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SETBACKS AND SURPRISES

Performance of single versus mixed coral species for transplantation to restore degraded reefs

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Coral transplantation has become a potential tool for the restoration of coral cover in degraded reef habitats. Yet, very few investigations have attempted to determine whether there is an advantage for at least two species to be used together in coral transplantation. It is hypothesized that corals would perform better in terms of survival and growth when transplanted in mixed- than in single-species plots. Single-species plots were compared with combinations of two species at several reef sites, using three separate coral species, namely, *Porites cylindrica*, *Pavona frondifera*, and *Hydnophora rigida*. *P. cylindrica* performed consistently well in terms of survival whether alone or in the presence of another species. In a stressful environment with strong wave action, *P. frondifera* performed better when mixed with *P. cylindrica* than when alone. However, this difference was not evident where wave action was weak. The influence of mixing on the growth rates of *H. rigida* and *P. frondifera* transplants could not be examined completely because of high mortality because of predation by the starfish *Acanthaster planci* and the gastropod *Drupella* sp. Interestingly, the presence of *P. cylindrica* appeared to minimize the impact of predation on *P. frondifera* transplants. The setback caused by predation stresses the importance of other factors that influence the outcome of restoration interventions. Future initiatives should take into consideration management measures when selecting sites in relation to wave action and predators, control predator outbreaks, and use coral species, e.g. *P. cylindrica* that are less susceptible to predation.

Key words: ***Acanthaster planci*, coral restoration, diversity, *Drupella*, partial mortality, *Pavona frondifera*, *Porites cylindrica*, predation**

Implications for Practice

- Effects of variable wave exposure and predation on coral transplants suggest that local environmental conditions have a great effect on the outcome of coral restoration efforts. This stresses the need to select carefully the coral species to use, particularly those that are known to be resilient to predation or variable water motion.
- The advantage afforded by one coral species over another depends on its competitive ability and also its adaptation to local conditions (e.g. the presence of predators and environmental factors).
- The presence of a coral species may minimize the predation mortality and survival under strong wave action of another; however, the advantage of mixing coral species on resulting growth of the transplants needs to be assessed further.

Introduction

In a world where coral reefs are under siege from both natural and anthropogenic challenges (Burke et al. 2011), efforts are under way to study how to ensure their continued provision of ecosystem services even as their biodiversity is diminished. One approach is the transplantation of corals into areas where they have been compromised but where the threats have been reduced subsequently, leaving hope that new communities may be established where needed (Edwards & Gomez 2007). Initial experiments have often dealt only with single-species transplantation (e.g. Yap et al. 1992; Gomez et al. 2011, 2014), a practice more common in the Caribbean, for example, where there are ongoing and continued attempts to save their framework building species, *Acropora palmata* (Williams & Miller 2010). There is a need to study the performance of mixed-species assemblages compared with those of single species because the former are expected to contribute more effectively to the successful reestablishment of the broader reef community as explained below.

Coral transplantation studies in the past have focused on examining the performance and feasibility of translocating coral species to areas with different environmental conditions (e.g. Birkeland et al. 1979; Yap & Gomez 1985; Dizon & Yap 2005). The practice in transplanting corals has been to attach fragments randomly onto suitable bare substrate (Yap et al. 1992; Villanueva et al. 2012), with less consideration given to the

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arrangement and composition of the transplants. Early experiments that involved mixed-species transplantation tested the influence of nutrient disturbance on corals that were attached to steel platforms above a sandy substrate (Dizon & Yap 2005). This study involves direct transplantation onto natural reef substrates for the purpose of restoring degraded patches, while at the same time examining the performance of single-species compared with mixed-species transplants.

Reef communities harboring multiple numbers of species are expected to have better chances of survival and persistence than single-species patches for the simple reason that various species possess different characteristics in terms of tolerance to environmental variability as well as to fluctuations in available resources (cf. Bellwood & Hughes 2001). Hardier species are expected to survive better as well as undergo continued growth and reproduction, while more sensitive species may eventually die out. More diverse reef areas are likely to continue to harbor some resilient species after the occurrence of disturbance (Nystrom & Folke 2001), whether in the form of rising sea surface temperatures and increased storm intensity, or anthropogenic impacts such as nutrient enrichment (Loya et al. 2001; Villanueva et al. 2006; San Diego-McGlone et al. 2008).

