Tissue loss rather than colony size determines the demographic fate of the branching coral *Acropora cervicornis*

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ABSTRACT: Partial mortality is a common process affecting coral colonies. Yet, the impact of tissue loss on the demography of the threatened reef-building coral *Acropora cervicornis* has been poorly investigated. This limits our understanding of how this species will fare under unfavorable environmental conditions. In this study, we examined the growth and survival of colonies with varying degrees of partial mortality, indicated by tissue loss, for 2 yr at 2 reefs in Puerto Rico. We found that irrespective of colony size, rates of coral growth and survival declined significantly once the proportion of dead tissue exceeded 20 % of the total colony size. Projections of state-matrix population models indicated that partial mortality could also have a negative impact at the population level. For instance, a 25 % increase in the number of colonies with >20 % tissue loss would reduce the time in which 75 % of the population is lost by 3 to 4 yr. Our results provide a new perspective on the effect of partial mortality on the demography and population dynamics of *A. cervicornis*. First, 20 % of tissue loss can be considered a threshold value in which colony fate and population growth are compromised. Second, colony size is not the most important determinant of a colony's demographic performance; instead, the surface area lost to partial mortality is a better predictor of colony growth and survivorship. Taking into consideration the relationship between partial mortality and the demographic fate of *A. cervicornis* can aid in the development of stronger conservation and restoration programs.

KEY WORDS: Acroporids · Coral demography · Coral population dynamics · Coral growth · Coral survival · Partial mortality

INTRODUCTION

Marine modular organisms such as corals grow by replicating partially self-maintaining multicellular units known as modules (Hughes & Jackson 1985, Vuorisalo & Tuomi 1986). This unique aspect of their biology allows modular organisms to remain viable even when a portion of their total number of modules (i.e. polyps in corals) die. These partial mortality events are common among scleractinian corals and can occur as a result of physical stress (i.e. sedimentation, high water temperature), human-induced mechanical damage (i.e. anchor-

ing), as well as by biological disturbances such as predation and disease outbreaks. Indeed, partial mortality, rather than whole colony mortality, is thought to be the major contributor to the total loss of tissue within coral populations (Hughes & Jackson 1985, Meesters et al. 1997a, but see Furby et al. 2017).

Reduction of colony size is the most obvious outcome of partial mortality. Becoming a smaller colony can compromise coral performance (Hughes & Jackson 1985, Hughes & Connell 1987, Sakai 1998), probably because a colony's energy budget is proportional to its size (Connell 1973, Elahi & Edmunds

2007). Partial mortality can also alter the pattern of energy allocation to vital functions. For instance, energy allocated to growth and reproduction could be diverted towards tissue repair (Williams & Miller 2010, Serrano et al. 2017). Colony viability could also be threatened when the exposed skeleton and dead tissue are colonized by aggressive fouling competitors and pathogens such as fungi, algae, and sponges (Hall 2001). Consequently, a reduction of live tissue can significantly reduce the vital rates of a colony compared with those of a similar-sized colony that has not suffered polyp loss.

Published studies provide conflicting results about how partial mortality affects coral survival, growth, and reproduction. For instance, Babcock (1991) found that colonies of the corals *Goniastrea aspera* and *G. favulus* suffering partial mortality were more likely to regress in size than undamaged colonies. Likewise, Meesters et al. (1994) reported that cores of *Orbicella annularis* with human-induced lesions grew 32% slower than unaffected control cores. In contrast, Pisapia et al. (2016) showed that the growth of *Acropora hyacinthus*, *Pocillopora* spp., *Porites* spp., and *Montipora* spp. was unaffected by the partial loss of tissue. In another study, Graham & van Woesik (2013) found no evidence to contend that partial mortality compromises the reproductive output of 3 Caribbean coral species, whereas Hall (1997) found that the reproductive capability of 3 species inhabiting a reef in Lizard Island, Australia, was reduced when losing live tissue. The relationship between partial mortality and survival also needs to be clarified. Hughes & Connell (1987), as well as Babcock (1991), found that tissue loss reduced colony survival. However, studies by Hall (1997) and Cumming (2002) demonstrated that partial mortality does not always result in lower survival rates. These contrasting results make any generalization about the relationship between tissue loss and the fate of coral colonies questionable, and thus should be explored at the species-specific level whenever it is possible.

Understanding how coral populations respond demographically to partial mortality is essential to properly evaluate the prospect of population persistence under unfavorable environmental conditions, such as elevated seawater temperature and high sedimentation rates. Of particular concern are those threatened species that contribute significantly to the structure and function of coral reefs. In this study, the relationship between partial mortality (measured as % of tissue loss) and the demographic fate of the threatened Caribbean reef-building coral *Acropora cervicornis* was evaluated. Specifically, we measured the effect of partial tissue loss on colony survival and growth rate. We also sought to determine which is a better predictor of colony growth and survival: colony size or colony condition (that is, whether the colony suffers partial mortality or not). Finally, we constructed and analyzed a matrix population model to evaluate the effect of partial mortality on local population growth rates. The relevant question we addressed with the model was: Will population growth rates be reduced if the number of colonies suffering partial mortality increases? The results of this study will (1) increase our understanding of how *A. cervicornis* responds demographically to the loss of tissues, (2) shed light on the potential susceptibility of populations to partial mortality, and (3) provide fundamental demographic information that will improve the design of conservation and management initiatives directed at restoring the integrity of coral reefs, one of the most threatened ecosystems in the world.

