Coral reef restoration in the Eastern Tropical Pacific: Feasibility of the coral nursery approach

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ABSTRACT

Due to the worldwide degradation of coral reefs, the active restoration of these ecosystems has received considerable attention in recent decades. This study investigated i) the feasibility of using coral nurseries for restoration projects, ii) the minimum size required for a *Pocillopora damicornis* (Pocilloporidae) coral fragment to survive and grow in a nursery, and iii) the optimal transplant size of a fragment when transplanted to a degraded reef at Gorgona Island (Colombian Pacific). For this investigation, 230 fragments were transplanted directly to El Remanso reef, and another 150 fragments were maintained in *in situ* nurseries. Every 2 months, the length, weight and survival of the fragments were recorded. After growing for 134 days in the nurseries, the 52 surviving fragments were transplanted to El Remanso reef, and after 5 months, the same variables were measured. Among the nursery-reared fragments, the largest (4 to <8 cm) had the

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highest survival and growth rates, whereas among the directly transplanted fragments, the smallest fragments (<2 cm) had the highest survival and growth rates. However, the nursery-reared fragments acquired greater structural complexity (arborescent morphology), and they were all alive 156 d after transplantation and presented a maximum linear growth rate of over 2 cm, which was higher than that of the directly transplanted fragments. Apparently, the arborescent morphology acquired during the nursery period provides advantages to the colonies that favor greater success when transplanted. Therefore, nursery-reared fragments of *P. damicornis* between 2 and 4 cm are the most appropriate for use in restoration projects.

Keywords: corallivory, fragment, growth, morphology, survival, transplant.

Implications for practice:

- Fragments of *P. damicornis* grown in *in situ* coral nurseries provide a viable alternative to direct transplantation of coral fragments for coral reef restoration in the Eastern Tropical Pacific. The arborescent morphology acquired by the fragments reared in the nurseries confers clear post transplantation advantages in terms of growth rates compared with directly transplanted fragments. Thus, coral reef managers and restoration practitioners in the region can use the coral nursery approach to improve the outcomes of future restoration projects.
- Knowing the optimal size to which a *P. damicornis* fragment should be reared in a nursery and transplanted to a target area promotes the optimal use of coral material during restoration projects.

INTRODUCTION

Coral reefs are highly productive and biologically diverse ecosystems that provide ecosystem services to more than 850 million people (Burke et al. 2011). Despite their importance, these ecosystems, including the coral reefs of the Eastern Tropical Pacific (ETP), have deteriorated dramatically in the last three decades (Moritz et al. 2018). During the El Niño events of 1982-

1983 and 1997-1998, extensive areas of coral reefs in the ETP died. The genus *Pocillopora*, which is the main reef builder in the region, was the most affected (Glynn et al. 2017).

Under this scenario, the active restoration of coral reefs has received considerable attention in recent decades (Rinkevich 2005). Coral nurseries can generate large quantities of coral material by exploiting fragmentation, which is a natural process of asexual propagation in some species (Shafir et al. 2006). Very small fragments can be reared in nurseries until they reach an adequate size for transplantation. Hence, understanding the effects of size on the growth and survival of fragments is essential for the efficient and cost-effective use of coral material for restoration (Raymundo & Maypa 2004).

In the ETP, few studies have been conducted on coral reef restoration (Guzmán 1991; Liñán-Cabello et al. 2010; Tortolero-Langarica et al. 2014; Figueroa-Camacho & Nava 2015). Because none of these studies involved the use of nurseries, evaluations of whether fragments reared in nurseries present post-transplant advantages over fragments that were directly transplanted (i.e., without a period of growth in a nursery) are needed (Afiq-Rosli et al. 2017; de la Cruz et al. 2015). In addition, although the effects of the initial coral fragment size on the growth and survival of the fragment have been investigated for several coral species in other regions of the world (Nagelkerken et al. 2000; Forsman et al. 2006), such effects should be explored in detail for corals of the genus *Pocillopora*, the eudominant coral species in the ETP. The only available data are from a study that reported that small fragments (1-2 cm in length) of *Pocillopora damicornis* (Linneaus, 1758) had the lowest survival (55%) and growth rate after transplantation, particularly in the back reef (Lizcano et al. 2018).

