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Volume 81 *Scholarly Contributions from the Membership and Others* Article 4

2023

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Recommended Citation

Dalman, Nancy; Spence, Dianna; Settele, Richard; Turner, David; Shirley, Andrew; and Schulze, Jill (2023) "Meiofauna Distribution Patterns on a Sandy Beach of Sapelo Island, Georgia," *Georgia Journal of Science*, Vol. 81, No. 2, Article 4.
Available at: https://digitalcommons.gaacademy.org/gjs/vol81/iss2/4

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Acknowledgements

We thank John Baxter, Timothy Hernandez, Kendall Maze, Sharon Schmidt, and Logan Young for assistance with sample collection and processing, and Tracy Foor for assistance with sample collection and meiofauna identification. We also thank the University of Georgia Marine Institute (UGAMI) on Sapelo Island for generous use of their facilities.

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MEIOFAUNA DISTRIBUTION PATTERNS ON A SANDY BEACH OF SAPELO ISLAND, GEORGIA

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ABSTRACT

Substantial abundance and diversity of intertidal invertebrates known as meiofauna are evident on a sandy beach of Sapelo Island, Georgia. Meiofauna are small, benthic, nearly ubiquitous animals. They consume microbes and detritus and are a food source for juvenile fish and ghost shrimp. Meiofauna were manually separated from sand samples collected from three intertidal zones and two depths during low tide in January, March, June, and October, 2017. Fifteen major meiofaunal taxonomic groups were identified in June, while only eight were observed in January; in all, there were sixteen groups observed. Highest meiofauna densities were found in the middle intertidal zone and in the top 5 cm of sand. Abundance was high year-round, and highest in the summer and fall months. Temperature, sand grain size, slope of the beach, and weathering processes may influence this meiofaunal variation. This research could contribute future insight into metazoan food webs and beach disturbances.

KEYWORDS

Meiofauna; beach; nematode; intertidal; Sapelo Island

INTRODUCTION

Exposed sandy beaches contain a diverse and abundant meiofaunal community (Brown and McLachlan 1990). Meiofauna are defined as organisms ranging in size from 50 – 500 micrometers that live in the interstices of sand grains and have greater species diversity and density per unit area than larger metazoans (Armonies and Reiss 2000; Reiss and Schmid-Araya 2008). They are ubiquitous near water, occurring in and on sediment surfaces from headwater streams (Cowell et al. 2004) to the deep trenches of the ocean (Tseleipides and Lampadariou 2004). The large interstitial spaces of sand, as compared to mud or silt sediments, make it an environment conducive to the presence of abundant meiofauna (McLachlan 1990). Early studies by McLachlan (McLachlan 1990, McLachlan et al. 1993) correlated sandy beach macrofauna abundance and species richness with beach morphodynamics, and a more recent study by Rodriguez et al (2001) confirmed a similar trend for beach meiofauna. In general, meiofauna abundance and diversity increase from steep, narrow, coarse - sand beaches to broad, flat beaches with finer sands (Rodriguez et al. 2001). Meiofaunal abundance is expected to be high on Sapelo Island beaches, given their wide, gentle slope and fine grain sands.

The majority of beach animals are sand – dwelling infauna, both macrofauna and meiofauna. Species composition, density, and biomass for macro – and meiofauna are largely affected by beach morphology and dynamics, however, a general tidally – controlled zonation is evident along most beaches (McLachlan and Jaramillo 1995). Sapelo Island sits almost in the center of the Georgia Bight and as such its beaches are considered dissipative with low wave energy, a broad, low – sloping intertidal zone, and fine grain sands (Giles and Pilkey 1965; Hoyt 1962). Studies on dissipative beaches in

Belgium have reported greatest macrofaunal species richness and density in the middle intertidal zone, which has approximately two periods of immersion each tidal cycle, and the lowest species richness in the high intertidal zone, where immersion typically only happens during spring high tides (Degraer et al. 1999; Degraer et al. 2003). Subsequent studies on these Belgian beaches found the zone of greatest meiofauna density varied on different beaches (Kotwicki et al. 2005). Abiotic factors such as sand grain size, organic content and oxygenation caused these variances (Kotwicki et al. 2005). In the rocky intertidal zone of South Africa's west coast, macrofauna were most abundant in the middle intertidal zone while the highest density of meiofauna were found in the low intertidal zone (Gibbons and Griffiths 1986). On this rocky coastline, the low intertidal zone had the greatest sand density of all the zones studied, which likely explains the prevalence of meiofauna in this region (Gibbons and Griffiths 1986). A comparable examination of meiofauna abundance and diversity has not been conducted across the intertidal zones of southeastern United States Atlantic sandy beaches.

Previous work has shown seasonal variation in sandy beach macroinvertebrate (Leber 1982) and meiofauna (Coull & Dudley 1985; Hourston et al. 2005) abundance with corresponding peak numbers in summer months. These patterns are likely linked to the annual cycle of temperature – controlled food availability and may include both top down control dictated by predator populations and bottom – up control due to food availability (Coull 1999). Meiofauna have short lifecycles, typically with 2 - 3 generations per year that may not be consecutive (Gerlach 1971). Lasker & Wells (1970) showed that the copepod *Asellopsis intermedia* mates in August but the nauplii do not hatch until the following May. Theisen (1966) observed several ostracod species have hibernating eggs in both natural and cultured conditions. Culture studies indicate that most species appear to reproduce at high temperatures, which agrees with peak abundance in the summer, although there are likely numerous other biological and physical factors that control meiofauna lifecycles (Coull 1999). For example, meiofauna abundance and diversity are inversely correlated with wave action (Wieser 1959), which tends to be greater during the winter. Regardless of the driving factors, there is strong evidence to support a summer - dominant seasonal pattern in meiofauna abundance on sandy beaches (Harris 1972; Hourston et al. 2005).

