



Projected shifts in coral size structure in the Anthropocene

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Abstract

Changes in the size structure of coral populations have major consequences for population dynamics and community function, yet many coral reef monitoring projects do not record this critical feature. Consequently, our understanding of current and future trajectories in coral size structure, and the demographic processes underlying these changes, is still emerging. Here, we provide a conceptual summary of the benefits to be gained from more comprehensive attention to the size of coral colonies in reef monitoring projects, and we support our argument through the use of case-history

examples and a simplified ecological model. We neither seek to review the available empirical data, or to rigorously explore causes and implications of changes in coral size, we seek to reveal the advantages to modifying ongoing programs to embrace the information inherent in changing coral colony size. Within this framework, we evaluate and forecast the mechanics and implications of changes in the population structure of corals that are transitioning from high to low abundance, and from large to small colonies, sometimes without striking effects on planar coral cover. Using two coral reef locations that have been sampled for coral size, we use demographic data to underscore the limitations of coral cover in understanding the causes and consequences of long-term declining coral size, and abundance. A stage-structured matrix model is used to evaluate the demographic causes of declining coral colony size and abundance, particularly with respect to the risks of extinction. The model revealed differential effects of mortality, growth and fecundity on coral size distributions. It also suggested that colony rarity and declining colony size in association with partial tissue mortality and chronic declines in fecundity, can lead to a demographic bottleneck with the potential to prolong the existence of coral populations when they are characterized by mostly very small colonies. Such bottlenecks could have ecological importance if they can delay extinction and provide time for human intervention to alleviate the environmental degradation driving reductions in coral abundance.



1. Introduction

In a rapidly changing world dominated by anthropogenic disturbances, there is a great need to understand the ways through which ecosystem function is being perturbed (Doney et al., 2012; Hoegh-Guldberg and Bruno, 2010; Hughes et al., 2018). Quantifying changes in the abundance of functionally important organisms is at the frontier of efforts to address this need, and analyses of long-duration records are the central means to inform understanding of the ecological changes underway. The combination of time-series analyses with hypothesis-driven research allows ecological changes to be projected into the future (Lindenmayer et al., 2015, 2010), and to conduct proactive resource management (Flower et al., 2017; Hughes et al., 2013). Coral reefs are among the ecosystems most at risk from climate change (Hoegh-Guldberg et al., 2007; Walther et al., 2002), and while monitoring efforts are capturing the widespread, rapid, and large declines in abundance of corals (Bruno and Selig, 2007; De'ath et al., 2012), these efforts are not doing enough to identify the fundamental mechanisms causing the losses of coral to occur, or to determine whether they might reverse on a time scale of decades-to-a-century.

Decadal-scale monitoring is essential to document the dynamics of long-lived organisms like corals. Most monitoring studies report changes in live

coral cover (Bruno et al., 2019; Perry et al., 2018; Stuart-Smith et al., 2018), defined as the planar percentage cover of corals, pooled among taxa. Coral cover has been used as the state variable describing coral abundance for decades (Bell and Galzin, 1984; Bruno and Selig, 2007; Hughes, 1994; Roy and Smith, 1971; Talbot, 1965; Wismer et al., 2019), and it is used to evaluate reef “condition”. Arguably the coral reef crisis is so acute (Hughes et al., 2010, 2017a) that a summative metric like coral cover may be sufficient to quantify the large losses of coral that have taken place, particularly as these losses push corals to the brink of ecological extinction (Carpenter et al., 2008; McCauley et al., 2015). However, while coral cover is a good place to start for quantifying coral loss and reef degradation, this metric cannot deliver the demographic insights that are needed to understand the causes and consequences of the events now underway (Edmunds and Riegl, 2020; Hughes, 1984; Hughes and Tanner, 2000).

The focus of most coral reef monitoring on coral cover limits our ability to understand the processes driving reef degradation and perturbing reef function, and while some programs are expanding to record a wider variety of population state variables, these efforts remain nascent in implementation or interpretation. The focus of reef monitoring is shifting from measurements of coral cover to analyses of changes in recovery rates over space and time using population models that incorporate some mechanistic principles (e.g., differential equation approach with logistic and exponential growth) (Gouezo et al., 2019; MacNeil et al., 2019; Mellin et al., 2019, 2016; Ortiz et al., 2018; Osborne et al., 2017). The expansion of methodological approaches has started to increase our ability to understand reef function and to assign causality to reef degradation (Ortiz et al., 2018). Even though the importance of applying demographic approaches to coral populations has been recognized for nearly 40 years (Connell, 1973; Hughes, 1984), this suite of available approaches remain under-utilized (Edmunds and Riegl, 2020). Demography reveals mechanisms that contribute to changes in coral cover by quantifying the contributions of vital rates (recruitment, growth, and mortality) to population dynamics (Caswell, 2001). By resolving the vital rates that control population growth, and by defining their confidence limits, demography can support the testing of multiple hypotheses and strong inference (Platt, 1964) in elucidating the causes of changing coral cover. Demographic information can also substantially improve estimates of extinction risk for coral taxa (Carpenter et al., 2008), and can objectively evaluate the likelihood that depleted populations can recover, go extinct, or remain in a state of rarity (Fig. 1).

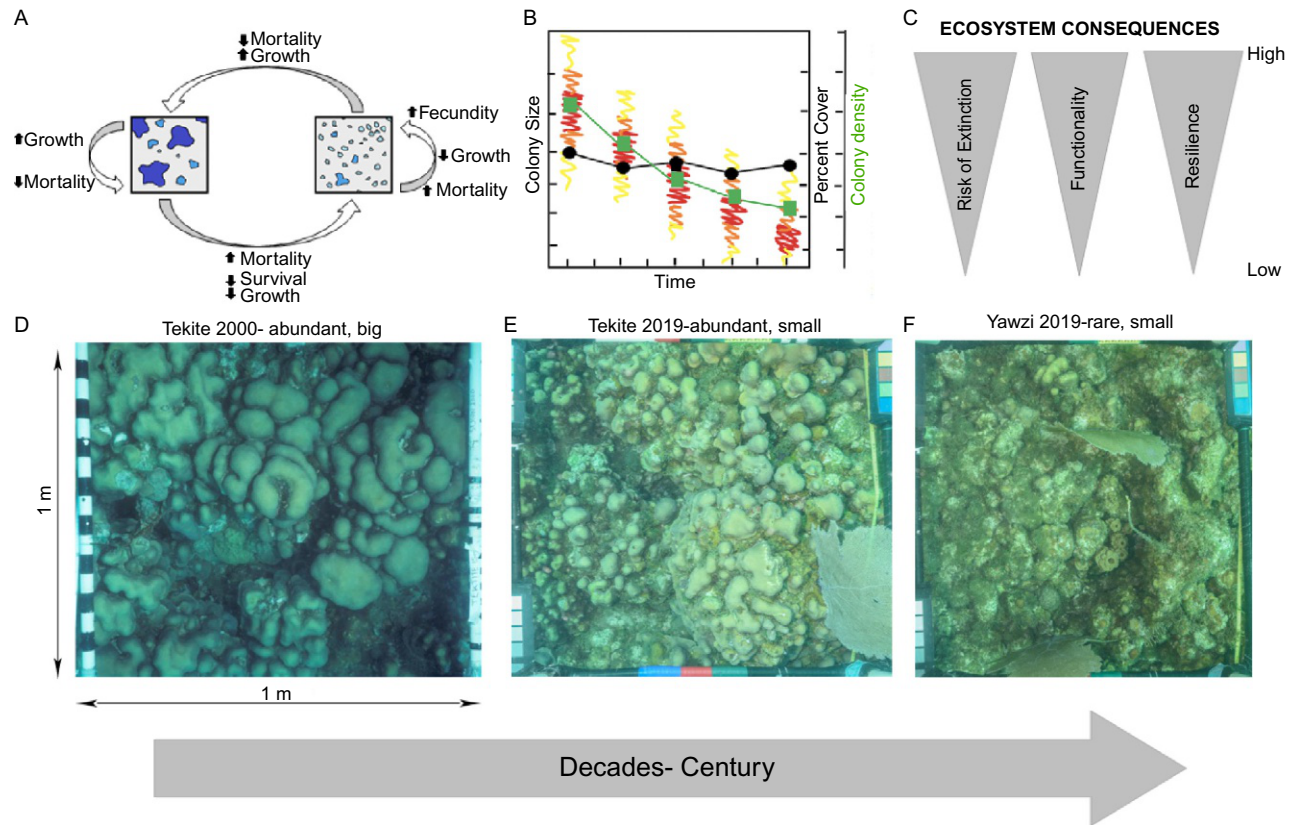


Fig. 1 See figure legend on opposite page.

Global climate change, ocean acidification, and other anthropogenic disturbances are accelerating coral mortality to favour demographic deficits in which more corals are killed than can be replaced through recruitment and growth (Hughes et al., 2017a, 2017b). Many coral reefs experience sequential disturbances that are overlapping in space and time (Ortiz et al., 2018; Wakeford et al., 2008), and sustain chronic stressors that elevate background mortality (Bythell et al., 1993; Wakeford et al., 2008). In addition to multiple disturbances, there is evidence that the growth rates of coral colonies have slowed (Cantin et al., 2010; De'ath et al., 2009; Edmunds, 2007) and rates of partial mortality have increased (Pisapia et al., 2016). Reduced growth rates, and multiple disturbances may alter the size-structure of coral populations, both due to different susceptibility of small versus large colonies, and enhanced partial mortality that reduces colony size. In some cases, larger colonies may survive a severe bleaching event (Barkley et al., 2018; Pisapia et al., 2019), but experience high rates of partial mortality and subsequent declines in colony size. These effects constraining colony growth, and reproduction, thereby degrading the capacity for population recovery following major disturbances (Hall and Hughes, 1996; Henry and Hart, 2005; Madin et al., 2020). With escalating effects of global climate change, it is expected that coral populations will have faster turnover (i.e., the rate at which individuals in the population are replaced) and will be increasingly dominated by smaller colonies (Riegl et al., 2012). There is a critical and immediate research need to better understand trends of declining size and abundance of coral colonies, and to clearly capture the demographic features of these changes.

