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REPORT

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Mediation of growth by conspecific neighbors and the effect of site in transplanted fragments of the coral *Porites attenuata* Nemenzo in the central Philippines

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Abstract To investigate facilitative and competitive effects of conspecific neighbors on coral growth, fragments of *Porites attenuata* were reciprocally transplanted between two reefs. Transplants were interspersed with dead coral fragments or live conspecifics and monitored for growth. Over 13 months, transplant performance differed between sites. Those from degraded Bais Bay grew significantly slower in all treatments compared with those from more pristine Apo Island, and Bais fragments branched less (Bais: 1.5 ± 0.16/transplant; Apo: 8.1 ± 0.66/transplant). Treatment effects were observed in Apo; fragments with live conspecifics branched less but grew taller, adding significantly more surface area than those with dead neighbors. Clonal fragments differed significantly in their responses, indicating environmentally induced effects. These interactions affected growth and morphology prior to physical contact between fragments. This illustrates a benefit of manipulating the biotic environment of early transplants: dense stocking in ocean nurseries could stimulate early growth, and subsequent spacing would allow lateral branching and reduce competition.

Keywords Scleractinia · Intraspecific interaction · Morphology · Growth · Transplantation · Philippines

Introduction

Active intervention is applied with increasing frequency to accelerate the recovery of destroyed or stressed coral reefs. In areas unlikely to recover by natural recruitment, but where coral re-establishment is deemed necessary, coral transplantation may be the only option. Corals may fail to recruit to unstable substrates due to past blast-fishing (Alcala and Gomez 1985; Aliño et al. 1985), or recruitment limitation (Pearson 1981; Sammarco and Andrews 1989; Sammarco 1991; Clark and Edwards 1995), or they may be outcompeted (Pearson 1981; Hughes 1994; Maida et al. 1995; Atrigenio and Aliño 1996), or being killed by benthic grazers (Sammarco 1980; Done and Potts 1992). Furthermore, limited data suggest that recruitment and/or recruit survival may be enhanced by the presence of established living coral colonies, suggesting that coral transplants could accelerate natural recovery (Birkeland 1977; Gittings et al. 1988; Clark and Edwards 1995). Transplantation has been used for decades as a tool to investigate coral responses to physical factors (see Birkeland et al. 1979; de Weerdt 1981; Pastorok and Bilyard 1985; Plucer-Rosario and Randall 1987; Gittings et al. 1988; Grigg and Dollar 1990; Hunte and Wittenberg 1992; Yap et al. 1992; West et al. 1993; Grigg 1995; Clark 1997; Custodio and Yap 1997). This knowledge has improved the success of coral reintroduction efforts.

Among the factors to be considered in transplantation efforts are potential interactions between coral transplants, and between transplants and organisms already present at the site to be restored. Coral interactions may be aggressive and inhibitory, and include overgrowth (Bak and Criens 1982; Rinkevich and Loya 1983; Buss 1990; Frank et al. 1995), weapon formation (Richardson et al. 1979; Chornesky 1983; Hidaka and Yamazato 1984; Hidaka 1985), growth or reproductive suppression (Rinkevich and Loya 1985a), allelopathy (La Barre et al. 1986), extrusion of mesenterial filaments (Lang 1971; Wellington 1980), and shading (Stimson 1985; Fisk and Harriot 1992). Alternatively, non-fusing interclonal contact that strengthens colonies in high-energy environments has been described as a non-aggressive, facilitative interaction (Bak and Criens 1982; Chornesky 1991).

The Philippines contains some of the most degraded reefs worldwide (Gomez 1997; Bryant et al. 1998) and lies within the area of richest coral species diversity (> 600 scleractinian species; Veron and Hodgson 1989).

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Growing interest in reef protection and recovery by government groups and local fishing communities, and the Philippines' historical involvement in terrestrial reforestation, suggest that research that develops and improves reef rehabilitation options should be prioritized. Coral transplantation was first investigated by Auberson (1982) and Alcala et al. (1982) as a potential rehabilitation approach. Yap and Gomez (1981, 1984, 1985) reported that transplants of *Acropora pulchra* grew more slowly and were more susceptible to sedimentation and seasonal differences in water temperature than naturally occurring colonies. Yap et al. (1992) compared growth and mortality in transplanted fragments of three dominant coral species to assess their suitability for restoration. They noted that life-history strategy played a role in the suitability of a species for transplantation; *Acropora hyacinthus* grew rapidly, but survived poorly. *Pocillopora damicornis* showed intermediate growth rates and high mortality during the first year, with eventual recovery. *Pavona frondifera* grew rapidly and showed lower mortality; this species was thought the most suitable for restoration. Fish diversity was enhanced, and fragments of *Porites cylindrica* grew significantly faster when transplanted in multi-species plots than in single-species plots, illustrating the benefits of higher diversity in polyculture vs single-species monoculture (Dizon and Yap 2000; Yap et al. 2000).

The effects of conspecific interactions have not been investigated in the context of coral transplantation for reef rehabilitation. Reef rehabilitation provides a unique opportunity to apply knowledge of coral interactions, derived from controlled field experiments, to improving the performance and re-establishment of transplants. This paper reports results of a study of the effects of conspecific neighbors on the growth of reciprocally transplanted fragments of the scleractinian *Porites attenuata* Nemenzo. In particular, the author's objectives were to: (1) test for a "neighbor effect" on growth and morphology of transplants placed in close proximity to conspecifics, and assess whether this effect was facilitative or competitive; and (2) evaluate the suitability of *P. attenuata* as a source species for transplantation for reef rehabilitation.

Materials and methods

The study sites were two reefs in the central Philippines: North Bais Bay and Apo Island Marine Reserve (Fig. 1). The reefs are 6 hours apart by boat. Although it was originally intended to select reefs in similar states of health, the Bais Bay reef proved to be more stressed from siltation and agricultural runoff. The experiment was set up in June 1996, at the start of the rainy season, based on findings by Yap and Gomez (1984) of slower growth in fragments transplanted during hot summer months. Twenty colonies of *Porites attenuata*, a dominant branching species, were haphazardly selected as donor colonies at each reef. Colonies were at 9- to 12-m depth and at least 10 m apart, to minimize the possibility that they were clonal (Potts 1976). Four unbranched fragments from each donor colony, at least 4 cm long, were carefully broken off near the base using hammer and chisel. Initial length of these branches varied insignificantly (ANOVA; $P = 0.5142$). Fragments were secured underwater into 1-inch segments of PVC pipe using Pioneer marine epoxy and haphazardly assigned to one of four treatments prior to permanent attachment to underwater platforms. Treatments were as follows:

- Transplantation within the source site, interspersed with dead fragments (AAD or BBD; A denotes Apo, B Bais, and D dead neighbor)
- Transplantation within the source site, with living conspecific fragments (AAL or BBL; L denotes live neighbor)
- Transplantation to the reciprocal site, interspersed with dead fragments (ABD or BAD; AB denotes from Apo to Bais, BA from Bais to Apo)
- Transplantation to the reciprocal site, with living conspecific fragments (ABL or BAL).

