

Supporting Information. Hall, T.E., A.S. Freedman, A.M. de Roos, P.J. Edmunds, R.C. Carpenter, and K. Gross. 2020. Stony coral populations are more sensitive to changes in vital rates in disturbed environments. *Ecological Applications*.

Appendix S1: Technical details and supplemental figures

Parameter values and justifications

x_0 , **diameter of a newly settled coral spat** We use a value of 0.4 mm, which is loosely based on Babcock (1991).

x_{\max} , **maximum diameter of a coral colony** Veron’s online factsheet reports that *P. verrucosa* colonies are “seldom more than 0.5 metres across” (<http://www.coralsoftheworld.org/>, accessed Jan. 20, 2020).

$g(x, C)$, **radial growth rate of a coral colony** To estimate the growth rate of *P. verrucosa*, we used annual monitoring data from the Mo’orea Coral Reef Long-Term Ecological Research (LTER) project for 2011 – 18. We use monitoring data from LTER sites 1 and 2 (both on Mo’orea’s north shore) and from 10 m depth on the outer reef. Monitoring consisted of annual visits to a permanent 40 m transect that contained several 0.5 m × 0.5 m quadrats spaced roughly 0.5 – 2 m apart (Edmunds, 2018). Quadrats were photographed in March or April of each year. Using the digital images, the diameter of the major and minor axis of each colony was recorded. The effective diameter of a colony is twice the geometric mean of the radii of the major and minor axis. To estimate the growth-rate function, we use pairs of data for which colonies can be (a) unequivocally identified as the same colony in consecutive years, (b) did not exhibit full or partial mortality (to the extent that observers could tell), and (c) remained entirely within the photographed quadrat in both years. Our analysis uses $n = 1003$ pairs of sizes in consecutive years available for analysis. Some of these pairs are generated by the same colony (for example, a single colony observed in four consecutive years generates three pairs

of consecutive observations), and thus would be expected to generate correlated residuals. Thus, the effective sample size is somewhat smaller than 1003, and the actual standard errors associated with our fitted growth curve are larger than a naive calculation would suggest. The data used for this analysis are deposited at <https://www.bco-dmo.org/dataset/808261>. We assumed that the growth increments that we observe reflect density-dependent growth rates. In other words, we expect that observed growth was reduced by crowding. For each year in our time series, we calculated the total coral cover across all quadrats at 10m depth for each LTER site. We then calculated a density-independent growth increment by dividing the observed growth increment by the coral cover in the initial year. That is, if a colony is observed to have size x_t at year t , and size x_{t+1} at year $t + 1$, and if the average coral cover at the particular LTER site in year t is C_t , then the density-independent growth increment is calculated as $y_t = (x_{t+1} - x_t)/(1 - C_t)$. We then regressed y_t vs. the size at the beginning of the time interval x_t , using a quadratic regression that is constrained to generate a fitted value of 0 when $x_t = x_{\max}$ (Fig. S2). Our fitted equation takes the form $y_t = b_0 + b_1x + b_2x^2 + \epsilon$, where the ϵ 's take the usual assumptions of independent and identically distributed Gaussian error. In other words, our fitted equation is

$$g(x, C) = (b_0 + b_1x + b_2x^2) \times (1 - C). \quad (\text{S1.1})$$

For our data, a constrained least-squares fit yields estimates of

$$\hat{b}_0 = 0.0123$$

$$\hat{b}_1 = 0.297$$

$$\hat{b}_2 = -0.643.$$

We do not report standard errors because accurate calculation of standard errors would require accounting for correlations among observations from the same colony, which is beyond the

scope of this analysis.

Finally, note that by equating a growth rate with an annual growth increment, we are essentially assuming that the growth rate is constant over the course of an entire year. Of course, in our model, the growth rate changes as the colony grows, so that the equivalence between the growth rate and the observed annual growth increment is inexact. However, growth rates are sufficiently slow, and change sufficiently slowly with changing colony size, that the loss in fidelity from using an observed annual growth increment to estimate a growth rate is minor.

