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

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► **To cite this version:**

Peter J. Edmunds, Steeve Comeau, Coulson Lantz, Andreas Andersson, Cherie Briggs, et al.. Integrating the Effects of Ocean Acidification across Functional Scales on Tropical Coral Reefs. *Bioscience*, 2016, pp.350-362. 10.1093/biosci/biw023 . hal-01304138

HAL Id: hal-01304138

<https://hal.sorbonne-universite.fr/hal-01304138>

Submitted on 20 Apr 2016

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



Journal:	<i>BioScience</i>
Manuscript ID	Draft
Manuscript Type:	Overview Article
Date Submitted by the Author:	n/a
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Key words:	Ocean acidification, coral reefs, functional scales
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Scale-dependency of ocean acidification on coral reefs

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Scale-dependency of ocean acidification on coral reefs

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.

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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 CO₂ 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 CaCO₃ (i.e., to persist as a calcified ecosystem) requires consideration of scaling effects.

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3 74 A defining feature of biological systems is the way in which multiple functional
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5 75 components sum to emergent properties that are not apparent at lower levels. In
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8 76 mutualistic symbioses, for example, the biology of the holobiont cannot be understood
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10 77 from the biology of the symbiotic partners, for it is their metabolic, functional, and
11
12 78 structural interactions that change through an association of their individual biological
13
14 79 traits (Edson et al. 1981, Brown et al. 2004). Phototrophic mutualisms like most reef
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16 80 corals illustrate this principle, for the combination of an animal host and algal symbiont
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18 81 facilitates nutritional polytrophy and nutrient recycling, which cannot be realized by the
19
20 82 symbiotic partners in isolation (Stambler 2011). Likewise, ecosystems achieve
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22 83 emergent properties through resilience, stability, and metabolic functionality that cannot
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24 84 be determined by summing effects on the species from which they are built.
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32 86 The ways by which biological properties vary among spatial, temporal, and functional
33
34 87 scales (Levin 1992), has a long history of investigation, with one of the best-known
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36 88 examples involving the scaling of traits with organism size (Schmidt-Nielsen 1984).
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38 89 There is a large theoretical and empirical treatment of the constraints placed upon
39
40 90 organism size by the ways in which biological traits vary with surface area and volume,
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42 91 and this principle is foundational to several domains of theory including the metabolic
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44 92 theory of ecology (MTE [Brown et al. 2004]) and Dynamic Energy Budget theory (DEB
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46 93 [Nisbet et al. 2000, Kooijman 2010]). These theories describe the rates at which
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48 94 organisms acquire resources from the environment and use the nutrients and energy
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50 95 therein for growth, maintenance, and reproduction to create outcomes that propagate
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52 96 among functional levels. Similar principles apply to ecological processes, and since
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3 97 the work of Levin (1992), scale-dependence has been engrained deeply in ecological
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5 98 science, with most studies of this topic showing that the scale of investigation affects the
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8 99 results obtained (Chave 2013). Thus, it is reasonable to expect that the effects of
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10 100 ocean acidification on coral reef communities and ecosystems cannot simply be
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12 101 estimated from carbonate deposition and dissolution rates determined with organismal
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14 102 and sub-organismal studies.
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20 104 We highlight the scale-dependence of deposition and dissolution of CaCO_3 on coral
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22 105 reefs with the objectives of stimulating research to: (1) predict whether coral reefs will
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24 106 persist as net depositors of CaCO_3 under future lower seawater pH, and (2) evaluate the
25
26 107 implications of changes in benthic community composition (e.g., Roff and Mumby 2012)
27
28 108 on the ability of coral reefs to maintain net deposition of CaCO_3 . We emphasize the
29
30 109 importance of these tasks and highlight areas of potential biological complexity that will
31
32 110 require attention in order to make progress in these areas. We devote less attention to
33
34 111 the complexity and the scale dependence of CaCO_3 dissolution processes, but we
35
36 112 acknowledge that this is equally important as the focus on CaCO_3 deposition. To
37
38 113 achieve our objectives, we consider coral reefs at the scales of cells, organisms,
39
40 114 populations, communities, and ecosystem (Fig 1). Within each scale, we describe
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42 115 traits that are likely to be important in determining responses to ocean acidification, and
43
44 116 identify means by which their effects cascade among levels of functionality. Finally, we
45
46 117 present a simple schematic, which illustrates the outcomes that might be possible
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48 118 through the use of appropriate theory to scale the effects of ocean acidification on coral
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50 119 reef calcification from cells to ecosystems. While our schematic is contextualized by
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120 empirical data from the literature, currently neither the empirical data nor the precise
121 theory has been developed to fully realize the potential of theoretical approaches.

Fig. 1

123 **Molecular and cellular effects of ocean acidification on coral reefs**

124
125 An appreciation of the biology of calcification in the Scleractinia requires understanding
126 of the evolutionary context of mineralization in this taxon. Scleractinians developed the
127 capacity to mineralize ~ 245 Ma ago (Stolarski et al. 2011), when the chemistry of
128 ancient seas was characterized by high concentrations of Mg relative to Ca, which
129 favored the deposition of the aragonite polymorph of CaCO₃ (Stanley and Hardie 1998).
130 Over geological time, aragonite deposition persisted within scleractinians despite a
131 transition to lower seawater Mg/Ca ratios from 190-40 Ma that chemically favored
132 deposition of the calcite polymorph of CaCO₃ (Stanley and Hardie 1998).

133
134 Although calcification is an innate feature of scleractinians, it is the presence of
135 chemically and physically favorable conditions for mineralization (i.e., elevated CaCO₃
136 saturation state, seawater Mg/Ca ratios > 2 that favor precipitation of aragonite, warm
137 temperatures, and clear seawater), and a mutualistic symbiosis with *Symbiodinium*
138 algae or zooxanthellae, that supports the deposition of the large quantities of CaCO₃
139 that are required for the construction of coral reef ecosystems. Symbioses with
140 *Symbiodinium* algae (Stambler 2011), as well as a diversity of microbes (Krediet et al.
141 2013), create some of the greatest challenges to understanding how calcification scales
142 up from cells to scleractinian colonies, and ultimately to reef ecosystems. These

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3 143 challenges arise from the complex and intertwined physiologies of the symbiotic
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5 144 partners, any one (or more) of which could mediate calcification through multiple
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8 145 pathways (e.g., directly involving mineralization, or indirectly through photosynthesis, or
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10 146 nutrient recycling) and determine the mechanisms by which it varies among functional
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13 147 scales.

