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Context-dependent effects of nutrient loading on the coral–algal mutualism

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Abstract. Human-mediated increases in nutrient availability alter patterns of primary production, impact species diversity, and threaten ecosystem function. Nutrients can also alter community structure by disrupting the relationships between nutrient-sharing mutualists that form the foundation of communities. Given their oligotrophic nature and the dependence of reef-building corals on symbiotic relationships, coral reefs may be particularly vulnerable to excess nutrients. However, individual studies suggest complex, even contradictory, relationships among nutrient availability, coral physiology, and coral growth. Here, we used meta-analysis to establish general patterns of the impact of nitrogen (N) and phosphorus (P) on coral growth and photobiology. Overall, we found that over a wide range of concentrations, N reduced coral calcification 11%, on average, but enhanced metrics of coral photobiology, such as photosynthetic rate. In contrast, P enrichment increased average calcification rates by 9%, likely through direct impacts on the calcification process, but minimally impacted coral photobiology. There were few synergistic impacts of combined N and P on corals, as the nutrients impact corals via different pathways. Additionally, the response of corals to increasing nutrient availability was context dependent, varying with coral taxa and morphology, enrichment source, and nutrient identity. For example, naturally occurring enrichment from fish excretion increased coral growth, while human-mediated enrichment tended to decrease coral growth. Understanding the nuances of the relationship between nutrients and corals may allow for more targeted remediation strategies and suggest how other global change drivers such as overfishing and climate change will shape how nutrient availability impacts corals.

Key words: coral growth; coral reefs; eutrophication; nutrients; photobiology; Symbiodinium; *symbiosis.*

Introduction

In most ecosystems, nitrogen (N) or phosphorus (P) limits primary production (Elser et al. 2007), but humans have increased the supply of these nutrients to well above the natural levels found in many systems (Vitousek et al. 1997*a*, *b*, Elser et al. 2007). Increases in nutrient loading can have severe consequences on the environment, often resulting in the dominance of species best suited to monopolize these new nutrient regimes, and the competitive exclusion of subordinate species (Tilman 1988, Smith et al. 1999). These changes result in declines in biological diversity, greater susceptibility to disturbances, and the loss of ecosystem services (Vitousek 1997*b*, Smith et al. 1999, Harpole and Tilman 2007). Aquatic systems may be particularly vulnerable to nutrient loading due to downstream transport of nutrients, making increasing nutrient delivery a primary threat to coastal ecosystems (Vitousek et al. 1997*a*).

Although anthropogenic enrichment often delivers both N and P, the concentration of each nutrient will differ with the source of enrichment. For example, regions with intense agricultural activity or urban development often have higher delivery of N to coastal waters (Howarth et al. 1996, Carpenter et al. 1998). In contrast, municipal and industrial wastewater, as well as runoff from regions with intense livestock production, often deliver substantial P to coastal systems (Conley et al. 2009). Geomorphology can also play a large role in shaping the identity of nutrient loads as soil type, age, and pH affect sorption of P and its downstream availability (Schachtman et al. 1998). Additionally, different N species (nitrate or ammonium) are often found in different anthropogenic or natural nutrient sources, and primary producers often have significant preferences for one vs. the other (Raven et al. 1992). Given that different nutrient sources frequently deliver different ratios or types of N and P, it is imperative to understand how altering the magnitude and identity of nutrients delivered to coastal systems will impact them.

On coral reefs, increasing nutrient availability may be a critical driver of degradation as it often promotes fast-growing algae that can hinder coral growth and survivorship (Mumby and Steneck 2008). The effects of these nutrients on algal communities of coral reefs have received considerable attention (McCook 1999,

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Szmant 2002, Burkepile and Hay 2006). Yet, there has been no quantitative synthesis of the impacts of nutrient availability on corals, the foundation species of these ecosystems. Although the negative impacts of nutrients are widely assumed (reviewed by Fabricius 2005), the direct effects of nutrients on corals are likely complex, as enrichment may affect both the coral host and their symbiotic dinoflagellates, *Symbiodinium* spp.

Understanding the individual impacts of N or P loading is important, as both nutrients may impact coral growth rates through a host of possible mechanisms. For example, N enrichment may inhibit coral growth by increasing the density of *Symbiodinium* within corals (Hoegh-Guldberg and Smith 1989, Muscatine et al. 1989). As a result, greater densities of *Symbiodinium* may monopolize dissolved inorganic carbon (DIC) for photosynthesis, limiting the DIC available for calcification and reducing growth rates (Muscatine et al. 1998). In contrast, P enrichment may have negligible effects on *Symbiodinium* (Muscatine et al. 1989, Godinot et al. 2011), but may impair coral growth by inhibiting the formation of calcium carbonate crystals and thereby hindering skeletal formation (Simkiss 1964, Dunn et al. 2012). However, some studies have documented positive effects of both N and P on coral growth (e.g., Meyer and Schultz 1985*b*, Holbrook et al. 2008, Godinot et al. 2011). These positive effects may be driven by physiological changes in the coral, such as increased photosynthetic output providing more energy to the coral or pH shifts within the coral tissue that facilitate calcification (Tambutte et al. 2011). Ultimately, the conflicting reports of negative and positive effects of nutrients on coral growth suggest that the effects of nutrient enrichment on the coral–algal mutualism may be context dependent.

