

An experimental test of the mechanism by which suspension feeding bivalves elevate seagrass productivity

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ABSTRACT: A field experiment utilizing mussel mimics and sediment nutrient enrichment was conducted to examine the effect of the mussel *Modiolus americanus* on meadows of the seagrass *Thalassia testudinum*. The experimental design tested the separate factors of increased habitat structure and increased nutrient enrichment resulting from the presence of the mussels. Nutrient enrichment had a significantly positive effect on sediment porewater nutrient concentrations and a significantly negative effect on leaf tissue C:N, C:P and N:P ratios. Increased habitat structure had a significantly positive effect on epiphytic grazer densities and a significantly negative effect on epiphytic biomass. In addition, calculated % light reduction by epiphytes was significantly reduced by structure and significantly increased by nutrient enrichment. This study showed that the direct effect of nutrient enrichment by mussel biodeposition produced the greatest positive response in productivity of *T. testudinum* in the seagrass meadows of St. Joseph Bay, Florida. In other systems experiencing eutrophication, however, it is possible that increased habitat complexity may have the greater effect on seagrass productivity.

KEY WORDS: Benthic-pelagic couple · Habitat complexity · Plant-animal interactions · Seagrass · *Thalassia testudinum* · Suspension feeding bivalves · *Modiolus americanus*

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INTRODUCTION

Nutrient and light availability are considered as 2 of the primary physical factors limiting seagrass distribution (see Dennison 1987, Short 1987 for reviews). Seagrasses are faced with a seeming paradox in their environmental requirements: as autotrophs, they need light to survive, but they are rooted under water, a medium that attenuates light much more strongly than air. In addition to light, they require mineral nutrients to photosynthesize and build tissue. Increases in nutrients in the overlying water column increases light attenuation as a result of plankton or epibiont growth,

often leading to the disappearance of seagrass (Orth & Moore 1983, Giesen et al. 1990, Larkum & West 1990, Duarte 1995, Short & Neckles 1999). Several recent studies have examined the effect of suspension feeding bivalves on changing nutrient and light availability to seagrasses.

A few studies have suggested that suspension feeding bivalves increase seagrass nutrient availability without the negative effect of increasing plankton density and reducing light availability. Reusch et al. (1994) demonstrated that the blue mussel *Mytilus edulis* doubled sediment porewater concentrations of ammonium and phosphate, and suggested that the mussels fertilize the seagrass *Zostera marina* by the deposition of feces and pseudofeces. Similarly, Reusch & Williams (1998) demonstrated that the introduced mussel *Musculista senhousia* fertilized beds of *Z. marina* at moderate bivalve densities. Mechanistically, it seems likely that as

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filter feeding bivalves transfer planktonic production from the water column to the benthos via feces and pseudofeces, they elevate seagrass productivity by increasing nutrient availability. However, the presence of filter feeding bivalves does more than add feces and pseudofeces to the benthos. A recent study investigating the positive interactions between suspension feeding bivalves and seagrass demonstrated that the presence of the mussel *Modiolus americanus* significantly increased the sediment nutrient pool available to seagrasses, as well as substantially reducing epiphytic biomass on the seagrass leaves (Peterson & Heck 2001). There are 3 alternative hypotheses as to why seagrasses associated with suspension feeding bivalves may have reduced epiphytic loads: (1) mussels may consume the epiphyte propagules in the water column before they attach to the plant, (2) the elevated productivity of the seagrasses increases blade production rates so that the leaves have less time to accumulate epiphytes, or (3) the presence of suspension feeding bivalves increases the structural complexity of the habitat, reducing predation pressures on epiphytic grazer species such as small gastropods and amphipods. This increased habitat complexity may result in elevated numbers of epiphytic grazers and consequently increased levels of epiphytic grazing. Regardless, the combination of increased sediment nutrient levels and reduced epiphytic loads significantly elevated the productivity of the seagrass *Thalassia testudinum* associated with *Modiolus americanus* (Peterson & Heck 2001). However, several questions remain about which mechanism (increased sediment nutrient levels or reduced epiphytic loads) is responsible for the increased seagrass productivity.

Using density manipulations of mussel mimics and nutrient enrichment of the sediments, the following questions were addressed by this study: (1) how do increasing habitat complexity and nutrient enrichment affect *Thalassia testudinum* short-shoot (SS) density, above-ground biomass, leaf morphometrics, leaf epiphytic loads and productivity and (2) which effect (nutrient enrichment or reduced epiphyte load) has the greater impact on seagrass productivity?

METHODS

The effects of nutrient enrichment and increased habitat structure on *Thalassia testudinum* were observed in St. Joseph Bay, Florida, in the northeastern Gulf of Mexico (30° 00' N, 85° 30' W). St. Joseph Bay is a protected shallow coastal embayment where the mean depth is 3 m and salinities usually range from 30 to 36‰ (Stewart & Gorsline 1962, Folger 1972). Temperatures vary seasonally from approximately 8 to 30°C (this study), and the mean tidal range is 0.5 m (Rudloe 1985).

The bay is oligotrophic with water column nitrogen and phosphorus values seldom exceeding 3 and 0.2 µM, respectively, and phytoplankton abundance is usually below 5 µg chl *a* l⁻¹ (Heck et al. 1998). Therefore, light availability for seagrasses is high, with approximately 40% of measured light at the water surface reaching the seagrass canopy (Heck et al. 1998).

St. Joseph Bay supports an extensive seagrass habitat dominated by large monospecific *Thalassia testudinum* beds interspersed with smaller patches of *Halodule wrightii*, unvegetated sand flats and small amounts of *Syringodium filiforme* (Iverson & Bittaker 1986). Only the shallowest portions of the seagrass habitat are exposed during low tides, and wave energy is minimal. Associated with these *T. testudinum* beds is the semi-infaunal tulip mussel, *Modiolus americanus*, which is found in densities as high as 2000 individuals m⁻² (Valentine & Heck 1993).

