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# Demography of the threatened coral Acropora cervicornis: implications for its management and conservation

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REPORT



# Demography of the threatened coral *Acropora cervicornis*: implications for its management and conservation

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Abstract Populations of Acropora cervicornis have collapsed throughout the Caribbean. This situation has prompted the initiation of many restoration efforts; yet, there are insufficient demographic data and analyses to effectively guide these initiatives. In this study we assessed the spatiotemporal variability of A. cervicornis vital rates. We also developed a population matrix model to (1) evaluate the risk of population extinction, (2) estimate population growth rates ( $\lambda$ ) considering different rates of colony fragmentation and fragment survival, (3) determine the demographic transition(s) that contribute the most to spatiotemporal differences in  $\lambda s$ , and (4) analyze the effectiveness of outplanting coral fragments of different sizes. The model was parameterized by following the fate of 300 colonies from 2011 to 2013 at two localities in Puerto Rico. Demographic transitions varied spatiotemporally, with a significant interaction between location and time period on colony fate. Spatiotemporal variations in  $\lambda$  were also observed. During the first year, populations exhibited  $\lambda s$ 

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below equilibrium (0.918 and 0.948), followed by a dramatic decline at both sites (0.535 and 0.709) during the second year. The lower  $\lambda$ s were caused by a decrease in the probability of stasis of large-sized colonies coupled with lack of sexual recruits and a meager contribution of asexual recruitment. Spatial variations in  $\lambda$ s were largely due to differences in the probability of medium-sized colonies advancing to the largest size class. The viability analysis forecasts that the populations will reach quasi-extinction levels of 25 % of the initial population size in <16 yrs. Numerical simulations indicate that outplanting fragments  $\geq$ 250 cm in total linear length (TLL) would result in a higher asymptotic population size than outplanting smaller fragments. We argue, however, that transplanting colonies  $\leq 100$  cm TLL will be a better management strategy because they can be produced faster and in higher numbers at coral nurseries.

**Keywords** Acropora cervicornis · Coral demography · Population viability analysis · Reef restoration

# Introduction

Coral reefs are among the most threatened ecosystems on earth. The structural and ecological integrity of approximately 60 % of coral reefs has been severely impacted by anthropogenic activities (e.g., water pollution), biological factors (e.g., diseases), and physical disturbances (e.g., bleaching events associated with elevated seawater temperature); by 2030, 90 % of reefs are expected to be compromised (Burke et al. 2011). Today, approximately half of the acroporid species, which are among the major reefbuilding corals worldwide, are listed as threatened by the International Union for Conservation of Nature (Carpenter et al. 2008). This list includes *Acropora cervicornis*, one of the most depleted species in the wider Caribbean. Populations of this coral have been decreasing dramatically (up to 97 % decline in abundance) throughout its geographical range since the late 1970s (Aronson and Precht 2001; Miller et al. 2002), and currently, it is considered a threatened species under the US Endangered Species Act (NMFS 2006). This is of concern not only because *A. cervicornis* is a major contributor to reef accretion but also because its branching morphology serves as nursery ground for multiple vertebrate and invertebrate species, thereby promoting coral reef biodiversity (Precht et al. 2002; Quinn and Kojis 2006).

Due to the decline of A. cervicornis and its ecological importance, efforts have been undertaken to revert its population decrease. In the USA and its territories, critical habitats have been protected, restoration programs have been launched, and research and monitoring programs have been initiated. Surprisingly, none of these conservation and restoration efforts are based on solid quantitative demographic analyses (Williams et al. 2006). The few population studies available have focused on estimating rates of colony growth, survival, and recruitment (Tunnicliffe 1981; Knowlton et al. 1990), but none have evaluated how variation in these demographic parameters affects local population growth ( $\lambda$ ). This hinders the effectiveness of conservation efforts because initiatives intended to improve the persistence of a population may fail to target those vital rates that have the greatest contribution to  $\lambda$ . Conservation management strategies also depend on quantitative predictions that can only be achieved by employing demographic analysis and modeling. Indeed, the lack of such analyses has been identified as an area of particular concern by the NOAA Acropora Biological Review Team (ABRT 2005) and the National Marine Fisheries Service (NMFS 2015).

Among the major goals of conservation and management efforts are first to arrest the decline of threatened populations and then to increase the rate of population growth until a "safe" population size is reached. The rate at which a population grows or declines is inevitably linked to its individuals' survival, growth, and reproduction. Therefore, effective conservation initiatives require knowledge of how variations in vital rates relate to variations in population growth. In this respect, population matrix models have become an important tool in conservation (Caswell 2001). However, relatively few scientists have applied population matrix models to answer specific management questions focusing on coral conservation (but see Linares et al. 2008; Vardi et al. 2012). Multiple factors make corals a complex subject for demographic studies. In many instances, corals are physically and practically hard to measure. Branching corals, for example, can form thickets that make it difficult to identify the physical boundaries of individual colonies. In fact, the literature focusing on the relationship between scleractinian coral vital rates and their population growth rates is scarce.