Because symbiotic relationships such as the coral–algal mutualism typically incur both costs and benefits to each participant (Herre et al. 1999), any factors that shift the cost–benefit ratio of the interaction for one or both participants have the potential to alter the dynamics of the symbiosis. For example, plant–mycorrhizae interactions, one of the best studied nutrient-sharing mutualisms, are frequently vulnerable to increases in nutrient loading (Hoeksema et al. 2010). In these mutualisms, plants provide more energy to mychorrhizal fungi when nutrients are limiting, but reduce energy delivery to mychorrhizae as nutrient levels increase, causing fungal populations to decline and plant growth to suffer (Johnson et al. 2008). Nutrient enrichment may ultimately reorganize plant communities by allowing species that are less dependent on mychorrizae to become competitively dominant when nutrient loading slows the growth of mycorrhizae-dependent species (Tilman 1988, Treseder 2004, Johnson et al. 2008). Whether enrichment-driven breakdowns in nutrient-sharing symbioses are ubiquitous or exclusive to plants and their mutualists is currently unclear. But, the coral–algal mutualism may be similarly vulnerable to increases in nutrient availability.

Here, we used meta-analysis of 208 independent experiments from 47 studies to quantify the impact of N and P loading on coral growth and photobiology. With our data set, we were able to assess: (1) How N vs. P impact corals differently, (2) how coral morphology and taxonomy influence responses to nutrients, and (3) how the source of nutrient enrichment determines the effect on corals. Our analyses reveal contrasting effects of N and P, illustrate the importance of nutrient source for coral growth, and suggest that there are common patterns across ecosystems in how altered nutrient supply affects the dynamics of nutrient-sharing mutualisms.

Materials and Methods

Coral growth is variously measured through calcification rates, skeletal extension rates, and changes in skeletal density. However, nutrient enrichment can affect each metric differently, making quantitative comparisons among them difficult. For example, Dunn et al. (2012) showed that in *Acropora muricata*, P enrichment caused increased extension rates, but reduced skeletal density. To account for these differences in our analyses, we divided coral growth responses into metrics of: (1) calcification rates, (2) extension rates, and (3) skeletal density. Similarly, nutrients can affect the density of chlorophyll within *Symbiodinium*, the density of *Symbiodinium* within corals, or both. Therefore, photobiology measurements were grouped as responses in: (1) chlorophyll *a* within *Symbiodinium* cells, (2) *Symbiodinium* cell density within coral hosts, (3) chlorophyll *a* density per unit area of coral (a product of *Symbiodinium* cell density and chlorophyll *a* per *Symbiodinium*), and (4) maximum gross photosynthesis of corals.

We compiled studies assessing the impact of N and P on any of the above metrics of coral growth and photobiology using ISI Web of Science (1978–2012). Search terms included key words such as "nutr* and coral," "coral growth," "nutr* and *Symbiodinium*," and so on. We identified additional studies by searching the references of studies identified in our Web of Science searches. For inclusion, studies were required to compare the effect of N and/or P between control and treatment corals on at least one of our metrics of coral growth or photobiology. To minimize confounding factors, studies that obtained measurements from corals growing on reefs, rather than controlled laboratory settings, were only included when the environments around control and treatment corals (e.g., depth, temperature, and so on) were controlled for as much as possible. As a result, studies that examined the response of corals to factors such as upwelling were not included due to co-occurring differences in temperature, which also impacts coral growth (e.g., Leichter and Genovese 2006). Similarly, measurements from studies

that manipulated factors in addition to N or P that could impact coral growth, such as the presence of competitors or coral predators (e.g., Burkepile and Hay 2009), were excluded from our data set as it was often difficult to decouple the effects of nutrients from other confounding factors. We restricted our analyses of photobiology to include only studies that assessed the impact of nutrient enrichment on *Symbiodinium* within the coral host rather than responses in culture.

We obtained data from the text of the studies, directly from the authors, or extracted measurements from digital PDFs using DataThief III V1.6 (software *available online*).[2] When studies reported growth rates throughout a time series, we averaged the measurements to calculate a mean effect for the whole study duration. For studies that provided measurements from multiple nutrient treatments (i.e., N and P independently) or across several enrichment levels, each treatment level was counted as an independent experiment. The exceptions to this were three studies that exposed the same corals to multiple enrichment levels through time (Appendix A). In these instances, we calculated the average growth rate through the entirety of the experiment to test the effect of nutrient identity, but excluded these results from tests of enrichment level.

We found 26 studies with 101 separate experiments from 17 species of coral that met all of our criteria for the analyses of nutrient loading on coral growth. Studies which reported the change in mass per unit volume of whole colonies through time were used in our analysis as measurements of both calcification rates and skeletal density. As a result, we were able to obtain 59 independent measurements of calcification from 21 studies, 37 measurements of skeletal extension rates from 14 studies, and 19 measurements of skeletal density from 5 studies (Appendix A). To assess the impact of nutrient enrichment on *Symbiodinium* and photosynthesis, we identified 21 studies with 107 separate experiments from 13 species of corals. We found 27 experiments from 8 studies that assessed how nutrient input alters chlorophyll *a* density within *Symbiodinium*, 38 experiments from 15 studies examining *Symbiodinium* density, 27 experiments from 11 studies examining chlorophyll *a* density per unit area of coral, and 15 experiments from 6 studies examining the gross photosynthetic rates of corals (Appendix B).

