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Distribution and Sediment Selection by the Mud Shrimp *Upogebia noronhensis* (Crustacea: Thalassinidea) and the Potential Effects on the Associated Macroinfaunal Community

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Abstract: Burrowers such as thalassinideans remobilize sediment in benthic ecosystems, altering granulometry, enhancing organic matter cycling and oxygenation. We characterized the distribution of the mud shrimp *Upogebia noronhensis* and the associated macroinfauna along a depth and granulometric gradient in a shallow subtidal area in the southern Brazilian coast. Mud shrimp densities were estimated by burrow opening count using 0.25 m² quadrats in three sediment zones: sand, sand-mud transition and mud. Macroinfaunal community descriptors and sediment granulometric characteristics were assessed. *U. noronhensis* average density varied from 0.6 to 145 individuals m^{-2} and was highest in the transition zone and lowest in the sand zone. Macrofauna in the sand zone was at least three times more abundant and 1.2 times richer, averaging 436.3 organisms and 39 species, while the transition and mud zones were more even in species distribution (species evenness > 0.7). The shrimp presence seems to be linked to a coarse sand content <80% and clay and silt <40% in the sediment, a compromise between gallery construction ability and filter-feeding suitability. High densities and aggregated distribution of mud shrimp, combined with alteration of sediment grain composition and organic matter, are likely to affect macroinfaunal abundance nearby the burrows.

Keywords: bioturbation; sediment reworking; ecosystem engineer; sublittoral; marine benthos

1. Introduction

Large sediment burrowers are normally regarded as ecosystem engineers [1,2] for their key role in transforming and rearranging the seafloor. During these activities, burrowing organisms change the biogeochemical characteristics of the sediment [3,4] in a process called bioturbation [2]. They alter the physical-chemical characteristics of the surrounding sediment and its nutrient exchange with the overlying water column. Bioturbation is defined by the sediment reworking caused by the activity of an animal and the ventilation derived by the water movement for respiration or feeding [2]. Bioturbation leads to a greater availability of dissolved oxygen and organic matter (OM) to deeper sedimentary layers, thus enhancing overall degradation and remineralization rates [5–8].

Burrowing activity may also facilitate the colonization of areas by other species that would not settle in otherwise undisturbed and dysaerobic/anaerobic sediments [9,10]. However, burrowers may

displace enough sediment to hamper or exclude other sympatric species from the burrow surroundings in an interaction known as amensalism [11–13].

Thalassinidean shrimps, commonly known as mud or ghost shrimps, are widely distributed, especially in sand and mud flats and shallow subtidal areas around the world [14–16]. These animals are burrow constructors that constantly tend and maintain their burrows [14,17]. As deposit or filter feeders, thalassinids ingest sediment particles and defecate sediment-laden fecal pellets [14,18,19]. They depend on burrows for shelter, feeding and finding a mate; except for a short pelagic larval phase, most thalassinidean species spend their whole life inside them. Thalassinideans are active sediment reworkers and are able to truly transform the habitat around them, conspicuously altering the physical properties and the appearance of the sediment and greatly influencing the community of other benthic organisms and the ecosystem functioning [14,20].

Bottom sediment is a major factor influencing the composition and abundance of benthic communities and is intrinsically related to thalassinidean burrow architecture [21,22]. Laboratory experiments and field studies with *Callianassa* species indicate that the type of sediment in which burrows are constructed can significantly influence the size of burrows created [21].

The mud shrimp *Upogebia noronhensis* inhabits sand and mud bottoms along the Brazilian coast from Maranhão State to the south coast of São Paulo State [23,24]. *U. noronhensis* feeds on small suspended food particles, which are collected by creating a water flux inside the burrow with its ventral appendages [24]. *U. noronhensis* is a filter feeding mud shrimp, considered an important bioturbator due to their active burrow construction and maintenance. The total length of an adult ranges between 15 and 35 mm; males burrow continuously into the sediment to seek females for mating and gallery linkages with fossorial mating encounters are common [24]. In our study area, reproduction occurs year-round, with increased mating activity during spring and summer [24]. The intense digging activity that is associated with a high population density (ca. 200 individuals m^{-2}) [24] makes *U. noronhensis* a key species for shaping the structure of the local benthic community [14,25,26]. The burrow lumen and walls are inhabited by species of bivalves, pinnotherid crabs and gobies [27,28]. In spite of that, the relationship among thalassinidean abundance, sediment grain size and the associated benthic infauna has not been investigated until now in the subtropical western Atlantic.

This study investigates the influence of a granulometric gradient on the distribution and density of *U. noronhensis*. It also tests for the presence of seasaonal changes in these population parameters. Furthermore, it examines the effect of the mud shrimp presence on associated benthic macrofauna, considering particle selection for burrow construction and influence on the organic matter content due to feeding activities. We hypothesize that higher densities of *U. noronhensis* would lead to lower abundance, species richness and diversity of benthic macroinfauna.

