Received: 11 October 2019 | Revised: 5 May 2020 | Accepted: 13 May 2020

DOI: 10.1111/gcb.15230

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Rewiring coral: Anthropogenic nutrients shift diverse coral–symbiont nutrient and carbon interactions toward symbiotic algal dominance

Jacob E. Allgeier[1] | Mona A. Andskog[1] | Enie Hensel[2] | Richard Appaldo[1] | Craig Layman[2] | Dustin W. Kemp[3]

[1]Department of Ecology, and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA

[2]Department of Applied Ecology, North Carolina State University, Raleigh, NC, USA

[3]Department of Biology, University of Alabama Birmingham, Birmingham, AL, USA

Correspondence
Jacob E. Allgeier, Department of Ecology, and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA.
Email: jeallg@umich.edu

Funding information
National Science Foundation, Grant/Award Number: OCE #0746164, OCE #2023507 and OCE #1948622; University of Alabama at Birmingham

Abstract

Improving coral reef conservation requires heightened understanding of the mechanisms by which coral cope with changing environmental conditions to maintain optimal health. We used a long-term (10 month) in situ experiment with two phylogenetically diverse scleractinians (*Acropora palmata* and *Porites porites*) to test how coral–symbiotic algal interactions changed under real-world conditions that were a priori expected to be beneficial (fish-mediated nutrients) and to be harmful, but non-lethal, for coral (fish + anthropogenic nutrients). Analyzing nine response variables of nutrient stoichiometry and stable isotopes per coral fragment, we found that nutrients from fish positively affected coral growth, and moderate doses of anthropogenic nutrients had no additional effects. While growing, coral maintained homeostasis in their nutrient pools, showing tolerance to the different nutrient regimes. Nonetheless, structural equation models revealed more nuanced relationships, showing that anthropogenic nutrients reduced the diversity of coral–symbiotic algal interactions and caused nutrient and carbon flow to be dominated by the symbiont. Our findings show that nutrient and carbon pathways are fundamentally "rewired" under anthropogenic nutrient regimes in ways that could increase corals' susceptibility to further stressors. We hypothesize that our experiment captured coral in a previously unrecognized transition state between mutualism and antagonism. These findings highlight a notable parallel between how anthropogenic nutrients promote symbiont dominance with the holobiont, and how they promote macroalgal dominance at the coral reef scale. Our findings suggest more realistic experimental conditions, including studies across gradients of anthropogenic nutrient enrichment as well as the incorporation of varied nutrient and energy pathways, may facilitate conservation efforts to mitigate coral loss.

KEYWORDS

coral reefs, eutrophication, fish nutrient supply, marine conservation, nitrogen, phase shift, phosphorus, Symbiodiniaceae, symbiosis

1 | INTRODUCTION

Understanding processes that drive nutrient dynamics within an ecosystem is a fundamental challenge in ecology. Nutrients are often limiting resources for productivity, and thus, knowledge of how nutrients cycle (i.e., via fluxes and pools) within ecosystems has important implications for theory as well as for conservation and management of ecosystems (Chapin, Matson, & Vitousek, 2011). Unlike many ecosystems where the availability of nutrients is often positively correlated with productivity, coral reefs provide a "nutrient paradox" in that they are among the most productive ecosystems in the world but typically thrive in highly oligotrophic environments. It is hypothesized that the high levels of coral reef productivity are due to extremely efficient nutrient recycling at both the organismal (e.g., coral–symbiotic algae) and ecosystem levels (Hatcher, 1988, 1990; Odum & Odum, 1955). But exogenous sources of nutrients, such as those from upwelling (e.g., Rougerie, Fagerstrom, & Andrie, 1992), plankton (e.g., Richter, Wunsch, Rasheed, Kotter, & Badran, 2001), fishes (e.g., Meyer, Schultz, & Helfman, 1983), and seabirds (e.g., Graham et al., 2018), also contribute to enhanced production on coral reefs. In contrast, anthropogenic nutrient enrichment is typically associated with negative impacts to coral reefs, with some important and interesting exceptions (e.g., see Szmant, 2002). Despite significant attention to this topic of nutrient enrichment (D'Angelo & Wiedenmann, 2014; Fabricius, 2005), our basic understanding of how altered nutrient availability changes coral nutrient dynamics remains limited.

Fundamental to coral reef nutrient dynamics and productivity are scleractinian corals that serve as the foundation species of these ecosystems. Their productivity and growth through calcification depend on internal nutrient and energy exchange between the coral host and the symbiotic algae (family: Symbiodiniaceae) within its tissues (Muscatine & Porter, 1977). Through photosynthesis, symbiotic algae provide organic carbon (C) to the coral host that in turn provides the algae with re-mineralized nutrients, for example, nitrogen (N) and phosphorus (P) (Muscatine & Porter, 1977). Corals also feed heterotrophically, and thus can vacillate along a continuum between heterotrophic and autotrophic nutrient acquisition to optimize efficiency under various conditions and resource availability, such as with nutrient enrichment (Anthony & Fabricius, 2000; Grottoli, Rodrigues, & Palardy, 2006; Houlbreque & Ferrier-Pages, 2009; Porter, 1976). But there are costs associated with shifts from heterotrophy to autotrophy that alter organismal nutrient cycling and influence productivity (Levas et al., 2016). For example, symbiotic algae are believed to be N-limited (Falkowski, Dubinsky, Muscatine, & McCloskey, 1993; Wiedenmann et al., 2013; Yellowlees, Rees, & Leggat, 2008), and under increased ambient availability of N have been shown to increase in density (Ezzat, Maguer, Grover, & Ferrier-Pagès, 2015; Falkowski et al., 1993; Muscatine, Falkowski, Dubinsky, Cook, & McCloskey, 1989). Increased symbiont density can stimulate competition for the intracellular pool of dissolved inorganic carbon (DIC) between the coral host and the symbiotic algae that require DIC for calcification of the coral skeleton and photosynthesis, respectively (Marubini & Davies, 1996, but see also Hoadley, Pettay, Dodge, & Warner, 2016). Such scenarios that many alter C or nutrient allocation may be associated with "harmful" effects from human nutrient inputs. Yet, depending on the coral species and the severity or duration of changing environmental conditions, shifts in nutrient acquisition can have variable outcomes (Anthony, Hoogenboom, Maynard, Grottoli, & Middlebrook, 2009; Grottoli et al., 2006; Palardy, Rodrigues, & Grottoli, 2008; Shantz, Lemoine, & Burkepile, 2016). Understanding underlying organismal mechanisms of how corals respond to such changes remains an important challenge for coral reef ecology and conservation.

Research to understand how coral respond to different regimes of nutrient availability (e.g., anthropogenic nutrient enrichment) often isolates potential drivers through experimental manipulations in laboratory settings. Such experiments can help identify mechanistic relationships, but one concern is that the experimental environment unlikely reflects the complex setting that typifies a coral reef. Furthermore, nutrients are often manipulated to reflect scenarios that can exceed even extreme anthropogenic enrichment conditions (reviewed by Szmant, 2002). This approach has been useful for determining thresholds of tolerance to high doses of nutrients, but the dynamic relationships that underpin the coral–symbiotic algae in situ, or under more realistic nutrient enrichment scenarios, have not been researched as extensively.

Here, we present a long-term (10 month) experiment to test how coral–symbiont C and nutrient relationships change under altered nutrient regimes; the experiment includes a recognized beneficial scenario—fish excretion (ammonium plus phosphate enrichment; Holbrook, Brooks, Schmitt, & Stewart, 2008; Huntington, Miller, Pausch, & Richter, 2017; Meyer et al., 1983; Shantz, Ladd, Schrack, & Burkepile, 2015; Shaver & Silliman, 2017), and a recognized detrimental scenario—anthropogenic fertilizer (ammonium plus nitrate plus phosphate enrichment; Dubinsky & Stambler, 1996; Fabricius, 2011; Thurber et al., 2014). We transplanted 128 coral fragments, from two species of scleractinian coral (*Acropora palmata* and *Porites porites*), onto 16 artificial reefs in The Bahamas, with two treatments: (a) varying densities of fish generated by differing artificial reef structures ($n = 16$ ARs, see Figure 1), and (b) moderate levels of nutrient enrichment from fertilizer ($n = 8$). For each fragment, we measured nine response variables that included: coral growth rate, symbiotic algal density, elemental nutrient content (C and N for coral and algal tissue and P for algal tissue), and natural abundance of stable isotopes ($\delta^{13}C$ and $\delta^{15}N$). Specifically, we had three objectives:

1. Test how nine response variables of coral and symbiotic algae change across the fish and anthropogenic nutrient gradient.
2. Test seven prevailing hypotheses generated from the literature of coral–symbiont nutrient and carbon relationships (see Figure 2) under the two nutrient regimes.
3. Quantify potentially unidentified coral–symbiotic algal nutrient and carbon relationships under the two nutrient regimes.