Analysis

To standardize the effect of nutrient enrichment on different metrics of coral growth and photobiology, we used a log response ratio in which effect sizes for each study were calculated as

$$\mathrm{LRR} = \ln\left(\frac{X_\mathrm{E}}{X_\mathrm{C}}\right)$$

where X_E is the mean response to nutrient enrichment, and X_C is the mean control response. This metric estimates the effect size as a proportionate change between the response and control groups such that values equal to zero signify no effect of enrichment, values less than zero indicate a negative effect of nutrient enrichment, and positive values indicate a positive response to nutrients. Log response ratios are often a useful metric when replication is low and Type II error can prevent the detection of biologically meaningful responses (Rosenberg et al. 1999, Harpole et al. 2011). Weighting effect sizes can account for inequality in study variance as well as increase the power and precision of tests by as much as 50–100% (Stewart 2010). Thus, we calculated weighted effect sizes using the inverse of the sampling variance, in which the variance for each effect size was

$$V_{\ln \mathrm{R}} = \frac{(s_\mathrm{E})^2}{n_\mathrm{E}(X_\mathrm{E})^2}\frac{(s_\mathrm{C})^2}{n_\mathrm{C}(X_\mathrm{C})^2}$$

where s_E and s_C are the variance of treatment and control groups, respectively, and n_E and n_C are the replication of each group. For all our analyses, we plotted standardized effect sizes against a standard normal distribution and calculated fail-safe numbers using Rosenthal's method to confirm the absence of publication bias.

Because responses may vary with experimental conditions among studies (e.g., temperature, light, and so on), we used mixed-effect models in MetaWin V2.0 that considered the treatment variable of interest as a fixed factor and study as a random factor (Rosenberg et al. 1999). We calculated weighted cumulative effect sizes and assessed significance by constructing standard 95% confidence intervals around the weighted mean effect size for each response variable examined. We tested the effect of nutrient enrichment on each metric of growth and photobiology for each nutrient type across all coral species. To determine if growth form had an impact on the response of corals to nutrients, we grouped corals by morphology (branching vs. mounding) and examined their response to each metric. We addressed taxonomic variation in responses to nutrients by repeating our analyses with *Acropora* spp. and *Porites* spp., the only two genera with enough replication for meaningful tests.

To test whether enrichment source affected coral growth, we divided studies into groups based on whether enrichment was the result of naturally occurring fish excretion, anthropogenic pollution, or experimental manipulations of nutrient levels. We used Welch's *t* tests to determine whether enrichment levels differed between N species (i.e., ammonium vs. nitrate) and tested whether N species had differential effects on coral growth and photobiology. To account for the effect of background N and P levels on responses, we used multiple regressions that included an interaction term for N and P to test for changes in the magnitude of effect

[2] http://datathief.org/

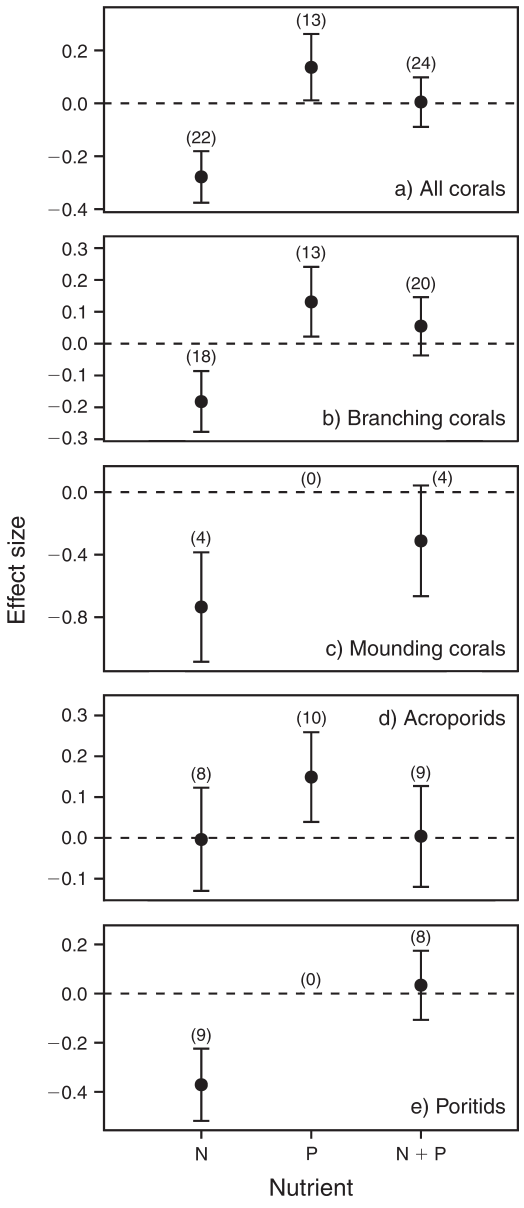

FIG. 1. Cumulative effect sizes for coral calcification rates in response to enrichment with nitrogen (N), phosphorus (P), or joint nitrogen and phosphorus (N + P). Effect sizes that are greater than zero indicate a significant positive effect, while those that are less than zero indicate a significant negative effect. Effect sizes which overlap zero indicate no significant effect. Responses are shown for: (a) all corals, (b) branching corals, (c) mounding corals, (d) *Acropora* spp., and (e) *Porites* spp. Data are means with 95% confidence intervals. Numbers in parentheses indicate the number of experiments used to calculate effect sizes.

size with control N and P levels for each of our metrics of growth and photobiology. For most organisms, there is a general expectation that performance peaks at an optimal level of nutrient supply, beyond which increases in nutrients have no impact or may even become toxic (Barboza et al. 2009). Therefore, using the MuMIn package in R (Barton 2012), we used AIC_c to select the best fit from linear and quadratic models to examine how the enrichment level and the ratio of N:P provided impacted the effect sizes for each metric of growth and photobiology.

