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13 FEVRIER 2018 UNIVERSITY OF LA ROCHELLE

Laboratoire Littoral, Environnement et SociétéS



# UNIVERSITÉ DE LA ROCHELLE ÉCOLE DOCTORALE GAY LUSSAC

Laboratoire Littoral, Environnement et SociétéS

# Thèse présentée par Thanh-Hien NGUYEN 13 February 2018

pour obtenir le grade de : Docteur de l'Université de La Rochelle

Spécialité : Biologie de l'environnement, des populations, écologie

# STRUCTURE AND FUNCTIONING OF THE BENTHIC COMMUNITIES IN THE EXTREME DYNAMIC INTERTIDAL MUDFLATS ALONG THE GUIANAS COASTS: TROPHIC FATE OF THE INFAUNA

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# Acknowledgements

The elaboration of this thesis would not have been possible without the supervision, collaboration and encouragement of many people to whom I would like to express my sincerest thanks.

First of all, I would like to thank my supervisors, Professor Christine Dupuy, Dr. Pierrick Bocher and Dr. Christel Lefrancois, for their continued support and contributions towards the compilation of this thesis and the work within it. Especially, Christine, you were always there for me, whether I needed to discuss data, papers, or my personal life, and listened to, and supported me throughout. Words could never be enough to express my gratitude.

Secondly, I would like to acknowledge the Ministry of Education and Training of Vietnam, the University of Science and Technology of Hanoi (USTH), who granted me a scholarship to pursue my PhD study. I am also grateful to my host institutions, LIENSs and University of La Rochelle, for kindly providing such a friendly working environment and for all the facilities needed for my thesis.

My special thanks also go to my husband for supporting every choice I have ever made. Thanks for helping me in many crucial points in my life, when I was about to give up, especially for your willingness to take care of our little son, therefore, I could totally focus on my study in France. For sure, you have endured having a PhD wife. Thank you for your patience, particularly, your trust in me through the three consecutive years I was living far away from home. For this and much more I will always be grateful to you.

I also want to thank to Jérôme Jourde for his invaluable guidance in macrofauna taxonomy and to Hélène Agogué for provided me great support and assistance during the "battle" with tiny specimens for molecular analyses. And to all the enthusiastic people who carried endless buckets of mud, your help was very much appreciated: Pierre-Yves Pascal, Celine Paris, Tony Bui, Antoine Gardel and, of course, Thierry Guyot for the map. Extra thanks go to Alexandre Carpentier for his expertise on trophic linkages.

Finally, to my friends who have come through these last few years with me, I would like to say thank you for your encouragement. Thanks to Mathilde, Benoit, Cyril, Anouk, Yann, Eva and Katherine for sharing with me so many great moments. You all made my days in La Rochelle the best.



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# CHAPTER 1 GENERAL INTRODUCTION

#### 1.1. Mechanisms structuring ecological communities

Generally, an ecological community is defined as naturally occurring group of species that are interacting in a unique habitat (Purves et al., 2004). This community is bound together by the network of influences that species have on each other and by the physical characteristics of the environment they inhabit. In intertidal flats, community structure have been long found to be regulated by sets of abiotic variables such as grain size, oxygen concentration, salinity, temperature, etc., to which the species in the community may respond differently (Warwick & Clarke, 1991; Coull, 1999; Lu et al., 2008; Schweiger et al., 2008). Particularly, the greater magnitude fluctuation of physical parameters in intertidal mudflats can put higher stress on the organisms inhabiting these areas (Woodin, 1974). Likewise, community structure is also massively influenced by the various biotic interactions, which mainly involve food availability and interconnections between species (Woodin & Jackson, 1979; Buffan-Dubau & Carman, 2000) (Fig. 1.1.).

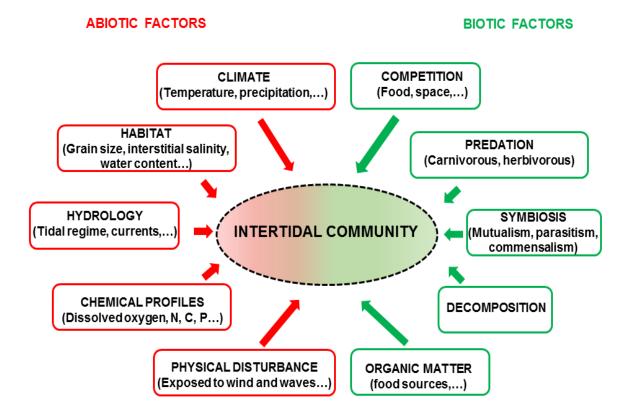


Figure 1.1. An example of abiotic and biotic parameters governing intertidal ecosystem

Within a community, organisms can interact with each other in varieties of ways, in which competition and predation are believed to strongly affect community dynamics and composition (Coneil, 1961a; Wilson, 1991; Hiltunen & Laakso, 2013). Competition occurs when the interactions between organisms result in a reduction of growth, survival or reproduction for both partners of the interactions (each species affected negatively). It commonly involves the use of a limiting resource (Schoener, 1974) (e.g. food, water, light, shelter, nesting site...) and can occur between individuals of the same species/population (intraspecific competition) as well as between individuals from different species/populations (interspecific competition). For example, competition for space among algae and sessile invertebrates is prevalent in benthic marine communities (Coneil, 1961b; Quinn, 1982) while other benthic invertebrates can compete for other subtle resources like oxygen (Ferguson et al., 2014) or food (Peterson and Black, 1987).

Different from competition, predation is the consumption of one living organism (prey, plant or host) by another (predator, grazers or parasite). This process takes place between trophic levels and it can have a major influence on the structure of communities. Azovsky et al. (1999) and Boates and Smith (1979) indicated shorebirds may deplete the densities of certain benthic preys. Additionally, the significant effects of epibenthic predators such as fish and crustacean on the infauna assemblages were largely reported (Virnstein, 1977; Gee et al., 1985; Azovsky et al., 1999; Hiddink et al., 2002). Given predation is pervasive: all organisms (plants, herbivores, and carnivores) within ecological communities are effectively predators of resources, these trophic interactions therefore provide the fundamental linkages among species (Polis et al., 1996) and play a critical role in structuring many ecosystems (Pearson & Rosenberg, 1978, 1987; Ambrose, 1984).

#### 1.2. Trophic structure and feeding relationships in ecological communities

The trophic interactions within ecological communities can be envisioned as food webs in which species are linked with each other in a trophic network of interconnections (Vander Zanden et al., 2016). In this network, all compartments (producers to consumers) are effectively predators of resources and resources for other predators. Energy enters the food webs through the photosynthetic fixation of carbon by primary producers (plants, algae, phototrophic prokaryotes, etc.). Many food webs also gain energy inputs through the decomposition of organic matter (detritus) with the help of bacterial activities (Thompson et al., 2012). Energy then moves from lower to higher trophic levels by consumption: herbivores (primary consumers) feed on primary producers; predators (secondary consumers) consume

herbivores, and may in turn be eaten by top predators. It is worth highlighting that some species feed at more than one trophic level, hence are termed omnivores. In addition, the meanings of a food web diagram are twofold: the flow of energy and the description of species interactions (Fig. 1.2.).

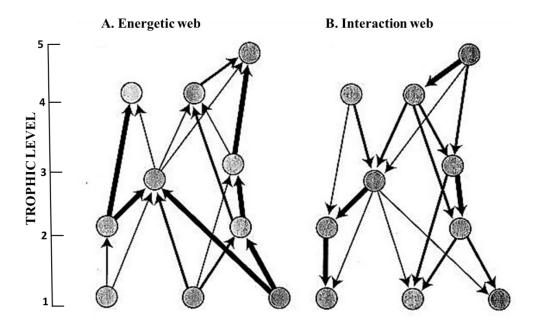


Figure 1.2. Food web structures: (A) Energetic web, depicting the pathways of mass or energy flow; and (B) Interaction web, showing the dynamically important food web linkages. Trophic species are encircled as nodes and arrows depict the links (modified from Vander Zanden et al., 2016).

Indeed, compartments of a food web may interact with one another by any of the interaction types mentioned above. Interactions between two species in one part of the web can affect species some distance away, depending on the strength and type of the interconnections. Particularly, adding a species (alien species introduction into a new area) or removing a species (as in a local extinction) has surprisingly far-reaching effects on many other species. The substantial damage in rice fields imposed by the alien species, Golden apple snail *Pomacea canaliculata*, has been a big lesson for any managers in Southeast Asia until now (Ichinose &Yoshida, 2001). Further, changing the food web structure can even cause acceleration of ecosystem collapse, for instance in the case of keystone species removal (Estrada, 2007; Curtsdotter et al., 2011). An example of this was the abrupt declines in populations of seals, sea lions, and sea otters over large areas of the northern North Pacific Ocean and southern Bering Sea during the last several decades. Springer et al. (2003) contended that such sequential collapses were triggered by the decimation of the keystone

species – the great whales, by post World War II industrial whaling, which consequently caused their foremost natural predators, killer whales, to begin feeding more intensively on the smaller marine mammals.

Moreover, the processes that define ecosystem functioning such as productivity, nutrients cycling and energy flow, etc., are typically linked through trophic interactions (Loreau, 2010). By representing both trophic interactions between species and energy links between them, food webs provide a natural framework for understanding species' ecological roles and mechanisms through which biodiversity reciprocally influences ecosystem function (Thompson et al., 2012).

#### 1.3. Ecological functioning in the view of trophic linkages

So far, several approaches have been proposed in attempts to assess the ecological functioning of benthic communities. The deployed methods regarding to this aspect focus on the type of the taxonomic units, whether species level or functional level, present in communities and their responses to environmental variables (Törnroos et al., 2015; Clare et al., 2015). Studies on ecological functioning, therefore, incorporate interactions between organisms and their environment into a concept that can portray ecosystem-level structure (Bremner et al., 2003).

Traditionally, ecological functioning of the marine benthic communities have been described through the variation in community structure, whereby changing pattern in taxonomic composition reflects the various ways of organisms interacting with their physical environmental characteristics. The changes in the occurrence of the species are subsequently interpreted as ecological processes. This approach has been widely used to investigate the response of organisms subjected to environmental alternation. For instance, Gray (1990) observed the adverse effect of oil drill activity on community structure of the soft-bottom benthic macrofauna resulting in decrease of total abundance and diversity while Olsgard & Gray (1995) highlighted the change in size structure to smaller-sized opportunistic species. Nevertheless, although this approach detects the responses of individual taxa to environmental stress, stressors overlap in space and time can cause difficulties to unravel which ecological functions are driving those responses.

Other studies tackled the ecological functioning of benthic communities by getting insight into the functional groups of the organisms present in the assemblages (Padilla & Allen, 2000; Pearson, 2001). In fact, individuals of benthic communities are classified according to their

similar functional attributes such as trophic group, feeding mode, morphology of the feeding apparatus, mobility, and so on (Bonsdorff & Pearson, 1999; Desrosiers et al., 2000). Given trophic interactions are central processes structuring marine ecosystems (Pearson & Rosenberg, 1978, 1987; Polis et al., 1996), this approach provides a stronger link between species and ecosystem functions. Therefore, it is essential to define precisely the trophic attributes of the targeted organisms.

The trophic attributes can be evaluated by several ways. The traditional methods such as stomach contents and faeces analysis have been appreciably used as the high degree of precision on prey type and size (Layman et al., 2012; Lourenço et al., 2017). However, these methods are often very time consuming. In addition, it have the main drawback when some prey items are often too deteriorated to be identified and others, with very small size class, are quickly digested and may never be detectable (Deagle et al. 2007; Pompanon et al., 2011). Nevertheless, in the advent of new technological tools, many previously unknown trophic linkages among ecosystems have been identified (Post, 2002; Gerwing et al., 2016). For instance, novel wide range of prey items were revealed, including microphytobenthos, meiofauna, macrofauna and insects in the shorebird Semipalmated Sandpiper diets by means of molecular scatology (Gerwing et al., 2016), which detected the presence of prey DNA in the faeces of the birds. Nonetheless, there is still major limitations of this method due to its high cost and shortage of the reference databank available for comparison. And more importantly, it does not give the proportion of each prey contributing to the diet. On the other hand, stable isotope analysis (Box 1) has proven to be a useful tool in trophic ecology with effectively application in diet reconstruction, determination of trophic levels and food web construction (Boecklen et al., 2011). The techniques, which use isotopic signatures from single/multiple elements (N, C, O, S,...) or from specific individuals compounds (fatty acids, amino acids,...), can range from simple, qualitative inferences based on the isotopic niche, to complex mixing models (Boecklen et al., 2011; Layman et al., 2012).

In this thesis, we used the variation in natural isotope abundances (isotopic signatures) of the two elements most commonly employed in a food web context: nitrogen (N) and carbon (C) (Layman et al., 2012). The use of stable isotopes is based on the precept "you are what you eat", whereby the isotope value of the consumer reflects that of the resource. Through trophic transfers, the ratios of heavy to light forms of elements (e.g. <sup>15</sup>N/<sup>14</sup>N, <sup>13</sup>C/<sup>12</sup>C) are stepwise enriched as the light isotopes of food items are more often utilized for biological processes then lost with excretion than the heavy forms. This shift, commonly known as fractionation, is

mass-dependent and hence varies more or less depending on the chemical element. Stable nitrogen isotope ratios ( $\delta^{15}$ N) become enriched by 3-4‰ between prey and predator tissues, thereby providing a measure of consumer trophic position (DeNiro & Epstein 1981; Minagawa & Wada 1984), whereas stable carbon isotope ratios ( $\delta^{13}$ C) vary substantially among primary producers with different photosynthetic pathways but exhibit little level enrichment (typically about 1‰). Therefore,  $\delta^{13}$ C is useful for identifying the original sources of dietary carbon for consumers (terrestrial vs. oceanic resources) (Hobson et al., 1994; France 1995). Most frequently, the bivariate plots of  $\delta^{15}$ N and  $\delta^{13}$ C then have been referred to trophic space, niche space, isotopic space or the isotopic niche. The ecological information derived from the stable isotope plots can be viewed as a proxy for a subset of the Hutchinsonian *n*-dimensional hypervolume (Hutchinson, 1957), which is distinct from, but in many circumstances should align closely with, aspects of the actual trophic niche (Layman et al., 2012).

Notwithstanding all mentioned benefits, the reduction of taxa to a small number of functional groups in the latter approaches of ecological functioning assessment might cause a loss of potentially important ecological information (Charvet et al., 1998). Besides, it is also possible that other interactions (e.g. with abiotic factors) or other ecological functions performed by organisms, which are important in structuring, ecosystems may be underestimated (Mancinelli et al., 1998).

#### Box 1. Stable isotope in a nutshell

- The isotope of an element is defined by the nucleon number, which is the sum of the number of protons and the number of neutrons in the atomic nucleus. While the number of protons and electrons remain constant in the neutral atom, the number of neutrons may vary within different atom species of the same element, characterizing the variant forms (isotopes) of an element. These forms have different atomic masses with the greater the number of neutrons, the heavier the isotope.
- Isotopes can be stable or unstable (radioactive). Stable isotopes do not emit radiations, whereas radioactive isotopes are unstable as their decaying atomic nuclei lose energy through radiations of particles or electromagnetic waves.
- The  $\delta$  notation is defined in per mille (‰), relative to a standard ratio as follow:  $\delta_{sample} = [(R_{sample} R_{standard})/R_{standard}] \times 1000$ , where R is the ratio of the measured stable isotope (e.g.  $^{13}$ C or  $^{15}$ N).
- Stable isotope analysis provides semi-quantitative information on both resource and habitat, which are commonly utilized to define ecological niche space (Newsome et al., 2007).
- Inferences derived from the isotopic data can depict feeding relationships and food web structure to a certain extent, but they are not direct characterization of diet such as those provided by foraging observation, stomach content and fecal analysis. Hence, when possible, stable isotope analysis should always augmented with additional trophic analytical methods to have a comprehensive understanding on the complexities that are manifest in the food webs (Layman et al., 2012).
- Advances in isotope mixing models allow transformation of isotopic data in to resource contribution value, thereby providing a standardized means of characterizing an organism's ecological niche (Boecklen et al., 2011).

#### 1.4. Ecological communities associated with the intertidal mudflats

A diverse of lifeforms occupying the mudflat has been well documented scattering around the world (Peterson & Peterson, 1979; Whitlatch, 1982). General compartments are microphytobenthos, microfauna, meiofauna, macrofauna, fish and birds (Fig. 1.2.). In some mudflats where sediment is characterized by larger mean grain sizes and relatively high sediment density, macroalgae (e.g. green algae *Ulva* and *Enteromorpha*) and macrophyte can additionally be a conspicuous element of this environment (Peterson and Peterson, 1979; Dyer et al., 2000).

#### Microphytobenthos

The surface of the mudflats is often apparently devoid of vegetation, however mats of microphytobenthos (MPB) are common. The MPB term usually refers to benthic microalgae, which mainly include Bacillariophyceae (diatoms) and Chlorophyceae (e.g. green algae), and also phototrophic prokaryotes, the cyanobacteria. To benthic community functioning, MPB not only influences nutrient, oxygen and carbon dioxide exchange at the sediment surface, but also plays a significant role in the sediment stabilization by producing a wide range of extracellular polymeric substances (EPS) which enhance the cohesion of the sediments (Consalvey et al., 2004; Agogué et al., 2014). And last but not least, it constitutes a substantial indispensable resource for the heterotrophic organisms (Miller et al., 1996; Herman et al., 2000).

The dynamics of MPB abundance and distribution are induced by both physical and biological parameters. Abiotic factors such as light, temperature, nutrient availability, etc.... have been generally considered the major parameters controlling the intensity of MPB reproducibility (Denis et al., 2012). On the other hand, MPB is also known to be affected by grazing activity imposed by epibenthic animals (e.g. Goldfinch & Carman, 2000; Hillebrand & Sommer, 2000). Additionally, in extreme conditions, MPB is able to regulate their photosynthesis by behavioral (migration) or physiological mechanisms to avoid photoinhibition damages (Cartaxana et al., 2011), thereby maintaining relative high abundance in the sediment. Given the high water content and mobile substrate of the intertidal mudflats can suppress growth of emergent macrophytes such as seaweeds (Yang et al., 2003), MPB is the primary source contributing significantly to the trophic base of intertidal mudflats

(Newell et al., 1995; Sauriau & Kang, 2000, Kang et al., 2003). It therefore evidently forms an important component of all shallow-water ecosystems (Miller et al., 1996).

