COMMUNITY RESPONSE TO THE REMOVAL OF A DOMINANT ALGA, *TURBINARIA ORNATA*, ON A CORAL REEF IN MOOREA, FRENCH POLYNESIA

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Abstract. Moorea's coral reefs have experienced a dramatic increase in the erect brown algae, *Turbinaria ornata*, over the past 30 years. This study holistically explored the effects of *Turbinaria* overgrowth on the coral reef ecosystem by surveying benthic assemblages and removing *Turbinaria* on 9 small coral heads. Another 9 coral heads were left as unmanipulated controls. Very low coral cover was found in the survey and it was negatively correlated with *Turbinaria* cover. Other macroalgae species were positively correlated with *Turbinaria* cover. Fish abundance and species richness were observed before and after *Turbinaria* removal. The reduction in *Turbinaria* resulted in an increase in wrasse (*Labridae*) visitation frequency and fish species richness. Settlement plates were used to determine the effect of *Turbinaria* removal on the recruitment of benthos. After three weeks of growing, there were significantly more encrusting algae on the plates from the removal sites and significantly more fleshy algae and sediments on plates from the control sites. Increased accessibility on the manipulated sites is likely to account for the increase in wrasse abundance and fish species richness, and the lack of early successional fleshy algae on the settlement plates.

Key words: coral-algal phase shift; Turbinaria ornata; *reef restoration; Moorea, French Polynesia; settlement; fish herbivory*

INTRODUCTION

Coral reefs worldwide are increasingly experiencing phase-shifts from scleractinian coral dominance to fleshy algal dominance (Hughes 1994; McCook 1999; Fabricius *et al.* 2005). The combined effects of climate change, water quality decline, coral disease, and over-fishing have caused widespread coral mortality (Hughes *et al.* 2003). Macroalgae are able to colonize struggling reefs because dead coral provides suitable substrate for algal settlement. The success and continued dominance of fleshy algae is then determined by both top-down and bottom-up control mechanisms (McManus and Polsenberg, 2004). The bottom-up control is determined by nutrient concentrations whereby eutrophication of oceanic water enhances algal blooms. Top-down control of algae is dependent on herbivore grazing, thus when overexploitation of grazers or disease-related mortality of grazers occurs, algae can proliferate.

Coral-algal phase shifts after natural disturbances have long been documented throughout coral reef history. Complete recovery from these shifts can occur within five to fifteen years depending on the degree of damages and environmental conditions (Pearson 1981; Adjeroud et al 2009). However, the rate and scale at which these shifts are occurring is higher than ever before. Increasing, anthropogenic disturbances compounded by eutrophication and overfishing are stalling and preventing the natural course reef recuperation (Diaz-Pulido et al 2009). Therefore, new methods of managing coral reefs and algal growth need to be explored.

While macroalgal dominance may not be the cause of coral health decline, it could play a role in preventing coral reef recovery. Coral and algae compete for space and resources (McCook *et al.* 2001). Experiments with brown algae and developing coral planulae have shown that brown algae can directly cause planulae mortality through allelopathy as well as indirectly through their associated microbes (Smith *et al.* 2006). Benthic algae can also deter coral growth through smothering, abrasion, and shading (McCook *et al.* 2001).

Not only can brown algae inhibit their coral competitors, they can also deter their predators. Phenolic compounds found in brown algae have been shown to prevent grazing by tropical fish (Van Alstyne and Paul, 1990). When erect brown algae was removed from Glover's Reef, Belize, abundance and biomass of blue-headed wrasse, blue tang, and spotlight parrotfish increased (McClanahan *et al.* 2000). While that study showed that certain grazers increase when several brown algae species are removed, it did not attempt to decipher if any one species of brown algae is more efficient at deterring herbivory. Some brown algae, such as *Turbinaria ornata*, have unpalatable physical structures that deter herbivores (Stiger and Payri 1999) and can serve as a refuge for other macroalgae (Bittick *et al.* 2010).

