PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes

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Abstract Restoration of degraded coral reef communities is dependent on successful recruitment and survival of new coral planulae. Degraded reefs are often characterized by high cover of fleshy algae and high microbial densities, complemented by low abundance of coral and coral recruits. Here, we investigated how the presence and abundance of macroalgae and microbes affected recruitment success of a common Hawaiian coral. We found that the presence of algae reduced survivorship and settlement success of planulae. With the addition of the broad-spectrum antibiotic, ampicillin, these negative effects were reversed, suggesting that algae indirectly cause planular mortality by enhancing microbial concentrations or by weakening the coral's resistance to microbial infections. Algae further reduced recruitment success of corals as planulae preferentially settled on algal surfaces, but later suffered 100% mortality. In contrast to survival, settlement was unsuccessful in treatments containing antibiotics, suggesting that benthic microbes may be necessary to induce settlement. These experiments highlight potential complex interactions that govern the relationships between microbes, algae and corals and emphasize the importance of microbial dynamics in coral reef ecology and restoration.

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Introduction

In many benthic marine systems, sessile organisms compete for limited substrata for settlement and growth (intertidal: Paine 1984; Dayton 1971; temperate reefs: Miller and Hay 1996; coral reefs: Jackson 1977; McCook et al. 2001). Competition is most obvious among neighboring individuals and includes direct physical mechanisms (e.g., overtopping, smothering; McCook et al. 2001; Box and Mumby 2007) and indirect mechanisms whereby an organism limits the competitive capacity of its neighbor through modification of its surroundings, including space preemption (Dobson and Hudson 1986; Hudson and Greenman 1998). For sessile tropical organisms, this latter mechanism also includes the production of allelochemicals (Bak and Borsboom 1984; Paul and Puglisi 2004; Gross 2003) or

stimulation of heterospecific pathogens (Nugues et al. 2004a; Smith et al. 2006). In addition to competition among adults, competition between adults and juveniles further shapes relative abundances of species within the wider community (Horn 1975; Caley et al. 1996).

The earliest life stages of many sessile species are typically poorer competitors than older and larger individuals (Sebens 1989; Maida et al. 2001; Vermeij and Sandin 2008). Adults can limit the success of potential competitors by targeting their sensitive life stages and preempting space preferred by their recruits (Grant 1977; Grizzle et al. 1996) or by releasing chemicals that deter heterospecifics from settling in surrounding areas (Maida et al. 2001; Grizzle et al. 1996; Bhadury and Wright 2004; Paul and Puglisi 2004). Despite the high vulnerability of juvenile organisms to competitive pressure, little evidence exists at present on the exact mechanisms that drive competitive dynamics between adults and heterospecific juveniles in benthic communities.

On coral reefs, competitive dynamics were historically studied as coral-coral interactions. However, over the last few decades degradation of coral reef ecosystems has been characterized by an increase in fleshy turf and macro-algal abundance in many regions resulting in an increased incidence of coral-algal interactions (Done 1992; Hughes 1994; Jackson et al. 2001; Wilkinson 2002; Hunter and Evans 1995; Gardner et al. 2003; Ledlie et al. 2007). While the increased abundance of fleshy algae is often attributed to their ability to actively overtake space previously occupied by corals, there is little direct evidence supporting this hypothesis (McCook et al. 2001). Experimental studies often find surprisingly minimal support for the ability of fleshy algae to directly kill and overgrow neighboring corals (e.g., McCook 2001; Jompa and McCook 2003; Nugues et al. 2004a) and the outcome of coral-algal interactions greatly depends on species specific factors that preclude generalization (Jompa and McCook 2003; Birrell et al. 2005). In addition, passive colonization of space previously occupied by stony corals that died from causes other than competition with algae (e.g., disease, bleaching) might often have been wrongfully interpreted as evidence for active competition between corals and algae. This observation clearly stresses that correlational approaches are not sufficient to determine the nature of competitive mechanisms driving the shift from coral to algal domination on degrading coral reefs.

In contrast to adult colonies, the earliest life stages of corals seem particularly sensitive to the presence of benthic turf and macroalgae, and many authors have suggested that the effect of algae on corals is strongest during the coral's earliest benthic stages (Hughes and Jackson 1985; Hughes 1989, 1996; McCook et al. 2001; Vermeij and Sandin 2008). Coral recruitment commonly declines when benthic algae become abundant in experimental (Rogers et al. 1984; Birrell et al. 2005; Hughes et al. 2007) and natural settings (Birkeland 1977; Hughes 1989; Edmunds and Carpenter 2001; Vermeij and Sandin 2008). Benthic algal assemblages can have direct negative impacts on coral recruitment through the preemption of settlement substrate (Birrell et al. 2005; Vermeij 2006; Mumby et al. 2007) and physical disturbance (e.g., abrasion, shading, smothering; McCook et al. 2001; Box and Mumby 2007). Additionally, algae can have indirect negative impacts on coral recruits through allelopathy (Gross 2003; Kuffner et al. 2006). Recent evidence suggests that a third functional group, namely microbes, can also play an important role in determining the outcome of coral-algal competition. Algae can harbor pathogenic microbes and transmit these to neighboring corals through direct contact, leading to disease and subsequent tissue mortality (Nugues et al. 2004b). Similarly, algae can release compounds [e.g., dissolved organic carbon, DOC (Wetzel 1982) or allelochemicals (Gross 2003)] that can enhance microbial activity through direct stimulation of the resident microbial community or by lowering a coral's defenses to such microbes, respectively. Either way, algal-induced increases of microbial abundance on the coral surface can cause hypoxia and subsequent coral tissue mortality (Mitchell and Chet 1975; Smith et al. 2006).