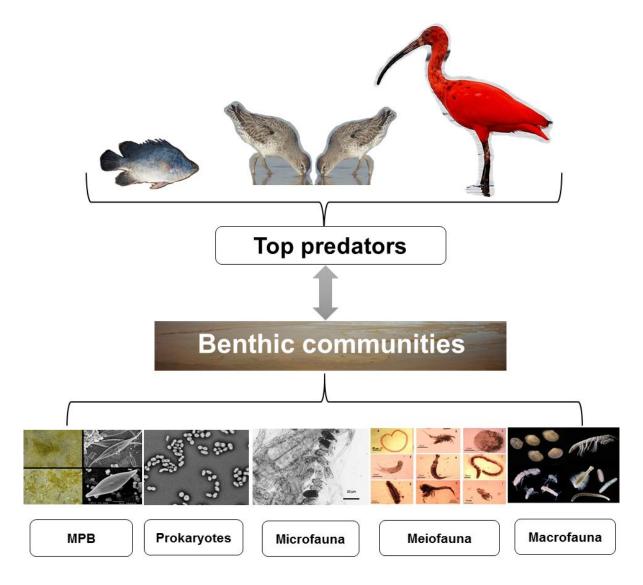


Figure 1.2. The benthic compartments and their top predators in the intertidal mudflat habitat

#### **Prokaryotes**

Prokaryotes (Archaea and Bacteria) are the smallest microorganisms of the benthic heterotrophic community with their size mostly ranging from  $0.5~\mu m$  to  $4.0~\mu m$  (Doetsch & Cook, 1973). They also contain autotrophic group in the case of cyanobacteria, which obtain their energy through photosynthesis and are the only photosynthetic prokaryotes able to produce oxygen. Prokaryotes play a fundamental role on the degradation and the remineralization of organic matter (van Nugteren et al., 2009). In the temperate intertidal

mudflats as well as in French Guiana mudflats, benthic bacteria are abundant (Pascal et al., 2009; Dupuy et al., 2015), and their production is as high (sometimes even higher) as MPB production (van Duyl et al., 1999; Pascal et al., 2009). In mudflat habitat, the bacterial cell abundances are often in the order of 10<sup>9</sup> cm<sup>-3</sup> of sediment (Schmidt et al., 1998; Lavergne et al., 2014; Dupuy et al., 2015) with a metabolism that can be either anaerobic or aerobic. Bacterial density and production decrease with depth and are higher in fine silty sediments compared to mudflats with coarser grain sizes (Carmen, 1990; Hamels et al., 2001). Numerous factors may influence bacterial abundance and production including abiotic factors (temperature, grain size, oxygen and organic matter concentration ...) as well as biotic factors such as the impact of the availability of resources (e.g. organic matter and/or inorganic nutrients) and predation pressure primarily induced by meiofauna or viruses (Lavergne et al., 2017). Nonetheless, although meiofauna feed on bacteria, they rarely reduce bacterial biomass (Pascal et al., 2009). Conversely, by removing dead cells from the microbial community, meiofauna can enhance bacterial growth rates (Meyer-Reil & Faubel, 1980; Montagna, 1984, 1995).

#### Microfauna

Microfauna are microscopic or very small unicellular eukaryote animals, usually referring to protozoans (e.g. flagellates and ciliates). Their size is variable but they are normally smaller than 60  $\mu$ m and larger than heterotrophic prokaryotes (e.g. bacteria). They show densities approximately in the order of  $10^3$  cm<sup>-3</sup> sediment. Microfauna mostly feed on bacteria (often by phagocytosis) but a few are fungivores, predators or detrivores (Fenchel, 1978; Sherr & Sherr, 1987).

#### **Flagellates**

Flagellate abundances range from 100 to several million individuals per ml of sediment (Gasol, 1993) and the highest abundances are found at the sediment surface (Alongi, 1991). Substantial flagellate densities have been observed in freshwater sediments (Gasol, 1993; Starink et al., 1996) but also in the marine environment (Hondeveld et al., 1994). Flagellates have different feeding types: phytophagous, bacteriovorous, carnivorous and even cannibal (Boenigk & Arndt, 2002). In benthic environments, only a quarter of heterotrophic flagellates are bacteriourous (Fenchel, 1986). It was indicated that flagellates do not structure the bacterial community since there are no correlation between bacterial and flagellate abundances (Alongi, 1991; Bak et al., 1991; Ekebom, 1999; Hamels et al., 2001). In contrast,

other authors found contradictory results highlighting strong links between flagellates and bacteria (Hondeveld et al., 1994, Bak & Nieuwland, 1997).

Flagellate abundances are consistently lower in muddy environments than in sandy ones (Bak et al., 1991; Bak & Nieuwland, 1993; Hamels et al., 2001). In muddy environments, most studies showed a declining trend of bacteria imposed by flagellates (Alongi, 1990; Epstein et al., 1992; Hondeveld et al., 1992; Bak & Nieuwland, 1993). Besides, it appears that the grazing rate was not influenced by season and temperature (Bak & Nieuwland, 1997), but might depend on protozoan size, bacterial abundances, and temperature (Moorthi, 2004). Nevertheless, most experimental researches showed a much lower rate of flagellate grazing on bacteria in benthic than in pelagic environments (Epstein & Shiaris, 1992; Starink et al., 1996).

#### **Ciliates**

Compared to flagellates, ciliates are larger, abundant in many benthic communities, and are more easily removed from sediment. Unlike flagellates, ciliates are more abundant in fine sediments than in coarse sediments (Fenchel, 1969; Kemp, 1988; Epstein, 1997). Thus, in favourable environments, such as fine sands, the biomasses of ciliates may be greater than those of meiofauna (Giere, 1993). On the other hand, in coarse sediments whose particles have a diameter greater than  $100 \, \mu m$ , the ciliates are scanty. Similarly, sediment clogged with organic matter is devoid of ciliates (Giere, 1993).

Most ciliates are bacteriores, but there are also scavengers, herbivores and predators. In the Baltic Sea, 50% of the benthic ciliates are bacteriores (Sich, 1990). Consumption rate of ciliates would reach 37 to 600 bacteria per ciliate per hour (Kemp, 1988; Epstein & Shiaris, 1992). Nonetheless, based on Kemp (1988) and Epstein et al. (1992), ciliates are not a significant vector for transferring bacterial production to the metazoan food web. In fact, the ratio between bacterial biomass and ciliate biomass is too low (0.6 in saltmarsh and 2.4 in saltwater pools). In mangrove sediments, this consumption is even lower (Alongi, 1986). Epstein & Shiaris (1992) also consider negligible the role of ciliates in the consumption of bacteria.

However, due to the technical difficulty in transporting high load of samples from French Guiana to France, as well as facing with such short limitation of studying time, the microfauna will be excluded in this thesis.

#### Meiofauna

Meiofauna is defined as all metazoans that pass through a 1 mm mesh size sieve and retain on a sieve of 40 μm (Higgins & Thiel, 1988). It constitutes an inconspicuous component of the benthic fauna but may provide the most abundant and diverse taxa in marine sediments. Some taxa, usually larvae of the macrofauna, are partly meiofauna during their juvenile stages (temporary meiofauna), but many taxa have species that are meiobenthic throughout their life cycle (permanent meiofauna). Permanent meiobenthos includes the Mystacocarida and many representatives of Rotifera, Nematoda, Polychaeta, Copepoda, Ostracoda and Turbellaria. An overall wide variety of food items including diatom, detritus, bacteria, ciliates, other meiofauna (by predation or scavenging) has been recorded corresponding to different meiofaunal taxa (Moens & Vincx, 1997). Given the capacity of meiofauna to distinguish between various food sources, numerous epistrate feeder nematodes, harpacticoids and oligochaetes often feed strictly on diatom (Pace & Carman, 1996; De Troch et al., 2005) while highly selective bacterivory is also observed in nematodes (Tietjen & Lee, 1977; Moens & Vincx, 1997), harparticoids (Carman & Thisle, 1985) and polychaetes (Gray, 1971).

In soft sediments, meiofauna may control MPB (Montagna et al., 1995) and vice versa, MPB supplies crucial food source for meiofauna, thereby sharply structuring meiofaunal distribution (Giere, 2009). There are also evidences of strong interactions between meiofauna and bacteria, such as higher abundance and diversity of meiofauna enhances bacterial productivity (Bonaglia et al., 2014), or the meiofaunal secretion may add a source of nutrients, thereby stimulating the development of bacteria (Moens et al., 2005). Further, by using enriched stable isotopic method, Pascal et al. (2009) observed double in bacterial consumption rate for the foraminifera *Ammonia tepida* (0.067 ngC ind<sup>-1</sup> h<sup>-1</sup>) in comparison to nematode community (0.027 ngC ind<sup>-1</sup> h<sup>-1</sup>). Additionally, meiofauna can be important prey for macrofauna such as polychaetes and fish (Gee, 1989; Coull, 1999). Recently, with the leaps in molecular technology, meiofauna has been even found in the diet of shorebirds thanks to the next generation DNA metabarcoding methods (Gerwing et al., 2016).

#### Macrofauna

Macrofauna, which includes all metazoans retained on a 1 mm mesh size sieve (Mees & Jones, 1977), is usually a major part of the total biomass of temperate zone mudflats and has a central role in the functioning of these ecosystems (Gray & Elliot, 2009). They represent a principle food source for higher trophic levels (e.g.crustaceans, fish and birds) and

fundamental consumers of lower trophic levels (e.g. MPB, detritus, meiofauna). Four major trophic groups of macrofauna are classified as surface deposit feeders, subsurface deposit feeders, carnivores/scavengers, and filter feeders/suspension feeders (Fauchald & Jumars 1979; Gage & Tyler, 1991; Wildish & Kristmanson, 1997). Generally, deposit feeders are believed to be more abundant in muddy habitats than the filter ones. Nevertheless, alternation of trophic mode in response to water flows and food fluxes has been also observed in some species (Laboy-Nieves, 2008). In addition, through their burrowing, feeding and respiration movements, macrofauna can enhance not only nutrients and organic matter release from sediments (Fukuhara & Sakamoto, 1987; Mermillod-Blondin et al., 2005) but also the bacterial activity (Mermillod-Blondin et al., 2005; Navel et al., 2011) and oxygen consumption (Lagauzère et al., 2009; Mermillod-Blondin et al., 2005).

#### Fish

During high tide, fish are one group of the top predators prevailing in these tropical habitats. Guiana coastal waters are home to a great diversity of fish. Many studies have been conducted on freshwater species, others on sub-tidal ones, while little work has been done on coastal species. Regarding to the French Guiana coast, Rojas-Beltran (1986) and Tito de Morais (1994) have achieved the first ichthyofauna inventory from the Papinabo creek (a tributary of Kourou river) and Cayenne river estuary. These studies confirmed the nursery role of mangrove for many species of crustaceans and fish, of which some are commercially important. Studies in temperate zones suggest that important patterns and mechanisms in the lifecycle of coastal fish species take place in intertidal mudflats such as small mullets, gobies and sea bass (e.g. Laffaille et al., 1998; Morrisson et al., 2002; Almeida, 2003). Meanwhile, in tropical zone, mudflats provide for the juvenile fish as important nursery functions as mangroves do (Tse et al., 2008).

In French Guiana, the two most common species highly associated with the intertidal mudflat are the Four-eyed Fish *Anableps anableps* and the Highfin goby *Gobionellus oceanicus*, of which *Gobionellus oceanicus* was the only fish species inhabiting in mud during low tide (Jourde et al., 2017). Pessanha et al. (2015) found that *Gobionellus oceanicus* consumed mainly detritus associated with diatoms. It coincided with the results of Vasconcelos Filho et al. (2003), whereby diatom consisted 87% of the food items found in this benthic goby stomach content analyses. Similarly, *Anableps anableps* was observed feeding on mud on the exposed shoreline at low water at the Surinam River (Zahl et al., 1977) while epibenthic algae

and arthropods (Insecta and Grapsidae) were described as important food for this species during its tidal migration in north Brazillian mangrove and Trinidad region (Wothke & Greven, 1998; Brenner & Krumme, 2007). In addition, fishing activities conducted on the intertidal shores highlighted the presence of many fish species.

#### Shorebirds

There are different species of waterbirds depending on mudflat for feeding, during at least one stage of their biological cycle. Small to medium size wading birds mostly specialized on intertidal mudflat habitats during the non-breeding period (van de Kam et al., 2004). They commonly feed, at low tide, on macrofaunal benthic preys (Colwell, 2010), while small-size species may also ingest biofilm (Kuwae et al., 2012). The study of Gerwing et al. (2016) revealed a novel wider range of preys in the diet of Semipalmated Sandpipers at their stopover mudflats in the Bay of Fundy, Canada, including diatoms, meiofauna (nematodes, copepods), the amphipod *Corophium voluntator*, bivalves, arachnids, crabs, fish eggs or juveniles, cnidarians, and even some terrestrial and freshwater insects.

Despite the recent decline of some species, particularly the Semipalmated Sandpiper (*Calidris pusilla*) (Morrison et al., 2012), the Guianas coast remains very important wintering grounds to millions of migrating birds (Boyé et al., 2009; Laguna Lacueva et al., 2012). Moreover, the predator guilds involve also high numbers of large size species as egrets (three species) and the Scarlet Ibis (*Eudocimus ruber*) foraging on the mudflats all year long. According to field observations (Bocher, pers. com.), they mainly feed on the Highfin goby (*Gobionellus oceanicus*), the benthic resident fish inhabiting on shallow mud or mud-sand bottoms in turbid and generally brackish water.

#### 1.5. The context of the thesis: Dynamics of the Guianas mudbanks

Locating between the Amazon and Orinoco Rivers, the 1500 km-long Atlantic coastline of South America (Fig. 1. 3.) is considered as the muddiest area on earth because of the large outflows of suspended sediment from the Amazon (Martinez et al., 2009). Every year, the Amazon discharges close to 800 million metric tons of sediment coming from Cordillera of the Andes, into the sea, of which 15-20% of this fluid mud is transported along the Guianas coast forming a series of huge mud banks. These mud banks, which are up to 5 m thick, 10-60 km long and 20-30 km wide (Froidefond et al., 2004; Anthony et al., 2011), in 2014 were

numbered 15 units (126 000 km²) at the time of our research. Particularly, under the influence of oceanic currents, tidal regime and waves generated by the trade wind, the mud banks are abraded on the east side and silted up on the west side, resulting in an over at least one km per year westward movement (Augustinus, 1978; Eisma et al., 1991; Anthony et al., 2011; Gensac et al., 2015). This unique "migrating" process can lead to rapid shoreline changes and a fast alternation of facies types, which might affect greatly the structure and functioning of its associated ecosystems.



Figure 1.3. Map of the Guianas coast (modified from Platon, 2012)

Actually, the emerged part of the mud bank is attached to the coast, encompassing the vast intertidal bare mudflats with the overgrown mangroves at the highest elevation (Augustinus, 1978; Froidefond et al., 2004) (Fig. 1.4.). Mangrove forest types and dominant species vary depending on the salinity of the water they grow in or near. Generally, the coastal mangroves are dominated by *Avicennia germinans* (De Granville, 1990), whereas mix stand of *Avicennia germinans* and *Rhizophora mangle* are found more on habitats that have a fluvio-marine influence. Particularly, in French Guiana, mangroves are intact but spread out due to

sedimentation and erosion along the coast, which forms many different habitat types. Mangroves often occur in fringe communities as a thin band along the coast, interrupted by sandy beaches and rocky headlands (Frazier, 1999).

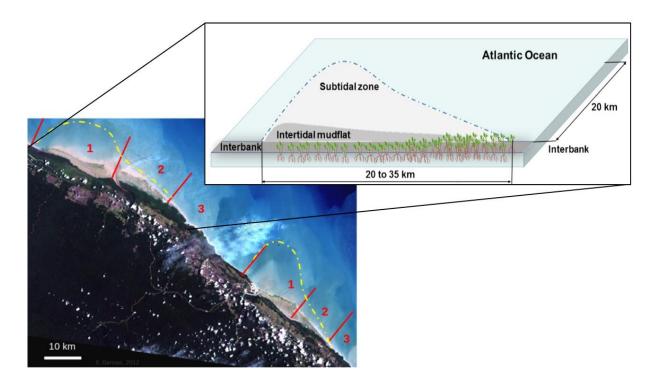


Figure 1.4. General structure of a mud bank along the Guianas coast: (1) Accumulation area; (2) Colonisation area; (3) Erosion area; Subtidal limit; (modified from Froidefond et al., 2004)

The considerable offshore extension of the mudflats is explicable by the extremely smooth slope (1:1600 in average) of the intertidal fringe. Soft tidal flat deposits are approximately 1 to 2 m thick and overlie a firm substratum of clay (Froidefond et al., 2004). Additionally, wave energy is strongly dampened by the fluid mud, which mostly occurs on the lee side of the mud shoals (Nedeco, 1968), thereby leading to a progressive stabilization of sediments. These deposits are gradually elevated and exposed to the air during the low tide periods then eventually colonized by the opportunistic tree mangrove (Fiot & Gratiot, 2006). In contrast, in the erosion area of the mud banks where the land is not protected from wave attacks, the mangrove forests are died off and the erosion of land can extend inland on several kilometres (Anthony et al., 2011). Nevertheless, by this process, the liquefied erosion muds are again suspended, and transferred to the accumulation area together with the high nutrient sediment-rich waters by means of oceanic currents, tides and wave forces (Gensac et al., 2015). In

French Guiana, around six major mudflats are recorded along the coast according to the dynamics of all mud banks from Amazon Estuary to coast of Venezuela (Froidefond et al., 2004). Despite the extreme morphodynamics of the mud banks, the intertidal mudflats are important nurseries for many coastal fish (Lowe-McConnell, 1962; Zahl et al., 1977; Brenner & Krumme, 2007) and also appear as important foraging areas for numerous local waterbirds and migrating shorebirds during their wintering period (Morrison & Ross, 1989; Boyé et al., 2009). Consequently, it was suspected a high productive and substantial ecological functioning of this ecosystem. However, the data on biodiversity, benthic community structure, and food web linkages of these mudflat habitats were hitherto scarce and mostly unknown.