In this study, we examined the demography of A. cervicornis at two localities in northeastern Puerto Rico from 2011 to 2013. The aims were to measure the spatiotemporal variability in vital rates and to use the demographic data to perform a population viability analysis. For the viability analysis, a size-based population matrix model was constructed to (1) determine whether the studied populations were stable ( $\lambda = 1$ ), increasing ( $\lambda > 1$ ), or decreasing ( $\lambda < 1$ ), (2) estimate quasi-extinction probabilities, (3) identify the demographic transition(s) that accounted for the observed spatiotemporal differences in  $\lambda$ by performing life table response analyses, (4) estimate  $\lambda$ under different rates of colony fragmentation and fragment survival, and (5) analyze the efficacy of different outplanting scenarios through numerical simulations. The numerical simulations were performed to assess (not predict) possible population trajectories of A. cervicornis for given conditions (Caswell 2001). This study is the first to use demographic modeling to better understand the population dynamics of the threatened coral A. cervicornis while evaluating the effect of different transplanting scenarios on population growth.

## Materials and methods

#### **Demographic data**

We surveyed suitable habitats within an area covering approximately 150 km<sup>2</sup> along the northeast coast of Puerto Rico to identify localities with a relatively high abundance of A. cervicornis colonies. The surveyed area encompassed coral reefs within La Cordillera Nature Reserve (LCNR), the Canal Luis Peña Nature Reserve (CLPNR), and the reef areas around the west side of the island of Culebra, zones where this coral has historically been prevalent (Wirt et al. 2015). We found very few extant populations and only two localities-Canal Luis Peña (CLP) and Palomino (PAL)with an adequate number of discernible colonies (no thickets) to study the demography of A. cervicornis. CLP (18°18'14"N, 65°20'15"W) is located within CLPNR on the island municipality of Culebra, approximately 30 km east of the Puerto Rico Island. PAL (18°21'3"N, 65°33'58"W) is located within LCNR, 6 km from the coastal municipality of Fajardo on the Puerto Rico mainland. The reef structure at both sites has a northeast orientation and is exposed to the easterly trade winds and long-period swells during the winter. Consequently, both sites are frequently exposed to moderate to strong wave action. Water quality is good (i.e., low turbidity, no terrigenous sediments) as none of the sites are directly

influenced by river-derived sediment, nutrient discharges, or coastal development. At the two sites, *A. cervicornis* colonizes a zone that was previously dominated by *A. palmata* but is currently dominated by octocorals and characterized by a low topographic relief. As mentioned above, the studied populations are not thickets as defined by the NMFS (2015), but rather have moderate densities of easily identified individual colonies distributed throughout the area. In this sense, the study can be understood as describing the demography of two populations in the process of forming (or not) a thicket. As *A. cervicornis* thickets are currently rare, these two populations are likely to be representative of the current state of populations of this coral within its range.

One hundred and fifty colonies were tagged at each site, at a depth of 3-5 m using numbered tags fixed with masonry nails to non-living substrate adjacent to the colony. Their survival, growth, and branch fragmentation were measured annually from 2011 to 2013. Colonies were considered dead if no live tissue was distinguishable or if the colony disappeared during the study period. Growth rates were estimated by comparing changes in total linear length (TLL) between surveys. Initial and final colony sizes were calculated as the sum of the lengths of all live portions of branches (Knowlton et al. 1990). To do this, a set of photographs was taken in situ from different angles with a scale by side (Mercado-Molina et al. 2014), which allowed us to measure all branches fully extended. This approach is an accurate estimate of the actual colony size of A. cervicornis as demonstrated by Mercado-Molina et al. (2014). The free software CPCe version 4.1 (Kohler and Gill 2006) was used to make all measurements.

#### **Recruitment and natural fragmentation**

At the two study sites, we randomly established thirty  $1 \text{ m}^2$ permanent quadrats along a 60 m<sup>2</sup> belt transect to assess sexual and asexual recruitment rates. All quadrats were marked with nails to facilitate relocation in subsequent surveys. Following Tunnicliffe (1981) and Knowlton et al. (1990), we defined sexual recruitment as a small crust showing a round or ellipsoidal morphology and measuring less than 10 cm in height with a vertical orientation. Asexual recruits were differentiated from sexual recruits by their orientation (horizontal vs. vertical), signs of obvious fragmentation, and size (TLL  $\geq 10$  cm) (Tunnicliffe 1981; Knowlton et al. 1990; but see Williams and Miller 2006). Rates of natural fragmentation were also estimated in situ by counting the number of broken branches and/or scars within a given colony and by comparing images between surveys to determine the number of branches that were lost (Tunnicliffe 1981; Mercado-Molina et al. 2015).

Visual inspections of the studied areas were performed every 3–4 months to evaluate the overall health of the marked colonies (looking for signs of disease or outbreaks of coral-feeding snails).

