PRIMARY RESEARCH PAPER

The role of freshwater inflow in lagoons, rivers, and bays

Terence A. Palmer · Paul A. Montagna · Jennifer Beseres Pollack · Richard D. Kalke · Hudson R. DeYoe

Received: 8 July 2010/Revised: 31 January 2011/Accepted: 12 February 2011/Published online: 5 March 2011 © Springer Science+Business Media B.V. 2011

Abstract The aim of this study was to compare the impact of different freshwater inflow volumes on benthic communities and water column dynamics in different estuary classes. Benthic and water column spatial dynamics were contrasted in lagoons (with no direct inflow sources), tidal rivers that empty directly into the Gulf of Mexico, and bar-built bay systems (with direct inflow sources) along the Texas (USA) coast to determine the role of inflow in regulating ecosystem structure and function. Chlorophyll-a and nutrient concentrations were inversely correlated with salinity and were thus highest in the river systems, but lowest in lagoons. All Texas estuary types studied have conservative mixing for silicate and ammonium but are sinks for nitrite plus nitrate and phosphate. Macrobenthic production (abundance and biomass) was lowest in rivers and highest in lagoons. Diversity was low in estuaries with salinities between 1 and 17, but increased with salinities of up to 30, before

Handling editor: Pierluigi Viaroli

T. A. Palmer $(\boxtimes) \cdot P.$ A. Montagna \cdot J. B. Pollack \cdot R. D. Kalke

H. R. DeYoe

Biology Department, University of Texas Pan American, 1201 W. University Dr, Edinburg, TX 78539, USA

decreasing in hypersaline conditions. Macrofaunal community structure divided the estuaries into two groups. The first group represented polyhaline communities and contained lagoons (East Matagorda, Matagorda, Christmas, and South Bays). The second group represented oligo-mesohaline community characteristics and contained the secondary bays (Lavaca Bay and Cedar Lakes) and rivers (San Bernard River, Brazos River, and the Rio Grande). The implications of these results for managing freshwater flows is that altered hydrology can change the character of estuarine systems regardless of their classification as bays, lagoons, or tidal rivers.

Keywords Benthos · Macrofauna · Meta-analysis · Nutrients · Salinity · Texas

Introduction

Estuaries are transitional zones where fresh water dilutes saline water in coastal embayments. This definition is a simplification of an increasingly complex topic (see Perillo, 1995). Classifying estuaries is difficult because of the unique combination of climate regime, river discharge, tidal range, and coastal geomorphology that each estuary possesses. Estuaries have been classified by their physiography (Pritchard, 1960, 1967), tidal range (Hayes, 1975, 1980), evolution and energy (Dalrymple et al., 1992), morphology (Fairbridge, 1980), and morphogenetic structure

Harte Research Institute for Gulf of Mexico Studies, Texas A&M University, Corpus Christi, 6300 Ocean Drive, Unit 5869, Corpus Christi, TX 78412, USA e-mail: terry.palmer@tamucc.edu

(Perillo, 1995). However, by simply classifying estuaries we begin to solve complex regulatory management problems, such as determining the inflow needed to maintain healthy and productive coastal ecosystems.

Historical studies have demonstrated the importance of freshwater inflow to estuarine systems, and have determined that inflow is a major factor driving estuary functioning and ecosystem health (Chapman, 1966; Benson, 1981). Inflows serve a variety of important functions in estuaries, including the creation and preservation of low-salinity nurseries, sediment and nutrient transport, allochthonous organic matter inputs, and the timing and extent of migration of critical estuarine species (Longley, 1994). From the early 1970s to 1990s, freshwater inflow studies along the Texas, USA coast focused on major bay systems (Longley, 1994). The major bay systems are also classified as bar-built estuaries (Pritchard, 1960; 1967) and restricted coastal lagoons (Perillo, 1995). These systems are composed of a river, a large open bay, and a connection to the Gulf of Mexico; thus fit the definition of an estuary.

Numerous studies have examined the effects of freshwater inflow on macrobenthos productivity in the major bay systems (Kalke & Montagna, 1991; Montagna & Yoon, 1991; Montagna & Kalke, 1992; 1995; Wilber & Bass, 1998; Russell et al., 2006; Kim & Montagna, 2009; Pollack et al., 2009; Shank et al., 2009). These studies demonstrated that regional scale processes and long-term hydrological cycles interact and regulate benthic abundance, productivity, diversity, and community structure. In particular, these studies established three major causes of changes in estuarine productivity of bay systems in Texas related to freshwater inflow: (1) year-to-year climatic variability in rain, temperature, and wind, which affects precipitation and evaporation, (2) a latitudinal climatic gradient of decreasing precipitation superimposed on a soil gradient of increasing sand content, which results in reduced inflow from northeast to southwest, and (3) salinity gradients within estuaries from rivers to the Gulf of Mexico. One goal of many of these studies was to demonstrate the required minimum inflow needs on an estuary-scale to maintain ecosystem health and productivity.

The major bay systems are not the only geomorphic estuary types along the western Gulf of Mexico coast. Another common feature is the lagoon, which is known locally as a minor bay. The lagoons lack direct river inflow and receive fresh water by ungaged runoff or as an indirect source via circulation from adjacent bays. The inter-bay connections are enhanced by the Gulf Intracoastal Waterway, which extends from Mexico to Florida, and prevailing southeasterly winds that drive currents within the lagoons toward the northeast. There are also riverdominated estuaries along this coast, which are drowned-river valley ecosystems that drain directly into the Gulf of Mexico rather than into a bay. In contrast, the major bays and lagoons are classic barbuilt estuaries (Pritchard, 1960, 1967). Because the lagoons and river-dominated estuaries are different from major bay estuaries, it is not known if any of the historical information is useful for estimating freshwater inflow requirements in these smaller systems. Ideally, a synoptic study of the entire coast would be performed to experimentally contrast the structure and function of bay, lagoon, and river estuaries, but this is literally impossible because of a lack of resources. Thus, the current study is a meta-analysis to compare estuary condition and biological response in the three types of estuary systems to determine if the character of lagoon and river estuaries is similar to bay estuaries.

After many years of development, there is now a well accepted framework that is the basis for a freshwater inflow determination methodology (Alber, 2002). The relationship between biology and hydrology is complex and embedded in food web and material flow dynamics of estuaries. A generic framework is that inflow hydrology drives estuarine condition and estuarine condition drives biological resource response (Fig. 1). Ultimately, biological resources in estuaries are affected by sediment and water condition, and often salinity is the main driver. Because the links between flow, salinity, and biology are unidirectional, all the resource based approaches are multi-step: first, the resource to be protected is identified; second, the salinity range or requirements of that resource are identified in both space and time; and third, the flow regime needed to support the required distribution of salinity is identified, usually using hydrodynamic and salinity transport models (Montagna et al., 2002a, b, 2009). Following this methodology, the approach used here is to link salinity to condition, and condition to benthic response.

Fig. 1 Conceptual model of inflow effects, modified from Alber (2002)



A meta-analysis was conducted using data collected from three river estuaries (Rio Grande, San Bernard River, and Brazos River), four lagoons (Christmas Bay, Cedar Lakes, East Matagorda Bay, and South Bay Coastal Preserve), and two wellstudied major bays (Lavaca and Matagorda Bays) in Texas, USA. For the current study, estuary condition is defined by water and sediment quality variables (i.e., salinity, temperature, dissolved oxygen, nutrients, chlorophyll-a, grain size, carbon, and nitrogen content) and the biological resource is benthos. Benthic organisms are excellent indicators of environmental effects of a variety of stressors because they are abundant, diverse, sessile, and long-lived relative to plankton (Pearson & Rosenberg, 1978; Kerans & Karr, 1994; Weisberg et al., 1997; Dauvin et al., 2010). Therefore, benthos are able to integrate temporal changes in ecosystem factors over long time scales and large spatial scales (Smith et al., 2001). Benthic macrofauna (body length > 0.5 mm) are especially sensitive to changes in inflow, and can be useful in determining its effects on estuarine systems over time (Remane & Schlieper, 1971; Montagna, 2000; Chainho et al., 2006). In the current study, benthic abundance, biomass, and diversity are measures of inflow response.

