Coral Reefs
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REPORT

The recovery of octocoral populations following periodic disturbance masks their vulnerability to persistent global change

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Abstract As the major form of coral reef regime shift, stony coral to macroalgal transitions have received considerable attention. In the Caribbean, however, regime shifts in which scleractinian corals are replaced by octocoral assemblages hold potential for maintaining reef associated communities. Accordingly, forecasting the resilience of octocoral assemblages to future disturbance regimes is necessary to understand these assemblages' capacity to maintain reef biodiversity. We parameterised integral projection models quantifying the survival, growth, and recruitment of the octocorals, *Antillogorgia americana*, *Gorgonia ventalina*, and *Eunicea flexuosa,* in St John, US Virgin Islands, before, during, and after severe hurricane disturbance. Using these models, we forecast the density of populations of each species under varying future hurricane regimes. We demonstrate that although hurricanes reduce population growth, *A. americana*, *G. ventalina*, and *E. flexuosa* each display a capacity for quick recovery following storm disturbance. Despite this recovery potential, we illustrate how the population dynamics of each species correspond with a longer-term decline in their population densities. Despite their resilience to periodic physical disturbance events, ongoing global change jeopardises the future viability of octocoral assemblages.

Keywords Ecological forecasting · Gorgonians · Hurricane disturbance · Integral projection models (IPMs) · Stochastic population growth rate (λ_s) · US Virgin Islands

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-024-02465-0.

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Introduction

Predicting the consequences of shifting community compositions in response to global change poses a major challenge throughout ecology and conservation (Bonebrake et al. 2018). Climatic- and human-mediated disturbances are degrading coral reefs worldwide (Hoegh-Guldberg et al. 2017), typified by reductions in scleractinian coral cover and increases in the prevalence of macroalgae (Graham et al. 2015). Yet, beyond coral-algal phase shifts, there is mounting evidence that on some Caribbean reefs, gorgonian octocorals are replacing scleractinian corals as the dominant benthic component in multiple reef environments (Ruzicka et al. 2013; Lenz et al. 2015; Tsounis and Edmunds 2017; Tsounis et al. 2018). Whilst unable to maintain the reef accretion associated with their scleractinian counterparts, arborescent octocorals can form dense underwater forests that modify light, current, and sedimentation patterns (Guizien and Ghisalberti 2017; Nelson and Bramanti 2020), and provide structural complexity (Rossi et al. 2020). Indeed, this maintenance of habitat heterogeneity is thought to facilitate the persistence of non-scleractinian reef taxa following

stony coral loss (Lenz et al. 2015). However, the ability of octocorals to play a role as a habitat-forming taxon relies upon their resilience to future disturbances linked to ongoing global change (Edmunds and Lasker 2022).

Octocorals are not novel components of Caribbean reefs but, following decades of disturbances and multiple thermal stress events, their coverage has expanded across many reefs, relative to that of scleractinian corals (Tsounis et al. 2018; Edmunds 2019a). Compared to scleractinians, octocorals are typically less susceptible to gradual changes in pH and water temperature (Gabay et al. 2014; Vargas et al. 2022), often resulting in reduced bleaching and mortality following heat stress events (Prada et al. 2010; Duarte et al. 2020; Steinberg et al. 2022), although this pattern is not universal (see Floros et al. 2004). Nevertheless, octocoral abundances can vary substantially over decadal time scales (Edmunds and Lasker 2016) mediated by the negative effects of abiotic and anthropogenic stressors (see Cerrano et al. 2005; Cupido et al. 2008; Ponti et al. 2014). Such variation poses challenges to predicting the population densities of octocorals on future reefs, particularly under disturbance regimes differing from the recent past (França et al. 2020).

Tropical storms impose a range of disturbances on coral reefs (Gardner et al. 2005). Throughout tropical octocoral assemblages, sediment abrasion, smothering, and colony detachment (due to damage to either the colony holdfast or basal skeleton), are significant sources of mortality that can make octocorals vulnerable to hurricane disturbance (Yoshioka and Yoshioka 1987, 1991). Predictions of the characteristics of future major storm events, arising as a consequence of global climate change, are highly varied and subject to debate (Knutson et al. 2019). Still, future storms of greater magnitude and frequency than in the recent past are likely to have strongly negative effects on octocoral assemblages and their associated communities (Lasker et al. 2020b). By quantifying the dynamics of octocoral assemblages following hurricanes, we can project their responses to varying future storm regimes (Edmunds et al. 2014; Edmunds and Riegl 2020), thereby enhancing our capacity to predict the ecological implications of scleractinian-octocoral regime shifts (Edmunds and Lasker 2016; Tsounis and Edmunds 2017).

Here, we used integral projection models (IPMs; Easterling et al. 2000) to project the impact of recurrent hurricanes on the population densities of the three most common octocoral species on the shallow reefs of St John, US Virgin Islands (Fig. 1): *Antillogorgia americana*, *Gorgonia ventalina* and *Eunicea flexuosa*. The reef communities of St John are typical of many Caribbean reefs that are now characterised by low (4–6%) scleractinian coverage (Jackson et al. 2014; Lenz et al. 2015; Edmunds 2019a) and high octocoral abundance (Edmunds and Lasker 2019). In St John, the annual survival and growth of tagged *A. americana*, *G. ventalina* and *E. flexuosa* colonies was documented between 2013 and 2019, with their recruitment quantified (i.e. the abundance of colonies < 5 cm tall) between 2014 and 2019, including during 2017 after Hurricanes Irma and Maria. Disturbances act upon populations and communities through impacts on individuals (Metcalf and Pavard 2007). Therefore, variation in per capita survival, growth, and reproduction, and how this is mediated by environmental conditions, underpins the response of populations to disturbances. We used IPMs to quantify the impact of hurricanes on the dynamics of *A. americana*, *G. ventalina* and

