Factors Controlling Net Ecosystem Metabolism in U.S. Estuaries

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ABSTRACT: High frequency dissolved oxygen data were analyzed to calculate primary production, respiration and net ecosystem metabolism (NEM) from 42 sites within 22 National Estuarine Research Reserves (NERR), 1995–2000. NERR sites are characterized by a variety of dominant plant communities including phytoplankton, salt marsh, seagrass, macroalgae, freshwater macrophyte, and mangrove, and are representative of the coastal bioregions of the United States. As expected from the wide diversity of sites, metabolic rates were temporally and spatially variable with the highest production and respiration occurring during the summer in Southeastern estuaries. Sites within different regions exhibited consistent seasonal trends in production, respiration, and NEM. Temperature was the most important environmental factor explaining within-site variation in metabolic rates; nutrient concentrations were the second most important factor. All but three of the 42 sites were heterotrophic (respiration was greater than production) on an annual basis. Habitat adjacent to the monitoring site, estuarine area, and salinity explained 58% of the variation in NEM. Open water sites or sites adjacent to mangroves or in marsh creeks were heterotrophic, while sites in or adjacent to submerged aquatic vegetation (eelgrass or macroalgal beds) were either autotrophic or near balance. Estuarine area was also a significant factor explaining variability in NEM; larger systems were closer to balance than smaller systems that trended toward heterotrophy. Freshwater sites were more heterotrophic than saline sites. Nutrient loading explained 68% of the variation in NEM among some of the sites. When these estimates were compared to the literature, metabolic rates from the NERR sites were much larger, often two to five times greater than rates from other estuarine and coastal systems. One explanation is that these small, generally shallow sites located near shore may have greater allochthonous organic inputs as well as significant benthic primary production than the large, deeper systems represented by the literature.

Introduction

Net ecosystem metabolism (NEM), the net effect of production and respiration, in coastal and estuarine environments is a means to evaluate whether such environments are sources or sinks of carbon (Smith and Hollibaugh 1993; Gattuso et al. 1998). By definition, NEM is positive (autotrophic) when production exceeds respiration and negative (heterotrophic) when respiration exceeds production. The magnitude of primary production and respiration varies widely among aquatic ecosystems from oligotrophic coral reefs and the open ocean to highly eutrophic streams, rivers and estuaries, as does NEM. Increased loading of nutrients leads to increased NEM by stimulation of production over respiration in marine mesocosms (Oviatt et al. 1986) and Waquoit Bay (D'Avanzo et al. 1996). In systems dominated by organic carbon loading such as Tomales Bay, California (Smith and Hollibaugh 1993, 1997), Satilla River, Georgia (Cai et al. 1999), and York River, Virginia (Raymond et al. 2000), NEM is heterotrophic. The balance between organic carbon and nutrient loading is critical in determining the balance between autotrophy and heterotrophy (Kemp et al. 1997; Eyre and McKee 2002).

Even within a single aquatic system, metabolic rates vary temporally and spatially. In San Francisco Bay, seasonal phytoplankton blooms shifted the system from heterotrophy to autotrophy (Caffrey et al. 1998). Variation along salinity and depth gradients has been observed in some estuaries. NEM changes from heterotrophy to autotrophy along the estuarine gradient (Howarth et al. 1996; Raymond et al. 2000). A similar pattern along depth gradients has also been observed, with shoals being more autotrophic than the typically light-limited channels (Kemp et al. 1997; Caffrey et al. 1998). While most metabolism studies have focused on the channels of large systems, this study focuses on the shallow, nearshore region of estuaries in the National Estuarine Research Reserve (NERR) system. Given their wide geographic distribution, NERRs are representative of the coastal bioregions of the United States.

A variety of techniques have been used to measure NEM from relatively simple budget calculations (e.g., LOICZ unpublished material; Smith and Hollibaugh 1997), to the addition of individually measured components of production and respiration (Kemp and Boynton 1980; Caffrey et al. 1998), or open water oxygen measurements (Odum 1956; Kemp and Boynton 1980). The LOICZ or biogeochemical stoichiometry approach incorporates simple box models of water, salinity,

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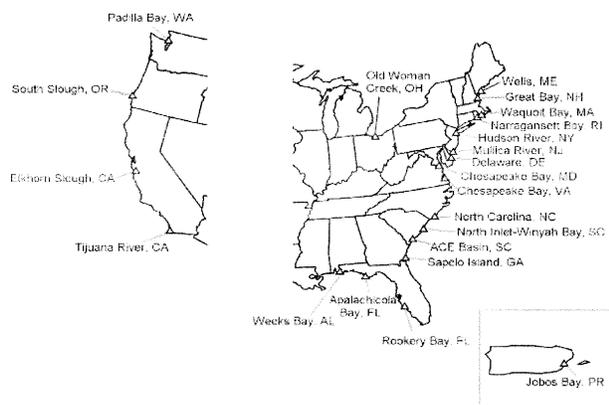
Fig. 1. Location of National Estuarine Research Reserve monitoring sites in the continental United States and Puerto Rico (not to scale).

nutrients, and an appropriate stoichiometric relationship between carbon and phosphorus to estimate NEM. This approach provides estuary-wide seasonal or annual estimates of NEM, but no estimate of production or respiration individually. Individual measurements of production and respiration can be summed to estimate NEM, although the propagation of errors associated with each individual measurement can be large, making it difficult to resolve whether NEM is positive or negative. In addition, isolating communities in bottles or chambers may lead to artifacts and unrealistic rates (Kemp and Boynton 1980). Technological advances have made continuous, high frequency measurements of dissolved oxygen increasingly easy and reliable. Primary production, respiration, and NEM can be calculated using the open water oxygen method (Odum 1956). Oxygen concentrations usually exhibit a characteristic diurnal pattern with concentrations increasing from morning into mid-afternoon as photosynthetic oxygen production outstrips respiratory processes. Declining oxygen concentrations occur during the late afternoon or evening as photosynthetic rate declines to zero with darkness. An important assumption is that observed changes in dissolved oxygen are due to biological processes, not advection. This implies that water masses passing by the sensor are laterally and vertically homogenous. Where this assumption is badly violated, metabolic rates will be incorrect (Kemp and Boynton 1980; Swaney et al. 1999).

The NERR System Wide Monitoring Program was established in 1995 to evaluate short-term variability and long-term changes in water quality at the NERR sites (Fig. 1). This study summarizes how metabolic rates calculated from water quality monitoring data change over a seasonal and annual basis, and to examine interannual trends in the dataset. It is the largest and most geographi-

cally diverse analysis of metabolic rates using identical measurements to date. Relationships among metabolic rates, physical, chemical, and biological factors are compared at several Reserves with extensive nutrient and chlorophyll a (chl a) data. The results are compared to literature values from other estuaries.

