)

Table 4: Consumption rate of *T. gratilla* on *G. salicornia* by season.

(Winter = January-March, Spring = April-June, Summer = July-September and Fall = October-December, based on water temperature.)

<u>Season</u>	<u>N</u>	<u>Mean Consumption (g/d)</u>	<u>SD</u>
Winter	51	12.76	9.13
Spring	18	11.62	7.71
Summer	84	8.69	6.34
Fall	18	8.23	6.67
Total	171	10.16	7.63

<u>Source</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>p</u>
Treatment	3	210.41	3.79	0.012
Error	167	55.53		
Total	170			

Table 5: Treatment (urchin density) has no effect on turf algae community diversity (H') in the Maintenance Experiment (ANOVA).

<u>Treatment</u>	<u>Number of pens</u>	<u>Mean H'</u>	<u>SD</u>
0 urchins/m ²	4	-3.07	0.139
1 urchin/m ²	4	-3.305	1.962
3 urchins/m ²	4	-3.673	0.057

<u>Source</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>p</u>
Treatment	2	0.0053	0.64	0.55
Error	9	0.0084		
Total	11			

Table 6: Closed (caged) turf algal communities are more diverse (H') than those communities caged to protect them from herbivory.

<u>Treatment</u>	<u>N</u>	<u>Mean</u>	<u>Standard Deviation</u>
Caged	8	4.26	0.36
Uncaged	8	3.00	1.32

t-test of differences (assuming unequal variance) df = 11, p = 0.009

Table 7: The taxa whose abundances lead to 90% of the difference between communities in the Caged and Uncaged plots (average dissimilarity: 37.97%). Six taxa are responsible for 50% and nine taxa are responsible for 66% of the difference between the two treatments.

<u>Taxon</u>	<u>Uncaged</u> <u>Av.Abund</u>	<u>Caged</u> <u>Av.Abund</u>	<u>Contrib%</u>	<u>Cum. %</u>
<i>Ceramium</i>	0.10	0.44	9.49	9.49
<i>Cyanobacteria</i>	0.71	0.53	9.05	18.54
<i>Centroceras</i>	0.20	0.43	8.42	26.96
<i>Herposiphonia</i>	0.76	0.50	8.16	35.11
<i>Hincksia</i>	0.46	0.30	7.78	42.90
<i>Enteromorpha</i>	0.11	0.36	7.45	50.34
<i>Polysiphonia</i>	0.61	0.46	7.19	57.53
<i>Sphacelaria</i>	0.43	0.25	7.00	64.53
<i>Bryopsis</i>	0.58	0.58	6.60	71.13
<i>Corallophila</i>	0.25	0.06	6.29	77.42
<i>Anotrichium</i>	0.08	0.26	5.25	82.67
<i>Taenioma perpusillum</i>	0.10	0.21	4.89	87.56
<i>Cladophora</i>	0.15	0.18	3.64	91.20

Table 8: An overview of dry weight biomass (g m^{-2}) values for various macroalgae at reefs <10m deep. Most invasive algae and blooms have much higher biomass values than most algae in their natural ranges in non-bloom conditions.

	<u>Alga(e)</u>	<u>Location</u>	<u>Biomass (g m^{-2})</u>	<u>Author(s) (year)</u>
Chlorophyta	<i>Caulerpa taxifolia</i>	Mediterranean*	55-518	Thibaut et al. (2004)
	Ulvales	Washington State*	3-60	Nelson et al. (2003)
Rhodophyta	<i>Digenia simplex</i> & <i>Laurencia inticata</i>	Bahamas*	600-2440	Lapointe et al. (2004)
	<i>Gracilaria</i> sp.	Brazil*	380-2540	Marinho-Soriano et al. (2002)
	<i>G. arcutata</i>	Philippines	1.7-25	Calumpong et al. (1999)
	<i>G. blodgettii</i>	Philippines	<1-26	Calumpong et al. (1999)
	<i>G. salicornia</i>	Philippines	<1-22	Calumpong et al. (1999)
	“	Kaneohe Bay*	971 [†]	This study
	“	Waikiki Beach*	431 [†]	Smith et al. (2004)
	<i>Kappaphycus</i> spp.	Kaneohe Bay*	1380 [‡]	Conklin and Smith (2005)
Phaeophyta	<i>Turbinaria ornata</i> & <i>Sargassum mangravense</i>	Tahiti*	133-192	Andréfouët et al. (2004)
	<i>Sargassum</i> spp., <i>Turbinaria</i> spp. & <i>Lobophora</i> spp.	Belize*	~250 [‡]	McClanahan et al. (2000)

*Indicates invasive algae or algal bloom conditions.

