

Spatial heterogeneity of benthos on the Carolina continental slope: large (100 km)-scale variation

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ABSTRACT: Large-scale spatial heterogeneity of macrofaunal and microbial communities was examined on the continental slope off North and South Carolina, USA, by comparing 3 sites, separated by 130 to 150 km and all at 850 m water depth. Significant variation was found among macrofaunal assemblages at all 3 sites, and between microbial counts at 2 sites. We investigated the hypothesis that 100 km scale heterogeneity was driven by variation in organic C flux to the sea floor. The northernmost site (Site III, off Cape Hatteras, NC) was found to have macrofaunal abundances ($> 55\,000\text{ m}^{-2}$) higher than any previously recorded from this depth, and significantly higher than those at Site II (off Cape Lookout, NC) ($21\,319\text{ m}^{-2}$) or Site I (off Charleston, SC) ($9\,438\text{ m}^{-2}$). Trends in macrofaunal abundance did not follow those of sediment TOC (total organic carbon), but agreed well with estimates of total carbon flux for the 3 sites. Mixing coefficients determined from profiles of naturally occurring ^{234}Th (half life 24 d) indicate that the sediments at Site III are mixed 2 to 6 times faster than at the other 2 sites, which is consistent with the trends in macrofaunal abundance and biomass. Using ^{14}C -based sedimentation rates and sediment carbon content, we estimated carbon flux to be 0.6, 20 and $>70\text{ g C m}^{-2}\text{ yr}^{-1}$ at Sites I, II and III, respectively. Inventories of ^{234}Th and downcore concentration profiles of dissolved SO_4^{2-} , ΣCO_2 and CH_4 within the sediment provided evidence that the flux of metabolizable carbon was greater at Site III than at the other sites. Polychaetes, which comprised 43, 74 and 65 % of the fauna at Sites I, II and III, respectively, exhibited lower diversity, higher dominance, and a completely different species composition at Site III than at the other 2 sites. *Scalibregma inflatum* and *Aricidea quadrilobata* comprised 33 % of total macrofauna at Site III, but were absent at Sites I and II. The species composition, high dominance, and prevalence of juveniles among polychaetes at Site III is suggestive of a response to organic enrichment. Enrichment of the Site III benthos is attributed to physical oceanographic and geophysical causes, including Gulf Stream-induced upwelling, a confluence of currents focused by bottom topography, and lateral inputs resulting from mass wasting processes. Despite significant differences in macrofaunal abundance, Sites I and II exhibited considerable overlap in microbial counts, polychaete species composition, dominance and diversity patterns.

INTRODUCTION

The continental slope environment has been acknowledged to be a location of remineralization and burial of large quantities of organic carbon (Premuzic et al. 1982, Walsh et al. 1985). Organic carbon on the slope and rise has been estimated to represent 90 % of the total inventory deposited during the Holocene in

marine sediments (Romankevich 1984). Approximately 26 % of the anaerobic carbon oxidation in marine sediments occurs between 200 and 2000 m water depth as a result of the significant carbon flux to the sea floor, even though that region represents only 9 % of the marine sediment area (Henrichs & Reeburgh 1987). It has been proposed that the slope acts as a major sink of excess atmospheric CO_2 generated by fossil fuel production via the export of shelf primary productivity (Walsh et al. 1985); however, other studies appear to refute this idea (Rowe et al. 1986, Biscaye et al. 1988).

The organic carbon in slope sediments is derived from shelf-exported material (both autochthonous as

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well as detrital) and overlying productivity (Rowe et al. 1986, Biscaye et al. 1988, Falkowski et al. 1988, Venkatesan et al. 1988, Walsh et al. 1988). Off the coast of New England, USA, as much as 30 % of the annual shelf production may be stored or degraded in slope sediments (Walsh 1991). Fresh deposits of phyto-detritus, which appear to be moving downslope, indicate that the slope experiences significant vertical inputs and horizontal transport of organic matter south of Georges Bank (Hecker 1990a). Localized areas of high productivity over the slope are associated with upwelling and intrusion events created by the interaction of the shelf/slope break and boundary currents such as the Gulf Stream (Janowitz & Pietrafesa 1980, Pietrafesa et al. 1985).

The slope environment is also rich in natural resources and has been exploited by commercial fisheries for invertebrates (Wigley & Theroux 1975) and fishes (Beamish & Chilton 1982, Merrett 1989) and by the petroleum industry (U.S. Dept. of Interior 1989). Despite considerable interest in diverse phenomena associated with the continental slope benthos, there is relatively little knowledge of the environments and processes that are responsible for structuring and maintaining benthic communities on the slope. The benthos has been studied in a number of basins and troughs occurring at upper slope depths, including the Santa Catalina Basin (Jumars 1975, Smith & Hamilton 1983, Smith et al. 1986, Smith et al. 1987), the San Diego Trough (Thistle & Eckman 1990), and the Porcupine Seabight (Gooday 1984). Among open slope environments, only the western Atlantic benthic communities have been examined systematically. Wigley & Theroux (1981) conducted a survey of the Middle Atlantic Bight benthos, describing taxonomic composition and geographic distributions of the macrofauna at 563 locations from 4 to 3000 m depth. The most thorough slope surveys may be a series of reports generated in response to concerns about exploratory drilling conducted on the North, Middle and South Atlantic Slope and Rise (Blake et al. 1985, Blake et al. 1987). These studies described a diverse set of communities off North and South Carolina at depths between 583 and 3494 m. More than one third of 900 benthic infaunal species described in these reports were new to science. In addition, several researchers have included Atlantic slope stations as part of depth zonation studies of deep-sea fauna (Sanders et al. 1965, Hessler & Sanders 1967, Rowe & Menzies 1969, Rowe et al. 1974, Grassle et al. 1975, Haedrich et al. 1975, Rowe et al. 1982, Hecker 1990b).

The objective of this study was to assess the spatial heterogeneity in microbial and macrofaunal communities among 3 slope sites in the South Atlantic Bight. Though only a small portion of the vast ocean floor has

been studied by biologists, it is clear that there is tremendous heterogeneity in faunal biomass, abundance, and composition (Rowe 1983, Gage & Tyler 1991). Most studies of non-vent systems on the continental slope and deeper point to the input of metabolizable organic material as a primary control on bacterial abundance (Deming & Yager 1992), and on benthic community structure (Smith & Hinga 1983, Graf 1989, Mayer 1989, Gooday & Turley 1990). Physical factors believed to influence benthic community composition and lifestyles in the deep sea include water depth (Jumars & Gallagher 1982), topography, flow regime (Levin & Thomas 1989), sediment grain size and degree of heterogeneity (Gray 1974, Rhoads 1974), and bottom-water oxygen concentration (Sanders 1969, Wishner et al. 1990, Levin et al. 1991).

In the present study, an attempt was made to identify the sources of observed heterogeneity, with regard to organic matter inputs and other chemical parameters. We hypothesized that variations among the 3 slope communities would be associated with differing input of organic carbon to the systems. Both macrofaunal and bacterial abundances were expected to be positively correlated with organic carbon flux and sediment total organic carbon, with microbes serving as a possible intermediary between organic matter and the macrofauna. To complement the biological data collected at each site (abundance, biomass, vertical distributions, and identification of major taxa), porewater profiles of sulfate, dissolved inorganic carbon, and methane, and solid-phase measurements of a naturally occurring particle tracer (^{234}Th , half life of 24 d) were used to understand the complex relationships among biological, chemical, and sedimentological processes. This study was part of a larger investigation aimed at investigating important spatial scales of variation in biogeochemical processes on the continental slope (Blair et al. 1989, DeMaster et al. 1989).

STUDY SITE DESCRIPTION

Three Mid-Atlantic continental slope sites were studied as part of this research project (Fig. 1). All were located in approximately 850 m water depth. The southernmost (Site I) and middle site (Site II) were separated by 150 km, whereas the middle and northernmost site (Site III) were separated by 135 km.

Site I was located at 32°52' N, 76°27' W, 177 km east of Charleston, South Carolina, USA. The slope of the sea floor here is slight (2 to 3°), and there is minimal fine-scale topography. The floor at this site appears current swept and small, symmetric ripples were visible occasionally (Fig. 2a). Arborescent foraminifera (1 to 3 cm, 4.0 m^{-2}) and small burrow openings (ca 0.5 cm

diameter, 2.9 m^{-2}) were the most common structures visible on the sediment surface. The dominant megafauna at this site included synaptobranchid eels *Synaptobranchus* spp. and rattail fish *Nezumia* spp.

The middle site (Site II) was located at $34^{\circ}15' \text{ N}$, $75^{\circ}44' \text{ W}$, 82 km east of Cape Lookout, North Carolina, USA. The slope here was approximately 15 to 20° . Site II was characterized by the presence of large numbers of biogenically produced pits (ca 15 cm diameter, 5 cm deep) and sediment mounds (ca 25 to 30 cm diameter, 5 to 10 cm high) covering up to 50 % of the sediment surface (Fig. 2b). Mound, pit and level microenvironments were sampled separately, but were combined for the present study, as they were shown to have little effect on the microbial or macrofaunal populations (Schaff 1991). Mounds were present at a density of approximately 1 m^{-2} , and pits at approximately 7.9 m^{-2} . Candidates for sediment mound and pit production included galatheid crabs *Munida valida*, a large burrowing sipunculan, and a burrowing holothurian (*Protankyra brychia* Verrill), all found in cores from this site. Other megafaunal bioturbators collected at this site included a large infaunal nemertean, and a spatangoid echinoid (possibly *Aeropsis* sp. or *Aceste* sp.). The dominant large epifauna at this site were *Munida valida*, synaptobranchid eels, rattail fishes and anemones.