#### Rationale and thesis layout

#### Problem statements

Recently, many attempts at unravelling the structure of intertidal food webs have been conducted as this type of habitat grants important food sources to many top predators as fish and shorebirds (Saint-Béat et al., 2013; Bocher et al., 2014, Catry et al., 2016, Gerwing et al., 2016). Despite the fact that the benthos compose the main compartments within mudflat communities, whose functioning can be extremely important to the total intertidal system (Amstrong et al., 1987; Danavaro et al., 2007), there is still a huge gap in the study of benthic communities along the Guianas coast. Especially, the sharp decrease of many migrating shorebird species in this region since 1980s (Morrison et al., 2012) indicates an urgent need to better understand the status of their potential food source as well as the impact of changing in benthic production on energy transfer between trophic levels, which subsequently affects those top predators. In addition, the benthic component is now being considered as an integral part of marine ecosystems due to its benthic-coupling suggesting the potential role in regulating sediment processes and providing food source to pelagic production (Ubertini et al., 2012; Griffiths et al. 2017).

Particularly, according to the IPCC (Intergovernmental Panel on Climate Change; IPCC 2007, 2013), the climate of the Amazonian Basin will evolve toward longer dry seasons and more intense rainfalls. Besides, the rapid sea level rising is expected to strongly affect the sedimentary plain increasing instability and vulnerability of the Guiana's littoral zone (Moisan et al., 2013). Among vulnerable littoral zones in the world, the Amazonian coast, in the northeast littoral zones of South America, appears as particularly sensitive areas subjected

to climate change (IPCC 2013). The first impacts of these changes are already observed: since 1970, the sea surface temperature mean along the Guiana's littoral zone has increased of ~0.6°C, with an acceleration since 1995, involving changes of fish community structure (Moisan et al., 2013). Given the fishery in French Guiana is the third most important economic activity after the space launching and gold-mining industries, it is therefore essential to investigate and evaluate the coastal biodiversity and its associated functioning of this region.

#### Research questions and objectives

This thesis is intended (i) to describe the structure and dynamics of the intertidal benthic infauna in the Guianas mudflats and (ii) to define its functioning in such highly unstable tropical muddy environments.

With a focus on the significance of meiofauna and macrofauna compartments and their connections with the primary food sources (microphytobenthos, mangrove leaves) as well as with the top predators (fish and shorebirds), I aimed to tackle several scientific questions:

- 1- How community structure and diversity of benthic infauna change across spatiotemporal variations over the Guianas mudflats?
- 2- How and to which extent the structure of benthic communities is associated with the specific community of predators in the intertidal trophic network?
- 3- What are the key factors that influence the structure of benthic assemblages?

#### Thesis layout

After this Chapter 1, which provides general information on the extreme dynamics of the Guianas intertidal mudflats, its associated communities, as well as the components needed to construct the intertidal food web and their trophic interactions, four chapters are further presented.

Chapter 2 gives an overview of benthic communities along the Amazonian coast. This chapter consists of two papers, which describe general structure and functional characteristics of macrofaunal assemblages and meiofaunal communities along a macroscale gradient from French Guiana to Suriname mudflats.

Chapter 3 defines the dynamics of infauna communities in relation to environmental variables. Two papers are presented as two parts in this chapter. Part one reveals the strong seasonal effects on the most abundant macrofauna representative - the Tanaidacea. The adaptation of these animals to cope with extreme environmental condition through life strategy and morphological development are also discussed. Part two highlights the seasonality and ecological zonation of meiofaunal assemblages with regards to the variation of both abiotic and biotic factors.

Chapter 4 emphasises on the trophic position of the main groups of meiofauna and macrofauna together with other food web compartments (microphytobenthos, fish, birds) basing on ratio of natural dual stable isotopes ( $\delta^{13}$ C,  $\delta^{15}$ N). A hypothesis that different trophic guild has different trophic level is tested. The results then are augmented with the morphological-base feeding guild assignments to elucidate their trophic linkages with other compartments. Mixing model is applied to calculate the contribution value of each compartment then built up a conceptual model of French Guiana intertidal food web.

General discussion, conclusions and perspectives will be included in the chapter 5.

# CHAPTER 2

AN OVERVIEW OF BENTHIC COMMUNITIES
INHABITING MUDFLAT HABITAT ALONG THE
GUIANAS COAST

It has been long known that mudflats are highly productive areas, which together with other intertidal habitats, are of great importance to large numbers of birds and fish. They provide vital feeding and resting areas for important populations of migratory, over-wintering and breeding waterfowl. Its high biological productivity has received much attention from many scientists with uncountable publications as the result. Nevertheless, until now, there is deficiency of a comprehensive understanding of the trophic fate of mudflat benthic communities (microphytobenthos, meiofauna, macrofauna) and their role in the larger intertidal food web (shorebirds and fish).

The coast sections of the South America located between the Amazon and Orinoco Rivers (1500 km) are considered as the most muddiest in the world because of the large flow of suspended sediment from the Amazon. The fluid mud is transported along the coasts of the Guianas by a complex interaction of waves, tidal forcing and wind coastal currents forming a series of huge mud banks. These mudflats migrate of one km per year and are distributed in at least 15 units of 10-60 km long and 20-30 km wide. They impose a geomorphological dynamic leading to rapid changes of shoreline and a fast alternation of facies types. Although the dynamics of these banks have been extensively studied in recent years, the state of knowledge on organisms associated with these highly unstable environments is still at an exploratory stage. Very few data on biodiversity, benthic community structure of these banks are available thus making its trophic structure mostly remained obscured. Accordingly, there is a serious need for a basic background on the ecological communities of this ecosystem since these mudflats appear as unique and productive ecosystems in the world and are expected to constitute critical foraging habitats for many avian and ichtic species during both phases of immersion as emersion.

In this chapter, an overview of the diversity and community patterns of macrofauna and meiofauna assemblages in the mudflats along the Guianas coast will be presented. The sampling stations were chosen presenting for a gradient of distance from the Amazon estuary, encompassing 3 to 4 sites located in the western Amazonian coast from French Guiana to Suriname mudflats. The distribution of macrofauna is contained in paper one while paper two reveals information regarding to meiofauna assemblages.

# PAPER 1

MACROFAUNA ALONG THE GUIANAS COAST



# Low Benthic Macrofauna Diversity in Dynamic, Tropical Tidal Mudflats: Migrating Banks on Guiana's Coast, South America

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Received: 14 January 2016 / Revised: 16 December 2016 / Accepted: 17 December 2016 © Coastal and Estuarine Research Federation 2017

**Abstract** In tropical South America, the mudflats of the Amazonian coast are unique because of their large size and unrivaled migration dynamics. On Guiana's coast, macrofaunal communities are believed to be well-adapted to these dvnamic conditions. In this study, the benthic macrofauna was sampled in April 2012 in the Awala-Yalimapo region of western French Guiana and at two sites in Suriname: Warappa Kreek and Bigi Pan. These sites are found 800, 920, and 1140 km from the Amazon delta, respectively. The richness, diversity, and densities of the macrofaunal communities in these mudflats are here described for the first time. Only 38 operational taxonomic units (OTUs) were recorded, among which two species were common and widely distributed: the tanaid crustacean Halmyrapseudes spaansi and the polychaete Sigambra grubii; the former represented 84% of all individuals collected, with densities reaching up to 73,000 individuals m<sup>-2</sup>. Most of the OTUs consisted of relatively small individuals (<10 mm in length). The very low richness and diversity and the small sizes of the organisms are likely linked

Communicated by Judy Grassle

Published online: 03 January 2017

**Electronic supplementary material** The online version of this article (doi:10.1007/s12237-016-0205-y) contains supplementary material, which is available to authorized users.

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to the instability and softness of the substrate on these mudflats. This study suggests that the differences in macrofaunal community composition among sites could be due to the migration stage of banks rather than the distance from the Amazon delta and associated effects of river discharge.

**Keywords** Amazon influence · Tropical mudflats · Soft-bottom macrobenthos · Communities · Dynamic habitat

#### Introduction

The mudflats of the Amazonian coast in South America are unique because of their size and dynamics. The coastline between the Amazon and Orinoco rivers (ca. 1500 km long), often referred to as the "Guianan coast," is considered the muddiest in the world because of the large flow of suspended sediment from the Amazon River (754 Mt year<sup>-1</sup>  $\pm$  9%; Martinez et al. 2009). The fluid mud is transported along the Guianan coast in a series of large migrating mudbanks resulting from complex interaction among waves, tides, wind, and coastal currents. The physical dynamics of these mudbanks have been studied extensively in French Guiana (Augustinus 1978; Eisma et al. 1991; Allison et al. 2000; Allison and Lee 2004; Baltzer et al. 2004; Gratiot et al. 2007; Anthony et al. 2010). These migrating mudflats, at least 15 in all, each 10–60 km long, 20–30 km wide (126,000 km<sup>2</sup>) area), and thickness up to 5 m, travel > 1 km year<sup>-1</sup> from Brazil to eastern Venezuela (Gardel and Gratiot 2005). The mudflats are associated with space-varying and time-varying depositional "bank" phases and erosional "inter-bank" phases, which lead to either rapid settlement or destruction of mangroves, depending on the level of accretion or erosion of the intertidal fringe. The specific characteristics of each sedimentary area depend on the tidal range and swells. These induce



strong sedimentation rates of homogeneous fluid mud, often several meters thick, while tides induce repeated sedimentation of several centimeters, depending on sediment availability (Gensac et al. 2015).

Although the dynamics of mudbanks along the Guianan coast have been studied extensively in recent years, data on infaunal biodiversity, community structure, and thus food web function are lacking for this highly dynamic and unstable environment. Macrofauna, sometimes defined as metazoans retained by a sieve with a 1-mm square mesh opening (Mare 1942; Bachelet 1990), is usually a major component of the total biomass and plays a central role in the functioning of these ecosystems (Gray and Elliot 2009). Surprisingly, only two studies on macrofaunal biodiversity and abundance have been conducted in this region over the last 30 years. The first provided data on the main operational taxonomic unit (OTU) occurring along Suriname's coast but lacked species-level identification for many organisms (Swennen et al. 1982). The second study was conducted in the Kaw estuary in French Guiana but had only a limited number of sampling stations (Clavier 1999). Despite these shortcomings, both studies found low macrofaunal diversity and the dominance of very few taxa such as tanaidaceans, although densities were highly variable depending on the habitat sampled. However, a recent study on the structure of meiofauna in French Guiana and Suriname mudflats indicates a very productive zone with a thick biofilm of microphytobenthos and prokaryotes (up to 1 mm thick; Gensac et al. 2015), coupled with a high abundance and biomass of meiofauna, mainly dominated by nematodes (Dupuy et al. 2015). Local sediment granulometry and organic matter content appeared to drive the size structure and functional characteristics of nematodes. Despite the high instability of mudflats in this region, chlorophyll a, biomass, and meiofauna abundance always tend to be higher than in other areas such as temperate European or tropical Australian and Vietnamese mudflats (Dupuy et al. 2015). Consequently, the question arises if this biofilm could be essential in food web function through direct trophic links with the macrofauna and thus support a rich benthic community.

In the present study, sediment characteristics, and richness, diversity, and density of the benthic macrofaunal communities, are documented at three sites along the coast of French Guiana and Suriname. It is hypothesized that differences in these characteristics are determined by the relative distance from the Amazon delta, the sediment source for these coastal mudbanks. It is also postulated that because of the highly dynamic nature of mudbanks, richness and diversity of macrofaunal benthic communities will differ from other tropical or temperate mudflats. Biometric measures (individual size/length) of macrofaunal organisms are documented in this study based on the premise that highly dynamic conditions along the Guianan coast limit the occurrence of large-bodied macrofaunal species. Consequently, it is expected that

findings of the present study will support the theory of a complex diversity-stability relationship, in which high environmental variability results in fewer species and greater evenness (Lehmann-Ziebarth and Ives 2006).

#### Methods

#### **Study Sites**

The study was conducted at one site in the Awala-Yalimapo region of western French Guiana, near the mouth of the Maroni River (05° 44′ 44″ N; 53° 55′ 36″ W), and at two sites in Suriname, Warappa Kreek, Commewijne District (05° 59' 33" N; 54° 55′ 50" W) and Bigi Pan, Nickerie District (05° 59′ 09" N; 56° 53′ 03" W), near the mouth of the Corentyne River (Fig. 1). The sites are located 800, 920, and 1140 km, respectively, from the Amazon delta. Tides at all three sites are semidiurnal with a range of 0.8–2.9 m. The Awala site was at the leading edge of a mudbank composed of very fluid mud and below a bare sandy beach. The site was adjacent to an area with young mangrove trees on somewhat consolidated mud. The Bigi Pan and Warappa sites were closer to the trailing edges of two different mudbanks and characterized by an erosive area (consolidated muds with microcliffs) crowded with dead trees lying in the mud, situated below a sandy shore that was partially colonized by adult mangrove trees. Sampling stations were below this erosive area.

#### **Sampling Strategy**

All intertidal stations were sampled in April 2012 (wet season). At each site, five to six stations close to the shore were visited on foot. They were positioned a priori using GPS, such that adjacent stations were separated by a 200 to 300-m distance. However, given the difficulty of sampling the soft sediment at low tide and of dealing with the fast moving ebbing or rising tides at high tide, actual stations were selected 5–15 m from the shore depending on mudflat conditions at the time of sampling. This explains variations in the distance between stations (Fig. 1). The mean distance among stations was  $285 \pm 20$  m (standard deviation (SD)) at Awala,  $340 \pm 105$  m (W10–W14) at Warappa and  $245 \pm 90$  m at Bigi Pan.

Additionally, the availability of a boat at Warappa Kreek allowed sampling a 2-km intertidal transect perpendicular to the shore (Fig. 1). There were nine stations on this transect, eight sampled by boat (W1–W8), and one (W9) sampled on foot. The mean distance ( $\pm$ SD) between stations was  $260 \pm 17$  m (W1–W9).

For each nearshore station, six replicate sediment samples were haphazardly collected, avoiding trampling the area, with a plastic corer (15-cm internal diameter) to a depth of 20 cm. For the intertidal transect at Warappa, a metal vacuum corer



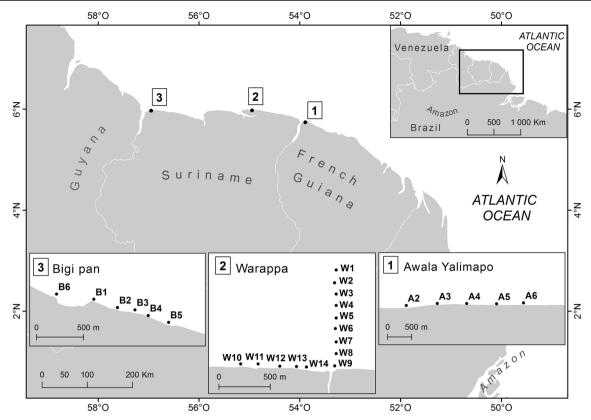


Fig. 1 Map showing the study area and the location of the study sites sampled in French Guiana and Suriname in April 2012, with locations of sampling stations at each study sites

with a 10-cm internal diameter was used, and two cores were combined into one sample. There were six of these combined samples per station (Bocher et al. 2007). Sampling from a boat or on foot yields identical estimates (Kraan et al. 2007). All samples were sieved through a 0.5-mm mesh, and organisms retained on the sieve were fixed in 70% ethanol.

#### **Sediment Characteristics**

At every station, a sediment sample was taken to a maximum depth of 4–5 cm to evaluate grain size. The sediment grain size was characterized using a Malvern Mastersizer 2000 (Malvern Instruments Ltd., UK) (size range 0.02–2000  $\mu$ m). Results were computed using Gradistat version 4.0 software and expressed as percentages of different grain size classes and geometric mean grain size. The different size classes given by Gradistat were grouped into four main categories: silt and clay (<63  $\mu$ m), fine sand (63–250  $\mu$ m), medium sand (250–500  $\mu$ m), and coarse sand (500–2000  $\mu$ m).

#### **Macrofaunal Sorting and Species Identification**

In the laboratory, samples were stained with the vital stain Rose Bengal to improve sorting and washed on a 0.5-mm mesh sieve. All individuals were first sorted into major taxonomic groups (e.g., annelids, tanaidaceans, crustaceans other than tanaidaceans, molluscs, and insects). In several cases, samples containing a high abundance of tanaidaceans were further subdivided using a Motoda box to estimate the total abundance of tanaids (Motoda 1959). Macroinvertebrates were identified using a Leica MZ205C stereomicroscope and, when necessary, an Olympus BH-2 compound microscope. Whenever possible, organisms were identified to the species level. Unfortunately, infaunal taxonomic literature is limited for this poorly studied, biogeographical region. To deal with the issue of identification to levels of species, genus, family, or higher, the term OTU is used in the present study. Faunal data available for statistical analyses were richness (i.e., number of OTU recorded) and density. These metrics were used to compute the occurrence (% of occurrence in stations of the whole data set or of a cluster where the OTU was recorded), frequencies (% of individuals of a given OTU out of all individuals recorded across all stations or for a cluster of stations), and the Shannon diversity index ((log 2) H'; Shannon and Weaver 1949). Biometric data (individual body length) were acquired using Leica stereomicroscope software (LAS).

#### **Statistical Analyses**

One-way analysis of variance (ANOVA) and post hoc Dunn's multiple comparison tests were performed on geometric mean grain size among sites (Awala, Bigi Pan, Warappa nearshore



stations, and Warappa offshore transect). Normality of the data was evaluated using a Shapiro-Wilk test. Taxonomic richness (S), density (N), and Shannon diversity index (H') data were not normally distributed (Shapiro-Wilk test P < 0.05), so Kruskal-Wallis one-way ANOVA on ranks was used to test for differences in each variable (S, N, and H') among sites. Subsequently, post hoc Dunn's pairwise multiple comparison tests were performed for the three variables to allow a comparison among sites.

Community statistical analyses were performed using Primer 6 software (Clarke and Gorley 2006). Hierarchical clustering and multidimensional scaling (MDS) of the stations were obtained from a Bray-Curtis similarity matrix computed with fourth root-transformed species densities. The SIMilarity PROFile routine ("SIMPROF" permutation tests) was used to identify genuine clusters (at a 5% significance level) to better define groups of stations using hierarchical clustering. The SIMilarity PERcentages routine (SIMPER) was performed to answer the questions of which OTU structured the clusters (90% cutoff for low contributions) and which contributed to dissimilarity. It was considered that a "good" discriminating OTU shows a ratio of dissimilarity to standard deviation between clusters (Diss/SD) > 1.5 (Wildsmith et al. 2009).