While the presence of microbes has been related to reductions in coral recruitment (Vermeij 2005; Kuffner and Paul 2004; Kuffner et al. 2006), the effects of microbes on the settlement of invertebrates are not necessarily negative as many larvae require a microbial film to successfully settle and metamorphose (e.g., Neumann 1979; Richmond 1987; Morse et al. 1988; Golbuu et al. 1995; Zaslow and Benayahu 1996; Leitz 1997; Heyward and Negri 1999). The dual and potentially contrasting role of microbes may critically influence the early dynamics of coral populations, and understanding these dynamics may be fundamental to developing effective reef restoration and conservation strategies.

In this paper, we investigate the indirect effects of benthic macroalgae on planular survival and recruitment success for the common reef-building coral *Montipora capitata* in the Hawaiian Islands. We begin by investigating patterns of coral recruitment relative to fleshy algal cover in the field. We then experimentally examine the independent and combined effects of algae and microbes on coral recruitment. Specifically, we (1) determine whether microbes increase pre-settlement mortality rates across a range of planular densities, (2) explore separate and joint effects of algae and microbes on planular survival and settlement success, and (3) evaluate effects of different algal species on planular survival rates.

Materials and methods

Study species

Montipora capitata is a common Hawaiian coral, comprising upwards of 31.8% of total cover in shallow reef habitats (0–10 m depth; M.J.A. Vermeij, unpublished data). *M. capitata* is a broadcast spawning species, typically releasing gametes in a synchronized pulse between 20:00 and 22:00 h, 1–4 nights following the new moon between June and August. Fertilized eggs develop into planulae, while in the pelagic environment, before returning to settle in the reef environment. Early recruits from the genus *Montipora* can be uniquely identified by their skeletal characteristics (Babcock et al. 2003).

Field study

A number of studies have reported negative relationships between fleshy algal cover and abundance of coral recruits (Birkeland 1977; Hughes 1989; Edmunds and Carpenter 2001), with 'recruits' being operationally defined as small colonies, typically less than 5 cm in diameter. A recent study, however, found a similar negative relationship between turf algal cover and abundance of single polyp coral individuals (Vermeij and Sandin 2008). Focusing on similarly small individuals, we quantify the relationship between fleshy algal cover and abundance of recent coral recruits on a Hawaiian reef.

The number of recent *Montipora* recruits (1–3 polyps or <3.22 mm^2) was quantified in 82 0.25 m^{-2} quadrats on the shallow (3–6 m) fore-reef at Kahekili Beach Park on northwestern Maui (20°56′08″N, 156°41′33″W). Quadrats were placed haphazardly in areas spanning a gradient of algal abundance (0–100% cover). Quadrats containing adult colonies were not sampled to avoid possible confounding effects of distance-dependent mortality of settlers relative to adults (Vermeij and Sandin 2008). Sampling occurred in September 2006, approximately 1 month after *Montipora capitata* spawned. Quadrats were photographed prior to sampling, and the abundance of macroalgae was quantified using image analysis software (Photoshop CS, Adobe Systems Inc.) and expressed as the percentage of total benthic surface covered by macroalgae. Macroalgae are defined here as all algae extending more than 1 cm above the reef substratum. All algae were then gently removed, and colonies of recently settled *Montipora* (three polyps or less) were counted in situ using an underwater magnifying glass.

The strength of the relationship between fleshy algal cover and recruit density was tested by Poisson regression. Two models of recruit density (δ_r) − constant, $\delta_r = \alpha$, and exponential with algal cover (*A*), $\delta_r = \alpha \exp (\beta A)$, where α and β are the algal-independent and algal-dependent terms, respectively, were compared for relative fit using a likelihood ratio test (Hilborn and Mangel 1997).

Experimental manipulations

Field collection and experimental design

All gametes used to rear planulae were collected from nine colonies of *M. capitata* that spawned egg/sperm packages on 25 July 2006 (20 45–21 45 h) at the shallow (5–8-m) fore-reef at Kahekili Beach Park. Gametes were collected by netting large colonies (>0.6 m) with cone-shaped nets made of transparent plastic sheeting. The nets were weighted down using a metal chain and had a removable 50-ml container at the top. When the collection tubes were 1/3 full of gametes, they were removed and stored, resulting in a combined total of 150 ml of gametes that were transported (<30 min) to the laboratory. Here, all the gametes were mixed in a 10-l container with 3 l of filtered (~25 μm) seawater. The gametes were left for 2 h to allow gamete bundles to break apart and fertilization to occur. All embryos were then pipetted out of the container and transported to six 3-l glass containers with filtered seawater to allow planular development to occur for 40 h. All seawater was filtered (~25 μm) to remove sediment and debris, but not microbes.

For each experiment, planulae were transferred from developmental containers to standard petri dishes (9-cm diameter). The dishes were filled with 40 ml of filtered seawater. Ninety-five percent of the water volume inside the dishes was changed daily during the first 3 weeks of the study and weekly thereafter. Dead planulae were simultaneously removed with the water changes. Under this experimental setting, coral planulae can be kept alive for >1 year (M.J.A. Vermeij, unpublished data). The entire experiment was carried out in an open laboratory, subjecting planulae to natural daily temperature (range 27.5 and 28.7°C) and light regimes (~10% of incident surface photosynthetically active radiation, PAR) for the duration of the experiments.

We used ampicillin, an antibiotic commonly used to reduce the abundance of coral associated microbes, in some of our experimental treatments. Ampicillin is related to penicillin and penetrates both gram-positive and gram-negative bacteria, making it a broad-spectrum antibiotic. Ampicillin was added to petri dishes at 100 μg ml^{-1}, a concentration sufficient to dramatically reduce the density of microbes present in each dish without becoming deleterious to the corals (Zaslow and Benayahu 1996; Kelman et al. 1998; Smith et al. 2006; F.L. Rohwer, personal communication). A reduction in planular mortality after the addition of antibiotics relative to controls is assumed to indicate some form of microbially driven mortality in treatments without antibiotics.

