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The effect of freshwater inflow on net ecosystem metabolism in Lavaca Bay, Texas

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Abstract

Estuaries and other coastal ecosystems depend on freshwater inflow to maintain the gradients in environmental characteristics that define these transitional water bodies. Freshwater inflow (FWI) rates in many estuaries are changing due to changing land use patterns, water diversions for human consumption, and climate effects, but there are no standard criteria to determine minimum inflow rates. An ecological indicator is required so models can be produced to predict how changing hydrology might affect estuarine metabolic rates, productivity, or impairment. One indicator of estuarine metabolic rates is net ecosystem metabolism (NEM). It is hypothesized that metabolic rates (as indicated by NEM) will depend on recently delivered FWI. To test this hypothesis, daily NEM was calculated from high frequency changes in dissolved oxygen measurements in a shallow water estuary, Lavaca Bay, Texas, USA and related to FWI and other environmental conditions. There was a significant relationship between NEM and cumulative ten-day FWI in upper Lavaca Bay, with more heterotrophic conditions occurring after high FWI events. No significant relationship existed between NEM and FWI in lower Lavaca Bay, where other environmental conditions, such as tidal forcing, may be more influential. An empirical model simulating NEM's response to FWI in upper Lavaca Bay was more accurate during moderate to high flows than during low base-flow conditions. Thus, quantity of FWI and distance from the inflow point source constrained the dependence of NEM on FWI. NEM can be quite variable over time and within a bay dominated by a river at one end and ocean exchange at the other end. The range of environmental gradients over time and within an estuary will determine how representative NEM at a single location is for an entire estuary. However, during high flow period pulses NEM can accurately predict shifts from balanced to heterotrophic conditions. Therefore, use of the NEM model as an indicator of FWI effects is constrained to regions in estuaries that are most effected by FWI because of proximity to the source or the size of FWI pulse events. The unique geologic, geographic, and climate signature's of individual estuaries will dictate the fit of this model in space and time. Inclusion of other environmental factors, such as temperature or irradiance, is necessary to improve the NEM model during low base-flow conditions. It is concluded that the NEM model does provide a useful indicator of FWI effects on ecosystem metabolic rates as it works well in the upper regions of Lavaca Bay and during freshwater inflow pulses where and when freshwater inflow has more influence than other environmental factors.
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Keywords: net ecosystem metabolism; estuarine metabolic rates; freshwater inflow; impairment; indicators; ecological indicators

1. Introduction

Estuaries and other coastal ecosystems depend on freshwater inflow to maintain the gradients in environmental characteristics that define these transitional water bodies (Ketchum, 1951; Pritchard, 1967). Freshwater inflow rates are changing in most estuaries because of changes in land use and cover, water diversion for human uses, and climate change effects. These changes generally result in decreased freshwater inflow, loss of pulsed events, and changes in the timing of pulses. Minimum freshwater inflow levels are required by many states and countries to protect estuarine ecosystems, but there is no standard approach or criterion to set inflow levels (Montagna et al., 2002a). Also, freshwater inflow is delivered from a watershed as a result of precipitation events; some of which can

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be highly variable. The typical precipitation pattern in South Texas, for example, results in relatively small base flows punctuated by large inflow events from frontal systems and tropical storm activity (Orlando et al., 1993). Freshwater inflow transports sediment, nutrients, and organic matter from a watershed to an estuary. Thus, the inherent variability in freshwater inflow affects sediment, nutrient, and organic loading to estuaries. Nutrient and organic loading have been linked to estuarine metabolic rates (D'Avanzo et al., 1996; Kemp et al., 1997; Caffrey, 2004). The measurement of metabolic rates may enable prediction of how changes in freshwater inflow might affect estuarine ecosystems, and, therefore, how human-influenced changes in freshwater inflow may affect ecosystem function.

Anthropogenic modification of freshwater inflow can change the structure of South Texas estuarine ecosystems. For example, restored inflow to Rincon Bayou Texas, after damming reduced freshwater inflow by 55%, resulted in infauna abundance, biomass, and diversity increases (Montagna et al., 2002b). Increased freshwater inflow restored the ecosystem characteristics of this salt marsh nursery habitat to the range required for estuarine dependent, commercially important species such as the brown shrimp, *Farfantepenaeus aztecus* (Riera et al., 2000). The effect of changes in freshwater inflow on estuarine ecosystem function is more difficult to measure, because it requires an indicator that can quantify metabolic processes within a defined area on relatively short temporal scales.

Net ecosystem metabolism (NEM), first proposed by H.T. Odum (1956) may provide an ecological indicator of human influenced changes in freshwater inflow and their effects on an estuarine ecosystem's metabolic rates that fulfills the above mentioned requirements. NEM is calculated by subtracting aerobic respiration 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 respiration rates. A negative NEM indicates a heterotrophic ecosystem where respiration rates exceed photosynthesis rates. Changes in NEM may be driven by environmental conditions that vary temporally on daily scales, such as freshwater inflow rates related to daily precipitation differences, or seasonal scales, such as annual cycles of temperature. Freshwater inflow, by delivering nutrients and organic matter from the watershed, should be an important influence on estuarine NEM.

The balance between heterotrophic and autotrophic estuarine conditions is a measure of an ecosystem's organic matter production relative to remineralization and has implications for the balance between nutrient assimilation and release. A heterotrophic ecosystem is supported by remineralization of stored or imported organic matter. Organic matter input from deltaic regions explained stable carbon isotope values in 25% of particulate organic matter samples in Lavaca Bay (Parker et al., 1989), and during periods of high freshwater inflows terrestrial organic carbon can be distributed throughout Texas bay systems (Jones et al., 1986). Thus, Texas estuaries have the potential to be net heterotrophic ecosystems if organic matter inputs are relatively labile. An autotrophic ecosystem buries or exports organic matter. High rates of organic production in estuaries have been attributed to high rates of nutrient inputs (Nixon et al., 1986). Increased allochthonous inputs of inorganic nutrients without concurrently increased allochthonous inputs of organic carbon tend to result in autotrophic estuarine conditions (Oviatt et al., 1986). Also, heterotrophic ecosystems regenerate and export nutrients, while autotrophic ecosystems require inputs of inorganic nutrients (Smith et al., 1991). The balance between allochthonous organic matter and nutrient inputs has been hypothesized to explain variability in estuarine NEM (Kemp et al., 1997). Thus, NEM may be used to indicate organic matter and nutrient sources and sinks.

Ecosystem metabolic rates can lead to dystrophic or hyperautotrophic conditions when oxygen production and consumption rates exceed the assimilation capacity provided by physical processes, such as diffusion and advection (Viaroli and Christian, 2003). NEM, as an indicator of metabolic rates in an ecosystem, may be useful to estimate dissolved oxygen impairment. Dissolved oxygen concentrations in Texas bays and estuaries are considered unimpaired if they remain sufficiently high to maintain these ecosystems in an aquatic life category designated by the Texas Commission on Environmental Quality (TCEQ) (Texas Administration Code, Title 30, Part 1, Ch. 307). If average daily dissolved oxygen concentrations drop below 5 mg $O_2\,l^{-1}$ or concentrations drop below 4 mg $O_2\,l^{-1}$ at anytime during a 24-h period, then that aquatic system is impaired with regard to requirements for an exceptional aquatic life category. The United States Environmental Protection Agency's 2002 303(d) list reported that, nationally, there were 4641 impaired water bodies listed for organic enrichment and low dissolved oxygen. Low dissolved oxygen/organic enrichment ranked fifth behind pathogens, metals, nutrients, and sedimentation on the list of the top 100 impairments. Dissolved oxygen impairment has led to the approval of 947 total maximum daily load (TMDL) programs, representing over 10% of the total number currently approved nationally. In Texas, low dissolved oxygen/organic enrichment ranks second behind pathogens on the list of top impairments. One effect of altered dissolved oxygen dynamics is the increase in bottom water hypoxia events during summer months (Applebaum et al., 2005). Causes of bottom water hypoxic conditions include water column stratification, nutrient enrichment, high rates of organic matter decomposition, high salinity, and high water temperatures (Officer et al., 1984; Pokryfki and Randall, 1987; Ritter and Montagna, 1999; Rabalais and Turner, 2001). A large imbalance between planktonic and benthic photosynthesis and respiration can result in waters becoming hypoxic or anoxic. Large areas of shallow water estuaries in Texas can become hypoxic during summer months when high levels of water column primary production, water column stratification, high benthic respiration rates, high water temperatures, high salinity, and reduced flushing by freshwater inflow and tides combine to reduce bottom water dissolved oxygen levels to dangerous levels for most aerobic organisms (<2.0 mg $O_2\,l^{-1}$). Over one-half of the estuaries in the Gulf of Mexico exhibit moderate to severe dissolved oxygen depletion

(<5.0 mg O_2 l^{-1}), a currently used indicator of aquatic ecosystem impairment (Bricker et al., 1999).