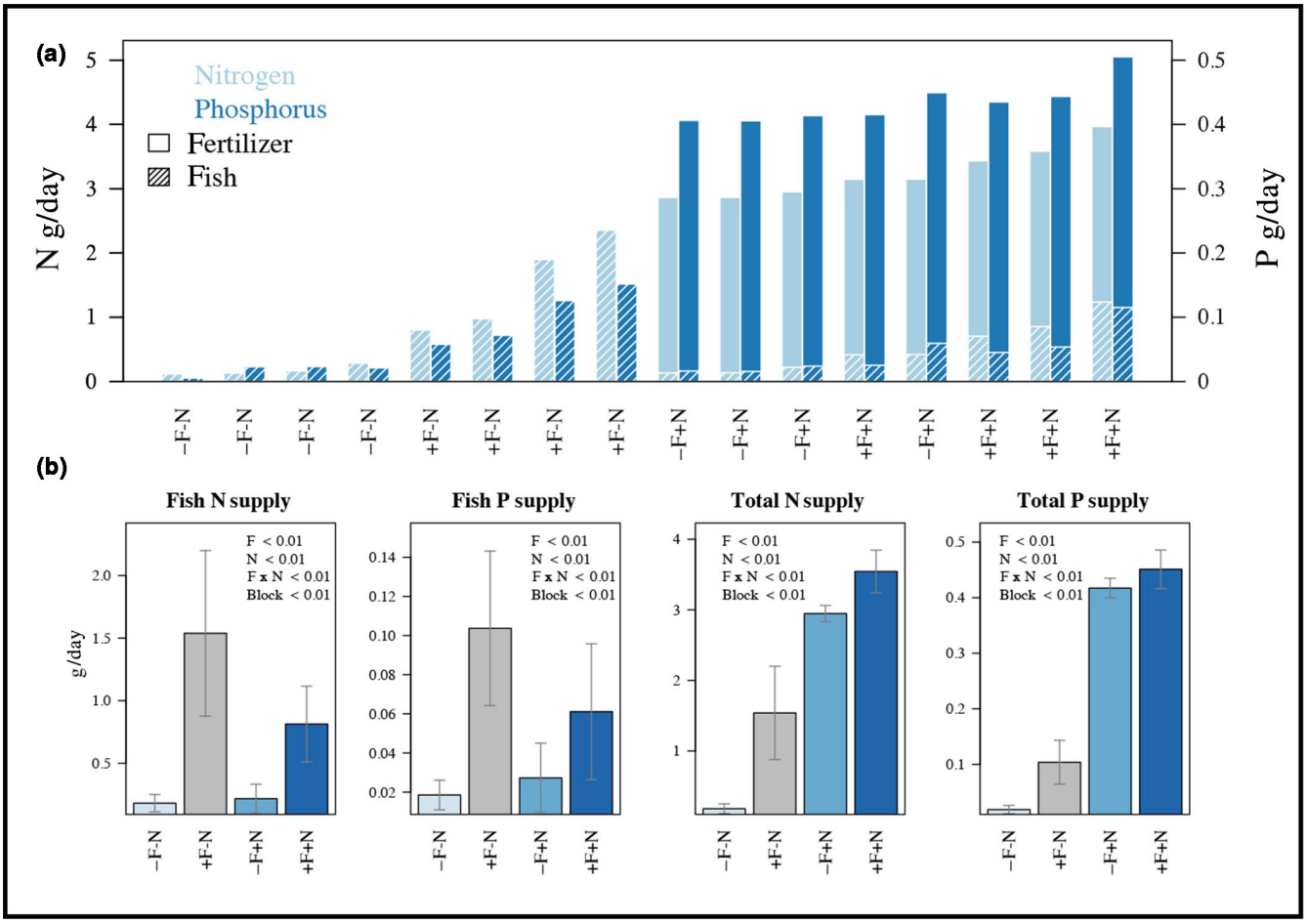


FIGURE 1 (a) Reef-level bar plots of nutrient input (four reefs per treatment), differentiating fish-mediated and fertilizer nutrients. (b) Treatment-level bar plots of nutrient input with significance tests. ±F = low/high fish treatment, ±N = absence/presence of fertilizer [Colour figure can be viewed at wileyonlinelibrary.com]

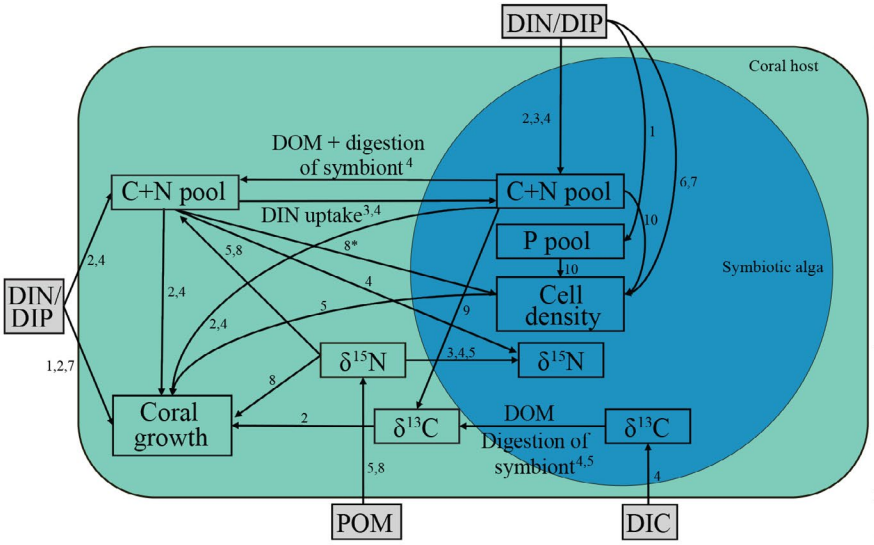
Our study had three key strengths: (a) it was a long-term field experiment, (b) the complex, non-lethal nature of nutrient enrichment design, and (c) the large number of response variables measured for both coral and algae. Key findings from our study were that coral growth rate increased with fish-mediated nutrients, but anthropogenic nutrients, surprisingly, had no additional effect. Nonetheless, we found that coral–symbiont associations were different under conditions of anthropogenic nutrients, whereby diverse nutrient and C relationships under fish-mediated nutrients shifted to being dominated by the algal symbiont. These findings provide new perspectives on how anthropogenic nutrients "rewire" coral–symbiont and coral–coral interactions, and we discuss how these might inform avenues of future research.

2 | METHODS

2.1 | Experimental design

The study was conducted in The Bight of Old Robinson, Abaco, The Bahamas (26.26697, -76.94126), a semi-enclosed bay dominated by seagrass that is interspersed with sand and hard bottom habitats (Yeager, Allgeier, & Layman, 2011). We took advantage of an ongoing, artificial reef nutrient enrichment study, see Allgeier et al. (2018). The study included 16 artificial reefs, constructed in December 2010 from 30 cinder blocks (~40 cm × 20 cm × 20 cm) in a pyramid shape (~100 cm × 80 cm at base, 60 cm height), on sparse seagrass habitat dominated by common turtle grass, *Thalassia testudinum*, at a depth of 3–4 m. Artificial reefs provide replicable units of discrete size from which ecological responses in the local ecosystem can be measured (Carr & Hixon, 1997; Hixon & Beets, 1989). Environmental conditions such as salinity, temperature (range from 29°C to 31°C), and irradiance are relatively consistent throughout the embayment (Allgeier, Layman, & Rosemond, 2011; Allgeier, Rosemond, Mehring, & Layman, 2010; Stoner, Layman, Yeager, & Hassett, 2011), thus likely varied little from reef to reef for the duration of the experiment, and were similar to conditions on nearby coral reefs (<1 km).

We manipulated nutrient regimes on reefs in two ways: (a) altered fish-mediated nutrient supply via manipulation of the reef structure (±F), and (b) nutrient enrichment via the addition of fertilizer (±N; Florikan 18-6-8 NPK 8 months, type 270; the N fraction of the fertilizer is 8.3:9.7 ratio NO_3^-:NH_4^+). These two treatments were imposed on the artificial reefs in a 2 × 2 factorial design with a randomized block (n = 16 reefs total in four blocks; see



References:
1. Godinot et al. (2011)
2. Tanaka et al. (2007)
3. Tanaka et al. (2015)
4. Tanaka et al. (2018)
5. Tremblay et al. (2015)
6. Wiedenmann et al. (2012)
7. Ezzat et al. (2015)
8. Houlbreque et al. (2015)
9. Furla et al. (2000)
10. Sterner and Elser (2002) (stoichiometry theory: luxury uptake)

*indirect: Feeding led to increased algal density. N must have passed through the coral first.

DIC/N/P, dissolved inorganic carbon/nitrogen/phosphorus; DOM, dissolved organic matter; POM, particulate organic matter

Component models that make up the complete SEM. Each model, described in the text, represents a general hypothesis generated from the literature (numbers in Figure 2 correspond with citations below).

Component model	Response	Predictor(s)
1	$C{:}N_{coral}$	$Nutrients_{ambient} + \delta^{15}N_{coral}$
Coral and algae can take up N from the water column and heterotrophically feed on particulate matter with consequences for increased $\delta^{15}N$ signature of the holobiont (Muscatine et al., 2005; Tanaka et al., 2007, 2015, 2018; Tremblay et al., 2015)		
2	$\delta^{13}C_{coral}$	$C{:}N_{symbiont} + \delta C^{13}{}_{symbiont}$
Dissolved organic carbon produced from the photosynthetic activity of the algae ($\delta^{13}C_{algae}$) is a primary source of C to coral and thus is expected to be positively correlated with $\delta^{13}C_{coral}$. Additionally, a larger C pool in the algae means that more C is available to be transferred to the coral (Tanaka et al., 2007,2015,2018).		
3	$C{:}N_{symbiont}$	$C{:}N_{coral} + Nutrients_{ambient}$
Ambient nutrients are expected to increase N concentrations in the algae (decreased C:N), and the recycling of nutrients via metabolic waste products is expected to influence the correlation between the coral C:N and algae C:N (Tanaka et al., 2007,2015,2018). The SEM cannot account for recycling (called feedback loops; Lefcheck et al., 2016) and the direction of N flow therefore goes from the coral to algae. The recycling of C and N is also expressed in component model 2.		
4	$\%P_{symbiont}$	$Nutrients_{ambient}$
P concentrations in symbiotic algae tend to increase with ambient phosphate concentrations (Godinot et al., 2011).		
5	$\delta^{15}N_{symbiont}$	$\delta^{15}N_{coral} + C{:}N_{coral}$
Coral heterotrophy of particulate matter from the water column, that is indicated by an increased $\delta^{15}N$ signature in the coral, can be a source of N that is mediated into the N cycling loop between the coral and algae (Muscatine et al., 2005, Tremblay et al., 2015).		
6	$Density_{symbiont}$	$Nutrients_{ambient} + C{:}N_{symbiont} + \%P_{symbiont} + C{:}N_{coral}$
Algae can take up nutrients from the water column increasing the nutrient pool available for their growth (Tanaka et al., 2007,2015, 2018), which can lead to increased algal density cm^{-2} (Ezzat et al., 2015; Wiedenmann et al., 2012)		
7	$Growth_{coral}$	$C{:}N_{coral} + \delta^{15}N_{coral} + \delta^{13}C_{coral} + C{:}N_{coral} + \%P_{symbiont} + Density_{symbiont} + Nutrients_{ambient}$
Energy from algal photosynthates plus most other compartments will, to various degrees, have an influence on the calcification rates and growth (mg $cm^{-2}day^{-1}$) of the coral (Ezzat et al., 2015; Ferrier-Pagès et al., 2000; Godinot et al., 2011; Houlbreque et al., 2015; Tanaka et al., 2007)		

