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The effects of the filter-feeding clam *Mercenaria mercenaria* on carbon cycling in experimental marine mesocosms

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ABSTRACT

The metabolism and the fate of ^{14}C labelled carbon was examined in 4 outdoor mesocosm (13 m^3) tanks containing both benthic and pelagic compartments. Mesocosms with (16/m^2) and without the clam, *Mercenaria mercenaria* were compared. System production, net and gross sedimentation of particulate carbon and benthic remineralization of dissolved inorganic nitrogen were all greater in mesocosms with clams. A filtration rate model, dependent on clam size and temperature, explained between 74–114% of the increased gross sedimentation in clam tanks relative to controls.

The higher production in the clam tanks was at least in part due to a greater flux of dissolved inorganic nitrogen from the benthos. Despite this greater production in the clam tanks, water column biomass remained similar to controls. Calculations based on the filtration rate model indicated that clams could have consumed between 30% and 46% of the excess biomass produced during the day. Loss of particles due to processes in the water column appeared to consume most of this excess biomass. Although clams enhanced production and sedimentation, they did not limit phytoplankton biomass in the water column through filtration.

1. Introduction

Filter feeding by benthic bivalves has long been recognized as a process which can increase transport of particulate matter from the overlying water to the benthos (Verwey, 1952; Haven and Morales-Alamo, 1966, 1972). Only recently, however, has such removal been viewed as an important factor in the cycling of material between the water column and benthos (Ott and Fedra, 1977; Kitchell *et al.,* 1979; Dame, 1980; Jordan and Valiela, 1982).

The effects of benthic filter feeders on system processes or specific components follow from the removal of particulate matter from the water column. Benthic filter feeders can enhance deposition (Verwey, 1952; Haven and Morales-Alamo, 1966, 1972; Ott and Fedra, 1977). The largely theoretical considerations of Cloern (1982) and Officer *et al.* (1982) predict that under certain conditions this removal may regulate phytoplankton biomass. Indeed, depletion of plankton biomass has been observed over dense assemblages of bivalves (Wright *et al.,* 1982; Carlson *et al.,* 1984;

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Cohen *et al.*, 1984; Nichols, 1985). Removal of suspended particles may limit the amount of substrate available for water column respiration (Ott and Fedra, 1977). Thus, benthic filter feeders appear to moderate water column processes and the dynamics of resident populations through transfer of suspended particles to the benthos.

Most investigations have centered on effects produced by removal of suspended particles, thus viewing filter feeding as a unidirectional process. Benthic metabolism is strongly related to pelagic production in shallow coastal areas; increased organic deposition to the sediment leads to enhanced nutrient regeneration, thereby refueling pelagic activity (Zeitzschel, 1980; Nixon, 1981; Kelly and Nixon, 1984; Kelly *et al.*, 1985). Few studies have considered the influence of benthic filter feeders on this return of nutrients to overlying water (e.g., Dame *et al.*, 1984; Murphy and Kremer, 1985). Clearly, benthic filter feeding should be investigated within the context of reciprocal exchange between water column and benthos.

This paper presents the results of a mesocosm experiment conducted at the Marine Ecosystems Research Laboratory (MERL) adjacent to Narragansett Bay, Rhode Island. The impact of a filter feeding bivalve, *Mercenaria mercenaria,* upon carbon flow through a shallow coastal ecosystem was examined under experimental conditions allowing for a reciprocal coupling of benthic and pelagic biogeochemical cycles. We followed the fate of ^{14}C added as sodium bicarbonate to the water column of mesocosms with and without *M. Mercenaria* as a component of the benthic community. We present results for the entire spring–summer period of the experiment, focusing upon the impact of this species on production, respiration, sedimentation, benthic storage and the biomass of particulate organic carbon in the water column. Some ancillary measurements on clam filtering rates and on nitrogen cycling are also presented in order to begin to delineate the mechanisms through which the noted effects on carbon flow were mediated.

2. Methods

a. Mesocosms. Four mesocosm tanks (Fig. 1) were employed during this study. Each mesocosm contains both seawater and sediments and is designed to simulate a shallow, unstratified coastal ecosystem such as Narragansett Bay, Rhode Island. The mesocosms closely resemble the Bay with respect to temperature, mixing (Nixon *et al.*, 1980), primary production (Oviatt *et al.*, 1981), nutrient concentrations and dynamics (Pilson *et al.*, 1980), phytoplankton (Vargo *et al.*, 1982) and benthic community structure (Grassle *et al.*, 1981; Frithsen, 1984).

The treatment of tanks and sediments is summarized in Table 1. Sediments were collected using a 0.25 m^2 box corer from a site north of Conanicut Island on Narragansett Bay (Hunt and Smith, 1983). The benthic macrofauna are dominated by two deposit feeders: the polychaete, *Mediomastis ambiseta* and the bivalve, *Nucula annulata* (Frithsen, 1984; Rudnick, 1984). *Mercenaria* occurs only rarely at this site

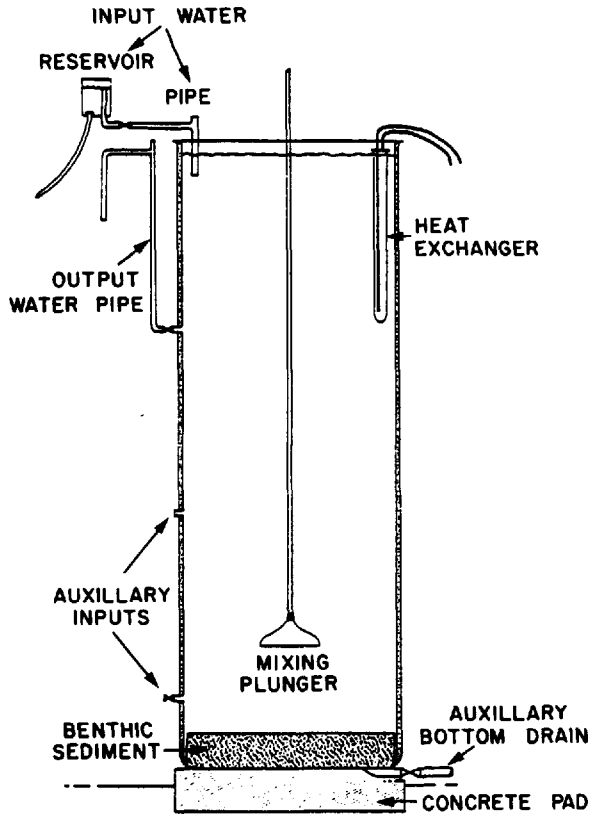

Figure 1. Diagram of a MERL Tank. Water depth is 5 m, volume 13 m^3. Sediment depth is 37 cm, area 2.52 m^2. Mixing is provided by a plunger which rotates, in eliptical orbit, 1 m off the bottom and operates on a 2 hrs. on—4 hrs. off schedule. Normally water is exchanged with Narraganset Bay at the rate of 480 l/day.

