Stony coral populations are more sensitive to changes in vital rates in disturbed environments

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Abstract

Reef-building corals, like many long-lived organisms, experience environmental change as a combination of separate but concurrent processes, some of which are gradual yet long-lasting, while others are more acute but short-lived. For corals, some chronic environmental stressors, such as rising temperature and ocean acidification, are thought to induce gradual changes in colonies' vital rates. Meanwhile, other environmental changes, such as the intensification of tropical cyclones, change the disturbance regime that corals experience. Here, we use a physiologically structured population model to explore how chronic environmental stressors that impact the vital rates of individual coral colonies interact with the intensity and magnitude of disturbance to affect coral population dynamics and cover. We find that when disturbances are relatively benign, intraspecific density dependence driven by space competition partially buffers coral populations against gradual changes in vital rates. However, the impact of chronic stressors is amplified in more highly disturbed environments, because disturbance weakens the buffering effect of space competition. We also show that coral cover is more sensitive to changes in colony growth and mortality than to external recruitment, at least in open populations, and that space competition and size structure mediate the extent and pace of coral-population recovery following a large-scale mortality event. Understanding the complex interplay among chronic environmental stressors, mass-mortality events, and population size structure sharpens our ability to manage and to restore coral-reef ecosystems in an increasingly disturbed future.

Keywords— coral reefs, environmental change, intraspecific competition, mathematical model, population dynamics, size structure

Introduction

Tropical reef-forming corals are celebrated worldwide for the spectacular and diverse marine communities they support (Huston, 1985; Knowlton et al., 2010), and for the ecosystem services that those communities provide (Moberg and Folke, 1999; Knowlton et al., 2010; Wild et al., 2011). Reef-building corals are also thought to be particularly vulnerable to ongoing environmental changes (Hoegh-Guldberg et al., 2007; Hughes et al., 2017), including rising sea temperatures, acidifying oceans, increased competition from macroalgae, and increased nutrient run-off and sediment loading in coastal waters. The aggregate effect of these changes may place many reefs in jeopardy of substantial ecological restructuring, if not wholesale collapse. The prospect of coral-reef degradation motivates robust and ongoing efforts to manage, to restore, and to protect reefs and the ecosystems they support (Hughes et al., 2017; Bruno et al., 2019).

A particular challenge to projecting how reefs will respond to environmental change or to management is that different components of environmental change will have different demographic consequences. In the case of corals, many coral reefs intermittently experience catastrophic mortality events from disturbances such as typhoons, predator outbreaks, bleaching, and disease. Environmental change is expected to increase the frequency and/or intensity of these disturbances (for example, tropical storms have recently become more powerful (Emanuel, 2005)). However, other aspects of environmental change — most notably rising sea temperatures and ocean acidification (OA) — simultaneously present chronic stressors that will alter the physiology and vital rates of individual coral colonies. For example, increasing temperature or decreasing calcification rates may reduce growth rates (De'ath et al., 2009); reduced skeletal density and/or increased microbioerosion might make colonies more susceptible to fragmentation or dislodgement from hydrodynamic stress (Madin et al., 2012; Reyes-Nivia et al., 2013); and recruitment of new colonies may be reduced by sublethal effects of bleaching (Ward et al., 2002) or increased macroalgal cover (Kuffner et al., 2006). Forecasting the aggregate impact of environmental change requires understanding how physiological responses to chronic stressors interact with changes in the disturbance regime that corals experience.

For example, Ortiz et al. (2018) recently showed that recovery rates from disturbances have slowed on the Great Barrier Reef, and suggested that these slower recovery rates may be a consequence of the combined effects of several chronic stressors. Restoration and management of coral reefs also benefits from an understanding of how chronic stressors and acute disturbances interact, as some stressors (e.g., sedimentation, fishing) may be more amenable to amelioration than others (e.g., tropical cyclones), especially at local scales.

Yet the interaction between chronic stressors and acute disturbances may be more nuanced than simply repeated episodes of death and recovery. In particular, size structure is known to be an important mediator of coral population dynamics. Over 30 years ago, Roughgarden et al. (1985) showed that sessile marine invertebrates with long-distance larval dispersal can undergo sustained population cycles driven by the interaction between age structure and density-dependent recruitment. Even when population cycles do not persist in perpetuity, populations may show damped oscillations in the recovery phase following a catastrophic disturbance. Pascual and Caswell (1991) showed that the same oscillations can appear in size-structured populations, thus establishing an important connection to stony corals, as vital rates of coral colonies often depend on colony size (Hughes, 1984; Hughes and Connell, 1987). Later work by Artzy-Randrup et al. (2007) suggested that density-dependent growth can stabilize these general dynamics and thus make population cycles less likely. Nevertheless, this theory makes it clear that a full consideration of coral populations' response to environmental change must account for the demographic consequences of size structure within the coral population.

The objective of this study is to investigate how gradual changes in coral colonies' vital rates driven by chronic stressors will interact with an increase in the frequency and intensity of disturbances, when vital rates depend on both colony size and population density. We investigate this question by developing and analyzing a physiologically structured population model (PSPM) of stony corals, building on theory developed by de Roos and colleagues (de Roos, 1997; Kirkilionis et al., 2001; de Roos et al., 2010; de Roos and Persson, 2013). Our core analysis consists of two parts. First, we investigate how size structure impacts coral population dynamics when coral populations experience stochastic mortality pulses from disturbances such as typhoons or predator outbreaks. Second, we conduct an elasticity analysis to quantify how changes in vital rates driven by chronic stressors might scale up to affect average coral cover, and ask how these sensitivities may depend on the frequency and intensity of mortality pulses.

Stony coral themselves are a hugely diverse taxon, with a vast array of growth morphologies, reproductive modes, and habitats. We do not attempt to capture the full range of this diversity here. Instead, we parameterize our model using data for the *Pocillopora verrucosa* species complex (see Edmunds et al. (2016)) as it occurs at 10 m depth on the fore reef of the north shore of Mo'orea, French Polynesia. We choose this species complex and habitat because it is well-studied and common on Mo'orea (Comeau et al., 2016; Holbrook et al., 2018; Doo et al., 2019), and has been a focus of other modeling efforts (Kayal et al., 2018). Our modeling framework is sufficiently general that it can be customized to other coral populations, although comparisons among different coral species are beyond the scope of this article.