The present study was performed as part of a TMDL assessment in Lavaca Bay, Texas (Montagna and Russell, 2003). NEM was calculated to determine its relationship to freshwater inflow and other environmental conditions. It was hypothesized that NEM in this shallow subtropical estuary was mainly dependent on the quantity of freshwater inflow recently delivered from the associated watershed, because of the nutrient and organic matter loading by inflow. It was further hypothesized that high inflow events could lead to dystrophic conditions that would be responsible for any dissolved oxygen impairments that might occur. The results of the analysis were used to produce a model for estimating NEM under different freshwater inflow conditions. Simulated and observed NEM rates were compared under a wide range of gauged freshwater inflow conditions into Lavaca Bay. Environmental conditions on days with differences between simulated and observed NEM rates were used to determine if other environmental conditions could be added to the model to make it more robust.

2. Methods and materials

2.1. Study site and experimental design

Since Odum's (1956) seminal work, open-water dissolved oxygen measurements have been used to provide spatially and temporally integrated estimates of metabolic processes in aquatic systems. Open-water dissolved oxygen methods have been used in a variety of estuaries to calculate NEM (Kemp et al., 1992; D'Avanzo et al., 1996; Borsuk et al., 2001; Caffrey, 2003). NEM is a calculation of the change in dissolved oxygen concentration resulting from biological processes in an aquatic ecosystem over a period of 24-h. The open-water dissolved oxygen method was applied to a suite of stations in Lavaca Bay, Texas, USA (Fig. 1) and employed high-frequency dissolved oxygen measurements.

The Lavaca River, discharging into the north-eastern region of the upper-bay, provides the major point source of freshwater inflow to Lavaca Bay. Spatial coverage was provided by sampling six different Texas Commission of Environmental Quality (TCEQ) sites. Stations LB 1–LB 6 correspond to TCEQ stations 17552, 17553, 13383, 17554, 13384, and 17555 respectively. Stations were spatially divided into upper-bay (stations 1–3), and lower-bay (stations 4–6) groups, which were partially separated by a shoreline constriction and the pylons of the Highway 35 over-pass (Fig. 1). The shoreline constriction and pylons combine to slow water movement into the lower bay.

Fifty-eight 24-h water quality monitoring samples, 22 water column nutrient samples, and 22 water column chlorophyll-a samples were taken at mid-depth over a two year period (2002–2003). Salinity, water temperature, and depth daily means were calculated from multiparameter sonde measurements. Water quality parameter measurements (dissolved oxygen concentration and saturation, temperature, pH, specific conductivity, depth, and salinity) were measured every 15 min at mid-depth of each station 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 data sondes have the following accuracy and units: temperature (±0.15 °C), pH (±0.2 units), dissolved oxygen (±0.2 mg l^{-1}), dissolved oxygen saturation (±2%), specific conductivity (±0.5% of reading depending on range), depth (±0.2 m), and salinity (±1% of reading or 0.1 ppt, whichever is greater). Salinity was automatically corrected to 25 °C.

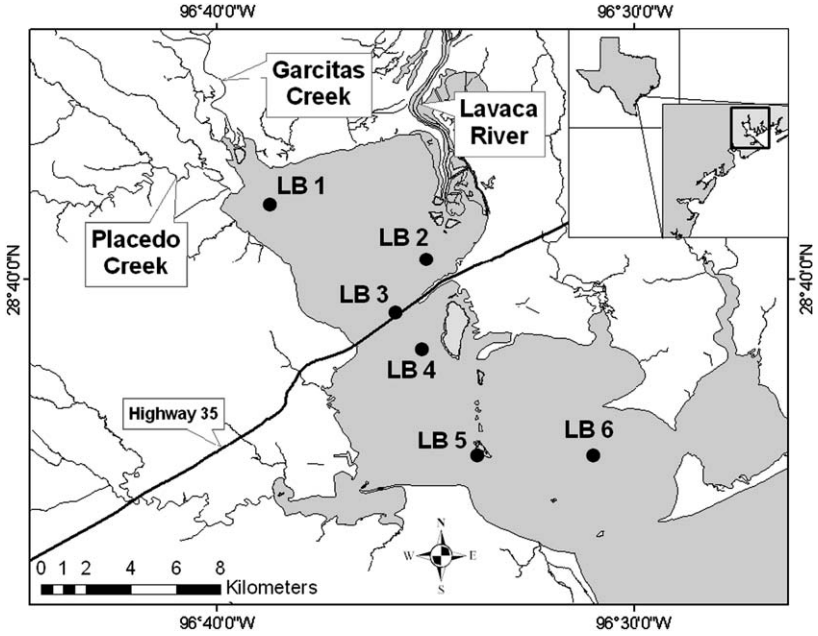

Fig. 1. Map of station locations in Lavaca Bay, Texas, USA. Stations 1–3 are geographically partially separated from stations 4–6 by the State Highway 35 bridge constriction and pylons. Lavaca River discharges into northeastern Lavaca Bay. Lavaca Bay is located on the western Gulf of Mexico Texas coastline (insert).

Chlorophyll-a was measured from two 10-ml sub-samples taken at mid-depth with a 1-l van Dorn bottle. Chlorophyll-a samples were filtered on site and stored in dry ice until returned from the field. Chlorophyll-a concentration was determined using non-acidification fluorometric techniques (Welschmeyer, 1994). Water column nutrient analyses for ammonium, phosphate, silicate, and nitrate plus nitrite were run on a Lachat Quikchem 8000 using standard colorometric techniques (Parsons et al., 1984; Diamond, 1994).

2.2. Atmospheric oxygen flux

Atmospheric oxygen flux must be estimated to separate physical and biological influences on dissolved oxygen concentration (Odum and Wilson, 1962). Texas estuaries experience sustained wind speeds commonly around 7–8 m s^{-1} (~13–18 mph), but commonly have daily variations in wind speed of 10 m s^{-1} (23 mph) (Texas Coastal Ocean Observation Network data at http://lighthouse.tamucc.edu/TCOON/HomePage;). Meteorological forcing dominates water exchange and circulation in South Texas estuaries because of shallow water depths (~2–4 m), small tidal range (~0.25 m), slow circulation due to relatively low freshwater inflow (~0–800 million m^3 y^{-1}), and long over-water fetches (Orlando et al., 1993). These characteristics combined with ample sunlight and high temperatures make South Texas estuarine ecosystems particularly amenable to open-water methods of estimating NEM (Kemp and Boynton, 1980). The two main assumptions for using open-water changes in dissolved oxygen concentration to calculate NEM are valid in Lavaca Bay. First, residence time, based on tidal exchange and freshwater inflow, can be as high as 77 days in Lavaca Bay (Armstrong, 1982). Long residence time combined with the relatively homogenous muddy bottom habitat of Lavaca Bay ensures that water moving past a fixed point in the estuary will have a similar metabolic history over a 24-h period. Secondly, the relatively high temperatures, ample sunlight, shallow water depth, and long residence times, should yield dissolved oxygen concentrations that retain a biologically controlled signal even after physical influences are accounted for.

Three equations to calculate wind-dependent diffusion coefficients (Odum and Wilson, 1962; Marino and Howarth, 1993; D'Avanzo et al., 1996) were compared to a constant coefficient of 0.5 g O_2 m^{-2} h^{-1} proposed by Caffrey (2004). The constant coefficient was similar to the wind-dependent coefficients at wind speeds from 0–5 m s^{-1}, but greatly underestimated air-sea exchange at winds greater than 8 m s^{-1} (Fig. 2). The three wind-dependent diffusion coefficient equations are similar when plotted over wind speeds from 0–10 m s^{-1} (Fig. 2). D'Avanzo et al. (1996), studying a shallow estuarine system in Waquoit Bay, Cape Cod, Massachusetts, estimated relatively higher air-sea exchanges over the entire range of wind speeds than that found for the wide range of ecosystems studied by Marino and Howarth (1993), which included deep open-ocean waters. The present study uses D'Avanzo et al. (1996) diffusion coefficient equations to calculate NEM because Lavaca Bay is a shallow-water system similar to Waquoit Bay.

