

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

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1 **ABSTRACT**

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

21

22 **KEY WORDS**

23 Land-based sources of pollution; resource management; mixed-effects meta-regression; evidence
24 synthesis

25

26 **1. INTRODUCTION**

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

45 experimental studies that quantify the effects of DIN (nitrate and ammonium) and DIP
46 (phosphate) on coral and coral-endosymbiont health.

47 Elevated nutrients on coral reefs can result from surface run-off, submarine groundwater
48 discharge, sewage discharge, aquaculture, or natural sources such as bird colonies or fish (Wear
49 and Thurber 2015, Graham et al. 2018, Otero et al. 2018, Adam et al. 2021), and different
50 sources have different characteristics. Natural sources tend to deliver ammonium, which is
51 highly bioavailable, while anthropogenic sources tend to introduce nitrate (Shantz and Burkepile
52 2014, Morris et al. 2019), which is less bioavailable and can lead to increased stress responses in
53 corals (Fernandes de Barros Marangoni et al. 2020, Burkepile et al. 2020). Phosphate may be
54 derived from natural and anthropogenic sources (Fernandes de Barros Marangoni et al. 2020),
55 but the relative anthropogenic addition of phosphate has lagged far behind that of nitrate (Vilmin
56 et al. 2018, Zhao et al. 2021). This unbalanced supply of nutrients in turn can negatively impact
57 biological functions in marine organisms (Wiedenmann et al. 2013, Ezzat et al. 2015, Morris et
58 al. 2019).

59 The effects of nutrient enrichment on corals can vary by life stage, taxonomy, and
60 nutrient type (D'Angelo and Wiedenmann 2014, Morris et al. 2019). Elevated nutrients may
61 increase the abundance of zooxanthellae, positively affecting photosynthetic function, but
62 beyond an optimal concentration, defined by Morris et al. (2019) as $1-3 \times 10^6$ cells cm^{-2} ,
63 overcrowding may occur and lead to negative outcomes such as shading, increased holobiont
64 temperature, and oxidative stress. In these cases, the addition of nutrients may result in a positive
65 response up to a point, beyond which the response may become negative (Tomascik and Sander
66 1985, Shantz and Burkepile 2014). A variety of negative growth-related responses have also
67 been reported in corals exposed to elevated nitrate and phosphate concentrations, including

68 decreased growth (Marubini and Davies 1996), decreased calcification (Silbiger et al. 2018), and
69 decreased skeletal density (Dunn et al. 2012). However, some studies have found either no direct
70 effects of ammonium and phosphate enrichment (Stambler et al. 1991) or positive responses,
71 such as increased growth rate (Koop et al. 2001).

72 The effects of DIN and DIP enrichment on coral larvae and juveniles have remained
73 relatively under-studied as compared to adults (Fabricius 2005, Humanes et al. 2016). Existing
74 data suggest that coral gametes and larvae are more sensitive to elevated concentrations of
75 ammonium (e.g., 1 μM) and phosphate (e.g., 0.1 μM) than adults, with responses including
76 reduced fertilization, abnormal embryo development, and reduced larval settlement (Wittenberg
77 and Hunte 1992, Fabricius 2005). Response to elevated nutrient concentrations also varies by
78 taxonomy, with differential and sometimes opposite effects observed among coral species in
79 nutrient enrichment experiments (Koop et al. 2001, Cox and Ward 2002, Kitchen et al. 2020).
80 This variability may be attributable to morphological differences, a variety of symbiont clades,
81 or other differences in adaptive capacity. Additionally, while the specific mechanisms are
82 complex, clear shifts in the composition of coral communities along water quality gradients have
83 been demonstrated (Tomascik and Sander 1987, Fabricius 2005, Fabricius et al. 2005, Oliver et
84 al. 2019).

85 It is clear that the magnitude and type of coral response depends on the species of nutrient
86 under enrichment (e.g. nitrate NO_3^- , ammonium NH_4^+ , or phosphate PO_4^{3-}); a 2014 meta-
87 analysis found that nitrogen enrichment reduced calcification but enhanced photosynthetic rate
88 on average, while phosphorus enrichment increased calcification and had little effect on
89 photosynthesis (Shantz and Burkepile 2014). Increased ammonium levels may mitigate the
90 adverse effects of heat stress by moderating the loss of endosymbionts (Zhou et al. 2017), and

91 corals experiencing temperature anomalies simultaneously with eutrophication can maintain
92 healthy zooxanthellae in their deeper tissues (Riegl et al. 2019), but may be more vulnerable to
93 disease (Caldwell et al. 2016, Aeby et al. 2020). Conversely, nitrate, has been linked to an
94 increased prevalence and duration of bleaching in corals experiencing temperature stress
95 (Burkpile et al. 2020), and corals that are acclimatized to high-nutrient conditions demonstrate a
96 greater propensity towards bleaching (Wooldridge and Done 2009). Adding an additional layer
97 of complexity, past research has found that coral response can depend not only on the type and
98 absolute concentration of nutrients, but also on the stoichiometric ratio of nitrogen to phosphorus
99 (Morris et al. 2019, Zhao et al. 2021).

100 Coral reefs exist across a wide range of dissolved nutrient concentrations, and this
101 variation in ambient conditions is critical context for experimental manipulation of nutrients
102 (Szmant 2002, D'Angelo and Wiedenmann 2014). For reference, we include reported ambient
103 nutrient concentrations on coral reefs in Hawai'i, Malaysia, and Australia, ranging from 0.1-0.38
104 μM DIP and 0.15 - 0.44 μM DIN (Fabricius et al. 2013, Nakajima et al. 2015, Silbiger et al.
105 2018). These ambient values are well below the elevated nutrient levels in experimental studies
106 (ranging from 0.06 - 202 μM DIN and 0.02 to 101 μM DIP in the studies included here),
107 however within-reef variation in dissolved inorganic nutrients can be high. Hawaiian reefs
108 receiving submarine groundwater discharge from an urbanized watershed had nutrient
109 concentrations ranging from 0.02 – 32.39 μM DIN and 0.04 – 0.89 μM DIP across the reef
110 (Lubarsky et al. 2018). Natural variation can be similarly high on remote atolls; for example soil
111 in forests preferred by seabirds on Palmyra had nitrate concentrations that were more than twelve
112 times higher than those in less preferred habitat, which can result in elevated DIN on adjacent
113 reefs (Young et al. 2010). Further information on reference values is detailed in Figure S1.

