

# On the Ecology of Oligochaetes: Monthly Variation of Community Composition and Environmental Characteristics in Two South Carolina Tidal Creeks

DAVID J. GILLETT<sup>1,\*</sup>, A. FREDERICK HOLLAND<sup>2</sup>, and DENISE M. SANGER<sup>3</sup>

<sup>1</sup> *Grice Marine Biological Laboratory, 205 Fort Johnson Road, Charleston, South Carolina 29412*

<sup>2</sup> *Hollings Marine Laboratory, 219 Fort Johnson Road, Charleston, South Carolina 29412*

<sup>3</sup> *South Carolina Department of Natural Resources Marine Resources Research Institute, 217 Fort Johnson Road, Charleston, South Carolina 29412*

**ABSTRACT:** In the tidal creeks of the southeastern United States, the numerically and ecologically dominant macrobenthic organisms are typically oligochaetes. Due to their relatively small size and difficult taxonomy, little is known about the short-term and seasonal changes in the oligochaetes of tidal creeks. This study presents a report of the spatial and temporal changes of the oligochaete taxa within and between two tidal creeks in southern South Carolina, at monthly intervals over a 13-month period. These changes are framed within the reference of monthly changes in benthic chlorophyll *a*, sediment composition, and porewater ammonia, as well as in the perspective of seasonal changes in the entire tidal creek macrobenthic community. The most abundant oligochaete found in this study was the tubificid *Monopylephorus rubroniveus*, followed by the naid *Paranais litoralis* and the tubificids *Tubificoides heterochaetus* and *T. brownae*. All of the oligochaetes exhibited strong month-to-month and spatial changes, indicative of changes in water quality and sediment habitat characteristics (e.g., low dissolved oxygen, high benthic chlorophyll *a*). There were significant correlations between the abundance of most species and either benthic chlorophyll *a* concentration or the silt-clay fraction of the sediment. Looking at short-term changes in this rapidly changing component of the macrobenthic community provides insight not only into the ecology of the oligochaetes, but also into the changes in the tidal creek ecosystem and their potential effects on other biota.

## Introduction

Salt marshes and tidal creeks are the pervasive, characteristic ecosystems of the southeastern United States coastal zone (Nummedal et al. 1977). Salt marshes and tidal creeks contain a diverse array of microhabitats and complex food webs, a reflection of their position as an interface between the estuary and the uplands (Mitsch and Gosselink 2000; Weinstein and Kreeger 2000). These are systems renowned for their high primary (Pinckney and Zingmark 1993; Mitsch and Gosselink 2000; Sullivan and Currin 2000) and secondary production (Sardá et al. 1995; Gillett et al. 2005), providing nursery grounds or year-round habitat for economically, ecologically, and recreationally important finfish and crustaceans (Weinstein 1979; Wenner and Beatty 1993; Kneib 1997; Coen et al. 1999).

Benthic macrofauna are an important component of tidal creek ecosystems as they provide an important food source for resident nekton (Wenner 1992; Stehlik and Meise 2000), affect sediment geochemical processes via bioturbation (Rice and

Rhoads 1989; Levin et al. 1997; Schaffner et al. 2001), and function as an important link in benthic-pelagic coupling, transferring energy from primary producers and decomposers to higher trophic levels (Diaz and Schaffner 1990; Kneib 1997; Posey et al. 2002). In the intertidal portions of tidal creeks in South Carolina, the most abundant macrobenthic organisms are oligochaetes (Sanger 1998; Lerberg et al. 2000; Van Dolah et al. 2000; Gawle 2002). Oligochaetes are nonselective, burrowing deposit feeders that consume vascular plant-derived detritus, microphytobenthos, and sediment-bound bacteria (Kendal 1979; Giere and Pfannkuche 1982). They are an energy rich food source for many nektonic predators (Cummins and Wuycheck 1971).

In the southeastern U.S., studies of tidal creek macrobenthos have not traditionally identified oligochaetes to the level of species or fully evaluated their roles in ecosystem processes (Teal 1962; Cammen 1979; Swearingen 1983; West 1985). In macrobenthic communities where oligochaetes do not comprise a large portion of the infauna, or where only one or two species exist, characterizing specimens as Oligochaeta may not adversely affect findings and conclusions. In tidal creeks, salt marshes, and other brackish, intertidal areas,

\* Corresponding author; current address: Biological Sciences Department, Virginia Institute of Marine Science, P.O. Box 1346, Gloucester Point, Virginia 23062; tele: 804/684-7740; fax: 804/684-7889; e-mail: gillett@vims.edu

oligochaetes are a diverse and important component of the macrobenthic community and should be identified to the species level (Diaz 1980; Sardá et al. 1995; Seys et al. 1999; Lerberg et al. 2000). In South Carolina, there are at least 15 species of oligochaetes that are part of the tidal creek and salt marsh macrobenthic community (Sanger 1998; Lerberg et al. 2000; Van Dolah et al. 2000; Gawle 2002). All species of oligochaetes do not respond to environmental gradients in the same manner (Sauter and Güde 1996; Seys et al. 1999; Verdonschot 2001; Calle Delgado 2006) and classifying them as *Oligochaeta* may obscure relationships between environmental factors and species-specific distributional patterns.

Environmental gradients exist both along the length of a tidal creek and among tidal creeks draining watersheds with different land cover; the macrobenthic community reflects these gradients (Lerberg et al. 2000). The upper most portions of creeks are stressful environments prone to large fluctuations in dissolved oxygen and salinity. These headwater habitats are exposed to air for many hours a day, are strongly influenced by the runoff from surrounding uplands, and serve as repositories for chemical and microbial contaminants (Sanger et al. 1999a,b; Lerberg et al. 2000; Mallin et al. 2000; Holland et al. 2004). These upper reaches are typically dominated by species of oligochaetes that are tolerant to the fluctuations and stressors (Lerberg et al. 2000; Van Dolah et al. 2000). The lower sections of tidal creeks are generally less physically variable environments that are influenced by the larger tidal rivers and open estuarine waters into which they drain (Hackney et al. 1976; Horlick and Subrahmanyam 1983; Van Dolah et al. 2000). The macrobenthic communities of the lower reaches are reflective of this lower variation, consisting of a more diverse array of species, including polychaetes, bivalves, and crustaceans, in addition to multiples species of oligochaetes. Watershed-scale differences in tidal creeks are generally a function of hydrology and pollutant loading, both of which are affected by proximity to the coastal ocean and the land use characteristics of the upland watershed (Lerberg et al. 2000; Mallin et al. 2001; Gawle 2002; Holland et al. 2004).

In order to assess anthropogenic effects on an ecosystem, one must be able to differentiate between changes in the macrobenthic community that are due to natural spatial and temporal variation from changes that are associated with anthropogenic stresses (Holland et al. 1977, 1987; Weisberg et al. 1997). In the southeastern U.S., there have been a variety of studies characterizing the macrobenthic community in relation to environmental conditions of tidal creeks and salt

marshes. Some studies have assessed the seasonal changes in the community (Cammen 1979; West 1985; Sanger 1998), whereas others were designed to assess spatial patterns occurring at a specific time of the year (Posey et al. 1995, 2002; Lerberg et al. 2000; Van Dolah et al. 2000; Gawle 2002). The within year differences in seasonal abundance of tidal creek macrobenthic communities (high abundance in the winter compared to the summer) are well documented (Sanger 1998; Gawle 2002; Holland et al. 2004). Less information was available for the magnitude of consecutive year-to-year variability of the macrobenthos in South Carolina tidal creeks and none of these existing studies investigated the short-term temporal variability in the oligochaete component of the tidal creek macrobenthic community.