FIGURE 2 Hypothesized C and nutrient relationships (or pathways) within the coral–algal symbiosis. Boxes are nutritional and physiological attributes of the coral (light blue) and the algal symbionts (dark blue). Arrows between boxes describe established pathways of nutrient and energy exchange between the coral and algae reported in the literature, as indicated by numbers and described by the component models in the table below. The hypothesized relationships outlined here are not specified in terms of directionality (positive or negative); however, output from the structural equation models provided directionality (Figure 4). DIC, dissolved inorganic carbon (i.e., bicarbonate); DIN, dissolved inorganic nitrogen (i.e., ammonium, nitrate); DIP, dissolved inorganic phosphorus (i.e., phosphate); DOM, dissolved organic matter (i.e., photosynthates, amino acids, lipids); POM, Particulate organic matter (i.e., phytoplankton and zooplankton) [Colour figure can be viewed at wileyonlinelibrary.com]

map Appendix S1). Fish-mediated nutrient supply was altered by reducing the physical complexity of the reefs by filling in the holes of the cinder blocks creating a smooth-sided structure. In doing so, fish biomass and community composition were substantially altered, but in a continuous manner, across reefs, that is, even the half of the reefs with low physical structure had varying fish biomass (Allgeier et al., 2018; Figure 1a; Appendix S1). Reefs were placed >150 m apart to minimize among-reef movement of more transient fish species (Carr & Hixon, 1995, 1997). Cross-reef enrichment due to fertilizer was not a concern due to the highly oligotrophic nature of the system with high rates of nutrient uptake by benthic and water column producers, and previous evidence in this system that nutrient effects do not extend beyond ~8 m away from reefs (Allgeier et al., 2018; Layman, Allgeier, & Montaña, 2016; Layman, Allgeier, Yeager, & Stoner, 2013). These conditions are consistent with previous findings on the effects of nutrient enrichment on water column nutrients from an oligotrophic embayment in Hawaii (Smith, Kimmerer, Laws, Brock, & Walsh, 1981).

2.2 | Nutrient enrichment

Fish-mediated nutrient supply was quantified by modeling species-specific nutrient supply rates onto repeated visual census data that estimated fish abundance and size. This approach has been conducted previously by the authors on these same reefs (see Allgeier et al., 2018), other artificial reefs nearby (Allgeier, Yeager, & Layman, 2013; Layman et al., 2013), and other coral reef ecosystems in the Caribbean (e.g., Allgeier, Layman, Mumby, & Rosemond, 2015), and is described in greater detail in Appendix S1. Importantly, because the exact density of fish could not be explicitly manipulated, the high/low fish treatment also provided a continuous gradient of fish-mediated nutrient supply across all 16 reefs used for Objectives 2 and 3 (Figure 1a).

Anthropogenic nutrient enrichment was simulated using PVC diffusers filled with slow-release fertilizer Florikan (18-6-8 NPK, type 270, 8 months; the N fraction of the fertilizer is 8.3:9.7 ratio NO_3^-:NH_4^+). Seven diffusers filled with ~500 g of fertilizer were suspended around each reef, on glass fritted poles, ~0.5 m above the substrate. Diffusers have been changed every 3 months since December 2010 as part of an ongoing enrichment study (Allgeier et al., 2018); they were changed every 2 months for the duration of this study to ensure more consistent enrichment effects. Because of the low ambient nutrient availability (<20 μg/L NH_4^+, <5 μg/L PO_4^-; Allgeier et al., 2010; Stoner et al., 2011) and high levels of uptake, water column nutrients are not a reliable source for estimating enrichment effects (Allgeier et al., 2013, 2018; Smith et al., 1981). Nutrient release rates from fertilizer were estimated by calculating the total mass loss of fertilizer on subset of diffusers ($n = 7$) after deployment for 90 days (2.7 ± 0.3 *SD*, 0.039 ± 0.0042 *SD*, g $reef^{-1}$ day^{-1}, for N and P, respectively; see Appendix S1 and Allgeier et al., 2018 for further detail).

The likelihood that the coral fragments (located <1.5 m from the diffusers and directly in the center of fish activity; Appendix S1) are affected by both sources of nutrients is high because previous work on these same reefs has shown that seagrass is affected by fish nutrient supply (Allgeier et al., 2013; Layman et al., 2013) and fertilizer (Allgeier et al., 2018) at a minimum of 3 m and up to 8 m from reefs (Appendix S1). We can accurately estimate the rates of nutrient supply from fishes moving within and around reefs, and from each nutrient diffuser, and thus the amount of nutrient supply at the reef scale. However, the complex nature of the environmental conditions, namely currents in a non-directional and tidal-dominated system, precludes estimation of the exact amount of nutrients that reach the coral fragments. For these reasons, we use our estimates of nutrient supply from fish and fertilizer to characterize the different nutrient regimes (fish only, and fish + anthropogenic nutrients) that a given coral fragment is exposed to, but we do not suggest that this precisely represents the specific nutrient supply rates or ratios that a given coral fragment experiences.

2.3 | Coral processing

Two phylogenetically diverse scleractinian species were used for this study: *A. palmata* and *P. porites*. In July 2015, corals were collected on nearby reefs at a depth of 2–3 m. Fragments were ~30–40 cm^2 in size. Before deployment to experimental reefs, the corals were photographed and weighed using the buoyant weight technique (Jokiel, Maragos, & Franziskey, 1978). Four individuals of each species were suspended above the reef using ~30 cm length of monofilament attached to a PVC rack ($n = 8$ per reef; figures 1 and 2 in Appendix S1).

In May 2016, all coral fragments were removed from experimental treatments and transferred in coolers filled with seawater and processed <5 hr after collection. Fragments were first weighed using the buoyant weight technique (Jokiel et al., 1978) before processing to separate coral tissue and algal cells. Coral calcification rate was calculated per day and normalized to coral surface area (mg cm^{-2} day^{-1}), which was determined using a single paraffin wax dipping at 65°C for 3 s (Stimson & Kinzie, 1991; Veal, Carmi, Fine, & Hoegh-Guldberg, 2010).

Host tissue was removed from the coral skeleton with an airbrush in 0.45 μm filtered seawater (Szmant & Gassman, 1990). The saltwater tissue slurry was homogenized for 10 s using a Tissue Tearor (BioSpec Products) and subsamples were taken and preserved in formalin for symbiotic algae density quantification. Cell enumerations were done via replicate hemocytometer counts ($n = 8$) using light microscopy. Symbiotic algal densities were normalized to the skeletal surface area determined by the foil method (Marsh, 1970).

Symbiotic algae and coral tissue were separated by a series of centrifugation washes. Each algal and coral fraction was microscopically verified to ensure homogeneity, and placed on pre-combusted Whatman GF/F glass microfiber filters, sealed in individual bags, and kept frozen at −20°C until analyzed. Elemental analysis for percent C and N, as well as the natural abundance of stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) for coral tissue and algae were measured using a Carlo Erba CHN Elemental Analyzer (Model NA1500) coupled to Thermo

Finnigan Delta V Isotope Ratio Mass Spectrometer via a Thermo Finnigan Conflo III Interface. Percent P was measured using dry oxidation-acid hydrolysis extraction followed by colorimetric analysis (Alpkem RF300). All elemental laboratory analyses were conducted at the University of Georgia, Center for Applied Isotope Studies.

2.4 | Statistical analysis

We used two statistical modeling approaches to accomplish our three objectives outlined above.

- *Objective 1* tested treatment-level effects (fish-mediated and fish + anthropogenic nutrients) on the nine measures of coral and algae. To do this, we ran a three-way ANOVA with an additional test for a block effect on all samples across all reefs (response = F(±) * N(±)*species + block).
- *Objective 2* tested how well seven hypotheses regarding coral–symbiont relationships, drawn from the literature (see Figure 2), explained the observed coral–symbiont interactions under the two nutrient regimes using confirmatory structural equation modeling.
- *Objective 3* extended the approach from *Objective 2* to quantify potentially unidentified coral–symbiont nutrient and carbon relationships under the two nutrient regimes using exploratory structural equation modeling.

Structural equation models (SEMs) are probabilistic models specifying causal relationships between predictor and response variables in a single network. SEMs can incorporate indirect effects by allowing response variables to be functions of other response variables (Grace et al., 2012). SEMs consist of multiple individual component models (i.e., here they are linear regressions) that each test for specific hypotheses. They can be used in a confirmatory manner to test these specific hypotheses (used for *Objective 2*) or in an exploratory manner to identify unspecified relationships and remove unimportant ones (used for *Objective 3*). Using the SEM approach, we were able to move beyond conventional approaches (e.g., ANOVA used for *Objective 1*) to identify and better understand the important coral–symbiont relationships as they pertain to different nutrient regimes of fish and anthropogenic enrichment.

We generated a single SEM that consisted of seven component models—each articulating a specific hypothesis that was drawn from the literature (Figure 2). This same model structure was used for *Objective 2* and *3* (see below). These hypotheses included relationships between coral and symbiont elemental content and natural abundance of stable isotopes, as well as symbiotic alga densities (cm^{-2}) and coral growth (mg cm^{-2} day^{-1}); see Figure 2 for the hypothesis-based component models and appropriate citations. The hypothesized relationships outlined in Figure 2 are not specified in terms of directionality (positive or negative); however, the output from the SEM provided directionality, an important benefit of using SEMs because past findings have found both negative and positive effects of, for example, nutrient supply on coral growth.

