



## Demographics and dynamics of two restored populations of the threatened reef-building coral *Acropora cervicornis*



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### ABSTRACT

*Acropora cervicornis* is one of the principal reef-building organisms in the Caribbean; it is also considered one of the most threatened coral species. Due to its ecological importance and critical status it is the focus of many restoration and management initiatives. However, studies that quantitatively measure the efficacy or feasibility of these efforts are mostly lacking. In this study, nursery-reared fragments of *A. cervicornis* were transplanted to two reefs in Puerto Rico as part of a reef rehabilitation program, and their survival, growth, and branch production were measured for a year. We also evaluated the effect of this restoration on the dynamics and viability of the fragment populations by means of a simple model. Survival of outplanted fragments surpassed 60%. Colony growth rate varied between  $0.20 \pm 0.18$  and  $0.29 \pm 0.21$  cm d<sup>-1</sup> (mean  $\pm$  SD) whereas branch production ranged between  $7.02 \pm 5.72$  and  $11.86 \pm 7.06$  (mean  $\pm$  SD) branches per fragment per year. Survival did not vary considerably with respect to fragment size. In contrast, large fragments ( $\geq 25$  cm) grew faster and tended to produce more branches than smaller ones. Model simulations indicate that (1) in the absence of recruitment, and without any subsequent human intervention, restored populations will decrease below a quasi-extinction level of 25% of the initial population size after just 3 years and (2) transplanting at least 20 colony fragments per year (12% of initial population) is sufficient to keep the restored populations above the 25% threshold. We conclude that *A. cervicornis* may be a feasible species for restoration projects given sustained human intervention and that transplanting fragments of at least 25 cm to reefs is an effective restoration protocol that requires minimum effort to maintain a viable restored population of this key reef-building coral.

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### Introduction

Since the late 1970s Caribbean coral reefs have lost approximately 80% of their coral cover (Gardner et al. 2003); putting at risk not only the functioning of this ecosystem, but also the ecological services that coral reefs provide to millions of people around the region. Scientists, managers, and local stakeholders have been looking for alternatives to prevent and/or reduce coral reef degradation by restoring depleted populations of major reef-building corals. *Acropora cervicornis* is one of the most important reef-forming species in the region not only because it is among the fastest growing corals (Tunncliffe 1981; Knowlton 1992) but also because it has the capacity to bind carbonate rubble and other reef materials (e.g. clastic sediment) that contribute to the stabilization

of the reef framework (Gilmore & Hall 1976). In addition, because of its branching morphology, *A. cervicornis* provides recruitment habitat for many commercial fishes (e.g. groupers and snappers). This species, however, has collapsed along its geographical range due to many biotic stressors (e.g. diseases, predator outbreaks), physical disturbances (e.g. hurricanes, increase in sea water temperature), and anthropogenic impacts (e.g. water pollution, ship groundings) (Miller et al. 2002). As a response to this situation, *A. cervicornis* has been listed as a threatened species under the United States Endangered Species Act (NMFS 2006). Since then it has been the focus of several population restoration projects (reviewed by Young et al. 2012).

An example of the efforts to promote the recovery of this coral has been the development of different fragment-based aquaculture techniques (e.g. A-frames, hanging ropes; reviewed by Young et al. 2012). The ultimate goal of such actions is to enhance the survival and growth of colony fragments (collected from wild populations) that later will be transplanted into selected sites (Edwards 2010; Griffin et al. 2012). This human-assisted asexual propagation

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has been put into practice in at least 12 localities in the Wider-Caribbean (Young et al. 2012).

Although culturing has been successful in increasing the number of colonies available for restoration programs (Hernández-Delgado & Suleimán-Ramos 2014; Hernández-Delgado et al. 2014) little is known about the demographic performance of the fragments once they have been transplanted into reefs. Moreover, the few published studies (e.g. Shinn 1966; Garrison & Ward 2008; Hollarsmith et al. 2012) have been modest in that (1) they only considered one aspect of the life-history transitions of coral transplants (growth or survivorship), (2) the sample sizes have been small (i.e.  $n \leq 45$ ; Hollarsmith et al. 2012) and (3) none of them considered the effect of these efforts at the population level (i.e. population growth rates, recruitment). This lack of knowledge has generated debate as to the suitability of *A. cervicornis* for reef restoration. For example, while the study by Hollarsmith et al. (2012) concludes that the species is a good candidate for restoration projects because none of the coral outplants ( $n = 45$ ) died during their 1 year study; Garrison and Ward (2008), who followed the fate of storm-generated fragments transplanted to a reef in Saint John, US Virgin Islands, argue otherwise because all transplants ( $n = 15$ ) died within 5 years.