In addition to the general consideration of added benefits afforded by a higher species richness to the overall persistence of a community, attention should be paid to actual processes involving the species themselves that allow them to coexist and, hence, maintain a particular level of diversity. Individual species are known to respond differently when they occur as monospecific patches, as opposed to when they have to share space and other resources with neighboring species (Dizon & Yap 2005; Elahi 2008). Some species are poorer competitors than others and, hence, survive and grow better in monocultures. Other species, in contrast, are better competitors and are able to grow and survive better than species they come in contact with (Rinkevich & Sakai 2001; Idjadi & Karlson 2007). Moreover, the presence of another coral species may (1) diffuse the impact of predation (De'ath & Moran 1998); (2) provide shading during thermal stress events (Ortiz et al. 2009), although this may also hinder light penetration during normal conditions (Baird & Hughes 2000); and (3) alter water motion in the reef, promoting coral settlement or protecting other corals from physical damage (Dollar 1982).

Here, investigations involving two-species interactions (Order Scleractinia) are described, focusing on their growth and survival in comparison with single-species performance. Three species were used, namely, *Porites cylindrica, Hydnophora rigida*, and *Pavona frondifera*, all present in significant numbers in the Bolinao-Anda reef complex in the northern Philippines. All three species are important framework builders of Indo-Pacific reefs (Veron 2000). Because of their local availability, they have been used in various studies (e.g. Yap et al. 1992; Dizon & Yap 2005; Vicentuan 2009; Yap 2009). *Porites cylindrica* is a branching colony distributed widely in the Bolinao area where there are some large degraded outcrops with surviving colonies at the lower depths (Gomez et al. 2014). This species was shown to be more silt tolerant in studies relating river discharge to diversity in Palau (Golbuu et al. 2011). Similarly, a number of degraded bommies of the foliose *P. frondifera* species occur in the more sheltered lagoonal areas, with some extensive communities evident at a site more open to the sea. On the other hand, the short digitate *H. rigida* colonies are found in less abundance in both exposed and sheltered areas.

The experiments were conducted in a lagoonal environment in Bolinao, northern Philippines, the site of a number of recent restoration efforts (e.g. Dizon et al. 2008; Shaish et al. 2008; Gomez et al. 2011, 2014). The objective was to restore coral cover of selected degraded bommies, and in doing so to determine whether it was effective to use single species or a combination of two species. The hypothesis was that corals would have better survival and growth when transplanted in mixed-species than in single-species plots.

Methods

Study Site

Experiments were conducted in the reef lagoon of Bolinao, Pangasinan, in the northwestern Philippines. Coral fragments derived from natural colonies within existing reef communities were transplanted on dead coral outcrops or 'bommies' at two sites, namely, Binlab and Malilnep (Fig. 1). At each site, three replicate bommies were selected among the other numerous bommies in the area which ranged in size from 1 m^2 to 10's of square meters and were located at depths of 1–3 m (from the sea surface to the tops of the bommies). The bommies at Malilnep are mainly dead massive *Porites* colonies, while at Binlab, they are composed of dead branching *Porites*. Bommies at Malilnep experience stronger water current as these are located along a channel that connects the lagoon with the outer reef (Gomez et al. 2011). On the other hand, bommies at Binlab are subjected to more turbid conditions as they are situated nearer to the main

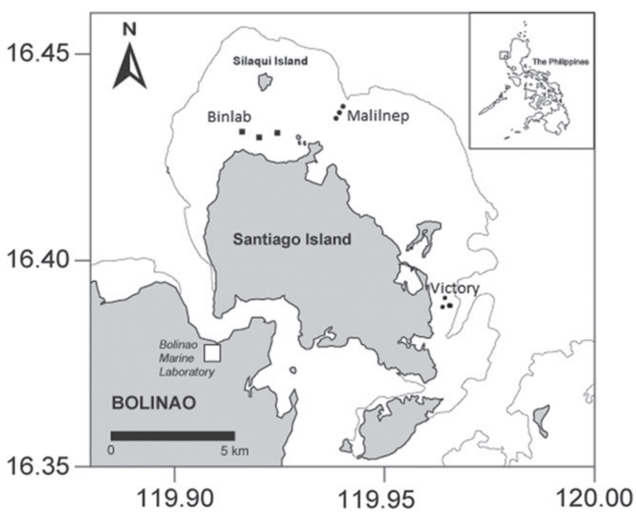

Figure 1. Map showing the source sites at Binlab (for *Porites cylindrica*) and Victory (for *Pavona frondifera*) and transplantation sites using the different species at Binlab and Malilnep.

island of Santiago. Oftentimes, underwater visibility in Binlab was as low as 2 m compared with the 5-m visibility in Malilnep.