Methods

This study used half-hourly records of dissolved oxygen collected by the NERR System Wide Monitoring Program, January 1995–December 2000. Dissolved oxygen, temperature, salinity, pH, and turbidity were measured with YSI data sondes. Data were collected from two sites at each of 22 Reserves (Fig. 1 and Table 1). Two sites were excluded from this analysis based on a previous study, which suggested that physical factors overwhelmed biological activity at these locations (Caffrey 2003). At these two sites, dissolved oxygen concentrations varied depending on water flow and rarely showed the characteristic diurnal pattern that was observed at all other sites. Sites were categorized based on the dominant habitat adjacent to the deployment site. Detailed descriptions of each site are available in Wenner et al. (2001). Water surface area (Table 1) was calculated based on individual descriptions of sites (Wenner et al. 2001) and generally represent subsystems (i.e., tidal creek or embayment) within the estuary as a whole.

All data has undergone extensive quality control and quality assurance to remove data collected when data sondes were malfunctioning (Wenner et al. 2001).

CALCULATIONS

Metabolic rates were calculated as described in Caffrey (2003). Oxygen flux (g O_2 m^{-2}) was calculated from the change in oxygen concentrations (DO) in g O_2 m^{-3} between half hour readings, accounting for air-sea exchange as described in Eq. 1 below.

$$\text{Oxygen flux} = \Sigma_{i=1}^{t} (\text{DO}_t - \text{DO}_{(t-1)}) * \text{water depth} - \text{air-sea exchange} \quad (1)$$

Oxygen flux during the daylight hours is net apparent production, while oxygen flux at night is night respiration. By convention, respiration is expressed as a positive number, thus night oxygen flux was multiplied by -1. Gross production is calculated as the sum of net apparent production plus the respiration occurring during daylight hours. Total respiration is the respiration for the entire 24-h period, by extrapolating night respiration to daylight hours. NEM was calculated by subtracting total respiration from gross production or more

TABLE 1. Characteristics of Reserve sites grouped by region including habitat type, $\log_{10}$ estimated water surface area (km²), average water depth, and tide range. Days of data used for analysis with 48 dissolved oxygen observations per day. SAV indicates submerged aquatic vegetation.

Region/Reserve (State)	Site	Abbreviation	Days of Data	Habitat Type	Water Surface Area, $\log_{10}$ (km²)	Water Depth (m)	Tide Range (m)
Caribbean and Gulf of Mexico							
Jobos Bay (Puerto Rico)	Station 10	JOB-10	562	Mangrove	−1.5	1.0	0.4
Jobos Bay	Station 9	JOB-09	528	Mangrove	−1.0	0.9	0.4
Rookery Bay (Florida)	Blackwater River	RKB-BR	419	Mangrove	−0.6	2.0	0.7
Rookery Bay	Upper Henderson	RKB-UH	1,106	Mangrove	−0.8	1.5	1.6
Apalachicola (Florida)	Bottom	APA-EB	784	Open water	1.2	1.8	0.5
Apalachicola	Surface	APA-ES	1,057	Open water	1.2	1.8	0.5
Weeks Bay (Alabama)	Fish River	WKB-FR	1,168	Open water	0.7	2.4	0.4
Weeks Bay	Weeks Bay	WKB-WB	1,191	Open water	0.7	1.3	0.4
Southeast							
Sapelo (Georgia)	Flume Dock	SAP-FD	752	Marsh	−0.6	2.5	2.4
Sapelo	Marsh Landing	SAP-ML	721	Marsh	0.2	6.0	2.4
ACE (South Carolina)	Big Bay Creek	ACE-BB	888	Marsh	−2.5	1.3	2
ACE	St Pierre	ACE-SP	871	Marsh	−1.7	1.8	2
North Inlet-Winyah Bay (South Carolina)	Oyster Landing	NIW-OL	1,187	Marsh	−1.1	1.5	1.4
North Inlet-Winyah Bay	Thousand Acre Creek	NIW-TA	1,201	Marsh	−1.9	1.2	1
North Carolina	Masonboro Inlet	NOC-MS	1,496	Marsh	−1.8	1.5	1.2
North Carolina	Zeke's Island	NOC-ZI	1,514	Marsh	−1.4	1.5	1.3
Mid Atlantic							
Chesapeake Bay (Virginia)	Goodwin Island	CBV-GI	926	SAV	0.0	1.0	0.7
Chesapeake Bay (Virginia)	Taskinas Creek	CBV-TC	1,296	Marsh	−1.2	1.3	0.8
Chesapeake Bay (Maryland)	Jug Bay	CBM-JB	424	Marsh	−2.3	1.7	0.8
Chesapeake Bay (Maryland)	Patuxent Park	CMB-PR	243	Marsh	−1.3	2.4	0.8
Delaware Bay (Delaware)	Blackwater Landing	DEL-BL	1,377	Marsh	0.4	1.8	0.9
Delaware Bay	Scotton Landing	DEL-SL	1,043	Marsh	0.0	1.8	1.5
Mullica River (New Jersey)	Buoy 126	MUL-B6	781	Open water	1.7	3.0	1.1
Mullica River	Lower Bank	MUL-BA	627	Open water	1.0	2.0	1.0
Northeast							
Old Woman Creek (Ohio)	State Route 2	OWC-SU	827	Open water	−1.2	0.5	
Old Woman Creek	State Route 6	OWC-WM	790	Open water	−1.2	0.6	
Hudson River (New York)	Tivoli South	HUD-TS	855	Marsh	−0.2	1.5	1.2
Narragansett Bay (Rhode Island)	Potters Cove	NAR-PC	973	Open water	−0.6	3.5	1.1
Narragansett Bay	T-wharf	NAR-TW	519	Open water	2.6	4.5	1.1
Waquoit Bay (Massachusetts)	Central Basin	WQB-CB	316	SAV	0.6	2.0	0.4
Waquoit Bay	Metoxit Point	WQB-MP	305	SAV	0.6	1.8	0.4
Great Bay (New Hampshire)	Great Bay Buoy	GRB-GB	785	SAV	1.4	4.8	2.1
Great Bay	Squamscott River	GRB-SQ	430	Open water	0.1	3.0	2.1
Wells (Maine)	Head of Tide	WEL-HT	274	Marsh	−1.7	0.7	2.6
Wells	Inlet	WEL-IN	1,099	Open water	0.1	3.5	2.6
Pacific							
Padilla Bay (Washington)	Bay View	PDB-BY	947	SAV	1.4	3.2	1.6
South Slough (Oregon)	Stengstacken Arm	SOS-SE	909	Marsh	−0.5	1.2	1.7
South Slough	Winchester Arm	SOS-WI	859	Marsh	−0.2	1.4	1.7
Elkhorn Slough (California)	Azevedo Pond	ELK-AP	1,656	Marsh	−2.4	0.7	0.2
Elkhorn Slough	South Marsh	ELK-SM	1,195	Marsh	−1.4	1.6	1.7
Tijuana River (California)	Oneonta Slough	TJR-OS	1,045	Marsh	−1.4	1.0	1.3
Tijuana River	Tidal Linkage	TJR-TL	509	Marsh	−2.1	0.8	1.3

simply by subtracting night respiration from net apparent production.