MATERIALS AND METHODS

Study species

The coral *Acropora cervicornis* is one of the major reef-building species in the Caribbean. This coral has suffered a dramatic decline in population abundances throughout its geographic extent, becoming extinct in many localities (Knowlton et al. 1990, Miller et al. 2002), including areas of Puerto Rico (Weil et al. 2003). The population decline that began in the early 1980s was triggered by a combination of disease (Aronson & Precht 2001) and predator outbreaks (Knowlton et al. 1990). Natural population recovery has been very rare, not only due to recurrent epizootic events (Williams & Miller 2005, Miller et al. 2014) but also because of low sexual and asexual recruitment (Knowlton et al. 1990, Quinn & Kojis 2005, Mercado-Molina et al. 2014), degradation of critical habitats (Goreau 1992, Hernández-Delgado et al. 2014), episodes of high thermal stress (Quinn & Kojis 2008), and intense physical disturbances (e.g. hurricanes; Goreau 1992). Currently, *A. cervicornis* is considered Critically Endangered by the International Union for Conservation of Nature (Aronson et al. 2008).

Study sites

This study was carried out at Canal Luis Peña (CLP) and Palomino (PAL) reefs. These reefs are located within Puerto Rico's Northeast Marine Corridor and

Culebra Island Habitat Focus Area (CLP: 18° 18′ 14″ N, 65° 2′ 15″ W; PAL: 18° 21′ 3″ N, 65° 35′ 58″ W). Both sites are characterized by a hard bottom dominated by octocorals (Mercado-Molina et al. 2015a). Water quality is relatively good because the sites are not directly influenced by a river or human-derived water discharges. The population of *A. cervicornis* at CLP and PAL consists of colonies scattered over the seabed rather than colonies forming a dense thicket, which was typical prior to the 1980s. Therefore, individual colonies were easily discernable and tractable. Given the current decimated status of *A. cervicornis* in the Caribbean, populations with scattered colonies rather than thickets are the current typical structure (NMFS 2015).

Partial tissue mortality and colony size

In total, 123 and 111 colonies were identified and tagged at CLP and PAL, respectively, at depths that varied between 3 and 5 m. Numbered aluminum tags were fixed to non-living substrate adjacent to (not in direct contact with) the colony with masonry nails. All colonies were photographed *in situ* (scale by side), and the images were processed using the software Coral Point Count (CPCe version 4.1; Kohler & Gill 2006) to obtain colony initial size. Following Knowlton et al. (1990) the size of the colony was calculated as the sum of the lengths of live portions of all branches (total live tissue, TLT) and expressed in cm (Table 1). TLT was used as the measure of colony size to make our results comparable to previous studies investigating the relationship between partial mortality and

Table 1. Summary of the demographic terms used in the study

Term	Definition	Unit
Colony size	Sum of the lengths of the live portions of all branches of a colony, expressed as total live tissue (TLT)	cm
Partial mortality	Sum of the lengths of the dead portions of all branches of a colony, expressed as total dead tissue (TDT)	cm
Total colony size	TLT + TDT	cm
Percent partial mortality	Proportion of dead tissue relative to total colony size. Calculated as [TDT / (TLT + TDT)] × 100	%
Relative colony growth	Defined as the proportional change in TLT and expressed as percent of change. Calculated as: [(Final size − Initial size) / Initial size] × 100	%

coral fate (e.g. Cumming 2002, Pisapia et al. 2016). Partial mortality, defined as total dead tissue (TDT), was measured as the sum of the lengths of portions with dead tissues (i.e. lesions) in all branches of a colony. The proportion of partial mortality was calculated by diving TDT by the total size of the colony, which in turn was calculated as the sum of TLT and TDT. Colonies were photographed from different angles to ensure that all branches were visible. To test whether larger colonies were more likely to experience partial mortality, we determined the relationship between colony size and percent of dead tissue using a Pearson correlation analysis. Because multiple comparisons were performed, the 0.05 significance level was adjusted using a Bonferroni correction.

Partial tissue mortality and colony growth

Relative growth, which expresses the change in colony size as a percentage of the initial size (Table 1), was our measure of coral growth. It was calculated as [(Final size − Initial size) / Initial size] × 100 for the 2011–2012 and 2012–2013 periods. Initial and final colony sizes were measured as explained above. Pearson correlation analysis was used to test if relative colony growth was related to percent partial mortality. To determine whether undamaged (= no partial mortality) colonies had a higher probability of increasing in size than those colonies showing partial mortality (= damaged), an odds ratio analysis was carried out. The odds ratio (OR) analysis, defined here as OR = $(N_{00} \times N_{11}) / (N_{01} \times N_{10})$, measures the association between binary variables which can be represented by a value of 0 and 1 (Pearson 2011), for instance, fate (growth = 1 or no growth = 0) vs. condition (no partial mortality = 1 or partial mortality = 0). Thus, N_{00} represents the number of colonies with partial mortality that did not grow during the study, N_{11} represents the number of colonies with no partial mortality that increased in size, and so forth. In our case, OR values >1 indicate that colonies with no partial mortality (1) are more likely to grow than to regress in size (0). A Mann-Whitney *U*-test was used to compare rates of relative growth between corals with different tissue conditions. To establish the relationship between partial mortality and the relative growth of colonies varying in size, we classified coral colonies into 3 size classes. Following Mercado-Molina et al. (2015a), colonies were classified as small (10–100 cm TLT), medium (101–250 cm), and large (>250 cm). Colonies that disappeared during the study were excluded from all analyses.

Partial tissue mortality and colony survival

The relationship between colony survival and the amount of tissue loss was evaluated using a logistic regression test. We also used the odds ratio analysis to determine whether undamaged colonies had a higher probability of survival than damaged colonies. Odds ratio values >1 indicate that colonies with no partial mortality (1) are more likely to survive than die (0). To avoid estimation problems for cells in which an event did not occur, the corresponding value of 0 was replaced by 1. Yate's correction was applied when expected values were <5 to prevent overestimation of statistical significance (Stamatis 2012). Chi-squared analysis was used to test whether colony survival was associated with size class. Colonies were considered dead if no live tissue was distinguishable.