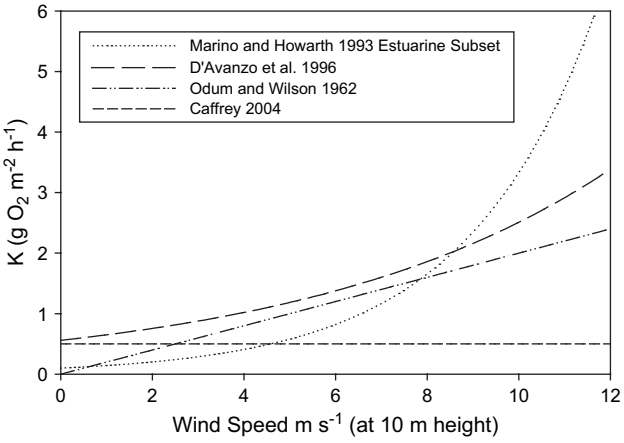

Fig. 2. Comparison of three wind dependent and one constant diffusion coefficients (K) at different wind speeds. Diffusion potential at higher wind speeds is underestimated by the constant coefficient.

2.3. Net ecosystem metabolism

NEM was calculated using open-water diurnal curve methods (Odum, 1956). Dissolved oxygen concentrations were converted to a rate of change in dissolved oxygen concentration by subtracting each 15-min measurement from the previous one. These rates of change per 15 min were then adjusted to control for diffusion of oxygen between the water column and the atmosphere by using percent saturation of dissolved oxygen in the water column, the wind dependent diffusion coefficient K (g O_2 m^{-2} h^{-1}) proposed by D'Avanzo et al. (1996), and wind speed data from the Texas Coastal Ocean Observation Network station at Sea Drift (located about 20 km SE of Lavaca Bay at 28° 24.4′ N 96° 42.7′ W) using the equation:

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

R_{dc} (mg O_2 l^{-1} 15 min^{-1})
= diffusion corrected DO rate of change,

R (mg O_2 l^{-1} 15 min^{-1}) = observed DO rate of change,

S_1 and S_2
= DO percent saturations at time one and two respectively,

K (g O_2 m^{-2} h^{-1}) = diffusion rate at 0% DO saturation.

Note: 1 g O_2 m^{-2} h^{-1} = 1 mg O_2 l^{-1} h^{-1} at a depth of one meter.

To calculate daily NEM the 15-min wind-diffusion corrected rates of dissolved oxygen change were then summed over a 24-h period, starting and ending at 08:00.

2.4. Statistical analysis

Principal component analysis (PCA) was used to quantify the temporal and spatial variability of environmental characteristics among stations. Results from the PCA were used to distinguish upper- and lower-bay station groups because of their respective distances from the mouth of the Lavaca River. NEM was regressed (step-wise linear regression) against cumulative ten-day freshwater inflow (FWI), salinity, water temperature, water column depth, water column chlorophyll-a, and water column nutrients. Freshwater inflow was calculated by summing all daily United States Geological Survey (USGS) gauged river flow (m^3 day^{-1}) into the bay during the ten days prior to sampling. A ten-day period was previously identified as the time interval that captures the response of estuarine benthic communities to freshwater inflow events (Kalke and Montagna, 1991; Montagna and Kalke, 1992), and it provides sufficient time to incorporate the duration of most rainstorms.

2.5. Net ecosystem metabolism model

An empirical model was produced for upper Lavaca Bay from the linear regression relationship between NEM at upper-bay stations and freshwater inflow into the bay. Simulated NEM was compared to observed NEM calculations during 2003. The difference between simulated and observed NEM was used to determine if inclusion of other environmental variables would improve the model performance. NEM, calculated from open-water dissolved oxygen measurements sampled quarterly at mid-depth at station 3 in 2004, was used to validate the NEM empirical model. Water quality was measured daily at Lavaca Bay station 3 for a week at a time during each season of 2004 (Russell, 2005). NEM validation results in 2004 were compared to those predicted from the relationship between 10-day cumulative freshwater inflow and NEM in 2002–2003. The comparison allows assessment of the capability of the NEM model to predict NEM under a wider range of environmental conditions than observed in 2002–2003.

3. Results

3.1. Range of environmental conditions

Observed NEM ranged from -2.62 mg O_2 l^{-1} d^{-1} to 1.74 mg O_2 l^{-1} d^{-1} (Table 1). Environmental characteristic measurements also varied widely over the two years of sampling (Tables 1 and 2). Salinity varied from 1.18 to 26.90 ppt and temperature from 20.89 to 30.99 °C. Ambient phosphate concentrations ranged from 0.01 to 5.52 μmol l^{-1}, silicate from 4.05 to 266.89 μmol l^{-1}, total inorganic nitrogen from 0.42 to16.89 μmol l^{-1}, and chlorophyll-a from 2.33 to 15.48 μg l^{-1}. Nitrogen to phosphorus ratios averaged 4.62 implying possible nitrogen limitation of primary production. Phosphorus concentrations generally decreased as water flowed down estuary implying a river source. Nitrogen concentrations were more spatially variable implying multiple sources. Nutrient concentrations remained fairly low at all stations and chlorophyll-a concentrations were higher at stations closer to the mouth of the Lavaca River than for those further down estuary except on 9/23/2003. High nutrient concentrations and low salinity measurements corresponded with a large freshwater inflow pulse on 9/23/2003, which pushed the chlorophyll maximum into the lower-bay.

3.2. Principal component analysis

Principal component analysis quantified the importance of each environmental variable to the total environmental variability. Principal components 1 and 2 accounted for 54.6% and 18.3% of the variance, respectively, for a combined 72.9% of the total variance of environmental conditions in Lavaca Bay (Fig. 3). Principal component 1 included variables that were dependent on freshwater inflow, e.g., high values of nutrient concentrations and low values of salinity. Principal component 2 represented seasonally changing environmental factors, e.g.,

Table 1
Monitoring dates by area of bay listing results for mean daily net ecosystem metabolism (NEM), salinity (Sal.), temperature (Temp.), and sonde deployment depth which is half the total water column depth

Date	Area	NEM (mg O_2 l^{-1} d^{-1})	Sal. (ppt)	Temp. (°C)	Depth (m)	Date	Area	NEM (mg O_2 l^{-1} d^{-1})	Sal. (ppt)	Temp. (°C)	Depth (m)
4/24/2002	Upper	−0.84	14.16	26.73	0.74	3/18/2003	Upper	−0.50	13.38	21.36	0.91
4/24/2002	Lower	−0.82	23.35	26.41	0.99	3/18/2003	Lower	−0.13	19.71	20.89	1.12
5/22/2002	Upper	−1.37	18.58	23.43	0.85	4/15/2003	Upper	−1.04	17.55	22.55	0.90
5/22/2002	Lower	−1.06	25.43	23.50	1.05	4/15/2003	Lower	−1.05	21.64	22.10	1.20
8/21/2002	Upper	−1.35	10.59	30.26	0.70	5/28/2003	Upper	1.74	18.73	26.71	0.87
8/21/2002	Lower	−0.78	15.60	30.33	0.92	5/28/2003	Lower	1.41	23.06	27.15	1.05
10/9/2002	Upper	−0.11	13.67	27.18	0.82	7/22/2003	Upper	−1.26	9.65	30.91	0.82
10/9/2002	Lower	−0.69	19.60	27.46	1.05	7/22/2003	Lower	−1.46	14.32	30.81	0.87
						8/19/2003	Upper	0.23	14.97	30.90	0.62
						8/19/2003	Lower	0.35	25.04	30.76	0.89
						9/23/2003	Upper	−2.62	3.87	25.55	0.81
						9/23/2003	Lower	0.65	12.19	25.73	1.08

Table 2
Monitoring dates by area of bay listing results for mean water column phosphate (PO_4), silicate (SIO_4), nitrate + nitrite + ammonium (DIN), chlorophyll-a (Chl-a), and cumulative ten-day freshwater inflow (FW)