Air-sea exchange, was estimated by Eq. 2 below

$$\text{Air-sea exchange} = \overline{satdeficit} * k_s * dt$$
$$\equiv [1 - (DO_{sat,t2} + DO_{sat,t1})200]$$
$$* k_s * dt \qquad (2)$$

where $\overline{satdeficit}$ is the mean fractional saturation def-

icit, ($DO_{sat,t1}$ $DO_{sat,t2}$) are the percent oxygen saturation (units −%) at t1 and t2 and dt is the time interval (hr) between t2 and t1. The time interval for all data was 0.5 h. The coefficient, k_s, was assumed to be 0.5 g O_2 m^{-2} hr^{-1} at zero O_2 and was used to estimate the air-sea exchange (Kemp and Boynton 1980). When the oxygen concentration for a time interval (($DO_{sat,t1}$ + $DO_{sat,t2}$)/200) is un-

dersaturated, oxygen diffuses from the air into the water and air-sea exchange is positive. If oxygen concentrations are supersaturated, oxygen diffuses out of the water into the air and air-sea exchange is negative. Previous research has shown that the rate of diffusion is dependent on wind speed (Copeland and Duffer 1964; Hartman and Hammond 1984; Marino and Howarth 1993; Raymond and Cole 2001), or current speed (Hartman and Hammond 1984). In order to evaluate the above approach, I analyzed the effect of wind speed on air-sea exchange compared to a constant diffusion coefficient using the equations from Hartman and Hammond (1984), Marino and Howarth (1993) and D'Avanzo et al. (1996).

Production rates were converted from oxygen to carbon assuming a photosynthetic quotient of 1.2 (O_2:CO_2 molar) and a respiratory quotient of 1 (O_2:CO_2 molar).

ANCILLARY DATA

Eight sites (ACE-BB, ELK-AP, ELK-SM, GRB-GB, GRB-SQ, HUD-TS, NIW-OL, NIW-TA) had monthly dissolved inorganic nitrogen (DIN) and phosphorus (DIP) data for 1995–2000 and four of these sites (GRB-GB, GRB-SQ, NIW-OL, NIW-TA) had additional chl *a* data. Alkalinity, Cl^-, and SO_4^{2-} were measured monthly at one site (HUD-TS). Dissolved organic carbon (DOC) was measured at two sites (NIW-OL, NIW-TA).

STATISTICAL ANALYSIS

Daily metabolic rate data were averaged by month and by season (winter: December–February; spring: March–May; summer: June–August; fall: September–November) for each year. Means and standard error of the mean were calculated for the annual data. Two approaches were used to examine the importance of different physical, chemical, and biological factors on metabolic rates. The first focused on seasonal variations in metabolic rates at the eight sites with ancillary data. The relationships among metabolic rate (production, respiration, and NEM) versus environmental variables (temperature, salinity, precipitation, the percent deviation of rainfall from average rainfall, and ancillary data) were analyzed with a backward stepwise linear multiple regression analysis (alpha to remove = 0.15) for each site. The second analysis examined variation in NEM among different sites. A backward stepwise multivariate general linear model with annual average NEM, habitat, depth, temperature, salinity, tide range, and estuarine surface area was performed. Estuarine surface area was log transformed. In addition, the relationship between nutrient (DIN or DIP) loading and NEM was examined using a linear re-

gression model. All statistical analyses were performed using SYSTAT.

Results

Average annual rate of gross primary production ranged from 2.3–28.1 g O_2 m^{-2} d^{-1} (Table 2). The site with the highest gross production also had the highest total respiration (32.3 g O_2 m^{-2} d^{-1}), while the lowest respiration rate was 4.4 g O_2 m^{-2} d^{-1} (Table 2). All but three sites were heterotrophic on an annual basis, with NEM varying from -7.6–0.9 g O_2 m^{-2} d^{-1} (Table 2).

SPATIAL AND SEASONAL TRENDS BY REGION

Most sites exhibited strong seasonal patterns with high rates of gross primary production and total respiration in the summer and low rates in the winter. One of the Delaware sites (DEL-BL) provided a good illustration of daily and seasonal variation (Fig. 2). Seasonal trends at Puerto Rico (JOB-09) were muted with little distinction between winter and summer (Fig. 2), perhaps due to the relatively small range in temperature (22°C–32°C). NEM also exhibited seasonal differences in rates at most sites, although there were more sites with weaker seasonal patterns than for production and respiration. Regional trends in interannual rates of metabolic rates were minimal, although distinct interannual trends were evident at a few individual sites (data not shown).

In the following sections, where gross primary production and respiration are discussed, only plots of production are shown. The trends in production and respiration were consistent at all sites.

CARIBBEAN AND GULF OF MEXICO

Seasonal patterns of production and respiration in this region were muted (Fig. 3). Gross production was highest in the summer at sites along the northern Gulf of Mexico (Apalachicola Bay and WKB-WB). The South Florida (Rookery Bay) and one of the Puerto Rican sites (JOB-09) had higher rates of gross production in the spring and summer, while the other sites (JOB-10 and WKB-FR) were very similar throughout the year (Fig. 3). Apalachicola Bay had lower metabolic rates than other Reserves in this region. All sites from this region were strongly heterotrophic, particularly the Rookery Bay sites (Fig. 4). The Blackwater River site in Rookery Bay (RKB-BR) was autotrophic only 1 d of the 419 d record. NEM exhibited consistent seasonal patterns of greater heterotrophy during the summer, except in Puerto Rico (JOB), which was most heterotrophic during the fall (Fig. 3).

SOUTHEAST

Production and respiration rates in the Southeast region were greatest in Georgia and decreased

TABLE 2. Annual average rates of gross primary production, total respiration, and NEM (NEM) in g O_2 m^{-2} d^{-1} at NERR sites.

