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Mechanisms underlying macroalgal phase shifts in coral reef ecosystems

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Mechanisms underlying macroalgal phase shifts in coral reef ecosystems

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution and Marine Biology

by

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September 2016

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September 2016

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ABSTRACT

Mechanisms underlying macroalgal phase shifts in coral reef ecosystems

by

Samantha Lee Davis

Coral reefs are currently threatened by both natural and human-driven disturbances, and climate change scenarios suggest that the health of future reefs is uncertain. To better inform management and preservation of coral reef ecosystems, it is critical that we understand the mechanisms that support recovery of coral habitat after coral mortality events. Macroalgae can inhibit coral recovery by preventing recruitment and growth of corals after a disturbance, leading to a shift in the dominant benthic community from coral to macroalgae. These macroalgal habitats do not support the same diversity of fish and other species as healthy coral reefs, and are thus undesirable on large scales. This dissertation addresses some processes that are important in the establishment and persistence of these macroalgal phase shifts. Through an enhanced understanding of macroalgal persistence, we may be able to identify (and protect) key species and processes that are critical to promoting coral reef recovery.

I used the macroalga *Turbinaria ornata* as a model species to examine the potential for herbivore-algal feedbacks that can promote persistent macroalgal phase shifts. This species is perennial and patches appear to persist inter-annually once established. In areas where macroalgae is present, *Turbinaria* largely dominates the benthic community. Results

of observational studies of tagged *Turbinaria* patches suggest that *Turbinaria* populations exhibit positive population growth (both number of adult thalli and patch area increased over a 2 year period). Several factors including high turnover rates of thalli, year-round reproduction, and a buffer of immature individuals that may act as a "seed bank" following a disturbance may contribute to the expansion of this species in the lagoons of Moorea.

In addition, I used field experiments to assess the potential for associational refuge to provide a mechanism for *Turbinaria* persistence in the lagoons of Moorea. Results from these experiments suggest that an associational refuge may facilitate persistence of *Turbinaria*, as predation on small vulnerable individuals (< 2 cm in length) is reduced when associated with larger, less palatable adults. However, the significance of this refuge depends on the local abundance of browsing herbivores that can consume macroalgae. An associational refuge that results in higher recruit survival in the presence of herbivory could represent a self-reinforcement mechanism that could facilitate the establishment and multi-generational persistence of *Turbinaria* patches on coral reefs.

To determine the effects of herbivore pressure on the development and persistence of a macroalgal community, I examined the effects of herbivores on mature (dominated by the late stage macroalga *Turbinaria ornata*) and early stage (dominated by turf algae) algal communities. Results suggest that the effects of herbivores depend upon the initial conditions of the benthic community, and this may have implications for management practices for disturbed, degraded and healthy reefs. Herbivores, particularly browsing fish that can consume mature macroalgae, appear to be limited in their capacity to remove established macroalgae. These critical species appear to be present in low abundance in some habitats, and are targeted as part of a local fishery. In contrast, other herbivores (grazers that consume turf algae and immature macroalgae) appear to readily limit the

development of macroalgal communities. I also found that herbivores differentially influence the richness of macroalgal communities depending on the initial macroalgal community. Specifically, an initial presence of the mature macroalga, *Turbinaria ornata,* enhanced richness of macroalgal assemblage even as herbivore pressure increased. At the same level of herbivore pressure, communities with *Turbinaria* present had greater richness than communities that initially were dominated by turf algae, even after two years. Results from this experiment provide some of the first empirical tests of hysteresis (path-dependency) in reef recovery, and reinforce the importance of different herbivore functional groups at different points along the recovery trajectory.

Overall, this research highlights characteristics of macroalgae and interactions between macroalgal and herbivore communities that can drive persistent macroalgal phase shifts in coral reef ecosystems. This information may be used to develop sustainable management and conservation strategies to preserve these valuable ecosystems and the services that they provide for local communities.

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Abstract

Turbinaria ornata (Turner 1848) is one of the most abundant macroalgal species in the lagoons of Moorea, French Polynesia. This species is both chemically and structurally defended against herbivory, and may serve as a model to understand the persistence of macroalgal assemblages in coral reef ecosystems. I used tagged *Turbinaria* patches to explore the demography of *Turbinaria* stages (adult, juvenile and recruit thalli), as well as the dynamics of patches over a 3-year period. Understanding the patch dynamics of this critical species could provide valuable information to aid management of macroalgae on coral reefs, and contribute to the development of more comprehensive strategies to promote coral recovery following coral mortality events. Over the course of this study, *Turbinaria* populations exhibited positive population growth (both number of adult thalli and patch area increased). High turnover rates of thalli, year-round reproduction, and herbivore resistance for thalli > 2 cm may contribute to the expansion of this species in the lagoons of Moorea. As macroalgae are known to negatively influence coral recovery processes, the development of effective conservation and management protocols may be improved by studies incorporating the dynamics of macroalgal populations in habitats at local scales.

Introduction

Macroalgae are fundamental structural components of many marine habitats including temperate and tropical reefs, providing shelter and food for a variety of organisms (Rönnbäck et al. 2007, Nelson 2009, Smale et al. 2013). The provisioning of ecosystem services (e.g., coastal protection, carbon sequestration, raw materials) can be of both financial and cultural value to local economies (Bennett et al. 2015). Some macroalgae, like the giant kelp *Macrocystis pyrifera*, may drive local biodiversity and biomass of associated species (Steneck et al. 2002, Graham 2004). The establishment and persistence of macroalgal assemblages have been studied as part of efforts to better understand, manage and preserve these critical ecosystems, especially in light of predicted and recent global changes (Dayton et al. 1998, Halpern et al. 2007, Byrnes et al. 2011). Many marine systems are experiencing an influx of invasive macroalgae, which may or may not provide similar ecosystem functions (Stachowicz et al. 2002, Occhipinti-Ambrogi and Savini 2003). For example, the invasive macroalga *Sargassum muticum* may alter diversity and abundance of multiple trophic levels, food web dynamics and thus ecosystem functioning (Sanchez and Fernandez 2005, Salvaterra et al. 2013). Attributes that could influence the establishment and persistence of macroalgae include r-selected traits like fast growth, high dispersal rates, and the ability to reproduce both sexually and asexually (Chapman et al. 2006).

Understanding the traits that enable successful establishment of marine macroalgae and promote persistence could improve management of threatened ecosystems, including coral reefs. Shifts from coral-dominated to macroalgal-dominated reefs have been documented globally (Done 1992, Hughes 1994, Bellwood et al. 2004, Hughes et al. 2007; but see Bruno et al. 2009), and these shifts can have significant negative consequences for reef biodiversity and abundance of critical species, as well as for local economies

(Wilkinson 1996). In the study of macroalgal phase shifts in coral reef systems, general focus has been on changes in the percent cover of macroalgae – less emphasis has been placed on the dynamics of macroalgal patches, though patch dynamics can be very important when considering the ecological impacts of coral – macroalgal interactions. For example, short-lived dynamic patches with high extinction rates may have shorter interaction times with recovering coral, while patches with lower extinction rates are capable of longer term interactions with coral (Mumby et al. 2005).

Turbinaria ornata (Turner 1848), a brown alga (order Fucales) that is distributed on coral reefs in much of the Indo-Pacific, has the potential for becoming a dominant space holder for extended periods of time. *Turbinaria* became dominant in the lagoons of Moorea, French Polynesia in the late 1980's to early 1990's (Done 1992), and again is becoming a space dominant on lagoon (but not fore reef) substrata following recent disturbances (Adam et al. 2011, Carpenter 2015). *Turbinaria* is patchily distributed on suitable hard substrata and its abundance can fluctuate through time. To better inform management and generate predictions concerning persistence of this species, it is necessary to understand both the demography of the species and the dynamics of their patches, neither of which has been done to date for this ecologically important species of macroalgae. In this study, I quantified stage-specific demographic attributes of *Turbinaria* as well as dynamics of *Turbinaria* patches over a 3-year period, which represented multiple complete turnovers of individual thalli.

Methods

Study Site and Focal Species

All fieldwork was conducted within the north shore lagoons of Moorea, French Polynesia (17º32’ S, 149º50’W) during 2012- 2015. Moorea is a high volcanic island in the Society Islands archipelago, located approximately 17 km northwest of Tahiti. The benthic communities of the north shore lagoons are characterized by a combination of scleractinian corals, mixed assemblages of turf algae, sessile invertebrates, and in some locations, patches of macroalgae.

Turbinaria ornata (Turner 1848) is one of the most abundant species of macroalgae at the study sites (Carpenter 2015), though other macroalgal taxa (including *Dictyota* spp., *Halimeda* spp., *Amansia rhodantha*, *Sargassum pacificum*, *Padina* spp.) are also present. *Turbinaria ornata* is found throughout the central and western Pacific, mostly in lagoon environments. Phenotypic plasticity facilitates the development of different morphotypes that are suited to either calm unidirectional flow (lagoon) or high-energy, wave-driven flow (reef crest) (Stewart 2008). *Turbinaria* is both structurally and chemically defended against herbivory, and the production of chemical defense compounds develop ontogenetically (Stiger et al. 2004). Sexual reproduction occurs year-round, and dispersal occurs on both local (fertilized zygotes develop on and settle within 1 m of parent thalli, Stiger and Payri 2005) and regional (floating rafts of reproductively mature thalli can travel >100 km) scales (Stiger and Payri 1999a, 1999b). *Turbinaria* also may be able to grow vegetatively from fragments (Prathep et al. 2007). Short distance dispersal and/or asexual reproduction can facilitate a “patchy” distribution of *Turbinaria ornata* thalli*,* whereby thalli are often found clustered together. There is also recent evidence that *Turbinaria* populations (along with other macroalgal taxa) may increase in response to increased substrate availability following coral mortality events (Carpenter 2015). Coral mortality within the lagoon habitats of Moorea has been spatially heterogeneous: some areas have declined in the cover of living coral while other areas have maintained similar living coral cover.

Demographic study

To characterize demographic attributes of *Turbinaria ornata,* I established tagged patches (N = 50) at one site (Site 1) in the north shore lagoon during austral winter (Aug-Sept) 2012. This site was located in a back reef environment characterized by a patchy distribution of dead and living coral bommies, separated by sand, rubble, and pavement. *Turbinaria ornata* patches are generally found on hard substrata (e.g., dead coral, pavement). For this study, a patch of *Turbinaria* was defined operationally as being >10 cm away from adjacent *Turbinaria* thalli; clusters of *Turbinaria* thalli growing closer together than 10 cm were considered part of the same patch. 10 cm was selected as the operational distance for distinct patches based on observations of a distinct region where an adult thallus (> 5 cm in height) might physically influence other individuals (via shading, abrasion, etc.). Individual patches were marked with numbered plastic tags affixed to the substrate using a marine epoxy. At each patch, I counted the number of individual thalli belonging to 3 different stages: recruits (< 2 cm thallus length), juveniles (2-5 cm), and adults (> 5 cm). Multiple upright branches occurring on a single holdfast were counted as one individual thallus. These stages are similar to those established by Stiger et al. (1999, 2005), and are largely based on physical characteristics (height) and reproductive potential (individuals > 5 cm are capable of reproduction). Recruits < 2 cm are more vulnerable to herbivory than juveniles and adults, which may be a result of lower phenolic content and/or less structural defense (Stiger et al. 2004, Davis 2016). To estimate the lifespan of *Turbinaria* thalli, I marked different cohorts by attaching a color-coded cable tie around adult and juvenile thalli during each survey. Because recruits (< 2 cm) are small and fragile, I was unable to tag them in this way. Between 2012 and 2015, I surveyed these patches 7 times (Sept. 2012, Dec. 2012, April 2013, July 2013, Jan. 2014, July 2014, and July 2015). At each subsequent survey, I counted the number of marked thalli present from prior cohorts (adults and juveniles marked with colored cable ties), counted and marked new adults and juveniles with colored cable ties, and counted recruits. Patch size was measured and area calculated using the formula for area of an ellipse ($A = pi*d_1/2*d_2/2$) as a general shape that could characterize the patches that occurred in irregular clumps or clusters. This enabled estimation of density of each stage, as well as total density of thalli within a patch.

During austral winter 2013, I began to follow permanently marked patches at 3 additional sites within the north shore lagoon (Sites 2-4, N = 30 patches per site). These sites were similar to Site 1 with respect to benthic composition. At these sites only adult thalli (> 5 cm) were marked, and area of the patches were estimated using the same methods as described above. Between 2013 and 2015, I surveyed these patches 3 times (July 2013, July 2014, and July 2015). At each survey, I counted the number of previously marked adults, counted and tagged new adults with colored cable ties, and estimated the area of the patch. Because of the large total area covered by these patches, I did not count the numbers of juveniles or recruits during surveys, although individual thalli in these stages were generally present at all survey times (personal observation). I used data from all four sites (N = 129 in 2013; 11 patches were lost between 2012-2013 at Site 1) to investigate temporal patterns of adult density and patch area.

Distribution of Turbinaria *stages and lifespan of adult and juvenile thalli*

Many benthic macroalgae, including *Turbinaria ornata*, maintain high propagule output by being reproductively active throughout the year (Lotze et al. 2000). I used the demographic data collected at Site 1 to determine the proportion of each *Turbinaria* stage present throughout the study period. These surveys included time points in austral summer and austral winter, so potential effects of seasonality on the relative proportions of stages could be evaluated. At each survey, I quantified the number of adults, juveniles and recruit thalli. The total number of adult thalli present in a patch was calculated by combining the surviving thalli from prior surveys (thalli tagged as adults and juveniles in prior survey), and the number of "new" adult thalli counted during the survey. This method of obtaining the total number of adults assumes that all individual thalli that survived and previously marked as juveniles grew to be > 5cm by the time of the next sampling period (the "new" stage status of tagged thalli was not recorded during subsequent surveys, i.e., thalli were only tagged once). Two points may justify this assumption: 1) The estimated growth rate of sister species *Turbinaria decurrens* is approximately 2 cm per month (Kaliaperumal and Rao 1975) and 2) The sampling intervals in this study were no less than 3 months. With a growth rate of ~ 2 cm per month, a juvenile thallus marked at 2 cm could grow to be > 5 cm in < 2 months, well within the time frame between survey periods. The total number of juvenile (2-5 cm) and recruit (< 2 cm) thalli were all "new" thalli counted (and marked in the case of juveniles) at a given time point. To determine whether the relative proportion of thalli differed among thalli or varied throughout the study, I calculated the relative proportion of each stage (adult, juvenile, recruit) for each patch and at each survey date, then used an ANOVA to test the separate and interactive effects (proportion of each stage ~ *Turbinaria* stage * survey date). Both *Turbinaria* stage and survey period were fixed effects in this model, and the response variable (proportion of thalli in each stage) was log transformed to approximate assumptions of normality (ln [proportion + 0.01]). Following this analysis, pairwise contrasts (Tukey's HSD) were used to compare the proportions for all stages and survey dates. All analyses and models were constructed using JMP (v.12 for Mac).

Using cohort 1 (originally marked in September 2012), I calculated separate mortality rates of adults and juveniles in each patch. Cohort 1 was selected for this analysis because thalli from this cohort were observed after the longest elapsed time (approximately 7 months). Assuming a constant per-capita mortality rate m for thalli in a given stage, such that: $dN/dt = -m\,N$, I calculated $m = [\ln(N_0) - \ln(N_t)]/(t)$, where N_0 is the initial number of thalli of a given stage, N_t is the number of thalli at time t, and t is time in months between surveys. To determine whether the monthly mortality rates differed among stages and/or survey dates (December 2012 and April 2013), an ANOVA was used ($m \sim$ stage*survey date), followed by Student's t tests to compare levels. All analyses and models were constructed using JMP (v.12 for Mac). I also estimated the half-life and turnover of *Turbinaria* thalli using adult and juvenile thalli in cohort 1. Assuming that m was constant, half-life ($t_{1/2}$) was calculated as: elapsed time in days x ln(2) / $[\ln(N_0 / N_f)]$ where $N_0 =$ initial number of thalli and N_f = final number of thalli. Half-life was calculated for each stage/cohort for all patches where the initial number of thalli was > 0. The turnover time for each stage/cohort was approximated by first calculating the estimated number of elapsed half-lives that would result in ~1% of the original cohort remaining (i.e., ~ 99% of the original cohort would have died) using the following equation: $1 = 100 * (1/2^n)$ and solving for n (number of elapsed half lives). After calculating n (n = 6.6), I then estimated this turnover time (time point where <1% of the original thalli would be expected to remain) for each stage/cohort by multiplying 6.6 by the half-life for each stage/cohort. The elapsed time between sampling periods was approximately 90 days between September-December 2012 and April-July 2013. To determine whether half-life and/or turnover differed among stages, the data were first log transformed to improve assumptions of normality, and ANOVAs were used to compare stages. All analyses were completed using JMP (v.12 for Mac).

