



Review

A systematic review and meta-analysis of the direct effects of nutrients on corals



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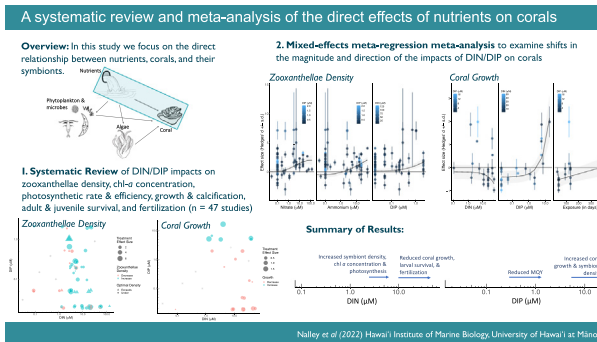
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HIGHLIGHTS

- Meta-analyses quantified theoretical relationships between nutrients and corals.
- Increasing nutrients cause shifts in magnitude and direction of impacts on corals.
- Nutrients at these concentrations also promote growth of coral competitors.
- Elevated nutrients can have negative direct and indirect effects on coral health.
- Impacts on coral symbionts are pronounced at high nutrient concentrations.

GRAPHICAL ABSTRACT



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ABSTRACT

Chronic exposure of coral reefs to elevated nutrient conditions can modify the performance of the coral holobiont and shift the competitive interactions of reef organisms. Many studies have now quantified the links between nutrients and coral performance, but few have translated these studies to directly address coastal water quality standards. To address this management need, we conducted a systematic review of peer-reviewed studies, public reports, and gray literature that examined the impacts of dissolved inorganic nitrogen (DIN: nitrate, nitrite, and ammonium) and dissolved inorganic phosphorus (DIP: phosphate) on scleractinian corals. The systematic review resulted in 47 studies with comparable data on coral holobiont responses to nutrients: symbiont density, chlorophyll *a* (chl-*a*) concentration, photosynthesis, photosynthetic efficiency, growth, calcification, adult survival, juvenile survival, and fertilization. Mixed-effects meta-regression meta-analyses were used to determine the magnitude of the positive or negative effects of DIN and DIP on coral responses. Zooxanthellae density (DIN & DIP), chl-*a* concentration (DIN), photosynthetic rate (DIN), and growth (DIP) all exhibited positive responses to nutrient addition; maximum quantum yield (DIP), growth (DIN), larval survival (DIN), and fertilization (DIN) exhibited negative responses. In lieu of developing specific thresholds for the management of nutrients as a stressor on coral reefs, we highlight important inflection points in the magnitude and direction of the effects of inorganic nutrients and identify trends among coral responses. The responses of corals to nutrients are complex, warranting conservative guidelines for elevated nutrient concentrations on coral reefs.

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1. Introduction

Coral reefs evolved in warm, oligotrophic waters and are thus adapted to life in low nutrient conditions. In the United States, estimated coastal nitrogen inputs have increased 4 to 8-fold from historic levels with industrial agriculture and increased human development (Howarth et al., 2002; Oelsner and Stets, 2019), and in 2000, it was estimated that >50 Tg of nitrogen year⁻¹ was deposited into coastal ecosystems globally via river input and submarine groundwater discharge alone, with this number expected to increase annually, which has wide-ranging impacts (Seitzinger et al., 2010; Beusen et al., 2013; Zhao et al., 2021). Coastal eutrophication is associated with lower water clarity (Cooper et al., 2007), phase shifts from coral to algal dominance and reduced habitat complexity (Adam et al., 2021), shifts in microbial processes (Vega Thurber et al., 2020), and decreased resilience to co-stressors, including thermal stress (Donovan et al., 2020; Burkepile et al., 2020). Nutrient addition from land-based sources of pollution (LBSP) is most readily measured and available for uptake by coral reef organisms in the form of dissolved inorganic nitrogen and phosphorus (DIN and DIP, respectively). The effects of DIN and DIP on corals have been well studied and reviewed to date (D'Angelo and Wiedenmann, 2014; Shantz and Burkepile, 2014; Morris et al., 2019; Zhao et al., 2021). However, coral reef resource managers still lack quantitative nutrient concentrations guidelines to effectively control LBSP and limit their effects on coral reef ecosystems. Thus, our study addresses this management need by conducting a systematic review and meta-analysis of experimental studies that quantify the effects of DIN (nitrate and ammonium) and DIP (phosphate) on coral and coral-endosymbiont health.

Elevated nutrients on coral reefs can result from surface run-off, submarine groundwater discharge, sewage discharge, aquaculture, or natural sources such as bird colonies or fish (Wear and Thurber, 2015; Graham et al., 2018; Otero et al., 2018; Adam et al., 2021), and different sources have different characteristics. Natural sources tend to deliver ammonium, which is highly bioavailable, while anthropogenic sources tend to

introduce nitrate (Shantz and Burkepile, 2014; Morris et al., 2019), which is less bioavailable and can lead to increased stress responses in corals (Fernandes de Barros et al., 2020; Burkepile et al., 2020). Phosphate may be derived from natural and anthropogenic sources (Fernandes de Barros et al., 2020), but the relative anthropogenic addition of phosphate has lagged far behind that of nitrate (Vilmin et al., 2018; Zhao et al., 2021). This unbalanced supply of nutrients in turn can negatively impact biological functions in marine organisms (Wiedenmann et al., 2013; Ezzat et al., 2015; Morris et al., 2019).

The effects of nutrient enrichment on corals can vary by life stage, taxonomy, and nutrient type (D'Angelo and Wiedenmann, 2014; Morris et al., 2019). Elevated nutrients may increase the abundance of zooxanthellae, positively affecting photosynthetic function, but beyond an optimal concentration, defined by Morris et al. (2019) as $1-3 \times 10^6$ cells cm⁻², overcrowding may occur and lead to negative outcomes such as shading, increased holobiont temperature, and oxidative stress. In these cases, the addition of nutrients may result in a positive response up to a point, beyond which the response may become negative (Tomascik and Sander, 1985; Shantz and Burkepile, 2014). A variety of negative growth-related responses have also been reported in corals exposed to elevated nitrate and phosphate concentrations, including decreased growth (Marubini and Davies, 1996), decreased calcification (Silbiger et al., 2018), and decreased skeletal density (Dunn et al., 2012). However, some studies have found either no direct effects of ammonium and phosphate enrichment (Stambler et al., 1991) or positive responses, such as increased growth rate (Koop et al., 2001).

The effects of DIN and DIP enrichment on coral larvae and juveniles have remained relatively under-studied as compared to adults (Fabricius, 2005; Humanes et al., 2016). Existing data suggest that coral gametes and larvae are more sensitive to elevated concentrations of ammonium (e.g., 1 μM) and phosphate (e.g., 0.1 μM) than adults, with responses including reduced fertilization, abnormal embryo development, and reduced larval settlement (Wittenberg and Hunte, 1992; Fabricius, 2005). Response to

elevated nutrient concentrations also varies by taxonomy, with differential and sometimes opposite effects observed among coral species in nutrient enrichment experiments (Koop et al., 2001; Cox and Ward, 2002; Kitchen et al., 2020). This variability may be attributable to morphological differences, a variety of symbiont clades, or other differences in adaptive capacity. Additionally, while the specific mechanisms are complex, clear shifts in the composition of coral communities along water quality gradients have been demonstrated (Tomascik and Sander, 1987; Fabricius, 2005; Fabricius et al., 2005; Oliver et al., 2019).

It is clear that the magnitude and type of coral response depends on the species of nutrient under enrichment (e.g. nitrate NO_3^- , ammonium NH_4^+ , or phosphate PO_4^{3-}); a 2014 meta-analysis found that nitrogen enrichment reduced calcification but enhanced photosynthetic rate on average, while phosphorus enrichment increased calcification and had little effect on photosynthesis (Shantz and Burkepile, 2014). Increased ammonium levels may mitigate the adverse effects of heat stress by moderating the loss of endosymbionts (Zhou et al., 2017), and corals experiencing temperature anomalies simultaneously with eutrophication can maintain healthy zooxanthellae in their deeper tissues (Riegl et al., 2019), but may be more vulnerable to disease (Caldwell et al., 2016; Aeby et al., 2020). Conversely, nitrate, has been linked to an increased prevalence and duration of bleaching in corals experiencing temperature stress (Burkepile et al., 2020), and corals that are acclimated to high-nutrient conditions demonstrate a greater propensity towards bleaching (Wooldridge and Done, 2009). Adding an additional layer of complexity, past research has found that coral response can depend not only on the type and absolute concentration of nutrients, but also on the stoichiometric ratio of nitrogen to phosphorus (Morris et al., 2019; Zhao et al., 2021).