The efficacy of ampicillin in reducing microbial concentrations in small-volume containers was addressed in a series of preliminary experiments. The total number of colony-forming units was determined in petri dishes filled with 80 ml of tropical seawater, where ampicillin was added to half of the units, and the others were left as untreated controls ($n = 3$). The treatment concentration of ampicillin was 100 µg ml^{-1}. After 24 h at 24°C, 250 µl of seawater from each of the experimental units was plated on two types of media: Zobell ($n = 3$) and TCBS ($n = 3$) and kept at 24°C for another 24 h after which the number of colony-forming units were counted. Ampicillin additions severely reduced the number of microbes [mean (SE), TCBS: +AMP 0.0 (0.0) ml^{-1} vs. −AMP 116.0 (66.9) ml^{-1}, Zobell: +AMP 25.7 (14.8) ml^{-1} vs. −AMP 1,628.4 (183.3) ml^{-1}], suggesting that ampicillin is able to severely reduce the abundance of coral reef microbes. From this experiment, we also tested for evidence of bottle effects, i.e., rapid increases of microbial concentrations observed in some small-container experiments. In the −AMP treatments, we tested for changes in the density of microbes through time by counting the number of colony-forming units at $t = 0$ and $t = 24$ h on the two media ($n = 3$). Microbial densities after 24 h did not significantly differ for the Zobell medium ($t = −0.36$, $p = 0.73$), and a small but significant increase (29.4%) was observed on the TCBS medium ($t = −2.93$, $p < 0.05$).

Experiment 1: Effects of microbes and planular density on survival

To determine whether planular mortality depended on microbial and planular density during the pre-settlement period, we compared planular survival rates across a density gradient (approximately 10, 50, 100, 200 and 400 planulae per dish, $n = 3$ per density). The effects of microbes on survivorship patterns were investigated by replicating the above gradient, with and without the addition of ampicillin. In total, 30 petri dishes were established [5 densities × 2 antibiotic treatments (−AMP/+AMP) each with three replicates]. After a 10-h acclimation period, the number of planulae was recorded in each dish as the starting density. Survivor density was then recorded as the number of individuals remaining after a 20-h period in each petri dish.

To determine if the relationship between planular density and survivorship varied as a function of developmental stage or age, this experiment was carried out separately for the pre-settlement period (when all planulae moved in the water column, $t = 43$–80 h post spawning) and the benthic exploration period (when >80% of the planulae moved across the bottom of the petri dish, $t = 80$–179 h post spawning). In the latter experiment, planulae were kept in 1-l glass containers filled with filtered seawater prior to the start of the experiment 80 h post-spawning.

Experiment 2: Effects of algae and microbes on planular survival and settlement

This experiment was designed to determine if algae negatively affected planular survival rates and whether such an effect was mediated by microbes. Samples of the locally abundant green alga *Ulva fasciata* (1.5 g wet weight) were collected at the same site as the coral gametes, at a depth of 1 m. *Ulva* is known to exude DOC (maximum rate: 60 mg l^{-1}d^{-1} per 5 g of algal dry weight; Brun et al. 2003) and allelochemicals known to affect invertebrates (Magre 1974; Johnson and Welsh 1985) into the surrounding water. *Ulva* may therefore enhance microbial abundance on or near adjacent coral colonies by stimulating growth rates through the release of DOC [see model by Kline et al. (2006)] or other waterborne chemical exudates that may weaken the coral's resistance to microbial infection (Gross 2003). Note that our study is not designed to discriminate between these two potential mechanisms.

A factorial experiment was used to compare the independent and combined effects of algae and microbes on planular survival. In this experiment, planulae were subjected to the following treatments: (1) the experimental control, without algae or ampicillin (−ALG/−AMP), (2) the antibiotic control, without algae but with ampicillin (−ALG/+AMP), (3) the algal treatment, with algae added, but no ampicillin (+ALG/−AMP), and (4) the combined treatment, with both algae and ampicillin (+ALG/+AMP). Five independent replicate dishes each with approximately 200 planulae were prepared for each treatment. Experiments were prepared and initiated 43 h after spawning.

The algal treatments were designed specifically to test for effects of substances released by the algae (DOC or allelopathic chemicals) on planular survival and settlement. Therefore, we added a physical algal replica to the −ALG treatments to control for the possibility that the structural change and/or shading artifacts inside the petri dish could alter survival and settlement dynamics. White plastic clippings constructed from egg-crate fragments cut to approximately the same size as the algal fragments (diameter 2–3 cm) were used as this procedural control. Because *U. fasciata* was growing during the experiment, algal fragments were regularly clipped to maintain their initial size.

At the start of the experiment (43 h post spawning), the number of planulae were recorded in each dish as the starting density. Survivor density was recorded daily, but overall survival in response to the various treatments was defined as the proportion of the initial density of individuals ($n = \sim 200$) still alive after approximately 2 weeks (361 h) in each petri dish. Similarly, the number of settlers was recorded when a surviving planula had (1) attached to the bottom, (2) made a calyx and (3) developed tentacles. Note that because settlement can depend upon the availability of

suitable substrate, we added standardized substrate to each dish 80 h after commencement of the experiment. A small piece of crustose coralline algae (CCA, 0.8 cm diameter), a terra-cotta chip (0.8 cm diameter) and a piece of egg-crate overgrown with diatoms (0.8 cm diameter) were added to each petri dish to provide planulae with a variety of different settlement substrata.