This project sought to determine 1) the minimum size required for the successful survival and growth of a fragment of *P. damicornis* in a coral nursery, 2) the optimal size of *P. damicornis* fragments for transplantation to a degraded reef, and 3) the feasibility of implementing coral nurseries in the ETP.

METHODS

Study area

The study was carried out on coral reefs within Gorgona National Natural Park, located 28 km from the Colombian Pacific mainland coast (2°58'10"N and 78°11'05"W; Fig.1). Fragments of *P. damicornis* (Schmidt-Roach et al. 2014) were collected from healthy colonies at La Azufrada reef (2°57'17.2"N, 78°10'34.8"W; Fig.1a). The nurseries were installed at El Muelle (2°57'41.8"N, 78°10'25.0"W; Fig.1b), and the transplant experiments were conducted at El Remanso (33°00'07.0"N, 78°09'59.2"W; Fig.1c). El Remanso once hosted a coral community with high cover (Glynn et al. 1982), although it is now dominated by rocks covered by algae and scattered coral colonies, mostly of the genus *Pocillopora*.

Coral nurseries

In July 2015, three 2x3 m fixed-rope coral nurseries (Levy et al. 2010; Fig.S1) were installed at El Muelle reef at 1.5 m below the minimum tidal level. The coral nurseries were fixed to the substrate with stainless steel rods. Every 2 months, sessile organisms were removed from all nursery structures. The fragments were assigned to five size treatments (<1, 1 to <2, 2 to <4, 4 to <6, and 6 to <8 cm in length) and randomly distributed within the nurseries. The number of replicates per treatment was 31 in all cases except in the 2 to <4 cm category, which included 27 replicates, for a total of 151 fragments. The fragments were tagged and then fixed to the nursery lines with thin plastic-covered copper wiring, which allowed them to be suspended in the water column.

From July to November 2015 (134 days), the survivorship and growth (in length and buoyant weight; Jokiel et al. 1978) of the fragments were estimated every 2 months. Fragments with 0% live tissue were considered dead. The buoyant weight (Davies 1989) was recorded in the laboratory with an electronic scale (Kern EMB 100-3, ±0.001g). The change in weight was calculated as a percentage of the increased weight relative to the initial weight. The length of the fragments was measured with a caliper (±0.05 mm precision).

Direct transplantation

In April 2015, 230 fragments were outplanted to El Remanso immediately after harvesting them from La Azufrada reef (i.e., without nursery rearing). These fragments were fixed to the substrate with cement, marked with a numbered aluminum plate, and placed in five rows (70 m long) parallel to the coastline at 2-3 m below the minimum tidal level. The size treatments were randomly distributed, and the number of replicates per treatment was <1 cm (*n*=52), 1 to <2 cm (*n*=56), 2 to <4 cm (*n*=45), 4 to <6 cm (*n*=45) and 6 to <8 cm (*n*=32), for a total of 230 fragments.

To measure linear growth, each fragment was photographed from the same angle during each field trip (n=5) performed during the year of study (April 2015 - April 2016; 366 days). The length of the fragment was estimated using free-software ImageJ (Schneider et al. 2012), and survival was evaluated via the same method used in the nurseries.

Transplantation of nursery-reared fragments

In November 2015, after 134 days of growth in the coral nurseries, the surviving fragments were transplanted to El Remanso. Due to strong wave action, only 52 out of 98 fragments were transplanted successfully. After transplantation, their size was measured and used as the initial value for further comparisons. The number of replicates per treatment was 1 to <2 cm (*n*=12), 2 to <4 cm (*n*=30), and 4 to <6 cm (*n*=10), for a total of 52 fragments. The fragments of <1 cm were not transplanted because only two fragments survived after the nursery-rearing period.

The depth, method of fixation, and marking of fragments were the same as that used in direct transplants. Five months (156 days) after transplantation, the fragments were measured for linear growth and survival following the same method used with the direct transplants.

Data analysis

The linear growth rate was estimated using the slope of the regression between the fragment height and the elapsed time for each fragment. For nursery-reared fragments, the increment in weight was also estimated. The mean growth rate and survival percentages for each size category were calculated in the three experiments. Because neither the linear extension rates nor the weight increment data showed homoscedasticity (Levene's test; $p<0.05$) or normality of the residuals (Shapiro-Wilks test; $p<0.05$), comparisons of growth rates between size classes and between experiments were performed with a randomized one-way ANOVA (10,000 randomizations) using the Manly approach (2007) for unequal variances.