#### **Demographic analysis**

A size-based matrix population model was constructed to analyze and simulate the dynamics of *A. cervicornis* at the study sites (Eq. 1).

$$\begin{pmatrix} s \\ m \\ l \end{pmatrix}_{t+1} = \begin{pmatrix} S_{ss} + (Pf)(\delta) & R_{sm} + (Pf)(\delta) & R_{sl} + (Pf)(\delta) \\ G_{ms} & S_{mm} & R_{ml} + (Pf)(\delta) \\ G_{ls} & G_{lm} & S_{ll} \end{pmatrix} \times \begin{pmatrix} s \\ m \\ l \end{pmatrix}_{t}$$
(1)

The number of small-sized colonies [s] ( $\leq 100$  cm TLL), medium-sized colonies [m] (101-250 cm TLL), and largesized colonies [l] (>250 cm TLL) at time t + 1 (one year into the future) equals the current number of colonies in each of the three size classes multiplied by a  $3 \times 3$  matrix of the transition probabilities among the size classes. The diagonal elements in the matrix are the probabilities of colonies surviving and remaining in their current size class. In the case of small-sized colonies, this value is given by the sum of two terms: (1) the probability of surviving and not growing to the next size class (stasis,  $S_{ss}$ ) and (2) the product  $(Pf)(\delta)$ , which represents the probability of a small-sized colonies producing another small-sized colonies by means of branch fragmentation (Pf), multiplied by the probability of the fragment surviving one year ( $\delta$ ). For each size class, the probability of colony fragmentation (Pf) was estimated as the number of colonies that fragmented divided by the total number of colonies. Annual fragment survival rates of 24 % at CLP and 32 % at PAL were estimated by following the fate of 100 loose fragments at each site between February 2012 and August 2013 (Mercado-Molina et al. 2014). The supradiagonal elements represent the contribution of the large-sized colonies classes to smaller ones by regressing in size due to partial mortality  $(R_{\rm sm})$ . medium-sized colonies and large-sized colonies also contribute to the small-sized colonies size class by branch fragmentation as described above. Lastly, the subdiagonal elements represent the probabilities of a colony growing to the next size class  $(G_{ms})$ . Sexual recruitment was not included in the transition matrix because no larval-derived recruits were observed during this study. With respect to asexual reproduction, we planned for two independent estimates of asexual recruitment (branch fragmentation and the appearance of colony

fragments in the recruitment plots) because we did not know a priori which would provide better data. Given that no asexual recruits were observed in these plots, we only use rate of branch fragmentation in the model. The transition probabilities were estimated by constructing transition frequency tables (Caswell 2001) for each locality and census period (2011–2012 and 2012–2013; Electronic Supplementary Materials, ESM, Table 1). The three size classes were chosen to incorporate size-specific patterns of vital transition rates while maintaining a sample size greater than 25 colonies for each size category.

Four transition matrices were generated, one for each site and census period. To determine whether the transition probabilities in these four matrices were independent of time and location, log-linear models were applied to a fourway contingency table. Following Caswell (2001), fate (F) was set as the response variable and time (T) and location (L) were set as the explanatory factors, conditional upon initial colony size (S). The model that best fit the data was determined by means of the scaled Akaike information criteria (AIC), calculated for log-linear models as AIC =  $G^2 - 2(df)$  (Caswell 2001), where  $G^2$  is the goodness-of-fit log-likelihood ratio statistic obtained from comparing the model with the saturated model and df is the degrees of freedom of the test. Log-linear models were also applied to a three-way contingency table developed for each of the size classes to examine the effect of time and location on the fate of colonies within each size class. 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 each matrix, the dominant eigenvalue was calculated to obtain the asymptotic finite rate of increase in the population ( $\lambda$ ) (Caswell 2001). Transition matrices were subject to a bootstrapping re-sampling procedure (10,000 simulations) to obtain the 95 % confidence intervals for  $\lambda$ . To determine the demographic transition(s) that accounted for most of the observed spatio-temporal differences in  $\lambda$ , a life table response experiment (LTRE) analysis was performed rather than an elasticity analysis. LTRE is a retrospective analysis that provides information on how much variation in a particular life cycle transition actually contributed to the observed differences in  $\lambda$  between treatments (years and localities in this study). Elasticity, on the other hand, is a prospective (predictive) analysis that looks at how  $\lambda$  could respond when a particular life cycle transition is perturbed (Caswell 2001).