***Turbinaria* patch dynamics**

During my surveys of *Turbinaria* patches at Sites 1-4 (surveyed annually during the austral winter 2013-2015), I observed two types of patch loss: lost tags (tag was not located during a particular sampling time) and patches where no thalli of any stage remained. For the former, no information could be estimated about these patches, so these were removed from subsequent analyses. However, patches classified as extinct (i.e., no thalli remained) were used to estimate annual patch extinction rates (2013-2014 and 2014-2015). A Chi-square test for two proportions was used to compare the proportion of extinct patches between years.

To estimate *Turbinaria* colonization rate to unoccupied reef substrata, I used annual (2013-2015) photographs of fixed quadrats (0.25 m^2) located on dead massive *Porites* bommies or pavement, N = 20). The location of the photoquadrats was similar to my study sites in back reef location and in benthic composition. I recorded the presence or absence of *Turbinaria* thalli for each photograph and calculated the estimated colonization rate as: number of colonization events (i.e., *Turbinaria* thalli were not present in one time period, then present at the next time period) / the total number of potential colonization events during that time period (i.e., number of quadrats with no *Turbinaria* thalli present). A Chisquare test for two proportions was used to compare the proportion of colonized patches between years.

Factors contributing to persistence of patches

I quantified population growth rate (λ) to assess patch persistence for the set of patches that persisted throughout the study. I calculated λ (population growth rate, N_{t+1}/N_t where N = number of adult thalli) for each patch surveyed during each annual period (2013-2014 and 2014-2015) and then calculated an annual mean using λ estimates for all patches present during a given time period. An ANOVA ($\lambda \sim$ Year with year as fixed categorical factor) was performed to test whether λ differed between years, following a log transformation of λ to meet assumptions of normality ($\ln[\lambda + 0.01]$). I then used post-hoc test to determine the significance of Year on the model coefficients.

When patch population growth is positive ($\lambda > 1$), the patches could be growing in size (i.e., footprint or patch area) and/or numerically (increasing number of adult thalli). Using only patches that were found at all 3 time points (N = 56), I compared the mean patch area (m^2) in 2013, 2014, and 2015 using a generalized linear model with exponential error distribution (patch area ~ Year with year as fixed effect), and then followed with a Type III Analysis of Deviance (log likelihood) test to determine the significance of Year on the model coefficients. Pairwise contrasts (using log-likelihood statistics) were used to compare each stage. The p-values for each comparison were computed and then adjusted for multiple comparisons using the Bonferroni correction method. I also compared the mean adult density (no. per $0.1m^2$) in patches for the three years of the study using a one-way ANOVA (adult densities were log transformed [ln(adult density + 1)] to meet assumptions of normality). The mean values for each year were then compared using a Tukey's HSD post-hoc analysis. All analyses were performed using JMP v.12 for Mac.

Even if $\lambda > 1$ and populations are growing, density-dependent effects (e.g., intraspecific competition) can lead to asymptotic growth as populations approach a local carrying capacity. To investigate the degree to which *Turbinaria* patches exhibited density-dependence, I first calculated the log difference in the adult density for each time period (2013-2014 and 2014-2015) as log (final adult density +1) – log (initial adult density +1). This metric can be interpreted as the difference in density between the first and second time period. I compared the log difference in adult density with the initial adult density for both time periods using linear regression. All analyses performed using JMP v. 12 for Mac.

Results

Demography study

Distribution of Turbinaria stages and lifespan of adult and juvenile thalli

All *Turbinaria* stages were present during both austral winter and summer sampling points. Throughout the 3-year study, recruits (< 2 cm) comprised the majority of the thalli in patches (~60-80%), followed by adults (> 5 cm, ~10-40%). Juveniles (2-5 cm) comprised ~20% of the thalli in patches throughout the study. There was a significant effect of stage ($P < 0.0001$), survey date ($P < 0.0001$), and the interaction between stage and survey date ($P < 0.0001$) on the distribution of thalli in *Turbinaria* patches ($F_{20,775} = 36.45$, $P < 0.001$, Figure 1). For most survey dates, the relative abundance of thalli in patches was highest for recruits, followed by adults and then juveniles, though the relative abundance of adults and juveniles switched during austral summer 2014 (the proportion of adults was lower than the proportion of juveniles).

The observed lifespan of *Turbinaria* thalli originally marked as adults in September 2012 (adult cohort 1) was between 3 and 7 months (Figure 2). Three months after this first adult cohort was marked (December 2012), only about 20% of these thalli remained (mean ± SE: 17 ± 3 %), and all were gone at the seven-month sampling (April 2013). The lifespan of *Turbinaria* thalli originally marked as juveniles in September 2012 was also between 3 and 7 months. Approximately 25% (mean ± SE: 22 ± 4 %) of the thalli originally marked as juveniles remained after 3 months (December 2012), and < 1% (mean ± SE: 0.5% ± 0.5) of these thalli remained after 7 months. There was a significant effect of both time and stage on the mean mortality rates of cohort 1 ($F_{3,139} = 13.6$, $P = 0.001$, Figure 3). Mortality rates for cohort 1 were significantly higher in December 2012 (mean ± SE: 0.43 ± 0.02) compared to April 2013 (mean ± SE: 0.26 ± 0.02, $P<0.001$), and adult mortality rate (mean ± SE: 0.37 ± 0.02) was significantly higher than juvenile mortality rate (mean ± SE: 0.31 ± 0.02, $P = 0.04$). These data from cohort 1 yield half-life estimates of 45 ± 4 days for adult thalli and 55 ± 7 days for juvenile thalli (mean ± SE). The estimated turnover time ranged from 299 ± 24 days for adults to 361 ± 43 days for juveniles (mean ± SE), suggesting that complete turnover of thalli would be expected to occur in less than 1 year. There was no significant difference in either half-life or turnover time between adults and juveniles ($F_{1,53} = 1.1$, $P = 0.3$).

Turbinaria patch dynamics

The annual extinction rate of *Turbinaria* patch was between 4 – 7% (2013-14: 6 extinctions of 86 patches, 2014-15: 2 of 59), which were not statistically different (χ^2 =

0.864, $P = 0.35$). Extinct patches were generally small (mean ± SE: 0.012 ± 0.003 m^2) compared to the median size of tagged patches (0.022 m^2).

Over the course of a year, colonization rates of *Turbinaria* to suitable, unoccupied substrata of the same area (photoquadrats) varied from 14 to 33%. There was no difference in colonization between years ($\chi^2 = 0.762$, $P = 0.383$). Caution should be exercised in interpreting these colonization rates given the small number of quadrats (≤ 20) that were available to make these estimates.

Factors contributing to persistence of patches

Population growth (λ) was positive (2013-2014 mean ± SE = 1.35 ±0.13; 2014-2015 mean ± SE: 1.18 ± 0.15) and did not differ statistically between years (ANOVA, $F_{1,106} = 0.08$, $P = 0.7$). With respect to patch size, there was a significant 50% increase in mean area from 2013 (mean ± SE: 0.04 ± 0.01 m^2) to 2015 (mean ± SE: 0.06 ± 0.01 m^2) ($X^2_{df = 2} = 6.41$, $P = 0.04$, Figure 4A).

The density of adult *Turbinaria* declined as the area of a patch increased (Fig. 4B; ANOVA, $F_{2,166} = 6.89$, $P = 0.001$). There was a 50% higher density of adults in a patch in 2013 (61 ± 3 adult thalli per 0.1m^2) compared with 2015 (44 ± 4 adult thalli per 0.1m^2).

To investigate the degree to which *Turbinaria* patches exhibited density-dependence, I compared the log difference in adult density with the initial adult density for both years using linear regression ($N = 76$ for 2013-2014 and $N = 51$ for 2014-2015, Figure 5). There was a significant negative relationship between the log difference in adult density and initial adult density for both 2013-2014 ($r^2 = 0.21$, ANOVA: $F_{1,75} = 21.09$, $P<0.0001$) and 2014-2015 ($r^2 = 0.24$, ANOVA: $F_{1,50} = 16.36$, $P = 0.0002$).The relationships (Fig. 5) revealed that adult density increased from one year to the next at low initial densities, however, adult density decreased from one year to the next at higher initial densities. These patterns are consistent with the operation of density dependence within *Turbinaria* patches.

Discussion

In this study of *Turbinaria* patches in the lagoons of Moorea, French Polynesia, results suggest that *Turbinaria* displays several characteristics that could support a persistent macroalgal phase shift in this habitat. *Turbinaria* is a perennial alga with all stages (immature recruits and juveniles, mature adults) of thalli present throughout all years of this study. In this study, ~ 80% of thalli in patches were immature (juveniles and recruits) during all sampling periods. The presence of immature individuals may act as a "seed bank" to maintain the population following a disturbance that removes adult thalli. *Turbinaria* thalli senesce and detach from their holdfasts throughout the year, especially during the austral summer. In this study, the lowest proportions of adult thalli in patches were recorded during December 2012 and January 2014. Frequent storms and high currents during this time of year in Moorea could result in mechanical displacement of adult and senescing thalli, facilitating long distance dispersal of the species via floating rafts of reproductive thalli (Stewart 2006, 2008). During this period, an existing "seed bank" of immature thalli that are less buoyant and thus less easily removed could enable persistence of a local population. *Turbinaria* thalli appear to be resistant to herbivory once they are larger than ~2 cm (Davis 2016).

Additionally, *Turbinaria* patch colonization rates exceeded extinction rates (14-33% per year vs. 4-7% per year), at least for the duration of this study. These rates are similar to other studies of macroalgal patch colonization and extinction rates in coral reef systems (mean annual colonization and extinction rates for *Dictyota pulchella*, 7-11% and 13-20% respectively, Mumby et al. 2005), and provide support for the observed increases of *Turbinaria ornata* in the north shore lagoons of Moorea (Carpenter 2015). *Turbinaria* displayed positive population growth (mean annual λ > 1, increasing patch area over time). Persistent marine macroalgae exhibit various life histories and survival strategies, which may have evolved as mechanisms to deal with stochastic disturbance regimes and resource availability (Engelen et al. 2005)**.** In their study of the coral reef macroalga *Sargassum polyceratium,* Engelen and Breeman (2005) parameterized a stage-based model and determined that the most significant stages for determining population growth (λ) varied depending on depth (shallow vs. deep) and disturbance regime. The population growth rates of *S. polyceratium* (λ = 0.54-1.03) were influenced by both reproductive thalli and asexual fragments: sexual reproduction was critical at all depths and habitats, though the incidence of a hurricane strengthened the contribution of asexual fragments to the population growth rate of deeper populations. In a similar study of the temperate macroalga *Sargassum muticum,* elasticity analysis revealed survival of non-reproductive fronds was the greatest contributor to positive population growth rates, suggesting that K-selected strategies may drive the invasion success of this species on temperate reefs (Engelen and Santos 2009). In the present study, mean annual growth rates of *Turbinaria* patches reflected overall positive population trends (λ > 1), though this study only characterized *Turbinaria* patches at a relatively homogenous depth (~1-2 m) and no significant disturbances were recorded during the period of study. *Turbinaria* is capable of both sexual and asexual reproduction – both strategies may contribute to the positive population growth and persistence of this species. At this point, the relative contribution of sexual and asexual reproduction to *Turbinaria* population growth is unclear, but characterizing these components could improve our understanding of the dynamics of these populations.

Competitive interactions between macroalgae and corals can take many forms and have differential impacts on the trajectory of coral recovery following a disturbance (Lirman 2001, Jompa and McCook 2003, Box and Mumby 2007, Rasher et al. 2011, Thurber et al. 2012). The longevity of macroalgal patches, rates of colonization vs. extinction, and functional morphology of specific macroalgal taxa can influence the duration, frequency and severity of coral-macroalgal interactions. Perennial macroalgae such as *Turbinaria* (or *Sargassum pacificum* – another locally abundant species in the back reef of Moorea) may preclude coral recruitment by occupying space for relatively long periods. In this study, relatively low extinction rates of *Turbinaria* patches over a 2-year period suggest the duration of interactions between coral and macroalgae could be enhanced by the presence of perennial macroalgae. In contrast, many macroalgal taxa, such as the corticated brown alga *Chnoospora implexa*, form dense but ephemeral mats that are highly seasonal and appear to have very little effect on the coral assemblage underneath these mats (Birrell et al. 2008)**.** Persistent macroalgal patches may also influence coral recovery as a result of specific macroalgal functional morphologies. Canopy-forming macroalgae, like *Turbinaria*, may have negative effects on coral recruitment and growth via abrasion, light reduction, and/or allelopathic effects (McCook et al. 2001, Jompa and McCook 2003, Hauri et al. 2010). However, these canopy-forming *Turbinaria* thalli may also offer protection by deterring herbivores and corallivores (Bulleri et al. 2013). Expanding the study of macroalgal patch dynamics and incorporating these dynamics with process-based studies of coral-macroalgal competition will be critical for evaluating the long-term outcomes of coral-macroalgal interactions.

Turbinaria appears to be among a subset of coral reef macroalgae that is capable of dominating reef benthos in persistent patches that could have significant consequences for the recovery of coral on degraded reefs following a disturbance. In this 2-year study of *Turbinaria* demography and patch dynamics, results suggest that *Turbinaria* populations exhibit positive population growth (both number of adult thalli and patch area increased). Several factors including high turnover rates of thalli, a buffer of immature individuals that may act as a "seed bank" following a disturbance, and herbivore resistance for thalli > 2 cm may contribute to the expansion of this species in the lagoons of Moorea. In addition, browsing fish that can consume macroalgae like *Turbinaria* (e.g., *Naso* spp.) are targeted by local fisheries, and are present in very low abundances (< 5 g m^{-2} in the back reef habitats, Han et al. 2016). Though results from this study suggest that intraspecific competition among adult thalli could produce density-dependence within patches, it is unclear the extent to which these processes limit *Turbinaria* population expansion. Understanding factors that determine the establishment and persistence of marine macroalgae will have significant consequences, as coral reefs around the world experience declines in coral cover and subsequent increases of suitable substrate for macroalgae. As macroalgae are known to negatively influence coral recovery processes, the development of effective conservation and management protocols may be improved by studies incorporating the dynamics of macroalgal populations in habitats at local scales.

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Figures

Figure 1: Proportion of thalli of *Turbinaria* by life stage in patches through time. The sample sizes (N = number of patches found) for each survey period are given for each survey date.

Figure 2. Proportion of thalli originally marked as adults and juveniles in Sept. 2012 remaining after 3, 7 and 10 months (mean ± SE). Number of patches were: 3 months: N = 48; 7 months, N = 42; 10 months , N = 39.

Figure 3. Mortality rates (month^{-1}) for adult and juvenile thalli in Cohort 1 in December 2012 and April 2013 (originally marked in September 2012, mean ± SE). The sample sizes (N = number of patches where initial count of thalli of a particular stage was > 0) were as follows: Adults December 2012 = 46, Adults April 2013 = 35, Juveniles December 2012 = 47, Juveniles April 2013 = 35.

Figure 4. A) *Turbinaria* patch area (m^2, mean ± SE) and B) *Turbinaria* adult thalli density (number per 0.1 m^2, mean ± SE) for 2013, 2014 and 2015 (N = 56 patches).

Figure 5. The relationship between relative change in adult density and initial adult density (number thalli per 0.1m^2). Relative change in adult densities from one year to the next was calculated as log (final adult density) – log (initial adult density). N = 76 for 2013-2014 and N = 52 for 2014-2015.

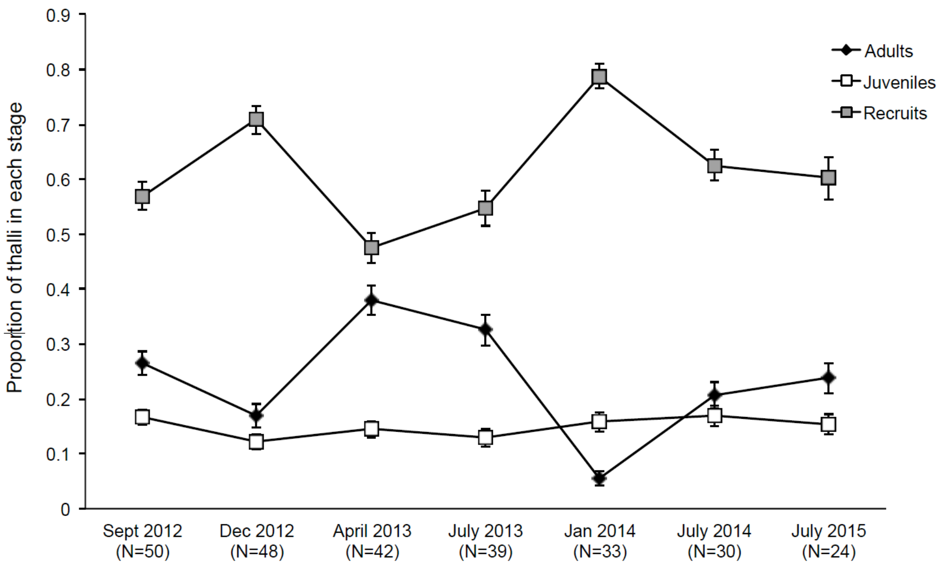
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proportion of thalli in each stage
Adults
Juveniles
Recruits
Sept 2012 (N=50)
Dec 2012 (N=48)
April 2013 (N=42)
July 2013 (N=39)
Jan 2014 (N=33)
July 2014 (N=30)
July 2015 (N=24)

Figure 1.

