

Evaluating the causal basis of ecological success within the scleractinia: an integral projection model approach

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Abstract Many tropical corals have declined in abundance in the last few decades, and evaluating the causal basis of these losses is critical to understanding how coral reefs will change in response to ongoing environmental challenges. Motivated by the likelihood that marine environments will become increasingly unfavorable for coral growth as they warm and become more acidic (i.e., ocean acidification), it is reasonable to evaluate whether specific phenotypic traits of the coral holobiont are associated with ecological success (or failure) under varying environmental conditions including those that are adverse to survival.

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Initially, we asked whether it was possible to identify corals that are resistant or sensitive to such conditions by compiling quantitative measures of their phenotypic traits determined through empirical studies, but we found only weak phenotypic discrimination between ecological winners and losers, or among taxa. To reconcile this outcome with ecological evidence demonstrating that coral taxa are functionally unequal, we looked beyond the notion that phenotypic homogeneity arose through limitations of empirical data. Instead, we examined the validity of contemporary means of categorizing corals based on ecological success. As an alternative means to distinguish among functional groups of corals, we present a demographic approach using integral projection models (IPMs) that link organismal performance to demographic outcomes, such as the rates of population

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growth and responses to environmental stress. We describe how IPMs can be applied to corals so that future research can evaluate within a quantitative framework the extent to which changes in physiological performance influence the demographic underpinnings of ecological performance.

Introduction

Rising concentrations of atmospheric carbon dioxide (CO₂) from the burning of fossil fuels have resulted in global climate change (GCC) that has increased global sea surface temperatures (SST) and perturbed the carbonate chemistry of seawater, thereby reducing the surface pH of oceans [i.e., ocean acidification (OA) (Kelly and Hofmann 2012)]. These changes have many biological consequences known best for their negative implications, such as the physiological stress associated with high temperature (Harley et al. 2006; Hoegh-Guldberg and Bruno 2010; Somero 2010), and in the marine environment, reduced skeletal accretion (e.g., calcification) and perturbed respiration and photosynthesis associated with OA (Hofmann et al. 2010; Rodolfo-Metalpa et al. 2011). The potential implications of these effects are serious, for within 100 years, atmospheric pCO₂ is projected to increase from 39 Pa to between 49.6 and 85.1 Pa (van Vuuren et al. 2011), thereby increasing SST 0.3–2.1 °C (depending on the climate change scenario) and reducing pH of the open ocean by 0.3 units (Feely et al. 2009; Sokolov et al. 2009; Kirtman et al. 2013). Relatively little is known of the effects of these conditions on coastal marine ecosystems, including coral reefs.

OA and elevated temperature are among the most prominent threats to ocean ecosystems (Hughes et al. 2003; Hoegh-Guldberg et al. 2007), and their interactive effects may represent an evolutionary impasse to the survival of tropical reefs as coral-dominated, calcifying systems (Silverman et al. 2009; Wild et al. 2011; Anthony et al. 2011). While it has rapidly become clear that the responses of corals to OA and thermal stress, individually or interactively, are not uniform among species (Loya et al. 2001; Pandolfi et al. 2011; Comeau et al. 2013), progress in understanding the causal basis of this variability has been slow. There are exceptions to this generality, notably with molecular genetic tools, for example, being used to clarify cellular function (Meyer et al. 2011; Miller et al. 2011), host taxonomy (Forsman et al. 2009; Stat et al. 2012), and the roles of *Symbiodinium* genotypes in affecting holobiont biology (Hennige et al. 2009; Putnam et al. 2012; Yuyama et al. 2012). There is a clear need for more information in order to understand the factors promoting coral success in the face of environmental challenges.

Corals have been categorized into functional groups based on the performance for at least four decades, with

two of the earliest studies partitioning corals by relative dependence on autotrophy and heterotrophy (Porter 1976) and degree of digestive aggression (Lang 1973). These studies began a period of phenomenological approaches to differentiating among corals based on phenotypic traits. This interest has re-emerged in the twenty-first century in efforts to categorize corals in ways that are insightful to understanding the causes and consequences of declines in coral cover (Loya et al. 2001; Darling et al. 2012, 2013), as well as declines that occurred prior to current concerns over climate change (Cramer et al. 2012). The renewed interest initially focused on approaches similar to the r-K life history classification of Stearns (1977), with the debate crystallizing around whether coral species can be categorized as “winners” or “losers” (Loya et al. 2001), or display “weedy” or “non-weedy” life history strategies (Knowlton 2001). This discussion is acquiring sophistication with, for example, studies partitioning hundreds of coral species among four life history strategies based on up to 11 features (Darling et al. 2012), or categorizing them as generalists or specialists based on the genetic diversity of their *Symbiodinium* (Fabina et al. 2012; Putnam et al. 2012). Other studies have characterized vulnerable and resistant corals on extant and fossil reefs based on key traits generated from the opinions of experts (van Woesik et al. 2012), disease-susceptible and disease-resistant corals based on mostly categorical traits (Diaz and Madin 2011), and bleaching-susceptible and bleaching-resistant corals based on mass transfer effects (van Woesik et al. 2012; see Patterson 1992).

While the aforementioned studies demonstrate that corals can be classified into functional groups, most studies have relied heavily on categorical data, which overlooks the resolution that can be obtained from continuous data available in the primary literature (Edmunds et al. 2011 and reinforced below). More importantly, virtually all studies of functional groupings of scleractinians provide no mechanism by which trait values can be scaled across the complex landscape of organismic biology to affect population-specific processes such as birth rates, death rates, longevity, and fecundity. These demographic properties are the best means through which the ecological successes of corals can be codified and quantified. With greater understanding of the causal basis of the aforementioned demographic properties, it should be possible to construct a mechanistic understanding of the effects of physical environmental conditions on the growth of coral populations. Madin et al. (2012a) provide one example in which demographic traits are linked to coral performance, and their analysis modeled lifetime reproductive output of *Acropora hyacinthus* as a function of the effects of seawater flow and OA on colony dislodgement, photosynthesis, and respiration.

Here, we advocate a demographic construct for scleractinian corals that provides an explicit means to couple organismic performance to ecological success. Similar approaches have been applied in other systems (Violle et al. 2007), for example, phytoplankton (Litchman and Klausmeier 2008) and bighorn sheep (Coulson et al. 2005), but have received little attention in studies of scleractinians (but see Burgess 2011; Madin et al. 2012a, b). Coupling physiological phenotypes to demographic properties is central to understanding the mechanistic basis of ecological success and, in the case of scleractinians, to predict which corals might function as ecological winners when faced with anthropogenic assaults. Arguably, understanding the causal basis of ecological success (and failure) among scleractinians on contemporary reefs is the most important objective to advance efforts to forecast the structure and function of coral reefs in the future.

We have structured our paper into two parts. First, we outline our efforts using existing continuously distributed data from the primary literature to characterize the phenotypes of scleractinian holobionts (i.e., the animal host plus the consortia of single-celled taxa they contain, including *Symbiodinium* dinoflagellates), and in so doing, underscore the current limitations to accomplishing this goal. Second, we describe how the well-developed tools of integral projection models (IPMs) can provide insights into trait-based explanations of ecological success. In conclusion, we identify key research areas critical to understanding and projecting coral assemblages in a future differing from recent times in a variety of physical conditions.