Experiment 3: Interspecific variability of algal effects on planular survival and settlement

To determine if the effects of algae on coral planulae were common across algal taxa, we compared the effects of four different species of macroalgae (the green alga *Ulva fasciata*, the red algae *Acanthophora spicifera* and *Pterocladiella caerulescens* and the brown alga *Sargassum polyphyllum*) on planular survival and settlement. These species represent a taxonomic spectrum of locally common algal species, together accounting for 26.1% of all algae at the collection site (M.J.A. Vermeij, unpublished data).

Algal fragments were collected at Kahekili at 1–2 m depth. Small samples of algae (1.5 g wet weight) were added to petri dishes and regularly clipped during the experiment to account for growth and thus maintain for constant size. Approximately 50 planulae (43 h post spawning) were added to each dish (n = 4 for each algal treatment). Survivorship and settlement rates were estimated as described in Experiment 2 above.

Statistical analyses

The design of this study enables comparisons of survivorship and settlement probabilities of *M. capitata* planulae across various treatments. Replication of planular treatments across independent petri dishes provides statistical power to assess the proportion of individuals surviving (or settling) under a particular condition. In addition, each planula within a petri dish provides another unit of replication testing for treatment effects on survivorship, as the variability of survivorship proportions is likely to be a function of the density of individuals within each replicate dish. We assumed that the probability of survivorship for individuals within petri dishes was a function of experimental conditions, but that survivorship of each individual was independent of the fate of neighbors within the dish. As such, we assumed that dish-specific survivorship data (i.e., proportion of surviving planulae relative to the starting density) and settlement data (i.e., proportion of settling planulae relative to starting density) were binomially distributed. Starting density is defined as the actual density of planulae in each petri dish at the beginning of each experiment. We aimed seeding petri dishes at starting densities of 10, 50,

100, 200 and 400 planulae per dish, but actual densities varied slightly from these targeted densities. To test specific hypotheses while addressing such statistical details of these survivorship data, we employed an explicit binomial error structure for all analyses.

Experiment 1

To estimate the interacting effects of density and microbial concentration on planular survival, we compared the relative fits of a series of complementary binomial regression models. We used a non-linear, exponential model to describe the survivorship probability in dish i, s_i, with density, ρ_i, as $s_i = \alpha \exp(\alpha \rho_i)$ where α and β are estimated parameters. The best-fit parameters were estimated by the Nelder–Mead optimization algorithm in R (http://www.R-project.org).

For both pre- and post-settlement data, we considered survivorship data (i.e., proportion of surviving planulae relative to the starting density) to address two questions: (1) was survivorship best described as density-dependent and (2) was the degree of density dependence similar or different in the +AMP treatments (+ALG and −ALG)? The importance of the density-dependent term, β, was determined independently for both ampicillin treatments (−AMP and +AMP) by comparing the fit of the complete model to the nested model with $\beta = 0$, i.e., assuming that density has no effect on planular survival. To test for differences of the density-dependent terms across ampicillin treatments, the relative fit of a full model was compared to the nested model, assuming the density-dependent terms to be the same across treatments (i.e., $\beta_{-AMP} \neq \beta_{+AMP}$ vs. $\beta_{-AMP} = \beta_{+AMP}$). In both cases, a likelihood ratio test was used to determine the degree of significance for the added parameter relative to the nested model. As such, we assumed that planular mortality was density dependent if β was significantly less than zero and that microbes mediated the density-dependent effect if the density dependence was significantly weaker in the +AMP treatments (i.e., $\beta_{-AMP} < \beta_{+AMP}$).

For the sake of completeness, we tested for the independence of the density independent terms, α_{-AMP} and α_{+AMP}, similarly as described above. Detailed statistical output is presented in the Supplemental Material.

Experiments 2 and 3

To test for differences among treatments within each experiment, we compared the relative fits of a broad suite of demographic models. We assumed that survivorship (or settlement) within each treatment was determined by a single parameter, s_x, such that the proportion of planulae surviving (or surviving and settling) at the end of the

experiment was binomially distributed around the expectation, $n_{j,x}s_x$, where n_j is the initial density in petri dish j exposed to treatment x. The goal was to determine the most parsimonious collection of parameters to describe the observed survivorship (or settlement) data across the four treatments. For each experiment, the best-fit values of 15 distinct parameter combinations were estimated (i.e., all combinations of parameters for each 1, 2, 3 and 4 total parameters; see Statistical Appendix). The best combination of parameters was selected using Akaike's Information Criteria (when the number of parameters was different) and based on an assumption of equal Bayesian prior expectations (when the number of parameters was the same). See Hilborn and Mangel (1997) for more details on this statistical approach.

Results

Field study

The density of *M. capitata* recruits decreased with increasing algal abundance in the field (Fig. 1). A negative exponential model was strongly favored over the nested model with constant recruitment ($p < 0.001$). Low recruitment in algal-dominated areas suggests either a direct or indirect negative effect of algae on coral planular settlement and survival.
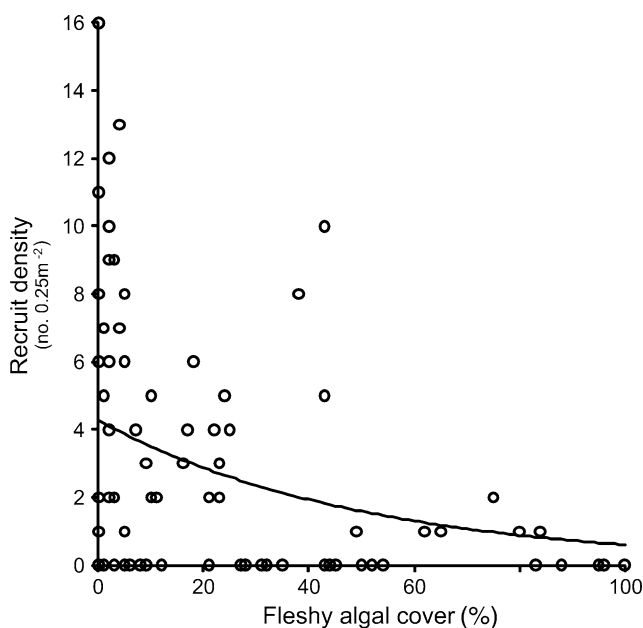

