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## **Sediment-Water Nutrient Exchange in Estuarine Sediments of Differing Trophic Status**

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Office of Ocean and Coastal Resource Management  
National Ocean Service  
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for a project entitled

**SEDIMENT-WATER NUTRIENT EXCHANGE IN ESTUARINE SEDIMENTS OF  
DIFFERING TROPHIC STATUS**

(Award No. NA27OR0215)

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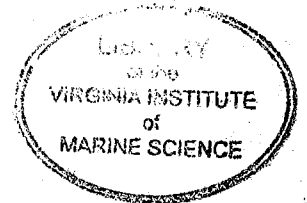
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by

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## ABSTRACT

The National Estuarine Research Reserve (NERR) system offers unique opportunities to carry out research in a variety of estuarine habitats. In both Virginia and North Carolina, NERR sites include both low salinity areas (Sweethall Marsh and Currituck Banks, respectively) and high salinity sites (Goodwin Islands and Masonboro Island, respectively) containing habitats with varied sediment types, light and nutrient conditions.

Eutrophication poses a threat to many estuaries. Among other impacts, increases in turbidity and nutrient concentrations may effect changes in estuarine autotrophic and heterotrophic processes. We investigated sediment community oxygen and carbon dioxide metabolism, and sediment-water exchange of nutrients ( $\text{NH}_4^+$ , nitrate + nitrite ( $\text{NO}_x^-$ ), and filterable reactive phosphate (FRP)) and assessed potential eutrophication-related impacts on benthic environments along natural light/depth gradients. Field studies provided baseline information on these processes, and the comparison between areas of high and low irradiance indicated potential changes attributable to turbidity increases in the water column. Field studies were conducted at the NERR sites listed above, in both sand and mud dominated areas.

Overall, significant effects of short-term light conditions were common for fluxes of  $\text{O}_2$ ,  $\text{CO}_2$ , and  $\text{NH}_4^+$ , but less so for  $\text{NO}_x^-$  and FRP. The greatest frequency of depth (long-term light) effects across all variables was at Goodwin Islands. Other sites had significant effects for one half or less of the analyses. "Mud" sites tended to demonstrate effects more often and with greater significance than sand sites. With the exception of Goodwin Islands, shallow (1 m) depths tended to be more "autotrophic" than 2 m deep sediments. In 1992 at Goodwin Islands, numerous effects

demonstrated that deeper sediments were more autotrophic. Effects of sediment type (sand vs. "mud") were notable on  $O_2$ ,  $CO_2$  and  $NH_4^+$  fluxes and less so on  $NO_x^-$  and FRP fluxes. However, differences among sites in combination with factors associated with date of sampling confound any pattern. Highly significant differences associated with salinity regime were only noted twice:  $O_2$  at Pmax and  $NO_x^-$  at Pmax. But in both cases there was also significant interaction with the date/depth treatment. For  $O_2$  there was a trend for fluxes in high salinity to exceed paired fluxes in low salinity, but no trend was discernible for  $NO_x^-$ .  $CO_2$  fluxes at Pmax demonstrated a less significant effect but no interaction. In this case low salinity regimes demonstrated greater autotrophy. Lastly, no discernible trends between regions (Virginia vs. North Carolina sites) could be noted with the exception of benthic respiration. Uptake of  $O_2$  in the dark for our North Carolina samplings tended to be higher than those for Virginia.

The patterns of flux direction vary among sites and chemical species. Masonboro and Goodwin Islands have sediments that are most likely to be autotrophic. Both are also potential sinks for  $NO_x^-$ ; but whereas Masonboro Island is also a sink for  $NH_4^+$  and FRP, Goodwin Islands are more likely to be a source for both. Sweethall and Currituck Banks have sediments which tend to be heterotrophic even though the one is largely "mud" and the other sand.  $NH_4^+$  and  $NO_x^-$  tend to be taken up by the sediments at Currituck Banks with FRP concentrations being too low to measure. At Sweethall  $NO_x^-$  is consistently effluxed, whereas the directions of  $NH_4^+$  and FRP fluxes are less predictable.



## INTRODUCTION

As a result of high and increasing human population densities in coastal areas, changes in agricultural practices and commercial/industrial development; estuaries and coastal waters are subject to historic and increasing anthropogenic impacts; generically termed "eutrophication" (Nixon, 1995). This broad term encompasses a number of environmental problems including elevated nutrient concentrations (cf. Neilson and Cronin, 1981), high water column turbidity (Meybeck et al., 1988; DeGroot and de Jonge, 1990), nuisance algal blooms (Lancelot and Mathot, 1987; Lancelot et al., 1987; Graneli et al. 1990), changes in the species composition of estuarine communities (Murray, 1983; Twilley et al., 1985), low dissolved oxygen concentrations (Taft et al., 1980; Officer et al., 1984; Seliger et al., 1985; Malone et al., 1988), fish kills (Vernberg, 1983; Connell and Miller, 1984; Turner et al., 1987), reduced fisheries yields (Seliger et al., 1985; Renaud, 1986), and unpleasant aesthetic impacts (Lancelot et al., 1987). Human activities increase both the point source and non-point source inputs of dissolved nutrients and nutrients derived from both organic and inorganic particulate matter. Particulates also affect water quality by increasing turbidity and reducing photosynthesis.

Although most studies of estuarine eutrophication have focused on the water column, estuarine sediments are an important component of the estuarine landscape. Benthic habitats support a diverse array of species, and include both heterotrophically-dominated sediments and autotrophically-dominated sediments such as those having submersed macrophyte and benthic microalgal communities (Rizzo et al., in press). The sediments are also the final (or at least long-term) repository for much of the organic matter entering the estuary or produced within it (Taft et al., 1980; Graf et al., 1982; Graf, 1987; Rudnick, 1989). In completely heterotrophic

sediments, the food and energy supply of benthic organisms is dependent on these inputs.

Aerobic heterotrophic metabolism of sediment organic matter produces two important impacts on the water column: nutrient input due to the remineralization of organic matter and the concomitant reduction of oxygen concentration due to respiration. Estuarine aquatic primary production may depend on the supply of nutrients derived from the breakdown of organic matter in the sediments (cf. Day et al., 1989). However, under high metabolic conditions in the sediments which occur in the mid to late summer months, concentrations of dissolved oxygen in the water column may be significantly reduced as nutrients are regenerated (Seliger et al., 1985; Stanley, 1985). Sediment oxygen consumption increases with increased organic input to the sediments (Taft et al., 1980; Kelly et al., 1985; Rydberg et al., 1990). The inputs derive from both external loadings (Meybeck et al., 1988; Christian et al., 1989) and sedimentation from the water column, resulting from increased primary production due to increased nutrient concentrations (Kelly et al., 1985; Rydberg et al., 1990). Thus, while heterotrophically-dominated sediments may be critical in maintaining aquatic primary and secondary production under relatively oligotrophic situations, sediment processes may also limit secondary productivity in hypereutrophic situations by creating hypoxic and/or anoxic conditions.

Autotrophically-dominated sediments are important in many estuaries as producers of organic matter and oxygen, as sinks for nutrients and as habitats for other species. Submerged macrophyte communities in the Chesapeake Bay estuary have suffered from eutrophication effects (Twilley et al., 1985). In addition to submerged macrophytes, estuarine sediments dominated by microalgal communities are quantitatively important primary producers. For instance, benthic microalgal primary productivity or biomass often equals or exceeds that of phytoplankton in many

estuaries, on a square meter basis (Pamatmat, 1968; Joint, 1978; Murray, 1983; Rizzo and Wetzel, 1985; 1986; Murray and Wetzel, 1987), and in some estuaries, benthic microalgal dominated communities can comprise between 33% to nearly 100% of the total benthos (Rizzo, 1991; Rizzo et al., 1992). In addition to high primary productivity, sediments supporting benthic microalgae can be net sources of oxygen to the water column rather than sinks (Rizzo, 1986; Rizzo et al., 1992) and release significantly less ammonium, and sometimes phosphate, to the water column than sediments dominated by heterotrophic processes (Rizzo et al., 1992). In fact, these sediments may often be nutrient sinks rather than sources (Rizzo et al., 1992). While the differences in nutrient and oxygen exchanges between heterotrophically-dominated and autotrophically-dominated sediments are striking, the characterization of these exchanges in transition zone (low light) has not been determined.

The emerging model of benthic processes regulating exchange of oxygen and nutrients and the environmental factors which affect these processes is not necessarily a simple one of balancing photosynthesis and aerobic respiration. Chemoautotrophy (e.g. nitrification), chemoheterotrophy of high C:N material (with inorganic N uptake), benthic macrofaunal metabolism and excretion, and physiochemical conditions (sediment redox conditions and position in the sediment profile) all play roles in determining the direction and quantity of exchange. In turn, the system's responses to increased turbidity and nutrient inputs are difficult to predict in transition zones. Yet the activity of sediments in these zones may determine the extent of such things as hypoxic events in a shallow estuary.

The potential impacts of a shift from autotrophic to heterotrophic sediments would have widespread impacts in some estuaries. This occurs naturally as water depth increases and light is

attenuated by the water column as a result of increasing depth. However, a trophic shift from a benthic microautotrophic community to a heterotrophic community could also result from eutrophication impacts associated with elevated nutrients, elevated turbidity, or both. Sediment heterotrophs (largely bacteria) might compete successfully for added nutrients such that disproportionately large increases in sediment microheterotrophs may bring about a trophic shift in the benthic community (Webb, 1981). Similarly, suspended particulate concentrations in the water column may increase from either direct watershed input or increased phytoplankton growth. Either factor reduces light penetration in the water column and results in reduction or elimination of benthic microalgae.

The response of benthic microalgae to eutrophication related changes in light or nutrient concentrations are not well-known. Admiraal (1977) has shown that benthic microalgal cultures can grow at high nutrient concentrations (1-10 mg-at N; ca. 1 mg-at P), although growth was severely inhibited. These concentrations are much greater than observed in even eutrophic estuarine areas (Heinle et al., 1980; Boynton and Kemp, 1985; Christian et al., 1989). In the Neuse River, North Carolina, autotrophically-dominated communities are restricted to shallower depths in the turbid, nutrient-rich oligohaline zone (occupying < 50% of the benthos) than in the relatively nutrient-poor, less turbid mesohaline areas (occupying nearly 100% of the benthos; Rizzo et al., 1992). For the York River estuary, ca. 38% of the total subtidal bottom area is potentially dominated by benthic microautotrophic communities (Rizzo, 1986). Sediment metabolic processes thus affect not only the type of benthic environment (autotrophic or heterotrophic) present in an area, but the sediment-water exchanges of nutrients. Changes in sediment metabolism are therefore important to the total estuarine ecosystem.

## OBJECTIVES & WORKING HYPOTHESES

We investigated sediment community oxygen metabolism and sediment-water exchange of nutrients (ammonium, nitrate + nitrite, and phosphate) and assessed potential eutrophication related impacts on benthic environments along natural light-depth gradients. Field studies provided baseline information on these processes, and the comparison between areas of high and low irradiance would indicate potential changes attributable to turbidity and nutrient increases in the water column. Microcosm studies involved both nutrient concentration and light manipulations. These latter studies are part of the master's thesis research of Susan K. Dailey at East Carolina University. Thus the results of the microcosm studies are presented in the thesis accompanying this report (Dailey, 1995). Field studies were conducted at four NERR sites in Virginia and North Carolina.

Stated as null hypotheses, our work addressed four questions:

1. Rates of sediment net community productivity at various light levels (1a), and rates of sediment community respiration (1b) do not vary between areas receiving high irradiance over the long term (sufficient to saturate benthic microalgal photosynthesis) and areas receiving reduced irradiance (intensities below levels of light-saturated photosynthesis).
2. The rates of nutrient exchange (ammonium, nitrate+nitrite, and phosphate) between sediments and the water column do not differ between long-term high and low light environments.

3. Rates of maximum sediment net community productivity ( $P_{max}$ )(3a) and sediment community respiration (3b) are the same for different sediment types (sand and mud), different salinity regimes, and different geographic areas.

