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## **Benthic respiration and nitrogen release in Buzzards Bay, Massachusetts**

by Gary T. Banta<sup>1,3</sup>, Anne E. Giblin<sup>2</sup>, John E. Hobbie<sup>2</sup> and Jane Tucker<sup>2</sup>

### ABSTRACT

The decomposition of organic matter and the regeneration of nitrogen in the sediments of Buzzards Bay, Massachusetts were examined by measuring benthic fluxes of oxygen and dissolved inorganic nitrogen (DIN). Benthic respiration ( $O_2$  consumption) rates measured from one site yielded an estimate of 65–80 g C  $m^{-2}$  oxidized annually. Comparing the annual release of DIN with the consumption of  $O_2$  led to an estimate of N loss from the benthic-pelagic system, most likely as  $N_2$  gas via denitrification, corresponding to 14–32% of the N remineralized from organic matter decomposition. Using path analysis, benthic flux rates of  $O_2$  and DIN over a seasonal cycle in Buzzards Bay were determined to be related to water temperature and sediment photosynthetic pigments (chlorophyll *a* and phaeopigments). The rate of DIN release was also negatively related to the particulate organic N (PON) pool as well. The relationship of benthic fluxes to sedimentary pigment concentrations suggested that pigments were good indicators of labile organic matter input to sediments. Macrofauna appeared to have a direct negative effect, as well as a positive indirect effect on DIN release. Benthic respiration rates were not related to sedimentary particulate organic C (POC) or PON content, or macrofaunal abundances. Release rates of DIN were also unrelated to POC pools.

Benthic flux rates measured at 12 sites in Buzzards Bay during August 1989 varied by less than a factor of 2 for benthic respiration and less than a factor of 3 for DIN release. The only environmental factor that emerged from path analysis as related (negatively) to the spatial pattern of benthic flux rates in August was water depth. Other factors, such as organic pools, pigment concentrations, macrofauna, and distance from the New Bedford sewage outfall were not related to the spatial patterns of benthic fluxes in Buzzards Bay. The combination of seasonal and spatial observations indicate that the processes oxidizing organic matter in Buzzards Bay sediments are controlled by temperature and the delivery of labile organic matter to the sediment surface. Benthic flux rates in Buzzards Bay were generally low, but N recycling efficiency was high, relative to similar coastal environments.

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## 1. Introduction

Primary production of coastal marine waters and the lower reaches of most estuaries is limited by availability of nitrogen (Ryther and Dunstan, 1971; Boynton *et al.*, 1982). In open ocean waters 82–94% of the N necessary to support primary production is regenerated as ammonium within the water column from the breakdown of organic matter produced in the euphotic zone (Eppley and Peterson, 1979). In contrast, Nixon (1981) observed that much of the N needed to support primary production in coastal waters is regenerated by organic matter decomposition in sediments. There is much variability, however, in the absolute amount of this N supporting primary production that is regenerated from sediments in different coastal environments.

Several factors affect the decomposition of organic matter within sediments. For example, organic matter decomposition is strongly temperature dependent (Nixon *et al.*, 1976), while benthic macrofauna can influence both the magnitude and timing of decomposition (Rhoads, 1974; Aller, 1980, 1982; Rudnick and Oviatt, 1986). Ultimately, however, rates of organic matter decomposition in sediments are controlled by organic matter supply to sediments, which is in turn a function of factors such as water depth and rates of primary production (Hargrave, 1973; Suess, 1980).

Benthic respiration ( $O_2$  uptake) is a good proxy for the numerous microbial reactions and processes responsible for the decomposition of organic matter in marine sediments. Benthic respiration rates, which include both the consumption of  $O_2$  by aerobic organisms and the oxidation of reduced compounds produced by anaerobic microbes (Jørgensen, 1982; Mackin and Swider, 1989), closely reflect rates of organic matter degradation (both aerobic and anaerobic decomposition) in sediments overlain by oxic waters.

Dissolved inorganic nitrogen (DIN) release from sediments is less tightly coupled to organic matter decomposition because DIN is lost from the benthos via processes such as denitrification or ammonium adsorption (Berner, 1974; 1980). Losses of N from coastal sediments by denitrification are often substantial, ranging between 15 and 60% of the organic N that is deposited on the sediments (Seitzinger, 1988). When decomposition rates are known (e.g., from benthic respiration), denitrification losses can be indirectly estimated from DIN release measurements given certain assumptions about the stoichiometry of the organic matter being decomposed (Nixon *et al.*, 1976; Nixon, 1981).

Although rates of benthic respiration and nutrient release have been reported for sediments in many environments (e.g., Nixon, 1981; Nixon and Pilson, 1983; Kemp *et al.*, 1982), the effects of multiple factors controlling the rates and seasonal dynamics of those benthic processes are difficult to separate. The purpose of this study was to examine the factors controlling the magnitude and seasonal patterns of rates of organic matter decomposition ( $O_2$  uptake) and DIN release for sediments of Buzzards Bay, Massachusetts. We did this in two ways. In the first case, we examined

benthic fluxes over a seasonal cycle (June 1988–September 1989) at one location in Buzzards Bay. In the second case, we compared benthic fluxes from 12 sites in Buzzards Bay measured at the same time, August 1989. In both cases we used path analysis, which investigates both the direct and indirect effects of variables on each other, to examine the factors controlling decomposition in Buzzards Bay. We thereby related benthic flux rates to environmental factors, sediment characteristics, and benthic macrofaunal abundances measured at the same times and locations.

## 2. Methods

We measured benthic respiration and nitrogen release 11 times from June 1988 to September 1989 at the Weepecket Island Station (WIS) in Buzzards Bay, Massachusetts, U.S.A. (Fig. 1). The WIS station has been the site of several biogeochemical studies (Martin and Sayles, 1987; Brownawell, 1986; McNichol *et al.*, 1988). Water depth at this station is 15 m and the bottom consists of fine silt-clay (Moore, 1963) with a benthic animal community dominated by *Nephtys incisa* and *Nucula annulata* (Sanders, 1958). The sediments and benthic community at this site are typical for much of the deeper portions of Buzzards Bay (Rhoads and Young, 1970; Sanders, 1958).

Measurements of benthic flux were most frequent during spring, summer, and fall when benthic respiration and DIN release rates were highest. At the time of each flux measurement, bottom water temperature was recorded and sediment samples were taken to measure organic C and N content, chlorophyll *a* and phaeopigment concentration, and macrofaunal abundances.

The same suite of measurements was made at 11 other sites in addition to WIS (Fig. 1) during August 1989 to characterize the spatial variability of benthic flux rates in the bay when they were at a seasonal maximum. The lettered stations (Fig. 1, Stations G–Q) were the same stations sampled by Sanders (1958, 1960) for macrofauna during the 1950's. The numbered stations (Stations 7–14) were sites along a transect between New Bedford harbor and the central basin of Buzzards Bay surveyed in 1987 by Rhoads and Hampson (SAIC, 1987) with SAIC's (Science Applications International Corporation) sediment profiling camera REMOTS® (Remote Ecological Monitoring of the Seafloor). Nine of the 11 other stations sampled were similar to WIS in that they had silty sediments (Moore, 1963) and were dominated by a *Nephtys-Nucula* macrofaunal assemblage (Sanders, 1958). Two stations (Stations G and H) had sandy sediments and the corresponding benthic community.

### *a. Benthic respiration and nutrient fluxes*

At each station SCUBA divers collected 3–4 intact sediment cores in 15 cm (inner diameter) PVC tubes. The tubes contained approximately 20–30 cm of sediment and

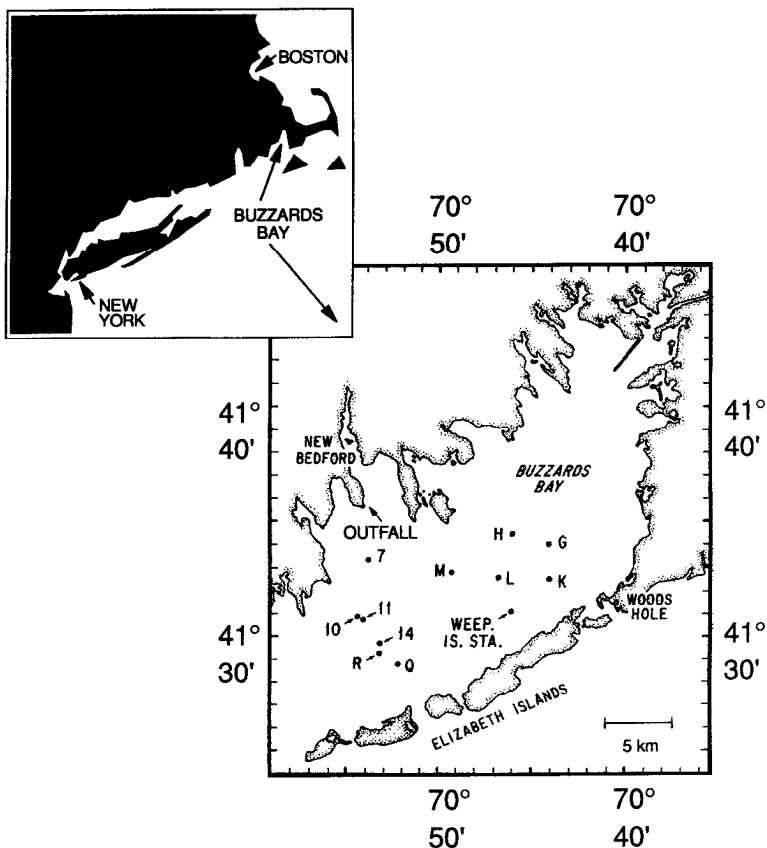


Figure 1. Stations sampled in Buzzards Bay. The Weepeket Island Station (WIS) was the site of our seasonal measurements. The lettered stations (G–R) are the same as described by Sanders (1958). The New Bedford REMOTS® (SAIC 1987) transect is represented by Stations 7–14 and Station R. The location of the New Bedford sewage outfall is also indicated.