Region/Reserve/Site	Production		Respiration		NEM	
	Mean	(SE)	Mean	(SE)	Mean	(SE)
Caribbean and Gulf of Mexico						
Jobos Bay 10	4.2	0.3	6.8	0.5	−2.6	0.4
Jobos Bay 09	5.7	0.4	10.0	0.6	−4.3	0.4
Rookery Bay Blackwater River	3.9	0.4	11.5	0.4	−7.6	0.3
Rookery Bay Upper Henderson	5.6	0.3	11.6	0.4	−5.9	0.3
Apalachicola Bottom	3.1	0.2	5.6	0.4	−1.6	0.2
Apalachicola Surface	2.8	0.2	4.4	0.3	−2.5	0.3
Weeks Bay Fish River	7.7	0.9	7.4	1.0	−2.2	0.3
Weeks Bay Weeks Bay	6.9	1.3	7.0	1.2	−2.0	0.3
Southeast						
Sapelo Flume Dock	18.4	1.5	22.1	1.7	−3.7	0.3
Sapelo Marsh Landing	9.2	0.8	11.1	1.0	−1.9	0.3
ACE Big Bay Creek	12.4	0.7	17.9	0.9	−5.4	0.7
ACE St. Pierre	12.0	0.6	14.7	0.8	−2.6	0.3
North Inlet-Winyah Bay Oyster Landing	7.0	0.3	7.9	0.4	−2.2	0.3
North Inlet-Winyah Bay Thousand Acre Creek	4.7	0.3	5.6	0.3	−3.0	0.2
North Carolina Masonboro Inlet	5.5	0.3	7.7	0.5	−0.9	0.2
North Carolina Zeke's Island	3.5	0.3	6.4	0.4	−0.9	0.2
Mid-Atlantic						
Chesapeake Bay Virginia Goodwin Island	5.2	0.4	4.7	0.5	0.5	0.2
Chesapeake Bay Virginia Taskinas Creek	8.9	0.6	8.5	0.7	−2.1	0.2
Chesapeake Bay Maryland Jug Bay	6.8	0.5	12.3	0.6	−5.6	0.4
Chesapeake Bay Maryland Patuxent Park	8.2	1.6	10.2	1.4	−2.0	0.4
Delaware Bay Blackwater Landing	11.2	1.0	13.9	1.2	−2.7	0.2
Delaware Bay Scotton Landing	9.4	0.9	11.0	1.1	−1.6	0.4
Mullica River Buoy 126	5.8	0.6	5.9	0.6	−0.03	0.2
Mullica River Lower Bank	2.7	0.3	4.8	0.5	−2.1	0.3
Northeast						
Old Woman Creek State Route 2	2.3	0.2	6.4	0.3	−4.1	0.3
Old Woman Creek State Route 6	2.7	0.2	6.3	0.4	−3.6	0.3
Hudson River Tivoli South	3.0	0.3	4.6	0.4	−1.6	0.2
Narragansett Bay Potters Cove	8.2	0.6	9.9	0.8	−1.7	0.3
Narragansett Bay T-wharf	8.0	1.0	9.4	1.2	−1.3	0.4
Waquoit Bay Central Basin	6.6	0.3	8.8	0.4	0.3	0.2
Waquoit Bay Metoxit Point	5.6	0.4	7.2	0.5	−0.1	0.4
Great Bay Great Bay Buoy	7.6	0.6	7.8	0.6	−0.2	0.2
Great Bay Squamscott River	6.5	0.6	7.1	0.7	−0.6	0.3
Wells Head of Tide	3.3	0.4	6.9	0.8	−3.6	0.5
Wells Inlet	5.1	0.5	4.9	0.5	0.9	0.3
Pacific						
Padilla Bay Bay View	11.4	1.1	11.7	1.0	−0.4	0.2
South Slough Stengstacken Arm	14.4	1.4	16.5	1.4	−2.1	0.2
South Slough Winchester Arm	10.0	0.9	11.3	1.0	−1.3	0.2
Elkhorn Slough Azevedo Pond	11.0	0.5	13.3	0.5	−2.2	0.2
Elkhorn Slough South Marsh	3.0	0.2	4.4	0.2	−1.4	0.2
Tijuana River Oneonta Slough	15.1	0.9	19.1	1.0	−4.0	0.3
Tijuana River Tidal Linkage	28.1	2.4	32.3	2.3	−4.1	0.4

with latitude (Fig. 5). All sites had peak summer rates except for the South Carolina site, ACE-SP, which had peak rates in the spring. Summer rates of production and respiration were about double those in the Gulf and Caribbean regions. Production and respiration in North Carolina often had a bimodal pattern, with peaks in both March–April and again in June–August (Fig. 6). Southeastern sites were similar to the Gulf and Caribbean sites in exhibiting a distinct seasonal pattern in NEM

(Fig. 5). Summer was the period with the greatest heterotrophy, except at two sites (ACE-SP and SAP-ML) that were most heterotrophic during the spring months (Fig. 5). Sites in the Southeast were usually balanced or autotrophic during the winter months. The North Carolina sites were the least heterotrophic of the Southeastern sites and were autotrophic or balanced during fall and winter months, particularly Zeke's Island (Fig. 6). One South Carolina site (NIW-OL) also became auto-
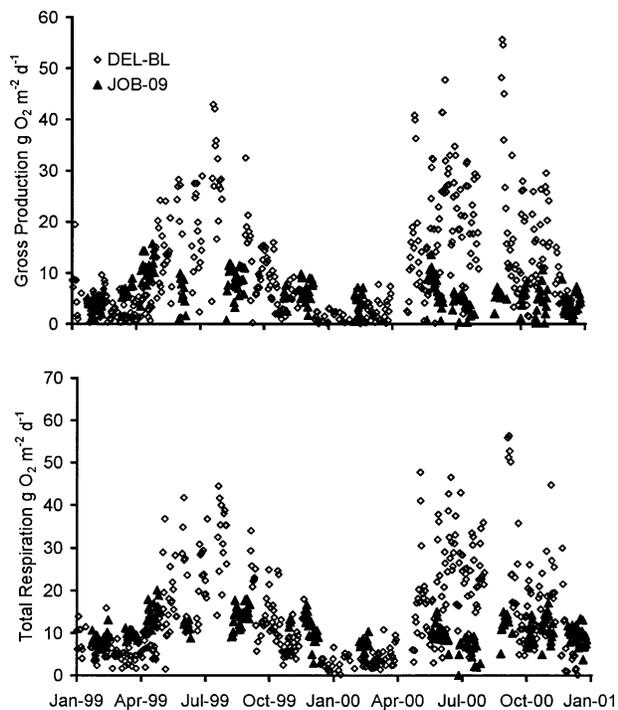
Fig. 2.   Daily gross production and total respiration (g O_2 m^{-2} d^{-1}) at Delaware Blackbird Landing (DELBL) and Jobos station 9 (JOB09), January 1999–December 2000.
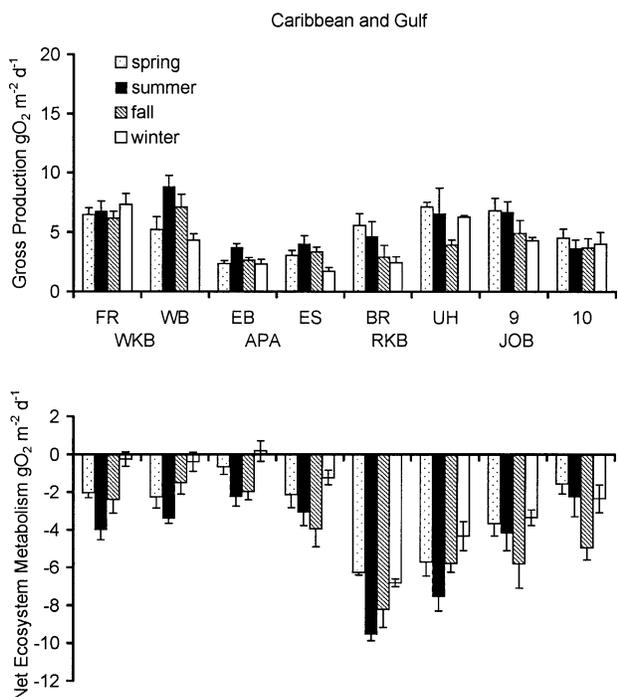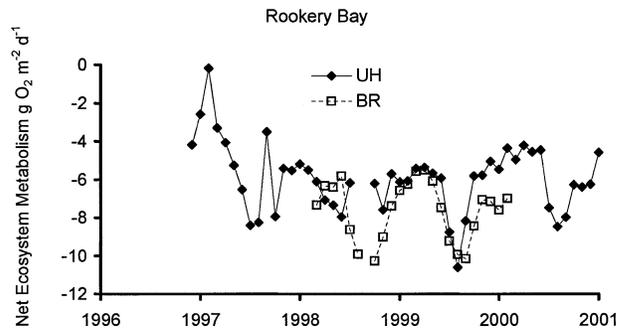

Fig. 4.   Monthly average NEM (g O_2 m^{-2} d^{-1}) at Rookery Bay Upper Henderson and Blackwater River, 1996–2000.

trophic (or balanced) every January or February (data not shown).