Environmental stochasticity (Morris and Doak 2002) was modeled by randomly selecting one of the two transition matrices constructed for the time periods 2011–2012 and 2012–2013. A total of 50,000 iterations (Stubben and Milligan 2007) were performed in which the selected matrix was post-multiplied by the initial population vector to obtain the stochastic lambda ( $\lambda_s$ ). During the iterations, transition matrices had equal probability of being selected. These stochastic trajectories were used to (1) estimate the probability of populations reaching quasi-extinction thresholds of 10, 15, 20, and 25 % of the initial population size, (2) estimate  $\lambda s$  for probabilities of colony fragmentation and fragment survival varying between 0.10 and 1.0, and (3) analyze the effectiveness of fragment transplantation as a management tool to aid in the recovery of A. cervicornis populations. In the latter case, we modified Eq. 1 by adding a recruitment vector as expressed in Eq. 2, where the elements  $R_s$ ,  $R_m$ , and  $R_l$  represent the numbers of small-sized colonies, medium-sized colonies and largesized colonies to be transplanted, respectively. Equation 2 is an open population model, in which coral transplants come from an external source (e.g., coral nurseries). To determine the most effective number and size of fragments to maintain a population equal or larger than the initial population size, Eq. 2 was projected for 20 yrs considering the outplanting of 25, 50, 75, or 100 small-sized colonies, medium-sized colonies, or large fragments per year.

$$\begin{pmatrix} s \\ m \\ l \end{pmatrix}_{t+1} = \begin{pmatrix} S_{ss} + (Pf)(\delta) & R_{sm} + (Pf)(\delta) & R_{sl} + (Pf)(\delta) \\ G_{ms} & S_{mm} & R_{ml} + (Pf)(\delta) \\ G_{ls} & G_{lm} & S_{ll} \end{pmatrix} \\ \times \begin{pmatrix} s \\ m \\ l \end{pmatrix}_{t} + \begin{pmatrix} R_{s} \\ R_{m} \\ R_{l} \end{pmatrix}_{t}$$

$$(2)$$

R.3.0.1 package popbio (Stubben and Milligan 2007; R Development Core Team 2014) was used to perform all demographics analyses. For log-linear analyses, the package MASS was used (Venables and Ripley 2002).

#### Results

#### **Transition rates**

During the first census period (2011–2012), the most frequent transition was stasis (colonies remaining within their original size classes), with large-sized colonies showing the highest transition value at both sites (Table 1). At CLP, the percentage of colonies (medium-sized colonies + largesized colonies) that retrogressed to a lower size class (28 %) was similar to the overall number of colonies (small-sized colonies + medium-sized colonies) that grew to a larger size class (29 %). In contrast, at PAL more colonies grew (38 %) than shrank (13 %). At both sites, shrinkage occurred more frequently on medium-sized colonies, whereas rates of size progression were similar between small-sized colonies and medium-sized colonies classes. Colony survival did not differ statistically between

Size class	2011–2012			2012–2013		
	S	М	L	S	М	L
CLP						
S	0.5010	0.3309	0.0581	0.3029	0.4262	0.3041
М	0.3272	0.3225	0.1851	0.1276	0.2325	0.2500
L	0	0.2580	0.7407	0	0.0465	0.2500
λ	0.918 (95 % CI 0.852-96)			0.535 (95 % CI 0.455-0.599)		
PAL						
S	0.4710	0.1456	0.0387	0.4365	0.3584	0.2507
М	0.3134	0.5000	0.1515	0.1428	0.2156	0.1951
L	0.0895	0.3400	0.7575	0	0.2549	0.4390
λ	0.948 (95 % CI 0.892-981)			0.709 (95 % CI 0.664-0.778)		

**Table 1** Size class transition probabilities of small-sized colonies sized (S:  $\leq 100 \text{ cm}$  in TTL), medium-sized colonies (M: 101-250 cm in TTL) and large-sized (L: > 250 cm TTL) colonies of *Acropora* 

*cervicornis* at two localities (Canal Luis Peña reef, CLP, and Palomino reef, PAL) in eastern Puerto Rico during two annual time periods

 $\lambda$  = estimated population growth rate; numbers within ( ) represent the lower and upper 95 % confidence intervals

size classes, varying between 82 and 96 % at CLP ( $\chi^2 = 3.77$ , df = 2, p > 0.05) and between 84 and 96 % at PAL ( $\chi^2 = 4.74$ , df = 2, p > 0.05). Overall survival rates (size classes pooled) did not differ significantly between sites (CLP: 88 %; PAL: 89 %;  $\chi^2 = 0.0955$ , df = 1, p > 0.05).

the second year (2012–2013), shrinkage During became the most frequent transition, as both mediumsized colonies and large-sized colonies experienced relatively high rates of tissue loss. In this time period, 46 and 37 % of the colonies (medium-sized colonies+ largesized colonies) transitioned to a smaller size class at CLP and PAL, respectively. On the other hand, the percentages of colonies (small-sized colonies + medium-sized colonies) growing into the next size class were lower than the previous year, 9 % at CLP and 21 % at PAL. Differences between sites in the proportion of colonies that progressed in size were associated with the low number of mediumsized colonies that grew to the largest class at CLP, as rates of progression of small-sized colonies were similar between sites (CLP: 13 %, PAL: 14 %). Significant differences in survival rates between size classes were evident during the second year (CLP:  $\chi^2 = 13.27$ , df = 2, p < 0.05; PAL:  $\chi^2 = 15.19$ , df = 2, p < 0.05). This was mostly due to the low number of small-sized colonies that survived from 2012 to 2013 (ESM Table 1). When comparing between time periods within study sites, survival rates differed significantly (CLP:  $\chi^2 = 24.93$ , df = 1, p < 0.05; PAL:  $\chi^2 = 9.15$ , df = 1, p < 0.05). Overall survival rates (size classes pooled) differed significantly between sites during the period 2012-2013, being significantly lower at CLP (CLP: 60 %; PAL: 75 %;  $\chi^2 = 13.13$ , df = 1, p < 0.05).

