Vol. 635: 233–242, 2020
https://doi.org/10.3354/meps13205

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 6

OPINION PIECE

Urgent need for coral demography in a world where corals are disappearing

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ABSTRACT: Coral reefs have long attracted attention because of their biological and economic importance, but this interest now has turned to examining the possibility of functional extirpation. Widespread declines in coral abundances have fueled the shift in motivation for studying reefs and catalyzed the proliferation of monitoring to record the changes underway. Despite appreciation of monitoring as a scientific endeavor, its primary use has continued to be the quantification of cover of coral, macroalgae, and a few other space holders. The limitations of coral cover in evaluating the consequences of changing coral abundance were highlighted decades ago. Yet neglect of the tools most appropriate for this task (demographic approaches) and continuing emphasis on a tool (coral cover) that is not ideal, indicates that these limitations are not widely appreciated. Reef monitoring therefore continues to underperform with respect to its potential, thus depriving scientists of the approaches necessary to project the fate of coral reefs and test hypotheses focused on the proximal causes of declining coral cover. We make the case that the coral reef crisis creates a need for coral demography that is more acute now than 4 decades ago. Modern demographic approaches are well suited to meet this need, but to realize their potential, consideration will need to be given to the possibility of expanding ecological monitoring of coral reefs to provide the data necessary for demographic analyses of their foundation taxon, the Scleractinia.

KEY WORDS: Scleractinia · Climate change · Monitoring · Population biology · Time series

1. INTRODUCTION

1.1. Present-day coral populations

The size of the scientific community studying coral reefs and the number of people visiting them for recreation and business have dramatically increased in the last few decades. Simultaneously, much funding is allocated to promote the understanding and conservation of coral reefs (GBRMPA 2018, NOAA 2018). Much of this attention is in response to the coral reef crisis (Bellwood et al. 2004, Hughes et al. 2010), which is a product of centuries of human exploitation and pollution, as well as globally warming seawater and declining ocean pH (Hoegh-Guldberg et al. 2007). This crisis is defined by large and globally distributed reductions in coral cover (Bellwood et al. 2004, Hughes et al. 2010), and it now threatens the ability of coral reefs to persist as calcifying ecosystems (Eyre et al. 2014).

There is a long and very successful history of describing the ecological condition of present-day coral communities based on the quantity of live coral on a reef system, as measured by planar cover (Hughes 1994, Connell et al. 1997, Bruno & Selig 2007, Jackson et al. 2014). Relative to the capacity of corals to deliver the ecological goods and services with which they have been associated (Moberg &

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Publisher: Inter-Research · www.int-res.com

Folke 1999, Wild et al. 2011), declining coral cover is considered undesirable, while stable or increasing cover is considered desirable (De'ath et al. 2012). High coral cover is consequently associated with positive reef 'health' (McField & Kramer 2007). Prior to the 1980s, it was assumed (with empirical support) that declines in coral cover on tropical reefs would be followed by increases to levels similar to those occurring before the disturbance (i.e. reef recovery; Pearson 1981). By the close of the 20th century, however, recovery following declines in cover became less common, and it is now routine to consider that damaged reefs will not recover (Hughes et al. 2017, Perry et al. 2018). This change in expectations has favored the widely held opinion that ongoing declines in coral cover will culminate in local extirpation of coral species, and perhaps, entire coral reefs (Carpenter et al. 2008, van Hooidonk et al. 2014).

