

# The Contribution of Benthic Nutrient Regeneration to Primary Production in a Shallow Eutrophic Estuary, Weeks Bay, Alabama

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**Abstract** Benthic oxygen, dinitrogen, and nutrient fluxes ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , and  $\text{PO}_4^{3-}$ ) were measured monthly during a 1-year period at two locations in Weeks Bay, a shallow (1.4 m) and eutrophic estuary in Alabama. Gross primary productivity (GPP), ecosystem respiration (R), and net ecosystem metabolism were determined from high-frequency dissolved oxygen measurements. Peak water column  $\text{NO}_3^-$  (55  $\mu\text{M}$ ) and chlorophyll *a* (138  $\mu\text{g/l}$ ) concentrations were measured during spring and fall, respectively. Sediments were a net source of  $\text{NH}_4^+$  (102  $\mu\text{mol m}^{-2} \text{h}^{-1}$ ) and  $\text{PO}_4^{3-}$  (0.9  $\mu\text{mol m}^{-2} \text{h}^{-1}$ ) but a sink for  $\text{NO}_3^-$  (−30  $\mu\text{mol m}^{-2} \text{h}^{-1}$ ). Benthic  $\text{N}_2$  fluxes indicated net N fixation (12  $\mu\text{mol N m}^{-2} \text{h}^{-1}$ ). Sediment oxygen demand (0.55  $\text{g O}_2 \text{m}^{-2} \text{day}^{-1}$ ) accounted for <10% of R (7.3  $\text{g O}_2 \text{m}^{-2} \text{day}^{-1}$ ). Despite high GPP rates (4.7  $\text{g O}_2 \text{m}^{-2} \text{day}^{-1}$ ), the estuary was net heterotrophic. Benthic regeneration supplied, on average, 7.5% and 4% of primary productivity N and P demands,

respectively. These results contrast with the conventional view that benthic regeneration accounts for a large fraction of phytoplankton nutrient demand in shallow estuaries.

**Keywords** Primary production · Respiration · Net ecosystem metabolism · Benthic flux

## Introduction

Estuaries are dynamic ecosystems located at the land–sea interface and characterized by high rates of primary production that support economically important food webs. Primary production is often limited by the supply of one or more of the nutrients: nitrogen (N), phosphorous (P), and silica which are supplied to estuaries from rivers, groundwater discharge, atmospheric deposition, tidal exchange with marine systems, or regeneration during organic matter decomposition (Paerl 2002). Although rivers generally supply most of the N to estuaries (Nixon 1995; Seitzinger et al. 2002), internal cycling of nutrients is also important because fluxes from the sediment may supply a significant proportion of nutrients utilized by primary producers in the water column (Nixon 1981; Fisher et al. 1982; Wollast 1993, Fulweiler et al. 2010). In addition, N fixation can be a source of new N to estuaries; however, N fixation rates tend to be lower in estuarine waters compared to rates in most freshwater ecosystems (Howarth et al. 1988; Marino et al. 2006).

Eutrophication is currently considered the most detrimental problem in estuaries and is often due to an increase of anthropogenic nutrient inputs (NRC 1993, 2000; Bricker et al. 1999). Ecosystem recovery from eutrophication is partially dependent on the internal recycling and regeneration of nutrients (Pinckney et al.

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2001). Tight coupling between benthic and pelagic processes in estuaries results in effective recycling and retention of nutrients, supporting high rates of primary production (Nixon 1981; Kemp et al. 1992).

In shallow estuaries, a large fraction of nutrients fueling water column primary production is regenerated in the sediments from the mineralization of phytodetritus (Jensen et al. 1990; Koho et al. 2008), releasing N and P to the water column, which may be utilized by primary producers. Under oxic conditions, nitrifying microbes in the sediment may oxidize  $\text{NH}_4^+$  to  $\text{NO}_2^-$  and subsequently  $\text{NO}_3^-$ , which may then be released to the water column and utilized by primary producers. Alternatively, under anaerobic conditions,  $\text{NO}_3^-$  may be utilized by heterotrophic bacteria and reduced to gaseous  $\text{N}_2$  during denitrification, resulting in a net efflux of  $\text{N}_2$  to the water column. Denitrification is often the primary sink of N in estuaries and is important because it removes bioavailable N from the ecosystem (Smith et al. 1985; Seitzinger 1987, 1988; Jorgensen and Sorensen 1988), potentially alleviating the impact of eutrophication. However, other processes, such as anaerobic ammonia oxidation (Anammox) and dissimilatory nitrate reduction to ammonium (DNRA), can co-occur and influence the ultimate fate of N (Brandes et al. 2007). Phosphate ( $\text{PO}_4^{3-}$ ) fluxes are also affected by  $\text{O}_2$  and redox potential of the sediment, and  $\text{PO}_4^{3-}$  is released from the sediments during periods of hypoxia/anoxia (Koop et al. 1990).

Factors influencing benthic–pelagic coupling include water column depth, temperature, and mixing events. Benthic–pelagic coupling is typically stronger in shallow estuaries than deeper coastal regions (Nixon 1981) because a greater proportion of the phytodetritus reaches the sediment surface (Hargrave 1973) where it may be mineralized and made available to primary producers in the water column (Oviatt et al. 1981, 1986; Jensen et al. 1990). Secondly, as water column temperature increases, rates of mineralization increase and there is a greater ammonium ( $\text{NH}_4^+$ ) release from the sediments that can support higher rates of water column primary production (Vouvé et al. 2000). However, sediments may contribute proportionally less to phytoplankton N demand than other sources of N during periods of increased primary production (Hopkinson 1987). Finally, mixing events such as sediment resuspension (e.g., wind events or storms) may disrupt benthic–pelagic coupling by the release of nutrients from the surface of sediment particles or resuspension of nutrient-rich porewaters (Porter et al. 2010). As a result, a sudden increase in net heterotrophy may be restored to net autotrophy merely a few days after a wind event (Lawrence et al. 2004). Furthermore, N released from mineralization in the sediments are often more labile than allochthonous sources of N and thus more often

incorporated into primary producer biomass (Boynton et al. 1995).

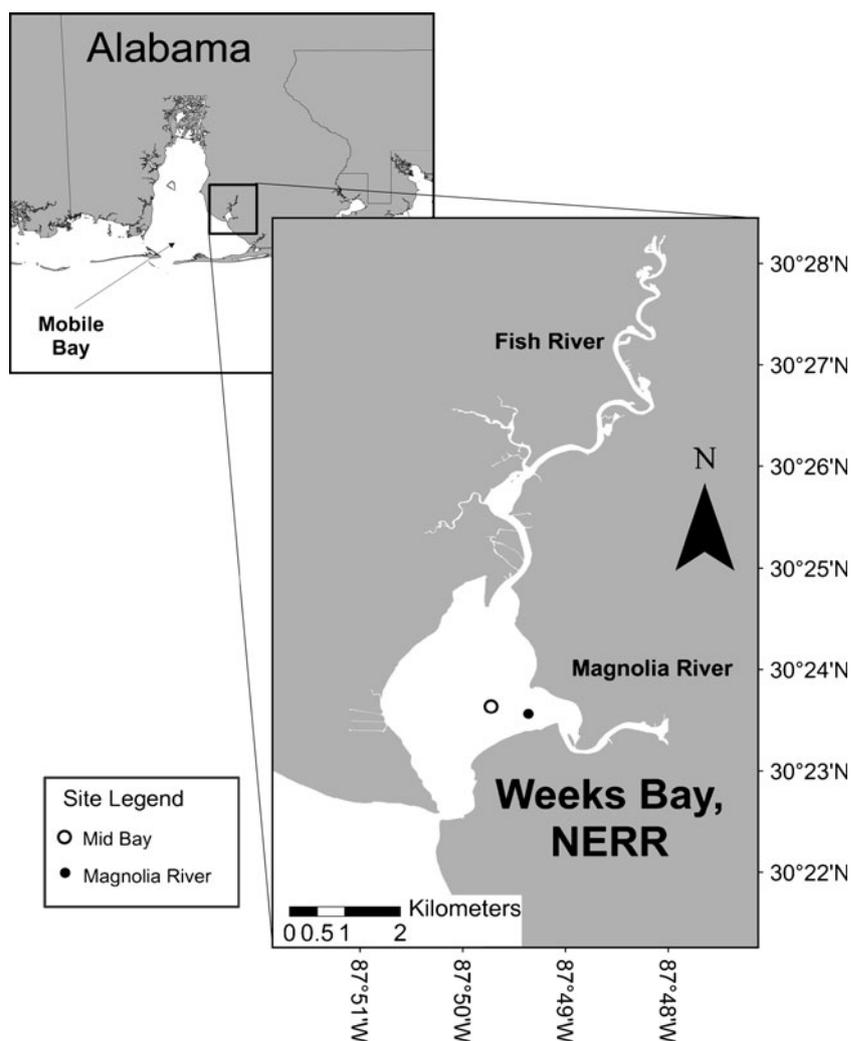
The overarching goal of our study was to examine the contribution of benthic nutrient recycling to water column primary production nutrient demand (PND) in Weeks Bay, Alabama, one of several eutrophic sub-estuaries bordering Mobile Bay. Weeks Bay is a shallow (1.4 m) microtidal (range=0.4 m) estuary with a small watershed (521 km<sup>2</sup>). Freshwater is delivered to Weeks Bay by Fish River located at the north end of the north–south longitudinal axis, and Magnolia River located at the east side of the east–west lateral axis (Fig. 1). The watersheds for these two rivers are highly agricultural with 59% of the land-use as row crops and pasture (Lehrter 2006). High nutrient inputs from both agricultural and residential land uses result in freshwater dissolved inorganic nitrogen (DIN) concentrations exceeding 140  $\mu\text{M}$  (Lehrter 2008). The high DIN concentrations in the tidal reaches, and within Weeks Bay, lead to high phytoplankton biomass throughout the year (Murrell and Caffrey 2005; Lehrter 2008), with chlorophyll *a* concentrations (Chl*a*) within the estuary sometimes exceeding 160  $\mu\text{g/l}$  (Canion 2008). Because the flux of organic matter reaching the benthos is a dominant factor controlling benthic nutrient regeneration (Kelly and Nixon 1984; Cowan and Boynton 1996), we hypothesize that benthic nutrient fluxes will provide a large fraction of N and P demand for water column primary producers in Weeks Bay.