114 Our study builds on a set of previous reviews that addressed the complex relationship
115 between nutrients and coral physiology and identified gaps for future research. Woods et al.
116 (2016) also used a meta-analysis to examine the effects of DIN/DIP on a fertilization success,
117 and Shantz and Burkepile (2014) used meta-analysis to assess broad trends in the effects of
118 elevated nitrogen and phosphorus on effect size (coral growth, calcification, and photobiology).
119 These studies identified a need for more experiments that incorporate a wider range of nutrient
120 concentrations to assess nonlinear responses and generate thresholds that can be used for
121 management. More experiments now exist to analyze these non-linearities, so we conducted
122 meta-regressions that quantify the shapes of the relationships between effect sizes (coral
123 response) and nutrient concentration. Foundational reviews (Szmant 2002, Fabricius 2005) have
124 been built upon by more recent reviews (D'Angelo and Wiedenmann 2014, Morris et al. 2019,
125 Zhao et al. 2021) that offer conceptual, mechanistic explanations of the direct and indirect effects
126 of nutrients on corals, but these studies also call for additional quantitative analyses of the
127 relationships between nutrients and coral responses. Our synthetic approach provides
128 quantitative support for these conceptual models and addresses important data gaps by using a
129 systematic review paired with mixed-effects meta-regression meta-analysis that focuses on the
130 interaction between DIN and DIP and identifies inflection points for these nutrients' effect sizes
131 on several coral physiological responses. Our meta-analysis of 47 studies thus represents decades
132 of intensive research and quantifies many of the mechanistic complexities underlying the effects
133 of local nutrient stressors on coral reefs.

134

135 **2. METHODS**

136 **2.1 Systematic Literature Review**

137 The approach used in this study followed that described previously in Tuttle et al. (2020),
138 Tuttle & Donahue (2020, 2022), and Nalley et al. (2021). We first identified reviews that
139 addressed the impacts of nutrients on reefs and on scleractinian corals (Szmant 2002, Fabricius
140 2005, D'Angelo and Wiedenmann 2014, Shantz and Burkepile 2014, Morris et al. 2019, Houk et
141 al. 2020, Zhao et al. 2021). Using these reviews to build a conceptual framework, we developed
142 a systematic search of peer-reviewed studies, public reports, and gray literature. This required the
143 compilation of an exhaustive list of terminology associated with nutrients, nutrient pollution,
144 corals, and various coral taxa of concern (see below). This list was optimized into a series of
145 search terms using the Web of Science format ([search term]* AND coral), which includes a
146 wildcard (*) and Boolean operator (AND), which were in turn combined into a composite search
147 term (Text S1). The composite search term was used to query eight databases and search engines
148 (Table S1), which are justified and described in Tuttle et al. (2020).

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

158 Bibtex and RIS files generated in the search were imported to a reference manager
159 (Mendeley Reference Manager 2020) where duplicates were removed, and unique citations (n =

160 10,911) were imported into Abstrackr, which was used for screening search results (Abstrackr
161 2020). Following the completion of a training set of reviews and discussion, which confirmed
162 consistency among review decisions, at least two reviewers screened each abstract and
163 determined whether it met the criteria for inclusion in this study based on the research questions
164 (n = 375). If the two reviewers did not agree, a third reviewer resolved the decision of whether a
165 study was relevant. Sources that were deemed relevant at the title-abstract screening stage were
166 further screened for eligibility using the PECO framework (population, exposure, comparison,
167 outcome; Text S2) (Morgan et al. 2018). Full texts that passed this stage of review (n = 93) were
168 then assessed a final time for comparability among studies of response measurement units (n =
169 47). This subset of comparable studies was then used for the final meta-analysis. It is important
170 to note that the primary focus of this meta-analysis was on manipulative experimental studies
171 rather than observational studies, which means that most of the included studies were conducted
172 in experimental tanks (see Text S2 for greater detail on selection criteria). Only 4 of the included
173 47 studies were field studies which focused on growth (3 studies), adult survival (1 study),
174 chlorophyll-*a* concentrations (1 study), and photosynthetic rate (1 study). A complete list of
175 studies included is provided in the Supplemental Materials (Text S3).

176

177 **2.2 Data Extraction**

178 A suite of information was collected from each study including the species studied,
179 collection site, experimental location, experimental parameters, nutrient concentrations
180 (ambient/control and experimentally added), and duration of study. If data were presented in
181 figures or graphs, they were extracted using Web Plot Digitizer to obtain quantitative values
182 (Rohatgi 2017). Response measurements were converted to a common unit when possible to

183 increase the number of studies using comparable metrics, which in turn increased meta-analytical
184 power. We considered the number of studies (i.e., articles) studying a particular response, as well
185 as the number of distinct experiments, where experiment is defined as a unique set of control-to-
186 treatment comparisons. This was done because a single study/article may contain multiple
187 unique experiments. Responses measured in fewer than three independent articles were not
188 included in the meta-analyses. If a minimum concentration of DIN or DIP was not reported (e.g.,
189 stated that it was below the detection limit), 0.1 μM and 0.02 μM were added as the minimum
190 treatment concentrations, respectively, which are conservative estimates based on the studies
191 included in this review (e.g., Marubini and Thake 1999).

192

193 **2.3 Analysis**

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

206 Eggs that are not successfully fertilized will not produce zygotes that develop into larvae and
207 eventually, adult reef-building corals. Hypotheses were developed to describe the nature of the
208 relationship between nutrients and responses, based on ecological processes and characteristics
209 (Table 1).

210 All analyses in this study were completed using R statistical software (R Core Team
211 2020). Effect sizes were generated for each experiment (i.e., treatments compared to a control)
212 using the *dosresmeta* package, which generates a standardized difference in mean (Hedges' *d*),
213 corresponding variances, and covariance matrices (Crippa and Orsini 2016). This value is
214 unaffected by unequal sample variances between treatments and controls, and it also corrects for
215 small sample sizes (Tuttle and Donahue 2020). For adult mortality, which tends to be measured
216 in binary terms (i.e., dead or alive), a risk-ratio was used to generate effect sizes for meta-
217 analyses; to ensure centering around zero and asymptotic normality, the natural log of the risk
218 ratio (i.e., log risk-ratio) and standard error of the log risk-ratio were used (Harrer et al. 2021).
219 The formulas used to generate the standardized effect sizes (Hedge's *d* and log risk-ratio) are
220 provided in the Supplemental Materials (Text S4). For all responses, concentrations of different
221 species of dissolved inorganic nitrogen were combined and considered together as one
222 concentration (DIN); for photosynthetic responses, ammonium and nitrate were considered
223 separately. The effects of DIN and DIP were treated as independent fixed effects for a given
224 response using an effect size that refers to the magnitude of the standardized difference in mean
225 of the response in treatment conditions from that of the control in the same experiment.

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

229 **Equation 1.** *Response Effect Size* \sim *DIN + DIP + random effects*

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

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

247 The exposure concentrations extracted in these analyses were compared to reference
248 concentrations of DIN and DIP. Ambient DIN and DIP concentrations were used from four
249 locations. The Hawai'i Ocean Timeseries reports open ocean surface concentrations of 0.03 μ M
250 for DIN and 0.03 μ M for DIP (Fujieki et al. 2021). Ambient concentrations of 0.75 μ M DIN and
251 0.1 μ M DIP were reported from a reef in Malaysia (Nakajima et al. 2015), and ambient

252 concentrations of 0.15 μM DIN and 0.15 μM DIP were used for an experiment simulating
253 conditions in Hawai'i (Silbiger et al. 2018). High ambient values were also reported from
254 Australia at 0.44 μM DIN and 0.38 μM DIP (Fabricius et al. 2013). Very high values at sites
255 with known impacts were also included for reference, where DIN was as high as 32.4 μM
256 (Lubarsky et al. 2018), and DIP was 2.6 μM (Silbiger et al. 2018). These points are included for
257 reference in plots for each coral response effect size and the corresponding exposure
258 concentrations. An annotated reference is provided in the Supplemental Materials (Fig. S1).

