PRODUCTION, RESPIRATION AND NET ECOSYSTEM METABOLISM IN U.S. ESTUARIES

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Abstract. Primary production, respiration, and net ecosystem metabolism (NEM) are useful indicators of ecosystem level trophic conditions within estuaries. In this study, dissolved oxygen data collected every half hour between January 1996 to December 1998 by the National Estuarine Research Reserve System Wide Monitoring Program were used to calculate primary production, respiration, and net ecosystem metabolism. Data from two sites at each of 14 Reserves were analyzed. On average, three quarters of the data available could be used to calculate metabolic rates. Data from two of the Reserves were used to evaluate the assumption of homogeneity of water masses moving past the oxygen sensor. Temperature was the single most important factor controlling metabolic rates at individual sites, although salinity was also important at about half the sites. On an annual basis, respiration exceeded gross primary production demonstrating that all but 4 of the 28 sites were heterotrophic.

Keywords: estuary, production, respiration, net ecosystem metabolism, dissolved oxygen

1. Introduction

Primary production, respiration and the balance between the two, or net ecosystem metabolism (NEM) vary widely across ecosystems, from highly productive salt marshes to oligotrophic ocean waters. NEM is a useful indicator of the trophic condition within estuaries, whether autochthonous or allochthonous sources of organic matter dominate. If NEM is positive, the system is autotrophic suggesting that internal production of organic matter dominates, while if NEM is negative, the system is heterotrophic and reliant on external sources of organic matter.

In aquatic ecosystems, a variety of techniques have been used to measure production, respiration and NEM. H.T. Odum first developed the method of calculating metabolic rates from diel oxygen curve data in the 1950s (Odum, 1956; Odum and Hoskins, 1958). Since then it has been applied in a wide variety of systems, including many different estuaries (Nixon and Oviatt, 1972; Kemp and Boynton, 1980; Oviatt *et al*., 1986; D'Avanzo *et al*., 1996; Swaney *et al*., 1999).

The National Estuarine Research Reserve (NERR) system currently includes 25 protected areas throughout the United States, including Puerto Rico. Each Reserve participates in the System Wide Monitoring Program (SWMP) to measure water quality parameters (temperature, salinity, dissolved oxygen, pH, turbidity, water depth) at a minimum of two sites. The goal of the NERR SWMP is to examine short-term variability and long-term changes in representative estuarine ecosystems (Wenner *et al*., 2001).

This paper assesses the feasibility of using water quality monitoring data to calculate metabolic rates. Data were examined to determine whether advection

Environmental Monitoring and Assessment **81**: 207–219, 2003.

was important in controlling oxygen dynamics at different sites. The relationships among metabolic rates (gross photosynthesis, respiration, and NEM), salinity and temperature were also evaluated for each site.

2. Methods

I used existing dissolved oxygen data from the NERR SWMP from January 1996 to December 1998 for this analysis. All data had undergone extensive quality control and quality assurance as described in Wenner *et al*. (2001). Data from 2 sites at 14 Reserves were analyzed (Table 1). Sites were chosen based on several factors including hydrography, habitat types near deployment, geographic location, and availability of ancillary data such as nutrient and chlorophyll concentrations.

2.1 CALCULATIONS

Oxygen is produced as a by-product of photosynthesis and consumed by respiration. In aquatic environments, oxygen concentrations usually exhibit a characteristic diurnal pattern with concentrations increasing from morning into mid afternoon as photosynthesis outstrips respiration. Declining oxygen concentrations occur during the late afternoon or evening as photosynthetic rate declines and throughout the night when photosynthesis does not occur. In addition to these biological processes, physical processes can also affect oxygen concentrations. Diffusion of oxygen across the air-water interface can increase or decrease water column concentrations, with diffusion from the air into the water occurring when the water is under saturated and vice versa when the water is supersaturated.

The diffusion, or air-sea exchange, was estimated by equation (1) below

$$\text{Air-Sea Exchange} = \left(1 - \frac{DO_{\text{sat},\,t2} + DO_{\text{sat},\,t1}}{200}\right) * 0.5 * \text{dt}$$

where $(DO_{\text{sat},\,t2} + DO_{\text{sat},\,t1})$ are the oxygen concentrations (units -%) for t1 and t2 and dt is the time difference, in hours, between t2 and t1. The time interval for all data was 0.5 hours. A coefficient of 0.5 g O_2 m^{-2} hr^{-1} at zero O_2 was used to estimate the air-sea exchange (J. Hagy and W.R. Boynton, pers. comm.). The units for air-sea exchange are g O_2 m^{-2}. Thus, when the average oxygen concentration for the time interval $(DO_{\text{sat},\,t2} + DO_{\text{sat},\,t1})/200)$ is under saturated, air-sea exchange is positive and oxygen diffuses from the air into the water. If oxygen concentrations are supersaturated, air-sea exchange is negative and oxygen diffuses out of the water into the air.