Determining potential mechanisms of *Thalassia*-mussel interactions. This experiment was designed to examine the effect of the structure of mussel beds and the nutrient loading caused by mussels on *Thalassia testudinum*. A 3 × 3 factorial incomplete randomized design was used for this experiment, which consisted of 2 factors; structure and nutrient enrichment. Structure had 3 levels: 0, 500 and 1500 mussels m⁻² levels. The structure treatment consisted of mussel mimics within the same shell length range (45 to 50 mm). Mimics were constructed by filling dead mussel valves with clean sand and using Ross cyanoacrylate cement (DURO™ non-toxic) to seal mussel shells together. In a heavily vegetated portion of a turtlegrass bed, these mimics were added randomly to 6 replicate 0.5 m² plots (71 × 71 cm) within 2 spatially separated treatment arrays (approximately 1.6 km). Mimics were sufficiently negatively buoyant to remain in place within the sediment for the duration of the experiment. The mussel densities used in this experiment approximate the range of abundances most often observed in the bay (Valentine & Heck 1993).

Nutrient enrichment had 3 levels (nutrient loading achieved by 0, 500 and 1500 mussels m⁻²). The nutrient addition treatment was accomplished by adding levels of nutrient approximating the biodeposition rates of *Modiolus americanus*. Previous literature values of mussel biodeposition rates were used to estimate the amount of nitrogen deposited by *M. americanus*. The average deposition of N g⁻¹ dry wt of mussel tissue from previous investigations is 1.537 × 10⁻³ g N d⁻¹ g⁻¹ tissue (Jordan & Valiela 1982, Kautsky & Evans 1987, Jaramillo et al. 1992). The concentrations of nutrients added to the sediments reflected those estimated for the 2 mussel densities used in the structure treatment (0.2348 g N d⁻¹ for 500 individuals m⁻²; 0.7044 g N d⁻¹ for 1500 individuals m⁻²). In the nutrient enrichment treatments,

sediment nutrients were increased with slow release Osmocote™ (cf. Williams 1980, McGlathery 1992) placed on the sediment surface of six 0.5 m² plots (n = 3 for nutrient enrichment produced by 500 and 1500 individuals m⁻²) within each array. Nitrogen and phosphorus were delivered to the sediments primarily in the form of ammonium phosphate and ammonium sulfate in a molar ratio of N:P ca 8:1. Nutrient additions were made monthly throughout the experiment except at the height of the growing season (June to August) when nutrient additions occurred at 2 wk intervals.

Finally, there was the structure × nutrient enrichment interaction treatment. These treatments contained both mussel mimics and the nutrient enrichment estimated for that density of mussels. The 3 × 3 factorial design was incomplete because the experiment did not include 2 of the interaction treatments. It did not include the 500 mimics m⁻² and nutrient enrichment for 1500 individuals m⁻² nor the 1500 mimics m⁻² and nutrient enrichment for 500 individuals m⁻² treatments. These were excluded because they are biologically unrealistic.

Plot margins of each treatment were marked by anchoring PVC frames to the sediment. Possible translocation of stored nutrients through the seagrass rhizomes out of or into the plots was prevented by severing the rhizomes around the perimeter of each plot. This process was repeated every 3 mo. All extant mussels in the plots were removed prior to the initiation of the experiment. This experiment was conducted for 1 yr. It was initiated on 18 September 1995, and concluded on 21 September 1996.

Treatment effects on SS density, above-ground biomass, leaf morphometrics, leaf productivity and epiphyte coverage were compared monthly by marking then collecting all SS from randomly selected 0.01 m² samples from each replicate plot during 1 growing season (6 mo). Leaf production was measured by using the modified leaf marking method of Zieman (1974). In the laboratory, the number of leaves, leaf width, leaf length, daily gross above-ground production, above-ground seagrass biomass, SS density and leaf epibiont biomass (mg SS⁻¹) were determined from the harvested SS. Epibiont mass was determined by scraping fouling organisms and algae from each leaf, then drying them to a constant mass (±0.01 mg) in an oven at 60°C. Following dry weighing, the ash weight was determined by ashing the samples at 500°C for 4 h. Ash-free dry weight (AFDW) was calculated as dry weight – ash weight.

Epiphyte grazers were collected every other month by suction sampling the area enclosed by a PVC cylinder (15.24 cm diameter × 150 cm height) held vertically at randomly selected locations on the sediment surface. After the sample was passed through a 0.5 mm sieve, each individual was identified to the lowest possible taxonomic classification.

Sediment nutrient concentrations were collected every other month for 1 yr using a PVC core (2 cm diameter, 15 cm depth). The sediment samples were dried at 80°C for at least 24 h and homogenized to a fine powder with a mortar and pestle. Total carbon and total nitrogen contents of the sediment samples were determined for each treatment by oxidation in a Carlo Erba Model 1500 CNS analyzer. Phosphorus content was measured using a modification of the method presented in Solorzano & Sharp (1980) for total particulate phosphorus determination.

To document any potential changes in N and P concentrations in leaves due to treatment effects, biomass specific changes in the concentrations of C, N and P in the dried leaves were measured following Fourqurean et al. (1992). Five randomly selected SS were taken from each treatment at the initiation of the experiment (September 1995), at the beginning of the growing season (May 1996) and at the conclusion of the experiment (September 1996). Leaves were gently scraped and washed in flowing tap water to remove epibionts and sediments that had adhered to the leaves. These washed samples were dried to a constant mass and homogenized by milling to a fine powder. The elemental contents of C, N and P of these seagrass leaves were then determined as described above. The data are presented as mol:mol ratios.

