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

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2 DATA STATEMENT

All data and code used in this study are available in the public repository: htts://github.com/enalley/nutrient_thresholds

3 EXECUTIVE SUMMARY

3.1 BACKGROUND

Corals evolved in warm, low nutrient waters and are adapted for efficient uptake of available nutrients. Chronic exposure of coral reefs to elevated nutrient conditions can have negative impacts on organism physiology and modify competitive interactions between organisms. Elevated nutrients on coral reefs, typically from surface run-off or submarine groundwater discharge, are often delivered in combination with other stressors, such as contaminants, sediment, and freshwater, or may co-occur with other local and global stressors, such as elevated temperatures, hypoxia, ocean acidification, or overfishing, and can reduce resilience to these other stressors. Coral responses to nutrient exposure are context-dependent, varying with coral and symbiont taxon, nutrient species (i.e., phosphate, ammonium, nitrate, or nitrite), and relative ratios of these species. The mechanisms by which nutrients impact corals typically involve other members of the coral holobiont, including the algal endosymbiont (zooxanthellae) and bacterial communities. Though many compounds are included under the umbrella of nutrients, this study focuses specifically on dissolved inorganic nitrogen (DIN: nitrate, nitrite, and ammonium) and phosphorus (DIP: phosphate), which are the most studied in relation to corals (D'Angelo and Wiedenmann 2014, Shantz and Burkepile 2014, Zhao et al. 2021).

DIN increases algal symbiont densities, which can lead to a transition from mutualism to a more parasitic relationship between zooxanthellae and the coral host (Morris et al. 2019). Higher symbiont concentrations can lead to oxidative stress and increased susceptibility to bleaching of the coral (Zhao et al. 2021). DIP, which generally occurs at much lower concentrations than DIN, can increase the growth rate of corals but reduce calcification, making corals more vulnerable to breakage (Dunn et al. 2012). The aim of this study was to examine these differing impacts of DIN and DIP on corals and their zooxanthellae in order to provide managers with a framework in which to develop nutrient management guidelines.

Because nutrients are essential for the function and health of corals and other organisms, management guidelines that address the transition from beneficial concentrations of nutrients to potentially harmful concentrations must be nuanced. Many of the negative impacts of elevated nutrient concentrations on corals may be a result of indirect relationships via other organisms, such as zooxanthellae or macroalgae. Finally, DIN and DIP may have unique effects on the coral and its holobiont, meaning that even at high concentrations, nutrients cannot be treated as a homogenous stressor. This combination means that the effects of nutrients on corals can be very difficult to tease apart, and as a result, management guidelines are challenging to develop. This report and the meta-analyses within aggregate available data to

identify trends and inflection points in nutrient-coral dynamics, and provide data that will aid in the creation of effective management goals.

3.2 METHODS

The approach used in this study followed that described previously in Tuttle et al. (2020), Tuttle & Donahue (2020, 2022), and Nalley et al. (2021). We conducted a systematic review of peer-reviewed studies, public reports, and gray literature that examined nutrient impacts on scleractinian corals and reviewed abstracts, texts, and data through a multi-step process that resulted in 47 studies with comparable data that could be compared for the following coral responses: symbiont density, chlorophyll *a* concentration, photosynthetic rate, photosynthetic efficiency (maximum quantum yield, MQY), growth, calcification, adult survival, juvenile survival and settlement, 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.

3.3 RESULTS

The mean exposure duration for nutrients in the experiments included in the meta-analyses was typically one to two months, with the exception of studies of larval survival (<1 day) and growth in adult corals (5 months). The most common response variable, zooxanthellae density, had almost twice as many studies included (21 studies) as the next closest response, chlorophyll *a* concentration (12 studies). 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 negative effects were seen in coral responses to increasing DIN, including reduced growth and survival. 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.

Zooxanthellae Density & Chlorophyll *a* Concentration:

- Chlorophyll *a* concentration depends on zooxanthellae density and the amount of chlorophyll per zooxanthellae cell
- Reduced zooxanthellae density and chlorophyll *a* concentration was seen at low (< 1 µM) DIN concentrations (i.e., nutrient limitation); reduced zooxanthellae density was also seen at combined concentrations of high DIN and low DIP.
- Zooxanthellae density increased with DIN and DIP; nitrate had more significant effects than ammonium, but few studies examined ammonium at high concentrations.
- Chlorophyll *a* concentration increased with DIN.

Photosynthetic Rate & Efficiency:

- The photosynthetic rate increased with nitrate but not with ammonium or DIP.
- Photosynthetic efficiency decreased with DIP but had no relationship with DIN.
- Photosynthetic efficiency fell below 0.5 (a threshold for resilience: D'Angelo and Wiedenmann 2014) at DIN concentrations >10 µM and DIP concentrations >0.5 µM.

Growth & Calcification:

- DIP had a positive relationship with coral growth (particularly at concentrations >5 µM), and DIN and exposure duration had slightly negative relationships.
- The effects of DIN and DIP on calcification were consistently negative, but the magnitude of these negative effects did not increase significantly with higher concentrations of DIN and DIP.

Adult Survival:

- Exposure duration had a significant effect on adult survival, but DIN and DIP did not.
- High nutrient concentrations can alter microbial assemblages, which can in turn increase disease prevalence in corals and lead indirectly to reduced survival.

Larval Survival & Fertilization Success:

- DIN had a negative relationship with larval survival, which encompassed measurements of both survival and settlement, and while the overall effect of DIP was generally negative, there was no significant relationship with the magnitude of the effect.
- DIN had a negative effect on fertilization.

3.4 CONCLUSIONS AND RECOMMENDATIONS

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 quantified 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 same concentrations of DIN and DIP that negatively impact coral physiological responses may also double the growth of reef macroalgae (Schaffelke and Klumpp 1998a) and result in phytoplankton blooms (Hayashida et al. 2020).

Future research should incorporate recent technological advances to better address the impacts of nutrients on the coral holobiont and the ecosystem in a more holistic fashion. Metabolomics allows for analysis of shifts in metabolic pathways in response to stressors and is particularly relevant for nutrients as a stressor. Increased knowledge of the role of the coral microbiome on disease, physiological function, and resilience has contributed to our understanding of the underlying mechanisms of negative responses of corals to nutrients and other stressors. Satellites, sensors, and autonomous monitoring systems also contribute to the ability to record chemical and biological fluctuations, even in remote locations, which has improved predictive capacity for anticipating responses to eutrophication and other stressors. Standardizing new data types as they become available will facilitate their future use in assessing trends and developing appropriate management guidelines in response.

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 it is important that managers use conservative guidelines for elevated nutrient concentrations on coral reefs. It is well documented that nutrients have significant negative direct and indirect effects on the overall health and resilience of corals, so 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).

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9 BACKGROUND

Nutrients can have diverse impacts on coastal ecosystems and communities. Coral reefs evolved in warm, oligotrophic waters and are adapted to life in low nutrient conditions. Nutrients are essential to core biological functions such as photosynthesis and DNA replication, and we expect changes in nutrient concentration to affect the health and physiology of all reef organisms, including the coral holobiont. Phytoplankton, macroalgae, coral endosymbionts, and microbial communities are particularly responsive to nutrient addition, and therefore eutrophication can alter their competitive interactions as well as their biology (Fig. 9.1). Each of these taxa responds in unique ways to the addition of nutrients, and their responses have cascading impacts on other members of the coral reef community. Elevated nutrients on coral reefs, typically from surface run-off or submarine groundwater discharge, are often delivered in combination with other stressors, such as contaminants, sediment, and freshwater, or may co-occur with other local and global stressors, such as elevated temperatures, hypoxia, ocean acidification, or overfishing, and can reduce resilience to these other stressors. These co-occurring stressors can also affect the way that corals, and other reef organisms, respond to changing nutrient concentrations.

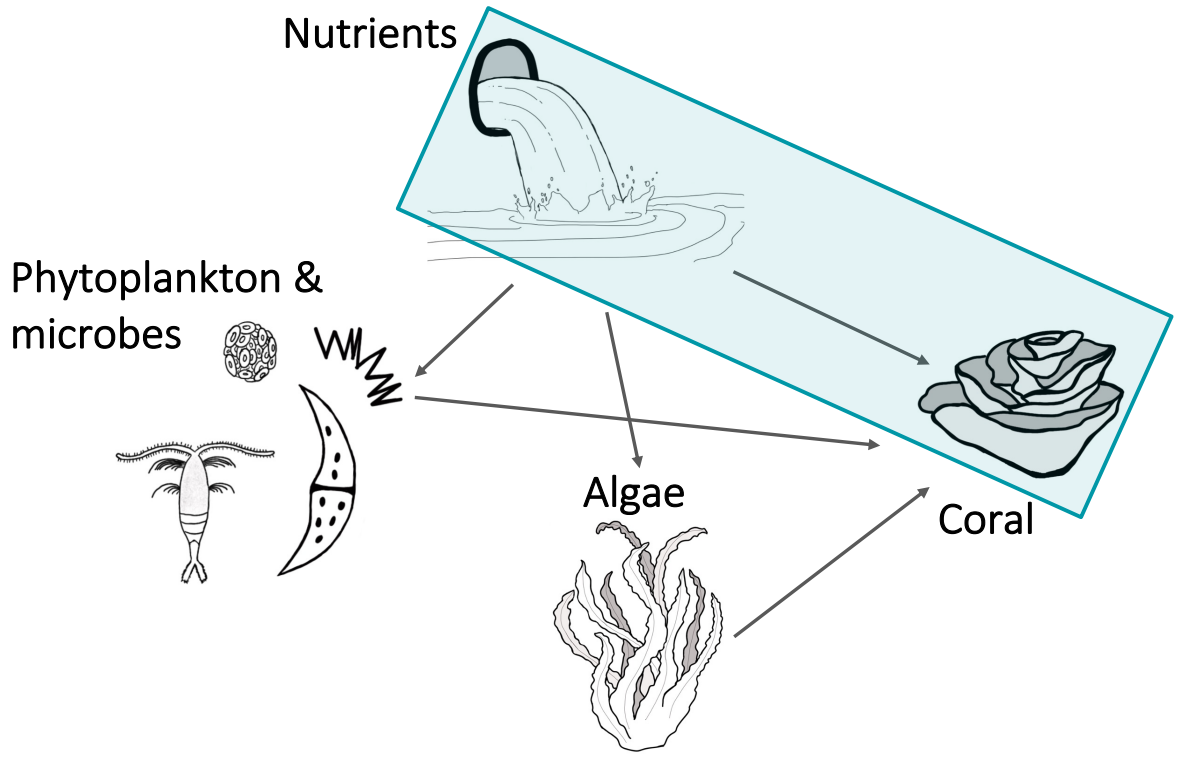

Figure 9.1. Schematic of nutrient impacts on reefs, in the context of corals. The arrows indicate the direct and indirect relationships among different reef taxa and corals, and the shaded box highlights the direct relationship between nutrient addition and corals, which is the focus of this study. *Schematic drawing by D. Wulstein.*

Reef-building corals are ecosystem engineers that shape habitat, provide shelter, and recycle nutrients and carbon back into the water column through biological mechanisms such as mucus sloughing and release of dissolved organic matter (Tanaka et al. 2008). Corals, algae, and other benthic organisms are constantly competing for space in reef ecosystems, and the addition of nutrients can accelerate shifts from coral dominance to benthos dominated by algae, cyanobacterial mats, or urchins (Littler et al. 2006, Norström et al. 2009, Vermeij et al. 2010, Ford et al. 2018). These phase shifts are often due to a combination of stressors such as increased sea surface temperature, nutrient loading, and overfishing (Hughes 1994, Burkepile and Hay 2006). Increased nutrient levels can also directly change the competitive relationship between corals and other benthic organisms, resulting in shifts from diverse coral-dominated systems to lower-diversity algal mats or heterotrophic-dominated communities (Villanueva et al. 2005, Fabricius et al. 2012). Nutrification has many direct effects on coral health and contributes to indirect impacts that can lead to community and ecosystem-level changes.

Many factors influence nutrient cycling on reefs, which makes the development of clear threshold guidelines for beneficial versus detrimental concentrations challenging (McCook 1999). Some organisms may excel at drawing down nutrients or converting them to other forms which are more biologically available to a variety of taxa and numerous critical biological processes. Community members are competing for access to nutrients, and some taxa, like algae, are more efficient than corals at acquiring nutrients and are therefore more likely to flourish under high-nutrient conditions (Naim 1993, Schaffelke and Klumpp 1998b, Burkepile and Hay 2006). In other cases, nutrient-induced phytoplankton blooms increase the competition between corals and other filter feeders and alter light attenuation through the water column (Hayashida et al. 2020). Corals rely on their integrated holobiont for access to nutrients, so their intake may lag behind that of their competitors (Glaze et al. 2021).

Cyanobacterial mats, which are becoming increasingly common on reefs worldwide, also exhibit unique responses to nutrients (Ford et al. 2018). Their rates of nitrogen fixation can far exceed that of algae or corals, and the composition of cyanobacteria may shift in response to the availability of nitrogen on reefs (Ford et al. 2018). This efficiency at nitrogen fixation means that cyanobacteria can have a competitive advantage on reefs with high phosphorus inputs, when the availability of nitrogen is limiting to other organisms (Ford et al. 2018). Similarly, on reefs that are dominated by turf or macroalgae, the abundance of microbes that thrive in high nutrient conditions increases as compared to reefs dominated by corals, which can set off the dissolved organic carbon-disease-algae-microorganism (DDAM) feedback loop and lead to increased disease prevalence (Haas et al. 2016, Caldwell et al. 2020).

Coral reefs are often associated with shallow, oligotrophic waters, and eutrophication in the water column causes drastic changes in the microbial and planktonic community (Bruno et al. 2003, Voss and Richardson 2006, Brodie et al. 2007). Influxes and shortages of nutrients can

alter assemblages of phytoplankton, heterotrophic plankton, zooplankton, and bacteria in ways that affect corals and other benthic organisms (Kürten et al. 2019). For example, phytoplankton can dissipate light, thus reducing available light for coral endosymbionts under normal light levels or protecting them from light levels that induce bleaching (Maina et al. 2008). Shifts in the microbial community can also increase coral disease-associated bacteria (Soffer et al. 2015), resulting in localized oxygen minimum zones causing coral hypoxia (Avendaño-Alvarez et al. 2017, Altieri et al. 2017).

In addition to the biological complexity of nutrient cycling on coral reefs, the sources of the nutrients themselves may affect their availability and toxicity in marine ecosystems (Shantz and Burkepile 2014). 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). 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 more than 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 (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).

Different nutrient 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 Marangoni et al. 2020, Burkepile et al. 2020). Phosphate may be derived from natural and anthropogenic sources (Fernandes de Barros Marangoni 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).

Fertilizers containing nitrogen and phosphorus are of particular concern for nutrient inputs, and as human population has increased, the global use of fertilizers has increased as well (Penuelas et al. 2020). As a result, reef areas near agricultural runoff have increased levels of nutrients (Brodie et al. 2007, Cooper et al. 2007). Terrestrial runoff is also a continuous threat to coral reefs carrying pollutants, sediment, and nutrients from land out to sea. Increased urbanization and the hardening and channelization of watersheds facilitates the

transport of high loads of sediment and nutrients to nearshore environments, and discharge of treated and untreated sewage also introduces nutrients to coral reefs that can reduce coral cover and cause other ecological shifts (Walker and Ormond 1982, Reopanichkul et al. 2009). Urban runoff can also contain nitrogen and phosphorus from lawn care, household cleaners, and sanitary waste (Field and Pitt 1990). Additionally, fish farm effluent can elevate nutrient levels in reef systems, which can negatively impact the reproductive capacity of corals (Loya et al. 2004, Quimpo et al. 2020).

Given the inherent complexity of this system, there are many components that are understudied. This review and analysis focus specifically on the direct relationship between inorganic nutrient addition and corals (Fig. 9.1). However, the relationships between corals and algae, plankton, and the microbial community in nutrient-enriched waters are also extremely important and merit review in future studies.

9.1 NUTRIENTS AND OTHER STRESSORS

Dissolved inorganic nutrients in coastal marine waters are often derived from terrestrial sources and are associated with other stressors, such as increased sediment loads, freshwater, and land-based pollutants (i.e., heavy metals, pesticides, plastics, etc.). The impacts of altered nutrient levels and ratios may also be exacerbated by stressors such as changes in irradiance and increased sea surface temperature (Donovan et al. 2020). The relationships between these compounding stressors are complex and nuanced.