The rest of this paper is structured as follows. In the Methods section, we introduce the mathematical model and describe how it is parameterized for *P. verrucosa*. The analysis of the model follows, and proceeds in two parts. First, we investigate the population dynamics predicted by the model under both undisturbed and intermittently disturbed conditions. Second, we conduct an elasticity analysis to investigate how coral cover responds to changes in colonies' vital rates under different disturbance regimes. The supplement provides technical details about parameter estimation and model implementation, computer code, and additional figures.

Methods

Model construction

Our development closely follows de Roos (1997). We classify individual coral colonies by their size, because size is often correlated with the demographic fate of individual colonies (Hughes and Connell, 1987). We measure a coral colony's size by its effective diameter x. In other words, if a colony's planar area is A, then the effective diameter x is defined by the familiar relation $A(x) = \pi\,(x/2)^2$. Let $n(t, x)$ give the density of coral colonies with size x at time t, such that $n(t, x)\,dx$ gives the population density of colonies with diameters between x and $x + dx$.

Let x_0 be the size of a newly settled and metamorphosed planula (i.e., a single polyp, often referred to as a spat) and let $x_{\max}$ be the maximum achievable colony size in the local habitat. The total coral cover at time t, measured as the proportion of available substratum covered, is given by

$$C(t) = \int_{x_0}^{x_{\max}} A(x)\, n(t, x)\, dx. \tag{1}$$

The proportion of available substratum is $1 - C(t)$. (As will be seen below, the model is defined to ensure $0 \leq C(t) \leq 1$.) Although our definitions of $C(t)$ and $1 - C(t)$ are most natural in the context of a monoculture, for a multi-species reef $C(t)$ can be interpreted as the cover of the focal population as a proportion of the habitat available to that species.

Three vital rates govern the predicted population dynamics. Each vital rate may depend on both a colony's size and the population's total cover. The growth rate of a colony is the rate at which its size changes with respect to time, written as $g(x, C)$. We assume that growth is deterministic, and depends only on the colony's size and the total population cover. The second vital rate is the background mortality rate, written as $\mu(x, C)$. This gives the rate at which colonies perish from chronic mortality, such as dislodgement, overgrowth, or disease. This rate does not include episodic mass mortality caused by mass bleaching, cyclones, or predator outbreaks. For simplicity, we assume that when a colony dies, the space that it occupied immediately becomes available to other living colonies. We also do not consider partial mortality, which may be important for many coral species.

The third vital rate is the recruitment rate. Following previous theory (Roughgarden et al., 1985; Artzy-Randrup et al., 2007), we will consider a single coral population that recruits predominantly via larval immigration; internal recruitment (i.e., self-seeding) is assumed to be negligible. Successful recruitment is limited by the available free space (Hughes and Jackson, 1985;

Connell et al., 1997). The rate at which new recruits arrive and settle is written as $s(C)$.

Collecting all model components gives the full model for coral population dynamics as (de Roos, 1997)

$$\frac{\partial n(t,x)}{\partial t} + \frac{\partial g(x,C)\,n(t,x)}{\partial x} = -\mu(x,C)\,n(t,x) \tag{2a}$$

$$g(x_0,C)\,n(t,x_0) = s(C). \tag{2b}$$

Eq. 2a is a balance equation that relates the change in the density of coral colonies to their growth and mortality. Eq. 2b is a boundary condition that adds new individuals to the population via external recruitment.

Parameterization for *Pocillopora verrucosa*

We parameterize our model based on the species complex *Pocillopora verrucosa* as it is found at 10 m depth on the north shore of Mo'orea, French Polynesia (Edmunds et al., 2016). No single data set contains all of the information that we need to parameterize the model fully. Thus, we pool information from several sources, including previously published data (Holbrook et al., 2018), our own annual photoquadrat monitoring data, and precedent set in earlier modeling studies (Muko et al., 2001; Artzy-Randrup et al., 2007). Details about parameter estimation can be found in Appendix S1.

We assume that the maximum attainable size of a *P. verrucosa* colony is $x_{\max}$ = 50 cm (Veron, 2000), and that a newly settled coral polyp has a diameter of $x_0 = 0.4$ mm (Babcock, 1991). To quantify growth rates, we first assume that the growth rate $g(x,C)$ takes the form

$$g(x,C) = g_0(x)\,(1-C)$$

where $g_0(x)$ gives a colony's growth rate in uncrowded conditions. Density-dependence is assumed to reduce growth in proportion to the available free space, equal to $1-C$ (Muko et al., 2001; Artzy-Randrup et al., 2007). To estimate $g_0(x)$ we use annual photoquadrat monitoring data of individual *P. verrucosa* colonies from this habitat for 2011–2018. These years followed a large die-off caused by an outbreak of crown-of-thorns seastars in 2002–10 and a cyclone in 2010 (Kayal et al., 2012; Holbrook et al., 2018). Thus, most coral colonies observed during these surveys were small ($x \leq 12$ cm). These data suggest that as corals become larger, coral growth rates increase, but at a decelerating rate, at least across the size ranges found in this data set. Thus, we fit a quadratic curve for $g_0(x)$, constrained so that the growth rate is 0 when a colony attains its maximal size, i.e., $g_0(x_{\text{max}}) = 0$ (Fig. 1A).

