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The potential for suspension feeding bivalves to increase seagrass productivity

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Abstract

Suspension feeding bivalves are commonly associated with seagrass habitats in the Gulf of Mexico and Caribbean Sea. Biodeposits of some suspension feeding bivalves have been shown to be high in nitrogen and phosphorus. Consequently, filter feeding bivalves may act as a bentho-pelagic couple bringing planktonic production to the benthos, thereby elevating submerged aquatic vegetation growth by increasing the nutrients available to the rhizosphere. Laboratory feeding experiments were used to calculate the filtration rate of a typical suspension feeding bivalve *Modiolus americanus*. Filtration rates were estimated to be 2.87 ± 0.82 l h^{-1} g tissue dry weight^{-1}. Consumption rates were estimated to be 9.41 ± 2.62 μg Chl *a* h^{-1} g tissue dry weight^{-1}. In addition, field experiments were used to calculate mean biodeposition rates. Biodeposition rates were estimated to be 2.25 ± 0.36 g dry wt material g tissue dry weight day^{-1}. Therefore, at mean field densities *M. americanus* are capable of depositing 218 kg dry weight material m^{-2} annually. These deposits will contain 215 g N and 7.1 g P. A flower pot experiment demonstrated that the biodeposits of *M. americanus* were capable of increasing the pore water nutrient content and a mussel density manipulation in the field revealed that the presence of mussels significantly reduced leaf tissue C:N and C:P ratios. Pore water ammonium and phosphate concentrations were four times greater in the highest mussel density than in the control treatments and the lower leaf tissue C:N and C:P ratios in the presence of mussels established that this increased pore water nutrient was available to the seagrass, *Thalassia testudinum*. Collectively, these experiments suggest that suspension feeding bivalves may be important resource conduits converting inaccessible PON and POP in the water column to elevated sediment nutrient levels within the rhizosphere available for absorption by submerged aquatic vegetation.

Keywords: Bentho-pelagic couple; Biodeposition; Plant–animal interactions; Seagrass; *Thalassia testudinum*; Suspension feeding bivalves; *Modiolus americanus*

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1. Introduction

Dense assemblages of filter feeding bivalves (e.g. mussels) remove suspended matter from the water column and deposit it as feces or pseudofeces on the bottom. Biodeposits from filter feeding bivalves may significantly contribute to the total suspended load in shallow coastal environments (Haven and Morales-Almo, 1966; Tenore and Dunstan, 1973; Kraeuter, 1976; Tsuchiya, 1980). Such biologically mediated sedimentation has the capacity to greatly exceed passive physical processes in the deposition of fine sediments in estuaries and coastal environments (Biggs and Howell, 1984). These biodeposits represent a potentially significant energy source to consumers (Vahl, 1980; Kautsky, 1981; Newell et al., 1982; Stewart, 1987). For example, Newell et al. (1982) calculated that one third of the annual production of particulate matter in a kelp bed area was from fecal matter originating from suspension feeding benthic animals. After bacterial enrichment, a significant proportion was reingested, leading these authors to conclude that a mussel 'fecal loop' plays a significant role in the circulation of nutrients and organic matter in a kelp community.

Additionally, filter feeders transform suspended material by changing particle size distributions in the water column and by converting particulate material into dissolved constituents or biomass via metabolism (Dame et al., 1980). Dame et al. (1985) suggested that feeding by bivalve aggregates may act as a positive feedback loop in which particulate nitrogen (phytoplankton) consumed by the filter feeding bivalves is rapidly remineralized to ammonium (NH_4). This ammonium is then available for plant growth. This model has been envisioned as a nitrogen retention mechanism as well as a process which accelerates the nitrogen cycle (Dame et al., 1989).

Previous studies have illustrated that filter feeding bivalves may control phytoplankton abundance through feeding and nutrient excretion activities (Dame et al., 1980, 1985, 1989, 1991; Cloern, 1982; Officer et al., 1982; Carlson et al., 1984; Prosch and McLachlan, 1984; Nichols, 1985; Doering and Oviatt, 1986; Boucher and Boucher-Rodoni, 1988; Dame and Dankers, 1988; Yamamuro and Koike, 1993). These studies generated great interest in the role that filter feeding bivalves have on phytoplankton growth dynamics and biomass. However, the influence that suspension feeding bivalves have on submerged aquatic vegetation has been largely ignored.