When considering the whole study period (2011–2013), only 53 % of the tagged colonies survived at CLP, compared with 67 % at PAL ( $\chi^2 = 5.90$ , df = 1, p < 0.05). Survival was size independent at CLP ( $\chi^2 = 5.44$ , df = 2, p > 0.05) but varied with respect to size at PAL ( $\chi^2 = 17.99$ , df = 2, p < 0.05).

#### Log-linear analysis

Results from the four-way contingency table indicate that both time (T) and location (L) had a significant effect on the demographic rates of A. cervicornis colonies (ESM Table 2). When comparing each model to the saturated model (TLSF), the model that considered the effects of time and location simultaneously (TLS, FST, FSL) was the one with the best goodness of fit (ESM Table 2). That is, transitions among size classes are better explained by the interaction between location and time than by the independent effect of each factor. Nevertheless, the model that included the effect of location while excluding the effect of time (TLS, FSL) had comparable AIC values to that of the model TLS, FST, FSL (ESM Table 3); therefore, TLS, FSL could also be considered a good approximation of the observed data. Indeed, the  $\Delta$ AIC value for TLS, FSL was below 2 indicating that the model has better support than the models TLS, FS and TLS, FST (ESM Table 3). This result suggests that location may be a more parsimonious ("better") predictor of colony fate than time. This is supported by the fact that, in contrast to location, time did not have a significant effect on the fate of small-sized colonies and large-sized colonies (ESM Table 2), either when tested against the null model (TL, F) or when tested against the model in which the factor location was included (ESM Table 2).

#### **Recruitment and colony fragmentation**

We did not observe the establishment of any sexual recruits or colony fragments within permanent quadrats. Branch fragmentation was rare. At CLP, only 7 % of the colonies fragmented during the first year, whereas 8 % of the colonies fragmented during 2012–2013. At PAL, 7 % of colonies showed signs of fragmentation during 2011–2012, while 10 % of the colonies fragmented during 2012–2013. The total number of fragments produced during the whole study period (2011–2013) was 26 and 25 at CLP and PAL, respectively. All resulting fragments were small-sized colonies (<100 cm TLL).

#### **Population growth**

During the first year of the study (2011–2012), populations at both localities exhibited growth rates that were close to, but significantly below 1.0, with no differences between locations (based on 95 % CI), at 0.91 for CLP and 0.94 for PAL (Table 1). During the second year,  $\lambda$ s decreased considerably at both sites (Table 1), with the decline being more dramatic at CLP than at PAL. Growth rates differed significantly between sites during 2012–2013 as well as when comparing between time periods (2011–2012 vs. 2012–2013) within locations (Table 1).

LTRE analyses indicate that at both sites, temporal differences in  $\lambda$ s (2011–2012 vs. 2012–2013) were largely related to a reduction in the stasis of large-sized colonies (P<sub>II</sub>; Fig. 1a, b). The spatial difference in  $\lambda$ s observed during 2012–2013 can be explained mostly by differences in growth between medium-sized colonies and large-sized

colonies ( $G_{lm}$ ), but also with an important contribution from differences in the stasis of small-sized colonies and large-sized colonies ( $P_{ss}$ ,  $P_{ll}$ ; Fig. 1c).

The estimated stochastic population growth rates were 0.717 (CI 0.715-0.718) and 0.844 (CI 0.843-0.845) at CLP and PAL, respectively. At these rates of decline, the population at CLP would reach any of the proposed quasiextinction levels in less than 14 yrs, whereas at PAL it would take between 16 and 20 yrs (Fig. 2). Numerical simulations indicate that the observed rates of colony fragmentation are not sufficient to maintain populations at equilibrium, even if all produced fragments show an annual survival rate of 100 % (Fig. 3a). On the other hand, given the observed fragment survival rates of 24 % at CLP and 32 % at PAL, the population at CLP would fail to reach equilibrium even for a probability of fragmentation of 1.0, whereas at PAL  $\lambda \ge 1$  can be obtained if the probability of fragmentation is greater than 80 % (Fig. 3b).

Figures 4 and 5 show the projected size of *A. cervicornis* populations under different outplanting (management) scenarios. Transplanting large-sized colonies resulted in a higher asymptotic population size in all cases. Nevertheless, the analysis also indicates that transplanting fewer than 25 colonies per year at CLP, regardless of size, would result in abundances below the initial population size. In contrast, at PAL, transplanting 25 colonies measuring more than 100 cm TTL would be sufficient to attain an asymptotic population size that surpasses the initial number of colonies. Transplanting small-sized colonies would be effective in attaining population viability ( $\lambda \ge 1$ ) as long as the number of transplants is  $\ge 50$ .



