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On the contribution of the benthos to pelagic production

by Peter H. Doering¹

ABSTRACT

Annual production and consumption of oxygen were compared in large outdoor mesocosms differing only in the presence or absence of an intact benthic community and associated sediments. Both daily apparent production and nighttime respiration of oxygen were greater in tanks with a benthos. The fluxes of oxygen into, and dissolved inorganic nitrogen out of the bottom were also greater in tanks with an intact benthos. In tanks with a benthos, calculated gross system production increased 33% relative to tanks lacking a benthos. Depending on assumed O:N ratios only 45–60% of this increase was attributable to differences in the flux of inorganic nitrogen from the benthos to the water column. Nearly 40% was evidently fueled by higher rates of recycling in the water column. Between 3 and 17% of the difference in production could not be attributed to either source. The benthos apparently affects production in the water column not only by supplying nutrients directly, but also by enhancing rates of pelagic recycling.

1. Introduction

In shallow coastal waters the benthos often represents a significant source of nutrients to the overlying water (Zeitzschel, 1980). As depth decreases, the proportion of primary production that is deposited on the bottom increases (Hargrave, 1973), and most of this material is respired by the benthic community (Oviatt *et al.*, 1981).

The resulting flux of inorganic nutrients back to the overlying water, can in large measure control seasonal fluctuations in water column concentrations (Pilson, 1985) and may supply a large proportion of the phytoplankton demand for nutrients (Hale, 1974; Rowe *et al.*, 1975; Nixon *et al.*, 1976; Table 1). In fact, local variation in phytoplankton productivity has been attributed to local variation in benthic flux of nutrients (Zeitzschel, 1980; Vetter and Hopkinson, 1985).

The idea that much of the nutrient demand for pelagic production derives from the benthos has gained wide acceptance but there is no general agreement concerning the extent of its importance (Garber, 1987). Indeed, even in shallow areas rates of nutrient recycling in the water column may be nearly sufficient to fuel primary production (Boynton and Kemp, 1985).

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Table 1. Some estimates of the percentage of phytoplankton nitrogen demand supplied by benthic flux.

Nutrient	% Phytoplankton nitrogen demand	Reference
DIN	12	Kautsky and Evans (1987)
DIN	11	Hopkinson (1987)
NH ₃	13–40	Boynton and Kemp (1985)
NH ₃	100	Murphy and Kremer (1985)
NH ₃	16–44	Pomroy <i>et al.</i> (1983)
DIN	20	Raine and Patching (1980)
DIN	22	Nixon <i>et al.</i> (1980b)
DIN	30–40	Rowe <i>et al.</i> (1977)
Total N	0	Hartwig (1976)
DIN	50	Davies (1975)

Estimates of the benthic contribution to the nutrient demand for production (Table 1) are generally calculated from a combination of benthic flux and pelagic production measurements. These calculations imply that productivity in shallow water is enhanced by benthic recycling of nutrients. There have been no manipulative experiments, at the ecosystem level, which quantify the influence of the benthos on production in the water column. The purpose of this report is to present results of just such a manipulation.

Large (13 m³) outdoor experimental mesocosms were used to compare similar systems, differing only in the presence or absence of an intact benthic community and associated sediments. Although production was greater in tanks with sediments, as might be predicted (Table 1), calculations suggested that benthic flux of nutrients could not entirely account for observed differences. The results imply that the benthos functions not only as a direct supplier of nutrients, but also enhances production by increasing rates of nutrient recycling in the water column itself.

2. Methods

a. Mesocosms. The mesocosms (Table 2) located outdoors, at the University of Rhode Island, Graduate School of Oceanography are simplified models of shallow, plankton-based coastal marine ecosystems. Production occurs in the water column, while the benthic community is heterotrophic. Temperature, light, mixing, water turnover and sediments (when present) are similar to the parent system, Narragansett Bay (Pilson *et al.*, 1979; Nixon *et al.*, 1980b; Oviatt *et al.*, 1986a).

b. Experimental design. Two mesocosms were assigned to each of two treatments; either, with or without an intact benthic community. Sediment for the tanks with a benthos was collected from mid-Narragansett Bay using a 0.25 m² box corer as described by Hunt and Smith (1983). In the no-benthos treatment, autochthonous material, produced during the experiment, was allowed to accumulate on the bottom.

Table 2. Summary of MERL mesocosm design. Tank construction is fiberglass reinforced resin with a white interior to maximize sunlight reflection. A 50 cm diameter plunger with 60 cm vertical excursion mixes a tank at a rate of 5 cycles/min for 2 hrs every 6 hrs. Sediments are collected from mid-Narragansett Bay.

