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Persistent benthic communities in the extreme dynamic intertidal mudflats of the Amazonian coast: an overview of the Tanaidacea (Crustacea, Peracarida)

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Abstract The extreme dynamics of the Amazonian coast and associated mudbanks raises questions about their unknown resistant infauna. In order to fill the gap, we investigated the seasonal variations of species composition, abundance and population structure of Tanaidacea in two dynamic mudbanks near the coast of French Guiana. Despite the low species richness recorded for this taxon, the very high densities and biomass of tanaids constituted a potential plentiful trophic resource for many coastal species, such as shorebirds, fish, shrimps, and crabs. The estuarine habitat at Sinnamary presented more tanaid species than the bare marine mudflat at Awala-Yalimapo. All species showed strong female-biased sex ratios and differed in range of total length and stage of maturity. The species with smaller body size with sexual maturity occurring at an earlier stage were dominant and widely distributed. Pore water salinity and predator pressure may be considered key factors driving seasonal variations of tanaid abundance and population structure. This study gives a novel insight into the macrobenthos communities along the highly dynamic Amazonian coast.

Introduction

Tanaidacea is an order of crustaceans which includes approximately 1,300 described species belonging to the superorder of Peracarida (Anderson and Blazewicz 2016). Most tanaids inhabit marine demersal environments either interstitially or in burrows, sometimes constructing tubes in sediment (Blazewicz-Paszkowycz et al. 2012). These crustaceans have been found in several types of marine habitats, from coastal mudflats to the deepest abyssal shelves, and even in extreme ecosystems such as underwater caves, hydrothermal vents, mud volcanoes and seabed pock-marks (Blazewicz-Paszkowycz et al. 2012). A few species have also been recorded in freshwater environments (Gardiner 1975; Bamber 2008). So far, although most tanaids are among the smallest macrobenthic organisms, their abundance, sometimes with surprisingly high densities, suggests their ecological importance in marine ecosystems (Marshall 1979; Delille et al. 1985; Baldinger and Gable 1996; Blazewicz-Paszkowycz and Jazdzewski 2000).

In spite of high densities recorded, for instance, in intertidal mudflats, the knowledge of tanaids in relation to their various and extreme environments has, paradoxically, been, until recently, limited. Studies on the abundance and dynamics of tanaids in intertidal habitats have mostly been carried out in

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the Americas (Gardiner 1975; Levings and Rafi 1978; Kneib 1992; Krasnow and Taghon 1997; Talley and Ibarra-Obando 2000; Lucero et al. 2006; Freitas-Junior et al. 2013), while fewer have been carried out in other continents (Johnson and Attrammadal 1982; Schrijvers et al. 1995).

On the coast of South America, tanaids can be very abundant, with densities often exceeding 10,000 ind. m^{-2} in intertidal mudflats (Swennen et al. 1982; Freitas-Junior et al. 2013). It has been observed that the fluctuation of tanaid density displays spatial and seasonal variations, while their various life strategies influence the population structure among different tanaidacean species (Leite et al. 2003; Freitas-Junior et al. 2013; Rumbold et al. 2014, 2015). In South American mudflat habitats, tanaids might occupy the same ecological niche as the very well-studied amphipod *Corophium volutator* found in the mudflats from northern Atlantic coasts. Tanaids could represent a prime and crucial food resource for many shorebirds and fish foraging on exposed or flooded mudflats (Swennen et al. 1982; Wakabara et al. 1993; Ferreira et al. 2005; Corrêa and Uieda 2007; Barreiros et al. 2009; Pennafirme and Soares-Gomes 2009). Despite their relevant function in many trophic webs in all the oceans, very few studies have been carried out on the abundance and function of this group on the gigantic intertidal mudbanks along the 1,500 km length of the Guiana's coast in South America. Only two studies have reported the presence of three tanaid species on the coasts of Suriname (Bacescu and Gutu 1975; Swennen et al. 1982) and French Guiana (Clavier 1999). The recent discovery of a fourth species, *Monokalliapseudes guianae* (Drumm et al. 2015), proves the lack of knowledge on these shrimp-like crutaceans in such an unique environment.

The 320 km of coast of French Guiana is strongly affected by the large amounts of fine-grained discharges from the Amazon River (Plaziat and Augustinus 2004; Lambs et al. 2007; Vantrepotte et al. 2013). Every year, the Amazonian suspended sediment load can reach about 800 million metric tons (Martinez et al. 2009). Around 15–20% of these sediments migrate north-westward (1–4 km year^{-1}) along the coast of the Guianas by means of ocean waves, tidal force and coastal currents. This singularity leads to the formation of the most morphodynamic mud banks in the world (Eisma et al. 1991; Allison et al. 2000; Froidefond et al. 2004; Gardel and Gratiot 2005; Anthony et al. 2011; Péron et al. 2013; Gensac et al. 2015). The structure of the mudbanks has been subdivided into three parts: the leading edge of the bank, the consolidated mudflat and the trailing edge (Gensac et al. 2015). The intertidal topography is smooth with a gentle slope of 1:2000 (Gardel and Gratiot 2005), and more than 85% of granulometric composition is silt and clay (Dupuy et al. 2015; Gensac et al. 2015). In addition, the mud properties and consolidation are not only associated with bed elevation within the tidal frame but also influenced by the seasonal changes,

which are mainly related to the decrease of rainfall in the dry season (Gratiot et al. 2007; Lambs et al. 2007; Anthony et al. 2011). However, contrary to many studies of this extreme ecosystem on Guiana's coast, the composition and the structure of the infauna remain largely unexplored. This study aimed to describe (1) the species richness of tanaidacean communities in the intertidal mudflats of French Guiana coast; (2) the population structure of three tanaid species; and (3) the abundances of the main species in relation to the different substrate characteristics and their responses to seasonal variables.

Materials and methods

Study sites

The study was carried out on two out of six mudbanks moving along the coast of French Guiana at the time of the study: Awala-Yalimapo (05°44′N, 53°55′W) and Sinnamary (05°27′N, 53°00′W) mudbanks. According to Plaziat and Augustinus (2004), the evolution of mudbanks in Awala-Yalimapo has been characterized by a gradual overall westward extension of the mud cape along the coast, without either intensive erosion or accretion, whereas in Sinnamary, the mudbank has undergone several consecutive accumulations and erosion phases (Fromard et al. 2004). During our sampling time, Sinnamary mudbank was migrating westward with most of the intertidal part having crossed the Sinnamary River Sector (Gensac et al. 2015; Fig. 1). Both mudbanks constitute a meso-tidal system with semidiurnal tidal range between 0.8 m (neap tide) and 2.9 m (spring tide). The choice of these sites was driven by their reliable location and notably their proximity to the main rivers, Sinnamary and Maroni. Nevertheless, they exhibit contrasting conditions as the Sinnamary station is more exposed to the river flow (estuarine mudflat), compared to Awala, which is less exposed and qualified as a seafront mudflat. The climate is tropical and humid, with a long rainy season from January to July (wet season) and a strict dry season from August to the end of December.

