CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

THE EFFECTS OF WATER FLOW AND SEDIMENTATION ON INTERACTIONS
BETWEEN MASSIVE *PORITES* AND ALGAL TURF

A thesis submitted in partial fulfillment
of the requirements for the degree of
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By

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Abstract

THE EFFECTS OF WATER FLOW AND SEDIMENTATION ON INTERACTIONS BETWEEN MASSIVE *PORITES* AND ALGAL TURF

By

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Interactions between scleractinian corals and benthic algae can be an important process structuring coral reef communities. The effects of algae on corals and vice versa are not fixed and may be influenced by abiotic factors such as sedimentation, a process often underlying reef degradation. In addition, the rate of sedimentation as well as the effects of trapped sediments may be mediated by water flow, which may influence coral-algal interaction dynamics. The first goal of this study was to test the hypothesis that gradients in sedimentation and flow on the fringing reefs and back reefs of the north shore of Moorea, French Polynesia, correlate with gradients in the frequency of massive *Porites*-turf interactions, as well as the outcomes of these interactions. In the back reef, *Porites*-algal turf interaction frequency increased by 73% as sedimentation decreased and flow increased. Along fringing reefs, interaction frequency increased by 97% as sedimentation increased. Results indicated that flow and sedimentation do not interact to influence the frequency or outcome of interactions, but rather exert significant independent effects.

The second goal of this research was to test the separate and joint effects of flow and sedimentation on coral-algal interactions in a controlled laboratory setting. Results

indicated that despite extensive damage to coral tissue across treatments, *Porites* growth as measured by the change in dry weight did not differ across treatments. This led to the hypothesis that massive *Porites* may allocate resources preferentially to the growth of tissues not in direct contact with algal turf, thus accounting for the maintenance of growth rates across treatments.

The third goal, therefore, was to test this hypothesis in the field along gradients of flow and sedimentation, and sedimentation alone, for 1 year. Coral growth was quantified as linear extension in three directions: vertical, and horizontal away from and towards the zone of interaction with algal turf. Results indicated that as sedimentation increased, both vertical extension and horizontal extension adjacent to the interacting algal turf decreased by approximately 80%. In contrast, growth of tissue away from the algal turf interaction doubled as sedimentation rate increased. Overall, these data suggest that massive *Porites* may be able to compensate for the reduction in growth along the zone of interaction by increasing growth rates of tissues away from the interacting turf.

The fourth and final goal was to identify a possible mechanism underlying the effects of sediment trapping by algal turf on corals. The hypothesis that spatial variation in sedimentation at the scale of a coral-algal interaction might be an additional important mechanism by which sediments influence coral-algal interactions was tested. For this study, the relative effects of sediment accumulation along interaction boundaries, on the surface of coral and algal tissue not in direct competition, and all possible location combinations was quantified. Results indicate that the accumulation of sediments along the coral-algal interface reduces the area of coral tissue damaged by 56% when sediments also are present on the non-interacting algal turf surface. Knowledge of how fine-scale

patterns of sediment deposition may affect the competitive outcome of coral-algal interactions has implications for the study of coral-algal dynamics as well as increasing understanding of the relative importance of sediment trapping by algal turf. Together, these results suggest that flow and sedimentation exert significant, individual, direct and indirect effects on interactions between massive *Porites* and algal turf.

Chapter 1

Introduction

Over the past century, coral reefs have been exposed increasingly to anthropogenic stressors including global climate change, overfishing, and pollution, resulting in an unprecedented decline in live coral cover worldwide (Hughes et al. 2003, Bellwood et al. 2004). An important process in the degradation of coral reefs is the shift from a coral-dominated to an algae-dominated state, known as a coral-algal phase shift (Done 1992, McCook et al. 2001). Coral and macroalgae are major benthic components of coral reefs and interactions between the two groups of taxa are a common feature on many coral reefs (Tanner 1995, Haas et al. 2010). Coral and algae are thought to compete for access to benthic substrata and light via a suite of mechanisms including overgrowth, shading and abrasion of corals by algae, allelopathy, and epithelial sloughing and mucus secretion (reviewed in McCook et al. 2001).

Of the few direct experimental tests for coral-algal competition, most studies demonstrate negative impacts of algae on corals but the effects are inconsistent and vary in magnitude. For example, most studies report bleached or dead corals in areas in contact with algae (Hughes 1989, Coyer et al. 1993, Tanner 1995), reduced coral growth (Miller and Hay 1996, Miller and Hay 1998), or no effect of algae on coral survival (Tanner 1995). Some studies have demonstrated that corals can overgrow algae (Bak et al 1977, McCook 2001) and in some cases algae can provide a settlement cue and induce metamorphosis of coral larvae (Heyward and Negri 1999). In one case, algae protected corals from bleaching by providing shade under high light conditions (Jompa and McCook 1998). Thus, although corals and algae may be competing for space and this

competition may explain algal overgrowth when corals are damaged or suffer mortality, algae may not outcompete corals directly (McCook et al. 2001). It is accepted generally that coral tissue damage and algal overgrowth might not indicate algal competitive superiority, but rather the competitive exclusion of algae from areas of healthy coral tissue (de Ruyter van Steveninck et al. 1988, McCook 2001).

Both corals and algae are required to maintain a healthy reef ecosystem as both provide critical habitat and food for a variety of marine organisms. However, some coral reefs are becoming increasingly dominated by benthic macroalgae due to anthropogenic disturbances that promote algal overgrowth of coral tissue (Birrell et al. 2008, Hughes 1994, Hughes et al. 2007, Knowlton & Jackson 2008, McCook et al. 2001). The ability of algae to outcompete or colonize corals thus may require the suppression of coral competitive ability following either an acute or chronic stressor, or a combination of stressors.

Of the few direct experimental tests of coral-algal competition following a disturbance, many have focused on reefs exposed to terrestrial runoff in the form of nutrients, pollutants, and sediments (McCook 2001, Jompa and McCook 2002, Nugues and Roberts 2003, Birrell et al. 2005, Haas et al. 2009). Carbonate and terrigenous sediments have widespread effects on coral settlement, recruitment, and reproduction and have been implicated as a major cause of reef degradation worldwide (Rogers 1990, Gilmour 1999, Wilkinson 2000, Fabricius et al. 2003). In contrast, studies of the effects of sediment on algae, such as filamentous algal turf, point to the enhancement of competitive ability through a process known as sediment trapping, resulting in the smothering and overgrowth of corals as well as decreased coral recruitment (Steneck

1997, Nugues and Roberts 2003, Birrell et al. 2005). The few studies directly examining the relationship between coral, algae, and sediments have reported conflicting results, from synergistic negative effects of sediments and algae on coral, to coral competitive superiority in areas of increased sedimentation (McCook 2001, Nugues and Roberts 2003). Sediments may exert significant direct and indirect effects on coral-algal interactions by (1) damaging or killing coral tissue that may indirectly lead to algal overgrowth of the newly opened space, or (2) by directly promoting algal overgrowth of live coral tissue. In addition, the few studies of the effects of sedimentation on coral-algal interactions reported variability in current velocities and directions, which may affect sediment delivery as well as mediate interactions between sediment-laden algal turf and coral. Therefore it is likely that the effects of sedimentation on coral-algal interactions are not fixed but may be dependent on other physical factors such as water flow.

The effects of water flow on the ecology of corals and algae include changes in growth (Jokiel 1978), distribution (Vosburgh 1977), and recruitment (Sammarco and Andrews 1989, Abelson and Denny 1997). In addition, primary production, respiration, and nutrient uptake of corals and algae have been shown to increase with increasing flow (Patterson et al. 1991, Atkinson and Bilger 1992, Genin and Karp 1994, Thomas and Atkinson 1997, Bruno and Edmunds 1998, Carpenter and Williams 2007). For example, under increased sea surface temperatures and irradiance, increased flow may facilitate the recovery of coral symbiodinium by enhancing mass-transfer rates of gases and nutrients (Nakamura et al. 2003). One study that investigated the effects of flow on the interactions between corals found that strong currents deflect the tentacles of aggressive corals and

may enhance the rate of tissue recovery by individuals damaged by more aggressive corals (Genin et al. 1994).

Currently, there have not been any studies directly testing the effects of water motion or sedimentation on coral-algal interactions. In fact, one only can speculate about the outcome of interactions from experiments involving either flow or sedimentation separately when in nature, rates of sedimentation may be highly dependent on the prevailing flow regime. In addition, increased flow may modify the effects of sediments entrained on the coral and/or algal surface through reductions in the diffusive boundary layer, thereby enhancing mass-transfer of solute, reducing hypoxia or hyperoxia, and diluting products of microbial activity (Weber 2009, Wangpraseurt et al. 2012). Therefore, it is essential to consider the separate and interactive effects of flow and sedimentation on coral-algal interactions.

The combined effects of flow and sedimentation on the interactions between coral and algae most likely will vary with flow speed and sediment load. For example, in coastal environments exhibiting high sediment input and relatively low flow, the competitive ability of corals may be reduced as a result of turbidity effects on light capture, direct smothering by sediments, and the alteration of chemical microenvironments (Fabricius 2005). Conversely, in areas of high flow where resuspension and transport of sediments reduces the effects of sedimentation, corals most likely will be favored as flow increases the uptake of nutrients and has the potential to remove or damage some competitive macroalgal species. In the present study, a series of field and laboratory experiments therefore were designed to quantify the effects of flow and sedimentation on interactions between coral and algae.

First, surveys were conducted to quantify coral-algal interaction frequencies and to make predictions of interaction outcomes along flow and sedimentation gradients on the north shore of Moorea, French Polynesia. In the field, water flow often varies over gradients of reef rugosity or with distance from areas of high wave action (Roberts and Suhayda 1983, Hearn et al. 2001, Lowe et al. 2005) while sedimentation rates often change with distance from a point source such as a stream or river (Randall and Birkeland 1978). Using natural, continuous flow and sedimentation gradients in the field allowed for an *in situ* test of the hypothesis that gradients in flow and sedimentation correlate with gradients in coral-algal interaction dynamics and benthic community composition. However, gradients in flow and sedimentation likely exist concurrently with gradients in nutrients, temperature, and herbivory, possibly confounding the effects of flow and sedimentation. Therefore, a laboratory experiment was designed to tease apart the separate and interactive effects of flow and sedimentation on the amount of *Porites* tissue damaged when in contact with algal turf.

The prevalence of massive *Porites* along fringing reefs exhibiting high sediment input and extensive colonization by algal turf has been well-documented, suggesting that *Porites* may be relatively robust to sedimentation and overgrowth by algal turf (Highsmith 1980, Barnes and Lough 1999). McCook (2001) showed that growth rates of *Porites lobata* in contact with algal turf increased with increasing terrestrial sediment and nutrient input. This led to the hypothesis that massive *Porites* may be able to allocate resources preferentially to increase the growth of tissues not in direct competition with algal turf, allowing it to maintain growth rates under increasing sedimentation. To test this hypothesis, interactions between massive *Porites* and mixed algal turf were

established for 1 year along gradients of flow and sedimentation and sedimentation alone on the north shore of Moorea, French Polynesia to quantify the patterns in *Porites* linear extension.