At each site, eight cement platforms, 1 m long by 0.3 m wide, were anchored into place 30 cm off the substrate in two rows, between 10 and 11 m deep. Each platform held two rows of nine fragments. Five test fragments of *P. attenuata* from the donor colonies mentioned above alternated with four treatment fragments (either live conspecifics or dead). Live treatment conspecifics, haphazardly obtained from donor colonies on each reef, were not measured for growth or morphology, though handling and preparation were identical to test fragments. Distance between neighbors within each row was 4.5 cm, and between rows on a platform, 11 cm. Fragments to be transplanted to each reciprocal site were transported by boat in aquaria with fresh seawater and aeration and affixed as described above. In summary, each reef housed a total of 8 platforms, with 2 platforms per treatment; a total of 10 replicates per treatment, and 80 transplanted fragments. Using clonal branches spread among treatments between two sites allowed detection of phenotypically plastic growth effects. Dead fragment neighbors were treated as controls for living, growing neighbors, to analyze the effect of interactions between live neighbors on growth rate and morphology.

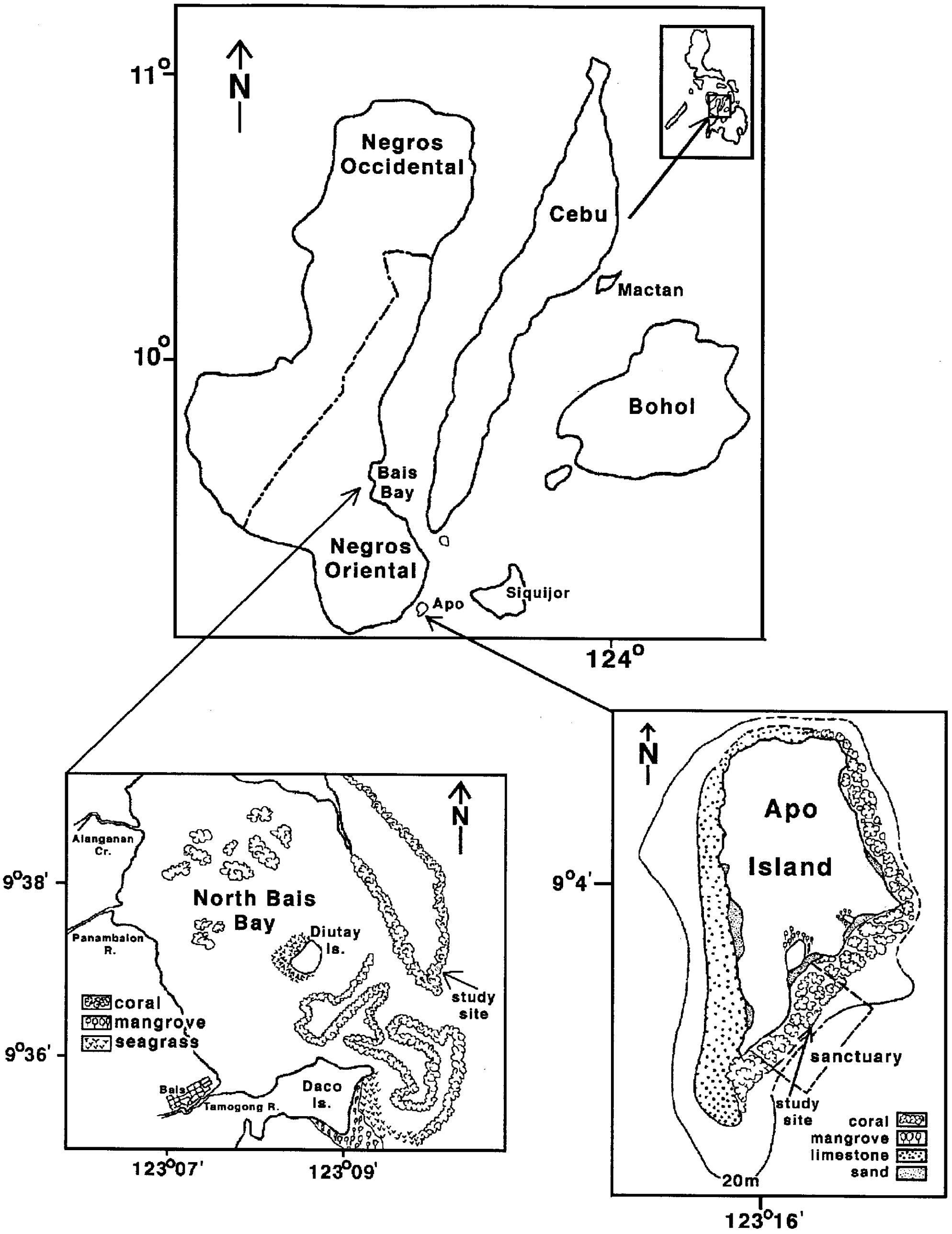
Transplants were censused for growth, injury, mortality, and partial mortality, signs of disease, and branching, approximately bimonthly from June 1996 to July 1997. Transplant length and basal width were measured using hand calipers for the first three sampling periods. However, fragments soon began to branch and develop basal discs, and branch buds and basal growth were not represented as a component of overall transplant growth when only hand measurements of total branch length and width were used. Therefore, video images were taken concurrently with caliper measurements. Estimates of fragment size were then obtained from video images using the public domain NIH Image Analysis program (developed for the Macintosh computer by the US National Institutes of Health, available at http://rsb.info.nih.gov/nih-image) by tracing the outline of each fragment, including basal disc, branches, and branch buds. Each transplant was then treated as a polygon, and the program calculated surface area of the polygon in square millimeters. All video shots were taken each month from the same position, to minimize image distortion. Differences in total length using calipers vs image analysis were not significant (ANOVA, $P = 0.3004$; $F = 1.807$), so hand measurements were not used for the last three sampling periods. The final census included video imaging for fragment size and branch position, the number of branches per fragment, and a final assessment of mortality, partial mortality, and injury/breakage. Negative growth resulted from either tip breakage or partial mortality. Fragments that broke off and disappeared between sampling periods were considered dead and were not replaced.