259

260 **3. RESULTS**

261 Meta-analyses were conducted for the following responses: zooxanthellae density,
262 chlorophyll *a* concentration, photosynthetic rate, maximum photosynthetic efficiency (F_v/F_m),
263 growth rate, calcification, adult survival, larval survival, and fertilization. The number of studies
264 and experiments within study included in each analysis are outlined in Table 2, along with the
265 range of exposure concentrations and the duration of treatment exposure. Model results for all
266 responses are summarized in Table 3.

267

268 **3.1 Photosynthetic Responses of the Coral Endosymbiont**

269 *Zooxanthellae Density:* Looking at general trends in the effect of DIN and DIP on
270 zooxanthellae density, the largest increases occurred at concentrations between 1-10 μM DIN
271 and 0.1-1 μM DIP (Fig 1a). Zooxanthellae densities were most likely to exceed a physiologically
272 optimal concentration ($1-3 \times 10^6$ cells cm^{-2} ; Morris et al. 2019) at medium to high concentrations
273 of DIN ($>3 \mu\text{M}$). Decreases in zooxanthellae density were seen at very low DIN and DIP

274 concentrations, which may be indicative of nutrient limitation, as well as at very high DIN
275 concentrations when DIP is concurrently low (Fig. 1a).

276 Because of the known differences in nitrate and ammonium impacts on zooxanthellae,
277 NO₃ and NH₄ were modeled separately, rather than together as DIN. A linear mixed-effects
278 meta-regression with a second order polynomial for NO₃ was used in this meta-analysis because
279 of the biological mechanisms underlying the relationship between zooxanthellae density and
280 NO₃ (i.e., increased to a maximum concentration and then decreased). Zooxanthellae density
281 increased significantly with the addition of NO₃ ($P < 0.0001$; Fixed effect estimates \pm SE: $1.91 \pm$
282 0.46), NH₄ ($P < 0.0001$; Fixed effect estimates \pm SE: 1.52 ± 0.18), and DIP ($P < 0.0001$; Fixed
283 effect estimates \pm SE: 3.29 ± 0.58) (Fig. 2a; Table S2). The range of concentrations examined for
284 NO₃ (0-128 μ M) far exceeded those tested for NH₄ (0-50 μ M) or DIP (0-2 μ M), so the
285 comparable effects of NH₄ and DIP at very high concentrations cannot be determined from this
286 dataset. There were differences between experiments that remain unaccounted for by the model
287 ($I^2 = 68.3\%$; $Q = 221$), but model fit was not improved with the addition of coral species or
288 exposure duration as fixed effects. Clear taxonomic or morphological trends were not observed
289 in the response of symbiont density to nutrient addition (Figs. S2-4a).

290 ***Chl-a Concentration:*** At concentrations of DIN that are observed on coral reefs,
291 concentrations of chl-*a* increased, particularly above 5 μ M DIN (Fig. 1b). Negative effects were
292 only seen at low concentrations of DIN ($< 3 \mu$ M) and may be indicative of nutrient limitation. A
293 linear mixed-effects meta-regression was used, and ammonium and nitrate were analyzed
294 together as DIN. Analyzing them separately did not improve model fit. DIN concentrations had a
295 significant positive effect on chl-*a* ($P = 0.0005$; Fixed effect estimate \pm SE: 0.95 ± 0.27), but
296 there was no significant relationship with DIP ($P = 0.997$; Fig. 2b; Table S3). The model

297 explained most of the heterogeneity between experiments ($I^2 = 43.3\%$; $Q = 77.6$), and adding in
298 species or exposure duration as fixed effects did not improve model fit (Figs. S2-4b).

299 ***Photosynthetic Rate:*** The impacts of elevated DIN and DIP on photosynthetic rate were
300 less clear than those seen with zooxanthellae density or chl-*a* concentrations (Fig. 1c). The best
301 fit model was a linear mixed-effects meta-regression with NO_3 and NH_4 analyzed independently
302 (Table S4). NO_3 had a significant positive effect on the photosynthetic rate ($P < 0.0001$; Fixed
303 effect estimates \pm SE: 1.84 ± 0.38), but NH_4 and DIP had no significant effect ($P > 0.05$) (Fig.
304 2c). Species and exposure duration were not included in the best fit model, but most of the
305 heterogeneity between experiments was explained well by the model ($I^2 = 36.3\%$; $Q = 31.4$).
306 There were no clear trends in the data that were attributable to species, taxonomic family, or
307 coral morphology (Figs. S2-4c). One outlier point (Stambler 1998) showed a significant negative
308 effect of ammonium on the photosynthetic rate, but this point represents corals that were adapted
309 to ambient high light conditions being exposed to high light and ammonium simultaneously.
310 Other corals in this experiment that were exposed to lower light conditions, which are likely on
311 eutrophic reefs, in addition to high ammonium concentrations had far less response in the
312 photosynthetic rate.

313 ***Photosynthetic Efficiency (Maximum Quantum Yield, MQY):*** At concentrations of DIN
314 and DIP greater than $10 \mu\text{M}$ and $0.5 \mu\text{M}$, respectively, the MQY dropped below 0.5, indicating
315 reduced resilience. Few studies examined MQY in response to low nutrient treatments, so it is
316 not clear how MQY may be affected by nutrient limitation (Fig. 1d). The best fit model was a
317 linear mixed-effects meta-regression model (Table S5). NO_3 and NH_4 were analyzed together as
318 DIN, because analyzing them independently did not improve model fit. DIN had no significant
319 effect on MQY ($P = 0.15$) (Fig. 2d). DIP had a significant negative effect on the MQY ($P <$

320 0.001, Fixed effect estimate \pm SE: -5.61 ± 1.01). *Acropora microphthalma* and *A. polystoma*, in
321 particular followed this trend (Fig. S2d), but including species in the model led to overfitting.
322 Most of the taxa examined were Acroporids, so there were no clear trends in response by
323 taxonomic family or morphology (Figs. S3-4d). There was considerable heterogeneity between
324 studies that was still unexplained by the best fit model ($I^2 = 72.5\%$; $Q = 54.5$), which may be
325 attributable to the relatively few studies that were available for MQY as compared to some other
326 responses.

327

328 **3.2 Coral Growth and Calcification**

329 **Growth:** Growth was measured as linear extension (mm day^{-1}). Increased growth only
330 occurred when the relative concentration of DIP was greater than that of DIN, but the
331 concentrations of DIP that caused a significant positive effect size are above those that are
332 typically seen on coral reefs, even in locations with considerable eutrophication (Fig. 1e). A
333 linear mixed-effects meta-regression was used to examine growth, and the best fit model
334 included exposure duration as a fixed effect. DIN had a small but significant negative effect on
335 the growth rate ($P = 0.007$; Fixed effect estimate \pm SE: -0.01 ± 0.004), and exposure duration
336 had a small but significant positive effect ($P = 0.03$; Fixed effect estimate \pm SE: 0.002 ± 0.001 ;
337 Table S6). DIP, however, had a strong significant positive effect on the growth rate ($P < 0.0001$;
338 Fixed effect estimate \pm SE: 0.16 ± 0.03), with positive effects occurring at DIP concentrations
339 above $5 \mu\text{M}$ (Fig. 2e). Coral species was not included in the best fit model, and there was very
340 little unexplained heterogeneity between studies that was not accounted for in the model ($I^2 =$
341 0.0% ; $Q = 15.2$). There were no clear taxonomic trends in the response (Figs. S2-3e). Only corals

342 with branching morphology were examined, so the effect of morphology could not be assessed
343 (Fig. S4e).