To better understand the mechanisms underlying the phenomenon of sediment trapping by algal turf, sediment samples were collected from various surfaces of coral and turf algae engaging in direct interactions. Repeated observations of unequal sediment accumulation on these surfaces led to the hypothesis that the mechanism behind the effects of sediment trapping on *Porites*-turf interactions is the accumulation of sediment along interaction margins rather than elsewhere on the turf surfaces not in direct competition with coral. This led to questions regarding the importance of spatial variation in sediment accumulation at the scale (cm) of coral-algal interactions, and further, whether this phenomenon might help explain how sediment trapping by algal turf promotes overgrowth of corals. Therefore, a second laboratory experiment was conducted to quantify the effects of spatial variation in sedimentation on the area of coral tissue damaged when in contact with algal turf.

Together, these studies seek to elucidate the connections between coral-algal interactions, a relatively small-scale biological process, and reef-scale forcing by flow and sedimentation by: 1) quantifying the abundance and diversity of coral-algal interactions along gradients of flow and sedimentation, and 2) using manipulative field and laboratory experiments to further elucidate the relationship between flow, sedimentation, and massive *Porites*-algal turf interactions.

Chapter 2

The separate and interactive effects of flow and sedimentation on the frequency and outcomes of massive *Porites*-algal turf interactions

Introduction

Competition for space and light among sessile benthic organisms is a key process structuring coral reef communities (Benayahu and Loya 1981, Lang and Chornesky 1990, Miller 1998, Karlson and Cornell 1999, McCook 1999). Coral and macroalgae are major benthic components of coral reefs and are thought to engage in competitive interactions via a suite of mechanisms including overgrowth, shading, abrasion, allelopathy, and epithelial sloughing and mucus secretion (reviewed by McCook et al. 2001). Until recently, it was thought that increased coral mortality accompanied by declining coral abundance was the direct result of competition with algae and subsequent overgrowth. It now increasingly is understood that algal overgrowth of corals is not necessarily the cause of coral mortality but rather may be a consequence of coral tissue damage or mortality following an external disturbance (McCook et al. 2001).

Many studies of coral-algal competition following a disturbance have focused on areas exposed to terrestrial runoff in the form of nutrients, pollutants and sediments (McCook 2001, Jompa and McCook 2002, Nugues and Roberts 2003, Birrell et al. 2005, Haas et al. 2009). Sedimentation in particular is considered a major cause of coral reef degradation through direct effects on coral reproduction, settlement and recruitment (Rogers 1990, Gilmour 1999, Wilkinson 2000, Fabricius et al. 2003, Fabricius 2005). By contrast, studies of the effects of sediment on algae, such as filamentous turf, point to the

enhancement of competitive ability through a process known as sediment trapping, resulting in the smothering and overgrowth of corals as well as decreased coral recruitment (Steneck 1997, Airoidi 1998, Nugues and Roberts 2003, Birrell et al. 2005). The few studies directly examining the relationship between coral, algae, and sediments have reported conflicting results, from synergistic negative effects of sediments and algae on coral, to coral competitive superiority in areas of increased sedimentation (McCook 2001, Nugues and Roberts 2003). Even where sedimentation facilitated algal overgrowth, coral tissue loss was small compared to loss due to sediment smothering and burial in the absence of an algal competitor. In addition, McCook 2001 and Nugues and Roberts 2003 reported variability in current velocities and directions, which may affect sediment delivery as well as mediate interactions between sediment-laden turf and coral. Therefore it is likely that the effects of sedimentation on coral-algal interactions are not fixed, but may be dependent on other physical factors such as water flow.

In general, increased water flow promotes the resuspension and transport of sediments, while low flow promotes sediment deposition and trapping (Abelson and Denny 1997, Steneck 1997, Birrell et al 2008). In the absence of sediments, primary production, respiration, and nutrient uptake by corals and algae have been shown to increase with increasing flow (Jokiel 1978, Patterson et al. 1991, Atkinson and Bilger 1992, Genin and Karp 1994, Thomas and Atkinson 1997, Bruno and Edmunds 1998, Carpenter and Williams 2007). Thus far, the potentially complex and interactive relationship between flow, sedimentation and the outcome of coral-algal interactions has not been investigated. In fact, speculation about the outcomes of interactions can only be derived from single-factor studies involving either flow or sedimentation in isolation.

Because the effects of sedimentation are likely to vary in different flow regimes, it is essential to consider the interactive effects of these important physical forces on coral-algal interactions.

In the field, flow often changes over gradients of reef rugosity or with distance from breaking waves (Roberts and Suhayda 1983, Hearn et al. 2001, Lowe et al. 2005) while sedimentation rates often change with distance from a point source such as a stream or river (Randall and Birkeland 1978). For this study, surveys of coral-algal interactions and predicted outcomes were conducted along flow and sedimentation gradients on the north shore of Moorea, French Polynesia. Using natural, continuous gradients in the field allowed for an *in situ* test of the hypothesis that gradients in flow and sedimentation correlate with gradients in coral-algal interaction dynamics and benthic community composition.

Secondly, in order to better understand the mechanisms underlying the effects of sediment trapping by algal turf, sediment samples were collected from various surfaces of massive *Porites* and turf algae in direct competition with one another. Repeated observations of unequal sediment accumulation on these surfaces led to the hypothesis that the mechanism behind the effects of sediment trapping on *Porites*-turf interactions may be the localized accumulation of sediment along interaction margins rather than accumulation elsewhere on the turf surfaces not in direct competition with coral.

Methods

Site Selection

In May 2010, three fringing reef and three back reef sites were chosen on the north shore of Moorea in order to sample gradients of flow and sedimentation (back reef) and gradients of sedimentation alone (fringing reef). On the north shore, unidirectional water flow moving over the reef dissipates with proximity to shore, where then it is redirected along shore at relatively constant speeds and back out to the open ocean through reef passes (Hench et al. 2008). In the back reef, this results in carbonate sediments are carried towards shore with the flow gradient, while along the fringing reefs, terrestrial sediments deposited near shore are carried downstream creating a gradient of terrestrial influence. For the purposes of this study, the three back reef sites were selected to sample a continuous reef along a hypothesized flow and sedimentation gradient, while the fringing reef sites were chosen based on proximity to sources of terrigenous sediments. Water flow along shore at these three sites is thought to remain relatively low and constant across the sedimentation gradients of interest (Alldredge, unpublished data, personal communication).

Relative Sedimentation and Flow Rates

At each of three sites within the fringing and back reef habitats, a 50-meter permanent transect was established at one to two meters depth and was subdivided into five, 10-meter zones, using rebar stakes to demarcate the borders of each zone. Bordering each zone at 0, 10, 20, 30, 40, and 50 meters, clod cards and sediment traps were deployed to measure relative flow and sedimentation rates. While clod cards do not

measure actual flow rates, the relative dissolution of clod cards provides an estimate of relative flow (Doty 1971, Jokiel and Morrissey 1993, Thompson and Glenn 1994).

Measurements at the upstream and downstream end of each 10m zone then were averaged to yield an average clod card dissolution and sedimentation rate for each zone.

Sediment traps were constructed according to the following MCR-LTER protocol (Alldredge, 2012), using PVC pipe with a 3:1 aspect ratio (5.2 cm internal diameter, 17.5 cm high) glued to a Plexiglas base and weighted down to the substratum with a lead weight. Traps were placed on the benthos every 10 m directly underneath the transect line for 24 hours. Sedimentation rates were estimated by vacuum filtering a 15-ml subsample from each trap onto pre-weighed 1- μ m pore size, 47-mm Whatman polycarbonate filters. Samples were dried at 70- $^{\circ}$ C overnight and then weighed to the nearest milligram.

Clod cards were constructed using the methods described in Thompson and Glenn (1994). Plaster of Paris was mixed with water and allowed to solidify in standard ice cube trays for 3 days at which point the clod cards were removed and allowed to dry before being sculpted to create a uniform shape and weight. Clod cards were attached to rebar stakes that were affixed to the reef benthos directly underneath the transect line. Because flow rates differed significantly between the fringing and back reef habitats, clod cards were deployed for 24 hours on the fringing reefs and for approximately seven hours in the back reef. The height of the clod cards above the benthos corresponded to the height of the sediment traps, approximately 17.5 cm above the benthos.

Acoustic Doppler Profilers (Nortek Aquadopp ADPs) were placed at the upstream and downstream end of each of the three back reef sites for seven hours every two weeks for six weeks to supplement the clod card data and compare dissolution rates with

measured flow speeds. ADPs were placed on the bottom at approximately two meters depth and at least 1.5 meters from surrounding structures. ADPs recorded depth averaged flow speeds every 60 seconds beginning 0.20 meters above the benthos. The number of 0.1-meter bins was adjusted to account for differences in depth of the benthos along the transects at each site, ranging from 13 to 17 bins. Because data obtained from clod cards indicated that flow along the fringing reefs was relatively low and constant, ADP data were not collected at these sites.

Clod cards and sediment traps were deployed every two weeks for a period of six weeks during the austral winter between May and July of 2010. A three-way ANOVA was used to test for an effect of sampling date (with site and zone as additional fixed factors) but after it was determined that there was no statistical difference between sampling dates, data were pooled to yield an average clod card dissolution and sedimentation rate within each zone for each of the three back reef and fringing reefs.

Benthic Composition, Interaction Frequencies, and Interaction Outcomes

Because the frequency of an interaction between massive *Porites* and turf algae may simply be a reflection of the abundance of the interacting taxa, benthic composition was estimated from surveys along each of the three fringing and back reef transects in order to estimate interaction frequency relative to the abundance of the interacting components. These interaction data were used to predict the outcome of the observed interactions. Three replicate 0.25 m² quadrats were divided into 25 subplots, each 10 x 10 cm. In each of the 25 subplots, the dominant taxon occupying > 50% of the subplot area was recorded including all hermatypic corals identified to species where possible, benthic

macroalgae genera, turf algae, sand, bare coral rock and rubble. The number of squares occupied by each component was summed and divided by 25 to yield percent cover, which then was averaged across replicates within each zone for each of the three back reef and fringing reefs. The frequencies of various coral-algal interactions were estimated by determining the predominant coral-algal interaction in each subplot according to the length of the interaction perimeter, counting the number of subplots dominated by each coral-algal interaction type and dividing by the total area of the quadrat to yield an estimate of the number of interactions per square meter of benthos. Results from replicate quadrats were averaged within each zone for all 3 back reef and fringing reef sites.

