Journal of Experimental Marine Biology and Ecology 330 (2006) 307 – 326

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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The soft-bottom macrobenthos of Gray's Reef National Marine Sanctuary and nearby shelf waters off the coast of Georgia, USA

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Received 2 September 2005; received in revised form 10 December 2005; accepted 15 December 2005

Abstract

As part of an ongoing ecological assessment of the Gray's Reef National Marine Sanctuary (GRNMS), a 58-km^2 marine protected area 32 km off the coast of Georgia, USA, surveys of benthic macroinfaunal communities, contaminant levels in sediments and biota, and general habitat conditions were conducted during 2000–2002 at 20 stations within the sanctuary and along three cross-shelf transects in nearby shelf waters. Macroinfaunal community structure and composition exhibited distinct cross-shelf patterns associated with sediment granulometry, depth and possibly other factors related to shoreline proximity (e.g., erosional effects, recruitment of estuarine species). Finer-scale spatial patterns of benthic fauna among stations within the sanctuary appear to be related to proximity to live-bottom habitat and other features of seafloor structure (e.g., rippled vs. flat sand). Population densities of dominant fauna within the sanctuary also varied considerably among years, resulting in shifts in the ranking of dominants at most stations. Chemical contaminants generally were at low background concentrations below probable bioeffect levels and thus are not a likely cause of the observed spatial patterns of benthic fauna. However, trace concentrations of pesticides, PCBs, and PAHs were detectable in sediments and biota throughout the study area, demonstrating that chemicals originating from human activities are capable of reaching the offshore sanctuary environment, possibly from atmospheric deposition or cross-shelf transport of materials outwelled through coastal sounds. Highly diverse infaunal assemblages also were observed within the sanctuary and nearby sites of similar depth, suggesting that the sanctuary is an important reservoir of marine biodiversity. Results of this study should be useful in addressing long-term science and management needs of the GRNMS and in furthering our understanding of broader ecological patterns and dynamics of the surrounding South Atlantic Bight (SAB) ecosystem.
Published by Elsevier B.V.

Keywords: Benthic communities; Environmental quality; Georgia continental shelf; Gray's Reef National Marine Sanctuary; Infaunal–benthoscape relationships; South Atlantic Bight

1. Introduction

The continental shelf off the coast of Georgia is a broad (>130 km) gradually sloping margin, with finer-sand/silt sediments along the inner shelf (within ca.

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0022-0981/$ - see front matter. Published by Elsevier B.V.
doi:10.1016/j.jembe.2005.12.036

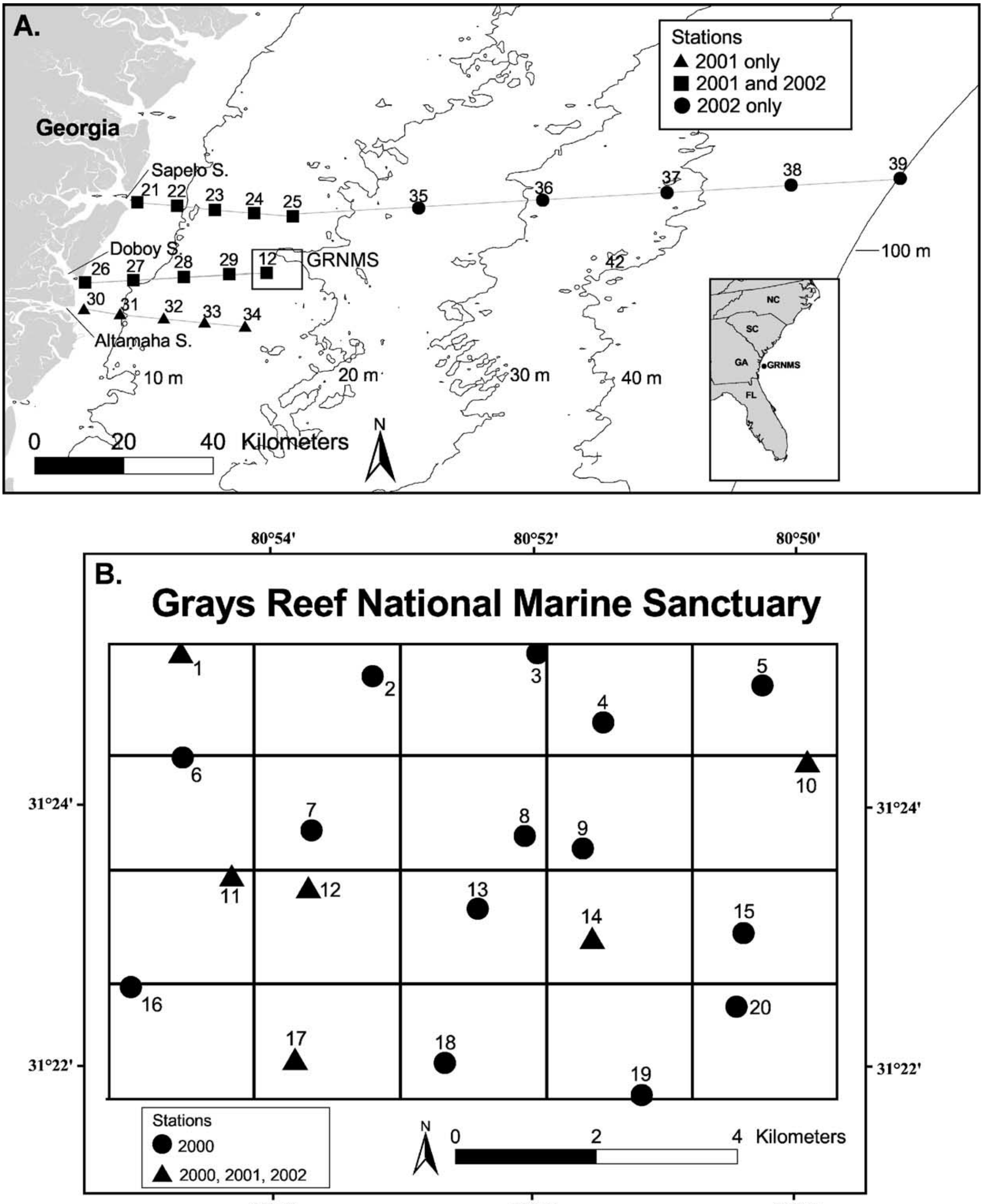


Fig. 1. Study area showing location of stations sampled (A) along three cross-shelf transects in April 01 and April–June 02, and (B) within GRNMS in April 00, April 01, and April–June 02.

22 km of shore) and coarser sands seaward to the shelf-slope break (Gorseline, 1963; Uchupi, 1967; Frankenberg, 1971). A particularly striking feature amidst these generally smooth unconsolidated substrates is Gray's Reef, a submerged hard-bottom area containing a high concentration of outcroppings (1–3 m high) and associated epifauna, commonly referred to as "live bottom" (Cummins et al., 1962). The rocky-reef topography with its diverse assemblage of epifaunal invertebrates (e.g., hard and soft corals, sponges, anemones, bryozoans, hydroids, ascidians, mollusks) attracts numerous species of benthic and pelagic fishes, as well as populations of protected species such as the threatened loggerhead sea turtle. This area was established as a National Marine Sanctuary in 1981 and named (sensu Hunt, 1974) in recognition of marine curator Milton B. Gray, who first used the area in the 1960s to obtain collections of reef-associated fauna for the University of Georgia Marine Institute. The Gray's Reef National Marine Sanctuary (GRNMS) is located 32 km off Sapelo Island, Georgia and encompasses 58 km^2 (Fig. 1A,B).

Much of the previous research at GRNMS has focused on fishes (e.g., Sedberry and Van Dolah, 1984; Sedberry, 1987, 1988; Gilligan, 1989; Parker et al., 1994; Furse, 1995; Sedberry et al., 1998) and benthic invertebrates and seaweeds associated with the live-bottom rocky outcrops (e.g., MRRI, 1982; Wenner et al., 1983; Searles, 1988). Hopkinson et al. (1991) also conducted a study of benthic community metabolism in live-bottom habitat at Gray's Reef. In contrast, there has been limited work on the ecology of unconsolidated sandy substrates, which characterize the majority of the seafloor within the sanctuary (ca. 75%, Kendall et al., 2005) and surrounding southeastern continental shelf (ca. 70%, Parker et al., 1983). There has been no prior system-wide description of macroinfaunal communities of GRNMS or of levels of chemical contaminants in sediments and biota of the sanctuary environment. With some notable exceptions (e.g., Frankenberg, 1971; Smith, 1971; Frankenberg and Leiper, 1977; Tenore et al., 1978; Hanson et al., 1981; Hopkinson, 1985), in general, there have been surprisingly few studies of the soft-bottom benthos along the continental shelf off Georgia. The benthos is a key component of coastal ecosystems, playing vital roles in detrital decomposition, nutrient cycling, and energy flow to higher trophic levels. Moreover, because of their relatively stationary existence within the sediments, benthic infauna can serve as reliable indicators of potential environmental disturbances to the seafloor.

In the present study, sampling of benthic macroinfaunal communities, contaminant levels in sediments and biota, and general habitat conditions was conducted over a 3-year period (2000–2002) at 20 stations within the sanctuary and along three additional cross-shelf transects in nearby shelf waters (Fig. 1A,B). Key objectives were (1) to develop a better understanding of the characteristics and patterns of benthic fauna and their relationship to potential environmental controlling factors, and (2) to document existing environmental conditions within the sanctuary in order to provide a quantitative benchmark for tracking any future changes due to either natural or human disturbances.

