

BENTHIC COMMUNITIES IN THE NORTHERN
GULF OF MEXICO HYPOXIC AREA:
POTENTIAL PREY FOR DEMERSAL FISH

A Thesis

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ABSTRACT

Bottom-water hypoxia ($\leq 2 \text{ mg O}_2 \text{ l}^{-1}$) usually occurs on an annual basis on the Louisiana/Texas continental shelf from mid-May through mid-September over a large area (up to 20,000 km² in mid-summer). The effects of hypoxia on the benthic infauna (potential prey) for demersal fish were examined, because changes in optimal diet can lead to negative impacts on growth and reproduction. Benthic samples were taken in three areas (inshore and offshore out of hypoxia and in the hypoxic area) during August 2003. Samples were also taken monthly from September 2003 to October 2004 at a fixed station (C6B) where summer hypoxia occurs consistently. The mean abundance of the benthic infauna in the three summer areas were not significantly different indicating similar prey abundances found in the study area. Diverse infaunal communities exist offshore of the hypoxic zone with similar species composition compared to the inshore but different compared to the hypoxic area. An abundance of benthos at the surface was not found at the summer 2003 hypoxic stations; therefore there was not an abundance of available prey at the surface. However, benthos migrated toward the surface at station C6B in June and July 2004 during hypoxia, providing an increase of prey at the surface compared to other months. During the spring months, the infaunal community was more diverse and abundant compared to the post hypoxic months (August, September, and October), which suggests fewer and less diverse potential prey in the fall for demersal predators. The most abundant prey items for demersal fish in the study area were polychaetes and secondarily molluscs. The benthic community abundances during the summer 2003 and 2004 were not expected and may be due to the storm events in summer 2003 and shorter duration of hypoxia in summer 2004.

INTRODUCTION

Oxygen depletion, or hypoxia, occurs worldwide in marine systems such as oxygen minimum zones, fjords, continental margins with upwelling systems, and in some coastal waters (Turner et al. 1987, Kamykowski & Zentara 1990). Hypoxia is commonly found on stratified continental shelves in shallow depths where carbon flux from high primary production falls to the seafloor and contributes to the organic-rich and reducing state of the sediment (Tyson & Pearson 1991). Coastal hypoxia resulting from anthropogenic eutrophication is occurring more frequently and is more severe than historically (Diaz & Rosenberg 1995). The severity of hypoxia and number of hypoxic areas are increasing in coastal waters that are stratified and receive inputs from watersheds with high nutrient loading (Rabalais 2002).

Coastal systems with hypoxia differ with regard to periodicity, severity and frequency of events (Diaz et al. 2004). Systems experience periodic (e.g., York River, Virginia), seasonal (e.g., German Bight, North Sea) or persistent (e.g., central Baltic Sea) hypoxia. The severity of hypoxia can be characterized as moderate (e.g., Seto Inland Sea, Japan) to severe (e.g., Long Island Sound, New York) (Diaz 2001). Fauna die in many of these systems or have limited or slow recovery or both (e.g., Kattegat, Sweden-Denmark). Fisheries may also be affected in ecosystems with hypoxia (Diaz 2001). The duration and severity of hypoxia is influenced by mixing processes such as winds, tides, currents and cooling of the surface waters, all of which promote destruction of the stratified layer and reoxygenation of the bottom water (Boesch and Rabalais 1991).

Severe seasonal hypoxia occurs on an annual basis in the northern Gulf of Mexico, west of the Mississippi River along the Louisiana coast and onto the northeastern coast of Texas (Figure 1). The commonly used definition of hypoxia for this area is dissolved oxygen ≤ 2 mg l⁻¹ based

on lack of catch in bottom trawls below this level (Renaud 1986, Rabalais et al. 1991). The water column is stratified through much of the year and persistently stratified from April – September. Nutrient loading from the Mississippi River promotes high primary productivity, which ultimately leads to high organic loading onto the seabed. Aerobic bacteria decompose the organic material, resulting in oxygen depleted below the pycnocline. The hypoxic area on the northwest Gulf of Mexico continental shelf is currently the world’s second largest coastal hypoxic area, with a bottom-water aerial coverage up to 20,000 km² (Rabalais et al. 2002a). Below the pycnocline, the water becomes and remains hypoxic for much of the summer with little or no exchange of oxygenated water from the surface. The inshore-offshore extent of bottom-water hypoxia is related to upwelling and downwelling favorable oceanographic regimes (Rabalais et al. 1994). Wind and waves produced by tropical cyclones during the summer will cause the water column to be mixed and allow the bottom water to be reoxygenated. The increased frequency of storms in the winter continues to mix the water column on the Louisiana continental shelf with hypoxia seldom occurring then but reforming in the spring.

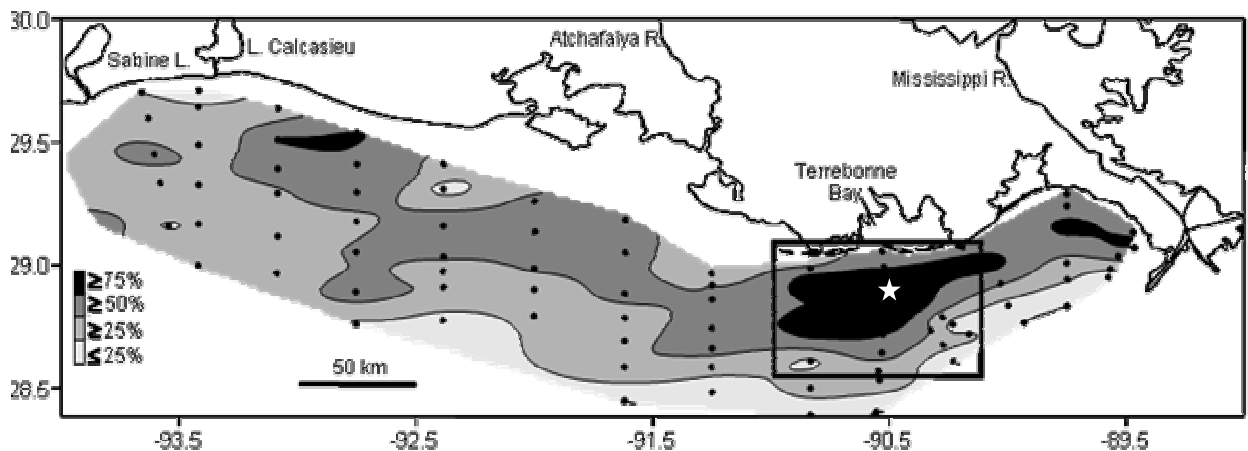


Figure 1. Mid-summer bottom-water hypoxia frequency of occurrence distribution (dissolved oxygen $\leq 2 \text{ mg l}^{-1}$) over the 60- to 80-station grid from 1985-2002 (modified from Rabalais et al. 2002b). The box represents the study area for this project. The star is station C6B.

Benthic infauna are an integral part of coastal ecosystems. They serve as prey, bioturbate the sediment allowing oxygen to penetrate to deeper depths, and form a component of the biogeochemical cycling of material in the sediments (Aller 1988, Solan et al. 2004). Benthic infauna are directly affected by hypoxia because they cannot move out of the low oxygen area, unlike demersal fish and shrimp. The survivorship of infauna is reduced in hypoxic environments because of intolerance to low oxygen and/or hydrogen sulfide (Theede et al. 1969, Burnett & Stickle 2001).

Infaunal community abundance, species richness, and biomass decline during and after hypoxia. The spring infaunal densities declined an order of magnitude on the inner Texas and Louisiana continental shelves following hypoxia (Harper et al. 1981, Gaston 1985, Rabalais et al. 2001a). Spring species richness, likewise, declined by a factor of four in these same studies. Similar trends were found in coastal waters of Sweden (Baden et al. 1990, Rosenberg & Loo 1988). A post-hypoxic community is usually dominated by r-selected species (low biomass, short-lived, high reproductive rate) like polychaetes, especially spionids (Harper et al. 1981, Gaston 1985, Niermann et al. 1990, Rabalais et al. 2001a).

The northern Gulf of Mexico is a highly productive coastal area that supports large yields of fish and shellfish for commercial and recreational fishers. Economically, the fishery in the northern Gulf of Mexico is important, producing about 600 million dollars in annual revenue (Chesney & Baltz 2001). There is disagreement as to whether the shrimp and recreational fishery economies of the northern Gulf of Mexico region are affected by hypoxia (Downing et al. 1999, Chesney & Baltz 2001, Diaz 2001, Zimmerman & Nance 2001). According to Diaz (2001), the Gulf of Mexico is the only hypoxic area comparable to the Baltic Sea or the Black Sea that has not yet suffered declines in fishery production. Fish species with life history

characteristics, such as demersal foraging, demersal spawning and low fecundity, and the fish that have nursery grounds subject to summer hypoxia may be the most impacted (Chesney & Baltz 2001). This includes Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and brown and white shrimp (*Farfantepenaeus aztecus*, *Litopenaeus setiferus*).

Demersal predators are affected by hypoxia by losing essential habitat for feeding, reproduction and protection from predators (Breitburg 2002). In the northern Gulf of Mexico, mobile organisms, such as demersal fish and shrimp leave the hypoxic area, either moving vertically up into the water column or horizontally into oxygenated waters (Craig et al. 2001, Rabalais et al. 2001b, Stanley & Wilson 2004, Craig & Crowder 2005). An increase in competition over food and space may result when demersal predators crowd together to avoid low oxygen (Eby & Crowder 2002). Also, the oxygenated areas that fish move into can be less suitable for growth and reproduction. In North Carolina reduction of available prey resulted in lower growth and production rates of juvenile Atlantic croaker (Eby et al. 2005). Change in available prey (Eby et al. 2005) and suboptimal temperatures (Craig & Crowder 2005) could impact fishery production. In areas of low oxygen the overall abundance and diversity of demersal predators decline (Renaud 1986, Howell & Simpson 1994).

Feeding behaviors of demersal fish change as a result of hypoxia. The common prey items for Atlantic croaker in northern Gulf of Mexico non-hypoxic offshore areas were primarily crustaceans but annelids and molluscs frequently occurred (Overstreet & Heard 1978). Both spot and Atlantic croaker in Texas preyed upon Arthropoda (> 60%), and Annelida (> 20%) (Matlock & Garcia 1983). Young Atlantic croaker also consumed more polychaetes than the adults who preferred larger mobile benthos like crustaceans (Sheridan et al. 1984). Shifts in diet composition from fewer crustaceans and molluscs to more hypoxia tolerant polychaetes and

anemones were found in benthic fish (Pihl et al. 1992, Pihl 1994). More severe hypoxia and the volume of overlying hypoxic waters may reduce the available prey or limit access of demersal fish to the area, both of which result in less prey available to demersal predators. Also, in post-hypoxic conditions the number of benthos do not return to the pre-hypoxic levels but decrease as fall recruitment of meroplankton is limited by reduced fall primary production or as predation pressure increases (Rabalais et al. 2001a).

Hypoxia influences the distribution of benthos in the sediment. During severe hypoxic conditions, benthos will migrate to the sediment surface to reach better-oxygenated sediment, and sometimes swim up into the overlying water (Rabalais & Turner 2001), to avoid toxic levels of hydrogen sulfide. In severe hypoxic conditions, bivalves extend their siphons into the water column to reach oxygenated water (Jorgensen 1980). In worst case scenarios, large numbers of macrobenthos emerge from the sediment so that their abundances in bottom trawls exceed the fish biomass (Baden et al. 1990). The emergence of stressed benthic organisms at the sediment surface results in an increased availability of benthos for demersal predators (Jorgensen 1980) since foraging occurs in the upper 0.5 cm of the sediment (Billheimer & Coull 1988).

The potential location of benthos with depth and bioturbation activity can be characterized by beryllium-7 (^7Be). Vertical distributions of short-lived particle-reactive radioisotopes such as ^7Be characterize the intensity and depth of bioturbation and potential location of macroinfauna with depth in the sediments. The cosmogenic radioisotope ^7Be is produced in the atmosphere and transferred to land by precipitation and dry deposition (Sommerfield et al. 1999). This radioisotope binds to fine sediment particles and is transported by major river systems, such as the Mississippi River, and transported to coastal areas (Baskaran et al. 1997). Beryllium-7 is a useful tool for bioturbation measurements in sediments because of its short half-life of 53 d and

because it can be readily and directly detected using low energy gamma spectrometers that measure its primary peak energy at 477 keV. Beryllium-7 penetrates to deeper depths by biological reworking of the sediment. Polychaetes belonging to the families Orbiniidae, Capitellidae and Maldinidae are head-down deposit feeders that bioturbate the sediment (Rice 1986, Pearson 2001). Other infaunal organisms, such as ophiuroids and shrimp, bioturbate the sediment as well. In addition, physical reworking of the sediment, such as downward transport due to deposition of fresh sediment (Sommerfield et al. 1999) and hurricanes (Wiberg 2000, Bentley et al. 2002), facilitate ^7Be penetration to deeper depths. If these biological and physical processes were not occurring, ^7Be would be found at the sediment surface until it becomes decayed within 53 d.

The area of frequent hypoxia in the northern Gulf of Mexico is well documented (Figure 1). Long-term data from station C6B (see Figure 1) indicate patterns of persistent and severe oxygen conditions in late spring through late summer (Rabalais et al. 2001a). Rabalais & Harper (1992) and Rabalais et al. (2001a, 2001b) report that summer hypoxia at station C6B lasts approximately three months. However, the duration and severity of hypoxia is variable due to Mississippi River nutrient loads, subsequent surface production, intensity of stratification related to Mississippi River discharges, and physical mixing of the water column from storms or thermal turnover. Historical studies of macroinfauna at station C6B under conditions of prolonged bottom-water hypoxia (reviewed by Rabalais et al. 2001a) provide data for further comparative studies. The area surrounding station C6B is also frequently focused on for studies of demersal fish and shrimp (Craig & Crowder 2005).

There are limited studies in the northern Gulf of Mexico concerning benthic communities outside of the area of frequent hypoxia. Likewise, how reduced or stressed benthos may affect

food availability and feeding for demersal predators over a large area of hypoxia is not known (Chesney & Baltz 2001). The main objective of this study was to determine the benthic community composition within and outside of the area of hypoxia in order to understand how the available prey for demersal fish was affected by low oxygen. A second objective was to examine the seasonality of potential prey in the area of frequent hypoxia. The questions I am asking are (1) What are the available prey within and outside of the area of hypoxia? (2) What are the seasonally available prey at station C6B? (3) Does hypoxia affect the vertical distribution of macroinfauna in the sediments and thus the availability of prey? and (4) Do seasonal beryllium-7 penetration depths reflect the vertical distribution of macroinfauna as an indicator of available prey?

METHODS

Benthic infauna were sampled over a broad area of hypoxia off the central coast of Louisiana in the summer of 2003 and at a single station over an annual cycle beginning in late summer of 2003. To determine the available prey in and outside of hypoxia, fifteen stations were sampled during the first two weeks of August 2003. The stations were divided into three areas, within hypoxia (2, 16, 25, 43, 58), inshore of hypoxia (1, 26, 27, 32) and offshore of hypoxia (37, 38, 42, 48, 49, 65). Bottom-water oxygen concentrations were obtained by a conductivity/temperature/depth (CTD) 911-plus meter with an attached SBE-43 oxygen transducer sensor calibrated against Winkler titrations (Mettler DL21 titrator). Except stations 1 and 2, a Hydrolab Surveyor 3 was deployed and calibrated according to specification and cross-checked with Winkler titrations (Mettler DL21 titrator).

A 12.2 m long mongoose bottom trawl (with 1.2 x 2.4 m doors) was towed for approximately 20 min to collect Atlantic croaker at all the summer stations except 1 and 2. If Atlantic croaker were caught in the trawl, then the fish stomachs were removed and fixed with 10% formaldehyde solution and later stored in 70% ethanol solution. The stomach content analysis was performed by J.K. Craig et al. at Duke Marine Laboratory. Box cores for macroinfauna were collected at the end location of each trawl. Two benthic stations (1 and 2) were sampled after the primary trawling/coring cruise from a smaller research vessel, due to the original ship being damaged in a collision that abruptly ended the cruise.

