Ecology of infaunal Mollusca in south Texas estuaries

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Abstract. The ecology of Texas estuaries is strongly influenced by latitudinal ecotones that exist along the northwestern Gulf of Mexico coastline. Long-term studies were conducted in four of the seven major estuarine ecosystems in Texas. The objective was to determine the role of climatic variability and concordant differences in freshwater inflow among the ecosystems in structuring benthic infaunal communities and maintaining secondary production. Mollusks are prominent members of the infauna in all benthic habitats of Texas estuaries. The abundance, biomass, and community structure of mollusks was measured along salinity gradients within the four south Texas estuaries. Infaunal samples were collected by divers using small (6.7 cm diameter) cores (so larger epibenthic mollusks were not collected). Overall, these Texas estuaries had a mean of 14 species of infaunal mollusks, with mean abundance of 7,500 individuals/m^2, and mean biomass of 2.4 g/m^2. Freshwater inflow is the dominant factor regulating variability of molluscan communities. Salinity is a surrogate for inflow, therefore, there are zoogeographic patterns within and among estuaries related to salinity patterns. There are seasonal, interannual, and latitudinal patterns of inflow, and these patterns are apparently regulating community structure, population dynamics, and secondary production in Texas estuaries. Recent water projects to enhance the amount of freshwater flowing into estuaries appear to have had an effect and have increased the number of mollusks in those areas. However the projects occurred during a naturally wet period, so it is difficult to differentiate natural versus anthropogenic changes. The response of mollusks to natural gradients and man-induced changes of freshwater inflow demonstrate the importance of this factor in regulating benthic communities.

A major component of benthic ecosystems in Texas estuaries, as is true elsewhere, is the Mollusca. Molluscan biomass dominates the macroinfauna in Lavaca, San Antonio, Corpus Christi, and Nueces Bays (Kalke and Montagna, 1991; Montagna and Kalke, 1992). During peak recruitment events, Mollusca can also dominate population abundance. However, differences in population size and community structure exist within and among Texas Bays.

There are seven major estuarine systems along 600 linear kilometers of coastline. The estuaries of Texas are remarkably diverse in spite of similar physiography (Fig. 1). This is due to a climatic gradient, which influences freshwater inflow. The gradient of decreasing rainfall, with concomitant freshwater inflow from north to south, is the most distinctive feature of the coastline (Table 1). Along this gradient, rainfall decreases by a factor of two, but inflow balance decreases by almost two orders of magnitude. The inflow patterns appear to group into four distinct types of estuaries that vary by about an order of magnitude each (Table 1). Each estuary-type also has distinctly different timing of peak inflow events. The northern estuaries receive peak inflow during the spring, the central estuaries are bimodal receiving peak inflows during the spring and fall, and the southernmost estuaries receive peak inflows during the fall (Texas Department of Water Resources, 1982). These distinct patterns are very important, because growth, reproduction, and migration of many species are keyed to seasonal events. The timing and magnitude of inundation is believed to regulate finfish and shellfish production (Texas Department of Water Resources, 1982).

We have been conducting long-term studies in four of the seven estuaries to determine the role of freshwater inflow in maintaining benthic productivity. The primary purpose of the current study was to determine the degree of influence of freshwater inflow in regulating zoogeographic differences of molluscan population size and community structure within and among Texas estuaries. The secondary purpose of this study was to assess the effects of two major water projects designed to increase freshwater inflows to estuaries to maintain or enhance productivity. One project was a mandated freshwater release schedule from a dam and the other was a diversion of river water to an estuary. The focus in this manuscript is on the infaunal mollusks.

METHODS

All seven Texas estuaries have similarities in their structure and physiography (Fig. 1). Barrier islands are parallel to the mainland along most of the coast. Between the islands and the mainland there are lagoons. The

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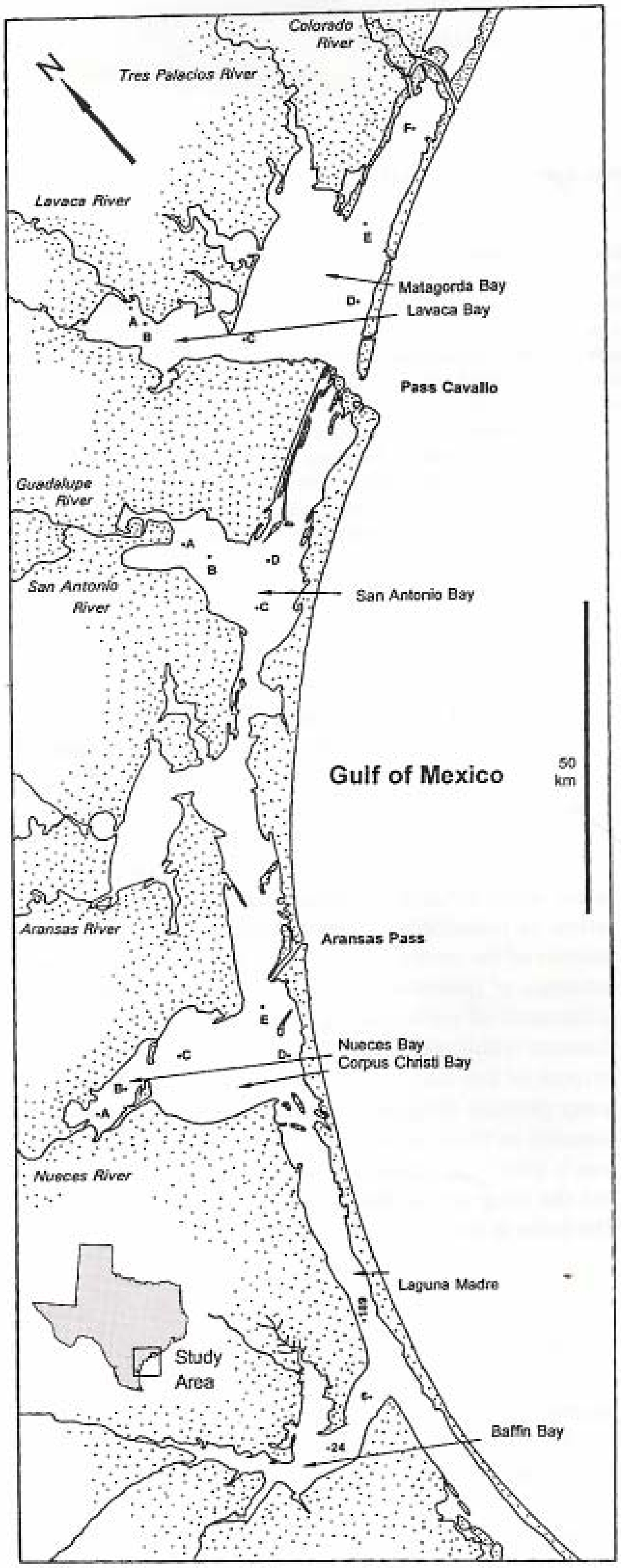

Fig. 1. Location of south Texas estuaries and sampling stations.