Today, the reefs of the French Polynesia are dominated by benthic brown algae (Stiger and Payri 2005). *Turbinaria* is the most prevalent of these macroalgae on Tahiti and Moorea, and these are some of the only locations in the world that *Turbinaria* has such widespread dominance. *Turbinaria*, however, was only observed in small quantities prior to 1980 and it was found solely in the Society and Austral Archipelagos (Stiger and Payri 1999; Andrefouet *et al.* 2004). Over the past 30 years, *Turbinaria* has come to dominate the back reefs of these areas and has spread to the Tuamotus (Martinez *et al.* 2007). The initial boom in *Turbinaria* has been attributed to intense cyclones and Crown of Thorns Starfish outbreaks decimating the reefs repeatedly, and the coral has yet to rebound from these damages. French Polynesia's reefs are critical to the people's culture and economy (United Nations Statistics Division) and if the reefs continue on their current trajectory, it is likely that they will continue to degrade. Since it is unfeasible to control disasters such as coral bleaching, crown of thorns outbreaks, cyclones, and ocean acidification, small scale reef management possibilities need to be explored.

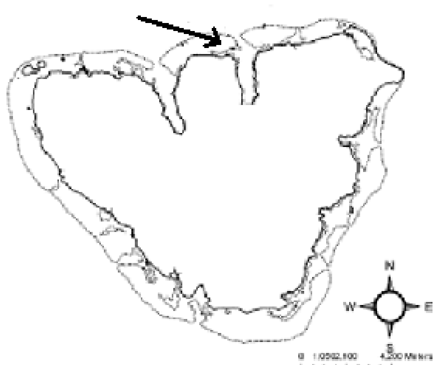

FIG. 1. The site sampled in this study is shown in this map of Moorea, French Polynesia. Base map courtesy of the Geospatial Innovation Facility, University of California, Berkeley.

One possible course of action would be to introduce human harvesting of *Turbinaria* to act as an artificial top-down control of the algae that are unpalatable to natural grazers. Past studies have shown that removal of all macroalgae has positive impacts on fish communities (McClanahan et al 2000; McClanahan et al 2002). However, the health of a reef is determined by much more than fish. While many aspects of coral-algal phase shifts have been studied extensively, there is a lack of attention to the connectivity of all these different processes on reefs. This study seeks to holistically examine different aspects of community change after the removal of the dominant brown algae, *Turbinaria ornata.* The goals of this study were to 1) observe the natural variation in coral and other algal cover in relation to *Turbinaria* cover, 2) assess how fish abundance and diversity changes when *Turbinaria* is removed, and 3) determine how *Turbinaria* removal affects new settlers on a reef. These three objectives will provide a more complete picture of how macroalgae can affect a coral reef environment and will highlight how intertwined different coral reef processes are.

METHODS

Study site

This study was conducted in the back reef on the West side of Avaroa pass entering Cook's Bay which is located on the North side of the island of Moorea, French Polynesia (17°28'48.89"S, 149°49'40.62"W; Fig 1). The site was centered around a metal pole that lies approximately 30 meters from the reef crest. The environment was characterized by solitary and conjoined coral heads situated on sand and coral rubble substrate. The depth ranged from 1.5-3.1 meters. The study took place between October 23rd and November 19th 2013.

The criteria for choosing a coral head was that it be between 3.5-5.5 meters circumference and have greater than or equal to 40% *Turbinaria* coverage. The substrate of each coral head was mostly composed of dead *Porites* coral. To randomize the selection of coral heads, three compass headings starting at the pole were chosen at random and the first six coral heads fitting the criteria on each heading were selected, giving a total of 18 coral heads. Along each heading, the six coral heads were alternately marked for manipulation or control. Coral heads that were to be manipulated were marked with pink flagging tape and control coral heads were marked with yellow flagging tape. All flagging tape was removed at the end of the study.

Field survey

The first portion of the study was a survey of the macroalgal and coral communities found on the coral head. To do this, *Turbinaria*, other algae, and coral cover were recorded as percentages in two 0.5 x 0.5 meter quadrats on each coral head selected. The first quadrat was placed in the area of highest *Turbinaria* density, which was then selected as the site for settlement plate attachment. The second quadrat was arranged so that it centered on the flagging tape. These areas with visible markers were chosen so that the quadrat was placed in the same area upon every visit. The algae were identified using the guide "South Pacific Reef Plants" (Littler and Littler 2003). Corals were identified using the guide "Coral Reef Animals of the South Pacific" (Gosliner et al. 1996). A generalized linear model (GLM) was employed using R (R Development Core Team, version 3.0.2, 2013) to determine if there were any correlations between *Turbinaria* coverage and other benthic organisms.