20–30 cm of overlying water. The tubes were brought back to the lab and placed in the dark at *in situ* temperatures. Tubes were held with tops open and submerged under running, filtered (Fulflo polypropylene wound-fiber cartridge filter, nominal pore size 1  $\mu\text{m}$ ) seawater for 0.5–3 d before benthic fluxes were measured.<sup>4</sup> Just prior to measuring fluxes the water overlying the sediment was replenished by flushing with fresh, filtered seawater while the cores were underwater. Care was taken not to disturb the sediment surface while flushing the overlying water. Afterwards, the core

4. Note: cores used for the January 1989 benthic flux measurements were held for 22 d before starting flux measurements. Water temperatures were low (3–7°C) during this period, so we expected little changes in flux rates over this time. Banta (1992) maintained sediment cores from WIS in the laboratory for periods of 2–3 months with little changes in flux rates.

tubes were sealed (enclosing water volumes of 3.5–5 l) with a plexiglass top equipped with a magnetic stirrer to mix the water column (Dornblaser *et al.*, 1989) and benthic flux rates were measured by monitoring the change in concentration of O<sub>2</sub> and dissolved inorganic N (DIN) in the overlying water.

Oxygen concentration was measured with a dissolved O<sub>2</sub> electrode (Orbisphere 2112) inserted through a port in the plexiglass top of the tube. Bottom water O<sub>2</sub> concentrations in the portions of Buzzards Bay that we studied are usually near saturation (Howes, pers. com.), so the O<sub>2</sub> concentrations in the core tubes at the start of the incubation were similar to O<sub>2</sub> concentrations in the field. At least five measurements of O<sub>2</sub> concentration were made at regular intervals throughout the incubation period (31–118 hr, depending on the rate of O<sub>2</sub> consumption) to ensure that the consumption of O<sub>2</sub> remained constant (linear) throughout the incubation. Benthic respiration rate was calculated as the slope of the linear regression of O<sub>2</sub> concentration versus time.

Immediately after O<sub>2</sub> concentration was measured, a 15 ml sample of overlying water was withdrawn with a syringe through sampling ports for DIN analysis. Seawater was added to replace the water removed. Water samples were processed as follows within 1 hr. Ammonium (NH<sub>4</sub><sup>+</sup>) was determined for duplicate 3 ml samples by the technique of Solorzano (1969) modified for a small sample size. Samples for nitrate (NO<sub>3</sub><sup>-</sup>) and nitrite (NO<sub>2</sub><sup>-</sup>) were frozen until later measurement using the cadmium reduction method (EPA) on a rapid flow analyzer (Alpkem RFA-300). Previous work suggested that the contribution of NO<sub>2</sub><sup>-</sup> to the DIN pool was insignificant for these sediments so only the combined NO<sub>3</sub><sup>-</sup> + NO<sub>2</sub><sup>-</sup> pool was measured in this study. Dissolved inorganic nitrogen (DIN) was calculated as the sum of NH<sub>4</sub><sup>+</sup> + NO<sub>3</sub><sup>-</sup> + NO<sub>2</sub><sup>-</sup>.

#### *b. Sediments*

At the same time as the flux cores 4 smaller sediment cores (2.5 cm inner diameter) were collected for sediment analysis. Two cores were sectioned for the analysis of particulate organic carbon and nitrogen (POC and PON, respectively). These cores were sectioned at 1 cm intervals to a depth of 10 cm, dried at 105°C, weighed, and ground. Carbonates were removed by fuming with concentrated HCl (Hedges and Stern, 1984). After acidification, samples were redried at 105°C, weighed, and analyzed for POC and PON using an elemental analyzer (Perkin Elmer 240C CHN). Concentrations of POC and PON were corrected for change in weight due to acidification.

Chlorophyll *a* and phaeopigments were measured in the top 5–10 cm of the two other small cores. These cores were sectioned at 1 cm intervals and extracted overnight with cold, buffered 100% acetone (a modification of Foreman, 1989). The sediment acetone mixture was centrifuged (8000 rpm) for 10 min and the absorbance of the supernatant at 665 and 750 nm was measured before and after acidification.

The equations of Lorenzen (1967) were used to calculate chlorophyll *a* and phaeopigment concentrations.

*c. Animals*

The abundance of benthic animals in Buzzards Bay were determined in three 6.5 cm diameter cores collected at each sampling occasion. The top 10 cm of these 3 cores was sieved for macrofauna through a 300  $\mu\text{m}$  sieve and preserved in formalin with Rose Bengal. Macrofauna were defined as those animals retained on a 300  $\mu\text{m}$  sieve. Taxa that are traditionally classified as meiofauna (i.e., nematodes, harpacticoid copepods, and ostracods) were not counted. Macrofauna were later counted and identified to at least family level. The most abundant taxa were identified to species.

*d. Data analysis-path analysis*

We tested the factors controlling benthic fluxes in Buzzards Bay using path analysis in two cases. In the first case, we did a path analysis of the effect of environmental, sediment, and biological variables on benthic flux rates (benthic respiration and DIN release) over the season at WIS. In the second case, we conducted a similar path analysis of factors controlling the spatial pattern of benthic flux rates from the 12 sites in Buzzards Bay we sampled in August 1989. In both cases, a separate path analysis was conducted for benthic respiration and DIN release rates.

Path analysis (Wright, 1934; Li, 1975; Sokol and Rohlf, 1981) allows the partitioning of correlations between variables into direct effects of one variable on another and indirect effects between variables due to correlations with other, common variables (Herbers, 1990). Path analysis thus allowed us to separate the direct and indirect effects of the environmental, sediment, and biological variables we measured on benthic fluxes. A second feature of path analysis is that the analysis is statistically valid when the predictor variables (*X*'s) are highly interrelated (intercorrelated). In contrast, multiple regression analysis is based on the assumption that all of the predictor variables (*X*'s) are uncorrelated. This is seldom the case in ecological data sets, such as those we present here. Path analysis therefore provides an appropriate alternative to multiple regression analysis in highly correlated data sets.

Path analysis is conducted with the help of path diagrams showing the *a priori*, hypothetical relationships (both direct and indirect) between predictor (environmental, sediment, and biological) variables and response (benthic flux) variables. Path diagrams for the seasonal data at WIS (Fig. 2, top) and for data from the 12 stations sampled in August 1989 (Fig. 2, bottom) show which relationships between the environmental, sediment, biological variables and the benthic flux rates we tested. Causal relationships are indicated by one-way arrows while correlational relationships (here only %C to %N) are indicated by two-directional arrows. Direct effects