Date	Area	PO_4 ($\mu mol\ l^{-1}$)	SIO_4 ($\mu mol\ l^{-1}$)	DIN ($\mu mol\ l^{-1}$)	Chl-a ($\mu g\ l^{-1}$)	FW (m^3)
4/24/2002	Upper	0.76	70.56	1.96	12.16	5160040
4/24/2002	Lower	0.61	42.64	1.08	6.39	5160040
3/18/2003	Upper	0.41	47.73	0.64	10.13	9097576
3/18/2003	Lower	0.01	4.05	0.96	10.73	9097576
4/15/2003	Upper	0.66	107.67	3.35	5.54	4883601
4/15/2003	Lower	0.55	94.14	1.36	5.39	4883601
5/28/2003	Upper	0.60	65.70	1.10	6.21	1706288
5/28/2003	Lower	0.47	32.99	2.11	5.62	1706288
9/23/2003	Upper	4.04	227.42	15.29	9.01	52393329
9/23/2003	Lower	2.38	166.34	9.16	11.64	52393329

high chlorophyll concentrations and low temperatures. Differences among sampling days resulted in three temporally distinct sample groups (Fig. 4A). These temporal groups coincided with high freshwater inflow events in March 2003 and September 2003, low freshwater inflow rates on all other dates, and seasonal environmental characteristics (Fig. 4A). Low freshwater inflow rates were characterized by high temperatures, salinity, and pH; and low chlorophyll-a, dissolved oxygen (Table 1), and nutrient concentrations (Table 2). The high freshwater inflow event in March 2003 was characterized by high chlorophyll-a, pH, and dissolved oxygen concentrations; moderate salinity; and low temperature and nutrient concentrations. The high freshwater inflow event in September 2003 was characterized by high nutrient concentrations; moderate temperature, chlorophyll-a; and low salinity, pH, and dissolved oxygen concentration. Station environmental conditions changed spatially with distance from the freshwater inflow source within each temporal group (Fig. 4B),

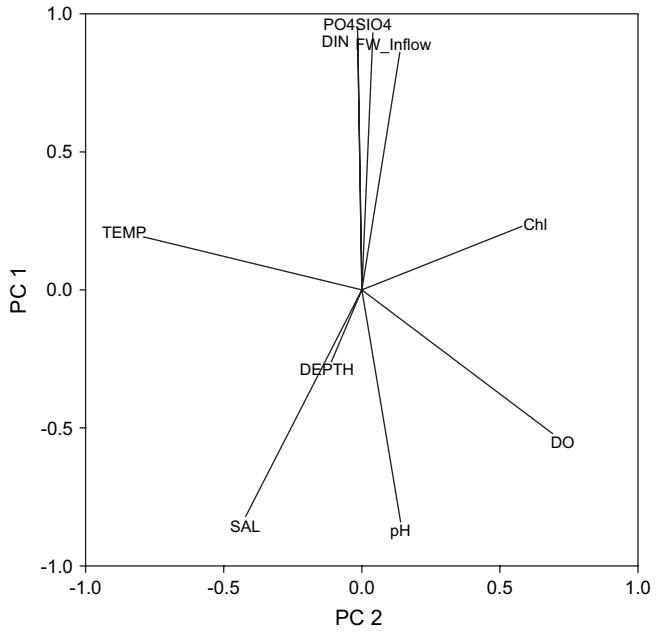

Fig. 3. Principal component (PC) analysis variable loads. PC 1 loads are determined by event driven environmental conditions, while PC 2 loads are determined by seasonal changes in temperature.

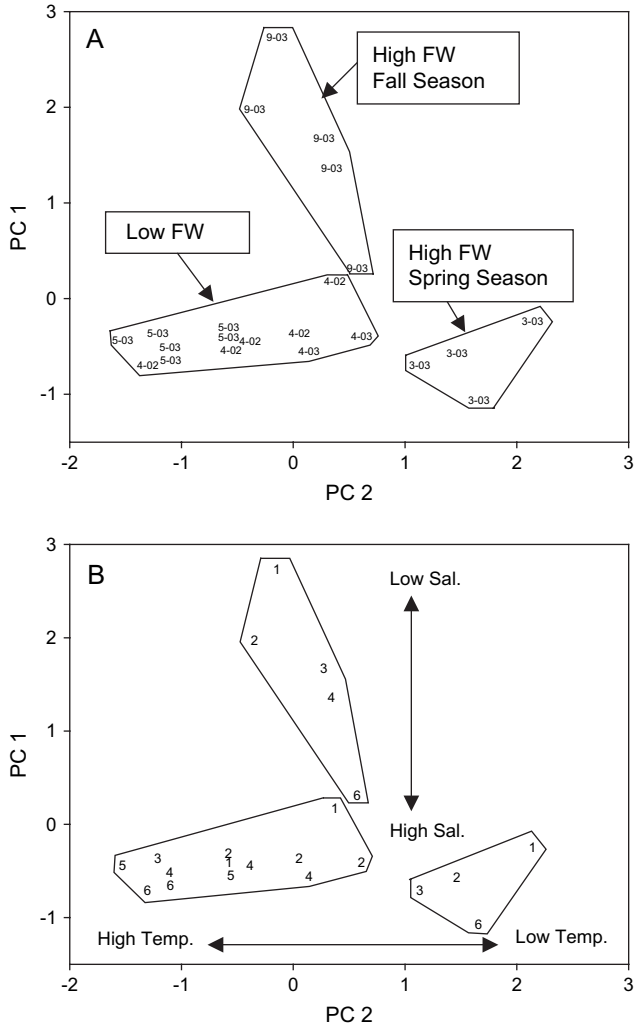

Fig. 4. Spatial and temporal separation of principal component (PC) station scores. A) Sampling dates used as symbols. High freshwater inflows during March and September 2003 resulted in two separate groups, with the remaining lower flow periods grouping together. B) Stations used as symbols. Stations separate along gradients of environmental conditions. Temperature is influential during all periods except September 2003 when salinity/freshwater inflow became more influential.

but there was no significant overall spatial separation among stations over all environmental conditions (Fig. 4B). The environmental characteristics that drove the temporal group spatial trends were different in each temporal group. Stations separated along a gradient of temperature, salinity, chlorophyll-a, and dissolved oxygen concentrations from upper to lower-bay during March. Stations separate along a temperature, chlorophyll-a, and dissolved oxygen gradient from upper to lower-bay during April and May. A salinity and nutrient gradient drove station separation in September. Depth had no covariance with other environmental characteristics except a weak covariance with salinity ($P = 0.026$). Freshwater inflow is this study and in past monitoring efforts (Montagna unpublished) co-varied with water column nutrient concentrations (Fig. 5), but in the present study had no significant relationship with water column chlorophyll-a concentrations, which are apparently seasonally driven.

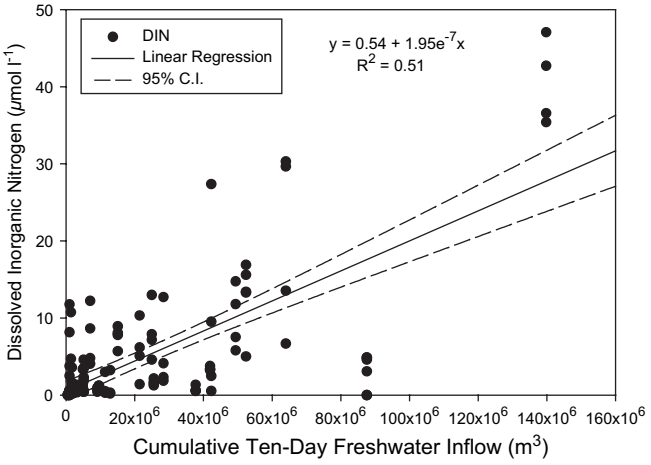

Fig. 5. Comparison of Lavaca Bay dissolved inorganic nitrogen concentrations and cumulative ten-day freshwater inflow from 1996 to 2003. Data from 1996–2001 courtesy of Paul Montagna, UTMSI. Best fit regression line (solid) and 95% confidence intervals (dashed).