2. Materials and Methods

The work was conducted in a shallow subtidal area from 6 to 15 m water depth on the west coast of Anchieta Island (23° 32′ S and 45° 05′ W) in Ubatuba, SE Brazil. Previous work has shown that this area is home to a large population of the thalassinidean shrimp *U. noronhensis* (up to 200 ind. m^{-2}), occurring along a depth and sedimentary gradient [24]. The sampled area is located near the rocky granitic shore of Anchieta Island, extending offshore in a gradient as follows: (1) coarse sand, (2) fine sand with silt and clay and (3) silt and clay, hereafter simply referred to as sand, transition and mud zones, respectively (Figure 1).
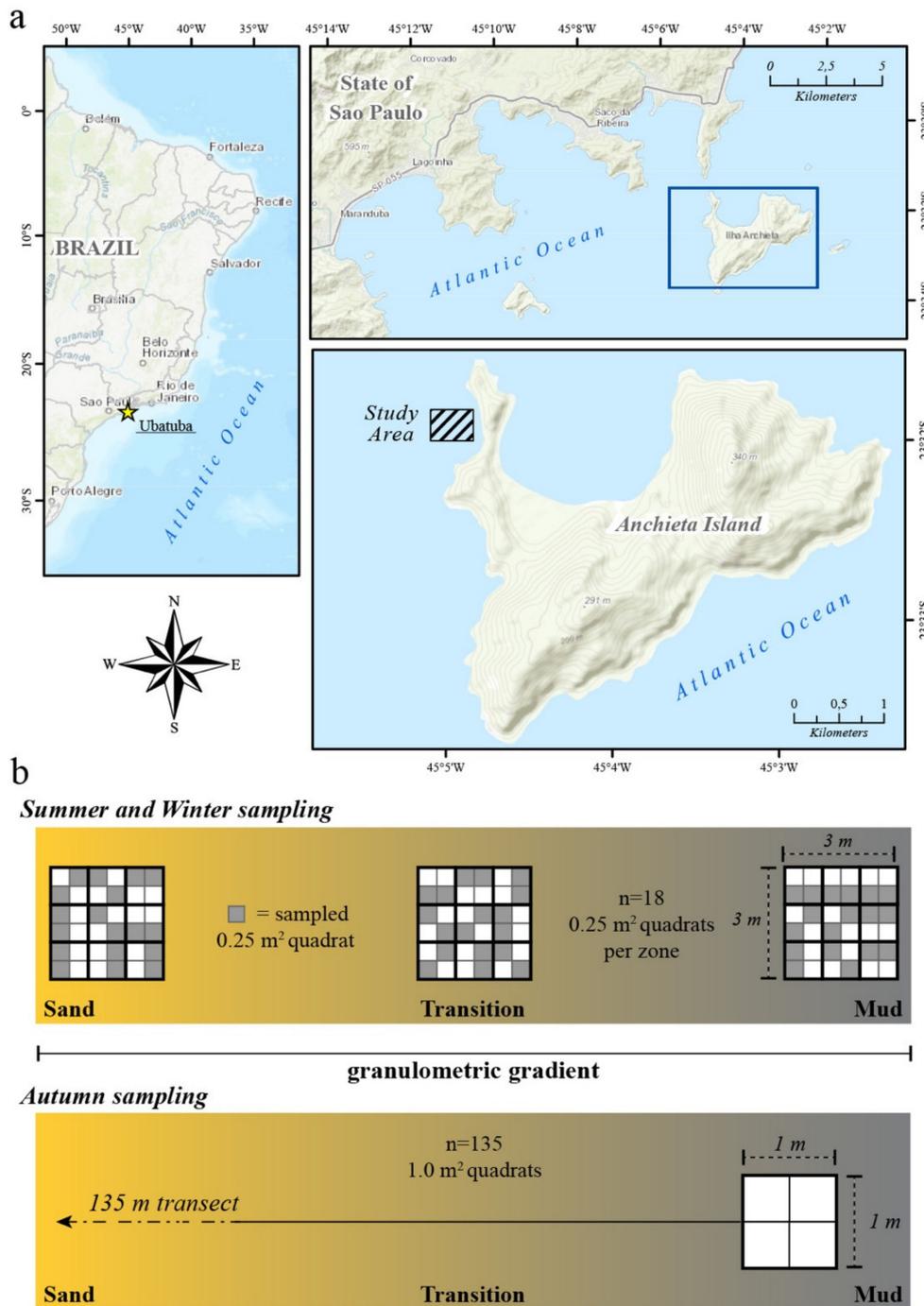
Figure 1. Study area and *U. noronhensis* sampling methods employed at Anchieta island, Ubatuba, Brazil. (**a**) Map showing the sampled area (hatched rectangle). The sediment gradient goes from mud to sand in an east to west transect. (**b**) Schematic representation of the sampling methods used to estimate *U. noronhesis* densities through burrow opening counts during summer and winter using a 9×9 m quadrat for each zone and the autumn sampling method using a 1×1 m quadrat along a 135 m transect. Representation not to scale.

Mud shrimp densities and distribution were assessed in a 9 m^2 (i.e., 3×3 m) area selected within each sediment zone. In this area, we used a 1 m^2 quadrat subdivided into four 0.25 m^2 squares to facilitate burrow opening counts (Figure 1b). Using scuba diving, *U. noronhensis* burrow openings were counted in only two 0.25 m^2 squares, randomly chosen within each 1 m^2 frame. Therefore, a total of 18 squares were counted for each sediment zone. To assess potential seasonal changes in *U. noronhensis*

distribution and density, this approach was performed in the same area during both austral summer (February) and austral winter (July).

The relationship between *U. noronhensis* densities and the co-occurring fauna was only assessed during the collection in the summer. For this, the macroinfauna of the three sediment zones were sampled in triplicates using a 0.1 m² van Veen grab. The nine resulting samples were then washed with filtered seawater in a 500 μm sieve and preserved in 70% ethanol. Animals were sorted out from the sediment under a dissecting microscope and identified to the lowest possible taxonomic level. Although *U. noronhensis* individuals were occasionally collected by the van Veen grab, this species was excluded from the macrofauna analysis as this collection method is not suitable for sampling mud shrimps [29]. For grain analysis and sediment zone characterization, each van Veen grab sample had subsamples taken from the first 5 cm layer of sediment.

In a separate sampling event during austral autumn (April), a second assessment of *U. noronhensis* density was made focusing on the effect of the mud shrimp on the grain size and organic matter content in the adjacent sediment. This scuba-based sampling used continuous counting of burrow openings along a 135 m transect across the sedimentary zone gradient, perpendicular to the coast (i.e., from 6 to 15 m depth, crossing the three zones) (Figure 1b). For this approach, all burrow openings were counted within a 1 m² quadrat placed at every meter of the 135 m transect (n = 135). In addition, ten 20 × 20 cm resin castings were made along the transect. Upon removal of the hardened resin casts, sediment samples from the burrow walls attached to the casts were carefully removed and collected. The granulometric characteristics along the transect were described with sediment collection from 33 van Veen grab samples. Sediment samples of the burrow walls were compared with the background adjacent sediment from the van Veen samples.

In the laboratory, the burrow casts were visually examined for any notable differences in burrow architecture in each of the three different zones. Final density of *U. noronhensis* (abundance per meter squared) was corrected using a ratio of 1.8 gallery openings per animal. This ratio was estimated with the data obtained from the resin casts, associating the number of burrow openings with the mud shrimp entrapped in resin, using the method described in Candisani et al. (2001) [24]. The burrow casts were also checked for entrapped commensal organisms.

For grain analysis, 2–3 g wet weight (ww) of the sediment samples were analyzed using sieving and pipetting and graded using the Wentworth scale. Total organic matter (TOM) was estimated by combustion at 500 °C for 4 h, and calcium carbonate ($CaCO_3$) content was estimated by sample acidification [30].

Data Analysis

The distribution of *U. noronhensis* individuals was calculated within and across sediment types (meters and tens of meters scales, respectively) using the Standardized Morisita Index (I_p) [31,32]. This index varies from −1.0 to 1.0, where random distributions give an I_p of zero, and positive values denote an aggregated distribution and negative values a uniform distribution [33]. The association between the *U. noronhensis* density assessment methods of direct individual count with resin cast entrapment and of indirect burrow opening count was confirmed with a Pearson's correlation test. We also tested the relationship between *U. noronhensis* density and sediment grain size with a Pearson's correlation test.

For each sediment zone, macroinfaunal communities were defined in terms of species richness (S), abundance (n), Pielou's evenness index (J') and Shannon diversity index (H'$_{(log\,e)}$). The macroinfaunal community composition was also described using multivariate methods [34]. Differences in abundance and species composition between sedimentary zones were tested using a one-way permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis distances. *p*-values were adjusted using the Monte Carlo approach. The PERMDISP procedure was used to test for homogeneity of dispersion of the data. A similarity percentage analysis (SIMPER) was used to assess the species similarity among samples in the same sedimentary zone and to rank species that contribute the most

to differences between zones (dissimilarity). A non-metric Multidimensional Scaling (nMDS) plot was used to graphically compare the community similarity among samples and zones. Grain size composition, calcium carbonate and TOM content were related to the zone replicates and to burrow walls and graphically expressed via Principal Coordinates Analysis (PCoA). Each pair relationship was also verified with a Pearson's correlation test. For all of the aforementioned multivariate analyses, we log-transformed (logX + 1) the species abundance data, so the less abundant or rare species were given more weight. The relationship between *U. noronhensis* density and macrofaunal density was tested with a Pearson's correlation test.