Mid-Atlantic

All sites within this region exhibited consistent seasonal trends in production and respiration, except for the Chesapeake Bay Maryland sites where limited sampling makes interpretations difficult. Summer production and respiration rates were often 1.5–2 times higher than rates in the other seasons (Fig. 7). Summer rates were comparable to those in the Southeast region. Rates ranged from being relatively low at one New Jersey site (MUL-BA) to high at the Delaware sites. As in the Southeast and Caribbean and Gulf of Mexico regions,

Fig. 3.   Seasonal gross production and NEM (g O_2 m^{-2} d^{-1}) in Caribbean and Gulf of Mexico region (mean + SE).
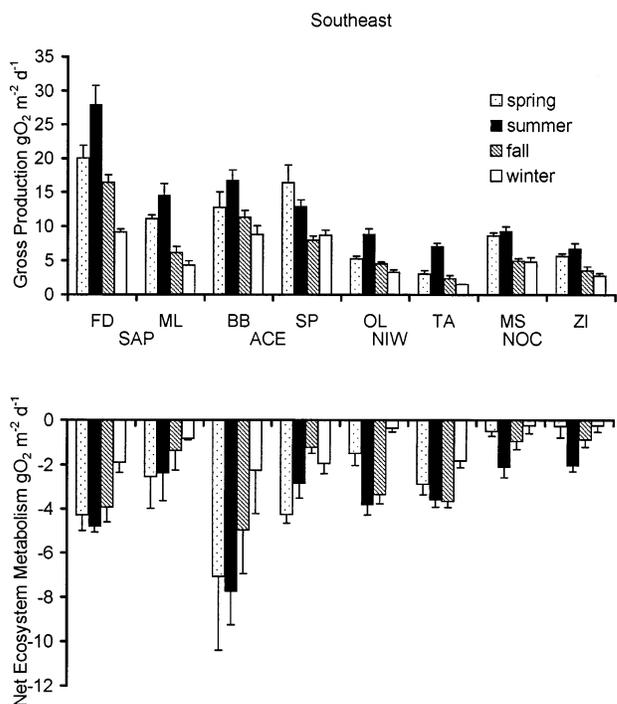
Fig. 5.   Seasonal gross production and NEM (g O_2 m^{-2} d^{-1}) in the Southeast region (mean + SE).
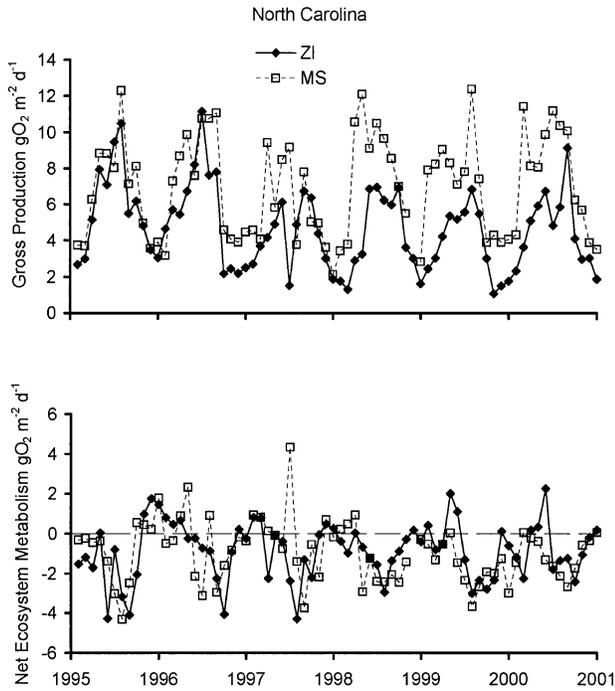
Fig. 6. Monthly average gross production and NEM (g O_2 m^{-2} d^{-1}) at North Carolina Masonboro Inlet and Zeke's Island, 1995–2000.

Fig. 7. Seasonal gross production and NEM (g O_2 m^{-2} d^{-1}) in the Mid Atlantic region (mean + SE).
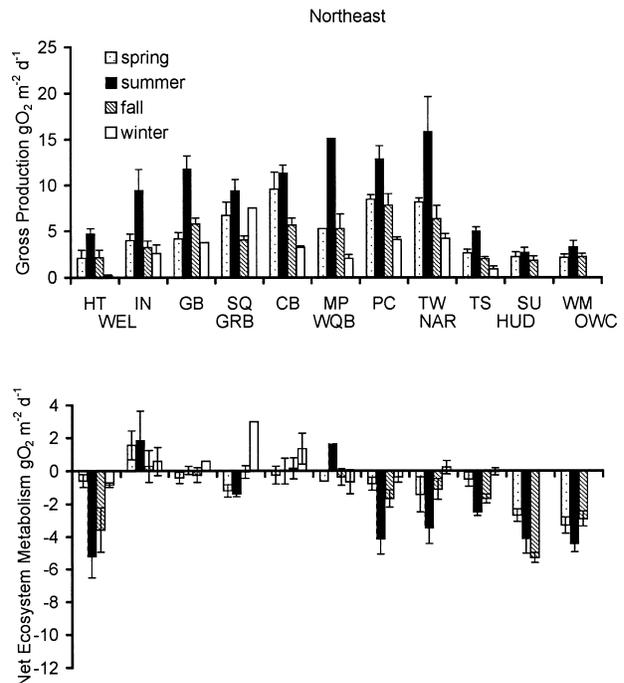
Fig. 8. Seasonal average gross production and NEM (g O_2 m^{-2} d^{-1}) in the Northeast region.

strong seasonal patterns in NEM were apparent, although the magnitude of NEM was variable among sites (Fig. 7). Maximum heterotrophy during the summer was consistently observed at all sites (excluding Chesapeake Bay Maryland). Two sites (CBV-GI and MUL-BA) were usually autotrophic or balanced during the other seasons.