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17 149 Calcification on coral reefs begins with molecular and cellular events, and
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20 150 understanding of the scale-dependence of calcification on coral reefs, and how it is
21
22 151 affected by ocean acidification, must embrace explanatory power at these most
23
24 152 reductionist levels (Fig 2A). This will best be achieved by exploiting theory with
25
26 153 sufficient complexity and flexibility to capture the emergent ecosystem-level features
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28 154 that are the summation of cellular events translated through organisms, populations,
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30 155 and communities/ecosystems (Fig 2E). Although gaps remain in understanding
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32 156 cellular mineralization in diverse coral reef taxa, knowledge is most complete for
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34 157 scleractinians (e.g., Cohen and McConnaughey 2003, Allemand et al. 2011), but is
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36 158 growing rapidly for calcified algae (Wizeman et al. 2014, McCoy and Kamenos 2015).
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39 159 We focus here on molecular and cellular aspects of calcification within the Scleractinia,
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41 160 but the investigative principles potentially are transferable to analyses of cellular
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43 161 calcification in algae that function as important organismic calcifiers on coral reefs. It is
44
45 162 not our objective to summarize the recent advances that have been made in
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47 163 understanding coral mineralization at the molecular and cellular levels, and interested
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49 164 readers are referred to comprehensive treatments of this topic (Cohen and
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51 165 McConnaughey 2003, Allemand et al. 2011, Tambutté et al. 2011, Venn et al. 2013).
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3 166 Instead, we highlight three areas with the potential to limit the quantity of CaCO_3
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5 167 deposited by scleractinians under conditions of elevated pCO_2 : (a) the organic matrix
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8 168 (Tambutté et al. 2008), (b) the chemical composition of calcifying fluids (Cohen et al.
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10 169 2009, Venn et al. 2013), and (c) the energetics of calcification (Anthony et al. 2002).
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15 171 Although organic matrix has long been known to occur within coral skeletons, attention
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17 172 to this facet of skeletogenesis has only recently been considered in effort to understand
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20 173 how corals respond to ocean acidification. The organic material of coral skeletons is
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22 174 composed of lipids, sugars, and proteins (for review see Tambutté et al. 2007). Among
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24 175 these components, acidic proteins appear to be essential for biomineralization (Drake et
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26 176 al. 2015), and interest in this material has focused on its roles in shaping the
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29 177 ultrastructure of the coral skeleton beyond what is possible through chemical
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31 178 precipitation alone (Mass et al. 2013). The potential for the organic matrix to modulate
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34 179 skeletal structure is attractive to the consideration of scaling in corals' calcification
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36 180 response to ocean acidification, as this concept bridges chemical and biological controls
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39 181 of coral skeletal morphology and, ultimately, the emergent properties of corallum shape
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41 182 that dictate how CaCO_3 is used to build coral reefs (Tambutté et al. 2015, Venn et al.
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43 183 2015).
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48 185 Recent research in coral calcification has underscored the role of the biology of the
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50 186 coral host in modifying the chemical composition of the fluid beneath the tissue and
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53 187 adjacent to the calcifying surface (Cohen et al. 2009, Ries 2011, McCulloch et al. 2012,
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55 188 Venn et al. 2013). Understanding the chemistry of this microenvironment is central to
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3 189 understanding how coral calcification occurs and the extent to which it is affected by
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5 190 ocean acidification. The important processes involve the flux of chemical species,
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8 191 notably the export of protons (H^+) from and the import of Ca^{2+} ions and dissolved
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10 192 inorganic carbon to the calcifying fluid, in order to maintain the sufficiently elevated
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12 193 saturation state necessary for $CaCO_3$ deposition (Cohen and McConnaughey 2003).
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17 195 Crystallographic properties of aragonite crystals accreted under OA conditions (Cohen
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19 196 et al. 2009), the boron isotope composition of those crystals (McCulloch et al. 2012),
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21 197 pH-sensitive dyes (Venn et al. 2013), and pH microelectrodes (Al Horani et al. 2003
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23 198 Ries 2011) each have been used to show that the pH of the coral calcifying fluid (CCF)
24
25 199 is elevated relative to surrounding seawater pH, and that acidification of the surrounding
26
27 200 seawater causes a reduction in pH of the CCF. These observations are critical,
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29 201 because they provide direct evidence of a mechanism by which ocean acidification
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31 202 impairs coral calcification. Proton removal involves active transport across cell
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33 203 membranes (Isa et al. 1980, Ries 2011, Zoccola et al. 2004), and this flux appears to be
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35 204 matched to the supply of dissolved inorganic carbon (DIC) from seawater and host
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37 205 tissue (Zoccola et al. 2004, Allemand et al. 2011, Allison et al. 2014) in order to support
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39 206 the deposition of $CaCO_3$. Understanding the processes determining the chemical
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41 207 composition of the CCF will be pivotal to understanding how calcification scales from
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43 208 cells to ecosystems to support the growth of coral colonies, populations, and
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45 209 communities/ecosystems.
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3 211 Finally, modification of the ionic milieu of the CCF represents physical work that is
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5 212 supported with metabolic energy. Faced with an increased thermodynamic challenge
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8 213 to precipitating CaCO_3 under ocean acidification (Erez et al. 2011, Ries 2011), it is
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10 214 appealing to suggest that ocean acidification depresses calcification due to increased
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12 215 metabolic costs (Cohen and Holcomb 2009, Erez et al. 2011). However, evidence of
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14 216 elevated aerobic respiration in corals exposed to ocean acidification is equivocal
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17 217 (Crawley et al. 2010, Kaniewska et al. 2012), and it is therefore unclear whether energy
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19 218 demands alone can explain why ocean acidification depresses calcification. This
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21 219 outcome does not exclude the possibility that changes in the allocation strategies of
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23 220 energy resources among metabolic sinks within corals could have a similar effect in
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25 221 depressing calcification. Analyses of the energetic costs of calcification (including both
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27 222 absolute costs and allocation strategies for metabolic energy) are, due to the power of
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29 223 the laws of thermodynamics, inherently attractive in considering scaling of physiological
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31 224 processes. This type of approach is already deeply engrained in several theoretical
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33 225 frameworks addressing the flux of energy among multiple scales of biological
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35 226 functionality (Brown et al. 2004, Kooijman 2010, Nisbet et al. 2000), including a recent
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37 227 model relating subcellular and physiological processes to population level impact of
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39 228 ocean acidification on calcification in coccolithophorids (Muller and Nisbet, 2014)
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43 230 The aforementioned areas of complexity governing cellular calcification in scleractinians
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45 231 provide an effective stage from which to consider how the products of cellular
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47 232 calcification determine ecosystem-level calcification (Fig. 2). Moreover, much of this
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49 233 complexity can be explained from the physical and chemical principles governing the
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234 deposition of CaCO_3 , and these same principles can provide pathways through which
235 the effects of ocean acidification as an agent of perturbation can be considered.