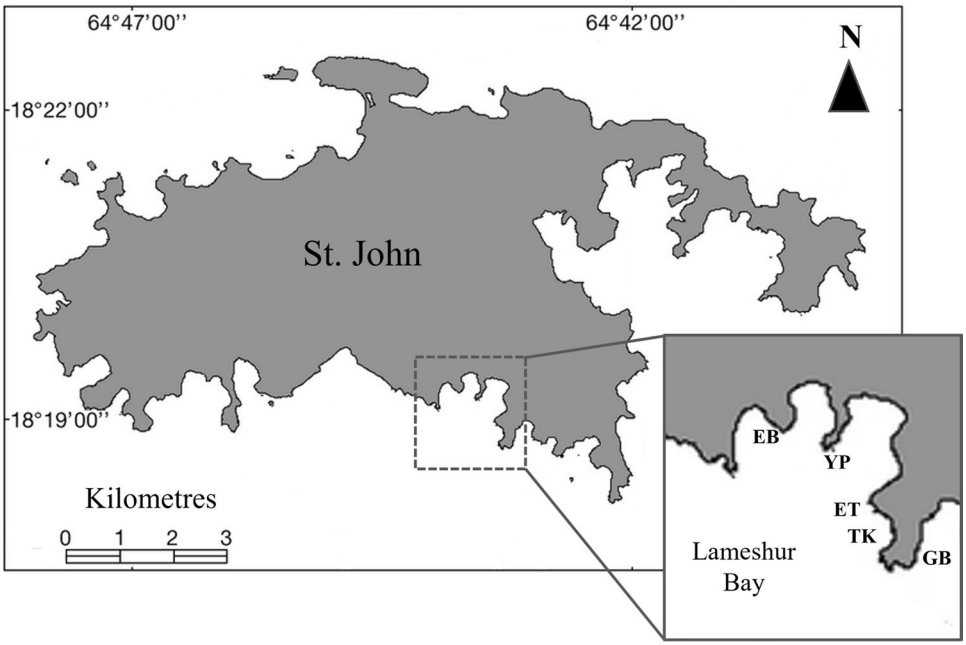

Fig. 1 A Map of St John, US Virgin Islands, showing the location of Europa Bay (EB), Grootpan Bay (GB), where the annual survival and growth of marked *Antillogorgia americana*, *Eunicea flexuosa*, and *Gorgonia ventalina* colonies were documented between 2013 and 2019. Between 2014 and 2019 the recruitment patterns of these three species were evaluated across both Europa Bay and Grootpan Bay, alongside the additional three sites, Tektite (TK), East Tektite (ET), and Yawzi Point (YP)

E. flexuosa, comparing the trajectories of each population before, during, and after severe hurricane disturbance. Next, we used stochastic IPM resampling (Metcalf et al. 2015) to forecast the population densities of each species under projected recurrent hurricane regimes. With this approach, we explore the mechanisms determining the long-term condition of octocoral populations, and test for the effects of recurrent hurricanes in mediating changes in the population structure of Caribbean octocoral communities.

Methods

Integral projection models

Integral projection models (IPMs) reflect how variation in the characteristics of individuals, as they undergo transitions in size (z to z') across the time interval t to $t+1$, translates into measures of population performance (Easterling et al. 2000). A general IPM (Eq. 1; see Table 1 for definitions) classifies individuals according to their position along a continuous size spectrum to describe how the size structure of a population at any discrete point in time, $\mathbf{n}(z', t+1)$, is contingent on its size structure at a previous time point, $\mathbf{n}(z, t)$, subject to the size dependant processes of survival and growth, $P(z', z)$, and reproduction, $F(z', z)$ (Eq. 2)

$$\mathbf{n}(z', t+1) = \int_L^U K(z', z)\mathbf{n}(z, t)\Delta z \tag{1}$$

$$K(z', z) = P(z', z) + F(z', z) \tag{2}$$

$$\text{Where}: P(z', z) = s(z) + g(z', z) \text{ and } F(z', z) = b(z) + pr^b(z) + C_0(z) \tag{3}$$

To complete an IPM, repeated observations of individuals are required to determine rates of growth (both positive and negative) and reproduction which, typically, centre around the size-dependant vital rates of survival probability (s), growth/shrinkage (g), fecundity (b), offspring survival probability (pr^b), and offspring size (C_0; Eq. 3). These vital rates are estimated over the size range U to L, which is equal to 10% above and below the minimum and maximum observed size of individuals, respectively (Merow et al. 2014). Here, we also included a ceiling size threshold (U_C; Supplementary S1), beyond which individuals retain the demographic properties of size U_C individuals (Ellner et al. 2016). A ceiling size threshold operates as a transition between a continuous and discrete state and thus prevents the eviction of very large individuals from the model (Williams et al. 2012). Throughout our framework, we defined U_C as equal to the maximum observed colony size, and therefore 10% below the value of U (Supplementary S1).

Table 1 A glossary of integral projection model (IPM) parameters

z	Refers to the state class of individuals. In an IPM the state of individuals can reflect their position along a continuous spectrum (i.e. size), in which case the transition of individuals between states is represented as z to z'
t	Refers to a discrete time point
$\mathbf{n}(..)$	A numerical vector describing the state-distribution of all individuals making up a population at a defined point in time
$s(z)$	The probability that an individual of state z survives the time interval t to $t+1$
$g(z', z)$	A probability curve determining the range and likelihood of possible states of individuals present at time $t+1$ given their state at time t
$b(z)$	The number of offspring produced by an individual of state z across the time interval t to $t+1$
$pr^b(z)$	The probability of offspring produced by an individual of state z surviving to the end of time interval t to $t+1$
$C_0(z)$	The size distribution of offspring produced by an individual of state z
P & F	Matrices describing the probabilities of individuals of state z at time t producing individuals of state z' at time $t+1$ given the state-specific patterns of survival and growth (P), and the state-specific patterns of reproduction (F)
U	The maximum size implemented within the IPM, typically estimated as being 10% greater than the maximum observed size for the population
U_C	Within our IPM model we implemented a transition of individuals between a continuous and discrete size class. This transition occurred once individuals attained a size equal to U_C (equal to the maximum observed size of individuals). As a consequence of this approach all individuals of a size larger than, or equal to, U_C are assumed to display the same characteristics of survival, growth, and reproduction. However, this approach ensures that our IPM does not 'evict' individuals that achieve the largest possible size during simulations (i.e. they can grow no larger). See Supplementary S1 for further details
L	The minimum size implemented within the IPM, typically calculated as being 10% below the smallest observed size for the population
R	The total number of offspring produced by a population across the time interval t to $t+1$
γ	A density-dependant coefficient that ensures the number of surviving recruits at time $t+1$ is weighted according to community size (all species pooled) at time $t+1$

To address the open and density-associated nature of octocoral assemblages, the IPM approach we adopted involved one further modification to the general framework: the replacement of the reproduction sub-kernel with a variable recruitment factor (γR; Eq. 4).

$$\mathbf{n}(z', t+1) = \gamma R C_0 + \int_L^U P(z', z)\mathbf{n}(z, t)\Delta z \quad (4)$$

The connectivity of reef environments, through larval dispersal pathways, ensures that localised populations represent a small component of a wider meta-community (Cowen and Sponaugle 2009). Thus, in open populations larval influx occurs largely independently of the dynamics of the existing population (Yau et al. 2014). Hence recruitment within our model was based on an independent recruit count (R); simply a value describing the number of new individuals introduced into the population during the period t to $t+1$. However, localised reef populations can exert a strong regulatory influence on larval settlement and the subsequent survival of recruits, influencing both space availability (Bramanti and Edmunds 2016; Doropoulos et al. 2017) and the fine-scale movements of settling larvae (Privitera-Johnson et al. 2015; Guizien and Ghisalberti 2017; Edmunds and Lasker 2019). Subsequently, the role of the independent recruit count in our IPM framework is weighted according to the density of the existing populations (γ).