Survivorship was compared between treatments in both experiments using survival data analysis, a non-parametric pair-wise comparison test based on the Kaplan–Meier function (Lee, 1992). For the statistical analyses, the programs Rundom Pro version 3.14 (Jadwiszczak 2009), SPSS version 23.0 (IBM statistics) and PAST version 3.01 (Hammer et al. 2001) were used with a level of significance of $\alpha=0.05$.

RESULTS

Survival and growth in the coral nurseries

After 134 days, 66.9% of the *P. damicornis* fragments in the nurseries survived. The highest survival was observed in size categories 2 to <4, 4 to <6 and 6 to <8 cm, and the lowest survival was observed for the smallest fragments (<1 and 1 to <2 cm; Fig.2) with statistical differences among size categories (logrank test: $X^2=75.12$, $p<0.001$). No encrusting-tissue growth over the wiring was observed in these fragments during the first 68 days, leading to fragment detachment and partial overgrowth by turf algae. After day 68, survival remained constant for all size categories except for the smallest category (<1 cm), which presented decreased survival over time. The survivorship curves of the <1 and 1 to <2 cm size classes were significantly different from the survivorship curves of all other size classes (TableS1; Fig.2).

Growth rates, based on both linear extension and weight increase, increased with initial fragment size (Figs.3a, b). The 6 to <8 cm fragments presented the highest linear growth rates (2.6 ±2.1

cm $year^{-1}$; $\bar{x}$ ±SD) and the highest percentage of increase in weight compared with the initial weight (313 ±153%). The 4 to <6 cm fragments presented a mean linear extension rate of 2.1 ±1.6 cm $year^{-1}$ and a mean increase in weight of 339 ±92%. The linear growth rates of the two largest size categories (4 to <6 cm and 6 to <8 cm) were significantly greater than those of the smaller ones (randomized one-way ANOVA: $F_{[4,\ 101]}$ =6.6, p<0.001), but no significant difference was found between the two largest ones (Table S2, Fig.3a). The variability of the growth rates increased as the size increased.

The 4 to <6 cm fragments exhibited the greatest increase in weight per year (339%; Fig. 3b), which was significantly greater than that of the other size categories (randomized one-way ANOVA: $F_{[4,\ 102]}$ =18.79, p<0.001) (TableS2, Fig.3b). After 4 months of growth, fragments <4 cm in initial size changed their morphology from a single or few branches to an arborescent morphology with greater structural complexity typical of *P. damicornis* colonies (Fig.S2). Although the fragments >4 cm did not exhibit the arborescent colony morphology at the end of the experiment, they presented new and thicker branches.

Survival and growth of the direct transplants

At 366 days after direct transplantation to El Remanso reef, the fragments had a survival rate of 66.4%. The fragments from 2 to <4 cm had the highest survival (75.6%), followed by those from 1 to <2 cm and 4 to <6 cm (both with 73%; Fig.4a). Compared to our expectations and the nursery observations, the largest fragments (6 to <8 cm) died faster than fragments with other sizes and exhibited a low survival rate (56%), similar to that of the smallest (<1 cm) fragments (54%) at the end of the experiment. The fragments from 1 to <2 cm maintained a stable and very high survival rate (96.4%) during the first 7 months, although their survival decreased during the last 5 months, which was consistent with the survival of the fragments from 4 to <6 cm. Significant differences in the survivorship curves were detected, only between the 1 to <2 and 6 to <8 cm sizes (logrank test: X^2 =4.44, p =.035, TableS1, Fig.4).

Fish bite marks were observed in most of the directly transplanted fragments, mainly at the distal ends of the new branches (Fig.S3). These bites removed living tissue and part of the calcareous skeleton.

An inverse relationship was observed between the fragment size and linear growth rate of the directly transplanted fragments (Fig.5a). This pattern was opposite to the pattern found in the nursery-reared fragments, both during the nursery growth phase (Fig.3) and after transplantation (Fig.5b). Only directly transplanted fragments with initials sizes of <1 cm and 1 to <2 cm showed positive growth rates (0.7 ±0.88 cm $year^{-1}$ and 0.24 ±0.9 cm $year^{-1}$, respectively), although these two rates were significantly different (randomized one-way ANOVA: $F_{[4, 148]}$ =27.8, $p<0.001$)(TableS2, Fig.5a). In contrast, all other sizes presented negative growth rates, with the largest fragments (4 to <6 and 6 to <8 cm) decreasing the fastest (-2.37 ±1.83 and -3.68 ±2.37 cm $year^{-1}$, respectively). However, the latter two rates did not differ significantly (TableS2, Fig.5a). The variation in the growth rates increased as the size of the fragments increased.