Data on colony size with species resolution has much to contribute to the understanding of coral demography, and it is one of the easiest to measure

Fig. 1 Schematic showing the importance of colony size structure: (A) how reduction in colony size favours positive feedback on decreasing population size (colonies varying in size shown in blue); (B) hypothetical results of repeated surveys of a coral community for coral cover (black circles), colony density (green squares), or colony size-frequency structure (heat map, red = abundant, yellow = rare), as a function of time, thus revealing stable cover but declining colony abundance; (C) changes in ecosystem properties that can be associated with reduced colony size, but which remain hidden with an emphasis on coral cover as the state variable for coral community condition; (D–F) representative coral assemblages at 9–14 m depth at two sites (Tekite and Yawzi Point) in US Virgin Islands that illustrate the general transitioned (but do not convey a time series) from abundant and large colonies in 2000 (D), to abundant and small colonies at the same site in 2019 (E), and at Yawzi Point, to rare and small colonies in 2019 (F).

aspects of coral populations. Not only is colony size easy to record underwater, but the ability to acquire this information is poised to quickly expand through the application of emerging technologies to image-based data (i.e., video and still images). These technologies are approaching the capacity for automated acquisition of colony sizes from images using machine learning and artificial intelligence (Beijbom et al., 2015; Pavoni et al., 2020; Williams et al., 2019). While previous studies have identified a path for inclusion of coral demography in monitoring (e.g., Edmunds and Riegl, 2020), the present contribution conceptually addresses the causes and implications of changing size of coral colonies. Contextualized by the ongoing trends affecting the size of coral populations, ecological theory, and contemporary technological sophistication, we address four objectives. First, we summarize the ecological importance of coral colony size as it pertains to the capacity to understand the causes and consequences of changing coral abundances. Second, we use decadal-scale time series data from two case-history studies to underscore examples in which coral cover is declining, coral colonies are becoming smaller, and coral populations are transitioning to rarity. Third, we apply a generalizable stage-structured matrix model for branching and massive corals to better understand which vital rates are most influential in creating the demographic changes underway in our case example sites. By applying this model, we predict the consequences of ongoing demographic shifts for the population persistence of reef corals. Finally, we highlight the kinds of questions focusing on coral population dynamics that can be addressed with demographic approaches, and use these examples to highlight the utility of demography and its implementation in coral biology.



2. The functional implications of coral colony size

Body size has profound importance in modulating the structure and function of unitary organisms, and ultimately limits their size within bounds determined by allometric scaling (Schmidt-Nielsen and Knut, 1984). In contrast, it has long been assumed that a colonial modular body plan provides escape from these constraints (Hughes, 2005; Sebens, 1987) because colonies can increase in size while conserving module dimensions (Sebens, 1987). Colonial scleractinian corals once were thought to provide a classic example of this body plan (Hughes, 2005; Jackson and Coates, 1986), and while early work indicated that at least some traits scaled allometrically with size (Jokiel and Morrissey, 1986), the notion that colony size is indeterminate and functional traits scale isometrically persisted for decades

(Hughes, 2005; Sebens, 1987). In contrast, recent work has reinforced the generality of allometry in colonial corals (Burgess et al., 2017; Edmunds and Burgess, 2016), with multiple traits, including for example fertility and growth, changing disproportionately with colony size (Burgess et al., 2017; Dornelas et al., 2017; Edmunds and Burgess, 2016). Allometric scaling in corals has important implications, because colony size varies greatly over time within the life of a single coral, and it varies greatly among colonies within a species. Moreover, if disturbances lead to overall reductions in colony size, there will be disproportionate consequences across multiple traits.

Small corals (i.e., ≤ 4 -cm diameter) are exposed to high risks of whole-colony mortality relative to larger (i.e., adult) colonies (Edmunds and Elahi, 2007; Hughes and Tanner, 2000). In general, the probability of whole-colony mortality decreases with colony size (Madin et al., 2020), while the extent of injury (e.g., partial mortality) is expected to increase with colony size (Henry and Hart, 2005; Hughes and Jackson, 1985; Madin et al., 2014). In part, this effect reflects the limited amount of coral tissue in small colonies, which can reduce resistance to partial mortality (Henry and Hart, 2005), whereas large colonies frequently experience a wide variety of partial mortality effects (Henry and Hart, 2005; Madin et al., 2020). With high risk of mortality, small corals are subject to strong selective pressure for rapid growth (Jackson, 1977). This trend favours prioritization of food resources to tissue and skeleton, but can lead to depletion of energy reserves (e.g., storage lipids (Anthony et al., 2009)). Depletion of reserves and selective pressure for rapid growth, can push small corals into a nutritional deficit from which they may be unable to escape whole colony mortality.

Small corals are not necessarily young (Hughes and Jackson, 1980), and big colonies can undergo fission to form small colonies with relatively old tissue. Some demographic traits such as reproduction are known to revert to their younger states upon fission (Hughes et al., 1992), while other traits may persist in the daughter colonies. When older traits are retained, the resulting small, but old, corals might respond to the environment in different ways, influenced by their history (Putnam et al., 2017), thereby making them functionally different to small and young corals (Kojis et al., 1985; Szmant-Froelich, 1985). Age-related phenomena that can carry over to small fission products can include the consequences of establishing symbiosis with dinoflagellate algae, for which an initially cosmopolitan genetic assemblage (e.g., consisting of multiple symbiont genotypes in a single host) might be winnowed over time (Little et al., 2004; Mieog et al., 2009). Moreover,

these effects can include the legacy of a reproductive status determined by age and colony (Kojis et al., 1985; Szmant-Froelich, 1985), and epigenetic effects mediated by parental history (Putnam et al., 2017).

Interactions between coral colonies and their fluid environment are also modulated by colony size (Madin et al., 2014; Patterson, 1992a, 1992b). For a given flow regime small corals operate at lower Reynolds numbers, while large colonies operate at higher Reynolds numbers (Patterson, 1992a, 1992b). Reynolds numbers give a measure of the ratio of inertial to viscous forces and are used to characterize the nature of the flow past a coral colony (Schlichting, 1979). As a result, colonies varying in size are affected differentially by turbulent flow and the propensity for mass transfer limitation of metabolically important gases and metabolites. Associated with these trends, flow speeds can modulate metabolic rates through the flux of metabolites between the tissue and seawater (Patterson, 1992a, 1992b). These effects vary as a function of colony size and shape, and create predictive capacity for favoured shapes and sizes of coral colonies under differing flow regimes (Patterson, 1992a, 1992b). Flow can also play strong roles in dislodging coral colonies, with the risks of dislodgement increasing with size and shapes of coral colonies (e.g., certain shaped colonies are more prone to dislodgement such as tabular and arborescent) (Madin et al., 2014). Mortality curves for these corals adopt a “bathtub-shape” with high mortality at both extremes of the colony size distribution (Madin et al., 2014).

Together, the aforementioned trends demonstrate that reductions in coral colony size and density will have profound implications that cannot be elucidated through measurements of coral cover alone (Fig. 1). Further, the multifaceted implications of a reduction in colony size at the population level indicate that the demographic consequences of this trend are likely to be complex. Reductions in colony size, for example, can support a variety of demographic outcomes, not just high risks of extinction, as has been suggested (Carpenter et al., 2008). To begin to distinguish among these possibilities, here we develop a stage-based matrix model for two functional groups of coral (massive and branching species) and compare the model output to empirical data from our case-studies. The kinds of population projections these models can produce have previously been used to evaluate the implications of decadal shifts in the colony size distributions of several corals (Edmunds and Riegl, 2020; Hughes, 1984). Specifically, we evaluate whether increased abundances of small colonies could accelerate the transition to functional extinction, due to concomitant declines in individual persistence and reproductive potential.



3. Temporal shifts in the size structure of coral populations

An increasing number of studies highlight the major changes underway in the abundance and community structure of scleractinian corals on tropical reefs (Hughes et al., 2018; Jackson et al., 2014; Pisapia et al., 2019). These changes can be attributed to multiple anthropogenic and natural disturbances (Hoegh-Guldberg et al., 2007; Hughes et al., 2010), but the gravest threats are posed by global climate change (Hoegh-Guldberg et al., 2007). In 2015–2017, extreme temperature anomalies triggered unprecedented coral mortality in all major coral reef regions throughout the world (Eakin et al., 2016, 2014). These events drastically altered the composition of coral assemblages on the Great Barrier Reef (GBR) (Hughes et al., 2018). The observed shifts in community structure relied upon the relative abundance of thermally sensitive branching corals, which exhibited severe changes in abundance (Hughes et al., 2018). Massive corals are comparatively more resilient to elevated temperatures (Hughes et al., 2018) than branching and encrusting species. Even though massive corals are more likely than branching corals to survive a bleaching event, they may experience high levels of partial mortality in response to the same stressor (Pisapia et al., 2019). However, shifts in the taxonomic composition of coral communities depend on both the frequency and severity of major disturbances such as bleaching (Pratchett et al., 2020).

Disturbances and taxonomic shifts in coral assemblages are often accompanied by changes in colony size distributions, commonly involving the selective loss of larger, reproductively mature colonies (Pisapia et al., 2019). However, changes in size-structure have been overlooked in most studies of coral bleaching, and most empirical attention has focused on measuring changes in live coral cover among taxonomic groups. Despite recognition of the importance of coral colony size, few studies have rigorously recorded colony size over time, and where sizes have been recorded, measurements rarely extend over decades (but see Kramer, 2003). A common reason for coral colony size to be measured in time-series analysis is to evaluate the effects of disturbances such as bleaching or storms (Edmunds and Elahi, 2007; Roff et al., 2014). To date, however, the colony size structure of coral communities has rarely been measured in the “recovery” phase following disturbances. This is unfortunate as such data are necessary to evaluate the extent to which the coral community returns to a holistic measure of pre-disturbance condition (Graham et al., 2015).

