Integrating the Effects of Ocean Acidification across Functional Scales on Tropical Coral Reefs

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Abstract:	There are concerns about the future persistence of coral reefs in the face of ocean acidification and warming, and while studies of these effects have advanced in the last decade, efforts have focused on pieces of the puzzle rather than integrating the pieces to evaluate ecosystem-level effects. The field is poised to begin this challenging task, and here we identify important information gaps at the functional levels of cells, organisms, populations, communities, and ecosystem that must be addressed to achieve the goal of integration. Addressing these gaps inherently is difficult for corals reefs that are complex systems whose response to ocean acidification is characterized by a suite of interdependent processes acting at multiple functional levels. Yet there are theoretical tools that can be embraced to good effect to understand how this ecosystem will respond to ocean acidification based on what is known of the functional biology of their component pieces.

Integrating the effects of ocean acidification across functional scales on tropical coral reefs

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Abstract

There are concerns about the future persistence of coral reefs in the face of ocean acidification and warming, and while studies of these effects have advanced in the last decade, efforts have focused on pieces of the puzzle rather than integrating the pieces to evaluate ecosystem-level effects. The field is poised to begin this challenging task, and here we identify important information gaps at the functional levels of cells, organisms, populations, communities, and ecosystem that must be addressed to achieve the goal of integration. Addressing these gaps inherently is difficult for corals reefs that are complex systems whose response to ocean acidification is characterized by a suite of interdependent processes acting at multiple functional levels. Yet there are theoretical tools that can be embraced to good effect to understand how this ecosystem will respond to ocean acidification based on what is known of the functional biology of their component pieces.

Introduction

The history of investigating the effects of ocean acidification on coral reefs is short, with initial studies appearing in the 1990's, and the first syntheses appearing in the new millennium (Kleypas et al. 2005, Gattuso and Hansson 2011). Most studies address the effects of ocean acidification on single species of corals and calcified algae in tanks (e.g., Gattuso et al. 1988, Langdon et al. 2000, Ries et al. 2009) and in situ (e.g., Kline et al. 2012), with a few addressing reef communities in mesocosms (e.g., Andersson et al. 2009, Dove et al. 2013, Comeau et al. 2015), or in situ near CO_2 vents (e.g., Fabricius et al. 2011) or areas of low pH (Barkley et al. 2015). In this paper we consider the challenges of integrating empirical studies conducted at a single functional scale to obtain a broader understanding of the effects of ocean acidification on coral reefs, and we propose experimental and theoretical means by which these challenges can be overcome. Without progress in these areas, it will remain impossible to integrate results from lower functional scales (e.g., species) to larger functional scales (e.g., communities and ecosystems) to predict how coral reef ecosystems will respond to ocean acidification. This is a general issue affecting ocean acidification research (Riebesell and Gattuso 2015, Andersson et al. 2015), but it has strong implications for coral reefs, where our capacity to predict whether they will maintain a positive balance between deposition and dissolution of $CaCO_3$ (i.e., to persist as a calcified ecosystem) requires consideration of scaling effects.

A defining feature of biological systems is the way in which multiple functional components sum to emergent properties that are not apparent at lower levels. In mutualistic symbioses, for example, the biology of the holobiont cannot be understood from the biology of the symbiotic partners, for it is their metabolic, functional, and structural interactions that change through an association of their individual biological traits (Edson et al. 1981, Brown et al. 2004). Phototrophic mutualisms like most reef corals illustrate this principle, for the combination of an animal host and algal symbiont facilitates nutritional polytrophy and nutrient recycling, which cannot be realized by the symbiotic partners in isolation (Stambler 2011). Likewise, ecosystems achieve emergent properties through resilience, stability, and metabolic functionality that cannot be determined by summing effects on the species from which they are built.

The ways by which biological properties vary among spatial, temporal, and functional scales (Levin 1992), has a long history of investigation, with one of the best-known examples involving the scaling of traits with organism size (Schmidt-Nielsen 1984). There is a large theoretical and empirical treatment of the constraints placed upon organism size by the ways in which biological traits vary with surface area and volume, and this principle is foundational to several domains of theory including the metabolic theory of ecology (MTE [Brown et al. 2004]) and Dynamic Energy Budget theory (DEB [Nisbet et al. 2000, Kooijman 2010]). These theories describe the rates at which organisms acquire resources from the environment and use the nutrients and energy therein for growth, maintenance, and reproduction to create outcomes that propagate among functional levels. Similar principles apply to ecological processes, and since the work of Levin (1992), scale-dependence has been engrained deeply in ecological science, with most studies of this topic showing that the scale of investigation affects the results obtained (Chave 2013). Thus, it is reasonable to expect that the effects of ocean acidification on coral reef communities and ecosystems cannot simply be estimated from carbonate deposition and dissolution rates determined with organismal and sub-organismal studies.

We highlight the scale-dependence of deposition and dissolution of $CaCO_3$ on coral reefs with the objectives of stimulating research to: (1) predict whether coral reefs will persist as net depositors of $CaCO_3$ under future lower seawater pH, and (2) evaluate the implications of changes in benthic community composition (e.g., Roff and Mumby 2012) on the ability of coral reefs to maintain net deposition of $CaCO_3$. We emphasize the importance of these tasks and highlight areas of potential biological complexity that will require attention in order to make progress in these areas. We devote less attention to the complexity and the scale dependence of $CaCO_3$ dissolution processes, but we acknowledge that this is equally important as the focus on $CaCO_3$ deposition. To achieve our objectives, we consider coral reefs at the scales of cells, organisms, populations, communities, and ecosystem (Fig 1). Within each scale, we describe traits that are likely to be important in determining responses to ocean acidification, and identify means by which their effects cascade among levels of functionality. Finally, we present a simple schematic, which illustrates the outcomes that might be possible through the use of appropriate theory to scale the effects of ocean acidification on coral reef calcification from cells to ecosystems. While our schematic is contextualized by empirical data from the literature, currently neither the empirical data nor the precise theory has been developed to fully realize the potential of theoretical approaches.