Information about the month-to-month changes of an important component of tidal creek ecosystems will provide ecological information about how environmental changes influence the macrobenthic community by measuring the biotic and physical changes at a time scale more appropriate to the organisms than traditional annual monitoring studies have done. The primary goal of this research was to characterize monthly and interannual changes in the oligochaete community and identify the environmental factors potentially influencing oligochaete abundance in the two creeks being intensively studied by the South Carolina Sea Grant Consortium and National Oceanic and Atmospheric Administration's Land Use - Coastal Ecosystem Study program. A secondary goal was to characterize the entire macrobenthic community in the summer and winter to provide a context against which the month-to-month changes could be evaluated and related to previous studies.

## Materials and Methods

### STUDY AREA

Malind and Okatee Creeks are located in the Okatee River basin near Bluffton, South Carolina, USA (Fig. 1), and drained a combination of developed and forested uplands, as well as *Spartina alterniflora* and *Juncus roemerianus* salt marshes. Based on the 1999 U.S. Geological Survey (USGS) National Aerial Photography Program images, Malind Creek drained 1,030 ha of upland and salt marsh with approximately 5.6% of the watershed classified as impervious cover. Malind Creek's watershed was comprised of 83% forested land cover, 8.1% urban, 0.9% urban-associated water (retention and golf course ponds), and 1.3% creek and salt marsh land cover. Okatee Creek's 2,576-ha watershed was estimated to consist of 59.9% forest, 26.7% urban, 2.4% urban-associated water, and

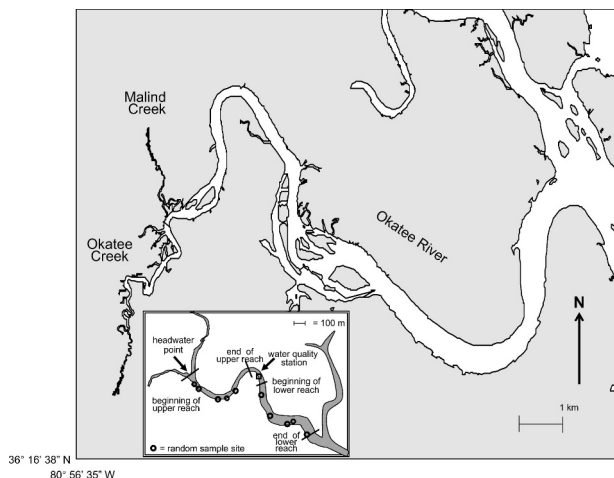


Fig. 1. A map of Okatee Creek and Malind Creek near Bluffton, South Carolina, USA. Inset, a schematic showing the sample design in a hypothetical creek. The creek is divided into two 750-m reaches, with a water quality station located between the two reaches. Five intertidal sampling sites were selected monthly in each reach at a random distance from the beginning of the reach and on a random side of the creek.

1.5% creek and salt marsh land cover. Eight percent of the non-salt marsh portion of the watershed was impervious cover. (Gillett et al. 2005). Both tidal creeks had approximately 3-m, semidiurnal tides with salinity and dissolved oxygen concentrations that fluctuated at diel and tidal cycles. Based upon the classification scheme of Lerberg et al. (2000) and Holland et al. (2004), the Okatee Creek watershed was classified as suburban and the Malind Creek watershed as forested.

Each creek was stratified into two 750-m reaches for sampling (Fig. 1). The upper reaches were approximately 1-m to 2-m wide from berm to berm, approximately 0.1-m deep at mean low water and  $\leq$  2-m deep at mean high water, and comprised of large amounts of intertidal habitat. The lower reaches were approximately 5-m to 6-m wide from berm to berm, approximately 0.5-m deep at mean low water and 3-m to 4-m deep at mean high water, and characterized by a persistent subtidal channel that was 2-m to 3-m wide at low tide.

#### SAMPLING

Approximately every 4 wk from January 2001 to January 2002, five intertidal sampling sites were selected within each reach at random distances from the beginning of the reach. Samples were collected on a random side of the creek at low tide at a point approximately 1.5 m below mean high tide to eliminate submersion bias within and among reaches. Samples were processed to determine benthic chlorophyll *a* (chl *a*) concentrations, pore-water ammonia concentrations, sediment composi-

tion, and the composition of the oligochaete assemblage or the entire macrobenthic community using the methods described below.

Benthic chl *a* samples were taken to a depth of 1 cm with a 38.5-mm<sup>2</sup> plastic core and placed on ice. Within 6 h, the cores were placed in 10 ml of 100% acetone in the dark, at 4°C for 24 h and agitated every 8 h. Samples were brought to room temperature, centrifuged for 2 min, and the chl *a* in the supernatant was measured with a UV-Vis spectrophotometer (Method 3.1 in Strickland and Parsons 1972).

Samples of surface sediment (upper 2–3 cm) were collected at each site and analyzed to determine percent water, percent silts and clays ( $<$  63  $\mu$ m), and percent sand ( $\geq$  63  $\mu$ m) using a modification of the pipette method (Plumb 1981), following Lerberg et al. (2000). Total organic carbon (TOC) content was measured for each sample by combustion of acidified and dried sediments in a CHN-S analyzer following Hedges and Stern (1984).

Two 11.9-cm<sup>2</sup> cores of sediment were collected from each site to a depth of 3 cm to determine porewater ammonia levels. Samples were kept on ice and processed within 6 h of collection. Each sample was homogenized, centrifuged, and the ammonia concentrations of the supernatant were measured using the salicylate-cyanurate colorimetric method (Hach Company 1994).

Samples for macrobenthos were collected to a depth of approximately 16 cm with a 45.6-cm<sup>2</sup> stainless steel core (Lerberg et al. 2000). The sample was sieved through a 500- $\mu$ m screen and the portion of the sample that remained on the screen was preserved in 10% sea water-buffered formalin with rose bengal stain. All organisms were separated from the detrital matter under magnification (3 $\times$ ) and the oligochaetes were counted and identified to the lowest possible taxonomic level. All macrobenthos in the February 2001, August 2001, and January 2002 samples were enumerated and identified to the lowest possible taxonomic level. One of every 10 benthic samples was re-processed by a South Carolina Department of Natural Resources benthic taxonomist. If the initial identification of a sample was not within 90% of the reprocessed value in terms of taxonomic composition and enumeration, all 10 samples were reidentified and recounted for the taxa in dispute.

The oligochaetes were identified based upon their body shape and setal structure, not their reproductive structures, due to the large number of worms collected and their varying levels of maturity. There was a degree of uncertainty about the identity of 564 specimens (6.7% of the oligochaetes) that had a similar setal structure and body shape to

*Tubificoides brownae* (Brinkhurst and Baker 1979), but could not be confidently identified as *T. brownae* using setal characteristics. These worms were classified as Tubificidae indeterminate (indet.).

Salinity, dissolved oxygen, pH, and water temperature, detailed in Gillett et al. (2005) and Buzzelli et al. (2007), were measured semicontinuously every 30 min at a site located between the upper and lower reaches of Malind and Okatee Creeks from January 2001 to January 2002. Daily rainfall data was also collected by the USGS at the mid-point water quality station (Buzzelli et al. 2007).

#### STATISTICAL ANALYSIS

SAS for Windows v 8.1 was used to evaluate the differences in benthic chl *a* concentration, porewater ammonia concentration, percent silts and clays, and percent TOC among month (January 2001–January 2002), creek (Malind or Okatee), and reach (upper or lower) using a 3-way analysis of variance (ANOVA; Littell et al. 1991). Many of the interaction terms in the chl *a* and ammonia models were significant, revealing a level of complexity that made clear interpretation very difficult. The creek effect in the ANOVA models for benthic chl *a* and porewater ammonia was not significant ( $p > 0.05$ ) and accounted for less than 1% of the variance, so the creek effect term was removed from the ANOVA models and the data for chl *a* and porewater ammonia were reanalyzed using a 2-way ANOVA with month and reach as treatment effects. These changes provided more interpretable results for both parameters, while preserving the terms of the model that contributed most of the variance.