Methods

Study area and sampling design

The objective of this study was to compare the biological response to freshwater inflow, and how it is affected by spatial variability of estuarine condition. These data were compiled to examine how the three estuary-type ecosystems differ spatially. Three river estuaries (Rio Grande, San Bernard River, and Brazos River), four lagoons (Christmas Bay, Cedar Lakes, East Matagorda Bay, and South Bay Coastal Preserve), and two major bays (Lavaca and Matagorda Bays) were sampled between September 2000 and July 2005 (Table 1). Lavaca Bay and Matagorda Bay are nested within the same estuary, although the larger Matagorda Bay has direct inflow from the Colorado River and Tres Palacios Rivers and indirect inflow from the Lavaca River via Lavaca Bay. The dataset used in this investigation assimilates data from several smaller investigations and is unbalanced. In the Rio Grande, two additional sampling stations were added to the existing three in 2002, bringing the number of stations to five. The sites were divided into northern and southern systems. The northern systems include the Brazos River, San Bernard River, Christmas Bay, Cedar Lakes, and East Matagorda Bay (Fig. 2), while the southern systems include the Rio Grande and South Bay Coastal Preserve (Fig. 3).

Station locations in all bays were chosen based on previous sampling experience, sediment type, depth found on National Oceanic and Atmospheric Administration navigation charts, and constraints of sampling logistics. In addition, stations within each bay or riverdominated estuary were chosen to represent both the salinity gradient within the estuary and a broad spatial coverage. All lagoons and river estuaries except for the Rio Grande are connected to the Gulf Intracoastal Waterway, a navigation channel that runs almost the entire length of the USA portion of the Gulf of Mexico.

Quarterly sampling occurred every October, January, April, and July between October 2000 and

System name	Region	Туре	Inflow $(m^3 s^{-1})$	Fiscal year						
				2001	2002	2003	2004	2005		
South Bay Coastal Preserve	South	Lagoon	-	2 (24)	2 (24)					
Rio Grande Estuary	South	River	13.9	3 (36)	3 (36)	5 (60)	5 (60)	5 (60)		
Christmas Bay Coastal Preserve	North	Lagoon	_		3 (36)	3(36)				
Cedar Lakes	North	Lagoon	_			2 (24)	2 (24)	2 (24)		
East Matagorda Bay	North	Lagoon	_	3 (36)						
San Bernard River Estuary	North	River	24.1			2 (24)	2 (24)	2 (24)		
Brazos River Estuary	North	River	263.0	3 (36)	3 (36)	3 (36)	3 (36)	3 (36)		
Lavaca-Colorado Estuary										
Lavaca Bay ^a	North	Major Bay	50.0	2 (24)	2 (24)	2 (24)	2 (24)	2 (24)		
Matagorda Bay ^b	North	Major Bay	100.8	2 (24)	2 (24)	2 (24)	2-4 (30)	4 (48)		
Totals				15 (180)	15 (180)	19 (228)	18 (198)	18 (216)		

 Table 1
 Estuarine ecosystems compared

Number of stations sampled at each location and year (with the total number of samples collected in parentheses). Fiscal year runs from October of the previous year to July of the recorded year. Inflow is the mean flow at the nearest upstream gaging station over the sampling period of each estuary. Data from: IBWC (2010; Rio Grande), LNRA (2010; Navidad River), and USGS (2010; all other rivers)

^a Combined inflow from Lavaca and Navidad Rivers

^b Combined inflow of Colorado and Tres Palacios Rivers



Fig. 2 Northern sampling stations. Dashed line Gulf Intracoastal Water Way

July 2005. In previous benthic studies (Kalke & Montagna, 1991; Montagna & Kalke, 1992; Montagna & Li, 2010; Montagna, 2000), quarterly sampling has been demonstrated as effective in capturing temporal benthic dynamics, while economizing on temporal replication. The timing of the sampling captured the major seasonal inflow events and temperature changes in Texas estuaries. Each quarter, three

replicate benthic samples were collected per station. During each sampling period ancillary environmental data were also collected.

Hydrographic measurements

Salinity, conductivity, temperature, pH, and dissolved oxygen were measured at each station during each



Fig. 3 Sampling locations within South Bay Coastal Preserve and Rio Grande

sampling trip using multiprobe water quality meters. A YSI 6920 multiprobe sonde was used to measure these parameters, except for in South Bay and the Rio Grande, where hydrography was measured using a Hydrolab Surveyor 4.

Chlorophyll and nutrient measurements

Water samples were collected during each sampling trip at the surface by hand and at the bottom (approximately 20 cm from the sediment–water interface) using a horizontally mounted Van Dorn bottle. Water for chlorophyll-*a* analysis was filtered onto Whatman GF/F 25 mm glass fiber filters and placed on ice (<4.0°C). Nutrient samples were filtered to remove biological activity (0.45 μ m polycarbonate filters) and also placed on ice (<4.0°C). Chlorophyll-*a* was extracted overnight and read on a Turner Model 10-AU fluorometer using a non-acidification technique (USEPA, 1997; Welschmeyer, 1994). Nutrient analysis was conducted using a LaChat QC 8000 ion analyzer with computer controlled sample selection and peak processing. Nutrients measured were nitrate + nitrate (Quikchem method 31-107-04-1-A), silicate (Quikchem method 31-114-27-1-B), ammonium (Quikchem method 31-107-06-5-A), and phosphate (Quikchem method 31-115-01-3-A).

Sediment measurements

Sediment characteristics were measured annually. At each site one 6.7-cm diameter sediment core sample was taken by diver or coring pole and sectioned at 0-3 cm and 3-10 cm depth intervals. Analysis

followed standard geologic procedures (Folk, 1964; E.W. Behrens, personal communication). A 20-cm³ sediment sample was mixed with 50 ml of hydrogen peroxide and 75 ml of deionized water to digest organic material in the sample. The sample was wet sieved through a 62- μ m mesh stainless steel screen using a vacuum pump and a Millipore Hydrosol SST filter holder to separate rubble and sand from silt and clay. After drying, the rubble and sand were separated on a 125 μ m screen. The silt and clay fractions were measured using pipette analysis. Percent contribution by weight was measured for four components: rubble (e.g., shell hash), sand, silt, and clay.

Sediment samples were measured for carbon and nitrogen isotopes δ^{13} C and δ^{15} N and the proportion of organic and inorganic carbon and nitrogen. Samples were measured using a Finnigan Delta Plus mass spectrometer linked to a CE instrument NC2500 elemental analyzer. The system uses a Dumas type combustion chemistry to convert nitrogen and carbon in solid samples to nitrogen and carbon dioxide gases. These gases are purified by chemical methods and separated by gas chromatography. The stable isotopic composition of the separated gases is determined by a mass spectrometer designed for use with the NC2500 elemental analyzer. Standard material of known isotopic composition was run every tenth sample for quality assurance.

Biological measurements

Macrobenthos were sampled during each sampling trip with core tubes held by divers or with a coring pole. The macrofauna were sampled with a 6.7-cm diameter tube (35.26 cm² area), and sectioned at depth intervals of 0-3 cm and 3-10 cm. Three replicates were taken within a 2 m radius. Samples were preserved in the field with 5% buffered formalin. In the laboratory, samples were sieved on 0.5 mm mesh screens, sorted, identified to the lowest taxonomic level possible and counted. Dry weight biomass was also measured for each macrofauna sample. Individuals were combined into higher taxa categories, e.g., Crustacea, Mollusca, Polychaeta, before being dried for 24 h at 55°C, and weighed. The carbonate shells of molluscs were dissolved using 1 N HCl and rinsed with fresh water before drying.

Analytical approach

The goal of this study was to investigate relationships between estuary condition as it is affected by freshwater inflow in three different estuary types. Lagoon, river, and major bay estuaries are located along the entire Gulf of Mexico coast, and nine in Texas were studied over a 5-year period. The control sites in this study were the major bay sites located in Lavaca Bay and Matagorda Bay (the Lavaca-Colorado Estuary), which has been well-studied (Ward & Armstrong, 1980; Wilber & Bass, 1998; Montagna, 2000; Montagna et al., 2008a; Kim & Montagna, 2009; Pollack et al., 2009). Control sites are needed in research studies to compare reference conditions to experimental conditions (Piegorsh & Bailer, 1997). Matagorda Bay, a primary bay, represents an area of greater marine influence, while Lavaca Bay, a secondary bay, represents an area with more freshwater influence. Data from these bays were collected during the entire study period for use in other projects, therefore, information is available to be applied to the current project to represent major open bay system control sites. These particular bays were chosen based on their sampling schedule and close proximity to most of the lagoon and river-dominated estuaries included in this study.

A meta-analysis approach, which applies quantitative methods to summarize evidence across studies (Arnqvist & Wooster, 1995), was used to aggregate the data over all samples to determine broad trends and relationships among estuaries. In this approach, every estuary sampled is represented by a point on a graph. This approach removes temporal variability so that only spatial variability is determined. A more detailed approach including temporal analyses can be viewed in Montagna et al. (2008b).