Fig. 1

Molecular and cellular effects of ocean acidification on coral reefs

An appreciation of the biology of calcification in the Scleractinia requires understanding of the evolutionary context of mineralization in this taxon. Scleractinians developed the capacity to mineralize ~ 245 Ma ago (Stolarski et al. 2011), when the chemistry of ancient seas was characterized by high concentrations of Mg relative to Ca, which favored the deposition of the aragonite polymorph of $CaCO_3$ (Stanley and Hardie 1998). Over geological time, aragonite deposition persisted within scleractinians despite a transition to lower seawater Mg/Ca ratios from 190-40 Ma that chemically favored deposition of the calcite polymorph of $CaCO_3$ (Stanley and Hardie 1998).

Although calcification is an innate feature of scleractinians, it is the presence of chemically and physically favorable conditions for mineralization (i.e., elevated $CaCO_3$ saturation state, seawater Mg/Ca ratios > 2 that favor precipitation of aragonite, warm temperatures, and clear seawater), and a mutualistic symbiosis with *Symbiodinium* algae or zooxanthellae, that supports the deposition of the large quantities of $CaCO_3$ that are required for the construction of coral reef ecosystems. Symbioses with *Symbiodinium* algae (Stambler 2011), as well as a diversity of microbes (Krediet et al. 2013), create some of the greatest challenges to understanding how calcification scales up from cells to scleractinian colonies, and ultimately to reef ecosystems. These challenges arise from the complex and intertwined physiologies of the symbiotic partners, any one (or more) of which could mediate calcification through multiple pathways (e.g., directly involving mineralization, or indirectly through photosynthesis, or nutrient recycling) and determine the mechanisms by which it varies among functional scales.

Calcification on coral reefs begins with molecular and cellular events, and understanding of the scale-dependence of calcification on coral reefs, and how it is affected by ocean acidification, must embrace explanatory power at these most reductionist levels (Fig 2A). This will best be achieved by exploiting theory with sufficient complexity and flexibility to capture the emergent ecosystem-level features that are the summation of cellular events translated through organisms, populations, and communities/ecosystems (Fig 2E). Although gaps remain in understanding cellular mineralization in diverse coral reef taxa, knowledge is most complete for scleractinians (e.g., Cohen and McConnaughey 2003, Allemand et al. 2011), but is growing rapidly for calcified algae (Wizeman et al. 2014, McCoy and Kamenos 2015). We focus here on molecular and cellular aspects of calcification within the Scleractinia, but the investigative principles potentially are transferable to analyses of cellular calcification in algae that function as important organismic calcifiers on coral reefs. It is not our objective to summarize the recent advances that have been made in understanding coral mineralization at the molecular and cellular levels, and interested readers are referred to comprehensive treatments of this topic (Cohen and McConnaughey 2003, Allemand et al. 2011, Tambutté et al. 2011, Venn et al. 2013).

Instead, we highlight three areas with the potential to limit the quantity of $CaCO_3$ deposited by scleractinians under conditions of elevated pCO_2: (a) the organic matrix (Tambutté et al. 2008), (b) the chemical composition of calcifying fluids (Cohen et al. 2009, Venn et al. 2013), and (c) the energetics of calcification (Anthony et al. 2002).

Although organic matrix has long been known to occur within coral skeletons, attention to this facet of skeletogenesis has only recently been considered in effort to understand how corals respond to ocean acidification. The organic material of coral skeletons is composed of lipids, sugars, and proteins (for review see Tambutté et al. 2007). Among these components, acidic proteins appear to be essential for biomineralization (Drake et al. 2015), and interest in this material has focused on its roles in shaping the ultrastructure of the coral skeleton beyond what is possible through chemical precipitation alone (Mass et al. 2013). The potential for the organic matrix to modulate skeletal structure is attractive to the consideration of scaling in corals' calcification response to ocean acidification, as this concept bridges chemical and biological controls of coral skeletal morphology and, ultimately, the emergent properties of corallum shape that dictate how $CaCO_3$ is used to build coral reefs (Tambutté et al. 2015, Venn et al. 2015).

Recent research in coral calcification has underscored the role of the biology of the coral host in modifying the chemical composition of the fluid beneath the tissue and adjacent to the calcifying surface (Cohen et al. 2009, Ries 2011, McCulloch et al. 2012, Venn et al. 2013). Understanding the chemistry of this microenvironment is central to understanding how coral calcification occurs and the extent to which it is affected by ocean acidification. The important processes involve the flux of chemical species, notably the export of protons (H^+) from and the import of Ca^{2+} ions and dissolved inorganic carbon to the calcifying fluid, in order to maintain the sufficiently elevated saturation state necessary for $CaCO_3$ deposition (Cohen and McConnaughey 2003).

Crystallographic properties of aragonite crystals accreted under OA conditions (Cohen et al. 2009), the boron isotope composition of those crystals (McCulloch et al. 2012), pH-sensitive dyes (Venn et al. 2013), and pH microelectrodes (Al Horani et al. 2003 Ries 2011) each have been used to show that the pH of the coral calcifying fluid (CCF) is elevated relative to surrounding seawater pH, and that acidification of the surrounding seawater causes a reduction in pH of the CCF. These observations are critical, because they provide direct evidence of a mechanism by which ocean acidification impairs coral calcification. Proton removal involves active transport across cell membranes (Isa et al. 1980, Ries 2011, Zoccola et al. 2004), and this flux appears to be matched to the supply of dissolved inorganic carbon (DIC) from seawater and host tissue (Zoccola et al. 2004, Allemand et al. 2011, Allison et al. 2014) in order to support the deposition of $CaCO_3$. Understanding the processes determining the chemical composition of the CCF will be pivotal to understanding how calcification scales from cells to ecosystems to support the growth of coral colonies, populations, and communities/ecosystems.

