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Synergistic nutrient colimitation across a gradient of ecosystem fragmentation in subtropical mangrove-dominated wetlands

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Abstract

We examined benthic algal response to nutrient enrichment by nitrogen (N), phosphorus (P), and N + P in mangrove wetlands of The Bahamas, to test the hypothesis that human impacts (fragmentation) on these ecosystems altered nutrient limitation, thereby changing the frequency and/or magnitude at which ecological synergies occurred. Fragmentation occurred due to road construction, resulting in reduced hydrological connectivity between the wetlands and marine environment. Strong, persistent, and synergistic nutrient colimitation occurred in both pristine and fragmented estuaries. Ecosystem fragmentation did not alter the biomass response to dual nutrient enrichment, but did alter the relative magnitude of the nonadditive response. That is, synergistic responses were less extreme in fragmented systems. This was supported by the strong, negative relationship between ambient algal biomass (a surrogate for background productivity) and the strength of synergistic responses ($R^2 = 0.69$ and 0.79, year 1 and year 2, respectively). Bahamian coastal ecosystems exhibited the greatest synergistic responses reported for a marine ecosystem, suggesting that the benthic algal communities associated with Bahamian wetlands are among the most nutrient-limited marine ecosystems. Our findings provide a case study illustrating how altered nutrient dynamics associated with land-use change may decrease the frequency and/or magnitude of synergistic responses to nutrients in aquatic ecosystems.

Coastal environments are among the most anthropogenically altered ecosystems on Earth (Lotze et al. 2006). Of the multiple stressors affecting these systems, two of the most conspicuous are altered hydrologic connectivity (Pringle 2001) and eutrophication (Lotze et al. 2006; Diaz and Rosenberg 2008). Hydrologic connectivity affects transport of nutrients, energy, and organisms, and can be increased or decreased as a result of human modification of landscapes (Pringle 2001). Eutrophication of coastal zones results from the downstream flux of nutrient loading and mobilization from agricultural, industrial, and municipal sources (Lotze et al. 2006; Diaz and Rosenberg 2008). A consequence of both of these stressors is altered nutrient availability, which has numerous implications for the structure and function of estuarine ecosystems (Dodds 2006; Conley et al. 2009; Paerl 2009). Yet, because coastal ecosystems have been so widely affected by these stressors, our understanding of how these systems functioned before human intervention is often unclear, presenting a dilemma for long-term conservation and restoration initiatives (Jackson et al. 2001; Paerl 2009).

In any ecosystem, determining which nutrient(s) most limit primary production is at the core of understanding nutrient dynamics and ecosystem function (Hecky and Kilham 1988; Elser et al. 2007; Tank et al. 2007). Recent research has demonstrated that ecosystems tend to be nutrient colimited, i.e., primary producers have a greater response to enrichment by multiple nutrients (typically N and P together) than to either nutrient independently, and at times the type of colimitation can be synergistic (Allgeier et al. in press). In this case, synergism is defined as a nonadditive form of colimitation that occurs when the producer response to dual-nutrient enrichment is greater than that predicted by the sum response to both nutrients independently (e.g., when N and P together > [N alone + P alone]) (Allgeier et al. in press).

Synergism generally results from oscillating nutrient limitation, whereby the ambient availability of nutrients is minimal, and given an increased supply of one nutrient, limitation shifts toward limitation by the other (Davidson and Howarth 2007). Thus, limitation oscillates between nutrients until either production is maximized or a tertiary factor becomes limiting (Arrigo 2005; Davidson and Howarth 2007). Synergistic responses to multiple-nutrient enrichment are predicted to occur most strongly in ecosystems that are extremely nutrient limited. But anthropogenic perturbations generally enhance the availability and supply rates of nutrients (Halpern et al. 2008; Conley et al. 2009; Paerl 2009). Therefore, it is logical to hypothesize that human modification of nutrient availability may decrease the frequency and/or magnitude at which ecological synergies occur.

Coastal waters of the subtropics and tropics in areas with low human population densities tend to be relatively nutrient poor, especially in the Caribbean (Lapointe and Clark 1992; Rivkin and Anderson 1997; Koch and Madden 2001). Yet land-use change associated with increasing population densities alters nutrient availability (Lapointe 1997). One of the most prevalent forms of land-use change in the region is physical fragmentation of coastal ecosystems due to road construction (Layman et al. 2004; Layman et al. 2007). Fragmentation generally occurs when roads bisect mangrove wetlands, causing a physical barrier between the associated wetland and the ocean. Fragmentation results in reduced hydrologic connectivity (i.e., tidal exchange) and is predicted to affect nutrient availability in

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Table 1. Ambient water-nutrient concentrations (μg L^{-1}) and salinity measured in March 2008 (year 1) for all unfragmented (uf1–uf3) and fragmented (f1–f4) sites. Values were averaged from $n = 8$ and $n = 4$ samples taken at each NDS plot in each of the unfragmented and fragmented sites respectively. bd = below detection limits for the analytical equipment used. SRP = soluble reactive phosphorus; TDP = total dissolved phosphorus.

