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Investigating fragment size for culturing reef-building corals (*Porites lobata* and *P. compressa*) in *ex situ* nurseries

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Abstract

Culturing small propagules of coral has the potential for high yield with low environmental impact, provided that mortality is low. This study investigated the size-specific mortality and growth of minute fragments (as small as 5 polyps) of two of the most abundant reef-building corals in Hawaii (*Porites lobata* and *P. compressa*). Two *ex situ* nursery systems differing in cost, design complexity, and labor intensity were compared. The first nursery experiment lasted for four months in a large tank with high water motion/surge and extensive manual cleaning to remove competitive algae. The corals were then transferred to a simple low-flow tank containing sea urchins (*Tripneustes gratilla*) and reduced cleaning, where they were grown for six more months (Nursery II). 'Nursery I' resulted in 92% of *P. lobata* and 73% of *P. compressa* fragments surviving and nearly doubling in area, in spite of a brief infestation by a nudibranch (*Phestilla sibogae*) that primarily fed on larger *P. compressa* fragments. There was a significant positive relationship between fragment size and growth rate, and survivorship was significantly different between donor colonies (genets), but there was no evidence of size-specific mortality. 'Nursery II' on the other hand had clear size-specific mortality and higher urchin damage for smaller fragments, resulting in moderate survivorship (78% for *P. lobata* and 76% for *P. compressa*), and only a slight increase in the total area covered by coral tissue. Fragments larger than 3 cm^2 were undamaged and had the highest survival and growth rates. This study illustrates how size-specific mortality can be reduced by *ex situ* nursery conditions.
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1. Introduction

Coral reef restoration efforts have traditionally relied on the transplantation of fragments or entire coral colonies from surrounding reefs (e.g. Maragos, 1974; Birkeland et al., 1979; Kojis and Quinn, 1981; Auberson, 1982; Harriott and Fisk, 1988; Guzman, 1991; Clark and Edwards, 1995; Rinkevich, 2005). The effectiveness of these efforts has varied greatly, depending on the protocols, habitat, and species selected, but in general, they were not regarded as ecologically sound management tools (Edwards and Clark, 1998; Rinkevich, 2005). The availability of source material for transplantation is one of the most important limitations in reef restoration, as the breakage and removal of coral material from source areas may result in further damage and reduced fecundity of donor colonies.

Direct coral transplantation efforts are potentially harmful to source reefs and to donor coral colonies,

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especially if the source reef is already in a state of decline. To address this concern, Rinkevich (1995, 2000) and Epstein et al. (2003) have suggested a "gardening" approach for restoring denuded coral reefs that is analogous to established terrestrial silviculture and reforestation methods. The "gardening" strategy uses aquaculture methodologies to establish sheltered *ex situ* or *in situ* nurseries, to farm and to mass-produce coral for mitigation and restoration efforts, for experimental studies, or for the marine aquarium industry (Shafir et al., 2001, 2003, 2006; Epstein and Rinkevich, 2001).

Propagation by fragmentation is a common asexual reproductive mode of many reef-building corals (Highsmith, 1982). This life history trait has been manipulated to artificially produce large quantities of fragments, or 'nubbins' as small as a few polyps, with high survival rates (Rinkevich, 1995, 2000; Shafir et al., 2001). Fragmentation can also produce large sample sizes with minimal genetic variation, which is ideal for experimentation (Shafir et al., 2003). One of the largest advantages of the gardening strategy is that coral nurseries can be started by a variety of means, many of which have little or no impact on the donor coral population, such as: (i) collecting fragments that were previously broken, overturned, or in imminent threat, (ii) using very small fragments (just a few polyps) taken from multiple donor colonies, or (iii) using coral colonies originating from field collected larvae (Gateno et al., 2000), or larval spat from settlement plates. The latter options have the added benefits of providing a nearly unlimited supply of source material, with minimal impact, while preserving the genetic diversity of the source population (Rinkevich, 2000, 2005; Delbeek, 2001). A coral nursery can provide refuge from size-specific mortality, until the colonies are large enough to be transplanted with a higher chance of survival (Rinkevich, 2005).