Log-linear analysis

Log-linear models were applied to a 3-way contingency table developed to establish whether size or condition (partial or no partial mortality) is a better predictor of colony fate (Cumming 2002). As suggested by Fingleton (1984), 0.5 was added to each cell value within the contingency tables to avoid estimation problems for values equal to 0. For the analyses, the package MASS (Venables & Ripley 2002) was run in R (R Development Core Team 2013).

Population modeling

We evaluated the effect of partial mortality in the performance of *A. cervicornis* at the population level by means of a 2-state transition matrix model, in which state was based on colony condition (see Eq. 1 below). The model did not include size because colony condition rather than size was a better predictor of colony fate (see below). The number of colonies within each category in time $t + 1$ equals the product of the 2 × 2 matrix (**A**) and the column vector representing the number of colonies in each category at time t. The matrix contains the transition probabilities between colony states. In Eq. (1), C_{ud} and C_d stand for undamaged (no partial mortality) or damaged (partial mortality) colony, respectively. Among the elements within the transition matrix, $C_{ud,ud}$ and $C_{d,d}$ represent the probability of an undamaged or damaged colony to survive and remain within its original category; $C_{d,ud}$ represents the probability of an undamaged colony to suffer partial mortality and

therefore change its state; and $C_{ud,d}$ represents the probability of a damaged colony to transition to the undamaged state by regenerating the lost tissue. The transition probabilities were based on the fate of all colonies, including those that died. The matrix population models do not include death as a state because death is an absorbing state (i.e. once entered, it cannot be left). Four matrices were constructed, one for each site and time period. The site-specific matrices were used to calculate the mean matrix, which was post-multiplied by the initial population vector to project population abundance over time and determine the time it would take for the populations to reach a level of 25% of the original population size (Mercado-Molina et al. 2015a). Various levels of partial mortality were tested (0, 25, 50, 75, and 100%). The model was not aimed at projecting the population dynamics of *A. cervicornis* under current or future population conditions, but simply to test whether increasing the proportion of colonies with partial mortality has a negative impact on local population growth. The package popbio (Stubben & Milligan 2007) was run in R (R Development Core Team 2013) to perform all demographics analyses.

$$\begin{pmatrix} C_{ud} \\ C_d \end{pmatrix}_{t+1} = \begin{pmatrix} C_{ud,ud} & C_{ud,d} \\ C_{d,ud} & C_{d,d} \end{pmatrix} \times \begin{pmatrix} C_{ud} \\ C_d \end{pmatrix}_t \quad (1)$$

RESULTS

Partial tissue mortality and colony size and growth

After adjusting the significance level, we did not find evidence to argue that the amount of tissue loss is related to colony size (Table 2).

Coral relative growth rates tended to decrease as the percent partial mortality increased (Fig. 1). Except for PAL during the first year of the study, the relationship was relatively strong, explaining over 60% of the variation. The low correlation value (−0.30) observed at PAL during 2011−2012 was related to 2 extreme values. When running the analysis without these 2 outliers, the r value increased to −0.48.

A threshold between the percent partial mortality and the probability of increasing in size was evident (Fig. 1). It showed that surpassing 20% of dead tissue limited colony growth. Results of the odds ratio analysis confirmed that colonies with ≤20% of partial mortality were more likely to grow than the colonies that had lost over 20% of their tissue (Fig. 2; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m597p147_supp.pdf).

Table 2. Results of the correlation analyses performed to explore the relationship between the percent partial mortality and colony size of *Acropora cervicornis*, considering total live tissue (TLT) and whole colony size (live + dead tissues). Significance level after Bonferroni correction = 0.008. CLP: Canal Luis Peña reef, PAL: Palomino reef

Year	CLP		PAL	
	r	p	r	p
TLT only				
2011	−0.017	0.85	0.168	0.09
2012	−0.301	0.01	−0.161	0.23
2013	−0.292	0.03	−0.272	0.09
Whole colony				
2011	0.19	0.04	0.19	0.04
2012	0.06	0.62	0.17	0.22
2013	0.23	0.09	0.29	0.07