Differences in macroinfauna densities and in diversity indexes among sediment zones were tested with a one-way Analysis of Variance (ANOVA). Differences in *U. noronhensis* densities between seasons (summer and winter) and sediment zones (transition and mud zones) were tested with a two-way mixed model ANOVA. In the latter case, we excluded the sand zone from the analysis because of the near absence of burrows in this zone. Pairwise post-hoc tests were performed with Student's *t*-tests or Tukey's test All data was tested for normality and homogeneity of variance and log-transformed (logX + 1) when necessary.

3. Results

3.1. Macroinfaunal Community Analysis

The sand zone was characterized by the dominance of coarse and medium sand grains (Appendix A, Table A1). Macrofauna from this area (Appendix A, Table A2) were mainly characterized by the presence of the polychaete *Exogone arenosa* and the gastropod *Caecum pulchellum*, which together contributed nearly 70% to the average similarity of the group (Table 1). This area presented the lowest diversity (mean H' = 1.8 ± SE 0.6), the greatest mean number of species found (mean S = 39.0 ± SE 8.7 species) and the lowest evenness of all areas (mean J' = 0.5 ± SE 0.1) (Appendix A, Table A3).

Table 1. Similarity percentages (SIMPER) of the most representative macrofaunal species (up to 90% cumulative contribution) collected in the three zones of the study area in summer. Average abundance is given in individuals m^{-2}. Sim./SD is the ratio of average similarity divided by its standard deviation (SD).

Species	Average Abundance	Average Similarity	Sim./SD	Contribution (%)	Cumulative Contribution (%)
		Sand—Average Similarity: 36.03			
Exogone arenosa	142.00	16.43	3.75	45.58	45.58
Caecum pulchellum	136.33	8.77	0.58	24.33	69.91
Pholoe sp.	23.67	3.78	8.60	10.49	80.41
Mactra sp.	13.67	1.22	0.58	3.39	83.80
Kinbergonuphis sp.	5.00	0.60	3.14	1.67	85.47
Corbula caribaea	15.33	0.57	1.01	1.59	87.06
Pseudorythoe ambigua	4.00	0.46	7.13	1.29	88.34
Ophiuroidea	5.67	0.44	1.32	1.21	89.55
Caecum sp.	4.00	0.41	0.58	1.13	90.69
		Transition—Average Similarity: 52.52			
Pholoe sp.	51.33	31.32	3.38	59.64	59.64
Nucula semiornata	7.67	3.88	2.46	7.38	67.02
Semelidae sp.	7.00	2.42	0.58	4.60	71.62
Ampelisca cristata	5.67	2.00	0.90	3.81	75.43
Caecum pulchellum	2.00	1.46	29.01	2.79	78.22
Diplodonta punctata	4.33	1.45	0.58	2.76	80.98
Lysidice schmardae	6.33	1.44	1.19	2.75	83.73
Corbula caribaea	4.00	1.21	0.58	2.30	86.03
Idunella titinga	3.00	1.01	0.58	1.93	87.96
Cumacea	2.67	0.97	2.46	1.85	89.80
Chione paphia	1.00	0.73	29.01	1.39	91.20
		Mud—Average Similarity: 43.63			
Ophiuroidea	8.67	21.24	12.49	48.68	48.68
Monokalliapseudes schubarti	4.67	7.18	0.87	16.46	65.14
Harmothoe sp.	2.67	5.91	4.98	13.54	78.68
Rathbunixa sayana	1.33	1.85	0.58	4.24	82.92
Nereididae sp.	1.33	0.93	0.58	2.12	85.05
Cabira incerta	0.67	0.82	0.58	1.89	86.93
Maldanidae sp.	2.00	0.82	0.58	1.89	88.82
Pseudoharpinia dentata	0.67	0.82	0.58	1.89	90.70

Sediments from the transition zone were composed mainly by fine and very fine sand with high calcium carbonate content (~80%; Appendix A, Table A1). The average similarity of the group was related mainly with the presence of the polychaete *Pholoe* sp. and the bivalve *Nucula semiornata*, which together contributed 67% to the group. Diversity was higher than in the other two areas (mean H′ = 2.5 ± SE 0.1) and the mean number of species was 32.3 ± SE 1.7 (Appendix A, Table A3).

In the mud zone, fine-grained sediments were more prominent and higher silt and clay contents were found (Appendix A, Table A1). A species of unidentified ophiuroid, the tanaid *Monokalliapseudes schubarti* and the polychaete *Harmothoe* sp., accounted for nearly 80% of the average similarity in the group. Despite the lower number of species found in this zone (mean S = 16.0 ± SE 1.5 species), diversity was relatively high (mean H′ = 2.4 ± SE 0.1), owing to the more even distribution of total abundance among species (Appendix A, Table A3).

In terms of species composition and abundance, macroinfaunal communities differed significantly among the three sedimentary zones (PERMANOVA Pseudo-F = 4.35, df = 2, p(MC) < 0.01) Appendix A, Table A4). The communities in sand and transition zones were more similar to each other (SIMPER average dissimilarity of 84%; (PERMANOVA t-test, p(MC) = 0.11), whereas the mud area was around 97% dissimilar to the other two sampled areas (PERMANOVA t-test, p(MC) < 0.02) (Figure 2). Abundance was significantly different among the three sedimentary zones (F = 130.39; df = 2; p < 0.001).

Figure 2. Non-metric Multidimensional Scaling (nMDS) showing the differences among the composition of macroinfaunal communities on the three sampling zones in summer. Numbers after S (Sand Zone), T (transition Zone) and M (Mud Zone) represent the van Veen grab replicate (n = 3) of each zone.

3.2. Upogebia Noronhensis Distribution

U. noronhensis individuals were rare in the sand zone, being found only in summer (0.6 ± 0.4 ind. m^{-2}; Table A1). The scarcity of animals prevented us from calculating a dispersion index for *U. noronhensis* in this area. The highest numerical densities were found in the transition zone with an average of approximately 144.6 ± 13.8 ind. m^{-2}. In the mud zone, the mean density was nearly three times lower than those found in the transition zone, i.e., approximately 53.8 ± 3.1 ind. m^{-2} (Figure 3). There were no significant differences in *U. noronhensis* densities in summer and winter (two-way ANOVA, F_{season} = 0.14; df = 1; p = 0.7140), but the total number of individuals was significantly higher in the transition zone (two-way ANOVA, F_{zone} = 57.25; df = 1; p < 0.001). There was no significant

