



## Gradients in primary production predict trophic strategies of mixotrophic corals across spatial scales

Fox, Michael D.; Williams, Gareth J.; Johnson, Maggie D.; Radice, Veronica Z.; Zgliczynski, Brian J.; Kelly, Emily L. A.; Rohwer, Forest L.; Sandin, Stuart A.; Smith, Jennifer E.

### Current Biology

DOI:  
[10.1016/j.cub.2018.08.057](https://doi.org/10.1016/j.cub.2018.08.057)

Published: 05/11/2018

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*  
Fox, M. D., Williams, G. J., Johnson, M. D., Radice, V. Z., Zgliczynski, B. J., Kelly, E. L. A., ... Smith, J. E. (2018). Gradients in primary production predict trophic strategies of mixotrophic corals across spatial scales. *Current Biology*, 28(21), 3355-3363.  
<https://doi.org/10.1016/j.cub.2018.08.057>

#### Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

#### Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 **Title:** *Gradients in primary production predict trophic strategies of mixotrophic corals across*  
2 *spatial scales*

3

4

5 **Authors:** Michael D. Fox<sup>1,2\*</sup>, Gareth J. Williams<sup>3</sup>, Maggie D. Johnson<sup>4</sup>, Veronica Z. Radice<sup>5</sup>,

6 Brian J. Zgliczynski<sup>1</sup>, Emily L.A. Kelly<sup>1</sup>, Forest L. Rohwer<sup>6</sup>, Stuart A. Sandin<sup>1</sup>, Jennifer E.

7 Smith<sup>1</sup>

8 <sup>1</sup>Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography,

9 University of California San Diego, La Jolla, CA, 92037 USA

10 <sup>2</sup>Lead contact

11 <sup>3</sup>School of Ocean Sciences, Bangor University, Anglesey LL59 5AB, UK

<sup>4</sup>Smithsonian Marine Station, Fort Pierce, FL, 34949 USA

12 <sup>5</sup>Global Change Institute, Australian Research Council Centre of Excellence for Coral Reef

13 Studies, University of Queensland, St. Lucia 4072, QLD, Australia

14 <sup>6</sup>Department of Biology, San Diego State University, San Diego, CA, 92182 USA

15 **\*Correspondence:** [fox@ucsd.edu](mailto:fox@ucsd.edu)

16

17

18

19

20

21

22

23

24

25 **SUMMARY**

26 Mixotrophy is among the most successful nutritional strategies in terrestrial and marine  
27 ecosystems. The ability of organisms to supplement primary nutritional modes along continua of  
28 autotrophy and heterotrophy fosters trophic flexibility that can sustain metabolic demands under  
29 variable or stressful conditions. Symbiotic, reef-building corals are among the most broadly  
30 distributed and ecologically important mixotrophs, yet we lack a basic understanding of how  
31 they modify their use of autotrophy and heterotrophy across gradients of food availability. Here  
32 we evaluate how one coral species, *Pocillopora meandrina*, supplements autotrophic nutrition  
33 through heterotrophy within an archipelago, and test if this pattern holds across species globally.  
34 Using stable isotope analysis ( $\delta^{13}\text{C}$ ) and satellite-derived estimates of nearshore primary  
35 production (chlorophyll-*a*, as a proxy for food availability), we show that *P. meandrina*  
36 incorporates a greater proportion of carbon via heterotrophy when more food is available across  
37 five central Pacific islands. We then show that this pattern is consistent globally using data from  
38 15 coral species across 16 locations spanning the Caribbean, Indian, and Pacific Oceans.  
39 Globally, surface chlorophyll-*a* explains 77% of the variation in coral heterotrophic nutrition,  
40 86% for one genus across 10 islands, and 94% when controlling for coral taxonomy within  
41 archipelagos. These results demonstrate, for the first time, that satellite-derived estimates of  
42 nearshore primary production provide a globally relevant proxy for resource availability that can  
43 explain variation in coral trophic ecology. Thus, our model provides a pivotal step towards  
44 resolving the biophysical couplings between mixotrophic organisms and spatial patterns of  
45 resource availability in the coastal oceans.

46 **Key Words:** Coral reef, Heterotrophy, Stable Isotopes, Phytoplankton, Nutrients, Chlorophyll-*a*,  
47 Oceanography, Remote Sensing

## 48 INTRODUCTION

49           Mixotrophic organisms can balance their reliance on different nutritional modes (i.e.,  
50 autotrophy and heterotrophy) in accordance with spatiotemporal fluctuations in resource  
51 availability. This trophic flexibility allows mixotrophs to adapt to a wide range of terrestrial and  
52 aquatic biomes, making mixotrophy one of the most ubiquitous nutritional strategies on earth [1].  
53 Most mixotrophs subsist along a continuum of autotrophy and heterotrophy, such as vascular  
54 plants that can supplement autotrophic nutrition along gradients of limiting resources through  
55 carnivory or mycoheterotrophy [2, 3]. Dynamic marine environments favor mixotrophic  
56 organisms, which are broadly distributed and provide crucial linkages for energy flow between  
57 trophic levels [4]. Many cnidarians and sponges have evolved a tight symbiosis with microalgae  
58 to sustain high rates of primary production in oligotrophic regions [5, 6]. Of these animals,  
59 mixotrophic reef-building corals form the foundation of one of the most biodiverse and  
60 productive marine ecosystems, yet our understanding of how corals adjust nutritional modes in  
61 response to natural gradients in resource availability (e.g., inorganic nutrients and particulate  
62 resources) remains limited [7]. Given their pantropical distribution, mixotrophic corals represent  
63 an opportunity to examine the biophysical coupling between resource availability and the trophic  
64 ecology of mixotrophic organisms across spatial scales.

65           Reef-building corals obtain energy from both autotrophy, via their endosymbiotic  
66 microalgae of the genus *Symbiodinium*, and heterotrophy via the capture of allochthonous  
67 particles [8]. While the physiological benefits of this trophic plasticity were acknowledged by  
68 early studies of coral biology [5], the ecological success of scleractinian corals has long been  
69 attributed to their symbiotic nature [9]. Indeed, photosynthetically fixed carbon translocated from  
70 endosymbionts to the coral host can contribute more than 100% of the daily metabolic

71 requirements of corals [10-12]; however much of the fixed carbon is respired or released as  
72 mucus rather than incorporated into host biomass [13, 14]. Heterotrophy on the other hand,  
73 provides corals with carbon and essential nutrients (e.g., nitrogen and phosphorus) that directly  
74 support growth and reproduction [15, 16]. The physiological importance of heterotrophy for  
75 corals is widely accepted, yet a disproportionate amount of research to date has focused on the  
76 role of endosymbionts in defining coral nutrition [7].

77 Heterotrophic nutrition can mitigate the negative effects of environmental stressors on  
78 coral physiology. For example, heterotrophy can increase coral recovery rates following acute  
79 stress, decrease overall mortality, and help reestablish the coral-algal symbiosis following  
80 thermally-induced bleaching [11, 17-19]. Heterotrophic nutrition can increase coral fecundity  
81 [15] and also facilitate calcification under low pH conditions, which is critical for coral growth  
82 and therefore the structural development and persistence of reefs through time [20, 21]. *In situ*,  
83 increased rates of heterotrophy by corals are often considered a response to the contrasting  
84 gradients of light and resource availability [22] and are thought to increase with depth [23].  
85 However, some corals may feed continuously across depth in areas where heterotrophic  
86 resources are more abundant [24, 25]. Food availability for corals is linked with nearshore  
87 primary production ( $PP_n$ ) [26]. Thus future reductions in  $PP_n$ , caused by increased ocean  
88 stratification [27] and moderate to strong El Niño events [28] likely represent an unanticipated  
89 stressor on the persistence of coral populations in a warming ocean. Understanding the  
90 relationship between  $PP_n$  and coral trophic ecology will improve our capacity to accurately  
91 predict the implications of global change on coral populations over space and time.

92 To date, our understanding of heterotrophic nutrition in corals is largely laboratory-based  
93 [7, 14, 16, 19, 29, 30], thus limiting our ability to assess coral feeding at broader, more

94 ecologically relevant scales. New techniques are required to propel our understanding of coral  
95 nutrition beyond individual colonies and to scale these patterns up to entire reef ecosystems. An  
96 essential first step is to link regional variation in environmental conditions with the biological  
97 responses of corals. Remotely sensed estimates of surface chlorophyll-*a* (chl-*a*) [31] have  
98 revealed significant increases in phytoplankton biomass in the nearshore regions of oceanic  
99 islands across the Pacific [26]. Notably, these satellite-derived chl-*a* estimates are correlated  
100 strongly with PP<sub>n</sub> throughout the photic zone as well as the relative abundance of zooplankton, a  
101 primary food resource for corals [32, 33]. Remotely sensed surface chl-*a* may therefore provide a  
102 globally relevant proxy for estimating PP<sub>n</sub> and heterotrophic resource availability on coral reefs.  
103 Similarly, stable isotope analyses ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of coral hosts and their endosymbionts can  
104 assess the relative contributions of heterotrophic and autotrophic nutrition across multiple coral  
105 species and spatial scales [18, 23, 24].

106       To test for a link between heterotrophic resource availability and the trophic response of  
107 mixotrophic corals, we compared the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of corals to satellite-derived estimates  
108 of PP<sub>n</sub> (using chl-*a* as a proxy for plankton biomass). At an archipelago scale, we measured the  
109 degree of heterotrophy in a common reef-building coral (*Pocillopora meandrina*) collected  
110 across depths (5-30 m) at five uninhabited islands in the Southern Line Islands of Kiribati (SLI)  
111 and modeled these against concurrent changes in PP<sub>n</sub>. To determine if the same relationship held  
112 globally, we synthesized published  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for 15 coral species from 16 locations  
113 across the Red Sea, Caribbean, Indian and Pacific Oceans and modeled these against  
114 climatological estimates of PP<sub>n</sub> for each location.

115

## 116 **RESULTS**

## 117 **Oceanographic context of the Southern Line Islands (SLI)**

118           The oceanic primary production gradient across the SLI is conspicuous, with  
119 climatological surface chl-*a* concentrations (2004-2015) separating the islands into distinct  
120 regions (Figure 1A, 1B). Surface chl-*a* (a proxy for PP<sub>n</sub>) was similar at the three southern islands  
121 (Flint, Vostok, and Millennium) while considerably higher and with less inter-annual variation at  
122 the northern two (Starbuck and Malden) ( $F_{4,55} = 27.48$ ,  $p < 0.01$ ; Tukey HSD: FLI, VOS, MIL <  
123 STA, MAL). The mean depth of light penetration at 490 nm (a proxy for light attenuation) from  
124 2004-2015 ranged from 29-35 m, which suggests the light environment on these islands does not  
125 differ markedly on decadal time scales. Inorganic nutrient concentrations were latitude-  
126 dependent and closely associated with the chl-*a* gradient (Figure 1C). Mean dissolved inorganic  
127 nitrogen (DIN) concentrations increased nine-fold (0.51-4.69  $\mu\text{mol}$ ) from south to north with a  
128 concomitant increase in soluble reactive phosphorus (SRP) (0.15-0.44  $\mu\text{mol}$ ,  $F_{4,40} = 70.66$ ,  $p <$   
129 0.01). Within islands, inorganic nutrient concentrations were homogenous in the upper 30 m and  
130 consistent with measurements from 2009 [34]. During our study, *in situ* irradiance was similar  
131 throughout the SLI and there was no pattern between islands (i.e., the more productive islands  
132 did not have reduced irradiance relative to the more oligotrophic islands). On sunny days, mean  
133 daily irradiance ranged from 374-546  $\mu\text{E m}^{-2} \text{ s}^{-1}$  and total integrated daily irradiance ranged from  
134 11.76-17.04  $\text{E m}^{-2} \text{ d}^{-1}$ .