Interaction data then were used to predict the outcome of the observed interactions. Within each subplot, the predominant coral-algal interaction was scored as an algal win based on the presence of bleached coral tissue, overgrowth by algae, or signs of abrasion. Interactions lacking these indicators were scored a coral “win.” The rationale for the scoring method is that in the absence of algal colonization or coral tissue damage, corals generally are thought to be superior competitors to algae (reviewed by McCook et al. 2001). The percentage of algal “wins” was determined by dividing the number of wins by the total number of interactions and these results were averaged within each zone for each of the three back reef and fringing reefs.

Sediment Accumulation

Sediment trapping has been shown to occur primarily on mixed filamentous algal turf (Steneck 1997) and because turf interactions with massive *Porites* spp. dominated the fringing reefs, only these interactions were sampled. In addition, because data from

sediment traps indicated that sedimentation was much greater on the fringing reefs than in the back reef, sediments were collected from massive *Porites*-algal turf interactions at the fringing reef sites only. Three massive *Porites*-turf interactions were selected within each zone after which sediment samples were collected from the surface of massive *Porites*, turf, and along the margins of their interaction. A 1-cm² sampling area was cleared of all sediment by using compressed air from a scuba tank to dislodge the sediments while minimizing disruption to the turf. Any remaining sediments were removed with a syringe. The areas then were sampled 24 hours later using a syringe to extract all the sediments that had accumulated. Sediments were sampled along the interaction margin and 2 cm away on the adjacent coral and algal surfaces. Sediments were filtered and weighed using the methods described previously.

Statistical Analyses

To quantify the flow and sedimentation gradients in the back reef and the sedimentation gradients along the fringing reefs, separate two-way ANOVAs were utilized with site and zone as fixed factors. If either clod card dissolution or sedimentation rates did not vary significantly between zones, they were not included as covariates in subsequent analyses. To test for a relationship between flow and sedimentation rate among sites, separate ANCOVAs were conducted for each habitat to test for an effect of site (categorical) and clod card dissolution (covariate) on the rate of sedimentation.

Back reef interaction frequency and outcome data were analyzed using ANCOVA to test for effects of site (categorical), clod card dissolution (covariate), and sedimentation

(covariate). All non-significant interactions ($p > 0.05$) with the covariates were sequentially eliminated from the model before testing any remaining significant interactions and main effects. In addition, if water flow significantly affected the rate of sedimentation, the residuals were used in the analyses of interaction frequencies and predicted outcomes. This allowed for analyses of the separate and interactive effects of flow and sedimentation while excluding the effects of flow on the rate of sedimentation itself. Fringing reef interaction frequency and outcome data were also analyzed using ANCOVA but clod card dissolution was removed from the model after it was determined that flow did not vary among zones.

Separate regressions were used to determine the extent to which the frequency of interactions in each habitat was explained by the product of the proportional abundances of *Porites* and algal turf. Lastly, sediment accumulation was analyzed using ANCOVA with surface (*Porites*, turf, or interaction) as the categorical variable and the sedimentation rate as a covariate. Data were found to meet the assumptions of normality and homogeneity of variances as assessed using Shapiro-Wilk's and Levene's tests, respectively.

Results

Flow and Sedimentation

Along the fringing reef sites, average sedimentation rates increased monotonically from 4.5 to 12 mg cm⁻² d⁻¹ with proximity to the sediment sources, while clod card dissolution was relatively constant, averaging ~ 9% dissolution over 24 hours. Sedimentation differed significantly across zones for all three sites (ANOVA, $F_{4,10} =$

33.18, $p < 0.0001$, Fig. 1C), while the percent dissolution of clod cards was not significantly different ($F_{4,10} = 2.19$, $p = 0.14$, Fig. 1A). The sedimentation gradients therefore were not confounded by gradients in water flow.

For the back reef sites, both clod card dissolution and sedimentation rates differed significantly across zones, however the gradients observed were not linear from the reef crest towards shore. Clod card dissolution rates ranged from 13 to 25% ($F_{4,10} = 13.32$, $p < 0.001$; Fig. 1B) over seven hours. Zones furthest upstream, closest to the reef crest averaged 18% clod card dissolution, while the upstream ADP recorded depth-averaged velocities of $\sim 0.14 \text{ m s}^{-1}$. Downstream clod card dissolution averaged 13% with ADP depth-averaged velocities of $\sim 0.11 \text{ m s}^{-1}$. Sedimentation ranged between ~ 3.8 and $7.7 \text{ mg cm}^{-2} \text{ d}^{-1}$ ($F_{4,10} = 19.47$, $p < 0.001$; Fig. 1B), with higher sedimentation in zones that experienced the lowest flow.

The relationship between clod card dissolution and sedimentation differed between the fringing reef and back reef. For both habitats, there was no significant interaction between site and clod card dissolution (ANCOVA, Back reef: $F_{2,9} = 0.98$, $p = 0.41$; Fringing reef: $F_{2,9} = 1.07$, $p = 0.38$) indicating that the effects of flow on sedimentation were consistent among sites. In the back reef, there was a significant effect of flow on the rate of sedimentation ($F_{1,11} = 58.26$, $p < 0.001$; Fig. 2B), such that with increasing flow, sedimentation decreased. Along the fringing reef, however, flow did not significantly affect rates of sedimentation ($F_{1,11} = 0.051$, $p = 0.82$; Fig 2A).

Benthic Composition

Over 70% of the benthos in both habitats was dominated by massive *Porites* spp. and mixed algal turf so only the abundances of these taxa were analyzed. Along the fringing reefs, the lack of variation in flow meant that it could be eliminated as a covariate in all fringing reef analyses, therefore site and sedimentation were included as the categorical variable and covariate, respectively. Massive *Porites* abundance decreased significantly with increasing sedimentation (ANOVA, $F_{1,9} = 82.39$, $p < 0.001$, Fig. 3a) while the abundance of turf increased significantly with increasing sedimentation (ANOVA, $F_{1,9} = 127.56$, $p < 0.001$, Fig 3b).

In the back reef, the significant inverse relationship between flow and sedimentation rate allowed for the use of the residuals from that regression in the remaining back reef analyses. In the back reef, massive *Porites* abundance increased significantly with increasing flow (ANCOVA, $p < 0.001$, Fig. 4a), while turf abundance decreased ($p = 0.013$, Fig. 4b). Sedimentation, however, did not have a significant effect on both *Porites* ($p = 0.53$) and turf abundance ($p = 0.67$).

Interaction Frequency

Along fringing reefs, interactions between massive *Porites* and turf algae increased significantly with increasing sedimentation, ranging from 0 to 69 interactions per m² (ANCOVA, $p < 0.001$, Table 1, Fig. 5a). This relationship was consistent across sites ($p = 0.730$). In the back reef, *Porites*-turf interaction frequency increased significantly with decreasing flow ($p = 0.00013$, Fig. 6a, Table 2) ranging from 14 to 52

interactions m^{-2} . In contrast to the fringing reef, interaction frequency was not significantly predicted by sedimentation in the back reef ($p = 0.72$, Table 2).

Interaction Frequency as a Function of Porites and Algal Turf Abundances

In both the back reef and fringing reef, the product of the proportional abundances of *Porites* and algal turf did not significantly predict the frequency of *Porites*-algal turf interactions (Back reef: $p = 0.36$; Fringing reef: $p = 0.68$).

Interaction Outcomes

For fringing reefs, the percentage of predicted turf “wins” differed significantly among sites (ANCOVA, $p = 0.0021$, Table 1), but increased significantly with increasing sedimentation among all sites from 0% to 100% ($p < 0.001$, Fig. 5b, Table 1).

In the back reef, flow was the only factor to significantly affect the percentage of predicted turf “wins” (ANCOVA, $p = 0.03$, Fig. 6b, Table 2), such that with increasing flow there was a reduction in the percentage of turf “wins”, from 95% to 37%.

Sediment Accumulation

There was a significant effect of sedimentation rate on the amount of sediment accumulated on the surface of massive *Porites*, algal turf, and along the margin of their interactions (ANCOVA, $F_{2,39} = 23.51$, $p < 0.001$, Table 3, Fig. 7). In general, as sedimentation increased, more sediment was retained along the margin of interactions (6.3 to $15 \text{ mg cm}^{-2} \text{ d}^{-1}$), whereas the least amount of sediment was retained on the surface of massive *Porites* (3.9 to $7.1 \text{ mg cm}^{-2} \text{ d}^{-1}$). Also, the distribution of sediments across the

different surfaces changed with overall sedimentation rate, with the magnitude of differences in sedimentation accumulation becoming more pronounced as reef sedimentation rate increased (Fig. 7).

Discussion

As coral reefs worldwide continue to degrade with persistent anthropogenic impacts, increasingly it is important that research continues to identify the factors and mechanisms that will determine the winners and losers of coral-algal competition. Processes that facilitate coral reef degradation include interactions between corals and algae as well as various abiotic factors such as sedimentation, yet the breadth of potential mechanisms are not well understood. For example, sedimentation has been implicated as a major cause of reef degradation, yet data presented here suggest that flow is a significantly better predictor of both massive *Porites*-algal turf interaction frequencies and outcomes than sedimentation.

Interestingly, flow and sedimentation do not interact to influence the frequencies of massive *Porites*-algal turf interactions, but rather, each exerts significant independent effects. Flow, however, was shown to significantly affect the rate of sedimentation, suggesting a separate, indirect effect of flow on massive *Porites*-algal turf interactions. These results are supported by previous observations of coral-algal competition in the presence of external disturbances or chronic stressor/s that reduce the ability of corals to competitively exclude algae (Banner 1974, Birkeland 1977, Wittenberg and Hunte 1992, Steneck et al. 1994, Connell et al. 1997, McCook 2001). In fact, in studies where experimental damage to coral tissue was inflicted in the absence of an abiotic or biotic

stressor, coral tissue regenerated and overgrew algae that initially had colonized the lesions, suggesting competitive superiority of otherwise healthy coral tissue (Meesters and Bak 1993, Meesters et al. 1994, 1997, van Woesik 1998). While explicit tests of the physiological effects of sedimentation and low flow on massive *Porites* were not conducted, their separate negative effects are well-documented and suggest that reductions in metabolism, growth, and survival could have major implications for coral-algal competitive outcomes (Dodge & Vaisnys 1977, Dallmeyer et al. 1982, Dodge & Lang 1983, Hubbard & Scaturo 1985, Tomascik & Sander 1985, Hubbard et al. 1987, Fabricius 2005).

