

Gulf Research Reports

Volume 9 | Issue 2

January 1995

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DOI: 10.18785/grr.0902.05

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Recommended Citation

Gaston, G. R., S. S. Brown, C. F. Rakocinski, R. W. Heard and J. Summers. 1995. Trophic Structure of Macrobenthic Communities in Northern Gulf of Mexico Estuaries. *Gulf Research Reports* 9 (2): 111-116.
Retrieved from <http://aquila.usm.edu/gcr/vol9/iss2/5>

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TROPHIC STRUCTURE OF MACROBENTHIC COMMUNITIES IN NORTHERN GULF OF MEXICO ESTUARIES

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ABSTRACT Trophic structure of estuarine benthic communities in the northern Gulf of Mexico was characterized according to the functional roles and geographic distributions of the macrobenthos. Macrobenthic organisms collected during two years of study were assigned to trophic groups to assess the relative utilization of detritus and other resources. Three groups of detritivores (surface-deposit feeders, subsurface-deposit feeders, and filter feeders) were numerically dominant among the benthos, each of which accounted for 25-30% of total abundance across regions. Carnivorous macrobenthos also comprised an appreciable portion (12%), while omnivores (<3%) and other groups (<4%) were poorly represented. Dominance by detritivores is consistent with current concepts regarding the role of macrobenthos in processing detritus of Gulf of Mexico estuaries.

INTRODUCTION

One of the central tenets of estuarine ecology is that organic detritus provides a major food source for estuarine benthic organisms (Darnell 1961; Day et al. 1989; D'Avanzo and Valiela 1990). Darnell (1961) was the first to study the role of detritus in Gulf of Mexico estuaries when he examined gut contents of consumers from Lake Pontchartrain, Louisiana (*vide* Day et al. 1989). Until recently, however, the scarcity of information on feeding biology of macrobenthic organisms prevented comprehensive studies of the trophic ecology (i.e., feeding ecology) of estuaries. Consequently, studies of the macrobenthic trophic ecology of northern Gulf of Mexico estuaries were lacking.

Several regional investigations of trophic structure were conducted recently to examine relationships between macrobenthic trophic structure and environmental gradients in Gulf of Mexico estuaries and nearshore waters (Flint and Kalke 1985, 1986a, 1986b; Gaston and Nasci 1988; Gaston et al. 1988, 1992; Gaston and Young 1992; Gaston and Edds 1994). These studies compared habitats or specific environmental characteristics of estuaries (e.g., salinity effects, contaminant effects), but were of limited geographic scope. By contrast, we compared estuaries on a broad geographical scale from Florida to Texas in order to examine variation in macrobenthic trophic structure and to assess the role of detritus and other resources. We also compared patterns of trophic structure observed in this study with those of previous studies.

METHODS

Sampling Design

Samples were collected from 201 estuarine stations (603 samples) from Anclote Anchorage, Florida to the Rio Grande River, Texas during July - August 1991 (100 stations) and 1992 (101 different stations) under the auspices of the U.S. Environmental Protection Agency Environmental Monitoring and Assessment Program (EMAP). A surface-area based, probabilistic sampling design was used to ensure that all estuarine "resource types" were equitably sampled and represented (Summers et al. 1992; Engle et al. 1994). Estuarine resource types included large estuarine systems (> 260 km²), small estuarine systems (> 2.6 km² but < 260 km²), and large tidal rivers (> 260 km² with aspect ratio > 20).

Sampling and Sample Analyses

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

Benthic samples were rewashed in the laboratory on a 500- μm screen, sorted to taxonomic groups for later identification and enumeration, and placed in labeled vials containing 70% ethanol. Ten percent of all sorted samples were resorted to ensure consistency and quality of work. When resorting revealed more than 10% error in removal of organisms, the previous ten samples completed by that sorter were reanalyzed. Organisms were identified to the lowest practical taxon and enumerated, and voucher specimens were compiled. Quality checks of identifications and counts were conducted by senior project taxonomists, and greater than 10% error resulted in reanalyses of samples. A complete description of quality assurance procedures used in this program is available in Heitmuller and Valente (1991) and Summers et al. (1992).