The scarcity of information on the demographic success of transplanted fragments, both at the colony and population level, limits our assessment of the efficacy of transplantation as an effective restoration tool. In this study, we quantified the survival, growth, and rate of branch production of *A. cervicornis* fragments transplanted to two reefs in Puerto Rico. We considered fragments of different sizes to measure the effect of size on the demographic performance of transplants. In addition, we evaluated the effect of this restoration on the dynamics and viability of the fragment population by (1) projecting the restored population into the future, and (2) determining the number of transplants necessary to maintain the restored population over a threshold of 25% of the original population size. Results of this study will help coral ecologists and managers in determining whether coral transplantation is a feasible approach for reef restoration.

## Methods

### Study sites

The study was carried out at Punta Soldado (PSOL) and Tamarindo (TAM) reefs, Culebra Island, Puerto Rico (Fig. 1). Both sites have an active nursery and restoration project run by the local NGO – Sociedad Ambiente Marino (SAM). The sites are characterized by low wave energy, and relatively good water quality (mean horizontal water transparency 7.7 m, Ruiz-Ramos et al. 2011). No differences in temperature or water transparency are evident between sites (Hernández-Delgado & Suleimán-Ramos, Sociedad Ambiente Marino, unpublished data). The area of transplantation is of low topographic relief (Mercado-Molina et al. 2014a) with a consolidated bottom where macrofauna is visually dominated by *Millepora* spp., *Diploria* spp. and *Porites* spp. However, macroalgae cover is higher at PSOL ( $\approx 37\%$ ) compared to TAM ( $\approx 17\%$ ).

### Fragment transplantation

A total of 170 fragments were transplanted at each site by stabilizing them directly to the substrate using concrete nails of 8 cm (length) and plastic cable ties (see Garrison & Ward 2008; Hollarsmith et al. 2012). All fragments were collected haphazardly from healthy colonies growing in situ nurseries by clipping at the base of branches projecting out of the principal branch. No more than two fragments were collected from the same donor colony. Transplantation took place at a depth of 3–4 m during May 2011.

All fragments were identified with a numbered tag tied to their respective nails (no tag was in direct contact to the transplant). Fragments were categorized in two size classes (small  $< 25$  cm and large  $\geq 25$  cm) following Mercado-Molina et al. (2014b).

### Survival

Survival (live tissue  $> 0\%$ ) was monitored 1 month after transplantation and every 3 months thereafter for 1 year (2011–2012). Kaplan–Meier Survival Analysis was used to compare fragment survival schedule between the studied sites and size classes.

### Growth and branch production

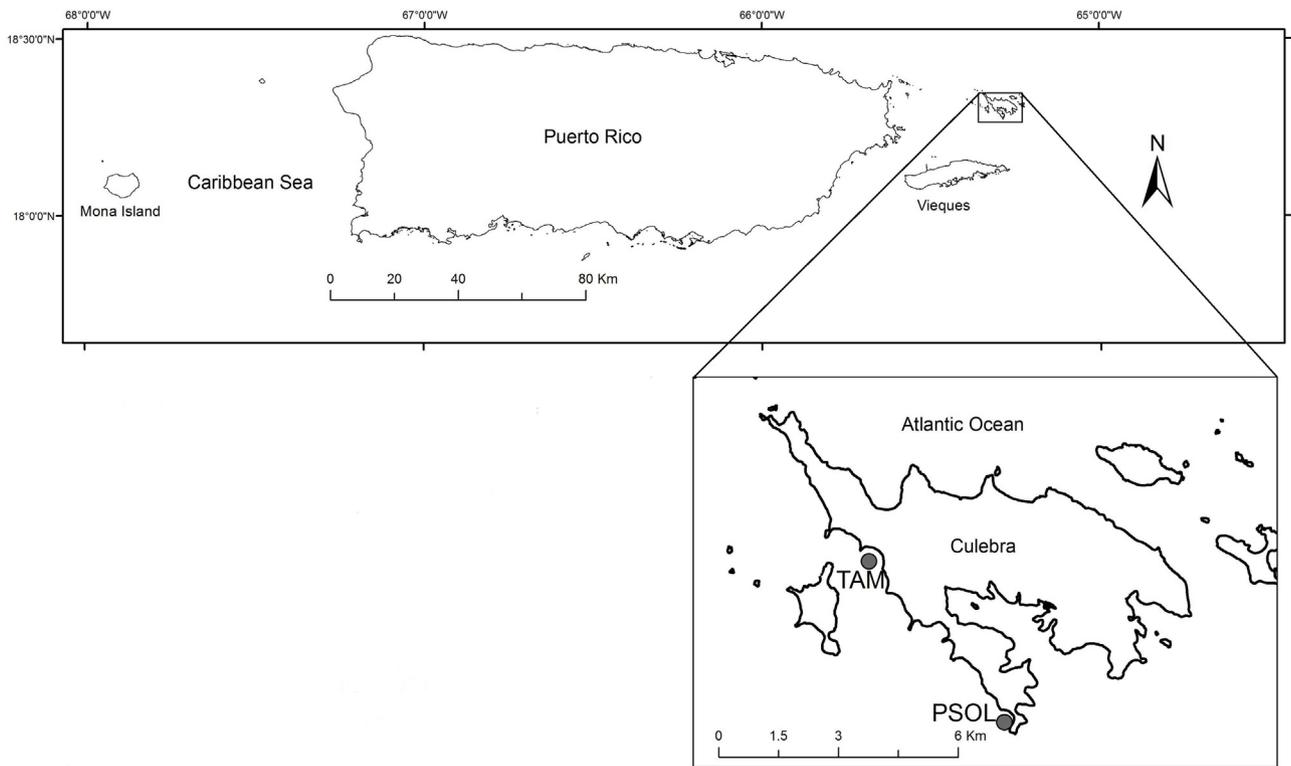
Growth rate of fragments was measured as the change in daily linear extension (final length – initial length/total number of days) and expressed as cm/day. Initial and final sizes were measured as the sum of the linear lengths of the live tissue portions of all branches, subtracting partial mortality from the total size when appropriate. Length of all branches was obtained by analyzing photographs (taken in situ scale-by-side) using the software Coral Point Count with Excel extensions (CPCe) (Kohler & Gill 2006). Fragments were photographed from different angles to ensure that all branches could be appreciated in their full extension. The suitability of this approach (image analysis) as estimator of actual fragment size for *A. cervicornis* was demonstrated by Mercado-Molina et al. (2014b). Growth rates were calculated for those fragments that survived to the end of the study, 104 and 112 at PSOL and TAM, respectively. Mann–Whitney *U*-test was used to compare overall growth rates between sites as well as to compare growth between size classes within each site because data were not normally distributed. Branch production, calculated as the number of new branches produced by fragments, was analyzed as explained earlier for rates of growth.