Sample collections and laboratory processes

Samples were collected in 2014 in the intertidal area during the wet season (WS, May–June) and late in the dry season (DS, November–December) at three stations in Awala-Yalimapo (Awa1, Awa2 and Awa3) and one station in Sinnamary (Sinna), (Table 1; Fig. 1). The three stations in Awala present a gradient of mud consolidation and were sampled along an intertidal transect parallel to the coast, while the station in Sinnamary was close to the estuary (Table 1). Considering the dynamics of the system, the samples were collected in the same habitat (the same consolidation stage
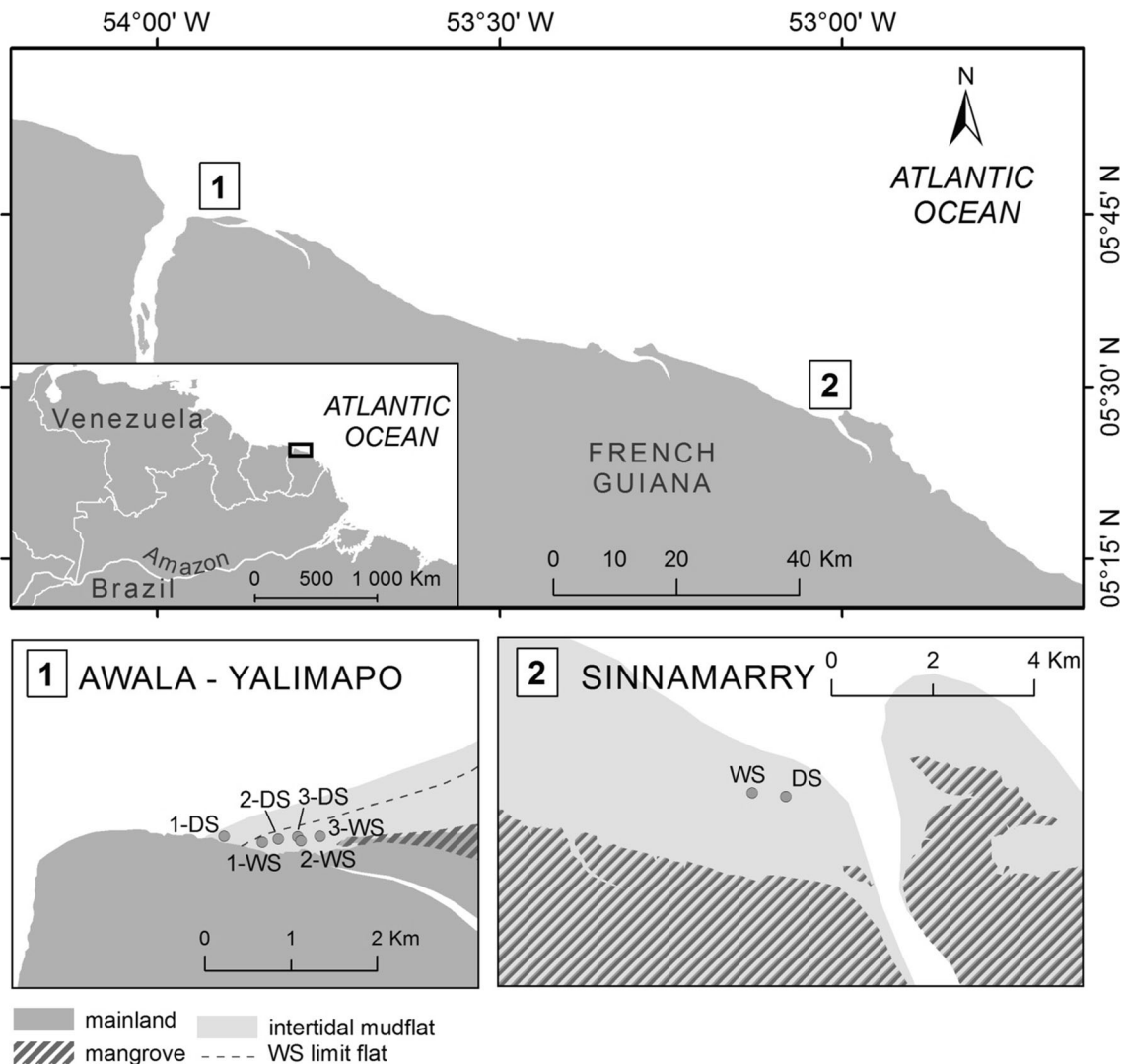
Fig. 1 Location of study sites and sampling stations on the Guiana coast

of mud) rather than in the same location in the two sampling seasons. Consequently, stations with the same name have different geographic coordinates according to the sampling season, as presented in Table 1. In addition, only in the dry season, during the lowest tidal level and apart from the sampling station, we collected tanaids at another station on the riverside waterfront mud in Sinnamary. This additional sampling was carried out due to the presence of prominent aggregations of infauna tubes on the surface of the sediment.

For each station, ten replicates were taken with a core (15 cm diameter) to a depth of 20 cm. The sediment was then sieved through a 500-μm mesh and the retained infauna were preserved in 70% alcohol (final concentration). At the same time, the sediment temperature (0-5 cm depth) was measured by thermal probe (Hobo Pro V2; USA). Pore water was extracted by means of Rhizon samplers (0–2 cm depth), and its salinity was estimated in situ using a refractometer (Atago S-10; Japan). Organic matter in the sediment was estimated

according to method of Wollast (1989) and presented as the percentage of total matter. Water content of the sediment was measured by the formula: water content $= [(M_t - M_s)/M_t] \times 100$, where M_t is the mass of the wet sediment and M_s is the mass of the oven-dried sediment (60 °C, 24 h).

