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Spatial and Temporal Variability and Drivers of Net Ecosystem Metabolism in Western Gulf of Mexico Estuaries

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ABSTRACT: Net ecosystem metabolism (NEM) is becoming a commonly used ecological indicator of estuarine ecosystem metabolic rates. Estuarine ecosystem processes are spatially and temporally variable, but the corresponding variability in NEM has not been properly assessed. Spatial and temporal variability in NEM was assessed in four western Gulf of Mexico shallow water estuaries. NEM was calculated from high-frequency dissolved oxygen measurements. Interbay, intrabay, and water column spatial scales were assessed for NEM, gross primary production (GPP), and respiration (R) rate variability. Seasonal, monthly, and daily temporal scales in NEM, GPP, and R were also assessed. Environmental conditions were then compared to NEM to determine which factors were correlated with each temporal and spatial scale. There was significant NEM spatial variability on interbay, intrabay, and water column spatial scales. Significant spatial variability was ephemeral, so it was difficult to ascertain which environmental conditions were most influential at each spatial scale. Significant temporal variability in NEM on seasonal, monthly, and daily scales was found and it was correlated to temperature, salinity, and freshwater inflow, respectively. NEM correlated strongly with dissolved oxygen, temperature, and salinity, but the relationships where different in each bay. The dynamics of NEM on daily scales indicate that freshwater inflow events may be the main driver of NEM in the semiarid estuaries studied. The variable nature of NEM found here is further evidence that it is not valid to use single station monitoring deployments for assessment of whole estuarine ecosystem metabolic rates in large ecosystems. The relationship between NEM and temperature, salinity, and freshwater inflow events could drive predictive models assessing the potential influence of projected climate change and watershed development scenarios on estuarine metabolic rates.

Introduction

Ecological processes in estuarine ecosystems are driven by a suite of environmental factors. Some influential environmental factors, such as seasonal temperature and irradiance, change in predictable ways. Others, such as freshwater inflow (FWI) and salinity, are less predictable and are often associated with ephemeral events. Estuaries and other coastal ecosystems by definition depend on FWI events to maintain the gradients in environmental characteristics that define these transitional water bodies (Ketchum 1951; Pritchard 1967). Nutrients and organic matter loaded by FWI have been linked to estuarine productivity, health, and function (D'Avanzo et al. 1996; Kemp et al. 1997; Caffrey 2004). Sediment, nutrients, and organic matter are delivered from a watershed as a result of precipitation events that can be highly variable. The typical precipitation pattern in south Texas results in small base flows punctuated by large inflow events caused by frontal systems or tropical storms (Orlando et al. 1993). Spatial and temporal variability in other environmental conditions may also modify estuarine ecosystem metabolic rates. Estuarine ecosystem metabolic rates could be affected by the interaction of nutrient and organic matter loading from rivers with light availability, temperature, dissolved oxygen, and salinity within the water column of the receiving estuarine system. A greater understanding of spatial and temporal variability in estuarine ecosystem metabolic responses to changing environmental conditions is needed. Understanding the relevant scales and magnitudes of ecosystem metabolic responses is becoming more important as many semiarid estuaries are threatened by environmental conditions that are changing due to climate change and watershed development.

Net ecosystem metabolism (NEM), first proposed by Odum (1956), may provide an ecological indicator of ecosystem metabolic rates that can be used to understand the relevant scales of estuarine ecosystem response to changing environmental conditions. NEM is calculated by subtracting aerobic respiration (R) rates from photosynthesis rates for all biological components contained in a defined body of water. A positive NEM indicates an autotrophic ecosystem where photosynthesis rates exceed R rates. A negative NEM indicates a heterotrophic ecosystem where R rates exceed photosynthesis rates. Changes in NEM may be driven by environmental conditions that vary temporally on daily scales, such as FWI rates related to daily

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precipitation differences, or seasonal scales, such as annual cycles of temperature. FWI, by delivering nutrients and organic matter from the watershed, should be an important influence on estuarine NEM.

Large spatial and temporal variability in estuarine environmental conditions have limited the scope of conclusions made from previous attempts to determine ecological metabolic responses to changing conditions. Caffrey (2004) completed one of the most comprehensive studies of spatial and temporal variability using NEM as an indicator of estuarine metabolic rates. Caffrey (2004) analyzed high frequency dissolved oxygen data from 42 sites within 22 National Estuarine Research Reserves (NERR) over a 5-yr period. The large, continent-wide scale of Caffrey's study limited the analysis of NEM variability to seasonal and interbay scales. Previous studies (Caffrey 2003; D'Avanzo et al. 1996) concluded that NEM results from only one or two carefully located sites and one depth could be representative of NEM in entire estuaries, but further analysis (Caffrey 2004) concluded that shallow nearshore areas are sometimes not representative of estuaries as a whole. Intrabay NEM results from previous studies were compared at stations less than 400 m (Caffrey 2003) and approximately 700 m apart (D'Avanzo et al. 1996), leaving the spatial variability of NEM in larger estuaries unquantified. A more recent study in a larger estuary, Lavaca Bay, Texas, concluded that spatial variability in NEM became apparent at distances greater than 6 km (Russell et al. 2006). As Caffrey (2004) points out, there may be an advantage to using open-water oxygen methods, which are usually spatially representative of a subsection of an estuary, when one wishes to detect the effects of changes in a watershed that may be more apparent in highly productive nearshore regions of an estuary. Comparisons of surface and bottom water NEM results have also been limited in number. Caffrey (2003) compared gross primary production (GPP), R, and NEM calculations from surface and bottom deployments at a site in Apalachicola Bay, Florida. Caffrey (2003) concluded that surface and bottom GPP and R results were not significantly different, but that NEM was significantly different. D'Avanzo et al. (1996) used comparisons of vertical profiles to assess the vertical and horizontal homogeneity of small (1.4 km length) subestuaries. Vertical dissolved oxygen (DO) profiles were assessed at the beginning of each 5 to 25 d continuous DO monitoring deployment. Net primary production and R were not significantly different in surface and bottom waters, but no attempt was made to compare NEM. The evidence suggests that it is problematic to use only one mid estuary NEM calculation to represent entire estuaries larger than 1.4 km in length. Evidence of depth differences in NEM between surface and bottom waters also greatly decreases the validity of using single depth DO measurements to calculate NEM. The spatial and temporal scales of variability of NEM must be better quantified if NEM is to be used as an indicator of the response of estuarine ecosystem metabolic rates to changing environmental conditions.

There are various different ways to measure NEM. The Land-Ocean Interactions in the Coastal Zone (LOICZ) method (Crossland et al. 2005), which uses a budgeting approach to estimate seasonal or annual estuary-wide NEM, can be used to compare metabolic rates among estuaries. Unlike the LOICZ method, which does not provide individual measurements of production or R, the measurement of metabolic rates in water enclosed in bottles or chambers can be summed to estimate NEM. Chamber affects on trapped biological communities cause the error of summing the individual production and R terms to be so large that it is difficult to determine the validity of the NEM calculation (Kemp and Boynton 1980). Open-water oxygen methods (Odum 1956) have become much more reliable as technology has provided easier, more reliable methods of continuously measuring DO in the water column. Open-water oxygen methods now provide relatively accurate estimates of primary production, R, and NEM, as long as the main assumption that observed oxygen changes are dominated by biological processes and not advection is not violated (Kemp and Boynton 1980; Swaney et al. 1999).

Here open-water oxygen methods are applied to quantify spatial and temporal variability and assess the relevant scales for quantifying NEM, GPP, and R rates. Information about the scales that ecosystem metabolic rates respond to changing environmental conditions is needed for use in future ecosystem modeling efforts. This study takes advantage of the uniquely situated western Gulf of Mexico estuarine system. The discrete nature of bay watersheds along the Texas coastline, when coupled with a steep FWI gradient along the coastline, provides a natural experiment of conditions necessary for assessing spatial and temporal variability of NEM, GPP, and R, and their responses to changing environmental conditions. Environmental conditions are compared to NEM to quantify their relative influences on metabolic rates. NEM, GPP, and R are compared at three different spatial scales: interbay (30 km), intrabay (4 km), and between surface and bottom water (1–3 m). NEM, GPP, and R are also compared at three temporal scales: daily, monthly, and seasonally. The validity of using NEM calculations on the spatial and temporal scales of routinely