Macrofaunal diversity was calculated using Hill's N1 diversity index (Hill, 1973). Hill's N1 was used because it has units of number of dominant species, and is more interpretable than most other diversity indices (Ludwig & Reynolds, 1988). Macrofaunal community structure was analyzed using non-metric multi-dimensional scaling (MDS) using a Bray-Curtis similarity matrix among stations to create a MDS plot (Clarke, 1993; Clarke & Warwick, 2001). Relation-ships within each MDS were highlighted using a Cluster Analysis using the group average method. Significant differences between each cluster were

tested using the SIMPROF permutation procedure using a significance level of 0.05. Data were $log_e(x + 1)$ transformed prior to MDS and Cluster analysis in Primer to decrease the effect of numerically dominant species on the interpretation of the community composition (Clarke & Gorley, 2006).

Water quality and sediment quality were each analyzed using principal component analysis (PCA). Correlations between the first two principal component scores from each PCA and macrofauna productivity measures (N1 diversity, biomass, and abundance) were determined to examine the relationship between physical variables and macrofaunal productivity. PCA and all univariate statistical analyses were performed using SAS software version 9.2 (SAS Institute Inc., 2009). Water quality data were log_e transformed prior to analysis. All sediment data except for carbon and nitrogen isotopes were arcsine square-root transformed because the data are proportional. Carbon and nitrogen isotope data were log_e transformed prior to analysis.

Results

Physical characteristics

Mean salinities ranged from 4.2 in the Rio Grande to 36.6 in South Bay (Table 2). Variation in salinity was smallest in the Rio Grande, South Bay, and Christmas Bay. Temperature ranges were similar for the northern systems (Brazos River, San Bernard River,

Table 2 Physical characteristics of the estuarine ecosystems

Christmas Bay, Cedar Lakes, and East Matagorda Bay; 21.2–23.5°C) while the two southern systems (Rio Grande and South Bay) had slightly higher temperatures (25.1 and 25.0°C; Fig. 4A). The coldest mean water temperatures were found at Christmas and Lavaca Bays (21.2 and 21.9°C, respectively). The greatest variability in temperatures was found within East Matagorda Bay and Cedar Lakes. There was no correlation between temperature and salinity.

Ammonium levels were the lowest in the two major bays, Lavaca and Matagorda Bays, and lagoons East Matagorda Bay and Christmas Bay, with values ranging from 1.0-1.5 µM compared with 4.8-7.6 µM in other bay systems (Table 2; Fig. 4B). These bays also had the most consistent ammonium concentrations, i.e., lowest variance. The river-dominated estuaries had the highest concentrations of ammonium (5.8–7.6 µM). Ammonium was negatively correlated with salinity among estuaries with the exception of South Bay, which had both high salinity and ammonium levels. The high mean ammonium concentration in South Bay was dominated by three very high ammonium concentrations (35 and 52 µM), one at the southern station in July 2001 and two at the northern gulf-ward station in July 2002. The mean without these anomalies is $1.5 \mu M$.

Phosphate and silicate concentrations were both inversely proportional to salinity (Table 2; Figs. 4C, 5A). The Rio Grande river estuary had the highest concentration of phosphate and second highest concentration of silicate (5.7 μ M and 163.1 μ M, respectively) while lagoons (South Bay and Christmas Bay)

Bay	Depth (m)	Temperature (°C)	Salinity	DO (mg l ⁻¹)	NH4 (μM)	NO _{<i>x</i>} (μM)	$\begin{array}{c} PO_4 \\ (\mu M) \end{array}$	Chl-a (µg/L)	N:P	N:Si	P:Si
RG	0.6	25.1	4.2	7.4	5.8	26.5	5.7	20.8	4.6	0.163	0.035
BR	2.3	23.3	8.6	6.7	7.6	40.4	2.3	9.2	17.7	0.243	0.014
SB	1.4	23.0	10.1	7.2	6.3	16.8	2.7	6.5	6.1	0.140	0.023
CL	0.3	23.5	15.4	8.8	4.8	5.9	1.5	5.0	3.9	0.078	0.020
LB	1.5	21.9	15.8	7.3	1.4	3.6	1.3	8.8	2.7	0.024	0.009
MB	2.8	23.5	22.8	6.7	1.0	2.3	1.0	8.5	2.2	0.024	0.011
EM	1.0	22.7	24.0	7.0	1.5	4.9	1.2	11.1	4.2	0.036	0.009
CB	1.2	21.2	25.8	7.3	1.1	1.2	0.4	5.6	2.7	0.025	0.009
SO	1.0	25.0	36.6	6.9	5.1	0.8	0.2	2.7	3.5	0.088	0.025

Average over all samples

BR Brazos River, *CB* Christmas Bay, *CL* Cedar Lakes, *EM* East Matagorda Bay, *MB* Matagorda Bay, *RG* Rio Grande, *SB* San Bernard River, *SO* South Bay, *DO* dissolved oxygen, NH_4 ammonium, NO_x nitrate + nitrite, PO_4 phosphate



Fig. 4 Mean (\pm standard error) salinity versus mean (\pm standard error). **A** Temperature, **B** ammonium, and **C** phosphate for lagoons, river-dominated estuaries, and major estuaries along the Texas coastline from 2001 to 2005. *BR* Brazos River, *CB* Christmas Bay, *CL* Cedar Lakes, *EM* East Matagorda Bay, *LB* Lavaca Bay, *MB* Matagorda Bay, *RG* Rio Grande, *SB* San Bernard River, *SO* South Bay





Fig. 5 Mean (\pm standard error) salinity versus mean (\pm standard error). A Silicate, B nitrate plus nitrite, and C chlorophyll*a* for lagoons, river-dominated estuaries, and major estuaries along the Texas coastline from 2001 to 2005. Bay abbreviations same as Fig. 4

had the lowest concentrations (0.2-0.4 µM and 9.3–48.2 µM, respectively). Despite similar salinities, lagoon Cedar Lakes, and major bay Matagorda Bay had silicate concentrations of at least 40 µM lower than major bay Lavaca Bay and lagoon East Matagorda Bay. River-dominated estuaries had the highest concentrations of nitrate plus nitrite, ranging from 16.83 μ M in the San Bernard River to 40.40 μ M in the Brazos River (Fig. 4B). Other estuaries examined along the Texas coast had much lower nitrate plus nitrite concentrations (0.8-5.9 µM). The Rio Grande chl-a had the highest mean concentration (20.80 µM), while South Bay had the lowest (2.69 μ M; Fig. 4C). Mean chl-a concentrations in the other estuaries ranged from 5.0 to 11.1 μ M.

Only the Brazos River had a high N:P ratio, 17.7 (Table 2). The other ecosystems, even the two other rivers had N:P ratios ranging from 2 to 6. N:Si ratios were uniformly high in rivers 0.14–0.24, and low in the higher salinity bays (0.02–0.09). P:Si ratios were high only in the Rio Grande (0.035) and lowest in the high salinity bays (~0.009). P:Si ratios declined with increasing salinity (Table 2).

Water quality parameters for each site were merged using principal component analysis (PCA; Fig. 6). The first and second principal components (PC1 and PC2) explained 39.7 and 21.7% of the variation within the data set, respectively (total 61.4%). Salinity was negatively related to phosphate, chlorophyll-a, dissolved inorganic nitrogen, and silicate along PC1 (Fig. 6B). Nitrogen to phosphorus ratios, water temperatures and dissolved inorganic nitrogen all correlated with positive PC2 values. Depth, dissolved oxygen, and pH did not explain much variation within the first two principal components. Station loading scores from the three river estuaries (Rio Grande, Brazos River, and San Bernard River) were separated from the minor and major bay estuaries along the PC1 axis (Fig. 6A). The river estuaries had higher mean dissolved inorganic nitrate, phosphate, and chlorophyll-a concentrations and lower mean salinities than any other estuary.