This study examined the feasibility of culturing of *Porites lobata* (abundant throughout the Pacific) and *P. compressa* (endemic to Hawaii) in *ex situ* nurseries. *Porites* is a ubiquitous circumtropical genus that provides the majority of the framework of Hawaiian coral reefs (Maragos, 1977) and many reefs worldwide (Veron, 2000). *Porites* is among the most widely distributed coral genera, both in terms of geography and in terms of habitats occupied. A combination of factors such as ubiquity, resilience and ecological importance makes *Porites* an excellent candidate as a model organism, provided that rapid culturing methods can be developed.

Here we examine the effects of fragment size on the survival and growth in two *ex situ* nursery types where the major causes of size-specific mortality (such as predation,

competition, sedimentation and incidental grazing) can be reduced. An additional obstacle for culturing *Porites* is infestation by corallivorous nudibranchs of the genus *Phestilla*. The nudibranchs are highly cryptic and lay egg cases hidden deep within crevices in live rock. *Phestilla* can reproduce rapidly and can decimate large colonies in aquaria in a matter of weeks (Gochfeld and Aeby, 1997). *Phestilla sibogae* was unintentionally introduced into one of our experimental systems; however, only one species (*P. compressa*) appeared to be preyed upon by this corallivore. *P. sibogae* was quickly eradicated, providing us with an opportunity to examine the effects of predation and feeding preferences.

2. Materials and methods

A 10-month long, two-phase (Nursery I, Nursery II) inland coral culturing study was conducted at the Waikiki Aquarium. Nursery I consisted of a large outdoor rectangular tank (approximately 3000 L capacity; $2.1 \times 1.2 \times 1.2$ m), exposed to full sunlight. The tank consisted of a siphon-surge tower that held approximately 700 L, producing an 11-L s^{-1} surge for 1 min at seven-minute intervals. The tank contained approximately 180 kg of live rock and was maintained at approximately 25–27 °C, by adjusting the amount of cool (ca. 24–25 °C) seawater that entered the tank (approximately 6 L min^{-1}). The seawater drawn from a below-ground well has been previously described to be high in inorganic nutrients (approximately: $SiO_3 \sim 200$ μM; $PO_4 \sim 0.6$ μM; $NO_3 \sim 5$ μM; $NH_4 \sim 2$ μM, from Atkinson et al., 1995; Carlson, 1999).

The coral donor colonies (two *P. compressa*, two *P. lobata*) and live rock were collected from Kualoa, Oahu, approximately 1 m depth, from a fringing reef characterized by patches of rubble and occasional small coral colonies. The colonies were acclimated to the tank conditions for one week, and then fragmentation was performed underwater using a chisel, tin snips and wire cutters to achieve a variety of sizes. A total of 432 fragments (216 per species, 108 per genet, 36 of each size category per genet) were affixed underwater onto 23 cm^2 unglazed ceramic tiles with marine epoxy (Splash Zone Compound, Woosley/Z-spar Inc., USA) in a split-plot experimental design. Each of the 12 arrays of 36 tiles was fixed to a 30 cm^2 tile for added weight and ease of manipulation. Each array of 36 tiles contained four blocks, one for each donor colony, consisting of nine fragments each. Each block contained three fragments of each non-overlapping size category: small (57 ± 6 mm^2), medium (126 ± 8 mm^2), and large (242 ± 22 mm^2), assigned a position within a block with

the pseudo-random number generator in SPSS v 11.0 (SPSS Inc).