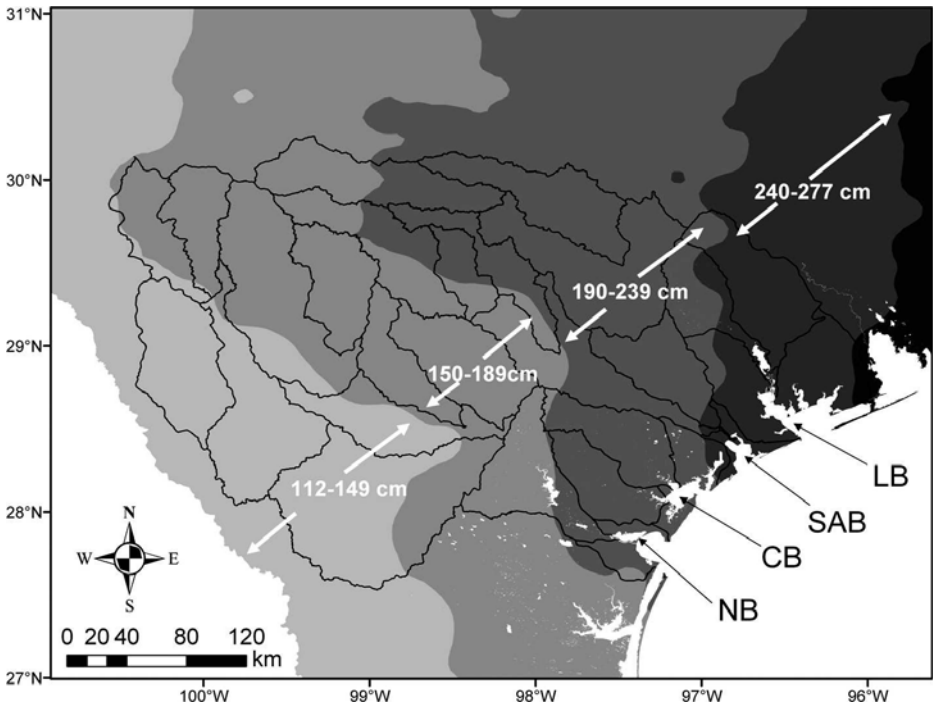


Fig. 1. East to west precipitation gradient (cm yr^{-1}) in Texas. The watershed locations (outlined in black) result in a northeast to southeast inflow gradient along the Texas coastline. Bays are shown with the following labels: Lavaca Bay = LB, San Antonio Bay = SAB, Copano Bay = CB, and Nueces Bay = NB.

monitored water quality data is assessed through intrabay and intrawater column comparisons. The potential for combining data from multiple bays to produce an NEM model that can respond to changing environmental conditions is assessed.

Methods and Materials

Study Area and Environmental Conditions

The southeastern coastline of Texas is dominated by a linked lagoonal system. This mostly subtropical system experiences annual water temperatures ranging from 10°C to 30°C. The Texas lagoonal estuaries are unique in that each major bay system receives FWI from only one or two major river-watershed systems. The lagoonal estuaries are physiographically similar, but differ due to a climatic gradient along the coast. Precipitation along the Texas coastline decreases from moderately wet conditions in northeastern watersheds to semiarid conditions in southwestern watersheds (Fig. 1). This climatic gradient influences FWI (Table 1), salinity,

TABLE 1. Location, mean 2004 USGS gauged freshwater inflow rates, and approximate watershed size of the study sites. Mean monthly freshwater (FWI) inflow, salinity, total nitrogen (N), total phosphorus (P), and total organic carbon volume loading (C) summaries for Texas estuaries. Residence (Res.) times (yr) influence nitrogen availability. Adapted from Longley (1994).

	Lavaca	San Antonio	Copano	Nueces
Latitude	28°38.4′N	28°24.4′N	28°6.9′N	27°51.6′N
Longitude	96°36.6′W	96°42.7′W	97°1.5′W	97°29.0′W
Mean inflow ($m^3\ s^{-1}$)	35.44	67.34	4.55	10.00
Watershed size (km^2)	2,110	15,063	2,172	43,439
FWI ($10^6\ m^3\ mo^{-1}$)	100	241	44	65
Salinity (‰)	13.17	11.94	10.94	21.49
N ($g\ m^{-3}\ yr^{-1}$)	3.18	10.8	1.93	2.1
P ($g\ m^{-3}\ yr^{-1}$)	0.48	2.25	0.4	0.43
C ($g\ m^{-3}\ yr^{-1}$)	19.6	34.2	12	6.3
N:P	6.63	4.8	4.83	4.88
C:N	6.16	3.17	6.16	3
Res. time (yr)	0.21	0.19	3.02	0.46
Res. time weighted N ($g\ m^{-3}\ yr^{-1}$)	0.66	2.09	5.83	0.97

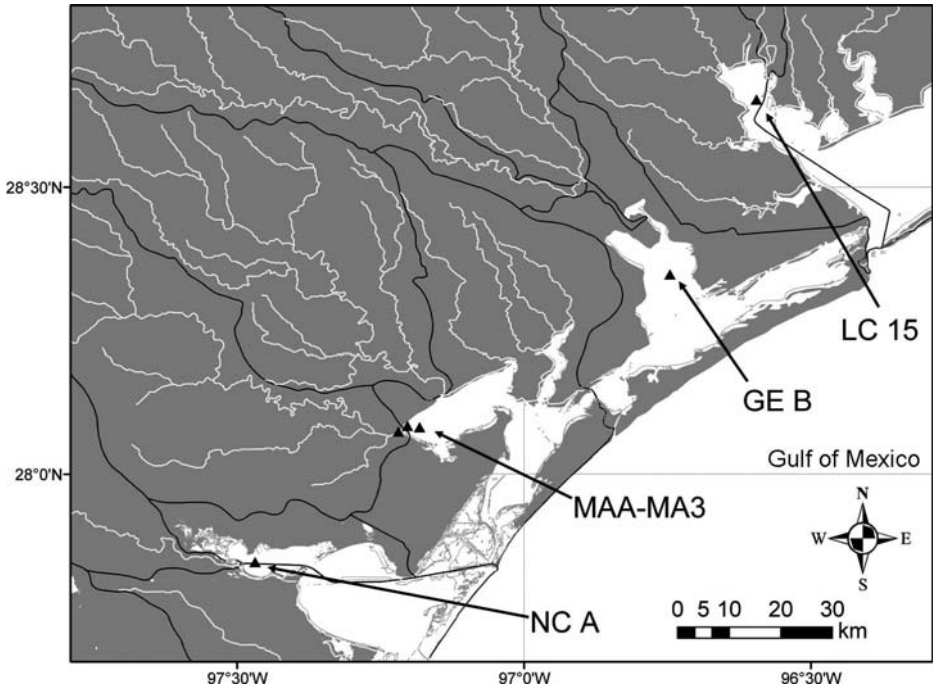


Fig. 2. Station locations in Lavaca Bay (LB), San Antonio Bay (SAB), Copano Bay (CB), and Nueces Bay (CB). Station names (estuary + station) are from Montagna and Kalke (1992). River systems within watersheds are shown with white lines and watersheds are shown with black lines.

nutrient loading, and residence time in Texas estuaries. Some data for Table 1 were compiled from those presented by Longley (1994), who assessed historical trends (1941–1987) in FWI and their effects on Texas estuaries. The climatic gradient results in a two orders of magnitude decrease in FWI from northeast to southwest (Montagna and Kalke 1995). Mean daily gauged river flow rates range from a high of 116 $m^3 s^{-1}$ in the Guadalupe River to a low of 28 $m^3 s^{-1}$ in the Aransas River (NOAA 1997). Freshwater flowing over the salt water dam into Nueces Bay can completely stop when removal of water from the ungauged region of the Nueces River is higher than flow rates. Actual daily differences in FWI among bays can also be much greater than mean daily FWI differences imply, because inflow is driven by short-lived and often localized precipitation pulses, rather than average base flows in the semiarid southwestern watersheds of Texas. Each estuarine system along the Texas coastline has river flow into a secondary bay, which is partially separated from a larger primary bay by a land constriction. The primary bays are either directly or indirectly connected to the Gulf of Mexico. Secondary bays have more direct influence from freshwater than primary bays. River flow results in a longitudinal salinity gradient within each secondary bay (Longley 1994). Past studies have taken advantage of these climatic and longitudinal gradients to determine FWI's influence on zoogeographic distributions (Montagna and Kalke 1992, 1995). Within the context of past studies, it is hypothesized that the influence of varying environmental conditions will affect estuarine NEM along the Texas coastline. The estuaries of Texas provide ideal environments for application of open-water NEM methodology. Texas estuaries fulfill all the requirements set forth by Kemp and Boynton (1980) for environments suitable for open-water NEM methods: shallow-water communities with long residence times, little physical circulation, and moderate metabolism.

Interbay Variability

Estuarine NEM variability may exist due to differences in FWI. It is hypothesized that NEM, GPP, and R are variable on interbay spatial scales (> 30 km). The present study's spatial sampling design included one station located in the FWI region in each of the following secondary bays: Lavaca Bay, San Antonio Bay, Copano Bay, and Nueces Bay (Fig. 2). Sampling was restricted to regions most affected by FWI because FWI's influence on estuarine ecosystem function does not extend into the lower half of a Texas secondary bay (Russell et al. 2006). The temporal sampling design included

weekly deployments during every quarter of 2004 at stations LC 15, GE B, and NC A in Lavaca, San Antonio, and Nueces Bays, respectively, and monthly at one (MAA) of three stations (MAA-MA3) in Copano Bay (Fig. 2). Limiting deployments to 1 wk avoided problems associated with instrument fouling. Stations MA2 and MA3 are used to assess intrabay variability in Copano Bay (see below). Stations were either at or very close to historically sampled locations. Station names follow the original naming convention (estuary + station) previously established by Montagna and Kalke (1995) for these locations. A two-way analysis of variance (ANOVA; alpha = 0.05) was used to test for significant NEM, GPP, and R differences between bays and seasons. Tukey's honestly significant difference (HSD) post-hoc analysis was used to test for significant differences among all pairwise comparisons.

Intrabay Variability

Ecosystem response to environmental conditions has been shown to be similar in the 6-km long region of water between river point sources of FWI and the mid region of Lavaca Bay (Russell et al. 2006). It is hypothesized that intrabay variability in NEM, GPP, and R does not exist within the upper region of Copano Bay (< 4 km), and that one station (MAA) can be used to represent the entire upper bay. To test this hypothesis a spatial sampling design was employed that included three synoptically sampled stations (MAA, MA2, and MA3) located along the longitudinal salinity gradient produced in upper Copano Bay by Aransas River FWI (Fig. 2). The temporal sampling design included sampling for 1-wk periods during the months of March, June, August, September, and November of 2004. A two-way ANOVA (alpha = 0.05) was used to test for significant NEM, GPP, and R differences between stations and months. Tukey's HSD post-hoc analysis was used to test for significant differences among all pairwise comparisons.