Nematodes and harpacticoid copepods tend to be the most abundant marine meiofauna taxonomic groups (Heip et al. 1985), with a general shift from predominantly nematodes in fine grain sands to primarily harpacticoid copepods in coarse sands (Coull 1970). Other common groups represented in the sandy beach meiofauna community include Turbellaria, Polychaeta, Ostracoda and Gastrotricha (Brown and McLachlan 1990). In contrast, the beach macrofauna community is dominated by Mollusca, Crustacea and Polychaeta. Meiofauna consume microbes and detritus and in turn are an important food source for beach macrofauna and juvenile fish. They therefore provide a critical link in several marine food webs.

The purpose of this study was to document the meiofaunal community structure at Nannygoat Beach (Sapelo Island, GA) during four different seasons. Sapelo Island is a sparsely inhabited, relatively pristine environment with little human traffic. Meiofauna abundance and diversity were examined during low tide at three different horizontal zones within the intertidal region and at two different depths in each zone. The present study provides data for a Georgia barrier island, for which little information on meiofaunal composition exists, and can serve as a baseline for future research on beach disturbances and environmental contamination.

MATERIALS & METHODS

The diagram shown in Figure 1 illustrates the theoretical framework that guided the data collection and analysis for the study. Species diversity and species abundance are identified as the outcomes of interest; tidal zone, depth, organic content, water content, and season are identified as predictors of these outcomes. Arrows in the diagram show the expected relationships among these variables. Every relationship (arrow) shown in the theoretical framework was checked with a simple bivariate model. A summary of the results is given in Table 1. Most relationships shown were confirmed, with exceptions noted in the table.

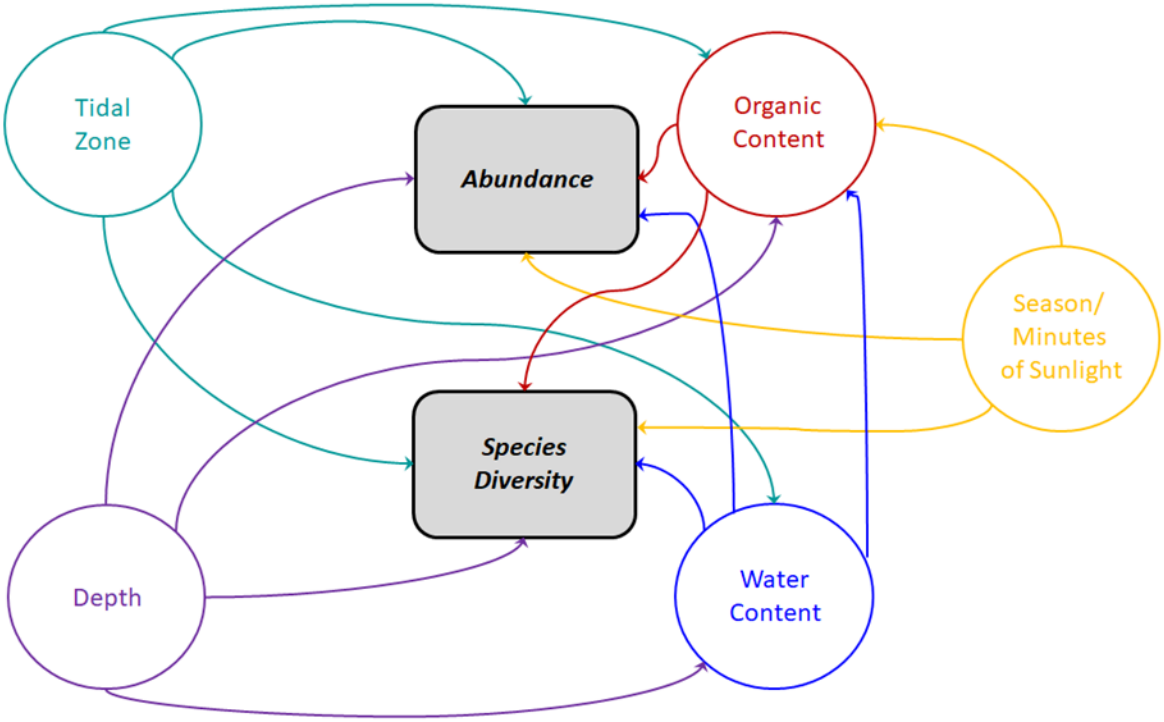

Figure 1. Relationships among environmental variables and the abundance of organisms and species diversity.

Table I. Verifications of relationships between variables connected in our theoretical framework, as depicted in Figure 1.

Explanatory variable	Response variable	Significance (p-value)	R^2	Confirmation
Tidal Zone	Organic Content	1E-14	0.2553	Very strong
Tidal Zone	Water Content	3E-15	0.2631	Very strong
Tidal Zone	Diversity	0.002	0.0483	Strong
Tidal Zone	Abundance	2E-16	0.3286	Very strong
Depth	Organic Content	0.820	---	Not confirmed
Depth	Water Content	0.230	---	Not confirmed
Depth	Diversity	0.061	0.0118	Weak
Depth	Abundance	0.0004	0.0530	Strong
Season	Organic Content	2E-16	0.4553	Very strong
Season	Diversity	0.023	0.0304	Confirmed
Season	Abundance	0.012	0.0371	Confirmed
Water Content	Organic Content	0.055	0.0126	Weak
Water Content	Diversity	0.450	---	Not confirmed
Water Content	Abundance	0.0002	0.0596	Strong
Organic Content	Diversity	0.0002	0.0592	Strong
Organic Content	Abundance	3E-5	0.0740	Very strong

Sampling was conducted during low tides in January, March, June, and October 2017 at three north to south locations on Nannygoat Beach (081°16’52”W, 31°23’50”N), Sapelo Island, GA. Samples were collected at spring low tide from three zones across each beach: high tide (mean high water for spring tides), middle tide, and low tide (mean low water for spring tides). GPS coordinates for each sampling site were recorded to ensure sampling occurred at the same locations in all seasons. One - meter square plots were marked in the sand, and corers (1” diameter) were used to collect sand (~125g sand total for each sample) from the 0-5 cm deep and from 5-10 cm deep. Triplicate 125g samples were collected for each location, tidal zone, and depth.