Coral Transplantation

Porites cylindrica fragments were collected from one of the bommies at Binlab, while *Pavona frondifera* transplants were sourced from Victory (Fig. 1). Fragments of *Hydnophora rigida* were collected from the outer reef of Malilnep. Initially, loose fragments (70–1000 cm^3 in size) or "corals of opportunity" (Edwards & Gomez 2007) that were healthy with no lesions were collected from these sites. These fragments were located a few meters away from each other and, thus, were assumed to have come from different mother colonies. Only if the transplant material was not enough were additional fragments collected from standing colonies (at least 10 independent colonies of each species) using side cutter pliers, taking less than 10% of each colony to minimize collateral damage (Epstein et al. 2001; Edwards & Gomez 2007). Some of the fragments were cut to standardize the sizes of the transplants. Collected fragments were placed in buckets and submerged in seawater while being transported to the transplant sites where they were attached to the coralline substrates directly with epoxy clay putty (an inert substance; Dizon et al. 2008), without resorting to artificial platforms or substrates. Fragments were randomly distributed among each of the three replicate bommies.

At Malilnep where the bommies were dead massive *Porites* colonies, holes were drilled using an improvised auger (i.e. a cold chisel with a perpendicular handle as described by Gomez et al. (2010)) in order to provide more secure attachment to the substrate. The holes were initially brushed to remove turf algae and silt, after which a small amount of epoxy clay putty was introduced before inserting the coral fragment. A live portion of the fragment was placed in direct contact with the calcium carbonate substrate to ensure natural attachment. At Binlab, the substrate of the bommies was porous compared with the ones at Malilnep, providing natural holes and spaces in between dead branches. Thus, after cleaning, coral fragments were simply wedged into available crevices. A small portion of epoxy was applied if needed.

Experimental Design

The first set of experiments involved transplants of *P. cylindrica* (32 cm^3 in size) and *H. rigida* (16 cm^3 in size), in single and mixed plots in Malilnep. However, it progressed only for a month because of selective predation by the crown-of-thorns starfish, *Acanthaster planci*, on *H. rigida*. The set-up of this experiment was the same as described below, that is, three replicate bommies with three treatment plots on each bommie but in only one site.

A second set of experiments used approximately equal-sized transplants of *P. cylindrica* and *P. frondifera* (32 cm^3 in size). It extended for 12 months. In this experiment, there were three replicate bommies at each of the two sites, that is, Malilnep and Binlab, each of which contained three independent plots representing the following treatments: (1) single-species plot for *P. cylindrica*; (2) single-species plot for *P. frondifera*; and (3) mixed-species plot containing both *P. cylindrica* and *P. frondifera*. As mentioned in the introduction, the objective was to compare the survival and the growth of corals transplanted in single-species plots with those in mixed-species plots. For the single-species plots, 40 fragments of *P. cylindrica* (for treatment 1) and 40 fragments of *P. frondifera* (for treatment 2) were attached on each bommie on a horizontal surface. For the mixed-species plots, 40 fragments of each of the two species were transplanted in an alternating arrangement on each bommie. Mixed-species plots covered a larger area than the single-species plots because each of them contained 80 fragments, and the spacing (approximately 15 cm) between transplants was the same in all treatments. A total of 240 fragments of each of the two species, *P. cylindrica* and *P. frondifera*, were used in each site (i.e. each site had three bommies and each bommie contained 80 fragments of each of the two species).

Monitoring

Survival of coral transplants per treatment and location was monitored monthly for the first 3 months and every 3 months thereafter. Transplants with no living tissue were considered dead. Corals that were initially detached were reattached as much as possible if still alive. Growth rates of coral transplants were measured in two ways, as linear increment in height and as radial increment. Height was measured from the bottom to the top of the transplant using a caliper. Radial increment was obtained by measuring the longest length (L) of each transplant and the widest width (W) perpendicular to L and computed as 1/2 SQRT ($L \times W$). This represented a slight modification of the geometric mean diameter of Clark and Edwards (1995). Growth rates in terms of height and radial increments were monitored every 3 and 6 months, respectively. These were standardized to obtain "mm per 30 days." Transplants that exhibited negative increments were excluded from the analyses as these values do not represent growth but shrinkage or partial mortality because of predation by *Drupella*.