Sediment: The addition of sediment to reef ecosystems can result in increased turbidity and greater amounts of deposited sediment, and sediment alone can have significant negative impacts on corals (Tuttle and Donahue 2020, 2022). Suspended and deposited sediment can also influence the availability of nutrients. High turbidity and high nutrient levels both result in lower available sunlight for coral endosymbionts (Storlazzi et al. 2015). Sedimentation can also result in tissue abrasions that leave corals more susceptible to disease-associated bacteria and other harmful microbes. Eutrophication can increase the prevalence of these microbes, which in turn increases the rate of coral disease and death (Bruno et al. 2003, Voss and Richardson 2006, Harvell et al. 2007). The magnitude of the impacts of sediment vary by the amount and duration of exposure, as well as the type of sediment (e.g., fine organic matter versus coarse grains) (Fabricius 2005).

Pollutants: Many nutrient sources are associated with agricultural runoff, and industrial fertilizers and pesticides are often associated with one another. Although only a few papers look at the synergistic effects between changes in nutrients and the addition of pollutants, it has been well established that pollutants can negatively impact corals (Nalley et al. 2021). From field data, it is also clear that these stressors co-occur and often affect similar systems,

potentially multiplying each other's effects (Ban et al. 2014). Sewage is a large contributor of coastal nutrients and is also associated with harmful bacteria and other pollutants (Wear and Thurber 2015).

Freshwater: With the increase in agriculture and the destruction of permeable natural filtration systems, such as wetlands and mangroves, nutrient-rich freshwater can enter coastal marine ecosystems (Field and Pitt 1990). Changes in salinity due to freshwater inputs can negatively impact coral health. With the addition of nutrients, these adverse effects can be more pronounced (Humphrey et al. 2008, Ban et al. 2014).

Irradiance: Increased nutrient levels can alter phytoplankton populations, which can have different impacts on coral health depending upon the ambient irradiance levels and sea-surface temperature. Phytoplankton can reduce light-induced bleaching but may also reduce available light for coral endosymbionts, resulting in decreased photosynthesis rates (Maina et al. 2008). Phosphate starvation and shifts in nutrient ratios can increase coral susceptibility to light- and temperature-induced bleaching events (Wiedenmann et al. 2013).

Temperature: Changes in dissolved nutrient levels can reduce coral tolerance to heat (D'Angelo and Wiedenmann 2014). While the prevalence of bleaching is largely attributable to high temperatures, elevated nitrogen has been correlated with an increased severity of the response (Donovan et al. 2020), and nutrient limitation has been linked to bleaching at lower temperatures (Morris et al. 2019). During periods of temperature stress, corals take up less nitrogen but their acquisition rate of phosphorus, which is used to sustain photosynthesis, increases significantly (Ezzat et al. 2016a).

The type of nitrogen is also important in the context of bleaching. 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). Conversely, nitrate has been linked to increased prevalence and duration of bleaching in corals experiencing temperature stress (Burkepile et al. 2020), and corals that are acclimatized to high-nutrient conditions demonstrate a greater propensity towards bleaching (Wooldridge and Done 2009). Corals experiencing temperature anomalies are also more vulnerable to disease, which may be exacerbated by simultaneous exposure to elevated nutrient concentrations (Caldwell et al. 2016, Aeby et al. 2020).

9.2 IMPACTS THROUGHOUT THE LIFE CYCLE OF A CORAL

Nutrient enrichment can have both direct and indirect effects on corals of all life stages. Like many other marine invertebrates, corals have a biphasic life cycle that alternates between small free-swimming larvae and large sessile adults. Metamorphosis from larva to sedentary

polyp is accompanied by extensive molecular and physiological changes (Ball et al. 2002, Strader et al. 2018). Stressors can therefore impact corals through different mechanisms, and at different magnitudes, at these distinct life stages (Richmond et al. 2018).

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 x 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).

On a population scale, the negative impacts of a stressor can be reflected not only in adult health and mortality, but also in reproduction and recruitment (i.e., failure to recolonize after a disturbance). Additionally, non-lethal stressors can have cumulative effects over the course of an organism's lifetime (Nalley et al. 2021). Therefore, effective management strategies should consider impacts across all coral life stages.

9.3 NUTRIENTS AS A STRESSOR COMPARED TO SEDIMENT AND POLLUTANTS

In related studies examining sediment (Tuttle and Donahue 2020, 2022) and pollutants (Nalley et al. 2021) we examined negative, unidirectional relationships between stressors and coral stress responses. For example, we determined the concentration of sediment that elicits a shift to negative effects and generated "No Observed Adverse Effect Levels" (NOAEL) and "Lowest Observed Adverse Effect Levels" (LOAEL) for each sediment-response relationship examined (Tuttle and Donahue 2020, 2022). Similarly, examining the impacts of a variety of pollutants on coral responses, we generated negative dose-response thresholds, effective concentrations (i.e., EC_{10} and EC_{50}), and LOAEL values (Nalley et al. 2021).

This study focuses on dissolved inorganic nitrogen (DIN, specifically nitrate and ammonium) and dissolved inorganic phosphorus (DIP, phosphate). Nitrogen is being introduced to reefs at increasing rates via atmospheric deposition, discharge, and runoff, and the amount of nitrogen being introduced has exceeded that of phosphate, which disrupts the relative balance of nutrients on reefs (Zhao et al. 2021). DIN and DIP have different anticipated impacts on corals, but the mechanisms are complex. Corals are heavily reliant on endosymbionts to assimilate these nutrients, which means that the relationship between corals and nutrients involves the holobiont, rather than a single organism (Morris et al. 2019). The sensitivity of corals to nutrients can vary by coral species, and the response of corals to different species of DIN (i.e., ammonium versus nitrate) can also vary greatly (Shantz and Burkepile 2014, Zhao et al. 2021). Further, increases in nutrients can have cascading impacts throughout the ecosystem (e.g., phytoplankton blooms), which can indirectly affect the availability of nutrients and the physiological function of corals (D'Angelo and Wiedenmann 2014).

When examining the relationship between excess nutrients and physiological responses of the coral holobiont, there are not always direct negative impacts. Adding nutrients may increase the abundance of zooxanthellae, which has positive effects on photosynthetic function. Beyond a slight elevation of nutrients, however, overcrowding may occur and cause negative outcomes like shading, increased holobiont temperature, and oxidative stress (D'Angelo and Wiedenmann 2014, Morris et al. 2019). In these cases, the addition of nutrients may result in a positive response up to a point, beyond which the response may become negative (Shantz and Burkepile 2014). The addition of nutrients also promotes the growth of coral predators, such as the crown-of-thorns starfish (*Acanthaster planci*), which can indirectly reduce coral survival (Birkeland 1989, Brodie et al. 2005). Other studies have indicated that nutrients supplied as pulses, or in short bursts typical of flooding events, may have less negative impacts on corals as compared to those applied in presses, which are continuous applications typical of sewage contamination or submarine groundwater discharge (van der Zande et al. 2021). To address this complexity in response directionality, we needed to account for the

interaction between nutrients and also the inflection points between positive and negative relationships.

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 – 0.38 µM DIP and 0.15 – 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 – 202 µM DIN and 0.02 – 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 – 32.39 µM DIN and 0.04 – 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).

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.

10 METHODS

10.1 SYSTEMATIC LITERATURE REVIEW

10.1.1 ARTICLE SEARCHES

The approach used in this study followed that described previously in Tuttle et al. (2020), Tuttle & Donahue (2020, 2022), and Nalley et al. (2021). We first identified reviews that addressed the impacts of nutrients on reefs and on scleractinian corals (D'Angelo and Wiedenmann 2014, Shantz and Burkepile 2014, Morris et al. 2019, Houk et al. 2020, Zhao et al. 2021). With this framing, we developed a systematic search of peer-reviewed studies, public reports, and gray literature. The scope of the study included all life stages of scleractinian corals found between 20-30 °C in the shallow, photic zone (<80 m). The justification for the search engines and databases used is described in detail in Tuttle et al. (2020), and a list is provided for reference in the Supplemental Materials of this report (Table S1). A comprehensive list of search terms was optimized using the Web of Science format ([search term]* AND coral), which includes a wildcard (*) and Boolean operator (AND).

To focus the search on endangered and threatened taxa as listed under the United States Endangered Species Act and those of particular interest in the U.S. Pacific Islands, the following genera were included specifically as search terms: *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*. A complete list of search terms has been included in the Supplemental Materials (Text S1).

10.1.2 ARTICLE SCREENING AND ELIGIBILITY CRITERIA

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 was included. Studies that were deemed relevant were further screened for eligibility based on the PECO framework (population, exposure, comparison, outcome) described in the Supplemental Materials (Text S2) (Morgan et al. 2018). Full texts that passed this stage of review (n = 93) were then assessed

a final time for response measurement comparability between studies (n = 47). This subset of studies was then used for the final 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). An additional list of studies that were not able to be included in our meta-analyses but that may be relevant for future studies that address the effects of other types of nutrients on coral health (e.g., organics, effluent, different types of fertilizer, etc.) is also included in the Supplemental Materials (Text S4).

10.2 DATA EXTRACTION

A single individual extracted data from articles that passed the final review stage, described above. A suite of information was collected from each study including the species studied, collection site, experimental location, experimental parameters, nutrient concentrations, and duration of study. If data were presented in figures or graphs, it was extracted using Web Plot Digitizer, which converts the data to 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) examining 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).

10.3 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 10.1).

Table 10.1. 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 Burkepile 2014).
Chlorophyll a concentration	▪ Chlorophyll *a* concentrations are dependent on the density of zooxanthellae, so chlorophyll *a* 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 *a* 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).

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):

$$Standardized\ Difference\ in\ Means: \frac{(sample\ mean_{treatment} - sample\ mean_{control})}{s} \times J$$

$$J\ (Correction\ Factor): 1 - \frac{3}{4(n_{treatment} + n_{control}) - 9}$$

$$S = \sqrt{\frac{(n_{treatment} - 1) \times SD^2_{treatment} + (n_{control} - 1) \times SD^2_{control}}{n_{treatment} + n_{control} - 2}}$$

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):

$$Treatment\ Risk\ (R_{treat}): \frac{n_{survived}}{n_{treatment}} \qquad Control\ Risk\ (R_{control}): \frac{n_{survived}}{n_{control}}$$

$$\log Risk\ Ratio: log_e(\frac{R_{treat}}{R_{control}})$$

$$SE_{logRR}: \sqrt{\frac{1}{n_{survival\ in\ treatment}} + \frac{1}{n_{survival\ in\ control}} - \frac{1}{n_{treatment}} - \frac{1}{n_{control}}}$$

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,

$$Response\ Effect\ Size \sim DIN + DIP + random\ effects$$

Positive effect sizes indicate an increase in the measured response as compared to the control, and negative effect sizes indicate a decrease in 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 nonlinearity, 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 (Fujieki 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 DIP µM (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 below (Fig. 10.1).

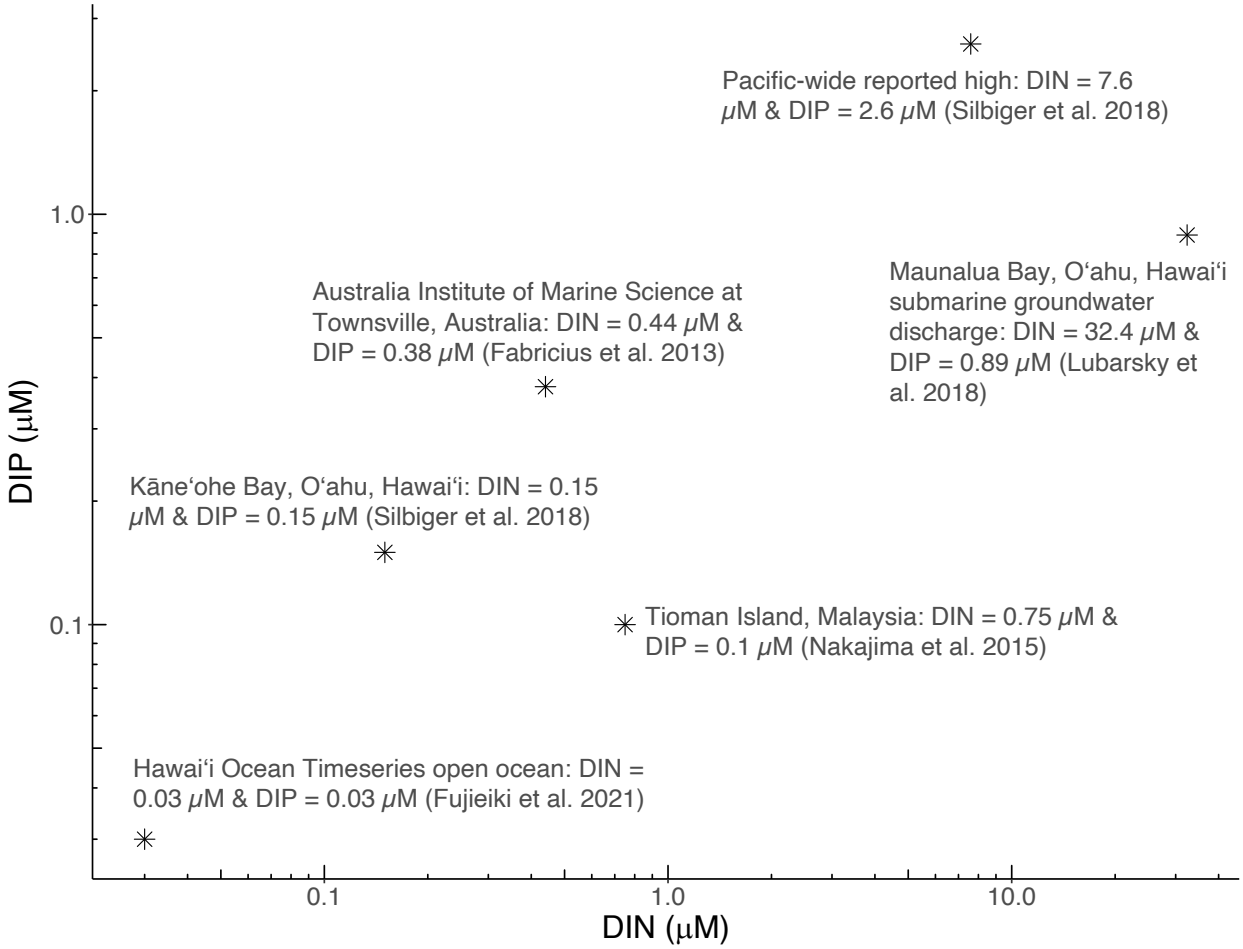

Figure 10.1. A diagram of the reference, ambient nutrient concentrations (grey stars) used in this study, which span open ocean to impacted coastal sites.

11 RESULTS

Meta-analyses were conducted for the following responses: zooxanthellae density, chlorophyll *a* concentration, photosynthetic rate, maximum photosynthetic efficiency (F_v/F_m), 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 11.1, along with the range of exposure concentrations and the duration of treatment exposure. Model results for all responses are summarized in Table 11.2.

Table 11.1. Coral responses examined using meta-analysis with ranges of predictors.

Response	Studies	Experiments	DIN (µM)	DIP (µM)	Mean Exposure Duration in days (Range)
Zooxanthellae Density	21[a]	36	0.08-128	0.02-2	33 (3-126)
Chlorophyll a 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, 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, 2010, 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. 2016b, 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)

Table 11.2. 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 between Experiments (based on I^2)**
Zooxanthellae Density (std. diff. in means)	NO_3^-: pos. quadratic NH_4^+: pos. linear DIP: pos. linear	moderate (68.3%)
Chlorophyll a Concentration (std. diff. in means)	DIN: pos. linear DIP: n.s.	moderate (43.3%)
Photosynthetic Rate (std. diff. in means)	NO_3^-: pos. linear NH_4^+: n.s. DIP: n.s.	low (36.3%)
Photosynthetic Efficiency (std. diff. in means)	DIN: n.s. DIP: neg. linear	high (72.5%)
Growth Rate (std. diff. in means)	DIN: neg. linear DIP: pos. linear Duration: pos. linear	low (0%)
Calcification (std. diff. in means)	DIN: n.s. DIP: n.s.	moderate (56.4%)
Adult Survival (log risk ratio)	DIN: n.s. DIP: n.s. Duration: neg. linear	low (23.1%)
Larval Survival (std. diff. in means)	DIN: neg. linear DIP: n.s.	moderate (61.1%)
Fertilization Success (std. diff. in means)	DIN: neg. linear DIP: n.s.	moderate (63.9%)

11.1 PHOTOSYNTHETIC RESPONSES OF THE CORAL ENDOSYMBIONT

11.1.1 ZOOXANTHELLAE DENSITY

Looking at general trends in the effect of DIN and DIP on zooxanthellae density, the largest increases occurred at concentrations between 1-10 µM DIN and 0.1-1 µM DIP (Fig. 11.1). Zooxanthellae densities were most likely to exceed a physiologically optimal concentration (1-3 x 10^6 cells cm^{-2}; Morris et al. 2019) at medium to high concentrations of DIN (>3 µM). 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. 11.1).

