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BENTHIC-PELAGIC COUPLING IN NORTHERN GULF OF MEXICO ESTUARIES: DO BENTHOS FEED DIRECTLY ON PHYTOPLANKTON?

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ABSTRACT Few of the dominant benthic taxa of the northern Gulf of Mexico feed directly on phytoplankton. Rather, most of them feed on near-bottom seston and detritus. This is in contrast to models for Chesapeake Bay and San Francisco Bay. We found that detritivores represented over 80% of the macrobenthic organisms and over 90% of the biomass in Gulf of Mexico estuaries. The paucity of benthos that consumed phytoplankton led us to hypothesize that macrobenthos in Gulf of Mexico estuaries had less effect on plankton communities than was documented in U.S. east coast and west coast estuaries, where benthic communities consumed much of the water-column production. We provided as evidence gut-contents analyses of dominant taxa, the feeding morphology of suspension feeders (especially clams), and the lack of vertical mixing or strong turbulent flow that is necessary for benthos to remove substantial portions of the phytoplankton.

INTRODUCTION

Recent investigations into estuarine trophic ecology established that benthic organisms in San Francisco Bay (Cloern 1982, Alpine and Cloern 1992) and Chesapeake Bay (Cohen et al. 1984, Gerritsen et al. 1994) may play a major role in maintaining water clarity. Dominant benthos of those estuaries feed directly on phytoplankton (water-column production) and may clear the water of certain planktonic organisms. In contrast, it is widely held that few suspension-feeding benthos of northern Gulf of Mexico estuaries feed directly on phytoplankton; rather, most of them are thought to ingest suspended organic matter (seston) from near the sediment-water interface or detritus on the sediment surface (Darnell 1961, Day et al. 1989, D'Avanzo and Valiela 1990, Gaston et al. 1995).

The purpose of our research was to determine whether dominant benthos of the northern Gulf of Mexico feed directly on phytoplankton. Before we could address the problem we had to answer several questions. Which benthos were numerical dominants? Which benthos were biomass dominants? How did these dominant species feed? Our results allowed us to determine whether trophic models proposed for Chesapeake Bay were applicable to Gulf of Mexico estuaries.

MATERIALS AND METHODS

Sampling and Analyses

Benthic samples were collected from 201 estuarine stations (603 samples) from Anclote Anchorage, Florida to the Rio Grande River, Texas during July - August of 1991 (100 stations) and 1992 (101 different stations) under the auspices of the Environmental Protection Agency (EPA)

Environmental Monitoring and Assessment Program (EMAP). A surface-area based, probabilistic sampling design was used to ensure that all estuaries were equitably sampled and represented (Summers et al. 1992, Engle et al. 1994).

Loran-C was used to locate sampling stations before water-quality parameters were measured and quantitative benthic macroinvertebrate samples were collected (see methods in Heitmuller and Valente 1991, Summers et al. 1992). Three (3) replicate macrobenthic samples were collected with a modified Van Veen grab (413 cm²). Samples were washed on a 500-um screen, transferred to bottles containing 10% buffered formalin and Rose Bengal as a vital stain.

Wet-weight and dry-weight biomass were determined by methods described in Gaston et al. (1996). Biomass values included only soft tissues. Molluscs were weighed without shells, tube-dwelling taxa without tubes, and encrusting taxa were scraped from their hosts.

Organisms were identified to the lowest practical taxon and enumerated. Quality checks of identifications and counts were conducted by senior project taxonomists, and greater than 10% error resulted in reanalysis of samples. Complete descriptions of methods and quality assurance procedures used in this program are available in Heitmuller and Valente (1991) and Summers et al. (1992).

Dominant Species

We used EMAP data and Gaston et al. (1995) for benthic biomass and abundance values in the study area. *Crassostrea virginica* (commercial oysters) biomass values were estimated from Eleuterius (1977), Louisiana Department of Wildlife and Fisheries information (unpublished data), Weston and Gaston (1982), and EMAP data.