135           Coral and endosymbiont  $\delta^{15}\text{N}$  values were influenced most strongly by location due to a  
136 baseline shift in  $\delta^{15}\text{N}$  of nitrate that occurs along the oceanic primary production gradient in the  
137 equatorial Pacific (lower  $\delta^{15}\text{N}$  values closer to the equator) [35]. As a result, coral and  
138 endosymbiont  $\delta^{15}\text{N}$  decreased from Flint to Malden. The endosymbiont fraction became more  
139 deplete in  $^{15}\text{N}$  with depth at all islands while coral host  $\delta^{15}\text{N}$  only declined with depth on

140 Starbuck (Tables S1, S2). C:N values were elevated in the coral host fraction on Starbuck and  
141 Malden, which indicates the nitrogen content of the coral and endosymbiont fractions did not  
142 increase along the nutrient gradient (Table S1). However, the overall chl-*a* content of *P.*  
143 *meandrina* endosymbionts increased from Flint to Malden (Island:  $F_{(4,60)} = 21.26$ ,  $p < 0.01$ ,  
144 TukeyHSD: FLI < VOS, MIL, STA < MAL). Pigment content generally increased from 10-30 m  
145 but was highly variable (Depth:  $F_{(2,60)} = 6.61$ ,  $p < 0.01$ , TUKEY HSD: 10m < 30 m, Figure S1).  
146 Endosymbiont density was positively correlated with chl-*a* content at 10 m depth across all  
147 islands (Pearson's correlation:  $t_{(1,25)} = 5.27$ ,  $p < 0.01$ ,  $r = 0.73$ ).

148

#### 149 **Isotopic evidence for coral heterotrophy across islands and depth**

150 The  $\delta^{13}\text{C}$  values of coral and endosymbiont tissues can be influenced by differences in  
151 photosynthetic rates (autotrophic nutrition) and by the incorporation of allochthonous food  
152 sources via particle capture (referred to herein as heterotrophic carbon). Decreased rates of  
153 photosynthetic fractionation cause coral host and endosymbiont  $\delta^{13}\text{C}$  values to decrease with  
154 depth [23]. Planktonic communities and POM are the primary heterotrophic resources for corals.  
155 On most coral reefs these resources are depleted in  $^{13}\text{C}$  (more negative  $\delta^{13}\text{C}$ ) relative to  
156 *Symbiodinium* spp. by at least 4-6 ‰ [25]. Thus, increased heterotrophic nutrition leads to a  
157 reduction in coral host  $\delta^{13}\text{C}$  values. The relative difference between the coral host and  
158 endosymbiont  $\delta^{13}\text{C}$  ( $\Delta^{13}\text{C} = \delta^{13}\text{C}_{\text{host}} - \delta^{13}\text{C}_{\text{endosymbiont}}$ ) can therefore be used to disentangle the  
159 relative effects of photosynthetic fractionation and incorporation of heterotrophic carbon. While  
160 not a quantitative estimate of the heterotrophic contribution to a corals metabolic demands, this  
161 isotopic proxy ( $\Delta^{13}\text{C}$ ) provides insight to deviations from a fully autotrophic diet and reliably  
162 tracks intra-island gradients in resource availability [18, 23, 24].



163 Coral host and endosymbiont  $\delta^{13}\text{C}$  values declined linearly with depth and  $\delta^{13}\text{C}$  for both  
164 fractions ranged from -14 to -18 ‰ across the SLI (Figure 1A-E, Table S1). Host  $\delta^{13}\text{C}$  was  
165 consistently lower than the endosymbiont fraction and was greatest at Flint (southernmost island)  
166 and lowest at Malden (northernmost). In contrast, endosymbiont  $\delta^{13}\text{C}$  did not vary among  
167 islands. As an additional proxy of coral heterotrophy we also examined the relative similarity of  
168 coral host  $\delta^{13}\text{C}$  and the mean  $\delta^{13}\text{C}$  of the reef associated zooplankton at each island ( $\Delta^{13}\text{C}_{\text{host-}}$   
169  $\text{zooplankton} = \delta^{13}\text{C}_{\text{host}} - \delta^{13}\text{C}_{\text{zooplankton}}$ ). Coral host  $\delta^{13}\text{C}$  values became more similar to zooplankton  
170  $\delta^{13}\text{C}$  (more depleted in  $^{13}\text{C}$ , lower  $\Delta^{13}\text{C}_{\text{host-zooplankton}}$ ) with increasing surface chl-*a*, indicating a  
171 greater incorporation of heterotrophic carbon at the more productive islands ( $\Delta^{13}\text{C}_{\text{host-zooplankton}} -$   
172  $F_{(1,3)} = 44.89, p = <0.01, r^2 = 0.94$ , Figure 1D). There was no relationship between coral and  
173 zooplankton  $\delta^{15}\text{N}$  ( $\Delta^{15}\text{N}_{\text{host-zooplankton}} - F_{(1,3)} = 0.97, p = 0.65$ ).

174 In contrast to the individual  $\delta^{13}\text{C}$  values of the corals and endosymbiont tissues,  $\Delta^{13}\text{C}$   
175 ( $\delta^{13}\text{C}_{\text{host}} - \delta^{13}\text{C}_{\text{endosymbiont}}$ ) varied as a function of chl-*a* across the SLI (Figure 2F-J, Table S1). *P.*  
176 *meandrina*  $\Delta^{13}\text{C}$  was most negative on islands with higher surface chl-*a*. On Flint and Vostok  
177 (most oligotrophic), *Pocillopora* exhibited increased reliance on heterotrophic carbon sources  
178 (more negative  $\Delta^{13}\text{C}$ ) as a function of depth (from 5 to 30 m depth: Flint: slope = -0.23,  $p < 0.01,$   
179  $r^2 = 0.97$  Vostok: slope = -0.19,  $p = 0.05, r^2 = 0.67$ , Figure 2I, 2J, Table S1). There was no depth  
180 dependence of  $\Delta^{13}\text{C}$  on Millennium, Starbuck, or Malden (Figure 2F, 2G, 2H). Importantly,  $\Delta^{13}\text{C}$   
181 was not related to coral surface area normalized chl-*a* concentrations (Pearson's correlation:  
182  $t_{(1,25)} = -1.89, p = 0.2, r = 0.1$ ) or endosymbiont densities ( $t_{(1,25)} = 1.65, p = 0.2, r = 0.25$ ).

183 Coral  $\Delta^{15}\text{N}$  and  $\Delta\text{C:N}$  values showed no consistent relationships with islands or depth  
184 (Table S2).  $\Delta^{15}\text{N}$  values on Millennium were similar with those of Flint and Vostok but did not  
185 increase with depth. On Starbuck and Malden,  $\Delta^{15}\text{N}$  values were generally lower and did not

186 vary with depth. Coral  $\Delta C:N$  was highest on Starbuck and Malden indicating greater  
187 concentrations of lipids in the animal fraction on the more productive islands.

### 188 **Global patterns of coral $\delta^{13}C$ and $\delta^{15}N$ in relation to nearshore primary production**

189 Coral  $\delta^{13}C$  and  $\delta^{15}N$  values vary with large-scale physical processes but  $\Delta^{13}C$  is most  
190 tightly coupled with surface chl-*a* across 16 locations spanning three ocean basins. Latitude was  
191 positively related to coral and endosymbiont  $\delta^{13}C$ , respectively, but this relationship did not  
192 explain a significant amount of variation due to the low  $\delta^{13}C$  values of *Madracis auretenra* on  
193 Curaçao (Figure S2, Table S4). Latitude was unrelated to  $\Delta^{13}C$ . Coral and endosymbiont  $\delta^{15}N$   
194 showed no coherent pattern when considered globally (Table S4). However, considering only  
195 *Pocillopora*, host and endosymbiont  $\delta^{15}N$  (but not  $\Delta^{15}N$ ) were well explained by latitude, chl-*a*,  
196 and estimated thermocline depth (Table S4).  $\delta^{15}N$  values were lowest in regions with shallower  
197 thermoclines and higher chl-*a*.

198 Coral and endosymbiont  $\delta^{13}C$  values were tightly constrained across species and  
199 geography and did not vary as a function of surface chl-*a* (Figure 3A-C, Table S2, S3). In  
200 contrast, surface chl-*a* explained 77% of the variation in mean coral  $\Delta^{13}C$  across 16 locations  
201 ( $F_{(1,14)} = 46.24$ ,  $r^2 = 0.77$ ,  $p < 0.01$ , Figure 3D, Table S3). Additionally, depth of the 22° isotherm  
202 (a proxy for thermocline depth) explained 51-69% of the variation in coral  $\Delta^{13}C$  (Figure S2,  
203 Table S4). Our findings indicate that mixotrophic corals incorporate a greater proportion of  
204 heterotrophic carbon (more negative  $\Delta^{13}C$ ) in regions where resource abundance is enhanced by  
205 shallower thermoclines and higher surface chl-*a* concentrations.

206 The linear relationship between  $\Delta^{13}C$  and surface chl-*a* is globally consistent, irrespective  
207 of taxonomic resolution or spatial scale. For all species, coral or endosymbiont  $\delta^{13}C$  values  
208 showed no relationship to chl-*a* but  $\Delta^{13}C$ , while variable, declined significantly with increased

209 chl-*a* (Tables S2, S3). This relationship was similar when constrained to an archipelago scale  
210 (islands within the same region averaged together) to account for potential geographic sampling  
211 biases ( $F_{(1,5)} = 18.35$ ,  $p = 0.01$ ,  $r^2 = 0.79$ ). Controlling for four coral families common to all  
212 islands, surface chl-*a* remained a significant predictor but explained less variation than the  
213 original model at an island-scale ( $F_{(1,14)} = 19.04$ ,  $p < 0.01$ ,  $r^2 = 0.58$ ). When we controlled for coral  
214 taxonomy within archipelagos this model explained much more variation ( $F_{(1,5)} = 74.31$ ,  $p < 0.01$ ,  
215  $r^2 = 0.94$ ). Across seven additional linear models that varied by total species number and  
216 sampling location, the slope of our observed relationship varied by 6% and explained 70-86% of  
217 the overall variation in coral  $\Delta^{13}\text{C}$  (Table S3). Coral host  $\delta^{13}\text{C}$  was only related to surface chl-*a*  
218 in the two most simplified models and endosymbiont  $\delta^{13}\text{C}$  was not related to surface chl-*a* in any  
219 model. Notably, surface chl-*a* explained 86% of the variation in *Pocillopora spp.*  $\Delta^{13}\text{C}$  alone  
220 from the Maldives and central Pacific with a similar slope and intercept to the global model  
221 (Table S3).

222

## 223 **DISCUSSION**

224       Mixotrophic corals benefit greatly from heterotrophic nutrition but the role of  
225 oceanographic processes in structuring food availability, and the associated responses of corals,  
226 have not been widely studied [24, 36, 37]. Our results indicate the trophic ecology of some corals  
227 is spatially flexible, such that corals will increase their use of heterotrophic nutrition when  
228 resources are abundant. Specifically, we provide empirical evidence that spatial gradients in  
229 nearshore primary production ( $\text{PP}_n$ ) around coral reef islands can directly influence the  
230 nutritional status of mixotrophic corals on shallow reefs. Most importantly, we demonstrate that  
231 heterotrophic carbon incorporation ( $\Delta^{13}\text{C} = \delta^{13}\text{C}_{\text{host}} - \delta^{13}\text{C}_{\text{endosymbiont}}$ ) is related to surface

232 chlorophyll-*a* (chl-*a*) at a global scale for multiple coral species across three oceans. We also  
233 illustrate that PP<sub>n</sub> gradients can influence coral trophic ecology across islands and archipelagos.  
234 Our findings support the recent observation that seabird-vectored nutrients may stimulate PP<sub>n</sub>  
235 and subsequently enhance the growth and biomass of coral reef fish populations [38]. Notably,  
236 our study is the first to link patterns of PP<sub>n</sub> with the nutrition of coral communities (Figure 3),  
237 which provides further evidence that variation in PP<sub>n</sub> has strong implications for coral reef  
238 ecosystem functioning at multiple scales and trophic levels.