Samples for meiofauna extraction were brought back to the University of Georgia Marine Institute lab on ice for processing. From each of the triplicate samples, 25g of sand were fixed and dyed in a 4% formalin and 1.5% Rose Bengal solution. The meiofauna were extracted using methods described in Armenteros et. al. (1980). Briefly, approximately 10 parts fresh water were added to one part sand and vigorously agitated for 30 s. The samples were allowed to settle for 30 s and the supernatant was decanted on a 45 µm mesh sieve. The process was repeated 5 times and the resulting sample and transferred to an 80% ethanol preservative solution. A Meiji stereo microscope (50x magnification) was used for initial identification of meiofauna. Further identifications were made using an Olympus compound microscope (100x magnification). Meiofauna were identified to the lowest taxonomic group possible.

Additional sand samples (~50g) were dried for 24 hours in a 70°C oven. Water content was calculated by subtracting dry weight from wet weight and is reported as percent of the total weight. Samples were subsequently ashed at 900°C for three hours. Final weight was subtracted from initial weight to calculate organic content and is reported as percent of total weight. Ashed samples were analyzed to determine sand grain size via the Wentworth Scale (Higgins and Thiel 1988). Median sediment diameters are presented in Φ units.

A final set of samples (50 g) were agitated in 200 ml diH_2O. The sand was allowed to settle and 50 ml of supernatant was filtered through 47mm A/E Gelman glass filters with vacuum (pressure no greater than 100 mm Hg). Filters were submerged in 25 mL of methanol and held at 0°C in the dark for 12 hours. Chlorophyll a measurements were made using an Aquaflor handheld fluorometer (Turner Designs, San Jose, CA). Methodological error resulted in chlorophyll analysis only being conducted with summer and fall samples.

Beach slope was measured at each intertidal zone location using a Bosch optical level set on a tripod. Meter sticks were used to find beach height.

Statistical analyses followed the recommendations of Sokal and Rohlf (1981). Analyses were performed with JMP® Pro 16.2.0 statistical software. For all tests we used a significance level of alpha=0.05. No significant differences were found between sampling locations on Nannygoat Beach in abundance ($F_{(2,212)}=1.483$, $p=0.229$), organic content (%) ($F_{(2,69)}=0.660$, $p=0.520$), water content (%) ($\chi^2=0.466$, $df=2$, $p=0.792$), chlorophyll (µg/L) ($F_{(2,33)}=2.147$, $p=0.133$), or median sediment diameter (Φ) ($\chi^2=5.358$, $df=2$, $p=0.069$). The Effective number of species differed by ≤10% between locations, therefore data for the three north to south sampling locations were combined for analyses.

We used parametric tests when data were normally distributed, or could be transformed to fit a normal distribution, and when homogeneity of variance existed among samples. We assessed normality with Shapiro-Wilk test and homogeneity of variance with Levene's test. In order to fit data to a normal distribution, we attempted a Box-Cox power series transformation Y^{λ} where $\lambda=-2, -1, -0.5, 0, 0.5, 1$, and 2 (Box and Cox 1964); $\log(Y)$; and $\log(Y+1)$ transformations. We used the transformation that best fit a normal distribution. When considering a single variable, we used Student's t-test for comparisons of two samples, and one-way ANOVA for comparisons of >2 samples. If an ANOVA was significant, we conducted simultaneous multiple pairwise comparisons with Tukey-Kramer Honestly Significant Differences (HSD) test, which guards against Type I errors and allows comparisons between samples of different sizes (Smith 1971).

We used non-parametric statistics when data did not meet the criteria of normality and homogeneity of variance. When considering a single variable, we used Wilcoxon Rank Sum test for comparisons of two samples, and Kruskal-Wallis test for comparisons of >2 samples. If a Kruskal-Wallis test was significant, we conducted simultaneous multiple pairwise comparisons with Dunn's test. Dunn's test incorporates Bonferroni's adjustment to alpha level to pairwise comparisons and guards against Type I errors by reducing the likelihood of getting a significant difference due to chance when conducting large numbers of unplanned comparisons (Dunn 1961).

None of the variables we analyzed (abundance, organic content (%), water content (%), chlorophyll (µg/L), and median sediment diameter (Φ)) had normally distributed parameter values. We transformed the following variables to normality: abundance, using $\log(Y+1)$; organic content (%), using $\ln(Y)$; and chlorophyll (µg/L), using $\log(Y)$. We could not transform water content (%) or median sediment diameter (Φ) to normality. In our tables, we present original (non-transformed) values of data for the purpose of communicating parameter values. Parameter values are presented as median±median absolute deviation (*MAD*). Median absolute deviation is a robust estimate of dispersion used with non-normally distributed data.