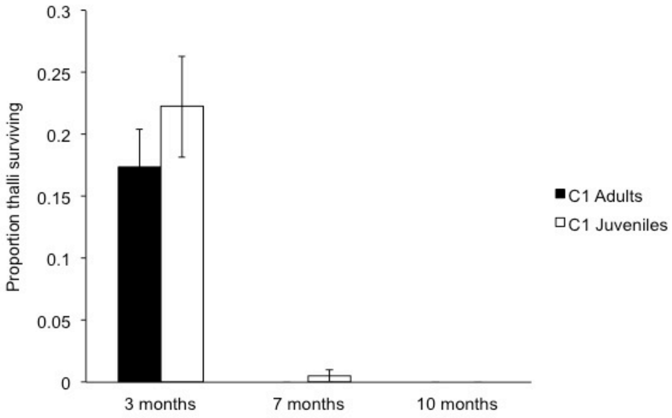
0.3
0.25
0.2
0.15
0.1
0.05
0
Proportion thalli surviving
3 months
7 months
10 months
■ C1 Adults
□ C1 Juveniles

Figure 2.

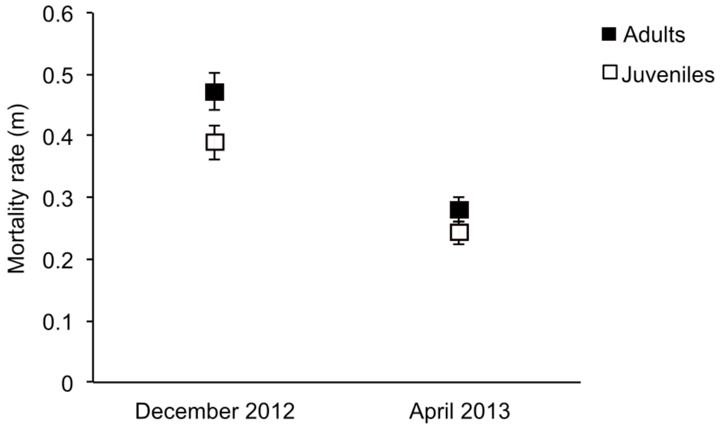
0.6
0.5
0.4
0.3
0.2
0.1
0
Mortality rate (m)
December 2012
April 2013
■ Adults
□ Juveniles

Figure 3.

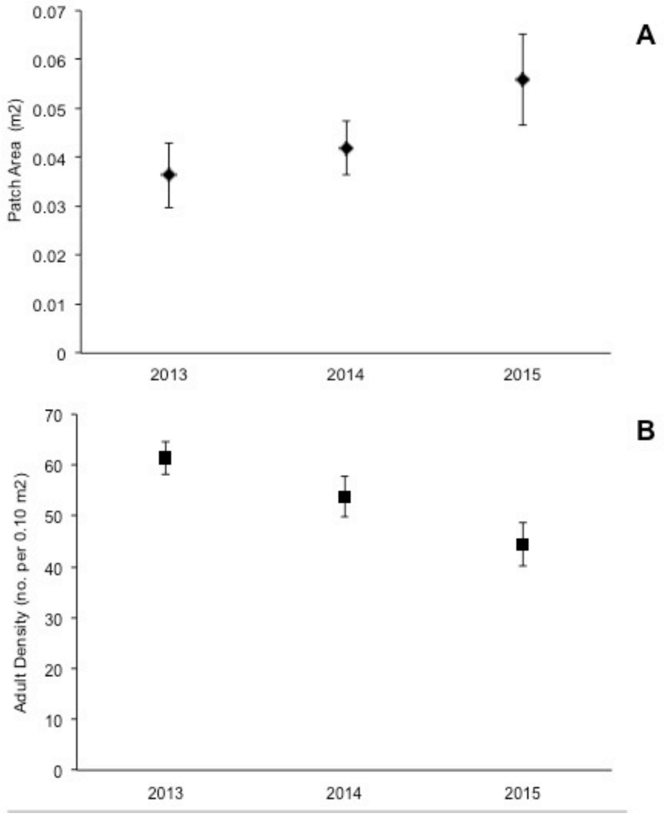
A
Patch Area (m2)
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
2013
2014
2015
B
Adult Density (no. per 0.10 m2)
70
60
50
40
30
20
10
0
2013
2014
2015

Figure 4.

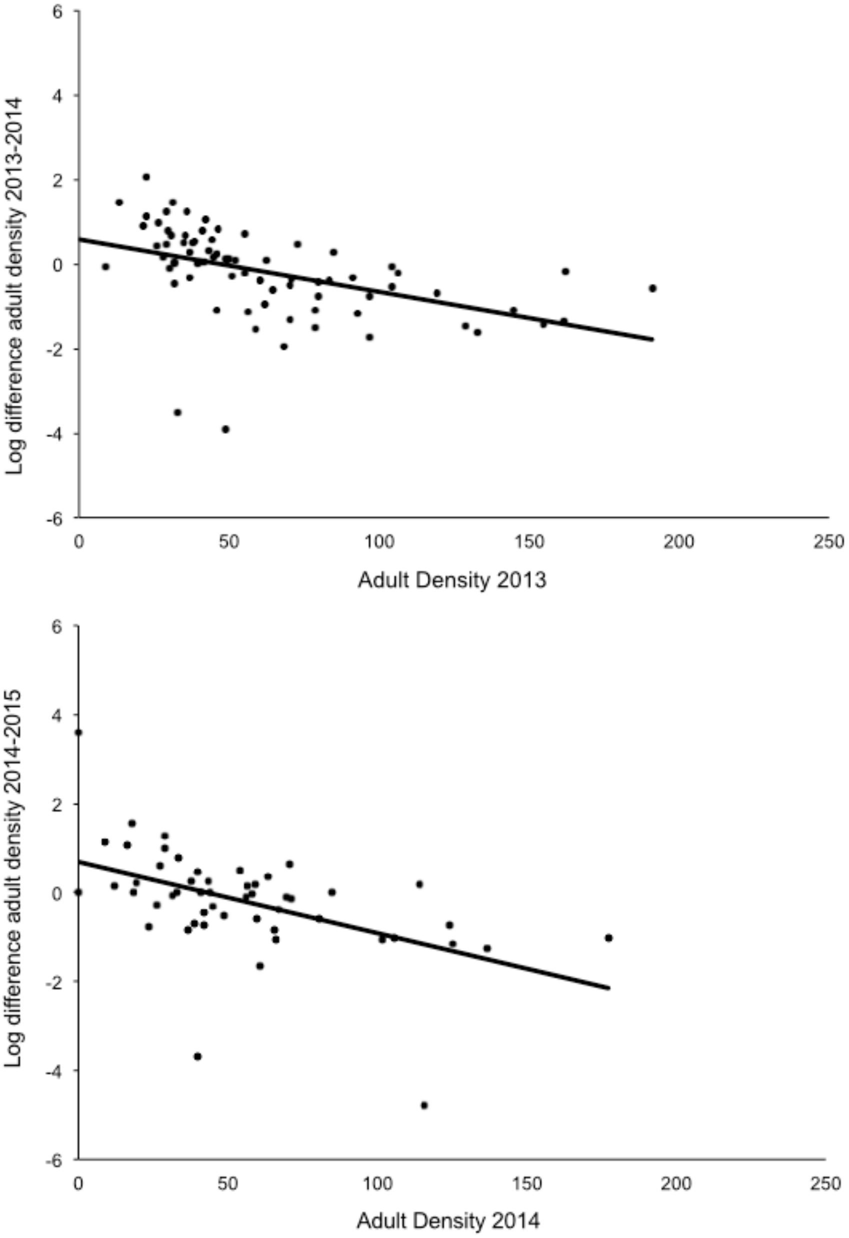
6
4
2
0
-2
-4
-6
Log difference adult density 2013-2014
0
50
100
150
200
250
Adult Density 2013
6
4
2
0
-2
-4
-6
Log difference adult density 2014-2015
0
50
100
150
200
250
Adult Density 2014

Figure 5.

II. Associational refuge facilitates phase shifts to macroalgae in coral reef ecosystems

Abstract

Coral reefs are among the most diverse and productive marine ecosystems, and are currently threatened by an increasing frequency and magnitude of natural and anthropogenic perturbations. Natural disturbances such as predator outbreaks and tropical storms can facilitate community shifts from coral to macroalgae. Such shifts have received considerable attention since macroalgae are known to inhibit coral recruitment, and thus hinder or prevent recovery to the coral-dominated state. It is critical, then, to understand mechanisms that permit the establishment and persistence of macroalgae. I addressed these issues using field experiments and herbivore assays in the lagoons of Moorea, French Polynesia. I tested the hypothesis that differences in vulnerability to herbivory across *Turbinaria* life stages may facilitate establishment of *Turbinaria*. Results suggest that *Turbinaria* may only be limited by herbivory as recruits (< 2 cm in length), which can lead to the establishment of *Turbinaria* if the alga survives the brief period when it is especially vulnerable to herbivores. I also tested whether vulnerable *Turbinaria* recruits experience a refuge from herbivory when they are associated with relatively unpalatable adults. This mechanism would promote persistence of a *Turbinaria* population once mature individuals become established. My results show that survival of recruits was higher when they were associated with *Turbinaria* adults than when alone. These feedbacks can limit the capacity of herbivores to control macroalgae and hence reverse the phase shift. I also explored the cost of such an association, and found that the sign (positive or negative) of a refuge can be spatially variable depending on local herbivory.

Introduction

Community phase or state shifts are characterized by a persistent change in the composition of dominant species, and are known to occur in a variety of ecosystems. Well-known examples include transitions between clear and turbid water states in shallow lakes (Scheffer et al. 1993), kelp-forests and urchin barrens on rocky reefs (Steneck et al. 2002), macroalgae and sessile invertebrates on temperate subtidal reefs (Rassweiler et al. 2010), and grassland and woody savannah (Dublin et al. 1990). In some instances, the alternative ecosystem state is undesirable from an ecological and/or economic perspective, which has led researchers to explore whether it is possible to predict impending shifts (Brock and Carpenter 2006, Scheffer et al. 2009, Bestelmeyer et al. 2011) and understand how readily the shift could be reversed. In addition, the 'reversibility' of a phase shift is directly related to whether different sets of stabilizing feedbacks exist to reinforce alternative ecosystem states. In coral reef ecosystems, transitions from a coral-dominated state to a macroalgae-dominated state may be persistent (e.g., Rogers and Miller 2006), and some have argued may not be easily reversed (e.g., Mumby et al. 2013; but see Dudgeon 2010). Thus developing an understanding of the mechanisms that might "trap" a tropical reef in a macroalgal state is critical in the development of effective management practices to prevent transitions to a macroalgae community and/or speed the return of the coral state.

Major disturbances such as tropical storms and outbreaks of coral predators that result in landscape scale loss of live coral can trigger community shifts on tropical reefs (Hughes et al. 2003). Such shifts are well-documented in the Caribbean (Hughes 1994, Mumby et al. 2007, Maliao et al. 2008) and to a lesser extent, the Indo-Pacific (Cheal et al., 2010, Bruno et al. 2009, Roff and Mumby 2012). Macroalgae-dominated reefs inhibit coral recovery through direct competitive interactions (McCook et al. 2001) as well as indirect effects such as altering the behavior of key herbivores (Chong-Seng et al. 2014). Tropical reefs that are dominated by macroalgae are considered to have reduced ecological and social value when compared to reefs dominated by coral (Scheffer et al. 2001, Folke et al. 2004, Nyström et al. 2008). Stabilizing feedbacks can help maintain reefs in a particular phase (Nyström et al. 2012), and on coral reefs, competitive interactions among coral and macroalgae can result in stabilizing feedbacks that enable a persistent reef configuration (Mumby and Steneck 2008). Herbivory is a critical process influencing the abundance and distribution of macroalgae in coral reef ecosystems (Carpenter 1986), and many species of macroalgae have structural and chemical defenses against herbivores (Hay 1991). Such defense mechanisms can result in positive interactions for macroalgae where at least one of the participants in the interaction benefits by a close physical association with the other (Levenbach 2008).

Associational refuges arise when the per capita benefits of close physical co-location outweigh the costs (e.g., reduced mortality rate > reduced growth rate, Hay 1986, Levenbach 2008, Barbosa et al. 2009). On temperate and tropical reefs, palatable macroalgae may be found in greater abundance and diversity in close associations with unpalatable species in situations where herbivory is intense (Levenbach 2009, Bittick et al. 2010, Loffler et al. 2014). An associational refuge is composed of at least 2 ecological interactions that have opposite demographic effects (e.g., competition and facilitation) such that the net effect (positive or negative) depends on the strength of each interaction and the physical or biological stress in the ecosystem (Levenbach 2009). Intraspecific associational defenses in species of tropical macroalgae have rarely been studied (but see Dell et al. 2016), however, this mechanism has been suggested to explain the persistence of grassland states in African savannah ecosystems (Caughley 1976). In this study, I examined the potential for and possible consequences of within-species associational refuge provision for vulnerable life stages of the tropical fucoid *Turbinaria ornata*.

Here I explore whether there is evidence that 1) differences in consumption by herbivores among *Turbinaria* life stages (sizes) may facilitate transitions from coral-dominated to macroalgae-dominated reefs and 2) associational refuges are a mechanism of self-reinforcement and replenishment of *Turbinaria* populations. Because chemical and structural defenses of *Turbinaria* individuals develop ontogenetically (Stiger et al. 2004), I hypothesize that vulnerability to herbivory is highest for new recruits and much lower for older adults. I also hypothesize that vulnerable recruit stages should have higher survival when they are in close association with less palatable adults. Furthermore, if an associational refuge does exist, then there should be a demographic cost to young *Turbinaria* that co-occur with older stages where herbivory is low. An associational refuge that results in higher recruit survival in the presence of herbivory could represent a self-reinforcement mechanism that may facilitate the establishment and multi-generational persistence of *Turbinaria* patches on coral reefs.

Methods

Study location and species

Fieldwork was conducted in the north shore lagoons of Moorea, French Polynesia (17º32' S, 149º50'W) during the austral winter in 2012- 2015. Moorea is a high volcanic island in the Society Islands archipelago, located approximately 17 km northwest of Tahiti. The benthic communities of the north shore lagoons are characterized by a combination of scleractinian corals, mixed assemblages of turf algae, sessile invertebrates, and in some locations, patches of macroalgae. *Turbinaria ornata* (Turner 1848) is the most abundant species of macroalgae at the study sites (Carpenter 2015). This species is found throughout the South Pacific, and has been documented as a dominant space holder for extended periods of time on hard substrates in the lagoons of Moorea in the late 1980's to early 1990's (Done 1992).The abundance and longevity of *Turbinaria ornata* in French Polynesia may be driven by morphology and/or reproductive traits. This species can thrive in a variety of reef environments – phenotypic plasticity facilitates the development of different morphotypes that are suited to either calm unidirectional flow (lagoon) or high-energy, wave-driven flow (reef crest) (Stewart 2008). *Turbinaria ornata* is both structurally and chemically defended against herbivory, and the production of chemical defense compounds develops ontogenetically (Stiger et al. 2004). Sexual reproduction occurs year-round, and offspring settle close to parent thalli (within 1 m, Stiger and Payri 2005). *Turbinaria* may also be able to grow vegetatively from fragments (Prathep et al. 2007).

Size-specific survivorship of Turbinaria

To test the hypothesis that there vulnerability of *Turbinaria* to herbivory decreases with increasing age/size of individual thalli, I conducted survival assays in the field in July 2013. I outplanted individuals in 5 distinct size classes on a reef in the lagoon for 7 days in two treatments: exposed to or protected from herbivory. Differences in consumption by herbivores were estimated as the proportion of surviving individuals in each size class in the herbivore exposed treatment discounted by the loss of individuals in the treatment without herbivores (presumably from handling). However, no *Turbinaria* were lost in any replicate of the herbivore exclusion treatment.