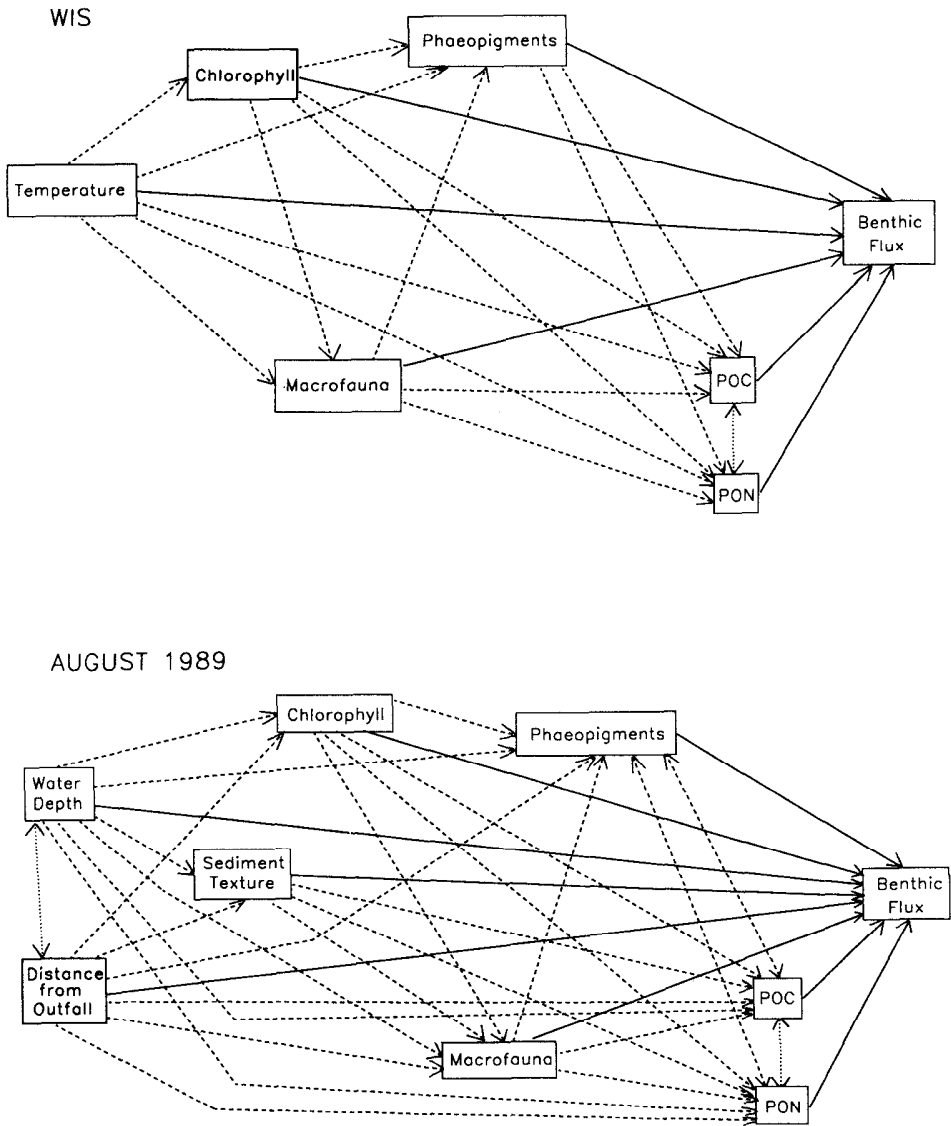


Figure 2. Initial path diagrams indicating the relationships between benthic fluxes, environmental, sedimentary, and biological variables tested with path analysis for seasonal data from the Weepeket Island Station (WIS) (top) and the bay-wide study during August 1989 (bottom). Causal relationships are indicated by one-way arrows while correlations are indicated by two-way arrows. Direct effects on benthic fluxes are indicated with solid lines while indirect effects are shown with dashed lines.



on benthic fluxes are indicated with solid lines while indirect effects are shown with dashed lines.

To conduct the path analyses, path coefficients were calculated by standardizing all variables to mean 0 and variance 1 and calculating multiple regression coefficients for each sub-model of a path diagram (Fig. 2); a sub-model is any group of predictor (i.e., causative) and criterion (i.e., response) variables that can be identified from the path diagram (Li, 1975; Sokol and Rohlf, 1981). In an iterative procedure similar to the backward elimination procedure used for multiple regressions, weak causal links were rejected and the models were redefined, simplified and retested (Li, 1975; Draper and Smith, 1981). This iterative procedure resulted in the simplest models that explained the observed data. Only variables that were significantly related to benthic fluxes, either directly or indirectly, were kept in the final models.

### 3. Results

#### a. Benthic respiration

The seasonal pattern of benthic respiration rates at WIS generally followed water temperature (Fig. 3, top), except in spring when respiration rates increased much more rapidly than temperature. In fact, benthic respiration began increasing in March while water temperature was still dropping. The second highest benthic respiration rate was measured in early May when the water temperature was only 11°C. Graf *et al.* (1982) observed a similar rapid increase in benthic respiration, despite only a slight increase in temperature, following the deposition of a phytoplankton bloom in Kiel Bight. Benthic respiration rates measured for 12 stations in Buzzards Bay during August 1989 ranged from a low of 18.7 mmol O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> at Station R to a high of 27.9 mmol O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> at Station M (Table 1). Water temperature was essentially constant (21–23°C) over the 3 weeks that we sampled these stations so these rates can be compared directly.

The benthic respiration rates we measured (Fig. 3, top; Table 1) are within the range of rates reported previously for Buzzards Bay for similar water temperatures. There is close agreement between our rates and those of Florek and Rowe (1983) at Station K and those of Howes (pers. com.) in outer New Bedford Harbor. Smith *et al.* (1973) and Rowe *et al.* (1975) measured benthic respiration rates that were 2–3 times higher, however, at Sanders' (1958) Station J (located between Station K and Woods Hole, see Fig. 1) than we did at nearby stations (eg., WIS, and Stations K and L). Spatial variability in benthic flux rates in Buzzards Bay may explain some of the differences between our results and these latter studies, as the lowest and highest benthic respiration rates we measured at the 12 stations in August 1989 differed by a factor of 1.5 (Table 1). Temporal variability in flux rates may also play a role in the observed differences. Banta *et al.* (1994) measured benthic respiration rates at WIS, Station 7 and Station R in 1990 that were in some case 1.5 times greater than during

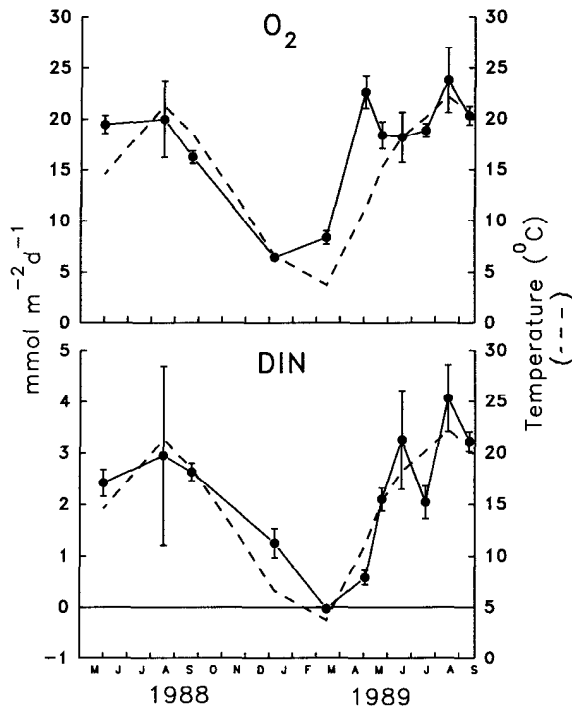


Figure 3. Seasonal pattern of benthic fluxes at the WIS (top—benthic respiration rates, bottom—dissolved inorganic nitrogen (DIN) release rates). All flux values are reported as mean  $\pm$  standard error of rates determined from 3–4 replicate cores. In both panels, water temperature is indicated by the dashed line.

Table 1. Benthic fluxes in Buzzards Bay during August 1989. Flux rate units are  $\text{mmol m}^{-2} \text{d}^{-1}$  and presented as means  $\pm$  standard errors for O<sub>2</sub> and DIN and means  $\pm$  propagated standard errors for O/N.

Station	O <sub>2</sub>	DIN	O/N
7	27.7 $\pm$ 2.7	4.8 $\pm$ 0.2	11.6 $\pm$ 0.7
10	22.9 $\pm$ 1.9	3.0 $\pm$ 0.3	15.5 $\pm$ 1.4
11	23.5 $\pm$ 1.4	3.0 $\pm$ 0.2	15.5 $\pm$ 1.9
14	21.8 $\pm$ 1.2	2.7 $\pm$ 0.2	15.9 $\pm$ 0.3
G	22.8 $\pm$ 0.8	3.4 $\pm$ 0.6	13.6 $\pm$ 2.0
H	24.4 $\pm$ 1.4	4.1 $\pm$ 0.3	12.0 $\pm$ 0.9
K	19.9 $\pm$ 1.2	2.0 $\pm$ 0.1	19.8 $\pm$ 1.5
L	20.8 $\pm$ 1.8	2.3 $\pm$ 0.6	17.8 $\pm$ 3.2
M	27.9 $\pm$ 0.9	5.0 $\pm$ 0.5	11.2 $\pm$ 2.1
Q	24.2 $\pm$ 1.2	2.1 $\pm$ 0.3	22.6 $\pm$ 2.6
R	18.7 $\pm$ 2.0	2.4 $\pm$ 0.4	17.4 $\pm$ 2.7
WIS	23.8 $\pm$ 3.2	4.1 $\pm$ 0.6	11.7 $\pm$ 2.7

similar times in 1988 and 1989. This fits well with Borkman and Turner's (1993) finding that the spring phytoplankton bloom in most parts of Buzzards Bay was more intense in 1990 than in 1989. In general, all measured benthic respiration rates for Buzzards Bay (Fig. 3, Table 1, Smith *et al.*, 1973; Rowe *et al.*, 1975, Florek and Rowe, 1983; Banta *et al.*, in 1994) are in the lower range of benthic respiration rates reported for other coastal environments (see Nixon 1981).

