Benthic enrichment in the Georgia Bight related to Gulf Stream intrusions and estuarine outwelling

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ABSTRACT

The distribution patterns of benthic biomass (microbiota, meiofauna, and macrofauna) over the expansive continental shelf of the Georgia Bight suggest nutrient inputs from intrusions of deep Gulf Stream waters at the shelf break. Estimates of microbiota were lower (4.8 μg adenylates/cm^3) in the mid shelf than in the inner (12.4 μg/cm^3) and outer shelf (6.1 μg/cm^3). The microbiota biomass increased southward along the shelf break towards an area of frequent intrusions off Florida. Meiofaunal biomass was highest (1267 μg dry wt/10 cm^2) in the mid shelf region off Georgia which receives infrequent intrusion waters. Macrofauna biomass, however, was highest (13.2 g AFDW/m^2) off Florida. Both nematode and copepod biomasses were inversely related with macrofaunal biomass over the entire shelf. Only nematode biomass correlated significantly with microbiota biomass. Sediment characteristics and organic matter and chlorophyll *a* contents were also measured.

The activity of the benthic fauna over the shelf also suggests nutrient inputs at the shelf break. Benthic surface respiration was generally higher along the inner shelf ($\sim$ 31 ml O_2 $m^{-2} \cdot h^{-1}$) and the rates decreased with distance offshore. However, off Florida some of the highest rates (41 to 47 ml $O_2 \cdot m^{-2} \cdot h^{-1}$) were found at the mid shelf and shelf break. Glucose flux was highest (1429 $\mu g \cdot cm^{-3} \cdot h^{-1}$) in the sediments off Florida. The rates increased southward along the inner shelf, mid shelf and shelf break stations. Glucose concentrations were also highest (1540 μg/cm^3) off Florida and lowest (120 μg/cm^3) in the mid shelf off Georgia. Carbon oxidations were highest along the inner shelf ($\sim$ 28 μmoles $CO_2 \cdot cm^{-2} \cdot h^{-1}$), and decreased offshore and southward along the shelf break. The average carbon oxidation in the sediments over the entire shelf was estimated at 101 g $C \cdot m^{-2} \cdot d^{-1}$. Based on the carbon oxidation to surface O_2 consumption, the lowest metabolic quotients or expenditure were found offshore (0.63) and southward (1.2) along the mid shelf and shelf break stations. Denitrification potential was generally constant along the inner shelf ($\sim$ 12 μmoles $N_2O \cdot cm^{-2} \cdot h^{-1}$). The highest rate (45 μmoles $\cdot cm^{-2} \cdot h^{-1}$) was measured at the shelf break off Savannah, Georgia, and the rates decreased southward along the shelf break. The mean denitrification potential was estimated at 2.1 mg $N \cdot m^{-2} \cdot d^{-1}$ for the entire shelf. Nitrogen fixation activity was highly variable (20 to

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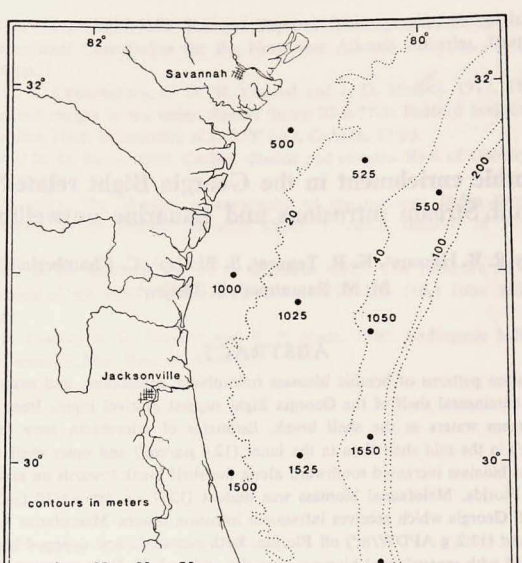

Figure 1. Location of benthic stations in the Georgia Bight.

150 pmoles $C_2H_4 \cdot cm^{-2} \cdot h^{-1}$) along the inner shelf. The rates at the shelf break were generally higher than those at mid shelf. Nitrogen fixation was estimated at about 283 $\mu g\ N \cdot m^{-2} \cdot d^{-1}$ over the entire shelf.

These results suggest that the shelf break benthos is enriched by intrusions of nutrient-rich, deep Gulf Stream waters off Florida. However, the mid shelf benthos is in general impoverished because of sporadic and patchy nutrient inputs from intrusions and meager nutrient enrichments from estuarine outwelling beyond the inner shelf.

1. Introduction

The Georgia Bight extends from Cape Hatteras, North Carolina, to Cape Canaveral, Florida (Fig. 1). The shelf sediments are approximately 96% sand and are moderately to well sorted. The daily climatological conditions are similar over most of the shelf.

River discharge (Atkinson *et al.*, 1978a), tidal outwelling from salt marshes (Odum, 1968), and intrusions of deep Gulf Stream water (Lee *et al.*, 1980) are the major sources of nutrients to the Bight. Because of the breadth of the shelf off Georgia and the barrier created by nearshore salinity fronts (Blanton and Atkinson, 1978), estuaries and rivers do not significantly contribute particulate organic matter and possibly inorganic nutrients to the shelf outside the nearshore zone (20 km offshore) (Haines and Dunstan, 1975).

Intrusions occur along the shelf break at frequencies of 5 to 14 days and are more common in summer than winter (Dunstan and Atkinson, 1976; Atkinson *et al.*, 1978b; Lee *et al.*, 1981). At the shelf break, intrusions of Gulf Stream water contributed 66,000 tons N (Lee *et al.*, 1981). This value is substantially higher than estimates of 12,000 and 7,500 tons N for continental runoff and atmospheric fallout in the Georgia Bight (Haines, 1975).

Enrichment due to this sporadic nutrient input should affect the benthic standing biomass and activity of the microbiota, meiofauna and macrofauna. In an earlier study of the shelf benthos off Georgia in the early spring (Tenore *et al.*, 1978) we found that the benthos along the shelf break was denser than the benthos of the mid and inner shelf. This present paper gives a descriptive account of the conditions over a wider range of the Georgia Bight during a summer cruise on the R/V *Columbus Iselin.*

2. Materials and methods

Twelve stations in the Georgia Bight were sampled in June 1977 (Fig. 1). The stations were spaced along four transects off the Savannah River, St. Catherines Island, St. Augustine, and Daytona Beach and provided samples from inner (20 to 30 km), middle (30 to 70 km), and outer (70 to 100 km) shelf regions. Bottom sediments were collected with a weighted stainless steel box corer (10 × 20 cm box) usually to a depth of 20 to 25 cm. The box core collected samples with a minimum of surface disturbance but certainly the sediment-water interface was disturbed. On retrieval, the overlying water was retained over the sediment. However, on standing the water did drain slowly between the sediment core and the box, with some percolation through the sediment. Samples for activity measurements and meiofauna were taken before this percolation occurred.

a. Sediment granulometry (Chamberlain and Tenore). The grain size distribution of approximately 50 g of the upper 2.5 cm of each core was determined by a wet sieve analysis at 1/4 ϕ intervals ($\phi = -\log_2$ [diameter, mm]) (Folk, 1974). The graphic mean, $M_z = \phi 16 + \phi 50 + \phi 84/3$, and the inclusive graphic standard deviation, $\sigma_I = (\phi 84 - \phi 16)/4 + (\phi 95 - \phi 5)/6.6$ were calculated for description of sediment samples (fine, medium or coarse).

A subcore (dia. 2.5 cm) of the top 1 cm was frozen onboard ship for sediment carbon-nitrogen analysis in the laboratory. Sediment samples were treated with cold phosphoric acid to remove carbonate and dried at 90°C for 24 hours. Organic carbon and nitrogen concentrations from triplicate samples were determined with a Model 240 Perkin-Elmer Elemental Analyzer. Values were calculated on the basis of pre-digested sample weight.

b. Benthic algal biomass (Bishop). The top 1 cm from replicate box cores was sampled by 2.5 cm diameter corer and kept frozen until analyzed in the laboratory. Sediment samples were freeze-dried, and chlorophyll *a* was extracted by shaking in hot methanol (80°C) (McIntire and Dunstan, 1975), and measured spectrophotometrically (Tett *et al.*, 1975).

c. Benthic metabolism (Pamatmat). Benthic surface respiration (change in O_2 concentration in the water circulating over relatively undisturbed sediment) was used to measure benthic metabolism (for complete details see Pamatmat, 1971a and b and 1975).