Effect of Turbinaria removal on fish

The second portion of the study involved manipulation of the coral heads to assess the influence of *Turbinaria* on the fish community. A before-after-control-impact (BACI, Smith 2002) approach was taken to limit possible confounding factors. Before removal, each coral head was characterized according to the methods below. Then, the *Turbinaria* was removed from the nine coral heads selected for manipulation by pulling off all thalli by hand and cutting off as much visible holdfast as possible with scissors.

Two aspects of the fish community were assessed: visitation frequency of the four main grazing fish families and diversity of visiting fish species. The four main grazing fish families were *Acanthuridae* (surgeonfish), *Pomacentridae* (damselfish), *Labridae* (wrasse), and *Scaridae* (parrotfish). These fish families were chose because during several hours of preliminary observation it was concluded that these were the most frequently spotted grazers on the reef. Before the field work, I studied "Reef Fish Identification: Tropical Pacific" (Allen et al. 2010) so that unique species and different morphologies of the same species could be properly identified. Frequency of visitation of the four families and fish diversity were measured during five minute observation sessions. One person tallied the number of times parrotfish, wrasse, damselfish, and surgeonfish visited the coral head and another person kept count of how many different fish species visited the coral head. The fish observation at each coral head was repeated four times: once prior to *Turbinaria* removal and three times after in the following 3 weeks. An analysis of covariance (ANCOVA) was used to asses the effect of *Turbinaria* removal on fish counts over the three weeks. The continuous variable for these analyses was time and the categorical variable was treatment (*Turbinaria* present and *Turbinaria* removed).

Effect of Turbinaria removal on settlement

The differences in colonization between coral heads whose *Turbinaria* had and had not been removed was assessed using settlement plates. The settlements plates were 4.5 x 4.5 cm squares, made of plaster of Paris, and were rough on one side. They were placed in a seawater tank at the Gump Station for 4 days to develop a biofilm prior to installation. The plates were then installed, rough side up, onto the *Turbinaria* removed and *Turbinaria* covered coral head using screws, washers, and plastic screw anchors. The plates were placed in the center of the first quadrat where *Turbinaria* density was the highest or had been the highest prior to removal. Each week, notes were taken on the color of the settlement plates and any identifiable colonized organisms. At the end of the three weeks, settlement plates and all hardware were removed and transported back to the lab. First, plates were placed in a dish, where they were submerged in seawater, and pictures were taken of each plate. Next, a transect was laid randomly along the length of the plate and examined under a microscope. Settlers were grouped into five categories (brown filamentous, brown encrusting, green filamentous, green encrusting, and pink coralline) and calculated as a proportion of the 45mm transect. Finally, everything was scraped from each plate onto filter paper using razors and brushes, placed in a drying oven for 48 hours, and weighed. A principle components analysis and discriminant analysis was done to differentiate the compositions of the settlement plates from each treatment. Individual *T*-tests were performed for each of the five settler categories and for total fleshy (green fleshy + brown fleshy) and total encrusting (green encrusting + brown encrusting + pink coralline). A Wilcox rank sum test was used to analyze the dry masses of the settlement plates from each treatment.

RESULTS

Field survey

Figure Percent *Turbinaria* cover was tested against percent coral cover and percent other algal cover in each of the two quadrats on all 18 coral heads. Coral cover was negatively correlated with *Turbinaria* cover (GLM(quasipoisson), X^2= 148.33, df=35, p<0.001, Fig 2). The mean coral cover was 5.33% and the mean *Turbinaria* cover was 56.33%. Of the mean coral cover, 4.22% was accounted for by *Porites* and 1.11% was *Pocillopora.* The maximum coral cover reported was a mere 25%.

