

Factors promoting coral-algal transition in coral transplantation experiments

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Coral transplantation experiments can provide a useful platform by which to examine the overgrowth of coral by algae under different environmental conditions. The proliferation of algae on coral reefs is a serious concern at present. Under optimal conditions for coral survival and growth in the field, algal overgrowth was made possible only after extensive damage to coral tissue by gastropod predation. This was not the case, however, in land-based tanks where conditions were suboptimal for coral growth and survival, and where there was an absence of both predators and herbivores. As coral tissue deteriorated, high nutrient conditions appeared to promote a greater abundance as well as diversity of algae, notably *Enteromorpha*, *Cladophora*, *Ceramium* and *Centroceras*. In contrast, algal cover on coral transplants in the field was dominated by the genus *Hypnea*. Composition and percentage

cover of algae did not differ significantly between previously live transplants and dead coral skeletons in most treatments (two different coral species, field versus land-based tanks). There was also no significant difference in algal colonization of previously live transplants of two coral species, *Porites cylindrica* and *P. rus*. The above findings are relevant to understanding coral-algal dynamics under conditions of human induced perturbation (e.g., the depletion of herbivores, high nutrient loading). In addition, these results suggest developmental trajectories a coral community can undergo following such perturbation because different algal genera presumably are grazed on by different species of herbivores, and hence support different trophic pathways.

KEYWORDS:

algal colonization; nutrient enrichment; coral transplantation; community development

INTRODUCTION

The rapid growth of macroalgae on coral reefs is a growing environmental concern. Algal proliferation is linked to increased nutrient loading (Lapointe 1997, Lapointe et al. 2004), or to the reduction in numbers of herbivores which leads to decreased grazing on macroalgae (Hughes 1994, Lapointe et al. 2004). Macroalgae are well known to be competitors of corals for space and light (Miller and Hay 1998, Lirman 2001, McCook et al.

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2001). They can cause damage to coral tissue, or the demise of coral colonies. However, the debate continues as to whether the algae themselves are capable of outcompeting, and then overgrowing, healthy coral colonies. It is believed that algal spores or filaments generally do not settle directly on live corals (McCook et al. 2001, Diaz-Pulido and McCook 2004). However, when established algae come in direct contact with corals on the reef, this can cause shading, tissue abrasion, and/or overgrowth (Quan-Young and Espinoza-Avalos 2006). Abrasive contact or overgrowth can eventually result in partial or total coral mortality. Live corals are also capable of overgrowing algae (Diaz-Pulido et al. 2009) and can inhibit algal growth as well (Jompa and McCook 2002, Nugues et al. 2004). It is widely believed that the coral must be weakened or killed first before algal invasion can occur (McCook et al. 1997, McCook 2001, Jompa and McCook 2002). In the Great Barrier Reef, for example, it appears that healthy *Porites lobata* are able to resist algal colonization or overgrowth by mucus secretion, so that a colony must be injured first before algae can invade (McCook 2001). Dead coral skeletons are frequently observed to be rapidly covered by algae (Diaz-Pulido and McCook 2002). Once established, algal populations tend to persist, thus hindering reestablishment of coral populations via recruitment (Birrell et al. 2005, Kuffner et al. 2006) or the regrowth of adult colonies.

Coral transplantation is a tool for coral restoration or reef rehabilitation at the local scale (Yap 2000). However, coral transplantation has met with varying degrees of success. Algal overgrowth is one major problem (Yap and Molina 2003, Dizon and Yap 2005, Palomar et al. 2009, Shaish et al. 2010). It can be a significant factor that hampers the success of coral restoration efforts because of reduced growth or mortality of the transplants. Under certain conditions, coral transplants appear unable to resist algal invasion, and eventually die, apparently because of smothering (Bruckner and Bruckner 2001, Dizon and Yap 2006). In several experiments, corals attached either to artificial substrates that were placed on the bottom, or directly to the reef substrate itself, suffered overgrowth by algae, and some of them succumbed after a period of time (Coyer et al. 1993, Potts 1977, Bruckner and Bruckner 2001). In some cases, algae were observed to cause bleaching of the underlying coral tissue (Rojas et al. 2008). The bleached tissue subsequently deteriorated. Contact with algae can cause direct stress to coral tissue, after which the algae proceed to overgrow the coral (Quan-Young and Espinoza-Avalos 2006). In experiments where the performance of coral transplants in the presence of algae was compared with that of corals in cleared plots, transplants in the latter instances survived better (Miller and Hay 1996, Soong and Chen 2003).