Site	SRP	TDP	NO_3^-–N	NH_4^+–N	Salinity
uf 1	0.9±0.9	4.3±3.3	3.0±1.3	4.9±0.5	34±0
uf 2	bd	2.9±1.6	3.03±1.4	5.2±0.3	34±0
uf 3	0.9±0.5	bd	0.3±0.9	8.1±0.9	40±0
unfrag means	0.60±0.3	2.4±1.27	2.13±0.91	6.06±1.03	36±2
f 1	2.7±2.7	4.5±1.9	0.5±0.25	14.3±0.7	37±0
f 2	bd	4.8±0.3	6.2±0.5	41.8±4	40±0
f 3	3.8±1.6	5.8±1.9	0.6±0	12.7±2.3	3±0
f 4	bd	0.4±0	3.2±1.4	22.7±5.2	10±0
frag means	1.61±0.96	3.76±1.26	2.61±1.35	22.86±6.67	22.5±9.37

two primary ways: 1) enhanced N availability via atmospheric fixation because nitrogen-fixing cyanobacteria tend to proliferate in systems with minimal tidal exchange (decreasing N limitation, and thus potentially increasing P limitation) (Smith 1984; Howarth et al. 1988; Howarth and Marino 2006), and 2) decreased P availability because a primary source of P to coastal ecosystems comes from oceanic upwelling (Smith 1984; Howarth et al. 1988; Howarth and Marino 2006). As such, fragmentation provides an ecosystem-scale context in which to independently test the relative importance of changes in hydrologic connectivity on nutrient dynamics because it is predicted to alter nutrient dynamics, but it is not directly (in this case) associated with anthropogenic nutrient loading.

Here we used single-nutrient (N and P) and dual-nutrient (N + P, herein NP) enrichment experiments across unaltered and fragmented wetlands in subtropical mangrove ecosystems of The Bahamas to accomplish two objectives: 1) to quantify nutrient limitation of benthic algae and determine whether response to N, P, or dual-nutrient enrichment was affected by fragmentation, and 2) to quantify the presence and strength of nonadditive responses to dual-nutrient enrichment in fragmented and unfragmented systems. We also compared our findings to published studies examining dual-nutrient limitation from other marine ecosystems. Our specific hypotheses were: 1) benthic algae would be colimited by N and P and would exhibit strong synergistic responses to dual-nutrient enrichment, and 2) ecosystem fragmentation would reduce synergistic responses to dual-nutrient enrichment.

Methods

Site description—The study was conducted in mangrove-dominated wetlands on Abaco Island, Bahamas, locally known as "tidal creeks." Bahamian tidal creeks receive little freshwater input because of small watershed size (essentially having no freshwater rivers or streams on any of the islands), little topographic relief, and porous calcium-carbonate geology. Reduced salinities in some systems (Table 1) are due to direct rainwater input. Creeks are typically characterized by a relatively narrow creek mouth that is the primary hydrologic conduit for tidal exchange ($\sim$ 0.8-m tidal range). The creeks typically broaden with increased distance from the mouth, graduating into expanses of shallow (< 1 m at low tide) wetlands with red mangrove (*Rhizophora mangle*) as the primary emergent vegetation. All of the creeks on our study, including those that were fragmented, were surrounded by land that is devoid of residential, industrial, or agricultural land use, and thus were assumed to have relatively low anthropogenic nutrient inputs. Ambient nutrient concentrations are extremely low in unaltered sites (Table 1).

Our study was conducted in three unaltered (unfragmented) tidal creeks and four fragmented tidal creeks during the months of February and March in 2008 and 2009. The unfragmented and fragmented sites ranged from $\sim$ 0.12 km^2 to $\sim$ 0.47 km^2 and from $\sim$ 0.001 km^2 to $\sim$ 0.3 km^2, respectively, with a maximum mean depth of $\sim$ 1.2 m at high tide. Tidal oscillations are reduced by $> 90\%$ in all of the fragmented sites used in this study (Layman et al. 2007). Ambient water nutrients in fragmented sites are slightly higher than in unfragmented sites (Table 1). More detail on these systems can be found in Layman et al. (2007) and Valentine-Rose et al. (2007*a,b*).

