Mass Bleaching Impacts in the Demography of the Caribbean Reef-building Star Coral *Monastraea annularis*: A Modeling Approach

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ABSTRACT

The northeastern Caribbean region experienced a record-breaking sea surface warming and prolonged mass bleaching during 2005. This event resulted in significant mortality of the principal Caribbean reef-building coral *Montastraea annularis*. We evaluated the demographics and size structure of a *M. annularis* population before, during, and after this event; stochastically simulated the population dynamics with different bleaching regimes over a period of 100 years, and determined the life cycle transitions that contributed most to population decline after recurrent events using a life table response analysis. Size-based transition matrices from 2001-2009 were constructed following individual colonies through time in 17 permanent photo-transects located in Culebra Island, Puerto Rico. Temporal variation in the population growth rate indicated a demographic equilibrium before the event, an increase in mortality for two years after the event, and demographic recovery by the third year. However, population size structure did not recover entirely. Stochastic simulation showed that viability of the population becomes strongly compromised with only 10% annual probability of bleaching, while a 20% probability led to population local extinction. Life table response analysis determined that mortality of small colonies accounted the most for population decline after the event. The natural history of *M. annularis* has showed that recovery by sexual recruitment alone is unlikely. The fate of present small colonies will determine the population viability in the near future. We conclude that the demography of *M. annularis* populations is highly susceptible to mass bleaching and that its viability is seriously comprised under the predicted global warming scenarios.

KEY WORDS: Mass coral bleaching, *Montastraea annularis*, projection matrix model, stochastic analysis

Impactos del Blanqueamiento Masivo en la Demografía del Coral de Estrella *Montastraea annularis*, Constructor de Arrecifes en el Caribe: Un Acercamiento de Modelaje

PALABRAS CLAVES: Blanqueamiento masivo, *Montastraea annularis*, acercamiento de modelaja

Impacts Blanchissement de masse dans la Démographie de la Coral Reef Caraïbes Renforcement des Étoiles *Monastraea annularis*: Une Approche de Modélisation

MOTS CLÉS: Blanchissement de masse, *Montastraea annularis, approche de modélisation*

INTRODUCTION

The predicted scenario for coral reefs around the world is alarming due to uncertainty on whether corals will be able to withstand forecasted increased frequencies of mass bleaching events (Hoegh-Guldberg 1999, Donner et al. 2005). As a result, the long-term impact of today's conservation and management strategies could be largely limited. For example, the record-breaking increase in sea surface temperature (SST) that took place during the summer/fall of 2005 resulted in the most severe mass bleaching event ever documented within the northeastern Caribbean region (Miller et al. 2009). During this event, more than 90% of scleractinian corals showed signs of thermal stress at different sites in US Virgin Islands and Puerto Rico (Hernandez-Delgado et al. 2006, Miller et al. 2009). This situation points towards the need to understand the response of principal reef-building coral populations to mass bleaching events in order to address issues concerning the improvement of coral reef resilience confronting climate change-related phenomena.

The mass bleaching event of 2005 was followed by an unprecedented mass coral mortality event between late 2005 and mid 2006 associated to a widespread white plague-like outbreak. It caused a significant mass mortality across different coral taxa, with particular impacts on populations of one of the principal Caribbean reef-building star corals, *Montastraea annularis* (Ellis and Solander), which suffered significant decline at multiple localities across the northeastern Caribbean (Hernández-Delgado et al. 2006, In prep., Miller et al. 2006, 2009). Although there have been previous *M. annularis* population dynamic modeling efforts (Edmunds and Elahi 2007), the demographic consequences of coral bleaching in this species are still unknown. This is of major concern because a complete evaluation of the population dynamics and demographic recovery following bleaching is necessary in order to be able to quantify and model the effects of mass bleaching and coral mortality in coral populations under the predicted global warming scenario. In this article, the demographic effects of the 2005 bleaching event on a *M. annularis* population in Puerto Rico

following Hernández-Pacheco et al. (2010 Accepted) are described and future implications are discussed.

METHODS

Study Site

The field work was conducted at Carlos Rosario Beach (CR), located within the Canal Luis Peña No-Take Natural Reserve (CLPNR) in Culebra Island, 28 km off eastern Puerto Rico (18°19'29" N, 65°19'60" W). This site has been monitored since 1997 for changes in benthic community structure. We used data from 2001 to 2009 to evaluate the population dynamics of *M. annularis* due to the continuous availability of permanent photographic records of coral colonies. The 2005 mass bleaching event impacted 97% of coral colonies at CR (Hernández-Delgado *et al.* 2006). All *M. annularis* colonies within our study transects bleached during the first week of the event in September 2005 and many surviving colonies remained pale even a year after. Further, isolated coral heads remained pale for 29 months. All methods are based on Hernández-Pacheco et al. (2010 Accepted).

