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Niche overlap of benthic macrofauna in a tropical estuary: diurnal variation

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Abstract: The complexity of estuaries allows for the establishment of diverse communities composed of species with different survival strategies. The vertical migration of animals in the sediment is linked to competition, escape from predators and adaptations to diurnal physio-chemical changes related to variations in water levels. The present study aimed to evaluate niche overlap and amplitude, as well as the composition and structure, of communities of polychaetes and molluscs between sediment aliquots during the day and at night. Data sampling was performed in the Tubarão River estuary. The highest individual occurrence was registered during the diurnal period. Communities of polychaetes varied significantly between sediment aliquots during the day and at night, while molluscs did not show diurnal variation. Niche overlap results for polychaetes showed higher values between aliquots during the night, while molluscs showed greater overlap during the day. This indicates that polychaetes and molluscs have different mechanisms of coexistence. This may be related to different attributes of species allowing for the division of resources among individuals. Examination of niche overlap provides insights into coexistence of mechanisms within benthic macroinvertebrate communities.

Keywords: Coexistence, hypersaline estuary, vertical migration, Mollusca, Polychaeta.
INTRODUCTION

Estuaries are considered highly productive, complex and heterogeneous ecosystems that depend on these habitats for feeding, reproduction, colonization, and protection against predators (Elliot & MCluscky 2002; Kennish 2002; Kaiser et al. 2005; Vasconcelos et al. 2007; Potter et al. 2010). Estuarine dynamics are influenced by seasonal, monthly & daily variations, and consequently the concentrations of organic matter, nutrients, and water level can oscillate during these periods (Dyer 1979). These variations come from chemical, physical and biological alterations, causing changes at spatial and temporal scales in the functioning of biological communities (Officer & Lynch 1981; Day et al. 2012; Medeiros et al. 2016).

Among the communities that inhabit estuarine ecosystems, benthic macroinvertebrates, mainly represented by Polychaeta and Mollusca, have important roles in the decomposition of organic matter, nutrient cycles, and energy fluxes (Nunes et al. 2008; Wildsmith et al. 2011; Tweedley et al. 2012). Benthic macroinvertebrates can migrate vertically within the sediment according to spatial and temporal scales, reacting to the variations of environmental conditions (Cardoso et al. 2010). Thus, vertical migration of organisms in the sediment can occur in function of their tolerance to limiting factors (e.g., light availability), life strategy (e.g., protection against predators) or feeding habits (Cardoso et al. 2010). This locomotive ability is related to the presence of determined functional traits of each species (e.g., related to feeding category, larvae development and body size) (Esselink & Zwarts 1989; Cruz-Motta 2005; Persson & Svensson 2006).

It has been observed in the sand/mudflats of estuaries, that the vertical locomotion of invertebrates is influenced according to light availability or tide cycle (Yannicelli et al. 2001). In this case, the pattern of vertical migration in relation to tide cycles, determines the density of macrofauna in the sediment as a form to escape adverse conditions. That is, during low tide, organisms can migrate to protect themselves from predators, while during higher tides, organisms, when moving vertically, can maximize foraging opportunities (Cardoso et al. 2010). Diurnal changes also generate vertical migration, regulated according to light availability, that alter the visibility, and consequently influence organisms’ survival in the presence of predators (Estlander et al. 2017). In addition, vertical migrations can also be enhanced when the organisms of a community share the same functional categories, this can result in greater niche overlap causing the development of strategies which, consequently, results in the use of different resources and organism coexistence (Silva-Camacho et al. 2017).

Hypervolume niche concept was stated by Hutchinson (1957) who considered a niche as multidimensional space in which species might be established in accordance with their demands relative to abiotic factors and resources. Abiotic factors limit species distribution through their physiological tolerance and space and food as resources limited through competition among species when they are scarce (Kraft et al. 2015). Some strategies developed by species viewing coexistence are: the species may use their resources differently in spatial and temporal scales (Devictor et al. 2010) or functional traits of species (Violle 2007) which allow them to explore a wider range or to specialize in a narrow range of resources (Devictor et al. 2010). In this way, these strategies are not only important to understand the mechanism underlying community assembly processes but also to understand how the complexity of species interactions influence their occurrence and their environment defining ecosystem functioning (Dehling & Stouffer 2018).