Statistical Analyses

Survival of transplants among treatments and sites was compared and tested using survival analysis (representing trends in mortality) with the Kaplan–Meier function (Lee 1992). Factors were then compared using log-rank statistics. The log-rank test is used to compare two or more groups of survival times or the times to event (i.e. survival or the number of transplants alive in this study). For survival and growth rates, the average per treatment for the three replicate bommies was calculated. Changes in growth rates through time by treatment and species were analyzed using repeated measures analysis of variance (ANOVA, Potvin et al. 1990) after data were tested, and transformed where necessary, for normality and homogeneity of variance. To obtain a clear result when comparing treatments (i.e. single vs. mixed-species plots), separate ANOVA tests were conducted

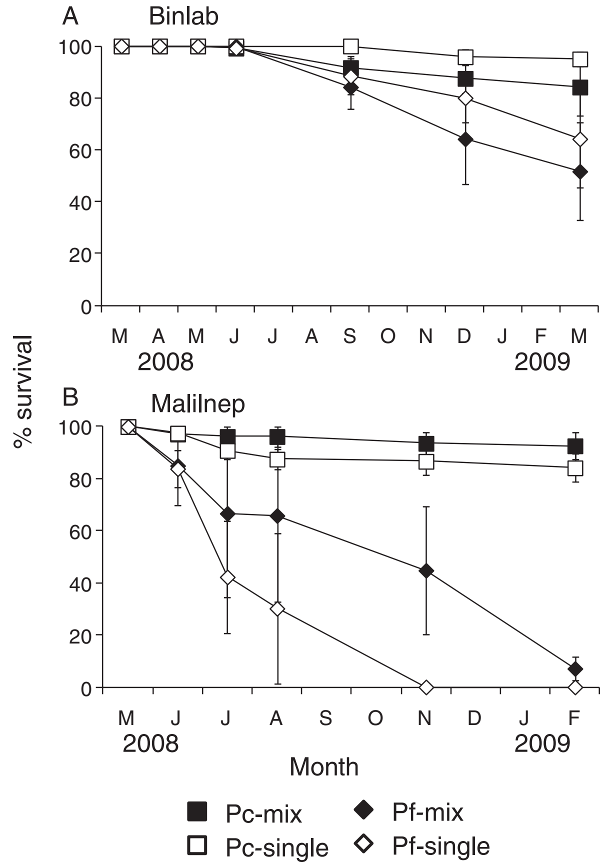

Figure 2. Survival of coral transplants of *Porites cylindrica* and *Pavona frondifera*, per treatment at (A) Binlab and (B) Malilnep through time. Error bars are standard errors of the means.

for each species per location. Bonferroni correction was applied on *p* values to account for the increase in statistical errors (Zar 1984). Factors with significant results in ANOVA were further tested using Tukey's honestly significant difference (HSD) *post hoc* test. All statistical analyses were conducted using Statistical Package for the Social Sciences (SPSS) software. The height and radial increments of *P. frondifera* at Malilnep could not be compared statistically between treatments (single- and mixed-species transplant plots) because of insufficient replicate samples for *P. frondifera* in the single-species transplant plots. (The samples were lost to mortality by predation.)

Results

Survival

As mentioned earlier, the *Hydnophora rigida* transplants were lost to predation by the crown-of-thorns starfish, while none of the *Porites cylindrica* were eaten by the predators. *P. cylindrica* had high percent survival in all treatments in both experiments, which ranged from 84 to 95% over a period of 12 months (Fig. 2). Survival of *P. cylindrica* showed no significant difference when transplanted as a monoculture or in a mixed-species treatment (Table 1). On the other hand, *Pavona frondifera* had a survival rate that ranged from 7% at Malilnep to 64% at Binlab (Fig. 2A & 2B). *Pavona frondifera* in mixed-species plots exhibited significantly higher survival rate than the transplants in single-species plots at Malilnep. In contrast, there was no statistically significant difference in survival of *P. frondifera* in mixed-species plots compared with that in single-species plots at Binlab (Table 1; Fig. 2B). Overall, Malilnep yielded the lowest survival of *P. frondifera* transplants.