All *Turbinaria* used in the assays were collected from the same location in the lagoon, where it is abundant on the tops of coral bommies that rise to ~ 1 m or less below the surface. Individuals selected for the assay all had minimal fouling by epiphytes and were not senescent. Thalli were placed into 5 size classes based on their length, which roughly correlated to age, as follows: Size Class 1: < 1 cm; Size Class 2: 1 to 2 cm; Size Class 3: 2 to 5 cm; Size Class 4: 5 to 8 cm; Size Class 5: > 8 cm. *Turbinaria* thalli were transported in seawater to the laboratory and placed in high flow aquaria within ~ 1 hr of collection. For the smallest individuals in Size Classes 1 and 2, scuba divers used a rock hammer and chisel to remove portions of dead coral substrate on which they were attached. These smallest individuals do not yet have holdfasts and if removed from their substrate, begin immediately to deteriorate (S.L. Davis, *unpublished data 2011*). Marine epoxy was used to affix pieces of substratum with small *Turbinaria* to galvanized mesh (30 cm x 30 cm) in running seawater in the laboratory. Larger size classes (Size Classes 3 to 5, all > 2 cm thallus length) were collected with holdfasts attached. These larger individual thalli were attached to mesh substrata directly using cable ties loosely placed around the thallus. A total of 25 individual thalli of a single size class were placed on each replicate mesh substrate; each replicate with 25 individuals of a single size class was randomly assigned to the herbivore exclusion (N = 3 per size class) or exposed to herbivory (N = 4 per size class) treatments. For the herbivore exclusion treatments, circular cages (~ 30 cm high by ~ 120 cm in circumference) constructed of galvanized wire mesh (2.5 cm mesh) were used to exclude fish and sea urchins, and no fish or urchins were observed within the cages during the course of the assays.

I deployed the assays on natural substrata in the lagoon at depths of 2 to 3 m for 7 days and counted the total number of individual thalli surviving out of the original 25 per replicate each day. An individual thallus was scored as “dead” when it was entirely consumed and therefore absent from the replicate substrate. I used a generalized linear model (*glm* function within the *stats* package for R, R Core Team 2013) with binomial error distribution to investigate the effects of size class (fixed) on survival (success) of individuals in replicates in the treatment exposed to herbivores only. As no individuals were lost in the herbivore exclusion treatment, this factor was not included in analysis. I used a Type III Analysis of Deviance on the coefficient estimates from the model to test the significance of size class on the mean survival of *Turbinaria* individuals. Following this, I performed simultaneous comparisons of coefficient estimates for each size class (Generalized Linear Hypothesis Simultaneous Tests for GLMs) using the package *multcomp* for R (Torsten et al. 2008). All statistical models and tests were completed using RStudio (version 0.97.551) for R Statistical Computing Package (R Team 2013).

Test for an associational refuge

If vulnerability to herbivory decreases with size or age of *Turbinaria*, vulnerable recruits may experience enhanced survival when associated with less vulnerable older (larger) stages. Here I tested whether presence of adults (thalli > 5 cm, Stiger et al. 2004) provided an associational refuge for small recruits (thalli < 2cm in length). To determine the effect of adults on the short-term survival of co-located *Turbinaria* recruits, I investigated the separate and interactive effects of adult density and exposure to herbivores on the survival of *Turbinaria* recruits (< 2cm in length) over 7 days. To manipulate the presence of fish and urchin herbivores, I used 2.5 cm galvanized wire mesh cages of the same design as used in the size-specific herbivory assay described above. During the experiment, I did not observe any fish or urchins inside of the cages. I used a partial cage control (2.5 cm galvanized wire mesh formed into semi-circle ~ 12 cm high and 60 cm circumference) for all replicates exposed to herbivores.

Turbinaria used in the experiment was collected from the lagoon habitat using the techniques described above and included adults (thalli > 5 cm) and recruits (thalli < 2 cm), transported to the laboratory in seawater, and placed in high-flow aquaria. Prior to the start of the experiment, 20 recruits were attached to 2.5 cm wire mesh using techniques described above. Adults were then affixed to the mesh to create four adult density treatments that were within the range of densities observed in the field (0 adults, 30 adults per m^2, 100 adults per m^2 and 200 adults per m^2). The replicates were arranged in a systematic block design in the field (i.e. increasing from lowest to highest *Turbinaria* adult density, N = 10 for each treatment). Though randomized block design is generally accepted as the strongest experimental design, systematic arrangement of replicates is generally appropriate for most ecological experiments where no gradient in physical or biological conditions exists within the experimental site (Hurlbert 1984). Within a block, replicates were spaced approximately 0.5-1m apart from one another in a rubble field adjacent to coral bommies. All replicates within a block were well within the estimated home ranges of the local browsing fish species (*N. literatus* = 6.8 ha and *N. unicornis* = 3.2 ha, Marshell et al. 2011), thus replicates within a block were likely exposed to similar local browsing pressures.

Immediately after transporting the focal *Turbinaria* to the reef, I counted the outplanted recruits to quantify the actual starting number. I maintained *Turbinaria* adult density treatments during the experiment by replacing lost adults twice during the experiment. After 7 days, I counted all remaining recruits to determine the number of individuals surviving in each replicate. Recruits that survived (and grew for 7 days) were easily distinguished from the much larger adults used to create variation in density of less palatable associates. To investigate the separate and interactive effects of *Turbinaria* adult density and presence of herbivores on the mean fraction of surviving *Turbinaria* recruits, I used a generalized linear model with binomial error distribution and block as a random effect (*glm* function in *stats* package for R, R Core Team 2013). I then used a Type III Analysis of Deviance on the coefficient estimates from the model to test the significance of variation in adult *Turbinaria* density and herbivore exposure treatment. Following this test, I performed simultaneous comparisons of the means of the interaction coefficient estimates (Tukey pairwise comparisons) using the package *multcomp* for R (Torsten et al. 2008). All statistical models and tests were conducted using RStudio (version 0.97.551) for R Statistical Computing Package (R Team 2013).

Since the net effect (positive or negative) of an intraspecific association varies with the level of herbivory, I quantified local herbivory at the location of this experiment in two ways. I estimated the local browsing pressure by implementing two separate 24 hr herbivory assays. Each assay consisted of a 24 hr deployment of a known biomass of the palatable macroalga *Sargassum pacificum. Sargassum* was selected with the assumption that fish species that would consume *Sargassum* (*Naso* spp.) would also consume *Turbinaria*, which has been observed on the fore-reef in Moorea. I collected mature *Sargassum* thalli from the reef crest where it is abundant and transported them in seawater back to the laboratory where they were placed in high flow aquaria within 1 hr of collection. For each replicate of the assay, 3 mature *Sargassum* thalli were damp weighed and then attached to a galvanized mesh square (37.5 cm x 37.5 cm) using cable ties, transported to the field (continuously submerged), and affixed to the reef. I quantified the mean proportional change in biomass ([final weight (g) – initial weight (g)] / initial weight (g) at the end of the 24 hr period; N = 2 separate 24 hr assays). I also quantified the abundance and size (total length in cm) of browsing fish species along four 50 x 5 m transects (for browser species list see Appendix). I used published information on length-biomass relationships to calculate the biomass of each fish (Brooks 2014).

Cost of the associational refuge

In the case of small *Turbinaria* individuals associated with larger, less palatable conspecifics, there may be both benefits of increased survival when exposed to herbivores counter-balanced by reduced growth, survivorship and perhaps recruitment via shading, space pre-emption or other forms of intraspecific competition with the older, larger life stages. The costs of an association (e.g., reduced growth and new recruitment) may take longer to manifest than the immediate effects of enhanced survival due to reduced herbivory. In addition, the relative levels of biological stress (i.e., herbivory) may also influence the net effect of an association, as the benefits (enhanced survival) may only be present when herbivory is sufficiently high (Levenbach 2008). To measure the potential cost of an intraspecific association, I manipulated the density of *Turbinaria* thalli > 2cm in height in replicate quadrats (37.5 cm x 37.5 cm) on the reef and followed the net population change, including survival, of recruits (initially ≤ 2 cm tall), growth to the next size class, and new recruitment over a five-week period during July and August 2015. This experiment was established at a site where there were dense patches of *Turbinaria* but where browsers were rare and browsing pressure low. I quantified the abundance and biomass of browsers, as well as the browsing pressure, using the same methods as described above.

Treatments were established by selecting areas where older *Turbinaria* were dense and assigning them at random to one of two treatments: an 'adult removal' treatment where all *Turbinaria* > 2 cm in height were removed by hand and an unmanipulated (control) treatment where naturally occurring older stages were left intact (N = 13 per treatment). In the removal quadrats, all thalli > 2cm in height were removed by cutting each thallus just above the holdfast. At the start of the experiment, I counted all visible recruits in every replicate, as well as the number of individual thalli removed or intentionally left. For the latter, I fastened a small cable tie around the base of each older-stage thallus to mark the individuals > 2 cm in length that remained in the unmanipulated plots. This provided the means to identify individuals in the control treatment that started as a recruit but grew to > 2 cm by the end of the experiment. After 5 weeks, I counted the number of individual thalli (recruits and new [untagged] juveniles that grew from the initial cohort of recruits). Because I was unable to distinguish recruits that were present at the start of the experiment that remained < 2 cm tall from those that were 'born' during the 5 weeks, the metric I used was change in the proportion of young *Turbinaria*, defined as [(number of final recruits + new juveniles) – number of initial recruits]/ number of initial recruits. This yields an estimate of the net population change of vulnerable life stages in low browsing conditions.

To analyze the effect of adult density treatment on the net population change, I used the non-parametric Kolmogorov-Smirnoff two-sample test, which compares samples without specifying an underlying distribution. All statistical models and tests were conducted using JMP statistical software (v.11).

Results

Size-specific survivorship of *Turbinaria*

All individuals of all size classes of *Turbinaria* survived the 7-day experiment when protected from herbivores. By contrast, when exposed to herbivory, survivorship was highly dependent on size (age) of the *Turbinaria* plant (Type III Analysis of Deviance, $X^2_{df = 4} = 133.31$, $P < 0.0001$, Table 1, Fig. 1). Individuals in Size Classes 1 and 2 (i.e., < 2 cm tall) had the lowest survival rates (54% and 67%, respectively; not significantly different (Generalized Linear Hypothesis Simultaneous Tests for GLMs, Tukey Contrasts, $P > 0.05$, Table 2), which were statistically different from survival of the three larger size classes ($P < 0.05$). For individuals > 2 cm tall (i.e., Size Class 3 and above), ≥ 97% survived (Fig. 1), suggesting an ontogenetic decline in the vulnerability of *Turbinaria* to browsers with increasing size (age).

Test for an associational refuge

The lagoon location of the associational refuge field experiment was characterized by the presence of large browsing fishes (biomass mean ± SE: 0.63 ± 0.36 grams / m^2, Appendix Table 1) and relatively high browser pressure (percent of palatable *Sargassum* consumed in 24 hrs mean ± SE: 50% ± 30). The experiment revealed that the survivorship of vulnerable *Turbinaria* recruits depended on the presence and density of older conspecifics, but only when exposed to browsers (Fig. 2, Tables 3-4; Type III Analysis of Deviance, $X^2_{df = 3} = 48.89$, $P < 0.0001$). When protected from herbivory, survivorship of recruits was at or near 100% for all adult *Turbinaria* density treatments, although there was a significant decline in recruit survivorship (to 93% ± 3%) at the highest density of associated adults (Fig.

2), which might reflect intraspecific competition. By contrast, when exposed to browsers, survivorship of recruits increased monotonically with increasing density of older conspecifics (Fig. 2). When exposed to browsers, survivorship of recruits was ~ 20% greater at the highest relative to lowest adult density treatment, and the survivorship of recruits in the highest adult density exposed to herbivores was statistically indistinguishable from the survivorship of recruits protected from herbivores at the same high density of adult *Turbinaria* (Tukey-adjusted pairwise tests).

Cost of the associational refuge

The lagoon location where the demographic cost of the associational refuge was estimated was characterized by extremely low densities of browsing fishes capable of consuming *Turbinaria* (no browsing fish were observed in any visual survey) and a much lower browsing rate on highly palatable macroalgae (percent of *Sargassum* consumed in 24 hrs mean ± SE: 13% ± 7). The experiment revealed that at this location of comparatively low browser pressure, the mean proportional change in abundance of vulnerable life stages of *Turbinaria* was positive regardless of whether older conspecifics were present or removed (Fig. 3), which can only have occurred due to the recruitment and/or growth of new thalli during the 5 week experiment. However, the relative increase in population size of vulnerable stages was 2.5 times greater when older conspecifics were removed (mean ± SE: 0.47 ± 0.1 in the absence of older conspecifics vs. mean ± SE: 0.18 ± 0.08 when they were present, KS Test, D = 0.54, P = 0.04, Table 5), confirming that the net effect of the associational refuge varied from positive to negative depending on the local degree of browsing pressure.

Discussion

In this study, I used field experiments to assess whether differences in consumption of *Turbinaria* life stages (sizes) by herbivores could support an associational refuge for *Turbinaria* recruits associated with larger conspecifics. In the lagoon habitats where this study was conducted, herbivores appeared to be limited in their capacity to fully consume (and thus exert control) on *Turbinaria* thalli larger than ~2 cm in length. This finding may support an associational benefit for recruits in dense patches of adults. The greatest benefit of association occurred when browsing pressure was sufficiently high so that the negative effects of intraspecific competition were overshadowed by the benefit of enhanced survival when protected from herbivory. At low levels of browsing, the costs of intraspecific competition appear to outweigh the benefits of the association. The results of this study suggest that 1) intraspecific associational refuge among *Turbinaria* thalli may be a mechanism for persistent macroalgal assemblages, and 2) variability in the abundance/biomass of browsers can have significant consequences for the trajectory of reef recovery and the development of reinforcing feedbacks that can promote macroalgal-dominated reefs.

In the context of macroalgal phase shifts in general, this study provides evidence that a refuge for vulnerable macroalgal life stages creates a reinforcing feedback mechanism that facilitates persistent macroalgal assemblages. Results presented here, along with the recent work of Dell et al. (2016) on *Sargassum polycystum* in Fiji, suggest that associational refuges can act as a stabilizing process to support macroalgal dominated reefs. Intraspecific associational refuges may be found in many macroalgal species that experience ontogenetic shifts in palatability such as *Turbinaria* and *Sargassum* (Stiger et al. 2004), suggesting that this mechanism may promote macroalgal dominance in other reef systems with different macroalgal taxa. Positive benefits of associations have been examined in coral reef macroalgae, though the focus has generally been on the effects of interspecific associations (e.g., mixed palatable macroalgae and *Turbinaria ornata,* Bittick et al. 2010; *Caulerpa sertularoides* and less palatable epiphytic cyanobacteria, Smith et al. 2010; palatable *Acanthophora spicifera* and the chemically-defended *Galaxaura rugosa,* Loffler et al. 2014). In these studies, the persistence of the more palatable species was facilitated via association with a less palatable species, enhancing macroalgal diversity and potentially promoting macroalgal dominance following reef disturbance. The sign (positive or negative) and strength of these associations depends on the local environment and whether herbivory produces sufficient biological disturbance levels such that an association between organisms becomes beneficial instead of competitive. At intermediate levels of consumer stress, reduced consumption within associations can outweigh the potential competitive costs (Levenbach 2009). In this study, spatial variation in browsing by herbivores revealed differential effects of the association between *Turbinaria* recruits and larger conspecifics.

Differences in browsing (i.e., consumer stress) could arise several ways. If browsing fish are present but avoiding foraging in dense patches of *Turbinaria,* vulnerable stages can become established and grow to a size/stage that is invulnerable. This might occur rapidly as the estimated growth rate for a sister species (*Turbinaria decurrens*) is ~ 2 cm per month (Kaliaperumal and Rao 1975). Browsers may avoid relatively unpalatable macroalgae (such as *Turbinaria ornata*) using visual cues to locate more preferred algae elsewhere, and thus as the density and frequency of unpalatable patches in a specific area increases, overall browsing pressure may decrease. Tootell & Steele (2015) observed that the distribution, behavior and condition of herbivorous fish tracked the availability of turf algae in the lagoons of Moorea, and browsing fish may respond similarly to availability of a preferred resource. Further, potential risk from predators may deter browsers as patches of *Turbinaria* become dense. Recent work on the Great Barrier Reef has suggested that browsing fish may avoid dense patches of macroalgae because of visual obstruction from predators (Hoey and Bellwood 2011). Though the maximum length of *Turbinaria* (30 cm, estimated for sister species *Turbinaria decurrens,* Kaliaperumal and Rao 1975) is much shorter than the *Sargassum* species studied on the Great Barrier Reef (> 1m), this may be a potential mechanism influencing smaller browsing fish. Although behavioral factors may influence local browsing pressure, abundance and biomass of browsing fish may also be limited by local fishing practices. Many browsing species (including the large-bodied *Naso spp.*) are targeted as part of the lagoon fishery on Moorea and elsewhere in the South Pacific (Kuster et al. 2005, Leenhardt et al. 2016). Regardless of the mechanism involved, reductions in browsing pressure could provide a reinforcing feedback that promotes a macroalgal phase shift through limited top-down control.