The predicted outcomes based on the massive *Porites*-algal turf interactions surveyed here was determined based on visible evidence of coral tissue damage resulting specifically from algal colonization. There are many limitations to this method, as the trajectory of interactions are likely not fixed over time, with the potential for seasonal variation in interaction dynamics (Haas et al. 2009). In the back reef, flow was the only factor to significantly affect the outcome of interactions such that increased flow significantly reduced the percentage of turf “wins”. In part, this may be due to the effects of flow on sedimentation rate, but once this effect is removed, the capacity of flow to mediate the relationship between massive *Porites*-algal turf interactions and sedimentation is still significant. Increased flow has been shown to increase the delivery of nutrients, primary productivity, and food capture in addition to enhancing rates of tissue recovery (Dennison and Barnes 1988, Patterson et al. 1991, Atkinson and Bilger 1992). These results emphasize the importance of flow as a physical factor controlling the

dynamics between corals and algae and suggest that the benefits of increasing flow have the potential to significantly counteract the negative effects of sedimentation.

Along fringing reefs in the absence of a flow gradient, sedimentation remains a significant factor affecting the frequencies and predicted outcomes of interactions. Specifically, massive *Porites*-algal turf interaction frequencies as well as the percentage of predicted turf “wins” increased with increasing sedimentation, suggesting a weakening of *Porites* competitive ability against sediment-laden turf algae. Potts (1977) suggested that algae-sediment mats cause localized smothering of coral margins, resulting in increased energy expenditure on sediment clearing rather than resisting algal colonization, resulting in successful algal overgrowth of coral tissue. Similarly, Nugues and Roberts (2003) hypothesized that the energy spent by corals on sediment removal from tissues not in direct competition with algae may reduce the energy available for defense along interaction margins, resulting in decreased growth of corals in contact with algae in areas of high sediment. In fact, Riegl and Branch (1995) demonstrated that with the addition of sediments, coral respiration accounts for ~ 130 % of daily carbon production with 65 % of total respiration allocated to mucus production but only 35 % to general metabolic requirements. Therefore, as filamentous algal turfs respond to increasing sediment accretion by increasing horizontal extension and percent cover (Kendrick 1991, Nugues and Roberts 2003), the ability of massive *Porites* to combat algal overgrowth may be reduced as a result of increased energy expenditure toward the removal of sediments. Still, little is known regarding the mechanism of turf proliferation in areas of high sedimentation whether by overgrowth of damaged or dead coral,

competitive dominance over established coral, or colonization and occupation of empty space.

Algal turfs “trap” and anchor sediments which may facilitate algal overgrowth of some corals (Steneck 1997, Airoidi 1998, Birrell et al. 2005), but the mechanisms of these effects have yet to be determined. One possible mechanism proposed here is the accumulation of sediments along coral-algal interaction margins compared to adjacent non-interacting massive *Porites* and algal turf surfaces. This may be a result of the secretion of coral mucus which when actively or passively removed, may become trapped along margins of interactions with turf algae. Therefore this fine-scale spatial variation in sediment accumulation may be an additional important mechanism by which sediments influence coral-algal interactions. It is unlikely that sediments trapped elsewhere on the algal surface not in direct competition with coral should have an effect on interaction dynamics, thus the term sediment trapping may be too broad and instead, it is the accumulation of sediments at the margin of interaction that has the greatest effect. It is here that coral polyps are in direct contact with algae and with the addition of sediment, the allocation of energy for defense may be reduced in favor of mitigating the effects of sediment. By contrast, where water flow and/or wave action effectively removes or reduces the effect of sediments, the reduction in energy expenditure for cleaning may be re-allocated for defense. Knowledge of how fine-scale patterns of sediment deposition may affect the competitive outcome of coral-algal interactions has implications for the study of coral and algal dynamics as well as increasing our understanding of the relative importance of sediment trapping by algal turf.

While these results may not be applied generally to other interaction types, these data highlight the importance of multiple factor studies of coral-algal dynamics, as the outcome of interactions are likely to be highly context-dependent. Specifically, variation in local, regional, and landscape scale effects of flow and sedimentation may have large implications for coral reef community structure and functioning through their separate direct and indirect effects on coral-algal interactions.

Tables

Table 1. Results of an ANCOVA assessing the effect of site (categorical) and sedimentation rate (covariate) on the frequency of massive *Porites*-algal turf interactions on fringing reefs.

Parameter	Source of Variation	df	MS	<i>F</i>	<i>p</i> -value
Interaction Frequency	Site	2	118.723	1.702	0.227
	Sedimentation rate	1	5234.684	52.388	< 0.001
	Error	11	69.736		
	Site*Sedimentation rate	2	25.860	0.325	0.730
	Error	9	79.486		
Percentage Turf “wins”	Site	2	0.127	11.390	< 0.001
	Sedimentation rate	1	0.616	55.082	< 0.001
	Error	11	0.011		
	Site*Sedimentation rate	2	0.019	2.054	0.184
	Error	9	0.009		

Table 2. Results of a two-way ANCOVA assessing the effect of site (categorical), % clod card dissolution (covariate), and sedimentation rate residuals (covariate) on the frequency of massive *Porites*-algal turf interactions and the percentage of turf wins in the backreef.

Parameter	Source of variation	df	MS	<i>F</i>	<i>p</i> -value
Interaction Frequency	Site	2	0.871	0.018	0.981
	Clod Card (CC) Dissolution	1	1705.028	35.942	< 0.001
	Sedimentation Residuals	1	319.775	6.741	0.721
	Error	10	47.439		
	CC dissolution*Sedimentation Residuals	1	63.664	1.395	0.268
	Error	9	45.636		
	Site*CC dissolution	2	35.943	0.743	0.510
	Error	7	48.405		
	Site*Sedimentation Residuals	2	46.202	0.937	0.451
	Error	5	49.286		
	Site*CC dissolution*Sedimentation Residuals	2	25.354	0.389	0.708
	Error	3	65.241		
Percent Turf “wins”	Site	2	0.128	0.128	0.882
	CC Dissolution	1	8.195	8.20	0.017
	Sedimentation Residuals	1	3.736	3.74	0.082
	Error	10	0.017		
	CC dissolution*Sedimentation Residuals	1	<0.001	0.002	0.967
	Error	9	0.018		
	Site*CC dissolution	2	0.033	2.411	0.160
	Error	7	0.014		
	Site*Sedimentation Residuals	2	<0.001	0.032	0.969
	Error	5	0.019		
	Site*CC dissolution*Sedimentation Residuals	2	0.005	0.178	0.845
	Error	3	0.029		

Figures

Figure 1. Average percent clod card dissolution (A,B) and sedimentation rate (C,D) for each of five, 10-meter zones. Data are means ($\pm$ SE) among three backreef and fringing reef sites ($n = 9$). Also included are average upstream and downstream flow rates ($n = 9$) among three backreef sites (B).

Figure 2. Sedimentation rates as a function of clod card dissolution along three fringing reef (A) and back reef (B) sites.

Figure 3. Percent cover of massive *Porites* (A) and algal turf (B) along a gradient of sedimentation. Data are from three fringing reef sites.

Figure 4. Percent cover of massive *Porites* (A) and algal turf (B) along a gradient of flow. Data are from three back reef sites.

Figure 5. Massive *Porites*-turf interaction frequency (A) and percent turf wins (B) along a gradient of sedimentation. Data are from three fringing reef sedimentation gradients.

Figure 6. Massive *Porites*-turf interaction frequency (A) and percent algal turf wins (B) along a gradient of flow. Data are from three backreef sites.

Figure 7. Sediment accumulation on the surface of massive *Porites*, algal turf, and on the margin of interaction along a gradient of fringing reef sedimentation. Data are from three fringing reef sites.

Chapter 3

The separate and interactive effects of flow and sedimentation on massive *Porites* tissue damage and linear extension when in direct contact with algal turf.

Introduction

Competition between scleractinian corals and benthic algae is a common feature on many coral reefs (Tanner 1995, Haas et al. 2010). Both corals and algae are required to maintain a functioning reef ecosystem as both provide critical habitat and food for a variety of marine organisms. However, some coral reefs are becoming increasingly dominated by benthic macroalgae due to anthropogenic disturbances that promote algal overgrowth of coral tissue (Birrell et al. 2008, Hughes 1994, Hughes et al. 2007, Knowlton & Jackson 2008, McCook et al. 2001). Studies of coral-algal competition following such disturbances raised questions as to whether the presence of algae is the cause or a consequence of coral mortality (McCook et al. 2001). It is now generally accepted that coral tissue damage and algal overgrowth might not indicate algal competitive superiority, but is instead a consequence of coral tissue damage or mortality following a disturbance (McCook et al. 2001). The ability of algae to outcompete or colonize corals thus may require the suppression of coral competitive ability following either an acute or chronic stressor, or combination of stressors.

Sedimentation is an important chronic stressor on coral reefs and currently is considered a major cause of reef degradation worldwide (Wilkinson 2000). Thus many studies of coral-algal competition following a disturbance focus on areas prone to sedimentation (McCook 2001, Jompa and McCook 2002, Nugues and Roberts 2003,

Birrell et al. 2005). Sediments have been shown to reduce coral reproduction, settlement, recruitment and growth (Rogers 1990, Gilmour 1999, Wilkinson 2000, Fabricius et al. 2003, Crabbe and Smith 2005, Fabricius 2005), while studies of the effects of sediment on algae such as filamentous algal turf point to the enhancement of competitive ability through the trapping of sediments, resulting in the smothering and overgrowth of corals as well as decreased coral recruitment (Steneck 1997, Airolidi 1998, Birrell et al. 2005). In nature, however, the effects of sediment on interactions between corals and algae may be mediated by other abiotic factors such as water flow.

In general, increased water flow promotes the resuspension and transport of sediments, while low flow promotes sediment deposition and trapping by algal turf (Abelson and Denny 1997, Steneck 1997, Birrell et al 2008). In the absence of sediments, primary production, respiration, nutrient uptake, and growth of corals and algae increase with flow (Jokiel 1978, Patterson et al. 1991, Atkinson and Bilger 1992, Genin and Karp 1994, Thomas and Atkinson 1997, Bruno and Edmunds 1998). Currently, there have not been any studies directly testing the effects of water motion or sedimentation on coral-algal interaction dynamics. In fact, speculation about the outcome of interactions between coral and algae derives from experiments involving either flow or sedimentation separately when in nature, rates of sedimentation may be highly dependent on the prevailing flow regime. In addition, increased flow may mediate the effects of trapped sediments through the reduction of the coral diffusive boundary layer, thereby enhancing mass-transfer of gases and nutrients, reducing hypoxia or hyperoxia, and diluting products of microbial activity (Weber 2009, Wangpraseurt et al. 2012).

In the field, flow often changes over gradients of reef rugosity or with distance from breaking waves (Roberts and Suhayda 1983, Hearn et al. 2001, Lowe et al. 2005), while sedimentation rates often change with distance from a point source such as a stream or river (Randall and Birkeland 1978). Further, gradients in flow and sedimentation have the potential to result in gradients of reef community structure through effects on coral-algal interactions. Previous studies of coral-algal interactions along gradients of flow and sedimentation suggest that in the field, flow and sedimentation exert significant independent effects on the frequency and predicted outcomes of massive *Porites*-algal turf interactions (Chapter 1). However, gradients in flow and sedimentation likely exist alongside nutrient, temperature, and herbivory gradients, possibly confounding the effects of flow and sedimentation. Therefore, a laboratory experiment was first designed to quantify the separate and interactive effects of flow and sedimentation on the amount of *Porites* tissue damaged when in contact with algal turf.