Sediment cores were taken with the box corer fitted with a collar designed to hold a fiberglass-epoxy cylindrical tube 33 cm long and 8.5 cm in diameter. Each core was sealed with a plexiglas piston fitted with an oxygen electrode and stirrer. The cores were transferred to a water bath at 19°C and incubated in the dark for 10 hours. Rates of oxygen uptake were calculated from the decrease in dissolved oxygen with time. After measuring total oxygen uptake, the cores were treated with enough buffered formaldehyde to make a 2% solution and their residual rate of oxygen uptake was determined as a measure of inorganic chemical oxidation.

d. Microbial activity and biomass (Hanson). Relative microbial activity was assessed by changes in O_2, CO_2, N_2O (denitrification potential) and C_2H_4 (nitrogen fixation activity) concentrations in the gas phase above sediment subsamples. Labelled glucose uptake and natural glucose concentration measurements provide an estimate of glucose flux in the sediment (Hanson, 1980). In general, bacteria are the main component of the microbiota that have the ability to assimilate (active uptake) glucose at natural glucose concentrations. To assess the relative carbon oxidation to aerobic respiration in shelf sediments, the change in CO_2 production to O_2 consumption was calculated. In addition, nitrogen fixation and denitrification activities were determined because these processes may be influenced by the amount of inorganic nitrogen and organic carbon inputs to the shelf system.

Glucose uptake was measured in sediment subcores (2.6 cm diameter) down to a depth of 10 cm. A total of 9 cores were taken from 3 replicate box cores. The sediment from each subcore was extruded from the core tube into a second and third tube so that the surface, 5 cm and 10 cm depths were exposed to the air. Labelled glucose (100 μl of D-(U-^{3}H)-glucose, 128 ng glucose/ml, 0.25 μCi) was

placed on the exposed layer and the cores incubated for exactly 15 minutes at 23°C. The sediment appeared oxic down to 10 to 15 cm at most stations, although there were pockets of FeS deposits throughout the sediment column. Although the lower sediment layers were exposed to air, it is unlikely that air had any great affect on glucose uptake in these "aerobic sediments". The reactions were terminated by removing the upper 2 mm of sediment into 10 ml of seawater plus formaldehyde (4%)-sulfuric acid (2N). For zero time controls, the exposed sediment layers (1 subcore) were flooded with 0.5 ml of 35% formaldehyde before the labelled substrate was added. A slurry of each 2 mm layer was mixed, centrifuged at 2000 × g for 5 minutes and the supernatant decanted. This wash procedure was repeated to remove ^{3}H-glucose. The sediment was dried (80°C), ground to a powder using a mortar and pestal, and dried to constant weight. Weighed samples (10 to 20 mg) were combusted on a Packard Oxidizer and counted by liquid scintillation. Values were corrected for quench and background.

Glucose flux was expressed as ng glucose • h^{-1} • cm^{-3} from the equation: Flux $= (c/C\mu t)\ (Sn + A)$, where c is the dpm in the sample (1 cm^3); C, the dpm per μCi; μ, the fraction of a μCi added; t, the incubation time (hours); Sn, the natural substrate concentration; and A, the substrate concentration added to the exposed sediment layers.

Natural glucose concentrations in the sediment were estimated by the method of Hicks and Carey (1968). Sediment from each zone in the core was placed in filtered seawater (0°C), mixed, allowed to settle, and the supernatant filtered through combusted Gelman glass fiber filters using Swinnex adaptors. The filtrate was stored at −20°C. Glucose in the filtered surface seawater was also measured and subtracted from the total concentration. The corrected value was converted to ng/cm^3 of sediment.

Relative microbial activity was measured in duplicate subcores of 10 cm depth, which were removed from three box cores. The 5 to 10 cm layers were placed in 250 ml serum bottles along with 10 ml of degassed seawater, stoppered and shaken intermittently while being flushed with helium for five minutes. Next, the 0 to 5 cm layer was placed in bottles with 10 ml of oxic seawater. Silicone grease was used to prevent gas exchange through the punctured stoppers. N_2O (0.2 ml) was added to the helium flushed bottles and acetylene (25 ml) added to all bottles. Acetylene does not influence carbon oxidation or oxygen uptake but blocks the terminal step in denitrification (N_2O to N_2) and is a gratuitous substrate (inhibitor of nitrogen fixation) for the enzyme nitrogenase. Consequently, potential N_2O production and nitrogen fixation activity were measured on the same sediments (Balderson *et al.*, 1976; Yoshinari *et al.*, 1977), along with measurements of carbon oxidation and aerobic respiration. Several gas samples (2.5 ml) were removed from each bottle over 120 hours and compressed in 2 ml Vacutainers. The gas was analyzed for CO_2,

C_2H_4, O_2, N_2O, and N_2 using a Carle Gas Chromatograph. Pure gases from Matheson Gas Company were used as standards. Linear regression was used to relate changes in each gas concentration with time. The rates were converted to moles of gas transformed • h^{-1} • cm^{-2} for O_2, N_2O, CO_2, and C_2H_4. Carbon oxidation to O_2 uptake or metabolic quotient was computed for the 0-5 cm sediment layer. The quotient provides a relative estimate of the metabolic expenditure of the benthos in the shelf sediments.

Microbial biomass was measured by adenylate extraction, which includes bacteria, fungi, algae, protozoans, and some meiofauna. Total adenylates (adenosine triphosphate, adenosine diphosphate, and adenosine monophosphate) were determined on 1 cm^3 of sediment by removing a 2 mm section from the surface, 5 cm, and 10 cm from triplicate cores, and extracting adenylates in 15 ml of boiling $NaHCO_3$ buffer (Bancroft *et al.*, 1976). The buffer was cooled to 0°C and then centrifuged for five minutes at 2000 × g. A 5 ml aliquot of the extract was transferred to a polyethylene vial and stored at −20°C. Adenylates were determined by bioluminescence (Karl *et al.*, 1978; Tenore *et al.*, 1978). The adenylate energy charge was calculated by the equation: E.C. = [ATP] + 1/2 [ADP]/[total adenylate], (Wiebe and Bancroft, 1975).

e. Meiofaunal density and biomass (Tietjen). Samples of meiofauna were obtained by inserting three plastic core tubes (1.5 cm diameter) to a depth of 5 cm into the three replicate box cores from each station. The samples were preserved in a 5% formalin buffered seawater containing Rose Bengal stain. In the laboratory the samples were washed through a set of two sieves with mesh openings of 0.500 mm and 0.044 mm. Animals that passed the larger sieve and were retained in the smaller were considered meiofauna.

Meiofauna biomass (wet weight) was determined and conversion factors used to estimate dry and ash-free dry weight. Dry weight conversions were obtained for representative individuals from each taxon that had been dried to constant weight at 90°C and weighed on a Mettler M5 Microbalance (± 1 μg).

f. Macrofaunal biomass (Tenore). At each station 15 box cores (at least 15 cm depth) were collected for macrofaunal biomass determinations. The samples were sieved through a 0.5 mm mesh on board and preserved in 5% buffered formalin containing Rose Bengal stain. In the laboratory, the stained macrofauna was picked from the remaining sediment (generally half the original core volume), gently patted with absorbent papers to remove excess water, and the total wet weight determined. The samples were then dried at 90°C for 24 hours and ashed at 475°C for 12 hours for ash-free weight (AFDW) determinations. The results represent data on preserved samples.

Table 1. Sediment data of samples collected in the Georgia Bight, June 1977.

Station	Water depth (m)	Distance offshore (km)	Graphic mean (Mz)	% Coarse ($> -1.0\phi$)	% Sand (-1.0 to 4.0ϕ)	% Silt and clay ($< 4.0\phi$)
500	14	26	0.243mm (2.04ϕ)	0.4	98.2	1.4
525	28	72	0.496mm (1.01ϕ)	1.4	97.8	0.8
550	45	111	0.409mm (1.29ϕ)	0.1	99.4	0.5
1000	13	17	0.314mm (1.67ϕ)	2.3	97.0	0.7
1025	25	60	0.590mm (0.76ϕ)	11.6	87.1	1.3
1050	44	113	0.483mm (1.05ϕ)	2.1	97.1	0.8
1500	18	11	0.325mm (1.62ϕ)	1.0	98.5	0.5
1525	31	48	0.382mm (1.39ϕ)	7.2	86.1	6.7
1550	39	85	0.314mm (1.67ϕ)	0.9	97.9	1.2
2000	14	17	0.149mm (2.75ϕ)	0.1	96.8	3.1
2025	28	41	0.191mm (2.39ϕ)	0.6	97.2	2.2
2050	68	74	0.165mm (2.60ϕ)	6.1	78.6	15.3

$\phi = -\text{Log}_2$ [Diameter, mm] Graphic Mean (M_z) $= \phi 16 + \phi 50 + \phi 84/3$

3. Results

a. Sediment granulometry and organic carbon and nitrogen content (Chamberlain and Tenore). The grain size of the sediment was predominantly medium sand ($M_z > 0.200$) except for the fine sand ($M_z < 0.200$) along the southernmost transect (Table 1). The sediments consisted mostly of quartzitic sand (-1.0 to 4.0ϕ) with lesser amounts of fecal pellets and shell fragments. The inclusive graphic standard deviation indicates that most of the sediments were moderately to well sorted (σ_I between 0.43ϕ and 0.83ϕ). The sediments at stations 1025, 1525 and 2050 were poorly sorted ($\sigma_I > 1.29\phi$).