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

356

357 **3.3 Mortality**

358 **Adult Tissue and Colony Survival:** Nutrient addition at concentrations that are regularly
359 observed on reefs had negative effects on the survival of adult corals; the largest negative effects
360 occurred at high nutrient concentrations (Fig. 1g). The best fit model was a linear mixed-effects
361 meta-regression that included exposure duration as a fixed effect, using the log risk ratio to
362 measure effect sizes. Exposure duration had a significant negative effect on the survival of adult
363 coral tissues and colonies ($P = 0.01$, Fixed effect estimate \pm SE: -0.002 ± 0.0007), but DIN and
364 DIP did not have significant effects (Table S8; Fig. 2g). There was minimal heterogeneity

365 between experiments that was unaccounted for by the best fit model ($I^2 = 23.1\%$, $Q = 26.0$).
366 Though species was not included in the best fit model, negative effects were observed in
367 *Acropora cervicornis* and *Agaricia tenuifolia* (Figs. S2-3g), but there were no clear trends based
368 on coral morphology (Fig. S4g).

369 **Larval Survival and Settlement:** Studies examined larval survival at a large range of DIN
370 and DIP concentrations (up to $\sim 100 \mu\text{M}$) (Fig. 1h). A linear mixed-effects meta-regression was
371 used in this analysis. DIN had a slight but significant negative effect on larval survival ($P =$
372 0.002 , Fixed effect estimate \pm SE: -0.005 ± 0.002) (Table S9; Fig. 2h), but DIP had no
373 significant effect on larval survival ($P = 0.48$). Though species and exposure duration were not
374 included in the best fit model, there was also heterogeneity between studies that was not captured
375 by the model ($I^2 = 61.1\%$, $Q = 111$). *Platygyra acuta* was the primary species examined at high
376 DIN concentrations (Fig. S2h), but no clear trend was seen based on taxonomic family or coral
377 morphology (Figs. 3-4h).

378 **Fertilization:** Few studies examined the impacts of low, environmentally relevant
379 nutrient concentrations on fertilization (Fig. 1i). The effects of elevated nutrient concentrations
380 were overwhelmingly negative, with the greatest negative effects occurring at low DIN ($\sim 1 \mu\text{M}$)
381 and higher DIP ($> 1 \mu\text{M}$). A linear mixed-effects meta-regression was used to examine the
382 relationship between nutrients and fertilization (Table S10). DIN had a significant negative effect
383 on fertilization ($P < 0.001$, Fixed effect estimate \pm SE: -0.01 ± 0.002), but DIP had no significant
384 effect ($P = 0.31$; Fig. 2i). Negative effects were particularly apparent in *Acropora longicyathus*
385 (Fig. S2i). All the *A. longicyathus* were from one study, but other species included in that study
386 (e.g., *Goniastrea aspera*) did not show the same trend (Harrison and Ward 2001). *Platygyra*
387 *acuta* also had a pronounced negative response to the addition of DIN (Fig. S2). There was still

388 considerable heterogeneity between studies that was not explained by the model ($I^2 = 63.9\%$, $Q =$
389 169), but with only two taxonomic families examined, clear trends were not determined based on
390 taxonomic family or morphology (Figs. S3-4i).

391

392 4. DISCUSSION

393 Meta-analyses were conducted for photosynthesis-related responses of coral
394 endosymbionts (i.e., zooxanthellae density, chlorophyll *a* concentration, photosynthetic rate, and
395 maximum photosynthetic efficiency), coral growth and calcification, and coral mortality
396 measures at several coral life history stages in response to elevated concentrations of dissolved
397 inorganic nitrogen and phosphorus (DIN and DIP). The mean exposure duration for the
398 experiments included was typically one to two months, except for larval survival (<1 day) and
399 growth of adult corals (5 months). Zooxanthellae density had nearly twice as many studies
400 included (21 studies) as the next closest response, chlorophyll *a* (12 studies). The relative
401 abundance of data for certain responses aided in the development of more refined
402 characterizations of these relationships. In general, elevated DIN concentrations, and in
403 particular nitrate, led to an increase in endosymbiont photosynthetic responses (zooxanthellae
404 density, chl-*a* concentration, and photosynthetic rate), while negative effects were seen in coral
405 responses to increasing DIN, including reduced growth and survival (Fig. 2). Increased DIP
406 affected endosymbionts by increasing zooxanthellae density but reducing photosynthetic
407 efficiency, but it had positive effects on coral growth. At concentrations of DIN and DIP below
408 10 μM and 0.3 μM , respectively, few direct effects are seen, and the concern for management
409 guidance should likely focus on competitive interactions between corals and macroalgae and/or
410 increased coral disease prevalence (Fig. 3).

411

412 **4.1 Summarizing Key Findings in the Context of Other Studies**

413 The relationship between zooxanthellae density and nutrients has been studied
414 extensively, and the biological mechanisms that drive increases in zooxanthellae density have
415 been considered in detail (Morris et al. 2019). Coral bleaching, which is the expulsion of
416 endosymbionts, can be driven by photo-oxidative stress or carbon limitation that occurs at high
417 temperatures that shift the coral-zooxanthellae metabolic relationship (Morris et al. 2019).
418 Phosphate limitation and shifts in the DIN to DIP ratio can also impact zooxanthellae and cause
419 coral bleaching (Morris et al. 2019). Elevated concentrations of DIN increase zooxanthellae
420 density, and elevated DIN in combination with DIP may be beneficial (Shantz and Burkepile
421 2014). When increases in DIN are not balanced with increased DIP, however, high zooxanthellae
422 density may lead to reduced health and increased vulnerability to co-occurring stressors like high
423 temperature.

424 Our meta-analysis quantifies this mechanistic relationship. Increases in zooxanthellae
425 density peaked at moderate nutrient concentrations, with increased density still occurring at
426 balanced high DIN-high DIP concentrations (Fig. 1a). The effect of nitrate on zooxanthellae
427 density increased significantly with low to moderate nitrate concentrations, but was less
428 pronounced at the highest concentrations (>50 μM). Zooxanthellae density only showed
429 significant increases at the highest ammonium concentrations (~10 μM) and also increased with
430 DIP, but to a far lesser extent than seen with nitrate. While the magnitude of the effect of DIN
431 and DIP on zooxanthellae density decreased at higher concentrations, the overall effect of
432 nutrient enrichment remained positive at the concentrations examined (up to 128 μM DIN and 2
433 μM DIP). These findings support previous descriptions of the theoretical mechanisms occurring

434 (D'Angelo and Wiedenmann 2014, Morris et al. 2019, Zhao et al. 2021) and further resolve the
435 demonstrated significant relationships between zooxanthellae, DIN, and DIP (Shantz and
436 Burkepile 2014).

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

456 zooxanthellae density under pulsed nutrient applications is also important for future work (van
457 der Zande et al. 2021).