After 144 days of growth, the fragments showed an increase in structural complexity, which consisted of new and thicker branches compared with the thin branches presented by the donor colonies of the La Azufrada reef (Fig.S4).

Survival and growth of the nursery-reared transplants

Five months (156 days) after transplantation to El Remanso, the nursery-reared fragments presented 100% survival (Fig.4b). No significant differences (randomized one-way ANOVA: $F_{[2,49]}$ =0.7, p =0.53) were observed between the growth rates of the different size categories, and fragments >2 cm grew at a rate of approximately 1.52 ±1.8 cm $year^{-1}$ (Fig.5b). None of the nursery-reared transplants showed fish bite marks, which occurred frequently in the directly-transplanted fragments.

Comparison between direct transplants vs. nursery-reared transplants

Despite that the survival of the nursery-reared transplants was 100% in all sizes, no statistical differences were found between the survival curves of the direct and nursery-reared transplants during the first 144 days (TableS3). However, the growth rate of the nursery-reared transplants was more than twice greater than the maximum growth rate of direct transplants (1.52 ±1.8 and 0.7 ±0.88 cm year^{-1}, respectively), and statistical differences for all size categories were found (randomized one-way ANOVA: $F_{[1,188]}$ =73.4, p<0.001)(TableS3).

DISCUSSION

Coral reef restoration approaches must be as efficient, cost-effective and practical as possible. In this paper, we considered two basic approaches: a) direct transplantation of fragments to a degraded reef immediately after harvesting from a healthy reef, and b) transplantation of fragments after a nursery-rearing period. We found that despite the reduced time and effort required for direct transplantation, rearing coral fragments in nurseries provided a clear advantage in terms of the growth of fragments after transplantation to a degraded area. Furthermore, these advantages were largely mediated by the effects of fragment size and morphology on survival and growth.

Size has frequently been considered a determining factor in the survival of both nursery-reared and directly transplanted fragments (Barton et al. 2017). During the nursery-rearing phase, we found that larger fragments presented greater survival rates, which is consistent with many previous reports, because smaller fragments are more susceptible to manipulation, competition by fouling organisms and predation (Raymundo & Maypa 2004; Okubo et al. 2007; Barton et al. 2017). However, positive size-dependent survival of fragments has not been observed in other studies (Bruno 1998; Mercado-Molina et al. 2014), and such survival did not occur in the directly transplanted fragments. In the latter case, both the smallest and largest fragments showed the lowest survival while intermediate sizes showed the highest survival.

Although low survival after transplantation of large fragments, due to dislodgement by strong wave action, has been previously observed (Shafir & Rinkevich 2013), in this study, fish predation was the most likely cause of mortality of large fragments, which was inferred from the presence of fish bite scars on some fragments (Palacios et al. 2014). Thus, it is also important to determine the negative effect that corallivory has on fragment growth and survival.

Positive size-dependent growth, as observed in the nursery fragments, has been reported previously (e.g., Raymundo & Maypa 2004). Other studies have also shown that the linear growth rate, both in fragments and coral colonies, is size dependent (Forsman et al. 2006; Okubo et al. 2007). It is believed that larger fragments provide a larger surface for feeding and photosynthesis and a greater amount of available resources that can be shared between polyps (Forsman et al. 2006). However, growth independent of size has also been reported (Kinzie & Sarmiento 1986).

Compared to the findings in the nurseries, the maximum growth rate of the directly transplanted fragments was well below the growth rates reported for *P. damicornis* in the ETP (Eakin 1996; Manzello 2010). The high variation found in the growth rates of the transplanted fragments, particularly the negative values, could be due to fish corallivory. The shape and location of bite scars on branch tips suggest that they were caused by the guinea fowl puffer, *Arothron meleagris* (Palacios et al. 2014), which is perhaps the most important corallivorous fish in the ETP (Guzmán & Robertson 1989). Hence, it is important to consider potential solutions to mitigate the effects that corallivores may have in the loss of biomass in restoration programs.