Each array of tiles was rotated and moved to a new position weekly, to reduce the possibility of positional effects within the tank. The tile surfaces surrounding coral tissue were carefully scraped clean of algae and sediment (mostly diatoms, filamentous and coralline algae) two to three times weekly, with a nylon toothbrush and a flat-tipped knife. The numbers of juvenile and adult *P. sibogae* were recorded, after their removal from the tank with a siphon. Photographs were taken weekly with an Olympus digital camera with an underwater housing in a fixed photo frame. Survival and percentage of healthy tissue were estimated from the photographs. Tissue damage was estimated on a scale of 1–4, with a score of '4' indicating no damage, '3'

indicating 1–10% damage, '2' indicating 10–30% and '1' indicating >30% tissue damage. Nubbin area (from an aerial perspective) was measured every three weeks from the photographs using ImageJ v.1.32 (National Institutes of Health, USA); the length of the tiles (48 mm) was used to calibrate the scale of the image. Nursery I entailed detailed monitoring, and was conducted for four months (September 15, 2004 to January 12, 2005). Nursery II lasted for six months (January 12 to June 5, 2005). In Nursery II, the nubbins were moved to a $2.7 \times 1.2 \times 0.6$ m, 1000 L capacity rectangular tank with air stones, low flow (~ 4 L min^{-1}) and no surge tower, containing ~ 40 kg of live rock, and 15 sea urchins (*Tripneustes gratilla*) where they were kept with minimal cleaning. Through the course of the experiment 5 sea urchins died, which were not replaced.
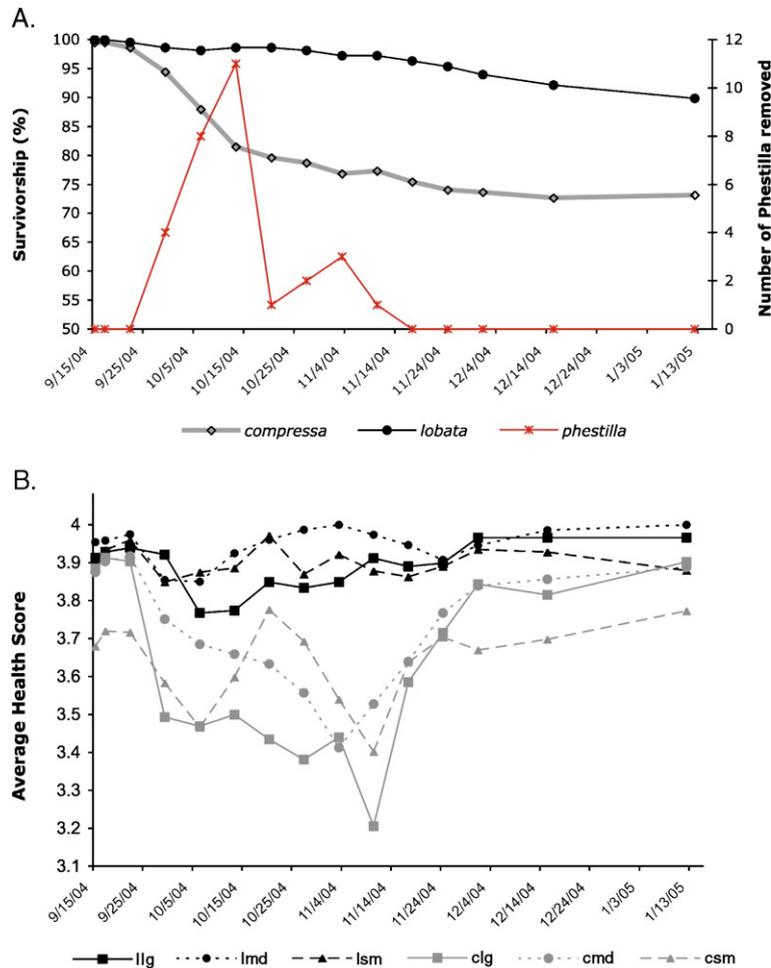

Fig. 1. A. Nursery I survivorship (%) and the numbers of *Phestilla sibogae* removed from the culture tank (on the secondary *y*-axis). B. Nursery I average health score (apparent tissue damage) for size categories (lg = large, md = medium, sm = small) of *P. lobata* (l) and *P. compressa* (c). Health was scored on the following scale of tissue damage: 1 = >50%, 2 = 10 to 30%, 3 = 1 to 10%, 4 = no apparent damage.