## Materials and Methods

### Field Collections

Sediments and site water were collected monthly at two sites, Magnolia River and Mid Bay, between April 2009 and March 2010 (Fig. 1). Surface and bottom water temperature, salinity, and dissolved oxygen (DO) were measured with a YSI Model 556 Multiparameter Meter. Bottom water for nutrients ( $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{NH}_4^+$ , and  $\text{PO}_4^{3-}$ ) and Chl*a* analyses were collected with a Niskin bottle and stored in acid-washed Teflon carboys. Sediment for Chl*a* and denitrification potentials were collected with an Eckman grab. Top 1-cm sediments were sectioned in the field from cores ( $n=3$ ) subsampled from the Eckman grab for Chl*a* determination. Sediment samples for Chl*a* determination were stored in acid-washed glass scintillation vials. Water for nutrient analyses, as well as sediments, were stored in a cooler in ice prior to return to the laboratory. Water samples for nutrient analyses were filtered within 3 h of collection. For denitrification potential experiments, the Eckman grabs were subsampled with six cores (3.8 cm diameter, 30.5 cm length) and sectioned into 0–3 cm and 3–6 cm depths and stored in acid-washed jars.

**Fig. 1** Map of Weeks Bay, Alabama, National Estuarine Research Reserve (NERR). Study sites are indicated by circles, at Magnolia River (*closed*) and Mid Bay (*open*), respectively



SCUBA divers collected four sediment cores (10.2 cm diameter, 50.8 cm length) for benthic flux experiments at each site. All cores were evaluated for intactness, and cores with sediment cracks or re-suspension were discarded. Sediment height was adjusted to approximately 30 cm. Sediment cores were stored in the dark in coolers and returned to the Dauphin Island Sea Lab.

#### Benthic Fluxes

Uncapped cores were submerged in tanks filled with unfiltered site water in an environmental chamber set at the average *in situ* water temperature of both sites. One core tube with unfiltered water from each site served as the blanks. Sediment cores and water-only cores were allowed to equilibrate for 12–14 h, along with GF/F filtered site water which was used as replacement water for water samples removed for nutrient and  $N_2/Ar$  analyses during the incubations. Blanks and

sediment cores were fitted with a cap with a suspended stir bar and two ports. Cores and blanks were capped underwater and checked to ensure the absence of bubbles. Capped cores were transferred to a water filled tank with a rotating magnet at the center that allowed the stir bars in each core to rotate. Water samples were collected five times during a 9–12-h period for determination of  $N_2/Ar$ ,  $O_2$ , and nutrient concentrations. Samples for  $N_2/Ar$  analysis were siphoned from the cores into 12-ml Labco Exetainer vials allowing the vial to overflow three times the volume of the vial and then immediately preserved with 250  $\mu$ l of 50% (wt  $vol^{-1}$ )  $ZnCl_2$  prior to capping. Vials were stored underwater in the environmental chamber until dissolved gas analysis. Samples for  $O_2$  analysis were also collected into Exetainers and preserved with Winkler reagents (Strickland and Parsons 1972) and analyzed within 24 h. Ten milliliters of water was collected from each core and filtered through GF/F filters and stored frozen (<1 month) at  $-20^\circ C$  for nutrient analyses.

## Denitrification Potential Rates

Sediment denitrification potential rates were measured with the acetylene inhibition technique (Sorensen 1978) as modified by Dollhopf et al. (2005). Because of inhibition of nitrification by acetylene, rates determined with this approach underestimate denitrification that would be supported by coupled nitrification–denitrification. Samples were collected from June 2009 to March 2010, at two depths (0–3 cm and 3–6 cm), in Magnolia River and Mid Bay sites. Once in the laboratory, sediments were allowed to acclimate in the dark to room temperature ( $25\pm 2^\circ\text{C}$ ). Twenty grams of homogenized sediment and 50 ml of filtered site water were added to each foil covered 120 ml Wheaton serum vial. Three slurries were amended with 250  $\mu\text{l}$  of a 20 mM  $\text{KNO}_3^-$  solution. Vials were sealed with a septum, capped, and flushed with  $\text{N}_2$ . Ten milliliters of acetylene was added and samples were incubated for an hour at room temperature on a shaker table. Headspace gas was removed and injected into 12 ml evacuated Labco Exetainer vials.

## Sample Analyses

Nutrient concentrations were determined using standard wet chemical techniques modified for the Skalar SAN<sup>+</sup> Autoanalyzer (Pinckney et al. 2001). Water column Chl *a* was determined by filtering 10 ml of site water onto a 25-mm-diameter Whatman GF/F glass fiber filter and extracted with 10 ml of 90% acetone for 24 h at  $-20^\circ\text{C}$ . Chl *a* was extracted from 2 ml of sediment with 10 ml of 90% acetone for 24 h at  $-20^\circ\text{C}$ . Chl *a* in the extracts was determined fluorometrically (Welschmeyer 1994). DO concentrations were determined with a Mettler DL-21 autotitrator with the Winkler method as described by Strickland and Parsons (1972). Whole core denitrification was determined by the  $\text{N}_2/\text{Ar}$  ratio measured with a membrane inlet mass spectrometer (MIMS) according to the method by Kana et al. (1994) and standard gas concentrations were determined according to Hamme and Emerson (2004). Oxygen was removed from the inflow gas upstream of the mass spectrometer during  $\text{N}_2$  analyses by using an in-line quartz column packed with copper turnings heated to  $600^\circ\text{C}$  (Eyre et al. 2002).  $\text{N}_2\text{O}$  concentrations from potential denitrification experiments were analyzed within 48 h of collection using a gas chromatograph with an electron capture detector (GC-2014 Shimadzu).

## Net Ecosystem Metabolism Calculations

One of the three main components of the National Estuarine Research Reserve System-Wide Monitoring Program (SWMP) is the monitoring of abiotic indicators of water quality including but not limited to temperature, salinity, and DO collected by automated dataloggers

(0.5 m above the sediment surface) at 15-m intervals. Gross primary production (GPP), ecosystem respiration (R), and net ecosystem metabolism (NEM) were determined from the water quality data from two of the NERR monitoring stations (Mid Bay and Magnolia River sites, Fig. 1) according to the open water method as described by Caffrey (2003, 2004). A major assumption of the diel oxygen curve method is that water masses passing by the sensor are laterally and vertically homogenous. In areas where physical processes such as advection and diffusion dominate over biological processes, metabolic rates may be either underestimated or overestimated (Kemp and Boynton 1984). The underlying assumptions, limitations, and calculations of this method are further discussed in detail in Caffrey (2003, 2004).