Monthly macroinfaunal samples were also taken from September 2003 to October 2004 at station C6B, located in 20 m water depth off Terrebonne Bay, Louisiana (28°52.10' N and 90°28.00' W). Bottom-water dissolved oxygen was measured with a Hydrolab Surveyor 3. Bottom-water oxygen measurements were also recorded continuously at 15 min intervals from

May 2003 to September 2004 with monthly exchanges of oxygen meters for maintenance, calibration, and cross-check with Winkler dissolved oxygen titrations. An oxygen meter (YSI 6600) with a precision of $\pm 0.2 \text{ mg l}^{-1}$ was deployed within 1 m from the seafloor on a free-standing moored buoy attached to an oil platform near station C6B. The C6B meter (YSI 6600) was removed on February 16, 2004 and the new meter (YSI 6600 EDS) installed on February 17, 2004 at C6C (28°52.12' N and 90°29.42' W). The new meter was attached to the leg of an oil platform at a similar depth (19 m). The near surface oxygen meter at C6B (in 9 m depth) was also moved to station C6C but placed at 2.4 m. Comparisons of CTD data and oxygen profiles over the year prior to moving the meters indicated that the two stations (~ 6 km apart) were similar in stratification and oxygen conditions. It was inappropriate to move the box coring location, because of differences in sediments related to the C6C platforms and the effects of petroleum production at station C6C. Station C6B was located near a non-production platform at a distance 100 m east from the structure to avoid platform-related effects (Rabalais et al. 1993).

Three GOMEX box cores (0.5 m high, 0.3 m long, 0.3 m wide, and surface area 0.09 m^2) were taken to sample benthic organisms (Boland & Rowe 1991). Smaller samples were taken from the box cores when the surface sediments were intact. A 0.02 m^2 standard Ekman grab was used to sample the macroinfauna. Vertical cores (10 cm long, 8 cm diameter) were sliced at 1 cm increments in order to determine the vertical distribution of infauna and ^7Be penetration. Infauna were separated from the sediment with a 0.5 mm sieve, fixed in 10% formalin solution, stained with vital Rose Bengal and transferred to 70% ethanol solution for storage. The benthic infauna were enumerated and identified to the lowest practical taxonomic level.

Sediment grain size and total organic carbon (TOC) samples were collected from approximately the top 5 cm of sediment with a 50 cm^3 syringe. Percent total organic carbon

($\pm 0.02\%$) was determined by drying and grinding the sediment, acidifying to remove calcium carbonates, and using a Perkin Elmer CHN Model 2400 elemental analyzer (Hedges & Stern 1984). Sediment grain size fractionation (± 0.0001 g) was determined by removing the organics with 3.5% hydrogen peroxide and dispersing the sediment with sodium hexametaphosphate ($2.55 \text{ g l}^{-1} \text{ H}_2\text{O}$) over night. The wet sediment was then passed through 1.0 mm, 500 μm , and 63 μm stacked sieves to obtain the very coarse sand, coarse sand, and medium, fine, and very fine sand, respectively, for total sand. The sediment that passed through all the sand sized sieves were divided into silt and clay fractions by timed gravimetric extraction to obtain the mud (silt + clay) percentage (Folk 1974). The sliced sections for the radioisotopic measurements were dried, ground, and sealed in Petri dishes and analyzed for ^7Be radioisotopes within 30 d using a Canberra low-energy gamma spectrometer for a 24 h period (Sommerfield et al. 1999).

The macroinfauna data were analyzed by using Statistical Analysis Software (SAS) version 9.1 (SAS Institute Inc. 2003). A nested two-way analysis of variance (ANOVA) test with the 'area' as a fixed factor and the 'stations' a nested factor in the 'area' was used. The nested ANOVA was performed by using the proc mixed statement to determine significant differences at an alpha level of 0.05 among the summer abundance and species richness values. *A-priori* contrasts were used to test pair-wise station area differences. Summer abundance data were $\log(y+1)$ transformed to meet assumptions of normality. A one-way ANOVA, was used to determine significant differences at an alpha level of 0.05 among the abundance and species richness values of the monthly samples. A post-hoc ANOVA test, Duncan's multiple range, was used to test monthly group-wise differences. To examine the similarity of the community composition among the station areas and months, Plymouth Routines in Multivariate Ecological Research (PRIMER) version 5.0 (Clarke & Warwick 2001) was used. Summer data of all

organisms in a sample were standardized and $\log(y+1)$ transformed (to minimize the effect of dominant species) in order to calculate the Bray-Curtis similarity index needed for the multidimensional scaling (MDS) plots and cluster dendrograms. For the annual cycle, species and numerical data of all organisms were standardized to develop the Bray-Curtis similarity index for the MDS plots and cluster dendrograms. To determine if the community composition was different among the three summer areas, an analysis of similarity (ANOSIM) was performed.

RESULTS

2003 Summer Survey

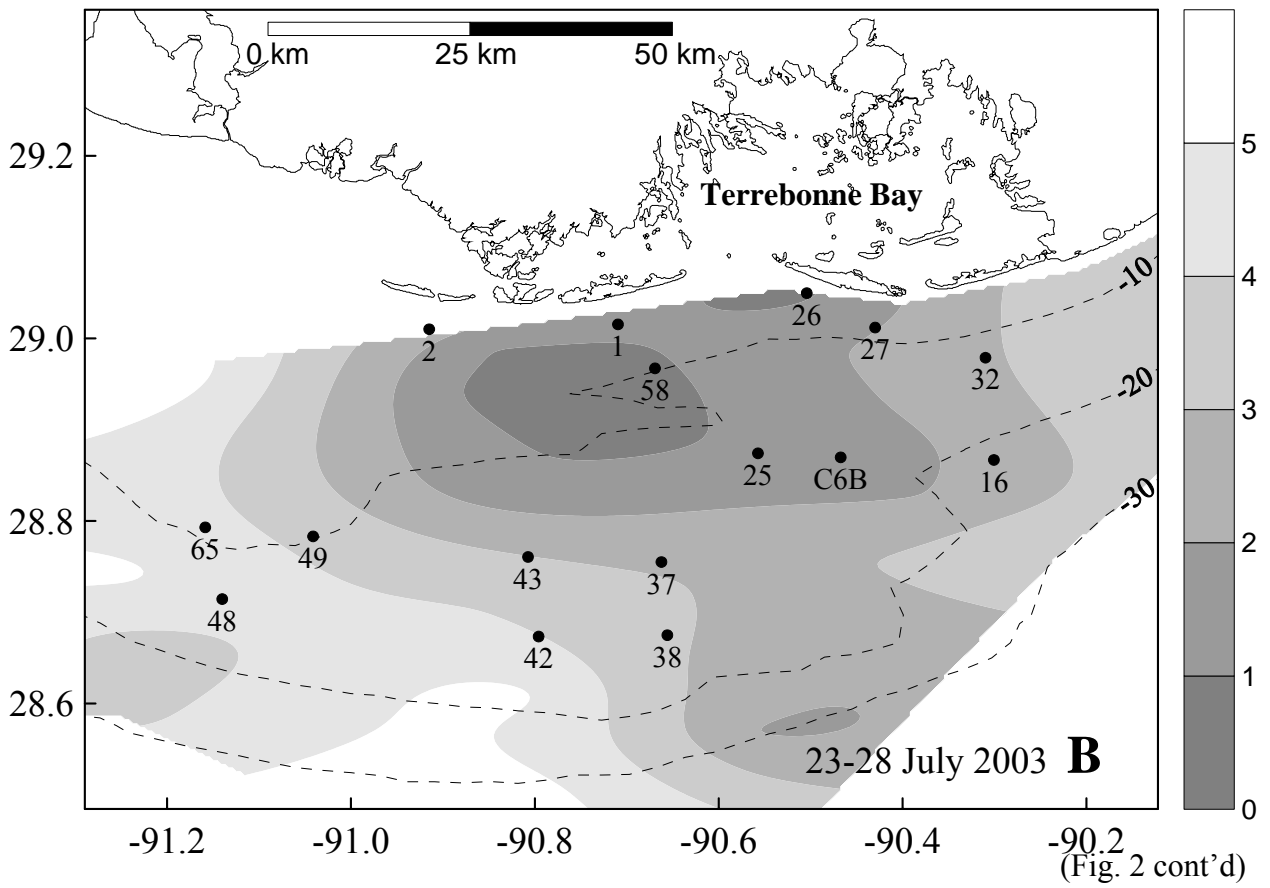
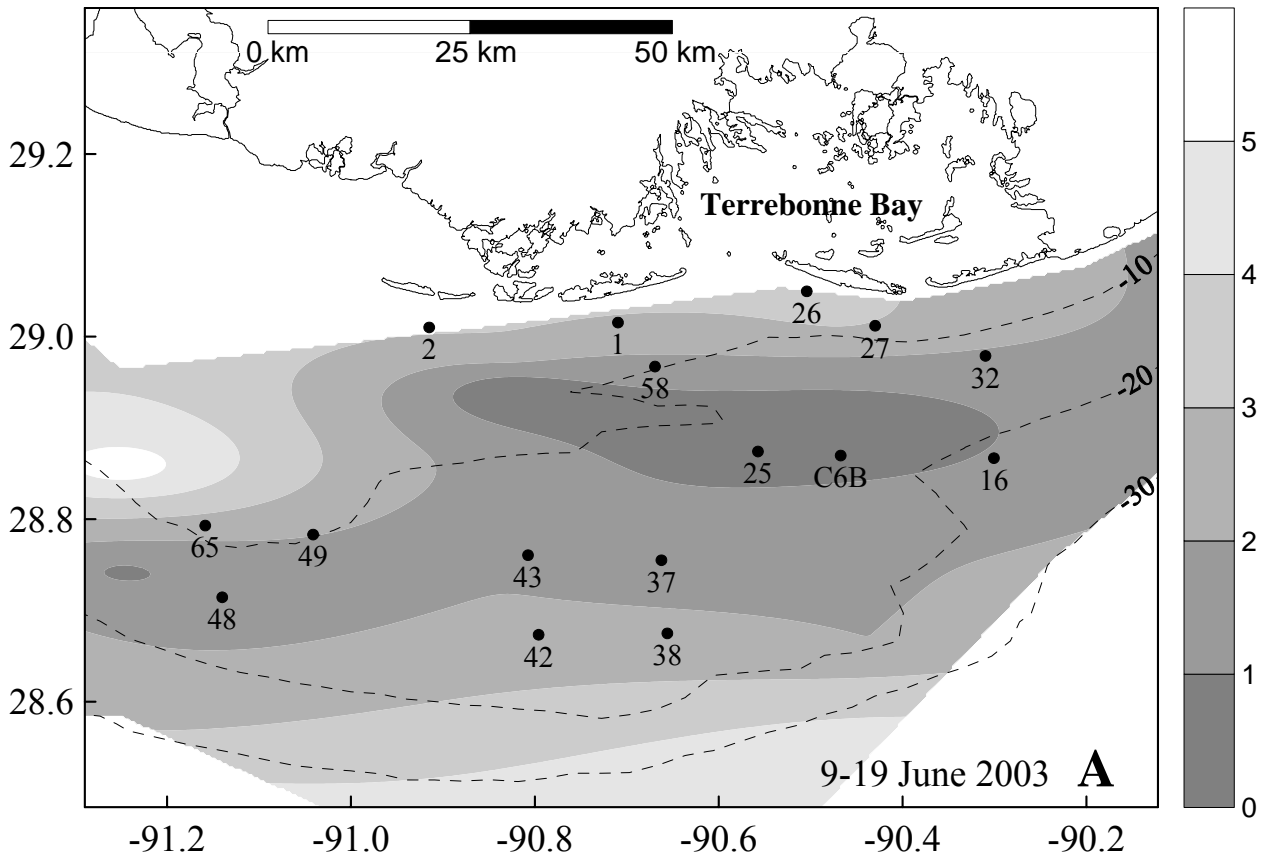
Hypoxic bottom-water covered a large portion of the study area in June (Figure 2A) but was disrupted by a series of tropical storms as illustrated by the dissolved oxygen distribution in late July (Figure 2B). In early August the area of hypoxia became larger (Figure 2C). In order to gain some understanding of oxygen conditions prior to the trawl and benthic sampling, the results from several cruises were mapped (Figure 2A,B,C) along with the long term frequency of hypoxia on the shelf (Figure 2D).

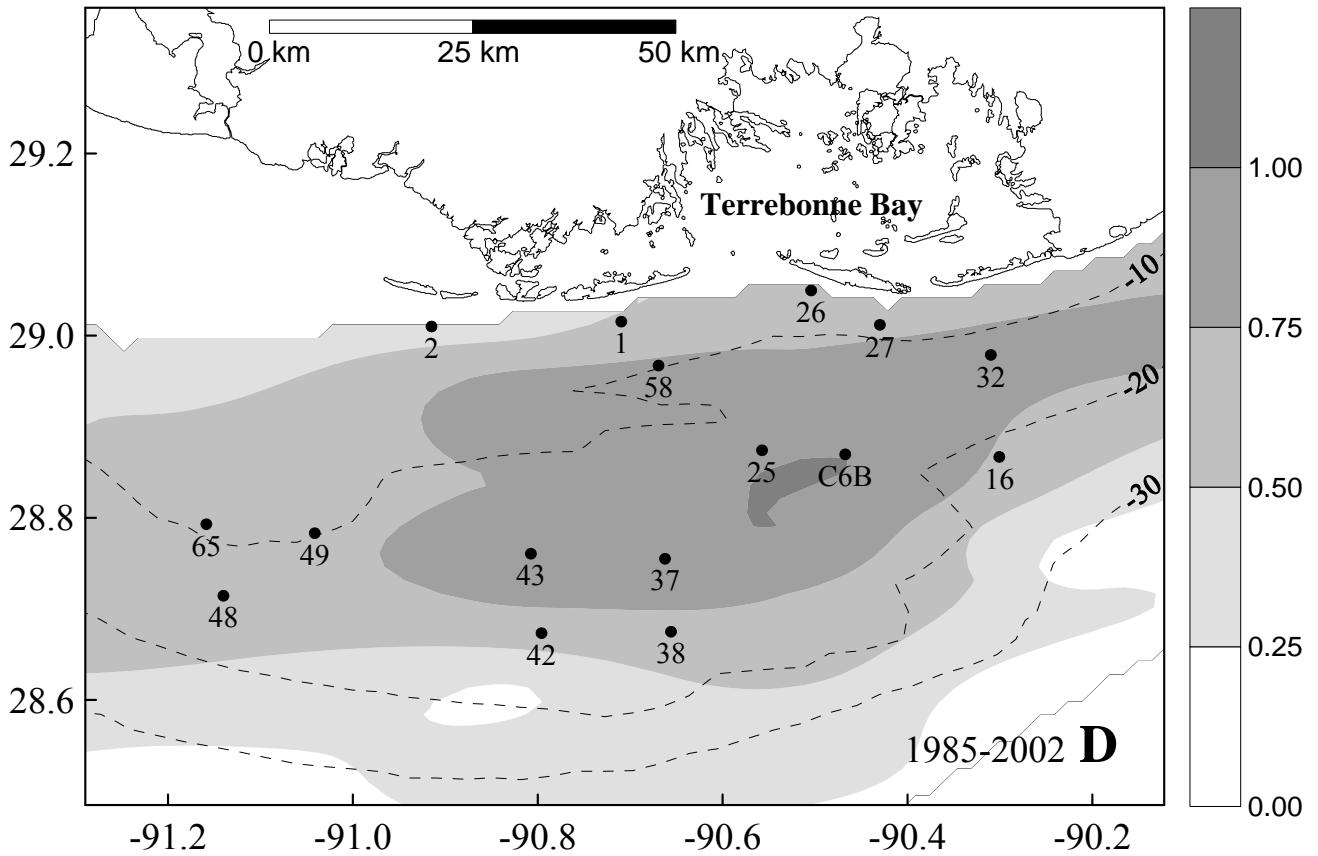
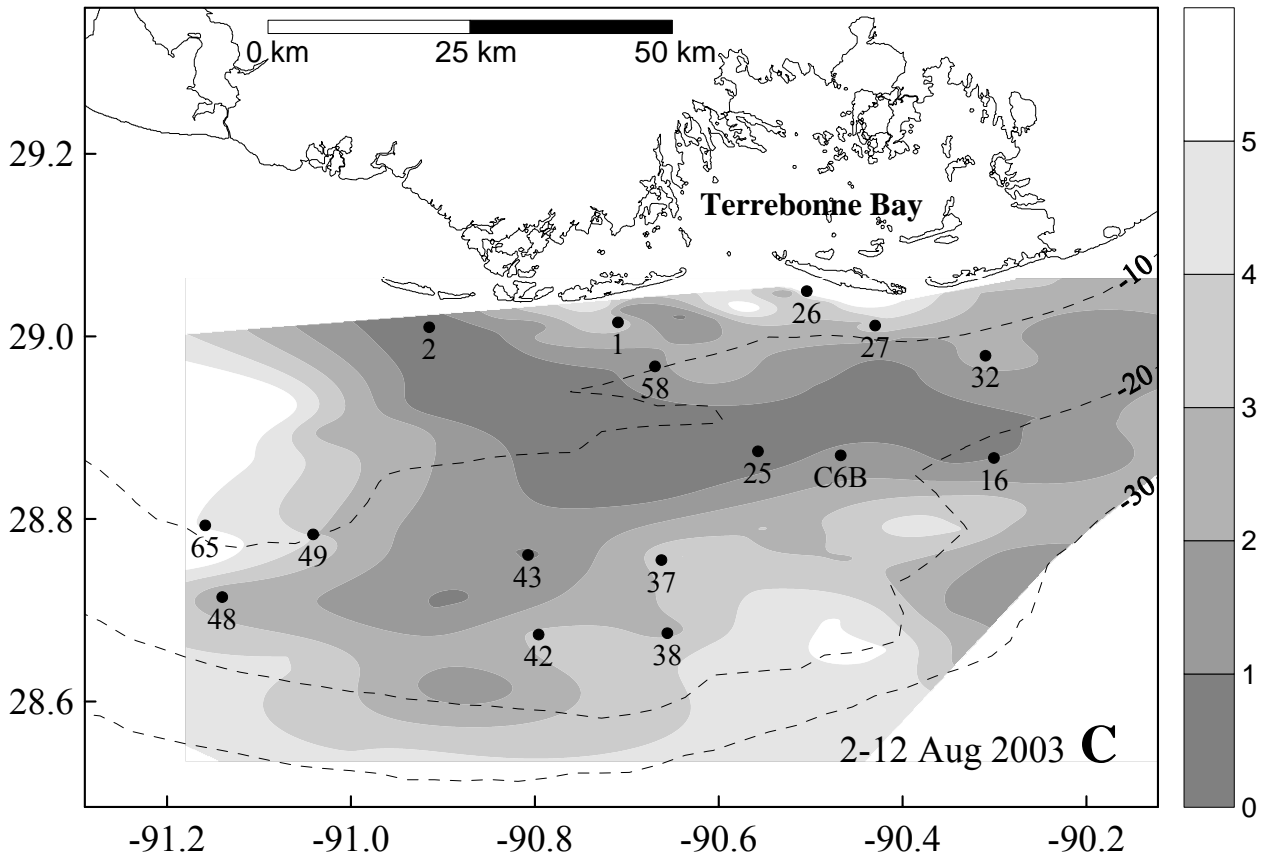
Mean dissolved oxygen conditions and depth determined the grouping of stations by inshore, hypoxia, and offshore (Figure 2C). The variability of environmental parameters averaged by these groups is illustrated in Figure 3 and Table 1. There was a general increase in depth from inshore to offshore. The offshore area bathymetry, however, was not uniform alongshore so that several non-hypoxic stations were located in depths similar to the hypoxic area. Sand content was most variable at the inshore stations with station 27 being very muddy. Sand content was lowest in the hypoxic area. Sediment TOC values were negatively related to sand content and ranged from 0.08 – 1.38%.