The absolute abundance of the five most abundant oligochaete taxa and total oligochaete abundance were also analyzed using a 3-way ANOVA with month, creek, and reach as the treatment effects. The population data for the remaining five oligochaete taxa were not analyzed due to their infrequent collection (< 5% of samples) and low abundance (< 0.5% of total abundance). To provide some insight into the potential relationships between the measured sediment variables (benthic chl *a*, sediment composition, TOC, and porewater ammonia) and the five most abundant oligochaete taxa, Pearson's correlation coefficients were calculated between each taxon, the total abundance of those taxa, and the environmental variables over the 13-mo data set using SAS for Windows v 8.1.

Analyzing the abundance patterns of the whole macrobenthic community with only one summer sample and two winter samples from different years potentially confounds within year and among year sources of variance. The winter data were evaluated to compare year-to-year variance. For these analyses, the five most abundant oligochaete taxa and the

four other nonoligochaete taxa were analyzed using a 3-way ANOVA with year (2001 and 2002), creek (Malind and Okatee), and reach (upper and lower) as treatment variables. The remaining taxa were not evaluated due to their infrequent collection (< 30% of samples).

The entire macrobenthic communities (i.e., oligochaetes and all other taxa) of Malind and Okatee Creeks in the upper and lower reaches were compared using the following community-level metrics: Shannon-Weiner Diversity index (H), species richness (S), evenness (E), and dominance (relative abundance of the dominant taxon) using a 3-way ANOVA with creek, reach, and year as treatment variables.

All data were either  $\log_{10}(x+1)$  or arcsine-square root transformed as appropriate to obtain normality and homogeneity of variance of the model residuals. The least square means of all significant ( $\alpha = 0.05$ ) treatments and interaction terms in the 2-way and 3-way ANOVAs were compared to evaluate differences among the treatments (Littell et al. 1991). Least square means contrasts were considered significant at  $\alpha = 0.05$ .

## Results

### SEDIMENT CHARACTERISTICS

Benthic chl *a* concentration varied significantly among month ( $p < 0.0001$ ) and between reaches ( $p = 0.0001$ ) in the 2-way ANOVA (Table 1). Month-to-month differences accounted for 94% of the model variance, with the highest concentrations occurring in the cooler months and the lowest in the warmer months (Fig. 2). The upper reaches typically had greater chl *a* concentrations than the lower reaches. The reach effect accounted for only 6% of the chl *a* abundance pattern.

Porewater ammonia concentrations varied significantly from month to month and between reaches (both  $p < 0.0001$ ; Table 1). Ammonia concentrations were highest in the summer and autumn (Fig. 2), with month-to-month variation accounting for 69% of the variance in the 2-way ANOVA model. The reach effect accounted for 25% of the variance, with higher ammonia concentrations in the upper reaches than in the lower reaches. The month-reach interaction term was significant ( $p = 0.0183$ ), but accounted for only 6% of the variance. The low porewater ammonia concentrations in both reaches during the cooler months likely contributed to the month-reach interaction.

Sediments in Malind and Okatee creeks were predominantly mixed mud, with mean silt-clay values ranging from 50% to 80% (Fig. 2). Sediment from Okatee Creek had a higher silt-clay content than Malind Creek ( $p = 0.0475$ ), and the creek-to-

TABLE 1. ANOVA summary of the monthly benthic environmental characteristics collected from January 2001 to January 2002, with the parameter evaluated, the number of samples, the model  $r^2$  and probability of significance, the F-statistic and degrees of freedom (model, error), the probability of significance of each treatment variable, significant interaction terms, and least square means contrasts. The least square means variables are in order from largest to smallest and an underline indicates the treatments were not significantly different at  $\alpha = 0.05$ . Benthic chlorophyll  $a$  and porewater ammonia were analyzed with 2-way ANOVA and percent mud and percent total organic carbon were analyzed with 3-way ANOVA. M = month, C = creek, 1 = January 2001, 2 = February, .... 13 = January 2002, ML = Malind, OC = Okatee.

Parameter	n	$r^2/p$	F/df	Month	Creek	Reach	Interactions	Month Effect	Creek Effect	Reach Effect
2-way ANOVA										
Benthic chl $a$ ( $\text{mg m}^{-2}$ )	258	0.460 < 0.0001	16.02 13, 244	< 0.0001	—	0.0001	—	3 2 1 13 4 12 5 8 11 6 7 10 9	—	Up low
Log <sub>10</sub> porewater ammonia ( $\text{mg l}^{-1}$ )	258	0.635 < 0.0001	16.15 25, 232	< 0.0001	—	< 0.0001	M $\times$ R	8 9 7 10 6 5 4 11 12 3 2 13 1	—	Up low
3-way ANOVA										
Arcsine (sq rt) percent silts and clays	259	0.116 0.0058	2.29 14, 244	0.1362	0.0475	0.0013	—	12 9 3 6 7 5 13 8 10 11 2 4	OC ML	Low up
Percent total organic carbon	255	0.070 0.2085	1.30 14, 240	0.1216	0.8113	0.8636	—	9 12 6 1 3 7 5 2 13 11 8 10 4	ML OC	Low up

creek differences accounted for 33% of the model variance. The lower reaches of both creeks had sediments with higher silt-clay content than the upper reaches ( $p = 0.0013$ ) with the reach effect accounting for 12% of the model variance. The silt-clay content did not vary from month to month (Table 1). The TOC content of the sediments of Malind and Okatee Creeks was moderate, between 1.6% and 3.7% (Fig. 2). There were no statistical differences among months or between creeks and reaches for TOC values (Table 1).

#### OLIGOCHAETES

Between January 2001 and January 2002, 9,834 oligochaetes were collected in 260 samples. Ten taxa were collected, no one taxon occurred in every sample, and 7 samples did not contain any oligochaetes. The oligochaete communities of Malind and Okatee Creeks were similar in composition to those in the intensively studied tidal creeks within the Charleston Harbor Estuary (CHE; located along the central coast of the South Carolina), but the abundances of all the taxa were onefold to twofold greater in Malind and Okatee Creeks than in the CHE. The dominant oligochaete was the tubificid *Monopylephorus rubroniveus* (Levinsen 1884), which comprised 74.2% of the oligochaetes and occurred in 73.5% of the samples. The naid *Paranais litoralis* (Müller 1773) comprised 11% of the oligochaetes and occurred in 30% of the samples. Tubificidae indet. comprised 6.7% of the total oligochaete abundance and was found in 43.5% of the samples (Table 2). In the upper reaches of both creeks, the oligochaete assemblage was numerically dominated by *M. rubroniveus*. In the lower reaches of Malind Creek, *P. litoralis* numerically dominated the oligochaete assemblage in the winter months and Tubificidae indet. dominated during the rest of the year. Similarly in Okatee Creek, *P. litoralis* was the most abundant oligochaete in the winter, but with Tubificidae indet. and *M. rubroniveus* numerically dominant during spring, summer, and autumn.

Total oligochaete density varied from month to month ( $p < 0.0001$ ), between creeks ( $p = 0.0009$ ), and between reaches ( $p < 0.0001$ ). Differences between the upper and lower reaches accounted for 58% of the variance, monthly differences accounted for 33%, and the remaining variance (9%) was explained by differences between Malind and Okatee Creeks. Total oligochaete abundance was much greater in the winter months than in the summer months. The upper reaches had a greater number of oligochaete taxa than the lower reaches, and typically Okatee Creek had greater oligochaete densities than did the comparable reach in Malind Creek (Fig. 3).