Finally, modification of the ionic milieu of the CCF represents physical work that is supported with metabolic energy. Faced with an increased thermodynamic challenge to precipitating $CaCO_3$ under ocean acidification (Erez et al. 2011, Ries 2011), it is appealing to suggest that ocean acidification depresses calcification due to increased metabolic costs (Cohen and Holcomb 2009, Erez et al. 2011). However, evidence of elevated aerobic respiration in corals exposed to ocean acidification is equivocal (Crawley et al. 2010, Kaniewska et al. 2012), and it is therefore unclear whether energy demands alone can explain why ocean acidification depresses calcification. This outcome does not exclude the possibility that changes in the allocation strategies of energy resources among metabolic sinks within corals could have a similar effect in depressing calcification. Analyses of the energetic costs of calcification (including both absolute costs and allocation strategies for metabolic energy) are, due to the power of the laws of thermodynamics, inherently attractive in considering scaling of physiological processes. This type of approach is already deeply engrained in several theoretical frameworks addressing the flux of energy among multiple scales of biological functionality (Brown et al. 2004, Kooijman 2010, Nisbet et al. 2000), including a recent model relating subcellular and physiological processes to population level impact of ocean acidification on calcification in coccolithophorids (Muller and Nisbet, 2014)

The aforementioned areas of complexity governing cellular calcification in scleractinians provide an effective stage from which to consider how the products of cellular calcification determine ecosystem-level calcification (Fig. 2). Moreover, much of this complexity can be explained from the physical and chemical principles governing the deposition of $CaCO_3$, and these same principles can provide pathways through which the effects of ocean acidification as an agent of perturbation can be considered.

Organismal effects of ocean acidification on coral reefs

Of the functional scales relevant to coral reefs, organisms have received the most attention in ocean acidification studies (Erez et al. 2011, Kroeker et al. 2013). The majority of studies have focused on calcification in corals, and less extensively, calcified algae (Kroeker et al. 2013). Most tropical corals and calcifying algae show decreased or parabolic (Castillo et al. 2014) calcification responses to ocean acidification, but results differ among taxa, including species, higher taxonomic levels, and functional groups (Chan and Connolly 2013, Comeau et al. 2014). The effects of ocean acidification on the fleshy macroalgae found on coral reefs have received less attention than the effects on calcified taxa, yet there is the potential for ocean acidification to “fertilize” macroalgal growth through stimulatory effects of high pCO_2 on photosynthesis and growth (Johnson et al. 2014).

Species-specific responses of organisms to elevated pCO_2 on coral reefs are caused by a variety of factors, including differing skeletal mineral solubility (i.e., low-Mg calcite vs. high-Mg calcite vs. aragonite), ability to regulate pH of the organism’s calcifying fluid, presence of protective shell layers, nutritional status, and ability to utilize CO_2 directly via photosynthesis (Ries et al. 2009). Variations in treatment conditions also are likely to contribute to variable results. For example, the experimental effect size for ocean acidification acting on calcification ranges from 0–100% for corals (Erez et al. 2011), and from ~0–50% for algae (Anthony et al. 2008, Comeau et al. 2013) when atmospheric pCO_2 is approximately double that of present-day values. In light of such variation, it is critical to understand why organisms with apparently similar mechanisms of calcification respond in very different ways to modification of seawater carbonate chemistry. A deeper comprehension of cellular mechanisms of calcification, and how they scale up to mediate organismal calcification (section 1 above) is of key importance in understanding the drivers of organismal-scale heterogeneity in calcification rates, and the means by which this variance cascades upwards to determine rates of calcification at higher functional levels (Fig. 2).

For corals and calcifying algae on tropical reefs there are many physiological characteristics that could drive variation in response to ocean acidification. For example, coral colony, algal thallus morphology, skeletal mineralogy, and organism size, have a strong potential to impact the response of reef organisms to ocean acidification (Fig. 2B). Among corals, differential sensitivity of calcification to seawater carbonate chemistry also could be driven by tissue thickness (Edmunds et al. 2012), gender and the mechanism of nutrient acquisition (Holcomb et al. 2012), and the assemblage of *Symbiodinium* clades within the tissue (Little et al. 2004). In coralline red algae, the Mg/Ca ratio of their calcite skeleton (which controls calcite solubility), as well as the abundance of ancillary minerals such as dolomite and brucite, vary amongst species (Nash et al. 2014). Nutrient availability also is potentially critical to influencing calcifying algal sensitivity to ocean acidification. For fleshy macroalgae, calcifying algae, and zooxanthellate corals, carbon acquisition strategies – the ability to use CO_2 directly and the presence of carbon concentrating mechanisms (CCMs) -- are critical in determining the potential fertilization effect of increasing pCO_2 on photosynthesis and growth (Raven et al. 2011), which could provide additional energy for calcification. Currently, the combination of features that determines taxon-specific susceptibility to ocean acidification in corals and calcifying algae is unknown, and studies addressing this problem have yet to identify one or more mechanisms that are common among multiple taxa (Chan and Connolly 2012, Comeau et al. 2014).

Scaling the effects of ocean acidification from organisms to populations to communities and ecosystems is complicated by: (1) coupling of calcification and photosynthesis at the organismal scale, as both are affected directly by environmental parameters such as water flow speed, temperature, and light/nutrient availability (Gattuso et al. 1999) (Fig. 2F), (2) non-linear relationships between organism growth and population growth, and (3) the complex ways by which species interactions (e.g., competition, predation, bioerosion, etc.) determine how populations responses sum to communities and ecosystems. Interestingly, the role of organism size in determining sensitivity to ocean acidification has received little attention for any reef taxon. However, a study on chitons showed that the severity of their metabolic response to OA was proportional to their body size (Carey and Sigwart 2014). Analyses of the relationships between organism size and sensitivity to OA in tropical organisms are missing from efforts to evaluate the effects of OA on coral reef ecosystems, and it is likely that this omission will need to be addressed in order to scale responses to OA across functional scales (Brown et al. 2004).

Population effects of ocean acidification on coral reefs

Quantifying the effects of ocean acidification on individual performance has been the mainstay of much of ocean acidification research, and the outcomes of these studies have resulted in numerous predications of how individuals might respond to a more acidic ocean (Gattuso and Hanson 2011, Kroeker et al. 2013). The challenge at the population level is to integrate individual responses, and to do so in a manner that will allow these effects to be propagated through multispecies interactions in order to scale up to the community level. It also is possible to investigate intra-species (i.e., population level) effects of ocean acidification on coral reef systems (Fig. 2).