We assume that mortality is density-independent, thus $\mu(x, C) = \mu(x)$. Following Madin et al. (2014), we expect that very small and very large colonies will experience larger mortality than intermediate-sized colonies; that is, the relationship between size and mortality will be "u-shaped". This shape arises because small coral colonies are more vulnerable to a wide variety of mortality types including overgrowth from space competitors, whereas large colonies are more vulnerable to dislodgement from hydrodynamic stress (Madin et al., 2014). Our photoquadrat data do not include enough large colonies to estimate the full relationship between mortality and colony size. Thus, we instead use size-specific mortality data reported by Madin et al. (2014) for corymbose corals at Lizard Island, Australia. Of the coral growth forms included in Madin et al. (2014), the corymbose growth form is most similar to the closed branching growth form of *P. verrucosa*, and thus we expect the qualitative shape of the mortality curve to be similar. However, we also expect that the acroporid species used by Madin et al. (2014) will have higher mortality than *P. verrucosa*, as verified by Holbrook et al. (2018)'s mortality data for *Pocillopora* recruits at Mo'orea. Thus, we fit a size-dependent survival curve to Madin et al. (2014)'s corymbose colony data, and then multiplied this curve by a constant factor to adjust the small-colony mortality to match the mortality from Holbrook et al. (2018) (Fig. 1B).

Finally, we assume that recruits arrive at a baseline rate s_0. Recruits successfully settle at a rate proportional to the amount of free space (Hughes and Jackson, 1985; Connell et al., 1997), giving

$$s(C) = s_0\,(1 - C).$$

Holbrook et al. (2018) report that *P. verrucosa* recruits large enough to be easily detectable in photoquadrats ($x = 0.03$ m) are found on the north shore of Mo'orea at an average rate of approximately 20 m^{-2} y^{-1}. Our growth and survival curves suggest that in uncrowded conditions roughly 40% of all recruits will survive long enough to grow to $x = 0.03$ m, giving an arrival rate of newly settling recruits of $s_0 \approx 20/.4 = 50$ recruits m^{-2} y^{-1}.

Numerical implementation

We implemented the model using two separate numerical procedures. We simulated dynamics from our model by using the Escalator Boxcar Train (EBT) method (de Roos, 1988, 1997). The EBT divides the population into many small cohorts, where each cohort consists of colonies that enter the population during a short time interval. A closed system of ordinary differential equations is developed that tracks the number and size of individuals in each cohort through time, and approximates the dynamics of the full model up to second-order precision. In addition to the EBT, we calculated the equilibrium population structure under undisturbed conditions by using the methods described in Kirkilionis et al. (2001). This procedure converts the model to an age-dependent renewal equation and solves for the equilibrium. More details are provided in Appendix S1. For the purposes of this article, the benefits of this second approach are to provide a more exact calculation under undisturbed conditions, and to build confidence that both methods have been implemented correctly. All analysis were implemented in R, version 3.5.2 (R Core Team, 2018). Computer code is provided in Data S1.

Analysis and results

First, we explore the population dynamics generated by the model under our baseline parameter set, both with and without mass-mortality events caused by disturbances such as typhoons or bleaching. Second, we conduct a sensitivity analysis to investigate how changes in vital rates driven by chronic stressors such as temperature or OA interact with mortality pulses to affect overall coral cover.

Population dynamics

Figure 2A shows total coral cover over time for 100 (undisturbed) years following a catastrophe that completely eliminates the resident coral population. Recovery following a catastrophe is characterized by transient oscillations of considerable magnitude that eventually decay as coral cover approaches a stable equilibrium. These oscillations have a period on the order of one full oscillation per 40–50 years, suggesting that coral populations may exhibit slow dynamics that unfold on the time scale of scientific careers and management horizons, or longer.

These transient oscillations in coral cover are driven by space competition between cohorts of colonies (Figs. 2B, S1). Immediately after a catastrophe, the reef is repopulated by immigrating larvae from other reefs. These new recruits grow quickly in uncrowded conditions, rapidly occupying the available space. As cover builds, crowding reduces both growth and subsequent recruitment, leading to a population that consists mostly of corals that are large enough to escape overgrowth, yet small enough to avoid being dislodged. Eventually these colonies grow large enough that dislodgment mortality increases, opening new substratum to usher in the next cohort of recruits. These population cohorts echo the dynamics observed in early theoretical work for sessile marine invertebrates with space-limited recruitment (Roughgarden et al., 1985; Pascual and Caswell, 1991; Artzy-Randrup et al., 2007), and can be visualized by plotting coral cover against a characteristic colony size (Fig. 2B). Here, we define the characteristic colony size such that colonies smaller than the characteristic size account for half the coral cover, and colonies larger than the characteristic size account for the other half of coral cover. We summarize size structure in this way because the average or median colony size is affected by the size structure's skew. Appendix S1: Fig. S1 provides an alternative visualization of these population oscillations.

For contemporary coral reefs, decades-long runs of undisturbed conditions are unlikely. To ask if similar dynamics appear in disturbed environments, we conducted simulations with stochastic mass-mortality events. We modeled two disturbance regimes. In the moderate-disturbance regime (Fig. 3A,B), each year had a 10% chance of an event such as bleaching or a typhoon in which 25%

of all colonies die (what we will subsequently call a “25% mortality event”), and a 4% chance of an 80% mortality event (such as a predator outbreak). In the high-disturbance regime (Fig. 3C,D), each year had a 20% chance of a 40% mortality event, and a 5% chance of a 95% mortality event. Mortality in these events was uniform across colony size.

These simulations show that size structure still mediates the recovery of coral populations following a widespread mortality event, even if fully formed population oscillations do not appear. Specifically, as long as a disturbance does not decimate a population (that is, when post-disturbance cover is $\geq 10\%$), the characteristic colony size will continue to increase following the disturbance (Fig. 3B,D). This suggests that, following a mild or moderate disturbance, recovery is initially driven by growth of surviving colonies as opposed to recruitment of new colonies. Consequently, cover will rebound more rapidly if the colonies that survive the disturbance are medium-size colonies that are able to grow most quickly in uncrowded conditions (Fig. 1A). Surviving colonies then grow rapidly to fill newly vacated space, to the extent that this growth is not impeded by dead coral skeletons. On the other hand, if the disturbance occurs when the population is dominated by large colonies, then physiological constraints will limit the survivors’ post-disturbance growth, despite the newly relaxed intraspecific competition. Thus, the population may fail to rebound to pre-disturbance cover in the first several years following a disturbance, even if those years are environmentally benign. On the other hand, when a severe disturbance reduces the coral population to very low cover ($\leq 10\%$), the surviving colonies are too sparsely distributed to rebuild cover through their growth. Instead, recovery must wait for a new cohort of recruits to arrive and to replenish the population.