The potential for suspension feeding bivalves to affect the growth dynamics of marine angiosperms may be great. Seagrass productivity is limited primarily by nutrient and light availability. If both are equally important, this creates an apparent environmental incongruity for seagrasses. Increasing water column nutrient levels results in elevated plankton and epiphytic growth which may decrease light availability for seagrasses. Therefore, seagrasses are usually limited to areas with relatively low water column nutrient concentrations. But, unlike phytoplankton, which rely exclusively on water column nutrient sources, seagrasses primarily takes up nutrients from the sediments by using roots (Agami and Waisel, 1986). Previous studies have demonstrated that sediment pore water is the primary source of nutrients for seagrass growth (Stewart, 1987). Because biodeposits of some suspension feeding bivalves are high in nitrogen and phosphorus (Kautsky and Evans, 1987, Jaramillo et al., 1992), filter feeding bivalves can potentially transfer planktonic production from the water column to the benthos via feces

and pseudofeces, and thereby enhance submerged aquatic vegetation growth by increasing the nutrients available in the rhizosphere.

Bertness (1984) investigated the interaction of cordgrass, *Spartina alterniflora*, and the semi-infaunal mussel, *Geukensia demissa*, demonstrating that the presence of this mussel at densities as high as 900 individuals m^{-2} increased net production and the above ground–below ground biomass ratio of *S. alterniflora*. Recently, Reusch et al. (1994) suggested that the blue mussel, *Mytilus edulis*, fertilizes eelgrass, *Zostera marina*, growth by the deposition of feces and pseudofeces. However, the effect that biodeposits of filter feeding bivalves have on seagrass productivity remains uncertain.

One conspicuous plant–animal association within seagrass habitats of the Gulf of Mexico and Caribbean Sea involves turtle grass, *Thalassia testudinum*, and the semi-infaunal suspension feeding tulip mussel, *Modiolus americanus* (Leach) (Rodriguez, 1959; Jackson, 1973; Young and Young, 1982; Lyons, 1989; Valentine and Heck, 1993). In St. Joseph Bay, Florida, extensive monotypic stands of *T. testudinum* contain patchily distributed clusters of *M. americanus*, making this location ideal for experimental manipulation and thus for determination of the significance of a seagrass–bivalve interaction. Using both laboratory and field experiments, the following questions were addressed: (1) what are the particle consumption, filtration and biodeposition rates of *Modiolus americanus*? (2) how does the nutrient content of biodeposits compare to that of naturally sedimenting material? (3) can the addition of biodeposits increase the nutrient content of sediment pore water? and (4) are these nutrients available to *Thalassia testudium*?

2. Study site

The potential effects of mussels on seagrass assemblages were observed in St. Joseph Bay, Florida, in the northeastern Gulf of Mexico (30° 00′ N, 85° 30′ W) during the summer (May–August) of 1996. St. Joseph Bay is a protected shallow coastal embayment where salinities usually range from 30 to 36‰ (Stewart and Gorsline, 1962; Folger, 1972; this study). 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 (J. Pennock, unpublished data). Phytoplankton abundance is also low, usually below 5μg/l. Therefore, photosynthetically active radiation (PAR) is high, with approximately 40% of measured light at the water surface reaching the seagrass canopy (Heck and Valentine, in press).

St. Joseph Bay supports an extensive seagrass habitat occupying ≈ 26 km^2 of shallow bay bottom (McNulty et al., 1972). This seagrass habitat is dominated by large monospecific stands of *Thalassia testudinum* interspersed with smaller patches of *Halodule wrightii*, unvegetated sand flats, and small patches of *Syringodium filiforme* (Iverson and Bittaker, 1986). Seagrass production is highly seasonal with blade biomass and density peaking near 150 g AFDW m^{-2} and 3000 blades m^{-2}, respectively, during summer months (Iverson and 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 and Heck, 1993). Mean densities of *M. americanus* at the study site were 625 individuals m^{-2}. Due to the great variability in mussel size between individuals, a linear regression of shell length to g tissue dry weight was constructed for *M. americanus*:

$$\text{tissue dry wt. weight} = -0.474 + 0.018*\text{shell length} \quad (1)$$

($r^2 = 0.92$; $n = 328$). This allowed a more precise comparison to be made on g dry wt tissue m^{-2} rather than on individuals m^{-2}. Based on this regression at mean field densities, there was 426 g tissue dry wt in each m^2 of sediment surface.

3. Materials and methods

3.1. Flow-through laboratory experiment

Consumption rate (matter ingested per unit time per unit mussel weight) (Hildreth and Crisp, 1976) was estimated using flow-through techniques. Using a modified equation of Northby (1976) consumption at time t (C_t) can be estimated by the equation:

$$C_t = f(Qb_t - Qm_t) \quad (2)$$

where f is the flow rate, Qb_t is the concentration of the rate-indicator substance at the outflow of the control tank and Qm_t is the concentration of the rate-indicator substance at the outflow of the experimental tank (Frechette and Bourget, 1985). The use of this equation requires the following assumptions: (1) that the control tanks are mounted in parallel with the experimental tanks, (2) there is zero consumption in the control tank, (3) that the flows between the experimental and control tanks are equal, and (4) that the experimental organisms occupy a negligible proportion of total tank volume.