$\mu(x, C)$, **coral mortality rate** First, we assume that coral mortality is independent of coral cover.

To estimate the size-dependence of coral mortality, we use data from corymbose corals on Lizard Island, Australia from Madin et al. (2014) (helpfully provided as a supplement to their paper). We modified their fit as follows. Because our model requires a mortality rate instead of an annual mortality, we fit a generalized linear model (GLM) with a complimentary-log-log (cloglog) link; Madin et al. used a more familiar logit link. Madin et al. used the log of the colony size as their predictor; however, fitting a quadratic model (on the link scale) with log diameter as the predictor yields very high mortality rates for small colonies (annual mortality rates of $> 99.9\%$ for colonies at $x = 3$ cm) that are not consistent with either our monitoring data or recent fits to similar data that appear in Kayal et al. (2018). Thus, we instead opted for a quadratic fit (again, on the link scale) with colony diameter as the lone predictor, even though this model is slightly AIC-worse than the fit with log diameter as the predictor (Δ AIC = 4.07). In terms of a mortality rate, this fit implies the following functional form for $\mu(x, C)$:

$$\mu(x, C) = \exp\left(a_0 + a_1x + a_2x^2\right). \quad (\text{S1.2})$$

Holbrook et al. (2018) report that, on the north shore of Mo'orea, the annual mortality of newly detectable *P. verrucosa* colonies (which they define to be $x \approx 3$ cm) is 35%. The fit to Madin *et al.*'s data suggests an annual mortality for $x = 3$ cm corals of 61% per year. Thus we adjusted the a_0 term in the model to give an annual mortality of 35% for colonies of size

$x = 3$ cm. Our estimated, adjusted coefficients are

$$a_0 = -0.3782$$

$$a_1 = -16.26$$

$$a_2 = 26.41.$$

s_0 , **coral recruitment rate** Holbrook et al. (2018) report that visible *P. verrucosa* recruits ($2 \leq x \leq 3$ cm) are found on the north shore of Mo'orea at an average rate of approximately 20 recruits $\text{m}^{-2} \text{y}^{-1}$. Our growth and survival curves suggest that in uncrowded conditions roughly 40% of all recruits will survive long enough to become detectable at this size, giving an arrival rate of newly settling recruits of roughly $s_0 \approx 20/.4 = 50$ recruits $\text{m}^{-2} \text{y}^{-1}$.

Calculation of the undisturbed equilibrium

In this section, we describe how the equilibrium of the model without disturbance can be calculated using the methods of Kirkilionis et al. (2001). What we present here is a simplified version of the methods in Kirkilionis et al. (2001), where we have retained only the components necessary to analyze our model. The full methodology in Kirkilionis et al. (2001) allows for the analysis of substantially richer models.

The essential approach of Kirkilionis et al. (2001) is to convert the model to an age-dependent renewal equation. To adapt some notation from Kirkilionis et al. (2001), let $b(t)$ represent the rate at which new colonies enter the population at time t . In our model, $b(t) = s(1 - C(t))$. Let $x(t - a, a)$ be the size at age a of a colony that settled at time $t - a$. Similarly, let $\mathcal{F}(t - a, a)$ be the proportion of colonies that settled at time $t - a$ and have survived to age a . Let $A(x) = \pi (x/2)^2$ be the area occupied by a colony of size x .

We first write a renewal equation for $C(t)$ by integrating over the the ages of all coral colonies present at time t :

$$C(t) = \int_0^\infty A(x(t - a, a)) \mathcal{F}(t - a, a) b(t - a) da. \quad (\text{S1.3})$$

Substituting in $b(t) = s(1 - C(t))$ gives

$$C(t) = s \int_0^\infty A(x(t-a, a)) \mathcal{F}(t-a, a) (1 - C(t-a)) da \quad (\text{S1.4})$$

At equilibrium, we require the time-independent (that is, translation invariant) form of this equation.

