Nutrient Stress and Coral Health: Bridging Physiology, Holobiont Dynamics, and Molecular Mechanisms

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ABSTRACT

Nutrient stress acts as a multiscalar and context-dependent driver of coral reef decline primarily driven by anthropogenic interference. Decades of physiological and ecological studies have established that nutrient stress elicits physiological responses from corals, but reveal species-specific variability dependent on nutrient identity, concentration, and stoichiometry, as well as intricate interactions with other stressors like climate change. Due to this complexity, a deeper mechanistic understanding of nutrient stress is necessary, with molecular biology research at the forefront of building conceptual models. This review synthesizes the current understanding of nutrient stress effects, bridging classical physiological observations with insights from omics research. We review how molecular approaches—spanning genetics, epigenetics, transcriptomics, and other omics (such as proteomics and lipidomics)—have been used to elucidate the underlying processes driving nutrient stress response in corals. We find that molecular evidence provides empirical support for the two prevailing models: the Phosphate Starvation Model (PSM) and the Greedy Symbiont Model (GSM), as well as novel mechanisms outside the scope of the two established models. However, molecular studies still remain underutilized, unevenly distributed across omic fields, and often lack correlation with physiological outcomes. Thus, we highlight the need for hypothesis-driven research which combines ecologically relevant nutrient conditions with multi-omic approaches and phenotypic responses across the coral holobiont. Calculated and intentional studies are required to understand the complexity of nutrient stress responses in order to further frameworks for coral resilience and inform conservation efforts in an increasingly eutrophied ocean already subject to a multitude of concurrent stressors.

1. The Complex Interplay Between Nutrients and Coral Health

1.1. Nutrient cycles and anthropogenic driven shifts

Natural nutrient cycling in the ocean functions as a series of sinks, sources, and internal recycling (Fig. 1a). Across the world's oceans, the two most common limiting factors to primary productivity are access to sunlight and nutrients–primarily nitrogen, phosphorus, iron, and silica (Bristow et al., 2017). Tropical and subtropical coastal waters, however, are primarily limited by nutrients due to existing in the euphotic zone (the depth to which sunlight can penetrate) in regions with plentiful sunlight (Lønborg et al., 2021). Because of this, nutrients are quickly removed from the water column by biological elements, resulting in ecosystems in tropical coastal waters being typically oligotrophic ecosystems. Currently, coastal waters globally are experiencing twice as much eutrophication as oligotrophication (Maúre et al., 2021) –a trend that is of particular concern to ecosystems constrained to tropical and subtropical waters such as warm-water coral reefs (Guan et al., 2015).

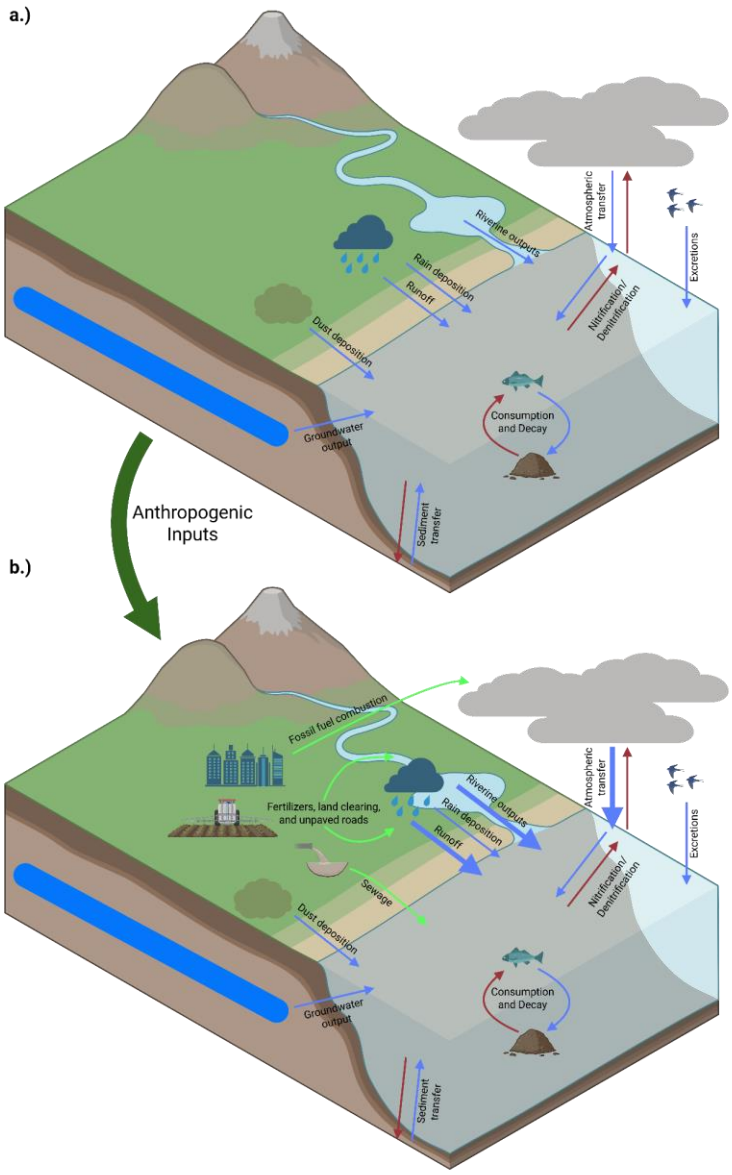

Figure 1. a) Generalized representation of the natural nutrient cycle in the ocean. Sinks include sedimentation, gas exchange into the atmosphere and denitrification, and uptake of nutrients by organisms, while sources come from river outputs, terrestrial runoff, groundwater, rain deposition, gas exchange from the atmosphere and nitrification, dust deposition, organismal excretions, reabsorption from sediment, and decomposition of decaying organic matter (Bristow et al., 2017; Chen & Nihoul, 2009). b) The nutrient cycle in the ocean when impacted by anthropogenic sources. New sources include fossil fuel combustion augmenting atmospheric deposition (Vitousek et al., 1997), sewage output (Chen & Nihoul, 2009), and activities which increase runoff and riverine outputs such as fertilizer use for crops (Matson et al., 1997; Vitousek et al., 1997), land clearing (Beaulac & Reckhow, 1982; Vitousek et al., 1997), and unpaved roads (Ramos-Scharrón & LaFevor, 2016; Ziegler & Giambelluca, 1997).

Coral reefs provide critical services for humans globally, including food, protection, economic benefits and local job opportunities, and cultural enrichment. It is becoming increasingly important to understand the anthropological impacts on coral reefs in the modern world where human civilization is ever expanding (Hughes et al., 2017). Human activities have long been disrupting the global nutrient cycles by augmenting natural nutrient sources through different sources (Fig. 1b). When combined with rainfall (Beaulac & Reckhow, 1982) these disruptions lead to runoff into coastal waters, enriching them with nutrients. This can have serious consequences, particularly in generally oligotrophic ecosystems such as coral reefs (Fabricius, 2005), and can facilitate shifts on reef ecosystems from being dominated by corals to becoming macroalgae dominated (Lesser, 2021).

1.2. Coral physiological responses to nutrient stress

Exposure to eutrophic conditions leads to various physiological and community-level responses in corals (Tables 1 and 2, Figure 2). Accordingly, eutrophication is negatively correlated with coral species diversity and cover (Duprey et al., 2016). While responses are complex and study-dependent, general trends exist: elevated nutrient concentrations tend to increase disease, symbiont density, bleaching, chlorophyll-*a* content, respiration, and mortality; while often decreasing growth and skeleton density. Some metrics, like photosynthesis, calcification, and photosynthetic efficiency show mixed results (Fig. 2). In addition, trade-offs have been also reported, where increased calcification rates lead to lower skeleton densities, making corals more fragile (Shantz & Burkepile, 2014). This complexity is driven by variations in nutrient type, concentration, combination, source, and state, as well as the coral species affected.

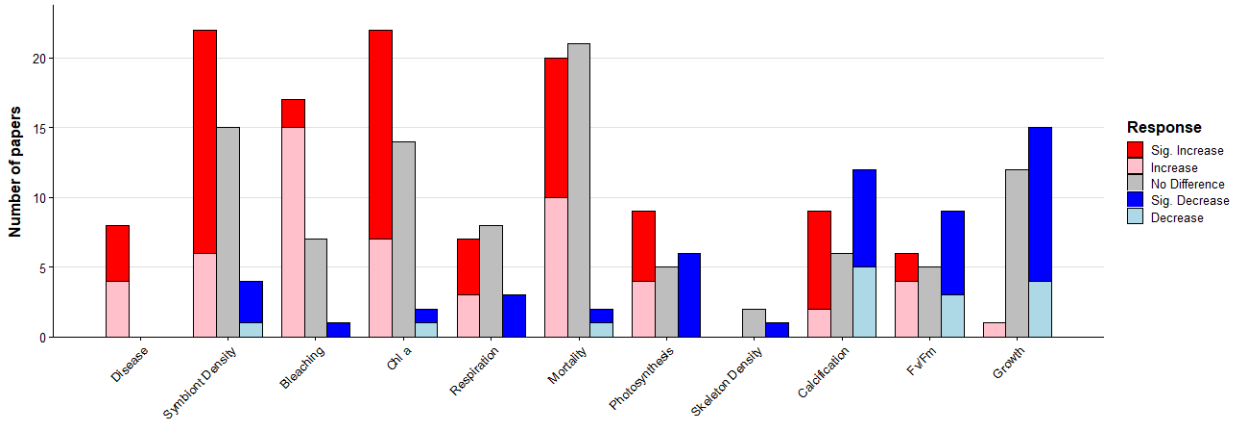

Figure 2. Summary of the results of the studies included in Table 1 which used elevated nutrient treatments or studied eutrophied conditions. The various metrics measured by the studies are on the x-axis and the number of studies that reported those results is on the y-axis. Chl a is the total concentration of Chlorophyll a and F_v/F_m is the maximum photosynthetic efficiency.

