

LETTER OPEN ACCESS

A New Conceptual Model of Tropical Seagrass Eutrophication: Evidence for Single Nutrient Management

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Correspondence: Bridget F. Shayka (bshayka@umich.edu)**Received:** 1 May 2024 | **Revised:** 18 July 2025 | **Accepted:** 24 July 2025**Funding:** Support for this study was provided by the David and Lucile Packard Foundation and National Science Foundation OCE (grant no. 1948622) to J.E.A.**Keywords:** epiphytes | eutrophication | management | nitrogen | nutrient pollution | phosphorus | phytoplankton | production | wastewater

ABSTRACT

Nutrient enrichment is one of the greatest threats to seagrass ecosystems globally. Current management is based on a temperate conceptual model of seagrass eutrophication where epiphytes and then phytoplankton cause light limitation and seagrass die-off. However, producers in tropical and subtropical systems respond differently to nutrients, suggesting a need for an updated conceptual model for these ecosystems. Using a long-term multifactorial seagrass enrichment experiment of nitrogen and phosphorus supply rates and ratios, we showed that seagrass growth was enhanced with increased phosphorus but not nitrogen supply and was never inhibited by epiphytes or shifts in seagrass community structure. A parallel experiment showed phytoplankton primarily responded to nitrogen enrichment. Our findings provide evidence for a new nutrient enrichment conceptual model in subtropical and tropical seagrass ecosystems, with a larger role played by phytoplankton. We suggest that management efforts to mitigate nitrogen supply alone may offer an effective starting point for reducing negative impacts of eutrophication, one of the most ubiquitous stressors to these imperiled ecosystems.

1 | Introduction

Nutrient enrichment of coastal waters is one of the most globally ubiquitous stressors, affecting 78% of U.S. coastal waters and 65% of European Atlantic coastal waters (Malone and Newton 2020). Downstream effects from excess fertilizer application and municipal wastewater result in eutrophication, trophic dead ends, and dead zones (Vitousek et al. 1997; Burkholder et al. 2007; Howarth 2008; Lapointe et al. 2019); thus, understanding the mechanisms that drive eutrophication is imperative for establishing standards for wastewater management. Yet, these mechanisms are often disputed (Cloern 2001; Conley et al. 2009) because nutrient enrichment typically occurs via multiple nutrients, which means that the supply rate of individual nutrients, and their ratio, may have differential impacts on primary production in coastal waters (Conley et al. 2009;

Allgeier et al. 2010). Despite being the focus of long-standing ecological inquiry (Redfield 1958; Tilman 1982; Sterner and Elser 2002), how producers respond to multinutrient enrichment remains an outstanding knowledge gap in many ecosystems with critical implications for management, particularly in coastal ecosystems.

Seagrass ecosystems are globally distributed and provide a wide array of services such as coastline protection, fish nursery habitat, nutrient filtration, pathogen control, sediment stabilization, and carbon storage (Dewsbury et al. 2016; Nordlund et al. 2016; Lamb et al. 2017; Moksnes et al. 2021; Shayka et al. 2023). Despite this, they are among the most imperiled ecosystems globally (Dunic et al. 2021) due to myriad human stressors, of which eutrophication is likely the most pervasive (Orth et al. 2006; Burkholder et al. 2007). The effects of eutrophication on