(Oviatt, pers. obs.), but sediment grain size (18% sand, 60% silt, 22% clay) compares favorably with that in the Providence River area (17% sand, 55% silt, 28% clay) where *Mercenaria* may exceed 60/m^2 (Oviatt *et al.*, 1984; Saila *et al.*, 1967). Until addition of radiocarbon the tanks were configured as in Figure 1. After addition, tanks were run in batch mode receiving no input from Narragansett Bay. Tanks configured in this manner for up to 7 months do not diverge either from the Bay or tanks receiving input from Narragansett Bay (Pilson *et al.*, 1980). Temperature ranged from 9 to 21°C and salinity from 26 to 29‰ during the course of the experiment.

Forty clams (16/m^2), *Mercenaria mercenaria,* (marked with nail polish and measured: anterio-posterior length) were planted in the sediments of each of two mesocosms. The other two, without clams, served as control tanks. Clam lengths ranged from 3.2 to 10.7 cm and averaged (±S.D.) 6.71 ± 1.89 cm and 6.73 ± 1.87 cm respectively in the two mesocosms. The size distribution approximated that given by

Stringer (1959) for Narragansett Bay. *Mercenaria* were collected from Sheffield Cove on Conanicut Island, Narragansett Bay, R.I.

Radiocarbon (^{14}C) (2 mCi in 2.5 l of filtered (1 μm) seawater) was added to each of the tank water columns at mid-depth during mixing as sodium bicarbonate (New England Nuclear, specific activity: 50 mCi/m mole).

b. Samples. The types of samples and frequency of their collection are summarized in Table 1. All water column samples were withdrawn by siphon from mid-depth while the mixers were operating and after homogeneity of the water column had been achieved (Nixon *et al.*, 1980).

Phytoplankton biomass was assessed by chlorophyll *a* analysis after Yentsch and Menzel (1963) and Lorenzen (1966).

Dissolved inorganic nitrogen was determined by standard techniques: ammonia after Solorzano (1969), nitrate-nitrate after Strickland and Parsons (1972) and Grasshoff *et al.* (1983). Total CO_2 concentration was derived from measurements of pH, alkalinity, temperature, and salinity as in Oviatt *et al.* (1986).

Radioactive dissolved inorganic carbon ($DI^{14}C$) was determined by purging duplicate acidified (5 ml 6N H_2SO_4) 250 ml water samples with N_2. CO_2 was removed from the gas stream by extraction in a phenethlyamine filled (5 ml) Vigreux column. The column was rinsed (5 ml) twice with scintillation cocktail (Beckman MP). The extraction procedure was 99.2 ± 0.07% (n = 2) efficient.

The phenethylamine-scintillation cocktail mixture was collected in a 20 ml vial and ^{14}C activity (dpm) determined on a liquid scintillation counter (external standard, channels ratio method with a Beckman LS-3105T counter). Samples were counted 3 times for 10 minutes. The 10 minute counting period usually resulted in counting errors of 1% or less with an efficiency of about 80%. The precision of the duplicate samples was ±5% of the mean.

The activity of ^{14}C on suspended particles ($PO^{14}C$) was determined by passing duplicate 1 liter water samples through 47 mm Gelman AE glass fiber filters (nominal pore size 0.4 μm). These were rinsed with 100 ml of filtered sea water to remove any soluble ^{14}C. The filters were transferred to 20 ml vials with 15 ml of scintillation cocktail and dpm were determined as above. Counting efficiency averaged about 85% and the precision of the duplicate samples 2.5% of the mean.

Sediment cores (5.067 cm^2, n = 8) were taken from each tank on 14 August, 1984, using a remote coring device (Frithsen *et al.*, 1983). A triangulation system employed at the water surface protected against coring the same location twice. In the laboratory, cores were sliced to obtain the following vertical intervals: 0–0.5 cm, 0.5–1.0 cm, 1–2 cm, 2–6 cm, 6–10 cm. All but the surface 0–0.5 cm were subcored (1.54 cm^2) to avoid smearing between layers. Two slices from each depth (1 from each of two cores) were placed in clean, preweighed vials and wet and dry weight (110°C) determined.

Table 1. Treatment of tanks before the experiment and types of samples and their frequency of collection during the 119 day experiment.

Time	Activity
24–28 Oct. 1983	Sediments collected; tanks on flow through.
20 March–2 April, 1984	Tanks drained: Epibenthic filter feeders, predators removed. Clams planted in sediments. Tanks on batch mode.
18 April	Addition of radiocarbon (2 mCi/tank).
18 April–14 August sampling	
Sample type	**Frequency**
Water column	
Chlorophyll *a*	Weekly
Zooplankton (net tow 153 μm)	Weekly
pH, Alkalinity	Weekly
Dissolved Inorganic ^{14}C (DI ^{14}C)	Weekly
Temperature	Weekly
Dawn-dusk-dawn	
Particulate ^{14}C	Weekly
Sediment	
Cores (^{14}C)	Final
Fluxes (DI ^{14}C, nutrients)	Fortnightly
Other	
Clam filtering rates	Monthly
Nutrients (NH_3, $NO_2 + NO_3$)	Fortnightly
Clam tissue ^{14}C	Final
Clam shell ^{14}C	Final

Radioactivity in the sediments was determined after Rudnick (1984). Sediment was ground and homogenized with mortar and pestle. Subsamples (about 50 mg) were transferred to preweighed, precombusted crucibles. Dry weight was determined after oven drying (60°C) for 24 hrs. Subsequent acidification with 300 ul of 6N H_3PO_4 volatilized DI^{14}C. Samples were burned at 950°C in a precombusted stream of oxygen (1 l/min) and the resultant radioactive CO_2 caught in a phenethylamine filled (5 ml) Vigreux column (Burnison and Perez, 1974). Treatment and counting of the samples were the same as those for DI^{14}C. Counting efficiences averaged about 80%. Estimates of dpm/m^2 of bottom, at each depth, from the 4 pools of slices varied from 11 to 100% of the mean (average ± 45%) and were summed to yield estimates of the total sediment inventory from 0–10 cm.