Table 1: Summary of studies reporting changes in coral physiology under various nutrient and secondary stressor conditions with the top number of parameter measurements represented. Note that multiple distinct results may be derived from a single study. The complete dataset encompassing all extracted data is provided in Supplementary Table S1. A solid row separation indicates a new study; a dashed separation indicates a different treatment, group, or species within the same study. Treatment/Condition is denoted as a combination of nitrogen condition - high or low (HN and LN, respectively) - phosphorus condition - high or low (HP and LP, respectively) and any additional stressors. Treatment/Condition is not differentiated between forms of each nutrient, such as nitrate and ammonia for nitrogen. Changes in physiological parameters were reported as an increase (+), decrease (-), or no difference (=) when compared to the studies controls or ambient conditions, with a star indicating that result was reported to be significant by that study. Percent changes were shown for studies that included them, as well as studies which did not include them but provided the information required to calculate them. Reported results are either relative to controls, low nutrient treatments, or temporal environmental differences depending on the study's experimental design. Exact nutrient ranges and forms reported by each study can be found in Supplementary Table S3, if reported by said study.

Treatment/ Condition	Type	Time frame	Species	Bleaching	Mortality	Disease	Growth	Calcification	Skeleton Density	Paper
HN	Tank	3 months	Montipora tuberculosa	=	=		=			Fabricius et al., 2013
HN	Field	14 months	Acropora longicyathus		=		-*	+*	=	Koop et al., 2001
HN	Field	14 months	Pocillopora damicornis		+*			-*		
HN	Field	14 months	Acropora palifera				=	-*		
HN	Field	14 months	Stylophora pstillata				-*	=		

HN	Field	30 years	General Caribbean species		+	404% +				Lapointe et al., 2019
HN	Tank	3 months	Acropora cervicornis		+		-*			Renegar & Riegl, 2005
HN	Meta Analysis	N/A	General coral species				-*	11% -*	=	Shantz & Burkepile, 2014
HN + Elevated CO_2	Tank	3 months	Acropora cervicornis		+		-			Renegar & Riegl, 2005
HN + Organic Enrichment	Tank	3 months	Acropora millepora		=		=			Fabricius et al., 2013
HN + Organic Enrichment	Tank	3 months	Montipora tuberculosa		=		=			
HN + Organic Enrichment + Thermal Stress	Tank	3 months	Acropora millepora		=		=			
HN + Organic Enrichment + Thermal Stress	Tank	3 months	Montipora tuberculosa		=		=			
HN + Thermal Stress	Field	10 weeks	Pocillopora spp.	+*	+*					Burkepile et al., 2020
HN + Thermal Stress	Tank	4 weeks + 10 days thermal	Stylophora pistillata	-*				+*		Ezzat et al., 2019
HN + Thermal Stress	Tank	3 months	Montipora tuberculosa		+*		=			Fabricius et al., 2013
HN + Thermal Stress	Field	6 months	Agaricia spp.	+	+					Wang et al., 2018
HNHP	Field	14 months	Acropora longicyathus		=		-*	=		Koop et al., 2001
HNHP	Tank	30 days	Montastrea annularis	+	=					Kuntz et al., 2005
HNHP	Tank	3 months	Acropora cervicornis		+		61% -*			Renegar & Riegl, 2005
HNHP	Meta Analysis	N/A	General coral species				-*	=	10% -	Shantz & Burkepile, 2014
HNHP	Field	3 months	Acropora cervicornis		-*		-			Shaver et al., 2017
HNHP	Field	3 years	General Caribbean corals		=	200% +*				R. L. Vega Thurber et al., 2014
HNHP + Elevated CO_2	Tank	3 months	Acropora cervicornis		+		-*			Renegar & Riegl, 2005
HNHP + Predation	Field	3 months	Acropora cervicornis		=		=			Shaver et al., 2017
HNHP + Thermal Stress	Field	6 months	Agaricia spp.	+	=					Wang et al., 2018
HNLP	Tank	10 weeks	Acropora polystoma	+			=			Buckingham et al., 2022
HNLP + Light Stress	Tank	5 weeks + light exposure	Montipora foliosa	+	+					Wiedenmann et al., 2013
HP	Field	14 months	Acropora longicyathus		=		-*	+*	-*	Koop et al., 2001
HP	Field	14 months	Pocillopora damicornis		+*			-*		
HP	Field	14 months	Acropora palifera				-*	+*		
HP	Field	14 months	Stylophora pstillata				=	-*		
HP	Tank	3 months	Acropora cervicornis		+		-*			Renegar & Riegl, 2005
HP	Meta Analysis	N/A	General coral species				+	9% +*	9% -	Shantz & Burkepile, 2014
HP + Elevated CO_2	Tank	3 months	Acropora cervicornis		+		-			Renegar & Riegl, 2005
HP + Thermal Stress	Field	6 months	Agaricia spp.	+	=					Koop et al., 2001
HNHP + Disease	Field	3 months	Montastrea annularis & Montastrea franksii		+*	+*				Bruno et al., 2003
HNHP	Field	3 years	General Florida Keys species		+*	+				Zaneveld et al., 2016
HN + Predation	Field	3 years	Porites spp.		+*	+*				

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Table 2: Summary of the reported results for changes to coral physiology under various nutrient and secondary stressor conditions with the top number of parameter measurements represented. Note that multiple distinct results may be derived from a single study. The complete dataset encompassing all extracted data is provided in Supplementary Table S2. Chl a is the total concentration of Chlorophyll a, R_d is the dark respiration rate, P_{max} is the maximum photosynthetic rate, and F_v/F_m is the maximum photosynthetic efficiency. Solid row separation indicates a new study; dashed separation indicates a different treatment, group, or species within the same study. Treatment/Condition is denoted as a combination of nitrogen condition - high or low (HN and LN respectively) - phosphorus condition - high or low (HP and LP respectively) and any additional stressors. Treatment/Condition is not differentiated between forms of each nutrient, such as nitrate and ammonia for nitrogen. Changes in physiological parameters were reported as an increase (+), decrease (-), or no difference (=) when compared to the studies controls or ambient conditions, with a star indicating that result was reported to be significant. Percent changes were shown for studies that included them, as well as studies which did not include them but provided the information required to calculate them. Exact nutrient ranges and forms reported by each study can be found in Supplementary Table S3, if reported by said study.

Treatment/ Condition	Type	Time frame	Species	R_d	Chl a	Symbiont Density	P_{max}	F_v/F_m	Paper
HN	Tank	1 month	Turbinaria reniformis	=	+/+*	-*	=		Béraud et al., 2013
HN	Tank	9 weeks	Pocillopra damicornis	=	+	=	+		Courtial et al., 2018
HN	Tank	3 weeks	Stylophora pistillata	+*		=			Fernandes de Barros Marangoni et al., 2020
HN	Field	14 months	Stylophora pstillata	=	+*	+*	=		Koop et al., 2001
HN	Tank	12 days	Porites cylindrica	=	=	=	-*		Nordemar et al., 2003
HN	Tank	3 days	Acropora aspera		=	=		+	Rosic et al., 2014
HN	Meta Analysis	N/A	General coral species		+*	+	+		Shantz & Burkepile, 2014
HN + Thermal Stress	Tank	1 week	Turbinaria reniformis	=	+*		+*		Béraud et al., 2013
HN + Thermal Stress	Tank	9 weeks	Pocillopra damicornis	+	+	=	+		Courtial et al., 2018
HN + Thermal Stress	Tank	17 days	Turbinaria reniformis	-*	280% +*		-*		Ezzat et al., 2016
HN + Thermal Stress	Tank	4 weeks + 10 days thermal	Stylophora pistillata		-*	-*	-*		Ezzat et al., 2019
HN + Thermal Stress	Tank	3 weeks	Stylophora pistillata	=		=			Fernandes de Barros Marangoni et al., 2020
HN + Thermal Stress	Tank	2 days	Porites cylindrica	=	=	=	-*		Nordemar et al., 2003
HNHP	Field	15 months	Pocillopora spp.	12% +	=	54% +*	29% +*		D. M. Becker et al., 2021
HNHP	Tank	6 weeks	Stylophora pistillata	+*	+*	+*	-*		Ezzat et al., 2015
HNHP	Tank	36 days	Porites compressa	=	+	+*	=	+*	Fox et al., 2021
HNHP	Tank	36 days	Pocillopora acuta	=	+	+*	+*	+*	
HNLP	Tank	6 weeks	Stylophora pistillata	-*	+*	+*	-*		Ezzat et al., 2015
HNLP	Tank	6 weeks	Stylophora pistillata		+*	+*	=		
HNLP + Light	Tank	5 weeks + 3 weeks light exposure	Euphyllia paradivisa		-	-		-	Wiedenmann et al., 2013
HP	Field	14 months	Stylophora pistillata	+	=	+*	+		Koop et al., 2001
HP	Meta Analysis	N/A	General coral species		=	=	=		Shantz & Burkepile, 2014