The study then consisted of a 3 × 3 factorial incomplete randomized design examining the possible mechanisms of *Thalassia*-mussel interactions: both structure and nutrient enrichment factors had 3 levels (0, 500 and 1500 individuals m⁻² or the appropriate nutrient addition equivalent for that density). Each treatment was replicated 3 times in each of 2 spatially separated experimental arrays. Repeated measures ANOVA was utilized to test for significant differences and interactions between structure and nutrient enrichment. Prior to any statistical analysis, ratio data was arcsine transformed. When either factor had a significant effect on the response variable and no interaction occurred, multiple comparison tests (Tukey's Studentized range) were used to test for significant differences between levels within the treatment. Results of the repeated measures ANOVA were considered to be significant if $p < 0.05$.

RESULTS

Sediment nutrient concentration

Nutrient enrichment had a significant effect on sediment C:N, C:P and N:P ratios over the course of the experiment (Fig. 1, Table 1). In addition, time had a significant effect on sediment nutrient ratios. As the

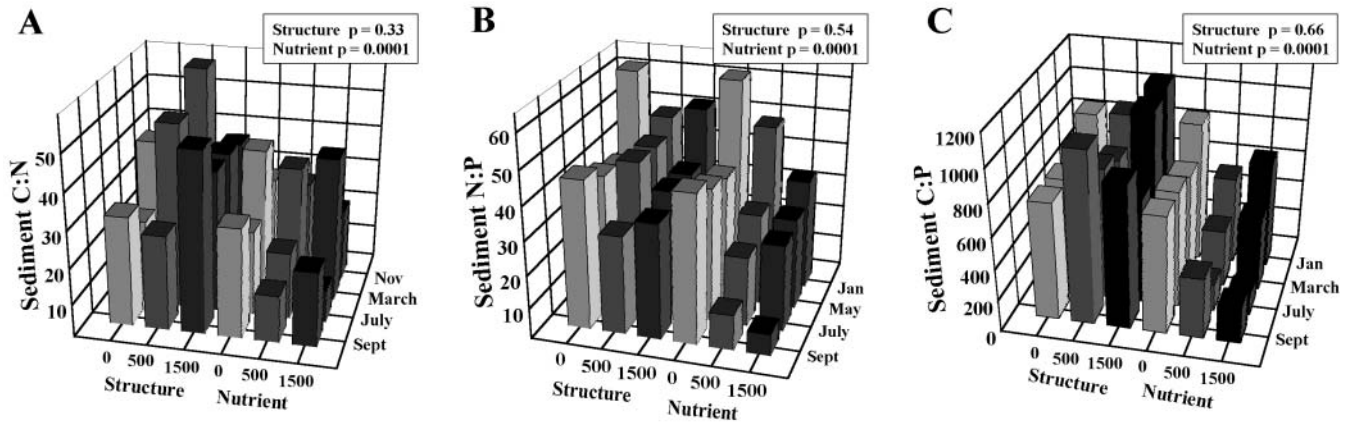


Fig. 1. 3-dimensional plots of the effects of different levels of structure and nutrient on (A) sediment C:N, (B) sediment N:P and (C) sediment C:P ratios by month. Note that the bars are means for each treatment and the 0 structure level and 0 nutrient level are the same data from the 0 structure 0 nutrient plots. The bars become darker with increasing structure or nutrient enrichment

experiment proceeded, sediment nutrient ratios (C:N, C:P and N:P) decreased in the nutrient enrichment treatments. Multiple comparison tests were not conducted because there was a significant time \times nutrient interaction. Conversely, structure (mussel mimics) had no effect on sediment nutrient ratios. However, there was a non-significant increasing trend in sediment C:P ratios with increasing levels of structure. Thus, structure may have enhanced the accumulation of organic material, but this did not significantly increase the nutrient levels of the sediments. Therefore, this experiment revealed that while structure did not affect sediment nutrient ratios, nutrient enrichment on the sediment surface did, and that the decreasing C:N and C:P ratios indicates that the nutrient addition treatments significantly increased the total nitrogen and total phosphorus pools of the sediments. N:P ratios were significantly reduced by nutrient enrichment ($p < 0.001$), revealing that within the sediments the total phosphorus pool was increasing at a rate greater than that of the total nitrogen pool.

***Thalassia testudinum* biomass and morphology**

SS densities ranged from 400 to 1600 SS m^{-2} in the structure treatments and from

Table 1. Repeated measures ANOVA from the 3×3 factorial experiment for sediment nutrient concentrations

Source	df	Type III SS	MS	F	p > F
<i>Sediment C:N ratio</i>					
Structure	2	0.0054	0.0027	1.15	0.3359
Nutrient	2	0.0513	0.0257	11.02	0.0005
Structure \times Nutrient	2	0.0003	0.0002	0.07	0.9297
Error (Treatment)	35	0.0489	0.0023		
Time	3	0.2094	0.0698	5.84	0.0014
Time \times Structure	6	0.0572	0.0100	0.80	0.5752
Time \times Nutrient	6	0.2119	0.0353	2.96	0.0132
Time \times Structure \times Nutrient	6	0.1380	0.0230	1.92	0.0905
Error (Time)	105	0.7530	0.0120		
Total	167				
<i>Sediment C:P ratio</i>					
Structure	2	0.0055	0.0027	0.43	0.6558
Nutrient	2	1.0138	0.5069	79.25	0.0001
Structure \times Nutrient	2	0.0098	0.0049	0.77	0.4770
Error (Treatment)	35	0.1343	0.0063		
Time	3	0.2302	0.0767	7.27	0.0003
Time \times Structure	6	0.1160	0.0193	1.83	0.1071
Time \times Nutrient	6	0.1308	0.0218	2.07	0.0700
Time \times Structure \times Nutrient	6	0.1499	0.0249	2.37	0.0399
Error (Time)	105	0.6652	0.0106		
Total	167				
<i>Sediment N:P ratio</i>					
Structure	2	0.0241	0.0120	0.64	0.5370
Nutrient	2	1.3198	0.6598	35.09	0.0001
Structure \times Nutrient	2	0.0797	0.0398	2.12	0.1450
Error (Treatment)	35	0.3949	0.0188		
Time	3	1.8624	0.6208	21.83	0.0001
Time \times Structure	6	0.1403	0.0234	0.82	0.5570
Time \times Nutrient	6	0.4385	0.0731	2.57	0.0270
Time \times Structure \times Nutrient	6	0.0928	0.0155	0.54	0.7730
Error (Time)	105	1.7916	0.0284		
Total	167				