interaction between sediment zones and season (two-way ANOVA, $F_{zone.season} = 0.15$; df = 1; $p = 0.6989$). There was no correlation between the number of *U. noronhensis* and macrofaunal density in the study area (Figure 3).
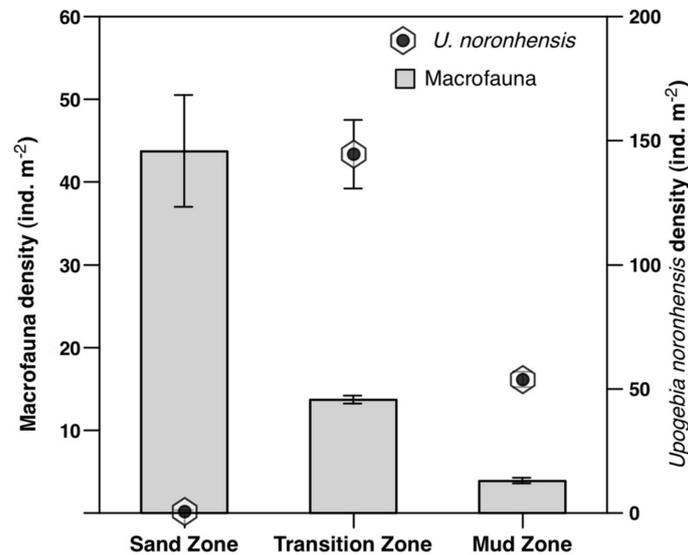
Figure 3. Macroinfaunal (n = 3, per zone) and *U. noronhensis* (n = 9, per zone) densities (ind. m^{-2}) in the Table 1.

The distribution pattern of *U. noronhensis* within the zones (except in the sand zone where few or no animals were found) was aggregated (Table A1). Values of Standardized Morisita Index (I_p) were around 0.5 in both the transition and mud zones, suggesting a clumped distribution. No differences in the burrow structure and shape between sediment zones were observed from the casts. The main difference was the shortening or bending of the lower central shaft of the common Y-shaped gallery due the presence of a gravel and deep shell layer (~10 cm) in the transition zone.

The comparison of the two methods of *U. noronhensis* density assessment has been validated with a significant correlation between the direct individual count from resin casts and the indirect method of burrow opening counts ($N_{(pairs)} = 10$; $r_{(Pearson)} = 0.67$; $p = 0.03$).

U. noronhensis abundance measurements along a continuous transect showed that this species occurred starting at the 55 m (8.1 m depth) of the transect, increasing in numbers to reaching up to 252 ind. m^{-2} at the 106 m (10.1 m depth) in the transition zone and decreasing again towards the mud zone (Figure 3; Appendix A, Table A5). Testing for a preferred type of sediment grain size, there was a positive correlation between *U. noronhensis* abundance and fine sand ($N_{(pairs)} = 34$; $r_{(Pearson)} = 0.47$; $p < 0.01$) and calcium carbonate ($N_{(pairs)} = 34$; $r_{(Pearson)} = 0.49$; $p < 0.01$) content (Figure 4; Appendix A, Table A5).

The granulometric gradient in the sampling area was evident as shown in Figure 4. The sand zone had a higher coarse grain and lower OM and calcium carbonate contents. The transition zone was mostly composed of finer fractions of sand, low OM and higher calcium carbonate. The mud zone was mostly composed of silt and significant fractions of clay and very fine sand with high OM and calcium carbonate contents. Compared to the grain size composition of the area, the burrow walls were lined with finer particles (clay, silt, very fine sand and fine sand) and a lower content of coarse and very coarse sand than adjacent sediments (Figures 4 and 5). Additionally, the total organic matter contents were higher in the walls of a burrow (ca. 0.7%) than in non-wall sediments (ca. 0.4%) from samples adjacent to the burrows (Appendix A, Table A5).
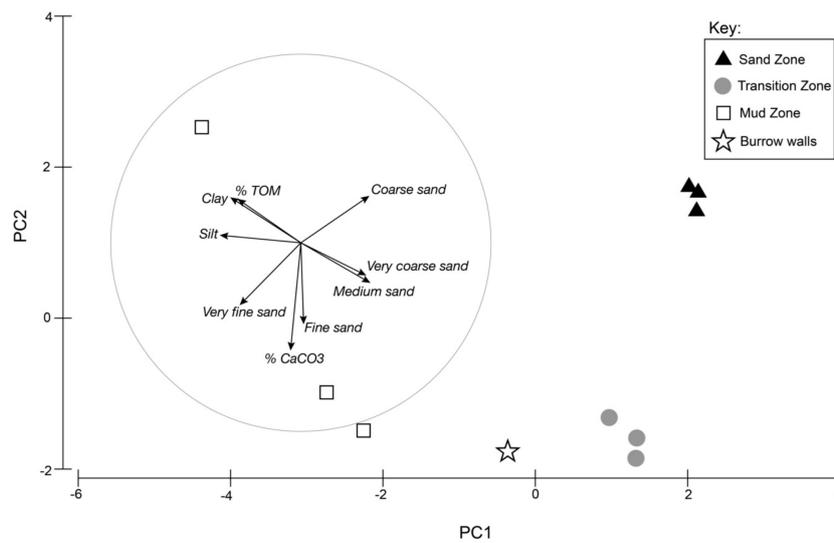
Figure 4. PCoA plot showing the sediment characteristics (vectors) for the three sampled sediment zones and for the burrow walls (symbols) in the autumn sampling. The first (PC1) and second (PC2) axes explain 55.5% and 30.0% of the total variation, respectively.
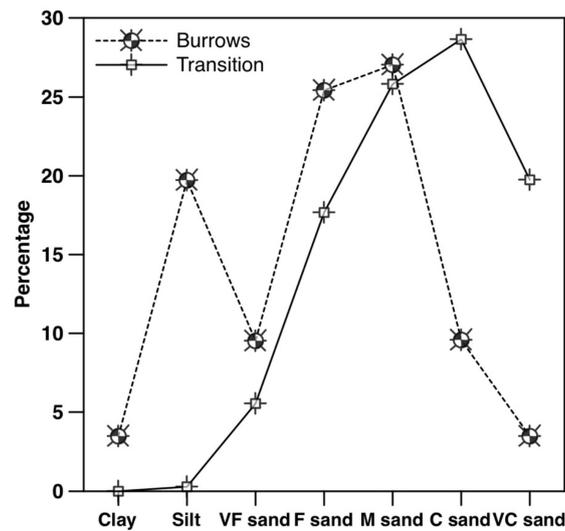
Figure 5. Percentage distribution of the several sediment grain size classes of the *U. noronhensis* burrow walls and adjacent sediments of the transition zone. VF sand = very fine sand; F sand = fine sand; M sand = medium sand; C sand = coarse sand; VC sand = very coarse sand.