LN	Field	16 months	Pocillopora damicornis	=	=	=	=	Koop et al., 2001
LN	Field	16 months	Acropora longicyathus	=		=	=	
LN	Field	16 months	Acropora palifera	=		=	=	
LN	Field	16 months	Stylophora pstillata	=		=	=	
LNLP	Field	16 months	Pocillopora damicornis	=	=	=	=	
LNLP	Field	16 months	Acropora longicyathus	=		=	=	
LNLP	Field	16 months	Acropora palifera	=		=	=	
LNLP	Field	16 months	Stylophora pstillata	=		=	=	
LP	Field	16 months	Pocillopora damicornis	=	=	=	=	
LP	Field	16 months	Acropora longicyathus	=		=	=	
LP	Field	16 months	Acropora palifera	=		=	=	
LP	Field	16 months	Stylophora pstillata	=		=	=	

The effects of nitrogen alone range from positive impacts on some symbiotic metrics such as photosynthetic efficiency or photosynthesis rate (Courtial et al., 2018; Ezzat et al., 2015; Koop et al., 2001)(Table 2) to non-significant impacts on others, such as chlorophyll-a content or symbiont density (Ezzat et al., 2019; Fabricius et al., 2013)(Tables 1 and 2), to detrimental effects on health and survival (Koop et al., 2001; Lapointe et al., 2019; Voss & Richardson, 2006)(Table 1). Phosphorus alone has been shown in a meta-study to have little effect on coral symbionts or photosynthesis, but may enhance growth and calcification at the expense of skeleton density (Shantz & Burkepile, 2014). While extreme concentrations can cause mortality (Koop et al., 2001; Renegar & Riegl, 2005), low to high levels often have minimal impact (Koop et al., 2001; Rosset et al., 2017). When both nitrogen and phosphorus are present in high concentrations, photosynthetic metrics may improve (Ezzat et al., 2015; Koop et al., 2001; Stambler et al., 1991), but this combination can increase the risk of bleaching, mortality, and disease (Ferrier-Pagès et al., 2000; Koop et al., 2001; Kuntz et al., 2005; Renegar & Riegl, 2005; Shantz & Burkepile, 2014; Shaver et al., 2017; R. L. Vega Thurber et al., 2014; Zaneveld et al., 2016) and disrupt symbiosis (Ezzat et al., 2015).

The source of nitrogen (urea, ammonium, or nitrate) also affects corals differently. For instance, urea from reef fish excretion appears to have little effect on coral bleaching or mortality (Burkepile et al., 2020), while ammonium sourced naturally (atmospheric deposition, upwelling, reef fish) or anthropogenically (fertilizer), is often beneficial, improving photosynthesis and growth metrics (Fernandes de Barros Marangoni et al., 2020; Holbrook et al., 2008). Nitrate, derived naturally (upwelling, nitrification) or anthropogenically (fertilizer runoff), is generally detrimental to symbiosis and can increase oxidative stress compared to ammonium (Ezzat et al., 2015; Fernandes de Barros Marangoni et al., 2020). The positive effect of ammonium likely stems from nitrate processing being more complex, harder to catalyze, and less energy-efficient (Ezzat et al., 2015; Raven et al., 1992).

Nutrient stress effects are also species-dependent. For instance, *Porites spp.* corals were seen to be more resilient to elevated nitrate and urea than *Acropora* and *Pocillopora spp.* (Burkepile et al., 2020). In one study of five species, *Pocillopora damicornis* was the only one with significant mortality under high nutrient conditions, with high variation in physiological responses across species (Koop et al., 2001). *In situ* experiments have shown species-specific differences in response to high nutrients: *Agaricia spp.* bleached more than controls, while *Siderastrea siderea* colonies showed increased disease prevalence (R. L. Vega Thurber et al., 2014). Another *in situ* study during a thermal event also found *Agaricia spp.* more prone to bleaching and death, while *S. siderea* was more likely to exhibit disease (Wang et al., 2018).

1.3. Nutrient interactions with other stressors

Nutrient stress has been shown to interact differently with thermal stress depending on the concentration and nitrogen:phosphorus (N:P) ratios. Larger spatial scale studies suggest that nutrient pollution has been linked to increased coral mortality and disease susceptibility during heat stress (Zaneveld et al., 2016), while increasing the corals susceptibility to bleaching during

heating events (Donovan et al., 2020; Wooldridge et al., 2017). In a study considering gradients of both nutrient and sedimentation loading (two processes that are often inextricable in field research), corals exposed to higher levels of loading had significantly lower thermal optimums for dark respiration rates and significantly lower maximal rates of gross photosynthesis–two metabolic parameters associated with thermal performance (D. M. Becker & Silbiger, 2020). The concentrations and ratios of nitrogen and phosphorus can also modulate the effects of this combination of stressors, as has been shown in a variety of manipulation studies.

One of these manipulation studies found that low levels of nitrogen and phosphorus may increase coral performance under thermal stress (D. M. Becker et al., 2021). High levels of nitrogen or nitrogen and phosphorus in combination can increase mortality and reduce bleaching recovery post-thermal events, though phosphorus alone has little effect (Wang et al., 2018). Elevated levels of nitrogen by itself during thermal stress can be detrimental to coral photosynthesis and calcification (Ezzat et al., 2016), but enrichment of both nitrogen and phosphorus can alleviate the effects of thermal stress on coral metabolism and calcification (Ezzat et al., 2016). When corals were exposed to elevated nitrate, thermal stress, and organic enrichment, they had significantly lower survival (Fabricius et al., 2013). The state of nitrogen will also change the interaction of these two stressors; nitrate exacerbates coral's inflammatory response to heat stress resulting in bleaching, while ammonium is beneficial under the same conditions (Zhang et al., 2023).

1.4. Mechanisms of nutrient stress in corals

There are two prevailing models for the mechanisms underlying nutrient stress's effect on coral physiology. The first, the Phosphate Starvation Model (PSM), was first outlined by Wiedenmann et al. (2013). In this model, corals in natural oligotrophic conditions are nitrogen limited (Dagenais-Bellefeuille & Morse, 2013), and their symbiont's thylakoid membranes are largely

composed of phospholipids. Under these conditions, an increase in environmental nitrogen levels (without an increase in phosphorus), will shift the limiting resource to phosphorus, causing the phospholipids in the thylakoid membranes to be replaced by sulfolipids, resulting in less efficient photosynthesis (Fig. 3). With a compromised photosynthetic apparatus, reactive oxygen species (ROSs) are produced and transferred back to the coral host, straining and destabilizing the symbiotic relationship. On the other hand, a balanced increase in both nutrients will drive an increase in symbiont cell division rates, without the substitution of phospholipids with sulfolipids, thus resulting in less destabilization (D'Angelo & Wiedenmann, 2014).

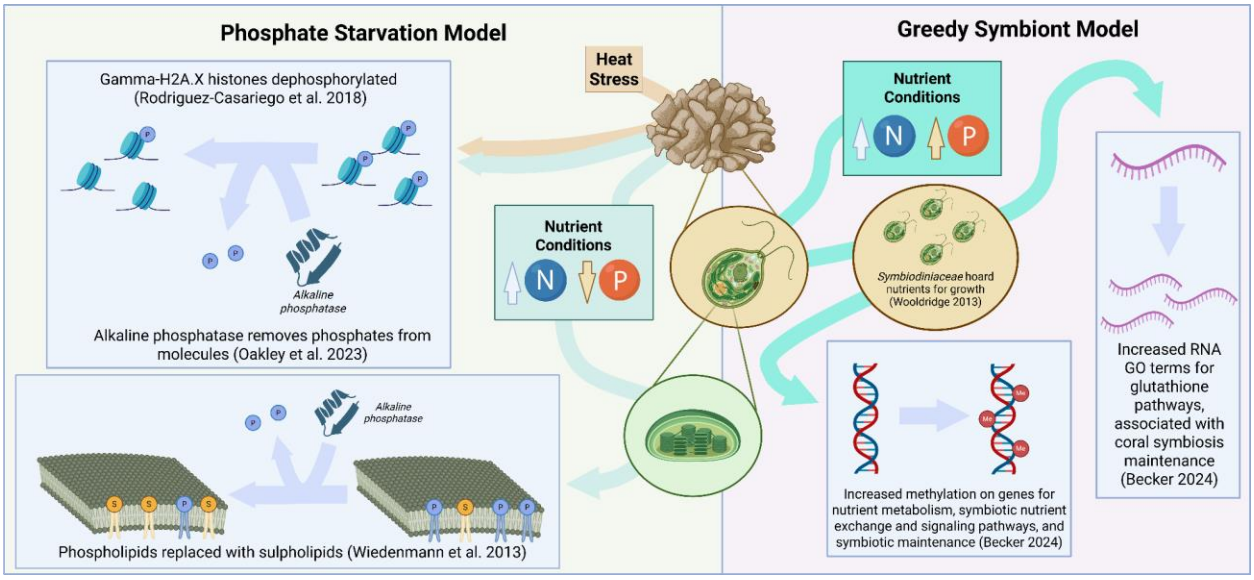

Figure 3. Diagram summarizing major molecular and physiological evidence supporting the Phosphate Starvation Model (PSM) and the Greedy Symbiont Model (GSM) In the case of PSM model, during imbalanced nutrient conditions where nitrogen is elevated relative to phosphorus, phosphate starvation causes phospholipids to be replaced with sulpholipids in the thylakoid membranes of Symbiodineaceae during increased alkaline phosphatase (ALP) activity. During imbalanced conditions with heat stress, gamma-H2A.X histones are dephosphorylated during increased ALP activity. In the case of the GSM Model, when both nutrients are elevated, the internal symbionts accumulate nutrients for population growth, instead of returning photosynthates to the coral host. This is reflected in the coral holobiont methylome where there is increased methylation of genes for nutrient metabolism, symbiotic

nutrient exchange and signaling pathways, and symbiotic maintenance, and in the transcriptome where GO terms for glutathione pathways associated with coral symbiosis maintenance are elevated.