Organic carbon and nitrogen values from sediment from the southernmost transect were several times higher than those from the rest of the region (Table 2). In general, organic carbon and nitrogen content increased (mean values in Table 2) offshore and southward in the shelf sediments. The inner shelf showed the highest latitudinal variation for organic nitrogen content.

b. Benthic algal biomass (Bishop). Benthic chloropyhll *a* was consistently lower at shelf break stations than at mid shelf or inshore stations (Table 3). Chlorophyll *a* values were lowest off Florida and the mean chlorophyll values increased northward. The inner and mid shelf sediments contained approximately twice as much chlorophyll *a* as the shelf break sediments. The percent degraded chlorophyll, on the other hand, was highest in the southernmost sediments in the Georgia Bight.

Table 2. Sediment organic carbon (%) and nitrogen (%) content on the continental shelf off Georgia and Florida in June, 1977.

	Organic carbon content			
Stations	Inshore	Mid shelf	Shelf break	Means
500-550	0.18	0.16	0.12	0.15
1000-1050	0.20	0.79	2.03	1.01
1500-1550	0.18	3.28	2.19	1.89
2000-2050	0.29	2.12	2.45	1.62
Means	0.21	1.59	1.70	
	Organic nitrogen content			
Stations	Inshore	Mid shelf	Shelf break	Means
500-550	.009	.004	.002	.005
1000-1050	.012	.012	.010	.011
1500-1550	.003	.031	.007	.014
2000-2050	.023	.018	.889	.310
Means	.012	.016	.227	

c. Benthic surface metabolism (Pamatmat). The rates of total oxygen uptake showed no statistically significant trends across the shelf or in a north-south direction (Table 4). In the two northernmost transects O_2 uptake decreased offshore, but in the two southernmost transects, the value at the inner and shelf break stations were higher than those at mid shelf. However, mean values indicate a tendency for rates to decrease across the shelf and to increase from north to south. The rates of chemical oxygen uptake averaged 25% of the total oxygen uptake.

d. Microbial biomass and activity (Hanson). Glucose flux at three depths in the sediment increased significantly ($P < 0.05$) across the shelf and in a north-south direction (Table 5). The flux decreased significantly ($P < 0.05$) with depth in the sediment but was unrelated ($P > 0.1$) to overlying depth of the water. A comparison

Table 3. Sediment chlorophyll *a* on the continental shelf off Georgia and Florida, June, 1977. Values in parentheses are percent phaeopigment.

	Sediment chlorophyll *a* ($\mu g \cdot g^{-1}$)			
Stations	Inshore	Mid shelf	Shelf break	Means
500-550	1.95 ± .63 (64)	2.01 ± .26 (53)	1.09 ± .53 (56)	1.7
1000-1050	2.76 ± .04 (66)	1.84 ± .37 (58)	0.73 ± .09 (64)	1.8
1500-1550	1.28 ± .46 (67)	1.45 ± .55 (72)	1.03 ± .50 (65)	1.3
2000-2050	0.47 ± .01 (74)	1.13 ± .36 (76)	0.55 ± .18 (69)	.72
Means	1.6	1.6	.85	

Table 4. Rates of total oxygen uptake and inorganic chemical oxidation (ml • m^{-2} • hr^{-1}) at 19°C in the Georgia Bight, June 1977.

	Inshore		Mid shelf		Shelf break		Mean and S.D.	
Stations	Total	Chemical	Total	Chemical	Total	Chemical	Total	Chemical
500-550	30	5	26	8	18	8	25	7
	36	6	28	10	15	6	± 8	± 2
1000-1050	34	2	26	11	11	3	21	5
	28	5	17	7	9	2	± 10	± 4
1500-1550	27	9	25	5	30	6	29	6
	24	7	23	2	47	5	± 9	± 2
2000-2050	31	6	20	5	25	5	31	7
	35		41	14	34	7	± 8	± 4
Means ± S.D.	31 ± 4	6 ± 2	26 ± 7	8 ± 4	23 ± 12	5 ± 2		

Overall Mean, Total Oxygen Uptake = 26 ± 9 (S.D.) ml O_2 • m^{-2} • hr^{-1}
Overall Mean. Inorganic Chemical Oxidation = 6 ± 3 (S.D.) ml O_2 • m^{-2} • hr^{-1}

Table 5. Glucose flux (^{14}C-glucose uptake) in southeastern continental shelf sediments at three depths. Values are ± 1 S.D.

			($ng \cdot cm^{-3} \cdot h^{-1}$)		
Depth	Stations	Inshore	Mid shelf	Shelf break	Means
	500-550	120 ± 51	170 ± 77	351 ± 139	217
Surface	1000-1050	160 ± 39	107 ± 6	145 ± 58	137
	1500-1550	168 ± 43	226 ± 73	291 ± 98	288
	2000-2050	446 ± 273	1429 ± 290	617 ± 315	829
	Means	234	484	351	
	500-550	210 ± 47	185 ± 23	290 ± 158	228
5 cm	1000-1050	136 ± 23	93 ± 7	192 ± 31	140
	1500-1550	227 ± 41	178 ± 58	336 ± 21	263
	2000-2050	255 ± 110	581 ± 231	374 ± 123	403
	Means	220	259	298	
	500-550	109 ± 45	70 ± 41	139 ± 98	106
10 cm	1000-1050	38 ± 12	19 ± 15	178 ± 17	78
	1500-1550	156 ± 23	96 ± 48	325 ± 152	192
	2000-2050	72 ± 15	338 ± 129	102 ± 14	171
	Means	94	130	186	

of Table 5 and 6 shows that glucose flux calculations were greatly affected by the concentrations of glucose in the sediments. Glucose concentrations were highest at mid shelf stations and decreased significantly with depth in the sediment (Table 6). With the exception of the sediment at stations 500 to 550, concentrations in the sediments increased significantly in a north-south direction.

Carbon oxidation (CO_2 production) in the surface sediment decreased across the shelf but showed some variation among the inner and mid shelf stations (Table 7a). Carbon oxidation at the shelf break decreased significantly ($P < 0.05$) in a north-south direction. In the subsurface sediment, carbon oxidation for the entire shelf decreased in a north-south direction (mean values in Table 7a) but did not change across the shelf (Table 7a). In general, the oxidations in the mid shelf were greater than those at the inner and shelf break stations. CO_2 production decreased significantly ($P < 0.05$) with depth of overlying water, and subsurface CO_2 production was highly correlated ($P < 0.01$) with glucose flux (glucose concentrations). Total oxygen demand of the sediments increased across the shelf and was significantly ($P < 0.5$) higher in the southernmost stations (Table 7b). The mean metabolic quotient (CO_2 production/O_2 demand) decreased across the shelf and decreased significantly ($P < 0.05$) in a north-south direction (Table 7a).

Nitrogen fixation (C_2H_4) and denitrification (N_2O) activities showed similar rela-

Table 6. Apparent glucose concentration (± 1 S.D.) in shelf sediment in the Georgia Bight.

Depth	Stations	Inshore	Mid shelf	Shelf break	Means
			(ng • cm^{-3})		
Surface	500-550	285 ± 184	245 ± 116	872 ± 369	467
	1000-1050	320 ± 50	120 ± 50	159 ± 76	199
	1500-1550	392 ± 87	298 ± 19	228 ± 63	306
	2000-2050	540 ± 258	1540 ± 295	334 ± 253	804
	Means	384	551	398	
5 cm	500-550	206 ± 74	210 ± 84	794 ± 380	403
	1000-1050	105 ± 19	24 ± 17	59 ± 11	63
	1500-1550	130 ± 34	220 ± 46	210 ± 40	187
	2000-2050	336 ± 308	833 ± 556	213 ± 107	461
	Means	194	322	319	
10 cm	500-550	118 ± 30	148 ± 58	617 ± 276	294
	1000-1050	100 ± 31	34 ± 13	163 ± 25	99
	1500-1550	108 ± 38	259 ± 173	234 ± 97	200
	2000-2050	148 ± 167	645 ± 499	170 ± 204	322
	Means	199	272	296	

Table 7. Carbon dioxide production, oxygen demand, ethylene production and nitrous oxide production in shelf sediments off Georgia and Florida. Values are ± 1 S.E.