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237 **Organismal effects of ocean acidification on coral reefs**

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

250

251 Species-specific responses of organisms to elevated pCO_2 on coral reefs are caused by
252 a variety of factors, including differing skeletal mineral solubility (i.e., low-Mg calcite vs.
253 high-Mg calcite vs. aragonite), ability to regulate pH of the organism’s calcifying fluid,
254 presence of protective shell layers, nutritional status, and ability to utilize CO_2 directly
255 via photosynthesis (Ries et al. 2009). Variations in treatment conditions also are likely
256 to contribute to variable results. For example, the experimental effect size for ocean

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3 257 acidification acting on calcification ranges from 0–100% for corals (Erez et al. 2011),
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6 258 and from ~0–50% for algae (Anthony et al. 2008, Comeau et al. 2013) when
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8 259 atmospheric pCO₂ is approximately double that of present-day values. In light of such
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10 260 variation, it is critical to understand why organisms with apparently similar mechanisms
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12 261 of calcification respond in very different ways to modification of seawater carbonate
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14 262 chemistry. A deeper comprehension of cellular mechanisms of calcification, and how
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16 263 they scale up to mediate organismal calcification (section 1 above) is of key importance
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18 264 in understanding the drivers of organismal-scale heterogeneity in calcification rates, and
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20 265 the means by which this variance cascades upwards to determine rates of calcification
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22 266 at higher functional levels (Fig. 2).
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29 268 For corals and calcifying algae on tropical reefs there are many physiological
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31 269 characteristics that could drive variation in response to ocean acidification. For
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33 270 example, coral colony, algal thallus morphology, skeletal mineralogy, and organism
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35 271 size, have a strong potential to impact the response of reef organisms to ocean
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37 272 acidification (Fig. 2B). Among corals, differential sensitivity of calcification to seawater
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39 273 carbonate chemistry also could be driven by tissue thickness (Edmunds et al. 2012),
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41 274 gender and the mechanism of nutrient acquisition (Holcomb et al. 2012), and the
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43 275 assemblage of *Symbiodinium* clades within the tissue (Little et al. 2004). In coralline
44
45 276 red algae, the Mg/Ca ratio of their calcite skeleton (which controls calcite solubility), as
46
47 277 well as the abundance of ancillary minerals such as dolomite and brucite, vary amongst
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49 278 species (Nash et al. 2014). Nutrient availability also is potentially critical to influencing
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51 279 calcifying algal sensitivity to ocean acidification. For fleshy macroalgae, calcifying
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3 280 algae, and zooxanthellate corals, carbon acquisition strategies – the ability to use CO₂
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6 281 directly and the presence of carbon concentrating mechanisms (CCMs) -- are critical in
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8 282 determining the potential fertilization effect of increasing pCO₂ on photosynthesis and
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10 283 growth (Raven et al. 2011), which could provide additional energy for calcification.
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12 284 Currently, the combination of features that determines taxon-specific susceptibility to
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14 285 ocean acidification in corals and calcifying algae is unknown, and studies addressing
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16 286 this problem have yet to identify one or more mechanisms that are common among
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20 287 multiple taxa (Chan and Connolly 2012, Comeau et al. 2014).
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24 289 Scaling the effects of ocean acidification from organisms to populations to communities
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26 290 and ecosystems is complicated by: (1) coupling of calcification and photosynthesis at
27
28 291 the organismal scale, as both are affected directly by environmental parameters such as
29
30 292 water flow speed, temperature, and light/nutrient availability (Gattuso et al. 1999) (Fig.
31
32 293 2F), (2) non-linear relationships between organism growth and population growth, and
33
34 294 (3) the complex ways by which species interactions (e.g., competition, predation,
35
36 295 bioerosion, etc.) determine how populations responses sum to communities and
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38 296 ecosystems. Interestingly, the role of organism size in determining sensitivity to ocean
39
40 297 acidification has received little attention for any reef taxon. However, a study on
41
42 298 chitons showed that the severity of their metabolic response to OA was proportional to
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44 299 their body size (Carey and Sigwart 2014). Analyses of the relationships between
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46 300 organism size and sensitivity to OA in tropical organisms are missing from efforts to
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48 301 evaluate the effects of OA on coral reef ecosystems, and it is likely that this omission
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302 will need to be addressed in order to scale responses to OA across functional scales
303 (Brown et al. 2004).

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305 **Population effects of ocean acidification on coral reefs**

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

315

316 Understanding population-level responses of scleractinians and calcifying algae to
317 ocean acidification requires linking the organismal-level responses of growth, survival,
318 and fecundity to population structure and demographic properties. Mathematical tools
319 for scaling up from individual performance to population dynamics are well developed
320 and have been applied widely to a diverse group of taxa (Caswell 2000). Structured
321 population models (Caswell 2000), in which individuals are classified according to one
322 (or several) state variable(s) that correlate(s) with demographic inputs, provide one
323 effective tool for this purpose. For scleractinians, colony size is a useful state variable
324 that frequently is measurable in ecological surveys, and is associated directly with