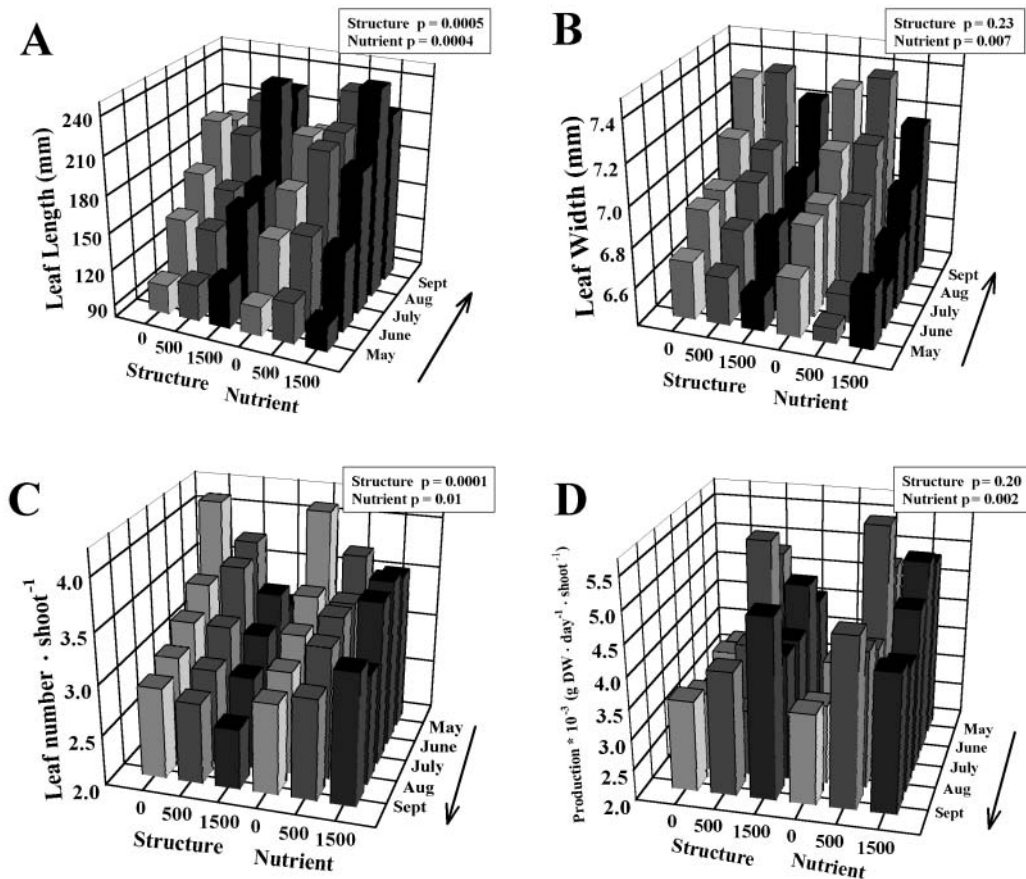


Fig. 2. 3-dimensional plots of the effects of different levels of structure and nutrient on *Thalassia testudinum* leaf morphology. (A) Leaf length in mm, (B) leaf width in mm, (C) leaf number shoot $^{-1}$ and (D) *Thalassia testudinum* productivity (g dry wt d $^{-1}$ shoot $^{-1}$) by month. Note that the bars are means for each treatment and the 0 structure level and 0 nutrient level are the same data from the 0 structure 0 nutrient plots. The bars become darker with increasing structure or nutrient enrichment

500 to 1700 m $^{-2}$ in the nutrient enrichment treatments over the duration of the experiment. The mean SS densities (\pm SD) by treatments over the course of the entire growing season (April to Sept) were 1016 ± 264 for the 500 mimics m $^{-2}$, 983 ± 227 for the 1500 mimics m $^{-2}$, 1067 ± 227 for the nutrient enrichment of 500 individuals m $^{-2}$ and 997 ± 235 for the nutrient enrichment of 1500 individuals m $^{-2}$. Neither structure nor nutrient enrichment had a significant effect on SS densities ($p = 0.66$ and $p = 0.61$, respectively; Table 2). Above-ground biomass ranged from 54 to 266 g dry wt m $^{-2}$ in the structure treatments, and from 74 to 294 g dry wt m $^{-2}$ in the nutrient enrichment treatments over the same time period. Again, neither structure nor nutrient enrichment had a significant effect on above-ground biomass ($p = 0.56$ and $p = 0.15$, respectively). However, structure and nutrient enrichment both had a significant effect on leaf length (Fig. 2, Table 2). Although multiple comparisons were not tested due to a significant time \times

structure \times nutrient interaction, the longest leaves were found consistently in the highest structure and highest nutrient treatments. In addition to leaf length, nutrient enrichment had a significantly negative effect on leaf width ($p = 0.007$), while structure had no effect ($p = 0.23$, Fig. 2). Because there was a significant time \times nutrient interaction, no within-treatment effects are discussed. Finally, structure and nutrient enrichment both had a significant affect on leaf number (Fig. 2). Structure had a negative effect on leaf number ($p = 0.0001$). Conversely, nutrient enrichment had a positive effect on leaf number ($p = 0.01$). Leaf number was also negatively affected by time ($p = 0.0001$). No within-treatment effects are discussed because of a significant time \times structure \times nutrient interaction. Overall, nutrient enrichment treatments resulted in seagrass SS with a greater number of narrower, longer leaves, while structure treatments resulted in SS with a fewer number of wider, longer leaves.