Because of the known differences in nitrate and ammonium impacts on zooxanthellae, NO_3 and NH_4 were modeled separately, rather than together as DIN. A linear mixed-effects meta-regression with a second order polynomial for NO_3 was used in this meta-analysis

because of the biological mechanisms underlying the relationship between zooxanthellae density and NO_3 (i.e., increased to a maximum concentration and then decreased). Zooxanthellae density increased significantly with the addition of NO_3 ($P < 0.0001$; Fixed effect estimates ± SE: 1.91 ± 0.46), NH_4 ($P < 0.0001$; Fixed effect estimates ± SE: 1.52 ± 0.18), and DIP ($P < 0.0001$; Fixed effect estimates ± SE: 3.29 ± 0.58) (Fig. 11.2; Table S2). The range of concentrations examined for NO_3 (0-128 µM) far exceeded those tested for NH_4 (0-50 µM) or DIP (0-2 µM), so the comparable effects of NH_4 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. S1-3a).

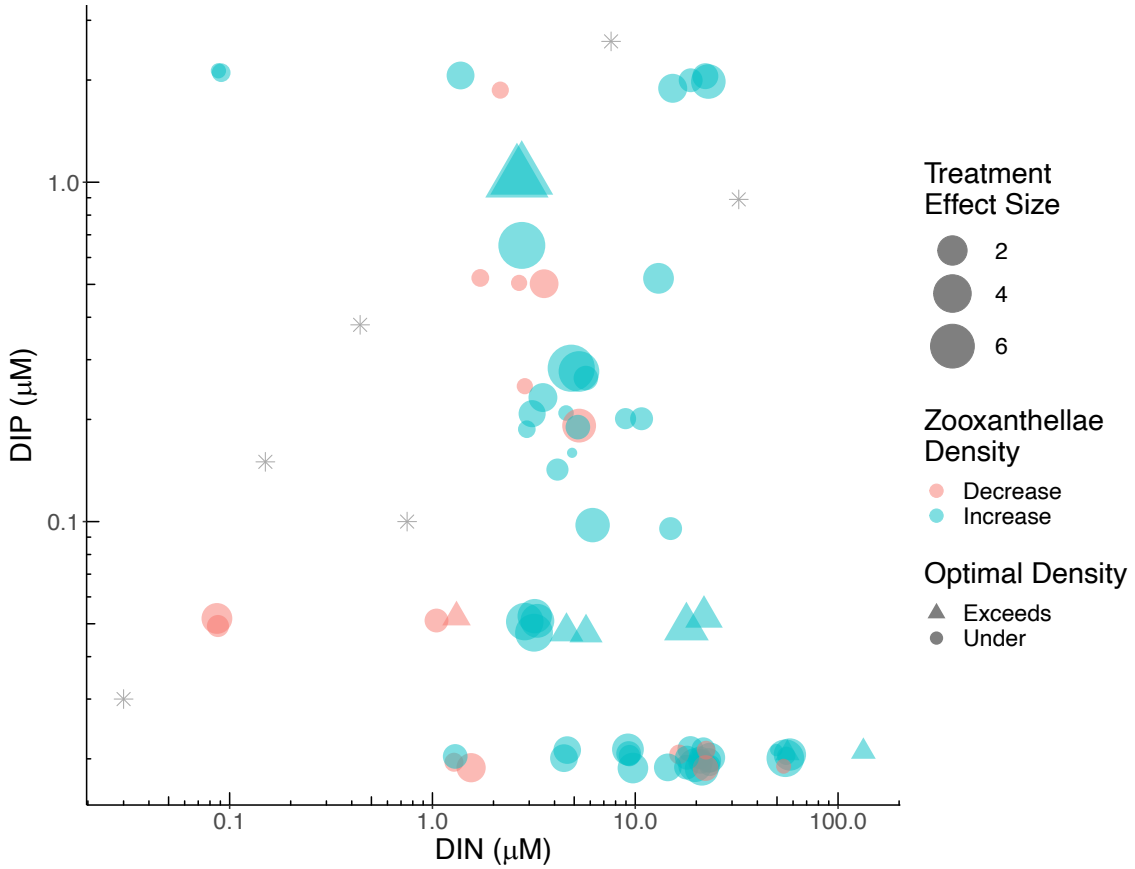

Figure 11.1. Effect sizes of DIN and DIP addition treatments on zooxanthellae density (10^6 cells cm^{-2}) in corals. The size of the point refers to the standardized difference in means between the treatment and the control in an experiment, and the color refers to whether zooxanthellae density increased (teal) or decreased (red). The shape indicates whether the concentration of zooxanthellae exceeded the optimal density (3 x 10^6 cells cm^{-2}) reported in Morris et al. (2019). The gray stars in the plot indicate ambient DIN and DIP conditions measured in the field at open ocean, unimpacted coastal, and impacted coastal sites. See Fig. 10.1 for a thorough explanation of the reference sites and concentrations.

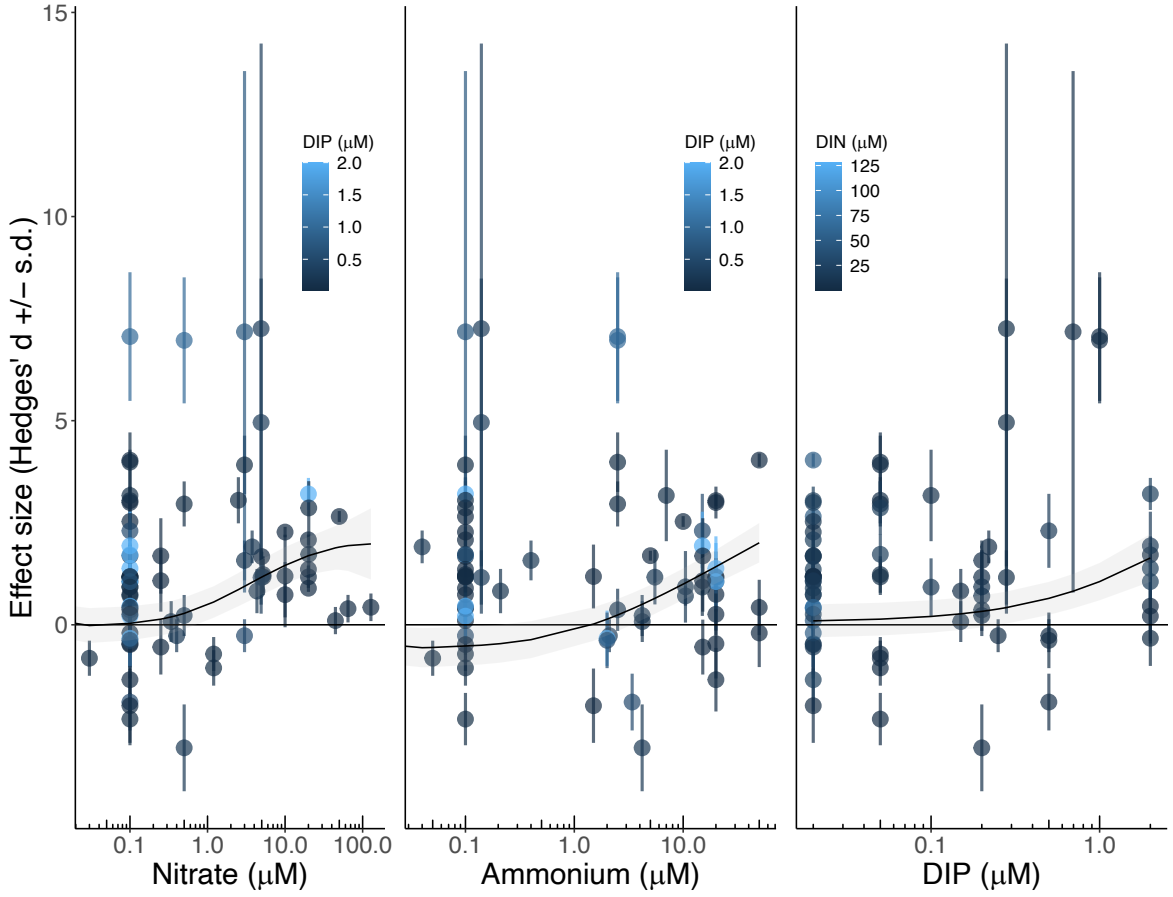

Figure 11.2. Effect size of DIN (nitrate and ammonium on the left) and DIP (right) on zooxanthellae density (10^6 cells cm^{-2}). Points indicate the standardized difference in means ± the standard deviation for each treatment condition as compared to the control. The model predicted fit line and 95% confidence interval are included for each fixed effect, with the other effects held constant at their median.

11.1.2 CHLOROPHYLL *A* CONCENTRATION

At concentrations of DIN that are observed on coral reefs, concentrations of chl-*a* increased, particularly above 5 µM DIN (Fig. 11.3). Negative 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 ± SE: 0.95± 0.27), but there was no significant relationship with DIP (P = 0.997; Fig. 11.4; 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. S1-3b).

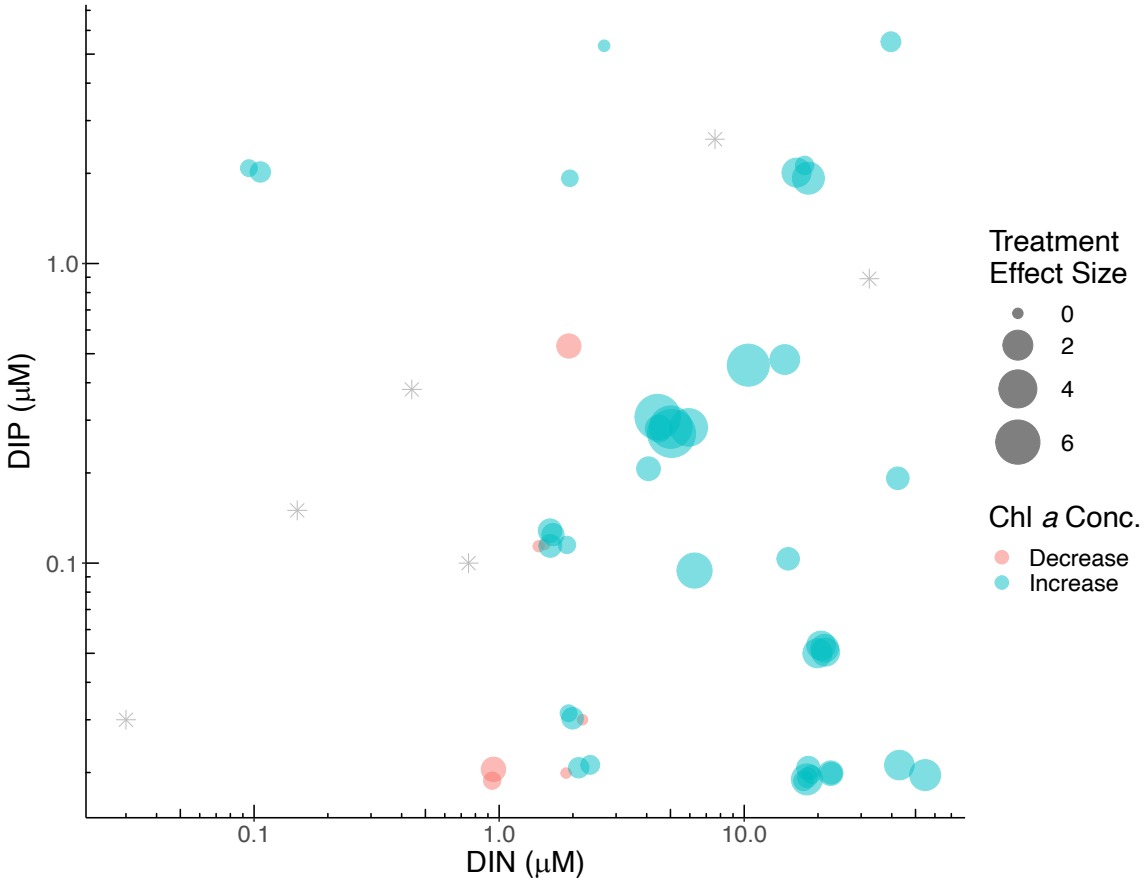

Figure 11.3. Effect sizes of DIN and DIP addition treatments on chlorophyll a concentrations (µg Chl a cm^{-2}) in corals. The size of the point refers to the standardized difference in means between the treatment and the control in an experiment, and the color refers to whether chlorophyll a concentrations increased (teal) or decreased (red). The stars indicate ambient DIN and DIP conditions measured in the field. See Fig. 10.1 for a complete description of reference data sources.

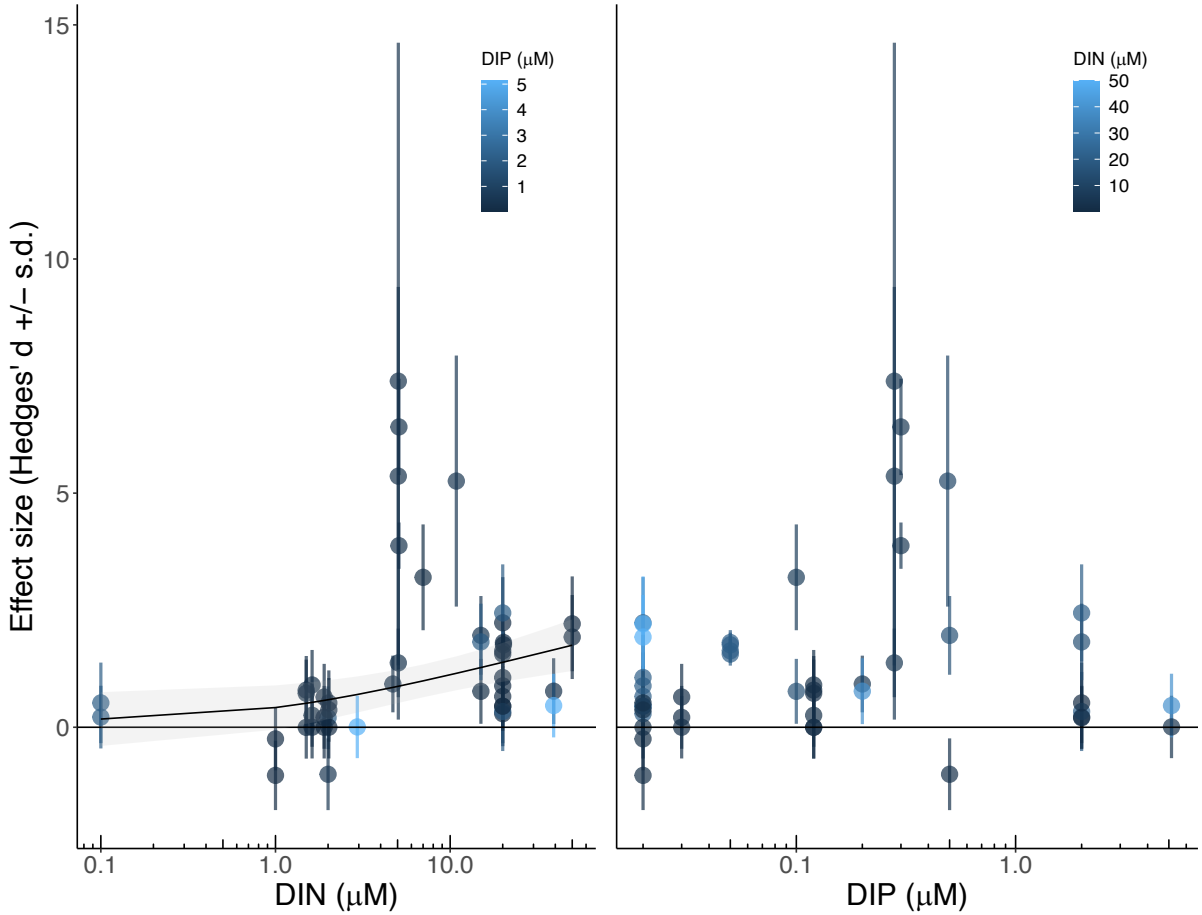

Figure 11.4. Effect size of DIN (left) and DIP (right) on chlorophyll a concentrations (μg Chl a cm^{-2}). Points indicate the standardized difference in means ± the standard deviation for each treatment condition as compared to the control. The model predicted fit line and 95% confidence interval are included for each nutrient, with the other held constant at its median. No predicted fit line indicates no significant relationship.

11.1.3 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. 11.5). The best fit model was a linear mixed-effects meta-regression with NO_3 and NH_4 analyzed independently (Table S4). NO_3 had a significant positive effect on the photosynthetic rate ($P < 0.0001$; Fixed effect estimates ± SE: 1.84 ± 0.38), but NH_4 and DIP had no significant effect ($P > 0.05$) (Fig. 11.6). 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. S1-3c). 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.