Therefore, we estimate a grazing density of 3 urchins m^{-2} for the entire experiment. The second nursery was intended to evaluate survival and growth in a more simple and inexpensive *ex situ* installation with minimal effort devoted to cleaning and maintenance.

2.1. Analysis

All polyps were counted from digital photographs for each individual fragment (from both coral species) at the beginning of the experiment, to determine if the area measured from digital photographs is a good proxy for the number of polyps. A linear regression indicated that area measurements, for both *Porites* species, strongly predicted initial polyp count, accounting for more than 90% of the variance in both species (*P. lobata* $r^2 = 0.916$, $p < 0.001$, $y = 0.61x + 0.75$, $n = 216$, and *P. compressa* $r^2 = 0.912$, $p < 0.001$, $y = 0.49x - 0.05$, $n = 216$). The fragments in this experiment were too small to develop branches or rugged topology; therefore, this method was used as a conservative estimate of growth. At the end of

the first nursery experiment, nubbins were placed in three categories based on the patterns of growth (1 = spherical growth, little or no tissue contact with tile; 2 = minor tissue growth on to tile; 3 = extensive tissue spreading over the tiles) to examine growth patterns among genets. Mortality between species, genets and size categories were compared using the Kaplan–Meir product-limit method of fitting survivorship curves, and comparison by Log rank, Breslow and Tarone–Ware non-parametric tests (Lee, 1992), and by Chi-Square tests. All statistical tests were preformed with SPSS v 11.0 (SPSS Inc).

3. Results

3.1. Nursery I

All 432 coral fragments survived subcloning and attachment procedures. Most tissue damage from fragmentation healed within the first few days and the fragment margins were grown over with tissue and small

Table 1
Survival, area increase, and growth rates for Nursery I and II

Source colony	Fragment size	Starting fragments (n)	Survival (%)	Initial size (mm^2±SD)	End size (mm^2±SD)	Avg. increase (%)	Growth rate (d^{-1} mm^2±SD)
Nursery I							
l1	lg	39	97.4	254.1±72.8	442.4±118.4	74.1	1.6±0.9
	md	30	93.3	129.0±24.7	328.7±111.8	154.7	1.7±0.9
	sm	39	97.4	64.0±17.3	210.3±73.5	228.8	1.2±0.5
l2	lg	33	84.8	240.6±57.3	373.8±115.8	55.4	1.1±0.7
	md	41	87.8	128.5±24.0	230.3±70.0	79.2	0.9±0.5
	sm	34	76.5	56.6±17.5	130.7±63.3	131.0	0.6±0.5
c1	lg	26	57.7	226.0±68.5	327.1±139.0	44.8	1.0±0.9
	md	40	62.5	123.6±24.0	294.5±117.2	138.3	1.4±0.9
	sm	42	73.8	52.2±19.1	155.6±105.1	198.2	0.9±0.8
c2	lg	46	78.3	248.0±69.2	355.6±122.0	43.4	0.9±0.9
	md	32	90.6	122.2±22.1	235.2±84.7	92.5	0.9±0.7
	sm	30	70.0	56.1±20.2	159.6±74.7	184.3	0.9±0.6
Nursery II: Starting count from end of Nursery I							
l1	lg	38	100.0	442.4±118.4	581.7±158.8	31.5	2.8±1.0
	md	28	100.0	328.7±111.8	402.5±120.5	22.5	2.3±1.0
	sm	35	92.1	210.3±73.5	238.9±81.1	13.6	1.5±0.6
l2	lg	20	71.4	373.8±115.8	471.3±173.8	26.1	1.9±1.2
	md	21	58.3	230.3±70.0	303.0±90.6	31.5	1.4±0.7
	sm	10	38.5	130.7±63.3	206.1±112.4	57.7	0.6±0.5
c1	lg	15	100.0	327.1±139.0	468.7±145.3	43.3	2.1±0.9
	md	21	84.0	294.5±117.2	370.0±177.0	25.6	2.0±1.3
	sm	15	48.4	155.6±105.1	178.2±91.3	14.5	1.0±0.7
c2	lg	35	97.2	355.6±122.0	435.0±128.5	22.4	1.5±1.1
	md	22	75.9	235.2±84.7	282.5±78.8	20.1	1.2±0.8
	sm	11	52.4	159.6±74.7	159.9±87.5	0.2	0.9±0.7