Diversity was estimated by Shannon's index (*H'*), Pielou's eveness index (*J'*), and Effective number of species, which is calculated as exp(*H'*). Effective number of species is not an index. In contrast to an index of diversity, Effective number of species offers an intuitive unit by measuring number of species. Effective number of species calculates the number of equally abundant species needed to generate a given *H'* value. By linearizing the relationship between richness and Shannon's index diversity, Effective number of species converts the Shannon index into true diversity (Jost 2006). We conducted pairwise comparisons of Shannon's index sequentially with Hutcheson's t-test (Hutcheson 1970).

To determine the degree to which organic content, water content, zone, depth, and season predicted abundance of organisms, a hierarchical multiple regression analysis was conducted. The first regression model included water content, organic content (log transformation) and zone as predictors of abundance. The second model added depth to the set of predictors, and the next model added season. Then the interaction between zone and season was added in the following model, with interaction between zone and depth introduced in the last model. Model analyses were conducted in R, version 4.1.1.

To determine the degree to which organic content, zone, depth, and season predicted species diversity, a hierarchical multiple regression analysis was conducted. The first regression model included only organic content (log transformation) and zone as predictors of diversity, because water content was not significant (Table 1). The second model added depth to the set of predictors, and the third model added season. Then the interaction between zone and season was added in the next model, followed by the interaction between zone and depth in the last model. Model analyses were conducted in R, version 4.1.1.

RESULTS

A total of 25,519 individuals were recorded from 216 samples (Table 2). The number of individuals per sample per 10cm^2 ranged from 1 to 831. Median abundance per sample was 56.0 individuals.

Table II. Taxonomic group frequencies throughout seasons.

Taxa	Winter	Spring	Summer	Fall	N_{Total}	% of Total
Nematoda	2947	3516	7190	7455	21,108	82.708
Gastrotricha	213	185	837	478	1,713	6.712
Tardigrada	4	9	8	1165	1,186	4.647
Platyhelminthes	137	109	303	20	569	2.230
Polychaeta	0	13	187	18	218	0.854
Annelida	15	57	116	26	214	0.839
Ostracoda	2	30	110	33	175	0.686
Arthropoda	48	44	50	18	160	0.627
Gnathostomulida	24	9	13	39	85	0.333
Gastropoda	0	0	25	2	27	0.106
Priapulida	0	2	11	13	26	0.102
Kinorhyncha	0	5	8	2	15	0.059
Collembola	0	0	12	0	12	0.047
Bryozoa	0	0	0	11	11	0.043
Total	3390	3979	8870	9280	25,519	100.0

Fourteen major taxonomic groups were observed. Nematoda were the most abundant (82.7%), followed by Gastrotricha (6.7%), Tardigrada (4.6%), and Platyhelminthes (2.2%). Individuals in the remaining 10 taxonomic groups accounted for <4.0% of all individuals observed. Eight to thirteen taxonomic groups were observed in any given season, and eight of the fourteen groups were observed during all four seasons (Table 2).

Meiofauna abundance was greater in the low and mid zones than the high zone ($F_{(5,209)}$=31.486, p<0.001; Table 3; Figure 2a). Within the low and mid zones, abundance was greater in shallow sediment than deep sediment (post-hoc Tukey HSD test, p<0.001 and p=0.001, respectively). Abundance varied across seasons ($F_{(3,211)}$=3.579, p=0.015; Table 3; Figure 2b). Summer showed more abundance than winter (post-hoc Tukey HSD test, p=0.036).

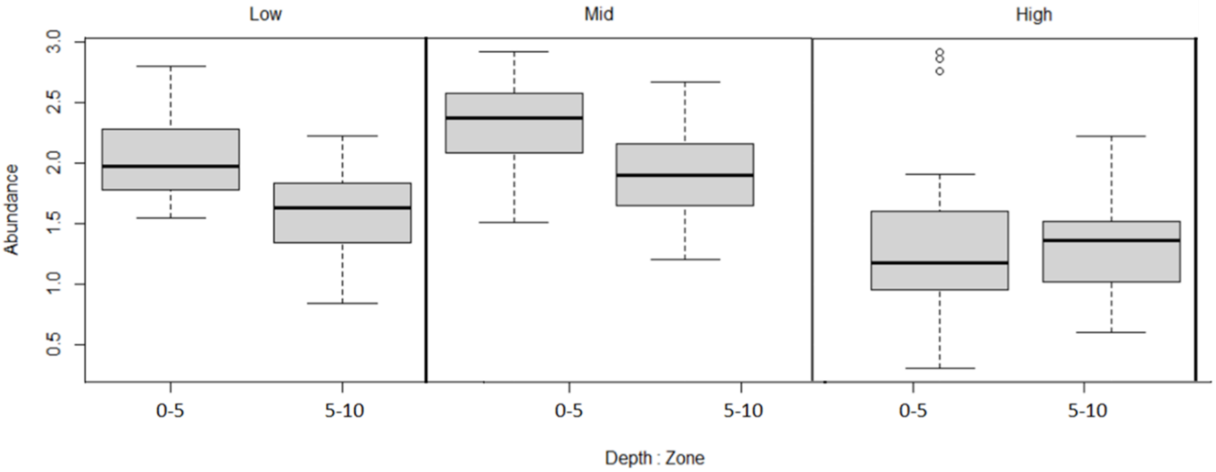

Figure 2a. Effects of intertidal zone and sediment depth on meiofauna abundance [log(ind. 10cm^{-2}+1)]. Dark lines represent the median; box extends from first quartile to third quartile; whiskers span from minimum to first quartile and from third quartile to maximum; open circles represent outliers.