## Data Treatment and Statistical Analyses

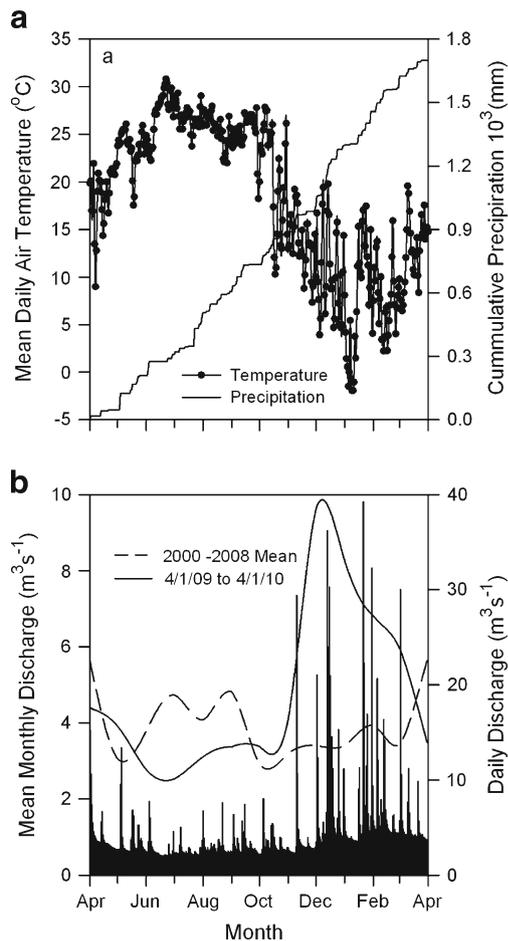
Linear regressions were then performed on the data to determine benthic flux rates in each core. Outliers were selected from all benthic flux data and removed, based on a modification of the method of Lancaster (1990) and Bowling et al. (2002): (1) a linear regression was performed with all data, and (2) any points where the absolute value of the residual was greater than two standard deviations of all absolute residuals was removed and the regression coefficients determined. This procedure resulted in the removal of measurements from each of the 922 measurements from the following: 72 ( $\text{N}_2$ ), 63 ( $\text{NO}_2^-$ ), 65 ( $\text{NO}_3^-$ ), 64 ( $\text{NH}_4^+$ ), 66 ( $\text{PO}_4^{3-}$ ), and 66 ( $\text{O}_2$ ) measurements from each of the 922 measurements. No less than four points were used for the regression. If the regression was not significant, the slope was assigned a value of zero. An average slope was obtained for the four sediment cores and the slope of the regression for the water blank was subtracted from this average after adjusting for the difference in the core water volumes.

Differences between sites in water column nutrients, Chl *a*, and benthic fluxes were examined using univariate analysis of variance (ANOVA). Relationships among water column parameters, water column nutrients, sediment and water column Chl *a*, and benthic fluxes were examined using a Pearson product–moment correlation.

## Results

### Environmental Characteristics

Average air temperature during the study period was  $18.3^\circ\text{C}$  and varied from  $-1.94$  to  $30.82^\circ\text{C}$  with a distinct seasonal pattern (Fig. 2a). Daily air temperature fluctuations in Weeks Bay can exceed  $11^\circ\text{C}$  and are associated with the passage of atmospheric fronts that generally result in short-lived precipitation events (Fig. 2a). Precipitation was evenly distributed throughout the study period (Fig. 2a). Daily



**Fig. 2** **a** Mean daily air temperature and cumulative precipitation and **b** mean monthly (solid line) and daily (bars) combined discharges from Fish and Magnolia rivers. In addition, the mean monthly discharge for the period of 2000–2008 is shown (dashed line)

combined freshwater discharge from the Magnolia and Fish Rivers averaged  $4.8 \text{ m}^3 \text{ s}^{-1}$  and varied from 2 to  $39.2 \text{ m}^3 \text{ s}^{-1}$  (Fig. 2b), with usually higher discharges in the winter months. Mean monthly winter river discharge during the study period exceeded monthly winter discharge for the 2000–2008 period by a factor of 3 (Fig. 2b).

#### Water Column Parameters

Average water temperature and salinity were  $21.1^\circ\text{C}$  and 7.0 PSU for Magnolia River, and  $21.3^\circ\text{C}$  and 6.4 PSU in Mid Bay (Fig. 3a–d). Highest water temperature and salinity were measured during the summer and early fall. During the winter, high freshwater discharge (Fig. 3d), the estuary was nearly fresh with salinities almost 0. The difference between bottom and surface water salinities during the monthly sampling events were  $<1$  PSU during the higher river flow periods, with the exception of the January sampling period when the salinity difference between the surface and bottom waters at Mid Bay was 5 PSU (Fig. 3d). Stratification was

greatest in the spring and fall when freshwater discharge was lowest. DO showed a significant inverse relationship with temperature (Pearson correlation,  $r=-0.436$ ,  $p=0.033$ ). The highest DO concentrations occurred during the winter and the lowest during the summer and early fall (Fig. 3e, f). The DO concentrations were below  $2 \text{ mg/l}$  during 8.1% (Mid Bay) and 4.6% (Magnolia River) of the time; sustained and frequent low DO events were measured during the August to October period at both sites.

#### Water Column Nutrients and Chlorophyll *a*

Both sites exhibited similar temporal trends in  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations.  $\text{NO}_3^-$  concentrations (Fig. 4a) were generally higher than those of  $\text{NH}_4^+$  except during summer (Fig. 4b), when water column temperatures were also higher (Fig. 3a, b). The lowest  $\text{NO}_3^-$  concentrations ranged between 0.2 and  $0.6 \mu\text{M}$  in the summer and peaked at  $55 \mu\text{M}$  in the spring and winter (Fig. 3a), when freshwater discharge into the estuary was high (Fig. 2b).  $\text{NO}_3^-$  was significantly negatively correlated with salinity ( $r=-0.603$ ,  $p=0.002$ ).  $\text{PO}_4^{3-}$  concentrations in both sites were lowest in July and highest during the December peak river flow period, with no significant differences between sites (ANOVA,  $p=0.90$ , Fig. 4c).

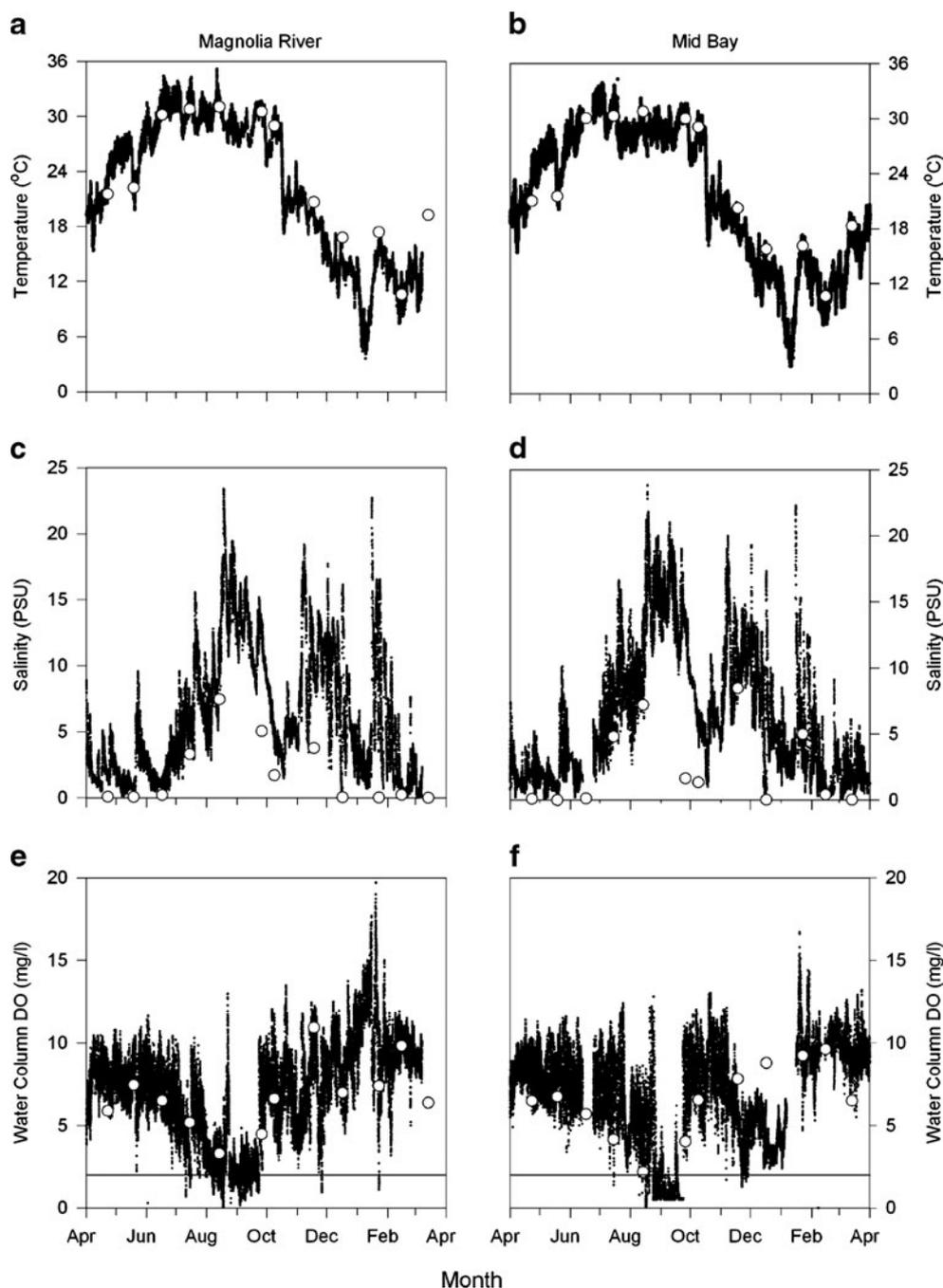
Average water column Chl *a* concentrations were  $49.6 \mu\text{g/l}$  at Magnolia River and  $36.0 \mu\text{g/l}$  at Mid Bay (Fig. 4d). Peak water column Chl *a* concentrations were  $132.8 \mu\text{g/l}$  in September at the Magnolia River and  $72.6 \mu\text{g/l}$  at Mid Bay in August (Fig. 4d). Sediment Chl *a* concentrations averaged  $3.30$  and  $2.18 \mu\text{g/g dw}$  sediment at the Mid Bay and Magnolia River sites, respectively, and showed an inverse temporal pattern with water column Chl *a* (Fig. 4d, e).