Researchers have used different parameters related to species’ niches, such as amplitude and niche overlap, associated with other parameters of functional traits that can aid in the understanding of species coexistence. However, the understanding of how benthic macrofauna species utilize their habitat resources in relation to vertical distribution, according to light availability (diurnal variation), has been neglected. Understanding the pattern of vertical distribution of species in the sediments of tropical estuaries and coexistence strategies of benthic macrofauna, is a key factor in describing the importance of these organisms in the maintenance of ecosystem functions. As such, the aim of this study was to evaluate amplitude and niche overlap, as well as the composition and structure of polychaete and mollusc communities between sediment aliquots during day and night periods. The questions that directed this study were: i) are there differences in the composition and taxonomic structure of polychaete and mollusc communities when comparing sediment aliquots analyzed during the day and night? and ii) does niche overlap and the overlap of polychaete and mollusc functional trophic groups occur, when comparing the sediment aliquots during day and night?
MATERIAL AND METHODS

Study area
The Tubarão River is located in the semiarid coast of the state of Rio Grande do Norte, northeastern Brazil (-5.09361111, -36.53916667) (Figure 1), inserted on the limits of the Sustainable Development Reserve of Ponta do Tubarão, a protected area with sustainable use administered by the state government. The Tubarão River is an estuarine system which extends a distance of 10 km, presents preserved mangrove vegetation and its surroundings have a variety of ecosystems such as marshes, Caatinga vegetation and dunes (Dias et al. 2007). Based on the precipitation standards, the climate of the region is characterized by higher evaporation rates and a lower pluviometric index with the rainy season occurring between February and May and the dry season occurring between June and January (INMET 2017). Additionally, the freshwater input comes from subterranean waters and from the lower precipitation of the region (Queiroz & Dias 2014, Medeiros et al. 2016).

The average rainfall between January and June is 161 mm (INMET 2010, 2017).

This study was performed throughout the estuary, where we defined three zones: upstream, intermediate and downstream. The sampling was carried out covering all the variation of the environmental variables of the estuarine ecosystem, from the continental drainage to the sea (Figure 1). The upstream zone presents lower profundity and higher evaporation rates with salinity varying between 30 and 50 and the predominant substrate is sandy and muddy. The intermediate zone presents salinity between 32 and 45, with muddy substrates. The downstream zone is located near the sea, with salinity between 35 and 45, and the predominant substrate is sandy with an abundance of gravel (Sales et al. 2016).

Sampling procedures
Samples were collected in May 2017, during the rainy season. In each zone (upstream, intermediate, and downstream) three sampling points were determined,
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totaling nine points across the estuary. The benthic macrofauna was sampled once during the day and at night, utilizing a PVC cylindrical core (16.67 cm²). The core was buried in the substrate (profoundity 10 cm) and posteriorly the sediment was partitioned in two aliquots: A1 (0 to 5 cm) and A2 (5 to 10 cm). The interval between diurnal and nocturnal sampling was 12 hours. The benthic macroinvertebrates were sampled in the intertidal region, always during low tide. The samples were washed in a 500 micro mesh sieve for the separation of benthic macrofauna. Organisms were preserved in 70% alcohol.

Laboratory procedures

In the laboratory, the organisms were separated and identified to the lowest possible taxonomic level with specialized keys for Polychaeta (Amaral & Nonato 1996; Amaral et al. 2006), and a specialized bibliography for Mollusca (Rios 2009; Tunnel Jr. et al. 2010). In addition, the Conquiliologistas site of Brazil was consulted (www.conchasbrasil.org.br) and the nomenclature followed the database Malacolog 4.1.1 (Rosenberg 2009).

