Associational refuge facilitates phase shifts to macroalgae in a coral reef ecosystem

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Abstract. Coral reefs are among the most diverse and productive marine ecosystems and are currently threatened by natural disturbances such as predator outbreaks and tropical storms that 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 to understand mechanisms that permit the establishment and persistence of macroalgae. Though many macroalgae are chemically and physically defended against herbivores as adults, these defenses may be lower during early life stages. One potential mechanism that could facilitate the establishment and persistence of macroalgae is an associational refuge whereby early life stages are protected from herbivory in close proximity of older, less palatable conspecifics. Using Turbinaria ornata as a model macroalga, I tested whether an associational refuge between different life stages could facilitate the establishment and long-term persistence of Turbinaria in the lagoons of Moorea, French Polynesia. Results suggest that Turbinaria may only be limited by herbivory as recruits, 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 recruits experience a refuge from herbivory when they are associated with relatively unpalatable adults, and found that survival of recruits was higher when they were associated with adults than when alone. I also found that the value of a refuge can be spatially variable because the association with adults has a growth and survivorship cost to recruits where herbivory was low. These mechanisms can promote persistent macroalgal assemblages and limit the capacity of herbivores to control macroalgae and reverse a phase shift.

Key words: associational refuge; coral reefs; facilitation; herbivory; macroalgae; phase shift.

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, including savannas, lakes, and temperate subtidal reefs (Dublin et al. 1990, Scheffer et al. 1993, Steneck et al. 2002, Rasseweiler et al. 2010). 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. The reversibility of a phase shift is directly related to the existence and strength of stabilizing feedbacks that can reinforce alternative ecosystem states. Thus, developing an understanding of the mechanisms that might trap an ecosystem in a particular state is critical in the development of effective...
management practices to prevent transitions to undesired states and/or speed the return of the desired state.

In coral reef ecosystems, transitions from a coral-dominated state to a macroalgal-dominated state may be persistent (e.g., Rogers and Miller 2006), and some have argued they may not be easily reversed (e.g., Mumby et al. 2013, but see Dudgeon et al. 2010). Examples of proposed stabilizing feedbacks on coral reefs include those resulting from competitive interactions among coral and macroalgae (Mumby and Steneck 2008), facilitative effects of coral on herbivores through habitat provision (Lee 2006), and Allee effects in corals, herbivores, and even coral predators (Babcock and Mundy 1992, Hughes et al. 2000, Edmunds and Elahi 2007). Strong stabilizing feedbacks can help maintain reefs in a particular phase (Nyström et al. 2012, Van de Leemput et al. 2016). Macroleaf-dominant reefs inhibit coral recovery through direct competitive interactions (McCoo et al. 2001) as well as indirect effects such as altering the behavior of key herbivores (Hoey and Bellwood 2011, 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). 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 could 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 (Littler et al. 1986).

Associational refuges arise when the per capita benefits of close physical proximity outweigh the costs to individuals in inter- or intraspecific aggregations (e.g., reduced mortality rate > reduced growth rate; Hay 1986, Levenbach 2008, Barbosa et al. 2009). On temperate and tropical reefs, palatable algal species may be found in greater abundance and diversity in close associations with unpalatable neighbors in situations where herbivory is intense (Leenbach 2009, Bittick et al. 2010, Loffler et al. 2014). Intraspecific associational refuges in species of tropical macroalgae have rarely been studied (but see Dell et al. 2016); however, studies of interspecific associational refuges in other ecosystems suggest that these facilitative processes may have community-level ramifications, such as enhanced local diversity among plants and macroalgae (Hay 1986, Hacker and Gaines 1997, Callaway et al. 2005), and could also form the basis of effective strategies for restoration of woodland habitats (Stutz et al. 2015). In this study, I examined the potential for and possible consequences of intraspecific associational refuge for early life stages of the tropical fucoid *Turbinaria ornata* in Moorea, French Polynesia.