The first and second principal components (PC1 and PC2) for sediment content along the Texas coast explained 54.1 and 17.8% of the variation within the data set (total 71.9%; Fig. 7). Lagoon systems had both the highest rubble content (East Matagorda Bay; 4.2% by weight) and the lowest rubble content (Cedar Lakes; 0.8%). Sand content was highest in the lagoon



Fig. 6 Plots of the first two principal components (PC) resulting from analysis of water quality data for all estuaries sampled. A PC station scores labeled by station and **B** PC loadings. Bay abbreviations same as Fig. 4

systems of South Bay (69.2%) and Cedar Lakes (59.9%), and in the Rio Grande river estuary (54.3%). Sand content was lowest in the San Bernard River (12.5%) and Matagorda Bay (19.9%). The Rio Grande and South Bay had the lowest sediment porosity (34.1 and 37.1%, respectively) while Matagorda Bay and the San Bernard River had the highest (63.9 and 61.7%, respectively). Clay content was highest in Matagorda Bay (45.3%) and lowest in



Fig. 7 Plots of the first two principal components (PC) resulting from analysis of sediment data for all estuaries sampled. A PC station scores labeled by station and **B** PC loadings. Bay abbreviations same as Fig. 4

Cedar Lakes (7.8%). δ^{15} N ranged from 4.1‰ in South Bay to 8.4‰ in East Matagorda Bay. The nitrogen content varied slightly along the coast, from 0.05% in Cedar Lakes to 0.12% in San Bernard River. Values of δ^{13} C ranged from -17.1‰ in San Bernard to -7.1‰ in the Rio Grande. East Matagorda Bay, South Bay, Christmas Bay, Cedar Lakes, Matagorda Bay, and the Rio Grande had the lowest silt contents (21.3-33.2%), whereas the San Bernard and Brazos Rivers had the highest (58.3-61.5%).



Fig. 8 Mean (\pm standard error) biomass versus mean (\pm standard error) macrofaunal abundance for lagoons, river-dominated estuaries, and major estuaries along the Texas coastline from 2001 to 2005. Bay abbreviations same as Fig. 4

Macrofauna

Macrofaunal abundance was positively correlated with biomass (Fig. 8). The estuaries divided into three groups based on abundance and biomass. The first group consisted of San Bernard River, Brazos River, and Lavaca Bay, which had both the lowest biomass $(0.5-0.8 \text{ g m}^{-2})$ and abundance $(3,800-5,200 \text{ n m}^{-2})$ of all the groups. The second group included Matagorda Bay, Cedar Lakes, and the Rio Grande, which had intermediate biomass (2.3-3.7 g m⁻²) and abundances $(7,700-10,300 \text{ nm}^{-2})$ relative to the other groups. The third group, which included South Bay, Christmas Bay, and East Matagorda Bay, had the highest biomass (6.9–10.9 g m⁻²) and abundances $(14,700-26,200 \text{ n m}^{-2})$. Individually, East Matagorda had the highest biomass (10.9 g m⁻²) and South Bay had the highest abundance (26,200 n m⁻²). The standard error of both abundance and biomass increased with the mean across all groups.

Mean macrofaunal abundance and biomass both decreased in salinities between 4 (Rio Grande) and 10 (San Bernard River; Fig. 9A, B). Mean abundance and biomass then increased with increasing salinities above 10. Macrofaunal diversity increased with increasing salinity, however, only where salinity values were above 20 (Fig. 9C). Mean diversity at



Fig. 9 Mean (\pm standard error) salinity versus mean (\pm standard error) macrofaunal. A Abundance, B biomass, and C N1 diversity for lagoons, river-dominated estuaries, and major estuaries along the Texas coastline from 2001 to 2005. N1 Diversity is reported for 35 cm². Bay abbreviations same as Fig. 4

the lower salinity estuaries, which included all of the river estuaries as well as Lavaca Bay and Cedar Lakes, only ranged from 2.3 to 2.6 dominant species per 35 cm^{-2} , whereas mean macrofaunal diversities

for Matagorda Bay and East Matagorda Bay (moderate salinities) were 4.2 and 5.1 species 35 cm^{-2} , respectively. Mean macrofaunal diversities for the highest salinity systems, South Bay and Christmas Bay, were 6.8 and 8.2 species 35 cm^{-2} , respectively. Standard errors for salinity were smallest at South Bay, Christmas Bay, and the Rio Grande stations. (0.3) compared to the other systems (0.7–1.7).

Apart from the low-salinity systems, biomass and abundance increased with increasing salinity (Fig. 9). Mean macrofaunal abundance was lowest when mean salinities were between 10 and 16 and increased as salinities increased or decreased from this salinity range (Fig. 9A). The macrofaunal biomass minima corresponded to a mean salinity of 10 at the San Bernard River, which again increased with both increasing and decreasing salinities. Above mean salinities of 24 (as at East Matagorda Bay), biomass decreased again. N1 diversity was consistently low (2.4–2.6) in estuaries with mean salinities below 16. Diversity increased with an increase in mean estuary salinity where mean bay salinities were above 22.

Multidimensional scaling (MDS) analysis of species abundances divided macrofaunal communities into two significantly different groups (P < 0.001) with at least 40% similarity among stations within each group (Fig. 10A). The two groups were 75% different from (25% similar to) each other (Fig. 10B). MDS Group 1 contained Lavaca Bay, San Bernard River, Brazos River, Cedar Lakes, and the Rio Grande. Within MDS Group 1, the macrofaunal communities of Lavaca Bay, San Bernard River, Brazos River, and Cedar Lakes were at least 50% similar to each other. MDS Group 2 contained East Matagorda, Matagorda, Christmas, and South Bays. Within MDS Group 2, there was at least 58% similarity in macrofaunal communities among East Matagorda, Matagorda, and Christmas Bays.

There were several differences between the two MDS community groups on a higher taxa level. Estuaries within MDS Group 2 contained a larger mean density of polychaete worms (6,000-18,200 m⁻²) than estuaries within MDS Group 1 (3,200-5,300 m⁻²). Two phyla, Phoronida (made up of solely *Phoronis architecta*) and Echinodermata (made up solely of the ophiuroid *Amphiodia atra*) were found at all estuaries in MDS Group 2 but no estuaries in MDS Group 1. Unidentified Anthozoa species occurred in average densities of 11-18 m⁻²

Fig. 10 Multidimensional scaling plot and cluster analysis of macrofauna communities for each estuary. Bay abbreviations same as Fig. 4. Clusters of macrofauna assemblages are significantly different to each other if they are separated by solid lines in the cluster analysis



in Group 2, but were absent in Group 1 except for in the Brazos River and Lavaca Bay, where densities were low $(3-5 \text{ m}^{-2})$. Unidentified Turbellaria species occurred in MDS Group 2 estuaries at average densities of 6–55 m⁻², however, Unidentified Turbellaria species were only found in the Brazos River (2 m^{-2}) of the MDS Group 1 estuaries.

Many species were unique to MDS Group 2, but no such unique species occurred in MDS Group 1. Individual species that were found exclusively to and universally throughout MDS Group 2 included polychaetes *Cirrophorus lyra*, *Aricidea catharinae* (60–981 m⁻²), *Branchioasychis americana* (35–347 m⁻²), *Axiothella* sp. A (20–134 m⁻²), *Euclymene* sp. B (1–118 m⁻²), *Melinna maculata* (8–71 m⁻²), *Glycera americana* (11–35 m⁻²), *Ceratonereis irritabilis* (2–30 m⁻²), *Malmgreniella* sp. (6–60 m⁻²), *Drilonereis magna* (1–20 m⁻²), cumacean *Oxyurostylis* sp. $(5-35 \text{ m}^{-2})$, pea crab *Pinnixa* sp. $(6-14 \text{ m}^{-2})$, gastropod *Turbonilla* sp. $(6-55 \text{ m}^{-2})$, phoronid *Phoronis* architecta (1–142 m⁻²), and ophiuroid *Amphiodia* atra (12–197 m⁻²; Table 3). Chironomid larvae were absent from Group 2 except for in Matagorda Bay (5 m^{-2}) . In MDS Group 1, chironomid larvae were present in low average abundances (2–75 m⁻²) except for at the Rio Grande, where abundances were on average 3500 m⁻². In all MDS Group 1 estuaries except for the San Bernard River, both unidentified ostracods (2–11 m⁻²) and the polychaete *Laeonereis* culveri (2–165 m⁻²) were present.