This approach may underestimate exchange during periods of high winds and overestimate exchange during calm periods, since previous research has shown that the rate of diffusion is dependent on wind speed (Copeland and Duffer, 1964;

Table I. Location of NERR sites and dominant habitat near site. The total number of days of observations available, average length of deployment, and the percent of dates with negative gross production or respiration.

Site Code	*Reserve*	*Site*	*Dominant Habitat*	*Total Days*	*Length of Deployment*	*Negative Observations*
					(days)	*(%)*
A	ACE, SC	Big Basin	Salt marsh	619	20	21
a		St Pierre	Salt marsh	478	19	21
B	Apalachicola, FL	Surface	Open water	788	18	27
B		Bottom	Open water	506	18	34
C	Chesapeake Bay,	Jug Bay	Fresh marsh	168	12	24
c	MD	Patuxent Park	Fresh marsh	118	11	19
D	Chesapeake Bay VA	Goodwin Island	Eelgrass	413	12	5
d		Taskinas Creek	Brackish marsh	829	14	17
E	Elkhorn Slough, CA	Azevedo Pond	Uplands	946	27	3
e		South Marsh	Salt marsh	716	28	12
F	Great Bay, NH	Great Bay Buoy	Open water	631	17	31
f		Squamscott River	Open water	276	18	20
G	Hudson River, NY	Sawkill	Uplands	442	18	69
g		Tivoli South	Fresh marsh	486	19	24
H	Jobos Bay, PR	Station 9	Mangrove	289	14	3
h		Station 10	Mangrove	327	14	6
I	Narragansett Bay,	Potters Cove	Open water	733	30	26
i	RI	T-wharf	Open water	330	27	38
J	North Inlet-Winyah Bay, SC	Oyster Landing	Salt marsh	822	14	12
j		Thousand Acre Creek	Salt marsh	856	14	27
K	Padilla Bay, WA	Bay View	Eelgrass	714	29	29
k		Joe Leary Slough	Upland	840	16	43
L	Rookery Bay, FL	Upper Henderson	Mangrove	585	15	12
l		Blackwater River	Mangrove	175	14	21
M	Weeks Bay, AL	Fish River	Open water	302	14	23
m		Weeks Bay	Open water	320	14	25
N	Waquoit Bay, MA	Central Basin	Macroalgae	313	14	8

Hartman and Hammond, 1984; Marino and Howarth, 1993).

For each time interval, air-sea exchange was subtracted from the change in oxygen concentrations (DO) in g O_2 m^{-3} multiplied by water depth (m) to give oxygen flux (g O_2 m^{-2}) as described in equation (2) below.

$$\text{Oxygen flux} = (DO_{t2}–DO_{t1}) * \text{water depth–air-sea exchange} \quad (2)$$

Oxygen fluxes during the daylight hours were summed to give net production and summed oxygen fluxes from night equaled night oxygen flux. Since respiration is defined as a positive quantity, night oxygen fluxes were multiplied by –1 to give a night respiration rate. Gross production and total (day + night) respiration rate were calculated using net production and night respiration values. Assuming a

constant respiration during the day and night, night respiration divided by hours of night equals the hourly respiration rate (g O_2 m^{-2} h^{-1}). Total respiration equals the hourly respiration rate multiplied by 24 h (g O_2 m^{-2} d^{-1}). Gross production is the net production plus the respiration occurring during daylight hours and was calculated by adding net production to the hourly respiration multiplied by the daylight hours. Net ecosystem metabolism was calculated by subtracting total respiration from gross production, or more directly by net production minus night respiration.

A major assumption of the diel oxygen curve method is that water masses passing by the sensor are laterally and vertically homogenous, i.e. they have the same metabolic history. 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, 1980).

2.2 STATISTICAL ANALYSES

Mean, median, 25th and 75th percentiles were calculated for air-sea exchange values for all sites except Goodwin Island. All values were eliminated from the dataset on dates where gross production and total respiration values were less than zero. The percent of dates with negative gross production or total respiration observations was determined for each site. In addition, paired t-tests were used to examine whether stratification had a significant effect on metabolic rates from the surface and bottom deployments in Apalachicola Bay or whether there was a significant variation in sites 400 m apart in Waquoit Bay. These were the only two Reserves with deployments close enough to test the assumption of homogeneity of water masses.

