# Survival, growth, and branch production of unattached fragments of the threatened hermatypic coral *Acropora cervicornis*

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## ABSTRACT

Fragmentation has been regarded as the most important reproductive strategy in the threatened reef building coral *Acropora cervicornis*. Before the Caribbean-wide collapse experienced by *A. cervicornis*, asexual reproduction may have served as an effective source of new colonies to sustain and/or enhance local population growth. However, baseline information on the demographic success of fragments in nature is limited, hampering our ability to estimate the real contribution of asexual fragmentation to current population growth. In this study, natural occurring fragments of *A. cervicornis* were monitored for 18 months at two sites in Puerto Rico in order to quantify their survival, growth, and branching dynamics. Fragment survivorship did not exceed 26%, growth rates were relatively low with mean values ranging between $0.0242 \pm 0.0168$ (SE) and $0.0906 \pm 0.0301$ (SE) cm d$^{-1}$, and fragments barely produced new branches. No significant differences were found when comparing these demographic traits for different size categories. The relative low rates of survival, growth and branch production of natural fragments suggest that asexual fragmentation may not currently be a significant source of recruits for populations of this threatened coral.

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## 1. Introduction

Before the 1980s, *Acropora cervicornis* was one of the most common and dominant reef building coral inhabiting Caribbean coral reefs (Tunnicliffe, 1983; Aronson and Precht, 2001). Several factors including, epizootic events (Precht et al., 2002; Williams and Miller, 2005), impacts of hurricanes (Knowlton et al., 1981), elevated sea surface temperature (Carpenter et al., 2008), and loss of habitat due to human activities (e.g. ship groundings, Griffin et al., 2012) led to a region-wide collapse. Localities have suffered population declines of up to 98% and many have experienced local extinctions (Knowlton et al., 1990; Miller et al., 2002; Precht et al., 2002). This scenario together with the fact that *A. cervicornis* has not shown much recovery in the localities where populations exist (National Marine Fisheries Service, 2012; Precht et al., 2002), has opened a debate within the USA-National Oceanic and Atmospheric Administration (NOAA) as to whether or not to reclassify the status of this coral from a threatened species to an endangered one.

The low natural capacity of *A. cervicornis* to recover (at least currently) is not only due to the impact of extrinsic disturbances leading to high mortality rates but is also hindered by limited sexual recruitment (Vargas-Angel et al., 2006; Vollmer and Palumbi, 2007). It is known that sexual reproduction is of little significance for population growth, either because: (1) mature colonies are unable to produce viable gametes (Quinn and Kojis, 2005, 2006), (2) fertilization rates are low (Quinn and Kojis, 2006; Vargas-Ángel et al., 2006), (3) larval settlement is precluded by high pre-settlement mortality or lack of proper settlement substrate, and/or (4) high post-settlement mortality due to predation and/or competition (Tunnicliffe, 1981; Ritson-Williams et al., 2009). Hence, it is understood that *A. cervicornis* relies almost exclusively on asexual fragmentation to propagate itself (Tunnicliffe, 1981; Highsmith, 1982; Knowlton, 1992).

The perceived relevance of asexual reproduction in the demography of *A. cervicornis* has led to the generalized belief that, at least at the local level, populations can sustain themselves by means of colony fragmentation (Tunnicliffe, 1981; Highsmith, 1982). Indeed, this paradigm was one of the reasons National Marine Fisheries Service classified *A. cervicornis* as a threatened rather than endangered species in 2006 (National Marine Fisheries Service, 2012). However, this conclusion was not based in empirical data about the demographic performance of asexual fragments under present coral reef conditions. Rather, the argument is based on the assumption that asexual reproduction has always been and remains as the main source of recruitment in this species, and that sexual recruitment was negligible even when the species was abundant.