Elasticity analysis

We now investigate how changes in colony-level vital rates driven by chronic disturbances such as rising sea temperatures or OA affect population cover. To do so, we quantify how a proportional change in a vital rate translates into corresponding proportional change in total cover; in other words, we conduct an elasticity analysis (de Kroon et al., 1986). To simplify matters, we suppose that changes in growth, mortality, or recruitment act independently of both colony size and coral density.

Mathematically, we introduce multiplication factors ϕ_g, ϕ_μ and ϕ_s, such that the modified growth, mortality, and recruitment rates are $\phi_g \times g(x, C)$, $\phi_\mu \times \mu(x, C)$ and $\phi_s \times s(C)$, respectively. We vary each multiplication factor individually, and track how the average coral cover changes in response. Multiplication factors are varied across a range of values to project the impact of varying degrees of chronic disturbance. However, specific experimental results can provide context. For example, Evensen and Edmunds (2016) showed that elevating seawater pCO_2 from ambient levels (~ 400 μatm) to levels projected at the end of the current century under pessimistic forecasts (~ 1000 μatm; Moss *et al.* 2010) decreases the horizontal linear extension rate of *P. verrucosa* colonies by 30%. This corresponds to a growth multiplication factor of $\phi_g = 0.7$.

To establish a baseline, we first consider how changes in vital rates impact coral cover in undisturbed environments. In this case, equilibrium cover is more sensitive to changes in growth and mortality, and considerably less sensitive to changes in recruitment (Fig. 4A). Large ($> 25\%$) decreases in growth eventually cause equilibrium cover to be lost at an accelerating rate, while non-linear effects of changes in mortality and recruitment are less pronounced. Next, we consider disturbed environments by simulating the same two disturbance regimes that we considered for Fig. 3. For each disturbance regime, we simulated 400 years of dynamics, and recorded average coral cover over the last 200 years. These simulations show that disturbance makes coral cover more sensitive to changes in any of the three vital rates (Fig. 4B,C). In other words, disturbance and changes in vital rates interact, as the effect of both combined is greater than the sum of the individual effects. In disturbed environments, average cover is still less sensitive to changes in recruitment than to changes in growth or mortality, but changes in any of these inputs have more pronounced effects under disturbed conditions.

To understand why small changes in vital rates have a bigger effect on coral cover in disturbed environments, we calculated the elasticity of total coral cover to changes in demographic inputs during the recovery period immediately following a local extirpation (Fig. 5). Elasticities here are defined in the usual way, as the proportional derivatives of the relationship between coral cover and the demographic multiplier ϕ evaluated at $\phi = 1$ (de Kroon et al., 1986). We compute the elasticity with respect to the direction of change caused by chronic environmental stressors (e.g., a decrease in growth or recruitment, and an increase in mortality). All elasticities are calculated with finite-difference approximations.

In the immediate aftermath of a local extirpation, coral cover is most sensitive to recruitment and growth of new colonies, and only minimally sensitive to mortality (Fig. 5). However, in the first few years of recovery, cover becomes increasingly sensitive to growth and mortality, and less so to recruitment. These elasticities are larger (in magnitude) than the elasticities observed at equilibrium (shown on the right axis of Fig. 5), especially for growth and recruitment. Coral populations are more sensitive to changes in vital rates after a disturbance because density-dependent crowding buffers the effect of demographic change in the long run, but acts only weakly in the uncrowded conditions created by a disturbance. As recovery continues, a more complicated pattern emerges, because changes in growth and mortality also affect the timing of the transient oscillations in population size. Despite these complicated patterns, cover remains only minimally sensitive to recruitment once the first few years of recovery have passed.

Discussion

This analysis suggests several insights into the population dynamics of reef-building corals. First, size structure and space competition can drive surprising dynamics even in populations that routinely experience mass mortality events. Roughgarden et al. (1985) and others have already established that size structure and space-limited recruitment can lead to population oscillations in sessile marine invertebrates in undisturbed conditions; we show here that those oscillations appear in models with size-dependent growth and mortality schedules similar to those observed in a common coral species complex, *Pocillopora verrucosa*.

For many of today's reefs, intermittent mortality pulses will disrupt the formation of regular population oscillations. However, recognizing that size structure causes coral cover to tend towards oscillation allows sharper projections coral recovery in disturbed environments, for two reasons.

First, when a new cohort of recruits settle and grow following a local extirpation (or near extirpation), coral cover can increase to levels that temporarily exceed the long-term carrying capacity. If a mortality pulse occurs at the peak of a nascent oscillation, coral cover should not necessarily be expected to rebound to pre-disturbance levels in the first several years following the disturbance, even if those years are environmentally benign. This possibility complicates the rapid evaluation of management actions to restore reefs after a disturbance. Second, fluctuations in size structure explain variation in the recovery of coral populations immediately after a moderate disturbance. Recovery after a moderate disturbance is driven by the growth of surviving colonies, and thus cover will rebound most quickly if the surviving colonies are able to grow rapidly when intraspecific space competition is relaxed. In our model, mortality pulses act independently of size, so size structure prior to a moderate disturbance dictate the pace of the post-disturbance rebound. If, instead, disturbance mortality depends on colony size, then the pace of recovery will be determined both by the size structure of the population at the time of the disturbance, and the size-selective mortality.

This analysis also suggests that occasional mass-mortality events make coral cover more sensitive to changes in vital rates driven by chronic environmental stressors. In the absence of disturbance, intraspecific space competition partially buffers the effect of changes in vital rates. Mass-mortality events continually reset coral populations to low densities where competition for space is less intense, and thus density-dependence is less effective at buffering simultaneous changes in underlying vital rates. Although we have presented our results as disturbance exacerbating coral sensitivity to chronic stressors, of course this interaction must flow in the other direction as well: chronic stressors will also make average coral cover more sensitive to changes in the frequency and magnitude of disturbance.