Relationships among temperature and salinity and metabolic rates for each site were determined using correlation analysis. Daily rates of gross production and total respiration were compared using a paired t-test. If production and respiration rates were significantly different from one another, then net ecosystem metabolism was significantly different from zero. All results are reported as non-significant when p values were greater than 0.05.

3. Results and Discussion

The total number of days of data available for the metabolic calculations was variable between sites (Table 1). A variety of factors contributed to the gaps in the data record: from logistical and personnel constraints, to weather (winter ice and freezing temperatures) to problems with instrument calibrations. The average length of deployment varied between 11 to 29 days among the different sites (Table 1). In general, most Reserves in the Southeast and along the Gulf Coast deployed the instruments for 7 days during the summer to minimize biofouling and instrument drift (Wenner *et al.*, 2001). Data for the three-year period was available at most sites, except for 5 sites (Chesapeake Bay MD Jug Bay, Chesapeake Bay VA

Goodwin Island, Great Bay Squamscott River, Narragansett Bay T-wharf, Rookery Bay Upper Henderson) that had only two years of data and 5 sites (Chesapeake Bay MD Patuxent Park, Rookery Bay Blackwater River, Weeks Bay Fish River, Weeks Bay, Waquoit Bay Metoxit Point) that had a single year of data.

Exchange of oxygen across the air-water interface can have a significant effect on concentration in the water column, particularly when the water is under saturated or supersaturated. Air-sea exchange averaged 0.1 $gO_2\ m^{-2}$ or less at most sites and rarely exceeded 0.2 $gO_2\ m^{-2}$ (Table 2). These values were comparable with previous estimates of air-sea exchange (Odum, 1956; Odum and Hoskins, 1958; D'Avanzo *et al*., 1996).

A fundamental assumption of this method is that water masses moving past the sensor are homogeneous. This assumption was examined in more detail using data from two of the Reserves where deployment sites were close. In Apalachicola Bay, one meter was deployed near the surface (0.6 m) and a second meter was deployed 1.2 m below the first and 0.4 m above the bottom. Gross production and respiration were not significantly different between the two depths (Figure 1), although NEM was significantly different ($p = 0.025$). Surface waters were significantly more heterotrophic than bottom waters, perhaps reflecting runoff from the adjacent bottomland hardwood swamp in the surface layer. In Waquoit Bay, two meters were deployed approximately 400 m apart for six weeks starting in November 1998 (Figure 2). Again there was no significant difference in gross production or respiration between the two deployment sites, while NEM was significantly different ($p = 0.001$). Previous research in Waquoit Bay has shown that mid-estuary deployments are representative of the estuary as a whole (D'Avanzo *et al*., 1996).

In addition to heterogeneity of water masses, the signal to noise ratio can also affect the success of this method. When metabolic rates are very low, the oxygen fluxes will be small and difficult to detect. Thus, estimating rates can be difficult when temperatures are low or in oligotrophic environments.

Physical processes appeared to control oxygen dynamics at only two out of the 28 deployment locations. At Hudson River Sawkill, 69% of the dates had negative gross production or respiration values. At this site, the YSI data sonde was deployed just upstream of a dam in the creek. Physical processes such as advection of different water masses and enhanced exchange across the air-water interface probably control the oxygen dynamics rather than biological processes. Thus, when stream flow was greater than 0.4 m^3/s, gross production and respiration were usually negative values. The other site with a relatively low percentage of useable observations was Padilla Bay Joe Leary Slough where 43% of the dates had negative gross production or respiration values. This small, intermittently flushed Slough drains agricultural fields and pastures. A dam and one-way tide gates restrict water flow between the Slough and Padilla Bay. High salinity and high DO water from Padilla Bay eelgrass beds seeped through the tide gates at high tides increasing

DO concentrations within the Slough. If high tide occurred at night, DO concentrations often increased which led to negative estimates of respiration.

The percentage of dates with negative values of gross production and respiration was also variable from 3% to 69%, although only 5 sites had percentages greater than 30%. On average, 23% of the data was eliminated (Table 1). Removing all data on dates with either negative gross production or respiration led to higher average annual gross production and respiration than if all data was used, although this had a minimal effect on net ecosystem metabolism. Several reasons justify removing data on dates with negative production and respiration. Respiration cannot be negative—there is no biological process that leads to the production of oxygen at night. Close scrutiny of the results from Hudson River Sawkill and Padilla Bay Joe Leary Slough as described above clearly demonstrate how heterogeneity of water masses led to impossible numbers. These same sort of physical processes occur at other sites. Some of these negative values were associated with

Table 2. Air-sea exchange in $gO_2\ m^{-2}$ using constant diffusion coefficient = 0.5 and calculated from equation 1. Number of observations used to estimate mean, median, 25^{th} and 75^{th} percentiles.