Partial tissue mortality and size-specific growth

The adverse effect of tissue loss on the growth of coral colonies was consistent among the different size classes (Table S2). Regardless of the size class, the mean growth rate of colonies with >20% partial mortality was negative, whereas for colonies that had lost ≤20% of their tissue, it was positive. Indeed, the likelihood of a colony with >20% partial mortality to exhibit positive growth did not surpass 10% (Fig. 2), while colonies with ≤20% of partial mortality showed a probability between 74% (large class) and 93% (medium class) at CLP and between 82% (medium class) and 90% (small class) at PAL (Fig. 2).
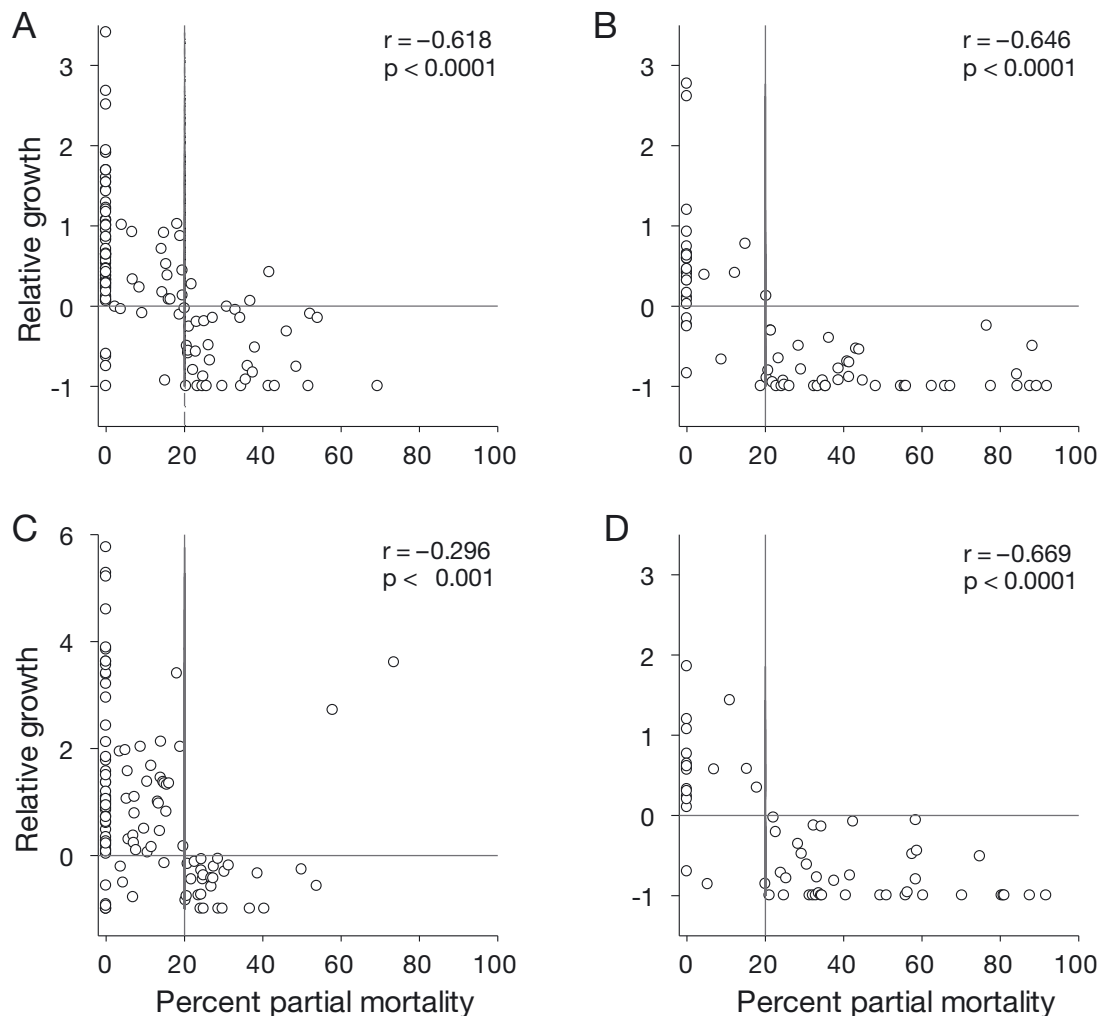

Fig. 1. Relationship between percent partial mortality and relative growth of *Acropora cervicornis*. Relative growth was calculated as [(Final size − Initial size) / Initial size] × 100. The horizontal line represents the value 0, where no change in size was observed. Values above 0 indicate positive growth, whereas values below indicate regression in size. The vertical line represents the 20% threshold level at which coral growth is compromised. Note that the scales of the *y*-axes vary. (A) Canal Luis Peña: 2011−2012; (B) Canal Luis Peña: 2012−2013; (C) Palomino: 2011−2012; (D) Palomino: 2012−2013
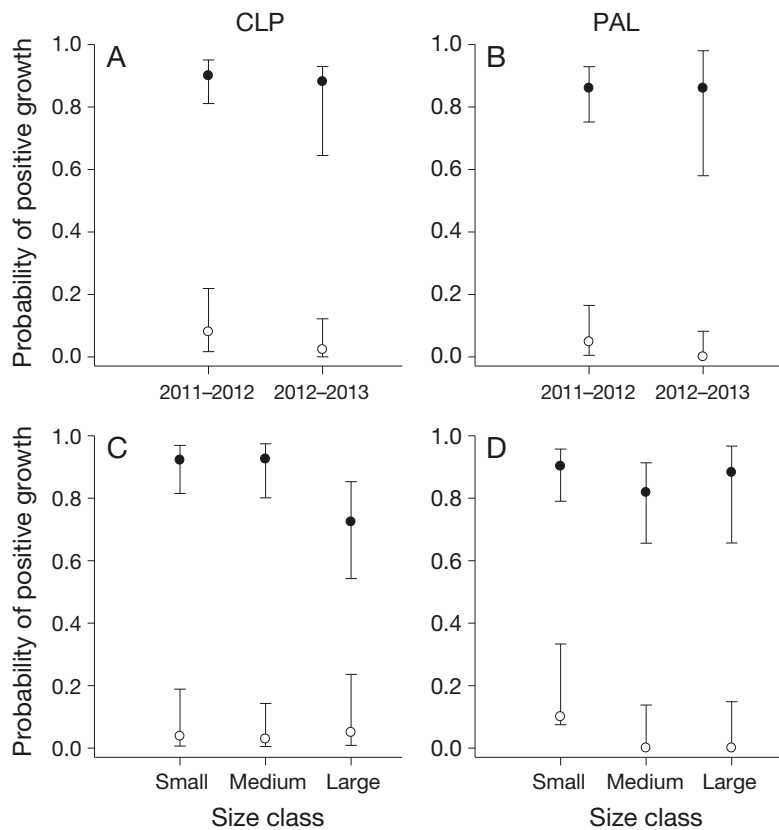
Fig. 2. (A,B) Temporal comparison of the probability of increasing in size between colonies of *Acropora cervicornis* affected by different levels of partial mortality. (C,D) Comparison at the size-specific level. (A,C) Canal Luis Peña (CLP); (B,D) Palomino (PAL). Closed circles = colonies with partial mortality ≤20%. Open circles = colonies with partial mortality >20%. Error bars represent 95% CI. Because no differences in growth rates were found between colonies with 0% partial mortality and colonies with 0% < x ≤ 20%, the 2 groups were pooled for the analyses. For size-specific analyses, temporal data were pooled within sites due to the small number of colonies with >20% of tissue loss that survived to the end of the study

Partial tissue mortality and survival

Results of the logistic regression analysis indicated that at CLP, the probability of colony survival decreased as the amount of tissue loss increased (Table S3). However, the survival pattern was not replicated at PAL, where the negative relationship between the variables was significant during 2012–2013 but not in 2011–2012 (Table S3). Nevertheless, as with the relative growth data, a threshold between the percent partial mortality and the probability of survival is unmistakable (Fig. 3). Results of the odds ratio analysis indicated that colonies with ≤20% partial mortality were between 6.5 and 28.7 times more likely to survive than colonies with >20% tissue loss (Fig. 4, Table S1).