Stations	Inshore	Mid shelf	Shelf break	Means
a. *Carbon dioxide* (nmoles • cm^{-2} • h^{-1})				
		Surface sediment		
500-550	24.5 ± 7.1 (8.8)*	15.3 ± 2.8 (25.5)	11.5 ± 2.9 (.81)	17.1 (11.7)
1000-1050	20.9 ± 8.0 (11.6)	9.9 ± 1.7 (6.6)	9.6 ± 3.8 (.94)	13.5 (6.4)
1500-1550	31.2 ± 8.2 (14.9)	16.2 ± 5.5 (2.4)	8.3 ± 3.6 (.39)	18.6 (5.8)
2000-2050	37.0 ± 6.9 (2.3)	13.7 ± 0.9 (1.0)	4.4 ± 1.3 (.37)	18.4 (1.2)
Means	28.4 (9.4)	13.9 (9.9)	8.5 (.63)	
Overall mean, 16.9 nmoles • cm^{-2} • h^{-1}				
		Subsurface		
500-550	9.2 ± 4.5	20.3 ± 15.6	0.7 ± 0	10.1
1000-1050	6.6 ± 1.6	11.6 ± 5.4	10.5 ± 4.3	9.6
1500-1550	7.8 ± 0.6	5.6 ± 0.4	10.7 ± 6.8	8.0
2000-2050	6.2 ± 1.8	6.7 ± 1.1	4.8 ± 2.0	5.9
Means	7.6	11.0	3.3	
Overall mean, 8.4 nmoles • cm^{-2} • h^{-1}				

Table 7. (continued)

Stations	Inshore	Mid shelf	Shelf break	Means
b. *Oxygen* (nmoles • cm^{-2} • h^{-1})				
500-550	2.8 ± 0.6	0.6 ± 0	14.2 ± 10.8	5.9
1000-1050	1.8 ± 0.9	1.5 ± 0.4	10.2 ± 2.8	4.5
1500-1550	2.1 ± 0.9	6.8 ± 3.6	3.2 ± 0.8	4.0
2000-2050	16.2 ± 3.5	13.9 ± 12.7	11.8 ± 6.9	14.0
Means	4.7	5.8	9.9	
Overall mean, 6.73 nmoles • cm^{-2} • h^{-1} (1.51 ml O_2 • m^{-2} • h^{-1})				
c. *Nitrous Oxide* (nmoles • cm^{-2} • h^{-1})				
500-550	13.5 ± 10.8	14.1 ± 7.7	45.9 ± 30.5	24.5
1000-1050	14.0 ± 9.3	22.6 ± 15.4	10.5 ± 3.5	15.7
1500-1550	19.5 ± 8.3	6.1 ± 4.4	7.0 ± 3.7	10.9
2000-2050	2.2 ± 1.3	1.7 ± 0.8	4.9 ± 2.2	2.9
Means	12.3	11.2	16.9	
d. *Ethylene* (pmoles • cm^{-2} • h^{-1})				
		Surface		
500-550	144.0 ± 100	15.1 ± 5.1	5.7 ± 0.6	54.9
1000-1050	22.6 ± 16.3	1.8 ± 0.8	10.3 ± 5.0	11.6
1500-1550	30.1 ± 16.2	11.5 ± 3.6	7.2 ± 3.1	16.3
2000-2050	107.7 ± 19.3	14.2 ± 3.8	59.6 ± 7.6	60.3
Means	76.3	10.7	22.1	
Overall mean, 36.3 pmoles • cm^{-2} • h^{-1}				
		Subsurface		
500-550	60.3 ± 21.0	170.5 ± 49.4	177.8 ± 135	136.
1000-1050	81.4 ± 33.5	72.4 ± 36.7	83.9 ± 26.7	79.2
1500-1550	50.1 ± 16.3	25.4 ± 4.7	38.7 ± 2.4	38.1
2000-2050	154.4 ± 60.1	45.5 ± 40.4	125.3 ± 23.1	108.
Means	86.6	78.3	105	
Overall mean, 90.3 pmoles • cm^{-2} • h^{-1}				

* Metabolic quotient

tionships in the 5-10 cm sediment layer of the Georgia Bight. Ethylene production in the surface sediments either decreased across the shelf (transects 500-550 and 1500-1550) or nitrogen fixation was lowest in the mid shelf compared to the inner and outer shelf areas (Table 7d). The mean values in a north-south direction

Table 8. Total adenylates (± 1 S.E.) at three sediment depths on the continental shelf off Georgia and Florida.

Depth	Stations	Inshore ($\mu g \cdot cm^{-3}$)	Mid shelf	Shelf break	Means
Surface	500-550	11.3 ± 7.4	1.3 ± 0.4	2.2 ± 1.0	4.9
	1000-1050	8.7 ± 2.2	5.8 ± 1.1	7.3 ± 2.0	7.3
	1500-1550	16.2 ± 5.3	6.8 ± 3.3	10.7 ± 5.9	11.2
	2000-2050	13.7 ± 0.7	5.1 ± 1.9	4.2 ± 1.4	7.7
	Means	12.4	4.8	6.1	
	Overall Mean, 7.8 $\mu g \cdot cm^{-3}$				
5 cm	500-550	1.1 ± 0.2	1.1 ± 0.3	0.88 ± 0.4	1.0
	1000-1050	1.8 ± 0.4	1.1 ± 0.2	1.2 ± 0.6	1.4
	1500-1550	4.7 ± 1.1	8.2 ± 6.4	1.7 ± 0.2	4.9
	2000-2050	2.9 ± 0.05	2.5 ± 1.2	1.6 ± 0.1	2.3
	Means	2.6	3.2	1.4	
	Overall Mean, 2.4 $\mu g \cdot cm^{-3}$				
10 cm	500-550	0.66 ± 0.04	0.88 ± 0.19	0.31 ± 0.09	0.62
	1000-1050	0.96 ± 0.22	0.58 ± 0.16	0.71 ± 0.25	0.75
	1500-1550	1.22 ± 0.09	0.97 ± 0.49	0.87 ± 0.12	1.02
	2000-2050	1.47 ± 0.40	1.14 ± 0.25	2.45 ± 0.53	1.65
	Means	1.15	.89	1.09	
	Overall Mean, 1.0 $\mu g \cdot cm^{-3}$				

Overall Mean integrated for top 10 cm, 65.9 mg • m^{-2}

showed the same general relationship over the shelf as did the glucose flux (glucose concentrations). The fixation in the subsurface sediment shows the same relations as the fixation in the surface sediment but were several times higher. The overall ethylene production in the subsurface sediments was highly correlated ($P < 0.01$) with surface total adenylates.

Potential nitrous oxide production decreased significantly in a north-south direction at the shelf break (Table 7c). With the exception of Station 2050, ethylene production and nitrous oxide production in the subsurface sediments show the same trend along the shelf break. Nitrous oxide production was significantly ($P < 0.05$) correlated with ethylene production in the subsurface sediment of the Georgia Bight.

In general, microbial biomass (total adenylates) was lowest in the mid shelf and increased in a north-south direction, except along the inshore stations (Table 8). Biomass decreased proportionately with depth in the sediment (Table 8), as did

Table 9. Mean meiofauna densities (No. • 10 cm^{-2}) for various taxa on the continental shelf off Georgia and Florida for June 1977.

	Station											
Taxon	500	525	550	1000	1025	1050	1500	1525	1550	2000	2025	2050
Nematoda	377	332	478	468	153	104	494	258	553	389	92	123
Foraminifera	9	44	128	5	2	3	17	38	42			
Harpacticoida	58	754	342	39	54	76	313	85	260	38	75	3
Ostracoda	1	5	5	1			3	2	6			
Polychaeta	9	26	37	55	15	12	29	12	24	11	7	4
Nauplii	20	130	167	5	7	10	49	16	33	5	1	
Hydrozoa		1	1		1			1				
Bivalvia	1	1	3	5	1		12	4	4			
Archiannelida				1		1				1	1	1
Gastrotricha	15	70	49	8	5	27	2	3	1			
Kinorhyncha	1	8	10		1	1	1			1		1
Isopoda					1	1						
Tardigrada	3	17	5				7	2	2			
Halacarida		1		1								
TOTAL	494	1389	1225	588	241	213	1057	520	927	446	176	132

Table 10. Mean meiofauna biomass (μg dry weight • 10 cm^{-2}) for various taxa on the continental shelf off Georgia and Florida for June 1977.