Let tildes denote equilibrium quantities. At equilibrium, the equation above becomes

$$\tilde{C} = s(1 - \tilde{C}) \int_0^\infty A(\tilde{x}(a)) \tilde{\mathcal{F}}(a) da \quad (\text{S1.5})$$

where $\tilde{x}(a)$ denotes the equilibrium size-at-age relationship, and $\tilde{\mathcal{F}}(a)$ denotes the equilibrium survival-to-age relationship.

To solve for \tilde{C} , we must know both $\tilde{x}(a)$ and $\tilde{\mathcal{F}}(a)$. These can be found by the following system of ODEs. First, for the equilibrium size-at-age relationship, we have

$$\begin{aligned} \frac{d}{da} \tilde{x}(a) &= g(\tilde{x}(a), \tilde{C}) \\ \tilde{x}(0) &= x_0. \end{aligned} \quad (\text{S1.6})$$

Second, we can follow eq. (4.19) of Kirkilionis et al. (2001) to show that $\tilde{\mathcal{F}}(a)$ solves

$$\begin{aligned} \frac{d}{da} \tilde{\mathcal{F}}(a) &= -\mu(\tilde{x}(a), \tilde{C}) \tilde{\mathcal{F}}(a) \\ \tilde{\mathcal{F}}(0) &= 1. \end{aligned} \quad (\text{S1.7})$$

To approximate the integral in eq. S1.5, write $\theta(a) = \int_0^a A(\tilde{x}(y)) \tilde{\mathcal{F}}(y) dy$. The integral in eq. S1.5 can then be computed with the ODE

$$\begin{aligned} \frac{d}{da} \theta(a) &= A(\tilde{x}(a)) \tilde{\mathcal{F}}(a) \\ \theta(0) &= 0. \end{aligned} \quad (\text{S1.8})$$

Finally, to determine a finite upper limit of integration for the integral in eq. S1.5, we choose a small survival probability ϵ , and a large age a_ϵ such that $\tilde{\mathcal{F}}(a_\epsilon) = \epsilon$. We then approximate the integral in eq. S1.5 with

$$\int_0^\infty A(\tilde{x}(a)) \tilde{\mathcal{F}}(a) da = \theta(\infty) \approx \theta(a_\epsilon). \quad (\text{S1.9})$$

The equilibrium value \tilde{C} is then found by solving $\tilde{C} = s(1 - \tilde{C})\theta(a_\epsilon)$ iteratively, where for each candidate guess of \tilde{C} , eqq. S1.6 – S1.8 are simulated from age 0 to age a_ϵ to compute $\theta(a_\epsilon)$.