4. The exchange rates of nutrients between sediment and water at  $P_{max}$  and in the dark are not related to salinity regime, sediment type, or geographic area.

## STUDY SITES

The North Carolina and Virginia National Estuarine Research Reserves (NERR) have preserved estuarine areas with a diversity of geomorphological, environmental and habitat characteristics in which human impacts have been minimal. Such sites allow determination of the characteristics of undisturbed estuarine areas, and provide opportunities for experimental studies of anthropogenic impacts of widespread interest to managers of coastal resources. We carried out field studies at four NERR sites: two in North Carolina and two in Virginia.

Masonboro Island (MI) comprises a barrier island-lagoon complex from subtidal sediments to salt-marsh ecosystems (Fig. 1). Salinities in the area are moderate to high, and a moderately high tide range (115 cm) results in extensive intertidal flats as well as subtidal habitats. Masonboro Sound is on North Carolina's list of "Outstanding Resource Waters". The report prepared for consideration of this status noted the "excellent water quality" of the waters behind Masonboro

Sound.

Currituck Banks (CB) is another undisturbed barrier island estuarine complex (Fig. 1). In contrast to Masonboro Island, Currituck Banks is far from any ocean inlet and consequently has a small tidal range and low salinities. The area supports both freshwater and saltmarsh vegetation, as well as an extensive maritime forest. Currituck Banks supports a high diversity of species due to the juxtaposition of northern (Virginian) and southern (Carolinian) biogeographic regions.

The Goodwin Islands (GI) site in the lower York River, Virginia comprises a polyhaline (16-22 ppt) estuarine landscape with salt marshes, forested wetlands, upland forest, submerged macrophyte beds, and intertidal and subtidal non-vegetated bottom (Fig. 2).

The Sweethall Marsh (SH) site is a tidal freshwater area (generally 0-0.5 ppt) of the Pamunkey River, a major tributary of the York River (Fig. 2). It consists of an extensive tidal freshwater marsh, intertidal flats, non-tidal bottomland hardwood forest, and upland ecosystems. In addition, the Pamunkey River remains one of the most pristine systems on the East Coast (NOAA, U.S. Dept. of Commerce and the Virginia Institute of Marine Science, 1990).

Thus, Masonboro and Currituck Sounds in North Carolina represent relatively undisturbed examples of high and low salinity lagoonal estuarine systems, respectively. Sweethall Marsh and Goodwin Islands in Virginia represent low and high salinity drowned river estuarine systems, respectively. Within each site, a diversity of habitats can be found including marshes, uplands, and both intertidal and subtidal sand and mud flats.

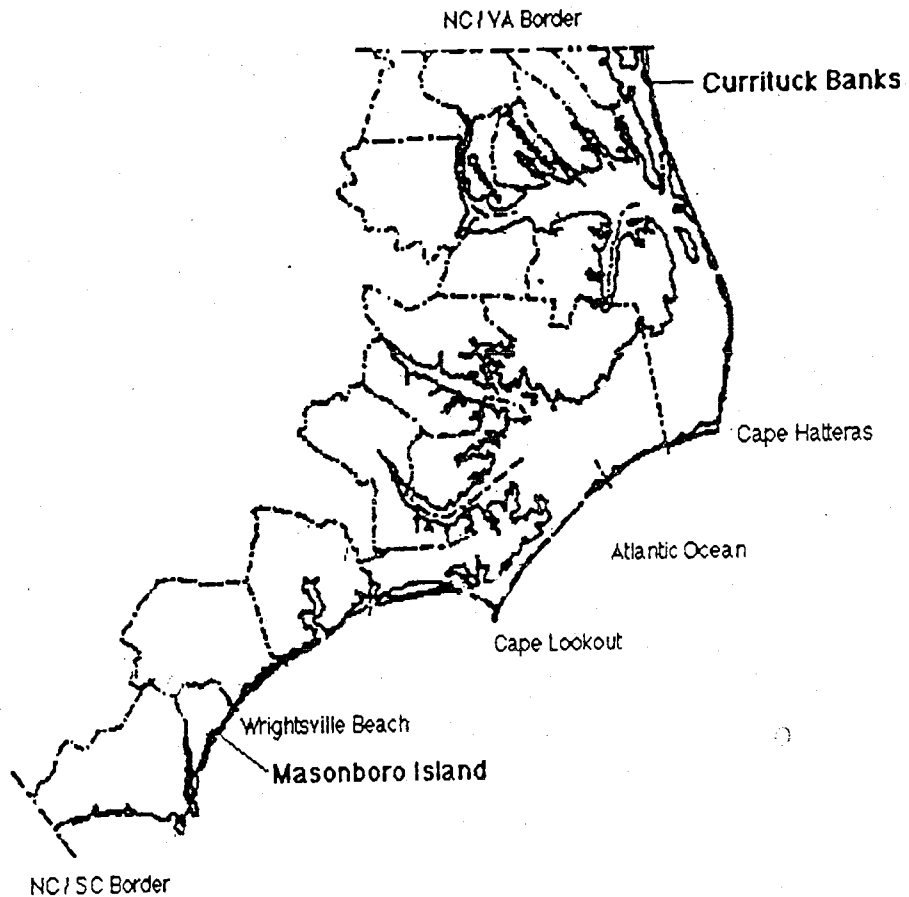


Figure 1. Location map for North Carolina National Estuarine Research Reserves showing Currituck and Masonboro study sites.



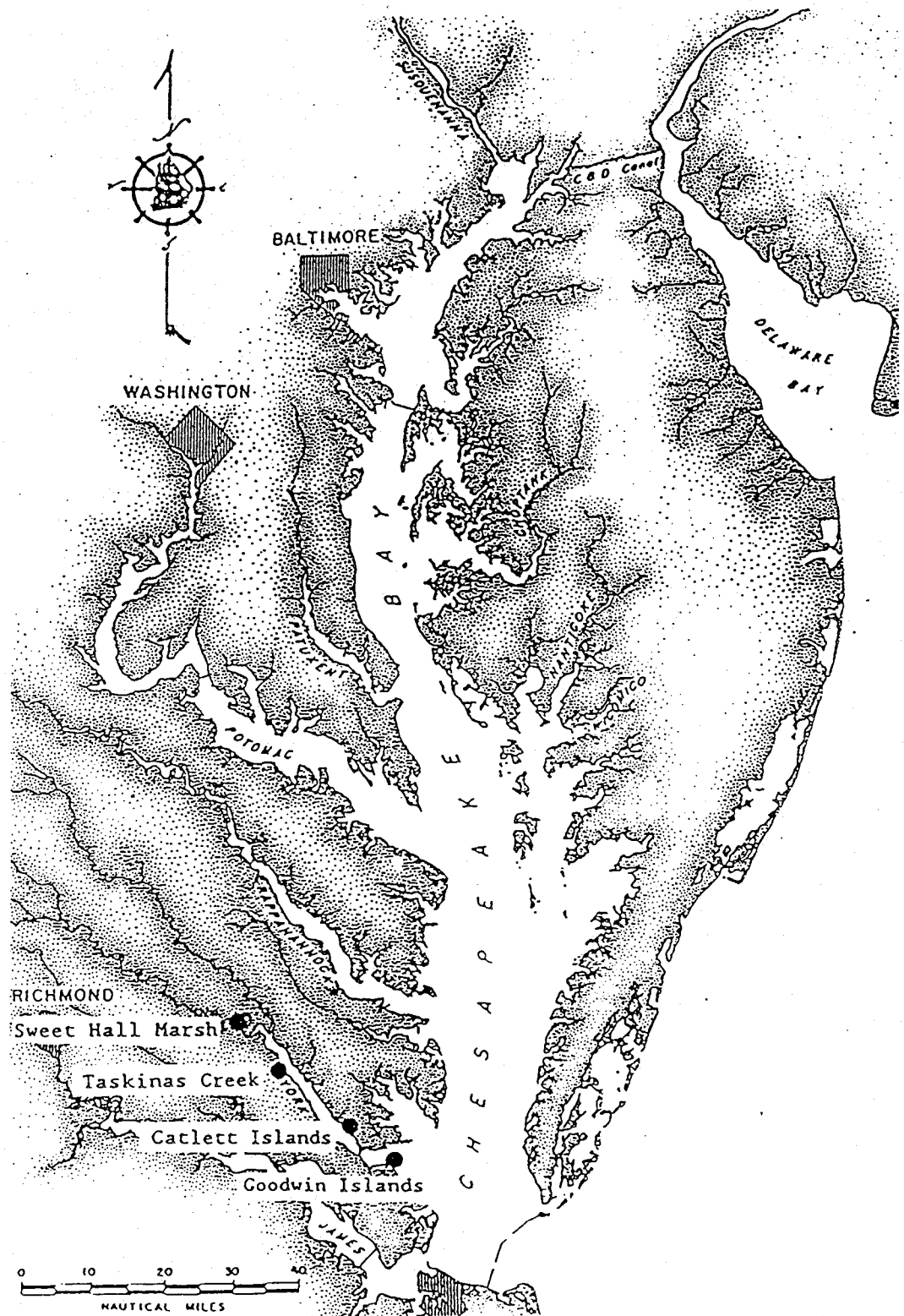


Figure 2. Location map for Virginia National Estuarine Research Reserves showing Sweet Hall Marsh and Goodwin Islands study sites.

## METHODS

### Field Studies

Sampling occurred during the periods from July through September 1992 and from July through August 1993. At each NERR site, areas of different sediment type were selected by visual inspection, or examination of sediment cores. In all but a few cases within each sediment type location, cores were taken from approximately 1 and 2 m depths. At each site measurements were taken of surface and bottom dissolved oxygen, temperature and salinity, and surface and submarine irradiance to determine water column light attenuation.

Sediment primary production and respiration rates were determined from changes in oxygen and, in some instances, carbon dioxide concentrations in light and dark core samples incubated over time. Net community production was calculated as the change in light cores from initial concentrations. Community respiration (sediment oxygen demand) was calculated as the change in concentration in dark cores compared to initial conditions. Hourly rates were determined by dividing each of the above by the incubation period. Sediment-water nutrient exchanges were calculated similarly from changes in nutrient concentrations during the same incubations.

Core incubation procedures were similar to those reported previously (Rizzo and Wetzel, 1985; Murray and Wetzel, 1987) and more recently modified by Lackey (1992) and Rizzo et al. (1992). Briefly, four plexiglass cores (37 mm dia.) containing intact sediments sampled by hand from the various sites were randomly assigned to one of the following light treatments: 100, 50, 25, and 12.5% of ambient surface irradiance for determinations of net community productivity and gross productivity, and in the dark for determinations of dark respiration. Cores were incubated under ambient temperature and light conditions in outdoor water baths. Neutral density

screening was used to achieve the given light intensities. Photosynthetically active radiation (PAR;  $\mu\text{mol photons } (\mu\text{Einsteins}) \times \text{m}^{-2} \times \text{sec}^{-1}$ ) was monitored during all incubations using a LiCor Model 185 Quantum meter equipped with a 2 pi, cosine corrected sensor. Each light-incubated core was wrapped with black rubber at the level of the sediment-water interface to prevent light from reaching the sediment from the sides. Each of these cores was sealed with rubber stoppers on either end. Cores were held under ambient temperature conditions in reduced light or dark for usually less than an hour from sampling until incubations were begun. Ambient water from each site was double-filtered: first through 1.2  $\mu\text{m}$  glass fiber filters (Whatman GF/C) and finally through 0.45  $\mu\text{m}$  membrane filters (Gelman GN-6). Filtration of site water for core incubations is preferable to corrections based on separate water column incubations because of occasional but frequent anomalous values for water column metabolic rates that lead to serious error in calculation of sediment rates. Ambient water overlying sediments in cores was withdrawn and immediately and gently replaced with filtered water. Representative cores were used for zero time measures by immediately withdrawing filtered water for analysis. Other cores were incubated for 2 to 4 hours. At that time all overlying water was withdrawn into a 60 cc syringe for analysis post incubation. Each treatment was represented by 4 cores.