Table 1. Gradients in Texas estuaries. Listed from north to south: area at mean low tide (Diener, 1975), mean annual rainfall (1951-1980; Larkin and Bomar, 1983), mean annual freshwater inflow balance (1941-1976; Texas Department of Water Resources, 1982), and mean annual commercial harvest (1962-1987; Texas Parks and Wildlife Department, 1988).

				Commercial Harvest	
Estuary	Area (km^2)	Rainfall (cm/yr)	Inflow (10^6 m^3/yr)	Finfish (10^3 kg/yr)	Shellfish (10^3 kg/yr)
Sabine-Neches	183	142	16,107	5	332
Trinity-San Jacinto	1,416	112	12,284	190	4,060
Lavaca-Colorado	1,158	102	3,242	100	2,076
Guadalupe	551	91	2,545	80	1,545
Mission-Aransas	453	81	190	207	1,453
Nueces	433	76	509	151	544
Laguna Madre	1,139	69	-947	834	147

lagoons are interrupted by drowned river valleys that form the bay and estuarine systems. There are Gulf inlets through the barrier islands, which connect the sea with the lagoon behind the island. The lagoon opens to a large primary bay. There is a constriction between the primary bay and the smaller secondary bay. The river flows into the secondary bay. Primary bays have greater marine influence and secondary bays have greater freshwater influence. So, as well as a latitudinal climatic gradient, there is a longitudinal salinity gradient within each estuary.

The similarity of the Texas estuaries allowed us to design a sampling program where we could use statistical control on confounding factors, *e.g.* Gulf exchange, circulation patterns, and alterations by humans. Four to six stations were chosen in each estuary (Table 2, Fig. 1) employing the same spatial sampling design that has been employed in previous studies of Texas estuaries (Montagna and Kalke, 1992). Two replicate stations (A and B) were in the secondary bay where freshwater influences are greatest. Two other replicate stations (C and D) were in the primary bay where marine influences are greatest. By using two stations in the freshwater-influenced zone and two stations in the marine-influenced zone, we were replicating effects at the treatment level and avoiding pseudoreplication (Hurlbert, 1984). There has been a diversion of the Colorado River into the east arm of Matagorda Bay, so we located two additional stations (E and F) there. The stations in Laguna Madre are located using a similar strategy. Two stations were located in Baffin Bay (6 and 24), and two stations were located in Laguna Madre in a seagrass bed (189G) and an unvegetated sand patch (189S) (Fig. 1).

Two major water projects were initiated during the course of this study. The purpose of both projects was to increase freshwater inflows to bays to enhance secondary productivity. In 1990, the Texas Water Commission

Table 2. Location of sampling stations and sampling periods.

Estuary	Bay	Name	Stations	Period
Lavaca-Colorado	Secondary	Lavaca Bay	A	1984-1994
	Secondary	Lavaca Bay	B	1988-1994
	Primary	Matagorda Bay	C, D	1988-1994
	Diversion	East Matagorda Bay	E, F	1993-1994
Guadalupe	Secondary	Upper San Antonio Bay	A, B	1987-1994
	Primary	Lower San Antonio Bay	C, D	1987-1994
Nueces	Secondary	Nueces Bay	A, B	1988-1994
	Primary	Corpus Christi Bay	C, D	1988-1994
	Primary	Corpus Christi Bay	E	1990-1994
Laguna Madre	Secondary	Baffin Bay	6, 24	1989-1993
	Primary	Laguna Madre	189G, 189S	1989-1993

ordered the City of Corpus Christi to release 151,000 ac-ft/yr (1.86 x 10^8 m^3/yr) to the Nueces Estuary from the Choke Canyon/Lake Corpus Christi reservoir system. The releases were mandated, because the City had not been releasing water. Stations A and B in Nueces Bay were used to assess the effects of this project (Fig. 1). The Colorado River was diverted into the eastern arm of Matagorda Bay by the creation of a flood diversion channel in 1991 and a dam in the river channel below the point of diversion in 1992. This project has diverted Colorado River water from the Gulf of Mexico into the eastern arm of Matagorda Bay. Stations E and F were sampled to assess the effect of this diversion into Matagorda Bay (Fig. 1). The current study is not a complete assessment of the efficacy of these two projects.

Replicate sediment samples (3) were taken within a 2 m radius at each of the stations in each estuary four times per year. Abundance and community structure were measured using the standard techniques that we (Montagna and Kalke, 1992) have been using since 1984. This includes sectioning 6.7 cm diameter cores (at 0-3 cm, and 3-10 cm) to examine the vertical distribution of infauna. Animals were then extracted using a 0.5 mm sieve, enumerated, and identified. Taxonomic authorities used were Abbott (1974), Turgeon *et al.* (1988), and Andrews (1992). Principal components analysis (PCA) was performed on all data sets to determine the relationship among stations in terms of species composition. Species composition was then pooled by bay within each estuary, and PCA was performed on these data to determine relationships among bays. Hydrographic data were recorded at each station using a Hydrolab Surveyor II (Hydrolab, Inc.). These measurements included: salinity, conductivity, temperature, dissolved oxygen, oxidation-reduction potential, pH, and depth. Salinity is reported as practical salinity units (psu).