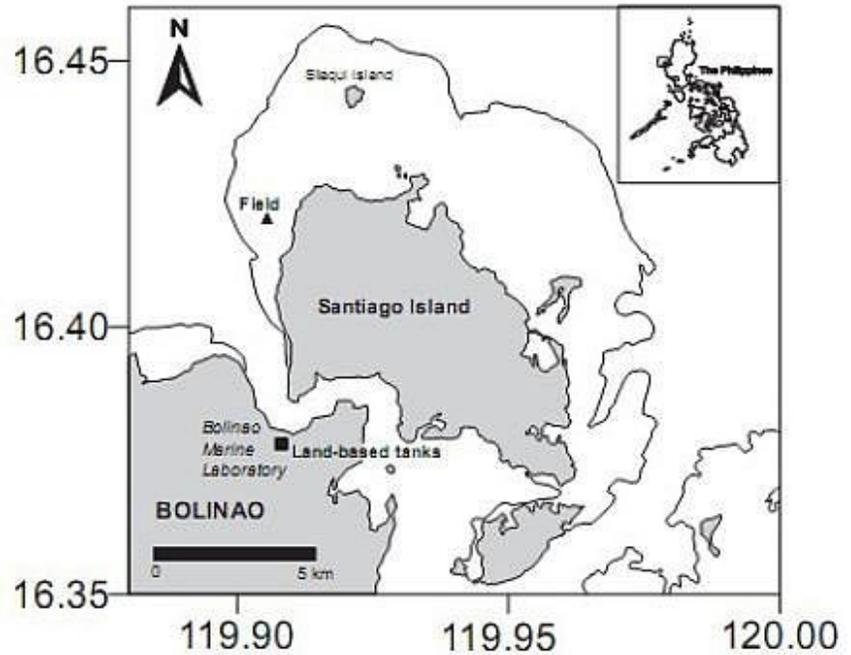


Figure 1. Map indicating location of grids containing coral transplants in the field and in the land-based tanks.

Coral transplantation experiments can serve as a useful platform for following closely the dynamics of algal colonization on corals, and other aspects of coral-algal interactions. A previous study (Yap and Molina 2003) compared responses of coral transplants of two species, *Porites cylindrica* and *P. rus* (Order Scleractinia), under different experimental conditions, viz. under natural conditions in the field, and in semi-enclosed land-based tanks. Coral transplants in the field are exposed to natural levels of light, temperature, water movement, nutrient levels, sedimentation and other factors crucial to growth and survival. However, corals are also subject to the full range of competition and predation from other species present in the natural community. Conditions in land-based tanks are controlled within certain ranges, but do not necessarily always approximate natural conditions.

In the present study, the process of algal overgrowth was examined in corals exposed to different experimental conditions as described above. Transplants were maintained and closely monitored until mortality occurred. In all cases, the previously live transplants were completely covered by macroalgae at the time of death, and were collected for analysis. Comparisons of algal cover were also made between previously live transplants and previously dead skeletons of the same species. The specific objectives of the study were: (1) to describe the process of algal colonization on previously live coral; (2) to compare patterns between two different hard coral species; and (3) to contrast trends between the natural environment and semi-enclosed

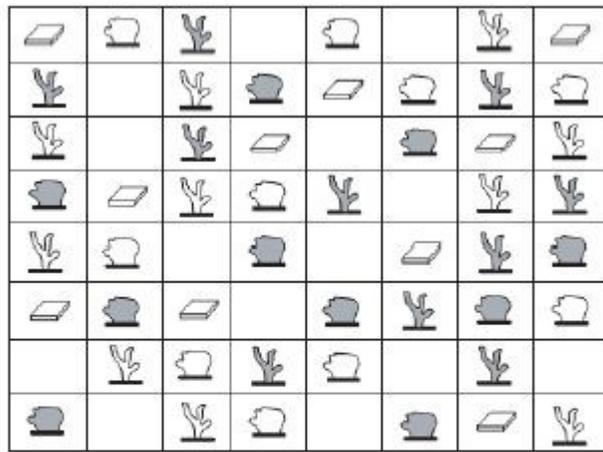


Figure 2. A model grid (1 m²) with 40 coral transplants (10 transplants for each treatment) arranged haphazardly. Dead coral blocks were for a separate experiment.

conditions in land-based tanks which represent sub-optimal conditions for coral growth and survival. The comparison of algal overgrowth of dead skeletons with that on previously live coral provided additional insight into the process of algal community establishment in a natural reef that contains varying proportions of live and dead coral cover, as well as non-living substrate. Overall, results of this study would provide greater understanding of the transition from coral to algal-dominated cover under different environmental conditions. Knowledge gained would also aid in predicting the different possible trajectories of coral community development following environmental disturbances that promote the proliferation of algae.

MATERIALS AND METHODS

Coral transplantation

In November 1996, branch fragments of two related coral species, *Porites cylindrica* and *P. rus*, were collected from different colonies in a shallow reef zone surrounding a sandy lagoon of about 3-4 m depth (off Santiago Island in Bolinao, northwestern Philippines, 16.42°N, 119.90°E, Fig. 1). The lagoon also served as the location of the field set-up. The latter consisted of 6 steel grids, each with an area of 1 m² and coated with white epoxy paint to minimize corrosion. These were raised approximately 20 cm off the bottom by means of angle bars driven into the substrate (Yap et al. 1998).

The coral fragments were cleaned of all encrusting organisms, cut to sizes within a narrow range (approximately 5-8

cm in length, with 1-3 small branches; initial weights are reported in Yap and Molina [2003]), and attached to acrylic plates with cyanoacrylate glue. Sixty (60) live transplants of each species were haphazardly arranged among the grids (10 in each, Fig. 2). An equal number of dead skeletons of the same species (cleaned with bleach and rinsed thoroughly with fresh water) were interspersed among the live corals. (The blocks illustrated in Fig. 2 were for a separate experiment.)