#### Benthic Fluxes

Sediment oxygen demand (SOD) was similar at Mid Bay and Magnolia River (ANOVA,  $p=0.054$ ) (Fig. 5a) and positively correlated with temperature ( $r=0.600$ ,  $p=0.002$ ). The annually integrated SOD flux at the Magnolia River and Mid Bay sites were  $0.5 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$  (range= $0.3$  to  $0.8 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) and  $0.6 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$  (range= $0.3$  to  $0.9 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ), respectively.

$\text{NH}_4^+$  fluxes were not different between sites ( $p=0.335$ ) and reached highest concentrations in the summer (Fig. 5b). The annually integrated  $\text{NH}_4^+$  flux at Magnolia River was  $88.2 \mu\text{mol N m}^{-2} \text{ h}^{-1}$  (range= $-10.0$  to  $340.4 \mu\text{mol N m}^{-2} \text{ h}^{-1}$ ) and  $116.8 \mu\text{mol N m}^{-2} \text{ h}^{-1}$  (range= $-25.5$  to  $355.0 \mu\text{mol N m}^{-2} \text{ h}^{-1}$ ) at Mid Bay.  $\text{NO}_3^-$  fluxes were similar between sites, (Fig. 5c) (ANOVA,  $p=0.80$ ), with uptake by sediments during high freshwater flow when overlying water concentrations were high.  $\text{NO}_3^-$  flux and  $\text{NO}_3^-$  concentration in the water column were negatively correlated ( $r=-0.416$ ,  $p=0.043$ ). During fall and winter months, periodic release of  $\text{NO}_3^-$  from the sediment to the

**Fig. 3** 15-min average for temperature (**a, b**), salinity (**c, d**), and dissolved oxygen (mg/l) (**e, f**) as measured by NERR data sondes located 0.5 m above the sediment surface. *Open circles* indicate bottom water temperature (**a, b**), difference between surface and bottom salinity (**c, d**), and bottom water oxygen on the date of sampling (**e, f**)



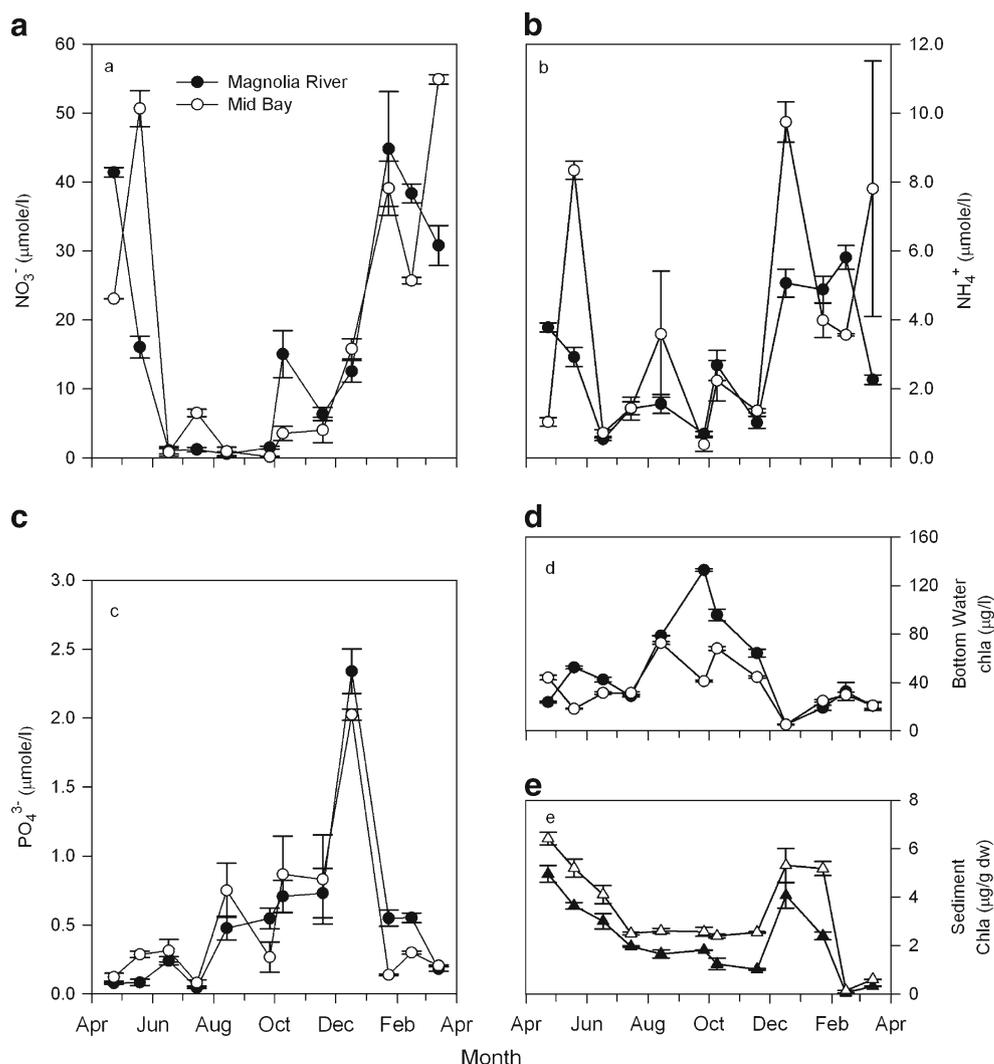
water column occurred at the Mid Bay site. The annually integrated  $\text{NO}_3^-$  flux in Magnolia River and Mid Bay sites were  $-33.7 \mu\text{mol N m}^{-2} \text{h}^{-1}$  (range= $-144.7$  to  $8.6 \mu\text{mol N m}^{-2} \text{h}^{-1}$ ) and  $-28.3 \mu\text{mol N m}^{-2} \text{h}^{-1}$  (range= $-128.7$  to  $64.1 \mu\text{mol N m}^{-2} \text{h}^{-1}$ ), respectively.

$\text{PO}_4^{3-}$  fluxes did not exhibit a detectable seasonal pattern (Fig. 5d). Both sites exhibited periodic release and uptake of  $\text{PO}_4^{3-}$  and were not significantly different (ANOVA,  $p=0.200$ ). The annually integrated  $\text{PO}_4^{3-}$  flux in Magnolia River and at Mid Bay were  $1.6 \mu\text{mol P m}^{-2} \text{h}^{-1}$

(range= $-4.1$  to  $9.1 \mu\text{mol P m}^{-2} \text{h}^{-1}$ ) and  $0.2 \mu\text{mol P m}^{-2} \text{h}^{-1}$  (range= $-4.2$  to  $6.4 \mu\text{mol P m}^{-2} \text{h}^{-1}$ ), respectively.

On an annual basis, there was  $\text{N}_2$  uptake by the sediments suggesting net N fixation (Fig. 6) and both sites exhibited similar rates (ANOVA,  $p=0.611$ ). There was a significant positive correlation between  $\text{N}_2$  flux and water temperature ( $r=0.450$ ,  $p=0.027$ ). The annually integrated  $\text{N}_2$  flux in Magnolia River was  $-8.7 \mu\text{mol N m}^{-2} \text{h}^{-1}$  (range= $-107.3$  to  $72.6 \mu\text{mol N m}^{-2} \text{h}^{-1}$ ) and  $-15.2 \mu\text{mol N m}^{-2} \text{h}^{-1}$  (range= $-125.7$  to  $27.4 \mu\text{mol N m}^{-2} \text{h}^{-1}$ ) at Mid Bay.