Turbinaria coverage was positively correlated with other fleshy algal coverage (GLM(quasipoison), X^2= 227.03, df=35, p=0.003, Fig 3). The other fleshy algae was calculated as a sum of the percent covers of the genera *Halimeda, Amansia, Dictyota, Padina, Colomenia, Asparagopsis*, *Sargassum*, and *Dictyosphaeria.* The mean other algae cover was 38.75% of which 24.31% was *Amansia*,

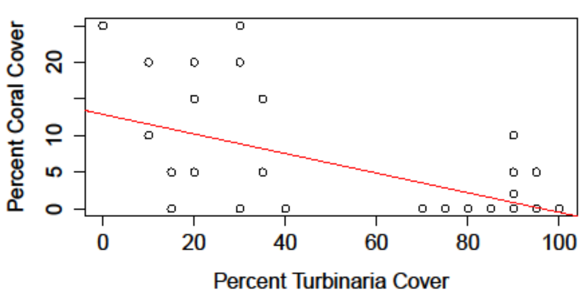

FIG. 2. This graph shows the inverse relationship between percent coral cover and percent *Turbinaria* cover from surveys of 18 coral heads.

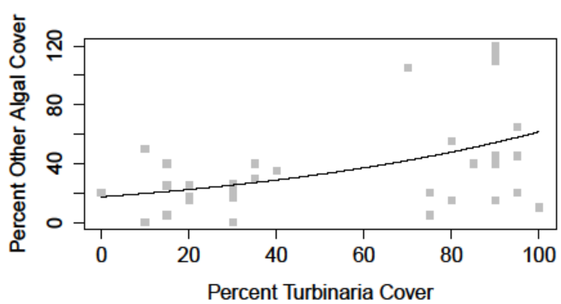

FIG. 3. This graph shows the relationship between percent *Turbinaria* cover and percent other macroalgal cover from surveys of 18 coral heads.

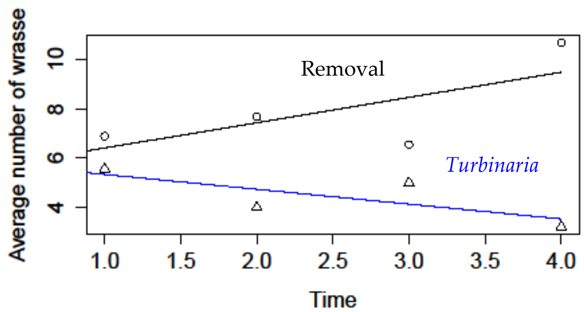

FIG. 4. This graph shows the change in wrasse visitation frequency over three weeks after *Turbinaria* removal

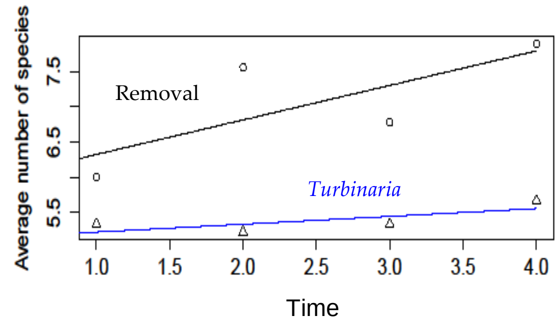

FIG. 5. This graph shows the change in total fish species richness over three weeks after *Turbinaria* removal.

8.19% was *Halimeda*, and 2.78% was *Dictyota*.

Effect of Turbinaria removal on fish

Fish counts were tested for an effect from the continuous variable, time and the categorical value, treatment. The frequency of wrasse visitation significantly increased as a result of *Turbinaria* removal over the 3 week period (Ancova: Treatment, $F_{1,68}$=22.87, p<0.001; Treatment*Time, $F_{1,68}$=6.14, p=0.02; Fig 4). The average number of wrasse visiting each *Turbinaria* removed coral head increased from 6.89 before removal to 10.67 three weeks after removal. The removal of *Turbinaria* did not have a significant effect on surgeonfish visitation frequencies (Ancova: Treatment, $F_{1,68}$=0.93, p=0.34; Treatment*Time, $F_{1,68}$=0.75, p=0.39). The sample size for damselfish and parrotfish were not large enough to analyze. Total number of fish species visiting the coral heads significantly increased after the removal of *Turbinaria* (Ancova: Treatment, $F_{1,68}$=8.27, p=0.005; Treatment*Time, $F_{1,68}$=0.53, p=0.47; Fig 5). At the removal site, mean species