4. Discussion

This work presented the distribution of the thalassinidean *U. noronhensis* along a sedimentary and depth gradient of a shallow subtidal area on the SE Brazilian coast and characterized the macrofaunal species composition and abundance in each main sediment zone. The effect of the presence of this burrowing shrimp on the local fauna is an open issue to be investigated. Nevertheless, the higher densities of *U. noronhensis* found in the transition zone may affect the local fauna as a less dense but more diverse and richer community of infauna was found in the transition zone in comparison to the sand and mud zones, also suggested in discussions on the effects of thalassinids on the benthic fauna [14,20]. However, we should emphasize that the change in faunal composition is also combined with the change in the sediment type between zones and this study was not designed to isolate the effect of sediment type from mud shrimp influence. Additionally, the granulometric characteristics of

the sediment change with depth. Coarser sediment are usually found in shallower areas close to the shore, whereas finer sediments tend to accumulate in the deeper areas in the center of the bays in the region, influencing the macrofauna distribution [35–37].

The macroinfaunal community found in the three sedimentary zones were typical for the SE Brazilian coast. The syllid polychaete *Exogone arenosa* is commonly associated with coarse sand substrate [38–40] as is the deposit feeder mollusk *Caecum pulchellum* [40]. The carnivorous polychaete *Pholoe* sp. was common in the sand zone and dominant in the transition zone [41,42]. Several bivalve species were present in the transition zone; the most important were semelids and *Nucula semiornata*, a typical deposit-feeder from shallow waters, found in a wide range of granulometric gradients [43,44]. The mud zone was characterized by the presence of ophiuroids and the tube-dwelling tanaid *Monokalliapaseudes schubarti*, a species that is associated with fine and organic-enriched sediments in the region [45,46]. Mud dwelling predators such as the polynoid polychaete *Harmothoe* sp. and the pinnotheridae crab *Rathbunixa sayana* were also common in the mud zone [40,47]. Several species of pinnotherid crabs are reported as commensals in thalassinidean burrows [48–50] but we found no direct evidence of *R. sayana* living in the burrows along with *U. noronhensis*.

Sediment reworking rates found for *U. pugettensis* suggests that *U. noronhensis* may generate high bioturbation due to their whole-year mating behavior, as males become more active in building new galleries when searching for a partner [24,26,51]. Therefore, *U. noronhensis* burrowing activities may still be sufficient to affect the surrounding fauna in zones of high abundances such as those observed in this study (ca. 140 ind. m^{-2} in average), particularly given the higher densities previously observed in the same area (ca. 200 ind. m^{-2}) [20,24,26,48]. Similarly, the bioturbation of *Upogebia pugettensis* is known to strongly affect the macroinfauna of tidal flats of the northwest coast of the United States [26]. A recent review by Pillay [20] notes the non-linearity of the response of the macroinfauna abundance and richness to the thalassinid density, which can be modulated by factors such as sediment type or benthic organisms considered (epifauna or infauna). In addition to shrimp abundance and richness, the bioturbation rate may also vary seasonally as evidence gathered for *U. noronhensis* indicates that these animals must be reworking more sediment than previously thought, particularly during the spring and summer months when mating activities are more intense [24].

U. noronhensis preferentially inhabited poorly sorted sediments with higher contents of fine and very fine sand (more than 80%) and calcium carbonate. The presence of fine grains is likely to be essential for the construction of the burrow, which was mainly composed of the smaller fraction of the sand and silt (see Figure 4). Our results pointed out that a high content of coarse sand in the sediment (<80%) may be too unstable for building and maintaining burrows, whereas sediments with more than 40% of clay and silt content may not be as suitable for these filter-feeding organisms. However, the transition zone is characterized by moderate contents of fine-grained material, which *U. noronhensis* uses to build its burrow. Fine grains may be glued together by the animal through an organic mucous matrix, which, together with the adhesion of organic debris, phytoplankton, benthic microalgae and other heterotrophic microorganisms [52,53], increase the organic content of the burrow wall (see [3,7,54]). It has been noted that the burrow walls may also trap finer sediment and food particles on which mud shrimp could feed [55,56]. We found the content of total organic matter 75% higher in *U. noronhensis* burrows when compared with the background sediment. In comparison, Dworschak [57] did not find significant differences in the organic content of burrows and the surrounding sediment and argued that a mucus lining is improbable for *U. pusilla.* However, there is mounting evidence showing that burrow walls have a higher content of organic matter than the surrounding sediment [7,52,53,55,56,58,59], suggesting that thalassinid shrimps may use food particles trapped on the burrow linings to feed [53,55,56,60]. We observed that *U. noronhensis* spends part of its time tending the burrow with sediment grains selected by its mouthparts (personal observation). This process may account for the selection of determinate grain sizes; *U. noronhensis* selected some particles to include in the burrow wall while rejecting others. It may also account for the inclusion of an organic secretion on the sediment grains just before tending the burrow. Of note, MacGinitie [61] observed *U. pugettensis* attaching loose sand

onto a glass tube, arguing that this would be impossible without some sort of cementing material involved. This question, however, remains to be tested explicitly. This burrow tending may also be related to the use of the burrow lining as a food source, suggesting that part of the animal diet may rely on deposit feeding, supplementing filter feeding. Many authors have observed this same behavior in related species, such as *Austinogebia edulis*, *Upogebia pugettensis*, *U. major* and *U. omissa* [52,55,56,60]. Griffen et al. [55] argued that burrow lining feeding may be especially important for smaller and younger individuals, as the area–volume ratio of the burrow wall surface versus the burrow lumen is higher for smaller individuals than found in adult burrows, therefore trapping significantly more food particles on the walls. This may also compensate for the smaller pumping capacity of smaller individuals [62], who may not rely as much on filter feeding as adults do. Besides filter feeding, Bosley et al. [58] found that *U. pugettensis* also feed on benthic organic particulates, although no direct evidence from molecular markers (stable isotopes and fatty acids) indicated that the source was also from the burrow linings. Given the evidence in this study from granulometry and organic matter content in burrow linings, we should also consider *U. noronhensis* as a species that is both filter and deposit feeding, including on the burrow lining.

Total abundance of mud shrimp was estimated through burrow opening counts, which is a rapid and reliable method [63–65]. Density estimates using a burrow to animal ratio of 1.8/1 ([24], for the same species and area) were up to ~250 ind. m^{-2}, similar to values found by Dworschak [66] and Hodgson et al. [67] for other *Upogebia* species. Burrow densities as high as 200 burrow openings per square meter for *U. omissa* have been reported [60]. Samples collected in the present study using the resin casting technique yielded abundance estimates from 10% to three times higher than those collected through burrow opening counts in the same sediment type (see Table A5). However, density estimates derived from casts are likely overestimated, as the castings were conducted mostly in the transition zone, where the shrimp densities are higher. In contrast, van Veen grab samples tended to underestimate *U. noronhensis* densities. For all nine van Veen grab samples collected in the present study, we obtained over 1800 specimens of macrofaunal organisms; only four of them were *U. noronhensis*. In the transition zone, where thalassinid densities were highest, only two animals were collected in three van Veen replicates. Both of them were small juveniles, which have much smaller and shallower burrows; larger animals are nearly impossible to collect using these remote samplers because adults mud shrimps can quickly retreat deeper into the burrow, out of the sampling device reach. Larger sampling efforts undertaken elsewhere with similar gear also failed to sample another species of upogebiid thalassinidean, *U. deltaura* [68], showing the difficulty in conducting studies that involve the relationships between macrofauna structure and large populations of bioturbators such as upogebiids.