The mortality of *P. frondifera* in Malilnep was due mainly to predation by corallivorous *Drupella* sp. gastropods and occasionally by *Acanthaster planci* starfish. In August 2008, one single-species and one mixed-species plot of *P. frondifera* (on one of three replicate bommies in Malilnep) were wiped out. The other two single-species plots of *P. frondifera* (on the two other bommies) still contained transplants, but one of these had only one transplant that experienced partial mortality. In the November 2008 monitoring, all remaining *P. frondifera* in the single-species plots at Malilnep died. On the other hand, less than six *P. frondifera* transplants survived in each of the two mixed-species plots after the last monitoring visit. In Binlab, only mild predation by *Drupella* sp. gastropods in some plots was observed.

Growth Rates

Growth rates in terms of height for *P. cylindrica* at Binlab were significantly higher when transplanted in mixed-species plots compared with single-species plots, although only during the first monitoring period (Fig. 3A; Table 2 showing significant time × treatment interaction). *Pavona frondifera* showed no significant growth differences when transplanted in mixed- or single-species plots (Table 2; Fig. 3A). At Malilnep, transplants of both *P. cylindrica* and *P. frondifera* exhibited no significant differences in growth rates in terms of height, whether transplanted in mixed or single-species plots (Table 2; Fig. 3B).

In terms of radial growth, *P. cylindrica* transplants in mixed-species plots at Binlab had significantly higher rates than the transplants in single-species plots (Fig. 4A; Table 2). For *P. frondifera* transplants, on the other hand, growth rates showed no significant differences between mixed- and single-species plots at this location (Table 2; Fig. 4A). However, radial growth rates of *P. frondifera* decreased significantly through time (Table 2). In the other location, Malilnep, transplants of *P. cylindrica*, had no significant differences in radial growth rates whether transplanted in mixed or in single-species plots (Table 2; Fig. 4B). A similar comparison could not be made for *P. frondifera* as the transplants in all single-species plots died out in the course of the experiment because of predation by corallivorous *Acanthaster planci* starfish and *Drupella* sp. gastropods.

Discussion

Of the three scleractinian species used, *Porites cylindrica* was the best survivor under all treatment conditions, making it a

Table 1. Results of log-rank statistics comparing the survival trends by species (*Pc*, *Porites cylindrica*; *Pf*, *Pavona frondifera*) and by treatment (single- vs. mixed-species transplant plots) at Binlab and at Malilnep. *p* Values in bold are significant at the 0.05 level after Bonferroni correction.

	Logrank			
	df	*Chi square*	*p*	Verdict
Binlab				
Species	2	14.62	**0.0001**	Pc > Pf
Single vs. mixed treatments	2	2.09	0.1483	Single = mixed transplants
	2	6.13	**0.013**	Pc single > Pf single
	2	8.59	**0.003**	Pc mixed > Pf mixed
	2	1.00	0.317	Pc single = Pc mixed
	2	1.58	0.209	Pf single = Pf mixed
Malilnep				
Species	2	148.74	**<0.001**	Pc > Pf
Single vs. mixed treatments	2	13.34	**0.0003**	Single < mixed transplants
	2	109.20	**<0.001**	Pc single > Pf single
	2	46.20	**<0.001**	Pc mixed > Pf mixed
	2	1.04	0.309	Pc single = Pc mixed
	2	13.74	**<0.001**	Pf single < Pf mixed