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

467 The gross photosynthetic rate and the photosynthetic efficiency (maximum quantum
468 yield, MQY) are also related to the abundance of zooxanthellae in corals. Elevated nutrients
469 impact photosynthesis directly via their availability for inclusion in essential molecules (e.g.,
470 ATP) and also indirectly through their cascading impacts in the coral holobiont (Morris et al.
471 2019). Past studies suggest that DIN has a very slight positive effect on gross photosynthesis,
472 and DIP has no significant effect; few studies examine the combination of DIN and DIP (Shantz
473 and Burkepile 2014). MQY is used as a measure of stress in plants, and values that fall below 0.5
474 indicate reduced resilience of corals to stressors (D'Angelo and Wiedenmann 2014). The best fit
475 model for photosynthetic rate examined nitrate and ammonium separately, and nitrate had a
476 significant positive effect on photosynthesis, while ammonium and DIP did not at the
477 concentrations examined (Fig. 2c). Conversely, DIN had no clear effect on MQY, but DIP had a
478 significant negative effect at the highest concentrations examined (Fig. 2d).

479 Coral growth can also be related to the density of zooxanthellae and their photosynthetic
480 output (Dunn et al. 2012). Coral growth can increase with the addition of phosphate, but
481 phosphate can also displace carbonate ions in the calcium carbonate crystal structure, meaning
482 calcification can simultaneously decrease (Dunn et al. 2012). This means that in elevated
483 phosphate conditions, corals can grow faster in terms of linear extension, but have less dense
484 skeletons. The effects of DIN and DIP on calcification can counteract one another, though the
485 degree of this effect varies by coral morphology (Shantz and Burkepile 2014). We found that
486 DIN had a negative effect on growth, but DIP had a positive relationship with coral growth
487 (measured as linear extension) that was particularly pronounced at concentrations $>5 \mu\text{M}$ (Fig.
488 2e), which is aligned with previous studies (Dunn et al. 2012). Growth effects, which are
489 typically measured in adults and take a while to manifest, also increased with the duration of
490 exposure. The effects of DIN and DIP on calcification were consistently negative (Fig. 1f), but
491 the magnitude of these negative effects did not increase significantly with higher concentrations
492 of DIN and DIP. Past reviews found that elevated DIN decreased calcification, while DIP
493 increased it, but when examined in combination we did not find a significant effect (Shantz and
494 Burkepile 2014). The effects may be more apparent, however, if there were additional studies
495 focusing on higher nutrient concentrations.

496 Impacts on zooxanthellae, photosynthesis, growth, and calcification are all expected to
497 affect the health and survival of adult corals. Adult corals did not exhibit a significant negative
498 response in survival with nutrient addition but survival did decrease with exposure duration. The
499 exposure duration used in experiments with adult corals was in some cases much longer than that
500 used in other studies, which may have contributed to its effect and the variability seen in the
501 data. It has been well documented that shifting nutrient concentrations can also alter the coral

502 microbiome and the broader microbial community of the reef, which in turn can result in
503 increased disease prevalence as an indirect effect of high nutrient concentrations on corals (Haas
504 et al. 2016, Ford et al. 2018, Vega Thurber et al. 2020). These indirect effects may take more
505 time to manifest, and thus, the duration of exposure is an important component of assessing adult
506 coral survival in high nutrient conditions.

507 Unlike adults, coral larvae and eggs are not reliant on photosynthesis for their survival.
508 Indirectly, nutrients contribute to the growth of disease-causing microorganisms and can alter the
509 biogeochemistry of coral reefs, which can have cascading impacts on the chemical cues and
510 delicate environmental balance required by these early life stages. DIN had a significant negative
511 relationship with larval survival and fertilization, but there was no significant effect of DIP (Figs.
512 2h-i). Past work using a different modeling approach found that phosphorous did have a negative
513 effect on fertilization, and while we did not find a significant effect, the reported effects were
514 primarily negative, suggesting this is an area in need of additional research (Woods et al. 2016).

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

522 The duration of the nutrient exposure varied by study, but it was not a significant
523 component of any of the best fit models used in this analysis, except for growth and adult
524 survival. The duration of exposure to elevated nutrient conditions may have different importance,

525 depending on the responses examined. For example, the time required to see impacts of elevated
526 nutrients on growth or adult mortality is likely much longer than that required to observe
527 measurable responses in photosynthetic variables. Similarly, most of the studies included in this
528 review and analysis used press treatment conditions, or a continuous application of elevated
529 nutrient concentrations. This is likely representative of the conditions experienced by corals on
530 reefs with elevated nutrient concentrations due to submarine groundwater discharge or continual
531 sewage outflow. It is not, however, typical of what would be expected if the primary route of
532 nutrient addition was through streams or surface runoff in storm events. These inputs tend to
533 occur periodically and are better represented in experimental conditions by pulse treatments, or
534 periodic addition of elevated nutrients. Experimental studies indicate that pulse nutrient additions
535 can actually be beneficial to corals, while continuous press conditions are more likely to have
536 negative impacts, making this an important topic for future studies (van der Zande et al. 2021).

537

538 **4.2 Recommendations for Future Research and Management**

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

548 of the complex metabolic processes occurring in the coral holobiont and surrounding community
549 that negatively impact the health of corals in high nutrient environments (Wegley Kelly et al.
550 2021).

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

561 Nutrients also influence the growth, function, and survival of other organisms on coral
562 reefs that have indirect impacts on the health of corals, which is important to consider in the
563 development of comprehensive ecosystem-wide management thresholds. To contextualize the
564 results of this study within the broader ecological scope of coral reefs and changing climate
565 conditions, it is also important to assess the nuanced indirect relationships among corals, algae,
566 cyanobacterial mats, urchins, sponges, and other benthic organisms and their responses to
567 nutrient additions (Littler et al. 2006, Norström et al. 2009, Vermeij et al. 2010, Ford et al. 2018).
568 The responses examined in this analysis are dynamically affected by co-occurring stressors and
569 responses in other organisms, as well as cascading indirect effects (Fabricius et al. 2010). Future

570 research should aim to address this interconnectedness to facilitate the development of
571 quantitative models that can more accurately capture the nuance of the system.

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

582

583 **5. CONCLUSIONS**

584 The results of this meta-analysis build on reviews that examined the overall effects of
585 DIN and DIP on coral responses (Shantz and Burkepile 2014), developed frameworks for the
586 mechanisms of ecological (D'Angelo and Wiedenmann 2014) and biological (Morris et al. 2019,
587 Zhao et al. 2021) impact of inorganic nutrients on corals, and offered guidelines for management
588 based on this information (Houk et al. 2020). By integrating DIN and DIP into the same analyses
589 and using mixed-effects meta-regressions, this study accounted for the variability between and
590 within studies while assessing the independent and interacting effects of DIN and DIP on a
591 variety of coral responses. In doing so, we were able to quantify relationships that have been
592 theoretically outlined in the past. In lieu of developing specific thresholds for the management of

593 nutrients as a stressor on coral reefs, we highlighted important inflection points in the magnitude
594 and direction of the effects of inorganic nutrients and identified trends among coral responses.
595 Importantly, the concentrations of DIN and DIP that negatively impact corals may double the
596 growth of reef macroalgae (Schaffelke and Klumpp 1998) and result in phytoplankton blooms
597 (Hayashida et al. 2020).