239 Our results support a working model that many corals will increase heterotrophy as a  
240 function of food availability. This is not surprising, as feeding in some coral species is nearly  
241 constant [16, 39] and heterotrophic nutrition is often a function of prey encounter rather than a  
242 necessity driven by metabolic deficit [40]. Consequently, patterns of PP<sub>n</sub> likely have significant  
243 influence on the nutritional status and energetic budgets of coral populations. Based on the  
244 strong agreement of our statistical analyses with this process-based model, we conclude that the  
245 nutritional status of mixotrophic corals is tightly coupled with patterns of PP<sub>n</sub> on a global scale.  
246 Specifically, using surface chl-*a* as a proxy for PP<sub>n</sub> we were able to estimate the  $\Delta^{13}\text{C}$  value of  
247 multiple coral species at 10 m depth. For example,  $\Delta^{13}\text{C}$  values were highly variable among  
248 thirteen species of coral from Jamaica (Table S2) [23], but when considered together, the mean  
249  $\Delta^{13}\text{C}$  converged on the value predicted by our linear regression. In another example, this  
250 relationship captured large seasonal variations in  $\Delta^{13}\text{C}$  reported for *Orbicella faveolata* in the  
251 northern Florida Keys at 8 m depth [41]. Using the climatological mean chl-*a* for this region  
252 (0.21 mg chl-*a* m<sup>-3</sup>), our model was able to approximate the inter-annual mean  $\Delta^{13}\text{C}$  (-1.1 ‰)  
253 reported by [41] within the error bounds of the linear regression ( $\Delta^{13}\text{C} = 0.6$  to  $-1.1$ ‰). We  
254 acknowledge that this relationship may not be relevant for all species, as corals demonstrate

255 diverse nutritional strategies [29, 39, 42] and differential feeding responses under stressful  
256 conditions [11, 43]. Furthermore, the relationship described here cannot resolve all variation in  
257 coral  $\Delta^{13}\text{C}$  driven by changes in metabolic demands associated with seasonality or environmental  
258 conditions (e.g., temperature, light, nutrients) [22]. This implies that the capacity of our model to  
259 predict coral trophic strategies will likely improve with the inclusion of additional environmental  
260 parameters. For example, in regions of strong seasonal upwelling, large drops in temperature can  
261 lower coral metabolic rates and suppress feeding during times of increased food availability [37].  
262 Most importantly, our results show that the relationship between  $\Delta^{13}\text{C}$  and surface chl-*a* is  
263 effectively constant, whether for a single species (*P. meandrina*) or a global composite of  $\Delta^{13}\text{C}$   
264 means derived from 15 species across 16 locations [24, 44].

265 Our findings also provide strong evidence that at smaller spatial scales (islands and  
266 archipelagos)  $\text{PP}_n$  can influence how a common coral species relies on heterotrophic nutrition  
267 across depths. In oligotrophic waters, corals primarily subsist on autotrophy in the particulate-  
268 deplete but well-illuminated shallows (more positive  $\Delta^{13}\text{C}$ ) and supplement with heterotrophy as  
269 particulate resource availability increases with depth [23, 24, 37, 44]. Consistent with this  
270 expectation, heterotrophic nutrition in *P. meandrina* increased with depth (more negative  $\Delta^{13}\text{C}$ )  
271 on the least productive islands in the SLI (Flint and Vostok). In more productive regions, deep-  
272 water internal waves frequently deliver inorganic nutrients and planktonic biomass from below  
273 the thermocline [44, 45], leading to increased surface chl-*a* and greater food availability at  
274 shallower depths [26, 33, 46]. Our results indicate that *P. meandrina* consumed more  
275 heterotrophic carbon (more negative  $\Delta^{13}\text{C}$ ) across all depths on Millennium, Starbuck and  
276 Malden. This reduction in  $\Delta^{13}\text{C}$  was driven by greater incorporation of carbon from zooplankton  
277 by the coral host (lower  $\Delta^{13}\text{C}_{\text{coral-zooplankton}}$ ). Coral C:N ratios also increased, consistent with

278 greater lipid content from heterotrophy in the host tissue, which can play an important role in  
279 coral resistance to and recovery following bleaching [47]. In contrast,  $\delta^{15}\text{N}$  values did not show  
280 consistent patterns across the SLI, suggesting that these changes in heterotrophy may be rather  
281 small in the context of the overall nutritional budget of the corals. Thus,  $\delta^{13}\text{C}$  may be a more  
282 informative proxy for detecting subtle changes in coral nutrition.

283         Satellite-derived estimates of  $\text{PP}_n$  provide useful estimates of food availability for  
284 shallow water corals, however these estimates do not capture all of the processes that influence  
285 food abundance and distribution on a given reef. For example, the  $\Delta^{13}\text{C}$  values on Millennium  
286 did not vary with depth as expected based on surface chl-*a* concentrations alone (chl-*a*  
287 concentrations similar to Flint and Vostok, Figure 1A). As the only atoll in the SLI, Millennium  
288 possesses a lagoon that exchanges water with the reef and the flushing of productive lagoon  
289 waters can influence  $\text{PP}_n$  [26]. Notably, spatially explicit downwelling of zooplankton-rich water  
290 from Palmyra Atoll's lagoon interacts with internal waves to homogenize food availability across  
291 depths, leading to static  $\Delta^{13}\text{C}$  values in *P. meandrina* from 10-30 m [24] and we hypothesize this  
292 is what is occurring at Millennium. Thus, where *inter-* and *intra-*island physical processes  
293 increase heterotrophic resources or re-distribute them throughout the water column, corals may  
294 feed opportunistically regardless of depth [17, 24].

295         To date, the physiological benefits of heterotrophic nutrition in corals have largely been  
296 determined in laboratory experiments (reviewed in [48]), though several studies have linked *in*  
297 *situ* feeding with resistance to and recovery following bleaching [11, 17]. As such, corals on  
298 reefs with elevated  $\text{PP}_n$  and greater access to heterotrophic resources may have a greater capacity  
299 to survive and recover from acute disturbances [49, 50]. On some coastal reefs, anthropogenic  
300 nutrient pollution can increase chl-*a* concentrations [51] and, more importantly, disrupt nitrogen

301 to phosphorus ratios (N:P) which can increase bleaching sensitivity in corals [52]. Our study  
302 identified 16 locations that span a three-fold gradient of naturally elevated surface chl-*a* (0.09-  
303 0.29 mg chl-*a* m<sup>-3</sup>) yet the highest values are 1.5-6 times lower than concentrations associated  
304 with increased bleaching sensitivity (>0.45 mg chl-*a* m<sup>-3</sup>) [53] and reduced species diversity in  
305 polluted locations (2 mg chl-*a* m<sup>-3</sup>) [54]. Thus, although in some coastal or more heavily  
306 impacted regions coral resistance to bleaching may not be correlated with surface chl-*a*, for  
307 many reefs slightly elevated chl-*a* likely confers benefits [55]. Future work to disentangle the  
308 roles of heterotrophic nutrition and background nutrient levels to coral persistence at will be  
309 valuable for refining projected coral reef trajectories in a warming ocean.

310 In conclusion, our study provides the first empirical evidence that coral trophic strategies  
311 track nearshore primary production (PP<sub>n</sub>) at multiple spatial scales. Our established relationship  
312 between coral nutrition ( $\Delta^{13}\text{C}$ ) and surface chl-*a* has high explanatory power and is based on  
313 freely available data. Importantly, our model can be applied to coral trophic ecology throughout  
314 the tropics because this metric of PP<sub>n</sub> is globally comprehensive. Previous investigations of  
315 upwelling and PP<sub>n</sub> on coral reefs have focused on the role of cooler, upwelled water to moderate  
316 temperatures and thus promote coral resistance to bleaching [56-59]. Given the strong  
317 connection between coral nutrition and PP<sub>n</sub> described here, the contribution of heterotrophy to  
318 coral recovery from bleaching has likely been underestimated in areas of naturally elevated PP<sub>n</sub>.  
319 As such, our model provides a framework to evaluate the importance of heterotrophy to the  
320 resilience of coral populations across regions with different background PP<sub>n</sub>. This information is  
321 essential for improving estimates of the response of corals, and other mixotrophic communities,  
322 to predicted variations in PP<sub>n</sub> in an era of global change.

323

324 **Acknowledgements**

325 We are grateful to the Environment and Conservation Division of the Republic of Kiribati for  
326 allowing us to conduct research within the Southern Line Islands. The authors thank the owner,  
327 captain, and crew of the M/Y Hanse Explorer for logistical support and field assistance. We also  
328 thank Jessica Glanz, Ellis Juhlin, Spencer Breining-Aday, Annika Vawter, and Ellen Williams  
329 for assistance in the lab. We thank the Moore Family Foundation, the Scripps family and several  
330 anonymous donors for their generous financial support. Finally, we are grateful to three  
331 anonymous reviewers for their time and valuable comments that have helped to improve this  
332 manuscript. VZR collected data from the Maldives with support from the XL Catlin Seaview  
333 Survey, funded by XL Catlin and the University of Queensland. MDF was supported by a Nancy  
334 Foster Scholarship from the NOAA Office of National Marine Sanctuaries.

335

336 **Author contributions**

337 Conceptualization: M.D.F., G.J.W., and J.E.S.; Methodology: M.D.F.; Investigation: M.D.F.,  
338 M.D.J., V.Z.R., B.J.Z, E.L.A.K., and J.E.S.; Writing – Original Draft: M.D.F, G.J.W., and J.E.S.;  
339 Writing – Review and Edits: All authors; Funding Acquisition: F.L.R., J.E.S., S.A.S.;  
340 Supervision: B.J.Z., F.L.R., J.E.S., S.A.S.