#### b. Benthic DIN release

Release rates of DIN ( $\text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$ ) at WIS (Fig. 3, bottom) ranged from a low of essentially 0  $\text{mmol N m}^{-2} \text{d}^{-1}$  in March to a maximum of 4.1  $\text{mmol N m}^{-2} \text{d}^{-1}$  in August. Nitrate ( $\text{NO}_3^-$ ) made up a relatively small proportion (<20%) of the DIN released from Buzzards Bay sediments during most of the year (data not shown) except in August 1989, when 57% of the DIN was released as  $\text{NO}_3^-$ , and in March 1989 and in early May 1989, when there were low rates (<0.1  $\text{mmol N m}^{-2} \text{d}^{-1}$ ) of  $\text{NO}_3^-$  uptake (data not shown).

The pattern for DIN release at WIS (Fig. 3, bottom) corresponded more closely to temperature changes over the season than did benthic respiration rates (Fig. 3, top). The spring maxima of DIN release rates occurred in June, much later than the maxima for benthic respiration rates. Thus, while benthic respiration and DIN release at WIS were correlated ( $r = 0.593$ ,  $p \leq 0.054$ ) over the entire study period indicating the linkage of these two processes, benthic respiration and DIN release were decoupled during the spring (correlation for March–June was  $r = 0.407$ ,  $p \leq 0.593$ ). During March, April, and May, benthic respiration rates increased dramatically, while DIN release rates were low. Benthic respiration and DIN release were tightly coupled during the rest of the year ( $r = 0.862$ ,  $p \leq 0.013$ ), however.

Sediment DIN release rates measured from the 12 stations during August 1989 generally followed the same pattern among stations as benthic respiration rates (Table 1). There were greater relative differences between stations for DIN release rates, than for benthic respiration rates. The benthic respiration rates differed between stations by a factor of 1.5 while DIN release rates differed by a factor of 2.4.

Our DIN flux rates for Buzzards Bay (Fig. 3, bottom; Table 1) agree quite closely with rates reported by others, both for Buzzards Bay (Rowe *et al.*, 1975; Florek and Rowe, 1983; Howes pers. com.) and other coastal areas (Nixon, 1981). This similarity of DIN release rates between environments is in contrast to the larger differences observed between environments for benthic respiration rates. This better agreement between Buzzards Bay and other areas for DIN release rates is in part due to the fact that we measured a wide range of DIN release rates in Buzzards Bay, from 0 to approximately 5  $\text{mmol N m}^{-2} \text{d}^{-1}$ , but measured a relatively narrow range of benthic respiration rates, from approximately 20 to 30  $\text{mmol O}_2 \text{m}^{-2} \text{d}^{-1}$ .

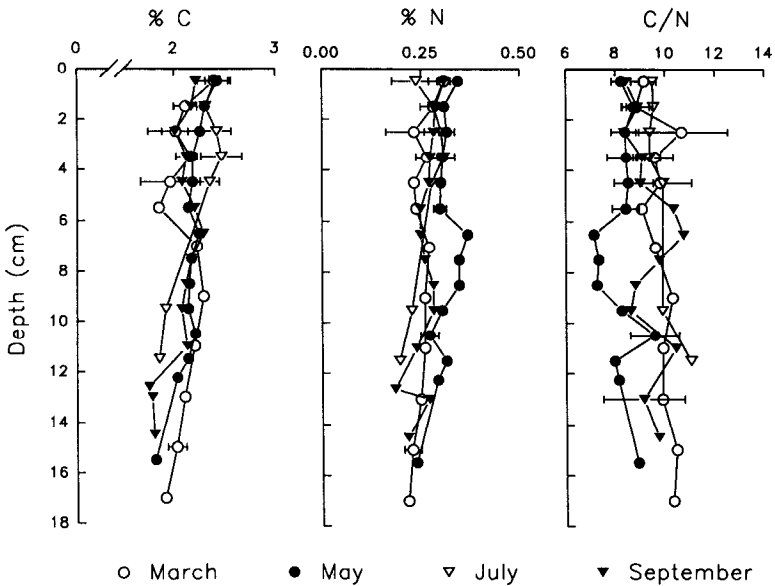


Figure 4. Profiles of sediment POC (left) and PON (middle) concentrations, and molar C/N ratios (right) from four representative times of the year during 1989 at the WIS. The POC and PON data are presented as percent of dry sediment and each value represents the mean  $\pm$  standard error of 2 replicate cores collected from the site. The C/N data are the ratio between the carbon and nitrogen molar concentrations for each depth and each value represents the mean  $\pm$  propagated standard error of 2 replicate cores collected from the site. Note, error bars are often smaller than the symbol size.

### c. Sedimentary POC and PON

Profiles of the sediment content of POC and PON at WIS changed little over the season (Fig. 4, left and middle). Throughout the year POC decreased with depth from 2.2–2.5% at the surface to slightly less than 2% at 16 cm depth (Fig. 4, left). A similar pattern was observed for PON which decreased from 0.3–0.4% at the surface to 0.2–0.3% at depth (Fig. 4, middle). Profiles of POC and PON for 10 of the 11 other stations we surveyed in August 1989 were similar to WIS, with POC values ranging between 1.3% and 2.6% and PON values ranging between 0.15% and 0.34% (Table 2; Banta, 1992). Station G was notably different from the other stations, with POC and PON concentrations less than 0.4% and 0.05%, respectively.

At WIS C/N was fairly constant (usually 8–10) with depth (Fig. 4, right), the 12 stations sampled during August 1989 had sediment C/N values ranging from 7 to 10 (data not shown, see Banta, 1992). There was little change in C/N with depth at any of these stations. The C/N of surface sediments at WIS changed slightly throughout the season, with C/N values being somewhat lower (8–9) in the late spring/early summer, higher (9–10) in the late summer, and lower again (approx. 9) in the fall (data not shown, see Banta, 1992). The slightly lower C/N ratios observed in May

Table 2. Sediment and other characteristics for the 12 stations sampled in August 1989. POC and PON (expressed as % dry weight) are averaged for the top 5 cm of the sediment. Phytoplankton pigment values are summed for the top 5 cm of the sediment. Distance is from the New Bedford sewage outfall (Fig. 1), the major point-source of N inputs into Buzzards Bay. The water depth of each station is presented under Z. Sediment texture is given in Udden-Wentworth  $\phi$  units. Errors, where given, are standard errors from duplicate cores from each station.

Station	POC (% dry weight)	PON	Chloro- phyll (mg m <sup>-2</sup> )	Phaeo- pigments	Macrofauna (thousands m <sup>-2</sup> )	Distance (km)	Z (m)	Sediment* Texture ( $\phi$ )
7	1.50 ± 0.04	0.177 ± 0.005	95 ± 3	653 ± 42	59.6 ± 18.6	4.1	10.4	6.1
10	1.87 ± 0.07	0.230 ± 0.006	105 ± 2	843 ± 9	99.9 ± 5.6	8.5	16.2	7.2
11	2.03 ± 0.01	0.262 ± 0.004	167 ± 17	815 ± 41	82.4 ± 2.6	8.7	15.2	(7.4)#
14	1.73 ± 0.01	0.235 ± 0.005	133 ± 2	837 ± 13	62.9 ± 6.1	10.7	18.9	7.5
G	0.30 ± 0.03	0.034 ± 0.03	103 ± 10	364 ± 26	20.8 ± NA	14.1	13.7	3.1
H	2.45 ± 0.01	0.307 ± 0.007	185 ± 17	709 ± 22	44.3 ± 2.6	11.3	14.0	(6.6)#
K	2.31 ± 0.08	0.298 ± 0.010	136 ± 24	589 ± 15	23.9 ± 2.1	14.9	15.2	7.4
L	2.21 ± 0.02	0.279 ± 0.009	188 ± 10	661 ± 1	76.2 ± 5.3	11.3	15.5	7.1
M	1.35 ± 0.09	0.155 ± 0.009	107 ± 1	640 ± 8	101.7 ± 7.1	8.1	14.9	6.1
Q	1.69 ± 0.03	0.217 ± 0.005	135 ± 2	886 ± 23	77.9 ± 10.9	12.6	16.8	6.3
R	1.64 ± 0.03	0.218 ± 0.013	107 ± 7	762 ± 23	66.2 ± 7.5	11.5	19.8	7.0
WIS	2.38 ± 0.02	0.295 ± 0.004	173 ± 2	656 ± 6	39.1 ± 1.6	13.7	15.2	(7.2)#

\*Sediment texture ( $\phi$ ) was calculated using Udden-Wentworth size intervals (Wentworth, 1922) from particle size data in Sanders (1958) for stations G–Q and from REMOTS<sup>(R)</sup> data (SAIC, 1987) for stations 7–14.