Although coral size and experimental duration could also affect the magnitude of coral responses to nutrients, there was not a wide enough range of either coral size or experimental duration for meaningful statistical analyses. Age of coral tissue can also influence growth rates (Elahi and Edmunds 2007), but was not reported in any of the studies that we used. Therefore, we cannot exclude the possibility that age played a role in the reported growth differences. However, most studies used in our analysis used similarly sized coral fragments cut from the distal portions of adult colonies, suggesting that the tissue age was similar among the corals in each study.

RESULTS

Studies used for our analyses of coral growth came from both manipulative experiments in the laboratory and field, as well as measurements taken along existing nutrient gradients. N and P enrichment ranged from 0.5–26 μmol/L and 0.11–26 μmol/L, respectively (Appendix A), which equated to levels that were 0.15–25.5 μmol/L higher than controls for N and 0.05–25.5 μmol/L higher for P. All of the studies used to explore the effects of nutrient availability on *Symbiodinium* and photosynthesis were tank-based, except for four field-based experiments (Appendix B). Nitrogen enrichment ranged from 1 to 50 μmol/L, while P enrichment trials spanned 0.5–4 μmol/L. This equated to nutrient levels 0.8–50 μmol/L and 0.4–4 μmol/L above control levels for N and P, respectively. For studies that enriched in N + P, the range for P was similar to the single nutrient studies, 0.3–4 μmol/L (0.28–4 higher than controls), while N levels were slightly more restricted than N-only trials, 5–20 μmol/L, (4–18 μmol/L higher than control levels).

Coral growth

Nitrogen enrichment resulted in significant declines in coral calcification (mean = −0.278, 95% CI = −0.376 to −0.181), which equated to 11% lower calcification rates on average (Fig. 1a). In contrast, P enrichment caused a significant increase in calcification; on average, 9% greater than controls (mean = 0.136, 95% CI = 0.011–0.262). When provided in concert, N + P had no effect on calcification (Fig. 1a). Branching corals made up >70% of the replicates for all enrichment treatments. Therefore, the effect of nutrients on calcification in branching corals was nearly identical to the effect on all corals (Fig. 1b). For mounding corals, N enrichment caused a greater inhibition of calcification than was seen in branching morphologies (Fig. 1c). Calcification in *Acropora* spp. was not inhibited by N or N + P, but was enhanced in the presence of P alone (mean = 0.149, 95%

CI = 0.039–0.259; Fig. 1d). For *Porites* spp., N enrichment caused a significant decline in calcification (mean = −0.371, 95% CI = −0.518 to −0.224; Fig. 1e). Although *Porites* spp. included both mounding and branching species, this reduction remained significant even when only branching *Porites* spp. were included (mean = −0.378, 95% CI = −0.523 to −0.233), suggesting the effect was not solely driven by morphology. N + P had no effect on calcification of *Porites* spp, and no studies documented the impact of P in isolation on calcification.

For coral extension rates, both N and N + P had significant negative effects (mean = −0.414, 95% CI = −0.740 to −0.089 and −0.231, 95% CI = −0.393 to −0.069 respectively; Appendix C: Fig. C1a). P enrichments increased extension rates by 35.4% over control corals, but this effect was not significant (mean = 0.248, 95% CI = −0.257 to 0.752), possibly due to high variability and low replication ($n = 5$). Enrichment had no significant effects on skeletal density. However, replication was low and there were trending negative effects of P and N + P enrichment, which caused a nearly 9% and 10% decline in skeletal density respectively (Appendix C: Fig. C1b).

When we assessed how background nutrient levels impacted the effect of enrichment, the only significant pattern was a decline in effect size as control nutrient levels rose for the effect of phosphorus on coral calcification rates (Appendix C: Table C1), suggesting that initial differences in nutrient limitation minimally influenced patterns in effect sizes. Similarly, enrichment level had little impact on effect sizes. In every case, linear models best described the relationship between enrichment level and effect size, but these best fit models yielded no significant relationships (Appendix C: Table C2). When we assessed how the ratio of N:P impacted corals, replication was only sufficient to examine studies that utilized ammonium and phosphorus for enrichment. For these studies, the relationship between effect size and N:P ratio was best explained by a quadratic model for calcification and skeletal extension and a linear model for skeletal density (Appendix C: Table C3). The ratio of N:P provided had a marginally significant effect on calcification and a significant effect on skeletal extension (df = 2, 8, $F = 4.26$, $P = 0.055$ and df = 2, 9, $F = 4.64$, $P = 0.041$, respectively; Appendix C: Fig. C2). In both cases, effect sizes peaked near the Redfield Ratio of 16:1, N:P; however, our results should be interpreted with caution, as the replication across the range of ratios provided was low and N:P ratios were confounded with enrichment level.

Coral photobiology

Nitrogen enrichment caused significant increases in the amount of chlorophyll *a* within the *Symbiodinium* of corals (mean = 0.204, 95% CI = 0.072–0.338; Fig. 2a), while enrichment with P caused a nearly 20% decline, but the 95% confidence intervals crossed zero slightly