Coral reefs exist across a wide range of dissolved nutrient concentrations, and this variation in ambient conditions is critical context for experimental manipulation of nutrients (Szmant, 2002; D'Angelo and Wiedenmann, 2014). For reference, we include reported ambient nutrient concentrations on coral reefs in Hawai'i, Malaysia, and Australia, ranging from 0.1 to 0.38 μM DIP and 0.15 to 0.44 μM DIN (Fabricius et al., 2013; Nakajima et al., 2015; Silbiger et al., 2018). These ambient values are well below the elevated nutrient levels in experimental studies (ranging from 0.06 to 202 μM DIN and 0.02 to 101 μM DIP in the studies included here), however within-reef variation in dissolved inorganic nutrients can be high. Hawaiian reefs receiving submarine groundwater discharge from an urbanized watershed had nutrient concentrations ranging from 0.02 to 32.39 μM DIN and 0.04 to 0.89 μM DIP across the reef (Lubarsky et al., 2018). Natural variation can be similarly high on remote atolls; for example soil in forests preferred by seabirds on Palmyra had nitrate concentrations that were more than twelve times higher than those in less preferred habitat, which can result in elevated DIN on adjacent reefs (Young et al., 2010). Further information on reference values is detailed in Fig. S1.

Our study builds on a set of previous reviews that addressed the complex relationship between nutrients and coral physiology and identified gaps for future research. Woods et al. (2016) also used a meta-analysis to examine the effects of DIN/DIP on a fertilization success, and Shantz and Burkepile (2014) used meta-analysis to assess broad trends in the effects of elevated nitrogen and phosphorus on effect size (coral growth, calcification, and photobiology). These studies identified a need for more experiments that incorporate a wider range of nutrient concentrations to assess nonlinear responses and generate thresholds that can be used for management. More experiments now exist to analyze these non-linearities, so we conducted meta-regressions that quantify the shapes of the relationships between effect sizes (coral response) and nutrient concentration. Foundational reviews (Szmant, 2002; Fabricius, 2005) have been built upon by more recent reviews (D'Angelo and Wiedenmann, 2014; Morris et al., 2019; Zhao et al., 2021) that offer conceptual, mechanistic explanations of the direct and indirect effects of nutrients on corals, but these studies also call for additional quantitative analyses of the relationships between nutrients and coral responses. Our synthetic approach provides quantitative support for these conceptual models and addresses important data gaps by using a systematic review paired with mixed-effects meta-regression meta-analysis that focuses on the interaction between DIN and DIP and identifies

inflection points for these nutrients' effect sizes on several coral physiological responses. Our meta-analysis of 47 studies thus represents decades of intensive research and quantifies many of the mechanistic complexities underlying the effects of local nutrient stressors on coral reefs.

2. Methods

2.1. Systematic literature review

The approach used in this study followed that described previously in Tuttle and Donahue (2020), Tuttle and Donahue (2020, 2022), and Nalley et al. (2021). We first identified reviews that addressed the impacts of nutrients on reefs and on scleractinian corals (Szmant, 2002; Fabricius, 2005; D'Angelo and Wiedenmann, 2014; Shantz and Burkepile, 2014; Morris et al., 2019; Houk et al., 2020; Zhao et al., 2021). Using these reviews to build a conceptual framework, we developed a systematic search of peer-reviewed studies, public reports, and gray literature. This required the compilation of an exhaustive list of terminology associated with nutrients, nutrient pollution, corals, and various coral taxa of concern (see below). This list was optimized into a series of search terms using the Web of Science format ([search term]* AND coral), which includes a wildcard (*) and Boolean operator (AND), which were in turn combined into a composite search term (Text S1). The composite search term was used to query eight databases and search engines (Table S1), which are justified and described in Tuttle and Donahue (2020).

The organismal scope of the study included all life stages of scleractinian corals found between 20 and 30 °C in the shallow, photic zone (<80 m) and the associated endosymbionts of these corals (Text S2 for criteria details). To focus the search on endangered and threatened taxa as listed under the United States Endangered Species Act and those of particular interest to coral reef managers in the U.S. Affiliated Pacific Islands, the following genera were included as part of the composite search term: *Acropora*, *Anacropora*, *Cantharellus*, *Dendrogyra*, *Euphyllia*, *Isopora*, *Montastraea*, *Montipora*, *Mycetophyllia*, *Orbicella*, *Pavona*, *Porites*, *Seriatopora*, *Siderastrea*, *Tubastraea*, *Alveopora*, *Astreopora*, *Favia*, *Favites*, *Goniastrea*, *Goniopora*, *Leptastrea*, *Leptoria*, *Lobophyllia*, *Millepora*, *Platygyra*, *Pocillopora*, and *Turbinaria* (Text S1).

Bibtex and RIS files generated in the search were imported to a reference manager (Mendeley Reference Manager, 2020) where duplicates were removed, and unique citations ($n = 10,911$) were imported into Abstrackr, which was used for screening search results (Abstrackr, 2020). Following the completion of a training set of reviews and discussion, which confirmed consistency among review decisions, at least two reviewers screened each abstract and determined whether it met the criteria for inclusion in this study based on the research questions ($n = 375$). If the two reviewers did not agree, a third reviewer resolved the decision of whether a study was relevant. Sources that were deemed relevant at the title-abstract screening stage were further screened for eligibility using the PECO framework (population, exposure, comparison, outcome; Text S2) (Morgan et al., 2018). Full texts that passed this stage of review ($n = 93$) were then assessed a final time for comparability among studies of response measurement units ($n = 47$). This subset of comparable studies was then used for the final meta-analysis. It is important to note that the primary focus of this meta-analysis was on manipulative experimental studies rather than observational studies, which means that most of the included studies were conducted in experimental tanks (see Text S2 for greater detail on selection criteria). Only 4 of the included 47 studies were field studies which focused on growth (3 studies), adult survival (1 study), chlorophyll-*a* concentrations (1 study), and photosynthetic rate (1 study). A complete list of studies included is provided in the Supplemental Materials (Text S3).

2.2. Data extraction

A suite of information was collected from each study including the species studied, collection site, experimental location, experimental parameters, nutrient concentrations (ambient/control and experimentally added), and duration of study. If data were presented in figures or graphs, they were extracted

using Web Plot Digitizer to obtain quantitative values (Rohatgi, 2017). Response measurements were converted to a common unit when possible to increase the number of studies using comparable metrics, which in turn increased meta-analytical power. We considered the number of studies (i.e., articles) studying a particular response, as well as the number of distinct experiments, where experiment is defined as a unique set of control-to-treatment comparisons. This was done because a single study/article may contain multiple unique experiments. Responses measured in fewer than three independent articles were not included in the meta-analyses. If a minimum concentration of DIN or DIP was not reported (e.g., stated that it was below the detection limit), 0.1 μM and 0.02 μM were added as the minimum treatment concentrations, respectively, which are conservative estimates based on the studies included in this review (e.g., Marubini and Thake, 1999).

2.3. Analysis

The responses considered in the meta-analysis were the density, chlorophyll *a* concentration, photosynthetic rate, and photosynthetic efficiency of zooxanthellae, as well as the growth, calcification, and mortality of coral. These responses were of particular interest for this study in part because of the established relationship between photosynthetic zooxanthellae and DIN. The relationship between DIP and coral growth, and consequently calcification, was also of interest. Finally, reduced coral mortality is a typical management objective, so it is important to consider this response as well, though the mechanisms of mortality in corals in response to elevated nutrients may be quite diverse and involve indirect effects. Mortality was examined at three distinct life stages. Adult survival included studies that assessed partial and total mortality of a coral colony. Larval survival was also examined and included studies that directly measured survival, as well as those that measured settlement. If a larva does not successfully recruit to the reef, it will not ultimately survive. Mortality was also examined in the context of fertilization. Eggs that are not successfully fertilized will not produce zygotes that

develop into larvae and eventually, adult reef-building corals. Hypotheses were developed to describe the nature of the relationship between nutrients and responses, based on ecological processes and characteristics (Table 1).