In the laboratory, the samples were washed again on a 300-μm-mesh sieve and stained with Rose Bengal. Tanaids were sorted and counted under a binocular microscope (×4; Olympus SZ30). A Motoda splitting box was applied to the replicates with very high abundances of tanaids (Motoda 1959). Observations of criteria for identification to species level were carried out using a stereomicroscope (×40; Leica M205 C). Species identifications were achieved according to the criteria from Bacescu and Gutu (1975) and Drumm et al. (2015). Specimens of each species were sorted and separated into three groups: males, females and juveniles, according to Rumbold et al. (2014). The sexual difference was based on the presence of genital cones in the male pereonite VI. All tanaids

Table 1 Station locations and general information

Site	Season	Code	Coordinates	Description
Awala-Yalimapo				
Station 1	Wet season 02/06/2014	Awa1-WS	05°44′44″N 53°55′38″W	The leading edge of the mudbank. Low intertidal elevation. Fluid mud at the surface
	Dry season 22/11/2014	Awa1-DS	05°44′46″N 53°55′53″W	
Station 2	Wet season 31/05/2014	Awa2-WS	05°44′44″N 53°55′24″W	500 m from the edge of the mudbank. Mid-intertidal elevation. Moderately compacted mud (soft mud).
	Dry season 30/11/2014	Awa2-DS	05°44′45″N 53°55′32″W	
Station 3	Wet season 01/06/2014	Awa3-WS	05°44′46″N 53°55′17″W	700 m from the edge of the mud bank. High intertidal elevation. Compacted mud, in front of pioneer stage of mangrove colonization
	Dry season 29/11/2014	Awa3-DS	05°44′46″N 53°55′25″W	
Sinnamary	Wet season 27/05/2014	Sinna-WS	05°28′27″N 53°01′54″W	The riverside of the mud bank. Estuary of Sinnamary River. Very soft mud
	Dry season 25/11/2016	Sinna-DS	05°28′24″N 53°01′32″W	

which measured less than the smallest identifiable males were considered as juveniles, except for those possessing visible ovisacs. Sex ratio [proportion of males = males/(males + females)] was then calculated based on Rumbold et al. (2012, 2014). When possible, at least 30 random individuals per replicate were measured under a stereomicroscope at the nearest 0.1 mm from the tip of the rostrum to the distal medial margin of the pleotelson (total length) and from the widest part of the carapace (total width). Biomass (wet mass) was calculated from body measurements using the equation: biomass $(\mu g) = 1.13 \times 400 \times LW^2$ [L = length (mm), W = width (mm)] as in Wieser (1960) and Warwick and Gee (1984).

Statistical analyses

All statistical analyses were conducted with STATISTICA 7. To evaluate the spatiotemporal variation of abiotic parameters and tanaids (factors: stations and seasons), two-way ANOVA was conducted on data of environmental variables, densities, biomasses and numbers of males, females and juveniles of *Halmyrapseudes spaansi*. Post hoc comparisons were performed with Tukey's HSD tests whenever there were significant differences of means in previous ANOVA tests. Student's *t* test was applied to compare the differences of density and biomass of *Dicapseudes surinamensis* in two seasons as it only occurred at one station. The chi-square test (χ^2) with Yates correction was used to verify the possible differences of sex ratio from an expected ratio 1:1. Principal component analysis (PCA) and Person's correlation coefficient were applied to elucidate the interaction between tanaids and environmental variables.

Results

Environmental parameters

Pore water salinity showed significant variation between seasons. In the dry season (DS), salinities were double to triple those in the wet season (WS) at all stations (two-way ANOVA, $p < 0.05$) (Table 2). Salinity was also significantly different between the four stations in DS and between both sites in the WS (Tukey HSD test, $p < 0.05$). Among all stations, Sinnamary had the lowest water salinity in the WS and DS, 8.2 ± 0.4 PSU and 16.0 ± 0.9 PSU, respectively. At Awala, salinity in the DS increased proportionally with the gradient of mud consolidation along the coast. The lowest value $(31.3 \pm 2.6$ PSU) was found at the fluid mud station (Awa1) while the consolidated mud flat (Awa3) had the highest value $(46.5 \pm 3.5$ PSU). In contrast, salinity was not significantly different between stations at Awala during the WS (Tukey HSD test, $p > 0.05$).

The mud temperature ranged from 29.4 °C (Awa2) to 31.5 °C (Awa3) in WS and from 29.0 °C (Awa1) to 33.2 °C (Awa3) in the DS. Sediment temperature showed no significant differences between stations in the WS (Tukey HSD test, $p > 0.05$). In the DS, Awa1 temperature was significantly lower than Awa2, Awa3 and Sinnamary, but it did not differ from the value of Awa1 in the WS. Awa2 had a higher mud temperature in the DS while no significant difference was found at Awa3 between the two seasons. Water contents did not differ between the four stations or between seasons (Table 2), except for the values measured at Sinnamary during the DS, which had significant difference with the water content at the same

Table 2 Means (± SD) of environmental variables in four stations

Stations	Pore water salinity (‰)	Mud temperature (°C)	Water content (%)	Organic matter (%)
Awa1-WS	14.3 ± 0.5 b	30.0 ± 0.3 abgf	63.4 ± 2.9 cd	6.8 ± 1.9 a
Awa2-WS	12.2 ± 0.5 ab	29.4 ± 0.5 abf	60.6 ± 4.4 cd	6.0 ± 1.3 a
Awa3-WS	14.9 ± 1.8 b	31.5 ± 0.4 cdef	57.6 ± 2.5 cd	6.2 ± 1.5 a
Sinna-WS	8.2 ± 0.4 a	31.0 ± 1.6 ac	54.9 ± 2.3 ac	5.6 ± 0.8 a
Awa1-DS	31.3 ± 2.6 c	29.0 ± 0.3 abe	58.3 ± 1.9 cd	5.3 ± 0.1 a
Awa2-DS	42.3 ± 3 c	32.1 ± 0.5 cdg	62.0 ± 7.9 cd	6.5 ± 0.8 a
Awa3-DS	46.5 ± 3.5 c	33.2 ± 0.1 cd	57.8 ± 1.6 cd	5.9 ± 0.6 a
Sinna-DS	16.0 ± 0.9 b	33.0 ± 1.6 c	71.7 ± 11.2 bd	11.3 ± 5.1 a

Lowercase letters represent differences as determined by the Tukey HSD post hoc test. Different letters in columns are significant at 5%

site in the WS (Tukey HSD test, $p < 0.05$). No significant differences between stations and seasons were found for organic matter of the sediments (two-way ANOVA, $p > 0.05$).

Diversity of Tanaids

Three species were present in the samples: *Halmyrapseudes spaansi*, *Discapseudes surinamensis* and *Monokalliapseudes guianae* (Fig. 2). Among those, *D. surinamensis* and *H. spaansi* are interstitially free-living species and are members of the family Parapseudidae, while *M. guianae* is a persistently tubiculous animal and belongs to the family Kalliapseudidae. The number of species at Sinnamary was higher than at Awala, with the occurrence of all three species. At Awala, only *H. spaansi* was present in the mudflat (Fig. 2). In addition, it is worth highlighting that *M. guianae* was first discovered from the second field trip in November 2014 and recently described as a new species (Drumm et al. 2015). The incident discovery of this new species from the extra station in the same mud bank at Sinnamary, but at a distance from the designed sampling location, increased the up-to-date records of tanaid species found in Guianan mudflats to 4 species: *D. holthuisi* (a single occurrence near the mouth of a tidal

creek in Suriname), *D. surinamensis*, *H. spaansi* and *M. guianae*. However, as we were not aware of its existence during our first sampling period in May 2014, no sample was collected, which consequently left data of *M. guianae* in the WS unavailable. For this reason, the information on *M. guianae* abundance was excluded from the statistical analyses and hence not considered in this study.