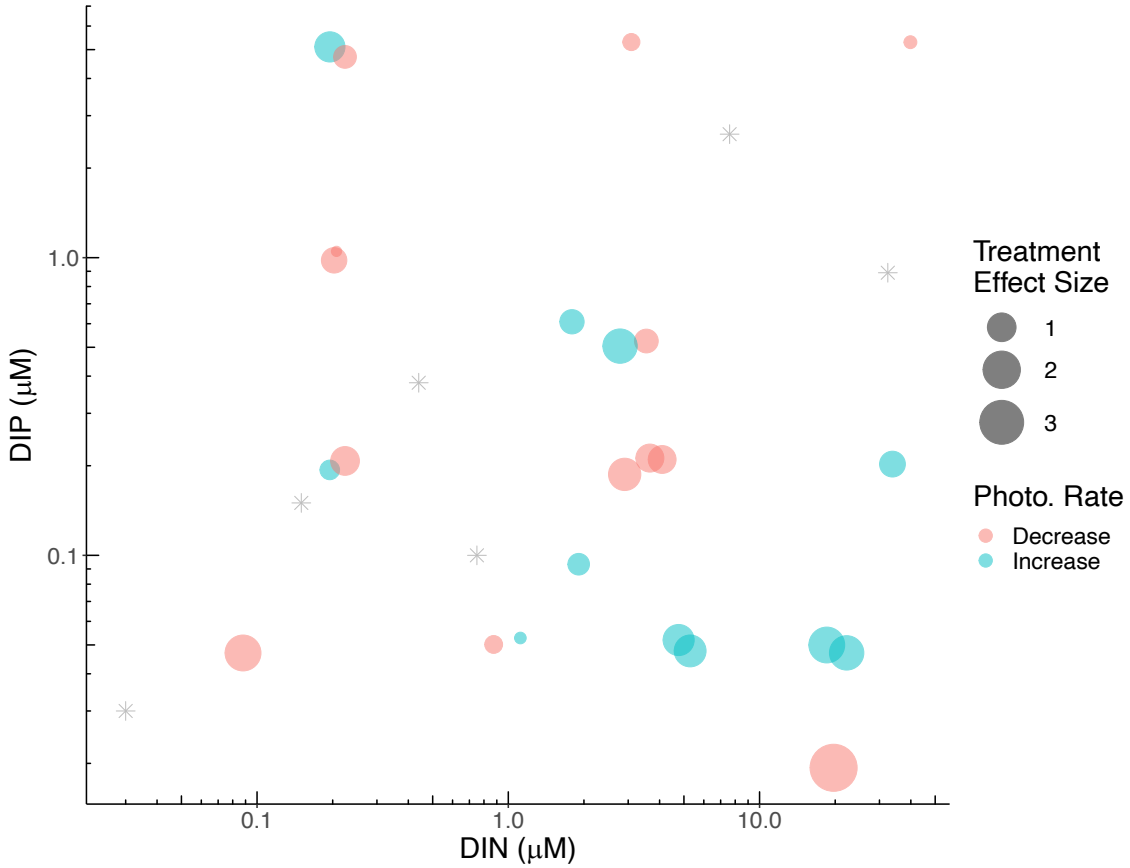

Figure 11.5. Effect sizes of DIN and DIP addition treatments on the gross photosynthetic rate (μmol O_2 cm^{-2} day^{-1}) in corals. The size of the point refers to the standardized difference in means between the treatment and the control in an experiment, and the color refers to whether the photosynthetic rate increased (teal) or decreased (red). The stars indicate ambient DIN and DIP concentrations measured in the field. See Fig. 10.1 for a complete description of reference data sources.

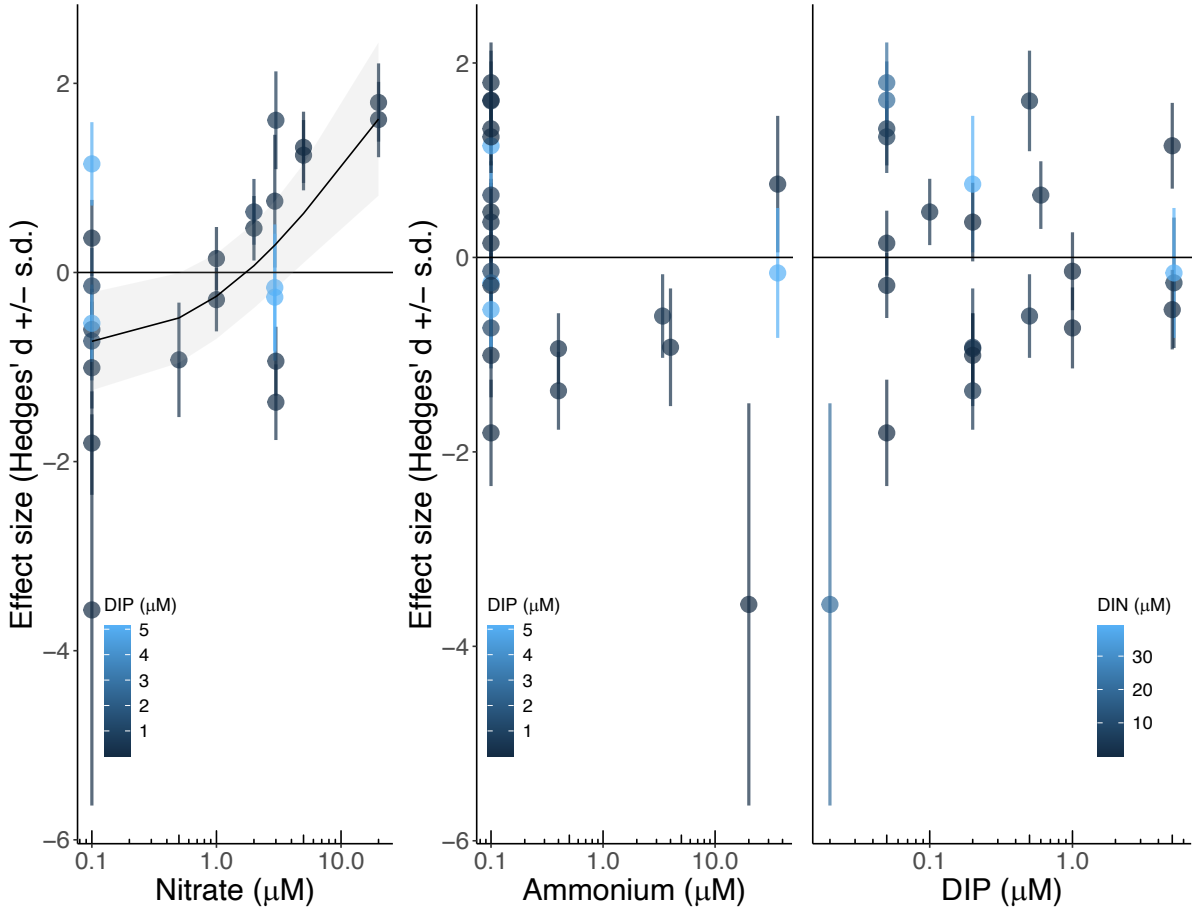

Figure 11.6. Effect size of DIN (left) and DIP (right) addition on the gross photosynthetic rate (μmol O_2 cm^{-2} day^{-1}). Points indicate the standardized difference in means ± the standard deviation for each treatment condition as compared to the control. Model-fitted lines are not included here because neither DIN nor DIP had a significant effect on the photosynthetic rate. No predicted fit line indicates no significant relationship.

11.1.4 PHOTOSYNTHETIC EFFICIENCY (MAXIMUM QUANTUM YIELD, MQY)

At concentrations of DIN and DIP greater than 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. 11.7). The best fit model was a linear mixed-effects meta-regression model (Table S5). NO_3 and NH_4 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. 11.8). DIP had a significant negative effect on the MQY (P < 0.001, Fixed effect estimate ± SE: -5.61 ± 1.01). *Acropora microphthalma* and *A. polystoma,* in particular followed this trend (Fig. S1d), but including species 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. S2-3d). 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.

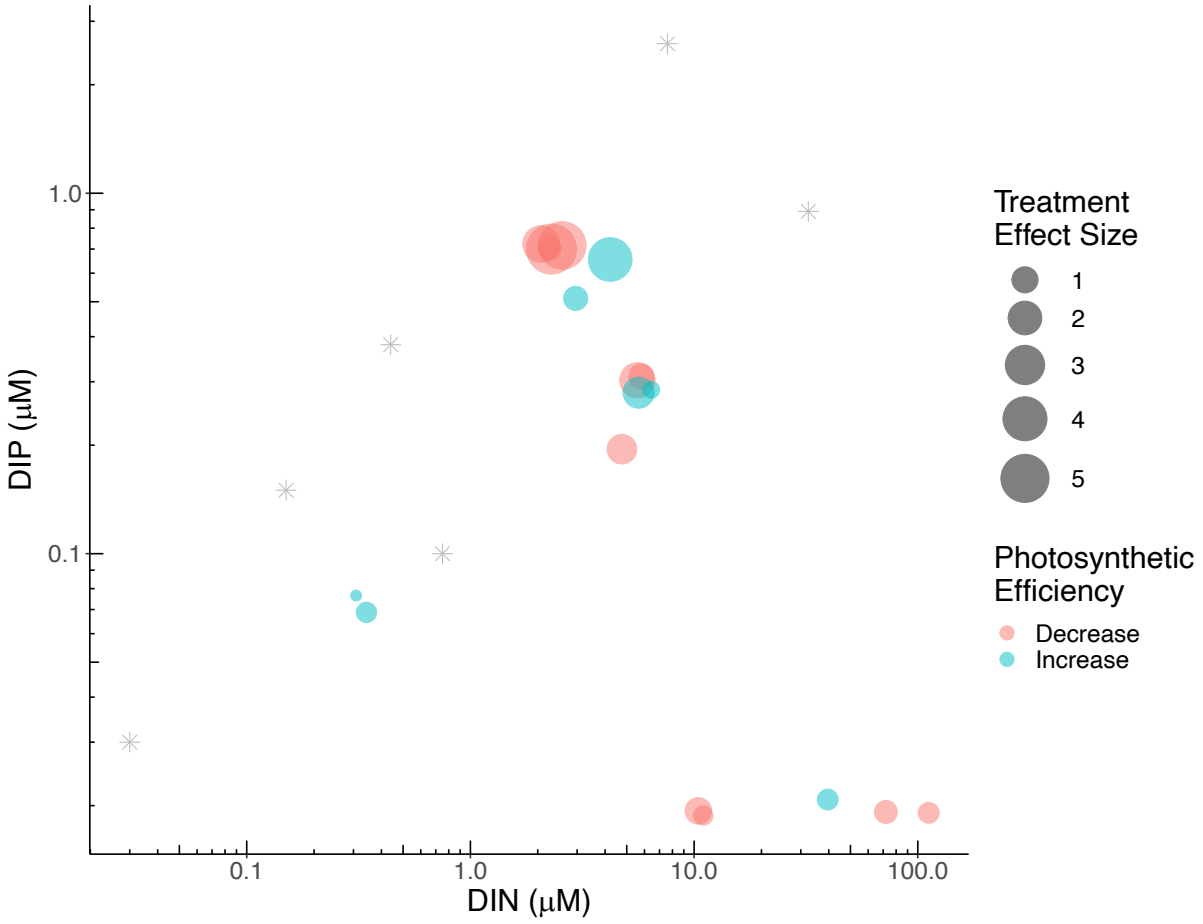

Figure 11.7. Effect sizes of DIN and DIP addition treatments on the photosynthetic efficiency (MQY - F_v/F_m) in corals. The size of the point refers to the standardized difference in means between the treatment and the control in an experiment, and the color refers to whether the photosynthetic rate increased (teal) or decreased (red). The stars indicate ambient nutrient conditions measured in the field. See Fig. 10.1 for a complete description of reference data sources.

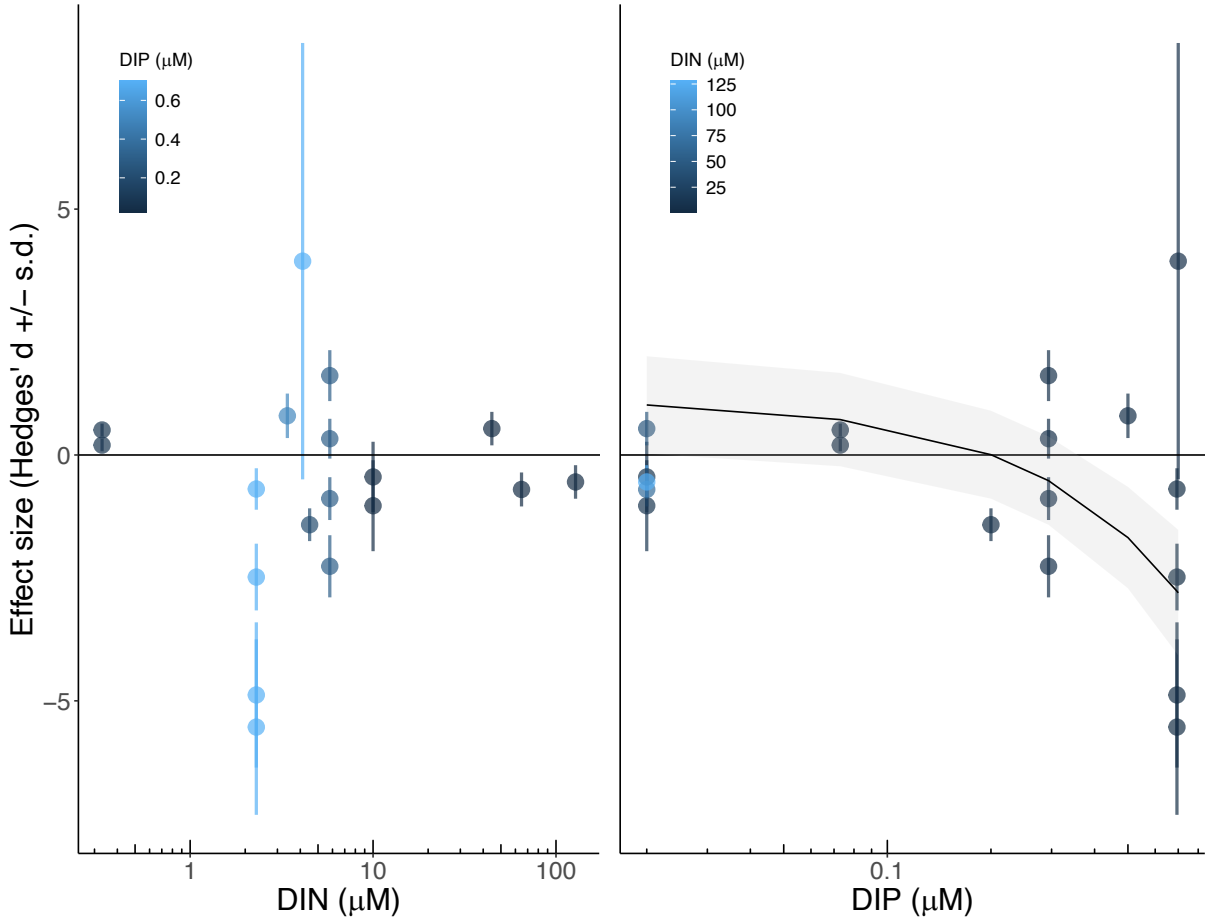

Figure 11.8. Effect size of nutrient enrichment treatments (left: DIN, right: DIP) on photosynthetic efficiency (i.e., maximum quantum yield, F_v/F_m). Points indicate the standardized difference in means ± the standard deviation for each treatment condition as compared to the control. The model predicted fit line and 95% confidence interval are included for DIP, with DIN held constant at its median. No predicted fit line indicates no significant relationship.

11.2 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. 11.9). 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 ± SE: -0.01 ± 0.004), and exposure duration had a small but significant positive effect (P = 0.03; Fixed effect estimate ± 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 ± SE: 0.16 ± 0.03), with positive effects occurring at DIP concentrations above 5 µM

(Fig. 11.10). 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. S1-2e). Only corals with branching morphology were examined, so the effect of morphology could not be assessed (Fig. S3e).