The rate-indicator substance for this flow-through experiment was an algal monoculture of the genus *Thalassiosira*. A randomized block design was used in this experiment. Six replicate flow-through chambers were mounted in parallel and randomly assigned to either treatment (three control; three mussels present). The bottom of each chamber was covered by approximately 3 cm of agar. Six mussels (approximate length 45 mm; constituting approximately 2% of the tank volume) were placed vertically into the agar of the experimental chambers and allowed to acclimate for 30 min. The flow rates in all six chambers were synchronized prior to each of the consumption rate estimations. The experiment was repeated four times with mussels that had not been used in previous trials ($n = 12$ for each treatment). After the initiation of the experiment, a known volume of water (250 ml) was collected from the outflow of each chamber every 5 min for 30 min. Output concentrations from control and experimental filtration chambers were measured by nephelometry, using a Turner Associates Model 111

fluorometer. In addition, acetone extracted chlorophyll *a* was collected on Whatman GF/C glass fiber filters used as an index of phytoplankton biomass was determined by fluorometry (Strickland and Parsons, 1972).

3.2. Biodeposition tubes field experiment

In the field, a randomized block design was used to estimate biodeposition rate and test for differences in nutrient content of sedimenting material. Four replicate pairs of PVC cylinders (50 cm in length, 19 cm ID) were tied to racks and attached to the sediment surface perpendicular to the dominant tidal flow. The design of the biodeposition tube followed that of Kautsky and Evans (1987) and Jaramillo et al. (1992). One cylinder of each replicate pair was randomly assigned to the experimental treatment ($n=4$ for each treatment). The tops of the cylinders were covered by Vexar™ mesh (20 mm ID), and a vexar mesh shelf was placed 50 mm below the cylinder lids.

Mussels were collected 24 h prior to the initiation of the experiment and held in aquaria allowing them to void their digestive tracts. Shell morphometrics were recorded and each individual was marked with numbered electrician wire tape. At the initiation of the experiment, mussels were randomly selected and placed between the mesh in the experimental cylinder of each pair. To avoid size specific biodeposition rates, mussels of all size ranges were randomly selected. Mussel biomasses within the cylinders ranged between 236 and 680 g tissue dry weight m^{-2}, which corresponded with the average field mussel biomass occurring in St. Joseph Bay (426 g tissue dry weight m^{-2}). Natural sedimenting material was collected in all the cylinders, while biodeposits were collected only in those containing mussels. Biodeposition was calculated as the amount of material collected in each mussel cylinder minus the average sedimentation obtained in the control cylinders. After 27 days the cylinders were retrieved from the field. The collected material within the cylinders were transferred to buckets and suspended while ten 40-ml aliquots were removed from each cylinder's sediment sample. Each aliquot was drawn through a glass fiber filter (2.4 cm Whatman GF/C glass fiber filters) and dried at 60°C to a constant mass. All ten filters were averaged together to estimate the total suspended load for each cylinder. Five filters were then randomly assigned for nutrient analysis or for ashing at 500°C for 5 h. Total carbon and nitrogen of the sedimented material was determined by combustion with the Carlo-Erba NA1500 (Sharp, 1974). Particulate organic phosphorus (POP) was converted to inorganic phosphorus by high temperature combustion. Residue polyphosphates were hydrolyzed with addition of hydrochloric acid. Total phosphorus was measured by the reactive phosphorus method. Extinction rates were read by spectrophotometric analysis at 885 nm (Fourqurean et al., 1992a). Differences between control and experimental cylinders in C:N and C:P ratios of the sedimented material were tested with one-way analysis of Variance (ANOVA).

3.3. Flower pot field experiment

A completely randomized design was used to conduct a 65-day in situ manipulation experiment within a monospecific grassbed of *Thalassia testudinum* in St. Joseph Bay,

Florida. Twelve plastic containers (15.24 cm in diameter; 0.75 l volume) were filled with sediment from which the organic material had been digested with 10% H_2O_2. The containers were randomly assigned to one of three mussel density treatments (0 individuals m^{-2}, 500 individuals m^{-2}, and 1000 individuals m^{-2}) and placed flush with the sediment surface of the grassbed. A single sediment plug (10 cc) was extracted from each container at the initiation of the experiment to establish initial nutrient concentrations and at the conclusion of the experiment to test for an increase in porewater nutrient levels. Pore water was collected by centrifugation and analyzed on an Alpkem Rapid Flow Analyzer 2 (RFA/2). Differences between the three treatments in sediment porewater ammonium and phosphate were tested with a one-way ANOVA.

3.4. Leaf tissue nutrient content experiment

A completely randomized design was used to perform density manipulations of live mussels in nine randomly assigned 0.25 m^2 plots within a heavily vegetated portion of a turtle grass meadow. Plot margins 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 experiment was conducted for three months (March 1996–May 1996).