Experimental design—Nutrient-diffusing substrates (NDS) have been widely used to determine nutrient limitation for primary production in freshwater ecosystems (Tank and Dodds 2003; Tank et al. 2007). Here we used four NDS treatments: N (0.5 mol L^{-1} NH_4Cl), P (0.5 mol L^{-1} KH_2PO_4), N + P (0.5 mol L^{-1} NH_4Cl + 0.5 mol L^{-1} KH_2PO_4), and a control (agar only) (Tank et al. 2007). Each treatment was incubated at each plot for 24–26 d. NDS experiments are short-term enrichments that are colonized by epiphytic and epibenthic (herein benthic) algae. The treatment that elicits the largest algal response (measured as μg cm^{-2} chlorophyll *a* (Chl *a*)), indicates the nutrient that is most limiting. Benthic algae are presumed to be especially important for nutrient uptake and primary production and are presumed to be a critical energy source to upper trophic levels of estuarine and wetland food webs (Johnson et al. 2006; Layman 2007; Valentine-Rose et al. 2007*a*). Because they represent an important component of the primary producer pool (Armitage et al. 2005, 2006),

Table 2. ANCOVA results for chlorophyll *a* response measured in nutrient treatments (N, P, and NP). For the ANCOVA, "distance" of plot from the mouth of the tidal creek was used as a covariate. For the ANCOVA, the predictor variable "Frag" indicates whether the treatment was from a fragmented or an unfragmented site.

Treatment	df	Sum of squares	*F*-value	*p*-value
Year 1				
Frag	1	11.952	53.751	<0.001
N	1	57.046	256.556	<0.001
P	1	31.341	140.952	<0.001
N×P	1	20.852	93.778	<0.001
Frag×N	1	1.292	5.81	0.017
Frag×P	1	4.868	21.891	<0.001
Frag×N×P	1	0.38	1.708	0.193
Distance	1	1.504	6.763	0.01
Error	151	33.575		
Year 2				
Frag	1	0.585	5.644	0.022
N	1	10.704	103.265	<0.001
P	1	6.832	65.909	<0.001
N×P	1	5.23	50.453	<0.001
Frag×N	1	0.025	0.239	0.627
Frag×P	1	0.576	5.556	0.023
Frag×N×P	1	0.212	2.042	0.16
Distance	1	0.028	0.266	0.609
Error	43	4.457		

benthic algae can be a useful proxy to measure nutrient limitation in these systems.

In year 1, eight and four plots of NDS were placed in each unfragmented and fragmented site, respectively (24 total plots in unfragmented sites and 16 total plots in fragmented sites). Plots were regularly spaced along a linear transect from the mouth to the terminal end of the tidal creek (i.e., there were different distances among plots because the size of creek systems varied). Each plot contained four replicates of each of the four treatments (16 individual nutrient diffusing assays plot^{-1}; 384 assays in unfragmented sites and 256 assays in fragmented sites). In year 2, two plots were placed in each site (unfragmented and fragmented) following the same design used in year 1, with the exception of one unfragmented creek that had three plots (seven plots with 96 assays in unfragmented and eight plots with 128 assays in fragmented sites). Chl *a* values from multiple replicates of a nutrient treatment were considered subsamples and were averaged within each plot.

NDS experiments were collected after 24–26 d, placed in foil, transported on ice and frozen for analysis following the protocol of Tank et al. (2007). All experiments at a given site were collected on the same day. Chl *a* content (μg cm^{-2} Chl *a*) of each sample was determined spectrophotometrically (Shimadzu 2100) for pheopigment-corrected Chl *a* (APHA 1995). Water-nutrient samples were taken in year 1 from each plot when the plates were retrieved at the end of the experiment. All samples were prefiltered through a 0.45 Whatman nylon-membrane filter, and all but NH_4 were frozen until analysis. Water samples were analyzed for NH_4 within 12 h of collection using a fluorometric method following Holmes et al. (1999) as modified by Taylor (2007). The concentration of total dissolved phosphorus (TDP) was determined using the persulfate digestion method, and the concentrations of soluble reactive phosphorus (SRP) and NO_3^- were determined with continuous-flow colorimetry.

Data analysis—Differences among nutrient-treatment effects in fragmented and unfragmented sites (Table 2) were analyzed with a three-factor analysis of covariance (ANCOVA) using the Generalized Linear Model (GLM) procedure in SAS version 9.1 (SAS Institute Inc., Cary, NC, USA) with α set at 0.05. Distance from the plot to the mouth of the tidal creek served as a covariate to account for the effect of location relative to potential sources of nutrients (e.g., the ocean as a source of P). Planned comparisons of three-factor joint means were made using the LSMEANS test with a Bonferroni adjustment in SAS (Milken and Johnson 1992). Chl *a* values were log transformed to meet assumptions of normality and homoscedasticity. In year 2, data from one fragmented site (f3) were not included in the analysis because they were lost during a storm event.