Gut-contents Analyses of Fresh Specimens

We collected live specimens of *Rangia cuneata* (common brackish-water clam) in Mississippi Sound at a subtidal site along East Beach Drive in Ocean Springs (Jackson Co., MS) and Back Bay near the old Biloxi Hospital (Harrison Co., MS) during June 1995. Specimens were collected by hand, transported to the laboratory on ice, then dissected for gut-contents analyses. Twenty-eight specimens of various sizes (20mm - 45mm) were dissected. Ingested material was removed from the siphon area (primarily pseudofeces) and foregut. We used compound and scanning-electron microscopes to identify and determine the likely sources of ingested material. Gut contents were compared with dominant organisms in water samples (20-liter containers filled with near-bottom water) taken during *R. cuneata* collections.

Macrobenthic Trophic Group Assignments

Benthic organisms were assigned trophic groups based on feeding behavior and food type. Trophic groups used in this study were surface-deposit feeders (SDF), subsurface-deposit feeders (SSDF), suspension and filter feeders (FF), carnivores (CARN), omnivores (OMNI), and others (XXX) (*sensu* Gaston et al. 1995). Thus, taxa that fed directly on phytoplankton were classified as suspension feeders. Trophic group assignments were based on morphological and behavioral characteristics of estuarine macrobenthos supported by peer-reviewed scientific literature, unpublished observations, and personal expertise of the authors.

Data Analysis

Macrobenthic abundance data from 201 stations were used to estimate relative proportions of each trophic group found in estuaries of the northern Gulf of Mexico. This analysis was completed using data from stations for 1991 and 1992 combined, as well as for each sampling year independently. Densities were mean numbers of individuals (m^{-2}) among all stations sampled. Biomass was calculated as mean biomass (m^{-2}) among all stations.

RESULTS

Suspension feeders composed the largest portion (67.5% of biomass) of the benthos in northern Gulf of Mexico estuaries (Table 1, Figure 1), and suspension-feeding bivalve molluscs had the greatest biomass among the dominants (49.7% of total dry-weight benthic biomass) (Table 2). Two bivalves contributed the most biomass,

Rangia cuneata (19.3% of total biomass; mean biomass, $1.37 g m^{-2}$), and *Crassostrea virginica* (approximately 20% of total biomass; approximately $1.2 g m^{-2}$) (Table 2). *Mulinia lateralis*, an abundant clam in many Gulf of Mexico estuaries, totaled only 0.44% of the biomass. Benthic trophic groups other than suspension feeders, including all deposit feeders, omnivores, and carnivores, totaled only 32.5% of the biomass (Table 1).

Abundance data were based on approximately 70,890 benthic organisms (840 taxa; mean density, 2846.4 organisms m^{-2}) from 201 stations (603 samples). The only species that occurred in abundance and contributed substantially in biomass was *Rangia cuneata* (mean biomass, $1.37 g m^{-2}$; mean density, 35 m^{-2}) (Table 2). The other abundant benthic organisms were small bodied and did not contribute significantly to total biomass as single species: *Mediomastus californiensis*, *Corophium cf. lacustre* (surface deposit-feeding amphipod; mean density, 178 m^{-2}), *Mulinia lateralis*, *Probythinella louisiana*, *Streblospio benedicti*, *Texadina sphinctostoma*, and several species of tubificid oligochaetes (Table 2).

Nearly equal proportions (25 - 30%) of the three categories of detritivores (FF, SDF, and SSDF) accounted for approximately 85% of the macrobenthic fauna in northern Gulf of Mexico estuaries (Figure 1). Carnivores (CARN), especially nemerteans, represented approximately 12% of total macrobenthic abundance, while omnivores (OMNI) and others (XXX) each accounted for less than 4% of total macrobenthic abundance.

Rangia cuneata gut contents included few planktonic organisms. Rather, ingested material was dominated by sand, silt, and clay particles (> 90%), a few benthic diatoms, frustules of dead diatoms, and bits of plant matter (Figure 2). There were many sand grains, much detritus, but few whole organisms. None of the dominant taxa observed in the plankton samples (minute navicular diatoms, centric diatoms, and calanoid copepods) were observed in the ingested material.