#Sediment texture ( $\phi$ ) was not measured directly at WIS. Sediment textures ( $\phi$ ) reported for stations H (Sanders, 1958) and 11 (SAIC 1987) were more coarse than we observed when we sampled these stations. For these 3 stations  $\phi$  was estimated by extrapolating between Sanders' (1958) stations. The sediment texture resulting from this extrapolation was confirmed by Moore's (1963) data.

and again in September probably reflected the inputs of algal organic matter to WIS sediments at those times. Seasonal changes in sediment C/N in other systems clearly follow the inputs of algal organic matter (eg., Marsh and Tenore, 1990; Sampou and Oviatt, 1991; Therkildsen and Lomstein, 1993). The changes we observed at WIS were small, however, suggesting that the inputs of fresh algal material were relatively low compared to these other systems.

#### d. Sedimentary pigments

Phaeopigment concentrations were considerably higher than chlorophyll *a* concentrations in the sediments of Buzzards Bay. Phaeopigments decreased slightly with depth, but concentrations remained high (15–20  $\mu\text{g}/\text{cc}$ ), even down to 10 cm (Fig. 5, right). Chlorophyll *a* concentrations were generally low, below 5  $\mu\text{g}/\text{cc}$  (Fig. 5, left), except in spring (especially May 1989).

Sedimentary stores of pigments (summed for the top 5 cm, the seasonally dynamic zone) showed marked seasonal variation at WIS (Fig. 6). The sediment chlorophyll *a* pool was quite low throughout the year except during the spring when there was a

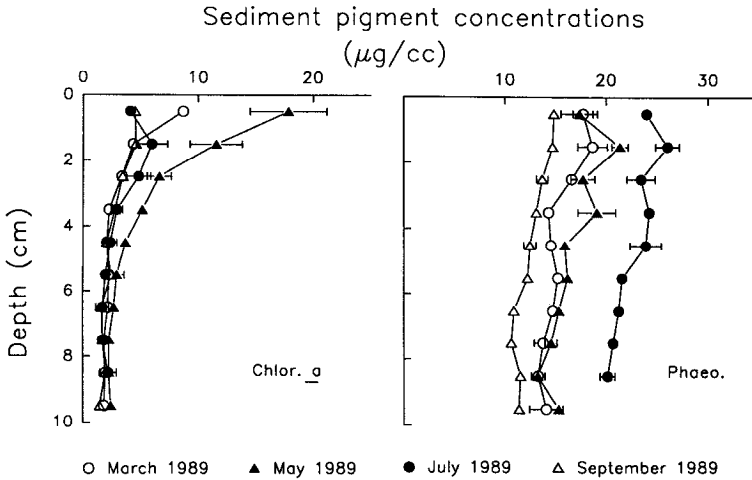


Figure 5. Profiles of sediment phytoplankton pigment concentrations from four representative times of the year during 1989 at the WIS. The data are presented as  $\mu\text{g}$  pigments per cubic cm of sediment and each value represents the mean  $\pm$  standard error of 2 replicate cores collected from the site.

sharp increase. This chlorophyll peak disappeared during the following few months. The seasonal pattern for integrated phaeopigment concentrations was more erratic than for chlorophyll *a*, but a late summer/fall peak in phaeopigment concentration was observed during both 1988 and 1989.

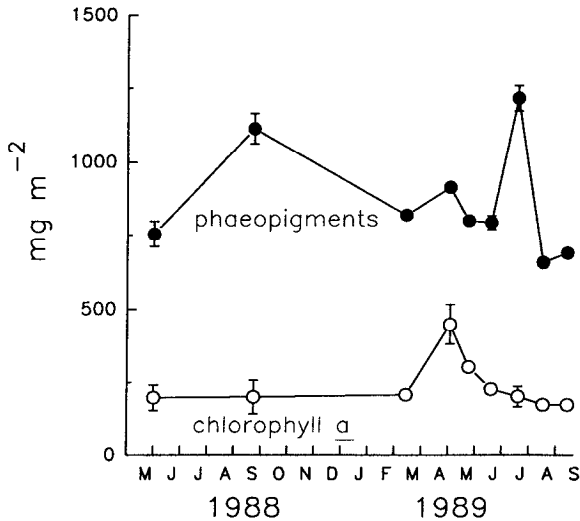


Figure 6. Integrated phytoplankton pigment concentrations at the WIS during 1989. Integrated concentrations are the sum of the chlorophyll *a* and phaeopigment concentrations for the top 5 cm but expressed on an areal basis as  $\text{mg pigment m}^{-2}$ . Values are the mean  $\pm$  standard error of 2 replicate cores collected at each sampling period from the site.

Pigment concentrations for the 12 stations in August 1989 were similar to WIS, with chlorophyll *a* concentrations ranging from 1.3 to 5.6  $\mu\text{g cc}^{-1}$  and phaeopigment concentrations of 11.2–20.8  $\mu\text{g cc}^{-1}$  (data not shown, see Banta, 1992). Station G was again an exception with significantly lower phaeopigment concentrations (4.4–8.7  $\mu\text{g cc}^{-1}$ ), although chlorophyll concentrations there were similar to the other stations. Integrated pigment stores (Table 2) were 95–173  $\text{mg m}^{-2}$  for chlorophyll and 364–886  $\text{mg m}^{-2}$  for phaeopigments. The similarity of pigment concentrations for all of the stations that we sampled in August 1989, including Station G, is consistent with Borkman and Turner's (1993) finding that algal concentrations, and presumably rates of primary production, are similar for most of Buzzards Bay. Pigment concentrations (chlorophyll + phaeopigments) for the 12 stations in August 1989 differed by only a factor of 2 compared to POC concentrations, which differed by a factor of 8.

Roman and Tenore (1978) measured lower sedimentary pigment concentrations (20–80  $\text{mg m}^{-2}$ ) for Buzzards Bay sediments than we did (Fig. 6, Table 2). They observed a winter/spring peak in sediment chlorophyll with the highest concentrations occurring in February–April, while we observed a peak later, in April–May. In both studies, the peaks in sediment chlorophyll concentrations occurred at the same time or just after increased chlorophyll concentrations in the water (Borkman and Turner, 1993) or peaks in primary production rates (Roman and Tenore, 1978). We did not observe the late summer/early fall peak in sediment chlorophyll that Roman and Tenore (1978) did. We did, however, measure a peak in sediment phaeopigments in July 1989 that may have reflected a summer peak in primary production. Borkman and Turner (1993) measured elevated water column concentrations of phaeopigments in central Buzzards Bay at that time, although water column chlorophyll *a* concentrations were low.

Sun *et al.* (1991) found depth profiles of chlorophyll *a* in two locations in Long Island Sound similar to the depth distributions we observed in Buzzards Bay (Fig. 5, left). Buzzards Bay sediments, however, often had more chlorophyll *a* at depth than Long Island Sound sediments. Recent comparisons of methods (Banta *et al.*, unpub. data) suggest we may have underestimated sedimentary chlorophyll *a* concentrations by 25% by not freezing the sediments before extracting the pigments (Sun *et al.*, 1991), so chlorophyll *a* concentrations at depth in Buzzards Bay sediments may in fact be greater. Even with our potential underestimate, Buzzards Bay had higher (approximately 2–10 fold) integrated chlorophyll *a* concentrations (Fig. 6, Table 2) than Long Island Sound for comparable times of the year.

#### *e. Benthic macrofauna*

Total macrofaunal abundances at WIS ranged between 25,000 and 60,000 individuals  $\text{m}^{-2}$  during 1989–90 (Fig. 7). There was a tendency for animal densities to be lower during summer. This pattern has been attributed to both increased predation

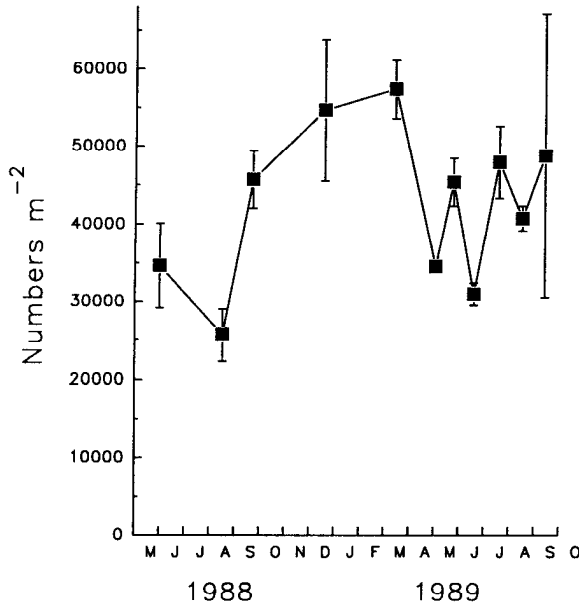


Figure 7. Abundances of macrofauna at the WIS during 1988 and 1989. Values are the mean  $\pm$  standard error of 2–3 replicate cores collected at each sampling period from the site.

during the summer and reduced food resources (Grassle *et al.*, 1985; Rudnick *et al.*, 1985; Wiltse *et al.*, 1984). Total macrofaunal abundances at the 12 sites sampled during August 1989 ranged from 21,000  $\text{m}^{-2}$  at Station G to 106,000  $\text{m}^{-2}$  at Station M (Table 2).