To determine the relative frequency and magnitude of nonadditive responses to multiple-nutrient enrichment we applied the Interaction Effect Index (IEI) (Allgeier et al. in press) to our data. The IEI provides a relative measure of the degree of non-additivity in response to multiple factors (in this case dual nutrient enrichment), by incorporating all response terms.

$$\text{IEI} = \ln[\text{response NP}/(\text{response N} + \text{response P})] \quad (1)$$

where response NP is the primary producer biomass reported for NP treatments and response N and response P are primary producer biomass reported for N and P treatments, respectively. IEI values close to zero, either positive or negative, are functionally additive (i.e., response NP = response N + response P). As IEI increases or decreases, the magnitude of the nonadditive effect becomes more synergistic or antagonistic, respectively (Allgeier et al. in press). We applied the IEI to all published experiments from marine systems (n = 105) that reported biomass per unit area or volume response to enrichment by N, P, and NP (Allgeier et al. in press). The raw data, initially reported in Elser et al. (2007), were obtained from the National Center for Ecological Analysis and Synthesis (2007).

To test for effects of fragmentation on the degree of synergy, we conducted two tests. First, we examined the difference in mean IEI values for fragmented and unfragmented sites using a *t*-test. Second, we expected synergies to be strongest in ecosystems with the lowest ambient production. If fragmentation enhanced the ambient production of an ecosystem, synergies would be expected to be weaker than they would otherwise be in a relatively unimpaired ecosystem. That is, the magnitude of the IEI value would be negatively correlated with ecosystem production. We used least-squares regression of the mean response to the control treatment for each site and the mean IEI value for each site to test for this

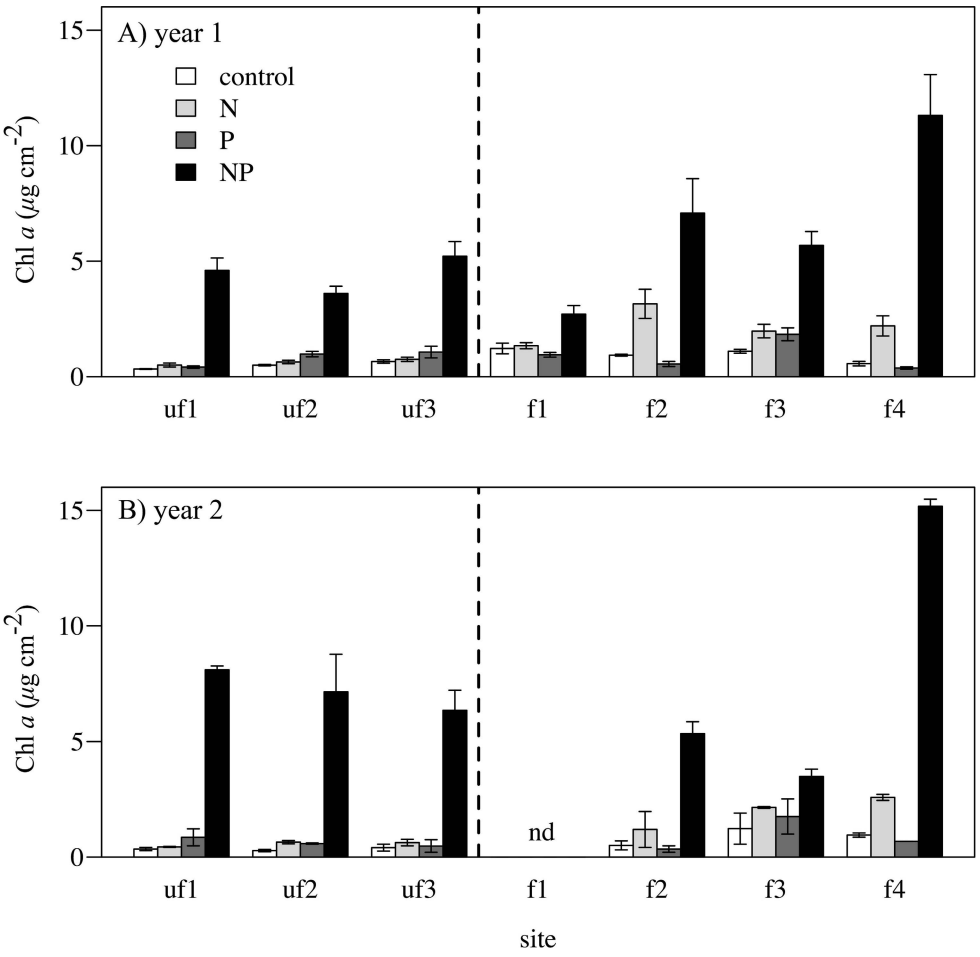

Fig. 1. Mean Chl *a* (μg cm^{-2}) response to nutrient diffusing substrate (NDS) across all unfragmented (uf1–uf3) and fragmented (f1–f4) sites for year 1 and year 2. Treatments are control, nitrogen (N), phosphorus (P), and nitrogen plus phosphorus (NP). Error bars indicate standard error based on four replicates per value. nd = no data (these experiments were lost in a storm).

relationship ($n = 7$ and 6 in year 1 and year 2, respectively). To verify that the relative size of the creek was not also an important variable to consider in our analysis, we regressed the ratio of creek surface area to volume (SA : V) with IEI. Because the relationship was not significant for either year ($p = 0.91$ and $p = 0.32$ for 2008 and 2009, respectively), creek size was not further considered. *T*-test and least-squares regression analyses were conducted in R software (R Development Core Team 2008).