Data Collection

Seventeen 10-m long permanent photo-transects at a 4-12m depth range were used. Each transect was divided into approximately 25 continuous images that on average covered a bottom area of 0.160 m^2 per image. Survival and size class transitions of coral colonies from 2001 to 2009 were measured by individually following the fate of 399 colonies through time. Colony size was estimated by measuring the colony planar area using Coral Point Count with Excel Extension version 3.5 (Kohler and Hill 2006). Colony fate was assessed by determining whether the colonies at time t were alive (> 0% live tissue cover) or dead (0% live tissue). If alive, it was determined whether they had grown, decreased in size, fused or split during the time interval (Caswell 2001).

Demographic Model

Eight size-based population projection matrices were constructed. The population was divided into three colony size classes; small [S] (0 - 50 cm^2), medium [M] (50 - 150 cm^2), and large [L] (> 150 cm^2). The number of colonies in each of the life cycle stages at time $t+1$ equals:

$$\begin{pmatrix} S \\ M \\ L \end{pmatrix}_{t+1} = \begin{pmatrix} P1 & R_{SM} & R_{SL} \\ G1 & P2 & R_{ML} \\ 0 & G2 & P3 \end{pmatrix} \cdot \begin{pmatrix} S \\ M \\ L \end{pmatrix}_t \quad \text{Equation 1}$$

where $P1$, $P2$, and $P3$ are the probabilities of small, medium, and large colonies, respectively, of remaining alive in the same size class for one year. The Gs represent growth transitions. In this case, $G2$ is the probability that a medium colony at time t will survive and grow into a large colony at time $t+1$. The Rs are size retrogressions (i.e. a

colony that becomes smaller by losing tissue through partial mortality). Recruitment is not considered in our matrices, as no recruits were seen in any of the photo-transects during the eight years of survey.

The real dominant eigenvalue and its corresponding right and left eigen vectors were calculated to obtain the asymptotic population growth rate (λ), the stable stage distribution (w), the reproductive value vector (v) and the sensitivity and elasticity matrices for every census period (Caswell 2001). A bootstrap analysis was carried out in order to determine 95% confidence intervals for the population growth rates by randomly selecting colonies from the data set, with replacement, until attaining the original sample size. Demographic transitions were calculated from this sample, a transition matrix was constructed and the λ calculated. The entire procedure was repeated 1000 times and asymmetric 95% confidence limits were determined from the 2.5th and 97.5th percentiles of the data.

For the stochastic simulation, four different annual bleaching event probabilities were used; 0%, 5% (one bleaching event for every 20 years), 10% (once every decade), and 20% (once every 5 years). This was based on the current recurrence trends of bleaching events documented in Puerto Rico ever the last three decades. In order to do this, two matrix distributions were generated; a distribution of "normal" or no-bleaching year matrices was generated by pooling the raw data from 2001 - 2005 and 2008-2009 censuses, and another distribution of bleaching year matrices with data from 2006 - 2007 censuses. Afterward, the population was projected 100 years into the future under each bleaching probability and the stochastic population growth rate, λ_s, was calculated by taking the arithmetic mean of the logs of the λ values (Caswell 2001). This procedure was repeated 1000 times using Mathcad Plus 6.0 MathSoft, Inc. Asymmetric 95% confidence intervals were estimated from the resulting distribution of λ_s. The number of colonies remaining alive after 100 years of stochastic projection from an initial population of 1000 colonies was also recorded. A life table response experiment (LTRE) was performed to quantify the population-level effect of the bleaching event in relation to the years prior and posterior to the episode (Hernández-Pacheco et al. 2010 Accepted).

RESULTS

Demographic Analysis

The *M. annularis* population was essentially at equilibrium during the four years prior to the mass bleaching event, exhibiting λ values not different from 1.0 (Table 1). The bleaching event resulted in a significant decline in λ to 0.806 during 2006 - 2007, and further to 0.747 during 2007 - 2008, just following the post-bleaching mass coral mortality (Table1). During the third census interval after the event (2008 - 2009), λ increased signifi-

cantly to a value not different from 1.0 (Table 1). The bleaching event increased the relative abundance of small colonies from 73% in 2004 to 97% after the event in 2007 as a result of major partial tissue mortality. Size retrogression of medium colonies was high, decreasing in relative abundance from 23% to 3% for the same years, respectively. The relative abundance of large colonies also decreased from 4.27% in 2004 to 0.4% in 2007. During 2008 - 2009, a decrease in the frequency of small colonies occurred from 97% to 82% as a result of further small physiological fragment mortality, and an increase in that of medium and large ones to 16.2 and 1.44%, respectively. The life table response experiment indicated that the significant decline in λ as a result of the ive bleaching event was due to increased post-bleaching mortality of small and medium-sized colonies. The significant increase in λ during 2008-2009 was mainly due to increased survivorship in small and medium colonies. Retrogressions and survivorship of large colonies had the smallest influences on either the decline or the subsequent increase in λ.

Stochastic simulation – The stochastic simulation indicated that *M. annularis* populations would remain viable for annual mass bleaching probabilities of less than 6% (Figure 1). Mean stochastic population growth rates decline very predictably and linearly with bleaching probability ($\lambda = -0.0014$ ($P_{bleaching}$) $+ 1.0025$). Mean proportion of initial colonies at the end of each simulation ($N_{t = 100}/N_{t = 0}$) declines geometrically with increasing bleaching probability (Figure 2). An annual bleaching probability of only 5% over 100 years would result in a decline of 64% in the abundance of colonies while annual bleaching probabilities between 10 and 20% would produce declines of 89% and 99% in the abundance of colonies, respectively (Figure 2).

DISCUSSION

Montastraea annularis Demographics

The *M. annularis* population showed temporal variation in growth rate before, during and after the 2005 mass bleaching and the 2006 post-bleaching mortality event. The population was in demographic equilibrium before the event, suffered a significant decline in growth rate for two years after the event, and demographically recovered by the third year. From one year to the next, *M. annulairs* showed high growth probabilities of small colonies supporting that its growth potential is probably size specific with strong selective pressure acting to maintain high growth rates of small colonies in order to escape vulnerable sizes (Hughes and Jackson 1985).

The observed population decline after the 2005 bleaching event was mainly caused by the significant decrease in survival of small colonies. Large and medium colonies suffered significant tissue loss during the process but did not experienced high mortality rates. Thus, the population viability depended mostly on the fate of small

Table 1. Mean asymptotic population growth rates for every census period and 95% confidence intervals

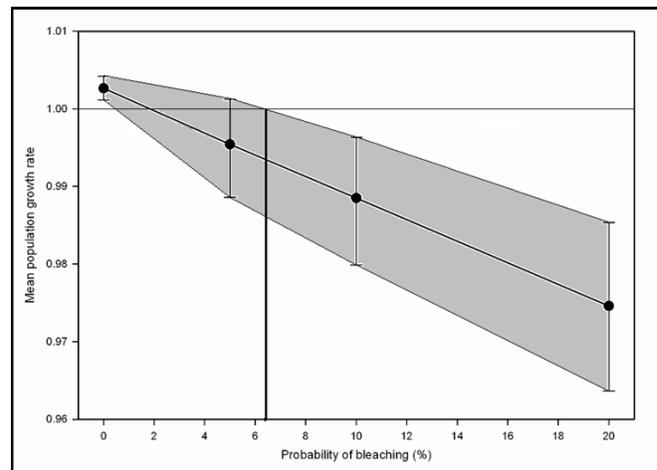| Census interval	λ	95% CI
2001-2002	0.945	(0.864, 1.014)
2002-2003	1.015	(0.938, 1.114)
2003-2004	1.085	(0.966, 1.167)
2004-2005	1.001	(0.965, 1.041)
2005-2006	0.939	(0.875, 0.991)
2006-2007	0.806	(0.734, 0.871)
2007-2008	0.747	(0.604, 0.914)
2008-2009	1.035	(0.980, 1.108)

Figure 1. Stochastic mean population growth rate of *Montastraea annularis* for different annual bleaching regimes. Vertical bar represents the maximum annual bleaching probability that the population must have in order
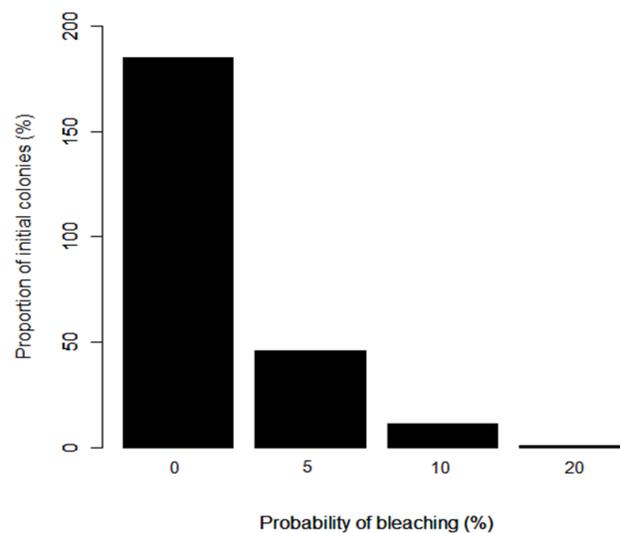