In a future of projected increases in environmental degradation and climate changes, it will be critical to continue to develop mechanistic understanding of feedbacks that support ecosystems (either desirable or undesirable states). These reinforcing feedbacks have been examined in many ecosystems including seagrasses (van der Heide et al. 2007), tropical forests (Cochrane et al. 1999, Laurance and Williamson 2001), and African savannas (van Langevelde et al. 2003). In coral reef systems, stabilizing feedbacks can promote reefs dominated by coral (i.e., intact herbivore guilds that can respond to increased algae and promote coral recovery following a coral mortality event, Adam et al. 2011) or macroalgae (i.e., suppression of browsing by dense macroalgal patches that promote macroalgal persistence, Hoey and Bellwood 2011). Targeted studies may be developed to assess these feedbacks through experimental techniques, and these feedbacks can then be supported or altered through local and national management practices to reinforce the desired ecosystem state. Resource management efforts have already benefitted from an increased understanding of ecological feedbacks (as well as social and economic feedbacks) that support the resilience of particular states. For example, the Sahel region of western and central Africa is plagued by cyclic periods of drought and famine, and temporal and spatial variability of rainfall limits growth of trees and crops in the region. Through analysis of over 30 years of data, Sendzimir et al. 2011 elucidated the underlying feedbacks between rainfall, soil and trees that maintained the ecosystem in an undesirable grassland state. Understanding these feedbacks facilitated the development of community-led management practices to enhance both the ecological and socio-economic resilience of the system. Using similar focused studies of reinforcing feedbacks in coral reef ecosystems, managers may be able to alter the trajectory of a recovering reef and promote a desirable ecosystem state (e.g., protecting and/or enhancing browsing fishes on degraded reefs to limit macroalgal proliferation).

This study demonstrates a potential feedback that can promote persistent assemblages of a dominant macroalga, *Turbinaria ornata,* in the lagoons of Moorea, French Polynesia. Following coral mortality events in the lagoon, hard substrate became available that could support new coral recruitment (and potential recovery of a coral-dominated reef) or macroalgal settlement and proliferation. When *Turbinaria* becomes established, it can support establishment of other palatable macroalgal species by providing an associational refuge, thus enhancing the local macroalgal diversity (Bittick et al. 2010). In this way, an associational refuge (either interspecific or intraspecific) can promote the continued development of macroalgal assemblages dominated by *Turbinaria.* However, the results of this study highlight the significant role of spatial variation: the strength of this feedback depends on whether browsing is sufficiently high that positive effects of association outweigh the costs. When developing management strategies that seek to disrupt such feedbacks, it will be critical to consider and account for spatial variation in the behavior and/or abundance of browsing species that support recovery of coral reefs to coral dominated benthic communities.

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Tables

Table 1. Results of Binomial GLM model (Recruit Survival ~ Size Class). Model for 2013 *Turbinaria* size class survival assays. Size class was a fixed effect. Null Deviance: 173.438 on 19 degrees of freedom. Residual Deviance: 40.133 on 15 degrees of freedom.

Coefficients	**Estimate**	**SE**	**z value**	**P (> |z|)**
(Intercept)	0.16	0.20	0.80	0.4
Size Class 2	0.55	0.29	1.87	0.06
Size Class 3	3.32	0.62	5.35	<0.0001
Size Class 4	4.44	1.0	4.32	<0.0001
Size Class 5	3.73	0.74	5.03	<0.0001

Table 2. Results of Simultaneous Pairwise Comparisons of Means for GLMs of coefficients for each size class. Estimated differences, standard error, Z values and Tukey-adjusted P values were calculated using the package *multcomp* for R statistical software.

	Estimate	**SE**	**z value**	**P (>|z|)**
S2 – S1 = 0	0.55	0.29	1.87	0.30
S3 – S1 = 0	3.31	0.62	5.35	<0.0001
S4 – S1 = 0	4.43	1.03	4.33	0.0001
S5 – S1 = 0	3.73	0.74	5.03	<0.0001
S3 – S2 = 0	2.77	0.62	4.44	<0.0001
S4 – S2 = 0	3.89	1.03	3.78	0.001
S5 – S2 = 0	3.18	0.75	4.27	0.0001
S4 – S3 = 0	1.12	1.16	0.96	0.85
S5 – S3 = 0	0.42	0.92	0.45	0.99
S5 – S4 = 0	-0.70	1.23	-0.57	0.98

Table 3. Coefficient estimates, error, Z value and P values from binomial GLM testing separate and interactive effects of herbivore exclusion (fixed) and adult density (fixed). Block was included as a random effect. Null deviance: 490.50 on 79 degrees of freedom. Residual deviance: 123.41 on 63 degrees of freedom.

Coefficient	Estimate	SE	z value	Pr(>|z|)
(Intercept)	2.976	0.39341	7.565	3.89E-14
densityINT	1.16628	0.54443	2.142	0.03218
densityLOW	19.03914	2064.12641	0.009	0.99264
densityNONE	19.04702	2053.21537	0.009	0.9926
Herbivores Present	-0.72466	0.371	-1.953	0.05079
block2	0.03719	0.38503	0.097	0.92305
block3	1.44586	0.53621	2.696	0.00701
block4	0.17439	0.39523	0.441	0.65904
block5	-0.44896	0.37139	-1.209	0.22672
block6	-1.65751	0.35549	-4.663	3.12E-06
block7	-1.01142	0.35106	-2.881	0.00396
block8	-0.98438	0.35105	-2.804	0.00505
block9	0.75585	0.44692	1.691	0.09079
block10	-0.36697	0.36627	-1.002	0.31638
densityINT:Herbivores Present	-1.82097	0.6171	-2.951	0.00317
densityLOW:Herbivores Present	-20.51203	2064.12643	-0.01	0.99207
densityNONE:Herbivores Present	-20.28294	2053.21538	-0.01	0.99212

Table 4. Analysis of Deviance Table for binomial GLM testing separate and interactive effects of herbivore exclusion (fixed) and adult density (fixed). Block was included as a random effect.

	X^2	**df**	**P ($>X^2$)**
Adult Density	31.35	3	<0.0001
Cage Type	3.98	1	0.04
Adult Density: Cage Type	52.91	3	<0.0001
Block	91.86	9	<0.0001

Table 5. Results of Kolmogorov-Smirnov Two-Sample Distribution Test for experimental test of the costs of association for *Turbinaria* recruits with adults/juveniles. Net population change was calculated as: [(final count of recruits + final count of new juveniles) - initial count of recruits]/initial count of recruits. There was a significant difference in the distributions of the two treatments (KS = 0.269, KSa = 1.37, D = 0.53, P = 0.04).

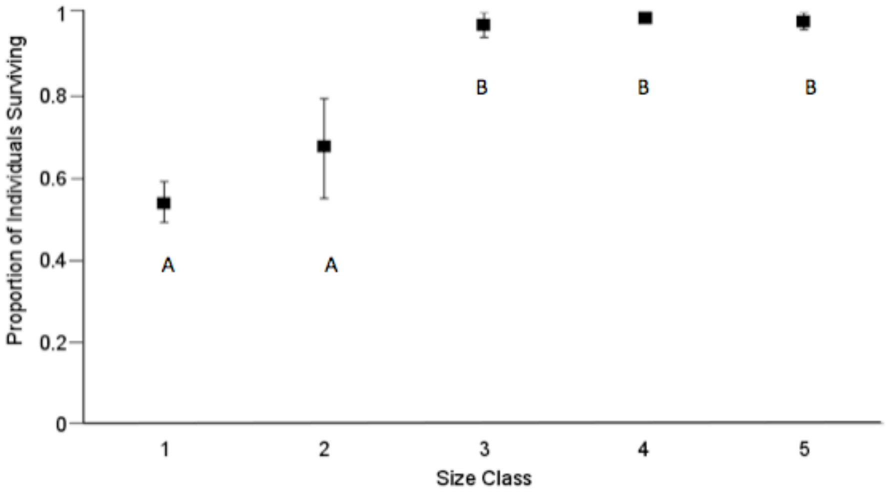
Level	**N**	**EDF at Maximum**	**Deviation from Mean at Maximum**
Control	13	0.538	0.971
Adult/Juvenile Removal	13	0	-0.971
Total	26	0.269	

Figures

Figure 1. Mean (± 1 SE) proportion of surviving *Turbinaria* thalli by size class when exposed to herbivores for 7 days (N = 4 for each size class). Statistical differences are denoted by different letters ($P < 0.05$).

Figure 2. Mean (± 1 SE) proportion of surviving recruits in the presence or absence of herbivores and a range in density of older conspecifics (N = 10 for each treatment). The experiment was deployed for 7 days. The proportion of surviving individuals for each treatment = final number of recruits / initial number of recruits. Letters indicate results of statisticalz tests (statistical difference is denoted by different letters, $P < 0.05$).

Figure 3. Mean (± 1 SE) net change in population size in the presence and absence of juvenile and adult conspecifics (N = 13 for each treatment). Net population change = [(final count of recruits + final count of new/unmarked juveniles) - initial count of recruits]/ initial count of recruits.



Proportion of Individuals Surviving
1
0.8
0.6
0.4
0.2
0
A
A
B
B
B
1
2
3
4
5
Size Class

Figure 1.

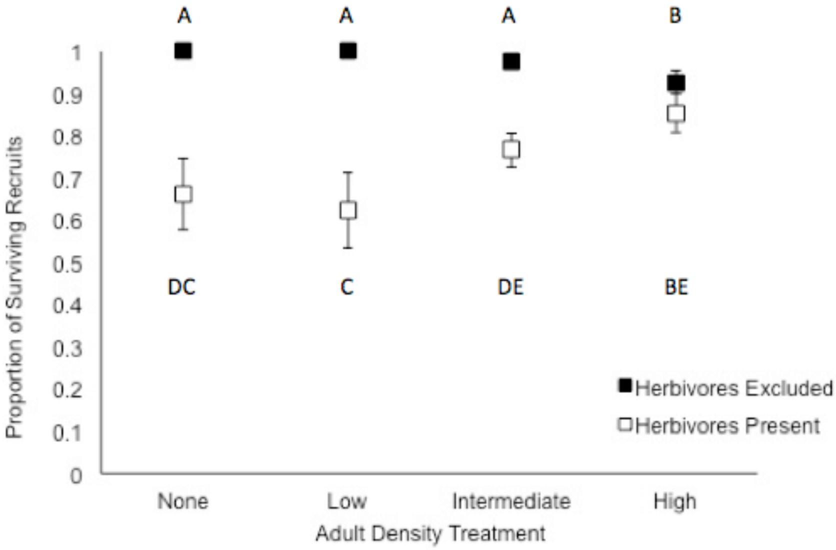

A
A
A
B
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proportion of Surviving Recruits
DC
C
DE
BE
■Herbivores Excluded
□Herbivores Present
None
Low
Intermediate
High
Adult Density Treatment

Figure 2.

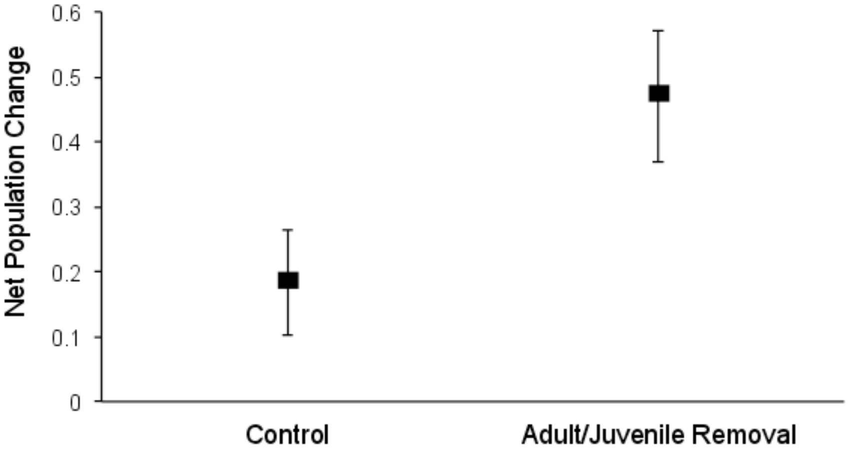

Net Population Change
0.6
0.5
0.4
0.3
0.2
0.1
0
Control
Adult/Juvenile Removal

Figure 3.

Supplementary Information

SI Table 1. Mean biomass of browsing fish used in estimation of browser biomass. During surveys, roving browsers on this list were counted and sized to the nearest cm. Using published length-weight relationships, I calculated the total biomass of browsers by adding estimates for these 5 species.

Browser Taxa	**Mean biomass (g/m^2)**	**SE**
Naso unicornis	0.15	0.15
Naso literatus	0.29	0.10
Calotomus carolinus	0.20	0.20
Kyphosus spp.	0	0
Naso spp.	0	0

III. The effect of reducing herbivory on the algal assemblage of a coral reef depends on the initial community state

Abstract

Top-down control by herbivores has been implicated as a key process influencing transitions among coral community states, especially in cases of algal dominance on Caribbean reefs. While the importance of herbivores to coral reef benthic communities is no longer in question, we currently know very little about how the strengths of consumer effects varies at different points in succession. If the herbivores in a system exert their greatest influence on early successional stages, but are unable to control late successional stages, the positive indirect effects of herbivores on coral recruitment and growth may be limited. This could also lead to a potential hysteresis or lag in the algal response to herbivory – where higher levels of herbivory are required to limit late successional stages than early stages. To determine how the effects of consumer pressure vary at different stages of algal succession, I manipulated 1) herbivory and 2) the initial algal community in field experiments in the north shore lagoon of Moorea, French Polynesia. Results from the two-year study suggest that the effects of reductions in herbivory on the macroalgal biomass, richness and species composition depend substantially on the initial state of the benthic community.

Introduction

Top-down control by herbivores has been implicated as a key process influencing transitions among coral community states, especially in cases of algal dominance on Caribbean reefs (Hughes 1994, Bellwood et al. 2004). Herbivory is a key interaction on coral reefs because it can prevent fast growing macroalgae from dominating the reef after coral mortality events. Consequently, top-down control of algae by herbivores has been well studied in coral reefs, and some groups, particularly parrotfishes (Mumby 2006) and sea urchins (Hughes 1994), have demonstrated a capacity to alter the dynamic trajectory of the benthic community by preventing shifts to macroalgal dominance on some reefs (Adam et al. 2011).

Though the importance of herbivores to coral reef benthic communities is no longer in question, we know less about how herbivore effects vary depending on the successional stage of the algal community. Mixed-species assemblages of turf algae quickly colonize and dominate early successional (i.e., immediately post disturbance) communities, while slower growing and more complex macroalgae may dominate during later stages of succession in the absence of herbivore control (Hixon and Brostoff 1996). Herbivores may exert the strongest effects at different points in algal succession, and these effects may be driven by morphology, diet specializations, and feeding behaviors that differ among herbivore functional groups. For example, scrapers, excavators and grazers that consume turf algae may be ineffective in the consumption and control of mature macroalgae (Burkepile and Hay 2008, 2010). If the herbivores in a system exert their greatest influence on early successional stages, but are unable to control later-successional stages, the positive indirect effects of herbivores on coral recruitment and growth may be limited.

There is increasing evidence that some herbivorous fishes (i.e., browsers that can consume mature macroalgae) can reverse a phase shift from coral to macroalgae once it has occurred (Bellwood et al. 2006, Hoey and Bellwood 2009, Burkepile and Hay 2010). However, removal of established macroalgae can become more difficult when there are few browser species or individuals (Bellwood et al. 2003, Hoey and Bellwood 2009) and/or macroalgae possess traits that effectively discourage herbivory (e.g. chemical and/or physical defenses, Hay et al. 1987, Hay and Fenical 1988). The difference in the trajectory of benthic community following coral mortality disturbance may depend on how much the algal state has progressed, that is whether the algal community in an early stage is dominated by turf algae, or a late-stage dominated by more herbivore-resistant macroalgae. If herbivores have differential abilities to control algal growth and development depending on the stage of the algal community, this could result in hysteresis or path dependence in the degradation vs. recovery trajectory of the benthic community (Mumby 2006, Mumby et al. 2007). There have been a number of reefs worldwide that have transitioned from coral-dominated to persistent macroalgal-dominated system (Done 1992, Hughes 1994, Hughes et al. 2007). Yet there is not yet sufficient understanding of how herbivores affect attributes of algal communities to assess whether this can contribute to hysteresis in the relationship between herbivory and macroalgae.