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seagrass have been well-studied in temperate systems. The current conceptual model describes nutrient enrichment leading to overgrowth, first by epiphytes or macroalgae and then phytoplankton, which each can lead to light limitation that reduces seagrass growth and ultimately leads to mortality (Cloern 2001; Lee et al. 2007; McGlathery et al. 2007; Schmidt et al. 2012; Lefcheck et al. 2018). However, the response of seagrass ecosystems to nutrient enrichment in tropical and subtropical environments with comparatively nutrient-poor waters may be different (Cloern 2001; Orth et al. 2006; McGlathery et al. 2007). For example, previous studies in oligotrophic subtropical ecosystems have demonstrated that under nutrient enrichment, epiphytes and macroalgae do not tend to overgrow seagrass and cause light limitation under experimental conditions (Fourqurean et al. 1995; Armitage et al. 2011; Allgeier et al. 2018) or across real-world enrichment gradients (Andskog et al. 2023). However, similar to temperate ecosystems, high levels of nutrient enrichment can increase water-column production, which can cause light limitation and negative impacts on seagrass (Burkholder et al. 2007; Schmidt et al. 2012). Thus, an alternative hypothesis for the mechanisms by which nutrient enrichment affects tropical and subtropical oligotrophic seagrass beds is that seagrass production is not inhibited by epiphytes or macroalgae and can even increase at low and possibly moderate levels of enrichment, but under high nutrient inputs, light limitation from phytoplankton should initiate events that result in seagrass die-offs (Figure 1). Testing this hypothesis is critically important for the management of tropical and subtropical seagrass beds because of the extent to which they are subject to nutrient enrichment, particularly from untreated municipal sources (Buchan 2000; Rangel-Buitrago et al. 2024).

Importantly, because nutrient enrichment typically occurs via inputs from multiple nutrients, an additional challenge for management is that input rates of individual nutrients (nitrogen [N] and phosphorus [P]) and their ratio (N:P) are expected to have differential effects on growth rates across different producer groups, for example, seagrass, phytoplankton, and epiphytes (Redfield 1958; Fourqurean and Zieman 2002; Ferdie and Fourqurean 2004; Orth et al. 2006; Conley et al. 2009). Thus, understanding the extent to which different producer groups in seagrass ecosystems can tolerate various nutrient supply rates and ratios remains a critical knowledge gap. Identifying a point of tolerance for each producer group at different supply rates and ratios is particularly relevant because reducing nutrient inputs to pristine levels is likely impossible due to the extent to which coastal waters are impacted by anthropogenic nutrients. Filling this knowledge gap is imperative to inform effective management in these ecosystems.

Here, we combine a long-term seagrass nutrient enrichment experiment with a complementary water-column experiment to quantify the effects of N and P supply rates and ratios on seagrass and phytoplankton growth rates in a subtropical coastal ecosystem in The Bahamas. Both experiments enriched producers across a factorial gradient of three levels of N and seven levels of P enrichment, creating a continuous gradient of N:P. Doing so allowed us to identify differential responses of each producer group to a range of anthropogenic nutrient enrichment that is typical for tropical and subtropical ecosystems. Specifically, we answered two questions:

Q 1. How do nutrient supply rates and ratios differentially affect seagrass, epiphyte, and phytoplankton growth?

Q 2. What are the optimal N:P ratios for seagrass and phytoplankton growth?

2 | Methods

The study was conducted in the Bight of Old Robinson, Abaco, The Bahamas—a shallow embayment within East Abaco Creeks National Park with a mosaic of seagrass meadows dominated by *Thalassia testudinum*. Twenty-one nutrient enrichment treatments and one control treatment were established on seagrass-dominated benthos and in clear bottles filled with seawater containing naturally occurring phytoplankton. Treatments for each experiment (seagrass and phytoplankton) were created by crossing three nitrogen treatments with seven phosphorus treatments to create 21 N:P treatments unique to each experiment (Supplementary Methods). Seagrass was enriched with fertilizer for 2 years, after which aboveground growth rate, shoot counts, seagrass community composition, herbivory, epiphyte biomass, and seagrass nutrient content (carbon, N, P) were measured. Phytoplankton were enriched with nutrients at the beginning of a 3-day incubation in bottles at the end of the seagrass experiment. Phytoplankton growth rates were quantified by measuring chlorophyll *a* on days 1 and 3. See methodological details for both experiments in the Supplementary Methods.