Abbreviations: l = *P. lobata*, c = *P. compressa*, lg = large, md = medium, sm = small, 1 and 2 = coral genets.
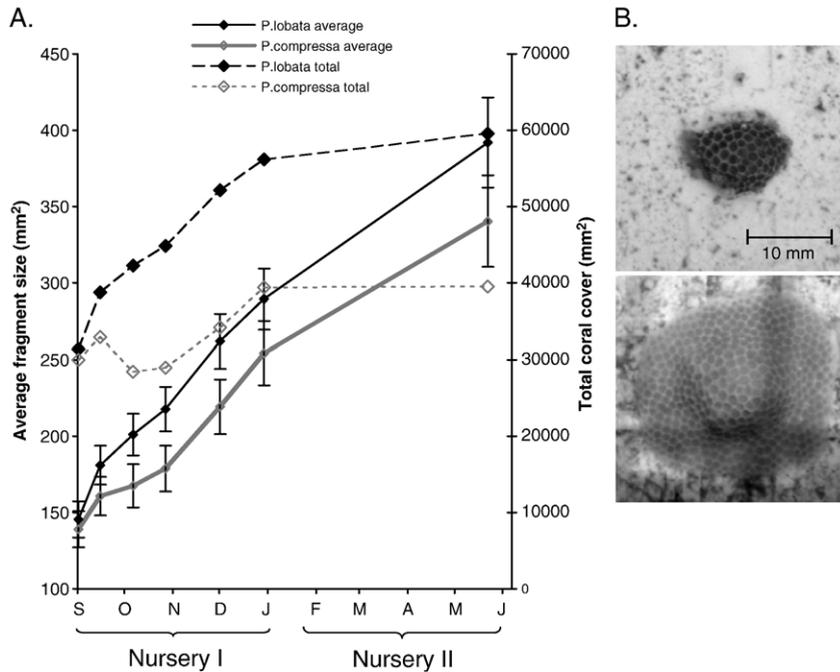
Fig. 2. A. Average fragment size, measured by area (mm^2) for *P. lobata* and *P. compressa* on the primary *y*-axis, and total area covered by coral tissue on the secondary *y*-axis. Error bars represent 95% confidence intervals of the mean. B. An example of a *P. lobata* nubbin that quadrupled in area over the course of four months; the upper photo taken after fragmentation on September 15, 2004, the lower photo was taken on January, 12, 2005.

polyps after the first week. The fate of *P. compressa* nubbins then became clearly associated with the unexpected appearance of *P. sibogae* nudibranchs. Adult *P. sibogae* (2–3 cm), probably collected as juveniles together with the *Porites* colonies, were discovered on the underside of the tiles on September 4th and were quickly eradicated; however, three egg masses were discovered underneath the tiles on October 6th and 13th and a brief second outbreak of juveniles (<1 mm length) followed before they were completely eradicated (see Fig. 1A).

Juvenile *Phestilla* predation was associated with increased coral mucus production and the loss of a thin layer of surface tissue, whereas adult predation resulted in patches of coral skeleton completely denuded of tissue. Even with a weekly protocol for monitoring and removal of *Phestilla*, the nudibranchs had significant impacts on the farmed corals. The nudibranchs were often discovered feeding on or in close proximity to *P. compressa* nubbins and were only rarely associated with *P. lobata* nubbins. *P. compressa* suffered higher tissue damage and mortality during the period of nudibranch infestation (Fig. 1A, B). Tissue loss and mortality fluctuated in accordance with the number of nudibranchs recorded, and tissue damage appeared more frequently on larger *P. compressa* nubbins, apparent from the low health scores (Fig. 1B).