341

342 **Declaration of Interests**

343 The authors declare no competing interests.



## References

- 344  
345
- 346 1. Selosse, M.-A., Charpin, M., and Not, F. (2016). Mixotrophy everywhere on land and in  
347 water: the grand écart hypothesis. *Ecol. Lett.*, doi: 10.1111/ele.12714.
  - 348 2. Ellison, A.M., and Gotelli, N.J. (2002). Nitrogen availability alters the expression of  
349 carnivory in the northern pitcher plant, *Sarracenia purpurea*. *Proc. Natl. Acad. Sci. USA*.  
350 99, 4409-4412.
  - 351 3. Matsuda, Y., Shimizu, S., Mori, M., Ito, S.I., and Selosse, M.A. (2012). Seasonal and  
352 environmental changes of mycorrhizal associations and heterotrophy levels in  
353 mixotrophic *Pyrola japonica* (Ericaceae) growing under different light environments.  
354 *Am. J. Bot.* 99, 1177-1188.
  - 355 4. Stoecker, D.K., Hansen, P.J., Caron, D., A. , and Mitra, A. (2017). Mixotrophy in the  
356 Marine Plankton. *Ann. Rev. Mar. Sci.* 9, 311-335.
  - 357 5. Muscatine, L., and Porter, J.W. (1977). Reef corals: mutualistic symbioses adapted to  
358 nutrient-poor environments. *Bioscience* 27, 454-460.
  - 359 6. Venn, A.A., Loram, J.E., and Douglas, A.E. (2008). Photosynthetic symbioses in  
360 animals. *J. Exp. Bot.* 59, 1069-1080.
  - 361 7. Ferrier-Pagès, C., Hoogenboom, M., and Houlbrèque, F. (2011). The role of plankton in  
362 coral trophodynamics. In *Coral Reefs: an ecosystem in transition*, Z. Dubinsky and N.  
363 Stambler, eds. (Netherlands: Springer), pp. 215-229.
  - 364 8. Furla, P., Allemand, D., Shick, J.M., Ferrier-Pagès, C., Richier, S., Plantivaux, A., Merle,  
365 P.-L., and Tambutté, S. (2005). The Symbiotic Anthozoan: A Physiological Chimera  
366 between Alga and Animal. *Integrative and Comparative Biology* 45, 595-604.
  - 367 9. Veron, J.E.N. (1995). *Corals in space and time: the biogeography and evolution of the*  
368 *Scleractinia*, (Cornell University Press).
  - 369 10. Muscatine, L., McCloskey, L.R., and Marian, R.E. (1981). Estimating the daily  
370 contribution of carbon from zooxanthellae to coral animal respiration. *Limnol. Oceanogr.*  
371 26, 601-611.
  - 372 11. Grottoli, A.G., Rodrigues, L.J., and Palardy, J.E. (2006). Heterotrophic plasticity and  
373 resilience in bleached corals. *Nature* 440, 1186-1189.
  - 374 12. Davies, P.S. (1984). The role of zooxanthellae in the nutritional energy requirements of  
375 *Pocillopora eydouxi*. *Coral Reefs* 2, 181-186.
  - 376 13. Falkowski, P.G., Dubinsky, Z., Muscatine, L., and Porter, J.W. (1984). Light and the  
377 bioenergetics of a symbiotic coral. *Bioscience* 34, 705-709.
  - 378 14. Tremblay, P., Maguer, J.F., Grover, R., and Ferrier-Pagès, C. (2015). Trophic dynamics  
379 of scleractinian corals: stable isotope evidence. *J. Exp. Biol.* 218, 1223-1234.
  - 380 15. Cox, E.F. (2007). Continuation of sexual reproduction in *Montipora capitata* following  
381 bleaching. *Coral Reefs* 26, 721-724.
  - 382 16. Ferrier-Pagès, C., Witting, J., Tambutte, E., and Sebens, K.P. (2003). Effect of natural  
383 zooplankton feeding on the tissue and skeletal growth of the scleractinian coral  
384 *Stylophora pistillata*. *Coral Reefs* 22, 229-240.
  - 385 17. Palardy, J.E., Rodrigues, L.J., and Grottoli, A.G. (2008). The importance of zooplankton  
386 to the daily metabolic carbon requirements of healthy and bleached corals at two depths.  
387 *J. Exp. Mar. Biol. Ecol.* 367, 180-188.

- 388 18. Rodrigues, L.J., and Grottoli, A.G. (2006). Calcification rate and the stable carbon,  
389 oxygen, and nitrogen isotopes in the skeleton, host tissue, and zooxanthellae of bleached  
390 and recovering Hawaiian corals. *Geochem. Cosmochim. Ac.* 70, 2781-2789.
- 391 19. Tremblay, P., Gori, A., Maguer, J.F., Hoogenboom, M., and Ferrier-Pagès, C. (2016).  
392 Heterotrophy promotes the re-establishment of photosynthate translocation in a symbiotic  
393 coral after heat stress. *Sci. Rep.* 6, 38112.
- 394 20. Drenkard, E.J., Cohen, A.L., McCorkle, D.C., de Putron, S.J., Starczak, V.R., and Zicht,  
395 A.E. (2013). Calcification by juvenile corals under heterotrophy and elevated CO<sub>2</sub>. *Coral*  
396 *Reefs* 32, 727-735.
- 397 21. Edmunds, P.J. (2011). Zooplanktivory ameliorates the effects of ocean acidification on  
398 the reef coral *Porites* spp. *Limnol. Oceanogr.* 56, 2402-2410.
- 399 22. Anthony, K.R., and Fabricius, K. (2000). Shifting roles of heterotrophy and autotrophy in  
400 coral energetics under varying turbidity *J. Exp. Mar. Biol. Ecol.* 252, 221-253.
- 401 23. Muscatine, L., Porter, J.W., and Kaplan, I.R. (1989). Resource partitioning by reef corals  
402 as determined from stable isotope composition. I  $\delta^{13}\text{C}$  of zooxanthellae and animal tissue  
403 vs depth. *Mar. Biol.* 100, 185-193.
- 404 24. Williams, G.J., Sandin, S.A., Zgliczynski, B., Fox, M.D., Furby, K., Gove, J.M., Rogers,  
405 J.S., Hartmann, A.C., Caldwell, Z.R., Price, N.N., et al. (2018). Biophysical drivers of  
406 coral trophic depth zonation. *Mar. Biol.* 165, 60.
- 407 25. Alamaru, A., Loya, Y., Brokovich, E., Yam, R., and Shemesh, A. (2009). Carbon and  
408 nitrogen utilization in two species of Red Sea corals along a depth gradient: Insights from  
409 stable isotope analysis of total organic material and lipids. *Geochem. Cosmochim. Ac.*  
410 73, 5333-5342.
- 411 26. Gove, J.M., McManus, M.A., Neuheimer, A.B., Polovina, J.J., Drazen, J.C., Smith, C.R.,  
412 Merrifield, M.A., Friedlander, A.M., Ehses, J.S., Young, C.W., et al. (2016). Near-island  
413 biological hotspots in barren ocean basins. *Nat Commun* 7, 10581.
- 414 27. Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L.,  
415 Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M., and Boss, E.S. (2006).  
416 Climate-driven trends in contemporary ocean productivity. *Nature* 444, 752.
- 417 28. Brainard, R.E., Oliver, T., McPhaden, M.J., Cohen, A., Venegas, R., Heenan, A., Vargas-  
418 Ángel, B., Rotjan, R., Mangubhai, S., and Flint, E. (2018). Ecological Impacts of the  
419 2015/16 El Niño in the Central Equatorial Pacific. *Bull. Amer. Meteor. Soc.* 99, S21-S26.
- 420 29. Hoogenboom, M., Rottier, C., Sikorski, S., and Ferrier-Pagès, C. (2015). Among-species  
421 variation in the energy budgets of reef-building corals: scaling from coral polyps to  
422 communities. *J. Exp. Biol.* 218, 3866-3877.
- 423 30. Houlbrèque, F., Tambutté, E., and Ferrier-Pagès, C. (2003). Effect of zooplankton  
424 availability on the rates of photosynthesis, and tissue and skeletal growth in the  
425 scleractinian coral *Stylophora pistillata*. *J. Exp. Mar. Biol. Ecol.* 296, 145-166.
- 426 31. Gove, J.M., Williams, G.J., McManus, M.A., Heron, S.F., Sandin, S.A., Vetter, O.J., and  
427 Foley, D.G. (2013). Quantifying climatological ranges and anomalies for Pacific coral  
428 reef ecosystems. *PLoS ONE* 8, e61974.
- 429 32. Croll, D.A., Marinovic, B., Benson, S., Chavez, F.P., Black, N., Ternullo, R., and Tershy,  
430 B.R. (2005). From wind to whales: trophic links in a coastal upwelling system. *Mar.*  
431 *Ecol. Prog. Ser.* 289, 117-130.

- 432 33. Hazen, E.L., and Johnston, D.W. (2010). Meridional patterns in the deep scattering layers  
433 and top predator distribution in the central equatorial Pacific. *Fish. Oceanogr.* 19, 427-  
434 433.
- 435 34. Kelly, L.W., Williams, G.J., Barott, K.L., Carlson, C.A., Dinsdale, E.A., Edwards, R.A.,  
436 Haas, A.F., Haynes, M., Lim, Y.W., McDole, T., et al. (2014). Local genomic adaptation  
437 of coral reef-associated microbiomes to gradients of natural variability and anthropogenic  
438 stressors. *Proceedings of the National Academy of Sciences of the United States of*  
439 *America* 111, 10227-10232.
- 440 35. Altabet, M.A. (2001). Nitrogen isotopic evidence for micronutrient control of fractional  
441  $\text{NO}_3^-$  utilization in the equatorial Pacific. *Limnol. Oceanogr.* 46, 368-380.
- 442 36. Leichter, J.J., and Genovese, S.J. (2006). Intermittent upwelling and subsidized growth of  
443 the scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay,  
444 Jamaica. *Mar. Ecol. Prog. Ser.* 316, 95-103.
- 445 37. Palardy, J.E., Grottoli, A.G., and Matthews, K.A. (2005). Effects of upwelling, depth,  
446 morphology and polyp size on feeding in three species of Panamanian corals. *Mar. Ecol.*  
447 *Prog. Ser.* 300, 79-89.
- 448 38. Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S., and MacNeil, M.A.  
449 (2018). Seabirds enhance coral reef productivity and functioning in the absence of  
450 invasive rats. *Nature* 559, 250.
- 451 39. Lewis, J.B., and Price, W.S. (1975). Feeding mechanisms and feeding strategies of  
452 Atlantic reef corals. *J. Zool.* 176, 527-544.
- 453 40. Maier, C., Weinbauer, M.G., and Pätzold, J. (2010). Stable isotopes reveal limitations in  
454 C and N assimilation in the Caribbean reef corals *Madracis auretenra*, *M. carmabi* and *M.*  
455 *formosa*. *Mar. Ecol. Prog. Ser.* 412, 103-112.
- 456 41. Swart, P.K., Saied, A., and Lamb, K. (2005). Temporal and spatial variation in the  $\delta^{15}\text{N}$   
457 and  $\delta^{13}\text{C}$  of coral tissue and zooxanthellae in *Montastraea faveolata* collected from the  
458 Florida reef tract. *Limnol. Oceanogr.* 50, 1049-1058.
- 459 42. Porter, J.W. (1976). Autotrophy, heterotrophy, and resource partitioning in Caribbean  
460 reef-building corals. *Am. Nat.* 110, 731-742.
- 461 43. Grottoli, A.G., Warner, M.E., Levas, S.J., Aschaffenburg, M.D., Schoepf, V., McGinley,  
462 M., Baumann, J., and Matsui, Y. (2014). The cumulative impact of annual coral  
463 bleaching can turn some coral species winners into losers. *Global Change Biol.* 20, 3823-  
464 3833.
- 465 44. Leichter, J.J., Wing, S.R., Miller, S.L., and Denny, M.W. (1996). Pulsed delivery of  
466 subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnol.*  
467 *Oceanogr.* 41, 1490-1501.
- 468 45. Leichter, J.J., Stokes, M.D., Hench, J.L., Witting, J., and Washburn, L. (2012). The  
469 island - scale internal wave climate of Moorea, French Polynesia. *J. Geophys. Res.*  
470 *Oceans* 117.
- 471 46. Sevadjian, J.C., McManus, M.A., Benoit-Bird, K.J., and Selph, K.E. (2012). Shoreward  
472 advection of phytoplankton and vertical re-distribution of zooplankton by episodic near-  
473 bottom water pulses on an insular shelf: Oahu, Hawaii. *Cont. Shelf. Res.* 50, 1-15.
- 474 47. Baumann, J., Grottoli, A.G., Hughes, A.D., and Matsui, Y. (2014). Photoautotrophic and  
475 heterotrophic carbon in bleached and non-bleached coral lipid acquisition and storage. *J.*  
476 *Exp. Mar. Biol. Ecol.* 461, 469-478.