Step 1: Assessing contemporary data

After decades of limited attention, the ecophysiology of tropical scleractinians has become a focus of research attention. In the 1970s and early 1980s, there was strong interest in coral ecophysiology (Muscatine et al. 1981; Dubinsky et al. 1984; Gladfelter 1985), and toward the end of this period, widespread coral bleaching maintained interest in this discipline (Glynn 1993; Gates and Edmunds 1999). Although attention waned in the 1990s, the ecophysiology of tropical reef corals is now being studied in great detail to evaluate the effects of GCC and OA on reef corals (Gattuso et al. 1998; Hofmann and Todgham 2010; Lesser 2013). Consequently, there is nearly a century of legacy data describing the ecophysiology of corals, with quantitative studies beginning as early as the 1920s (Vaughn 1914; Yonge and Nicholls 1930; Wellington et al. 2001). Not unsurprisingly, however, a century of research spans a wide range of methodological and technological sophistication, as well as paradigm shifts in comprehension of the

functional biology of this taxon (Lesser 2004; Davy et al. 2012).

One of the most profound changes in understanding of the biology of tropical reef corals has involved the discovery of high genetic diversity among their *Symbiodinium* symbionts (Rowan and Powers 1991; LaJeunesse et al. 2010; Stat et al. 2012) and an expansion of the notion of symbiosis in the Scleractinia to embrace microbes (Lesser et al. 2004; Apprill et al. 2009). These symbionts can have a striking effect on the physiology of the holobiont (Lesser et al. 2004; Jones et al. 2008; Putnam et al. 2012), and through changes in their genetic assemblages, can play important roles in the capacity of corals to improve their tolerance of environmental stress (Jones et al. 2008; Baskett et al. 2009; Gates and Ainsworth 2011). In the present study, we address the advantages to be gained by applying IPMs to reef corals, and do so by focusing on the physiology and ecology of the holobiont as an emergent property of its interactions with symbionts. This should not be construed to mean that variation in the genetic variants of the *Symbiodinium* (or microbial flora) is unimportant in the application of IPMs to corals, rather it recognizes the current state of empirical research necessary to achieve this goal. We note however that the effects of varying *Symbiodinium* type ultimately can be included in the IPM construct, essentially in the same way as any other variable that is important in determining demographic traits.

In 2009, we first became interested in the ecophysiology of reef corals when we sought empirical data to inform dynamic energy budget (DEB) models for scleractinians (Muller et al. 2009), and to test the aspects of coral biology that have become deeply engrained in the fabric of this discipline (e.g., depth-dependent reductions in growth rates) (Edmunds et al. 2011). Our initial effort included data for 73 species from 126 studies, yet it provided only weak support for apparently well-established patterns of variation in coral phenotypes among differing physical conditions and dissimilar taxa (Edmunds et al. 2011). Given the well-established differences we wished to test for general application, it seemed unlikely that the results of our analyses of compiled data reflected ecological reality. Rather, we suspected that our null results were a product of methods that differed among studies, as well as of outdated perspectives of the ways in which biological properties might differ among functionally dissimilar groups of corals. Outdated perspectives are common in older literature, because, for example, early studies overlooked the importance of seawater flow to coral biology (Patterson 1992) and the genetic variation hidden within *Symbiodinium* symbionts (Pochon and Gates 2010). We returned to compiling ecophysiological data for scleractinians in 2010 when we sought to evaluate the fate of corals in warmer and more acidic seas, and our compilation supported the hypothesis that some corals

Table 1 Compilation of 12 phenotypic traits that are widely available in peer-reviewed literature for the six most commonly studied genera

Trait	<i>Acropora</i>	<i>Goniastrea</i>	<i>Orbicella</i>	<i>Montipora</i>	<i>Pocillopora</i>	<i>Porites</i>
Calcification	0.56 ± 0.12 (28)	0.41 ± 0.03 (2)	0.35 ± 0.12 (2)	0.20 ± 0.05 (6)	0.39 ± 0.04 (26)	0.29 ± 0.03 (53)
Chlorophyll- <i>a</i>	2.23 ± 0.46 (9)	14.78 ± 4.50 (6)	10.23 ± 1.13 (30)	18.38 ± 4.99 (9)	5.08 ± 1.17 (14)	8.08 ± 1.62 (23)
Linear extension	109.5 ± 17.7 (19)	6.0 ± 0.8 (8)	6.6 ± 0.6 (17)	17.7 ± 6.8 (5)	50.0 (1)	12.1 ± 0.5 (127)
Lipid content	2.56 ± 0.71 (4)	8.00 ± 3.00 (2)	2.04 ± 0.24 (2)	4.43 ± 1.21 (3)	0.17 (1)	5.44 (1)
Mitotic index	2.68 ± 0.72 (10)	0.28 (1)	4.43 ± 0.66 (9)	1.20 ± 0.30 (2)	2.59 ± 1.81 (2)	3.52 ± 0.56 (10)
Polyp density	70.2 ± 18.3 (6)	5.3 ± 1.6 (3)	3.9 ± 1.0 (11)	158.5 (1)	71.2 ± 15.7 (5)	65.2 ± 2.8 (32)
Protein	3.70 ± 0.30 (2)	5.05 ± 0.35 (2)	2.40 ± 1.36 (6)	3.83 ± 0.81 (6)	0.26 ± 0.04 (8)	2.47 ± 0.87 (8)
<i>Symbiodinium</i> density	6.65 ± 4.44 (32)	2.66 ± 0.90 (6)	2.69 ± 0.40 (13)	1.55 ± 0.38 (8)	0.97 ± 0.28 (6)	5.98 ± 3.41 (14)
Tissue thickness	1.60 ± 0.30 (3)	3.20 ± 0.40 (2)	0.24 ± 0.01 (11)	0.90 (1)	0.65 ± 0.25 (2)	5.26 ± 0.26 (47)
Tissue biomass	3.08 ± 0.91 (8)	16.10 (1)	7.68 ± 0.77 (24)	7.48 ± 0.48 (2)	1.83 ± 0.33 (2)	12.51 ± 2.03 (8)
Respiration	0.37 ± 0.09 (7)	0.74 ± 0.04 (2)	0.79 ± 0.15 (26)	0.82 ± 0.27 (3)	1.68 ± 0.71 (4)	0.62 ± 0.12 (8)
Photosynthesis	1.00 ± 0.11 (5)	3.24 ± 0.07 (2)	2.61 ± 0.34 (19)	3.30 ± 0.34 (3)	4.75 ± 1.69 (4)	2.55 ± 0.55 (6)

Traits are calcification ($\mu\text{mol CaCO}_3 \text{ cm}^{-2} \text{ h}^{-1}$), chlorophyll-*a* content ($\mu\text{g cm}^{-2}$), linear extension (mm year^{-1}), lipid content (mg cm^{-2}), mitotic index (%), polyp density (polyps cm^{-2}), protein (mg cm^{-2}), *Symbiodinium* density ($\times 10^6$ cells cm^{-2}), thickness (mm), biomass (mg cm^{-2}), dark aerobic respiration ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$), and maximum rate of photosynthesis ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$) for *Acropora*, *Goniastrea*, *Orbicella* (formerly *Montastraea*), *Montipora*, *Pocillopora*, and *Porites*. Trait values (mean ± SE [n]) were used to support a cluster analysis (Fig. 1) illustrating similarities among these genera

are functioning as ecological winners while others around them are less successful (i.e., are losers) (sensu Loya et al. 2001). Further, a trait-based analysis of coral performance over ecological (i.e., on extant reefs) and geological time (i.e., the fossil record) revealed that the evolutionary fate of coral species was largely independent of taxon. We inferred, therefore, that the fate of corals was more strongly dependent on holobiont phenotypes than taxonomy, and subsequently implemented a modeling effort to evaluate the features of winning and losing corals in a phenotype-based construct (Edmunds et al. 2014).