During the recovery phase following major disturbances, the colony size structure of coral populations could adopt a wide variety of forms, each with distinct ecological implications. In a few cases, disturbances have favoured negatively skewed frequency distributions (i.e., populations in which large colonies are more common than small colonies (Bak and Meesters, 1999; Meesters et al., 2001). More frequently, there is a progressive decline in colony size as large and old colonies are degraded through partial mortality and fission (Edmunds and Elahi, 2007). Mean colony size can also be depressed with size distributions becoming positively skewed through high rates of sexual recruitment (Bak and Meesters, 1999). In a metapopulation, persistent recruitment from distant locations to maintain abundance of small colonies, even when small corals have high rates of mortality, can continue until the source populations for the coral larvae are negatively impacted by disturbances. Distinguishing among the aforementioned demographic mechanisms of changing size structure (e.g., the effects of recruitment versus partial mortality and fission) is necessary to interpret the long-term causes and implications of disturbance and declines in coral abundance.

To illustrate temporal shifts in the size structure of coral populations, we present time-series data describing coral populations on two coral reefs, one from the Caribbean (U.S. Virgin Islands, Fig. 2A–I) and one from the Indo-Pacific (the Persian Gulf, Fig. 2J–O). Our objective in presenting these data is not to suggest that are representative of all reefs, rather to present evidence supporting our assertion that coral colonies are declining in size on at least some modern reefs. A comprehensive analysis testing for similar effects on biogeographic scales remains an important research need.

There is evidence that coral colonies are becoming smaller on the reefs we selected as case examples, although we recognize that a diversity of trends for this state variable (i.e., colony size) have been reported (e.g., Babcock, 1991; Bak and Meesters, 1999). Our data from two locations reveal consistent shifts in the size-frequency distributions of four coral species, thus favouring high abundances of small versus large colonies (Fig. 2). These trends are not unique to these species or these locations (Fong and Glynn, 2001, 1998; Hernández-Pacheco et al., 2011; Hughes and Tanner, 2000), yet as described above, congruent results do not imply congruent demographic mechanisms, and without understanding the processes driving these changes, it is impossible to project their impacts on future coral communities. While extinction remains one possible outcome of these trends, it is also possible that shrinkage, fission, and rarity could represent a pathway towards a cryptic regime shift (sensu Hughes et al., 2010).

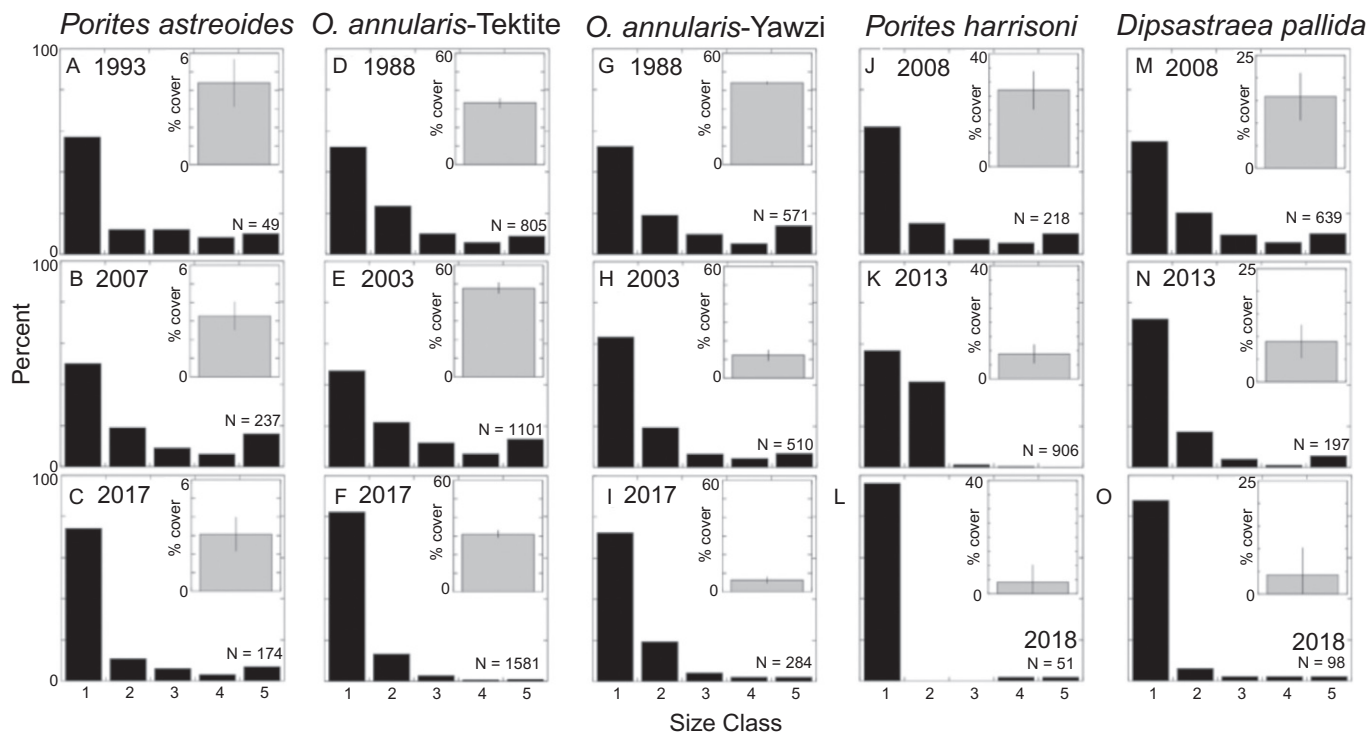


Fig. 2 Declining sizes of scleractinian colonies over a decades in the Caribbean and Persian Gulf. Bar graphs show the percentage distribution of colonies among five size classes defined by dividing the 90th percentile size range into five equal portions and adding larger colonies to size class 5. (A–C) Population structure in St. John (U.S. Virgin Islands) of *Porites astreoides* at 3–9-m depth in 1993, 2007, and July 2017 (A–C), *Orbicella annularis* at Tektite (14-m depth) in 1988, 2003, and July 2017 (D–F), and *O. annularis* at Yawzi Point (9-m depth) in 1988, 2003, and July 2017 (G–I); inset bar graphs show coral cover in the year of each size class analysis (note ordinates differ between *P. astreoides* and *O. annularis*). *P. astreoides* accounted for 16% of the coral cover throughout the study, and *O. annularis* accounted for 76% (Tektite) and 86% (Yawzi Point) of the coral cover throughout the study. Population structure in the Persian Gulf (Ras Ghanada, Abu Dhabi, UAE) for *Porites harrisoni* in 2008, 2013, and 2018 (J–L), and for *Dipsastraea pallida* in 2008, 2013, and 2018 (M–O). Data sources: (Edmunds, 2015, 2013; Edmunds and Elahi, 2007; Edmunds and Lasker, 2016; Riegl et al., 2017; Riegl and Purkis, 2015) and new data.

This shift might involve reduced ecological success of small colonies and a paucity of coral recruits, which together could favour population stabilization in a greatly reduced abundance (Fig. 2). Such an outcome would represent a vestige of the former community structure, but avoidance of extinction maintains the possibility of population recovery, and buys time for human intervention to increase the likelihood of coral population recovery.

Below we use stage-structured population matrix models to address mechanistic pathways culminating in coral populations of rare and small colonies. We project population structure into the future for both a branching and a massive coral in order to explore the consequences of the demographic trends that are underway on present day reefs (Fig. 2). These analyses are designed to highlight how a small number of processes, that can be relatively easily monitored in the field, can influence size distributions in a way that may not be captured by measuring coral cover alone.



4. Modelling changes in size distributions of coral populations

To distinguish between potential alternative demographic mechanisms that cause shifts in the size structure of coral populations, we use a stage-structured matrix population model after Caswell (2001) (Model code is available as a digital supplement, and at DOI: <https://doi.org/10.5281/zenodo.3926845>). Further, to account for potential differences in inherent life-history strategies (Pratchett et al., 2020), we parameterize the model for both a generalized branching coral and a generalized massive coral (Table 1). We use the models to explore the impacts of variation in three vital rates on the stable coral population size structure. First, we evaluate the role of increased whole-colony mortality, as might be caused by bleaching or disease (Hughes et al., 2017b; Weil, 2004). Second, we assess the role of declining colony growth (e.g., linear extension), which may be a consequence of increased environmental stress (Pratchett et al., 2015). Third, we explore the role of reduced fecundity, which may occur when stressed corals incur metabolic costs that reduce the resources available for spawning (Hughes et al., 2019; Szmant and Gassman, 1990).

Although we address a simplified system in which each vital rate varies independently of any other, this approach reveals the extent to which changes in each vital rate can create distinct outcomes with regard to the population size structure. By coupling changes in vital rates to their “signatures” in shifts in colony size structure, we generate hypotheses that

Table 1 Empirical data used to define the set of parameters (population reproduction, growth, partial mortality, and whole colony mortality) in the model matrix for branching and massive corals.

Model Parameters	(a) Branching	(b) Massive	Sources
Reproduction			
Minimum size for reproduction (projected planar area, cm ²)	~100	50	Hall and Hughes (1996), Stimson (1978)
Fecundity (eggs cm ⁻² y ⁻¹)	232	1198	Harrison and Wallace (1990)
Larval survival (maximum) (% y ⁻¹)	Exponential function with 50% mortality in 37 day	Exponential function with 50% mortality in 37 day	Graham et al. (2008)
Recruit survival function	Type 3; 100% at t ₀ , 50% ^a at t ₁	Type 3; 100 at t ₀ , 35% ^b at t ₁	Dunstan and Johnson (1998) ^a , Edmunds (2000) ^b
Recruits larva ⁻¹	0.000009	0.000009	Bramanti et al. (2015)
Growth			
Linear extension (mm y ⁻¹)	74	10	Pratchett et al. (2015)
Partial Mortality			
Colonies affected (% of colonies in 3 years)	65	90	Pisapia et al. (2016)
Severity (% tissue loss from each colony in 3 years)	5–30%	2–35%	Pisapia et al. (2016)
Whole colony mortality			(a) Branching
(% y ⁻¹ by size)	7.1% for 0.25 cm ²	6.9% for ≤50 cm ²	Kayal et al. (2018)
	2.0% for 3147 cm ²	4.1% for 51–150 cm ²	(b) Massive
		3.3% for 151–250 cm ²	Edmunds (2015), Edmunds and Elahi (2007)
		3.4% for ≥250 cm ²	

Whole colony mortality was calculated: (a) for branching corals for *Pocillopora* on the north shore of Moorea [Fig. 2E, in (Kayal et al., 2018)]. (b) for massive corals for *Orbicella annularis* by averaging data collected over 5 years intervals over 15 years (Yawzi, St. John) and 25 years (Tekite, St. John), divided by 5 to estimate annual rates (Edmunds, 2015; Edmunds and Elahi, 2007). However, the two taxa *Pocillopora* and *Orbicella annularis* do not represent the generic branching and massive corals in the model.

can be used to link observed changes in colony size distributions to their causal mechanisms.