The synergistic effects of chronic and acute disturbance on coral cover suggest an interesting implication for reef management and restoration. To the extent that efforts to ameliorate the impacts of chronic and acute disturbance are distinct, the benefits of ameliorating both types of disturbance may be less than the sum of the benefits of ameliorating either type of disturbance individually. Managing to lessen the impact of one type of disturbance on reefs not only creates a direct benefit, but it also creates an indirect benefit by reducing the interaction between the managed and unmanaged disturbance type. This eases the burden on managers, as it suggests that managing for either type of disturbance alone may be more efficacious than if the disturbance types had additive effects on coral cover. Of course, fully ameliorating the combined effects of acute and chronic disturbances will require managing for both, and addressing the ultimate driver of enhanced environmental disturbance — anthropogenic changes to the global environment — will combat both chronic and acute disturbances at once.

Our results also suggest that coral populations will be more sensitive to changes in colony growth or mortality rates than to changes in recruitment (Fig. 4). The relative robustness of coral cover to changes in recruitment is noteworthy because our assumption of constant recruitment is a clear simplification. In reality, we expect external recruitment to vary through time, likely substantially (Graham et al., 2008; Thompson et al., 2018). However, because recruitment has only a mild impact on average coral cover, it follows that coral populations should be relatively insensitive to fluctuations in external recruitment. Of course, one population's external recruits are another population's spawned gametes, and thus region-wide declines in coral cover must trigger comparable declines in recruitment across a metapopulation, if gamete production in corals is proportional to live tissue area (Hall and Hughes, 1996), and thus also proportional to total cover. The region-wide, metapopulation dynamics of several coral reefs coupled by larval migration, complete with local size structure and density-dependence, would be an intriguing topic for further study.

Our results also help to resolve why different demographic processes appear to drive the recovery of coral cover in recent empirical studies. Gilmour et al. (2013) showed that growth of surviving coral colonies drove recovery of an acroporid-dominated oceanic reef in Western Australia after a mass bleaching event. In contrast, Holbrook et al. (2018) argued that larval recruitment drove the recovery of pocilloporid cover at the Mo'orean reefs on which our model parameterization is based, following a near extirpation caused by corallivory and cyclone damage. Comparison of these two cases shows that, for the Western Australia study, bleaching reduced coral cover to 5 – 10%, while for the Mo'orean study, coral cover at its post-disturbance nadir was <0.5%. While this is only one of many differences between the two studies, it accords with our result that growth of surviving colonies can restore cover in the immediate wake of a disturbance as long as enough colonies survive, while recruitment becomes more important immediately after a near extirpation.

The present work follows in a rich tradition of using population- or community-dynamic models to quantify the sensitivity of coral growth or cover to coral demography (e.g., Hughes and Tanner, 2000; Riegl and Purkis, 2009; Baskett et al., 2010; Fabina et al., 2015). As befits modeling studies, these analyses simplify coral-reef ecosystems in different yet complementary ways. For example, Riegl and Purkis (2009) model competition among several coral species groups, while Baskett et al. (2010) and Fabina et al. (2015) embed coral dynamics in a larger community context that features competition with macroalgae. To the extent that common trends appear across these analysis, the survival of established coral colonies, either under background conditions or during times of acute stress, is regularly identified as an important determinant of coral-population growth and cover, while external larval recruitment has only a weak effect on coral growth and cover. None of these patterns are universal, however. For example, Riegl and Purkis (2009) found that coral cover and coral community composition were comparably driven by recruitment and survival. Differences among sensitivity analyses testify to the diversity of reef systems that have motivated those studies, and to the many different aspects of coral-reef communities (e.g., population growth, cover, resilience, species composition) to which sensitivity can be evaluated.

The present model invokes a number of additional simplifying assumptions, any one of which provides scope for additional study. First, we have assumed that internal recruitment (that is, self-seeding by local colonies) is negligible. Empirical evidence for the importance of internal recruitment of corals varies widely (Sammarco and Andrews, 1989; Gilmour et al., 2009; Jones et al., 2009; van Oppen et al., 2011). Additional simulations of our model (not shown) suggest that self-seeding dampens population oscillations, because high coral cover generates high larval production, which partially counteracts the reduction in recruitment caused by a dearth of available substratum. Second, we have assumed that when a coral colony dies, the space that it occupied immediately becomes available to living colonies or new recruits. This assumption is more appropriate for some causes of mortality, such as hydrodynamic dislodgement, than others, such as corallivory or bleaching. In these latter cases, dead coral skeletons need to be removed through breakage, bioerosion, or dissolution before surviving colonies or new recruits can occupy the newly available space. This lag between a colony's death and the removal of its dead skeleton may further promote population oscillations in coral cover.

Third, we have assumed that changes in colony growth and mortality caused by chronic stressors act independently of colony size. For mortality at least, we expect that size-dependent mortality is driven by multiple mechanisms. Namely, when colonies are small, mortality is likely inversely related to size because smaller colonies are most susceptible to overgrowth by conspecific or heterospecific space competitors (Ferrari et al., 2012). On the other hand, when colonies are large, mortality is positively related to size because large colonies are more susceptible to dislodgement from hydrodynamic stress (Madin et al., 2014). If, for example, a chronic stressor such as ocean acidification increases mortality by making coral skeletons less dense and hence more brittle (Fantazzini et al., 2015), we might expect the mortality of large coral colonies to increase more rapidly than the mortality of small coral colonies. If data were available to quantify the size-dependent effects of chronic stressors more precisely, it would be straightforward to incorporate those effects into this modeling framework.

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Figure legends

Figure 1. Growth and mortality functions used in the model. A: Density-independent growth rate in m / yr vs. colony diameter. This plot shows g_0, the growth rate in uncrowded conditions. B: Annual mortality vs. colony diameter, based on data for corymbose colonies reported in Madin et al. (2014), and adjusted to match 35% small-colony mortality for $x = 0.03$ m colonies reported in Holbrook et al. (2018) (shown by the point in red). This plot shows annual mortality as a proportion, although mortality enters the model as the equivalent rate.