DISCUSSION

Benthos that dominated northern Gulf of Mexico estuaries included few large, deep-burrowing suspension feeders that typify large estuaries of the United States east coast (Schaffner et al. 1987, Diaz and Schaffner 1990), a major distinction in trophic status of the two regions (Gaston et al. 1995). Gulf of Mexico estuaries generally lack dense populations of large clams, such as *Mercenaria mercenaria*, perhaps because these estuaries lack the tidal energy required for turbulent flow near the sediment-water interface. Gerritsen et al. (1994) discussed the importance of such energy to the feeding of large bivalves in Chesapeake Bay.

BENTHIC-PELAGIC COUPLING

TABLE 1

Benthic community trophic structure for northern Gulf of Mexico estuaries. Data collected at 201 randomly selected stations (603 samples).

Trophic Group	Biomass (g m ⁻²) (percentage of total)	Mean number of organisms (m ⁻²) (percentage of total)
Suspension Feeders	4.76 (67.5)	712.7 (25.0)
Surface Deposit Feeders	1.14 (16.2)	833.2 (29.3)
Subsurface Deposit Feeders	0.55 (7.8)	782.5 (27.5)
Carnivores	0.53 (7.5)	349.9 (12.3)
Omnivores	0.04 (0.5)	63.2 (2.2)
Other	0.04 (0.5)	104.9 (3.7)
TOTALS	7.06 (100)	2846.4 (100)

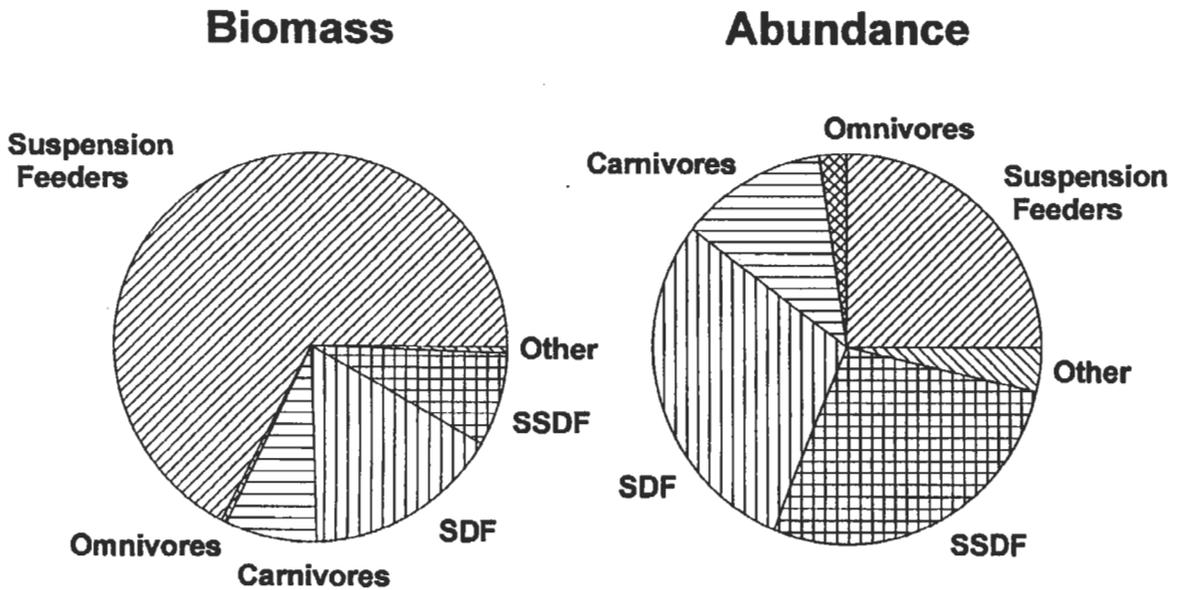


Figure 1. Benthic trophic structure of northern Gulf of Mexico estuaries, by biomass and by abundance. Proportions are percentage values.

TABLE 2

Dominant benthic taxa (1991-1992). Data for 201 randomly selected stations in northern Gulf of Mexico estuaries. Values are dry-weight biomass. Species with low density values were grouped as higher taxa for brevity.