A robust parameterization of a matrix model for a given coral population requires a substantial quantity of empirical data (which currently is unavailable for most corals), in part because changes in colony size structure in nature are likely to emerge from a combination of demographic mechanisms that can be statistically challenging to distinguish. Therefore, we use a generalizable parameterization for two coral types—branching and massive—grounded in empirical data but not intended to apply to a specific taxon. We seek a coarse-grain analysis with which we can illustrate the utility of the approach in aligning empirical changes in colony size distributions with mechanisms associated with specific vital rates. An emergent property of this approach is the development of benchmarks for projected population structure against which empirical population structure can be tested for goodness of fit. As we posit below, concordant size structuring likely arises from variation in specific vital rates, identification of which can support pro-active recommendations for the design of long-term monitoring and event sampling therein. In applying a stage structured matrix model we recognize that there are other demographic approaches that have been applied to scleractinian corals (Edmunds and Riegl, 2020), one of the earliest of which was a size based matrix model (Hughes, 1984). Each approach has strengths and limitations, and it is not our objective to advocate for a specific approach (or to review the methods available). Rather, we seek to shed light on the demographic mechanisms that can cause diagnostic variation in coral colony size, and explore the likelihood of local extirpation as one possible outcome of declining size and reduced abundance of coral colonies.

Matrix population models describe how individuals within a population change in state (size) over time. They can also incorporate recruitment and mortality, allowing them to capture overall population growth as well as population structure. In particular, the leading eigenvector of a matrix population model, λ , represents the population's exponential growth rate. The population grows when $\lambda > 1$, it shrinks when $\lambda < 1$ and asymptotically approaching zero, which indicates local extirpation and perhaps regional extinction (Caswell, 2001). The leading eigenvalue is also associated with an eigenvector, \vec{x} , which gives the population's stable size distribution. When the stable size structure of a population is reached, the numerical abundance of the population may still change while the relative contribution of each size-class to the population structure remains fixed (i.e., stable).

A stable stage distribution has been observed in natural coral populations after about a decade without disturbances (Riegl and Purkis, 2015), and serves as a useful way to explore “equilibrium dynamics” in a population. While useful for the theoretical evaluation, whether a stable stage structure is reached depends on the extent to which the population is closed (i.e., self-seeded) versus open (with recruits originating from spatially separated populations). The present analysis assumes a closed population and makes no direct reference to any export or import of larvae. Thus, the matrix model can be thought of either as encompassing the sum of all life-history parameters of several well-connected sub-populations (that themselves are isolated from other populations), or as representative of a single, primarily self-seeding locality. Either are realistic and encountered in nature.

Our matrix model describes a population of corals with a vector \vec{x}_t , whose entries define the number of coral colonies within each of a series of classes. Size is most easily defined as the planar surface area of living tissue (in cm^2), but the exact measurement of size is of no consequence here, and our model consists of four types of classes: Class I, diminutive corals that have not yet recruited to a reef (i.e., larvae); Class II, recruits that are new settlers to the reef (i.e., corals < 1 mm diameter); Class III, a set of classes of increasing size representing juveniles that are small and sexually immature (i.e., $< \sim 100 \text{ cm}^2$ in planar area for branching corals, $< 50 \text{ cm}^2$ for massive corals); and Class IV, a set of classes of increasing size representing sexually mature adults ($> 100 \text{ cm}^2$ for branching corals, $> 50 \text{ cm}^2$ for massive corals). The projection matrix \mathbb{A} simulates state transitions over time:

$$\vec{x}_{t+1} = \mathbb{A} \cdot \vec{x}_t.$$

This projection matrix \mathbb{A} is the composite of matrices representing the production of new individuals (fecundity, \mathbb{F}) and state transitions among existing individuals that represent growth, shrinkage, or stasis. The latter is traditionally represented as the product of the growth matrix \mathbb{G} and the diagonal survival matrix \mathbb{S} . However, in corals, state transitions are complicated by the possibility that individuals not only increase in size but may also shrink due to partial mortality and fission (Edmunds and Elahi, 2007; Hughes and Tanner, 2000). We represent the probability of partial mortality with the diagonal matrix \mathbb{M} and use two matrices \mathbb{G} and \mathbb{P} to represent the probabilities of state transitions to larger (via growth) and smaller (via partial mortality) size classes:

$$\mathbb{A} = \mathbb{F} + [\mathbb{G}(\mathbb{I} - \mathbb{M}) + \mathbb{P}]\mathbb{S}$$

where \mathbb{I} is the identity matrix.

We use generalized functions grounded in empirical data to represent reproductive and size transitions as a function of colony size (discussed in detail in the appendix). We model the production of larvae by adults as a positive linear function of adult size (Hall and Hughes, 1996). A proportion of these larvae successfully settle on the reef as new recruits, and the remainder perish. Corals that have recruited to the reef survive with a probability that is a saturating function of colony size. This effect is driven by the high rates of mortality of small colonies (Hughes and Jackson, 1985) and the low rates of complete mortality of large colonies, augmented by a greater probability of partial mortality every year (Edmunds and Elahi, 2007; Hughes and Jackson, 1985), which favours transition to a smaller size class. We model growth as linear extension of colony margins using a mean linear extension rate of 7.5 cm y^{-1} for branching corals and 1 cm y^{-1} for massive corals (Table 1). Larger corals are also more likely to experience partial mortality (e.g., damage due to physical impacts, corallivory, etc.) because of their greater spatial extent (Edmunds and Elahi, 2007; Hughes and Jackson, 1985). When injuries are sufficiently extensive, they can cause a coral to decrease in size, thus causing a transition to a smaller size class. Thus, corals can “shrink” and transition from larger to smaller size-classes.

We begin with a baseline set of parameters (Table 1) that produce coral populations with positive growth ($\lambda = 1.11$ for branching corals, $\lambda = 1.08$ for massive corals) and, having reached a stable size structured stage, a mean colony size of 6297 cm^2 for branching corals and 67 cm^2 for massive corals. The larger branching colony would be consistent, for example, with a large plate of *Acropora hyacinthus*, and the smaller massive colony would be consistent, for example, with a hemispherical colony of *Astrae curta* (both for an Indo-Pacific reef), but taxonomic concordance is neither implied nor intended. Increases in mortality of established corals (i.e., juveniles and adults), decreases in growth rate, and reductions in fecundity all reduce the population's growth rate, with large alterations in these vital rates creating a demographic deficit in population size (i.e., where $\lambda < 1$), indicating that local population extirpation is inevitable (Figs. 3A–C). Overall, the model was less sensitive to reductions in growth rate (i.e., larger proportionate reductions were required for population growth to fall below replacement rate) than increases in mortality or decreases in fecundity. However, because our model represents a hypothetical case study, we do not view this as a definitive prediction that reductions in growth rate are of little concern. Rather, our particular scenarios indicate that, so long as growth rates are sufficient for a few colonies to reach reproductive size, populations can be

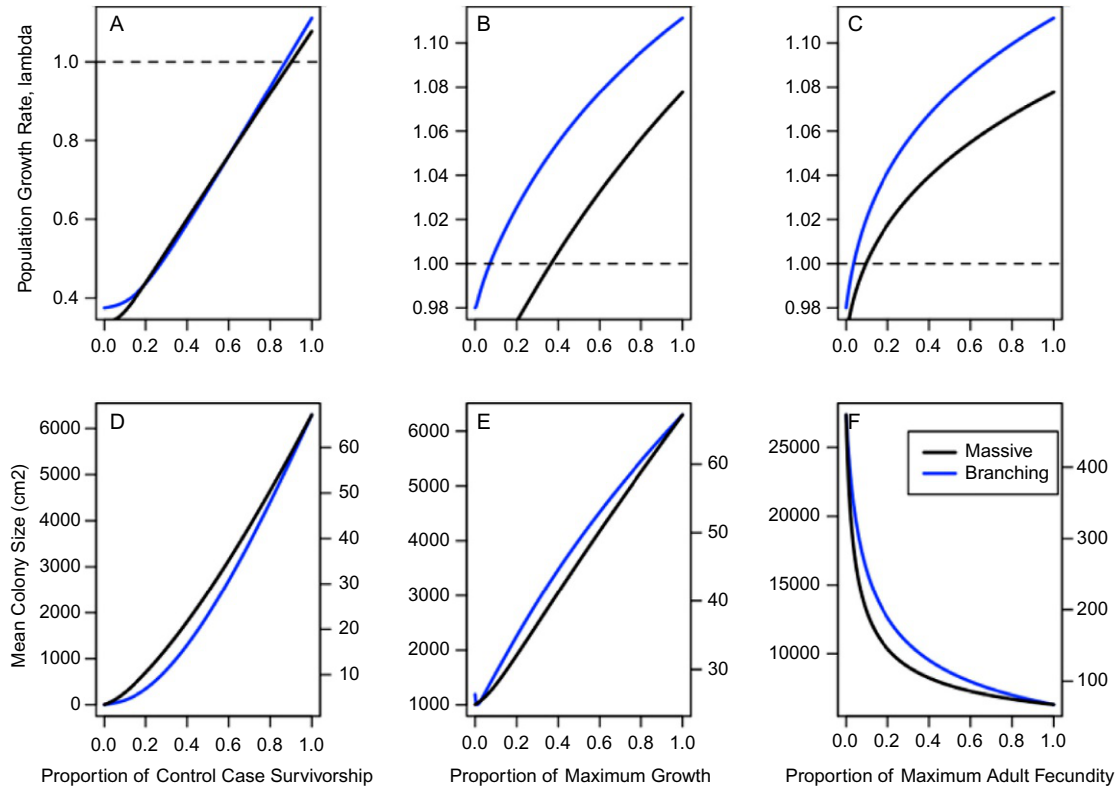


Fig. 3 Predicted coral population growth rates (top row A–C) and mean colony sizes (bottom row D–F) as vital rates are changed for both branching (blue) and massive (black) corals. Increases in mortality drive reductions in survivorship, reducing growth rate and mean size (left column). Decreases in growth rate drive similar patterns, though shifts are non-monotonic due to a loss of recruits that increases mean colony size at the lowest growth rates (middle column). While reductions in fecundity decrease the population growth rate, mean colony size actually increases due to the reduction in recruitment and, consequently, juvenile size classes. Trends are the same for both colony types, but note the larger mean sizes of branching corals. Dashed lines (top row) show the minimum population growth rate ($\lambda = 1$) for population persistence.