Using *T. ornata* as a model species, I explore whether there is evidence of differences in consumption by herbivores among *Turbinaria* life stages (sizes) that can support associational refuges as a mechanism of self-reinforcement and replenishment of *Turbinaria* populations. Because chemical and structural defenses of *Turbinaria* individuals develop ontogenetically and are highest for mature thalli (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 if recruit stages are more vulnerable to herbivory, recruits should have higher survival when they are in close association with less palatable adults. However, the long-term effects of association are complex, composed of both competitive costs (e.g., competition among individuals for light, nutrients, or attachment space) and associative benefits (e.g., reduced mortality due to herbivory). The relative strength of an associational refuge may depend on the strength of herbivory—when herbivory is low, there should be a demographic cost for young *Turbinaria* that co-occur with older stages. Intraspecific competition for resources such as light and attachment spaces within macroalgal beds could result in reduced recruitment, growth, or survival for young *Turbinaria* recruits as documented for other interspecific macroalgal communities (Carpenter 1990, Creed et al. 1997). It is thus critical to evaluate the potential for an associational refuge that results in higher recruit survival in the presence of herbivory to represent a self-reinforcement mechanism that could promote persistence of macroalgae such as *Turbinaria* on coral reefs.
**Methods**

**Study location and species**

Fieldwork was conducted in the north shore lagoons of Moorea, French Polynesia (17°32′ S, 149°50′ W), during the austral winters of 2012–2015. 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) (Agardh 1848) is the most abundant species of macroalgae in the lagoons of Moorea (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 1980s to early 1990s (Done 1992). The abundance and longevity of *T. ornata* in French Polynesia may be driven by morphological and/or reproductive traits. Though *T. ornata* is consumed by some herbivorous fishes on some reefs (Mantyka and Bellwood 2007, Rasher et al. 2013), this alga is both structurally and chemically defended against herbivory, and the production of chemical defense compounds develops ontogenetically (Stiger et al. 2004), suggesting that there may be differences in the susceptibility to herbivory at different life stages. Sexual reproduction occurs year-round, and most offspring settle close to parent thalli (generally within 1 m; Stiger and Payri 2005).

**Size-specific survivorship of Turbinaria**

To test the hypothesis that the vulnerability of *Turbinaria* to herbivory decreases with increasing age/size of individual thalli, survival assays were conducted in July 2013. Individuals in five size classes were outplanted on a reef in the lagoon for 7 d 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 exposure treatment discounted by the loss of individuals in the treatment without herbivores (presumably from handling).

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 (and thus may be a physical refuge from herbivorous fishes). Individuals selected for the assay all had minimal fouling by epiphytes and were not senescent. Thalli were placed into five size classes based on their length, which is related to ontogeny (Kalaparamul and Rao 1975, Stiger et al. 2004; Table 1). *Turbinaria* thalli were transported in seawater to the laboratory and placed in high-flow aquaria within ~1 h of collection. For the smallest individuals in Size Classes 1 and 2 (which together I term recruits), scuba divers used a rock hammer and chisel to remove portions of dead coral substrate on which they were attached. These smallest individuals have weak holdfasts and, if removed from their substrate, begin to deteriorate immediately (S. L. Davis, personal observation). Marine epoxy was used to affix pieces of substrate with small *Turbinaria* to galvanized wire mesh (30 × 30 cm) in running seawater in the laboratory. Larger size classes (Size Classes 3 [juveniles] and 4–5 [adults]) all had thalli >2 cm in length, and they were collected with holdfasts attached. These larger individual thalli were attached to the mesh directly using cable ties loosely placed around the thallus. Though collection methods differed between the smallest and largest size classes, these methodologies are not expected to differentially influence herbivory. Since small *Turbinaria* remained attached to natural substrate, this method closely approximates herbivory conditions in situ. Additionally, macroalgae attached to mesh were readily consumed by herbivores in other assays (S. L. Davis, personal observations). To create a cohort of individuals for each replicate, a total of 25 individual thalli of a single size class were placed on each replicate mesh substrate; and replicates with 25 individuals of a single size class were

| Size class | Size range | Approximate age of thallus |
|------------|------------|----------------------------|
| 1          | <1 cm      | <14 d                      |
| 2          | 1–2 cm     | 14–28 d                    |
| 3          | 2–5 cm     | 28–70 d                    |
| 4          | 5–8 cm     | 70–112 d                   |
| 5          | >8 cm      | >112 d                     |

*Note:* The approximate age of the thallus was calculated using the published growth rate for closely related *Turbinaria decurrens* (2 cm per month; Kalaparamul and Rao 1975).
haphazardly assigned to the herbivore exclusion (N = 3 mesh substrates per size class) or exposed to herbivory (N = 4 mesh substrates per size class) treatments. For the herbivore exclusion treatments, circular cages (approximately 30 cm high and 120 cm in circumference) constructed of galvanized wire mesh (2.5 cm mesh) were used to exclude fish and sea urchins.

The assays were deployed on natural substrates at a site where Turbinaria was rare at depths of 2–3 m for 7 d. At the end of the assay, the total number of individual thalli surviving out of the original 25 per replicate was recorded. An individual thallus was recorded as dead when it was entirely consumed and therefore absent from the replicate substrate. Diver observations of browsing fishes (e.g., Naso spp.) consuming Turbinaria on the fore reefs of Moorea (A. Brooks, personal communication) and actively foraging in the experimental area suggest that dead individuals were likely consumed by browsers.

A generalized linear model (glm function within the stats package for R [R Core Team 2013]) with binomial error distribution was used to investigate the effect of size class (fixed) on survival (success) of individuals in replicates in the treatment exposed to herbivores only. No individuals were lost in any size class when herbivores were excluded using cages; thus, this factor was not included in analysis. A Type III analysis of deviance on the coefficient estimates from the model was used to test the significance of size class on the mean survival of Turbinaria individuals, followed by 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).

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. It is thus critical to test whether presence of adults (thalli >5 cm; Stiger et al. 2004) could provide an associational refuge for recruits (thalli <2 cm in length). To determine the effect of adults on the short-term survival of associated Turbinaria recruits, the separate and interactive effects of adult density and exposure to herbivores on the survival of Turbinaria recruits (<2 cm in length) were tested experimentally over 7 d. Galvanized wire mesh (2.5 cm) cages of the same design as used in the size-specific herbivory assay described above were used to manipulate the presence of fish and urchin herbivores. Diver surveys throughout the experiment revealed no fish or urchins inside of the cages. A partial cage control (2.5-cm galvanized steel wire mesh formed into a semicircle approximately 12 cm high and 60 cm circumference) was used as a cage control for all replicates exposed to herbivores.

Turbinaria used in the experiment (adult thalli >5 cm and recruit thalli <2 cm) were collected from the lagoon habitat using the techniques described previously, transported to the laboratory in seawater, and placed in high-flow aquariums. Prior to the start of the experiment, 20 recruits were attached to 2.5-cm wire mesh using techniques described above. Immediately after transporting the focal Turbinaria recruits to the reef, the actual starting number of recruits was quantified, because some recruits were lost during transport. Before initiating the experiment, divers ensured that all remaining recruits were securely attached to the substrate. Each replicate mesh was haphazardly assigned to one of four adult density treatments based on surveys of natural Turbinaria patches in the north shore lagoons (0 adults, 30 adults per m², 100 adults per m², and 200 adults per m²) and either caged or left open to herbivore access. Adult Turbinaria were attached to the mesh using cable ties, distributing adult thalli among the recruits so that recruits were adjacent to canopy-forming adults. Replicates were arranged in a systematic block design where caged and cage control treatments for each Turbinaria adult density treatment were paired and interspersed along a line parallel to the reef crest from lowest to highest adult density (N = 10 for each treatment, one full set of replicates in each block). This method was selected to minimize within-block variation due to herbivore behavior, as dense patches of macroalgae may be avoided by browsers (sensu Hoey and Bellwood 2011). Blocks were spaced ~3 m apart, and within a block, replicates were spaced ~0.5–1 m apart from one another in a rubble field scattered with coral bommies. All replicates within a block were well within the estimated home ranges of the local browsing fish species
(Naso literatus = 6.8 ha and Naso unicornis = 3.2 ha; Marshall et al. 2011); thus, replicates within a block were exposed to similar local browsing pressure. Turbinaria adult density treatments were maintained by replacing lost adults once during the experiment. Few adults were lost during the 7 d experiment.

After 7 d, all remaining recruits were counted to determine the number of individuals surviving in each replicate. Recruits that survived (and grew for 7 d) were easily distinguished from the much larger adults used to create variation in density of adults. For eight of the 40 replicates in the caged treatments, the final number of recruits was slightly greater than the initial number (increases ranged from 1 to 3 individuals). It is likely that new Turbinaria thalli grew from fragments of old holdfasts that remained on the natural substrate over the course of the experiment. This common form of vegetative growth for Turbinaria (Kaliaperumal and Rao 1975, Stiger and Payri 2005, Prathep et al. 2007) likely occurred in the uncaged treatments as well.

A generalized linear model with binomial error distribution and block as a random effect was constructed to investigate the separate and interactive short-term effects of Turbinaria adult density and presence of herbivores on the mean fraction of surviving Turbinaria recruits. The maximum fraction of surviving recruits was constrained to 100% to perform this analysis. This analysis was followed by a Type III analysis of deviance using the methods and R packages described previously. The R package lsmeans (Lenth 2016) was used to back-transform coefficients from the binomial GLM to probabilities. Tukey-adjusted pairwise comparisons were computed on logit scale and then transformed to proportions. These statistical models and tests were conducted using RStudio (version 0.97.551) for R Statistical Computing Package (R Core Team 2013).

Cost of association

By definition, an associational refuge occurs when the benefit outweighs the demographic cost of an association. In the case of small Turbinaria individuals associated with larger, less palatable conspecifics, there may be benefits of increased survival when exposed to herbivores (i.e., reduced predation) counterbalanced by reduced growth, survivorship, and perhaps recruitment via shading, space preemption, 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) also influence the net effect of an association, as the benefits (enhanced survival) may only be present when herbivory is sufficiently high to outweigh any competitive costs (Levenbach 2008). To estimate the potential cost of intraspecific association, I manipulated the density of Turbinaria thalli >2 cm in length in replicate quadrats (37.5 x 37.5 cm) on the reef and followed the net population change (which includes survival of recruits initially ≤2 cm in length, growth to the next size class, and new recruitment) over a five-week period during July–August 2015. 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 a site in the north shore lagoon where there were dense patches of thalli of older Turbinaria (similar densities to experimental patches created for the short-term experiment) and assigning patches to one of two treatments: a removal treatment where all Turbinaria >2 cm in length were removed by hand and an unmanipulated (control) treatment where naturally occurring older stages were left intact (N = 13 replicates per treatment). In the removal quadrats, all thalli >2 cm in length were removed by cutting each thallus just above the holdfast. At the start of the experiment, the number of visible recruits in each replicate as well as the number of individual thalli removed or intentionally left was recorded. For the latter, a small cable tie was fastened around the base of each older-stage thallus to mark the individuals >2 cm in length that remained in the unmanipulated plots. In this way, individuals in the control treatment that started as a recruit but grew to >2 cm by the end of the experiment could be distinguished from marked individuals. After 5 weeks, the number of individual thalli present, composed of both recruits and new (untagged) juveniles that grew from the initial cohort of recruits, was recorded. The change in the proportion of young Turbinaria, defined as [(number of
final recruits + new juveniles) — number of initial recruits/number of initial recruits, was quantified as it was impossible to distinguish recruits that were present at the start of the experiment that remained < 2 cm in length from those that recruited during the 5 weeks. This yields an estimate of the net population change of vulnerable life stages in low-browsing conditions.

A nonparametric Kolmogorov-Smirnov two-sample test, which compares samples without specifying an underlying distribution (Sokal and Rohlf 1969), was used to examine the potential cost of association in Turbinaria (the effect of adult density treatment on the net population change). Statistical models and tests were conducted using JMP statistical software (v.11, SAS Institute Inc., Cary, North Carolina, USA).

**Herbivory assays**

Since the net effect (positive or negative) of an intraspecific associational defense is predicted to vary with the level of herbivory, local herbivore pressure at both experimental sites was quantified in two ways. First, the local browsing pressure was estimated by implementing two separate 24-h herbivory assays at each site. To obtain an independent assessment of herbivory, each assay consisted of a 24-h deployment of a known biomass of the palatable brown macroalga *Sargassum pacificum*, which is consumed by *Naso* spp. in many reef systems (Rasher et al. 2013), including Moorea (video observation). Mature *Sargassum* thalli were collected from the reef crest where the species is abundant and transported in seawater to the laboratory where they were placed in high-flow aquaria within 1 h of collection. For each replicate, three mature *Sargassum* thalli were each spun in a salad spinner to constant weight and then attached to a galvanized mesh square (37.5 × 37.5 cm) using cable ties, transported to the field, and affixed to the reef (N = 3 replicate squares per assay). At the end of the 24-h period, the mean proportional change in biomass ((final weight (g) – initial weight (g))/initial weight (g); N = 3) was quantified. The mean proportional change in *Sargassum* biomass was then calculated for each site using the two 24-h assays. Additionally, the abundance and size (total length in cm) of browsing fish species were also quantified along four 50 × 5 m transects (for browser taxa list, see Appendix S1: Table S7). Published length–biomass relationships were used to calculate the biomass of each fish (Brooks 2014).

**RESULTS**

**Size-specific survivorship of Turbinaria**

All individuals of all size classes of *Turbinaria* survived the 7-d experiment when protected from herbivores. By contrast, when exposed to herbivory, survivorship was highly dependent on size (ontogeny) of the *Turbinaria* thallus (Fig. 1; Type III analysis of deviance, $X^2 = 133.31$, df = 4, $P < 0.0001$; Appendix S1: Table S1). Individuals in Size Classes 1 and 2 (i.e., <2 cm in length) had the lowest survival rates (54% and 67%, respectively; not significantly different [generalized linear hypothesis simultaneous tests for GLMs, Tukey contrasts, $P = 0.3$; Appendix S1: Table S2]), which were statistically lower than survival of the three larger size classes ($P < 0.001$). For individuals >2 cm in length (i.e., Size Class 3 and above), ≥97% survived (Fig. 1), indicating an ontogenetic decline in the vulnerability of *Turbinaria* to browsers with increasing size.

**Test for an associational refuge**

The location of the associational refuge field experiment was characterized by the presence of

![Fig. 1. Mean (±1 SE) proportion of surviving *Turbinaria* thalli by size class when exposed to herbivores for 7 d (N = 4 for each size class). Statistical differences are denoted by different letters (P < 0.05).](image-url)
large browsing fishes (biomass mean ± SE, 0.63 ± 0.36 grams/m²) and relatively high brow-ser pressure (percentage of palatable Sargassum consumed in 24 h mean ± SE, 50% ± 30). The experiment at this site 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; Type III analysis of deviance, $X^2 = 48.89$, df = 3, $P < 0.0001$; Appendix S1: Tables S3 and S4). When protected from herbivory by cages, survivorship of recruits was at or near 100% for all adult Turbinaria density treatments, although there was a significant decline in recruit survivorship (to mean ± SE, 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 associated older conspecifics. 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; Appendix S1: Table S5).

**Cost of associational refuge**

The location of the experimental assessment of potential costs of associational refuge was selected for the high percent cover of Turbinaria patches to facilitate experimental manipulation (Carpenter 2015). Estimates of the local abundance of browsing fish conducted concurrently with the experiment suggested low densities of browsing fishes capable of consuming Turbinaria (no browsing fish were observed in any visual survey) and a low browsing rate on highly palatable macroalgae (percent of Sargassum consumed in 24 h 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 of new thalli and/or growth of thalli that were initially too small to see 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. 0.18 ± 0.08 when older conspecifics were present; KS Test, $D = 0.54$, $P = 0.0461$; Appendix S1: Table S6), suggesting that the net effect of the associational refuge could depend 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 produce an associational refuge for *Turbinaria* recruits that are co-located 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. Under low-browsing conditions, *Turbinaria* population growth was positive, despite the apparent costs of association (intraspecific competition, potentially for light and/or nutrients). Together, these results suggest that the persistence or expansion of *Turbinaria* may be dependent on an intraspecific associational refuge where herbivory is sufficiently high. Although an intraspecific associational refuge among *Turbinaria* thalli may be a mechanism for macroalgal persistence, variability in the abundance/biomass of browsers can have significant consequences for the trajectory of reef recovery and the development of such reinforcing feedbacks that promote macroalgae-dominated reefs.

In the context of macroalgal phase shifts in general, this study provides evidence that a biogenic 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 macroalgae-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 sertularioides* 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 net effect (positive or negative) and strength of these associations depend on the local environment and whether herbivory produces sufficient biological disturbance levels such that an association between organisms becomes beneficial instead of harmful. At intermediate levels of consumer pressure, reduced consumption within associations can outweigh the potential competitive costs (Levenbach 2009). Variation in browsing pressure could explain the observed differential effects of the association between *Turbinaria* recruits and larger conspecifics.

In this study, the tests for the presence of an associational refuge and the potential costs of association necessarily were conducted in different reef locations and in different years due to logistical constraints, and thus, direct statistical comparisons are not possible. Nonetheless, these results support the inference that variation in the strength of herbivory could significantly influence the net effect of an association. Though grazing herbivores may prevent macroalgal establishment when macroalgal thalli are small and indistinguishable from turf algae (e.g., Burkepile and Hay 2010), the time frame for macroalgal suppression by grazers (and browsers) may be relatively limited, which highlights the need for additional study of spatial and temporal variability in macroalgal browsing on coral reefs. Differences in browsing (i.e., consumer stress) could arise several ways. If browsing fish are present but avoid 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 closely related species...
Turbinaria decurrens) is ~2 cm per month (Kalaiaperumal and Rao 1975). Using this estimate, Turbinaria thalli may be vulnerable to herbivory for <1 month (Table 1). Browsers may avoid relatively unpalatable macroalgae (such as T. ornata) using visual cues to locate more preferred algae elsewhere, and thus, as the density and frequency of unpalatable patches in a specific area increase, overall browsing pressure may decrease. Tootell and Steele (2015) observed that the distribution, behavior, and condition of grazing fish herbivores 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. Behavioral studies of fish browsers on the Great Barrier Reef suggest that browsing fish may avoid dense patches of macroalgae because of visual obstruction from predators (Hoey and Bellwood 2011). In this study, browsing assays suggested that level of browsing and the cover of Turbinaria could be inversely related. This observation of a browser–macroalgal cover relationship is consistent with Hoey and Bellwood’s observations, although further work is needed to elucidate the mechanism underlying this relationship. Indeed, though the maximum length of Turbinaria (30 cm, estimated for T. decurrens; Kalaiaperumal and Rao 1975) is much smaller than the Sargassum species studied on the Great Barrier Reef (>1 m), this may be a potential mechanism influencing smaller browsing fish. In addition to behavioral factors that can 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 change, 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 (e.g., intact herbivore guilds that can respond to increased algae and promote coral recovery following a coral mortality event; Adam et al. 2011) or macroalgae (e.g., suppression of browsing by dense macroalgal patches that promote macroalgal persistence; Hoey and Bellwood 2011). Targeted studies could assess these feedbacks through experimental techniques, and these feedbacks can then be conserved or altered through local and regional 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 yr 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 socioeconomic 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, T. ornata, in the lagoons of Moorea, French Polynesia. Following coral mortality events in the lagoon, hard substrate becomes 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 facilitate 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 may depend on whether browsing is sufficiently high that positive effects of association outweigh the costs. Spatial variability in environmental parameters can be a significant determinant of the trajectory of reef recovery (Van Nes and Scheffer 2005) and must be considered in the development of management strategies to promote coral recovery following a disturbance. When developing management strategies that seek to disrupt feedbacks that promote macroalgal states, 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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