ALGAE-CORAL INTERACTIONS: MEDIATION OF CORAL SETTLEMENT, EARLY SURVIVAL, AND GROWTH BY MACROALGAE

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ABSTRACT

Degraded coral reefs are often colonized by macroalgae, which can impede coral reestablishment. However, impacts of abundant macroalgae have not been well-established for juvenile stages of coral. This study examined the effects of morphology and chemistry of four species of macroalgae on the early life history of the coral *Pocillopora damicornis* in laboratory aquaria. Morphologies of *Sargassum polycystum* and *Laurencia papillosa* significantly inhibited larval settlement (*S. polycystum* and *L. papillosa*: <30% settlement, vs. algae-free control: 60% settlement), while their exudates enhanced settlement (*S. polycystum*: 67% ± 6%; *L. papillosa*: 71% ± 4%; control: 20% ± 4%). Neither morphology nor exudates of *Halimeda opuntia* and *Peyssonnelia rubra* significantly affected larval settlement. Juveniles survived less in aquaria containing *H. opuntia*, while survival was facilitated in aquaria with *P. rubra*. Growth was also affected differentially; colonies growing with *L. papillosa* (5 ± 0.8 polyps per colony) and *S. polycystum* (4 ± 0.1 polyps/colony) were significantly smaller at three months than those growing with *H. opuntia* (6 ± 0.9 polyps/colony) and *P. rubra* (6 ± 0.6 polyps/colony). These data suggest that the effects of macroalgae on early life history stages of corals are complex and long-term, and vary between species.

Introduction

Coral reefs are degrading worldwide (Wilkinson, 2002) and efforts to understand the processes affecting recovery are in their most initial stages (e.g., Connell *et al.*, 1997; Hughes *et al.*, 1999). Degraded reefs often undergo a phase shift from abundant

corals to abundant macroalgae (Done, 1992; Hughes, 1994). Such shifts can result in lower fish biomass, coral biodiversity, and productivity, with a resulting loss of income for those dependent on reef resources. There is a widespread concern that this degradation is the result of human impact, though the relationship between anthropogenic stress and coral-to-algae phase shifts are poorly understood (McCook, 1999; Szmant, 2002).

Macroalgae and corals are competitors and increased abundance of macroalgae will lead to declines in coral populations (McCook, 1999). Brown fleshy algae colonize most of the hard substratum (dead corals and limestone) of previously dynamited reefs in the Central Philippines (Calumpong *et al.,* 1997a; 1997b), and a similar condition was observed in Kenyan lagoons (McClanahan *et al.,* 1996) and Jamaican reefs after a severe overfishing and mass mortality of the echinoid, *Diadema antillarum* (Hughes, 1994). Macroalgae are capable of overgrowing corals (Coyer *et al.,* 1993; Miller and Hay, 1996), which reduces coral cover, growth, and fecundity (Tanner, 1995). In addition, algae also cause abrasion and tentacle retraction, facilitating algal overgrowth and inhibiting feeding in corals (Coyer *et al.,* 1993; Miller and Hay, 1996). Experimental algal reduction in Kenyan lagoons increased coral cover by 5% within 6 months (McClanahan *et al.,* 1999).

Previous studies have reported that various algal species contain secondary metabolites which may function as anti-microbial and anti-fouling agents (Schmitt *et al.,* 1995; Hay,1996), herbivore deterrents, or as allelopathic agents to invertebrate larvae (Hay, 1996). Schmitt *et al.* (1995) exposed bryozoan larvae, *Bugula neritina,* to extracts of the brown alga *Dictyota menstrualis.* The alga was found to inhibit settlement and cause mortality and abnormal or reduced development in larvae settling near the thallus. Similarly, larvae of *B. neritina* and *Hydroides elegans,* a polychaete tube worm, either were immediately killed or failed to settle when exposed to waters conditioned with the algae *Dictyota sandvicensis* and *Laurencia cartaginea* (Walters *et al.,* 1996).

In contrast, some macroalgae have facilitative effects on invertebrate and coral larvae settlement. Aplysiid veligers showed high settlement and metamorphosis in the presence of certain algal species, suggesting that the algae release a metamorphosis cue for this species (Switzer-Dunlap and Hadfield, 1977; Otsuka *et al.*, 1981). Larval metamorphosis and settlement in polychaetes (Walters *et al.*, 1996), abalones (Morse and Morse, 1996; Jensen *et al.*, 1990), the crown-of-thorns starfish (Johnson *et al.*, 1991), and corals (Morse and Morse *et al.*, 1998; Heyward and Negri, 1999) were also found to be triggered by specific species of algae.