2.1 | Q1 Analysis

We hypothesized that P supply and N:P would have the strongest effects on growth rates because P is the primary limiting nutrient in this ecosystem (Smith 1984; Allgeier et al. 2010), and nutrient ratios are important predictors of growth (Sterner and Elser 2002). To test this, we used a global linear model: $Growth\ rate = (N \times P) + (N \times Experiment) + (P \times Experiment) + (NP \times Experiment)$. All parameters were standardized from each experiment ($Standardized\ value = (X - mean) / (2 \times sd)$) so that the results could be compared in the same model. N, P, and NP (the N:P ratio) were fixed continuous predictors. “Experiment” was included as a fixed categorical predictor with two levels (seagrass and phytoplankton) to identify differential responses by the producer groups. Model selection via AIC was used to determine the best-fit model (i.e., model with the lowest AIC). If “Experiment” (independent term or interactions) was retained in the best model, we ran independent models for each experiment with standardized data ($Growth\ rate = (N \times P) + N + P + NP$) using AIC to identify the top models for each producer ($\Delta AIC < 5$). To identify other factors that may have contributed to seagrass growth (blade area, blade height, epiphyte biomass, herbivory, community composition [richness, diversity], shoot count, and seagrass nutrient content and ratios [C, N, P, C:N, C:P, N:P]), relationships between growth rate and these other seagrass response measures were quantified using Pearson’s correlation coefficient (Pearson’s *r*), and significance of the Pearson’s *r* values was assessed (*p*-value < 0.05 was significant).