The high abundances of *U. noronhensis* found in the study area, especially in the transition zone, are likely to also be related to other sedimentary and biological issues. *U. noronhensis* galleries normally reach sediment depths up to 18 centimeters [24]; in the transition zone, a layer rich in shell fragments is found below 10 centimeters, which may further help stabilizing galleries. Interestingly, nearby areas with similar granulometric characteristics but without the deep shell layer did not harbor large numbers of *U. noronhensis* (personal observation). In addition, the dispersion pattern of *U. noronhensis* was aggregated both within and across the sediment zones. Evidence from the same species within the study area suggest juveniles settle on adult burrows [24], which is probably the main mechanism generating such dispersal and producing high densities. *U. noronhensis* may achieve high densities (>120 ind. m^{-2}) when sediment grain composition is ideal. Considering the clumped distribution and high densities attained in the region and the mud shrimp sediment reworking through burrowing, gallery maintenance and feeding activity, the role of *U. noronhensis* is likely to be significantly affecting the adjacent macroinfauna abundance and composition. These effects have yet to be directly proven with an experimental approach, such as with experiments using exclusion and transplant of the mud shrimp [26,65,69,70]. Although more direct evidence is needed, all these characteristics make *U. noronhensis* an important potential candidate as an ecosystem engineer in finer grained shallow unconsolidated areas in the southeastern Brazilian coast.

Appendix A

Table A1. *Upogebia noronhensis* (n = 9) mean density (ind. m^{-2} ± SE), Standardized Morisita Index (I_p) (n = 18) and sediment parameters in the three sample zones during the summer and winter periods. Sand classes: VF sand = very fine sand; F sand = fine sand; M sand = medium sand; C sand = coarse sand; VC sand = very coarse sand.

	Summer			**Winter**		
	Sand	**Transition**	**Mud**	**Sand**	**Transition**	**Mud**
U. noronhensis (ind. m^{-2} ± SD)	0.6 ± 0.42	144.6 ± 13.82	53.8 ± 3.10	0	135.9 ± 14.54	54.1 ± 10.38
I_p	−0.61 *	0.50	0.50	n/a [†]	0.50	0.51
Distribution	uniform *	aggregated	aggregated	n/a [†]	aggregated	aggregated
Depth (m)	7	10	14	7	10	14
VC sand (%)	13.7	5.4	0.5	5.9	11.3	2.2
C sand (%)	42.2	9.0	2.8	46.1	14.2	6.4
M sand (%)	37.5	11.5	5.7	40.4	21.3	10.0
F sand (%)	6.1	20.2	6.5	6.6	38.5	15.3
VF sand (%)	0.6	20.1	8.0	0.5	11.3	30.0
Silt (%)	0	21.3	57.4	0.1	0	31.0
Clay (%)	0	12.1	19.1	0	0	5.2
CaCO$_3$ (%)	54.2	79.9	60.9	61.6	80.4	78.6

* Very low mud shrimp density, only three quadrats had burrow openings; [†] not available, no burrow openings counted.

Table A2. Macrofaunal species collected in the three zones (Sand, Transition and Mud) of the study area. Numbers are in ind. 0.01 m^{-2}. R1, R2 and R3 refer to the van Veen grab replicate (n = 3) of a given area.

	Zones								
Taxon	**Sand**			**Transition**			**Mud**		
	R1	**R2**	**R3**	**R1**	**R2**	**R3**	**R1**	**R2**	**R3**
GASTROPODA									
Caecum pulchellum	0	280	129	2	2	2	0	0	0
Caecum sp.	0	6	6	0	0	0	0	0	0
Aesopus stearnsi	1	0	0	0	0	0	0	0	0
Turbonilla dispar	0	1	0	0	0	0	0	0	0
Turbonilla sp.	0	1	0	0	1	0	0	0	0
Alvania auberiana	0	1	0	0	0	0	0	0	0
Assiminea succinea	0	1	0	0	0	0	0	0	0
Macromphalina argentina	0	1	1	0	0	0	0	0	0
Natica sp.	0	4	0	0	0	0	0	0	0
Vitrinella sp.	0	1	2	0	6	1	0	0	0
Bulla striata	0	0	5	3	1	0	0	0	0
Calyptraea centralis	0	0	1	0	0	0	1	0	0
Fissurellidae sp.	0	1	1	0	0	0	0	0	0
Not identified	0	0	1	0	0	0	0	0	0

Table A2. *Cont.*

Taxon	Zones								
	Sand			Transition			Mud		
	R1	R2	R3	R1	R2	R3	R1	R2	R3
BIVALVIA									
Puberella crenata	1	0	0	0	0	0	0	0	0
Lirophora paphia	0	4	0	1	1	1	0	0	0
Crassinella marplatensis	1	1	1	0	0	0	0	0	0
Corbula caribaea	1	39	6	0	5	7	0	0	1
Corbula cubaniana	0	0	0	0	0	0	1	0	5
Corbula patagonica	0	0	0	0	0	0	0	1	2
Corbula sp.	0	0	2	0	0	0	0	1	0
Abra aequalis	1	0	0	0	0	0	0	0	0
Abra lioica	1	0	0	0	0	0	0	0	0
Abra sp.	0	3	8	5	0	0	0	0	0
Macoma sp.	1	0	0	0	0	0	0	0	0
Tellina sp.	1	3	4	1	1	0	0	0	4
Ervilia sp.	3	0	0	0	0	0	0	0	0
Pitar fulminatus	0	4	30	1	1	0	0	0	0
Pitar rostratus	0	1	1	1	0	1	0	0	0
Chama sp.	0	4	2	0	0	0	0	0	0
Nucula semiornata	0	1	0	11	4	8	0	0	0
Thracia similis	0	3	4	1	0	5	0	0	0
Phacoides pectinata	0	1	0	0	0	0	0	0	0
Mactra sp.	0	23	18	1	1	0	0	0	0
Lioberus castaneus	0	0	1	0	0	0	0	0	0
Diplodonta punctata	0	0	0	0	7	6	0	0	0
Glycymeris sp.	0	0	1	0	0	0	0	0	0
Pandora bushiana	0	0	0	2	0	0	0	0	0
Entodesma patagonicum	0	0	0	1	0	1	0	0	0
Clathrolucina costata	0	0	0	1	0	1	0	0	0
Trachycardium muricatum	0	0	0	2	0	0	0	0	0
Anadara sp.	0	0	0	0	0	0	0	0	1
Veneridae sp.	1	27	0	0	0	0	0	0	0
Mytilidae sp.	0	1	0	0	0	0	0	0	0
Lucinidae sp.	0	1	0	0	0	0	0	0	0
Ungulinidae sp.	0	5	2	1	0	0	0	0	0
Cardiidae sp.	0	0	1	0	0	1	0	0	0
Carditidae sp.	0	0	1	0	0	0	0	0	0
Tellinidae sp.	0	0	0	1	0	0	0	0	0
Semelidae sp.	0	0	0	0	11	10	0	0	1
SCAPHOPODA									
Polyschides tetraschitus	0	0	0	0	1	0	0	0	0
POLYPLACOPHORA									
Ischnochiton sp.	1	0	1	0	0	0	0	0	0
THALASSINIDEA									
Upogebia noronhensis	0	0	2	0	2	0	0	0	0
CARIDEA									
Automate sp.	0	2	0	0	0	0	0	0	0
Processa hemphilli	0	0	0	0	1	0	0	2	0
Alpheus floridanus	0	0	0	0	0	0	1	0	1
BRACHYURA									
Tetraxanthus rathbunae	0	1	0	0	0	0	0	0	0
Persephona mediterranea	0	0	0	0	1	0	0	0	0
Acantholobulus bermudensis	0	0	0	0	0	2	0	0	0
Rathbunixa sayana	0	0	0	0	0	0	2	2	0
Xanthidae sp.	0	0	1	0	0	0	0	0	0
AMPHIPODA									
Tiburonella viscana	1	0	0	0	1	0	0	0	0
Idunella titinga	1	1	0	4	5	0	0	0	0
Ampelisca cristata	0	7	3	10	6	1	0	1	0
Ampelisca pugetica	0	0	0	0	0	1	0	0	0