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3 325 demographic rates (Hughes 1984). Thus, if ocean acidification was found (for
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5
6 326 example) to reduce per capita fecundity (as life-history theory suggests; Mumby and
7
8 327 van Woerik 2014) or to weaken colony skeletons by favoring bioerosion and decreasing
9
10 328 skeleton density (Andersson and Gledhill 2013, Tambutté et al. 2015), thereby
11
12 329 increasing vulnerability of larger colonies to breakage, structured population models can
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14 330 translate these colony-level inputs to long-term population growth and structure.
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20 332 Population projection matrices (Caswell 2000) and integral projection models (IPMs,
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22 333 Easterling et al. 2000) are types of structured population models that offer fully
23
24 334 developed suites of tools for scaling up from individuals to populations. These models
25
26 335 can be easily modified to accommodate additional phenomena that may prove essential
27
28 336 for understanding the organismic responses of corals and calcifying algae to ocean
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30 337 acidification, and ultimately, for scaling the effects to the population level (Edmunds et
31
32 338 al. 2014). For example, mesocosm experiments can be used to define the
33
34 339 relationships between $p\text{CO}_2$ and colony growth, which can be integrated into field-based
35
36 340 demographic models evaluating change in colony size over time to explore directly the
37
38 341 effects of ocean acidification on the intrinsic rate of population growth (i.e., λ [Edmunds
39
40 342 et al. 2014]). There is a wide spectrum of viable permutations to such models that are
41
42 343 feasible. We describe some of the potentially more valuable modifications below.
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48 344
49
50 345 First, structured population models can be expanded to include dead corals. This
51
52 346 would be a valuable expansion of theory if bioerosion or dissolution of dead or
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54 347 weakened corals modulates the availability of surfaces suitable for settlement of coral
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3 348 larvae, or if it impacts carbonate chemistry in a way that feeds back upon local CaCO_3
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6 349 deposition and colony growth. Recent work highlights the importance of reef
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8 350 dissolution under elevated pCO_2 and depressed seawater saturation with respect to
9
10 351 CaCO_3 minerals (Andersson and Gledhill 2013, Comeau et al. 2015). Second, state
11
12 352 variables other than colony size may be worth considering, especially if other individual-
13
14 353 level characteristics are important for determining responses to ocean acidification. In
15
16 354 particular, genetic structure may prove to be an important individual-level covariate,
17
18 355 especially if adaptation through rapid evolution or trans-generational plasticity (Mumby
19
20 356 and van Woesik 2014) buffers individual-level demography against environmental
21
22 357 change. Third, structured population models can be embedded in a spatial context if,
23
24 358 for example, the impacts of ocean acidification are experienced differently across
25
26 359 different reef locations (e.g., fore-reef vs. back-reef) that are connected by propagule
27
28 360 dispersal. Fourth, density-dependence or inverse density-dependence may be added
29
30 361 if population density feeds back onto colony- or individual-level demographic rates (e.g.,
31
32 362 through self-shading, or competition for nutrients). Finally, structured population
33
34 363 models can be integrated into multi-species models to capture ecological interactions
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36 364 with other benthic taxa (e.g., inhibition of larval recruitment by fleshy macroalgae) that
37
38 365 can mediate changes in community structure (Gaylord et al. 2014). Conceptually,
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40 366 multi-species models often are often associated with the community scale (discussed
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42 367 below), although the mathematical distinction between single- and multi-species models
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44 368 often is often small.
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3 370 The tools of population ecology, including structured population models, often are
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6 371 developed to focus on long-term responses, such as a population's eventual growth rate
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8 372 and structure in terms of distributions of individuals varying in age or size. In the
9
10 373 context of an environmental covariate such as ocean acidification that is likely to change
11
12 374 slowly over decades-to-centuries (Gattuso and Hansson 2011), it may be valuable to
13
14 375 analyze short-term 'transient' biological responses to these conditions, as well as the
15
16 376 potential for acclimation of coral and other reef calcifiers. The analysis of short-term
17
18 377 responses (i.e., transients as defined against the time-scale of changes affecting
19
20 378 ecological systems) to changing environmental conditions is a mathematical frontier in
21
22 379 population ecology (Hastings 2004), but short-term responses also can be quantified
23
24 380 through simulations instead of through empirical approaches. Understanding short-
25
26 381 term population responses of coral reef calcifiers exposed to chronic pCO₂ exposure
27
28 382 may be important, especially for interfacing models with management timetables, and
29
30 383 for validating models on human time scales. Importantly, the outputs (projections) from
31
32 384 population level models of how species and species interactions will respond to ocean
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34 385 acidification must provide compatible inputs to community and ecosystem scale
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36 386 modeling efforts.
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388 **Community and ecosystem effects of ocean acidification on coral reefs**

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50 390 The processes of interest for understanding the impact of ocean acidification at the
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52 391 scale of coral reef communities and ecosystems are inter- and intra-specific
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54 392 interactions, net ecosystem production (NEP = primary production – total respiration),
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3 393 and net ecosystem calcification ($NEC = \text{gross calcification} - \text{gross CaCO}_3 \text{ dissolution}$)
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5 394 (Fig. 2D,E). The chief emergent properties arising from populations that influence
6
7
8 395 these processes are species composition (and the functional capabilities of each taxon),
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10 396 abundance of soft- and hard- substrata, diversity, richness, and the community
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12 397 assemblage at a particular point in time (Fig. 4). Multiple communities differing in
13
14 398 these features contribute to the response to ocean acidification observed at the
15
16 399 ecosystem level. Characterizing the response of coral reef ecosystems to ocean
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18 400 acidification can be achieved through direct measurements, but these efforts need to be
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20 401 matched with theoretical approaches that can be used to reveal how effects at lower
21
22 402 functional levels affect the ecosystem scale. Critically, the combination of empirical
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24 403 and theoretical approaches will be necessary to evaluate the implications of shifts in
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26 404 benthic community composition on the ability of coral reef ecosystems to maintain net
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28 405 deposition of CaCO_3 under different ocean acidification regimes.
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36 407 Coral reef ecosystem functionality is dependent on the net primary production and net
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38 408 calcification of individual populations within the communities that comprise the
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40 409 ecosystem. Differential effects of ocean acidification on the population growth rates of
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42 410 corals and calcifying algae will lead to shifts in their relative abundance, as mediated by
43
44 411 changes in the ability of these species to persist and maintain calcified structures.
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46 412 Changes in relative abundance of these taxa have important implications, as corals and
47
48 413 calcifying algae are unequal functionally, with some serving as primary reef builders and
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50 414 some as secondary reef builders, cementers, and/or consolidators. Resource
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52 415 competition among coral taxa (e.g., for space) likely will modulate changes in coral
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3 416 species abundance in cases where coral cover remains high by, for example,
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6 417 intensifying the ecological consequences of reduced colony growth rates. Such effects
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8 418 are likely to extend to interactions among corals and other members of the community,
9
10 419 notably macroalgae, and could have strongly non-linear or threshold effects. For
11
12 420 instance, ocean acidification could accentuate the rate at which phase shifts from a
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14 421 coral- to a macroalgal- dominated state occur if ocean acidification negatively impacts
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16 422 corals while enhancing the growth of macroalgae.
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22 424 Fundamentally, the growth of coral reefs is dependent on CaCO_3 deposition exceeding
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24 425 dissolution and destruction as defined by simple mass balance (Eyre et al. 2014):
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29 427 $\text{Net CaCO}_3 \text{ accumulation} = \text{Gross calcification} - \text{Gross CaCO}_3 \text{ dissolution} - \text{CaCO}_3$
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31 428 $\text{export (Equation 1)}$
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34 429