Mussels were added randomly to plots at treatment densities of 0, 500, and 1500 individuals m^{-2} ($n=3$ for each density). Within 7 days of planting, the mussels had reattached themselves into natural positions. These densities approximate the range of abundances most often observed in the bay (Valentine and Heck, 1993).

To document any potential changes in nitrogen and phosphorus concentrations in blades due to treatment effects, five shoots were randomly collected from each plot after 3 months and biomass specific changes in the concentrations of carbon, nitrogen and phosphorus in the dried blades were measured following Fourqurean et al. (1992a). 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 ascertained for each treatment. Leaf tissue C and N were determined by oxidation in a Carlo Erba Model 1500 CNS analyzer. Phosphorus content was measured using a modification of the method presented in Solorzano and Sharp (1980) by Fourqurean et al. (1992b) for total particulate phosphorus determination.

4. Results

4.1. Flow-through laboratory experiment

Outflow concentrations from the control chambers were 4.28 ± 0.61 μg Chl *a* ($n=12$) while those of the experimental chambers were 3.48 ± 0.61μg Chl *a* ($n=12$). Using the modified equation of Northby (1976), the consumption rate of *Modiolus americanus* was

calculated to be 9.41±2.62 μg Chl *a* h^{-1} g^{-1} tissue dry wt., while the filtration rate was calculated to be 2.87±0.82 l h^{-1} g^{-1} tissue dry wt.

4.2. Biodeposition tubes field experiment

Natural sedimentation within the biodeposition tubes ranged from 33 to 173 g dry wt. m^{-2} day^{-1}, while biodeposition varied from 431 to 1171 g dry wt. m^{-2} day^{-1} (equivalent to 1.013–2.75 g dry wt. g tissue dry $wt.^{-1}$ day^{-1}). The corresponding values for ashfree dry wt. were 26–112 g m^{-2} day^{-1} and 234–677 g dry wt. m^{-2} day^{-1} (0.55–1.59 g dry wt. g tissue dry $wt.^{-1}$ day^{-1}) for sedimentation and biodeposition, respectively. Combining all replicates, the average natural sedimentation rate was 120 g dry wt m^{-2} day^{-1} and the average biodeposition rates was 959 g dry wt m^{-2} day^{-1} (2.25 g dry wt. g tissue dry wt^{-1} day^{-1}). C:N ratios were significantly lower for biodeposits than for naturally sedimented material ($p<0.001$, $F=22.29$, df=7) (Fig. 1). Correspondingly, C:P ratios were significantly lower for biodeposits ($p=0.03$, $F=5.77$, df=7). However, N:P ratios were not significantly different between the two treatments ($p=0.277$, $F=1.32$, df=7).

4.3. Flower pot field experiment

Pore water nutrient concentrations increased dramatically from the initiation to the conclusion of the experiment. The mean values for ammonium (NH_4) in the control, 500 mussel m^{-2} and 1000 mussel m^{-2} treatments at the initiation of the experiment were 151, 608 and 227 μM NH_4. After 65 days in the field, the pore water concentration of NH_4 in the treatments were 1391, 5224 and 8803 μM NH_4 (Fig. 2a). At the highest mussel density treatment, pore water ammonium levels increased by a factor of 38. Similarly, the mean values for phosphate (PO_4) in the control, 500 mussel m^{-2} and 1000 mussel m^{-2} treatments at the initiation of the experiment were and 101, 56 and 63 μM PO_4 and at the conclusion of the experiment the pore water concentrations of PO_4 were 65, 185 and 461 μM (Fig. 2b). Over the course of the experiment, pore water PO_4 levels decreased in the control treatments and increased in the highest mussel treatments by a factor of 7. The pore water nutrient concentrations of both NH_4 and PO_4 demonstrated a significant positive response to the presence of filter feeding bivalves ($p=0.001$, $F=19.73$, df=11 and $p<0.001$, $F=23.19$, df=11, respectively).

4.4. Leaf tissue nutrient content experiment

Thalassia testudinum leaf tissue C:N exhibited a significant decline from 16.31±0.38 in the 0 mussel treatment, to 14.85±0.67 in the 500 mussel treatments, to 13.37±0.38 in the 1500 mussel treatments ($p=0.001$, $F=26.306$, df=2) (Fig. 3). Differences were significant for all treatment combinations (Student–Newman–Keuls method). A similar pattern was observed for treatment effects on leaf tissue C:P which declined from 774.62±25.84 to 702.52±39.80 to 658.74±28.21 with increasing mussel densities ($p=0.012$, $F=10.113$, df=2). However, leaf tissue N:P demonstrated no significant change with increasing mussel densities ($p=0.62$, $F=0.51$, df=2).