All analyses in this study were completed using R statistical software (R Core Team, 2020). Effect sizes were generated for each experiment (i.e., treatments compared to a control) using the *dosresmeta* package, which generates a standardized difference in mean (Hedges' *d*), corresponding variances, and covariance matrices (Crippa and Orsini, 2016). This value is unaffected by unequal sample variances between treatments and controls, and it also corrects for small sample sizes (Tuttle and Donahue, 2020). For adult mortality, which tends to be measured in binary terms (i.e., dead or alive), a risk-ratio was used to generate effect sizes for meta-analyses; to ensure centering around zero and asymptotic normality, the natural log of the risk ratio (i.e., log risk-ratio) and standard error of the log risk-ratio were used (Harrer et al., 2021). The formulas used to generate the standardized effect sizes (Hedge's *d* and log risk-ratio) are provided in the Supplemental Materials (Text S4). For all responses, concentrations of different species of dissolved inorganic nitrogen were combined and considered together as one concentration (DIN); for photosynthetic responses, ammonium and nitrate were considered separately. The effects of DIN and DIP were treated as independent fixed effects for a given response using an effect size that refers to the magnitude of the standardized difference in mean of the response in treatment conditions from that of the control in the same experiment.

Effect sizes were used as response variables indicating the magnitude of the deviation from the control in mixed-effects meta-regressions that incorporated covariance matrices based on the heterogeneity within studies using the *mixmeta* package (Sera et al., 2019). For example,

$$\text{Response Effect Size} \sim \text{DIN} + \text{DIP} + \text{random effects} \quad (1)$$

Positive effect sizes indicate an increase in the measured response as compared to the control, and negative effect sizes indicate a decrease in

Table 1

Hypothesized relationships between nutrient addition and physiological responses in corals, based on previous research.

Response	Frameworks for hypothesized relationships
Zooxanthellae density	Low zooxanthellae density is expected at low nutrient concentrations due to nutrient limitation. Increasing nutrient concentrations should reduce the impact of limitation, resulting in increased zooxanthellae growth up to a point where density is limited after a threshold level (Morris et al., 2019; Zhao et al., 2021). Nitrate, ammonium, and phosphate are expected to have independent effects on zooxanthellae density (Shantz and Burkepille, 2014).
Chlorophyll <i>a</i> concentration	Chlorophyll <i>a</i> concentrations are dependent on the density of zooxanthellae, so chlorophyll <i>a</i> concentrations are expected to increase with zooxanthellae density.
Photosynthetic Rate	Chlorophyll is essential for photosynthesis, but the rate of photosynthesis is likely limited when zooxanthellae and chlorophyll exceed a threshold density and cause light interference (Morris et al., 2019). As with the other photosynthetic responses, it is expected that the photosynthetic rate will have a relationship with nutrient addition that is mechanistically related to the relative increases in zooxanthellae density.
Photosynthetic Efficiency (Maximum Quantum Yield, MQY)	MQY refers to the maximum number of photons that are emitted per photon absorbed, so it is expected that MQY will be impacted by nutrient limitation and will lag in response to changes in zooxanthellae density and chlorophyll <i>a</i> concentrations (D'Angelo and Wiedenmann, 2014).
Growth	Growth in corals is expected to have a different response to nutrient addition than photosynthetic parameters because of the biological mechanisms involved. Specifically, it has been demonstrated that corals can use phosphate to create skeletons, so the addition of DIP is expected to have a positive relationship with growth (Dunn et al., 2012). The addition of nitrogen can lead to phosphate limitation, so it is expected that DIN will have a negative linear relationship with growth (Morris et al., 2019).
Calcification	Phosphate can replace carbonate ions in the coral skeletal structure in elevated phosphate conditions, resulting in skeletons that are more irregular and porous, so even if growth increases, a negative relationship is expected between DIP and calcification (Dunn et al., 2012).
Adult Survival (Partial and Complete)	The resilience of adult corals is enhanced by their photosynthetic capacity and growth, so survival is expected to decrease at nutrient concentrations that reduce zooxanthellae density, chlorophyll concentrations, and photosynthetic rate/efficiency (D'Angelo and Wiedenmann, 2014).
Larval Survival and Settlement	High nutrient concentrations are associated with a higher abundance of pathogenic bacteria that may negatively impact larval survival and settlement (Quimpo et al., 2020).
Fertilization	It is expected that at the high nutrient concentrations associated with reduced water quality, fertilization will decline (Woods et al., 2016).

Table 2
Coral responses examined using meta-analysis with ranges of predictors.

Response	Studies	Experiments	DIN Range (μM)	DIP Range (μM)	Mean Exposure Duration in days (Range)
Zooxanthellae Density	21 ^a	36	0.08–128	0.02–2	33 (3–126)
Chlorophyll <i>a</i> Concentration	12 ^b	23	0.1–50	0.02–5	41 (5–252)
Photosynthetic Rate	9 ^c	11	0.1–39	0.02–5	61 (21–252)
Photosynthetic Efficiency (Maximum Quantum Yield)	7 ^d	12	0.3–128	0.02–0.7	60 (3–105)
Growth Rate	6 ^e	8	0.1–50	0.02–16	147 (21–406)
Calcification	7 ^f	20	0.2–50	0.02–5	35 (14–168)
Adult Survival	5 ^g	8	0.1–33	0.02–5	47.5 (5–90)
Larval Survival	3 ^h	16	0.65–202	0.08–101	0.7 (0.02–4)
Fertilization	6 ⁱ	18	0.06–202	0.02–100	51 (2–240)

^a (Muscatine et al., 1989; Stambler et al., 1991, 1994; Marubini and Davies, 1996; Stimson, 1997; McGuire, 1997; Stambler, 1998; Ferrier-Pages et al., 2001; Miller, 2013; Wiedenmann et al., 2013; Béraud et al., 2013; Tanaka et al., 2014b; Tanaka et al., 2014a; Devlin, 2015; Ezzat et al., 2015, 2019; Higuchi et al., 2015; Courtial et al., 2018; Rice et al., 2019; Bednarz et al., 2020) *Chapters 4 and 5 from Devlin, 2015 were included as independent studies.

^b (Muscatine et al., 1989; Stambler et al., 1991, 1994; Muller-Parker et al., 1996; Stambler, 1998; Marubini and Thake, 1999; Koop et al., 2001; Tanaka et al., 2017; Tanaka et al., 2010; Tanaka et al., 2014b; Bednarz et al., 2020).

^c (Marubini, 1996; Marubini and Davies, 1996; Stambler, 1998; Koop et al., 2001; Ferrier-Pages et al., 2001; Béraud et al., 2013; Ezzat et al., 2016; Courtial et al., 2018; Bednarz et al., 2020).

^d (Liu et al., 2009; Fabricius et al., 2013; Miller, 2013; Wiedenmann et al., 2013; Béraud et al., 2013; Higuchi et al., 2015; Bednarz et al., 2020).

^e (Marubini and Thake, 1999; Bucher and Harrison, 2000; Koop et al., 2001; Jompa and McCook, 2002; Dunn et al., 2012; Devlin, 2015).

^f (Marubini, 1996; Marubini and Davies, 1996; Holcomb et al., 2010; Béraud et al., 2013; Devlin, 2015; Tanaka et al., 2017) *Chapters 4 and 5 from Devlin, 2015 were included as independent studies.

^g (Kuntz et al., 2005; Renegar and Riegl, 2005; Kline et al., 2006; Fabricius et al., 2013; Samlansin et al., 2020).

^h (Harrison and Ward, 2001; Humphrey et al., 2008; Lam et al., 2015).