†Indicates dry weight values calculated using equations from Larned (1997): *G. salicornia* (dry) \approx 0.083*wet wt; *K. alvarezii* (dry) \approx 0.092*wet wt.

‡Indicates an estimate of dry weight, wet weight of 2500 g m^{-2} given: dry weight \approx 0.1*wet weight (multiplying factor based on values for other algae)

Taxon	Cage 1 Control	Cage 2 Low	Cage 3 Medium	Cage 4 Low	Cage 5 Medium	Cage 6 Control	Cage 7 Medium	Cage 8 Control	Cage 9 Low	Cage 10 Low	Cage 11 Control	Cage 12 Medium
<i>Anotrichium</i>	0	0	0	0.2	0	0	0	0	0.1	0.1	0	0
<i>Bryopsis</i>	0	0.8	0.3	0.5	0.6	0.5	0.6	0.6	0.5	0.5	0.7	0.2
<i>Centroceras</i>	0	0.1	0.1	0	0.4	0.2	0.1	0.4	0.1	0.4	0	0.1
<i>Ceramium</i>	0.1	0	0	0.1	0.4	0.1	0.1	0.1	0.1	0.3	0	0
<i>Champia vieillardii</i>	0	0	0	0	0	0	0	0	0	0.1	0	0
<i>Cladophora</i>	0.3	0	0.5	0	0.1	0	0.5	0.2	0	0	0.2	0.5
<i>Corallophila</i>	0	0	0	0	0.1	0	0.4	0.1	0.1	0.1	0.1	0
cyanobacteria	0.5	0.9	0.5	0.9	1	0.4	0.8	1.2	0.7	0.7	0.7	0.9
diatoms	0.2	0.4	0.2	0	0.2	0.2	0.2	0.1	0	0.1	0.2	0.3
<i>Enteromorpha</i>	0	0.1	0.5	0	0	0.1	0	0	0	0.2	0.2	0
<i>Feldmannia</i>	0	0	0.2	0	0	0.2	0.1	0	0	0	0	0.1
Gelidiales	0	0	0	0	0	0	0	0	0	0.2	0	0.1
<i>Herposiphonia</i>	0.2	0.3	0.4	0.4	0.4	0.4	0.6	0.8	0.3	0.4	0.7	0.4
<i>Hincksia</i>	0.1	0.5	0.4	0.4	0.5	0.6	0.6	0.5	0.5	0.5	0.2	0.7
<i>Hypnea spinella</i>	0	0	0	0	0	0.1	0.1	0	0.2	0.3	0	0.1
<i>Jania</i>	0.1	0	0	0.1	0	0	0	0	0	0	0	0
<i>Polysiphonia</i>	0.2	0.7	0.4	0.5	0.2	0.6	0.5	0	0.5	0.5	0.4	0.7
<i>Tricleocarpa</i>	0.5	0	0.4	0.1	0.3	0.1	0.2	0.5	0.7	0.4	0.2	0.3
<i>Sphacelaria</i>	0.2	0	0	0	0.1	0	0.1	0	0.1	0.1	0	0
<i>Taenioma perpusillum</i>	0	0	0	0	0	0	0	0	0	0.2	0	0.1
<i>Wrangella</i>	0	0	0	0	0	0	0	0.3	0	0	0	0

Appendix A: Taxon lists and relative abundances for the turf communities in the Maintenance Experiment.