The present paper originated as an effort to use empirical data describing coral phenotypes to codify our general phenotype-based model projecting present-day reefs into a future of warmer and more acidic seas (Edmunds et al. 2014). Conceptually, we intended to select corals identified as ecological winners or losers based on changes in their absolute and relative abundance on contemporary reefs between 1981 and 2010 (Edmunds et al. 2014), and then define their phenotypes based on continuously distributed measurements of select traits. Our objective was to use the ecological categories and their corresponding phenotypic properties as parameter values in a population model from which we could evaluate emergent properties of the population. The phenotypic properties of corals were defined by 12 traits that are widely available in peer-reviewed literature: calcification ($\mu\text{mol CaCO}_3 \text{ cm}^{-2} \text{ h}^{-1}$), chlorophyll-*a* content ($\mu\text{g cm}^{-2}$), linear extension (mm year^{-1}), lipid content (mg cm^{-2}), mitotic index (%), polyp density (polyps cm^{-2}), protein (mg cm^{-2}), *Symbiodinium* density (cells cm^{-2}), tissue thickness (mm), total biomass (mg cm^{-2}),

dark aerobic respiration ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$), and maximum rate of photosynthesis ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$) (Table 1). We used these data to assess phenotypic differences among groups of corals exemplifying the functional group concept for this taxon (e.g., Loya et al. 2001). We first contrasted massive *Porites* spp. and *Acropora* spp. that represent the concept of ecological winners and losers, respectively (Loya et al. 2001; van Woesik et al. 2011), and rejected the null hypothesis of no difference between taxa for six traits (biomass, tissue thickness, linear extension, photosynthesis, chlorophyll-*a*, and calcification; $t > 2.222$, $df \geq 9$, $P \leq 0.034$); six additional traits did not differ between these genera ($t \leq 0.917$, $df \leq 44$, $P \geq 0.128$). The weak phenotypic discrimination among coral taxa that have been extensively studied for the select traits was revealed when they were clustered based on similarities generated from all 12 traits (Fig. 1). Hierarchical clustering was conducted (with Primer 6 software) using Gower similarity of group averages based on maximum standardized mean trait values across genera. Similarity profile permutations tests (SIMPROF) identified no statistically significant clusters ($\pi = 1.315$, $P = 0.8$). Even though the database had grown 4.6-fold for all records of the aforementioned traits compared to our previous work (Edmunds et al. 2011; Electronic Supplementary Material 1) and is now focused on 6 genera, we were unable to show that ecologically distinct taxa differed in terms of their multivariate phenotypes.

The inability to link empirical trait values to ecological success in reef corals prompted a re-evaluation of the criteria used to define winning and losing corals, and the utility of linear reasoning to couple trait values with performance.

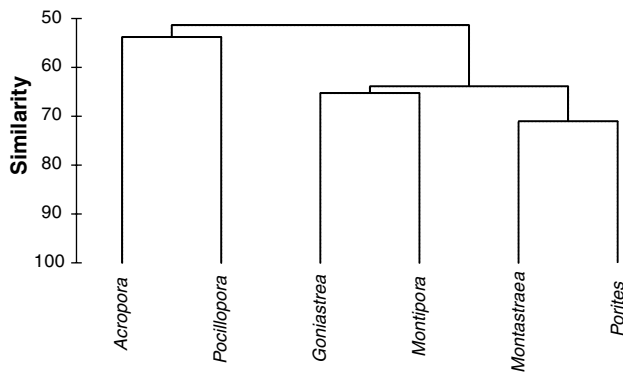


Fig. 1 Hierarchical clustering dendrogram based on mean values for 12 traits obtained for 6 coral genera that have been reported in peer-reviewed literature and linked to stress responses (Online Supplementary Material 1). Hierarchical clustering is based on Gower similarity of group means of maximum standardized mean trait values across genera (PRIMER v6; Clarke and Gorley 2006) where nodes show similarity groupings

This re-evaluation identified four important constraints on progress toward characterizing ecological success in corals, or more generally, phenotypically characterizing ecologically meaningful functional groupings of corals:

1. Defining winners and losers based on changes in abundance (percent cover or number of colonies) provides a poor indicator of ecological performance measured in a demographic currency.
2. The relationships between fine-scale physiological traits, coarse-scale coral characteristics (e.g., differences among genera or morphologies), and ecological responses are complex and nonlinear.
3. There is no theoretical construct for scleractinians to inform a mapping of fine-scale physiological traits onto coarse-scale coral characteristics, particularly in the context of multivariate physical forcing.
4. Synthesis of phenotypic data for scleractinians is impeded by a lack of more uniform methodology, common units, and effective model taxa that can be used to generate continuously distributed values of physiological traits.

Step 2: A demographic approach for coupling organismic performance to ecological success in the scleractinia

The benefits of a demographic approach to identifying winning and losing corals

The extent to which scleractinian corals achieve ecological success (i.e., win) or failure (i.e., lose) ultimately will

be reflected in their population dynamics. Therefore, principles of population persistence derived from population models (Caswell 2001) can be applied to this task. Specifically, over ecological time, populations of winning and losing corals should be defined by population growth rates that are above and below replacement, respectively. Each adult must, on average, replace itself with one offspring during its lifetime in order to function as a “winner.”

Models of coral populations often have derived population growth from age- or stage-structured representation of population dynamics using (standard or modified) Leslie matrices, which contains information on age- or stage-dependent survival and reproduction (e.g., Hughes 1984; Fong and Glynn 1998, 2000; Hughes and Tanner 2000; Edmunds and Elahi 2007). In Leslie matrices, the parameter defining population growth without density dependence is given by the dominant eigenvalue of the matrix, denoted as λ (Caswell 2001). Once the population achieves a stable age/stage distribution (indicated by the eigenvector corresponding to the eigenvalue λ), the population grows or shrinks by a constant factor (i.e., λ) at each time interval. In a currency that is mechanistically related to “ecological success,” winning corals can therefore be defined rigorously by $\lambda > 1$ and losing corals by $\lambda \leq 1$ (Caswell 2001). A demographic approach to defining ecological success offers advantages over common measures of abundance (like percentage cover), which are related only loosely to demographic processes (Hughes and Tanner 2000; Edmunds and Elahi 2007; Darling et al. 2013). Stable coral cover can, for example, hide impending population decline (Hughes and Tanner 2000), and categorizing corals based on changes in cover (Loya et al. 2001; Edmunds et al. 2014) has the potential to generate functional groupings with equivocal ecological relevance.