**Fig. 4** Monthly average water column nutrients  $\text{NH}_4^+$  (a),  $\text{NO}_3^-$  (b),  $\text{PO}_4^{3-}$  (c), water column Chla (d), and sediment Chla (e) at Magnolia River (black circles) and Mid Bay (white circles). Error bars indicate standard error of the mean ( $n=3$ )



### Denitrification Potential Rates

A site by depth and date between groups ANCOVA revealed a main effect for time ( $p<0.001$ ), site ( $p<0.001$ ), and depth ( $p<0.001$ ). The Magnolia River site had consistently higher rates of denitrification potential than the Mid Bay site for both depth profiles (Fig. 7). At the Magnolia River site, the average ( $\pm 1$  SD) denitrification potential rates from the 0–3 cm depth were 31.4 (11.1)  $\text{nmol cm}^{-3} \text{ h}^{-1}$  and at Mid Bay they were 19.5 (7.6)  $\text{nmol cm}^{-3} \text{ h}^{-1}$ . In comparison, average denitrification potential rates for the 3–6 cm depth at Magnolia River were 23.3 (6.8)  $\text{nmol cm}^{-3} \text{ h}^{-1}$  and 19.9 (9.7)  $\text{nmol cm}^{-3} \text{ h}^{-1}$  at the Mid Bay site.

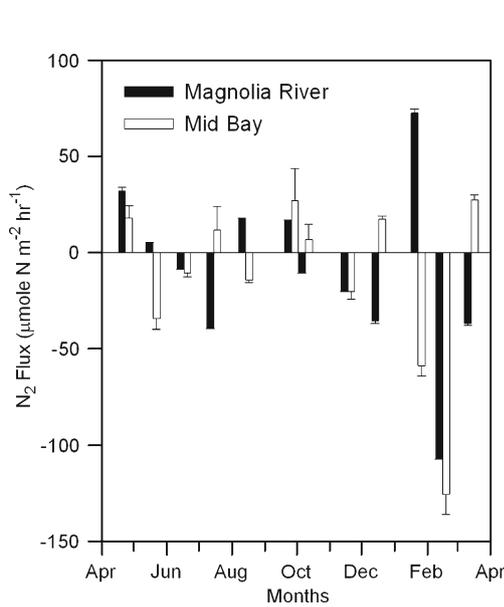
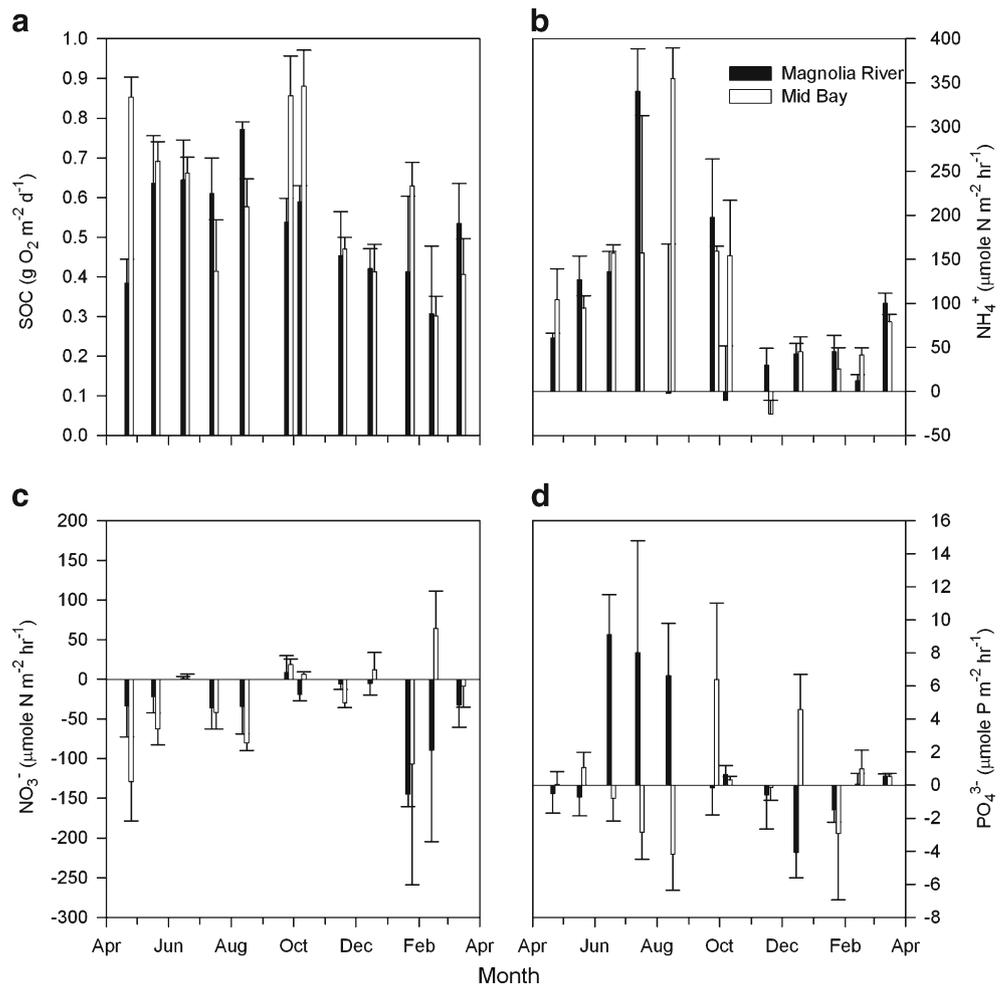
### Net Ecosystem Metabolism

GPP rates at the Magnolia River site were higher than at the Mid Bay site (one-way ANOVA,  $p<0.001$ ) (Fig. 8a, b). GPP rates for the duration of the study were 3.4 and 5.9  $\text{g O}_2$

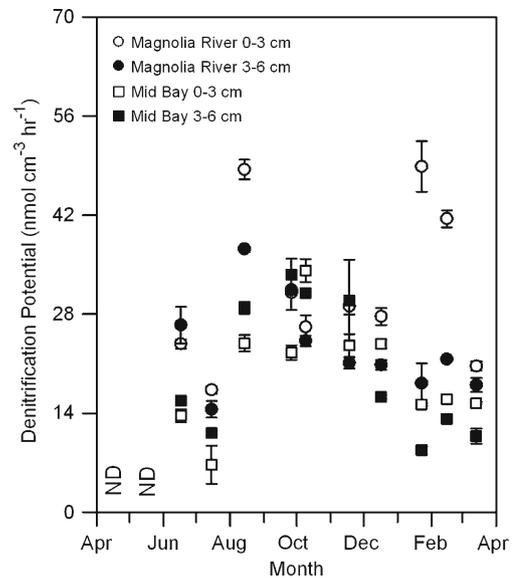
$\text{m}^{-2} \text{ day}^{-1}$  at the Mid Bay and Magnolia River sites, respectively. The highest monthly average GPP at Magnolia River was 8.3  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$  in November and at Mid Bay, 5.9  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$  in August. A Pearson correlation revealed GPP was positively correlated with water temperature ( $r=0.645$ ,  $p<0.001$ ), pH ( $r=0.533$ ,  $p=0.007$ ), Chla ( $r=0.514$ ,  $p=0.010$ ), and negatively correlated with water column  $\text{NO}_3^-$  ( $r=-0.435$ ,  $p=0.034$ ),  $\text{NO}_2^-$  ( $r=-0.473$ ,  $p=0.020$ ), and  $\text{NH}_4^+$  ( $r=-0.470$ ,  $p=0.019$ ).

R rates exhibited a strong seasonal pattern at both sites (Fig. 8c, d), increasing from spring to summer and decreasing in the fall and winter. For the duration of the study period, R rates were higher at the Magnolia River site (8.3  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) than the Mid Bay site (6.2  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) (ANOVA,  $p<0.001$ ). The highest monthly average R rates occurred in September (12.3 at Magnolia River and 11.5 at Mid Bay  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ). A Pearson correlation indicated that R was significantly positively correlated with water temperature ( $r=0.608$ ,  $p=0.002$ ), salinity ( $r=0.774$ ,  $p<0.001$ ), pH ( $r=0.531$ ,  $p=0.008$ ), Chla ( $r=0.646$ ,  $p<0.001$ ), and gross

**Fig. 5** Monthly average benthic fluxes of SOC (a),  $\text{NH}_4^+$  (b),  $\text{NO}_3^-$  (c), and  $\text{PO}_4^{3-}$  (d) at Magnolia River (black) and Mid Bay (white). Error bars indicate standard error of the mean ( $n=4$ ). Positive fluxes indicate an efflux from the sediment and negative fluxes indicate an influx into the sediment