In the present study, I examined the effects of a gradient in herbivory on the abundance and diversity of macroalgal communities on coral reefs, and how these effects depend on the initial state of the algal community. Here I contrast the effects of variation in herbivory on 1) early stage algal communities dominated by epithelial turf algae and 2) late stage communities dominated by macroalgae. By manipulating herbivory and initial algal community simultaneously, this study is able to examine whether the effects of variation in herbivory on algal diversity and community composition depend on the initial community state. In a broad sense, my experiment mimicked the effect of fishing on herbivores, which can reduce both herbivore body size and abundance (Jennings et al. 1999, Dulvy et al. 2004, Graham et al. 2005), to better understand how altered herbivorous fish communities can influence the development and persistence of macroalgal states.

Methods

Study Location and Focal Species

Field-work was carried out in the mid-lagoon (2-3 m depth) on the north shore of Moorea, French Polynesia (17.32° S, 149.50° W). Patch reefs in this location were composed of both living and dead coral substrate (mostly massive and mounding species of *Porites*) with little macroalgae present, and these coral bommies were separated by sand.

I selected *Turbinaria ornata* as the focal species for the manipulations as it represents a late-stage macroalgal community that is abundant in some areas of the lagoons of Moorea (Stiger and Payri 1999, Stewart 2008, Carpenter 2015). *Turbinaria* is both structurally and chemically defended against herbivory, which may contribute to its abundance in some areas of the lagoon (Stiger et al. 2004). Facilitative relationships have been documented for the macroalga *Turbinaria ornata* in Moorea, French Polynesia (Bittick et al. 2010); the presence of *Turbinaria* was found to enhance local macroalgal diversity and potentially, persistence of macroalgal assemblages via an associational defense (Bittick et al. 2010; Davis 2016).

Experiment to test effect of differential herbivory on the abundance and diversity of macroalgae

I experimentally explored the effects of variation in herbivory on 1) the establishment of macroalgae, 2) the species composition of the algal community and 3) the species richness of the community after 2 years. A gradient in herbivory was created using a semi-permeable cage design that consisted of treatments with different numbers and sizes of entrance holes in the top and sides of the cages. Each cage was a 37.5 x 37.5 x 37.5 cm box constructed out of plastic coated wire lattice with a 2.5 cm mesh size. To create differential herbivory across treatments, openings were made in the mesh to enable a larger fish to gain access to the cage. Treatment hole sizes were 2.5 x 2.5 cm, 5 x 5 cm, 7.5 x 7.5 cm, and 10 x 10 cm; additionally there was a completely exposed treatment (no cage, SI Table 1). The duration of the experiment was 24 months, which is a period equivalent to 2-3 complete turnovers of *Turbinaria ornata* in this system (Davis 2016). Herbivory treatments were crossed with two initial states of the benthic community, which were turf algae or mature *Turbinaria*.

For each replicate of each treatment, 4 unglazed terra cotta tiles (15 cm x 15 cm) were attached rough-side up to provide a uniform substrate for sampling. Tiles were seasoned for several weeks on the reef, which allowed initial development of the epithelial (turf) algal matrix, then allocated at random to one of the two initial community state groups. The initial benthic community of turf algae was designed to explore the effects of herbivory on establishment of macroalgae; there were 3 replicates of each herbivory treatment except for the lowest hole size (2.5 x 2.5 cm), which had 6 replicates. The second set of initial benthic community treatments started with mature *Turbinaria ornata* (replicates had similar biomass compared to natural patches of *Turbinaria* on lagoon reefs). *Turbinaria* was collected by chiseling natural substrate that contained adult and juvenile stage *Turbinaria*. I selected pieces of substratum that contained thalli of *Turbinaria* that were not senescent and that had minimal fouling. *Turbinaria*-laden substratum was returned to the lab in seawater, maintained in high-flow outdoor aquaria where they were attached to seasoned tiles using marine epoxy to affix pieces of chiseled substratum to a tile; all tiles were deployed to the field within 24 hrs of *Turbinaria* collection. There were 5 replicates of each of the 5 herbivory treatments. For this initial community state, two of the four tiles in each replicate contained *Turbinaria* and the remaining two tiles started with just turf to provide foraging opportunities to both browsers (fish that consume mature macroalgae) and grazers (fish that primarily consume turf algae). Treatments were deployed in a randomized block design in the field.

After 24 months, cages were transported to the laboratory in seawater and placed in high flow aquaria. Tiles were processed within 48 hrs of collection. For each replicate, all macroalgae were removed (fleshy and filamentous forms), identified to the lowest possible taxon and weighed to the nearest 0.1 g (damp weight). To obtain estimates of dry mass, subsamples of each macroalgal taxon then were placed in a pre-weighed aluminum weigh boats and dried to a constant weight at 120°C. Several samples of each macroalgal taxon were collected and processed as described above to obtain both damp and dry weight estimates. To convert experimental damp weights to dry weights for use in statistical analyses, I used the slopes derived from fitted linear relationships between damp and dry weights for each macroalgal taxon. For the initially *Turbinaria* dominated treatments, only the tiles that initially received mature algae were included in the analyses.

Assay of the experimental herbivory treatments

To obtain an independent estimate of fish herbivory for each herbivory treatment, I baited each of the cage treatments with a palatable macroalga (*Sargassum pacificum)* and mixed turf algae (collected on pieces of rubble from farmerfish (*Stegastes* spp.) territories) for 6 consecutive days and recorded herbivore visitations using remote video cameras (GoPro HD Hero2). These assays were conducted at the experimental site for all cage types. All video was recorded during peak herbivorous fish activity times of 1000-1400 (T. Adam, *pers. comm*). Between 15-20 hours of video was recorded and analyzed for each treatment (SI Table 1). During video analysis, observers identified each individual foraging event or 'visit' when a fish took bites of algae (turf or macroalgae) that was inside of the cage (fish could be partially in the cage as long as consumption occurred within the cage). The duration of time spent taking bites was recorded (foraging time in minutes), and these individual fish were later identified to species (or genus if species was unclear from the video) and total length (cm) of the individual fish was recorded. Biomass of each fish was calculated using the estimated length of each individual fish observed foraging in baited cages and published length-weight relationships for herbivorous fish (Brooks 2014). The video resolution was not sufficient to estimate the number of bites (though the observers were able to identify when a fish was eating), so the foraging metric used to quantify herbivore pressure was biomass weighted foraging time (g mins per hr). To calculate this metric, the estimated biomass (g) of each individual fish was multiplied by the time that particular individual fish spent foraging in the treatment (foraging time in minutes). The sum of all individual biomass-weighted foraging minutes was added together for each treatment, and then divided by the total amount of video recorded for each baited cage treatment (hours).

Statistical Analyses

To determine the separate and interactive effects of herbivory treatment and initial algal community type on the final macroalgal biomass, I used an ANOVA with herbivory treatment and initial community type as fixed factors (macroalgal biomass ~ herbivory treatment * initial community type). Richness was the total number of taxa of macroalgae in each experimental replicate, and analyzed using a generalized linear model with Poisson error distribution (richness ~ herbivory treatment (fixed) * initial community type (fixed)). A log-likelihood test (χ^2) was performed to determine the significance of the separate and interactive terms. Post-hoc analyses were performed using the *lsmeans* package for R (Lenth 2016). I also calculated Pielou's J, which is the relative abundance (evenness) of macroalgal taxa present on experimental tiles (J = Shannon's Diversity Index H'/ ln (number of species)) using the vegan package for R statistical software (Oksanen et al. 2015).The separate and interactive effects of herbivory treatment (fixed) and initial community type (fixed) on evenness were analyzed using an ANOVA. To standardize the sampling area, I used two experimental tiles per replicate to quantify biomass, richness and evenness. For experimental tiles that were initially outplanted with *Turbinaria,* only two tiles were present in a given replicate; however, for experimental tiles that initially began with turf algae only, there were four experimental tiles in each replicate cage. I selected two of these tiles at random for use in these analyses.

Variation among treatments in the composition of the macroalgal community at the end of the experiment was explored based on species-specific biomass. A redundancy analysis (RDA, Legendre and Legendre 2012) was used to characterize the macroalgal communities present using ordination techniques. I constructed a community matrix with log-transformed biomass data (g dry weight) for each macroalgal taxon. RDA analysis is an extension of multiple linear regression where multiple response and/or explanatory variables can be used. RDA selects the linear combination of response variables that minimizes the total residual sum of squares. In this case, the explanatory factor was an interaction term (herbivory treatment*initial community state), and the response variables were log-transformed biomass data for each macroalgal taxon. Analysis was conducted using the vegan package for the programming language R (Oksanen et al. 2015).

Results

Herbivory treatment assay

Experimental cages created variation in access for herbivorous fish and thus produced differences in herbivory (SI Table 1). A total of 928 visits were observed in video recording during the six-day period (SI Table 2). No herbivores were observed feeding in the treatment with the smallest opening. Mean body size (biomass) of visiting herbivorous fishes in the remaining treatments increased monotonically with increasing hole size (Fig 1b; $F_{3,924} = 4.9$, $P < 0.005$), with the average biomass of an individual feeding in the two highest herbivory treatments being 5 - 6 times greater than in the lowest herbivory treatment (5 x 5 cm hole size) that was visited. Total biomass-weighted foraging (g minutes/hr) also increased monotonically as size of cage openings increased, although there was a substantial increase in this estimate of herbivory between the 7.5 cm and 10 cm hole size treatments (Fig. 1a). Relatively few fish were observed foraging in cages with intermediate opening sizes (5 cm and 7.5 cm) whereas cages with the largest (10 cm) holes and the fully exposed treatment had higher and more similar visitation rates (SI Table 3) of fishes that on average were larger in size. Overall, the experimental design created differentiation across treatments for both the visitation rate and mean body size of herbivorous fishes that fed among the treatments.

Patterns of macroalgal biomass, richness and composition

After 24 months, there was a striking difference between the initial community states in the standing biomass of macroalgae for a given herbivory treatment (Fig. 2). For both initial states, biomass of macroalgae declined with increasing herbivory, although there was an interaction between initial state and herbivory treatment (ANOVA, $F_{9,33} = 9.9$ $P < 0.0001$, Table 1). Overall there was an order of magnitude more macroalgal biomass when the community started with mature *Turbinaria* compared to turf. Indeed, the mean biomass of macroalgae in the highest herbivory treatment where *Turbinaria* initially was present was similar to the lowest level of herbivory when the initial state was turf algae (Fig. 2).

For species richness, patterns across levels of herbivory differed as a function of initial community state (significant interaction between herbivory treatment and initial community state; log-likelihood test, $\chi^2_{df = 9} = 58.5$, $P <0.001$, Table 2). Pairwise comparisons (Tukey's adjusted pairwise tests) were non-significant for all comparisons of the interaction term. For the tiles that initially began with turf communities, richness of the final macroalgal community was very low (0-1 macroalgal taxa present). Consequently, the evenness of these tile communities was undefined. There was no significant effect of either herbivory treatment or initial tile type on species evenness (ANOVA, $F_{6,24} = 0.97$, $P = 0.4$, Table 3). For the set of treatments that began as turf, both mean richness and mean evenness declined rapidly as herbivory increased. These results suggest that most herbivory levels can sufficiently limit macroalgal richness. By contrast, for treatments that initially started with *Turbinaria*, richness was similar and high across all herbivory treatments except the fully exposed (ambient) herbivory treatment (Fig. 3).

The composition of macroalgal communities also varied across herbivore treatments as a function of initial community state (Fig. 4). In general, *Turbinaria* was a major component of the assemblage at all levels of herbivory when it was the initial state, whereas this species only occurred at the lowest two herbivory treatments when turf was the staring community. Redundancy analysis (RDA) with one explanatory variable (term combining initial state and herbivory treatment) revealed that the first two axes accounted for 84% (68% and 16% respectively) of the total variance (Table 6). Although compositions of the two initial states were distinctly different, they were most similar at the lowest herbivory treatment and most different at the highest, which reflected a general trend of increasing divergence in final community composition between initial states as the level of herbivory increased (Fig. 4). The comparatively greater compositional similarly of the two initial community states at the lowest herbivory levels reflected the high representation of *Turbinaria* in both assemblages. Species values (Table 6) reveal that separation along the x-axis (RDA 1) was due to *Laurencia* and *Lobophora*, vs. species of thalloid red algae (*Peyssonnelia*, *Galaxaura*), whereas that along RDA 2 primarily was due to brown algae (*Turbinaria*, *Dictyota*) vs. the red alga *Amansia.*

Discussion

Results of this study show that the effect of variation in herbivory depended on the initial state of the algal community, which resulted in substantially different patterns of macroalgal biomass, richness, and evenness across the same gradient in herbivory. One manner by which this could occur is if there is hysteresis in the relationship between herbivory and macroalgae such that more herbivory is required to remove mature macroalgae than is needed to suppress their establishment (Mumby et al. 2013). Discontinuity in a driver – response relationship depending on initial community state, such as suggested by the patterns reported here, has been used to infer hysteresis in several natural communities from long time series of data (Bestelmeyer et al. 2011). Experimental evidence of divergence in responses due to different initial condition has been regarded as compelling support for hysteresis (Schröder et al. 2005). The present study is among the first - if not the first - to report experimental support for initial state dependency in the herbivory – macroalgae relationship for a coral reef. One critical issue is whether the 2-year duration of the experiment was sufficiently long for the manipulated system to move beyond initial transient dynamics to approximate steady state conditions. Successive cohorts of *Turbinaria* thalli were tagged throughout this experiment, which suggested that the time scale was sufficient. Individual thalli at the lowest herbivory levels recruited continuously throughout the experiment and that these individual thalli had a half-life of ~ 40 days and had a turnover time of ~ 250-300 days (Davis 2016). Thus the experiment spanned 2-3 complete population turnovers of the most space dominant species of macroalgae.

In principle, hysteresis can give rise to alternative stable states (Beisner et al. 2003). The concept that alternative basins of attraction can occur in coral reef ecosystems has been highly controversial and the subject of considerable debate (Dudgeon 2010, Mumby et al.

2013, van de Leemput et al. 2016). While definitive experimental evidence has been lacking for coral reefs (Mumby et al. 2013), results of the present experiment provide strong support for the existence of hysteresis and are consistent with the concept of alternative basins of attraction. Here, depending on the initial state of the algal community, the same herbivory treatment resulted in a benthic community that either was more dominated by macroalgae, which greatly hinders coral recruitment (Kuffner et al. 2006), or by cropped turf that is accessible to recruitment by settling coral larvae (Mumby et al. 2007).

While empirical evidence for alternative basins of attraction on coral reefs has been equivocal, simple models have highlighted a myriad of mechanisms that theoretically could result in alternative stable states (Mumby et al. 2007, Fung et al. 2011). This has underscored the critical need for a better mechanistic understanding of reinforcing feedbacks in natural systems (van de Leemput et al. 2016). In the current study system, *Turbinaria* facilitates other more-palatable macroalgae by establishing enemy-free space (Bittick et al. 2010). *Turbinaria* thalli become relatively resistant to herbivory after an individual thallus grows through an early but short period of vulnerability (< 2 cm thallus height, Davis 2016). Further, herbivores may avoid foraging in spaces dominated by this macroalga, providing an associational refuge for young stages (Davis 2016) and also for more palatable species (Bittick et al. 2010). Stage-structured invulnerability to herbivory that results in structural refuges for young conspecifics and for more palatable macroalgae are mechanisms that result in strong reinforcing feedbacks (Dell et al. 2016). Data presented here suggests that although *Turbinaria* may be a facilitator, it can be overgrown when herbivory falls too low to remove more palatable macroalgal competitors (such as *Amansia* or *Sargassum*). For these same low levels of herbivory, however, palatable species like *Amansia* remained scarce when *Turbinaria* was not present initially.

Interactions among macroalgae (including facilitation and competition) can have consequences for persistence of macroalgal phase shifts on degraded reefs. Once established, macroalgae can limit recovery of corals through several mechanisms, including space pre-emption, shading and allelopathic effects (McCook et al. 2001, Rasher and Hay 2010). Though it is clear that outcomes of coral-algal interactions depend on species-specific traits of both corals and macroalgae (Rasher et al. 2011), both the relative frequency of occurrence and duration of coral-algal interactions also may depend in part on interactions among macroalgae. For example, a macroalgal species with perennial, dense holdfasts and thalli (such as *Amansia rhodantha* or *Halimeda* spp.) may outcompete slow-growing corals for space. However, local herbivore pressure could limit the abundance of these potential competitive dominants in favor of other more herbivore-resistant species such as *Turbinaria ornata,* which have different growth forms and physiology and thus the potential for different competitive interactions with corals (Jompa and McCook 2003).