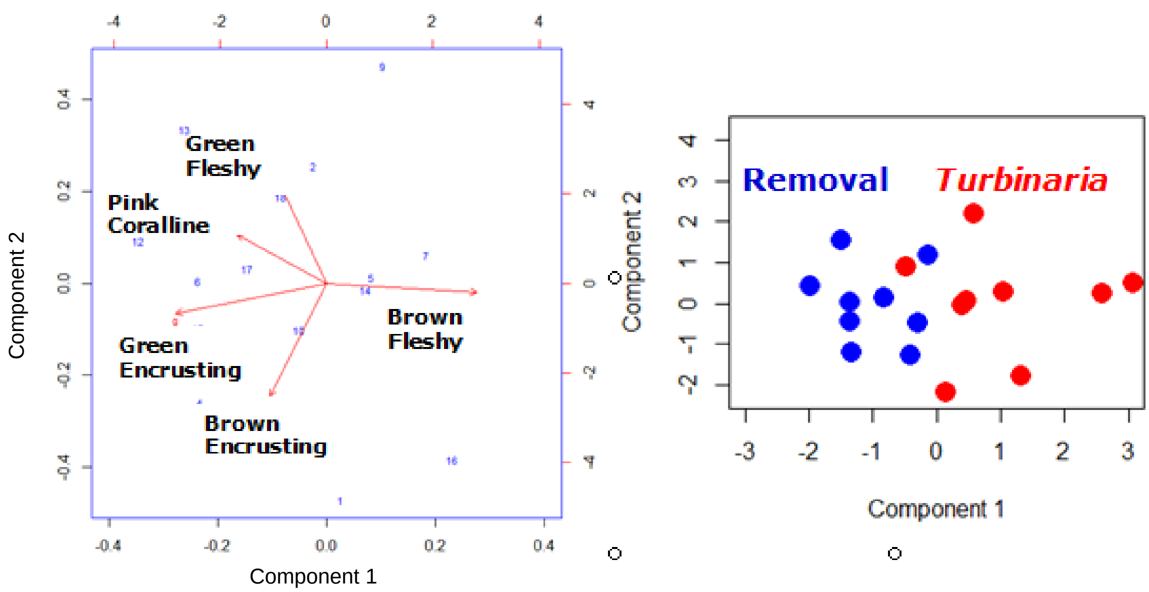

FIG. 6. These two figures both represent a principle components analysis of the settlers on the plates from both treatments. The figure to the left shows the distribution of the different characteristics amongst the plates and the graph on the right highlight which plates came from which treatment (red=*Turbinaria*, blue= removal). Pictures of settlement plates can be found in Appendix A and B.

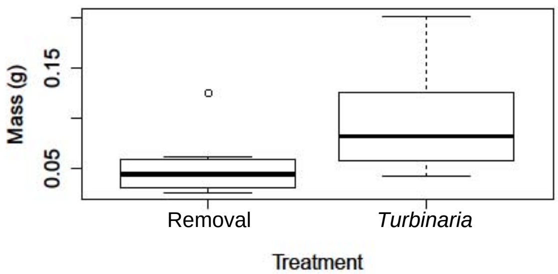

FIG. 7. This box plot shows the differences in dry mass of the settlers from the plates. There was significantly higher mass at the *Turbinaria* sites.

richness increased from 6 prior to removal to 7.89 three weeks after removal.

Effect of Turbinaria removal on settlement

The composition of algae on the plates from the removal sites were significantly different from those at the *Turbinaria* sites (Wilks-Lambda, Discriminant Analysis: df=5, p<0.001). The principle components analysis (Fig 6) shows that plates from the removal sites tended to be characterized more by green encrusting algae and *Turbinaria* plates were characterized more by brown fleshy algae. While pink coralline, brown encrusting, and green fleshy did not play as large a role in distinguishing the plates, these algae did tend to be more characteristic of the removal plates. *T*-tests run for each individual settler category confirmed that there was significantly more brown fleshy algae at the *Turbinaria* sites and significantly more green encrusting algae at the removal sites (*t*-test: brown fleshy, $t_{bf}(17)=3.10$, $p_{bf}<0.01$; green encrusting, $t_{ge}(17)=8.41$, $p_{ge}<0.001$). The categories were then combined into fleshy and encrusting. There was significantly more fleshy algae at the *Turbinaria* sites and significantly more encrusting at the removal sites (*t*-test: fleshy, $t_f(14.2)=2.18$, $p_f=0.04$; encrusting, $t_e(15.5)=3.97$, $p_e<0.01$) . The dry mass of the settlers was significantly lower on the plates from the removal sites (Wilcox rank-sum test: W=14.5, p=0.02; Fig 7). The mean mass at the removal sites was 0.05g and the mean mass at the *Turbinaria* sites was 0.10g.