Although the growth rates of the nursery-reared transplanted fragments were also below those reported for the ETP (Eakin 1996, Manzello 2010), their greater structural complexity translates into a larger surface for feeding and photosynthesis that allows them to have more energetic resources when compared to the direct transplants (Forsman et al. 2006). Moreover, during the nursery-rearing period, the fragments could grow in all directions because they were suspended in the water column, which allows them to have higher growth rates and acquire the natural arborescent morphology of *P. damicornis* in a short time, which seems to double the growth rates after transplantation when compared to direct transplants. Thus, the arborescent morphology seems to minimize the negative impact of corallivory and other physical disturbances (Epstein & Rinkevich 2001). Therefore, raising coral fragments in nurseries for at least 4 months before their transplantation could significantly improve the success of restoration programs by enhancing the increase of coral biomass in a shorter period of time.

The results show that the optimal size of nursery-reared fragments for transplantation is between 2 and 4 cm (with a minimum rearing period of 134 days), which had the highest growth rate. The direct transplantation is not recommended, because mechanical or biological agents (i.e., corallivorous fish) could severely affect the survival and growth of these fragments.

Restoration programs, which rely on limited coral material, have to be as efficient as possible and cannot afford high levels of mortality and biomass loss. A solution is the use of nurseries, because the nursery-rearing period allows the fragments to increase their three-dimensional structural complexity, which contributes to a greater growth rate after transplantation and accelerates the gain of coral biomass in the long term. In addition, knowing the minimum size in which a coral fragment should be used in a nursery, would allow future restoration programs to maximize the use of coral material from donor colonies, because a greater number of fragments can be extracted per colony if the same initial quantity of coral material is provided, and the post-transplant success of the reared fragments is greater.

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FIGURES

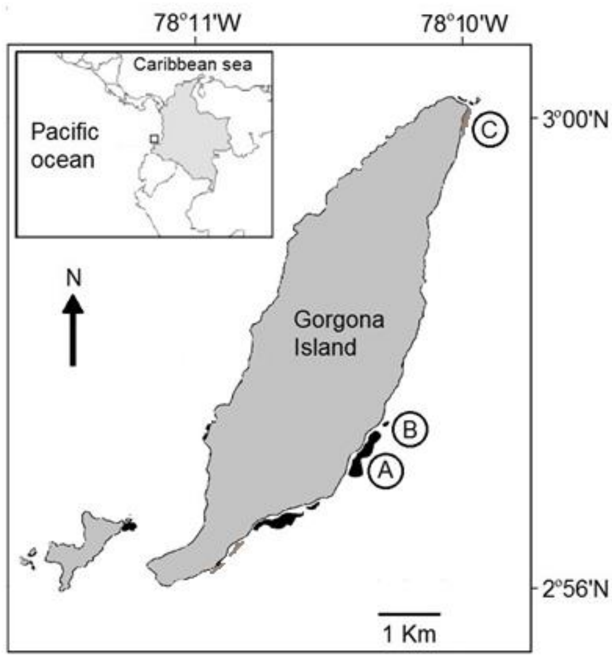

Figure 1. Location of Gorgona National Natural Park along the Colombian Pacific coast. Study locations: (A) La Azufrada, (B) El Muelle and (C) El Remanso. Coral reefs (dark black) and coral communities (grey) are also shown.

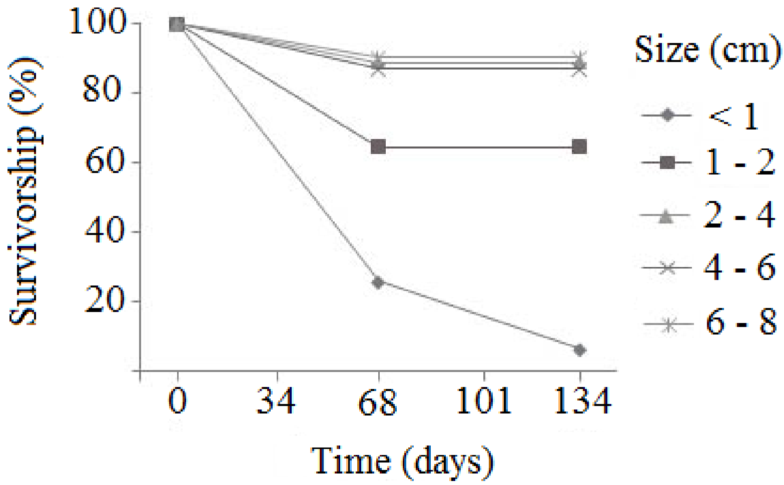

Figure 2. Survivorship of *Pocillopora damicornis* fragments with five initial size treatments after 134 days of growth in nurseries.