Relationship between physical characteristics and macrofauna

PC1 (inflow gradient) from the principal components analysis on water quality data was significantly and

Table 3 Mean species abundance (n m^{-2}) list of species that make up 90% of all individual organisms as a coast-wide average

Species name	Taxa	BR MDS- 1	CL MDS- 1	LB MDS- 1	RG MDS- 1	SB MDS- 1	CB MDS- 2	EM MDS- 2	MB MDS- 2	SO MDS- 2	Mean n	Mean %	Cum. %
Mediomastus ambiseta	Р	2036	3475	2333	3101	1127	4463	7359	3891	1525	3257	29.8	29.8
Streblospio benedicti	Р	2335	1422	518	1311	2340	327	496	574	4775	1567	14.3	44.1
Oligochaetes (unidentified)	0	183	2013	2	831	248	126	16	572	6370	1151	10.5	54.6
Cirrophorus lyra	Р	0	0	0	0	0	3892	1544	116	231	643	5.9	60.5
Tharyx setigera	Р	0	0	2	0	0	1466	32	67	2996	507	4.6	65.1
Chironomid larvae	Ι	17	75	2	3533	28	0	0	5	0	407	3.7	68.9
Polydora caulleryi	Р	13	0	0	0	4	1009	158	122	1058	263	2.4	71.3
Aricidea catharinae	Р	0	0	0	0	0	981	827	60	166	226	2.1	73.3
Prionospio heterobranchia	Р	0	0	0	0	0	0	0	0	2033	226	2.1	75.4
Capitella capitata	Р	47	142	31	1	28	0	0	0	1743	221	2.0	77.4
Cossura delta	Р	8	0	206	0	0	307	426	383	449	198	1.8	79.2
Nemertea (unidentified)	Ν	166	63	73	243	118	327	173	182	248	177	1.6	80.8
Lumbrineris parvapedata	Р	0	0	0	0	0	717	559	76	0	150	1.4	82.2
Mulinia lateralis	М	3	8	310	46	24	63	741	15	12	136	1.2	83.4
Apseudes sp. A	С	0	0	0	0	0	0	0	1171	0	130	1.2	84.6
Sphaerosyllis sp. A	Р	0	0	0	0	0	47	0	11	875	104	1.0	85.6
Gyptis vittata	Р	3	0	10	0	12	378	229	128	6	85	0.8	86.4
Branchioasychis americana	Р	0	0	0	0	0	225	347	36	142	83	0.8	87.1
Periploma orbiculare	М	0	0	0	0	0	646	0	37	0	76	0.7	87.8
Mysella planulata	М	0	0	0	0	4	370	87	30	0	55	0.5	88.3
Ampelisca abdita	С	0	122	104	0	0	47	32	34	112	50	0.5	88.8
Paraprionospio pinnata	Р	8	4	12	0	8	67	244	106	0	50	0.5	89.2
Amphiodia atra	0	0	0	0	0	0	118	197	101	12	48	0.4	89.7
Clymenella torquata	Р	0	0	0	0	0	284	126	7	0	46	0.4	90.1
Total (top 90%)		4819	7323	3602	9067	3939	15860	13591	7722	22750	9853	90.1	
Total (all)		5176	7654	3801	10272	4089	17913	14678	8672	26189	10938	100.0	

Abbreviations for ecosystems same as Table 1. MDS-1 and MDS-2 denote groupings of estuaries in multidimensional scaling analysis. Taxa groups: C crustacean, I insect, M mollusc, N nemertean, P polychaete, O other

negatively correlated with both macrofaunal abundance $(r = -0.75, P \le 0.02)$ and N1 diversity $(r = -0.77, P \le 0.02)$ but non-significantly and negatively related to macrofaunal biomass $(r = -0.53, P \le 0.15)$. A positive PC1 value (in Fig. 6) indicates high concentrations of dissolved inorganic nitrogen, phosphate, silicate and chl-*a* and low salinity values. Therefore, the negative correlations between PC1 and both diversity and abundance means that as salinity increases and selected nutrients decrease, macrofaunal abundance, and diversity increase. There were no significant

correlations between PC2 from the water quality PCA or either of the first two PCs from the sediment quality PCA with the three macrofaunal productivity variables.

Discussion

Comparisons between adjacent rivers and lagoons

The results of the current study indicate that riverdominated estuaries have more in common with one another than they do with lagoons, even when the lagoons are adjacent to and within the same climatic subregion as the river estuaries. The Brazos River and Rio Grande river estuaries had similarly low macrofaunal abundance, biomass, and diversity, despite being located in different climatic subregions along the Texas coast. The same was true for the Christmas Bay and South Bay lagoon systems, which had similarly high macrofaunal abundance, biomass, and diversity. Community structure was also similar in Christmas Bay and South Bay and different from the Rio Grande and Brazos River, which were similar. The differences between the river estuaries and lagoon systems are related to the magnitude of freshwater inflow relative to the estuary size, because the rivers have much lower salinities and higher nutrient and chlorophyll-a levels than the lagoons (Figs. 4, 5).

The four northernmost systems comprise Christmas Bay and Cedar Lakes lagoon systems, and the San Bernard and Brazos River estuaries. This allowed for an interesting synoptic comparison between two lagoons and two rivers in the same region. Christmas Bay receives little or no direct freshwater inflow, which makes this bay a typical lagoon in Texas. It does have an indirect connection with the Gulf of Mexico via Cold and San Luis Passes, and some exchange with the Gulf Intracoastal Waterway. Previous studies have identified four characteristics which make this bay unique: (1) diversity is highest in summer, (2) diversity is dominated by Mollusca, (3) Streblospio benedicti (a polychaete) is not common, let alone the dominant species, and (4) the community structure represents a climax community (Montagna, 2003). These unique characteristics may be due to a small data set (only 2 years) and with a larger data set these trends may disappear; or Christmas Bay habitats may be truly unique, rich, and relatively pristine. The latter explanation is likely true because Christmas Bay is a preserve and has a typical climax community with the highest abundance, biomass, and diversity of all systems studied (Figs. 8, 9). The Christmas Bay macrofaunal community was significantly different from the community in nearest lagoon system, Cedar Lakes (Fig. 10; Montagna et al., 2008b). In fact, the macrofaunal community in Cedar Lakes had more in common with the communities in the San Bernard and Brazos River estuaries. The mean ammonium concentration, temperature, and salinity of Cedar Lakes were closer to those of the San Bernard River and Brazos River then they were to those of Christmas Bay. The similarity of Cedar Lakes to the northern river estuaries is caused by fresh water from the San Bernard River entering Cedar Lakes via the Gulf Intracoastal Waterway.

Comparing minor bay lagoons versus major bays

Rivers and lagoons each share some similarities with major bays. Lavaca Bay, which is a small secondary bay that receives direct freshwater flows from the Lavaca River, has similar values for salinity and some nutrients (phosphate, nitrite and nitrate) to Cedar Lakes, which is the freshest lagoon. Lavaca Bay and Cedar Lakes also share some similarity in benthic characteristics with the river estuaries because they all have relatively low macrofaunal abundance (4,000–12,000 n m⁻²), biomass (1–3 g m⁻²), and diversity (N1 \approx 2.5).

In contrast, the other lagoons (Christmas Bay, East Matagorda Bay, and South Bay) are more saline and have lower nutrients and chlorophyll-a concentrations. These lagoons share some similarity in benthic characteristics, which are much greater than that found in the rivers, with macrofaunal abundance ranging from 15,000 to 27,000 n m⁻², biomass ranging from 7 to 11 g m^{-2} , and N1 diversity ranging from 5 to 8. Matagorda Bay has greater inflow than Lavaca Bay (Table 1), but also a larger volume to dilute that inflow. Interestingly, Matagorda Bay, which is the primary bay of the Lavaca-Colorado Estuary, has similar abundance and biomass to the rivers, but similar diversity to the lagoons. The high diversity in Matagorda Bay is likely due to the proximity and close connection to exchange with the Gulf of Mexico, which allows marine species to move freely into and out of the bay. The rivers and lagoons have very different community structures; Lavaca Bay resembles the rivers, whereas Matagorda Bay resembles the lagoons.

Estuary condition and benthic response

The coast-wide analytical approach utilized in this study aggregated data over all samples to determine broad-scale trends and relationships among estuaries along the Texas coast. Strong coast-wide correlations existed between salinity and chemical variables although differences between northern and southern estuaries were not observed (Table 2; Figs. 4, 5, 6). As salinity increased, phosphate, silicate, nitrate, and chlorophyll-a concentrations decreased. The decrease was near linear only for silicate, indicating a coastwide trend of conservative mixing for this compound. In contrast, all nutrients decreased very rapidly with a small increase (up to 20 ppt) salinity, consistent with the idea that the ecosystems were sinks for nutrients. Nutrient and nutrient-silicate ratios are indicators of the trophic status of water courses, and a typical N:P ratio of a system in balance is expected to be near 16 (Redfield, 1958; Falkowski, 2000). The Brazos River had a high N:P ratio of 17.7 rather than the expected ratio of 16. In contrast, all the other ecosystems had low ratios below 6.1, indicating that phosphate could be limiting in the Brazos River, but nitrogen is likely limiting in all the other systems. The N:Si and P:Si ratios indicate that silicate is in excess in all the ecosystems and not likely a limiting factor for any. The finding that the estuaries are retaining nutrients is not surprising and consistent with the idea that estuaries have a filter function where nutrients are consumed and incorporated into biomass (Schubel & Kennedy, 1984).