Figure 2. Model dynamics under the baseline parameter set for *P. verrucosa*. A: Total coral cover (as a proportion of available substrate) vs. time for 100 undisturbed years following a catastrophe that completely eliminates existing coral cover. The dashed horizontal line shows the equilibrium cover to which the dynamics eventually converge. B: Phase portrait showing the size (diameter) of a characteristic coral colony vs. the coral cover of the population. The characteristic colony size is defined such that colonies smaller than the characteristic size account for exactly half of the coral cover. Panel B shows 300 years of undisturbed dynamics following a catastrophe, and the red dot shows the equilibrium point to which the dynamics eventually converge.

Figure 3. Population oscillations driven by size structure persist in moderately disturbed environments, but not in highly disturbed environments. A: Total coral cover (as a proportion of available substrate) vs. time for 150 years in the "moderate-disturbance" regime. Tick marks on the top axis show the timing of small (above the axis) or large (below the axis) mortality pulses. B: Characteristic colony size vs. coral cover for the same dynamics. Characteristic colony size is defined in the same way as in Fig. 2. The red dot shows the equilibrium under undisturbed conditions. C,D: Parallel plots for the "high-disturbance" regime, where mortality events are more frequent and more severe. Displayed dynamics follow a "burn-in" period of 200 years to eliminate transients.

Figure 4. Average coral cover is more sensitive to changes in vital rates in disturbed environments. Each panel shows the proportional change in average coral cover in response to a proportional change in a single vital rate: either growth (black), mortality (violet), or recruitment (green). Within each panel, changes in vital rates are shown so that the putative effect of chronic environmental stress increases from left to right. A: No disturbance. B: Infrequent, moderate disturbance. C: Frequent, severe disturbance. Results in panel A are based on equilibrium calculations, while results in panels B and C are based on stochastic simulations.

Figure 5. Elasticity of coral cover to vital rates changes considerably during the years following a local extirpation. Lines show the elasticity of total coral cover to changes in colony growth (black), mortality (violet), and recruitment (green), as a population rebuilds following a local extirpation. Elasticities are defined with respect to the change in vital rates caused by chronic environmental stress; that is, with respect to a decrease in growth or recruitment, and with respect to an increase in mortality. Elasticities show how coral cover changes at each time point in response to changing one vital rate for the entire time course of the recovery following a local extirpation. Arrowheads on the right axis show the long-run elasticity of the equilibrium cover in undisturbed environments.

Figures

Figure 1:

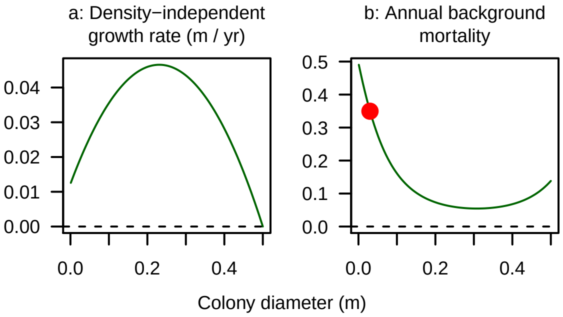


Figure 2:

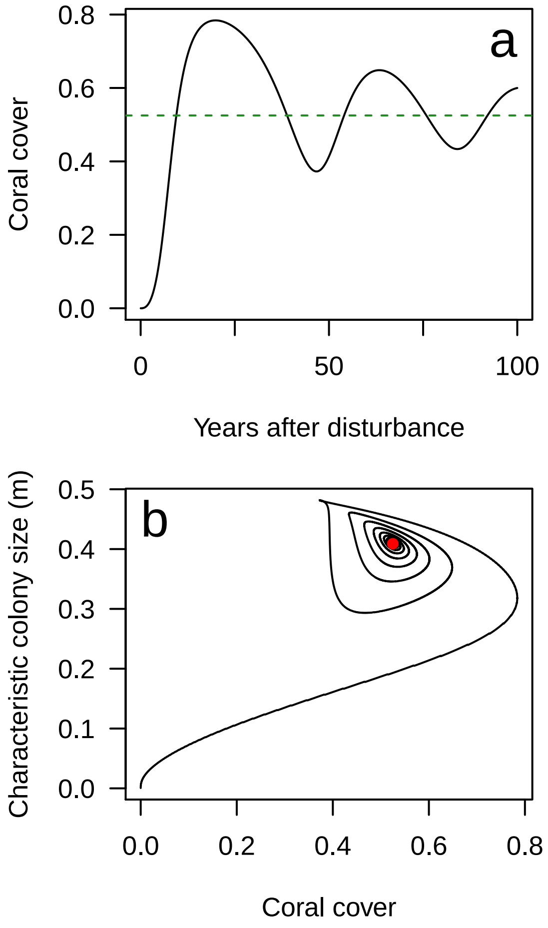

a
Coral cover
0.0
0.2
0.4
0.6
0.8
0
50
100
Years after disturbance
b
Characteristic colony size (m)
0.0
0.1
0.2
0.3
0.4
0.5
0.0
0.2
0.4
0.6
0.8
Coral cover

Figure 3:

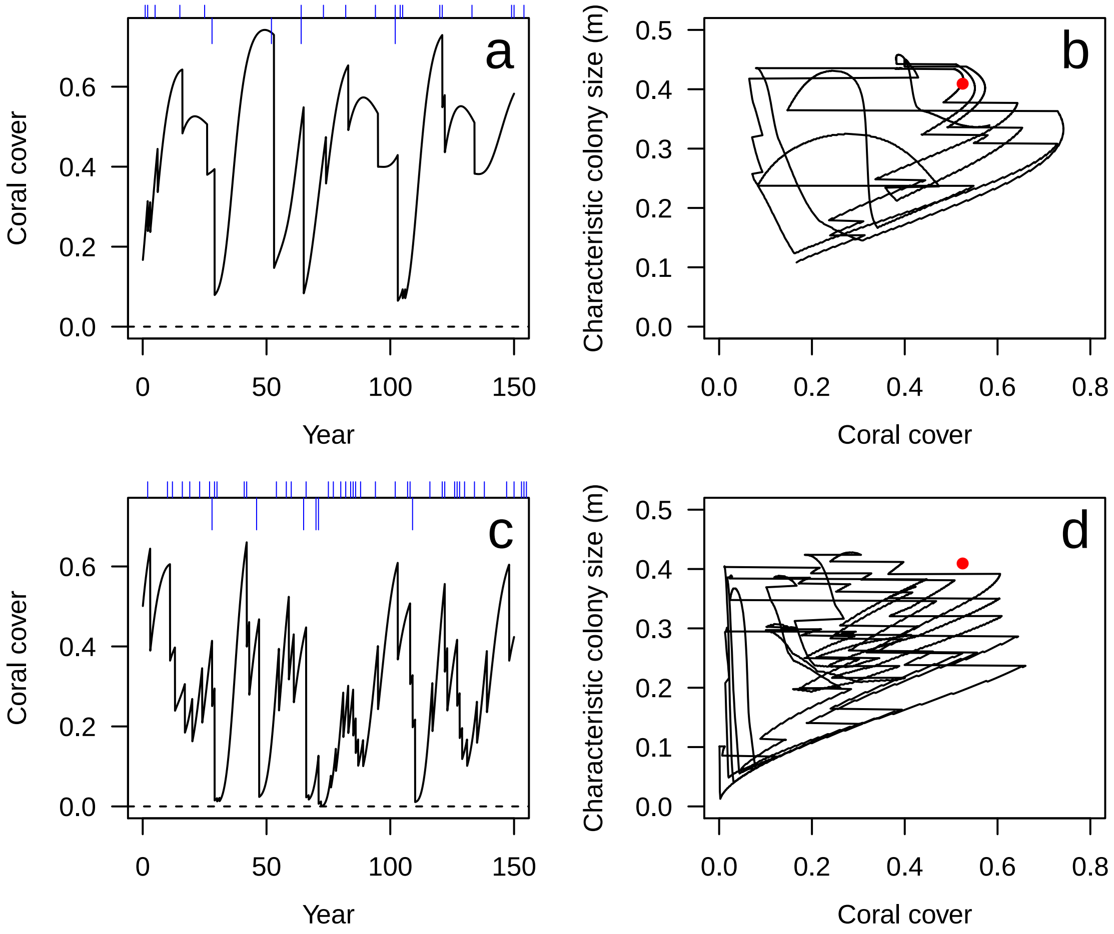

a
Coral cover
0.0
0.2
0.4
0.6
Year
0
50
100
150
b
Characteristic colony size (m)
0.0
0.1
0.2
0.3
0.4
0.5
Coral cover
0.0
0.2
0.4
0.6
0.8
c
Coral cover
0.0
0.2
0.4
0.6
Year
0
50
100
150
d
Characteristic colony size (m)
0.0
0.1
0.2
0.3
0.4
0.5
Coral cover
0.0
0.2
0.4
0.6
0.8

Figure 4:

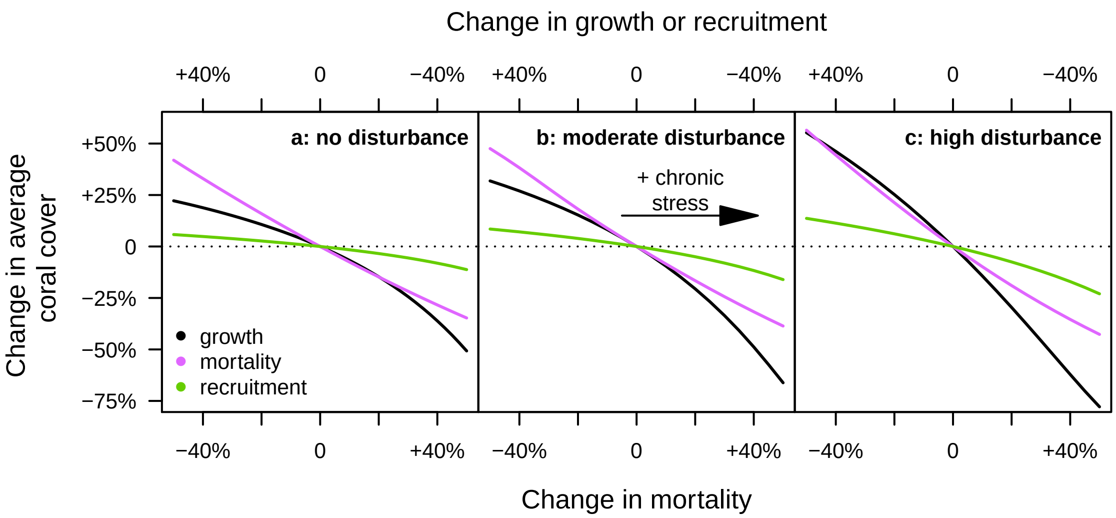
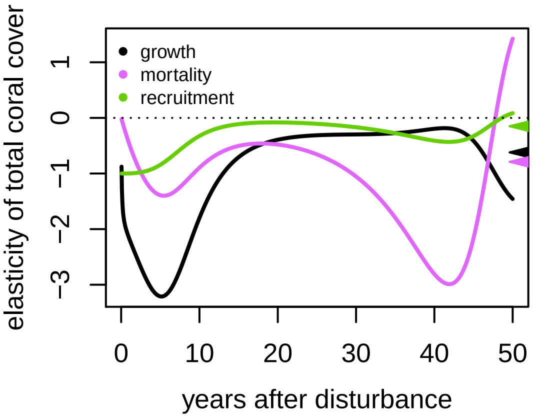

Change in growth or recruitment
+40%
0
−40%
+40%
0
−40%
+40%
0
−40%
a: no disturbance
b: moderate disturbance
c: high disturbance
+ chronic stress
Change in average coral cover
+50%
+25%
0
−25%
−50%
−75%
● growth
● mortality
● recruitment
−40%
0
+40%
−40%
0
+40%
−40%
0
+40%
Change in mortality

Figure 5:


elasticity of total coral cover
1
0
−1
−2
−3
0
10
20
30
40
50
years after disturbance
● growth
● mortality
● recruitment

Appendix S1: Technical details and supplemental figures

To accompany: Tessa E. Hall, Andrew S. Freedman, André M. de Roos, Peter J. Edmunds, Robert C. Carpenter, and Kevin Gross. 2020+. “Stony coral populations are more sensitive to changes in vital rates in disturbed environments.” *Ecological Applications*.