Tanaid density and biomass variations

The tanaid *H. spaansi* was the most abundant and widely distributed species at the two sites. Densities and biomasses of *H. spaansi* differed significantly between stations and seasons (two-way ANOVA, $p < 0.05$) (Table 4). The highest mean density was found at Sinnamary during the WS ($24,259 \pm 10,857$ ind. m^{-2}). The station Awa2-WS was the second most abundant station for this species ($12,488 \pm 22,975$ ind. m^{-2}) but was not significantly different from Sinna-WS. However, this tanaid showed a strong patchy distribution with, for instance, a density up to c. 77,000 ind. m^{-2} in one of the replicates in Awa2-WS. The other two stations in Awala had lowest *H. spaansi* mean densities in the WS, ranging between 1,244 and 1,429 ind. m^{-2} and showed no

Fig. 2 The three tanaidacean species per age and sex occurring on the French Guiana coast
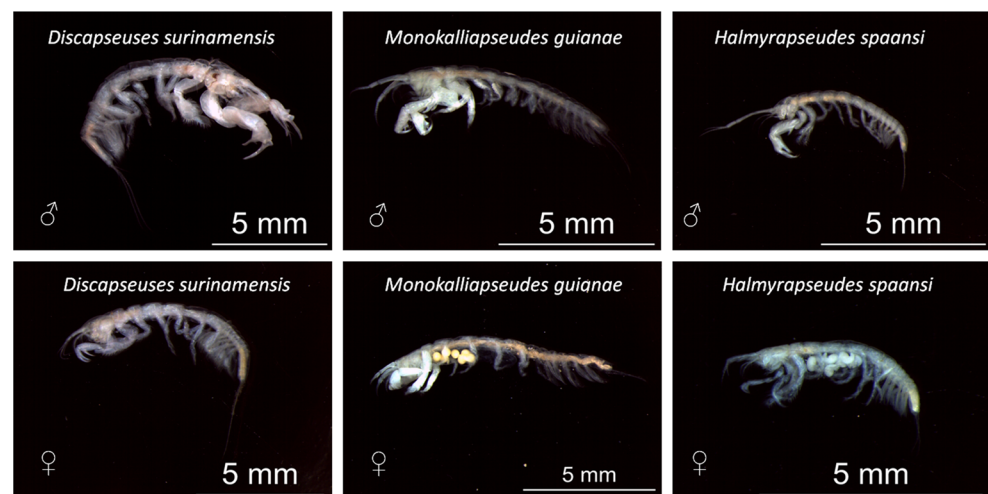
Table 3 Mean densities and biomasses (±SD) and range (min–max) of *Halmyrapseudes spaansi* and *Discapseudes surinamensis* at the four stations.

Stations	*Halmyrapseudes spaansi*		*Discapseudes surinamensis*	
	Density (ind/m^2)	Biomass (g/m^2)	Density (ind/m^2)	Biomass (g/m^2)
Awa1-WS	1,244 ± 514 (280–2,072) b	1.5 ± 0.7 (0.2–2.5) b	0	0
Awa2-WS	12,488 ± 22,975 (616–77,065) ab	12.1 ± 24.2 (0.3–80.5) ab	0	0
Awa3-WS	1,429 ± 2,579 (0–7,168) b	0.9 ± 2.2 (0.0–6.9) b	0	0
Sinna-WS	24,259 ± 10,857 (8,736–38,528) a	19.8 ± 9.7 (6.8–37.0) a	241 ± 132 (56–504) b	1.7 ± 0.3 (0.4–2.9) b
Awa1-DS	431 ± 509 (112–1736) b	0.2 ± 0.2 (0.1–0.8) b	0	0
Awa2-DS	28 ± 40 (0–112) b	0.015 ± 0.020 (0.000–0.06) b	0	0
Awa3–DS	11 ± 24 (0–56) b	0.009 ± 0.020 (0–0.08) b	0	0
Sinna-DS	12,566 ± 6,541 (6,048–24,192) ab	10.9 ± 6.5 (5.4–23.8) ab	291 ± 231 (0–784) b	1.6 ± 0.4 (0.0–4.5) b

Lowercase letters represent differences as determined by the Tukey HSD post hoc test. Different letters within columns are significant at 5%

significant differences between each other (Tukey HSD test, $p > 0.05$), but significant differences from Sinna-WS. In samples from the DS, despite the number of *H. spaansi* decreased by half, and no significant difference was found between densities between the two seasons at Sinnamary (Tukey HSD test, $p > 0.05$). In Awala in the DS, there was a drastic reduction in number in all stations where the mean number dropped to 431 ind. m^{-2}, 28 ind. m^{-2} and 11 ind. m^{-2} in Awa1-DS, Awa2-DS and Awa3-DS, respectively.

The variations of *H. spaansi* biomass were strongly correlated with the density changes. Sinna-WS, thus, had the highest mean biomass (19.8 ± 9.7 g. m^{-2}) while the lowest biomass was found at Awa3-DS (0.009 ± 0.020 g. m^{-2}). In contrast, density and biomass of *D. surinamensis*, the species only occurring at Sinnamary, did not significantly differ between seasons (*t* test, $p > 0.05$). However, due to its larger body size, despite presenting much lower densities (40–100 times less than *H. spaansi* density), its biomass contributed to 6–12% total tanaid biomass in Sinnamary in both seasons (1.7 ± 0.3 g. m^{-2} and 1.6 ± 0.4 g. m^{-2} in the WS and DS, respectively) (Table 3).

Sex and age ratio

The number of males, females and juveniles of *H. spaansi* were significantly different among stations and seasons (two-way ANOVA, $p < 0.001$) (Table 4) and the sex ratio of this species was skewed towards females (χ^2 test, $p < 0.05$) (Fig. 3). The sex ratio was of 0.36 in the WS and 0.29 in the DS at Sinnamary and of 0.47 in the WS and 0.33 in the DS at Awala. Observation of ovigerous females and juveniles in both seasons for all stations suggested that reproduction occurred over the whole year but with potential differences in intensity. In addition, the percentage of juveniles increased from 26.1 to 47.8% in Awala, and decreased from 31.6 to 10.0% in Sinnamary in the WS and DS, respectively (data not shown). With regard to *D. surinamensis*, the sex ratio

decreased from 0.73 in the WS to 0.50 in the DS, while the proportion of juveniles increased from 6.9% in the WS to 25.0% in the DS.