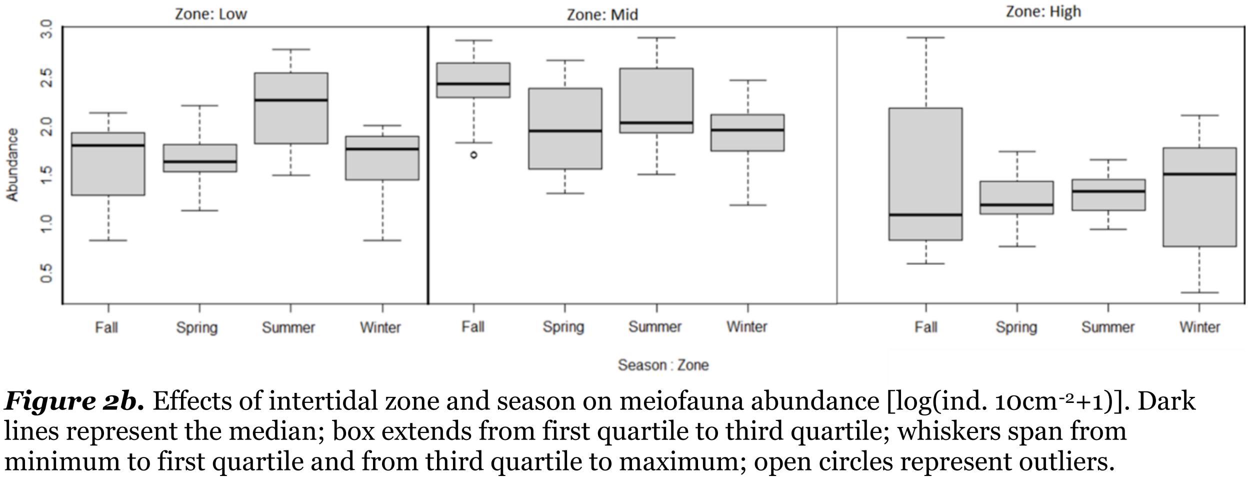

Figure 2b. Effects of intertidal zone and season on meiofauna abundance [log(ind. 10cm^{-2}+1)]. Dark lines represent the median; box extends from first quartile to third quartile; whiskers span from minimum to first quartile and from third quartile to maximum; open circles represent outliers.

Table III. Parameter values of meiofauna abundance and diversity in relation to intertidal zone, sediment depth, and season.

	Abundance (ind. 10cm^{-2})		**# taxonomic groups**	**Shannon index (H')**	**Pielou's evenness (J')**	**Effective # of species**
	median	**±*MAD***				
Depth, Zone						
0-5cm, Low	88.0	±48.0	13	0.641	0.243	1.898
0-5cm, Mid	230.5	±122.5	13	0.598	0.227	1.818
0-5cm, High	14.0	±10.0	12	1.026	0.413	2.789
5-10cm, Low	41.0	±22.0	11	0.830	0.334	2.294
5-10cm, Mid	76.0	±36.5	12	0.482	0.194	1.620
5-10cm, High	22.0	±12.5	11	0.453	0.189	1.573
Season, Zone						
Winter, Low	59.0	±31.0	6	0.463	0.258	1.792
Winter, Mid	93.0	±39.0	7	0.261	0.134	1.298
Winter, High	33.5	±28.0	8	1.114	0.536	3.047
Spring, Low	43.0	±9.0	11	0.626	0.261	1.871
Spring, Mid	89.5	±64.0	11	0.517	0.216	1.677
Spring, High	15.0	±7.0	9	0.541	0.246	2.197
Summer, Low	190.0	±130.0	12	0.721	0.290	2.485
Summer, Mid	109.0	±71.0	13	0.860	0.335	2.565
Summer, High	21.0	±8.0	4	0.244	0.176	1.276
Fall, Low	60.0	±28.0	13	0.747	0.291	2.111
Fall, Mid	275.5	±129.0	11	0.366	0.153	1.442
Fall, High	11.0	±8.0	12	0.804	0.324	2.236

MAD = median absolute deviation

Meiofauna diversity estimated by Shannon index (*H'*) did not show a clear pattern across intertidal zone or sediment depth (Table 3, Figure 3a). Pairwise comparisons of *H'* were significantly different among all combinations of zone and depth. Diversity was greatest in shallow sediment of the high intertidal zone and lowest in the deep sediment of the high intertidal zone. While there was no clear pattern in diversity when considering the interaction of zone and season, overall, the Shannon index diversity was highest in the summer, followed by fall, and lowest in winter and spring (Table 3; Figure 3b).