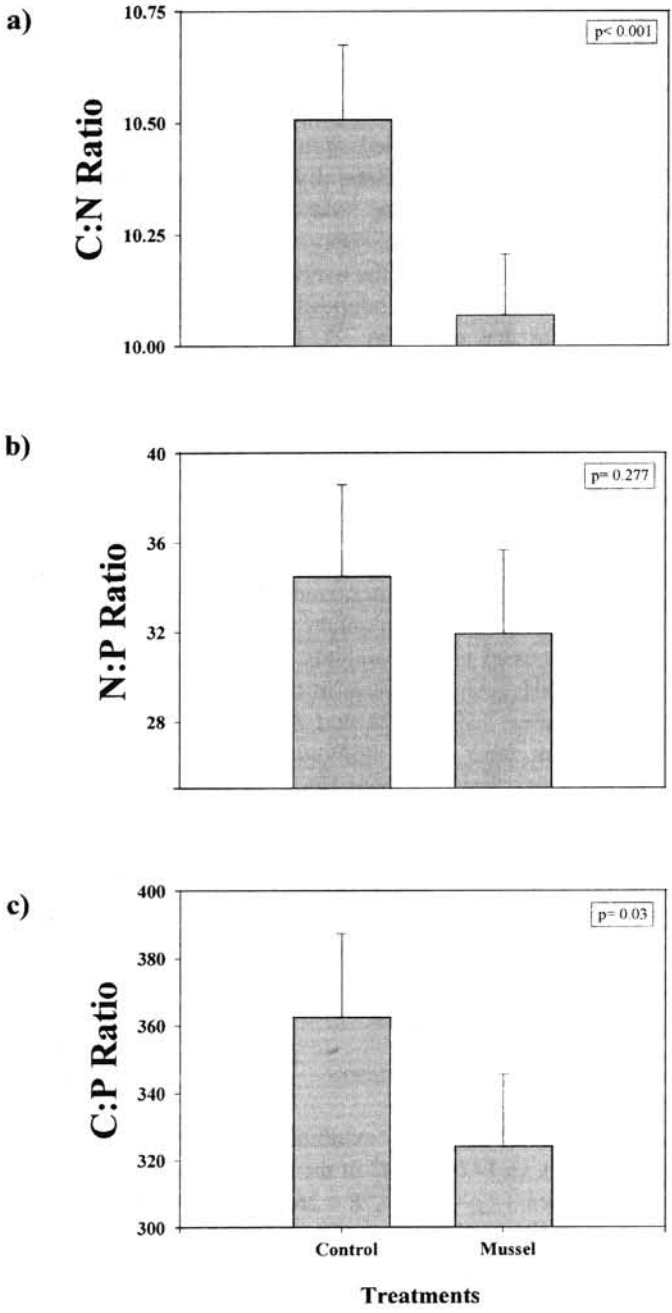

Fig. 1. (a) C:N, (b) N:P and (c) C:P ratios of *Modiolus americanus* biodeposits and naturally sedimenting material from the biodeposition tube experiment (Bars = mean ± 1 S.D.).