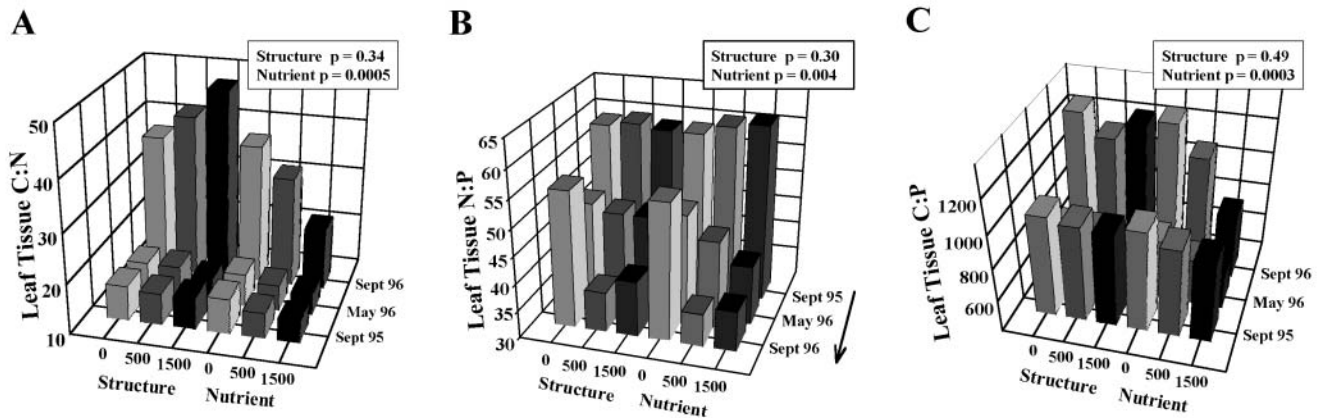


Fig. 3. 3-dimensional plots of the effects of different levels of structure and nutrient on *Thalassia testudinum* leaf tissue (A) C:N, (B) N:P and (C) C:P ratios by month. Note the change in direction of the time axis indicated by the arrow in (B). Note that the bars are means for each treatment and the 0 structure level and 0 nutrient level are the same data from the 0 structure 0 nutrient plots. The bars become darker with increasing structure or nutrient enrichment

Leaf tissue C:N, C:P and N:P concentrations

Structure had no significant impact on leaf tissue C:N or C:P ratios ($p = 0.34$ and $p = 0.49$, respectively) (Fig. 3, Table 2). In contrast, nutrient enrichment had a significant effect on both C:N and C:P leaf tissue ratios. C:N ratios ranged from 13 to 31 in the structure treatments with a mean of 18 ± 6 in treatments with nutrient enrichment for 500 mussels m^{-2} and 15 ± 3 in treatments with nutrient enrichment for 1500 mussels m^{-2} . There was also a significant effect of time on both ratios. Leaf tissue N:P ratios were significantly reduced by nutrient enrichment ($p = 0.004$). Therefore, while structure had no effect on leaf tissue nutrient ratios, nutrient enrichment treatments significantly increased the amount of N and P in the leaves. The N:P ratio changes suggest that the leaves are accumulating more P and may eventually become N-limited.

Primary production

Structure had no significant effect on *Thalassia testudinum* production ($p = 0.20$) (Fig. 2, Table 2). However, net above-ground primary production (NAPP) responded positively with increasing nutri-

Table 2. *Thalassia testudinum*. Repeated measures ANOVA from the 3×3 factorial experiment for response variables

Source	df	Type III SS	MS	F	p > F
<i>Shoot density</i>					
Structure	2	57 355.55	28 677.77	0.43	0.6548
Nutrient	2	68 022.22	34 011.11	0.51	0.6059
Structure \times Nutrient	2	56 533.33	28 266.67	0.42	0.6588
Error (Treatment)	35	2 342 333.33	66 923.81		
Time	4	772 685.19	193 171.30	6.12	0.0001
Time \times Structure	8	175 422.22	21 927.78	0.70	0.6953
Time \times Nutrient	8	445 866.67	55 733.33	1.77	0.0885
Time \times Structure \times Nutrient	8	677 911.11	84 738.89	2.69	0.0089
Error (Time)	140	4 416 000.00			
Total	209				
<i>Above-ground biomass</i>					
Structure	2	1 868.70	934.35	0.59	0.5644
Nutrient	2	6 509.73	3 254.87	2.05	0.1540
Structure \times Nutrient	2	11 303.81	5 651.91	3.56	0.0468
Error (Treatment)	21	33 373.06	1 589.19		
Time	4	171 716.27	42 929.07	43.68	0.0001
Time \times Structure	8	14 482.39	1 810.30	1.84	0.0805
Time \times Nutrient	8	7 652.84	956.61	0.97	0.4625
Time \times Structure \times Nutrient	8	29 885.86	3 735.73	3.80	0.0008
Error (Time)	84	82 560.73			
Total	139				
<i>Leaf length</i>					
Structure	2	156 077.73	78 038.86	7.66	0.0005
Nutrient	2	160 025.43	80 012.71	7.85	0.0004
Structure \times Nutrient	2	19 066.46	9 533.23	0.94	0.3926
Error (Treatment)	1027	10 461 594.10	59.48		
Time	4	9 346 087.26	2 336 521.81	260.32	0.0001
Time \times Structure	8	98 421.60	12 302.69	1.37	0.2040
Time \times Nutrient	8	344 189.79	43 023.72	4.79	0.0001
Time \times Structure \times Nutrient	8	170 725.55	21 340.69	2.38	0.0149
Error (Time)	4108	36 871 900.98			
Total	5169				

Table 2 (continued)