Fig. 1 The negative relationship between the density of *Montipora* coral recruits (one to three polyps) and increasing fleshy algal cover on the reef at Kahekili Beach Park between depths of 3–6 m. The *line* represents the best-fit model; recruits per 0.25 m² = 4.28 exp (−0.02 × algal cover)

Planular developmental phases

At approximately 40 h post spawning, planulae of *M. capitata* started swimming up and down within the water column. After 79 h post-spawning, planulae gradually started moving across the petri dish bottom, but settlement did not occur until 179 h post spawning. The period between 43 and 80 h post spawning was hence deemed pre-settlement period, the period between 80 and 179 h post spawning was deemed the benthic exploration phase, and the actual settlement period covered the 179–456 h post spawning interval. Some planulae did not settle after 457 h and either kept swimming or lay motionless on the bottom of the petri dish until the experiment was terminated at 1,032 h post spawning.

Experiment 1

Proportional mortality rates of planulae increased with increasing planular density during the pre-settlement period when all planulae were swimming in the water column. During the early settlement period, mortality rates decreased overall, but still increased with increasing planular density (Fig. 2 a, b). When ampicillin was added, planular mortality rates decreased by 74.3% and by 6.7% during the pre- and early post-settlement periods, respectively, across all densities (Fig. 2).

Experiment 2

Average planular survival rates were reduced in the presence of macroalgae relative to controls (Fig. 3). When algae were present, the percentage of surviving planulae dropped between 9 and 55% (mean 39%, SD 14) relative to 53 and 81% for the controls (mean 63%, SD 8). Mortality rates generally declined as planulae started exploring the bottom (∼80 h). Settlement was first observed 179 h post-spawning in the −ALG and −AMP treatment and followed soon thereafter in all other treatments, albeit that settlement was extremely low in both of the +AMP treatments (Fig. 4). Planulae that had not settled after 457 h did not settle for the remainder of the experiment (1,032 h) and either kept swimming or lay motionless on the bottom of the petri dish. In both of the antibiotics treatments, less than 3% of the surviving planulae settled, and settlement success approached zero, with no effects of algal presence. Without antibiotics, i.e., with microbes present, settlement rates were not affected by the presence of algae, and 15.3% (SD 18.7, $n = 5$) and 30.0% (SD 15.1, $n = 5$) of the surviving planulae had settled in the +ALG and −ALG treatment after 457 h, respectively. Less than 1% of the planulae settled on crustose coralline algae,
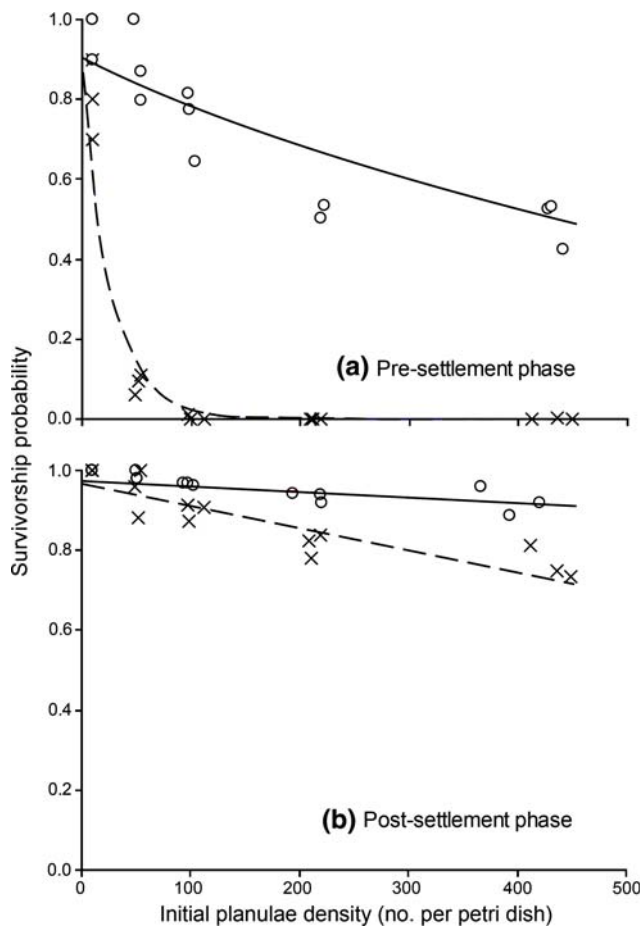
Fig. 2 Survivorship of *Montipora* planulae shown as the probability that planulae survive for 20 h as a function of planular density during the **a** pre-settlement period (starting 43 h post spawning) and **b** post-settlement period (starting 179 h post spawning). *Markers* indicate the observed survivorship probabilities when microbes are absent (*solid line*) or present (*dashed line*). *Lines* indicate best-fit models when microbes are absent (*solid line*) or present (*dashed line*). See Electronic Appendix S1 and S2 for statistical details

Fig. 3 Survivorship of *M. capitata* planulae (mean proportion +1 SE) of planulae surviving between 131 and 361 h post spawning in absence (−) or presence (+) of algae and absence or presence of microbes (+AMP, −AMP, respectively). *Letters* above the bars indicate significant differences ($p < 0.05$) between values based on maximum likelihood analyses. See Electronic Appendix S3 for statistical details