Measurement of niche breadth and overlap

Niche breadth and overlap analyses were performed to quantify how many species and functional guilds partitioned the spaces as resource between aliquots. The Morisita simplified index (Krebs 1989) was calculated to analyze the niche overlap of the functional trophic groups of polychaetes and molluscs between day and night aliquots based on abundance data. The index value varies from zero to one: when the index is zero or close to zero, the overlap is low or absent, while when equal to or close to one, the niche overlap is high or total. To analyze the taxonomic niche breadth and functional trophic amplitude of polychaetes and molluscs groups, the Shannon-Wiener (H') diversity index was used based on abundance data (Shannon & Weaver 1949), which corresponds to the niche breadth, considered high when close to one. These analyses were carried out in the “spaa” package, in the statistical software program R 1.9.0 (R Development Core Team 2017).

Composition and taxonomic structure

For the analysis of the composition and taxonomic structure of polychaetes and molluscs communities, species richness was analyzed using the Shannon-Wiener (H') index and Pielou (J') equitability. Species richness reflects the number of different species in an area, while the Shannon-Wiener index considers the richness and species equitability, both abundant and rare (Shannon & Weaver 1949). The Pielou (J') equitability index reflects the uniformity and species' distribution (Pielou 1966).

Functional trophic guilds

Macrofauna benthic taxa were classified within functional trophic guilds according to the food resources consumed, based not only on the type of resource, but also on the morphological and behavioral mechanisms of acquisition, following Fauchald & Jumars (1979) and Muniz & Pires (1999) for polychaetes and Linden et al. (2017), Mikkelsen & Bieler (2008) and Rosenberg et al. (2009) for molluscs (Table 1). Five guilds were considered for polychaetes: Carnivore (Car), Deposit feeder: digger (DC) e Deposit feeder: surface (DS), Filter feeder (Fil), Omnivore (Omn), while six guilds were considered for molluscs: Carnivore, Filter feeder, Herbivore (Her), Omnivore, Scavenger (Sce), and Suspension feeder (Sus). Functional trophic guilds were chosen as they reflect the distribution of resources in the ecosystem, the mechanism of adaptation and coexistence of species, in addition to influencing ecosystem processes, such as energy flow and nutrient cycle (Pearson & Rosenberg 1978; Dolbeth et al. 2015).

Table 1. Functional trophic guilds of polychaetes and molluscs and their importance in demonstrating the relationships of organisms with the ecosystem.

| Functional trophic guilds | Rationale |
|--------------------------|-----------|
| Carnivore                | Reflects the distribution of resources in the ecosystem and the adaptation of the species to the habitat. As well as influencing ecosystem processes such as energy flux and nutrient cycling (Pearson & Rosenberg 1978; Dolbeth et al. 2015). |
| Deposit feeder: digger   |           |
| Deposit feeder: surface  |           |
| Filter feeder            |           |
| Herbivore                |           |
| Omnivore                 |           |
| Scavenger                |           |
| Suspension feeder        |           |

Data analyzes

To test the differences in the taxonomic composition and trophic guilds of polychaetes and molluscs between the sediment aliquots during the day and night, a Permutational Multivariate Analysis of Variance (PERMANOVA) (with 9999 permutations, p ≤0.05) was performed, considering a factor (aliquots) with two fixed levels (A1 and A2) for day and night. For this, the abundance data was transformed into square
root values and a Bray-Curtis matrix was utilized as a dissimilarity measurement. To verify differences in the taxonomic structure of the polychaetes and molluscs between sediment aliquots during the day and night, analyses of univariate significance were applied to species richness, Shannon-Wiener index, and Pielou equitability, considering a factor (aliquots) with two fixed levels (A1 and A2) for day and night (PERMANOVA; 9999 permutations; \( p \leq 0.05 \)). For this analysis the coefficient of euclidean distance was utilized as a measure of dissimilarity. All the analyses were performed using the statistical software PRIMER-6 + PERMANOVA (Anderson et al. 2008).