Understanding population-level responses of scleractinians and calcifying algae to ocean acidification requires linking the organismal-level responses of growth, survival, and fecundity to population structure and demographic properties. Mathematical tools for scaling up from individual performance to population dynamics are well developed and have been applied widely to a diverse group of taxa (Caswell 2000). Structured population models (Caswell 2000), in which individuals are classified according to one (or several) state variable(s) that correlate(s) with demographic inputs, provide one effective tool for this purpose. For scleractinians, colony size is a useful state variable that frequently is measurable in ecological surveys, and is associated directly with demographic rates (Hughes 1984). Thus, if ocean acidification was found (for example) to reduce per capita fecundity (as life-history theory suggests; Mumby and van Woesik 2014) or to weaken colony skeletons by favoring bioerosion and decreasing skeleton density (Andersson and Gledhill 2013, Tambutté et al. 2015), thereby increasing vulnerability of larger colonies to breakage, structured population models can translate these colony-level inputs to long-term population growth and structure.

Population projection matrices (Caswell 2000) and integral projection models (IPMs, Easterling et al. 2000) are types of structured population models that offer fully developed suites of tools for scaling up from individuals to populations. These models can be easily modified to accommodate additional phenomena that may prove essential for understanding the organismic responses of corals and calcifying algae to ocean acidification, and ultimately, for scaling the effects to the population level (Edmunds et al. 2014). For example, mesocosm experiments can be used to define the relationships between pCO_2 and colony growth, which can be integrated into field-based demographic models evaluating change in colony size over time to explore directly the effects of ocean acidification on the intrinsic rate of population growth (i.e., λ [Edmunds et al. 2014]). There is a wide spectrum of viable permutations to such models that are feasible. We describe some of the potentially more valuable modifications below.

First, structured population models can be expanded to include dead corals. This would be a valuable expansion of theory if bioerosion or dissolution of dead or weakened corals modulates the availability of surfaces suitable for settlement of coral larvae, or if it impacts carbonate chemistry in a way that feeds back upon local $CaCO_3$ deposition and colony growth. Recent work highlights the importance of reef dissolution under elevated pCO_2 and depressed seawater saturation with respect to $CaCO_3$ minerals (Andersson and Gledhill 2013, Comeau et al. 2015). Second, state variables other than colony size may be worth considering, especially if other individual-level characteristics are important for determining responses to ocean acidification. In particular, genetic structure may prove to be an important individual-level covariate, especially if adaptation through rapid evolution or trans-generational plasticity (Mumby and van Woesik 2014) buffers individual-level demography against environmental change. Third, structured population models can be embedded in a spatial context if, for example, the impacts of ocean acidification are experienced differently across different reef locations (e.g., fore-reef vs. back-reef) that are connected by propagule dispersal. Fourth, density-dependence or inverse density-dependence may be added if population density feeds back onto colony- or individual-level demographic rates (e.g., through self-shading, or competition for nutrients). Finally, structured population models can be integrated into multi-species models to capture ecological interactions with other benthic taxa (e.g., inhibition of larval recruitment by fleshy macroalgae) that can mediate changes in community structure (Gaylord et al. 2014). Conceptually, multi-species models often are often associated with the community scale (discussed below), although the mathematical distinction between single- and multi-species models often is often small.

The tools of population ecology, including structured population models, often are developed to focus on long-term responses, such as a population's eventual growth rate and structure in terms of distributions of individuals varying in age or size. In the context of an environmental covariate such as ocean acidification that is likely to change slowly over decades-to-centuries (Gattuso and Hansson 2011), it may be valuable to analyze short-term 'transient' biological responses to these conditions, as well as the potential for acclimation of coral and other reef calcifiers. The analysis of short-term responses (i.e., transients as defined against the time-scale of changes affecting ecological systems) to changing environmental conditions is a mathematical frontier in population ecology (Hastings 2004), but short-term responses also can be quantified through simulations instead of through empirical approaches. Understanding short-term population responses of coral reef calcifiers exposed to chronic pCO_2 exposure may be important, especially for interfacing models with management timetables, and for validating models on human time scales. Importantly, the outputs (projections) from population level models of how species and species interactions will respond to ocean acidification must provide compatible inputs to community and ecosystem scale modeling efforts.

Community and ecosystem effects of ocean acidification on coral reefs

The processes of interest for understanding the impact of ocean acidification at the scale of coral reef communities and ecosystems are inter- and intra-specific interactions, net ecosystem production (NEP = primary production – total respiration), and net ecosystem calcification (NEC = gross calcification – gross $CaCO_3$ dissolution) (Fig. 2D,E). The chief emergent properties arising from populations that influence these processes are species composition (and the functional capabilities of each taxon), abundance of soft- and hard- substrata, diversity, richness, and the community assemblage at a particular point in time (Fig. 4). Multiple communities differing in these features contribute to the response to ocean acidification observed at the ecosystem level. Characterizing the response of coral reef ecosystems to ocean acidification can be achieved through direct measurements, but these efforts need to be matched with theoretical approaches that can be used to reveal how effects at lower functional levels affect the ecosystem scale. Critically, the combination of empirical and theoretical approaches will be necessary to evaluate the implications of shifts in benthic community composition on the ability of coral reef ecosystems to maintain net deposition of $CaCO_3$ under different ocean acidification regimes.

Coral reef ecosystem functionality is dependent on the net primary production and net calcification of individual populations within the communities that comprise the ecosystem. Differential effects of ocean acidification on the population growth rates of corals and calcifying algae will lead to shifts in their relative abundance, as mediated by changes in the ability of these species to persist and maintain calcified structures. Changes in relative abundance of these taxa have important implications, as corals and calcifying algae are unequal functionally, with some serving as primary reef builders and some as secondary reef builders, cementers, and/or consolidators. Resource competition among coral taxa (e.g., for space) likely will modulate changes in coral species abundance in cases where coral cover remains high by, for example, intensifying the ecological consequences of reduced colony growth rates. Such effects are likely to extend to interactions among corals and other members of the community, notably macroalgae, and could have strongly non-linear or threshold effects. For instance, ocean acidification could accentuate the rate at which phase shifts from a coral- to a macroalgal- dominated state occur if ocean acidification negatively impacts corals while enhancing the growth of macroalgae.

