The demography of hurricane effects on two coral populations differing in dynamics

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Abstract. On most tropical coral reefs, decades of disturbances have ratcheted down coral cover to create low abundance communities. In such a state, the reefs of St. John, US Virgin Islands, were hit by two Category 5 hurricanes in September 2017, yet the effects on two sites dominated by Orbicella annularis were minor in terms of coral cover. To explore the implications of this outcome, the fates of O. annularis colonies were determined from photoquadrats and used to prepare size-based matrix models for the year preceding the storms and the four months bracketing the storms. The populations displayed contrasting dynamics from 1988 to July 2017, with coral cover declining from 43% to 5% at Yawzi Point but remaining at ~30% at Tektite. Over this period, colony sizes declined, with ≥82% having planar areas ≤50 cm² (i.e., the smallest size class) by July 2017, and while densities declined from 47 to 8 colonies/m² at Yawzi Point, they increased from 36 to 51 colonies/m² at Tektite. Hurricanes Irma and Maria depressed coral cover by 1–4%, transitioned colonies into the smallest size class (>87% by November), killed 27% and 5% of the colonies in the smallest size class at Yawzi Point and Tektite, respectively, and depressed the 5-yr intrinsic rate of population growth (λ) to 0.53–0.87. Twenty-year projections suggested these demographic effects will not have ecologically meaningful impacts on population size, at least compared to projections initiated assuming Hurricanes Irma and Maria had not occurred. With low cover of O. annularis distributed among many small colonies, future disturbances may play more important roles in winnowing the few remaining host genotypes rather than further depressing coral cover.

Key words: Caribbean; demography; ecology; Orbicella; Scleractinia; St. John.

INTRODUCTION

Coral reefs are products of their scleractinian foundation species (Jones et al. 1994, Wild et al. 2011), whose capacity for depositing large quantities of CaCO₃ is central to their constructional roles (Wild et al. 2011, Pratchett et al. 2015), which operate in concert with other calcified taxa, notably algae (Adey 1998). The last few decades have not been conducive to scleractinians maintaining this functional role, as their percentage cover has been depressed by multiple disturbances (Bruno and Selig 2007, Jackson et al. 2014). Given the high rate at which seawater has warmed (Hughes et al. 2017a), much of the attention to the coral reef crisis has focused on bleaching (Hughes et al. 2017b), but there also has been considerable work on the effects of ocean acidification (Kornder et al. 2018). The threats to corals from other disturbances, like diseases and sedimentation, have not abated however, but decades of studying them provide reason to expect that future cases of the same disturbances will have predictable outcomes. In the Anthropocene epoch (Zalasiewicz et al. 2011), in which the biosphere and the physico-chemical environment in which it operates differs from the recent past, expectations of the ecological impacts
of well-known disturbances may need to be re-evaluated.

Hurricanes provide interesting examples of this phenomenon, because the severity of their impacts on coral reefs, as well as on other marine and terrestrial habitats, has been recorded for centuries (Rappaport and Fernández-Partagás 1997). Over the last 50 yr, studies of hurricanes on coral reefs have been published with regularity (Woodley et al. 1981, Harmelin-Vivien 1994, Edmunds 2019), and their consequences have been codified in ecological theory addressing community diversity, stability, and resilience (Connell 1978). Yet unexpected and nuanced effects of hurricanes on coral reefs continue to be reported. For example, throughout the Florida Reef Tract in 2005, multiple hurricanes cooled seawater through wind-driven vertical mixing, thus alleviating the consequences of bleaching (Manzello et al. 2007), and throughout the Caribbean, clonal proliferation of the columnar-lobate colonies of O. annularis is accentuated on steep reef slopes in the paths of frequent hurricanes (Foster et al. 2013). In St. John, Hurricanes Irma and María impacted the island within 14 d as Category 5 storms, yet the effects were small on reefs at 7–14 m depth on the south shore (1–4% change in absolute coral cover) because decades of degradation had created low cover coral communities that were resilient to disturbances (Edmunds 2019). The modest effect of the recent hurricanes on coral reefs in St. John is, in part, a product of the earlier removal of delicate species such as Acropora spp. (Zhang et al. 2014), and they reveal the complex implications of managing coral reefs for high resilience (Bellwood et al. 2004, Darling and Côté 2018).

The effects of hurricanes on coral communities mostly have been determined through coral cover, but this state variable has limited value in elucidating mechanisms of change and future population trajectories (Hughes and Tanner 2000). These challenges are accentuated as coral cover declines to single-digit levels, when most existing sampling regimes have limited statistical power (Cunningham and Lindenmayer 2005) to resolve change, and the disconnect between coral cover and vital rates (e.g., mortality, recruitment, population growth; Hughes and Jackson 1985) impedes interpretation of the trends in changing coral cover. Critically, it is impossible to know from coral cover alone at what point declines in abundance are ecologically meaningful with respect to future population dynamics, and when cover is sufficiently low that local extirpation might be imminent. Demographic approaches (sensu Caswell 2001, Riegl et al. 2017) are well suited to addressing these issues, but their reliance on vital rates (i.e., recruitment, death, growth, etc.) defined by individual colonies has deterred their widespread application in coral reef science.

The present study focuses on the population biology of the Caribbean coral, Orbicella annularis, on two shallow reefs off St. John, US Virgin Islands, where the ecological history of this species has been described over three decades (Edmunds 2013, 2015). Most recently, their response to two hurricanes of unprecedented strength has been quantified (Edmunds 2019), with this earlier paper providing a 30-yr temporal context to the present analysis. Interested readers should refer to this paper for more ecological detail regarding the effects of these storms on the reefs at Yawzi Point and Tektite, and to Browning et al. (2019), Cox et al. (2019), and Edmunds et al. (2019) for details of the physical and biological consequences of these events in St. John. O. annularis dominates both study reefs in St. John, one at 9 m depth (Yawzi Point) and one at Tektite (14 m depth), with each displaying contrasting coral community trajectories over 32 yr, most recently culminating in a non-significant, ≤3.7% change in absolute coral cover following the hurricanes of September 2017 (Edmunds 2019). For the reasons described above, the ecological meaning of these changes is equivocal on a percentage cover scale, notably at Yawzi Point where the reef had only 6.3% coral cover before the most recent hurricanes (Edmunds 2019). The objectives of the present study are to (1) use size-based matrix models (after Hughes 1984) to quantify the demographic responses of O. annularis to the recent hurricanes on two reefs off St. John (Edmunds 2019), (2) place these effects in a decadal history over which the response of this species to hurricanes has previously been reported (Edmunds 2019), and (3) use 20-yr projections to provide a context within which the implications of catastrophic hurricanes for present-day, O. annularis reefs can be evaluated.
METHODS