Fig. 1 Results of the life table response experiment analysis showing the contribution of each life cycle transition to the population growth rate of *Acropora cervicornis* after accounting for the effect of time, 2011–2012 versus 2012–2013, at Canal Luis Peña (**a**) and Palomino (**b**) and between locations during the 2012–2013 period (**c**). Positive

and negative values indicate transitions that contribute to and suppress local population growth, respectively. Note the difference in scale in the y-axis in (c). S = stasis, G = growth, R = retrogression; s = small, m = medium, l = large

**Fig. 2** Population viability analysis for *Acoprora cervicornis* populations studied at Canal Luis Peña (CLP) and Palomino (PAL). Each trajectory represents the cumulative probability of quasiextinction over time. Various trajectories are explored based on the threshold at which the population would be considered functionally (or quasi-) extinct—from 10 % (a 90 % reduction) to 25 % of the population size in 2011





#### Discussion

### Spatiotemporal variability in vital rates

Studies directed at understanding the population dynamics of *A. cervicornis* have been relatively scarce. Knowlton et al. (1990) found that the rates of survival and growth of this coral varied both temporally and spatially. Our results support these findings. The spatiotemporal variability observed in this study is, however, somewhat surprising. Knowlton et al. (1990) attributed most of the mortality they observed to high predation rates by the snail *Coralliophila* spp. and the polychaete *Hermodice carunculata*. In contrast, the 2 yrs in which we measured the vital rates can be categorized as "normal" in the sense that no major disturbances such as hurricanes, bleaching, predator outbreaks, or epizootic events directly impacted the two study sites. Moreover, the conditions at the study localities remained similar in terms of water quality, wave exposure, and biotic composition. Thus, this study suggests that even in the absence of a major disturbance, the vital rates of this species can be susceptible to minor or moderate local variations in environmental parameters. The only potentially stressful event that occurred during the study period was a heavy rainfall event (356 cm, an anomaly of 215 % in relation to mean monthly rainfall) during June 2013 (Hernández-Delgado et al. 2014), 4 months before the last survey. Extreme rainfall events have been associated with high mortality of scleractinian corals, including A. cervicornis, due in part to a drop in seawater salinity (Morton 2002; Hernández-Delgado et al. 2014). There is evidence that a reduction in salinity can limit the capacity of a coral to survive short-term increases in seawater temperature (Coles and Jokiel 1978). Low salinity can also impair coral physiological efficiency (Kerswell and Jones 2003) with possible costs to colony development. However, we cannot





Fig. 4 Simulated trajectories of the *Acoprora cervicornis* population size over time at Canal Luis Peña using different numbers and sizes of transplanted colonies based on the stochastic mean matrix. *Solid line* =

initial population size ( $N_0 = 144$ ); *closed circles* = population trajectory with no outplants; *open circles* = small-sized outplants; *closed triangles* = medium-sized outplants; *open triangles* = large-sized outplant

determine the specific causal factors for the significant decline in survival and growth rates during the period 2012–2013.

Life history trade-offs may explain the apparently high susceptibility of this species to low/moderate levels of environmental variation. It is understood that *A. cervicornis* allocates most of its energetic resources toward rapid growth at the expense of other biological functions (Palmer et al. 2010). The resource allocation trade-off hypothesis postulates that an individual's energetic budget is finite and that resources invested in one function cannot be used for another (Bazzaz et al. 1987). Hence, it is likely that *A. cervicornis*' poor ability to cope with environmental changes is a result of a resource allocation strategy favoring rapid colony growth over other life history traits

directed to assure colony survival, such as maintenance, tissue regeneration and repair, and a stronger immune response (Palmer et al. 2010; Ruiz-Diaz et al. 2013). The literature on life history trade-offs in corals is very limited; nonetheless, the immune response of acroporids appears to be weaker in relation to that of slower-growing massive corals (Palmer et al. 2010).

Results of the log-linear analysis suggest that spatial variation in the demography of *A. cervicornis* may be larger than temporal variation within the same location. Such differences were more evident in medium-sized colonies. During 2011–2012, the probability of a medium-sized colonies remaining within its size class or retrogressing into the smaller size class was noticeably lower and higher, respectively, at PAL. In contrast, during the second year,