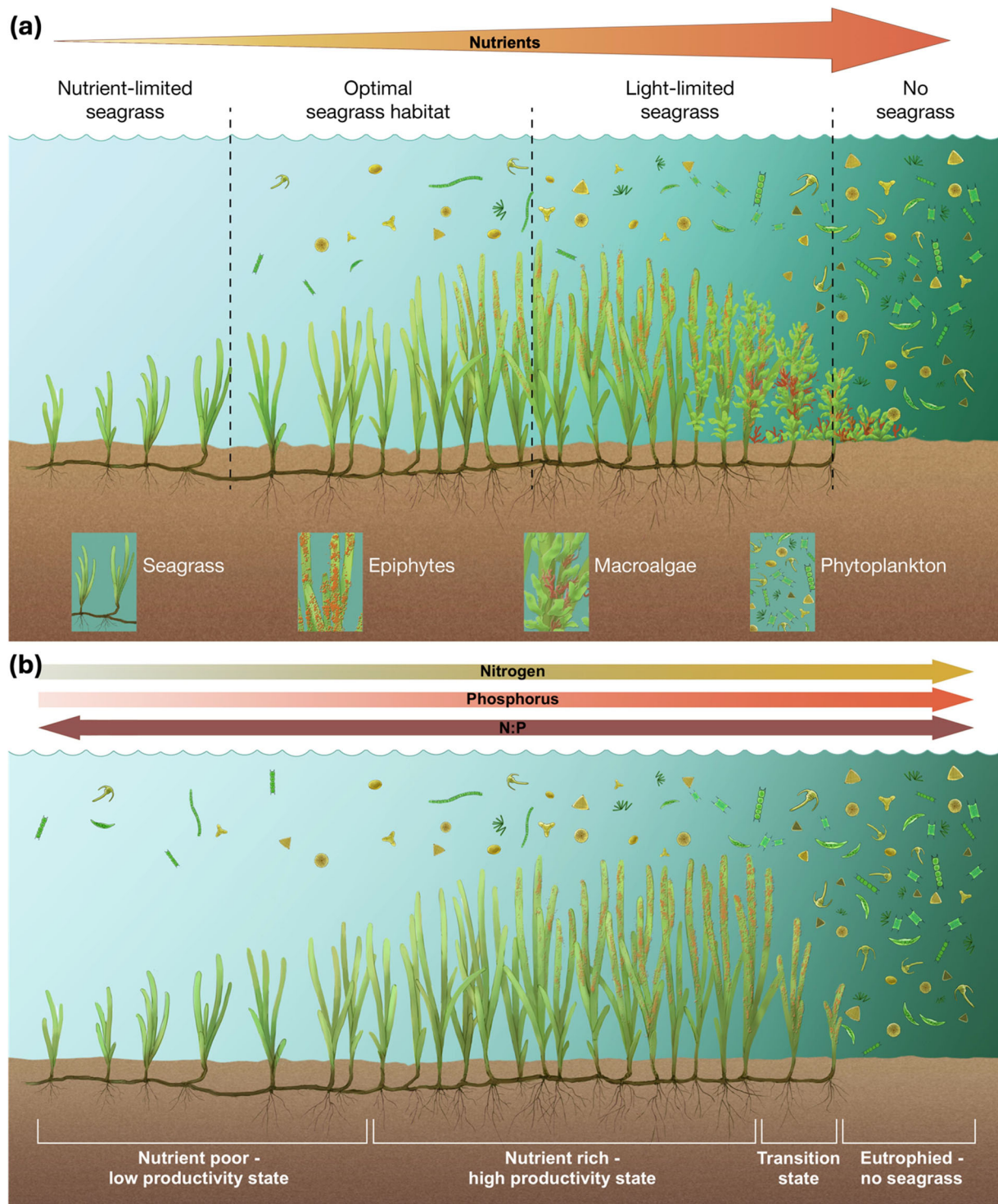


FIGURE 1 | (a) Depiction of current conceptual model for temperate systems: Enrichment leads to overgrowth, first by epiphytes or macroalgae and then phytoplankton. Note in this depiction, nitrogen and phosphorus are not considered independently and are represented as a whole as “Nutrients.” Depiction adapted from Wazniak et al. (2007). (b) Depiction of tested hypothesis for oligotrophic tropical and subtropical systems: Nitrogen and phosphorus affect phytoplankton and seagrass independently and do not cause epiphyte overgrowth but do cause shading by phytoplankton, resulting in ecosystem responses that are different than those in temperate systems. Producers not drawn to scale. Illustrations by John Megahan.

2.2 | Q2 Analysis

We hypothesized that the relationship between growth rate and N:P would be nonlinear and that growth rates would be optimized at 30:1 for seagrass and 16:1 for phytoplankton, based on previous

findings (Redfield 1958; Fourqurean and Zieman 2002). Linearity was tested by comparing the AIC of Generalized Additive Models (GAMs) ($Growth\ rate = s(NP)$) and linear models ($Growth\ rate = NP$) for each experiment on untransformed data. We used the best-fit line (GAM or linear) for each experiment based on the

model with the lowest AIC to determine the N:P ratio at which the growth rate was highest.

To better inform management recommendations, we used our data to predict growth rates under a broad range of nutrient enrichment scenarios that are representative of real-world conditions in coastal ecosystems (see Figure 3 caption for references). To do this, we used individual linear models for unstandardized seagrass and phytoplankton growth rates ($Growth\ rate = N + P + NP$) with N, P, and N:P as independent continuous parameters to interpolate our results within the experimental treatment ranges and extrapolate our results to ranges of N and P seen throughout the literature. All analyses for Q1 and Q2 were conducted using R v4.4.0.

3 | Results

Q1: Models that included both experiments showed that P supply had a much stronger effect on seagrass than phytoplankton growth (the latter not being significant) (Figure 2a). N supply doubled phytoplankton growth but inhibited seagrass growth (Figure 2b), and increased N:P had a more negative effect on phytoplankton than seagrass (Figure 2d,e and Table S1). The variables retained in all of the top models ($\Delta AIC < 5$) were: N, P, Experiment, and Experiment $\times$ N (global), P (seagrass growth), and N and N:P (phytoplankton growth) (Figure 2c and Table S2).