The Atlantic croaker stomach content data were not available at the time this paper was being prepared. A premature conclusion about the relationship between available prey in the sediment and stomach content, in relation to hypoxia was avoided. Future discussion is planned among the scientists involved to interpret the prey selectivity by the demersal fish.

The mean abundances of macroinfauna in the three areas (Figure 4) were not significantly different from each other ($F_{2, 5.96} = 2.12, p < 0.2019$). The mean abundances for the area groups ranged from about 3,500 individuals m^{-2} to about 7,000 individuals m^{-2} . The highest

Fig. 2. Map of the 15 summer stations and one seasonal station (C6B) located in the vicinity of Terrebonne Bay, Louisiana. Bottom-water dissolved oxygen data were taken (A) 9-19 June 2003 (M. Murrell unpubl. data) (B) 23-28 July 2003 (N.N. Rabalais unpubl. data) (C) 2-12 August 2003 (J.K. Craig unpubl. data) and (D) the frequency of occurrence of hypoxia in the area by Rabalais et al. 2002b. Shades of gray in A, B, C represent bottom-water dissolved oxygen in mg l^{-1} and D is the frequency of mid-summer hypoxia occurring from 1985-2002.





mean abundance ($\sim 15,000$ individuals m^{-2}) was found inshore at station 26 and the lowest mean abundance ($\sim 2,000$ individuals m^{-2}) was found at the hypoxic station 43. The mean species richness values per Ekman grab among the three areas (Figure 5) were significantly different ($F_{2, 8.54} = 6.22$, $p < 0.0215$). The highest species richness was in the offshore area, which was significantly different from the hypoxic area ($F_{1, 8.20} = 12.45$, $p < 0.0075$) but not the inshore area ($F_{1, 6.66} = 3.52$, $p < 0.1049$). The mean species richness was 17 for inshore, 13 for hypoxia, and 26 for offshore (Figure 5).

The infauna was composed mostly of polychaetes, but molluscs, echinoderms and crustaceans were also abundant in most areas (Figure 6). The spionids, *Paraprionospio pinnata* and *Prionospio pygmaea*, were the most abundant polychaetes in the inshore area. The common molluscs inshore were *Mulinia lateralis* and *Tellina versicolor*. Compared with the other two areas, the inshore area contained the highest percentage (6.3%) of echinoderms, which were the brittle star *Hemipholis elongata*. The most numerous crustacean inshore was the cumacean *Oxyurostylis smithi*. Platyhelminthes were found in low numbers at most inshore stations but were not part of the hypoxic or offshore infauna. The highest percentage of polychaetes (86.2%) and the lowest percentage of crustaceans (0.6%) were found in the hypoxic area. The common polychaete in the hypoxic area was the spionid *P. pinnata*, which was almost twice as abundant as the second ranked polychaete *Magelona* sp. H. The most abundant mollusc in the hypoxic area was *Nuculana acuta*. The few crustaceans found in the hypoxic area were mostly the amphipod *Ampelisca* sp. A. Polychaetes (65.1%) were less abundant in the offshore area compared to the inshore and hypoxic areas. Molluscs, crustaceans, sipunculans, and nemerteans were a greater proportion of the benthic community in the offshore area compared to the other two (Figure 6). The most common polychaete offshore was *P. pinnata*, but many other species

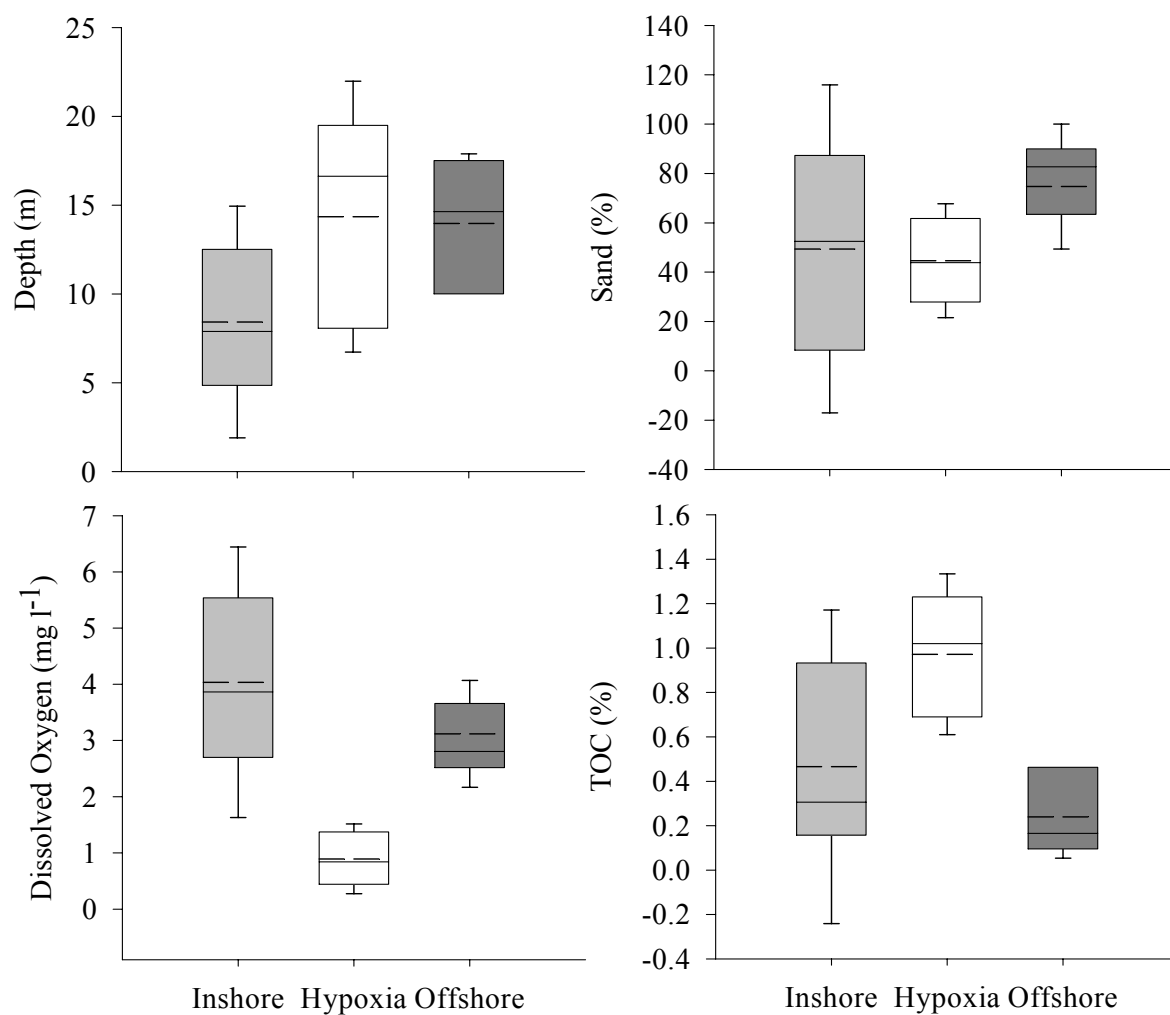


Figure 3. Box plots by area of summer environmental data, depth (m), bottom-water dissolved oxygen (mg l^{-1}), percent sand, and percent total organic carbon. The whiskers are 95% confidence intervals, the dotted line is the mean and the solid line is the median.

Table 1. Location, depth of water, bottom water quality and sediment characteristics of 15 summer stations sampled during August 2003 in coastal Louisiana. I = inshore, H = hypoxia, O = offshore, STAT = station, LAT = latitude, LON = longitude, DO = dissolved oxygen, SAL = salinity, TEMP = temperature and TOC = total organic carbon.

LOCATION				BOTTOM WATER				SEDIMENT		
AREA	STAT	LAT (N)	LON (W)	DEPTH (m)	DO (mg l ⁻¹)	SAL (psu)	TEMP (°C)	TOC (%)	MUD (%)	SAND (%)
I	1	29.02	90.71	7.50	3.87	30.10	29.67	0.21	21.94	78.06
I	26	29.05	90.50	4.00	6.03	31.96	28.92	0.14	9.56	90.44
I	27	29.01	90.43	8.38	4.07	33.47	27.86	0.40	97.83	2.17
I	32	28.98	90.31	13.88	2.38	34.56	27.40	1.11	73.04	26.96
H	2	29.01	90.91	6.10	0.64	32.30	28.39	1.38	81.60	18.40
H	16	28.87	90.30	21.13	1.23	35.68	26.26	1.08	56.18	43.82
H	25	28.87	90.56	16.63	0.24	35.47	25.65	0.69	62.57	37.43
H	43	28.76	90.81	17.63	0.84	35.24	25.42	1.02	43.62	56.38
H	58	28.97	90.67	10.13	1.52	34.74	27.12	0.69	32.84	67.16
O	37	28.75	90.66	17.50	2.57	34.40	27.06	0.46	24.39	75.61
O	38	28.67	90.66	15.88	2.54	35.20	25.81	0.08	10.08	89.92
O	42	28.67	90.80	17.38	3.26	35.12	26.17	0.47	21.13	78.87
O	48	28.71	91.14	13.38	2.45	34.79	26.54	0.18	9.70	90.30
O	49	28.78	91.04	10.38	3.04	34.53	26.99	0.10	13.43	86.57
O	65	28.79	91.16	8.88	4.85	34.36	27.25	0.15	13.98	86.02

of polychaetes were as abundant, for example *P. pygmaea*, *Ampharete* sp. A and *Tharyx* cf. *annulosus*. The molluscs *T. versicolor*, *Nassarius acutus* and *N. acuta* were common offshore. Like the polychaetes, there were several abundant species of crustaceans. Amphipods, *Americhelidium americanum* and *Ampelisca abdita*, were common at every station. The cumacean *O. smithi* was also abundant in the offshore area. Nemerteans (*Nemertea* sp. A) were also abundant offshore.

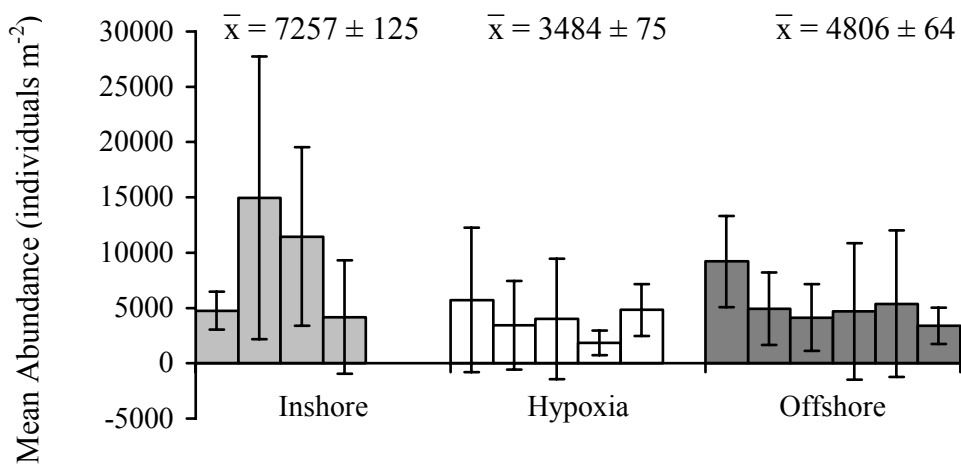


Fig. 4. Mean abundance of macroinfauna for each station (bar) \pm 95% confidence intervals and the mean (\pm 95% confidence intervals) abundance (\bar{x}) per area. Bars (stations) are in numerical order from left to right, Inshore (1, 26, 27, 32), Hypoxia (2, 16, 25, 43, 58) and Offshore (37, 38, 42, 48, 49, 65).

The community composition of the three areas was not distinctively different according to the cluster analysis (Figure 7). There were three main clusters. One group was composed of some offshore stations and one inshore station 26. Another cluster of stations was the other offshore stations and two hypoxic stations. The third major group contained two hypoxic stations and all the inshore stations except station 26, which was clustered with the offshore stations.