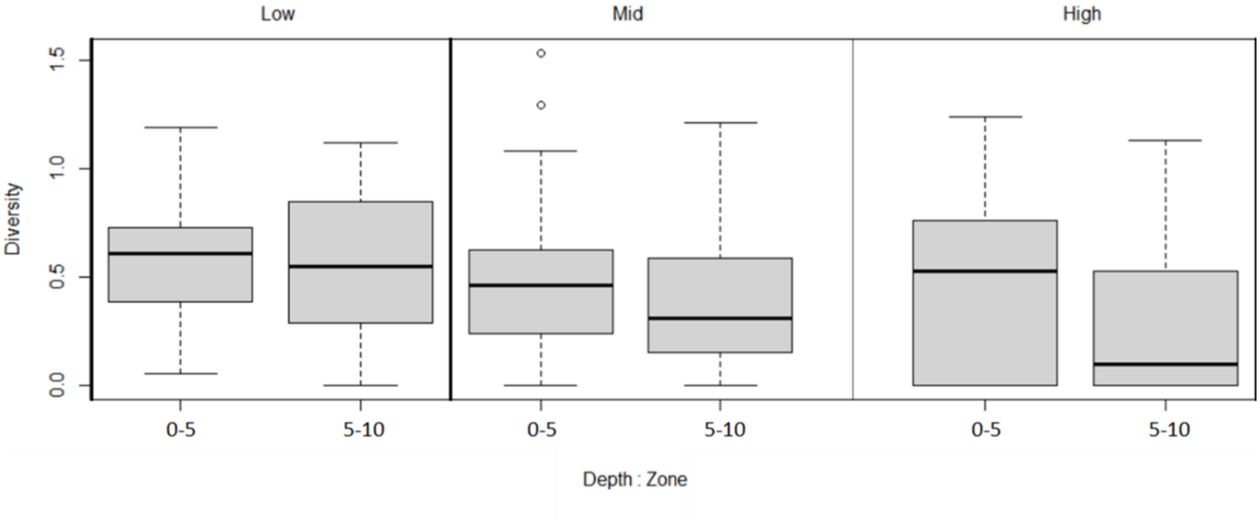

Figure 3a. Effects of intertidal zone and sediment depth on meiofauna diversity (*H'*). Dark lines represent the median; box extends from first quartile to third quartile; whiskers span from minimum to first quartile and from third quartile to maximum; open circles represent outliers.

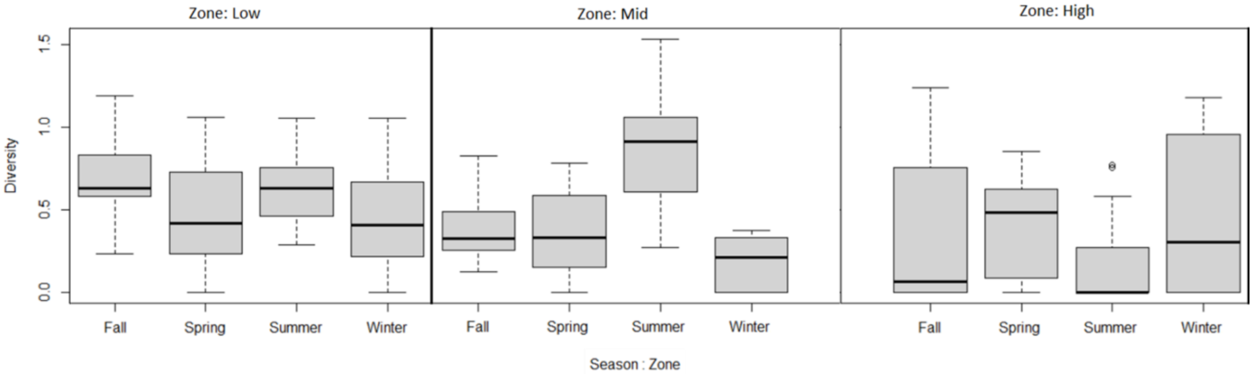

Figure 3b. Effects of intertidal zone and season on meiofauna diversity (*H'*). Dark lines represent the median; box extends from first quartile to third quartile; whiskers span from minimum to first quartile and from third quartile to maximum; open circles represent outliers.

Sediment characteristics varied more among intertidal zones than between sediment depths (Table 4). Organic content (%) ($F_{(5,66)}$=4.786, *p*=0.001), water content (%) (χ^2=19.470, *df*=5, *p*=0.002), and chlorophyll (µg/L) ($F_{(5,30)}$=3.798, *p*=0.009) were greater in the low intertidal zone than the high zone. Within each tidal zone, no differences existed between shallow and deep sediment for organic content, water content, or chlorophyll. Median sediment diameter (Φ) varied among intertidal zone and sediment depth (χ^2=25.996, *df*=5, *p*<0.001). Sediment diameter was smallest in the deep sediment of the high intertidal zone and greatest in the shallow sediment of the low and high intertidal zones.

Table IV. Physical characteristics of sediment at Nannygoat Beach.

Zone, Depth	**Organic content (%)**				**Water content (%)**				**Chlorophyll (µg/L)**				**Sediment diameter (median Φ)**			
	median	**±*MAD***	***p***	**§**	**median**	**±*MAD***	***p***	**§**	**median**	**±*MAD***	***p***	**§**	**median**	**±*MAD***	***p***	**§**
Low, 0-5cm	0.830	±0.112	***	A,B	19.975	±1.436	**		35.965	±8.630	**	A	2.450	±0.150	***	B
Low, 5-10cm	0.859	±0.225		A	22.124	±1.225		A	25.987	±9.680		A	2.000	±0.400		
Mid, 0-5cm	0.659	±0.137		A,B,C	18.408	±2.479			29.573	±5.567		A	2.400	±0.100		
Mid, 5-10cm	0.675	±0.154		A,B,C	19.849	±4.001			18.752	±3.564		A,B	2.300	±0.000		
High, 0-5cm	0.537	±0.193		B,C	8.028	±4.655		B	26.910	±9.099		A,B	2.500	±0.050		B
High, 5-10cm	0.451	±0.115		C	9.451	±5.324		B	11.395	±1.889		B	1.700	±0.200		A

MAD = median absolute deviation
*** $p<0.001$; **$p<0.01$; *$p<0.05$; *n.s.* not significant
§ Categories with different letters indicate significant pairwise differences

One focal point of the study was to determine the degree to which water content, organic content, zone, depth, and season predicted abundance of organisms (Figure 1). Table 5 shows the regression coefficients obtained from the hierarchical multiple regression analysis conducted to address this question. Hierarchical multiple regression adds independent variables in steps. In each step, regression coefficients are generated for the independent variables predicting the dependent variable, and for the interactions between independent variables. For example, Model 1 includes the independent variables water content, organic content, and zone. Water content and organic content do not contribute significantly to Model 1, but zone does. Adjusted R^2 values are given for each model. Model 1 explains approximately one-third of the observed variation in abundance (Adjusted $R^2=0.328$, $p<0.001$). Change in R^2, located in the bottom row of Table 5, shows the change in Adjusted R^2 value with each step. As variables are added to the models, regression coefficients change. Variables remain in the models as long as they are significant. Once variables lose significance, they are removed from the models, unless they have a significant interaction with another independent variable. For example, introducing the interaction between zone and season and the interaction between zone and depth resulted in highly significant increases to the model R^2 values. When the interaction between zone and season was introduced in Model 5, the independent contribution of season was no longer statistically significant. When the interaction between zone and depth was introduced in Model 6, the independent contribution of depth was no longer statistically significant. The individual components season and depth need to remain in the model because of the significant interactions between zone and season and between zone and depth.