2. Methods

The first sampling event (April 2000) focused on the 20 stations within GRNMS to document baseline characteristics of sanctuary resources (Fig. 1B). A random-sampling design was applied to support probability-based estimates of condition relative to various measured environmental indicators. The resulting sampling framework was a 58-km^2 grid of 20 individual cells, 2.9 km^2 each. One station was randomly located within each cell. The second sampling event (April–May 2001) included additional sites outside the sanctuary along three cross-shelf transects extending from the mouths of Sapelo, Doboy, and Altamaha Sounds out to depths of GRNMS, ca. 20 m (Fig. 1A). Sampling was conducted at a total of 20 stations: three cross-shelf transects of five stations each, including one of the previous Year-2000 stations within the sanctuary (Station 12) serving as the seaward end of the middle (Doboy Sound) transect; and five additional Year-2000 stations within the sanctuary boundaries (Stations 1, 10, 11, 14, and 17). In the third year (April–June 2002), the Sapelo Sound transect was extended out to the shelf break (ca. 100 m). Sampling was conducted at 20 stations, including 10 stations along the Sapelo transect (2 km offshore to shelf break), five stations along the original Doboy Sound transect (inclusive of Station 12 within GRNMS as the seaward end of this transect), and the five additional stations within GRNMS (1, 10, 11, 14, and 17) where sampling had occurred over both prior years. The three cross-shelf transects provided a means of examining broad spatial patterns in benthic assemblages and sediment contaminant levels in relation to both natural factors (e.g., depth, sediment characteristics) and potential anthropogenic factors (e.g., proximity to land-based sources of contaminants). The repeated-sampling sites within GRNMS (total of six inclusive of Station 12) provided a means of examining among-year temporal variability.

During all 3 years, samples were collected at the various stations for characterization of general habitat conditions (depth, temperature, salinity, pH, dissolved oxygen, total organic carbon, grain size), concentrations of sediment contaminants (metals, pesticides, PCBs, PAHs), diversity and abundance of macroinfauna (>0.5 mm), and aesthetic quality (presence of anthropogenic debris, visible oil, noxious sediment odor, and water clarity based on secchi depths). During the first year, samples of benthic and demersal fauna (the ark shell *Arca zebra* and black sea bass *C. striata*) also were collected at targeted sites within GRNMS (by divers for the mollusks, and by fish traps for the fish) and analyzed for concentrations of chemical contaminants in tissues. Black sea bass were selected because of their abundance and commercial value, with a focus on adult fish of legal size (mean total length was 10 in., the size limit in 2000). Ark shells were selected for analysis because of their abundance in the area and exposure susceptibility (being sessile filter-feeders).

Physical properties of water (salinity, conductivity, dissolved oxygen, pH, and temperature) were measured at all stations in 2000–2001, and seven of the 20 stations in 2002 (1, 10, 11, 14, 17, 21, 26) with a Hydrolab (DS3) multi-probe data logger. Measurements were obtained where possible at both the surface and near-bottom. A Seabird CTD also was used in 2002 to obtain surface-to-bottom profiles of salinity and temperature at the remaining 13 Yr-02 stations (22, 23, 24, 25, 35, 36, 37, 38, 39, 27, 28, 29, 12). Dissolved oxygen (DO) and pH were not recorded at these latter stations due to the lack of appropriate probes for these variables on the CTD unit.

Sediment samples for macroinfaunal analysis were collected at each station in triplicate using a 0.04-m^2 Young grab sampler. Each replicate was sieved in the field through a 0.5-mm mesh screen and preserved in 10%-buffered formalin with rose bengal. Samples were shipped to the laboratory and transferred to 70%-ethanol. Animals were then sorted from sample debris under a dissecting microscope and identified to the lowest practical taxon (usually to species).

The upper 2–3 cm of sediment from additional multiple grabs were taken at each station, combined into a single station composite, and then sub-sampled for analysis of metals, organic contaminants (PCBs, pesticides, PAHs), total organic carbon (TOC), and grain size. TOC and grain size were analyzed using protocols modified from Plumb (1981). TOC content of sediment was measured on a CHN elemental analyzer (at 950 °C combustion temperature). Methods for analysis of chemical contaminants followed those of Sanders (1995), Fortner et al. (1996), Kucklick et al. (1997), and Clum et al. (2002). While matrix-specific extraction methods were required for some chemicals (e.g., all metals except Hg), follow-up instrumental analyses were the same for both sediments and tissues. Inductively coupled plasma mass spectrometry (ICP/MS) was used for the following suite of metals: Al, Cr, Cu, Fe, Mn, Ni, Sn, As, Cd, Pb and Zn. Ag and Se were analyzed using graphite furnace atomic absorption (GFAA). Cold vapor atomic absorption (CVAA) spectroscopy was used for analysis of Hg. The organic PCBs and pesticides were analyzed by dual-column gas chromatography with electron capture detection (GC-ECD). An ion-trap mass spectrometer equipped with a gas chromatograph (GC/MS-IT) was used for analysis of PAHs. Lists of method detection limits (MDLs) for all targeted chemicals in both sediments and tissues may be obtained by request to the senior author.

Effects Range-Low (ERL) and Effects Range-Median (ERM) sediment quality guideline (SQGs) values from Long et al. (1995) were used (where available) to help in interpreting the biological significance of observed contaminant levels in sediments. ERL values are lower-threshold bioeffect limits, below which adverse effects of the contaminants on sediment-dwelling organisms are not expected to occur. In contrast, ERM values represent mid-range concentrations of chemicals above which adverse effects are more likely to occur. Individual concentration-to-SQG comparisons were made for all chemicals with available SQG values. Overall sediment contamination from multiple chemicals also was expressed through use of mean ERM quotients (sensu Long et al., 1998, 2000; Long and MacDonald, 1998; Hyland et al., 1999). The mean ERM quotient is the mean of the ratios of individual chemical concentrations in a sample relative to corresponding published ERM values. A useful feature of this method is that overall contamination in a sample from mixtures of multiple chemicals present at varying concentrations can be expressed as a single number that can be compared to values calculated the same way for other samples (either from other locations or sampling occasions).

A variety of data-analysis methods were used to characterize benthic communities and examine patterns in relation to other measured environmental variables. Spatial patterns in the distribution of benthic communities, including both within-sanctuary and broader cross-shelf variations, were examined using normal (*Q* mode) cluster analysis (Boesch, 1977). Group-average sorting (=unweighted pair–group method, Sneath and Sokal, 1973) was used as the clustering method and Bray–Curtis similarity (Bray and Curtis, 1957) was used as the resemblance measure. Analyses were run on double-square-root transformed abundances (combined over replicates within a station) using the PRIMER software package (Clarke and Gorley, 2001). Following the species reduction procedure included in PRIMER, rare species (i.e., those representing <1% of the total abundance of a sample) were excluded from the analysis to improve clustering interpretability. Results were expressed as a dendrogram in which samples were ordered into groups of increasingly greater similarity based on resemblances of component-species abundances. Canonical discriminant analysis was applied in conjunction with the cluster analysis to determine whether the separation of site groups could be explained by various measured abiotic environmental variables (sensu Green and Vascotto, 1978; Hyland et al., 1991). This latter analysis, performed with the CANDISC procedure in SAS (2003), sought to derive a reduced set of discriminant (canonical) functions that best described the separation of the pre-declared site groups, based on data represented by the different abiotic environmental variables. Total Structure Coefficients (TSC), which are the correlations between the original variables and the discriminant scores on each function, provided a measure of the relative contribution of each variable to group separation.

The role of seafloor landscape, or benthoscape (Zajac et al., 2000), as a potential source of within-sanctuary spatial patterns also was examined. A map of benthoscape features within the sanctuary, developed recently by Kendall et al. (2005), provided a basis for this analysis. The map was produced through combined analysis of sonar imagery, including multibeam bathymetry and sidescan-sonar backscatter, with additional ground-truth data from towed-camera video transects and diver observations. Spatial overlays, produced with ArcView, were used to compare station classifications derived from the cluster analysis of benthic data (from the 20 GRNMS stations in 2000) to the mosaic of benthoscape types depicted in the map.

Analysis of variance (ANOVA) and Tukey's Honestly Significant Difference (HSD) multiple-comparison test were used in conjunction with several of the above analyses to examine statistical differences in benthic and abiotic environmental variables among various stations, site groups, and benthoscape types. Benthic variables included number of species, H' diversity (Shannon and Weaver, 1949) derived with base-2 logarithms, density (m^{-2}) of total fauna (all species combined), and density (m^{-2}) of numerically dominant fauna. Lists of top-ranked dominant fauna at the six repeated-sampling stations within GRNMS also were compared to determine how variable the dominance structure at these sites was from year to year. Among-year differences in densities were measured statistically with ANOVA and Tukey's HSD test. All ANOVAs and multiple-comparison tests were based on procedures in SAS (2003).

3. Results and discussion

3.1. Cross-shelf spatial patterns of benthic fauna

Results of *Q*-mode cluster analysis of benthic data from stations along the three cross-shelf transects are presented as a dendrogram in Fig. 2. Application of a Bray–Curtis similarity value of 0.3 as a separation rule yielded four major site groups, denoted as A, B, C and D. There is a distinct cross-shelf pattern in the distribution of these site groups. Group A consists of the three inshore stations within 2 km of land (21, 26, and 30; mean depth 8.1 m, range 4–10 m), Group B consists of inner-shelf stations within 9–17 km of land (mean depth 10.5 m, range 7–13 m), Group C consists of middle-shelf stations within 17–66 km of land and inclusive of sites in GRNMS (mean depth 19.2 m, range 10–43 m), and Group D consists of the deepest station (39) at the shelf break (77 km from land, 105 m depth).