The seven component models were run using the *piecewiseSEM* package in R following Lefcheck (2016) to generate two outcomes (one for each objective). For *Objective 2*, we conducted a confirmatory analysis to test for support for the specified hypotheses, herein referred to as the *Confirmatory model*. For *Objective 3*, using the same initial SEM with the seven component models, we incorporated a stepwise process to explore important unspecified relationships and eliminate specified relationships that were not significant from *Objective 2* (Figure 2). By considering alternative models, we identified the best candidate model according to AICc (corrected for sample size) and Fisher's *C* statistic (Grace et al., 2012), herein referred to as the *Exploratory model*.

The stepwise process was conducted as follows: (a) Shipley's test of directional separation (Shipley, 2009) was run across the component models to determine missing significant relationships between variables present in the SEM; (b) the missing relationships were added, and this alternative model was run to determine the significance of model relationships, whereby those with $p > .1$ were removed—this step was conducted because some models with marginally significant relationships had lower AICc (Burnham & Anderson, 2002); and (c) we then tested a series of candidate models by removing any nonsignificant relationships ($p > .05$). The goodness of fit (Fisher's *C* statistic) and AICc were used to assess the best model. To assess model validity, we plotted residuals against fitted values for each component model. The data were hierarchically structured and thus each component model included random effects for block, reef, and species. Although understanding the species-level effects is of interest, we used species as a random effect for two reasons: (a) despite being significant in our treatment-level analyses, there were no significant interactions between the species term and either nutrient treatment, suggesting that although there was a different mean effect by species, the magnitude of change across treatments was similar (i.e., different intercept but not slope); and (b) given the number of parameters of interest, we had insufficient data to run separate models for each species and for each nutrient regime, as the ratio of sample size to variables should not be less than five (Grace et al., 2012). Variables that did not follow a normal distribution were either log- or square root-transformed.

The *Confirmatory model* and *Exploratory model* approach were both applied to each nutrient regime scenario in our experiment, for example, using the continuous gradient of fish-mediated nutrient supply with no fertilizer (+F-N or −F-N), and fish-mediated nutrient supply with fertilizer (+F+N or −F+N). This resulted in four separate SEMs (two each for *Objective 2* and *3*), each represented by path diagrams, allowing simple visualization of important relationships (or pathways) in the model (e.g., Figure 4). Standardized regression coefficients for each relationship and conditional r^2 values for each component model were used to compare differences among models.

3 | RESULTS

The experimental design created significantly different nutrient regimes across treatments (Figure 1b), consistent with previous

research on these reefs (Allgeier et al., 2018). Of the 128 individual coral fragments, 13 died (3, 5, 3, and 2, from −F-N, +F-N, −F + N, and +F+N treatments, respectively), only one of which was *P. porites*. An additional eight were excluded due to large tissue lesions that likely affected fragment growth (half of which were from fertilized reefs), leaving 47 and 60 live coral fragments of *A. palmata* and *P. porites*, respectively.

Objective 1: Coral growth (mg cm^{-2} day^{-1}) and coral C:N increased significantly in the presence of high fish-mediated nutrient supply, but anthropogenic nutrients had no additional negative or positive effect (Figure 3). There were no significant effects due to anthropogenic nutrient enrichment (Figure 3). The interaction term between fish and anthropogenic nutrients was never significant. Species differed in the magnitude of their response to treatments in all cases, with the exception of symbiotic algal $\delta^{15}N$ in which there was no significant difference. In no case did species differ in the direction of the response, i.e., there were no significant treatment–species interactions. A significant block effect was found for algal C:N ($p = .05$), algal $\delta^{13}C$, and algal $\delta^{15}N$.

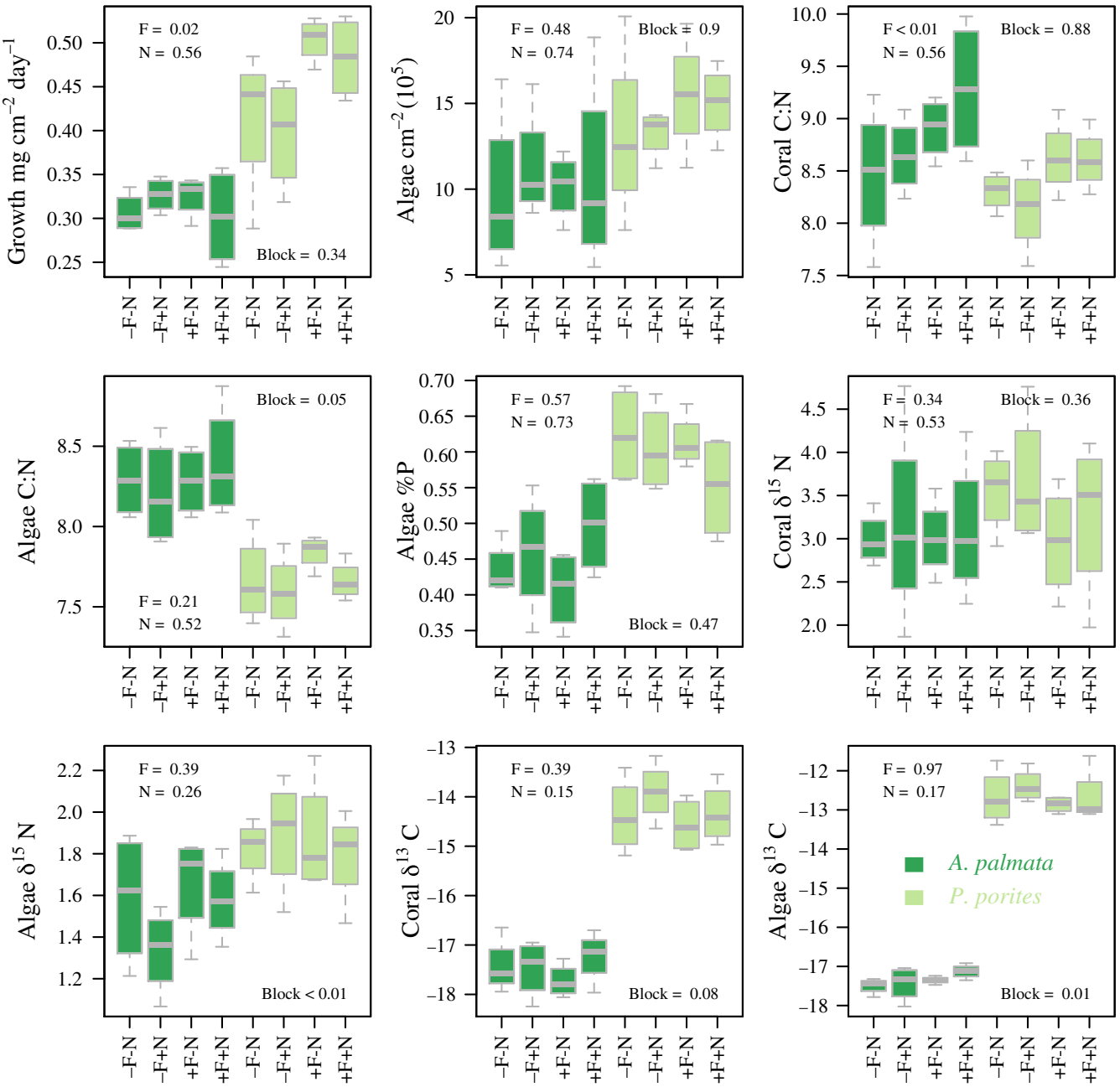


FIGURE 3 Treatment-level means for each of the nine variables, measured for each coral fragment, with associated significance for a three-way ANOVA, including a test for a block effect. ±F = low/high fish treatment, ±N = absence/presence of fertilizer. There were no significant F * N interactions. Species differed in the magnitude of their response to treatments in all cases, with the exception of symbiotic algal $\delta^{15}N$ in which there was no significant difference. In no case did species differ in the direction of the response, that is, there were no significant treatment–species interactions. *Porites porites* and *Acropora palmata* are light green and dark green, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

Objective 2: Our *Confirmatory model* allowed us to test seven hypotheses of coral–symbiotic algal nutrient and carbon interactions drawn from the literature (Figure 2), and found limited support for most under either nutrient regime scenario (Figure 4). These hypotheses were characterized by specific coral–symbiotic algae nutrient relationships, called "pathways" following Grace et al., 2012, and are indicated by black and red arrows (positive and negative, respectively) of which only a few were significant ($p < .05$, solid arrows; Figure 4). Key findings from these models were: (a) the overall hypothesis support was similar across the two nutrient regimes, largely because most pathways were not significant in either ($p > .05$, dashed arrows; Figure 4a,b); (b) algal %P positively affected algal density ($p < .05$) in the fish-only treatments (Figure 4a; Figure 2, component model 6); (c) coral $\delta^{13}C$ was positively correlated with coral growth ($p < .05$) only under the fish only regime (Figure 4c; Figure 2, component model 7); (d) under the anthropogenic nutrient regime, coral $\delta^{15}N$ was negatively correlated with coral C:N ($p < .05$; Figure 4b; Figure 2, component model 1); (e) Component model 2 was partially confirmed by the correlation between algal and coral $\delta^{13}C$; and (f) Component model 3 was partially confirmed in that algal C:N is correlated to coral C:N. In summary, the *Confirmatory models* did not provide an overall good fit to the data in either nutrient regime scenario; Fisher's *C* *p*-value = 0, and a model is interpreted as being consistent with the data if the Fisher's *C* statistic is small and its *p*-value is large, that is, $\alpha > 0.05$ (Grace et al., 2012).