A similar set-up was established using land-based tanks (at the Bolinao Marine Laboratory of the Marine Science Institute located about 5 km south of the field site) using three (3) white plastic tanks measuring 153x95x42 cm and filled with seawater. Each tank contained two plastic grids on which the specimens were placed. Thus the experimental design for the land-based tanks included a blocking factor (tank x grid). Another major difference was that water flow through the tanks was continuous for only 9 h, from 0800H to 1700H, after which it was shut off following prescribed procedures at the marine laboratory.

The experimental treatments, thus, were as follows: *P. cylindrica*, live, FIELD; *P. cylindrica*, dead, FIELD; *P. rus*, live, FIELD; *P. rus*, dead, FIELD; *P. cylindrica*, live, TANKS; *P. cylindrica*, dead, TANKS; *P. rus*, live, TANKS; *P. rus*, dead, TANKS.

Description and measurement of algal settlement patterns

The corals were maintained and monitored until mortality occurred, in this case, being defined as loss of >95% of the living coral tissue. All previously living transplants that died were retrieved. At the same time, an equal number of dead skeletons were collected haphazardly for direct comparison (Table 1). This procedure was repeated every time mortality of live transplants occurred. We termed this “opportunistic” sampling because it was based solely on the frequency of natural transplant mortality (i.e., no corals were deliberately sacrificed). But since an equivalent number of dead skeletons were always collected, this sampling procedure allowed for direct comparisons between previously live and dead transplants. However, it resulted in unequal sample sizes representing the different time intervals, as well as differences in the sampling intervals themselves, ranging from a few days to as long as 3 months. The experiment was terminated after one year when significant mortality had occurred in more than one treatment.

On each sample, the surface area of the skeleton that was covered by algae was carefully measured using a grid (calibrated in millimetres), then digitized to quantify algal cover. The algae were identified to genus level. If clumps of algae were seen to be overgrowing other mats of algae underneath, then total surface area was estimated to exceed 100%. This explains results of percent cover greater than 100%. If a clump consisted of more than one genus, then the reported surface area for each genus was simply the total divided by the number of genera.

After algae were identified and quantified, the coral

skeletons were cleaned and dried, and their surface area determined following the procedure of Hoegh-Guldberg (1988).

Environmental factors

In both the field and the land-based tanks, the following environmental factors were measured, with detailed procedures as well as results reported in Yap and Molina (2003): light, temperature, salinity, dissolved oxygen in the water, nutrients (ammonium and nitrate), sedimentation and water exchange.

Statistical analyses

One-way analysis of similarities (ANOSIM) (Clarke 1993, Clarke and Gorley 2001) was used to test for significant differences among treatments in terms of algal composition and percentage cover. A test of similarities in percentages (SIMPER) determined which algal groups contributed most to the similarity within treatments, as well as to the differences among them. In addition to percent cover as a measure of abundance, analyses were run on data converted to presence/absence. Abundance data were 4th root transformed to give weight to rare genera.

RESULTS

Field conditions

From December 1996 until December 1997, mortality in transplants of *P. cylindrica* in the field was noted on only three occasions, namely, in February, July and October (Fig. 3a). The largest number of mortalities (16 or 27% of the original number) occurred in February, and was due to predation by the gastropod *Drupella*. After this, inverted funnels were installed on the legs of the field set-ups to prevent further access of this predator to the corals.

All the dead transplants from the February sampling were overgrown by the alga *Hypnea* (Rhodophyceae) (average cover 65.3 %). An

equivalent number of previously dead skeletons were also largely covered by this genus (78.6%) followed by the genus *Lithothamnion* (Rhodophyceae).

During each of the monitoring visits in July and October, only one (1) transplant was recorded as dead, and algal cover was noted only for the previously live sample in October. In both instances, there was a higher diversity of algae observed on the previously dead skeletons compared to the previously live ones (Fig. 3a).