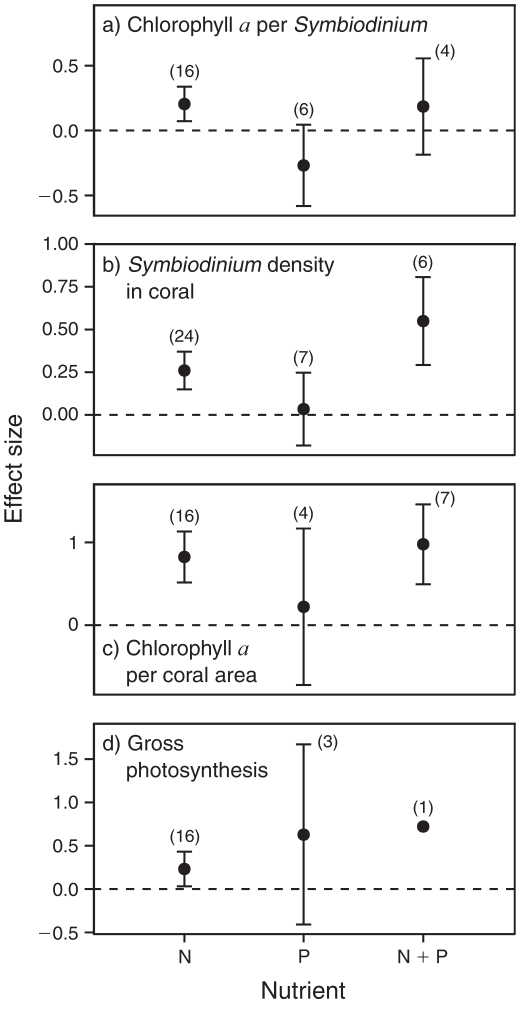

FIG. 2. Cumulative effect sizes of nutrient enrichment on different metrics of photobiology of corals: (a) the density of chlorophyll *a* within individual *Symbiodinium*, (b) the density of *Symbiodinium* within corals, (c) the density of chlorophyll *a* per area of coral, and (d) gross photosynthesis. Statistics as in Fig. 1.

(mean = −0.269, 95% CI = −0.582 to 0.045), likely due to low replication ($n = 6$). When provided together, both nutrients resulted in an average 15% increase in chlorophyll *a* and a similar mean effect to N alone, although the effect of N + P was not significant (mean = 0.185, 95% CI = −0.186 to 0.556).

N enrichment resulted in higher *Symbiodinium* densities than in control corals (mean = 0.260, 95% CI = 0.150–0.370), and when N and P were provided together, the effect size more than doubled (mean = 0.549, 95% CI = 0.292–0.806; Fig. 2b). There was no effect of P on *Symbiodinium* density. Accordingly, because both N and N + P enrichments increased the chlorophyll *a* in *Symbiodinium* and the *Symbiodinium* density in corals, the effects of these enrichments on chlorophyll *a* per unit of coral tissue were even more pronounced. Both N and N + P significantly increased

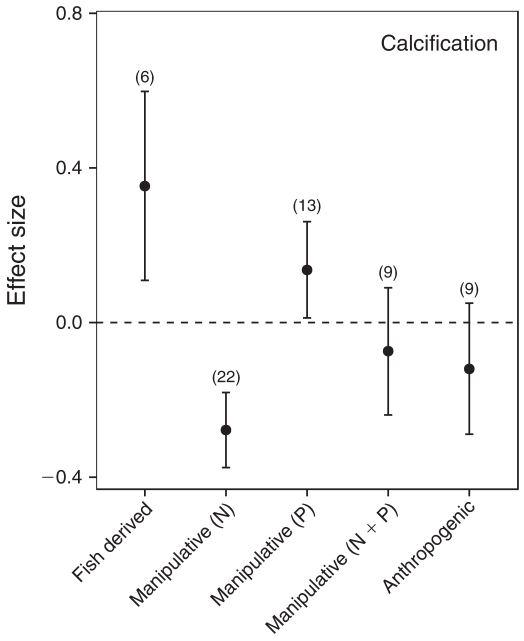

FIG. 3. Cumulative effect sizes of fish-derived (naturally occurring), manipulative, or anthropogenic nutrient enrichment on the calcification rates of corals. Nutrients provided for manipulative studies are indicated in parentheses on the *x*-axis. Statistics as in Fig. 1.

the density of chlorophyll *a* in corals (mean = 0.824, 95% CI = 0.516–1.133 and mean = 0.978, 95% CI = 0.494–1.146, respectively; Fig. 2c), whereas again, P had no effect. Our analysis of gross photosynthetic rates revealed that N enrichment elicited higher rates of photosynthesis (mean = 0.232, 95% CI = 0.032–0.432), while the effect of P was nonsignificant and highly variable and N + P lacked sufficient replication for analysis (Fig. 2d). Because ~80% of the studies that examined nutrients and coral photobiology were conducted on branching corals, we did not attempt comparisons between functional groups or genera. There were no significant effects of enrichment level or N:P ratio on any of our metrics of photobiology for which we had sufficient data to analyze (Appendix C: Tables C2 and C3).

Enrichment source

Enrichment source was analyzed to determine whether naturally occurring enrichment processes impacted coral growth differently than did anthropogenic pollution or manipulative enrichment. We found six experiments from five studies examining the effect of natural, fish-derived enrichment (fish excretion) on coral calcification rates. Two experiments from two studies reported the effect of this type of enrichment on extension rates of corals and one experiment reported the effect on skeletal density. In all cases, the effect of natural enrichment on corals was positive, although due to low replication, only significant for calcification (mean = 0.353, 95% CI = 0.109–0.598; Fig. 3). In contrast, when enrichment was the result of anthropogenic pollution, such as wastewater delivery or high levels of agricultural runoff, nutrients resulted in a 5% decline in average calcification rates (mean = −0.120, 95% CI = −0.289 to 0.050), although the 95% confidence intervals slightly crossed zero. In manipulative experiments, N enrichment resulted in significant declines in calcification (mean = −0.278, 95% CI = −0.375 to −0.181) and extension rates (mean = −0.476, 95% CI = −0.870 to −0.081), while P enrichment caused increased calcification (mean = 0.136, 95% CI = 0.012 to 0.261), but had no effect on other growth metrics. N + P enrichment caused significant reductions in extension rates (mean = −0.508, 95% CI = −0.751 to −0.264), but had no effect on calcification or skeletal density. We were unable to explore the impact of enrichment source on coral photobiology because all but two studies were from manipulative experiments.