	Station											
Taxon	500	525	550	1000	1025	1050	1500	1525	1550	2000	2025	2050
Nematoda	113.1	99.6	148.6	143.4	45.9	31.2	148.2	77.4	165.9	116.7	27.6	26.9
Copepoda	75.4	980.2	444.6	50.7	70.2	98.8	406.9	110.5	338.0	49.4	97.5	3.9
Polychaeta	46.5	134.4	191.2	284.4	77.6	62.0	149.9	62.0	124.0	56.9	36.2	20.7
Other*	4.5	53.0	70.3	2.7	1.8	3.3	26.3	15.7	38.1	1.4	0.3	0.4
TOTAL	239.5	1267.2	854.7	481.2	195.5	195.4	731.3	265.5	666.0	224.4	161.6	61.9

Overall mean, 444.9 μg dry weight • 10 cm^{-2}

* Includes Foraminifera, Hydrozoa, Gastrotricha, Kinorhyncha, Archiannelida, Tardigrada, Halicarida, Ostracoda, Isopoda, Nauplii and Pelecypoda

glucose flux (glucose concentrations). Adenylate energy charge ratio showed no significant relation across the shelf or in a north-south direction. The ratio was relatively constant with depth in the sediment, e.g., the surface ratio was 0.650; 5 cm, 0.618; 10 cm, 0.622 with a Coefficient of Variation (C.V.) of about 20%.

e. Meiofauna densities and biomass (Tietjen). The dominant taxonomic groups present along the four transects were: nematodes (61%), copepods (24%), polychaetes (4%), and foraminifera (3%) (Table 9). Mean nematode densities for the entire shelf were significantly lower at the mid shelf (209 individuals/10 cm^2) than at inshore (432) and shelf break stations (314). Conversely, mean copepod densities for the entire shelf were significantly higher at mid shelf stations (242 individuals/10 cm^2) than at inshore (112) and shelf break (170).However, the densities along some transects (1000-1500) did not confirm this trend. General differences in the distribution of copepods, polychaetes, foraminifera, and total meiofauna were not observed across the Shelf. However, the mean densities of nematodes and copepods were higher along Stations 500 to 550 and 1500 to 1550 (396 and 384 individuals/10 cm^2, respectively). The differences in copepod densities were highly significant ($P < 0.01$).

While nematodes (average individual dry weight of ~ 0.3 μg) comprised 61% of the total number of meiofauna individuals, their dry weight accounted for only 23% of the total biomass along the four transects (Table 10). Copepods (average individual dry weight of 1.4 μg) comprised 50% of the biomass; and polychaetes, the largest animals present, comprised 22% of the biomass. All remaining taxa accounted for only 4% of meiofaunal biomass.

No relationships were seen between the distribution of nematodes, copepods, or total meiofaunal densities and mean grain size or sedimentary chlorophyll. Inverse relationships did exist, however, between meiofaunal densities and both organic carbon ($r = 0.52$, $P < 0.05$) and nitrogen ($r = 0.57$, $P < 0.05$). A significant ($P < 0.05$) relationship also was found between the distributions of microbial biomass and nematodes ($r = 0.79$) but not copepod biomass. Nematode and copepod biomass were both inversely correlated with macrofaunal biomass ($r = -0.52$ for both).

f. Macrofaunal biomass (Tenore). Macrofaunal biomass values, with the exception of that from Station 2025 (13 g AFDW/m^2), were generally low (< 9 g AFDW/m^2) but significantly higher than those collected previously in early spring (Tenore *et al.*, 1978). The biomass showed no significant spatial differences on the shelf (Table 11). Higher biomasses along Stations 2000 to 2050 did however, coincide with an area of continual nutrient enrichment due to Gulf Stream intrusions off Florida. Although biomass was highest in the fine sand sediments off Florida the infaunal biomass showed no correlation with sediment particle size.

Table 11. Macrofauna biomass on the continental shelf off Georgia and Florida, June 1977. Values are given as the mean ± 1 SD of 15 samples.

Stations	Inshore	Mid shelf	Shelf break	Means
		Wet weight ($g \cdot m^{-2}$)		
500-550	8.01 ± 3.09	28.79 ± 44.24	32.76 ± 65.85	23.2
1000-1050	79.64 ± 61.16	20.50 ± 11.17	33.14 ± 37.00	44.4
1500-1550	28.30 ± 16.35	69.89 ± 75.96	17.39 ± 12.04	38.5
2000-2050	44.36 ± 27.83	111.51 ± 109.32	67.14 ± 31.44	74.2
Means	40.1	57.1	37.6	
		Ash free dry weight ($g \cdot m^{-2}$)		
500-550	0.68 ± .34	2.17 ± 2.91	2.67 ± 5.36	1.84
1000-1050	8.48 ± 7.48	1.35 ± 0.59	2.13 ± 2.45	3.99
1500-1550	2.26 ± 1.38	5.24 ± 5.67	1.21 ± 0.88	2.90
2000-2050	3.73 ± 2.84	13.22 ± 18.93	4.53 ± 2.60	7.06
Means	3.16	5.49	2.64	

4. Discussion

Intrusions of Gulf Stream water onto the continental shelf of the Georgia Bight affects both the spatial and temporal patterns of nutrients on the outer shelf (Lee *et al.*, 1981). Intruded waters generally remain in the outer shelf area although occasionally they are found in the nearshore zone, i.e., within 20 km off Georgia (Blanton and Atkinson, unpublished data). The nutrients in these intruded waters are utilized by phytoplankton along the shelf break and the newly produced organic matter may be either mineralized in the water column (Haines and Dunstan, 1975) or deposited on the outer shelf (Hargrave, 1973; Rowe *et al.*, 1975; Thiel, 1978). However, the deposition of the particulate organic matter may not be evenly distributed over the outer shelf due to the magnitude of Gulf Stream eddies and to irregular movement of the outer shelf waters in the Georgia Bight (Atkinson, 1977; Atkinson *et al.*, 1978a).

Nearshore benthos may be enriched by estuarine outwelling from expansive *Spartina* marshes along the coast and river outflow from Georgia and the Carolinas (Odum, 1968; Goldberg, 1971). However, salinity fronts along the Georgia coast probably restrict a substantial exchange of materials and nutrients from the estuaries and rivers with outer shelf waters (Blanton and Atkinson, 1978; Yoder *et al.*, 1981). Coastal currents also may play a major role in the lateral dispersion of nutrients (Atkinson *et al.*, 1978a) and may confine the deposition of estuarine nutrients within the coastal zone. About 75% of the freshwater is retained inshore of the 20 m depth contour (Atkinson *et al.*, 1978a). These salinity fronts and coastal

currents may explain why estuarine detritus was not a significant fraction of the particulate organic carbon in the waters beyond 20 km offshore (Haines and Dunstan, 1975). Consequently, because of these physical regimes along the coast and outer shelf, and the breadth of the Georgia continental shelf (~ 100 km), nutrients from the coast and intrusions probably rarely reach the mid shelf benthos.

In general, most of our work on benthic faunal communities in the Georgia Bight (Tenore *et al.*, 1978 and herein) supports the literature that nutrients in the intrusion waters of the Gulf Stream are directly or indirectly important to the enrichment of the outer Georgia shelf ecosystem (Lee *et al.*, 1981), and nutrient inputs from the estuaries and rivers into the nearshore region are restricted from mixing with outer shelf waters (Atkinson *et al.*, 1978a; Yoder *et al.*, 1981). And, where the data do not conform with the literature, sporadic deposition of particulate organic matter, unfavorable bottom substrate for fauna colonization or both are proposed. However, the finer sediments off Florida possessed some of the highest measurements of benthic activity and biomass in the Georgia Bight.

a. Sediment granulometry and organic carbon and nitrogen. Our sediment analysis for the Georgia Bight agrees with previously published work (Milliman *et al.*, 1972; Gorsline, 1963; Emery, 1968). The patchiness of the sediment size distribution confirms earlier textural analysis for stations studied by Tenore *et al.* (1978). The variation in the graphic mean can usually be attributed to the amount of shell fragment or fecal mud present in the sample. Station 500 had a finer sediment composition probably due to input from the Savannah River (Kingery, 1973). The fine sediments in the southernmost transect may be due to higher deposition of particulate organic matter and fecal production by fauna in the water column as well as by the benthos. The organic carbon and nitrogen content in the northern area was higher than previously reported (Tenore *et al.*, 1978).

b. Benthic algal biomass. Algal biomass (chlorophyll *a*) showed a general increase in a south-north direction which may be related to the deposition of phytoplankton during the northern movement of nutrient-rich intrusion waters over the shelf (Atkinson, 1977). Chlorophyll *a* concentrations were similar to those reported earlier (Tenore *et al.*, 1978).

c. Benthic surface metabolism. The areal distribution of oxygen uptake rates on the shelf are generally consistent with the hypothesis that nutrient-rich intrusions enhance benthic community metabolism at the shelf break off Florida, an area of frequent intrusions. However, estuarine outwelling of nutrients and particulate matter does not appear important to benthic metabolism beyond 20 km offshore because the rates at the inshore stations off Georgia are similar to the rates off Florida. Oxygen uptake rates in Georgia Bight sediments are about 25 to 50% of those measured by Smith (1971) at a more inshore (7 km) station off Sapelo Island.