3.3. Linear regression analysis

Step-wise linear regression analysis comparing NEM with chlorophyll-a, PO_4, SIO_4, dissolved inorganic nitrogen, depth, salinity, freshwater inflow, dissolved oxygen, pH, temperature, and depth measurements resulted in only salinity (Fig. 6A) having a weak but significant relationship ($P \leq 0.0001, R^2 = 0.25$) with NEM. Geographically separating the data at upper- and lower-bay stations produced more and less significant relationships, respectively, between salinity and NEM. Salinity correlated strongly with NEM in upper Lavaca Bay (linear regression $P \leq 0.0001, R^2 = 0.46$) (Fig. 6B). The most autotrophic NEM (3.43 mg $O_2\,l^{-1}\,d^{-1}$) in upper Lavaca Bay occurred during times of high salinity (18.70 ppt) and low freshwater inflow. The most heterotrophic NEM (-2.89 mg $O_2\,l^{-1}\,d^{-1}$) in upper Lavaca Bay occurred during times of low salinity (7.32 ppt) implying that freshwater constituent loading may be important. Lower Lavaca bay NEM, however, had an insignificant correlation with salinity (linear regression $P = 0.1645$, $R^2 = 0.06$) (Fig. 6C). The largest response in NEM (3.10 mg $O_2\,l^{-1}\,d^{-1}$) in lower Lavaca Bay, however, occurred during lowered salinity (19.66 ppt) when the influence of freshwater inflow was greatest in the lower reaches of the bay.

Salinity and freshwater inflow (FWI) had a significant inverse relationship ($P \leq 0.0001, R^2 = 0.51$) (Fig. 7). Covariance between salinity and FWI may explain why addition of FWI did not significantly improve the regression fit when salinity was also added to the step-wise regression analysis. Also, salinity is a function of many processes and integrates freshwater inflow, evaporation, and tidal exchange. Thus, the relationship between NEM and FWI was analyzed with linear regression analysis, even though FWI had an almost identical relationship to NEM as did salinity. NEM in upper Lavaca Bay had a significant linear relationship with FWI ($P \leq 0.0001, R^2 = 0.43$) (Fig. 8A). There was no significant relationship between NEM and FWI in lower Lavaca Bay ($P = 0.5684, R^2 = 0.01$) (Fig. 8B).

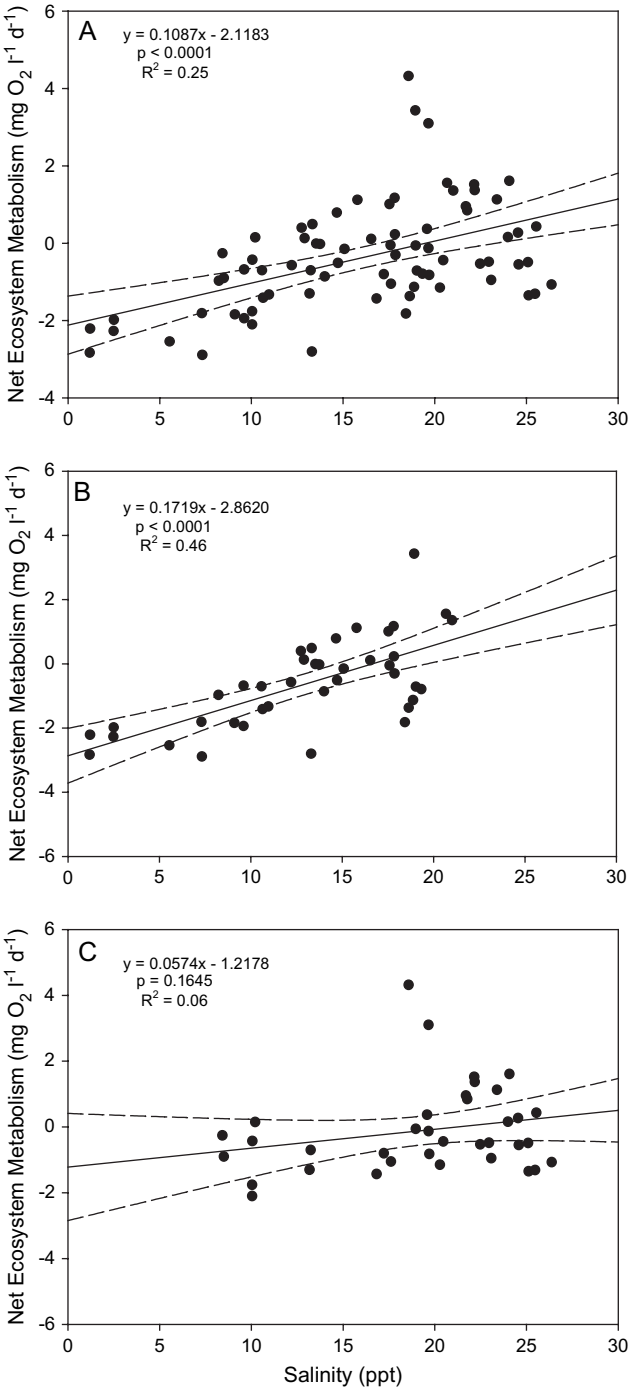

Fig. 6. Lavaca Bay net ecosystem metabolism relationship to salinity (linear regression line and 95% confidence intervals). A) All data combined. Significantly more bay-wide heterotrophic conditions correspond to periods of low salinity. B) Upper-bay data only. Increased heterotrophy with lower salinity is evident in upper-bay regions. C) Lower-bay data only.

3.4. Net ecosystem metabolism model

The empirical NEM model for upper Lavaca Bay was as follows:

$$\mathrm{NEM} = 0.14 - \left(4.81 \times 10^{-8}\right)\mathrm{FWI}$$

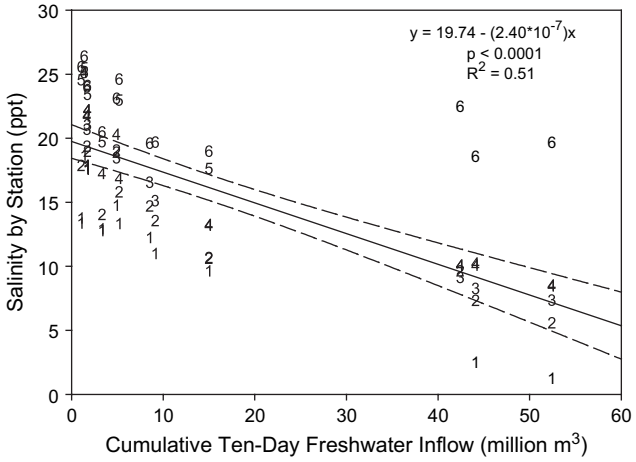

Fig. 7. Relationship between average daily salinity and cumulative ten-day freshwater inflow (linear regression line and 95% confidence intervals). Stations 1–4 closer to mouth of the Lavaca River are more affected by freshwater inflow than station 6 further down estuary.

where NEM is net ecosystem metabolism (mg O_2 l^{-1} d^{-1}) and FWI is cumulative ten-day freshwater inflow (m^3). This model was produced from the linear regression equation comparing NEM to FWI in upper Lavaca Bay.

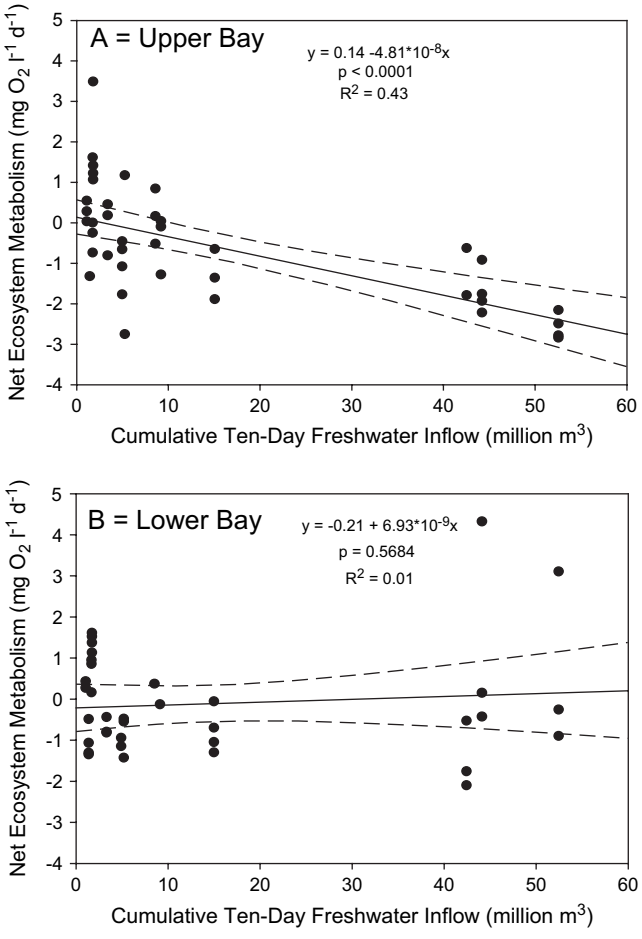

Fig. 8. Comparison of net ecosystem metabolism and cumulative ten-day freshwater inflow (linear regression line and 95% confidence intervals) in A) upper and B) lower Lavaca Bay. Freshwater inflows influence on NEM is spatially limited to the upper bay.