Differences between ammonium and nitrate enrichment were analyzed only for studies of calcification, chlorophyll *a* within *Symbiodinium*, and *Symbiodinium* density due to lack of replication for other metrics. For coral growth studies, when ammonium was the sole source of N enrichment, N concentrations were over 1.5 times higher than when nitrate was used for enrichment (13.59 μmol/L vs. 8.07 μmol/L respectively; $t = 2.11$, df = 18.07, $P = 0.05$). Similarly, for studies of photobiology ammonium was provided at nearly three times higher concentrations than nitrate in single N enrichment studies (20.62 μmol/L vs. 7.66 μmol/L; $t = 4.13$, df = 59.17, $P = 0.001$).

Nitrate caused a significant reduction in calcification (mean = −0.476, 95% CI = −0.583 to −0.369), while there was no effect of ammonium (mean = −0.037, 95% CI = −0.150 to 0.075; Fig. 4a). Nitrate also caused a significant increase in chlorophyll *a* density within *Symbiodinium* (mean 0.278, 95% CI = 0.017–0.538), but again ammonium had no effect (Fig. 4b). In contrast, only ammonium caused a significant increase in the *Symbiodinium* density within coral tissue (mean = 0.508, 95% CI = 0.334–0.683; Fig. 4c), while nitrate had a trending positive, but nonsignificant, effect (mean = 0.106, 95% CI = −0.036 to 0.249).

DISCUSSION

Nutrient loading represents one of the greatest threats to the function of coastal ecosystems (Vitousek et al. 1997*a*). Our analyses of the effects of nutrient loading on the coral–algal mutualism both supports and challenges some commonly held beliefs concerning the impact of nutrients on corals. In general, our data support the broadly held notion that nitrogen inhibits coral growth (reviewed by Fabricius 2005). However, we show that these effects are context dependent and vary with coral taxa, N identity (ammonium vs. nitrate), enrichment source (fish excretion vs. anthropogenic nutrients), and the presence or absence of P. Furthermore, rather than suppressing growth as has been commonly assumed, P

enrichment enhances calcification in corals, but may compromise skeletal integrity. Nitrogen drives the effects of nutrient loading on coral photobiology, but acts synergistically with P in co-enrichments to further increase *Symbiodinium* populations. Ultimately, our analyses suggest that changing nutrient loading patterns in coastal oceans will impact the dynamics of the coral–algal mutualism and may alter their susceptibility to stressors associated with global climate change.

Nitrogen enrichment decreased coral growth (Fig. 1) while increasing all metrics of coral photobiology (Fig. 3). These patterns are consistent with proposed N-induced inhibition of growth via DIC limitation whereby abundant *Symbiodinium* fix carbon so rapidly that it becomes limiting for calcification in the coral (Muscatine et al. 1989). Unexpectedly, this is dependent on nitrogen identity with nitrate causing strong reductions in calcification, but ammonium having no effect (Fig. 4). Significantly higher concentrations of ammonium vs. nitrate could have contributed to this pattern. However, if the magnitude of enrichment were the primary driver of patterns in coral growth, then coral growth rates should have been lower in ammonium enrichment studies than in nitrate enrichment experiments. Yet, we showed that nitrate strongly inhibited coral growth, while ammonium had no effect.

Instead, the different effects of N identity may be driven by differential utility of ammonium and nitrate by *Symbiodinium* and subsequent changes in the delivery of photosynthate to coral hosts. Coral calcification is enhanced during periods of photosynthesis (Gattuso et al. 1999), presumably through internal changes in pH or the delivery of surplus oxygen or photosynthetic products to the coral host (Tambutte et al. 2011). However, unlike ammonium, nitrate utilization by photoautotrophs requires an energetically costly reduction (Patterson et al. 2010), potentially reducing the benefits that *Symbiodinium* provide to the coral by decreasing the surplus energy available for transfer to the host when nitrate is the dominant N source. This may also explain increases in *Symbiodinium* density under ammonium but not nitrate enrichment, as marine microalgae often have higher specific growth rates when using ammonium vs. nitrate due to the differential costs of utilization (Raven et al. 1992).

The density and species composition of mutualists may also shape the response of symbioses to altered abiotic conditions. For example, species-specific plant traits shape the diversity and abundance of their mychorrizal associates (Eom et al. 2000), consequentially impacting the response of plants to enrichment (Johnson et al. 2008). Here, taxa-specific differences in *Symbiodinium* density may have shaped the response of different coral taxa to nutrient enrichment, with N inhibiting calcification more strongly in mounding morphologies and Poritids than in branching morphologies or Acroporids (Fig. 1). *Symbiodinium* densities are typically lower in branching vs. mounding corals (Li et al. 2008), and Poritids had twice the *Symbiodinium* density of Acroporids (mean = 2.608×10^6 vs. 1.133×10^6, respectively) in our data set. These differences may result in lower rates of DIC use, and consequently, less DIC limitation in Acroporids and branching corals. Additionally, mass transfer rates are faster in branching corals, allowing replenishment of DIC from the water column more rapidly than in mounding corals and further mitigating carbon limitation associated with higher *Symbiodinium* densities under nutrient enrichment (van Woesik et al. 2012). This taxonomic variation in responses to nutrients means that coral species composition could influence the vulnerability of reefs to nutrient loading. For example, in the Caribbean almost half of reef-building corals are Poritids or mounding species, possibly making these reefs more susceptible to the negative effects of excess nutrients than reefs in regions such as the Indo-Pacific with more Acroporids and branching corals.