The large number of massive *Porites* commonly observed along fringing reefs exhibiting high sediment input and extensive colonization by algal turf has been well-documented, suggesting that massive *Porites* may be relatively robust to sedimentation and overgrowth by algal turf (Barnes and Lough 1999, Highsmith 1980). McCook (2001) showed that *Porites lobata* overgrew algal turf on reefs with high terrestrial sediment and nutrient input. This led to the hypothesis that colonies of massive *Porites* may be able to preferentially allocate resources towards the growth of tissues not in direct competition with algal turf, allowing the colony to maintain or even increase growth rates under increasing sedimentation. To test this hypothesis, a second field experiment was designed whereby staged interactions between massive *Porites* and algal turf were maintained for 1

year along gradients of flow and sedimentation, and sedimentation alone, on the north shore of Moorea, French Polynesia to quantify the patterns in *Porites* linear extension across a colony engaged in interactions with algal turf.

Methods

Flume Experiment

A fully-factorial laboratory experiment was designed to test the separate and interactive effects of high versus low flow and the presence or absence of sedimentation on the extent of massive *Porites* tissue damaged when in contact with algal turf. Specific pairwise and *a priori* contrasts were conducted to test the hypotheses that (1) high flow reduces the area of *Porites* tissue damaged when in contact with algal turf, (2) the addition of sediments under low flow results in significantly more damage to *Porites* tissue, and (3) there is no effect of sedimentation on the area of *Porites* tissue damaged when in contact with algal turf under high flow.

The experimental setup was designed to administer constant water flow and sedimentation simultaneously using twelve, half-meter long, half-pipe PVC flumes. The half-pipe design was necessary in order to be able to access the flumes for cleaning and administer sediments. In order to manipulate and maintain constant water flow, three manifolds were supplied with seawater and fitted with 4 valves that controlled the flow of water entering each of 4 flumes. A honeycomb of flow straighteners was placed at the upstream end of each flume to regulate turbulence. At the downstream end, a flow control valve was inserted that was used in conjunction with the upstream valve to control the rate of water flow through each flume (Fig. 1 and 2).

Flow rates were maintained daily using the combination of inflow and outflow control valves to account for variation in the water pressure leaving the seawater filtration system. Flow speeds were determined from Acoustic Doppler Profile data collected in May-July of 2010 from three back reef (high flow) and fringing reef (low flow) sites on the north shore of Moorea, with 0.25 m s^{-1} as the 'high flow' and 0.05 m s^{-1} as the 'low flow'. To measure flow in the flumes, patches of fluorescein dye were introduced at the upstream end of each flume and the amount of time it took to be expelled at the downstream end was recorded, allowing for estimates of flow rates in m s^{-1} . Because this method is relatively imprecise, the volume of water exiting each flume was measured over a period of 10 seconds to provide supplementary estimates of flow rates. Flow rates were recorded every day to ensure maintenance of treatment conditions.

Sediments were collected from the upper 5 cm of a nearby fringing reef (~ 2-m depth) that is exposed to both carbonate and terrigenous sediments. Sediments were filtered to remove larger particles or shell fragments greater than $500 \mu\text{m}$ and isolate smaller grain sand and silt sediments (Weber et al. 2006). To constantly administer sediments, a system of reservoirs and pumps were designed to deliver suspended sediments to individual flumes (Fig. 2). First, a 2,461-liter reservoir was equipped with 3 circulation pumps (Aquaclear 110) that continuously stirred a sediment stock suspension. Every 30 minutes, a timer turned on a pump that delivered this stock suspension to a smaller 76-liter tub that was raised approximately 1.5 m above the flume system to allow the sediment solution to be gravity fed to each flume. The timer controlled the filling of the tub in order to maintain a sediment solution delivery rate of $\sim 20 \text{ mg cm}^{-2} \text{ d}^{-1}$, corresponding to the high sedimentation rates recorded along the fringing reefs described

in Chapter 1. To ensure maintenance of treatment conditions, sedimentation rates were recorded every other day by using Sculpy Putty to attach a 2-cm² piece of astro-turf adjacent to the staged interactions for approximately 1 hour. Sediments then were removed by agitating the astro-turf in a bucket of freshwater. Sedimentation rates were estimated by vacuum filtering each sample onto pre-weighed 1-μm pore size, 47-mm Whatman polycarbonate filters. Samples were dried at 70 °C overnight and weighed to the nearest mg.

Interactions were staged by adjoining massive *Porites* and algal turf-covered coral fragments of similar area (approximately 50 cm² to ideally situate interactions within each flume) with an interaction margin of approximately 2 cm that was consistent across treatments. Corals and algal turfs were collected from the back reef environment to avoid sampling from areas subject to chronic sedimentation, thus reducing the potential for predisposed phenotypic responses of corals to sedimentation (Anthony 2000).

Interactions were held in place and oriented so that the interaction margin ran parallel to the direction of flow using Sculpy Putty that was affixed approximately 20 cm from the downstream end of each flume. The response variables measured included the area of coral tissue damaged as well as the change in *Porites* buoyant mass that was then converted to dry weight. Initial and final photographs of the *Porites* nubbins were analyzed using Image J software to outline the area of bleached coral tissue. After three weeks, *Porites* and algal turf surface area was measured using the foil method (Marsh 1970) to normalize the area of damaged tissue. This design only allowed for three replicates of each of the four treatments in each trial so the experiment was repeated once with each trial lasting 3 three weeks.

Statistical Analyses

A three-way ANOVA was first used to test for an effect of trial on the area of *Porites* tissue damaged across treatments. After it was determined that there was no effect of trial, data were pooled across trials and analyzed using a two-way ANOVA to test for relative differences in *Porites* dry weight as well as the area of damaged tissue using planned pairwise comparisons across treatments. Additionally, *a priori* contrasts were utilized to compare high versus low flow with sediment and no sediment treatments combined. Data met the assumptions of normality and homogeneity of variances as assessed using Shapiro Wilk's and Levene's tests, respectively.

Field Experiment

Three fringing reef and three back reef sites were chosen on the north shore of Moorea, French Polynesia that exhibited gradients in flow and sedimentation (back reefs) and sedimentation alone (fringing reefs) as described in Chapter 1. The three fringing reefs exhibited gradients in sedimentation along shore emanating from either a small river mouth or stream. Fringing reef sites were chosen based on proximity to sources of terrigenous sediments draining from open fields or uninhabited forest. Water flow along shore at these three sites remains relatively low ($< 15 \text{ m s}^{-1}$) and constant over the observed sedimentation gradients (Chapter 1). The back reef sites were selected in order to sample a continuous reef environment along gradients of both flow and sedimentation. Back reef sites were established at least 75 meters from one another along unidirectional flow and sedimentation gradients extending from the reef crest towards shore (Chapter 1).

At each of three sites within each habitat, a 50-meter permanent transect was established approximately 10 meters behind and perpendicular the reef crest on the benthos at one to two meters depth and was subdivided into five, 10-meter zones to sample the gradient at discrete intervals. Interactions between massive *Porites* and mixed algal turf were staged by adjoining nubbins of similar size (approximately 100 cm²) and shape to a Plexiglas plate. Coral nubbins again were collected from the back reef environment and allowed to acclimate in the lab with natural light and flow-through seawater. Before interactions were staged, coral nubbins were stained for 24 hours in Alizarin red (Dustan 1975) and then buoyant weighed (to nearest tenth of a mg) in order to measure linear extension and growth at the end of the experiment. To facilitate removal of the coral nubbins for final buoyant weight measurements, a bolt was affixed to the underside of each nubbin using Z-spar (Splash Zone A-788 epoxy) with a wing nut on the underside of the plate to hold it in place.

Algal turf nubbins were affixed to the Plexiglas using Z-spar. Two holes were drilled in opposite corners of the Plexiglas in order to attach the plates to the benthos. Within each zone, three replicate interactions were placed randomly on the benthos and oriented so that the interaction margin ran parallel to the direction of flow. To minimize flow interference by adjacent coral bommies, interactions were placed > 1 m from the nearest upstream bommie or feature. Measurements of linear extension were made from the Alizarin red stain line to the edge of the colony at the top, toward the zone of interaction, and away from the zone of interaction on the opposite side of the colony. The results were averaged within each zone for all three sites.

Statistical Analysis

To determine the separate and interactive effects of flow and sedimentation on massive *Porites* linear extension, separate analyses of covariance (ANCOVAs) first were conducted for each habitat to determine the effect of flow on the rate of sedimentation, with site as a categorical variable and clod card dissolution as a covariate (Chapter 1). The residuals from these ANCOVAs then were used in subsequent analyses of *Porites* linear extension using separate ANCOVAs for each habitat, with growth surface (categorical; top, toward interaction, opposite interaction), clod card dissolution (covariate), and the sedimentation residuals (covariate) as the factors of interest. Use of the residuals allowed for the exclusion of variation in sedimentation rate due to flow, thus focusing on the effects of sedimentation alone. Site was eliminated as a factor after it was determined that there were no significant differences ($p > 0.1$) in flow or sedimentation among sites. All non-significant interactions ($p > 0.05$) were eliminated from the final model before testing the remaining interactions and main effects. Data were found to meet the assumptions of normality and homogeneity of variances as assessed using Shapiro-Wilk and Levene's test, respectively.

Differences in coral dry weight could not be tested due to extensive overgrowth of both coral and algal turf resulting in attachments between the two taxa that could not be broken without compromising the coral sample. Therefore, only linear extension data are reported.

Results

Flume Experiment

Flow and sedimentation treatments generally were maintained throughout the experiment. Variation in flow across the different flumes was a result mainly of changes in water pressure, therefore the valves were adjusted accordingly every morning, afternoon, and evening. The low flow treatments were maintained between the range of 0.04 and 0.05 m s⁻¹ while the high flow treatments were maintained between 0.21 and 0.25 m s⁻¹. Variation in sedimentation was inherent to the gravitational design. As the smaller 76-liter tub drained, the rate of sedimentation decreased as a result of reduced pressure forcing the suspended sediment through the tubes. As the tub was refilled, pressure increased and sedimentation rate increased. This resulted in sedimentation rates ranging from 17 to 20 mg cm⁻² d⁻¹. Altogether, the variation in flow and sedimentation was limited to within a small range of values.