Table 1 provides a comparison of benthic fauna among the four site groups. There were clear cross-shelf differences in species composition. Dominant fauna of Group A included common estuarine species, reflecting the close proximity of these stations to land and potential sources of estuarine larvae. Many of the Group A dominants (e.g., the polychaetes *Streblospio benedicti*, *Tharyx acutus*, *Mediomastus* spp., *M. ambiseta*, *M. californiensis*, *Eumida sanguinea*, *Polycirrus eximius*) were absent or rare at stations further offshore in Groups C and D. In comparison, dominant fauna of Groups C and D included many species that were absent or rare at inshore Group A sites (e.g., the gastropod *Caecum johnsoni*, the polychaete *Protodorvillea kefersteini*, the cephalochordate *Branchiostoma* spp., the bivalve *Crassinella dupliniana*, the amphipod *Bathyporeia parkeri*, the scaphopod *Cadulus quadridentatus*, and the isopod *Ptilanthura tenius*). Site Group B included dominants common to both adjacent groups, but which overlapped to a greater extent with the more seaward Site Group C. Dominants of the outer-shelf Group D consisted of species present in other site

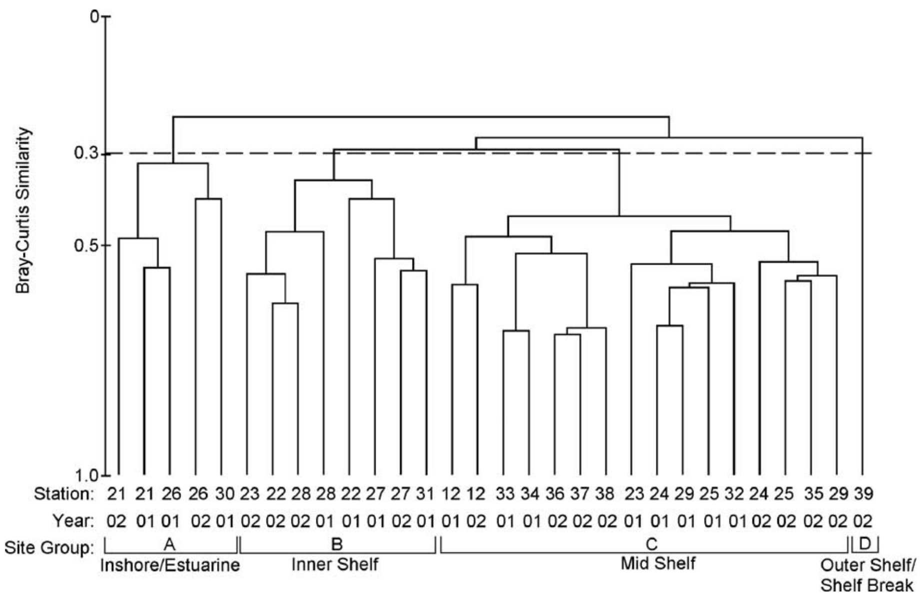


Fig. 2. Dendrogram resulting from clustering of stations sampled in April 01 and April–June 02, using group-average sorting and Bray–Curtis similarity. Each station-year combination is represented by three combined replicate samples (0.04 m^2 each). The analysis was performed on double-square-root transformed abundances after removing rare species (i.e., those representing <1% of total abundance of a sample). A similarity level of 0.3 (dotted line) was used to define major site groups (A–D).

groups, especially the adjacent Group C. A notable characteristic of the Group D dominants was their extremely low densities. A full species list may be obtained by request to the senior author.

There were notable among-group differences in species abundances, richness, and diversity (Table 1). Densities were highest at inshore Group A sites and lowest at the shelf-break Group D site. The high faunal densities at Group A sites are characteristic of such estuarine species and may be attributable to typically high nutrient supplies in these inshore areas, though appreciable inputs to the outer shelf can occur as well due to deepwater Gulf Stream intrusions along the shelf break (Tenore et al., 1978). H′ diversity increased with increasing depth, consistent with similar patterns noted along the continental shelf off New England (Neff et al., 1989), in the middle Atlantic Bight (Boesch, 1979), and in the SAB off Cape Lookout (Day et al., 1971). In contrast, species richness was highest at stations within the mid-shelf Group C, especially those in GRNMS. Similarly, in a prior study of benthic fauna in close association with live-bottom areas throughout the SAB (MRRI, 1982; Wenner et al., 1983), it was found that numbers of species were higher at mid-shelf sites in comparison to inner-shelf and outer-shelf sites, and that changes were more related to varying degrees of topographic complexity and habitat heterogeneity than to depth or distance from shore.

Abiotic environmental variables among the various benthic site groups are compared in Table 2. There were no major differences in DO or pH along any of the transects; mean DO values of 7.3 mg L^{-1} and mean pH values of 7.9 were the same for all groups measured. We were unable to obtain measurements of these two variables at the outer-shelf Group D site, however data from a station of similar depth (100 m) off Charleston, South Carolina revealed values in this same range (DO 7.5 mg L^{-1}, pH 8.5; J. Hyland, unpublished data). The high DO levels observed in this study are well above a reported benthic hypoxic-effect-threshold of about 1.4 mg L^{-1} (Diaz and Rosenberg, 1995), as well as most State standards of 5 mg L^{-1} or lower. TOC content of sediments was found at moderately low levels throughout the study area (2.1–4.1 mg g^{-1}), which are typical of shelf waters in this region (Tenore et al., 1978) and well below a reported range (>36 mg g^{-1}) associated with a high risk of disturbance from organic over-enrichment (Hyland et al., 2005). TOC values, though low overall, were slightly higher at both the inshore Group A and outer-shelf Group D sites (4.0 and 4.1 mg g^{-1}, respectively), compared to the two groups in-between (2.1–2.6 mg g^{-1}), due possibly to respective influences of coastal outwelling and deepwater Gulf Stream intrusions (Tenore et al., 1978).

With respect to remaining abiotic variables, Group A sites compared to those further offshore generally had

Table 1
Benthic characteristics by site group

Site group	Taxon	Dominant fauna			Mean density (m^{-2})[a]	Mean # taxa $grab^{-1}$	Mean H′ ($grab^{-1}$)[b]	Mean # taxa ($Sta.^{-1}$)[c]
		Mean density m^{-2}	Cum. %	% Freq.[d]				
A	*Mediomastus* spp. (P)	3257	28	67	11743	36	3.24	66
	Polycirrus eximius (P)	2008	45	47				
	Tharyx acutus (P)	1162	55	47				
	Streblospio benedicti (P)	572	60	67				
	Mediomastus ambiseta (P)	423	63	47				
	Tubificidae (O)	407	67	93				
	Spiophanes bombyx (P)	372	70	80				
	Exogone rolani (P)	247	72	60				
	Eumida sanguinea (P)	245	74	53				
	Mediomastus californiensis (P)	205	76	53				
B	*Mediomastus* spp. (P)	1003	20	33	4958	29	3.66	54
	Spiophanes bombyx (P)	550	31	96				
	Owenia fusiformis (P)	469	41	42				
	Oxyurostylis smithi (C)	306	47	79				
	Sabellaria vulgaris (P)	176	51	25				
	Mediomastus ambiseta (P)	152	54	58				
	Tellina spp. (B)	152	57	29				
	Eudevenopus honduranus (C)	145	60	83				
	Protohaustorius wigleyi (C)	127	62	50				
	Rhepoxynius epistomus (C)	108	64	42				
C	*Caecum johnsoni* (G)	389	7	56	5901	50	4.57	98
	Ericthonius brasiliensis (C)	377	13	27				
	Protodorvillea kefersteini (P)	309	18	69				
	Tubificidae (O)	281	23	77				
	Branchiostoma spp. (Ch)	226	27	71				
	Spiophanes bombyx (P)	197	30	96				
	Echinoidea (E)	193	33	58				
	Crassinella dupliniana (B)	173	36	48				
	Parapionosyllis longicirrata (P)	163	39	75				
	Bathyporeia parkeri (C)	134	41	27				
D	*Polygordius* spp. (P)	75	5	33	1550	37	4.89	74
	Sipuncula (S)	67	9	67				
	Spionidae (P)	67	13	100				
	Armandia maculata (P)	58	17	100				
	Cadulus quadridentatus (Sc)	58	21	67				
	Cirratulidae (P)	58	25	100				
	Lucinidae (B)	58	28	67				
	Spionidae Genus F (P)	58	32	67				
	Onuphidae (P)	50	35	33				
	Ptilanthura tenuis (C)	50	39	67				

P = Polychaeta, G = Gastropoda, B = Bivalvia, C = Crustacea, O = Oligochaeta, E = Echinodermata, S=Sipuncula, Sc= Scaphopoda, Ch = Cephalohordata.

[a] All taxa combined.

[b] Calculated using base 2 logarithms.

[c] Total number of taxa at a station (3 replicate, 0.04-m^2 grabs combined) averaged over all stations within the same site group.

[d] Percentage of samples in which taxon occured.

shallower depths, slightly warmer water, lower salinity, and a much higher silt-clay content of sediments (Table 2). Percent silt-clay, in particular, averaged 16.3% at Group A sites, compared to a mean of 0.3% for Group C sites (inclusive of GRNMS) and <2% for remaining sites. The warmer and less saline condition of water at this time of year for stations nearest to land was especially pronounced at Station 30 near the entrance of Altamaha Sound (near-bottom T=22.4 °C, S=22.8 ppt), which is presumably attributable to the larger river flow exiting the Altamaha River relative to the other two sounds (Amft et al., 2002; Chunyan and Blanton, 2002). Altamaha Sound is at the mouth of the Altamaha River, the largest river in Georgia. Doboy Sound, adjacent to

Table 2
Summary of abiotic environmental variables by site group

Variable	Site group means				ANOVA results	
	A	B	C	D	*F*-value	*Pr*>*F*
Depth (m)	8.1	10.5	19.2	105.0	50.66	<0.0001
Temperature (°C)	21.8	19.7	19.3	20.1	11.35	<0.0001
DO (mg/L)	7.3	7.3	7.3	–	0.03	0.9690
pH	7.9	7.9	7.9	–	1.82	0.2037
% Silt-clay	16.3	1.3	0.3	1.7	16.35	<0.0001
Mean ERM quotient	0.007	0.009	0.005	0.011	3.60	0.0267
Phi (median particle size)	1.50	2.33	1.22	1.43	8.29	0.0005
TOC (mg/g)	4.0	2.6	2.1	4.1	2.08	0.1278
Salinity (‰)	29.9	34.8	35.8	36.3	8.81	0.0004
Distance from shore (km)	2	12	42	145	12.92	<0.0001

Included are the site group means and univariate test statistics for significance of among-group differences (df=3,24 for F-statistics). Values for T, DO, pH, and S are from near-botttom measurements.