These data reveal a number of diverse functions of macroalgae on reefs; some deterrent and competitive to corals; others, beneficial. The application of such information to coral colonization and recovery after disturbance has only recently been considered in light of observations of competitive replacement of corals by macroalgae. One factor which may affect coral reestablishment is the ability of larvae to recognize highly specific physical and chemical cues (Morse and Morse, 1996; Babcock and Mundy, 1996). To date, very few species of algae are known to facilitate coral larval settlement. In degraded reefs where these settlement cues are absent, recolonization and recovery may be inhibited. A better understanding of the species that inhibit or facilitate coral settlement and/or early survival is therefore essential. Natural recovery via larval recruitment may be slow to non-existent, depending on the nature of the disturbance (Birkeland, 1977; Alcala and Gomez, 1985). Since data suggest that the mechanisms by which algae mediate coral recruitment on reefs are highly variable and species-specific, it is important to quantify these interactions in all stages of the coral life history. This is particularly important for species of algae with the potential to dominate in disturbed reef communities. In this study, we present experimental evidence on the facilitative and inhibitory effects of four common species of algae on the settlement, early survival, and growth of the coral *Pocillopora damicornis*. We hypothesize that an alga can affect settling larvae in two ways: either morphologically, due to possible shading, abrasion, or influences

on water movement of the microhabitat; or chemically, through waterborne chemicals which may either deter or attract larvae.

Materials and Methods

Larvae collection

Pocillopora damicornis colonies were collected off Bantayan, Dumaguete City (9°19.800N, 123°18.693E), central Philippines prior to new moon. Larvae collection in the laboratory followed the protocol described in Raymundo *et al.* (1997). Colonies were placed in separate buckets supplied with running seawater each night. Bucket outlets drained into 125μ plankton mesh cups which collected the planulae as they were released. Since differences in settlement success in larvae from different parents have been documented from the Bantayan population (Raymundo and Maypa, 2004), larvae in these preliminary experiments were obtained from a single parent colony, rather than pooling larvae from different parents. Although this limited the interpretation of our results, it avoided the possibility that the results observed were due to behavioral differences in larvae from different parents, rather than responses to the algal treatments. Spent colonies were returned to the reef after spawning.

Effect of morphology on settlement and survival

Experimental set-up. Planulae used in this experiment were collected during two peak spawning days from a single colony. Five control aquaria were stocked with 90 planulae and contained 12 glass substrates, previously conditioned in salt water, roughened and fitted tightly at the bottom. This ensured maximum contact between algae and planulae by providing only upper glass surfaces for settlement. The planulae were allowed to settle for 48 h without aeration, after which settlement was censused on all plates. Aquaria were subsequently supplied with running seawater for eight hours during the day and aeration at night. All aquaria were cleaned weekly for the three-month duration of the study.

Halimeda opuntia, Laurencia papillosa, Sargassum polycystum and *Peyssonnelia rubra* were chosen for this study.

All algae were abundant on surveyed reefs in the central Philippines, and represented four distinct morphologies: *Halimeda opuntia* thalli are calcareous with articulated segments; *L. papillosa* is fleshy; *S. polycystum* has a bushy-frondose morphology; and *P. rubra* is coralline and foliose. All algae collected were allowed to acclimate in laboratory tanks supplied with running seawater for two to four days. Algal thalli were cleaned of epiphytes and only intact thalli were used in the experiments. Replicate aquaria (n=6 per alga) were set up as described above. To test for the effect of morphology on larval settlement, larvae (n=90 per aquarium) were provided with three possible choices for settlement: (1) four plates with a single thallus of the assigned alga in the center of the plate; (2) four with an artificial algal thallus made of plastic coated wire and nylon stocking, mimicking the morphology of the algae inside the aquarium but without chemical exudates and thallus movement; and (3) four empty plates. Stocking, settlement, and censusing were carried out as described above.

Settlement, survival and growth. Coral spat were counted after 48 h. The distance between each coral spat to the nearest living or artificial thallus was recorded, and position of each spat on the plates was mapped. Coral spat were monitored for survival, mortality, and growth weekly after settlement until colonies were three months old, the algae being maintained in the tanks for the duration of the study. Mortality was noted by the absence of mapped spat during the subsequent census. Growth was measured by the increase in polyp number.

Effect of waterborne chemicals on settlement

The method used in this study was modified from that of Walters *et al.* (1996). Algae collected from the field were cleaned of epiphytes and allowed to acclimate for two days in laboratory tanks supplied with running seawater. For each species, intact algae were chosen and rinsed with synthetic seawater (Coralife Salts®). Algae-to-water volume ratio was 1:10. Algae in buckets were left uncovered, unaerated, and unstirred for 24 h under

natural light conditions. After 24 h, the algae-conditioned water was immediately poured into 1 L beakers (n=6 per alga) rinsed with synthetic seawater. A roughened, unconditioned glass substrate was also placed in each beaker tilted at an angle of 15° and 30 planulae were immediately added. Synthetic seawater and natural seawater controls were set up in an identical fashion. Planulae were left to settle for 48h. Half of the water in each beaker was changed every three days with either fresh algae-conditioned water or control water. Settlement and survival were monitored for 10 days.