NORTHEAST

All Reserves in this region had peak production and respiration rates during summer (Fig. 8). Few reserves collected data during winter months due to ice cover, but where data were available (e.g., Wells), rates were often near zero. The high winter primary production rate observed at Great Bay Squamscott should be interpreted with caution because it represented just 3 d from the entire 430-d record. Production and respiration rates were quite low year-round compared to the other regions, usually less than 5 g O_2 m^{-2} d^{-1}, in Ohio and one Maine site (WEL-HT). In contrast to the other regions, the Northeast region did not exhibit a coherent seasonal pattern in NEM (Fig. 8). Several sites in this region (Waquoit Bay, Wells Inlet, and Great Bay Great Bay sites) were balanced or autotrophic and showed little consistent seasonal variation. NEM at the other sites was heterotrophic, with the greatest degree of heterotrophy usually occurring in the summer at the five of the sites
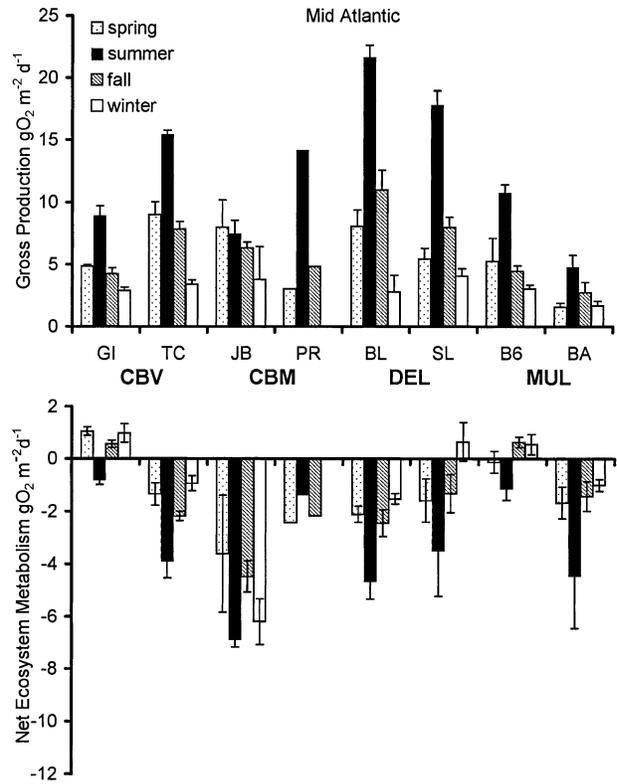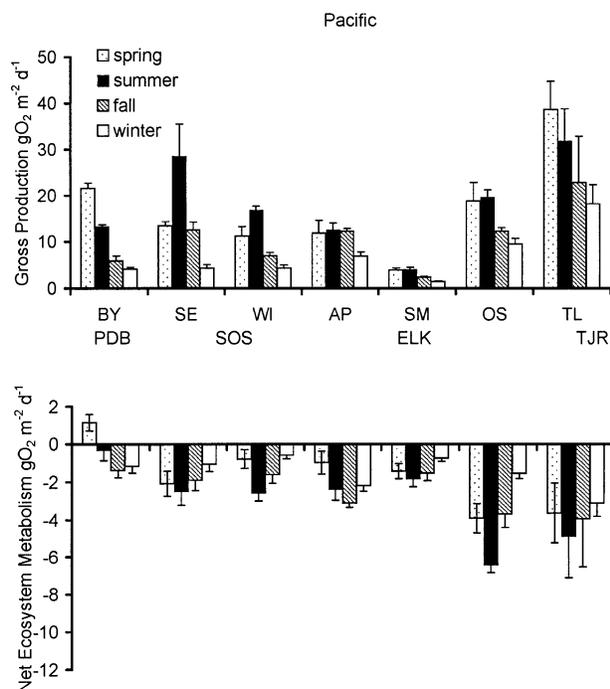
Fig. 9.   Seasonal gross production and NEM (g O_2 m^{-2} d^{-1}) in the Pacific region (mean + SE).

(WEL-HT, OWC-WM, HUD-TS, and Narragansett Bay sites).

PACIFIC

Sites in this region span the greatest geographical and climatic gradients, so it is not surprising that seasonal patterns were not consistent. Only Oregon (SOS) sites exhibited the typical summer peak in production and respiration rates that were observed in the Southeast, Mid-Atlantic, and Northeast regions. Southern California (TJR) and Washington (PDB) sites had peak rates in the spring (Fig. 9). Central California (ELK) sites did not show any consistent seasonal trends. The California sites had both the highest (TJR-TL) and lowest (ELK-SM) production and respiration rates in this region. Seasonal patterns in NEM in this region were consistent with patterns observed in other regions, namely, heterotrophy at most sites in the summer. Padilla Bay Bayview was consistently autotrophic in the spring and balanced in the summer.

FACTORS CONTROLLING METABOLIC RATES

The seasonally averaged data shown in Figs. 3, 5, 7, 8, and 9 confirm the importance of temperature for the entire dataset. Stepwise multiple regression was used to examine how monthly metabolic rates (gross production, respiration, and NEM) were related to physical (temperature, salinity, rainfall, deviation from normal rainfall), chemical (DIN, DIP, TN, TP, DOC) and biological (chl *a*) variables. Regression models for all metabolic rates at the eight sites with ancillary data were significant, with one exception (Table 3). The regression models explained 20–90% of the variation in metabolic rates. The coefficients of determination (r^2) were generally higher for gross production and respiration than NEM. Temperature was a significant factor in 22 out of 24 models. Nutrient concentrations were a significant factor in six out of eight NEM models, three out of eight gross production models, and four out of eight respiration models (Table 3). Nitrogen was most often the nutrient included in the regression models, except at HUD-TS, which is freshwater, and NIW-OL, where phosphorus was significant. Precipitation was a significant factor in the production, respiration and NEM regression models at the ELK-SM site and for several of the models at the NIW sites and for production at GRB-SQ (Table 3).

AIR-SEA EXCHANGE

Oxygen diffusion across the water surface can be a significant physical process affecting oxygen concentrations in the water. Dissolved oxygen conditions used to compare air-sea exchange encompass values observed at most of the reserves (between 0–200% saturation) (Wenner et al. 2001). The gas transfer coefficient, k, was calculated for wind speeds between 0 and 10 m s^{-1}. The values using a constant coefficient were most similar to those based on wind-dependent coefficients at wind speeds between 0–5 m s^{-1}, although this technique greatly underestimated air-sea exchange relative to wind-dependent calculations when winds exceeded 8 m s^{-1} (Fig. 10). How these different assumptions about air-sea exchange affect metabolic rates is complex. If the site was consistently windy over the 24-h period, higher air-sea exchange values would lead to high production and respiration values, but little change in NEM compared to estimates based on a constant k. If the site experienced a diurnal wind pattern of strong winds during the day and calm conditions at night, higher air-sea exchange during the day would lead to enhanced production, but no change in respiration, with NEM becoming more autotrophic. Air-sea exchange has a proportionately larger effect on the metabolic rate calculations in shallow water depths than in deep water. At 1 m water depths, air-sea exchange represented about 25% of the oxygen flux, while at 8 m it was less than 5% (data not shown).