Results

Significant interactions between nutrient treatments and levels of fragmentation in both years necessitated multiple comparisons of joint treatment means rather than the interpretation of simple main effects (Table 2). NP treatments elicited the greatest algal responses in all fragmented and unfragmented sites in both years (Figs. 1, 2). Single-nutrient treatments (N or P alone) did not differ significantly from controls or from one another in unfragmented sites in either year (Fig. 2). At fragmented sites in year 1 and year 2, algal biomass of N treatments was significantly higher than that of controls and P treatments, which did not differ significantly from each other (Fig. 2). In year 1, algal biomass on controls and on treatments of N alone differed significantly between fragmented and unfragmented sites, but in year 2, only single-nutrient treatments of N differed between fragmented and unfragmented sites (Fig. 2). The effect of distance was significant in year 1 alone (Table 2). The lack of a significant effect of distance in year 2 is probably due to decreased sample size.

Strong synergistic responses to dual-nutrient enrichment were found at every site for both years (Fig. 3). The mean IEI values for unfragmented sites were 1.19 ± 0.12 ($\pm$ 1 SE) and 2.60 ± 0.16 in year 1 and year 2, respectively, representing a 228% and 1246% increase in biomass response above the predicted response from an additive model (response NP = response N + response P). The mean IEI values for fragmented sites were 0.69 ± 0.18 and 1.64 ± 0.23 in year 1 and year 2, respectively, and represented 95% and 416% increases in biomass above additivity. Our findings from year 2 experiments represent five of the highest IEI values recorded for any marine ecosystem.

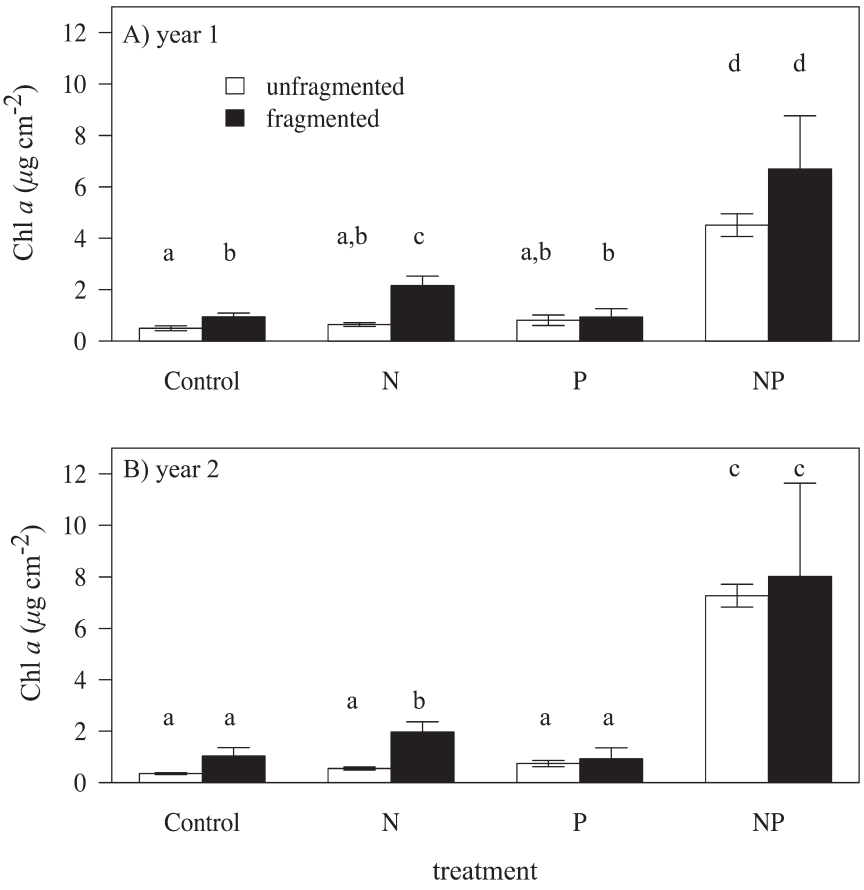

Fig. 2. Comparison of mean Chl *a* (μg cm^{-2}) response to nutrient-diffusing substrate (NDS) between unfragmented (white) and fragmented (black) estuaries. Treatments are control, nitrogen (N), phosphorus (P), and nitrogen plus phosphorus (NP) for year 1 and year 2. Error bars indicate standard error. Letters above columns indicate significant differences in joint mean comparisons (Bonferroni corrected, $p < 0.05$).