DISCUSSION

The presence of *Turbinaria* naturally influences its surrounding macroalgal and coral communities. *Turbinaria*, however, affected these groups in opposite ways. Coral cover was negatively correlated with *Turbinaria* cover (Fig 2). Many studies have shown similar negative correlations between other macroalgae and corals as reviewed by compete for space, resources, and light (McCook et al. 2001). *Turbinaria* has many competitive advantages that may be causing this negative correlation. The erect, canopy-forming thalli of *Turbinaria* shade corals in the vicinity, depriving them of the sunlight necessary for their photosynthetic symbionts. It also has a leathery and spiny structure which causes abrasion of coral tissue when current or surge moves the thalli.

Some macroalgae assume tactics that target corals during the sensitive recruitment stages. While the direct mechanism is unknown, corals are less likely to settle in areas of high macroalgal growth and instead prefer crustose coralline algae (Birrell et al 2008). If a planulae does settle in the vicinity, certain algae have been found to have both direct and microbe-mediated allelopathic properties that are particularly lethal to vulnerable developing coral planulae (Vermeij et al 2008). It has been hypothesized that this creates a positive feedback loop: algae releases chemicals that stimulate microbial activity on the surface of corals causing tissue mortality which opportunistically provides substrate for more algal growth (Smith et al 2006). The combined effects of these macroalgal competitive mechanisms can physiologically stress corals which in turn can reduce fecundity and growth (Hughes et al 2010). Thus, macroalgae has deleterious effects at every stage in a corals life cycle making it no surprise that the mean percent coral cover was a mere 5.33%.

Turbinaria cover tended to be lower where coral cover was higher which may be because some corals have defensive mechanisms against algal overgrowth (Fig 2). Studies have shown that healthy corals are able to prevent attachment and survival of macroalgal recruits (Diaz-Pulido and McCook 2004). *Porites* corals slough off their surface tissue taking all unwanted settlers with it, and then "resheet" with live tissue (McManus and Polsenberg 2004). This may be a contributing factor to why 79% of the coral recorded was *Porites*. *Porites* has been dubbed a "winner" amongst corals for its lower susceptibility to bleaching (Loya et al 2001) and its low favorability for crown of thorns starfish (De'ath and Moran 1998). In contrast, *Pocillopora* has been dubbed a "loser" for not possessing these qualities which may explain why its overall coverage was a meager 1.11%.

The algae found nestled amongst the *Turbinaria* may contribute to the negative effects on coral health. The most abundant algae recorded were *Amansia* (62%), *Halimeda* (21%), and *Dictyota* (7%). Past studies have shown that each of these algae significantly reduces coral settlement in its vicinity (Diaz-Pulido et al 2010).

While coral was negatively correlated with *Turbinaria* cover, other algae was positively correlated with *Turbinaria* cover (Fig 3). This suggests that *Turbinaria* may act as an herbivory refuge for other algae. *Turbinaria* has a cylindrical thallus that is attached to a substrate by a long holdfast. Algae have ample space to grow in this understory between the substrate and the dense canopy of thalli. Since the thalli are spiny and rigid they act as a physical barrier to grazing because fish are discouraged from swimming through them (Bittick et al 2010). In addition, *Turbinaria* produces high levels of phenolic compounds (Stiger et al 2004) which it releases in part to deter herbivory (Van Alstyne and Paul 1990).