Fig. 4 Settlement of *M. capitata* planulae (mean proportion + 1 SE). The proportion of planulae that survived and settled 361 h post spawning is shown in absence (−) or presence (+) of algae and absence or presence of microbes (+AMP, −AMP, respectively). Note that none of the planulae in the +Algae, +AMP treatment survived and/or settled. *Letters* above the bars indicate significant differences ($p < 0.05$) between values based on maximum likelihood analyses. See Electronic Appendix S4 for statistical details

terra-cotta chips or substrates overgrown with diatoms, and no preference for any of these potential settlement substrates was observed (χ^2, $p > 0.05$). Planulae generally settled on the petri dish surfaces except in the +ALG and −AMP treatment where 92.7% of the settlers settled directly on the macroalgal surfaces (SD 40.8, $n = 4$).

Overall, antibiotic treatments greatly reduced settlement success, whereas algal presence did not. Settlement was similar between the +ALG/−AMP and the −ALG/−AMP treatments, although the majority of planulae settled on algal surfaces in the +ALG/−AMP treatment, despite the presence of alternative settlement substrata. The majority of settlers on algal surfaces (i.e., 52 out of a total 54) died between 457 and 1,032 h, whereas all individuals that had settled on the dish surface survived.
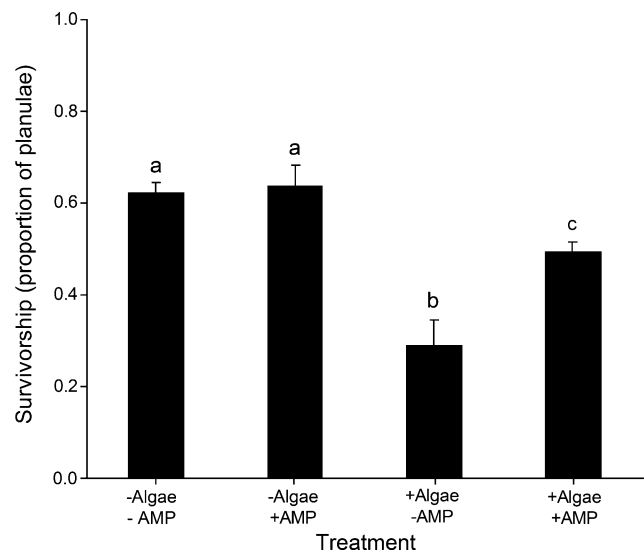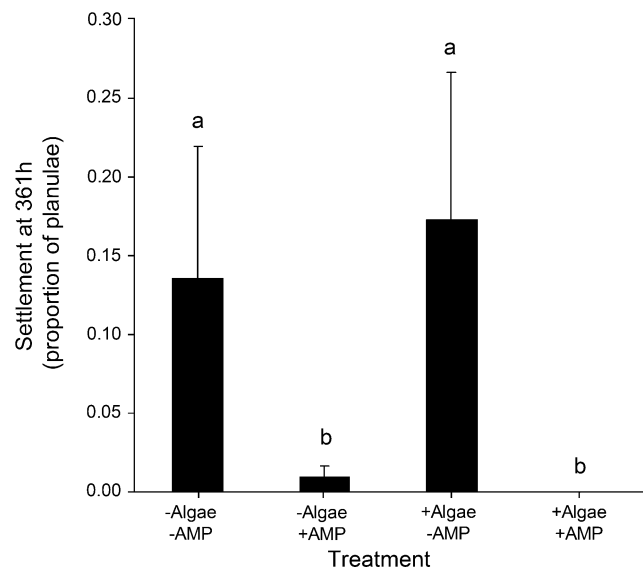
Experiment 3

The degree to which algae increased planular mortality rates differed among algal species (Fig. 5a) and became
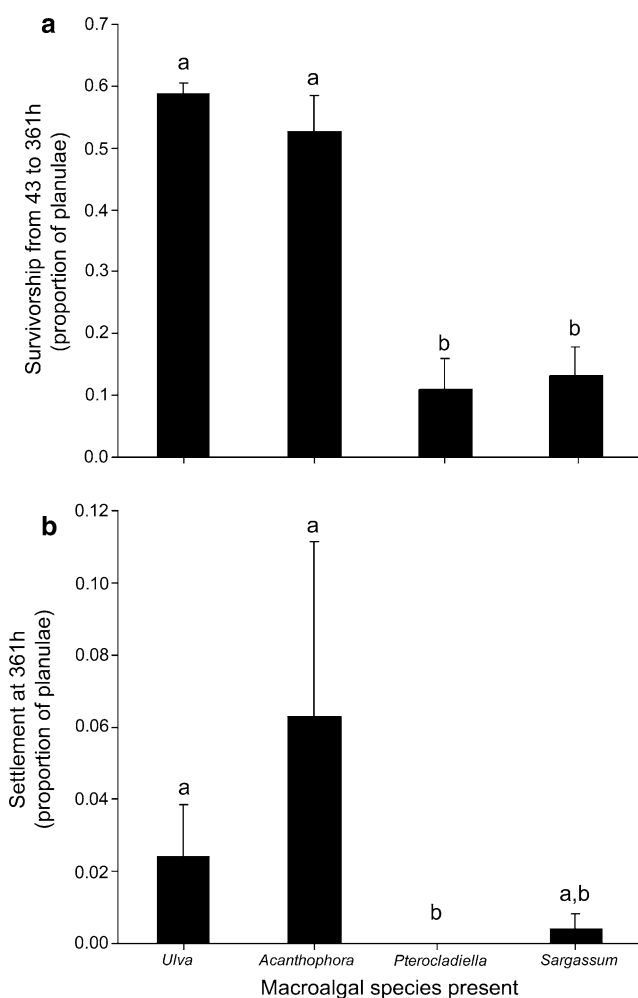
Fig. 5 **a** Survivorship and **b** settlement of *M. capitata* planulae (mean proportion +1 SE) as a response to the presence of four common Hawaiian macroalgal species. Note that none of the planulae in the *Pterocladiella* treatment settled. *Letters* above the bars indicate significant differences ($p < 0.05$) between values based on maximum likelihood analyses. See Electronic Appendix S5 for statistical details