- 477 48. Houlbrèque, F., and Ferrier-Pagès, C. (2009). Heterotrophy in tropical scleractinian  
478 corals. *Biol Rev Camb Philos Soc* 84, 1-17.
- 479 49. Levas, S.J., Grottoli, A.G., Hughes, A., Osburn, C.L., and Matsui, Y. (2013).  
480 Physiological and biogeochemical traits of bleaching and recovery in the mounding  
481 species of coral *Porites lobata*: implications for resilience in mounding corals. *PLoS one* 8,  
482 e63267.
- 483 50. Anthony, K.R.N., Hoogenboom, M.O., Maynard, J.A., Grottoli, A.G., and Middlebrook,  
484 R. (2009). Energetics approach to predicting mortality risk from environmental stress: a  
485 case study of coral bleaching. *Funct. Ecol.* 23, 539-550.
- 486 51. Wooldridge, S.A. (2009). Water quality and coral bleaching thresholds: Formalising the  
487 linkage for the inshore reefs of the Great Barrier Reef, Australia. *Mar. Pollut. Bull.* 58,  
488 745-751.
- 489 52. Wiedenmann, J., D'Angelo, C., Smith, E.G., Hunt, A.N., Legiret, F.-E., Postle, A.D., and  
490 Achterberg, E.P. (2012). Nutrient enrichment can increase the susceptibility of reef corals  
491 to bleaching. *Nat. Clim. Chang.* 3, 160-164.
- 492 53. Wooldridge, S.A. (2016). Excess seawater nutrients, enlarged algal symbiont densities  
493 and bleaching sensitive reef locations: 1. Identifying thresholds of concern for the Great  
494 Barrier Reef, Australia. *Mar. Pollut. Bull.*
- 495 54. Duprey, N.N., Yasuhara, M., and Baker, D.M. (2016). Reefs of tomorrow: Eutrophication  
496 reduces coral biodiversity in an urbanized seascape. *Global Change Biol.* 22, 3550-3565.
- 497 55. Williams, G.J., Gove, J.M., Eynaud, Y., Zgliczynski, B.J., and Sandin, S.A. (2015). Local  
498 human impacts decouple natural biophysical relationships on Pacific coral reefs.  
499 *Ecography* 38, 751-761.
- 500 56. Karnauskas, K.B., and Cohen, A.L. (2012). Equatorial refuge amid tropical warming.  
501 *Nat. Clim. Chang.* 2, 530-534.
- 502 57. Karnauskas, K.B., Cohen, A.L., and Gove, J.M. (2016). Mitigation of Coral Reef  
503 warming across the Central Pacific by the equatorial undercurrent: a past and future  
504 divide. *Sci. Rep.* 6.
- 505 58. Riegl, B., Glynn, P.W., Wieters, E., Purkis, S., d'Angelo, C., and Wiedenmann, J. (2015).  
506 Water column productivity and temperature predict coral reef regeneration across the  
507 Indo-Pacific. *Sci Rep* 5, 8273.
- 508 59. Wall, M., Putschin, L., Schmidt, G.M., Jantzen, C., Khokiattiwong, S., and Richter, C.  
509 (2015). Large-amplitude internal waves benefit corals during thermal stress. *Proc. R. Soc.*  
510 *B.* 282, 20140650.
- 511 60. Smith, J.E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., Lewis, L., Obura,  
512 D., Rohwer, F., and Sala, E. (2016). Re-evaluating the health of coral reef communities:  
513 baselines and evidence for human impacts across the central Pacific. *Proc. R. Soc. B* 283,  
514 20151985.
- 515 61. Johnston, E.C., Forsman, Z.H., Flot, J.-F., Schmidt-Roach, S., Pinzón, J.H., Knapp,  
516 I.S.S., and Toonen, R.J. (2017). A genomic glance through the fog of plasticity and  
517 diversification in *Pocillopora*. *Sci. Rep.* 7, 5991.
- 518 62. Williams, G.J., Knapp, I.S., Maragos, J.E., and Davy, S.K. (2010). Modeling patterns of  
519 coral bleaching at a remote Central Pacific atoll. *Mar. Pollut. Bull.* 60, 1467-1476.
- 520 63. Williams, G.J., Smith, J.E., Conklin, E.J., Gove, J.M., Sala, E., and Sandin, S.A. (2013).  
521 Benthic communities at two remote Pacific coral reefs: effects of reef habitat, depth, and  
522 wave energy gradients on spatial patterns. *PeerJ* 1, e81.

- 523 64. Williams, I.D., Baum, J.K., Heenan, A., Hanson, K.M., Nadon, M.O., and Brainard, R.E.  
524 (2015). Human, Oceanographic and Habitat Drivers of Central and Western Pacific Coral  
525 Reef Fish Assemblages. PLoS ONE 10, e0120516.
- 526 65. Hughes, A.D., Grottoli, A.G., Pease, T.K., and Matsui, Y. (2010). Acquisition and  
527 assimilation of carbon in non-bleached and bleached corals. Mar. Ecol. Prog. Ser. 420,  
528 91-101.
- 529 66. Nahon, S., Richoux, N.B., Kolasinski, J., Desmalades, M., Pages, C.F., Lecellier, G.,  
530 Planes, S., and Lecellier, V.B. (2013). Spatial and temporal variations in stable carbon  
531 ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic composition of symbiotic scleractinian corals. PloS  
532 One 8, e81247.
- 533 67. Grottoli, A.G., and Wellington, G.M. (1999). Effect of light and zooplankton on skeletal  
534  $\delta^{13}\text{C}$  values in the eastern tropical Pacific corals *Pavona clavus* and *Pavona gigantea*.  
535 Coral Reefs 18, 29-41.
- 536 68. Moran, R., and Porath, D. (1980). Chlorophyll determination in intact tissues using N,N-  
537 Dimethylformamide. Plant Physiol. 65, 478-479.
- 538 69. Wellburn, A.R. (1994). The spectral determination of chlorophylls a and b, as well as  
539 total carotenoids, using various solvents with spectrophotometers of different resolution.  
540 J. Plant Physiol. 144, 307-313.
- 541 70. Stimson, J., and Kinzie, R.A. (1991). The temporal pattern and rate of release of  
542 zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-  
543 enrichment and control conditions J. Exp. Mar. Biol. Ecol. 153, 63-74.
- 544 71. Zar, J.H. (2007). Biostatistical Analysis, Fifth Edition, (New Jersey: Prentice-Hall, Inc.).
- 545 72. Bates, D., Mächler, M., Bolker, B.M., and Walker, S. (2015). Fitting linear mixed-effects  
546 models using lme4. J. Stat. Software 67, 1-48.
- 547 73. Barton, K. (2015). MuLIn: Multi-Model Inference. R Package version 1.13.4.
- 548 74. Hurvich, C.M., and Tsai, C. (1989). Regression and time series model selection in small  
549 samples. Biometrika 76, 297-307.
- 550 75. Rebert, J.P., Donguy, J.R., Eldin, G., and Wyrski, K. (1985). Relations between sea level,  
551 thermocline depth, heat content, and dynamic height in the tropical Pacific Ocean. J.  
552 Geophys. Res. Oceans 90, 11719-11725.
- 553 76. Lindell, D., and Post, A.F. (1995). Ultraphytoplankton succession is triggered by deep  
554 winter mixing in the Gulf of Aqaba (Eilat), Red Sea. Limnol. Oceanogr. 40, 1130-1141.  
555  
556  
557  
558  
559  
560  
561  
562  
563  
564  
565  
566  
567  
568

569 **Figure Legends**

570

571 **Figure 1. Oceanographic climate of the Southern Line Islands.**

572 **A** Satellite-derived climatological means of surface chlorophyll-*a* in the Southern Line Islands  
573 from 2004-2015. **B** Boxplot of annual mean chl-*a* concentrations calculated for each of the most  
574 proximate pixels to an island. The box represents lower and upper quartiles with the median  
575 value shown as a black line. Whiskers represent the minimum and maximum values that are not  
576 greater than 1.5 times the difference between the upper and lower quartiles. All data beyond this  
577 limit are displayed as points. **C** Mean inorganic nutrient concentrations across all depths (5, 10,  
578 15, 25, 30 m; n=3 per depth). Error bars are  $\pm$  1SE. For dissolved inorganic nitrogen (DIN),  
579 letters denote significant differences at the  $p < 0.05$  level and for soluble reactive phosphorus  
580 (SRP) differences are denoted with i or ii. **D** Mean differences between coral host and  
581 zooplankton  $\delta^{13}\text{C}$  ( $\Delta^{13}\text{C}_{\text{coral-zooplankton}}$ ) across the SLI as a function of mean surface chl-*a*. All data  
582 are from corals at 10 m (n=5) and the zooplankton values were calculated as the mean of  
583 duplicate samples from three different sites on the leeward coast (n=3) of each island. The line  
584 represents best-fit linear regression ( $p < 0.01$ ,  $r^2 = 0.94$ ) and the shaded region represents  $\pm$  1SE  
585 of the linear fit. See also Figure S1.

586

587 **Figure 2. *Pocillopora meandrina* host and endosymbiont  $\delta^{13}\text{C}$  and  $\Delta^{13}\text{C}$  across depth in the**  
588 **SLI.**

589 Islands are ordered top to bottom from north to south, in order of decreasing surface chl-*a*. Data  
590 are presented for depths 5-30 m in 5 m intervals (n=6 per island) In plots **A-E**, the lines are  
591 provided to help visualize the relationship between tissue  $\delta^{13}\text{C}$  and depth in the coral host (solid)  
592 and endosymbiont (dashed) fractions. In plots **F-J** the dashed line represents  $\Delta^{13}\text{C}$  ( $\delta^{13}\text{C}_{\text{host}} -$   
593  $\delta^{13}\text{C}_{\text{endosymbiont}} = 0$ , or no difference in  $\delta^{13}\text{C}$  between coral host and endosymbiont tissues. All  
594 data points and error bars represent mean values  $\pm$  1SE (n = 5) except for Flint 30 m (n = 3).  
595 Lines of best fit are displayed for significant linear regressions of  $\Delta^{13}\text{C}$  as a function of depth at  
596 each island. Shaded areas represent  $\pm$  1SE of the linear fit and error bars represent  $\pm$  1SE of the  
597 mean. See also Figure S1 and Table S1-2.

598

599

600 **Figure 3. Global patterns of coral and endosymbiont  $\delta^{13}\text{C}$  and  $\Delta^{13}\text{C}$  as a function of surface**  
601 **chl-*a*.**

602 **A** Locations from the global data set are depicted in the maps with the first three to four letters of  
603 each location corresponding to the island name in the magnified regions for the **(a)** Maldives, **(b)**  
604 central Pacific, and **(c)** Caribbean basin. The Gulf of Eilat is shown only in the global map.  
605 Regions of lower surface chl-*a* are shown in blue and areas of higher surface chl-*a* in red. **B**  
606 Boxplot of annual mean surface chl-*a* data from 2004-2015 for all islands. Shaded boxes indicate  
607 the five SLI. **C** Mean coral and endosymbiont  $\delta^{13}\text{C}$  as a function of surface chl-*a*. **D** Mean  $\Delta^{13}\text{C}$   
608 ( $\delta^{13}\text{C}_{\text{coral}} - \delta^{13}\text{C}_{\text{endosymbiont}}$ ) as a function of surface chl-*a*. Mean values for Jamaica (JAM), Gulf of  
609 Eilat (EIL), and all atolls in the Maldives (except MAA) are composite means of all species  
610 sampled at that location (see Table S6 for a complete list). Chl-*a* estimates are based on data  
611 from between the 7 and 13 most proximate pixels to each sampling location and represent the  
612 climatological mean from 2004 to 2015. The line represents best-fit linear regression ( $p < 0.001$ ,  
613  $r^2 = 0.77$ ) and the shaded region represents  $\pm$  1SE of the linear fit. See also Figure S2 and Tables  
614 S3-S4.

615 **STAR METHODS**

616

617 **CONTACT FOR REAGENT AND RESOURCE SHARING**

618 Further information and requests for resources and reagents should be directed to and will be  
619 fulfilled by the Lead Contact, Michael Fox (fox@ucsd.edu).