Five common taxa (*Nucula annulata*, *Nephtys incisa*, *Mediomastus ambiseta*, *Cylichna oryza*, and spionid polychaetes) usually made up 76 to 95% of the macrofaunal community in Buzzards Bay (data not shown, see Banta, 1992). The exception was Station G, where these species represented only 40% of the animals present. Station G had the sandiest sediments of the sites we sampled and many of the species found there were typical of sandier regions of Buzzards Bay (Sanders, 1958).

The macrofaunal abundances we measured were 3 to 92 times higher than those of Sanders (1958) who observed a range of 1100 to 6100 individuals  $\text{m}^{-2}$  from 9 muddy stations in Buzzards Bay during October and November 1955. Our macrofaunal densities agree more closely with R. Whitlatch *et al.* (unpub. manuscript), who resampled Station R in 1975–76 and found an annual average of 62,000 individuals  $\text{m}^{-2}$ . The macrofaunal community of Buzzards Bay is similar to other muddy bottom communities in southern New England, such as those in Long Island Sound (Sanders, 1956) and Narragansett Bay (Grassle *et al.*, 1985).



Table 3. Correlation matrix between benthic fluxes, sediment parameters and benthic animal abundances for measurements at the WIS in Buzzards Bay during 1988–1989. Correlations significant at  $p \leq 0.05$  are indicated with an asterisk, \*. Correlations marginally significant at  $p \leq 0.10$  are indicated by (\*).

	Benthic Respi- ration	DIN Release	Temper- ature	POC	PON	Chloro- phyll Conc.	Phaeo- pigment Conc.
DIN Release	0.58	—					
Temperature	0.64(*)	0.92*	—				
POC	0.44	0.12	0.17	—			
PON	0.68(*)	0.16	0.12	0.82*	—		
Chlorophyll Conc.	0.26	-0.54	-0.53	0.19	0.50	—	
Phaeopigment Conc.	-0.18	-0.30	0.03	-0.22	-0.44	0.08	—
Benthic Animals	-0.66(*)	-0.36	-0.25	-0.34	-0.68(*)	-0.45	0.12

#### f. Results of path analyses

i. *Seasonal study*—WIS. Benthic respiration and DIN release rates increased exponentially with temperature, which could be empirically described by the equation:

$$\text{Benthic Flux} = a + b * e^{cT}$$

where  $T$  is temperature and  $a$ ,  $b$ , and  $c$  are constants. The constants  $a$ ,  $b$ , and  $c$  were estimated using a Marquardt curve-fitting procedure (Marquardt, 1963) as  $-0.02$ ,  $5.5$ , and  $0.0635$  for benthic respiration, and  $-2.5$ ,  $2.1$ , and  $0.049$  for DIN release, respectively. We used these exponential relationships in path analyses to test the role of temperature, along with other environmental factors, in regulating benthic flux rates over the season at WIS based on the hypothesized relationships indicated in Figure 2 (top). Correlations between variables in the path analyses for WIS are given in Table 3. The high correlations of fluxes with temperature were expected because the flux data were fit to the seasonal temperature pattern to determine the exponential relationship used in the path analysis. In effect, the variables other than temperature included in the path analyses were tested to see if they explained any of the seasonal pattern of benthic fluxes (Fig. 3) once the effect of temperature was removed.

Based on path analysis, the seasonal pattern of benthic respiration at WIS could be related to temperature and sediment chlorophyll  $a$  concentration (Fig. 8, top). These two variables explained 77.4% of the seasonal variability in benthic respiration rates at WIS. Temperature alone explained 41.6% of the seasonal pattern of benthic respiration, while chlorophyll  $a$  concentration alone explained only 6.6%. That temperature and chlorophyll together explained so much more than the sum of the two of them alone indicates that chlorophyll explained a great deal (an extra 35%) of

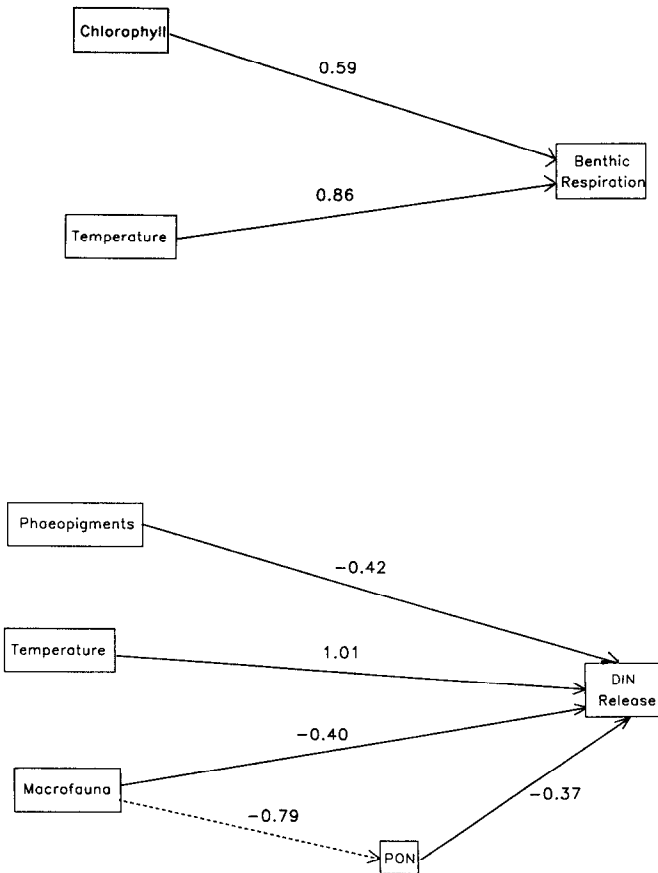


Figure 8. Final results of path analysis for the WIS benthic flux data (top—benthic respiration, bottom—DIN release). Values associated with the causal arrows are path coefficients.

the seasonal benthic respiration pattern after the effect of temperature was accounted for.

The final path diagram for the seasonal pattern of benthic DIN release at WIS (Fig. 8, bottom) was more complicated than that for benthic respiration. Again temperature was most important for explaining the seasonal pattern in DIN release as indicated by the magnitude of its path coefficient. In fact, temperature alone could explain 85.3% of the DIN pattern. The rest (up to 98.1%) of the seasonal pattern of DIN release at WIS could be explained if PON, phaeopigments, and macrofauna were also included in the model. That is, changes in DIN release rates over the season that were not related to temperature were related to changes in these other three variables. Note, however, that all of the path coefficients for these variables are smaller than 0.5 (absolute value), so the influences of these variables on DIN release were much weaker than that of temperature (path coefficient = 1.01).

Table 4. Correlation matrix between benthic fluxes, environmental variables, sediment parameters, and benthic animal abundances for measurements made during August 1989 at 12 stations in Buzzards Bay. Correlations significant at  $p \leq 0.05$  are indicated with an asterisk, \*. Correlations marginally significant at  $p \leq 0.10$  are indicated by (\*).

	Benthic Respi- ration	DIN Release	POC	PON	Chloro- phyll Conc.	Phaeo- pigment Conc.	Benthic Animals	Dist. from Outfall	Water Depth (Z)
DIN Release	0.86*	—							
POC	-0.20	-0.17	—						
PON	-0.29	-0.23	0.98*	—					
Chlorophyll Conc.	-0.19	-0.15	0.73*	0.71*	—				
Phaeopigment Conc.	-0.05	-0.29	0.50(*)	0.46	0.15	—			
Benthic Animals	0.19	0.28	0.12	0.03	-0.11	0.31	—		
Dist. from Outfall	-0.65*	-0.58*	0.08	0.16	0.34	-0.26	-0.65*	—	
Water Depth (Z)	-0.66*	-0.66*	0.14	0.19	0.04	0.52(*)	0.10	0.42	—
Sediment Texture ( $\phi$ )	-0.27	-0.28	0.86*	0.86*	0.42	0.72*	0.36	-0.10	0.41

ii. *Spatial study—August 1989.* The relationships between environmental, sedimentary, and biological parameters (Table 2) and the spatial variability in benthic flux rates measured in Buzzards Bay during August 1989 (Table 1) were also tested using path analysis (Fig. 2, bottom). In addition to the variables included in the WIS path analyses, water depth ( $Z$ ), distance of the station from the New Bedford sewage outfall (the major point source of nutrient inputs to Buzzards Bay; Gliblin and Foreman, 1991), and sediment texture ( $\phi$ ) were included in the path analyses of the August 1989 fluxes. Bottom water temperature was approximately the same at all stations in August 1989 and was therefore not considered in these path analyses. Correlations between these variables are given in Table 4.