When considering only colonies with >20% partial mortality, the relationship between survival and the amount of tissue loss was variable. For instance, no significant relationship was found during the first year of the study; however, between 2012 and 2013, colony survival tended to decrease as the percent partial mortality increased (Table S3). These results suggest that the probability of survival is not directly related to the amount of tissue that a colony has lost.

Partial tissue mortality and size-specific survival

Our data also demonstrated that, irrespective of colony size, colonies with partial mortality >20% were less likely to survive than those colonies with ≤20% tissue loss (Fig. 4). We also found that although the probability of mortality decreased as colony size (in TLT) increased, the differences in survival among size classes were not significant (CLP: χ^2 = 5.75, df = 2, p = 0.06; PAL: χ^2= 1.11; df = 2, p = 0.58). Similarly, the survival of colonies with 0–20% partial mortality was not associated with size classes (CLP: χ^2 = 1.26, df = 2, p = 0.53; PAL: χ^2 = 0.681; df = 2, p = 0.711).

Colony fate: partial tissue mortality vs. colony size

Log-linear analyses indicated that condition (0–20% or >20% partial mortality) rather than size was a better predictor of colony fate. This statement holds true for both time periods and sites. For instance, none of the models that take into consideration the effect of size on colony relative growth and survival was significant, contrary to the models that considered the effects of condition (Tables S4 & S5). The effect of the interactions between size and condition were non-significant.

Partial tissue mortality and population dynamics

Increasing the number of colonies with partial mortality by a proportion of 25% during each time step in the simulation caused the simulated populations to
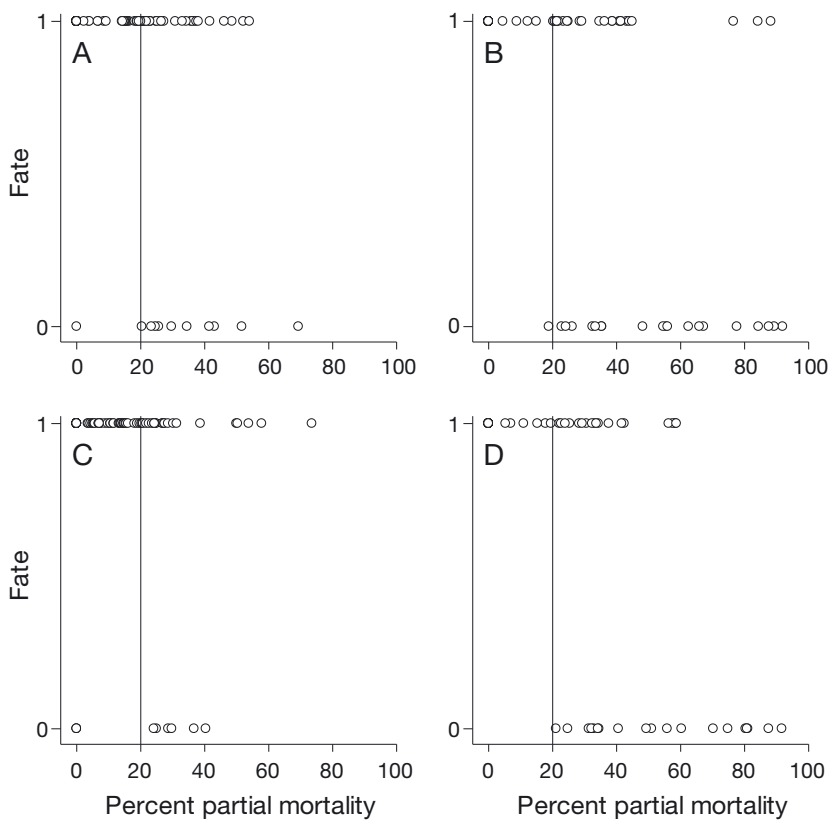
Fig. 3. Relationship between percent partial mortality and colony survival of *Acropora cervicornis*. Fate 0 or 1 refers to a colony that died or survived, respectively. The vertical line represents the 20% threshold level at which the probability of colony survival is compromised. (A) Canal Luis Peña: 2011–2012; (B) Canal Luis Peña: 2012–2013; (C) Palomino: 2011–2012; (D) Palomino: 2012–2013

reach a level of 25% of the initial population size 3 to 4 yr sooner (Fig. 5).

DISCUSSION

The functioning of Caribbean coral reefs is dependent on the population performance of major ecosystem engineers, including the threatened coral *Acropora cervicornis*. Efforts to promote the population recovery of this species need to be grounded in the understanding of the demographic processes that drive changes in population size. Because population growth is linked to the rates of colony growth, survival, and reproduction, it is critical to understand the processes that influence such vital rates. The present study is the first to directly evaluate the demographic and population response of *A. cervicornis* to varying levels of tissue loss, a common phenomenon in

coral reef ecosystems that needs to be better integrated into studies of coral demography.

Contrary to the results presented here, Lirman et al. (2010) found that the growth rates of nursery-reared *A. cervicornis* colonies increased when colonies were subject to artificial partial mortality. Sánchez & Lasker (2004), who also found similar results for the octocoral *Pseudopterogorgia bipinnata*, considered this response as an overcompensation process to the partial loss of tissues. The contrasting results between our study and the works by Sánchez & Lasker (2004) and Lirman et al. (2010) can be explained by the way in which partial mortality is defined. In the case of Sánchez & Lasker (2004) and Lirman et al. (2010), partial tissue loss was produced by the physical detachment of colony branches (i.e. fragmentation), whereas for our study, partial mortality was considered as the death of coral tissue due to natural causes and without the physical separation of the dead portion (e.g. skeleton). Fragmentation and dead tissue are often used without discrimination when referring to partial mortality in corals. However, because it is likely that colonies may show different demographic responses to the 2 forms of tissue loss, it is important to distinguish between fragmentation and the death of the tissue when analyzing the effects of partial mortality on coral demography.