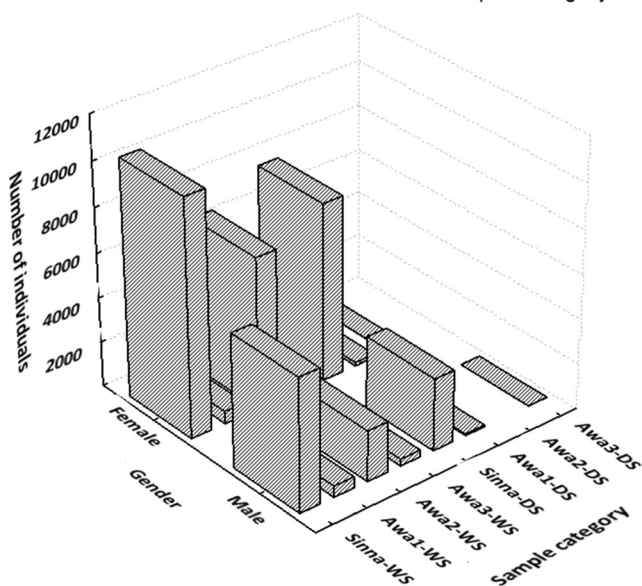### Size frequency distribution

H. spaansi was the smallest tanaid species in the French Guiana mudflat, with total length ranging from 1.1 to 6.4 mm (Fig. 4). The mean total length of females, males and juveniles in the WS were 4.4 ± 0.7 mm, 4.5 ± 0.6 mm and 2.5 ± 0.4 mm, respectively. The mean sizes of females and males decreased in the DS , with a mean total length of 3.9 ± 0.4 mm for females and 4.1 ± 0.4 mm for males. The mean juvenile length remained around 2.5 mm in both seasons. The juveniles of *H. spaansi* differed in length between stations (Kruskal–Wallis test, $p < 0.05$) with Awa3-DS hosting smaller *H. spaansi* juveniles than at other stations. There were

Table 4 Results of two-way ANOVA for comparison of *Halmyrapseudes spaansi* males, females, juveniles between different stations in two seasons (since this is the only species occurring at all stations).

Comparison		SS	df	MS	F	p
Male	Station	2.64E + 08	3	88,033,622	21.92467	*
	Season	41184500	1	41,184,500	10.25695	*
	Station × season	24221641	3	8,073,880	2.01079	–
	Error	2.89E + 08	72	4,015,278		
Female	Station	1.07E + 09	3	3.57E + 08	12.63484	*
	Season	1.35E + 08	1	1.35E + 08	4.79415	*
	Station × season	1.32E + 08	3	44,154,514	1.56426	–
	Error	2.03E + 09	72	28,227,066		
Juvenile	Station	2.45E + 08	3	81,644,192	12.99372	*
	Season	1.24E + 08	1	1.24E + 08	19.81114	*
	Station × season	1.28E + 08	3	42,608,466	6.78116	*
	Error	4.52E + 08	72	6,283,359		

*Significant difference at 5%

Fig. 3 Bivariate distribution of Chi-square test with Yates correction results, at level of 0.05, to verify the possible differences among *H. spaansi* sex ratio per station and season

no significant differences in total length between adult females and adult males between stations. However, both females and males in the WS were respectively larger than the females and males found in the DS (Kruskal–Wallis test, $p < 0.05$). The smallest differentiated male was 3.4 mm long, while the smallest female was 3.3 mm.

D. surinamensis had a total mean length which ranged from 4.5 to 12.8 mm. The smallest differentiated male was 6.2 mm while the smallest female was 7.0 mm. The mean total length of males was 8.6 ± 1.6 mm in WS and 8.8 ± 1.0 mm in the DS while this was 9.2 ± 1.5 mm and 8.4 ± 0.9 mm for females. Males did not significantly differ from females in total length between two seasons (two-way ANOVA test, $p > 0.05$).

M. guianae showed a wide range in total length, which fluctuated from 1.7 to 13.4 mm. The beginning of sexual differentiation occurred at 4.6 mm and 4.9 mm for males and females, respectively. *M. guianae* females (7.5 ± 1.8 mm in the DS) were larger than males (6.1 ± 1.0 mm in the DS) (Mann–Whitney U test, $p < 0.001$).

Tanaid distributions in relation to environmental parameters

Axes 1, 2 and 3 of the PCA explained 94.1% of the variation of the six original variables (axis 1: 48.6%; axis 2: 29.5%; and axis 3 explained 15.9%) (Fig. 5). Axis 1 was correlated with the density of *D. surinamensis* and organic matter, while the second axis was represented by pore water salinity. *H. spaansi* was well represented by both axes 1 and 2. The sediment temperature was not well represented by axis 3 since it was

correlated to the three factors together (Factor 1: −0.61; Factor 2: −0.41; Factor 3: 0.63). Multiple regression analyses indicated significant positive correlations between organic matter and water content, and between *D. surinamensis* and *H. spaansi* densities (Pearson's correlation, $p < 0.05$).

Vector projection and mapping variables showed a clear discrimination of tanaid distribution correlated to sampling sites and seasonal changes (Fig. 6). At Sinnamary, the stations were characterized by high abundance of both *D. surinamensis* and *H. spaansi*, and lower pore water salinity in comparison with stations at Awala. The density of *D. surinamensis* and organic matter increased from the WS to the DS at Sinnamary, but there was no significant correlation between these two variables. On the right side of axis 1, stations collected from Awala were grouped and seemed to be characterized only by *H. spaansi* with lower density. The seasonal induced-change was found along axis 2, which was represented by a gradient of pore water salinity. Samples collected in WS with lower salinity were all mapped on the upper part of axis 2, while the DS samples were placed on the lower part of axis 2, except for Awa1. The station Awa1 in the DS stayed close to the bunch of Awala stations in the WS, where it had similar sediment temperature, water content, and organic matter (Turkey HSD test, $p > 0.05$) except for its higher salinity.