The northernmost site (Site III) was located at $35^{\circ}24' \text{ N}$, $74^{\circ}48' \text{ W}$, 61 km northeast of Cape Hatteras, North Carolina. In this general region the sea floor contains numerous canyons, ridges and gullies cutting across the slope. Sampling for this study was carried out on a broad ($>1 \text{ km}$) expanse between canyons. The slope at the sampling area was approximately 30 to 35° . A dominant feature of this site was the presence of white tubes (5 to 12 cm long, up to 154 m^{-2}) belonging to the foraminiferan *Bathysiphon filiformis* (Fig. 2c) (Gooday et al. 1992). Other major epifauna at this site included the eel pout *Lysenchelys verilli*, the anemone *Actinauge verilli* and the witch flounder *Glyptocephalus cynoglossus*.

Many aspects of the oceanography of the Carolina shelf and slope region are described in papers in Atkinson et al. (1985). Several major North Atlantic currents influence the 3 sites (Johnson 1989). The bottom flow is dominated by the Deep Western Boundary Current (Barrett 1965, Rowe & Menzies 1968). This current forms from cold Labrador Sea water and flows counter to the Gulf Stream from north to south along

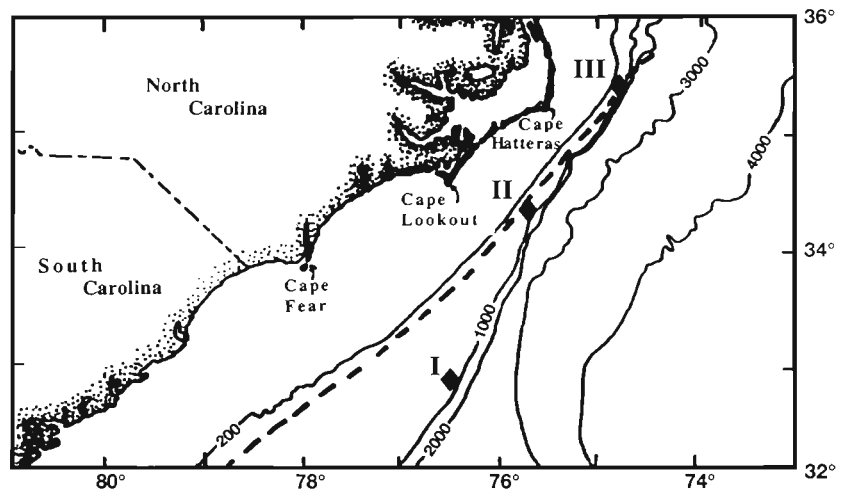
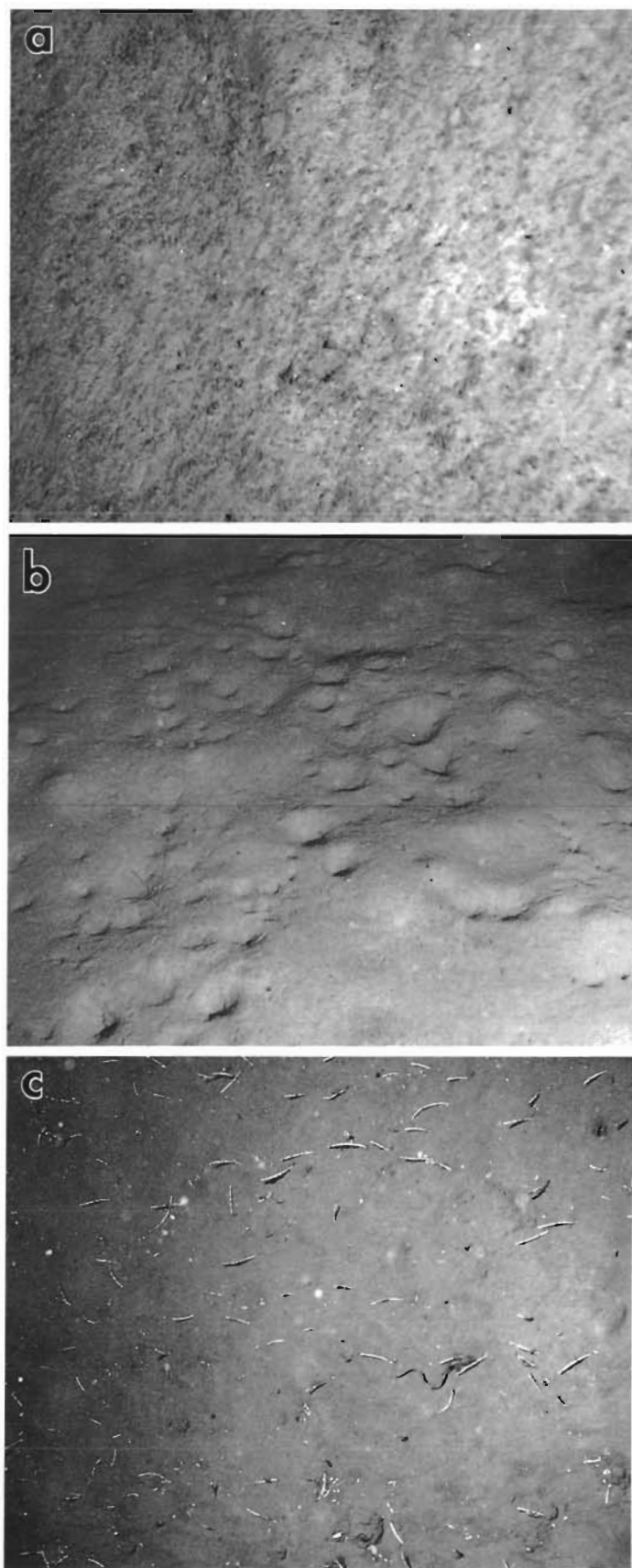


Fig. 1. Location of continental slope study sites in approximately 850 m water depth. Dashed line indicates the main axis of the Gulf Stream

the slope (US Department of Interior 1989). The Gulf Stream dominates surface flow, and may impinge on the bottom at over 800 m water depth (Rowe & Menzies 1968, Johnson 1989). The Gulf Stream generally follows the continental slope northeast from Florida to Cape Hatteras (Fig. 1), where it turns east and flows into the central Atlantic Ocean. Associated with the Gulf Stream off North Carolina are numerous, highly variable meanders, filaments and eddies which may lead to local upwelling conditions on the shelf/slope break off of Cape Hatteras (Pietrafesa et al. 1985). The Virginia Current flows south along the continental shelf in the Mid-Atlantic Bight and converges with the Gulf Stream near Cape Hatteras (Csanady & Hamilton 1988). The deeper Gulf Stream waters, which are in contact with slope waters along isopycnals, contain the local nutrient maximum. Advection of these waters during wind-induced events and seasonal overturn favor high primary productivity on the upper slope and continental shelf (Csanady & Hamilton 1988).

MATERIALS AND METHODS

Biological sample collection and shipboard processing. Samples were collected in August/September 1988, June 1989, October 1989 and August 1990. On all dates except June 1989, sampling was by divers. Sediments for faunal and some chemical analyses were collected using $15 \times 15 \times 20 \text{ cm}$ Ekman-style boxcorers (0.0196 m^2) fitted with two to four $7 \times 7 \times 15 \text{ cm}$ subcores. Twenty-nine Ekman cores (4 from Site I, 14 from Site II and 11 from Site III) were examined. Cores from the June 1989 cruise were taken using a ship-deployed 0.25 m^2 USNEL Mark III box-



core. On board, four to six $7 \times 7 \times 15$ cm subcores were inserted into each of 4 USNEL cores (2 at Site II and 2 at Site III) as part of the subsampling procedure. In most cases, two 49 cm^2 subcores from each USNEL or Ekman core were processed for infaunal analysis. Other subcores were collected for microbial counts, radiochemical, solid-phase chemical, organic geochemical, porewater chemical and grain-size analyses.

Upon recovery, subcores designated for infaunal analysis were subdivided as quickly as possible into 0–2, 2–5, 5–10 and 10–15 cm vertical fractions and sieved. The top 2 fractions were sieved on a $63 \mu\text{m}$ screen and the bottom 2 on a $300 \mu\text{m}$ screen. All samples were preserved in 10 % buffered formalin.

Microbial samples were taken from cores using sterile 10 cm^3 syringes or glass tubes of the same diameter. Samples were taken from 2 boxcores in August 1988 at Site I, from 13 boxcores at Site II (4 in August 1988, 3 in June 1989 and 6 in October 1989) and from 8 boxcores at Site III (2 in June 1989 and 6 in October 1989). In August 1988 and June 1989, 2 replicate samples were collected from each core. Samples were extruded and sectioned into 1 cm vertical fractions down to between 11 to 15 cm (depending on the core depth). The sediment samples were preserved in sterile test tubes by adding 9 ml of 2.5 % glutaraldehyde (made up using $0.2 \mu\text{m}$ filtered seawater) and were kept under refrigeration until counting was carried out.

Laboratory analyses of biota. Macrofaunal samples were returned to the laboratory, stained with rose bengal, rewashed through a $300 \mu\text{m}$ screen (to separate macrofauna from meiofauna), examined under a dissecting microscope and identified to the lowest possible taxon.