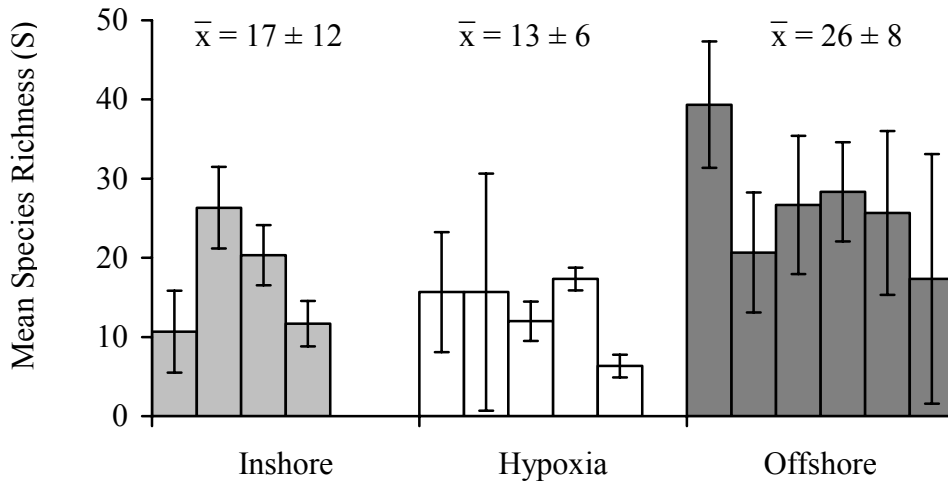


Fig. 5. Species richness of infauna at each station (bar) \pm 95% confidence intervals and the mean (\pm 95% confidence intervals) species richness (\bar{x}) for each of three areas. Bars (stations) are in numerical order from left to right, Inshore (1, 26, 27, 32), Hypoxia (2, 16, 25, 43, 58) and Offshore (37, 38, 42, 48, 49, 65).

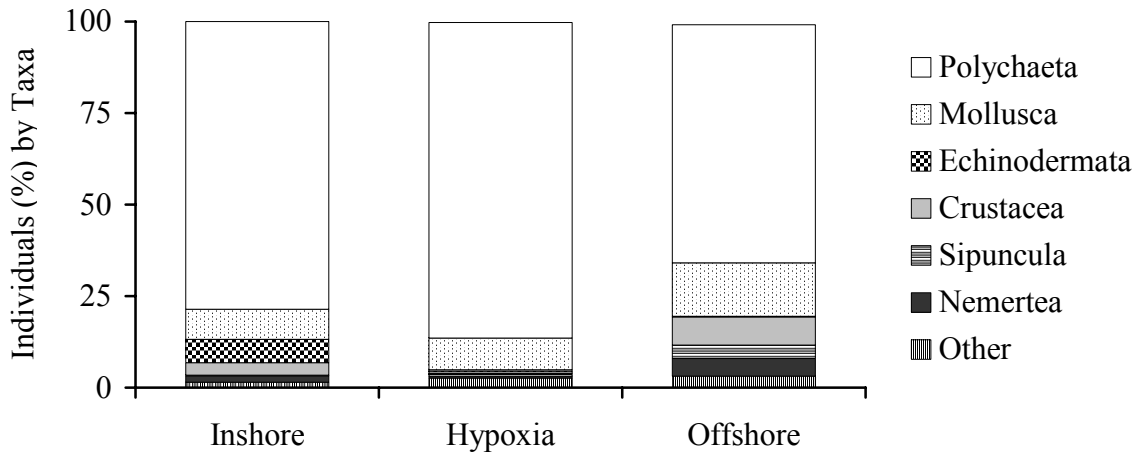


Fig. 6. Percent of individuals by major taxonomic group for summer samples (all stations and replicates pooled per station group). 'Other' refers to Chordata (gobies and lancelets), Cnidaria, Phoronida, Platyhelmenthes, Echiura, and Hemichordata.

The MDS plot showed a similar grouping of stations but on two dimensions (Figure 8). The stress value, indicating distortion (Clarke & Warwick 2001) was less than 0.2 and thus represented a useful two-dimensional plot. The correlation values (R) of the ANOSIM analysis suggest similarity or differences in the community composition among the station groups. An R value > 0.5 suggests differences with some overlap, and values < 0.25 characterize communities that are similar or have few differences (Clarke & Warwick 2001). The inshore area and the hypoxic area were similar in community composition ($R = -0.044$). The inshore and offshore areas were slightly different with some overlap in community composition ($R = 0.421$). The hypoxic and the offshore area differed in community composition ($R = 0.600$).

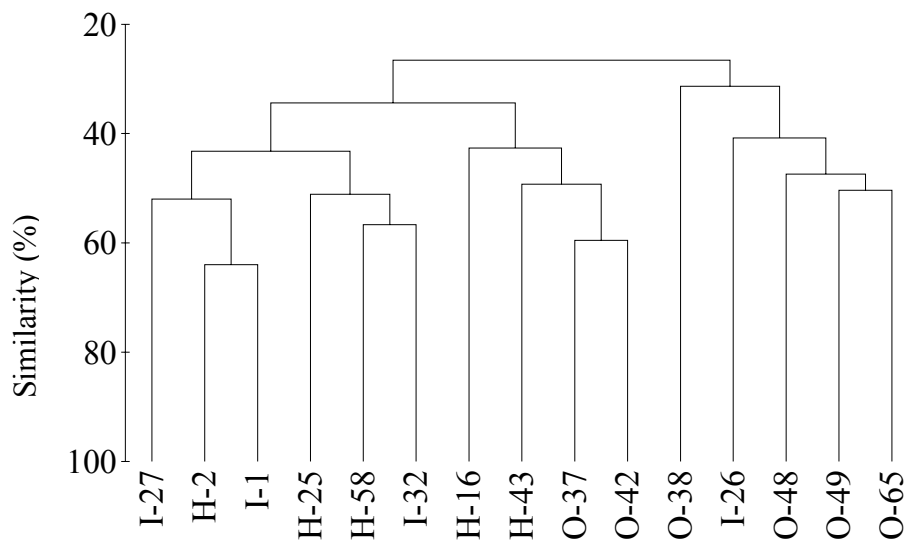


Fig. 7. Clustering dendrogram of summer stations macroinfaunal data using $\log(y + 1)$ standardization and Bray-Curtis similarity index. The labels refer to area (Inshore, Hypoxia, Offshore) and station number.

The vertical distribution of macroinfauna in the inshore area was either infauna at the surface and much less abundance deeper in the core or infaunal abundances throughout the depth of the core (Figure 9). The greatest number of individuals in a 1 cm section, nearly 70 individuals section^{-1} , was found in a short sandy core at the inshore station 26 (Figure 9), which the box

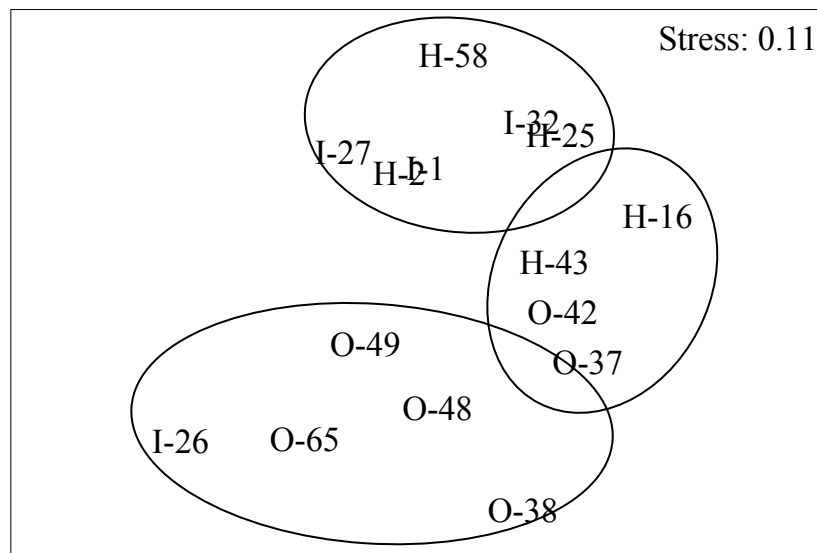


Fig. 8. Two-dimensional multidimensional scaling (MDS) ordination for summer station macroinfaunal data (replicates averaged) from log (y+1) transformation and standardized data using a Bray-Curtis similarity index. The similarity is > 35% for the stations circled. The labels refer to station group (Inshore, Hypoxia, Offshore) and station number.

corer could not penetrate deeply. The hypoxic stations did not show any obvious patterns in the vertical distribution of infauna (Figure 10). Some of the highest abundances in the hypoxic area were found at the surface (stations 2, 58) while other abundant infauna were mid-depth in the cores. The patterns of infauna in the offshore area were similar to the inshore area with either high abundances at the surface (stations 37, 49, 65) or very few organisms throughout the core depth (Figure 11). An exception was station 37, the distribution of infauna abundance was highest between 1 and 3 cm either indicating that the surface benthos were consumed or the surface (0-1 cm) was lost during slicing. The box corer did not penetrate as deeply at some stations in the offshore area due to high sand content (i.e, stations 38, 49 and 65). There was a variety of benthos at the surface sediment (0-1 cm) inshore compared to the hypoxic area. The most abundant were the spionids, *Prionospio pygmaea* and *Paraprionospio pinnata*, but molluscs, *Mulinia lateralis* and *Abra aequalis*, were also abundant.

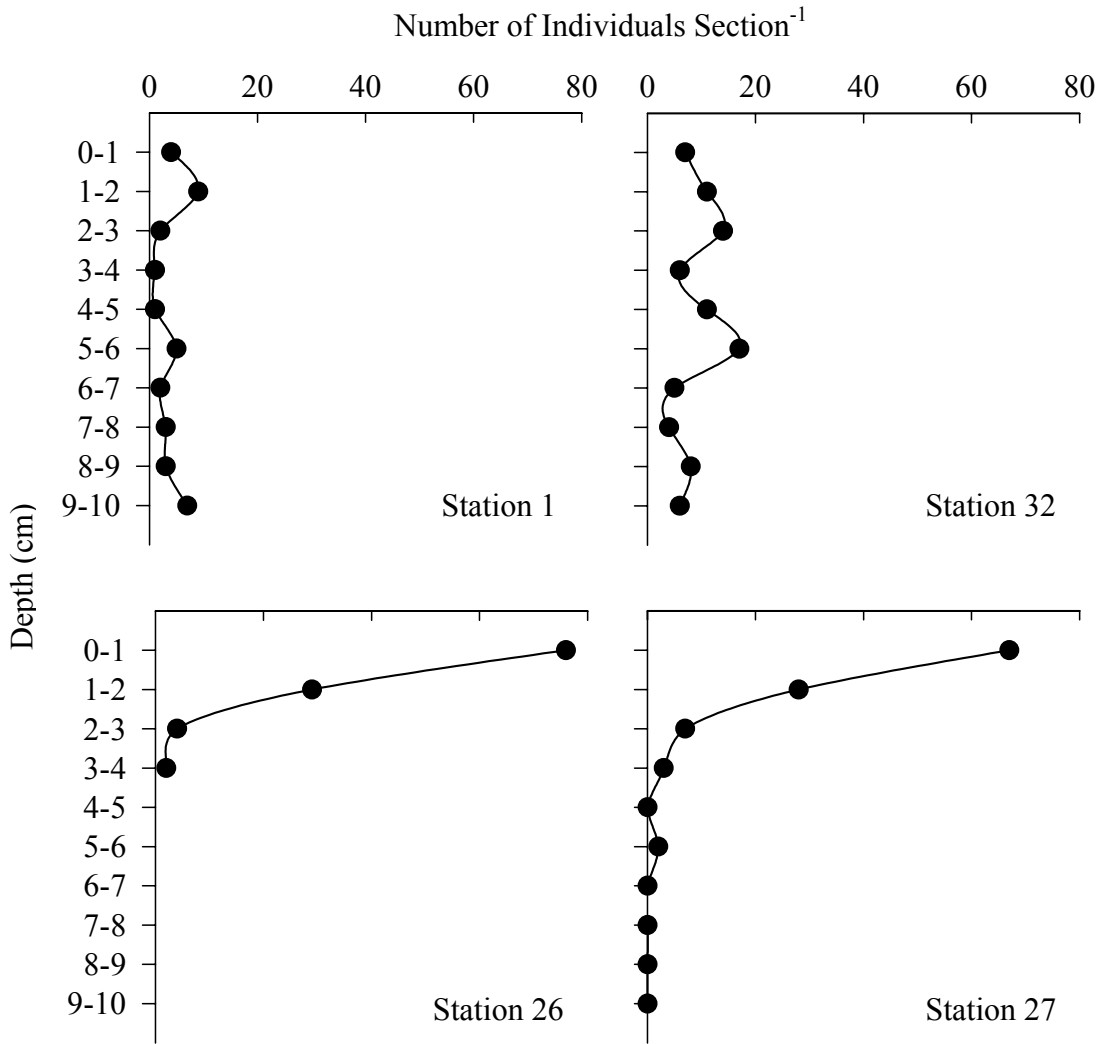


Fig. 9. Vertical distribution of macroinfaunal abundance in four inshore stations.

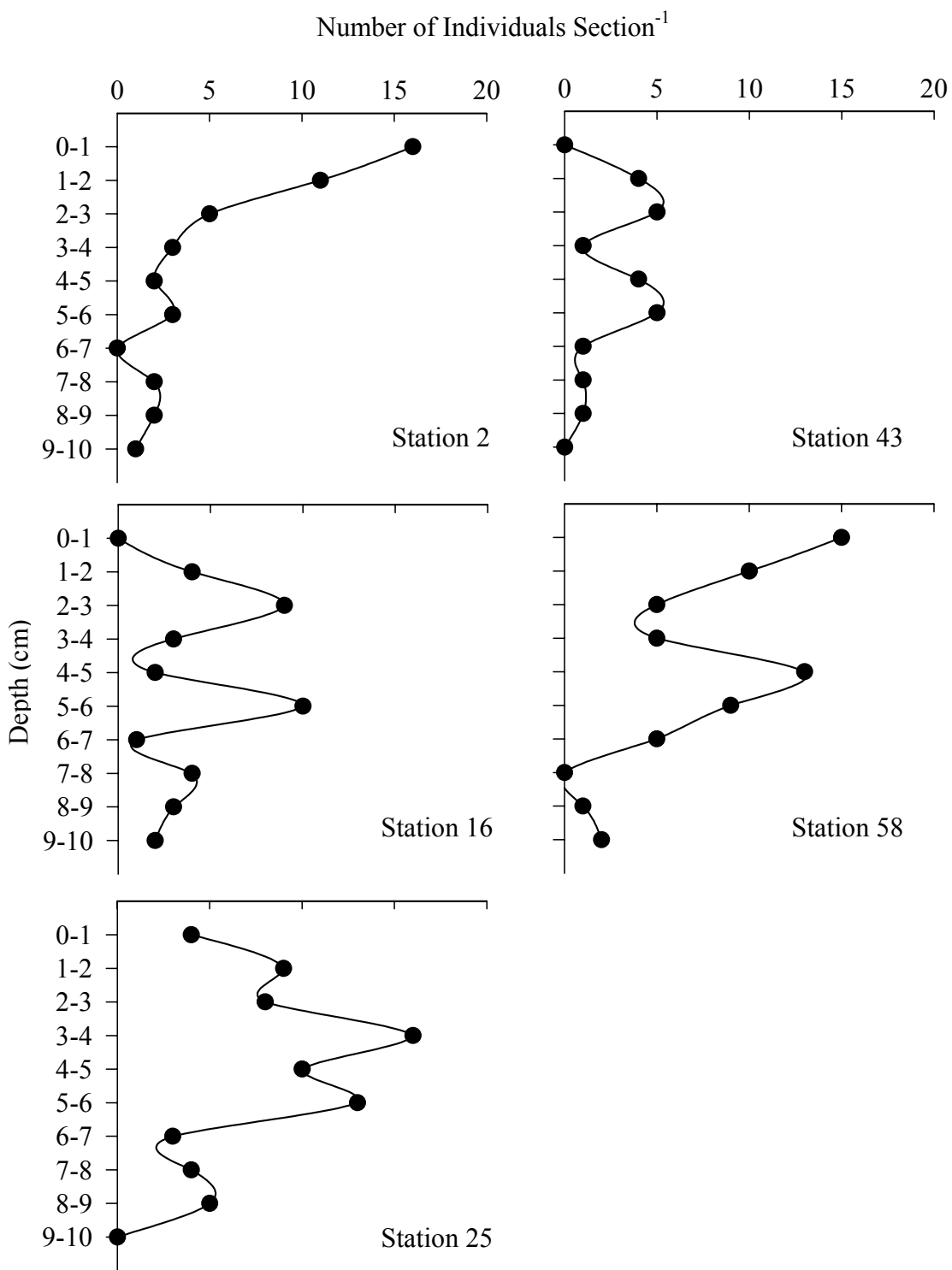


Fig. 10. Vertical distribution of macroinfaunal abundance in five hypoxic stations.