Taxa	Trophic Group	Biomass(g m ⁻²)	Density(m ⁻²)
<i>Rangia cuneata</i> (Bivalvia)	FF	1.37	35
<i>Mulinia lateralis</i> (Bivalvia)	FF	0.03	129
Other Bivalves*	SDF	0.70	<5
	FF	1.42	<9
<i>Probythinella louisiana</i> (Gastropoda)	SDF	< 0.10	109
<i>Texadina sphinctostoma</i> (Gastropoda)	SDF	< 0.10	79
<i>Caecum johnsoni</i> (Gastropoda)	OMNI	< 0.10	47
<i>Mediomastus californiensis</i> (Annelida)	SSDF	< 0.20	386
<i>Streblospio benedicti</i> (Annelida)	SDF/FF	< 0.01	85
<i>Paraprionospio pinnata</i> (Annelida)	SDF/FF	< 0.01	58
<i>Spiochaetopterus costarum</i> (Annelida)	FF	< 0.01	54
Amphipoda	SDF	< 0.10	230
Tubificidae	SSDF	< 0.10	110
Nemertea	CARN	0.05	105

* includes *Crassostrea virginica* (commercial oysters)

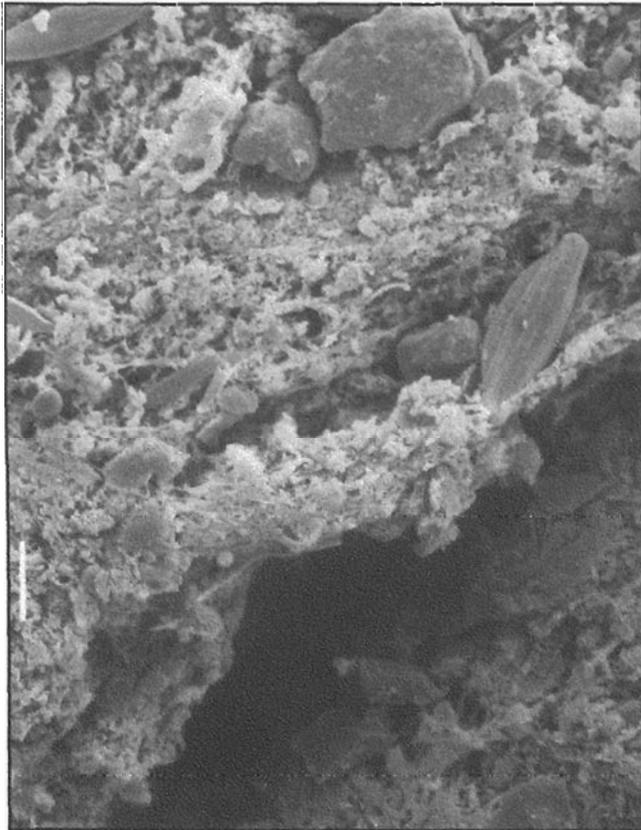


Figure 2. Scanning electron micrograph of *Rangia cuneata* gut contents. *R. cuneata* specimens were collected in Mississippi Sound (Harrison and Jackson Co., MS) during 1995. Particles of sand, silt, clay are evident, as are a few diatoms. Scale = 10 microns.

The only large suspension feeders of Gulf of Mexico estuaries that represented enough biomass to potentially affect phytoplankton production were *Rangia cuneata* and *Crassostrea virginica*. Do these species feed directly on phytoplankton? It appears unlikely that phytoplankton are a major portion of their diets. These two species lack the long siphons that characterize bivalves of other estuaries (e.g., *Mya arenaria*, *Tagelus plebius*), leaving them to feed in the benthic boundary layer (an area of reduced turbulence) near the sediment-water interface (see Muschenheim and Newell 1992). Although benthos can remove substantial amounts of phytoplankton in shallow systems with strong turbulent flow (Newell 1988, Sornin et al. 1990, Sullivan et al. 1991, Ulanowicz and Tuttle 1992), oysters in Gulf of Mexico estuaries feed primarily on near-bottom seston and detritus (Galtsoff 1964, Soniat et al. 1984, Soniat and Ray 1985) and to a lesser extent on phytoplankton (Stickney 1984). Without the regular (tidal) mixing energy to expose oysters to upper water-column phytoplankton, Gulf of Mexico oysters could not have an estuarine-wide effect on phytoplankton biomass.