**RESULTS**

Composition and taxonomic structure of polychaete and mollusc communities

A total of 1,329 individuals were captured and distributed across 19 and 21 polychaete and mollusc taxa, respectively (Supplementary material: T1; Figure 2). The highest individual occurrences (705) were captured with higher abundances registered in aliquot A1 for the polychaetes Cirratulidae (28%), Spionidae (25%), capitellidae (12%), and the bivalve Anomalocardia flexuosa (11%), while the polychaetes Orininiidae (20%), Amphiaretidiae (15%), and the bivalve A. flexuosa (10%) had the highest abundances in aliquot A2 (Figure 2). During the night, 624 individuals were captured with higher abundances registered in aliquot A1 for the polychaetes Cirratulidae (28%), spionidae (8%), and the bivalve A. flexuosa (8%). In aliquot A2, the polychaetes Cerratulidae (25%) and bivalves A. flexuosa (17%) & Phacoidea pectinatus (15%) were most abundant (Figure 2).

PERMANOVA results show that the polychaetes group varied significantly between the sediment aliquots during the day (Pseudo-\( F_{1,37} = 2.3226; p = 0.027 \)) as well as during the night (Pseudo-\( F_{1,41} = 2.8135; p = 0.007 \)). The molluscs did not present variation between the day and night sediment aliquots, (day: Pseudo-\( F_{1,37} = 1.4734; p = 0.21 \); night: Pseudo-\( F_{1,37} = 1.9075; p = 0.079 \)). The species richness, Shannon-Wiener index, and Pielou equitability varied significantly between sediment aliquots during the day and night for polychaetes and molluscs (Table 2).

Overlap and breadth of polychaetes and molluscs taxonomic niches

Overlap results showed higher values between the aliquots for polychaetes during the night and molluscs during the day (Table 3). For polychaetes niche breadth, the taxa Orininiidae, Amphiaretidiae, Pilargidae, and Onuphidiae were found to exhibit higher values when comparing day aliquots, while Amphiaretidiae, Pilargidae, Onuphidiae, Dorvilleidae, and Nereidiae demonstrated higher values at night (Table 3). The molluscs, Veneridae sp., A. succinea, and Macoma sp.1, exhibited higher niche breadths during the day and P. pectinatus, B. varium, C. cariabae, S. fragilis at night (Table 3).

Overlap and breadth of functional trophic guilds

The functional trophic guilds of polychaetes that obtained higher proportions were Deposit feeder: digger, Deposit feeder: surface, Carnivore and Filter feeder, while for molluscs, the abundant guilds were Filter feeder, Suspension feeder, and Scavenger (Figure 3). For the polychaetes community, the guilds Deposit feeder: digger (42%), Carnivore (24%), and Deposit feeder: surface (21%) were most abundant in aliquot A1, while Deposit feeder: digger (44%), Deposit feeder: surface (33%) and filter feeder (11%) were most abundant in aliquot A2 during the day. During the night, Deposit feeder: digger (50%), Carnivore (18%), Deposit feeder: surface (15%) and filter feeder (14%) presented higher abundance proportions in aliquot A1, and Deposit feeder: digger (49%), Carnivore (27%), Deposit feeder: surface (18%) in aliquot A2. Significant differences in the abundance of trophic guilds were observed only between day and night periods for Molluscs (Pseudo-\( F_{1,68} = 4.05; p = 0.0513 \)) and between aliquots for polychaetes (Pseudo-\( F_{1,76} = 2.98; p = 0.0368 \)).

The functional trophic groups of polychaetes, Carnivore, Deposit feeder: surface and Omnivore exhibited higher breadth during the night while Filter feeder were more representative during the day (Table 4). For the molluscs, the only functional trophic group with higher amplitude was Suspension feeder for both day and night periods (Table 4).