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

605

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613

614 **DATA STATEMENT**

615 All data generated during this study, along with code used to analyze data and generate figures,

616 are shared in the public repository: https://github.com/enalley/nutrient_thresholds

617

618

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Table 1. Hypothesized relationships between nutrient addition and physiological responses in corals, based on previous research.

Response	Frameworks for Hypothesized Relationships
<i>Zooxanthellae density</i>	<ul style="list-style-type: none"> ▪ Low zooxanthellae density is expected at low nutrient concentrations due to nutrient limitation. Increasing nutrient concentrations should reduce the impact of limitation, resulting in increased zooxanthellae growth up to a point where density is limited after a threshold level (Morris et al. 2019, Zhao et al. 2021). ▪ Nitrate, ammonium, and phosphate are expected to have independent effects on zooxanthellae density (Shantz and Burkepille 2014).
<i>Chlorophyll a concentration</i>	<ul style="list-style-type: none"> ▪ Chlorophyll <i>a</i> concentrations are dependent on the density of zooxanthellae, so chlorophyll <i>a</i> concentrations are expected to increase with zooxanthellae density.
<i>Photosynthetic Rate</i>	<ul style="list-style-type: none"> ▪ 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.
<i>Photosynthetic Efficiency (Maximum Quantum Yield, MQY)</i>	<ul style="list-style-type: none"> ▪ MQY refers to the maximum number of photons that are emitted per photon absorbed, so it is expected that MQY will be impacted by nutrient limitation and will lag in response to changes in zooxanthellae density and chlorophyll <i>a</i> concentrations (D'Angelo and Wiedenmann 2014).
<i>Growth</i>	<ul style="list-style-type: none"> ▪ 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).
<i>Calcification</i>	<ul style="list-style-type: none"> ▪ 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).
<i>Adult Survival (Partial and Complete)</i>	<ul style="list-style-type: none"> ▪ 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).
<i>Larval Survival and Settlement</i>	<ul style="list-style-type: none"> ▪ High nutrient concentrations are associated with a higher abundance of pathogenic bacteria that may negatively impact larval survival and settlement (Quimpo et al. 2020).
<i>Fertilization</i>	<ul style="list-style-type: none"> ▪ It is expected that at the high nutrient concentrations associated with reduced water quality, fertilization will decline (Woods et al. 2016).

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

Response	Studies	Experiments	DIN Range (μM)	DIP Range (μM)	Mean Exposure Duration in days (Range)
<i>Zooxanthellae Density</i>	21 ^a	36	0.08-128	0.02-2	33 (3-126)
<i>Chlorophyll a Concentration</i>	12 ^b	23	0.1-50	0.02-5	41 (5-252)
<i>Photosynthetic Rate</i>	9 ^c	11	0.1-39	0.02-5	61 (21-252)
<i>Photosynthetic Efficiency (Maximum Quantum Yield)</i>	7 ^d	12	0.3-128	0.02-0.7	60 (3-105)
<i>Growth Rate</i>	6 ^e	8	0.1-50	0.02-16	147 (21-406)
<i>Calcification</i>	7 ^f	20	0.2-50	0.02-5	35 (14-168)
<i>Adult Survival</i>	5 ^g	8	0.1-33	0.02-5	47.5 (5-90)
<i>Larval Survival</i>	3 ^h	16	0.65-202	0.08-101	0.7 (0.02-4)
<i>Fertilization</i>	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. 2016, Courtial et al. 2018, Bednarz et al. 2020)

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

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

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

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

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

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

Table 3. Model results with influential nutrient concentration ranges. All models included experiment as a random effect and used a covariance structure based on experiment to account for heterogeneity between studies. Statistically non-significant relationships are noted with ‘n.s.’.

Response (Effect Size Measurement)	Effect Size Relationship and Direction	Unexplained Heterogeneity between Experiments (based on I²)
<i>Zooxanthellae Density (std. diff. in means)</i>	NO ₃ ⁻ : pos. quadratic NH ₄ ⁺ : pos. linear DIP: pos. linear	moderate (68.3%)
<i>Chlorophyll a Concentration (std. diff. in means)</i>	DIN: pos. linear DIP: n.s.	moderate (43.3%)
<i>Photosynthetic Rate (std. diff. in means)</i>	NO ₃ ⁻ : pos. linear NH ₄ ⁺ : n.s. DIP: n.s.	low (36.3%)
<i>Photosynthetic Efficiency (std. diff. in means)</i>	DIN: n.s. DIP: neg. linear	high (72.5%)
<i>Growth Rate (std. diff. in means)</i>	DIN: neg. linear DIP: pos. linear Duration: pos. linear	low (0%)
<i>Calcification (std. diff. in means)</i>	DIN: n.s. DIP: n.s.	moderate (56.4%)
<i>Adult Survival (log risk ratio)</i>	DIN: n.s. DIP: n.s. Duration: neg. linear	low (23.1%)
<i>Larval Survival (std. diff. in means)</i>	DIN: neg. linear DIP: n.s.	moderate (61.1%)
<i>Fertilization Success (std. diff. in means)</i>	DIN: neg. linear DIP: n.s.	moderate (63.9%)

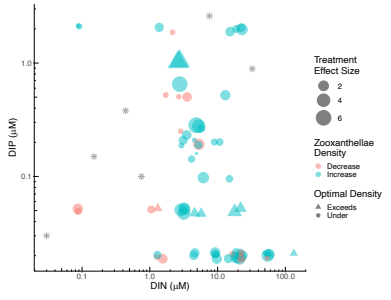
FIGURES

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

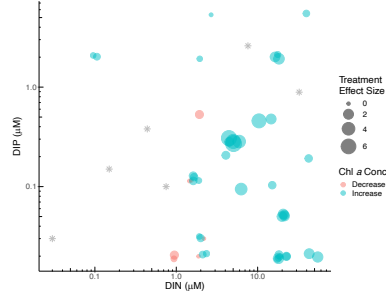
Figure 2. Effect size of DIN (left) and DIP (right) on (A) zooxanthellae density (10^6 cells cm^{-2}) – 21 studies, (B) chlorophyll a concentration ($\mu\text{g Chl a cm}^{-2}$) – 12 studies, (C) photosynthetic rate ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ day}^{-1}$) – 9 studies, (D) MQY (F_v/F_m) – 7 studies, (E) growth (mm day^{-1}) – 6 studies, (F) calcification ($\text{mg CaCO}_3 \text{ cm}^{-2} \text{ day}^{-1}$) – 7 studies, (G) adult tissue and colony survival (% survival) – 5 studies, (H) larval survival and settlement (%) – 3 studies (*note: two points with large vmd were removed from this plot for scale*), and (I) fertilization (%) – 6 studies. Points indicate the standardized difference in means +/- 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. *This figure should be a 2-column fitting image.*