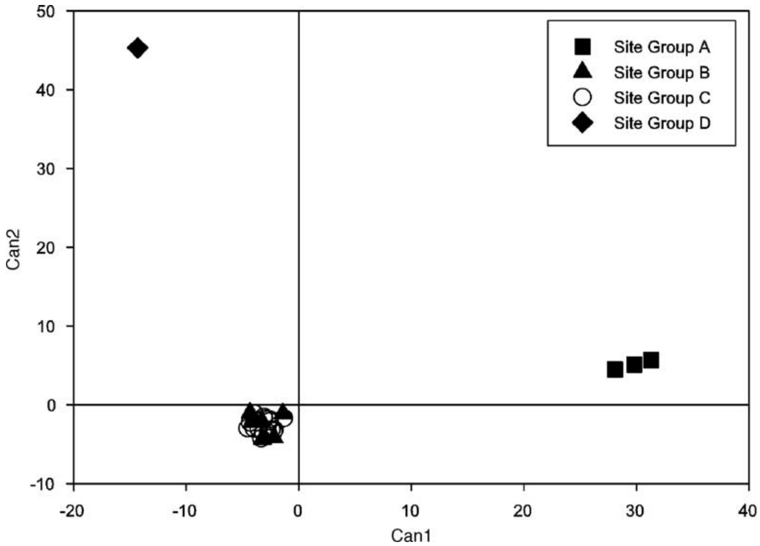
the middle transect, has no major upland sources of freshwater, but receives some low-salinity water from the Altamaha River via the Intracoastal Waterway, connecting marsh channels, and tidal exchange with Altamaha's near-coastal plume. Sapelo Sound, with no direct connection to Altamaha or other rivers, has the least amount of net outward water transport among the three sounds.

The fine-grained sediment particles, found at highest concentrations nearest the mouths of the three sounds, represent a potential source for sorption of any chemical contaminants in the run-off entering these systems and ultimately the offshore ecosystem. However, chemical contaminants in sediments appeared to be at low background levels throughout the study area. None of the stations had mean ERM quotients high enough to suggest significant risks of adverse effects on benthic fauna. Hyland et al. (1999) reported a high incidence of impaired benthic assemblages in southeastern estuaries at mean ERM quotients above a critical point of about 0.06 (78% of samples in that range) and a low incidence of effects (5% of samples) at mean ERM quotients below 0.02. Although in the present study we are dealing with offshore benthic fauna, none of the stations had mean ERM quotients in this upper bioeffect range (which are the most applicable data known to us for comparison). All values are well within the reported low-risk range (Table 2).

Canonical discriminant analysis was used to determine whether the separation of the cluster groups could be explained by such abiotic environmental factors (sensu Green and Vascotto, 1978; Hyland et al., 1991). Abiotic variables that displayed minimal variation across the four groups (i.e., DO and pH, Table 2) were not included in the analysis. Results revealed that the first two canonical functions are significant (CAN 1: $p<0.0001$, df=24, 50; CAN 2: $p<0.0001$, df=14, 36) and together account for 98.5% of the among-group variation in abiotic variables (56.7% and 41.8%, respectively). A plot of the discriminant scores on each of these two functions (Fig. 3) shows a strong separation of Site Group A stations from the other site groups on the CAN 1 axis, and of Site Group D from the other groups on the CAN 2 axis. Comparison of the TSCs reveals that the first canonical function (CAN 1) is most highly correlated with % silt-clay, thus explaining the wide separation of siltier, inshore Group A stations from the sandier, offshore stations comprising Groups B, C, and D. There is an additional slight separation on the CAN 1 axis of Group D from Groups B and C, reflecting the slightly higher percentage of silt-clay at this deepest station compared to the shallower Group B/C sites. TSCs for salinity and temperature also indicate relatively high correlations on CAN 1, and thus their possible further influence on the separation of Group A stations from the others. In addition to having sediments with higher silt-clay content, Group A stations were slightly warmer and less saline, revealing characteristics that are probably all due to the closer proximity of Group A stations to land and the influence of the coastal sounds. Additional unmeasured controlling factors related to land proximity also could be contributing to these patterns. These include physical factors (e.g., erosional effects near the mouths of sounds) and biological factors (e.g., closer proximity of Group A sites to sources of recruitment by estuarine species).

The canonical plot (Fig. 3) also reveals that the second canonical function explains most of the variation between Group D and remaining groups. TSCs for CAN 2 indicate that the strongest correlations on this function are with depth (foremost) and the related factor of distance from shore. The next strongest correlation was with mean ERM quotients. Though mean ERM quotients vary significantly among the three site groups (Table 2), the values are not in the range associated with a high risk of adverse effects on benthic fauna (as discussed above) and thus are not likely to be the cause of the observed faunal patterns.

These results suggest that granulometric characteristics of sediment (i.e., % silt-clay) and depth are major controlling factors contributing to the observed cross-shelf patterns in benthic fauna. Variations between Groups B and C, though not distinguishable in the



Variable	TSC	
	Can1	Can2
Depth	-0.3650	<u>0.8299</u>
Temperature	0.6975	0.2714
Salinity	-0.6978	-0.0795
TOC	0.3735	0.2838
% Silt-clay	<u>0.9631</u>	0.2220
Mean ERM quotient	0.2270	0.3096
Phi	0.1747	0.0017
Distance from shore	-0.4096	0.5167

Fig. 3. Separation of site groups on the first and second canonical components derived from canonical discriminant analysis performed on abiotic environmental variables. Can 1 = first canonical variable (56.7% of variability); Can 2 = second canonical variable (41.8% of variability). Total structure coefficients (TSC) of abiotic variables on both functions are also listed; coefficients considered important in each function are underlined.

present canonical plot (Fig. 3), may be attributable to subtle differences in these same factors. A comparison of Group B and C stations (Table 2), for example, reveals a transition from medium to coarse sands (with lower phi and % silt-clay values) and to slightly deeper water depths, respectively. As mentioned above, differences in salinity, temperature and other unmeasured factors related to shoreline proximity (e.g., erosional effects, recruitment of estuarine species) may be contributing to these patterns as well.

3.2. Within-sanctuary patterns of benthic fauna and relationship to benthoscape structure

3.2.1. Diversity and abundance of benthic fauna

A total of 349 taxa were identified from the 20 stations sampled at GRNMS in Year 2000 (Table 3). Though not depicted in the table, these fauna were comprised mostly of polychaete worms (45% by species, 16% by abundance), mollusks (27% by species, 67% by abundance), and crustaceans (22% by species, 7% by abundance). These three taxonomic groups represented 90% or more of the fauna, both by % species and % abundance. Particularly strong dominants (10 most abundant) throughout the sanctuary (all samples combined) in decreasing order were the bivalves *Ervilia* sp. A and *Crassinella lunulata*, the cumacean *Oxyurostylis smithi*, the gastropod *C. johnsoni*, the sipunculid *Aspidosiphon muelleri*, the cephalochordate *Branchiostoma* spp., actiniarian anthozoans, and the polychaetes *Spio pettiboneae* and *Spiophanes bombyx*. The most abundant of these species was *Ervilia* sp. A, which represented 56% of the total faunal abundance and occurred in 75% of the samples. The high abundance of

Table 3
Characteristics of benthic macroinfauna (>0.5 mm) at stations in GRNMS in April 2000

Station	Mean density (m^{-2}) [a]	Mean no. taxa $(grab^{-1})$ [a]	Mean H′ diversity $(grab^{-1})$ [a, b]	Total no. taxa $(station^{-1})$ [c]
1	2542	32	4.32	66
2	5775	58	4.71	113
3	5217	53	4.84	102
4	4492	52	4.81	96
5	4083	57	5.13	98
6	2617	31	3.81	62
7	2233	32	4.38	57
8	9850	59	4.07	117
9	3125	41	4.52	84
10	7967	64	4.46	115
11	6650	34	2.16	71
12	5933	49	4.00	96
13	40,642	40	0.89	81
14	50,258	45	0.82	89
15	4300	46	4.26	94
16	1642	27	4.23	53
17	3608	42	4.49	80
18	5900	41	3.98	85
19	1858	47	4.46	91
20	423	45	4.62	86

Three replicate grabs (0.04 m^2 each) were taken at each station.
[a] Averaged over 3 replicates.
[b] Calculated using base 2 logarithms.
[c] Total number of taxa from 3 replicates combined. Grand total from all 20 stations in 2000 = 349 taxa.

Ervilia, in excess of 10^4 m^{-2}, reflects its potential importance from a trophic perspective. Sedberry (1985), for example, reported that the largest percentage by number (38%) of prey consumed by tomtate, *Haemulon aurolineatum*, in the SAB consisted of *Ervilia*. Another dominant infaunal species occurring at GRNMS, the lancelet *Branchiostoma* spp., also was reported by Sedberry as representing the largest volume (41.6%) of prey consumed by tomtate. The role of these faunas as preys for fishes feeding on sandy substrates within the sanctuary is the subject of an ongoing companion study.

Macroinfaunal assemblages within GRNMS were highly diverse. As noted above, from just this one sampling occasion, a total of 349 different taxa were identified from the 60 individual, 0.04-m^2 grab samples (representing a total area of just 2.4 m^2) (Table 3). The actual number of species encountered is probably higher, given that some taxa were identified only to the lowest practical identification level (LPIL). Mean number of taxa per grab ranged from 27 to 64 (median = 45) and mean H′ diversity ranged from 0.82 to 5.13 (median = 4.3). The mean number of taxa per grab at one of these sites (Station 12) during a subsequent sampling event (May 2001) was 89, which is a very sizable number for the relatively small sampling area of the 0.04-m^2 grab.