Table A2. *Cont.*

Taxon	Zones								
	Sand			Transition			Mud		
	R1	R2	R3	R1	R2	R3	R1	R2	R3
Phoxocephalopsis zimmeri	0	4	0	0	0	0	0	0	0
Globosolembos smithi	0	0	1	0	0	0	0	0	0
Photis longicaudata	0	0	2	6	1	0	0	0	0
Ericthonius brasiliensis	0	0	1	0	0	1	0	0	0
Monoculodes nyei	0	0	0	1	0	0	0	0	0
Cheiriphotis megacheles	0	0	0	0	0	2	0	0	0
Pseudoharpinia dentata	0	0	0	0	0	0	1	0	1
Caprellidae sp.	0	7	3	1	0	0	0	0	0
Lysianassidae sp.	0	2	1	2	0	0	0	0	0
Isaeidae sp.	0	0	2	0	0	0	0	1	0
Aoridae sp.	0	0	3	0	0	1	0	0	0
Ampeliscidae sp.	0	0	0	0	0	1	0	1	0
Not identified	1	0	2	0	1	0	0	0	0
POLYCHAETA									
Kinbergonuphis sp.	2	9	4	0	0	0	0	0	0
Exogone arenosa	281	65	80	0	3	5	0	0	0
Hermundura fauveli	1	0	0	0	0	0	0	0	0
Lysidice schmardae	1	8	3	4	1	14	0	0	0
Pseudorythoe ambigua	2	2	8	0	4	0	0	0	0
Glicine multidens	0	1	10	0	0	3	0	0	0
Syllis sp.	0	0	7	1	0	0	0	0	0
Ninetta sp.	0	0	1	0	0	0	0	0	0
Neanthes sp.	0	0	0	0	3	0	0	0	0
Owenia fusiformis	0	0	0	0	1	0	0	0	2
Magelona variolamellata	0	0	0	0	14	2	0	0	0
Loandaria americana	0	0	0	0	2	0	0	0	0
Lisidice ninetta	0	0	2	0	1	1	0	0	0
Glicera americana	0	0	0	0	0	1	0	0	0
Lumbrineris sp.	0	0	0	0	1	0	0	0	0
Cabira incerta	0	0	0	0	0	0	1	0	1
Harmothoe sp.	0	0	0	0	0	0	2	3	3
Scoloplos (Leodamas) sp.	0	0	0	0	0	0	3	0	0
Isolda pulchela	0	0	0	0	0	0	0	1	0
Maldanidae sp.	0	0	0	0	0	0	1	0	5
Nereididae sp.	0	0	0	1	0	0	3	1	0
Spionidae sp.	0	0	0	0	0	0	2	0	0
Pholoe sp.	16	17	38	59	35	60	0	0	0
Sabellidae sp.	0	0	0	0	0	1	0	0	0
Eunice sp.	0	0	0	0	0	0	0	0	1
Euclimelia sp.	0	0	0	0	0	0	0	6	0
Ancistrosyllis jonesi	0	0	0	0	0	1	0	0	0
Notomastus lobatus	0	0	0	0	0	0	0	0	2
Terebellidae sp.	0	0	0	0	0	1	0	0	0
ISOPODA									
Munna cananeia	0	0	0	1	0	1	0	0	0
Anthuridae sp.	0	1	0	0	1	1	0	0	0
Politolana sp.	0	0	0	0	0	0	1	0	0
TANAIDACEA									
Monokalliapseudes schubarti	0	0	0	0	0	0	7	6	1
Tanais sp.	0	1	1	4	0	1	0	0	0
CUMACEA sp. 1	0	0	2	5	1	2	0	0	0
HIRUDINEA sp. 1	0	0	1	0	0	0	0	0	0
OPHIUROIDEA sp. 1	1	12	4	0	1	0	9	8	9
ECHINOIDEA sp. 1	3	0	0	0	0	0	0	0	0
NEMERTINEA sp. 1	6	0	2	0	0	0	0	1	2
PRIAPULIDA sp. 1	0	0	3	0	0	0	0	0	0
ECHIURA sp. 1	0	0	0	0	0	0	0	0	3
ACTINIARIA sp. 1	0	0	4	0	0	0	0	2	1
PYCNOGONIDA sp. 1	0	2	1	0	1	0	0	0	0
Branchiostoma sp.	0	2	1	0	1	0	0	0	0
TOTAL	329	562	422	134	130	147	35	37	46

Table A3. Macrofaunal community descriptors obtained for the three sampled zones and results for one-way ANOVA and post-hoc Tukey testing for differences among sediment zones. Numbers 1 to 3 are replicates. S = sand zone; T = transition zone; M = mud zone; S = species richness; n = total number of individuals; J′ = Pielou evenness index; H′$_{(\log e)}$ = Shannon diversity index. Mean and standard error (SE) are included for each descriptor in each zone. Asterisk (*) indicates significant *p*-values ($p < 0.05$). For Tukey pairwise tests, zones (S, T and M) linked with the same line are not statistically different.

Zone	Sample	S	n	J′	H′($\log_e$)
Sand	S1	22	328	0.25	0.77
	S2	44	562	0.56	2.14
	S3	51	419	0.67	2.63
	Mean (±SE)	*39 ± 8.73*	*436.33 ± 68.10*	*0.49 ± 0.12*	*1.84 ± 0.55*
Transition	T1	29	134	0.69	2.34
	T2	35	129	0.80	2.84
	T3	33	147	0.70	2.45
	Mean (±SE)	*32.33 ± 1.76*	*136.66 ± 5.36*	*0.73 ± 0.03*	*2.54 ± 0.15*
Mud	M1	14	35	0.87	2.29
	M2	15	37	0.88	2.38
	M3	19	46	0.90	2.66
	Mean (±SE)	*16.0 ± 1.52*	*39.33 ± 3.38*	*0.83 ± 0.00*	*2.44 ± 0.11*
1-way ANOVA	F	7.64	130.39	5.42	1.23
	df	2	2	2	2
	p	0.02 *	<0.001 *	0.04 *	0.35
Tukey		S T M	S T M	M T S	T M S

Table A4. Results of the 1-way permutational multivariate analysis of variance (PERMANOVA) and pairwise *t*-tests using Bray-Curtis distances testing for differences on the composition of macroinfaunal communities among three sedimentary zones. *p*-values were adjusted using the Monte Carlo approach [*p*(MC)]. *p*-values for tests of homogeneity of dispersion (PermDisp) are shown [*p*(PermDisp)]. Asterisk indicates values under 5% probability.