The potential utility of a demographic approach to comparing ecological success among coral species can be seen in other biological systems where similar approaches have been applied. λ has a strong history as a means to evaluate population performance and viability (Caswell 2001), with examples coming from many taxa as diverse as grizzly bears (Mace and Waller 1998), whales (Fujiwara and Caswell 2001), spotted owls (Noon and Biles 1990), ungulates (Coulson et al. 2005), sea turtles (Crowder et al. 1994), precious octocorals (Bramanti et al. 2009), Tasmanian devils (Lachish et al. 2007), and plants (Ramula et al. 2008; Crone et al. 2011). In terrestrial plants, for example, much demographic data are available to assess the patterns and process of population growth. Buckley et al. (2010) synthesized demographic models having both spatial and temporal replication from 50 species, with multiple populations (≥ 2) per species and multiple matrices (≥ 2) per population. They identified the species for which population growth rates declined through time, as well as the sources

of variation in population growth rates among species. Temporal variation in population growth rates was mostly due to variation in post-seedling survival (rather than adult fecundity), herbivory, and fire (Buckley et al. 2010). An analysis such as that utilized by Buckley et al. (2010) could be used to good effect with tropical reef corals, specifically to identify ecological winners and losers in communities exposed to disturbances such as storms, predatory sea stars, thermal stress, and OA.

Compared to research in other systems, demographic studies on corals are rare. Only a handful of studies have quantified λ (e.g., Hughes 1984; Hughes and Tanner 2000; Edmunds and Elahi 2007; Edmunds 2011; Hernández-Pacheco et al. 2011; Madin et al. 2012b), despite long-standing efforts to promote demographic analyses of this important taxon (Connell 1973; Hughes and Jackson 1985; Hughes 1996). The implications of the scarcity of studies on the demography of scleractinian corals are now being felt acutely as biologists focus on determining which corals might function as winners or losers, as well as the causal basis of these outcomes, in an era of strong effects of GCC and OA (Hoegh-Guldberg 2012). While there are several studies that associate ecological success with mean trait values (Darling et al. 2012, 2013), or model the influence of environmental and biological traits on fecundity (Madin et al. 2012a), most efforts have favored phenomenological links among the functional levels and have not explicitly addressed the conditions favoring population persistence (e.g., those involving λ).

Integral projection models (IPMs) for corals

A promising way to integrate organismal-level performance with population-level outcomes is through an integral projection model (IPM [Easterling et al. 2000; Coulson 2012]). IPMs evaluate the role of continuous traits in driving population dynamics and create the potential to scale up the effects of GCC and OA on individual-level performance to evaluate population-level consequences. IPMs are an extension of discrete time, discrete age/stage models based on the Leslie matrix. While Leslie matrices are based on discrete classes, IPMs accommodate continuous classes or states (e.g., continuously distributed size) in a predictive framework (in discrete time, as in the Leslie matrix). IPMs share many of the features that have made matrix projection models popular: estimation of population growth (λ), state-specific reproductive values, the stable population phenotypic distribution, and identification of the parameters to which λ is most sensitive. Furthermore, IPMs are a better representation of transient dynamics than traditional discrete matrix models, because demographic rates change in a gradual, rather than abrupt, manner across an organism's life history. IPMs also perform better for small

datasets (<300 individuals) than traditional matrix models because they require fewer parameters to describe vital rates of a population's growth, which are integral in the calculation of λ (Ramula et al. 2008). To date, IPMs have not been applied widely to scleractinians (but see Burgess 2011; Madin et al. 2012b), or to other "corals" (i.e., octocorals, Bruno et al. 2011).

We describe how IPMs can be used to identify winning and losing corals as well as the physiological traits driving these ecological outcomes (Fig. 2; Box 1). The IPM is a relatively well-developed technique, and it is not our goal to provide a comprehensive description of the theory and mechanics of IPMs. Furthermore, the flexibility of constructing the IPM means that we would do it injustice if we set about providing a simple "recipe." Therefore, we assume the reader has some familiarity with IPM methodology and assumptions (e.g., as described in Easterling et al. 2000; Ellner and Rees 2006, 2007; Rees and Ellner 2009; Coulson 2012); without this basic knowledge, the flexibility of IPMs may give the wrong impression that they are complicated. Finally, we note that any difficulties involved with obtaining the necessary data for applying IPMs to corals should not detract from the importance of assessing winning and losing corals in a demographic framework.

The simplest representation of an IPM involves a description of the number of individuals $n(y, t + 1)$ at time $t + 1$ with a given state y as a product of the number of individuals $n(x, t)$ at time t with state x and a kernel $k(y, x, \theta(t))$ representing all possible transitions from state x (in time t) to state y (in time $t + 1$) under the environment $\theta(t)$, integrated over all states x :

$$n(y, t + 1) = \int k(y, x, \theta(t))n(x, t)dx. \quad (1)$$

The kernel, $k(y, x, \theta(t))$, is analogous to the projection matrix (e.g., Leslie matrix). While there is flexibility in the mathematical definition, it is typically expressed as the fecundity $f(x, y, \theta(t))$ of individuals of state x producing those of state y plus the product of the survival $s(x, \theta(t))$ of those in state x and the growth $g(x, y, \theta(t))$ from state y to state x :

$$k(y, x, \theta(t)) = f(x, y, \theta(t)) + s(x, \theta(t))g(x, y, \theta(t)). \quad (2)$$

$\theta(t)$ describes the environment as it affects growth, fecundity, and survivorship. In essence, the functions describe how individuals with states enter the population (through birth and immigration), leave the population (through death and emigration), and how the state of an individual changes through time (e.g., growth from one time step to the next causing a transition between size classes). The functions can be generated from statistical models fit to empirical data and, therefore can be linear, nonlinear,