Results

Effect of morphology on settlement, survival, and growth

All larvae in both control and treatment aquaria settled preferentially on the conditioned glass substrata, but settlement varied significantly among algal species (Table 1, Fig. 1; Kruskal-Wallis, $p = 0.0002$). Settlement was highest in aquaria with *P. rubra* (57 % $\pm$ 2.6) and *H. opuntia* (50.7% $\pm$ 1.6), but these were not significantly different from control aquaria. In *L. papillosa* and *S. polycystum* treatments, settlement was significantly lower (<30%). This suggests that the bushy frondose morphology of *S. polycystum* and the turf-forming *L. papillosa* are inhibitory to the settlement of *P. damicornis*. Settlement patterns, expressed as mean distance of spat to the nearest algal thallus, were similar in all algal treatments except in *H. opuntia* aquaria; mean settling distance of planulae was significantly closer to *H. opuntia* (20.5 $\pm$ 2.7; ANOVA, $p = 0.016$) than to *P. rubra, S. polycystum, and L. papillosa* (Table 2).

In general, highest mortality occurred during the first week, approximating Type III survivorship; succeeding weeks were significantly lower in all treatments and control aquaria (Table 1, Fig. 2; Friedman's test, $p < 0.05$). First week survival in *L. papillosa, S. polycystum* and *H. opuntia* aquaria was significantly lower than in *P. rubra* and control aquaria. At the end of the study period, similar survival patterns were seen between algal treatments though percent total survival differed between

Table 1. Summary of results of Kruskal-Wallis (KW) and ANOVA (AN) tests between algal treatments for the Morphology experiment and Waterborne chemical assay. C = Control; Pr = *Peysssonnelia rubra;* Ho = *Halimeda opuntia;* Lp = *Laurencia papillosa;* Sp = *Sargassum polycystum.*

Life history	p-value	*Post-hoc* test
Effect of morphology		
Settlement	0.0002 (KW)	C=Pr=Ho>Lp=Sp
Survival (12 weeks)	0.0001 (KW)	Pr>C>Ho>Lp>Sp
Growth (no. of polyps)	0.0067 (AN)	Pr>C>Ho>Lp=Sp
Effect of waterborne chemicals		
Settlement	0.0008 (KW)	Lp=Sp>Hp=Pr=C
Survival (10 days)	0.0005 (KW)	C=Lp=Pr=Ho>Sp

Figure 1. Maypa and Raymundo: Percent settlement (mean ± SE) of *Pocillopora damicornis* larvae in aquaria with living and artificial algal thalli. C = Control; Pr = *Peysssonnelia rubra;* Ho = *Halimeda opuntia;* Lp = *Laurencia papillosa;* Sp = *Sargassum polycystum.*

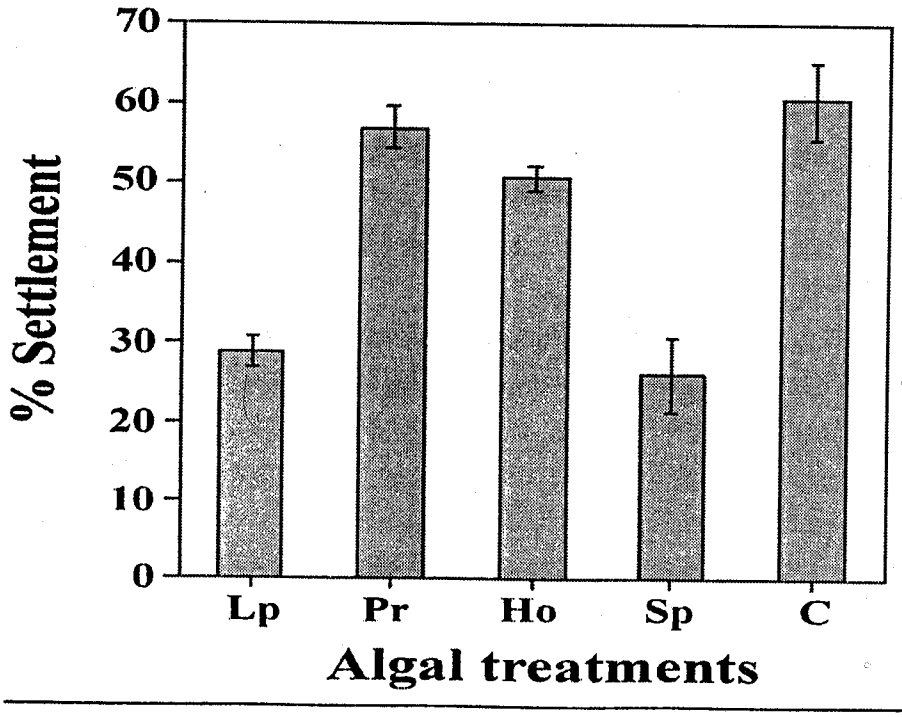


Table 2. Settlement distance of juvenile colonies to the nearest alga/fake alga and correlation between survival and distance to nearest alga/fake alga. r=Pearson Product Moment correlation coefficient. Only significant results ($p<0.05$) are presented.