Intrawater Column Variability

Stratification events can separate surface and bottom waters into layers with different environmental conditions. It is hypothesized that NEM, GPP, and R in shallow water estuaries are variable on small vertical spatial scales (meters) as a result of stratification events. The water column was simultaneously sampled 0.5 m from the surface and 0.25 m from the bottom to quantify differences between depths. Because stratification in these shallow bays can be ephemeral, the temporal sampling design included deployments lasting for 1-wk periods every quarter during 2004 at stations LC 15, GE B, and NC A in Lavaca, San Antonio, and Nueces Bays, respectively, and monthly at station MAA in Copano Bay (Fig. 2). A *t*-test (alpha = 0.05) was used to test for significant NEM, GPP, and R differences between surface and bottom water for all data pooled together and then within each separate week and bay. Grouping the data into separate weeks allowed analysis of significant differences between consecutive days with and without stratification events. A previously developed water column stratification index (Sigma Sal.; Ritter and Montagna 1999) was calculated for each station every 15 min by subtracting surface salinity from bottom salinity. A threshold of 5‰ difference between top and bottom salinity was used to designate stratification events. This was compared to the Sigma NEM that was calculated by subtracting surface and bottom NEM rates.

Temporal Variability

Environmental conditions change on daily to seasonal time scales. It is hypothesized that estuarine NEM, GPP, and R are variable on daily, monthly, and seasonal temporal scales. The main effects of daily, monthly, and seasonal variability on NEM, GPP, and R were analyzed during the above mentioned ANOVA and *t*-tests.

During sampling, DO and other water quality parameters were measured every 15 min at surface and bottom depths using YSI series 6 multiparameter data sondes. Models 6920-S and 600XLM data sondes with 610-DM and 650 MDS display loggers were used. The series 6 parameters have the following accuracy and units: temperature ($\pm$ 0.15°C), pH ($\pm$ 0.2 units), DO ($\pm$ 0.2 mg l^{-1}), DO saturation ($\pm$ 2%), specific conductivity ($\pm$ 0.5% of reading depending on range), depth ($\pm$ 0.2 m), and salinity ($\pm$ 1% of reading or 0.1‰, whichever is greater). Salinity was automatically corrected to 25°C.

NEM was calculated using open-water diurnal DO curve methods first proposed by H. T. Odum in 1956 and modified for use in a variety of estuaries since then (Odum and Hoskin 1958; Kemp and Boynton 1980; D'Avanzo et al. 1996; Caffrey 2004; Russell et al. 2006). Briefly stated, DO concentrations were converted to a rate of change in DO concentration. These rates of change were then adjusted to control for diffusion of oxygen between the water column and the atmosphere. This was achieved by using percent saturation of DO in the water column, the wind dependent diffusion coefficient K (g O_2 m^{-2} h^{-1}), proposed by D'Avanzo et al. (1996), K/10 for bottom waters during periods of salinity stratification, and wind data from Texas

Coastal Ocean Observation Network (TCOON) stations using the equation:

$$R_{dc} = R - ((1 - ((S_1 + S_2)/200))K/4)$$

where R_{dc} = diffusion corrected oxygen concentration rate of change per 15 min, R = observed oxygen concentration rate of change per 15 min, S_1 and S_2 = DO percent saturations at time one and two, respectively, and K = diffusion coefficient at 0% DO saturation per hour.

$$K = 0.56e^{(0.15x)}$$

where x is wind speed (m s^{-1}) at 10 m height above water.

To calculate daily NEM the 15-min diffusion corrected rates of DO change were then summed over a 24-h period, starting and ending at 8AM. NEM is the balance between GPP and R. Net community production (NCP) and R were estimated from daytime and nighttime diffusion corrected DO concentration changes, respectively. GPP was then estimated by adding NCP to R, with the assumption that nighttime and daytime R rates are similar. GPP and R can be affected by temperature effects on physiological mechanisms (Caffrey 2003). GPP is also influenced by light availability (D'Avanzo et al. 1996). It is hypothesized that GPP and R rates will generally follow the seasonal temperature cycle, with higher rates during summer. The exception to this pattern may be during discrete FWI events when allochthonous organic matter loading or nutrient inputs may stimulate aerobic R rates or primary production, respectively.

NEM results from each bay were compared to temperature, salinity, DO concentration, depth, pH, wind speed, and 10-d cumulative FWI using stepwise multiple regression analysis to assess their relationships in each of the four bays. NEM in Copano Bay was compared to surface irradiance measurements using regression analysis. Environmental condition data were gathered from various sources. Hourly irradiance data were gathered from the University of Texas at Austin's Marine Science Institute in Port Aransas, Texas (Dunton unpublished data). Hourly wind speed was downloaded from the TCOON stations located closest to each study site. FWI was downloaded from United States Geological Survey (USGS) gauged river flow (m^3 d^{-1}) into each bay. Flow gauges in the Lavaca, Guadalupe, Aransas, and Nueces Rivers are numbered USGS 08164000, 08188800, 08189700, and 08211500, respectively. Placedo and Garcitas creeks, which also drain into upper Lavaca Bay, are monitored by USGS stations 08188800 and 08164600, respectively. Variability and correlations among environmental conditions and water quality parameters was assessed using principal component analysis (PCA).

Results

Significant interbay differences in NEM, GPP, and R were found between bays, but an interaction between bays and season complicated the interpretation of trends ($p < 0.01$; Fig. 3). The nature of the interaction was that Copano Bay station MAA in the Mission-Aransas estuary was more heterotrophic in winter than the other bays and remained net heterotrophic throughout the year. San Antonio Bay station GE B in the Guadalupe estuary was more autotrophic than the other three bays during spring and summer, but Nueces Bay station NC A in the Nueces-Corpus estuary was more autotrophic during fall. A large spike in GPP (6.08 ± 1.76 mg O_2 l^{-1} d^{-1}) and R (4.24 ± 0.74 mg O_2 l^{-1} d^{-1}) was measured during spring at station GE B in San Antonio Bay. Lavaca Bay station LB 15 in the Lavaca-Colorado estuary fell within the range of the other three bays, but declined from autotrophic conditions in winter to heterotrophic conditions by summer. NEM tended to be most autotrophic during winter and most heterotrophic during summer (Fig. 3) in all the bays but San Antonio Bay, which responded differently to changing conditions, and Copano Bay, which tended to be relatively heterotrophic throughout the entire year. Overall there was no clear seasonal pattern to NEM, GPP, and R.

Significant intrabay differences in NEM, GPP, and R were found among Copano Bay stations (MAA-MA3; $p = 0.049$), but the overall differences were hard to interpret due to a significant interaction between NEM and month ($p < 0.01$; Fig. 4). Station MA3 was more autotrophic during June than the other two stations, and MA2 was more autotrophic during November. August results at station MAA (0.8 ± 1.44 mg O_2 l^{-1} d^{-1}) are omitted due to loss of bottom water data. Throughout 2004, stations MA2 and MA3 generally tended to be less metabolically active than station MAA with both higher GPP and R at station MAA than at MA2 or MA3.

No overall significant differences were found between surface (−0.74 ± 0.48 mg O_2 l^{-1} d^{-1}) and bottom (−1.12 ± 0.48 mg O_2 l^{-1} d^{-1}) NEM with all data pooled together. There was significantly ($p < 0.05$) more heterotrophic bottom water at station NC A in Nueces Bay only during October and at station GE B in San Antonio Bay only during July and October (Fig. 5). It is possible this is a consequence of benthic aerobic R and sediment oxygen demands during warm water salinity stratification. Bottom water was significantly more autotrophic than surface water in most bays during January when turbidity in the water column tends to