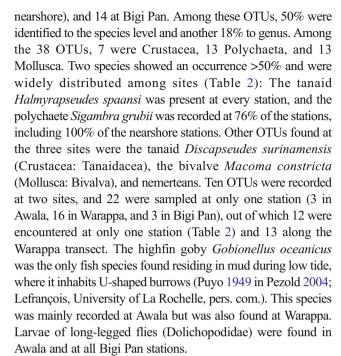
#### Results

#### **Sediment Characteristics**

No obvious granulometric gradient was detected among the three study sites based on their distance from the Amazon delta. The intertidal substrate was devoid of macrovegetation and was mostly comprised of fine silt and clay (Table 1; ESM 1) at every site. Thus, mud accounted for >99% of the total sediment in all nearshore stations of Awala and Warappa. In Bigi Pan, sand accounted for almost 10% (B1, B5, and B6), with mud content ranging between 89.3 and 98.6%. On the Warappa transect, at stations W1 to W6, sand percentages were higher, reaching almost 25% at the most remote station (W1). Transect stations closest to the coast (W7 and W8) had a similar mud content to nearshore stations. Mean grain size was consistently <10 µm for all nearshore stations (Table 1). Values differed significantly among sites (one-way ANOVA, F = 17.236, df = 3, P < 0.001). Post hoc Dunn's multiple comparison tests indicated that the mean grain size for Warappa transect stations was significantly different from Awala and Warappa nearshore stations (P < 0.05), but not from Bigi Pan (P > 0.05).

#### Richness

Thirty-eight OTUs were identified across the three study sites (Table 2), 16 at Awala, 28 at Warappa (22 offshore, 11



Mean taxonomic richness differed significantly among sites (Kruskal-Wallis one-way ANOVA on ranks, H = 14.201, df = 3, P = 0.003). However, a post hoc Dunn's multiple comparison test showed that mean taxonomic richness differed significantly only between Bigi Pan and both Warappa groups (P < 0.05). At the site scale, total richness by station was 3-11 OTUs in Awala (Table 2), and mean richness (Fig. 2a) ranged from 1.3 (A2) to 5.8 OTUs (A5). At Warappa stations, total richness ranged from 2 to 11 OTUs. Whereas 6-11 OTUs were recorded at transect stations, total richness was lower at nearshore stations with 2-7 OTUs (Table 2). This difference, however, was not supported by mean richness, which ranged from 2.5 to 3.0 OTUs per station for the whole site (Fig. 2a) (post hoc Dunn's pairwise multiple comparison test between Warappa transect and nearshore stations P > 0.05). At Bigi Pan, total and mean richness (7–9 and 4.0–5.2 OTUs, respectively) were homogenous and among the highest recorded in the present study.

#### **Densities and Diversities**

Considering all OTU values by station, individual densities ( $\pm$ SD) ranged widely from 72  $\pm$  56 ind. m<sup>-2</sup> at A2, up to 31,000  $\pm$  27,000 ind. m<sup>-2</sup> at B3 (Fig. 2b), which contributed to the significant differences recorded among sites (Kruskal-Wallis one-way ANOVA on ranks, H = 20.072, df = 3, P < 0.001). A post hoc test identified differences among Bigi Pan and both Awala and Warappa transect stations, as well as between Warappa nearshore and transect stations (P > 0.05), but not between Warappa nearshore stations and Awala (P > 0.05).



**Table 1** Location and sedimentary characteristics of the 25 stations sampled in April 2012 in French Guiana and Suriname

Study site		Station coordinate	es	Sediment characte	eristics
	Station	Latitude	Longitude	Mean grain size μm	Sediment <63 μm
Awala-Yalimapo	A2	53° 55′ 26.3″ W	5° 44′ 44.1″ N	5.9	100
	A3	53° 55′ 16.5″ W	5° 44′ 44.7″ N	5.9	100
	A4	53° 55′ 07.2″ W	5° 44′ 44.7″ N	5.6	99.9
	A5	53° 54′ 57.8″ W	5° 44′ 44.6″ N	5.5	100
	A6	53° 54′ 49.3″ W	5° 44′ 44.9″ N	5.3	100
Warappa					
Transect stations	W1	54° 54′ 45.6″ W	6° 00′ 36.0″ N	19.2	76.5
	W2	54° 54′ 46.7″ W	6° 00′ 27.4″ N	14.9	80.3
	W3	54° 54′ 45.6″ W	6° 00′ 19.8″ N	9.5	89.9
	W4	54° 54′ 45.6″ W	6° 00′ 12.1″ N	16.6	78.3
	W5	54° 54′ 45.6″ W	6° 00′ 03.8″ N	12.2	86.0
	W6	54° 54′ 46.1″ W	5° 59′ 59.6″ N	14.1	81.9
	W7	54° 54′ 45.6″ W	5° 59′ 47.6″ N	6.0	99.5
	W8	54° 54′ 45.6″ W	5° 59′ 39.7″ N	6.8	97.4
Nearshore stations	W9	54° 54′ 45.6″ W	5° 59′ 31.5″ N	6.6	96.5
	W10	54° 55′ 50.1″ W	5° 59′ 32.9″ N	5.5	99.7
	W11	54° 55′ 28.8″ W	5° 59′ 31.2″ N	5.3	99.8
	W12	54° 55′ 23.6″ W	5° 59′ 31.3″ N	5.5	99.8
	W13	54° 55′ 12.4″ W	5° 59′ 31.1″ N	5.7	98.6
	W14	54° 55′ 05.7″ W	5° 59′ 30.8″ N	5.7	99.5
Bigi Pan	B1	56° 53′ 28.6″ W	5° 59′ 17.7″ N	7.9	92.7
	B2	56° 53′ 20.5″ W	5° 59′ 14.9″ N	6.5	96.4
	В3	56° 53′ 14.5″ W	5° 59′ 14.1″ N	6.4	97.3
	B4	56° 53′ 10.0″ W	5° 59′ 12.2″ N	5.9	98.6
	В5	56° 53′ 03.0″ W	5° 59′ 09.9″ N	8.6	91.2
	В6	56° 53′ 41.3″ W	5° 59′ 19.5″ N	9.5	89.3

Lowest values (100–300 ind. m<sup>-2</sup>) were recorded at Awala and at the most distant stations along the offshore transect. This contrasted with densities recorded, up to ca. 11,000 ind. m<sup>-2</sup> at nearshore Warappa stations and up to ca. 31,000 ind. m<sup>-2</sup> at Bigi Pan, where densities were always >10,000 ind. m<sup>-2</sup>. The W8 station was singular within the offshore transect since it presented a density comparable to nearshore stations (Fig. 2b). No significant difference was found, however, between densities at Bigi Pan and Warappa nearshore stations (Dunn's post hoc test, P > 0.05). Indeed, some stations at Bigi Pan showed high variability, with replicates ranging by two orders of magnitude, from 484 ind. m<sup>-2</sup> to ca. 40,000 ind. m<sup>-2</sup>.

In this study, only three species represented >1% of the total of individuals counted per station: *H. spaansi* (84.5%), *S. grubii* (7.9%), and *D. surinamensis* (5.3%). Each of the remaining OTU accounted for <0.4% of all individuals counted.

Taxonomic diversity (Shannon index H'), which reflects taxonomic richness and the relative densities of the OTU, differed among stations within sites, ranging from twofold in

Bigi Pan up to tenfold in Awala. Thus, mean  $H' \pm SD$  ranged from  $0.17 \pm 0.41$  to  $1.74 \pm 0.30$  (Fig. 2c).

#### Size of Macrobenthic Organisms

An important common characteristic of the macrobenthic community in intertidal mudflats of the Guiana's coast was the small size of most individuals. Among the three most common OTUs, no individuals were >13 mm long. Mean length ( $\pm$  SD) of *H. spaansi* was  $3.8 \pm 1.0$  mm (1.7-8.6 mm, n=653),  $7.8 \pm 2.8$  mm (2.5-12.9 mm, n=146) for *D. surinamensis*, and  $6.6 \pm 1.7$  mm (2.1-13.0 mm, n=40) for the polychaete *S. grubii*. The shell length (greatest anteroposterior length) of all bivalves was 2.1 to 8.4 mm, with the exception of *M. constricta* ( $11.2 \pm 5.1$  mm, n=6) and *Tagelus plebeius*, with two individuals with a shell length of 11.9 and 12.7 mm. The most common gastropods, *Assiminea succinea* and *Cylichnella bidentata*, had a mean shell height ( $\pm$ SD) of  $1.3 \pm 0.3$  mm (n=54) and of  $2.1 \pm 0.4$  mm (n=15), respectively. Few annelids exceeded 20 mm. The largest organisms



Table 2 Densities (ind. m<sup>-2</sup>) of each OTU for the 25 stations (coded by letters) sampled in April 2012 in French Guiana and Suriname

OTU	Awala	_ e			¾ 	Warappa													Big	Bigi Pan					0	Occ.
	A2 /	A3 A	A4 A5	5 A6	- W1	1 W2	2 W3	3 W4	. W5	M6	W7	W8	6M	W10	W11	W12	2 W13	3 W14	– 14 B1	B2	B3	B4		B5 B6	%	
Crustacean Halmyrapseudes spaansi Discapseudes surinamensis Gnathiidae Isopoda Mysidacea Uca maracoani Callinectes bocourti	18 2 9	206 52	54 242	42 18	3 10	49 20	59	10	69	69 10	20 10 10	2255	10,951	5538	1846	3136	5 4462	2 5296		8	13,190 <i>27,95</i> ′ 2428 9	_	97	7966 16,84 1873 2688	6 1	100 28 16 12 8 8
Polychaetes Sigambra grubii Lumbnineridae Heteromastus sp. Mediomastus sp. Alitta sp.	1 45 1	152 179	_	896 63			59	108	69 50 50	20 167 10	20 10 10 29	137	275	1272	1075	. 162.	1075 1622 1774	4 1935	35 645	780	430	475		269 278		76 28 28 28 24
Orbinidae Streblospio gynobranchiata Phyllodoce sp. Polychaeta Capitella sp. Capitellidae Glycinde multidens Nephtys sp.	<u>.</u> ,	6	188 18	6	20	10			10	10	39			6	6				36			18				0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Oligochaetes Oligochaeta Nemertea Nemertea Molluscs	6		6			10		39		10	29	10		18			18	6	6		6				61 (4	36
Bybalves Macoma constricta Mulinia cleryana Ennucula dahnasi Nuculana concentrica Euryellina trinitatis Tagelus plebeius Tellinidae			36	9 2 18	49 10	20 20	10	10						6			27			18	6 6	6	18	6 6	~ ~ ~	42 20 21 8 4 4 4
Castropods Assiminea succinea Cylichnella bidentata Odostomia solidula Olivella olssoni Parvanachis obesa Turbonilla sp. Insects	J	9 81		341 81	1 20 10 10	29	10	39	39	10										6 6	27	36	6	27	6, 4, –	36 24 16 4 4 4 4



 Table 2 (continued)

OTU	Awala	la				Warappa	pa												Bi	Bigi Pan					Occ.
	A2	A2 A3 A4 A5 A6 W1 W2	A4	A5	A6 V	W1 \		V3 V	V4 W	/5 W	W3 W4 W5 W6 W7 W8	7 W.	6M 8		M 0	W10 W11 W12 W13 W14	12 W	713 W	/14 B1	B2	B3	B4	B5	B6	%
Dolichopodidae larvae Insecta larvae				54 18 45	18 45														27	27 242	36	63	143	6	32
Gobionellus oceanicus Total number of OTU per	$\kappa$	54	54 27 9 7 7 11	9 9 11 9	6 6	-		7	9		6 8	9	7	27	4	33	5	36	∞	∞	6	6	7	6	24
station  Total number of OTU per site 16	16				2	28 (22; 11)	: 11)												14						

Total number of OTU per station and per site (in Warappa, values in brackets refer to the number of OTU for transect and nearshore stations, respectively). Total occurrences (Occ.) (percentage of stations where the OTU were present) for each OTU over the whole study area are also given

was the fish, *G. oceanicus*, with a mean length of  $14.3 \pm 5.1$  mm (n = 28) and maximum length of 32.9 mm.

#### **Macrofaunal Assemblages**

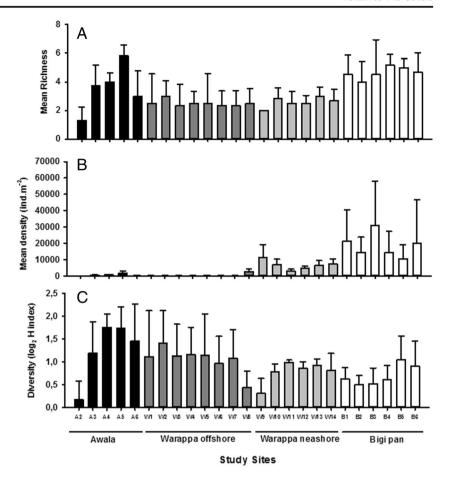
Hierarchical clustering of stations using SIMPROF and MDS revealed four clusters (Fig. 3; ESM 2): Awala (A), Bigi Pan (B), Warappa nearshore (Wn), and Warappa offshore (Wo); and two outliers: A2 and W7. All were organized in two main clusters, with the offshore Warappa stations (W1-W6) found to be clearly different from all inshore stations. The exception was W8, a priori considered an offshore station, which appeared similar to the inshore Warappa stations, and the outlier W7. In general, the four clusters (A, B, Wn, and Wo) grouped stations from the same site. Station W7 was distinct from both nearshore cluster (A, B, and Wn) and Wo, remaining in an intermediate position more closely associated with the Wo stations. Station A2 was in the nearshore stations cluster but segregated from the three assemblages A, B, and Wn.

The main OTUs contributing to similarity within site clusters are shown in Table 3 (SIMPER results). The tanaid H. spaansi appeared to be the main contributor, especially at nearshore stations in Warappa and Bigi Pan. The polychaete S. grubii characterized nearshore assemblages (A, B, Wn). Moreover, these two species were responsible for >90% of the similarity within the Wn cluster. The remaining OTUs in Table 3 were typical of different clusters. Thus, the gastropod A. succinea, the fish G. oceanicus, and polychaete S. gynobranchiata distinguished cluster A. Cluster B was distinguished by the tanaid D. surinamensis, the capitellid polychaete Heteromastus sp., and the Dolichopodidae insect family. The offshore cluster (Wo) was typified by an unidentified lumbrinerid polychaete (cf. Abyssoninoe sp. likely to be an undescribed species, Carrera-Parra, El Colegio de la Frontera Sur, pers. com.), the gastropod C. bidentata, the polychaetes Alitta sp., Mediomastus sp., and an unidentified orbiniid polychaete (cf. Scoloplos sp.).

Concerning the outliers (A2 and W7), OTU frequencies  $(100 \times Ni / Nt)$ , where Ni is the density of OTU and Nt is the total density at the station) were used to describe the faunal community structure (Table 3). Thus, A2 was mainly characterized by S. grubii and H. spaansi and thus explains its inclusion in the nearshore station cluster. In the W7 cluster, the most important species were the capitellid polychaetes (other than Mediomastus sp., as well as oligochaetes. Species characteristic of other clusters, such as H. spaansi and S. grubii (nearshore clusters), D. surinamensis (B), and the Lumbrineridae species (Wo), that were also present in W7, also likely contributed to explain W7 intermediate status.



**Fig. 2** Mean richness (**a**), mean densities (**b**), and mean *H'* diversity (**c**) measured at the 25 stations sampled in April 2012 in French Guiana and Suriname (*A* Awala, *B* Bigi Pan, *W* Warappa)



The OTUs mainly responsible for similarities within clusters were the main OTUs allowing discrimination among clusters (Table 4). However, distinguishing OTU could be split into two categories: "typical" OTU, mainly, if not exclusively, recorded from one cluster (e.g., A. succinea, Alitta sp., C. bidentata, D. surinamensis, Dolichopodidae, G. oceanicus, Heteromastus sp.,

Lumbrineridae; ESM 3) and "ubiquitous" OTU (e.g., *H. spaansi*), widely distributed throughout the study area and whose contributions to dissimilarities were likely due to differences in their distribution (densities and density variability) among stations within clusters (ESM 3). Thus, *S. grubii* was both a typical species and a ubiquitous species in the nearshore clusters.

**Fig. 3** Non-metric multidimensional scaling (MDS) ordination compiled from fourth root-transformed OTU densities (ind. m<sup>-2</sup>) based on Bray Curtis similarities of the 25 stations sampled in April 2012 in French Guiana and Suriname (*A* Awala, *B* Bigi Pan, *W* Warappa); overlaid clusters (*black lines*; 50% Bray-Curtis similarity level) correspond to genuine clusters defined by the SIMPROF routine (5% significance level)

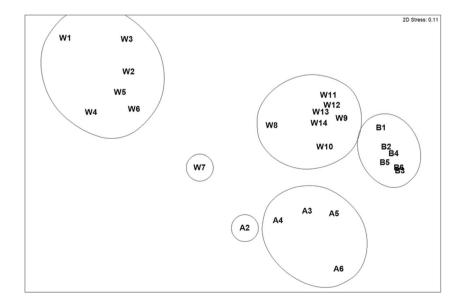




Table 3 Average percent similarities within clusters and percent OTU contribution to the average similarities within clusters identified in the study area in April 2012

J 1						
Stations	A	В	Wo	Wn	A2	W7
Average similarity (%)	56.2	77.2	60.5	70.6	_	_
Halmyrapseudes spaansi (T)	21.3	40.7	20.7	56.4	25.0	11.1
Sigambra grubii (P)	26.7	16.8		36.7	62.5	11.1
Assiminea succinea (G)	19.5					
Gobionellus oceanicus (F)	15.4					
Streblospio gynobranchiata (P)	7.5					
Discapseudes surinamensis (T)		13.4				5.6
Heteromastus sp. (P)		10.2				5.6
Dolichopodidae (I)		8.9				
Lumbrineridae (P)			19.9			5.6
Cylichnella bidentata (G)			18.9			
Alitta sp. (P)			18.4			
Mediomastus sp. (P)			7.0			16.7
Orbiniidae (P)			6.6			
Nemertea					12.5	
Capitellidae (P)						22.2
Oligochaeta						16.7

SIMPER: OTU contribution cutoff>90%. For outliers A2 and W7, individual frequencies within stations are shown (cutoff>90% of total abundance within each station). Letters in parenthesis indicate the faunal group to which the individual OTU belongs

A Awala, B Bigi Pan, Wo Warappa offshore, Wn Warappa nearshore, P polychaetes, T tanaids, G gastropods, F fishes, I insects

#### **Discussion**

The 1500-km coast between the Amazon and Orinoco River deltas is a unique system, comprised of an array of migrating, shifting mudbanks (Anthony et al. 2010). The biological communities in these mudflats are poorly known. Previous studies dealing with intertidal macrofaunal communities in Suriname (Swennen et al. 1982) and French Guiana (Clavier 1999) were restricted to a few mudflat sites and limited in taxonomic resolution, focusing only on major taxa. The present study was thus constrained by the lack of previous taxonomic work in the region, given the few available studies and the nature of the substrate compared to the east coast of the Amazon estuary (Kober and Barlein 2006; Braga et al. 2011; Venturini et al. 2011; Botter-Carvalho et al. 2014). It is thus likely that some individuals sampled belong to undescribed species (e.g., within the Lumbrineridae). Among the 19 identified species in the present study, 14 were previously recorded from the Brazilian coast east of the Amazon estuary, whereas 13 had been previously observed in the Caribbean Basin. Only one species, the tanaid D. surinamensis, has never been previously collected outside the study area (Bacescu and Gutu 1975).