Taxon	Cage 1	Cage 2	Cage 3	Cage 4	Cage 5	Cage 6	Cage 7	Cage 8
<i>Anotrichium sp.</i>	0.3	0.3	0.2	0.3	0.2	0.3	0.2	0.3
<i>Bryopsis spp.</i>	0.5	0.5	0.2	0.8	0.5	1.1	0.3	0.7
<i>Centroceras spp.</i>	0.2	0.6	0.6	0.1	0.3	0.5	0.7	0.4
<i>Ceramium spp.</i>	0.5	0.5	0.6	0.4	0.2	0.2	0.8	0.3
<i>Cladophora spp.</i>	0.1	0.1	0.1	0.3	0.4	0.2	0.1	0.1
<i>Corallophila sp.</i>	0	0.2	0	0.1	0	0	0.1	0.1
Cyanobacteria	0.6	0.4	0.5	0.4	0.6	0.5	0.7	0.5
Diatoms	0	0.2	0.1	0	0	0.1	0	0.1
<i>Enteromorpha spp.</i>	0.3	0.5	0.3	0.2	0.4	0.6	0.3	0.3
<i>Feldmannia sp.</i>	0	0	0	0	0	0.1	0	0.2
Gelidaceae	0	0.1	0	0.1	0	0	0	0
<i>Gracilaria salicornia</i>	0	0.1	0	0	0	0	0.1	0.3
<i>Herposiphonia spp.</i>	0.6	0.8	0.5	0.4	0.3	0.6	0.4	0.4
<i>Hincksia sp.</i>	0.6	0.4	0.2	0.2	0.2	0.4	0.1	0.3
<i>Hypnea spinella</i>	0	0	0	0.1	0	0	0	0
<i>Polysiphonia spp.</i>	0.4	0.3	0.1	0.5	0.6	0.6	0.6	0.6
<i>Sphacelaria spp.</i>	0.2	0.3	0.2	0.1	0.4	0.4	0.4	0
<i>Taenioma perpusillum</i>	0.2	0.3	0.6	0.1	0	0	0.3	0.2
<i>Trichoglea sp.</i>	0	0	0	0	0	0	0.1	0
<i>Wrangelia sp.</i>	0	0.3	0	0	0	0.1	0	0

Appendix B: The taxa and their relative abundances for Caged plots in the Herbivore Exclusion experiment.

Taxon	Cage 1	Cage 2	Cage 3	Cage 4	Cage 5	Cage 6	Cage 7	Cage 8
<i>Anotrichium sp.</i>	0	0.1	0	0.2	0	0	0.1	0.2
<i>Bryopsis spp.</i>	0.7	0.6	0.4	0.6	0.5	0.6	0.8	0.4
<i>Centroceras spp.</i>	0	0.4	0	0.1	0	0.2	0.3	0.6
<i>Ceramium spp.</i>	0	0.2	0	0.3	0.2	0	0	0.1
<i>Cladophora spp.</i>	0.1	0.1	0	0.1	0.2	0	0.4	0.3
<i>Corallophila sp.</i>	0	0.1	0.4	0	0.5	0.6	0.1	0.3
Cyanobacteria	0.9	0.9	0.9	0.8	0	0.6	0.7	0.9
Diatoms	0.2	0.1	0.1	0	0	0.2	0.2	0.1
<i>Enteromorpha spp.</i>	0	0	0	0.1	0	0.2	0.2	0.4
<i>Feldmannia sp.</i>	0	0.1	0.1	0	0	0	0	0
Gelidaceae	0	0	0	0	0	0	0	0
<i>Gracilaria salicornia</i>	0.1	0.1	0	0	0	0.1	0	0.1
<i>Herposiphonia spp.</i>	0.8	0.5	0.6	1.1	0.6	0.9	0.8	0.8
<i>Hincksia sp.</i>	0.6	0	0.8	0.5	0.5	0.4	0.7	0.2
<i>Hypnea spinella</i>	0	0	0	0	0	0	0	0
<i>Polysiphonia spp.</i>	0.3	0.6	1.3	0.3	0.7	0.6	0.6	0.5
<i>Sphacelaria spp.</i>	0.1	0.8	0.2	0.3	0.7	0.5	0.4	0.4
<i>Taenioma perpusillum</i>	0.1	0.1	0	0.3	0.1	0	0.1	0.1
<i>Trichoglea sp.</i>	0	0	0	0	0	0	0	0
<i>Wrangelia sp.</i>	0	0	0	0	0	0	0.1	0

Appendix B: The taxa and their relative abundances for Uncaged plots in the Herbivore Exclusion experiment.