Model parameterisation: colony survival and growth

We parameterised our IPMs using survival, growth, and recruitment data collected between 2013 and 2019 from *A. americana*, *G. ventalina*, and *E. flexuosa* populations at shallow water sites (< 10 m depth) along the south shore of St John, US Virgin Islands (18.34° N, 64.73° W; Fig. 1). We monitored colony survival and growth between 2013 and 2019 using annual tagging surveys conducted within approximately 60 m^2 sections of reef at Europa Bay and Grootpan Bay. To present an overall forecast of the viability of octocoral assemblages exposed to recurrent hurricane disturbance, we consider the differing octocoral communities at Europa Bay and Grootpan Bay as a single assemblage. Thus, survival and growth data are pooled across sites to represent a population covering 120 m^2 of reef. In 2013, we marked *A. americana* ($n = 207$) and *G. ventalina* ($n = 200$) colonies by fixing aluminium tags at the base of each colony, with the height (cm) of each colony recorded as the distance between the colony holdfast and the tip of the longest branch. In 2014, we applied the same approach to mark *E. flexuosa* colonies ($n = 254$). Annually, we measured the heights of all tagged colonies, with new individuals marked over time to replace those not found or lost through mortality. Over subsequent surveys, we recorded colony survival using a binary format reflecting whether mortality had occurred (i.e. 0 = dead, 1 = survived). We defined mortality as one of three events: (1) a marked colony remained fixed in place but visually was dead (i.e. its tissue had disappeared with its skeleton often colonised by algal turf), (2) a tag was found fixed in place but without its associated colony, and (3) neither a colony nor its associated tag were relocated over two successive surveys (*i.e.* 2 years).

Using the empirical data, we modelled colony survival and growth as a function of colony height using generalised linear models (GLMs; see supplementary S2). Prior to analysis, colony heights were square root transformed. We modelled survival probability as a function of colony height using a binomial GLM with survey year included as a fixed effect. Colony growth was modelled as the linear relationship between colony height in year t and colony height in year $t+1$, with survey year again included as a fixed effect. In both cases, we initially included site (Grootpan Bay *vs.* Europa Bay) as a random effect using the R package '*lme4*' (Bates et al. 2015), however, we dropped this term to select the most parsimonious model after checking model BIC scores (Supplementary S2). Subsequently, we implemented our GLMs using the base R function '*glm*' (R Core Team 2022). Next, to account for the effect of variance in growth on population performance, we extracted the residuals from our growth models for each species, to model variability in colony height at time $t+1$ as a function of colony height at time t, using a nonlinear gamma GLM to ensure variance remained non-negative. Within our IPMs, this approach ensured the standard deviation in modelled colony growth could vary according to initial colony size.

Model parameterisation: recruitment

We quantified species-specific recruitment patterns using quadrat surveys carried out at 5 sites along the south coast of St John: Grootpan and Europa Bays between 2014 and 2019, Tektite and East Tektite between 2015 and 2019, and Yawzi Point between 2017 and 2019 (Fig. 1). Collecting data from Tektite, East Tektite, and Yawzi Point, in addition to Europa Bay and Grootpan, increased the number of recruits observed, and, therefore, presumably the accuracy of our inferred recruitment rates. Including these additional sites allowed us to inspect recruitment over a greater range of adult densities. However, we acknowledge that our assessment of this relationship cannot exclude the possibility that both recruitment and adult abundances are independently related to differences in hydrodynamics across the different sites. Annually, at each site, we recorded the number and size (height, cm) of new recruits (≤ 5 cm) across eight 0.25 m^2 quadrats randomly positioned along 10 m fixed transects, six at Grootpan Bay, Europa Bay and East Tektite,

and 3 transects at Tektite and Yawzi Point. Meanwhile, we recorded the number and size of juvenile and adult colonies (> 5 cm height), henceforth referred to collectively as adult colonies, across ten 1 m^2 quadrats along the same transects. Following evidence of density-dependent recruitment within the octocoral assemblages of St John (Privitera-Johnson et al. 2015), we used these records of recruit and adult colony densities, pooled across sites and years, to calculate density-associated recruitment (γR) for *A. americana*, *G. ventalina*, and *E. flexuosa* (see supplementary S3). Firstly, we scaled observed densities (individuals m^{-2}) to represent individuals per 120 m^2 to correspond with the area over which we quantified colony survival and growth. Next, we modelled the relationship between observed recruit and total (all species pooled) adult colony densities for each species. We implemented these models using the *'gamlss'* and *'gamlss.dist'* R packages (Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2019), to apply generalised additive models (GAMs) set to a zero-adjusted gamma distribution (ZAGA; a continuous non-negative distribution that includes zero); from which we extracted the intercept (R) and slope (γ) coefficients. Finally, to allow for new individuals to be iteratively combined into each population during projection (*see below*), we modelled the recruit size distributions (C_0) of each species using the *'Fitdistrplus´* R package (Delignette-Muller and Dutang 2015), with recruit colony size data pooled from across annual surveys at the different sites.

Quantifying instantaneous hurricane impact

To evaluate the impacts of Hurricanes Irma and Maria on *A. americana*, *G. ventalina*, and *E. flexuosa*, we estimated population growth rates (λ_P) across our IPMs. In a general IPM (Eq. 1), the estimate of long-term population growth rate (λ), equal to the dominant eigenvalue of the discretised K kernel (Ellner et al. 2016), provides a relative measure of population performance (Groenendael et al. 1988; Crone et al. 2011). However, since recruitment was not directly incorporated into our open population IPMs (Eq. 4), we can only estimate the dominant eigenvalue of sub-kernel P (henceforth λ_P), representing a measure of standing stock viability (Yau et al. 2014). With populations typically unable to grow without recruitment, λ_P operates on a scale of $0 < \lambda_P < 1$, with 1 representing populations at equilibrium (*i.e.* self-sustaining in the absence of recruitment). We parameterised separate IPMs describing the dynamics of *A. americana*, *G. ventalina*, and *E. flexuosa* during each year between 2013 and 2019. For each species, this approach provided multiple models reflecting population dynamics during non-disturbance years (2013/14 [*A. americana* and *G. ventalina* only], 2014/15, 2015/16, and 2016/17), one model characterising population dynamics following hurricane exposure during 2017/2018, and one outlining post-disturbance dynamics (2018/19). We note, here, that our models are based on data collected at annual intervals. Although, Hurricanes Irma and Maria occurred separately, they took place merely weeks apart and during the same survey interval. Thus, in spite of their severity, we are unable to distinguish their individual impacts. Following parameterisation, we discretised each IPM using the mid-point rule (sensu Zuidema et al. 2010) and calculated λ_P. We determined the variance in these λ_P estimates using 95% Jack-Knife resampling without replacement, with the 95% confidence intervals of these resampled distributions used to evaluate for significant differences among species, and years.