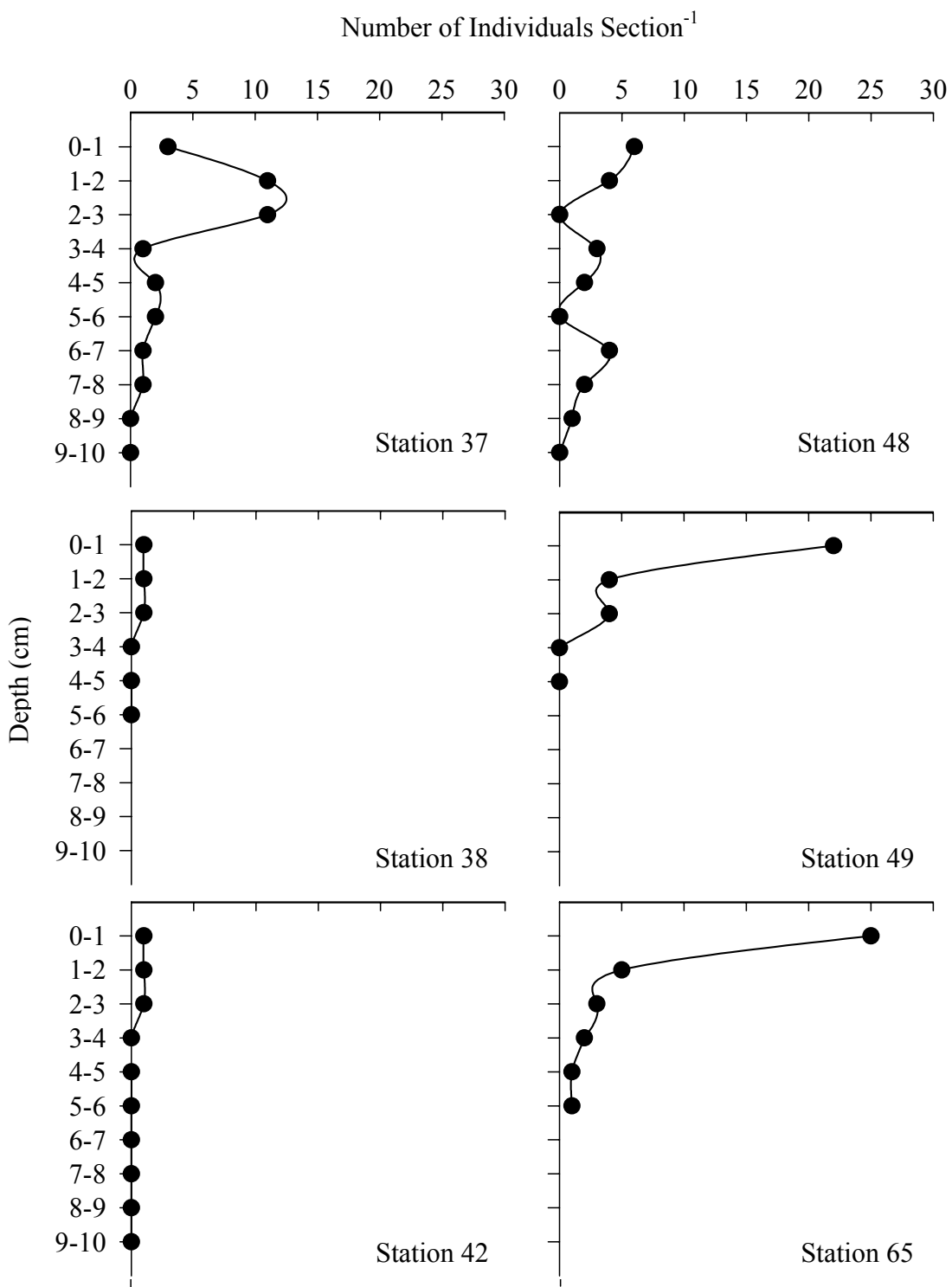


Fig. 11. The vertical distribution of macroinfaunal abundance in the offshore stations.

2003-2004 Annual Cycle

Oxygen conditions were similar to the long-term annual cycle at station C6B. The highest surface oxygen concentrations were in March and May 2004 with a peak of about 13 mg l^{-1} and 15 mg l^{-1} , respectively. In summer 2004 the surface dissolved oxygen decreased to about 6 mg l^{-1} and remained at that level through October (Figure 12). The surface-water dissolved oxygen ranged from $3 - 16 \text{ mg l}^{-1}$ from September 2003 to October 2004 (Figure 12). The bottom-water was hypoxic from May to August in summer 2003 and from early June to late August in summer 2004 except for short periods in mid-July 2003 and mid-August 2004 (Figure 12). There were 111 d of hypoxia in May-August 2003, but only 60 d for the same period in 2004.

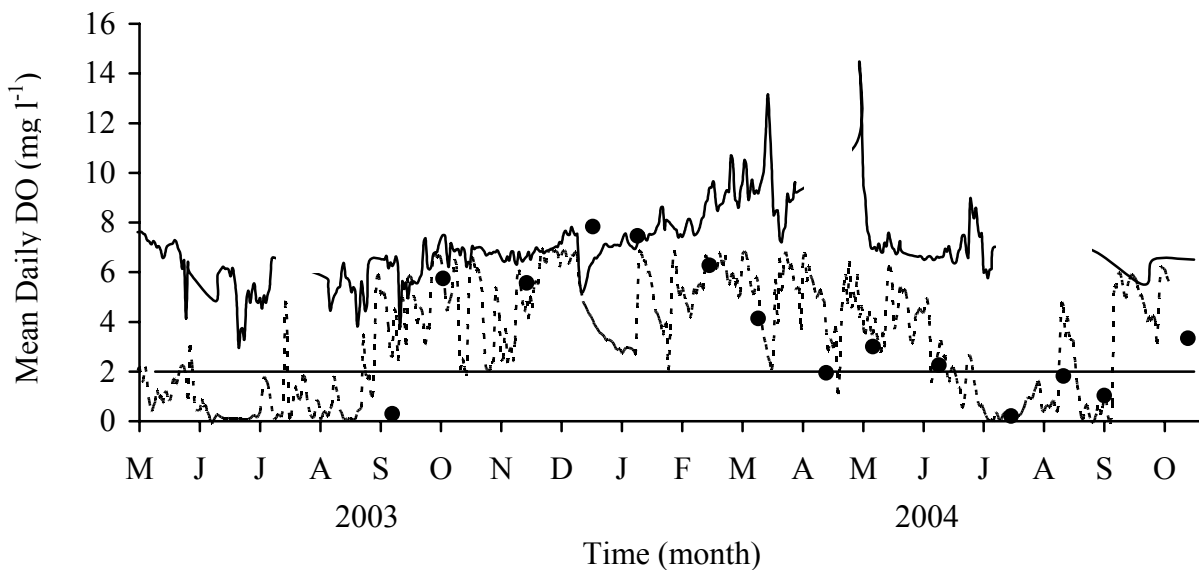


Fig. 12. Mean daily dissolved oxygen (DO) (surface is the solid line and bottom is the dotted line) from May 2003 to October 2004 at station C6B as measured by the YSI 6600 and YSI 6600 EDS oxygen probes. Solid circles refer to bottom dissolved oxygen measurements taken by the Hydrolab Surveryor 3 before box coring. A blank area in the surface line indicates no data. Solid line at 2 mg l^{-1} is a reference line for hypoxic water.

Sediment characteristics were consistent among months with a few exceptions. Sediment TOC was close to 1.80% from September 2003 to September 2004 with an increase in May 2004

to 2.25% and a decrease to 0.72% in October 2004 (Figure 13). Grain size was consistently sandy-mud sediment (~ 97% mud) for most months except for October 2004 when the sediment was sandier (~ 55% sand).

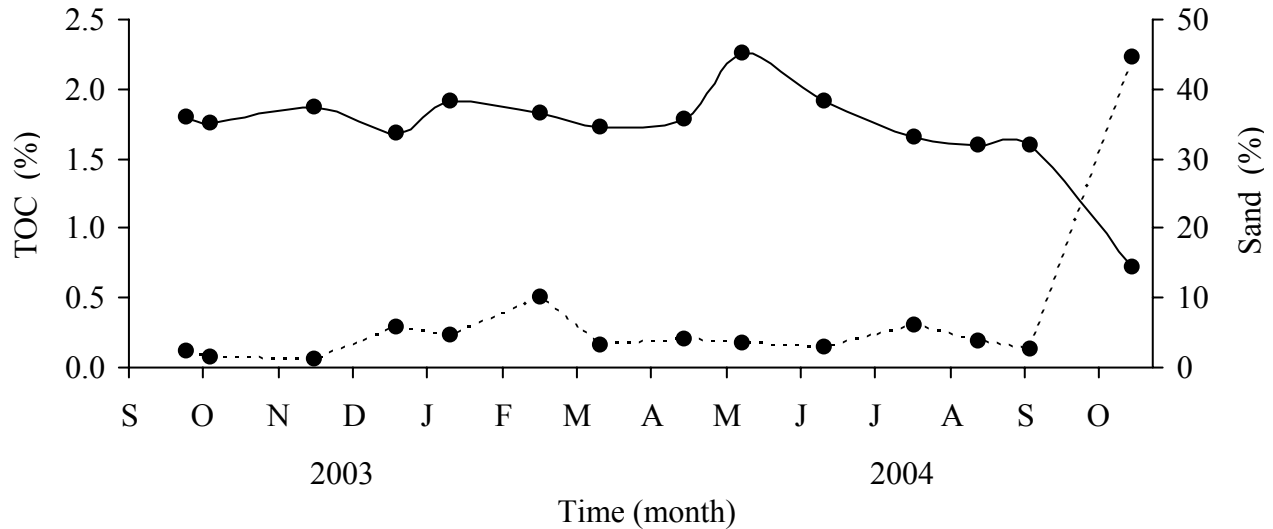


Fig. 13. Percent total organic carbon (solid line) and percent sand (dashed line) of monthly sediments from station C6B (September 2003 to October 2004).

The mean abundance of the macroinfauna ranged from 385 to 2548 individuals m^{-2} over the course of the year (Figure 14). Abundance was low during the fall months of September – December 2003 and generally increased in winter and spring. High variability of macroinfaunal abundance occurred in the spring. The highest abundance was in April 2004 (Table 2, Figure 14), but declined in May 2004 to 2000 individuals m^{-2} and remained near this level for June and July 2004. Following the hypoxic period of June and July 2004, the macroinfauna abundance in August 2004 significantly decreased to 800 individuals m^{-2} and was less than 600 individuals m^{-2} in September and October 2004 (Table 2), similar to the fall and winter means of 2003. The trend for mean species richness per Ekman grab was similar to the mean abundance. Species richness was low in September - December 2003, increased in the following winter and spring,

and early summer then declined in August through October (Figure 14). There was similarity in monthly mean species richness values over the annual cycle (Table 2). Generally, the species richness was above 10 except during the post hypoxic months of September - November 2003 and August - October 2004.

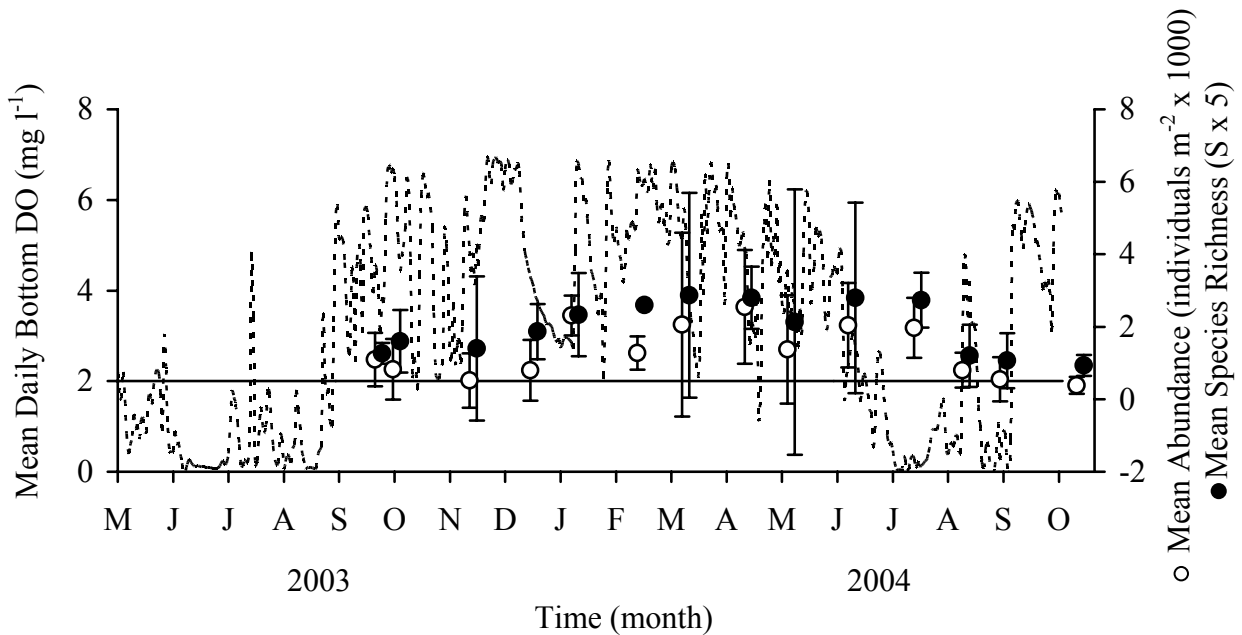


Fig. 14. Mean daily bottom dissolved oxygen (DO, mg l^{-1}) from May 2003 to October 2004 as the dotted line. Monthly mean abundance ($\text{individuals m}^{-2} \times 1000$) \pm 95% confidence intervals as white dots and mean species richness ($S \times 5$) \pm 95% confidence intervals from September 2003 to October 2004 as black dots. Abundance values are shown two days prior to the sampling date and species richness values are displayed two days after the sampling date to clarify the data presentation.

Polychaetes dominated the benthic community with greater than 50% of the individuals throughout the year. Molluscs, crustaceans, and nemerteans, however, were also abundant (Figure 15). The four most abundant infauna were *Paraprionospio pinnata*, *Nemertea* sp. A, *Armandia maculata*, and *Magelona* sp. H (Figure 16). The spionid polychaete *P. pinnata* was the most abundant through the year and was dominant in September 2003 and July - October 2004 when the other three species declined. The common molluscs were *Nuculana acuta*,

Natica pusilla, and *Abra aequalis*. Most of the crustaceans were caridean shrimp (*Alpheus*), amphipods (*Americhelidium*) and cumaceans (Diastylidae) and were common through most of the year. No crustaceans were found in August and October 2004, and few were found in September 2004 (Figure 15).

Changing patterns in community structure resulted in three groups of > 45% similarity in the cluster analysis (Figure 17). The post-hypoxic months (September to October 2003 and August to October 2004) clustered together. The months of November 2003 - January 2004 and February - July 2004 formed the other two groups. These groupings were similar in the MDS plot (Figure 18). Community composition in September and October of both years were similar; however, September 2003 and 2004 grouped more closely than October 2003 and 2004 (Figure 18).

From September through November 2003, low abundances of mostly *Sigambra tentaculata* and *Cossura* sp. A occurred with depth in the vertical cores (Figure 19). In December 2003 and January 2004 the higher abundances of infauna (mostly *Aricidea wassi*, *Cossura* sp. A and *Tharyx* cf. *annulosus*) were deeper in the sediment at 2 – 7 cm. In February and March 2004, especially in March 2004, *A. wassi*, *C. sp. A*, and *Nuculana acuta* dominated. From April to May 2004 many *C. sp. A* moved to deeper depths. The majority of the macroinfauna were at the surface in June, July, and August 2004. The highest number of organisms per section (dominated by *A. wassi*) was found at the surface in July 2004. Low abundances of *Gyptis vittata* and *Paraprionospio pinnata* in September and *C. sp. A* and *S. tentaculata* in October were found throughout the core.