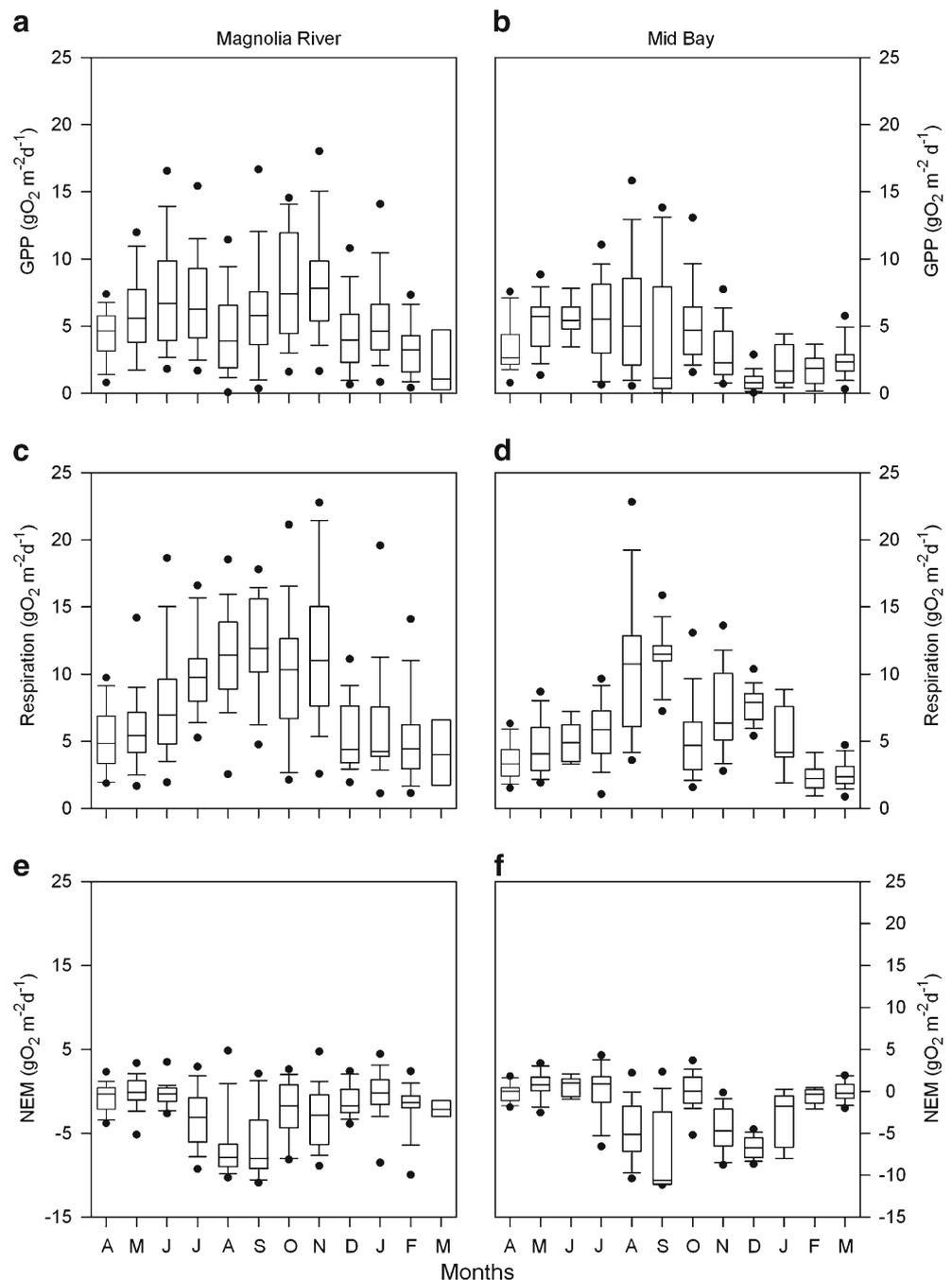


**Fig. 6** Monthly  $\text{N}_2$  fluxes at Magnolia River (black) and Mid Bay (white). Error bars indicate standard error of the mean ( $n=4$ ). Positive fluxes indicate an efflux from the sediment and negative fluxes indicate an influx into the sediment



**Fig. 7** Box plot of monthly GPP, respiration, and NEM at Magnolia River (black) and Mid Bay (white) sites. In the box plots, the median (horizontal line) and the 25 (bottom of the box) and 75 (top of the box) percentiles, as well as the 10th and 90th percentiles (error bars) are shown

**Fig. 8** Denitrification potential rates at Magnolia River and Mid Bay at 0–3 cm and 3–6 cm depths. Error bars indicate standard error of the mean ( $n=3$ ). ND not determined



primary production ( $r=0.543$ ,  $p=0.006$ ), and negatively correlated with water column  $\text{NO}_3^-$  ( $r=-0.664$ ,  $p<0.001$ ),  $\text{NO}_2^-$  ( $r=-0.657$ ,  $p<0.001$ ), and  $\text{NH}_4^+$  ( $r=-0.412$ ,  $p=0.045$ ).

NEM rates indicated that the system was usually net heterotrophic ( $\text{NEM}<0$ ; i.e.,  $\text{R}>\text{GPP}$ ) (Fig. 8e, f). Although the Magnolia River site exhibited higher GPP and R rates than the Mid Bay site, both had similar NEM rates ( $-2.2$  at Mid Bay and  $-2.4$  at Magnolia River  $\text{g O}_2 \text{m}^{-2} \text{day}^{-1}$ , ANOVA,  $p=0.137$ ). NEM was significantly positively correlated with water column  $\text{NO}_3^-$  concentrations ( $r=0.442$ ,

$p=0.031$ ) and negatively correlated with salinity ( $r=-0.672$ ,  $p<0.001$ ) and R ( $r=-0.753$ ,  $p<0.001$ ).

## Discussion

### Nutrients and Chla

The DIN and DIP concentration ranges measured at the two sampling stations in Weeks Bay were similar to those

**Table 1** Phytoplankton nutrient demand (PND) for N and P ( $\mu\text{mol m}^{-2} \text{day}^{-1}$ ) calculated from monthly mean GPP and the Redfield ratio and the sediment N and P contribution (%) to PND

	Magnolia River		Mid Bay		Magnolia River		Mid Bay	
	N demand	Sediment DIN contribution	N demand	Sediment DIN contribution	P demand	Sediment P contribution	P demand	Sediment P contribution
April	1267	2	1048	0	79	0	66	0
May	1,628	6	1,570	2	102	0	98	1
June	2,238	6	1,734	9	140	7	108	0
July	1,949	16	1,701	7	122	7	106	0
August	1,166	0	1,773	15	73	9	111	0
September	1,770	12	1,189	15	111	0	74	9
October	2,173	0	1,600	10	136	0	100	0
November	2,191	1	879	0	137	0	55	0
December	840	4	150	38	53	0	9	49
January	1,544	0	397	0	97	0	25	0
February	843	0	364	29	53	0	23	4
mean	1,601	4	1,128	11	100	2	70	6

previously measured in this estuary (Schreiber and Pennock 1995, Canion 2008; Murrell and Caffrey 2005) with peak  $\text{NO}_3^-$  concentrations (Fig. 4a) measured during higher freshwater discharge into the estuary (Fig. 2b). In contrast to DIP, which does not exhibit a clear spatial trend, DIN concentrations in Weeks Bay decrease from high values near the rivers to low concentrations at the Bay mouth (Canion 2008). DIN concentrations during the study period did exhibit a statistically significant inverse relation with salinity ( $\text{NH}_4^+ - r = -0.534, p = 0.007$ ;  $\text{NO}_3^- - r = -0.603, p = 0.002$ ), but DIN concentrations were not significantly different at the two sites, presumably because of the proximity of these stations to each other (ANOVA,  $p = 0.376$ ). Similarly,  $\text{PO}_4^{3-}$  were comparable at the two stations with highest concentrations measured in December, coinciding with lowest in water column Chla (Fig. 4d) and high sediment Chla concentrations (Fig. 4e).

The high concentrations of nutrients in the rivers delivering freshwater to Weeks Bay (Lehrter 2008) lead to nutrient concentrations within the estuary (Fig. 4) that can exceed those in other northern Gulf of Mexico estuaries by up to an order of magnitude (Cowan et al. 1996; Mortazavi et al. 2000a; Twilley et al. 1996; Murrell et al. 2009; Putland and Iverson 2007). For example, Weeks Bay DIN concentrations were nearly 75% higher than the maximum in Mobile Bay system (Cowan et al. 1996) and five times higher than in Pensacola Bay (Murrell et al. 2009), two nearby river-dominated estuaries.

Water Chla concentrations reached peak values (Fig. 4d) during the late summer and early fall when freshwater to the estuary was low (Fig. 2b) and dropped to low values during the high river flow period. Lehrter (2008) found an inverse

relation between freshwater discharge and water column Chla in the sub-estuaries of Mobile Bay (including Weeks Bay) similar to patterns described for the upper San Francisco Bay (Cloern et al. 1985) and the upper reaches of the Rhode River estuary (Jordan et al. 1991). It suggests that, during high discharge events, this short residence estuary becomes an extension of the river leading to high water column DIN concentrations but low phytoplankton, which is presumably washed out the system (Eyre 2000).