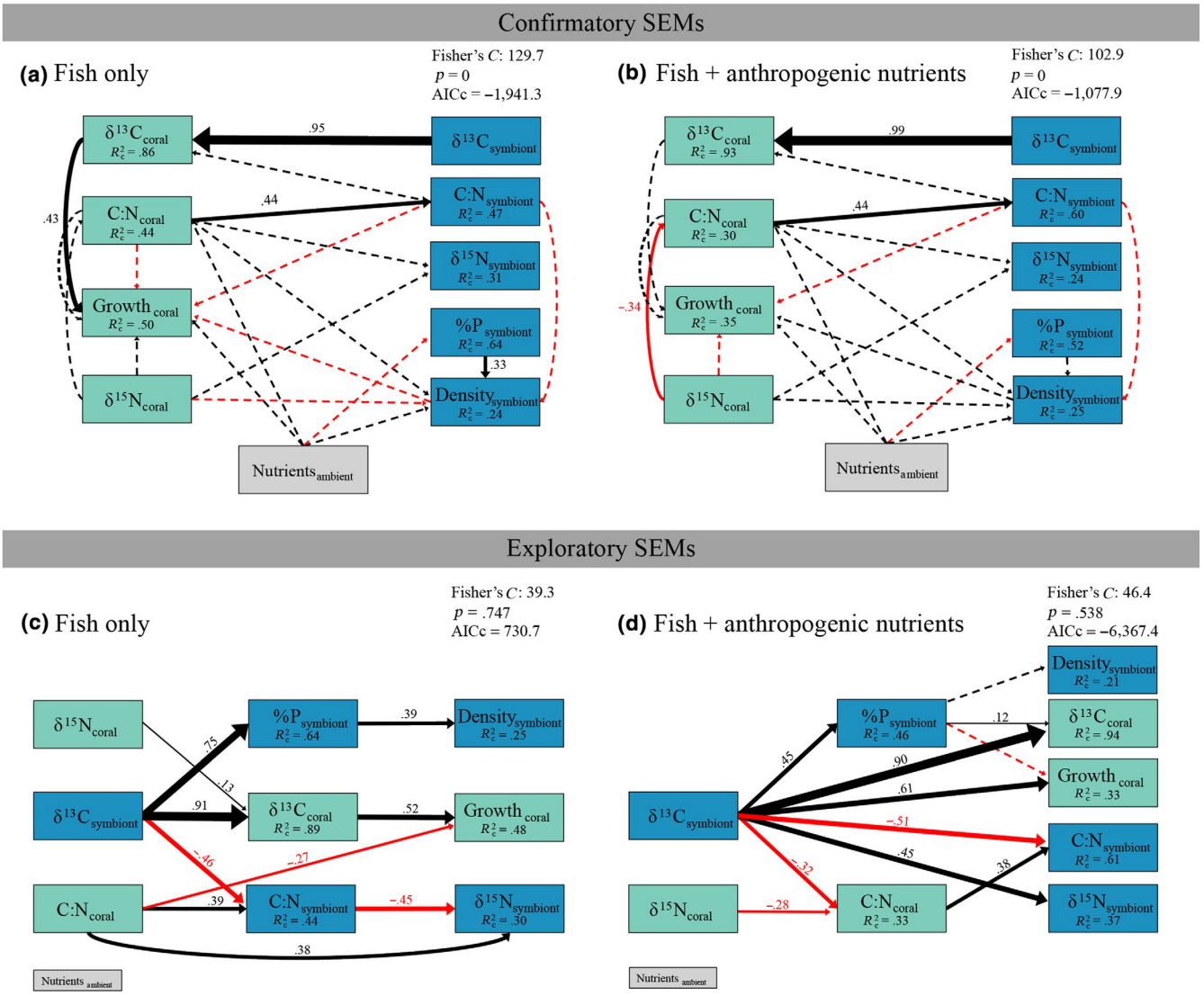


FIGURE 4 Path diagrams of the *Confirmatory* (a, b) and *Exploratory* (c, d) structural equation models (SEMs) that depict the significant (solid arrows) and nonsignificant (dashed arrows) relationships between coral (light blue) and algal (dark blue) variables in a single SEM. Arrow thickness corresponds to the standardized regression coefficient (−1 to 1), and arrow color refers to the direction of the relationship (black: positive; red: negative). The confirmatory models include all of the tested hypotheses. The exploratory models are the best-fit models generated through a stepwise process for each nutrient enrichment scenario. Excluded variables (those that were not important for the model) are shown in smaller boxes (ambient nutrients in c and d). Model statistics include conditional R^2 (R^2_c) for the response variable of each component model, Fisher's *C* (a lower score indicating a better fit), *p*-value ($\alpha = 0.05$), and AICc for each complete SEM [Colour figure can be viewed at wileyonlinelibrary.com]

Objective 3: Our goal was not to belabor confirmation or rejection of the literature-generated hypotheses, particularly because they were all generated under different conditions and with various coral species. Instead, a primary motivation was to use previous findings to frame our *Exploratory models* with the objective to identify novel pathways and generate new hypotheses from which to motivate future research (Grace et al., 2012; Lefcheck, 2016). The *Exploratory models* were generated using the *Confirmatory model* as the initial model structure to begin the stepwise model selection process. For both nutrient regimes, the Shipley's test of directed separation indicated that many significant, and reasonably plausible, pathways were missing. The *Exploratory models* allowed us to identify the pathways that most accurately represent coral–symbiont interactions by including previously missing, and excluding non-significant, relationships to generate the best-fit model (see Figure 4 for differences in AICc scores between *Confirmatory models* and *Exploratory models*).

A key finding from the *Exploratory models* was that under the fish only regime, coral–symbiotic algal interactions were more diverse in terms the number of significant pathways between variables (Figure 4c); under elevated anthropogenic nutrient enrichment, these pathways became strongly mediated through the algal symbiont (Figure 4d). A useful aspect of SEMs is that they identify which variables could not be explained by any other parameter in our model, called exogenous variables. Under the fish only regime, there were three exogenous variables, coral δ^{15}N, algal δ^{13}C, and coral C:N. In contrast, under the anthropogenic nutrient regime, there was only one exogenous variable, algal δ^{13}C, highlighting the dominance of this variable for all pathways.

The *Exploratory model* for the fish-only nutrient regime showed that coral growth was directly affected by coral δ^{13}C (positively) and coral C:N (negatively; Figure 4c; Figure 2, component model 7). Under the fish-only nutrient regime, coral growth was indirectly mediated through coral δ^{13}C by two factors: symbiotic algal δ^{13}C (positive)—this strong correlation confirmed that corals derive most of their C via algal produced photosynthate (Figure 2, component model 2); and coral δ^{15}N (positive)—showing that heterotrophic feeding also positively contributes C flow to the coral. Symbiotic algal density had no direct or indirect effect on coral growth. Ambient nutrients were excluded from the best-fit model, as they did not significantly affect any other variable and did not improve the model fit—an expected finding because the random effect on reef in our model largely accounted for the variation in nutrient input. When this random effect was removed, ambient nutrients positively affected coral C:N and coral growth.

The best-fit *Exploratory model* under the anthropogenic nutrient scenario showed that coral growth was only influenced by symbiotic algal δ^{13}C (Figure 4d). Despite being nonsignificant, effects of algal %P on coral growth (negative) and on symbiont density (positive) were retained in the model because of an improved fit relative to the model without these pathways (ΔAICc 7,209.3). An additional difference associated with the presence of anthropogenic nutrients was the decoupling of coral–coral C or nutrient pathways, for example, under the fish-alone nutrient regimes, there were three direct and one indirect, coral–coral C or nutrient pathways, whereas under the anthropogenic regime, there was only one. Environmental nutrients were excluded from the best-fit model as it was not significantly affected by any other variable and did not contribute substantially to the model fit.

4 | DISCUSSION

The mechanisms that underpin how coral respond to anthropogenic nutrient enrichment and the degree to which this relates to global declines in coral reef health remain poorly understood (D'Angelo & Wiedenmann, 2014; Szmant, 2002). Central to this problem is identifying how nutrient enrichment can alter the interaction between the coral host and its symbiotic algae. Previous work has been dominated by experiments that expose coral to high levels of nutrients that often exceed those found on eutrophied reefs, with the expectation of negative effects on coral. The goal of our study was to shift perspectives by exploring the effect of in situ enrichment from "beneficial" nutrients (fish excretion only), and the combination of "beneficial" and "harmful" (anthropogenic nutrients), where all treatments were a priori anticipated to be non-lethal. Whereas findings from our treatment-level analyses corroborate previous research showing beneficial effects of fish-mediated nutrients for coral growth (Holbrook et al., 2008; Huntington et al., 2017; Meyer et al., 1983; Shantz et al., 2015; Shaver & Silliman, 2017), anthropogenic nutrients were found to be relatively benign. These findings contrast general expectations of negative effects of nutrient enrichment, but support findings that moderate enrichment may positively affect coral growth (D'Angelo & Wiedenmann, 2014; Shantz et al., 2016). Despite this, a more comprehensive analysis of all coral and symbiotic algae relationships revealed that anthropogenic nutrients highly altered internal nutrient and carbon relationships such that they were dominated by the algal symbiont. These findings highlight a striking parallel between how anthropogenic nutrients promote symbiont dominance with the holobiont, and how they promote macroalgal dominance at the coral-reef scale (D'Angelo & Wiedenmann, 2014; Fabricius, 2005). We hypothesize that our experiment captured coral in a transition state, from a mutualistic symbiosis to a potentially antagonistic interaction (D'Angelo & Wiedenmann, 2014; Shantz et al., 2016), and provide a new perspective on the mechanisms by which a single stressor—nutrient enrichment—can compromise coral such that they are more susceptible to additional stressors such as overfishing or climate change.

Our experimental design allowed us to analyze results categorically at the treatment-level (ANOVAs), and in a continuous regression framework (SEMs). From the treatment-level perspective, findings revealed that fish-mediated nutrients enhanced coral growth rates—corroborating previous findings (Holbrook et al., 2008; Huntington et al., 2017; Meyer et al., 1983; Shantz et al., 2015). Addition of anthropogenic nutrients did not change

the overall positive effect of fish-mediated nutrients, demonstrating that we achieved our goal of non-lethal enrichment, which was supported by an ~90% survivorship of transplanted coral—a high success rate for coral transplantation (Okubo, Taniguchi, & Motokawa, 2005). At face value, this finding contrasts previous findings that anthropogenic nutrients are detrimental for coral growth and survival (Fabricius, 2005; Marubini & Davies, 1996), particularly because the fertilizer treatment did not significantly alter any response variable. However, this is an important finding in light of the results from our more comprehensive SEM analysis, as it demonstrates coral were able to maintain net positive growth and homeostasis in internal nutrient pools despite changes in the way in which the coral mediates nutrients between these pools. One hypothesis supporting these findings is that coral have likely evolved relatively high levels of flexibility in coping with variable nutrient inputs at the reef scale from sources, such as upwelling (Rougerie et al., 1992) and great variation in consumer-mediated nutrient supply (Allgeier, Layman, Mumby, & Rosemond, 2014), but also spatially within reefs at more localized scales (Graham et al., 2018; Holbrook et al., 2008; Meyer et al., 1983; Savage, 2019; Shantz et al., 2015). In a more general sense, these findings suggest that the outward appearance of coral at the individual or reef scale may be an insufficient measure of stress, and that additional assessment of nutrient and energy pathways may be needed to assess reef health.