Most present-day coral reef biologists effectively study coral populations characterized by low cover and low densities of coral colonies (Edmunds 2018, Hughes et al. 2018, Riegl et al. 2018). Now that the cover of many corals, as well as the abundances of their colonies, is greatly reduced compared to only a few decades ago, it is valuable to consider whether the dynamics of these emerging small populations can be effectively measured through coral cover alone. As noted decades ago for corals (Loya 1978, Pichon 1978) and more recently for terrestrial plants (Elzinga et al. 2009), the planar coverage of the substratum by sessile taxa provides limited resolution in evaluating trajectories of changing abundance, particularly when population sizes are small. In this opinion piece, we make the case that it is timely to revisit the recommendations of Connell (1973) and Hughes (1984), who appealed for demographic approaches to understand the mechanisms underlying changes in coral cover. The importance of coral cover in quantifying the coral reef crisis, and for contextualizing decades of hypothesis-driven investigations of coral reef biology, cannot be overstated. However, we contend that there is an urgent need to augment measurements of coral cover with demographic approaches in order to fully understand the significance of the coral reef crisis, and to transition to a new era of solution-oriented science with the potential to prolong the survival of coral populations (van Oppen et al. 2015). Modern demographic approaches provide tools suitable for augmenting ongoing studies of coral cover, and they have the capacity to deliver statistically bounded projections of coral population structure into the future. They can also be used to test hypotheses regarding the demographic causes of changing coral cover, and 'what if' scenarios addressing future population trajectories. Such prospective analyses offer the potential to inform the design of conservation strategies intended to enhance (or restore) the structure and ecological functions of coral communities.

1.2. Strengths and limitations of coral cover measures

Coral cover refers to the summed incidences of corals within a sampling area, where 'incidences' are defined by the methods employed to evaluate abundance (Loya 1978). They can refer to points falling on coral colonies encountered in point-count surveys along a transect (English et al. 1997), in quantitative planar images of coral reefs (Kohler & Gill 2006), or intercept lengths along a transect that correspond to coral colonies upon which the transect is placed (Loya 1978). Coral cover can also describe the projected area of a colony on a belt- or photo-transect (Aronson et al. 1994, English et al. 1997), or the 3-dimensional area in a survey processed with structure-from-motion software (Storlazzi et al. 2016). When these data are expressed as a percentage of the dot population used in the survey, the transect length, or the sample area (respectively), they provide a measure of relative coral cover. Other combinations of approaches have been used to measure coral cover, and their strengths are discussed elsewhere (Dodge et al. 1982, Edmunds et al. 1998, Riegl 1999, Rogers & Miller 2001, Lam et al. 2006, Pante & Dustan 2012).

While coral cover has served as a critical state variable that has fueled decades of scientific advances in understanding coral reefs (Bruno & Selig 2007, Jackson et al. 2014), as a summative statistic it cannot evaluate several critical properties of coral populations (Fig. 1). First, it cannot reveal how cover is allocated among colonies of different size (e.g. many small, versus few large). Second, it provides no information on the processes driving variation in cover (e.g. settlement versus colony persistence), and as a result, third, changes in cover do not allow accurate projection of how coral cover will change in the future. These limitations were described decades ago (Connell 1973, Hughes 1984), but they have not resulted in widespread adoption of demographic approaches in the study of coral populations. Coral cover remains an effective tool to capture the severity of the coral reef crisis (Hughes et al. 2018), and to publicize the dire implications of the losses that are underway (Morton 2019), but demography has much to offer in testing the roles of various mechanisms