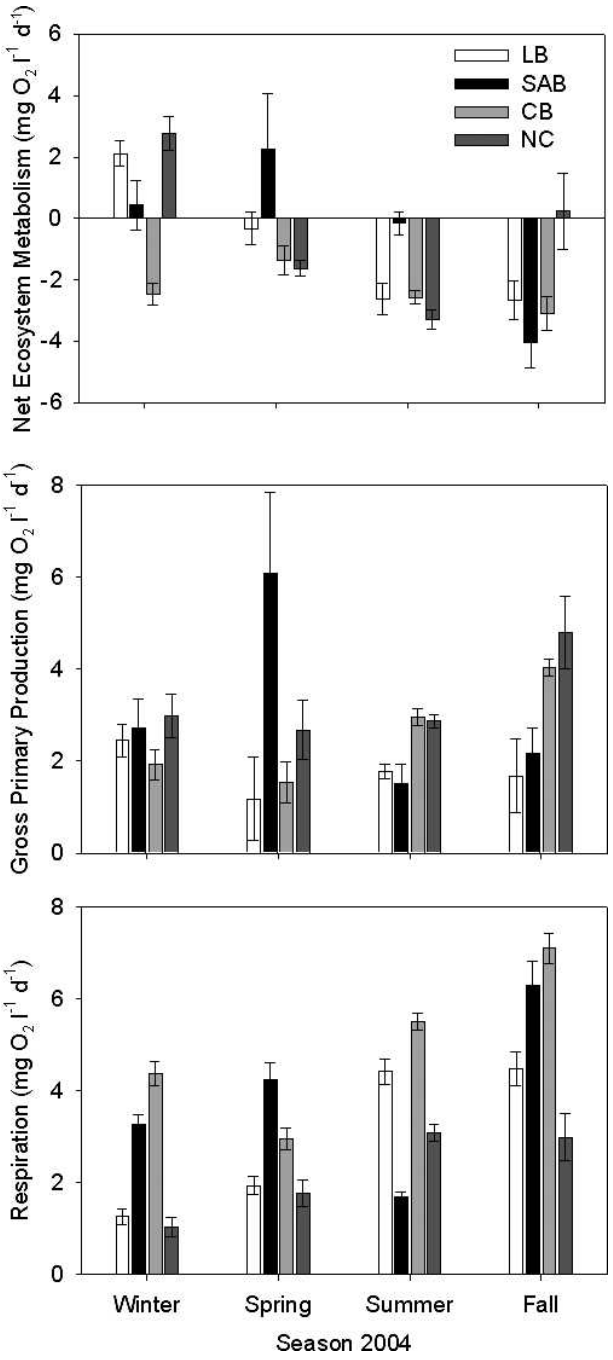


Fig. 3. Seasonal and interbay variability in net ecosystem metabolism, gross primary production, and respiration rates (mean ± 1 SE) for all stations and samples in Lavaca Bay (LB), San Antonio Bay (SAB), Copano Bay (CB), and Nueces Bay (NB).

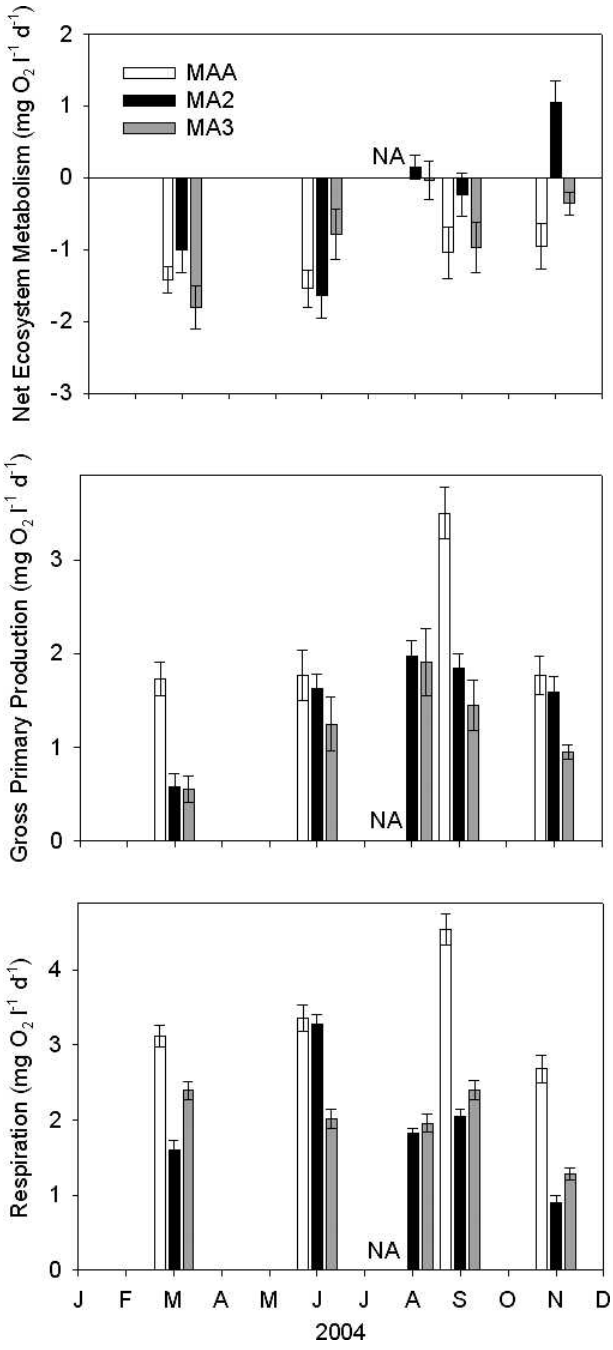
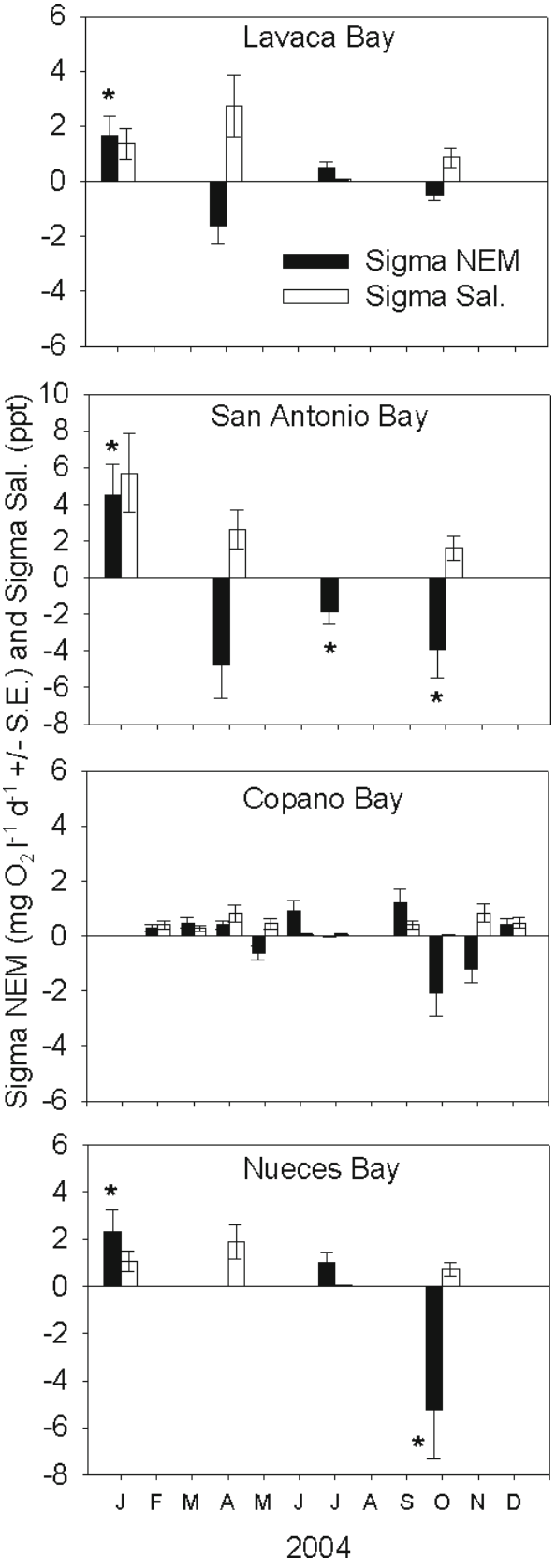


Fig. 4. Monthly and intrabay variability in net ecosystem metabolism, gross primary production, and respiration rates (mean ± 1 SE) for replicates at stations in Copano Bay. Note: Bottom depth data missing for August at station MAA.

decrease. Significant differences between surface and bottom water NEM mainly occurred during periods of significant vertical salinity stratification ($p < 0.01$). Sigma Sal. values greater than one yielded relatively larger Sigma NEM results than those observed during more vertically homogenous conditions, which suggests that there may be some threshold value for the effect of salinity stratification on NEM differences. Significant differences between surface and bottom NEM did occur during periods with a marked lack of salinity stratification,



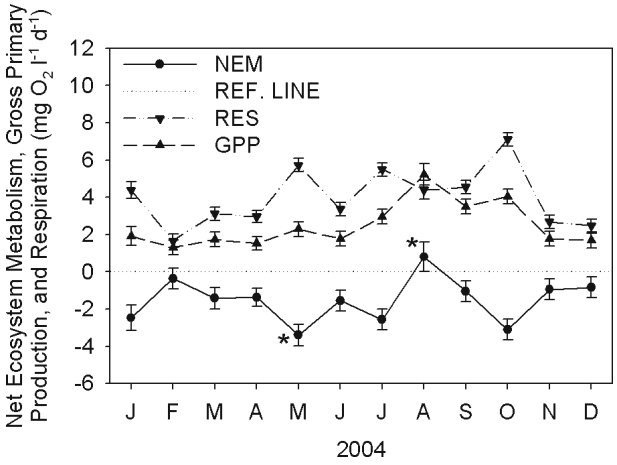


Fig. 6. Monthly variability in daily net ecosystem metabolism, gross primary production, and respiration in Copano Bay (mean ± 1 SE). Significantly different ($p < 0.001$) NEM values denoted by *.

implying that other factors, such as NEM dynamics after inflow events, may be important to consider. No significant differences in GPP or R between surface and bottom waters were found.

The most temporally complete data set was from Copano Bay station MAA and had 138 samples from 69 d in 12 different weeks. There were significant NEM, GPP, and R differences at station MAA among months ($p < 0.01$; Fig. 6). The most heterotrophic NEM conditions occurred during the months of May (-3.40 ± 0.56 mg O_2 l^{-1} d^{-1}) and October (-3.11 ± 0.56 mg O_2 l^{-1} d^{-1}). R increased from a base level of 3.0–4.0 mg O_2 l^{-1} d^{-1} to significantly elevated levels of 5.6–7.1 mg O_2 l^{-1} d^{-1} during May, July, and October. Late summer-early fall months tended to have slightly higher GPP values than other months.