evident 64 h after the algae were added. Mortality rates were higher for planulae in treatments with *S. polyphyllum* or *P. caerulescens* in comparison to the other two algal species. Mortality was lowest for planulae in treatments with *U. fasciata*, the alga used in our main experiment, and was intermediate for *A. spicifera*, although mortality rates in response to these species became similar after 311 h.

Planulae settled in all algal treatments, but settlement was extremely low when planulae were confronted with *S. polyphyllum* and *P. caerulescens*. In the latter case, all settlers had died after 361 h, and only 0.6% of the initial number of planulae settled on average in the *Sargassum* treatment (Fig. 5b). Only the settlers in the *Acanthophora* and *Ulva* treatment that had settled on the petri dish surface survived until 1,032 h. Planulae never settled on *Acanthophora*, but did so with all other algal species. During the

highest levels of settlement, 26.7% (SD 9.4, *n* = 2) of the surviving planulae settled on *Sargassum* (at *t* = 265 h) and 79.1% (SD 39.6, *n* = 4) on *Ulva* (at *t* = 256 and 361). None of the settlers on algal surfaces survived beyond 457 h.

Discussion

Algal-induced, microbe-mediated mortality of planulae

Many coral reefs are shifting from domination by reef-building corals to domination by fleshy algae, though the mechanisms leading to this transition remain unclear (McCook et al. 2001). Passive colonization of space previously occupied by stony corals is often interpreted as evidence for active competition between corals and algae through overgrowth, abrasion and shading. However, few studies have experimentally tested whether algal growth is a cause rather than a consequence of coral mortality (McCook et al. 2001). The studies that have examined whether algae can kill adult coral colonies have rarely found evidence that active overgrowth of live coral tissue occurs (McCook 2001; Jompa and McCook 2003; Nugues et al. 2004b). Much less is known about the interaction between coral larvae and algae, but understanding these interactions is important for the development of effective reef restoration activities.

For many marine species, it is during the early life-history stages that most population-structuring dynamics occur (Caley et al. 1996; Vermeij and Sandin 2008). For example, settlement and survivorship of coral recruits have been shown to be reduced in areas of high fleshy algal cover (Birkeland 1977; Hughes 1989; Edmunds and Carpenter 2001). On the reefs of Hawaii, we demonstrate a clear, negative relationship between density of early life-history corals (1–3 polyps) and fleshy algal cover (Fig. 1). Further, we demonstrate experimentally that algae, microbes and coral planulae have dynamic relationships that change though time and can be species specific.

Here, we found evidence that algal-induced, microbe-mediated mortality occurs for the earliest life-history stages of the common Hawaiian reef-building coral *M. capitata*. We found that when planulae are in the presence of fleshy algae during their benthic exploration and settlement phases, their mortality rates increase relative to controls. However, this increase in mortality was greatly reduced when antibiotics were added, suggesting that microbes caused the increase in mortality. Algae are known to exude organic compounds (e.g., excess photosynthate/DOC: Khailov and Burlakova 1969; Wetzel 1982; Cole et al. 1982; Stanley et al. 2003), which can lead to accelerated microbial growth (Cole et al. 1982; Aluwihare et al. 1997; Aluwihare and Repeta 1999), and in turn can result in coral

mortality, likely as a result of hypoxia (Kline et al. 2006; Smith et al. 2006). A second explanation for our findings is that algae exude allelopathic chemicals that lower the resistance of planulae to opportunistic microbes. Planulae may then become more susceptible to microbial infection, either through primary pathogens or because the natural microbial community increases in abundance as it can no longer be controlled by the coral's defense mechanisms. Planulae naturally harbor antimicrobial compounds (Lindquist et al. 1992; Lindquist 2002; Koh 1997; Slattery et al. 1999), indicating that microbes may negatively affect planulae when both co-occur in the natural environment. Regardless of the specific mechanism, this study and that of Smith et al. (2006) suggest that algae may shift the competitive balance between microbes and corals, including their planulae, leading to increases in coral mortality rates. These indirect, algal-induced sources of coral mortality complement a variety of other known mechanisms leading to coral mortality, such as disease (Harvell et al. 1999), predation (Cumming 1999) and environmental stress (Hoegh-Guldberg 1999).

Likelihood of proposed scenario in a reef setting

Our results show that the presence of four algal species, representing very different life-history strategies, all lead to increased planular mortality rates, highlighting the potential negative effects that fleshy algae have on the earliest life stages of corals. A negative relationship between algal abundance and recruit density was also observed in the field (Vermeij and Sandin 2008; Fig. 1), lending support for the field relevance of our small-scale experimental results. Our data suggest that algal community structure plays an important role in determining the local survival probabilities of coral planulae as different algal species affect planulae in different ways (Fig. 5). Species-specific effects of macroalgae on adult or juvenile corals have been observed elsewhere (Jompa and McCook 2003; Birrell et al. 2005; Smith et al. 2006), and because tropical macroalgal species vary so widely in their growth rates, physiology and, specifically, release rates of allelochemicals (Gross 2003) and/or photosynthates (Khailov and Burlakova 1969; Brylinsky 1977), it is unlikely that generalizations can be made about the effects of all "fleshy" or "macro"-algae on coral-microbe-algal interactions.