ⁱ (Cox and Ward, 2002; Bassim and Sammarco, 2003; Lam et al., 2015; Renegar, 2015; Serrano et al., 2018; Kitchen et al., 2020).

the measured response as compared to the control. Experiment was included as a random effect in all models to account for variation between controlled experimental settings. In most cases an experiment included just one coral species, so it was not possible to include species as an additional orthogonal random effect. Given the number of taxa examined, including species as a fixed effect resulted in overfitting for most models. For this reason, differences between species were qualitatively considered but were not included in the final best fit models. Linear models with and without polynomial terms that address nonlinear relationships were compared when appropriate based on underlying hypotheses about the relationship between the response and the predictor.

Probabilistic model selection was based on Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) scores. The I^2 statistic and Cochrane's Q were used to examine variation that is explained by differences between studies. Lower values of each indicate less heterogeneity between experiments. Model fit was visually assessed using quantile-quantile plots of the residuals. Models were tested for sensitivity by comparing results using linear and polynomial models to account for apparent non-linearity, as well as the addition of exposure duration and species.

The exposure concentrations extracted in these analyses were compared to reference concentrations of DIN and DIP. Ambient DIN and DIP concentrations were used from four locations. The Hawai'i Ocean Timeseries reports open ocean surface concentrations of 0.03 μM for DIN and 0.03 μM for DIP (Fujiiki et al., 2021). Ambient concentrations of 0.75 μM DIN and 0.1 μM DIP were reported from a reef in Malaysia (Nakajima et al., 2015), and ambient concentrations of 0.15 μM DIN and 0.15 μM DIP were used for an experiment simulating conditions in Hawai'i (Silbiger et al., 2018). High ambient values were also reported from Australia at 0.44 μM DIN and 0.38 μM DIP (Fabricius et al., 2013). Very high values at sites with known impacts were also included for reference, where DIN was as high as 32.4 μM (Lubarsky et al., 2018), and DIP was 2.6 μM (Silbiger et al., 2018). These points are included for reference in plots for each coral response effect size and the corresponding exposure concentrations. An annotated reference is provided in the Supplemental Materials (Fig. S1).

3. Results

Meta-analyses were conducted for the following responses: zooxanthellae density, chlorophyll *a* concentration, photosynthetic rate, photosynthetic efficiency (maximum quantum yield), growth rate, calcification,

adult survival, larval survival, and fertilization. The number of studies and experiments within study included in each analysis are outlined in Table 2, along with the range of exposure concentrations and the duration

Table 3

Model results with influential nutrient concentration ranges. All models included experiment as a random effect and used a covariance structure based on experiment to account for heterogeneity between studies. Statistically non-significant relationships are noted with 'n.s.'.

Response (Effect size measurement)	Effect size relationship and direction	Unexplained Heterogeneity (based on I^2)
Zooxanthellae density (std. diff. in means)	NO_3^- : positive quadratic NH_4^+ : positive linear DIP: positive linear	Moderate
Chlorophyll <i>a</i> concentration (std. diff. in means)	DIN: positive linear DIP: n.s.	Moderate
Photosynthetic rate (std. diff. in means)	NO_3^- : positive linear NH_4^+ : n.s. DIP: n.s.	Low
Photosynthetic efficiency (std. diff. in means)	DIN: n.s. DIP: negative linear	High
Growth rate (std. diff. in means)	DIN: negative linear DIP: positive linear Duration: positive linear	Low
Calcification (std. diff. in means)	DIN: n.s. DIP: n.s.	Moderate
Adult survival (log risk ratio)	DIN: n.s. DIP: n.s. Duration: negative linear	Low
Larval survival (std. diff. in means)	DIN: negative linear DIP: n.s.	Moderate
Fertilization success (std. diff. in means)	DIN: negative linear DIP: n.s.	Moderate

of treatment exposure. Model results for all responses are summarized in Table 3.

3.1. Photosynthetic responses of the coral endosymbiont

3.1.1. Zooxanthellae density

Looking at general trends in the effect of DIN and DIP on zooxanthellae density, the largest increases occurred at concentrations between 1 and 10 μM DIN and 0.1 and 1 μM DIP (Fig. 1a). Zooxanthellae densities were most likely to exceed a physiologically optimal concentration ($1\text{--}3 \times 10^6$ cells cm^{-2} ; Morris et al., 2019) at medium to high concentrations of DIN ($>3 \mu\text{M}$). Decreases in zooxanthellae density were seen at very low DIN and DIP concentrations, which may be indicative of nutrient limitation, as well as at very high DIN concentrations when DIP is concurrently low (Fig. 1a).

Because of the known differences in nitrate and ammonium impacts on zooxanthellae, nitrate and ammonium were modeled separately, rather than together as DIN. A linear mixed-effects meta-regression with a second order polynomial for nitrate was used in this meta-analysis because of the

biological mechanisms underlying the relationship between zooxanthellae density and nitrate (i.e., increased to a maximum concentration and then decreased). Zooxanthellae density increased significantly with the addition of nitrate ($P < 0.0001$; Fixed effect estimates \pm SE: 1.91 ± 0.46), ammonium ($P < 0.0001$; Fixed effect estimates \pm SE: 1.52 ± 0.18), and DIP ($P < 0.0001$; Fixed effect estimates \pm SE: 3.29 ± 0.58) (Fig. 2a; Table S2). The range of concentrations examined for nitrate (0–128 μM) far exceeded those tested for ammonium (0–50 μM) or DIP (0–2 μM), so the comparable effects of ammonium and DIP at very high concentrations cannot be determined from this dataset. There were differences between experiments that remain unaccounted for by the model ($I^2 = 68.3\%$; $Q = 221$), but model fit was not improved with the addition of coral species or exposure duration as fixed effects. Clear taxonomic or morphological trends were not observed in the response of symbiont density to nutrient addition (Figs. S2-4a).

3.1.2. Chl-a concentration

At concentrations of DIN that are observed on coral reefs, concentrations of chl-a increased, particularly above 5 μM DIN (Fig. 1b). Negative