The average rate for the entire shelf is about the same as at a depth of 40 m off Cape Cod (30 ml $O_2 \cdot m^{-2} \cdot h^{-1}$) although the latter was measured in November at a lower temperature (13°C) (Smith, 1978). The range of values is well within those obtained by Thomas *et al.* (1977) from the New York Bight. There is a definite seasonal cycle of oxygen uptake on the northern shelf as a result of temperature changes (Smith, 1978; Thomas *et al.*, 1977). Seasonal cycles caused by temperature, however, are greatly reduced on the shallow southeastern continental shelf (Smith, 1971) and could be even further dampened farther offshore near the Gulf Stream. Seasonal cycles, however, are also affected by changes in primary production, sedimentation of organic matter to the bottom and intrusions of nutrient-rich waters (Pamatmat, 1971b).

d. Microbial activity and biomass. The biomass of the microbiota in the mid shelf region was lower than the inner and shelf break regions of the Georgia Bight. In general, microbiota biomass did not decrease with distance offshore except across the narrow shelf off Daytona Beach, Florida and the microbiota biomass along the inner shelf off Georgia were not much different from those off Florida. We suspect coastal currents and salinity fronts probably restrict the lateral diffusion of nutrients into the mid shelf zone, while nutrient rich intrusion waters rarely penetrate across the expansive shelf off Georgia. Adenylate concentrations were in the range of adenosine triphosphate concentrations of 1-10 μg/g of sediment reported for this and other continental shelves (Yingst, 1978; Pamatmat and Skjoldal, 1974; Ernst, 1970; Hodson *et al.*, 1976; Tenore *et al.*, 1978).

Total adenylates were converted to carbon for comparison with the literature by assuming adenosine triphosphate (ATP) is 0.4% of total organic carbon (Paerl and Williams, 1976). Based on the adenylate energy charge, ATP makes up nearly 60% of the total adenylates in these sediments. The overall mean concentration of 65.9 mg/m^2 (Table 8) was used to compute a microbial biomass of 9.9 g C/m^2 for the entire shelf. A biomass of 10.5 g C/m^2 was found earlier (Tenore *et al.*, 1978). The microbial biomass of 9-11 g C/m^2 off Georgia and Florida is low compared to the 15 to 50 g C/m^2 found in the sediments of an upwelling area off NW Africa (Christensen and Packard, 1977).

The ATP in these sediments include not only single cell microorganisms but also protozoa and some meiofauna. We estimated the meiofaunal biomass at 445 μg dry wt/10 cm^2 (Table 11). Assuming 35% of the meiofauna dry weight is carbon, meiofauna contributed less than 2% of the microbial biomass. It appears that the meiofauna represent a much smaller fraction of the microbiota in the Georgia Bight than other systems (Sikora *et al.*, 1977; Yingst, 1978).

Adenylate energy charge ratio is an approximate measure of the physiological condition or growth state of the microbiota in the ecosystem (Wiebe and Bancroft, 1975; Karl *et al.*, 1978; Hanson, 1980). This measurement indicates that the growth

state of the microbiota was constant over the entire shelf and with sediment depth. Because of the within station variability (~ 20% C.V.), significant differences between stations could not be detected. However, the microbiota in the sediments of the Georgia Bight possess an energy charge ratio of 0.6 to 0.7, which is not different from values reported for marsh soils and other sediment systems (Wiebe and Bancroft, 1975; Karl *et al.*, 1978; Pamatmat and Skjoldal, 1979; Hanson, 1980). In a bacterial culture, an adenylate energy charge ratio of 0.8 represents an exponential growth state whereas the ratio < 0.6 represents a stationary growth state (Wiebe and Bancroft, 1975; Hanson, 1980; Karl *et al.*, 1978).

In situ rates are difficult to obtain, as retrieval and alteration of benthic samples could greatly change actual metabolic rates (Davies, 1975). The rates reported here while relative, provide interesting insights into spatial patterns of several metabolic processes of the benthos in the Georgia Bight. There is little information on carbon oxidation rates in continental shelf and deep oceanic sediments. The rate of carbon oxidation of 101 $gC \cdot m^{-2} \cdot d^{-1}$ in these sediments is approximately 65% of the rate estimated off NW Africa (Christensen and Packard, 1977). At this rate, the benthos would consume 29% of the phytoplankton produced daily in the Georgia Bight (Haines and Dunstan, 1975).

The metabolic quotients (CO_2O_2), at each station indicate that the microbiota were probably more efficient utilizers of organic matter offshore and southward along mid shelf and shelf break stations in the Georgia Bight. The lower quotients off Florida suggest higher benthic production in the area. This region off Florida is noted for its shellfish beds. However, full evaluation of the metabolic quotients over the entire Georgia Bight require information on the deposition rates of particulate organic matter.

Nitrogen fixation and denitrification activities are influenced by nitrogen and energy sources in the system (Hanson, 1977). Nitrogen fixation in the surface sediments coincided with the region of frequent upwelling. Although intrusion waters are high in nitrogen, only extremely high concentrations of inorganic nitrogen (> 200 μg-at N/l) suppress bacterial nitrogen fixation (Hanson, 1977; Teal *et al.*, 1979). The low fixation rates in the Georgia Bight suggest that the process is limited by the availability of energy. However, the mean fixation activity in the sediments off Georgia was more than 100 times greater than rates found for deep sea sediments from the northeastern Atlantic Ocean (Hartwig and Stanley, 1978). Cognizant of the problems in extrapolation of ethylene production data, a rough estimate of the amount of nitrogen fixed in the shelf sediments was made. Based on the theoretical ratio of 3:1, which is the number of electrons required to fix a mole of N_2 relative to the number needed to reduce C_2H_2 (Hardy *et al.*, 1973), nitrogen fixation could supply approximately 283 $\mu g\ N \cdot m^{-2} \cdot d^{-1}$. A similar value (330 $\mu g\ N \cdot m^{-2} \cdot d^{-1}$) was reported earlier (Tenore *et al.*, 1978). The mean rate for

denitrification at 5 to 10 cm depth, based on nitrous oxide production, was 2.1 mg $N \cdot m^{-2} \cdot d^{-1}$. This rate is an order of magnitude lower than reported by Vanderborght *et al.* (1977) for muddy sediment along the Belgian coast (30 mg $N \cdot m^{-2} \cdot d^{-1}$) or by Valiela and Teal (1979) in Atlantic salt marshes (24 to 120 mg $N \cdot m^{-2} \cdot d^{-1}$).

e. Meiofaunal density and biomass. Physical conditions greatly influence composition and density in benthic systems (Wieser, 1960; McIntyre, 1969; Tietjen, 1969, 1971, 1977; Coull, 1970). Sediment grain size *per se* seems to exert a strong influence on total meiofaunal densities only when large sediment size class differences appear (e.g., muds vs. sands, sands vs. gravels, etc.). Although the sediments are all moderately to well-sorted sand in the Georgia Bight, they may have exerted some direct influence on meiofauna densities (apparently more on nematodes than copepods).

The inverse correlation between organic carbon and nitrogen values and meiofaunal densities was somewhat unexpected. This relation has not been found elsewhere (Tietjen, 1969, 1971, 1977, 1980; Coull, 1970; Cantelmo, 1978). Other abiotic and biotic factors may usually supersede the importance of sedimentary carbon and nitrogen, e.g., the nutritional value of the deposited particulate organic matter and the rate of its decomposition. In addition, bacteria are an important source of food for sublittoral marine meiofauna (Gerlach, 1978), but almost nothing is known about bacteria-meiofauna interactions under natural or semi-natural (experimental) field conditions (McIntyre *et al.*, 1970; Boucher and Chamroux, 1976; Tietjen, 1980). However, Yingst and Rhoads (1978) present data for Long Island Sound that suggest increases in meiofaunal densities are preceded by increases in microbial (ATP) biomass by one month.

A significant correlation between nematodes, but not copepods, and microbial biomass was observed in the present study. However, the response times of meiofauna to "blooms" of microbes are unknown. Studies of meiofauna life histories under experimental conditions suggest that the response time to a sustained increase in microbial productivity may be a few weeks under conditions prevailing on the Georgia shelf (Tietjen and Lee, 1972, 1977; Heip, 1972; Zurlini *et al.*, 1978).