Benthic fluxes of DI^{14}C and the various nitrogen species were measured by following concentration changes over time within a chamber covering the entire benthos. Flux methodology and chamber operation is described in Kelly *et al.* (1985). Precision of DI^{14}C samples averaged 1.2% of the mean (n = 3), ammonia 5%, and nitrate + nitrite

3.5% (both $n = 3$). Incubation time varied inversely with temperature and ranged from 4 to 9 hours over the course of the experiment. The decline in oxygen concentration, although not reported here, was always linear over the incubation period (average $r = 0.990 \pm 0.019$, $n = 28$). Fluxes were calculated following Kelly *et al.* (1985), except a 3 or 4 point time series and linear regression of concentration on time were used to better estimate fluxes.

Clams were retrieved from the tanks on 21 August 1984, allowed to void their guts for 24 hours and frozen until analysis. Seven clams from each of the two treatment tanks, spanning the range of sizes were shucked, and regressions of dry tissue weight (including adductor muscle) and shell weight against length determined. For analysis of ^{14}C activity, tissue was treated in the same manner as sediments, while shells were pulverized and 50 mg subsamples evaluated for inorganic ^{14}C. These subsamples were dissolved in 225 ml of deionized water through acidification with 10 ml of concentrated HCl (pH < 2) and analyzed for $DI^{14}C$ as above.

Estimates of μCi/clam in tissue (precision ± 19% of the mean, $n = 2$) were related to clam length by power functions; the exponent for each tank was about 2.3 (Tank 13: $r = 0.98$, $p < 0.05$, Tank 14: $r = 0.89$ $p < 0.05$, $n = 14$ in both cases). These regressions enabled calculation of the amount of label contained in clam tissue in each tank.

Estimates of μCi/clam shell (precision ± 22% of the mean, $n = 2$) were linearly related to a composite variable, growth in length during the experiment multiplied by shell weight (Tank 13: $r = 0.90$ $p < 0.05$, Tank 14: $r = 0.89$ $p < 0.05$, $n = 14$ in both cases). Shell weights were calculated from power functions of shell weight on length ($r = 0.99$ $p < 0.05$ for each tank, $n = 7$ in both cases). Growth of extraneous unmarked clams was assumed to be the average of their size class. Clams which died during the experiment were not included in these calculations. The above relationships allowed estimation of ^{14}C activity in the shell of each clam in the two treatment tanks.

c. Carbon. ^{14}C dpm have been converted to total labelled carbon using the specific activity (dpm/μgC) of the dissolved inorganic carbon in the water column, calculated from $DI^{14}C$ measurements and total CO_2 derived from pH and alkalinity. Except where noted, dpm have been converted to total labelled carbon using average values of specific activity (dpm/μgC) for each tank (Controls: T-12 = 12.58 ± 1.86, T-15 = 11.89 ± 2.26. Treatments: T-13 = 11.39 ± 2.47, T-14 = 11.59 ± 2.27).

d. Sedimentation. Net sedimentation of organic carbon was determined from the amount of ^{14}C in the sediment at the end of the experiment as estimated from core samples. In treatment tanks, the amount of labelled carbon in *Mercenaria* tissue was added to the core estimates, as the latter included small animals but not clam tissue.

Gross sedimentation was calculated as net sedimentation plus the amount of labelled carbon remineralized over the experiment as measured by flux of $DI^{14}C$. This flux was estimated from concentration changes within a chamber. Deposition of $DI^{14}C$ in clam

shell either directly from the water or from organic matter respired by the clams (Dillaman and Ford, 1982) causes the measured flux to underestimate remineralization. Thus, labelled carbon in clam shells was treated as remineralized carbon in the calculation of gross sedimentation.

e. System production and respiration. Production and night respiration were estimated from sequential dawn-dusk-dawn measurements of ^{14}C dpm on particles in the tank water column. Production was calculated by subtracting the dawn particulate dpm from the dusk particulate dpm. The difference in activity was converted first to μg C/l using the weekly specific activity measured at dusk, then to gC/m^2 and lastly divided by the number of hours between the two samples to yield an hourly rate of production. The hourly rate was multiplied by the actual day length to give daily production. Night loss of particulate matter (system night loss) was calculated similarly using the difference between the dusk and subsequent dawn samples.

Production as measured here is the net system production of particles (system production) which occurs above and beyond losses due to respiration and sedimentation during the day, while night losses include sedimentation and respiration of particles by the water column and benthos. Loss of particulate matter due to processes in the water column (water column night loss) can be calculated by subtracting the losses due to sedimentation and benthic respiration from system night loss. These losses amount to gross sedimentation during the night. Gross sedimentation at night was computed by adjusting estimated total gross sedimentation for the average night fraction (0.39) over the experiment of the 24 hour day. This same procedure was used to derive the nocturnal proportion of other processes which were estimated over the entire day.

f. Integration. In most instances data are summarized in the Results section using values derived from trapezoidal integration over the time period from Julian Day 109 (18 April, 1984: ^{14}C addition) to Julian Day 227 (14 August, 1984: final coring of sediments) inclusive or 119 days.

Control and treatment means are compared using the Student's *t*-test (Winer, 1971). This procedure does not account for errors induced by adding various quantitites together (e.g., as for gross sedimentation). All tests reported have 2 degrees of freedom.

g. Consumption of labelled carbon by clams. Clam filtering rates were measured by a flow through technique using water from clam treatment tanks, 6 times during the experiment between 25 May and 7 August (13.5–21.5°C). Individual clams, representing the range of those in the tanks, were placed in 4 sealed plastic chambers (500 ml). A fifth, empty chamber, served as a control. Ambient water, from either of the clam treatment tanks, was pumped through the chambers and 100 ml samples

collected from the inflow and outflow. These were assessed for ^{14}C activity on particles as described earlier. Flow rates were measured at the outflow of each chamber using a graduated cylinder and stopwatch. Filtration rates were calculated as:

$$\frac{[IN] - [OUT]}{[OUT]} \times \text{flow rate}$$

and were corrected for the control. This formulation best approximates the true filtration rate when the concentration inside the chamber is not measured, as with the closed system here (Hildreth and Crisp, 1976). At least 3 measurements were made on each clam, while siphons were extended, generally over a period of 3 to 4 hours. The average decline in dpm on particles between inflow and outflow was 18 ± 7.8%. Measurements with differences of less than 10% were considered invalid. Flow rate through the chambers averaged 112 ± 33 ml/min and ranged from 59 ml/min at 13.5°C to 181 ml/min at 21.5°C. A total of 41 measurements were used to derive a filtration rate model dependent on length of clam and temperature. The model (Doering and Oviatt, 1986) was:

$$\log FR = 0.96 \log L + 0.95 \log T - 0.47$$

$$r = 0.634, F = 12.83, df = 2.38, p < 0.05$$

where:

L = length in cm, T = temperature in °C and FR = filtering rate in ml/min.