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There is lack of quantitative data describing the dynamics of naturally occurring fragments (e.g. survivorship and growth). Moreover, the few available studies show contrasting results with regard to fragment survivorship. For example, Bak and Criens (1981) as well as Knowlton et al. (1981) followed the fate of unattached fragments and found that most of them (98%–100%) died within 5 months. In both studies the elevated mortality was associated to a disease outbreak. On the other hand, Bowden-Kerby (2001) measured survivorship for a period of between 6 and 7 months and reported survival rates varying between ≈55% and ≈90% in fragments selectively placed on coral rubble. Given the contrasting survival estimates, the aim of this study was to shed light on the demographic performance of natural fragments by describing not only their survival but also their growth and branching dynamics at two sites in Puerto Rico where *A. cervicornis* is relatively abundant. The results of this work should enhance our competence to make effective conservation and management decisions to preserve this key reef building coral species.

## 2. Materials and methods

### 2.1. Study sites

The survival, growth, and branch production of natural unattached fragments were investigated at two reefs in the northeast coast of Puerto Rico: Canal Luis Peña (CLP, 18°18′14.12″N: 65°20′15.29″W) and Palomino (PAL, 18°21′3.95″N: 65°33′58.79″W) (Fig. 1). CLP and PAL are characterized by low topographic relief and clear water with moderate to high wave energy. CLP is a colonized pavement while PAL is a reef crest formerly dominated by *Acropora palmata*. At both sites gorgonians are the major benthic macrofauna component with a relatively high natural abundance of *A. cervicornis* colonies.

### 2.2. Survival

A total of 100 fragments were collected at each site (CLP and PAL) and tethered by attaching a 1.5 m long monofilament line tied to a nail driven into the substrate, at depths of 3 m–4 m. This method, previously used by Bowden-Kerby (2001) as well as by Williams and Miller (2010), and recommended by Bruckner and Bruckner (2001), to study the dynamics of unattached fragments of Acroporids (*A. cervicornis* and *A. palmata*), was chosen because Acroporids are typical of reef zones frequently exposed to high energy due to wave action. Placing fragments within a study area without attaching them to a line would result in fragments being swept away and lost during events of a strong surge (i.e. Bowden-Kerby, 2001; Williams and Miller, 2010). This makes it impossible to accurately determine the fate of fragments displaced outside the study area. On the other hand, attaching fragments to a monofilament line allows the natural movement of the fragments over the seabed while allowing their fate and growth to be determined (Bowden-Kerby, 2001; Williams and Miller, 2010).

The study area covered ≈100 m² where *A. cervicornis* naturally occur. As such, the experimental area enclosed both suitable microhabitats where fragments can be wedged so that they could attach and then survive and grow, as well as microhabitats where fragment survival could be compromised (e.g. sediment patches). Fragments were haphazardly placed in groups of three to five (approximately 0.5 m apart one of each other) every 5 m in the reef in order to avoid bias against any particular microenvironment. It was assumed that the final positioning of any given fragment was a consequence of their natural displacement due to water motion (i.e. Bowden-Kerby, 2001). All fragments were identified by a numbered plastic tag tied to their corresponding nail.