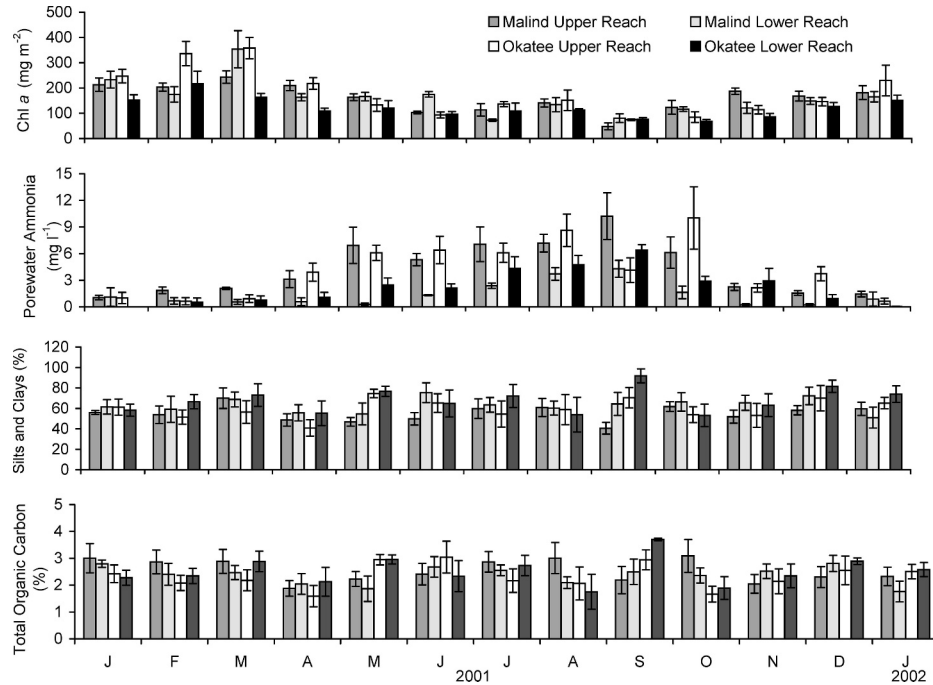


Fig. 2. Monthly means of sediment characteristics, benthic chlorophyll *a*, porewater ammonia, percent silts and clays, and total organic carbon in the upper and lower reaches of Malind and Okatee Creeks collected from January 2001 through January 2002. Error bars represent  $\pm 1$  SE.

The five most abundant oligochaetes were *M. rubroniveus*, *P. litoralis*, *Tubificoides heterochaetus* (Michaelson 1926), *T. brownae*, and Tubificidae indet. Significant monthly patterns in the abundance of each oligochaete taxon were observed (Table 3). The highest densities of all taxa, except for *T. heterochaetus*, were observed in the winter months, typically in February or March; the abundance of *T. heterochaetus* remained constant throughout the year (Fig. 3). Month-to-month differences explained most of the variation in the 3-way ANOVA models of *P. litoralis* (97%), *T. brownae* (83%), and Tubificidae indet. (85%). For these 3 taxa, there were no significant differences in abundance

TABLE 2. The relative abundance and frequency of occurrence of all oligochaetes collected from Malind and Okatee Creeks combined from January 2001 to January 2002.

	Percent Composition	Frequency of Occurrence
<i>Monopylephorus rubroniveus</i>	74.15	73.46
<i>Paranais litoralis</i>	10.99	30.00
Tubificidae indet.	6.66	43.46
<i>Tubificoides heterochaetus</i>	5.05	33.46
<i>Tubificoides brownae</i>	2.72	33.08
<i>Monopylephorus irroratus</i>	0.39	4.62
<i>Tubificoides wasseli</i>	0.02	0.77
Enchytraeidae	0.01	0.38
Naididae	0.01	0.38
<i>Nais elinguis</i>	0.01	0.38

between reaches or creeks, except for *P. litoralis*, which had greater abundance in Malind Creek compared to Okatee Creek (Table 3). Most of the variance for *M. rubroniveus* (73%) and *T. heterochaetus* (83%) was explained by the reach term, whereas the month-to-month and creek-to-creek effects were small ( $< 15\%$  of the variance). Abundance of *M. rubroniveus* and *T. heterochaetus* was much greater in the upper reaches of Malind and Okatee Creeks. The abundance of *M. rubroniveus* was also significantly higher in Okatee Creek compared to Malind Creek (Fig. 3).

There were significant ( $p < 0.05$ ), positive correlations between the abundance of *M. rubroniveus* ( $r = 0.297$ ), *P. litoralis* ( $r = 0.215$ ), and *T. brownae* ( $r = 0.130$ ) with benthic chl *a* concentration. *P. litoralis* abundance was negatively correlated with the concentration of porewater ammonia ( $p = 0.002$ ,  $r = -0.197$ ). There was a significant, negative correlation between the abundance of *T. heterochaetus* and the percent silt and clay in the sediment ( $p = 0.008$ ,  $r = -0.165$ ). None of the measured sediment variables were correlated with the abundance of Tubificidae indet. The sum total abundance of the 5 most abundant oligochaete taxa was only correlated with the concentration of benthic chl *a* ( $p < 0.0001$ ,  $r = 0.313$ ), similar to 3 of the component taxa.

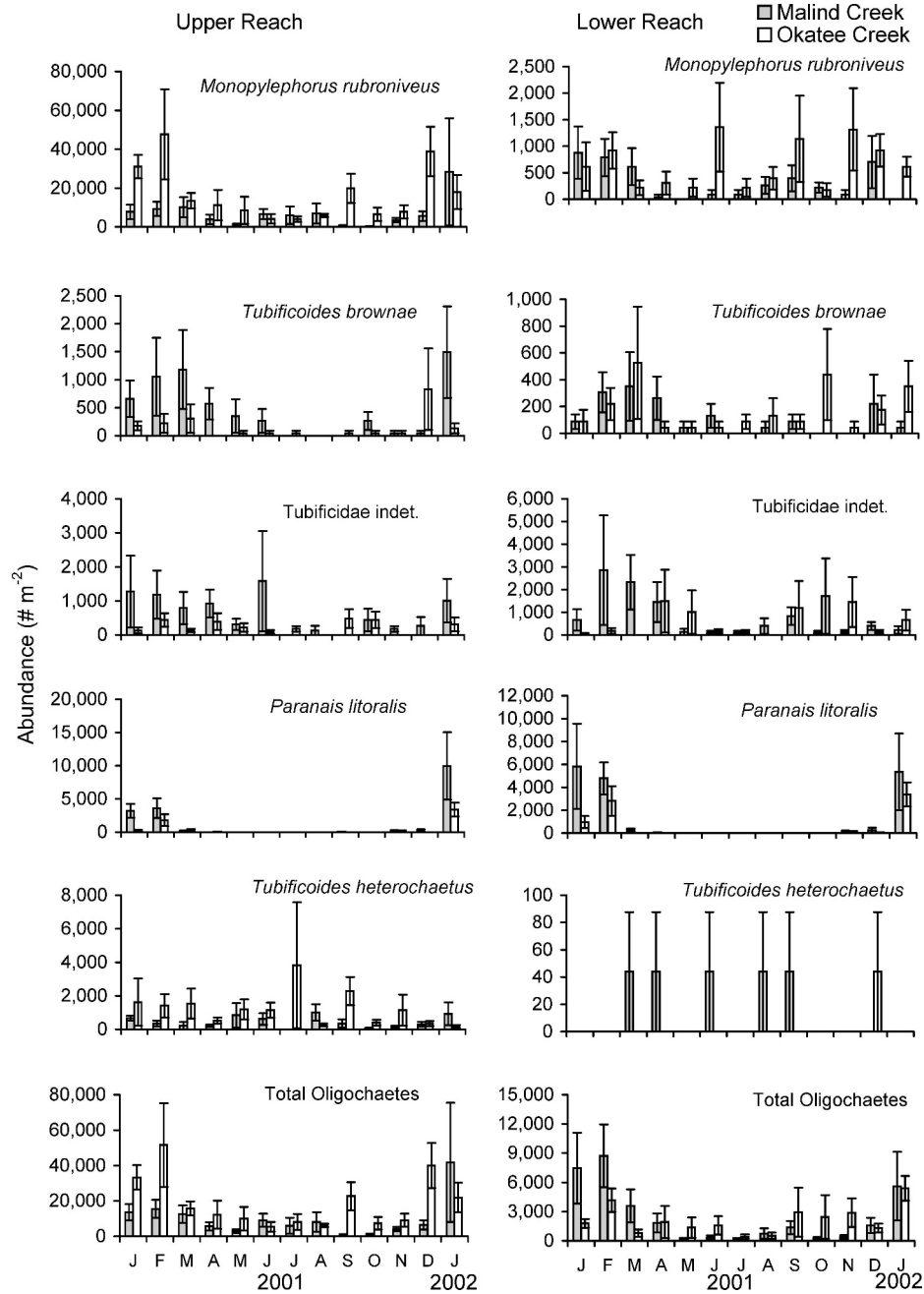


Fig. 3. Monthly mean abundance of the five most abundant oligochaetes and the sum of all oligochaetes in the upper and lower reaches of Malind and Okatee Creeks from January 2001 through January 2002; note the differing scales on the y-axes. Error bars represent  $\pm 1$  SE.