Rapid growth rates after fragmentation could be an adaptive response of *A. cervicornis* to the process itself, given that branch fragmentation is the most important reproductive strategy in this coral (Tunnicliffe 1981). Sánchez & Lasker (2004) suggested that faster growth rates of branching corals after fragmentation are due to the redirection of energy towards the affected area to induce the apical growth of 'dormant' branches. *A. cervicornis*, on the other hand, responds differently to non-fragmentation-derived tissue loss. For instance, and against expectations, colonies did not regenerate the lost tissue; instead, they formed a calcified bulge (or neoplasia, Bak 1983) at the interface between live and dead tissues. There is evidence that some coral species in the Pacific are also unable to regenerate the portion of
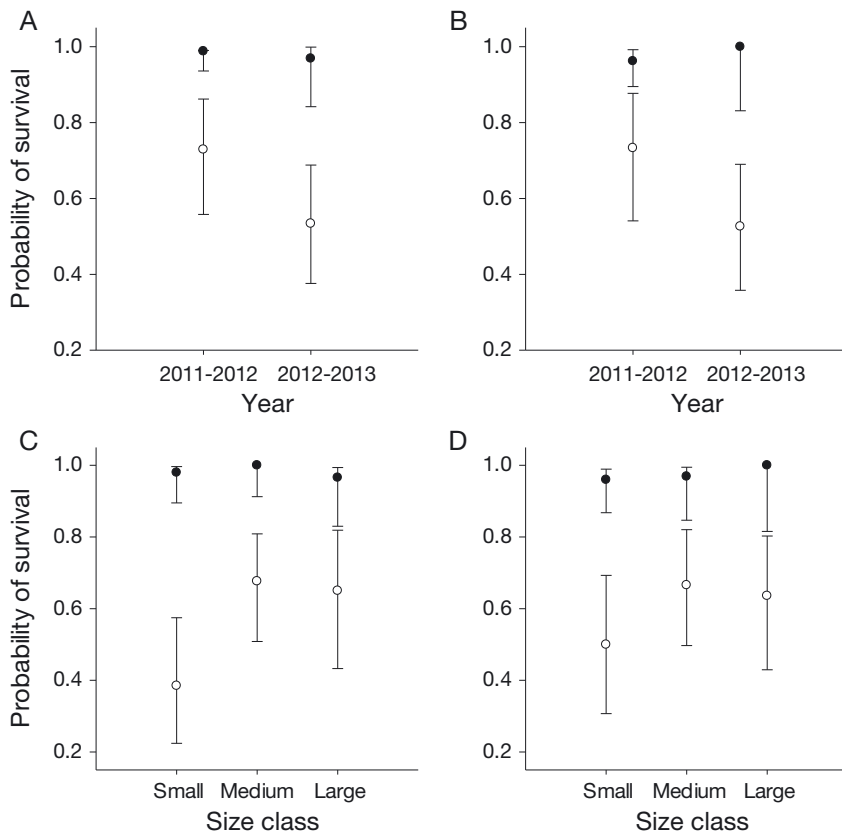
Fig. 4. (A,B) Temporal comparison of the probability of survival between colonies of *Acropora cervicornis* affected by different levels of partial mortality. (C,D) Comparison at the size-specific level. Canal Luis Peña (A and C); Palomino (B and D). Other details as in Fig. 2

tissue that has been lost (Pisapia et al. 2016). These results challenge the perceived notion that all modular organisms can recover from partial mortality (see arguments by Sánchez & Lasker 2004, Pisapia et al. 2016).

The causal factors driving tissue mortality at the studied locations are unknown. We do know, however, that extreme stressor events such as thermal anomalies, storms, predator/disease outbreaks, or sediment/nutrient loads did not occur during the study period. It is possible that other processes that are not readily noticeable and that are not necessarily considered as major stressors triggered the death of tissues. For instance, the number of colonies suffering partial mortality was higher at the end of 2012. The year 2012 was a time period characterized by higher levels of solar radiation (SR) in Puerto Rico (Puerto Rico Agricultural Water Management, https://pragwater.com). There is evidence suggesting that exposure to high SR can lead to colony mortality, induce physiological stress, and slow down the growth of *A. cervicornis* (Lesser & Farrell 2004, Torres et al.
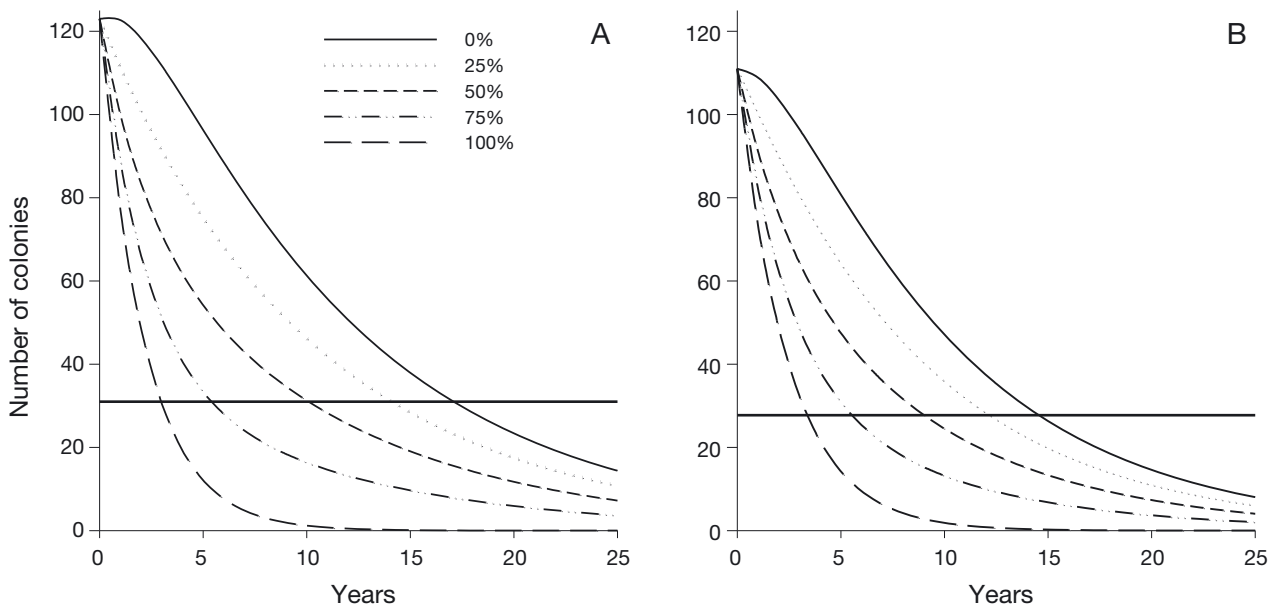