The Yawzi Point (9 m) and Tektite (14 m) sites have been surveyed with annual resolution since 1987 (Edmunds 2000, 2013, Edmunds and Lasker 2016), and the present study focuses on the population biology of *Orbicella annularis* at these sites. This species has dominated the coral fauna in both locations since at least 1987, and at each site, the analyses are based on the abundance of colonies in 10 contiguous photoquadrats (1 × 1 m, n = 30) along each of three 10-m transects. At each site, the transects are permanently marked, parallel to one another and 5 m apart, and they were established in 1987 to evaluate the impacts of coral bleaching (Roberts 1987). Here, new data are presented from surveys conducted in July 2017, November 2017, and July 2018, the first two of which sampled just before, and shortly after, the hurricanes that passed ≤86 km from St. John (Edmunds 2019). The results of these surveys are placed in a longer history using a 32-yr time-series, of which the present study is a part, with these surveys sampled at 5-yr intervals to match the resolution of previous demographic analyses of *O. annularis* (Edmunds and Elahi 2007, Edmunds 2015).

*Orbicella annularis* is one of the most extensively studied Caribbean corals (Knowlton et al. 1992), and it serves as a foundation species of profound importance (Knowlton et al. 1992, Foster et al. 2007, 2013). Over the last 50 yr, region-wide declines in abundance of this species, driven by storms, bleaching, diseases, and algal overgrowth (Edmunds and Elahi 2007, Bruckner 2012), have focused attention on its population biology (e.g., Burgess 2011, Hernandez-Pacheco et al. 2011, Foster et al. 2013) to evaluate whether it is likely to sustain its ecological roles in the future. Such studies require identification of coral colonies, but this unit of individuality can be equivocal for this species, because colonies undergo fission to form columnar aggregates, in which lobes on a common framework share a host genotype (i.e., they are ramets of a genet; Heyward and Collins 1985). Sampling of *O. annularis* in St. John has confirmed this host genetic structuring (Edmunds et al. 2014), but it did not preclude the possibility of sexual origin for adjacent lobes (D. Levitan, unpublished data).

Following Connell (1973), colonies of *O. annularis* are defined as autonomous areas of tissue, even if adjacent colonies share a common antecedent framework. First, the results from photoquadrats are used to describe *O. annularis* populations over time. Second, by tracking colonies of *O. annularis* between sampling intervals, vital rates (mortality and intrinsic population growth, $\lambda$) are compared over time, including before and immediately after Hurricanes Irma and Maria. Analysis of the demographic implications of the hurricanes focused on a contrast of photoquadrats recorded in July 2017 and November 2017 in order to describe the immediate effects of the storms (e.g., scouring, dislodgement, breakage), rather than delayed effects over the following year, such as could arise from disease (Knowlton et al. 1981), or macroalgal blooms. Finally, the demographic implications of these hurricanes are evaluated using 20-yr projections of *O. annularis* populations, starting either with the pre-storm, or the post-storm, population structure.

Field surveys and image analysis

Thirty photoquadrats at each site were recorded annually using a Nikonos V camera fitted with Kodachrome 64 film prior to 2000, and digital cameras thereafter, with the resolution changing from 3.34 MP to 36.3 MP (2017 onwards). The images analyzed herein were recorded in March 1988, June 1993, July 1998, 2003, 2008, 2013, 2016, and 2017, November 2017, and July 2018. Nine of these samplings were part of the routine time-series, but the November 2017 sampling was implemented to assess the effects of Hurricanes Irma and Maria. These years were subsampled from the 32-yr record to provide an overview of the trends in coral cover affecting these reefs; the changes are reported for every year in Edmunds (2013), and Edmunds and Lasker (2016). The slides were professionally digitized (4000 dpi) and analyzed using either CPCe (Kohler and Gill 2006) or CoralNet software (with manual annotation; Biejom et al. 2015). In both cases, 200 random dots were superimposed on each image, with the number of dots falling on each substratum expressed as a proportion of the dot population providing a measure of percentage cover (Menge 1976). The present analysis reports the...
percentage cover of all corals and *O. annularis*, with a full description of changes in benthic communities over nearly three decades summarized elsewhere (Edmunds 2000, 2013, 2019, Edmunds and Lasker 2016).

The photoquadrats were also used to evaluate the size, density, and fate of colonies of *O. annularis*. First, colonies were enumerated in photoquadrats, and their size (cm², planar area) was determined using Image J software (Abramoff et al. 2004). These data were used to calculate colony density (colonies/m²), sizes, and their distribution among four size classes: I ≤ 50 cm², II > 50 cm² and ≤150 cm², III > 250 cm² and ≤250 cm², and IV > 250 cm². These size classes sampled the range of colony sizes of this species at Yawzi Point in 1988 (i.e., with ≥39 colonies/size class), and their use in previous demographic analyses of *O. annularis* at Yawzi Point and Tektite (Edmunds and Elahi 2007, Edmunds 2015) mandated their use in the present analysis to support backward compatibility. Second, spatially corresponding photoquadrats were paired between sampling intervals, and colonies were tracked between July 2016 and July 2017, and between July 2017 and November 2017, to measure growth, survivorship, and cases of fission and fusion. Only identifiable colonies that were fully within photoquadrats were tracked, which restricted the number of colonies that could be tracked, particularly when photoquadrat positioning was inaccurate, lighting was poor, or colonies were obscured by macroalgae. For trackable colonies, their sizes were measured at each sampling, fission products were recorded, and cases of fusion or mortality were scored.