### Sexual recruitment and natural fragmentation (asexual recruitment)

Asexual and sexual recruitment were monitored at a quarterly basis for 1 year in thirty 1 m<sup>2</sup> permanent quadrats randomly placed along three 10 m  $\times$  1 m transects separated 10 meters from each other. Following Tunnicliffe (1981) and Knowlton et al. (1990) sexual recruits were defined (a priori) as a small crust showing a round or ellipsoidal morphology and measuring less than 10 cm in height. Asexual recruits were differentiated from sexual recruits by looking at (1) its orientation (horizontal vs. vertical), (2) signs of obvious fragmentation, and (3) fragment size ( $> 10$  cm in total linear length) (Tunnicliffe 1981; Knowlton et al. 1990). Rates of natural fragmentation were also measured in situ by identifying scars within each colony fragment (Tunnicliffe 1981) as well as by counting the number of broken (missing) branches when comparing images between surveys.

### Population modeling

The restored populations were projected for 15 years by iterating Expression (1), where  $N$  is the number of fragments at time  $t$  and 3 months into the future ( $t + 1$ ), and  $\lambda$  is the growth rate of the population. During the iterations,  $\lambda_t$  was randomly drawn from the set of  $\lambda$ 's that were calculated for each of the 3 months intervals (four in total) using the expression  $N_{t+1}/N_t$ . Initial population size was set as 170 fragments. To simulate population trajectories under different outplanting scenarios, we followed the same procedure as above using Expression (2), where  $R$  represents the input of new fragments to the population every 3 months. Simulations started with the equivalent of 10 fragments per year, increasing



**Fig. 1.** Map showing the study sites. Punta Soldado (PSOL) and Tamarindo (TAM).

the number by 10 until reaching a value of 100 outplants per year. In both cases, a total of 10,000 simulations were performed to estimate the mean and 95% confidence intervals (not shown on Fig. 5C and D for graph clarity). The fit of the model was tested by comparing the values observed during the study with the predicted values using chi-square analysis as well as by correlating the observed vs. expected dynamics. All analyses were carried out with R software (R Development Core Team, <http://www.R-project.org>).