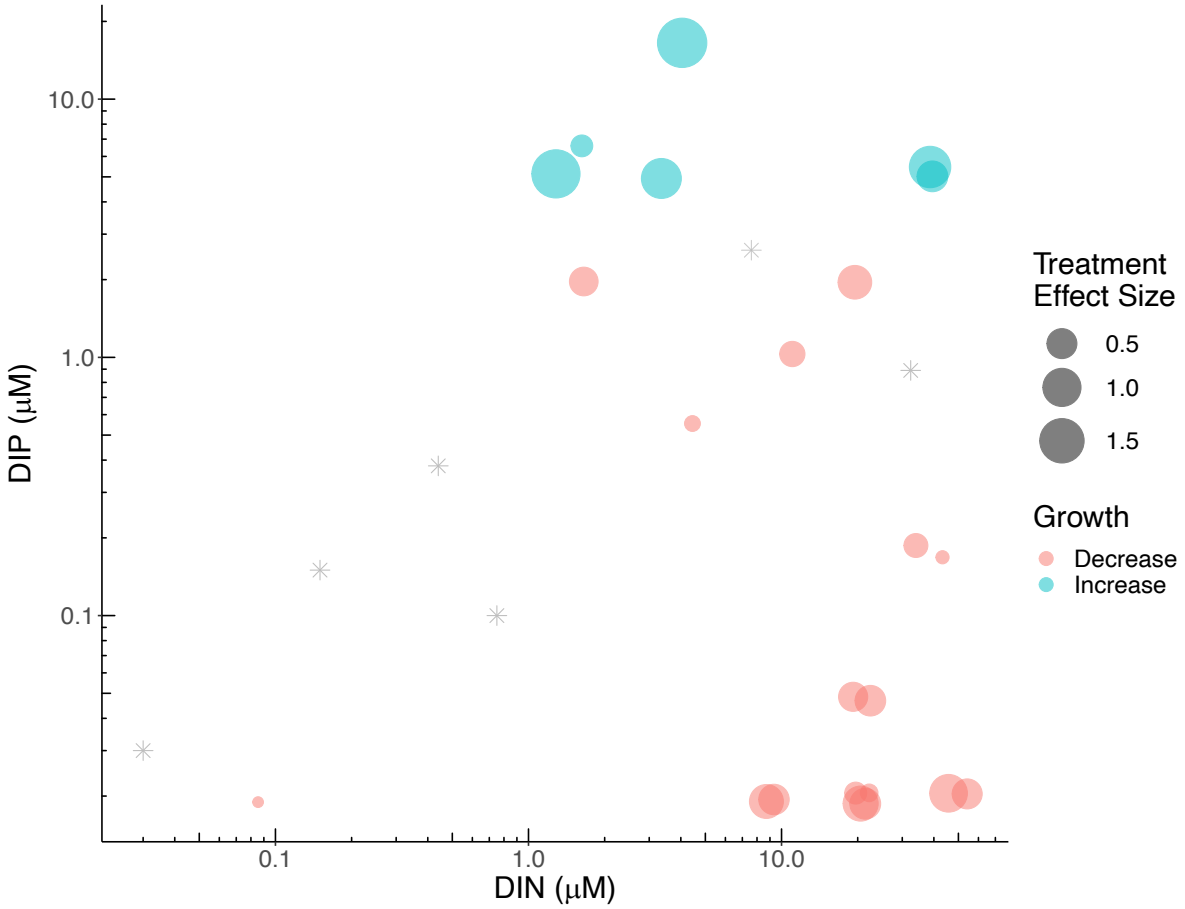

Figure 11.9. Effect sizes of DIN and DIP addition treatments on linear extension (mm day^{-1}) in corals. The size of the point refers to the standardized difference in means between the treatment and the control in an experiment, and the color refers to whether the growth rate increased (teal) or decreased (red). The stars indicate ambient conditions measured in the field. See Fig. 10.1 for a complete description of reference data sources.

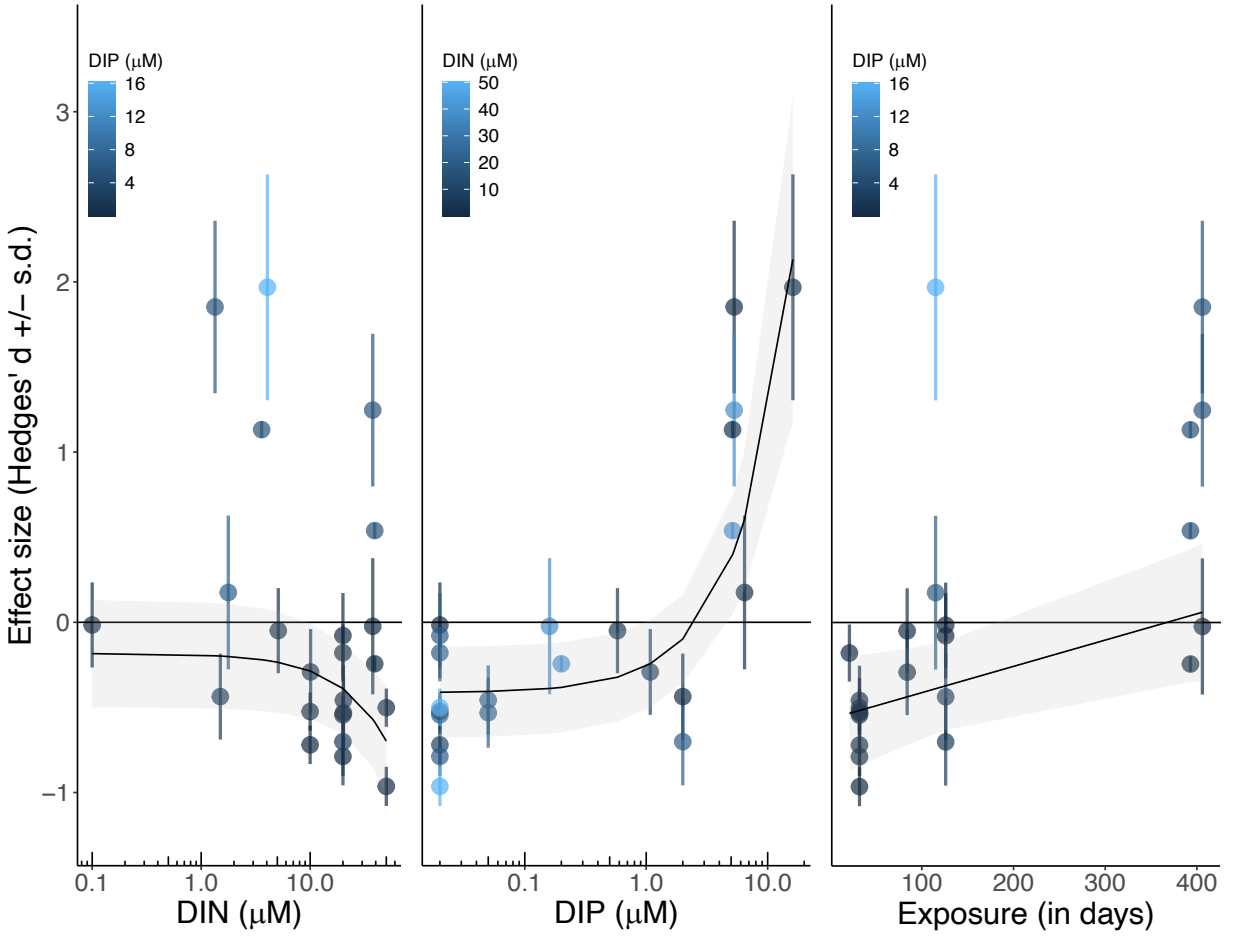

Figure 11.10. Effect size of nutrient (left: DIN, right: DIP) treatments on coral growth (mm day^{-1}). Points indicate the standardized difference in means ± the standard deviation for each treatment condition as compared to the control. The model predicted fit line and 95% confidence interval are included for DIP, with DIN held constant at its median.

11.3 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 1-20 µM, when DIP was less than 0.2 µM (Fig. 11.11). 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. 11.12; 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. S1-3f).

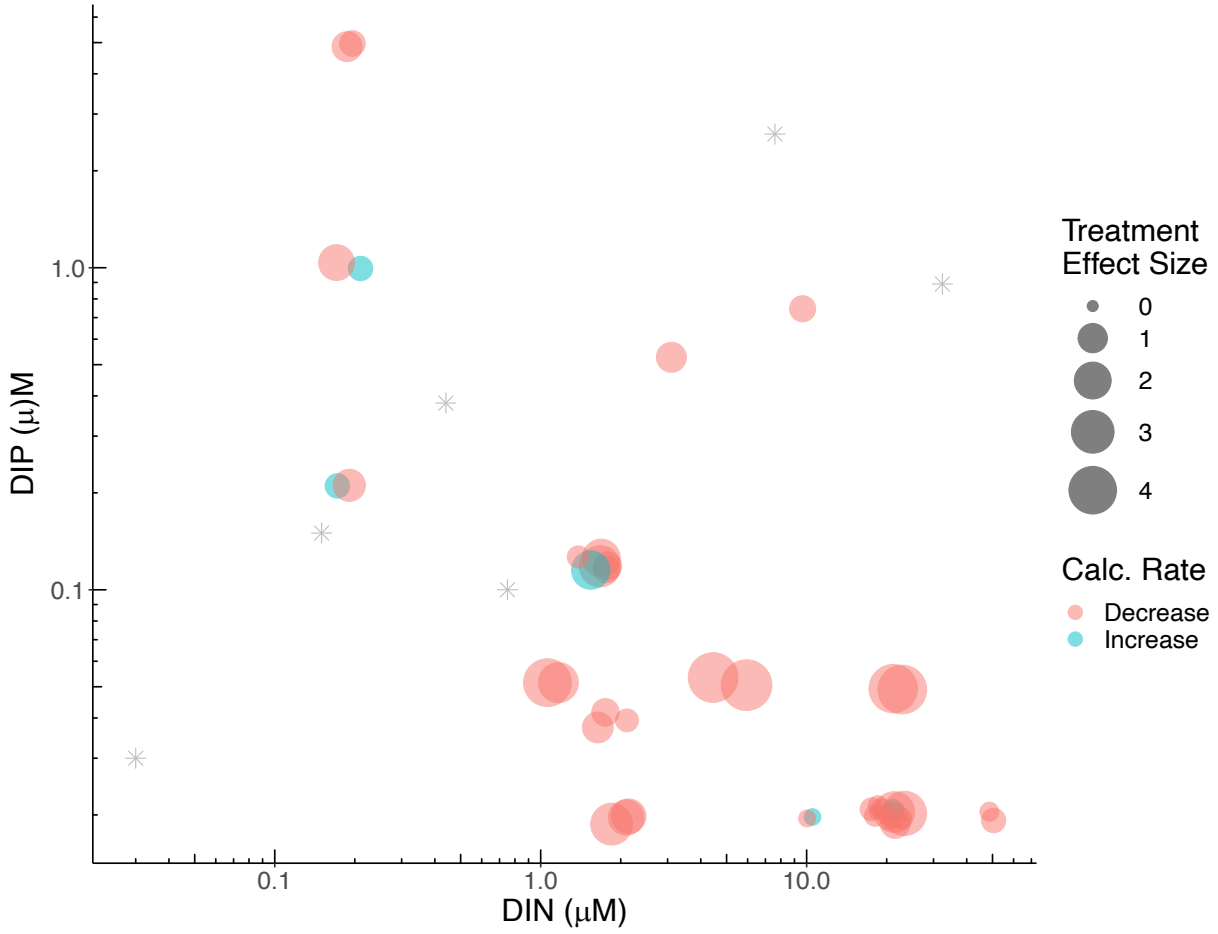

Figure 11.11. Effect sizes of DIN and DIP addition treatments on calcification (mg $CaCO_3$ cm^{-2} day^{-1}) in corals. The size of the point refers to the standardized mean difference between the treatment and the control in an experiment, and the color refers to whether the growth rate increased (teal) or decreased (red). The stars indicate ambient conditions measured in the field. See Fig. 10.1 for a complete description of reference data sources.

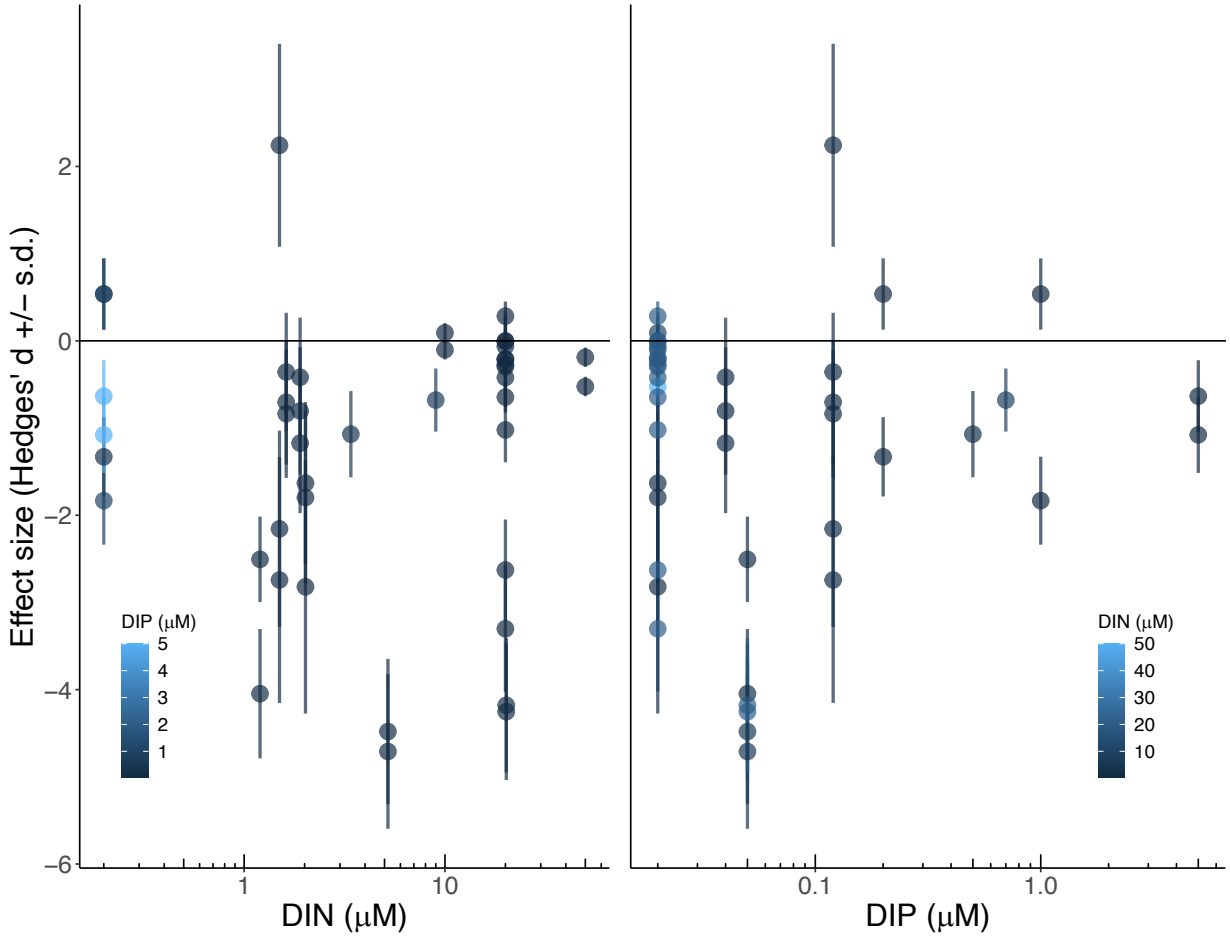

Figure 11.12. Effect size of nutrient (left: DIN, right: DIP) treatments on calcification (mg $CaCO_3$ cm^{-2} day^{-1}) in corals. Points indicate the standardized mean difference ± the standard deviation for each treatment condition as compared to the control. Model predictions are not included for DIN or DIP, because they did not have significant relationships with the magnitude of the effect on coral calcification rate.

11.4 MORTALITY

11.4.1 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. 11.13). 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 ± SE: -0.002 ± 0.0007), but DIN and DIP did not have significant effects (Table S8; Fig. 11.14). 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 tenufolia* (Figs. S1-2g), but there were no clear trends based on coral morphology (Fig. S3g).