Fig. 5 Simulated trajectories of Acoprora cervicornis population size over time at Palomino using different numbers and sizes of transplanted colonies based on the stochastic mean matrix. Solid line = initial

most of the spatial variation in the dynamics of mediumsized colonies could be attributed to differences in their probability of advancing to the large size class. It is unclear why medium-sized colonies were more susceptible than small-sized colonies and large-sized colonies to spatiotemporal variability. Nevertheless, we noticed that at the beginning of the study, and particularly at CLP, mediumsized colonies exhibited the highest proportions of dead tissue. It has been suggested that differences in the ratio of live to dead tissue can have important implications for the demographic performance of corals (Meesters et al. 1997; Oren et al. 1997; Ruiz-Diaz et al. unpublished data). For instance, there is an inverse relationship between the potential of a colony to regenerate lost tissue and the ratio between the size of a lesion (e.g., dead tissue) and size of the colony (Sousa 1984; Oren et al. 1997; Ruiz-Diaz et al. unpublished data). Lower regeneration capability not only

population size ( $N_0 = 150$ ); closed circles = population trajectory with no outplants; open circles = small-sized outplants; closed triangles = medium-sized outplants; open triangles = large-sized outplant

limits the growth of a colony but also increases its probability of dying (Meesters et al. 1997; Hall 2001).

The significant spatiotemporal variability of A. cervicornis demographic rates observed in this study contrasts with rates for A. palmata in Florida (Vardi et al. 2012). That study estimated higher and more stable population growth rates ( $\lambda s = 0.97 - 1.05$ ) over 6 yrs (with the exception of a hurricane year,  $\lambda = 0.71$ ), and transition rates that did not vary considerably among reefs. This suggests, as previously noted by Williams et al. (2006), that the demography of A. cervicornis is more dynamic and variable than that of A. palmata, which is unexpected given that the two species share similar life history traits. Considering the differences observed here, although only based on two sites and 2 yrs, conservation recommendations and initiatives should be species specific, not generic, when possible.

#### Population dynamics and viability analysis

During the first year of this study, colony survival varied between 88 and 89 %. These annual rates are comparable to those found by Knowlton et al. (1990) during the initial years of their study. Yet the lack of sexual recruitment, as well as relatively low rates of colony fragmentation, resulted in a population decline at both sites ( $\lambda < 1$ ). The absence of sexually derived recruits was not a surprise, as this coral is characterized by limited sexual reproduction (Tunnicliffe 1981; Knowlton et al. 1990). On the other hand, the rarity of natural fragmentation was unexpected as it is accepted that colony fragmentation is the main mode of reproduction in A. cervicornis, even in areas where the degree of wave exposure is low (Tunnicliffe 1981; Knowlton et al. 1990). A possible explanation for the low rates of fragmentation is that current size structures are below a threshold at which water-related drag forces or mechanical instability can induce branch breakage (Highsmith 1982). Tunnicliffe (1982) identified 40 cm as the minimum colony height at which waves can induce branch breakage in A. cervicornis; at our study sites, only ten colonies exceeded that height (eight at CLP and two at PAL). Mean colony height varied between 19.42 cm  $(\pm 8.88; SD)$  at PAL and 23.00 cm  $(\pm 9.26; SD)$  at CLP.

During the second year, reductions in population growth of  $\sim$  24 and 38 % were documented at PAL and CLP, respectively. These lower  $\lambda$ s were due not only to insignificant rates of recruitment but also to the combination of lower colony survival, little colony growth, and higher levels of colony shrinkage. As indicated by the life table response analysis, the lower probability of large-sized colonies surviving and remaining within the largest size class was the demographic transition that contributed most to the observed temporal reduction in  $\lambda$ s. Although large-sized colonies survived better than small-sized colonies- and medium-sized colonies, they exhibited higher transitions to smaller size classes, particularly to the smallest size class. Higher proportions of colonies <250 cm TTL may increase the risk of population extinction. First, small-sized colonies survive poorly compared with largesized colonies. Second, it is recognized that there is a positive linear relationship between sexual reproductive output and colony size (Hughes 1984). Third, large-sized colonies tend to produce a greater number of branches than small-sized colonies (Mercado-Molina et al. 2015), which is essential for a species that relies mostly on branch fragmentation for propagation. It can be argued that populations are currently shifting toward smaller populations dominated by small-sized colonies, which are generally characterized by low demographic performance. This exacerbates the poor prospect of population persistence.

Determining the minimum viable size at which a population is capable of recovering is critical for its conservation. We know that the number of colonies required to maintain a coral population needs to be large, particularly for broadcast spawners (Hernández-Pacheco et al. 2011); but determining an exact number is not currently possible. Quasi-extinction thresholds are a way of estimating the probability of extinction without knowing the critical level at which a given population becomes functionally extinct. Four different quasi-extinction thresholds were considered for the studied populations, and even under the most conservative scenario (10 %), the studied populations can become functionally extinct in  $\leq 20$  yrs. This result provides quantitative support to the generalized perception that populations of A. cervicornis continue to decline rapidly throughout their geographical range (NMFS 2015). Therefore, populations of A. cervicornis should be of conservation concern, especially when our analyses did not consider the consequence of possible extreme events such as hurricanes or disease outbreaks. The insignificant contribution of asexual reproduction to local population growth together with the fact that loose fragments of A. cervicornis survive poorly (Mercado-Molina et al. 2014) leads us to believe that the studied populations will not recover or sustain themselves without intervention. This underscores the need for human involvement to ensure the viability of A. cervicornis in northeastern Puerto Rico.