#### THE ENTIRE MACROBENTHIC COMMUNITY

For the three sampling dates that the entire macrobenthic community was evaluated (February 2001, August 2001, and January 2002), 41 taxa were identified. The whole community, like the oligochaetes, was similar in composition to those from creeks in CHE but abundance was greater for every

taxon in Malind and Okatee Creeks except for *Streblospio benedicti* (Webster 1879). Oligochaetes comprised 85.4% of the organisms collected, 13.7% were polychaetes, and 0.9% were other taxa, including nemertean, crustaceans, and bivalves provides a summary of the taxonomic data, including the absolute and relative abundance of each taxon by month, creek, and reach. Thirty-four taxa

TABLE 3. Summary of 3-way ANOVAs of the oligochaetes collected from January 2001 to January 2002, with the parameter evaluated, the number of samples, the model  $r^2$  and probability of significance, the F-statistic and degrees of freedom (model, error), the probability of significance of each treatment variable, significant interaction terms, and least square means contrasts. The least square means variables are in order from largest to smallest and an underline implies the treatments were not significantly different at  $\alpha = 0.05$ . M = month, C = creek, R = reach, 1 = January 2001, 2 = February ..., 13 = January 2002, Up = upper, Low = lower, ML = Malind, and OC = Okatee.

Parameter	n	$r^2/p$	F/df	Month	Creek	Reach	Interactions	Month Effect	Creek Effect	Reach Effect
$\text{Log}_{10}$ <i>Monopylephorus rubroniveus</i> (# m <sup>-2</sup> )	260	0.454 < 0.0001	14.59 14, 245	0.0032	< 0.0001	< 0.0001	—	2 12 1 3 8 11 6 9 13 10 7 4 5	OC ML	Up Low
$\text{Log}_{10}$ <i>Paranais litoralis</i> (# m <sup>-2</sup> )	260	0.680 < 0.0001	37.14 14, 245	< 0.0001	0.0010	0.0957	—	2 13 1 3 11 12 4 9 8 6 7 5 10	ML OC	Up Low
$\text{Log}_{10}$ <i>Tubificoides heterochaetus</i> (# m <sup>-2</sup> )	260	0.453 < 0.0001	13.49 15, 244	0.0336	0.0894	< 0.0001	C × R	9 6 8 4 1 2 12 5 3 13 11 10 7	OC ML	Up Low
$\text{Log}_{10}$ <i>Tubificoides brownae</i> (# m <sup>-2</sup> )	260	0.150 0.0003	2.88 15, 244	0.0007	0.3581	0.5065	C × R	2 3 13 1 4 12 10 5 6 9 7 11 8	ML OC	Up Low
$\text{Log}_{10}$ Tubificidae indet. (# m <sup>-2</sup> )	260	0.092 0.0417	1.78 14, 245	0.0526	0.0751	0.5062	—	2 4 3 13 9 10 1 5 6 11 12 7 8	ML OC	Up Low
$\text{Log}_{10}$ total Oligochaetes (# m <sup>-2</sup> )	260	0.370 < 0.0001	10.28 14, 245	< 0.0001	0.0009	< 0.0001	—	2 1 13 3 12 11 9 6 4 8 10 5 7	OC ML	Up Low

were collected from the lower reaches of Malind and Okatee Creeks, compared to only 25 from the upper reaches. Density was approximately 2.5 times greater in the upper reaches than in the lower reaches:  $8.8 \times 10^5$  ind m<sup>-2</sup> versus  $3.4 \times 10^5$  ind m<sup>-2</sup>. Figure 4 illustrates the complex changes in abundance that occurred between years, creeks, and reaches, as well as among seasons for 7 important macrobenthic organisms.

The results of the tests for differences in abundance of the 5 most abundant oligochaetes and 4 selected nonoligochaetes – *S. benedicti*, *Polydora cornuta* (Bosc 1802), *Neanthes succinea* (Frey and Leurkart 1847), and nemerteans – between years, creeks, and reaches are summarized in Table 4. Year-to-year differences were not significant for *P. litoralis*, *T. brownae*, and Tubificidae indet. There were significant differences in abundance of *M. rubroniveus* ( $p = 0.0325$ ), *S. benedicti* ( $p = 0.0008$ ), *P. cornuta* ( $p = 0.0240$ ), and *N. succinea* ( $p = 0.0316$ ) between years. Yearly differences accounted for 94% of the variance in the *S. benedicti* model and were the only significant effect. Year-to-year differences accounted for between 5% and 24% of the variance for *M. rubroniveus*, *P. cornuta*, and *N. succinea*. All of these species were more abundant in winter 2001 compared to winter 2002 (Fig. 4).

Creek differences were only significant for *M. rubroniveus* ( $p = 0.0046$ ) and nemerteans ( $p = 0.0015$ ) and accounted for 23% and 97% of the variance, respectively. *M. rubroniveus* was more abundant in Okatee Creek and nemerteans were more abundant in Malind Creek.

Of the macrobenthos analyzed, *M. rubroniveus* ( $p = 0.0001$ ), *T. heterochaetus* ( $p < 0.0001$ ), and *P. cornuta* ( $p = 0.0090$ ) had significant differences between reaches. Reach accounted for 47% of the variance for *M. rubroniveus* and 91% for *T. heterochaetus*. Both of the oligochaetes had greater abundance in the upper reaches compared to the lower reaches. *P. cornuta* had greater abundance in the lower reaches of Malind and Okatee Creeks compared to the upper reaches, which accounted for 32% of the variance in the 3-way ANOVA model. There were significant interactions in the *M. rubroniveus*, *P. cornuta*, and *N. succinea* models that accounted for 18%, 44%, and 69% of the variance, respectively (Table 4). These interactions illustrate the complexity of the year-to-year and spatial variation in the macrobenthic community.