620 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

621 The Southern Line Islands, of the Republic of Kiribati consist of four low-lying limestone  
622 islands (Flint, Vostok, Starbuck, and Malden) and one atoll (Millennium) (Figure 1A). These  
623 coral-dominated islands [60] represent reef ecosystems that have likely adapted to long-term  
624 differences in inorganic nutrient availability and primary production (PP) due to variation in  
625 regional oceanography in the absence of local human impacts. All research was conducted on the  
626 leeward (west) fore reef habitat of each island between October and November 2013. Sites were  
627 selected based on previously published data and were representative of island-scale averages for  
628 benthic community structure [60].

629 For the first part of this study, we sought to compare the trophic ecology of a common  
630 reef-building coral across a natural, long-term gradient in nearshore primary production. We  
631 chose to examine a species that is widely distributed coral throughout the Pacific and Indian  
632 oceans, *Pocillopora meandrina*. We recognize the challenges of accurately identifying  
633 *Pocillopora* species visually in the field given the high level of morphological plasticity within  
634 this genus [61]. However, the relative abundance of *P. meandrina* throughout the Line Islands  
635 [62, 63] supports our identification. We removed approximately 2-3 cm<sup>2</sup> branch tips from the  
636 top-center of five similarly sized colonies of *P. meandrina*. All sampled colonies were separated  
637 by at least 5m when abundant and collections were made strictly along the isobaths at each  
638 depth. Samples in the SLI were collected at 5, 10, 15, 20, 25, 30 m on each island and placed in  
639 individual UV protective sample bags. During transport to the research vessel, samples were  
640 stored in the dark and on ice and then frozen at -20° C until analysis.

641 We also examined the relationship between coral trophic ecology and nearshore primary  
642 production on a global scale using previously published coral isotope data from the literature.  
643 Coral host tissue and endosymbiont  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were acquired from published studies  
644 (Table S4). Only data from studies that collected corals at 10 m depth and presented independent  
645 means of host and endosymbiont fractions were included. This depth was selected because it is  
646 among the most commonly surveyed depth on fore reef habitats [60] and therefore most relevant  
647 to previous studies of coral reef benthic communities. When isotopic means were not provided in  
648 a table, values were extracted from figures using Data Thief 3.0 ([www.datathief.org](http://www.datathief.org)). If multiple  
649 coral species were sampled at the same location, their isotopic values were averaged to create a  
650 site-specific mean in order to avoid pseudoreplication among each level of chl-*a* in our statistical  
651 analyses.

652

## 653 **METHOD DETAILS**

### 654 *Oceanographic context of the Southern Line Islands*

655 To quantify differences in ambient inorganic nutrient concentrations across the SLI,  
656 triplicate water samples (50mL) were collected at 5, 10, 15, 20, and 30 m at each site, filtered  
657 (0.7  $\mu\text{m}$  GF/F filters, Whatman) and frozen at  $-20^\circ\text{C}$  until analysis. Samples were analyzed for  
658 dissolved inorganic nitrogen ( $\text{DIN} = \text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$ ) and soluble reactive phosphorus  
659 (SRP) at the University of Hawaii Hilo EPSCoR analytical laboratory. Inter-island variation in  
660 nutrient concentrations were compared using a two-way fixed factor analysis of variance  
661 (ANOVA) to examine the effects of island and depth and their possible interaction. Assumptions  
662 of normality and homoscedasticity were verified by using the Anderson-Darling test and  
663 Levene's test, respectively. There was significant interaction between island and depth for DIN



664 ( $F_{16,40} = 5.083$ ,  $p < 0.001$ , Figure 1C). This interaction, however, was driven by differences in  
665 nutrient concentrations at the same depths across islands. The only intra-island differences across  
666 depth occurred on Malden (Tukey HSD: 5 m < 15, 25, 30 m) and the difference was  $< 0.5 \mu\text{mol}$ .  
667 Phosphate concentrations did not vary with depth but differed among islands ( $F_{4,40} = 70.66$ ,  $p <$   
668  $0.001$ ). As such, we considered inorganic nutrient concentrations to be homogenous throughout  
669 the upper 30 m and pooled the data to present an integrated mean for the water column. *In situ*  
670 photosynthetically active radiation (PAR) was recorded with a LI-COR  $4\pi$  quantum sensor (LI-  
671 1400, LICOR USA) that was deployed at 10 m depth for 2-4 diel cycles at each island. The  
672 relative light environment at each island over longer time scales was assessed by determining the  
673 depth of light penetration at 490 nm (K490) from the MODIS data package, *sensu* [26].

674 To quantify patterns of island-scale PP we used the eight-day  $0.0417^\circ$  ( $\sim 4\text{-km}$ ) spatial  
675 resolution product of chl-*a* ( $\text{mg m}^{-3}$ ) derived from the Moderate Resolution Imaging  
676 Spectroradiometer (MODIS; <https://modis.gsfc.nasa.gov/>). Data were obtained for 2004-2015  
677 (12 years) to provide climatological means of surface chl-*a* concentrations across the SLI, *sensu*  
678 [6]. Briefly, pixels that fell within 3.27 km of the 30 m isobath of each island were excluded to  
679 avoid data confounded by optically shallow water. Next, a full pixel width (4.4 km) buffer region  
680 was extended beyond the 3.27 km exclusion zone and used to select a single band of pixels  
681 around each island. These pixels were averaged to create island-scale climatological estimates of  
682 chl-*a* concentrations as a proxy for nearshore PP and heterotrophic resource availability.

683 The mean number of pixels used around the smallest oceanic islands in this study  
684 (Palmyra Atoll and all islands in the SLI) was 13. Therefore, climatological chl-*a* estimates were  
685 derived for other locations using the mean of the 13 most proximate pixels along shore of the  
686 collection site. This standardized the spatial areas considered for the PP climatologies at each

687 location and allowed for more ecologically relevant estimates along continental coastlines such  
688 as in the Red Sea or from large islands, such as Jamaica.

689 By using chl-*a* data from optically clear waters we avoid confounding data from  
690 nearshore waters that may be influenced by terrestrial runoff or other anthropogenic impacts  
691 [31]. Consequently, our chl-*a* estimates are not made on the reef and may therefore  
692 underestimate the overall chl-*a* concentration and plankton abundance. However, this proxy to  
693 nearshore primary production is a powerful predictor of the biological responses of coral reef  
694 communities, most notably corals and planktivorous fish [55, 64]. Satellite-derived chl-*a*  
695 estimates from 29 Pacific islands also accurately reflect phytoplankton biomass throughout the  
696 euphotic zone [26]. The mean chl-*a* concentration at each island during our cruise in October-  
697 November 2013 mirrored the long-term climatologies for the region and was strongly correlated  
698 with *in situ* DIN concentrations ( $r = 0.97$ ). Thus, we believe that remotely sensed chl-*a*  
699 accurately reflect surface chl-*a* conditions near coral reef environments over longer time scales  
700 and that this metric provides a relevant estimate of food abundance for coastal mixotrophs in the  
701 tropics.

702

### 703 *Stable isotope analysis of Pocillopora across islands and depths in the SLI*

704 Coral host and endosymbiont fractions were isolated following established methods [18,  
705 23, 24, 65]. An airbrush was used to remove tissue from the skeleton using 10 mL of 0.07  $\mu\text{m}$   
706 filtered seawater (FSW). The resulting blastate was homogenized with an electric tissue  
707 homogenizer. The animal fraction was isolated through centrifugation at 2,000g for 5 min to  
708 pellet most of the endosymbionts. The supernatant (animal fraction) was decanted and the  
709 symbionts fraction was suspended in 2 mL of FSW, centrifuged again. The supernatant from this

710 was added to the animal fraction, which was centrifuged a final time to pellet any residual  
711 endosymbionts and 2 mL were loaded onto a pre-combusted GF/F filter (Whatman). To  
712 minimize the contamination of the endosymbiont fraction by coral host tissue (and therefore  
713 optimize our ability to detect true heterotrophic signals), the endosymbiont fraction was then  
714 resuspended in 5 mL FSW, pressure filtered through 83 and 20  $\mu\text{m}$  nitex mesh and pelleted at  
715 2,000 g. This filtration was repeated once more before 1 mL of the endosymbiont fraction was  
716 loaded onto a pre-combusted GF/F. Each sample was briefly rinsed with 1 mL 1N HCl to remove  
717 calcium carbonate from the coral sample and rinsed with 1 mL of DI water [66]. Acidified and  
718 non-acidified samples were tested against each other to ensure that rinsing with a weak acid did  
719 not affect nitrogen isotope values. We examined acidification effects on both tissue fractions  
720 ( $n=5$ ) using paired t-tests and found no effect of this light acidification on  $\delta^{15}\text{N}$  of either tissue  
721 type ( $t_{\text{host}}=1.50$ ,  $p=0.21$ ;  $t_{\text{symbiont}}=-0.08$ ,  $p=0.94$ ). No differences were observed for  $\delta^{13}\text{C}$  either;  
722 suggesting  $\text{CaCO}_3$  contamination is minimal following this protocol with *P. meandrina* ( $t_{\text{host}}=-$   
723  $1.69$ ,  $p=0.17$ ;  $t_{\text{symbiont}}=-0.42$ ,  $p=0.69$ ). The mean offset between acidified and non-acidified  
724 samples were:  $\delta^{13}\text{C}_{\text{host}}=-0.02 \pm 0.02 \text{‰}$ ,  $\delta^{15}\text{N}_{\text{host}}=-0.01 \pm 0.02\text{‰}$ ,  $\delta^{13}\text{C}_{\text{symbiont}}=-0.03 \pm 0.15\text{‰}$ ,  
725  $\delta^{15}\text{N}_{\text{symbiont}}=-0.03 \pm 0.02\text{‰}$ . As such, we elected to briefly acidify each sample to minimize the  
726 risk of  $\text{CaCO}_3$  contamination and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were determined from the same sample.

727 The isolated fractions were analyzed for  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\mu\text{g C:N}$  with a Costech 4010  
728 Elemental Combustion Analyzer interfaced with a Thermo Finnigan Delta Plus XP stable isotope  
729 mass spectrometer (San Jose, CA) at Scripps Institution of Oceanography. Isotopic values are  
730 expressed as  $\delta^{13}\text{C}/^{15}\text{N}$ , where  $\delta = 1000 \times [(R_{\text{sample}} / R_{\text{standard}}) - 1]$  and  $R_{\text{sample}}$  or  $R_{\text{standard}}$  are the ratio  
731 of the heavy to light isotope in parts per thousand, or per mil (‰). The  $\text{C}^{13}/\text{C}^{12}$  and  $\text{N}^{15}/\text{N}^{14}$  ratios  
732 are expressed relative to the levels of  $^{13}\text{C}$  in Vienna-Pee Dee Belemnite (V-PDB) and  $^{15}\text{N}$  in

733 atmospheric N<sub>2</sub>. Repeated measurements (n=60) of internal working standards exhibited a  
734 precision of 0.01‰ for δ<sup>13</sup>C and 0.2‰ for δ<sup>15</sup>N. The internal standards of calcium carbonate and  
735 ammonium sulfate were calibrated against NBS 18 and IAEA-1, respectively. Ten percent of all  
736 samples (n=18) were run in duplicate with a measurement error ± 0.12‰ for δ<sup>13</sup>C and ± 0.31‰  
737 for δ<sup>15</sup>N.