Survivorship (live tissue > 0%) or death (live tissue = 0%) of fragments was monitored one month after the start of the study and at six month intervals thereafter from February 2012 to August 2013. To
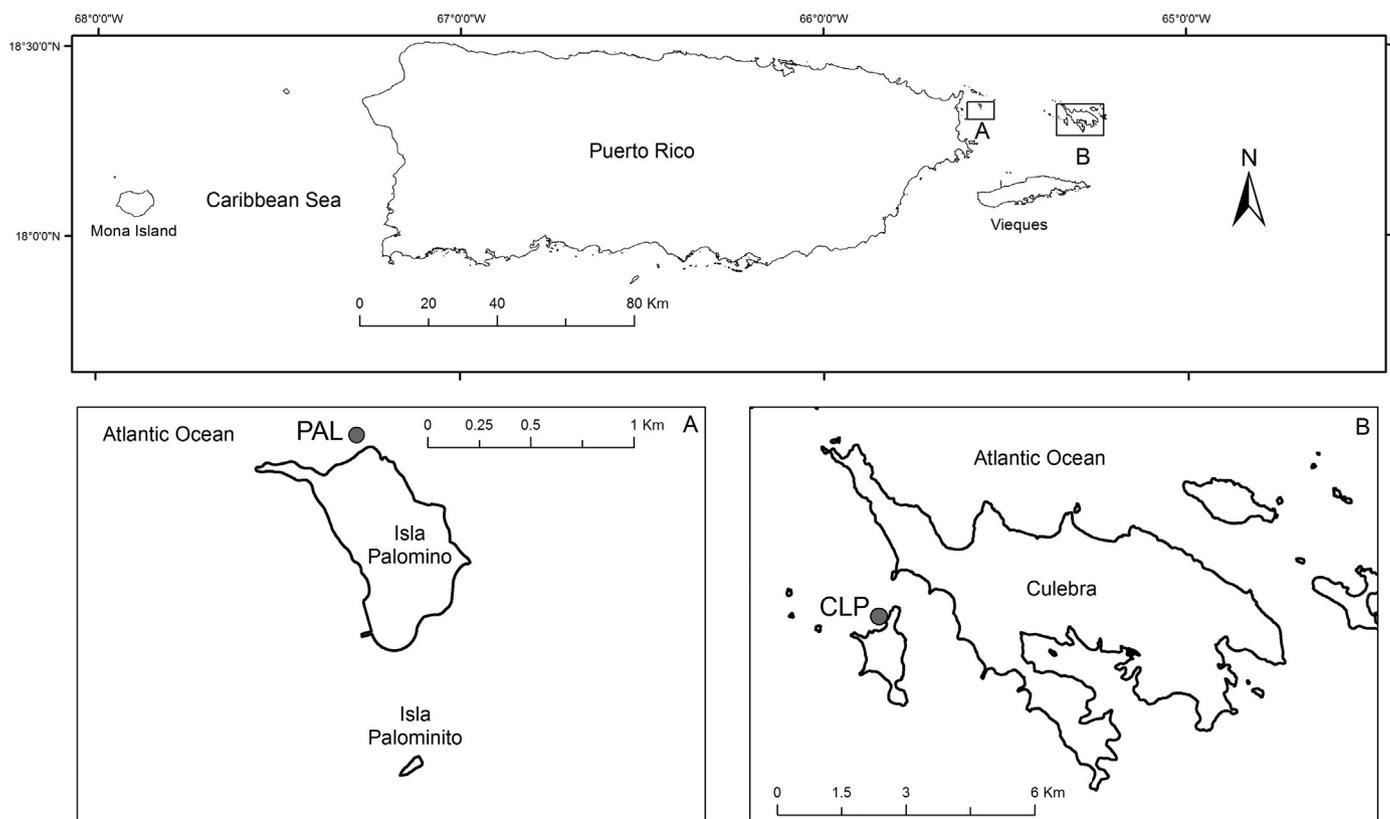


**Fig. 1.** Map showing the two study sites, CLP = Canal Luis Peña and PAL = Palomino.

evaluate whether the cumulative probability of survival varied significantly between sites and size classes (see below) Kaplan–Meir Survival analyses were performed.