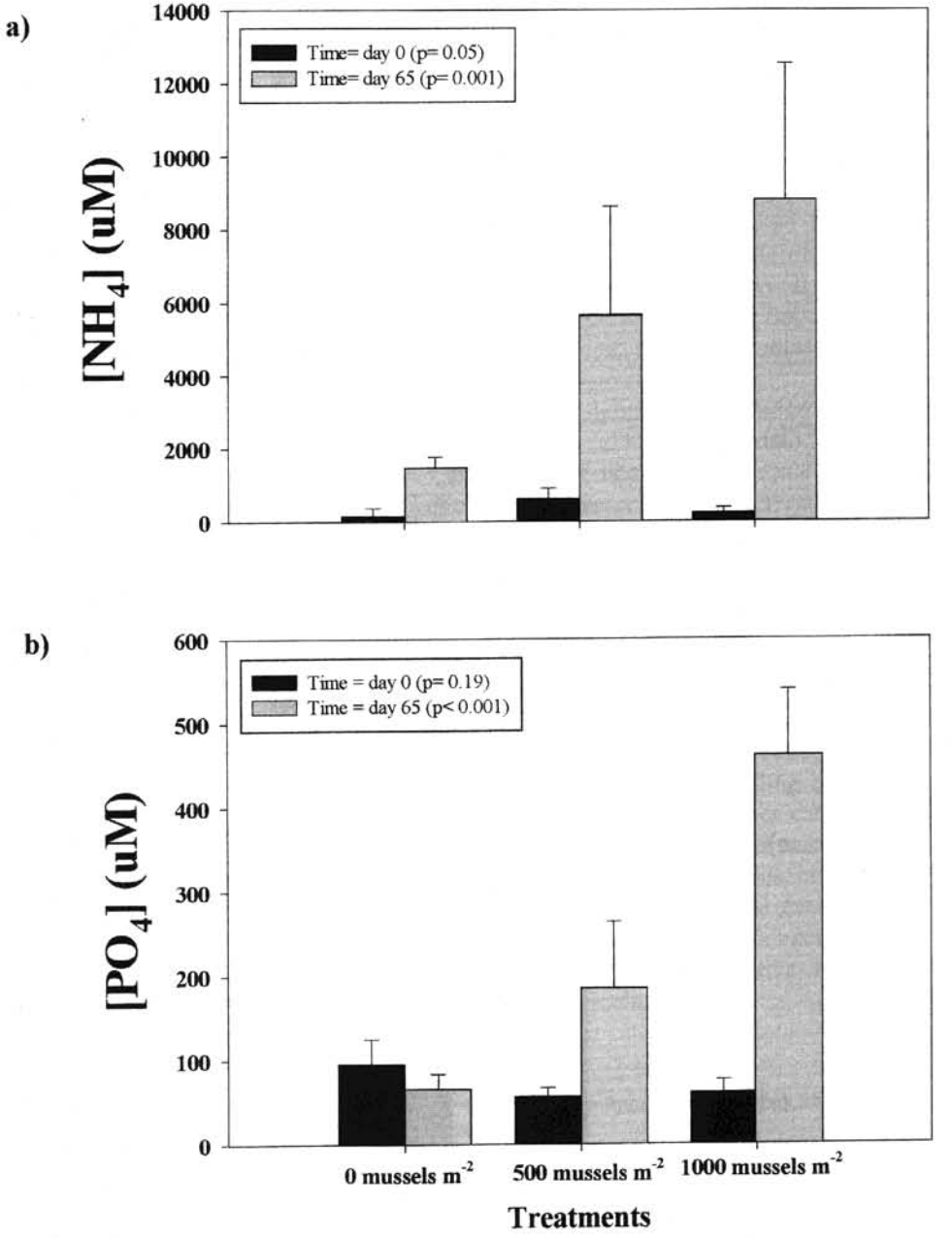

Fig. 2. (a) Pore water ammonium concentration comparison between control, 500 mussels m^{-2} and 1000 mussels m^{-2} at day 0 and day 65, respectively. (b) Pore water phosphate concentration comparison between control, 500 mussels m^{-2} and 1000 mussels m^{-2} at day 0 and day 65, respectively (Bars = mean ± 1 S.D.; differing letters indicate significant differences between treatments using Student–Newman–Keuls multiple comparison method).