References: Appendix S1

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Supplemental figures

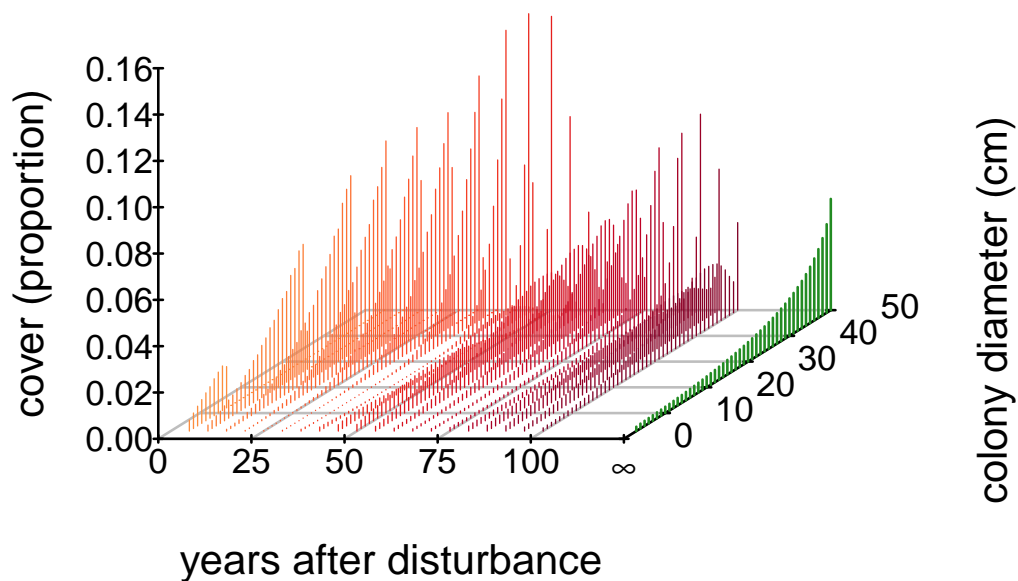


Figure S1: **Oscillations in coral cover are driven by space competition between pulses of recruits.** This display shows the size structure of the coral population for 100 undisturbed years following a catastrophe that completely eliminates existing coral cover. For ease of visualization, this display divides coral colonies into discrete size classes of 2 – 3 cm diameter, 3 – 4 cm diameter, . . . , 49 – 50 cm diameter, and shows the cover accounted for by colonies in each size class, expressed as a proportion of the total available space. Warm colors (orange and red) show size structure for years 5, 10, . . . , 100. The green histogram shows the equilibrium size structure to which the dynamics eventually converge.

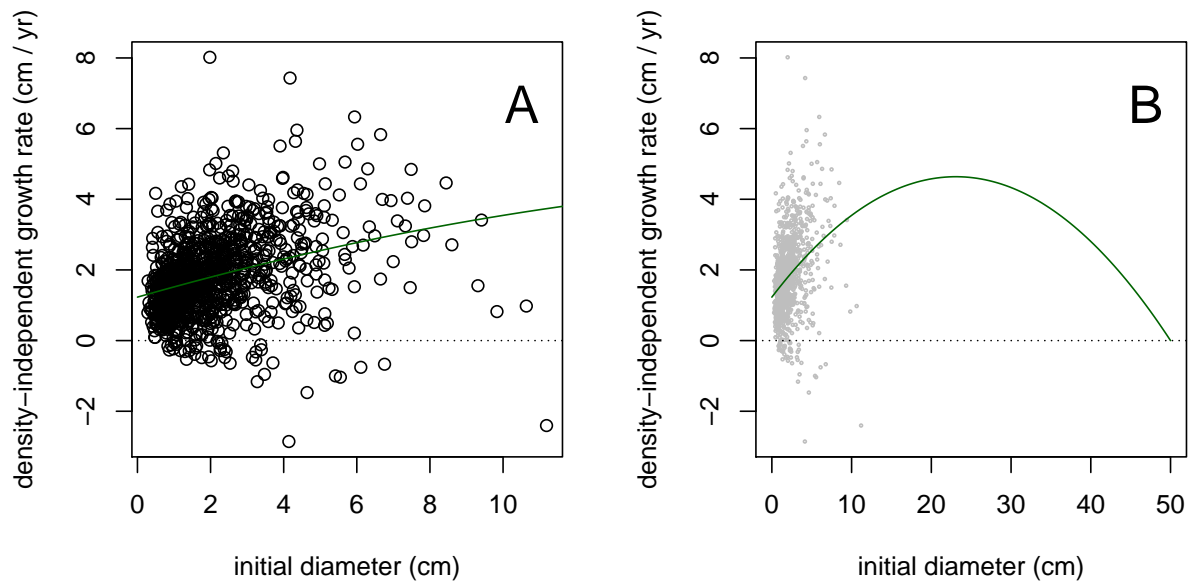


Figure S2: **Estimated growth rate for *Pocillopora verrucosa*.** A: Annual growth increment (corrected for crowding) vs. coral colony size for monitoring data from LTER sites 1 and 2 on Mo'orea's north shore, and best constrained least-squares fit of eq. S1.1. B: As in panel A, but extended over the full range of coral colony sizes.