Source	df	SS	MS	Pseudo-F	*p*(MC)	*p*(PermDisp)
Zones	2	15,414	7707.2	4.35	0.004 *	0.959
Residual	6	10,611	1768.4			
Total	8	26,025				
t-test:	Groups			t	*p*(MC)	*p*(PermDisp)
	Sand	Transition		1.4906	0.117	1.00
	Sand	Mud		2.1955	0.018 *	1.00
	Transition	Mud		2.4613	0.009 *	0.202

Table A5. *U. noronhensis* densities and sediment characteristics along the sampled transect in autumn. Sediment data are represented in percentages. Shaded rows represent data collected along with resin casts. Sand classes: VC sand = very coarse sand; C sand = coarse sand; M sand = medium sand; F sand = fine sand; VF sand = very fine sand.

Transect Distance/ Depth (m)	Density (ind.m^{-2})	VC Sand	C Sand	M Sand	F Sand	VF Sand	Silt	Clay	Gravel	OM	CaCO$_3$
13/6.8	0	2.2	70.8	23.2	3.5	0.3	0.1	0	0	< 0.1	61.8
25/7.4	0	7.8	41.2	44.9	6.6	0.7	0	0	0.9	< 0.1	70.9
50/8.1	0	19.4	26.5	31.1	12.2	5.1	0	0	5.7	0.2	77.9
55/8.1	11.1	12.4	21.2	40.1	19.9	3.2	0.1	0	2.7	0.1	78.4
56/8.3	56.7	23.3	22.7	32.8	13.8	3.1	0	0	4.3	0.1	80.3
57/8.4	78.9	18.7	25.9	34.9	12.4	1.9	0	0	6.1	0.2	81.6
58/8.5	67.8	11.3	22.5	45.8	17.0	1.4	0	0	2.1	0.1	83.1
59/8.5	125.0	7.3	14.5	44.6	23.5	7.2	0	0	2.9	<0.1	84.1
61/8.7	186.7	13.8	20.1	35.1	20.4	6.0	0	0	4.7	0.2	81.2
63/8.8	250.0	13.5	27.7	40.7	15.9	1.6	0	0	0.7	<0.1	82.6
64/8.8	92.2	9.9	18.9	41.1	21.0	5.2	0	0	3.9	< 0.1	81.0
66/8.8	100.0	8.0	16.7	36.4	31.0	7.4	0.4	0	0.3	0.2	80.9
69/8.9	300.0	11.6	17.7	33.8	28.1	5.4	0.1	0	3.3	0.3	80.9

Table A5. *Cont.*

Transect Distance/ Depth (m)	Density (ind.m^{-2})	VC Sand	C Sand	M Sand	F Sand	VF Sand	Silt	Clay	Gravel	OM	CaCO$_3$
71/9.1	104.4	13.3	19.2	32.1	27.8	5.9	0.2	0	1.4	0.1	80.6
74/9.1	155.6	11.3	15.4	32.5	26.8	9.2	0.4	0	4.5	0.2	82.2
75/9.1	375.0	5.4	11.5	26.5	32.6	8.8	15.3	0	0.0	0.1	81.1
77/9.2	350.0	8.5	13.7	30.7	31.8	11.5	0.1	0	0.4	0.3	81.1
77/9.2	124.4	14.8	19.4	29.5	27.0	7.6	0	0	1.8	0.1	83.2
78/9.3	38.9	8.2	11.9	22.0	29.2	8.5	19.8	0	0.4	0.2	79.3
80/9.4	48.9	7.7	13.7	34.0	35. 5	9.1	0	0	0.1	0.1	82.3
85/9.5	54.4	13.6	21.7	27.9	25.3	5.4	0	0	6.1	0.1	84.3
86/9.6	31.1	10.1	18.5	21.8	16.1	12.1	17.8	0	3.5	0.2	83.0
87/9.5	210.0	8.1	11.2	22.4	29.0	8.8	19.8	0	0. 7	0.2	82.0
90/9.5	60.0	19.0	22.1	21.8	19.9	9.2	0.1	0	7.9	0.2	83.6
91/9.5	132.2	15.5	22.8	25.7	20.5	10.2	0.7	0	4.6	0.1	82.6
92/9.5	200	11.9	20.0	23.6	20.0	6.5	8.5	9.3	0	0.5	79.4
95/9.7	165.6	11.3	20.9	20.6	13.8	11.5	12.0	5.9	3.8	0.2	83.2
96/9.7	325	12.2	14.3	15.9	21.0	9.9	12.7	11.0	3.1	0.3	81.8
96/9.7	145.6	5.0	14.3	17.3	24.5	10.2	17.9	5.5	1.3	0.2	81.9
100/9.9	77.8	5.4	13.8	18.5	24.3	14.2	22.6	0	1.2	0.2	81.3
105/10.1	121.1	11.0	17.5	17.4	22.1	12.7	18.2	0	1.0	0.2	82.7
109/10.1	225	4.7	11.8	14.2	24.1	16.0	23.5	5.3	0.3	0.2	78.5
110/10.1	111.1	6.5	14.7	18.3	26.5	14.7	19.3	0	0	0.1	84.2
112/10.3	125.6	4.3	9.9	12.7	19.2	25.3	17.1	11.4	0	0.2	81.6
114/10.4	33.3	2.5	10.4	15.4	21.3	21.3	23.4	5.8	0	0.4	82.4
115/10.4	121.1	3.5	8.9	12.4	24.3	22.4	28.1	0.1	0.2	0.3	81.2
118/10.5	50.0	5.5	11.9	14.1	20.4	22.5	17.1	8.5	0	0.4	74.4
119/10.0	53.3	5.3	11.9	12.9	16.4	17.6	21.2	14.1	0.6	0.7	70
120/10.1	91.1	3.3	8.1	9.5	13.9	20.9	34.5	9.9	0	0.6	79.6
122/10.4	30.0	2.1	10.6	14.5	18.0	25.2	23.6	5.9	0	0.5	81.9
127/11.1	0.0	1.4	7.2	10.4	11.4	24.7	34.9	10.0	3.7	0.1	81.1
129/11.2	37.8	1.1	6.1	9.1	9.1	23.8	37.3	14.0	0	0.8	77.5
130/11.4	5.6	2.1	7.0	11.5	11.5	16.5	42.1	9.3	0	0.8	78.4
133/11.8	45.6	0.5	5.7	9.8	8.7	18.8	39.1	17.4	0	1.9	76.9

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