Macrobenthic Trophic Group Assignments

Each of the macrobenthic organisms identified during the study period was assigned to a trophic group 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 and Nasci 1988). 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. Count data for species that fed by more than one method were evenly divided among the feeding groups assigned to that species (e.g., spionid polychaetes feed both on suspension matter and surface detritus; hence FF/SDF).

Data Analysis

Macrobenthic abundance data from 201 randomly selected base stations were used to estimate relative proportions of each trophic group found in estuaries of the northern Gulf of Mexico (i.e., Louisianian Province). This province-wide analysis was completed using data from randomly selected base stations for 1991 and 1992 combined, as well as for each sampling year independently. In addition to year-to-year comparisons, community structure was compared among four regions of the Louisianian Province. Regional comparisons were based on data from 86 stations (16 in Texas, 13 in Louisiana, 44 in Mississippi-Alabama, 13 in Florida) that represented five estuaries in each region, selected *a priori*. All four regions were sampled each year. We selected only stations that occurred in embayments or lagoons for regional comparisons, which allowed comparisons of similar habitats.

Twenty-eight taxa were considered numerical dominants in this study (i.e., mean density ≥ 22 individuals m^{-2}). Densities were mean numbers of individuals (m^{-2}) among all stations sampled.

Differences in macrobenthic trophic structure were evaluated using a log-likelihood ratio or G-test ($\alpha = 0.05$) employing intrinsic hypotheses (Zar 1984). Null hypotheses tested whether trophic group frequency distribution (trophic structure) was independent of sampling year and region. Distributions within six feeding groups were compared between two years and among four regions (i.e., 2×6 and 4×6 contingency tables). These analyses were completed using the relative abundance of each trophic group weighted for (multiplied by) the number of stations represented. The calculated test statistic was compared to the chi-square distribution, using $(r-1)(c-1)$ degrees of freedom (d.f. = 5 for between years, and 15 for among regions). Finally, in addition to comparisons of trophic structure (G-tests), comparisons of mean total macrobenthic density (m^{-2}) among regions were made using Wilcoxon paired T-tests ($\alpha = 0.05$) based on the ten most abundant taxa in each region.

RESULTS

Approximately 70,890 macrobenthic organisms (840 taxa; mean density, 2846.4 organisms m^{-2}) from 201 stations (603 samples) were collected. These stations were numerically dominated by *Mediomastus californiensis* (subsurface-deposit feeding polychaete; mean density, 386 m^{-2}), *Corophium cf. lacustre* (surface-deposit feeding amphipod; mean density, 178 m^{-2}), *Mulinia lateralis* (filter-feeding bivalve; mean density, 129 m^{-2}), juvenile and unidentifiable tubificid oligochaetes (subsurface-deposit feeders; mean density, 110 m^{-2}), *Probythinella louisiana* (surface-deposit feeding gastropod; mean density, 109 m^{-2}), *Streblospio benedicti* (surface-deposit/filter-feeding polychaete; mean density, 85 m^{-2}), and *Texadina sphinctostoma* (surface-deposit feeding gastropod; mean density, 79 m^{-2}) (Table 1).

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 (Table 2). 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. Results from G-tests indicated that trophic distributions were not different between 1991 and 1992 ($G = 4.1$, critical value = 11.070; do not reject H_0), despite apparent shifts in the relative abundance of SSDF and FF (Table 2).

Significant differences in macrobenthic trophic structure were not found among large estuaries from the four geopolitical regions ($G = 9.4$, critical value = 24.996; do not reject H_0), despite relatively greater numbers of CARN in Louisiana and Florida, and fewer SDF in Louisiana (Table 3). Greater proportional representation by

MACROBENTHIC TROPHIC STRUCTURE OF ESTUARIES

TABLE 1

Numerically dominant macrobenthic taxa collected in Gulf of Mexico estuaries (1991-1992). Data for 201 randomly selected stations (603 samples).