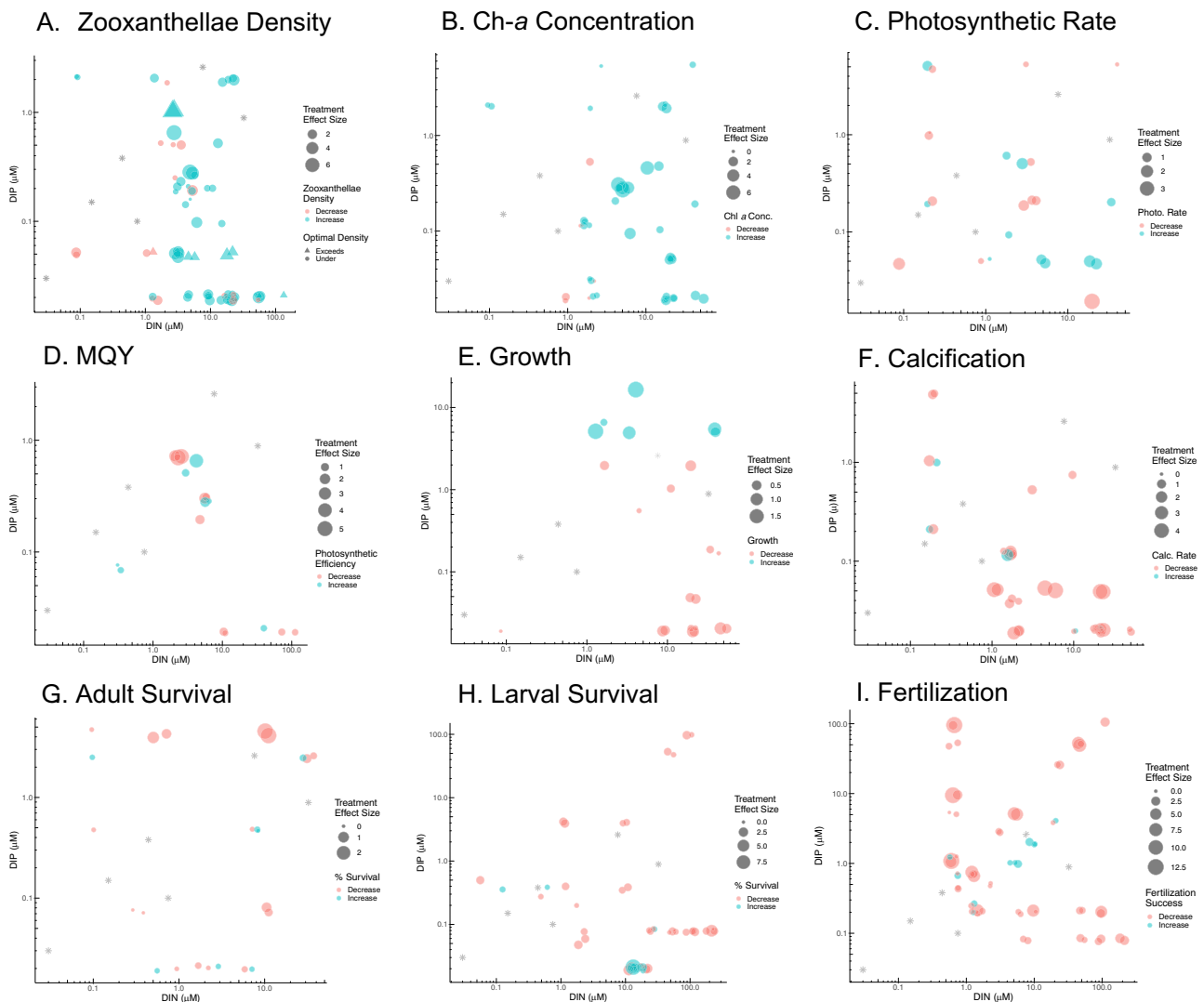


Fig. 1. Effect sizes of DIN and DIP addition treatments on (A) zooxanthellae density (10^6 cells cm^{-2}) – 21 studies, (B) chlorophyll *a* concentration ($\mu\text{g Chl } a \text{ cm}^{-2}$) – 12 studies, (C) photosynthetic rate ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ day}^{-1}$) – 9 studies, (D) MQY (F_v/F_m) – 7 studies, (E) growth (mm day^{-1}) – 6 studies, (F) calcification ($\text{mg CaCO}_3 \text{ cm}^{-2} \text{ day}^{-1}$) – 7 studies, (G) adult tissue and colony survival (% survival) – 5 studies, (H) larval survival and settlement (%) – 3 studies, and (I) fertilization (%) – 6 studies. The size of the point refers to the standardized mean difference between the treatment and the control in an experiment, and the color refers to whether the effect size increased (teal) or decreased (red). The stars indicate ambient conditions measured in the field at open ocean, coastal, and impacted sites. See Fig. S1 for a complete description of reference data sources. For (A), the shape indicates whether the concentration of zooxanthellae exceeded the optimal density (3×10^6 cells cm^{-2}) reported in Morris et al. (2019).

effects were only seen at low concentrations of DIN (<3 μM) and may be indicative of nutrient limitation. A linear mixed-effects meta-regression was used, and ammonium and nitrate were analyzed together as DIN. Analyzing them separately did not improve model fit. DIN concentrations had a significant positive effect on chl-*a* ($P = 0.0005$; Fixed effect estimate \pm SE: 0.95 ± 0.27), but there was no significant relationship with DIP ($P = 0.997$; Fig. 2b; Table S3). The model explained most of the heterogeneity between experiments ($I^2 = 43.3\%$; $Q = 77.6$), and adding in species or exposure duration as fixed effects did not improve model fit (Figs. S2-4b).

3.1.3. Photosynthetic rate

The impacts of elevated DIN and DIP on photosynthetic rate were less clear than those seen with zooxanthellae density or chl-*a* concentrations (Fig. 1c). The best fit model was a linear mixed-effects meta-regression with nitrate and ammonium analyzed independently (Table S4). Nitrate had a significant positive effect on the photosynthetic rate ($P < 0.0001$; Fixed effect estimates \pm SE: 1.84 ± 0.38), but ammonium and DIP had no significant effect ($P > 0.05$) (Fig. 2c). Species and exposure duration were not included in the best fit model, but most of the heterogeneity between experiments was explained well by the model ($I^2 = 36.3\%$; $Q = 31.4$). There were no clear

trends in the data that were attributable to species, taxonomic family, or coral morphology (Figs. S2-4c). One outlier point (Stambler, 1998) showed a significant negative effect of ammonium on the photosynthetic rate, but this point represents corals that were adapted to ambient high light conditions being exposed to high light and ammonium simultaneously. Other corals in this experiment that were exposed to lower light conditions, which are likely on eutrophic reefs, in addition to high ammonium concentrations had far less response in the photosynthetic rate.

3.1.4. Photosynthetic efficiency (maximum quantum yield, MQY)

At concentrations of DIN and DIP >10 μM and 0.5 μM , respectively, the MQY dropped below 0.5, indicating reduced resilience. Few studies examined MQY in response to low nutrient treatments, so it is not clear how MQY may be affected by nutrient limitation (Fig. 1d). The best fit model was a linear mixed-effects meta-regression model (Table S5). Nitrate and ammonium were analyzed together as DIN, because analyzing them independently did not improve model fit. DIN had no significant effect on MQY ($P = 0.15$) (Fig. 2d). DIP had a significant negative effect on the MQY ($P < 0.001$, Fixed effect estimate \pm SE: -5.61 ± 1.01). *Acropora microphthalma* and *A. polystoma*, in particular followed this trend (Fig. S2d), but including species