Discussion

The most significant result of this study was that habitat adjacent to the monitoring site explained

TABLE 3. Regression models of gross production, respiration, and NEM at sites with ancillary data. Variables included in the model were temperature (T), salinity (S), precipitation (Pr), and percent deviation from normal precipitation (Pd), dissolved inorganic nitrogen (DIN) (or NO_3^- at HUD-TS), dissolved inorganic phosphorus (DIP), total nitrogen (TN), total phosphorus (TP), alkalinity (A), chloride (Cl^-), sulfate (SO_4^{2-}), dissolved organic carbon (DOC), and Chl a (C). Significant factors at $p < 0.05$.

| Site	Gross Production		Respiration		NEM		Variables Included in Models in Addition to T, S, Pr, and Pd
	r^2	Significant Factors	r^2	Significant Factors	r^2	Significant Factors	
ACE-BB	0.27	T	0.56	T, S, DIN	0.56	T, S, DIN	DIN, DIP
ELK-AP	0.43	T, DIN, DIP	0.43	T, S	0.26	S, DIN, DIP	DIN, DIP
ELK-SM	0.30	T, Pr	0.40	T, Pr	0.17	S, Pd	DIN, DIP
GRB-GB	0.65	T	0.72	T	0.06	None	DIN, DIP, C
GRB-SQ	0.71	T, S, Pr, C	0.76	T, C	0.56	T, DIN	DIN, DIP, C
HUD-TS	0.56	T, Cl^-	0.84	T, Cl^-, SO_4^{2-}, DIP	0.83	T, Pr, Pd, A, Cl^-, SO_4^{2-}, DIP	NO_3^-, DIP, A, Cl^-, SO_4^{2-}
NIW-OL	0.79	T, Pr, TP, DOC, C	0.89	Pd, DOC, C	0.69	T, TP, C	DIN, DIP, TN, TP, DOC, C
NIW-TA	0.82	T, TN, DOC, C	0.78	T, S, Pr, Pd, DIN, C	0.41	T, Pr, Pd, DIN	DIN, DIP, TN, TP, DOC, C
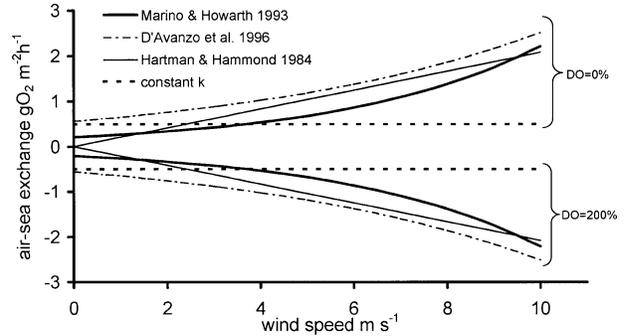
Fig. 10. Air-sea exchange (g O_2 m^{-2} h^{-1}) versus wind speed m s^{-1} where air-sea exchange was calculated using either a constant gas transfer coefficient (constant k) or one proportional to wind speed based on equations from Hartman and Hammond (1984), Marino and Howarth (1993), or D'Avanzo et al. (1996).

the general trends in NEM among different sites (Fig. 11). Sites adjacent to mangroves or in marsh creeks were heterotrophic, often strongly heterotrophic. Sites adjacent to submerged aquatic vegetation (eelgrass or macroalgal beds) were either autotrophic or near balance. Open water sites were generally heterotrophic, although the variation between sites was large. Several factors likely contribute to these patterns including hydraulic residence time, nutrient and organic loading. Habitat, estuarine area, and salinity were significant factors explaining 58% of the variation in NEM among the different sites, while region, temperature, tide range, and water depth were not significant ($p < 0.01$).

Estuarine area may determine the ratio of allochthonous organic inputs to autochthonous production, with small systems being dominated by terrestrial or marsh organic inputs. In the marsh creeks and open water sites, nutrient inputs supporting phytoplankton production may become more important than allochthonous organic inputs from the marsh or uplands as systems get bigger. This pattern was observed in other marsh estuarine systems where large bays and sounds were au-
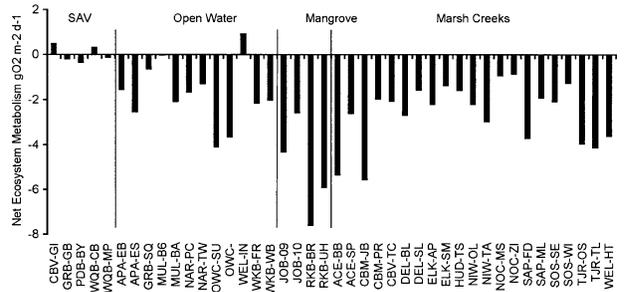

Fig. 11. NEM (g O_2 m^{-2} d^{-1}) for open water, mangrove, marsh, and submerged aquatic vegetation (SAV) habitats.
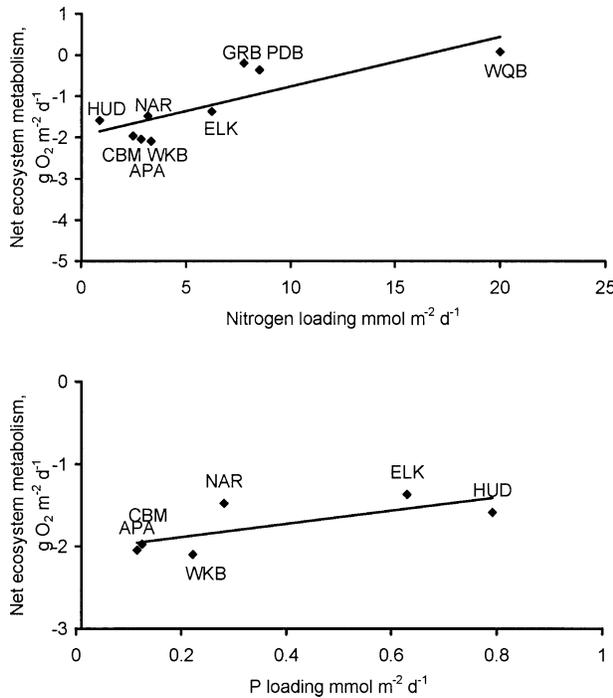
Fig. 12. NEM versus nitrogen loading (mmol N m^{-2} d^{-1}) or phosphorus loading (mmol P m^{-2} d^{-1}).

totrophic, while tidal creeks were heterotrophic (Hopkinson 1988). The pattern for SAV sites was quite different than that observed in marsh creeks or open water sites. As area increased systems became more heterotrophic. The relative balance between SAV production, plankton production, and organic loading may explain this pattern.

The influence of salinity suggests that spatial gradients along estuaries are a fairly consistent feature across different estuaries. That is, oligohaline, mesohaline, or euhaline zones behave similarly in terms of NEM. This may reflect generally higher terrestrial inputs enhancing respiration over pro-

duction, higher turbidity leading to light limited production and thus greater heterotrophy in oligohaline zones compared to euhaline zones.

The multiple regression models at individual sites (Table 3) suggested that nutrient concentrations covary with metabolic rates. Nutrient concentrations at any point in time represent a balance between inputs, internal processing, and export; the nutrient supply or nutrient loading rate is likely a better determinant of metabolic rates. In the MERL mesocosms, increased DIN loading led to more autotrophy (Oviatt et al. 1986). Similarly, the Childs River, which had the highest nutrient loading among three sub estuaries in Waquoit Bay, was more autotrophic than Sage Lot Pond (D'Avanzo et al. 1996). Estimates of DIN loading were available for 9 of the sites and ranged from 1 mmol m^{-2} d^{-1} in the upper Hudson River to 20 mmol m^{-2} d^{-1} in Waquoit Bay. NEM was significantly more autotrophic under conditions of higher nitrogen loading ($R^2 = 0.68$, $p < 0.01$; Fig. 12), suggesting that production was enhanced over respiration at higher nitrogen loading rates. Phosphorus loading showed a similar pattern, although it was not statistically significant. Further studies to estimate nutrient and organic loading rates for each of the sites are necessary to establish whether this relationship holds across all habitat types.