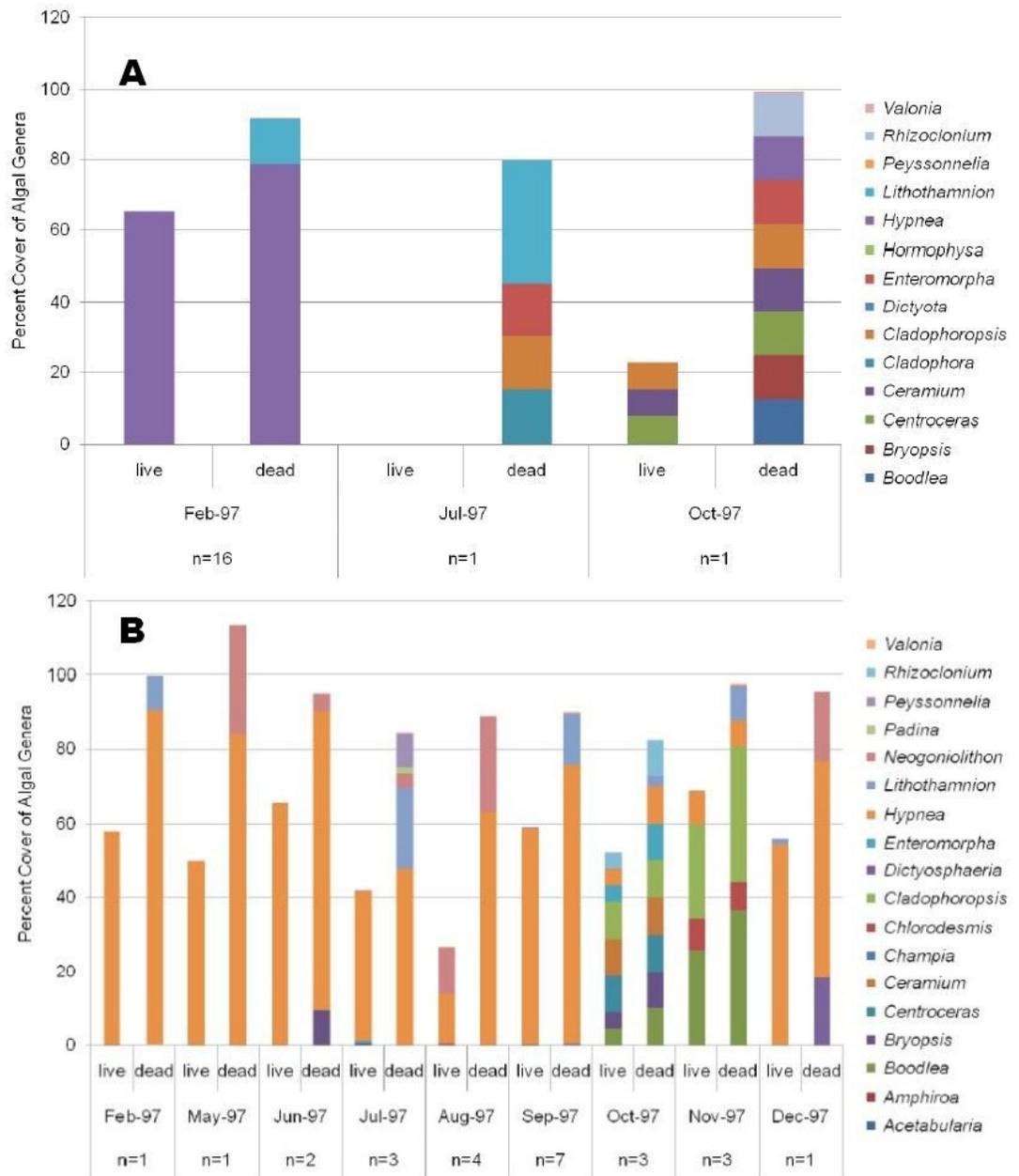


Figure 3. Percent cover of algal genera recorded over time in the field. A) *P. cylindrica*, B) *P. rus*. "n" as in Table 1.

More frequent mortalities, though still involving relatively low numbers (ranging from 1 to a one-time maximum of 7), were recorded for transplants of *P. rus* in the field (Fig. 3b). In the majority of cases, from February to September 1997, both previously live and previously dead corals were largely covered by *Hypnea*. A difference in algal composition was documented during the months of October and November, which then reverted back to a dominance by *Hypnea* in December.

Altogether, for both species, a total of 43 live corals out of an original number of 120, or 36%, were completely covered by algae in a span of one year under field conditions. The most significant factor observed to have triggered this shift was predation.

Statistically significant differences in both presence/absence and percent algal cover between previously live and previously dead corals were detected for *P. cylindrica* only (Table 2). The difference was mainly attributed to the presence of the genus *Lithothamnion* which occurred in significant quantities on dead skeletons compared to live colonies.

There were no statistically significant differences between the two coral species in terms of both presence/absence and percent algal cover for previously live and dead corals.

Controlled conditions in tanks

More frequent mortalities of coral transplants, and in higher numbers (ranging from 1 to a one-time maximum of 16), were observed for both species in the land-based tanks (Fig. 4a and 4b). Altogether, a total of 89 originally live transplants out of an initial total of 120, or 74%, were completely covered by algae within a period of approximately one year. The occurrences of mortality were not synchronized. Thus, there appeared to be no regular temporal pattern in the demise of corals associated with algal colonization.

In terms of both presence/absence and percent algal cover, no statistically significant differences were detected between previously live and previously dead corals of both species. Similarly, there were no statistically significant differences between the two coral species.