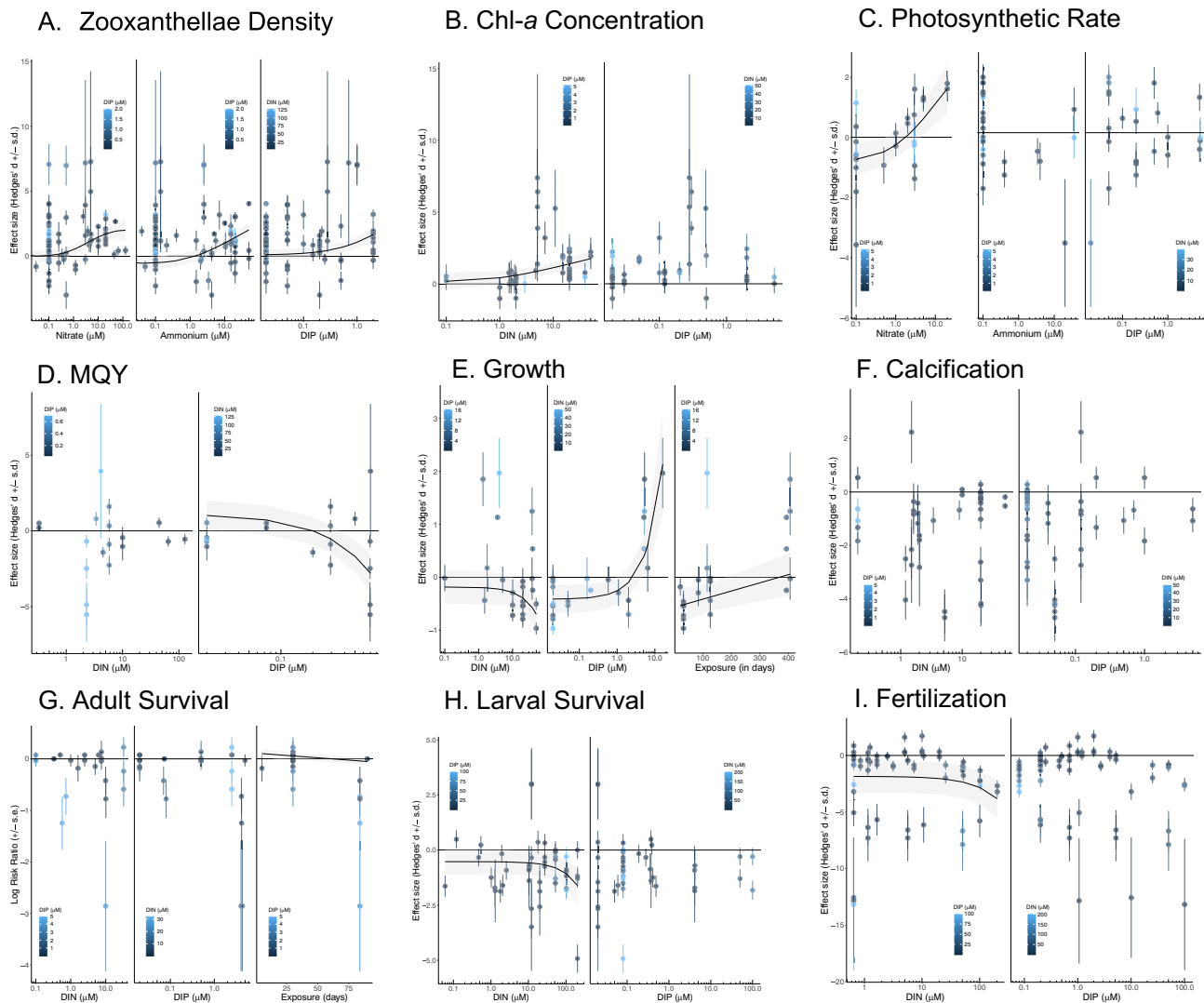


Fig. 2. Effect size of DIN (left) and DIP (right) on (A) zooxanthellae density (10^6 cells cm^{-2}) – 21 studies, (B) chlorophyll *a* concentration ($\mu\text{g Chl a cm}^{-2}$) – 12 studies, (C) photosynthetic rate ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ day}^{-1}$) – 9 studies, (D) MQY (F_v/F_m) – 7 studies, (E) growth (mm day^{-1}) – 6 studies, (F) calcification ($\text{mg CaCO}_3 \text{ cm}^{-2} \text{ day}^{-1}$) – 7 studies, (G) adult tissue and colony survival (% survival) – 5 studies, (H) larval survival and settlement (%) – 3 studies (note: two points with large vmd were removed from this plot for scale), and (I) fertilization (%) – 6 studies. Points indicate the standardized difference in means \pm the standard deviation for each treatment condition as compared to the control. The model predicted fit line and 95 % confidence interval are included for each fixed effect, with the other effects held constant at their median.

in the model led to overfitting. Most of the taxa examined were Acroporids, so there were no clear trends in response by taxonomic family or morphology (Figs. S3-4d). There was considerable heterogeneity between studies that was still unexplained by the best fit model ($I^2 = 72.5\%$; $Q = 54.5$), which may be attributable to the relatively few studies that were available for MQY as compared to some other responses.

3.2. Coral growth and calcification

3.2.1. Growth

Growth was measured as linear extension (mm day^{-1}). Increased growth only occurred when the relative concentration of DIP was greater than that of DIN, but the concentrations of DIP that caused a significant positive effect size are above those that are typically seen on coral reefs, even in locations with considerable eutrophication (Fig. 1e). A linear mixed-effects meta-regression was used to examine growth, and the best fit model included exposure duration as a fixed effect. DIN had a small but significant negative effect on the growth rate ($P = 0.007$; Fixed effect estimate \pm SE: -0.01 ± 0.004), and exposure duration had a small but significant positive effect ($P = 0.03$; Fixed effect estimate \pm SE: 0.002 ± 0.001 ; Table S6). DIP, however, had a strong significant positive effect on the growth rate ($P < 0.0001$; Fixed effect estimate \pm SE: 0.16 ± 0.03), with positive effects occurring at DIP concentrations above $5 \mu\text{M}$ (Fig. 2e). Coral species was not included in the best fit model, and there was very little unexplained heterogeneity between studies that was not accounted for in the model ($I^2 = 0.0\%$; $Q = 15.2$). There were no clear taxonomic trends in the response (Figs. S2-3e). Only corals with branching morphology were examined, so the effect of morphology could not be assessed (Fig. S4e).

3.2.2. Calcification

The effects of nutrient addition on calcification were primarily negative, but there were insufficient studies to assess the impacts of nutrient limitation or high concentrations of both DIN and DIP. In general, the greatest decreases in calcification were seen at DIN concentrations between 1 and $20 \mu\text{M}$, when DIP was $< 0.2 \mu\text{M}$ (Fig. 1f). Though these concentrations of DIN are higher than would be typical on an unimpacted reef, they are within the range of concentrations measured on impacted reefs. A linear mixed-effects meta-regression was used in this analysis. Increasing concentrations of DIN and DIP did not have a significant effect on calcification (all $P > 0.05$; Fig. 2f; Table S7). There was also considerable heterogeneity between studies that was not captured by the model ($I^2 = 55.9\%$; $Q = 90.6$), but coral species and exposure duration were not included in the best fit model. There were no clear trends in calcification that were attributable to species, taxonomic family, or morphology (Figs. S2-4f).

3.3. Mortality

3.3.1. Adult tissue and colony survival

Nutrient addition at concentrations that are regularly observed on reefs had negative effects on the survival of adult corals; the largest negative effects occurred at high nutrient concentrations (Fig. 1g). The best fit model was a linear mixed-effects meta-regression that included exposure duration as a fixed effect, using the log risk ratio to measure effect sizes. Exposure duration had a significant negative effect on the survival of adult coral tissues

and colonies ($P = 0.01$, Fixed effect estimate \pm SE: -0.002 ± 0.0007), but DIN and DIP did not have significant effects (Table S8; Fig. 2g). There was minimal heterogeneity between experiments that was unaccounted for by the best fit model ($I^2 = 23.1\%$, $Q = 26.0$). Though species was not included in the best fit model, negative effects were observed in *Acropora cervicornis* and *Agaricia tenuifolia* (Figs. S2-3g), but there were no clear trends based on coral morphology (Fig. S4g).

3.3.2. Larval survival and settlement

Studies examined larval survival at a large range of DIN and DIP concentrations (up to $\sim 100 \mu\text{M}$) (Fig. 1h). A linear mixed-effects meta-regression was used in this analysis. DIN had a slight but significant negative effect on larval survival ($P = 0.002$, Fixed effect estimate \pm SE: -0.005 ± 0.002) (Table S9; Fig. 2h), but DIP had no significant effect on larval survival ($P = 0.48$). Though species and exposure duration were not included in the best fit model, there was also heterogeneity between studies that was not captured by the model ($I^2 = 61.1\%$, $Q = 111$). *Platygyra acuta* was the primary species examined at high DIN concentrations (Fig. S2h), but no clear trend was seen based on taxonomic family or coral morphology (Figs. S3-4h).

3.3.3. Fertilization

Few studies examined the impacts of low, environmentally relevant nutrient concentrations on fertilization (Fig. 1i). The effects of elevated nutrient concentrations were overwhelmingly negative, with the greatest negative effects occurring at low DIN ($\sim 1 \mu\text{M}$) and higher DIP ($> 1 \mu\text{M}$). A linear mixed-effects meta-regression was used to examine the relationship between nutrients and fertilization (Table S10). DIN had a significant negative effect on fertilization ($P < 0.001$, Fixed effect estimate \pm SE: -0.01 ± 0.002), but DIP had no significant effect ($P = 0.31$; Fig. 2i). Negative effects were particularly apparent in *Acropora longicyathus* (Fig. S2i). All the *A. longicyathus* were from one study, but other species included in that study (e.g., *Goniastrea aspera*) did not show the same trend (Harrison and Ward, 2001). *Platygyra acuta* also had a pronounced negative response to the addition of DIN (Fig. S2). There was still considerable heterogeneity between studies that was not explained by the model ($I^2 = 63.9\%$, $Q = 169$), but with only two taxonomic families examined, clear trends were not determined based on taxonomic family or morphology (Figs. S3-4i).