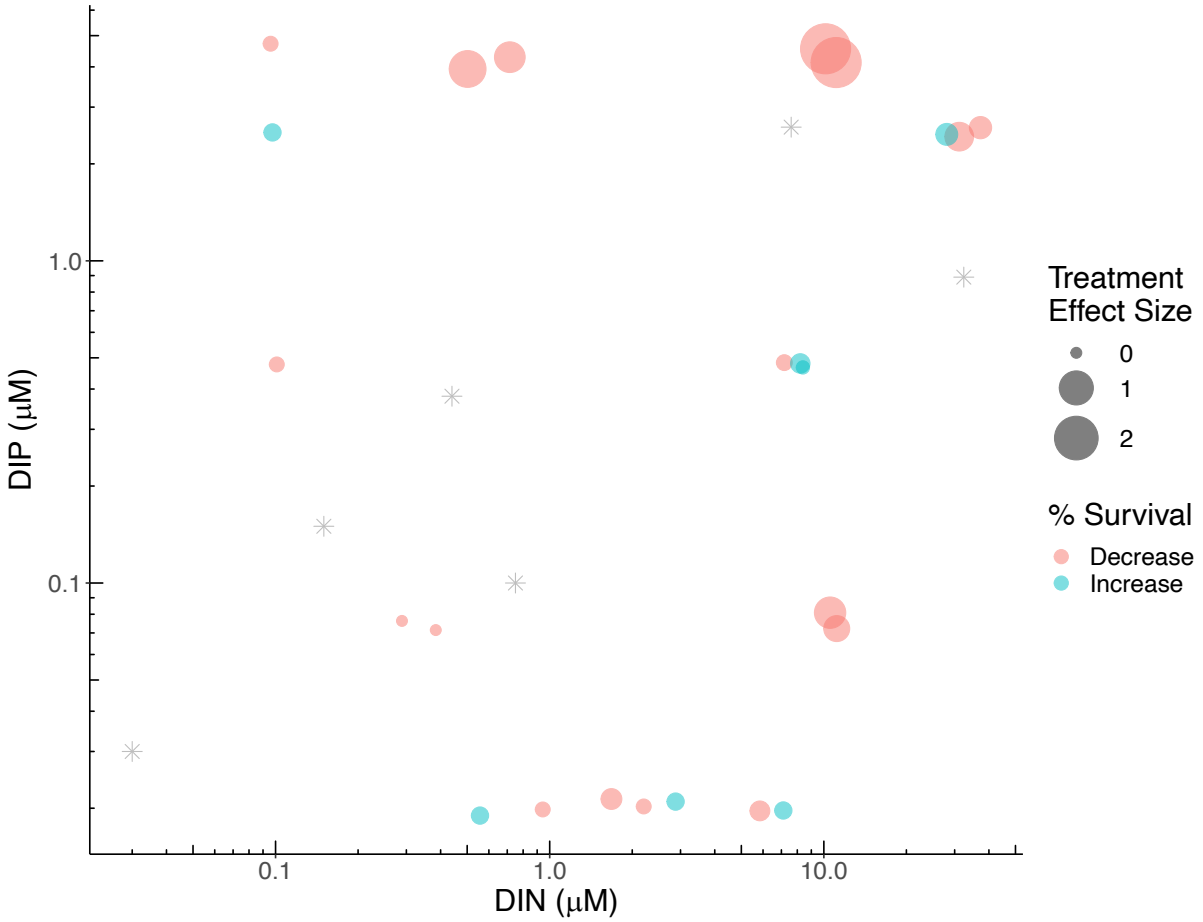

Figure 11.13. Effect sizes of DIN and DIP addition treatments on adult mortality (% survival) in corals. The size of the point refers to the log risk ratio between the treatment and the control in an experiment, and the color refers to whether the percent survival increased (teal) or decreased (red). The stars indicate ambient conditions measured in the field. See Fig. 10.1 for a complete description of reference data sources.

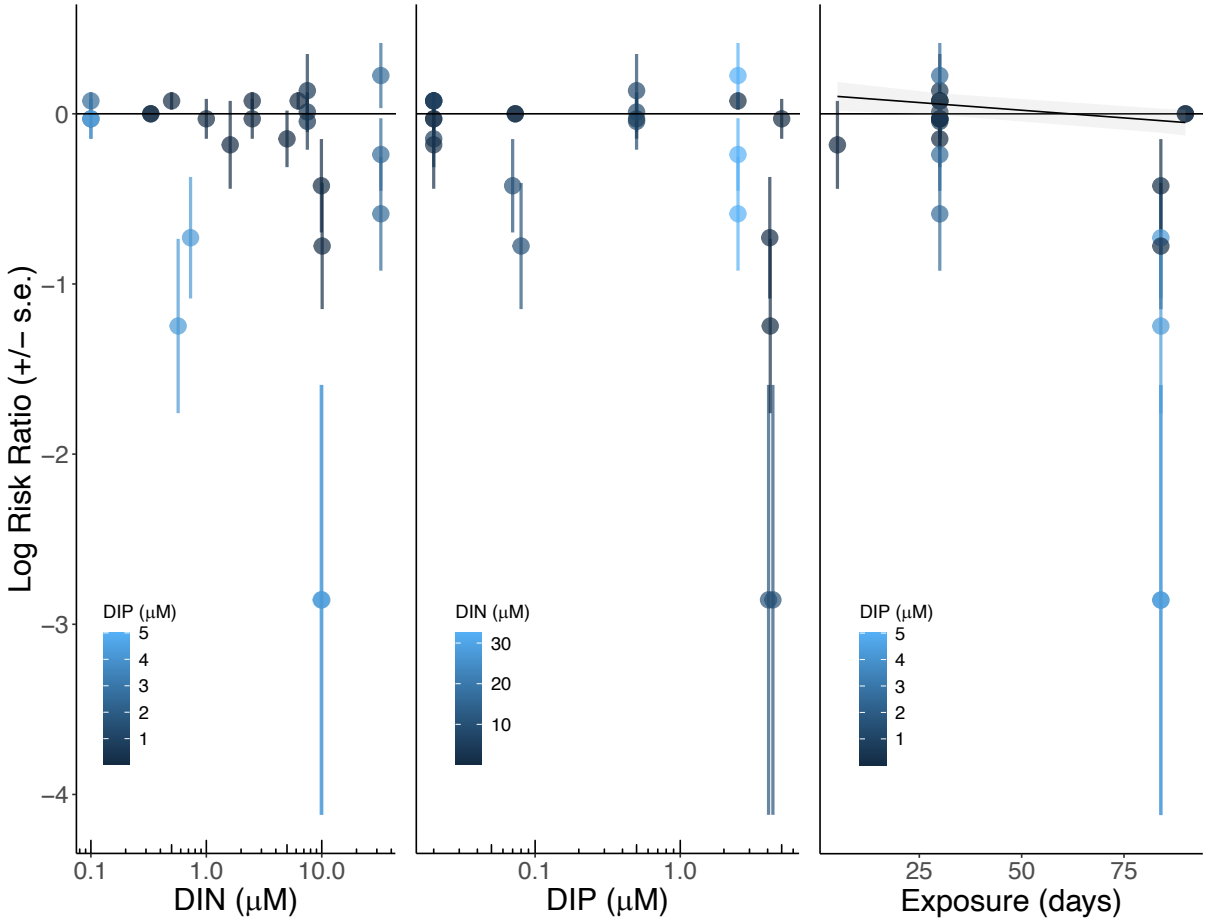

Figure 11.14. Effect size of nutrient (left: DIN, right: DIP) treatments on adult survival (%) in corals. Points indicate the log risk ratio ± the standard error for each treatment condition as compared to the control. The model predicted fit line and 95% confidence interval are included for each nutrient, with the other held constant at its median. Exposure duration in days was also held constant at its median. No predicted fit line indicates no significant relationship.

11.4.2 LARVAL SURVIVAL

Studies examined larval survival at a large range of DIN and DIP concentrations (up to ~100 µM) (Fig. 11.15). 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 ± SE: -0.005 ± 0.002) (Table S9; Fig. 11.16), 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. S1h), but no clear trend was seen based on taxonomic family or coral morphology (Figs. 2-3h).

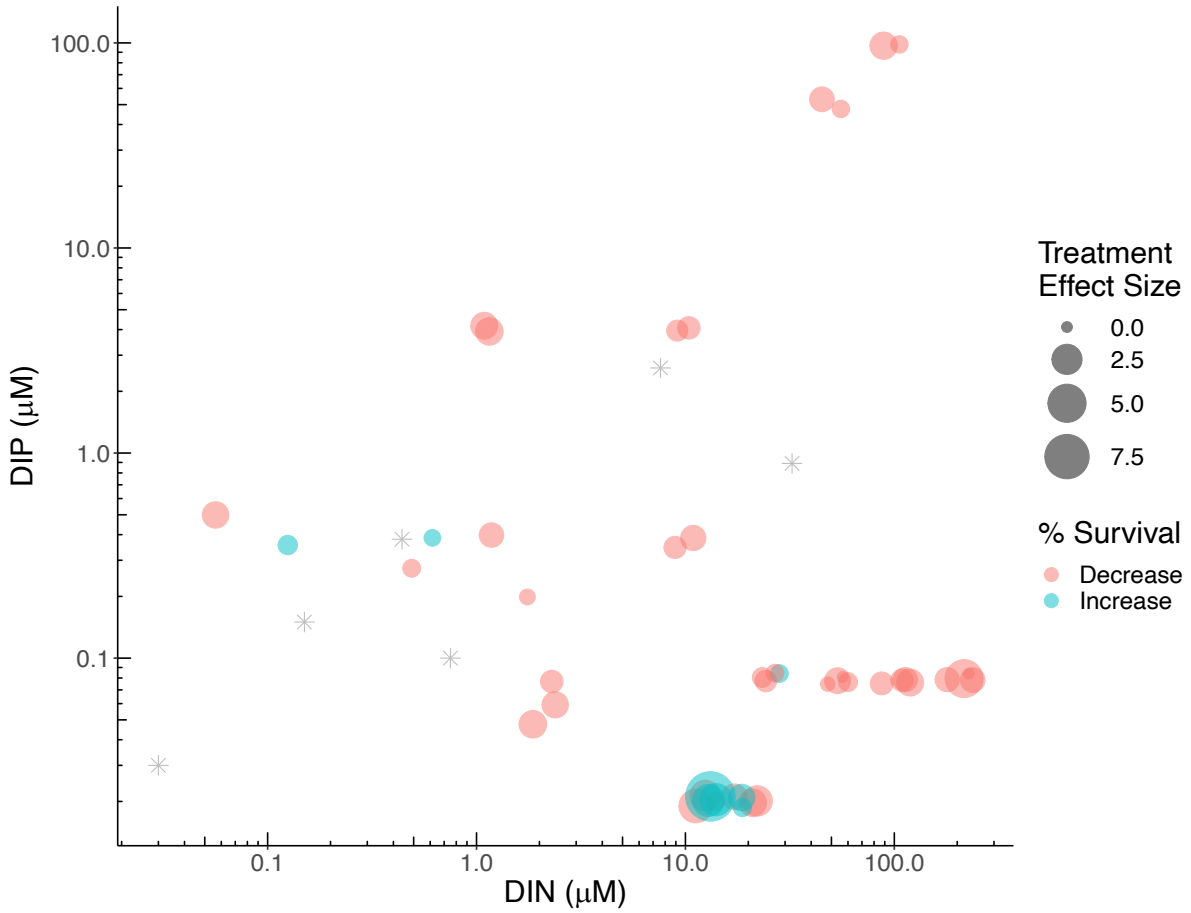

Figure 11.15. Effect sizes of DIN and DIP addition treatments on larval survival in corals. The size of the point refers to the standardized mean difference between the treatment and the control in an experiment, and the color refers to whether the percent survival increased (teal) or decreased (red). The stars indicate ambient conditions measured in the field. See Fig. 10.1 for a complete description of reference data sources.

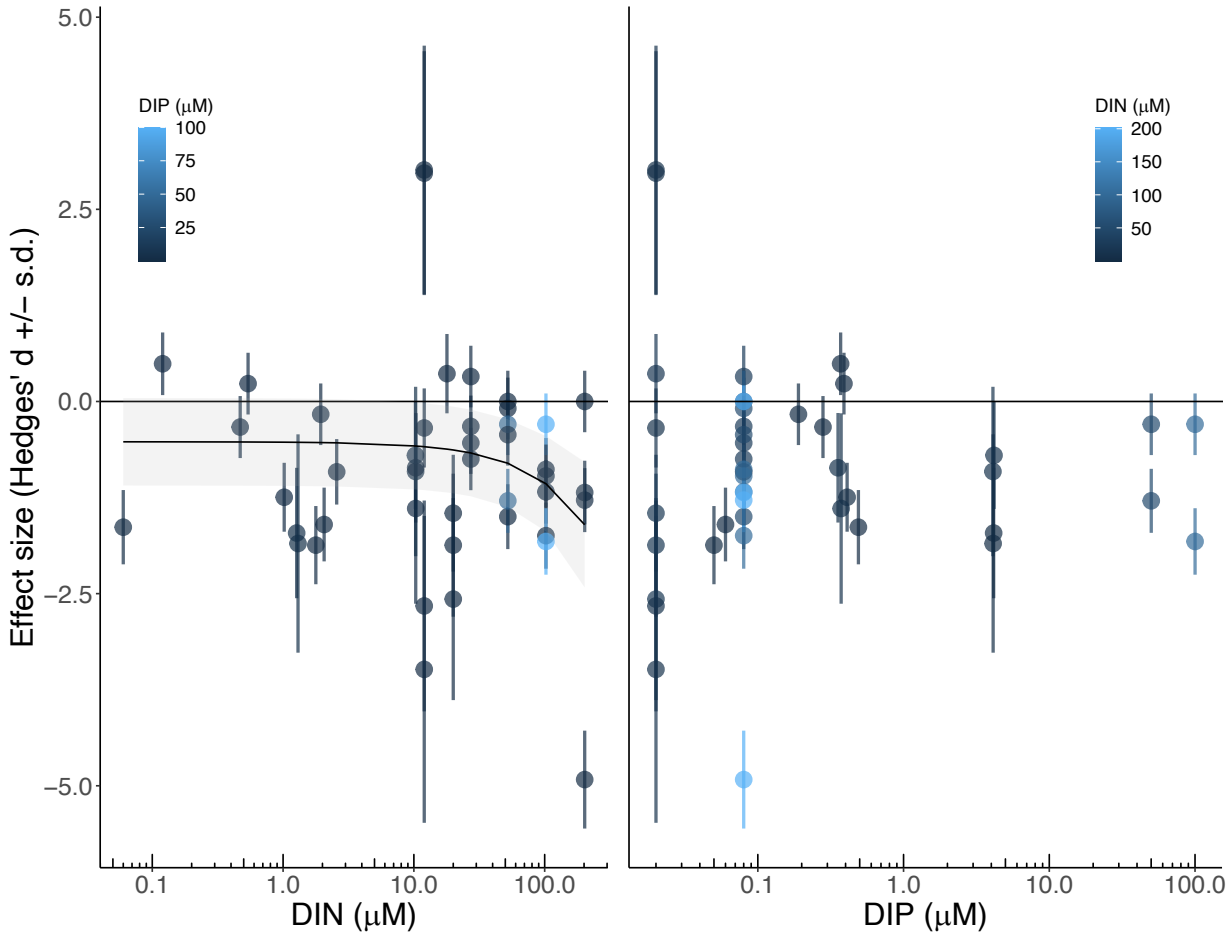

Figure 11.16. Effect size of nutrient (left: DIN, right: DIP) treatments on larval survival and settlement (%) in corals. Points indicate the log risk ratio ± the standard error for each treatment condition as compared to the control. The model predicted fit line and 95% confidence interval are included for DIN, with DIP held constant at its median. No predicted fit line indicates no significant relationship.

11.4.3 FERTILIZATION

Few studies examined the impacts of low, environmentally relevant nutrient concentrations on fertilization (Fig. 11.17). The effects of elevated nutrient concentrations were overwhelmingly negative, with the greatest negative effects occurring at low DIN (~1 µM) and higher DIP (> 1 µM). 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 ± 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. 11.18). 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. S1i). 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. S2-3i).