The inverse relationship between macrofauna and nematode biomass observed on the Georgia shelf might reflect predation, competition, or other interactive effects. The same suggestion has been made by Elmgren (1978) to explain an inverse relationship between macro- and meiofaunal biomass observed in the Baltic Sea. The macrofauna:meiofauna biomass ratio ranged from 1.8:1 to 82.5:1 on the Georgia shelf. In Mediterranean muds and New England sands this ratio ranges from < 1:1 to 15:1, respectively (Guille and Soyer, 1974; Wigley and McIntyre, 1964). The significance of this ratio is unclear. McIntyre (1964) observed an inverse relation-

ship between macro- and meiofauna on the Fladen ground of the North Sea and ascribed high meiofauna production to a possible competitive advantage of meiofauna over macrofauna. On the other hand, macrofauna might prey on meiofauna. Meiofauna are found in the guts of macrobenthos (Smidt, 1951; Tietjen, 1969; Bell and Coull, 1978; Buzas, 1978) and these authors suggest that this indicates meiofauna as a food for macrobenthos.

Total meiofaunal biomass showed no obvious relation to outwelling along the coast of Georgia and upwelling at the shelf break. However, the biomass at the shelf break (except Station 2050) was greater than that at several mid shelf and inshore stations. Among the inshore stations, meiofaunal biomass increased from Georgia to Florida (except Station 2000), discounting the possible significance of outwelling and discharge from Georgia estuaries and rivers beyond 20 km offshore.

f. Macrofaunal biomass. Previously Tenore *et al.* (1978) reported that biomass values of inshore stations in the spring were significantly lower than mid shelf and outer stations. This was attributed to an unstable sedimentary regime and low nutrient input, especially of organic nitrogen. This distribution trend was not seen in the present summer study. The overall higher densities found in this present June study could be summer enrichment associated with seasonal changes. For example, all biomass values in June 1977 were significantly higher than those from the same stations occupied in March 1976. Elevated biomass could indicate seasonal fluctuations, larval recruitment to the benthos and/or a response to organic enrichment such as benthic microalgal production or sedimentation of pelagic production. But regardless of this possible seasonal fluctuation, the standing crop of macrobenthos of the mid shelf was patchy and suggested occasional areas of high benthic biomass in an area otherwise low in benthos compared to inner and outer shelf. Because intrusions can influence the mid shelf region in the summer (Atkinson, pers. comm.) the observed patchiness could reflect spatial and temporal patterns of enrichment to the benthos.

The macrofauna of the Georgia Bight is characterized by small species with short generation times that could respond more quickly to intermittent and patchy nutrient inputs. We often approach the study of benthos as communities that are stable at least in terms of species composition and dominance. In environments such as the Georgia Bight that receive intermittent inputs of nutrients, the benthic community structure is probably less stable and the population dynamics (recruitment, growth, survivorship) of individual species are much more prominent.

Biomass values reported are lower than those from other shelf environments and reflect the oligotrophic characteristics of this region. High values off the Florida reflect nutrient enrichment due to intrusions and subsequent sedimentation of particulate organic matter.

5. Conclusion

The spatial patterns of infaunal biomass and activity in the Georgia Bight suggest that intrusions of nutrient-rich Gulf Stream water at the shelf break are fairly constant and important to offshore benthic communities. However, nutrient enrichment by intrusions in the mid shelf is less common and more sporadic, and this would explain the generally low, but patchy standing stock of benthic fauna off Georgia. Estuaries, frequently considered major sources of nutrients to the outer continental shelf systems (Odum, 1968; Goldberg, 1971), may not supply sufficient nutrients to enhance the benthos beyond 20 km off Georgia. From the acreage of *Spartina* marshes and the number of major rivers in the southeast that flow through these marshes, one would expect a greater influence in benthic biomass and activity off Georgia than off Florida. Possible explanations for why this is not so include: (1) low nitrogen content of the detritus washed out of the estuary and (2) the presence of salinity fronts and alongshore currents that effectively restrict offshore transport of nutrients and particulate matter.

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REFERENCES

Atkinson, L. P. 1977. Modes of Gulf Stream intrusion into the South Atlantic Bight shelf waters. Geophys. Res. Lett., *4*, 583–586.

Atkinson, L. P., J. O. Blanton, and E. B. Haines. 1978a. Shelf flushing rates based on the distribution of salinity and freshwater in the Georgia Bight. Est. Coast. Mar. Sci., *7*, 465–472.

Atkinson, L. P., G. Paffenhofer, and W. M. Dunstan. 1978b. The chemical and biological effect of a Gulf Stream intrusion off St. Augustine, Florida. Bull. Mar. Sci., *28*, 667–679.

Balderson, W. L., B. Sherr, and W. J. Payne. 1976. Blockage by acetylene of nitrous oxide reduction in *Pseudomonas perfectomarinus*. Appl. Environ. Microbiol., *31*, 504–508.

Bancroft, K., E. A. Paul, and W. J. Wiebe. 1976. Extraction of adenosine triphosphate from marine sediments with boiling bicarbonate. Limnol. Oceanogr., *21*, 473–480.

Bell, S. S., and B. C. Coull. 1978. Field evidence that shrimp predation regulates meiofauna. Oecologia, *35*, 141–148.

Blanton, J. O. and L. P. Atkinson. 1978. Physical transfer processes between Georgia tidal inlets and nearshore waters, *in* Estuarine Interactions, M. L. Wiley, ed., Academic Press, New York, pp 515–532.

Boucher, G. and S. Chamroux. 1976. Bacteria and meiofauna in experimental sand ecosystem. I. Material and preliminary results. J. exp. mar. Biol. Ecol., *24*, 237–249.

Buzas, M. A. 1978. Foraminifera as prey from benthic deposit feeders: Results of predator exclusion experiments. J. Mar. Res., *36*, 617–625.

Cantelmo, F. R. 1978. The ecology of sublittoral meiofauna in a shallow marine embayment. Ph.D. Thesis, City University of New York, 137 pp.

Christensen, J. P. and T. T. Packard. 1977. Sediment metabolism from the northwest African upwelling system. Deep-Sea Res., *24*, 331–343.

Coull, B. C. 1970. Shallow water meiobenthos of the Bermuda Platform. Oecologia, *4*, 325–357.

Davies, J. M. 1975. Energy flow through the benthos in a Scottish sea loch. Mar. Biol., *31*, 353–362.

Dunstan, W. M. and L. P. Atkinson. 1976. Sources of new nitrogen for the South Atlantic Bight, *in* Estuarine Processes, Vol. 1, M. L. Wiley, ed., Academic Press, New York, pp 69–78.

Elmgren, R. 1978. Structure and dynamics of Baltic benthos communities, with particular reference to the relationship between macro- and meiofauna. Kieler Meeresforsch. Sonderheft., *4*, 1–22.

Emery, K. O. 1968. Relict sediments on continental shelves of world. Am. Assoc. Pet. Geol. Bull., *52*, 445–464.

Ernst, W. 1970. ATP als indikator fur die biomasse marine sedimente. Oecologia, *5*, 56–60.

Folk, R. L. 1974. Petrology of Sedimentary Rocks. Hemphill Publishing Co., Austin, Tx., 192 pp.

Gerlach, S. A. 1978. Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. Oecologia, *33*, 55–69.

Goldberg, E. D. 1971. River-ocean interactions, *in* Fertility of the Sea, Vol. 1, J. D. Costlow, ed., Gordon and Breach, New York, pp 143–156.

Gorsline, D. S. 1963. Bottom sediments of the Atlantic shelf and slope off the Southern United States. J. Geol., *71*, 422–440.

Guille, A. and J. Soyer. 1974. Bionomie benthique de plateau continental de la cote catalane francaise. 8. Macrofaune et meiofaune, rapports quantitatifs et biocenotiques. Vie Milieu, *24*, 301–320.

Haines, E. B. 1975. Nutrient inputs to the coastal zone: The Georgia and South Carolina shelf, *in* Estuarine Research, Vol. 1, M. L. Wiley, ed., Academic Press, New York, pp 303–324.

Haines, E. B. and W. M. Dunstan. 1975. The distribution and relation of particulate or organic materials and primary productivity in the Georgia Bight. Est. Coast. Mar. Sci., *3*, 431–441.

Hanson, R. B. 1977. Nitrogen fixation (acetylene reduction) in a salt marsh amended with sewage sludge and organic carbon and nitrogen compounds. Appl. Environ. Microbiol., *33*, 846–852.

—— 1980. Measuring microbial activity to assess detrital decay and utilization, *in* Marine Benthic Dynamics, K. R. Tenore and B. C. Coull (eds.), University of South Carolina Press, Columbia, South Carolina, pp 347–357.

Hardy, R. W. F., R. C. Burns, and R. D. Holsten. 1973. Application of acetylene-ethylene assay for measurement of nitrogen fixation. Soil. Biol. Biochem., *5*, 47–81.