River-dominated estuaries such as the Rio Grande, Brazos River, and San Bernard River had lower salinity ranges and tended to have higher concentrations of nutrients. In contrast, lagoons such as South Bay, Christmas Bay, and East Matagorda Bay had higher salinities and lower nutrient concentrations. In South Bay, the mean ammonium concentration was similar to those of the river estuaries and Cedar Lakes, even though South Bay had the highest mean salinity of all estuaries sampled. The high mean ammonium concentration at South Bay was largely influenced by three very high ammonium concentrations (32–52 μ M) in July 2001 and 2002. While the causes of the high ammonium concentrations are unknown, the mean without these anomalies $(1.5 \ \mu M)$ is similar to other lagoons with salinities above 20 (1.0-1.5 µM) and lower than the river estuaries (5.8–7.6 μ M). With this anomaly removed, the negative trend between salinity and ammonium concentration is stronger. The negative correlations between salinity and all measured nutrient concentrations are likely to be due to dilution of freshwater inflows by saline waters in the estuaries. While not studied here, it is thought that agricultural and urban areas are dominant sources of nutrients in the watersheds (Howarth et al., 2002; Bricker et al., 2007). The reference sites, Lavaca Bay and Matagorda Bay were relatively neutral (i.e., had PC1 values near zero) when compared to most rivers and lagoons in this study (Fig. 6). This neutrality demonstrates the difference between these two major bays compared to the two types of ecosystems (river and lagoon estuaries).

Salinity is probably the most important environmental variable influencing macrofauna organism distribution in northern Gulf of Mexico estuaries (Rakocinski et al., 1997). At salinities above 20 within Texas estuaries, macrofaunal densities increased with increasing salinity (Fig. 9A). Biomass and abundance were lower for river-dominated estuaries (low salinities) and high for lagoons, except Cedar Lakes (high salinities, Fig. 9). Salt tolerance plays a major role in estuarine systems; organisms can be killed if there is too much or too little inflow (Gunter, 1961; Montagna et al., 2002a, b; Palmer et al., 2002). Palmer et al. (2002) studied the Nueces Delta, Texas marsh and determined low biomass and abundance in upper estuary areas can be attributed to high flow velocities and a lack of salinity-tolerant species. Flow velocities that are too high can prohibit organic matter from depositing in the sediments, which would stimulate benthic productivity. However, flow velocities cannot be the only factor in causing decreased macrofaunal biomass and abundance because flow velocities in Cedar Lakes are relatively low. Other possible mechanisms include the low-salinity suppression of benthic predators (Wilber, 1992), or the release from bottom-up limitation due to nutrient stimulation (Sutcliffe, 1972).

Species diversity in estuaries along the Texas coast increased with increasing salinity (Fig. 9). These results support those from previous studies in showing that species diversity increases from nearly freshwater to seawater within Texas, USA (Montagna & Kalke, 1992; Palmer et al., 2002), South Africa (Schlacher & Wooldridge, 1996), Portugal (Sousa et al., 2006; Teixeira et al., 2008), northwest Europe (Ysebaert et al., 1998, 2003), Baltic Sea (Zettler et al., 2007), and many other estuaries. The current diversity versus salinity plot did not follow the

"Remane curve," whereby diversity maxima occur at both high and low salinities (Remane, 1934; Remane & Schlieper, 1971; Paavola et al., 2005). One possibility for reduced diversity at low salinities in this current study is that insect taxa (chironomid larvae, diptera spp.) were grouped into higher taxa groups than species and therefore may have caused an underestimation of diversity at low salinities. It is also possible that the lowest average salinities in this study (mean salinity of 4), which occurred at the Rio Grande, were not low enough to yield a diverse number of oligohaline species. In the Lavaca-Colorado Estuary, Texas, insects as a group were not found to be good indicators of the existence of a salinity gradient, but rather served as indicators of freshwater conditions (Pollack et al., 2009).

The significant negative correlation between macrofaunal metrics (macrofaunal abundance and diversity) and the water quality PC1 implies a negative correlation between dominance by inflows and macrofaunal productivity in estuaries (Fig. 6). A positive PC1 score correlates with estuaries with high nutrient concentrations and low salinities. Therefore, PC1 approximates freshwater inflow dominance in an estuary. The lack of any significant correlation between other sediment or water quality PCs suggests that on a coast-wide basis, inflow is the most important factor influencing macrofaunal communities.

Multivariate analysis provides the ability to determine indicator taxa and to investigate which taxa are driving the changes between different communities (Hewitt et al., 2005). Macrofaunal community structure was divided into two major types (Fig. 10). The first type contained communities found in the Rio Grande, Brazos River, San Bernard River, Lavaca Bay, and Cedar Lakes. The estuaries in this first group all had mean salinities below 16, and hence represented oligohaline (salinity 0.5-5) and mesohaline (salinity 5-18) conditions (Venice Classification system; Anonymous, 1958). The second macrofaunal community grouping contained Matagorda, East Matagorda, Christmas, and South Bays. The estuaries in this second group had mean salinities above 22 and hence represented a more polyhaline (salinity 18-30) community (Venice Classification system; Anonymous 1958). The estuaries of the first type are subject to a greater range of flows and water quality-related fluctuations because of the strong influence that rivers have on them (Figs. 4, 5). The estuaries of the second type have relatively stable nutrient concentrations and salinities. Stability, as indicated by low variance of condition metrics is likely the factor driving this response.

The oligo-mesohaline community type had the lowest mean diversity and biomass values in this study (Fig. 9). The only common organism in this group, which was also rare in the polyhaline group, was Chironomid larvae (Table 3). Chironomid larvae have been shown to be more common in oligohaline conditions in many estuaries (Grenon, 1982; Schlacher & Wooldridge, 1996; Seys et al., 1999; Fuentes et al., 2005; Brammer et al., 2007; Dimitriadis & Cranston, 2007), however, certain species of chiromonids also exist at higher salinities elsewhere (Carew et al., 2007; Dimitriadis & Cranston, 2007; Keats & Osher, 2007). Chironomid larvae were more abundant in the upper reaches of the marsh of Rincon Bayou, Texas, rather than downstream near the bay (Palmer et al., 2002). However, in that study, the high relative abundance was attributed to the broader salinity range that occurred upstream in the Rincon Bayou.

Many species were found in the polyhaline estuaries in addition to species found in the oligomesohaline estuaries. Species that were found exclusively in and universally throughout the polyhaline estuaries included polychaetes Cirrophorus lyra, Aricidea catharinae, Branchioasychis americana, Axiothella sp. A, Euclymene sp. B, Melinna maculata, Glycera americana, Ceratonereis irritabilis, Malmgreniella sp., Drilonereis magna, cumacean Oxyurostylis sp., pea crab Pinnixa sp., gastropod Turbonilla sp., phoronid Phoronis architecta, and ophiuroid Amphiodia atra. The increase in the number of species found in the polyhaline estuaries is due to an increased number of marine species (Remane & Schlieper, 1971). There appears to be a tipping point at salinities of about 17-21 where coastal systems change from oligo-mesohaline to polyhaline community characteristics. In comparison, macrobenthic community structure was divided by a salinity of approximately 15 in a South African estuary (Schlacher & Wooldridge, 1996). Macrofauna community structure was divided into three salinity zones; polyhaline, mesohaline, and oligohaline zones in two northwest European estuaries (Ysebaert et al., 1998, 2003). Differences between the tipping point in the current study and those from these other studies may be attributed to many factors, including differences in salinity variance among study areas.

In the current study of rivers, lagoons, and major bays along the Texas Coast, several key points arise that are relevant to the management of environmental flows of freshwater to the coast. On one hand, there is a degree of uniqueness among the nine systems studied. This is common in estuarine ecology and has been termed the "estuarine signature" of the system (Turner, 2001). Whereas all estuaries will have some differences from one another, it is striking that along the Texas coast, rivers share similarities with one another and lagoons share similarities among one another as well. Each system has a characteristic community that is strongly influenced by the interactions of hydrology, sediments, and nutrients. Another striking finding is that the rivers resemble at least one major secondary bay (Lavaca Bay), and the lagoons resemble at least one major primary bay (Matagorda Bay). This indicates that much of the research performed on the major bays is directly comparable and thus of value in assessing the environmental flow needs of rivers and lagoons. This finding is useful not only for describing previously poorly studied estuaries in Texas or the rest of the world, but also for allowing speculation on how future increases or decreases in inflow and resulting changes in estuarine condition may change biological resource response. This information regarding relationships of macrofaunal communities among different types of estuaries is also useful in managing other coastlines of the world where differing estuarine types exist alongside each other because it demonstrates that common traits exist that are directly comparable and system-specific information is not necessary in order to make these comparisons.