**Demographic analyses**

The size and fates of colonies of *O. annularis* were used to prepare 4 × 4, size-based Leslie matrices (Hughes 1984) for July 2016–July 2017, and July 2017–November 2017. Matrices and vital rates for 1988–1993, 1993–1998, 1998–2003 (Yawzi Point and Tektite), 2003–2008, and 2008–2013 (Tektite) were obtained from previously published results (Edmunds and Elahi 2007, Edmunds 2015). The 16 transition probabilities in each matrix were calculated from the fates of colonies that began the study intervals in one of four size classes, and through growth, shrinkage, stasis, or death, remained in the same size class, transitioned among size classes, or died. Bootstrap resampling (with replacement) was used to generate 1000 versions of each matrix and mortality estimates in order to calculate 95% confidence intervals (CI) on vital rates. Resamplings were conducted in Excel (Microsoft Office 365 ProPlus) using the Resampling Stats 4.0 add-in (statistics.com LLC) running in a Windows 7 operating system.

The matrices were used to calculate the intrinsic rate of population increase (λ), the rate at which the population converged to a stable size structure (the damping ratio, ρ), and stable stage distribution of the colonies (right eigenvector), using the Pootools 2.4 add-in (Hood 2010) to Excel 2000 operating on a 32-bit PC platform. Prospective perturbation analyses (Caswell 2000) were conducted using elasticity matrices to reveal the influence of each transition in modifying λ. Retrospective perturbation analyses (i.e., Life Table Response Experiments [LTRE]; Caswell 2000) were used evaluate how variation in vital rates before versus after the hurricanes led to changes in λ. Retrospective analyses were conducted after Caswell (2001) and Cockrell and Sorte (2013). In the matrices of contributions that LTRE generates, positive values of the matrix elements indicate parameters that caused an increase in λ following the hurricanes, whereas negative values indicate parameters that cause a decrease in λ (Caswell 2001).

The previous demographic analyses of *O. annularis* (i.e., Edmunds 2015) were based on 5-yr intervals with the rationale that 5 yr was necessary to record the effects of slow growth in this species. In the present study, matrices based on 4-month intervals were used to capture the effects of Hurricanes Irma and Maria, and matrices with 12-month intervals over the preceding year were used as a baseline against which the effects of the hurricanes on *O. annularis* were compared. The advantage of using these two periods of time for the study was to focus the post-hurricane analysis on immediate mortality and partial mortality, rather than delayed effects occurring during the following year. This sampling regime was close to that employed nearly 30 yr ago to evaluate the effects of Hurricane Hugo on the same reefs (Edmunds and Witman 1991) and corresponds to the sampling regime used to describe the effects of Hurricanes Irma
and Maria on coral community ecology of the study reefs (Edmunds 2019). To contrast λ between the present and previous studies, values over 1 yr were raised to the power of 5, and the rates over 4 months were raised to the power of 15. While this made them comparable to values measured over 5 yr (as in Edmunds 2015), estimates over short periods are prone to errors, which are reflected in high values and large CI.

To test for the demographic implications of Hurricanes Irma and Maria on *O. annularis*, populations were projected starting with the vector describing the population in the 30-m² study areas in July 2017 (i.e., before the hurricanes) or November 2017 (i.e., after the hurricanes). Projections were completed with the most recently available 4 × 4 matrix calculated over 5 yr, which was over 2008–2013 for Tektite (Edmunds 2015) and 1998–2003 for Yawzi Point (Edmunds and Elahi 2007), and included recruitment of *O. annularis* that was estimated from adjacent shallow areas in St. John (5–9 m depth) over 20 yr (equivalent to eight colonies 30 m⁻² 5 yr⁻¹; Edmunds 2015). Recruits were added to size class I at each iteration, with four iterations projecting the population 20 yr. The final population vector was used to estimate coral cover assuming colony sizes in each size class were normally distributed so that an average colony in size class I had an area of 25 cm², in size class II an area 100 cm², in size class III an area of 200 cm², and in size class III an area of 250 cm².

**RESULTS**

**Decadal-scale changes in coral communities**

The reefs dominated by *Orcicella annularis* at Yawzi Point and Tektite changed in different ways over 32 yr (Fig. 1A). At Yawzi Point, mean coral cover (±SE) was 43% ± 3% in 1988, but declined to 6% ± 2% in July 2017, with large declines in the 5-yr intervals ending after Hurricane Hugo in 1989 (i.e., 1993), and Hurricanes Marilyn and Luis in 1995 (i.e., 1998). From 1988 to 2018, ≥60% of the coral cover was *O. annularis* complex, and the decline reflected a loss of *O. annularis*, as shown by the 81% reduction in mean colony density from 1988 to July 2017. While coral cover and *O. annularis* density declined from 1988, mean colony size increased by 50% from 76 cm² in 1988 to 114 cm² in 1993, but declined by 71% from 1993 to July 2017 (mean size = 33 cm²).

At Tektite, mean coral cover (±SE) was 33% ± 3% in 1988, but increased to 48% ± 3% in 2003 and then declined to 31% ± 2% by July 2017 (Fig. 1B). *O. annularis* accounted for ≥72% of coral cover, and the mean colony size increased from 68 ± 3 cm² in 1988 to 93 ± 6 cm² in 2003 and then declined to 27 ± 1 cm² in July 2017. Mean density (±SE) increased by 90% from 1988 (36 ± 6 colonies/m²) to 2013 (68 ± 9 colonies/m²) but declined to 53 ± 8 colonies/m² in July 2017.

The 32-yr period covered by these analyses encompassed three major hurricane episodes, with Hurricane Hugo on 18 September 1989 (with maximum wind speeds of 214 km/h, a pressure of 94.6 kPa, and 12 cm of rain on the day of impact), Hurricanes Marilyn and Lenny in 1995 (6 and 16 September, respectively, with maximum wind speeds of 217 km/h and 177 km/h, a pressure of 94.1 and 95.7 kPa, and 4 cm and 13 cm of rain on the day of impact), and Hurricanes Irma and Maria in 2017 (6 and 20 September, respectively, with maximum wind speeds of 298 km/h and 266 km/h, a pressure of 92.0 and 91.7 kPa, and 17 cm and 11 cm of rain on the day of impact). When these storms impacted St. John, Hurricane Hugo was a Category 4 storm on the Saffir-Simpson hurricane scale, Luis and Marilyn were Category 2 and 3, respectively, and Hurricanes Irma and Maria were Category 5 (see Edmunds 2019).