Discussion

Diversity of Tanaidaceans in Guiana's mudflats

In this study, for the first time, the population structure of three tanaidacean species of the Guiana mudflats and the abundance of the two dominant species have been described. Differences in distribution were observed between the three species. Thus, *Halmyrapseudes spaansi*, *Discapseudes surinamensis* and *Monokalliapseudes guianae* were present on the estuarine mudflat in Sinnamary while only *H. spaansi* was found in the bare mudflat of Awala. The occurrence of *H. spaansi* with high densities and biomasses at all stations implies a wider range of habitats for this smaller tanaid species, as well as its probable major role in the mudflat ecosystem. To date, this species was found inhabiting the bare mudflat habitats with the most prominent density in comparison with other infauna species of French Guiana and Suriname (Bacescu and Gutu 1975; Jourde et al. 2017), and less abundantly in the eastern mangrove habitats such as the Brazilian Amazonian Coast (Beasley et al. 2010) and northern Brazilian salt marshes (Braga et al. 2011). In contrast, the larger tanaid *D. surinamensis* was exclusively abundant (up to c. 8,000 ind. m^{-2}) in the consolidated part of a long existing mudbank, while it rarely occurred in the leading edge of the mudflat (Swennen et al. 1982; Jourde et al. 2017). This conformed to
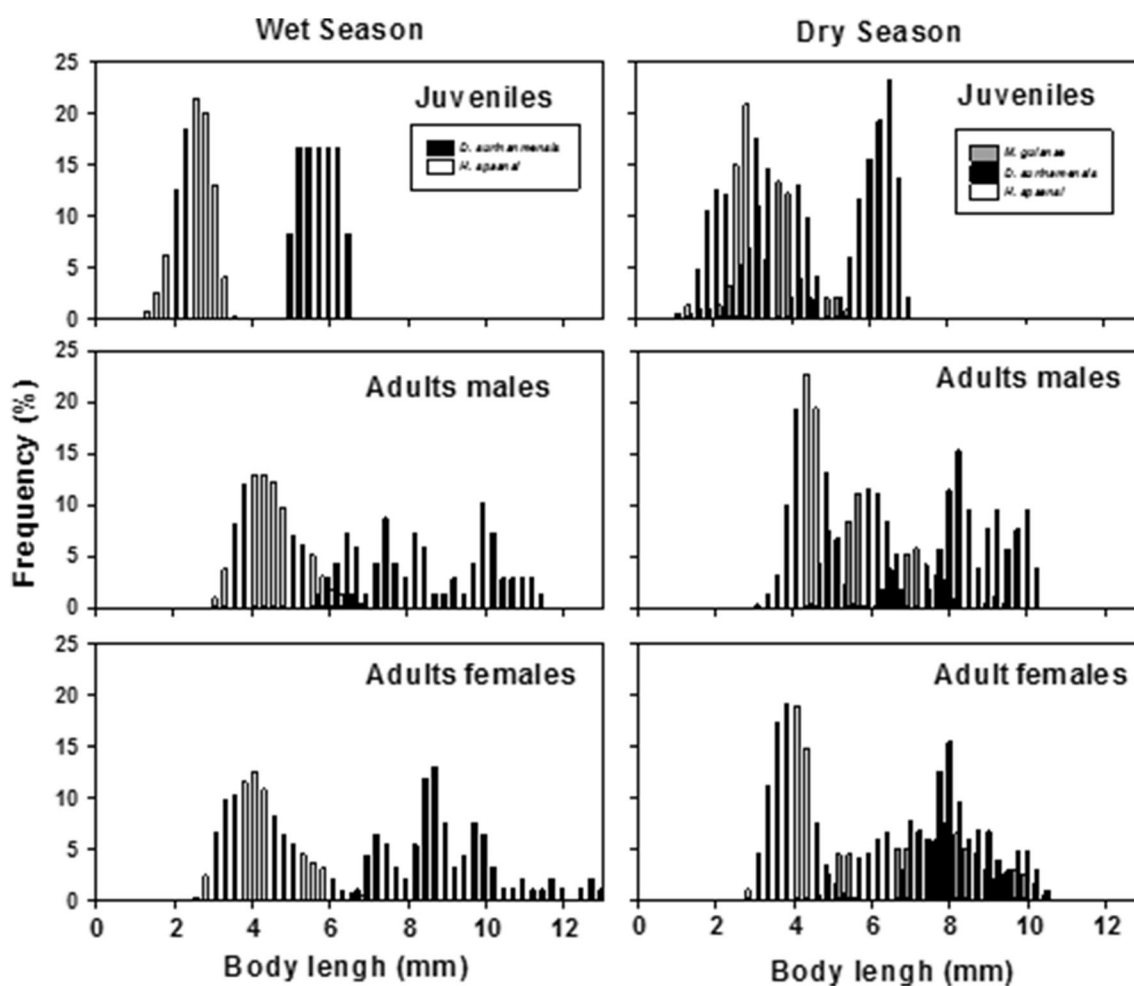
Fig. 4 Frequency distribution of the total length of males, females and juveniles of three tanaid species occurring in French Guiana

our results as *D. surinamensis* was only found at Sinnamary (the relatively stable center part of a migrating mudflat) except for the much lower densities of this species.
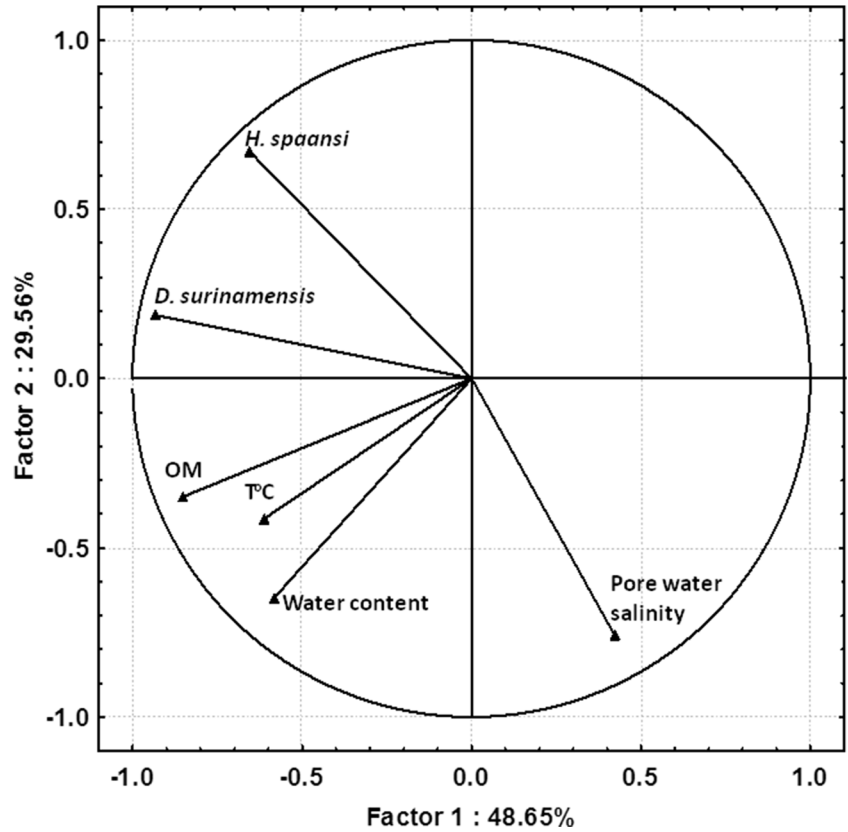
Spatial distribution

Changing sediment properties, wave-induced shear stress, and duration of submergence and exposure are believed to be among the most important factors structuring intertidal infaunal assemblages (Hertweck 1994; Raffaelli and Hawkins 1996). In agreement, our results showed a distinct segregation of the distribution of tanaid species in relation to different substrate characteristics between both sampling mudflats. Diversity and density of tanaids were higher in the mudbank of Sinnamary. A possible reason could be lower pore water salinity and mitigating wave energy at this station in comparison with those of the seafront bare mudflat at in Awala. Furthermore, the Sinnamary station was located on the middle part of a migrating mudbank, in which the sediment was more stabilized (Lefebvre et al. 2004; Gensac et al. 2015) relative to the one collected on the leading edge of the mudflat at Awala,

which has undergone an accretion stage with highly dynamic muddy substrates. The higher macrofauna diversity and biomass on the estuarine mudflats was also reported in Artigas et al. (2003), while the same tendency of very low benthic diversity at the head of the Awala mudbank was observed in the studies of Dupuy et al. (2015) for meiofauna community and Jourde et al. (2017) for macrofauna community.