Despite nudibranch predation, survival of *P. lobata* and *P. compressa* nubbins over the four-month course of the first nursery was high, 92% and 73% respectively (Table 1). During this period, fragments of both species nearly doubled in average area covered by coral tissue in 119 days (Fig. 2A). When calculating the total area of all surviving fragments, *P. lobata* increased during this period by 79%, while *P. compressa* briefly decreased, before rebounding after eradication of the nudibranchs
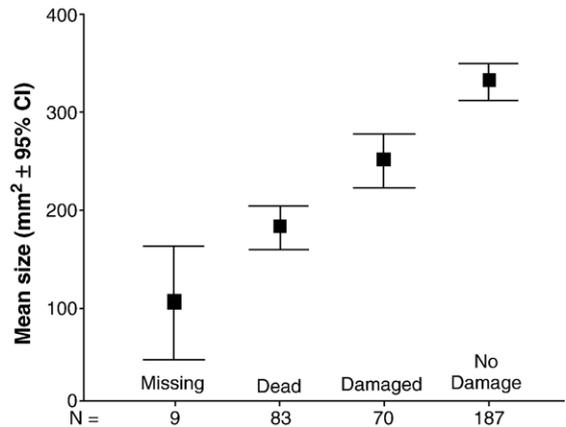

Fig. 3. The mean size (and 95% confidence interval) of the nubbins prior to introduction to sea urchins, and the resulting fate of the nubbins in Nursery II.

Table 2
Comparisons of survivorship distributions between species, genets, and size categories in the first nursery experiment

	df		Log rank		Breslow		Tarone–Ware		Verdict
			Statistic	p	Statistic	p	Statistic	p	
I. Between species	1		35.00	0.0000	36.29	0.0000	35.71	0.0000	l>c
II. Between genets within species	3	P. lobata	7.16	0.0075	7.19	0.0073	7.17	0.0074	l1>l2
	3	P. compressa	3.91	0.0479	3.72	0.0538	3.82	0.0506	c2>c1
III. Between size categories within species *	2	P. lobata	1.55	0.4615	1.55	0.4604	1.55	0.4610	ns
	2	P. compressa	1.70	0.4285	1.81	0.4039	1.76	0.4158	ns
IV. Between size categories within a single genet	2	l1	1.69	0.4291	1.69	0.4291	1.69	0.4291	ns
	2	l2	3.51	0.1731	3.50	0.1737	3.50	0.1734	ns
	2	c1	0.02	0.9924	0.02	0.9915	0.01	0.994	ns
	2	c2	3.49	0.1749	3.62	0.1634	3.56	0.1688	ns

Abbreviations: l = *P. lobata*, c = *P. compressa*, ns = not significant.
 * Pooled between individuals.

for a net gain of 31% (Fig. 3). The average increase in area was 1.2 mm^2 d^{-1} and 0.97 mm^2 d^{-1} for *P. lobata* and *P. compressa* respectively, which corresponds to 0.54 polyps d^{-1} and 1.34 polyps d^{-1} respectively (assuming the linear relationship estimated previously).

The fastest growing fragment was a medium-sized *P. lobata* nubbin with a low profile that rapidly grew onto the surface of the tile and doubled in surface area in only 5 weeks (3.9 mm^2 or 1.8 polyps d^{-1}, Fig. 2B). Fragments as small as 5–6 polyps (6–8 mm in diameter) survived; smaller *P. lobata* fragments grew at a slower average rate than larger fragments, while smaller *P. compressa* fragments grew at similar rates to larger fragments (Table 1). However, when excluding nubbins that had experienced predator damage and those that grew by two-dimensional spreading onto the tiles, there was a significant relationship between initial fragment size and growth rate (*P. compressa*: $r^2 = 0.49$, [$y = 0.0034x + 0.336$], $F = 33.08$, $p < 0.001$; *P. lobata*: $r^2 = 0.26$, [$y = 0.003x + 0.4034$], $F = 25.99$, $p < 0.001$).