| Taxa | Trophic Group | Mean Density (m ⁻²) |
|-----------------------------------|---------------|---------------------------------|
| <i>Mediomastus californiensis</i> | SSDF | 386 |
| <i>Corophium cf. lacustre</i> | SDF | 178 |
| <i>Mulinia lateralis</i> | FF | 129 |
| unidentified Tubificidae | SSDF | 110 |
| <i>Probythinella louisiana</i> | SDF | 109 |
| <i>Streblospio benedicti</i> | SDF/FF | 85 |
| <i>Texadina sphinctostoma</i> | SDF | 79 |
| <i>Paraprionospio pinnata</i> | SDF/FF | 58 |
| <i>Spiochaetopterus costarum</i> | FF | 54 |
| <i>Caecum johnsoni</i> | OMNI | 47 |
| <i>Myriochele oculata</i> | SSDF | 41 |
| <i>Hobsonia florida</i> | SDF | 40 |
| unidentified Nemertea | CARN | 36 |
| <i>Crassinella lunulata</i> | FF | 35 |
| Nemertea sp. B | CARN | 35 |
| <i>Rangia cuneata</i> | FF | 35 |
| Nemertea sp. A | CARN | 34 |
| <i>Tubificoides heterochaetus</i> | SSDF | 33 |
| <i>Parandalia sp. A</i> | CARN | 32 |
| <i>Ampelisca abdita</i> | FF | 27 |
| <i>Notomastus latericeus</i> | SSDF | 26 |
| <i>Magelona sp. H</i> | SDF | 26 |
| <i>Acteocina canaliculata</i> | CARN | 24 |
| <i>Balanus sp.</i> | FF | 24 |
| <i>Prionospio pygmaea</i> | SDF/FF | 24 |
| unidentified Maldanidae | SSDF | 23 |
| <i>Prionospio perkinsi</i> | SDF/FF | 23 |
| <i>Phoronis muelleri</i> | FF | 23 |
| <i>Petricola pholadiformis</i> | FF | 22 |

TABLE 2

Macrobenthic community trophic structure by year for northern Gulf of Mexico estuaries. Data collected from 201 randomly selected stations (603 samples).

| Trophic Group | Mean number of organisms m ⁻² (proportions of each group) | | | | | |
|---------------|--|--------|--------|--------|--------|--------|
| | 1991 & 1992 | | 1991 | | 1992 | |
| SDF | 833.2 | (29.3) | 724.8 | (29.7) | 943.3 | (28.9) |
| SSDF | 782.5 | (27.5) | 532.5 | (21.9) | 1035.0 | (31.7) |
| FF | 712.7 | (25.0) | 737.7 | (30.3) | 687.9 | (21.1) |
| CARN | 349.9 | (12.3) | 278.3 | (11.4) | 422.8 | (13.0) |
| OMNI | 63.2 | (2.2) | 77.4 | (3.2) | 48.8 | (1.5) |
| OTHER | 104.9 | (3.7) | 86.2 | (3.5) | 123.8 | (3.8) |
| TOTALS | 2846.4 | (100) | 2436.5 | (100) | 3261.6 | (100) |

CARN in Louisiana estuaries was primarily due to high abundance of *Acteocina canaliculata* (Gastropoda), nemerteans, and *Glycinde solitaria* (Polychaeta). Stations in large estuaries of Florida also contained a higher proportion of CARN, including *Acteocina canaliculata*, nemerteans, and the carnivorous polychaetes *Lumbrineris* sp., *Goniadides carolinae*, and *Polygordius* sp. While macrobenthic trophic structure was found to be relatively similar among large estuaries from the four regions, results from Wilcoxon paired T-tests indicated that mean total macrobenthic density differed among regions ($P < 0.003$). Macrobenthos more densely populated estuaries of Mississippi-Alabama (mean density, 3160.5 m⁻²) than estuaries of Texas (mean density, 1990.5 m⁻²), Louisiana (mean density, 1994.8 m⁻²), or Florida (mean density, 2441.2 m⁻²).