The second model, proposed by Wooldridge (2013), refers to the breakdown of the exchanges between the host and symbionts, which we will refer to as the Greedy Symbiont Model (GSM). Accordingly, under oligotrophic conditions *Symbiodiniaceae* proliferation is nutrient-limited, resulting in an abundance of carbon-based photosynthates which are transferred to the coral host. However, if nutrient loading occurs, the symbionts use the excess carbon for proliferation, thus stopping the exchange of photosynthates to the corals (Fig. 3). This, in turn, disrupts the host's carbon-concentrating mechanisms which provide the CO2 needed by the symbionts, resulting in a negative feedback loop where the exchange of photosynthates and CO2 is further disrupted. Under CO2 limitation, the electron transport chain (ETC) in the photosynthetic apparatus becomes inhibited, causing damage to the photosystems. Similar to the PSM, this damage produces ROSs at a detriment to the symbiotic relationship. It should be noted that while both models assume ROS release is a key component causing the symbiotic breakdown, there is evidence to suggest that ROS release is not the cause of bleaching but rather only correlated with it under certain conditions, or is not released at all during stress (Diaz et al., 2016; Krueger et al., 2015; Schlotheuber et al., 2024; Tolleter et al., 2013). This breakdown of the nutrient exchange model is further supported by Ezzat et al. (2015), which found that photosynthate translocation went down when both nitrogen and phosphate were enriched simultaneously, and Rädecker et al. (2021) which saw a similar breakdown occurring during heat stress.

There is evidence to support both the phosphate starvation and breakdown of exchange models, and, as they are not mutually exclusive, both may play a role in creating the complexity seen in coral response to nutrient stress. The PSM explains why corals can stay healthier when

nitrogen and phosphorus are balanced (Koop et al., 2001) and the breakdown of exchange model explains the reduction of photosynthate translocation during nutrient enrichment (Ezzat et al., 2015; Rädecker et al., 2021) and why algal symbiont populations have been seen to increase during heat stress prior to bleaching (Rädecker et al., 2021). Due to the complex and varied impact nutrient stress has on corals (Tables 1 and 2), it is difficult to create a comprehensive model through collection of physiological data alone. For this, mechanistic approaches are needed, such as through molecular biological techniques. Studies utilizing these techniques are better suited to discover the root causes of stress response, such as in Wiedenmann et al. (2013) where lipidomics were employed to find differences in phospholipid to sulfolipid ratios leading to the proposed PSM. However, relative to the field as a whole there are few studies assessing nutrient stress in corals utilizing molecular biology, leading to large knowledge gaps and unexplained conflicting results.

2. Molecular Mechanisms Underlying Coral Responses to Nutrient Stress

Coral responses to nutrient stress are diverse and often conflicting (Fig. 2) and thus it is pertinent that more mechanistic approaches are used for a universal framework to be developed. For this, molecular approaches can provide the necessary context underlying observed physiological responses, particularly genetics, epigenetics, transcriptomics, and other omics, including metabolomics, proteomics, and lipidomics. These fields provide insights into biological processes occurring within organisms from molecular to cellular scales while modulating and regulating each other, resulting in bottom-up effects which influence an organism's phenotype and its interactions with its environment. Because of this, each field may provide unique information on how organisms react to shifting environmental conditions within their lifetimes or across generations, if the molecular acclimatizations are inheritable.

2.1. Genetic and genomic studies

Many genetic studies have focused on identifying genetic markers for coral populations living in eutrophied conditions. For instance, a gene-by-environment and genotype-by-environment association study found stress tolerance and antioxidant capacity loci associated with heat and nutrient stress effect and responses in *Acropora millepora* (Jin et al., 2016). Although nutrient concentrations were not directly quantified, additional studies correlated poor water quality to Single Nucleotide Polymorphisms (SNPs) in coral genomes. By using seascape genomics, one of these studies identified 65 putative SNPs across three coral species of New Caledonia (southwestern Pacific) associated with higher levels of chlorophyll (Selmoni et al., 2021). Another study in *A. millepora* discovered that two SNP markers were significantly correlated with areas of poor water quality, low surface temperature, and high annual surface temperature range, with 48-58% of the variability in these SNPs being explained by nitrate concentrations and surface temperature (Jin et al., 2016). Although they did not correlate nutrient stress directly to SNPs, a third study used a Bayesian belief network model and predicted that alleles for a bleaching tolerance gene in that same species would be be higher in areas exposed to high nitrate and sea surface temperature (Jin et al., 2020).

Genetic analyses have also been used to study other components of the coral holobiont. Accordingly, variable evolutionary responses of individual Symbiodineaceae genotypes were seen when exposed to increases in temperature and nitrogen as they adapted to their environment. While some showed decreased chlorophyll content, photosynthetic efficiency, and growth rate, others responded oppositely (Bayliss et al., 2019). Similarly, differences in Symbiodineaceae species in coral hosts in eutrophied and ambient treatments have been identified using Internal Transcribed Spacer (ITS) 2 ribosomal DNA (Hall et al., 2018), with these regions even being used to find a significant relationship between symbiont species and nitrate levels *in situ* (Bai et al., 2024). *Symbiodinaceae* ITS gene sequencing showed lower levels of diversity in an impacted reef when nutrient levels were elevated, indicating potential

stress (Bai et al., 2024). Metagenomics were used to find how the structure and function of microbial communities in the coral holobiont shifted over time. This study found that *Porites compressa* holobiont communities exposed to elevated levels of nitrogen and phosphate together saw genes associated with virulence as well as carbohydrate and RNA metabolism become more abundant (R. Vega Thurber et al., 2009).

Collectively, genetic and genomic studies have identified loci and holobiont characteristics associated with nutrient stress and eutrophication, offering valuable insights into coral responses under challenging conditions. While these approaches tend to focus on specific components or long-term adaptive signals, they complement other lines of research by highlighting historical and regional patterns of nutrient exposure, especially in systems with sustained eutrophication or across multiple generations, and underscore the importance of integrating genetic, physiological, and environmental data to achieve a more holistic understanding of nutrient stress in corals.

2.2. Epigenetic studies

Changes in environmental conditions must be met by appropriate acclimatory responses modulating phenotypic states. Such plasticity is driven by the combination between genetic diversity and the modulation of gene function through epigenetic regulatory mechanisms (Ecker et al., 2018; Vogt, 2022). Epigenetics, defined as “the study of molecules and mechanisms that can perpetuate alternative gene activity states in the context of the same DNA sequence” (Cavalli & Heard, 2019) accounts for both context-dependent and independent modifications in genome function, driven by shifting energetic states in the cell resulting from changing in environmental parameters (Wallace & Fan, 2010).

A study from Rodriguez-Casariego et al. (2018) provided one of the first links between nutrient metabolism, thermal stress and epigenetic regulation in corals, finding that when occurring concurrently with thermal stress, nutrient enrichment was associated with gamma-H2A.X formation (phosphorylation of the histone variant H2A.X, also known as the “guardian of the genome” due to its role in double stranded DNA-repair). However, when only nitrogen was present, gamma-H2A.X levels decreased, suggesting that phosphorus was being depleted by its use in the formation of the gamma-H2A.X foci The links between seawater nutrient regimes and epigenetic regulation in corals were further corroborated by studies establishing linkages between DNA methylation profiles and phenotypes in corals subject to seasonal variation on reefs in Bonaire (Hackerott et al., 2023). A study by Becker (2025), provided additional insights by using a high-resolution whole genome DNA methylation approach, Whole Genome Bisulfite Sequencing (WGBS). Here, *Pocillopora* corals exposed to low level, long term *in situ* nutrient enrichment experienced increased symbiont densities and higher levels of DNA methylation on genes involved in nutrient metabolism, symbiotic nutrient exchange and signaling pathways, and symbiotic maintenance. Concurrently, genes for environmental response and regulation for these same corals had lower levels of DNA methylation which was associated with decreased gene expression.

Overall, the development of epigenetic studies in marine organisms, and notably in coral reefs, has proven to be extremely challenging for multiple reasons ranging from methodological to logistic. However, more and more studies are being published, progressively filling the many gaps still existing in this field, most commonly studying DNA methylation and in some cases (although less) histone modifications (Fuller, Mansoor, Guzman, et al., 2025; Fuller, Mansoor, Jeanne Dit Fouque, et al., 2025) and small RNA regulation (Ashey et al., 2025) predominantly during responses to thermal stress. Yet, in the case of nutrient stress, epigenetic studies are still largely underdeveloped. Among those, only a single study has implemented analyses with

enough resolution to link DNA methylation levels with the expression of particular genes during responses to nutrient stress (D. Becker, 2025). Thus, additional efforts are required to fully elucidate not only the general contribution of epigenetic regulation to environmental nutrient regimes, but especially to understand the mechanistic basis linking environmental to energetic to epigenetic to ecological responses in corals. For this purpose, more laboratory-based experimental studies will be required in order to control the multiple variables contributing to these responses, which will complement the growing amount of observational studies coming from the field, striking a better balance between mechanistic and ecologically realistic studies.