RESULTS

SALINITY REGIMES

There were large differences in salinity from year to year in all estuaries (Fig. 2). The years 1985-1986 and 1992-1993 were wet periods with concordant low salinities. These wet periods occur during periods when an El Niño event is occurring in the western Pacific Ocean. The intervening time between El Niño events is dry. Texas suffers through a series of flood and drought periods regulated by global climatic events. There are generally lower salinities in the spring and higher salinities in the summer, because of seasonal inflow and evaporation patterns.

Salinity in the Lavaca-Colorado Estuary ranged from 0-36 psu (Fig. 2). The lowest salinities always occurred in the secondary bay at stations A and B. After the diversion of the Colorado River, Stations E and F exhibited low salinities that are more typical of the secondary bay.

Salinity in the Guadalupe Estuary ranged from 0-32 psu (Fig. 2). During flood periods, this estuary is uniformly low (0-10 psu) in salinity. This is unusual compared to other Texas estuaries. It is caused by the high rate of inflow into a relatively small estuary (Table 1). The high turnover rate and low rate of exchange of marine water with the Gulf of Mexico exacerbate this trend. During extreme flooding the entire estuary can be at or near 0 psu. During drought periods, there can be a gradient of salinity.

Salinity in the Nueces Estuary ranged from 2-45 psu

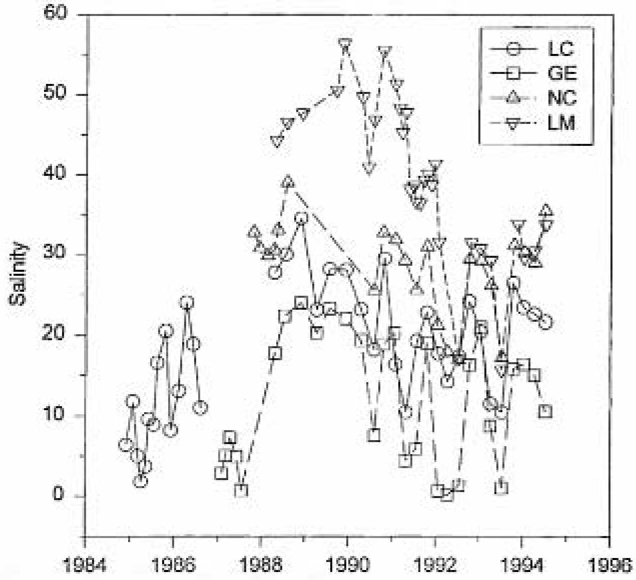

Fig. 2. Mean bottom salinity (psu) at all stations during each sampling period. (GE = Guadalupe Estuary; LC = Lavaca-Colorado Estuary; LM = Laguna Madre-Baffin Estuary; NC = Nueces Estuary).

(Fig. 2). Prior to 1991, salinities in the estuary were uniform and high. In 1991, after a series of mandated freshwater releases, salinities declined in the secondary bay. Salinities in the secondary bay were much lower than in the primary bay, where they had been similar in 1987-1988. Heavy rain in 1992-1993 reduced salinity further.

Salinity in the Laguna-Baffin Estuary ranged from 10-60 psu (Fig. 2). Seasonal fluctuations are less evident in this system. Changes occur system-wide when there are large climatic events, *e.g.* the 1992-1993 El Niño event. There is little salinity gradient in this ecosystem, because freshwater inflow and exchange with the Gulf of Mexico is restricted.

COMMUNITY STRUCTURE

In the Lavaca-Colorado Estuary, stations A and B were almost identical (Fig. 3A). Station F, at the mouth of the river diversion was also similar to A and B. Stations C and E were similar, and both these stations are nearly equidistant from freshwater input and Gulf exchange. Station D, near the pass, was the most different station of all. The pattern elucidated in the PCA was driven by the greater number of species that were found in station D, near the Gulf pass (Table 3). Also, species dominance patterns were different. The dominant bivalves were from the genus *Periploma* at stations C and D, whereas *Mulinia lateralis* (Say, 1822) was dominant at stations A, B, E, and F where there is freshwater influence. Gastropod species were more uniformly distributed throughout the estuary. The dominant gastropods were *Nassarius acutus* (Say, 1822) and *Acteocina canaliculata* (Say, 1826). Bivalves were always dominant over gastropods. Gastropods were most common in Lavaca Bay where they constituted 32% of the population at station A and 49% at B. In contrast, gastropods represented only 24% in C, 14% in D, 16% in E, and 20% in F.

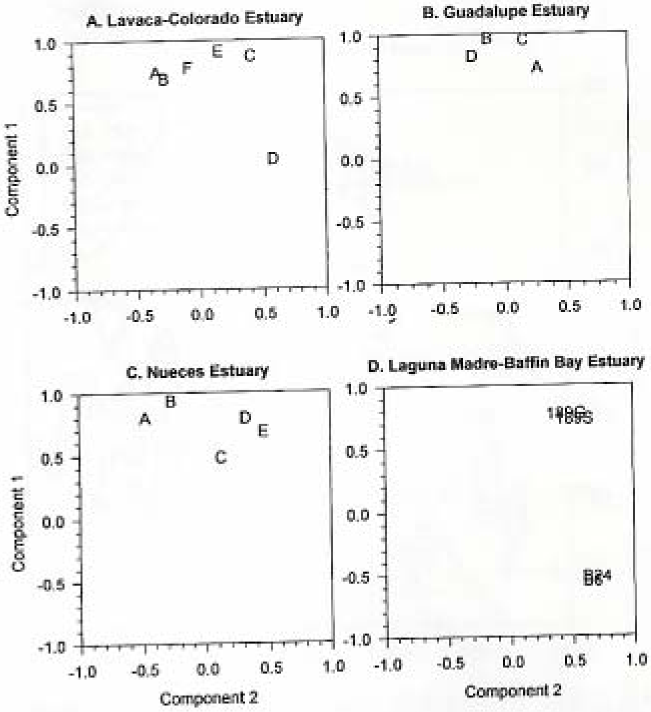

Fig 3. Principal components analysis of molluscan communities at each station over the entire study period within estuaries.