Acknowledgments The field work for this study was supported by the Texas Water Development Board, Research and Planning Fund, Research Grants, authorized under the Texas Water Code, Chapter 15, and as provided in §16.058 and §11.1491. This support was administered by the Board under interagency cooperative contracts 2001-483-362, 2002-483-414, 2003-483-471, 2004-483-012, 2005-483-541, and 2006-483-026. Much of the analytical work was supported by grant number NA09NMF4720179 from the National Oceanic and Atmospheric Administration under the Comparative Assessment of Marine Ecosystem (CAMEO) program. The study also benefitted by partial support from the University of Texas at Austin, Marine Science Institute, and

Texas A&M University—Corpus Christi. Larry Hyde, Christopher Kalke, Jeff Baguley, Marc Russell, Julie Kinsey, and others aided in field collections. Tracy Villareal and Lynn Tinnin performed nutrient analyses and measurements. Carrol Simanek also provided significant help in data management. Anne Evans and Laura Ryckman provided help with the initial development of this manuscript. Review and advice on earlier drafts was provided by the Bay and Estuaries Division of the Texas Water Development Board. This manuscript was improved with the assistance of two anonymous reviewers.

References

- Alber, M., 2002. A conceptual model of estuarine freshwater inflow management. Estuaries 25: 1246–1261.
- Arnqvist, F. R. & D. Wooster, 1995. Meta-analysis—synthesizing research findings in ecology and evolution. Trends in Ecology and Evolution 10: 236–240.
- Benson, N. G., 1981. The freshwater-inflow-to-estuaries issue. Fisheries 6: 8–10.
- Brammer, A. J., Z. R. Rodriguez del Rey, E. A. Spalding & M. A. Poirrier, 2007. Effects of the 1997 Bonnet Carre Spillway opening on infaunal macroinvertebrates in Lake Pontchartrain, Louisiana. Journal of Coastal Research 23: 1292–1303.
- Bricker, S., B. Longstaff, W. Dennison, A. Jones, K. Boicourt, C. Wicks & J. Woerner, 2007. Effects of nutrient enrichment in the nation's estuaries: a decade of change. NOAA Coastal Ocean Program Decision Analysis Series No. 26, National Centers for Coastal Ocean Science, Silver Spring, MD: 322 pp.
- Carew, M. E., V. Pettigrove, R. L. Cox & A. A. Hoffmann, 2007. The response of Chironomidae to sediment pollution and other environmental characteristics in urban wetlands. Freshwater Biology 52: 2444–2462.
- Chainho, P., J. L. Costa, M. L. Chaves, M. F. Lane, D. M. Dauer & M. J. Costa, 2006. Seasonal and spatial patterns of distribution of subtidal benthic invertebrate communities in the Mondego River, Portugal—a poikilohaline estuary. Hydrobiologia 555: 59–74.
- Chapman, E. R., 1966. The Texas basins project. In Smith, R. F., A. H. Swartz & W. H. Massmann (eds), A Symposium on Estuarine Fisheries, Vol. 95. American Fisheries Society, Washington, DC: 83–92.
- Clarke, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143.
- Clarke, K. R. & R. N. Gorley, 2006. Primer v6: User Manual/ Tutorial. Primer-E, Plymouth, UK.
- Clarke, K. R. & R. M. Warwick, 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd ed. Primer-E, Plymouth, UK.
- Dalrymple, R. W., B. A. Zaitlin & R. Boyd, 1992. A conceptual model of estuarine sedimentation. Journal of Sedimentary Petrology 62: 1130–1146.
- Dauvin, J. C., G. Bellan & D. Bellan-Santini, 2010. Benthic indicators: from subjectivity to objectivity—where is the line? Marine Pollution Bulletin 60: 947–953.

- Dimitriadis, S. & P. S. Cranston, 2007. From the mountains to the sea: assemblage structure and dynamics in Chironomidae (Insecta: Diptera) in the Clyde River estuarine gradient, New South Wales, south-eastern Australia. Australian Journal of Entomology 46: 188–197.
- Fairbridge, R. W., 1980. The estuary: its definition and geodynamic cycle. In Olausson, E. & I. Cato (eds), Chemistry and Biogeochemistry of Estuaries. Wiley, New York: 1–35.
- Falkowski, P. G., 2000. Rationalizing elemental ratios in unicellular algae. Journal of Phycology 36: 3–6.
- Folk, R. L., 1964. Petrology of Sedimentary Rocks. Hemphill's Press, Austin, TX: 155.
- Fuentes, C., A. J. Green, J. Orr & J. S. Olafsson, 2005. Seasonal variation in species composition and larval size of the benthic chironomid communities in brackish wetlands in southern Alicante, Spain. Wetlands 25: 289– 296.
- Grenon, J.-F., 1982. The macrobenthic fauna of the Eastmain Estuary (James Bay, Quebec), before the diversion. Naturaliste Canadien 109: 793–802.
- Gunter, G., 1961. Some relations of estuarine organisms to salinity. Limnology and Oceanography 6: 182–190.
- Hayes, M. O., 1975. Morphology and sand accumulation in estuaries. In Cronin, L. E. (ed.), Estuarine Research, Vol. 2. Academic Press, New York: 3–22.
- Hayes, M. O., 1980. General morphology and sediment patterns in tidal inlets. Sedimentary Geology 26: 139–156.
- Hewitt, J. E., M. J. Anderson & S. F. Thrush, 2005. Assessing and monitoring ecological community health in marine systems. Ecological Applications 15: 942–953.
- Hill, M. O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427–432.
- Howarth, R. W., E. W. Boyer, W. J. Pabich & J. N. Galloway, 2002. Nitrogen use in the United States from 1961–2000 and potential future trends. Ambio 31: 88–96.
- International Boundary and Water Commission, 2010. Rio Grande Historical Mean Daily Discharge Data. IBWC [available on internet at http://ibwc.gov/wad/DDQ BROWN.htm]. Accessed Nov 2010.
- Kalke, R. D. & P. A. Montagna, 1991. The effect of freshwater inflow on macrobenthos in the Lavaca River Delta and Upper Lavaca Bay, Texas. Contributions in Marine Science 32: 49–71.
- Keats, R. A. & L. J. Osher, 2007. The macroinvertebrates of *Ruppia* (widgeon grass) beds in a small Maine estuary. Northeastern Naturalist 14: 481–491.
- Kerans, B. L. & J. R. Karr, 1994. A benthic index of biotic integrity (B-IBI) for rivers of the Tennessee Valley. Ecological Applications 4: 768–785.
- Kim, H. & P. A. Montagna, 2009. Implications of Colorado River (Texas, USA) freshwater inflow to benthic ecosystem dynamics: a modeling study. Estuarine, Coastal and Shelf Science 83: 491–504.
- Lavaca-Navidad River Authority, 2010. Lake Texana ~ Palmetto Bend Project Historical Spillway & Row Releases. LNRA [available on internet at http://www.lnra.org]. Accessed Jan 2010.
- Longley, W. L. (ed.), 1994. Freshwater Inflows to Texas Bays and Estuaries: Ecological Relationships and Methods for Determination of Needs. Texas Water Development Board

and Texas Parks and Wildlife Department, Austin, TX: 386. http://midgewater.twdb.state.tx.us/bays_estuaries/ Publications/FreshwaterInflows-EcologicalRelationships andMethodsforDeterminationofNeeds-1994.pdf.