Weeks Bay water column Chla concentrations are also consistently higher than those of other shallow sub-estuaries along Mobile Bay (Dog River and Fowl River estuaries) (Lehrter 2008) despite the relatively short distance (<100 km) separating their watersheds. The higher DIN and Chla concentrations in Weeks Bay reflect the impact of agricultural land use in its watershed (Lehrter 2006). The percentage of the Weeks Bay watershed that is covered with row crops (26%) greatly exceeds those of the Dog (2.4%) and Fowl River (9.8%) watersheds (Lehrter 2006).

#### Ecosystem Metabolic Rates

High nutrient availability in nearshore marine systems can lead to high NEM by stimulation of production over respiration (Oviatt et al. 1986; D'Avanzo et al. 1996). GPP rates in Weeks Bay are considerably higher than other Gulf of Mexico estuaries (Caffrey 2004), consistent with the higher DIN and water column Chla concentrations within this estuary relative to other northern Gulf of Mexico estuaries (Pennock et al. 1999). GPP values were, for example, twice those in Apalachicola Bay (Caffrey 2004), a larger river-

dominated estuary in the Gulf of Mexico, where average water column DIN concentrations are 9  $\mu\text{M}$  (Pennock et al. 1999) and Chla concentrations rarely exceed 10  $\mu\text{g/l}$  (Mortazavi et al. 2000b; Putland and Iverson 2007).

Despite the 73% higher GPP rates at the Magnolia River site compared to that at the Mid Bay station, NEM values were similar for the two sites ( $-2.2$  at Mid Bay and  $-2.4$  at Magnolia River  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) because of higher R rates at the Mid Bay site (Fig. 8c, d). Increased anthropogenic inputs of N and P have shifted many ecosystems towards net heterotrophy such that R rates are higher than GPP (Smith and Hollibaugh 1993), and Weeks Bay is consistent with this trend.

NEM in Weeks Bay was negatively correlated with salinity. Caffrey (2003) also found a significant negative correlation between NEM and salinity at a site located near the mouth of Weeks Bay. In western Gulf of Mexico Texas estuaries, NEM and salinity are also negatively correlated (Russell and Montagna 2007). Increased freshwater input results in increased concentrations of inorganic nutrients resulting in an initial increase in autotrophy, which is followed by increased heterotrophy due to the increase in organic matter availability (Russell and Montagna 2007).

The high R rates in Weeks Bay led to low concentrations in bottom water column DO during the August to October period (Fig. 3e, f) when the water column appeared to be stratified (Fig. 3c, d). While GPP rates were high, it was not sufficient during this period to compensate for the high R rates. The persistence of low oxygen waters in deeper estuaries is often attributed to water column stratification that prevents the mixing of surface oxygen-rich waters with bottom waters that have low DO concentrations (Hagy et al. 2004). The sustained low water column DO in Weeks Bay (Fig. 3c, d) is surprising because of its shallow depth. However, the late summer–early fall low DO concentrations in this estuary (Fig. e, f) occurred when water column was stratified (Fig. 3c, d) and R rates were high (Fig. 3c, d).

The rapid return to normoxic conditions in Weeks Bay at the end of September (Fig. 3e, f), and freshening of the estuary (Fig. 3c, d), was accompanied by the passage of an atmospheric front that caused air temperatures to decline by  $6.95^\circ\text{C}$  during a 24-h period (Fig. 2a). In contrast to the nearby Mobile Bay, where bottom water DO concentrations following destratification events can be quickly exhausted (Park et al. 2007), Weeks Bay DO remained normoxic for the majority of the remainder of the study period (Fig. 3e, f). This could be resulting from lower R rates in the fall and winter compared to summer months (Fig. 8c, d), coupled to a shallow depth in this estuary that allows for mixing of surface and bottom waters.

## Benthic Respiration

Benthic respiration and water temperature in Weeks Bay were positively correlated ( $r=0.60$ ,  $p<0.05$ ), but benthic respiration rates (range= $0.3$ – $0.9 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) were much lower than that observed for other estuarine systems that experience similar temperature ranges (Twilley et al. 1996). For example, water temperatures in Plum Island Sound vary from 4 to  $23^\circ\text{C}$  while sediment  $\text{O}_2$  uptake rates vary by a factor of 8.5 (Giblin et al. 2010). In addition to temperature, organic carbon content and supply rate (Jensen et al. 1990), as well as bioturbation (Zimmerman and Benner 1994), can influence sediment oxygen consumption. Input of terrigenous organic matter can supply a large fraction of material deposited in the sediments that fuels benthic respiration (Zetsche et al. 2011). This terrigenous material also reduces light penetration and lowers *in situ* water column and benthic production rates. In systems with limited freshwater supply, *in situ* production of highly labile phyto-detritus will dominate the source of organic matter for the benthos, and could potentially lead to high benthic respiration and N and P regeneration rates (Caffrey et al. 1993; Witte et al. 2003). In Weeks Bay, freshwater discharge is low compared to other Gulf of Mexico estuaries (Twilley et al. 1996), but water column DIN can reach 50  $\mu\text{M}$  (Fig. 4a) and Chla concentrations can exceed 130  $\mu\text{g/l}$  (Fig. 4d). Therefore, we expected high benthic respiration in Weeks Bay compared to estuaries that have a larger terrigenous contribution and lower water column Chla concentrations. Benthic respiration in Weeks Bay (Fig. 5a), however, was within the lower range of that reported for the Gulf of Mexico river-dominated systems (Cowan et al. 1996; Twilley et al. 1996). For example, Mobile Bay, with a higher river flow ( $1,800 \text{ m}^3 \text{ s}^{-1}$ , Park et al. 2007) and lower DIN concentrations (maximum 14  $\mu\text{M}$ ) as well as water column Chla concentrations (range= $0.4$  to 22  $\mu\text{g/l}$ ), has a mean benthic respiration of  $0.56 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$  (Cowan et al. 1996), and this value is remarkably similar to that measured in Weeks Bay ( $0.6 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ). Benthic respiration in Weeks Bay accounts for  $<10\%$  ( $0.6$  of  $7.25 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) of R. This contribution to R is much smaller than that measured in other estuarine systems. Hopkinson and Smith (2005), based on a compilation of estuarine data, estimate a mean benthic respiration of  $1.1 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ , contributing to 23–37% of R.

## Benthic N and P Fluxes

The range in  $\text{NH}_4^+$  fluxes in Weeks Bay (Fig. 5b) was similar to that measured in some nearshore marine and estuarine systems along the Gulf of Mexico (Flint and Kamykowski 1984; Teague et al. 1988), North Carolina (Fisher et al. 1982), and the Parker River Estuary (Giblin

et al. 2010), with higher rates of benthic  $\text{NH}_4^+$  flux in the summer (Kemp and Boynton 1984; Cowan and Boynton 1996; Cowan et al. 1996). However, compared to other Gulf of Mexico estuaries, Weeks Bay  $\text{NH}_4^+$  fluxes were higher than those measured in Escambia (Murrell et al. 2009; Smith and Caffrey 2009) and Apalachicola (Mortazavi et al. 2000a) Bays, Florida and Mobile Bay, Alabama (Cowan et al. 1996). These higher  $\text{NH}_4^+$  fluxes may reflect higher organic matter availability in Weeks Bay sediments as indicated by high sediment *Chl a* concentrations (Fig. 4e). Benthic  $\text{NH}_4^+$  fluxes peaked 3–4 months following the peak in sediment *Chl a* concentrations (Fig. 4e), similar to observations in Chesapeake and Mobile Bays which showed a lag between peak sediment *Chl a* and nutrient release (Cowan and Boynton 1996; Cowan et al. 1996).

There was no apparent seasonal trend in benthic fluxes of  $\text{PO}_4^{3-}$  and  $\text{NO}_3^-$  (Fig. 4d, c). The  $\text{PO}_4^{3-}$  flux integrated over the study period was similar to the annual averages reported for nearby estuaries (Cowan et al. 1996, Mortazavi et al. 2000c). However, in contrast to Mobile Bay where there is a net  $\text{NO}_3^-$  efflux from the sediments to the water column (Cowan et al. 1996), in Weeks Bay there was an influx of  $\text{NO}_3^-$ :  $-33.7 \mu\text{mol N m}^{-2} \text{h}^{-1}$  (Magnolia River) and  $-28.3 \mu\text{mol N m}^{-2} \text{h}^{-1}$  (Mid Bay) into the sediments. The uptake of  $\text{NO}_3^-$  by the sediments in Weeks Bay was not accompanied by a comparable  $\text{N}_2$  efflux, suggesting that processes other than denitrification (e.g., DNRA) were consuming  $\text{NO}_3^-$ . Although denitrification is considered the primary N sink in estuaries,  $\text{NO}_3^-$  removal processes such as DNRA may be underestimated in many ecosystems (Burgin and Hamilton 2007), and may be an important sink for  $\text{NO}_3^-$  in estuarine and marine ecosystems (Christensen et al. 2000; Tobias et al. 2001; An and Gardner 2002; Gardner et al. 2006). Because DNRA is often linked to sulfur oxidation, the availability of reduced sulfur compounds may also favor DNRA over denitrification (Brunet and Garcia-Gil 1996; An and Gardner 2002). The high sulfide concentrations in Weeks Bay sediments (1.4 to 1.6 mM; Caffrey et al. 2007) support this contention. DNRA may have important implications within the estuary because, instead of removing N from the ecosystem, it is converting it to a more bioavailable form ( $\text{NH}_4^+$ ). Further investigations are required to determine the relative importance of DNRA versus denitrification in this estuary.