Fundamentally, the growth of coral reefs is dependent on $CaCO_3$ deposition exceeding dissolution and destruction as defined by simple mass balance (Eyre et al. 2014):

Net $CaCO_3$ accumulation = Gross calcification – Gross $CaCO_3$ dissolution – $CaCO_3$ export (Equation 1)

Whereas the calcification and dissolution terms in this relationship can be defined by components falling under lower functional levels (e.g., cellular, organismal, and population, or sediment grain, skeleton, and community, respectively), $CaCO_3$ dissolution and export are terms that feature prominently at the community level, but can also be important for individuals (Fig. 2). There are biogeochemical techniques with the potential to quantify the performance and function of coral reefs at the ecosystem scale that effectively incorporate $CaCO_3$ dissolution and export into predictive models of coral reef ecosystem accretion, while embracing the need to integrate the contributions of lower functional levels to ecosystem function. For example, simultaneous measurements of seawater dissolved inorganic carbon and total alkalinity (TA) over space and time can be used to quantify relative levels of net ecosystem calcification and net ecosystem organic carbon production (Fig. 2; Gattuso et al. 1996, Suzuki and Kawahata 2003, Watanabe et al. 2006, Lantz et al. 2014). Evaluating TA anomalies relative to offshore conditions also provides information whether a reef is net calcifying (depletion of TA) or net dissolving (repletion of TA). These ecosystem properties are a function of performances at lower functional levels, but we have a poor quantitative understanding of the relative importance of community members within a given functional level to ecosystem-level processes.

Combining theory and observation

Nearly half a century ago, Levins (1966) argued that models in ecology can be organized by the balance they strike among the countervailing axes of realism, precision, and generality. Furthermore, he suggested that although models may enjoy two of these desirable characteristics simultaneously, no model can be realistic, precise and general all at once. Although the virtues of Levins's scheme are debatable, the core observation that models are subject to trade-offs is indisputable. No model or modeling approach is suited uniformly for all scientific purposes, in the same way that no single empirical approach renders all other approaches inferior. Thus, we should not expect a "Grand Unifying Theory" of the effects of ocean acidification on coral reefs to emerge that simultaneously unites all the scales of biological organization at which ocean acidification and its impacts can be described (Fig. 2). Instead, the science of ocean acidification on coral reefs will advance by embracing a suite of complementary modeling approaches and their associated strengths.

The preceding sections have suggested several theoretical tools that may be useful for the study of ocean acidification, and which take different approaches to understanding complex, multi-scale behavior (Box 1). For example, both DEB and MTE flow from the philosophy that much of the variation observed in the natural world can be explained by appealing to a fundamental collection of first principles --- such as the allometric scaling of metabolic rates and the allocation of assimilated energy. Although these approaches do not strive for pinpoint predictions for any particular time and place, they can inform a conceptual backbone that unites disparate observations of the effects of ocean acidification. In contrast, contemporary computing power has enabled detail-rich computer simulations of highly specific and complex systems. Such computing power can be deployed to study complex systems as varied as the different genetic pathways within a single cell (so-called systems biology; Kitano 2002), or the interactions among thousands to millions of individuals in an ecosystem (often called individual- or agent-based models; Grimm et al. 2005). These approaches emerged from the philosophy that a detailed understanding of the rules that govern behavior within a complex system can enable profitable exploration of the emergent properties of that system through computer simulation. Lying somewhere between these two extremes are compartmental models (including stage-structured models) that have featured prominently in population and community ecology. Compartmental models do not strive for the same broad universality as DEB or MTE, but also require strategic assumptions about which sources of biological variation must be incorporated into a model, and which can be ignored.

Finally, just as theory and empiricism benefit from a diverse collection of approaches, theory and empiricism themselves provide complementary routes to scientific progress, and thus both benefit from a vigorous exchange of ideas. Indeed, both theory and experimentation can inspire new hypotheses that motivate evaluation from a complementary perspective. The learning that ensues may suggest refinement of the hypothesis, or even wholesale rejection.

Summary and future directions

Given the rapid changes in seawater carbonate chemistry that are being driven by anthropogenic effects, and the long time necessary to reverse these effects once CO_2 emissions are reduced (Ciais et al. 2013), there are compelling reasons to be concerned about the impacts of ocean acidification on coral reefs (Gattuso et al. 2014). We still lack basic understanding of the time that it takes for a coral reef to transition from net deposition to net dissolution, and how such a process would reduce structural complexity of the reef and impair its ecological function (e.g., habitat provisioning [Fabricius et al. 2014], wave buffering, etc.). It is clear that theoretical approaches, in addition to the multi-scale approaches outlined above, will be needed to evaluate the impact of a reef transitioning from net deposition to net dissolution (and the reverse). Such approaches have the capacity to model the effect of ocean acidification on emergent properties (species composition, diversity, richness) that influence the functionality (species interactions, NEP, NEC) of coral reef ecosystems. Against this backdrop, there are several research priorities that should be addressed to improve the synthetic capacity of ocean acidification studies on coral reefs that may ultimately help mitigate the deleterious impacts of CO_2-induced ocean acidification:

Since the threat of ocean acidification for calcified marine ecosystems first became apparent, there has been a massive increase in empirical studies designed to document the effects on organisms. Future progress will depend upon the integration of these observed effects and the application of theory to these massive datasets. Powerful and appropriate theory already is available for this task, and significant effort should be allocated to adapting and expanding this theory to coral reef applications.

Although integrating the effects of ocean acidification across multiple functional scales (Fig. 2) will advance the field, there are still many pieces missing from the puzzle. Major needs include: (i) greater attention to the effects of OA on processes (e.g., recruitment, competition, predation, bioerosion, $CaCO_3$ dissolution) that mediate connections between functional scales on coral reefs; (ii) improved understanding of the ways in which physical and chemical aspects of the environment modulate biological responses to ocean acidification; (iii) expansion of taxonomic breadth of ocean acidification experiments; (iv) improved understanding of population-level impacts of ocean acidification; and (5) improved understanding of how population-level impacts of OA sum to community- and ecosystem-level impacts.