For comparison, numbers of taxa (e.g., based on the median value of 45 for the 20 sites in 2000) are over twice as high as those at sites of comparably high salinity (> 30 ppt) sampled with the same methods in estuaries throughout the southeastern U.S. (median value for 38 sites = 19; J. Hyland, unpublished data). Moreover, the total number of taxa found at any given station from the three replicate grabs combined (0.12 m^2) ranged from 53 to 117 (Table 3). Boesch (1977), working at similar shelf depths in the Middle Atlantic Bight (MAB), generally found fewer than 60 species in six larger, 0.1-m^2 grabs combined, thus less species in about five times the sampling area. Similarly, based on results of an offshore monitoring program conducted in the 1980s, Blake and Grassle (1994) found that the diversity of benthic infauna at deeper, slope-to-rise sites off the Carolinas was much higher in comparison to similar depths in the middle and North Atlantic, and was attributed to a higher diversity of sediment types. Van Dolah et al. (1997), in a study conducted with methods identical to ours at sandy sites of similar depths off the coast of South Carolina, also found a high diversity of macroinfauna, with mean numbers of species ranging from comparable values of 34–70 species 0.04 m^{-2}. In the above-mentioned study of live-bottom habitats throughout the SAB (MRRI, 1982; Wenner et al., 1983), which included a station within GRNMS, divers used suction samplers to collect macroinvertebrates from sand veneers in close association with the live-bottom outcrop. Although a difference in methods precludes direct comparisons with the present study, these authors also reported a high diversity of benthic fauna and attributed it to high topographic complexity.

3.2.2. Spatial patterns of benthic fauna

Data from the 20 stations sampled at GRNMS in April 2000 also were used to examine within-sanctuary spatial patterns of these fauna. Results of cluster analysis, performed with the same methods used for analysis of cross-shelf patterns, show that stations separate into two major site groups, denoted A and B, at a Bray–Curtis similarity of 0.55 (Fig. 4). Site Group A consists of Stations 1, 6, 7, and 11 co-located in the northwest sector of the sanctuary (Fig. 1). The larger Group B, consisting of the remaining 16 stations, was further divided into two subgroups at a similarity of 0.63. Note that these division points are at much higher levels of similarity compared to the value (0.30) that defined the broader cross-shelf groupings. In general, the fauna of Group A stations appeared to be less diverse and abundant in comparison to other sanctuary sites (Fig. 5, Table 3). Numbers of species and densities were highest at B1 and B2 stations, respectively. Dominant (five most abundant) species and corresponding rank orders also varied among the three site groups (Fig. 5). However, all of these species were fairly common throughout the sanctuary. Though some species were significantly more abundant in one site group compared to others (also see Table 7 below), none of these species were unique to a specific group. *Ervilia* sp. A was particularly abundant at B2 stations, with mean densities in excess of 10^4 m^{-2}.

3.2.3. Abiotic environmental characteristics

Key abiotic environmental characteristics of the sanctuary based on April 2000 data (Table 4) included depths typically between 17 and 19.4 m (based on interquartile range; median = 18.9 m); euhaline (oceanic) salinities, typically between 33.8–34.1 ppt (median = 33.9); very high DO levels, typically between 7.9 and 8.2 mg L^{-1} (median = 7.92); low levels of organic carbon in sediments, typically between 1–2 mg g^{-1} (though one station, 17, had a moderate level of 19.7 mg g^{-1}); and coarse sediments consisting mostly of sand with some shell hash and gravel-size particles. There was no fine (silt-clay) fraction of sediment apparent in these samples. Given their generally narrow

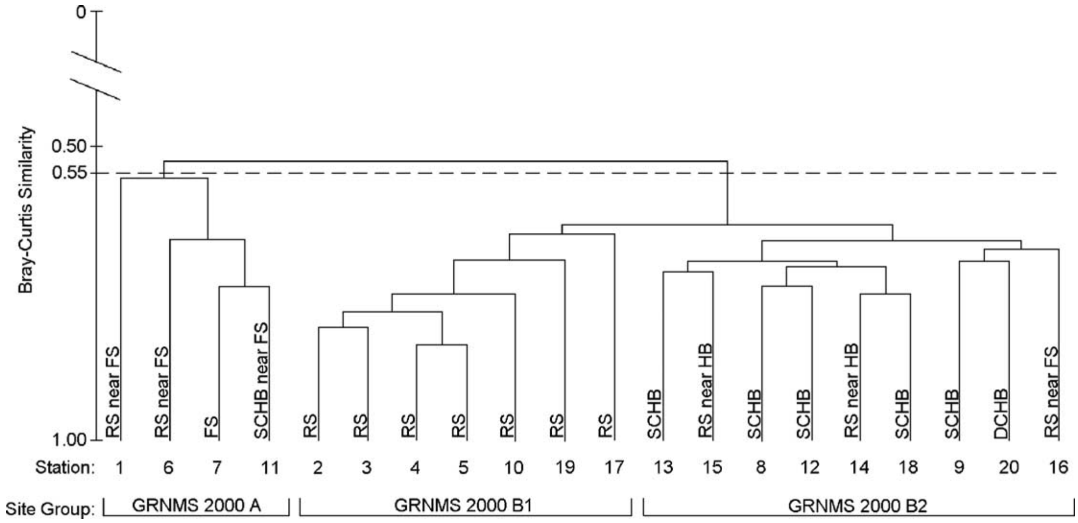


Fig. 4. Dendrogram resulting from clustering of 20 stations sampled within GRNMS in April 2000, using group-average sorting and Bray–Curtis similarity. Samples within each station are combined over all three replicates. Letter code next to each station number refers to corresponding benthoscape category (see companion Fig. 6). RS = rippled sand, FS = flat sand, DCHB = densely colonized hard bottom, SCHB = sparsely colonized hard bottom (from Kendall et al., 2005).

ranges among the various GRNMS stations, it is unlikely that these factors are the cause of the observed spatial patterns of benthic fauna within the sanctuary.

Chemical contaminants in sediments throughout the sanctuary appeared to be at low background concentrations, below probable bioeffect levels. There were no

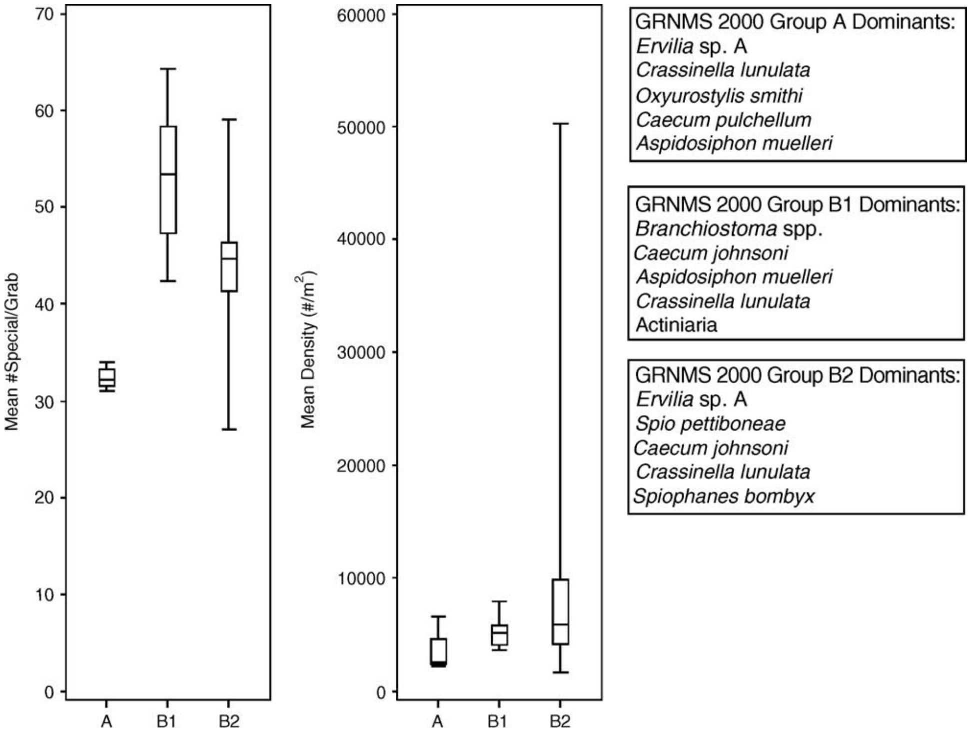


Fig. 5. Comparison of benthic species richness (mean # species grab^{-1}), mean density (# individuals m^{-2}), and dominants (5 most abundant species in decreasing order) at GRNMS Site Groups A, B1, and B2. For plots of species richness and density, boxes are inter-quartile ranges, horizontal lines within boxes are medians, and whisker endpoints are high-low extremes.