Biomass samples from Site I were taken from 2 boxcores each in August 1988 and August 1990. From Site II they were collected from 2 boxcores each in October 1989 and August 1990. Biomass samples from Site III were collected from 2 boxcores in October 1989 and 3 boxcores in August

Fig. 2. Photographs of the study sites. (a) Site I, 177 km SE of Cape Fear, NC, 850 m water depth. Small-scale features are agglutinating foraminiferans. (b) Site II, 82 km E of Cape Lookout, NC, 850 m water depth. Sediments are heavily pocked by pits (15 cm diameter) and mounds (25 to 30 cm diameter). (c) Site III, 61 km NE of Cape Hatteras, NC, 850 m water depth. White tubes (2 to 12 cm) belonging to the agglutinating foraminiferan *Bathysiphon filiformis* protrude from the sediment

1990. Since the samples were too small to weigh reliably, macrofaunal biomass was estimated from volume, determined using water displacement techniques. Macrofauna were blotted on absorbent towels and placed in microcentrifuge tubes containing a known amount of seawater. An effort was made, using jewelers forceps, to remove non-living materials such as tubes, shells and sediment in guts. The tubes were centrifuged at a slow rate in order to submerge all of the animals. A microsyringe was then used to draw off and measure the water displaced by the infauna. This step was subject to some error, but we estimate it to be no more than 10 %. Volume was converted to biomass using the minimum conversion factor (1.02 g cm^{-3}) provided by Snider et al. (1984). This method for determining biomass was used in order to keep the animals intact for further study.

In the laboratory, only selected microbial samples, corresponding to the top cm of the vertical fractions examined for macrofauna (0–1, 2–3, 5–6 and 10–11 cm), were prepared and counted. Microbial samples were diluted 1000 \times , dyed and counted using the acridine orange direct count method as described by Hobbie et al. (1977) and modified for sediments (Deming pers. comm., Levin & Thomas 1989).

Chemical analyses. Tube cores were subsampled for methane with cut-off 3 ml syringes. The 3 ml of sediment were extruded into 9 ml serum bottles (Wheaton) containing 1 ml of 1N KOH. The bottles were sealed with black rubber stoppers (Bellco Biotech) and vigorously shaken. A sample of 3 to 5 ml of headspace was removed from the bottle with a syringe by displacement with water. The syringe sample was analyzed on a Shimadzu Mini-2 Gas Chromograph equipped with a Valco 6-port loop injector, a flame ionization detector and a Molecular Sieve 5A column (1/8" o.d. \times 6', 100/120 mesh) maintained at 100 °C.

Porewater was collected for sulfate and ΣCO_2 (dissolved inorganic carbon) analyses with a sediment press (Reeburgh 1967). The concentration of dissolved sulfate was determined by the gravimetric analysis of the precipitated barium sulfate (Chanton 1985). For analysis of ΣCO_2 , 1 ml of porewater was sealed in a 3 ml serum vial (Wheaton) with a crimped red rubber stopper. Samples were either processed immediately or stored at 4 °C until analysis. Each sample was acidified with 0.2 ml of 2M H_3PO_4 . The resulting CO_2 was removed from the sample with helium (30 ml min^{-1}). The gas mixture was dried by passage through a Nafion dryer (Perma Pure). The CO_2 was separated from N_2/O_2 with a 1/8" o.d. \times 1' long column of Unibeads 1S (80/100 mesh, Alltech Assoc.) and quantitated with a thermal conductivity detector (GowMac).

Several grams of wet sediment was lyophilized for quantification of total organic carbon (TOC). After

weighing the dry sediment sufficient 4N HCl was added to eliminate CaCO_3 . The samples were left overnight with acid before drying *in vacuo*. The dried sediment was weighed again to determine carbonate loss. TOC content was measured on a Carlo Erba EA 1108 CHNS analyzer.

To utilize ^{234}Th as a particle tracer, both ^{234}Th and its parent, ^{238}U , must be measured (Aller & Cochran 1976). Sediment samples collected at 1 cm intervals were dried, ground, and then leached with near boiling 6N HCl for a period of 4 to 6 h. U and Th were separated using ion exchange techniques, with the chemical yield monitored by the addition of a $^{232}\text{U}/^{228}\text{Th}$ spike (DeMaster et al. 1985). After extraction into a 0.4M TTA (thenoyltrifluoroacetone)/benzene solution, the thorium isotopes and uranium isotopes were evaporated onto stainless steel planchets. The beta activity of ^{234}Th (and its daughter, ^{234}Pa) was measured on a low level anti-coincidence beta system, whereas the Th chemical yield and U activities were determined using an alpha spectrometer. An unspiked Th sample was processed to correct for the natural levels of ^{232}Th in the sediment samples.

Statistical analyses. Species diversity indices and rarefaction curves were generated using PRARE software (provided by J. F. Grassle). Infaunal data were log-transformed prior to statistical analysis because of inhomogeneity in the variances. All count data were analyzed using the SAS software GLM procedure (SAS Institute Inc. 1982). Microbial and macrofaunal counts were initially surveyed for site, cruise, site by cruise, core and subcore effects. Bacterial inventories were calculated for several vertical ranges; 0–5, 0–6, and 0–11 cm, by interpolating between existing points and calculating a total for that depth range. Site by cruise and subcore effects on bacteria and macrofauna were found to be nonsignificant and were removed to simplify the comparison. A posteriori least square means tests were used to clarify areas of significant difference within the data set. Biomass results were analyzed using ANOVA procedures in Statview 512+ software for the Macintosh. Percentage data (feeding groups, taxonomic groups and vertical distributions) were transformed to normalize distributions (arcsin square root; Sokal & Rohlf 1969) and compared using the same ANOVA procedures.

RESULTS

Sediment texture and chemistry

The hemipelagic sediments at Site I are a calcareous sandy mud containing as much as 72 % carbonate by weight. At Sites II and III, the hemipelagic deposits

consist of a calcareous sandy silt, which generally contains less carbonate (30 to 60 % by weight) than at Site I. Sediment grain size distributions at the 3 sites were similar, though Site II had more fine sediments (Table 1). Sediment TOC varied little in the upper 15 cm at each site. TOC was highest at Site II (2.1 %), intermediate at Site III (1.7 to 1.8 %) and lowest at Site I (1.2 %) (Table 1).

Table 1 Mean sediment characteristics for the upper 5 cm of sediment at Sites I, II and III

	Site I 870 m	Site II 850 m	Site III 850 m
% Sand	34	20	31
% Silt	37	43	43
% Clay	29	37	26
% TOC	1.2–1.6	2.0–2.5	1.5–1.7

Dissolved sulfate was depleted to a greater extent at Site III than at Sites I and II (Fig. 3a). The concentration of dissolved inorganic carbon (ΣCO_2), the principal remineralization product, was significantly higher at Site III than at the other 2 sites (Fig. 3b). Methane was detected above background levels only at Site III (Fig. 3c).

Fig. 4 shows excess ^{234}Th profiles from Sites I, II and III. ^{234}Th activity tracks particles deposited at the sediment-water interface over a period of about 5 half lives (i.e. over 100 d time scales). The magnitude of the mix-

ing coefficient, D_b , reflects the intensity of biological particle reworking in the seabed. The ^{234}Th D_b values from the 3 study sites show significantly greater mixing intensity ($p < 0.05$) at Site III (mean = $23 \text{ cm}^2 \text{ yr}^{-1}$, range 15 to $30 \text{ cm}^2 \text{ yr}^{-1}$) than at Site II (mean = $4.0 \text{ cm}^2 \text{ yr}^{-1}$, range = 2 to $9 \text{ cm}^2 \text{ yr}^{-1}$) or Site I (mean = $8.7 \text{ cm}^2 \text{ yr}^{-1}$, range = 1 to $17 \text{ cm}^2 \text{ yr}^{-1}$). No significant difference ($p > 0.05$) in the mixing coefficients was observed between Sites I and II.

The inventory of ^{234}Th in the seabed (integrated excess activity with depth) is a good indicator of the particle flux during the 3 or 4 mo prior to core collection. The mean ^{234}Th inventory from Site III cores ($25 \pm 7 \text{ dpm cm}^{-2}$) is 2 to 5 times greater ($p < 0.05$) than that observed in cores from Site II ($9.7 \pm 6.1 \text{ dpm cm}^{-2}$) or in cores from Site I ($4.4 \pm 1.9 \text{ dpm cm}^{-2}$). In a comparison of ^{234}Th inventories at Sites I and II, no significant difference ($p > 0.05$) was observed.

Bacterial counts

Bacterial samples were taken as paired subsamples (within a core), but initial statistical analysis (GLM test) for subsample variation showed no effect ($p > 0.05$). Thus, the subsamples from within each core were averaged for between-site and temporal comparisons. We observed high variation in microbial densities at the 3 sites (Fig. 5). Average surface (0–1 cm) values ranged from $1.76\text{--}1.96 \times 10^9 \text{ ml}^{-1}$ at Site I, $0.69\text{--}2.48 \times 10^9 \text{ ml}^{-1}$ at Site II, and $1.22\text{--}1.94 \times 10^9 \text{ ml}^{-1}$ at Site III.