DISCUSSION

Benthic macroinvertebrate communities are important functional components of estuarine ecosystems. Macrobenthic organisms alter physical and chemical conditions at the sediment-water interface, promote the decomposition of organic matter, recycle nutrients for photosynthesis, and transfer energy to other food-web components (e.g., Rhoads 1974; Boesch et al. 1976; Diaz and Schaffner 1990; Day et al. 1989). Our use of functional trophic groups to characterize the role of macrobenthos in estuaries incorporates estimates of macrobenthic community structure, and assesses or infers community function. This approach is essential to understanding estuarine ecosystems, because

it provides information about food-resource availability and food-web interactions, and may be useful for assessing differences in ecosystem structure and function over space and time.

We hypothesize that changes in proportions of trophic groups among estuaries are reflective of food allocations. For instance, estuarine habitats with an abundance of suspended food might be expected to be dominated by suspension feeders, but only when the food is limiting and/or it is ingested before reaching the bottom (Gaston and Nasci 1988). Once at the sediment surface it may be consumed by SDF, or if it is in abundance and sedimentation rates exceed consumption rates, it may be buried and consumed by SSDF. Certainly the distribution and structure of benthic macroinvertebrate communities in estuaries is governed by many interacting environmental parameters and anthropogenic factors. Species richness and abundance have been shown to vary along a number of environmental gradients including salinity (e.g., Sanders et al. 1965; Boesch 1971; Boesch 1977; Flint and Kalke 1985; Gaston and Nasci 1988), substrate or sediment type (e.g., Boesch 1973; Flint and Kalke 1985; Llanso 1985; Diaz and Schaffner 1990), and dissolved oxygen concentration (Boesch and Rosenberg 1981; Gaston 1985; Rabalais and Harper 1992). Many contaminants partition to sediments, creating a major sink and potential source for organism exposure that affect benthic distributions. For example, Gaston and Young (1992) found that sediment contaminants altered the macrobenthic trophic structure of estuaries in Louisiana.

TABLE 3

Macrobenthic community trophic structure by region for northern Gulf of Mexico estuaries (1991-1992). Data collected from 86 stations (258 samples) in selected large estuaries from four geopolitical regions.

| Trophic Group | Mean number of organisms m ⁻² (proportions of each group) | | | | | | | |
|---------------|--|--------|---------|--------|------------|--------|---------|--------|
| | TX (16) | | LA (13) | | MS-AL (44) | | FL (13) | |
| SDF | 408.1 | (20.5) | 258.9 | (13.0) | 1103.9 | (34.9) | 597.9 | (24.5) |
| SSDF | 584.1 | (29.4) | 402.3 | (20.2) | 682.5 | (21.6) | 446.4 | (18.3) |
| FF | 646.7 | (32.5) | 723.3 | (36.2) | 643.5 | (20.3) | 430.2 | (17.6) |
| CARN | 229.5 | (11.5) | 578.6 | (29.0) | 457.2 | (14.5) | 603.5 | (24.7) |
| OMNI | 56.0 | (2.8) | 8.1 | (0.4) | 163.3 | (5.2) | 31.7 | (1.3) |
| OTHER | 66.1 | (3.3) | 23.6 | (1.2) | 110.1 | (3.5) | 331.5 | (13.6) |
| TOTALS | 1990.5 | (100) | 1994.8 | (100) | 3160.5 | (100) | 2441.2 | (100) |

The numerical dominance by detritivores (85% of macrobenthic fauna) in this study is indicative of the major role of detritus in northern Gulf of Mexico estuaries. Quantities of detritus are provided to estuaries from several sources, most notably vascular plant and planktonic production (reviewed by Day et al. 1989). The fate and trophic significance of organic detritus to estuaries has been discussed in detail elsewhere (e.g., Darnell 1967; Heard 1982; Day et al. 1989; D'Avanzo and Valiela 1990; Schwinghamer et al. 1991; Kristensen et al. 1992) and will not be reviewed here, except to emphasize the salient points of this study. Understanding densities of macrobenthic organisms supported by the detrital food chain in the study area should facilitate future development of estuarine food webs and energy-flow models, and provide a more accurate assessment of the functional roles of macrobenthos in processing detritus.