Figure 2. Proportion of initial colonies of *Montastraea annularis* remaining after 100 years of stochastic projection for different annual bleaching probabilities. The proportion of remaining colonies was calculated by dividing the number of colonies at $t = 100$ by 1000, the number of colonies at $t = 0$.

colonies. In a matrix model such as the one presented by Hernández-Pacheco et al. (2010 Accepted), colony fission was understood as a form of asexual reproduction. Because of this, retrogressions of medium colonies to small ones had a positive effect on λ. However, the magnitude of this "positive" effect was not strong enough to overcome the negative effect of increased mortality in small colonies.

Three years after the bleaching event, the population showed life cycle transitions similar to transitions before the event. Thus, the demographic effects of the bleaching event on the *M. annularis* population were observed a year after colonies got bleached and lasted for two years after the event started in September, 2005. This relatively quick demographic recovery, driven mostly by the increase in survival of small colonies, was unexpected, given the high elasticity in the survival of medium and large colonies reported by Hughes and Tanner (2000), and by Edmunds and Elahi (2007).

Demographic Recovery in the Absence of Sexual Recruitment

Recovery in coral populations has often be analyzed in terms of recruitment dynamics (Arthur et al. 2006, Golbuu *et al.* 2007, Sheppard et al. 2008). However, the *M. annularis* population in Culebra Island, Puerto Rico showed significant demographic recovery even in the complete absence of sexual recruits (Hernández-Pacheco et al. 2010 accepted). In the past decades, *M. annularis* populations from Jamaica and U.S. Virgin Islands have also experienced similar scenarios. Hughes and Tanner (2000) only found a single recruit in 16 years for a *M. annularis* population in Jamaica; while in St. John, U.S. Virgin Islands, the density of juvenile corals (number of colonies less or equal to 4 cm diameter per 10 m^2) was less than 2 in 10 years (Edmunds and Elahi 2007). No single *M. annularis* coral recruits have ever been documented in permanent monitoring sites across Puerto Rico, even in those that go back to 1997 (Hernández-Delgado, unpub. data). Therefore, recovery of today's population solely by sexual recruitment is unlikely. Our analysis showed that the fate of surviving, small colonies, and not the number of new recruits, will be determining the viability of *M. annularis* populations in the near future.

***Montastraea annularis* Populations in a Global Warming scenario**

The stochastic analysis indicated that the viability of *M. annularis* populations will strongly depend on the frequency of recurrent mass bleaching and mass mortality events. It also revealed that an annual bleaching probability of only 5% (once every 20 years) will result in a dramatic population reduction of 54% after 100 years; while an annual probability of 20% (once every 5 years) will result in a 99% reduction. This is highly significant under the predicted rise in SSTs across the Caribbean for the next decades (Hoegh-Guldberg 1999). Not all bleaching events have the same intensity (Glynn 1993) and our simulations are based on a single strong event. However, this event represented an exceptional opportunity to model the possible fate of coral reefs in the Caribbean if future warming episodes and mass bleaching events would be as catastrophic as forecasted.

As local management and conservation strategies are limited, global strategies are still far from reality. A world-wide meta-analysis contrasting change in percent coral cover between marine protected areas (MPAs) and non protected areas concluded that MPAs were effective in preventing coral cover loss (Selig and Bruno 2010). No-take MPAs have also shown to be effective in decreasing biological stresses on corals, but their capacity to reduce physical stresses, such as elevated SSTs, is highly limited (Mumby and Steneck 2008). Côté and Darling (2010) concluded that MPAs – the ultimate management strategies of today's governments – do not confer protection against thermally induced bleaching, and that future conservation strategies must be oriented toward the effective reduction in global green house gases emissions. The strong negative relationship between bleaching frequency and population growth rate of *M. annularis* reveals that the viability of this major reef-builder will be largely dependent on SSTs remaining below its maximum annual thermal threshold. Therefore, coral reef accretion in the Caribbean is highly compromised unless meaningful rapid reductions in rising global temperature drivers take place. Otherwise, the future of coral reefs will remain largely obscure.

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