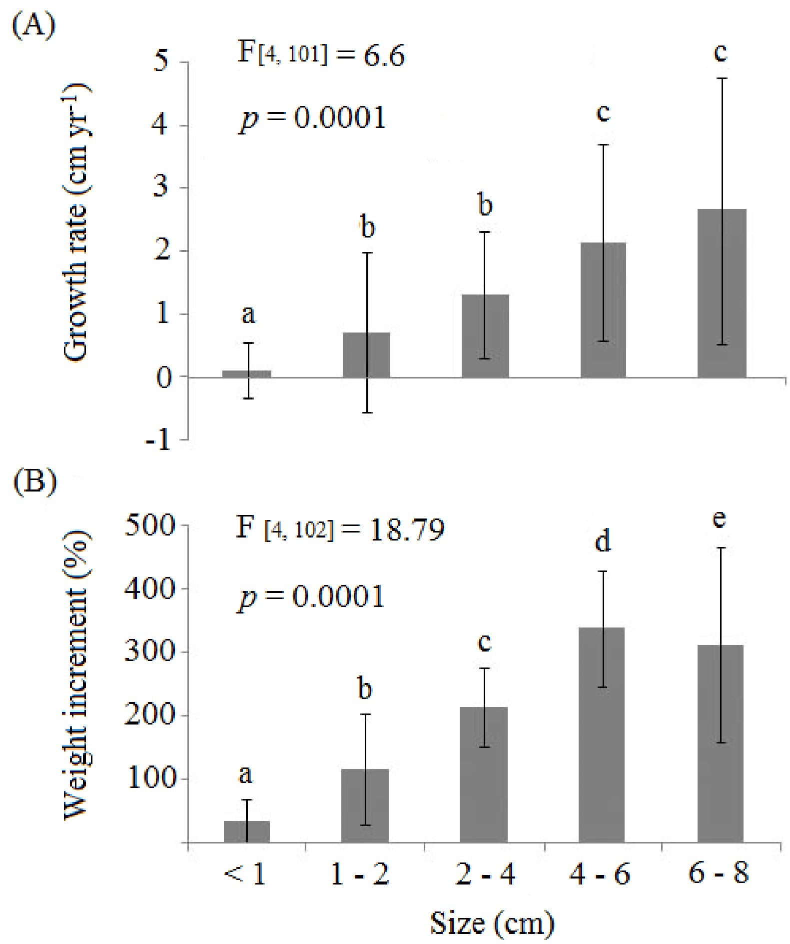

Figure 3. Mean (± SD) growth rates of *Pocillopora damicornis* fragments during 134 days of growth in fixed rope nurseries. (A) Linear growth rate (cm year^{-1}), and (B) increase in weight as percentage of initial weight. Letters group the size categories in which no statistically significant differences ($\alpha = 0.05$) were detected.