At the end of the first nursery phase, 36% and 49% (*P. lobata* and *P. compressa* respectively) of the nubbins grew in a primarily two-dimensional manner onto the tiles (category 3; Table 3). Chi-Square tests indicated that there were no significant differences between spreading categories among size classes (Likelihood Ratio = 0.862 $df = 4$, $p = 0.931$), but it was significantly heterogeneous among coral genets (Table 3). There were substantial differences in survivorship curves between species, and between genets within species (Table 1), which were highly significant (Table 2), but there were no significant differences for survivorship between the three size categories. A Chi-Square test of survivorship across size categories also revealed no difference (Likelihood Ratio = 0.162, $df = 2$, $p = 0.922$), or for a subset of the data in which all nubbins that had tissue damage (from predation) were excluded (Likelihood Ratio = 0.993, $df = 2$, $p = 0.993$).

3.2. Nursery II

Although there were no *Phestilla* infestations over the six-month period of the second nursery, the fate of the coral colonies appeared to be related to sea urchins (*T. gratilla*) in the culture tank. The urchin density in this nursery (~ 3 m^{-2}) greatly reduced the need for manual cleaning of the tiles; however, the urchins appear to have grazed the coral tissue, as evidenced by white scrape marks, particularly at the edges and tops of the smaller nubbins. Survivorship continued to differ among colonies (Table 1). In contrast to Nursery I, a pattern of size-specific mortality was evident in Nursery II. Smaller nubbins had lower survival across all genets (Table 1). There was also a relationship between the size of the fragment at the start of Nursery II, and the resulting fate of the nubbin. Smaller nubbins became detached from the tiles, or died; medium-sized nubbins had minor tissue damage from urchin grazing, while the largest had no evidence of damaged tissue (Fig. 3).

4. Discussion

4.1. Nursery I

Methods that use smaller coral propagules, have the lowest environmental impact and the highest potential yield, but also face the highest mortality (Rinkevich, 2005). Factors that are known to result in size-specific mortality, such as sedimentation, grazing, predation, and competition (Sato, 1984), were limited as much as possible during the first nursery experiment. We successfully reared nubbins as small as 10 mm^2 (average 57 ± 6 mm^2) and

Table 3
Chi-Square tests of spreading categories for each coral genet

		Spreading category			Total
		1	2	3	
Genet	l1	22	23	45	90
	l2	37	20	13	70
	c1	15	6	19	40
	c2	15	9	24	48
Total		89	58	101	248

Chi-Square tests	Value	df	p
Pearson Chi-Square	23.649	6	0.001
Likelihood Ratio	25.45	6	0.000

(1 = spherical, volumetric growth, little tissue contact with tiles; 2 = some tissue contact and growth over the tiles; 3 = extensive tissue spreading two-dimensionally over the tiles) p values are for two-sided tests. l = *P. lobata*, c = *P. compressa*, 1 and 2 = coral genets.

their survivorship was not significantly different from the largest size category (average 242 ± 22 mm^2). The period immediately following subcloning from donor colonies is likely to be one of the most sensitive and vulnerable periods for survivorship of small fragments *in situ* (Shafir et al., 2006), yet we found no evidence of size-specific mortality over the course of 119 days. Small nubbins had high survivorship (70–90%), and more than doubled in size (net increase of 131%–228%) on average (Table 1). These outcomes have positive implications for the potential to culture *Porites* (and probably other genera) from small propagules.