Five intact colonies were selected at each reef in the vicinity of the platforms, for reference measurements. Two branches were marked with cable ties on each colony. Due to the difficulty in obtaining clear video shots of individual branches within a colony, total length and width at base were measured by hand calipers on marked branches during each sampling period.

Weekly growth rate was considered the most accurate growth assessment, because some fragments died prior to the end of the study, and all fragments were of similar initial length. This was calculated per fragment as the total increase in surface area divided by the number of weeks of growth. All data were tested for normality with Kolmogorov's test and for homoscedasticity using Levene's test. Non-normal data were normalized using Box-Cox transformations (Velleman 1997) and a square-root transformation was used for heteroscedastic variances. Site quality differences were very apparent; transplants growing in Apo were visibly healthier and survived better than those at Bais Bay. A three-way ANOVA was used on square-root transformed data to analyze the effects of site of origin, site of growth, and neighbor on the entire data set. Because neighbor effects were apparent only for transplants growing in Apo, the effects of neighbor and site of origin on mean weekly growth (Box-Cox exponent = 0.28) and final branching number (Box-Cox exponent = 0.7644) were tested using two-way ANOVA on only Apo data. The ranked differences between factors were tested with Bonferroni post-hoc tests (Velleman 1997). Final colony morphology in Apo-grown transplants was analyzed by testing for a neighbor effect on directional branching. Branch orientation was described as either (1) facing outer margins and/or the center of the growth platforms, where more space was available, or (2) facing growing neighbors, where more crowding occurred. Branch counts were transformed (Box-Cox exponent = 0.7644) and tested with a two-way ANOVA using branch orientation and presence of living vs dead neighbors as predictors. An additional ANOVA on log-transformed branch counts per fragment on open corners vs inner rows further quantified the effect of available space on branching.

For the Bais data, an analysis of factors affecting mortality was deemed appropriate, since neighbor effects had no significant effect on transplant performance. Cox's Proportional Hazard Analysis software (Sall and Lehman 1996) was used to determine if treatment (i.e., with live or dead neighbor), site of origin (Apo or Bais reefs), or early growth rate (growth within the first sampling

Fig. 1 Map of the central Philippines showing the study sites



interval after transplantation) affected later survival. This test calculates a risk ratio associated with each factor potentially affecting the fate of the transplants. Three possible fates were defined: (1) death during the time interval between two sampling periods (a total of five intervals within which a fragment could die), (2) dying at the end of the study (declining fragment health, gradual tissue loss, no basal growth), or (3) healthy and growing at the end of the study.

Results

General trends in transplant performance

Performance was defined as transplant growth and survival. Several general patterns emerged as fragments grew at both sites. Fragments originally from Apo grew faster than those from Bais at both sites, and fragments growing at Apo grew faster and survived better than those growing at Bais (transformed growth rate Box-Cox exponent = 0.425; ANOVA; F = 76.627, $P \leq 0.0001$). Therefore, both site of origin and site of growth had greater effects on transplant performance than did neighbor in the overall analysis (Table 1, Fig. 2). Transplants growing at Apo showed steady linear extension, slightly higher than that of reference colonies (Fig. 2). By January 1997 (7 months post-transplant), basal disc development and branching accelerated greatly. Those growing in Bais, however, showed much slower growth, with little or no basal growth and little branching. To determine whether growth differed between sampling periods, suggesting either a seasonal effect or a post-transplant stress effect, growth differences between the five sampling periods were tested at both sites. Neighbor effects were not significant within intervals of growth between sampling periods, and so were eliminated from the analysis. Results showed significant differences in growth between time periods, primarily between the first time period post-transplantation, and all others (Table 2). Growth rate increased between sampling periods, though the increase was generally not significant. This suggested an immediate stress effect of transplantation overcome by the second sampling, and no evidence of a seasonal effect on growth.

In Apo, growth rate increases were largest after the first (August 1996) and third (January 1997) sampling periods, which corresponded with the development of basal discs and accelerated branching. Bais data showed different results. The growth curve of reference colonies was similar to those at Apo, though growth rate was slower at Bais (Fig. 2). However, transplants grew much less than reference colonies at Bais after the first sampling period (Fig. 2). Fragments also branched much less at Bais (final census: 1.54 ± 0.16 branches per fragment) than at Apo (final census: 8.1 ± 0.66 branches per fragment). In addition, site of fragment origin did not affect growth rate in Bais, though it did in Apo (Table 2). Since fragments were treated identically at both sites and transplantation to both reefs was simultaneous, these observations suggest a cumulative effect of the less-optimum environment on growth.

Neighbor effects

Because a neighbor effect was not detectable in transplants growing in Bais – growth rate and final colony morphology were not significantly different in any of the Bais treatments – an analysis of the effect of neighbor was carried out only for fragments growing at Apo. Fragments growing next to live neighbors added significantly more surface area faster than those next to dead neighbors (Table 3, Fig. 3), and were significantly longer than those next to dead neighbors at 13 months (ANOVA; F = 6.77, $P = 0.01$ 1; Bonferroni post-hoc test $P = 0.011$). This enhancement of growth rate by close neighbors illustrates an early positive effect on growth. In addition, fragment source differences were significant; those originally from Apo grew faster than those from Bais (Table 3, Fig. 3). Conversely, fragments with live neighbors branched much less than those with dead neighbors, and site of origin did not affect branching (Table 3, Fig. 4). The effect on the number of branches produced was much more pronounced than that on growth rate. These differences – greater linear growth and reduced lateral branching with live neighbors – suggest a competitive interaction mediating colony morphology by inhibiting branch production. Clonal pairs in the two treatments differed significantly in the number of branches they produced (Wilcoxon signed rank test; z = 3.9578, $P \leq 0.0001$), showing that differences in colony morphology were environmentally induced. The author hypothesized directional branching, with fewer branches on colony sides adjacent to neighbors. However, the number of branches oriented toward and away from living neighbors did not vary (ANOVA; F = 1.125, $P = 0.29$); branching was three-dimensional. Colonies at the corner of platforms also did not show greater branching in response to more available space

Table 1 Three-way analysis of variance of effect of neighbor (live vs dead), fragment source (Apo vs Bais), and site of growth (Apo vs Bais) on mean weekly growth (over 13 months) of coral transplants at two sites