While manipulative laboratory experiments such as ours are likely to have artifacts such as unnatural water flow and limited space, they are also extremely useful in studies of coral planulae as it is difficult to study their behavior in the field due to their small size and high mobility. Much of what we know today about planulae is derived from studies where planulae were kept in the laboratory, e.g., habitat recognition (e.g., Harrington et al. 2004), complex and adaptive behavior (e.g., Vermeij et al. 2006) and metamor-

phic responses to microbial biofilms (Webster et al. 2004). Nevertheless, caution is required when speculating about the commonality of these phenomena in a field environment. We argue that these laboratory results identify the presence of algal-induced, microbe-mediated mortality of corals and planulae. However, several factors will influence its expression in the field, including (1) water flow, as reduced flow in benthic microhabitats and/or within the benthic boundary layer will contribute to higher DOC/allelochemicals accumulation in the direct vicinity of the algal thallus (Bak and Borsboom 1984) and thus increase mortality rates, (2) coral colony size as small colonies (typical for recent coral settlers) are more likely than larger colonies to fall entirely within the spatial scale over which a single alga can stimulate microbial communities and (3) algal abundance because in areas where fleshy algae are abundant the water column is more likely to be enriched in DOC/allelochemicals, increasing the spatial scale over which corals may be impacted.

Small coral colonies, especially recent settlers, are likely to be more prone to algal-induced, microbially mediated mortality, especially when fleshy algae are highly abundant, suggesting that benthic community structure is important in developing reef restoration strategies. This expectation is corroborated by phenomenological observations that coral recruitment is indeed lower in areas where the abundance of fleshy algae is high (Rogers et al. 1984; Hughes 1989; Edmunds and Carpenter 2001; Birrell et al. 2005; Kuffner et al. 2006; Hughes et al. 2007; Mumby et al. 2007) and mortality rates of colonies increase towards smaller colony sizes (Nugues 2002; Vermeij 2006; Vermeij and Sandin 2008). In contrast to these correlational studies, our study and that of Kuffner et al. (2006) provide a mechanistic pathway linking fleshy algal growth to coral mortality, such that stimulation of microbial communities by macroalgal production can increase recruitment failure in tropical stony corals. Subsequent investigations of microbial concentrations and benthic community composition in reef environments are necessary to test these hypotheses across broader spatial and temporal scales.

Successful recruitment is further hampered as the planulae in this study often settled on the algal surfaces, a phenomenon that has been observed in other algae–planulae interactions (Nugues and Szmant 2006). Planulae that settle in macroalgal-dominated areas thus not only suffer from increased indirect, algal-induced mortality, but also experience lower recruitment success as algae are unlikely to serve as stable substratum for future colony growth. Again, species-specific effects likely confound the generality of this statement as planulae of other coral species actively avoid macroalgae (Baird and Morse 2004; Kuffner et al. 2006).

The effect of microbes on successful coral recruitment varies among planular developmental stages

During the planktonic and benthic exploration phase (43–79 and 80–179 h post-spawning, respectively), treatments without ampicillin showed increased planular mortality, either directly (pre-settlement phase) or indirectly through algal stimulation (benthic exploration phase). Many coral planulae possess antimicrobial compounds to oppose the detrimental effects of microbes (Lindquist et al. 1992; Lindquist 2002; Koh 1997; Slattery et al. 1999). However, mortality becomes unavoidable when coral planulae are present in high densities. At high planular densities, microbial populations likely increase as nutrients become available after lysis of dead planulae, while overall transmission probabilities increase. Caution is required when applying these findings to the field, as planular densities in this study are likely artificially high due to a lack of dilution and planular dispersal. Nevertheless, they suggest a strong influence of microbes and planular age on survivorship during the earliest stages of a coral's life.

Interestingly, ampicillin additions reduced settlement success following the benthic exploration phase (>179 h). In all ampicillin treatments, settlement success approached zero, possibly suggesting that microbes are needed for successful planular settlement. Bacterial biofilms are indeed known to serve as attractants for coral settlement and/or may be needed to induce metamorphosis (Neumann 1979; Richmond 1987; Morse et al. 1988; Golbuu et al. 1995; Zaslow and Benayahu 1996 and references therein; Leitz 1997; Heyward and Negri 1999; Negri et al. 2001; Webster et al. 2004). Microbes in a reef environment appear to contribute to higher planular mortality during the pre-settlement and benthic exploration phase, but may be important for successful settlement and/or metamorphosis in scleractinian corals (see also: Zaslow and Benayahu 1996; Negri et al. 2001; Webster et al. 2004). These apparently opposing effects of microbial presence on planular survival and settlement could be a result of distinct microbial communities that may reside in the water column versus on the benthos (Frias-Lopez et al. 2002).

Conclusion

Microbes have been shown to cause coral mortality when pathogens reach susceptible colonies, leading to coral disease (Harvell et al. 1999; Lesser et al. 2007 and references therein), and when natural microbial communities become fertilized (Kuntz et al. 2005; Smith et al. 2006). Furthermore, microbes influence coral population structure (Vermeij 2005) and serve as a mediating component in coral-algal interactions, either directly (Nugues et al.

2004a; Kuffner et al. 2006) or indirectly (Smith et al. 2006, this study). We are only now beginning to understand the role that microbes play in mediating ecological processes and/or in structuring communities. Future research should seek to understand how coral/algal/microbial interactions vary across space, time and across different forms of natural and anthropogenic disturbances. The unexplored interactions that exist between macroscopic reef organisms and microbes deserve critical attention in the light of increasing pollution and degradation of reef systems worldwide.

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