738         The amount of heterotrophic carbon incorporated by *Pocillopora* was inferred by  
739 calculating the difference between the δ<sup>13</sup>C values of the coral host and endosymbiont fractions  
740 ( $\Delta^{13}\text{C} = \delta^{13}\text{C}_{\text{host}} - \delta^{13}\text{C}_{\text{endosymbiont}}$ ) [23]. This metric has been shown to accurately track intra-  
741 island variations in resource availability across sites and depth in this coral species within the  
742 Line Islands [24]. To verify that the dominant coral food sources (e.g. zooplankton and  
743 particulate organic matter (POM)) had more negative δ<sup>13</sup>C values than the coral host and  
744 endosymbiont tissue [23, 67] (to ensure accurate interpretation of the Δ<sup>13</sup>C metric), we collected  
745 reef-associated POM (2 L seawater filtered onto 25 mm GF/F) and zooplankton (>133 μm,  
746 collected across full diel cycles using an autonomous plankton sampler, *sensu* [24]) from 10 m  
747 depth at 3 leeward sites per island. Both sample types were concentrated on pre-combusted GF/F  
748 filters and briefly acidified as above. For each zooplankton filter (n=3 per island), duplicate  
749 subsamples were averaged together to account for the heterogeneous distribution of plankton  
750 across the filter.

751         To extract chlorophyll-*a*, endosymbionts were pelleted from 2 mL of coral blastate from  
752 each coral at 10, 20, and 30 m. The animal fraction was decanted and the algal pellet was  
753 homogenized in 1 mL in *N,N*-dimethylformamide (DMF) and the pigments were extracted for 24  
754 hrs at 4 °C following [68]. The sample was then centrifuged for 5 min at 7,000 x g to remove all  
755 particulate debris and the supernatant was analyzed with a diode array spectrophotometer

756 (Agilent, UV-vis 8453) following the equations of [69] for a spectrophotometer with 1 nm  
757 resolution. Pigment concentrations were normalized to surface area of each coral fragment  
758 determined by wax dipping [70], initial blastate volume, and solvent volume. Endosymbiont  
759 density was quantified by 6 replicate counts on a Hausser hemocytometer and normalized to  
760 initial blastate volume and coral surface area.

## 761 **QUANTIFICATION AND STATISTICAL ANALYSIS**

762 To determine if coral host tissue was more similar to its dominant prey source  
763 (zooplankton) on more productive islands, we examined the difference between the coral host  
764 tissue with zooplankton  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values at each island using only corals from 10 m (to be  
765 consistent with the depth of zooplankton collections). We used a one-way ANOVA to test for  
766 differences in zooplankton  $\delta^{13}\text{C}$  among islands. Assumptions of normality and homoscedasticity  
767 were verified by using the Anderson-Darling test and Levene's test, respectively. Zooplankton  
768  $\delta^{13}\text{C}$  did not vary among islands ( $F_{(4,10)} = 1.59$ ,  $p = 0.5$ ) so we used island-specific zooplankton  
769  $\delta^{13}\text{C}$  values to examine the relationship between coral host and zooplankton  $\delta^{13}\text{C}$  ( $\Delta^{13}\text{C}_{\text{host-}}$   
770  $\text{zooplankton}$ ). We used a standard linear model to assess the relationship between  $\Delta^{13}\text{C}_{\text{host-}}$   
771  $\text{zooplankton}$  and  $\Delta^{15}\text{N}_{\text{host-}}$   $\text{zooplankton}$  as a function of surface chl-*a* at each island.

772 Spatial variability in  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and C:N and their relative differences between tissue  
773 fractions ( $\Delta$ ) across depths and islands was examined using an analysis of covariance  
774 (ANCOVA) on mean values ( $n=5$  per depth except Flint 30 m,  $n=3$ ) to account for non-  
775 independence among replicate samples within each level of depth. Assumptions of normality and  
776 homoscedasticity were verified by using the Anderson-Darling test and Levene's test,  
777 respectively. We included depth as a covariate to test for differences in the slope of the  
778 relationship between tissue chemistry and depth across the SLI (significant interaction term) and

779 for differences in the magnitude of the heterotrophic signal (significant effect of island).  
780 Significant differences in the slopes of island-specific regressions of mean values vs. depth were  
781 determined individually in pairwise contrasts [71].

782 Coral pigment content was log transformed to satisfy the assumptions of normality and  
783 homoscedasticity and compared across islands and depth with a two-way fixed factor ANOVA.  
784 The relationship between coral pigment content and endosymbiont density and their respective  
785 influence on coral  $\Delta^{13}\text{C}$  was examined using Pearson's correlations for all coral samples from 10  
786 m pooled across the SLI (n=25).

787

#### 788 *Global relationships between coral isotopic ratios and nearshore primary production*

789 The physiology and trophic strategies of scleractinian corals vary considerably across  
790 taxa [29]. We acknowledge that averaging the  $\Delta^{13}\text{C}$  estimates of multiple species reduces our  
791 ability to examine species-specific patterns and intra-site variability, but this allowed us to test  
792 our observed relationship in the most statistically rigorous fashion. To account for the influence  
793 of coral taxonomy on our observed relationship between  $\Delta^{13}\text{C}$  and surface chl-*a*, we refined the  
794 global dataset to only include data from coral families that were replicated in at least two  
795 separate locations (intra-archipelago replication excluded). The resulting dataset thus excluded  
796 samples from the Acroporidae and Meandrinidae (Jamaica) and Oculinidae (Maldives) families  
797 from the mean  $\Delta^{13}\text{C}$  estimates at those locations. The resulting family-level dataset contained  
798  $\Delta^{13}\text{C}$  estimates from all 16 locations but only for corals from four families (Agariciidae,  
799 Astrocoeniidae, Faviidae, Pocilloporidae). Using this refined dataset, we tested the consistency  
800 of our observed linear relationship between  $\Delta^{13}\text{C}$  and chl-*a* at both island and regional scales.

801 To examine the influence of spatial autocorrelation on heterotrophy estimates from  
802 geographically clustered islands, we fitted a linear mixed effects model (lme4 package for R  
803 [72]) with region included as a random effect (model 1) on the intercept as: mean  $\Delta^{13}\text{C} \sim \text{mean}$   
804  $\text{chl-}a + (1|\text{Region})$ . Region explained zero percent of the model variance while surface chl-*a* was  
805 a significant predictor variable ( $p < 0.01$ ,  $r^2 = 0.78$ ). To further address this concern, we  
806 compared the performance of this model with a standard general linear model (model 2)  
807 (residuals of our data were normally distributed, were not auto-correlated, and showed no sign of  
808 heteroscedasticity) using Akaike Information Criterion (MuMIn package [73]) corrected for  
809 small sample size AICc [74]. Both models confirmed that chl-*a* was a significant predictor  
810 variable and indicated that the effect of surface chl-*a* concentration on coral  $\Delta^{13}\text{C}$  was consistent  
811 within and across regions, regardless of ocean basin ( $p < 0.01$ ). The slope and y-intercept of both  
812 models were identical; therefore we selected the more parsimonious general linear model of  
813 island means as the model of best fit ( $\Delta\text{AICc} = -5.19$  relative to model 1).

814 To test for a spatial bias driven by uneven sampling within individual regions (1-6 islands  
815 per archipelago), we collapsed the island-mean estimates of heterotrophy into regional means  
816 (i.e. data from each island of an archipelago were averaged, thereby reducing the influence of  
817 spatial autocorrelation within archipelagos). Our expectation was that significant regional bias  
818 would reduce performance of the regional general linear model (model 3). Notably, this  
819 approach had no significant effect on model performance (model 2:  $F_{1,14} = 44.44$ ,  $r^2 = 0.77$ ,  $p <$   
820  $0.001$ ; model 3:  $F_{1,5} = 18.35$ ,  $r^2 = 0.79$ ,  $p = 0.01$ ). Therefore, we used the standard general linear  
821 model of island-specific  $\Delta^{13}\text{C}$  estimates to most accurately capture the variation across all 16  
822 locations.

823 To further assess the performance of our selected linear model we performed a sensitivity  
824 analysis to assess the influence of taxonomy and geography on model performance by reducing  
825 the model in a step-wise fashion (Table S3). First, we tested for a significant relationship  
826 between surface chl-*a* and all coral  $\delta^{13}\text{C}$  and  $\Delta^{13}\text{C}$  data for 15 species. Next, we removed islands  
827 whose mean  $\Delta^{13}\text{C}$  value was created from multiple species (i.e., Jamaica, Eilat) and for a species  
828 with uniquely deplete  $\delta^{13}\text{C}$ , *Madracis spp.* [23]. Then, we further reduced the model to include  
829 only data from a single species at all locations (excluding Jamaica and using *Stylophora pistillata*  
830 from the Gulf Eilat due to its genetic relatedness to *Pocillopora*). Finally, we examined the most  
831 simplistic model, only  $\delta^{13}\text{C}$  and  $\Delta^{13}\text{C}$  data for *Pocillopora* from the Line Islands and the  
832 Maldives. We calculated coefficients of variation for the slope and y-intercept terms across all  
833 models (excluding model with raw data) to assess overall variation. See Table S3 for statistical  
834 summaries of each model, respectively.

835 Finally, to disentangle the influence of geography vs. oceanographic processes related to  
836 resource availability (i.e., PP and upwelling) on coral and endosymbiont  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values  
837 we examined linear relationships between absolute latitude (as a proxy for light and temperature)  
838 and estimated thermocline depth (as a proxy for resource delivery potential, as internal wave  
839 delivery of subthermocline resources are more probable in regions with shallower thermoclines  
840 [75]). Thermocline depth was estimated as the depth of the 22° isotherm computed using  
841 objectively analyzed mean SST averaged across all available decades from the World Ocean  
842 Atlas (<https://www.nodc.noaa.gov/OC5/woa13/>). Thermocline depth in the tropical Pacific is  
843 well estimated by the depth of the 20° isotherm [75], however, we used the 22° isotherm in order  
844 to include the Gulf of Eilat in our analysis, which can be mixed to depths in excess of 600 m [76]  
845 and did not go below 22° in the world ocean atlas database. Mean temperatures from the surface