Oxygen determinations were made using polarographic methods (Model 2607, Orbisphere Laboratories Inc, Geneva). The water from the syringe was carefully extruded into a centrifuge tube, the oxygen probe was inserted and the concentration was measured after the reading stabilized (ca. 1 to 2 min). A 1 ml sample was then withdrawn into a syringe for the measurement of total inorganic carbon (TIC). A stopcock sealed the water inside the syringe which was kept in the cold until analysis using a Capni-Con 4 Total  $\text{CO}_2$  Analyzer (Cameron Instruments Co., Port

Aransas, TX). The remaining water was then removed and filtered through a 0.45  $\mu\text{m}$  filter (Gelman GN-6) for storage in the cold until nutrient analyses could be run. Ammonium analyses were conducted on the day of sampling. Other analyses were conducted within a few days and kept refrigerated until time of analysis. If nitrate + nitrite ( $\text{NO}_x^-$ ) and filterable reactive phosphate (FRP) analyses could not be performed within a few days of sampling, the samples were stored frozen (ca.  $-20^\circ\text{C}$ ). Nutrient analyses followed the method of Solorzano (1969) for ammonium, Scientific Instruments Corporation (1981) for nitrate + nitrite, and U.S.E.P.A. (1979) for phosphate.

Sediments at each field site were characterized by determinations of total carbon and total nitrogen (Model 440 CEC Elemental Analyzer; Leeman Labs, 1990), and grain size (U.S.G.S., 1977). The above analyses were conducted on the surface 1 or 2 cm of representative cores.

### Statistical Methods

Data were managed using EXCEL spreadsheets, and statistical analyses were conducted using the same package. Two-way analyses of variance (ANOVAs) were used to test null hypotheses on appropriate transformed data. Fluxes could be represented as both positive (efflux from sediments) and negative (influx) values both among treatments and among replicates. Barlett's test of homogeneity of variance was used on representative results (Sokal and Rohlf, 1981), and transformations were considered warranted. To transform each variable (e.g.,  $\text{O}_2$  flux) the most negative flux over all samples was determined and one unit was subtracted from it. The absolute value of this sum was then added to all fluxes for this variable, and the natural log was taken for each resultant sum.

Details of each ANOVA design are given in the associated sections of the results. The overall logic was to pair samplings having as much in common as possible but representing alternate treatments for the main effect (e.g., sand vs. "mud" or low vs. high salinity regime). A more elaborate multiway ANOVA design was not used because: (1) environmental constraints on sampling resulted in considerable asymmetry among treatments and (2) significant interaction terms in multiway ANOVA designs are often difficult to interpret.

## RESULTS

### Environmental factors

As desired for our study, the four NERR sites represented a variety of environments as summarized in Tables 1 and 2. Salinity ranged from 1 to 23 ppt with SH and CB being oligohaline, as expected (Table 1). Light conditions during the taking of cores varied greatly among sampling dates. However, with the exception of a very dark day on 8/14/92 at CB, light was near or above photosynthetically saturating conditions for benthic microalgae during incubations. The second attempt to obtain samples at CB was in October 1992 when temperatures were less than during other sampling times.

Those sites designated as sand had % sand contents greater than 95% with the exception of two sites at CB which had somewhat lower percentages (Table 2). The designation of "mud" was less descriptive. Percent sand in these sites ranged from 8 to 95%. SH truly had muddy sediments with the majority of the sediment being clay. However, at the other locations it was difficult or impossible to find sediments with a truly small grain size.

Table 1. Summary of environmental conditions during sampling. Hydrologic variables are averaged from surface and bottom samples. Sediment type: S=sand, M=mud based on visual inspection. Light measured as photosynthetically active radiation (PAR;  $\mu\text{Einstein m}^{-2} \text{ s}^{-1}$ ). Attn. = vertical diffuse downwelling attenuation coefficient for PAR).

Site	Date	Depth (m)	Sediment Type	Temp. ( $^{\circ}\text{C}$ )	Salinity (psu)	Light (PAR)	Attn. ( $\text{m}^{-1}$ )
Goodwin	7/24/92 <sup>23</sup>	1	S	27	14		
		2	S	27	15		
	7/25/92 <sup>24</sup>	1	M	25	15		
		2	M	25	15		
	6/14/93 <sup>3</sup>	1	M	21	14	195	1.71
		2	M	22	14	230	1.82
	6/18/93 <sup>14</sup>	1	S	23	14	900	2.49
		2	S			1300	1.14
Sweethall	8/7/92 <sup>6</sup>	1	M	27	1		
		2	M	27	1		
	6/16/93 <sup>15</sup>	1	M	25	1	710	2.04
		2	M	25	1	710	2.04
Currituck	8/14/92	1	S				
	10/21/92	1	S	12		1050	2.98
		2	S			1100	4.61
	6/21/93	1	M	27	2	1250	3.29
		2	S	27	2	1400	2.21
	6/22/93	1	S				
		2	S				
	Masonboro	8/26/92	1	S	29	23	1100
2			S	29	23	1600	2.76
8/27/92		1	M	28	22	950	2.42
6/29/93		1	S				
		2	S				

Table 2. Summary of edaphic factors. Values are averages from samples of representative cores for the surface 1 cm.

Site	Date	Depth m	Sed. Type S or M*	Texture			Contents	
				Sand	Clay	Silt	C	N
				%	%	%	%	%
<b>Goodwin Islands</b>								
	7/24/92	1	S	99.1	1.6	0.6	0.12	0.00
		2	S	97.5	2.0	0.8	0.15	0.01
	7/25/92	1	M	79.6	8.8	9.0	0.61	0.06
		2	M	88.1	7.0	7.7	0.60	0.06
	6/14/93	1	M	71.7	6.1	12.2	0.60	0.05
		2	M	86.6	6.4	8.7	0.30	0.00
	6/15/93	1	S	98.5	1.1	0.7	0.06	0.00
		2	S	97.7	1.2	0.7	0.12	0.01
<b>Sweethall Marsh</b>								
	8/7/92	1	M	11.5	55.0	41.6	4.14	0.32
		2	M	13.4	53.5	29.0	2.43	0.21
	6/16/93	1	M	7.6	57.6	38.3	1.78	0.24
		2	M	8.1	59.0	36.7	1.20	0.18
<b>Currituck Banks</b>								
	8/14/92	1	S	101	0.1	0.0	0.04	0.00
	10/21/92	1	S	NA	NA	NA	NA	NA
		2	S	NA	NA	NA	NA	NA
	6/21/93	1	M	75.6	6.2	38.2	1.385	0.175
		2	S	89.8	1.8	5.5	0.11	0.01
	6/22/93	1	S	89.3	0.9	2.7	0.31	0.03
		2	S	96.0	0.6	1.7	0.10	0.00
<b>Masonboro Island</b>								
	8/26/92	1	S	98.6	1.1	0.1	0.79	0.00
		2	S	98.3	1.3	0.2	0.79	0.00
	8/27/92	1	M	94.7	4.1	3.5	0.46	0.03
	6/29/93	1	S	96.0	2.2	0.7	0.24	0.00
		2	S	97.3	1.4	0.2	0.05	0.00
* S and M refer to coarse and fine grained textures based on visual inspection.								

### Format for interpreting results

The overall purpose of this project was to evaluate the influence of factors on the relationship between autotrophy and heterotrophy (trophic status) in determining the flux of materials between sediments and water column. In assessing the influence of environmental factors on flux, we evaluated differences relative to those conditions which provided the greatest indication of autotrophy. For the fluxes of  $\text{CO}_2$ ,  $\text{NH}_4^+$ ,  $\text{NO}_x^-$ , and FRP greater uptake of the material by sediments or less release is indicative of enhanced autotrophy. For  $\text{O}_2$  flux the opposite would be true: greater release or less uptake.

This project and report are hypothesis-driven as described in the OBJECTIVES & WORKING HYPOTHESES section. As we address the hypotheses in the RESULTS section, we present data on fluxes through summaries of ANOVAs. The original data are listed in the appendix.

### Short-term light effects

Each sampling involved the incubation of sets of four cores under five conditions of light ranging from darkness to near full sunlight (totaling 20 cores). This was done (1) to assess the response of the benthic community to short-term light conditions and (2) to obtain contrasting flux results for respiration in darkness and near maximum photosynthesis ( $P_{\text{max}}$ ). Representative results are shown from a 1 m site of sandy sediments at Goodwin Islands (24 July 1992) (Fig. 3). The short-term response to light is obvious for  $\text{O}_2$  and  $\text{CO}_2$  fluxes (Fig. 3a). A light response was not always found, however (Fig. 3b). Summaries of 2-way ANOVAs for each measured flux type with depth and incubation light condition are shown in Tables 3, 4, 5, 6 and 7 for  $\text{O}_2$ ,  $\text{CO}_2$ ,  $\text{NH}_4^+$ ,



# Goodwin Islands

1m Sand Site; 24 June 1992

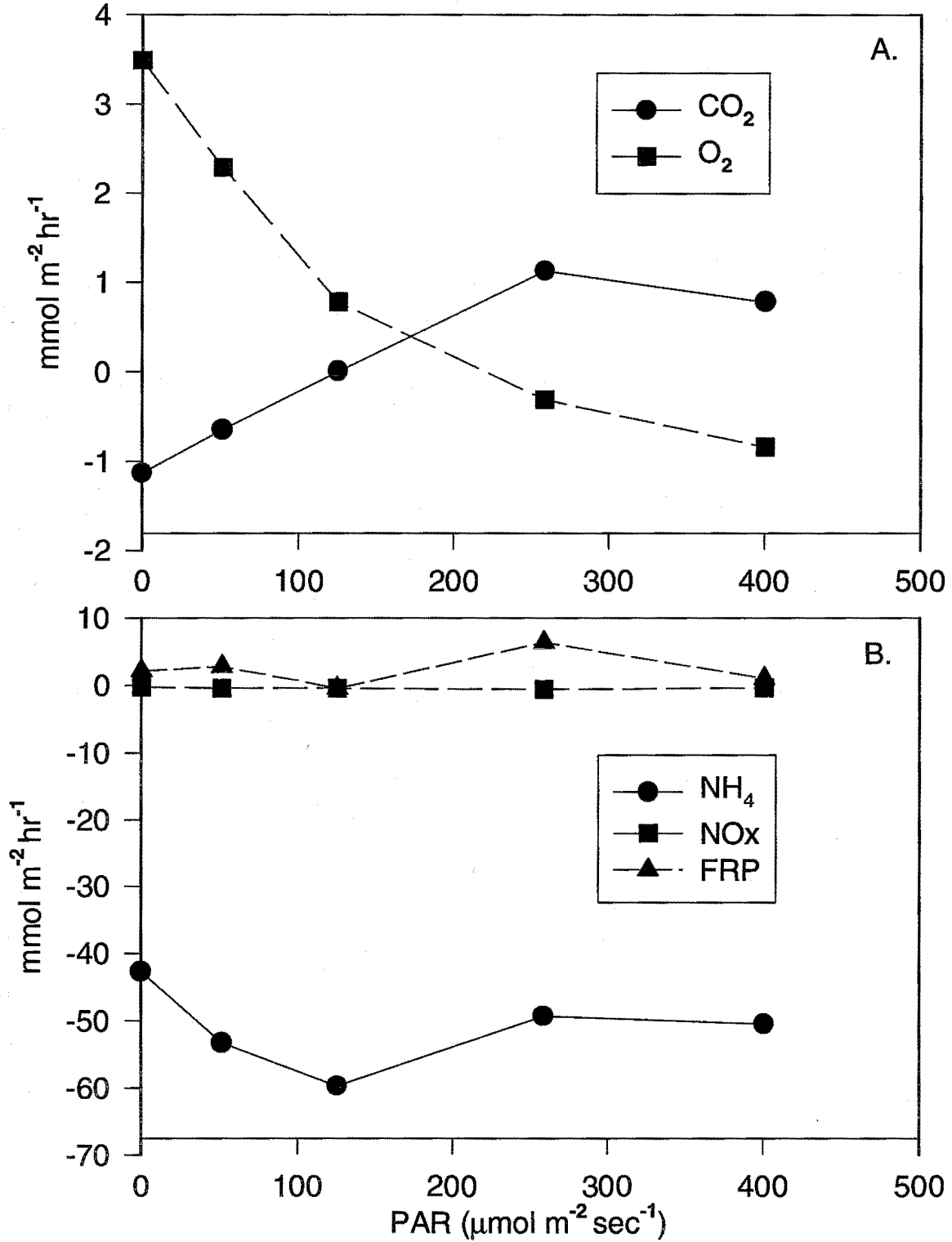


Figure 3.  $\text{O}_2$  and  $\text{CO}_2$  (A) and nutrient (B) exchanges relative to PAR intensity for shallow sand sediment from Goodwin Islands.