Hargrave, B. T. 1973. Coupling carbon flow through some pelagic and benthic communities. J. Fish. Res. Board. Can., *30*, 1317–1326.

Hartwig, E. O. and S. O. Stanley. 1978. Nitrogen fixation in the Atlantic deep-sea and coastal sediments. Deep-Sea Res., *25*, 411–417.

Heip, C. 1972. The reproductive potential of copepods in brackish water. Mar. Biol., *12*, 219–221.

Hicks, S. E. and F. G. Carey. 1968. Glucose determinations in natural waters. Limnol. Oceanogr., *13*, 361–363.

Hodson, R. E., O. Holm-Hansen, and F. Azam. 1976. Improved methodology of ATP determination in marine environment. Mar. Biol., *34*, 143–149.

Karl, D. M., J. A. Haugnsers, L. Campbell and O. Holm-Hansen. 1978. Adenine nucleotide extraction from multicellular organisms and beach sand: ATP recovery, energy charge ratios, and determination of carbon/ATP ratios. J. exp. mar. Biol. Ecol., *48*, 185–197.

Kingery, F. A. 1973. Textural analysis of shelf sands off Georgia coast. Unpub. M.S. Thesis, California State Univ., San Diego, 75 pp.

Lee, T. N., L. P. Atkinson, and R. Legeckis. 1981. Detailed observations of a Gulf Stream spin-off eddy on the Georgia continental shelf, April, 1977. Deep-Sea Res. (in press).

McIntire, G. L. and W. M. Dunstan. 1975. Methods of analysis of *Spartina alterniflora* for carbohydrates, chlorophyll and iron. Georgia Marine Science Center, Technical Report 75-4.

McIntyre, A. D. 1964. Meiobenthos of sublittoral muds. J. Mar. Biol. Ass. U. K., *44*, 665–674.

—— 1969. Ecology of marine meiobenthos. Biol. Rev., *44*, 245–290.

McIntyre, A. D., A. L. S. Munro, and J. H. Steele. 1970. Energy flow in a sand ecosystem, *in* Marine Food Chains, J. H. Steele, ed., Oliver and Boyd, Edinburgh, pp 19–31.

Milliman, J. D., O. H. Pilkey and D. A. Ross. 1972. Sediments of the continental margin off the Eastern United States. Geol. Soc. Amer. Bull., *83*, 1315–1334.

Odum, E. P. 1968. A research challenge: Evaluating the productivity of coastal and estuarine water. Proc. 2nd Sea Grant Conf., Grad. School Oceanography, Univ. of Rhode Island, Newport, pp. 63–64.

Paerl, H. W. and N. J. Williams. 1976. The relationship between adenosine triphosphate and microbial biomass in diverse aquatic ecosystem. Int. Rev. Gesamten Hydrobiol., *61*, 659–664.

Pamatmat, M. 1971a. Oxygen consumption by the seabed. IV. Ship-board and laboratory experiment. Limnol. Oceanogr., *16*, 536–550.

—— 1971b. Oxygen consumption by the seabed. VI. Seasonal cycle of chemical oxidation and respiration in Puget Sound. Int. Revue ges. Hydrobiol., *56*, 769–793.

—— 1975. *In situ* metabolism of benthic communities. Cah. de Biol., *16*, 613–633.

Pamatmat, M. M. and H. R. Skjoldal. 1974. Dehydrogenase activity and adenosine triphosphate concentration of marine sediments in Lindaspollene, Norway. Sarsia, *56*, 1–11.

—— 1979. Metabolic activity, adenosine phosphates and energy charge of below ground biomass of *Juncus roemerianus* Scheele and *Spartina alterniflora* Loisel. Est. Coastal Mar. Sci., *9*, 79–90.

Rowe, G. T., C. H. Clifford, K. L. Smith, and P. L. Hamilton. 1975. Benthic nutrient regeneration and its coupling to primary productivity in coastal waters. Nature, *255*, 215–217.

Sikora, J. P., W. B. Sikora, C. W. Erkenbrecher, and B. C. Coull. 1977. Significance of ATP, carbon, and caloric content of meiobenthic nematodes in partitioning benthic biomass. Mar. Biol., *44*, 7–14.

Smidt, E. L. B. 1951. Animal production in the Danish Waddensea. Medd. Dan. Fish, Havunders., *11*, 1–151.

Smith, K. L., Jr. 1971. Structural and functional aspects of a sublittoral community. Ph.D. Thesis, University of Georgia, Athens. 160 pp.

—— 1978. Benthic community respiration in the N. W. Atlantic Ocean: *In situ* measurements from 40 to 5200 m. Mar. Biol., *47*, 337–347.

Teal, J. M., I. Valiela, and D. Beilo. 1979. Nitrogen fixation by rhizosphere and free-living bacteria in salt marsh sediments. Limnol. Oceanogr., *24*, 126–132.

Tenore, K. R., C. F. Chamberlain, W. M. Dunstan, R. B. Hanson, B. Sherr and J. H. Tietjen. 1978. Possible effects of Gulf Stream intrusions and coastal runoff on the benthos of the continental shelf of the Georgia Bight, *in* Estuarine Interactions, M. L. Wiley, ed., Academic Press, New York, pp 577-598.

Tett, P., G. K. Mahlon, and G. M. Hornberger. 1975. A method for the spectrophotometric measurement of chlorophyll *a* and pheophytin *a* in benthic microalgae. Limnol. Oceanogr., *20*, 887–895.

Thiel, H. 1978. Benthos in upwelling regions, *in* Upwelling Ecosystems, R. Boje and M. Tomczak, eds., Springer-Verlag, New York, pp 124–138.

Thomas, J. P., W. C. Phoel, F. W. Steimle, J. E. O'Reilly and C. A. Evans. 1977. Seabed oxygen consumption. New York Bight apex. Limnol. Oceanogr. Spec. Symp., *2*, 354–369.

Tietjen, J. H. 1969. The ecology of shallow water meiofauna in two New England estuaries. Oecologia, *2*, 251–291.

—— 1971. Ecology and distribution of deep-sea meiobenthos off North Carolina. Deep-Sea Res., *18*, 941–957.

—— 1977. Population distribution and structure of the free-living nematodes of Long Island Sound. Mar. Biol., *43*, 123–136.

—— 1980. Population structure and species composition of the free-living nematodes inhabiting sands of the New York Bight Apex. Est. Coast. Mar. Sci., *10*, 61–73.

Tietjen, J. H. and J. J. Lee. 1972. Life cycles of marine nematodes. Influence of temperature and salinity on the development of *Monhystera denticulata* Timm. Oecologia, *10*, 167–172.

—— 1977. Feeding behavior of marine nematodes, *in* Ecology of Marine Benthos, B. C. Coull, ed., University of South Carolina Press, Columbia, pp 22–36.

Valiela, I. and J. M. Teal. 1979. The nitrogen budget of a salt marsh ecosystem. Nature, *280*, 652–656.

Vanderborght, J. P., R. Wollsat, and G. Billen. 1977. Kinetic models of diagenesis in disturbed sediments. Part 2. Nitrogen diagenesis. Limnol. Oceanogr., *22*, 794–803.

Wiebe, W. J. and K. Bancroft. 1975. Use of the adenylate energy charge ratio to measure growth state of natural microbial communities. Proc. Nat. Acad. Sci., *72*, 2112–2115.

Wieser, W. 1960. Benthic studies in Buzzards Bay. II. The meiofauna. Limnol. Oceanogr., *5*, 121–137.

Wigley, R. and A. D. McIntyre. 1964. Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Martha's Vineyard. Limnol. Oceanogr., *9*, 485–493.

Yingst, J. Y. 1978. Patterns of micro- and meiofaunal abundance in marine sediments measured with adenosine triphosphate assay. Mar. Biol., *47*, 41–54.

Yingst, J. Y. and D. C. Rhoads. 1978. Seafloor stability in central Long Island Sound. Part II. Biological interactions and their potential importance for seafloor erodibility, *in* Estuarine Interactions, M. L. Wiley, ed., Academic Press, pp 245-260.

Yoder, J. A., L. P. Atkinson, J. O. Blanton, D. R. Deibel, D. W. Menzel, and G.-A. Paffenhofer. 1981. Plankton Dynamics of the Southeastern Shelf. (Submitted).

Yoshinari, T., R. Hynes, and R. Knowles. 1977. Acetylene inhibition of nitrous oxide reduction and measurement of denitrification and nitrogen fixation in soil. Soil Biol. Biochem., *9*, 177–184.

Zurlini, G., I. Ferrari, and A. Nassogne. 1978. Reproduction and growth of *Euterpina acutifrons* (Copepoda:Harpacticoida) under experimental conditions. Mar. Biol., *46*, 59–64.

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