Forecasting recurrent hurricane impact

To explore how changing hurricane disturbance regimes could influence the viability of *A. americana*, *G. ventalina*, and *E. flexuosa* on St John, we used stochastic IPM resampling (Metcalf et al. 2015) to forecast the performance of *A. americana*, *G. ventalina*, and *E. flexuosa* under varying future hurricane scenarios. Firstly, we present a scenario of no recurrent hurricanes as a baseline to provide insight into the differing dynamics of the study species. Next, the Caribbean currently experiences hurricane (all categories) return times of between 5- and 35-years (0.2 to ~ 0.03 annual occurrence probability), with a mean anticipated return time of 11.6-years (~ 0.09 annual probability) (Gardner et al. 2005; Keim et al. 2007). However, we lack sufficient evidence for accurately predicting future shifts in the frequency of hurricane storms (Knutson et al. 2019; Dixon et al. 2022), and thus our remaining scenarios explore how both projected declines (see Knutson et al. 2019) and increases (see Bhatia et al. 2018) in hurricane frequencies could impact the dynamics of octocoral communities. In scenarios 2, 3, and 4, we present recurrent hurricane regimes during which the frequency of hurricane occurrence declines by 0.5% annually (equivalent to a 20% decline in the North Atlantic predicted by 2055; Knutson et al. 2019) from initial return times of 5-, 11.6-, and 35-years, respectively. Meanwhile, in scenarios 5, 6, and 7, we present recurrent hurricane regimes during which the frequency of hurricanes increases by 12.5% by 2035, and then by 25% by 2100 (as forecasted by Bhatia et al. 2018); again, originating from initial return times of 5-, 11.6-, and 35-years, respectively. Crucially, across each of these scenarios, the occurrence of a hurricane in any given year is determined independently of events imposed during any previous years.

Using each species-specific IPM series, we projected the annual dynamics of *A. americana*, *G. ventalina*, and *E. flexuosa* until 2100, under each of our aforementioned hurricane scenarios. We used colony abundances and heights recorded during our quadrat surveys in 2019 to empirically determine

the size structure of the local *A. americana*, *G. ventalina*, and *E. flexuosa* populations. Pooling these data from across our sites, to maintain our focus on the broader viability of octocoral assemblages on St John, we determined an initial size structure ($\mathbf{n}_0$) for each species, from which we initiated our simulations. During our simulations, the annual likelihood of a hurricane was randomly determined according to the annual hurricane occurrence probabilities associated with each scenario. In the event a hurricane occurred during any given iteration, we used the IPM kernels corresponding with 2017/18 (capturing the impact of Hurricanes Irma and Maria) to represent local dynamics. For non-hurricane years, the IPMs used were randomly selected from those formulated for the intervals between 2013 and 2017. Finally, our λ_P analysis (see *Results*) dictated that for addressing a non-hurricane iteration immediately preceded by a simulated hurricane period, we should implement the IPMs corresponding with the interval period 2018/19 to represent a recovery phase.

During each simulation, we retained the size distributions of each population following each iteration ($\mathbf{n}_t$). With these sequential size distributions, we determined a series of population sizes (N_t), which were used to calculate a stochastic measure of population growth rate (λ_s; sensu Lewontin and Cohen 1969) (Eq. 5):

$$\log(\lambda_s) = E[\log\left(\frac{N_{t+1}}{N_t}\right)] \tag{5}$$

We repeated all simulations 1000 times to estimate variance in λ_s for each population, using the 95% confidence intervals of each resampled distribution to evaluate for differences among scenarios and species.

Results

Instantaneous hurricane impact

Hurricanes Irma and Maria coincide with a decline in population growth rate in *A. americana*, *G. ventalina*, and *E. flexuosa* (Fig. 2). Our estimates of λ_P were low (*i.e.* $\lambda_P < 0.75$) for *A. americana*, *E. flexuosa*, and *G. ventalina* during the annual period associated with Hurricanes Irma and Maria (2017/18). Values of λ_P operate on a scale between 0 and 1, reflecting the proportional retention of population size over time (excluding the recruitment of new individuals). Accordingly, estimates of $\lambda_P \leq 0.75$ represent a 25% decline in population size. These observed declines in population size corresponded with the temporal shifts in colony survival we observed across the three species (Fig. 3a–c). In 2017/18, coincident with Hurricanes Irma and Maria, *G. ventalina* experienced a marked decline in the survival of

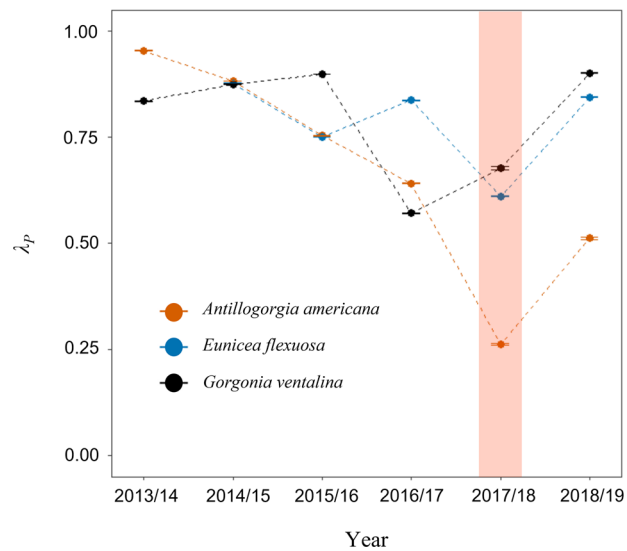

Fig. 2 Interaction plot showing temporal variation in population growth (λ_P) for *Antillogorgia americana*, *Eunicea flexuosa*, and *Gorgonia ventalina*. The red bar denotes timing of Hurricanes Irma and Maria. Error bars display ± 95% CI based on Jack-Knife resampling in which we repeated our analyses 1000 times, each time omitting 5% of our sample without replacement

larger colonies (i.e. > 20.25 cm), in comparison with other interval periods (Fig. 3c). During this same period, *A. americana* and *E. flexuosa* also experienced lower rates of survival, although the relative trend of increasing survival with colony size was maintained (Fig. 3a and b). In contrast, individual colony growth patterns remained unaffected by hurricane disturbance (Fig. 3d–f). However, our findings indicate that hurricane disturbance is unlikely the sole agent underpinning the observed decline in population growth rate as, although our estimates of λ_P for both *A. americana* and *E. flexuosa* were at their lowest in 2017/18, declines in λ_P were also evident in the years prior to hurricane disturbance (Fig. 2).