Factor	df	F	*P* value	Post-hoc rank
Neighbor	1	0.087	Not significant	Dead > Live; $P = 0.767$
Fragment source	1	15.23	0.0001	Apo > Bais; $P = 0.00015$
Site of growth	1	92.95	≤ 0.0001	Apo > Bais; $P = 0.0000$
Growth × source	1	5.867	0.0167	–
Growth × neighbor	1	7.859	0.0058	–

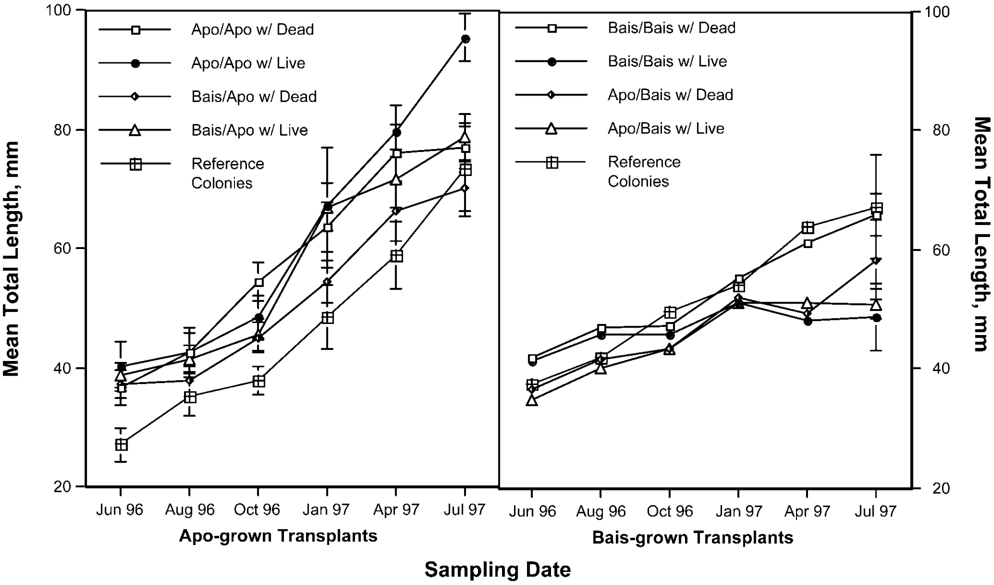


Fig. 2 Mean weekly growth rates of *P. attenuata* fragments reciprocally transplanted between two sites, subjected to two treatments (with live neighbor and with dead neighbor). $n=20$ fragments/treatment-site; $n=5$ reference colonies; mean ±SE

Table 2 Results of two-way ANOVA on the effect of post-transplant growth interval and site of transplant origin on mean weekly growth rate. (Site of origin: Apo vs Bais; growth intervals: *1*=6/96–8/96; *2*=8/96–10/96; *3*=10/96–1/97; *4*=1/97–4/97; *5*=4/97–7/97)

Factor	df	F	*P* value	Post-hoc rank
Apo-growing transplants				
Growth interval	4	39.72	≤ 0.0001	1 < 2; $P=0.0000$ 1 < 3; $P=0.0000$ 1 < 4; $P=0.0000$ 1 < 5; $P=0.0000$ 3 < 5; $P=0.0027$ 2 < 5; $P=0.0002$
Site of origin	1	9.295	0.0025	Apo > Bais: $P=0.00248$
Bais-growing transplants				
Growth interval	4	9.357	≤ 0.0001	1 < 2; $P=0.0000$ 1 < 3; $P=0.0000$ 1 < 4; $P=0.0016$ 1 < 5; $P=0.0039$
Site of origin	1	2.539	Not significant	–

Table 3 Results of two-way ANOVA for effect of neighbor on mean weekly growth rate and colony morphology in Apo-grown transplants for 13 months of growth ($n=20$ fragments/treatment; neighbors: either dead or live; sites: either Apo or Bais)

Source	df	F	*P* value	Post-hoc rank
Effect on mean weekly growth				
Neighbor	1	4.185	0.0442	Live > Dead; $P=0.0442$
Site of origin	1	23.907	≤ 0.0001	Apo > Bais; $P=0.0000$
Effect on branch number				
Neighbor	1	20.953	< 0.0001	Dead > Live; $P=0.0328$
Site of origin	1	0.378	0.602	Not significant

(corner fragments: 5.65±0.81 branches/fragment; inner fragments: 7.29±0.66 branches/fragment, ANOVA; $F=2.5446$, $P=0.1152$). It is possible that directional growth might occur at a later stage, as fragments grow into contact.

As mortality and partial mortality in Bais-growing transplants were very high, the author tested for the possibility that neighbor (live vs dead), site of origin, or early growth rate might affect later fate. Results are presented in Table 4. No significant differences were seen; all fragments had an equally "hazardous" existence at the less favorable site. The presence of live conspecifics did not affect fragment fate, and coming from the healthier site (Apo) did not afford any advantage. In addition, no link existed between early growth rate and later survival; fragments that initially grew well did not necessarily survive better.

Site quality

The most obvious effect on transplant performance was the environmental quality difference between the two sites: Bais Bay was disturbed by fishing, siltation, and

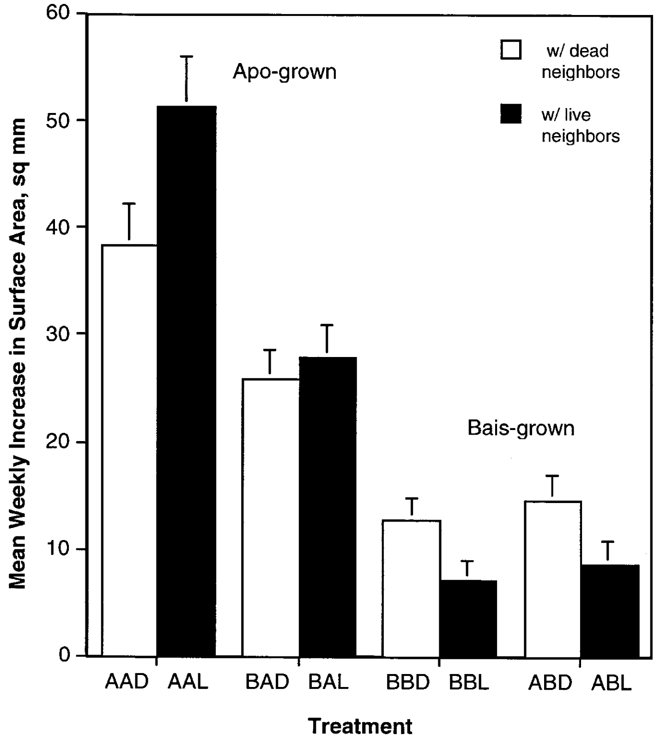


Fig. 3 Mean weekly growth rate of *P. attenuata* transplants in two treatments, growing at two sites. *AAD/BBD* Within-site transplants growing with dead neighbors; *AAL/BBL* within-site transplants, live neighbors; *BAD/ABD* between-site transplants, dead neighbors; *BAL/ABL* between-site transplants, live neighbors. $n=20$ fragments/treatment-site; mean ±SE