The detritivores that numerically dominated estuaries of the northern Gulf of Mexico included few deep-burrowing forms that typify some large estuaries of the United States east coast (Diaz and Schaffner 1990). The SSDF were dominated by *Mediomastus californiensis*, a species of polychaete that inhabits shallow tubes. *M. californiensis* was abundant throughout the study area. There also were dense populations of FF species that inhabited the sediment-water interface, such as bivalves (especially *Mulinia lateralis*). The SDF included a greater diversity of species than the SSDF or FF. Gastropods *Probythinella louisianae* and *Texadina sphinctostoma* and several species of tube-dwelling spionid polychaetes densely populated many estuaries of Louisiana and Texas.

There have been few studies of the macrobenthic trophic structure of Gulf of Mexico estuaries. The numerical dominance by detritivores in this study generally is similar to results from Calcasieu Estuary, Louisiana (>90% detritivores; Gaston and Nasci 1988; Gaston et al. 1988), Corpus Christi Bay, Texas (generally >90%; Flint and Kalke 1985, 1986a, 1986b), and low-salinity nearshore waters off Cameron, Louisiana (an offshore extension of the Calcasieu Estuary; Gaston 1985; Gaston et al. 1985; Gaston and Edds 1994). We found higher proportions of CARN in the present characterization of all northern Gulf of Mexico estuaries than were reported for either Calcasieu Estuary or Corpus Christi Bay, perhaps reflective of the fine sediments in the latter two estuaries. Generally, greater proportions of CARN occur in sandy habitats. The ratio of carnivorous macrobenthos (i.e., infaunal predators) may be as high as 0.25 in sand or as low as 0.12 in mud (Ambrose 1984), but may vary widely depending on the predatory species that dominate each habitat. Furthermore, standing crops of CARN may vary as a function of production rates of primary consumers.

Thus, even though the ratios of trophic groups may be similar among regions, species that play those roles, and their functional behavior may vary. For instance, several species of nemerteans (CARN) and the polychaete *Sigambra tentaculata* (CARN) dominated most fine-sediment habitats in Louisiana, goniadid polychaetes such as *Glycinde solitaria* (CARN) dominated sandy mud throughout the study area, and a variety of predatory macrobenthos, especially the annelid *Polygordius* spp. (CARN), dominated sandy habitats in Florida and Texas. Each of those species plays a particular role as a CARN in the macrobenthic community, almost certainly selects and ingests specific foods, and attains its food in a unique manner. The value of using trophic groups to study macrobenthos is that trophic analyses allow characterization of a habitat by inclusion of all taxa, and results in establishment of a broad-scale model of macrobenthic resource allocation. However, the inferences that can be drawn from such a study are only as strong as the information on those species that compose each trophic group. Particular functions, population variations, and feeding of species in each region must now be analyzed before details on energy transfer at smaller scales can be interpreted. Such studies will allow researchers to establish the source and fate of energy resources of a given estuary to help interpret and test our functional model. Data of this study demonstrated the general distributions and densities of each trophic group, assessed the unique trophic characteristics of estuarine regions, and gave insight into the numerically dominant species involved.

One of the major advantages of the probability-based sampling design used for this study was the application of the data to broad-scale characterizations of estuaries in the Gulf of Mexico. These characterizations can be used to assess the condition of estuarine resources in the study area (Summers et al. 1992) and provide testable hypotheses concerning many aspects of estuarine function. This study provided a baseline for future examination of specific relationships between macrobenthic trophic structure and environmental or contaminant variables of Gulf of Mexico estuaries (see Engle et al. 1994; Brown et al. Ms.).

ACKNOWLEDGMENTS

The authors gratefully acknowledge the help of personnel at the University of Mississippi, especially A. McAllister, R. Woods, T. Randall, and C. Lehner. We also thank S. LeCroy, D. Hard, and J. McLelland at the Gulf Coast Research Laboratory (GCRL), and personnel at the Gulf Breeze EPA Laboratory, especially J. Macauley and V. Engle. This project was funded under a Cooperative Agreement between EPA and GCRL (CR818218-01) and a subcontract from GCRL to the University of Mississippi.

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