Extending our analysis by using SEMs to fit more complex models revealed a more nuanced understanding of the dynamics of the coral–symbiont system. Our *Confirmatory model* approach allowed us to simultaneously test seven hypotheses of coral–symbiont inorganic nutrient and carbon interactions drawn from the literature in a single SEM that was applied independently to the fish-only (F+N− and F-N−), and the fish + anthropogenic nutrient regimes (F+N+, F-N+; Figures 2 and 4a,b). These models confirmed an essential energy pathway of C transfer between coral and algae with the directional positive relationship between coral and algal $\delta^{13}C$ (Figure 4a,b)—a hallmark relationship of all animal–algal mutualisms that indicates algae are providing their host with fixed C through photosynthesis (Venn, Loram, & Douglas, 2008). Whereas other hypothesized relationships were confirmed (e.g., coral $\delta^{13}C$–coral growth, coral C:N–algal C:N, coral $\delta^{15}N$–coral C:N, algal %P–algal density), the overall poor model fit for both *Confirmatory models* suggests that coral growth is more likely mediated through additional pathways.

Building on our *Confirmatory models* and the hypotheses provided by the past work (e.g., cited studies in Figure 2), a key outcome of our *Exploratory models* was that the anthropogenic nutrient regimes fundamentally restructured nutrient and C coral–symbiont interactions (Figure 4). Under conditions of fish-only nutrients, coral growth was supported directly by two pathways: (a) increased availability of N in coral tissue (negative relationship with coral C:N) and (b) higher availability of photosynthate (positive relationship with coral $\delta^{13}C$; Tanaka, Suzuki, & Sakai, 2018; Tremblay, Grover, Maguer, Hoogenboom, & Ferrier-Pages, 2014; Tremblay, Maguer, Grover, & Ferrier-Pages, 2015). Coral growth was additionally supported by two indirect pathways: (a) the positive relationship between algal $\delta^{13}C$ and coral $\delta^{13}C$ showing a positive relationship between algal photosynthesis and coral growth, and (b) the positive relationship with coral $\delta^{15}N$ suggesting that coral were also feeding heterotrophically (Muscatine et al., 2005) and that this positively influenced growth.

In contrast to the more diverse pathways that underpinned coral growth under fish-only nutrient enrichment, coral growth was likely only supported by photosynthate from the algae in the anthropogenic nutrient regime as indicated by a direct positive pathway from algal $\delta^{13}C$ (Muscatine et al., 2005). In fact, a key finding from the *Exploratory* anthropogenic nutrient model was overall algal dominance of all nutrient and C pathways (Figure 4d). For example, algal $\delta^{13}C$ was linked to every other variable in the model, with the exception of coral $\delta^{15}N$, via six direct and two indirect pathways, whereas in the fish-only model, algal $\delta^{13}C$ was associated with only three direct and three indirect pathways. These findings are consistent with the past work that shows that moderate nutrient levels can increase algal dominance in the holobiont without necessarily having an effect on coral growth (Tanaka, Miyajima, Koike, Hayashibara, & Ogawa, 2007). However, algal proliferation may lead to stress and increasingly antagonistic interactions for the coral—the primary mechanism for this being that increased algal densities create a greater demand of resources on the coral, shifting the mutualism toward antagonism with negative consequences for growth or calcification (Marubini & Davies, 1996), and/or increased susceptibility to bleaching (Baker & Cunning, 2012; Wiedenmann et al., 2013). Yet, we found no evidence that algal cell density increased in response to the anthropogenic nutrient enrichment regime. Instead, we found that algal cell density was no longer significantly predicted by any coral or algal variables (Figure 4d), as was the case under the fish-only conditions (e.g., $\%P_{algae}$ was positively related to algal density; Figure 4c). It is possible, however, that the increased ambient availability of nutrients from our fertilizer disrupted internal nutrient dynamics such that the algal density was more strongly governed by extrinsic nutrient availability. Furthermore, previous research has shown that the presence of nitrate from anthropogenic nutrients (that includes NO_3^- and NH_4^+, whereas fish excretion is exclusively NH_4^+) would, in of itself, encourage algal proliferation within the host (Ezzat et al., 2015; Shantz et al., 2016). As such, it is possible that other metrics of symbiont growth would have supported this expectation (e.g., increased cell size, or density per host protein or lipid content). Nonetheless, we hypothesize that we did not find increases in algal density because of the moderate level of our enrichment regime. We suggest this provides further support that our experiment captured coral at a transition state whereby further increases in ambient nutrient availability would result in increased algal densities with potentially harmful implications for the coral host.

Our findings help identify new, and hone existing, hypotheses that we hope can inform future research to understand coral–symbiotic algal interactions and how they respond to changing environmental conditions. Resulting Hypothesis 1: *Considering*

interactions between the coral host and the algal symbiont in a traditional food web context may be a useful framework through which to quantitatively understand coral health. The successful application of SEMs in our analysis highlights the potential utility of framing the complex coral–algal symbiont relationships in a food web context whereby food web networks (e.g., Dunne, Williams, & Martinez, 2002), or interaction strengths (e.g., McCann, Hastings, & Huxel, 1998), could directly quantify the diversity and stability of these interactions under changing environmental conditions. The use of isotopes, either natural abundance or tracers, could also complement this approach by providing means to quantify interaction strengths. Resulting Hypothesis 2: *Coral–symbiotic algal interactions exist along a continuum between mutualism and antagonism that is highly dynamic*. Our findings provide new evidence in support of this long-standing hypothesis by showing that anthropogenic nutrients can to some extent appear benign (e.g., no effect on growth), but also fundamentally shift internal processes. This strongly suggests that corals can persist under highly variable relationships with their symbiont. Similar evidence suggests that coral subjected to short-term temperature shift can exhibit substantial reconfiguration of their coral–symbiont interactions that appear "benign" in that they do show pronounced external changes (Morris, Voolstra, Quigley, Bourne, & Bay, 2019). Therefore, it appears that the transition state that we hypothesize captured in our study may also occur from additional stressors. A key challenge is to extend experiments to include an even greater range of nutrients (or other stressors) such that species interaction dynamics can be more rigorously captured. Resulting Hypothesis 3: *The ratio (N:P) of nutrient supply may be more important than supply rate for understanding nutrient enrichment for coral*. This hypothesis is rooted in the resource ratio hypothesis (Tilman, 1982), ecological stoichiometry (Sterner & Elser, 2002), and more contemporary work with corals (e.g., Wiedenmann et al., 2013). It is also supported by this study in that the N:P ratio across the two nutrient regimes differed more than the nutrient supply rates (Allgeier et al., 2018). Previous work has supported the hypothesis that fishes supply nutrients at an optimal ratio for coral, and this may be disrupted by the low N:P ratio of anthropogenic nutrients (Allgeier et al., 2014). However, testing this requires overcoming the fundamental challenge for any field-based study where water movement and/or fish movement are present, that is, knowing the exact amount of nutrients coral is subjected to—a key limitation in this study.

Substantial debate remains over the role of anthropogenic nutrient enrichment for coral health (see discussion in Bruno, Cote, & Toth, 2019). A key challenge is that nutrient enrichment often does not result in drastic changes in ambient nutrient availability, making it difficult to quantify net effects to ecosystems. For example, in a long-term study over the course of nearly four decades in the Floriday Keys, Lapointe, Brewton, Herren, Porter, and Hu (2019) found a marginal increase in dissolved inorganic nitrogen over time, and negligible increases in NH_4^+, NO_3^-, or PO_4^{3-}, despite the tremendous amount of nutrients entering the system from the Florida Everglades. While Lapointe et al. (2019) claimed that these increases in DIN led to reduced coral cover, research in the same region reported that that live coral cover was positively correlated to the proximity to shore on 84 patch reefs, indicating that increased land-based nutrients may actually be promoting coral health (Lirman & Fong, 2007). The fact that outcomes to nutrient enrichment on coral reefs are so variable, plus findings from our study, provides a strong case that nutrient enrichment effects on coral reefs maybe in fact common, but simply highly cryptic. The significance of this for conservation is that improved monitoring of coral reefs to understand the degree to which they are stressed, may require additionally sampling coral and algal tissue to characterize nutrient and energy pathways.

Insights from our research may also benefit the study of coral survivorship, and development beyond early recruitment—processes that are considered to be essential for maintaining reef resilience (Doropoulos et al., 2016; Gleason & Hofmann, 2011). Immediately following settlement, coral are particularly susceptible to stressors (Graham, Baird, & Connolly, 2008), and further understanding of the nutrient and energy pathways that underpin the early colonization of the coral by symbiotic algae may provide important insights into this critical life history stage (Graham, Baird, Connolly, Sewell, & Willis, 2013; Harii, Yasuda, Rodriguez-Lanetty, Irie, & Hidaka, 2009; Humanes et al., 2017). Furthermore, this approach may help identify individuals or species that may be most resilient to stress associated with transplantation. Our findings suggest that utilization of more realistic experimental conditions, including studies across gradients of anthropogenic nutrient enrichment as well as the incorporation of quantifying nutrient and energy pathways, may facilitate conservation efforts to mitigate coral loss.