Treatment	Settlement Distance (mm)	r
Halimeda opuntia	20.5 ± 2.7	0.54
Laurencia papillosa	31.4 ± 4.2	0.56
Sargassum polycystum	38.0 ± 3.3	0.65
Peyssonelia rubra	37.8 ± 5.0	0.16
artificial *S. polycystum*	41.1 ± 2.4	0.23

Figure 2. Maypa and Raymundo: Percent weekly survival (mean ± SE) of *Pocillopora damicornis* larvae in different algal treatment aquaria. N = 6 aquaria/treatment; N = 5 control aquaria.

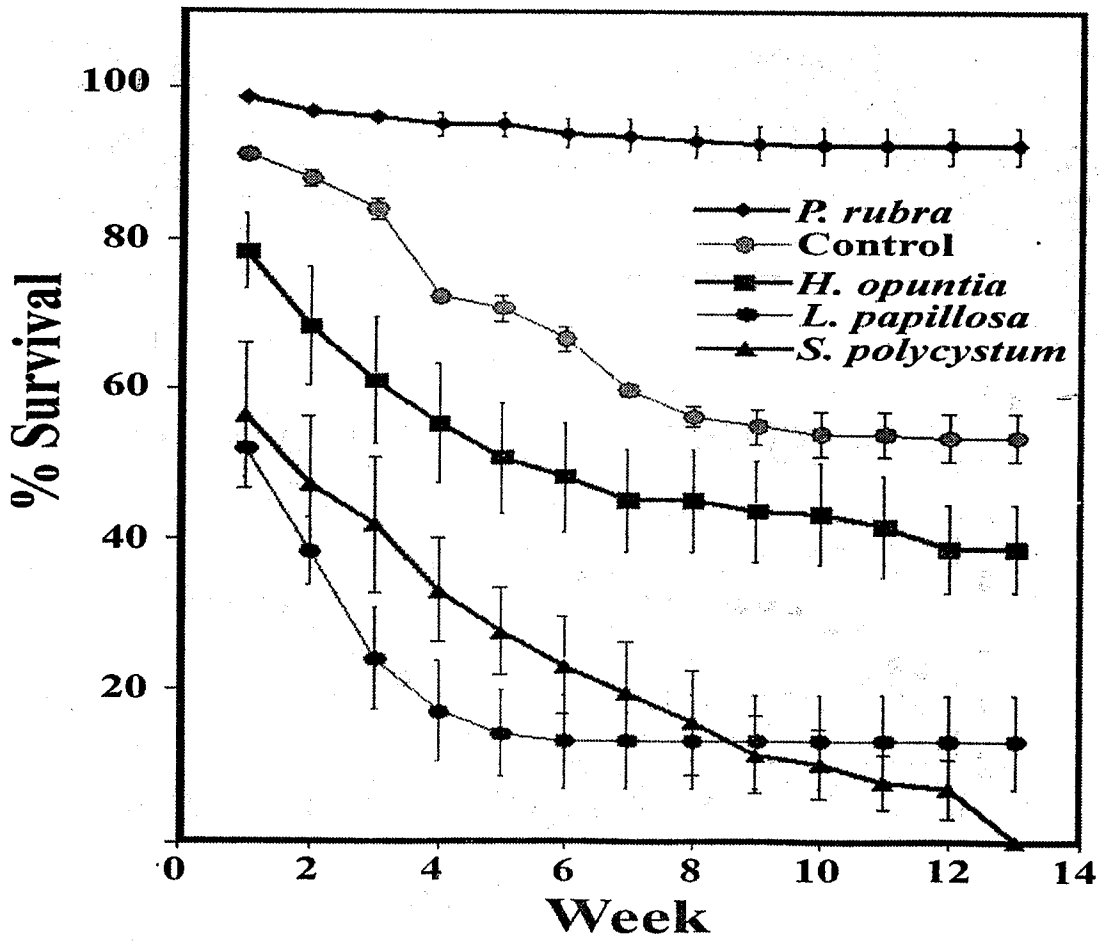
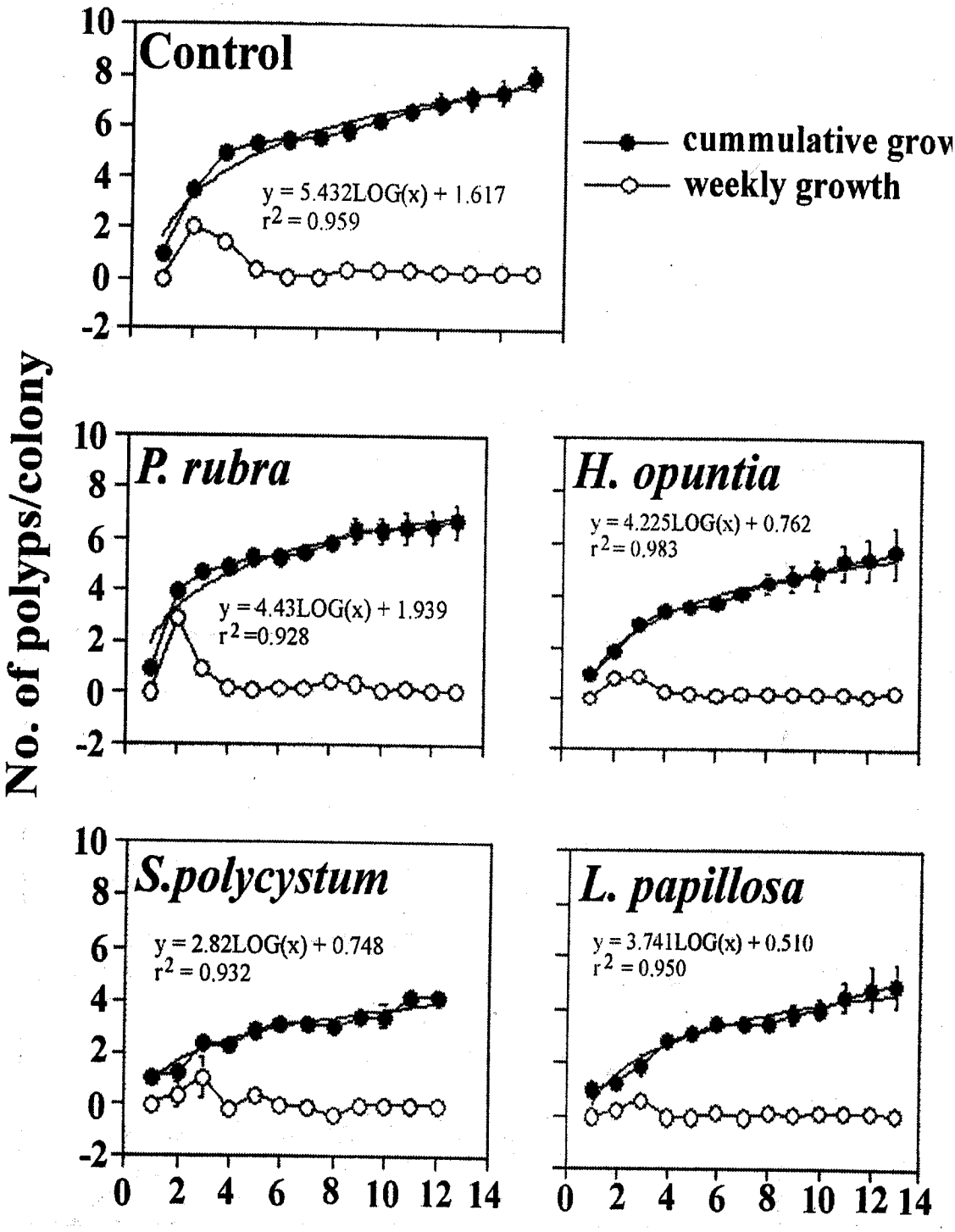