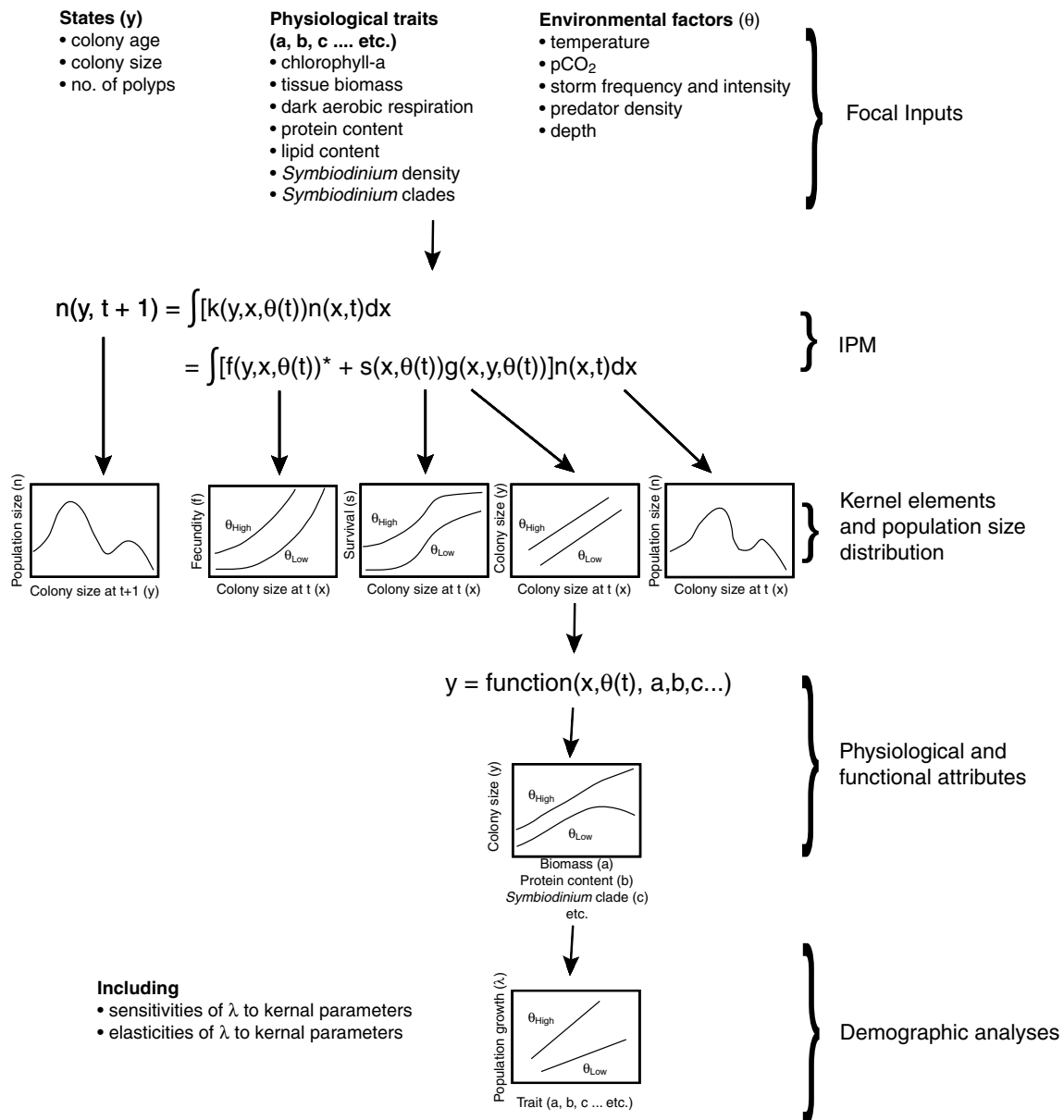


Fig. 2 Schematic illustrating the application of an integral projection model (IPM) to corals to link holobiont physiology, individual colony-level performance (i.e., survival, growth, and fecundity), and population-level (demographic) outcomes (i.e., population growth, λ) as a function of environmental factors (θ). The population is structured by colony states [y] (e.g., colony size), which vary among individual corals. The colony state of each individual determines the individual’s fecundity (f), growth/fission (g), and survival (s), generating the kernel elements (k(y,x,θ(t))) of the IPM. In this example, physiological traits [a, b, c, etc.], and environmental factors [θ], determine vital demographic rates (i.e., kernel elements) through their effects on the colony states. Physiological traits can affect the multiple kernel elements independently or interactively through multiple pathways. Shown here for clarity is just the effect of attributes such as biomass,

protein content, and *Symbiodinium* clades on colony growth. We display the relationships in each kernel for two sets of environmental conditions (θ_{high} and θ_{low}, e.g., high and low water temperature) for illustration, but environmental conditions can be discrete or continuous. Kernel elements are used to evaluate population growth (λ), from low population density, as a function of environmental conditions and physiological traits (“Demographic analyses”). Additional analyses can determine the sensitivity and elasticity of the population growth factor to changes in the parameters defining the kernels; refer to text and Box 1 for further details. *This term is replaced with r(x,y) in an open population. a, b, c... etc., a variety of physiological traits and functional attributes that can affect demographic rates, n number of colonies, y size of colony at time (t) t + 1, x = size of colony at time t

additive, or nonadditive, or derived from mechanistic models (e.g., DEBs, Edmunds et al. 2011) explicitly modeling how energy is converted into growth and fecundity (Fig. 2). Growth can be measured in ways most relevant to the morphology and physiology of the study species, and can include linear extension, change in surface area, increase in biomass, or calcification. The fecundity kernel incorporates all the processes from larval release to recruitment.

In the mathematical terms implementing how the environment affects growth, fecundity, and survivorship, previous representations of IPMs (e.g., Rees and Ellner 2009) have implemented $\theta(t)$ as stochastic environmental variation based on the distribution of data around growth, fecundity, and survivorship relationships. To understand the response of corals to future environmental change, however, $\theta(t)$ might represent a predictably changing environmental variable that influence these kernel elements. For example, if $\theta(t)$ is a representation of OA (e.g., pCO₂), then it might alter the growth rate through time, while $\theta(t)$ representing temperature might affect how a temperature-dependent change in symbiont density or genetic composition influences bleaching susceptibility. Under multiple environmental changes, $\theta(t)$ then becomes a vector where each element represents a different aspect of the environment. To illustrate this overall approach, we provide an example that connects coral size distribution dynamics to OA in Box 1.

Incorporating physiology into a coral IPM

Coral physiological characteristics (Table 1), or any other types of coral characteristics that connect environmental change to coral colony performance, can enter into the IPM in a number of ways (Box 1 is just one example). For physiological traits that vary among populations or species, the trait for a given population or species might drive the shape of the IPM kernel (e.g., faster growth for corals in habitats allowing faster calcification) and allow comparison of expected coral dynamics among populations or species. In this case, the physiological trait is a property of the whole population (or species) and it modifies the parameters that define the kernel elements for that population. For example, coral populations in shallow water may have a different genetic compliment of *Symbiodinium* than coral populations in deeper water. If *Symbiodinium* composition alters the slope of the colony growth function (or any other function in the kernel elements), then the effects of changing *Symbiodinium* composition on the dynamics of multiple populations (or species) can be predicted.

For traits that vary continuously within populations (i.e., among individuals), the physiological trait can enter into the IPM in a number of ways. The trait itself might be a component of the state y , in addition to size, that directly

affects survival, growth, or fecundity, such that the model captures the joint distribution of colony size and that trait in the population. In such a case, for example, survival, growth, or fecundity might vary depending on the population density or genetic variation in the endosymbiotic *Symbiodinium* and, therefore, would also be influenced by interactive effects with a variety of other factors including seawater temperature and colony size. Another way in which the physiological trait can enter into the IPM is by its indirect affects with colony size. For example, Madin et al. (2012a, b) modeled a size-structured coral population with environment-dependent reductions in calcification that reduced skeletal density, which in turn decreased the survival of larger colonies due to dislodgment during storms (i.e., survival was a function of colony size, given its skeletal density). Finally, for traits that vary both within and among populations (as is the case for the traits in Table 1), then a combination of the two approaches is feasible (e.g., dynamically following *Symbiodinium* density within populations as part of state y , where the maximum density might vary with species).

How physiological characteristics are described in the function of the IPM depends on the research question and the extent of the basic knowledge of the physiology of the study species. The IPM is flexible enough to handle many different configurations of the pathways by which physiology affects growth, survival, or fecundity, and has the potential to consider the effects of the host and *Symbiodinium* (including genetic variation in these algae) independently.

Some considerations in applying IPMs to corals

There are several issues that need to be considered when applying IPMs to corals, but these issues have solutions that render IPM approaches highly attractive for corals. As with previous coral matrix models (Hughes and Tanner 2000; Fong and Glynn 1998, 2000; Edmunds and Elahi 2007), the growth function $g(x,y,\theta(t))$ in a coral IPM needs to also account for fragmentation and fission that occur in many coral species. The implication is that the growth function will have to allow for negative growth, and the individuals (ramets) arising from fragmentation will have to be added to $n(y,t + 1)$.