Rangia cuneata are widely distributed in oligohaline habitats of Gulf of Mexico estuaries, and are known to be nonselective suspension feeders (Olsen 1976, Harrel and McConnell 1995) that depend on the presence of organic

matter for larval settlement and survival (Sundberg and Kennedy 1993). *R. cuneata* gut-contents analyses confirmed that these clams feed on detritus and/or seston of the benthic boundary layer, rather than on phytoplankton directly.

We recognize that chlorophyll a in the water column results from both phytoplankton (water-column production) and resuspended benthic microalgae (Christensen and Kannevorff 1985, Day et al. 1989, Baines and Pace 1991, Graf 1992). Biomass of resuspended benthic diatoms may exceed that of phytoplankton in some estuaries (Baillie and Welsh 1980, de Jonge and van Beusekom 1992), and may provide the major diet of bivalves (Muschenheim and Newell 1992). Similarly, vascular plants (seagrasses and marsh vegetation) provide substantial detritus in some habitats (Heffernan and Gibson 1983, Fry 1984, Shaffer and Sullivan 1988). These observations and our analyses lead us to the conclusion that food ingested by bivalves in Gulf of Mexico estuaries likely originated from a variety of sources, but consisted mostly of seston and detritus. Of course, seston and detritus may include suspended benthic microalgae and suspended or sedimented phytoplankton. Therefore, it is inappropriate to assume that either *R. cuneata* or *C. virginica* feed exclusively on phytoplankton.

Although few of the dominant taxa in northern Gulf of Mexico estuaries feed directly on phytoplankton, certainly some benthos may ingest phytoplankton selectively. These may include taxa capable of feeding above the sediment-water interface in the water column, such as barnacles and bryozoa (attached to structure), benthos attached to seagrass blades, and mussels attached to structure or in shallow water. Yet, these taxa represent a small portion of the biomass in Gulf of Mexico estuaries, and would affect limited areas with little impact overall on the estuary.

We suggest that the models proposed for benthos of Chesapeake Bay, in which bivalves effectively removed over 50% of the annual primary production in some regions (Gerritsen et al. 1994), do not apply to Gulf of Mexico estuaries. We also suggest that additional oyster stocking, as proposed for improved water clarity in Chesapeake Bay (Ulanowicz and Tuttle 1992), would have little effect on overall water clarity in Gulf of Mexico estuaries. Gulf of Mexico estuaries are relatively shallow with small tidal amplitude. As a result, oyster distribution in Gulf of Mexico estuaries is confined to relatively narrow habitats, which limits potential for stocking effects. Furthermore,

water clarity problems in Gulf of Mexico estuaries cannot be solved simply. Turbidity is related to environmental variables such as erosion and sediment transport, bioturbation, enhanced deposition of particulates by feeding of benthos, presence and density of seagrasses, and sediment stabilization by benthic algae or tube-dwelling taxa (Stickney 1984, Day et al. 1989, Diaz and Schaffner 1990). Wind-driven tides regularly exceed lunar tides and may account for many variations in water clarity (Stickney 1984). Human-related factors affect turbidity in Gulf of Mexico estuaries as well, including shrimp trawling (de Groot 1984, Gaston 1990, Hutchings 1990, Riemann and Hoffmann 1991), shell dredging (Tarver 1972, Tarver and Dugas 1973, Francis et al. 1994), and secondary effects of urban runoff, sewage discharge, and other human activities (Stickney 1984).

Our understanding of the fundamental conception of trophic exchange in estuaries changed during the past few years. Scientists once believed that vascular plant biomass was the key to understanding estuarine productivity, but evidence showed that benthic and planktonic algae played a major role in many systems (Haines 1979, Fry 1984). Today there is a temptation to assume that benthic suspension feeders depend entirely on phytoplankton, based on evidence in San Francisco Bay (Cloern 1982, Alpine and Cloern 1992) and Chesapeake Bay (Cohen et al. 1984, Gerritsen et al. 1994). We suggest that such a premise is unfounded in Gulf of Mexico estuaries, where relatively few taxa feed directly on phytoplankton, and detritus-based trophic ecosystems depend primarily on near-bottom seston and detritus.

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