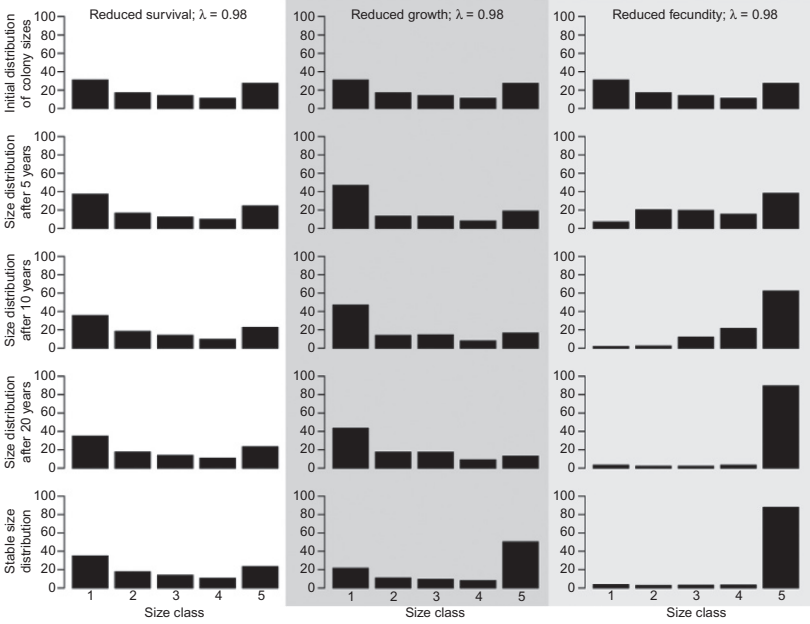
sustained. Predicting how population structure changes over time is more complex than evaluating whether the population increases in density. Mean colony size decreases with increasing mortality and decreasing colony growth rate (Figs. 3D and E, Figs. S1–2), though in the latter case this decrease is non-monotonic. In contrast, reductions in fecundity causes an increase in mean colony size, due to a reduction in recruitment that leads to a relative increase in abundance of the larger colonies (Figs. 3F, Fig. S3).

How long does it take a coral population to show a demographic response to a change in vital rates? Although multi-year (and possible decadal) datasets are necessary to empirically answer this question (particularly to establish baseline estimates of population size distributions and growth rates), our model reveals how changes in mortality, growth, and fecundity can cause shifts in size distributions within a few years (Fig. 4), though it may take several decades to reach the new stable stage distribution (Fig. 5). Variation in each vital rate produce distinctive shifts in the colony size distributions with differences between branching and massive morphologies: increased mortality decreases the probability of state transitions to larger size classes and reduces abundance especially of the largest size classes. Reduced growth preferentially removes individuals of intermediate size, initially bolstering the relative abundance of the smallest size-classes (either recruits or small tissue fragments) and, at steady state, a few large individuals (with higher abundance of larger corals for branching compared to massive corals). Reduced fecundity increases the relative abundance of the largest individuals, which survive but fail to support large propagule classes with increased abundance of larger colonies more pronounced for branching compared to massive corals (Fig. 4).

Our model simplifies reality in order to make conceptual advances, and in due course will require ecologically relevant treatment of a wider variety of demographic traits in order to achieve its potential in advancing coral reef science. For example, while there is strong evidence for some coral populations that they reach stable size distribution (Riegl and Purkis, 2015), this is unlikely to be the case in fully open populations, or those that reflect a combination of open and closed structuring that vary in relative importance over time (Caley et al., 1996). Thus, especially if strong connectivity among several populations is present, reductions in fecundity of the focal population may have a different, or entirely absent, expression in size distribution than our simplified model reveals. In the case of stabilization to favour abundant large colonies, such an outcome might reflect a diagnostic feature of the storage effect (Chesson, 1984) (e.g., large and old individuals

A

Branching corals



B

Massive corals

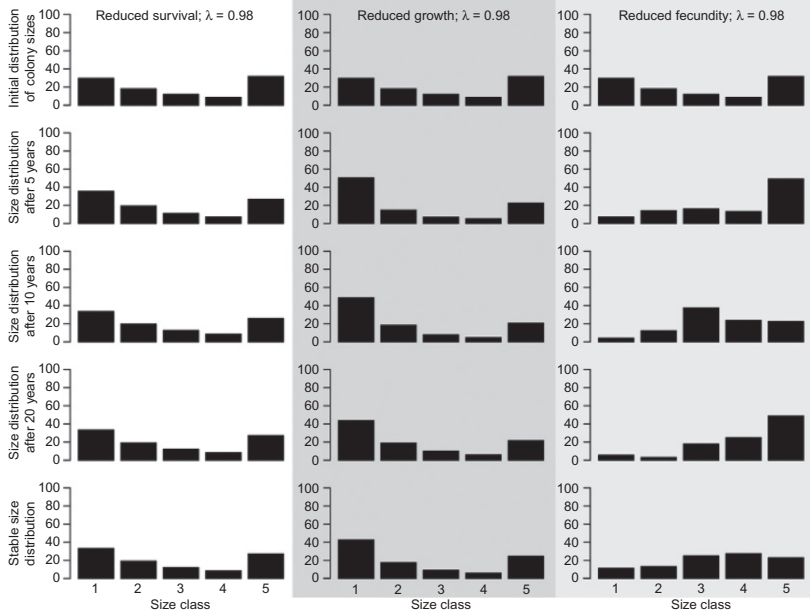


Fig. 4 See legend on next page.

“store” the demographic signal of historic recruitment until such point in the future when recruitment is/can be successful. Hence *Orbicella* in the Caribbean seems to persist as a stable population for decades without any effective sexual recruitment.). Also partial mortality can have important influences on size-structure, but it is highly context-specific with regards to the type of disturbance, environment, and species affected. In its effect on overall population size, it is usually subordinate to changes in fecundity and overall mortality. Similarly, fission is often an important process in population dynamics, however, its effect may also be subordinate. None of the aforementioned arguments suggests anything other than the overwhelming importance of obtaining colony size-dependent information in order to fully understand coral population dynamics. While real coral populations are subject to a combination of changes in their vital rates over time, our findings show how incorporating demography into coral monitoring can provide insights into the mechanisms driving changes in coral cover. Importantly, the model highlights the complex interaction of processes affecting size frequency distributions rather than document an absolute tendency toward reductions in colony size.

Overall, our model highlights two important results. First, the model formally represents the expectation that changes in coral vital rates (i.e., decreases in survivorship, linear extension, and fecundity) drive reductions in coral population growth. Importantly, the relationships between these parameters and population growth rate are non-linear (Fig. 3, top row).

Fig. 4 Coral populations shift in size distribution under different environmental conditions favouring dissimilar effects on key vital rates. For both (A) branching and (B) massive corals, reductions in survival and growth cause a shift towards smaller colony size classes, whereas reductions in fecundity cause an increase in mean colony size as small (young) colonies are lost from the population. For all cases, demographic parameters are set such that population growth rates are 0.98 (e.g., a 2% decrease in population size per year). While changes in colony size distribution are perceptible within a decade for reductions in survival and growth, it can take several decades for coral distributions to equilibrate to the new, larger, stable size distribution when fecundity is reduced. Top row: initial distribution of colony sizes, given by the stable stage distribution of the “control” matrix. Middle rows: stage distributions expected five and 10 years after the vital rate has shifted. Bottom row: stable stage distribution that will emerge from specific changes in one of three vital rates. Stable stage distributions are computed by dividing the juvenile and adult size classes (i.e., corals that would be detected when surveying a reef among five size classes defined by dividing the 90th percentile size range into five equal portions and adding larger colonies to size class 5 (as in Fig. 2).

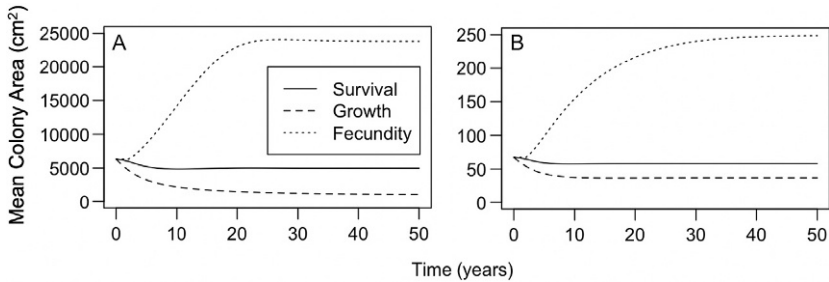


Fig. 5 Rate of change in mean coral colony size under different vital rates. For branching (A) and massive (B) corals, reductions in survival (solid line) and growth (dashed line) cause decreases in coral colony size. These declines are most precipitous when growth rates are affected and, in the latter case, may require decades (e.g., for branching corals) before the new mean size of corals is achieved. In contrast, reductions in fecundity (dotted lines) cause substantial increases in mean coral size due to the loss of the smallest (juvenile) size classes. For massive corals, which exhibit the slowest growth rates, this demographic shift takes the longest period of time, with the new stable size distribution not achieved for several decades.