Site Code	*Site*	*Number of Observations*	*Mean*	*Median*	*25^{th}*	*75^{th}*
A	Big Basin	37,919	0.09	0.07	0.02	0.18
a	St Pierre	27,369	0.08	0.05	0.02	0.13
B	Surface	26,960	0.03	0.02	-0.02	0.08
b	Bottom	35,578	0.02	0.02	-0.01	0.05
C	Jug Bay	8,016	0.14	0.15	0.09	0.21
c	Patuxent Park	5,445	0.05	0.07	0.02	0.10
d	Taskinas Creek	40,060	0.04	0.04	0.01	0.08
E	Azevedo Pond	44,874	0.05	0.07	-0.01	0.14
e	South Marsh	34,116	0.04	0.04	0.01	0.06
F	Great Bay Buoy	29,466	0.00	0.00	-0.02	0.02
f	Squamscott River	13,106	0.02	0.02	0.00	0.03
G	Sawkill	20,920	-0.00	-0.00	-0.02	0.00
g	Tivoli South	23,221	0.03	0.03	0.01	0.05
H	Station 9	14,603	0.08	0.08	0.02	0.15
h	Station 10	17,024	0.03	0.03	-0.01	0.08
I	Potters Cove	35,360	0.01	0.00	-0.02	0.03
i	T-wharf	842	0.02	0.02	0.01	0.03
J	Oyster Landing	41,592	0.04	0.03	0.00	0.08
j	Thousand Acre Creek	40,252	0.06	0.05	0.02	0.10
K	Bay View	40,940	0.01	0.02	-0.02	0.04
k	Joe Leary Slough	39,464	0.12	0.12	0.06	0.17
L	Upper Henderson	9,807	0.15	0.16	0.12	0.19
l	Blackwater River	27,349	0.12	0.13	0.08	0.18
M	Fish River	14,346	0.02	0.04	0.00	0.06
m	Weeks Bay	15,024	0.01	0.00	-0.05	0.06
N	Central Basin	15,035	-0.02	-0.01	-0.05	0.02