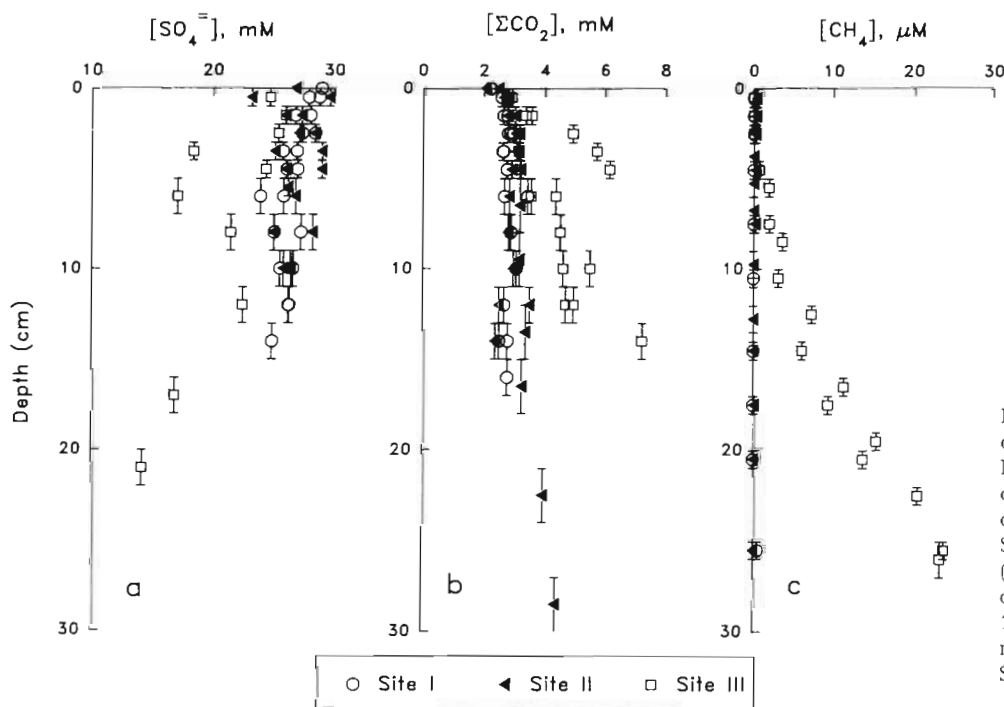


Fig. 3. Sediment porewater chemistry profiles for Sites I, II and III. (a) Dissolved sulfate concentration as a function of depth within sediment. Samples from 1988 and 1989. (b) ΣCO_2 (dissolved inorganic carbon) concentrations from 1988 and 1989. (c) Dissolved methane concentrations from SeaLink cruises in 1989 and 1991

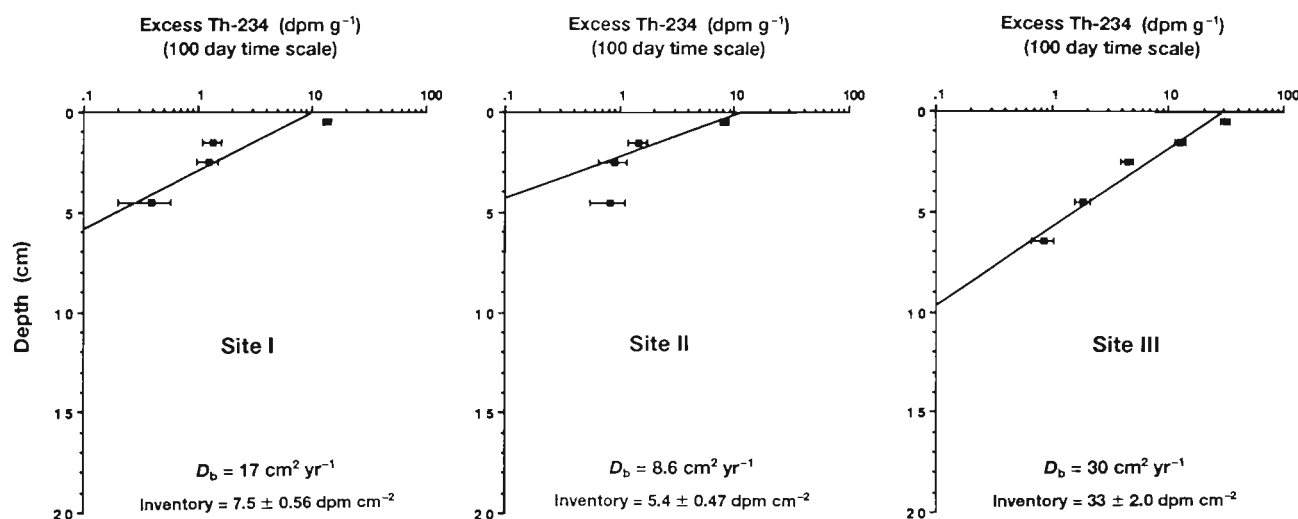


Fig. 4. Representative ^{234}Th profiles from Sites I, II and III. The mixing coefficient, D_b , is considered to be an indicator of the intensity of bioturbation in the seabed. The sediments at Site III exhibited the highest rates of particle mixing

Comparison of microbial abundances and vertical distribution between Sites I and II during the September 1988 cruise revealed no significant differences at any depth interval or for the inventory (0–6 cm) values. Site

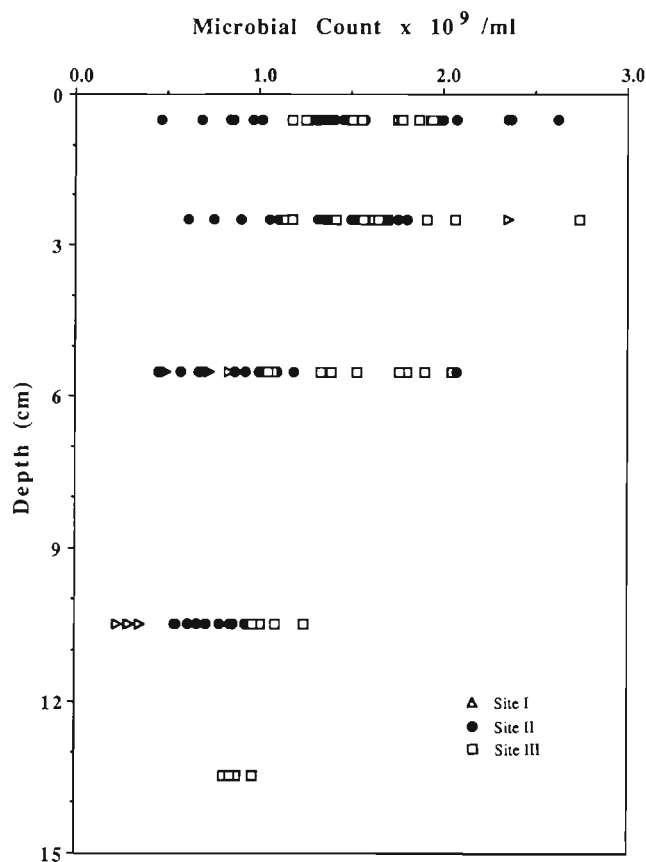


Fig. 5. Acridine orange direct counts of bacteria in sediments from Sites I, II, and III

III had greater bacterial abundances than Site II at all depth intervals in October 1989 ($p < 0.004$), and in all but the 0–1 cm fraction in June 1989 ($p < 0.015$). The 0–6 cm inventory values for both cruises also followed this pattern ($p = 0.004$ in October 1989, $p = 0.004$ in June 1989). No direct comparisons were made between Sites I and III because the 2 sites were sampled on different cruises. However, if all data from each site were combined, Site III would exhibit higher counts in the 5–6 cm ($p = 0.025$) and 10–11 cm ($p = 0.001$) intervals (Fig. 5).

Temporal comparisons of bacterial densities (within sites) were possible only at Sites II and III, as Site I was visited only once. These comparisons must be interpreted with caution, because coring methods differed in June from the other cruises, and because analytical artifacts could have introduced apparent temporal variability. Both Sites II and III exhibited similar temporal variations. At Site II, means for all depth intervals and 0–6 cm inventories for the 3 cruise dates exhibited similar trends with September 1988 > June 1989 > October 1989. The pattern of temporal variation in bacterial densities also was apparent down core at Site II. Site III was visited twice, allowing for comparison of June 1989 and October 1989. The means for the surface fraction were not different, but the 2–3, 5–6 cm and 0–6 cm inventory values were higher in June 1989 than October 1989, as observed at Site II.

Macrofaunal biomass

Biomass (average g wet wt of macrofauna $\text{m}^{-2} \pm 1 \text{ SD}$) at Site III ($54.52 \pm 14.44 \text{ g m}^{-2}$) was more than 6 times higher than at Site I ($7.19 \pm 5.51 \text{ g m}^{-2}$, $p < 0.001$) and Site II ($8.16 \pm 3.99 \text{ g m}^{-2}$, $p < 0.001$), which were not signifi-

cantly different from each other ($p = 0.77$) (Fig. 6a). Mass per individual was computed by dividing the total mass per core by the number of individuals counted. Site III had 3.4 times more mass per individual (1.00 ± 0.30 g ind.⁻¹) than Site II (0.29 ± 0.20 g ind.⁻¹, $p = 0.004$) but was not significantly higher than Site I (0.57 ± 0.60 g ind.⁻¹, $p = 0.199$) (Fig. 6b). Sites I and II were not significantly different ($p = 0.432$). A very broad range of animal sizes was observed at Site I. No information about temporal variation in biomass is available because biomass estimates for each site were made from one time only.

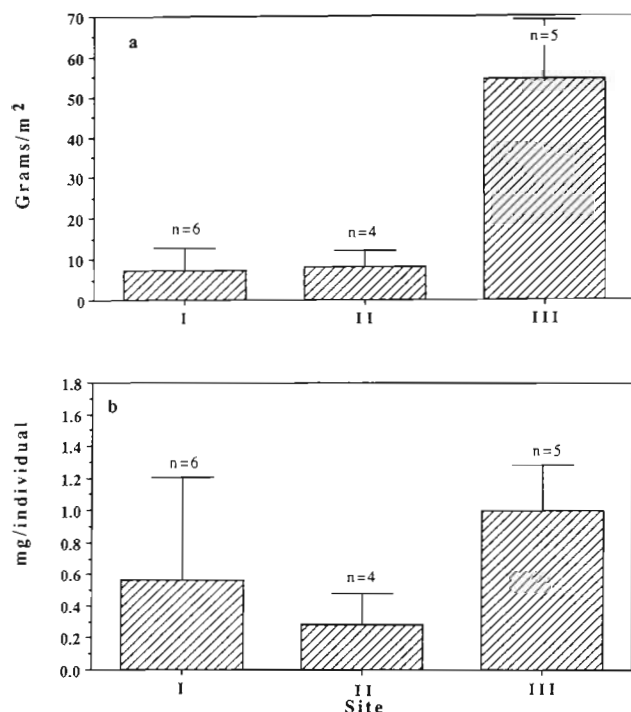


Fig. 6. (a) Biomass in g wet wt m⁻² (mean \pm 1 SD) at Sites I, II and III. n = no. of 49 cm² subcores (15 cm deep) that were included in the analysis. (b) Biomass in mg wet wt ind.⁻¹ (mean \pm 1 SD) at Sites I, II and III. Data were obtained by dividing the g wet wt per subcore by the number of individuals in each subcore

Macrofaunal abundance and vertical distributions

Average macrofaunal abundances varied by a factor of 2 to 6 among sites (Fig. 7). Site I had an average total macrofaunal density (\pm 1 SD) of 9439 ± 3134 m⁻², Site II averaged 21319 ± 5001 m⁻² and Site III 55483 ± 15396 m⁻². Comparisons of mean abundances per core for individual cruise dates show Site II > Site I ($p < 0.0001$) in September 1988, and Site III > Site II ($p < 0.01$) in June 1989 and October 1989. Because Sites I and III were not sampled at the same time, no direct comparisons were made.