$$N_{t+1} = N_t \lambda_t \quad (1)$$

$$N_{t+1} = N_t \lambda_t + R \quad (2)$$

## Results

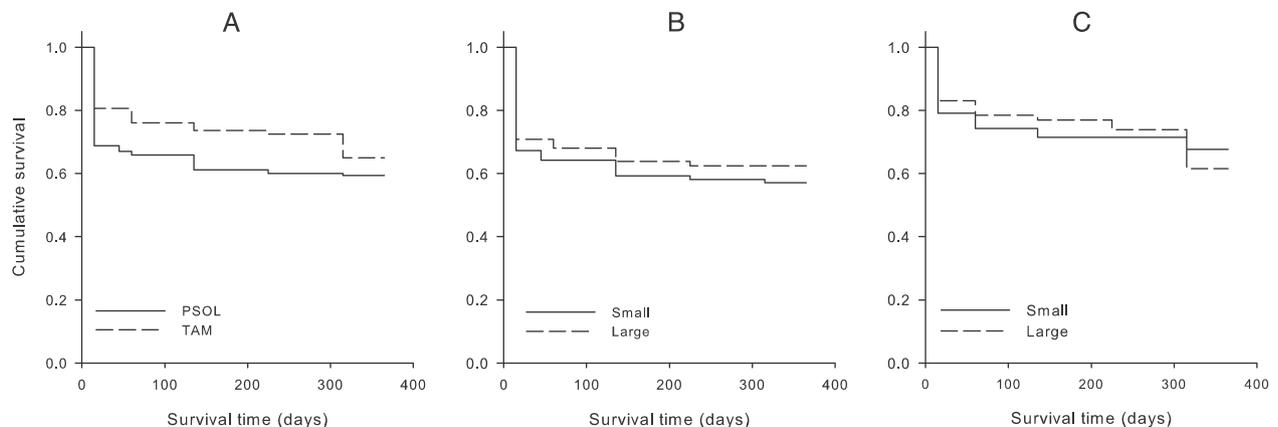
### Survival

Survival did not differ significantly between PSOL and TAM (KM log-rank test,  $p > 0.202$ ; Fig. 2A); indicating, that survival patterns

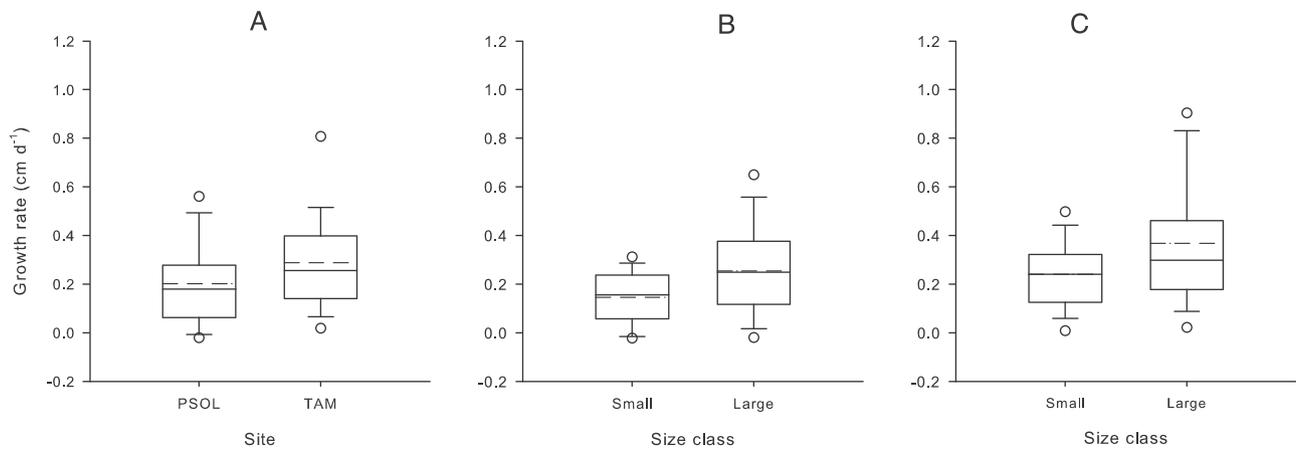
were similar at both sites. In general, mortality of fragments was high during the first month after transplantation when 77% (at PSOL) and 50% (at TAM) of the total mortality occurred. Thereafter, very few fragments died (Fig. 2A). At the end of the year 61.17% and 65.88% of the fragments survived at PSOL and TAM, respectively. No significant differences in survival were found between small and large fragments (KM log-rank test,  $p > 0.05$ , Fig. 2B and C).

### Growth

Growth rates of transplanted fragments differed significantly between sites (Mann Whitney  $U$ -test,  $p < 0.001$ ). At PSOL, fragments grew at mean rates of  $0.20 \pm 0.18$  ( $\pm$ SD)  $\text{cm d}^{-1}$  (median =  $0.18 \text{ cm d}^{-1}$ ) whereas at TAM the mean growth rate was  $0.29 \pm 0.21$  ( $\pm$ SD)  $\text{cm d}^{-1}$  (median =  $0.26 \text{ cm d}^{-1}$ ) (Fig. 3A). With respect to size-specific growth, at both sites, large fragments grew more rapidly than smaller ones (Mann Whitney  $U$ -test,  $p < 0.001$ , Fig. 3B and C, see Supplementary Fig. S1).