Figure 3. Maypa and Rymundo: Commulative and weekly growth rates to 13 weeks expressed as number of polyps per juvenile colony of *Pocillopora damicornis* in different algal treatments (mean ±



treatments. Total percent juvenile survival was highest in *P. rubra* (92.5% ± 2.4) and was significantly lower in *H. opuntia* (39% ± 5.8), *L. papillosa* (13.2% ± 6.2), and *S. polycystum* (0%; Kruskal-Wallis $p<0.05$).

Survival of *P. damicornis* juveniles was affected by their distance from the nearest alga or artificial alga inside the aquarium. Distance of juvenile colonies from *L. papillosa, H. opuntia, S. polycystum* and artificial *S. polycystum* were all significantly positively correlated with survival; the greater the distance between spat and algal thallus, the longer spat survived (Table 2; $p =< 0.05$). *Laurencia papillosa, H. opuntia, S. polycystum* and artificial *S. polycystum* thus had a negative influence on spat survival. No significant correlation was seen in *P. rubra* and all other artificial algae on juvenile survival. These results suggest that both morphologies of *S. polycystum* (bushy frondose) and *L. papillosa* (turf-forming) are inhibitory to both larval settlement and juvenile colony of *P. damicornis*. Although *H. opuntia* did not have any significant effect on larval settlement, it was inhibitory to juvenile survival.