## 2.3. Growth and branching dynamics

To estimate the rate of growth we calculated the change in daily linear extension by subtracting the initial size of any given fragment from its final size and dividing the difference by the total number of days. Both initial and final sizes were measured as the sum of the linear length of live tissue in all branches. Branch size was determined from in-situ photographs (scale-by-side) that latter were processed using the software Coral Point Count with Excel extensions (CPCe) (Kohler and Gill, 2006). All fragments were photographed from different angles in order to appreciate all branches fully extended. The appropriateness of digital image analysis in determining colony size was validated by measuring 50 colonies (ranging in size from 9cm to 545cm) in situ as well as using the CPCe software. T-test analysis was used to compare the mean colony sizes calculated with the two approaches, and no significant difference was found. Moreover, results of a regression analysis showed that image analysis is a good estimator of actual colony size ($r^2 = 0.966$, $p < 0.01$). Growth rates were calculated for those fragments that survived for at least six months because very few fragments survived to the end of the study. Mann–Whitney $U$-test was used to compare growth rates between sites and size treatments (see below) because data did not fulfill the requirements of normal distribution and homoscedasticity, despite several data transformation attempts. Branch production, calculated as the number of new branches produced by fragments, was analyzed as explained for growth rates.

## 2.4. Size classes

In order to measure the effect of the size on survivorship, growth, and branching, we categorized fragments into four total linear length size-classes: 1) <15 cm, 2) 15–25 cm, 3) >25–35 cm, and 4) >35 cm. These size-classes were chosen in order to include at least 20 fragments in each size-class within the observed range of fragment sizes. Because the demographic parameters did not differ significantly between class 1 and class 2 and between class 3 and class 4 fragments were pooled in two size classes (small: ≤25 cm and large: >25 cm) for further analysis.

# 3. Results

## 3.1. Survival

Survival curves did not differ significantly between fragments at CLP and those at PAL (KM log-rank test, $P > 0.05$, Fig. 2A), indicating that fragment survival followed a similar pattern at both sites. In general, survival was highest during the first month ($\approx 90\%$) of the study declining considerably thereafter (Fig. 2A). At the end of the study only 19% and 26% of the fragments survived at CLP and PAL, respectively. No significant differences in survival were found between small and large fragments (KM log-rank test, $P > 0.05$, Fig. 2B, 2C).

## 3.2. Growth

Growth rates did not differ significantly between fragments at CLP and those at PAL (Mann–Whitney test, $P > 0.05$). At CLP fragments grew at mean rates of $0.0906 \pm 0.0301$ (SE) cm d$^{-1}$ (median = 0.0345 cm d$^{-1}$) whereas at PAL the mean grow rate was $0.0242 \pm 0.0168$ (SE) cm d$^{-1}$ (median = 0.0121 cm d$^{-1}$) (Fig. 3A). With respect to size-specific growth, no significant differences were found between small and large fragments neither at CLP nor at PAL (Mann–Whitney test, $P > 0.05$, Fig. 3B, 3C).

## 3.3. Branch production

Rates of branch production did not differ significantly between sites (Mann–Whitney test, $P > 0.05$). Fragments at CLP produced in average $0.811 \pm 0.204$ (SE) (median = 0.00) new branches per fragments per year whereas at PAL, the mean branch production was $1.387 \pm 0.322$ (SE) (median = 0.00) (Fig. 4A). Likewise, no significant difference in ramification rates between small and large fragments was found (Mann–Whitney test, $P > 0.05$, Fig. 4B, 4C).