Effect of Turbinaria removal on fish

When *Turbinaria* and its associated fish-deterring properties were removed from the coral head, the visitation frequency of wrasses significantly increased (Fig 4). The wrasses observed in Moorea, primarily *Thalassoma Hardwicke*, feed on small invertebrates and zooplankton found close to the substrate (fishbase.org). The removal of *Turbinaria* likely exposed many invertebrate rich areas on top of the coral head that were previously protected. Wrasses were often observed nibbling at solitary detached thalli floating through the water column yet were not often seen grazing in dense *Turbinaria* stands. This reasserts that the structure of *Turbinaria* is a physical barrier to grazing. It also suggests that many small invertebrates take refuge amongst the *Turbinaria* thalli as well as underneath them.

There was no significant effect of removal on surgeonfish. This was surprising since surgeonfish were found to be the dominant herbivores on the reef and they were never observed eating *Turbinaria*. However, this may be because surgeonfish prefer to graze young and filamentous algae and the algae exposed by *Turbinaria* removal was late stage, fleshy algae (fishbase.org). Thus, surgeonfish were primarily observed grazing around the vertical sides of the coral head where it is hard for macroalgae such as *Turbinaria* to attach.

Fish species richness increased after the removal of *Turbinaria*. This is likely due to the exposure of new microhabitats. Small fish and invertebrates are exposed to their fish predators which in turn trickles down the food chain and increases overall diversity of fish frequenting the site. The heterogeneous substrate provides crevices for shelter and protection. These structures are crucial because without them, larger herbivores are predated at a higher rate and a shift towards smaller fish body size is observed (Mumby and Steneck 2008). Macroalgae cannot provide the 3D structural protection that hard corals can. This creates another feedback loop favoring algal growth because smaller fish have less potential for controlling macroalgae. Experimental reductions of macroalgae in Belize (McClanahan et al 2000) and Kenya (McClanahan et al 2002) have documented an increase in both abundance and size of several fish species after one week and one year respectively. Very clear differences were observed on the settlement plates from the two treatments (Fig 6).

Effect of Turbinaria removal on settlement

The higher amounts of brown fleshy and combined fleshy algae on the plates from the

Turbinaria sites suggests that *Turbinaria* can influence both what settles and which settlers survive. Due to the close proximity at the *Turbinaria* sites, new recruits may be the offspring of algae in their immediate vicinity (Diaz-Pulido and McCook 2004). Also, placement in the highest density *Turbinaria* area could have reduced the grazing pressure on the new recruits. The higher amounts of green encrusting and combined encrusting algae at the removal sites suggest that there was higher grazing pressure and minimal influences from other algae. These results are reinforced by the dry mass calculations (Fig 7). The dry mass data also takes sediments into account. Fleshy algae are much more likely to trap sediments than encrusting algae so sediment may contribute to the higher mass at the *Turbinaria* sites.

As mentioned above, macroalgae can negatively affect coral planulae, but the microenvironment of the substrate also plays a role in coral recruitment. Past studies have shown that both sediments and filamentous algal turfs reduce coral settlement (Birrell et al 2005). Alternatively, crustose coralline algae increase coral settlement (Vermeij and Sandin 2008). Therefore, while no coral settled during this study, if the plates were left in the water longer it is more likely that coral would settle at the removal sites over the *Turbinaria* sites.

Conclusions

All of the significant results from the *Turbinaria* removal experiments have positive implications for coral reef recovery. Long term effects should be further studied and manual removal of *Turbinaria* should be considered as a restoration ecology method on a local scale. In the interest of enhancing tourist appeal, some hotels on Moorea already partake in reef restoration by developing artificial reefs. Hotels and tourist operations, therefore, may be interested in exploring this new option. Furthermore, the phenolic compounds in *Turbinaria* are of use in the cosmetic industry and harvesting it has been considered for years in Tahiti (Andrefouet et al. 2004). Thus, *Turbinaria* removal would be beneficial from both an economic and ecological perspective.