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 $x_t = x_{\mathrm{max}}$ (Fig. S2). Our fitted equation takes the form $y_t = b_0 + b_1 x + b_2 x^2 + \epsilon$, where the ϵ's take the usual assumptions of independent and identically distributed Gaussian error. In other words, our fitted equation is

$$g(x, C) = (b_0 + b_1 x + b_2 x^2) \times (1 - C). \tag{S1.1}$$

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 $\mu(x, C)$:

$$\mu(x, C) = \exp\left(a_0 + a_1 x + a_2 x^2\right). \tag{S1.2}$$

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 $\mathrm{m}^{-2}\ \mathrm{y}^{-1}$. 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 $\mathrm{m}^{-2}\ \mathrm{y}^{-1}$.

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:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

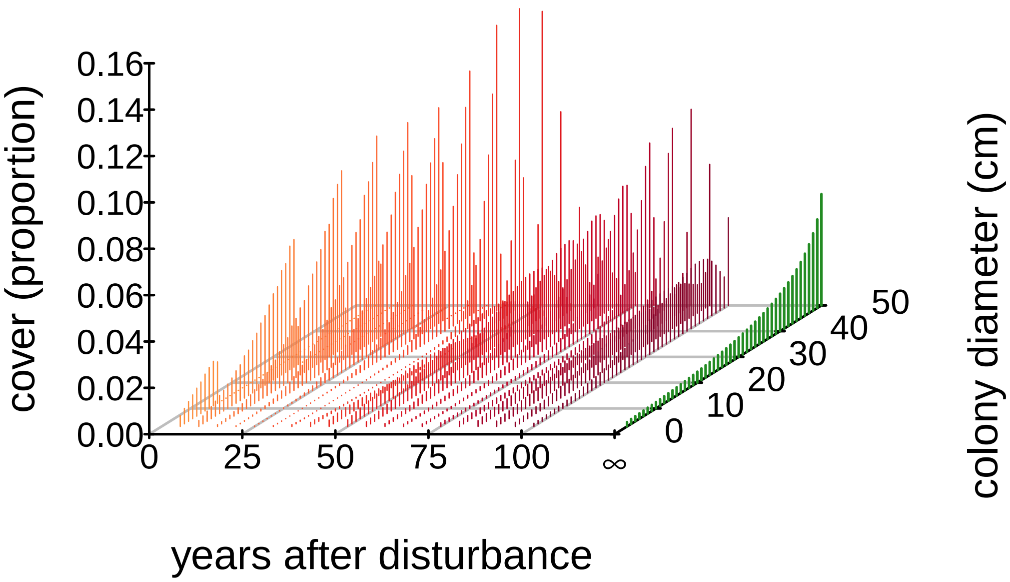

Figure S1: **Oscillations in coral cover are driven by space competition between pulses of recruits.** This display shows the size structure of the coral population for 100 undisturbed years following a catastrophe that completely eliminates existing coral cover. For ease of visualization, this display 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 $5, 10, \ldots, 100$. The green histogram shows the equilibrium size structure to which the dynamics eventually converge.

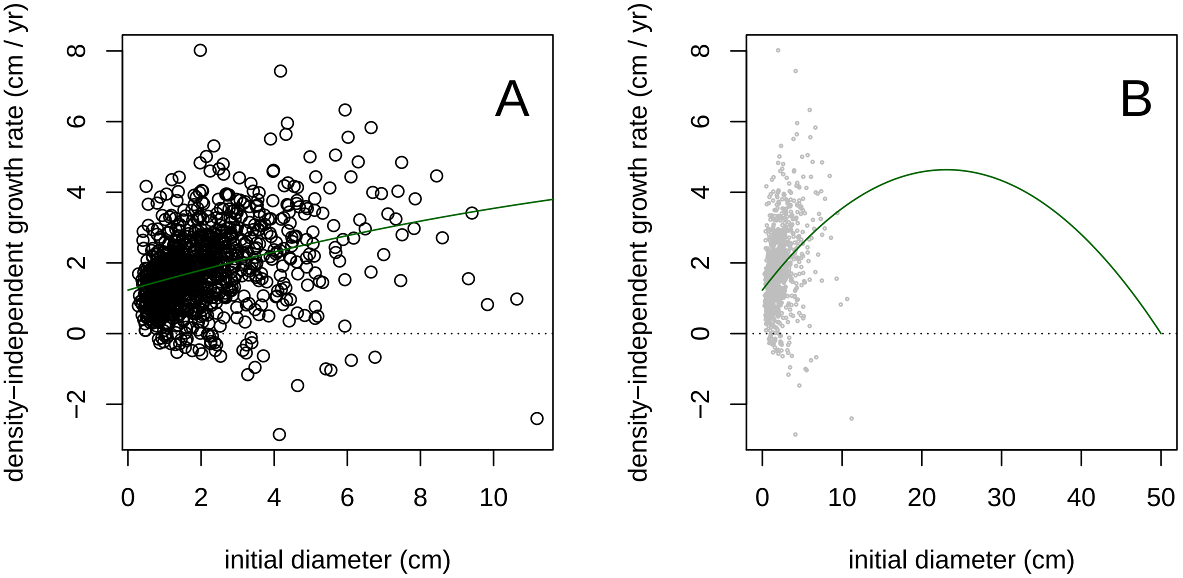

Figure S2: **Estimated growth rate for *Pocillopora verrucosa*.** A: Annual growth increment (corrected for crowding) vs. coral colony size for monitoring data from LTER sites 1 and 2 on Mo'orea's north shore, and best constrained least-squares fit of eq. S1.1. B: As in panel A, but extended over the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