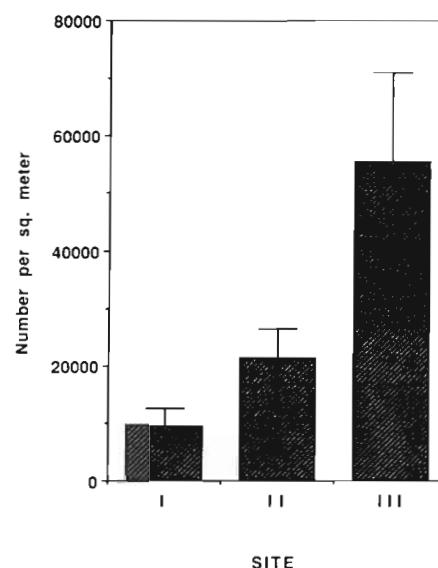


Fig. 7 Macrofaunal abundance (>0.300 mm) at Sites I, II and III (mean \pm 1 SD)

A comparison of the distribution of macrofauna among vertical fractions revealed a significantly higher proportion ($p < 0.05$) of the macrofauna in the top vertical fraction at Sites I (67.1 %) and III (61.1 %) than at Site II (46.1 %), and a higher proportion in the 2–5 cm fraction at Site II (39.4 %) (Fig. 8). Few animals were found below 5 cm; 7 % at Site I and 14 % at Sites II and III (Fig. 8). The dominant deep-dwelling animals were oligochaetes and capitellid, coarctid, maldanid and paraonid polychaetes.

Temporal comparisons of vertical distribution and total macrofaunal abundance were made for the different cruises at Sites II and III. Site II revealed little variation in vertical distribution or total abundances among the 3 cruise dates, with one exception. Abundances in the 2–5 cm vertical fraction from October 1989 (102 ± 27 core⁻¹) were almost twice those in June 1989 (58 ± 7 core⁻¹, $p = 0.039$).

Comparison of June and October 1989 distribution and abundance data for Site III revealed differences in the surface (0–2 cm) fraction and total macrofauna counts only. October 1989 surface counts (381 ± 99 core⁻¹) were over twice those of June 1989 (153 ± 48 core⁻¹). This difference (228 animals core⁻¹) accounted for 91 % of the difference in the total core average abundance observed between the 2 cruise dates ($p < 0.004$). Surface disturbance caused by use of the larger (0.25 m²) core in June may have accounted for some of the observed temporal difference, but the increased numbers of juvenile polychaetes present in October suggests that recruitment took place in summer or fall.

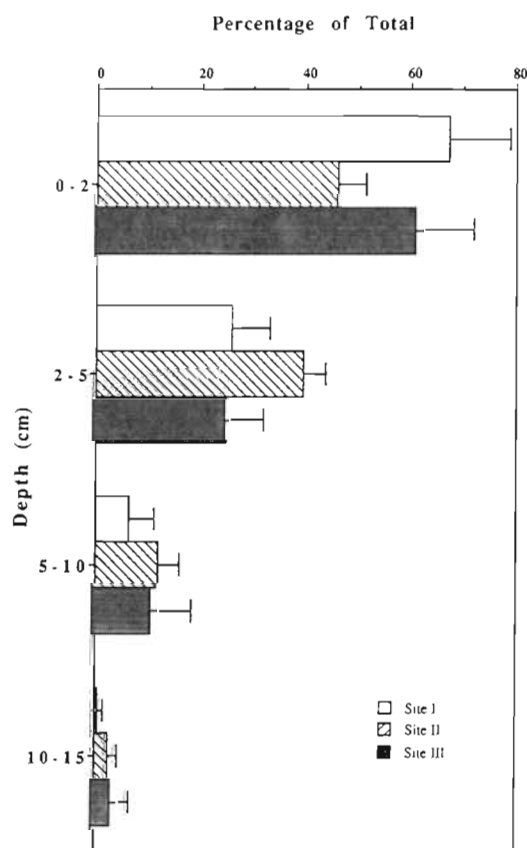


Fig. 8. Vertical distribution of macrofauna (>0.300 mm) in sediments at Sites I, II and III (mean \pm 1 SD)

Taxonomic representation

The macrofaunal taxonomic composition at the 3 sites (Fig. 9) was largely typical of bathyal depths. Annelids comprised the largest fraction at each of the sites, but

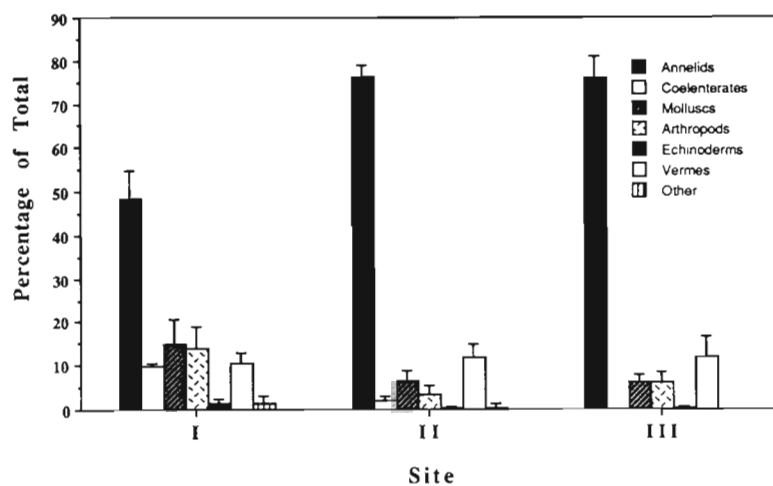


Fig. 9. Representation of major macrofaunal taxa in sediments at Sites I, II, and III (mean \pm 1 SD)

were far less common at Site I (48.3 %, $p < 0.05$) than at Sites II (76.2 %) and III (75.8 %). Site I had a greater proportion of coelenterates (9.8 %, $p < 0.05$), molluscs (14.8 %, $p < 0.05$), and arthropods (13.9 %, $p < 0.05$) than the other 2 sites (Fig. 9). Echinoderms and other vermes (including nemerteans, sipunculans and turbellarians) accounted for similar proportions at all 3 sites. Other miscellaneous taxa, such as chaetognaths and poriferans, were notably rare at all 3 sites.

Polychaete community structure

As the dominant macrofaunal taxon at each site, polychaetes were examined in detail. Polychaetes comprised 43.0 % of all animals counted at Site I, 74.0 % at Site II and 65.3 % at Site III. Sites I and II had similar polychaete species present, but Site III exhibited a surprisingly different composition (Appendix I). All but 3 of the 33 polychaete species collected at Site I (*Diplocirrus* sp. 1, *Tabia* sp. 1 and *Questa* sp. 1) were found at Site II. Of the 34 polychaete species described at Site III, 17 were found at Site II. These comprised only 4.0 % of the total polychaetes present at Site III (the nereid *Ceratocephale loveni* alone accounted for 3.3 % of this total), but 29.4 % at Site II. Thirteen species found at Site III also were present at Site I. They accounted for 3.6 % of the total polychaetes at Site III (with *C. loveni* comprising 3.3 %), and 36.0 % of the polychaetes at Site I. Thus, with the exception of *C. loveni*, the overlap of species at Site III with Sites I and II was limited to rare species (ones which represent < 0.02 % of the total at Site III).

None of the top 12 polychaete species from Site III were among the most abundant at Sites I or II (Table 2). The 4 top-ranking species that overlapped at Sites I and II, the chrysopetalid *Dysponetus* sp. 1, the cossurid *Cossura longocirrata*, the capitellid *Barantolla* sp. 1 and the dorvilleid *Meiodorvillea minuta*, together represented 32.5 % of the total polychaetes at Site I and 34.8 % at Site II.

Polychaete diversity was examined for the 3 sites using the Shannon-Weiner information index (H), graphical rarefaction techniques and species dominance curves. Diversity was similar at Site I ($H = 4.656$) and Site II ($H = 4.572$), but much lower at Site III ($H = 2.757$). Plots of expected species numbers versus sample size generated by rarefaction of pooled core data (Fig. 10a) revealed that Sites I and II had the highest species richness, and Site III had much lower richness.