In the Guadalupe Estuary, all of the stations were somewhat alike in terms of community structure (Fig. 3B). There was more of a gradient from stations A to B to C to D in terms of abundance of individual species (Table 3). This was true for the dominant species, *e.g. Texadina sphinctostoma* (Abbott and Ladd, 1953), *Acteocina canaliculata*, and *Mulinia lateralis*. The brackish water species, *Rangia cuneata* (Sowerby, 1831) only occurred in stations A and B. In general, there were more species in the marine end of the estuary where stations C and D are located. However, there were much higher abundances of species in the freshwater end of the estuary where stations A and B are located (Table 3). In spite of these trends, the PCA indicated that there may be more affinity between stations A and C, and stations B and D may be more alike (Fig. 3B). This trend may be explained by the unusual circulation pattern in San Antonio Bay. Freshwater enters the estuary near station A, and travels southwest along the shoreline toward station C. Marine water enters the bay near station D and travels north toward station B. The species community pattern in the PCA is driven by the number of gastropods versus the number of bivalves. Gastropods were most common at station A (80% of the population) and station C (58%). In contrast, gastropods represented only 41% in B and 30% in D.

In the Nueces Estuary, stations A and B in Nueces Bay were almost identical (Fig. 3C). Stations D and E were very similar, and station C was somewhat different from all other stations. Stations D and E are nearest the Aransas Pass in Corpus Christi Bay. Station C is in the upper part of Corpus Christi Bay. The pattern elucidated in the PCA was driven by the greater number of species that were found in stations D and E, near the Gulf pass (Table 3), and some species unique to station C. In stations A and B, the dominant species were the bivalves, *Mulinia lateralis* and *Macoma mitchelli* Dall, 1895. In contrast, at stations D and E, gastropods were always dominant, where they constituted 46% of the population at station D and 33% at E. Gastropods represented only 7% in A and B, and 16% in C. Station C was different from the rest in that the dominant bivalves were from the family Nuculanidae (Table 3).

The Laguna Madre-Baffin Bay system exhibited the most varied molluscan communities within an ecosystem (Fig. 3D). This trend was due to the difference caused by

Table 3. Infaunal molluscan distribution in Texas estuaries. Mean number/m^2 for entire study period (see Table 1) at each station.

	Lavaca-Colorado Estuary						Guadalupe Estuary				Nueces Estuary					Laguna Madre-Baffin Bay			
Class/Order/Family/Species	A	B	C	D	E	F	A	B	C	D	A	B	C	D	E	189G	189S	6	24
Gastropoda																			
Gastropoda (unidentified)	95	95	95	0	0	0	12478	0	0	284	0	0	0	189	95	221	95	0	95
Mesogastropoda																			
Hydrobiidae																			
Texadina spinctostoma (Abbott & Ladd, 1953)	189	189	0	0	0	0	14683	5138	4781	934	0	0	0	0	0	0	0	0	0
Littorinidae																			
Littorina ziczac (Gmelin, 1791)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0
Vitrinellidae																			
Vitrinella floridana Pilsbry & McGinty, 1946	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0
Vitrinellidae (unidentified)	0	0	0	0	0	0	0	0	0	142	0	0	0	662	0	0	0	0	0
Caecidae																			
Caecum johnsoni Winkley, 1908	0	0	165	95	95	0	0	0	95	95	0	0	236	425	95	0	0	0	0
Caecum pulchellum Stimpson, 1851	0	0	0	0	0	95	0	95	0	95	0	0	0	0	0	2518	1395	0	0
Cerithiidae																			
Diastoma varium (Pfeiffer, 1840)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	359	95	0	0
Cerithium lutosum Menke, 1828	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	303	221	0	0
Epitoniidae																			
Epitonium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0	0
Calyptraeidae																			
Crepidula fornicata (Linné, 1758)	0	0	0	284	0	0	0	0	95	95	0	0	95	95	0	265	142	95	0
Neogastropoda																			
Columbellidae																			
Anachis ostreiocola Sowerby, 1882	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	95	0	0	0
Anachis semiplicata Stearns, 1873	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	158	0	0	0
Mitrella lunata (Say, 1826)	0	0	95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nassariidae																			
Nassarius acutus (Say, 1822)	189	158	113	189	189	95	0	0	95	0	0	0	189	95	95	95	0	0	0
Nassarius vibex (Say, 1822)	0	0	0	189	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0
Pyramidelloida																			
Pyramidellidae																			
Boonea impressa (Say, 1822)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0
Eulimastoma teres (Bush, 1885)	142	307	189	0	284	95	95	95	95	142	0	95	0	0	0	0	0	0	0
Eulimastoma sp.	0	0	0	0	189	0	567	95	0	126	95	0	0	236	0	0	0	0	0
Odostomia gibbosa (Bush, 1909)	155	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odostomia sp.	284	189	0	0	0	0	0	0	95	0	0	0	0	0	0	0	0	0	0
Pyramidella crenulata (Holmes, 1859)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	189	95	0	0
Pyrgiscus sp.	0	142	138	95	0	0	0	0	189	165	0	0	189	284	378	340	425	0	0
Sayella crosseana (Dall, 1885)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	189	118	0	0
Cephalaspidea																			
Acteonidae																			
Rictaxis punctostriatus (C. B. Adams, 1840)	0	0	0	0	0	0	0	0	0	0	0	0	0	1135	473	0	0	529	511
Scaphandridae																			
Acteocina canaliculata (Say, 1826)	321	662	95	189	591	284	95	189	189	216	95	236	0	113	0	0	0	95	95

(continued)

Table 3. Continued.