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36 430 Whereas the calcification and dissolution terms in this relationship can be defined by
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38 431 components falling under lower functional levels (e.g., cellular, organismal, and
39
40 432 population, or sediment grain, skeleton, and community, respectively), CaCO_3
41
42 433 dissolution and export are terms that feature prominently at the community level, but
43
44 434 can also be important for individuals (Fig. 2). There are biogeochemical techniques
45
46 435 with the potential to quantify the performance and function of coral reefs at the
47
48 436 ecosystem scale that effectively incorporate CaCO_3 dissolution and export into
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50 437 predictive models of coral reef ecosystem accretion, while embracing the need to
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52 438 integrate the contributions of lower functional levels to ecosystem function. For
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3 439 example, simultaneous measurements of seawater dissolved inorganic carbon and total
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5 440 alkalinity (TA) over space and time can be used to quantify relative levels of net
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7 441 ecosystem calcification and net ecosystem organic carbon production (Fig. 2; Gattuso
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9 442 et al. 1996, Suzuki and Kawahata 2003, Watanabe et al. 2006, Lantz et al. 2014).
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11 443 Evaluating TA anomalies relative to offshore conditions also provides information
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13 444 whether a reef is net calcifying (depletion of TA) or net dissolving (repletion of TA).
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15 445 These ecosystem properties are a function of performances at lower functional levels,
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17 446 but we have a poor quantitative understanding of the relative importance of community
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19 447 members within a given functional level to ecosystem-level processes.
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26 27 449 **Combining theory and observation**

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29 450 Nearly half a century ago, Levins (1966) argued that models in ecology can be
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31 451 organized by the balance they strike among the countervailing axes of realism,
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33 452 precision, and generality. Furthermore, he suggested that although models may enjoy
34
35 453 two of these desirable characteristics simultaneously, no model can be realistic, precise
36
37 454 and general all at once. Although the virtues of Levins's scheme are debatable, the
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39 455 core observation that models are subject to trade-offs is indisputable. No model or
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41 456 modeling approach is suited uniformly for all scientific purposes, in the same way that
42
43 457 no single empirical approach renders all other approaches inferior. Thus, we should
44
45 458 not expect a "Grand Unifying Theory" of the effects of ocean acidification on coral reefs
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47 459 to emerge that simultaneously unites all the scales of biological organization at which
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49 460 ocean acidification and its impacts can be described (Fig. 2). Instead, the science of
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3 461 ocean acidification on coral reefs will advance by embracing a suite of complementary
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5 462 modeling approaches and their associated strengths.
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10 464 The preceding sections have suggested several theoretical tools that may be useful for
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12 465 the study of ocean acidification, and which take different approaches to understanding
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14 466 complex, multi-scale behavior (Box 1). For example, both DEB and MTE flow from the
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16 467 philosophy that much of the variation observed in the natural world can be explained by
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18 468 appealing to a fundamental collection of first principles --- such as the allometric scaling
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20 469 of metabolic rates and the allocation of assimilated energy. Although these
21
22 470 approaches do not strive for pinpoint predictions for any particular time and place, they
23
24 471 can inform a conceptual backbone that unites disparate observations of the effects of
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26 472 ocean acidification. In contrast, contemporary computing power has enabled detail-
27
28 473 rich computer simulations of highly specific and complex systems. Such computing
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30 474 power can be deployed to study complex systems as varied as the different genetic
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32 475 pathways within a single cell (so-called systems biology; Kitano 2002), or the
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34 476 interactions among thousands to millions of individuals in an ecosystem (often called
35
36 477 individual- or agent-based models; Grimm et al. 2005). These approaches emerged
37
38 478 from the philosophy that a detailed understanding of the rules that govern behavior
39
40 479 within a complex system can enable profitable exploration of the emergent properties of
41
42 480 that system through computer simulation. Lying somewhere between these two
43
44 481 extremes are compartmental models (including stage-structured models) that have
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46 482 featured prominently in population and community ecology. Compartmental models do
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48 483 not strive for the same broad universality as DEB or MTE, but also require strategic
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3 484 assumptions about which sources of biological variation must be incorporated into a
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6 485 model, and which can be ignored.
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10 487 Finally, just as theory and empiricism benefit from a diverse collection of approaches,
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12 488 theory and empiricism themselves provide complementary routes to scientific progress,
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15 489 and thus both benefit from a vigorous exchange of ideas. Indeed, both theory and
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17 490 experimentation can inspire new hypotheses that motivate evaluation from a
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20 491 complementary perspective. The learning that ensues may suggest refinement of the
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22 492 hypothesis, or even wholesale rejection.
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24 493