Pearson's correlations showed that seagrass growth was not correlated with epiphyte biomass (which was generally low across the enrichment gradient and showed no overgrowth; Figure S1), herbivory, community composition (richness, diversity—demonstrating no increase in macroalgal cover; Figure S1), shoot count, or seagrass nutrient content or ratios (C, N, P, C:N, C:P, N:P) (Table S3). Seagrass growth was positively correlated with blade area (Pearson's $r = 0.91$, p -value = <0.001) and blade height (Pearson's $r = 0.86$, p -value = <0.001) (Table S3).

Q2: Seagrass growth rates decreased nonlinearly (Figure 2d), and phytoplankton growth rates decreased linearly with higher N:P (Figure 2e). Optimal growth rates for both producers were at the lowest N:P treatments (Figure 2d,e).

Interpolating seagrass and phytoplankton growth linearly through the full range of N and P enrichment in our study and extrapolating them to encompass N and P ranges reported in coastal waters helped identify potential responses of seagrass and phytoplankton to relative nutrient loading rates in other coastal ecosystems (Figure 3). Highest seagrass growth rates were found at low N and high P supply, while the highest phytoplankton growth rates were found at high N (Figure 3).

4 | Discussion

The long-standing debate over whether N, P, or both limit primary production in coastal ecosystems has been an obstacle for managing anthropogenic nutrient enrichment. Which nutrient(s) limit primary production can differ geographically, and in particular between temperate and tropical and subtropical coastal ecosystems (Smith 1984; Conley et al. 2009; Allgeier

et al. 2010). The source of anthropogenic nutrients to coastal waters can also vary between regions, with sewage being a larger source of inputs in the tropics because many island nations lack wastewater management infrastructure (Howarth 2008; Malone and Newton 2020; Rangel-Buitrago et al. 2024). A novel feature and key strength of our experimental design is that we spanned a range of N and P supply rates and ratios that realistically encompass the levels of nutrient enrichment that typify inputs to tropical and subtropical coasts. Two key findings emerged. First, seagrass growth rates increased in response to P enrichment with no evidence of epiphyte overgrowth or shifts in community composition. Second, N supply, more than P or N:P, strongly increased phytoplankton growth. Our findings are important for the management of tropical and subtropical seagrass because they suggest that an effective approach would be to (1) not focus efforts on reducing P inputs because seagrass appears to be highly tolerant to enrichment from this nutrient, and (2) instead focus on reducing N inputs which would reduce the potential for light limitation of seagrass by phytoplankton.

The ability of our experiment to explicitly test the importance of nutrient supply rates and ratios is novel and has important implications for both ecological theory and management. Our hypothesis that N:P would have strong effects on producer groups was predicated based on substantial previous research (Sterner and Elser 2002) and evidence of strong nutrient colimitation in this system (Allgeier et al. 2010). The assumption that different producer groups should have differential responses to a particular nutrient ratio is also consistent with previous management emphasis on dual-nutrient reduction strategies (Conley et al. 2009). Despite this, supply ratios were not the most important factor in predicting growth in our study. We found that P is more important than the supply ratio for seagrass, likely due to strong P-limitation in this system (Smith 1984; Allgeier et al. 2010), but that N and N:P both impact phytoplankton production, with N having a larger effect. The implications are two-fold: (1) theory that has largely been developed in temperate systems can be improved by additionally considering producers in oligotrophic systems (Allgeier et al. 2018; Brines et al. 2022; Andskog et al. 2023), and (2) management in tropical and subtropical seagrass ecosystems may be effective by focusing efforts on mitigating a single nutrient—N.