Massive *Porites* tissue in contact with algal turf became pale after approximately three days across all treatments. This most likely was an artifact of the side-by-side arrangement of the nubbins, as coral tissues at the center of the interaction plane were exposed to less light and water flow compared to tissues not in direct contact with algal turf. This damage accounted for approximately 1 cm² of the total damage measured at the end of the experiment. In the high flow treatments (with and without sediment), the area of coral tissue damaged remained nearly constant at 1 cm² (Fig. 3), suggesting that sediments did not have a significant effect on the area of coral tissue damaged under high flow (ANOVA, $F_{1,20} = 1.70$, $p = 0.21$). By contrast, coral in the low flow treatments displayed significantly more damage and showed signs of bleaching after approximately

two weeks compared to the high flow treatments ($F_{1,20} = 125.52$, $p < 0.001$). At this point, algal turf in the low flow, sediment addition treatment began to colonize the newly-opened space, resulting in significantly greater coral tissue damage averaging 5.02 ± 0.26 cm^2 (mean $\pm$ SD) compared to the low flow, no sediment treatment with damaged areas averaging 2.88 ± 0.37 cm^2 ($F_{1,20} = 30.39$, $p < 0.001$, Fig. 3). Despite the variable extent of coral tissue damage, massive *Porites* dry weight did not differ significantly among treatments (ANOVA, $F_{3,20} = 0.33$, $p = 0.80$, Fig 4).

Field Experiment

Due to the absence of a flow gradient along the fringing reefs, flow was not included as a covariate in the fringing reef growth analyses, leaving sedimentation and growth surface as the categorical variable and covariate, respectively. Sedimentation exerted significantly different effects on *Porites* linear extension across the three growth surfaces measured (ANCOVA, $F_{2,63} = 72.07$, $p < 0.001$, Fig 5). As sedimentation increased, vertical linear extension decreased from 1.1 to 0.2 cm/yr (Fig. 5 “Top”). Similarly, the extension of tissues adjacent to the algal turf interaction decreased from 0.8 to 0 mm/yr with increasing sedimentation (Fig. 5 “Toward interaction”). By contrast, horizontal extension of tissue away from the interaction increased from 0.6 to 1.2 cm/yr with increasing sedimentation (Fig. 5 “Opposite of Interaction”).

In the back reef, flow and sedimentation exerted independent significant effects on *Porites* linear extension, but the effects were not consistent across the 3 growth surfaces measured (Table 1). Similar to the fringing reefs, as sedimentation increased in the back reef, vertical linear extension decreased from 1.6 to 0.4 cm/yr (Fig. 6 “Top”), as

did extension adjacent to the algal turf interaction (0.6 to 0.05 cm/yr, Fig. 6 “Toward interaction”), while horizontal extension of tissue away from the interaction increased from 0.15 to 1.3 cm/yr with increasing sedimentation (Fig. 6 “Opposite interaction”). The back reef also exhibited a gradient in flow that not only influenced the rate of sedimentation as previously shown (Chapter 1), but also acted independently from sedimentation to influence *Porites* growth when in contact with algal turf. Specifically, as flow decreased vertical linear extension decreased (Fig. 6 “Top”), as did the extension of tissues adjacent to the algal turf interaction (Fig. 6 “Toward interaction”), whereas horizontal extension of tissue away from the interaction increased (Fig. 6 “Opposite interaction”). Finally, these results indicate that flow and sedimentation do not interact in the field to influence massive *Porites* growth when in contact with algal turf (Table 1).

Discussion

Sedimentation has long been viewed as an important agent of coral reef degradation (reviewed in Rogers 1990 and Fabricius 2005) through effects on coral recruitment, physiology, reproduction, and growth. An important factor determining the magnitude of degradation is the concentration of sediment and the duration of exposure, both of which are influenced by hydrodynamic processes (Phillip and Fabricius 2003, Fabricius 2005, Storlazzi et al. 2009). Spatial and temporal variation in hydrodynamic forcing has been shown to significantly affect the rate of deposition, residence time, resuspension, and advection of both marine and terrestrial sediments (Storlazzi et al. 2009). Water flow therefore is likely to exert indirect effects on a number of

physiological and ecological processes by altering the delivery, concentration and duration of sediment exposure.

The results presented here also suggest that flow also has a significant effect on massive *Porites*-algal turf interactions independent of sedimentation. These results support patterns described in Chapter 1, where field surveys revealed that flow exerts significant effects on the frequency and outcome of *Porites*-algal turf interactions. In addition, flow accounted for a much larger proportion of the variation in interaction frequencies and was a significant factor influencing the outcome of interactions. While sedimentation also had a significant independent effect on interaction frequency, it did not affect the outcome of interactions. Further, the current study reveals that only under low flow do sediments influence massive *Porites*-algal turf interactions, while under high flow, the effects of sediments are reduced. In part, this may be due to the effects of increased flow on the rate of sedimentation but as the sedimentation rates achieved here remained relatively constant across treatments, it is likely that flow was modifying the interaction between sedimentation, massive *Porites*, and algal turf, such that the effects of sedimentation are enhanced under low flow and lessened under high flow.

The results of the lab experiment also support previous studies demonstrating that massive *Porites* growth, as measured by the change in dry weight, is not affected by sedimentation or interactions with algal turf over a period of 7 months (McCook 2001), despite measureable damage to coral tissue (Barott et al. 2009). What is not evident from the flume experiment is how massive *Porites* is able to maintain growth rates despite high sedimentation and algal overgrowth.

One mechanism which may explain the negligible difference in coral dry weight across treatments in the flume experiment may be that massive *Porites* is able to increase rates of linear extension of tissues away from the site of algal turf interactions, as revealed by the field experiment. Barnes and Lough (1999) found that *Porites* linear extension decreased from ~ 1.3 to 1.15 cm/y after severe sedimentation, yet this study did not involve an algal competitor nor was linear extension measured across different areas of the *Porites* colony. While the rates of linear extension measured here are typical of those observed for massive *Porites* in areas of high sedimentation, this is the first to report variability in within colony growth rates in response to sedimentation and interactions with turf algae. An observation of *Porites* tissue damage, death, or algal overgrowth therefore might not indicate algal dominance over coral but rather, the localized loss of coral tissue along the zone of interaction with turf algae. In fact, overgrowth of massive *Porites* by algal turf in areas of high sedimentation might not represent a net loss of coral colony area if *Porites* growth rate away from the zone of interaction is greater than or equal to the rate of overgrowth by algal turf.

The implications of these findings for understanding coral-algal interactions are three-fold. First, it is well-understood that both coral and algae coexist on coral reefs and both are vital to reef functioning and persistence. However, many consider algal overgrowth of corals as evidence of algal competitive superiority that may potentially lead to a phase shift from a coral-dominated to algae-dominated state. As coral reefs are under increasing anthropogenic pressure, coral mortality indeed may result in algae-dominated reefs, however the results presented here suggest that the advancement of algae onto living coral tissue does not necessarily indicate algal competitive superiority

nor does it point to eventual reef degradation into an algal-dominated state. In fact, some robust corals such as massive *Porites* may be able to withstand local, isolated algal overgrowth in favor of growth and maintenance of tissues not in direct competition.

Second, the ability of corals to withstand or prevent algal overgrowth likely is influenced by other biotic and abiotic factors. For example, previous work showed that in areas of low flow and high sedimentation, *Porites* is more likely to be in contact with algal turf than in areas of high flow or reduced sedimentation (Chapter 1), yet may be able to maintain growth rates as demonstrated here. The sedimentation rates recorded in the back reef and fringing reefs of Moorea vary between ‘normal’ and ‘high’ as described in Rogers (1990), suggesting that only in areas of extremely high chronic sedimentation ($>100 \text{ mg cm}^{-2} \text{ d}^{-1}$) where damage to coral tissue is extensive (Dodge et al. 1974, Cortes and Risk 1985, Tomascik and Sander 1985, Acevedo and Morelock 1988, Lewis 1997, Van Woesik and Done 1997, Wesseling et al. 2001, Philipp and Fabricius 2003), is the threat of algal proliferation and dominance imminent. Therefore, thresholds in either the concentration or duration of sediment exposure may exist beyond which the effects become lethal for certain coral species.

Finally, the results presented here highlight the importance of multi-factor experiments in studies of coral-algal competition. One of the major challenges to predicting community dynamics in a changing climate is our ability to understand the potential for interactive, direct, and indirect effects of multiple biotic and abiotic factors at different spatial and temporal scales. While these studies do not suggest an interactive effect of flow and sedimentation, there are other concurrent factors that undoubtedly will exert significant, potentially interactive effects such as pCO_2 , temperature, nutrients, and

herbivory. Additionally, these findings underscore the importance of reef-scale variation in the physical factors that affect coral-algal interactions, the understanding of which is critical to our ability to predict the fate of coral reefs in a changing climate.

Tables

Table 1. Results of an ANCOVA assessing the effect of % clod card dissolution (covariate), and sedimentation rate residuals (covariate) on the linear extension of massive *Porites* at three surfaces (top, inside adjacent to turf interaction, and outside away from turf interaction).

Source of Variation	df	MS	<i>F</i>	<i>p</i> -value
Surface	2	0.734	17.615	<0.001
Clod card (CC) dissolution	1	0.006	0.138	0.712
Sedimentation Residuals	1	0.005	0.126	0.724
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Surface*CC dissolution	2	0.679	16.295	<0.001
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Error	35	0.042		
Surface*CC dissolution*Sedimentation Residuals	2	0.028	0.667	0.520
Error	33	0.042		

Figures

Figure 1. Flume and manifold setup. A) Cradle with space for 4 flumes, B) Upstream water flow control valve, C) Honeycomb of flow straighteners, D) Downstream water flow control valve, E) Placement of staged interactions.

Figure 2. Schematic of laboratory experimental setup. A) Assembled flumes, B) Filtered seawater supply manifold, C) Sediment delivery tubes extending from stock tank to 6 flumes, D) 20 gal suspended sediment stock tank, E) Pump and hosing connecting suspended sediment reservoir to 20 gal stock tank, F) 650 gal suspended sediment reservoir, G) Pumps stir constantly to keep sediments suspended.

Figure 3. Results of flume experiment. Data represents average area ($\pm$ SE) of damaged coral tissue in contact with algal turf under high flow, high flow + sediment, low flow, and low flow + sediment. Data are pooled from 2 trials.

Figure 4. Results from the flume experiment showing the overall change in dry weight of massive *Porites* (normalized to colony area) in contact with algal turf under conditions of high flow, high flow + sediment, low flow, and low flow + sediment. Data are means ($\pm$ SE) from two, 3-week trials.

Figure 5. Results from the field experiment showing vertical (top) and horizontal linear (toward interaction and opposite interaction) extension of massive *Porites* tissue when in contact with algal turf along a gradient of sedimentation. Data are from three fringing reef sites.

Figure 6. Results from the field experiment showing vertical (top) and horizontal linear (toward interaction and opposite interaction) extension of massive *Porites* tissue when in contact with algal turf along a gradient of flow and sedimentation. Data are from three backreef sites.