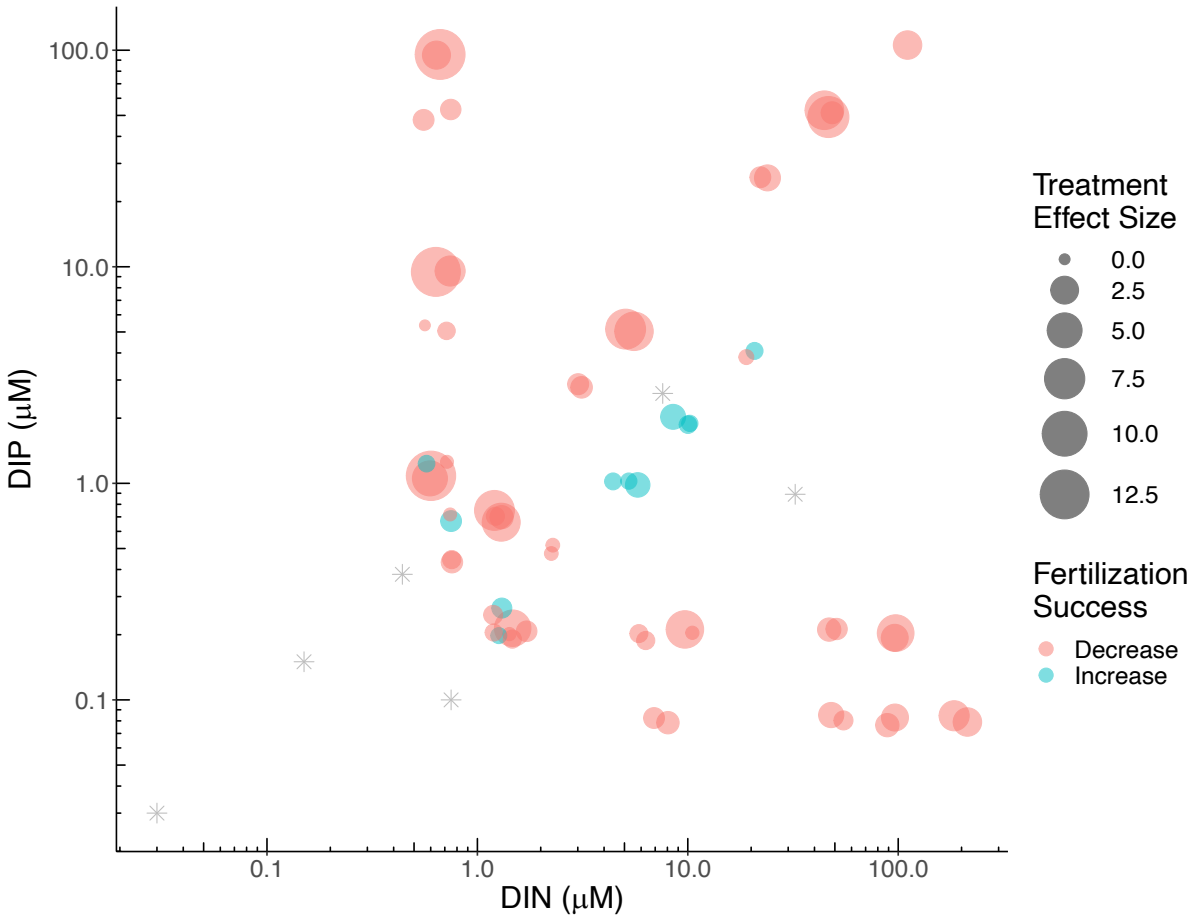

Figure 11.17. Effect sizes of DIN and DIP addition treatments on fertilization success (% fertilized) in corals. The size of the point refers to the standardized mean difference between the treatment and the control in an experiment, and the color refers to whether the percent fertilization increased (teal) or decreased (red). The stars indicate ambient conditions measured in the field. See Fig. 10.1 for a complete description of reference data sources.

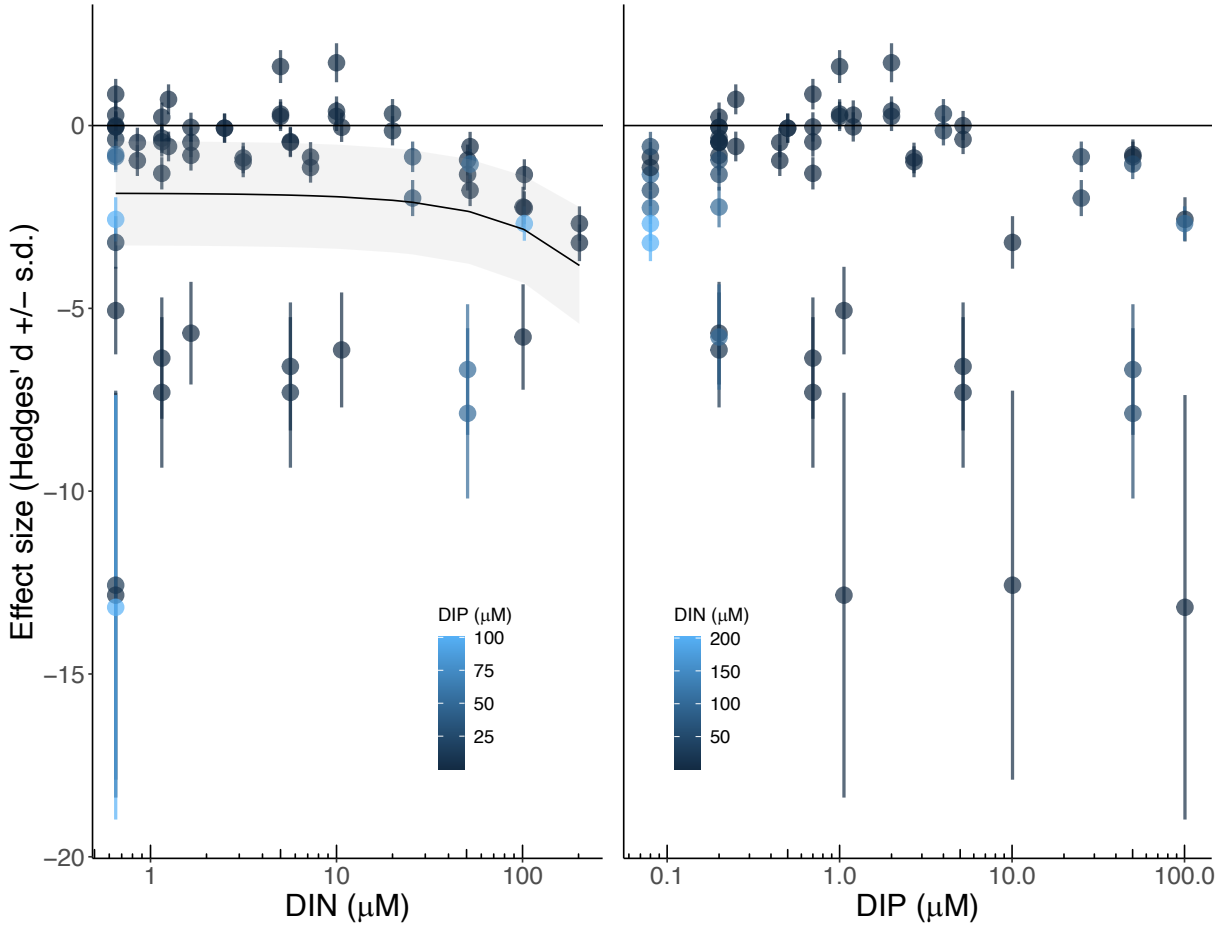

Figure 11.18. Effect size of nutrient (left: DIN, right: DIP) treatments on fertilization (%) in corals. Points indicate the log risk ratio ± the standard error for each treatment condition as compared to the control. The model predicted fit line and 95% confidence interval are included for DIP, with DIN held constant at its median. No predicted fit line indicates no significant relationship.

12 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 negative effects were seen in coral responses to increasing DIN, including reduced growth and survival. 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. 12.1).

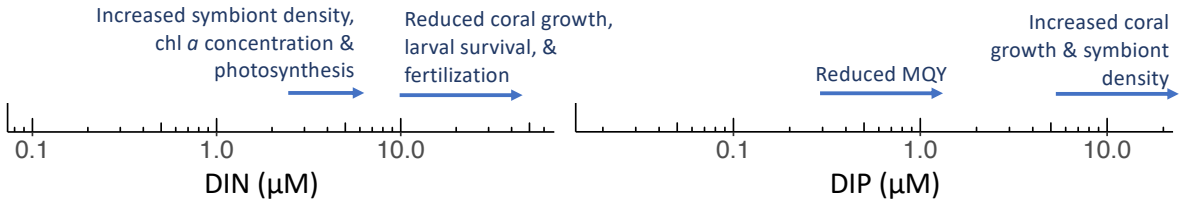

Figure 12.1. Responses associated with increasing nutrient (left: dissolved inorganic nitrogen, DIN and right: dissolved inorganic phosphorus, DIP) concentrations. Arrow locations and directions align with the concentration at which the effect becomes apparent. For reference, ambient concentrations referred to in this review ranged from 0.15 µM to 32.4 µM for DIN and from 0.1 µM to 2.6 µM for DIP (Fig. 10.1). MQY is maximum quantum yield, or photosynthetic efficiency (F_v/F_m).

12.1 SUMMARIZING KEY FINDINGS IN 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. 11.1). 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. 11.3). At higher DIN concentrations, chlorophyll *a* followed the same trend as zooxanthellae density (Fig. 11.4). The effect of DIN on chlorophyll *a* increased above 2 µM, peaking between 5-10 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. 11.6). Conversely, DIN had no clear effect on MQY, but DIP had a significant negative effect at the highest concentrations examined (Fig. 11.8).

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. 11.10), 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. 11.12), 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 3-5 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 1998a). At these same nutrient concentrations, zooxanthellae density and chlorophyll *a* 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).

12.2 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., Hawai'i: <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. 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).

12.3 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 1998a) 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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14 SUPPLEMENTAL MATERIALS

14.1 SUPPLEMENTAL TEXT

Text S1. Full Search Terms.

The following search was run through each DSE listed in Tuttle et al (2020), and the number of results were recorded and saved as RIS (.ris) or Bibtex (.bib) files:

All ((nutrient* AND Acropora) OR (nutrient* AND Anacropora) OR (nutrient* AND Cantharellus) OR (nutrient* AND Dendrogyra) OR (nutrient* AND Euphyllia) OR (nutrient* AND Isopora) OR (nutrient* AND Montastraea) OR (nutrient* AND Montipora) OR (nutrient* AND Mycetophyllia) OR (nutrient* AND Orbicella) OR (nutrient* AND Pavona) OR (nutrient* AND Porites) OR (nutrient* AND Seriatopora) OR (nutrient* AND Siderastrea) OR (nutrient* AND Tubastraea) OR (nutrient* AND Alveopora) OR (nutrient* AND Astreopora) OR (nutrient* AND Favia) OR (nutrient* AND Favites) OR (nutrient* AND Goniastrea) OR (nutrient* AND Goniopora) OR (nutrient* AND Leptastrea) OR (nutrient* AND Leptoria) OR (nutrient* AND Lobophyllia) OR (nutrient* AND Millepora) OR (nutrient* AND Platygyra) OR (nutrient* AND Pocillopora) OR (nutrient* AND Turbinaria) OR (nutrient* AND coral) OR (enrich* AND coral) OR (eutroph* AND coral) OR ("phase shift*" AND coral) OR ("bottom up" AND coral) OR (nutrif* AND coral) OR (bloom* AND coral) OR ("harmful algal bloom" AND coral) OR (phosphorus AND coral) OR (groundwater AND coral) OR ("DIN" AND coral) OR ("DIP" AND coral) OR (fertiliz* AND coral) OR (fertilis* AND coral) OR (cesspool* AND coral) OR (sewage AND coral) OR (septic AND coral) OR (OSDS AND coral) OR (ammoni* AND coral) OR (discharg* AND coral) OR (upwelling AND coral) OR (nitr* AND coral))

Text S2. PECO Eligibility Criteria adapted from Tuttle et al. (2020):

Population: All life stages of all shallow (photic zone, ≤80 m depth) scleractinian coral genera in all warm-water ocean basins (20°–30 °C).

Exposure: Exposure to dissolved inorganic nitrogen and dissolved inorganic phosphorus, including experimental application in both short- and long-term exposures in the laboratory.

Comparison: Coral samples experimentally compared to nutrients were compared to appropriate control samples.

Outcome(s): Endpoints that were included were physiological, physical, behavioral, developmental, and ecological. These included but were not limited to fertilization, larval survival, adult survival, growth, calcification, maximum photosynthetic efficiency, photosynthetic rate, chlorophyll *a* concentration, and zooxanthellae density. Outcomes were either binary or continuous variables.

Text S3. Complete List of Studies.

A list of all studies that were included in the analyses is available on GitHub:
https://github.com/enalley/nutrient_thresholds/blob/main/NutrientsS3_IncludedStudies.xlsx

Text S4. Observational Studies.

A list of all the full texts that were reviewed is available on GitHub:
https://github.com/enalley/nutrient_thresholds/blob/main/NutrientsS4_ReviewedStudies.xlsx

14.2 SUPPLEMENTAL TABLES

Supplemental Table 1. Search specifications for each database or search engine, reprinted from Nalley et al. (2021).

DSE Category	DSE Name (Abbreviation)	DSE Scope	Search specification(s)	Search dates
Bibliographic databases:	1) *Web of Science* (WoS)*, All Databases*	General science	Topic (titles, authors, abstracts, keywords); 'All Databases' include: (a) WoS Core Collection (SCI-EXPANDED, ESCI), (b) Biological Abstracts, (c) SciELO Citation Index, & (d) Zoological Record	All years (1950 - present)
	2) *JSTOR*	General academic	Abstract, All content	Any time
	3) *Aquatic Sciences and Fisheries Abstracts* (ASFA)	Aquatic and marine science	Abstract	Any time
	4) *Dissertations & Theses Global* (PQDT)	Global dissertations and theses	Abstract	Any time
Organizational databases:	5) *James Cook University One Search* (JCU)	Australian University dissertations and theses	Abstract, Dissertation/Thesis	Any time
	6) *ReefBase*	Proceedings of the International Coral Reef Symposium	Title; also Keywords for taxon-specific search terms	Any time
	7) *Science.gov*	United States federal government science	Full record (no 'Abstract' option)	Any time
	8) *Great Barrier Reef Marine Park Authority (GBRMPA) Elibrary*	Australian federal government science	All of ELibrary, Type = Report	Any time

Supplemental Table 2. Zooxanthellae density linear mixed-effects meta-regression model specifications, examining NO_3 (second order polynomial), NH_4, and DIP. Experiment was included as a random effect (I^2 = 68.3%%; Q = 221). Model components in italics were significant. DRMA-z is the Z-value for the dose-response meta-analysis.

Fixed Effect	P-value	Estimate (SE)	95% CI	DRMA-z
Intercept	*0.002*	*-0.84 (0.27)*	*-1.37, -0.30*	*-3.08*
log_{10} NO_3				
1	*<0.0001*	*1.91 (0.46)*	*1.00, 2.81*	*4.14*
2	0.08	*-0.45 (0.26)*	*-0.95, 0.06*	*-1.74*
log_{10} NH_4	*<0.0001*	*1.52 (0.18)*	*1.17, 1.87*	*8.46*
log_{10} DIP	*<0.0001*	*3.29 (0.58)*	*2.16, 4.42*	*5.71*

Supplemental Table 3. Chlorophyll *a* concentration linear mixed-effects meta-regression model specifications. Experiment was included as a random effect (I^2 = 43.3%; Q = 77.6). Model components in italics were significant.

Fixed Effect	P-value	Estimate (SE)	95% CI	DRMA-z
Intercept	0.66	0.14 (0.31)	-0.48, 0.75	0.44
log_{10} DIN	*0.0005*	*0.95 (0.27)*	*0.42, 1.48*	*3.50*
log_{10} DIP	0.997	-0.002 (0.60)	-1.17, 1.17	-0.004

Supplemental Table 4. Photosynthetic rate linear mixed-effects meta-regression model specifications. Experiment was included as a random effect (I^2 = 36.3%; Q = 31.4). Model components in italics were significant.

Fixed Effect	P-value	Estimate (SE)	95% CI	DRMA-z
Intercept	*0.004*	*-0.84 (0.29)*	*-1.41, -0.27*	*-2.90*
log_{10} NO_3	*<0.0001*	*1.84 (0.38)*	*1.10, 2.57*	*4.88*
log_{10} NH_4	0.73	-0.13 (0.37)	-0.85, 0.59	-0.35
log_{10} DIP	0.28	0.53 (0.50)	-0.44, 1.50	1.07

Supplemental Table 5. Photosynthetic efficiency linear mixed-effects meta-regression model specifications. Experiment was included as a random effect (I^2 = 72.5%; Q = 54.5). Model components in italics were significant.

Fixed Effect	P-value	Estimate (SE)	95% CI	DRMA-z
Intercept	*0.02*	*1.18 (0.52)*	*0.16, 2.20*	*2.26*
DIN	0.15	-0.01 (0.001)	-0.02, 0.003	-1.53
DIP	*<0.0001*	*-5.62 (1.01)*	*-7.60, -3.63*	*-5.55*

Supplemental Table 6. Growth linear mixed-effects meta-regression model specifications. Experiment was included as a random effect, and exposure duration was included as a fixed effect (I^2 0.0%; Q = 15.2). Model components in italics were significant.

Fixed Effect	P-value	Estimate (SE)	95% CI	DRMA-z
Intercept	*0.05*	*-0.39 (0.19)*	*-0.77, -0.004*	*-1.98*
DIN	*0.007*	*-0.01 (0.004)*	*-0.02, -0.003*	*-2.71*
DIP	*<0.001*	*0.16 (0.03)*	*0.10, 0.22*	*5.02*
Exposure Duration	*0.03*	*0.002 (0.0007)*	*0.0001, 0.003*	*2.14*

Supplemental Table 7. Calcification linear mixed-effects meta-regression model specifications. Experiment was included as a random effect (I^2 = 56.4%; Q = 91.7). Model components in italics were significant.