Tank diameter	1.83 m
Tank height	5.49 m
Water surface area	2.63 m ²
Water depth	5.00 m
Water volume	13.1 m ³
Sediment area	2.53 m ²
Sediment depth	0.37 m
Water column turnover	27 days

Periodic scrubbing of the bottom with a plastic pad prevented colonization by benthic fauna.

The experiment commenced on June 11, 1985 and terminated 365 days later on June 10, 1986. Ambient water from Narragansett Bay flowed through all mesocosms at a rate of 480 l/day to produce a turnover time of 27 days.

c. Measurements. Daily apparent system production and nighttime system respiration were estimated weekly by measuring dawn-dusk-dawn oxygen concentrations in the tank water column. Dissolved oxygen was measured by the Winkler titration (Carritt and Carpenter, 1966). Dawn minus dusk concentrations were corrected for diffusion to yield an estimate of daily apparent production by the system (Oviatt *et al.*, 1987). The difference between the concentrations at dusk and the following dawn estimated nighttime respiration (Oviatt *et al.*, 1987).

Biomass of phytoplankton was determined weekly by analysis of chlorophyll *a* after Yentsch and Menzel (1963) and Lorenzen (1966) as modified by Lambert and Oviatt (1986).

The concentrations of dissolved inorganic nitrogen ($\text{DIN} = \text{NH}_3 + \text{NO}_2 + \text{NO}_3$) in tank water columns was determined weekly. A pooled sample from three depths was filtered and frozen until analysis using a Technicon autoanalyzer (Lambert and Oviatt, 1986).

Detritus deposited on the bottom of the tanks without sediment was sampled by a diver using a vacuum system (Lambert and Oviatt, 1986). At each sampling, two circular rings (0.049 m²) were vacuumed clear of floc. The floc from each ring was collected in an appropriately sized vessel, allowed to settle and the supernatant decanted. The resulting floc solutions were centrifuged weighed, dried (60°C) and weighed again. Dried floc was ground and aliquots analyzed for organic carbon by high temperature combustion (950°C) to CO₂ (Rudnick and Oviatt, 1986). Collections were made every two weeks in summer, monthly in the winter and always occurred within a week of benthic flux measurements.

Benthic macrofaunal samples from tanks with sediment were collected with a flow-through coring device (5.06 cm², Frithsen *et al.*, 1983) 13 times during the experiment at approximately monthly intervals. A total of 87 and 89 cores were taken from each of the two tanks. These were about evenly distributed between quarters of the year, so that no one season was over represented.

Cores were sliced to yield a 0 to 2 cm and a 2 to 6 cm depth fraction. These were preserved in 10% buffered formalin containing rose bengal and washed through a nest of sieves (0.5 and 0.3 mm). Animals were identified and enumerated with the aid of a stereomicroscope.

The exchanges of DIN and oxygen across the sediment water interface were measured using a clear plexiglass chamber (vol = 300 l) which encapsulated the entire benthos (Doering *et al.*, 1987). Fluxes were calculated from initial and final samples withdrawn by siphon after mixing with a hand operated stirring bar. Control bottles were simultaneously incubated on top of the chamber to correct for changes occurring in the water itself. Incubation time varied inversely with temperature, and oxygen concentration was not allowed to fall below 80% saturation. A total of nine measurements was taken throughout the year, being more frequent when water temperatures exceeded 5°C.

Fluxes were measured in both tanks with a benthos but in only one of the tanks with no benthos (Tank 15). Data from this no-benthos tank were used to estimate fluxes in the remaining replicate (Tank 2). Oxygen consumption was estimated from a relation with the amount of floc accumulated on the bottom.

$$\text{Oxygen consumption (mg O}_2\text{/m}^2\text{/hr)} = -3.75 - 0.196 * \text{Floc (g C/m}^2\text{);}$$
$$r = 0.79, F = 8.97, df = 1,8, p < 0.05.$$

DIN flux was estimated by assuming that fluxes in both tanks exhibited similar O:N ratios.

d. Statistical analysis. Daily apparent system production, nighttime system respiration and benthic fluxes were integrated over time to yield annual estimates. Annual production and respiration measurements were compared using the *t*-test. Benthic fluxes in the two benthos tanks were compared individually to those measured in the one no-benthos tank using the paired *t*-test. Pairing was by date of measurement. Accumulation of floc on the bottoms of tanks without sediment was also compared using the paired (by date) *t*-test.