Table 4
Summary of station depth, water quality, and sediment data for stations sampled within GRNMS in April 2000

Station	Depth (m)	Near-bottom water				TOC (mg g^{-1})	% Gravel	% Sand	Mean ERM quotient
		Temp (°C)	Salinity (ppt)	D.O. (mg L^{-1})	pH				
1	17.5	17.8	33.6	8.4	7.9	1.1	0.00	99.87	0.0039
2	19.3	17.9	33.7	8.2	7.9	1.1	3.36	96.14	0.0023
3	19.4	17.9	33.8	8.3	7.9	1.5	0.00	99.45	0.0039
4	20.8	17.9	33.8	8.2	7.9	1.2	0.00	99.74	0.0063
5	21.1	17.6	34.1	8.2	7.9	0.8	0.00	99.82	0.0038
6	18.0	17.9	34.0	7.9	7.9	1.3	0.00	99.79	0.0036
7	16.0	17.9	34.0	7.9	7.9	1.3	0.00	99.53	0.0037
8	14.5	18.2	33.9	8.1	7.6	4.9	9.41	90.04	0.0021
9	19.7	18.2	33.9	8.2	7.9	1.2	0.00	99.56	0.0016
10	19.0	17.7	34.1	8.2	7.9	1.4	4.39	94.73	0.0015
11	16.7	17.9	34.0	7.9	8.0	1.9	0.00	99.69	0.0040
12	17.0	17.9	34.1	7.9	8.0	4.2	0.00	99.37	0.0038
13	18.7	17.9	34.2	7.9	8.0	1.8	0.00	99.46	0.0040
14	19.3	18.0	33.7	7.7	8.0	1.4	3.57	96.19	0.0128
15	18.1	18.0	33.9	7.7	8.0	1.5	0.00	99.76	0.0020
16	15.2	18.0	34.1	8.0	8.0	1.3	3.55	96.18	0.0051
17	19.6	17.9	34.3	7.9	8.0	19.7	15.53	83.79	0.0238
18	17.0	17.9	34.3	7.9	8.0	2.7	6.25	93.38	0.0054
19	19.0	18.0	33.9	7.6	8.1	1.6	0.00	99.29	0.0022
20	19.2	18.0	33.9	7.7	8.0	1.3	2.23	97.51	0.0025

A silt-clay fraction was absent in all samples.

stations within the sanctuary with mean ERM quotients in the range (i.e., above a critical point of 0.06, sensu Hyland et al., 1999) associated with a high incidence of impaired benthic condition (Table 4). Also, there were no stations in which individual contaminants exceeded their corresponding upper-level ERM SQG values (Table 5). One station, representing just 5% of the sanctuary's area, had a moderate concentration of copper (103 μg g^{-1}) that was above the lower-level ERL guideline value of 34 μg g^{-1}, but still below the higher ERM value of 270 μg g^{-1}. Though the source could be natural or anthropogenic, the concentration of copper at this station was higher than the concentrations typically observed in other southeastern coastal areas remote from contaminant sources (Windom et al., 1989). Also, trace concentrations of man-made pesticides (DDT, chlorpyrifos) and other chemical substances from human sources (PCBs, PAHs) were detectable in sediments throughout the sanctuary (Table 5), though not at concentrations likely to cause significant bioeffects. The low sediment contamination is most likely attributable to the remote location of this offshore environment and the sandy nature of the substrate (i.e., absence of a silt-clay fraction).

Contaminants measured in tissues of target demersal/benthic species, black sea bass *C. striata* and the ark shell *A. zebra*, were also below human-health guidelines (where available), based on a limited sample population of 10 fish fillets and 9 ark-shell composites (Table 6). However, moderate concentrations of lead, just below the FDA (1993b) Level of Concern value of 3 μg g^{-1} dry wt., were found in one fish sample (2.6 μg g^{-1}) and one ark-shell sample (2.9 μg g^{-1}). Similar to results for sediments, tissues of both species contained trace concentrations of additional chemical contaminants associated with human sources (pesticides, PCBs, PAHs), further demonstrating that such materials are making their way to the offshore sanctuary environment, albeit at low concentrations, either by atmospheric deposition or underwater cross-shelf transport from land. The detection of trace concentrations of these contaminants in sediments along the cross-shelf transects during the two subsequent sampling events provides additional support for this point.

3.2.4. Infaunal–benthoscape relationships

Given the low background levels of chemical contaminants and the generally narrow ranges in other measured environmental variables among the various GRNMS stations, it is unlikely that such factors were a major cause of observed within-sanctuary spatial patterns of benthic fauna. Therefore, the role of seafloor structure, or benthoscape, as a potential source of these patterns was examined. Advances in seafloor mapping

Table 5
Chemical contaminants present at detectable concentrations in sediments at GRNMS (from 20 sites in 2000, and 6 of the same 20 sites in 2001 and 2002)

Analyte	Mean	Range		SQG	
		Min	Max	ER-L	ER-M
Metals (ug/g dry wt., unless otherwise indicated)					
Aluminum (%)	0.04	0.01	0.08	–	–
Arsenic	1.46	0.12	4.09	8.2	70
Cadmium	0.08	<MDL	0.35	1.2	9.6
Chromium	1.93	<MDL	8.60	81	370
Copper	3.78	<MDL	103.00	34 (1)	270
Iron (%)	0.13	0.03	0.39	–	–
Lead	0.67	0.01	2.19	46.7	218
Manganese	21.62	7.36	46.40	–	–
Mercury	0.00	<MDL	0.003	0.15	0.71
Nickel	2.31	0.91	5.00	20.9	51.6
Selenium	0.10	<MDL	0.72	–	–
Silver	0.03	<MDL	0.93	1	3.7
Tin	0.02	<MDL	0.28	–	–
Zinc	9.70	<MDL	40.80	150	410
PAHs (ng/g dry wt.)					
Acenaphthylene	0.01	<MDL	0.46	44	640
Anthracene	0.00	<MDL	0.04	85.3	1100
Benzo(a)anthracene	0.01	<MDL	0.05	261	1600
Biphenyl	1.10	<MDL	8.40	–	–
Chrysene + triphenylene	0.00	<MDL	0.04	–	–
Dibenz (a,h + a,c)anthracene	0.00	<MDL	0.03	63.4	260
2,6 Dimethylnaphthalene	0.14	<MDL	2.35	–	–
Fluoranthene	0.18	<MDL	0.63	600	5100
1-Methylnaphthalene	1.85	<MDL	9.12	–	–
2-Methylnaphthalene	3.55	<MDL	16.30	70	670
1-Methylphenanthrene	0.01	<MDL	0.17	–	–
Naphthalene	6.71	<MDL	32.50	160	2100
Phenanthrene	0.92	<MDL	1.75	240	1500
Pyrene	0.02	<MDL	0.29	665	2600
1,6,7 Trimethylnaphthalene	0.01	<MDL	0.04	–	–
Total PAHs [a]	0.72	<MDL	32.50	4022	44,792
Total PCBs (ng/g dry wt.)	3.68	2.19	6.23	22.7	180
Pesticides (ng/g dry wt.)					
Chlorpyrifos	0.03	<MDL	0.13	–	–
Endosulfan ether	0.00	<MDL	0.03	–	–
Heptachlor	0.00	<MDL	0.02	–	–
Hexachlorobenzene	0.00	<MDL	0.02	–	–
Lindane	0.00	<MDL	0.03	–	–
DDT [c]	0.00	<MDL	0.09	–	–
Total DDT [b]	0.00	<MDL	0.09	1.58	46.1

For computing the mean concentration, a value of zero was used for any station where the concentration of the analyte was < the corresponding method detection limit (MDL). Also listed are corresponding sediment quality guideline (SQG) values (Long et al., 1995). Number of sites where SQGs were exceeded is indicated in parentheses.

[a] Without Perylene.

[b] Total DDTs = 2′4′-DDD + 4′4′-DDD + 2′4′-DDE + 4′4′-DDE + 2′4′-DDT + 4′4′-DDT.

[c] DDT = 2′4′-DDT + 4′4′-DDT.

techniques over the last decade have produced a growing body of new literature on the study of benthic community structure and dynamics in relation to benthoscape characteristics (e.g., Zajac, 1999, 2001; Zajac et al., 2000, 2003; Kostylev et al., 2001; Brown et al., 2002).

The above-mentioned map of benthoscape features within GRNMS, developed recently by Kendall et al.

Table 6
Chemical contaminants present at detectable concentrations in edible tissues of black sea bass and ark shells at GRNMS sites in April 2000

Analyte	Black Sea Bass (n=10)			Ark Shell (n=9)			FDA guideline
	Mean	Range		Mean	Range		
		Min	Max		Min	Max	
Metals (μg/g dry wt.)							
Aluminum	48.72	40.40	61.80	89.86	59.30	182.00	–
Arsenic	58.52	6.76	89.30	63.57	<MDL	93.00	215.0 [a]
Copper	0.41	0.19	1.17	5.96	<MDL	8.02	–
Iron	1.90	<MDL	16.90	147.89	60.70	294.00	–
Lead	0.30	<MDL	2.64	0.40	<MDL	2.92	3.0 [a]
Manganese	0.13	<MDL	0.55	17.11	<MDL	26.70	–
Mercury	0.23	0.11	0.59	0.05	<MDL	0.12	5.0 [b]
Nickel	2.20	<MDL	21.70	1.37	<MDL	3.80	350.0 [a]
Selenium	2.83	2.43	3.35	6.79	5.13	10.30	–
Silver	0.05	<MDL	0.18	3.24	1.60	4.66	–
Zinc	24.33	<MDL	47.30	114.11	<MDL	211.00	–
PAHs (ng/g dry wt.)							
2-Methylnaphthalene	2.62	<MDL	26.20	16.07	<MDL	48.50	–
Total PAHs w/o Perylene	2.62	<MDL	26.20	22.93	<MDL	110.30	–
PCBs (ng/g dry wt.)							
Total PCBs	10.52	5.23	19.90	2.11	1.25	2.68	10,000.0 [c]
Pesticides (ng/g dry wt.)							
Chlorpyrifos	0.10	<MDL	0.60	0.14	<MDL	0.84	–
DDE [d]	0.73	0.35	1.93	0.26	<MDL	0.41	25,000.0 [b]
DDT [d]	0.09	<MDL	0.26	<MDL	<MDL	<MDL	25,000.0 [b]
Total DDTs [e]	0.82	0.35	2.19	0.26	<MDL	0.41	25,000.0 [b]
Dieldrin	0.10	<MDL	0.41	0.04	<MDL	0.35	1500.0 [b]
Endosulfan ether	0.02	<MDL	0.24	<MDL	<MDL	<MDL	–
Heptachlor	0.03	<MDL	0.10	<MDL	<MDL	<MDL	1500.0 [b]
Heptachlor epoxide	0.27	<MDL	2.69	2.87	2.18	3.59	1500.0 [b]
Hexachlorobenzene	0.07	<MDL	0.13	0.01	<MDL	0.06	–
Lindane	0.79	0.15	1.34	0.94	0.73	1.13	–
Mirex	0.22	<MDL	0.86	<MDL	<MDL	<MDL	500.0 [b]
Trans-nonachlor	0.17	<MDL	0.39	<MDL	<MDL	<MDL	–
Lipids (% dry wt.)	1.53	0.85	3.00	6.20	4.73	7.18	–

All concentrations are reported on a dry-weight basis. FDA guideline values are included (where available) and have been converted to dry weight by multiplying published wet-weight values by a factor of 5. For computing the mean concentration, a value of zero was used for any sample in which the concentration of the analyte was < the corresponding MDL. There were no cases where FDA guidelines were exceeded.