From this model, consumption of labelled carbon by the clams in each tank was calculated. Clams in each tank were divided into 4 size classes. The daily consumption of an average sized clam in each size class was calculated as the filtration rate × dpm/l on suspended particles × submergence time (24 hrs in our case). A daily consumption of particulate dpm was thus calculated for each week of the experiment. Data for each size class were integrated over the 119 day experiment and converted to total labelled carbon as described above. This value was multiplied by the number of clams in each size class and expressed on an areal basis.

Mean size of clams in each size class was determined by averaging initial and final lengths. The lengths upon recovery of unmarked clams were included in these calculations.

3. Results

The addition of *Mercenaria* to the benthos of the mesocosms was successful. Of the marked clams in Tank 13, 35 were recovered live, 5 dead and 3 extraneous clams were found. In Tank 14, 38 were recovered alive, 2 dead and 1 extraneous clam was found. A thorough search of the control tanks revealed no *Mercenaria*.

A final accounting of the activity (^{14}C) added to each of the tanks appears in Table 2. About 26% of the label added to each tank could not be accounted for at the

Table 2. Initial amount of ^{14}C added as sodium bicarbonate to the tanks and the final activity on water column particulates, in the sediments (and clams where appropriate) and as dissolved inorganic carbon. The amount lost by draining tanks after severe rain storms is also included. The amount lost to air represents the fraction missing at end of experiment. Units are microcuries/tank.

	Controls		Treatments	
	T-12	*T*-15	*T*-13	*T*-14
Water Column				
Initial $DI^{14}C$	2022	1989	2009	2013
Final $DI^{14}C$	1198	1154	1087	1099
Final particulates	23	11	12	7
Benthos				
Final sediments	190	163	228	181
Clam tissue	—	—	42	77
Clam shell	—	—	69	65
Rain overflow	64	169	55	55
Final total	1475	1497	1493	1484
Lost to air or				
Dissolved organic carbon	547	492	516	529

end of the experiment and is assumed to have been lost to the atmosphere or remained in the water column as dissolved organic carbon which was not measured.

a. Sedimentation. Although ranges of values for accumulation of labelled organic carbon in the sediments (excluding clam tissue) of treatment and control tanks did not overlap, the difference was not striking ($t = 1.51$, $p < 0.40$, Table 3). There was significant incorporation of label in clam tissue, and when this is taken into account, net sedimentation increased on average by 60% (7.6 g C/m^2) in treatments relative to controls (Table 3: $t = 8.54$, $p < .02$).

The time course of measured benthic $DI^{14}C$ remineralization is depicted in Figure 2. On several occasions, a flux of $DI^{14}C$ was not detected and these were assumed to be zero. Inspection of the integrated values (Table 2) revealed no difference between control and treatment ($t = 0.66$, $p < 0.5$). When the activity in clam shell is considered however, benthic remineralization of $DI^{14}C$ in treatments was on average 57% greater than in controls ($t = 2.88$, $p < 0.20$).

Gross sedimentation (net sedimentation and benthic remineralization) was 58% greater in treatment than controls increasing on average by 14.2 g C/m^2 ($t = 7.25$, $p < 0.02$). Of this increase 47% was attributable to greater respiration by the benthic community, 32% to incorporation into clam tissue and 21% to storage in the sediment and small animals included in core samples.

b. Water column particulate matter. The standing stock of ^{14}C activity on suspended particles at dusk is shown in Figure 3. Time weighted mean standing stocks (Table 4)

Table 3. Sediment inventory (0–10 cm), net sedimentation, integrated benthic remineralization and gross sedimentation of labelled organic carbon during the 119 day experiment. ^{14}C activity is converted to total labelled carbon using the following average specific activities *T*-12: 12.58 dpm/μgC, *T*-15: 11.89 dpm/μgC, *T*-13: 11.39 dpm/μgC, *T*-14: 11.59 dpm/μgC.

	Controls		Treatments	
	T-12	*T*-15	*T*-13	*T*-14
Sediment inventory				
μCi/m^2	75.5	64.7	90.5	72.0
gC/m^2	13.3	12.1	17.6	13.8
Clams				
Tissue				
μCi/m^2	—	—	16.7	30.4
gC/m^2	—	—	3.3	5.8
*Net sedimentation**				
gC/m^2	13.3	12.1	20.9	19.6
$\bar{X}$ ± SD	12.7 ± 0.9		20.3 ± 0.9	
Benthic DI ^{14}C remineralization				
Flux μCi/m^2	71.2	57.8	56.8	79.7
gC/m^2	12.6	10.8	11.1	15.3
Clam shells				
μCi/m^2	—	—	27.5	25.6
gC/m^2	—	—	5.4	4.9
Gross sedimentation**				
gC/m^2	25.9	22.9	37.3	39.8
$\bar{X}$ ± SD	24.4 ± 2.1		38.6 ± 1.8	

*In control tanks net sedimentation was calculated from the amount of labelled carbon in cores. In tanks with clams, net sedimentation represents the sum of ^{14}C in cores and clam tissue.

**In control tanks gross sedimentation is the sum of net sedimentation and benthic remineralization, as calculated from flux measurements. In tanks with clams, gross sedimentation is the sum of net sedimentation, benthic flux and activity in clam shells.

were similar in treatments and controls ($t = 0.11$, $p > 0.60$). Chlorophyll *a* ($t = 1.41$, $p < 0.40$) and integrated zooplankton biomass ($t = 0.16$, $p > 0.60$) showed the same pattern (Table 5). Fluctuations in total chlorophyll *a* generally mirrored those in C-14 activity on water column particulates (Fig. 3) (Spearmans rank correlation coefficient Tank 12: 0.513, $p = 0.02$; Tank 15: 0.585, $p = 0.009$; Tank 13: 0.343, $p = 0.08$; Tank 14: 0.821, $p < 0.005$).