**Fig. 2.** Kaplan–Meier plots showing percent of survival of fragments: (A) between sites (pooling by size), (B) between size classes at Punta Soldado (PSOL), and (C) between size classes at Tamarindo (TAM).



**Fig. 3.** Box plots comparing median growth ( $\text{cm d}^{-1}$ ) of fragments with the 75th and 95th percentiles: (A) between sites (pooling by size), (B) between size classes at Punta Soldado (PSOL), and (C) between size classes at Tamarindo (TAM). Solid and dashed horizontal lines within the box represent the median and the mean, respectively. Open circles represent maximum and minimum values.

Supplementary Fig. S1 related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jnc.2015.01.001>.

#### Branch production

Branching dynamics followed a similar pattern to that of growth rates. Rates of branch production differed significantly between sites (Mann Whitney  $U$ -test,  $p < 0.001$ , Fig. 4A). Fragments at PSOL produced on average  $7.02 \pm 5.72$  ( $\pm$ SD) (median = 6.00) new branches per fragments per year whereas at TAM the mean branch production was  $11.86 \pm 7.06$  ( $\pm$ SD) (median = 12.00). Likewise, there was a tendency for large fragments to produce more branches than smaller ones (Fig. 4B and 4C, see Supplementary Fig. S1), but difference in branch production between small and large transplants was significant only at PSOL (Mann Whitney  $U$ -test,  $p < 0.001$ , Fig. 4B).

#### Sexual recruitment and natural fragmentation (asexual recruitment)

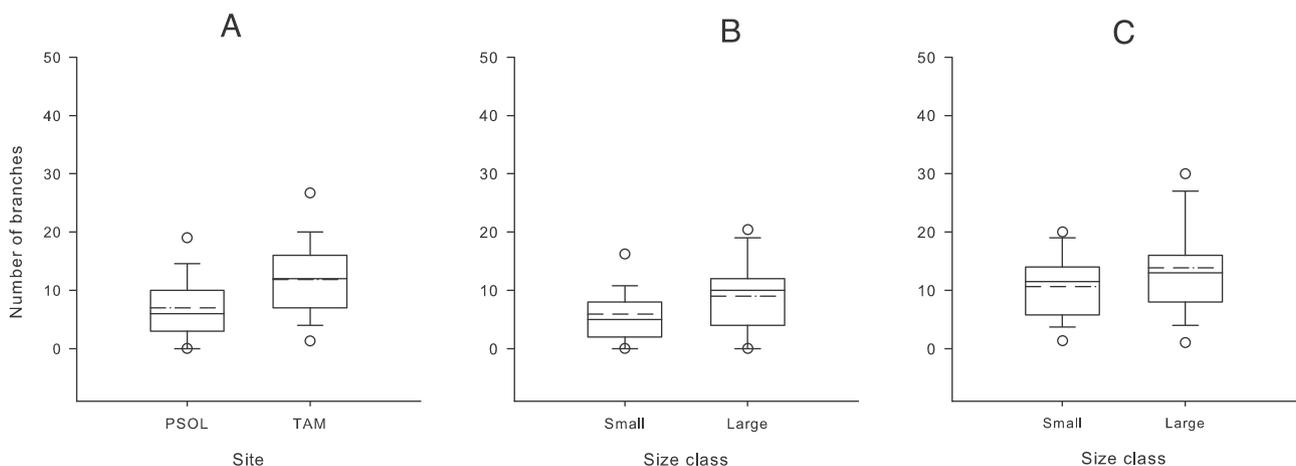
No asexual or sexual recruits were found within the permanent quadrats during the study period. Fragmentation of outplants was very rare with only nine (9) colonies fragmenting: three (3) at PSOL and six (6) at TAM.