Although the population growth rates we obtained for each species varied between years, our estimates reveal congruent temporal patterns across the relative growth rates of the three species. *A. antillogorgia*, *E. flexuosa*, and *G. ventalina* each exhibit declines in λ_P between 2013/14 (2014/15 in *E. flexuosa*) and 2017/18, followed by an increase in 2018/19 (Fig. 2). *A. americana* was the only species to display population growth rates close to population equilibrium ($0.95 < \lambda_P \approx 1$; $\lambda_P = 0.956$ [95% CI: 0.955, 0.957]). However, this estimate occurred during our initial population surveys in 2013/14, with λ_P in *A. antillogorgia* diminishing over subsequent surveys to 0.290 [0.286, 0.293] in 2017/18. Likewise, *E. flexuosa* experienced a reduction in λ_P which declined to 0.611 [0.610, 0.612] in 2017/18. Meanwhile, in *G. ventalina* λ_P reached its lowest value ($\lambda_P = 0.567$ [0.566, 0.569]) in 2016/17, a year before Hurricanes Irma

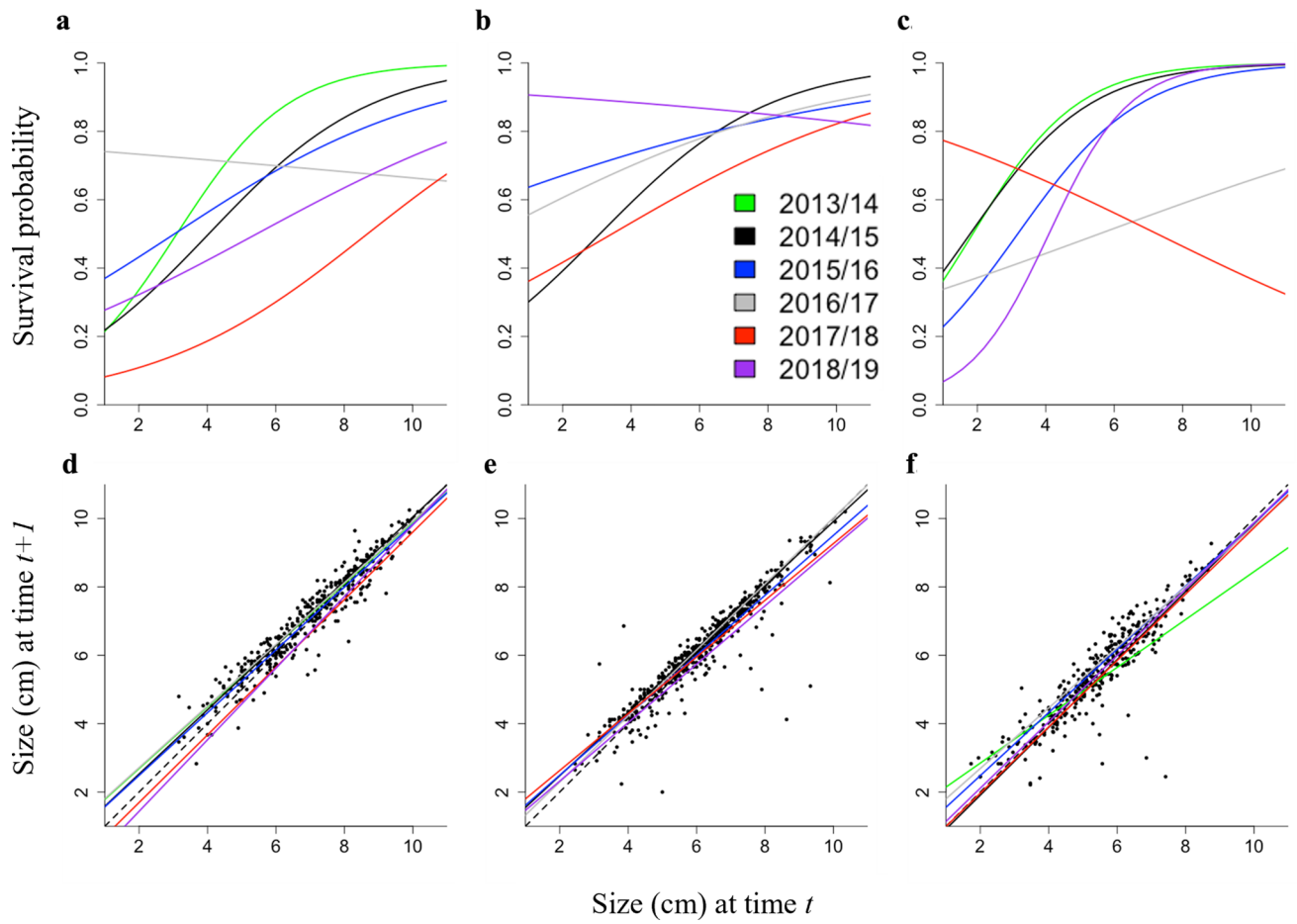

Fig. 3 Annual variation in colony survival ([**a**] *Antillogorgia americana*, [**b**] *Eunicea flexuosa*, and [**c**] *Gorgonia ventalina*), and the relationship between colony size (height in cm; square root transformed) at time t and size at time $t+1$ ([**d**] *A. americana*, [**e**] *E. flexuosa*, and [**f**] *G. ventalina*) recorded from tagged octocoral colonies on the shallow reefs of St John between 2013 and 2019. Dashed lines on the growth panels (**d**–**f**) denote the zero-growth threshold (i.e. size at t = size at $t+1$)

and Maria. In 2018/19, following hurricane disturbance, all three species displayed a recovery in population growth rate (*i.e.* $\lambda_P^{2018/19} \geq \lambda_P^{2017/18}$), with λ_P in both *E. flexuosa* and *G. ventalina* returning to broadly similar values to estimates observed during earlier surveys (*A. americana*: 0.587 [0.584, 0.591]; *E. flexuosa*: 0.845 [0.844, 0.846]; *G. ventalina*: 0.889 [0.888, 0.890]; Fig. 2).