Concentrations of nutrients and chlorophyll *a* in the tank water columns were evaluated by a two factor ANOVA. The factors were date and treatment (with or without sediment). Replicate mesocosms were nested within the sediment effect and assumed to be random. This nested model is equivalent to a repeated measures design and is summarized in Winer (1971).

Table 3. Summary of calculations used to estimate the difference in production between benthos and no-benthos treatments and the percentage of the nitrogen demand of this difference, which is accounted for by benthic flux of dissolved inorganic nitrogen (DIN) and pelagic recycling.

1. Gross System Production (GSP) = System Apparent Production + Nighttime System Respiration
2. Water Column Respiration (WCP) = 2*Nighttime System Respiration – Benthic Respiration
3. Treatment Production Difference (moles O₂) = GSP (Benthos) – GSP (No-Benthos)
4. Treatment Water Column Respiration Difference (moles O₂) = WCR (Benthos) – WCR (No-Benthos)
5. Convert (3) and (4) from units of O₂ to units of N assuming O:N ratio of 17.25:1 or 13.25:1
6. Treatment Benthic Flux Difference (moles N) = DIN Flux (Benthos) – DIN Flux (No-Benthos)
7. Percentage of Treatment Production Difference accounted for by differences in Benthic Flux of DIN

$$\frac{\text{Treatment Benthic Flux Difference (moles N)}}{\text{Treatment Production Difference (moles N)}} \times 100$$

8. Percentage of Treatment Production Difference (moles N) accounted for by recycling of N in the water column

$$\frac{\text{Treatment Water Column Respiration Difference (moles N)}}{\text{Treatment Production Difference (moles N)}} \times 100$$

e. Calculations. The purpose of the calculations summarized in Table 3 is to determine the source of inorganic nitrogen (benthic flux or water column recycling) which may have fueled an observed difference in production between tanks with and without an intact benthos. The logic of this analysis is that since by design, input of nutrients from Narragansett Bay did not vary with treatment, any treatment difference in production arose from treatment differences in benthic flux or water column recycling of nitrogen. Thus, any treatment difference (Benthos-No Benthos) in production should equal the treatment difference in benthic flux plus the treatment difference in water column recycling. Three treatment differences must be estimated, all in units of nitrogen.

Treatment differences are calculated by subtraction of treatment means (Benthos-No Benthos). Production is estimated as gross system production of oxygen (see below) and the treatment difference in production converted to a nitrogen demand assuming an O:N ratio. Water column recycling of nitrogen is estimated from water column respiration of oxygen (see below). Again the treatment difference is converted to units of nitrogen assuming an O:N ratio. The treatment difference in benthic flux of nitrogen is calculated from estimates of benthic flux of DIN.

The percentage of the treatment difference in production (moles N) accounted for

by the treatment difference in benthic flux of DIN is calculated by dividing the latter by the former. The percentage attributable to water column recycling is calculated similarly.

The quantities used in the calculations are yearly totals derived by trapezoidal integration of variables measured over time. Units are therefore in moles O_2 or $N/m^2/year$. Given the annual character of these estimates, the equations in Table 3 assume that system-apparent production and nighttime respiration each occur over $1/2$ an average day. Benthic flux data, measured on an hourly time scale, were first expressed as 24 hour rates and then integrated to yield a yearly total. Details of the oxygen production and respiration calculations are given below.

Gross system production of oxygen is calculated by summing daily apparent system production and nighttime system respiration. This calculation assumes that nighttime and daytime respiration are equivalent. Gross system production represents production without any respiratory loss. It is fueled by the flux of nutrients from the benthos and recycling in the water column. Both these processes occur continuously (24 hours/day).

Water column respiration of oxygen is calculated as twice nighttime system respiration less benthic respiration. This quantity estimates the amount of oxygen consumed in the water column during 24 hours. The calculation assumes that (1) the respiration measured in the entire system is the sum total of respiration by the benthic and pelagic communities and (2) that nighttime and daytime respiration are equivalent.

Both gross system production and water column respiration are in units of O_2 . These are converted to units of nitrogen (N) using a molar O:N ratio of either 17.25 or 13.25 (Redfield, 1958). The former value of the ratio, based on the composition of the plankton, assumes that all nitrogen is converted to nitrate while the latter assumes ammonia as an end product (Alvarez-Borrego *et al.*, 1975; Redfield, 1958).