The present study allowed identification of two distinct communities whose differences depend on the level in the

Ratios of dissimilarity to standard deviation (Diss./SD) and the percent contributions of various OTU to dissimilarities (Contrib %) between clusters identified in the study area in April 2012 Table 4

	A/B		A/Wo		A/Wn		B/Wo		B/Wn		Wo/Wn	
Average dissimilarity (%)	60.14		84.68		60.87		89.72		50.52		81.09	
	Diss/SD	Diss/SD Contrib%	Diss/SD	Diss/SD Contrib%	Diss/SD	Contrib%	Diss/SD	Contrib%	Diss/SD	Contrib%	Diss/SD	Contrib%
Halmyrapseudes spaansi (T)	5.6	24.6			2.9	20.8	8.7	19.2	2.1	11.9	3.7	19.6
Sigambra grubii (P)	1.8	3.7	6.3	11.7	1.6	8.1	7.6	10.2	2.1	5.3	4.9	19.1
Discapseudes surinamensis (T)	2.0	14.4					2.0	11.0	2.0	19.2		
Heteromastus sp. (P)	7.0	8.5					8.1	6.1	7.8	10.6		
Assiminea succinea (G)			4.7	0.6	4.6	12.2	2.2	3.7	2.2	6.4		
Alitta sp. (P)			5.9	6.4			8.1	4.6			6.7	7.2
Cylichnella bidentata (G)			4.7	6.7			5.8	4.8			5.0	7.6
Lumbrineridae (P)			3.2	9.7			3.6	5.4			2.3	7.6
Gobionellus oceanicus (F)	3.7	6.5	3.3	6.7	1.7	7.1						
Dolichopodidae (I)							3.1	6.2	3.1	10.8		

Dnly OTU detected by SIMPER as good discriminating OTU (Diss/SD > 1.5; Wildsmith et al. 2009) are presented. Highest contributions (>10%) are in bold face. Letters in parenthesis as in Table A Awala, B Bigi Pan, Wo Warappa offshore, Wn Warappa nearshore



intertidal (mean high water vs mean medium and low water) rather than the distance from the Amazon estuary as originally hypothesized. The nearshore communities of the three sites fit partially with descriptions already reported by Clavier (1999) and Swennen et al. (1982), as tanaid species are highly abundant and dominant taxa. Thus, H. spaansi and D. surinamensis reached densities of up to 73,000 and 8000 ind. m<sup>-2</sup>, respectively, in the present study. Both previous studies reported dominance of tanaids at most of the sampling sites, i.e., up to 67,000 ind. m<sup>-2</sup> in the Kaw estuary, French Guiana, although the species was not identified (Clavier 1999), and mean abundances of 16,000 ind. m<sup>-2</sup> for H. spaansi and 20,500 ind. m<sup>-2</sup> for D. surinamensis in a coastal lagoon near Krofajapasi, Suriname (Swennen et al. 1982). H. spaansi and S. grubii, which are widely distributed in the studied area, were the main species in nearshore communities in the present study. S. grubii is common along the coast of Brazil in different soft-bottom habitats (Lana et al. 1997; Venturini et al. 2011; Braga et al. 2011; Botter-Carvalho et al. 2014). This ubiquitous species seems enough of a generalist to exploit the highly unstable mudflats of the coast of Guiana. These two dominant species can locally make up >90% of the observed densities (Warappa), although S. grubii seems to be typical of nearshore communities as it was almost completely absent from the offshore intertidal community at Warappa. This dominance by a very few species and the low taxonomic richness xplain the low Shannon diversity index values for the nearshore macrofaunal communities here reported. Furthermore, each site appeared to have its own characteristic density ratios between the two dominant species as well as a characteristic OTU. Indeed, the singularity of the Warappa nearshore community was precisely in the huge contribution of *H. spaansi* and *S. grubii* to the exclusion of most other OTUs, whereas Awala and Bigi Pan were more diverse and differed in their site-specific OTU. These local differences cannot be explained by sediment characteristics, as there was no obvious gradient at mean high water among the sites. Consequently, as reported by Dupuy et al. (2015) for meiofauna, differences in macrofaunal assemblages are mainly attributed to local conditions, especially the migration stage of banks, at the scale examined in the present study. The Awala stations were located at the leading edge of a mudbank, characterized by very fluid mud, and were close to a mangrove colonization area, whereas stations at Bigi Pan and Warappa were closer to the trailing edges of two mudbanks characterized by an erosive regime and mature mangrove trees. A complex interaction of local physical factors could explain the differences in macrofaunal benthic assemblages among sites, but unfortunately, it was not possible to measure these characteristics, except for sediment grain size.

The mid and lower tidal level community at Warappa was not described by Swennen et al. (1982) and Clavier (1999) and thus appears to be unknown prior to this study. This sparse but diverse community comprises >50% of all macrobenthic

OTUs recorded (22 out of 38), with more than half found to be site specific (13). *H. spaansi* was present, but in low densities, and *S. grubii* almost absent. A lumbrinerid (cf. *Abyssoninoe* sp.), together with *Alitta* sp. and the gastropod *C. bidentata*, dominates this community. Sediment granulometric composition may also partially explain the difference in taxonomic faunal composition between nearshore and offshore stations. Most notably, the offshore sediments at Warappa had a higher proportion of coarse sand. Another possible explanation for the differences between the offshore and nearshore stations might be a higher nutrient supply inshore due to the proximity of sources of estuarine and mangrove leaf decomposition. The subtidal extent of the offshore community at Warappa is unknown.

Low diversity seems to be a major feature of bare intertidal mudflats. Previous studies on tropical mudflats showed that 10-32% of the species account for 80 or 95% of the individuals reported (Vargas 1987; Wolff et al. 1993; Dittmann 1995). In the present study, H. spaansi constituted 84% of all individuals sampled. Thus, tanaids H. spaansi, widely distributed, D. surinamensis, locally very abundant, and probably the tanaid Monokalliapseudes guianae that prefers estuarine conditions (Drumm et al. 2015) clearly constitute the major component of the macrobenthic communities along the 1500-km length of Guiana's coast. A fourth tanaid species, Discapseudes holthuisi, described from Suriname by Bacescu and Gutu (1975), was not recorded in the present study. Tanaids might occupy the same ecological niche and importance as the wellstudied amphipod Corophium volutator in temperate systems. In bare mudflats of the Bay of Fundy and Europe, C. volutator can occur at densities of 10,000 s ind. m<sup>-2</sup> (Hawkins 1985; Murdoch et al. 1986; Peer et al.1986; Møller and Riisgård 2006). Like corophids (Meadows and Reid 1966; Peer et al. 1986; Møller and Riisgård 2006), tanaids live in burrows (Bacescu and Gutu 1975) and are believed to be surface deposit feeders that mostly feed on biofilms they collect by scraping the mud surface with their long appendages.

Conversely, some differences between Guiana's mudflats and those in temperate zones have also been identified. Thus, although 580 species of marine molluscs have been recorded from the Guiana's coast (Massemin et al. 2009), only 13 species (seven bivalves and six gastropods) were recorded in the present study. They globally show very low occurrences and densities and would not contribute significantly to the total biomass of macrofauna, since they are typically small. Most of the 580 molluscan species are restricted to subtidal and deeper levels, and few species seem able to live on the very soft and dynamic substrate of tidal mudflats. Only the gastropods A. succinea at Awala and C. bidentata in offshore Warappa were sufficiently abundant to contribute significantly to the local community structure. None of them, however, reached abundances comparable to those of the widespread gastropod Hydrobia ulvae, considered the most common



deposit feeder in European intertidal mudflat communities (Newell 1979), where they can reach several thousands of individuals per square meter (Dekker 1989; Bocher et al. 2007).

Insects are rarely included in studies of marine coastal macrofauna. However, they can be major components of coastal infaunal communities in low salinity areas such as the Baltic Sea (Hummel et al. 2016). The long-legged flies (Dolichopodidae) are known to include marine representatives (Hinton 1976) and can thus be considered a component of infaunal communities during larval stages. In the present study, they were recorded at several stations, sometimes with relatively high densities (up to 700 ind. m<sup>-2</sup>). Adults were also observed at the surface of the mud at low tide and could be part of the mudflat food web by feeding on the surface biofilm (Pollet and Brooks 2008).

The highfin goby, G. oceanicus, was present in most Awala samples. Like insect larvae, fishes are not usually included in studies of benthic macrofaunal communities since they are mobile and not necessarily well sampled by benthic cores. This estuarine resident (Andrade-Tubino et al. 2008) is widely distributed from the state of Virginia in the USA to southern Brazil and occurs in soft bottoms along coasts and estuaries (Robins et al. 1999). At low tide, G. oceanicus individuals remain in water-filled burrows (U-shaped in Awala) that they excavate in the mud (Puyo 1949 in Pezold 2004; Lefrançois, University of La Rochelle, pers. com.). In the present study, this fish species was patchily distributed at low tide but sometimes reached densities up to 50 ind. m<sup>-2</sup>. The individuals collected were <33 mm in length and were likely juvenile that depend on this habitat during early, nursery stages (Wyanski and Targett 2000; Gomes and Bonecker 2014; Gomes et al. 2014). Although the species is considered to be a detritivore (Vasconcelos Filho et al. 2003), there is evidence from field observations and stomach contents that it can also feed on tanaids (Lefrançois, unpublished results). Thus, densities of the benthic goby could either be related to the importance of the surface biofilm as a food source or/and to high densities of tanaids as an abundant food source.

The highly dynamic conditions of the intertidal mudflats of the Guianas, related to the high variability of environmental factors (e.g., high physical forcing and large variable freshwater input), should limit settlement success and the adaptive capacities especially of large-sized species in very soft mobile mud. A previous study on the meiofauna at the same sites documented a very high abundance of these small organisms, especially nematodes, which was higher than that reported in other areas worldwide (Dupuy et al. 2015). However, the production of these mudflat ecosystems is expected to be very high and largely subject to export. Based on the results of the present study, future research should focus on the resilience capacity, via shifts in functional benthic groups due to adaptation or resistance to local stress conditions, especially strong physical instability, of all community components of the mudflat ecosystem.

Acknowledgements This study was funded by the University of La Rochelle, the CNRS, and the National Fish and Wildlife Foundation via the New Jersey Audubon Society. The authors thank Sophie Maillé from GEPOG in French Guiana for technical support, Thierry Guyot (LIENSs laboratory) for the map, Michel Le Duff (IUEM UBO) for his very valuable help with mollusk taxonomy, and The Microscopic Logistical Department of the Laboratory LIENSs. We are also grateful to the two anonymous referees for their very valuable comments and suggestions.

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## PAPER 2

MEIOFAUNA ALONG THE GUIANAS COAST

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#### Research papers

### Structure and functional characteristics of the meiofauna community in highly unstable intertidal mudbanks in Suriname and French Guiana (North Atlantic coast of South America)



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#### ARTICLE INFO

Article history:
Received 24 January 2015
Received in revised form
22 September 2015
Accepted 24 September 2015
Available online 9 October 2015

Keywords:
French Guiana
Suriname
Unstable intertidal mudbanks
Chlorophyll a
Organic matter content
Prokaryotes
Meiofauna

#### ABSTRACT

The North Atlantic coast of South America is influenced by the Amazon River. This coast is considered the muddiest in the world due to the enormous suspended sediment input from the Amazon River. The mobility of the sediment imposes a geomorphological dynamic with a rapid change of shoreline and fast alternation of facies types of the sediment. This study first describes the spatial and functional structure of meiofauna communities of highly unstable intertidal flats along coasts of French Guiana and Suriname in relation to environmental variables. Six sampling sites, composed mainly of muddy sediment, were located 700 km (Kourou) to 1200 km (Nickerie) from the mouth of the Amazon River. The granulometry, chlorophyll a biomass, prokaryote abundance, percentage of organic matter, meiofauna abundance and feeding guilds of nematodes in sediment stations were independent of the distance of the Amazon River mouth and likely were more influenced by the local dynamism of migration of mudbanks. Meiofauna was not more abundant when the sediment was dominated by the finest sediment particles and also when chlorophyll a and prokaryotes, potential prey of meiofauna, were greater. However, as a percentage, small nematodes (biomass of  $0.07 \pm 0.001 \,\mu\mathrm{g}$  ind<sup>-1</sup>), which are mainly epigrowth-feeders, were more abundant in very fluid mud. Local granulometry and organic matter content appeared to be driving factors of the size structure and functional characteristics of nematodes. Despite the high instability of mudflats, chlorophyll a biomass and meiofauna abundance always tended to be higher toward other world areas. No foraminifera among the six stations of the study were found. Very fluid mud with physical instability of sediment caused a large perturbation to the settlement of meiofauna; the least amounts of chlorophyll a biomass and prokaryotic and meiofauna abundances were found there. Thus, the probable mobility of sediment may select for smaller meiobenthic organisms, mainly epigrowthfeeders nematodes, and disturb the larger organisms in the sediment, and, therefore, they would not permit the settlement of the foraminifera. In addition, no non-permanent meiofauna largely was found in the sediment.

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#### 1. Introduction

The coast between the Amazon and Orinoco Rivers (1500 km) in South America is considered the muddiest in the world due to the enormous suspended sediment input from the Amazon River (754 Mt y $^{-1}\pm9\%$ ) (Martinez et al., 2009). Thus, a large amount of fluid mud is transported from the Amazon River mouth in a northwestern direction along the coasts of the Guianas, including French Guiana and Suriname, by a complex interaction of waves, tidal

forces, and coastal currents. These complex interactions result in the formation of a series of large mudbanks that are distributed in at least 15 units 10–60 km long and 20–30 km wide and migrate 1 km y $^{-1}$  (Allison et al., 2000). They impose a geomorphological dynamic leading to rapid changes of shoreline and fast alternation of facies type (Anthony et al., 2010). The intertidal area, bordered by mangroves, represents approximately 5% of the entire mudbank. Although these emerged mudflats are unique in the world considering their high dynamic processes and particular instability, the diversity and structure of communities as well as food web functionality associated with these mudbanks are mostly unknown.

Intertidal soft sediment habitats rank among the most productive ecosystems on Earth, largely owing to the primary

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production of highly diverse assemblages of benthic diatoms (Underwood and Kromkamp, 1999). Indeed, at every low tide, the intertidal flats are rapidly covered by mats of microalgae (microphytobenthos [MPB]) (Underwood and Kromkamp, 1999). Diatoms have the ability to migrate through fine sediments according to the tidal and daily irradiation cycles in order to find optimal light conditions for their growth. The MPB constitutes a complex biofilm in association with prokaryotic communities, mainly composed of bacteria in the sediment surface (van Duyl et al., 1999). These prokaryotes play a fundamental role through the degradation and remineralisation of nutrients. The components of biofilm (MPB and prokarvotes) are considered key ecosystem engineers in food webs. In addition, diatoms are known to be important trophic sources for many benthic organisms (meiofauna and macrofauna), and the prokaryotes can represent a complementary food source for meio- and macrofauna (Moens and Vincx, 1997; Pascal et al., 2008a, b; Pascal et al., 2009).

Meiobenthos occurs in all types of sediments and is thus able to reside in a wide variety of habitats (subtidal and intertidal areas). Nevertheless, the texture of the sediment is an important variable for structure and composition of meiobenthic assemblages (Schwinghamer, 1981; Semprucci et al., 2010, 2011). Abundance of benthic organisms is generally higher toward fine grains due to a concomitant increase of food availability (Balsamo et al., 2010; Heip et al., 1992). Meiofauna is generally considered to constitute recurrent taxa, such as nematodes, copepods, and foraminifera, and non-permanent taxa, such as small gastropods, small bivalves, and small annelids. In mudflats, nematodes are consistently considered the most abundant meiobenthic taxa (Boucher and Lambshead, 1995). Some authors have suggested that the ecological significance of nematodes is crucial in terms of food web relationships (reviewed in Balsamo et al., 2012; Heip et al., 1985; Platt and Warwick, 1980), production of detritical organic matter. and recycling of nutrients, thereby enriching the coastal waters to support marine benthic production. Nematodes are functionally diverse, as they can be herbivores, bacterivores, deposit feeders, epigrowth feeders, or predators (Pascal et al., 2008b; Rzeznik-Orignac et al., 2003).

The spatial structure of meiofauna assemblages has been well studied in temperate mudflats (Pascal et al., 2008b; Rzeznik-Orignac et al., 2003) and tropical mangrove areas (Alongi, 1987;

Chinnadurai and Fernando, 2007; Debenay et al., 2002; Xuan et al., 2007). Nevertheless, studies of bare tropical mudflat meiofauna are scarce and completely absent for the Guiana coast areas submitted to high dynamic processes, leading to a strong instability rarely met among coastal ecosystems.

The present study first describes the spatial and trophic functional structure of meiofauna communities of intertidal flats along the French Guiana and Suriname coasts in relation to environmental variables such as granulometry, chlorophyll *a* biomass, prokaryote abundance, and percentage of organic matter in sediment. The sampling stations are influenced by the Amazon flume, considered the largest and muddiest river in the world, and the choice of the stations presented a gradient of influence of the river from east to west (from French Guiana to Suriname). Second, three types of mud facies (fluid mud, moderately compacted mud, and compacted mud) were sampled on the intertidal mudflats of Awala (French Guiana), and their meiofauna communities were compared. We hypothesised that in highly unstable intertidal mudbanks:

- Compositions and abundances of meiofauna were different according to the grain size and particularly the fraction of fine sediment particles.
- Meiofauna was more abundant when MPB biofilm containing diatoms and prokaryotes, which are potential prey for meiofauna, was more abundant.