Our study identified several important ways in which the temperate conceptual model of nutrient enrichment in seagrass ecosystems is inadequate for tropical and subtropical systems. First, we did not find a correlation between epiphyte biomass and seagrass growth, a key expectation in temperate seagrass ecosystems (McGlathery et al. 2007). Importantly, this relationship was not altered due to herbivory because we also found no correlation between growth and herbivory. These findings are supported by other research in subtropical systems showing that epiphyte growth due to nutrient enrichment does not lead to decreased seagrass growth (Fourqurean et al. 1995; Armitage et al. 2011; Allgeier et al. 2018; Andskog et al. 2023). While previous studies were not able to isolate the effects of nutrient supply rates and ratios, we explicitly tested for this using realistic nutrient inputs that were within the range of supply rates seen in coastal waters (Figure 3). Second, in temperate systems, the expectation is that there are community composition shifts due to macroalgae overgrowing seagrass (Burkholder et al. 2007; McGlathery et al. 2007). We

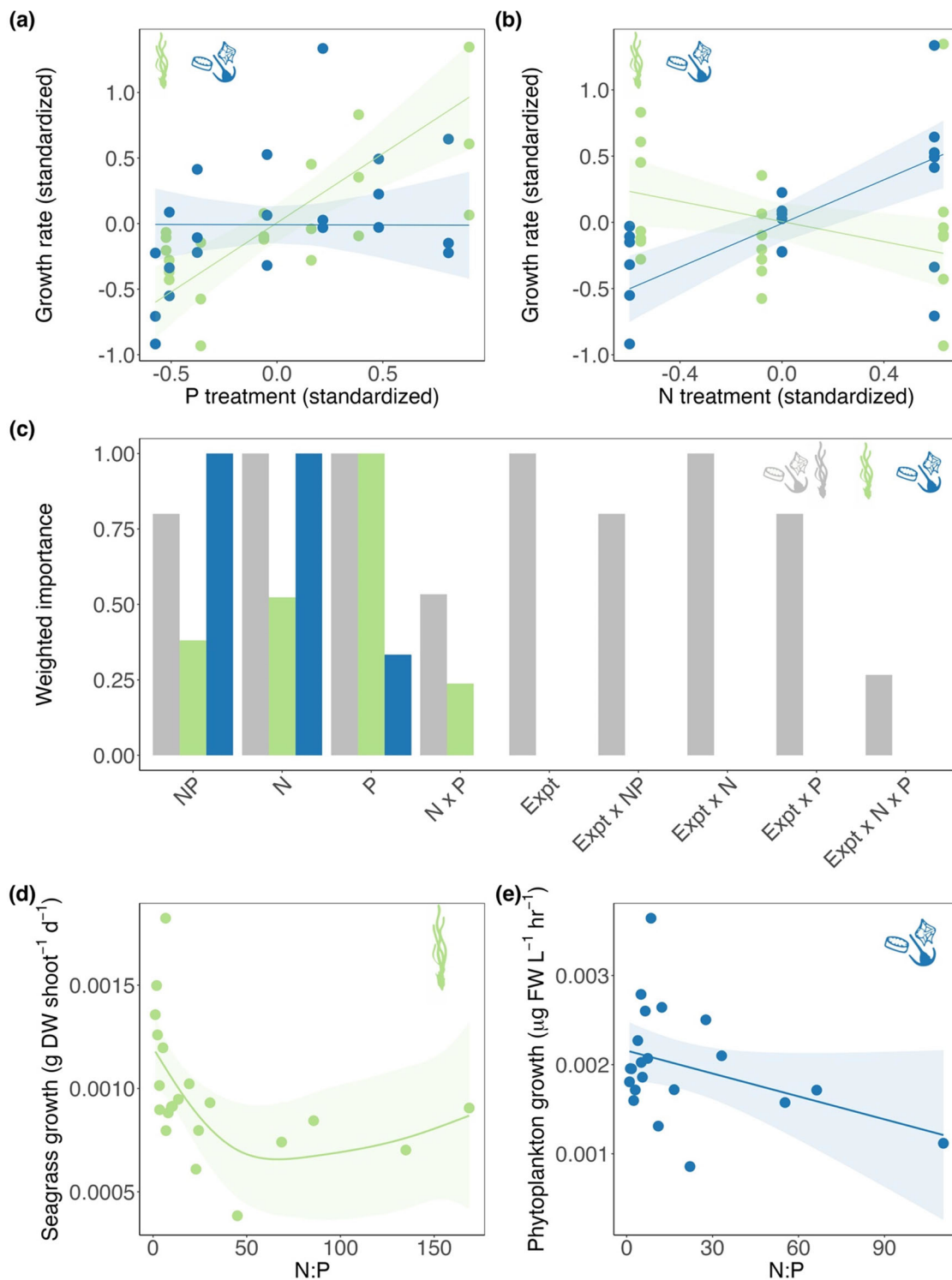


FIGURE 2 | Relationship between standardized growth rates (seagrass—green, phytoplankton—blue) and standardized phosphorus (a) and nitrogen (b) treatments. Lines are estimated marginal mean trendlines with 95% confidence intervals. (c) Weighted