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Legends

Fig. 1. Illustrations of the scales of observations described in the present study and characteristic of contemporary investigations of the effects of ocean acidification on corals, algae, and coral reefs. A) Cellular level: scanning electron micrograph of a cross section of the aragonite skeleton (left) and body wall (right) of *Acropora cervicornis* showing *Symbiodinium* nestled in the oral endoderm (1 µm scale bar, lower right). B) Organism level: polyps of *Montastraea cavernosa* (each ~ 1 cm width). (C) Organism level: a single cultured colony of *A. pulchra* growing in the back reef of Moorea. (D) Population level: a population of multiple colonies of *P. verrucosa* on the outer reef of Moorea. (E) Community level: a coral reef community composed of a diversity of corals, algae and other taxa on the outer reef of Palmyra Atoll. (F) Ecosystem level: satellite image of Tetiaroa Atoll in the south Pacific. Photo credits: A: J. Ries, B: P. Edmunds, C: C. Lantz, D: P. Edmunds, E: M. Johnson, and F: Google Earth.

Fig. 2. Summary of functional scales at which the effects of ocean acidification on the calcification on coral reef calcifiers is currently being evaluated. An important goal of this research is integrating results across functional scales to better understand the emergent properties of ecosystem-level calcification in a more acidic ocean. This ecosystem-level response is a summation of events at lower functional scales, but we currently lack the empirical and theoretical tools necessary to scale with ecological relevance among these levels. Our construct

distinguishes among calcification at the scale of (A) cells, (B) organisms, (C) populations, and (D, E) communities and ecosystems, all of which are forced to some extent by environmental factors (F); these scales serve as a construct within which the challenges can be articulated, and solutions discussed, thereby leading to effective integration. At each scale, traits are described that address the factors modulating calcification, and arrows among the scale describe the direction of scaling effect. At the population (C) and community (D) scales, we emphasize the complexity added through the presence of multiple categories of benthic organisms (corals, macroalgae [MA], and crustose coralline algae [CA]) that vary in abundance through space and time. Ecosystem-level processes (E) represent the highest level of complexity that we seek to understand. At this levels efforts will likely focus on community metabolism and its response to key large-scale responses to ocean acidification. For illustrative purposes, we focus on the interactive effects of dissolved inorganic carbon (C_T) and total alkalinity (A_T) on the balance between gross primary production (GPP) and respiration (R) and $CaCO_3$ deposition (G) and dissolution (D).

Box 1

Four approaches (A-D) and the potential outcomes (E) of quantitative scaling of the effects of ocean acidification on coral reef calcifiers in order to estimate the effects on community calcification.

(A) **Simple extrapolation** utilizes empirical data describing physiological responses of reef calcifiers to differing pCO_2 regimes, and extrapolates these responses based on community composition. As an illustration, we show a quadrat recorded at 17-m depth on the outer reef of Moorea in 2006 that was used as a basis to create a reef community in a flume for which calcification as function of pCO_2 was determined. To extrapolate the effects of ocean acidification, the community structure in 2006 was used to evaluate the percentage cover of CCA and the population size structure scleractinians belonging to branching, mounding, or sheeting functional groups. Based on these data, community calcification (g m^{-2} d^{-1}) was calculated under present day conditions (~ 400 µatm pCO_2) and those expected by the end of the current century (~1000 µatm pCO_2) (E). CCA cover was taken as 20%, the mean size of corals in the three function groups were calculated (shown in histograms) and their mean densities were 13.9, 5.0, and 6.9 colonies m^{-2} for branches, mounds, and plates. Coral surface areas were calculated from the relationship between diameter and area (as determined for *Pocillopora verrucosa* from $y = 2.493.x^{2.312}$ where y is area [cm^2] and x is diameter [cm]), and assuming mounds were hemispheres, and sheets were circles. Organismic rates of calcification at different pCO_2 values were obtained from Comeau et al. 2013, 2014, 2015).

(B) The **experimental** approach relies on direct measurements of net community calcification, which in our recent work (Comeau et al. 2015) exploits communities assembled from specimens collected from the outer reef (17-m depth) and assembled at ecologically relevant densities (as assessed from percent cover) in a 5.0 x 0.3 m flume. These communities included carbonate pavement, which was added to capture the effects of dissolution in this aspect of the community.

(C) **Processed based** posits that reef-scale calcification can be understood based on first principles of biological organization. The Metabolic Theory of Ecology [MTE; Brown et al. 2004]) for example, uses allometric scaling to predict emergent property of an ecosystem (such as the net calcification rate) using power-law relationships between physiology and colony size, and abundance and colony size. Integrating the former relationship over size-frequency distributions yields a net calcification rate for the entire reef. A mature MTE for coral reefs has yet to appear, and so we illustrate a hypothetical scaling relationships inspired by MTE (Enquist et al. 2003, West et al. 2009) and informed by empirical data describing the size-frequency structure of branching, mounding, and sheeting corals (as in 2006 at 17-m depth) and empirically calcification rates at the organismic level (both as in A above). The product of the scaling relationships between average calcification rate per size class (y) and area (x) and average abundance per size class (y) and area (x) yields the total calcification per size class (y) as a function of area (x). Integration of the values among area categories provides an estimate of community calcification under ambient and elevated pCO_2. While power laws provide good fits for observed coral scaling, as expected by theory, quadratic functions fit better for observed patterns of coral abundance (red).

(D) The **simulation** approach builds an *in silico* replica of an ecosystem that incorporates all known rules of how individuals in a complex system behave and interact, and then explores emergent ecosystem behavior through simulation under various environmental scenarios. This approach is exemplified by individual-based models (Grimm and Railsback 2005), and is illustrated by the recent Madingley model (Harfoot et al. 2014), which claims to provide “a mechanistic General Ecosystem Model … that is both global and applies in all terrestrial and marine environments.” The difference between analytical theory and computer simulation often is one of dimensionality: theory strives to describe ecosystem structure and function through a few key variables and parameters, while simulation uses brute computing power to portray an ecosystem in fine detail. Of course, computer simulations require intricate knowledge about how the entities in the simulation behave and interact. Such knowledge can be and often is provided by experimental evidence and first-principles theory (Harfoot et al. 2014), and thus computer simulations rely deeply on the advances provided by other approaches to scientific discovery. IBMs specifically for coral-reef ecosystems have yet to appear, and so we illustrate the approach with a cartoon.

(E) **Community calcification** calculated using the approaches described above (A-D) to reveal differences in rates depending on scaling technique; it is not yet possible to evaluate calcification rates from first principles using simulation techniques (shown as “?”). The research challenge faced by the coral reef ocean acidification community is expanding existing theory to capitalize on the strengths of each domain while understanding the sources of mismatches in predictions and uncertainties in the properties of the predictions. Theoretical estimates shown here reflect quadratic fits for the scaling of coral abundance.