Fig. 5. Simulated population trajectories under scenarios in which the proportion of colonies suffering >20% partial mortality varied (0, 25, 50, 75, 100%). Percentages represent the proportion of colonies within the populations that had lost >20% of the living tissue. The horizontal line represents 25% of the initial population size. (A) Canal Luis Peña; (B) Palomino

2007). It is important to note, however, that we lack *in situ* SR data (e.g. at the site-specific level); therefore, the possible negative effect of SR on *A. cervicornis* demographics at the studied sites remains a hypothesis that needs to be tested.

Determining the causes of mortality is essential to better understand the relationship between tissue loss and coral demographics. For example, partial mortality derived from a disease (e.g. white band disease) or Caribbean ciliate infection would compromise the immune system; consequently, the likelihood of total recovery may be lower than the recovery from mechanically derived (e.g. abrasion) or predation injuries that do not necessarily compromise the immune system. We are not aware of any study explicitly comparing the demographic and population response of corals to different causes of partial mortality. We would expect, however, that for *A. cervicornis* the negative association between the amount of tissue lost and colony fate will persist independently of the causes (see Shaver et al. 2017). In the case that differential responses do exist with respect to sources of mortality, we hypothesized that the threshold in which the amount of tissue loss imperils colony fate would be higher for mechanically derived damage. This is because, as mentioned above, the immune system of mechanically damaged corals should not be as compromised as it would be in the case of coral colonies affected by biological agents.

A. cervicornis failed to recover the lost tissue irrespective of colony size. Likewise, Ruiz-Diaz et al. (2016a) found that colony size was not a good predictor of the capacity of lesion recovery in the octocoral *Gorgonia ventalina*. We also observed that lack of tissue regeneration was sustained over time, which is in accordance with Shaver et al. (2017), who noted that colonies of *A. cervicornis* failed to recover tissues predated by the corallivorous snail *Coralliophila abbreviata*. The regeneration of a lesion in corals appears to be linked to the ratio of live to dead tissue, likely because the energetic resources that can be devoted to tissue recovery increase as the area of healthy tissues surrounding the dead area increases (Meesters et al. 1997b, Oren et al. 1997, Ruiz-Diaz et al. 2016a,b). In *A. cervicornis*, however, the tubular nature of the branches, as well as their spatial arrangement within the colony (branches are not in direct contact with each other), limits the amount of live tissue from which energy can be derived locally for the regeneration process. At the same time, the disruption of tissue connectivity by patches of dead tissues may be impeding energy transfer between healthy areas.

Neoplasia, which may serve as a physical barrier for repelling the spread of colonizing organisms, is energetically costly, with a significant adverse effect on coral growth (Bak 1983). The overall lower growth rates of colonies with partial mortality (>20%) could also be attributed to competition against epibionts, particularly algae (e.g. turf and *Ramicrusta* spp.) and sponges (e.g. *Desmapsama anchorata*) that colonized the exposed skeleton of many colonies. Lack of regeneration may not only suppress coral growth, but may also increase the probability of coral death (Meesters et al. 1997b, Hall 2001). Colonies with high partial mortality (>20%) were more likely to die than colonies with partial mortality below 20%. This result concurs with Shaver et al. (2017), who also observed that colonies of *A. cervicornis* suffering tissue loss due to predation by *C. abbreviata* were 5 times more likely to suffer death than undamaged colonies, even when the predator was removed. Failure to recover the lost tissue can result in higher algae colonization rates of the exposed skeleton (van Woesik 1998, Shaver et al. 2017). *A. cervicornis* is a poor competitor (at least against algae and sponges), as it invests more energy in growth than in defense or maintenance (Palmer et al. 2010, Darling et al. 2012). The poor competitive ability of *A. cervicornis* together with fewer energetic resources to invest in producing new tissues may allow superior competitors to eventually overgrow and kill the colony.

Colony condition rather than colony size was a better predictor of *A. cervicornis* survival and growth. This result was surprising, as is it generally accepted that for modular organisms, size largely determines the schedule of life-history transitions (Jackson & Hughes 1985). Our finding is in accord with Cumming (2002), who also found that the loss of tissue rather than the size of a colony was a better predictor of colony fate for pocilloporid corals and acroporid corals with small and compact branches. However, Cumming (2002) found that the fate of acroporid corals with arborescent morphologies, similar to that of *A. cervicornis*, were unaffected by the loss of tissue. The differential response to partial mortality between *A. cervicornis* and the arborescent acroporids of the Pacific could be attributed to species-specific life history traits or to different causes of tissue loss. It is important to note that the amount of tissue lost by the species studied by Cumming (2002) was mostly small (≤5%), which is consistent with our

finding that the demographic fate of *A. cervicornis* is only compromised once the proportion of the tissue loss exceeded 20% of the total colony size.