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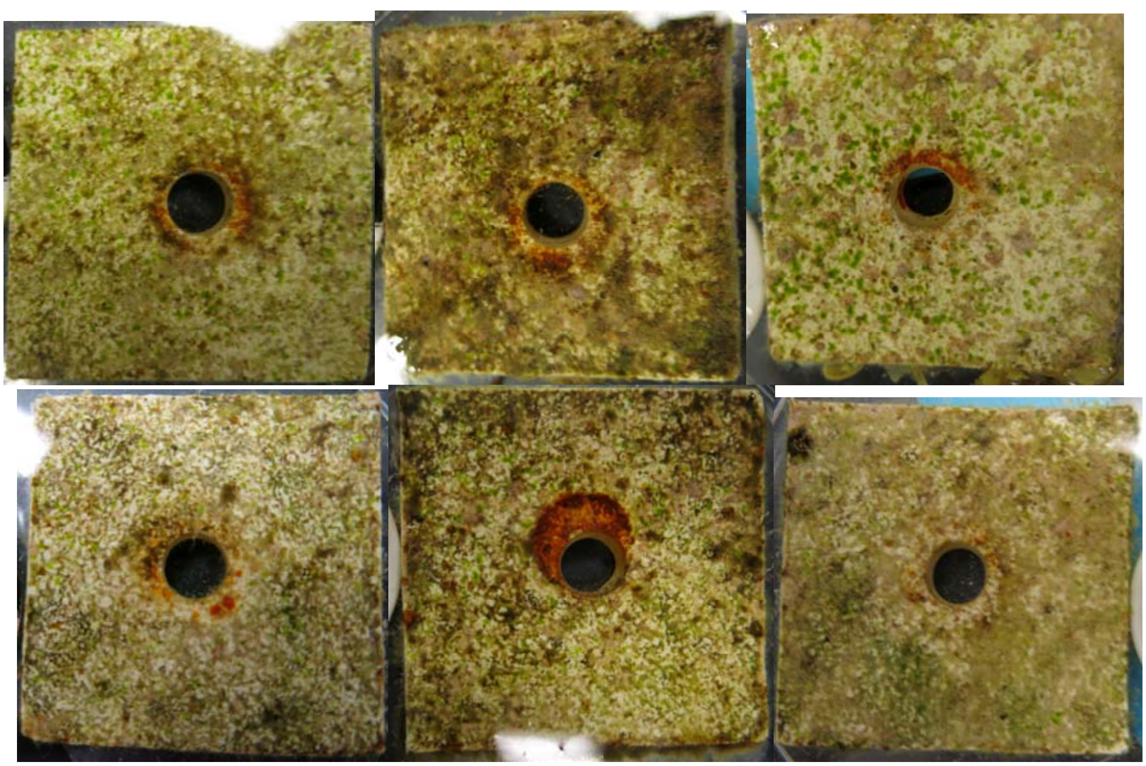
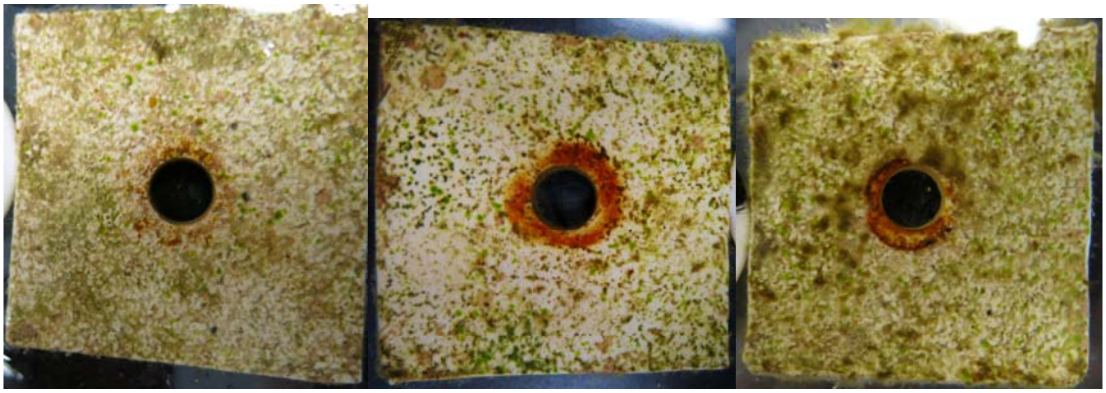
APPENDIX A

These are pictures of settlement plates that were attached to the removal sites. The plates were 4.5 x 4.5 cm and were made of plaster of Paris.





APPENDIX B

These are pictures of settlement plates that were attached to the *Turbinaria*/control sites. The plates were 4.5 x 4.5 cm and were made of plaster of Paris.