Relative dominance of individual polychaete species at each site was compared

Table 2. The 12 most abundant polychaete species at Sites I, II and III

Rank	Site I		Site II		Site III	
	Species	% of tot. polych.	Species	% of tot. polych.	Species	% of tot. polych.
1	<i>Dysponetus</i> sp. 1	15.8%	<i>Meiodorvillea minuta</i>	14.3%	<i>Scalibregma inflatum</i>	26.3%
2	<i>Cossura longicirrata</i>	9.6%	<i>Dysponetus</i> sp. 1	9.7%	<i>Aricidea quadrilobata</i>	23.6%
3	<i>Paraonis cerruti</i>	6.1%	<i>Cossura longicirrata</i>	7.6%	<i>Cossura soyeri</i>	13.8%
4	<i>Microrbinis lineae</i>	5.3%	<i>Paraonis uncinatus</i>	5.6%	<i>Chaetozone</i> sp. 1	12.4%
5	<i>Hesionura</i> sp. 1	4.4%	<i>Ophelia profunda</i>	3.9%	<i>Ceratocephale loveni</i>	3.3%
6	<i>Questa</i> sp. 1	4.4%	<i>Flabelligella</i> sp. 1	3.8%	<i>Schistomeringos caecus</i>	2.3%
7	<i>Barantolla</i> sp. 1	3.5%	<i>Barantolla</i> sp. 1	3.6%	Phyllodocidae sp. 2	2.2%
8	<i>Dysponetus</i> sp. 2	3.5%	<i>Tachytrypane</i> sp. 1	3.1%	<i>Lumbrineris fragilis</i>	1.6%
9	<i>Meiodorvillea minuta</i>	3.5%	<i>Tharyx</i> sp. 1	3.1%	<i>Artacana</i> sp. 1	0.7%
10	Ampharetidae sp. 1	2.6%	<i>Levensenia gracilis</i>	2.9%	Ophelidae sp. 1	0.5%
11	Dorvillea sp. 1	2.6%	Owennidae sp. 1	2.5%	<i>Levensenia</i> sp. 1	0.5%
12	Spionidae sp. 1	2.6%	<i>Paraonis</i> sp. A	2.2%	Dorvilleidae sp. 3	0.5%

by plotting the species rank (highest to lowest) versus the cumulative percentage of the total number of individuals (Fig. 10b). The top 3 polychaete species comprised 31.5, 31.6 and 63.7 % of the total polychaetes at Sites I, II and III, respectively. Thus, dominance was considerably higher at Site III than the other 2 sites.

All polychaete species were assigned to feeding categories (surface-deposit feeders, subsurface-deposit feeders, carnivores or filter feeders) using classifications in Fauchald & Jumars (1979), with some modifications based on personal observations. These categories were then summed and relative percentages for each group were determined for each site (Fig. 11). The dominant feeding type at all 3 sites was subsurface-deposit feeding. Site III polychaetes had the highest percentage of subsurface-deposit feeders (70.9 %) followed by Site II (63.5 %) and Site I (54.2 %), although only Sites III and I were significantly different ($p < 0.05$). The proportion of carnivorous polychaetes exhibited the inverse of this pattern, with Site I having the greatest proportion (29.6 %), Site II intermediate values (20.2 %) and Site III (11.1 %) the lowest proportion (all values significantly different, $p < 0.05$). Representation of surface-deposit feeders was similar at all 3 sites (16 to 18 %; $p > 0.05$). Filter feeders were rare at Sites II and III (< 1 %), and no filter-feeding polychaetes were found at Site I. However, other non-polychaete, filter-feeding taxa were present at Site I (e.g. solitary corals).

DISCUSSION

Sources of spatial heterogeneity

This study revealed significant heterogeneity in macrofaunal community structure along the Carolina continental slope on a 100 km scale. Large differences were documented in both the density and composition

of the macrofaunal community at 3 sites ≤ 150 km apart from one another. Bacterial densities varied only between Sites II and III.

Macrofaunal heterogeneity was hypothesized to derive from differences in metabolizable carbon flux, and thus food availability, at the 3 sites. The flux of total organic carbon can be estimated by combining measurements of sediment organic carbon content with estimates of sedimentation rates over the past 300 to 500 yr. Based on the assumption that the ^{14}C age of the organic matter at the sediment-water interface has remained constant over the dating interval, sedimentation rates at Sites I and II were estimated to be $0.0067 \text{ cm yr}^{-1}$ and 0.16 cm yr^{-1} , respectively (DeMaster et al. unpubl.). ^{14}C measurements from a Site III core produced similar ages for all material down to 2 m sediment depth (DeMaster et al. unpubl.). From these Site III data it is not possible to distinguish between continuous sedimentation at a rate of $> 0.5 \text{ cm yr}^{-1}$, episodic mass sediment movement, or a combination of the two. Hecker (1990a) noted greatest deposition of phytodetrital particles on the middle slope, and a down-slope movement of phytodetritus over time on the continental slope south of Georges Bank. Depositional events of this nature may be important sources of metabolizable carbon to slope benthic communities.

Total organic carbon (TOC) in surface sediments, which was highest at Site II, intermediate at Site III and lowest at Site I (Table 1), was not correlated with macrofaunal biomass (Fig. 6) or abundance (Fig. 7). The TOC data in our study do not agree with previously reported values by Blake et al. (1987), which indicated Site I $<$ Site II $<$ Site III. In both studies, however, TOC alone appears to be a poor indication of food availability to the macrofauna, based on site differences in macrofaunal biomass and densities. The lack of relationship between TOC and infauna has been shown in previous studies in the deep sea (Sanders et al. 1965, Rowe et al.

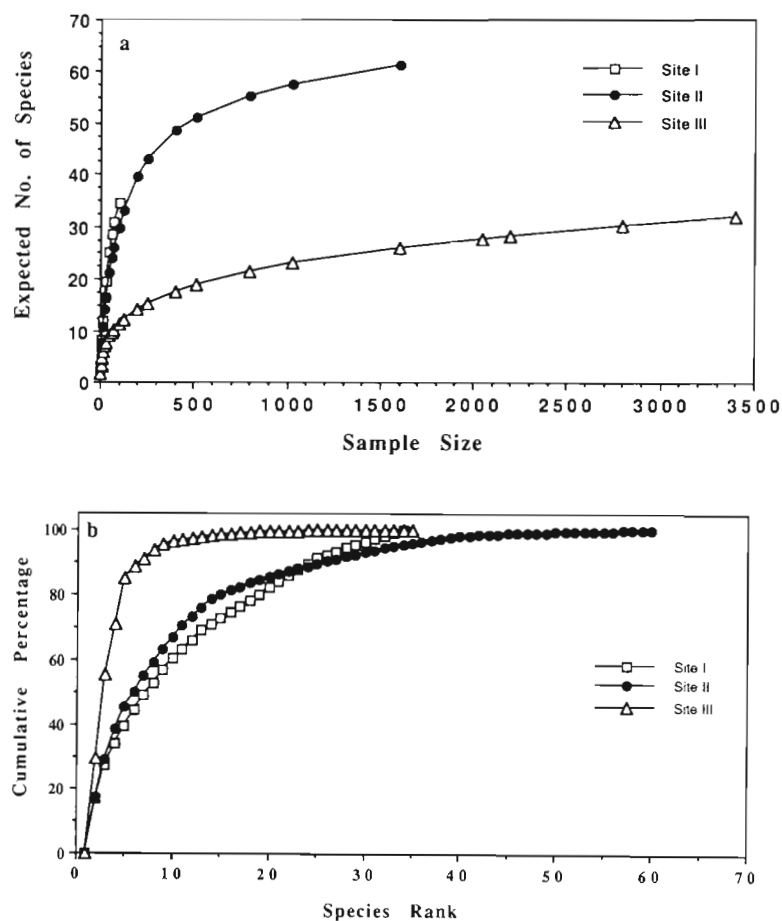


Fig. 10. (a) Rarefaction curves giving expected polychaete species richness as a function of sample size for pooled data at Sites I, II and III. (b) Dominance curves showing cumulative percentage of polychaete species at Sites I, II and III

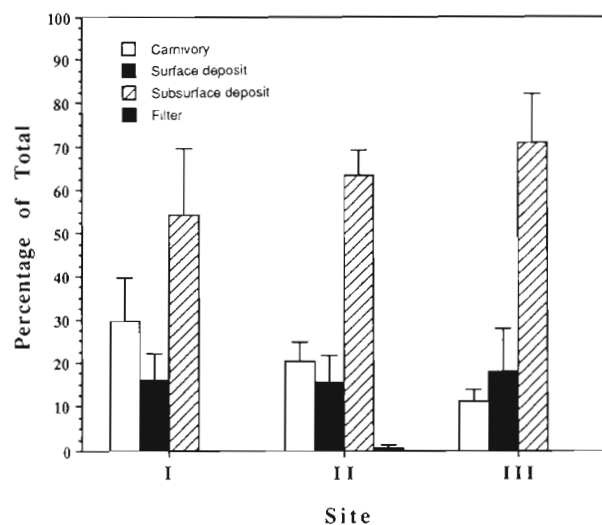


Fig. 11 Representation of polychaete feeding types at Sites I, II and III (mean \pm 1 SD)

1974), and is often attributed to the inability of TOC measures to distinguish between refractory and labile (utilizable) organic carbon. In addition, we suggest that the flux of labile carbon, rather than the pool size, primarily controls infaunal populations.

Thus, a more appropriate indication of food availability may derive from estimates of carbon flux at each site. Multiplication of surface TOC concentration (Table 1) by the sedimentation rates described above, gives estimated fluxes of 0.6, 20 and $>70 \text{ g C m}^{-2} \text{ yr}^{-1}$ for Sites I, II and III, respectively. The Site I flux estimate is in the same range as that reported for the Sargasso Sea ($0.7 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Deuser & Ross 1980) and slightly less than estimates for the Mid Atlantic Bight slope (1.1 to $2.1 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Anderson et al. 1988). The Site II value is higher than sediment-trap based carbon flux estimates from a 1295 m site slightly SW of the study area ($5.4 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Hinga et al. 1979), and from 500 m isobaths in the Mid-Atlantic Bight (9.9 to $11.3 \text{ g C m}^{-2} \text{ yr}^{-1}$), but within the range estimated from ^{210}Pb accumulation for the same region (Walsh 1989). The Site III estimates are comparable to values from upwelling regions in the coastal eastern Pacific (40 to $70 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Henrichs & Farrington 1984, Martin et al. 1987), and higher than many reported from shallow bays and inlets in North America ($36 \text{ g C m}^{-2} \text{ yr}^{-1}$ in Buzzards Bay, Massachusetts; Henrichs & Farrington

1987, 40 to $65 \text{ g C m}^{-2} \text{ yr}^{-1}$ in Alaskan bays calculated from Canfield 1989). Our slope estimates represent the total rather than metabolizable fraction of carbon, but the estimated increase from Sites I to II to III corresponds well with observed changes in macrofaunal abundance.