**Demographic effects of Hurricanes Irma and Maria**

Hurricanes Irma and Maria had small effects on the two *O. annularis* populations. At Yawzi Point, there was a non-significant (t = 0.560, df = 58, P = 0.577) decline in mean coral cover (±SE) from 6% ± 2% in July 2017 to 5% ± 2% in November 2017, and colony density and size were unchanged (9 colonies/m² and ~ 32 cm², respectively). At Tektite, the decline in mean coral cover (±SE) from July 2017 (31% ± 2%) to November 2017 (27% ± 2%) was not significant (t = 1.417, df = 58, P = 0.162), and colony density and size remained unchanged (~52 colonies/m² and 27 cm², respectively).

At Yawzi Point, 184 colonies were surveyed from July 2016 to July 2017, and 80% were in size class (I), 19% in size class II, and 1% in size class
III; there were none in size class IV. Between samplings, most (92%) size class I colonies remained in this size class, and while 91% of size class II colonies remained in the same size class, there was a 46% chance that these colonies transitioned to size class I through fission; 8% of size class I colonies died, but none died in size class II (Table 1). Because of fission of size class II colonies, the population maintained positive growth ($\lambda = 1.012$) without recruitment. Between July 2017 and November 2017, 150 colonies were repeatedly surveyed: 83% started in size class I, 16% in size class II, and 1% in size class III. Over 4 months, 67% of size class I colonies remained in this size class, and 31% died, and while 46% of size class II colonies remained in the same size class, 29% died. With sparse observations over a short period, the 4-month matrix requires caution in interpretation, but with $\lambda < 1$, the population was declining. The lower bootstrapped value ($\lambda_b = 0.958$) suggests the rate of decline was greater than the single empirical value (Table 1).

At Tektite, 1206 colonies were tracked from July 2016 to July 2017: 88% were in size class I, 12% in size class II, 1% in size class III, and no colonies were in size class IV (Table 1). Overall, the July 2016–July 2017 matrix was similar to that for Yawzi Point, showing that 95% of size class I colonies remained in size class I, as did colonies in size classes II and III (80% and 89%, respectively; Table 1). Twenty-five percent of colonies shrank from size class II to I, and 22% shrank from size class III to either II or I. There was a 22% probability of size class III colonies transitioning to size class IV. Mortality in size classes I and II was 6% and 1%, respectively, and with little fission, the population declined without

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**Fig. 1.** Coral abundance from March 1988 to November 2011 on reefs dominated by *Orbicella annularis* at (A) Yawzi Point (9 m depth) and (B) Tektite (14 m depth). Data from 1988 to 2013 are subsets of annual time-series (Edmunds 2013, 2019) that have been used to support demographic analyses at 5-yr increments (Edmunds and Elahi 2007, Edmunds 2015), and are combined with three samplings over 12 months from July 2017 that quantify the effects of Hurricanes Irma and Maria (September 2017). Black = mean ($\pm$SE) combined coral cover (% left ordinates) of which *O. annularis* complex (sensu Knowlton et al. 1997) represents 60–96% by year ($n = \sim 30$ yr $^{-1}$), blue = mean ($\pm$SE) colony density (colonies/m$^2$, right ordinates) of *O. annularis*, and red = mean ($\pm$SE) colony size (cm, right ordinate) of *O. annularis* ($n = 200–1605$ colonies/yr). Vertical dashed lines show the occurrence of five major hurricanes impacting these reefs from 1989.
Table 1. Summary of Leslie matrices and elasticity matrices describing populations of *Orbicella annularis* at Yawzi Point and Tektite from July 2016 to July 2017 (A & C, before Hurricanes Irma and Maria), and from July 2017 to November 2017 (B & D, after Hurricanes Irma and Maria).

| Parameter | I | II | III | IV | Stable distribution (%) |
|-----------|---|----|-----|----|-------------------------|
| **Yawzi Point** | | | | | |
| A) July 2016–July 2017 (12 months) | | | | | |
| Leslie matrices | | | | | |
| I | 0.918 | 0.457 | 0.000 | 0.000 | 58 |
| II | 0.020 | 0.914 | 0.000 | 0.000 | 12 |
| III | 0.000 | 0.029 | 1.000 | 0.000 | 30 |
| IV | 0.000 | 0.000 | 0.000 | 0.000 | 0 |
| Dead | 0.047 | 0.000 | 0.000 | 0.000 | |
| Fusion | 0.048 | 0.143 | 0.000 | 0.000 | |
| N | 147 | 35 | 2 | 0 | |
| λ | | | | | 1.012 |
| λb | | | | | 1.018 |
| ρ | | | | | 0.463 |
| Elasticity matrices | | | | | |
| I | 0.463 | 0.047 | 0.000 | 0.000 | |
| II | 0.047 | 0.442 | 0.000 | 0.000 | |
| III | 0.000 | 0.000 | 0.000 | 0.000 | |
| IV | 0.000 | 0.000 | 0.000 | 0.000 | |
| B) July 2017–November 2017 (4 months) | | | | | |
| Leslie matrices | | | | | |
| I | 0.669 | 0.292 | 0.000 | 0.000 | 0 |
| II | 0.024 | 0.458 | 0.000 | 0.000 | 0 |
| III | 0.000 | 0.000 | 1.000 | 0.000 | 100 |
| IV | 0.000 | 0.000 | 0.000 | 0.000 | 0 |
| Dead | 0.270 | 0.250 | 0.000 | 0.000 | |
| Fusion | 0.032 | 0.041 | 0.000 | 0.000 | |
| N | 124 | 24 | 2 | 0 | |
| λ | | | | | 0.999 (0.997) |
| λb | | | | | 0.958 (0.879) |
| ρ | | | | | 1.432 (2.938) |
| Elasticity matrices | | | | | |
| I | 0.000 | 0.000 | 0.000 | 0.000 | |
| II | 0.000 | 0.000 | 0.000 | 0.000 | |
| III | 0.000 | 0.000 | 1.000 | 0.000 | |
| IV | 0.000 | 0.000 | 0.000 | 0.000 | |
| **Tektite** | | | | | |
| C) July 2016–July 2017 (12 months) | | | | | |
| Leslie matrices | | | | | |
| I | 0.951 | 0.250 | 0.111 | 0.000 | 84 |
| II | 0.027 | 0.800 | 0.111 | 0.000 | 13 |
| III | 0.000 | 0.021 | 0.889 | 0.000 | 3 |
| IV | 0.000 | 0.000 | 0.222 | 0.000 | 1 |
| Dead | 0.038 | 0.000 | 0.000 | 0.000 | |
| Fusion | 0.020 | 0.014 | 0.000 | 0.000 | |
| N | 1057 | 140 | 9 | 0 | |
| λ | | | | | 0.993 |
| λb | | | | | 0.997 |
| ρ | | | | | 1.011 |
| Elasticity matrices | | | | | |
| I | 0.716 | 0.030 | 0.003 | 0.000 | |
| II | 0.032 | 0.150 | 0.004 | 0.000 | |
| III | 0.000 | 0.007 | 0.058 | 0.000 | |
| IV | 0.000 | 0.000 | 0.000 | 0.000 | |
recruitment ($\lambda = 0.993$). Between July 2017 and November 2017, 1255 colonies were repeatedly surveyed: 87% were in size class I, and $\geq 64\%$ remained in their initial size class for size classes I, II, and III. Over 4 months, mortality in size classes I, II, and III was 9%, 4%, and 7%, respectively, but with shrinkage and fission of colonies in size classes II and III, the net effect was equivocal with respect to population growth. While the empirical $\lambda$ was 1.093, the boot-strapped mean value was 0.991.