- Ludwig, J. A. & J. F. Reynolds, 1988. Statistical Ecology: A Primer on Methods and Computing. Wiley, New York: 368.
- Montagna, P. A., 2000. Effect of freshwater inflow on macrobenthos productivity and nitrogen losses in Texas estuaries. Final Report to Texas Water Development Board, Contract No. 2000-483-323, University of Texas Marine Science Institute Technical Report Number TR/00-03, Port Aransas, TX: 78 [available on internet at http://www.twdb.state.tx.us/rwpg/rpgm_rpts/2000483323.pdf].
- Montagna, P. A., 2003. Effect of freshwater inflow on macrobenthos productivity in minor bay and river-dominated estuaries—FY03. Final Report to Texas Water Development Board, Contract No. 2003-483-471, University of Texas Marine Science Institute Technical Report Number TR/03-03: 56 [available on internet at http://www.twdb. state.tx.us/rwpg/rpgm_rpts/2003483471.pdf].
- Montagna, P. A. & R. D. Kalke, 1992. The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces Estuaries, Texas. Estuaries 15: 307–326.
- Montagna, P. A. & R. D. Kalke, 1995. Ecology of infauna mollusca in south Texas estuaries. American Malacological Bulletin 11: 163–175.
- Montagna, P. A. & J. Li, 2010. Effect of freshwater inflow on nutrient loading and macrobenthos secondary production in Texas. In Kennish, M. J. & H. W. Paerl (eds), Coastal Lagoons: Critical Habitats of Environmental Change. CRC Press, Taylor & Francis Group, Boca Raton, FL: 513–539.
- Montagna, P. A. & W. B. Yoon, 1991. The effect of freshwater inflow on meiofaunal consumption of sediment bacteria and micophytobenthos in San Antonio Bay, Texas, USA. Estuarine, Coastal and Shelf Science 33: 529–547.
- Montagna, P. A., M. Alber, P. Doering & M. S. Connor, 2002a. Freshwater inflow: science, policy, management. Estuaries 25: 1243–1245.
- Montagna, P. A., R. D. Kalke & C. Ritter, 2002b. Effect of restored freshwater inflow on macrofauna and meiofauna in upper Rincon Bayou, Texas, USA. Estuaries 25: 1436–1447.
- Montagna, P. A., T. A. Palmer, R. D. Kalke & A. Gossmann, 2008a. Suitability of using a limited number of sampling stations to represent benthic habitats in Lavaca-Colorado Estuary, Texas. Environmental Bioindicators 3: 156–171.
- Montagna, P. A., T. A. Palmer & J. B. Pollack, 2008b. Effect of freshwater inflow on macrobenthos productivity in minor bay and river-dominated estuaries—synthesis. Final Report to Texas Water Development Board, Contract No. 2006-483-026, Texas A&M University—Corpus Christi: 110 [available on internet at http://www.twdb.state. tx.us/RWPG/rpgm_rpts/20064830026_MinorBays.pdf].
- Montagna, P. A., E. M. Hill & B. Moulton, 2009. Role of science-based and adaptive management in allocating environmental flows to the Nueces Estuary, Texas, USA. In Brebbia, C. A. & E. Tiezzi (eds), Ecosystems and Sustainable Development VII. WIT Press, Southampton, UK: 559–570.

- Paavola, M., S. Olenin & E. Leppakoski, 2005. Are invasive species most successful in habitats of low native species richness across European brackish water seas? Estuarine, Coastal and Shelf Science 64: 738–750.
- Palmer, T. A., P. A. Montagna & R. D. Kalke, 2002. Downstream effects of restored freshwater inflow to Rincon Bayou, Nueces Delta, Texas, USA. Estuaries 25: 1448– 1456.
- Pearson, T. H. & R. Rosenberg, 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology 16: 229–311.
- Perillo, G. M. E., 1995. Definition and geomorphologic classification of estuaries. In Perillo, G. M. E. (ed.), Geomorphology and Sedimentology of Estuaries. Developments in Sedimentology, Vol. 53. Elsevier Science BV, Amsterdam: 17–47.
- Piegorsh, W. W. & A. J. Bailer, 1997. Statistics for Environmental Biology and Toxicology. Chapman & Hall, London: 579 pp.
- Pollack, J. B., J. W. Kinsey & P. A. Montagna, 2009. Freshwater inflow biotic index (FIBI) for the Lavaca-Colorado Estuary, Texas. Environmental Bioindicators 4: 153–169.
- Pritchard, D. W., 1960. Lectures on estuarine oceanography. In Kinsman, B. (ed.), Johns Hopkins University: 154 pp.
- Pritchard, D. W., 1967. What is an Estuary: Physical Viewpoint. In Lauff, G. H. (ed.), Estuaries. American Association for the Advancement of Science, Washington, DC: 3–5.
- Rakocinski, C. F., S. S. Brown, G. R. Gaston, R. W. Heard, W. W. Walker & J. K. Summers, 1997. Macrobenthic responses to natural and contaminant-related gradients in northern Gulf of Mexico estuaries. Ecological Applications 7: 1278–1298.
- Redfield, A. C., 1958. The Biological control of chemical factors in the environment. American Scientist 46: 205–221.
- Remane, A., 1934. Die Brackwasserfauna. Verhandlungen der Deutschen Zoologischen Gesellschaft 36: 34–74.
- Remane, A. & C. Schlieper, 1971. Biology of Brackish Water. Wiley, New York: 372 pp.
- Russell, M. J., P. A. Montagna & R. D. Kalke, 2006. The effect of freshwater inflow on net ecosystem metabolism in Lavaca Bay, Texas. Estuarine, Coastal and Shelf Science 68: 231–244.
- SAS Institute Inc., 2009. SAS/STAT[®] 9.2 User's Guide, 2nd ed. SAS Institute Inc., Cary, NC, USA: 7886 pp.
- Schlacher, T. A. & T. H. Wooldridge, 1996. Axial zonation patterns of subtidal macrozoobenthos in the Gamtoos Estuary, South Africa. Estuaries 19: 680–696.
- Schubel, J. R. & V. S. Kennedy, 1984. The estuary as a filter: an introduction. In Kennedy, V. S. (ed.), The Estuary as a Filter. Academic Press, New York.
- Seys, J., M. Vincx & P. Meire, 1999. Spatial distribution of oligochaetes (Clitellata) in the tidal freshwater and brackish parts of the Schelde estuary (Belgium). Hydrobiologia 406: 119–132.
- Shank, G. C., K. Nelson & P. A. Montagna, 2009. Importance of CDOM distribution and photoreactivity in a shallow Texas estuary. Estuaries and Coasts 32: 661–677.

- 67
- Smith, R. W., M. Bergen, S. B. Weisberg, D. Cadien, A. Dalkey, D. Montagne, J. K. Stull & R. G. Velarde, 2001. Benthic response index for assessing infaunal communities on the southern California mainland shelf. Ecological Applications 11: 1073–1087.
- Sousa, R. S. Dias & J. C. Antunes, 2006. Spatial subtidal macrobenthic distribution in relation to abiotic conditions in the Lima estuary, NW of Portugal. Hydrobiologia 559: 135–148.
- Sutcliffe, W. H. Jr., 1972. Some relations of land drainage, nutrients, particulate material, and fish catch in two eastern Canadian bays. Journal of the Fisheries Research Board of Canada 29: 357–362.
- Teixeira, H., F. Salas, A. Borja, J. M. Neto & J. C. Marques, 2008. A benthic perspective in assessing the ecological status of estuaries: the case of the Mondego estuary (Portugal). Ecological Indicators 8: 404–416.
- Turner, R. E., 2001. Of manatees, mangroves, and the Mississippi River: is there an estuarine signature for the Gulf of Mexico? Estuaries 24: 139–150.
- United States Environmental Protection Agency, 1997. Method 445.0, In vitro determination of chlorophyll *a* and pheophytin *a* in marine and freshwater algae by fluorescence. USEPA, National Exposure Research Laboratory, Cincinnati, OH [available on internet at http://www.epa.gov/ microbes/m445_0.pdf].
- United States Geological Survey, 2010. WaterWatch (Stations 08116650, 08117500, 08162500, 08162600 & 08164000).
 USGS [available on internet at http://waterwatch.usgs.gov]. Accessed Dec 2010.
- Ward, G. H. Jr., & N. E. Armstrong, 1980. Matagorda Bay, Texas, its hydrography, ecology, and fishery resources. Report FWS/OB5-81/52, U.S. Fish and Wildlife Service, U.S. Department of the Interior: 230.
- Weisberg, S. B., J. A. Ranasinghe, D. M. Dauer, L. C. Schaffner, R. J. Diaz & J. B. Frithsen, 1997. An estuarine benthic index of biotic integrity (B-IBI) for the Chesapeake Bay. Estuaries 20: 149–158.
- Welschmeyer, N. A., 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. Limnology and Oceanography 39: 1985–1992.
- Wilber, D. H., 1992. Associations between freshwater inflows and oyster productivity in Apalachicola Bay, Florida. Estuarine, Coastal and Shelf Science 35: 179–190.
- Wilber, D. H. & R. Bass, 1998. Effect of the Colorado River diversion on Matagorda Bay epifauna. Estuarine, Coastal and Shelf Science 47: 309–318.
- Ysebaert, T., P. Meire, J. Coosen & K. Essink, 1998. Zonation of intertidal macrobenthos in the estuaries of Schelde and Ems. Aquatic Ecology 32: 53–71.
- Ysebaert, T., P. M. J. Herman, P. Meire, J. Craeymeersch, H. Verbeek & C. H. R. Heip, 2003. Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe. Estuarine, Coastal and Shelf Science 57: 335–355.
- Zettler, M. L., D. Schiedek & B. Bobertz, 2007. Benthic biodiversity indices versus salinity gradient in the southern Baltic Sea. Marine Pollution Bulletin 55: 258–270.