The Chl *a* response within the control treatment, representing a measure of ambient algal production, was negatively correlated to IEI values ($R^2 = 0.79$, $p < 0.001$ and $R^2 = 0.69$, $p < 0.05$, in year 1 and year 2, respectively; Fig. 4a,c). *T*-tests revealed that IEI values from fragmented sites were significantly different than those from unfragmented sites in year 2 (*t*-test, $t_6 = 3.4$, df = 6, $p = 0.01$) but not in year 1 (*t*-test, $t_7 = 1.3$, df = 7, $p = 0.11$; Fig. 4b,d).

Discussion

Our findings demonstrate strong and persistent nutrient colimitation and synergisms in both unaltered and anthropogenically altered Bahamian estuaries. Specifically, over 2 yr (7 sites, 55 experimental units and 880 total assays) all experiments indicated N+P colimitation, and all sites demonstrated synergistic responses to dual-nutrient enrichment. The classic model of biogeochemical supply of nutrients to coastal ecosystems predicts two primary inputs: 1) down-stream transport from terrestrial ecosystems, supplying nutrients at concentrations of high N relative to P, and 2) tidal exchange that delivers mobilized nutrients at concentrations of low N relative to P from oceanic upwelling (Smith 1984; Howarth et al. 1988). Our findings of substantial nutrient colimitation and strong synergistic responses to dual-nutrient enrichment suggest that both of these mechanisms may play a relatively small role in delivery of nutrients to Bahamian coastal ecosystems. This is highlighted by the fact that even though fragmentation was found to alter nutrient availability and to increase ambient algal production (as discussed below), nutrient colimitation was still prevalent and strong in every study site.

Our findings regarding the implications of ecosystem fragmentation for nutrient limitation did not support our a priori predictions. We expected that reduced tidal exchange would decrease N-limitation and concomitantly NP-limitation because of two underlying mechanisms. First, we expected enhanced N supply rates because waters that do not experience significant tidal exchange tend to promote the presence of N-fixing microbes and algae (e.g., cyanobacteria) (Howarth and Marino 2006). Second, because fragmentation drastically decreased tidal exchange, and thus would reduce a potential source of P from incoming seawater (given the potential of nearby coastal upwelling), we predicted an increase in P limitation. But our study demonstrated that the largest effect of fragmentation was enhanced N limitation while P and NP limitation remained relatively similar to unfragmented sites.