⁷Be radioisotopes were not detected in March, July and October 2004 (Figure 20). A ⁷Be penetration depth of 3 cm was measured in April, and in May the deepest depth of ⁷Be

Table 2. Post-hoc analysis of variance (Duncan's multiple range test) of mean abundance (individuals m⁻²) and mean number of species mo⁻¹. Months are arranged in decreasing numerical order of values from left to right. Underlined months are not significantly different from each other.

	P VALUE	MONTH
MEAN ABUND.	< 0.0001	<u>4/04</u> <u>1/04</u> <u>3/04</u> <u>6/04</u> <u>7/04</u> 5/04 2/04 9/03 10/03 8/04 12/03 9/04 11/03 10/04
MEAN NO. SPECIES	0.0014	<u>3/04</u> <u>6/04</u> <u>4/04</u> <u>7/04</u> <u>2/04</u> 1/04 5/04 <u>12/03</u> 10/03 11/03 9/03 8/04 9/04 10/04

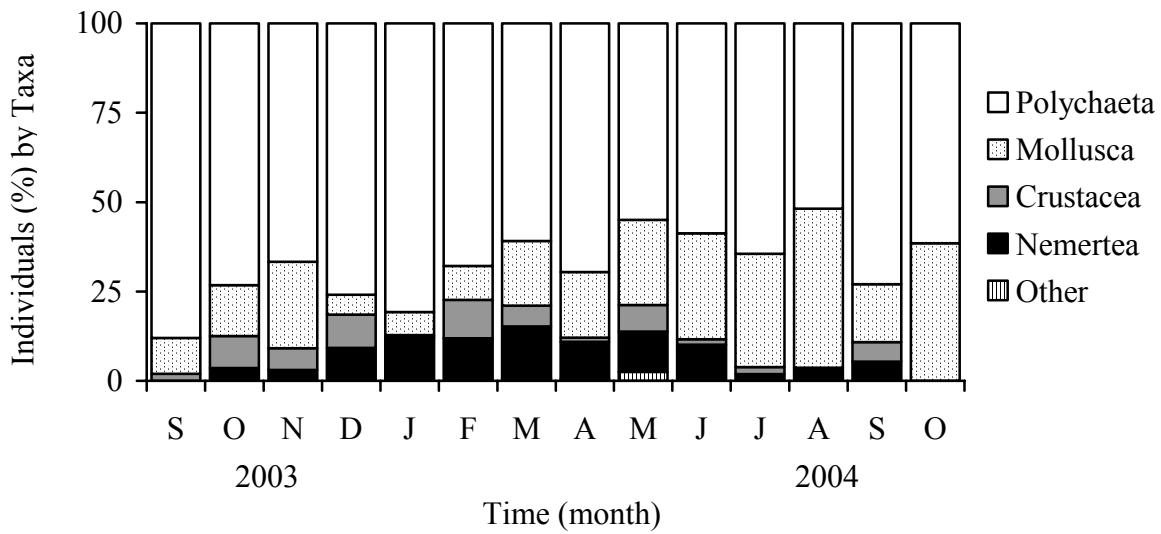


Fig. 15. Percent of individuals by major taxonomic group for station C6B from September 2003 to October 2004. 'Other' refers to Echinodermata and Osteichthyes.

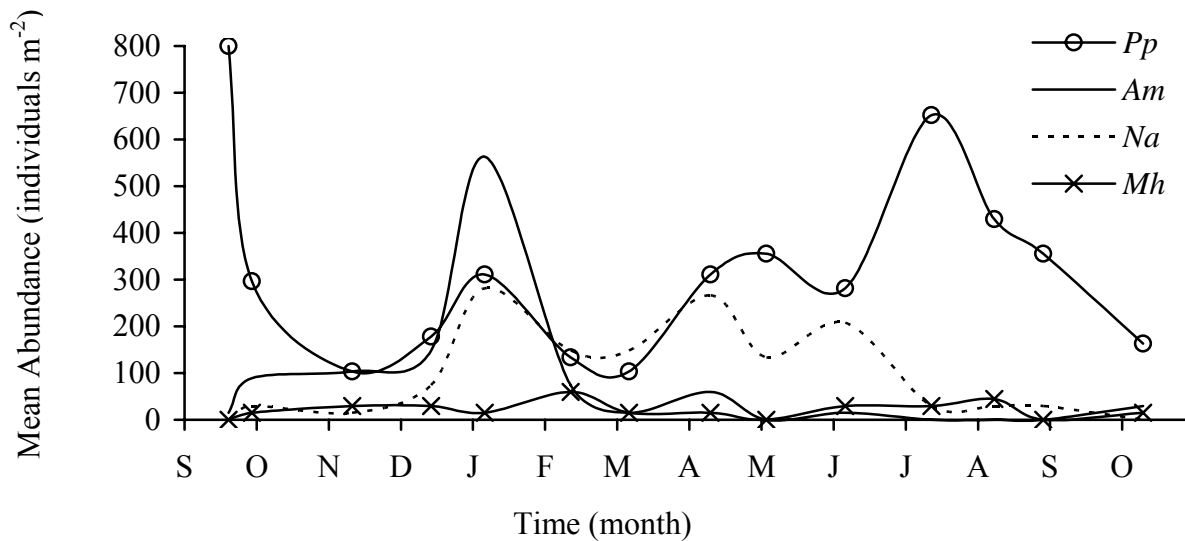


Fig. 16. The mean abundance of *Paraprionospio pinnata* (*Pp*), *Armandia maculata* (*Am*), *Nemertea* sp. A (*Na*), and *Magelona* sp. H (*Mh*) for each month during 2003-2004 sampling at station C6B.

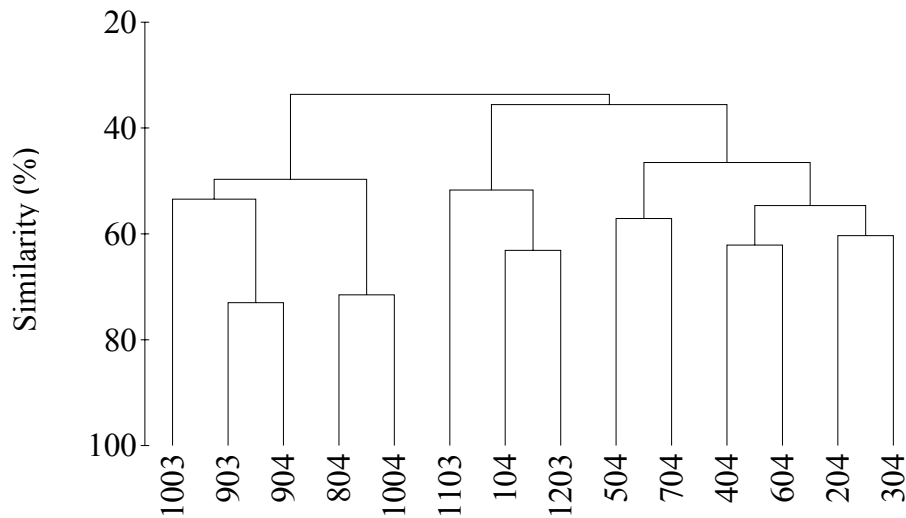


Fig. 17. Clustering dendrogram of the mean monthly macroinfaunal data at station C6B using the Bray-Curtis similarity matrix with standardization. The numbers refer to the month and year of the sample.

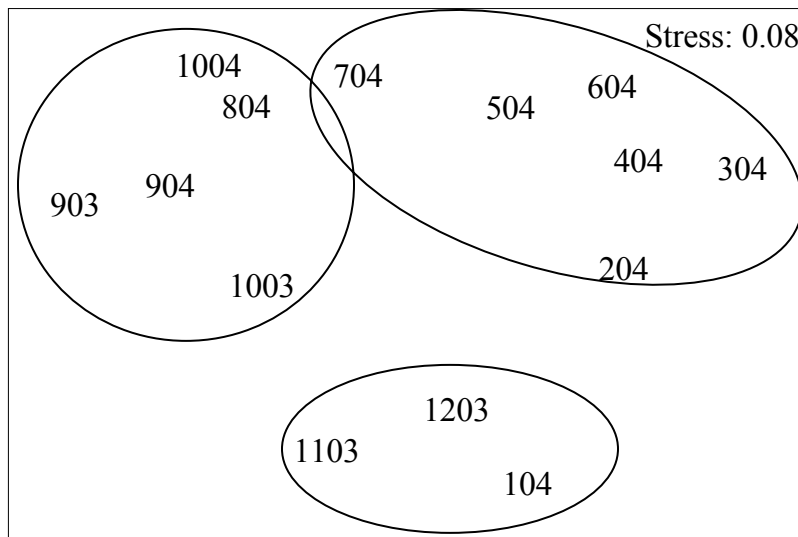


Fig. 18. Two-dimensional multi-dimensional scaling (MDS) ordination for station C6B mean monthly macroinfaunal samples. The points within the circles have > 45% similarity and refer to month and the year of sampling.

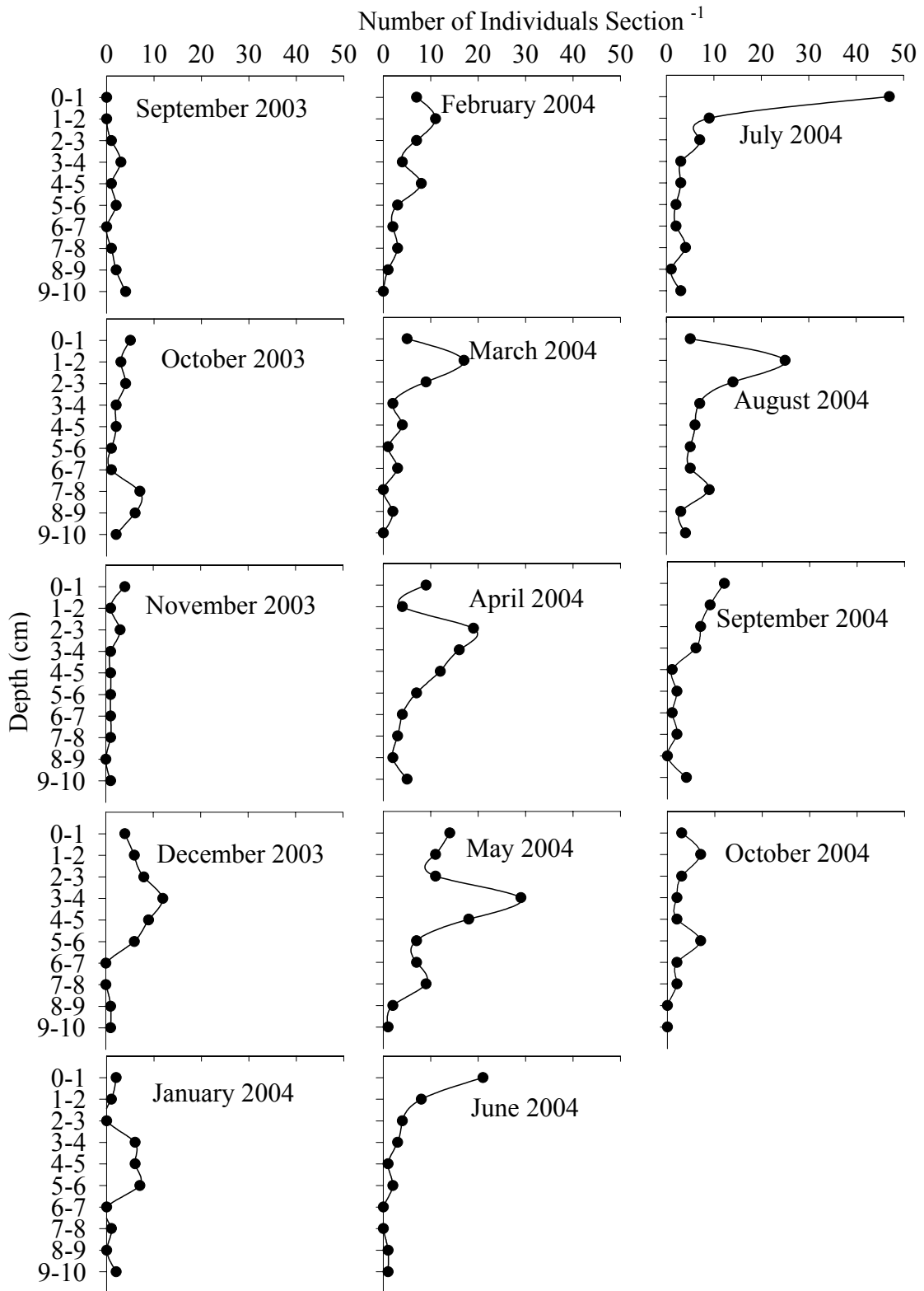


Fig. 19. Vertical distribution of macroinfaunal abundance at station C6B from September 2003 to October 2004.

penetration was 9 cm, with high counts of radioisotopes at 1, 3 and 9 cm. The June radioisotope depth indicated biological reworking to a depth of 7 cm. Beryllium-7 penetration was at a depth of 1 cm in August and deeper to 7 cm in September (Figure 20).

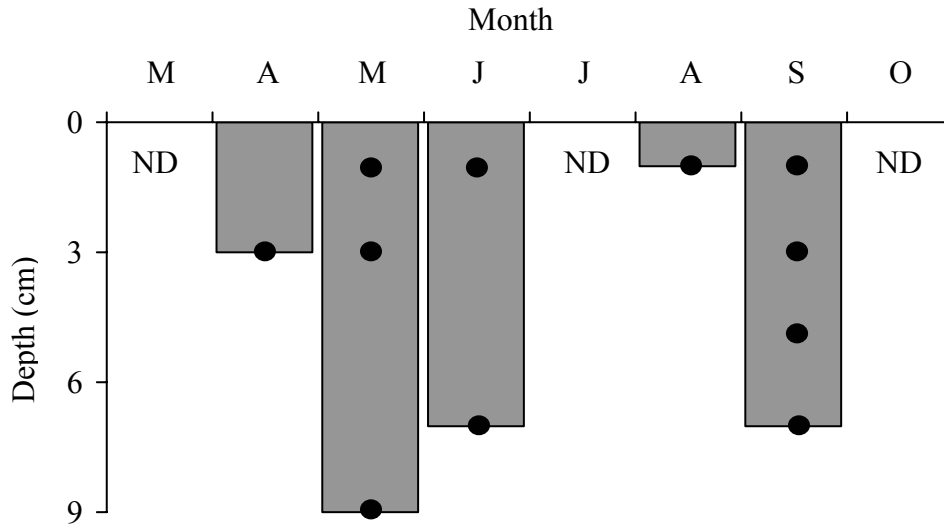


Fig. 20. ^7Be penetration for sediments of C6B from March through October 2004. Black dots are raw counts of ^7Be radioisotopes greater than the detector limit of 20 counts per 24 h period. ^7Be radioisotopes were not detected (ND) in the March, July and October samples.

DISCUSSION

A continuous band of summer hypoxia usually parallels the Louisiana coast (Rabalais et al. 2002a). The distribution of hypoxia during summer 2003 differed from the long-term average because of a mid-summer storm. In June 2003 the bottom-water hypoxia was approximately 4800 km² (M. Murrell, unpubl. data) covering the eastern Louisiana shelf (Figure 2A). Tropical Storm Claudette crossed the study area on July 14, 2003, mixing the surface and bottom waters, resulting in a patchy distribution of hypoxia a week later on July 23-28 (N. N. Rabalais, unpubl. data) (Figure 2B). By August 2, 2003 the bottom area of hypoxia increased as stratification of the water column strengthened and the decomposition of organic material at the seabed continued (Figure 2C). The stations for this study were concentrated within the 2-12 August 2003 hypoxic area (Figure 2C). Stations 25, 43, and 58 were located within an area of $\geq 75\%$ frequency of mid-summer hypoxia for the period 1985-2002 (Fig. 2D). Station 16 and 2 were found in an area with $\geq 50\%$ and $\geq 25\%$ respectively. Station 2 was located outside of the area where hypoxia is usually measured (Figure 2D). The inshore stations (1, 26, 27) were found in an area with $\geq 50\%$ frequency and station 32 in an area of $\geq 75\%$ frequency. The offshore stations 37, 38, 42, 48, 49 and 65 were located in areas with a $\geq 50\%$ or $\geq 75\%$ chance of mid-summer hypoxia (Figure 2D). Although some of the offshore stations were not hypoxic when sampled in summer 2003, hypoxia may have occurred previously (Figure 2D). Similarly, some hypoxic stations may have been non-hypoxic for some unknown period prior to sampling. The distribution of summer 2003 hypoxia sampled for this study was similar to the previously reported frequency of hypoxia for the area (Rabalais 2001a).