Class/Order/Family/Species	Lavaca-Colorado Estuary						Guadalupe Estuary				Nueces Estuary					Laguna Madre-Baffin Bay			
	A	B	C	D	E	F	A	B	C	D	A	B	C	D	E	189G	189S	6	24
Atyidae																			
Haminoea antillarum (Orbigny, 1841)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5578	1418	0	0
Haminoea succinea (Conrad, 1846)	0	0	0	0	189	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalvia																			
Bivalvia (unidentified)	158	142	118	701	0	95	0	0	189	662	0	0	189	189	0	94	0	0	0
Nuculoida																			
Nuculanidae																			
Nuculana acuta (Conrad, 1832)	95	0	95	252	725	0	0	0	0	95	0	95	851	284	252	0	0	0	0
Nuculana concentrica Say,1824	142	284	221	142	95	0	0	0	0	95	0	0	473	0	0	0	0	0	0
Mytiloida																			
Mytilidae																			
Amygdalum papyrium (Conrad, 1846)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	265	95	0	0
Brachidontes exustus (Linné, 1758)	95	95	0	0	0	95	0	378	0	0	0	0	0	0	0	520	95	0	0
Arcoida																			
Arcidae																			
Anadara ovalis (Bruguière, 1789)	0	0	0	95	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0
Ostreoida																			
Ostreidae																			
Crassostrea virginica (Gmelin, 1791)	0	95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veneroida																			
Kelliidae																			
Aligena texasiana Harry, 1969	0	0	95	95	0	0	0	0	95	246	0	95	0	605	378	0	0	0	0
Montacutidae																			
Mysella planulata (Stimpson, 1851)	378	142	95	95	0	0	0	0	0	643	0	95	331	0	0	0	0	0	0
Crassatellidae																			
Crassinella lunulata (Conrad, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	189	0	0	0	0	0	0
Cardiidae																			
Laevicardium mortoni (Conrad, 1830)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	126	95	0	0
Mactridae																			
Mactra fragilis Gmelin, 1791	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	359	95	0	0
Mulinia lateralis (Say, 1822)	714	544	1429	260	7162	993	6145	6802	2920	1642	1377	2902	697	1721	615	95	315	352	1150
Rangia cuneata (Sowerby, 1831)	0	0	0	0	0	0	578	142	0	0	0	0	0	0	0	0	0	0	0
Solenidae																			
Ensis minor Dall, 1900	350	0	0	0	0	0	0	95	95	473	0	95	0	0	0	0	0	0	0
Solen viridis Say, 1821	0	0	0	0	0	0	0	0	0	0	0	0	0	189	0	0	0	0	0
Tellinidae																			
Macoma brevifrons (Say, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0	0
Macoma mitchelli Dall, 1895	464	228	95	236	189	1059	431	441	244	490	1305	977	95	0	0	0	0	0	0
Macoma tenta (Say, 1834)	0	0	0	95	0	0	0	0	0	95	0	0	189	189	189	0	0	0	0
Tellidora cristata Récluz, 1842	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0
Tellina sp.	378	284	0	95	0	0	0	95	0	95	0	0	425	189	378	189	0	0	0
Tellina tampaensis Conrad, 1866	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	95	0	0
Tellina texana Dall, 1900	0	0	0	95	0	0	0	0	0	0	0	0	0	0	0	95	95	0	0

(continued)

Table 3. Continued.

Class/Order/Family/Species	Lavaca-Colorado Estuary						Guadalupe Estuary				Nueces Estuary					Laguna Madre-Baffin Bay			
	A	B	C	D	E	F	A	B	C	D	A	B	C	D	E	189G	189S	6	24
Semelidae																			
Abra aequalis (Say, 1822)	0	0	0	176	0	0	0	0	0	0	0	0	95	0	189	0	0	0	0
Solecurtidae																			
Tagelus divisus (Spengler, 1794)	0	0	0	0	0	0	0	0	0	0	0	0	0	284	0	0	0	0	0
Tagelus plebeius (Lightfoot, 1786)	433	0	0	0	0	0	0	0	189	189	0	0	284	0	0	0	0	0	0
Veneridae																			
Anomalocardia auberiana (Orbigny, 1842)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	189	662	0	0
Chione cancellata (Linné, 1767)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	993	165	0	0
Mercenaria campechiensis (Gmelin, 1791)	0	0	0	95	0	0	0	0	95	95	0	0	0	95	0	0	0	0	0
Myoida																			
Myidae																			
Paramya subovata (Conrad, 1845)	0	0	0	700	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corbulidae																			
Corbula contracta Say, 1822	0	0	0	819	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hiatellidae																			
Hiatella arctica (Linné, 1767)	0	0	0	536	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyoida																			
Lyonsiidae																			
Lyonsia floridana Conrad, 1849	0	0	95	0	0	0	0	0	95	0	0	189	95	189	0	0	0	0	0
Pandoridae																			
Pandora trilineata Say, 1822	0	95	0	95	0	0	0	0	0	95	0	0	0	0	0	0	0	0	0
Periplomatidae																			
Periploma margaritaceum (Lamarck, 1801)	0	0	425	1182	0	0	0	0	95	0	0	0	0	0	0	0	0	0	0
Periploma orbiculare Guppy, 1878	0	0	378	1179	0	0	0	0	0	315	0	0	268	126	95	0	0	0	0
Scaphopoda																			
Dentaliida																			
Dentaliidae																			
Dentalium texasianum Philippi, 1849	0	0	0	95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

the seagrass habitats of Laguna Madre, versus the open bay habitats characteristic of Baffin Bay. Stations 189G and 189S were identical, and stations 6 and 24 were identical (Fig. 3D). Gastropods were rich in Laguna Madre (13 species in stations 189G and 11 species in 189S), but few in Baffin Bay (3 species each at stations 6 and 24) (Table 3). Only one bivalve species, *Mulinia lateralis*, was ever found in Baffin Bay. In contrast, 11 species were found in station 189G and 9 species were found in station 189S. Because of the concomitant low numbers of individuals found in Baffin Bay, the proportion of each class was similar. Gastropods dominated this ecosystem, 77% at station 189G, 71% at 189S, 67% at 6, and 38% at 24.

Community characteristics varied among the estuaries as well as within the estuaries (Table 4). Salinity generally increased from north to south. The lowest salinity, open-bay station (Guadalupe A) had the highest abundance and biomass indicating high productivity. The only high-salinity station with high abundance and biomass was the seagrass habitat of Laguna Madre (station 189G). The hypersaline environments of Baffin Bay had the lowest abundances and biomasses. Diversity was generally highest near Gulf passes and in the seagrass habitats. Overall, these Texas estuaries had a mean of 14 species of small infaunal mollusks, with a mean abundance of 7,500 individuals/m², and mean biomass of 2.4 g/m².

Table 4. Summary of zoogeographic distributions and estuarine characteristics: mean salinity (psu), number of species, abundance (N/m^2), and biomass (g/m^2) for each station over the entire study period.