Our study brings to light new perspectives and hypotheses about the effects of nutrient enrichment for coral. We provided additional support for the important role that consumers play in mediating nutrients in near-shore environments (Allgeier, Burkepile, & Layman, 2017) and highlighted the cryptic effects anthropogenic nutrients can have in these systems. Interestingly, the patterns that emerge in our findings also parallel our understanding of the impacts of nutrient enrichment on coral reefs at the ecosystem scale—anthropogenic nutrients shunt energy away from coral pathways and through algal pathways. This pattern can only be speculated on at this point, but is suggestive of the consistent manner in which human activity tends to rewire ecological interactions at different scales of biological organization.

ACKNOWLEDGEMENTS

J.E.A. was supported by a National Science Foundation DDIG and a National Science Foundation Postdoctoral Fellowship during this project with current support by a Lucille and David Packard Fellowship and National Science Foundation OCE #1948622, and C.L. by National Science Foundation OCE #0746164 and start-up funds from NCSU. D.W.K. was supported by start-up funds provided by the University of Alabama at Birmingham. We would like to thank Mark Warner, two reviewers and the editor for thoughtful

comments that greatly improved the manuscript, and Dillard Bray for his intellectual support of these ideas. We would also like to thank the Bahamian Government for permission to conduct our research (permit #0933604008).

AUTHOR CONTRIBUTION

J.E.A. and D.W.K. designed the experiment and conducted laboratory analyses; J.E.A., D.W.K., R.A., and E.H. conducted fieldwork; M.A.A. and J.E.A. conducted analyses; J.E.A. wrote the first draft with significant writing contributions from M.A., D.W.K., C.L., and E.H.

DATA AVAILABILITY STATEMENT

Data is available in the supplementary information of this manuscript.

ORCID

Jacob E. Allgeier https://orcid.org/0000-0002-9005-6432

REFERENCES

Allgeier, J. E., Burkepile, D. E., & Layman, C. A. (2017). Animal pee in the sea: Consumer-mediated nutrient dynamics in the world's changing oceans. *Global Change Biology*, *23*, 2166–2178. https://doi.org/10.1111/gcb.13625

Allgeier, J. E., Layman, C. A., Montaña, C. G., Hensel, E., Appaldo, R., & Rosemond, A. D. (2018). Anthropogenic versus fish-derived nutrient effects on seagrass community structure and function. *Ecology*, *99*, 1792–1801. https://doi.org/10.1002/ecy.2388

Allgeier, J. E., Layman, C. A., Mumby, P. J., & Rosemond, A. D. (2014). Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Global Change Biology*, *20*, 2459–2472. https://doi.org/10.1111/gcb.12566

Allgeier, J. E., Layman, C. A., Mumby, P. J., & Rosemond, A. D. (2015). Biogeochemical implications of biodiversity loss across regional gradients of coastal marine ecosystems. *Ecological Monographs*, *85*(117), 132.

Allgeier, J. E., Layman, C. A., & Rosemond, A. D. (2011). Variation in nutrient limitation and seagrass nutrient content in Bahamian tidal creek ecosystems. *Journal of Experimental Marine Biology and Ecology*, *407*, 330–336. https://doi.org/10.1016/j.jembe.2011.07.005

Allgeier, J. E., Rosemond, A. D., Mehring, A. S., & Layman, C. A. (2010). Synergistic nutrient co-limitation across a gradient of ecosystem fragmentation in subtropical mangrove-dominated wetlands. *Limnology and Oceanography*, *55*, 2660–2668. https://doi.org/10.4319/lo.2010.55.6.2660

Allgeier, J. E., Yeager, L. A., & Layman, C. A. (2013). Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. *Ecology*, *94*, 521–529. https://doi.org/10.1890/12-1122.1

Anthony, K. R. N., & Fabricius, K. E. (2000). Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *Journal of Experimental Marine Biology and Ecology*, *252*, 221–253. https://doi.org/10.1016/S0022-0981(00)00237-9

Anthony, K. R. N., Hoogenboom, M. O., Maynard, J. A., Grottoli, A. G., & Middlebrook, R. (2009). Energetics approach to predicting mortality risk from environmental stress: A case study of coral bleaching. *Functional Ecology*, *23*, 539–550. https://doi.org/10.1111/j.1365-2435.2008.01531.x

Baker, A., & Cunning, R. (2012). Excess algal symbionts increase the susceptibility of reef corals to bleaching. *Nature Climate Change*, *3*, 259. https://doi.org/10.1038/nclimate1711

Bruno, J. F., Cote, I. M., & Toth, L. T. (2019). Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? *Annual Review of Marine Science*, *11*(11), 307–334.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information theoretic approach* (2nd ed.). New York, NY: Springer-Verlag.

Carr, M. H., & Hixon, M. A. (1995). Predation effects on early post-settlement survivorship of coral reef fishes. *Marine Ecology-Progress Series*, *124*, 31–42. https://doi.org/10.3354/meps124031

Carr, M. H., & Hixon, M. A. (1997). Artificial reefs: The importance of comparisons with natural reefs. *Fisheries*, *22*, 28–33. https://doi.org/10.1577/1548-8446(1997)022<0028:ARTIOC>2.0.CO;2

Chapin, F. S., Matson, P. A., & Vitousek, P. (2011). *Principles of terrestrial ecosystem ecology* (2nd ed.). New York, NY: Springer.

D'Angelo, C., & Wiedenmann, J. (2014). Impacts of nutrient enrichment on coral reefs: New perspectives and implications for coastal management and reef survival. *Current Opinion in Environmental Sustainability*, *7*, 82–93. https://doi.org/10.1016/j.cosust.2013.11.029

Doropoulos, C., Roff, G., Bozec, Y. M., Zupan, M., Werminghausen, J., & Mumby, P. J. (2016). Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. *Ecological Monographs*, *86*, 20–44.

Dubinsky, Z., & Stambler, N. (1996). Marine pollution and coral reefs. *Global Change Biology*, *2*, 511–526. https://doi.org/10.1111/j.1365-2486.1996.tb00064.x

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, *5*, 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Ezzat, L., Maguer, J.-F., Grover, R., & Ferrier-Pagès, C. (2015). New insights into carbon acquisition and exchanges within the coral–dinoflagellate symbiosis under NH^{4+} and NO^{3-} supply. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*. https://doi.org/10.1098/rspb.2015.0610

Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin*, *50*, 125–146. https://doi.org/10.1016/j.marpolbul.2004.11.028

Fabricius, K. E. (2011). Factors determining the resilience of coral reefs to eutrophication: A review and conceptual model. In Z. Dubinsky & N. Stambler (Eds.), *Coral reefs: An ecosystem in transition* (pp. 493–505). Dordrecht, the Netherlands: Springer. https://doi.org/10.1007/978-94-007-0114-4

Falkowski, P. G., Dubinsky, Z., Muscatine, L., & McCloskey, L. (1993). Population control in symbiotic corals. *BioScience*, *43*, 606–611. https://doi.org/10.2307/1312147

Gleason, D. F., & Hofmann, D. K. (2011). Coral larvae: From gametes to recruits. *Journal of Experimental Marine Biology and Ecology*, *408*, 42–57. https://doi.org/10.1016/j.jembe.2011.07.025

Grace, J. B., Schoolmaster, D. R., Guntenspergen, G. R., Little, A. M., Mitchell, B. R., Miller, K. M., & Schweiger, E. W. (2012). Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere*, *3*, 44. https://doi.org/10.1890/ES12-00048.1

Graham, E. M., Baird, A. H., & Connolly, S. R. (2008). Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral Reefs*, *27*, 529–539. https://doi.org/10.1007/s00338-008-0361-z

Graham, E. M., Baird, A. H., Connolly, S. R., Sewell, M. A., & Willis, B. L. (2013). Rapid declines in metabolism explain extended coral larval longevity. *Coral Reefs*, *32*, 539–549. https://doi.org/10.1007/s00338-012-0999-4

Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S., & MacNeil, M. A. (2018). Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature*, *559*, 250–253. https://doi.org/10.1038/s41586-018-0202-3

Grottoli, A. G., Rodrigues, L. J., & Palardy, J. E. (2006). Heterotrophic plasticity and resilience in bleached corals. *Nature*, *440*, 1186–1189. https://doi.org/10.1038/nature04565

Harii, S., Yasuda, N., Rodriguez-Lanetty, M., Irie, T., & Hidaka, M. (2009). Onset of symbiosis and distribution patterns of symbiotic

dinoflagellates in the larvae of scleractinian corals. *Marine Biology*, *156*, 1203–1212. https://doi.org/10.1007/s00227-009-1162-9

Hatcher, B. G. (1988). Coral reef primary productivity – A beggar's banquet. *Trends in Ecology & Evolution*, *3*, 106–111. https://doi.org/10.1016/0169-5347(88)90117-6

Hatcher, B. G. (1990). Coral reef primary productivity – A hierarchy of patterns and process. *Trends in Ecology & Evolution*, *5*, 149–155.

Hixon, M. A., & Beets, J. P. (1989). Shelter characteristics and Caribbean fish assemblages – Experiments with artificial reefs. *Bulletin of Marine Science*, *44*, 666–680.

Hoadley, K. D., Pettay, D. T., Dodge, D., & Warner, M. E. (2016). Contrasting physiological plasticity in response to environmental stress within different cnidarians and their respective symbionts. *Coral Reefs*, *35*, 529–542. https://doi.org/10.1007/s00338-016-1404-5

Holbrook, S. J., Brooks, A. J., Schmitt, R. J., & Stewart, H. L. (2008). Effects of sheltering fish on growth of their host corals. *Marine Biology*, *155*, 521–530. https://doi.org/10.1007/s00227-008-1051-7

Houlbreque, F., & Ferrier-Pages, C. (2009). Heterotrophy in tropical scleractinian corals. *Biological Reviews of the Cambridge Philosophical Society*, *84*, 1–17. https://doi.org/10.1111/j.1469-185X.2008.00058.x

Humanes, A., Fink, A., Willis, B. L., Fabricius, K. E., de Beer, D., & Negri, A. P. (2017). Effects of suspended sediments and nutrient enrichment on juvenile corals. *Marine Pollution Bulletin*, *125*, 166–175. https://doi.org/10.1016/j.marpolbul.2017.08.003

Huntington, B. E., Miller, M. W., Pausch, R., & Richter, L. (2017). Facilitation in Caribbean coral reefs: High densities of staghorn coral foster greater coral condition and reef fish composition. *Oecologia*, *184*, 247–257. https://doi.org/10.1007/s00442-017-3859-7

Jokiel, P. L., Maragos, J. E., & Franziskey, L. (1978). Coral growth: Buoyant weight technique. In D. R. Stoddart & R. E. Johannes (Eds.), *Coral reefs: Research methods*. UNESCO monographs on oceanographic methodology (pp. 529–542). Paris, France: UNESCO.