Source	df	Type III SS	MS	F	p > F
<i>Leaf number</i>					
Structure	2	17.3417	8.6708	11.46	0.0001
Nutrient	2	7.0518	3.5259	4.66	0.0102
Structure × Nutrient	2	0.1881	0.0940	0.12	0.8832
Error (Treatment)	297	224.6951	0.7566		
Time	4	139.5855	34.8964	43.98	0.0001
Time × Structure	8	8.3565	1.0446	1.32	0.2309
Time × Nutrient	8	11.3679	1.4210	1.79	0.0790
Time × Structure × Nutrient	8	18.3960	2.2995	2.90	0.0033
Error (Time)	1188	942.5995			
Total	1519				
<i>Leaf tissue C:N ratio</i>					
Structure	2	0.0054	0.0027	1.15	0.3359
Nutrient	2	0.0513	0.0257	11.02	0.0005
Structure × Nutrient	2	0.0003	0.0002	0.07	0.9297
Error (Treatment)	35	0.0490	0.0023		
Time	2	0.4004	0.2002	106.97	0.0001
Time × Structure	4	0.0112	0.0028	1.49	0.2217
Time × Nutrient	4	0.0601	0.0150	8.02	0.0001
Time × Structure × Nutrient	4	0.0092	0.0023	1.23	0.3131
Error (Time)	70	0.0786			
Total	125				
<i>Leaf tissue C:P ratio</i>					
Structure	2	0.0009	0.0005	0.74	0.4894
Nutrient	2	0.0149	0.0075	11.94	0.0003
Structure × Nutrient	2	0.0038	0.0019	3.02	0.0706
Error (Treatment)	35	0.0132	0.0006		
Time	2	0.1158	0.0579	208.59	0.0001
Time × Structure	4	0.0016	0.0004	1.46	0.2314
Time × Nutrient	4	0.0089	0.0022	8.10	0.0001
Time × Structure × Nutrient	4	0.0013	0.0003	1.20	0.3263
Error (Time)	70	0.0117			
Total	125				
<i>Leaf tissue N:P ratio</i>					
Structure	2	0.0046	0.0023	1.29	0.2954
Nutrient	2	0.0253	0.0127	7.13	0.0043
Structure × Nutrient	2	0.0035	0.0018	0.99	0.3867
Error (Treatment)	35	0.0373	0.0018		
Time	2	0.1858	0.0929	82.02	0.0001
Time × Structure	4	0.0091	0.0023	2.00	0.1384
Time × Nutrient	4	0.0269	0.0067	5.94	0.0031
Time × Structure × Nutrient	4	0.0068	0.0017	1.50	0.2368
Error (Time)	70	0.0476			
Total	125				
<i>Thalassia production</i>					
Structure	2	3.3081	1.6541	1.75	0.1979
Nutrient	2	15.4012	7.7006	8.15	0.0024
Structure × Nutrient	2	7.2202	3.6101	3.82	0.0384
Error (Treatment)	35	19.8310	0.9443		
Time	4	23.9325	5.9831	9.76	0.0001
Time × Structure	8	6.2718	0.7839	1.28	0.2656
Time × Nutrient	8	5.3410	0.6676	1.09	0.3790
Time × Structure × Nutrient	8	8.7099	1.0887	1.78	0.0933
Error (Time)	140	51.5010	0.6131		
Total	209				

ent enrichment. Unlike structure, nutrient addition produced significantly greater productivity ($p = 0.002$). While NAPP ranged from 2.57 to 5.05 g dry wt $m^{-2} d^{-1}$ over the entire growing season for the no structure-no nutrient treatments, it ranged from 2.4 to 6.63 g dry wt $m^{-2} d^{-1}$ for the structure treatments and from 3.4 to 8.04 g dry wt $m^{-2} d^{-1}$ for the nutrient enrichment treatments. Mean NAPP for 500 mimics m^{-2} was 4.17 ± 0.94 g dry wt $m^{-2} d^{-1}$ and 4.42 ± 0.96 g dry wt $m^{-2} d^{-1}$ for 1500 mimics m^{-2} . Similarly, NAPP for the nutrient enrichment treatments was 4.77 ± 1.23 g dry wt $m^{-2} d^{-1}$ and 4.75 ± 0.88 g dry wt $m^{-2} d^{-1}$ for the 500 and 1500 individuals m^{-2} nutrient addition treatments, respectively. Although there appeared to be a trend of increasing *T. testudinum* productivity with increasing structure over the course of the experiment, it was not significant. In contrast, nutrient enrichment did significantly elevate *T. testudinum* productivity.

Epiphytic biomass

Overall, nutrient enrichment had no significant effect on epiphytic biomass ($p = 0.30$) (Fig. 4, Table 3). However, in July and August there appeared to be increased epiphytic biomass with increased levels of nutrients. Conversely, structure did have a significant effect on epiphytic biomass ($p < 0.001$). Epiphytic biomass on the leaves was significantly decreased in structure treatments every month except July. Therefore, although nutrients had no significant effect on epiphyte biomass on the leaves (and may actually stimulate epiphyte growth), structure treatments resulted in significantly lower epiphytic leaf loads. Using an equation from Fong & Harwell (1994), the % light reduction attributed to the presence of epiphytic loads on the seagrass leaves was calculated. Repeated measures ANOVA based on the calculated % light reduction by epiphytes revealed that structure resulted in significantly less light reduction ($p = 0.001$),