Initial reductions in these rates result in relatively small shifts in population growth rates (λ), but as further declines in vital rates occur, the corresponding reductions in λ become more precipitous. Second, our model predicts that when each shift in vital rate acts in isolation, it produces a demographic “signature” in the colony size distribution that is expressed within years to decades (Fig. 5). These signatures highlight the intrinsic value of demographic data: knowledge of coral size distributions (and changes therein) may provide critical early warning signs for researchers and managers seeking to predict population trajectories, and qualitative shifts in size structure may reflect distinct demographic drivers (Fig. 2). However, care is needed not to over-interpret such patterns, since a variety of combinations of different demographic parameters can lead to similar size-distributions (Condit et al., 2017).



5. Tractable questions and the data with which they can be answered

We have placed our treatment of coral colony size structure in a context within which some of the key implications of declining size and abundance of coral colonies are highlighted. Even a cursory evaluation of these features reveals the broad extent to which coral colony size can affect the response of coral populations to environmental conditions and, therefore,

the capacity for corals to persist in a world disturbed by anthropogenic effects. We present select evidence that coral colonies are becoming smaller and rarer on two reefs (Fig. 2), and through modelling, we reveal how variation in three vital rates can contribute to transitions of coral colonies into small size classes (Fig. 4). These effects are expressed through different demographic mechanisms creating distinctive signatures in the shape of the colony size distributions for the two most common morphological groups of reef-building corals (massive and branching taxa). By projecting a hypothetical coral population 10+ years into the future, our results suggest that rarity and small colony size does not necessarily lead to extinction ($\lambda \geq 1$) over decades. While decades are trivial in duration relative to the geological history of coral reefs, and the ecological history of many coral species (Babcock, 1991; Darke and Barnes, 1993; Devlin-Durante et al., 2016; Hughes and Jackson, 1980; Lough and Barnes, 1997), decades are relevant to the capacity of humans to develop tractable solutions to the coral reef crisis. Persistence of small and rare corals over multiple decades effectively buys time to develop solutions to the crisis, and staves off potential apathy and dismay at the prospect of preventing climate change from driving widespread extinctions of reef corals (Jackson, 2008).

Appeals for greater use of demographic tools to address the dynamics of coral populations have been made for more than 40 years (Connell, 1973; Hughes, 1984), and recently these appeals have been repeated (Edmunds and Riegl, 2020) as the global crisis affecting coral populations intensifies (Hughes et al., 2018). At a time when widespread coral extinctions are considered likely (Carpenter et al., 2008; Hoegh-Guldberg et al., 2007), the need for accurate and precise coral demography has never been more acute. As we highlight above, and has been described elsewhere (Edmunds and Riegl, 2020), there are unique needs for new data to which coral reef monitoring must respond in order to fully exploit the potential of demography to advance the discipline and answer critical questions addressing coral reef conservation, functionality, and management. Given the rapid advances in computer-aided image analysis, colony size distribution information probably will be easy to obtain from images in the near future.

A demographic approach can serve to identify early indicators of reef degradation and could provide insights into reef recovery potential. For instance, a distribution dominated by larger colonies may indicate that recruitment is currently limited, or that recent disturbances had a disproportionate impact on smaller colonies. Conversely a distribution where larger colonies are under-represented may indicate that recent disturbances caused selective loss of larger colonies and hence reproductive potential, which may

reduce recovery capacity. It may however, be challenging to identify a particular distribution as “conducive to future coral population growth”, thus a key need for coral reef monitoring is maintaining the capacity for repeated sampling of identical areas of reef. Some suggestions to support this outcome are detailed in [Edmunds and Riegl \(2020\)](#). Below we highlight four themes to which coral demography could be productively applied.

5.1 Risks of extinction

The possibility that reef corals will be locally extirpated or become extinct is the ultimate outcome of the coral reef crisis, and these possibilities are becoming more likely as the crisis intensifies ([Hughes et al., 2018](#)). Accurately characterizing these risks is a critical aspect of managing endangered species ([Powles et al., 2000](#)), and is a mandatory step in the development of effective conservation strategies ([Jackson, 2008](#)). The risks of premature estimates of extirpation and extinction are considerable, as they undermine efforts to develop solutions and challenge the credibility of scientific endeavour. Population viability analysis (PVA) is a well-established means to address risk of extinction for endangered species, and it offers a formal procedure to evaluate the probability that a population will persist for a specified time into the future ([Boyce, 1992](#)). To our knowledge, PVA has only been applied to one coral species in a single location ([Muko et al., 2014](#)), and thus consideration of risks of extinction for reef corals largely remain a matter of speculation ([Carpenter et al., 2008](#)). A wide variety of demographic tools, including those similar to the approach described above, offer great potential in addressing the critical questions of *which corals are threatened by extinction* and *how long can current populations persist with low densities of small colonies?*

5.2 Ecosystem functionality

The ecological value of coral reefs is to a large extent dependent on the framework-building capacity of reef corals and the maintenance of a positive carbonate budget. Only if reef structures can be maintained, will the habitat required for the reef’s biodiversity continue to exist. Since the potential of corals to form interlocking frameworks of skeletons depends on their sizes, any prediction of future carbonate budgets and framework dynamics will be greatly assisted by adequate demographic information of the reef builders. Demographic approaches can evaluate the capacity of coral colonies to continue to contribute coral skeletons to future reef communities, and when combined with explicit models of community metabolism (such as MTE

(Brown et al., 2004)) and net accretion (Perry and Alvarez-Filip, 2019), can objectively evaluate the form in which the three-dimensional structure of coral reefs will persist.

5.2.1 Community and ecosystem resilience

Community and ecosystem resilience (Gunderson, 2000) are central concepts of modern coral reef ecology and their conservation (Hughes et al., 2010), yet these concepts continue to be addressed mostly with the same state variable used to quantify coral abundance (i.e., cover). Yet as dynamic and multifaceted concepts, coral cover offers an incomplete means to evaluate rates of future change. Coral habitats with similar coral cover may nonetheless have very different community structure (e.g., different size-frequency distribution of corals) which will have a plethora of implications (described above). Demographic tools are well designed to address these implications, and offer statistically robust tools to address the rate of future changes in coral community structure, and the extent to which future populations are functionally equivalent to (or different from) those of the past.

5.3 Necessary changes in coral reef monitoring

An implicit outcome of projected shifts in the size-structure of coral populations, where there are both fewer and smaller coral colonies, is that the needs for effective ecological sampling will differ from those designed and implemented in an era when corals thrived. These needs are also likely to differ from those of the recent past as photogrammetry (Burns et al., 2015; Ferrari et al., 2017) and computer-aided analyses (Bejbom et al., 2015; Pavoni et al., 2020; Williams et al., 2019) become economically and ecologically viable. Importantly, obtaining the necessary information from high quality images will likely require relative small changes in the next generation of software tools developed to support automated and semi-automated analysis of images. Without a time machine, the sampling conducted now, and the images that are archived, will remain the only means to quantify how reefs are changing, and thus there is an urgent need to build new capacity into ongoing sampling regimes for coral communities (Flower et al., 2017; Kramer et al., 2020). These should include sampling of larger numbers of replicate and permanently marked areas with high resolution images that preserve colour, shape, and size information for even the smallest of coral colonies.

Supplementary materials

An R markdown file containing the mathematical model and the simulations needed to reproduce the paper's results can be found at <https://doi.org/10.5281/zenodo.3926845>.

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Author contributions

MSP motivated the questions that gave rise to the workshop in which all authors participated. MMcW crafted an outline of the paper that was fleshed out and written as a complete draft by CP, PJE, HVM, and BR. HVM drafted the demographic model, the products of which were fueled by input from CP, PJE, and BR. All authors contributed to revisions and edits. MSP largely funded the workshop.

References

- Anthony, K.R., Hoogenboom, M.O., Maynard, J.A., Grottoli, A.G., Middlebrook, R., 2009. Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. *Funct. Ecol.* 23, 539–550.
- Babcock, R.C., 1991. Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. *Ecol. Monogr.* 61, 225–244.
- Bak, R.P., Meesters, E.H., 1999. Population structure as a response of coral communities to global change. *Am. Zool.* 39, 56–65.
- Barkley, H.C., Cohen, A.L., Mollica, N.R., Brainard, R.E., Rivera, H.E., DeCarlo, T.M., Lohmann, G.P., Drenkard, E.J., Alpert, A.E., Young, C.W., 2018. Repeat bleaching of a Central Pacific coral reef over the past six decades (1960–2016). *Commun. Biol.* 1, 177.
- Beijbom, O., Edmunds, P.J., Roelfsema, C., Smith, J., Kline, D.I., Neal, B.P., Dunlap, M.J., Moriarty, V., Fan, T.-Y., Tan, C.-J., 2015. Towards automated annotation of benthic survey images: variability of human experts and operational modes of automation. *PLoS One* 10, e0130312.
- Bell, J.D., Galzin, R., 1984. Influence of live coral cover on coral-reef fish communities. *Mar. Ecol. Prog. Ser.* 15, 265–274.
- Boyce, M.S., 1992. Population viability analysis. *Annu. Rev. Ecol. Syst.* 23, 481–497.
- Bramanti, L., Iannelli, M., Fan, T.-Y., Edmunds, P.J., 2015. Using demographic models to project the effects of climate change on scleractinian corals: *Pocillopora damicornis* as a case study. *Coral Reefs* 34, 505–515.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Bruno, J.F., Selig, E.R., 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2, e711.
- Bruno, J.F., Côté, I.M., Toth, L.T., 2019. Climate change, coral loss, and the curious case of the parrotfish paradigm: why don't marine protected areas improve reef resilience? *Ann. Rev. Mar. Sci.* 11, 307–334.
- Burgess, S.C., Ryan, W.H., Blackstone, N.W., Edmunds, P.J., Hoogenboom, M.O., Levitan, D.R., Wulff, J.L., 2017. Metabolic scaling in modular animals. *Invertebr. Biol.* 136, 456–472.
- Burns, J.H.R., Delparte, D., Gates, R.D., Takabayashi, M., 2015. Utilizing underwater three-dimensional modeling to enhance ecological and biological studies of coral reefs. *Int. Arch. Photogramm. Remote Sens. Inf. Sci.* 40, 61.
- Bythell, J.C., Gladfelter, E.H., Bythell, M., 1993. Chronic and catastrophic natural mortality of three common Caribbean reef corals. *Coral Reefs* 12, 143–152.

- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* 27, 477–500.
- Cantin, N.E., Cohen, A.L., Karnauskas, K.B., Tarrant, A.M., McCorkle, D.C., 2010. Ocean warming slows coral growth in the central Red Sea. *Science* 329, 322–325.
- Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., Chiriboga, A., Cortés, J., Delbeek, J.C., DeVantier, L., 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321, 560–563.
- Caswell, H., 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*, second edn Sinauer Associates, Inc Sunderland MA.
- Chesson, P.L., 1984. The storage effect in stochastic population models. In: *Mathematical Ecology*. Springer, pp. 76–89.
- Condit, R., Pérez, R., Lao, S., Aguilar, S., Hubbell, S.P., 2017. Demographic trends and climate over 35 years in the Barro Colorado 50 ha plot. *For. Ecosyst.* 4, 17.
- Connell, J.H., 1973. Population ecology of reef-building corals. *Biol. Geol. Coral Reefs* 2, 205–245.
- Darke, W.M., Barnes, D.J., 1993. Growth trajectories of corallites and ages of polyps in massive colonies of reef-building corals of the genus *Porites*. *Mar. Biol.* 117, 321–326.
- De'ath, G., Lough, J.M., Fabricius, K.E., 2009. Declining coral calcification on the Great Barrier Reef. *Science* 323, 116–119.
- De'ath, G., Fabricius, K.E., Sweatman, H., Puotinen, M., 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Natl. Acad. Sci.* 109, 17995–17999.
- Devlin-Durante, M.K., Miller, M.W., Caribbean Acropora Research Group, Precht, W.F., Baums, I.B., Carne, L., Smith, T.B., Banaszak, A.T., Greer, L., Irwin, A., 2016. How old are you? Genet age estimates in a clonal animal. *Mol. Ecol.* 25, 5628–5646.
- Doney, S.C., Ruckelshaus, M., Duffy, J.E., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., 2012. Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.* 4, 11–37.
- Dornelas, M., Madin, J.S., Baird, A.H., Connolly, S.R., 2017. Allometric growth in reef-building corals. *Proc. R. Soc. B Biol. Sci.* 284, 20170053.
- Dunstan, P.K., Johnson, C.R., 1998. Spatio-temporal variation in coral recruitment at different scales on Heron Reef, southern Great Barrier Reef. *Coral Reefs* 17, 71–81.
- Eakin, C.M., Rauenzahn, J.L., Liu, G., Heron, S.F., Skirving, W.J., Geiger, E.F., Burgess, T.F., Strong, A.E., 2014. Will 2014–2015 be the next big El Niño? If so, what might it mean for coral reefs? *Reef Encount.* 29, 30–35.
- Eakin, C.M., Liu, G., Gomez, A.M., De La Cour, J.L., Heron, S.F., Skirving, W.J., Geiger, E.F., Tirak, K.V., Strong, A.E., 2016. Global coral bleaching 2014–2017: status and an appeal for observations. *Reef Encount.* 31, 20–26.
- Edmunds, P.J., 2000. Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. *Mar. Ecol. Prog. Ser.* 202, 113–124.
- Edmunds, P.J., 2007. Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. *Mar. Ecol. Prog. Ser.* 341, 1–13.
- Edmunds, P.J., 2013. Decadal-scale changes in the community structure of coral reefs of St. John, US Virgin Islands. *Mar. Ecol. Prog. Ser.* 489, 107–123.
- Edmunds, P.J., 2015. A quarter-century demographic analysis of the Caribbean coral, *Orbicella annularis*, and projections of population size over the next century. *Limnol. Oceanogr.* 60, 840–855.
- Edmunds, P.J., Burgess, S.C., 2016. Size-dependent physiological responses of the branching coral *Pocillopora verrucosa* to elevated temperature and PCO₂. *J. Exp. Biol.* 219, 3896–3906.

- Edmunds, P.J., Elahi, R., 2007. The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecol. Monogr.* 77, 3–18.
- Edmunds, P.J., Lasker, H.R., 2016. Cryptic regime shift in benthic community structure on shallow reefs in St. John, US Virgin Islands. *Mar. Ecol. Prog. Ser.* 559, 1–12.
- Edmunds, P.J., Riegl, B., 2020. Urgent need for coral demography in a world where corals are disappearing. *Mar. Ecol. Prog. Ser.* 635, 233–242.
- Ferrari, R., Figueira, W.F., Pratchett, M.S., Boube, T., Adam, A., Kobelkowsky-Vidrio, T., Doo, S.S., Atwood, T.B., Byrne, M., 2017. 3D photogrammetry quantifies growth and external erosion of individual coral colonies and skeletons. *Sci. Rep.* 7, 16737.
- Flower, J., Ortiz, J.C., Chollett, I., Abdullah, S., Castro-Sanguino, C., Hock, K., Lam, V., Mumby, P.J., 2017. Interpreting coral reef monitoring data: a guide for improved management decisions. *Ecol. Indic.* 72, 848–869.
- Fong, P., Glynn, P.W., 1998. A dynamic size-structured population model: does disturbance control size structure of a population of the massive coral *Gardineroseris planulata* in the Eastern Pacific? *Mar. Biol.* 130, 663–674.
- Fong, P., Glynn, P.W., 2001. Population abundance and size-structure of an eastern tropical Pacific reef coral after the 1997–98 ENSO: a simulation model predicts field measures. *Bull. Mar. Sci.* 69, 187–202.
- Gouezo, M., Golbuu, Y., Fabricius, K., Olsudong, D., Mereb, G., Nestor, V., Wolanski, E., Harrison, P., Doropoulos, C., 2019. Drivers of recovery and reassembly of coral reef communities. *Proc. R. Soc. B* 286, 20182908.
- Graham, E.M., Baird, A.H., Connolly, S.R., 2008. Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral Reefs* 27, 529–539.
- Graham, N.A., Jennings, S., MacNeil, M.A., Mouillot, D., Wilson, S.K., 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518, 94–97.
- Gunderson, L.H., 2000. Ecological resilience—in theory and application. *Annu. Rev. Ecol. Syst.* 31, 425–439.
- Hall, V.R., Hughes, T.P., 1996. Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* 77, 950–963.
- Harrison, P.L., Wallace, C.C., 1990. Reproduction, dispersal and recruitment of scleractinian corals. *Ecosyst. World* 25, 133–207.
- Henry, L.-A., Hart, M., 2005. Regeneration from injury and resource allocation in sponges and corals—a review. *Int. Rev. Hydrobiol.* 90, 125–158.
- Hernández-Pacheco, R., Hernández-Delgado, E.A., Sabat, A.M., 2011. Demographics of bleaching in a major Caribbean reef-building coral: *Montastraea annularis*. *Ecosphere* 2, 1–13.
- Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. *Science* 328, 1523–1528.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., et al., 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742.
- Hughes, T.P., 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. *Am. Nat.* 123, 778–795.
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551.
- Hughes, R.N., 2005. Lessons in modularity: the evolutionary ecology of colonial invertebrates. *Sci. Mar.* 69, 169–179.
- Hughes, T.P., Jackson, J.B.C., 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science* 209, 713–715.
- Hughes, T.P., Jackson, J.B.C., 1985. Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* 55, 141–166.

- Hughes, T.P., Tanner, J.E., 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81, 2250–2263.
- Hughes, T.P., Ayre, D., Connell, J.H., 1992. The evolutionary ecology of corals. *Trends Ecol. Evol.* 7, 292–295.
- Hughes, T.P., Graham, N.A., Jackson, J.B., Mumby, P.J., Steneck, R.S., 2010. Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* 25, 633–642.
- Hughes, T.P., Linares, C., Dakos, V., Van De Leemput, I.A., Van Nes, E.H., 2013. Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends Ecol. Evol.* 28, 149–155.
- Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B., Kleypas, J., van de Leemput, I.A., Lough, J.M., Morrison, T.H., et al., 2017a. Coral reefs in the Anthropocene. *Nature* 546, 82–90.
- Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., et al., 2017b. Global warming and recurrent mass bleaching of corals. *Nature* 543, 373–377.
- Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Liu, G., 2018. Global warming transforms coral reef assemblages. *Nature* 556 (7702), 492–496.
- Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Chase, T.J., Dietzel, A., Hill, T., Hoey, A.S., Hoogenboom, M.O., Jacobson, M., Kerswell, A., Madin, J.S., Mieog, A., Paley, A.S., Pratchett, M.S., Torda, G., Woods, R.M., 2019. Global warming impairs stock–recruitment dynamics of corals. *Nature* 568 (7752), 387–390. <https://doi.org/10.1038/s41586-019-1081-y>.
- Jackson, J.B.C., 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am. Nat.* 111, 743–767.
- Jackson, J.B., 2008. Ecological extinction and evolution in the brave new ocean. *Proc. Natl. Acad. Sci.* 105, 11458–11465.
- Jackson, J.B.C., Coates, A.G., 1986. Life cycles and evolution of clonal (modular) animals. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 313, 7–22.
- Jackson, J.B.C., Donovan, M.K., Cramer, K.L., Lam, V.V., 2014. Status and Trends of Caribbean Coral Reefs. Global Coral Reef Monitoring Network, IUCN, Gland.
- Jokiel, P.L., Morrissey, J.I., 1986. Influence of size on primary production in the reef coral *Pocillopora damicornis* and the macroalga *Acanthophora spicifera*. *Mar. Biol.* 91, 15–26.
- Kayal, M., Lenihan, H.S., Brooks, A.J., Holbrook, S.J., Schmitt, R.J., Kendall, B.E., 2018. Predicting coral community recovery using multi-species population dynamics models. *Ecol. Lett.* 21, 1790–1799.
- Kojis, B.L., Quinn, N.J., Claerboudt, M.R., 1985. Living coral reefs of northeast New-Guinea. In: *Proc. Fifth Int. Coral Reef Congr. Tahiti*, pp. 323–328.
- Kramer, P.A., 2003. Synthesis of coral reef health indicators for the western Atlantic: results of the AGRRA program (1997–2000). *Atoll Res. Bull.* 496 (3), 1–57.
- Lindenmayer, D.B., Likens, G.E., Krebs, C.J., Hobbs, R.J., 2010. Improved probability of detection of ecological “surprises.” *Proc. Natl. Acad. Sci.* 107, 21957–21962.
- Kramer, N., Tamir, R., Eyal, G., Loya, Y., 2020. Coral morphology portrays the spatial distribution and population size–structure along a 5–100 m depth gradient. *Front. Mar. Sci.*
- Lindenmayer, D.B., Burns, E.L., Tennant, P., Dickman, C.R., Green, P.T., Keith, D.A., Metcalfe, D.J., Russell-Smith, J., Wardle, G.M., Williams, D., 2015. Contemplating the future: acting now on long-term monitoring to answer 2050’s questions. *Austral Ecol.* 40, 213–224.
- Little, A.F., Van Oppen, M.J., Willis, B.L., 2004. Flexibility in algal endosymbioses shapes growth in reef corals. *Science* 304, 1492–1494.
- Lough, J.M., Barnes, D.J., 1997. Several centuries of variation in skeletal extension, density and calcification in massive *Porites* colonies from the great barrier reef: a proxy for