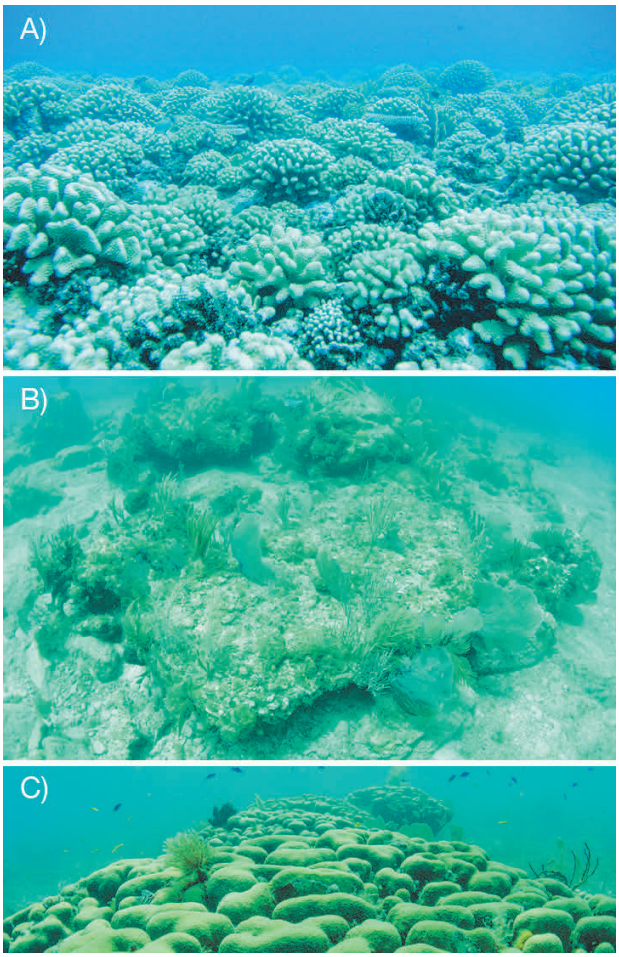

Fig. 1. (A) Coral cover is effective at measuring coral abundance (for example, in Moorea, French Polynesia, in 2018), but it has limited capacity to identify the causal processes of changing abundances. (B) The utility of coral cover in measuring abundance declines when cover is depleted (as in St. John, US Virgin Islands, in 2018), as it cannot evaluate how coral biomass is distributed among coral colonies. (C) This problem is acute for corals that undergo fission, like the Caribbean coral *Orbicella annularis*

(e.g. adult mortality vs. poor recruitment) in causing declining coral cover, and in objectively evaluating the likelihood of population recovery (or extirpation).

Expanding the types of variables used to quantify coral populations is more important now than it was 35 yr ago (cf. Hughes 1984), because many coral populations are transitioning to low abundance states (Edmunds 2018, Riegl et al. 2018), in which the risks of extirpation intensify (Riegl et al. 2017, 2018), and the limitations of coral cover as a state variable are highlighted. As we describe in Section 2, the demographic approaches available for the analysis of coral populations have evolved statistically and mathematically from those advocated in the 1980s and 1990s (Hughes 1984, Bak & Meesters 1998). Moreover, computational advances allow these approaches to be easily applied to appropriate data and, therefore, they are poised to deliver timely advances in understanding of the dynamics of coral populations and communities. Existing monitoring projects can supply much of the data necessary to achieve this potential, but some may require modification (described below) to deliver the detail required to harness the full potential of demography. A demographic understanding of the causes of historic variation in sizes of coral populations is necessary to project the population structure into the future and test hypotheses regarding the effects of intensifying environmental stressors and possibilities of alternative outcomes.

Demographic approaches require the measurement of vital rates (probabilities of growth, survival, fecundity) causing population sizes to change. Individuals in populations are often subdivided by size, age, or life stage, and vital rates between or within these states are calculated. In corals, 'individual' usually refers to autonomous tissue areas (sensu Connell 1973) that are typically also colonies, or sometimes polyps, as in solitary corals (e.g. *Fungia* and *Balanophyllia*; Fadlallah 1983, Goffredo & Chadwick-Furman 2003, Goffredo et al. 2004, Elahi et al. 2016), but the genetic identity of 'individual' colonies is usually not addressed. Genetic identity can be important due to fragmentation and other asexual reproduction (Highsmith 1982, McFadden 1991), which are common in corals and can create systems of genets (genetically unique individuals) and ramets (replicates of a single genet). Within genets, ramets share genetically identical host tissue, and they may not share common demographic fates.

Partitioning of individuals within the population (i-states) can be on continuous (e.g. smoothly changing biomass or colony sizes) or discrete (grouping of colonies into size classes) scales, as can their responses to environmental conditions (e.g. through changes in fecundity and/or growth). The structure of populations determines the type of demographic model most suitable for modeling changes in population size. Although coral population dynamics are made complex by colony growth, shrinkage, fission, and fusion, these effects should not deter the application of demographic models that are applied in other ecosystems to populations that arguably are more complex than those of scleractinians (Caswell 2001). Some of the best known methods for quantifying vital rates, and using them for projection, are life tables (Fadlallah 1983, Bramanti et al. 2015), matrix projection models (Hughes & Jackson 1985, Gotelli 1991, Fong & Glynn 1998), coupled ordinary differential and difference

equations (Sebens 1982), partial differential equations, delay differential equations (Metz & Diekmann 1986, Nisbet 1997), integral projection models (Tuljarpurkar & Caswell 1997, Easterling et al. 2000, Hastings & Gross 2012), or cellular automata (Mumby 2006).