[a] FDA Level of Concern for contaminants in shellfish. Value is lowest of multiple values reported by FDA for humans of various ages consuming either crustaceans or molluscs at the 90th percentile consumption rate. Values (converted from wet weight to dry weight) are from: FDA (1993a) for As, FDA (1993b) for Pb, FDA (1993c) for Ni.

[b] FDA Action Level for poisonous or deleterious substances in human food and animal feed (level for edible portion of fish is given). FDA, 1994.

[c] FDA Tolerance for unavoidable residues of PCBs in fish and shellfish. FDA, 1984.

[d] DDE=2′4′-DDE+4′4′-DDE; DDT=2′4′-DDT+4′4′-DDT.

[e] Total DDTs=2′4′-DDD+4′4′-DDD+2′4′-DDE+4′4′-DDE+2′4′-DDT+4′4′-DDT.

(2005), provided a basis for this analysis (Fig. 6). Four benthoscape types were identified in this latter study as follows:

- *Sand plain (flat sands, FS):* Coarse unconsolidated sediment occurring as a flat plain with no sudden changes in relief and <1% colonization by sessile epifaunal invertebrates. Thickness is variable, but may be only a few centimeters overlying flat limestone. Bioturbation is visible from polychaetes, echinoderms, and burrowing fishes and ranges from reworking of surface material to mound building and other excavations.
- *Rippled sand (RS):* Unconsolidated sediment deposited in sufficient thickness such that regular ridges or waves are formed. Typically, ridges are 6–10 cm

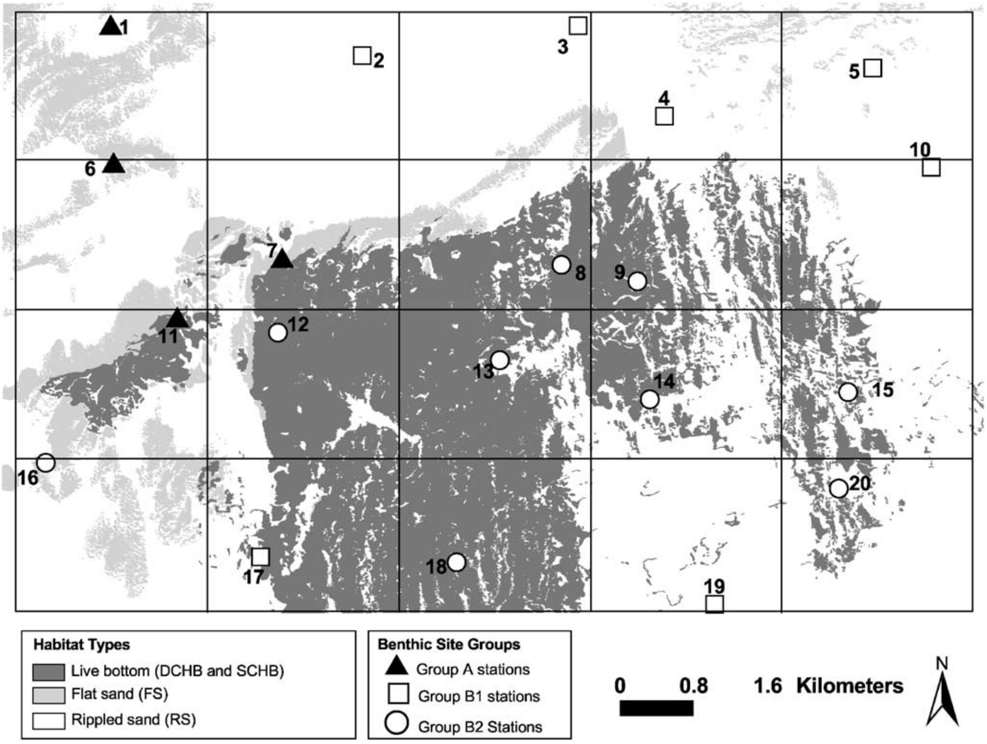


Fig. 6. Map of GRNMS showing relationship of benthic site-group designations (from Fig. 4) to bottom habitat structure (from Kendall et al., 2005). Note: Densely colonized hard bottom (DCHB) and sparsely colonized hard bottom (SCHB) features originally described by Kendall et al. (2005) are combined into a single "live bottom" category for the purpose of the present analysis.

high from crest to trough, and 40–60 cm long from crest to crest. Troughs are often dominated by coarser material such as shell fragments, while crests are primarily composed of sand. Density of colonization by sessile epifaunal invertebrates is <1% as in flat sands.

- *Sparsely colonized hard bottom (SCHB):* Low-relief bottom composed of partially exposed limestone substrate, sparsely colonized (1–60% of bottom) by sessile epifaunal invertebrates such as soft corals, sponges, and tunicates. A thin veneer of sand 1–2 cm thick may cover much of the bottom, but is thin enough to allow sessile benthic organisms to attach to the limestone.
- *Densely colonized hard bottom (DCHB):* Bottom composed of exposed limestone substrate densely colonized (60–100% of bottom) by assemblages of sessile epifaunal invertebrates. The limestone may be flat with little vertical relief or include ledges, overhangs, and other changes in bathymetry. Ledges typically have a vertical relief of 0.5–2 m.

Spatial overlays (produced with ArcView) were used in the present study to compare station classifications derived from the above cluster analysis of benthic infaunal data (Fig. 4) to the distribution of habitat types depicted in the map (Fig. 6). There is a fairly close match between the spatial pattern of benthic site groups and the mosaic of habitat (benthoscape) types. Site-Group A stations (1, 6, 7, 11) are all located in the northwest quadrat of the sanctuary, in or near substrates designated as flat sand (FS). Flat sands, occupying about 8% of the sanctuary seafloor (Kendall et al., 2005), are the most predominant in the northwest and southwest portions of the sanctuary. Site-Group B1 stations (2, 3, 4, 5, 10, 17, 19) are all located in substrates designated as rippled sands (RS). This is the most spatially extensive benthoscape feature, representing about 67% of the sanctuary seafloor (Kendall et al., 2005). Live bottom, including sparsely to densely colonized hard-bottom substrates (SCHB, DCHB), is predominant in the middle to south-mid portions of the sanctuary. SCHB substrates cover about 25% of the sanctuary seafloor, while DCHB is much more concentrated, representing <1% (Kendall et al., 2005). Most Site-Group B2 stations (with the exception of Station 16) fall in or near these live-bottom substrates. Further differentiation of infaunal patterns between the two types of live-bottom habitat was not possible with the present study design, especially given the concentrated nature of DCHB substrates (thus the two are combined in the Fig. 6 map).

Benthic community characteristics were compared across the various benthoscape elements, with the SCHB and DCHB substrates combined into a single live-bottom category (Table 7). The flat-sand category incorporated all Site-Group A stations (from Fig. 4) in addition to Station 16, which was a member of the B2 site group but included here because of its close proximity to a large flat-sand area. The rippled-sand category consisted of all Site-Group B1 stations, and the live-bottom category consisted of all remaining stations (corresponding largely to Site Group B2). In general, infauna in flat sands was the least abundant and diverse. Rippled sands supported the highest diversity (with significantly highest number of species and H′) and moderately high densities. Live-bottom areas supported the highest density of infauna and moderately high numbers of species. However, the high density of infauna in live-bottom was due primarily to an enormous bloom of the clam *Ervilia* sp. A. Without *Ervilia*, total faunal densities (all other species combined) at live-bottom sites were below that of rippled sands. Rippled sands also supported significantly higher densities of three other dominants, the gastropod *C. johnsoni*, the sipunculid *A. muelleri*, and the cephalochordate *Branchiostoma* spp.

The relatively close match between spatial patterns of benthic site-groups and the mosaic of benthoscape types provides evidence to suggest that benthoscape structure plays an important role in the distribution of infaunal assemblages within the sanctuary. Such an effect occurs on spatial scales smaller than the broad cross-shelf patterns in benthic fauna discussed above in relation to such factors as depth, grain size, and shoreline proximity. At this time, we are unable to identify with certainty the specific factors that explain differences in faunal patterns among the various benthoscape features. However, potential sources may include variations in level of substrate complexity, predation effects from foraging fishes, bioturbation effects from large motile epifauna, amount and quality of food, or currents and other hydrologic conditions that may be affecting sediment dynamics (e.g., the thickness and stability of sediment veneers) as well as larval settlement. Regarding this latter point, Zajac et al. (2003) suggested that changes in hydrologic conditions enhancing larval settlement may explain higher densities of dominant fauna found in transition zones between different benthoscape elements in Long Island Sound.

Table 7
Comparison of benthic community characteristics by benthoscape type

	Benthoscape type			ANOVA results			
	Flat sand (F)	Rippled sand (R)	Live bottom (L)	*F*-value	*df*	*Pr*>F	Sig. diff.[a]
Component stations:	*(1, 6, 7, 11, 16)*	*(2, 3, 4, 5, 10, 17, 19)*	*(8, 9, 12, 13, 14, 15, 18, 20)*				
Mean # taxa grab $^{-1}$	31	53	46	25.95	2,57	<0.0001	F L R
Mean H grab^{-1}	3.8	4.7	3.4	7.13	2,57	0.0017	L F R
Mean # taxa station^{-1} (pooled replicates)	62	99	91	18.48	2,17	<0.0001	F L R
Mean density grab $^{-1}$ (# m^{-2}): All fauna	3137	5244	15,528	5.61	2,57	0.0059	F R L
Mean density grab $^{-1}$ (# m^{-2}): All fauna[b]	2183	5215	3805	16.36	2,57	<0.0001	F L R
Mean density grab^{-1} (# m^{-2}):							
•*Ervilia* sp. A	953	29	11,723	5.54	2,57	0.0063	R F L
•*Crassinella lunulata*	253	314	235	0.42	2,57	0.6563	L F R
•*Oxyurostylis smithi*	185	117	170	1.50	2,57	0.2314	R L F
•*Caecum johnsoni*	55	530	254	11.16	2,57	<0.0001	F L R
•*Aspidosiphon muelleri*	177	354	124	11.18	2,57	<0.0001	L F R
•*Branchiostoma* spp.	45	595	78	9.10	2,57	0.0004	F L R
•Actiniaria	20	262	13	2.81	2,57	0.0686	L F R
•*Spio pettiboneae*	42	130	256	3.14	2,57	0.0511	F R L
•*Spiophanes bombyx*	113	154	204	5.20	2,57	0.0084	F R L

Sparsely and densely colonized hard bottom are combined into a single “live bottom” (L) category.