Another particularly important issue to consider is the spatial scale at which inferences regarding winning and losing corals are to be made in relation to the spatial scale of larval dispersal. This determines whether a population is closed (e.g., where input into the local population is linked directly to reproductive output of the population) or open to immigration from other sources (where local recruitment is uncoupled from local reproductive output). The extent to which a population is open or closed to larval input from

other populations will determine whether fecundity needs to be estimated, and how local fecundity is linked to local recruitment. Previous applications of IPMs to plants and ungulates have not included dispersal, so the study populations were considered “closed.” In contrast, at the spatial scale of a local coral reef (i.e., ≤ 20 km [Mittelbach et al. 2001]), or a typical coral field study, most coral populations might be considered “open,” or at least partly open, to immigration of larvae from other nearby reefs.

Most previous applications of matrix models to coral populations assumed that recruitment into the population was uncoupled from fecundity (Hughes and Tanner 2000; Edmunds and Elahi 2007). In such cases, the projection matrix omitted fecundity and just included transitions between size classes (i.e., survival and growth) with recruitment included as a constant (Box 1), whose value is determined empirically in the field, and can be space-dependent (Roughgarden et al. 1985). Madin et al. (2012a, b) applied IPM to both open and closed coral populations (see also Box 1). In summary, in a closed population, the fecundity kernel needs to be estimated; in an open population, the fecundity kernel is replaced by the recruitment kernel, which describes the number of recruits of a given size into the population. Importantly, the IPM framework can describe a “semi-open” population with emigration and immigration (Coulson 2012), although this adjustment increases the quantity of data required for the model. Ideally, some estimate of local larval retention should be obtained (see Burgess et al. 2014 for more details).

Obtaining data for an IPM

To prepare an IPM and use it for the purpose we propose, it is necessary to (1) identify the traits that contribute most to coral growth, survival, and reproduction; (2) describe functions relating such traits to growth, survival, and reproduction, as well as their environmental dependencies; and (3) calculate λ and evaluate how sensitive it is to changes in the parameters describing the relationships between traits and vital rates (e.g., Box 1, Online Supplementary Material 2; see supplement of Ellner and Rees 2006 for another example with R code). In many cases, fundamental principles of biology or the basic biology of the Scleractinia and their *Symbiodinium* symbionts can be used to inform the choice of proximal traits that are informative with regard to variation in growth, survival, and reproduction, and whether traits vary across populations or species, or vary continuously within populations. For instance, the size of coral colonies, which varies among individuals, is a critical feature determining whole-colony fecundity (Hall and Hughes 1996), the probability of dislodgement during storms (Denny et al. 1985; Massell and Done 1993; Madin and Connolly 2006), and the mass transfer

of key metabolites that can affect the availability of energetic resources required for reproduction (Patterson 1992; Hoogenboom and Connolly 2009). Likewise, it is becoming increasingly clear that genetic variants of *Symbiodinium* hosted by different individuals, populations, or species of corals have important roles in determining the fitness of the holobiont (Putnam et al. 2012). As we describe above, incorporating into IPMs the physiological consequence for the holobiont of hosting multiple, dissimilar, or changing combinations of genetically distinct *Symbiodinium* spp. is an important research objective in order to realize the full potential of these tools. Currently, this objective is beyond the scope of what can be accomplished with the state of the empirical and theoretical literature.

Obtaining the data in the field necessary to support an IPM approach requires an effort similar to that necessary to monitor permanent areas of reef (Hughes 1996; Burgess 2011; Bruno et al. 2011; Coulson 2012). One critical difference in comparison with much of the contemporary monitoring efforts on coral reefs is that the fate of individual colonies needs to be recorded, rather than changes in percent cover of species or groups of species. Monitoring individual colonies is inherently more time-consuming than measuring area (or percentage cover), because it requires censusing individuals at two or more points in time. Furthermore, delineating colonies (especially individual ramets belonging to a clonal genotype [a genet] that reflect fragmentation rather than sexual recruitment) will be more difficult for some species (e.g., *Acropora cervicornis* and *Porites irregularis*) than others (e.g., *Orbicella* [formerly *Montastraea annularis* complex, and *Acropora hyacinthus*). Indeed, the scarcity of demographic studies on corals exists, in part, because of the difficulty in attributing changes in colony size to growth, fusion, fission, recruitment, and partial mortality at the data collection stage. In a practical sense, the utility of applying IPMs to corals will be limited to some extent by the growth form of the study species, which influences how data collected in the field (such as circumference, length, height, and 2D surface area) relate to physiologically relevant metrics of size (such as biomass).

Analysis of the IPM: what can an IPM tell us?

Once each element of the IPM kernel has been defined, numerical representation of the kernel provides a matrix of conversion from state(s) x to state(s) y that can be treated in a manner analogous to a Leslie matrix (e.g., Easterling et al. 2000; Ellner and Rees 2006, 2007; Rees and Ellner 2009; Coulson 2012). Specifically, after discretizing the continuum of possible states into bins of size Δx and analyzing the kernel across the matrix of all possible combinations of x and y (defined at the midpoints of their bins),

the resulting matrix of $k(x,y,\theta(t))\Delta x$ represents the transition matrix for each time step. The leading eigenvalue (λ) of this matrix then is the population growth factor, the corresponding right eigenvector v is the vector of size- or physiological state-specific reproductive values, and the corresponding left eigenvector w is the stable population phenotypic distribution. See Online Supplementary Material 2 for a detailed description of this analysis. The eigenvalue and eigenvectors can be interpreted in this way under the assumption that the population has reached a stable age/size/phenotype distribution.

Rather than using λ to evaluate “what if” scenarios (Crone et al. 2011), or to make projections into the future (i.e., as in traditional matrix models [Hughes and Tanner 2000; Edmunds and Elahi 2007]), the most useful information that an IPM reveals is how changes in the relationship between physiology and performance (e.g., survival, growth, and fecundity) influence long-term population growth rate (at low density). This is done by perturbing the model to examine how model predictions vary as model parameters are altered, with these procedures termed sensitivity analysis (perturbations in absolute units; $d\lambda/dp_i$ for each parameter p_i , given by $v(y_1)w(y_2)/\langle v, w \rangle$ for sensitivity to the transition from state y_2 to state y_1) and elasticity analysis (perturbations in proportional units; $p_i d\lambda/(\lambda dp_i)$, given by $k(y_1, y_2)v(y_1)w(y_2)/(\lambda \langle v, w \rangle)$ for sensitivity to the transition from state y_2 to state y_1 ; Caswell 2001).

Perturbation analysis in previous matrix models or IPMs in other systems suggests that the patterns of variation in the demographic parameters contributing to λ are likely to be more complex (e.g., Franco and Silvertown 2004) than the simple classification of corals into a few dimensions (e.g., Darling et al. 2012, 2013). In other words, two coral species with similar mean colony growth rates, for example, may have very different contributions of survival, growth, and fecundity toward their overall λ . A demographic approach to link variation in continuous traits to ecological success allows for an assessment of whether species with similar mean trait values have different population growth rates. Furthermore, some mean trait values related to competitive ability or stress tolerance, for example, may be different between two species, but make a similar relative contribution toward λ in both species (Franco and Silvertown 2004; Coulson et al. 2005). Previous analyses on Soay sheep and Yellowstone wolves, for example (Coulson et al. 2010, 2011), show that a wide range of population responses is possible depending on which parameter is perturbed. Furthermore, depending on which parameter is influenced by environmental change, almost any type of population change can occur. With Yellowstone wolves, for example (Coulson et al. 2011), the population growth rate was more sensitive to changes in the shape and variation in the growth and trait inheritance function than of the

survival and recruitment function. Furthermore, altering the mean environment had greater population-level consequences than changing the variability in environmental conditions. Sensitivity and elasticity analyses can be more useful at informing management decisions because, as opposed to the predictions of population numbers that try to forecast the future, such analyses identify which demographic processes are most important to the future, and therefore where management efforts might be most effective (Crouse et al. 1987; Crone et al. 2011).