2. DATA NEEDS AND LOGISTICAL IMPLICATIONS OF DEMOGRAPHIC MODELS

Whatever their mathematical basis, demographic approaches can leverage data typically provided through monitoring of coral reefs, and we contend that there is much to be gained by more fully integrating demography into coral monitoring (Fig. 2). The data requirements for demographic models, relative to those required to evaluate abundances through measurements of cover, range from modest to burdensome depending on the approach. The simplest of demographic information is provided by measuring colony sizes, which can be harnessed to test for variation in colony size-frequency structure across space or time (Bak & Meesters 1998, 1999). While surveys conducted at a single time cannot address trajectories of change (Condit et al. 1998), they reveal the effects of disturbances through unequal representation of colony sizes (Bak & Meesters 1998, 1999). To quantify trajectories of change, repeated measurements of the same colonies, or population, are required. These measurements are obtained by retaining the continuously distributed nature of colony size or by assigning colonies to size classes, such that growth increases colony size, and promotes transitions among size classes. Below we summarize the strengths and limitations of 5 demographic approaches that have been applied to reef corals.

2.1. Life tables (LTs)

LTs estimate rates of growth, reproduction (including recruitment), and mortality for a cohort of individuals (tracking individuals from birth to death results in 'horizontal' LTs), or a sub-sample of the population (for which measurements of birth and death results in 'vertical' LTs). Age- or stage-specific survival rates (growth, stasis, shrinkage) can be estimated using data organized in LTs (Williams et al. 2002, Skalski et al. 2005). LTs usually also report maternity (i.e. fertility) schedules that indicate the proportion of the population that reproduces, as well as the fecundity of mature individuals. As a common objective of demographic approaches is to increase the accuracy with which populations can be projected into the future, survival and maternity schedules from LTs are used to parameterize cohort-based