3. Results

The concentrations (Table 4) of the dissolved inorganic nitrogen species in the water column were unaffected by the presence or absence of an intact benthos (ANOVA main effect $p > 0.57$ in all cases). Although each nutrient showed significant seasonal trends (f -test for effect of DATE $p < 0.01$ in all cases), the lack of a treatment effect was persistent throughout the year (f -test for DATE X TREATMENT interaction $p > 0.90$ in all cases).

In tanks with a benthos, concentrations of chlorophyll *a* appeared higher than in the no-benthos treatment. The difference was statistically significant on only 4 of 53 dates.

The average amount of floc ($gram\ C/m^2$) accumulated on the bottoms of the two tanks without sediment was similar (tank 2: $\bar{x} \pm SD = 20.79 \pm 15.84\ n = 11$, tank 15: $22.34 \pm 19.05\ n = 12$). Mean accumulation was not statistically different (paired t -test $p > 0.59$).

Table 4. Mean \pm SD concentrations of dissolved inorganic nitrogen nutrients ($\mu\text{moles/l}$) and chlorophyll *a* ($\mu\text{g/l}$)

Sediments	DIN	NH ₃	NO ₂ + NO ₃	Chl <i>a</i>
T-12	0.70 \pm 1.28	0.30 \pm 0.36	0.40 \pm 1.12	7.42 \pm 7.14
T-14	1.70 \pm 2.64	0.86 \pm 1.20	0.84 \pm 1.64	5.79 \pm 5.85
No sediment				
T-2	1.07 \pm 2.23	0.56 \pm 1.27	0.51 \pm 1.27	4.44 \pm 3.14
T-15	0.77 \pm 1.51	0.32 \pm 0.42	0.44 \pm 1.25	4.79 \pm 3.39

The benthic macrofauna in both tanks with sediment was dominated by deposit feeders: the polychaete, *Mediomastus ambiseta*, and the protobranch bivalve *Nucula annulata*. Together these accounted for 60–70% of the mean macrofaunal abundance in the tanks (Table 5). These species dominate the macrofaunal community at the site from which the sediments were collected (Grassle *et al.*, 1985).

Annual apparent system production (Fig. 1) of oxygen was significantly greater in tanks with sediment than in those without (*t*-test, equal variances $t = 10.41$, $df = 2$, $p < 0.01$; *f*-test for equal variance $p > 0.50$). Annual nighttime respiration was also significantly greater in tanks with sediment (*t*-test, equal variances $t = 5.86$, $df = 2$, $p < 0.03$; *f*-test for equal variance $p > 0.40$).

Comparison of benthic fluxes in the replicate with no benthos, with each of the two replicates with a benthos indicated that consumption of oxygen and production of DIN were both significantly lower in the tank without sediment (paired *t*-tests for oxygen $t = 7.70$ and 7.62 , $df = 8$, $p < 0.05$; paired *t*-tests for DIN $t = 5.14$, and 5.85 , $df = 8$, $p < 0.05$). Annual fluxes are depicted in Figure 1.

Calculations. Calculated gross system production and water column respiration of oxygen were both on average greater in mesocosms with a benthos (Table 6). Relative to the no benthos treatment, gross system production rose by 33% and water column respiration by 18% in the presence of an intact benthos.

Depending on the conversion factor, a nitrogen input of 0.91 to 1.19 moles/m²/year

Table 5. Composition of the macrofauna in the two tanks with sediment. Values are mean number/m² based on cores ($n = 87$ for tank 12, $n = 89$ for tank 14) taken during the experiment. C.V. = coefficient of variation, % total = percent of mean total macrofauna.

	Tank 12			Tank 14		
	Mean	CV	% Total	Mean	CV	% Total
<i>Mediomastus ambiseta</i>	17519	43	44	23500	42	54
<i>Nucula annulata</i>	7864	80	20	8835	76	20
<i>Chaetozone</i> spp.	5313	57	13	3036	66	7
<i>Leptocheirus pinguis</i>	4008	318	10	—	—	—
<i>Aricidea</i> spp.	—	—	—	2262	126	5
Total Macrofauna	39866	46	—	43509	46	—