Table V. Regression Coefficients for Variables Predicting Abundance (Baseline: Zone=High, Season=Fall, Depth=Shallow (0-5)).

	Model 1	**Model 2**	**Model 3**	**Model 4**	**Model 5**	**Model 6**
Water Content	0.002	0.004				
(ln) Organic	0.124	0.138				
Zone						
Low	0.393^{***}	0.366^{***}	0.488^{***}	0.486^{***}	0.209	0.449^{**}
Mid	0.712^{***}	0.688^{***}	0.778^{***}	0.778^{***}	0.931^{***}	1.155^{***}
Depth						
Deep (5-10)		-0.271^{***}	-0.267^{***}	-0.266^{***}	-0.266^{***}	0.043
Season						
Winter				-0.219^{**}	-0.169	-0.169
Spring				-0.201^{*}	-0.207	-0.207
Summer				0.066	-0.144	-0.144
Zone*Season						
Low-Winter					0.179	0.185
Low-Spring					0.231	0.231
Low-Summer					0.699^{***}	0.699^{***}
Mid-Winter					$-0.331^{\wedge}$	$-0.331^{\wedge}$
Mid-Spring					-0.214	-0.214
Mid-Summer					-0.068	-0.068
Zone*Depth						
Low-Deep						-0.480^{***}
Mid-Deep						-0.448^{***}
Adjusted R^2	0.328^{***}	0.385^{***}	0.384^{***}	0.426^{***}	0.470^{***}	0.507^{***}
Change in R^2		0.057^{***}	-0.001	0.042^{***}	0.044^{**}	0.037^{***}

^ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Similarly, the degree to which water content, organic content, zone, depth, and season predicted species diversity was also considered (Figure 1). Table 6 shows the regression coefficients obtained from the hierarchical multiple regression analysis conducted to address this question. We did not include water content in the model in Table 6 because prior analysis showed there was no relationship between water content and species diversity (Table 1). When season was added to the model, the independent contribution of organic content was no longer statistically significant. Informed by this observation alongside the guiding theoretical diagram and the finding that season was already found to be a highly significant predictor of organic content, season was retained for subsequent models, and organic content was dropped, as shown in Model 4. When the interaction between zone and season was introduced in Model 5, the model R^2 saw a highly significant increase from 9% to about 28%, a much greater increase than was achieved from any other predictor. This suggests the interaction between Zone and Season is by far the strongest predictor of species diversity among the variables being considered. The interaction between zone and depth was also found to be significant when it was introduced in Model 6.

Table VI. Regression Coefficients for Variables Predicting Diversity (Baseline: Zone=High, Season=Fall, Depth=Shallow (0-5)).

	Model 1	**Model 2**	**Model 3**	**Model 4**	**Model 5**	**Model 6**
(ln) Organic	0.140*	0.137*	– 0.024			
Zone						
Low	0.128^	0.130*	0.220**	0.206***	0.307**	0.202^
Mid	0.044	0.045	0.104	0.095^	– 0.016	– 0.066
Depth						
Deep (5-10)		– 0.089^	– 0.091^	– 0.091^	– 0.090*	– 0.194**
Season						
Winter			– 0.124	– 0.113^	0.087	0.087
Spring			– 0.075	– 0.071	0.010	0.010
Summer			0.089	0.080	– 0.215*	– 0.215*
Zone*Season						
Low-Winter					– 0.327*	– 0.330*
Low-Spring					– 0.234	– 0.234^
Low-Summer					0.155	0.155
Mid-Winter					– 0.275^	– 0.275^
Mid-Spring					– 0.010	– 0.010
Mid-Summer					0.729***	0.729***
Zone*Depth						
Low-Deep						0.211*
Mid-Deep						0.100
Adjusted R^2	0.068***	0.080***	0.087***	0.091***	0.279***	0.288***
Change in R^2		0.012	0.007	0.004	0.188***	0.009

^ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

DISCUSSION

The results are compatible with the framework given in Figure 1, and further illuminate the relationships among the predictors and outcomes. Specifically, the framework shows no explicit interactions among variables, but the models reveal significant zone-season and zone-depth interactions in predicting both abundance and diversity. In addition, because zone, depth, and season help to drive water content and organic content, the model hierarchies demonstrate that when zone, depth, season, and their interactions are accounted for, water content and organic content do not add further predictive value.

The meiofauna community on one of Sapelo Island's sandy beaches was overwhelmingly composed of nematodes in all tidal zones and sand depths measured. This finding agrees with numerous studies from other sandy beaches (Coull 1999; Harris 1972; Warwick 1971). Despite the prevalence of nematodes, the meiofaunal diversity was high and included 16 different animal taxonomic groups. Gastrotricha, Annelida, Platyhelminthes, Arthropoda, Ostracoda, Tardigrada and Polychaeta were likewise common, with Kinorhyncha, Priapulida, Gastropoda, Gnathostomulida, Collembola, Bryozoa, Copepoda, and Sarcomastigophora also present but in lower numbers. Seasonally, diversity showed a marked decrease with 13 - 15 taxonomic groups present in the summer and fall but only 8 groups present in the winter (locations, zones and depths combined). The seasonal trend in diversity is consistent with previous work (Hourston et. al. 2005) and likely is influenced by seasonal water temperature fluctuations (Harris 1972).