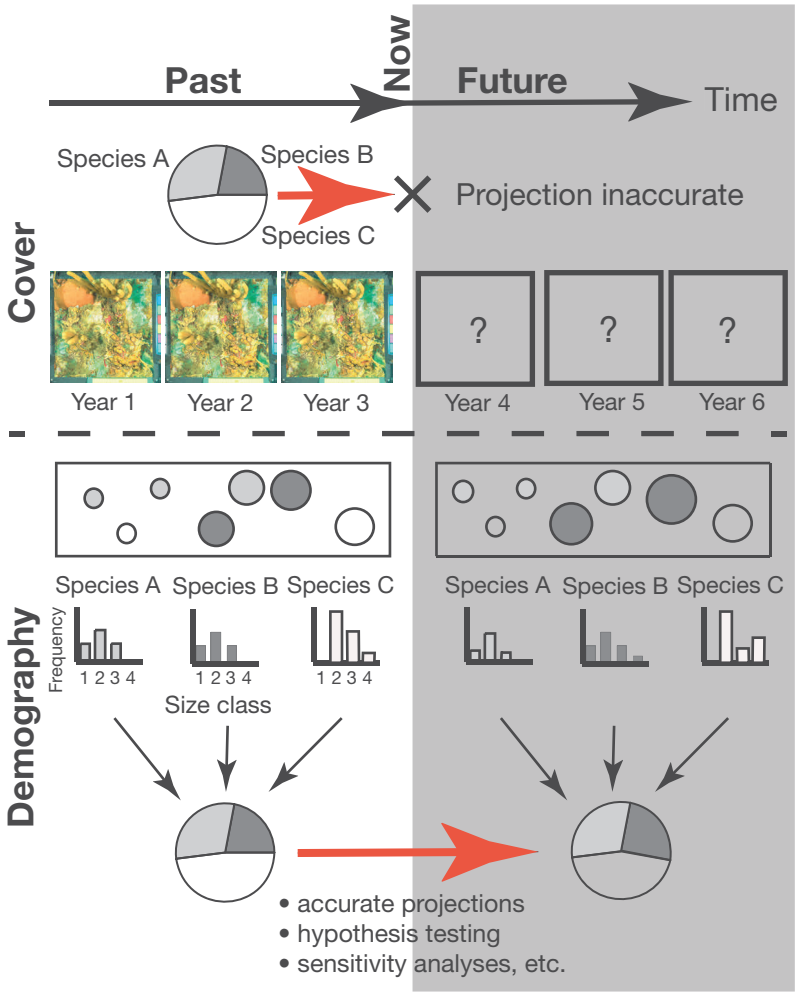

Fig. 2. Strengths and limitations of monitoring coral communities by measuring coral cover versus coral colony abundance. Monitoring over the Past (Years 1–3) supports projections into the Future (Years 4–6) for multiple species (Species A, B, and C). Projections by cover tend to be inaccurate and have limited ability to test mechanistic hypotheses; demography better addresses mechanisms of change by tracking the fates of colonies (circles) and their size distributions (bar graphs). Demographic models (see Section 2 for details) support accurate population projections and have a strong ability to test hypotheses regarding the causes and consequences of changing population abundances

models, such as matrix projection models (see Section 2.2). Both horizontal and vertical LTs have been used to model coral populations (Edmunds & Elahi 2007, Doropoulos et al. 2015, Edmunds 2015, Riegl & Purkis 2015, Riegl et al. 2017, 2018, Soto-Santiago et al. 2017). The strengths of LTs are their easy application and their wide distribution throughout the literature. The limitations of LTs are that they tend to serve as repositories for the information required to develop more sophisticated demographic models. Therefore, LTs should be considered a required step, but not the ultimate goal, of a demographic analysis.

2.2. Matrix projection models (MPMs)

MPMs (Hughes 1984, Gotelli 1991, Caswell 1997, 2001, Rees & Ellner 2009) consist of matrices with column entries reporting transition probabilities of colonies among classes. In MPMs, corals are usually grouped by size rather than age, because size is a poor predictor of coral age (Hughes & Jackson 1980, Hughes 1984, Hughes & Connell 1987). The matrix defines the probabilities of growing or remaining in the same size classes, reproducing, or dying. Backward class-transitions are possible by partial mortality or fragmentation. When prepared as Markov chains, MPMs describe life-event probabilities within populations until (and including) death (Tanner et al. 1996, Caswell 2001, 2019, Lowe et al. 2011), and when prepared as Leslie or Lefkovich matrices (Caswell 2001), they describe variation in population structure and include the effects of fecundity. Survival and fertility probabilities in MPMs are fixed, and the same survival, death, and reproductive regimes repeat throughout the projection (i.e. the Leslie matrix is invariant). Diverse life histories that include elements like inter-annual variability in life-history parameters, or the influence of changing environment, are modeled using several matrices that are alternated to represent sequences of good and bad years (Hughes 1984, Fong & Glynn 2001, Vardi et al. 2012, Riegl et al. 2017, 2018).

The strengths of MPMs lie in their inherent mathematical simplicity that reduces the burden of supplying the data they require, and their computational requirements can be satisfied by PCs and spreadsheet software. MPMs have limitations, however, notably requiring continuously distributed size to be discretized into size classes. The boundaries of these classes, as well as the number of replicates in each class, affect the model predictions and sensitivities (Caswell 2019).

2.3. Integral projection models (IPMs)

IPMs consider demographic rates influenced by continuously varying measures of size (Ellner & Rees 2006, Merow et al. 2014, Rees et al. 2014), and they evaluate the transitions of individuals between times using a kernel that has a flexible mathematical definition. Fecundity, growth, and mortality typically have unique kernels, with each expressed as a continuous function of size and having the capacity to quantify the effects of the environment. Each relationship captures ecological reality, as size-dependency can adopt a variety of forms and can be based on empirical data, or predictive models like dynamic energy budgets (Kooijman 2009, Smallegange et al. 2017) or the metabolic theory of ecology (Brown et al. 2004).

To date, only a few studies have applied IPMs to scleractinians (Edmunds et al. 2014, Elahi et al. 2016, Kayal et al. 2018) or octocorals (Bruno et al. 2011), but these applications, together with examples in the terrestrial vertebrate literature (Coulson et al. 2011), illustrate their analytical power relative to other demographic approaches. The strength of IPMs lies in their ability to capture ecological realism through the treatment of size as a continuously distributed variable, and the effects of varying environmental conditions through empirical and mathematical approaches. Consideration of environmental effects in IPMs has great appeal in addressing the effects of global climate change (warming) and ocean acidification through first principles (e.g. the Arrhenius function) and empirical data (e.g. seawater pH). The advantages of IPMs also compose their chief limitations, which arise from their demands for large quantities of data (including fecundity, which is logistically challenging to obtain) and computational complexity.