importance of terms from top models ($\Delta AIC < 5$) for each model (full [gray], seagrass only [green], phytoplankton only [blue]). Value of 1 represents occurrence in all top models. Adjusted R^2 for best models: full = 0.56, seagrass = 0.50, phytoplankton = 0.67. Seagrass (d) and phytoplankton (e) growth rates by N:P ratio. Lines are fitted GAM and linear trends with 95% confidence intervals for seagrass and phytoplankton, respectively, and were the best-fit models (Seagrass AICs—GAM: -280.9, linear model: -277.1; Phytoplankton AICs—both models: -249.1). Maximum growth rates for both were at the lowest N:P - 1.2 for seagrass and 1.0 for phytoplankton. DW = dry weight, FW = fresh weight.

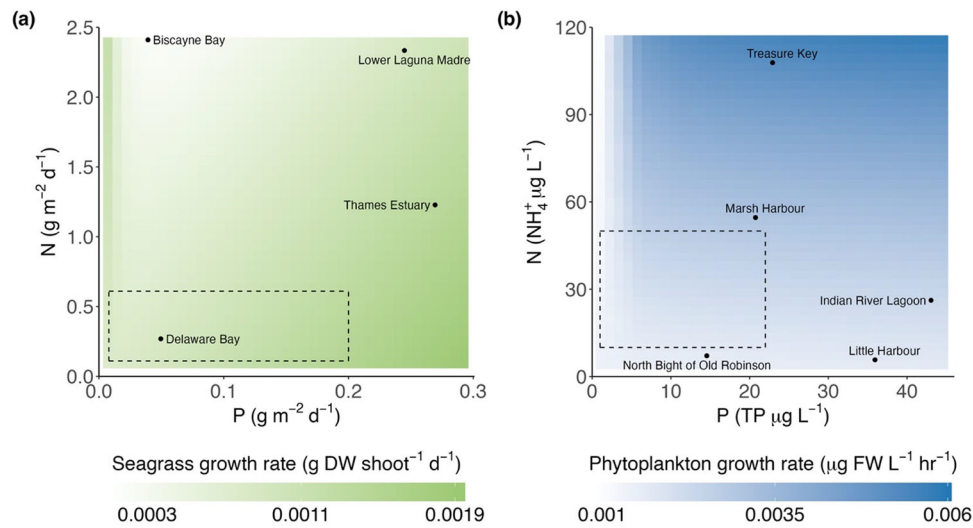


FIGURE 3 | Extrapolation of seagrass (a) and phytoplankton (b) growth rates beyond experimental conditions. Dashed boxes represent experimental treatment limits. Ranges of extrapolated data encompass N and P conditions seen in tropical and subtropical coastal waters in the literature (Heck et al. 2006; Caccia and Boyer 2007; Rebich et al. 2011; Stoner et al. 2011; Lapointe et al. 2023)—Note: Limited number of datapoints is a reflection of limited reports of supply rates of both N and P to tropical and subtropical coastal areas. Locations in (b) are in The Bahamas, except Indian River Lagoon, FL, USA. DW = dry weight, FW = fresh weight, NH_4^+ = ammonium, TP = total phosphorus.