Figure 3. Responses associated with increasing nutrient (left: dissolved inorganic nitrogen, DIN and right: dissolved inorganic phosphorus, DIP) concentrations. Arrow locations and directions align with the concentration at which the effect becomes apparent. For reference, ambient concentrations referred to in this review ranged from $0.15 \mu\text{M}$ to $32.4 \mu\text{M}$ for DIN and from $0.1 \mu\text{M}$ to $2.6 \mu\text{M}$ for DIP (Fig. S1). MQY is maximum quantum yield, or photosynthetic efficiency (F_v/F_m). *This figure should be a 2-column fitting image.*

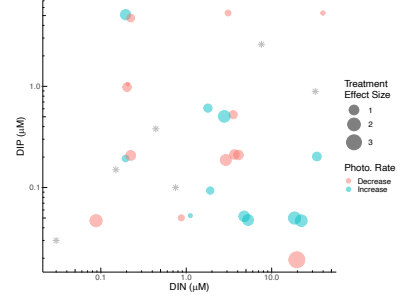
A. Zooxanthellae Density



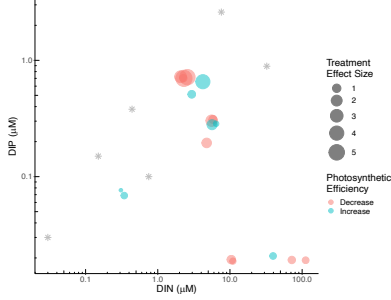
B. Chl-a Concentration



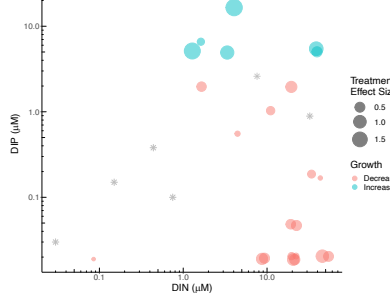
C. Photosynthetic Rate



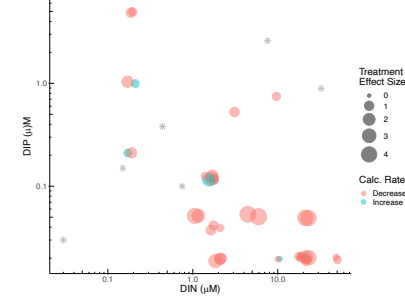
D. MQY



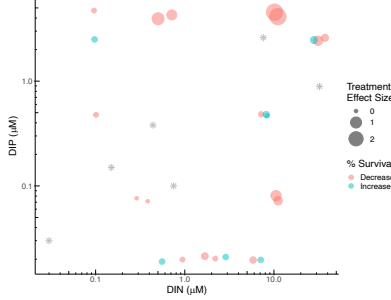
E. Growth



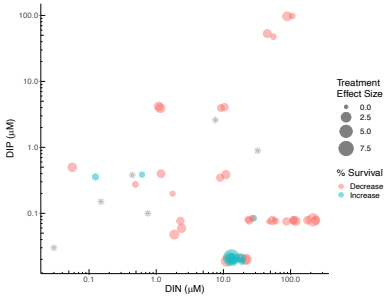
F. Calcification



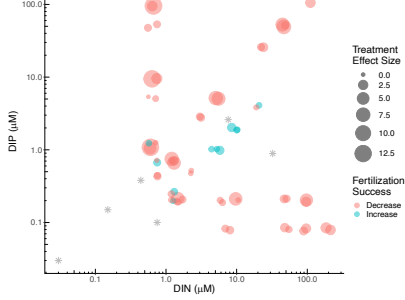
G. Adult Survival



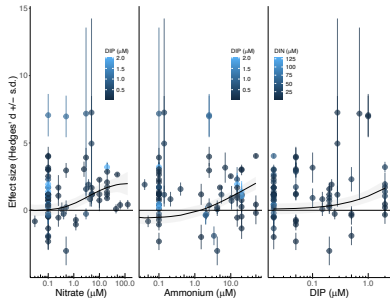
H. Larval Survival



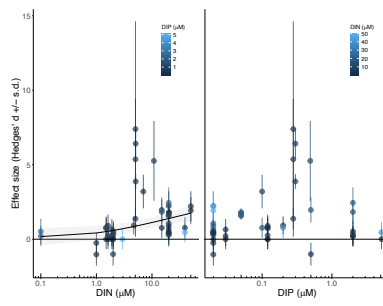
I. Fertilization



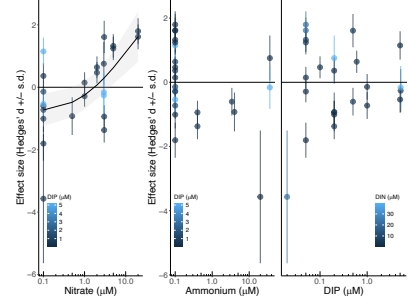