Growth rates expressed as increase in polyp number per colony are shown in Figure 3. Colony growth was highest during the second and third weeks in all treatments and control aquaria, slowing and becoming fairly constant afterward. A significant difference was found in weekly growth rates between treatments (ANOVA, $F = 194.62$, $p = 0.0001$). At the end of the monitoring period, the total number of polyps per colony was significantly different between treatments (Table 1). The mean colony size in *H. opuntia* (6 ± 0.9 polyps per colony) and *P. rubra* (6 ± 0.6 polyps/colony) was not significantly different from those in the control (7 ± 0.5 polyps/colony) but was significantly higher than *L. papillosa* (5 ± 0.8 polyps/colony) and *S. polycystum* (4 ± 0.1 polyps/colony) aquaria. These findings are consistent with the settlement and survival results. The bushy frondose *S. polycystum* and turf-forming *L. papillosa* consistently inhibited the early stages of *P. damicornis* life history, while the effects of the calcareous and coralline algae, *H. opuntia* and *P. rubra,* varied.

Growth curves followed a logarithmic curve; colonies exhibited rapid initial growth, which then tapered off (Fig. 3). The lack of significant difference between slopes of growth regression lines in the different treatments indicates that growth rates showed similar trends over the three-month period (ANCOVA, $F = 1.27$, $p = 0.1242$).

Waterborne Chemical Assay

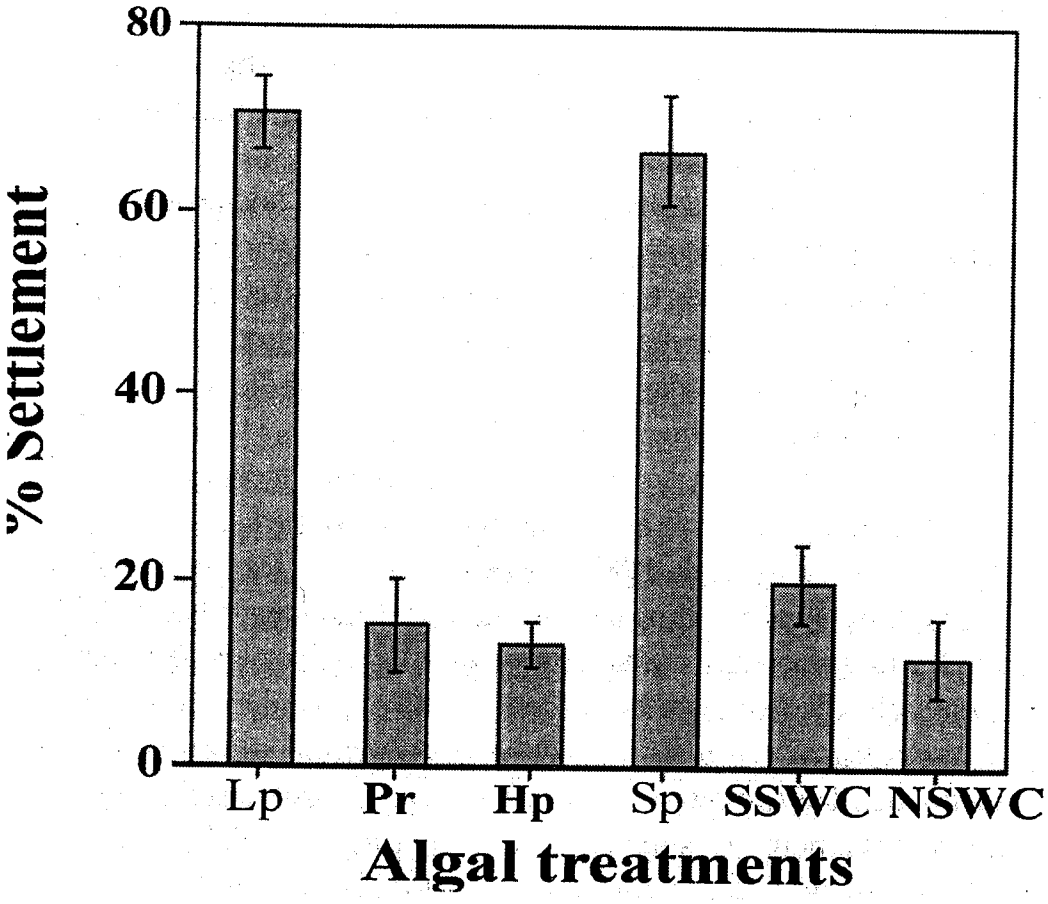
All planulae that settled by 24 hr settled on the bottom of the beakers in all algae conditioned water treatments and controls. No spat were found on the unconditioned glass plates. Settlement success of larvae varied significantly between treatments and controls. Settlement was significantly higher in *L. papillosa*- ($70.7\% \pm 4$) and *S. polycystum* (66.7 ± 6.1) conditioned water than in all others (Table 1, Fig. 4). Settlement in *H. opuntia*- and *P. rubra*- conditioned water and both controls was less than 21% and larvae that failed to settle during the first 24 h settlement period (approximately 80% per beaker) remained free-swimming during the subsequent 10-day observation period. In contrast, those that did not settle in *L. papillosa*- (29%) and *S. polycystum* – (33%) conditioned water died after 24 h.