Sediment porewater measurements of SO_4^{2-} , CH_4 and ΣCO_2 (Fig. 3) provide further evidence for differences in availability of metabolizable organic matter at the 3 study sites. Sulfate is a terminal electron acceptor in the anaerobic degradation of organic matter (Claypool & Kaplan 1974). To a first approximation, differences in the concentration gradient and depth of depletion in sediments can be attributed to differences in microbial sulfate reduction rate and by inference, flux of metabolizable organic carbon to the seabed (Berner 1978, Jørgensen 1982, Martens & Klump 1984). Thus, the lower sulfate concentrations observed at Site III suggest that a greater flux of labile C is reaching that site. Similarly, the higher concentrations of the principal remineralization product, ΣCO_2 , would argue for

higher rates of organic matter delivery and degradation at Site III. Methane is produced primarily when the flux of metabolizable carbon to the seabed is great enough to deplete sulfate concentrations to below approximately 1 mM (Martens & Berner 1974). Its presence above detection levels only at Site III is compelling evidence that organic fluxes are greater at that location. Site III sediments contained many large (>300 µm) centric diatom frustules, further indication of input from productive overlying waters.

In addition, profiles of sediment oxygen concentrations (generated with oxygen microelectrodes onboard ship) exhibited depletion of oxygen by 3 mm at Site III, 5 mm at Site II and 6 mm at Site I (B. Bebout pers. comm.). Though absolute oxygen values on board ship differ from those occurring *in situ*, the relative differences in depletion depth between sites are consistent with the SO_4^{2-} , CH_4 and ΣCO_2 profiles (Fig. 3). These profiles all suggest greatest organic matter utilization, and thus availability of labile components at Site III.

In continental margin environments in which carbon flux is primarily controlled by lateral transport from the continental shelf, food availability may be inversely related to water depth and distance from shore (Sanders & Hessler 1969, Rowe et al. 1974, Rowe et al. 1982, Carney et al. 1983). Enhancement of surface production from upwelling also may explain regionally-elevated deep-sea benthic production (Smith & Hinga 1983). In the present study, water depth was held approximately constant (850 m \pm 30 m) among the sites. Distance from sources of production and hydrodynamic conditions remain as possible causes for the differences in food input.

In this study the apparent carbon utilization patterns determined from the porewater profiles (Fig. 3) exhibit some support for the hypothesis that organic input to the seafloor decreases with increasing distance from shore or distance from the shelf/slope break (200 m isobath). Of the 3 sites, Site I was furthest from shore (177 km) and from the shelf/slope break (77.7 km), Site II was intermediate (82 km from shore; 13.9 km from the shelf/slope break) and Site III was closest (61 km from shore and only 5.6 km from the shelf/slope break). However, these distances fail to explain trends in community structure.

Communities at Sites I and II were most similar, while the distance to the shelf/slope break was similar at Sites II and III. The differences in macrofaunal abundances at Sites I and II may be better explained by the lower sedimentation rate at Site I, which is probably the result of periodic sweeping by the Gulf Stream. The greater organic matter flux at Site III probably results from a combination of Gulf Stream-induced upwelling (Pietrafesa 1990), lateral transport resulting from downslope mass wasting processes (Sanford et al. 1990), and a confluence of deep-water, slope and west-

ern boundary currents that may be focused by bottom topography (Johnson 1989, Csanady & Hamilton 1988).

²³⁴Th mixing coefficients and inventories

As described previously, the mixing coefficient is a good indicator of the intensity of particle mixing (i.e. bioturbation) occurring in the seabed. The greater mixing intensity at Site III as compared to Sites I and II is probably a result of the greater number of macrofauna present in the seabed. Conveyor-belt feeders such as maldanid polychaetes and oligochaetes were more common at Site III than the other sites (Appendix I). In addition, many of the macrofauna at Site III were somewhat larger than at the other 2 sites (Schaff 1991), suggesting a larger step length in the mixing process (Wheatcroft et al. 1990) and consequently enhanced particle reworking. The case has been made that the increased abundance of macrofauna at Site III relative to the other sites may be the result of the increased carbon flux. The ¹⁴C data used to calculate the sedimentary organic carbon flux characterize the flux on a time scale of several hundred to a few thousand years. The ²³⁴Th inventories provide a snapshot of the relative particle flux from the water column during the 3 or 4 mo prior to core collection. This short-term flux of material probably is more important in determining the abundance of macrofauna (and their activity levels) than the long-term flux. The mean ²³⁴Th inventory is 2 to 5 times greater at Site III than at Sites I or II, which is consistent with the higher abundance of macrofauna, the greater mixing intensity, and the enhanced carbon utilization rate at this site.

Bacterial abundance

Bacterial counts were not consistent with the hypothesized gradient of organic flux, sediment TOC or with macrofaunal abundances, except at the deepest levels within the sediments. Sites I and II had similar microbial abundances, but Site III had higher abundances than Site II. Several alternative factors, including grazing pressure, sediment disturbance, differing quality of sediment organic matter, or methodological artifacts, may be responsible for this lack of correlation (Deming & Baross in press). Counts provide a static view of microbial communities and do not reveal the origin or activity level of the bacterial cells. Since grazing by protozoa, meiofauna, or macrofauna may remove bacterial production and leave numbers low (Kemp 1987, Kemp 1990 and references therein), measurements of microbial growth rates might more accurately link microbial processes to organic flux. However, many deep-sea and anaerobic

bacteria are believed to expend most energy on maintenance rather than biomass production (Novitsky 1987, Deming & Baross in press). Under these circumstances counts combined with measures of respiration or enzymatic activity may be most appropriate (J. Deming pers. comm.).

Macrofaunal community structure

The differences in organic flux at the 3 sites appears to exert numerous effects on animal community structure. A 5-fold difference in macrofaunal density (Fig. 7) and a 7-fold difference in biomass (Fig. 6a) were observed among the sites. Average macrofaunal densities at Site III ($55\,482\text{ m}^{-2}$) were more than twice as high as any known slope environment at similar depths (Blake et al. 1987), and were comparable to littoral or shallow, organic-rich environments (Kneib 1984, Dauer et al. 1984, Sacco 1990). Previous work at a 604 m station on the slope off Cape Hatteras revealed densities of $53\,000\text{ m}^{-2}$ ($300\text{ }\mu\text{m}$ screen) (Blake et al. 1987). Sanders et al. (1965) reported macrofaunal densities ($420\text{ }\mu\text{m}$ screen) of $21\,000\text{ m}^{-2}$ at 300 m depth, but only 2979 m^{-2} at 823 m depth along a Gay Head-Bermuda transect. Other studies of infauna on the Atlantic slope used larger screen sizes to separate macrofauna and resulted in much lower estimates of animal densities [Cerame-Vivas & Gray 1966: 1.0 inch (= ca 25 mm); Maurer & Leathem 1981: 0.5 mm; Wigley & Theroux 1981: 1.0 mm].

Abundances measured in this study off Cape Lookout, NC (Site II) of $21\,319\text{ m}^{-2}$ were slightly higher than those reported by other investigators from nearby sites at comparable depth. Blake et al. (1987) reported densities of $18\,144\text{ m}^{-2}$ at 583 m depth off Cape Lookout. Macrofaunal densities at Site I averaged $9\,438\text{ m}^{-2}$ and were similar to values listed by Blake et al. (1987) for South Atlantic sites at this depth (850 m).

Patterns of diversity and dominance also were distinct among sites. Sites I and II had diversities similar to other slope environments (Blake et al. 1987). The very low species richness (Fig. 10a) and high dominance (Fig. 10b) at Site III resembles community patterns observed in the eastern Pacific oxygen minimum zone at comparable depths (Levin et al. 1991) and in shallow, organic-rich sediments (Pearson & Rosenberg 1978, Ritz et al. 1989, Weston 1990). The Shannon-Wiener diversity index for polychaetes at Site III was even lower than values reported for the nearby lower Chesapeake Bay and inner continental shelf off Virginia (Dauer et al. 1984), but comparable to diversity indices for macrofauna at several upper slope stations in the South Atlantic Bight (Tenore 1985).

Site III is unusual in having species that are cosmopolitan, and in some cases, indicators of organic

enrichment. Sites I and II had component species typical of other Atlantic slope stations (Blake et al. 1987), yet none of the dominant polychaete species at those sites were important at Site III (Table 2). Two of the species found exclusively at Site III, *Scalibregma inflatum* and *Lumbrineris fragilis*, have been identified in studies of polluted areas (Rygg 1985, Aschan & Skullerud 1990). The dominant Site III species, *S. inflatum* (26.7 % of total polychaetes), is a widespread species, found from Europe to Antarctica in intertidal to abyssal (4436 m) depths (Hartmann & Fauchald 1971, Kudenov and Blake 1978, Blake 1981). *S. inflatum* appeared early in successional sequences following pollution abatement in one study of a Swedish estuary (Rosenberg 1976) and has been proposed to be an indicator of enriched or polluted areas (Rosenberg et al. 1987, Gray & Pearson 1982). The second-ranked species at Site III, *Aricidea quadrilobata*, is also a widespread, highly eurybathic species. It has been described in collections from New England to the Sea of Japan at depths ranging from 6 to 2500 m (Strezlov 1973).