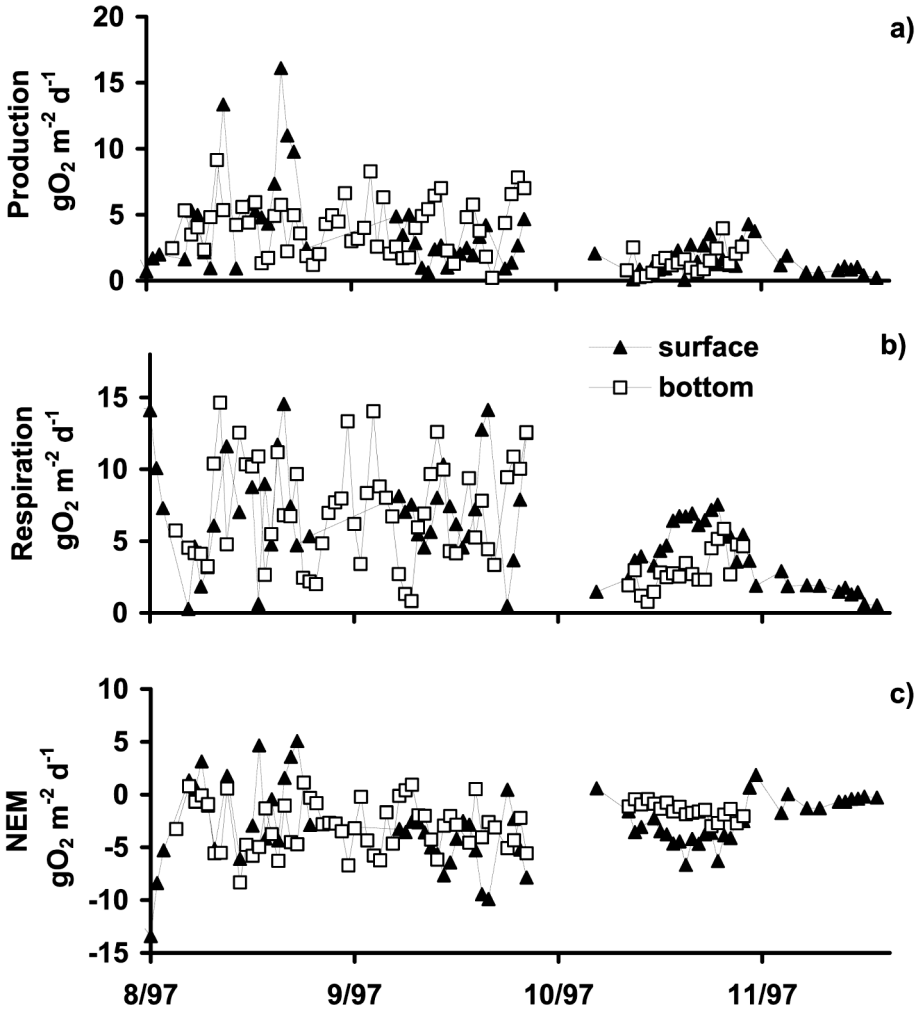

Figure 1. Comparison of a) gross production b) total respiration and c) net ecosystem metabolism (g O_2 m^{-2} d^{-1}) between Apalachicola Bay surface and bottom deployments.

a rapid change in salinity, suggesting the movement of a different water mass past the sensor. These physical processes probably occur intermittently perhaps associated with fronts or strong currents. A more complete analysis of the data is needed to determine whether heterogeneity of water masses is responsible for negative values at other sites.

Average annual gross production and total respiration rates were calculated at each site. The lowest average annual gross production and total respiration rates occurred at the Hudson River Sawkill site, a small freshwater creek. Rates were also generally low at Hudson River Tivoli South, North Inlet-Winyah Bay Thousand Acre Creek and Weeks Bay Fish River (Figure 3). The highest rates occurred at the Elkhorn Slough Azevedo Pond, Padilla Bay Bayview and ACE Basin St. Pierre, which were nearly double the rates at the other sites. Across all sites average gross production and respiration were significantly correlated (Figure 3, $r = 0.82$, $p < 0.01$). Average annual respiration was significantly greater than average annual gross production, except at 4 of the sites where gross production was sig-

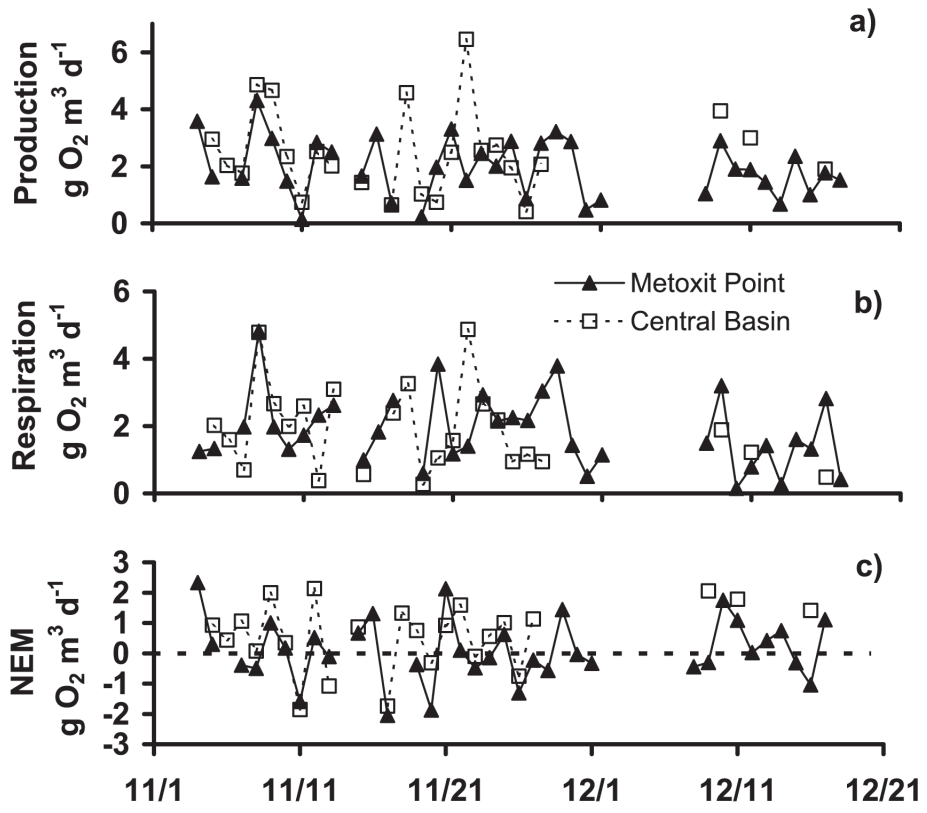

Figure 2. Comparison of a) gross production b) total respiration and c) net ecosystem metabolism (g O_2 m^{-2} d^{-1}) between Central Basin and Metoxit Point stations in Waquoit Bay in 1998.