#### Population modeling

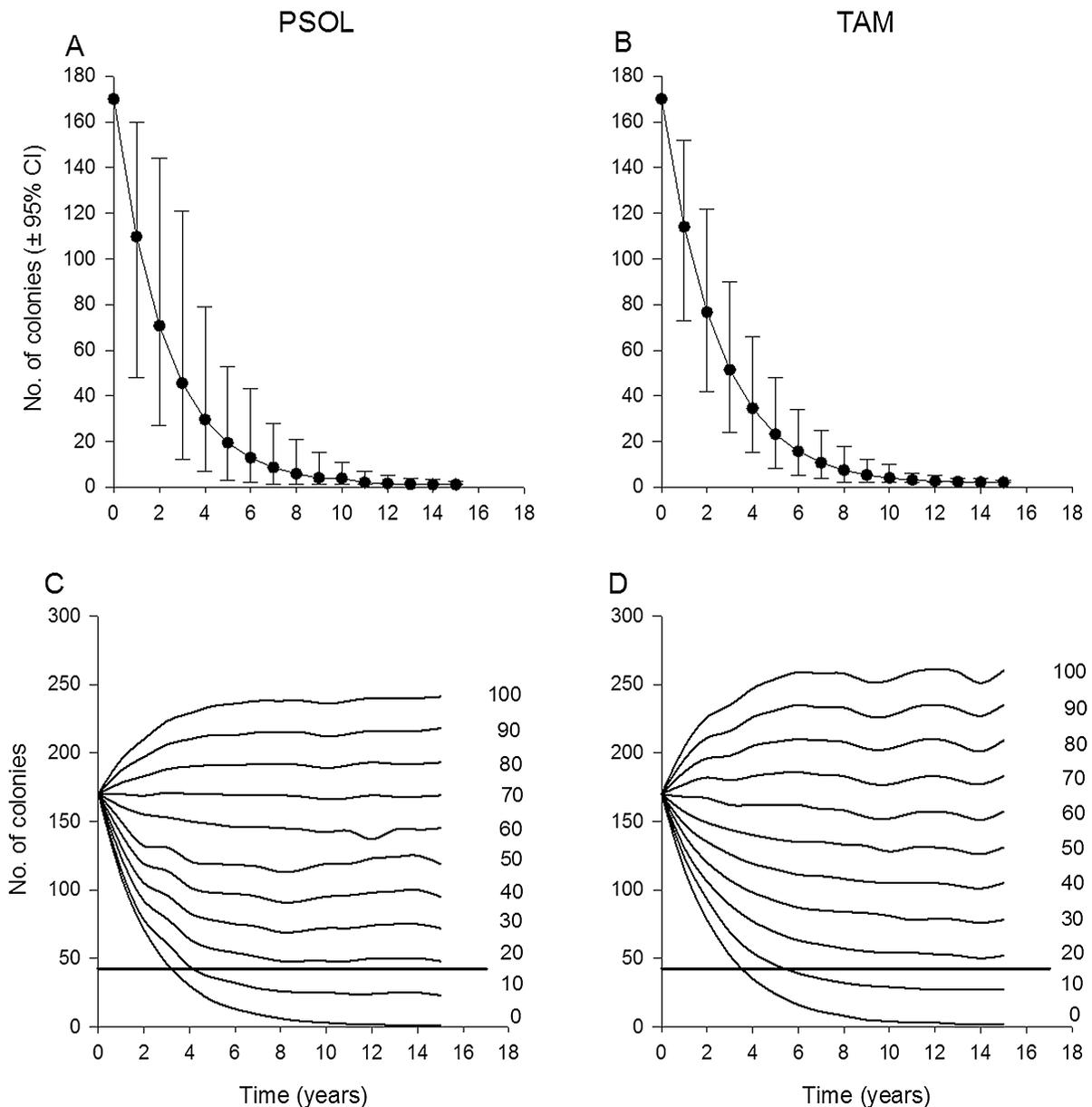
Results of the simulations indicate that in the absence of recruitment a mean population size below 25% of the initial number of transplants ( $\approx 43$  fragments) will be reached by the 4th year, and extinction ( $N = 0$ ) by the 11th year (Fig. 5A and B). It would require transplanting 20 colony fragments per year to keep both populations above the 25% threshold (Fig. 5C and D). To obtain a restored population equal or larger than the initial ( $N_0 = 170$ ) it would be necessary to transplant between 60 and 70 fragments per year. All the transplanting scenarios produced steady state dynamics by approximately the 8th year. No significant differences were found between observed and predicted mean population sizes (PSOL:  $\chi^2 = 4.359$ ,  $df = 4$ ,  $p = 0.3595$ ; TAM:  $\chi^2 = 1.513$ ,  $df = 4$ ,  $p = 0.824$ ). Furthermore, the models accounted for over 80% of the variation in fragment abundance (PSOL:  $r_{\text{Pearson}} = 0.82$ ; TAM:  $r_{\text{Pearson}} = 0.85$ ). These results indicate that the model is able to simulate the dynamics of fragment at both sites with relatively high accuracy.

#### Discussion

The aim of this study was to evaluate whether transplanting nursery-reared fragments of *A. cervicornis* is a viable approach to restore depleted or locally extinct populations of this coral. We took a more comprehensive approach than previous studies



**Fig. 4.** Box plots comparing median branch production (no. of branches per fragment per year) with the 75th and 95th percentiles: (A) between sites (pooling by size), (B) between size classes at Punta Soldado (PSOL), and (C) between size classes at Tamarindo (TAM). Solid and dashed horizontal lines within the box represent the median and the mean, respectively. Open circles represent the maximum and minimum values.