# 4. Discussion

A major goal of this study was to provide baseline information about the dynamics of A. cervicornis natural fragments. When compared to the survival of established colonies (Knowlton et al., 1990), our results indicate that survival of loose fragments is relatively poor, as only 19% (CLP) and 26% (PAL) of the fragments survived after 18 months. Moreover, most of the fragments (at both sites) were progressively losing tissue at a mean rate of approximately 7 mm d$^{-1}$. At this pace, it could be
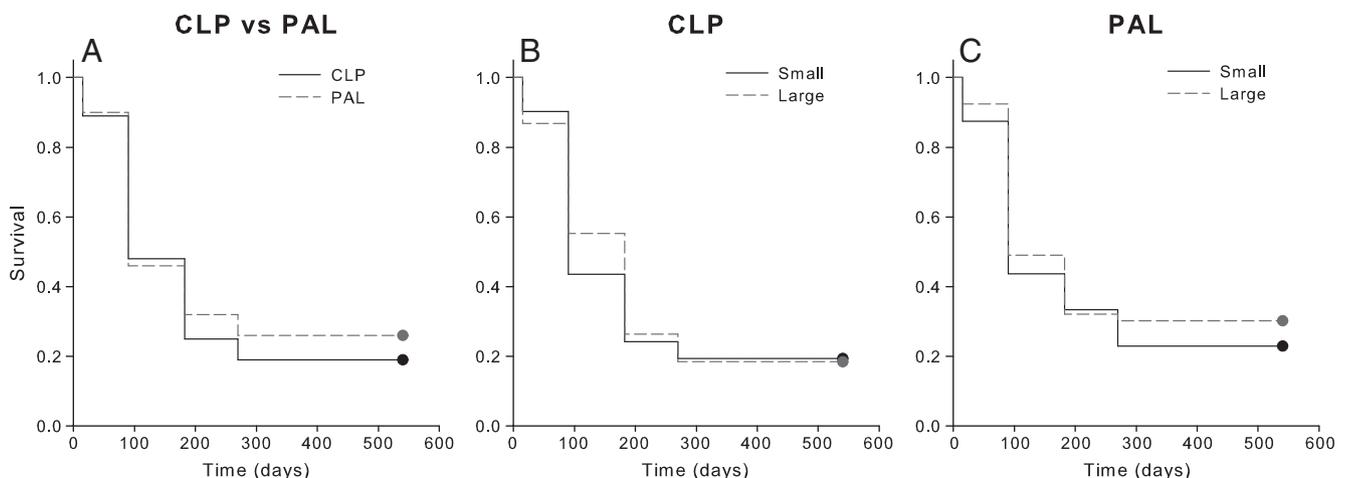


**Fig. 2.** Kaplan–Meier plots showing percent survival of fragments between (A) sites (pooling by size) and (B) size classes at Canal Luis Peña, and (C) and at Palomino.
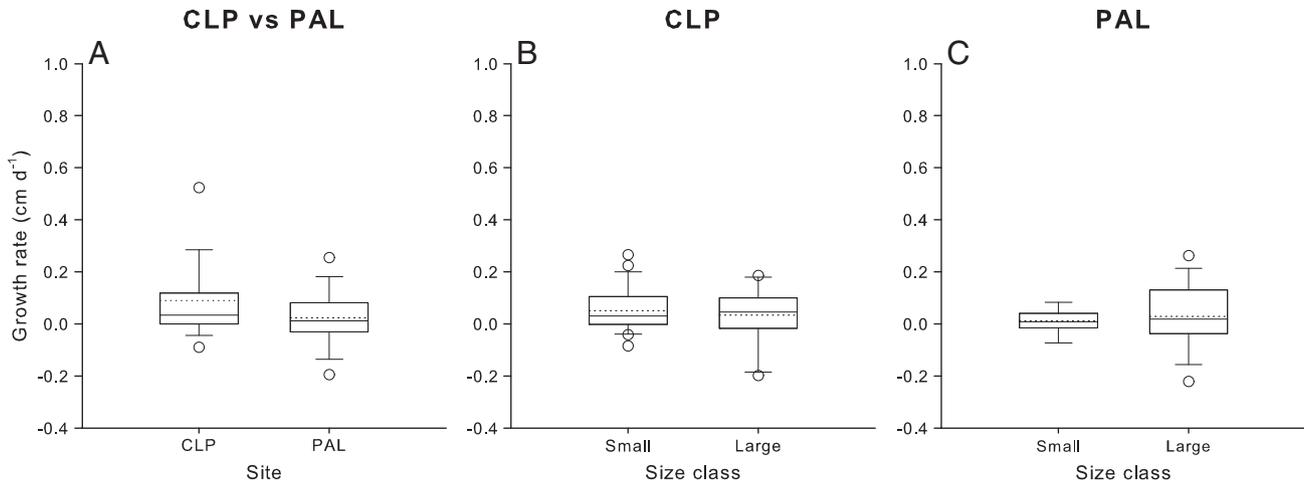
**Fig. 3.** Box plots comparing median growth (cm d$^{-1}$) of fragments with the 25th and 75th percentiles, (A) between sites (pooling by size), (B) between size classes at Canal Luis Peña, (C) between size classes at Palomino. Vertical lines that end in a horizontal stroke are the upper and lower adjacent values. Open circles represent outliers. Dash line represents the mean value.