27 494 **Summary and future directions**

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32 496 Given the rapid changes in seawater carbonate chemistry that are being driven by
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34 497 anthropogenic effects, and the long time necessary to reverse these effects once CO₂
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36 498 emissions are reduced (Ciais et al. 2013), there are compelling reasons to be
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38
39 499 concerned about the impacts of ocean acidification on coral reefs (Gattuso et al. 2014).
40
41 500 We still lack basic understanding of the time that it takes for a coral reef to transition
42
43 501 from net deposition to net dissolution, and how such a process would reduce structural
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45
46 502 complexity of the reef and impair its ecological function (e.g., habitat provisioning
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48 503 [Fabricius et al. 2014], wave buffering, etc.). It is clear that theoretical approaches, in
49
50 504 addition to the multi-scale approaches outlined above, will be needed to evaluate the
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53 505 impact of a reef transitioning from net deposition to net dissolution (and the reverse).
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55 506 Such approaches have the capacity to model the effect of ocean acidification on
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3 507 emergent properties (species composition, diversity, richness) that influence the
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6 508 functionality (species interactions, NEP, NEC) of coral reef ecosystems. Against this
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8 509 backdrop, there are several research priorities that should be addressed to improve the
9
10 510 synthetic capacity of ocean acidification studies on coral reefs that may ultimately help
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12 511 mitigate the deleterious impacts of CO₂-induced ocean acidification:
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17 513 Since the threat of ocean acidification for calcified marine ecosystems first became
18
19 514 apparent, there has been a massive increase in empirical studies designed to document
20
21 515 the effects on organisms. Future progress will depend upon the integration of these
22
23 516 observed effects and the application of theory to these massive datasets. Powerful
24
25 517 and appropriate theory already is available for this task, and significant effort should be
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27 518 allocated to adapting and expanding this theory to coral reef applications.
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34 520 Although integrating the effects of ocean acidification across multiple functional scales
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36 521 (Fig. 2) will advance the field, there are still many pieces missing from the puzzle.
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38 522 Major needs include: (i) greater attention to the effects of OA on processes (e.g.,
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40 523 recruitment, competition, predation, bioerosion, CaCO₃ dissolution) that mediate
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42 524 connections between functional scales on coral reefs; (ii) improved understanding of the
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44 525 ways in which physical and chemical aspects of the environment modulate biological
45
46 526 responses to ocean acidification; (iii) expansion of taxonomic breadth of ocean
47
48 527 acidification experiments; (iv) improved understanding of population-level impacts of
49
50 528 ocean acidification; and (5) improved understanding of how population-level impacts of
51
52 529 OA sum to community- and ecosystem-level impacts.
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531 Acknowledgements

532

533 This research resulted from a workshop convened from 16-19 June 2014 at the WIES
534 Boone Center on Santa Catalina Island, funded by the US National Science Foundation
535 (OCE-1041270 to PJE and RCC), the Moorea Coral Reef LTER (NSF OCE-1236905),
536 California State University, Northridge (CSUN), and the University of Southern
537 California. We are grateful to our friends and colleagues who knowingly or unwittingly
538 contributed to the ideas expressed above, although we are entirely responsible for the
539 content of this paper. This is contribution number xxx of the CSUN Marine Biology
540 Program and a contribution to the Ocean 2015 Initiative.

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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

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3 817 distinguishes among calcification at the scale of (A) cells, (B) organisms, (C)
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5 818 populations, and (D, E) communities and ecosystems, all of which are forced to
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8 819 some extent by environmental factors (F); these scales serve as a construct
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10 820 within which the challenges can be articulated, and solutions discussed, thereby
11
12 821 leading to effective integration. At each scale, traits are described that address
13
14 822 the factors modulating calcification, and arrows among the scale describe the
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16 823 direction of scaling effect. At the population (C) and community (D) scales, we
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18 824 emphasize the complexity added through the presence of multiple categories of
19
20 825 benthic organisms (corals, macroalgae [MA], and crustose coralline algae [CA])
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22 826 that vary in abundance through space and time. Ecosystem-level processes (E)
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24 827 represent the highest level of complexity that we seek to understand. At this
25
26 828 levels efforts will likely focus on community metabolism and its response to key
27
28 829 large-scale responses to ocean acidification. For illustrative purposes, we focus
29
30 830 on the interactive effects of dissolved inorganic carbon (C_T) and total alkalinity
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32 831 (A_T) on the balance between gross primary production (GPP) and respiration (R)
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34 832 and $CaCO_3$ deposition (G) and dissolution (D).
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834 **Box 1**

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

838 **(A) Simple extrapolation** utilizes empirical data describing physiological responses of
839 reef calcifiers to differing pCO₂ regimes, and extrapolates these responses based on
840 community composition. As an illustration, we show a quadrat recorded at 17-m depth
841 on the outer reef of Moorea in 2006 that was used as a basis to create a reef
842 community in a flume for which calcification as function of pCO₂ was determined. To
843 extrapolate the effects of ocean acidification, the community structure in 2006 was used
844 to evaluate the percentage cover of CCA and the population size structure
845 scleractinians belonging to branching, mounding, or sheeting functional groups. Based
846 on these data, community calcification (g m⁻² d⁻¹) was calculated under present day
847 conditions (~ 400 µatm pCO₂) and those expected by the end of the current century
848 (~1000 µatm pCO₂) (E). CCA cover was taken as 20%, the mean size of corals in the
849 three function groups were calculated (shown in histograms) and their mean densities
850 were 13.9, 5.0, and 6.9 colonies m⁻² for branches, mounds, and plates. Coral surface
851 areas were calculated from the relationship between diameter and area (as determined
852 for *Pocillopora verrucosa* from $y = 2.493 \cdot x^{2.312}$ where y is area [cm²] and x is diameter
853 [cm]), and assuming mounds were hemispheres, and sheets were circles. Organismic
854 rates of calcification at different pCO₂ values were obtained from Comeau et al. 2013,
855 2014, 2015).