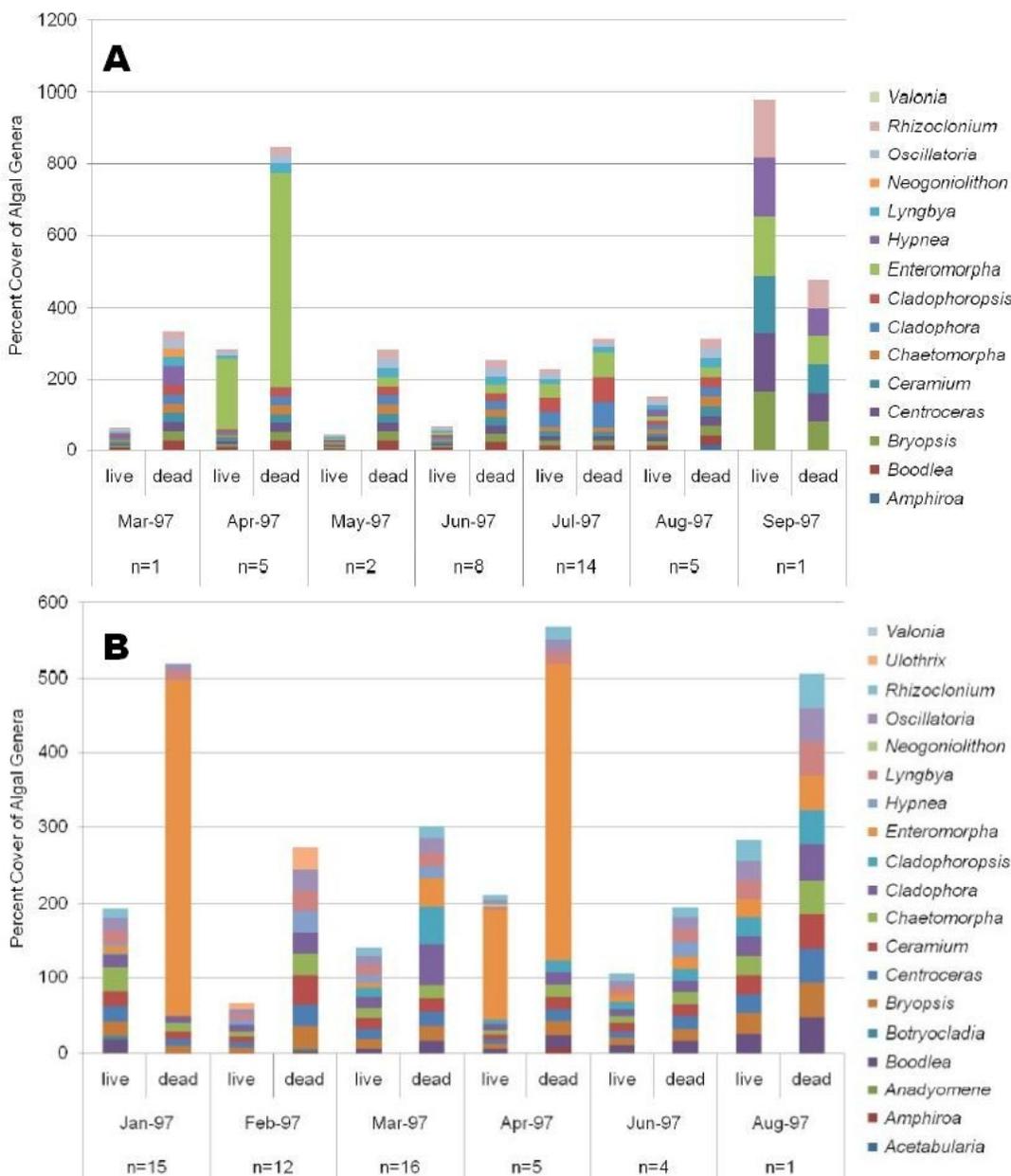


Figure 4. Percent cover of algal genera recorded over time in the land-based tanks. A) *P. cylindrica*, B) *P. rus*. "n" as in Table 1.

Comparison between the field and land-based tanks

Significant differences in terms of both presence/absence of algal genera as well as percent cover were documented between the field and the land-based tanks (Table 2). The genus *Hypnea* (Rhodophyceae) was consistently present, and was also the most abundant in field corals (live and dead, both species; Table 3a, 3b).

For transplants in the land-based tanks, a greater variety of genera were found to be dominant, including *Enteromorpha* (Chlorophyceae), characteristically growing on *P. cylindrica* (live and dead), *Cladophora* (Chlorophyceae), commonly found on dead skeletons of *P. rus*, and *Ceramium* (Rhodophyceae) and *Centroceras* (Rhodophyceae), both consistently present on live specimens of *P. rus* (Table 3a). Overall, the mean number of observed genera was higher for all treatments in the land-based tanks (Fig. 5).

Mean percent cover of algae was also greater in the land-based tanks than in the field (Fig. 6). Similarly, the Shannon index of algal diversity was consistently higher for corals in the land-based tanks (Fig. 7).

DISCUSSION

Coral mortality and algal colonization

The end point for coral mortality was almost complete coverage of originally live transplants by algae. In the field, significant algal colonization occurred only after the death and removal of coral tissue, caused by predation by the gastropod *Drupella* (Cumming 1999). Thus, under optimal conditions for coral survival and growth, a disturbance triggered the transition from coral to algal cover.

Transplants that remained alive at the end of the experiment did not manifest large-scale deterioration or death of their tissue (due to grazing, disease or some other stress factors), and also apparently were able to successfully resist algal invasion (McCook 2001, Diaz-Pulido et al. 2009). There were essentially no differences in trends between the two

coral species (*Porites cylindrica* and *P. rus*).