Estuary	Station	Salinity	Species	Abundance	Biomass
Lavaca-Colorado	A	15	18	4,700	1.13
	B	19	18	3,800	0.40
	C	24	18	4,000	0.40
	D	29	26	8,100	1.99
	E	22	10	9,700	1.38
	F	17	8	2,800	2.02
Guadalupe	A	7	8	35,000	5.93
	B	11	11	13,600	2.95
	C	15	17	9,700	1.65
	D	16	23	7,400	8.43
Nueces	A	23	4	2,900	1.05
	B	27	9	4,800	2.61
	C	31	8	5,000	0.92
	D	32	22	7,200	0.55
	E	28	15	3,500	0.77
Laguna Madre	189G	38	24	13,000	10.41
	189S	38	20	5,000	1.34
Baffin Bay	6	40	4	1,900	0.25
	24	42	4	1,100	1.00

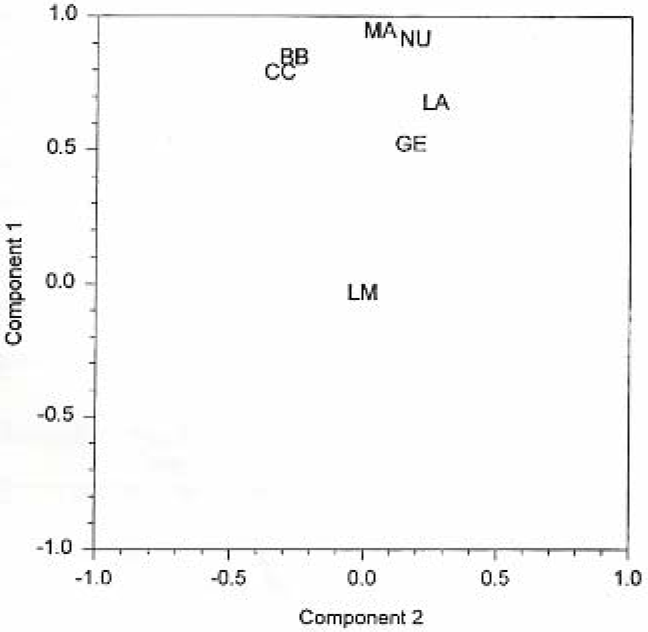

Fig 4. Principal components analysis of molluscan communities in each bay over the entire study period. (BB – Baffin Bay; CC – Corpus Christi Bay; GE – Guadalupe Estuary (San Antonio Bay); LA – Lavaca Bay; LM – Laguna Madre; MA – Matagorda Bay; NU – Nueces Bay).

Each estuary is generally composed of two bays, except for the Guadalupe Estuary (Fig. 1). The seagrass-dominated, hypersaline Laguna Madre was very different from all the open-bay habitats in terms of species composition (Fig. 4). The two secondary bays that receive the most freshwater inflow (Lavaca and San Antonio Bays) were alike and shared a similar space in the PCA diagram (Fig. 4). The restricted freshwater inflow into Nueces Bay caused that community to appear more like a primary bay community than a secondary bay community. The two most-saline bays in south Texas (Corpus Christi and Baffin Bays) were alike. In general, the first PCA axis is separating communities on a gradient from seagrass to fresh to saline habitats. The second PCA axis appears to be separating large open bays from smaller closed bays.

The infaunal molluscan community in Texas estuaries was dominated by the dwarf surf clam, *Mulinia lateralis* (Table 5). *M. lateralis* populations were more abundant in the more freshwater bays of the northern part of the study area. Only in Laguna Madre, which is dominated by seagrass beds, were other species found to dominate. Salinity alone is not the only factor determining mollusk distributions or dominance. Estuarine physiography is also very important. For example, *M. lateralis* was found in Lavaca Bay and Matagorda Bay, but was at highest density in stations C and E, which have moderate inflow influence, and

Table 5. Dominant species in each estuary, with overall mean abundance (N/m²) in parentheses.

Estuary	1st Dominant	2nd Dominant	3rd Dominant
Lavaca-Colorado	*Mulinia lateralis* (1900)	*Macoma mitchelli* (400)	*Acteocina canaliculata* (400)
Guadalupe	*Texadina sphinctostoma* (6400)	*Mulinia lateralis* (4400)	*Macoma mitchelli* (400)
Nueces	*Mulinia lateralis* (150)	*Macoma mitchelli* (50)	*Rictaxis punctostriatus* (300)
Laguna Madre	*Haminoea antillarum* (400)	*Caecum pulchellum* (500)	*Chione cancellata* (600)
Baffin Bay	*Mulinia lateralis* (800)	*Rictaxis punctostriatus* (500)	*Acteocina canaliculata* (100)

moderate mean salinities near 23 psu (Table 3). But, in the higher-salinity Baffin Bay (about 41 psu), it was still the dominant species (Table 3). *M. lateralis* was abundant in the Guadalupe Estuary where salinities ranged from 7-16 psu, but was most abundant in stations A and B where the salinity was low, about 9 psu (Table 3). *M. lateralis* was also equally present in most stations in the Nueces Estuary, where mean salinities ranged from 23 to 32 psu (Table 3). On average, *M. lateralis* was more dense in the secondary bays than in the primary bays from San Antonio Bay south to Baffin Bay. The only exception was in Matagorda Bay, but here it also occurred nearer the freshwater inflow sources, and was rare near the Gulf pass.

There was a great deal of temporal variability with respect to the densities of all these organisms. However, this was most exemplified by *Mulinia lateralis* (Fig. 5). The temporal patterns within estuaries were similar, but of different magnitude. The periods between 1987-1988 and 1992-1993 were good years for *M. lateralis* in the central estuaries (Fig. 5A). This pattern was not as distinct in the southern estuaries (Fig. 5B). The good years corresponded to wet years which followed, or occurred during El Niño events. *M. lateralis* practically disappeared from Baffin Bay during 1990-1992 corresponding to the occurrence of a severe brown-tide bloom. Large-scale climatic events seem to be controlling *M. lateralis* populations.

DISCUSSION

On one hand, there appears to be a typical, open-bay, "Texas molluscan" community. The community is dominated by small bivalves. Typically the small bivalves represent two-thirds of the community. The dominant species are *Mulinia lateralis* and *Macoma mitchelli*. The estuarine-wide pattern is influenced by the patterns near the river mouth, where bivalves can be as high as 90% of the population. The dominance of these clams is important to the entire trophic structure of Texas estuaries, because *M. lateralis* is the predominant food source for black drum, *Pogonias cromis* (Goode, 1884) (fide Martin, 1979).