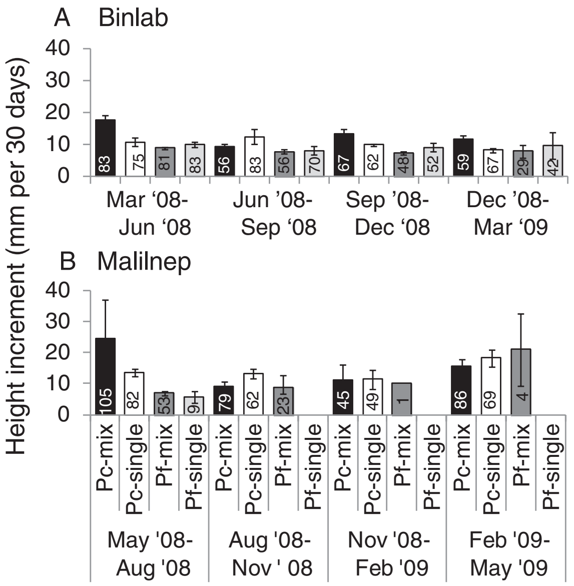

Figure 3. Height increment (mm per 30 days) of coral transplants at (A) Binlab and (B) Malilnep. Error bars represent the standard errors of the means. The values on each bar are number of fragments that exhibited growth between monitoring periods. There are no values for Pf-single in Malilnep following August 2008 because all of the *Pavona frondifera* in single-species plots on the three replicate bommies died out owing to predation by *Drupella* sp. and *Acanthaster planci*. Also, the height increment for Pf-mix in Malilnep from November 2008 to February 2009 has no error value as only one transplant registered a positive height increment or growth. The other surviving *P. frondifera* transplants ($n = 70$) during this period experienced partial mortality and did not register a positive height increment or growth.

good candidate for the restoration of coral cover in degraded reef habitats (Gomez et al. 2014). A recent coral transplantation study in Palau comparing *P. cylindrica* with *Acropora digitifera* similarly showed the former to be a better survivor (Golbuu et al. 2011). On the other hand, *Hydnophora rigida* succumbed entirely to predation by the starfish *Acanthaster planci* in the early part of the experiment, although it had performed reasonably well in a previous investigation (Vicentuan 2009). *H. rigida* transplants in the study by Vicentuan (2009) were protected from *A. planci* as these were attached to elevated platforms established in sandy areas of the reef lagoon.

Does the presence of other sessile benthic organisms affect the survival and growth of certain species? The literature on the interaction of two or more species tends to demonstrate negative effects, whether it be actual predation (e.g. Lang 1971) or the broader range of competition (Lang & Chornesky 1990; Chadwick & Morrow 2011) including temporal shifts (Chornesky 1989). Possible facilitation of survival or growth by the presence of other species has not been as widely investigated (Bruno et al. 2003; Dizon & Yap 2005).

A beneficial effect of mixing species was manifested in the growth performance of the transplants. At its native habitat in Binlab, *P. cylindrica* had greater height and radial increments over time when in the presence of another coral species. In the same environmental setting (Binlab), *P. frondifera* showed no significant difference in growth, whether alone or in the mixed-species treatment. No noticeable advantage in terms of growth was conferred on *P. frondifera* by the presence of another species. When superior competitors are situated next to poorer competitors, the former are expected to be able to exert their advantage and perform better, e.g. in terms of growth (Idjadi & Karlson 2007) as demonstrated by the *P. cylindrica* transplants in the present and past studies (Dizon & Yap 2005). On the other hand, poorer competitors should perform better when in monospecific aggregations (Idjadi & Karlson 2007). However, *P. frondifera*, the less competitive species in this study (as demonstrated in Dizon & Yap 2005), did not exhibit better performance in monospecific compared with mixed plots. Apparently, the growth of *P. frondifera* transplants was interrupted by the predation of the corallivorous gastropod, *Drupella* sp. (PC Cabaitan 2007, The Marine Science Institute, University of the Philippines, personal observation).

Table 2. Results of repeated measures ANOVA of height and radial colony increments of coral transplants (*Porites cylindrica* and *Pavona frondifera*) in different treatments (single- and mixed-species transplant plots) at Binlab and Malilnep. *p* Values in bold are significant at the 0.05 level after Bonferroni correction. n.d. means no data.

	Height increment								*Radial colony increment*							
	Porites cylindrica				Pavona frondifera				Porites cylindrica				Pavona frondifera			
Effects	df	*MS*	F	p	*df*	*MS*	F	p	*df*	*MS*	F	p	*df*	*MS*	F	p
Binlab																
Time	3	21.23	4.75	0.02	3	2.71	0.29	0.83	1	0.00	0.00	1.00	1	0.82	46.38	**<0.01**
Treatment	1	43.88	4.78	0.09	1	9.00	0.74	0.44	1	1.62	33.77	**<0.01**	1	0.02	0.11	0.76
Time × treatment	3	24.91	5.57	**0.01**	3	0.65	0.07	0.98	1	0.03	0.20	0.68	1	0.00	0.22	0.66
Malilnep																
Time	3	95.56	1.91	0.18			n.d.		1	7.30	2.47	0.19		n.d.		
Treatment	1	7.09	0.04	0.84					1	1.47	0.50	0.52				
Time × treatment	3	69.14	1.38	0.29					1	2.14	0.72	0.44				