nificantly greater than respiration (Chesapeake Bay VA Goodwin Island) or they were equal (Waquoit Bay Central Basin, Padilla Bay Bayview and Hudson River Sawkill) (Figure 3). When daily gross production and respiration rates were compared using a paired t-test, respiration was significantly greater than gross production at all sites except for Padilla Bay Bayview, Waquoit Bay Central Basin, and Hudson River Sawkill where there was no significant difference between rates. At Chesapeake Bay VA Goodwin Island, gross production was significantly greater than respiration. At three of these sites, eelgrass (Chesapeake Bay VA Goodwin Island, Padilla Bay Bayview) or macro algae (Waquoit Bay Central Basin) dominated. It was surprising that the Padilla Bay Bayview site was not net autotrophic given the extensive intertidal beds of eelgrass in the Bay. However, the instrument was deployed in a deep channel adjacent to the grass beds rather than in the grass beds proper. Another site that was probably influenced by nearby eelgrass beds was Great Bay Buoy, which was only slightly heterotrophic. Sites from Chesapeake Bay MD, Rookery Bay and ACE Basin were very heterotrophic, probably because of high organic inputs from adjacent marshes and mangroves.

Temperature and metabolic rates were significantly correlated at most of the 27 YSI deployment sites (Waquoit Bay Metoxit Point was not included due to the small amount of data available) (Table 3). Gross production and temperature were correlated at 23 sites; respiration and temperature were correlated at 26 sites, while

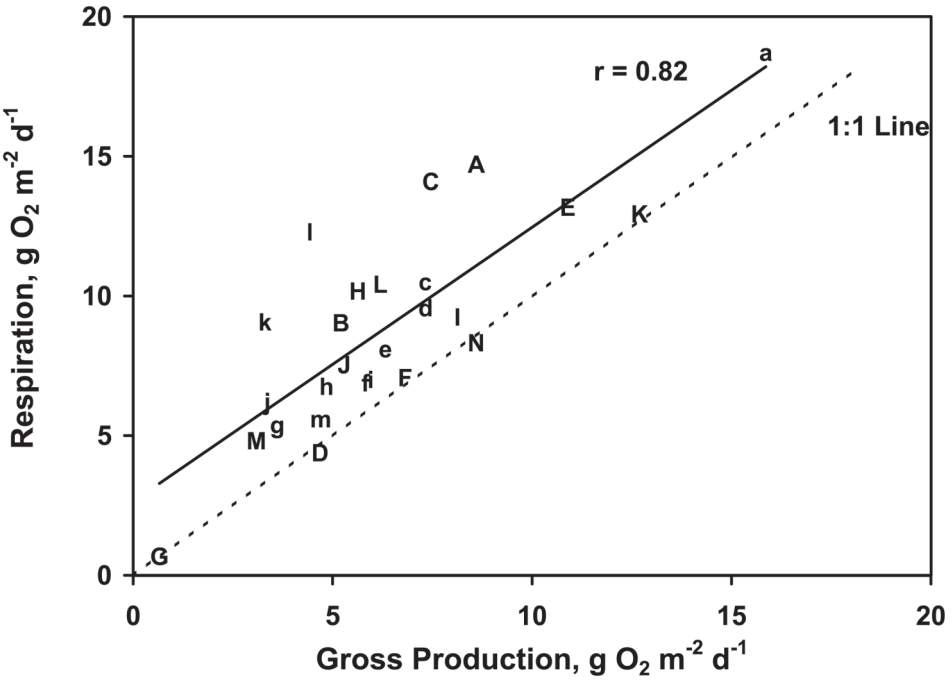

Figure 3. Average annual rate of production and respiration in g O_2 m^{-2} d^{-1} among NERR sites. Site codes in Table 1.

Table 3. Correlation coefficients for temperature, salinity, Gross Production (Pg), Total Respiration (R) and net ecosystem metabolism (NEM)($p < 0.05$ at NERR sites). ns – non significant ($p > 0.05$). # is number of observations