4. Discussion

Meta-analyses were conducted for photosynthesis-related responses of coral endosymbionts (i.e., zooxanthellae density, chlorophyll *a* concentration, photosynthetic rate, and maximum photosynthetic efficiency), coral growth and calcification, and coral mortality measures at several coral life history stages in response to elevated concentrations of dissolved inorganic nitrogen and phosphorus (DIN and DIP). The mean exposure duration for the experiments included was typically one to two months, except for larval survival (< 1 day) and growth of adult corals (5 months). Zooxanthellae density had nearly twice as many studies included (21 studies) as the next closest response, chlorophyll *a* (12 studies). The relative abundance of data for certain responses aided in the development of more refined characterizations of these relationships. In general, elevated DIN concentrations, and in particular nitrate, led to an increase in endosymbiont photosynthetic responses (zooxanthellae density, chl-*a* concentration, and photosynthetic rate), while

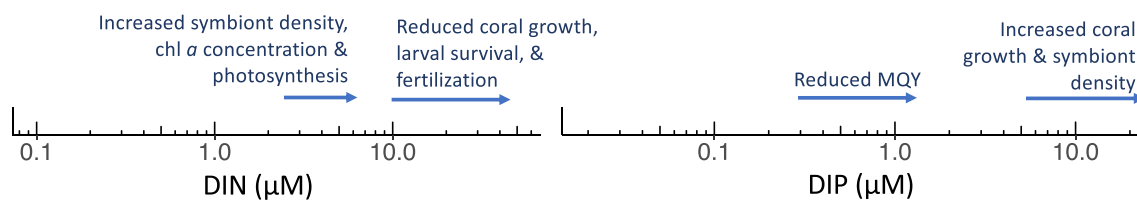


Fig. 3. Responses associated with increasing nutrient (left: dissolved inorganic nitrogen, DIN and right: dissolved inorganic phosphorus, DIP) concentrations. Arrow locations and directions align with the concentration at which the effect becomes apparent. For reference, ambient concentrations referred to in this review ranged from $0.15 \mu\text{M}$ to $32.4 \mu\text{M}$ for DIN and from $0.1 \mu\text{M}$ to $2.6 \mu\text{M}$ for DIP (Fig. S1). MQY is maximum quantum yield, or photosynthetic efficiency (F_v/F_m).

negative effects were seen in coral responses to increasing DIN, including reduced growth and survival (Fig. 2). Increased DIP affected endosymbionts by increasing zooxanthellae density but reducing photosynthetic efficiency, but it had positive effects on coral growth. At concentrations of DIN and DIP below 10 μM and 0.3 μM , respectively, few direct effects are seen, and the concern for management guidance should likely focus on competitive interactions between corals and macroalgae and/or increased coral disease prevalence (Fig. 3).

4.1. Summarizing key findings in the context of other studies

The relationship between zooxanthellae density and nutrients has been studied extensively, and the biological mechanisms that drive increases in zooxanthellae density have been considered in detail (Morris et al., 2019). Coral bleaching, which is the expulsion of endosymbionts, can be driven by photo-oxidative stress or carbon limitation that occurs at high temperatures that shift the coral-zooxanthellae metabolic relationship (Morris et al., 2019). Phosphate limitation and shifts in the DIN to DIP ratio can also impact zooxanthellae and cause coral bleaching (Morris et al., 2019). Elevated concentrations of DIN increase zooxanthellae density, and elevated DIN in combination with DIP may be beneficial (Shantz and Burkepile, 2014). When increases in DIN are not balanced with increased DIP, however, high zooxanthellae density may lead to reduced health and increased vulnerability to co-occurring stressors like high temperature.

Our meta-analysis quantifies this mechanistic relationship. Increases in zooxanthellae density peaked at moderate nutrient concentrations, with increased density still occurring at balanced high DIN-high DIP concentrations (Fig. 1a). The effect of nitrate on zooxanthellae density increased significantly with low to moderate nitrate concentrations, but was less pronounced at the highest concentrations (>50 μM). Zooxanthellae density only showed significant increases at the highest ammonium concentrations (~10 μM) and also increased with DIP, but to a far lesser extent than seen with nitrate. While the magnitude of the effect of DIN and DIP on zooxanthellae density decreased at higher concentrations, the overall effect of nutrient enrichment remained positive at the concentrations examined (up to 128 μM DIN and 2 μM DIP). These findings support previous descriptions of the theoretical mechanisms occurring (D'Angelo and Wiedenmann, 2014; Morris et al., 2019; Zhao et al., 2021) and further resolve the demonstrated significant relationships between zooxanthellae, DIN, and DIP (Shantz and Burkepile, 2014).

Although coral species-specific responses to elevated nutrient concentrations are well-documented in the literature (Tomascik and Sander, 1987; Koop et al., 2001; Cox and Ward, 2002; Fabricius, 2005; Fabricius et al., 2005; Oliver et al., 2019; Kitchen et al., 2020), we were unable to include taxonomy as a random effect in our model due to limitations of the data and the meta-analysis process. To account for variability between experiments (i.e., for every comparison to a control), it was necessary to include experiment as a random effect. As most experiments included in the meta-analysis included only one species, it was not possible to simultaneously include taxonomic effects without model overfitting. Therefore, while species-level differences are largely captured by the random effect of experiment, it is possible that taxonomic exclusion may contribute to the unexplained heterogeneity in the data (i.e., high I^2 values). This heterogeneity may also be attributable to influential factors that were not available to be included in this meta-analysis, such as zooxanthellae clade (Morris et al., 2019). While we provide quantitative responses across coral species in this study, determining species-specific responses to elevated nutrient concentrations within a meta-analysis framework remains an important avenue for future work. The duration of exposure to nutrients did not significantly influence the zooxanthellae density, but all the studies in this analysis used press (i.e., continuous) rather than pulse (i.e., episodic) exposure conditions. There is a great deal of variability in how press conditions are applied experimentally, and this may influence the overall response. Press conditions are more likely than pulse to have a negative impact on coral health, so examining zooxanthellae density under pulsed nutrient applications is also important for future work (van der Zande et al., 2021).

The concentration of chlorophyll *a* per coral surface area is dependent on the concentration of zooxanthellae. As with zooxanthellae density, Shantz and Burkepile (2014) found that DIN alone and DIN combined with DIP increased chlorophyll *a* concentrations, while DIP alone did not have any significant effect. We similarly found that at low DIN concentrations, chlorophyll *a* decreased (i.e., nutrient limitation); however, at low DIN and high DIP, increases in chlorophyll *a* were reported (Fig. 1b). At higher DIN concentrations, chlorophyll *a* followed the same trend as zooxanthellae density (Fig. 2b). The effect of DIN on chlorophyll *a* increased above 2 μM , peaking between 5 and 10 μM . DIP had no effect on chlorophyll *a* by comparison, but there were few studies at higher DIP concentration ranges.

The gross photosynthetic rate and the photosynthetic efficiency (maximum quantum yield, MQY) are also related to the abundance of zooxanthellae in corals. Elevated nutrients impact photosynthesis directly via their availability for inclusion in essential molecules (e.g., ATP) and also indirectly through their cascading impacts in the coral holobiont (Morris et al., 2019). Past studies suggest that DIN has a very slight positive effect on gross photosynthesis, and DIP has no significant effect; few studies examine the combination of DIN and DIP (Shantz and Burkepile, 2014). MQY is used as a measure of stress in plants, and values that fall below 0.5 indicate reduced resilience of corals to stressors (D'Angelo and Wiedenmann, 2014). The best fit model for photosynthetic rate examined nitrate and ammonium separately, and nitrate had a significant positive effect on photosynthesis, while ammonium and DIP did not at the concentrations examined (Fig. 2c). Conversely, DIN had no clear effect on MQY, but DIP had a significant negative effect at the highest concentrations examined (Fig. 2d).

Coral growth can also be related to the density of zooxanthellae and their photosynthetic output (Dunn et al., 2012). Coral growth can increase with the addition of phosphate, but phosphate can also displace carbonate ions in the calcium carbonate crystal structure, meaning calcification can simultaneously decrease (Dunn et al., 2012). This means that in elevated phosphate conditions, corals can grow faster in terms of linear extension, but have less dense skeletons. The effects of DIN and DIP on calcification can counteract one another, though the degree of this effect varies by coral morphology (Shantz and Burkepile, 2014). We found that DIN had a negative effect on growth, but DIP had a positive relationship with coral growth (measured as linear extension) that was particularly pronounced at concentrations >5 μM (Fig. 2e), which is aligned with previous studies (Dunn et al., 2012). Growth effects, which are typically measured in adults and take a while to manifest, also increased with the duration of exposure. The effects of DIN and DIP on calcification were consistently negative (Fig. 1f), but the magnitude of these negative effects did not increase significantly with higher concentrations of DIN and DIP. Past reviews found that elevated DIN decreased calcification, while DIP increased it, but when examined in combination we did not find a significant effect (Shantz and Burkepile, 2014). The effects may be more apparent, however, if there were additional studies focusing on higher nutrient concentrations.