The bottom-water dissolved oxygen at C6B progressed through a typical seasonal cycle. The surface dissolved oxygen at C6B was approximately 7 mg l⁻¹ for most of the study period, but

increased to 13 and 15 mg l⁻¹ in March and May 2004, respectively. The duration of the low oxygen, however, was not as prolonged in summer 2004 as in previous years. Gaston (1985) and Harper et al. (1981) documented hypoxia on the western coast of Louisiana and upper coast of Texas as early as May, near anoxia in mid-summer and return of non-hypoxia in early August. Hypoxia at C6B is usually periodic beginning in March, expands in distribution and duration in May through August, and is present through late September (Rabalais et al. 2002b). Spring nutrient input from the Mississippi River supports high primary productivity that results in supersaturated surface oxygen conditions (Figure 12). The high productivity as indicated by high surface oxygen concentrations (6 May 2004) results in an increased flux of organic matter to the seabed. The increase in sedimentary TOC (Figure 13) in May likely reflects the high surface production of the prior week. TOC values at C6B (~ 1.80%) for much of the annual cycle were greater than the TOC values for sediments over the broader area of summer 2003. The highest TOC value in summer was 1.38% at the hypoxic station 2. These higher TOC values at station C6B were consistent with their muddy composition; mud content at station 2 was also high. TOC values were consistent with what is known from the study area, with most values less than 1.0% (Rabalais et al. 1993). Some of the highest values of TOC were found in the hypoxic area, which indicates potential carbon source for benthic food webs.

Sandy sediments dominate close to barrier islands or further offshore, both in the area of delta destructional sands of the last deltaic cycle (Fitzhugh 1983). The sand content of the Mississippi River discharge settles close to the delta and finer sediments are carried by westward currents to the hypoxic area (Curran 1960). The sediment at C6B was similar throughout the year (~ 97% mud) as in the Rabalais et al. (2001a) study. Similar sedimentary characteristics (~ 90% mud) characterized the western inshore Louisiana shelf (Gaston 1985). The sediment of the

inshore area in the Harper et al. (1981) study was mostly silts and clays, but offshore the sediment consisted of more sand, similar to the summer 2003 offshore stations of this study. The exception to muddy sediment at C6B was in October 2004 (Figure 13) following the passage of Hurricane Ivan in September. The sediment composition changed to sandier sediment (~ 45% sand) in October 2004. Sediment variability, usually sandy silt or silty sand was observed previously at C6B (Rabalais et al. 2001a). Hurricanes are major disturbance events that resuspend and transport sediments in the C6B area (Rabalais et al. 2001a). The currents from these storms can expose the compact clay layer beneath accumulated muddy sediment or transport the mud from the area and deposit a meter or more of sandy sediment (N.N. Rabalais, pers. comm.). C6B and the summer 2003 station 27 (98% mud) were the muddiest stations in the study area. The hypoxic station 2 was 82% mud, with a high TOC value of 1.38%.

Demersal predators, like Atlantic croaker, prefer muddy substrates with high organic content (Gunter 1938, Parker 1971, Pearson 1929). Sand and hard substrates are unsuitable for juvenile croaker. The stations with the most suitable habitat characteristics of muddy sediment and high TOC values are located in the hypoxic area (Table 1).

Hypoxia effects differ with sediment characteristics (Nilsson & Rosenberg 1994). Infauna of soft substrates are more resistant to low oxygen than those of hard or sandy substrates (Theede et al. 1969), because benthos in muddy sediment are adapted to the hydrogen sulfide and reducing conditions and are capable of prolonged survival during hypoxia. Within the hypoxic area the lowest abundance of macroinfauna was found at station 58, where the sediment was sandy and the dissolved oxygen was higher compared (Table 1 and Figure 4) to hypoxic station 2. Very low oxygen (0.64 mg l^{-1}) was found at station 2 and the sediment was the muddiest in the hypoxic area, which may explain why the greatest abundance of macroinfauna was found (Table

1, Figure 2). These examples of differences in abundance could be due to the dichotomy suggested by Theede et al. (1969). On the other hand, the location of station 2 was close to the edge of hypoxia as measured in the survey and may not have experienced hypoxia for an extended period prior to sampling of the benthos. The combination of sandy sediment and low oxygen may be more stressful than hypoxia alone on benthic communities, because some infauna are not resistant to hydrogen sulfide and hypoxic sediment conditions. The sediment alone does not fully characterize the benthic composition, but the interaction of hypoxia and hydrogen sulfide within the sediment may influence which benthos survive (Nilsson & Rosenberg 1994).

Oxygen stress can significantly reduce the number of species in a community without affecting the total abundance (Nilsson & Rosenberg 1994) as seen in this study (Figure 4). The benthic infauna, as potential prey for demersal predators, was similar in abundances across the shelf. Hypoxia did not significantly affect the abundances for several potential reasons. (1) An abundance of opportunistic benthos may be able to survive and recruit to maintain population levels similar to non-hypoxic surroundings (Dauer et al. 1992). (2) Nekton predators are usually not found in the hypoxic area (Craig et al. 2001), therefore predation would not affect the benthic community like the non-hypoxic areas. (3) Disruption of hypoxia by a tropical storm may have moderated the severity of hypoxia.

Species richness was significantly different in the hypoxic area compared to the non-hypoxic offshore area (Figure 5). Some taxonomic groups (e.g., Crustacea and Echinodermata) or selective species may be less resistant to oxygen stress than others and die resulting in a reduction of species richness (Theede et al. 1969, Mangum & Van Winkle 1973). The offshore non-hypoxic area had a similar benthic community composition (Figure 5, 7, 8) as the inshore non-hypoxic area most likely due to the sandy nature of the sediment common to both areas.

The offshore area was more diverse in major taxa than the inshore area including a larger percentage of crustaceans (Figure 6). Although the abundances of organisms were not significantly different among the summer areas, the species richness and community composition differed within and outside of hypoxia (Figure 5, 8).

Because some demersal fish move to non-hypoxic areas (inshore or offshore of the low oxygen, e.g., Craig et al. 2002), the benthic infaunal composition changes (Figure 6, 8) may result in less preferred prey for demersal fish. The displacement of demersal feeding fish by hypoxia could also lead to increased energy expended due to migration, which may overall result in negative impacts on fish growth and reproduction. Conversely, demersal fish, like the Atlantic croaker forage opportunistically on any available prey (Overstreet & Heard 1978). Displacement of Atlantic croaker by hypoxia from suitable habitat, therefore, may not be as detrimental to the population as predicted because alternative prey remain available. However, my current examination of preliminary stomach content analyses by J.K. Craig (pers. comm.) indicate that croaker may be a selective opportunist, because there is a greater variety of taxa (e.g. Brachyura, Gammaridea, Dendrobrachiata, Mysidacea, *Squilla empusa*) in the stomachs than in the sediment samples. Furthermore, the collection of macroinfauna by box coring seldom captures the less abundant, highly motile benthos like the crustaceans that are heavily preyed upon. Discrepancies between stomach content and benthic community composition from a box core need to be taken into consideration when determining electivity of prey by demersal predators.

Polychaetes were the most abundant individuals in each of the three areas and the seasonal station and would be the most available prey for demersal predators within the study area. In the hypoxic area two abundant polychaetes, *Paraprionospio pinnata* and *Magelona* sp. H, are

known to be resistant to extremely low dissolved oxygen concentrations (Diaz and Rosenberg 1995, Yokoyama 1995), would therefore compose most of the community, and be the most available prey. The two most abundant polychaetes at station C6B were *P. pinnata* and *Armandia maculata* (Figure 16) similar to the results, especially in September-October 2003 of Rabalais et al. (2001a). Benthos such as penaeid shrimp, portunid crabs, and brittle stars that actively move through or above the sediments require more oxygen for metabolism and have lower survival under low oxygen conditions (Theede et al. 1969). Larger demersal fish tend to consume crustaceans in non-hypoxic conditions (Overstreet & Heard 1978, Matlock & Garcia 1983); however, in the hypoxic area and after summer hypoxia at C6B, few crustaceans were found and were not available as food items (Figure 6).

In July 2004 the infaunal abundance did not decline at station C6B as expected based on prior studies when hypoxia/anoxia occurred in the bottom water (Figure 14) (Rabalais et al. 2001a). The benthos did not decline in July after the oxygen levels fell below 2 mg l⁻¹ (Figure 14) possibly because the period of hypoxia prior to sampling was only 19 days compared to the low abundance following at least 30 days of hypoxia in Rabalais et al. 2001a. The most abundant infauna were the polychaete *Paraprionospio pinnata* and the bivalve *Nuculana acuta*. Harper et al. (1981) also found some polychaetes and bivalves to be the most abundant and least affected by hypoxia. In another study, the abundance of *P. pinnata* was 52 individuals m⁻² in July and increased to 973 individuals m⁻² in September (Gaston 1985), which was just the opposite in this study. Some benthos such as gastropods (*Nassarius* spp.) and the polychaete (*Glycera dibranchiata*) use gas bubbles, oxygen reservoirs, or high oxygen affinity hemoglobin to survive during hypoxia until activating anaerobic respiration (Mangum & Van Winkle 1973). The lack of decline in the July 2004 abundance may be due to these or similar survival techniques.

No studies in the northern Gulf documented a high infaunal abundance (similar to spring abundance) when conditions were almost anoxic (Figure 12). Usually the summer abundances drastically decrease with the onset of hypoxia (Harper et al. 1981, Gaston & Edds 1994, Rabalais et al. 2001a). At oxygen concentrations $\leq 0.5 \text{ mg l}^{-1}$ macroinfauna are found dead on the seafloor (Rabalais et al. 2001b). The bottom oxygen at C6B fell to 0.5 mg l^{-1} only 14 d before sampling occurred in July 2004. It is possible that the July samples were taken at the beginning of declining abundances.

In late summer 2004 (August and September) the abundances of infauna declined following continued low oxygen concentrations (Figure 14). Although the macroinfaunal abundance was low, the bottom water was well oxygenated. The combination of summer hypoxia and the physical disturbance of the sediment (Dernie et al. 2003) by Hurricane Ivan may have resulted in the low abundance of macroinfauna in October 2004 (Figure 14). Another possibility is that demersal predators returned to the oxygenated area of C6B and consumed the infauna. Low abundances may have also occurred due to low macroinfaunal recruitment in the fall.

The winter months (November –January 2004) were similar to each other but different in community composition compared to other periods. Winter months follow a period of predation, a decrease in food supply, colder temperatures and fewer planktonic recruits. The other group of months (February – July) occur when there is higher surface water production in the spring resulting in increased food resources that would support infaunal meroplankton and eventually provide food resources in the sediment for opportunistic surface deposit feeders (e.g., TOC in May 2004).

The vertical distribution patterns of the benthos in summer 2003 were unexpected (Figure 9, 10, 11). The inshore area had the most organisms at the sediment surface (~70 individuals

section⁻¹ at station 26 and 27), therefore probably the most available prey for potential demersal fish. The benthos were concentrated at the sediment surface in offshore stations 49 and 65 but with lower abundances at the surface compared to the inshore area. In the inshore and offshore area, the benthos found at the surface section were composed of surface deposit feeders and suspension/filter feeders (Table 3) indicating that the benthos were distributed vertically as expected in the well-oxygenated sediment. The lowest abundance of infauna near the sediment surface was at hypoxic stations 2 and 58 (~15 individuals section⁻¹). A similar pattern among the remaining hypoxic stations was not found. The hypoxic stations did not all have surface deposit feeders at the surface (Table 3). Some were subsurface feeders and carnivores thus providing evidence of migration to the sediment surface.

Table 3. Feeding guilds of abundant infauna at the summer and C6B stations. SDF = surface deposit feeder, SSDF = sub-surface deposit feeder, SF = suspension feeder and C = carnivore. Guilds were taken from Gaston & Nasci (1988), Rakocinski et al. (1997), and Gaston (1998).

TAXA	GUILD			
	SDF	SSDF	SF	C
<i>Abra aequalis</i>	X			
<i>Aricidea wassi</i>	X			
<i>Cossura</i> sp. A	X			
<i>Gyptis vittata</i>				X
<i>Magelona</i> sp. H	X			
<i>Mediomastus californiensis</i>		X		
<i>Mulinia lateralis</i>			X	
<i>Nemertea</i> sp. A				X
<i>Nuculana acuta</i>		X		
<i>Paraprionospio pinnata</i>	X			
<i>Prionospio pygmaea</i>	X			
<i>Sigambra tentaculata</i>				X
<i>Tellina versicolor</i>	X		X	
<i>Tharyx</i> cf. <i>annulosus</i>	X			

The expected pattern of infaunal migration to the surface under hypoxic conditions, however, was evident at station C6B. The greater abundance of infauna at a depth of 4 cm in May shifted to the surface in June and July (Figure 19). As a result there would be more available prey at the surface for demersal fish during hypoxia. The most available food source were polychaetes, especially *Paraprionospio pinnata*, *Mediomastus californiensis*, *Sigambra tentaculata*, and *Gyptis vittata*. Not all of these are surface deposit feeders (Table 3). Due to sub-surface deposit feeders found near the surface, migration upward to better oxygenated conditions may occurred. As noted by Jorgensen (1980) and Baden et al. (1990), benthos migrate to the surface during hypoxia as the upward migration of the redox layer reduces the suitable habitat, resulting in increased prey availability at the sediment-water interface. The infauna at the surface of the sediment in each of the station groups (Inshore, Hypoxia, Offshore) and at station C6B would be the most likely available prey for demersal fish.

At C6B an annual cycle of vertical distribution reflecting seasonal temperatures, primary production, hypoxic conditions, and predation was documented. There were few infauna in the upper sections of the vertical cores in the post hypoxic months of September through November 2003 (Figure 19). In December 2003 and January 2004, higher abundances of *Aricidea wassi*, *Cossura* sp. A, *Mediomastus californiensis*, and *Tharyx* cf. *annulosus* were deeper in the sediment (~ 5 cm). The vertical distribution in March 2004 may reflect recent recruitment because of the abundance of *A. wassi*, *C. sp. A*, and *Nuculana acuta* at the surface. In April and May 2004 there were higher abundances with increasing depths as surface feeders (*C. sp. A*) moved deeper into the sediment possibly due to better food resources or predator avoidance. From June to July the benthos, such as *A. wassi* and *Abra aequalis*, moved toward the surface where the sediments were more oxygenated. The highest number of organisms per section was

found in the surface layers in July 2004 (Figure 19), when the dissolved oxygen concentration was lowest (Figure 12). Consumption of *A. wassi* and *Paraprionospio pinnata* by demersal fish may have occurred in August 2004 (when the bottom-water became oxygenated for a short period) as suggested by their low abundance in the 0-1 cm above their highest abundance in the 1-2 cm section. In fall 2004, the September and October vertical distribution of benthos may represent post-predation numbers or recent recruitment or both. In September and October surface samples, surface deposit feeders were mostly found, except for *Sigambra tentaculata*, *Mediomastus californiensis*, and *Gyptis vittata* (Table 3).

The ^7Be distributions were most likely caused by bioturbation and not other physical processes. Downward transport of ^7Be into the sediment can be produced by physical or biological mixing or deposition of new sediment. Physical reworking of cohesive muddy sediments by waves and currents is likely to be restricted to the upper few millimeters of the seabed. An exception is during hurricanes and tropical storms (Bentley et al. 2002), which impacted the study area only once during the period of observation. Also, the location of C6B is relatively far away from large sources of fresh sediment and therefore the seasonal variation of ^7Be is not due to seasonal sediment deposition. The depth of ^7Be penetration did not always correspond with the vertical distribution of the benthos. ^7Be and vertical distributions displayed similar patterns in the months of April, July and August 2004 (Figure 19, 20). No detection of ^7Be radioisotopes in July may be a result of the severe oxygen depletion (limited mobility and activity of bioturbators). The least ^7Be penetration depth in August was representative of the abundance of surface deposit feeders at the sediment surface and no bioturbators or any other infauna at depth. From the radioisotope penetration depths, the most likely availability of prey

for demersal predators was in August, for which the vertical distribution of abundance indicated potential feeding by demersal predators (Figure 19, 20).