Table 3. Summary of analyses of variance addressing the null hypothesis that oxygen flux is independent of long-term light regime (as indexed through depth of sampling). The ANOVAs are two-way such that incubation light conditions are considered also. A "\*" and **bolded** entry indicates significance at  $p \leq 0.01$ .

Site	Date	Sed. Type S or M**	p among Depths	p among PAR	p interact.
<b>Goodwin Islands</b>					
	7/24/92	S	1.99e-02	<b>*6.54e-12</b>	7.44e-01
	7/25/92	M	<b>*2.50e-04</b>	2.80e-02	3.36e-01
	6/14/93	M	<b>*9.24e-14</b>	<b>*2.03e-09</b>	<b>*4.60e-03</b>
	6/15/93	S	<b>*2.86e-03</b>	<b>*5.98e-13</b>	5.53e-02
<b>Sweethall Marsh</b>					
	8/7/92	M	<b>*1.06e-03</b>	4.77e-01	1.12e-01
	6/16/93	M	2.33e-01	3.29e-01	4.71e-01
<b>Currituck Banks</b>					
	8/14/92	S			
	10/21/92	S	1.35e-02	8.81e-01	8.71e-01
	6/21/93	M			
	6/22/93	S	3.45e-01	<b>*1.41e-03</b>	5.61e-02
<b>Masonboro Island</b>					
	8/26/92	S	8.94e-01	<b>*3.06e-13</b>	9.82e-01
	8/27/92	M			
	6/29/93	S	9.75e-01	<b>*7.02e-13</b>	3.88e-01
** S and M refer to coarse and fine grained textures based on visual inspection.					

Table 4. Summary of analyses of variance addressing the null hypothesis that inorganic carbon flux is independent of long-term light regime (as indexed through depth of sampling). The ANOVAs are two-way such that incubation light conditions are considered also. A "\*" and **bolded** entry indicates significance at  $p \leq 0.01$ .

Site	Date	Sed. Type S or M**	P among Depths	p among PAR	p interact.
<b>Goodwin Islands</b>					
	7/24/92	S	<b>*6.65e-07</b>	<b>*2.63e-10</b>	3.25e-01
	7/25/92	M	<b>*1.22e-06</b>	2.68e-02	1.20e-01
	6/14/93	M			
	6/15/93	S	<b>*8.89e-05</b>	<b>*3.44e-03</b>	2.01e-02
<b>Sweethall Marsh</b>					
	8/7/92	M	2.90e-01	7.78e-01	<b>*6.22e-03</b>
	6/16/93	M			
<b>Currituck Banks</b>					
	8/14/92	S			
	10/21/92	S	4.53e-01	3.49e-01	3.64e-01
	6/21/93	M			
	6/22/93	S	1.32e-01	5.11e-02	3.35e-02
<b>Masonboro Island</b>					
	8/26/92	S			
	8/27/92	M			
	6/29/93	S	7.71e-01	<b>*6.78e-11</b>	1.80e-01
** S and M refer to coarse and fine grained textures based on visual inspection.					

Table 5. Summary of analyses of variance addressing the null hypothesis that ammonium flux is independent of long-term light regime (as indexed through depth of sampling). The ANOVAs are two-way such that incubation light conditions are considered also. A "\*" and **bolded** entry indicates significance at  $p \leq 0.01$ .

Site	Date	Sed. Type S or M**	p among Depths	p among PAR	p interact.
<b>Goodwin Islands</b>					
	7/24/92	S	3.47e-01	<b>*9.27e-03</b>	7.41e-01
	7/25/92	M	1.76e-02	1.90e-01	4.85e-01
	6/14/93	M	<b>*1.31e-05</b>	<b>*2.00e-05</b>	7.83e-02
	6/15/93	S	5.43e-01	4.03e-02	8.65e-01
<b>Sweethall Marsh</b>					
	8/7/92	M	<b>*7.31e-04</b>	4.75e-01	5.29e-01
	6/16/93	M	4.75e-01	5.86e-02	5.71e-01
<b>Currituck Banks</b>					
	8/14/92	S			
	10/21/92	S	2.10e-02	5.65e-01	5.71e-01
	6/21/93	M			
	6/22/93	S	1.79e-01	1.98e-02	4.97e-01
<b>Masonboro Island</b>					
	8/26/92	S	9.31e-01	4.20e-02	6.47e-01
	8/27/92	M			
	6/29/93	S	4.64e-01	1.74e-01	9.25e-01
** S and M refer to coarse and fine grained textures based on visual inspection.					

Table 6. Summary of analyses of variance addressing the null hypothesis that nitrate plus nitrite flux is independent of long-term light regime (as indexed through depth of sampling). The ANOVAs are two-way such that incubation light conditions are considered also. A "\*" and **bolded** entry indicates significance at  $p \leq 0.01$ .

Site	Date	Sed. Type S or M**	p among Depths	p among PAR	p interact.
<b>Goodwin Islands</b>					
	7/24/92	S	<b>*1.76e-22</b>	3.66e-01	5.46e-01
	7/25/92	M	6.90e-01	2.73e-01	6.40e-01
	6/14/93	M	5.02e-01	1.93e-01	2.36e-01
	6/15/93	S	7.38e-01	3.39e-02	5.04e-01
<b>Sweethall Marsh</b>					
	8/7/92	M	<b>*2.29e-03</b>	4.82e-01	6.24e-01
	6/16/93	M	4.32e-01	3.26e-01	2.23e-01
<b>Currituck Banks</b>					
	8/14/92	S			
	10/21/92	S	<b>*7.96e-05</b>	7.38e-01	1.62e-01
	6/21/93	M			
	6/22/93	S	9.96e-01	5.09e-01	8.36e-01
<b>Masonboro Island</b>					
	8/26/92	S	<b>*5.37e-03</b>	2.60e-01	2.39e-01
	8/27/92	M			
	6/29/93	S	3.99e-01	9.81e-02	5.81e-01
** S and M refer to coarse and fine grained textures based on visual inspection.					

Table 7. Summary of analyses of variance addressing the null hypothesis that filterable reactive phosphate flux is independent of long-term light regime (as indexed through depth of sampling). The ANOVAs are two-way such that incubation light conditions are considered also. A "\*" and **bolded** entry indicates significance at  $p \leq 0.01$ .

Site	Date	Sed. Type	p among Depths	p among PAR	p interact.
<b>Goodwin Islands</b>					
	7/24/92	S	1.27e-02	<b>*4.00e-03</b>	2.58e-01
	7/25/92	M	8.97e-02	6.42e-01	6.14e-01
	6/14/93	M	<b>*5.69e-03</b>	2.46e-01	7.36e-01
	6/15/93	S	1.16e-01	1.09e-01	1.66e-01
<b>Sweethall Marsh</b>					
	8/7/92	M	<b>*2.35e-03</b>	1.64e-01	1.18e-01
	6/16/93	M			
<b>Currituck Banks</b>					
	8/14/92	S			
	10/21/92	S			
	6/21/93	M			
	6/22/93	S			
<b>Masonboro Island</b>					
	8/26/92	S	<b>*7.33e-09</b>	<b>*2.15e-04</b>	<b>*4.04e-03</b>
	8/27/92	M			
	6/29/93	S	9.49e-01	3.45e-01	2.58e-01

\* S and M refer to coarse and fine grained textures based on visual inspection.

Table 8. Summary of analyses of variance addressing the null hypothesis that fluxes are independent of short term light regime. A "\*" is significance at  $p \leq 0.05$ , a "\*\*\*" is significance at  $p \leq 0.01$ , a blank is not significant, and NA is not available. I is interaction significant at  $p \leq 0.05$ , II at  $p \leq 0.01$ . (L>D) represents flux in light more "autotrophic" than in dark. (D>L) represents flux in light more "heterotrophic" than in dark.

Site	Date	Sed. Type	O2	CO2	NH4
		S or M*	"	"	"
<b>Goodwin Islands</b>					
	7/24/92	S	** (L>D)	** (L>D)	** (L>D)
	6/15/93	S	** (L>D)	** I	* (L>D)
<b>Currituck Banks</b>					
	10/21/92	S			
	6/22/93	S	** (L>D)	I	* (L>D)
<b>Masonboro Island</b>					
	8/26/92	S	** (L>D)	NA	* (L>D)
	6/29/93	S	** (L>D)	** (L>D)	
<b>Goodwin Islands</b>					
	7/25/92	M	* (L>D)	* (L>D)	
	6/14/93	M	** II	NA	** I
<b>Sweethall Marsh</b>					
	8/7/92	M		II	
	6/16/93	M		NA	
* S and M refer to coarse and fine grained textures based on visual inspection.					

$\text{NO}_x^-$ , and FRP, respectively. These have been further summarized for the incubation light treatment in Table 8. (The complete listing of mean flux values is given in the Appendix).

Effects were more commonly significant in sand than "mud" sites and more commonly significant with  $\text{O}_2$ ,  $\text{CO}_2$  and  $\text{NH}_4^+$  fluxes than with  $\text{NO}_x^-$  or FRP fluxes. In most cases the pattern of effect was associated with greater autotrophy in the light compared to the dark. However, significant interaction terms associated with the depth treatment were found in 5 analyses; and for the one significant incubation light effect with  $\text{NO}_x^-$ , the direction was reversed from that expected.

Although there were confounding factors and nonsignificant incubation light effects, the general patterns of response are shown in Figure 3.  $P_{\text{max}}$  values, as measured by  $\text{O}_2$  or  $\text{CO}_2$  fluxes, were often reached under our incubation conditions.  $\text{CO}_2$  and  $\text{NH}_4^+$  patterns were similar and often mirrored the curve for  $\text{O}_2$  flux.  $\text{NO}_x^-$  and FRP fluxes were less affected by incubation light conditions.

#### Depth or long-term light effects

Hypotheses 1 and 2 were evaluated using a series of 2-way ANOVAs with depth sampled and incubation light conditions as the 2 treatments. To test the null hypothesis that sediment net community productivity was not different between depths (Hypothesis 1a), we analyzed  $\text{O}_2$  and  $\text{CO}_2$  results from each day's sampling in which both deep and shallow samplings were made from the same sediment type (Tables 3 and 4). Individual core fluxes within a light and depth treatment were used as replicates. Although GI demonstrated a depth effect on all days tested, consistent differences were not noted at other sites. Significant effects were only seen for  $\text{O}_2$  flux at SH and CB in 1992 but not 1993. In 5 of 7 cases at GI when significance was found, the deeper site had



the higher productivities (Table 9). The reverse was true for other significant conditions.

To isolate the possibility that a depth effect may occur for respiration (Hypothesis 1b) separate from one for primary productivity, we conducted a second group of 2-way ANOVAs. In this case our treatments were date and depth. Further, we did separate ANOVAs for sand and "mud" sediments and used fluxes from individual cores as replicates. Three to 6 dates were used for each ANOVA. Respiration, measured as either  $O_2$  or  $CO_2$  flux in the dark, did not demonstrate a significant depth effect under any conditions (Table 10).

Hypothesis 2 was analyzed in the same manner as Hypothesis 1a but for  $NH_4^+$ ,  $NO_x^-$ , and FRP fluxes. Separate ANOVAs were calculated for each date when two depths were sampled of the same sediment type. Treatments were incubation light condition and depth with individual core values as replicates.