Lapointe, B. E., Brewton, R. A., Herren, L. W., Porter, J. W., & Hu, C. M. (2019). Nitrogen enrichment, altered stoichiometry, and coral reef decline at Looe Key, Florida Keys, USA: A 3-decade study. *Marine Biology*, *166*, 31.

Layman, C. A., Allgeier, J. E., & Montaña, C. G. (2016). Mechanistic evidence of enhanced production on artificial reefs: A case study in a Bahamian seagrass ecosystem. *Ecological Engineering*, *95*, 574–579.

Layman, C. A., Allgeier, J. E., Yeager, L. A., & Stoner, E. W. (2013). Thresholds of ecosystem response to nutrient enrichment from fish aggregations. *Ecology*, *94*, 530–536. https://doi.org/10.1890/12-0705.1

Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Levas, S., Grottoli, A. G., Schoepf, V., Aschaffenburg, M., Baumann, J., Bauer, J. E., & Warner, M. E. (2016). Can heterotrophic uptake of dissolved organic carbon and zooplankton mitigate carbon budget deficits in annually bleached corals? *Coral Reefs*, *35*, 495–506. https://doi.org/10.1007/s00338-015-1390-z

Lirman, D., & Fong, P. (2007). Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. *Marine Pollution Bulletin*, *54*, 779–791. https://doi.org/10.1016/j.marpolbul.2006.12.014

Marsh, J. A. (1970). Primary productivity or reef-building calcareous red algae. *Ecology*, *51*, 255–263. https://doi.org/10.2307/1933661

Marubini, F., & Davies, P. S. (1996). Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. *Marine Biology*, *127*, 319–328. https://doi.org/10.1007/BF00942117

McCann, K. S., Hastings, A., & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, *395*, 794–798. https://doi.org/10.1038/27427

Meyer, J. L., Schultz, E. T., & Helfman, G. S. (1983). Fish schools – An asset to corals. *Science*, *220*, 1047–1049. https://doi.org/10.1126/science.220.4601.1047

Morris, L. A., Voolstra, C. R., Quigley, K. M., Bourne, D. G., & Bay, L. K. (2019). Nutrient availability and metabolism affect the stability of coral-symbiodiniaceae symbioses. *Trends in Microbiology*, *27*, 678–689. https://doi.org/10.1016/j.tim.2019.03.004

Muscatine, L., Falkowski, P. G., Dubinsky, Z., Cook, P. A., & McCloskey, L. R. (1989). The effects of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. *Proceedings of the Royal Society B-Biological Sciences*, *236*, 311–324.

Muscatine, L., Goiran, C., Land, L., Jaubert, J., Cuif, J. P., & Allemand, D. (2005). Stable isotopes (delta C-13 and delta N-15) of organic matrix from coral skeleton. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 1525–1530.

Muscatine, L., & Porter, J. W. (1977). Reef corals – Mutualistic symbiosis adapted to nutrient-poor environments. *BioScience*, *27*, 454–460.

Odum, H. T., & Odum, E. P. (1955). Trohic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs*, *25*, 291–320.

Okubo, N., Taniguchi, H., & Motokawa, T. (2005). Successful methods for transplanting fragments of *Acropora formosa* and *Acropora hyacinthus*. *Coral Reefs*, *24*, 333–342. https://doi.org/10.1007/s00338-005-0496-0

Palardy, J. E., Rodrigues, L. J., & Grottoli, A. G. (2008). The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. *Journal of Experimental Marine Biology and Ecology*, *367*, 180–188. https://doi.org/10.1016/j.jembe.2008.09.015

Porter, J. W. (1976). Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. *The American Naturalist*, *110*, 731–742. https://doi.org/10.1086/283100

Richter, C., Wunsch, M., Rasheed, M., Kotter, I., & Badran, M. I. (2001). Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature*, *413*, 726–730. https://doi.org/10.1038/35099547

Rougerie, F., Fagerstrom, J. A., & Andrie, C. (1992). Geothermal endoupwelling – A solution to the reef nutrient paradox. *Continental Shelf Research*, *12*, 785–798. https://doi.org/10.1016/0278-4343(92)90044-K

Savage, C. (2019). Seabird nutrients are assimilated by corals and enhance coral growth rates. *Scientific Reports*, *9*, 4284. https://doi.org/10.1038/s41598-019-41030-6

Shantz, A. A., Ladd, M. C., Schrack, E., & Burkepile, D. E. (2015). Fish-derived nutrient hotspots shape coral reef benthic communities. *Ecological Applications*, *25*, 2142–2152. https://doi.org/10.1890/14-2209.1

Shantz, A. A., Lemoine, N. P., & Burkepile, D. E. (2016). Nutrient loading alters the performance of key nutrient exchange mutualisms. *Ecology Letters*, *19*, 20–28. https://doi.org/10.1111/ele.12538

Shaver, E. C., & Silliman, B. R. (2017). Time to cash in on positive interactions for coral restoration. *PeerJ*, *5*, e3499. https://doi.org/10.7717/peerj.3499

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, *90*, 363–368. https://doi.org/10.1890/08-1034.1

Smith, S. V., Kimmerer, W. J., Laws, E. A., Brock, R. E., & Walsh, T. W. (1981). Kaneohe bay sewage diversion experiment – Perspectives on ecosystem responses to nutrient perturbation. *Pacific Science*, *35*, 279–402.

Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton, NJ: Princeton University Press.

Stimson, J., & Kinzie, R. A. (1991). The temporal pattern and rate of release of zooxanthellae from the reef coral pocillopora-damicornis under nitrogen-enrichment and control conditions. *Journal of Experimental Marine Biology and Ecology*, *153*, 63–74.

Stoner, E. W., Layman, C. A., Yeager, L. A., & Hassett, H. M. (2011). Effects of anthropogenic disturbance on the abundance and size

of epibenthic jellyfish Cassiopea spp. *Marine Pollution Bulletin*, *62*, 1109–1114. https://doi.org/10.1016/j.marpolbul.2011.03.023

Szmant, A. M. (2002). Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? *Estuaries*, *25*, 743–766. https://doi.org/10.1007/BF02804903

Szmant, A. M., & Gassman, N. J. (1990). The effects of prolonged bleaching on the tissue of biomass and reproduction of the reef coral *Montastreat annularis*. *Coral Reefs*, *8*, 217–224.

Tanaka, Y., Miyajima, T., Koike, I., Hayashibara, T., & Ogawa, H. (2007). Imbalanced coral growth between organic tissue and carbonate skeleton caused by nutrient enrichment. *Limnology and Oceanography*, *52*(3), 1139–1146.

Tanaka, Y., Suzuki, A., & Sakai, K. (2018). The stoichiometry of coral-dinoflagellate symbiosis: Carbon and nitrogen cycles are balanced in the recycling and double translocation system. *The ISME Journal*, *12*, 860–868. https://doi.org/10.1038/s41396-017-0019-3

Thurber, R. L. V., Burkepile, D. E., Fuchs, C., Shantz, A. A., McMinds, R., & Zaneveld, J. R. (2014). Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. *Global Change Biology*, *20*, 544–554. https://doi.org/10.1111/gcb.12450

Tilman, D. (1982). *Resource competition and community structure*. Princeton, NJ: Princeton University Press.

Tremblay, P., Grover, R., Maguer, J. F., Hoogenboom, M., & Ferrier-Pages, C. (2014). Carbon translocation from symbiont to host depends on irradiance and food availability in the tropical coral *Stylophora pistillata*. *Coral Reefs*, *33*, 1–13. https://doi.org/10.1007/s00338-013-1100-7

Tremblay, P., Maguer, J. F., Grover, R., & Ferrier-Pages, C. (2015). Trophic dynamics of scleractinian corals: Stable isotope evidence. *Journal of Experimental Biology*, *218*, 1223–1234. https://doi.org/10.1242/jeb.115303

Veal, C. J., Carmi, M., Fine, M., & Hoegh-Guldberg, O. (2010). Increasing the accuracy of surface area estimation using single wax dipping of coral fragments. *Coral Reefs*, *29*, 893–897. https://doi.org/10.1007/s00338-010-0647-9

Venn, A. A., Loram, J. E., & Douglas, A. E. (2008). Photosynthetic symbioses in animals. *Journal of Experimental Botany*, *59*, 1069–1080. https://doi.org/10.1093/jxb/erm328

Wiedenmann, J., D'Angelo, C., Smith, E. G., Hunt, A. N., Legiret, F. E., Postle, A. D., & Achterberg, E. P. (2013). Nutrient enrichment can increase the susceptibility of reef corals to bleaching. *Nature Climate Change*, *3*, 160–164. https://doi.org/10.1038/nclimate1661

Yeager, L. A., Allgeier, J. E., & Layman, C. A. (2011). Effects of heterogeneity at multiple spatial scales on fish community assembly. *Oecologia*, *167*, 157–168. https://doi.org/10.1007/s00442-011-1959-3

Yellowlees, D., Rees, T. A., & Leggat, W. (2008). Metabolic interactions between algal symbionts and invertebrate hosts. *Plant, Cell and Environment*, *31*, 679–694. https://doi.org/10.1111/j.1365-3040.2008.01802.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Allgeier JE, Andskog MA, Hensel E, Appaldo R, Layman C, Kemp DW. Rewiring coral: Anthropogenic nutrients shift diverse coral–symbiont nutrient and carbon interactions toward symbiotic algal dominance. *Glob Change Biol*. 2020;26:5588–5601. https://doi.org/10.1111/gcb.15230