expected that at least 5–7 of the remaining living fragments would die during the next four to six months reducing the overall survivorship to 12% at CLP and 19% at PAL by the 24th month. There are other studies that report lower survivorship of loose fragments of *A. cervicornis* (Bak and Creins, 1981; Knowlton et al., 1981); however, both studies attributed the elevated mortality to a disease outbreak. During the study no evidence of white band or other diseases was observed in any of the fragments.

The relatively high mortality of unattached fragments may be a consequence of their inability to reattach to the substratum (Forrester et al., 2011; Williams and Miller, 2010). At both sites, less than 5% of the fragments successfully reattached. Lying loose on the substrate may increase the susceptibility of fragments to recurrent movement, resulting in a significant loss of live tissue due to abrasion. At the same time, the probability of landing on unfavorable locations where their survivorship could be compromised (e.g. sediments patches, Lirman, 2000; Bowden-Kerby, 2001) is likely to increase with time. Nevertheless, very few of the dead fragments (5 at CLP and 1 at PAL) were covered by sand/sediments even when sand/sediments patches were not rare within the study area.

We did not find evidence that survivorship of fragments varied significantly with size. This result contrasts with the pattern reported by Bowden-Kerby (2001), who also evaluated the effect of fragment size on survivorship in *A. cervicornis* and found that survival increases with size. Our study differs from Bowden-Kerby (2001) in that: 1) he used fragments smaller than 22 cm whereas this study considers the natural size-frequency distribution of the fragments, 2) he selectively placed the fragments within a rubble zone whereas in our study fragments were positioned haphazardly over the study area, and 3) he performed his study in an area protected from wave action (i.e. backreef zone) whereas our study sites are exposed reefs where *A. cervicornis* naturally occur. Lack of size-specific survivorship has been also reported for fragments of other coral species that rely on asexual fragmentation for their propagation such as *A. palmata* (Lirman, 2000) and *Madracis mirabilis* (Bruno, 1998) as well as for the hydrocoral *Millepora complanata* (Lewis, 1991).