Comparison to Other Systems

The results of this study were compared to other metabolic rates in estuarine and coastal systems. NEM was estimated for a variety of locations, ten of them at or near NERR sites (Table 4). There was good agreement between estimates at four of the sites (Waquoit Bay, Chesapeake Bay Virginia-York River, Apalachicola Bay-Boynton, and Elkhorn Slough). The estimate from Central Basin and Metoxit Point was bracketed by the measurements in the three sub watersheds of Waquoit Bay

TABLE 4. Comparison of NEM (g C m^{-2} y^{-1}) at Reserve SWMP sites and literature values. [1] indicates references from LOICZ web site (http://data.ecology.su.se/MNODE/).

Reserve	SWMP	Other Study	Citation
Waquoit Bay	−154	−397 to +18	D'Avanzo et al. (1996)
Narragansett Bay	−388	80	Smith and Hollibaugh (1993)
		26 to 43	Nixon et al. (1995)
		14	Smith (LOICZ)[1]
Hudson River	−287	−30	Howarth et al. (1996)
Patuxent River (CBM-PR)	−458	−15	Hagy and Kemp (LOICZ)[1]
York River (CBM-TC)	−153	−100	Raymond et al. (2000)
Apalachicola Bay	−348	−366	Boynton (1975, East Bay only)
		13.1	Marsh (LOICZ)[1]
Mobile Bay (WKB-WB)	−344	−31	Marsh (LOICZ)[1]
Elkhorn Slough (ELK-SM)	−257	−219	Caffrey (LOICZ)[1]
Duplin River (SAP-ML)	−701	1,082	Hopkinson (1988)
Rookery Bay	−1,034	−76	Twilley (1988)

(D'Avanzo et al. 1996). Elkhorn Slough South Marsh site was quite similar to the Slough-wide estimate based on a biogeochemical budget. Summer measurements of metabolic rates in East Bay by Boynton (1975) were similar to the measurements at that site. The estimate of NEM in Apalachicola Bay as a whole based on a biogeochemical budget suggests that the bay as a whole is autotrophic. The East Bay site is in the oligohaline portion of Apalachicola Bay and receives drainage from a bottomland hardwood swamp as well as the river, perhaps contributing to heterotrophy at this site. The East Bay site does not appear to be representative of Apalachicola Bay as a whole. NEM from the other six sites (Narragansett Bay, Hudson River, Patuxent River, Mobile-Weeks Bay, Duplin River, and Rookery Bay) were all more heterotrophic than the literature estimates (Table 4). This is not surprising given that literature estimates were for the entire system, or large reaches in the case of the Hudson (i.e., the oligohaline section), or adjoining systems in the case of Mobile and Weeks Bays. The shallow Reserve sites may have been more strongly influenced by allochthonous organic inputs from nearby marshes (Hudson, Patuxent, and Duplin Rivers) or land runoff (Narragansett and Weeks Bays). In Rookery Bay, Twilley (1988) estimated that mangrove detritus contributed about 345 g C m^{-2} y^{-1} to the estuary. Decomposition of this organic material supported heterotrophic conditions in the Bay (Twilley 1988), although NEM in tidal creeks was thirteen times more heterotrophic than in the Bay (Table 4). In the Duplin River, NEM was strongly autotrophic because the mass balance estimate included salt marsh as well as tidal creeks and estuary, although the tidal creeks themselves were strongly heterotrophic (Hopkinson 1988). These comparisons between literature-whole system and site-specific values are consistent with earlier findings that size makes a difference, that is, smaller systems are more heterotrophic than larger systems.

Smith and Hollibaugh (1993) summarized the metabolism estimates from marsh, estuarine, and coastal systems. They observed that estuarine and coastal systems were generally heterotrophic and became more heterotrophic as gross primary production increased (Fig. 13). The Texas bays and the Georgia coast were the most heterotrophic (Smith and Hollibaugh 1993). The results from the NERR sites generally followed this trend (Fig. 13), although the rates of production and NEM were two to five times greater than the systems summarized in Smith and Hollibaugh (1993). Several factors are likely responsible for the high rates of production and NEM at the NERR sites relative to the literature values. Water depth averaged 1.9
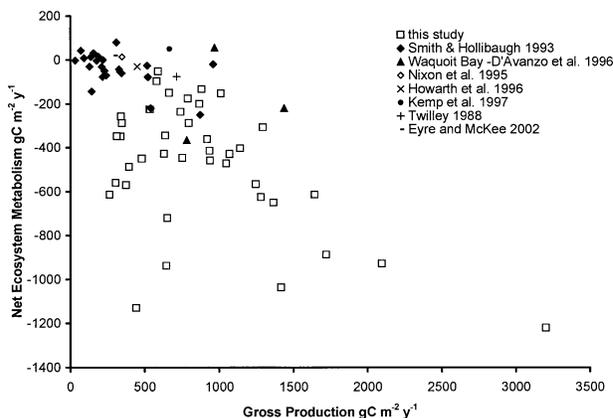

Fig. 13.   NEM (g C m^{-2} y^{-1}) versus gross primary production (g C m^{-2} y^{-1}) for Reserve SWMP sites, and literature values.

m at these sites with only six sites exceeding 3 m water depth. Benthic production is likely enhanced in these shallow regions compared to the often light-limited channels and deep water where many estuarine studies focus. These areas are also closest to the land margins and may intercept nutrient runoff that could enhance local production. Other studies have also observed heterotrophy in estuaries, including the York and Satilla estuaries and the upper Hudson River (Howarth et al. 1996; Cai et al. 1999; Raymond et al. 2000). Both the York and Satilla have large fringing marshes that may be a source of allochthonous organic matter that is respired in the estuary. The freshwater tidal reaches of the Hudson River have few fringing marshes, yet the river is heterotrophic (Howarth et al. 1996). Allochthonous organic inputs from agriculture appear to be fueling the high respiration rates observed in this system (Howarth et al. 1996). The results of this study are consistent with the observation that estuaries generally appear to be heterotrophic (Heip et al. 1995; Gattuso et al. 1998), perhaps because of the balance between organic carbon and nutrient loading (Kemp et al. 1997; Eyre and McKee 2002).

Different approaches used to estimate NEM can provide unique insights into the factors controlling metabolic rates. Mass balance or LOICZ style biogeochemical budgets may be more appropriate for estimating estuary-wide NEM on a seasonal or annual basis. Although with the careful selection of monitoring stations that are representative of the estuary as a whole, the open water oxygen method can be used to estimate estuary-wide metabolic rates. This method can provide a detailed picture of production, respiration, and NEM at a daily timescale that is unavailable with any other method. While the results of this study show that metabolism estimates from subsystems such as tidal

creeks are not representative of the estuary as a whole, that can be an advantage in some situations. Detecting changes in the watershed, such as increased nutrient loading, may be more apparent in the shallow highly productive nearshore regions than out in the channel. Future advances in our understanding will come as this method is combined with the emerging in-situ nutrient analyzer technology to provide an unprecedented and detailed picture of the interaction between metabolism and nutrient concentrations.

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