Measurements made with the MIMS suggest that integrated over the study period there was little to no net benthic  $\text{N}_2$  loss (Fig. 6). However, there were instances when  $\text{N}_2$  flux was positive. Interestingly, denitrification potential measurements showed measurable activity by the denitrifier community during all months examined (Fig. 7). With the exception of January and February (0–3 cm), peak in potential denitrification rates were measured when water column  $\text{NO}_3^-$  concentrations were low (Fig. 4a). River flow

generally peaks in the summer (Fig. 2b). However, unusually higher river discharge occurred during the winter months during the study period leading to high water column  $\text{NO}_3^-$  concentrations. The higher response to  $\text{NO}_3^-$  during the summer, when water column temperatures were higher, compared to winter months suggests, higher summer abundances or activity of the denitrifying community. It remains to be seen if the denitrifying community will be able to respond to higher water column  $\text{NO}_3^-$  concentrations during the summer when benthic respiration rates are high and higher sulfate reduction rates are expected (Miley and Kiene 2004). The higher sulfate reduction rates can lead to high pore water sulfide concentrations, inhibiting the nitrifying and denitrifying activity (Joye and Hollibaugh 1995; Brunet and Garcia-Gil 1996; Porubsky et al. 2009).

On an annual basis there was a small  $\text{N}_2$  uptake by the sediments, suggesting that net N fixation was occurring in Weeks Bay sediments similar to observations from Corpus Christi Bay (McCarthy et al. 2008) and Narragansett Bay (Fulweiler et al. 2007). In Corpus Christi Bay, net N fixation occurred during periods of normoxia and net denitrification during periods of hypoxia (McCarthy et al. 2008). With the exception of the February fluxes, the range of net  $\text{N}_2$  fixation at this site is similar to reported values for sub-tidal unvegetated sediments (Newell et al. 2002) and in sub-tropical estuaries (McCarthy and Gardner 2002; Ferguson et al. 2007). Generally,  $\text{N}_2$  fixation associated with sulfate reduction has been measured in seagrass beds (Welsh et al. 1996) and in wetlands (Santruckova et al. 2010), where supplies of labile organic carbon support the energy requirements for fixing  $\text{N}_2$ . High sulfide concentrations in Weeks Bay (1.4 to 1.6 mM; Caffrey et al. 2007) suggest that sulfate reduction in this estuary is occurring, and if an abundant labile carbon source is available, then a significant fraction of energy generated by sulfate reducers may then be routed to  $\text{N}_2$  fixation.

#### Phytoplankton Nutrient Demand

Monthly phytoplankton nutrient demand (PND) calculated using mean monthly GPP and the Redfield ratio was used to estimate the potential contribution of the sediment to water column primary production (Table 1). Only a small fraction of DIN and P, regenerated from the sediment, could potentially support primary production in the water column. Our estimates suggest sediments were contributing 0–18% DIN, 0–9% P for primary production at Magnolia River, and 0–38% DIN, 0–49% P for primary production at Mid Bay (Table 1). Based on the two stations monitored, on average benthic fluxes supply 4–11% and 2–6% of N and P requirements for water column primary producers, respectively (Table 1).

The exceptionally high contribution from the sediment to phytoplankton P demand in December at the Mid Bay site occurred during a period with low GPP (Fig. 8a) and

exceptionally high P flux (Fig. 5d). These results are similar to other sub-tropical estuaries where, during periods with low GPP, the sediments can supply a large proportion of the N and P required for primary production (Cowan et al. 1996; Cowan and Boynton 1996). In south San Francisco Bay, benthic nutrient fluxes increase during and immediately following an algal bloom because of increased organic matter deposition, supplying a large fraction of PND (Grenz et al. 2000). However, the overall contribution of benthos to PND is also small in South San Francisco Bay (Grenz et al. 2000). In the Providence River estuary, benthic nutrient fluxes in the summer months only provide 5–30% and 3–20% of the N and P, respectively, of PND (Fulweiler et al. 2010).

The contribution of benthic regenerated nutrients to water column primary production can be highly variable spatially and temporally. Boynton and Kemp (1985) calculated that the sediments contributed between 13% and 40% of the N required for primary producers in Chesapeake Bay, while Cowan and Boynton (1996) estimated that benthic regeneration contributed to 0–93% of N and 0–168% of P demand in the same estuary, respectively. In the Georgia Bight, sediment regeneration only contributed to 11% of the N demand for primary production (Hopkinson 1987). In Mobile Bay, the sediments contribute between 0 and 94% N (mean 36%) and 0 and 83% P (mean 25%) required for primary production (Cowan et al. 1996), similar in magnitude to another coastal plain estuary where benthic regeneration supplied 24% N and 12% P for primary production (Pratihary et al. 2009).

Water column respiration in Weeks Bay exceeds benthic respiration by a factor of 9 and, on average, consumes  $6.6 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ . Assuming a respiration quotient of 1 and the Redfield ratio, water column respiration can potentially result in regeneration of  $1,993 \text{ } \mu\text{mol N m}^{-2} \text{ h}^{-1}$  and  $125 \text{ } \mu\text{mol P m}^{-2} \text{ h}^{-1}$ , suggesting that water column regeneration can supply a large fraction of water column N and P demand (Table 1). Higher water column contribution to nutrient regeneration is also the case in Apalachicola Bay, a nearby shallow estuary, where, for example, water column N regeneration exceeded benthic  $\text{NH}_4^+$  flux by a factor of 4.7, and supplies a large fraction of water column nutrient demand (Mortazavi et al. 2000a).

Based on a compilation of data for estuaries with a mean depth of 6.4 m, Hopkinson and Smith (2005) estimated benthic respiration to be two to four times lower than water column respiration. The lower contribution of benthic to water column respiration in Weeks Bay could reflect the influence of factors other than organic input (allochthonous vs. autochthonous) and temperature on benthic respiration (Hopkinson and Smith 2005). Shallow estuaries can experience frequent resuspension events as a result of tides and storms (Liu and Huang, 2009). Field data (Hopkinson 1985,

1987) and modeling efforts (Wainright and Hopkinson 1997), as well as experimental data (Stahlberg et al. 2006), suggest that resuspension of bottom sediments enhances mineralization rates. At the mesocosm scale, resuspension events are shown to increase mineralization rates by a factor of 5, and field data suggest that the input of organic matter to the water column following resuspension events increases water column bacterioplankton production (Wainright 1987; Ritzrau and Graf 1992), and can drive shallow nearshore marine systems towards heterotrophy (Lawrence et al. 2004). Several mechanisms have been suggested to account for higher mineralization rates in the water column compared to the benthos. During resuspension events, pore dissolved organic matter and nutrients are released into the water column (Hopkinson 1985; Morin and Morse 1999), therefore increasing substrate and nutrient availability. In addition, bacteria from the sediments can also be transported into the water column (Garstecki et al. 2002). The resulting increase in the heterotrophic community, and organic matter exposure for longer time periods to oxic conditions, can lead to more efficient mineralization rates (Stahlberg et al. 2006). The net impact of these factors is an overall stimulation of R rates, with an increase in water column respiration and a concomitant decline in sediment respiration (Wainright and Hopkinson 1997), presumably because of higher organic matter degradation rates in the water column (Wainright and Hopkinson 1997). The dominance of water column respiration in Weeks Bay is consistent with the hypothesis that, in this 1.4-m-deep estuary, resuspension events are leading to a higher fraction of labile organic matter being remineralized in the water column. Canion (2008) observed that turbidity increased from 10 to 60 NTU with sustained wind speeds  $>5 \text{ ms}^{-1}$ , and varied from 5 to  $>15 \text{ NTU}$  as a result of tides during period with wind speeds were  $<5 \text{ ms}^{-1}$ . Similarly, Novoveská (2011) reported that during a 3-h storm, turbidity values increased from  $<15$  to 135 NTU during another mooring at Weeks Bay. Thus, in this eutrophic estuary, rates of R are high but the benthos makes a minor contribution to the overall nutrient regeneration and nutrient removal via denitrification. The current state of knowledge on whole system respiration (Hopkinson and Smith 2005) and the extent of the contribution of water column regeneration to primary production is lacking. Future research addressing the controls on ecosystem respiration and water column nutrient regeneration, particularly in shallow and highly impacted estuaries, will lead to better constraints on the role of these ecosystems in acting as filters for land-derived nutrients and organic carbon.

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