#### 2. Materials and methods

#### 2.1. Study sites

The intertidal mudflats studied are located along the French Guianese coast in front of the city of Kourou and village of Awala-Yalimapo and on the Surinamese coast near the River of Warappa and city of Nickerie (Fig. 1). All stations were sampled in April 2012 (wet season) at low tide in the upper area of the intertidal mudflats. The tides of the considered coast sections are semidiurnal with a tidal range of 0.8 m (neap tides) to 2.9 m (spring tides).

The median sediment grain size was characterised using a Malvern Mastersizer 2000 (Malvern Instruments, Ltd., UK) (size



Fig. 1. Map showing the study area and location of samples collected in French Guiana and Suriname.

Table 1
Granulometric parameters and organic matter content (OM) (%) of the different stations in French Guiana and Suriname areas.

Station	Mud (%)	Sand (%)	Mean grain size (μm)	Median grain size (μm): D50	Sample type	Textural group	Sediment Name	OM (%)
Kourou	81	19	14.08	10.96	Bimodal	Sandy mud	Fine Sandy Medium Silt	4.44
Awala St1	88.76	11.24	7.96	5.86	Bimodal	Sandy mud	Fine Sandy Fine Silt	5.99
Nickerie	89.65	10.35	9.75	6.54	Bimodal	Sandy mud	Very Coarse Sandy Fine Silt	5.55
Warappa	99.78	0.22	5.45	5.15	Unimodal	Mud	Fine Silt	6.21
Awala St4	99.92	0.08	5.62	5.51	Unimodal	Mud	Fine Silt	6
Awala St5	100	0	5.48	5.45	Unimodal	Mud	Fine Silt	5.99

range 0.02–2000 mm). This analysis allowed definition of different sediment textural groups by the relative abundance (percent volume) of mud (diameter  $<63~\mu m)$  and sand (diameter between 63 and 2000  $\mu m)$  according to the Udden-Wentworth scale. Data processing was performed using the GRADISTAT programme (Blott and Pye, 2001).

The sampled mudflat at Kourou (05°10′40.45″N; 52°38′53.74″ W) is the closest study site to the Amazon River mouth at a distance of 700 km (Fig. 1). At Kourou, one station was sampled (Table 1). The Awala mudflat station is located 850 km from the Amazon River mouth (Fig. 1). On this mudflat, contrary to other sites, samples were collected at three stations along a transect parallel to the coastline, presenting an alternation of facies type: Station A (St A) (05°44′44.6″N; 53°55′36.2″W), with very fluid mud (very soft mud); Station B (St B) (05°44′44.7″N; 53°55′07.2″ W), with moderately compacted mud (soft mud) and Station C (St C) (05°44′44.6″N; 53°54′57.8″W), with compacted mud just before young mangroves. Warappa and Nickerie are located 1000 km and 1200 km from the Amazon River mouth, respectively (Fig. 1). One station per site was sampled at Warappa (soft mud) (05°59′32.9″ N; 54°55′50.1″W) and at Nickerie (soft mud) (05°59′09.9″N; 56°53′03″W).

For each triplicate sample, the top 2-cm layers from three 15-cm diameter cores were sliced and gathered together. Each sediment sample was homogenised directly in the field in a sterile box and was subdivided for further analysis (storage conditions differed according to parameters).

#### 2.2. Environmental parameters

Organic matter content (OM) (weight loss after incineration) of the sediment was estimated by weight loss at  $450\,^{\circ}\text{C}$  for  $24\,\text{h}$  (Wollast, 1989) from three replicated cores (deep frozen for later analysis). The OM was expressed as the percentage of total matter.

Three replicated cores were used for algal biomass determination, which was assessed using chlorophyll a (Chl a) as a proxy and measured using fluorometry (640 nm, Turner TD 700, Turner Designs, USA) according to the method of Lorenzen (1966). Extraction of Chl a was obtained using freeze-dried sediment extracted at night in darkness in 4 °C, 90% acetone and centrifuged (10 min, 3500g, 8 °C). The Chl a biomass was expressed as  $\mu g \mu g^{-1}$  dry weight (DW) sediment or  $\mu g$  Chl a m<sup>-2</sup>.

Heterotrophic prokaryotic abundance (PA) was quantified by flow cytometry according to Lavergne et al. (2014). Sub-samples of the top 2 cm of the sediment were fixed with 0.2-µm filtered formaldehyde (vol/vol) (2% final concentration) and stored at 4 °C up to 3 months before analysis. Thawed samples were homogenised, prepared, and analysed as follows: (1) Sample preparation and extraction: dilution (1:1000–1:2000) in a detergent mix (sodium pyrophosphate [0.01 M]+Tween 80 [0.1%]), vortexing step, and 30 min of incubation at 4 °C. After the vortexing step, a sonication separation for 30 s (60 W) in ice with a sonication probe (3 mm) was applied. An aliquot of the sample was stained with SYBRGreen I (1:10,000) for 15 min in the dark and analysed by flow cytometry (see analysis details below); and (2) the

remaining part of the sample was centrifuged at low speed (1 min at 1000g at 4 °C). The pellet was then resuspended in the detergent mix, and step 1 was repeated once. Each sample was analysed for 30 s at low flow speed with a FacsCanto II cytometer (3-laser, 8-colour [4-2-2], BD Biosciences) using DIVA software. Fluorescent beads (Fluoresbrite Multifluorescent 1-µm microspheres, Polysciences, Germany) were added to each sample and simultaneously analysed. Stained cells were differentiated according to their green fluorescence (FL1) from SYBRGreen I staining and side-scatter properties (SSC). Picophytobenthic cells also were discriminated from heterotrophic prokaryotes by their red autofluorescence (FL3) and SSC properties and were excluded from final prokaryotic counts, measured on a gate SSC-FL1 (Marie et al., 2001). Accurate cell concentrations were performed using TruCount beads (BD-Biosciences) (excitation: red laser at 633 nm; emission: FL5 660/20 nm). Abundances were expressed as cells per cubic centimetre or millilitre of fresh sediment (cell cm<sup>-3</sup> or cell  $mL^{-1}$ , respectively).

#### 2.3. Meiofauna abundance

Meiofauna abundance and group composition were obtained from three replicated cores. The top 2 cm of sediment from each core were preserved in absolute ethanol (vol/vol). Samples (50 mL) were sieved through 50  $\mu m$  before staining with rose Bengal and observation under a binocular loupe (Zeiss). A sample splitter (Motoda box as Rzeznik-Orignac et al., 2003) was used to obtain an aliquot containing at least 100 individual nematodes for the abundance estimation.

The abundance of other meiobenthic taxa (i.e., copepods and ostracodes) was too low to be evaluated in split samples and, therefore, was quantified using whole samples. Abundances were expressed as individuals per cubic centimetre (ind  ${\rm cm}^{-3}$ ) or individuals per 10 cm<sup>2</sup> (ind 10 cm<sup>-2</sup>). The sizes (length and width) of nematodes were measured for at least 100 specimens picked haphazardly through a calibrated ocular micrometre. Three different size classes were made: small nematodes (mean length:  $300 \pm 30 \,\mu\text{m}$ ; mean width:  $18 \pm 5 \,\mu\text{m}$ ), medium nematodes (mean length:  $695 \pm 130 \,\mu\text{m}$ ; mean width:  $26 \pm 9 \,\mu\text{m}$ ), and large nematodes (mean length:  $1500 \pm 160 \,\mu\text{m}$ ; mean width:  $75 \pm 10 \,\mu\text{m}$ ). The biovolume was calculated using Warwick and Price (1979) formula:  $V=530LW^2$ , where V=biovolume (nl), L=length (mm) and W=width (mm). Biovolume was then converted in biomass, considering specific density as  $1.13 \,\mu g \, nl^{-1}$  (Wieser, 1960). The corresponding biomasses were: small nematodes:  $0.07 \pm 0.001 \,\mu g$ ind<sup>-1</sup>, medium nematodes:  $0.32 \pm 0.01 \,\mu g$  ind<sup>-1</sup>, and large nematodes:  $5.73 \pm 0.01 \,\mu g \, ind^{-1}$ .

From each of the three replicates, 100 nematodes were randomly withdrawn and mounted on slides in anhydrous glycerol to prevent dehydration (Seinhorst, 1959) and observed under a  $100 \times$  oil immersion objective (Axioskop 2, Zeiss). All nematodes were then classified into four trophic groups according to Wieser (1953, 1960) as follows: 1A (selective deposit-feeders), 1B (non-selective deposit-feeders), 2A (epigrowth-feeders), and 2B (omnivorous-carnivores).

#### 2.4. Statistical analysis

In the results section, all values are presented as means  $\pm$  SD. Variations in environmental variables or meiofauna abundances according to the sites were tested using Fisher tests or Wilks-Lambda tests after testing for data normality. For non-normal data, Wilcoxon tests were applied. The relationships between environmental parameters and meiofauna were assessed by principal component analysis (PCA). Pearson's correlations were used to measure and test the correlations between environmental variables and meiofauna. These analyses were performed with the XLSTAT 2014 software.

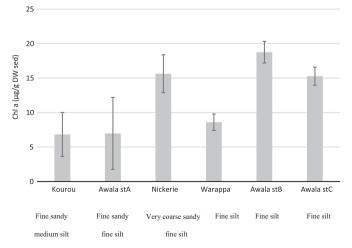
#### 3. Results

#### 3.1. Environmental variables

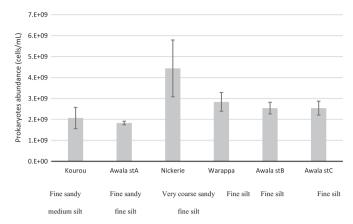
At Kourou, sediment was classified as fine sandy medium silt (Table 1). The Awala mudflat stations presented an alternation of three facies types: St A with very fluid mud (very soft mud) and composed of fine sandy silt; St B with moderately compacted mud (soft mud) and composed of fine silt; St C with compacted mud and composed of fine silt (Table 1). Warappa mudflat sediment was composed of fine silt, while Nickerie mudflats were made up of very coarse sandy fine silt (Table 1). In summary, the median grain size (MGS) among the six sampling stations ranged from 5.4 to11.0  $\mu$ m, and the percentage of mud in these six stations (81.0% at Kourou, 88.76% at Awala St A, 89.65% at Nickerie, and more than 99% at Awala St B, St C and Warappa [Table 1]) was independent of the distance to the Amazon River from east to west (from French Guiana to Suriname).

The percentage of OM mass in the sediment ranged from 4.4% (Kourou) to 6.2% (Warappa) (Table 1). Only one value for Kourou was significantly different from other stations (Wilcoxon, p < 0.05).

The mean Chl a biomass of the top 2 cm of the sediment varied from 7–19  $\mu$ g Chl a g<sup>-1</sup> DW sediment (corresponding to 70–190 mg Chl a m<sup>-2</sup>) (Fig. 2). The Chl a biomasses were the lowest at Kourou and Awala St A (large SD, no significant difference found between values, Fisher, p > 0.05), and the maximum Chl a biomass was recorded at Awala St B (significant difference between Kourou and Awala St B, Fisher, p < 0.05). Along the Awala transect, where facies was modified between St A to St C, the Chl a biomass was greatest in the intermediate moderately compacted muddy station



**Fig. 2.** Chlorophyll a (Chl a) biomass (mean  $\pm$  SD) of the top 2 cm of sediment at different stations in French Guiana and Suriname areas, classified according to sediment type. st=station.



**Fig. 3.** Prokaryote abundance (mean  $\pm$  SD) of the top 2 cm of sediment at different stations in French Guiana and Suriname areas, classified according to sediment type. st=station.

(St B:  $18.77 \pm 1.57 \,\mu g$  Chl a  $g^{-1}$  DW sediment) (significant difference between the three stations at Awala, Fisher, p < 0.05).

Heterotrophic prokaryotic (PA) cell abundance ranged from  $1.8-4.4\times10^9$  cells mL<sup>-1</sup> wet sediment in the 2-cm layer (Fig. 3). Prokaryotic cell numbers were lowest at the Kourou and Awala stations but higher at Nickerie (significant difference, Fisher, p<0.05), despite a large abundance variability  $(4.4\times10^9\pm1.36\times10^9$  cells mL<sup>-1</sup>). Along the Awala transect, prokaryotes were less abundant at St A. At St B and St C, no significant differences were observed (Fisher, p<0.05).

#### 3.2. Meiofauna abundance

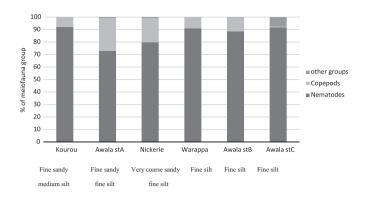
For the entire study area, total abundances of meiobenthos ranged from about  $88\text{-}220\,\text{ind}\,\text{cm}^{-3}$  (corresponding to 1760 ind  $10\,\text{cm}^{-2}$  to 4400 ind  $10\,\text{cm}^{-2}$  at Awala St A and Awala St C, respectively) (Fig. 4). The mean value for the six stations was 136 ind cm $^{-3}$ .

Along the Awala transect, a gradient of total abundances of meiobenthos appeared. The lowest abundances were recorded in the very fluid mud station (St A), a medium value was recorded in the moderately compacted mud station (St B), and the highest abundances were observed in the compacted mud station located at the edges of mangroves (St C) (significant differences between St A, B, and C at Awala, Fisher, p < 0.05).

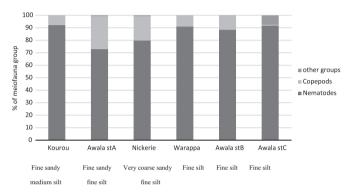
For all sampled stations, nematodes represented the most dominant taxon, contributing 73–92% of total meiobenthos abundance at Awala St A and Warappa, respectively (Figs. 4 and 5). Copepods contributed 0.5–26% of the meiobenthos abundance in Warappa and Awala St A, respectively (Figs. 4 and 5). The other groups (ostracodes, plathelminthes, small bivalves, and small gastropods) accounted for a very low percentage of the meiobenthos (less than 1%). One exception included ostracodes representing 8% of the total abundance at the Warappa station, and, in parallel, at this same station copepods were at very low abundance (0.5%). Surprisingly, no foraminifera were found among the six study sites.

Along the Awala transect, the percentage of nematodes increased, while the percentage of copepods decreased from St A to St C (from 26% in very fluid mud to 8.7% in compacted mud before mangroves).

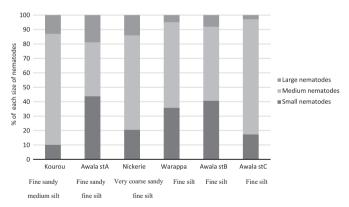
At all stations except Awala St A, the size class of medium nematodes (biomass of  $0.32\pm0.01~\mu g~imd^{-1}$ ) was the most dominant, contributing to 51-77% of total nematode abundance at Awala St B and Awala St C, respectively (Fig. 6), with significant differences between Kourou and Awala St A, Nickerie and Awala St A, and Warappa and Awala St C (p < 0.05). Significant differences



**Fig. 4.** Meiofauna abundance (mean  $\pm$  SD) of the top 2 cm of sediment at different stations in French Guiana and Suriname areas, classified according to sediment type. st=station. Other groups=sum of plathelminthes, ostracodes, small gastropods and small bivalves.



**Fig. 5.** Percentage of meiofauna group at different stations in French Guiana and Suriname areas, classified according to sediment type. st=station. %=percentage. Other groups=sum of plathelminthes, ostracodes, small gastropods and small bivalves.

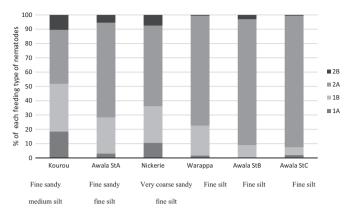


**Fig. 6.** Percentage of the size classes of nematodes at different stations in French Guiana and Suriname areas, classified according to sediment type. Classifications were as follows: small nematodes (mean length:  $300\pm30\,\mu m$ ; mean width:  $18\pm5\,\mu m$ ); medium nematodes (mean length:  $695\pm130\,\mu m$ ; mean width:  $69\pm130\,\mu m$ ; mean width:  $18\pm0\,\mu m$ ); and large nematodes (mean length:  $18\pm0\,\mu m$ ); mean width:  $18\pm0\,\mu m$ );  $18\pm0\,\mu m$ );  $18\pm0\,\mu m$ );  $18\pm0\,\mu m$ );  $18\pm0\,\mu m$ ) and  $18\pm0\,\mu m$ );  $18\pm0\,\mu m$ ) are percentage.

were observed for large nematode abundances between Nickerie and Warappa (p < 0.05). No significant difference was observed for small nematode abundances among all stations.

Along the Awala transect, the percentage of medium nematodes increased, while the percentage of small nematodes decreased from St A to St C from 44% in very fluid mud to 17% in compacted mud before mangroves (significant difference between three stations at Awala, Fisher, p < 0.05).

The proportion of nematodes gathered per trophic guilds was presented in Fig. 7. Epigrowth-feeders (2 A) were dominant in the



**Fig. 7.** Percentage of each feeding type of nematodes at different stations in French Guiana and Suriname areas, classified according to sediment type. 1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epigrowth feeders; 2B, omnivorous-carnivorous. st=station. %=percentage.

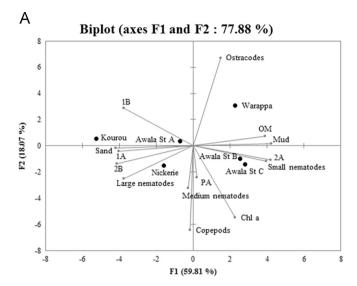
different stations increasing in proportion through the granulometric gradient, with the lower proportion at Kourou (38% of nematode community) and the maximum recorded at Awala St C (92%) (significant difference, Fisher, p < 0.05). The second dominant feeding type was non-selective deposit feeders (1B), inversely proportional to 2 A and ranging from 5 to 33% at Awala St C to Kourou (significant difference, Fisher, p < 0.05). Selective deposit-feeders (1A) and omnivorous–carnivores (2B) represented an average proportion of 6 and 5%, respectively. The medium and small nematodes belonged largely to epigrowth-feeders (2A) guild while large ones were from the 4 guilds, but the omnivorous–carnivores (2B) were represented by the large nematodes.