The demographic properties of $O.\ annularis$ at Yawzi Point and Tektite differed between the year before the hurricanes and the 4 months bracketing the storms (Table 1). The hurricanes increased the damping ratio ($\rho$), especially at Yawzi Point ($\rho$ increased from 2.938 [1.432 over 4 months]) vs. Tektite ($\rho$ increased from 1.168 to 1.594 [1.168 over 4 months]). The increase in $\rho$ after the hurricanes revealed an accelerated tempo of convergence to a stable distribution of colony sizes that differed between sites and times. The stable distribution (Table 1) shows a stronger dominance of small colonies at Tektite (84% of colonies) vs. Yawzi Point (58% of colonies) before the storms. After the storms, so few colonies remained at Yawzi Point that transitions either were zero or were based on small sample sizes. Based on limited data, the stable distribution at this site was more uniform than before the storms, with size class I colonies representing 51% of the population.

Prospective perturbation analyses of the populations at Yawzi Point and Tektite showed that prior to the hurricanes, they were most sensitive to the number of small colonies that remained small (i.e., the I—I transition). Over the four months encompassing the hurricanes, the populations were most sensitive to larger colonies that remained large (i.e., the III—I and IV—I transitions; Table 1). Retrospective perturbation analyses evaluating the roles of hurricane-associated changes in matrix transitions in driving variation in $\lambda$ revealed that the
decline in population growth at Yawzi Point was weakly affected by the reduction in likelihood that size class II colonies would grow into size class III colonies (i.e., this transition changed from 0.029 to 0.000; Table 2). At Tektite, retrospective analysis revealed that the change in population growth ($\lambda$) was associated with the reduction in probability of size class III remaining in this size class (i.e., this transition changed from 0.889 to 0.643), and instead transition to smaller size classes, and increased probability that size class IV colonies would transition to size class III (Table 2).

Demographic context and population projections

The demographic underpinning to 30 yr of changing abundances of *O. annularis* at Yawzi Point and Tektite (Fig. 1) involves a loss of the largest colonies (Fig. 2), which changed the distribution of colonies among the four size classes between 1988 and July 2017 at Yawzi Point ($\chi^2 = 51.82$, df = 3, $P < 0.001$) and Tektite ($\chi^2 = 300.60$, df = 3, $P < 0.001$). By July 2017, there were no colonies $>250$ cm$^2$, and colonies $>150$ cm$^2$ were rare at Yawzi Point (2% of colonies) and absent at Tektite. These trends were accentuated by Hurricanes Irma and Maria, which resulted in a slightly increased relative abundance of colonies in size class I from July 2017 (83% of colonies) to November 2017 (87% of colonies) at Yawzi Point ($\chi^2 = 3.66$, df = 3, $P = 0.300$), and an increase at Tektite (86% in July 2017 vs. 99% in November 2017; $\chi^2 = 175.88$, df = 3, $P < 0.001$).

Whole colony mortality drove the disappearance of larger colonies at both sites, with 3–5% of size class IV colonies dying annually between 1988 and 2003 at Yawzi Point and 1–8% dying annually between 1988 and 2008 at Tektite (Fig. 3). As colonies transitioned into smaller size classes through partial mortality, whole colony mortality of size class I colonies reduced population size at Yawzi Point (where 10–11% of size class I colonies died annually from 1988 to 2003), but had a smaller effect at Tektite, where 4–7% of size class I died annually. Against this backdrop, whole colony mortality in the year preceding Hurricanes Irma and Maria (July 2016–July 2017) was unremarkable relative to the preceding 30 yr, with annual mortality of size class I corals amounting to 5% at Yawzi Point and 4% at Tektite (Fig. 3). Whole colony mortality over the following 4 months was high, with 27% of size class I and 25% of size class II corals dying at Yawzi Point and 5% of size class I corals dying at Tektite (Table 1, Fig. 3). At both sites, the size of corals dying in size class I was small, with dead colonies at Yawzi Point having a mean ($\pm$SE) size of $17 \pm 2$ cm$^2$ ($n = 34$) and $8 \pm 1$ cm$^2$ ($n = 53$) at Tektite.