**Fig. 5.** Mean projected abundances of the restored populations (with 95% of confidence intervals) for the (A) PSOL and (B) TAM over a 15 years period. Mean population size of the restored populations at (C) PSOL and (D) TAM for 15 years under different recruitment scenarios. Number of fragments yr<sup>-1</sup> represented by the numbers on the right axis. Confidence intervals of 95% were obtained in graph C and D for clarity. Horizontal solid line represents the threshold population size of 43 fragments (approximately 25% of the initial population size).

(e.g. Shinn 1966; Garrison & Ward 2008; Hollarsmith et al. 2012) in that (1) we evaluated survival, growth, and branching rates to better understand the demography of fragments outplanted to the reef substrate (not growing in nursery units), (2) we examined the effect of size on the demographic performance of fragments, and (3) we analyzed the viability of the restored population by projecting it into the future using the estimated survival and fragments outplanting (recruitment) rates as the model parameters.

A good measure of the feasibility of a population restoration program is by how much a particular management strategy enhances the vital rates of a population vis-a-vis the naturally observed rates. The absence of naturally occurring unattached fragments within the studied sites prevented the direct comparison of their demographic performance against transplanted (stabilized) fragments. Nevertheless, our results indicate that fixing fragments to the reef substrate using nails and cable ties can improve considerably

fragment survival. Published estimates of annual survival of natural unattached fragments of *A. cervicornis* ranges between 0% and 32% (Bak & Crieis 1981; Knowlton et al. 1981; Mercado-Molina et al. 2014b); these values are considerably lower than the annual survivorship we report here for outplanted fragments which exceeded 60%. Williams and Miller (2010) as well as Forrester et al. (2011) also found that stabilizing fragments of *A. palmata* (using cable tie) to the reef substrate enhanced significantly their survival with respect to unstabilized fragments.

Mercado-Molina et al. (2014b) related the relatively low survival rates of *A. cervicornis* loose fragments (with respect to stabilized fragments) to their low reattachment rates. Attachment failure may result in fragments being continuously tumbled by waves/water movement causing a significant loss of live tissue due to abrasion. In addition, the probability of landing on an unsuitable microhabitat such as sediment patches increases with time

(Lirman 2000; Bowden-Kerby 2001). In contrast, stabilizing coral fragments to a fixed structure (a nail in this case) reduces sediment scour and/or burial by keeping the fragments in an upright position while restricting mobility; thereby, increasing their chance of survival.

An interesting aspect of the survival pattern observed in this study is that most of the mortality occurred within the first month after transplantation. Following the first month, fragments survived relatively well with rates varying between 90.20% and 98.97% per 3 months. A possible explanation for the early mortality observed at both sites could be “handling stress” (Yap et al. 1992; Clark & Edwards 1995; Forrester et al. 2012). It has been shown that handling makes transplant more susceptible to foraging/predation (Chasqui-Velasco et al. 2007), bleaching (Forrester et al. 2012), and diseases (Forrester et al. 2012). Unfortunately, we were unable to identify the specific source of mortality in this study.

The initial size of transplantation did not affect the survival of transplants. This outcome is somewhat surprising since it is generally understood that coral survival increases with size (Connell 1973; Hughes & Jackson 1985). Nonetheless, similar results have been reported for natural unattached fragments of *A. cervicornis* (Mercado-Molina et al. 2014b), for loose fragments of *A. palmata* (Lirman 2000) and *Madracis mirabilis* (Bruno 1998) as well as for transplants of the corals *Porites cylindrica* and *P. rus* (Yap et al. 1998).

Stabilizing fragments may not only improve their survival but may also increase significantly their growth. The growth rates reported here for *A. cervicornis* outplants are at least 4× greater in relation to what have been reported for unattached ones (Mercado-Molina et al. 2014b). The relatively high growth of stabilized transplants with respect to unattached fragments may be a consequence of the latter allocating more energy toward tissue repair and reattachment than to growth (Williams & Miller 2010).