In contrast to the negative effects of nitrogen, P enrichment increased calcification rates of corals (Fig. 1), but had no effect on extension rates or skeletal

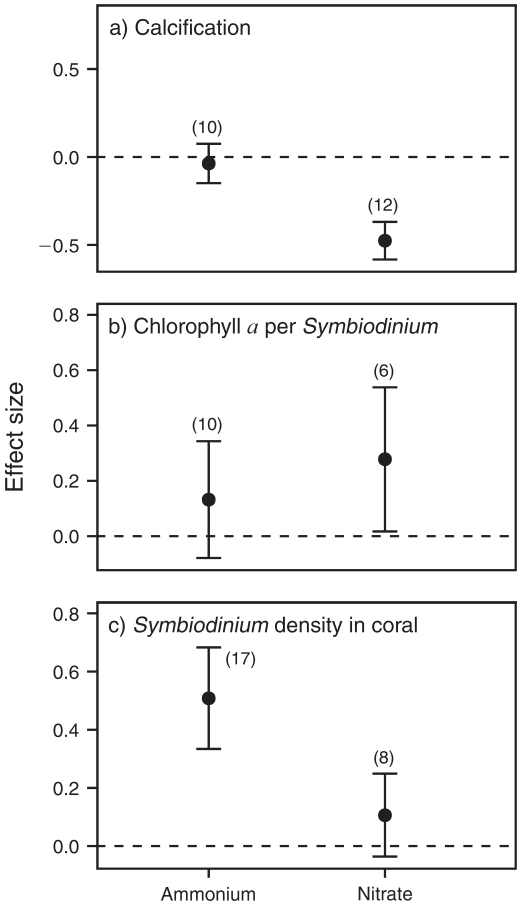

FIG. 4. Cumulative effect sizes for the impact of ammonium or nitrate on: (a) the calcification rates of corals, (b) the concentration of chlorophyll *a* within *Symbiodinium*, and (c) the density of *Symbiodinium* in coral tissue. Statistics as in Fig. 1.

density. This pattern was surprising given that phosphorus inhibits calcium carbonate precipitation (Lin and Singer 2006). However coral calcification involves active biomineralization, rather than passive precipitation of $CaCO_3$ (Tambutte et al. 2011). Dunn et al. (2012) proposed that corals incorporate $CaHPO_4$ into the skeleton when phosphate is abundant, allowing calcification to proceed at high phosphorus levels, but distorting the skeletal lattice and creating a more porous coral skeleton. While we found no significant evidence of reduced skeletal density to support this hypothesis, five of six measurements in our analysis reported decreased skeletal density under P enrichment. Decreased skeletal density, but increased rates of calcification seem to be at odds with one another. However, because calcification was often measured via changes in coral mass, rates of calcification may not have changed significantly. Rather, corals may have incorporated a greater amount of heavy $CaHPO_4$ into their skeletons, instead of $CaCO_3$, resulting in heavier, but more porous skeletons as Dunn et al. (2012) suggested. Increased porosity leads to greater susceptibility of corals to boring organisms and breakage (Caroselli et al. 2011), potentially making them more vulnerable to disturbances under P enrichment.

Synergistic effects of N and P on primary production are common across a variety of ecosystems (Elser et al. 2007). However, the coral–*Symbiodinium* mutualism adds complexity, with nutrients directly affecting both the coral and their mutualists. The only synergistic effect of N and P in our analyses was on *Symbiodinium* density with N + P enrichment having more than twice the effect of N alone and 15 times more than P alone (Fig. 2b). Despite super-additive responses in *Symbiodinium* and the apparent increase in photosynthesis, the effects of N + P on coral growth were largely additive (Fig. 1). Thus, for *Symbiodinium* growth, enrichment with N + P over the range of levels provided appears to shift nutrient limitation to whichever of the two is least abundant, yielding synergistic effects. Yet for calcification, N enrichment appears to shift limitation to DIC, regardless of P level. Furthermore, P may actually alleviate DIC limitation in part by replacing carbonate in the skeletal lattice with HPO_4 (Dunn et al. 2012), effectively canceling out the negative effect of N and explaining the absence of effects of N + P in our analyses. Ultimately, N and P appear to impact the coral–*Symbiodinium* mutualism in fundamentally different ways.

One surprising pattern in our analyses was the differential effect of enrichment source on corals. Natural enrichment via fish excretion always enhanced coral growth (Fig. 3). In contrast, human-derived nutrients, whether from manipulative experiments or anthropogenic pollution, tended to have negative effects on corals. Differences in nutrient identity, concentration, and consistency between fish excretion and human-derived nutrients, as well physical parameters like the flow rates around corals, may drive these differential effects. For example, fish excretion delivers primarily ammonium and P (Meyer and Schultz 1985*a*), while anthropogenic enrichment tended to deliver more nitrate, which easily leaches from soils relative to phosphorus (Appendix A). Our analyses show that nitrate tends to slow coral growth, while ammonium has little effect (Fig. 4). Further, the combined ammonium and P delivered by fishes may benefit corals more than N-dominated anthropogenic sources, as N-only enrichment drove decreases in coral calcification (Fig. 1). Fishes may also be a source of particulate organic matter that corals could ingest, further enhancing their growth rates (Meyer and Schultz 1985*a*).