The final results of the path analysis indicated that the spatial variability of both benthic respiration and DIN release measured in August 1989 across Buzzards Bay were best explained by water depth ( $Z$ ) alone (final path diagrams not shown). In both cases the path coefficient was  $-0.66$  which is the same as the correlation coefficient between benthic respiration or DIN release and  $Z$  (Table 4) because only one variable remained in the final model. All other variables dropped out of the model, including distance from the New Bedford sewage outfall which also had a significant negative correlation with benthic fluxes. The spatial pattern of benthic fluxes in the open portions of Buzzards Bay, where most of our stations were located, did not appear to be heavily influenced by the outfall. This does not eliminate the possibility of a more local effect of the outfall on benthic processes in and near New Bedford Harbor (SAIC, 1987).

#### 4. Discussion

##### a. Organic matter oxidation estimated from benthic fluxes

We integrated the seasonal benthic respiration and DIN flux data (Fig. 3) and estimated that  $5,210 \text{ mmol O}_2 \text{ m}^{-2}$  were consumed and  $686 \text{ mmol N m}^{-2}$  were

released at WIS annually. This O<sub>2</sub> consumption represented both aerobic respiration and the reoxidation of most of the reduced sulfur compounds produced from sulfate reduction (Jørgensen, 1977) and corresponded to an oxidation of 63 g C m<sup>-2</sup> yr<sup>-1</sup>. Our estimate of annual carbon oxidation at WIS increased to 65–80 g C m<sup>-2</sup> yr<sup>-1</sup> when we added the amount of C oxidized anaerobically but not reoxidized with O<sub>2</sub> (or included in O<sub>2</sub> consumption measurements) due to the reduced S that was permanently buried.<sup>5</sup>

Our annual carbon oxidation estimate agrees quite well with McNichol *et al.* (1988) who estimated that 69 g C m<sup>-2</sup> were oxidized annually at WIS. They based their estimate on changes in porewater profiles of dissolved inorganic carbon over a seasonal cycle. Both of these estimates are significantly lower, however, than the 142 g C m<sup>-2</sup> yr<sup>-1</sup> estimated by Rowe and McNichol (1991) based on flux measurements in the same region of Buzzards Bay. This range of C oxidation estimates reflects both the temporal and spatial heterogeneity of benthic processes in Buzzards Bay sediments.

#### b. Chlorophyll diagenesis

Chlorophyll was detected in sediments down to 10 cm at all sites and throughout the year at WIS. The background level of chlorophyll *a* found in the deeper portions of the sediment may represent a complexed or refractory form of chlorophyll which persists in the sediment (Furlong and Carpenter, 1988), and if so, is unlikely to indicate recent inputs of planktonic material. An alternative explanation for the deep chlorophyll, however, is that chlorophyll was quickly mixed to depth in Buzzards Bay sediments by benthic animals.

We used the diagenetic modelling approach of Sun *et al.* (1991) on our seasonal chlorophyll profiles at WIS. They proposed the following simplified diagenetic equation for chlorophyll in sediments (ignoring sedimentation and assuming that chlorophyll degradation is 1st-order):

$$\frac{\partial C}{\partial t} = D_B \frac{\partial^2 C}{\partial x^2} - k_d C \quad (1)$$

where  $C$  = chlorophyll *a* concentration,  $t$  = time,  $D_B$  = biogenic particle mixing coefficient,  $x$  = depth, and  $k_d$  = the 1st-order decay constant for chlorophyll *a*. Assuming the following boundary conditions:

$$\begin{aligned} x = 0, \quad C &= C_0 \\ x \rightarrow \infty, \quad C &= C_\infty \end{aligned}$$

5. The amount of reduced S buried at WIS was calculated based on the range of sedimentation rates (0.05–0.3 cm yr<sup>-1</sup>) reported in McNichol *et al.* (1988) and a range of reduced S concentrations (130–240 μmol S cm<sup>-3</sup>) for sediment greater than 10 cm deep at WIS measured in 1984 and 1985 (Hobbie, unpub. data). The amount of carbon oxidized was assumed to be 1 mole for every mole of oxygen consumed or 2 moles for every mole of reduced sulfur buried.

the steady state solution to Eq. (1) is:

$$C = (C_0 - C_\infty) \exp(-x\sqrt{k_d/D_B}) + C_\infty. \quad (2)$$

We used a Marquardt (1963) procedure to fit chlorophyll *a* profiles at WIS (Fig. 5, left) to Eq. (2) and solved for  $k_d/D_B$ . Based on Martin and Sayles' (1987) estimates of animal mixing rates ( $D_B = 6\text{--}17 \text{ cm}^2 \text{ yr}^{-1}$ ) at WIS we estimated the decomposition rates of chlorophyll,  $k_d$ . In most cases our  $k_d$ 's were much lower ( $0.005\text{--}0.03 \text{ d}^{-1}$ ) than the  $k_d$ 's ( $0.02\text{--}0.04 \text{ d}^{-1}$ ) reported by Sun *et al.* (1991), implying that chlorophyll is degraded more slowly in Buzzards Bay sediments than in Long Island Sound sediments. One would have to invoke extremely high bioturbation rates ( $D_B$ 's =  $50\text{--}200 \text{ cm}^2 \text{ yr}^{-1}$ ) to generate the chlorophyll profiles we observed with the higher rates of chlorophyll degradation that Sun *et al.* (1991) reported. While we must be somewhat cautious in comparing rates of chlorophyll degradation calculated in this way with those of Sun *et al.* (1991) because of the differences in chlorophyll extraction techniques used in the two studies, the implication that chlorophyll degrades more slowly in Buzzards Bay sediments than in Long Island Sound sediments is consistent with the somewhat lower benthic flux rates in Buzzards Bay compared to other coastal environments.

### *c. N cycling based on O/N benthic flux ratio*

The ratio of moles of oxygen (O) consumed to moles of N released by the sediments at WIS was 15.2 on an annual basis for 1988–89. The measured O/N ratio would have been between 15.4 and 19.4 if there had been no reduced S buried, that is, if all reduced S had been reoxidized with  $\text{O}_2$  (thus increasing  $\text{O}_2$  consumption rates) instead of buried. These O/N ratios are slightly higher than the expected value (13.25) for the mineralization of phytoplankton material containing C and N in the Redfield ratio to its inorganic constituents,  $\text{CO}_2$  and  $\text{NH}_4^+$  (Nixon *et al.*, 1976). The O/N ratios that we measured indicate that less DIN was released from sediments than was mineralized. A likely explanation is the loss of N from sediments as  $\text{N}_2$  via denitrification (Nixon *et al.*, 1976; Nixon, 1981).

Based on O/N ratios (Nixon *et al.*, 1976) we calculated that denitrification may be annually removing up to 14–32% of the N remineralized at WIS. This corresponds to average rates of denitrification of  $0.33\text{--}0.87 \text{ mmol N m}^{-2} \text{ d}^{-1}$ . These denitrification rates are in the lower end of rates measured in other coastal areas, based both on direct measurements of denitrification (Seitzinger *et al.*, 1984) and estimates from O/N flux ratios (Nixon, 1981), where usually 15–60% of the N mineralized is removed annually by denitrification (Seitzinger, 1988). Buzzards Bay thus appears to be relatively efficient at recycling the organic N deposited on the sediments back to the overlying water as DIN. Working at the same site in 1990, Banta *et al.* (1994) estimated denitrification based on O/N ratios to remove 22% of N mineralized on an annual basis at WIS, agreeing quite well with the estimates we give here. Using,

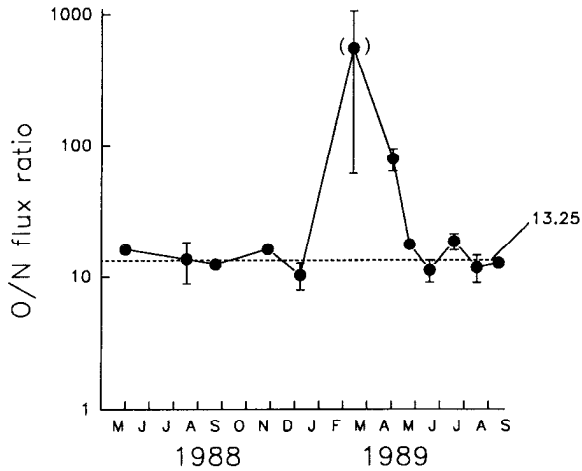


Figure 9. Seasonal pattern of the molar ratio of sediment  $O_2$  consumption (benthic respiration) rate to DIN release rate (mol O/ mol N) at the WIS. Error bars are propagated standard errors. Note the log scale for O/N and also note that DIN flux during March 1989 was essentially 0, so the O/N ratio for March is quite approximate, as indicated by the parentheses.

however, another indirect method to estimate denitrification (based on laboratory measurements of  $NH_4^+$  production rates), Banta *et al.* (1994) estimated that denitrification may remove 48% of the remineralized N at WIS annually. The higher rate of denitrification given by this second method indicates both some of the uncertainties of indirect methods of estimating denitrification and some of the variability in the denitrification process itself.