Fluxes of  $NH_4^+$  were largely independent of depth for sand habitats but significant differences were found on 3 of 4 dates in "mud" (Tables 5 and 9). When differences were most significant ( $p \leq 0.01$ ), the shallow depth displayed the more autotrophic pattern. This was not the case on the 2 occasions when significance was at the 0.05 level.

Depth effects occurred for  $NO_x^-$  fluxes on 4 occasions of the 10 analyzed (Tables 6 and 9). They occurred once at each of the NERR sites, were all highly significant, and indicated greater autotrophy in the shallow sediments. FRP fluxes demonstrated significant depth effects on 4 of 7 occasions (Tables 7 and 9). At CB the ambient concentrations of FRP were below the limits of detection. Highly significant interaction occurred in MI sand in 1992, significant effects in SH "mud" and GI sand had deep sediments more autotrophic, and the reverse occurred in GI mud.

Overall, the greatest frequency of depth effects across all variables was at GI (Table 9). Other

Table 9. Summary of analyses of variance addressing the null hypothesis that fluxes are independent of long-term light regime (as indexed through sampling depth). A “\*” is significance at  $p \leq 0.05$ , a “\*\*” is significance at  $p \leq 0.01$ , a blank is not significant, and NA is not available. I and II indicate significant interaction at  $p \leq 0.05$  and  $0.01$ , respectively. A (1>2) and (2>1) entry refers to depth comparison relative to autotrophic status.

Site	Date	Sed. Type S or M'	O2	CO2	NH4
<b>Goodwin Islands</b>					
	7/24/92	S	*(2>1)	** (2>1)	
	6/15/93	S	** (2>1)	**I(1>2)	
<b>Currituck Banks</b>					
	10/21/92	S	*(1>2)		
	6/22/93	S		I	
<b>Masonboro Island</b>					
	8/26/92	S		NA	
	6/29/93	S			
<b>Goodwin Islands</b>					
	7/25/92	M	** (2>1)	** (2>1)	*(2>1)
	6/14/93	M	**II(1>2)	NA	**I(1>2)
<b>Sweethall Marsh</b>					
	8/7/92	M	** (1>2)	II	** (1>2)
	6/16/93	M		NA	

' S and M refer to coarse and fine grained textures based on visual inspection.

Table 10. Summary of analyses of variance addressing the null hypothesis that community respiration is independent of long term light regime (i.e., depth). Two way ANOVAs included depth and date as treatments. Data were separated by sediment texture for separate analyses. A “\*\*” and **bolded** entry indicates significance at  $p \leq 0.01$ .

	Sediment	Variable	Number	p	p
	Type		of	among	among
	S or M**		Dates	Depths	Dates
	S	O <sub>2</sub>	6	1.28e-01	<b>*1.11e-04</b>
	M	O <sub>2</sub>	4	8.11e-01	<b>*1.41e-03</b>
	S	CO <sub>2</sub>	3	2.77e-01	1.12e-02
	M	CO <sub>2</sub>	4	2.49e-01	<b>*7.55e-11</b>

\*\* S and M refer to coarse and fine grained textures based on visual inspection.

sites had significant effects for one half or less of the analyses. "Mud" sites tended to demonstrate effects more often and with greater significance than sand sites. With the exception of GI, shallow (1 m) depths tended to be more "autotrophic" than 2 m deep sediments. In 1992 at GI, numerous effects demonstrated that deeper sediments were more autotrophic.

### Sediment type effects

Hypotheses 3 and 4 describe outcomes relative to sediment type, salinity regime and geographic region. Hypothesis 3 relates to effects on productivity and respiration (as measured with  $O_2$  and  $CO_2$ ), whereas hypothesis 4 relates to effects on fluxes of  $NH_4^+$ ,  $NO_x^-$  and FRP. As incubations that would allow for hypothesis testing were conducted on separate days, and light conditions differed among sampling dates; a normalization procedure was employed. We chose to test the hypotheses with two sets of cores from each appropriate date and site combination. For a given sampling one set was from dark incubations; the other was the set of cores under the incubation light condition that provided the maximum efflux of  $O_2$  (or minimum influx)(Pmax). All fluxes associated with those cores were used in ANOVAs even if maximum flux was not achieved for that chemical species.

Sediment type, salinity regime and geographic region were all considered as paired conditions: sand vs. "mud", oligohaline vs. mesohaline, and Virginia vs. North Carolina, respectively. Two-way ANOVAs were employed having sampling date and depth pairs as one treatment and the appropriate condition of potential effect as the second treatment (e.g., sediment type). For testing the effects of sediment type, pairings involved consecutive dates from the same NERR site and depth in which we sampled different sediment types on each date .

Table 11. Summary of analyses of variance addressing the null hypothesis that material flux is independent of sediment type (sand vs. "mud"). Two way ANOVAs included sediment type and date/depth as treatments. Fluxes designated as Pmax were associated with maximum O2 efflux, and fluxes designated as R for respiration were from dark incubations. A "\*" and **bolded** entry indicates significance at  $p \leq 0.01$ .

	Flux		Number	p	p
	Type	Variable	of	among	among
			Date	Sed. Type	Date
			/Depths		/Depths
	Pmax	O2	6	<b>*1.14e-09</b>	<b>*1.04e-16</b>
	R	O2	6	4.72e-01	<b>*1.16e-03</b>
	Pmax	CO2	3	<b>*2.15e-04</b>	<b>*3.13e-07</b>
	R	CO2	3	<b>*7.91e-07</b>	1.65e-02
	Pmax	NH4	6	<b>*2.86e-07</b>	1.24e-01
	R	NH4	6	<b>*2.44e-07</b>	<b>*4.48e-03</b>
	Pmax	NOx	6	6.39e-01	4.86e-01
	R	NOx	6	3.16e-01	1.05e-01
	Pmax	FRP	5	9.22e-02	<b>*9.52e-05</b>
	R	FRP	5	1.75e-02	1.65e-01

Net community productivity, as measured as Pmax fluxes of both O<sub>2</sub> and CO<sub>2</sub>, was significantly affected by sediment type (Hypothesis 3a) (Table 11). However, all ANOVAs had highly significant interaction terms such that no directional distinction could be made consistently. NCP as measured by O<sub>2</sub> tended to be higher in sand than "mud"; but as measured by CO<sub>2</sub>, productivity was greater in "mud" in 2 of 3 pairings.

The impact of sediment type on respiration was evaluated in two ways (Hypothesis 3b). As measured by CO<sub>2</sub>, it was significantly affected by sediment type but again with significant interaction (Table 11). Generally the greater respiration occurred in sand, but incubations of "mud" at GI in 1992 gave anomalous negative fluxes (influxes to the sediment in the dark). No significant difference was found between sediment types for respiration as measured by O<sub>2</sub> flux in the dark. Interaction was significant as was a date effect. In fact, all four O<sub>2</sub> and CO<sub>2</sub> flux ANOVAs had a significant, but uninteresting, date effect.

Sediment type effects on other fluxes involved ANOVAs of both dark fluxes and when O<sub>2</sub> was Pmax (Hypothesis 4) (Table 11). Effects of sediment were highly significant for NH<sub>4</sub><sup>+</sup> flux both at Pmax and in the dark. Both ANOVAs, also, had highly significant interactions. No consistent pattern relative to sediment type and direction or magnitude of effect could be seen. No significant effects of any kind were noted for NO<sub>x</sub><sup>-</sup> fluxes. An effect was found for FRP flux in the dark (0.05 < p < 0.01), but not at Pmax. Although there was no significant interaction, a pattern of effect is not discernible.

In summary sediment effects were notable on O<sub>2</sub>, CO<sub>2</sub> and NH<sub>4</sub><sup>+</sup> fluxes and less so on NO<sub>x</sub><sup>-</sup> and FRP fluxes. However, differences among sites in combination with factors associated with date of sampling confound any pattern development.

### Salinity Effects

To assess the influence of salinity regime on material flux, we conducted a series of two-way ANOVAs on data from dark incubations and at Pmax. Samplings were paired between GI and SH and between SH and MI. Pairings involved data from core sets having similar depths and sediment types from the closest dates. For example data from 1 m "mud" sediments from GI in 1992 were paired with those from 1 m "mud" from SH during the same year. The four cores in a sampling were considered replicates. For O<sub>2</sub>, NH<sub>4</sub><sup>+</sup> and NO<sub>x</sub><sup>-</sup> fluxes eight pairings were used.

Highly significant differences associated with salinity regime were only noted twice: O<sub>2</sub> at Pmax and NO<sub>x</sub><sup>-</sup> at Pmax (Table 12). But in both cases there was also significant interaction with the date/depth treatment. For O<sub>2</sub> there was a trend for fluxes in high salinity to exceed paired fluxes in low salinity, but no trend was discernible for NO<sub>x</sub><sup>-</sup>. CO<sub>2</sub> fluxes at Pmax demonstrated a less significant effect but no interaction. In this case low salinity regimes demonstrated greater autotrophy.

### Geographic Region Effects

The last potential influence considered was that associated with the geographical differences between the Virginia and North Carolina NERR sites. We tested pairings of comparable depth, sediment type, and year of sampling for the two sites possessing similar salinity regimes across geographical regions (i.e., GI with MI and SH with CB). Again fluxes in darkness and at Pmax were considered separately. Because of the dominance of sand at CB and "mud" at SH, only one pairing existed between these sites. Five pairings of the six in the ANOVAs were between GI and MI. Further, only O<sub>2</sub>, NH<sub>4</sub><sup>+</sup> and NO<sub>x</sub><sup>-</sup> fluxes were represented at both pairings.

Table 12. Summary of analyses of variance addressing the null hypothesis that material flux is independent of salinity regime. Two way ANOVAs included salinity regime and depth/date as treatments. Fluxes designated as Pmax were associated with maximum O2 efflux, and fluxes designated as R for respiration were from dark incubations. A "\*" and **bolded** entry indicates significance at  $p \leq 0.01$ .

Flux Type	Variable	Number of Date /Depths	p among Salinity Regime	p among Dates /Depths
Pmax	O2	8	<b>*1.17e-18</b>	<b>*7.75e-10</b>
R	O2	8	3.09e-01	<b>*9.50e-06</b>
Pmax	CO2	5	3.33e-02	1.61e-01
R	CO2	5	6.23e-02	3.99e-02
Pmax	NH4	8	1.32e-01	<b>*3.71e-04</b>
R	NH4	8	1.17e-01	<b>*1.83e-10</b>
Pmax	NOx	8	<b>*3.53e-10</b>	<b>*7.04e-20</b>
R	NOx	8	8.13e-02	<b>*2.80e-03</b>
Pmax	FRP	2	NA	NA
R	FRP	2	NA	NA

H is high and L is low salinity regime.



Table 13 . Summary of analyses of variance addressing the null hypothesis that material flux is independent of geographic region (VA vs. NC). Two way ANOVAs included region and date/depth as treatments. Fluxes designated as Pmax were associated with maximum O2 efflux, and fluxes designated as R for respiration were from dark incubations. A “\*” and **bolded** entry indicates significance at  $p \leq 0.01$ .

Flux Type	Variable	Number of Date /Depths**	p among Region	p among Date /Depths
Pmax	O2	6	<b>*6.79e-10</b>	<b>*2.69e-15</b>
R	O2	6	<b>*4.12e-09</b>	<b>*3.56e-04</b>
Pmax	CO2	3	NA	NA
R	CO2	3	NA	NA
Pmax	NH4	6	1.07e-01	<b>*5.01e-03</b>
R	NH4	6	<b>*8.94e-03</b>	<b>*1.16e-06</b>
Pmax	NOx	6	1.20e-01	4.78e-01
R	NOx	6	<b>*7.11e-03</b>	5.87e-02
Pmax	FRP	5	NA	NA
R	FRP	5	NA	NA

\*\* Only ANOVAs using both locations within a region were used. These included 5 samplings from a match of GI with MI and 1 sampling from a match of SH and CB.