Conditions in the land-based tanks appeared to be more stressful for the corals (Yap and Molina 2003), where a larger number of transplants of both species were observed at more frequent intervals to be covered by algae. Details on the differences in environmental conditions between the field and land-based tanks are given in Yap and Molina (2003). Both coral predators and algal grazers were conspicuously absent in the

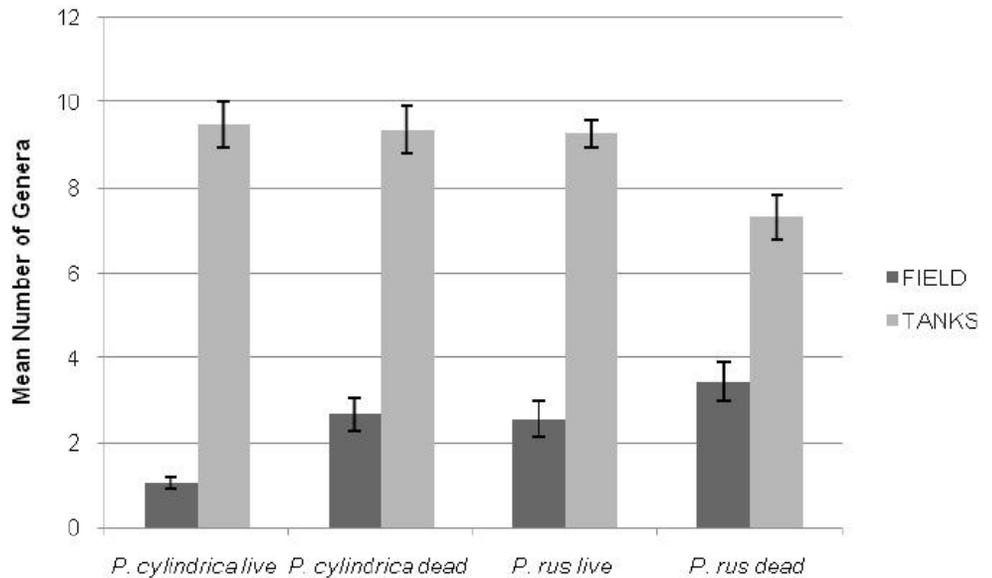


Figure 5. Mean number of algal genera observed for the different treatments. Error bars are standard errors.

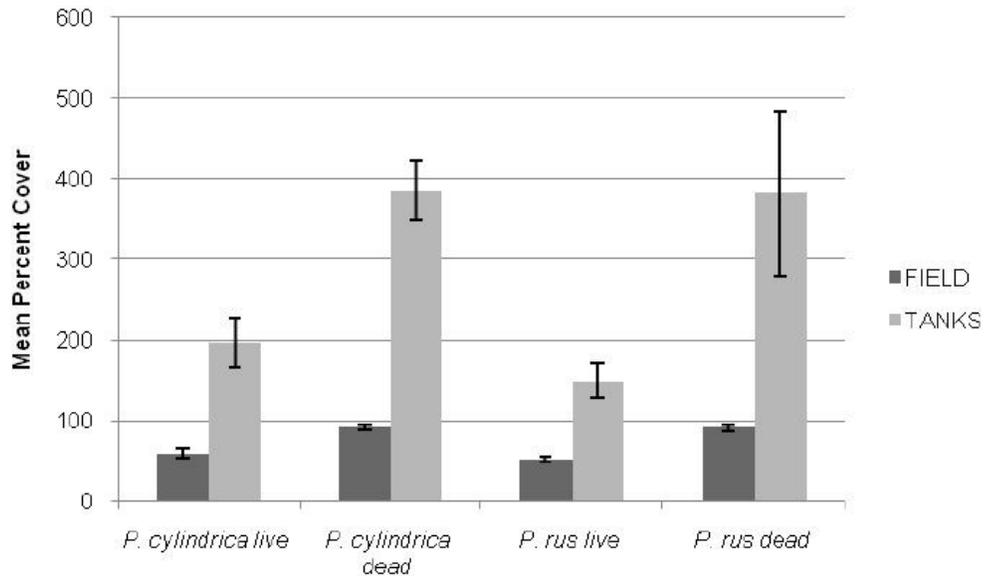


Figure 6. Mean percent cover of algae observed for the different treatments. Error bars are standard errors.