Survival to 10 d of settled juvenile colonies was 100% in all control and algal treatments, except in *S. polycystum*. Survival in *S. polycystum*-conditioned water was significantly lower than controls and other treatments (Kruskal-Wallis, $p = 0.0005$). Spat mortality was observed daily, starting from the first day after settlement; none survived to the 10th day. This suggests that the exudates of *S. polycystum* were toxic to *P. damicornis* juvenile colonies but apparently not to larvae prior to 24 hr old.

Discussion

Settlement and metamorphosis in many marine invertebrate larvae are controlled by sensory recognition of, and responsiveness to, environmental stimuli and exogenous chemical cues provided by reef biota (reviewed in Pawlik, 1992; Morse and Morse, 1996). In this study, the variation in responses to morphology and exudates

Figure 4. Maypa and Raymundo: Percent settlement (mean ± SE) of *Pocillopora damicornis* larvae in different algae-conditioned water and controls. Pr = *Peysssonnelia rubra;* Ho = *Halimeda opuntia;* Lp = *Laurencia papillosa;* Sp = *Sargassum polycystum;* SSWC = Synthetic seawater control; NSWC = Natural sea water control; N = 6 aquaria/treatment; N = 5 control aquaria.



can be partially explained by shading. Adult *Pocillopora* spp. thrive best at high light levels as they are considered shade intolerant (Stimson, 1985). Coral planula larvae are photosensitive, responding to light as a cue for settlement, and shading—by algae or other corals—can negatively affect coral settlement, survival, and growth (Rogers, 1979; Stimson, 1985; Harrison and Wallace, 1990; Miller and Hay, 1996; Babcock and Mundy, 1996). Algal canopy consistently inhibited recruitment and growth of the coral, *Oculina arbuscula,* and shading and abrasion were suggested as

the competitive mechanisms used by the algae (Miller and Hay, 1996). Miller (1995) found that the growth of *O. arbuscula* increased by 180-560% when grown in shallow areas where algae canopy was removed. Similarly, in our study, *S. polycystum* and *L. papillosa* and their artificial algae formed a canopy-like layer in each aquaria, thereby shading the substrata and reducing settlement. *H. opuntia* did not appear to affect larval settlement in aquaria, but in reef habitats, thalli tend to spread laterally close to the substrate and form dense mats. This may potentially shade coral larvae and juveniles on reefs.

Inhibition of *P. damicornis* juvenile survival and growth by the algal morphologies may also be attributed to abrasion. Spat survival of *P. damicornis* can be negatively affected by the presence of algae (Harrigan, 1972; Harriott, 1983), and an inverse relationship between densities of the coral *Balanophyllia elegans* and macroalgae has been reported (Coyer *et al.*, 1993). Algal abrasion facilitates algal overgrowth and exhausts energy reserves by reducing feeding time and requiring energy for surface cleaning (Potts, 1977; Fadlallah, 1983; Coyer *et al.*, 1993; Tanner, 1995). In this study, algal brushing did not influence settlement since water was left undisturbed in the aquaria for 48 h. However, algal abrasion negatively affected the survival and growth of juvenile colonies in *H. opuntia, L. papillosa* and *S. polycystum* aquaria. The continuous daily inflow of seawater in each aquarium caused enough water movement to result in slow whipping actions of algal thalli. It was observed that most juvenile colonies that died early or showed partial mortality were those settled close to an alga, i.e., within the "abrasion zone." In *H. opuntia* settlement distance of juveniles was significantly closer to the alga (0.05 mm – 3 mm), compared to other algal treatments and controls. Juveniles that settled close to the alga died early or showed partial mortality. These negative effects may be a compounded result of brushing and metabolic deficits from algal shading (Miller and Hay, 1996). Although water movement in the aquaria was minimal, water movement to a varying degree is always present in the natural habitat. When coral larvae settle near an alga, or the available

settlement surfaces limit the choice of larvae to fleshy macroalgae vicinities, mortality is a possible consequence.