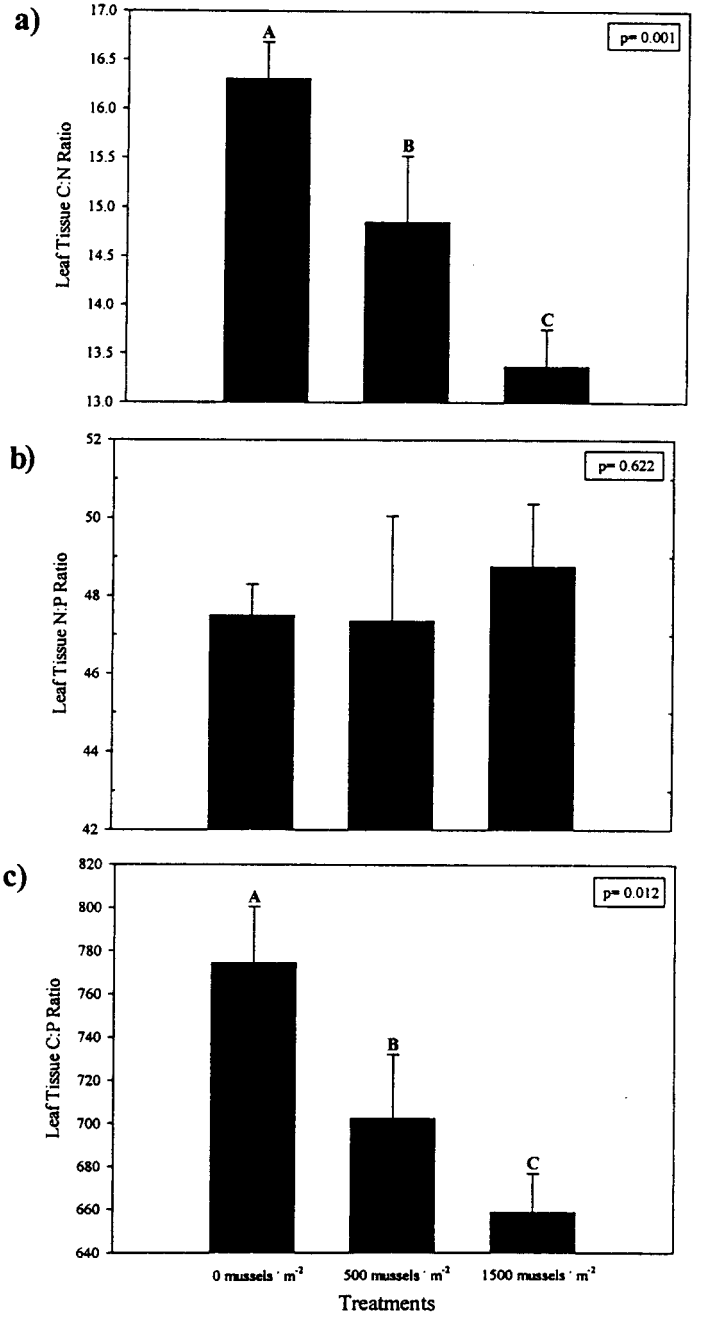

Fig. 3. (a) Leaf tissue C:N ratio comparison between between control, 500 mussels m^{-2} and 1500 mussels m^{-2}. (b) Leaf tissue C:P ratio comparison between control, 500 mussels m^{-2} and 1500 mussels m^{-2} (Bars = mean ± 1 S.D.; differing letters indicate significant differences between treatments using Student–Newman–Keuls multiple comparison method).

5. Discussion

The experimental consumption rates of *Modiolus americanus* for this study were compared to five models used in the literature to estimate consumption of suspended particles by filter feeding bivalves (Table 1). Models from the literature are all functions of size, temperature, or both. Four of the models predicted filtration rates within a close margin of the actual measured filtration rates for *M. americanus*. However, the model of Cloern (1982) significantly overestimated the actual filtration rate (Table 1). In these laboratory experiments, *M. americanus* was demonstrated to be capable of consuming twice the amount of Chl *a* present in the water column in St. Joseph Bay. It is possible, however, that the low Chl *a* content of the water column in St. Joseph Bay may be the direct consequence of the high consumption rates of *M. americanus* and other suspension feeding bivalves.

Organic matter deposited as feces may represent a significant proportion of nutrient potentially available to submerged aquatic vegetation. C:N and C:P ratios have been employed to assess the nutritional values of food, bacteria and detritus (Russell-Hunter, 1970; Kautsky and Evans, 1987; Parson et al., 1977). Lower C:N and C:P ratios indicate higher concentrations of nitrogen or phosphorus. Accordingly, comparisons of C:N ratios between naturally sedimenting particles and mussel biodeposits yield insights into the characteristics of both materials. Biodeposits of *M. americanus* were greatly enriched in both nitrogen and phosphorus, but C:N ratios for biodeposits analyzed in this study were higher than that of previously published studies (Jordan and Valiela, 1982; Kautsky and Evans, 1987; Jaramillo et al., 1992). C:N and C:P ratios were still significantly lower for biodeposits than that of naturally sedimenting material. Approximately half of the particulate nitrogen and carbon consumed by mussels is expelled as feces (Jordon and Valiela, 1982; Hawkins and Bayne, 1985), while the corresponding amount for phosphorus may be as high as 94% (Kuenzler, 1961). Bivalve molluscs can eliminate between 5 and 50% of total nitrogen excretion in the form of amino acids, but this phenomenon is highly seasonal and is usually associated with periods of starvation and/or gametogenesis when catabolism of protein provides a reserved energy supply (Bayne and Scullard, 1977). Previous studies have shown that ammonia excretion rates for bivalve molluscs increase with temperature and show a positive logarithmic relationship to body weight (Duerr, 1968; Bayne and Scullard, 1977).

Table 1
Comparison of filtration models from the literature with the estimates from the flow-through experiments for *Modiolus americanus* (L = shell length, T = temperature, W = weight)

Filtration model	Filtration estimate (ml ind^{-1} min^{-1})	Reference
$[(L^{0.96})(T^{0.95})]/2.95$	24.73	Doering and Oviatt (1986)
$5.12L^{0.967}$	21.92	Doering and Oviatt (1986)
$2.59W^{0.73}$	23.15	Coughlan and Ansell (1964)
$0.76W^{-0.40}$	17.82	Officer et al. (1982)
$168W^{0.67}$	65.86	Cloern (1982)
Actual	20.38	This study

Table 2
Comparison of biodeposition rates from the literature with the estimates from the biodeposition tubes for *Modiolus americanus*

Species	Biodeposition rate (g N day^{-1} g tissue dry wt^{-1})	Reference
Mytilus edulis	5.055×10^{-4}	Kautsky and Evans (1987)
Choromytilus chorus	2.066×10^{-3}	Jaramillo et al. (1992)
Mytilus chilensis	2.378×10^{-3}	Jaramillo et al. (1992)
Modiolus demissus	1.200×10^{-3}	Jordan and Valiela (1982)
Modiolus americanus	2.47×10^{-3}	This study
	6.92×10^{-3}	This study

Biodeposition rates of nitrogen for *Modiolus americanus* are consistent with those previously reported for most other suspension feeding bivalves (Table 2). The estimates of this field experiment reveal that if all of the nutrient within the biodeposits of *M. americanus* were available to *Thalassia testudinum*, then on an annual basis biodeposits would provide eight times greater nitrogen and seven times greater phosphorus than required for maximal leaf growth in *T. testudinum* (Patriquin, 1972). If all of this nutrient were directly available to the plant, then the requirements for maximal leaf growth in *Thalassia* would be achieved through the biodeposits of 1/6th of the biomass of *M. americanus* present in the average m^2 of sediment surface in St. Joseph Bay.