Site Code	*Site*	*#*	*Temperature effects*			*Salinity effects*		
			Pg	*R*	*NEM*	*Pg*	*R*	*NEM*
A	Big Basin	489	0.33	0.35	–0.16	0.13	ns	0.23
a	St Pierre	378	0.34	0.48	–0.18	ns	ns	ns
B	Surface	575	0.36	0.27	–0.08	0.17	ns	ns
b	Bottom	334	0.27	0.23	ns	0.20	0.29	–0.22
C	Jug Bay	128	ns	0.23	–0.38	ns	ns	–0.34
c	Patuxent Park	96	0.58	0.43	0.21	ns	ns	ns
D	Goodwin Island	392	0.64	0.67	–0.68	–0.16	–0.19	ns
d	Taskinas Creek	688	0.52	0.65	–0.38	0.13	0.16	–0.10
E	Azevedo Pond	918	0.48	0.52	0.09	0.39	0.46	ns
e	South Marsh	630	0.35	0.38	–0.11	0.23	0.22	ns
F	Great Bay Buoy	435	0.44	0.49	–0.06	0.29	0.25	0.14
f	Squamscott River	221	0.39	0.40	ns	ns	ns	ns
G	Sawkill	137	–0.34	0.19	–0.51	ns	ns	ns
g	Tivoli South	369	0.50	0.61	–0.45	ns	ns	ns
H	Station 9	280	0.30	0.41	–0.23	0.14	0.31	–0.25
h	Station 10	307	0.22	0.21	ns	ns	–0.20	0.21
I	Potters Cove	542	0.47	0.55	–0.33	ns	ns	ns
i	T–wharf	205	0.19	0.19	ns	–0.18	–0.21	ns
J	Oyster Landing	723	0.47	0.71	–0.53	0.16	0.16	ns
j	Thousand Acre Creek	625	0.44	0.56	–0.34	0.29	0.37	–0.24
K	Bay View	507	0.30	0.30	ns	–0.11	ns	–0.18
k	Joe Leary Slough	479	–0.18	0.30	0.46	–0.09	0.27	0.33
L	Upper Henderson	515	ns	0.30	–0.47	ns	ns	ns
l	Blackwater River	138	ns	0.36	–0.51	0.24	ns	0.48
M	Fish River	233	ns	ns	ns	0.37	ns	0.38
m	Weeks Bay	240	0.68	0.64	ns	ns	ns	–0.33
N	Central Basin	288	0.47	0.46	ns	ns	ns	ns

net ecosystem metabolism and temperature were correlated at 19 sites. This is consistent with the idea that biological processes are controlling metabolic rates at these sites, with warmer temperatures leading to higher metabolic rates. At most sites, higher temperatures generally resulted in more heterotrophic conditions.

In contrast, salinity and metabolic rates were significantly correlated at about half of the sites (Table 3). At most sites, gross production and respiration were low when salinity was low. Low salinities likely reflect greater freshwater inputs that may reduce the water residence time, leading to a greater flushing of the planktonic communities out of tidal creeks or estuaries. In contrast, at half the sites, NEM and salinity were positively correlated (more autotrophic at higher salinities) and half the sites were negatively correlated (more heterotrophic at higher salinities). This may reflect differing inputs of nutrients or organic matter associ-

ated with freshwater runoff at individual sites. Nutrient rich freshwater runoff could enhance production over respiration leading to more autotrophic conditions, while organic rich freshwater runoff could lead to more heterotrophic conditions.

Average salinity ranged between 0 and 39 at the Reserve deployment sites with freshwater conditions occurring at Chesapeake Bay Maryland and Hudson River sites throughout the three-year period. Jobos Bay sites were consistently hypersaline. The range in salinity within each site could also be large, up to 30 PSU or more at several sites (ACE St Pierre, Apalachicola East Bay Surface and Bottom, Elkhorn Slough Azevedo Pond, Great Bay Squamscott River, and North Inlet-Winyah Bay Oyster Landing). Higher gross production generally occurred at sites with salinity between 25–30 that had a moderate salinity range less than 10 PSU (Padilla Bay Bayview, Waquoit Bay Central Basin, Narragansett Bay Potters Cove), although production was also high at the freshwater sites in Chesapeake Bay Maryland. However, there was no trend among respiration, net metabolism, salinity, or salinity range.

4. Conclusions

Dissolved oxygen data collected as part of a routine water quality monitoring program can be used to estimate metabolic rates. However, it is important to select sites where biological processes dominate over physical processes. Despite the fact that NERR SWMP monitoring stations were not chosen with the intention of measuring metabolic rates, most of the data collected at these sites provided useful estimates of metabolic rates. Only two sites, Hudson River Sawkill Creek and Padilla Bay Joe Leary Slough, were the exception where physical processes consistently dominated oxygen dynamics.

Metabolic parameters are useful indicators of ecosystem condition, although their interpretation may not be as clear-cut as other indices such as degree of hypoxia or benthic diversity. These data can be used to answer such questions as: 1) how productive are estuaries relative to one another; 2) what is the balance between production and consumption of organic matter within these systems; and 3) how are these systems changing over time?