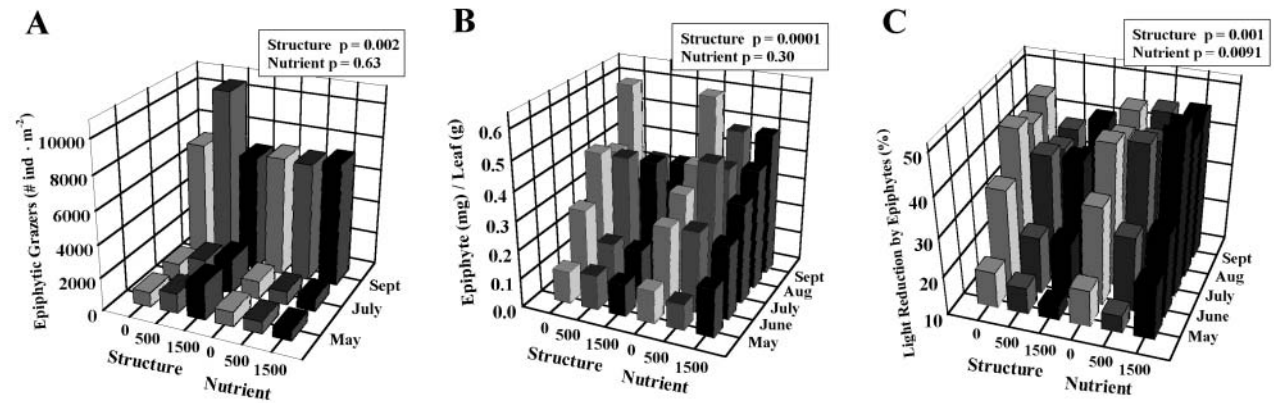


Fig. 4. 3-dimensional plots of the effects of different levels of structure and nutrient on (A) epiphytic grazer densities (individuals m^{-2}), (B) epiphyte biomass (mg epiphyte AFDW g^{-1} leaf dry wt) and (C) % light reduction (calculated by the equation of Fong & Harwell 1994) by month. Note that the bars are means for each treatment and the 0 structure level and 0 nutrient level are the same data from the 0 structure 0 nutrient plots. The bars become darker with increasing structure or nutrient enrichment

Table 3. Repeated measures ANOVA from the 2×3 factorial experiment for epiphytic grazer density and epiphyte biomass

Source	df	Type III SS	MS	F	p > F
<i>Epiphyte biomass</i>					
Structure	2	0.1986	0.0994	19.04	0.0001
Nutrient	2	0.0135	0.0068	1.29	0.2954
Structure \times Nutrient	2	0.0186	0.0093	1.78	0.1926
Error (Treatment)	35	0.1097	0.0052		
Time	4	1.7631	0.4408	73.53	0.0001
Time \times Structure	8	0.1175	0.0147	2.45	0.0196
Time \times Nutrient	8	0.0481	0.0060	1.00	0.4395
Time \times Structure \times Nutrient	8	0.0563	0.0070	1.17	0.3239
Error (Time)	140	0.5035	0.0060		
Total	209				
<i>Epiphytic grazer density</i>					
Structure	2	55 729 605	2 786 4 802	8.55	0.0019
Nutrient	2	3 110 320	1 555 160	0.48	0.6271
Structure \times Nutrient	2	6 779 154	3 389 577	1.04	0.3710
Error (Treatment)	35	68 446 165	3 259 341		
Time	2	734 068 363	36 703 4 181	102.91	0.0001
Time \times Structure	4	43 000 876	1 075 0 219	3.01	0.0322
Time \times Nutrient	4	10 887 590	2 721 897	0.76	0.5469
Time \times Structure \times Nutrient	4	6 104 370	1 526 092	0.43	0.7741
Error (Time)	70	149 788 667	3 566 396		
Total	125				
<i>% Light reduction by epiphytes</i>					
Structure	2	802.4735	401.2367	22.45	0.0001
Nutrient	2	211.6291	105.8146	5.92	0.0091
Structure \times Nutrient	2	54.3082	27.1541	1.52	0.2420
Error (Treatment)	35	375.3704	17.8748		
Time	2	14 444.6898	3 611.1725	80.37	0.0001
Time \times Structure	4	313.1051	1 039.1381	0.87	0.5442
Time \times Nutrient	4	302.6027	37.8253	0.84	0.5687
Time \times Structure \times Nutrient	4	468.1667	58.5208	1.30	0.2535
Error (Time)	140	3 774.2356	44.9314		
Total	209				

while nutrient enrichment resulted in significantly greater light reduction ($p = 0.009$).

Similarly, nutrient enrichment did not significantly affect epiphytic grazer densities ($p = 0.63$), while structure did ($p = 0.002$) (Fig. 4, Table 3). There were significantly greater densities of epiphytic grazers associated with the structure treatments. There was also a significant effect of time on epiphytic grazer densities. Multiple comparison analysis was not conducted due to a significant time \times structure interaction. Overall, structure resulted in significantly lower epiphytic biomass on the leaves and greater epiphytic grazer densities, while nutrient had no significant effect on either epiphytic biomass or grazers.

DISCUSSION

In shallow coastal waters, suspension feeding bivalves often dominate the benthos in numbers as well as in biomass. In the Gulf of Mexico and the Caribbean Sea these filter feeders are usually associated with seagrass. A previously conducted field experiment examined the positive interactions between the suspension feeding mussel *Modiolus americanus* and the seagrass *Thalassia testudinum* (Peterson

& Heck 2001). Their mussel density manipulations resulted in the doubling of the total nitrogen and total phosphorus levels of the sediments and, thus, the significant reduction of leaf tissue C:N and C:P ratios; demonstrating that the mussels increased the sediment nutrient content and that these increased nutrients were biologically available to the plant. *T. testudinum* responded to the presence of mussels by significantly increasing leaf lengths and productivity. In addition, the presence of mussels resulted in a significant reduction in epiphytic loads on the seagrass leaves. Consequently, when mussels were present in seagrass meadows, they elevated seagrass productivity through either increased nutrient resource pools or reduced epiphytic loads on the leaves.