Species diversity ( $H'$ ) values were moderately low, ranging between 0 and 2.9, with most samples having values between 1.0 and 2.5. Species richness ( $S$ ) ranged from 3 to 17 species, with a mean of 7.7 species per sample. The differences between creeks accounted for 52% of the variance in  $H'$ , and the

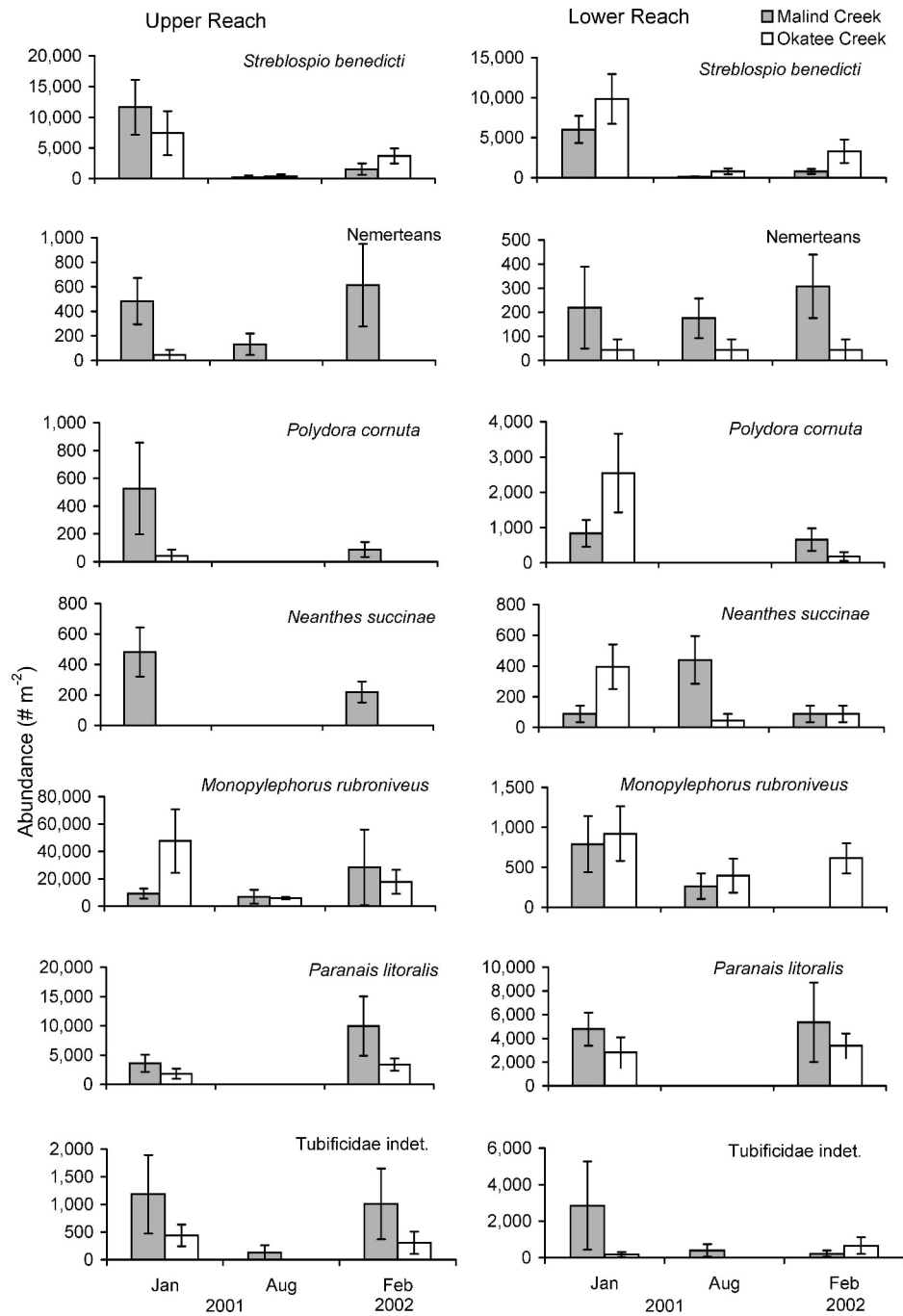


Fig. 4. Monthly mean abundance of the four most abundant nonoligochaete fauna and the three most abundant oligochaetes in the upper and lower reaches of Malind and Okatee Creeks collected in February 2001, August 2001, and January 2002; note the differing scales on the y-axes. Error bars represent  $\pm 1$  SE.

differences between years accounted for 71% of the variability in *S*. Dominance was generally greater than 40% and evenness (*E*) was typically greater than 0.5. Diversity was similar between years and reaches, but *H'* values were significantly higher in

Malind Creek compared to Okatee Creek ( $p = 0.0361$ ). *S* was greater in the winter of 2001 than 2002, but was similar between both reaches and creeks (Table 4). No differences in dominance or *E* values were found between years, creeks, or reaches.

TABLE 4. Summary of the 3-way ANOVAs of selected oligochaete, nonoligochaete taxa, and community metrics collected in February 2001 and January 2002, with the parameter evaluated, the number of samples, the model  $r^2$  and probability of significance, the F-statistic and degrees of freedom (model, error), the probability of significance of each treatment variable, significant interaction terms, and least square means contrasts. The least square mean variables are in order from largest to smallest and an underline indicates the treatments were not significantly different at  $\alpha = 0.05$ . Y = year, C = creek, R = reach, 2001 = February 2001, 2002 = January 2002, Up = upper, Low = lower, ML = Malind, and OC = Okatee.

Parameter	n	$r^2/p$	F/df	Year	Creek	Reach	Interactions	Year effect	Creek effect	Reach effect
$\log_{10}$ <i>Monopylephorus rubroniveus</i> (# m <sup>-2</sup> )	40	0.530 < 0.0001	9.87 4, 35	0.0325	0.0046	0.0001	Y × C	2001 2002	OC ML	Up Low
$\log_{10}$ <i>Paranais litoralis</i> (# m <sup>-2</sup> )	40	0.055 0.5599	0.70 3, 36	0.9421	0.3430	0.2880	—	2001 2002	ML OC	Up Low
$\log_{10}$ <i>Tubificoides heterochaetus</i> (# m <sup>-2</sup> )	40	0.508 < 0.0001	12.40 3, 36	0.1750	0.2636	< 0.0001	—	2001 2002	OC ML	Up Low
$\log_{10}$ <i>Tubificoides brownae</i> (# m <sup>-2</sup> )	40	0.014 0.9122	0.18 3, 36	0.7745	0.5264	0.8542	—	2001 2002	ML OC	Up Low
Tubificidae indet. (# m <sup>-2</sup> )	40	0.076 0.4111	0.98 3, 36	0.3579	0.1710	0.7166	—	2001 2002	ML OC	Low Up
<i>Streblospio benedicti</i> (# m <sup>-2</sup> )	40	0.281 0.0073	4.69 3, 36	0.0008	0.5476	0.5394	—	2001 2002	OC ML	Up Low
<i>Polydora cornuta</i> (# m <sup>-2</sup> )	40	0.432 0.0070	3.47 7, 32	0.0240	0.6099	0.009	Y × R	2001 2002	OC ML	Low Up
<i>Neanthes succinea</i> (# m <sup>-2</sup> )	40	0.398 0.0011	5.79 4, 35	0.0316	0.1300	0.8642	C × R	2001 2002	ML OC	Up Low
$\log_{10}$ Nemertean (# m <sup>-2</sup> )	40	0.253 0.0138	4.06 3, 36	0.8198	0.0015	0.6192	—	2001 2002	ML OC	Up Low
Shannon-Weiner Diversity (H')	40	0.202 0.0143	3.04 3, 36	0.128	0.0361	0.1706	—	2001 2002	ML OC	Low Up
Evenness (E)	40	0.088 0.3404	1.15 3, 36	0.8682	0.5137	0.0918	—	2002 2001	ML OC	Low Up
Species Richness (S)	40	0.256 0.0130	13.66 3, 36	0.0053	0.0752	0.6610	—	2001 2002	ML OC	Low Up
Percent Dominance	40	0.129 0.1696	1.77 3, 36	0.7502	0.1057	0.1252	—	2002 2001	OC ML	Up Low

## Discussion

Given their relatively sessile nature after settlement, the survival and reproduction of macrobenthic organisms are subject to the environmental changes occurring around them in the ecosystem. Changes in water quality, food availability, and predation pressure will alter the abundance and composition of the macrobenthic community, which is why they are so useful in monitoring of ecosystem health (Peterson et al. 1996; Weisberg et al. 1997; Van Dolah et al. 1999). Where longer-lived organisms provide an integration of the ecosystem environmental processes, shorter-lived organisms like oligochaetes provide a more rapid response to environmental changes. This type of responsive community dynamic may not provide valuable information in those systems where there is a degree of environmental stability, but they are important in systems like tidal creeks, where there are frequent changes in environmental conditions.