[a] Means connected by bars are not significantly different at α = 0.05, based on Tukey's HSD test.

[b] Without *Ervilia* sp. A.

Variations in hydrologic conditions affecting the stability and complexity of sediment may be a particularly important factor explaining differences between flat and rippled sands. A frequently shifting sediment veneer for example would not be an optimal condition for the survival of newly settled larvae and recruitment of many benthic species. Another important source of sediment disturbance could be bioturbation effects from large motile invertebrates, which appear to be particularly active in flat sands (Kendall et al., 2005). Benthic diversity and abundances were in fact lowest in this benthoscape feature. In contrast, the greater complexity and heterogeneity of rippled sands (e.g., with notable variations between ridge crests and troughs), may explain the higher diversity of benthic fauna in these sediments. As noted above, MRRI (1982, also Wenner et al., 1983) proposed that high diversity of infauna found in close proximity to live-bottom areas throughout the SAB may be attributable to the greater habitat complexity. In the present study, sediments near live bottom supported moderately high numbers of benthic species and the highest densities (i.e., when the dominant bivalve *Ervilia* sp A was included). However, diversity and abundance without *Ervilia* were lower in sediments near live bottom, compared to the open rippled-sand areas. Such differences could be related to predation pressures of fishes congregating around the reefs and foraging in the adjacent sands. Posey and Ambrose (1994), for example, noted feeding-induced "halos" of depressed benthic abundance surrounding live-bottom ledges off the North Carolina coast. Efforts to develop a better understanding of how the structure and dynamics of benthic communities vary in relation to such factors across the various benthoscape features should be a focus of future study.

Table 8
Comparison of mean densities (m^{-2}) of the two most abundant species for each year at each of the six repeated-sampling stations (1, 10, 11, 12, 14, 17)

Station	Year	Taxon	Mean density (m^{-2})
1	00	*Aspidosiphon muelleri*	375
		Crassinella lunulata	308
	01	*Crassinella lunulata*	400
		Spiophanes bombyx	358
	02	*Ervilia concentrica*	242
		Metharpinia floridana	208
10	00	Branchiostoma (LPIL)	2250
		Caecum johnsoni	625
	01	Branchiostoma (LPIL)	1092
		Caecum johnsoni	592
	02	*Filogranula* sp. A	775
		Sphaerosyllis piriferopsis	500
11	00	*Ervilia* sp. A	4725
		Crassinella lunulata	267
	01	*Spiophanes bombyx*	342
		Protodorvillea kefersteini	167
	02	*Semele nuculoides*	258
		Ervilia concentrica	175
12	00	*Ervilia* sp. A	1933
		Ophiuroidea (LPIL)	492
	01	*Protodorvillea kefersteini*	2400
		Erichthonius brasiliensis	2075
	02	*Erichthonius brasiliensis*	3700
		Ervilia concentrica	867
14	00	*Ervilia* sp. A	46,908
		Tectonatica pusilla	433
	01	*Spio pettiboneae*	542
		Spiophanes bombyx	367
	02	Cnidaria (LPIL)	317
		Rhynchocoela (LPIL)	58
17	00	*Caecum johnsoni*	517
		Spio pettiboneae	425
	01	*Fabricinuda trilobata*	5750
		Tubificidae (LPIL)	1000
	02	*Caecum johnsoni*	917
		Fabricinuda trilobata	850

3.3. Temporal (among-year) variability of benthic fauna

Data from the six repeated-sampling sites within GRNMS (1, 10, 11, 12, 14, 17) provided a basis for examining among-year temporal variability in population densities of dominant fauna. A comparison of the two most abundant species for each station-year combination (Table 8) shows that the dominance patterns at most stations were not repeatable precisely from year to year. While most of these species were present at a given station consistently each year, their abundance rank orders shifted considerably among years. Table 9 further demonstrates significant among-year differences in several of these species, namely the sipunculid *A. muelleri*, the cephalochordate *Branchiostoma* spp., the bivalve *Ervilia* sp. A, and the polychaetes *P. kefersteini* and *S. pettiboneae*. *Ervilia* sp. A was an especially striking example, with peak abundances at half of these stations in 2000 (4725 m^{-2} at Station 11, 1933 m^{-2} at Station 12, and 46,908 m^{-2} at Station 14) and a complete absence thereafter.

Prior studies similarly have demonstrated the temporally dynamic nature of benthic fauna in shelf waters off Georgia. Frankenberg (1971), in a study of temporal variability at a site of similar habitat type (coarse sand, 21 m) and very close to Gray's Reef, characterized benthic assemblages with sequential seasonal peaks of population density that were not repeatable from year to year. The dominant seasonal pattern in this latter study was a summer pulse in density of *Branchiostoma caribaeum* (comparable to our *Branchiostoma* spp.)

Table 9
Among-year comparison of mean densities (m^{-2}) of the two highest ranked species overall at each repeated-sampling station (i.e., ranked over all years within a station)

Station	Species	Mean density (m^{-2})			ANOVA results				
		2000	2001	2002	*F*	*Pr*>*F* [a]	Sig. diff. [b]		
1	*Crassinella lunulata*	308	400	192	1.0	0.425	02	00	01
	Aspidosiphon muelleri	375	33	192	12.5	0.007	01	02	00
10	*Branchiostoma* spp.	2250	1092	133	19.6	0.002	02	01	00
	Filogranula sp. A	492	567	775	0.2	0.861	00	01	02
11	*Ervilia* sp. A	4725	0	0	16.9	0.003	02	01	00
	Spiophanes bombyx	117	342	67	3.8	0.085	02	00	01
12	*Erichthonius brasiliensis*	42	2075	3700	0.6	0.579	00	01	02
	Protodorvillea kefersteini	25	2400	275	7.9	0.021	00	02	01
14	*Ervilia* sp. A	46,908	0	0	10.8	0.010	02	01	00
	Spio pettiboneae	192	542	0	6.5	0.031	02	00	01
17	*Caecum johnsoni*	517	583	917	0.9	0.471	00	01	02
	Fabricinuda trilobata	8	5750	850	4.3	0.069	00	02	01

[a] F-test based on 2,6 degrees of freedom.
[b] Means connected by bars are not significantly different at $\alpha = 0.05$, based on Tukey's HSD test.

with population lows of <100 m^{-2} from September to March, increases starting in April, and highs of about 1200–1300 m^{-2} from June to July. Our present study appears to have captured the beginning of this summer aggregation of *Branchiostoma* in samples from 2000 to 2001 at Station 10 (2250–1092 m^{-2}, respectively, Table 8). MRRI (1982, Wenner et al., 1983) also reported seasonal (winter vs. summer) changes in species composition and abundance of macroinvertebrates collected from sand veneers in close association with live-bottom outcrop at Gray's Reef and sites of similar depth throughout the SAB.

Changes in population densities on seasonal scales have been attributed to variable patterns in reproduction, larval settlement, and growth usually associated with variations in temperature (Osman, 1977; Wenner et al., 1983). Frankenberg (1971) further attributed the extreme seasonal variation in benthic fauna in shelf waters off Georgia to their short life cycles and meroplanktonic larvae. Seasonal variations in predation by fishes also could contribute to seasonality of benthic prey species (Frankenberg and Leiper, 1977; Wenner et al., 1983).

The present study was not designed to address monthly seasonal variations throughout any given year. However, distinct variations in temperature recorded over the three sampling events, which occurred from early April in 2000 to mid-June in 2002, suggest that the observed among-year differences in density of benthic fauna may be partly attributable to such seasonal factors. Mean temperatures among the six stations, despite the relatively narrow range in month of year, steadily increased from 17.9 °C in early April 2000, to 19.3 °C in late April/early May 2001, to 26.9 °C in mid-June 2002 (graphic not included). There was also a consistent increase in salinity and decrease in DO with increasing temperature over the three different sampling periods (salinity: 34.0, 35.9, and 37.3 ppt in 2000, 2001, and 2002, respectively; DO: 8.0, 7.2 and 6.0 mg L^{-1} in 2000, 2001, and 2002, respectively). While seasonality may be a factor, it is also possible that these year-to-year differences in population densities are the result of within-station patchiness and the inability to control for such micro-scale spatial variability due to the remote sampling nature of bottom grabs and limited sample replication (i.e., three grabs per each station-year combination). Regardless of source, these results demonstrate the importance of long-term repeated observations in helping to understand the structure and dynamics of these assemblages.

Acknowledgements

This work was sponsored by the Gray's Reef National Marine Sanctuary (GRNMS) Office and the Center for Coastal Environmental Health and Biomolecular Research (CCEHBR), of the National Centers for Coastal Ocean Science (NCCOS), National Oceanic and Atmospheric Administration (NOAA). Special recognition is given to Barry Vittor and Associates (Mobile, AL) for assistance with the analysis of macroinfaunal samples and to members of the CCEHBR Chemical Contaminants Research Group for contaminant analyses. We also thank various members of the scientific sampling teams from GRNMS and NCCOS, as well as the ship crew from the NOAA Ship FERREL, for their invaluable field support. **[SS]**

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