2.3. Transcriptomic studies

Transcriptomic analyses have been among the most implemented molecular approaches in coral molecular ecology (Cleves et al., 2020), linking environmental change to physiological processes (Barshis et al., 2013). For instance, it has been reported that *Stylophora pistillata* corals upregulated genes involved in ion transporter activity and downregulated genes linked to phospholipid biosynthesis under low phosphorus conditions (Page et al., 2025). Similarly, nitrogen limitation in *Cladocopium goreaui* cultures led to the upregulation of genes linked to nutrient transport. However, when heat stress was combined with nitrogen limitation, genes involved in apoptosis and antioxidant response were also upregulated (Zhou et al., 2021). Phosphorus-starved *Fugacium kawagutii* cultures upregulated genes involved in heat stress responses and energy production (S. Lin et al., 2019). Importantly, only two studies used a standard nutrient enrichment treatment. Accordingly, a short-term ammonium enrichment and thermal stress experiment on *Acropora aspera* colonies reported enriched GO terms associated with nutrient stress, metabolism, apoptosis, protein synthesis and degradation, and photosynthesis (Rosic et al., 2014). In addition, a long-term nutrient stress experiment found that *Pocillopora* corals under nutrient stress, which caused increased symbiont densities, were associated with GO terms related to glutathione pathways for redox balancing between host and

symbiont as well as protein synthesis and glucose metabolism for symbiosis maintenance (D. Becker, 2025).

Interestingly, several studies have exposed corals and symbionts to extreme nutrient conditions. One of them exposed *Duncanopsammia peltata* corals to chronic and extremely high nutrient concentrations (roughly 6.5 times higher nitrate and 8 times higher phosphate than the highest reported reef concentrations), identifying changes in molecular interaction networks associated with fatty acid (FA) metabolism, oxidative phosphorylation, and immunity (Huang et al., 2025). Similarly, exposure of *Pocillopora damicornis* to high ammonium concentrations (100 uM/l) resulted in the upregulation of transcripts involved in apoptosis and downregulation of transcripts involved in metabolism and signal transduction (Yuan et al., 2017). Extreme conditions were also studied in the case of symbionts, such as phosphate limitation in clade A symbiont cultures (882 uM/l nitrate and 2 uM/l phosphate). These experiments revealed a downregulation of genes for phosphorous metabolism, which was exacerbated by the incorporation of heat stress, along with the downregulation of genes involved in nitrogen intake, assimilation, photosynthesis, and photosynthate transporters, while upregulating genes for general metabolism, FA degradation, and oxidative phosphorylation (Li et al., 2024). *Cladocopium goreaui* cultures exposed to elevated nitrogen (up to 441 uM) and heat stress showed lower expression of photosynthesis-related genes (Huang et al., 2025). Finally, *Fugacium kawagutii* cultures exposed to high levels of dissolved organic phosphorus (a form associated with anthropogenic disturbance) upregulated processes associated with photosynthesis and stress response (S. Lin et al., 2019).

Although few studies utilized *in situ* research, one of them identified the differential expression of the transcription factor NF-κB (linked to immune and stress response) in *Galaxea fascicularis* corals, roughly 2 times higher on eutrophied reefs compared to pristine reefs (Z. Lin et al.,

2017). In the case of *Duncanopsammia peltata* corals from an unprotected eutrophied reef, conflicting transcriptomic results were reported depending on the methods used (Huang et al., 2025). Lastly, field manipulation studies assessing microbial communities have been also implemented, such as the case of water nutrient enrichment using fertilizer release Jessen et al. (2013). This work used 16S genes to identify higher amounts of nitrogen fixing and denitrifying bacterial species in high nutrient treatments, although resulting nutrient concentrations were not measured. Bai et al. (2024) positively correlated bacteria and archaea communities to nitrate levels using 16S genes. They found that corals in higher nutrient environments had higher levels of *Firmicutes*, a class of bacteria potentially beneficial under stress, and that holobiont bacterial communities in a protected reef had higher interconnectivity, suggesting greater stability.

Transcriptomic studies have been influential in advancing understanding of coral nutrient stress, especially through work on free-living Symbiodiniaceae cultures. Their extension to the intact coral holobiont will further enhance ecological relevance, particularly regarding host regulation of symbiont nutrient supply (Cui et al., 2022). Differences among experimental designs (such as nutrient ratios that induce phosphorus limitation, elevated nutrient concentrations relative to reef conditions, or an exclusive focus on molecular responses) highlight the value of future work that more closely mirrors naturally occurring environmental conditions. Thus, integrating ecologically realistic nutrient manipulations with physiological validation will strengthen links between transcriptomic patterns and functional outcomes, helping to build a more comprehensive picture of nutrient stress mechanisms in corals.

2.4. Other omics approaches

The lipidomics-based work of Wiedenmann et al. (2013), in which the PSM was proposed (see section 1.4), represents one of the most important omic approaches. This work also

incorporated proteomics, revealing significantly elevated alkaline phosphatase (ALP) activity (an enzyme responsible for liberating phosphate from molecules such as phospholipids (Lapointe, 1997)) in symbionts under nutrient-imbalanced conditions. A complementary field-based lipidomic study revealed that eutrophication led to higher quantities of lipids and lipid profiles associated to coral poor health (Kim et al., 2021). Further proteomic evidence from a reciprocal transplant experiment showed that, upon transplant to nutrient enriched environment, *Stylophora pistillata* corals displayed stress responses including reduced antioxidant activity likely caused by the UV attenuation associated with the eutrophication (Kramarsky-Winter et al., 2009). Studies focusing on coral symbionts also reported enzymatic stress responses under high nutrient conditions, including reduced antioxidant activity, along with the increase of biomarkers of lipid peroxidation in *Cladocopium goreaui* (Huang et al., 2025). Oakley et al. (2023) used proteomic approaches in free-living *Symbiodinium microadriaticum*, further supporting these findings by showing that when treatments with N:P ratios approximated the Redfield ratio, proteomes converged regardless of total nutrient concentrations. In contrast, imbalanced nutrients—in particular when combined with thermal stress—led to enrichment of proteins associated with photosynthesis, lipid metabolism, and phosphate acquisition, including increased ALP activity. Finally, different efforts have used microbiomic approaches to document shifts in the coral holobiont during eutrophication (e.g., Thurber et al. (2009)), including links between ammonium enrichment during disturbances to microbial communities and disease outbreaks. (C. C. Becker et al., 2024).

However, omics approaches beyond genomics and transcriptomics remain underdeveloped, with metabolomics and glycomics largely unexplored. Given their ability to more directly capture the realized phenotype of corals (as demonstrated by Wiedenmann et al. (2013)) these approaches represent a significant opportunity to advance the field. Integrating such data with existing molecular and physiological studies will be key to resolving the mechanistic links

between nutrient stress and coral holobiont function, and to developing more robust theoretical frameworks.

2.5. Molecular evidence for mechanistic models of coral nutrient stress

Of the studies reviewed above, the results of four of them provide evidence for the two proposed mechanistic models for nutrient stress (Fig. 3). Wiedenmann et al. (2013) proposed the PSM based on the ratios of phospholipids to sulpholipids in Symbiodineaceae lipidomes paired with increased ALP activity in conditions of high nitrogen and low phosphorus. Under similar nutrient conditions but with the addition of thermal stress, Rodriguez-Casariego et al. (2018) found that coral gamma-H2A.X histones became more dephosphorylated. In support of these results, Oakley et al. (2023) saw nutrient imbalance increasing abundances of proteins associated with lipid metabolism and photosynthesis, as well as elevating ALP activity in corals when high N:P ratios, both with and without thermal stress.

The findings of these studies reinforce each other as ALP could dephosphorylate histones and phospholipids, lipid metabolism proteins being required for catalyzation of phospholipids, and photosynthesis proteins being utilized to stabilize compromised photosynthetic machinery. However, though studies have observed ALPs dephosphorylating histones (Ekman, 1991; Tuleva et al., 1998) and phospholipids (Ehle et al., 1985; Santos et al., 2022) under specific conditions, whether they play this role in the coral holobiont has not been explored. Finally, an interesting caveat for the PSM from Huang et al. (2025) is that elevated ALP activity was also detected in corals under balanced but elevated nutrient conditions. This could provide a bridge between both models, or indicate that ALP activity may be involved in a more general stress response rather than just one due to nutrient imbalance. Thus, further research on ALP's function in coral stress response is needed.

On the other hand, only a study by Becker (2025) found evidence consistent with the GSM, but combining two different omic approaches. Accordingly, epigenomic analyses revealed increased levels of DNA methylation in genes linked to responses to nutrient stress and in symbiosis such as nutrient metabolism, symbiotic nutrient exchange and signaling pathways, and symbiotic maintenance. In addition, transcriptomic analyses identified an increase in RNA GO terms for glutathione pathways which the author discussed as having been associated with coral symbiosis maintenance. Both of these results occurred in tandem with increased symbiont densities in the corals.