The C:N:P ratios of plants have been used to assess the nutrient status of phytoplankton (Redfield, 1958) and macrophytes (Gerloff and Krombholtz, 1966). The amount of nitrogen or phosphorus, relative to carbon, in plant tissues is a function of the availability of N or P in the environment. Forqurean et al. (1992b) found that leaf tissue C:N and C:P of *T. testudinum* decreased with increasing pore water soluble reactive phosphorus and ammonium. Furthermore, the N:P ratio of seagrass leaf tissue reflected the relative availability of N and P in the environment. In this study, pore water nutrients increased dramatically in the presence of *M. americanus* and a subsequent decline in leaf tissue C:N and C:P was observed with increasing mussel densities. This indicates that the increased nutrient concentration of the sediments is biologically available to the plant and that plants in association with suspension feeding bivalves have an increased nutrient content within their leaf tissue. Thus, *T. testudinum* has more resources available for growth when associated with *M. americanus*.

Numerous organisms have been shown to have a profound influence on the communities they live in through habitat or resource modification (Jones et al., 1994). Previous investigators have demonstrated a positive effect of suspension feeding bivalves on plant production. Bertness (1984) found that the fecal material from *Geukenia demissa* stimulated growth of *Spartina alterniflora* on which the mussels were attached. Similarly, Reusch et al. (1994) documented enhanced growth of *Zostera marina* in the presence of the suspension feeding blue mussel, *Mytilus edulis*. These studies emphasize the stimulating effect of biodeposition on benthic plant production. In the grass system of St. Joeseph Bay, the mussels can be envisioned as transforming the unavailable particulate organic nitrogen and phosphorus in the water column into

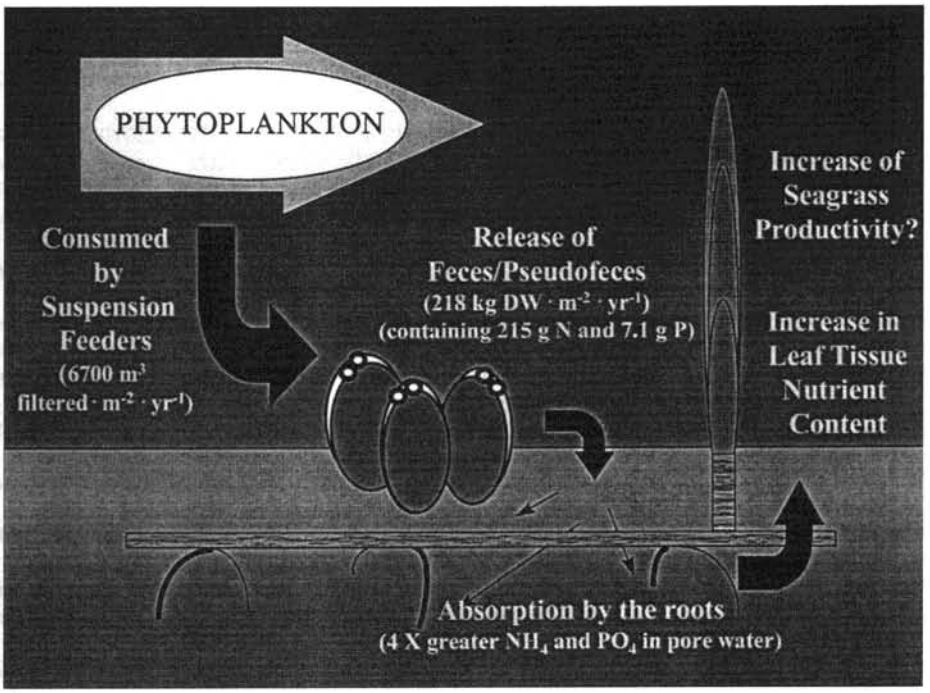

Fig. 4. Conceptual model of the role of *Modiolus americanus* in seagrass assemblages of *Thalassia testudinum*. The annual estimates of filtration and biodeposition are listed.

accessible nitrogen and phosphorus in the sediments (Fig. 4). The estimates of *M. americanus* biodeposition rates suggest that these organisms are capable of transferring a significant amount of nitrogen and phosphorus from the water column to the benthos. Consequently, their ecological impact may be great. It is conceivable that *M. americanus*, by increasing the sediment nutrient level, may create new habitable areas for colonization by *T. testudinum* or maintain sufficient nutrient levels for the continued existence of *T. testudinum* in stressful environments.

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