The normal range of FWI (0–50 million m^3 per 10-days) was captured during our sampling period. Two large pulses during late 2002 (>150 million m^3 per 10-days) were an abnormal condition resulting in a 200-year flood in much of South Texas (Fig. 9) and are considered beyond the range of the present model. No samples were taken during colder winter months, and therefore, this empirical model is only valid for estimating NEM within a limited temperature range (21–30 °C). One interesting characteristic of inflow is that it either is present or not, consequently there are base flows near zero or pulses during floods (Fig. 9). This results in a lack of data for calibration of the NEM model in the range of moderate freshwater inflows (Fig. 8).

The upper Lavaca Bay NEM simulation for years 2002 and 2003 is driven by precipitation events because FWI is the only forcing variable in the model (Fig. 10). The largest departures between simulated and observed NEM values occur during low inflow periods. The predicted NEM values have a much tighter fit to observed NEM during FWI events in 2003, but abnormally high inflows occurred between sampling periods of 2002, thus NEM required bounding conditions so it would not fall below −5 g O_2 l^{-1} d^{-1}, which is an unrealistic value. Additional factors that could be included in the upper Lavaca Bay NEM model were assessed by examining the environmental conditions during sample dates when observed and simulated NEM rates did not closely match. Most of the differences between observed and simulated NEM rates occurred during times of low freshwater inflow (Fig. 10). A close examination of environmental conditions on these dates identifies an interesting trend. Dates with more autotrophic observed NEM rates than predicted by the model simulation were clear and sunny, while dates with more heterotrophic observed rates than predicted were cloudy. This implies that including daily irradiance rates may produce a more robust NEM model. However, no irradiance measurements were taken close to Lavaca Bay during this study. The closest continuously monitoring irradiance meter in the region is located at The University of Texas at Austin's Marine Science Institute, in Port Aransas TX, too far from Lavaca Bay to justify

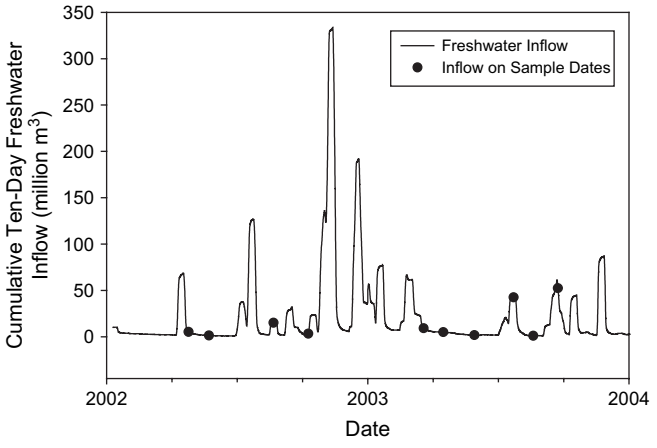

Fig. 9. Cumulative ten-day gauged freshwater inflow into Lavaca Bay, Texas. Circles denote sample dates.

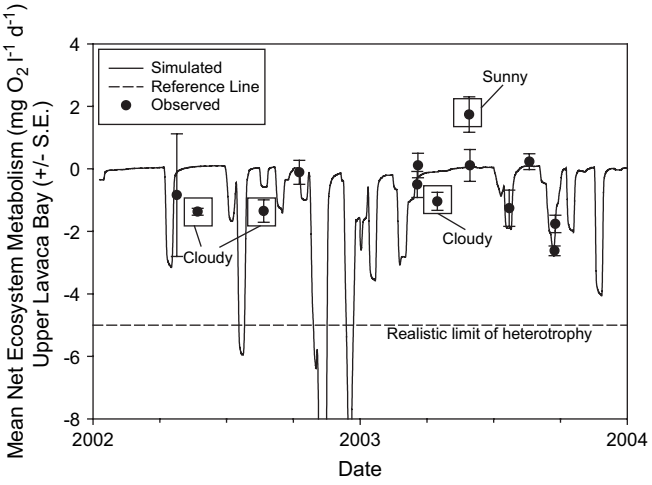

Fig. 10. Simulated daily NEM (solid line) compared to observed NEM (circles) for 2002 and 2003. The largest deviations between simulated and observed NEM's occur during low freshwater inflow periods.

using the data. A comparison of NEM from a bay closer to a continuously monitoring irradiance meter is required to better assess the influence of daily changes in irradiance on NEM. Other environmental factors such as temperature may have more influence on NEM rates than found in this study. Most of the sampling occurred during late spring, summer, or early fall. Extending sampling into winter months should provide a large enough temperature range to better assess the influence of temperature on NEM.

3.5. Model validation

The NEM model was validated against measurements taken at station 3 during quarterly sampling in 2004. The data exhibit a pattern of increased heterotrophy with increased FWI similar to that from 2002–2003 (Fig. 11A). The NEM predicted by the simple empirical model, however, did not fit with the 2004 validation data (linear regression, $P = 0.0783$ and $R^2 = 0.06$). This lack of fit is mainly due to increased scatter during periods of low FWI because a good fit between observed and predicted NEM is observed at higher FWI values. The scatter at low FWI appears to be related to seasonal temperature conditions. Samples taken during colder winter months tended to be more autotrophic than predicted and samples taken later in the year when water temperatures had warmed tended to be more heterotrophic. The larger temperature range (11–30 °C) of samples in 2004 contributed to a significant relationship between NEM and temperature ($P < 0.0001$, $R^2 = 0.45$) which was not found during 2002 and 2003 sampling (Fig. 11B). The 2004 NEM data may, thus, not represent a good validation dataset since half of the data were collected outside the environmental/temporal limits of the NEM model. The 2004 validation dataset does, however, lend support for inclusion of temperature in future modeling efforts of NEM over wider ranges of environmental conditions.

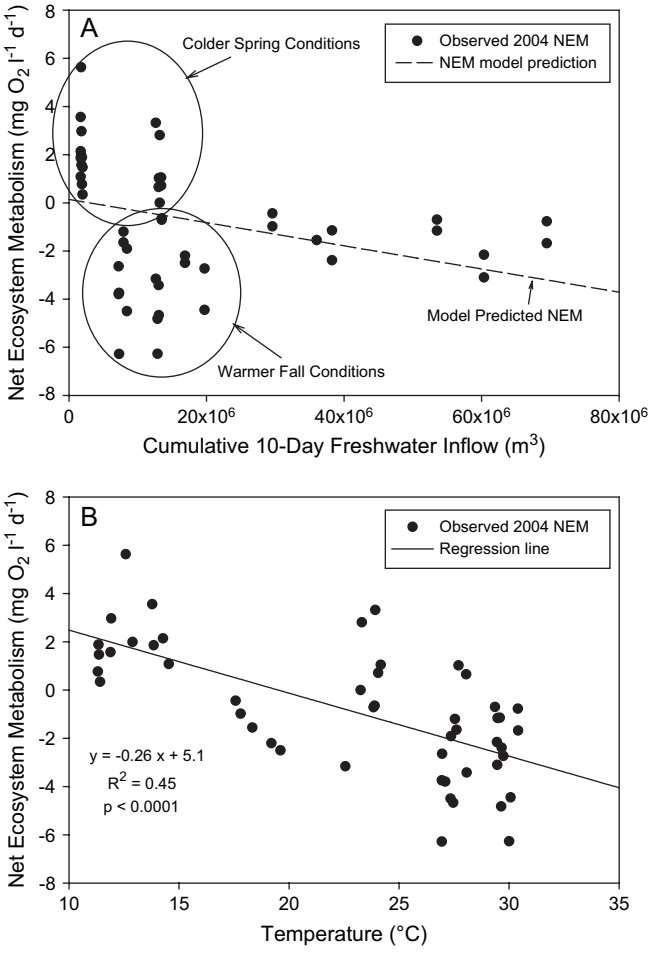

Fig. 11. NEM validation data during 2004. A) Ten-day cumulative inflow influence on NEM. NEM was more heterotrophic at higher freshwater inflows. Data, scattered during periods of low freshwater inflow, grouped together by temperature and season. B) Temperature influence on NEM.