The purpose of this study was to test which effect of the presence of mussels (increased sediment nutrient levels or decreased epiphytic loads on the leaves) had the greatest impact on seagrass productivity. By using mussel mimics and nutrient additions to the sediment surface, this experiment allowed the 2 potential mechanisms of increasing seagrass productivity to be uncoupled and tested. Similar to the previously conducted mussel addition manipulations (Peterson & Heck 2001), the nutrient enrichment treatments increased the amount of total nitrogen and total phosphate in the sediments, altering leaf tissue C:N and C:P ratios. In this experiment, structure had no effect on sediment nutrient levels or on leaf tissue nutrient content. Prior to this investigation, it might have been argued that the increased habitat complexity resulting from the presence of mussels enhances the accumulation of detrital material. The increasing C:N ratios of the sediments associated with the mimics in this study seemingly support this; however, structure produced no significant changes in the sediment nutrient ratios. Therefore, this experiment indicates that the increase in sediment nutrient pools and leaf tissue levels in the previously conducted live mussel density manipulation (Peterson & Heck 2001) can be attributed solely to the effect of biodeposition.

While SS densities and above-ground biomass were unaffected by either structure or nutrient enrichment, the plant's morphology was significantly altered by both factors. Structure resulted in SS with significantly fewer, longer leaves. In contrast, nutrient enrichment treatments resulted in SS with significantly more, narrower and longer leaves. In the previous live mussel manipulation experiment (Peterson & Heck 2001), the presence of mussels resulted in significant changes in leaf number and length. Seagrass SS had fewer leaves in mussel treatments early in the growing season. However, by the end of the growing season this trend had reversed and seagrass SS had more leaves in the mussel treatments than did the control treatments

with no mussels. From this experiment, we can infer that mussel structure had a greater influence on SS leaf number early in the growing season, while mussel biodeposition had a greater impact in the late growing season. Interestingly, in the factorial experiment both structure and nutrient enrichment resulted in significantly longer leaves.

In this experiment, productivity of *Thalassia testudinum* was significantly altered by nutrient enrichment, though not by structure. Increased rates of productivity were measured for every month of the growing season for both factors, and these elevated rates of productivity reached levels twice those of the no structure-no nutrient enrichment treatments. However, only nutrient enrichment had a significantly positive effect on *T. testudinum* productivity. Therefore, this experiment demonstrates that the effect of nutrient enrichment resulting from mussel biodeposition is the primary factor responsible for elevating seagrass productivity in St. Joseph Bay.

In the previous live mussel density manipulation experiment (Peterson & Heck 2001), the presence of *Modiolus americanus* significantly reduced epiphytic biomass on the seagrass leaves. In this experiment, structure resulted in significantly reduced epiphytic loads on the leaves. Nutrient enrichment had no significant effect on epiphytic biomass. This experiment allows 2 of the alternative hypotheses, presented in the 'Introduction' for explaining reduced epiphytic loads on the leaves of seagrasses associated with mussels, to be rejected. If the mussels were consuming the epiphyte propagules in the water column before they attached to the plant, then one would not expect to see a decrease in epiphytic loads on leaves in the structure treatments (since the mimics were incapable of consumption). Similarly, if elevated blade production rates were responsible for reducing epiphytic loads by giving the leaves less time to accumulate epiphytes then, since both structure and nutrient enrichment have had similar rates of blade production, they should have similar epiphytic loads, which they did not. The third alternative, that the presence of suspension feeding bivalves increases the structural complexity of the habitat reducing predation pressures on epiphytic grazer species, cannot be rejected.

Quantitative suction sampling of the structure and nutrient enrichment treatments revealed that structure significantly increased the densities of epiphytic grazers, while nutrient enrichment had no effect. Therefore, this experiment seems to suggest that the presence of the mussels elevates epiphytic grazer densities, which are responsible for the reduced epiphyte loads on the leaves of seagrasses associated with mussels.

Using an equation from Fong & Harwell (1994), the % light reduction attributed to the presence of epiphytic loads on the seagrass leaves was calculated. Both structure and nutrient had a significant effect on light reduction by epiphytes. Structure significantly reduced epiphytic shading, while nutrient significantly increased light reduction by epiphytes. The role of epiphytes in attenuation of light has been well demonstrated (for review see Orth & van Montfrans 1984, Neckles et al. 1993). Although structure had no significant effect on *Thalassia testudinum* productivity in this experiment, the dramatic decrease in epiphytic biomass and consequent % light reduction by epiphytes resulting from the structure treatment suggests that the presence of mussels could play a significant role in increasing seagrass productivity where epiphytic loads are greater than those observed in St. Joseph Bay.

The experimental design allowed both the independent and interactive effects of structure and nutrient enrichment to be examined. Comparing the effects of structure and nutrient enrichment with those of the live mussel manipulations revealed the relative importance of each factor on *Thalassia testudinum* productivity. Nutrient enrichment produced a similar response in sediment nutrient pools as that of the live mussel manipulations, while structure had no effect on sediment nutrient concentration. Similarly, structure resulted in significantly reduced epiphytic loads similar to those of the live mussel manipulations. The results of this experiment indicate that the productivity of the *T. testudinum* community in St. Joseph Bay is limited primarily by nutrient availability.

The overall significance of this study lies in its attempt to understand the processes that control the productivity and abundance of seagrass. This study tested the different effects of 2 beneficial consequences of *Modiolus americanus* on seagrasses. First, *M. americanus* was found to have a major influence on sediment nutrient enrichment. Aggregates of *M. americanus* significantly increased the nutrient pool of nitrogen and phosphate available to *Thalassia testudinum*. Hence, *M. americanus* patches may serve as nutrient 'hot spots' within seagrass assemblages. The dramatic increase in phosphate may have an even more significant impact on seagrasses where carbonate sediments dominate. Second, the epiphytic biomass on the leaves of *T. testudinum* was significantly altered by the presence of *M. americanus*. Although the impact of these reduced epiphytic loads resulted in increased production only near the end of the growing season, the extension of elevated productivity may have substantial consequences on the stability of seagrass assemblages. This may be particularly important to areas experiencing increased levels of eutrophication.

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