A. Zooxanthellae Density



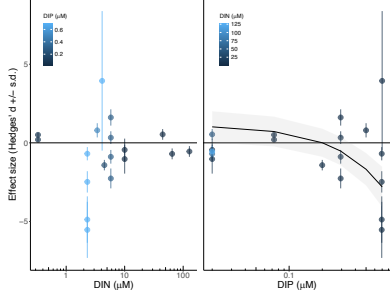
B. Chl-a Concentration



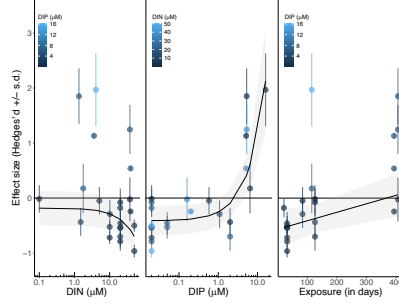
C. Photosynthetic Rate



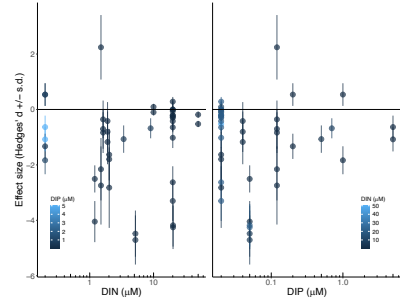
D. MQY



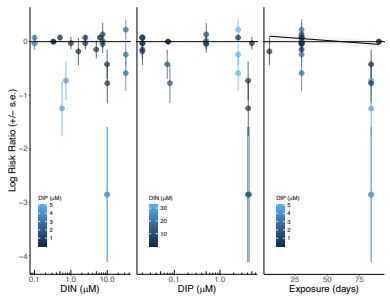
E. Growth



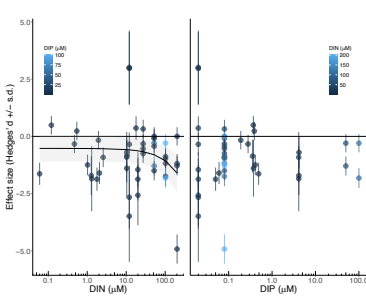
F. Calcification



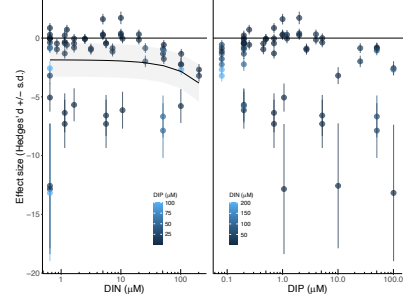
G. Adult Survival

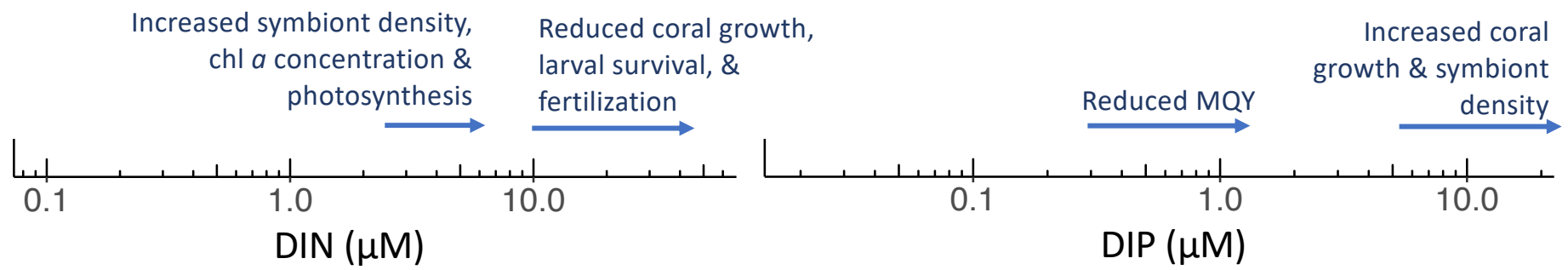


H. Larval Survival



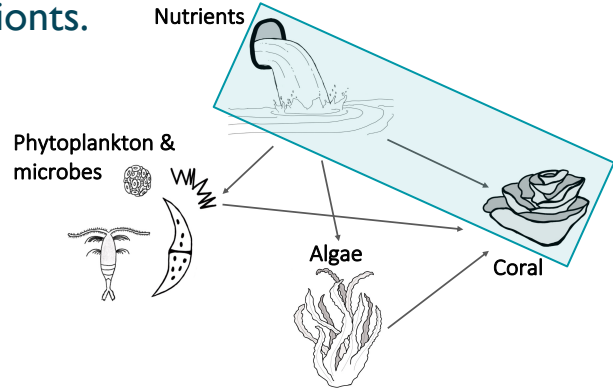
I. Fertilization





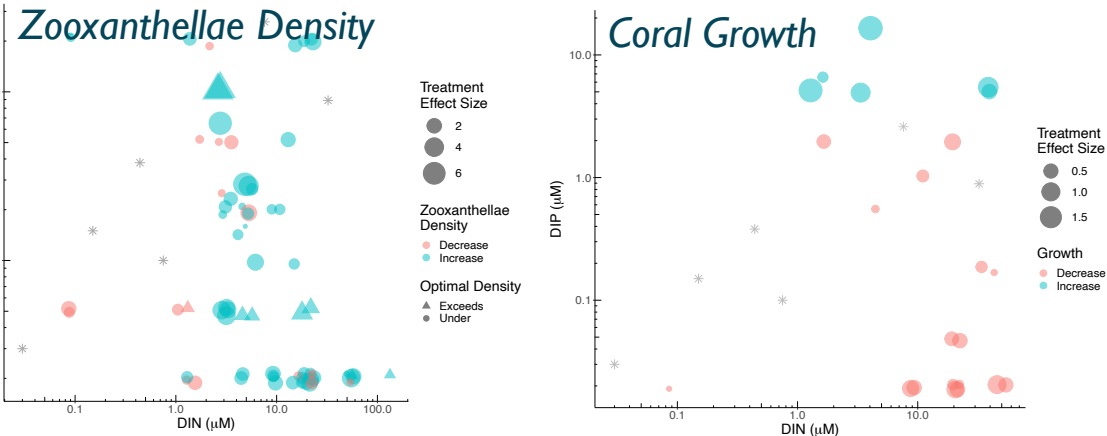
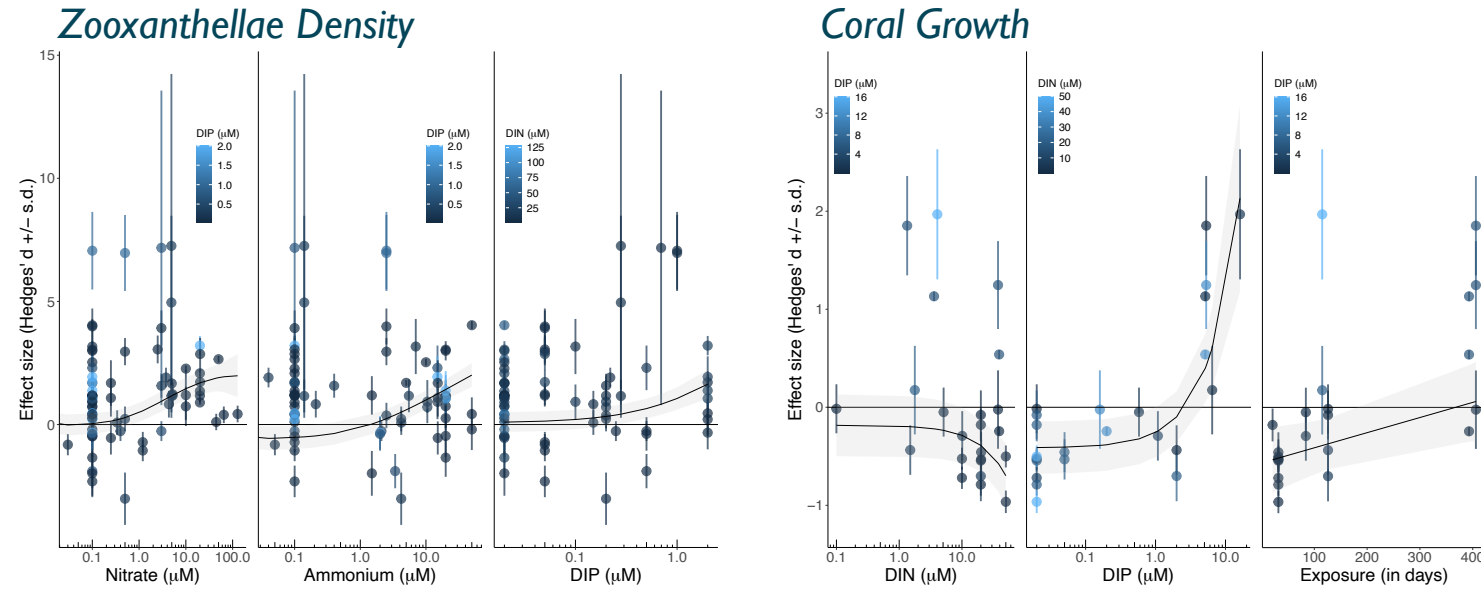
A systematic review and meta-analysis of the direct effects of nutrients on corals

Overview: In this study we focus on the direct relationship between nutrients, corals, and their symbionts.



I. Systematic Review of DIN/DIP impacts on zooxanthellae density, chl-*a* concentration, photosynthetic rate & efficiency, growth & calcification, adult & juvenile survival, and fertilization (n = 47 studies)

2. Mixed-effects meta-regression meta-analysis to examine shifts in the magnitude and direction of the impacts of DIN/DIP on corals



Summary of Results:

