Contents lists available at ScienceDirect

Aquatic Botany

Short communication

An experimental assessment of herbivory and nutrient effects on a small-scale in a coral reef macroalgal community

Caitlin R. Fong*

University of California Santa Barbara, Department of Ecology, Evolution, and Marine Biology, 552 University Rd, Santa Barbara, CA 93106, USA

ARTICLE INFO

ABSTRACT

Understanding spatial variation in top–down vs. bottom–up control may help resolve some of the conflicts among research findings on the controlling processes of marine plant communities. In this study, I manipulate herbivory and nutrient limitation on assembled communities of coral reef macroalgae. I conducted two identical 10-day manipulative experiments 20 m and 12 days apart and measured change in biomass of the 4 assembled species, *Padina boryana* (Thivy), *Halimeda opuntia* (L. J.V.Lamouroux), *Galaxaura divaricata* (L. Huisman and R.A.Townsend), and *Dictyota bartayresiana* (J.V.Lamouroux). I found that the response of all individual species varied markedly between the two sites. Between the two sites, *P. boryana* and *D. bartayresiana* responded differently to manipulations whereas *H. opuntia* and *G. divaricata* differed in growth magnitude and variance. The difference in final biomass between the two sites was most pronounced for the opportunistic algal species, suggesting small-scale spatial variation might be more important for these types of macroalgae. The constant environmental conditions during the study period suggest that small-scale spatial differences may affect the processes controlling community structure.

1. Introduction

Spatial variation in top–down vs. bottom–up control can strongly affect community structure, and understanding this spatial variation may help resolve some of the conflicts among research findings on the controlling processes of marine plant communities. In marine plant communities, spatial variation in top–down vs. bottom–up control has been most thoroughly explored in seagrass communities, where both top–down control by herbivores (White et al., 2011) and bottom–up control by nutrient limitation (Burkholder et al., 2013) vary spatially. This variation may result in population and community level differences. Shoot density, leaf length, shoot size, epiphyte load, and nutrient content can vary more substantially at 10 s than 1000 s of meters (Burkholder et al., 2013; Castejón-Silvo and Terrados, 2012). Hence, top–down and bottom–up processes have been demonstrated to vary on a small-scale spatial.

Researchers on coral reef macroalgae have demonstrated that top–down control by herbivores varies spatially across habitat (Hay et al., 1983), structural complexity (Vergés et al., 2011), and depth (Hay et al., 1983). Bottom–up control via nutrient limitation also varies spatially, though research is more limited; for example, tissue nutrient content can vary between sites (Fong et al., 2001), which has been attributed to spatial differences in nutrient availability. A meta-analysis by Burkepile and Hay (2006) suggests that on coral reefs, nutrient effects are only important when herbivory is reduced. This context dependency of nutrients suggests there may be a spatial pattern where greater nutrient effects are observed in areas of reduced herbivory.

Spatial differences in macroalgal palatability may be a result of spatial differences in herbivore pressure and nutrient availability. In temperate systems, algae collected inshore can be more palatable to grazers than algae collected offshore (e.g. Bolser and Hay, 1996; Taylor et al., 2003). Bolser and Hay (1996) found a difference in chemical defense between the two sites and suggest that this effect may be due to spatial differences in grazing pressure because macroalgae experimentally exposed to grazers increased chemical defenses (e.g. Pavia and Toth, 2000). Though, there is evidence that macroalgal palatability may vary spatially due to differences in grazing and perhaps nutrient availability, experimental evidence is that top–down and bottom–up process vary spatial is still needed.

In this study, I test the effects of herbivore exclusion and nutrient addition at an inshore and offshore site using a fully crossed design to illuminate both main effects and the interaction of these controllers on an assembled macroalgal community. I conducted this experiment at an inshore and offshore site separated by 20 m

* Tel.: +1 8184569168; fax.: +1 8058933998.
E-mail address: cat.fong@lifesci.ucsb.edu

2. Experimental

I conducted two experimental manipulations 12 days and 20 m apart to quantify inshore vs. offshore differences in the processes controlling coral reef macroalgal communities. The offshore site was 30 m from the reef edge while the inshore site was 50 m from the reef edge. I manipulated herbivory with fish exclosures and nutrients with slow release fertilizer additions. Research was conducted at the University of California's Gump South Pacific Research Station on the western fringing reef of Cook's Bay in Moorea, French Polynesia. One set of manipulations was conducted 30 m from the reef edge while the other was 50 m from the reef edge, which were at ½ and 1 m depths, respectively.

I surveyed the benthos for macroalgae on hard bottom substrate and herbivorous fish densities at my 2 study sites to compare the benthic macroaglae and fish communities between the inshore and offshore site. I used a 1-m^2 quadrat with 81 points for the point intercept technique to quantify percent hard bottom. Also using the point intercept technique, I then calculated percent cover of macroalgae (algae taller than 1 cm) on hard surfaces. The benthos was surveyed randomly along a 30 m transect horizontal with respect to the reef edge at 5 points (at 30 m from reef edge, $n = 10$; at 50 m from reef edge, $n = 14$). Benthic surveys were conducted on 26 May 2010 and 29 May 2010. All herbivorous fish were counted within a 25×2 m belt transect, including fish in the water column above the reef. Fish were categorized as either Scaridae or Acanthuridae, the major grazing families on this reef (at 30 m from reef edge, $n = 10$; at 50 m from reef edge, $n = 10$). Fish surveys were conducted throughout the experimental dates between 1000 h and 1400 h.

I assembled communities of macroalgae and manipulated both herbivory and nutrient addition to measure top–down and bottom–up processes on macroalgal communities. I assembled communities of the 4 most common species of macroalgae on this reef, putatively *Padina boryana* (Thivy), *Halimeda opuntia* (L. J.V.Lamouroux), *Galaxaura divaricate* (synonym to *G. fasciculata*) (L. Huisman & R.A.Townsend), and *Dictyota bartayresiana* (J.V.Lamouroux). These four species have been successfully used in artificial assemblages in mesocosms to determine effects of nutrient additions (Fong and Fong, 2014). I collected macroalgae from the same location in the field, sorted them by species, and cleaned algal thalli of all sediment and epiphytes. I then spun macroalgae for 1 min in a salad spinner to remove excess water. I weighed thalli into 5 g bundles for a total weight of 20 g and attached them to 15×15 mesh experimental units with cable ties.

Using a full factorial design, I crossed five levels of nutrient treatment with two levels of herbivory treatment for a total of ten treatment combinations. I replicated each treatment combination 5 times for a total of 50 experimental units. My nutrient treatments were 0, 5, 10, 15, and 20 grams of Osmocote (19% N, 6% P) encased in a mesh bag secured to the bottom of each experimental unit. Gil et al. (2013) demonstrated successful enrichment at these levels on a nearby reef. Experimental units were placed a minimum of 1 m apart to minimize the effect of nutrient diffusion between treatments. My two levels of herbivory were open and closed exclusion cages constructed with 1 cm mesh to partition the effects of large herbivores and small mesograzers. This size mesh is comparable to grazer exclusion cages used in other studies (for example, see Carpenter, 1986). Cages were 20 cm tall cylinders with a 15 cm diameter, which were attached to the mesh with the assembled macroalgal community. Experimental units were deployed flush to the substrate and scrubbed every other day to remove fouling. After 10 days, experimental units were retrieved from the field and macroalgae were sorted and weighed as before. Final weights were log transformed to meet assumptions and used for statistical analysis.

I analyzed data from each site with a 2-factor MANOVA with caging and nutrient addition as fixed factors as species response in my assembled communities cannot be considered independently. Significant MANOVAs were followed with a 2-factor ANOVA with caging and nutrient addition as fixed factors. When data associated with a main effect consisted exclusively of complete loss, I dropped that factor (e.g. 'uncaged') and conducted a 1-factor ANOVA.

Surveys indicated that community composition shifted to an increase in macroalgae at the site further from the reef edge. To understand differences in community structure, I conducted the same experiment at each location 12 days apart; the offshore experiment occurred from 2 April 2010 to 12 April 2010 and the inshore experiment occurred from 14 April 2010 to 24 April 2010. Data will not be compared statistically to avoid temporal psuedoreplication; thus, it is impossible to separate spatial and temporal effects. However, this study was conducted over a 30-day period in one season in a relatively constant tropical system and the two periods had no significant differences in temperature (t-test, $p = 0.968$), solar radiation (t-test, $p = 0.472$) or rainfall (t-test, $p = 0.775$). Additionally, observed tides in Moorea are remarkably small and high tide remains constant at noon throughout the tidal cycle (Hench et al., 2008).

3. Results

Fish and benthic communities varied between the inshore and offshore sites. The offshore site had 3 times as many acanthurids as scarids (∼3 vs. ∼1 m^{-2}) while no fish observed in surveys of the inshore site. The offshore site was dominated by *H. opuntia* and *Galaxaura divaricata* and had no *P. boryana* or *D. bartayresiana*. *H. opuntia* occupied 10.4 ± 3.9 SE % of the hard benthos while *G.*

Table 1

Summary of statistical analyses.

Offshore				
MANOVA- All species	Whole model			$p < 0.0001$
	Nutrients			$p = 0.0608$
	Herbivory			$p < 0.0001$
	Interaction			$p = 0.0199$
ANOVA- Individual species		df	Sum of squares	p value
Galaxaura divaricata	Nutrients	4	0.763	$p = 0.9774$
	Cage	1	1.68	$p = 0.3251$
	Nutrients × cage	4	2.61	$p = 0.8179$
Halimeda opuntia	Nutrients	4	13.9	$p = 0.1857$
	Cage	1	0.064	$p = 0.8636$
	Nutrients × cage	4	9.36	$p = 0.3731$
Padina boryana	Nutrients	4	22.0	$p = 0.2304$
Dictyota bartayresiana	Nutrients	4	29.3	$p = 0.0457$
Onshore				
MANOVA- All species	Whole model			$p = 0.0011$
	Nutrients			$p = 0.5378$
	Herbivory			$p = 0.0003$
	Interaction			$p = 0.8804$
ANOVA- Individual species		df	Sum of squares	p value
G. divaricata	Nutrients	4	1.13	$p = 0.8830$
	Cage	1	0.049	$p = 0.8235$
	Nutrients × cage	4	1.59	$p = 0.8018$
H. opuntia	Nutrients	4	0.344	$p = 0.9381$
	Cage	1	0.049	$p = 0.7388$
	Nutrients × cage	4	0.285	$p = 0.9555$
P. boryana	Nutrients	4	22.6	$p = 0.0710$
	Cage	1	51.5	$p < 0.0001$
	Nutrients × cage	4	6.96	$p = 0.5826$
D. bartayresiana	Nutrients	4	0.234	$p = 0.9689$
	Cage	1	6.08	$p = 0.0006$
	Nutrients × cage	4	2.49	$p = 0.2421$