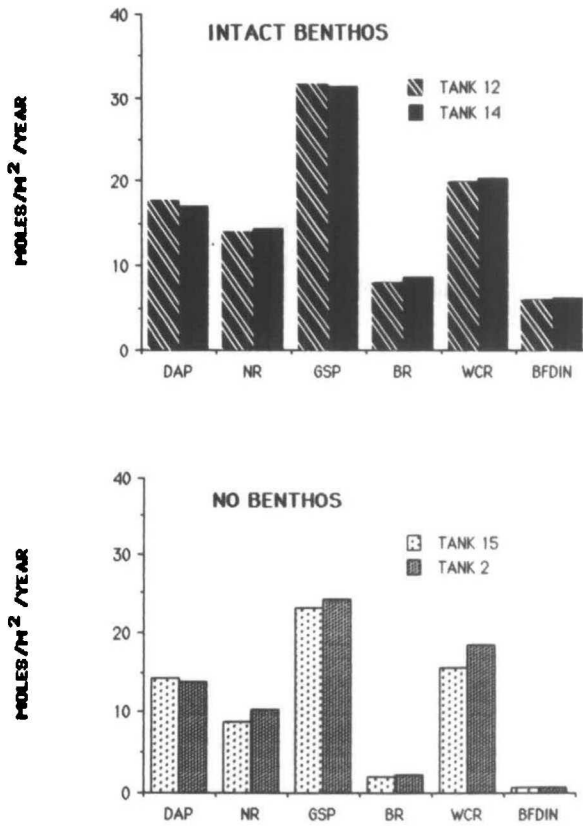


Figure 1. Annual metabolism of oxygen and benthic release of dissolved inorganic nitrogen in tanks with and without an intact benthic community. DAP = daily apparent system production, NR = nighttime system respiration, GSP = gross system production of oxygen calculated as in Table 3, BR = benthic consumption of oxygen, WCR = water column respiration as calculated in Table 3. BFDIN = Benthic flux of dissolved inorganic nitrogen. All units are moles O₂/m²/year excepting BFDIN which is in (moles N/m²/year) × 10.

Table 6. Average differences (Benthos–No Benthos) between treatments (moles N/m²/year) in gross system production, water column respiration and benthic flux. Also given is the percentage of nitrogen required to support the observed difference in production supplied by benthic flux and water column respiration. Calculations were made assuming two different O:N ratios. Parenthetical numbers refer to calculations in Table 3.

O:N	Gross production difference (3, 5)	Water column respiration difference (4, 5)	Benthic flux difference (6)	% of gross production difference		Total
				Benthic flux (7)	Water column respiration (8)	
17.25	0.915	0.348	0.539	59	38	97
13.25	1.191	0.453	0.539	45	38	83

would account for the increase in production observed in tanks with a benthos (Table 6). Calculations indicate that the benthos supplied between 45 and 60% of the nitrogen demand while pelagic regeneration supplied nearly 40%. Depending on the conversion factor, between 83 and 97% of the total demand was satisfied by benthic and pelagic sources.

4. Discussion

a. Assumptions. Benthic fluxes were measured in only one of the no-benthos mesocosms and thus the fluxes of both oxygen and dissolved inorganic nitrogen were estimated for the other replicate. Oxygen flux was calculated from a regression relating the amount of organic carbon on the bottom to oxygen consumption. In view of previous field and laboratory studies (Kemp and Boynton, 1981; Kelly and Nixon, 1984) which have demonstrated the importance of organic deposition to benthic flux, the existence of such a relationship in the present case is not surprising.

DIN flux was estimated assuming that both tanks exhibited similar O:N benthic flux ratios. Significant correlation between oxygen consumption and nitrogen release by sediments has been demonstrated previously (Nixon *et al.*, 1976). During the same experimental period, two other no-benthos tanks were being dosed with similar amounts of inorganic nitrogen and phosphorous but different amounts of silicon (Doering *et al.*, 1989). A plot of oxygen consumption versus DIN flux is shown in Figure 2. Data from both tanks fall within the same range, and the O to N relationship is apparently the same. The regression of oxygen on DIN flux is statistically significant ($p < 0.05$ $df = 1,17$) but with a low correlation ($r = 0.587$) due to one outlier. Exclusion of this point from the regression raises the correlation coefficient to $r = 0.823$. Although not replicates in the strictest sense, these data lend credence to the idea that O:N ratios did not vary substantially between no-benthos tanks treated similarly.

Calculating the nitrogen demand of production and the amount provided by pelagic recycling required the assumption of O:N ratios. The nitrogen demand of the difference in gross production (Table 6) could have been calculated by first converting oxygen to carbon employing a photosynthetic quotient of 1.2 which obtains in MERL mesocosms (Oviatt *et al.*, 1986b), followed by conversion of carbon to nitrogen assuming a Redfield ratio of 106C:16N. This procedure yielded a demand of 0.99 mole N/m²/year which lies between the two estimates in Table 6.