There are two exceptions to this "generalized Texas community," where gastropods are dominant: San Antonio Bay and Laguna Madre. Laguna Madre is dominated by seagrass-bed habitats, and diversity and standing stocks are generally very high. This is a direct result of the value of the seagrass habitats. San Antonio Bay is unusual in that it is dominated by freshwater inflow. This is due to high turnover rates of water and low rates of marine exchange. It appears that hydrography and physiography are responsible for the different kind of community found in San Antonio Bay.

During the entire study period, except for 1989, there was a continuous brown-tide bloom in Laguna Madre and Baffin Bay (Stockwell *et al.*, 1993). Other brown-tide blooms have had catastrophic effects on bivalves (Shumway, 1990). Effects have ranged from reproductive or recruitment failures (Bricelj *et al.*, 1987; Tracey, 1988), to adverse effects on feeding (Tracey, 1988; Tracey *et al.*, 1988; Bricelj and Kuenstner, 1989), to a toxic effect (Draper *et al.*, 1989; Tracey *et al.*, 1990; Gainey and Shumway, 1991). So, it is possible that the trend reported here is not normal, and could be due to the effects of a brown tide. We know that *Mulinia lateralis* feeds on the organisms that produce brown tide (Montagna *et al.*, 1993), so it is likely that the changes in Baffin Bay are related to an effect on larvae, reproduction, or are completely unrelated to brown tide. If the brown tide has had an effect on bivalves in Laguna Madre, then the conclusion that gastropods dominate in the Laguna is not a generality, but sim-

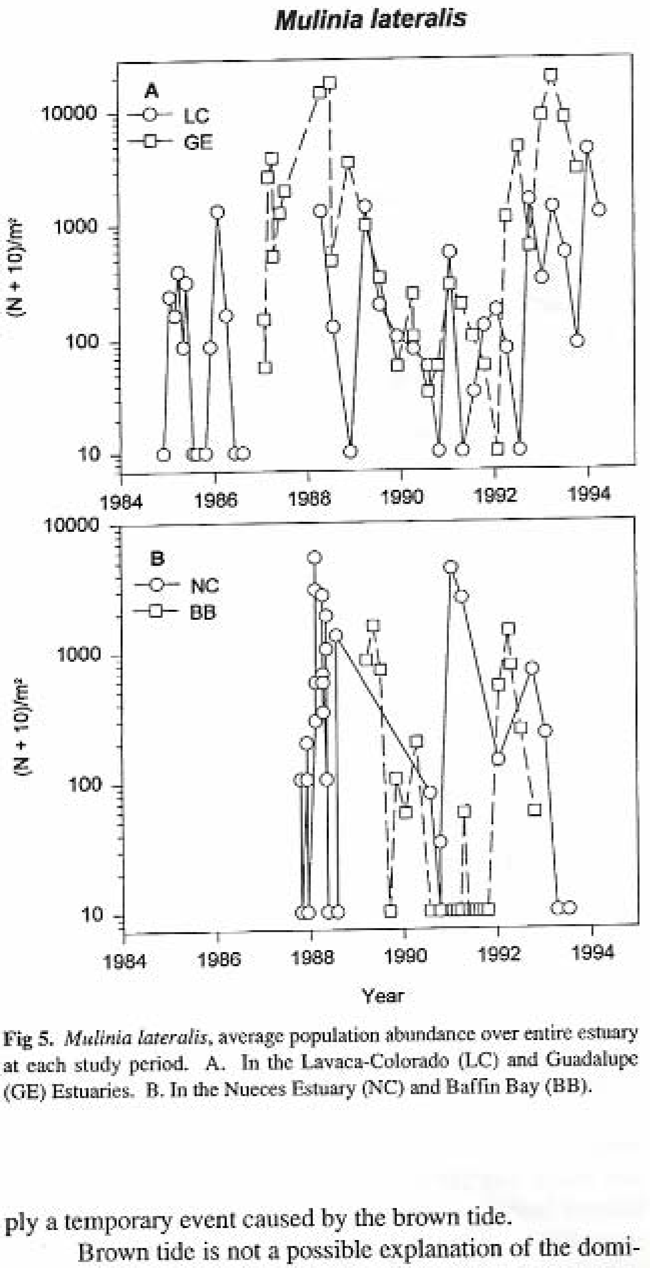

Fig 5. *Mulinia lateralis*, average population abundance over entire estuary at each study period. A. In the Lavaca-Colorado (LC) and Guadalupe (GE) Estuaries. B. In the Nueces Estuary (NC) and Baffin Bay (BB).

ply a temporary event caused by the brown tide.

Brown tide is not a possible explanation of the dominance by gastropods in San Antonio Bay. In fact, San Antonio Bay has a large population of *Mulinia lateralis* (Fig. 5). It is merely that the population of *Texadina sphinctostoma* is enormous at the mouth of the Guadalupe River (Table 3). The unidentified gastropods in these samples are all very small juveniles, and are also likely to be *T. sphinctostoma*. San Antonio Bay is also less like other Texas bays in terms of physiography. The demarcation between the primary and secondary bay is less distinct (Fig. 1), and there is very indirect exchange between the bay and the Gulf of Mexico. In San Antonio Bay most living freshwater species are found in the upper bay and along the western shoreline, being conspicuously absent from the eastern shore (Parker, 1959). The distribution of *Rangia cuneata* in upper San Antonio Bay and along the western shoreline conforms with the dominant freshwater flow pattern (Ladd, 1951). In general, the average pattern in the Guadalupe Estuary is masked by an unusual pattern of freshwater species near the river and the circulation pattern.

Ecological studies over the years have demonstrated the importance of salinity as a factor in affecting the distribution of marine and estuarine organisms. The number of species, but not necessarily the observed total biomass, increases as one proceeds along a salinity gradient from the freshwater side of a large estuary to the open sea (Springer and Woodburn, 1960; Gunter, 1961). This trend is also evident among Texas Mollusca (Table 4). The dominant species found in the current study are *Mulinia lateralis* and *Texadina sphinctostoma* (Table 3). The distribution of these species is strongly linked to long-term environmental conditions, although responses to flood conditions may result in rapid population changes.