Chapter 4

The effects of fine-scale spatial variation in sedimentation on the area of massive

***Porites* tissue damaged when in contact with algal turf**

Introduction

Over the past century, coral reefs have been exposed increasingly to anthropogenic induced stressors including global climate change, overfishing, and pollution, resulting in an unprecedented decline in coral reefs worldwide (Hughes et al. 2003, Bellwood et al. 2004). An important process in the degradation of coral reefs is the shift from a coral-dominated to an algae dominated state, known as a coral-algal phase shift (Done 1992, McCook et al. 2001). What remains unclear, however, are the mechanisms underlying algal overgrowth of corals and the potential of various biotic and abiotic factors to influence coral-algal dynamics. For example, sedimentation resulting from urbanization, development, and agriculture has been regarded as a major threat to coral reefs in the Caribbean and Pacific (Rogers 1990, Fabricius 2005), yet little is known about how sediments influence interactions between coral and algae.

Sediments have been shown to reduce coral reproduction, settlement, recruitment and growth (Rogers 1990, Gilmour 1999, Wilkinson 2000, Fabricius et al. 2003, Crabbe and Smith 2005, Fabricius 2005), while studies of the effects of sediment on algae such as filamentous algal turf point to the enhancement of competitive ability through the trapping of sediments, resulting in the smothering and overgrowth of corals as well as decreased coral recruitment (Steneck 1997, Airoidi 1998, Birrell et al. 2005). The few studies directly examining the relationship between coral, algae, and sediments have

reported conflicting results, from synergistic negative effects of sediments and algae on coral, to coral competitive superiority in areas of increased sedimentation (McCook 2001, Nugues and Roberts 2003). Sediments may exert significant direct and indirect effects on coral-algal interactions by: (1) damaging or killing coral tissue that may indirectly lead to algal overgrowth of the newly opened space, or (2) by directly promoting algal overgrowth of live coral tissue.

Previous field studies described in Chapter 1 revealed that at the scale of massive *Porites*-algal turf interactions, more sediment accumulates along the margin of interaction where *Porites* and algal turf are in direct contact, compared to on coral and algal turf surfaces not in direct competition. This accumulation most likely is the result of active or passive removal of sediments by massive *Porites*, which then becomes trapped among algal turf filaments at the interaction margin. This led to questions regarding the importance of spatial variation in sediment accumulation at the scale of a coral-algal interaction (cm), and the hypothesis that accumulation of sediments along interaction margins facilitates algal overgrowth of massive *Porites* whereas sedimentation on the non-interacting algal turf surface has no effect.

Methods

A fully factorial laboratory experiment was designed to test the effects of sediment accumulation on the non-interacting surfaces of massive *Porites* and algal turf, and along the margin of their interaction including all treatment combinations for a total of seven treatments.

Massive *Porites* and mixed algal turf-covered coral pieces of similar size (50 cm²) were collected from the back reef of the north shore of Moorea, French Polynesia and allowed to acclimate in the lab with flow through seawater and natural light for approximately five days before the start of the experiment. Corals and algal turfs were assigned randomly to each of the seven treatments and placed adjacent to one another so that the algal turf filaments were in contact with the neighboring *Porites*. Interactions were staged in 1-liter plastic containers that were submerged in a 1,550-liter tank equipped with flow through seawater. Two 8 x 4 cm rectangles were cut in opposite walls of each container and covered with 1 x 1 mm mesh to allow water to flow through while reducing debris from settling on the interactions. Staged interactions were affixed in the center of each container using Sculpy Putty, which allowed for daily cleaning and clearing of sediments applied the previous day. Treatment replicates were divided evenly among 4 elevated cinderblocks within the tank, with one replicate from each treatment represented on each block for a total of four replicates. The water level in the tank was kept just below the lip of the treatment containers to force seawater to flow through rather than over the containers. Each morning for 18 days, the four groups of replicates were rotated to a different cinderblock and replicates were randomized on the individual cinderblocks to account for differences in proximity to seawater input and position relative to the sun.

Marine sediments were collected from the upper five cm of a sandy fringing reef (1-2 m) on the north shore of Moorea that is subjected to chronic sedimentation from a small stream draining from uninhabited forest. Although the physical and chemical properties of the sediments were not quantified, sediments were wet sieved to exclude

particles greater than 500 μm , such as large carbonate sands or shell fragments (Weber et al 2006). Sediments were added daily from a prepared sediment stock solution with a concentration of 8 mg/ml of sediment. A syringe was used to extract 5 ml of this solution for application onto a 2 x 1 cm swath on the appropriate surface, yielding a sedimentation rate of approximately 20 $\text{mg cm}^{-2} \text{d}^{-1}$, corresponding to the sedimentation rate experienced on the north shore fringing reefs of Moorea (Chapter 1). Sediments were applied daily, after cleaning and removal of the previous day's sediments.

Initial and final photographs were taken of the coral surface in contact with algal turf and analyzed using Image J to trace the area of coral tissue damaged after three weeks. Damage to the coral tissue was determined based on the color of the tissue in the area of contact relative to non-interacting tissues. Faded or bleached tissues as well as tissues colonized by algal turf were considered damaged.

Statistical Analysis

Data were analyzed using ANOVA with specific *a priori* contrasts testing for differences between treatments described in Table 1. Data met the assumptions of normality and homogeneity of variances as determined by Shapiro-Wilk's and Levene's tests, respectively.

Results

As a result of the placement of the interactions, coral polyps in direct contact with algal turf presumably experienced less light and water flow, resulting in some damage to the coral tissue independent of treatment. Measureable and significant differences in the

relative area of tissue damaged were found across *a priori* treatment comparisons. First, sediment accumulation on the non-interacting surfaces of both *Porites* and algal turf resulted in more damage to the coral tissue than sedimentation on either the *Porites* (ANOVA $F_{1,14} = 6.42$, $p = 0.024$) or algal turf ($F_{1,14} = 10.72$, $p = 0.006$) surfaces in isolation (Fig. 1). Further, addition of sediments along the margin of *Porites*-algal turf interactions when sediments were also present on the non-interacting *Porites* and algal turf surfaces resulted in significantly less coral tissue damage than when sediments were placed only on the non-interacting surfaces ($F_{1,14} = 22.60$, $p < 0.001$), suggesting that sediments along the margin of interaction mediate interactions between *Porites* and algal turf (Fig. 2). Similarly, when sediments were present on the algal surface, the addition of sediments along the margin of interaction resulted in significantly less damage to the coral tissue ($F_{1,14} = 14.29$, $p = 0.002$, Fig. 3). In contrast, when sediments were present on the non-interacting *Porites* surface, there was no additional effect of sediments along the interaction margin ($F_{1,14} = 0.11$, $p = 0.74$, Fig. 4).

Discussion

Terrestrial runoff of sediments has been identified as a major threat to coastal coral reefs through effects on coral reproduction, settlement, and recruitment (as reviewed in Rogers 1990 and Fabricius 2005). In addition, the proliferation of macroalgae in areas prone to increased sedimentation has been implicated in phase-shifts from coral-dominated to algae-dominated reefs (Fabricius 2005). Despite widespread evidence of sediment trapping by mixed algal turf, little is known about the mechanism of the effects of sediments on the interactions between coral and algae. Repeated observations of

increased sediment accumulation along the margin of *Porites*-algal turf interactions (Chapter 1) led to the hypothesis that localized spatial variation in sediment accumulation may play an important role in the effects of sedimentation on *Porites*-algal turf interactions. Taken together, the results presented here suggest that localized spatial variation in sedimentation can have significant impacts on the trajectory of *Porites*-algal turf interactions. First, sediments can directly impact *Porites* tissue health when in contact with algal turf as previously demonstrated (Rogers 1990, Gilmour 1999, Wilkinson 2000, Fabricius et al. 2003, Crabbe and Smith 2005, Fabricius 2005). In addition, however, sediments may also exert indirect effects by modifying the interactions between *Porites* and algal turf. For example, sediments along the margin of *Porites*-algal turf interactions reduce the area of coral tissue damaged compared to when sediments are only present on the non-interacting coral and algal surfaces. What is not clear from this experiment, however, is the mechanism underlying this effect.

Corals are known to harbor an array of bacteria, some of which are thought to be species-specific (Ritchie and Smith 1997, Rohwer et al. 2002). These bacteria may sequester limiting nutrients from the surrounding water that then may be acquired by their host corals in addition to producing antibiotics that may prevent colonization by invasive bacteria (Rohwer et al. 2002). Therefore, coral hosts may regulate and select for external microbial symbionts that are advantageous under certain conditions (Reshef et al. 2006, Zilber-Rosenberg and Rosenberg 2008). However, benthic algae have been known to secrete hydrophobic allelochemicals, chemicals that stimulate growth of harmful coral-associated microbes, and chemicals that exhibit antimicrobial properties that may harm or kill beneficial coral-associated microbes (Smith et al. 2006, Rasher and

Hay 2010, Morrow et al. 2011, Rasher et al. 2011). In addition, many algal species exude chemical compounds that provide chemical defense against herbivores and inhibit microbial growth (Paul and Hay 1986, Nagle and Paul 1999, Goecke et al. 2010). Further, Wangpraseurt et al. 2012 reported an increase in the thickness of the diffusive boundary layer (DBL) at the *Porites*-algal turf interface which may result in lower metabolic rates and the accumulation of metabolites released by both *Porites* and algal turf. However, algal turf may need to be in direct contact with coral tissue in order for metabolites to reach high enough levels to stimulate microbial activity, or coral tissue damage or death (Vu et al. 2009, Rasher and Hay 2010). Rasher et al. (2011) showed that only when corals and algae are in direct contact, do these chemicals damage coral tissue. Therefore, the accumulation of sediments along the coral-algal interface may act as a physical buffer to direct contact of algal turf filaments with coral tissue. In this way, sediments in this zone may reduce the transfer of chemicals and metabolites from algal turf to *Porites*.

It is important to note that the effects of sediment addition to the non-interacting algal turf surface did not differ from when sediments were added to the coral surface, indicating that despite the trapping of sediments, no additional damage was inflicted to the coral tissue. This contradicts previous studies citing the enhancement of algal turf competitive ability when trapped sediments are present (Steneck 1997, Airoidi 1998, Birrell et al. 2005). One possible explanation for this may be the reduced organic content of the sediments used here. Weber and colleagues (2006) reported that nutrient-rich silts high in organic matter resulted in greater photophysiological stress in *Montipora peltiformes* compared to carbonate sediments. Subsequent research demonstrated that

sediments high in organic content killed corals through microbially induced hypoxia, reduced pH, and increased sulfide content (Weber 2009). While these experiments were conducted in the absence of an algal competitor, it is possible that sediments trapped among algal turf filaments induce similar microbial processes. The organic content of sediments utilized here was not analyzed but because a sulfur smell was not detected and the sediments did not turn black, it is likely that sulfate reducing bacteria were scarce if at all present (Cline and Richards 1969, Kelly 1988, Weber 2009). Therefore, future studies researching the effects of sedimentation on coral-algal interactions should characterize the nutrient and organic content of the sediments as the ability of sediments to physically buffer interaction between corals and algae may be overridden by the tendency of sediments high in organics to stimulate microbial activity.