Four variables of the 6 tested showed significant "regional" effects at  $p < 0.01$ : dark fluxes (R) for  $O_2$ ,  $NH_4^+$  and  $NO_x^-$ ; and Pmax for  $O_2$  (Table 13). However, highly significant interactions were also found for each. No discernible trends between regions could be noted with the exception of benthic respiration. Uptake of  $O_2$  in the dark for our North Carolina samplings tended to be higher than those for Virginia.

## DISCUSSION

There is a growing literature on material fluxes between sediments and water column where light may directly influence rates and direction of fluxes (e.g., Rizzo and Wetzel, 1986; Rizzo et al., 1992). This work adds to that general knowledge through the examination of fluxes at four NERR sites. In doing so, we also have assessed the potential for shallow sediments to impact nutrient cycling and productivity at these sites and the influences that various environmental factors have on that potential. What has become obvious, from our work here and elsewhere, and that of others, is that there is no simple set of conditions that predict fluxes with a high degree of accuracy. Rather, regulation of flux direction and magnitude results from the interaction of a host of factors both biotic and abiotic and in, on and above the sediment surface. Herein we discuss our findings with respect to the influences of short-term irradiance, depth (and hence long-term irradiance), sediment type, salinity regime and geographic region.

The success in evaluating the various environmental factors was dependent upon our sampling representative sediments at each NERR site. There arose limitations to the symmetrical experimental design originally planned. With the exception of SH, sampled sediments had high sand contents. This was true even for those considered "mud." GI was the only site where two

sediment types could be distinguished and sampled for both depths during both years. Second, weather prevented adequate sampling at CB. This NERR site resides on the eastern side of Currituck Sound, whereas the most convenient boat ramp is on the western side. With the shallow depth and large fetch of the Sound, travel to the site is problematic. Lastly, at MI truly "mud" sediments were only up creeks which are hard to approach on low tides. As a result of these limitations some factors were better evaluated for influence on fluxes than others.

Short-term and long-term light conditions were best evaluated. Sediment type was adequately evaluated, but salinity regime and geographic region were not as well tested.

Overall, significant effects of short-term light conditions were common for fluxes of  $O_2$ ,  $CO_2$ , and  $NH_4^+$ , but less so for  $NO_x^-$  and FRP. The greatest frequency of depth (long-term light) effects across all variables was at Goodwin Islands. Other sites had significant effects for one half or less of the analyses. "Mud" sites tended to demonstrate effects more often and with greater significance than sand sites. With the exception of Goodwin Islands, shallow (1 m) depths tended to be more "autotrophic" than 2 m deep sediments. In 1992 at Goodwin Islands, numerous effects demonstrated that deeper sediments were more autotrophic. Effects of sediment type (sand vs. "mud") were notable on  $O_2$ ,  $CO_2$  and  $NH_4^+$  fluxes and less so on  $NO_x^-$  and FRP fluxes. However, differences among sites in combination with factors associated with date of sampling confound any pattern. Highly significant differences associated with salinity regime were only noted twice:  $O_2$  at Pmax and  $NO_x^-$  at Pmax. But in both cases there was also significant interaction with the date/depth treatment. For  $O_2$  there was a trend for fluxes in high salinity to exceed paired fluxes in low salinity, but no trend was discernible for  $NO_x^-$ .  $CO_2$  fluxes at Pmax demonstrated a less significant effect but no interaction. In this case low salinity regimes demonstrated greater

autotrophy. Lastly, no discernible trends between regions (Virginia vs. North Carolina sites) could be noted with the exception of benthic respiration. Uptake of  $O_2$  in the dark for our North Carolina samplings tended to be higher than those for Virginia.

#### Directional considerations

All of the fluxes measured in the dark and at  $P_{max}$  were reduced to the direction relative to the sediment surface: + is effluxed into the water column and - is influxed into the sediment (Table 14). As stated previously, efflux of  $O_2$  and influx of the other chemical species constituted net autotrophy. The reverse directions were considered net heterotrophy. We assessed the directions of flux as another, less formal, form of meta-analysis. Patterns were evident that were site specific. These patterns demonstrate how difficult it is to develop predictive capabilities in determining direction let alone rates of exchange for specific nutrient and gas species..

Although  $O_2$  always influxed in the dark, as expected, efflux at  $P_{max}$  only occurred in slightly over one half of the samplings. MI showed the shift from heterotrophy to autotrophy in every case, GI showed it in sand always and twice in "mud." In contrast the sandy sediments of CB never showed an efflux of  $O_2$ . Wind mixing across the shallow sound may maintain turbidity levels that prevents the establishment of an extensive microalgal assemblage. The mud of SH demonstrated the shift in only one sampling. Thus it appears that sand sediments are more likely to act as sources of  $O_2$  to the water column than "mud" sediments under comparable conditions.

The results with  $CO_2$  were less conclusive. On 6 occasions there was a influx of  $CO_2$  in the dark. This may result from chemolithotrophy, chemical disequilibrium within the inorganic carbon couplings or some unexplained methodological problem. Influx or efflux could occur in the light

Table 14. Summary of directions of fluxes in darkness (first sign) and at Pmax (second sign). A "+" is efflux and a "-" is influx to sediments.

Site	Date	Depth	Sed. Type S or M*	Directional Flux				
				O2	CO2	NH4	NOx	FRP
		m						
<b>Goodwin Islands</b>								
	7/24/92	1	S	-/+	+/-	-/-	-/-	+/+
		2	S	-/+	+/-	-/-	+/+	+/+
	7/25/92	1	M	-/-	-/-	+/+	-/-	+/+
		2	M	-/+?	-/-	+/+	-/-	+/-
	6/14/93	1	M	-/+	NA	+/-	-/-	-/-
		2	M	-/-	NA	+/+	-/-	+/+
	6/15/93	1	S	-/+	-/-	+/+	-/-	-/+
		2	S	-/+	+/-	+/+	-/-	-/-
<b>Sweethall Marsh</b>								
	8/7/92	1	M	-/+	-/-	+/-	+/+	-/+
		2	M	-/-	-/-	+/+	+/+	-/-
	6/16/93	1	M	-/-	NA	+/-	+/+	NA
		2	M	-/-	NA	-/-	+/+	NA
<b>Currituck Banks</b>								
	8/14/92	1	S	NA	NA	NA	NA	NA
	10/21/92	1	S	-/-	+/+	-/-	-/-	NA
		2	S	-/-	+/+	-/-	-/-	NA
	6/21/93	1	M	-/-	+/+	+/-	-/+	NA
		2	S	-/-	+/-	-/-	-/-	NA
	6/22/93	1	S	-/-	+/-	+/-	-/-	NA
		2	S	-/-	+/+	+/-	-/-	NA
<b>Masonboro Island</b>								
	8/26/92	1	S	-/+	NA	-/-	+/-	-/-
		2	S	-/+	-/-	-/-	+/+	-/-
	8/27/92	1	M	-/+	NA	-/+	-/-	+/-
	6/29/93	1	S	-/+	+/-	-/+	-/+	-/-
		2	S	-/+	+/-	-/-	-/+	-/-

\* S and M refer to coarse and fine grained textures based on visual inspection.

at Pmax (as determined by O<sub>2</sub>). In keeping with the results with O<sub>2</sub>, MI and GI were autotrophic at Pmax. Influx was also observed at the other sites, but with 4 samplings at CB efflux continued at Pmax. Again the sediments at CB are seen as net heterotrophic.

Patterns associated simply with photosynthesis and respiration are less evident with the three micronutrients. At GI and SH, NH<sub>4</sub><sup>+</sup> generally effluxed in both the dark and at Pmax. In contrast at MI and CB, NH<sub>4</sub><sup>+</sup> generally influxed. Thus the direction was not necessarily the opposite of that for O<sub>2</sub>, the same as CO<sub>2</sub>, or linked to sediment type. A regional difference might be noted, but acceptance of such an association would require more consideration.

NO<sub>x</sub><sup>-</sup> fluxes appeared largely independent of incubation light conditions and were highly site specific in pattern. GI and CB were sites of nearly uniform influx, and at MI fluxes evenly distributed between in and out of sediments. However, only effluxes were found at SH. The sediments at SH had the least sand and most silt and clay contents which would be conducive to anaerobiosis near the sediment surface. One would normally consider that such conditions would limit nitrification relative to sandy sediments. Yet the efflux may indicate that such muds support considerable nitrification. Further, as these sediments were heterotrophic, there would be a supply of NH<sub>4</sub><sup>+</sup> and a lack of microalgal uptake. Lastly, the scenario of an active nitrifying population is supported by the influx of CO<sub>2</sub> in the dark.

FRP fluxes occurred in either direction at all sites for which data were available. At CB the ambient concentration of FRP was below the limits of detection for both years' samplings. In 1993 at SH FRP concentration was also too low to measure. At GI every possible pattern of flux was represented: -/-, +/+, -/+, and +/- . At SH in 1992 influx and efflux occurred. No interpretation is warranted for either site. The only site for which a conclusion can be drawn is

MI. These sediments demonstrated influx in almost all circumstances. The one efflux was for "mud" in the dark. As this site is autotrophic at Pmax, we infer that a substantial use of the influxed FRP is made by the microalgae.

In conclusion, the patterns of flux direction vary among sites and chemical species. MI and GI have sediments that are most likely to be autotrophic. Both are also potential sinks for  $\text{NO}_x^-$ ; but whereas MI is also a sink for  $\text{NH}_4^+$  and FRP, GI is more likely to be a source for both. SH and CB have sediments which tend to be heterotrophic even though the one is largely "mud" and the other sand.  $\text{NH}_4^+$  and  $\text{NO}_x^-$  tend to be taken up by the sediments at CB with FRP concentrations being too low to measure. At SH  $\text{NO}_x^-$  is consistently effluxed, whereas the directions of  $\text{NH}_4^+$  and FRP fluxes are less predictable.

### Significance

One goal of the NERR program seeks to provide information for sound management of these reserves, and all coastal resources. This project aided this goal by providing data on the effects of one major eutrophication-related impact in estuaries on metabolic processes in benthic environments: increased water column turbidity. Turbidity increases may be associated with runoff from non-point sources or, as we see with CB, may be associated with wind mixing in large shallow lagoons.

These field studies also demonstrate the importance of shoal areas in terms of both primary productivity and nutrient cycling. We have gathered this information for a number of different estuarine environments and showed that each acts somewhat uniquely from the others.

Conclusions based on this research for a diverse number of habitats and over a broad geographic area increases the validity of generalizations to other areas. This extends our research of recent years (Rizzo and Wetzel, 1985; 1986; Rizzo et al., 1992; Rizzo and Christian, in press).

We have begun to take another statistical approach with this growing data base beyond that of using ANOVAs. We have developed several multiple linear regression models of our results from the Neuse River Estuary (Rizzo et al., 1992; Lackey, 1992) using  $O_2$ ,  $NH_4^+$  and  $NO_x^-$  as dependent variables and a variety of environmental factors as independent variables (Rizzo and Christian, in press). In the master's thesis by Dailey (1995) funded in part by this grant, she has included benthic organisms as predictive variables of flux. Interpretations of this approach also proved to be problematic. Whereas chlorophyll a concentrations explained significant amounts of variance in  $O_2$  and  $NH_4^+$  fluxes at Pmax, fluxes in field cores incubated in the dark had little variance explained by organismal indices. In microcosms more variance of dark fluxes was explained by organisms. She attributed this to the breakup of the redox discontinuity layer in the microcosms and decrease in chemical oxygen demand. Again, one comes to the conclusion that much remains to be understood before accurate prediction is possible.

The work described herein at these NERR sites is applicable to a number of national research priorities at the time of funding and site specific research and management objectives. We compared the net community productivity and community respiration of sediments from high and low salinity areas to indicate the functional response of benthic communities to salinity. A national priority was to establish the relationship between freshwater inflows (i.e. changes in salinity) and primary and/or secondary productivity. In North Carolina, one management priority was to determine the potential impacts of a salinity increase (e.g. creation of an inlet resulting



from a major storm) on ecological processes in the reserve. In Virginia, several proposals would withdraw a substantial portion of the natural freshwater input to the York River, threatening Virginia NERR sites with increasing salinity as well. We did find statistically significant effects associated with salinity regime, especially for productivity. However, as we have reiterated, no simple pattern has emerged. In other words, salinity may well have an impact, but we do not have the information necessary to predict the effect of that impact.