**DISCUSSION**

The macrobenthic community of the Tubarão River varied quantitatively and qualitatively between day and night periods, exhibiting a pattern of vertical distribution in the sediment, possibly determined by ecological preferences and as a result of the interactions between species throughout the estuary which was corroborated with Hutchinson’s niche concept (Hutchinson 1957) who stated that a combination of abiotic and biotic factors
Figure 2. Abundance (%) of polychaetes and molluscs taxa in aliquots during the diurnal and nocturnal periods in the Tubarão River estuary, Macau-RN, northeastern Brazil. The box sizes are determined by the abundance of taxa.
influence species occurrences in given habitats relative to their preferences. These results are an important contribution to understanding how macrobenthic communities interact with each other and select their preferential habitats in tropical estuaries. Other studies (e.g., Poole & Stewart 1976) have demonstrated that variation in benthic macroinvertebrates communities exists in function of sediment profundity, which corroborates our results. A study conducted in an estuary of Portugal found that the vertical migration patterns of macroinvertebrates depend mainly on the size and feeding behavior of individuals (Cardoso et al. 2010).

Over short time-scales, individuals can move within sediments as a result of feeding behavior or to escape from predators (Goeij et al. 2001; Person & Svensson 2006). This may be the reason why the polychaete and mollusc presented functional and taxonomic differences between sediment aliquots. Vertical migration behavior can also be observed in other communities, such as zooplankton, which migrate from the water column to submerged macrophytes, avoiding open water predators (Sagrario & Balseiro 2010). Our results showed that polychaetes and molluscs had a greater abundance in aliquot A2 at night when compared to the day period. This result may be related to a survival strategy used by these taxonomic groups to escape from predators (e.g., fish) at night. In contrast, the considerable increase in nocturnal carnivorous polychaetes may be related to feeding behavior and food availability for these species at night. Other factors that can generate vertical migration are reproductive processes that occur mainly during

Table 2. PERMANOVA values for the taxonomic diversity of polychaetes and molluscs between day and night sediment aliquots (A1 e A2), in the Tubarão River estuary, Macau-RN, northeastern Brazil.

| Polychaeta | Day (A1xA2) | Night (A1xA2) |
|------------|-------------|---------------|
| Df | SS | MS | Pseudo-F | P(perm) | Df | SS | MS | Pseudo-F | P(perm) |
| Richness | 1 | 156.06 | 156.06 | 39.373 | 0.0001 | 1 | 110.01 | 110.01 | 32.225 | 0.0001 |
| Shannon-Wiener | 1 | 10.542 | 10.542 | 44.901 | 0.0001 | 1 | 8.0869 | 8.0869 | 28.991 | 0.0001 |
| Pielou | 1 | 4.2535 | 4.2535 | 38.865 | 0.0001 | 1 | 1.9306 | 1.9306 | 12.44 | 0.001 |

| Mollusca | Day (A1xA2) | Night (A1xA2) |
|----------|-------------|---------------|
| Df | SS | MS | Pseudo-F | P(perm) | Df | SS | MS | Pseudo-F | P(perm) |
| Richness | 1 | 39.014 | 39.014 | 29.061 | 0.0001 | 1 | 66.125 | 66.125 | 15.651 | 0.0001 |
| Shannon-Wiener | 1 | 4.7689 | 4.7689 | 33.107 | 0.0001 | 1 | 3.9247 | 3.9247 | 16.981 | 0.0002 |
| Pielou | 1 | 2.6835 | 2.6835 | 22.399 | 0.0001 | 1 | 1.9569 | 1.9569 | 15.462 | 0.0004 |

Table 3. Results of the niche overlap of polychaetes and molluscs abundance between day and night periods in the Tubarão River estuary, Macau-RN, northeastern Brazil.