Recurrent hurricane impact

We reveal that patterns in the future population densities of *A. americana*, *E. flexuosa,* and *G. ventalina* in St John remain largely consistent, irrespective of their exposure to varying recurrent hurricane regimes (Fig. 4). *E. flexuosa* exhibited the highest values of λ_s, but, neither *A. americana*, *G. ventalina*, nor *E. flexuosa*, exhibited positive population growth ($\lambda_s > 1$) under any recurrent hurricane scenario (Table 2 and Fig. 4). Whilst λ_s was greater in *G. ventalina* than *A. americana*, the relative impacts of the differing recurrent hurricane regimes were similar in both species, with each maintaining faster population growth under less frequent, or declining, hurricane disturbances (Table 2). Meanwhile, our estimates of λ_s for *E. flexuosa* were typically higher in scenarios reflecting increasing hurricane likelihood (Table 2). Only *A. americana* displayed its highest λ_s during our "no hurricane" scenario, whilst both *E. flexuosa* and *G. ventalina* showed greater population growth rates in the hurricane scenarios beginning with an initial hurricane return time of 11.6-years (Table 2).

Across our simulations, neither *A. americana*, *E. flexuosa,* nor *G. ventalina* were able to maintain population densities above or equal to the empirical densities recorded in 2019 (Fig. 4). We used colony abundances and heights recorded during our final population census in 2019 to determine an initial size structure for each species, from which we initiated all of our recurrent hurricane forecasts. For each species, this provided an initial measure of population density (colonies m^{-2}: *A. americana* = 1.84, *E. flexuosa* = 3.18, *G.*

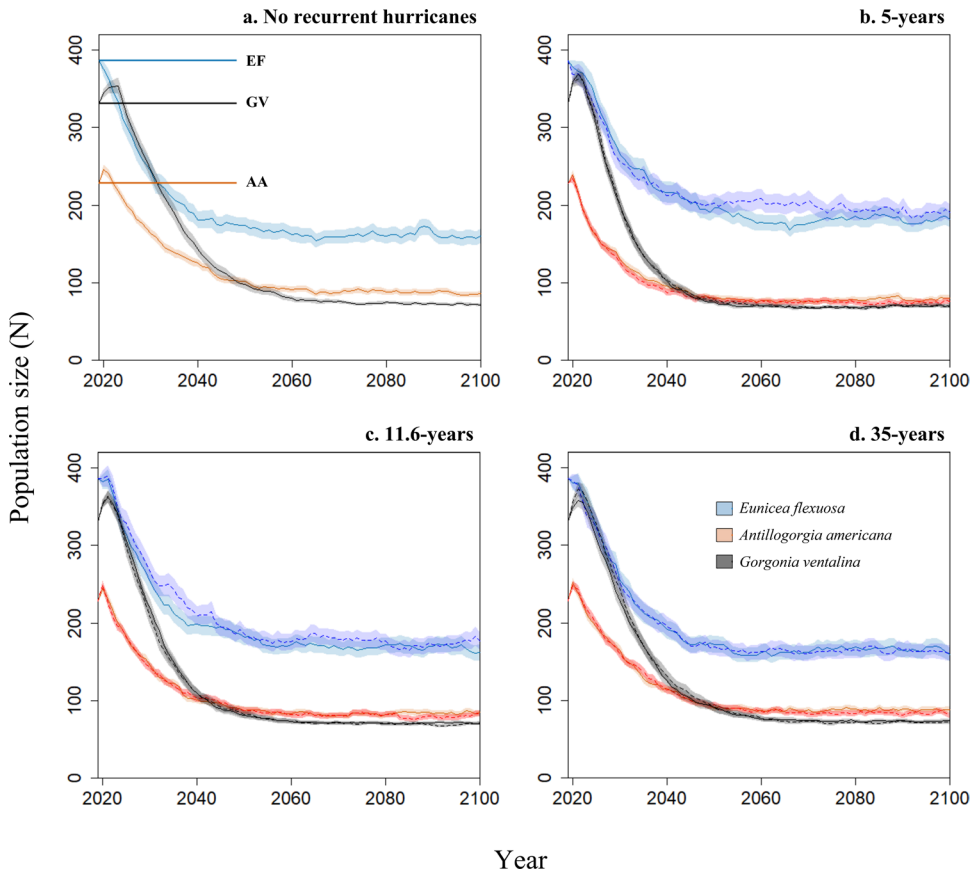

Fig. 4 Projected population densities for *Antillogorgia americana*, *Eunicea flexuosa*, and *Gorgonia ventalina* between 2019 and 2100 when exposed to (**a**) no hurricanes, (**b**) initial hurricane return times of 5-years, (**c**) initial hurricane return times of 11.6-years, and (**d**) initial hurricane return times of 35-years. Solid lines show projected densities corresponding with a decline in hurricane frequency relative to initial conditions, and dashed lines show projected densities corresponding with an increase in hurricane frequency relative to initial conditions. Horizontal bars on panel **a** compare the initial population densities (individuals 120 m^{-2}) used for *A. americana* (AA), *E. flexuosa* (EF), and *G. ventalina* (GV) with the projected densities for each population. Shaded regions represent ± 95% CI based on 1000 simulations during which hurricane disturbance was determined using a random number generator

ventalina = 2.76). Across our simulations, stochastic population growth remained close to equilibrium ($0.9 < \lambda_s \approx 1$) in all three species, with each able to attain stable population densities regardless of the recurrent hurricane scenario imposed (Fig. 4). However, across all simulations, these stable population densities were smaller than those used as the initial condition for each simulation (colonies m^{-2}. *A. americana* & *G. ventalina* = < 0.83, *E. flexuosa* = ~ 1.67), corresponding with a 47% decline in population size in *E. flexuosa*, a 55% decline in *A. americana*, and a 70% decline in *G. ventalina* by 2060 (Fig. 4). Across all scenarios the declines in population densities reported for *A. americana*, *E. flexuosa,* and *G. ventalina* correspond with a loss of individuals across the colony size spectrum, although this loss was more evident in larger sized colonies (Figs. 5 and S7).

Discussion

Forecasting the dynamics of octocoral assemblages exposed to recurrent disturbances is crucial for evaluating their capacity for enduring ongoing global change. However, here we illustrate that whilst the dynamics of octocoral assemblages can recover from the negative impacts of hurricane disturbance, these periodic recovery intervals may be masking ongoing declines in the condition of octocoral assemblages.