#### Restoration

Outplanting nursery-grown coral fragments (colonies) to selected sites using stabilization techniques such as epoxy/ cement and cable ties has been considered an effective tool for restoring depleted populations of Caribbean acroporid species (Bowden-Kerby 2001; Williams and Miller 2010; Mercado-Molina et al. 2015). Simulations indicate that transplanting large fragments would result in higher asymptotic population sizes. Nevertheless, considering that coral nurseries are usually initiated with coral fragments ≤15 cm TLL (Quinn and Kojis 2006; Herlan and Lirman 2009; Lirman et al. 2010, 2014), it would take at least 3 yrs in a good growth environment for a colony to reach ≥250 cm TLL (Lirman et al. 2010, 2014; Hernández-Delgado et al. 2014). This time lag may be critical for the persistence of the targeted populations, if, as shown in this study, populations experience a 'bad' year in which approximately half of the colonies are lost. An alternative approach is to focus the management plan on transplanting at least 50 ( $\sim$  33 % of the initial population size in the case of this study) small ( $\leq 100$  cm TLL) colonies per year. Results from Mercado-Molina et al. (2015) suggest that 25 cm TLL is an effective initial size for colony transplantation as the coral outplants survive, grow, and produce branches relatively well. Nursery-reared fragments can reach this size in less than 5 months (Hernández-Delgado et al. 2014).

Coral conservation initiatives can be costly (Edwards et al. 2010; Vardi et al. 2012). Yet reef restoration projects could be both economically and logistically feasible as long as members of the local community are part of the effort (Hernández-Delgado and Suleimán-Ramos 2014; Hernández-Delgado et al. 2014; Forrester et al. 2014). In Puerto Rico, for instance, the community-based non-government organization Sociedad Ambiente Marino (SAM) outplanted over 2000 colonies per year (employing nails and cable ties) with an initial budget of US\$90,000 yr<sup>-1</sup>, compared with ~US\$600,000 yr<sup>-1</sup> estimated for a similar (but not community-based) project in the Florida Keys (see Vardi et al. 2012). Taking into consideration the total cost of the SAM operation, the unit cost of a transplant is estimated at US\$45.

In conclusion, this study is based on demographic data collected for 2 yrs at two localities. It is likely that this data set has not captured all of the temporal and spatial variability in vital rates that this species can exhibit. Particularly, the impacts of hurricanes, mass bleaching, and disease outbreaks are absent from our analyses because none occurred during the study period. In spite of these limitations, this study has identified important aspects of the demography and dynamics of A. cervicornis. (1) This study highlights significant spatiotemporal variability in vital rates, even in the absence of a major disturbance. This stresses the apparent susceptibility of this species to low/moderate levels of environmental variability. (2) The overall effect of spatial variation on the demographic fate of A. cervicornis was stronger than the effect of temporal variation. Accordingly, restoration efforts should be partitioned among several small projects rather than allocating all the resources into one site. This action will enhance the persistence of the species if localized extirpation occurs due to spatial variability. Such results also imply that continuous demographic monitoring is essential, as real-time knowledge of the spatial and temporal variation may be necessary to fine-tune management plans in accordance with the observed population trends and/or conditions. (3) The observed contribution of asexual recruitment is meager and therefore not a significant factor in the population dynamics of the species. This challenges the generalized but insufficiently demonstrated belief that under current coral reef conditions, colony fragmentation is capable of sustaining local populations (NMFS 2006). (4) Rather, it is variation in the stasis of large-sized colonies, plus the growth and partial tissue mortality of medium-sized colonies that contributes most to variations in population growth rates.

The numerical projections performed in this study are not aimed at predicting what will happen to the population, but rather at evaluating the possible influences of the observed spatiotemporal demographic attributes on the population dynamics of *A. cervicornis* (Caswell 2001). Such projections are informative in guiding management and conservation strategies given that they incorporate the effects of the prevailing environmental conditions on colony vital rates (Caswell 2001). In this sense, even in the absence of a major perturbation, population growth rates are below equilibrium and the population viability analysis indicates quasi-extinction in less than two decades. Including the effect of major disturbances in the analysis will only make more ominous an already dismal scenario for A. cervicornis. Restoring populations by outplanting fragments is a feasible strategy, but one that requires sustained human intervention (Mercado-Molina et al. 2015). Finally, this study raises the first quantitatively supported red flag with regard to the long-term persistence of A. cervicornis. Major restoration efforts along the lines proposed in this study are necessary at a regional scale if we want to reverse the demise of this important Caribbean coral. We understand, however, that only through the collective publication of demographic data and analyses from other Caribbean localities and time periods by other research groups will we start to gain a comprehensive appreciation of the spatial and temporal variability in the demography and dynamics of this species.

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