Macroalgae produce compounds that may affect survival and recruitment of benthic invertebrates and thus play a role in structuring marine communities (Hay and Fenical, 1988). The inhibitory and facilitative effects of algal compounds on invertebrate larvae have been documented (e.g., Morse *et al.,* 1984; Morse *et al.,* 1998; Schmitt *et al.,* 1995). In this study, the exudates of both *S. polycystum* and *L. papillosa* enhanced settlement. The lack of evidence of toxicity to larvae of *L. papillosa,* in spite of the presence of gland cells containing haloterpenoids (Young *et al.,* 1980), suggests that other water soluble compounds may be released by the alga that enhanced larval settlement. Alternatively, different species of invertebrate larvae might show differential responses to the same compound. Despite the proven toxicity of *Laurencia* terpenoids (Hay and Fenical, 1988), settlement and metamorphosis of *Aplysia* larvae were enhanced in the presence of *Laurencia* spp. (Switzer-Dunlap and Hadfield, 1979).

Unlike *Laurencia,* the secondary metabolites of brown algae, including *Sargassum,* are water- soluble and are released into the environment (Hay and Fenical, 1988). Pachidictyol-A from *D. menstrualis* (Schmitt *et al.,* 1995) caused death and abnormal development in the bryozoan *B. neritina* (Schmitt *et al.,* 1995) while exudates and boiled extracts of *Sargassum* spp. facilitated larval settlement and metamorphosis of the hydroid *Coryne uchidai* (Nishira, 1968). Similarly, larvae of *B. neritina* and the polychaete tube worm, *Hydroides elegans,* showed differential settlement responses to the same *Sargassum*-conditioned water (Walters *et al.,* 1996). Our results are consistent with previous studies. Settlement of *P. damicornis* larvae was enhanced in S. *polycystum*-conditioned water but juvenile survival was inhibited. This again suggests that invertebrate larval types respond differentially to the same algal exudates. Larval threshold differences and varying sensitiveness in different life stages in response to a particular compound or class of compounds may explain this (Walters *et al.,* 1996). Alternatively, differences in

potency and release rates of metabolites in different species may also contribute to the observed responses of different larvae. Moreover, in the case of *S. polycystum,* although the exudates of the alga enhanced larval settlement, algal thalli inhibited settlement. This shows that the positive effects of the chemical exudates can be overridden by the negative effects of morphology. Continued exposure of *P. damicornis* larvae and juvenile colonies to *S. polycystum* exudates, compounded by shading and abrasion, may explain the high mortality observed in the aquaria. These effects may partially explain the consistent absence of scleractinians in most reefs colonized by beds of *Sargassum* in the Central Philippines.

Coralline crustose algae such as *Peyssonnelia* sp. and *Hydrolithon reinboldii,* facilitate settlement and metamorphosis of *Acropora spp.* larvae (Morse *et al.,* 1996). In this study, neither the morphology nor exudates of the red crustose alga, *P. rubra,* had any discernable facilitative or inhibiting effects on *P. damicornis* larvae. This contrast with the results of Heyward and Negri (1999); 50% of *Acropora millepora* larvae were induced to metamorphose in response to *Peyssonnelia* sp. methanol extracts. However, our results showed higher colony survival in aquaria with *P. rubra* than that of the control, suggesting a chemical influence. The absence of shading and algal abrasion in *P. rubra* aquaria may have contributed to this high survival, but the potential exists for fast growing crustose coralline algae to overgrow coral juveniles (Babcock and Mundy, 1996). *Lobophora,* a crustose-foliose brown alga, can occasionally overgrow corals (De Ruyter van Steveninck *et al.,* 1988).

Halimeda spp. produce diterpenoids that may only be released through mechanical damage of the alga (Paul and Fenical, 1984). In the natural habitat, where herbivores are present, mechanical damage of algal thalli is a regular occurrence and these metabolites may be frequently released. Production of metabolites in *Halimeda* spp. increases with increasing herbivory pressure (Paul and Van Alstyne, 1988), suggesting that heavily grazed areas

may affect coral larval settlement and juvenile colony growth differently from areas with lesser pressure.

In hermatypic corals, calcification is dependent on light (Barnes and Taylor, 1973; Chalker, 1981) and coral morphology may be a function of light levels (Goreau, 1963). Reef flora that has the potential to alter substratum illumination, such as canopy-forming species, can affect the species distribution and composition of a reef. Shade-intolerant species may be selected against in such an environment. In degraded reefs already colonized by macrophytes, coral recolonization may be dependent on the species of algae present. It has been suggested in many studies that development of extensive coral growths in many shallow tropical environments may be dependent on the near elimination of macrophytes either by sea urchin and fish grazing (Hughes, 1994; Mumby, 2004) or human intervention by algal weeding or cropping (McClanahan *et al.,* 1999). In addition, coral reef degradation often involves a phase-shift from coral to macroalgae (Hughes, 1994; McCook, 1999). To prevent this phase-shift, there is an urgent need to protect herbivorous fish populations and minimize terrestrial run-off and nutrient inputs to the sea (McCook, 1999; Mumby, 2004). In reefs where long-term, severe damage has already occurred, selective algal cropping and weeding should be explored in conjunction with establishment of marine reserves, to protect herbivore populations as a management tool for rehabilitating degraded coral reefs.

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