Texadina sphinctostoma populations increase following peaks in freshwater inflow (Harper, 1973; Matthews *et al.*, 1974). This is apparently a breeding response caused by a salinity decline (Harper, 1973). *T. sphinctostoma* carries its eggs on the shell and undergoes direct development with the young ready to assume adult existence upon emerging from the egg. *T. sphinctostoma* is commonly reported as one of the most dominant gastropod inhabitants of the river-influenced upper bays of the Texas coast (Ladd, 1951; Ladd *et al.*, 1957; Parker, 1959; Harper, 1973; Matthews *et al.*, 1974; Gilmore *et al.*, 1976; White *et al.*, 1983, 1989; Staff *et al.*, 1985).

Mulinia lateralis is an extremely hardy species, ranging from Prince Edward Island, Canada, to Yucatan, Mexico, and in salinities from 5 to 80 ppt (Parker, 1975). It is an opportunist of adversity because it can colonize rapidly after a disturbance event such as dredging or heavy rain (Flint *et al.*, 1981; Flint and Younk, 1983). It is one of the more abundant mollusks in the low-salinity bay heads of the Gulf coast (Hopkins *et al.*, 1973). In San Antonio Bay, Matthews *et al.* (1974) and Harper (1973) reported *M. lateralis* widely distributed from brackish water to higher salinity as found here. Both reports indicated that the close resemblance of *Rangia cuneata* juveniles and *M. lateralis* may have resulted in numerous misidentifications at the low salinity stations. In Laguna Madre (Alazan Bay) *M. lateralis* was the most abundant and widespread mollusk (Martin, 1979; Cornelius, 1984). *M. lateralis* is widely reported from other bays around the Gulf and Atlantic coasts of the U.S. Spawning was observed in the Tred Avon River, Maryland, and Chesapeake Bay where it was observed to have a continuous period of setting from a single spawning cycle from May through November (Shaw, 1965; Holland *et al.*, 1977). In Alazan Bay, Texas, Cornelius (1984) observed juveniles in all months except December, and Poff (1973) observed year-round spawning in Trinity Bay, Texas. *M. lateralis* has a very short generation time and is capable of successfully spawning at 3 mm in length which is approximately 60 days old (Calabrese, 1969a). Embryo survival and development for *M. lateralis*, as it is with *R. cuneata*, is dependent on certain salinity and temperature ranges. *M. lateralis* developed into normal larvae throughout the salinity range of 15 to 35 ppt and the temperature range of 10 to 30°C (Calabrese, 1969b). This clam is an important food item to bottom feeding organisms, *i.e.* the black drum (Pearson, 1929; Breuer, 1957; Simmons and Breuer, 1962; Martin, 1979) and to the greater and lesser scaup ducks [*Aythya marila nearctica* Stejneger, 1885, and *A. affinis* (Eyton, 1838), respectively] (Cronan, 1957). Large rafts of scaup ducks were observed in upper San Antonio Bay in November 1988 corresponding to high densities of *M. lateralis* (pers. obs.).

Humans have had an enormous impact on coastal ecosystems in general, and Texas is no exception. Recently, intervention has been attempted by State agencies to try and conserve or enhance natural resources. Two projects occurred during the current study: a mandated freshwater release schedule in Nueces Bay, and a diversion of the Colorado River to the east arm of Matagorda Bay. Both projects appear to have had a desirable effect, if this is defined as enhanced molluscan communities. The physical effect of both projects is obvious from the lowered salinity values that have occurred (Fig. 2, Table 4). In the Nueces Estuary, the stations A and B had very high salinities, and no longer exhibit this characteristic. There were generally low abundances and diversity prior to the mandated releases, and there is now a productive community. In the Lavaca-Colorado Estuary, station F is now very much like station A in terms of salinity and species composition. Both projects appear to have had the desired effects. However, there are two caveats. The changes that occurred in the Nueces Estuary coincided with an El Niño event, and therefore may have occurred without the releases. The changes that occurred in the Lavaca-Colorado Estuary are also being mitigated by siltation, which threatens to close the diversion or restrict freshwater inflow. Only after several more years of sampling, to determine the long-term effect, can we be certain that these two projects will have lasting value.

Freshwater inflow has obvious benefits to estuaries. Only Texas estuaries with high freshwater inflow rates support a productive shellfish industry (Table 1). The distribution and abundance of *Mulinia lateralis* demonstrates the importance of inflow and the physical characteristics of estuaries. The variability of salinity patterns is more important than the absolute salinity values. *M. lateralis* occurs most frequently in Baffin Bay, which is hypersaline, and Lavaca Bay and San Antonio Bay, which are both low-salinity regions. However, all three bays are secondary bays. This means that freshets have large impacts on these systems, and salinity values change rapidly. If only absolute values of salinity were important, then these patterns would not exist. It is more likely that recruitment events for *M. lateralis* are initiated by a large change in the salinity value, which predominantly occurs in secondary bays. *M. lateralis* is apparently a good indicator species of freshwater inflow effects.

In the present study, we have concentrated on the effects of physical factors, *e.g.* freshwater inflow, estuarine physiography, and time. Obviously, biological interactions are also occurring. However, we have little information to determine how to separate effects due to physical factors and biological interactions, *e.g.* competition and predation.

There are obviously interactions among three geophysical factors which regulate and control the structure and function of molluscan communities in Texas estuaries. These factors are climate (which regulates rates of freshwater inflow), estuarine physiography (which regulates circulation patterns and the degree of marine exchange), and the presence of specific habitats (particularly seagrass beds). These factors control the landscape of the estuary and this determines both the makeup and productivity of the molluscan community. Climate and physiography interact to control the salinity patterns among and within the estuaries. The salinity patterns are good surrogates for indicating the effects of climate and physiography, but salinity itself is not the controlling factor. It is clear that freshwater inflow is very important in maintaining estuarine productivity. The potential for enhancing marine resources by water management projects appears to be a fruitful endeavor, but this must be confirmed with long-term ecosystem-level research.

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