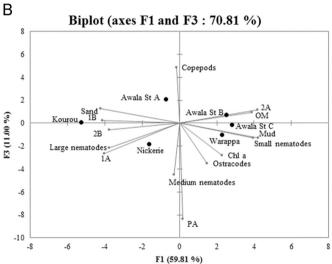
#### 3.3. Relationship between environmental parameters and meiofauna

Factor plans 1, 2, 3, and 4 of the PCA together explained 97.0% of the observed variability in each sample (Fig. 8) (axis 1: 59.8%, axis 2: 18.1%, axis 3: 11.0%, and axis 4: 8.1%). The variables OM content, small and large nematode abundances, and percentage of mud and sand, and the 4 feeding guilds of nematodes were represented by factor plan 1. The variables Chl a biomass, copepod, and ostracodes abundance were represented by factor plan 2. The PA abundance was represented by factor plan 3, and medium nematode abundance was represented by factor plan 4.

Only significant correlations were presented here and in Table 2: the OM content was positively correlated with small nematode abundance, 2A feeding type and percentage of mud, and negatively correlated with 1A feeding type, 2B feeding type and percentage of sand (Table 2; Fig. 8). The % of mud was correlated with 2A feeding type but negatively correlated with 1A, 1B and 2B feeding type and % of sand. The result of % of sand was inverted as above. Small nematode abundance was positively correlated with 2A feeding type and percentage of mud but negatively correlated with 1A feeding type, 2B feeding type and % of sand. Large nematodes abundance was positively correlated with 2B and 1A feeding type and percentage of sand, but negatively correlated with 2A feeding type and % of mud. Moreover, copepod abundance was negatively correlated with ostracodes abundance (Table 2; Fig. 8). 1A feeding type was positively correlated with 2B feeding type but negatively correlated with 2A feeding type. 1B feeding type was negatively correlated with 2 A feeding type and finally, 2A feeding type was negatively correlated with 2B feeding type.

The PCA exposed a clear separation of different clusters corresponding to the sampling sites, driven by their abiotic and biotic parameters of the four factor plans (Fig. 8, factor plan 4 not shown). Kourou site exhibited the lowest percentage of mud (81%)





**Fig. 8.** Principle component analyses calculated using six observations (samples of six sites: Kourou, Nickerie, Warappa, and Awala Stations A, B, and C) and 14 variables (mud, sand, OM, PA, Chl a, small, medium, and large nematods, copepods, and ostracodes abundance, and the 4 feeding type of nematodes). (A) Biplot F1  $\times$  F2 and (B) biplot F1  $\times$  F3. For each variable, the circle of correlation is reported. Observations were reported in the circle of correlation. Abbreviations: Chl a: chlorophyll a biomass; mud: percentage of mud; sand: percentage of sand; OM: organic matter mass; PA: prokaryotic cell numbers; 1A, 1B, 2A and 2B: feeding guilds of nematodes (see material and methods part for details); st= station.

mud), lowest OM content, lowest Chl a biomass and the lowest nematode abundance of small one. The same station exhibited the highest percentage of sand (19%), a part of large nematode abundance and 1A, 1B, 2B feeding type. In contrast, the Awala St B and St C were very muddy (100% mud) and showed high OM content, Chl a biomass and the highest percentage of 2A feeding type and, at St B, high abundance of small nematodes and presence of copepods. The Warappa station was mainly represented in factor plan 2 and was characterised by the highest abundance of ostracodes and average Chl a biomass; it was slightly represented in factor plan 1, characterised by a very muddy sediment and rich OM. Nickerie was represented in factor plans 2 and 3, characterised by high Chl a biomass and prokaryotic and copepod abundances. Awala St A was well represented in factor plan 3, characterised by the lowest PA abundance. In addition, Awala St A exhibited 89% mud, the lowest Chl a biomass, the lowest prokaryotic and meiofauna abundances, but the highest proportion of small nematodes and copepods.

#### 4. Discussion

The coasts of French Guiana and Suriname in South America are considered the muddiest in the world due to the enormous suspended sediment input from the Amazon River. Our six sampling sites were located 700 km (Kourou) to 1200 km (Nickerie) from the mouth of the Amazon River.

Our work clearly demonstrated that the distribution of the environmental parameters measured (median grain size, OM content, Chl a biomass, and prokaryotic cell abundance) was independent of the distance of the Amazon River mouth among sampling sites of the four study sites. The mean grain size ranged from 5.4 to 11 um among the six sampling sites, and the percentage of the mud in these six stations was independent of the distance to the Amazon River, from east to west (from French Guiana to Suriname). The environmental parameters probably were more influenced by the local dynamism of the migration of the mudbanks (Allison et al., 2000). Indeed, mudbanks are under strong influence of waves, tides, wind, and coastal currents, generating the movement of fluid mud, which moves more than  $1 \text{ km y}^{-1}$  (Allison et al., 2000). These migrant banks impose a geomorphological dynamic, leading to rapid, local changes of the shoreline (Anthony et al., 2010). In the same manner, distribution and structure of Chl a and meiofauna were independent of the distance to the Amazon River. Further studies are needed at a smaller scale to measure the physical conditions of the resuspension of the sediment (i.e., bed friction velocity) (Dupuy et al., 2014; Orvain et al., 2014).

The postulated hypothesis tested was that compositions and abundances of meiofauna were different according to the grain size and particularly the fraction of fine sediment particles. In the literature, muddy sediments are characterized by high meiofaunal. and in particular, nematode abundances (Giere, 2009; Heip et al., 1985). Yamanaka et al. (2013) found an increase of meiofauna abundance with increasing particle size (183-230 μm median particle size) on shallow- and intermediate-slope beaches. Coull (1999) argued that abundance values tend to be highest in organically enriched muds but lowest in clean sands. This postulated hypothesis is not corroborated with the present dataset, where sediments are very muddy, compared to the studies of Coull (1999). In fine silt sediment, meiofauna was as abundant as fine sandy medium silt or very coarse sandy fine silt. However, this hypothesis is corroborated with the different size classes of nematodes; small nematode abundance (mainly dominated by 2A feeding type) is positively correlated with higher percentage of mud (fine silt sediment) and OM content, and, inversely, large nematode abundance (mainly dominated by 2B feeding type) is negatively correlated with higher percentage of mud and OM content. Consequently, granulometry and OM content appear to be driving factors of the size structure and functional characteristics of nematodes. Nonetheless, sediment texture is also likely to have a strong structuring influence on nematodes. Thus, in percentage, small nematodes, mainly dominated by epigrowth-feeders nematodes, are more abundant in very fluid mud (Awala St A: 44%) compared to compacted bare mud in front of mangroves (Awala St C: 17%). This result could be explained by the sediment texture in Awala St A-the high fluidity of mud may result in high physical instability of the sediment (tidal currents, wave action, or input of resuspended sediment), causing a large perturbation to the settlement of the meiofauna. The lowest values of Chl a biomass, prokaryotes, and meiofauna abundances were recorded at Awala St A. Thus, the likely high mobility of sediment selects for smaller meiobenthic organisms and epigrowth-feeders nematodes and disturbs the larger organisms in the sediment as omnivorouscarnivores nematodes (2B). Kapusta et al. (2005) recorded the lowest abundance of meiofauna in unstable sediment in a channel

**Table 2**Pearson's correlations and *p*-values between environmental variables and meiofauna. PA=Prokaryotes abundance; Chl a=Chlorophyll *a* biomass; 1A, 1B, 2A and 2B; feeding guilds of nematodes (see Section 2 for details) - no correlation.

Pearson's correlation														
Variables	PA	Chl a	ОМ	Small nematodes	Medium nematodes	Large nematodes	Copepods	Ostracodes	Mud	Sand	1A	1B	2A	2B
PA	1	-	_		-	-	-	-	-	-	-	-	-	-
Chl a		1	-	_	_	-	_	-	-	_	-	-	_	_
OM			1	0.935	-	-	-	-	0.847	-0.847	-0.96	-	0.851	-0.872
Small nematodes				1	-	-	-	-	0.894	-0.894	-0.884	-	0.893	-0.875
Medium nematodes					1	-	-	-	-	-	-	-	-	-
Large nematodes						1	-	_	-0.871	0.871	0.848	-	-0.865	0.921
Copepods							1	-0.882	-	-	-	-	-	-
Ostracodes								1	_	-	-	-	-	-
Mud									1	-1	-0.883	-0.877	0.952	-0.954
Sand										1	0.883	0.877	-0.952	0.954
1A											1	-	-0.927	0.894
1B												1	-0.95	-
<b>2A</b> p-Values													1	-0.928
PA	0	_	_	_	_	_	_	_	_	_	_	_	_	
Chl a		0	_	_	_	_	_	_	_	_	_	_	_	_
OM			0	0.006	_	_	_	_	0.033	0.033	0.002	_	0.031	0.023
Small nematodes				0	_	_	_	_	0.016	0.016	0.019	_	0.016	0.022
Medium nematodes					0	-	-	-	-	-	-	-	-	-
Large nematodes						0	-	-	0.024	0.024	0.033	-	0.026	0.009
Copepods							0	0.019	-	-	-	-	-	_
Ostracodes								0	-	-	-	-	-	_
Mud									0	< 0.0001	0.019	0.021	0.003	0.003
Sand										0	0.019	0.021	0.003	0.003
1A											0	-	0.007	0.016
1B												0	0.003	-
2A													0	0.007

in the Tramandai-Armazem estuary in southern Brazil, and highest abundance of meiofauna, especially large species, in a sheltered area (i.e., seagrass beds). Yamanaka et al. (2013) demonstrated that the most significant factor affecting meiofauna was exposure to waves and currents.

The second postulated hypothesis was that meiofauna was more abundant when biofilm of Chl a and prokaryotes, both representing potential prey for meiofauna, were more abundant. This hypothesis was not corroborated with the present dataset. In this study, no correlation was found between meiofauna abundance and their potential prey. The interpretation is (1) the bacterivory in meiofauna is considered as minor factor in the regulation of the prokaryote pool, and bacteria do not constitute a preferentially ingested resource (no top-down control of bacteria [Pascal et al., 2008b]); and (2) despite the fact that herbivory is largely extended in meiofauna and confirmed here by the dominance of the epigrowth-feeders (2A) in different stations, the primary production largely supplies their food needs in intertidal mudflats. Finally, meiofauna uses only a negligible part of carbon from primary production (Middelburg et al., 2000; Moens et al., 2002; Pinckney et al., 2003; Rzeznik-Orignac and Fichet, 2012; van Oevelen et al., 2006). Food availability also does not appear to limit meiofaunal abundance (no top-down control of MPB [Coull, 1999]). Furthermore, Tolhurst et al. (2010) did not find a correlation between meiofauna and Chl a biomass. It appears that further investigations are needed to assess the primary production and meiofauna grazing rates in order to obtain reliable data of carbon flux in benthic ecosystems of the coasts of the Guianas.

Soft mudflats are characterised as containing important biofilms of MPB (Du et al., 2009; Herlory et al., 2004; Perkins et al., 2003; Underwood and Kromkamp, 1999; Underwood and Paterson, 2003) and having high meiofaunal abundances (Heip et al.,

1985) compared to sandy sediment. In the present study, in banks with muddy sediment of French Guiana and Suriname, the same tendency was found. For example, in stations with fine silt (muddy), Chl a biomass was 9–19  $\mu$ g Chl a g<sup>-1</sup> DW sediment but lower in stations exhibiting sandy mud (around 7  $\mu$ g Chl a g<sup>-1</sup> DW sediment). Similar values are found in European upper-shore mudflats (8.5–21  $\mu$ g Chl a g<sup>-1</sup> DW sediment [Herlory et al., 2004; Orvain et al., 2014; Underwood, 2010]), and lower values are found in sandflats of the Severn estuary (mean of  $5 \mu g$  Chl a  $g^{-1}$  DW sediment [Underwood, 2010]). However, the Chl a data from the literature presented above were obtained from the first 200, 500, or 1000 µm of the surface sediment, whereas data obtained in this study correspond to the first 2 cm of mud. In this case, the Chl a biomass is likely to have been diluted with sediment devoid of that used for MPB analysis. A supplementary study analysing the top 0.5 mm of the sediment surface in a few stations in French Guiana and Suriname showed that Chl a biomass could reach up to  $180 \,\mu g$  Chl a  $g^{-1}$  DW sediment in fine silt sediment (Awala St B and St C) and  $80 \,\mu g$  Chl a  $g^{-1}$  DW sediment in sandy mud sediment (Kourou) (unpublished results, Dupuy, personal communication). This supplementary study demonstrated that in intertidal sandy mud sediments and fine silt sediments of French Guiana and Suriname, primary producer biomass tends to be greater than in other tropical or European flats.

Prokaryotic abundance was within the same range as that of European mudflats ( $2 \times 10^9$  cells cm $^{-3}$ ) at Brouage (Lavergne et al., 2014; Orvain et al., 2014), and in the review of Schmidt et al. (1998), bacterial abundance remains stable, around  $10^9$  cells cm $^{-3}$ .

In our study, the meiofaunal community was constituted of only six taxa including small organisms of macrofauna (bivalves and gastropods). In other studies on intertidal flats, number of taxa was variable but in tropical area tend to welcome more taxa: in Mangrove forest of Vietnam, 11 taxa were described (Xuan et al., 2007) while 7 taxa were recorded in Southeast coast of India (Chinnadurai and Fernando, 2007). In sandy sediment of Maldives in Indian Ocean, from 17 to 20 different taxa were collected (Semprucci et al., 2010, 2011). In temperate area, the number of taxa varied from 4 to 13 taxa (Bohórquez et al., 2013; Soetaert et al., 1995) and was similar to our results (7 taxa: Alongi, 1987; 6 taxa: Rzeznik-Orignac et al., 2003). The hypothesis for explaining the lower number of taxa in tropical mudflat in French Guiana, is that mudflat is highly physically instable. Few taxa can survive in such fluid mud in the mudbanks.

On Guianas coast, total abundances of meiofauna were particularly high, ranging from 88 to 220 ind cm<sup>-3</sup> (corresponding to  $1760 \text{ ind } 10 \text{ cm}^{-2} \text{ to } 4400 \text{ ind } 10 \text{ cm}^{-2}) \text{ compared with other}$ studies on intertidal flats, where abundances were lower (1000 ind 10 cm<sup>-2</sup>; Coull, 1999; Heip et al., 1985; Platt and Warwick, 1980). In the Brouage mudflats (Atlantic French coast), the mean abundances were 2000 ind 10 cm<sup>-2</sup> (Rzeznik-Orignac et al., 2003). Similar abundances previously were observed by Montagna et al. (1995) in Marennes Oléron Bay (Atlantic French coast) and by others in European estuaries, such as Gironde, Tagus, and Westerschelde (Soetaert et al., 1995), or the mudflats of the Lynher estuary in Cornwall (Warwick and Price, 1979). Abundances of meiofauna in mangroves provided in the literature correspond to the lower values found in our study: 1156-2082 ind 10 cm<sup>-2</sup> in Vietnam (Xuan et al., 2007); a maximum of 735 ind 10 cm<sup>-2</sup> in mangroves of Nha Trang Bay (Vietnam); (Mokievsky et al., 2011) and 500 ind 10 cm<sup>-2</sup> in a tropical tidal flat of northeastern Australia (Dittmann, 2000). The highest value of meiofauna abundance was found by Vanhove et al. (1992), with 6707 ind 10 cm<sup>-2</sup> in the Bruguiera mangroves in Gazi Bay (Kenya). In conclusion, meiofauna abundance observed in French Guiana and Suriname was almost always higher than in other world areas, with the exception of mangroves in Gazi Bay (Kenya) (Vanhove et al., 1992).

As a constituent of meiofauna, nematodes represent the most common and abundant taxon in this study. They are also commonly found in European Atlantic mudflats (Montagna et al., 1995; Platt and Warwick, 1980; Rzeznik-Orignac et al., 2003) and mangrove ecosystems (Alongi, 1989; Chinnadurai and Fernando, 2007; Mokievsky et al., 2011; Xuan et al., 2007). Nematodes seem to be less prominent in Cuban mangroves (Lalana-Rueda and Gosselck, 1986) and Cape York Peninsula mangroves in Australia (Alongi, 1987).

Harpacticoid copepods are usually found as the second-most common taxon in terms of occurrence but are present at much lower abundances compared to nematodes in this study. Copepods are more related to coarse or sandy sediments in tropical area (Semprucci et al., 2010), or mangrove ecosystems (Chinnadurai and Fernando, 2007; Xuan et al., 2007) or in many European mudflats (Montagna et al., 1995; Platt and Warwick, 1980; Rzeznik-Orignac et al., 2003).

Interestingly, and, for the first time on bare mudflat habitat, no foraminifera were found among the six studied stations. Indeed, foraminifera mainly were found in the mangroves with a richness reaching up to 44 species and abundances reaching up to 2000 foraminifera 50 cm<sup>-3</sup>, but they were rare or absent in the open mudbanks (Debenay et al., 2002). The hypothesis for explaining the unexpected absence of this taxa is that the high physical instability of the mudflat does not allow foraminifera to survive in such fluid mud in the mudbanks as previously related by Debenay et al. (2002). Nevertheless, this hypothesis must be tested by experimental approach.

Further studies in this area are needed in order to better describe the local species richness of the meiofauna, and especially for nematodes. This presents a difficult challenge, since very few data from coasts of the Guianas are available, and many species will have to be described.

#### 5. Conclusions

On coasts of the Guianas, in the North Atlantic coast of South America in sandy mud sediment and fine silt sediment, biomass of primary producers tended to be greater toward the other world areas, and meiofauna abundance data were almost always higher, despite the high instability of mudflats. Meiofauna was not more abundant when the sediment was composed of the finest sediment particles and also when Chl a and prokaryotes, potential preys of meiofauna, were greater. But, epigrowth-feeders (2A) nematodes and small ones (biomass of  $0.07 \pm 0.001 \,\mu g \, ind^{-1}$ ) were largely well adapted in very fluid and unstable mud stations with probably no limitation of food source (e.g. microphytobenthos). No foraminifera were found among the six stations of the study. Very fluid mud with physical instability of sediment caused a large perturbation for the settlement of meiofauna; the least amounts of Chl a biomass and prokaryotic and meiofauna abundances were found there. Thus, the probable mobility of sediment may select for smaller meiobenthic organisms and disturb the larger organisms in the sediment, and, therefore, would not permit the settlement of foraminifera. In addition, temporary meiofauna (e.g. very small macrofauna) was largely found in the sediment.

#### Acknowledgments

The authors are grateful from Sophie Maillé from GEPOG in French Guiana for the technical support, and Thierry Guyot (LIENSs laboratory) for the Map. The authors are grateful to the "Plateau microscopie" of the LIENSs laboratory of the University of La Rochelle. The work was financially supported by the CNRS and the University of La Rochelle. This research was supported through a PhD grant for Hien Thanh Nguyen from the USTH (University of Hanoï) of Vietnam.