3.6. Indicator of impairment

The Lavaca Bay ecosystem would have had dissolved oxygen impairment if NEM rates had resulted in a dystrophic state (<5 mg O_2 l^{-1}) for sufficient periods of time. It was assumed that a 70% dissolved oxygen saturation in the water column was the threshold below which dystrophy begins. Dissolved oxygen saturation of 70% corresponds to dissolved oxygen concentration just over 5 mg O_2 l^{-1} at average Lavaca Bay salinity and temperature, which is the 24-h threshold of mean dissolved oxygen concentration impairment set by TCEQ. Simulated daily NEM rates were compared to daily oxygen diffusion rates from the atmosphere, using D'Avanzo et al. (1996) wind-dependant diffusion coefficients, at observed average daily wind speeds (Fig. 12). The simulated NEM and diffusion rates from upper Lavaca Bay indicate that this system did not become dystrophic and was not impaired for dissolved oxygen concentrations during 2003, which experienced more normal precipitation events than 2002. Potential dystrophic conditions existed only on days when wind speeds were very low (<2 m s^{-1}), thereby limiting diffusion rates, and

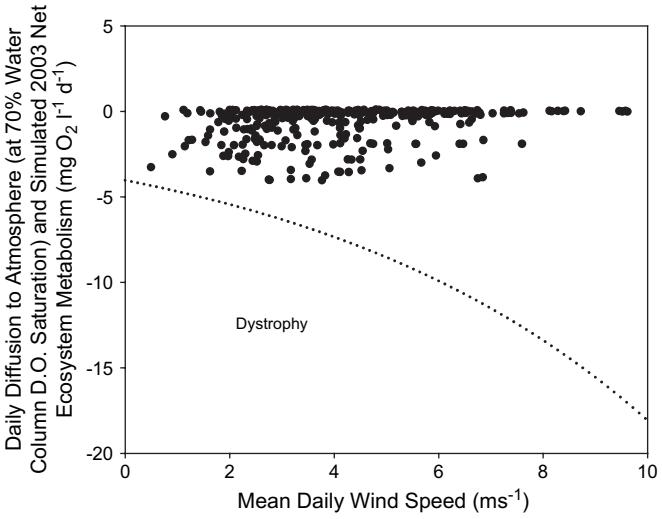

Fig. 12. Simulated daily NEM in upper Lavaca Bay during 2003 compared to the threshold of dystrophic estuarine conditions. Simulated NEM rates of biological oxygen consumption never exceeded the assimilation capacity provided by diffusion.

FWI was high (>100 million m^3). The combination of low wind speeds and high FWI did not occur for sufficient periods of time in Lavaca Bay during 2003 to cause dystrophic conditions.

4. Discussion

4.1. Indicator of freshwater inflow effects

The use of NEM as an indicator of freshwater inflow effects in estuaries is constrained spatially by the proximity of estuarine areas to freshwater inflow point sources and temporally to periods of moderate to high FWI pulses. In this study, freshwater inflow mainly influenced NEM in the upper reaches of Lavaca Bay closest to the river mouth (Fig. 8A). The relatively low freshwater inflows into Lavaca Bay are diluted by salt water in the first 8 km or so from the river mouth. Dilution results in environmental conditions, such as temperature, salinity, dissolved oxygen and chlorophyll concentrations, that vary along gradients between upper and lower bay regions (Fig. 4B). No relationship was found between FWI and NEM in lower Lavaca Bay (Fig. 8B). Therefore, the use of NEM as an indicator of freshwater inflow effects in Lavaca Bay works well in the upper bay where environmental conditions are mostly influenced by freshwater inflows, and becomes more accurate during periods with pulses of FWI.

4.2. Application to other ecosystems

The constraints of using net ecosystem metabolism as an indicator of freshwater inflow effects will hold true in other estuarine systems, but the spatial and temporal breakpoints where FWI ceases to be the dominant environmental factor influencing NEM will vary depending on the unique geographic, geologic, and climate signature of each estuary. The position of the river/ocean influence breakpoint and, therefore, the spatial extent for application of our NEM model is primarily a function of residence time. For example, the NEM model would be expected to be a useful indicator of freshwater inflow effects further down estuary in an estuary with a short residence time than in one, such as Lavaca Bay, with a long residence time. Freshwater inflow's influence on ecosystem metabolic rates would dominate over other environmental factors much further down estuary in an estuary with a shorter residence time. The unique signature of an estuary will also influence the range of up and down-estuary "sloshing" of the river/ocean water influence breakpoint due to seasonal and stochastic precipitation changes and in doing so will constrain where the NEM model is applicable.

4.3. Magnitude of heterotrophy

Previous research calculating ecosystem metabolic rates using open-water methods determined that respiration rates could reach almost 4.0 mg O_2 l^{-1} d^{-1} in Copano and Nueces Bay, Texas (Ward, 2003). Nighttime ecosystem respiration rates measured using open-water methods in a shallow water estuary (~1 m depth) during warmer months has been reported to range between 5–10 g O_2 m^{-2} d^{-1} (D'Avanzo et al., 1996). Benthic chamber measurements of sediment oxygen demand have been used to calculate oxygen flux into the sediments of 0.2–1.3 g O_2 m^{-2} d^{-1} in Nueces Bay and 0.3–1.9 g O_2 m^{-2} d^{-1} in San Antonio Bay, Texas during 1995 (Montagna unpublished). Odum and Hoskin (1958) measured sediment oxygen demand of 1–2 g O_2 m^{-2} d^{-1} in various Texas bays using benthic chambers. Light-dark bottle measurements of water column respiration in upper Lavaca Bay during 2002–2003 resulted in an average rate of 1.32 mg O_2 l^{-1} d^{-1} for the water column (Russell and Montagna, 2004). When benthic chamber and dark bottle oxygen consumption are combined, ecosystem respiration rates are estimated to be at least 2 mg O_2 l^{-1} d^{-1} in Texas. Odum and Hoskin (1958) compared light-dark bottle, benthic chamber, and open-water estimates of metabolic processes and concluded that the enclosed methods estimates were 2–10 times smaller than open-water estimates. Therefore, a conservative estimate of corresponding open-water respiration rates from the above mentioned bottle and chamber studies is between 2–10 mg O_2 l^{-1} d^{-1}. Observed NEM rates during the present study never exceeded −3 mg O_2 l^{-1} d^{-1} (Table 1) and calculations of respiration using open-water methods in Lavaca Bay during 2004 never exceeded 5 mg O_2 l^{-1} d^{-1} (Russell, 2005). Therefore, simulated heterotrophic NEM results presented here that exceed −5 mg O_2 l^{-1} d^{-1} should be considered unrealistic even during very high inflows (Fig. 11).

4.4. Spatial variability of nutrient inputs

The lack of a relationship between NEM and FWI in the lower bay may be due to its location with respect to sources

of nutrient loading from FWI. Gauged river inflow provides 49% of the nutrient loads to the Lavaca-Colorado estuarine system (Longley, 1994). Gauged river flow enters upper Lavaca Bay via the Lavaca River. Nutrients in this inflow travel approximately 6–8 km before they reach the lower bay. Nutrient concentrations decrease with distance from the mouth of the Lavaca River (Jones et al., 1986 and Table 2), likely due to assimilation into biomass, and thus are reduced by the time water reaches the lower bay. Other sources of nutrient inputs, such as those from atmospheric deposition, runoff from adjacent land and creeks, and tidal pumping, must provide a larger proportion of the nutrient loads in the lower bay than the freshwater dominated upper bay. The most autotrophic NEM values in lower Lavaca Bay took place during a large freshwater event when salinity was reduced to ~20 ppt at station LB 6 and nutrients (DIN = 5.01 μmol l^{-1}) and chlorophyll-a (12.28 μg l^{-1}) were higher than at any other time during the study. Thus, FWI can have an effect on lower-bay metabolic rates, but only during very high river discharges when river constituent loading becomes the dominant source of nutrients. Tidal entrainment and atmospheric deposition combined to provide up to 40% of the nitrogen loads to Nueces Bay, Texas under non-flood conditions (Brock, 2001), which indicates these sources can be very important in Texas. Regenerated nutrients from upper-bay decomposition of allochthonous organic matter will integrate freshwater loads over time, and this combined with a relatively steady flux of nitrogen from the atmosphere and tidally entrained waters helps explain the lack of a short-term response to increased freshwater inflow in lower Lavaca Bay NEM.