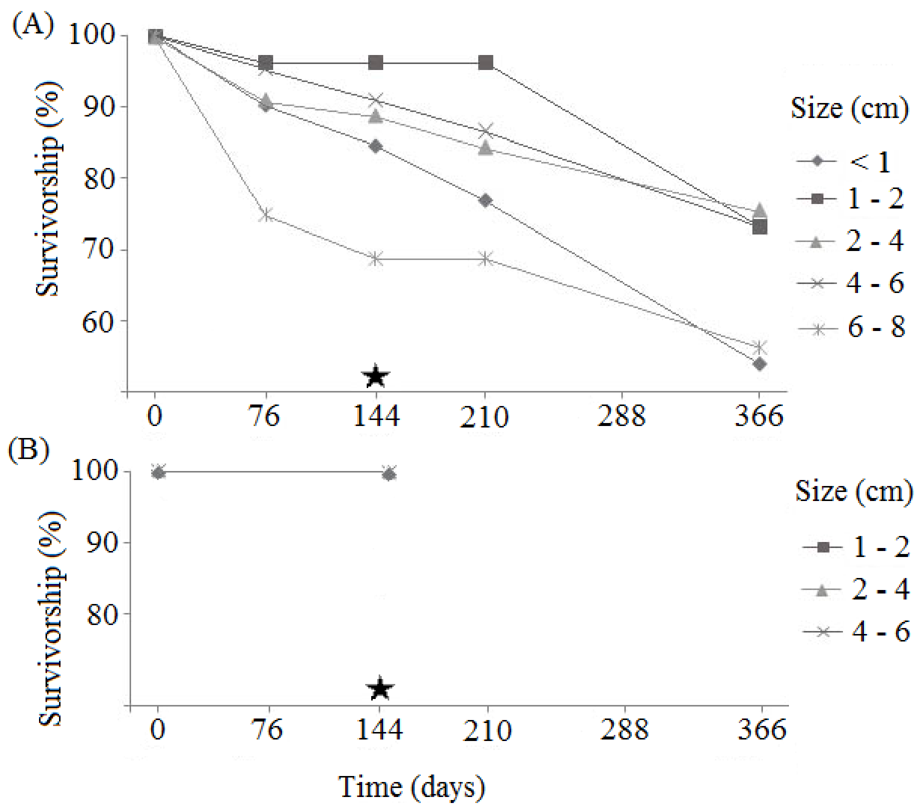

Figure 4. Survivorship of direct (A) and nursery-reared transplanted fragments (B) of *Pocillopora damicornis* at the coral community of El Remanso after 144 days (★) of transplantation. The long term (366 days) survivorship of direct transplanted fragments is also shown.

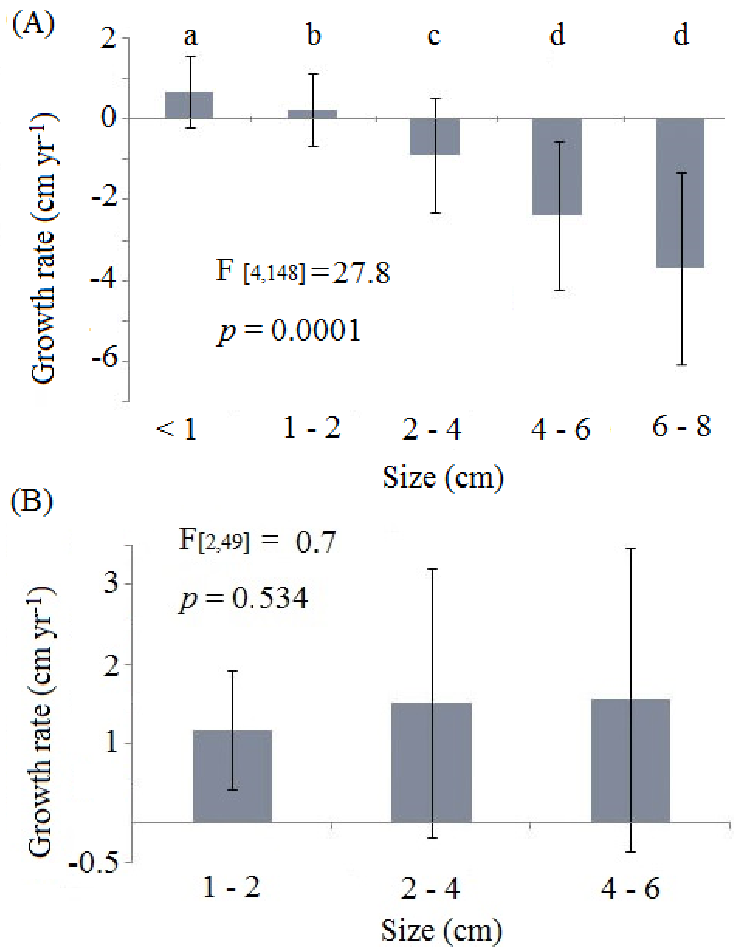

Figure 5. Mean (± SD) linear growth rate (cm year^{-1}) by size category of directly (A) and nursery-reared transplanted fragments (B) of *Pocillopora damicornis* at the coral community of El Remanso. Statistically significant differences between size categories are indicated by different letters in panel (A), while no differences were observed in panel (B) (Randomized one-way ANOVA, α = 0.05).