Significant changes in NEM between consecutive days only occurred 10 times out of a potential 339 sequential samples during this study. All but one of these changes in NEM between consecutive days occurred during one specific week in April. Daily NEM at station MAA in Copano Bay became significantly more heterotrophic from February 18 to 19. During the week of monitoring in April, significant changes in NEM occurred four times at both station MAA and NC A. Daily differences in GPP were similar to NEM in that there were very few

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Fig. 5. Monthly average difference of bottom and surface NEM's (Sigma NEM) and the average difference of bottom and surface salinity (Sigma Sal.) for each bay. Positive values mean that the bottom water is more autotrophic or more saline than the surface water. Weeks with significantly different ($p < 0.05$) Sigma NEM values are labeled with an asterisk (*).

TABLE 2. Average daily water temperatures (T; °C), salinities (Sal; ‰), measurement depth (D; m), and USGS gauged average cumulative daily freshwater inflow (FW; 10^5 m^3) by month (2004) and bay system.

	Lavaca				San Antonio				Copano				Nueces			
	T	Sal	D	FW	T	Sal	D	FW	T	Sal	D	FW	T	Sal	D	FW
January	13	22	1.3	12	13	18	1.2	45	16	9	0.4	3	15	23	0.9	0.7
February				15				51	17	11	0.7	3				0.9
March				15				52	20	12	1.3	2				11
April	21	22	1.0	26	21	9	0.9	69	21	4	0.5	13	20	5	0.7	111
May				71				70	24	1	0.8	16				113
June				86				68	29	1	0.9	1				40
July	30	0	1.2	21	30	0	1.2	69	30	1	0.7	4	29	1	0.8	103
August				3				64	29	2	1.0	3				9
September				2				59	28	6	1.1	4				26
October	27	8	1.2	8	27	13	1.3	63	28	7	0.8	2	28	1	0.8	1
November				106				73	22	7	0.9	7				28
December				5				75	18	7	0.5	2				22
Average	23	10	1.2	31	23	10	1.2	63	24	6	0.9	5	23	11	0.8	39

days that were different than the mean ($p < 0.01$). No significant GPP differences existed between consecutive days. Daily differences in R were significant ($p < 0.01$), but like GPP were not found on consecutive days.

Water temperature followed a seasonal cycle with lows during winter months and highs during summer (Table 2). Daily average temperature ranged from a low of 10°C at station GE B in San Antonio Bay during January to a high of 32°C at station MAA in Copano Bay during August. Nueces Bay station NC A had slightly lower temperatures than the other three bays throughout the year. Temperatures during deployments tended to remain stable, but in some weeks daily temperature changed about 1°C, and on a few occasions, water temperatures decreased by as much as 7°C in 24 h. Rapid temperature changes were most often associated with decreasing salinity (-2‰ d^{-1}) during April storm events.

Irradiance followed a seasonal cycle similar to temperature with highest irradiance rates in summer and lowest rates during winter. A few exceptions to this trend were observed during large precipitation events during April and May when irradiance decreased markedly.

Salinity was highest during January and remained that way until April (Table 2). Large FWI (up to 182 $\times$ 10^6 m^3 d^{-1}) beginning in April and continuing through most of early summer resulted in large decreases in salinity (dropping as much as 23‰) in all bays. All four bays had salinity at or near zero by July. The least amount of change in salinity occurred at the stations in Copano Bay, which started the year relatively fresh (8‰). Copano Bay remained relatively fresh throughout the year with an annual daily average salinity of 6‰. Salinity began to recover towards prespring levels by September in all four bays.

FWI followed the expected pattern, at least during the first 3 mo of the year, of decreasing flow from northeast to southwest along the Texas coastline (Table 2). San Antonio Bay, located to the south of Lavaca Bay, is fed by a much larger watershed than Lavaca Bay. San Antonio Bay receives, on average, higher flows than Lavaca Bay even though the San Antonio Bay watershed receives less annual precipitation per km^2. FWI increased as much as 100×10^5 m^3 d^{-1} in April and remained high in Lavaca, San Antonio, and Nueces Bays through early summer. Copano Bay received a shorter duration and less extreme freshwater pulse (16×10^5 m^3 d^{-1}) starting in April and ending in May. Freshwater inflow into Copano Bay decreased to spring levels (2×10^5 m^3 d^{-1}) in June and was low throughout most of the remaining year. Nueces Bay experienced another large FWI event in July (103×10^5 m^3 d^{-1}). San Antonio Bay FWI were proportionally the least affected by the spring runoff events as average inflow rates are generally higher than the other bays (Table 2).

PCA reduced the large data set (8 variables, n = 421) of mean daily environmental and water quality measurements (temperature, depth, DO concentrations, salinity, pH, FWI, and wind speed) into 3 principal components that explained a total of 70% of the environmental variability (Table 3). Principal component one, explaining 34.1% of the total variability, included factors associated with seasonal changes, such as temperature, salinity, and corresponding physical changes in DO. Principal component two, explaining a further 18.8% of the total variability, included factors associated with precipitation events such as FWI and wind speed. Principal component three, explaining an additional 16.9% of the total variability, included those factors associated with different bays such as depth and pH.

TABLE 3. Principal component variation explained and loading scores for principal components 1–3 (PC 1–3). The most influential factors in each principal component are in bold.

PC	% Variation	Cumulative % variation	
1	34.14	34.14	
2	18.77	52.91	
3	16.90	69.81	
Variable	PC 1	PC 2	PC 3
Temperature	**−0.43**	−0.10	0.02
Depth	−0.06	−0.20	**−0.44**
Dissolved Oxygen	**0.37**	0.04	0.31
Salinity	**0.36**	−0.03	−0.27
PH	−0.07	−0.18	**0.61**
Wind speed	0.02	**0.57**	−0.12
FWI	0.09	**0.61**	0.17

A limited data set (n = 229) with two additional variables, total daily irradiance and mean daily chlorophyll *a* concentrations, was included in a separate PCA (data not shown). Irradiance covaried with temperature ($p < 0.01$, $R^2 = 0.39$) and no significant change in NEM was observed over the range of irradiance measured. Chlorophyll *a* also had a nonsignificant relationship with NEM. Irradiance and chlorophyll *a* were not included in later analyses so sample numbers could be maximized.

Predicting NEM from Environmental Variables

Stepwise multiple regression analysis of NEM and environmental conditions showed similar results in all four bays (Table 4). Salinity, temperature, and DO concentration, which the PCA estimates to account for just 34.1% of the total environmental variability, were the strongest predictors of NEM. DO concentrations are physically linked to salinity and temperature, and so DO concentration's relationship with NEM may partially represent salinity and temperature's influences on NEM. Temperature variability explained between 20% in San Antonio Bay and 86% in Nueces Bay of the variability in measured DO concentrations. Salinity, temperature, and DO concentration combined to explain around 80% of the variability in NEM. The importance of each environmental condition changed among bays. The most autotrophic conditions took place during periods of high salinity, low temperatures, and high DO concentrations. High FWI, and corresponding low salinities, and wind speeds were associated with periods of more heterotrophic NEM.

TABLE 4. Stepwise multiple regression models of NEM and environmental variability. The three most influential significantly related variables on NEM are listed for each bay, except for Lavaca Bay, which had only two significantly related variables.

Bay	Variable	Partial R^2	Model R^2
San Antonio Bay	Dissolved Oxygen	0.62	0.62
	Temperature	0.08	0.70
	Salinity	0.06	0.76
Lavaca Bay	Dissolved Oxygen	0.79	0.79
	Temperature	0.05	0.84
Copano Bay	Dissolved Oxygen	0.25	0.25
	Temperature	0.26	0.51
	Salinity	0.08	0.59
Nueces Bay	Salinity	0.47	0.47
	Dissolved Oxygen	0.13	0.60
	Temperature	0.19	0.79

San Antonio Bay station GE B had variable NEM values over a large range of temperatures (13–30°C; Fig. 7). Copano Bay stations MAA-MA3 had relatively stable NEM values over a similar range of temperatures (16–30°C), but were not significantly related to temperature. Lavaca and Nueces Bay stations LB 15 ($p < 0.01$, $R^2 = 0.45$) and NC A ($p < 0.01$, $R^2 = 0.24$) had decreasing NEM values with increasing temperatures.

NEM was variable over the range of salinity (0–25‰) found during the study (Fig. 8). Copano Bay stations MAA-MA3 NEM also had no response to salinity, but salinity did not change as much as in other bays ranging from 0‰ to 14‰. Lavaca Bay station LB 15 ($p < 0.01$, $R^2 = 0.40$) and Nueces Bay station NC A ($p < 0.01$, $R^2 = 0.47$) had significantly increasing NEM, that is increasing autotrophy, as salinity increased from 25‰ to 0‰.

The covariance of salinity and temperature makes it difficult to separate each factor's influence on NEM, which is especially important in Lavaca and Nueces Bays where both salinity and temperature individually correlate with NEM. An analysis of residual variability in NEM explained by each factor after accounting for the other during stepwise linear regression helped to unravel the signals. When DO was not factored into the multiple regression analysis, both factors had a significant influence on NEM at station LB 15 in Lavaca Bay. Salinity explained the majority of NEM variance ($p < 0.01$, $R^2 = 0.39$). The influence of temperature on NEM was much reduced but it still helped to explain another 3% of the variability ($p < 0.04$). Even though salinity and temperature covaried during 2004, inclusion of both factors in estimates of NEM improves accuracy.