The intent of this study was to examine the benthic infauna as potential prey for demersal fish in their preferred habitat that becomes unsuitable during extended periods of bottom-water hypoxia. The benthic community structure of the hypoxic area was unexpected. In this study, sediment properties may have been a more important factor than oxygen conditions in determining benthic community structure. The reoxygenation of the water column by storms in 2003 and the shorter period of hypoxia at C6B did not impact the benthic community like previous years with longer periods of severe hypoxia. The impact of hypoxia on benthic infaunal communities and their potential as prey for demersal fish, and therefore local fishery and recreational economies, requires a longer-term analysis of the range of hypoxic conditions across the suitable fish habitat. Future studies that frequently monitor benthic communities over the entire shelf in early-spring to late-summer when bottom water becomes hypoxic and back to non-hypoxic are needed to understand the effects of hypoxia on benthic food webs.

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APPENDIX 1. MACROINFAUNA IDENTIFICATION AT THE SUMMER STATIONS AND SEASONAL STATION C6B

Table 4. Benthic infauna at the summer stations during August 2003 off the coast of Louisiana.
 *** Benthic organisms could not be identified to family level

PHYLUM	FAMILY	LOWEST TAXON IDENTIFIED
Annelida	Ampharetidae	<i>Ampharete</i> sp. A
		<i>Amphicteis gunneri</i>
		<i>Melinna cristata</i>
		<i>Sabellides</i> sp. A
	Amphinomidae	<i>Paramphinome</i> sp. B
		<i>Pseudoeurythoe ambigua</i>
	Aphroditidae	Aphroditidae
	Capitellidae	<i>Decamastus</i> sp. A
		<i>Mediomastus californiensis</i>
		<i>Notomastus latericeus</i>
		<i>Notomastus daueri</i>
	Chaetopteridae	<i>Mesochaetopterus capensis</i>
	Chrysopetalidae	<i>Bhawania heteroseta</i>
	Cirratulidae	<i>Chaetozone</i> sp. A
		<i>Chaetozone</i> sp. D
		<i>Cirriformia</i> sp. B
		<i>Tharyx</i> cf. <i>annulosus</i>
	Cossuridae	<i>Cossura</i> sp. A
	Flabelligeridae	<i>Diplocirrus</i> sp. A
	Glyceridae	<i>Glycera americana</i>
		<i>Glycera</i> sp. C
		<i>Ophioglycera</i> sp. A
	Goniadidae	<i>Goniada littorea</i>
Hesionidae	<i>Gyptis vittata</i>	
Lumbrineridae	<i>Lumbrineris verrilli</i>	
Magelonidae	<i>Magelona pettiboneae</i>	
	<i>Magelona</i> sp. B	
	<i>Magelona</i> sp. H	
	<i>Magelona</i> sp. I	
Maldanidae	<i>Asychis elongatus</i>	
	<i>Clymenella torquata</i>	

(Table 4. cont'd)

	<i>Euclymene</i> sp. B
Nephtyidae	<i>Aglaophamus verrilli</i>
	<i>Nephtys incisa</i>
	<i>Ceratocephale oculata</i>
Nereidae	<i>Neanthes micromma</i>
	<i>Neanthes succinea</i>
Onuphidae	<i>Diopatra cuprea</i>
	<i>Onuphis oculata</i>
	<i>Onuphis</i> sp. A
Opheliidae	<i>Armandia maculata</i>
Orbiniidae	<i>Leitoscoloplos fragilis</i>
	<i>Leitoscoloplos robustus</i>
	<i>Scoloplos capensis</i>
Owenidae	<i>Owenia fusiformis</i>
Paraonidae	<i>Aricidea fragilis</i>
	<i>Aricidea wassi</i>
	<i>Cirrophorus americanus</i>
	<i>Cirrophorus</i> sp.
	<i>Levinsenia gracilis</i>
Phylloceidae	<i>Anaitides longipes</i>
	<i>Anaitides</i> sp.
	<i>Phyllodoce arenae</i>
Pilargidae	<i>Ancistrosyllis jonesi</i>
	<i>Sigambra bassi</i>
	<i>Sigambra tentaculata</i>
Poecilochaetidae	<i>Poecilochaetus johnsoni</i>
Polynoidae	<i>Lepidasthenia</i> sp. A
	<i>Lepidonotus sublevis</i>
Sabellidae	<i>Megalomma bioculatum</i>
	<i>Megalomma</i> sp. A
Sigalionidae	<i>Sthenelais</i> sp. A
Spionidae	<i>Paraprionospio pinnata</i>
	<i>Prionospio cirrifera</i>
	<i>Polydora socialis</i>
	<i>Prionospio cristata</i>
	<i>Prionospio pygmaea</i>
	<i>Prionospio steenstrupi</i>
	<i>Scolelepis squamata</i>
	<i>Scolelepis texana</i>
	<i>Spiophanes bombyx</i>

(Table 4. cont'd)

		<i>Spiophanes missionensis</i>
		<i>Spiophanes wigleyi</i>
		<i>Amaeana trilobata</i>
		<i>Neoamphitrite</i> sp. A
		<i>Spilocuma watlingi</i>
		<i>Oxyurostylis smithi</i>
		<i>Leucon americanus</i>
		Ostracoda sp. 1
		Ostracoda sp. 2
		<i>Ampelisca abdita</i>
		<i>Ampelisca</i> sp. A
		<i>Batea catharinensis</i>
		<i>Microprotopus shoemakeri</i>
		<i>Photis macromana</i>
		<i>Listriella barnardi</i>
		<i>Americhelidium americanum</i>
		<i>Uromunna hayesi</i>
		<i>Albunea paretii</i>
		<i>Emerita talpoida</i>
		<i>Leptochela serratorbita</i>
		<i>Trachypenaeus similis</i>
		<i>Callianassa</i> sp.
		<i>Lucifer faxoni</i>
		<i>Ogyrides alphaerostris</i>
		<i>Processa</i> sp.
		<i>Persephona mediterranea</i>
		<i>Osachila</i> sp.
		Decapodid
		<i>Pinnixia</i> sp.
		unidentified juvenile
		<i>Speocarcinus</i> sp.
		<i>Pagurus</i> sp.
		unidentified juvenile
Chordata	Branchiostomidae	<i>Branchiostoma caribaeum</i>
	Gobiidae	goby
Cnidaria	***	Athenaria
	***	Thenaria
Echinodermata	Ophiidermatidae	<i>Hemipholis elongata</i>
	***	Holothuroidea

(Table 4. cont'd)

Echiura	Echiuridae	<i>Thalassema hartmani</i>
Hemichordata	Ptychoderidae	<i>Balanoglossus</i> sp.
Mollusca	Arcidae	<i>Anadara ovalis</i>
		<i>Barbatia candida</i>
		<i>Barbatia tenera</i>
	Buccinidae	<i>Cantharus cancellarius</i>
	Cerithiidae	<i>Cerithium muscarum</i>
		<i>Cerithium</i> sp.
	Corbulidae	<i>Corbula krebsiana</i>
	Epitoniidae	<i>Epitonium</i> sp.
	Mactridae	<i>Mulinia lateralis</i>
	Marginellidae	<i>Hyalina avena</i>
		<i>Hyalina</i> sp.
	Nassariidae	<i>Nassarius acutus</i>
	Naticidae	<i>Natica pusilla</i>
		<i>Polinices duplicatus</i>
		<i>Tectonatica pusilla</i>
	Nuculanidae	<i>Nuculana acuta</i>
	Nuculidae	<i>Nucula proxima</i>
	Pyramidellidae	<i>Odostomia gibbosa</i>
		<i>Odostomia laevigata</i>
		<i>Turbonilla portoricana</i>
		<i>Turbonilla</i> sp.
	Retusidae	<i>Volvulella texasiana</i>
	Scrobiculariidae	<i>Abra aequalis</i>
	Tellinidae	<i>Phylloda squamifera</i>
		<i>Tellina versicolor</i>
	Veneridae	<i>Chione cancellata</i>
		<i>Chione</i> sp.
	Vitrinellidae	<i>Vitrinella floridana</i>
	***	unidentified bivalve
	***	unidentified gastropod
Nemertea	***	Nemertea sp. A
	***	Nemertea sp. B
Phoronida	Phoronidae	<i>Phoronis</i> sp.
Platyhelminthes	***	Polycladida
Sipuncula	Aspidosiphonidae	<i>Aspidosiphon</i> sp.
	Golfingiidae	<i>Golfingia</i> sp.
		<i>Phascolion</i> sp.
	***	Sipuncula sp. B

Table 5. Benthic infauna at station C6B from September 2003 to October 2004 off the coast of Louisiana. *** Benthic organism could not be identified to family level

PHYLUM	FAMILY	LOWEST TAXON IDENTIFIED
Annelida	Ampharetidae	<i>Ampharete</i> sp. A <i>Sabellides</i> sp. A
	Amphinomidae	<i>Paramphinomes</i> sp. B
	Capitellidae	<i>Mediomastus californiensis</i> <i>Notomastus latericeus</i>
	Chaetopteridae	<i>Mesochaetopterus capensis</i>
	Cirratulidae	<i>Tharyx</i> cf. <i>annulosus</i> <i>Chaetozone</i> sp. D
	Cossuridae	<i>Cossura</i> sp. A
	Flabelligeridae	<i>Brada villosa</i>
	Glyceridae	<i>Glycera</i> sp. C
	Hesionidae	<i>Gyptis vittata</i>
	Magelonidae	<i>Magelona pettiboneae</i> <i>Magelona</i> sp. H <i>Magelona</i> sp. I
	Maldanidae	<i>Asychis elongatus</i>
	Nephtyidae	<i>Aglaophamus verrilli</i> <i>Nephtys incisa</i>
	Onuphidae	<i>Diopatra cuprea</i>
	Opheliidae	<i>Armandia maculata</i>
	Oweniidae	<i>Owenia fusiformis</i>
	Paraonidae	<i>Aricidea wassi</i> <i>Cirrophorus americanus</i>
	Pilargidae	<i>Ancistrosyllis jonesi</i> <i>Sigambra tentaculata</i>
	Polynoidae	Genus sp. C <i>Lepidasthenia</i> sp. A
	Sigalionidae	<i>Sthenelais</i> sp. A
	Spionidae	<i>Paraprionospio pinnata</i> <i>Polydora socialis</i> <i>Prionospio cirrifera</i> <i>Prionospio cristata</i>

(Table 5. cont'd)

		<i>Prionospio steenstrupi</i>
		<i>Amaeana trilobata</i>
Arthropoda	Terbellidae	<i>Alpheus</i> sp.
	Alpheidae	<i>Ogyrides alphaerostris</i>
	Ogyrididae	<i>Trachypenaeus similis</i>
	Penaeidae	<i>Speocarcinus lobatus</i>
	Goneplacidae	<i>Speocarcinus</i> sp.
	Xanthidae	unidentified juvenile
	Albuneidae	<i>Lepidopa websteri</i>
	Isaeidae	<i>Photis macromana</i>
	Oedicerotidae	<i>Americhelidium americanum</i>
		<i>Ameroculodes</i> sp. A
	Ampeliscidae	<i>Ampelisca</i> sp. A
	Liljeborgiidae	<i>Listriella barnardi</i>
	Diastylidae	<i>Oxyurostylis smithi</i>
	***	Ostracoda sp. 1
	Idoteidae	<i>Edotea montosa</i>
	Munnidae	<i>Uromunna hayesi</i>
Chordata	Gobiidae	goby
Echinodermata	Ophiactidae	<i>Hemipholis elongata</i>
Mollusca	Scrobiculariidae	<i>Abra aequalis</i>
	Arcidae	<i>Anadara ovalis</i>
		<i>Anadara transversa</i>
	Cerithiidae	<i>Cerithium</i> sp.
	Ungulinidae	<i>Diplodonta semispera</i>
	Naticidae	<i>Natica pusilla</i>
	Nassariidae	<i>Nassarius acutus</i>
	Nuculanidae	<i>Nuculana acuta</i>
	Tellinidae	<i>Phylloda squamifera</i>
		<i>Tellina versicolor</i>
	Vitrinellidae	<i>Vitrinella floridana</i>
	Retusidae	<i>Volvulella texasiana</i>
Nemertea	***	Nemertea sp. A
	***	Nemertea sp. B
Platyhelminthes	***	Polyclacida

APPENDIX 2. REFERENCES FOR MACROINFAUNA IDENTIFICATION

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APPENDIX 3. GRAIN SIZE COMPOSITION FOR SUMMER AND C6B SEDIMENT SAMPLES

Table 6. Location and sediment composition of 15 summer stations sampled during August 2003 in coastal Louisiana. I = inshore, H = hypoxia, O = offshore.

LOCATION		COMPOSITION (%)							
AREA	STATION	VERY COARSE SAND	COARSE SAND	MEDIUM, FINE, VERY FINE SAND	CLAY	SILT	TOTAL SAND	TOTAL MUD	
I	1	0.26	0.05	99.69	51.47	48.53	78.06	21.94	
I	26	0.01	0.01	99.98	96.99	3.01	90.44	9.56	
I	27	1.34	1.38	97.29	92.67	7.33	2.17	97.83	
I	32	7.98	0.28	91.75	77.38	22.62	26.96	73.04	
H	2	6.30	1.03	92.67	69.84	30.16	18.40	81.60	
H	16	0.89	0.91	98.20	67.00	33.00	43.82	56.18	
H	25	24.98	0.17	74.86	82.85	17.15	37.43	62.57	
H	43	1.21	0.30	98.50	88.26	11.74	56.38	43.62	
H	58	7.52	0.45	92.03	69.78	30.22	67.16	32.84	
O	37	1.74	0.29	97.97	89.07	10.93	75.61	24.39	
O	38	8.93	1.24	89.83	94.90	5.10	89.92	10.08	
O	42	1.97	0.20	97.83	84.05	15.95	78.87	21.13	
O	48	0.17	0.02	99.81	88.21	11.79	90.30	9.70	
O	49	0.57	0.10	99.33	91.12	8.88	86.57	13.43	
O	65	0.22	0.02	99.76	95.94	4.06	86.02	13.98	

Table 7. Location and sediment composition of station C6B from September 2003 to October 2004 in coastal Louisiana.

LOCATION		COMPOSITION (%)						
MONTH	STATION	VERY COARSE SAND	COARSE SAND	MEDIUM, FINE, VERY FINE SAND	CLAY	SILT	TOTAL SAND	TOTAL MUD
Sept. 2003	C6B	1.34	1.38	97.29	92.67	7.33	2.17	97.83
Oct. 2003	C6B	24.25	5.71	70.05	89.95	10.05	1.51	98.49
Nov. 2003	C6B	10.73	6.13	83.14	93.33	6.67	1.13	98.87
Dec. 2003	C6B	1.34	0.93	97.73	94.44	5.56	5.78	94.22
Jan. 2004	C6B	10.43	3.49	86.08	71.08	28.92	4.60	95.40
Feb. 2004	C6B	1.57	1.17	97.26	86.60	13.40	10.14	89.86
Mar. 2004	C6B	1.93	2.76	95.31	92.70	7.30	3.18	96.82
Apr. 2004	C6B	3.90	1.71	94.38	91.65	8.35	3.94	96.06
May 2004	C6B	6.68	5.78	87.54	97.08	2.92	3.32	96.68
Jun. 2004	C6B	2.41	2.89	94.70	89.37	10.63	2.83	97.17
Jul. 2004	C6B	1.62	1.31	97.07	71.92	28.08	5.94	94.06
Aug. 2004	C6B	2.92	1.35	95.73	80.92	19.08	3.63	96.37
Sep. 2004	C6B	3.05	1.78	95.16	74.56	25.44	2.67	97.33
Oct. 2004	C6B	1.21	0.28	98.51	53.67	46.33	44.45	55.55

VITA

Melissa Millman Baustian grew up in the eastern Iowa small town of St. Donatus. She attended Dubuque Senior High School and graduated in May 1999. She attended Iowa State University and graduated in May 2003 with a Bachelor of Science degree in biology. Soon after, she moved to Louisiana to work at Louisiana Universities Marine Consortium (LUMCON). In the fall of 2003 she began her Master of Science program at Louisiana State University in the Department of Oceanography and Coastal Sciences.