We observed patterns in the variation of λ_P across *A. americana*, *E. flexuosa*, and *G. ventalina* consistent with previous work highlighting both the detrimental impact of hurricane disturbances on Caribbean octocoral communities, and their capacity for quick recovery following the return of optimal conditions (Tsounis and Edmunds 2017; Lasker et al. 2020b). Across *A. americana*, *E. flexuosa*, and *G. ventalina*, declines in λ_P coincided with changes in the survivorship dynamics of each species. Differential patterns of commonness and rarity can arise across species and populations due to the accumulation of small differences among their survival, growth, and reproductive dynamics (McWilliam et al. 2022). Logically, small shifts within the survival, growth, and recruitment of *A. americana*, *E. flexuosa*, and *G. ventalina* could, therefore, over time compound into trajectories of population decline. Elevated mortality is routinely documented in octocoral assemblages following physical disturbances, occurring mainly as a result of substratum failure (Cerrano et al. 2005; Linares et al. 2005; Cupido et al. 2008). Meanwhile, the reversal in size-mediated survival observed in *G. ventalina* during 2017/18, but not in *A. americana* or *E. flexuosa*, corresponds with morphological differences among the species. The fan-shape of *G. ventalina*

Table 2 Stochastic population growth rate (λ_s) for *Antillogorgia americana*, *Eunicea flexuosa*, and *Gorgonia ventalina*, across 1000 simulations projecting population growth under varying hurricane regimes. We address a series of recurrent hurricane regimes, starting with (a) no hurricanes, and then hurricanes with return times of (b) 5-years, (c) 11.6-years, and (d) 35-years, with the likelihood of hurricane occurrence then either increasing or decreasing. Cell shading used to highlight within-species patterns in λ_S, with dark shades denoting higher growth rates. Error displayed as ± 95% CI based on 1000 simulations during which hurricane disturbance was determined using a random number generator

Return time scenario		*Antillogorgia americana*	*Eunicea flexuosa*	*Gorgonia ventalina*
a. No Hurricanes		0.985 [0.985, 0.986]	0.985 [0.985, 0.986]	0.980 [0.980, 0.981]
b. 5-years	Decreasing	0.983 [0.983, 0.984]	0.987 [0.986, 0.988]	0.980 [0.980, 0.980]
	Increasing	0.982 [0.981, 0.983]	0.987 [0.987, 0.988]	0.980 [0.979, 0.980]
c. 11.6-years	Decreasing	0.985 [0.985, 0.986]	0.985 [0.985, 0.986]	0.980 [0.980, 0.981]
	Increasing	0.984 [0.984, 0.985]	0.985 [0.985, 0.986]	0.980 [0.980, 0.981]
d. 35-years	Decreasing	0.985 [0.984, 0.985]	0.985 [0.985, 0.986]	0.980 [0.980, 0.980]
	Increasing	0.984 [0.984, 0.985]	0.986 [0.986, 0.987]	0.980 [0.980, 0.980]

elevates colony vulnerability to wave-mediated detachment compared to the slender branching morphologies of *A. americana* and *E. flexuosa* (Birkeland 1974; Lasker et al. 2020a). During 2018/19, following the dissipation of hurricane conditions, the survival patterns of *A. americana*, *E. flexuosa*, and *G. ventalina* showed evidence of population recovery towards their pre-disturbance condition. However, even with this recovery, the dynamics of *A. americana*, *E. flexuosa*, and *G. ventalina* documented over 6 years appear insufficient for maintaining their current population densities.

The declining trajectory in λ_P for *A. americana*, *E. flexuosa*, and *G. ventalina* throughout the duration of this study suggests that hurricane disturbance is not definitively responsible for the observed declines in population growth rate. Yet, these temporal patterns highlight the potential role of hurricane disturbance as a thinning mechanism, maintaining the condition and diversity of local benthic assemblages. Disturbances play an integral role in mediating community composition (Connell 1979). Recurrent disturbance prevents species assemblages from reaching their carrying capacity and, by non-randomly suppressing individuals across different life-cycle stages, can prevent populations from saturating available space and resources (Beckage et al. 2009; Dornelas 2010). Indeed, the disturbances generated by catastrophic hurricanes are an ecologically important mechanism mediating the diversity and health of forest ecosystems (Connell 1978; Xi et al. 2019; Sharma et al. 2021). Thus, throughout benthic reef assemblages, in which demographic rates, and therefore population growth, are influenced by density-dependent effects (Vermeij and Sandin 2008; Privitera-Johnson et al. 2015; Bramanti and Edmunds 2016; Doropoulos et al. 2017), the periodic removal of established individuals by hurricanes may inhibit the dominance of communities by one or only a few species, thus maintaining diversity.

Despite comprising annual observations over 6 years (2013–2019), the dynamics upon which we based our projections for *A. americana*, *E. flexuosa*, and *G. ventalina* are not predicted to sustain their current population densities over the next 30-years. The long-term decline in population densities that we project, relative to the population growth that has resulted in the existing populations, must be attributed to some combination of higher adult mortality, slower colony growth (which exposes colonies to small colony mortality rates over prolonged periods) and/or lower recruitment, which can be further subdivided into patterns of larval supply (i.e. production) and early post-settlement mortality. However, it is unknown whether any or all of these potential drivers will change, for better or worse, over time spans greater than our study timeline. Populations persisting within environments characterised by periodic disturbances can prioritise demographic strategies associated with maximising their short-term fitness (i.e. boom and bust cycles; McDonald et al. 2016). These strategies carry an energetic cost to long-term population growth (Cant et al. 2023), but can increase the ability for populations to grow following disturbance and thus warrant greater attention in