In general, fragments grew very slowly. The estimated mean growth rates (total linear length), 0.0906 ± 0.0301(SE) cm d$^{-1}$ at CLP and 0.0242 ± 0.0168 (SE) cm d$^{-1}$ at PAL, are similar or lower than what has been found for a single branch in colonies attached to the substrate and/or a rigid structure (Lirman et al., 2010; Shinn, 1966). Williams and Miller (2010) suggest that low growth rates of unattached fragments (with respect to those firmly attached) is related to a trade-off in the allocation of energy between tissue repair and attachment versus growth. Slow growth may have important consequences for the dynamics of *A. cervicornis* populations. First, it may take longer for a fragment to
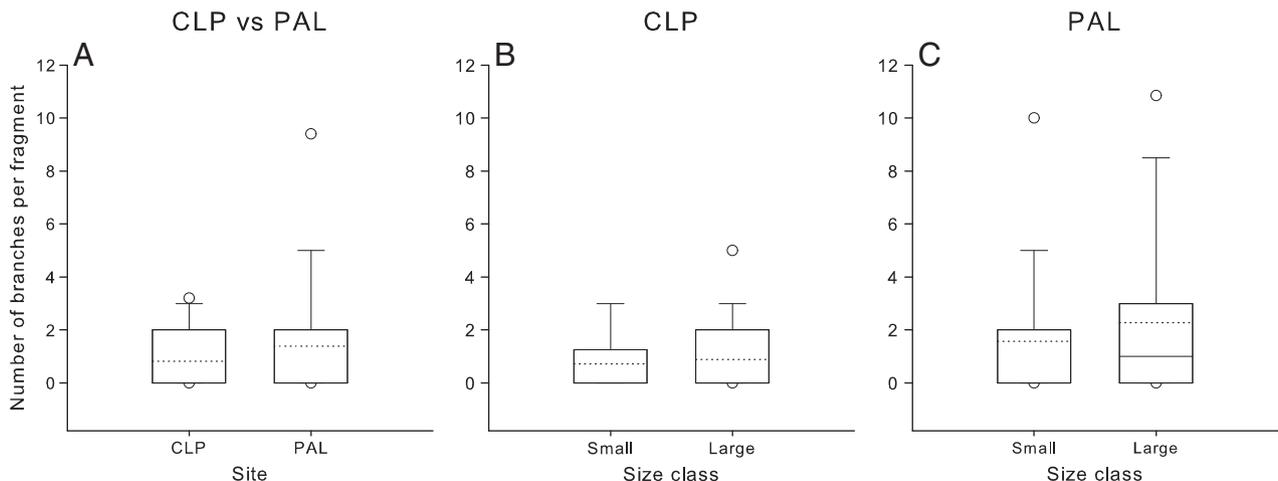


**Fig. 4.** Box plots comparing branch production of fragments with the 25th and 75th percentiles, (A) between sites (pooling by size), (B) between size classes at Canal Luis Peña, (C) between size classes at Palomino. Vertical lines that end of a horizontal stroke are the upper and lower adjacent values. Open circles represent outliers. Dash line represents the mean value.

reach a "refuge size" in which mortality risk associated with physical or biological disturbances is reduced (Hughes and Jackson, 1985; Sebens, 1987). Second, it may take longer for a fragment to reach the effective reproductive size (e.g. Lirman, 2000; Okubo et al., 2007; Smith and Hughes, 1999).

The branching dynamics followed a similar pattern to that of growth rates in the sense that no significant differences were found between sites and size classes. More importantly, branching rates were also very low. Fragments barely produced new branches probably because most energy was used to regenerate the continuous loss of tissue, as explained above. In order to promote population growth, fragments must be able not only to survive well and grow relatively fast but also need to produce branches. Therefore, the fact that loose fragments are not a significant source of additional fragments (assuming that the higher the number of branches within a colony the higher the probability of branch fragmentation) may be of concern because it may slow down the natural capacity of *A. cervicornis* populations to recover from local population collapses.

Attaching a monofilament line to a coral fragment did not cause tissue abrasion and/or partial mortality of the tissue in contact with the monofilament. In fact, in most cases coral tissue overgrew the monofilament (see electronic Supplement 1). Thus, it can be concluded that the effect of tethering on fragment survival and growth was negligible. Nonetheless, an inevitable consequence of the method is the restriction of the total distance that a fragment can move (Williams and Miller, 2010). This may result in a lower survival estimate if tethering decreases the probability of the fragment settling in a suitable microhabitat. We understand, however, that the bias is rather low because typical of high energy zones, the studied areas surrounding the tethered fragments included many localities suitable for the establishment of loose fragments (e.g. crevices and denuded reef areas, etc.). On the other hand, if tethering lowers the probability of fragments settling in unsuitable microhabitats such as sediment patches, then the survival estimates of tethered fragments are somewhat inflated.

In conclusion, the relatively low survival, growth, branching, and reattachment rates observed during this study suggest that the contribution of asexual fragmentation to current population growth in *A. cervicornis* is lower than generally assumed; and therefore may not be sufficient by itself for natural population recovery in this species.

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