The positive relationship between the growth rate and size of nubbins is most likely because larger colonies have more combined resources to share among polyps, a larger surface area for feeding, and more polyps available to divide. Yap et al. (2003) also found a positive relationship between the size and growth rates with *Porites* species growing in the field and in a culture system. They also found that the same genets had significantly lower growth and survivorship in the culture system, than in the field, which they attributed to lower water motion and competition with algae (most other environmental factors were within a similar range). Lough and Barnes (2000) determined that average linear extension rate in massive *Porites* from the Great Barrier Reef and from Hawaii is approximately 12.9 mm per year. From our area measurements (excluding category 2 and 3; nubbins that grew primarily two-dimensionally), we estimated a linear extension rate of approximately 9.8 mm per year for *P. lobata* (e.g. $\sqrt{(0.82 \text{ mm}^2 \text{ per day} \times 365 \text{ days per year})/\pi}$) and 10.3 mm per year for *P. compressa*. This indicates that small *Porites* fragments in the *ex situ* nurseries were growing at rates similar to full-sized colonies in the wild.

Differences in genet-specific mortality (Table 2), were likely to be largely attributable to *Phestilla* predation, but significant differences were still present when nubbins with visible *Phestilla* damage were excluded, which suggests that genet-level factors (such as prior health or acclimatization, colony size, or genetic differences), may also have a major influence on nubbin survival. Nubbins that grew primarily by two-dimensional growth (spreading category 3) were homogeneous among size categories, but were significantly different among coral genets (Table 3). This may also be due to genetic or physiological differences of the parent colony, or it could be influenced by the shape of the nubbin, or its original position on the parent colony. Genet-level differences in nubbin performance should be investigated further, and could have important implications, depending on the underlying causes (for example if colonies that are resilient to specific environmental conditions could be identified).

One of the difficulties in culturing *coral* species is the potential introduction of *corallivorous* predators. *P. sibogae* has a rapid life cycle (Hadfield, 1977) and juveniles are cryptic (similar in size and appearance to a single coral polyp). Eggs can be hidden deep within crevices in live rock, and their veliger larvae may infiltrate open seawater systems. Precautionary measures, such as the use of well seawater, quarantine of nubbins and live rock (for weeks or more), and biocontrol with *Phestilla* predators (Gochfeld and Aeby, 1997), are methods to reduce the chances of infestation. In spite of these precautions, *Phestilla* were introduced to the first phase of this study. Fortunately, the flat tile surfaces allowed for their detection and rapid eradication. Only *P. compressa* nubbins appeared to be affected (Table 1, Fig. 1A, B), which is likely due to a strong species-specific feeding preference documented previously for *Phestilla* species on *P. compressa* (Ritson-Williams et al., 2003). Tissue damage was more often visible on larger nubbins, (Fig. 1B), which could be attributable to stronger chemical cues, or because the larger nubbins offered more shelter (*Phestilla* were frequently found under the overhangs of larger nubbins).

4.2. Nursery II

Although scrape marks from urchin grazing were clearly evident on smaller nubbins, it is not certain if the tissue damage was caused primarily by urchin grazing, or secondarily after the tissue had already died from other factors that differ between the first and second nursery experiments (such as time, water motion, rainfall, season, etc.). These other possibilities do not account for the observation that the largest nubbins grew at rates that were substantially faster than in the first

nursery (1.5–2.8 mm^2 d^{-1}, Table 1), yet consistent with the positive linear relationship between size and growth rate. Urchin damage also appeared to occur where urchins had access to algae growing at the borders of the coral tissue. Nubbins above 3 cm^2 were large enough to become a significant obstacle in the path of an urchin and colonies above this size rarely had any damage (Fig. 3). These larger fragments exhibited fast growth and high survival rates, most likely because they were large enough to escape incidental urchin grazing.

The Nursery I conditions were moderately labor intensive, entailing approximately 20 person hours for fragmenting 432 nubbins and 75 h per month for cleaning algae from the tiles; Nursery II required very little labor, approximately 8–15 h per month. A two-phased *ex situ* nursery could take advantage of the strengths of both types of culturing systems; small fragments could be reared with the more labor-intensive method until they are at least 3 cm^2 or larger and can avoid incidental grazing by urchins. Future studies should more closely examine alternative grazers or alternate methods for rearing small fragments (such as suspension), and the ideal size for transplanting to the field.

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