By contrast, system production of particulate carbon (Fig. 4; Table 4) in treatments was double that of controls ($t = 4.94$, $p < 0.05$). Both system night loss ($t = 3.06$, $p < 0.10$) and water column night loss ($t = 1.96$, $p < 0.20$) of particles were on average a factor of two higher in tanks with clams than in controls.

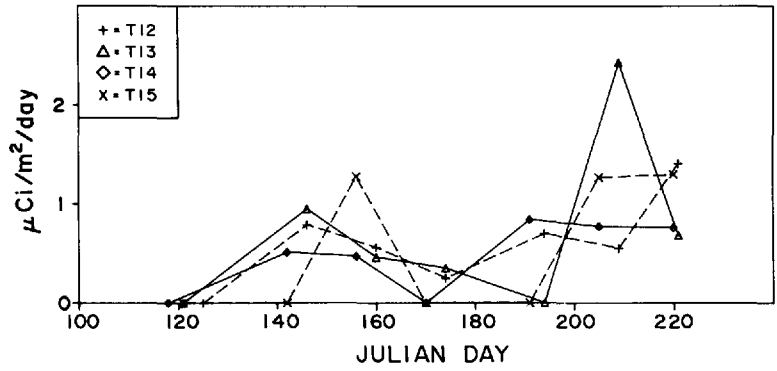

Figure 2. Benthic flux of dissolved inorganic ^{14}carbon (DI^{14}C) in microcuries/m^2/day. Positive values indicate flux out of the sediment. Control Tanks (dashed line): *T*12, *T*15. Treatment Tanks (solid line): *T*13, *T*14.

c. Consumption of labelled carbon by clams. Consumption of labelled carbon by the clams in each treatment tank, calculated from the filtering rate model appears in Table 6. Assuming that *Mercenaria* filters 100% of the time we estimate that on average in the two treatment tanks the clams consumed about 16.2 ± 2.0 g C/m^2. There is sufficient evidence in the literature to show that *Mercenaria* exhibits rhythmic cycles of shell opening and closing and therefore is not always active (Bennett, 1954; Brown *et al.*, 1956).

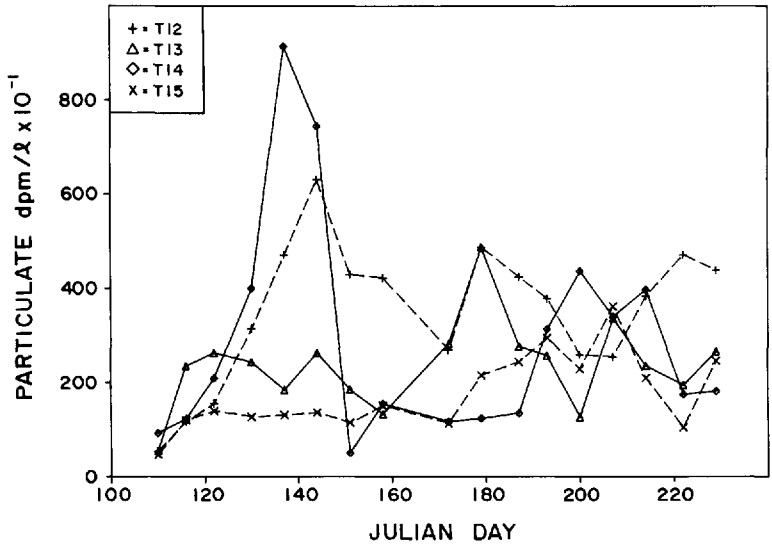

Figure 3. Activity of ^{14}C on water column particles in disintegrations per minute (dpm) per liter of tank water. Control Tanks (dashed line): *T*12, *T*15. Treatment Tanks (solid line): *T*13, *T*14.

Table 4. Water column standing stock, integrated system production, and system and water column night loss of labelled particulate carbon during the 119 day experiment. Values are integrations of weekly measurements except for water column night loss which was calculated.*

	Controls		Treatments	
	T-12	*T*-15	*T*-13	*T*-14
Standing stock (gC/m^2)				
Time weighted $\bar{x}$	1.45	0.78	1.02	1.29
$\bar{X} \pm SD$	1.1 ± 0.5		1.2 ± 0.2	
System particulate production				
Integrated gC/m^2	11.9	11.6	22.8	28.4
$\bar{X} \pm SD$	11.8 ± 0.2		25.6 ± 4.0	
System night loss				
Integrated gC/m^2	13.8	19.6	27.9	36.0
$\bar{X} \pm SD$	16.7 ± 4.1		32.0 ± 5.7	
Water column night loss				
Calculated gC/m^2	3.7	10.7	13.4	20.5
$\bar{X} \pm SD$	7.2 ± 5.0		17.0 ± 5.0	

*Water column night loss is calculated by difference: system night loss − gross sedimentation at night. The former was measured directly. The latter was calculated by partitioning gross sedimentation into a daytime and nightime fraction. The average proportion of darkness over the 24 hour day during the experiment was 0.39. Thus, 39% of total gross sedimentation was assumed to have occurred at night.

Loosanoff (1939) and Van Winkle *et al.* (1976) have both modeled activity patterns of *Mercenaria*. The former model is based on temperature while the latter on both temperature and salinity. Since both these parameters were measured during the present investigation, estimation of the time spent filtering was possible. Using our data, Loosanoff's (1939) model predicts 81% and Van Winkle *et al.*'s (1976) 65%. Adjusted average consumption estimates in the two different tanks appear in Table 7.

d. Dissolved inorganic nitrogen (DIN). Reliable estimates for the benthic flux of DIN ($NH_3 + NO_2 + NO_3$) were obtained only for the period between Julian dates 191 and

Table 5. Integrated standing stock of Chlorophyll *a* and zooplankton (net tow) biomass over the 119 day experiment. Values are integrations of weekly measurements.

	Controls		Treatments	
	T-12	*T*-15	*T*-13	*T*-14
Chlorophyll *a* g/m^2	1.8	1.2	1.8	2.3
Zooplankton g dry weight/m^2	38.3	13.9	28.7	27.4

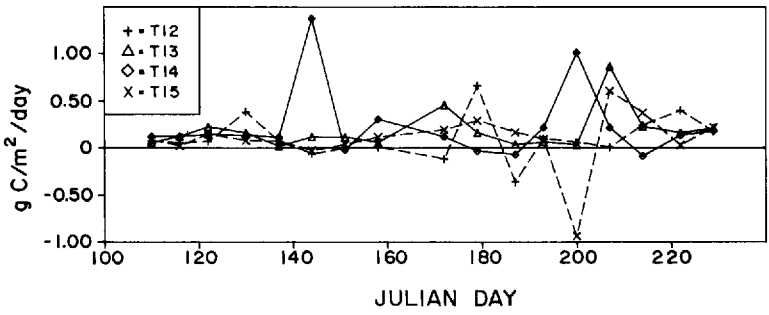

Figure 4. System production of carbon (g C/m^2/day) in the mesocosms over the course of the experiment. Values are based on dawn to dusk fluctuations in water column ^{14}C particles. Control Tanks (dashed line): *T*12, *T*15. Treatment Tanks (solid line): *T*13, *T*14.