Over the 30 yr preceding Hurricanes Irma and Maria, the intrinsic rate of population change ($\lambda$, without recruitment) differed between Yawzi Point and Tektite (Fig. 4). While $\lambda$ remained $\sim 0.6$ over 15 yr at Yawzi Point, indicating a population declining in size (Fig. 1), at Tektite it remained close to 1 in four of five intervals spanning a quarter century, indicating a population of largely stable size. Although $\lambda$ values calculated over short intervals (i.e., July 2016–July 2017 and July 2017–November 2017) are less accurate than those calculated over longer intervals (note larger CI for these periods versus 5-yr periods in Fig. 4), the values indicate that the year preceding Hurricanes Irma and Maria was a period of relative stability at both sites (i.e., $\lambda \sim 1$). The following four months was a period of strong decline in population size, with the lowest mean

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Table 2. Matrices of contributions showing the outcome of retrospective perturbation analyses using Life Table Responses Experiment (LTRE; Caswell 2000) of the population matrices for *Orbicella annularis* at (A) Yawzi Point, and (B) Tektite before (July 2016–July 2017), and after (July 2017–November 2017), Hurricanes Irma and Maria.

| Parameter      | I        | II       | III      | IV       |
|----------------|----------|----------|----------|----------|
| **A) Yawzi Point** |          |          |          |          |
| I              | 0.000    | 0.000    | 0.000    | 0.000    |
| II             | 0.000    | 0.000    | 0.000    | 0.000    |
| III            | 0.000    | $-0.029$ | 0.000    | 0.000    |
| IV             | 0.000    | 0.000    | 0.000    | 0.000    |
| **B) Tektite** |          |          |          |          |
| I              | $-0.034$ | 0.002    | 0.080    | 0.074    |
| II             | $-0.060$ | 0.003    | 0.139    | 0.143    |
| III            | $-0.161$ | 0.009    | 0.375    | 0.385    |
| IV             | 0.000    | 0.001    | $-0.025$ | 0.071    |

Notes: Values show the contribution of each transition from the two periods on the rate of population growth ($\lambda$) for *O. annularis*. Negative values indicate transitions that contributed to population decline, and positive values indicate transitions that contributed to population growth.
value of \( \lambda \) (adjusted to 5 yr as described in Methods) recorded at Yawzi Point (\( \lambda = 0.528 \)). Lambda also was depressed at Tektite (mean bootstrapped value of \( \lambda = 0.873 \)) with the CI suggesting this could be the lowest value recorded at this site in 30 yr (Fig. 4).

To evaluate the future implications of Hurricanes Irma and Maria, 20-yr projections were completed with the population vectors characterizing each population before (July 2017) and after the storms (November 2017; Fig. 5). Regardless of the effects of the hurricanes, the population of

Fig. 2. Size-frequency structure (percentage of colonies) of *Orbicella annularis* populations at (A) Yawzi Point, and (B) Tektite in 1988, July 2017, and November 2017 based on four size classes: I \( \leq 50 \text{ cm}^2 \), II \( > 50 \text{ cm}^2 \) and \( \leq 150 \text{ cm}^2 \), III \( > 150 \text{ cm}^2 \) and \( \leq 250 \text{ cm}^2 \), and IV \( > 250 \text{ cm}^2 \). Sample sizes (number of colonies) shown in each plot.

Fig. 3. Mortality of *Orbicella annularis* in four size classes (as in Fig. 2) over 3–5 intervals of 5 yr (1988–2013), 1 yr (July 2016–July 2017), or 4 months (July 2017–November 2017) at Yawzi Point (A) or Tektite (B). Except for the final sampling (July 2017–November 2017, *), mortalities were scaled proportionately to 1 yr regardless of the interval over which they were calculated. All values are empirical means \( \pm 95\% \) CI as determined from 1000 bootstrap resamplings (with replacement) of the raw data. n/d means no data.
O. annularis at Yawzi Point will be exceptionally small in 20 yr. There will be \(\leq 1.4\) colonies/m\(^2\), \(\geq 72\%\) of the colonies will be \(\leq 50\) cm\(^2\) in size (and \(\geq 97\%\) \(\leq 150\) cm\(^2\)), and the combined cover will be \(\leq 0.6\%). Hurricanes Irma and Maria reduced 20-yr projected coral cover from 0.6% to 0.3%.

### DISCUSSION

#### Overview

When Hurricanes Irma and Maria hit St. John in September 2017, they were unprecedented in human memory for their magnitude and back-to-back occurrence within 14 d (Cox et al. 2019). Destruction on land was extensive (Cox et al. 2019), and in one sheltered bay on St. John, there was broadscale (i.e., 1.28 km\(^2\)) burial under ~25 cm of re-suspended and transported marine sediment (Browning et al. 2019). Yet on coral reefs on the south shore of St. John, the damage to scleractinians at 7–14 m depth was minor when quantified through percentage cover (Edmunds et al. 2019; and also off St. Thomas, Gochfeld et al., unpublished manuscript), and benchmarked against expectations based on the high coral mortality that resulted from previous storms impacting Caribbean reefs (Woodley et al. 1981, Edmunds and Witman 1991, Rogers et al. 1991). Leading reasons for the limited underwater effects of Hurricanes Irma and Maria on coral reefs is that colonies of more delicate scleractinians had already been killed prior to September 2017 (Zhang et al. 2014), allowing these reefs to acquire resilience through adversity and the low coral abundance that it favors (Edmunds 2019). Regardless of the causes of this resilience, statistical power in detecting changes in low coral cover (i.e., for rare organism) is likely to be low in time-series analyses that were designed for coral-dominated reefs (i.e., where coral is common; e.g., Cunningham and Lindenmayer 2005). Moreover, where changes are detected in low abundance coral communities, inferring ecological meaning from small absolute change (that can be relatively large) probably is unreliable (MacKenzie et al. 2005). Demographic approaches (sensu Hughes 1984, Caswell 2001, Riegl et al. 2017) provide appropriate tools for such situations (Riegl et al. 2017), and here, they reveal the effects of Hurricanes Irma and Maria on Orbicella annularis.

Addressing the objectives of the present study generated three domains of results. First, the analyses show that the small changes in coral
Hurricanes Irma and Maria accentuated a decadal trend for declining cover, as well as increasing abundance of diminutive colonies (i.e., <50 cm$^2$) that are subject to high mortality (Hughes and Jackson 1980, Hughes and Tanner 2000, Edmunds 2015). Hurricanes Irma and Maria hastened the shrinkage, fission, and fracturing of large colonies into small colonies that had a high chance of dying. Coral cover barely detected the summation of these categorical events. Second, the 32-yr time-series of coral abundance at Yawzi Point and Tektite reveals the large extent to which percentage coral cover provides an incomplete record of variation in the population biology of *O. annularis*.