The two O:N ratios employed here assume that decomposition of plankton-derived organic matter terminates either in nitrate or ammonia. Since dissolved inorganic nitrogen in the water column was about evenly divided between ammonia and NO_x, the actual O:N ratio of decomposition probably lies somewhere between the two extremes. The two estimates of pelagic nitrogen recycling place limits on the actual value.

b. Production. In the MERL systems, production occurs primarily in the water

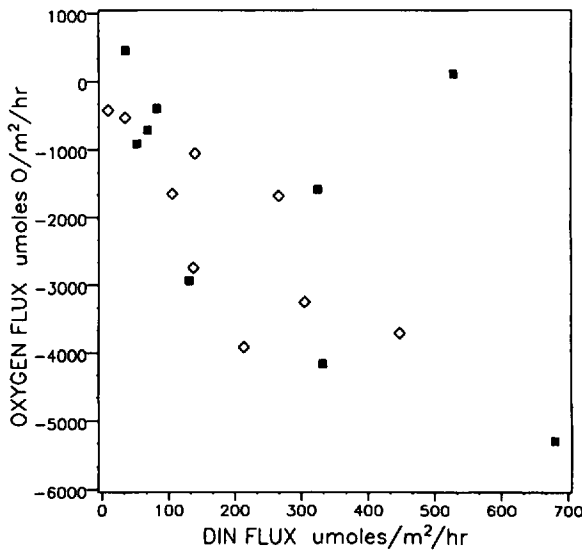


Figure 2. Benthic consumption of oxygen and production of dissolved inorganic nitrogen (DIN) from the bottoms of two no-benthos tanks receiving equivalent doses of nitrogen and phosphorous but differing amounts of silicon. (■) Tank 5, N + P + Low Si (◇) Tank 9, N + P + High Si.

column while the benthos is heterotrophic. These systems are thus ideal for examining the effects of the benthos on pelagic production. In mesocosms with an intact benthos, measured annual apparent production increased by 23% relative to mesocosms lacking a benthos. This statistically significant result verifies and quantifies the implications of field studies: the benthos makes a substantial contribution to production in the water column.

By design, both treatments received an equivalent input of nutrients from ambient Narragansett Bay water. Concentration of dissolved inorganic nitrogen did not vary as a function of the presence or absence of a benthos. Any treatment-related difference in production must therefore have resulted from differences in rates of internal recycling of nutrients by the benthos or in the water column.

The calculations (Table 3) partition recycling into benthic and pelagic components. The interesting result is that the higher gross system production in tanks with an intact benthos was not entirely a function of the greater benthic flux of nutrients in this treatment. Only 45–60% of the Benthos-No Benthos difference in production was attributable to the disparity in benthic flux between treatments. Nearly 40% was evidently fueled by a relatively higher rate of water column recycling in tanks with a benthos. These results suggest that the effect of the benthos on pelagic production is two fold. The benthos enhances production directly by supplying nutrients and indirectly by increasing regeneration rates in the overlying water column.

The benthos may stimulate pelagic heterotrophic activity in a number of ways.

Oviatt *et al.* (1986a) note that as production increases, respiration, and thus recycling of plant nutrients, in the water column also increases. The increased pelagic production fueled by nutrients derived from the benthos could thus result in higher pelagic recycling rates.

Secondly, release of dissolved organic nitrogen (DON) compounds from the benthos could stimulate bacterial activity in the water column. Although not measured here, DON may comprise about 10% of the total benthic nitrogen flux in some areas (Hopkinson, 1987). If true here, decomposition of these compounds would account for 13–17% of the calculated increase in pelagic recycling of nitrogen.

In relatively shallow coastal areas resuspension of bottom sediments may be substantial (Rhoads, 1973). In fact, resuspension of bottom sediments in MERL mesocosms is similar to that in Narragansett Bay (Santschi *et al.*, 1982; Oviatt and Nixon, 1975). Decomposition of resuspended material in the water column might also enhance rates of pelagic nutrient recycling.

The biogeochemical link, comprising the flow of inorganic nutrients, from benthos to water column has been well established over the past 10–20 years (Garber, 1987). The potential existence of additional links, which may influence the processing of organic matter in the overlying water, deserves further investigation. Such interactions may form an integral part of oxygen and nutrient dynamics in shallow waters and may be important to consider when predicting effects of environmental manipulations.

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