| Niche overlap/ Taxonomic Niche breadth | Polychaeta | Day | Night |
|---------------------------------------|------------|-----|-------|
| A1 vs. A2 | 0.47 | 0.88 |
| Orbiniidae | 0.47 | 0.17 |
| Ampharetidae | 0.47 | 0.57 |
| Pilidae | 0.51 | 0.56 |
| Onuphidae | 0.45 | 0.56 |
| Dorvilleidae | - | 0.63 |
| Nereididae | 0.11 | 0.48 |
| Cirratulidae | 0.03 | 0.37 |
| Gonadidae | - | 0.21 |
| Capitellidae | 0.19 | 0.28 |
| Spionidae | 0.20 | 0.10 |
| Syllidae | - | 0.24 |

| Niche overlap/ Taxonomic Niche breadth | Mollusca | Day | Night |
|---------------------------------------|----------|-----|-------|
| A1 vs. A2 | 0.81 | 0.61 |
| A. flexuosa | 0.20 | 0.54 |
| Macomosp.1 | 0.29 | 0.17 |
| P. pectinatus | 0.27 | 0.68 |
| B. varium | - | 0.63 |
| Veneridae sp. | 0.33 | - |
| A. succinea | 0.32 | - |
| C. cariabaea | - | 0.63 |
| S. fragilis | - | 0.63 |
| Macomosp.2 | - | 0.56 |
| B. striata | - | - |
Table 4. Overlap of polychaetes and molluscs functional trophic groups between day and night periods in the Tubarão River estuary, Macau-RN, northeastern Brazil.

| Functional overlap       | Polychaeta     | Day | Night |
|--------------------------|----------------|-----|-------|
| Deposit feeder: digger   | 0.20           | 0.36|
| Deposit feeder: surface  | 0.28           | 0.41|
| Omnivore                 | 0.34           | 0.41|
| Carnivore                | 0.04           | 0.47|
| Filter feeder            | 0.19           | 0.09|

| Mollusca                 | Day | Night |
|--------------------------|-----|-------|
| Filter feeder            | 0.24| 0.38  |
| Suspension feeder        | 0.38| 0.56  |
| Scavenger                | 0.32| -     |

The significant differences of the mollusc trophic guilds between the aliquots may be explained by the reduction in abundance of the three species that demonstrated the highest abundance during the day. The variation in the contribution of Suspension feeders occurred mainly by the elevation of Phacoides pectinatus density during the day. Some species of the Lucinidae family, such as Phacoides pectinatus, have specializations for surviving in environments with a lower oxygen content, under these conditions these species are likely to have symbiosis with sulfide oxidant bacteria (Taylor & Glover 2006), which allows for the displacement of individuals to areas of deep sediment.

It is possible that the higher abundance of Actina flexuosa in both aliquots was due to the fact that the sampling period included the start of the rainy season, which is linked to the greatest reproductive activity of the specie (Boehs et al. 2008). This may also explain the high proportions of polychaete families, Capitellidae and Cirratulidae, according to Giangrande & Simonetta (1993) and Gibbs (1971). These authors showed that these species from both families increase their reproductive activity during the month of May.

seasonal fluctuations (Cardoso et al. 2010), although this was not tested in this study.

The high niche overlap observed for the polychaete and mollusc indicates that there are coexistence mechanisms working in these communities, thus allowing the partitioning of resources between individuals. However, the mechanisms of coexistence that act on polychaetes and molluscs, act at opposing times. Different times for daily foraging are strategies used by individuals to reduce competition, allowing the partition and coexistence of food (Sánchez-Hernández et al. 2011). The different types of trophic guilds used by the species in this study may explain their coexistence. According to Kneitel & Chase (2004), alternative traits can enable the exploration of the same type of resource by different strategies, ensuring coexistence between species. This may explain the fact that in this study we found different types of trophic guilds, such as Filter feeder, Deposit feeder: digger, Deposit feeder: surface and Suspension feeder, that utilize the same type of resource, with different methods of capture.

Figure 3. Percentage of functional trophic guilds during the day and night in the Tubarão River estuary, Macau-RN, northeastern Brazil. (A) functional trophic guilds of polychaetes, and (B) functional trophic guilds of molluscs.
CONCLUSION

In conclusion, the polychaetes and mollusks groups occupied different functional guilds and presented dynamics of vertical migration in the sediment during the diurnal period, which may be a strategy used by species to obtain food resources, reproduce and persist in the environment under adverse conditions (for example, escape predation). These results provide information on the mechanisms of coexistence of macroinvertebrate communities and may support other studies aimed at the conservation of tropical estuaries.