Outside of the established models, there were various studies which found unique alternative mechanisms (Fig. 4). For instance, elevated nitrogen levels (both alone and in tandem with phosphorus) seem to drive changes in holobiont bacterial communities towards bacteria that aid in stress tolerance or interact with nitrogen, while making them less connected and thus less stable (Bai et al., 2024; Jessen et al., 2013). Oakley et al. (2023) found that under nutrient imbalance, proteins related to metabolism and photosynthesis increased while population growth was significantly reduced, indicating a decoupling of photosynthesis and cell proliferation under phosphate stress. Huang et al. (2025) discovered a transcriptional basis for a mechanism of nutrient stress, supported by the upregulation of symbiont transcripts linked to antioxidant activity and fatty acid metabolism. Fatty acid (FA) catabolism stimulated by lipid peroxidation may generate ATP that supports cellular maintenance processes, including protein repair via HSP90 or enhanced alkaline phosphatase (ALP) activity to recover phosphate under phosphorus stress, consistent with the PSM. Elevated ALP activity could also reflect increased extracellular ATP signaling, which has been associated with immune responses related to inflammation or cell death (Trautmann, 2009). In addition, ALP has been implicated in coral calcification by hydrolyzing pyrophosphates that inhibit aragonite precipitation (Domart-Coulon et al., 2001), offering a potential explanation for reports of elevated calcification under

high-nutrient conditions (Ezzat et al., 2016), although direct mechanistic links remain to be established. BothHuang et al. (2025) and Kramarsky-Winter et al. (2009) also reported reduced antioxidant activity, possibly reflecting ROS levels that exceed antioxidant capacity and thereby stimulate antioxidant pathway regulation. Notably, Huang et al. (2025) observed contrasting results between analytical approaches, with KEGG enrichment indicating increased fatty acid metabolism signals, while GSEA suggested downregulation of these pathways; lipid catabolism, however, was consistently identified as enriched.

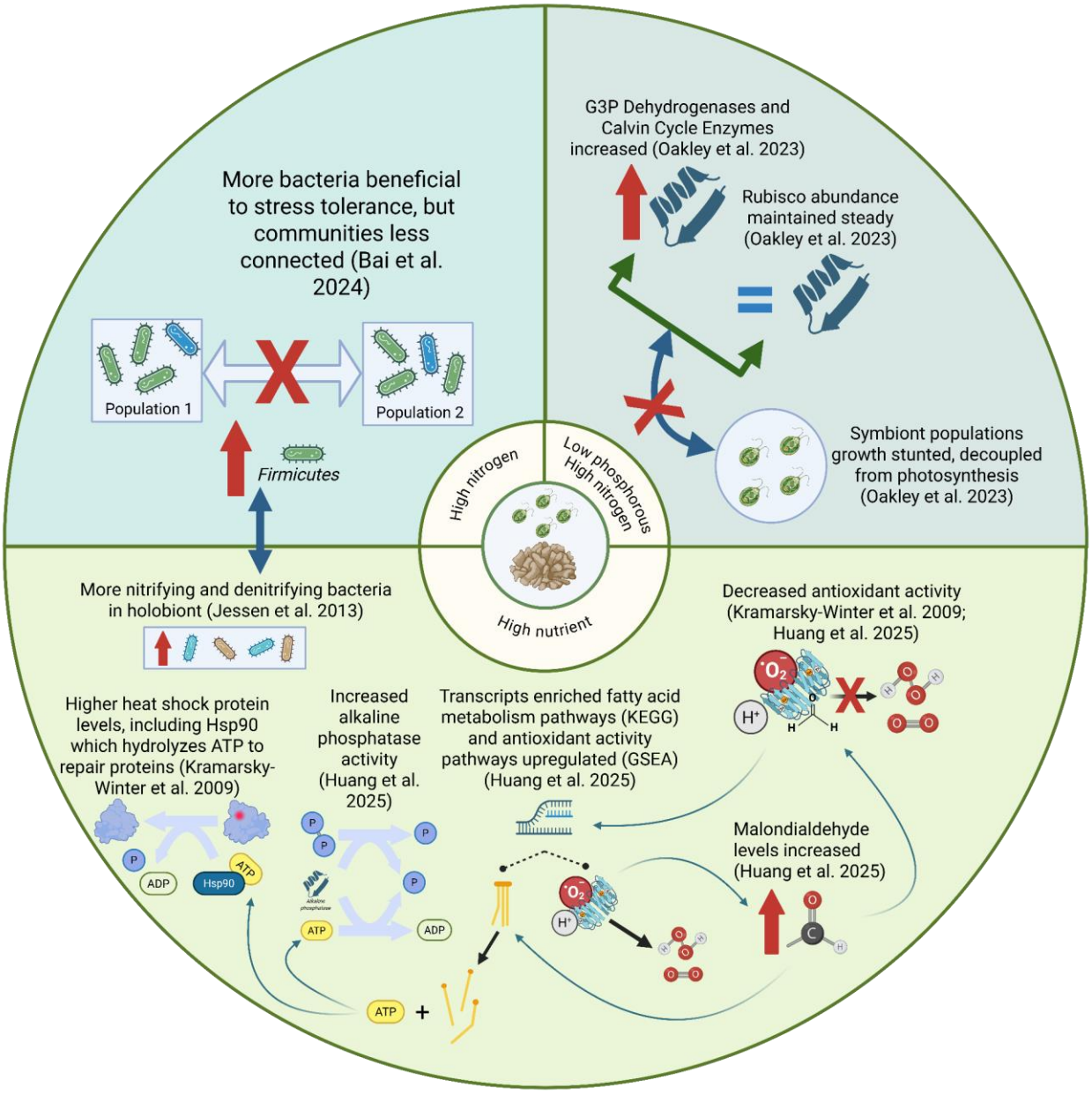

Figure 4: Omic mechanisms triggered by nutrient stress on the coral holobiont. High nitrogen levels modify the holobiont's bacterial communities by increasing bacteria associated with stress tolerance and biological nitrogen cycling while lowering the connectivity of bacterial communities across colonies. In the case of free living symbionts, high nitrogen and low phosphorus conditions cause photosynthesis-related proteins to be maintained or increased while symbiont population growth is decreased. As a result, photosynthesis is prioritized over growth. In the case of high overall nutrient conditions, transcriptional antioxidant activity pathways are upregulated due to increased levels of ROSs, as suggested by the increase in malondialdehyde (a byproduct of lipid peroxidation) resulting in the suppression of antioxidant activity. Increased levels of malondialdehyde are also linked to lipid peroxidation, as reflected by the upregulation of transcripts involved in fatty acid metabolism pathways, resulting in catabolism of lipids and production of ATP. The produced ATP can then be used by Hsp90 to repair proteins, or degraded by elevated levels of ALP to recover phosphate or reduce inflammation. Additionally, the increased ALP activity in turn hydrolyzes pyrophosphates, stimulating calcification.

3. Conclusions

Nutrient stress represents a multiscalar and context-dependent driver of coral reef decline, whose effects are shaped by nutrient identity, concentration, stoichiometry, source, species-specific traits, and interactions with additional stressors such as warming and eutrophication. While decades of physiological and ecological studies have established broad patterns in coral responses to nutrient enrichment, they have also revealed substantial variability that cannot be reconciled without mechanistic insight. Molecular approaches (spanning genetics, epigenetics, transcriptomics, and other omics) have begun to illuminate the underlying processes governing nutrient stress, providing empirical support for both the Phosphate Starvation and Greedy Symbiont models as well as evidence for novel mechanisms, highlighting their potential complementarity. However, these approaches remain underutilized, unevenly distributed across molecular scales, and often constrained by ecologically unrealistic experimental designs or a lack of integration with physiological outcomes. Advancing the field will require coordinated, hypothesis-driven studies that combine ecologically relevant nutrient manipulations with multi-omic profiling and validated phenotypic measurements in intact coral holobionts. Such efforts

526 are essential not only to resolve long-standing uncertainty surrounding nutrient stress
527 mechanisms, but also to refine predictive frameworks for coral resilience and inform effective
528 management strategies in an increasingly eutrophied and warming ocean.
529

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Supplement

Supplementary Table S1: Changes to coral physiology under various nutrient and secondary stressor conditions. A solid row separation indicates a new study, but a dashed separation indicates a different treatment, group, or species within the same study. Treatment/Condition is denoted as a combination of nitrogen condition - high or low (HN and LN respectively) - phosphorus condition - high or low (HP and LP respectively) and any additional stressors. Treatment/Condition is not differentiated between forms of each nutrient, such as nitrate and ammonia for nitrogen. Changes in physiological parameters were reported as an increase (+), decrease (-), or no difference (=) when compared to the studies controls or ambient conditions, with a star indicating that result was reported to be significant by that study. Percent changes were shown for studies that included them, as well as studies which did not include them but provided the information required to calculate them. Reported results are either relative to controls, low nutrient treatments, or temporal environmental differences depending on the study's experimental design. Exact nutrient ranges and forms reported by each study can be found in Supplementary Table S3, if reported by said study.