While initial (1987) and final (2018) coral cover documents losses of 90% at Yawzi Point and 18% at Tektite, the dynamics of colonies describe contrasting results. The population density of *O. annularis* declined by 62% at Yawzi Point but increased by 43% at Tektite, and mean colony size declined by ~60% at both sites as colonies transitioned from large to small sizes. Moreover, the intrinsic rate of population growth ($\lambda$) calculated up until 2013 revealed a declining population at Yawzi Point, but a stable or increasing population at Tektite. Hurricanes Irma and Maria pushed both populations into decline (mean boot-strapped $\lambda$ < 1.0); they accelerated the tempo of change ($\rho$ increased) and modified the stable distribution of colony sizes. Finally, 20-yr projections initiated with differing population vectors (i.e., before versus after the hurricanes) revealed outcomes that are unlikely to represent ecologically meaningful differences. These outcomes reflect the limited ability of acute disturbances (i.e., hurricanes) to modify the ongoing trajectories of change affecting coral populations on reefs that already are in a degraded state. Such disturbances may, however, mediate coral host genetic diversity by winnowing small colonies to remove host genotypes and their clonal replicates.

**The demographic responses to two hurricanes**

Based on state variables that are ubiquitous in studies of coral reef community structure (Connell 1997, Bruno and Selig 2007, van Woesik and Jordán-Garza 2011), Hurricanes Irma and Maria did not have statistically discernable effects on
the coral communities at Yawzi Point and Tektite (Edmunds 2019). These storms did, however, lead to a 30% increase in cover of macroalgae, which already covered 41% of these reefs when the hurricanes hit (Edmunds 2019). Using demographic state variables defined by the fate of colonies of O. annularis, the effects of the hurricanes were more nuanced, yet important. The clearest effect was accentuation of the decade-long trend for declining colony size (Edmunds 2015), which transitioned virtually all (≥87%) colonies at Yawzi Point and Tektite to the ≤50 cm² size class from which colonies were removed through mortality. Mortality of the smallest colonies at Yawzi Point was high (27% in four months) compared to previous survey periods and effectively removed 63 colonies from the population. At Tektite, a 5% mortality rate over 4 months removed more colonies (67) from the larger population at this site compared to Yawzi Point. The large magnitude of these mortality rates is underscored by extrapolating them to a 5-yr interval, as previously employed in demographic analyses of O. annularis at these sites (Edmunds and Elahi 2007, Edmunds 2015), over which 67% of size class I colonies would be killed at Tektite, and all colonies in this size class would be killed at Yawzi Point. When scaled to 1 yr, the hurricane-mediated mortality of size class I colonies at Yawzi Point (81%) would be higher than eight comparable values recorded for an O. annularis population at Culebra Island, Puerto Rico, (at ≤14 m depth) from 2001 to 2009 (1–34%; Hernandez-Pacheco et al. 2011). In comparison with the same study, the mortality of size class I colonies at Tektite would be higher than recorded in six of eight years, with higher rates in Culebra Island as a result of bleaching from 2005 to 2006 (30–34%; Hernandez-Pacheco et al. 2011).

As Hurricanes Irma and Maria also redistributed the cover of Orbicella annularis from large (i.e., in July 2017) to small (≤50 cm²) colonies (i.e., by November 2017), the effects of the storms on coral cover were small (Edmonds 2019). These demographic events were reflected in the sensitivity of population growth (λ) to specific transition probabilities in the Leslie matrices (Table 1), as revealed in prospective perturbation analyses. At both sites, λ shifted from being most sensitive to the fate of the smallest colonies from July 2016 to July 2017, to the fate of larger colonies from July 2017 to November 2018. These effects were revealed in slight declines in λ to <1.0 at Yawzi Point and Tektite (for the 5 yr, boot-strapped mean λ), with retrospective perturbation analyses (i.e., LTRE after Caswell 2000) suggesting the declines in λ were caused by different processes at each site. At Yawzi Point, the hurricane-associated change in the probability of size class II colonies (which were >50 cm² but ≤150 cm²) transitioning to size class III colonies appeared to have the strongest effect in depressing λ. In contrast, at Tektite, the hurricane-associated decline in the boot-strapped mean value for λ was most strongly affected by the increase in size class IV colonies transitioning to size class III, the reduction in size class III colonies remaining in this size class, and presumably, exiting the population by transitioning to size class I. These conclusions regarding demographic processes, however, have to be interpreted with caution because the transition probabilities at both sites are based on a small number of colonies for the larger size classes, which makes them prone to stochastic effects.

A decline in coral colony size is a common response to adverse conditions by tropical scleractinians (Hughes and Tanner 2000, Riegl and Purkis 2015, Riegl et al. 2017, but see Pisapia et al. 2016 for a case of the alternate trend), and on many reefs, it is a feature of the globally intensifying coral reef crisis (Fong and Glynn 1998, Hernandez-Pacheco et al. 2011, Riegl et al. 2017). Such declines might not be detected in analyses of coral cover, because cover is insensitive to the ways in which it is distributed among colonies (Hughes and Jackson 1985). Declining colony size has important implications, however, because mortality rises with declining colony size (Hughes and Jackson 1980), fecundity increases with size (Szmant-Froelich 1985, Hughes et al. 1992), and sexual maturity is determined by the interaction of age and size (Kojis and Quinn 1985, Szmant-Froelich 1985, Chornesky and Peters 1987). For Orbicella annularis, colonies probably are not sexually mature until they have ~100 cm² of tissue (Szmant-Froelich 1985), which corresponds to a planar area of ~50 cm² (as in the present study) assuming colonies are hemispherical. By November 2017, this cutoff was exceeded by only 13% of the colonies at Yawzi Point and Tektite, indicating that few of...
the colonies were capable of producing gametes. In the short term, these trends might not measurably affect recruitment of *O. annularis* in St. John, because this species reproduces by mass spawning in open populations (Levitan et al. 2004), which prevents a local stock–recruitment relationship (Caley et al. 1996), and has recruited in St. John at low rates for decades (Edmunds et al. 2011). Over a longer period, however, a regional decline in fecundity will undermine the possibility of future episodic high recruitment that has been hypothesized as important for maintaining populations of this species (Hughes and Jackson 1985, Edmunds and Elahi 2007).