The results presented here highlight the importance of fine-scale (cm), localized variation in sedimentation at the scale of massive *Porites*-algal turf interactions. Many questions remain unanswered that would further elucidate the mechanisms underlying the ability of sedimentation to buffer interactions between coral and algae. First, how do sediments along the margin of interaction mitigate the effects of algae? Is it chemically or physically mediated? Further, how do various properties of sediments influence interactions, such as organic and nutrient content, and grain size? The answers to these questions will help us to better understand the dynamic nature of coral-algal interactions and the factors that influence them as well as allow us to make local and regional scale predictions regarding the trajectory of sediment-induced phase shifts.

Tables

Table 1. Results of an ANCOVA assessing the effect of % clod card dissolution (covariate), and sedimentation rate residuals (covariate) on the linear extension of massive *Porites* at three surfaces (top, inside adjacent to turf interaction, and outside away from turf interaction).

Source of Variation	df	MS	<i>F</i>	<i>p</i> -value
Surface	2	0.734	17.615	<0.001
Clod card (CC) dissolution	1	0.006	0.138	0.712
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Error	33	0.042		

Figures

Figure 1. Average area of damaged massive *Porites* tissue when sediments are added to the non-interacting surface of algalturf, *Porites*, and both algal turf and *Porites*. Data are means ($\pm$ SE; n = 4).

Figure 2. Average area of damaged massive *Porites* tissue when sediments are added to the non-interacting surface of *Porites* and algal turf (a), and on *Porites*, algal turf, and the margin of interaction (b). Data are means ($\pm$ SE; $n = 4$).

Figure 3. Average area of damaged massive *Porites* tissue when sediments are added to the non-interacting surface of algal turf (a), and on algal turf as well as the margin of interaction (b). Data are means ($\pm$ SE; n = 4).

Figure 4. Average area of damaged massive *Porites* tissue when sediments are added to the non-interacting surface of *Porites*, and on *Porites* as well as the margin of interaction. Data are means ($\pm$ SE; n= 4).

Chapter 5

Summary

As coral reefs worldwide continue to degrade with persistent anthropogenic pressure, it is important that future research continues to identify the factors and mechanisms that will determine the winners and losers of coral-algal interactions. Processes that facilitate coral reef degradation include interactions between corals and algae as well as various abiotic factors such as sedimentation, yet the breadth of potential mechanisms are not well understood. For example, sedimentation has long been viewed as an important agent of coral reef degradation (reviewed in Rogers 1990 and Fabricius 2005) through effects on coral recruitment, physiology, and reproduction. An important factor determining the magnitude of degradation is the concentration of sediment and the duration of exposure, both of which are influenced by hydrodynamic processes (Phillip and Fabricius 2003, Fabricius 2005, Storlazzi et al. 2009). Spatial and temporal variation in hydrodynamic forcing has been shown to significantly affect the rate of deposition, residence time, resuspension, and advection of both marine and terrestrial sediments (Storlazzi et al. 2009). Water flow therefore is likely to exert indirect effects on a plethora of physiological and ecological processes by altering the delivery, concentration and duration of sediment exposure. In addition, the studies presented here suggest that flow also has a significant effect on massive *Porites*-algal turf interactions independent of sedimentation.

Data presented in Chapter 1 suggest that flow is a significantly greater predictor of both massive *Porites*-turf interaction frequencies and outcomes. In the back reef of

Moorea, massive *Porites*-turf interaction frequencies increased with decreasing flow and increasing sedimentation and under these conditions, turf was predicted to win more often. Even as massive *Porites* abundance decreased along these gradients, the frequency of *Porites*-turf interactions increased suggesting that coral competitive ability may be suppressed thus allowing for successful overgrowth by turf. Interestingly, flow and sedimentation did not interact to influence the frequencies of *Porites*-turf interactions but rather, each exerted significant independent effects. Flow, however, was shown to significantly affect the rate of sedimentation, suggesting a separate, indirect effect of flow on *Porites*-turf interactions. Also, in the back reef, flow was the only factor to significantly affect the outcome of interactions such that increased flow significantly reduced the percentage of turf “wins”. In part, this may be due to the effects of flow on sedimentation rate but once this effect is removed, the capacity of flow to mediate the relationship between massive *Porites*-turf interactions and sedimentation is significant. Therefore, flow likely is an important physical factor controlling the dynamics between corals and algae, and the benefits of increasing flow have the potential to significantly counteract the negative effects of sedimentation.

Further, the flume study described in Chapter 2 revealed that only under low flow do sediments influence *Porites*-algal turf interactions, while under high flow, the effects of sediments are reduced. In part, this may be due to the effects of increased flow on the rate of sedimentation but as sedimentation rates remained relatively constant across treatments, it is likely that flow was modifying the interaction between sedimentation, *Porites*, and algal turf, such that the effects of sedimentation are enhanced under low flow and lessened under high flow. In addition, differences in flow appeared to significantly

affect the area of coral tissue damaged regardless of sedimentation, corroborating the field survey results in Chapter 1.

The potential for water flow to alter the relationship between sediment-laden turf and coral may lie in the alteration of coral diffusive boundary layer thickness under different flow regimes. As flow increases and the diffusive boundary layer thins, the resulting increase in particle capture and mass-transfer of solutes may confer increased energy to the coral (Sebens 1984, Sebens et al 1998), which then may be utilized to either remove sediments or prevent algal overgrowth. Similarly, thinner boundary layers may help to dislodge trapped sediments. By contrast, thicker boundary layers in lower flow may facilitate the retention of sediment particles and reduce energy acquisition from particle capture and nutrient uptake, thus reducing the available energy that might otherwise be allocated for defense along interaction margins.

In the absence of a flow gradient, such as experienced along the north shore fringing reefs of Moorea, sedimentation remained a significant factor affecting the frequencies and outcomes of interactions. Specifically, massive *Porites*-turf interaction frequencies as well as the percentage of turf “wins” increased with increasing sedimentation. Potts (1977) suggested that algae-sediment mats cause localized smothering of coral margins, resulting in increased energy expenditure on sediment clearing rather than resisting algal colonization, resulting in successful algal overgrowth of coral tissue. Similarly, Nugues and Roberts (2003) hypothesized that the energy spent on sediment removal elsewhere on the coral colony not in direct competition with algae may reduce the energy available for defense along interaction margins, resulting in decreased growth of corals in contact with algae in areas of high sediment. It is well-

documented that filamentous turf in particular responds to increasing sediment accretion by increasing horizontal extension and percent cover (Kendrick 1991, Nugues and Roberts 2003). Still, little is known regarding the mechanism of turf proliferation in areas of high sedimentation, whether by overgrowth of damaged or dead coral, competitive dominance over established coral, or colonization and occupation of empty space.

It is well-documented that algal turfs “trap” and anchor sediments which may facilitate algal overgrowth of some corals (Steneck 1997, Airoidi 1998, Birrell et al. 2005), but the mechanisms of these effects have yet to be determined. The mechanism proposed in Chapter 3, that the accumulation of sediments along interaction margins has a greater affect on *Porites*-algal turf interactions than accumulation on the adjacent non-interacting *Porites* and turf surfaces, was rejected. Instead, it appeared that sediments along the margin of *Porites*-algal turf interactions reduced the area of coral tissue damaged compared to when sediments were only present on the non-interacting coral and algal surfaces. Sediments along the coral-algal interface may act as a physical buffer to direct contact of algal turf filaments with coral tissue, reducing the transfer of harmful allelochemicals and microbial growth-inducing chemicals from algal turf to *Porites*. Algal turf filaments may need to be in direct contact with coral tissue in order for metabolites to reach high enough levels to stimulate microbial activity, or coral tissue damage or mortality (Vu et al. 2009, Rasher and Hay 2010, Rasher et al. 2011).

Sedimentation on massive *Porites*-turf interactions also resulted in differential spatial allocation of resources to tissue growth as described in Chapter 2, such that under increasing sedimentation *Porites* tissue growth increased in areas not in direct contact with turf with and with a vertical profile that reduced sediment retention. The ability of

Porites to allocate resources to these tissues may help explain why *Porites* dry weight did not change among treatments in the Chapter 2 flume experiment. This phenomenon also might help explain the findings of Nugues and Roberts (2003), such that if *Porites* is maintaining or increasing growth of non-interacting tissues, the corresponding increase in energy expenditure may lead to tissue loss along interaction margins.

The implications of these findings for understanding coral-algal interactions are significant. First, it is well-understood that both coral and algae coexist on coral reefs and a balance of both is vital to reef functioning and persistence. Despite this knowledge, many consider algal overgrowth of corals as evidence of algal competitive superiority that may potentially lead to a phase shift from a coral-dominated to algae-dominated state. As coral reefs are under increasing anthropogenic pressure, coral mortality indeed may result in algae-dominated reefs, however the results presented here suggest that the advancement of algae onto living coral tissue under increasing sedimentation does not necessarily indicate algal competitive superiority nor does it point to eventual reef degradation into an algal-dominated state. In fact, some robust corals such as massive *Porites* may be able to withstand local, isolated algal overgrowth in favor of growth and maintenance of tissues not in direct competition. In addition, the ability of sediments to mediate interactions between coral and algae is highly dependent on the prevailing flow regime through effects on sediment deposition, transport, and resuspension. Further, the effects of sediments already entangled or trapped among algal filaments or coral polyps may be mediated by water flow, suggesting that flow can significantly affect coral-algal interactions through direct effects on corals and indirect effects on sedimentation. As such, the potential for reef or even regional scale patterns in coral-algal responses to

sedimentation and flow may significantly alter community structure and function, as interaction outcomes are likely to be highly context-dependent.

With rapid global climate change resulting in more frequent and intense storms, increasing water flow from wave action and freshwater runoff and sedimentation may significantly impact a variety of reef processes including interactions between coral and algae. In addition, with ever-expanding agriculture and development of island nations, the rate and chemical nature of sediments are likely to change with important implications for coral reefs and the people who rely on them. Understanding the dynamic processes that drive interactions between coral and algae is critical in order to predict the trajectory of coral-algal phase shifts, protect reefs heavily impacted by sedimentation, or restore damaged reefs. As anthropogenic climate change, tourism, overfishing, and pollution continue to decrease coral cover worldwide, it is important that future research integrates our knowledge of fine-scale physiological and biological process with other abiotic factors that affect coral reefs at the local, regional, and global scale.

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