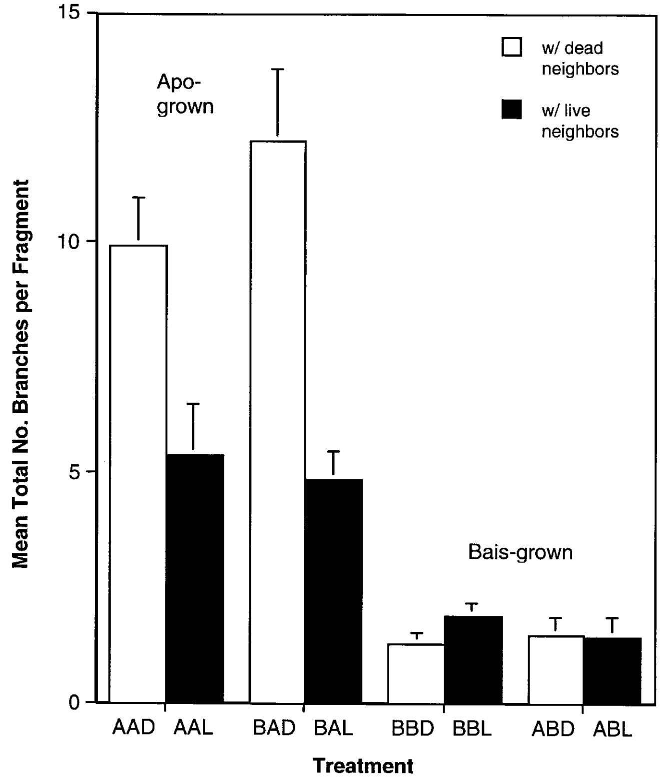


Fig. 4 Mean total number of new branches of *P. attenuata* transplants in two treatments at two sites. *AAD/BBD* Within-site transplants, with dead neighbors; *AAL/BBL* within-site transplants, live neighbors; *BAD/ABD* between-site transplants, dead neighbors; *BAL/ABL* between-site transplants, live neighbors. $n=20$ fragments/treatment-site; mean ±SE

agricultural runoff, while Apo reef was subjected to none of these stresses. At 1 year, transplant mortality was 6.25% in Apo (5 out of 80 fragments died or were lost) and the remaining transplants were healthy and growing well. In contrast, 1-year mortality at Bais was 25% (20 out of 80) and many of the remaining transplants were partially dead and died within months after the last sampling. All transplants at Bais were equally susceptible to the various factors contributing to high mortality, irrespective of treatment ($\chi^2=12$, $P=0.4457$).

Sources of mortality and injury

A summary of mortality and injury at both sites is presented in Table 5. Cause of mortality was usually not determined. Many fragments at Bais died slowly, showing a steady loss of pigmentation and slower growth over several weeks, followed by tissue necrosis starting at the base and progressing upward.

Without strong basal support, fragments were fragile and easily broken; several were lost. Bais-growing fragments were more impacted by biotic agents, which included flatworms, a red filamentous alga, a boring polychaete, and a disease (discussed below) (Table 5).

The most interesting condition affecting the health of Bais transplants was the appearance of discrete, multifocal, white lesions, 4 mm in diameter, in August 1996, which first appeared at the base of several fragments. By January 1997, 10% of the transplants were infected, and lesions had spread from the base. A total of 23 fragments (29%) eventually developed lesions; six of these were originally from Apo and 17 from Bais. Several infected fragments subsequently died (Table 5). Healthy colonies on the reef developed similar lesions. By the following year, a transect survey on this reef indicated that 45% of colonies within the genus *Porites* were manifesting these signs of disease. This disease, *Porites* ulcerative white spot disease (PUWS), is currently under investigation (Raymundo 2000).

Table 4 Results of Cox's Proportional Hazard Analysis for Bais-grown transplants; effects of early weekly growth rate, treatment, and site of origin on survival ($n=20$ fragments/treatment; neighbor: live or dead neighbor; site of origin: Apo or Bais; early growth rate: growth during first sampling interval)

Source	df	Risk ratio	χ^2	*P* value
Neighbor	1	0.555	1.579	0.2088
Site of origin	1	1.45	0.646	0.4214
Early growth rate	1	1.0012	0.605	0.4367

Table 5 Summary of injury and mortality of transplanted fragments ($n = 80$ fragments growing at each site). *PUWS* *Porites* Ulcerative White Spot Disease

Breakage, loss of fragment	Death (cause unknown)	Partial mortality (PM)	Disease (PUWS)	PUWS with later PM/death	Ectoparasite/borers
Apo-grown transplants					
3	2	0	0	0	0
Bais-grown transplants					
7	14	21	22	12	4

Discussion

Adult colony morphology and size must be considered when determining the density and spacing of coral transplants if corals are to be introduced with their long-term re-establishment in mind. The author's results illustrate an effect on both growth rate and colony form long before fragments came into physical contact. Transplants with live neighbors were 4.5 cm apart, and those with dead neighbors were approximately 10.5 cm apart. Two years post-transplantation, most transplants had grown into contact, yet significant effects on morphology were detectable within the first 6 months, when branching began. Because clonal branches responded differently within the treatments, genetic factors could not explain observed effects; differences in growth rate and form were clearly environmentally induced. Colonies growing close to living neighbors grew longer and added more surface area faster, but branched less than those with dead neighbors. It is likely that faster increase in surface area with live neighbors was a short-term effect. Greater branching of fragments next to dead neighbors should eventually result in greater surface area surpassing that of fragments branching less.