IPMs allow questions like “How are population dynamics influenced by reductions in calcification rate” to be addressed (e.g., Madin et al. 2012b; Box 1), which clearly is relevant to evaluating the ecosystem-level consequences of OA. Reductions in calcification rate can reduce skeletal density and increase the vulnerability of larger colonies to dislodgment during storms (Madin et al. 2012b). Additionally, depressed calcification also reduces colony growth rates, which in turn reduces survival and reproductive rate, since colonies will be smaller, less fecund, and remain in more vulnerable size classes for longer than under normal growth rates (Madin et al. 2012b).

Codifying the construct and future research

We do not present novel theory or methods, but instead advocate the application of emerging quantitative approaches from other systems (Crone et al. 2011; Coulson 2012) to scleractinian corals. We have been motivated in this effort by the striking changes that have taken place on tropical reefs, specifically leading to the widespread reduction in cover of scleractinian corals (Bruno and Selig 2007; Déath et al. 2012), as well as reductions in coral linear extension, potentially as a consequence of increased seawater temperature and OA (Déath et al. 2009). These changes have, in part, fueled a growing emphasis on identifying the winners and losers among the coral fauna on contemporary and future reefs in warmer and more acidic seas (Fabricius et al. 2011). This emphasis has been characterized by limited progress in evaluating the causal basis of ecological success or failure among coral taxa (Loya et al. 2001), and therefore provides a compelling context within which new approaches can be proposed. It is widely accepted that “weedy” corals will fare better than “non-weedy” corals on the reefs of tomorrow (Knowlton 2001), and that thermal resilience will be critical for survival in a warmer future (Brown and Cossins 2011; Edmunds et al. 2014). These traits, however, have not been evaluated in the context of impacts on long-term demography such as the population growth factor λ , nor have they been evaluated for relative importance against one another. We advocate the application of a demographic approach, where IPMs are

just one example [see de Roos and Persson (2012) for other examples linking individual-level process to population dynamics] that couple trait-based analyses to demographic approaches for scleractinian corals, and suggest it can serve as an effective template for further research. We do not imply this is the only template that can advance studies of the causal basis of winning and losing among scleractinian corals on contemporary reefs. Rather, we propose that a demographic approach is essential to overcome the impasse to progress in coupling organismic performance to population success under future climate change. Given the daunting prospect of collecting the empirical data necessary to prepare IPMs for reef corals, it is clear that properly understanding the mechanistic basics of future coral community structure remains difficult and represents a topic where shortcuts are unlikely to reveal profoundly useful discoveries. Coral reef biologists will need to rise to this challenge in order to make robust progress toward understanding the future of coral reefs. Such progress has been clearly demonstrated in other biological systems, and there is reason to expect this success can be transferable to coral reefs.

We hope that by identifying the lack of existing data as an impediment to illustrating our proposed framework with an empirical example, we can emphasize that there is much work to be done in the future. To advance a demographic approach, we recommend that experimental investigations of scleractinian corals should focus on three themes:

- I. Given the complexity of the hierarchical studies we are advocating, it will be increasingly important to focus initial efforts on coral species for which comprehensive data can be obtained. The construction of multi-factorial analyses of response variables coupled to λ is exceptionally challenging and would benefit from a major research initiative supported through different laboratories. The judicious selection of study species may facilitate access to a large quantity of legacy data that could accelerate progress in the construct illustrated herein. As model species become better studied, the taxonomic breadth of the analyses can be expanded to test other species for traits favoring greater capacity to respond in favorable ways to environmental challenges.
- II. Our perusal of the literature in support of Step 1 of this paper underscored the difficulty faced with legacy data. Some of the limitations associated with these data can be solved by careful attention to measurement units and appropriate normalization. We have found data on a percentage scale among the most difficult to combine in synthetic analyses, and for this reason discourage the use of this scale. Associated with the quality of data that can be mined from legacy studies is the problem of accessing records, and we therefore recommend

the establishment of a global open-access database for coral physiological data (e.g., www.coraltraits.org).

- III. We believe the approach we advocate has the potential to advance the identification of demographically successful taxa among the scleractinian fauna of contemporary coral reefs. This process is critical if we are to understand in what form the reefs of the future will exist, and what functional attributes will characterize the ecological goods and services provided by these ecosystems. The potential of this approach will only be realized if physiological studies are designed with an eye to inform the causal basis of demographic rates.

Box 1

Elements of an IPM for corals

Here, we provide an example functional form for fitting data to construct a coral IPM. This example is included for illustration, and the exact functional form of the IPM might vary with the coral and environmental factor(s) under consideration. First, we indicate how a basic coral IPM can be constructed for a stable environment, and then indicate how this model might extend to include a variable environmental factor. In Electronic Supplementary Material 2, we indicate the numerical tools for analyzing such an IPM.

Basic IPM

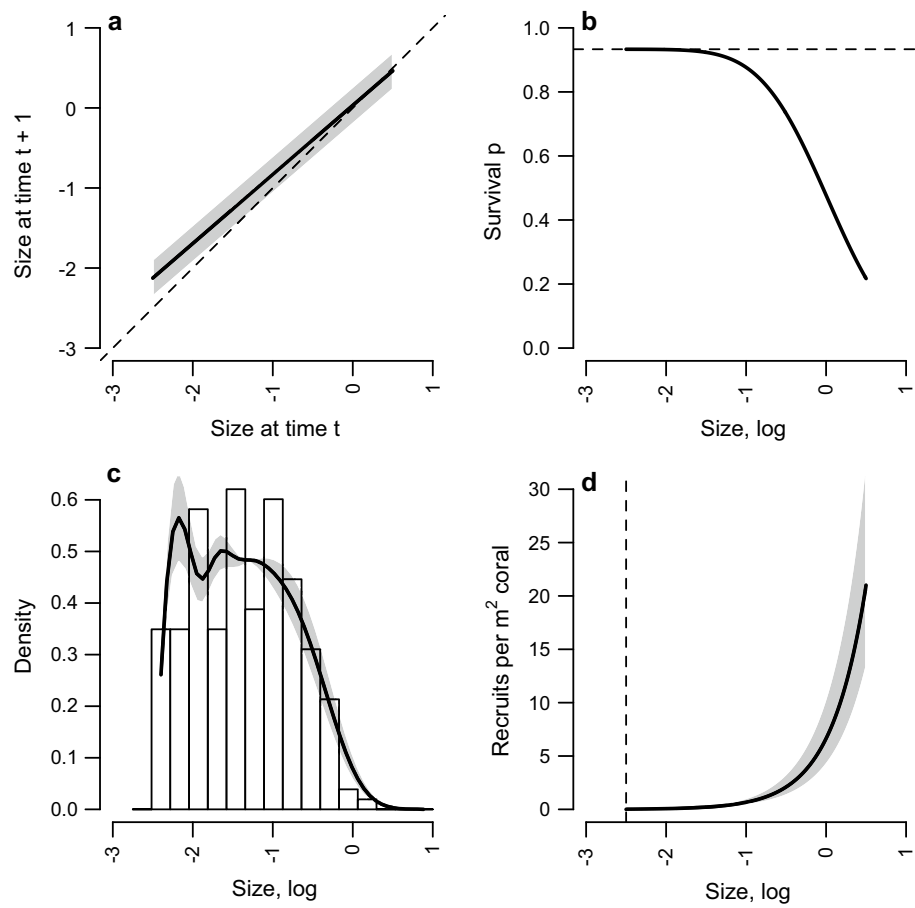
A coral IPM requires data relating colony size in 1 year to size (through growth, stasis, or shrinkage) and survival probability and contribution of offspring to the population in the following year (Eq. 2). Growth and mortality relationships can be calculated by measuring survival and changes in colony size in consecutive years. Growth is captured best with a power function because it is multiplicative (Fig. 3a), which also means that the IPM will operate more effectively on log-transformed size data, resulting in a linear function for the probability of growing from x to y during the year:

$$g(x, y) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(y-(mx+c))^2}{2\sigma^2}}$$

Size-independent survival processes can be captured as probabilities with error, $b + \varepsilon$ (dashed line, Fig. 3b), whereas size-dependent survival processes can be captured as a logistic function (solid curve, Fig. 3b). Combining the two gives

$$s(x) = (b + \varepsilon) \logit^{-1}(mx + c + \varepsilon).$$

Fig. 3 Example relationships describing the ways by which size translates into organismic and demographic properties required in the preparation of an IPM: **a** growth, **b** survival, **c** population density, and **d** recruitment



while colony fecundity is typically a function of size (i.e., number of polyps; Hall and Hughes 1996), many coral species are broadcast spawners, and so contributions to the recruitment from inside and outside the population are difficult to estimate. If modeling the population as an open system where recruitment is constant independent of the local population, the IPM intrinsic growth rate (λ) measured in the absence of this recruitment will indicate population decline, because the population has no intrinsic capacity to sustain itself. This rate of population decline can be used as a common currency when comparing environmental change scenarios. However, if the outside recruitment rate q can be estimated and/or expected to be associated with environment, then the population can be projected through time until it reaches a stable growth factor and size distribution for different environmental scenarios, using

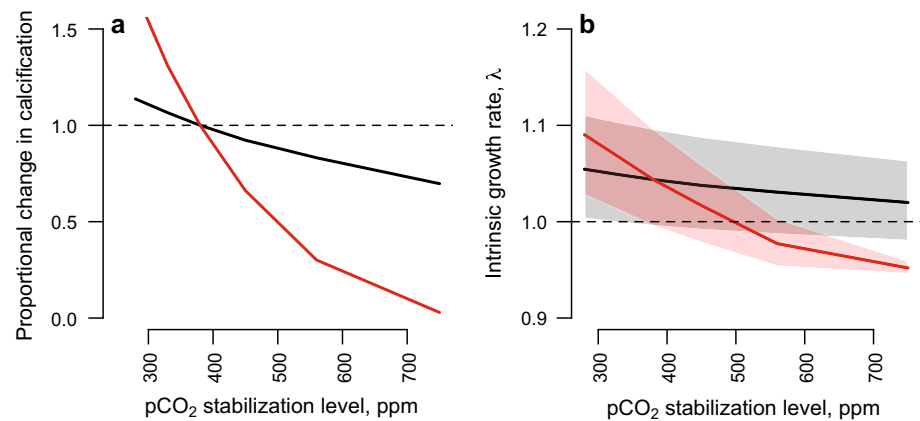
$$r(y) = q \quad \text{if } y \leq \text{recruitment size}$$

Then, the relative cover (i.e., the sum of colony areas) of populations for different scenarios can be contrasted, providing another common currency. This relative cover approach is problematic, because it compares populations that are limited by recruitment, but does not incorporate density-dependent processes, such as competition.

When modeling the population as a closed system where all recruitment depends on the local population size, the IPM intrinsic growth rate is a currency for the propensity for the populations to recover from low abundance such that density-dependent factors are negligible (e.g., following a storm, bleaching episode, or COTS outbreak). This definition of λ is equivalent to population (or engineering) resilience (Madin et al. 2012a, b) and makes no assumptions about the onset to density-dependent processes as space on the reef saturates. Closed system modeling can be justified if interconnected populations all tend to occupy similar habitats and environmental changes operate at scales larger than the meta-population, and therefore affect all populations similarly. In this case, a closed meta-population model will provide an approximation for local dynamics. Assuming a constant environment, an individual's contribution to recruitment q (recruits per unit colony area) can then be varied until the IPM stable size distribution (first eigenvector) best fits the empirical size distribution (Fig. 3c, d).

$$r(x, y) = \begin{cases} qx & \text{if } x > \text{recruitment size and } y \leq \text{recruitment size} \\ 0 & \text{if } x \leq \text{recruitment size} \end{cases}$$

Fig. 4 Relationships describing the ways by which increasing pCO₂ might be translated into calcification rates (a) and rate of population growth (b) for corals categorized as losers (black line) or winners (red line)



Once the recruitment parameter q has been estimated, the stable population growth factor (λ) can be calculated. In reality, recruitment within most coral populations will lie between the extremes of complete independence or dependence on local demography. Altering the recruitment function accordingly can model such a system where the data are available for parameterization.

Integrating environmental effects on physiological traits

Environmental variables (e.g., ocean pH) that influence physiological traits (e.g., calcification and cellular chemistry) can be manipulated experimentally to determine their effects on different demographic rates (e.g., growth, mortality, and fecundity). In some cases, the effect of environment on demographic rates can be estimated mechanistically (e.g., storm intensity on mechanical survival probability, Madin and Connolly 2006). Mechanistic effects are preferable, because they can be expected to operate similarly in novel environments (i.e., environments not considered in manipulative experiments) (Kearney et al. 2010).

For an example, we explore the effects of decreasing calcification rates in the future, a physiological trait that is responsive to increasing in sea surface temperature (SST) and decreasing aragonite saturation state (Ω_{arag}) due to OA (Anthony et al. 2008). For brevity, we illustrate the IPM approach using one of the scenarios modeled by Madin et al. (2012a), in which declining calcification impacts growth rate (i.e., material density is not affected, and therefore the mechanical integrity of coral skeleton and reef substrate is constant). Figure 4a shows how calcification rate is expected to change for two existing relationships of calcification with SST and Ω_{arag} (Anthony et al. 2008; Silverman et al. 2009), at least based on existing estimates of SST and Ω_{arag} for future pCO₂ stabilization scenarios (Cao and Caldeira 2008). Relative changes in future calcification rate are applied directly to mean growth probability (i.e., the intercept c in the growth function):

$$g(x, y, \theta(t)) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(y-(mx+c(\theta(t))))^2}{2\sigma^2}}$$

The population growth factor (λ) is plotted for the two coral calcification response scenarios as a function of stabilized atmospheric pCO₂ (Fig. 4b). Confidence intervals (shaded bands around the lines) reflect many sources of uncertainty, primarily the fitted recruitment parameter q . This coral species is predicted to become a “loser” for the red-colored calcification response scenario when pCO₂ levels reach approximately 500 ppm; it is predicted to remain a “winner” on average for the black-colored calcification response scenario.

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