In addition to removing small amounts of tissue from *O. annularis* populations, the transition of large colonies to smaller size classes, which die at elevated rates, also removes host genotypes. As *O. annularis* relies on extensive asexual reproduction for population growth (Barnes 1973, Knowlton et al. 1992, Foster et al. 2007), most frequently through fission (Hughes and Tanner 2000), the mortality of small colonies removes host genotypes or clonal replicates of specific host genotypes (i.e., genets and ramets, respectively; Heyward and Collins 1985). Ramets of individual genets therefore are likely to be spatially co-located, and the probability that mortality removes unique genotypes will depend on the degree of separation of affected colonies. Regardless of whether mortality removes genets or ramets, the summation of ramet mortality has the potential to remove multiple genets (Foster et al. 2007). Losses of *O. annularis* genets, as probably occurred during Hurricanes Irma and Maria, will deplete the population of host genotypes and increase the susceptibility to select disturbances such as diseases and bleaching (Reusch et al. 2005, Baums et al. 2006, van Woesik and Jordán-Garza 2011).

**Placing recent events in a decadal context**

When placed in the 31-yr history of Yawzi Point and Tektite (Edmunds and Elahi 2007, Edmunds 2013, 2015), the effects of the 2017 hurricanes on the cover, abundance, and size of *Orbicella annularis* colonies emerge as extensions of ongoing trends. At Yawzi Point, three decades of declining values of these state variables were accentuated by Hurricanes Irma and Maria. At Tektite, the same state variables shared a more complex history, but their values in 2017 were more coherent with the previous two years than with the effects of the hurricanes. This interpretation is consistent with the size-frequency structure of the populations in 1988 and 2017, mortality at Tektite, and the intrinsic rates of population growth (λ) at both sites. At Yawzi Point, however, the high mortality of size class I and II colonies from July to November 2017 reveals the role of the recent hurricanes in removing host genotypes. These observations reveal the extent to which well-known disturbances (i.e., hurricanes) acting on present-day reefs cannot reliably be predicted from historic occurrences of similar events (e.g., Woodley et al. 1981, Harmelin-Vivien 1994).

**Projecting coral populations**

While it is beyond the scope of the present study to consider how population dynamics might be affected by host genotype mortality, insight into future population structure can be provided by demographic projections (sensu Caswell 2001). Projections are not forecasts (Caswell 2001), and their efficacy is based on the assumption that previous performance is indicative of future performance under conditions similar to those of the past. If this assumption is correct, the 20-yr projections conducted herein indicate whether Hurricanes Irma and Maria have appreciably altered the likely future of *O. annularis* populations.

These projections assumed that the future performance of colonies can be described by the products of Leslie matrices prepared from changes over 1998 to 2003 at Yawzi Point and from 2008 to 2013 at Tektite (as in Edmunds and Elahi 2007, Edmunds 2015), and vectors describing each population prior to (July 2017) or after (November 2017) the hurricanes. At Yawzi Point, these projections corroborated previous analyses that indicated local extirpation was imminent (Edmunds and Elahi 2007), and suggest that by 2037, ≤0.6% of the reef would be covered by live *O. annularis*. This coverage is equivalent to one 9 cm diameter colony in 1 m², and whether or not these reefs were hit by two category 5 hurricanes effectively determined whether such a colony might be found in 1 m² or 2 m², twenty years later. At Tektite, the projections suggested that *O. annularis* would persist on this reef with
low cover (i.e., ~15%) through 2037, with the final cover being 16% (if the hurricanes had not occurred) or 12% (with the hurricanes). In all four projections, the populations remained dominated by size class I colonies, and there were no size class IV colonies either at the start or at the end of the 20-yr projections.

A critical issue in evaluating the present 20-yr projections (Fig. 5) is whether the differences between projections initiated with, and without, hurricane effects are ecologically meaningful? An unequivocal answer to this question is beyond the scope of this study, as it requires information on future environmental conditions and the response of *Orbicella annularis* to these conditions. Moreover, it is likely to require demographic approaches more sophisticated than employed herein (e.g., integral projection models; Edmunds et al. 2014), potentially to create the capacity for population viability analyses (PVA; Brook et al. 2000). However, 30 yr of time-series analyses of these populations provides context within which the projected changes can be evaluated, and within this history, the projected differences arising from the hurricanes are minor. For example, at Yawzi Point, the difference of 0.3% cover between projections is less than the variation in cover between consecutive years from 1987 to 2017, and at Tektite, the difference of ~4% between projections is comparable to the variation that previously has occurred over 3–4 yr at this site (Edmunds 2013, 2019).

**Summary**

The present study describes the impacts of two hurricanes on the population biology of *Orbicella annularis*, on reefs where the effects of the same storms on coral cover have been reported in detail (Edmunds 2019). For reefs between 7 and 14 m depth, the earlier study reported coral community resilience to storm effects as a result of decades of degradation (Edmunds 2019), largely as predicted (Gross and Edmunds 2015), and the present study sought to identify the demographic basis of this response, at least for one species at two sites. While demographic analyses corroborate the early conclusion by demonstrating resistance of *O. annularis* populations to hurricanes, this outcome hides re-arrangement of coral cover among colonies differing in size, as well as enhanced rates of complete mortality of small colonies. Given the small sizes of the coral populations that were studied, and their dominance by diminutive colonies when the hurricanes hit, these trends may represent ecologically meaningful winnowing of coral host genotypes that might lead to greater future sensitivity of the populations to disturbances. As biologists and resource managers revise their approaches to studying coral reefs to address the new reality of low abundance coral populations (Edmunds 2018), demographic techniques and identification of host genotypes will need to be more seriously considered as mandatory tools of coral reef time-series analyses (van Woesik and Jordán-Garza 2011).

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