- seawater temperature and a background of variability against which to identify unnatural change. *J. Exp. Mar. Biol. Ecol.* 211, 29–67.
- MacNeil, M.A., Mellin, C., Matthews, S., Wolff, N.H., McClanahan, T.R., Devlin, M., Drovandi, C., Mengersen, K., Graham, N.A., 2019. Water quality mediates resilience on the great barrier reef. *Nat. Ecol. Evol.* 3, 620–627.
- Madin, J.S., Baird, A.H., Dornelas, M., Connolly, S.R., 2014. Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecol. Lett.* 17, 1008–1015.
- Madin, J.S., Baird, A.H., Baskett, M.L., Connolly, S.R., Dornelas, M.A., 2020. Partitioning colony size variation into growth and partial mortality. *Biol. Lett.* 16, 20190727.
- McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. *Science* 347, 1255641.
- Meesters, E.H., Hilterman, M., Kardinaal, E., Keetman, M., De Vries, M., Bak, R.P.M., 2001. Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. *Mar. Ecol. Prog. Ser.* 209, 43–54.
- Mellin, C., Aaron MacNeil, M., Cheal, A.J., Emslie, M.J., Julian Caley, M., 2016. Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.* 19, 629–637.
- Mellin, C., Matthews, S., Anthony, K.R., Brown, S.C., Caley, M.J., Johns, K.A., Osborne, K., Puotinen, M., Thompson, A., Wolff, N.H., 2019. Spatial resilience of the great barrier reef under cumulative disturbance impacts. *Glob. Change Biol.* 25, 2431–2445.
- Mieog, J.C., Olsen, J.L., Berkelmans, R., Bleuler-Martinez, S.A., Willis, B.L., van Oppen, M.J., 2009. The roles and interactions of symbiont, host and environment in defining coral fitness. *PLoS One* 4, e6364.
- Muko, S., Arakaki, S., Tamai, R., Sakai, K., 2014. An individual-based model for population viability analysis of the brooding coral *Seriatopora hystrix*. *Ecol. Model.* 277, 68–76.
- Ortiz, J.-C., Wolff, N.H., Anthony, K.R., Devlin, M., Lewis, S., Mumby, P.J., 2018. Impaired recovery of the great barrier reef under cumulative stress. *Sci. Adv.* 4, eaar6127.
- Osborne, K., Thompson, A.A., Cheal, A.J., Emslie, M.J., Johns, K.A., Jonker, M.J., Logan, M., Miller, I.R., Sweatman, H.P., 2017. Delayed coral recovery in a warming ocean. *Glob. Change Biol.* 23, 3869–3881.
- Patterson, M.R., 1992a. A chemical engineering view of cnidarian symbioses. *Am. Zool.* 32, 566–582.
- Patterson, M.R., 1992b. A mass transfer explanation of metabolic scaling relations in some aquatic invertebrates and algae. *Science* 255, 1421–1423.
- Pavoni, G., Corsini, M., Cignoni, P., 2020. A state of the art technology in large scale underwater monitoring. *ERCIM News*.
- Perry, C.T., Alvarez-Filip, L., 2019. Changing geo-ecological functions of coral reefs in the Anthropocene. *Funct. Ecol.* 33, 976–988.
- Perry, C.T., Alvarez-Filip, L., Graham, N.A., Mumby, P.J., Wilson, S.K., Kench, P.S., Manzello, D.P., Morgan, K.M., Slangen, A.B., Thomson, D.P., 2018. Loss of coral reef growth capacity to track future increases in sea level. *Nature* 558, 396.
- Pisapia, C., Anderson, K.D., Pratchett, M.S., 2016. Temporal consistency in background mortality of four dominant coral taxa along Australia's great barrier reef. *Coral Reefs* 35, 839–849.
- Pisapia, C., Burn, D., Pratchett, M.S., 2019. Changes in the population and community structure of corals during recent disturbances (February 2016–October 2017) on Maldivian coral reefs. *Sci. Rep. Nat. Publ. Group* 9, 1–12.
- Platt, J.R., 1964. Strong inference. *Science* 146, 347–353.
- Powles, H., Bradford, M.J., Bradford, R.G., Doubleday, W.G., Innes, S., Levings, C.D., 2000. Assessing and protecting endangered marine species. *ICES J. Mar. Sci.* 57, 669–676.

- Pratchett, M.S., Anderson, K.D., Hoogenboom, M.O., Widman, E., Baird, A.H., Pandolfi, J.M., Edmunds, P.J., Lough, J.M., 2015. Spatial, temporal and taxonomic variation in coral growth—implications for the structure and function of coral reef ecosystems. *Oceanogr. Mar. Biol. Annu. Rev.* 53, 215–295.
- Pratchett, M.S., McWilliam, M.J., Riegl, B., 2020. Contrasting shifts in coral assemblages with increasing disturbances. *Coral Reefs*, 1–11.
- Putnam, H.M., Barott, K.L., Ainsworth, T.D., Gates, R.D., 2017. The vulnerability and resilience of reef-building corals. *Curr. Biol.* 27, R528–R540.
- Riegl, B., Purkis, S., 2015. Coral population dynamics across consecutive mass mortality events. *Glob. Change Biol.* 21, 3995–4005.
- Riegl, B.M., Bruckner, A.W., Rowlands, G.P., Purkis, S.J., Renaud, P., 2012. Red Sea coral reef trajectories over 2 decades suggest increasing community homogenization and decline in coral size. *PLoS One* 7, e38396.
- Riegl, B., Cavalcante, G., Bauman, A.G., Feary, D.A., Steiner, S., Purkis, S., 2017. Demographic mechanisms of reef coral species winnowing from communities under increased environmental stress. *Front. Mar. Sci.* 4, 344.
- Roff, G., Bejarano, S., Bozec, Y.-M., Nugues, M., Steneck, R.S., Mumby, P.J., 2014. Porites and the Phoenix effect: unprecedented recovery after a mass coral bleaching event at Rangiroa atoll, French Polynesia. *Mar. Biol.* 161, 1385–1393.
- Roy, K.J., Smith, S.V., 1971. Sedimentation and Coral Reef Development in Turbid Water: Fanning Lagoon.
- Schlichting, H., 1979. Boundary layer theory. McGraw-Hill, New York, Fig. CAPTIONS Solid Curve Disp. Exact Solut. Differ. Exact Solut. Eighth QLM Iteration T Fig. Than, p. 10.
- Schmidt-Nielsen, K., Knut, S.-N., 1984. Scaling: Why Is Animal Size So Important? Cambridge University Press.
- Sebens, K.P., 1987. The ecology of indeterminate growth in animals. *Annu. Rev. Ecol. Syst.* 18, 371–407.
- Stimson, J.S., 1978. Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. *Mar. Biol.* 48, 173–184.
- Stuart-Smith, R.D., Brown, C.J., Ceccarelli, D.M., Edgar, G.J., 2018. Ecosystem restructuring along the great barrier reef following mass coral bleaching. *Nature* 560, 92.
- Szmant, A., Gassman, N.J., 1990. The effects of prolonged “bleaching” on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* 8, 217–224.
- Szmant-Froelich, A., 1985. The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). In: *Proc 5th Int Coral Reef Symp*, pp. 295–300.
- Talbot, F.H., 1965. A description of the coral structure of Tutia reef (Panganyika territory, East Africa), and its fish fauna. In: *Proceedings of the Zoological Society of London*. Wiley Online Library, pp. 431–470.
- Wakeford, M., Done, T.J., Johnson, C.R., 2008. Decadal trends in a coral community and evidence of changed disturbance regime. *Coral Reefs* 27, 1–13.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389.
- Weil, E., 2004. Coral reef diseases in the wider Caribbean. In: *Coral Health and Disease*. Springer, pp. 35–68.
- Williams, I.D., Couch, C., Beijbom, O., Oliver, T., Vargas-Angel, B., Schumacher, B., Brainard, R., 2019. Leveraging automated image analysis tools to transform our capacity to assess status and trends on coral reefs. *Front. Mar. Sci.* 6, 222.
- Wismer, S., Tebbett, S.B., Streitt, R.P., Bellwood, D.R., 2019. Spatial mismatch in fish and coral loss following 2016 mass coral bleaching. *Sci. Total Environ.* 650, 1487–1498.