Conditions	Type	Species	Bleaching	Mortality	Disease	Growth	Calcification	Skeleton Density	Paper
HNHP	Field	*Pocillopora spp.*							Becker et al. 2021
HN & Thermal Stress	Tank	*Turbinaria reniformis*					=		Béraud et al. 2013
HNHP & Disease	Field	*Montastrea annularis & Montastrea franksii*		+*	+*				Bruno et al. 2003
HNHP	Tank	*Acropora polystoma*				500% +*			Buckingham et al. 2022
HNLP	Tank	*Acropora polystoma*	+			=			
HN & Thermal Stress	Field	*Acropora spp.*	+*	=					Burkepile et al. 2020
HN & Thermal Stress	Field	*Pocillopora spp.*	+*	+*					
HN & Thermal Stress	Field	*Porites spp.*	=	=					
HN & Thermal Stress	Field	*Porites spp.*	=	=					

HN	Tank	*Pocillopra damicornis*				-	Courtial et al. 2018
HN & Thermal Stress	Tank	*Pocillopra damicornis*				-	
HN	Field	*Acropora spp.*	+				Donovan et al. 2020
HN & Thermal Stress	Field	*Acropora spp.*	+				
HN	Field	*Pocillopora spp.*	+				
HN & Thermal Stress	Field	*Pocillopora spp.*	+				
HNHP	Tank	*Stylophora pistillata*				+*	Ezzat et al. 2015
HN (NO_4)	Tank	*Stylophora pistillata*				+*	
HN (NO_3)	Tank	*Stylophora pistillata*				+	
HN & Thermal Stress	Tank	*Turbinaria reniformis*				-*	Ezzat et al. 2016
HN	Tank	*Stylophora pistillata*				+*	Ezzat et al. 2019
HN & Thermal Stress	Tank	*Stylophora pistillata*	-*			+*	
HN	Tank	*Acropora millepora*	=	=	=		Fabricius et al. 2013
HN & Thermal Stress	Tank	*Acropora millepora*		+*	=		
HN & Organic Enrichment	Tank	*Acropora millepora*		=	=		
HN & Organic Enrichment & Thermal Stress	Tank	*Acropora millepora*		=	=		
HN	Tank	*Montipora tuberculosa*	=	=	=		
HN & Thermal Stress	Tank	*Montipora tuberculosa*		+*	=		
HN & Organic Enrichment	Tank	*Montipora tuberculosa*		=	=		
HN & Organic Enrichment & Thermal Stress	Tank	*Montipora tuberculosa*		=	=		
HN (NO_3−)	Tank	*Stylophora pistillata*				-*	Fernandes de Barros Marangoni et al. 2020
HN (NH_4+)	Tank	*Stylophora pistillata*				=	
HN (NO_3−) & Thermal Stress	Tank	*Stylophora pistillata*				-*	
HN (NH_4+) &	Tank	*Stylophora pistillata*				-*	

Thermal Stress								
HN	Tank	*Stylophora pistillata*			60% -			Ferrier-Pagès et al. 2000
HNHP	Tank	*Stylophora pistillata*			25% -			
HP	Tank	*Stylophora pistillata*			30% -			
HNHP	Tank	*Pocillopora acuta*				-		Fox et al. 2021
HNHP	Tank	*Porites compressa*				-		
HN	Field	*Porites lutea & Porites lobata*			-			Gil 2013
HN	Field	*Acropora longicyathus*		=	-*	+*	=	Koop et al. 2001
HNHP	Field	*Acropora longicyathus*		=	-*	=		
HP	Field	*Acropora longicyathus*		=	-*	+*	-*	
LN	Field	*Acropora longicyathus*		=	=	=	=	
LNLP	Field	*Acropora longicyathus*		=	=	=	=	
LP	Field	*Acropora longicyathus*		=	=	=	=	
HN	Field	*Acropora palifera*			=	-*		
HP	Field	*Acropora palifera*			-*	+*		
LN	Field	*Acropora palifera*		=	=	=	=	
LNLP	Field	*Acropora palifera*		=	=	=	=	
LP	Field	*Acropora palifera*		=	=	=	=	
HN	Field	*Pocillopora damicornis*		+*		-*		
HNHP	Field	*Pocillopora damicornis*		211-271% +*				
HP	Field	*Pocillopora damicornis*		+*		-*		
LN	Field	*Pocillopora damicornis*		=	=	=	=	
LNLP	Field	*Pocillopora damicornis*		=	=	=	=	
LP	Field	*Pocillopora damicornis*		=	=	=	=	
HN	Field	*Stylophora pstillata*			-*	=		
HNHP	Field	*Stylophora pstillata*			-*			
HP	Field	*Stylophora pstillata*			=	-*		
LN	Field	*Stylophora pstillata*		=	=	=	=	
LNLP	Field	*Stylophora pstillata*		=	=	=	=	
LP	Field	*Stylophora pstillata*		=	=	=	=	
HNHP	Tank	*Agaricia tenuifolia*	+	=				Kuntz et al. 2005
HNHP	Tank	*Montastrea annularis*	+	=				
HNHP	Tank	*Porites furcata*	=	=				

HN	Field	General Caribbean species		+	404% +			Lapointe et al. 2019
HNHP	Tank	*Stylophora pstillata*		=				Muscatine et al. 1989
HN	Tank	*Acropora cervicornis*		+	-*			Renegar and Riegl 2005
HN & CO2	Tank	*Acropora cervicornis*		+	-			
HNHP	Tank	*Acropora cervicornis*		+	61% -*			
HNHP & CO2	Tank	*Acropora cervicornis*		+	-*			
HP	Tank	*Acropora cervicornis*		+	-*			
HP & CO2	Tank	*Acropora cervicornis*		+	-			
HNLP	Tank	*Euphyllia paradivisa*	+					Rosset et al. 2017
LNHP	Tank	*Euphyllia paradivisa*	=					
LNLP	Tank	*Euphyllia paradivisa*	+					
HN	Meta Analysis	General coral species			-*	11% -*	=	Shantz and Burkepile 2014
HNHP	Meta Analysis	General coral species			-*	=	10% -	
HP	Meta Analysis	General coral species			+	9% +*	9% -	
Nutrient enrichment	Meta Analysis	General coral species			31% -			Shantz et al. 2016
HNHP	Field	*Acropora cervicornis*		-*	-			Shaver et al. 2017
HNHP & Predation	Field	*Acropora cervicornis*		=	=			
HNHP	Tank	*Porites compressa & Montipora caiptata*				56% -*		Silbiger et al. 2018
HNHP	Field	*Agaricia spp.*	400-700% +*					Vega Thurber et al. 2014
HNHP	Field	General Caribbean corals		=	200% +*			
HNHP	Field	*Siderastrea siderea*			100% +			
HN	Tank	*Siderastrea siderea*			+*			Voss and Richardson 2006
HN	Field	*Siderastrea siderea*			+*			
HN & Thermal Stress	Field	*Agaricia spp.*	+	+				Wang et al. 2018
HNHP & Thermal Stress	Field	*Agaricia spp.*	+	=				
HP & Thermal Stress	Field	*Agaricia spp.*	+	=				
HN & Thermal Stress	Field	*Siderastrea siderea*			+			
HNHP & Thermal Stress	Field	*Siderastrea siderea*			+			
HP &	Field	*Siderastrea siderea*			+			

Thermal Stress						
HNLP & UV Stress	Tank	*Montipora foliosa*	+	+		Wiedenmann et al. 2013
Water quality & Thermal Stress	Field	General Great Barrier Reef Species	+			Wooldridge and Done 2009
HN & Thermal Stress	Field	General Great Barrier Reef Species	+			Wooldridge 2009
HNHP	Field	General Florida Keys species		-		Zaneveld et al. 2016
HNHP	Field	General Florida Keys species		+*	+	
HNHP & Predation	Field	General *Porites* corals		+		
HN & Thermal Stress	Field	*Porites spp.*		+*		
HN & Predation	Field	*Porites spp.*		+*	+*	
HN & Thermal Stress	Tank	*Acropora hyacinthus*	+			Zhang et al. 2023

Supplementary Table S2: Changes to coral physiology under various nutrient and secondary stressor conditions. Chl a is the total concentration of Chlorophyll a, R_d is the dark respiration rate, P_{max} is the maximum photosynthetic rate, and F_v/F_m is the maximum photosynthetic efficiency. Solid row separation indicates a new study, but a dashed separation indicates a different treatment, group, or species within the same study. Treatment/Condition is denoted as a combination of nitrogen condition - high or low (HN and LN respectively) - phosphorus condition - high or low (HP and LP respectively) and any additional stressors. Treatment/Condition is not differentiated between forms of each nutrient, such as nitrate and ammonia for nitrogen. Changes in physiological parameters were reported as an increase (+), decrease (-), or no difference (=) when compared to the studies controls or ambient conditions, with a star indicating that result was reported to be significant. Percent changes were shown for studies that included them, as well as studies which did not include them but provided the information required to calculate them. Exact nutrient ranges and forms reported by each study can be found in Supplementary Table S3, if reported by said study.