In addition, both *D. surinamensis* and *H. spaansi* are members of the family Parapseudidae, which probably contains omnivorous feeders (Kudinova-Pasternak 1991), whereas *M. guianae* belongs to the Kalliapseudidae, a family believed to be filter feeders based on the rows of long plumose setae on the chelipeds (Drumm 2005; Fonseca and D'Incao 2006; Blazewicz-Paszkowycz et al. 2012). The habitat of *M. guianae* therefore differed from the two other species, since it was strictly limited to the riverside waterfront mud during low tide. This result concurred with the studies of Dankers and Beukema (1983) and Kamermans (1993), which also pointed out that the occurrence of some suspension feeders was restricted to the lower intertidal where their filter feeding benefited from longer submergence. Meanwhile, the

Fig. 5 Principal components and classification analysis. The projection of variables: *D. surinamensis* density, *H. spaansi* density, pore water salinity, water content, organic matter (*OM*) and sediment temperature (*T°C*) on the factor-plane (1 × 2)

two deposit feeders, *D. surinamensis* and *H. spaansi*, showed a very patchy distribution in the intertidal mudflats, which is consistent with the studies of Clavier (2000) and Jourde et al. (2017). A patchiness pattern has been observed quite frequently in the intertidal macrobenthic assemblages (Kraan et al. 2009), which is conceivably linked with the patchy

Fig. 6 Principal components and classification analysis. Projection of the stations on the factor-plane (1 ×). *Dotted ellipse* sampling site groups; *plain ellipse* seasonal groups
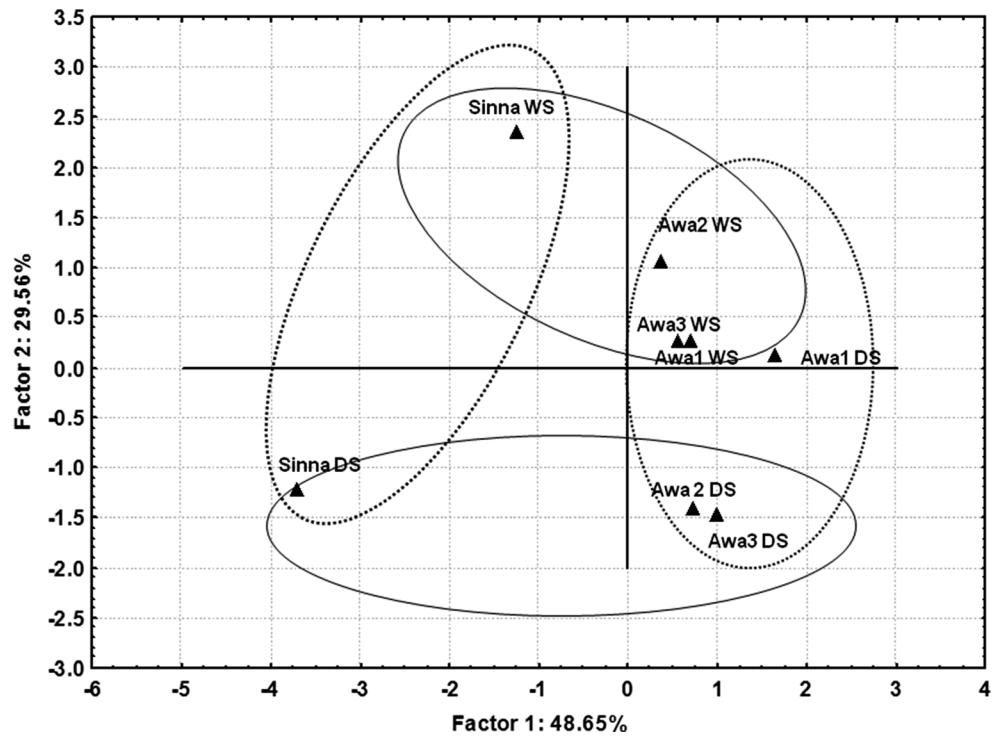
distribution of their potential food source such as the microphytobenthos (Beukeman and Cadée 1997; Compton et al. 2013).

The abundance of tanaids also differed spatially between stations in the mudflat of Awala. The stations Awa1 to Awa3 were sampled along a gradient of increasing sedimental consolidation, which, on the other hand, respectively presented an intertidal transect from the low toward high tide water marks. According to Dupuy et al. (2015) and Jourde et al. (2017), the granulometry in the Awala mudflat was largely compounded of fine mud and was similar in all three stations. In this study, the wet season presented no significant differences of pore water salinity, OM, water content and sediment temperature among the three stations. However, despite all these similarities, the mean density of tanaids (H. spaansi) increased from low towards mid-intertidal level and then decreased again in the high tide area. Similar patterns of distribution were observed in several studies such as Kneib (1984, 1992), Beukeman and Cadée (1997) and Dittmann (2000). In those studies, the natant predators were believed to control the infauna at lower tidal level. Hence, the macrobenthos densities increased with intertidal elevation, as the foraging time of aquatic predators is constrained by the frequency and duration of tidal submersion. Secondly, the desiccation effect on the high tide area during exposure duration (Beukeman 1976; Hertweck 1994) could be a possible elucidation for the lower density of tanaids in the high tide comparing to in the midtidal level. In this present study, the mean density of tanaids in the mid-tidal level was ten times higher than the ones at the low and high tide stations. In contrast, during the DS, when environmental conditions became harsh, the distribution of H. spaansi was completely different, and it was found mostly in the low tide station, while in the mid-tidal and high-tidal levels, the densities drastically decreased.