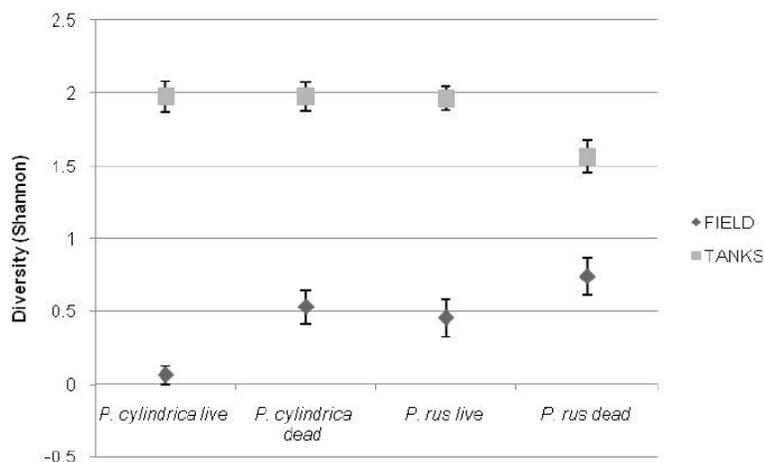


Figure 7. Mean diversity (Shannon) of algal groups calculated for the different treatments. Error bars are standard errors.

Table 1. Sampling protocol in the field (A) and the land-based tanks (B). Numbers indicate live corals sampled. An equivalent number of dead skeletons were sampled at the same time.

A. Field		
Sampling date	<i>Porites cylindrica</i>	<i>Porites rus</i>
Feb 97	16	1
May 97	0	1
June 97	0	2
July 97	1	3
Aug 97	0	4
Sept 97	0	7
Oct 97	1	3
Nov 97	0	3
Dec 97	0	1
Total sampled	18-live 18-dead	25-live 25-dead
Initial total	60-live 60-dead	60-live 60-dead
B. Land-based tanks		
Sampling date	<i>P. cylindrica</i>	<i>P. rus</i>
Jan 97	0	15
Feb 97	0	12
Mar 97	1	16
Apr 97	5	5
May 97	2	0
June 97	8	4
July 97	14	0
Aug 97	5	1
Sept 97	1	0
Total sampled	36-live 36-dead	53-live 53-dead
Initial total	60-live 60-dead	60-live 60-dead

tanks (pers.obs.). Light levels were several times higher in the field (395.79 ± 275.28 to $1880.73 \pm 166 \mu\text{E m}^{-2}\text{s}^{-1}$) than in the land-based tanks (172.67 ± 91.42 to $877.19 \pm 420.94 \mu\text{E m}^{-2}\text{s}^{-1}$) as the latter had been shaded to minimize bleaching of the corals. Water exchange was also greater in the field (0.15 ± 0.09 to 1.70 ± 0.11 DF [diffusion factor]) than in the land-based tanks (0.18 ± 0.04 to 1.37 ± 0.38 DF) because water circulation in the former location remained unimpeded. Both light and water turbulence are critical for coral growth and survival (Jokiel 1978, Yentsch et al., 2002).

Values of the other parameters, namely, temperature, salinity, and dissolved oxygen, were similar between the field and the land-based tanks. On the other hand, nutrient levels were significantly higher in the land-based tanks than in the field. Values of ammonium measured at different times of the year ranged between 0.99 and 1.51 micromoles in the field, compared to 1.18-3.60 micromoles in the land-based tanks (Yap and Molina 2003). Nitrate levels varied between 0.28 and 0.49 micromoles in the field, compared to 0.76-2.05 micromoles in the land-based tanks.

It appears that sub-optimal conditions in the land-based tanks, particularly lower levels of light and water exchange, led to a decline in health of the coral transplants. In addition, nutrient enrichment combined with the conspicuous absence of algal grazers probably promoted the proliferation of a higher diversity of algal genera (reviewed in Burkepile and Hay 2006). As the health of the corals in the tanks deteriorated over time, they likely became more susceptible to algal invasion.

In the majority of treatments, the initial presence of coral tissue in previously live transplants did not appear to influence the course of algal

Table 2. Statistically significant results from ANOSIM and SIMPER analyses comparing between groups. A) Data transformed to presence/absence, B) Percent cover data (4th root transformed).

A. Presence/absence				
Between groups	Analysis of Similarities (ANOSIM)	Similarity Percentages (SIMPER)		
		Pairwise Test (R)	Average dissimilarity	Discriminating genera
Comparison of presence				
Between live and dead				
<i>P. cylindrica</i> FIELD	0.678	42.43	<i>Lithothamnion</i>	dead > live
Between field and land-based tanks				
<i>P. cylindrica</i> live	0.884	93.83	<i>Enteromorpha</i>	TANKS > FIELD
<i>P. cylindrica</i> dead	0.965	95.24	<i>Cladophora</i>	TANKS > FIELD
<i>P. rus</i> live	0.829	84.72	<i>Lyngbya</i>	TANKS > FIELD
<i>P. rus</i> dead	0.706	86.85	<i>Hypnea</i>	FIELD > TANKS
B. Percent cover				
Between groups	Analysis of Similarities (ANOSIM)	Similarity Percentages (SIMPER)		
		Pairwise Test (R)	Average dissimilarity	Discriminating genera
Comparison of abundance				
Between live and dead				
<i>P. cylindrica</i> FIELD	0.68	35.28	<i>Lithothamnion</i>	dead > live
Between field and land-based tanks				
<i>P. cylindrica</i> live	0.879	94.48	<i>Hypnea</i>	FIELD > TANKS
<i>P. cylindrica</i> dead	0.966	95.55	<i>Hypnea</i>	FIELD > TANKS
<i>P. rus</i> live	0.821	87.74	<i>Hypnea</i>	FIELD > TANKS
<i>P. rus</i> dead	0.705	88.19	<i>Enteromorpha</i>	TANKS > FIELD

Table 3. Results from SIMPER comparison within treatments. A) Data transformed to presence/absence, B) Percent cover data (4th root transformed).