221 (Fig. 5). The range of fluxes for treatment and control overlap only during the first measurement (Julian Dates 191–194). In general, treatment fluxes were higher than control fluxes (Median Test, $P < 0.05$; Siegel, 1956). Nevertheless, all values fell within the range reported for Narragansett Bay at similar temperatures (Nixon *et al.*, 1976). By contrast water column concentrations (μM ± S.D.) were similar over the period of flux measurements (Julian Date 189–225: control *T*-12: 2.29 ± 0.90, *T*-15: 2.30 ± 1.19, treatments: *T*-13: 2.11 ± 1.02, *T*-14: 2.19 ± 0.75, $n = 8$ in each case).

Table 6. Integrated consumption of particulate carbon by clams during the 119 day experiment. Calculations were made for an average size clam in each of 4 size classes based on a filtering rate model and the ^{14}C dpm/l on particles in the tank water column. Values represent integrations of weekly estimates.

Clam length (cm)	Consumption gC/clam	# at end	Consumption
	Tank 13		
3.58 ± 0.28	0.567	3	1.7
4.47 ± 0.28	0.700	6	4.2
5.88 ± 0.46	0.913	15	13.7
8.27 ± 0.98	1.264	14	17.7
			37.3 gC/Tank
			14.8 gC/m^2
	Tank 14		
3.71 ± 0.39	0.650	4	2.6
4.69 ± 0.41	0.800	4	3.2
5.99 ± 0.45	1.043	14	14.6
8.29 ± 1.04	1.406	17	23.9
			44.3 gC/Tank
			17.6 gC/m^2
		$\bar{X}$ ± SD gC/m^2	16.2 ± 2.0

Table 7. Average (n = 2 treatment tanks) integrated clam consumption (gC/m^2) during the 119 day experiment adjusted for time spent filtering. Also given are the percentages of the difference, between control and treatment, in gross sedimentation which the clams could have consumed.

Time filtering	Average consumption	% Gross sed. difference
100%	16.2 ± 2.0	114
81%	13.1 ± 1.6	92
65%	10.5 ± 1.3	74

4. Discussion

a. Expected results. Previous investigations of filter feeders led us to expect the results shown in Table 8, which follow directly from the filtration and ingestion of suspended particles. Addition of *Mercenaria* to the tanks should have increased the transport of labelled carbon (gross sedimentation) to the benthos (Haven and Morales-Alamo, 1966, 1972; Dame *et al.*, 1980). Storage of carbon in clam tissue and biodeposition should have contributed to higher net sedimentation (Haven and Morales-Alamo, 1966, 1972; Ott and Fedra, 1977). The concentration, in the water column, of labelled particulate carbon, chlorophyll *a* or both should have decreased (Cloern, 1982; Officer *et al.*, 1982; Cohen *et al.*, 1984; Nichols, 1985). Such a decrease should have accompanied a decline in respiration in the water column (Ott and Fedra, 1977), and an increase in benthic remineralization (Murphy and Kremer, 1985).

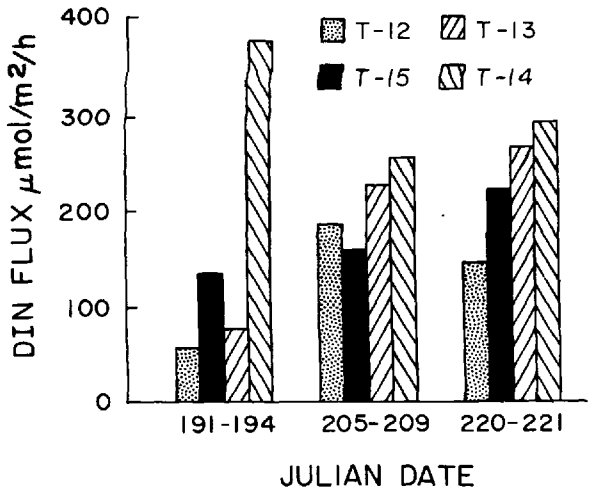

Figure 5. Flux of dissolved inorganic nitrogen (DIN) from the benthos to the water column in the mesocosms in $\mu mol/m^2/hr$. Julian dates refer to the dates upon which fluxes were measured in the 4 tanks (2 tanks on each date). Each bar represents one measurement. Control Tanks: $T12$, $T15$. Treatment Tanks: $T13$, $T14$.

Table 8. Comparison of qualitative results of this study and expected results based upon the literature.

	This study	Literature
1) Gross sedimentation	increase	increase*
2) Storage in clams	significant	significant**
3) Filtration by clams account for sedimentation	yes	yes***
4) Benthic respiration	increase	increase†††
5) Pelagic biomass	no change	decrease†
6) Production	increase	?
7) Pelagic respiration	increase	decrease**
8) Filtration by clams control pelagic biomass	no	yes††

*Dame *et al.*, 1980; Haven and Morales-Alamo, 1966; 1972
**Ott and Fedra, 1977
***Jordan and Valiela, 1982; refs. in*
†Wright *et al.*, 1982; Cohen *et al.*, 1984; Carlson *et al.*, 1984
††Nichols, 1985; Cloern, 1982; Officer *et al.*, 1982
†††Murphy and Kremer, 1985

b. Increased sedimentation. In general, our results, pertaining to sedimentation, agree with predictions from the literature (Table 8). Gross sedimentation (the total amount of labelled carbon removed from the water column) increased on average by 14.2 g C/m^2 in tanks with clams. Estimates of consumption of labelled carbon by the clams (Table 7) accounted for 74 to 114% of this increase, indicating that filtration of suspended particles enhanced sedimentation.