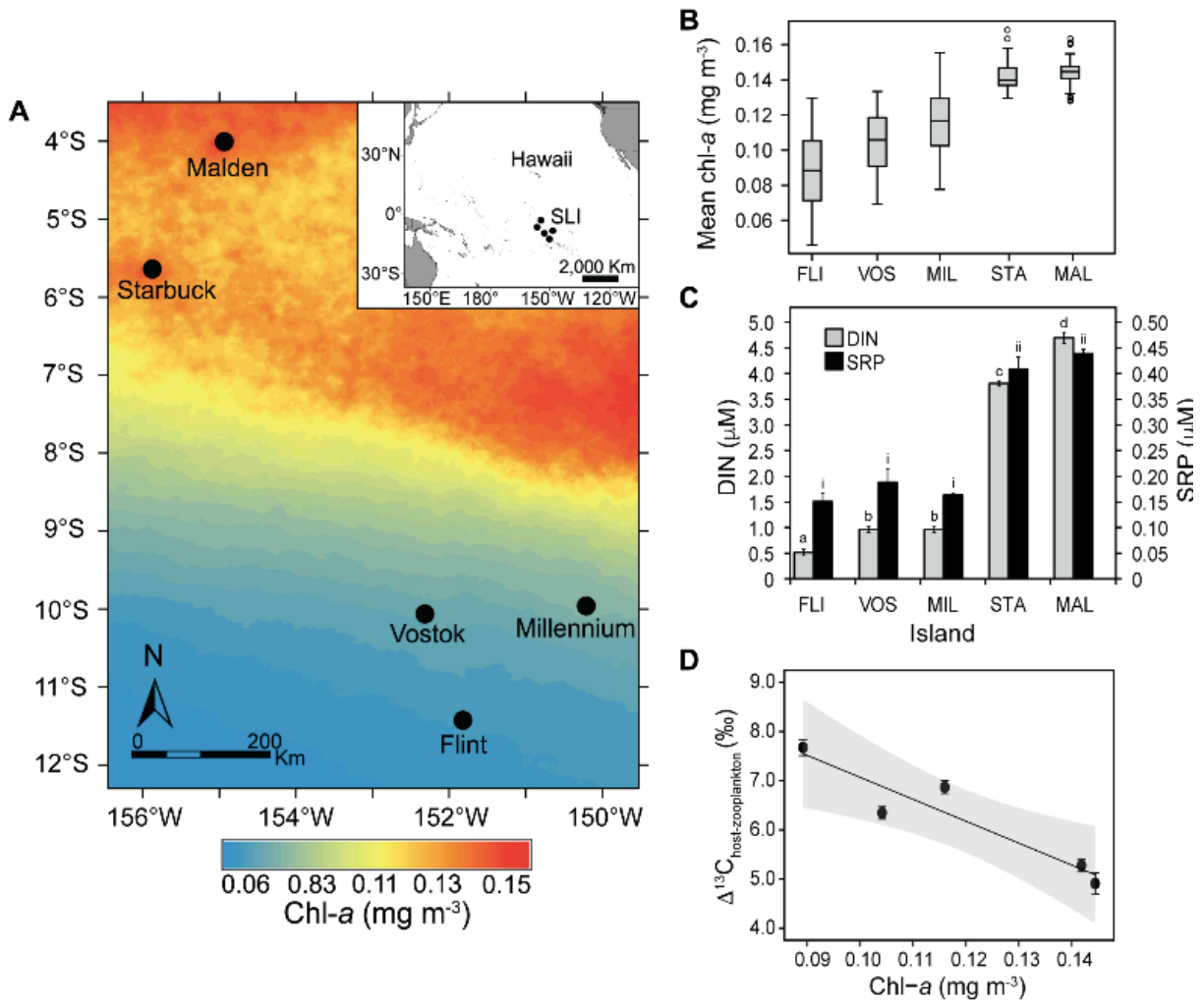
846 to 1000m were determined for each island in the global dataset using a horizontal average of a 1°  
847 x 1° box centered on each island [24]. Depth of the 22° isotherm was estimated from linear fits  
848 of temperature vs. depth for a temperature of 14-28° ( $r^2 > 0.95$  for all models), which provided  
849 independent estimates of thermocline depth for each location. To account for the geographic  
850 proximity of several atolls in the Maldives, the atolls from this region were consolidated into  
851 north, central, and south groups (isotope data averaged across two atolls per region). Thus, the  
852 degrees of freedom in this analysis differed slightly from the global model presented above (df =  
853 11 vs. 13). We compared linear models (Table S4) based on mean isotope values as described  
854 above. We also examined coral and endosymbiont  $\delta^{15}\text{N}$  and  $\Delta^{15}\text{N}$  across the Pacific and Indian  
855 oceans and for only *Pocillopora* from the Line Islands and the Maldives to control for regional  
856 oceanographic differences and elucidate how oceanic  $^{15}\text{N}$  baselines influence coral  $\delta^{15}\text{N}$ . All  
857 statistical analyses were completed using R (R Core Team 2013 and related packages).

## 858 **DATA AND SOFTWARE AVAILABILITY**

859 The datasets generated during and/or analyzed during this study have been deposited in the  
860 Mendeley Data repository at: <http://doi:10.17632/dhvyrxcxhw.1> The data sets we have  
861 deposited include: Annual surface chl-*a* concentrations determined for each location in the  
862 global analysis, *Pocillopora* host and endosymbiont  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , C:N data from the Southern  
863 Line Islands, Inorganic nutrient concentrations from the Southern Line Islands, and Sea Surface  
864 Temperature data for upper 1000 m from the World Ocean's Atlas

865  
866  
867  
868  
869  
870  
871  
872  
873  
874  
875

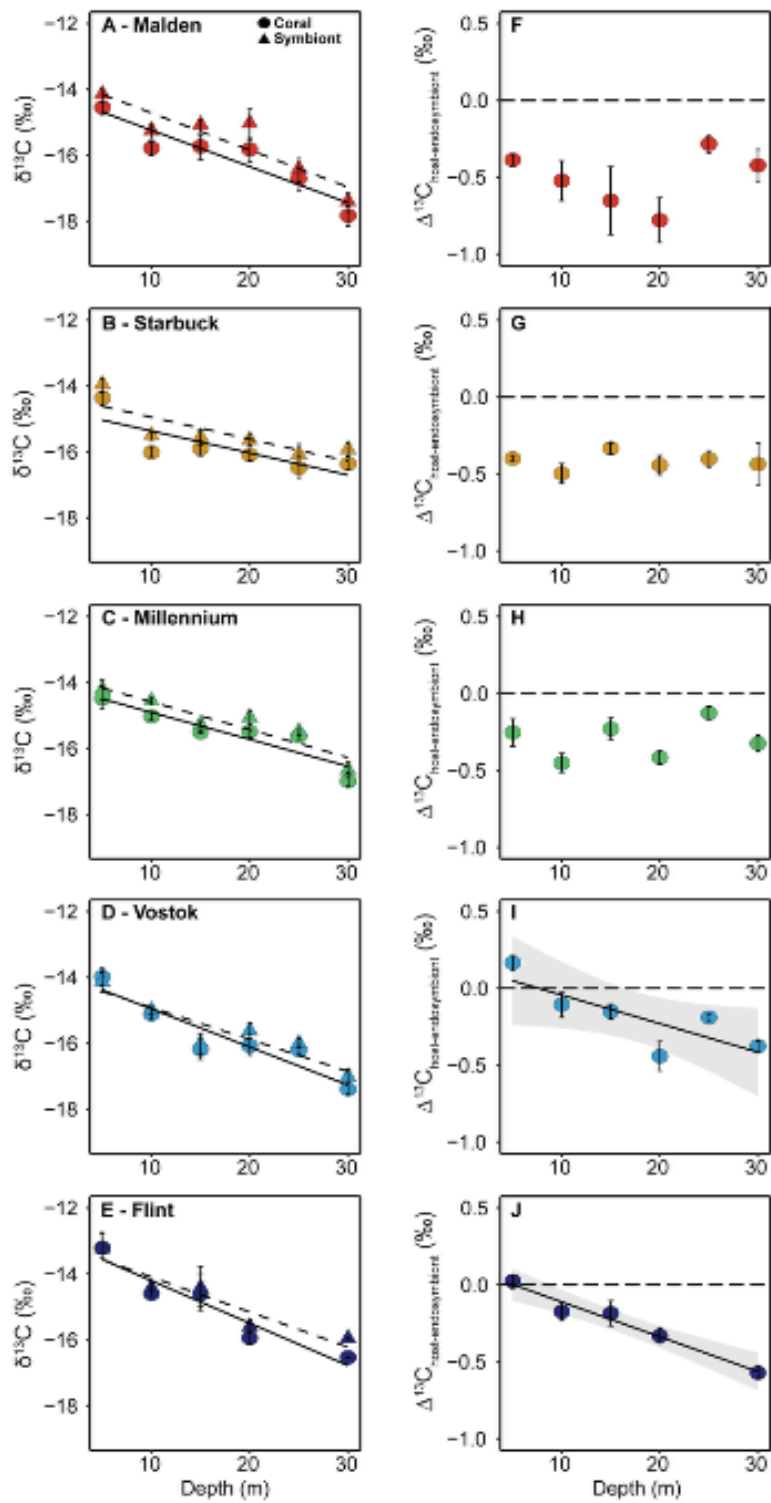
876 Figure 1  
 877



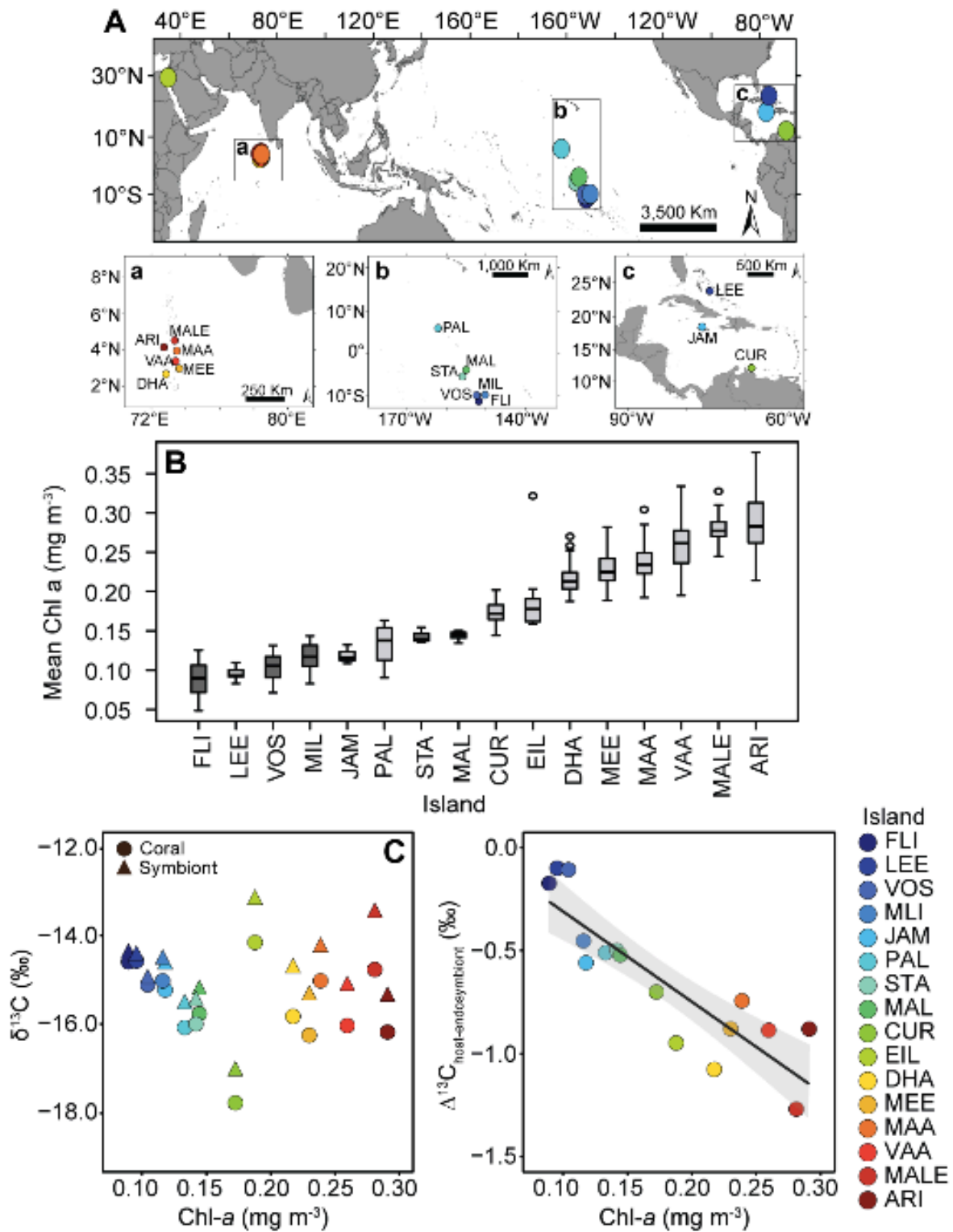
878  
 879  
 880  
 881  
 882  
 883  
 884  
 885  
 886  
 887  
 888  
 889

890 Figure 2

891  
892  
893  
894  
895  
896  
897  
898  
899  
900  
901  
902  
903  
904  
905  
906  
907  
908  
909  
910  
911  
912  
913  
914  
915  
916  
917  
918  
919  
920  
921  
922  
923  
924  
925  
926  
927  
928  
929  
930  
931  
932  
933  
934



935 Figure 3  
936



937