FWI was summed over 10 d prior to sampling and the total volume is labeled as the 10-d cumulative FWI (Fig. 9). The cumulative FWI volumes ranged from near zero in Copano Bay to near 200 million m^3 in Nueces Bay. Data were not obtained in all ranges in all bays. No data was obtained from zero to 30 million m^3 in San Antonio Bay, and little data was obtained above 7 million m^3 in Copano Bay. FWI volumes in Nueces Bay were bimodal, with data at the low end and high end, but none in the middle.

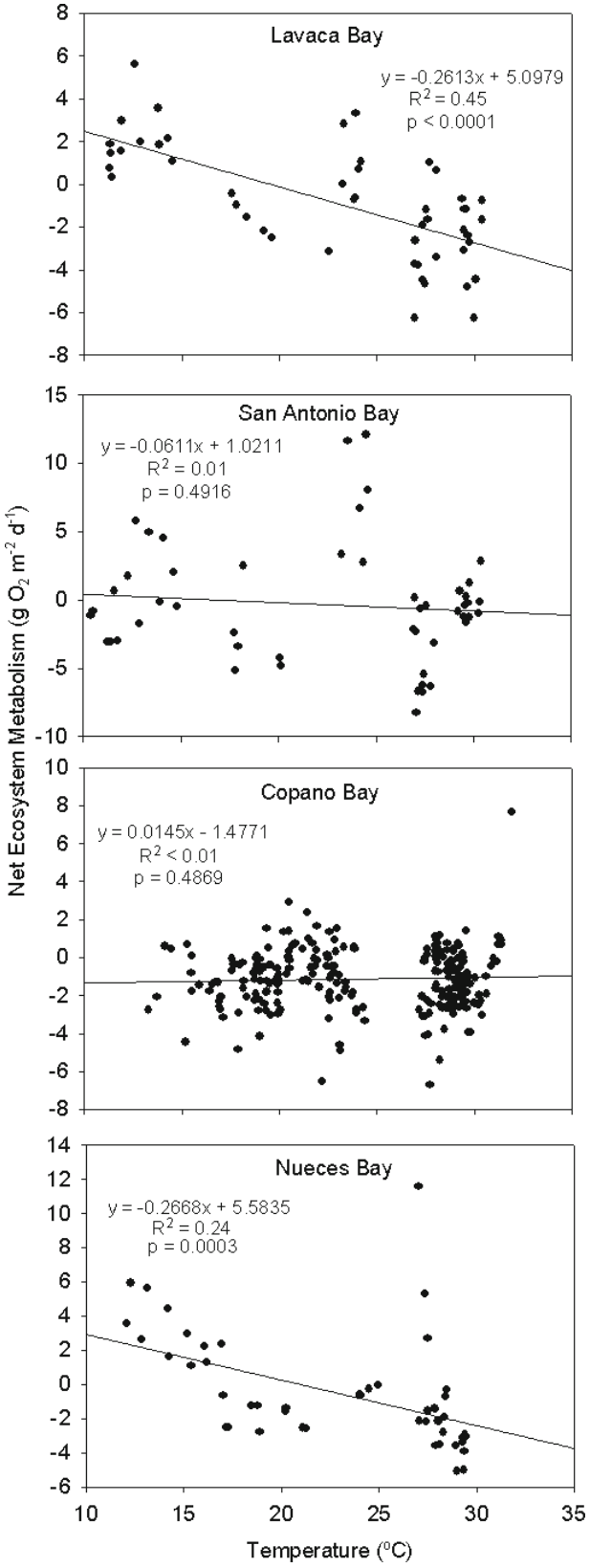


Fig. 7. Relationship between net ecosystem metabolism and temperature in four bays. San Antonio Bay, Lavaca Bay, Copano Bay, and Nueces Bay.

Station GE B in San Antonio Bay had highly variable NEM values clustered into two separate FWI ranges, but there was no obvious pattern with increasing FWI (Fig. 9). San Antonio Bay FWI rates are generally higher than the other three bays, and so the range of FWI was small, and more data in the low range, with little or no flow, may be required to assess the relationship between NEM and FWI in San Antonio Bay.

Copano Bay stations had relatively more heterotrophic NEM values at most FWI rates than the other three bays (Fig. 9). Average NEM at stations MAA-MA3 increased from slightly heterotrophic during the lowest FWI to zero at FWI less than 2 million m^3. Less data exist for evaluating NEM above FWI of 2 million m^3, but the results show a more heterotrophic trend in NEM as FWI increases to 7 million m^3. The limited samples collected at FWI above 7 million m^3 in Copano Bay occurred during one particularly large inflow event in April. NEM values started out autotrophic (Fig. 10) and then became very heterotrophic after a day of FWI of around 30 million m^3 and then became autotrophic again for a day or two as FWI slackened to around 7 million m^3 d^{-1}. NEM values returned to more moderate heterotrophic values as FWI slowed to 2 million m^3 d^{-1}.

Lavaca Bay station LB 15 NEM results show a similar pattern to Copano Bay results over a similar range of FWI (Fig. 9). Lavaca Bay NEM results became autotrophic at FWI of 2 million m^3 before becoming very heterotrophic at FWI of 8 million m^3. The NEM response to moderate FWI in Lavaca Bay varied widely between FWI of 10–20 million m^3. Some of this variability may be due to relatively autotrophic conditions observed during a period of subsiding FWI after a large precipitation event. At FWI greater than 20 million m^3, NEM results became heterotrophic. Clusters of NEM values were related to seasonal changes in salinity and temperature. Autotrophic conditions predominated during high salinity conditions in winter, but heterotrophic conditions prevailed during low salinity in fall.

Both stations MAA in Copano Bay and LB 15 in Lavaca Bay had similar lagged NEM responses to FWI pulses (Fig. 11). In April, large increases in GPP took place about 3 d after a pulse of FWI in both Lavaca Bay and Copano Bay. The large spike in GPP caused the bays to become more autotrophic following high heterotrophy immediately after the

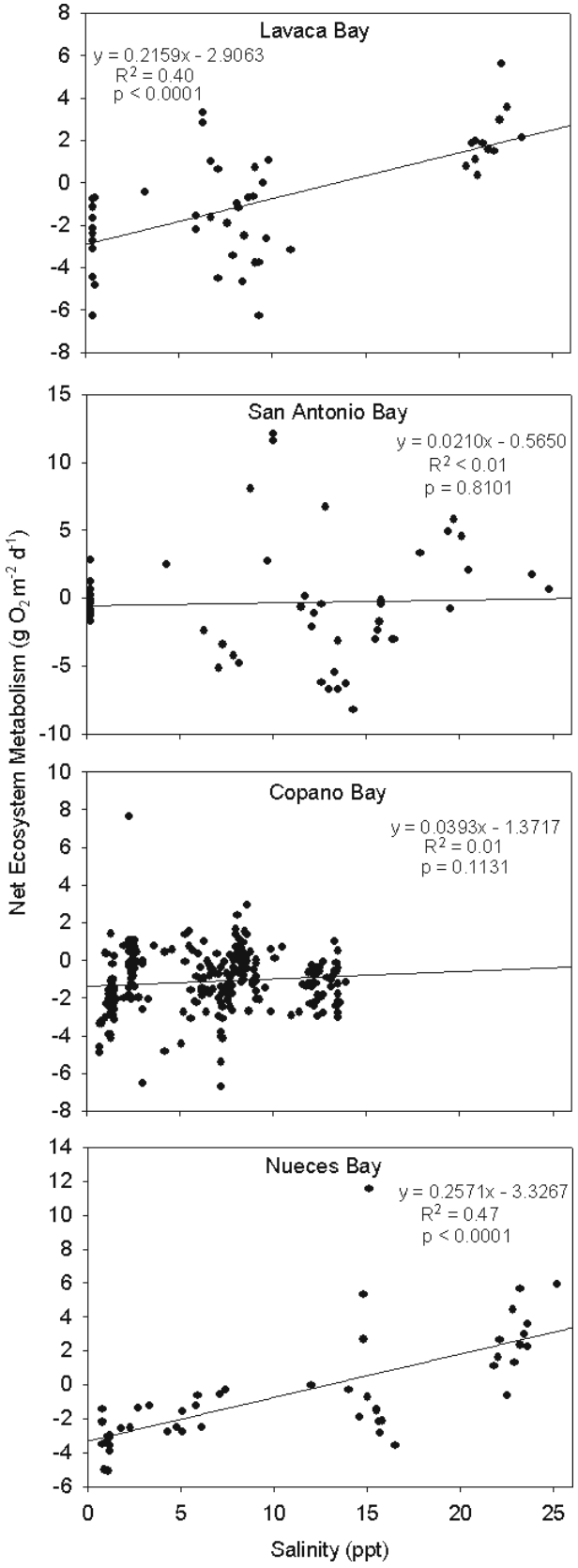


Fig. 8. Relationship between net ecosystem metabolism and salinity in four bays. San Antonio Bay, Lavaca Bay, Copano Bay, and Nueces Bay.

FWI pulse. Within 4 d after the inflow pulse, NEM began to fall indicating that conditions were again becoming net heterotrophic.