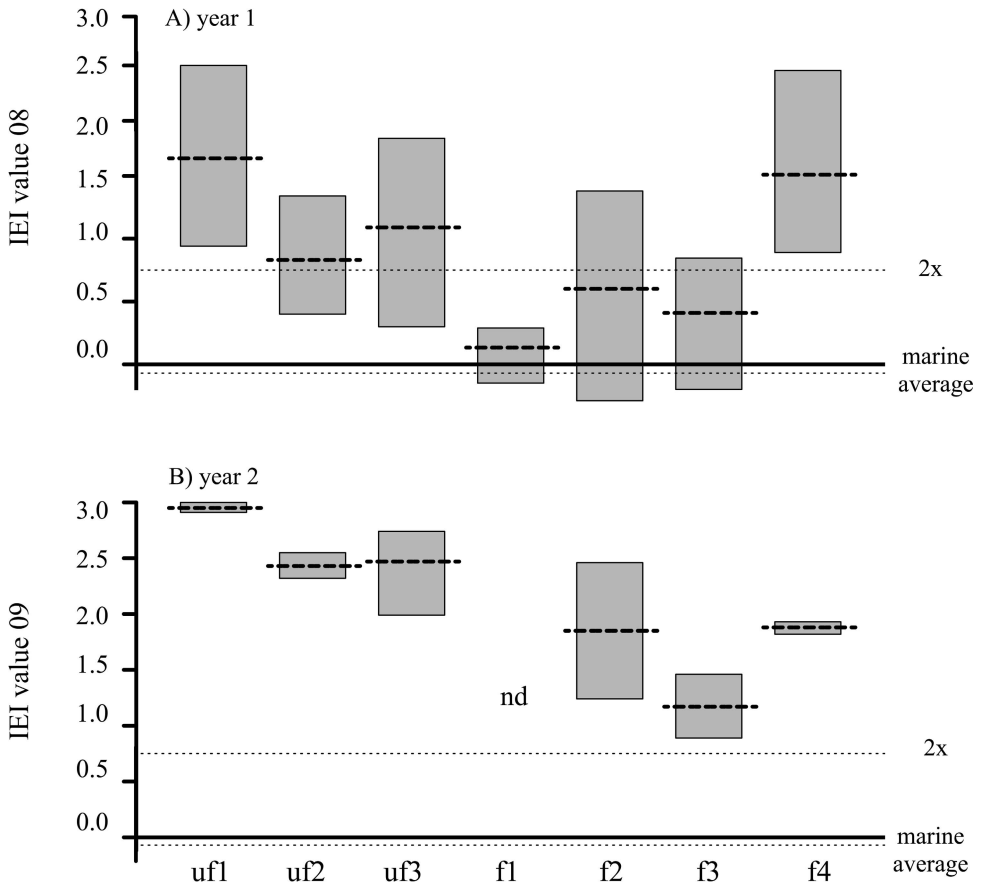

Fig. 3. Comparisons of IEI values for unfragmented (uf1–uf3) and fragmented (f1–f4) sites for (A) year 1 and (B) year 2. The gray bar represents the total range of values per site. The dashed black line on each bar represents the mean value per site. The line indicated by "2×" delineates a synergistic nonadditive IEI value that is approximately twice as large as additivity. The line indicated as "marine avg." represents the mean IEI value (-0.02 ± 0.10) for 105 published marine studies (Allgeier et al. in press). Raw data for marine studies were obtained via the public data repository of the National Center for Ecological Analysis and Synthesis. nd = no data.

Our ongoing research suggests that fragmented sites undergo substantial daily oscillations in dissolved oxygen concentration, often reaching anoxic conditions at night (C. A. Layman unpubl.). Low oxygen levels may release bound P from sediments, which would enhance algal production and facilitate a shift toward N limitation (Wetzel 2001). Thus, P inputs to the ecosystem would be from the benthos (from sediment-bound P release), where the NDS experiments were conducted. Conversely, our findings of greater availability of NH_4^+ in fragmented sites (Table 1), suggests that the system is also receiving N inputs at the air–water interface (the part of the water column from which samples were taken), potentially from N-fixing microbes such as cyanobacteria. Because fragmented sites can be stratified due to lack of tidal flow, nutrient limitation may vary in upper and lower parts of the water column. Regardless of the mechanism, it is clear that the relatively greater ambient nutrient availability in fragmented sites facilitated enhanced algal production (control mean Chl *a* (μg cm^{-2}) year 1: 0.93 ± 0.09 and 0.47 ± 0.03; year 2: 0.89 ± 0.23 and 0.35 ± 0.04, fragmented and unfragmented, respectively).

The IEI provides a quantitative measure of how primary producers in a particular system respond to dual-nutrient enrichment. We found strong synergistic responses across all sites for both years (Fig. 3). Our findings from year 1 represent the third highest IEI values (i.e., greatest synergistic effect) recorded for all experiments reported in the literature up to 2007, and 5 of the 15 values we recorded from year 2 were greater than all published marine experiments up to 2007. The maximum IEI values 2.38 (year 1) and 3.00 (year 2) demonstrated an increase of 980% and 1909% above additivity. Likewise, of the total 54 experiments reported in our study, only three (from fragmented sites) had an IEI value that was lower than the average IEI value for all marine studies (IEI = -0.02 ± 0.1) (Fig. 3). These data emphasize the nature of nutrient limitation in Bahamian coastal ecosystems and highlight them as among the most nutrient-limited marine ecosystems yet recorded.

While the magnitude of the response to the NP treatment was similar between fragmented and unfragmented sites (Fig. 2), the IEI values deviated significantly (in one of the two years examined) (Fig. 4d). This deviation was due to