Impacts on zooxanthellae, photosynthesis, growth, and calcification are all expected to affect the health and survival of adult corals. Adult corals did not exhibit a significant negative response in survival with nutrient addition but survival did decrease with exposure duration. The exposure duration used in experiments with adult corals was in some cases much longer than that used in other studies, which may have contributed to its effect and the variability seen in the data. It has been well documented that shifting nutrient concentrations can also alter the coral microbiome and the broader microbial community of the reef, which in turn can result in increased disease prevalence as an indirect effect of high nutrient concentrations on corals (Haas et al., 2016; Ford et al., 2018; Vega Thurber et al., 2020). These indirect effects may take more time to manifest, and thus, the duration of exposure is an important component of assessing adult coral survival in high nutrient conditions.

Unlike adults, coral larvae and eggs are not reliant on photosynthesis for their survival. Indirectly, nutrients contribute to the growth of disease-causing microorganisms and can alter the biogeochemistry of coral reefs,

which can have cascading impacts on the chemical cues and delicate environmental balance required by these early life stages. DIN had a significant negative relationship with larval survival and fertilization, but there was no significant effect of DIP (Figs. 2h-i). Past work using a different modeling approach found that phosphorous did have a negative effect on fertilization, and while we did not find a significant effect, the reported effects were primarily negative, suggesting this is an area in need of additional research (Woods et al., 2016).

Experimental studies examining increases in algal growth in response to nutrient addition found similar relationships as have been observed with corals. Specifically, *Sargassum* growth doubled from 3 to 5 μM of DIN and 0.3–0.5 μM of DIP, but reduced growth was seen at low and high nutrient concentrations (Schaffelke and Klumpp, 1998). At these same nutrient concentrations, zooxanthellae density and chlorophyll α spike as well, but the response of coral growth to nutrient addition is much slower. Spikes in coral growth require an order of magnitude higher concentrations of DIP than those required to rapidly increase algal growth.

The duration of the nutrient exposure varied by study, but it was not a significant component of any of the best fit models used in this analysis, except for growth and adult survival. The duration of exposure to elevated nutrient conditions may have different importance, depending on the responses examined. For example, the time required to see impacts of elevated nutrients on growth or adult mortality is likely much longer than that required to observe measurable responses in photosynthetic variables. Similarly, most of the studies included in this review and analysis used press treatment conditions, or a continuous application of elevated nutrient concentrations. This is likely representative of the conditions experienced by corals on reefs with elevated nutrient concentrations due to submarine groundwater discharge or continual sewage outflow. It is not, however, typical of what would be expected if the primary route of nutrient addition was through streams or surface runoff in storm events. These inputs tend to occur periodically and are better represented in experimental conditions by pulse treatments, or periodic addition of elevated nutrients. Experimental studies indicate that pulse nutrient additions can actually be beneficial to corals, while continuous press conditions are more likely to have negative impacts, making this an important topic for future studies (van der Zande et al., 2021).

4.2. Recommendations for future research and management

Technological advances have expanded our capacity to assess responses in ways that were unimaginable in recent years. For example, metabolomics can now quantify shifts in an organism's metabolic pathways in response to stressors, such as elevated nutrient concentrations. These shifts are driven not only by changes in the coral's physiology, but also by the coral's endosymbionts and microbiome (Sogin et al., 2017). Metabolomics and transcriptomics shed light on the importance of the type of zooxanthellae present for nutritional processes, immune response, and overall resilience (Matthews et al., 2017). The type of nutrient also impacts the composition of the coral's microbial community, which can have implications for the holobiont health (Rice et al., 2019). These tools have an enormous capacity to improve our understanding of the complex metabolic processes occurring in the coral holobiont and surrounding community that negatively impact the health of corals in high nutrient environments (Wegley Kelly et al., 2021).

In addition to advances that have improved the capacity to understand what is happening on a molecular scale, technology has also strengthened our ability to monitor and assess trends at an increasingly global scale. Chlorophyll concentrations can be monitored across the ocean in real-time using satellites, which has contributed to improved predictive capacity for algae blooms as a result of eutrophication events. Sensors, gliders, and buoys can also record chemical and biological fluctuations in remote locations. With these new advances come enormous amounts of data that can be incredibly valuable to answer specific questions. However, to harness the capacity of these datasets to identify trends on global or molecular scales, it is essential that measurements and reporting be standardized.

Though this can be challenging as new methods become available, it is critical to the future utility of these data.

Nutrients also influence the growth, function, and survival of other organisms on coral reefs that have indirect impacts on the health of corals, which is important to consider in the development of comprehensive ecosystem-wide management thresholds. To contextualize the results of this study within the broader ecological scope of coral reefs and changing climate conditions, it is also important to assess the nuanced indirect relationships among corals, algae, cyanobacterial mats, urchins, sponges, and other benthic organisms and their responses to nutrient additions (Littler et al., 2006; Norström et al., 2009; Vermeij et al., 2010; Ford et al., 2018). The responses examined in this analysis are dynamically affected by co-occurring stressors and responses in other organisms, as well as cascading indirect effects (Fabricius et al., 2010). Future research should aim to address this interconnectedness to facilitate the development of quantitative models that can more accurately capture the nuance of the system.

Our results are aligned with existing guidelines (e.g., Hawaii: <2.85 μM DIN and American Samoa: benchmarks of 1.61–2.41 μM DIN), as response shifts occurred around 2–3 μM DIN for zooxanthellae density and chlorophyll concentration (Hawaii State Department of Health, 2014; Houk et al., 2020). Negative effects on photosynthetic efficiency were seen at DIP concentrations above 0.3 μM , and growth of brittle skeletons increased at 5 μM DIP. It is important to note, however, that negative impacts were seen for fertilization, larval survival, and calcification, even if they did not increase in magnitude with increasing nutrient concentrations. Management strategies should focus on limiting nutrient inputs through increased agricultural and aquaculture efficiency, expanded wetland and estuary restoration, and improved sanitation systems (Zhao et al., 2021).

5. Conclusions

The results of this meta-analysis build on reviews that examined the overall effects of DIN and DIP on coral responses (Shantz and Burkepile, 2014), developed frameworks for the mechanisms of ecological (D'Angelo and Wiedenmann, 2014) and biological (Morris et al., 2019; Zhao et al., 2021) impact of inorganic nutrients on corals, and offered guidelines for management based on this information (Houk et al., 2020). By integrating DIN and DIP into the same analyses and using mixed-effects meta-regressions, this study accounted for the variability between and within studies while assessing the independent and interacting effects of DIN and DIP on a variety of coral responses. In doing so, we were able to quantify relationships that have been theoretically outlined in the past. In lieu of developing specific thresholds for the management of nutrients as a stressor on coral reefs, we highlighted important inflection points in the magnitude and direction of the effects of inorganic nutrients and identified trends among coral responses. Importantly, the concentrations of DIN and DIP that negatively impact corals may double the growth of reef macroalgae (Schaffelke and Klumpp, 1998) and result in phytoplankton blooms (Hayashida et al., 2020).

The responses of corals to nutrients as a stressor are complex and involve numerous other organisms including phytoplankton, endosymbionts, and other members of the holobiont (e.g., disease-causing microbes), so managers may opt to use conservative guidelines for elevated nutrient concentrations in coastal waters near coral reefs. Elevated nutrient concentrations can reduce the resilience of corals and other reef taxa to co-occurring stressors, like high temperatures or sedimentation, so management plans that employ the precautionary principle and adopt conservative guidelines will best account for these multiple interacting stressors.

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Data statement

All data generated during this study, along with code used to analyze data and generate figures, are shared in the public repository: https://github.com/enalley/nutrient_thresholds

CRediT authorship contribution statement

Eileen M. Nalley: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Writing – original draft, Writing – review & editing. **Lillian J. Tuttle:** Conceptualization, Data curation, Methodology, Project administration, Writing – review & editing. **Emily E. Conklin:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Alexandria L. Barkman:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Devynn M. Wulstein:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Madeline C. Schmidbauer:** Investigation, Methodology, Writing – review & editing. **Megan J. Donahue:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

Data availability

All code is freely available on GitHub, and the link is provided in the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.159093>.

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