The increase in gross sedimentation derived from several sources. Assimilation of labelled carbon into clam tissue represented 32%, substantiating the contention of Ott and Fedra (1977) that filter feeders may comprise a significant storage compartment. Although the difference was slight, on average about 21% of the increase appeared attributable to free detritus and small animals sampled by cores. Presumably, permanent deposition of clam feces and psuedofaeces contributed to this greater sedimentary storage (e.g. Haven and Morales-Alamo, 1966, 1972). The greatest proportion (47%) of the increase in gross sedimentation was attributable to remineralization of labelled carbon by the benthic community. Because *Mercenaria* incorporates CO_2 for shell growth from both the surrounding water and from respiration, in unknown proportion (Dillaman and Ford, 1982) it is not possible to attribute the increase in benthic community remineralization to respiration by the clams themselves or to remineralization of sedimentary detritus.

c. Suspended particles. Despite the greater transport of particulate matter from the water column to the benthos in tanks with clams, the standing stock of suspended particles measured either as labelled carbon, chlorophyll *a*, or net tow biomass was

similar to controls (Tables 4 and 5). By contrast, system production of particulate carbon in tanks with clams was essentially double that of controls (average difference: 13.8 g C/m^2).

Was this increase in production sufficient to account for the greater sedimentation in tanks with clams? System production as measured here already includes losses due to sedimentation during the day. For example, if all material produced during the day, sedimented immediately, system production would be zero. Since system production was positive in all tanks, it can be concluded that production was more than sufficient to account for daytime sedimentation. The difference in gross sedimentation between tanks with and without clams averaged 14.2 g C/m^2 over the 119 day experiment. Of this difference, 39% or 5.5 g C/m^2 presumably sedimented at night. The excess biomass of 13.8 g C/m^2, accumulated during the day in clam tanks is more than sufficient to account for this.

These results are at variance with recent suggestions founded on field observations and modelling efforts (Table 8). The concentration of suspended particles in the water column was unaffected by the density of *Mercenaria* employed in this investigation. Increased sedimentation did not accompany a decrease in suspended particles. Rather, the greater sedimentation in tanks with clams was fueled by higher production.

Following Cloern (1982) and Officer *et al.* (1982), who suggested that benthic filter feeders may control phytoplankton biomass, we now consider the factors which prevented this increased production from accumulating in the water column of the tanks with clams. It is clear from the above discussion of system production, that these factors must act at night. The possible nocturnal fate of the excess biomass produced in these tanks is shown in Table 9. Although significant, either filtration of particles by clams, or gross sedimentation (which includes filtration) account for less than half. Nocturnal loss of particulate matter in the water column (Table 4) was on average, double that of controls. The increase (9.8 g C/m^2) accounted for 71% of the excess biomass (Table 9). Note that water column night loss was calculated by difference and is quite variable (Table 4). Gross sedimentation was calculated by addition of several components all with associated experimental error. Thus, it is not surprising that losses due to both processes account for 111% of the excess biomass (Table 9). Nevertheless, these considerations indicate that *Mercenaria* neither represented the primary source of loss for pelagic biomass nor decreased catabolic processes in the water column. More likely, destruction of particles in the water column was the major heterotrophic loss of pelagic biomass.

The cause of this increased pelagic loss of suspended particles in the clam treatments remains obscure. Possibilities include: increased zooplankton grazing, alteration of phytoplankton community structure and enhanced bacterial activity.

Zooplankton grazing was not measured, but the similarity in biomass (as measured by net tow) among treatments (Table 5) argues against the latter possibility. In fact bivalve filter feeders may remove some zooplanktonic forms (Carlson *et al.*, 1984),

Table 9. Possible fate of excess biomass, relative to controls, produced during the day in tanks with clams. Both absolute magnitudes (g C/m^2) of and percentage of excess biomass (13.8 g C/m^2) accounted for by various processes acting at night are shown. Twenty-four hour rates have been adjusted to nighttime rates through multiplication by 0.39; the average nighttime fraction during the experiment. Values for feeding by clams are adjusted for time spent filtering as in Table 7. Both gross sedimentation and loss rate of particles in the water column (water column night loss) are based on the difference between control and treatment means.

Process	g C/m^2	% of excess biomass
Feeding by clams		
100%	6.3	46
81%	5.1	37
65%	4.1	30
Gross sedimentation	5.5	40
Water column night loss	9.8	71

perhaps reducing pelagic grazing pressure on phytoplankton. Again, however, biomass data (Table 5) do not support such a contention in our experiment.

Alteration of phytoplankton community structure has been correlated with benthic filter feeders (Carlson *et al.*, 1984; Cloern, 1982). Phytoplankton biomass in northern San Francisco Bay is dominated by neritic diatoms, while in the south, where there is an abundance of filter feeding bivalves, small diatoms and microflagellates predominate (Cloern, 1982). In general, respiration rates of unicellular algae tend to increase with decreasing size (Banse, 1976). In addition, flagellates may respire more of their own production than diatoms (Smith, 1977). Shifts in phytoplankton community structure, either from diatoms to flagellates or from larger to smaller cells might have contributed to the observed increase in loss of particles in the pelagic compartment of the clams treatments.

Such changes in the quality or size of suspended particulate matter may also stimulate bacterial or microheterotrophic activity in the water column. Although comparative evidence is sparse, diatoms may settle more readily than flagellates (Smetacek, 1984). In general, benthic grazing may select against forms which sink rapidly (e.g., large diatoms) (Cloern, 1982). Thus, benthic filter feeders might promote the growth of phytoplankton which are more likely to be grazed or decomposed in the water column. This indirect effect might also account for the observed difference in nocturnal loss of particulate matter in the water column. The data necessary to examine these latter two possibilities are unavailable for the present experiment.

d. Increased production. Addition of *Mercenaria* to the mesocosms increased system production by a factor of two. Such a response to herbivore grazing has been

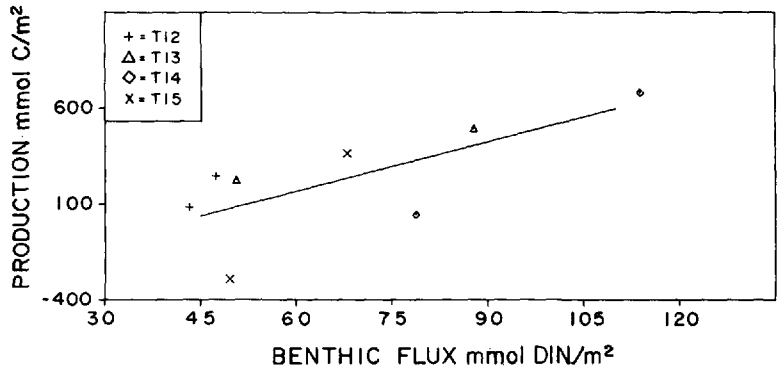

Figure 6. Relationship of benthic flux of dissolved inorganic nitrogen (DIN) in m mol/m^2 and daily apparent carbon production (m mol C/m^2). Points were derived by integrating over the two time intervals defined by the three flux measurements in Figure 5. Control Tanks: *T*12, *T*15. Treatment Tanks: *T*13, *T*14. The line has a slope of 8.6 m mol C/m mol N and is statistically different from zero ($p < 0.05$), $r = 0.716$.

demonstrated previously and in part derives from enhanced nutrient recycling through herbivore excretion (Hargrave, 1970; Cooper, 1973; Sterner, 1986).