Indirect competition between corals, i.e., no physical contact between competitors (Lang and Chornesky 1990), has rarely been described. Overtopping by table corals, resulting in low survival of shaded colonies, provides one example (Stimson 1985; Fisk and Harriot 1992). However, a shading effect was not operating here, and the method by which neighbors were affecting each other was unclear. Chemical mediation is one possibility; allelopathy is a well-established means of defense in soft corals (Sammarco et al. 1983 ; Bak and Borsboom 1984 ; Porter and Targett 1988). Chemical signals (isomones) in corals were described by Rinkevich and Loya (1985b) as a means of directing intracolony growth. In related studies, the authors described differing growth responses in the coral *Stylophora pistillata*; clonal branches fused when in physical contact, but retreated from each other when placed 0.5 cm apart (Rinkevich and Loya 1983, 1985b), suggesting chemical communication between close, but untouching, branches. Antimicrobial chemical defense has been documented in 100 scleractinian species (Koh 1997), and Koh and Sweatman (2000) demonstrated that extracts of *Tubastrea faulkneri* effectively reduced competition by killing coral larvae. Distance between colonies can determine the type of interaction between neighbors; smaller distances (i.e., physical contact, or as little as 5 mm apart) results in greater tissue damage (Chornesky 1983). My results suggest a chemical communication between close allogeneic neighbors that resulted in inhibited branching, possibly delaying physical contact, but stimulating branch extension.

Phenotypic plasticity is common in corals; they alter morphology and physiology in response to a variety of environmental changes (Dustan 1979; Davies 1980; Foster 1980; Rinkevich and Loya 1983; McCloskey and Muscatine 1984; West et al. 1993; Montebon and Yap 1997). The morphological differences between treatments at Apo are an example of phenotypic plasticity, as a clonal design was used. Growth plasticity could be manipulated when arranging and spacing transplanted fragments. Unbranched fragments could be grown in ocean nurseries in high densities prior to permanent attachment, to stimulate early growth. Older, branched clonal fragments could be permanently arranged in clusters to facilitate fusion (Hildemann et al. 1980; Bak and Criens 1982; Hidaka 1985; Willis and Ayre 1985) to form large colonies. Placement of clusters must allow for colony expansion, to avoid growth inhibition from competition with neighbors.

A related issue requiring further study is the potential benefit of transplanting in polyculture. Polyculture that establishes multispecies, clusters, or patches results in higher genetic diversity and habitat complexity, and would support a greater diversity of reef-associated fauna than would monoculture. Dizon and Yap (2000) suggested that competitive inhibition in monospecific stands may explain the lower growth rate observed in monoculture plots of *Porites cylindrica*, and this is consistent with the effect on branching seen in this study. However, interspecific competition often results in dominance hierarchies or competitive networks which may hinder the establishment of less-aggressive species (Bak et al. 1982; Rinkevich et al. 1992; Aerts 1998). Therefore, the placement of transplants requires a consideration of intraspecific effects not only on growth and form, but also on potential impacts from more aggressive species. Clearly, consideration of the diversity of interactions in which any single species may be involved is beyond the scope of most rehabilitation efforts, but a familiarity with available information on coral interactions can provide a starting point. An understanding of the factors mediating coral growth can and should be used to manipulate colony form and growth rate to achieve more effective results in restoration efforts. This should be considered a primary focus of reef restoration ecology.

One primary concern suggested by these results is the quality of the sites that will donate and receive transplants. Studies involving transplanting to a poor-quality site (Birkeland et al. 1979) or suboptimum conditions (Clark 1997) show that coral often fails to re-establish. Two points are clear: (1) stressed corals from a degraded site are easily established under optimal conditions, and (2) transplants taken from high-quality sites perform better than those from degraded sites. Clonal fragments taken from Bais grew significantly faster at Apo that they did at Bais (Figs. 3 and 4), despite the stress of long-distance transport. Fragments from Apo, on the other hand, grew faster than those from Bais at both sites (Fig. 3). In addition, the data suggested a difference in susceptibility to disease (PUWS): the majority of fragments infected with PUWS were from Bais, though all transplants were presumably exposed simultaneously after transplantation had occurred, and were growing in identical conditions. These differences may be explained genetically: Apo fragments could simply have come from more-resistant stock, or by past environmental influences; Apo fragments were taken from healthy colonies on a pristine reef and therefore responded better to stress when exposed to it.

The potential impact of coral disease on reef rehabilitation has not yet been evaluated. However, reports of diseases on reefs are increasing (Richardson 1998; Harvell et al. 1999) and require consideration. Transplant stress lowers a coral's natural resistance, leading to increased susceptibility to local pathogens. In addition, introducing a disease via infected, but asymptomatic, coral transplants is a very real concern. In this study, only fragments at Bais developed PUWS, but the effect was considerable and the disease has impacted the entire reef. So little is known about disease etiology (Antonius 1995) and so few diseases have been adequately documented and studied (Richardson 1998) that it may be possible to transplant fragments harboring potential pathogens without being aware that they are diseased. A detailed survey of the source reef, to identify colonies with any obvious symptoms of documented diseases, would be a first step in preventing a transplantation effort from becoming a facilitator in the spread of a disease.

A recent increase in the number of publications on coral transplantation as a management strategy is proof of the interest it is generating among coral reef workers. However, the prohibitive cost, labor-intensive initial stage, substrate area which can be reasonably "replanted" relative to the vast areas of denuded reef, and potential damage inflicted on donor reefs present real challenges (see Harriot and Fisk 1988; Edwards and Clark 1998). Coral transplantation may be most effectively used in conjunction with other restoration and management strategies, such as substrate stabilization and the use of seeded or cultured colonies. Certainly, naturally fragmenting species are most suitable for the method presented here, and fragments must be obtained from as many colonies as possible to maximize genetic diversity in the recipient site (Rinkevich 1995). In addition, the sexual reproductive mode of many species, including *P. attenuata*, remains undocumented; fragment transplantation may be the only viable means of preserving or reintroducing species that sexually reproduce rarely or not at all. Events such as dynamite blasting, hurricanes, and ship groundings generate enormous numbers of fragments without permanently altering water quality, and recent attempts to recover such areas by stabilizing fragments have shown some success (Gittings et al. 1994; Becker and Mueller 1999; Jaap 1999; Quirolo 1999). This study demonstrates that interactions resulting from the placement of fragments in close proximity can mediate the performance of transplants. Biological interactions and morphological plasticity can be manipulated to achieve more effective growth and re-establishment of transplanted coral.