Fixed Effect	P-value	Estimate (SE)	95% CI	DRMA-z
Intercept	0.11	-0.53 (0.34)	-1.19, -0.13	-1.58
log_{10} DIN	0.10	-0.40 (0.24)	-0.88, 0.08	-1.64
log_{10} DIP	0.42	-0.49 (0.62)	-1.70, 0.71	-0.80

Supplemental Table 8. Adult survival linear mixed-effects meta-regression model specifications. Experiment was included as a random effect (I^2: 23.1%; Q = 26.0). Model components in italics were significant.

Fixed Effect	P-value	Estimate (SE)	95% CI	DRMA-z
Intercept	*0.01*	*0.17 (0.07)*	*0.04, 0.31*	*2.51*
log_{10} DIN	0.25	-0.07 (0.06)	-0.19, 0.05	-1.15
log_{10} DIP	0.25	-0.10 (0.08)	-0.26, 0.07	-1.14
Exposure Duration	*0.01*	*-0.002 (0.001)*	*-0.003, -0.0004*	*-2.58*

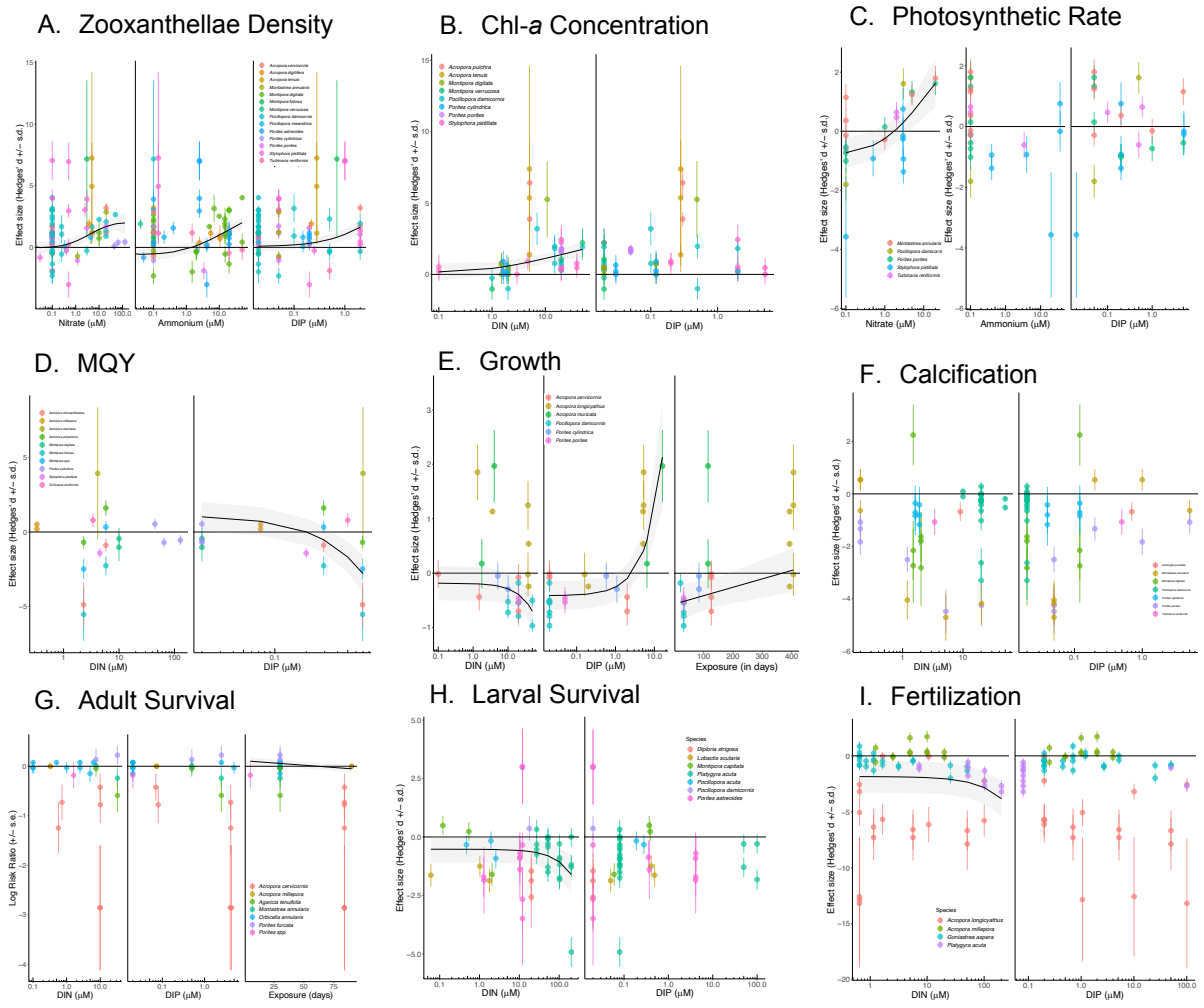
Supplemental Table 9. Larval survival linear mixed-effects meta-regression model specifications. Experiment was included as a random effect (I^2 = 61.1%; Q = 111). Model components in italics were significant.

Fixed Effect	P-value	Estimate (SE)	95% CI	DRMA-z
Intercept	0.07	-0.52 (0.29)	-1.09, 0.05	-1.80
DIN	*0.002*	*-0.005 (0.002)*	*-0.01, -0.002*	*-3.16*
DIP	0.48	-0.002 (0.003)	-0.01, 0.004	-0.71

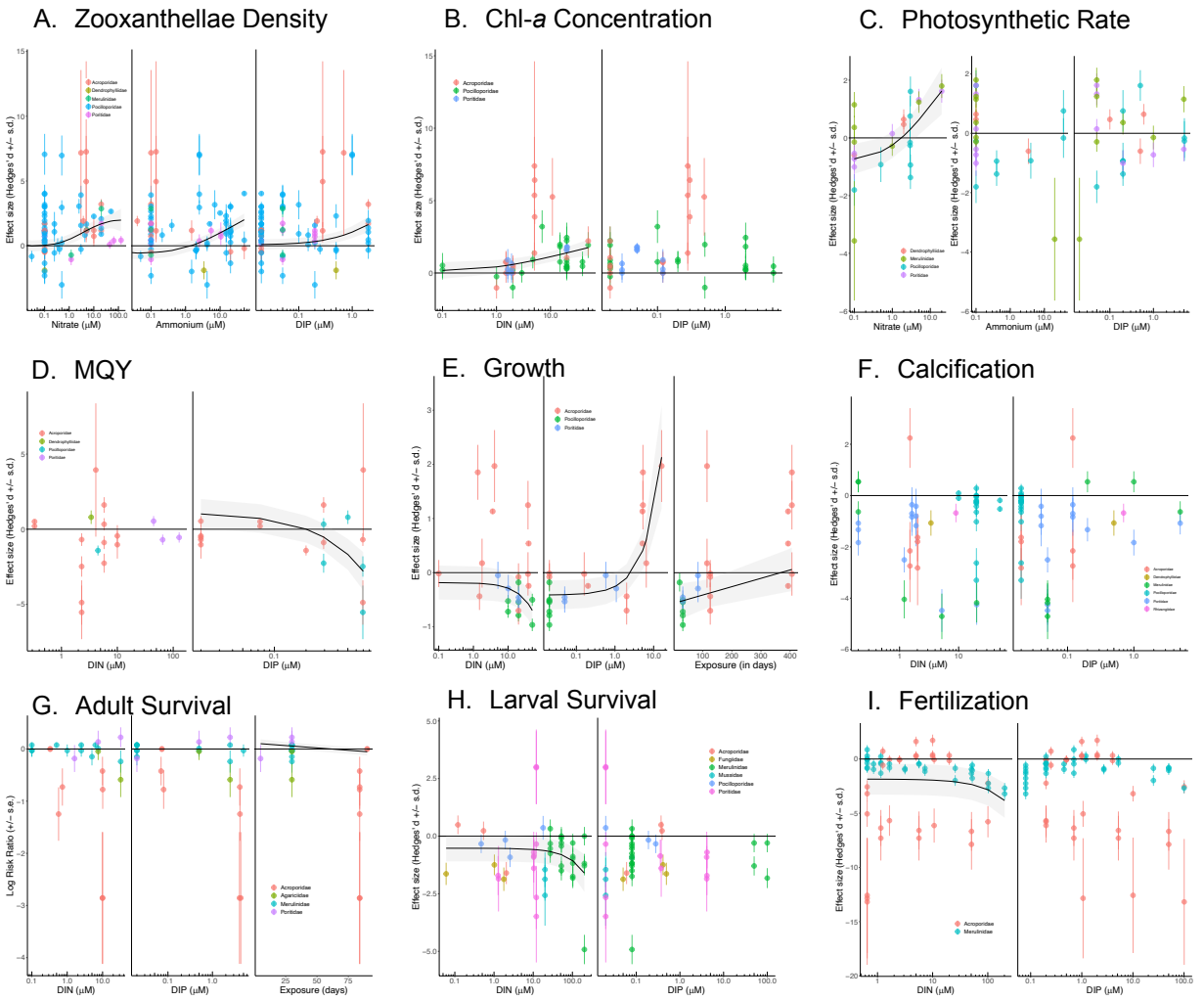
Supplemental Table 10. Fertilization linear mixed-effects meta-regression model specifications. Experiment and species were included as random effects (I^2 = 63.9%; Q = 169). Model components in italics were significant.

Fixed Effect	P-value	Estimate (SE)	95% CI	DRMA-z
Intercept	*0.01*	*-1.85 (0.73)*	*-3.27, -0.42*	*-2.54*
DIN	*<0.001*	*-0.01 (0.002)*	*-0.01, -0.01*	*-5.03*
DIP	0.31	-0.003 (0.003)	-0.01, 0.002	-1.02

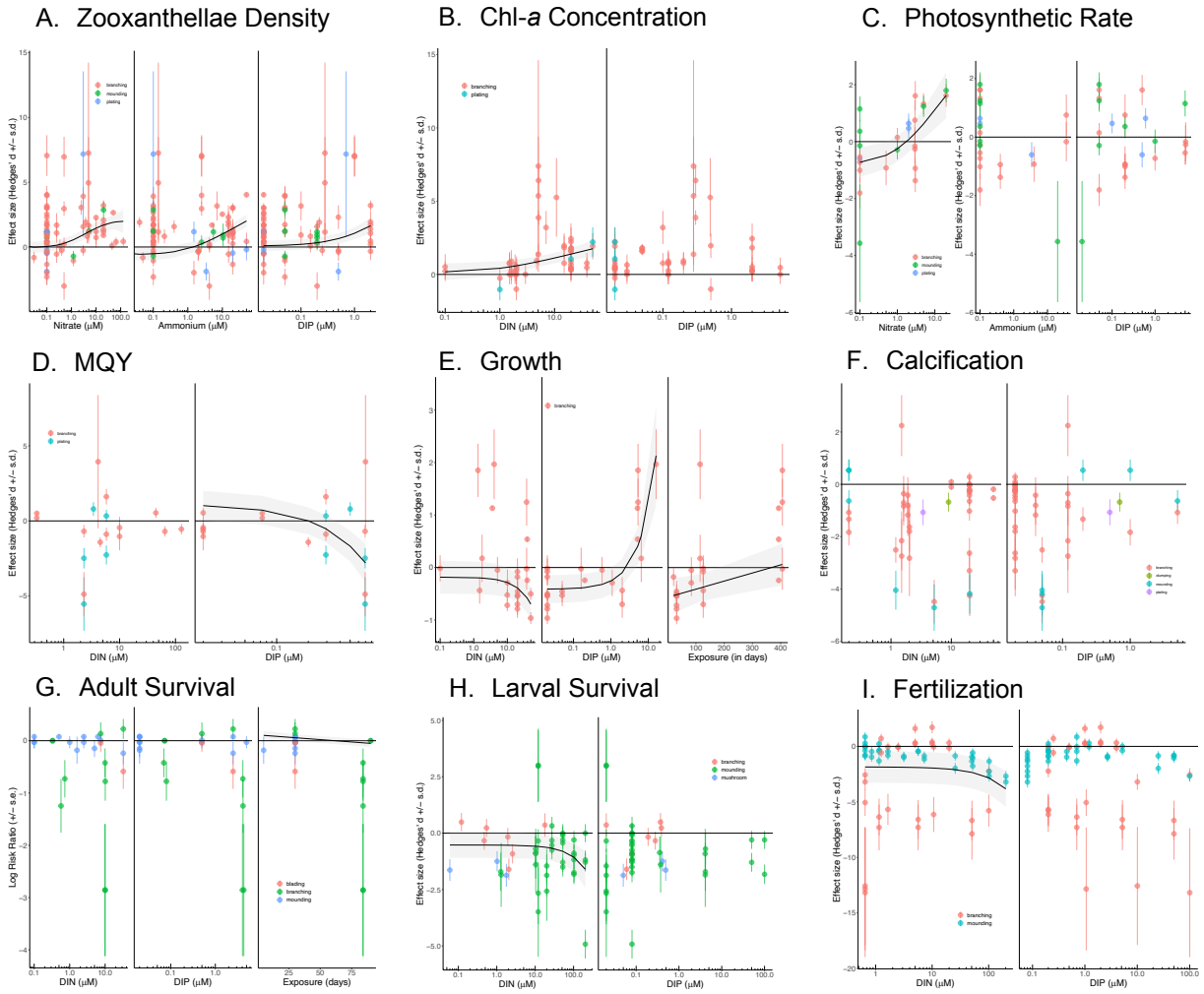
14.3 SUPPLEMENTAL FIGURES



Supplemental Figure 1. Effect size of (A) nitrate, ammonium, and DIP on zooxanthellae density (10^6 cells cm^{-2}) – n = 21 studies, (B) DIN and DIP on chl-a concentration (µg Chl a cm^{-2}) – 12 studies, (C) nitrate, ammonium, and DIP on the photosynthetic rate (µmol O_2 cm^{-2} day^{-1}) – 9 studies, (D) DIN and DIP on the MQY (F_v/F_m) – 7 studies, (E) DIN and DIP on growth (mm day^{-1}) – 6 studies, (F) DIN and DIP on calcification (mg $CaCO_3$ cm^{-2} day^{-1}) – 7 studies, (G) DIN and DIP on adult tissue and colony survival (% survival) – 5 studies, (H) DIN and DIP on larval survival and settlement (% survival - note two points with large vmd were removed for clarity) – 3 studies, and (I) DIN and DIP on fertilization success (%) – 6 studies. Points are colored by species. Statistically significant model results (relationships between the nutrient and effect size) are shown as lines and gray shaded area (mean ± 95% CI). The absence of a line indicates that there was no statistically significant relationship between nutrient addition and the effect size.



Supplemental Figure 2. Effect size of (A) nitrate, ammonium and DIP on zooxanthellae density(10^6 cells cm^{-2}) - 21 studies, (B) DIN and DIP on chl-a concentration (µg Chl a cm^{-2}) – 12 studies, (C) nitrate, ammonium, and DIP on the photosynthetic rate (µmol O_2 cm^{-2} day^{-1}) – 9 studies, (D) DIN and DIP on the MQY (F_v/F_m) – 7 studies, (E) DIN and DIP on growth (mm day^{-1}) – 6 studies, (F) DIN and DIP on calcification (mg $CaCO_3$ cm^{-2} day^{-1}) – 7 studies, (G) DIN and DIP on adult tissue and colony survival (% survival) – 5 studies, (H) DIN and DIP on larval survival and settlement (% survival - note two points with large vmd were removed for clarity) – 3 studies, and (I) DIN and DIP on fertilization success (%) – 6 studies. Points are colored by taxonomic family. Statistically significant model results (relationships between the nutrient and effect size) are shown as lines and gray shaded area (mean ± 95% CI). The absence of a line indicates that there was no statistically significant relationship between nutrient addition and the effect size.



Supplemental Figure 3. Effect size of (A) nitrate, ammonium and DIP on zooxanthellae density(10^6 cells cm^{-2}) - 21 studies, (B) DIN and DIP on chl-a concentration (µg Chl a cm^{-2}) – 12 studies, (C) nitrate, ammonium, and DIP on the photosynthetic rate (µmol O_2 cm^{-2} day^{-1}) – 9 studies, (D) DIN and DIP on the MQY (F_v/F_m) – 7 studies, (E) DIN and DIP on growth (mm day^{-1}) – 6 studies, (F) DIN and DIP on calcification (mg $CaCO_3$ cm^{-2} day^{-1}) – 7 studies, (G) DIN and DIP on adult tissue and colony survival (% survival) – 5 studies, (H) DIN and DIP on larval survival and settlement (% survival – note two points with large vmd were removed for clarity) – 3 studies, and (I) DIN and DIP on fertilization success (%) – 6 studies. Points are colored by coral morphology Statistically significant model results (relationships between the nutrient and effect size) are shown as lines and gray shaded area (mean ± 95% CI). The absence of a line indicates that there was no statistically significant relationship between nutrient addition and the effect size.