A second national water management priority addressed by this work concerns research contributions to elucidation of the nutrient budgets of the reserves. We determined the sediment-water nutrient exchanges concomitantly with the determinations of sediment metabolism. In terms of sediment management goals, this work addresses the priority of determining the relationship of sediments to habitat type by comparing the nutrient flux processes and  $O_2$  and  $CO_2$  metabolism characteristics of systems differing in grain size as well as other bulk sediment properties. The sediments of the NERR sites can be either sources or sinks for nutrients. Some of the regulation, as to their contribution to water column nutrient concentrations, is associated with the immediate light conditions; but most is related to the long-term history and location of the sediments. Thus the sediments of each site play a different role than others. In fact for the four NERR sites studied, no two show the same patterns for all chemical species investigated. This may be taken with some degree of exasperation, but it confirms our earlier tenet that no simple set of factors directs fluxes across the sediment surface. Rather, it is a challenge to begin to piece together the mechanisms and interactions that regulate fluxes. What we have done is add substantially to the base of knowledge that must be developed before a predictive understanding is possible.

## LITERATURE CITED

- Admiraal, W. 1977. Tolerance of estuarine benthic diatoms to high concentrations of ammonia, nitrite ion and orthophosphate. *Mar. Biol.* 43: 307-315.
- Boynton, W.R. and W.M. Kemp. 1985. Nutrient regeneration and oxygen consumption by sediments along an estuarine salinity gradient. *Mar. Ecol. Prog. Ser.* 23: 45-55.
- Christian, R.R., W.M. Rizzo and D.W. Stanley. 1989. Influence of riverine nutrient loading on the Neuse River Estuary, North Carolina. National Undersea Research Program Research Report 89-2. Rockville, MD pp. 19-40.
- Christian, R.R., J.N. Boyer and D.W. Stanley. 1991. Multi-year distribution patterns of nutrients within the Neuse River Estuary, North Carolina. *Mar. Ecol. Prog. Ser.* 71:259-274.
- Connell, D.W. and G.J. Miller. 1984. *Chemistry and Ecotoxicology of Pollution*. John Wiley & Sons. New York, N.Y.
- Dailey, S. K. 1995. Interactions of benthic communities and material fluxes across the sediment-water interface in North Carolina and Virginia estuaries. M. S. Thesis, East Carolina University. 120 pp.
- Day, J.W., Jr., C.A.S. Hall, W.M. Kemp and A. Yanez-Arancibia. 1989. *Estuarine Ecology*. John Wiley & Sons. New York, N.Y. 558 pp.
- DeGroot, E.G. and V.N. de Jonge. 1990. Effects of changes in turbidity and phosphate influx on the ecosystem of the Ems estuary as obtained by a computer simulation model. *Hydrobiologia* 195: 39-47.
- Graf, G. 1987. Benthic energy flow during a simulated autumn bloom sedimentation. *Mar. Ecol. Prog. Ser.* 39: 23-29.
- Graf, G., W. Bengtsson, U. Diesner, R. Schulz and H. Theede. 1982. Benthic response to sedimentation of a spring phytoplankton bloom: Process and budget. *Mar. Biol.* 67: 201-208.
- Graneli, E., K. Wallstrom, U. Larsson, W. Graneli and R. Elmgren. 1990. Nutrient limitation of primary production in the Baltic Sea area. *Ambio* 19: 142-151.
- Heinle, D.R., C.F. D'Elia, J.L. Taft, J.S. Wilson, M. Cole-Jones, A.B. Caplins and L.E. Cronin. 1980. Historical Review of Water Quality and Climatic Data from Chesapeake Bay with Emphasis on Effects of Enrichment. U.S. EPA Chesapeake Bay Program Final Report, Grant# R806189010. Chesapeake Research Consortium, Inc. Publication No. 84. Annapolis, M.D. 128 pp.

- Joint, I.R. 1978. Microbial production of an estuarine mudflat. *Estuarine Coastal Mar. Sci.* 7: 185-195.
- Kelly, J.R., V.M. Berounsky, S.W. Nixon and C.A. Oviatt. 1985. Benthic-pelagic coupling and nutrient cycling across an experimental eutrophication gradient. *Mar. Ecol. Prog. Ser.* 26: 207-219.
- Lackey, G.J. 1992. Effects of light and nutrients on primary productivity across the freshwater-seawater interface of the Neuse River estuary, North Carolina. M.S. Thesis. East Carolina University, Greenville, N.C.
- Lancelot, C., G. Billen, A. Sournia, T. Weisse, F. Colijn, M.J.W. Veldhuis, A. Davies and P. Wassman. 1987. Phaeocystis blooms and nutrient enrichment in the continental coastal zones of the North Sea. *Ambio* 16: 38-46.
- Lancelot, C. and S. Mathot. 1987. Dynamics of a Phaeocystis-dominated spring bloom in Belgian coastal waters. I. Phytoplanktonic activities and related parameters. *Mar. Ecol. Prog. Ser.* 37: 239-248.
- Leeman Labs. 1990. Operating Instructions: CEC Elemental Analyzer Model 440. Lowell, M.A.
- Malone, T.C., L.H. Crocker, S.E. Pike and B.W. Wendler. 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Mar. Ecol. Prog. Ser.* 48: 235-249.
- Meybeck, M., G. Cauwet, S. Dessery, M. Somville, D. Gouleau and G. Billen. 1988. Nutrients (Organic C, P, N, Si) in the eutrophic River Loire (France) and its estuary. *Estuarine, Coastal and Shelf Science* 27: 595-624.
- Murray, L. 1983. Metabolic and structural studies of several temperate seagrass communities, with emphasis on microalgal components. Ph.D. dissertation. College of William and Mary. Williamsburg, V.A. 90 pp.
- Murray, L. and R. L. Wetzel. 1987. Oxygen production and consumption associated with the major autotrophic components in two temperate seagrass communities. *Mar. Biol. Prog. Ser.* 38:231-239.
- National Oceanic and Atmospheric Administration and Virginia Institute of Marine Science. 1990. Chesapeake Bay National Estuarine Research Reserve System in Virginia. Draft Environmental Impact Statement and Draft Management Plan. U.S. Dept. of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service. Washington, D.C. 260 pp.

Neilson, B.J. and L.E. Cronin. 1981. Estuaries and Nutrients. Humana Press. Clifton, N.J. 643 pp.

Nixon, S. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41: 199-219.

Officer, C.B., R.B. Biggs, J.L. Taft, L.E. Cronin, M.A. Tyler and W.R. Boynton. 1984. Chesapeake Bay anoxia: Origin, development, and significance. *Science* 223: 22-27.

Pamatmat, M.M. 1968. Ecology and metabolism of an intertidal sandflat. *Int. revue ges. Hydrobiol.* 53: 211-298.

Renaud, M.L. 1986. Hypoxia in Louisiana coastal waters during 1983: Implications for fisheries. *Fishery Bull.* 84: 19-26.

Rizzo, W.M. 1986. The community metabolism and nutrient dynamics of a shoal sediment in a temperate estuary, with emphasis on temporal scales of variability. Ph.D. dissertation. College of William and Mary. Williamsburg, V.A. 113 pp.

Rizzo, W.M. 1993. Sediment-water phosphate exchange in the Neuse River, North Carolina. Report No. 275. University of North Carolina Water Resources Research Institute, Raleigh, NC.

Rizzo, W.M. 1990. Nutrient exchanges between the water column and a subtidal benthic microalgal community. *Estuaries* 13:219-226.

Rizzo, W.M. and R.L. Wetzel. 1985. Intertidal and shoal benthic community metabolism in a temperate estuary: Studies of spatial and temporal variability. *Estuaries* 8: 342-351.

Rizzo, W.M. and R.L. Wetzel. 1986. Temporal variability in oxygen metabolism of an estuarine shoal sediment. pp. 227-239. In: D.A. Wolfe (ed.). *Estuarine Variability*. Academic Press, Inc. New York, N.Y. 509 pp.

Rizzo, W.M. and R.R. Christian. In press. Significance of subtidal sediments to heterotrophically-mediated oxygen and nutrient dynamics in a temperate estuary. *Estuaries*.

Rizzo, W.M., G.J. Lackey and R.R. Christian. 1992. Significance of eutrophic, subtidal sediments to oxygen and nutrient cycling in a temperate estuary. *Mar.Ecol.Prog.Ser.* 86: 51-61.

Rizzo, W.M., S. K. Dailey, G.J. Lackey, R.R. Christian, B. E. Berry, and R. L. Wetzel. in press. A metabolism-based trophic index for comparing the ecological values of shallow water sediment habitats. *Estuaries*.

- Rudnick, D.T. 1989. Time lags between the deposition and meiobenthic assimilation of phytodetritus. *Mar. Ecol. Prog. Ser.* 50: 231-240.
- Rydberg, L., L. Edler, S. Floderus and W. Graneli. 1990. Interaction between supply of nutrients, primary production, sedimentation and oxygen consumption in SE Kattegat. *Ambio* 19: 134-141.
- Scientific Instruments Corporation. 1981. Nitrite or nitrate + nitrite in water or seawater. Pleasantville, N.Y.
- Seliger, H.H., J.A. Boggs and W.H. Biggley. 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. *Science* 228: 70-73.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*, 2nd ed. W. H. Freeman and Co., New York. 859 pp.
- Solorzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. *Limnol. Oceanogr.* 14: 799-801.
- Stanley, D.W. 1985. Nationwide review of oxygen depletion and eutrophication in estuarine and coastal waters: Southeast region. A report to Brookhaven National Laboratory and NOAA. East Carolina University, Institute for Coastal and Marine Resources, Greenville, N.C.
- Taft, J.L., W.R. Taylor, E.O. Hartwig and R. Loftus. 1980. Seasonal oxygen depletion in Chesapeake Bay. *Estuaries* 3: 242-247.
- Turner, R.E., W.W. Schroeder and W.J. Wiseman, Jr. 1987. The role of stratification in the deoxygenation of Mobile Bay and adjacent shelf bottom waters. *Estuaries* 10: 13-19.
- Twilley, R., W. Kemp, K. Staver, J.C. Stevenson and W. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. *Mar. Ecol. Prog. Ser.* 23: 179-191.
- U. S. Environmental Protection Agency. 1979. *Methods for Chemical Analysis of Water and Wastes*. Environmental Monitoring and Support Laboratory. Cincinnati, Ohio.
- U.S. Geological Survey. 1977. *National Handbook of Recommended Methods for Water-Data Acquisition*. U.S. Dept. Interior, Reston, V.A.
- Vernberg, W.B. 1983. Responses to estuarine stress. pp. 43-63. In: B.H. Ketchum (ed.). *Ecosystems of the World, 26: Estuaries and Enclosed Seas*. Elsevier Scientific Publ. C., New York, N.Y.

Webb, K.L. 1981. Conceptual models and processes of nutrient cycling in estuaries. pp. 25-46.  
In: B.J. Neilson and L.E. Cronin (eds.). Nutrient Enrichment in Estuaries. Humana Press.  
Clifton, N.J. 643 pp.

**APPENDIX**

Summary tables of flux data from 1992 and 1993.