Growth and branching rates varied significantly between sites. Data collected by the local NGO Sociedad Ambiente Marino, which has run an *A. cervicornis* nursery at both sites for over 10 years, indicates that both temperature and water quality (e.g. transparency) are very similar between sites (Hernández-Delgado & Suleimán-Ramos unpublished data). Hence, spatial differences in growth and branching dynamics cannot be attributed to differences in these physical parameters. On the other hand, there is evidence that mean macroalgae cover differs between sites (TAM: 17%; PSOL: 37%). It is known that competition between coral and macroalgae can adversely affect coral growth (Ferrari et al. 2012). Indeed, Forrester et al. (2011) demonstrated that the growth of stabilized fragments of the congeneric species *A. palmata* increased significantly when adjacent macroalgae were removed. Thus, lower growth rates at PSOL could be attributed, in part, to the negative effect that macroalgae have on corals (Ferrari et al. 2012). This study, nevertheless, was not designed to isolate the effects of these factors on transplants growth and branching dynamics but rather to compare the demographic performance of fragments of different sizes. At both sites, large fragments grew much faster and produced more branches than smaller ones. Thus, even when spatial differences were detected in the growth and branching rates of transplants, these differences were overwhelmed by the size effect (small vs. large). Size-dependent growth/branching pattern may be the result of large fragments having more resources to allocate toward growth (Garrison & Ward 2008) thanks to a greater surface area that can increase (1) the interception rate with food particles from the water column and (2) the area exposed to sunlight (Soong & Chen 2003). At the same time, large coral fragments may display better competitive abilities against macroalgae resulting in higher growth rates (Yap et al. 1992; Ferrari et al. 2012).

The finding that growth rates are influenced by the initial size of transplantation has practical implications for the design of management and conservation plans. Fragments  $\geq 25$  cm could be

considered an effective initial size of transplantation because compared to smaller ones, large fragments may reach much faster (1) a “refuge size” in which colonies can better cope with physical or biological disturbances (Hughes & Jackson 1985), and (2) an effective reproductive size (e.g. Lirman 2000; Smith & Hughes 1999; Okubo et al. 2007); thus improving the chances of *A. cervicornis* to naturally rebound from local population collapse. Moreover, the tendency of fragments  $\geq 25$  cm to produce a relative high number of new branches may be an important aspect to weigh if the restored population is to be considered a rapid source ( $\approx 1$  year) of fragments to (1) sustain the population itself, (2) serve as donor population to restore other sites or (3) to establish/expand coral gardening and nurseries programs.

Our model simulations indicate a reduction of approximately 90% in fragment abundance after 6 years (Fig. 5). This sharp reduction supports the conclusion of Garrison and Ward (2008) that *A. cervicornis* is not suitable for restoration. However, our simulations also indicate that with minimal human intervention it is possible to assure the persistence of a restored population. In this respect, for an initial population of 170 fragments, transplanting  $\approx 20$  coral fragments per year may be enough to maintain population size over the 25% of the initial number of transplants. Meanwhile, transplanting between 60 and 70 fragments per year would maintain the original population size (Fig. 5A and B). In our experience (and for the scale of this work) transplanting 70 colonies per year does not represent a significant logistical or economical constraint as it can be easily achievable within 1 or 2 days of work (a combined 8 h, 4 divers, 2 dives, 2 h per dive, 20 fragments per diver). The costs of a restoration project may vary considerably depending on the scale and the location of the impacted sites. However, if restoration projects are community/volunteers-based as is the case for many Caribbean restoration projects (Hernández-Delgado & Suleimán-Ramos 2014; Hernández-Delgado et al. 2014; Forrester et al. 2014) the financial burden may be significantly eased. Although fragments can be collected from previously transplanted colonies, having nursery units close to the site of restoration is desirable to reduce any possible negative impact associated with harvesting fragments from the restored populations. For the specific case of the studied sites in Culebra, nursery units run by SAM can produce between 1920 and 5760 coral fragments (branches) per year (Hernández-Delgado et al. 2014). Therefore, 70 coral fragments could be easily available for several restoration initiatives at a yearly basis.

To conclude, *A. cervicornis* rely heavily on branch fragmentation for its propagation. Nevertheless, as has been found for wild populations (Mercado-Molina et al. unpublished data), fragmentation was rare during this study. The combination of low fragmentation rates, low reattachment rates, and low survival of unattached fragments may be keeping this coral from recovering by itself. Human intervention is, therefore, necessary to promote population stability/growth. We provide quantitative evidence to argue that *A. cervicornis* outplants survive, grow, and produce branches much better than what has been reported for natural unattached fragments. Thus, stabilizing nursery reared fragments to the reef substrate or to a fixed structure (e.g. nails) could be considered an effective approach to promote the recovery of this species. Active management, however, is necessary to ensure the viability of the restored populations. Transplanting fragments  $\geq 25$  cm is preferable because they exhibit higher growth and branching rates than smaller ones. Lastly, population restoration programs must be implemented in combination with other conservation/management initiatives that may, for example, reduce coastal pollution and/or increase the abundance and biomass of herbivores (e.g. the establishment of Marine Protected Areas). Together, these actions can help mitigate the negative effect of coral diseases and the increase in seawater temperature; disturbances that are more difficult to manage.

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