Our study reveals that losing >20% of living tissue is a threshold at which the growth and survival of *A. cervicornis* are significantly compromised. This threshold was consistent among size classes, which supports our finding that colony condition rather than colony size is a better predictor of colony fate. Lower probability of survival and growth in colonies with >20% partial tissue loss, irrespective of colony size, indicates that tissue loss in large colonies may be as critical as for small colonies. It is not clear why 20% of tissue loss is a key turning point for colony fate. However, it is known that the interception rate of food particles from the water column as well as the area exposed to sunlight increases with surface area (Soong & Chen 2003). Therefore, it could be hypothesized that losing >20% of the total amount of tissue reduces colony size to a level at which energy acquisition is not sufficient to satisfy the energetic and physiological demands of the whole colony. Size may become important, however, in the absence of partial mortality. For instance, Lirman et al. (2014), Mercado-Molina et al. (2015b, 2016), and Goergen & Gilliam (2018) found that mean growth rates (i.e. absolute change in size) of undamaged *A. cervicornis* colonies increase with size. A plausible explanation for this relationship is that larger colonies are better at resource acquisition, i.e. light and food particles in the water column (Soong & Chen 2003, Garrison & Ward 2008).

The relationship between partial mortality and the demographic performance of *A. cervicornis* could be confounded if a relationship exists between the amount of tissue lost and the rates at which it is lost. To test this possibility, we conducted a correlation analysis and found that this relationship is neither strong nor significant (r = 0.027; p = 0.782). It could also be argued that the negative association between partial mortality and the growth and survival of the coral is only true if there are no major acute disturbances, or if measurements were not taken within a period of continuous stress. Although common coral stressors (e.g. thermal anomalies, storms, predator/ disease outbreaks) did not occur during the study period, we understand that such an argument is not necessarily true. Mercado-Molina et al. (2015a) reported survival rates varying between 88% (CLP) and 89% (PAL) during the first year of the study (2011–2012). These survival rates are among the highest reported for *A. cervicornis*. By the second year (2012–2013), however, survival rates declined to 60% (CLP) and 75% (PAL). Because periods of low survivorship are indicative of stressful environmental or demographic conditions (Ricklefs & Wikelski 2002), demographically speaking our study can be divided into a good (2011–2012) and a bad (2012–2013) year, or a good (PAL) and a bad (CLP) site. The fact that the relationship between the demographic performance of *A. cervicornis* and colony condition persisted both in space and time led us to conclude that undamaged colonies of *A. cervicornis* will grow faster and survive better than damaged colonies irrespective of the prevailing environmental conditions.

Although our data suggest that losing >20% of live tissue increases the probability of death, it is important to note that death is not necessarily the end point of partial mortality. As such, we are not arguing that the loss of tissues is driving colony mortality (or vice versa). Indeed, it is not clear whether colony death is a consequence of several cumulative tissue die-back events, or whether partial tissue mortality is the visible indication of an irreversible death process. In the field, we have observed the rapid death of apparently healthy (no partial mortality) colonies, but these events are rare. More commonly, we note that mortality is caused by several partial (and presumably independent) mortality events.

The paucity of knowledge about the processes affecting the population dynamics of *A. cervicornis* is regarded as one of the major limitations for the development of species-specific conservation and management plans (Williams et al. 2006, NMFS 2015). In contrast to results reported by Roth et al. (2010), we found that the negative relationship between partial mortality and colony fate transcended to the population level. Simulations showed that increasing the proportion of colonies with >20% partial mortality reduced the time in which the populations can reach a level of 25% of the initial population size by an average of 3–4 yr. This period may be critical for the population persistence of *A. cervicornis*, which is very susceptible to low/moderate variations in environmental conditions (Williams et al. 2006) and can suffer drastic declines in population growth rates very rapidly (Mercado-Molina et al. 2015a). The assessment of partial mortality becomes particularly imperative because size (based on live tissue) will not act as a 'refuge' of colony demographic performance when a substantial amount of tissue has been lost (i.e. >20% of the total colony size). Therefore, condition (partial morality vs. non-partial mortality) of a colony must be taken into consideration, perhaps analogous to the importance of coral diseases, when evaluating the possible trajecto-

ries of *A. cervicornis* populations. Populations varying in the number of colonies suffering partial mortality will show different dynamics, and therefore different management strategies may be required. Those populations with a high proportion of damaged colonies (i.e. >20% of tissue loss) should be prioritized in conservation management.

From the perspective of active restoration, the extirpation of the dead portion of the colony, followed by the outplanting of the undamaged fragment to the reef substrate could be a strategy to be considered. Outplanting coral fragments using low-cost techniques such as nails and cable ties is an efficient way to propagate the species (Hollarsmith et al. 2012, Mercado-Molina et al. 2015b, Goergen & Gilliam 2018). Reducing the amount of dead tissue should result in higher survival and growth rates. The proposed approach would also increase the population size, as affected colonies can be split into several fragments. Having a higher number of healthy colonies would increase the chances of population persistence of key Caribbean reef species.

In conclusion, this study provides evidence to argue that the demographic performance of *A. cervicornis* is negatively impacted if a colony loses >20% of its tissue. However, as stated above, we are not arguing that partial mortality is necessarily the causal factor for the diminished demographic performance in *A. cervicornis*. What our study shows is that independent of causes leading to tissue mortality, (1) if there is >20% tissue loss, the probability of growing and surviving are significantly compromised, (2) the negative association between partial mortality and the demographic performance of *A. cervicornis* was consistent in space and time, and (3) partial mortality rather than colony size is a better predictor of colony fate. Our conclusions must be interpreted within the context of a declining population (Mercado-Molina et al. 2015a) as observed in this study. Partial mortality may have less of an impact on demographics within the context of a growing population or a more resilient coral species.

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