Fishing has been implicated as one of the major factors that can facilitate a shift from corals to macroalgae on tropical reefs (Mumby 2006), which can occur when reduced herbivory from fishing results in loss of control of macroalgae. A common management practice in this context is to reduce fishing mortality via catch restrictions or spatial harvest refugia. There is evidence that increased grazing pressure within reserves due to reduced fishing mortality can maintain sufficiently low abundance of macroalgae to result in enhanced rates of coral replenishment and recovery (Mumby et al. 2007, Mumby and Harborne 2010). However, results of the present study suggest that the effect of reducing fishing-imposed mortality on coral reef herbivores may depend on whether or not a reef already is dominated by macroalgae. In Moorea and elsewhere, fish capable of consuming mature macroalgae (‘browsers’, e.g., *Naso* spp.) tend to be larger and less abundant - and the functional guild less speciose - compared to species that can prevent macroalgae from being established (Han et al. 2016). This may make the browser functional group disproportionately sensitive to fishing pressure relative to other groups of herbivorous fishes. The experimental design I used simulated the effects of fishing on reducing average body size and abundance of fishes, and results suggest that the response dependency on initial state of the algal assemblage may have arisen by differential effects of treatments on browsers vs. grazers. This highlights the need to understand the mechanism creating the divergent response to different initial states, as well as how fishing pressure affects various functional groups of herbivores.

The results of this study may also contribute additional understanding of the relationship between consumer disturbance (i.e., herbivory) and diversity of primary producers. Two general relationships between consumer pressure and diversity and have been explored in the literature: unimodal (diversity maximized at intermediate consumer pressure) and inverse (diversity declines monotonically with increasing consumer pressure, reviewed by Lubchenco and Gaines 1981). Unimodal responses may result from strong competitive hierarchies among prey that at least initially are counteracted by selective consumption of the competitive dominant (Paine 1966, 1974). Alternatively, diversity may exhibit an inverse relationship with consumer pressure if subordinate competitors are preferred by consumers (Lubchenco 1978), or if competitive networks and/or weak competition among prey eliminate the possibility of a single competitive dominant (Buss and Jackson 1979). Results of the experiment here suggest that a facilitative prey species (*Turbinaria ornata*) can produce another diversity-consumer relationship. In this study, a “threshold” response was observed when a facilitator species (*Turbinaria ornata*) appeared to promote macroalgal diversity as consumer pressure increased until a critical threshold was reached. Where the facilitator species was not initially present, both richness and evenness declined monotonically with increasing consumer pressure. Conceptual models incorporating facilitation into the ecological theory about the effects of consumers on prey diversity have suggested that adding a facilitator may increase total community diversity, but these effects have only been considered with respect to unimodal relationships suggested by the "compensatory mortality" or "intermediate disturbance hypothesis" models (e.g. Hacker and Gaines 1997). Though little is known about the competitive relationships among coral reef macroalgae, this study reinforces the need to incorporate such interactions into the ecological theory of consumer-diversity relationships, specifically in systems where outcomes of species interactions may be spatially or temporally variable. This research also points to possible hysteresis in the relationship between herbivory and coral reef benthic macroalgae, and reinforces the idea that conservation of complementary functional groups of herbivores may be needed to prevent macroalgal dominance following coral reef disturbances.

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Tables

Table 1. Results of ANOVA test of factors influencing final macroalgal biomass (biomass ~ herbivory treatment * initial tile community).

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	9	98916.2	10990.7	9.8792	<.0001
Error	33	36712.7	1112.5		
C. Total	42	135628.9			

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Treatment	4	4	34408.81	7.73E+00	0.0002
Tile type	1	1	32469.76	2.92E+01	<.0001
Treatment*Tile type	4	4	25591.96	5.75E+00	0.0013

Table 2. Results of Poisson GLM testing effects of treatment and initial tile community on final macroalgal richness (richness ~ herbivory treatment* initial tile community).

Whole Model Test

Model	-LogLikelihood	L-R ChiSquare	DF	Prob>ChiSq
Difference	29.25056	58.5011	9	<.0001
Full	65.54633			
Reduced	94.79689			

Goodness Of Fit Statistic	ChiSquare	DF	Prob>ChiSq
Pearson	20.5146	33	0.9558
Deviance	22.8631	33	0.9066
AICc			

Effect Tests

Source	DF	R ChiSqua	Prob>ChiSq
Treatment	4	34.54093	<.0001
Tile_ID	1	33.0202	<.0001
Treatment*Tile_ID	4	22.54587	0.0002

Parameter Estimates

Term	Estimate	Std Error	L-R ChiSquare	Prob>ChiSq	Lower CL	Upper CL
Intercept	-1.0229	268.03306	0.0076732	0.9302	-74.1836	0.747514
Treatment[2.5]	2.500352	268.03309	27.048367	<.0001	0.765684	75.50461
Treatment[5]	2.180812	268.03311	8.9104768	0.0028	0.28487	75.3139
Treatment[7.5]	1.27831	268.03335	0.0733667	0.7865	-1.22367	74.77152
Treatment[10]	-6.72696	1072.1321	4.4654265	0.0346	-298.243	-0.07314
Tile_ID[Turfl]	-2.32032	268.03306	33.0202	<.0001	-75.4407	-0.54917
Treatment[2.5]*Tile_ID[Turf]	2.229163	268.03309	15.091453	0.0001	0.399916	75.4274
Treatment[5]*Tile_ID[Turf]	2.143238	268.03311	8.2372673	0.0041	0.249847	75.41717
Treatment[7.5]*Tile_ID[Turf]	0.966299	268.03335	0.0042938	0.9478	-1.53553	74.39212
Treatment[10]*Tile_ID[Turf]	-6.81583	1072.1321	5.3160827	0.0211	-298.238	-0.16125

Table 3. Results of two-way ANOVA testing effects of treatment and initial tile community on final species evenness (evenness ~ herbivory treatment* initial tile community). Evenness calculated as Pielou's J.

Source	DF	Sum of Square	Mean Square	F Ratio	Prob > F
Model	6	0.2196034	0.036601	0.9788	0.4609
Error	24	0.8973947	0.037391		
C. Total	30	1.116998			

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	0.5406967	0.082115	6.58	<.0001
Treatment[2.5]	0.0273036	0.093139	0.29	0.7719
Treatment[5]	0.0990739	0.078626	1.26	0.2198
Treatment[7.5]	0.0525667	0.078626	0.67	0.5102
Treatment[10]	-0.018912	0.078626	-0.24	0.812
Tile_ID[Turfl]	0.0162451	0.080892	0.2	0.8425
Treatment[2.5]*Tile_ID[Turf]	0.0934894	0.099855	0.94	0.3585
Treatment[5]*Tile_ID[Turf]	0	0	.	.
Treatment[7.5]*Tile_ID[Turf]	0	0	.	.
Treatment[10]*Tile_ID[Turf]	0	0	.	.

Source	Nparm	DF	Sum of Square	F Ratio	Prob > F
Treatment	4	1	0.01931616	0.5166	0.4792
Tile_ID	1	0	0	.	.
Treatment*Tile_ID	4	1	0.03277602	0.8766	0.3585

Table 4. Loadings for each macroalgal taxon with total variance explained by RDA1 and RDA2.

Macroalgal Taxa	**RDA1**
Turbinaria ornata	2.26E+00
Lobophora spp.	-4.25E-01
UnID Red	-1.06E-16
Amansia rhodantha	2.59E+00
Filamentous red (unknown)	-6.33E-01
Galaxaura spp.	8.00E-03
Cladophora spp.	-1.27E-23
Halimeda spp.	1.42E+00
Laurencia spp.	-4.32E-03
Peyssionnella spp.	9.53E-03
Asparagopsis taxiformis	-1.39E-01
Hypnea spp.	-1.12E-01
Filamentous Brown (unknown)	1.22E-01
Dictyota spp.	2.73E-01
Filamentous green (unknown)	9.18E-02
UnID Coralline (unknown)	2.71E-01
Caulerpa serrulata	3.09E-03
Neomeris spp.	4.66E-02
Padina spp.	6.33E-02
Valonia spp.	2.05E-01
Rosenvingea spp.	1.07E-01
Sargassum pacificum	1.12E-01
Variance Explained	0.6816

Figures

Figure 1a. Estimate of herbivory (biomass-weighted foraging time in g minutes/hr) by herbivory treatment. Treatment numbers correspond to opening size dimension (2.5 cm x 2.5 cm, 5 cm x 5 cm, etc.) in cage treatments.

Figure 1b. Total Fish biomass in grams (mean ± SE) by herbivory treatment (N = 928). The biomass of the following treatments were significantly different: Ambient > 10 = 7.5 = 5 (Tukey HSD, $P < 0.05$). No herbivory was observed in the 2.5 herbivory treatment.

Figure 2. Biomass (dry weight in grams, mean ± SE) of all macroalgae at the end of 24 months for each herbivory treatment where tiles initially contained either turf algae (green squares) or *Turbinaria* (brown squares). Post-hoc analyses (Tukey's HSD) indicated which treatments differed significantly; treatments not connected by the same letter are significantly different.

Figure 3. Species richness (mean ± SE) and Evenness (Pielou's J mean ± SE) for both tile types along the gradient in herbivory. Tiles initially seasoned with turf algae represented by green squares (N = 6 for herbivore pressure treatment 1, N = 3 for all other treatments) and tiles initially outplanted with *Turbinaria ornata* (N = 5 for all treatments) represented by brown squares.

Figure 4. Biomass (dry weight in grams, mean ± SE) for each macroalgal taxon at the end of 24 months for each herbivory treatment where tiles initially contained either turf algae (top; a) or *Turbinaria* (bottom; b). For tiles that initially began with turf algae: N = 6 for herbivore pressure treatment 1, N = 3 for all other treatments. No macroalgae was present in any of the replicates of herbivory treatment 10.5cm. For tiles that were initially outplanted with *Turbinaria ornata,* N = 5 for all treatments.

Figure 5. Ordination plot from redundancy analysis (RDA) of macroalgal taxa present on experimental tiles at the end of the experiment. Centroids for each factor (herbivory treatment and initial algal community) are plotted with dispersion ellipses using 0.9 confidence limits of the standard deviation of treatment scores. For the tiles that initially contained only turf, no macroalgae was present in any of the replicates of herbivore treatment 4 after 24 months; thus this treatment was not included in this analysis. For the tiles that initially contained only turf, the area of the ellipses for two herbivory treatments was zero (hole size 7.5 cm and ambient herbivory).

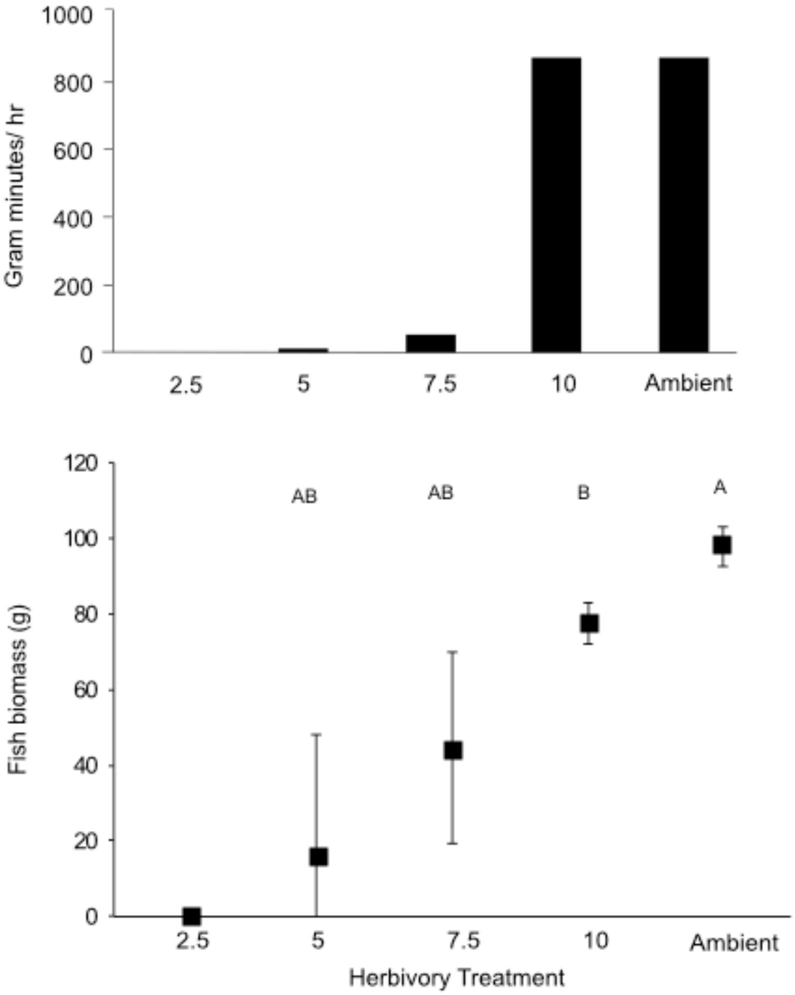
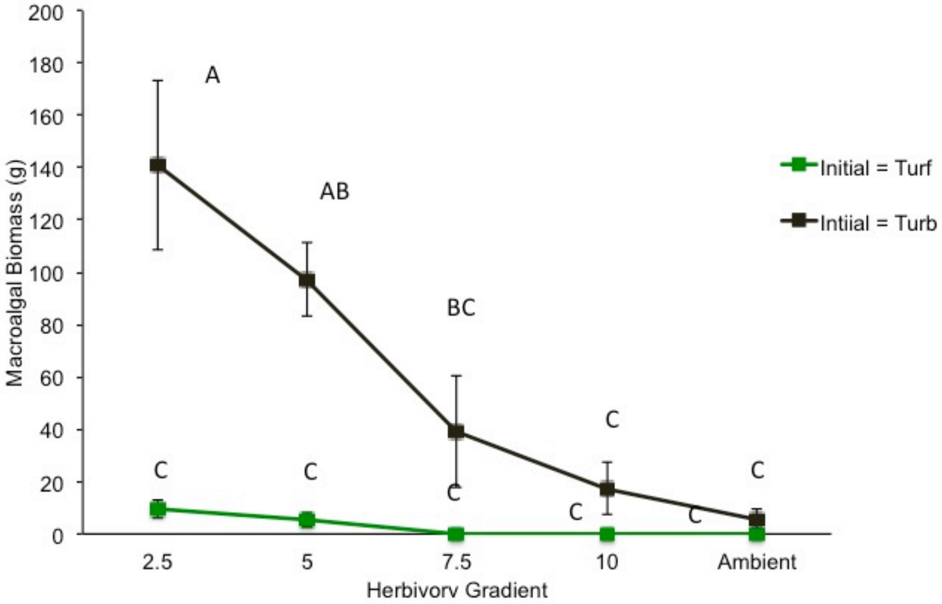


Figure 1a (top) and 1b (bottom).



Macroalgal Biomass (g)
200
180
160
140
120
100
80
60
40
20
0
2.5
5
7.5
10
Ambient
Herbivory Gradient
Initial = Turf
Intiial = Turb
A
AB
BC
C
C
C
C
C
C
C
C
C

Figure 2.

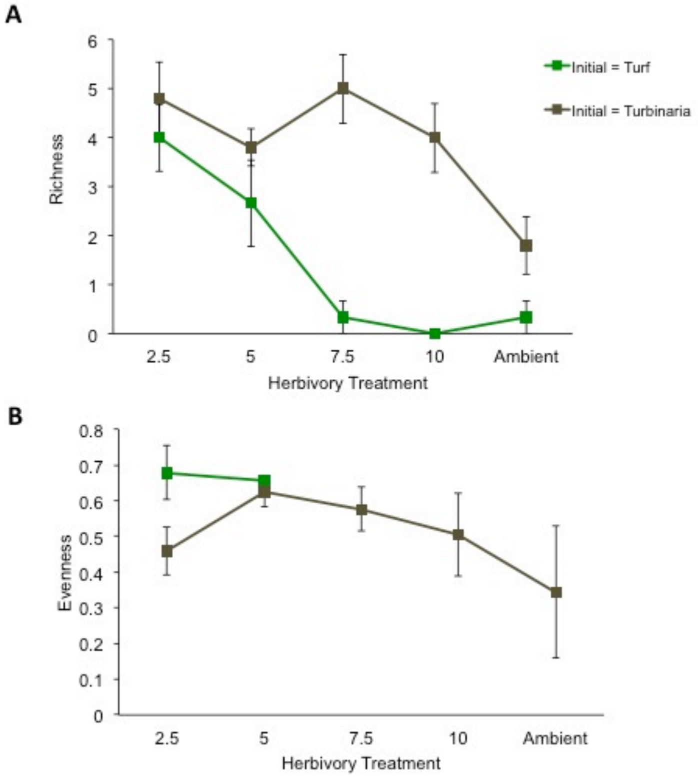

A
6
5
4
3
2
1
0
Richness
Initial = Turf
Initial = Turbinaria
2.5
5
7.5
10
Ambient
Herbivory Treatment
B
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Evenness
2.5
5
7.5
10
Ambient
Herbivory Treatment

Figure 3.