Date	Site	Sediment type	Depth	% light	Irradiance uE/(m <sup>2</sup> x s)	O2 Avg Flux mg/(m <sup>2</sup> x h)	O2 Flux STD	CO2 Avg Flux mmol/(m <sup>2</sup> x h)	CO2 Flux STD	NH4 Avg Flux mmol/(m <sup>2</sup> x h)	NH4 Flux STD	NOx Avg Flux mmol/(m <sup>2</sup> x h)	NOx Flux STD	FRP Avg Flux mmol/(m <sup>2</sup> x h)	FRP Flux STD
07/23/92	GI	Sand	1m	0	0	-36.2	13.7	3.49	1.44	-42.7	6.9	-0.3	0.1	2.1	1.1
07/23/92	GI	Sand	1m	12.5	51	-20.6	9.2	2.29	0.73	-53.3	9.4	-0.4	0.1	2.8	4.4
07/23/92	GI	Sand	1m	25	125	0.1	21.1	0.78	0.98	-59.7	7.4	-0.4	0.1	-0.5	1.2
07/23/92	GI	Sand	1m	50	259	36.2	20.9	-0.31	1.18	-49.3	4.2	-0.3	0.2	6.4	4.0
07/23/92	GI	Sand	1m	100	401	25.1	12.7	-0.84	1.03	-50.5	2.9	-0.4	0.0	1.0	1.2
07/23/92	GI	Sand	2m	0	0	-32.0	6.7	1.86	0.47	-30.0	13.5	13.1	1.2	1.2	2.2
07/23/92	GI	Sand	2m	12.5	51	-19.6	7.4	0.77	0.30	-53.1	10.6	11.7	2.9	-0.6	0.9
07/23/92	GI	Sand	2m	25	124	18.4	7.1	-1.04	0.55	-55.3	7.4	11.6	1.5	-0.4	0.9
07/23/92	GI	Sand	2m	50	255	54.7	22.4	-2.67	0.41	-50.4	6.4	14.1	4.4	1.8	1.0
07/23/92	GI	Sand	2m	100	396	48.1	28.3	-2.99	1.34	-40.9	19.9	11.1	0.9	0.5	1.9
07/24/92	GI	Mud	1m	0	0	-53.8	15.9	-2.71	1.92	127.4	117.9	-11.8	1.1	12.9	18.8
07/24/92	GI	Mud	1m	12.5	95	-43.0	16.5	-2.45	0.96	104.6	52.0	-9.4	3.0	10.2	5.8
07/24/92	GI	Mud	1m	25	190	-47.7	18.7	-1.71	1.81	95.7	66.0	-9.0	1.5	10.8	8.0
07/24/92	GI	Mud	1m	50	413	-38.1	30.8	-4.15	0.65	85.3	98.6	-8.3	4.1	6.0	9.6
07/24/92	GI	Mud	1m	100	704	-36.0	9.7	-2.53	2.23	99.1	100.8	-9.7	1.2	11.0	17.0
07/24/92	GI	Mud	2m	0	0	-44.9	15.2	-3.12	1.74	146.8	151.5	-10.1	1.8	25.8	49.1
07/24/92	GI	Mud	2m	12.5	93	-21.7	14.7	-5.55	1.72	76.9	117.9	-9.1	1.4	1.9	1.9
07/24/92	GI	Mud	2m	25	196	-14.1	31.0	-6.15	1.24	12.7	12.2	-9.9	2.2	0.9	2.3
07/24/92	GI	Mud	2m	50	359	26.2	26.7	-6.98	1.04	34.9	38.3	-9.2	0.9	4.0	3.9
07/24/92	GI	Mud	2m	100	756	-13.3	16.1	-6.51	0.14	1.8	7.7	-9.1	0.7	-1.0	0.9
converted to $\mu\text{mol}/\text{m}^2/\text{h}$ x 1000 $\mu\text{mol}/\text{m}^2/\text{h}$															
08/13/92	CB	Mud	1m	100	NA			NA	NA	0.7	44.2			NA	NA
08/13/92	CB	Mud	1m	100	NA			NA	NA	-28.8	7.7			NA	NA
08/13/92	CB	Mud	1m	100	NA	-15.6	5.4	NA	NA	-15.1	1.3	-6.4	3.8	NA	NA
08/13/92	CB	Mud	1m	0	NA	-11.2	5.6	NA	NA	15.7	47.8	-3.7	4.6	NA	NA
08/13/92	CB	Mud	1m	0	NA			NA	NA	-11.0	2.6			NA	NA
08/13/92	CB	Mud	1m	0	NA			NA	NA	-10.7	1.5			NA	NA
10/20/92	CB	Sand	1m	0	NA	-6.6	1.6	0.28	0.14	-22.2	16.3	-5.4	1.6	NA	NA
10/20/92	CB	Sand	1m	12.5	NA	-12.0	5.5	0.30	0.28	-33.7	8.3	-2.6	1.6	NA	NA
10/20/92	CB	Sand	1m	25	NA	-10.8	5.9	0.55	0.54	-29.7	13.0	-4.3	1.5	NA	NA
10/20/92	CB	Sand	1m	50	NA	-13.9	6.5	0.24	0.05	-31.4	3.6	-4.3	1.2	NA	NA
10/20/92	CB	Sand	1m	100	NA	-15.2	10.1	0.14	0.17	-41.7	9.1	-5.2	0.9	NA	NA
10/20/92	CB	Sand	2m	0	NA	-23.3	23.8	1.16	1.45	-23.9	18.5	-2.1	0.9	NA	NA
10/20/92	CB	Sand	2m	12.5	NA	-22.7	20.4	0.59	0.59	-28.5	28.1	-2.6	1.3	NA	NA
10/20/92	CB	Sand	2m	25	NA	-16.2	7.8	0.22	0.18	-31.8	10.5	-1.7	1.5	NA	NA
10/20/92	CB	Sand	2m	50	NA	-22.0	5.1	0.13	0.17	-35.7	12.9	-1.9	1.8	NA	NA
10/20/92	CB	Sand	2m	100	NA	-25.2	6.0	-0.02	0.09	-29.1	11.3	-0.4	4.1	NA	NA
08/06/92	SH	Mud	1m	0	NA	-32.3	7.9	-0.06	0.14	58.4	25.1	11.5	5.6	-3.7	1.4
08/06/92	SH	Mud	1m	12.5	NA	-2.8	11.3	0.52	0.61	6.8	16.1	7.2	12.1	-0.8	1.1
08/06/92	SH	Mud	1m	25	NA	18.7	23.0	-0.13	0.37	-7.0	4.2	1.7	7.7	-0.5	1.2
08/06/92	SH	Mud	1m	50	NA	39.3	34.3	-0.90	0.62	-3.2	13.9	2.2	8.3	0.4	1.8
08/06/92	SH	Mud	1m	100	NA	14.3	29.4	-0.16	1.16	1.5	14.8	3.6	13.3	-1.8	5.1
08/06/92	SH	Mud	2m	0	NA	-31.6	8.3	-0.13	0.34	71.5	44.4	14.9	1.9	-4.1	1.4
08/06/92	SH	Mud	2m	12.5	NA	-30.5	5.3	-0.24	0.09	82.9	73.2	15.4	9.2	-2.0	0.6
08/06/92	SH	Mud	2m	25	NA	-62.9	40.2	-0.40	0.25	122.4	131.2	12.2	13.0	-4.2	1.6
08/06/92	SH	Mud	2m	50	NA	-45.7	21.7	0.84	1.33	68.5	80.8	11.1	5.9	-4.4	2.3
08/06/92	SH	Mud	2m	100	NA	-44.5	6.0	0.23	0.15	63.2	80.1	23.0	8.0	-2.9	1.3
08/25/92	MI	Sand	1m	0	0	-13.1	3.4	NA	NA	-7.8	13.9	0.3	1.1	-3.7	1.0
08/25/92	MI	Sand	1m	12.5	99	20.2	10.8	NA	NA	-22.8	1.8	-1.4	0.8	-3.2	0.6
08/25/92	MI	Sand	1m	25	218	40.1	24.5	NA	NA	-23.5	5.2	-2.4	0.5	-4.2	0.6
08/25/92	MI	Sand	1m	50	444	98.2	56.2	NA	NA	-18.7	16.9	-2.2	0.9	-5.2	0.9
08/25/92	MI	Sand	1m	100	949	146.4	36.5	NA	NA	-29.4	16.0	-2.4	1.5	-5.4	0.9





Date	Site	Sediment type	Depth	% light	Irradiance uE/(m <sup>2</sup> x s)	O2 Avg Flux mg/(m <sup>2</sup> x h)	O2 Flux STD	CO2 Avg Flux mmol/(m <sup>2</sup> x h)	CO2 Flux STD	NH4 Avg Flux mmol/(m <sup>2</sup> x h)	NH4 Flux STD	NOx Avg Flux mmol/(m <sup>2</sup> x h)	NOx Flux STD	FRP Avg Flux mmol/(m <sup>2</sup> x h)	FRP Flux STD
08/25/92	MI	Sand	2m	0	0	-12.2	2.0	-6.71	9.35	-17.3	1.5	0.1	1.5	-8.2	0.3
08/25/92	MI	Sand	2m	12.5	98	26.9	8.9	-7.20	9.47	-19.1	2.7	-0.3	0.9	-6.2	2.7
08/25/92	MI	Sand	2m	25	219	39.2	19.4	-9.62	11.70	-25.7	3.2	-1.1	0.9	-10.8	1.5
08/25/92	MI	Sand	2m	50	431	95.6	30.6	-8.65	10.14	-22.4	5.5	1.9	5.1	-8.1	2.1
08/25/92	MI	Sand	2m	100	891	135.7	13.1	-13.66	14.59	-24.4	15.0	0.1	1.8	-12.1	1.4
08/26/92	MI	Mud	1m	0	0	-25.4	1.3	NA	NA	-5.3	2.0	-7.3	3.8	3.2	3.4
08/26/92	MI	Mud	1m	12.5	68	-16.2	3.2	NA	NA	-2.4	2.1	-7.2	3.8	0.0	1.2
08/26/92	MI	Mud	1m	25	149	-0.5	6.0	NA	NA	-6.6	0.6	-10.2	0.3	-0.4	0.7
08/26/92	MI	Mud	1m	50	315	30.8	24.2	NA	NA	-5.1	1.2	-9.0	1.8	2.9	1.3
08/26/92	MI	Mud	1m	100	695	80.0	20.1	NA	NA	2.0	8.0	-7.5	5.7	-0.1	0.4

Date	Site	Sediment type	Depth	% light	Irradiance uE/(m <sup>2</sup> x s)	O2 Avg Flux mg/(m <sup>2</sup> x h)	O2 Flux STD	CO2 Avg Flux mmol/(m <sup>2</sup> x h)	CO2 Flux STD	NH4 Avg Flux mmol/(m <sup>2</sup> x h)	NH4 Flux STD	NOx Avg Flux mmol/(m <sup>2</sup> x h)	NOx Flux STD	FRP Avg Flux mmol/(m <sup>2</sup> x h)	FRP Flux STD
06/28/93	MI	Sand	1m	0		-19.5	1.9	1.34	1.17	-24.9	13.2	-0.3	0.8	-2.2	0.7
06/28/93	MI	Sand	1m	12.5		-10.6	12.3	0.92	0.65	32.4	136.7	-0.2	2.0	-2.0	1.1
06/28/93	MI	Sand	1m	25		33.9	17.9	-0.58	0.72	-39.1	13.5	-0.6	0.8	-2.4	0.4
06/28/93	MI	Sand	1m	50		58.4	19.8	-0.61	0.58	-49.5	11.6	-1.5	0.7	-1.8	0.6
06/28/93	MI	Sand	1m	100		136.1	46.0	-3.06	1.08	4.1	128.8	2.4	5.0	-1.2	1.4
06/28/93	MI	Sand	2m	0		-23.7	4.9	2.09	1.06	-32.4	6.6	-1.0	0.7	-2.4	1.4
06/28/93	MI	Sand	2m	12.5		0.5	18.6	2.43	0.77	-31.9	14.4	-1.3	0.4	-2.3	1.3
06/28/93	MI	Sand	2m	25		42.6	9.4	-0.41	0.77	-40.7	9.0	3.4	8.5	2.1	7.4
06/28/93	MI	Sand	2m	50		69.5	26.4	-1.53	0.74	-50.6	19.0	-0.3	1.0	-2.9	2.2
06/28/93	MI	Sand	2m	100		100.5	53.8	-3.60	1.79	-48.6	3.2	3.5	2.9	-0.8	1.8