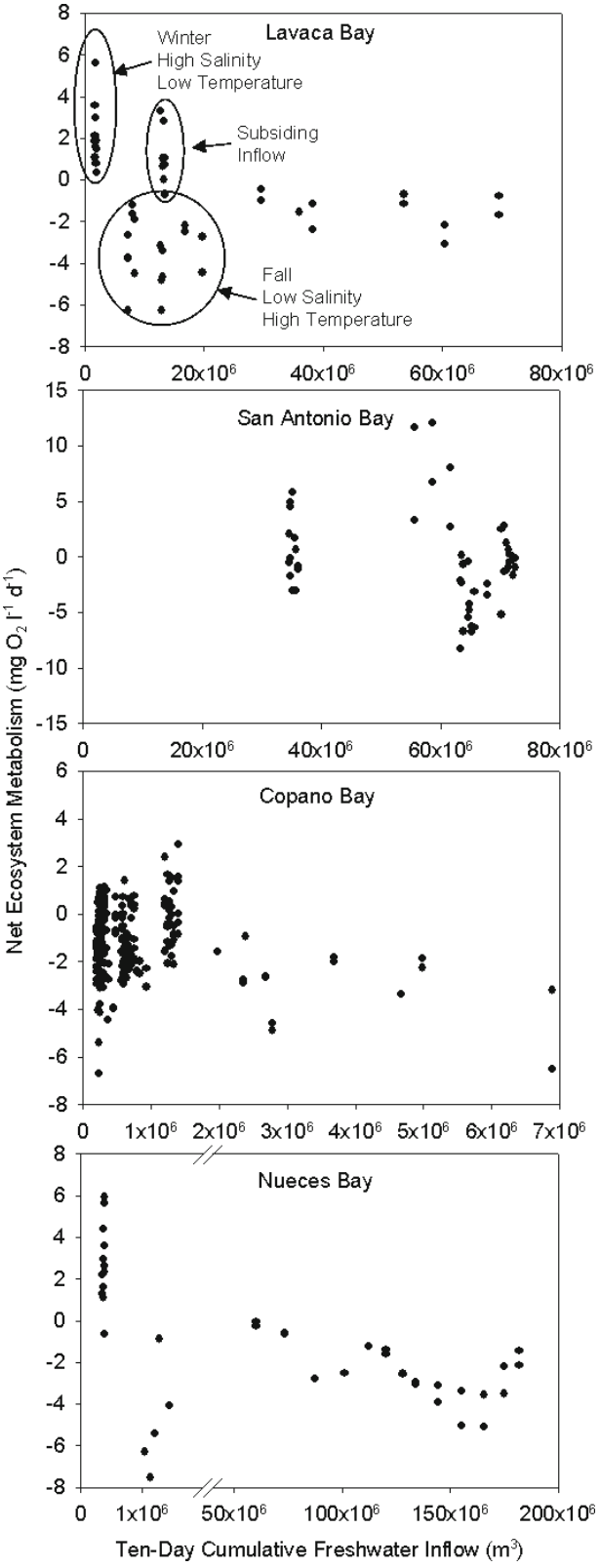
Nueces Bay station NC A NEM results exhibited more heterotrophic conditions at higher FWI volumes (Fig. 9). NEM values were relatively high at very low FWI of 0.5 million m^3, but became very heterotrophic around FWI of 2 million m^3. At FWI of 50–200 million m^3, NEM values were moderately heterotrophic. There was a huge flood in Nueces Bay where FWI reached 180 million m^3. This extreme range of FWI experienced by Neuces Bay and the subsequent lack of data to define the relationship between NEM and FWI at more moderate FWI volumes restricts interpretation.

Discussion

NEM is driven by environmental conditions. Temporal variability of environmental conditions, and NEM, followed both seasonal and event driven patterns. The scale that is relevant for modeling NEM depends on the spatial and temporal variability of these environmental conditions in the modeled system. Three of the most variable environmental conditions during the present study were temperature, salinity, and DO concentration. The accuracy of using NEM as an ecological indicator depends on measurements taken at the appropriate temporal and spatial scales of environmental variability.

Temporal Variability

NEM was significantly different among seasons (Fig. 3). Changes in temperature and salinity are influential at this temporal scale. Caffrey (2003) concluded that seasonal temperature variability explained most intrasite NEM variability. She found that NEM and temperature were correlated at 19 out of 28 NERR sites, but temperature's influence may be magnified by larger temperature ranges in the mostly temperate NERR estuaries. In western Gulf of Mexico subtropical estuaries there is a significant correlation between NEM and temperature, salinity, and DO concentrations (Table 4). The range of NEM in the western Gulf of Mexico found during the present study corresponds well with those from other Gulf of Mexico and southeastern U.S. sites (Caffrey 2004), but there appears to be more influence from FWI and corresponding salinity changes in some bays. Copano Bay stations MAA-MA3 and San Antonio Bay station GE B



exhibited little NEM response to changing temperature (Fig. 7). Higher temperatures at Lavaca Bay station LB 15 ($p < 0.01$, $R^2 = 0.45$) and Nueces Bay station NC A ($p < 0.01$, $R^2 = 0.24$) were associated with greater heterotrophic conditions and the relationship between temperature and NEM remained significant ($p < 0.04$) after accounting for the influence of salinity. Past research concludes that seasonally changing temperatures can have a major influence on NEM, but in the western Gulf of Mexico temperature's influence may be limited by the reduced temperature range, and seasonal or precipitation event driven salinity patterns may be more important.

NEM in western Gulf of Mexico estuaries was also significantly different among months (Fig. 6). On weekly to monthly scales, ephemeral events, such as storms, may become more influential on NEM than seasonally changing environmental conditions. Storms can result in rapid salinity changes as pulses of FWI mix with estuarine water. Caffrey (2003) found that salinity had a significant correlation with NEM in about half of NERR sites. She also found that NEM was positively correlated with salinity at 6 sites and negatively correlated in the other 7 sites. In western Gulf of Mexico estuaries, NEM was negatively correlated with salinity at stations LB 15 and NC A in Lavaca and Nueces Bay, respectively. Copano Bay stations MAA-MA3 and San Antonio Bay station GE B did not exhibit a simple, definable seasonal or monthly NEM response to changing salinity. Copano Bay stations experienced a much reduced range of salinity than did the other three bays, and station GE B may have responded differently to the FWI pulse in spring because of lower ratios of organic carbon to nutrients (Table 1) in San Antonio Bay FWI. Salinity changes may be an indicator of freshwater constituent loading in San Antonio Bay. In San Antonio Bay a drop in salinity and more autotrophic NEM probably indicates increased nutrient loading. The same drop in salinity could represent increased organic loading in the other three bays that have higher ratios of organic carbon to nutrients than San Antonio Bay (Table 1). Summer R rates at stations in Lavaca, Copano, and Nueces Bays increased without a corresponding increase in GPP after large magnitude FWI decreased salinity (Fig. 3). An alternate explanation for the lack of response of GPP during a FWI event is that the magnitudes of

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Fig. 9. Relationship between net ecosystem metabolism and 10-day cumulative freshwater inflow in four bays. San Antonio Bay, Lavaca Bay, Copano Bay, and Nueces Bay. San Antonio Bay and Copano Bay with event dynamics above 10-day cumulative freshwater inflows of 7×10^6 m^3 excluded from the data set.

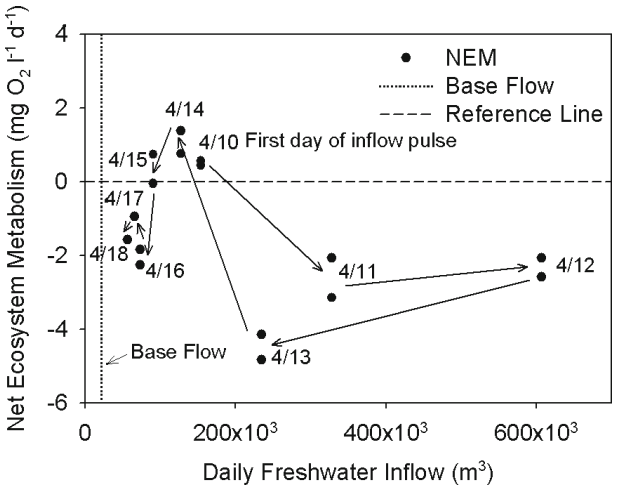

Fig. 10. Temporal response of net ecosystem metabolism to rapidly changing daily freshwater inflow in Copano Bay. Dotted vertical line represents base flow conditions (Aransas River 2002–2005 USGS median gauged freshwater inflow = 22×10^3 m^3 d^{-1}).

FWI observed during the present study represent large disturbances to the planktonic primary producer community. Past research supports the idea that salinity and its relationship with FWI delivered constituents is an influential factor on NEM on monthly time scales, but daily NEM dynamics and the lack of nutrient loading data during the present study makes it difficult to quantify these relationships in western Gulf of Mexico bays.

Large daily variability in estuarine metabolic rates has been reported by D'Avanzo et al. (1996) and Caffrey (2004). In this study almost all of the significant differences between daily NEM occurred during FWI pulses in April 2004. FWI rates during the April deployment in Lavaca Bay increased from 125 to 5,366 m^3 s^{-1} between April 10 and 12. The FWI rate into Copano Bay was 168 m^3 s^{-1} just 2 d before the deployment period in April, but had returned to more normal rates of 1 m^3 s^{-1} by the end of the deployment. The ephemeral and variable nature of FWI events means it is important to integrate FWI over more than 1 d to capture its influence on NEM. With the potential of large changes in NEM on daily time scales it is also important to sample multiple daily periods so that daily variability does not bias analysis at longer temporal scales. At least 7 d within each month were sampled in the present study and this produced large enough sample sizes to find significant differences between months even when within month daily variability was high.