Conditions	Type	Species	Chl a (total)	R_d	Symbiont Density	P_{max}	F_v/F_m	Paper
HN	Tank	*Stylophora pistillata*	+*		=		=	Fernandes de Barros Marangoni et al. 2020
HN & Thermal Stress	Tank	*Stylophora pistillata*	=		=		-*	
HN & Thermal Stress	Tank	*Turbinaria reniformis*	+*	=		+*		Béraud et al. 2013
HN & Thermal Stress	Tank	*Turbinaria reniformis*	+/+*	=	-*	=		
HN & Thermal Stress	Field	*Porites spp.*						Zaneveld et al. 2016
HNHP	Tank	*Pocillopra damicornis*	+	+	=	+		Courtial et al. 2018
HNHP	Tank	*Euphyllia paradivisa*			+			Rosset et al. 2015
HNHP	Tank	*Turbinaria reniformis*	350% +*					Ezzat et al. 2016
HN	Tank	*Turbinaria reniformis*	=					
HNHP &Thermal Stress	Tank	*Turbinaria reniformis*	280% +*	-*		-*		
HN & Thermal Stress	Tank	*Porites compressa & Montipora caiptata*		+			=	Silbiger et al. 2018
HN	Tank	*Porites cylindrica*	=	=	=	-*		Nordemar et al. 2003
Water quality & Thermal Stress	Tank	*Porites cylindrica*	=	=	=	-*		
HN & Thermal Stress	Tank	*Euphyllia paradivisa*			+		-	Rosset et al. 2017
HN & Thermal Stress	Tank	*Euphyllia paradivisa*			=		=	
HN & Thermal Stress	Tank	*Euphyllia paradivisa*			+		=	
HN & Thermal Stress	Tank	*Acropora polystoma*			600% +*		=	Buckingham et al. 2022
HN & Thermal Stress	Tank	*Acropora polystoma*			=		-*	
HN & Thermal Stress	Tank	*Stylophora pistillata*	+*	-*	+*	-*		Ezzat et al. 2015
HN & Thermal Stress	Tank	*Stylophora pistillata*	+*		+*	=		
HN & Thermal Stress	Tank	*Stylophora pistillata*	+*	+*	+*	-*		
HNLP	Tank	*Stylophora pistillata*		+*		+*		Ferrier-Pagès et al. 2000
LNHP	Tank	*Stylophora pistillata*		+*		+*		
LNLP	Tank	*Pocillopora damicornis*	+*					Snidvongs and Kinzie 1994
HNHP	Tank	*Pocillopora damicornis*	=					
HNLP	Tank	*Pocillopora damicornis*	=					

HNLP	Field	*Pocillopora damicornis*	=		=	=	=	Koop et al. 2001
HNLP	Field	*Pocillopora damicornis*	=		=	=	=	
HNHP	Field	*Acropora longicyathus*	=			=	=	
HN	Field	*Acropora longicyathus*	=			=	=	
HN	Field	*Pocillopora damicornis*	=		=	=	=	
HP	Field	*Acropora longicyathus*	=			=	=	
HNHP	Field	*Acropora palifera*	=			=	=	
HN & CO2	Field	*Acropora palifera*	=			=	=	
HP & CO2	Field	*Acropora palifera*	=			=	=	
HNHP & CO2	Field	*Stylophora pstillata*	=			=	=	
HP	Field	*Stylophora pstillata*	=			=	=	
HNHP	Field	*Stylophora pstillata*	=			=	=	
LP	Field	*Acropora longicyathus*			+*			
LNLP	Field	*Stylophora pstillata*	+*	=	+*	=		
LN	Field	*Stylophora pstillata*	=	+	+*	+		
LP	Field	*Stylophora pstillata*	+*					
LNLP	Tank	*Stylophora pstillata*	+*		+*			Muscatine et al. 1989
LN	Tank	*Stylophora pstillata*	=		=			
LP	Tank	*Stylophora pstillata*	+*		+*			
LNLP	Tank	*Stylophora pistillata*		+*		+*		Ferrier-Pagès et al. 2000
LN	Tank	*Pocillopora damicornis*	=		=			Stambler et al. 1991
LP	Tank	*Pocillopora damicornis*	+*		+*			
LNLP	Tank	*Pocillopora damicornis*	+*		+*			
HP	Meta Analysis	General coral species	+*		+	+		Shantz and Burkepile 2014
HNHP	Meta Analysis	General coral species	=		=	=		
HN	Meta Analysis	General coral species	+*		+			
HP	Field	*Pocillopora spp.*	=	12% +	54% +*	29% +*		Becker et al. 2021
HNHP	Tank	*Pocillopora verrucosa*		40% +*	60% -	30% -*	-*	Pogoreutz et al. 2017
HN	Tank	*Acropora millepora*					+	Fabricius et al. 2013

HP	Tank	*Montipora tuberculosa*				+		
HN	Tank	*Acropora millepora*				-*		
HP	Tank	*Montipora tuberculosa*				-*		
HNHP	Tank	*Stylophora pistillata*	-*		-*	-*		Ezzat et al. 2019
HNHP	Tank	*Montipora foliosa*			+		-	Wiedenmann et al. 2013
HN	Tank	*Euphyllia paradivisa*	-		-		-	
LN	Tank	*Pocillopra damicornis*	+	=	=	+		Courtial et al. 2018
HN	Tank	*Stylophora pistillata*	+		=		-*	Fernandes de Barros Marangoni et al. 2020
HN	Tank	*Stylophora pistillata*	=		=		-*	
HN & Thermal Stress	Tank	*Stylophora pistillata*	+*		+*		=	
HN & Thermal Stress	Tank	*Stylophora pistillata*	+		+*		+	
HN	Tank	*Acropora hyacinthus*			=			Zhang et al. 2023
HN	Tank	*Acropora hyacinthus*			+*			
HN	Tank	*Acropora hyacinthus*			-*			
HP	Tank	*Acropora hyacinthus*			+*			
HNHP	Tank	*Porites compressa*	+	=	+*	=	+*	Fox et al. 2021
HNHP	Tank	*Pocillopora acuta*	+	=	+*	+*	+*	
HN	Field	*Acropora muricata*	+		+			Chauvin et al. 2011
HN	Tank	*Acropora aspera*	=		=		+	Rosic et al. 2014

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908 Supplementary Table S3: Treatment/Condition for studies from Tables 1 and 2 and
909 Supplementary Tables S1 and S2 which provided these details for their research.
910 Concentrations are in μM and are labeled as the nitrogen condition - high or low (HN and LN
911 respectively) or the form of nitrogen used - phosphorus condition - high or low (HP and LP
912 respectively) - depletion levels for each, or the ambient/control conditions if stated.

LN	HN	Nitrate low	Nitrate high	Ammonium low	Ammonium high	LP	HP	HNHP	HNLP	LNHP	LNLP	Nutrient depletion (N & P)	Ambient/ Control (N & P)	Type	Paper
					3								0.7 & 0.5	Tank	Béraud et al. 2013
			1 to 6.4		1 to 11		0.9 to 4.6						1.085 & 0.183	Field	Bruno et al. 2003

								4.5 & 0.6	73 & undetectable	0.06 & 5.7		Neither detectable		Tank	Buckingham et al. 2022
		2.8	7.1	2.7	9.4								0.28 & 0.14	Field	Burkepile et al. 2020
		0.37	4.4-11.4											Field	Chauvin et al. 2011
								3 & 0.5				<0.1 & <0.05	0.5 & 0.1	Tank	Courtial et al. 2018
			2.5		2.5			3 & 1					0.5 & 0.05	Tank	Ezzat et al. 2015
	2							2 & 0.5					0.5 & 0.1	Tank	Ezzat et al. 2016
					2							0.08 & 0.05	0.5 & 0.2	Tank	Ezzat et al. 2019
			4.23										0.23 & N/A	Tank	Fabricius et al. 2013
			3		3								0.5 & 0.2	Tank	Fernandes de Barros Marangoni et al. 2020
		0.5		0.04	19.5	0.09	2.8	18.5 & 2.4					0.54 & 0.09	Tank	Ferrier-Pagès et al. 2000
		1	7			0.06	2.24	7 & 2.24			1 & 0.06		0.1 & 0.06	Tank	Fox et al. 2021
0.66	5.8												0.6 & N/A	Field	Gil 2013
3.85 to 14.39	14.24 to 39.14			0.9 to 11.45	11.3 to 36.2	0.52 to 2.34	2.4 to 5.14	36.2 & 5.14			0.9 & 0.5		0.65/1.34 & 0.2/0.16	Field	Koop et al. 2001
		2.5	7.5	5	25	0.5	2.5	32.5 & 2.5			7.5 & 0.5			Tank	Kuntz et al. 2005
					20		2	20 & 2						Tank	Muscatine et al. 1989
			16										1.4-2.1	Tank	Nordemar et al. 2003
		5	10			2	4							Tank	Renegar and Riegl 2005
								6.5 & 0.3					0.7 & 0.006	Tank	Rosset et al. 2017
								6.5 & 0.3	38 & 0.189	0.006 & 3.6	0.7 & 0.0006			Tank	Rosset et al. 2017
		0.62			15		1.2	15 & 1.2					1 & 0.3	Tank	Snidvongs and Kinzie 1994
					15	0.5	2		15 & 0.5				2 & 0.1	Tank	Stambler et al. 1991
								3.91 & 0.27					1.15 & 0.035	Field	Vega Thurber et al. 2014
			3					2.85 & .127					0.557 & 0.025	Field	Voss and Richardson 2006
								3.18 & 0.34					0.71 & 0.14	Field	Wang et al. 2018
									3 & 0.07			0.7 & 0.006	6.5 & 0.3	Tank	Wiedenmann et al. 2013
														Field	Zaneveld et al. 2016
			9		9									Tank	Zhang et al. 2023

Supplemental Citations

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