Fishes could also alter rates of nutrient uptake by increasing mixing in the water column via their movement around corals and facilitating mass transfer. Additionally, water flow may influence the impact of different nutrient sources. For example, downstream plumes from river discharge on the Great Barrier Reef range from 0.26 μmol/L to 16.1 μmol/L N, depending on distance from shore and the water currents at each site (Schaffelke and Klumpp 1998). Similarly, when nutrients are delivered in discrete pulses, such as via fish excretion or upwelling events, currents and tidal flushing can quickly dissipate nutrients from an area and modify either their positive or negative impact (Hatcher and Larkum 1983). As a result, water flow can act as either a dissipater or deliverer of nutrients depending on the origin of enrichment, potentially modifying the differential effects of nutrients.

Animals are often important sources of limiting nutrients across many disparate ecosystems. For example, large ungulates can facilitate primary production in terrestrial systems via urine and dung deposits (Burkepile 2013). Likewise, fishes often deliver important limiting nutrients in oligotrophic ecosystems (Allgeier et al. 2013) and can be important sources of nutrients on coral reefs (Burkepile et al. 2013). Thus, overfishing on coral reefs, an important driver of change in these ecosystems (Hughes et al. 2007), could disrupt the critical link between fish excretion and corals and dramatically alter production and coral growth (Layman et al. 2011). Given that increasing human populations along coastlines result in both overfishing and increased input of anthropogenic nutrients to coastal waters (Halpern et al. 2008), the trajectory of current global change may mean that corals suffer from a reduction of beneficial nutrient sources and an increase in detrimental ones.

Excess nutrients may also increase coral susceptibility to the effects of climate change such as coral bleaching, due to the effects of nutrient availability on *Symbiodinium*. Wooldridge and Done (2009) suggested that nutrient-induced increases in *Symbiodinium* density drove correlations between water column nitrogen and bleaching on the Great Barrier Reef. Additionally, Cunning and Baker (2012) found that elevated *Symbiodinium* densities in corals increased their susceptibility to

bleaching due to increased production of reactive oxygen species during periods of thermal/light stress. Thus, the nutrient-induced increases in *Symbiodinium* from both N and N + P enrichment that we show (Fig. 2) may make corals more vulnerable as bleaching conditions become more common. Furthermore, N enrichment in the absence of increased P can lead to P starvation of *Symbiodinium*, further increasing bleaching susceptibility (Wiedenmann et al. 2012). As a result, the simultaneous loading with N and P, such as from fish excretion, may actually be less harmful to, or even benefit, corals under bleaching conditions.

Nutrients also interact with other important drivers of coral reef decline that warrant consideration. For example, disease is a strong driver of coral decline on reefs worldwide (Bruno et al. 2007), and although nutrients influence the pathology of coral diseases (Vega Thurber et al. 2014), the role of specific nutrients in coral epidemiology remains unknown. Similarly, interactions between nutrient loading and ocean acidification require critical analysis. Increased atmospheric CO_2 lowers oceanic CO_3^{2-} concentrations and impairs calcification (Hoegh-Guldberg et al. 2007). How DIC-limited photosystems of enriched corals will respond to these changes remains unclear, but preferential use of CO_3^{2-} by *Symbiodinium* could exacerbate the negative effects of nutrients as CO_2 levels rise (Marubini et al. 2008). Our analysis also highlights several gaps in our understanding of the effects of nutrient loading on reefs. In particular, experiments assessing a wider range of enrichment levels are needed to assess nonlinear responses to enrichment. For example, Gil (2013) documented a unimodal growth curve for *Porites* spp. across a gradient of enrichment in which peak growth occurred between 1 μmol/L and 3 μmol/L N and declined above this level. In our analyses, almost 75% of the studies we found used enrichment levels higher than these peak values, potentially explaining the linear decline in coral growth with increasing enrichment levels that we found and the absence of expected unimodal responses to nutrient enrichment. Ultimately, our work emphasizes the importance of nutrient availability to the health of coral reefs and that a more nuanced understanding of impact of nutrients on corals is sorely needed.

At a more fundamental level, our analyses provide insight into the effects of nutrient loading on symbiotic interactions. Cost–benefit trade-offs in symbioses are often state dependent, and exogenous factors such as nutrient availability, may dictate where such interactions fall along the continuum of mutualism and parasitism (Leung and Poulin 2008). For example, Wooldridge (2010) proposed that the coral host maintains active control of N delivery to *Symbiodinium* in order to regulate symbiont populations. In this case, N loading may alter the cost–benefit trade-off for *Symbiodinium* by alleviating dependence on host-derived N. In turn, this disrupts the coral's control over *Symbiodinium* populations, leading to increased competition between the host and symbiont for DIC and photosynthate, which may be monopolized by the now N-replete *Symbiodinium* for population growth. Increased *Symbiodinium* populations and slower coral growth under N enrichment documented here support these hypotheses that nutrient enrichment can potentially decouple this mutualism. In analogous plant–mycorrhizae (Hoeksema et al. 2010) and legume–*Rhizobium* (Zahran 1999) symbioses, increased nutrient availability from nutrient loading can reduce the benefits provided by symbionts to plant hosts and push these interactions from mutualism to parasitism. Our study reveals similar patterns in the responses of foundational marine species and suggests that there may be general patterns in how nutrient-sharing mutualists respond to nutrification. Understanding patterns such as these are a fundamental goal of ecology and provide insight into how global change will impact community structure and function.

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Supplemental Material

Appendix A

Summary of studies used for the analysis of nutrients on coral growth (*Ecological Archives* E095-175-A1).

Appendix B

Summary of studies used for the analysis of nutrients on coral photobiology (*Ecological Archives* E095-175-A2).

Appendix C

Supplemental figures and tables detailing the impact of nutrients and enrichment conditions on additional metrics of coral growth and photobiology (*Ecological Archives* E095-175-A3).