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Supplementary Material 1. Composition, numerical abundance and functional trophic guilds of the taxa of Polychaeta and Mollusca captured at day and at night in the Tubarão River Estuary, Macau-RN, northeastern of Brazil. Functional trophic guilds: Car—Carnivore | Fil—Filter feeder | Her—Herbivore | DC—Depositor feeder: digger | DS—Deposite feeder: surface | Omn—Omnivore | Sce—Scavenger | Sus—Suspension feeder.

| Benthic macroinvertebrate communities | Day (A1/A2) | Night (A1/A2) | Trophic functional guilds |
|--------------------------------------|------------|--------------|--------------------------|
| **Polychaeta**                       |            |              |                          |
| Orbiniidae                           | 36/8       | 23/1         | DC                       |
| Ampharetidae                         | 27/6       | 23/8         | DS                       |
| Oweniidae                            | 1/0        | 0/0          | DC                       |
| Pilargidae                           | 11/3       | 9/3          | DC                       |
| Onuphiidae                           | 5/1        | 6/2          | Omn                      |
| Dorvilleidae                         | 9/0        | 4/8          | Car                      |
| Nereididae                           | 41/1       | 13/3         | Car                      |
| Cirratulidae                         | 165/1      | 149/21       | DC                       |
| Glyceridae                           | 1/0        | 0/0          | Car                      |
| Goniadidae                           | 16/0       | 33/3         | Car                      |
| Capitellidae                         | 77/4       | 11/1         | DC                       |
| Lumbrineridae                        | 2/0        | 6/1          | Omn                      |
| Goniadidae                           | 1/0        | 7/0          | DS                       |
| Stenaspidae                          | 4/0        | 12/0         | DS                       |
| Spionidae                            | 55/3       | 45/1         | Fil                      |
| Syllidae                             | 56/0       | 14/1         | Car                      |
| Sabelidae                            | 3/0        | 7/0          | Fil                      |
| Paraonidae                           | 1/0        | 0/0          | DS                       |
| Ophelidae                            | 0/0        | 1/0          | DC                       |
| **Polychaeta total abundance:**      | 538        | 416          |                          |

| Mollusca                              |            |              |                          |
| Anomalocardia flexuosa                | 75/4       | 45/14        | Fil                      |
| Macomasp.1                            | 21/2       | 23/1         | Fil                      |
| Phacoides pectinatus                  | 12/0       | 16/14        | Sus                      |
| Veneridae                             | 17/2       | 37/0         | Fil                      |
| Bittium varium                        | 0/3        | 2/1          | Sus                      |
| Tagelus divisus                       | 1/0        | 3/0          | Sus                      |
| Assiminea succinea                    | 9/1        | 17/0         | Sce                      |
| Caryocorbula caribaea                 | 0/0        | 2/1          | Fil                      |
| Acteocina bidentada                   | 7/0        | 14/0         | Sus                      |
| Sphynia fragilis                      | 2/0        | 2/1          | Sus                      |
| Neritina virginia                     | 0/0        | 0/2          | Her                      |
| Ervilia subcancellata                 | 0/0        | 2/0          | Fil                      |
| Paradentalium sp.                     | 0/0        | 1/0          | Omn                      |
| Tagelus sp.                           | 1/0        | 1/0          | Sus                      |
| Haminaea antillarum                   | 4/0        | 1/0          | Sus                      |
| Volvarina sp.                         | 1/0        | 0/0          | Car                      |
| Amygdalium papyrium                   | 0/0        | 5/0          | Sus                      |
| Chione sp.                            | 0/0        | 1/0          | Fil                      |
| Haminaea sp.                          | 0/0        | 1/0          | Sus                      |
| Macoma sp.2                           | 0/0        | 3/1          | Sus                      |
| Bulla striata                         | 2/0        | 0/0          | Her                      |
| **Mollusca total abundance:**         | 164        | 211          |                          |

Macroinvertebrate total abundance: 702 627
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Response