Fig. 1

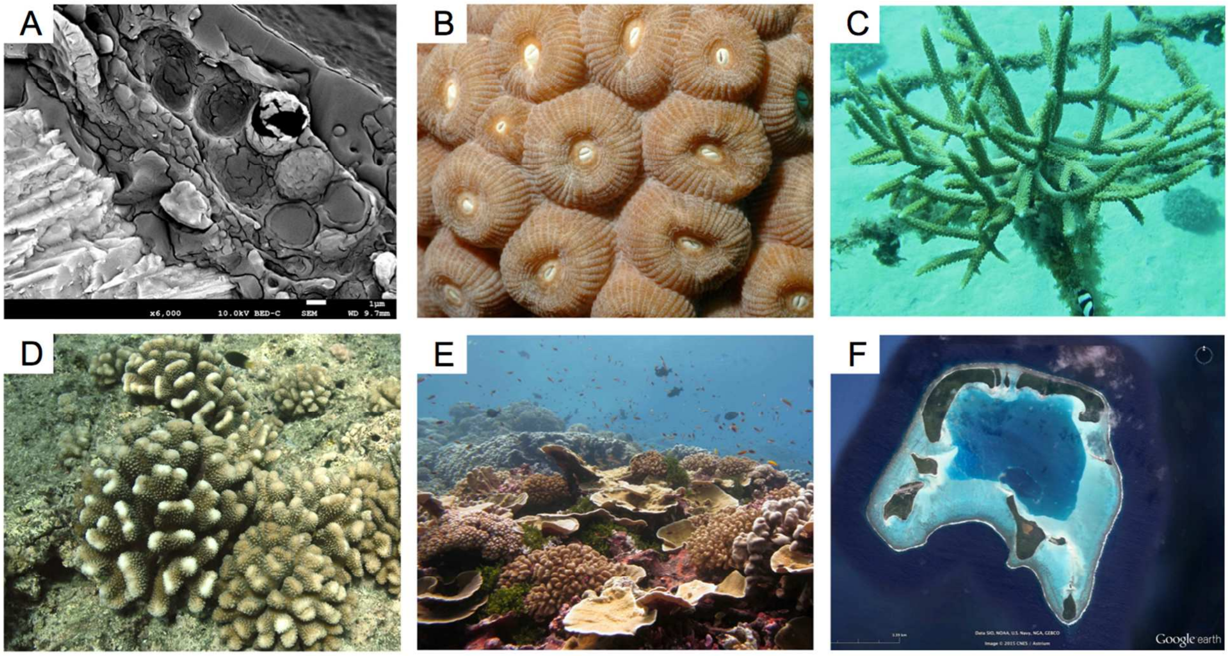
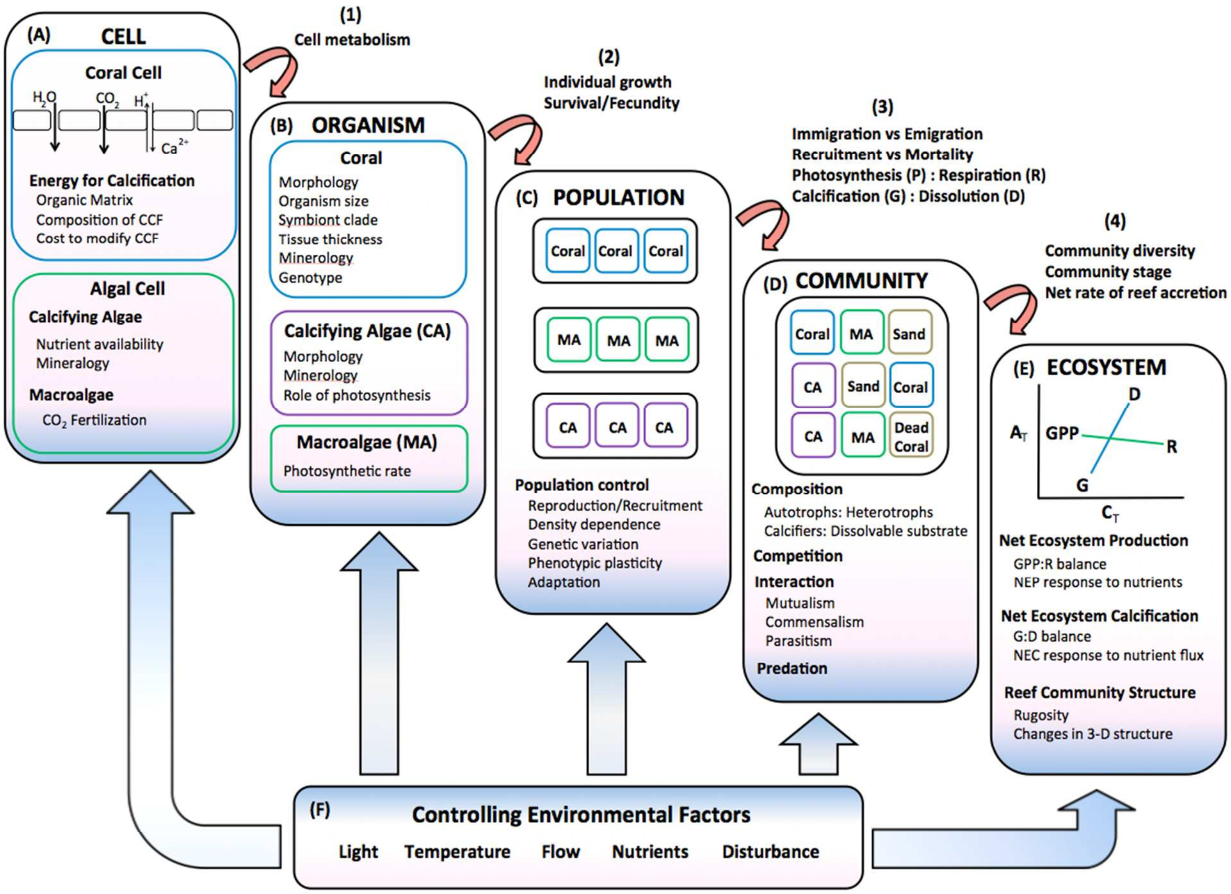
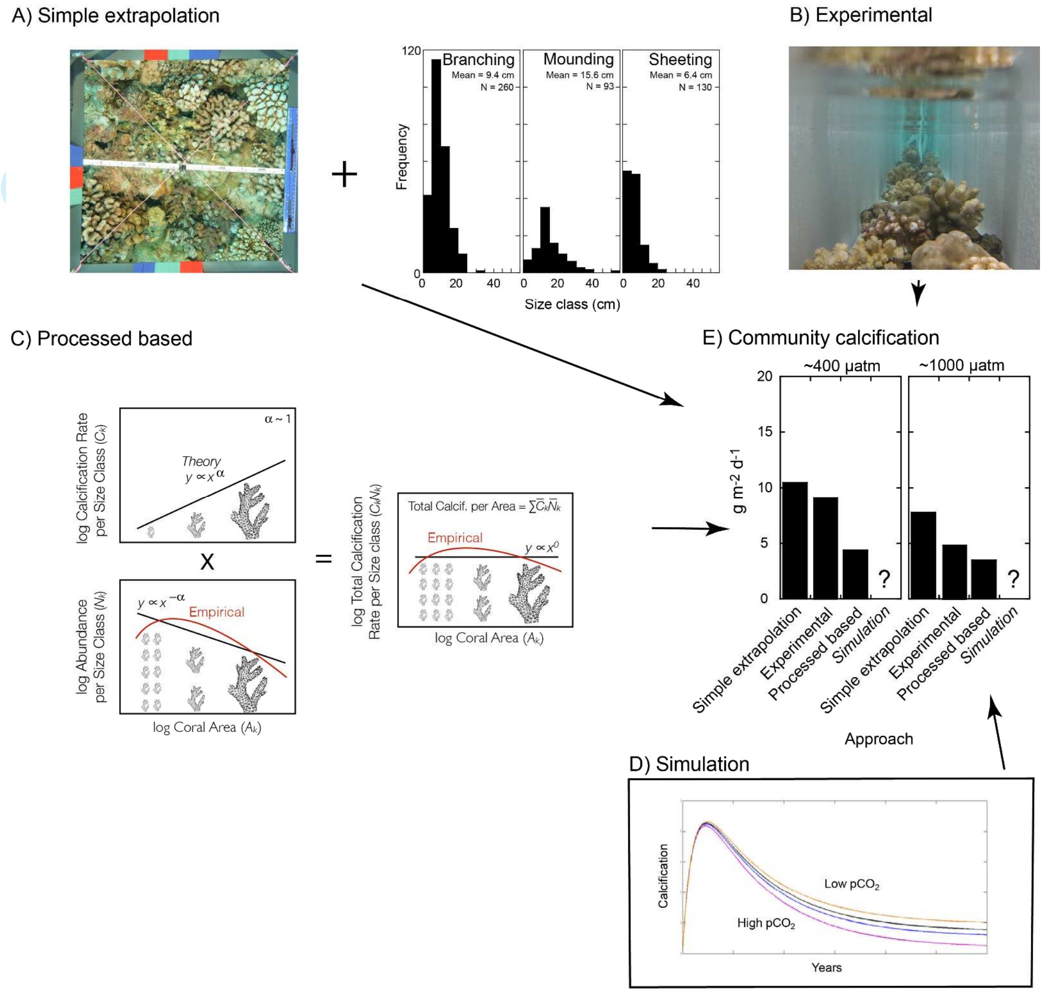