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3 856 (B) The **experimental** approach relies on direct measurements of net community
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6 857 calcification, which in our recent work (Comeau et al. 2015) exploits communities
7
8 858 assembled from specimens collected from the outer reef (17-m depth) and assembled
9
10 859 at ecologically relevant densities (as assessed from percent cover) in a 5.0 x 0.3 m
11
12 860 flume. These communities included carbonate pavement, which was added to capture
13
14
15 861 the effects of dissolution in this aspect of the community.
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17 862 (C) **Processed based** posits that reef-scale calcification can be understood based on
18
19 863 first principles of biological organization. The Metabolic Theory of Ecology [MTE;
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21
22 864 Brown et al. 2004] for example, uses allometric scaling to predict emergent property of
23
24 865 an ecosystem (such as the net calcification rate) using power-law relationships between
25
26 866 physiology and colony size, and abundance and colony size. Integrating the former
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29 867 relationship over size-frequency distributions yields a net calcification rate for the entire
30
31 868 reef. A mature MTE for coral reefs has yet to appear, and so we illustrate a
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33
34 869 hypothetical scaling relationships inspired by MTE (Enquist et al. 2003, West et al.
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36 870 2009) and informed by empirical data describing the size-frequency structure of
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38
39 871 branching, mounding, and sheeting corals (as in 2006 at 17-m depth) and empirically
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41 872 calcification rates at the organismic level (both as in A above). The product of the
42
43 873 scaling relationships between average calcification rate per size class (y) and area (x)
44
45 874 and average abundance per size class (y) and area (x) yields the total calcification per
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48 875 size class (y) as a function of area (x). Integration of the values among area
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50 876 categories provides an estimate of community calcification under ambient and elevated
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53 877 pCO₂. While power laws provide good fits for observed coral scaling, as expected by
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55 878 theory, quadratic functions fit better for observed patterns of coral abundance (red).
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3 879 (D) The **simulation** approach builds an *in silico* replica of an ecosystem that
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6 880 incorporates all known rules of how individuals in a complex system behave and
7
8 881 interact, and then explores emergent ecosystem behavior through simulation under
9
10 882 various environmental scenarios. This approach is exemplified by individual-based
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12 883 models (Grimm and Railsback 2005), and is illustrated by the recent Madingley model
13
14 884 (Harfoot et al. 2014), which claims to provide “a mechanistic General Ecosystem Model
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16 885 ... that is both global and applies in all terrestrial and marine environments.” The
17
18 886 difference between analytical theory and computer simulation often is one of
19
20 887 dimensionality: theory strives to describe ecosystem structure and function through a
21
22 888 few key variables and parameters, while simulation uses brute computing power to
23
24 889 portray an ecosystem in fine detail. Of course, computer simulations require intricate
25
26 890 knowledge about how the entities in the simulation behave and interact. Such
27
28 891 knowledge can be and often is provided by experimental evidence and first-principles
29
30 892 theory (Harfoot et al. 2014), and thus computer simulations rely deeply on the advances
31
32 893 provided by other approaches to scientific discovery. IBMs specifically for coral-reef
33
34 894 ecosystems have yet to appear, and so we illustrate the approach with a cartoon.
35
36 895 (E) **Community calcification** calculated using the approaches described above (A-D)
37
38 896 to reveal differences in rates depending on scaling technique; it is not yet possible to
39
40 897 evaluate calcification rates from first principles using simulation techniques (shown as
41
42 898 “?”). The research challenge faced by the coral reef ocean acidification community is
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44 899 expanding existing theory to capitalize on the strengths of each domain while
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46 900 understanding the sources of mismatches in predictions and uncertainties in the
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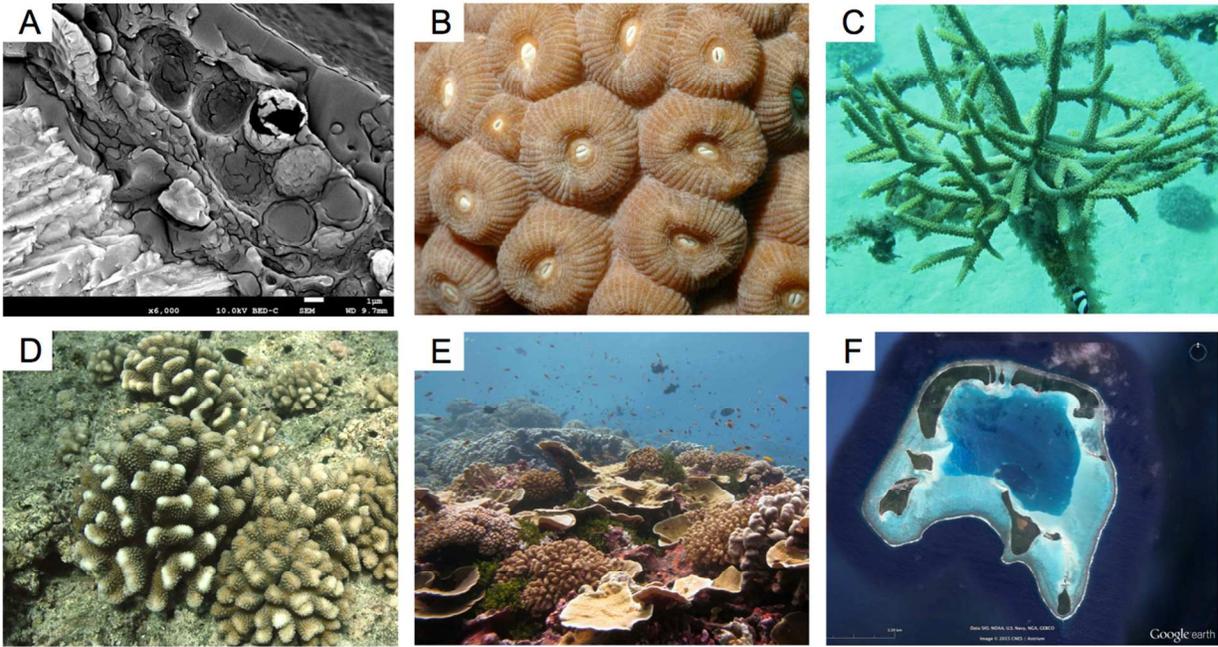
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3 901 properties of the predictions. Theoretical estimates shown here reflect quadratic fits for
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904 Fig. 1