Over the 13 mo of this study, the macrobenthic community of Malind and Okatee Creeks were dominated by two species of oligochaetes (*M. rubroniveus* and *P. litoralis*) and, to a lesser degree, the spionid polychaete *S. benedicti*. Though a number

of other taxa were found in the creeks, those 3 species were always the most abundant. This same pattern has been observed in almost all of the tidal creeks that have been investigated in South Carolina: *M. rubroniveus* dominates the upper reaches of the creeks throughout the year and *P. litoralis* and *S. benedicti* dominate the lower reach communities in the winter and summer, respectively (Lerberg et al. 2000; Van Dolah et al. 2000; Holland et al. 2004). While these species are community dominants, they do not tell the whole story of changes in the tidal creeks. The other less abundant taxa still provide insight into the spatial and temporal changes that occur there.

## THE ENVIRONMENTAL SETTING

As the macrobenthic community data would imply, many of the temporal and spatial patterns in environmental characteristics observed in Malind and Okatee Creeks were similar to those reported from tidal creeks in the CHE (Lerberg et al. 2000; Holland et al. 2004). Fluctuations in water quality parameters (e.g., salinity, pH, dissolved oxygen) were much larger and the benthic chl *a* levels in Malind and Okatee Creeks were approximately

twice the amount found in CHE tidal creeks (Gawle 2002). These differences appear to have been a function of the physical attributes of Malind and Okatee creeks (i.e., size of the watershed, tidal range, proximity to the ocean; Buzzelli et al. 2007), compared to the tidal creeks of the CHE. These attributes affect nutrient input and flushing rate, and are possibly the cause of greater macrobenthic abundance in Malind and Okatee Creeks.

As was expected, the silt-clay composition of the sediments of Malind and Okatee Creeks did not appreciably change during the study and both creeks had silt-clay percentages similar to other forested and suburban tidal creeks in South Carolina (Lerberg 1997; Sanger 1998; Gawle 2002). The trend of more silts and clays in the lower reaches was also noted by Lerberg (1997) and is thought to be function of particle settling rate. The absence of detectable patterns in the temporal and spatial measures of TOC, similar to Sanger (1998), likely indicates a relatively constant input of refractory organic material from the uplands and salt marshes to the sediments of the creeks.

The annual pattern of high benthic chl *a* in the winter and early spring and low levels in the summer was related to increased turbidity (Gillett personal observation) combined with intense herbivory and bioturbation in the summer. This temporal pattern was similar to those observed in North Inlet, South Carolina (Pinckney and Zingmark 1993), and the most upstream sites of Ems Estuary, The Netherlands (de Jonge and Colijn 1994). The proximity to the uplands in the upper reaches of Malind and Okatee Creeks may have provided increased nutrient concentrations compared to the lower reaches, leading to higher levels of benthic chl *a* in the upper reaches compared to the lower reaches (e.g., McClelland and Valiela 1998; reviewed in Cahoon 1999; Posey et al. 2002). This, again, is in agreement with the patterns observed by de Jonge and Colijn (1994), who reported increasing chl *a* concentrations with increased proximity to uplands in the Ems Estuary. Microphytobenthic production was not measured and cannot be directly linked to oligochaetes in Malind and Okatee Creeks. The data in this study do show that the abundance of the dominant oligochaetes and benthic chl *a* followed similar spatial and temporal patterns, implying the importance of benthic primary production to the growth and reproduction of oligochaetes.

While there were not strong creek-to-creek differences in the sediment composition, chl *a*, or porewater ammonia, there were significant differences in the dissolved oxygen, pH, salinity range, and flushing rates between Malind and Okatee Creeks. These differences were a function of land

cover, watershed size, orientation, and rainfall characteristics between the two creeks. Compared to Okatee Creek, Malind Creek had a greater flushing rate, greater salinity fluctuation over a tidal cycle, greater frequency of hypoxia (< 5% air saturation), and a lower annual net ecosystem metabolism (Gillett et al. 2005; Buzzelli et al. 2007), which combined to create a more stressful environment in Malind Creek with less particulate organic matter as a food source to the benthos. These differences are most clearly reflected in the greater abundance of the community dominant *M. rubroniveus* in Okatee Creek compared to Malind Creek. Differential predation pressure could also be invoked to explain the differences in the abundance of oligochaetes between the creeks, but the abundance of benthivorous shrimp and fishes was greater in Okatee Creek than in Malind Creek during the summer and winter (Sanger unpublished data). The greater macrobenthic abundance in Okatee Creek in spite of the marked difference in predator abundance, strongly suggests that food supply and water quality had a greater effect on oligochaetes in these tidal creeks than predation pressure.

#### OLIGOCHAETES AND OTHER MACROBENTHOS

*Monopylephorus rubroniveus* is a eurytolerant oligochaete found throughout the world and is the numerically dominant macrobenthic organism in small tidal creeks in South Carolina (Milligan 1996; Lerberg et al. 2000; Gawle 2002). Beyond being the most abundant oligochaetes in Malind and Okatee Creeks, *M. rubroniveus* was also the most responsive organism to the environmental differences between the two creeks and throughout the year. The dominance of *M. rubroniveus* occurred because it has a competitive advantage over most macrobenthos in ecosystems that experience frequent hypoxia, with a lethal time 50 (LT<sub>50</sub>) in hypoxia (< 5% air saturation) greater than 11.5 d. *S. benedicti* and *P. litoralis* have an LT<sub>50</sub> of less than 1.8 d and 24 h, respectively (Llansó 1992; Calle Delgado 2006).

The lower abundance of *M. rubroniveus* in lower reaches of both creeks is indicative of reduced environmental stressors in the lower reaches (Lerberg et al. 2000; Van Dolah et al. 2000; Holland et al. 2004), which allows for greater abundance of other species of oligochaetes and polychaetes, especially *P. litoralis* and *S. benedicti*. These other annelids utilize the same food sources as, and possess a reproductive advantage over, *M. rubroniveus*. Typical of most estuarine tubificid oligochaetes, *M. rubroniveus* can only reproduce sexually and produces 6–8 embryos per cocoon, with 1–2 cocoons per mating (Stephenson 1972; Giere and Pfannkuche 1982; Gillett personal observation). *P.*

*litoralis* reproduces primarily via asexual paratomy creating a number of clones in a short time frame (18 times increase in 3 mo; Giere and Pfannkuche 1982), and *S. benedicti* produces a large number of offspring (20–130 larvae per individual; Levin 1984; Bridges and Heppell 1996).

Further contributing to the disparate dominance of *M. rubroniveus* in the upper reaches compared to the lower reaches, McCann and Levin (1989) demonstrated that juvenile *S. benedicti* growth and survivorship was negatively affected by the presence of the oligochaete *Monopylephorus evertus* at densities similar to the *M. rubroniveus* densities observed here. This would suggest that once a population of *M. rubroniveus* establishes itself at high densities, possibly during periods of hypoxia, it may be able to retain its dominance during times without hypoxic stress. Conversely, competition for food and limited recruitment may limit the abundance and dominance of *M. rubroniveus* in the lower reaches of tidal creeks.

The naid *P. litoralis* was the only nontubificid oligochaete collected in large numbers from Malind and Okatee Creeks. Nilsson et al. (1997) have suggested that temperatures above 25°C may be lethal to *P. litoralis* and that optimum growth of this oligochaete is 18°C or below. Mean daily water temperatures in Malind and Okatee Creeks were less than 20°C only from November through March (the only times when *P. litoralis* were found) and often in excess of 30°C during the other months of the year (Gillett et al. 2005). This pattern would strongly suggest that temperature plays an important role in limiting when *P. litoralis* can occur in tidal creeks. *P. litoralis* sensitivity to hypoxia and sulphides (Gamenick et al. 1996; Calle Delgado 2006) prevent it from burrowing deep into the sediment to escape predation like the other macrobenthos typically do, making it more vulnerable to migratory benthivorous nekton. The ability to reproduce asexually and sensitivity to high temperatures (Nilsson et al. 1997) and low dissolved oxygen (Calle Delgado 2006) accounted for the marked increases and declines in abundance observed through out the year. These traits also separate *P. litoralis* from the other oligochaetes typically found in the tidal creeks of South Carolina; *P. litoralis* are responsive to high levels of benthic primary production, but are unable to survive warm temperatures and periodic hypoxia.