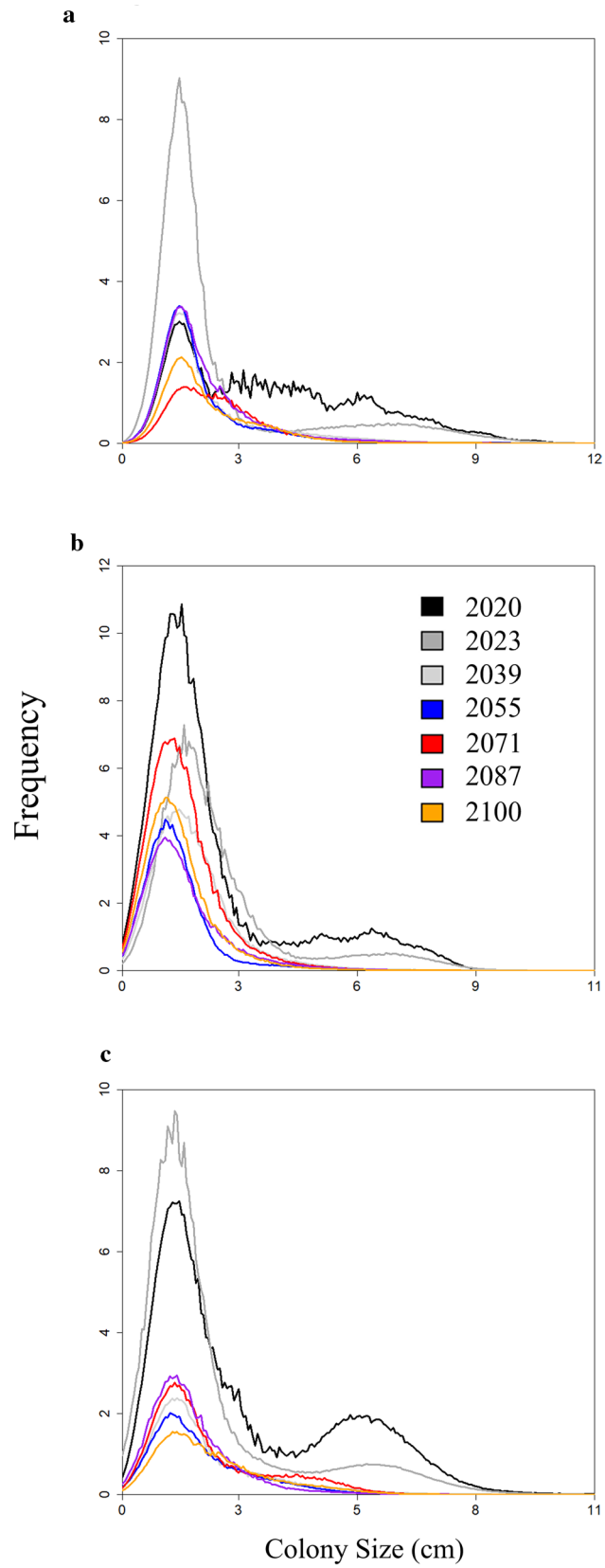

Fig. 5 Temporal patterns in the size frequency distributions of (**a**) *Antillogorgia americana*, (**b**) *Eunicea flexuosa*, and (**c**) *Gorgonia ventalina* between 2020 and 2100 under a scenario of no recurrent hurricane disturbance. Colony size (height, cm) shown on a square root transformed scale

assessments of frequently disturbed environments (Cant et al. 2022). Indeed, the viability of octocoral populations is often underpinned by intermittent demographic processes (e.g. Lasker et al. 1998; Santangelo et al. 2012). Simulating the dynamics of a population of *Corallium rubrum* over a 500-year period, Bramanti et al. (2009) demonstrate how the population is expected to undergo ~ 50-year oscillations in population density and the relative dominance of smaller- or larger-sized colonies. Accordingly, with these simulations based on detailed demographic data compiled across decades of field surveys (Abbiati et al. 1991, 1992; Santangelo and Abbiati 2001; Bramanti et al. 2003, 2005), it is important that we acknowledge the possibility that our survey, conducted between 2013 and 2019, did not capture the intermittent behaviours necessary for recreating pertinant periodic oscillations in the *A. americana*, *E. flexuosa*, and *G. ventalina* populations.

Alternatively, our demographic census show the *A. americana*, *E. flexuosa*, and *G. ventalina* populations are characterised by a large number of smaller-sized colonies (i.e. < 9 cm tall; Figs. 5 and S7). Although the peak in the number of smaller colonies does diminish over time, this composition persists in each species across our simulations. Initially, this structural composition suggests that, for each species, the low survivorship of larger-sized colonies (i.e. > 20.25 cm tall) is contributing to a winnowing in the relative prevalence of larger-sized colonies. Across our simulations, this loss of larger-sized colonies is then not being offset, as the growth and survival dynamics of smaller, and/or newly settled, colonies are insufficient for replenishing the numbers of larger colonies. Concurrently, the recruitment of new individuals across the populations of *A. americana*, *E. flexuosa*, and *G. ventalina* is positively associated with the density of the existing assemblage (Fig. S5). With increased colony densities supporting the entrainment of drifting planula larvae (Sponaugle et al. 2002), enhancing fertilisation success (Coma and Lasker 1997), and reducing post-settlement predation (Randall 1967), positive density-associated recruitment is characteristic of at least some octocoral assemblages (Privitera-Johnson et al. 2015). Yet, positive density-associated recruitment can make natural assemblages sensitive to the loss of individuals. Accordingly, on St John, the persistent loss of larger colonies could drive a steady decline in the relative abundance, and densities, of *A. americana*, *E. flexuosa*, and *G. ventalina* populations.

Regardless of the drivers of change in the present octocoral populations, our findings suggest that, despite their

capacity for recovery following periodic disturbances, octocoral populations may be vulnerable to the continuing impacts of global change. Indeed, this sensitivity may be masked by the ability for octocoral populations to recover quickly. We acknowledge here that our projections of *A. americana*, *E. flexuosa*, and *G. ventalina* assume that the impacts of any future disturbances will be equivalent to the impacts of Hurricanes Irma and Maria in 2017/18. This kind of event-specific assumption is a necessary caveat of IPM kernel resampling projections (Metcalf et al. 2015). However, during 2017/18, the coral reefs of St John were exposed to two severe hurricanes (Edmunds 2019b; Lasker et al. 2020b). Thus, our empirical data reflect the cumulative result of two hurricanes and therefore, likely overestimates the magnitude of less severe events. In the future, *A. americana*, *E. flexuosa*, and *G. ventalina*, may experience less severe recurrent disturbances, thus providing environmental conditions promoting population growth. Our work provides important insight into the dynamics of shallow water octocoral assemblages following exposure to recurrent disturbances. Although not as prominent as coral-macroalgal phase shifts, regime shifts involving non-scleractinian invertebrates occur in many reef environments worldwide (Norström et al. 2009). Here, we report the viability of one such alternative taxon (i.e. octocorals) under future global change scenarios, which remains overlooked compared to other reef states (Tsounis and Edmunds 2017). With the potential for both antagonistic and synergistic outcomes from changes in the frequency and intensity of disturbances, predicting the future impacts of severe tropical storms is complex (Knutson et al. 2019). Consequently, it is important that we continue to evaluate how simultaneous changes in the frequency and magnitude of hurricane storms will affect the future condition of octocoral assemblages.

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Author's contribution PJE, HRL, LB and GT conceived the initial project design. LB and GT collected colony survival and growth data, whilst HRL and AMQ designed and implemented the recruitment and colony density surveys. JC and LB led the implementation of all analyses, with PJE, GT, and AMQ assisting in the interpretation of collected demographic data. JC led manuscript write up with all authors contributing to its development.

Data availability The recruitment and adult abundance data used in this study are publicly available from the BCO-DMO database (https://www.bco-dmo.org/dataset/851382/data and https://www.bco-dmo.org/dataset/851382/data). As stipulated by our research funding, the colony survivorship and growth data used in this study will also be made publicly available. However, at the time of submission, these data are being utilised as part of ongoing research into the survivorship of octocoral populations and will therefore be uploaded to a public repository upon acceptance of this additional research. For the purposes of transparency, a copy of these data were enclosed as part of our manuscript submission. All R scripts used in the analyses presented throughout this manuscript and the associated supplementary material have been uploaded to the lead authors GitHub page, and are publicly avalible at (https://zenodo.org/doi/10.5281/zenodo.10605306)

Declarations

Conflict of interest All authors certify that they have no conflicting interests to declare that are relevant to the content of this article.

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