Fig. 2


(A) CELL
Coral Cell
H2O
CO2
H+
Ca2+
Energy for Calcification
Organic Matrix
Composition of CCF
Cost to modify CCF
Algal Cell
Calcifying Algae
Nutrient availability
Minerology
Macroalgae
CO2 Fertilization
(1)
Cell metabolism
(B) ORGANISM
Coral
Morphology
Organism size
Symbiont clade
Tissue thickness
Minerology
Genotype
Calcifying Algae (CA)
Morphology
Minerology
Role of photosynthesis
Macroalgae (MA)
Photosynthetic rate
(2)
Individual growth
Survival/Fecundity
(C) POPULATION
Coral Coral Coral
MA MA MA
CA CA CA
Population control
Reproduction/Recruitment
Density dependence
Genetic variation
Phenotypic plasticity
Adaptation
(3)
Immigration vs Emigration
Recruitment vs Mortality
Photosynthesis (P) : Respiration (R)
Calcification (G) : Dissolution (D)
(D) COMMUNITY
Coral MA Sand
CA Sand Coral
CA MA Dead Coral
Composition
Autotrophs: Heterotrophs
Calcifiers: Dissolvable substrate
Competition
Interaction
Mutualism
Commensalism
Parasitism
Predation
(4)
Community diversity
Community stage
Net rate of reef accretion
(E) ECOSYSTEM
AT
GPP
D
R
G
CT
Net Ecosystem Production
GPP:R balance
NEP response to nutrients
Net Ecosystem Calcification
G:D balance
NEC response to nutrient flux
Reef Community Structure
Rugosity
Changes in 3-D structure
(F) Controlling Environmental Factors
Light Temperature Flow Nutrients Disturbance

Box Fig. 1


A) Simple extrapolation
+
Frequency
120
0
Branching
Mean = 9.4 cm
N = 260
Mounding
Mean = 15.6 cm
N = 93
Sheeting
Mean = 6.4 cm
N = 130
0 20 40
Size class (cm)
B) Experimental
C) Processed based
log Calcification Rate per Size Class (C_k)
α ~ 1
Theory
$y \propto x^{\alpha}$
X
log Abundance per Size Class (N_k)
$y \propto x^{-\alpha}$
Empirical
log Coral Area (A_k)
=
log Total Calcification Rate per Size class ($C_k N_k$)
Total Calcif. per Area = $\sum \bar{C}_k \bar{N}_k$
Empirical
$y \propto x^{0}$
log Coral Area (A_k)
E) Community calcification
~400 µatm
~1000 µatm
g m-2 d-1
20
15
10
5
0
?
?
Simple extrapolation
Experimental
Processed based
Simulation
Approach
D) Simulation
Calcification
Low pCO$_2$
High pCO$_2$
Years