Despite a large decline in diversity during the winter sampling, there appeared to be only a modest decrease in abundance during that season (Table 2). This disparity can be explained by the consistent presence of the most dominant taxonomic groups (Nematoda, Gastrotricha, Tardigrada, Platyhelminthes, and Annelida) in all seasons and the corresponding decline in less numerically abundant taxonomic groups during the winter months. Harris (1972) reported similar winter declines in less prevalent groups such as Tardigrada; this group, along with others present in the summer and fall at Sapelo (Polychaeta, Gastropoda, Priapulida), were largely absent during winter sampling. The relationship between density and temperature is likely attributable to effects on reproduction rather than mortality. For example, Barnett (1970) reported a decline in copepod reproductive success at temperatures comparable to winter temperatures at Sapelo Island. Likewise, Harris (1972) found a rapid reduction in copepod nauplii through the fall and into the winter, about two weeks prior to adult copepod population decrease. Harris's (1972) study was conducted on a beach in England, where temperatures are, on average, cooler year – round than at Sapelo Island.

Meiofauna abundance was greatest in the middle intertidal zone, where the sand is submerged approximately half of the time. The low intertidal zone had the next highest overall meiofauna abundance, while the high intertidal zone, which is characterized by low organic and water content, had the lowest meiofauna abundance. Sapelo Island beaches can be considered low energy, dissipative and tidally - driven environments (Howard and Reineck 1981). Current and previous work indicates that sand grain size in the middle intertidal zone of Sapelo Island's beaches is considered fine but shows a slightly coarser grain size overall than the low intertidal zones, which may allow for better oxygenation and flushing of sand (Howard and Dorjes 1972; Rodriguez et al. 2003). This hypothesis is supported by highest dissolved oxygen readings in interstitial water from the middle intertidal zone (data not shown). Studies done at either high wave energy, reflective beaches (Hooge 1999) or low wave energy, dissipative beaches (Rodriguez et al. 2001) confirm that the mid intertidal zone has the highest meiofauna densities; aerobic interstitial conditions appear balanced with organic inputs in this region (McLachan and Turner 1994).

In contrast to abundance, meiofauna diversity was greatest in the high intertidal zones: zonal diversity ranged from 8 – 16 taxonomic groups, with diversity generally inversely correlated to tidal zone. There were no taxonomic groups that were unique to any single zone, rather groups were present in all three zones or in two adjacent zones (i.e. – low and mid zones or mid and high zones). However, certain groups, notably Tardigrada, exhibited a distinctly patchy distribution within sites. The beaches on Sapelo Island, almost centrally located in the Georgia Bight, experience some of the largest tidal fluctuations in the southeastern United States (Frey and Howard 1986). Sand, even in the uppermost reaches of the high intertidal zone is drier than that in the middle or low zones, but is still regularly inundated with highly – turbid, nutrient – rich water during most high tides. This may account for the larger diversity seen in Sapelo Island's high intertidal zone as compared to other beaches with a smaller tidal range. Further, the high intertidal zone of Sapelo Island beaches transitions from the intertidal beach to the adjacent dunes and interdune meadows; the high diversity of meiofauna in this area may also result from some community overlap between these habitats. The exception to the large diversity in the high intertidal occurs in the summer when significantly drier sand (Table 4) may drive the meiofauna deeper than the 10cm measured. Overall, the sands of a Sapelo Island beach appear to support a highly varied assemblage of meiofauna taxonomic groups that is fairly uniform across tidal zones.

Our results are consistent with previous studies that have reported meiofauna on fine grain sandy beaches as being most concentrated in the upper 5cm of sand (Harris 1972; Kotwicki et al. 2005; Rodriguez et al. 2003). Food in the form of diatoms is also generally most abundant in the upper layer of sand, where sunlight penetration is greatest. A study conducted on a South Carolina sandy beach showed a positive correlation between diatom and meiofauna abundances (Montaga et al. 1983). While there is some vertical migration of diatoms within the sand, this movement is generally limited to the upper few millimeters (Joint et al. 1982). Further, Haardt and Nielsen (1980) showed that light attenuation occurs more rapidly in fine grain sand than in coarse sand due to increased scattering. It should be noted, however, that interstitial algal migrations on Sapelo Island beaches are prompted by both light and tidal cycles (Asplund and Cottingham 1991). Since samples in this study were always taken during low tide, the vertical distribution of meiofauna may vary at different points in the tidal cycle, if food availability is a primary determinant in location. Oxygen availability, which decreases with depth, may also play a crucial role in meiofaunal vertical zonation (Kotowicki et al. 2005)

Meiofauna diversity and abundance patterns on Sapelo Island beaches follow those of other sandy beaches globally (Coull 1999; Harris 1972; Kotowicki et al. 2005). Future studies will examine additional sampling points at each site to clarify whether many of these organisms exhibit patchy distribution, as suggested by our Tardigrada data. Additional physical characteristics (dissolved oxygen levels, temperature, etc.) will also be measured to determine whether specific environmental parameters may play a role in influencing the meiofaunal communities.

ACKNOWLEDGEMENTS

We thank John Baxter, Timothy Hernandez, Kendall Maze, Sharon Schmidt, and Logan Young for assistance with sample collection and processing, and Tracy Foor for assistance with sample collection and meiofauna identification. We also thank the University of Georgia Marine Institute (UGAMI) on Sapelo Island for generous use of their facilities.

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