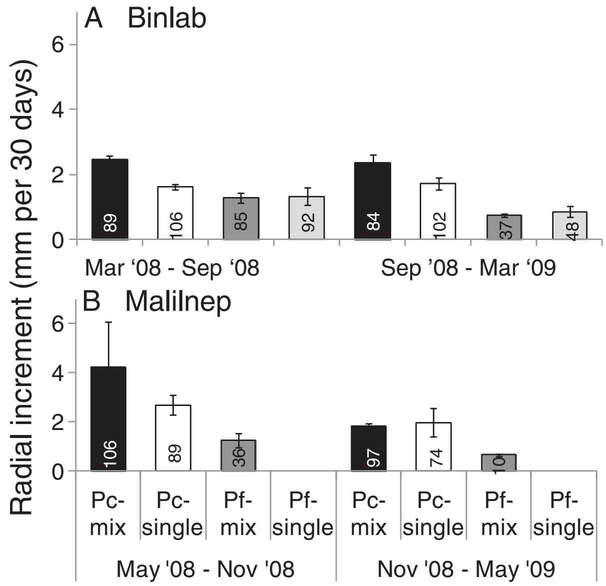

Figure 4. Radial increment (mm per 30 days) of coral transplants at (A) Binlab and (B) Malilnep. Error bars represent the standard errors of the means. The values on each bar are number of fragments that exhibited growth between monitoring periods. There are no values for Pf-single in Malilnep following August 2008 because all of the *Pavona frondifera* in single-species plots on the three replicate bommies died out due to predation by *Drupella* sp. and *Acanthaster planci*.

At Malilnep, the site more exposed to potential predation especially by *A. planci* because of its proximity to the outer reef (Gomez et al. 2011), *P. cylindrica* behaved similarly in terms of growth, whether in single or in mixed plots. Here, no advantage conferred by the presence of another species was observed. The two treatments in Malilnep yielded comparable outcomes because the majority of the *P. frondifera* transplants eventually succumbed to predation by *Drupella* sp. and *A. planci*. The early mortality of the *P. frondifera* transplants did not allow the assessment of the effects of species mixing on their growth.

In terms of survival at both sites, there was no apparent advantage for *P. cylindrica* when another species was present. On the other hand, at the more dynamic or stressful environment of Malilnep, *P. frondifera* survived better in mixed-species plots, possibly because of the protection from wave action as well as the predation that may have been afforded by the successfully established *P. cylindrica* transplants. As also noted elsewhere, *P. cylindrica* was generally avoided by the crown-of-thorns starfish (De'ath & Moran 1998).

Mixing two coral species, depending on their competitive ability, resulted in enhanced growth and survivorship, which varied in different environments. The enhanced effect of mixing on the growth performance of *P. cylindrica* transplants was apparent in only one site (Binlab). The otherwise similar performance of *P. cylindrica* between the two treatments in Malilnep may be attributed to the mortality of *P. frondifera* transplants, which also hindered the assessment of the performance of a poorer competitor in a monospecific treatment. Hence, the relative influences of mixing different coral species under varying environmental conditions on the performance of transplants needs to be assessed further. Overall, the results of these experiments provide insights into the potential benefit of mixing coral species in transplantation to a particular environment, which can contribute to the success of coral restoration.

Another factor that has been given less consideration but which represents a significant setback for coral restoration efforts is predation on coral transplants (Ferse & Kunzmann 2009; Omori 2011; Gomez et al. 2014). The predators had caused partial and whole colony mortalities of transplants. In this study, the presence of one species minimized the effect of predation on another coral species, an unexpected but positive outcome. The sporadic nature of the population dynamics of coral predators and the ability to alter their preference for coral prey according to the available coral assemblage (Turner 1994; De'ath & Moran 1998; Pratchett 2007; Morton & Blackmore 2009) require a local-specific approach in assessment of the impact of predation on coral restoration interventions. To mitigate the impact of predation, coral species that are not susceptible to predation should be utilized in monocultures or in combination with other more vulnerable species. Transplantation activities should also be conducted during the seasons when the abundance of predators like *Drupella* sp. is known to be low.

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