The water quality, and possibly predation, impart a strong seasonal dynamic in *P. litoralis* abundance in Malind and Okatee Creeks that has also been found in similar forested and suburban creeks in South Carolina (Sanger 1998; Gawle 2002). The pattern of high abundance for a few months followed by complete absence has also been

reported for *P. litoralis* and other naid oligochaetes in the northeast U.S. and the Baltic Sea (Giere and Pfannkuche 1982; Cheng et al. 1993; Gamenick et al. 1996). In these areas, high densities of *P. litoralis* were observed in the spring or early summer and sometimes in the autumn, with low abundance or absence in the late summer and winter. The temporal abundance patterns appear to be the same as in South Carolina, though temporally shifted because of latitudinal differences in temperature distributions.

The oligochaetes designated as Tubificidae indet. offer an example of the problem associated with lumping two or more species into one taxon, as often happens with oligochaetes. These worms were a mix of tubificid species that could not be consistently distinguished by their setal characteristics alone (Lerberg personal communication). While Tubificidae indet. was a substantial portion of the macrobenthic community in Malind and Okatee Creeks, there were no statistically significant spatial or temporal trends in abundance as seen in the other oligochaetes. The authors believe that the lack of pattern was in part due to the polyphyletic nature of the classification, wherein species-specific distribution patterns obscured each other when analyzed together. Without the ability to distinguish the patterns in abundance at the species level, it is impossible to determine if Tubificidae indet. were relatively tolerant of the physical conditions in the tidal creeks, maintaining a constant level of abundance while the other species fluctuated around them, or if the component species of Tubificidae indet. respond in inverse ways, canceling each other out when they were analyzed together.

*T. heterochaetus* is an estuarine species typically associated with sandy to mixed sediments and sites that either consistently have low salinity or large daily salinity fluctuations (Diaz 1980; Milligan 1996; Lerberg 1997; Seys et al. 1999). *T. heterochaetus* was found almost exclusively in the upper reaches of the creeks, indicating the fluctuation of saline estuarine water at flood tide and low salinity runoff and groundwater at ebb tide. The monthly abundance patterns of *T. heterochaetus* were unique compared to the other oligochaete taxa: remaining relatively constant year-round, even through the summer when abundance of the other oligochaetes was low. The absence of large changes in abundance are indicative of either life history differences or stressor avoidance or tolerance in *T. heterochaetus* compared to the other oligochaetes typically found in tidal creeks. The majority of reproductive *T. heterochaetus* were observed in May and July whereas the reproductive individuals of the other taxa were most commonly observed during autumn and winter. This would indicate that the recruitment of

*T. heterochaetus* occurs primarily in the summer, offsetting mortality losses due to spring-summer predation that were observed in most of the other species. The affinity of *T. heterochaetus* for low salinity waters in the upper most reaches of the tidal creeks also may provide some protection from estuarine predators.

*T. brownae* is a cosmopolitan species found in coastal areas throughout the world (Milligan 1996), though it was not very abundant in Malind and Okatee Creeks. Spatially, the monthly abundance pattern was similar to that of most other oligochaetes found in Malind and Okatee Creeks, indicating an affinity for periods of high benthic chlorophyll. The abundance of *T. brownae* populations are limited in the upper reaches of Malind and Okatee Creeks, because of its sensitivity to hypoxia (Gillett personal observation), while it is likely restricted in the lower reaches by low fecundity problems of the other tubificid oligochaetes. As such, *T. brownae* has the limitations but none of the advantages of *M. rubroniveus* and never reached high abundances in most South Carolina tidal creeks.

Of the other species of oligochaetes collected, *Monopylephorus irroratus* and *Tubificoides wasseli* are rare species in the intertidal portions of South Carolina tidal creeks (Sanger 1998; Lerberg et al. 2000; Gawle 2002). *M. irroratus* is more abundant in subtidal creek habitats and on the surface of the salt marsh; *T. wasseli* is more abundant in the subtidal portions of tidal creeks and deeper water sites (e.g., Sanger 1998; Van Dolah et al. 2000). The naid oligochaete *Nais elinguis* (Muller 1773) was only observed once, and while commonly found around the world in freshwater, tidal freshwater, and sometimes in brackish environments, it is rarely observed in higher salinity waters like tidal creeks and was probably nothing more than an anomaly (Brinkhurst 1982; Verdonshot 1999).

The spionid *S. benedicti* was the most abundant polychaete found in this study. *S. benedicti* is important to the tidal creek ecosystems of the southeast because it is larger than *M. rubroniveus* and it dominates the macrobenthic community in the lower reaches where *M. rubroniveus* is not as abundant. As such, it likely provides an important route for benthic-pelagic coupling and secondary production (Posey et al. 1995, 2002; Lerberg et al. 2000). In the upper reaches, its intolerance to hypoxia and the negative effects that high densities of oligochaetes are reported to have on *S. benedicti* growth and reproduction appear to limit its abundance despite the rich food sources (McCann and Levin 1989; Llansó 1992; Calle Delgado 2006), relegating it to the lower reaches of Malind and Okatee Creeks. *S. benedicti* displayed a similar seasonal pattern of abundance in Malind and

Okatee Creeks as in other small creeks of South Carolina, with considerably higher abundance in the winter compared to the summer.

Though it was the second most abundant non-oligochaete present, the abundance of the spionid polychaete *P. cornuta* was small (0.96% of total macrobenthic abundance) in comparison to the three dominant species (*M. rubroniveus*, *S. benedicti*, and *P. littoralis*). *P. cornuta* probably has only a minor ecological role in the tidal creek macrobenthic community, filling a similar ecological niche to *S. benedicti* (i.e., a tube building facultative filter-deposit feeder), though *S. benedicti* appears better adapted to, and more abundant in, intertidal creek habitats.

The final two macrobenthic organisms of note that were collected in the seasonal sampling of Malind and Okatee Creeks were *N. succinea* and nemerteans, neither of which displayed significant seasonal patterns in abundance. As mentioned above, the seasonal abundance patterns that were observed in the other macrobenthic taxa were probably a response to predation, temperature distributions, and hypoxic stress. Nemerteans and *N. succinea* are larger and more mobile than the other macrobenthic taxa in Okatee and Malind Creeks. These traits may explain their consistent, albeit low, abundances. Mobility allows an escape from hypoxia and rapid growth to a large size may have provided a refuge from predation by shrimp, though both of these characteristics probably made them a more desirable prey item for larger, visual predators like fish. Again, like *P. cornuta*, these organisms are common estuarine inhabitants that did not appear to be very responsive to environmental conditions in tidal creeks.

## Conclusions

The results of this study demonstrate the importance of understanding the intraannual variability of the macrobenthic community when interpreting the influences of physical and biological characteristics of an ecosystem, especially one with communities dominated by environmentally responsive organisms with a rapid turnover time like oligochaetes. These spatial and temporal changes are easily overlooked if one constrains the observation of the community to a single month or season within a year, as typically done in most benthic monitoring programs. Looking at fine-scale temporal changes in the oligochaete community would suggest that monitoring of seasonal or quarterly time scales may be more appropriate in systems dominated by oligochaetes, though the appropriate sampling scheme will depend upon the environmental parameters or stressors in which one is interested (Gawle 2002; Holland et al. 2004).

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