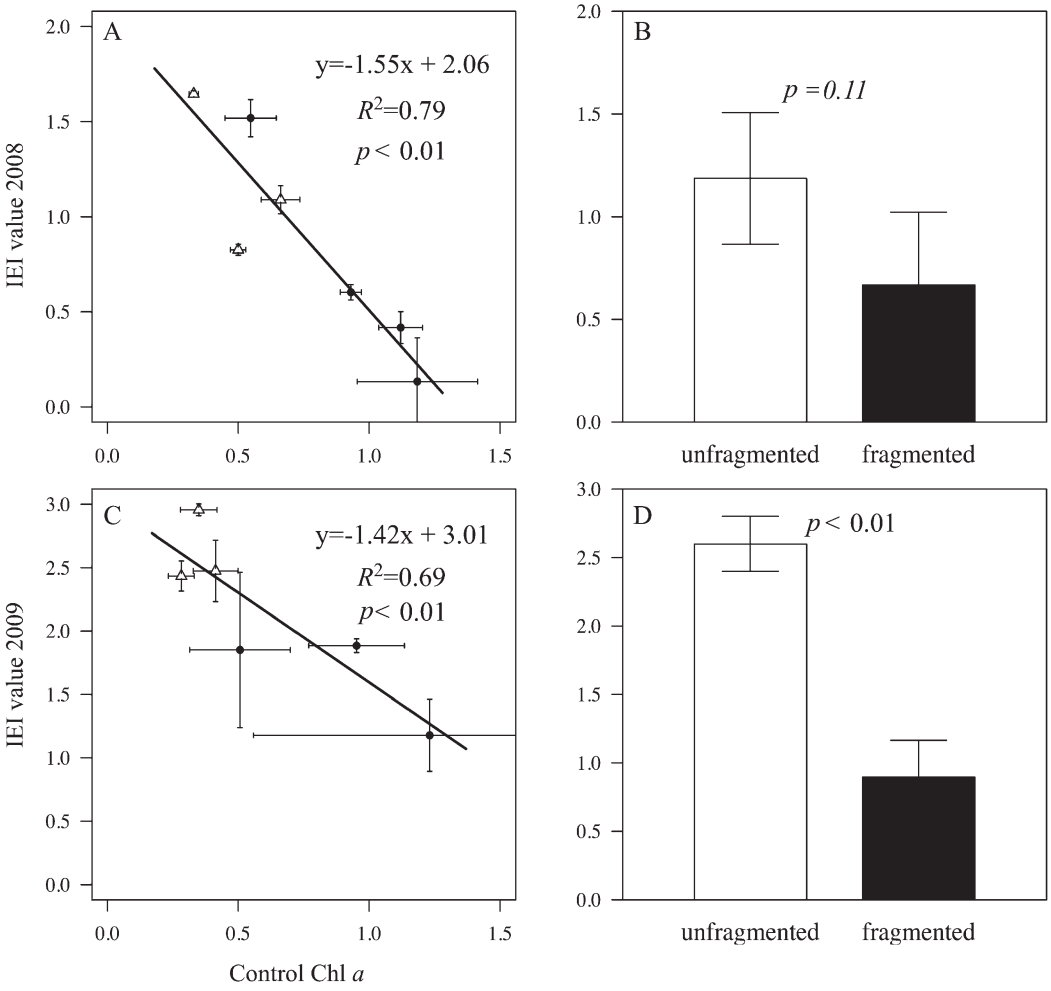

Fig. 4. (A, C) Linear regression between the average Chl *a* values (Chl *a* cm^{-2}) for control treatments at a given site and the respective IEI values for that site for year 1 and 2. Chl *a* values are a way to represent ambient algal production and thus are a useful proxy for baseline ecosystem productivity. Closed circles indicate fragmented sites ($n = 4$; $n = 3$ in year 2) and open triangles indicate unfragmented sites ($n = 3$) averaged for years 1 and 2. (B, D) Average IEI values for all unfragmented and fragmented sites in year 1 and year 2.

the relatively large response to single-nutrient enrichment found in fragmented sites. For example, in unfragmented sites the response to the NP treatment was 457% and 957% greater than that of the P treatment (the greatest single nutrient response) in year 1 and year 2, respectively. In comparison, the NP treatment in fragmented sites was only 211% and 294% greater than that of the N treatment (the greatest single nutrient treatment) in year 1 and year 2, respectively.

The disparity in IEI values between unfragmented and fragmented sites supports the hypothesis that human activity may be altering the relative frequency and/or magnitude at which synergisms occur. The IEI compares the *net* response to enrichment by single and dual nutrients because each value is not control-corrected. Thus, the IEI value is inclusive of the background productivity of the ecosystem and quantifies the net ecosystem response to enrichment as opposed to simply the effect size of a specific experiment. The negative relationship between the Chl *a* response to the control treatment and the IEI value suggests that as an ecosystem increases in ambient algal production (e.g., via anthropogenic alteration) the relative strength of synergistic effects decrease (Fig. 4a). Though fragmentation does not represent direct anthropogenic nutrient loading, it is indicative of the alterations in nutrient cycling that are likely associated with this kind of land-use change.

Our findings provide a case study illustrating how altered nutrient dynamics associated with land-use change may be decreasing the frequency and/or magnitude of synergies in aquatic ecosystems. As has been stressed in the ecological literature, anthropogenic impacts to ecosystems have drastically altered the "ecological baseline" and have skewed our understanding of basic ecological processes and mechanisms (Jackson et al. 2001). In this same context, physical alterations of coastlines may be skewing our understanding of nutrient dynamics in the prehuman era (Jackson et al. 2001; Knowlton and Jackson 2008). Basic understanding of how unaltered systems function is imperative if we are to fully grasp the ecological repercussions of the human footprint.

Acknowledgments

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