A. Presence/absence						
Within a group	Similarity Percentages (SIMPER)					
	Field			Land-based tanks		
	Average similarity	Consistently present	Contribution to similarity	Average similarity	Consistently present	Contribution to similarity
<i>P. cylindrica</i> live	88.24	<i>Hypnea</i>	100	78.33	<i>Enteromorpha</i>	12.58
<i>P. cylindrica</i> dead	79.80	<i>Hypnea</i>	74.66	78.53	<i>Enteromorpha</i>	14.21
<i>P. rus</i> live	44.08	<i>Hypnea</i>	87.37	75.87	<i>Ceramium & Centroceras</i>	12.98
<i>P. rus</i> dead	46.98	<i>Hypnea</i>	54.91	54.14	<i>Cladophora</i>	15.9
B. Percent cover						
Within a group	Similarity Percentages (SIMPER)					
	Field			Land-based tanks		
	Average similarity	Consistently most abundant	Contribution to similarity	Average similarity	Consistently most abundant	Contribution to similarity
<i>P. cylindrica</i> live	83.99	<i>Hypnea</i>	100	68.54	<i>Enteromorpha</i>	13.60
<i>P. cylindrica</i> dead	79.61	<i>Hypnea</i>	67.48	73.48	<i>Enteromorpha</i>	14.75
<i>P. rus</i> live	47.95	<i>Hypnea</i>	91.41	66.90	<i>Centroceras</i>	12.98
<i>P. rus</i> dead	48.10	<i>Hypnea</i>	80.39	49.08	<i>Enteromorpha</i>	16.22

settlement, as there was no significant difference in algal composition and abundance between previously live and dead coral substrates collected at the same time. The general absence of a significant difference in algal composition and abundance between previously live and dead coral substrates collected at the same time may indicate a negligible influence of either succession or seasonality.

Trends in algal composition and abundance

Since, for the most part, patterns of algal cover were found to be similar between previously live and dead coral, it appears that the process of algal invasion and eventual overgrowth of coral took place in a similar manner regardless of whether live tissue existed previously, or a skeleton was completely bare. The exception was the *P. cylindrica* transplants in the field that were grazed by *Drupella* in the early part of the experiment. The genus *Lithothamnion*, a red crustose coralline alga, had greater cover on dead than on previously live corals. Crustose coralline algae are poor competitors with corals (Littler 1972).

In addition, when comparing dead skeletons of *P. cylindrica* in the field and the land-based tanks, the same genus (*Lithothamnion*) had a higher rate of occurrence in the field. Experimental manipulations of levels of herbivory and nutrients have shown that crustose corallines are favored in unfertilized, grazed treatments (Miller et al. 1999, Belliveau and Paul 2002). Nutrient levels were lower and grazing was significant in the field compared to the land-based tanks (Yap and Molina 2003).

The greatest differences in algal composition and abundance occurred between corals in the field and in the land-based tanks. There was a higher diversity of algal genera in the tanks. The genus *Enteromorpha*, a green alga, was dominant on previously live and dead specimens of *P. cylindrica*. Another green alga, *Cladophora*, was the most abundant on dead skeletons of *P. rus*. On the other hand, previously live specimens of this coral species were predominantly covered by the red algae *Ceramium* and *Centroceras*.

Taxonomically distinct genera may share characteristics (productivity and susceptibility to grazers) that influence the

structure of algal communities (Littler 1980, Steneck and Dethier 1994). *Ceramium* and *Centroceras* are both turf algae and are favored under conditions of low grazing (Miller et al. 1999, Lotze et al. 2001) and high nutrients (McClanahan et al. 2002). *Enteromorpha* and *Cladophora* are highly palatable relative to other algal genera and are considered opportunistic (Littler 1980, Dodds and Gudder 1992). The absence of grazing in the land-based tanks apparently favored the proliferation of these genera.

In the field, *Hypnea*, a red alga, was the genus consistently present and most abundant on transplants of both coral species. This genus resists grazing, is relatively unaffected by nutrients, and is more efficient in utilizing light relative to other genera of smaller sizes (Steneck and Dethier 1994, Burkepile and Hay 2006). It also coexists with corals without inflicting damage (Jompa and McCook 2003).

Different kinds of algae are characterized by varying morphologies, chemical defenses against grazers, as well as degrees of palatability. Thus, a range of animal (not to mention microbial) types are expected to be associated with them. The resulting food webs that are built around these relationships would also be different. All of these factors would play a role in determining the development trajectory a coral reef community would undergo following environmental disturbance.

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CONTRIBUTIONS OF INDIVIDUAL AUTHORS

Helen T. Yap and Reverie Alvarez-Molina conceptualized the experimental design. Data gathering was done by RAM. RAM and CSB performed the data analysis. The manuscript was written by HTY and CSB.

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