Most of the NERR sites (23 out of 27) were significantly heterotrophic with respiration exceeding production on an annual basis. Some of the sites were very heterotrophic suggesting high inputs of organic matter from adjacent marshes and mangroves. Three of the sites that were not heterotrophic were dominated by either eelgrass or macro algae.

Temperature and salinity were important variables explaining some of the daily variations in metabolic rates. However, other factors such as nutrient and chlorophyll concentrations, solar irradiance, nutrient loading, organic loading and residence time may be important in controlling metabolic rates. Nutrient loading (D'Avanzo *et al*., 1996), organic loading (Smith and Hollibaugh, 1997) and the

ratio of nutrient to organic loading (Kemp *et al*., 1997) have been hypothesized to explain variations in rates of net ecosystem metabolism in different estuaries. Future manuscripts will examine how these factors explain variations in metabolic rates both within and between NERR sites.

Acknowledgements

This analysis would not have been possible without the dedication of the National Estuarine Research Reserve Research Coordinators and technicians. I thank Betty Wenner, Mike Arendt, and others at SC DNR, along with the Central Data Management Office, Belle Baruch, USC for critically evaluating the data used for this analysis. Chuck Nieder made available stream flow data from Sawkill Creek. He, Lee Edmiston and Doug Bulthius also provided useful insights about their NERR sites. I thank Fred Holland, Walter Boynton, Jim Hagy, and Mike Murrell for many helpful discussions and Jim Kremer, Jonathan Pennock, Erik Smith, and Virginia Engle for their critical reviews of this manuscript. The Estuarine Reserve Division of NOAA provided funding for this project.

References

Copeland, B.J. and Duffer, W.R.: 1964, 'Use of a Clear Plastic Dome to Measure Gaseous Diffusion Rates in Natural Waters', *Limnology and Oceanography*, **9,** 494–499.

D'Avanzo, C., Kremer, J.N. and Wainright, S.C.: 1996, 'Ecosystem Production And Respiration In Response To Eutrophication In Shallow Temperate Estuaries', *Marine Ecology Progress Series,* **141,** 263–274.

Hartman, B. and Hammond, D.E.: 1984, 'Gas Exchange Rates Across the Sediment Water and Air-Water Interfaces in South San Francisco Bay', *Journal of Geophysical Research,* **89,** 3593–3603.

Kemp, W.M. and Boynton, W.R: 1980, 'Influence of Biological and Physical Processes on Dissolved Oxygen Dynamics in an Estuarine System: Implications for Measurement of Community Metabolism', *Estuarine, Coastal and Marine Science,* **11,** 407–431.

Kemp, W.M., Smith, E.M., Marvin-Dipasquale, M., and Boynton, W.R.: 1997, 'Organic Carbon Balance and Net Ecosystem Metabolism in Chesapeake Bay', *Marine Ecology Progress Series,* **150,** 229–248.

Marino, R. and Howarth, R.W.: 1993, 'Atmospheric Oxygen Exchange in the Hudson River: Dome Measurements and Comparison with Other Natural Waters', *Estuaries,* **16,** 433–445.

Nixon, S.W. and Oviatt, C.A.: 1972, 'Preliminary Measurements of Midsummer Metabolism in Beds of Eelgrass, Zostera marina', *Ecology,* **53,** 150–153.

Odum, H.T.: 1956, 'Primary Production in Flowing Waters', *Limnology And Oceanography,* **1,** 102–117.

Odum, H.T. and Hoskins, C.M.: 1958, 'Comparative Studies on the Metabolism of Marine Waters', *Publications of the Institute of Marine Science, Texas* **5,** 16–46.

Oviatt, C.A., Keller, A.A., Sampou, P.A., and Beatty, L.L.: 1986, 'Patterns of Productivity During Eutrophication: a Mesocosm Experiment', *Marine Ecology Progress Series,* **28,** 69–80.

Smith, S.V. And Hollibaugh, J.T.: 1997, 'Annual Cycle and Interannual Variability of Ecosystem Metabolism in a Temperate Climate Embayment', *Ecological Monographs,* **67,** 509–533.

Swaney, D.P., Howarth, R.W. and Butler, T.J.: 1999, 'A Novel Approach for Estimating Ecosystem Production and Respiration in Estuaries: Application to the Oligohaline and Mesohaline Hudson River', *Limnology and Oceanography,* **44,** 1509–1521.

Wenner, E.L., Holland, A.F., Arendt, M.D., Edwards, D. And Caffrey, J.M.: 2001, 'A Synthesis of Water Quality Data from the National Estuarine Research Reserve System-Wide Monitoring Program', Report to NOAA Estuarine Reserve Division.