4.5. Other influences on net ecosystem metabolism

Variability in upper Lavaca Bay NEM became larger as FWI decreased. Other environmental factors may become more influential than FWI during low base-flow periods. Multiple freshwater point sources present at Lavaca Bay (i.e., creeks and streams) may have led to the relatively larger variability in NEM during low FWI periods. Placedo and Garcitas Creeks, which are usually insignificant freshwater point sources compared to the Lavaca River, can contribute up to about half of the total flow into Lavaca Bay during low freshwater inflow periods and can contribute up to 100 times more inflow than the Lavaca River during rare localized precipitation events. Localized differences in land use/land cover may influence NEM as the proportion of freshwater inflow from these local watersheds becomes more prevalent. Shallow depths in the upper bay may also contribute to the higher NEM variability during low inflow periods when water clarity tends to increase. The effects of variable daily irradiance on daytime ecosystem production (D'Avanzo et al., 1996) and microphytobenthic photosynthesis rates (Blanchard and Montagna, 1992) may explain some of the variability in NEM at shallow depths. Finally, FWI's influence on NEM may not be linear. Lack of NEM data during moderate and very high freshwater inflows, makes it difficult to assess the shape of the relationship curve. NEM likely responds in a more complex manner to increases in FWI than was assumed in this study. In addition to FWI, other physical factors that effect photosynthesis and respiration (e.g., irradiance and temperature) could be included in the model.

Freshwater inflow alone does not drive NEM in estuaries, but rather the organic and inorganic loads contained in that inflow does. Howarth et al. (1991) concluded that increased organic carbon, sediment, and nutrient loading in freshwater inflow into the Hudson River Estuary since European settlement have had significant effects on estuarine metabolism. Nutrient loading (D'Avanzo et al., 1996) and organic loading (Smith and Hollibaugh, 1997) have been proposed to influence NEM rates in estuaries. The ratio of nutrient to organic loading in freshwater inflows has also been hypothesized to explain NEM variability in estuarine systems (Kemp et al., 1997). Caffrey (2004) concluded that 68% of the variation in NEM among 42 National Estuarine Research Reserve (NERR) sites could be explained by changes in nutrient loads from freshwater inflow. Concentrations of limiting nutrients, e.g., dissolved inorganic nitrogen, increase as a function of freshwater inflow in Lavaca Bay (Fig. 5), but dissolved inorganic nitrogen (DIN) had no significant relationship with NEM in the present study. The lack of a relationship between nutrients and NEM may stem from measurement of nutrient concentrations instead of calculations of nutrient loads. Biological utilization of nutrients may result in ambient nutrient concentrations that are very different than the concentrations initially loaded into an ecosystem. Nutrient loads into Lavaca Bay, however, have been calculated (Longley, 1994), and it was concluded that nutrient loads were sufficient for assimilation of organic carbon loading. This implies that primary production in Lavaca Bay is not limited by nutrients alone, which in part explains the lack of response of NEM to changes in nutrients. High turbidity and subsequent light limitation of primary production has been suggested as an explanation for the lack of nutrient limitation (Longley, 1994). Organic matter loads, delivered to the bay from the watershed by freshwater inflow, may also be responsible for the heterotrophic response of upper Lavaca Bay NEM to increased freshwater inflow. Organic matter loads may be processed in the upper reaches of Lavaca Bay and might not be transported to lower reaches, because no significant relationship between freshwater inflow and NEM was found in lower Lavaca Bay.

4.6. Single versus multiple station monitoring

Significant intra-bay spatial differences in the relationship between freshwater loading and NEM could not have been found in many past estuarine metabolic rate studies because NEM has often been measured at only one or two closely located stations per estuary (D'Avanzo et al., 1996; Caffrey, 2003). Previous research concluded that NEM is not significantly different at distances <1.4 km and assumed that a single station NEM measurement was representative of entire estuarine systems (D'Avanzo et al., 1996; Caffrey, 2003). The present study's results indicate that NEM is variable between upper and lower bay areas at distances <6 km and thus a single

station NEM measurement is not representative of the entire estuary. Differences in each estuaries unique geographic, geologic, and climate signature will determine how representative a single calculation of NEM is of that entire estuary. High rates of biological production or consumption of oxygen, and little dilution in shallow, warm waters may magnify NEM spatial differences in Texas bays. This implies that single station monitoring of metabolic rates in estuaries with similar characteristics to those in Texas is not representative of entire estuaries and that monitoring programs should include multiple station locations along the salinity gradient between river freshwater inflow and oceanic water.

4.7. Heterotrophic metabolic state

Net heterotrophy implies that upper Lavaca Bay functions as a net carbon sink. The NEM model predicts more heterotrophy during higher inflow periods. Stable isotope measurements from samples taken between the Lavaca River and the mouth of Lavaca Bay estimated that 25–50% of particulate organic matter samples had a terrestrial origin (Parker et al., 1989). The signal of a terrestrial origin in particulate organic matter decreased with distance from the river, but in years with high FWI terrestrial carbon was detected throughout the system. Net heterotrophy in upper Lavaca Bay is consistent with other estuaries, such as Chesapeake Bay, where the upper bay acts as a terrestrial carbon sink and as a source of regenerated nutrients for areas further down stream (Kemp et al., 1997).

Only aerobic processes are accounted for by NEM. Anaerobic processes taking place below the oxic surface layer of the sediment remineralize organic matter without consuming oxygen. Therefore, estuarine ecosystems are more heterotrophic than estimated by NEM. Depth integrated sulphate reduction rates can contribute up to 49% of carbon oxidation in coastal sediments (Holmer, 1999). Using this ratio, organic carbon oxidation in shallow water ecosystems of Texas, could be twice that estimated by NEM. Little information exists for determining sulfate reduction rates under different environmental conditions, but evidence suggests that the complexity of organic matter (Kristensen et al., 1995) and periodicity of oxygen depletion (Aller, 1994) can have significant effects on anaerobic microbial processes. Quantification of sulphate reduction rates in Corpus Christi Bay, Texas is currently underway (Sell and Morse, 2006). Currently, NEM can only be used to estimate organic matter oxidation due to aerobic processes until better quantification of anaerobic metabolism under different environmental conditions is completed. Net heterotrophic NEM results, thus, should be viewed as underestimations of the total heterotrophic nature of Texas estuarine ecosystems.

4.8. Potential indicator of impairment

NEM has potential as an indicator of dissolved oxygen impairment. Although Lavaca Bay had been listed as impaired for dissolved oxygen on the state 303d list, dissolved oxygen conditions remained above impairment levels during the current study (Fig. 12). It is not surprising to find dissolved oxygen concentration above the impaired threshold, because the combination of calm conditions and large freshwater inflows do not occur regularly. Large freshwater inflow events are usually associated with storm events that have high wind speeds. A comparison of NEM with dissolved oxygen concentrations in a more impaired bay is needed to further assess whether NEM can be useful as an indicator of dissolved oxygen impairment.

5. Conclusion

The NEM model presented here is a useful indicator of freshwater inflow effects on ecosystem metabolic rates in regions of an estuary where freshwater inflow is the dominant environmental factor. The NEM model can accurately predict shifts from balanced to heterotrophic conditions during periods of moderate to large pulses of freshwater inflow. During periods of high freshwater inflow pulses, upper Lavaca Bay became more heterotrophic. It is hypothesized that the increased heterotrophy results from the combination of increased oxidation of organic matter loads and light limitation of primary production. This implies that changes in watershed hydrology, and organic or nutrient enrichment could be influential on estuarine metabolic rates. Inclusion of other environmental factors, such as temperature and irradiance, would improve the NEM model performance during periods of low freshwater inflow. NEM measurements taken over a wider range of environmental conditions, such as those from the validation data set, may provide the data necessary for an NEM model that estimates the effects on estuarine metabolic rates from large anthropogenic changes in environmental conditions and hydrology.

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