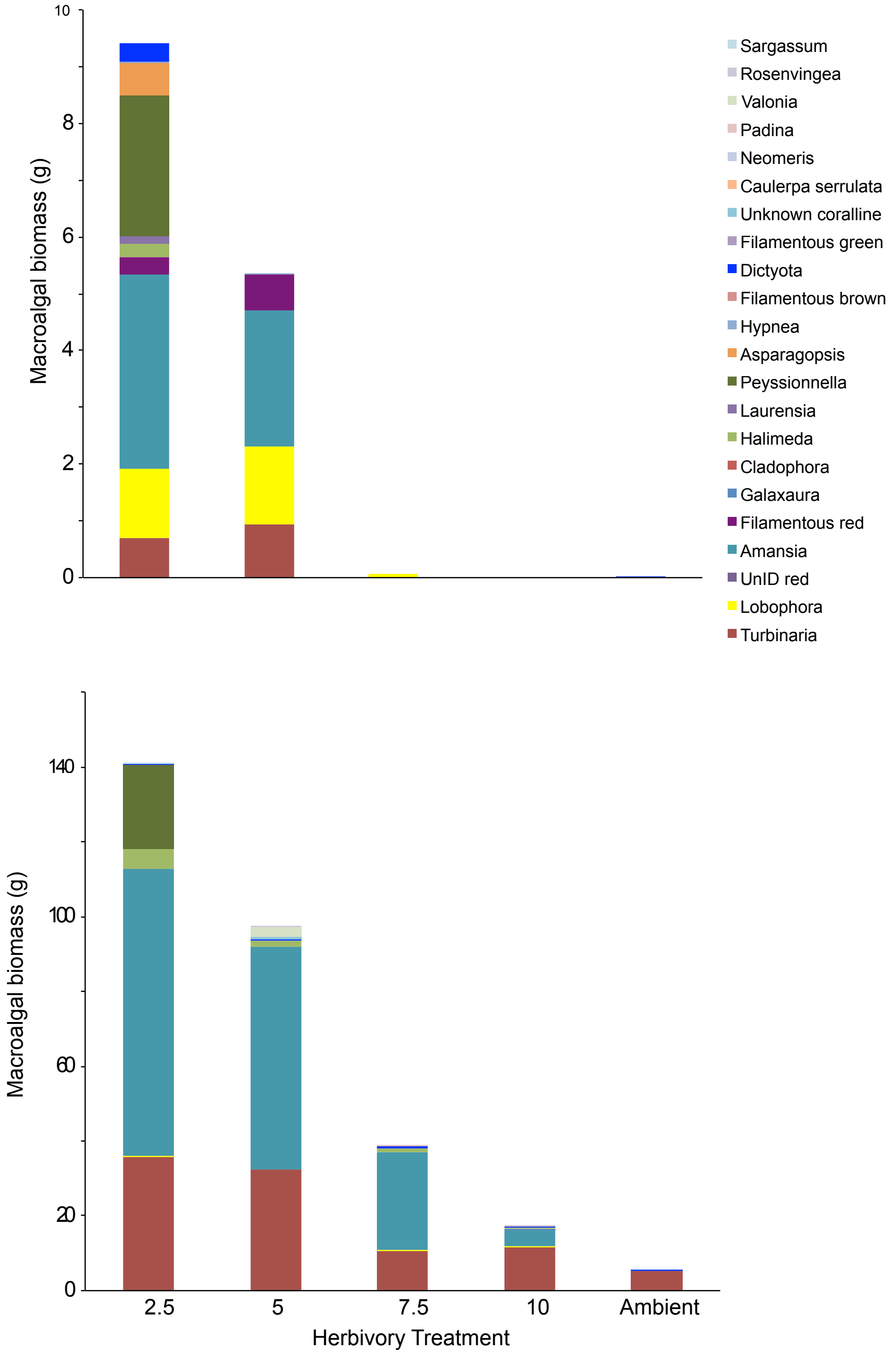


Figure 4a (top – tiles with initial turf community) and 4b (bottom – tiles initially dominated by *Turbinaria*).

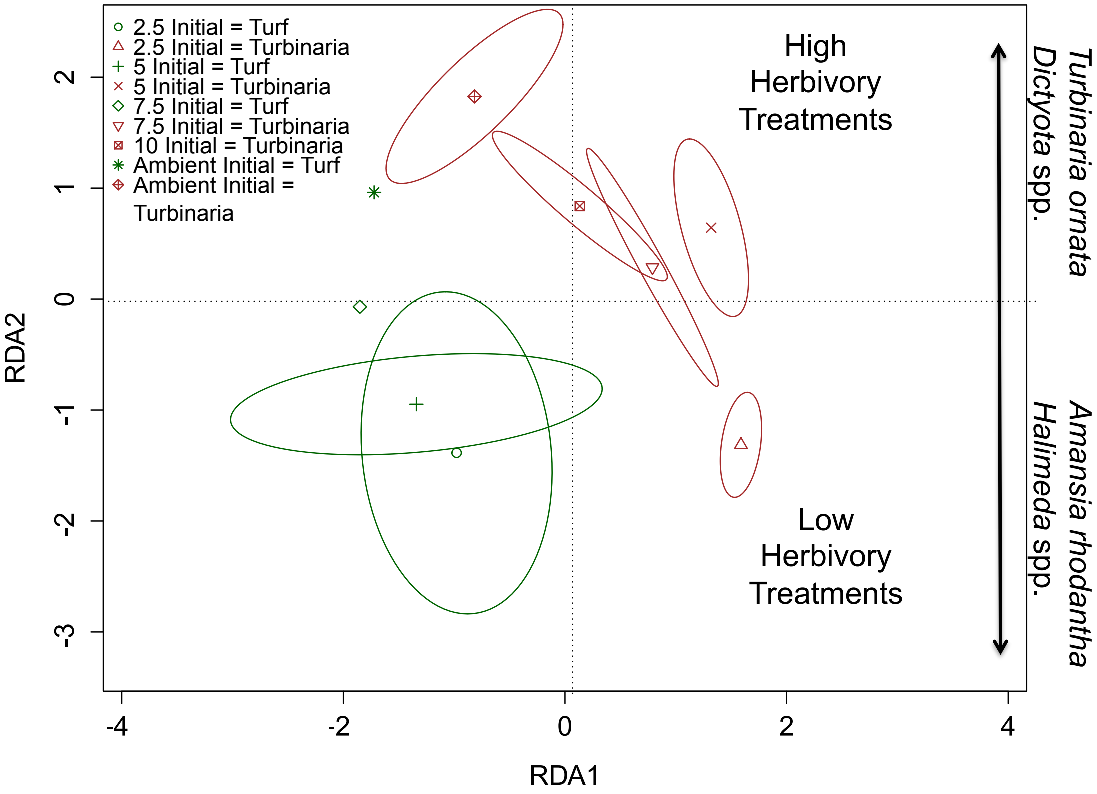

○ 2.5 Initial = Turf
△ 2.5 Initial = Turbinaria
+ 5 Initial = Turf
× 5 Initial = Turbinaria
◇ 7.5 Initial = Turf
▽ 7.5 Initial = Turbinaria
⊠ 10 Initial = Turbinaria
✳ Ambient Initial = Turf
⊕ Ambient Initial = Turbinaria
High Herbivory Treatments
Low Herbivory Treatments
Turbinaria ornata
Dictyota spp.
Amansia rhodantha
Halimeda spp.
RDA2
RDA1
2
1
0
-1
-2
-3
-4
-2
0
2
4

Figure 5.

Supplementary Information

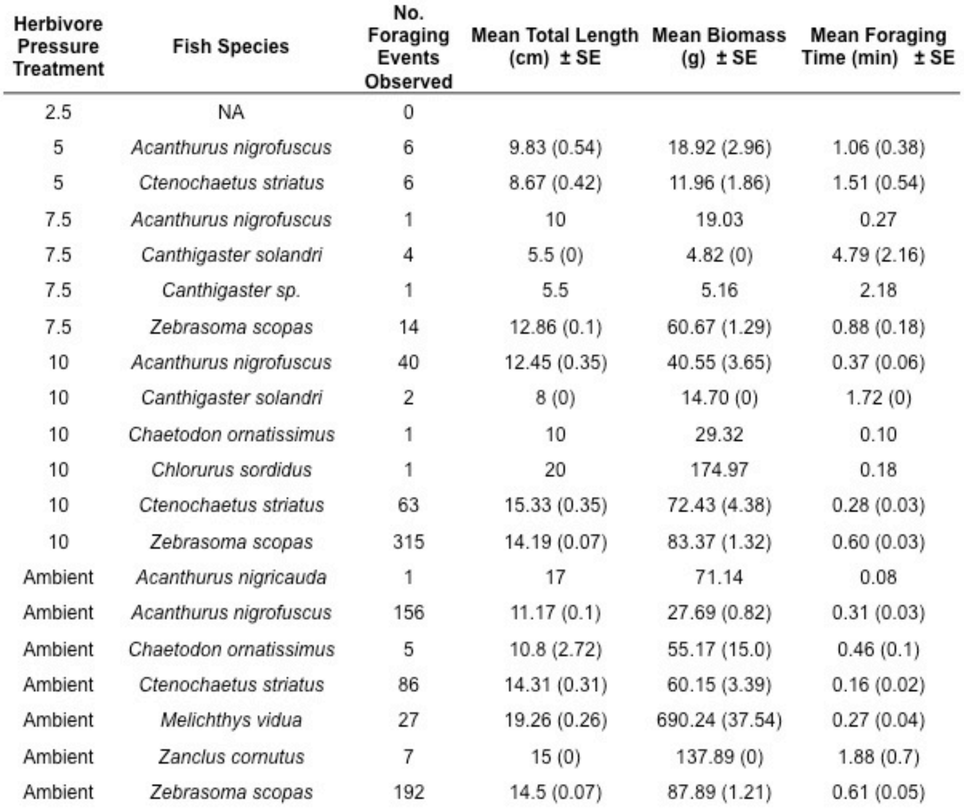
SI Table 1. Cage design for herbivory gradient experiment.

Herbivory Treatment	Size of Openings (dimensions in cm)	Total Area of Openings Allowing Fish Access (cm^2)
1	2.5 x 2.5	0
2	5 x 5	440
3	7.5 x 7.5	450
4	10 x 10	480
5	Full access	563

SI Table 2. Summary of herbivory gradient assay. For six consecutive days, each of the five herbivory treatments was baited with palatable macroalgae (*Sargassum pacificum)* and turf algae. Video was recorded during peak herbivory periods (1000-1400) each day. All recorded video for each herbivory treatment was analyzed for total number of foraging events observed and biomass-weighted foraging time per hour of video (g minutes/hr).

Herbivory Treatment	No. Foraging Events Observed	Total Recorded Video (hh:mm:ss)	Biomass-weighted foraging time per hour of video (grams*mins/hr)
2.5	0	21:25:04	0
5	12	18:10:17	13.71
7.5	20	15:42:29	54.59
10	422	21:11:16	872.53
Ambient	474	21:23:16	872.67

SI Table 3. Summary of herbivory gradient assays. Total number individual fish observed (mean ±SE), fish total length in cm (mean ±SE), biomass in grams (mean ±SE), and foraging time in minutes (mean ±SE) by fish species for each herbivory treatment. Means were calculated using N = number of foraging events observed for each fish species.



Herbivore Pressure Treatment	Fish Species	No. Foraging Events Observed	Mean Total Length (cm) ± SE	Mean Biomass (g) ± SE	Mean Foraging Time (min) ± SE
2.5	NA	0			
5	*Acanthurus nigrofuscus*	6	9.83 (0.54)	18.92 (2.96)	1.06 (0.38)
5	*Ctenochaetus striatus*	6	8.67 (0.42)	11.96 (1.86)	1.51 (0.54)
7.5	*Acanthurus nigrofuscus*	1	10	19.03	0.27
7.5	*Canthigaster solandri*	4	5.5 (0)	4.82 (0)	4.79 (2.16)
7.5	*Canthigaster sp.*	1	5.5	5.16	2.18
7.5	*Zebrasoma scopas*	14	12.86 (0.1)	60.67 (1.29)	0.88 (0.18)
10	*Acanthurus nigrofuscus*	40	12.45 (0.35)	40.55 (3.65)	0.37 (0.06)
10	*Canthigaster solandri*	2	8 (0)	14.70 (0)	1.72 (0)
10	*Chaetodon ornatissimus*	1	10	29.32	0.10
10	*Chlorurus sordidus*	1	20	174.97	0.18
10	*Ctenochaetus striatus*	63	15.33 (0.35)	72.43 (4.38)	0.28 (0.03)
10	*Zebrasoma scopas*	315	14.19 (0.07)	83.37 (1.32)	0.60 (0.03)
Ambient	*Acanthurus nigricauda*	1	17	71.14	0.08
Ambient	*Acanthurus nigrofuscus*	156	11.17 (0.1)	27.69 (0.82)	0.31 (0.03)
Ambient	*Chaetodon ornatissimus*	5	10.8 (2.72)	55.17 (15.0)	0.46 (0.1)
Ambient	*Ctenochaetus striatus*	86	14.31 (0.31)	60.15 (3.39)	0.16 (0.02)
Ambient	*Melichthys vidua*	27	19.26 (0.26)	690.24 (37.54)	0.27 (0.04)
Ambient	*Zanclus cornutus*	7	15 (0)	137.89 (0)	1.88 (0.7)
Ambient	*Zebrasoma scopas*	192	14.5 (0.07)	87.89 (1.21)	0.61 (0.05)

SI Table 4. Proportion of total dry biomass for each macroalgal taxon after 24 months on tiles initially covered with turf. Presented for each herbivory treatment. For herbivory treatment 1, N = 6; for all other herbivory treatments, N = 3.

Macroalgal Taxa	2.5	5	7.5	10	Ambient
Turbinaria	0.07	0.18	0.00	NA	0.00
Lobophora	0.13	0.26	1.00	NA	0.00
UnID red	0.00	0.00	0.00	NA	0.00
Amansia	0.36	0.45	0.00	NA	0.00
Filamentous red	0.03	0.12	0.00	NA	0.00
Galaxaura	0.00	0.00	0.00	NA	0.00
Cladophora	0.00	0.00	0.00	NA	0.00
Halimeda	0.03	0.00	0.00	NA	0.00
Laurensia	0.01	0.00	0.00	NA	0.00
Peyssionnella	0.26	0.00	0.00	NA	0.00
Asparagopsis	0.06	0.00	0.00	NA	0.00
Hypnea	0.00	0.00	0.00	NA	0.00
Filamentous brown	0.00	0.00	0.00	NA	0.00
Dictyota	0.03	0.00	0.00	NA	1.00
Filamentous green	0.00	0.00	0.00	NA	0.00
Unknown coralline	0.00	0.00	0.00	NA	0.00
Caulerpa serrulata	0.00	0.00	0.00	NA	0.00
Neomeris	0.00	0.00	0.00	NA	0.00
Padina	0.00	0.00	0.00	NA	0.00
Valonia	0.00	0.00	0.00	NA	0.00
Rosenvingea	0.00	0.00	0.00	NA	0.00
Sargassum	0.00	0.00	0.00	NA	0.00

SI Table 5. Proportion of total dry biomass for each macroalgal taxon after 24 months on tiles initially deployed with *Turbinaria ornata* attached. Presented for each herbivory treatment (N = 5 for all treatments).

Macroalgal Taxa	**2.5**	**5**	**7.5**	**10**	**Ambient**
Turbinaria	0.25	0.33	0.27	0.67	0.93
Lobophora	0.00	0.00	0.01	0.01	0.01
UnID red	0.00	0.00	0.00	0.00	0.00
Amansia	0.54	0.61	0.67	0.24	0.01
Filamentous red	0.00	0.00	0.00	0.01	0.00
Galaxaura	0.00	0.00	0.00	0.03	0.00
Cladophora	0.00	0.00	0.00	0.00	0.00
Halimeda	0.04	0.02	0.02	0.01	0.00
Laurensia	0.00	0.00	0.00	0.00	0.00
Peyssionnella	0.16	0.00	0.00	0.00	0.00
Asparagopsis	0.00	0.00	0.00	0.00	0.00
Hypnea	0.00	0.00	0.00	0.00	0.00
Filamentous brown	0.00	0.00	0.00	0.00	0.00
Dictyota	0.00	0.01	0.02	0.03	0.06
Filamentous green	0.00	0.00	0.00	0.00	0.00
Unknown coralline	0.00	0.01	0.00	0.00	0.00
Caulerpa serrulata	0.00	0.00	0.00	0.00	0.00
Neomeris	0.00	0.00	0.00	0.00	0.00
Padina	0.00	0.00	0.00	0.00	0.00
Valonia	0.00	0.03	0.00	0.00	0.00
Rosenvingea	0.00	0.00	0.00	0.00	0.00
Sargassum	0.00	0.00	0.00	0.00	0.00