2.4. Differential and difference equation models (DEMs)

DEMs employ equations to account for demographic processes. These can be linear or non-linear differential equations if the variable of interest is continuously changing, or difference equations (DE) if discrete time-steps can be rationalized based on the variable of interest (growth in corals is continuous, but reproduction in many species is discrete). Most frequently, ordinary, autonomous differential equations (i.e. ODEs) are employed (Wolanski et al. 2004, Mumby et al. 2007, Riegl & Purkis 2009, Bas-

kett et al. 2010, Melbourne-Thomas et al. 2011, van Woesik et al. 2018).

Delay differential equations, in which derivatives of the unknown function are written in terms of the values of the function at a preceding time, can be employed when present-day growth is dependent on historic growth (Kuang 1993, Gurney & Nisbet 1998, Li et al. 2014, Fattahpour et al. 2019). Across several equations, rates of graduation of individuals (most frequently, a fraction of the entire population) from one size class to the next, can be made continuous. DEMs are mathematically related to MPMs by a matrix being used as shorthand for a system of equations. Hence, equivalent models can be expressed in either format (i.e. DEMs or MPMs). While ODEs and DEs have been widely used in the analysis of coral cover (Mumby et al. 2007, van Woesik et al. 2018), only a few applications address coral size distributions (Sebens 1982, Riegl & Purkis 2009, Riegl et al. 2013, Baskett et al. 2014). The strengths of DEMs are their flexibility in allowing precise statements with regards to the population variables of interest. Colony sizes can be treated as discrete classes or as continuous variables, the structure of DEMs is inherently flexible, and modeling results can be contextualized by previous applications in other systems (e.g. Caswell 1997). Also, once a problem is formulated as equations, simulation can be implemented while remaining within the defined mathematical structure. The limitations are that equations must be precisely defined (i.e. dimensional analysis is important) and that mathematical elegance (i.e. compact equations with clear-cut dynamic properties) can come at the cost of ecological realism.

2.5. Individual-based models (IBMs)

These models focus on individual organisms and local interactions, and they typically capture a diversity of functions that are unique to individuals and are often variable among them. IBMs have been widely applied in multiple branches of ecological and evolutionary biology, where they have been developed to consider variation among individuals expressed at functional levels of space, ontogeny, phenotype, cognition, and genotype (DeAngelis & Mooij 2005). Through these functional levels, it is possible to evaluate how system-level properties arise from the summation of individual performance. The model design can be codified in an overview, design concept, and details protocol (Grimm et al. 2006), within which the mathematical equations relating model elements are defined through theoretical and empirical relationships.

Despite the apparent suitability of IBMs for modeling complex populations of colonial scleractinians, applications of this type of modeling in the coral system remain rare. Muko et al. (2014) applied IBMs to scleractinians for population viability analysis. While IBMs can provide attractive tools that are well matched to modeling the complex fates of individual coral colonies, their reliance on rich detail of individual performance creates substantial challenges to coral reef monitoring programs limited by time and money.

3. WHAT DEMOGRAPHY CAN (AND CANNOT) DO FOR CORAL REEF SCIENCE

While coral cover provides limited insights into the mechanisms causing it to decline, or whether the trends are likely to vary in the future (Hughes 1984), these limitations can be addressed with demographic approaches. Demographic models do not provide crystal balls to forecast the future, but they employ the empirical relationships between population and environment to project likely or plausible future dynamics. Critically, projections (as opposed to forecasts) anticipate future changes in population size assuming a very carefully prescribed set of future environmental conditions whose effects have been established with historic empirical research (Caswell 2001). Through such mechanisms, it is possible to identify future population trajectories (i.e. to anticipate change) given specific conditions, and to test hypotheses in a 'what if' context. Statistical rigor can be added through sensitivity analyses (Saltelli et al. 2004, Caswell 2019), which evaluate the changes in magnitude of outcomes (such as population growth rate) in response to explicit changes in demographic parameters (such as survival rates, fertility). With sensitivity analysis providing forward-looking capacity, and LT response experiments (Caswell 2001, 2019) a related, backward-looking approach, demographic models can offer insight into why populations change, and assist in the identification of likely life stage targets (e.g. recruits vs. adults) for conservation action.