Other fates for N released from organic matter (besides DIN release and denitrification) sediments not measured or considered in the above calculations, such as DON release, would lead to errors in our estimates of denitrification. A few studies (eg., Nixon *et al.*, 1976; Christensen *et al.*, 1983; Lomstein and Blackburn, 1992; Enoksson, 1993) have shown that DON flux from sediments can be high at times. If DON flux is important in Buzzards Bay as well, then our estimates of denitrification based on O/N ratios may be in error.

While the annual budget indicates that Buzzards Bay was fairly efficient at recycling N to the overlying water during 1988 and 1989, the recycling efficiency did vary significantly throughout the season as indicated by the large seasonal variation of O/N ratios at WIS (Fig. 9). The very large O/N ratios observed in the spring 1989 suggest that denitrification rates were highest at that time. In March, there was essentially no DIN release from the sediments suggesting that all of the DIN released by decomposition was either denitrified or taken up. The uptake of  $NO_3^-$  during spring (data not shown) also suggests that denitrification was quite active at that time.

The high O/N ratios in the spring occurred when sediments in Buzzards Bay typically receive large inputs of fresh detritus following the winter/spring phytoplankton bloom (Roman and Tenore, 1978). Spring maxima in denitrification rates related to the deposition of phytoplankton detritus following phytoplankton blooms have been observed elsewhere (Jensen *et al.*, 1988). We observed high concentrations of chlorophyll in WIS sediments during spring (Fig. 5, left) indicating the presence of fresh algal material, although this chlorophyll may have come from the deposition of planktonic algal material, the presence of benthic diatoms, or both. Diatoms were present at WIS in the spring of 1989 (personal observation) and in 1990 (Banta *et al.*, 1994) and the bottom of Buzzards Bay is within the euphotic zone ( $> 1\%$  surface light) throughout much of the year (Turner and Borkman, 1993). Inputs of fresh algal organic matter from benthic sources have also been shown to have a similar stimulatory effect on denitrification rates (Jørgensen and Sørensen, 1985) as does the settlement of phytoplankton blooms on the sediment surface, so whether the algal material was of planktonic or benthic origin, denitrification rates were likely to have been stimulated in the spring at WIS.

Benthic diatoms present during the spring may have had a second potential effect on N recycling at WIS. Benthic algae might have taken up DIN both from the overlying water (possibly the  $\text{NO}_3^-$  uptake we measured in March and early May) and from the DIN released by organic matter decomposition (Andersen and Kristensen, 1988; Sundbäck *et al.*, 1991). We minimized or eliminated this potential role of benthic algae in N cycling in our study, though, because we incubated our sediment cores in the dark. Cores were typically held at least overnight before flux measurements were made so benthic diatoms, when they were present, had probably stopped taking up DIN (Andersen and Kristensen, 1988; Risgaard-Petersen, 1992) before we measured fluxes. We therefore conclude that the N missing from the DIN release was due to denitrification and not algal uptake, given the conditions under which we incubated cores. Given the relatively shallow nature of Buzzards Bay, future studies should attempt to address the potential role of benthic algae in benthic N cycling, however.

The O/N ratios observed for the 12 stations sampled during August 1989 ranged from a low of 11.2 at Station M to a high of 22.6 (Table 1). Several stations (7, G, H, M and WIS) had values quite close to, or actually below, the expected value of 13.25 suggesting efficient recycling of N to the overlying water at that time. The remaining 7 stations had values ranging from 15.5 to 22.6 which are more typical of other coastal areas (Nixon 1981). Assuming that these O/N ratios were maintained throughout the season (and ignoring S burial) only 1% or less of the N released by decomposition at the first group of stations may be removed from sediments via denitrification, while 13–43% may be removed from the second group of stations. It is clear after examining the O/N ratio in August in relation to the seasonal O/N ratio at WIS that one must be cautious in interpreting one-time O/N measurements as indicators of

denitrification rates over the whole season, but it appears that denitrification rates may be quite low in many areas in Buzzards Bay.

*d. Controls of benthic fluxes*

Organic matter oxidation in Buzzards Bay sediments is controlled mostly by temperature and the supply of fresh, degradable organic matter. We conclude this based on the results of the path analyses for benthic respiration rates, where temperature and variables which either indicate the presence of fresh planktonic organic matter (i.e., chlorophyll) or control the inputs of that organic matter (i.e., Z) explain the temporal and spatial patterns of benthic respiration rates in Buzzards Bay. Few of the bulk sediment parameters that we measured appeared to have an important effect on organic matter decomposition. Benthic respiration rates in Buzzards Bay thus reflected the current mineralization of a small amount of reactive organic matter that was recently deposited, but not easily measurable within the bulk pool of refractory organic matter within the sediment. For example, benthic respiration rates and pigment concentrations differed between stations in August 1989 by factors of 1.5 and 2, respectively, while POC concentrations differed by a factor of 8. Furthermore, lower benthic respiration rates and thus slower rates of organic matter decomposition are consistent with lower concentrations of chlorophyll *a* in the water column and lower rates of primary production in Buzzards Bay compared to many other coastal environments (Roman and Tenore, 1978; Borkman and Turner, 1993). Phytoplankton pigments appear to be much better indicators of the deposition of fresh, labile planktonic organic matter than bulk sediment parameters such as POC in Buzzards Bay.

Nitrogen cycling and the resulting release of DIN from Buzzards Bay sediments is a function of several complex processes, and thus affected by many factors. Based on the path analyses of DIN release rates, temperature and the input of fresh organic matter are again the most important factors, but other factors such as benthic animals and benthic algae play important roles in N cycling in Buzzards Bay. The dominating importance of temperature in controlling N cycling is seen from the very strong relationship between temperature and DIN release rates at WIS (Fig. 8, bottom). That DIN release is ultimately tied to the decomposition of organic matter is seen both from the strong dependence of DIN release rates on temperature and from the inverse relationship of DIN release with Z, which determines in part the delivery rate of degradable organic matter to the sediment.

The relationship between DIN release and organic matter pools is quite complicated and dynamic, however. The release of DIN at WIS was negatively related to PON pools, which seems contradictory. One interpretation of this might be that the PON pool in the sediment is rapidly mobilized and released as DIN from the sediment. Thus, the PON pool decreased as fluxes increased.

The negative relationship between DIN release and phaeopigment concentration



(Fig. 8, bottom) is in contrast to the positive relationship observed between benthic respiration and chlorophyll (Fig. 8, top). Because phaeopigments are decomposition products of chlorophyll, we suggest that phaeopigment concentration may indicate the age of planktonic organic matter within sediments. The release rate of DIN from the sediment may decrease as phytoplankton detritus is decomposed and becomes poorer in quality because N is preferentially released relative to C as detritus decomposes and ages (Rice and Rhoads, 1989). The limited number of studies which combine the analysis of sedimentary pigments (especially phaeopigments) and organic matter decomposition make a general evaluation of this assumption difficult at present. Furlong and Carpenter (1988) suggested that both chlorophyll and phaeopigments indicate the presence of reactive organic matter in sediments, but they did not distinguish whether phaeopigments were less degradable than chlorophylls. In their study, as well as in ours, phaeopigments were a much larger component (approx. 90%) of the sedimentary pigment pool than chlorophyll, suggesting that chlorophyll is quickly transformed into phaeopigments as algal organic matter degrades. That the release of DIN is negatively related to both PON and phaeopigments suggests that DIN release falls off quickly as fresh organic matter pools are depleted and transformed into more refractory states.

Finally, benthic animals appeared to have two effects on DIN release in Buzzards Bay, a direct negative effect and an indirect positive one. One mechanism by which animals may directly reduce DIN release rates is by enhancing denitrification (Henriksen *et al.*, 1980; Kristensen *et al.*, 1991). Stronger than the direct negative effect on DIN release, however, was macrofauna's negative effect on the size of PON pools, possibly due to direct consumption of sediment organic matter or to stimulation of decomposition of sediment organic pools (Aller, 1988; Kristensen and Blackburn, 1987). The negative relationship between PON quantity and DIN release combined with the macrofauna's negative effect on PON pools resulted in macrofauna having an indirect positive effect on DIN release. Thus, macrofauna at WIS appeared to both decrease and increase DIN release rates through different mechanisms.

In conclusion, organic matter decomposition in Buzzards Bay sediments, as indicated by benthic respiration, is controlled by temperature and the inputs of fresh organic matter. Benthic N cycling is more complex. Being coupled to organic matter decomposition it is also driven by temperature and organic matter inputs, but it is also influenced by other factors such as benthic animals and benthic algae. Finally, based on an indirect estimate, the amount of remineralized N which is denitrified is relatively low compared to other estuaries, suggesting that N recycling in Buzzards Bay is relatively efficient.

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