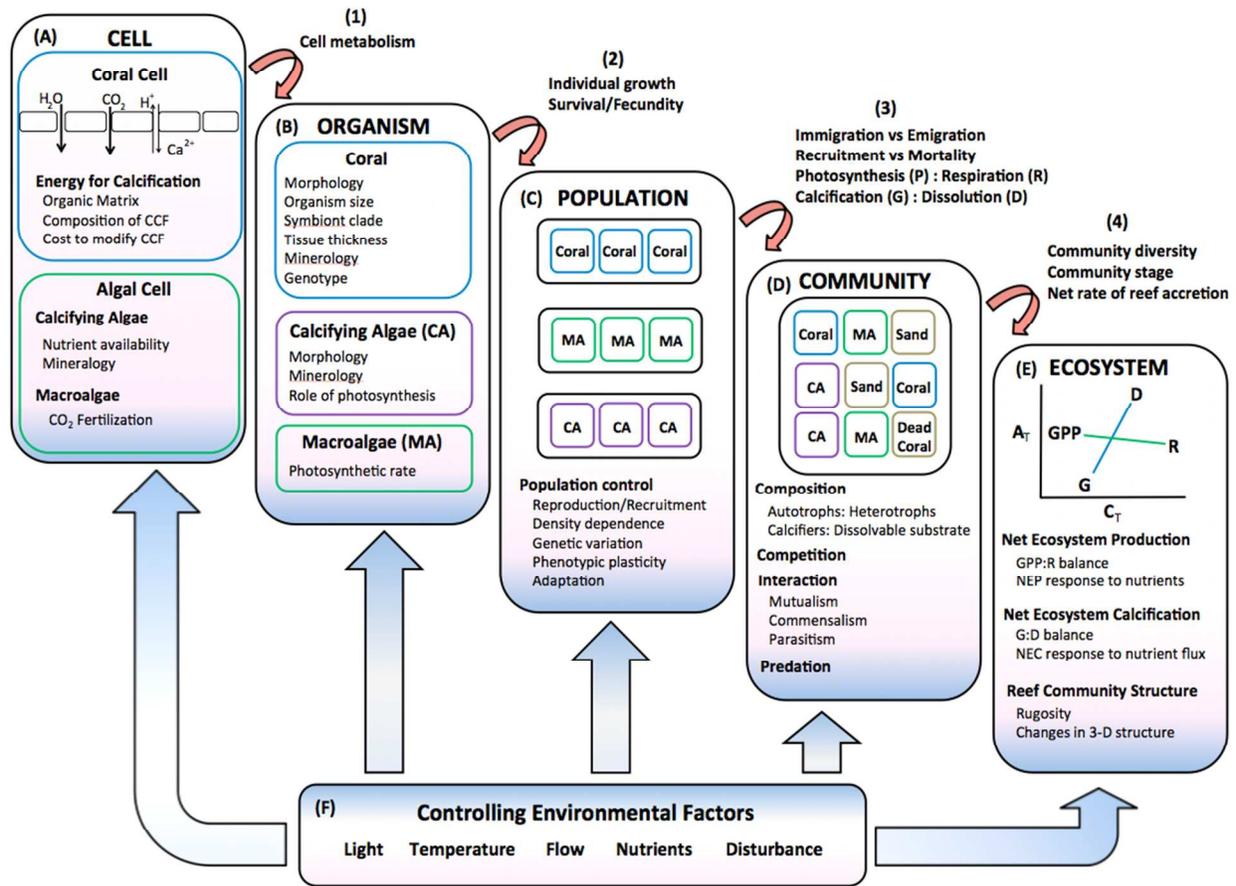
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907 Fig. 2



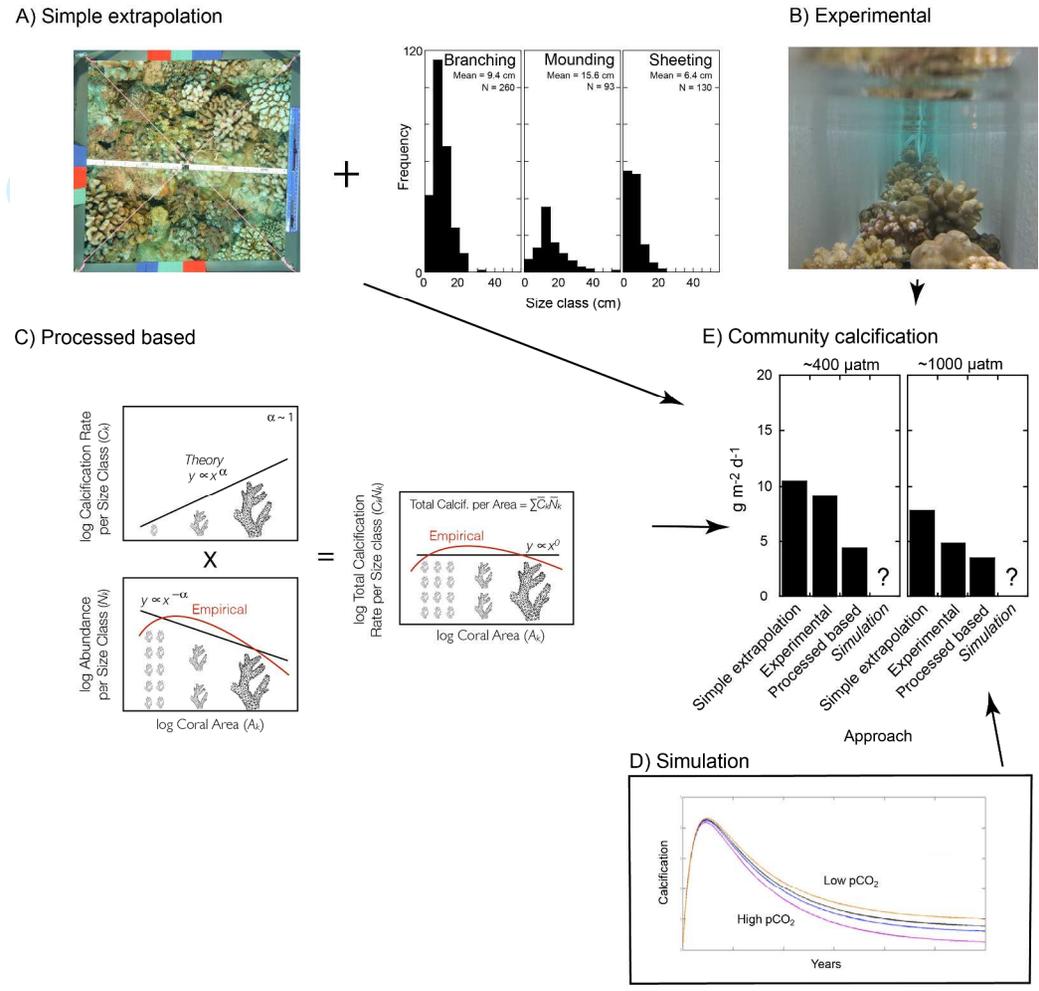
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909 Box Fig. 1



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