Benthic remineralization of DIN was greater in tanks with clams (Fig. 5). Despite a considerable input of DIN from the benthos, water column concentrations were low (about 2 μM) and relatively invariant (range: 0.6–3.8 μM) in all tanks during the period encompassed in Figure 5 (JD 191–221). Even the lowest benthic flux measured (*T* 12: 57 μ mol/m^2/hr) would have raised the water column concentration by 7.3 μM in this 30 day period. DIN, remineralized by the benthos, was probably utilized by phytoplankton in the water column. The three flux measurements, in each tank, define two periods over which the total integrated DIN flux from the benthos can be estimated. These have been plotted against system carbon production for each of these periods in Figure 6. The relationship may be described by a linear equation with a slope of about 8.6 m mol C/m mol N ($r = 0.716$, $p < 0.05$). If it is assumed that nitrogen was incorporated into organic matter according to the Redfield ratio of C/N = 6.625, then it can be calculated that the benthic flux of DIN fueled about 77% (6.625/8.6) of the daily apparent production in all tanks. This correlation implies that the higher production in the treatments was at least in part due to the higher benthic flux of DIN in these tanks.

e. Benthic DIN flux. Several sources may account for the increased benthic flux of DIN: clam death and subsequent decomposition, excretion and bioturbation. Of the two treatments, Tank 14 had both the lowest clam mortality (2) and the higher benthic DIN flux. Tank 13 had the highest clam mortality (5) and the lower benthic flux. These observations suggest an inverse correlation between magnitude of benthic flux and clam mortality which is contrary to expectation were clam mortality important.

It can be roughly calculated that the total benthic flux during the experiment for Tank 14 was 660 m mol DIN/m^2. Assuming, as did Officer *et al.* 1982, that 8% of a bivalve's dry mean weight is nitrogen it can be calculated that clam mortality accounted for 38 m mol DIN/m^2 or about 6% of the total flux.

It is clear from laboratory studies, that the activities of benthic macrofauna may enhance nutrient exchange between the sediment and water column (Aller, 1982; Yingst and Rhoads, 1980; Hylleberg, 1975). The mechanisms by which this enhancement occurs may include stimulation of bacterial activity (Yingst and Rhoads, 1980), flushing of pore water (Gust and Harrison, 1981) and macrofaunal excretion (Aller and Yingst, 1978). The former two mechanisms result from bioturbation.

Neither bioturbation nor clam excretion were measured during the study and their relative importance cannot be determined. However, using the equation of Srna and Baggaley(1976), relating ammonia excretion (at 20°C) in *Mercenaria* to dry weight, it can be calculated that the clams could have excreted 36 and 52 μmol NH_3/m^2/hr in Tanks 13 and 14 respectively ($\bar{X} = 44 \pm 11$ μmol/m^2/hr). For any of the three sets of benthic flux measurements (Fig. 5), the average clam contribution of 44 μ mol NH_3/m^2/hr, accounts for between 34 and 63% of the difference between control and treatment means ($\bar{X} = 48 \pm 15\%$, $n = 3$). Such calculations indicate that excretion by clams may contribute significantly to benthic nutrient flux and thus to production in the overlying water.

f. System effects of bivalves. Our results are significant for several reasons. Change in pelagic standing stock of particulate biomass over space (e.g., Cohen *et al.*, 1984) or time (e.g. Nichols, 1985) has often been used as an indicator of benthic filter feeder effects. The effects of *Mercenaria* were not observed as changes in standing stock of particles but as changes in the rate processes (production, respiration, sedimentation) which control standing stock. Although filter feeders may alter water column concentrations of particles, lack of such changes do not indicate a lack of filter feeder influence on material cycles.

Our results suggest that to view removal of pelagic particulate matter by benthic filter feeders as (1) a simple, additive loss term and (2) as the only influence on material cycles is inadequate. The experimental results indicate a stimulatory feedback effect from filter feeder to water column producer which tends to counter-act the potential negative effect of grazing on standing stock. This apparently occurs through enhanced return of nutrients from the bottom. Because our experimental regime excluded horizontal advection, these feedbacks may be accentuated relative to field sites with high exchange rates. However, the residence time of water in our experiment (4 months) compares favorably with that in south San Francisco Bay (5 months in summer, Conomos, 1979) where filter feeders may control phytoplankton biomass (Cloern, 1982). Clearly, the residence time of water in areas subjected to benthic filtering pressure will determine the importance of these feedbacks. Nevertheless,

models which seek to predict the impact of benthic filter feeders on phytoplankton populations (e.g., Officer *et al.*, 1982) or other system components should include such interactions (e.g., Sterner, 1986).

Our data indicate that *Mercenaria* increases nitrogen remineralization and that this effect may in part explain its influence on carbon cycling. Thus, studies which focus on the effects of filter feeders on both nutrients (e.g. Dame *et al.*, 1984) and carbon should be encouraged.

Many of our results could not have been predicted from information in the current literature (Table 9). Most available data pertain to dense assemblages of benthic filter feeders. The density of *Mercenaria* employed here is moderate, even for Narragansett Bay, where there is a thriving fishery, and for the East Coast of the U.S. in general (MacKenzie, 1979; Saila *et al.*, 1967; Pratt, 1953). The differences between our observations and the literature may stem from this difference in density. We suggest that the effects of filter feeders on system function vary with density and that the variations are not only quantitative but, more importantly, qualitative. Such qualitative effects are apparent in laboratory studies of herbivore density and primary production, where production is stimulated at low density and depressed at high density (Hargrave, 1970; Cooper, 1973).

An important implication of our work is that introduction of a single heterotrophic species can, without any external addition of nutrients, increase production of particulate carbon and enable a greater transport of carbon to the sediments. Such increases in production and transport of carbon occur not as a function of nutrient enrichment, but rather of nutrient recycling.

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