Seasonal variations

The seasonal changes in the abundance of tanaids were observed not only at Awala but also at Sinnamary. In the DS, the densities of the dominant H. spaansi declined sharply at Awala (70–99%) and by 50% at Sinnamary compared to the WS. Surprisingly, no seasonal difference in D. surinamensis densities was observed. The reduction in H. spaansi densities could be related to the escalating salinity in pore water (Figs. 5, 6). A profound increase in the value of the pore water salinity was recorded in the DS. At Sinnamary, although the pore water salinity values were double in the DS, the mudflat remained brackish (mesohaline habitat), whereas all stations at Awala moved from mesohaline in the WS to euhaline (Awa1, S > 30‰) and even to hyperhaline (Awa2, Awa3, S > 40‰) during the DS. This phenomenon could be due to the large decrease of precipitation in the DS and to a higher evaporation rate as a result of high temperature with constant duration of light exposure. Nevertheless, at Sinnamary, this impact was mitigated by the water discharge from the river, which possibly led to the maintenance of the species composition but with lower density of the most abundant species, H. spaansi. At Awala, the vigorous decline of tanaid densities was inversely proportional to the value of pore water salinity, which increased from low toward high tidal level, since periods of light exposure are shorter on the low intertidal where light penetration is restricted by highly turbid waters (Orvain et al. 2012; Geng et al. 2016). However, according to the literature, H. spaansi is seemingly highly adaptive to a wide range of salinity as it was abundantly recorded from any type of Guianan coastal habitats, from estuaries, intertidal mudflats, lagoons (Bacescu and Gutu 1975; Swennen et al. 1982) and even from saltmarshes (Braga et al. 2011) and mangroves (Beasley et al. 2010). Moreover, the densities of H. spaansi were significantly positively correlated with the presence of D. surinamensis (multiple regression analysis, p < 0.05). We suggest pore water salinity could be an important factor but not the only one that contributes to the seasonal change in tanaid abundance.

Menge (1995) found that indirect effects explained around 40% of the change in community structure when biotic and abiotic parameters were manipulated, and the predator–prey interaction was the most common type of indirect effect within these food webs. Observations of tanaids as an important food for some North American waders during their wintering period along the Amazonian coast were found in the studies of Bacescu and Gutu (1975) and Spaans (1978, 1979). Therefore, the occurrence of numerous migrating waders foraging on the mudflats along the coastline of French Guiana in the DS would be a further factor that possibly altered the tanaid abundance. Every year, the number of shorebirds such as sandpipers Calidris spp. migrating from North America can reach up to a million along the Guiana coast (Boyé et al. 2009). Our results agree with the findings of Peer et al. (1986), Hamilton et al. (2006) and Cheverie et al. (2014), which showed a decreasing tendency in prey density induced by a sudden increase of predators. Hamilton et al. (2006) also observed an 80% reduction in amphipod abundance in the Bay of Fundy and the predation by Semipalmated Sandpipers Calidris pusilla was responsible for approximately 55% of density loss. At Awala, the decreasing proportion of large adult tanaids (>3.3 mm) in comparison to the number of small juvenile (<3.3 mm) in the remained assemblages during the DS might be the result of size-selective feeding behavior of shorebirds during low tide (Peer et al. 1986, Hamilton et al. 2003, Cheverie et al. 2014) or fish during high tide (Kneib 1984, 1992). Moreover, both H. spaansi and D. surinamensis have been found in the stomach content of some migrating birds (Bacescu and Gutu 1975) and fish (Nguyen T.H., unpublished data).

Population structures

The sex ratio of *H. spaansi* and *D. surinamensis* showed the dominance of females whatever the mudflat or season considered. This strong female-biased sex ratio has frequently been found in other tanaid populations (Leite et al. 2003; Rumbold et al. 2012; Freitas-Junior et al. 2013). To date, several explanations have been proposed, which are mostly related to the different behavior of males and females during the reproductive stage (Wenner 1972; Mendoza 1982). The male tanaids were believed to have higher mortality due to their actively crawling to search for their mates, which possibly made male tanaids more exposed to predator. According to our results, a seasonal declining trend in proportion of males in relation to their predator's occurrence was observed that may support this hypothesis. Another possibility included intense competition among males to access females during their mating periods. The intrasexual battles over females, which might get the male tanaids serious injuries, were recorded in Highsmith (1983) and Thiel and Hinojosa (2010).

Finally, the reproductive activity took place in both seasons, which is in accordance with those of other tropical peracarid species (Thiel and Hinojosa 2010). The presence of both juveniles and ovigerous females in the population demonstrated strong evidence of a continuous reproductive strategy, which is beneficial for small crustaceans that carry few eggs. Nevertheless, the size of males and females in the DS was smaller than that in the WS. It is interesting that the mean total length of males and females in *H. spaansi* population was reduced during the foraging period of the migrating and wintering shorebirds. This result, therefore, supports the prey size selection tendency of the sandpipers (Peer et al. 1986; Hamilton et al. 2006). No such change was detected for *D. surinamensis*, which could be due to its relative low density in the samples. In addition, Rumbold et al. (2015) postulated that the sooner the crustaceans reach adulthood, the higher chance they can reproduce before being consumed by predators, which consequently result in more successful recruitment of the population. So the smallest size at sexual maturity of *H. spaansi* (M: 3.4 mm; F: 3.3 mm) could have been a remarkable advantage of this species, making *H. spaansi* the most abundant and widely distributed species in Guiana's mudflats. In contrast, *D. surinamensis*, with a larger maturity size (M: 6.2 mm; F: 7.0 mm), may be more impacted by predation, leading to unsuccessful recruitment, then gradually reducing its population size and/or narrowing its distribution. *M. guianae* is seemingly more adaptive, as its sexual maturity was reduced to 4.5 mm for males and 4.9 mm for female, although its adult size is as large as *D. surinamensis*. Furthermore, in this population, males are significantly smaller than females. This implies its capability of optimizing the chance to survival, as larger females would increase the fecundity rate (Rumbold et al. 2012) while

smaller males might reduce the risks of predation (Kakui 2015). And last but not least, by building residential tubes, *M. guianae* not only increases its protection from the predators (Johnson and Attramadal 1982) but might also contribute to the stabilization of the sediment it inhabits (Krasnow and Taghon 1997).

Conclusions

Tanaids are the major component of benthic communities in intertidal mudflats along the coast of Guiana in terms of both density and biomass. Despite the extreme morphodynamics of these mudbanks, the three species, especially *Halmyrapseudes spaansi*, are dominantly and patchily distributed in soft mud, offering a potential abundant trophic resource for many predator species. *H. spaansi* widely inhabits bare marine mudflats and estuarine habitats, whereas *D. surinamensis* and *M. guianae* seem to be less tolerant and occupy a more reduced part of the estuaries. The seasonal changes in densities of the tanaids were possibly driven by both abiotic and indirect factors, which were, respectively, pore water salinity and suspected predator pressure. All three species exhibited a dominance of females over males in their population structure. The differences in sexual maturity stages and size reflected the varieties of tanaid life strategies, among which species with smaller size and earlier adulthood seemed to be more resistant, hence being opportunistically developed. Nevertheless, further detailed studies are required to highlight the importance of tanaids in the structuring and functioning of this unique complex local food web in the absence of other macrofauna groups such as bivalves or large worms.

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