Another unusual feature of the Site III fauna was the preponderance of early life history stages and reproductive adults. Large numbers of juvenile *Scalibregma inflatum*, *Cossura soyeri*, *Ceratocephale loveni* and *Aricidea quadrilobata* were present in the upper sediments at Site III (Levin et al. in press). At Sites I and II, reproductive adults and juveniles of any species were rarely seen. These observations, combined with the presence of organophilic species, suggest that the infaunal assemblage at Site III is more typical of enriched, shallow, cold-water settings than of most deep-sea environments studied previously.

The dramatic differences in community composition and structure among sites off North Carolina form a sharp contrast to the latitudinal homogeneity reported by Tenore (1985) for shelf and upper slope macrofauna from Florida to South Carolina. Tenore's study noted strong seasonality in species composition and speculated that seasonal variation was moderated by current regimes. Observed temporal variations in the present study could not be tied to seasonal patterns due to the haphazard timing of cruises. However, physical oceanographic processes and bottom topography are almost certainly responsible for spatial (among-site) variations in macrofaunal communities in the present study.

CONCLUSIONS

Major trends among the 3 sites examined in this study are summarized in Table 3. Macrofaunal community structure at the 3 sites displayed considerable heterogeneity. Site III had 5.8 times ($55\,482\text{ ind. m}^{-2}$) the density of Site I ($9\,438\text{ ind. m}^{-2}$) and 2.6 times that of

Table 3. Summary of faunal trends among Sites I, II and III

Aspect of community structure	Trend
Macrofaunal abundance	III > II > I
Bacterial abundance	III > II = I
Macrofaunal biomass	III > II = I
Macrofauna vertical distribution	III = II = I
Diversity (rarefaction)	III < II = I
Dominance	III > II = I
Species composition	III ≠ II = I

Site II (21319 ind. m⁻²). Macrofaunal biomass was 6 times higher at Site III than at Sites I and II, which were not different. ²³⁴Th mixing coefficients at Site III were 2 to 6 times greater than at the other 2 sites, consistent with the increased abundance and biomass measurements. Bacterial abundances were also higher at Site III than Site II, but Sites I and II were not different. Site III displayed a higher degree of macrofaunal dominance, lower diversity and lower species richness than the other 2 sites, which were similar. Polychaete species composition at Sites I and II also was similar, and overlapped little with Site III. Bacterial counts at Sites II and III exhibited considerable temporal variation, with September 1988 > June 1989 > October 1989 at Site II and June 1989 > October 1989 at Site III, whereas macrofaunal densities showed little temporal variation among these 3 cruise dates over 13 mo.

Variations in organic input are hypothesized to be responsible for the heterogeneity observed at these 3

sites. Site III appears to have a much higher input of biologically-utilizable carbon. Differences in organic input to the 3 sites have been estimated on long time scales (hundreds of years) from measurements of sedimentation rate and TOC, and on short time scales (weeks to months) from porewater ΣCO₂, SO₄²⁻, and CH₄ profiles as well as ²³⁴Th inventories. Variations in food availability are most likely due to Gulf Stream impingement on the sea floor at Site I (diminishing deposition), lateral focusing of sediment induced by downslope mass wasting processes, as well as localized upwelling and an unusual confluence of currents in the Site III area.

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Appendix I. Total numbers of macrofaunal taxa collected at Sites I, II, and III. Species identifications are given for polychaetes only. The numbers of 196 cm² boxcores sorted were 4, 14, and 11 for Sites I, II and III respectively

Taxon	Site I	Site II	Site III	Taxon	Site I	Site II	Site III
Polychaetes				Cossuridae			
Acrociiridae				<i>Cossura longocirrata</i>	11	165	0
<i>Flabelligella</i> sp. 1	2	83	0	<i>Cossura soyeri</i>	0	0	536
Undet. Acrociiridae sp.	0	0	1	Dorvilleidae			
Ampharetidae	3	17	1	<i>Meiodorvillea minuta</i>	4	308	0
Aphroditidae	0	1	0	<i>Dorvillea</i> sp. 1	3	6	0
Arabellidae				nr. <i>Schistomeringos caecus</i>	0	0	89
<i>Drilonens</i> sp. 1	2	12	2	Undet. Dorvilleidae sp. 2	0	11	0
Bogoeidae	0	0	4	Undet. Dorvilleidae sp. 3	0	0	18
Capitellidae				Undetified spp.	0	0	1
<i>Barantolla</i> sp. 1	4	77	0	Eunicidae	0	3	0
<i>Capitella</i> sp. A	0	7	0	Fauvellopsidae			
<i>Capitella</i> sp. 1	0	12	0	<i>Fauvellopsis</i> nr. <i>scabra</i>	1	3	0
<i>Heteromastus</i> sp. 1	0	12	0	Flabelligeridae			
Unidentified spp.	0	5	1	<i>Diplocirrus</i> sp. 1	2	0	0
Chrysopetalidae				<i>Tabia</i> sp. 1	2	0	0
<i>Dysponetus gracilis</i>	1	25	0	Undet. Flabelligeridae sp. B	0	16	0
<i>Dysponetus</i> sp. 1	18	210	3	Undet. Flabelligeridae sp. C	0	22	0
<i>Dysponetus</i> sp. 2	4	2	1	Unidentified spp.	0	4	0
Undet. Chrysopetalidae sp. A	0	8	0	Glyceridae			
Undet. Chrysopetalidae sp. B	0	0	7	<i>Glycera</i> nr. <i>mimica</i>	2	15	0
Cirratulidae				Goniadidae			
<i>Tharyx</i> sp. 1	2	66	0	<i>Goniada</i>	1	1	0
<i>Chaetazone</i> sp. 1	0	13	482	Hesionidae			
<i>Caullerellia</i> sp. 1	0	2	0	<i>Hesionella</i>	2	19	0
Undet. Cirratulidae sp.	0	2	0	Lacydoniidae			
Unidentified spp.	0	23	8	<i>Paralacydonia paradoxa</i>	0	1	0

Appendix I (continued)

Taxon	Site I	Site II	Site III	Taxon	Site I	Site II	Site III
Lumbrineridae				Sphaerodoridae			
<i>Lumbrineris fragilis</i>	0	0	64	Undet. Sphaerodoridae sp.	0	0	11
<i>Ninoe</i> sp. 1	0	12	0	Unidentified spp.	3	9	0
Undet. Lumbrineridae sp. A	2	8	0	Spionidae			
Maldanidae	0	98	134	<i>Prionospio</i> sp. 1	0	12	0
Nephtyidae				<i>Auropsio dibranchiata</i>	2	16	0
<i>Nephtys</i> sp. 1	1	7	2	Undet. Spionidae sp.	3	9	0
Nereidae				Unidentified spp.	0	14	3
<i>Ceratocephale loveni</i>	1	46	128	Sternaspidae			
Onuphidae	1	4	2	<i>Sternaspis scutata</i>	0	2	0
Opheliidae				Syllidae	0	57	6
<i>Tachytrypae</i> sp. 1	1	68	0	Terebellidae			
<i>Ophelia profunda</i>	2	85	7	<i>Polycirrus</i> sp. 1	0	0	6
<i>Ophelia</i> sp. 1	0	22	1	<i>Nicolea</i> sp. 1	0	0	13
Undet. Opheliidae sp.	0	0	20	Unidentified spp.	0	10	0
Unidentified spp.	0	1	0	Trichobranchidae			
Orbiniidae				<i>Artacana</i> sp. 1	0	0	29
<i>Microrbinis lineata</i>	6	2	0	Unknown/juvenile	0	25	8
<i>Scolopsis</i> sp. 1	0	1	0	Terebelliform juveniles	0	0	236
Owennidae	1	53	1				
Paraonidae				Other taxa			
<i>Aricidea catherinae</i>	1	8	0	Porifera	2	0	0
<i>Aricidea quadrilobata</i>	0	0	915	Anthozoa			
<i>Cirrophorus lyra</i>	0	15	0	Anemones	17	50	0
<i>Levensenia gracilis</i>	1	62	0	Corals	21	2	0
<i>Levensenia</i> sp. 1	5	8	19	Nemertinea	25	243	615
<i>Paraonis uncinatus</i>	1	121	1	Oligochaeta	22	57	581
<i>Paraonis cerruti</i>	7	11	0	Sipuncula	11	93	1
<i>Paraonis</i> sp. A	2	47	0	Priapulida	0	9	119
<i>Paraonis</i> sp. B	0	1	0	Mollusca			
Unidentified spp.	0	102	0	Gastropoda	4	7	92
Phyllodocidae				Aplacophora	14	64	44
<i>Hesionura</i> sp. 1	5	14	1	Bivalvia	28	76	219
Undet. Phyllodocidae sp. 1	0	4	0	Scaphopoda	12	26	28
Undet. Phyllodocidae sp. 2	0	0	86	Crustacea			
Undet. Phyllodocidae sp. 3	0	2	0	Acarina	3	11	0
Unidentified spp.	0	2	0	Cumacea	2	1	1
Pilargidae				Tanaidacea	41	80	233
<i>Ancistrosyllis</i> sp. 1	0	3	9	Isopoda	9	7	88
Undet. Pilargidae sp. 1	0	1	0	Amphipoda	3	6	21
Questidae				Echinodermata			
<i>Questa</i> sp. 1	5	0	0	Ophiuroidea	3	6	0
Sabellidae	0	17	1	Echinoidea	3	4	22
Scalibregmatidae				Chaetognatha	0	1	0
<i>Scalibregma inflatum</i>	0	0	1018	Unidentified Vermes	1	14	1
Sigalionidae	0	16	3				

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