The dynamic range of NEM can be quite large over the course of a FWI event. The best example of this was observed during April in Copano Bay when sampling took place starting just after a large inflow

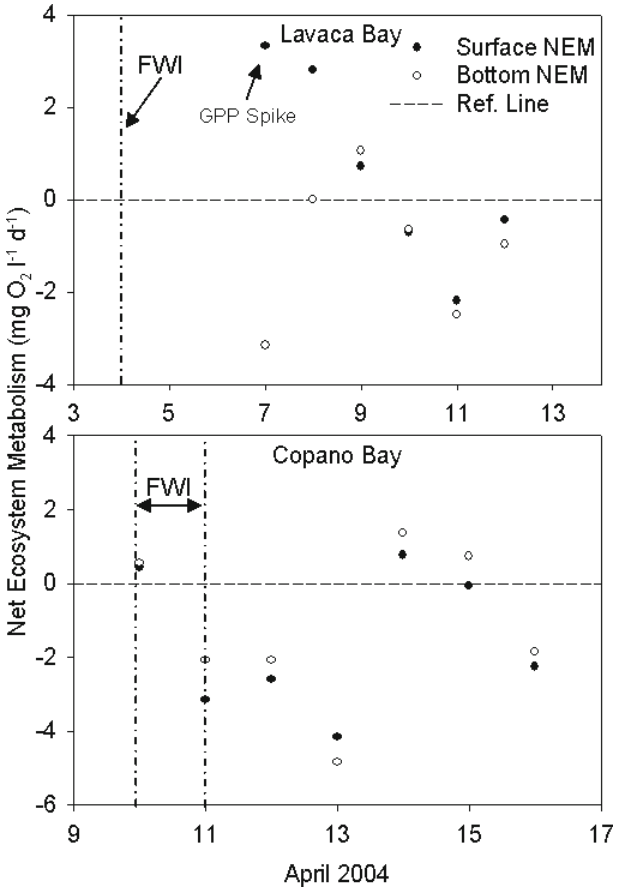

Fig. 11. Daily net ecosystem metabolism in surface and bottom samples in Lavaca Bay and Copano Bay. Vertical reference lines are the day of freshwater inflow (FWI) events. Spikes in gross primary production (GPP) are also labeled.

event had started and continued until freshwater subsided (Fig. 10). As FWI increases during an event it is thought that the ratio of nutrients to organic matter will increase during an initial pulse of dissolved nutrients and then will decrease as more terrestrial organic particulates are eroded from a watershed (Jones et al. 1986; Parker et al. 1989). NEM should become more autotrophic, due to increased nutrient loading, as FWI begins to increase from base flow levels. As FWI continues to increase and begins to disturb the planktonic community, NEM will become more heterotrophic due to increased organic matter consumption by benthic microheterotrophs. Evidence for this pattern of ecosystem response to changes in FWI is provided by the event dynamics during April's inflow event in Copano Bay (Fig. 10), as well as a similar response seen in Lavaca Bay (Fig. 11). NEM was initially net autotrophic, which may be due to primary producers responding to the initial dissolved nutrient pulse that precipitation events

bring to estuaries. After 3 d, NEM values were much more heterotrophic due to increased R and decreased GPP, which implies dominance of metabolic rates by labile organic matter processing. On the third day after inflow began, R was very high and GPP in the surface was beginning to increase while GPP in bottom waters remained low. As FWI continued to subside and conditions stabilized, the ecosystem again became net autotrophic with R decreasing and GPP greatly increasing. The lagged GPP response to a FWI pulse was also seen at station LB 15 in Lavaca Bay (Fig. 11). This autotrophic response could be due to the release of dissolved nutrients into the water column as benthic organisms processed organic matter loads and planktonic primary producers reestablished themselves in the upper bay. Overall the ecosystem was on average net heterotrophic during and after the FWI event. The combined result of event dynamics follows the general pattern of response of increased heterotrophy with increased FWI and lowered salinity. During our analysis of factors correlated with NEM (Table 4), it was assumed that the relationship between FWI and NEM was linear, which may not be valid. FWI dynamics may be more influential on NEM than presented here, and the FWI may be the most influential environmental factor in Copano Bay where temperature and salinity effects are negligible.

Spatial Variability

The largest of the three spatial scales (interbay) exhibited the most significant differences in NEM, and among the bays, FWI exhibits the largest range compared to other environmental factors. Other differences among bays include the presence of specific estuarine habitat types (i.e., seagrass beds or marsh) and salinity differences (Caffrey 2004), as well as nutrient and organic matter loading differences from each bay's watershed (Howarth et al. 1991; Kemp et al. 1992; D'Avanzo et al. 1996; Eyre and McKee 2002; Wang et al. 2003). The link between the last three factors in the present study is FWI. FWI, through its effect on nutrients, turbidity, and salinity, can determine the estuarine community structure of aerobic organisms in Texas estuaries (Montagna and Kalke 1995). Nutrients and organic matter are mainly delivered through FWI because Texas estuaries are microtidal (Whitledge 1989a,b; Longley 1994). Kemp et al. (1997) hypothesized that the ratio of nutrient to organic loading explains variations in estuarine NEM, where lower ratios result in more heterotrophic conditions. Large variability in environmental conditions on daily to seasonal temporal scales in this study interact with interbay differences in a way that makes separating out each specific bay's average response to specific environmental conditions difficult. Each of the four bays was unique in its response to changing conditions during at least one time period in 2004. The metabolic response in each bay to changing environmental conditions should be considered individually, and data from different bays should not be pooled together.

NEM values among stations in Copano Bay were not significantly different on intrabay scales. Significant differences among Copano Bay stations did occur during select months in 2004. Station MAA, which is closer to the Aransas River mouth than stations MA2 and MA3, was more heterotrophic than the two downstream stations during at least one sampling period in 2004. This difference was significant in June and November (Fig. 4). As noted by Caffrey (2004), individual station NEM measurements are not always representative of metabolic rates in entire estuaries. Results in Copano Bay occasionally exhibited small, but statistically significant, intrabay differences at distances between 2 and 4 km. This indicates that more intensive spatial sampling is required before routinely monitored single station DO data can be used to represent NEM for estuaries greater than 6 km in length.

Significant differences in NEM between surface and bottom waters rarely occurred in the shallow water estuaries of the western Gulf of Mexico. This is not surprising since the bays in the present study have depths that rarely exceed 3 m. When significant differences between surface and bottom water NEM did occur, it was almost always associated with significant salinity stratification events (Fig. 5). Salinity differences between surface and bottom waters, at times, became as large as 9‰ in shallow water columns (< 3 m depth). If similar stratification events take place at other sites then DO monitoring from a single depth may result in depth specific NEM values. Large influences of metabolic processes occurring in, and on, bottom substrates can be the driving force behind water column NEM rates. This should be especially true in the shallow, muddy, bottom environments of some Texas bays. Autotrophic benthic microalgal communities in Texas Bays have been implicated as being as productive during winter months as seagrass beds are during summer months and may be responsible for the autotrophic conditions seen during January in this study (Russell and Montagna 2004). NEM values may become even more nonrepresentative of an entire estuary if, during a 24-h cycle, stratification boundary layers move over the depth of the DO probe deployment. It may be more informative to use split depth monitoring, as employed in the present study, with daily samples at a station being treated as replicates only when salinity is vertically homogeneous. Routine DO monitoring, which is

often measured at one depth, needs to be thoroughly checked for anomalies in salinity to rule out stratification of the water column.

Any change in NEM could be ecologically significant given proper conditions. We have previously demonstrated the use of NEM as a potential indicator of DO impairment in estuaries (Russell et al. 2006). If NEM becomes statistically more heterotrophic for a significant length of time then DO concentrations may reach impaired levels as NEM reduces DO concentrations faster than can be replaced through exchange with the atmosphere or overlying waters. If NEM becomes just 0.5 mg O_2 l^{-1} d^{-1} more heterotrophic than the buffering capacity afforded by lateral advection of water masses or oxygen transfer from the atmosphere then, over a 2-d period, DO concentrations will drop 1.0 mg O_2 l^{-1}. This could represent a severe disturbance in environments with DO concentrations already reduced by high temperatures and high salinities, conditions that are relatively common in Texas bays (Ritter and Montagna 1999). Relatively small changes in NEM can be responsible for ecosystems that suffer from reoccurring hypoxia or anoxia.

NEM, as an indicator of estuarine ecological metabolic rates, is only useful for assessing the effect of climate change and watershed development if it responds in a predictable manner to changing environmental conditions. This research demonstrates that NEM does respond predictably to changing environmental conditions, such as temperature, FWI, and salinity regimes, and is a good indicator of estuarine ecological metabolic rates. The use of NEM as an indicator of estuarine ecosystem metabolic rates requires that measurements be taken at appropriate spatial and temporal scales. The NEM temporal variability is more prevalent than spatial variability in western Gulf of Mexico estuaries and this variability exists at daily, monthly, and seasonal scales. Temporal NEM variability is most strongly related to FWI dynamics, DO concentrations, and seasonal temperature changes. The nature of individual estuaries response to changing environmental conditions is dictated by factors specific to that system, which might include residence time, organic matter to nutrient load ratios, and mean FWI rates. The scales of variability and environmental drivers described here could be useful in developing predictive models to assess the potential influence of projected climate change and watershed development scenarios on estuarine metabolic rates.

Acknowledgments

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DUNTON, K. unpublished data. The University of Texas at Austin's Marine Science Institute, 750 Channell View Drive, Port Aransas, Texas 78373.

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