4. APPEAL FOR ACTION

To address the need for solution-oriented science in response to the coral reef crisis, and to better inform

reef management decisions with the potential to attenuate local coral mortality, there is an urgent need to improve the predictive capacity for future changes in coral population sizes. The challenges of implementing demographic approaches are modest relative to the great effort required to accurately record changes in coral reefs over time, and they offer the potential to leverage existing data already being generated from biological monitoring of coral reefs. In addition to emphasizing the importance of long-term measurements of coral abundance, the gravity of the coral reef crisis demands a rigorous treatment of processes causing coral populations to change in size. There also is a pressing need to improve the accuracy with which projections of future changes in coral population size can be made, including providing objective evaluations of the likelihood of local extirpation (and whether this can be avoided). The resources now allocated to monitoring coral reefs are greater than ever before, but there remains much competition among specific tasks for which this support might be used: we contend that there is much to be gained by increasing the priority accorded to the measurement and book-keeping of coral colony size over time.

Many data remain to be mined from existing time series analyses of coral reef communities to advance the goal of effective use of demography, particularly where legacy image-based data are available. However, adjustments of existing (and new) projects will facilitate the future development of demographic approaches in coral reef science, and we suggest these efforts might judiciously be focused on 4 tasks:

(1) Establish the capacity for repeated sampling of the same areas of reef, particularly to allow identical populations and coral colonies to be surveyed over multiple years. While repeated sampling of fixed areas of reef already is routinely accomplished in many monitoring programs, unique numbering and relocation of specific colonies is likely to remain a time-consuming task for some time to come. This challenge might find a solution in emerging image-based approaches (described below).

(2) As demography strictly is the study of populations (sensu stricto, Lawrence 2005) the tools of this discipline are most effective when applied at the species level. Unfortunately, the resolution of many coral species continues to be challenging, particularly underwater (Edmunds et al. 2016), and, therefore, the choice of taxa for demographic analyses must be made with close attention to the ease with which colonies can be identified to species underwater. For the time being, this may mean that some taxa will remain intractable to traditional demographic approaches, although the increasing ease with which coral host genotypes can be identified with genetic approaches is shifting the notion of genetically identifying members of a study population from speculation to reality (Sheets et al. 2018).

(3) Exploit image-based techniques to record coral communities along belts, quadrats, or plots (rather than line-intercept approaches), with images scaled to capture the planar extent of individual colonies. Such images preserve the opportunity for retrospective analysis of coral colony sizes and basic demographic properties, even if these features are not integral to the immediate sampling regime. Fine-grained spatially referenced photomosaics and structure-from-motion imagery (Pedersen et al. 2019, Rossi et al. 2019) offer the greatest promise in increasing the ease with which coral colonies can be measured and tracked over time, particularly when it becomes possible to pair the images with fully automated analytical tools.

(4) Wherever resources of time and money are available, coral reef monitoring programs should consider expanding their inclusion of state variables from coral cover to measures of coral colony abundance and size. This task will require defining coral colonies by size and consideration of the best means to count coral colonies along the boundaries of the sampling units (Zvuloni et al. 2008). Management of these data in parallel with coral cover will create the opportunity for flexible demographic approaches in which size can be treated categorically (e.g. MPMs, Edmunds 2015) or as a continuous variable (e.g. IPMs, Edmunds et al. 2014).

Acknowledgements. We dedicate this paper to Professor Joseph Connell, whose pioneering work on coral populations at Heron Island, Australia, and the legacy of colleagues he trained and inspired, made the present contribution possible. Writing of this paper was made possible through partial support from the NSF (to P.J.E., DEB 13-50146 and OCE 16-37396). This is contribution number 297 of the CSUN Marine Biology Program.

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Editorial responsibility: Karen Miller, Hobart, Tasmania, Australia

Submitted: August 26, 2019; Accepted: November 25, 2019
Proofs received from author(s): January 24, 2020