did not find shifts in community composition toward macroalgal dominance, which is also supported by other enrichment studies in subtropical ecosystems (Armitage et al. 2011; Allgeier et al. 2018). There have been documented shifts in seagrass community composition from one seagrass species to another under high levels of enrichment (Fourqurean et al. 1995; Armitage et al. 2011; Howard et al. 2016), but these shifts do not involve macroalgal overgrowth as is predicted in the temperate conceptual model. High levels of nutrient enrichment in tropical systems can, however, lead to overgrowth of seagrass by macroalgae (Liu et al. 2016; Luo et al. 2022, Luo et al. 2024), but based on our findings and others (Armitage et al. 2011; Allgeier et al. 2018; Andskog et al. 2023), we hypothesize that this largely occurs because seagrass growth is inhibited by light limitation from phytoplankton. Third, our results suggest that levels of nutrient enrichment that mirror real-world conditions do not necessarily have negative effects on seagrass growth in this system. Although we found a slight decrease in aboveground growth with higher N supply—possibly due to shifts in energy allocation to belowground production (Esquivel et al. 2022) that we did not measure—P supply had exclusively positive impacts on seagrass growth.

Consistent with the temperate conceptual model, light limitation can impair tropical and subtropical seagrass ecosystems, and increased water-column production is an important and common mechanism for this (Greening and Janicki 2006; Burkholder et al. 2007). We found that phytoplankton growth was promoted by increased N supply, not P, as was expected due to strong P limitation in this system (Smith 1984; Allgeier et al. 2010). Although our water-column experiment was a short-term enrichment, it is still reflective of the dynamics by which phytoplankton experience enrichment due to: (1) high flushing rates within coastal waters, and (2) the fact that phytoplankton respond to nutrient enrichment much more quickly than seagrass. Nonetheless, the differences in timescales of our two enrichment studies is a limitation, and our findings may not hold for a system with low

flushing rates (McGlathery et al. 2007). Additional tests along observational gradients of enrichment would be useful to further vet our findings. Nonetheless, because many coastal ecosystems are well-flushed, our findings have important implications for the management of wastewater in tropical and subtropical seagrass ecosystems.

Reducing nutrient inputs to seagrass ecosystems should be a priority in coastal areas. Our findings provide evidence that an important first step toward effective management would be reducing the input of N alone because N has the greatest effect on phytoplankton growth and thus should minimize the effect of light limitation via water-column shading. Nutrients have been managed individually for decades (Conley et al. 2009), and the processes for N and P removal from wastewater are separate, see, for example, Rout et al. (2021) for further detail. Therefore, in locations that lack nutrient management, a focus on N may be the most effective starting point. A concurrent reduction in P would likely also be beneficial, and when possible, mitigation of both should occur. However, the effect of P on phytoplankton growth was insignificant, and importantly, P increases seagrass production, with no clear negative effects found in this study and other long-term experimental and observational studies in similar ecosystems (Armitage et al. 2011; Allgeier et al. 2018; Andskog et al. 2023). It is possible that increased seagrass production from P enrichment could be an unforeseen benefit due to increases in carbon storage, but additional research on enrichment effects on belowground production is needed before this can be determined. It is clear that a complete cessation of anthropogenic nutrient enrichment is unlikely in the near future. Nonetheless, the widespread impairment from nutrient enrichment necessitates even modest steps toward mitigation. Our findings provide clear evidence that initial efforts to mitigate N alone in tropical and subtropical seagrass should have important consequences for the health and sustainability of a globally important marine ecosystem.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code used in this manuscript can be accessed at: https://github.com/Allgeier-Lab/Shayka_ConLetts

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supplementary Materials: conl13133-sup-0001-SupMat.docx