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References

Aerts LAM (1998) Sponge/coral interactions in Caribbean reefs: analysis of overgrowth patterns in relation to species identity and cover. Mar Ecol Prog Ser 175:241–249

Alcala AC, Gomez ED (1985) Recolonization and growth of hermatypic corals in dynamite blasted coral reefs in the Central Visayas, Philippines. Proc Int Symp Biogeogr and Evol Southern Hemisphere 2:645–661

Alcala AC, Gomez ED, Alcala LC (1982) Observations on survival and growth of coral transplants in central Philippines. Kalikasan Philipp J Biol 11:136–147

Aliño PM, Banzon PV, Yap HT, Gomez ED, Morales JT, Bayoneto RP (1985) Recovery and recolonization on a damaged backreef area at Cangaluyan Is. (northern Philippines). Proc 5th Int Coral Reef Congr 4:279–284

Antonius A (1995) Incidence and prevalence of coral diseases on coral reefs. What progress in research? Coral Reefs 14:224

Atrigenio MP, Aliño PM (1996) Effects of the soft coral *Xenia puertogalerae* on the recruitment of scleractinian corals. J Exp Mar Biol Ecol 203:179–189

Auberson B (1982) Coral transplantation: an approach to the re-establishment of damaged reefs. Kalikasan Philipp J Biol 11(1):158–172

Bak RPM, Borsboom JLA (1984) Allelopathic interaction between a reef coelenterate and benthic algae. Oecologia 63:194–198

Bak RPM, Criens SR (1982) Experimental fusion in Atlantic *Acropora* (Scleractinia). Mar Biol Lett 3:67–72

Bak RPM, Termaat RM, Dekker R (1982) Complexity of coral interactions: influence of time, location of interaction and epifauna. Mar Biol 69:215–222

Becker LC, Mueller E (1999) The culture, transplantation, and storage of *Montastraea faveolata*, *Acropora cervicornis*, and *A.*

palmata: what we learned so far. In: Proc Int Conf on Scientific Aspects of Coral Reef Assessment, Monitoring, and Restoration, Fort Lauderdale, 14–16 April, Conference Program Abstr, p 53

Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc 3rd Int Coral Reef Symp 1:15–21

Birkeland C, Randall RH, Grimm G (1979) Three methods of coral transplantation in the thermal effluent area at the Tanguisson power plant. Tech Rep 60, University of Guam Marine Laboratory

Bryant D, Burke L, McManus J, Spalding M (1998) Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, Washington, DC

Buss LW (1990) Competition within and between encrusting clonal invertebrates. Trends Ecol Evol 5:352–356

Chornesky EA (1983) Induced development of sweeper tentacles on the reef coral *Agaricia agaricites*: a response to direct competition. Biol Bull 165:569–581

Chornesky EA (1991) The ties that bind: interclonal cooperation may help a fragile coral dominate shallow high-energy reefs. Mar Biol 109:41–51

Clark T (1997) Tissue regeneration rate of coral transplants in a wave exposed environment, Cape D'Aguilar, Hong Kong. Proc 8th Int Coral Reef Symp 2:2069–2074

Clark S, Edwards AJ (1995) Coral transplantation as an aid to reef rehabilitation: evaluation of a case study in the Maldive Islands. Coral Reefs 14:201–213

Custodio HM III, Yap HT (1997) Skeletal extension rates of *Porites cylindrica* and *Porites* (*Synarea*) *rus* after transplantation to two depths. Coral Reefs 16:267–268

Davies PS (1980) Respiration in some Atlantic reef corals in relation to vertical distribution and growth form. Biol Bull 158:187–194

Dizon RM, Yap HT (2000) Growth differences in *Porites cylindrica* nubbins transplanted to monospecific and multispecific plots. Proc 9th Int Coral Reef Symp Progr Abstr p 132

Done TJ, Potts DC (1992) Influences of habitat and natural disturbances on contributions of massive *Porites* corals to reef communities. Mar Biol 114:479–493

Dustan P (1979) Distribution of zooxanthellae and photosynthetic chloroplast pigments of the reef-building coral *Montastraea annularis* Ellis and Solander in relation to depth on a West Indian coral reef. Bull Mar Sci 29(l):79–95

Edwards AJ, Clark S (1998) Coral transplantation: a useful management tool or misguided meddling? Mar Pollut Bull 37(8):474–487

Fisk DA, Harriot VJ (1992) Are understory coral communities recruitment limited? Proc 7th Int Coral Reef Symp 1:517–520

Foster AB (1980) Environmental variation in skeletal morphology within the Caribbean reef corals *Montastraea annularis* and *Siderastrea siderea*. Bull Mar Sci 30(3):678–709

Frank U, Brickner I, Rinkevich B, Loya Y, Bak RPM, Achituv Y, Ilan M (1995) Allogeneic and xenogeneic interactions in reef-building corals may induce tissue growth without calcification. Mar Ecol Prog Ser 124:181–188

Gittings SR, Bright TJ, Choi A, Barnett RR (1988) The recovery process in a mechanically damaged coral reef community: recruitment and growth. Proc 6th Int Coral Reef Symp 2:225–230

Gittings SR, Bright TJ, Hagman DK (1994) The MV Wellwood and other large vessel groundings: coral reef damage and recovery. In: Ginsberg RN, Smith FGW (eds) Proc Colloquium Global Aspects of Coral Reefs, Miami, pp 174–180

Gomez ED (1997) Reef management in developing countries: a case study in the Philippines. Coral Reefs 16(Suppl):S3–S8

Grigg RW (1995) Coral reefs in an urban embayment in Hawaii; a complex case history controlled by natural and anthropogenic stress. Coral Reefs 14:253–266

Grigg RW, Dollar SJ (1990) Natural and anthropogenic disturbance on coral reefs. In: Dubinsky Z (ed) Ecosystems of the world, vol 25: coral reefs. Elsevier, Amsterdam, pp 439–452

Harriot VJ, Fisk DA (1988) Coral transplantation as a reef management option. Proc 6th Int Coral Reef Symp 2:375–379

Harvell CD, Kim K, Burkholder JM, Colwell RR, Epstein PR, Grimes DJ, Hofmann EE, Lipp EK, Osterhaus ADME, Overstreet RM, Porter JW, Smith GW, Vasta GR (1999) Emerging marine diseases–climate links and anthropogenic factors. Science 285:1505–1510

Hidaka M (1985) Tissue compatibility between colonies and between newly settled larvae of *Pocillopora damicornis*. Coral Reefs 4:111–116

Hidaka M, Yamazato K (1984) Intraspecific interactions in a scleractinian coral, *Galaxea fasicularis*: induced formation of sweeper tentacles. Coral Reefs 3:77–85

Hildemann WH, Jokiel PL, Bigger CH, Johnston IS (1980) Allogeneic polymorphism and alloimmune memory in the coral *Montipora verrucosa*. Transplantation 30:297–301

Hughes TIP (1994) Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. Science 265:1547–1557

Hunte W, Wittenberg M (1992) Effects of eutrophication and sedimentation on juvenile corals. II. Settlement. Mar Biol 114:625–631

Jaap WC (1999) An historical review of coral reef restoration in Florida. In: Proc Int Conf on Scientific Aspects of Coral Reef Assessment, Monitoring, and Restoration, Program Abstr, p 111

Koh EGL (1997) Do scleractinian corals engage in chemical warfare against microbes? J Chem Ecol 23(2):379–398

Koh EGL, Sweatman H (2000) Chemical warfare among scleractinians: bioactive natural products from *Tubastraea faulkneri* Wells kill larvae of potential competitors. J Exp Mar Biol Ecol 251:141–160

La Barre SC, Coll JC, Sammarco PW (1986) Competitive strategies of soft corals (*Coelenterata*: Octocorallia): III. Spacing and aggressive interactions between alcyonaceans. Mar Ecol Prog Ser 28:147–156

Lang J (1971) Interspecific aggression by scleractinian corals. I. The rediscovery of *Scolymia cubensis* (Milne Edwards & Haime). Bull Mar Sci 21:952–959

Lang JC, Chornesky EA (1990) Competition between scleractinian reef corals – a review of mechanisms and effects. In: Dubinsky Z (ed) Ecosystems of the world, vol 25: coral reefs. Elsevier, Amsterdam, pp 209–251

Maida M, Sammarco PW, Coll JC (1995) Preliminary evidence for directional allelopathic effects of the soft coral *Sinularia flexibilis* (Alcyonacea: Octocorallia) on scleractinian coral recruitment. Bull Mar Sci 56:303–311

McCloskey LR, Muscatine L (1984) Production and respiration in the Red Sea coral *Stylophora pistillata* as a function of depth. Proc R Soc Lond B222:215–230

Montebon ARF, Yap HT (1997) Growth responses of the scleractinian coral *Porites cylindrica* Dana to water motion. Proc 8th Int Coral Reef Symp 2:1065–1070

Pastorok RA, Bilyard GR (1985) Effects of sewage pollution on coral-reef communities. Mar Ecol Prog Ser 21:175–189

Pearson RG (1981) Recovery and recolonization of coral reefs. Mar Ecol Prog Ser 4:105–122

Plucer-Rosario G, Randall RH (1987) Preservation of rare coral species by transplantation and examination of their recruitment and growth. Bull Mar Sci 41(2):585–593

Porter JW, Targett NM (1988) Allelochemical interactions between sponges and corals. Biol Bull 175:230–239

Potts DC (1976) Growth interactions among morphological variants of the coral *Acropora palifera*. In: Mackie GO (ed) Coelenterate ecology and behavior. Plenum Press, London, pp 79–88

Quirolo C (1999) Coral nursery project at Western Sambo Reef, Florida Keys. Reel Relief, Florida

Raymundo LJH (2000) Coral reef rehabilitation in the Philippines: the role of biotic interactions in coral reestablishment. PhD Thesis, Cornell University, Ithaca

Richardson CA, Dustan P, Lang JC (1979) Maintenance of living space by sweeper tentacles of *Montastraea cavernosa*, a Caribbean reef coral. Mar Biol 55:181–186

Richardson LL (1998) Coral diseases: what is really known? Trends Ecol Evol 13:438–443

Rinkevich B (1995) Restoration strategies for coral reefs damaged by recreational activities: the use of sexual and asexual recruits. Restoration Ecol 3:241–251

Rinkevich B, Loya Y (1983) Intraspecific competitive networks in the Red Sea coral *Stylophora pistillata*. Coral Reefs 1:161–172

Rinkevich B, Loya Y (1985a) Intraspecific competition in a reef coral: effects on growth and reproduction. Oecologia 66:100–105

Rinkevich B, Loya Y (1985b) Coral isomone: a proposed chemical signal controlling intraclonal growth patterns in a branching coral. Bull Mar Sci 36(2):319–324

Rinkevich B, Shashar N, Liberman T (1992) Nontransitive xenogeneic interactions between four common Red Sea sessile invertebrates. Proc 7th Coral Reef Symp 2:833–839

Sall J, Lehman A (1996). JMP Start statistics. SAS Institute. International Thomson, Belmont

Sammarco PW (1980) *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J Exp Mar Biol Ecol 45:245–272

Sammarco PW (1991) Geographically-specific recruitment and post-settlement mortality as influences on coral communities: the cross-continental shelf transplant experiment. Limnol Oceanogr 36:495–514

Sammarco PW, Andrews JC (1989) The Helix experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. Limnol Oceanogr 34:896–912

Sammarco PW, Coll JC, La Barre S, Willis S (1983) Competitive strategies of soft corals (Coelenterata: Octocorallia): allelopathic effects on selected scleractinian corals. Coral Reefs 1:173–178

Stimson J (1985) The effect of shading by the table coral *Acropora hyacinthus* on understory coral. Ecology 68:40–53

Velleman PF (1997) Data desk, vol 6.0 statistics guide. Data Description, Ithaca

Veron JEN, Hodgson G (1989) Annotated checklist of the hermatypic corals of the Philippines. Pac Sci 43(3):234–287

de Weerdt WH (1981) Transplantation experiments with Caribbean *Millepora* species (Hydrozoa, Coelenterata), including some ecological observations on growth forms. Bijdr Dierk 51(1): 1–19

Wellington GM (1980) Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. Oecologia 47:340–343

West JM, Harvell CD, Walls A-M (1993) Morphological plasticity in a gorgonian coral (*Briareum asbestinum*) over a depth cline. Mar Ecol Prog Ser 94:61–69

Willis BL, Ayre DJ (1985) Asexual reproduction and genetic determination of growth form in the coral *Pavona cactus*: biochemical genetic and immunogenic evidence. Oecologia 65:516–525

Yap HT, Gomez ED (1981) Growth of *Acropora pulchra* (Brook) in Bolinao, Pangasinan, Philippines. Proc 4th Int Coral Reef Symp 2:207

Yap HT, Gomez ED (1984) Growth of *Acropora pulchra*. II. Responses of natural and transplanted colonies to temperature and day length. Mar Biol 81:209–215

Yap HT, Gomez ED (1985) Growth of *Acropora pulchra*. III. Preliminary observations on the effects of transplantation and sediment on the growth and survival of transplants. Mar Biol 87:203–209

Yap HT, Aliño PM, Gomez ED (1992) Trends in growth and mortality of three coral species (Anthozoa: Scleractinia), including effects of transplantation. Mar Ecol Prog Ser 83: 91–101

Yap HT, Montebon ARF, Sabater MG, Gomez ED (2000) Prospects for coral reef rehabilitation: a Philippine case study. Proc 9th Int Coral Reef Symp Progr Abstr, p 352