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## CHAPTER 3

FACTORS STRUCTURING THE BENTHIC

COMMUNITIES IN FRENCH GUIANA MUDFLATS

The major challenge for benthic ecology is defining the parameters responsible for natural changes in ecological community structure. In fact, a variety of biological and physical factors can contribute to such changes. These factors act hierarchically and synergistically to control community structure. On one hand, the abiotic variables such as grain size, salinity, temperature, oxygen concentration have been long believed to limit the distribution of infauna in the soft sediment habitats. And on the other, the importance of biotic factors such as competition and predation in structuring infaunal communities is also widely recorded. Additionally, in soft bottom habitats, the biggest drawback to the infaunal lifestyle is lack of a securing "anchor" in the sediment. Given the sediment disturbance could alter the community structure through its effect on the abundance and occurrence of the different species in the ecosystem, the extreme instability of the Guianas mudflats is therefore expected to negatively impact their associated benthic organisms.

Chapter 3 involves the spatial and temporal biodiversity patterns of benthic communities (macrofauna and meiofauna) in the French Guiana mudflats. Both taxonomic and functional approaches were applied in order to describe the community structure and to relate it with the environmental parameters between the mudflats. At all sampling events, benthic assemblages reflected the gradient of mud consolidation, as well as habitat differences (estuarine vs. bare seafront mudflats). Both abiotic and biotic parameters during wet and dry season were taken into account. The main factors influencing infauna structure were then determined with the aid of multivariable analysis. Results on the dynamics of the most abundant macrofauna representative, the Tanaidacea, are presented in paper 3. The seasonality and spatial distribution of meiofauna assemblage are the content of paper 4.

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## PAPER 3

DYNAMICS OF THE TANAIDACEA

### CrossMark

#### ORIGINAL PAPER

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

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Received: 6 January 2017 / Revised: 28 February 2017 / Accepted: 2 March 2017 © Senckenberg Gesellschaft für Naturforschung and Springer-Verlag Berlin Heidelberg 2017

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

Communicated by J. Gutt

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Published online: 18 March 2017

Réserve Naturelle Nationale de l'Amana, Awala-Yalimapo, Guyane française, France 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.

**Keywords** Tanaidacea · Intertidal mudflat · Population structure · Spatio-temporal variations · French Guiana

#### 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



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<sup>-2</sup> 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<sup>-1</sup>) 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



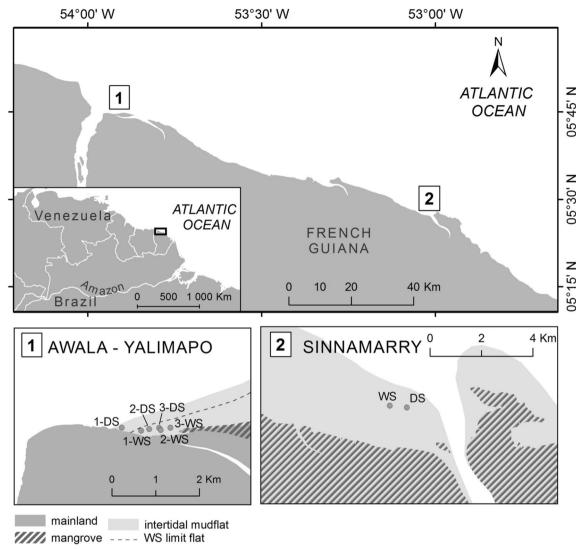


Fig. 1 Location of study sites and sampling stations on the Guiana coast

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 = [( $M_t - M_s$ )/  $M_t$ ] × 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	Awa1-DS	05°44′46″N	
	22/11/2014		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	Awa2-DS	05°44′45″N	
	30/11/2014		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
	Dry season	Awa3-DS	05°44′46″N	stage of mangrove colonization
	29/11/2014		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	Sinna-DS	05°28′24″N	
	25/11/2016		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  $(\chi^2)$  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.



#### **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,  $8.2 \pm 0.4$  PSU and  $16.0 \pm 0.9$  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 (%o)	Mud temperature (°C)	Water content (%)	Organic matter (%)
Awa1-WS	14.3 ± 0.5 b	$30.0 \pm 0.3 \text{ abgf}$	$63.4 \pm 2.9$ cd	6.8 ± 1.9 a
Awa2-WS	$12.2 \pm 0.5 \text{ ab}$	$29.4 \pm 0.5 \text{ abf}$	$60.6 \pm 4.4 \text{ cd}$	$6.0 \pm 1.3 \ a$
Awa3-WS	$14.9 \pm 1.8 \ b$	$31.5 \pm 0.4 \ cdef$	$57.6 \pm 2.5 \text{ cd}$	$6.2 \pm 1.5 \text{ a}$
Sinna-WS	$8.2 \pm 0.4 \ a$	$31.0 \pm 1.6$ ac	$54.9 \pm 2.3 \ ac$	$5.6\pm0.8~a$
Awa1-DS	$31.3 \pm 2.6$ c	$29.0 \pm 0.3$ abe	$58.3 \pm 1.9 \text{ cd}$	$5.3\pm0.1~a$
Awa2-DS	$42.3 \pm 3$ c	$32.1 \pm 0.5 \text{ cdg}$	$62.0 \pm 7.9 \text{ cd}$	$6.5\pm0.8~a$
Awa3-DS	$46.5 \pm 3.5 \text{ c}$	$33.2 \pm 0.1 \text{ cd}$	$57.8 \pm 1.6 \text{ cd}$	$5.9 \pm 0.6 \ a$
Sinna-DS	$16.0 \pm 0.9 \ b$	$33.0 \pm 1.6 \text{ c}$	$71.7 \pm 11.2 \text{ bd}$	$11.3 \pm 5.1 \text{ a}$

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

Fig. 2 The three tanaidacean species per age and sex occurring on the French Guiana coast

Discapseuses surinamensis

Monokalliapseudes guianae

5 mm

halmyrapseudes spaansi

5 mm

Discapseuses surinamensis

Monokalliapseudes guianae

Halmyrapseudes spaansi

Halmyrapseudes spaansi

Famm

5 mm

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  $(24,259\pm10,857 \text{ ind. m}^{-2})$ . The station Awa2-WS was the second most abundant station for this species  $(12,488\pm22,975 \text{ ind. m}^{-2})$  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<sup>-2</sup> 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<sup>-2</sup> and showed no



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

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 ( $19.8\pm9.7~\rm g.~m^{-2}$ ) while the lowest biomass was found at Awa3-DS ( $0.009\pm0.020~\rm g.~m^{-2}$ ). 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 ( $1.7\pm0.3~\rm g.~m^{-2}$  and  $1.6\pm0.4~\rm g.~m^{-2}$  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 ( $\chi^2$  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

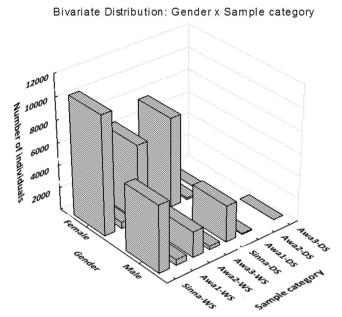
*H. spaansi* was the smallest tanaid species in the French Guiana mudflat, with total length ranging from 1.1 to 6.4 mm (Fig. 4). The mean total length of females, males and juveniles in the WS were  $4.4\pm0.7$  mm,  $4.5\pm0.6$  mm and  $2.5\pm0.4$  mm, respectively. The mean sizes of females and males decreased in the DS , with a mean total length of  $3.9\pm0.4$  mm for females and  $4.1\pm0.4$  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).

Comparis	son	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 $\times$ 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		_

<sup>\*</sup>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  $8.6 \pm 1.6$  mm in WS and  $8.8 \pm 1.0$  mm in the DS while this was  $9.2 \pm 1.5$  mm and  $8.4 \pm 0.9$  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 ( $7.5 \pm 1.8$  mm in the DS) were larger than males ( $6.1 \pm 1.0$  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<sup>-2</sup>) 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



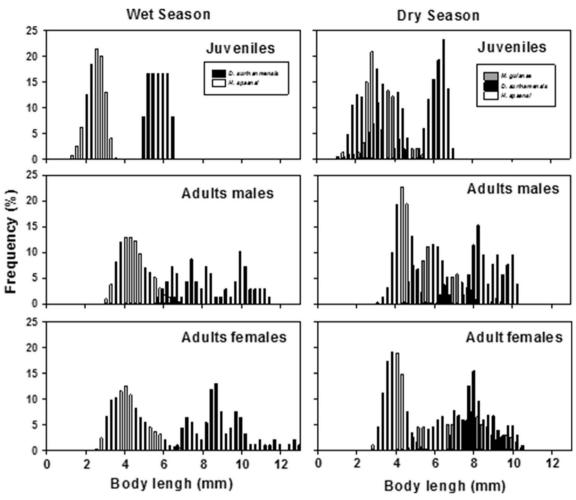


Fig. 4 Frequency distribution of the total length of males, females and juveniles of three tanaid species occurring in French Guiana

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**

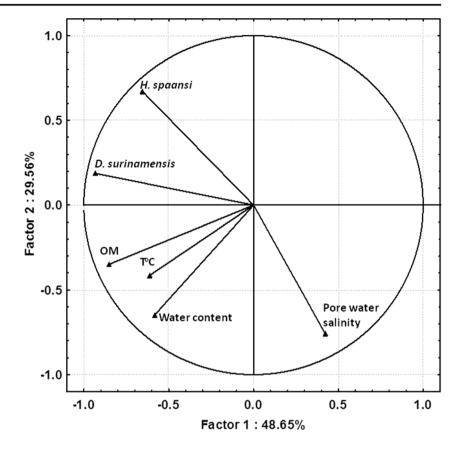
Changing sediment properties, wave-induced shear stress, and duration of submergence and exposure are believed to be among the most important factors structuring intertidal infaunal assemblages (Hertweck 1994; Raffaelli and Hawkins 1996). In agreement, our results showed a distinct segregation of the 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 atin 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



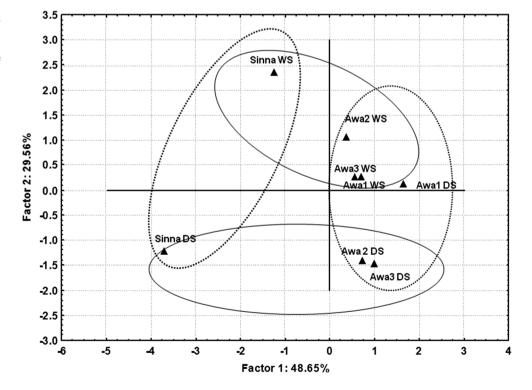
Fig. 5 Principal components and classification analysis. The projection of variables: D. surinamensis density, H. spaansi density, pore water salinity, water content, organic matter (OM) and sediment temperature  $(T^{\infty}C)$  on the factorplane  $(1 \times 2)$ 



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.

Acknowledgements The authors are grateful to Antoine Gardel, from CNRS Guiana, for the technical support in the field, and Thierry Guyot (LIENSs laboratory) for the map. The work was financially supported by the CNRS, the CNRS Guiana, the University of La Rochelle and the European Fund for Regional Development (FEDER). This research was supported through a 911 PhD grant to HienThanh Nguyen, from the USTH (University of Science and Technology of Hanoi) - Vietnam Academy of Science and Technology.

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# PAPER 4

DYNAMICS OF THE MEIOFAUNA

# Seasonality and ecological zonation of meiofaunal assemblages in highly dynamic intertidal mudflats along the Amazonian coast in French Guiana

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In preparation for Science of the Total Environment

# Introduction

In almost every marine ecosystems, benthic communities are recognised as important components and are fundamental to maintain the ecological integrity and biodiversity of the marine environment as a whole (Australian EPA, 2016). Among those, meiofauna is among the most abundant and diverse groups that widely distribute from tidal flats to deep-sea trenches (Giere, 2009). Despite their relative small size ( $40 \mu m - 1000 \mu m$ ), the ubiquity of meiofauna suggests its significant contribution to overall ecosystem functioning (Coull, 1999). The modification of sediment properties induced by meiofauna activities has been directly and indirectly affected various ecosystem services, such as sediment stabilization or waste removal (Schratzberger and Ingels, 2017). By its occurrence in the stomach content of several macrofauna and fish species (Coull, 1999), and recently even in the diet of shorebirds (Gerwing et al., 2016), meiofauna has been known as essential food sources for higher trophic levels (Danovaro et al., 2007). In soft sediment habitats, higher meiofaunal density and diversity have been observed showing significant effects on facilitating biomineralization (Nascimento et al., 2012) and stimulating bacterial denitrification and nitrification. These processes consequently enhance nutrient regeneration and, to a certain extent, can mitigate environmental degradation in habitats subjected to eutrophication (Coull, 1999; Bonaglia et al., 2014).

The distribution of meiofauna is heterogeneous with changes in density and species composition mainly driven by various environmental factors and biotic interactions (Wolowicz et al., 2011). Unravelling meiofaunal distribution patterns is of importance to better understanding the functioning of this infauna group in the ecosystems. In intertidal habitats, benthic communities usually follows a zonation of varying environmental variables from the high towards the low tidal level, corresponding with changes in sediment properties, wave exposure and the duration of submergence and exposure (Dittmann, 2000, Chappuis et al., 2014). In the sediment, besides the effect of seasonality, meiofaunal abundance and species composition are spatially structured by various abiotic and biotic factors along both horizontal

and vertical dimensions (Wolowicz et al., 2011). The horizontal differences are often reflecting the large scale of hundreds of metres, where physical parameters such as salinity, grain size and temperature and their variations are among the key factors determining the meiofaunal communities (Steyaert et al., 2003). In contrast, vertical distribution is differentiated at the scale of few centimetres with strong correlations with oxygen availability in the sediment (Joint et al., 1982; Taheri et al., 2014) as well as with the proximity to the primary food source (Wolowicz et al., 2011). Nevertheless, little has been done to explore the interaction between the horizontal and vertical distribution patterns of meiofaunal assemblages (Vieira and Fonseca, 2013). This is particularly true in the case of French Guiana mudflats, where the number of meiofaunal studies is still extremely scarce. Besides, this lack of studies sounds rather contradictory with the fact that meiofauna abundance was much higher compared to other productive habitats elsewhere (Dupuy et al., 2015). Meiofauna also played a significant functional role on bioturbation of sediment fluxes, implying their substantial influence on both physical structure of the sediment matrix and distribution of organic matter (Aschenbroich et al., 2017).

Unlike the majority of coastal environments, the French Guiana shoreline experiences massive fine-grained sediment discharge from the Amazon River, which consequently contribute to the formation of a series of alternating huge mudbanks along its coast (Plaziat and Augustinus, 2004; Anthony and Dolique, 2004, Lambs et al., 2007). These mudbanks, which may be up to 5 m-thick, 10 to 60 km-long, 20 to 30 km in width (Froidefond et al., 1988; Alison et al., 2000), continuously migrate westward under the influences of ocean waves and coastal currents (Plaziat and Augustinus, 2004; Anthony et al., 2011). The longshore structure of the mudbanks contains three parts: the leading edge of the bank, the consolidated mudflat and the trailing edge (Péron et al., 2013; Gensac et al., 2015). Among which, the development of the leading edge induced by excessive mud accretion from Amazonian discharge as well as from the supply of the mudbank trailing edge erosion is responsible for the mudbank migrating phenomenon (Lefbvre et al., 2004; Gensac et al., 2015). On the shoreward dimension, the intertidal mudflat formed by the migration of the mudbanks is divided into two areas: the seafront and the inner part (Gensac et al., 2015). The seafront exhibits higher sediment reworking rate imposed by wave effect, whereas the inner part undergoes a constant sedimentation process (Anthony et al., 2011; Gensac et al., 2015). These highly dynamics of the sediment are therefore supposed to have the strong impact on its associated benthic organisms and especially nematodes due to its consistent benthic lifestype.

In order to address the question on whether and to which extent the meiofaunal assemblages will be defined by the unique characteristics of French Guiana mobile mudflats, the profiles of meiofauna were compared in different intertidal habitats and seasons. It was notably hypothesized that meiofauna would show a weak vertical zonation in the high frequent reworked sediment (fluid mud) compared to the more stabilized and consolidated one. This study aimed (i) to investigate the distribution patterns of meiofauna along a consolidation gradient of the sediment subjected to seasonal impact, (ii) to reveal if there are any key factors determining the distribution and composition of meiofauna communities, and therefore, (iii) to understand the ecological functioning of meiofauna in this unique environment.

#### Materials and methods

Study sites

The study sites were located within two migrating mudbanks on the coast of Sinnamary and Awala-Yalimapo, in French Guiana (Fig. 1). Both mudbanks were characterized by meso-tidal regimes with semidiurnal tidal range between 0.8 m (neap tide) and 2.9 m (spring tide). The climate was tropical with two distinctive seasons: wet season (January-July) and dry season (August-December). The sites in Sinnamary and Awala were chosen for their characteristics of estuarine and seafront mudflat, respectively.

In June 2014 (wet season - WS), one very soft mud station was sampled at the riverside of the mudflat in Sinnamary (Sinna-WS, 05°28′27″N; 53°01′54″W). At the seafront mudflat Awala, three stations were sampled along the gradient of mud consolidation. Awa1-WS (05°44′44″N; 53°55′38″W) was at the leading edge of the mudbank, in the low tide zone and characterized by fluid mud. Awa2-WS (05°44′44″N; 53°55′24″W) was at 500 m away from the leading edge of the mudbank, possessing mid-intertidal level with moderate compacted mud (soft mud). Awa3-WS (05°44′46″N; 53°55′17″W) was at 700 m from the leading edge, in front of the pioneer stage of the mangrove colonization, high tidal elevation and the sediment was compacted mud. Likewise, in December 2014 (dry season - DS), samples were collected at the four stations: Sinna-DS (05°28′24″N; 53°01′32″W), Awa1-DS (05°44′46″N; 53°55′53″W), Awa2-DS (05°44′45″N; 53°55′32″W) and Awa3-DS (05°44′46″N; 53°55′25″W). Despites slight differences in geographical position, due to the westward extension process of the mudbanks (migrating) (Plaziat and Augustinus, 2004; Fromard et al., 2004; Gensac et al.,

2015), the four stations sampled in the DS presented the same characteristics as described above in the WS.

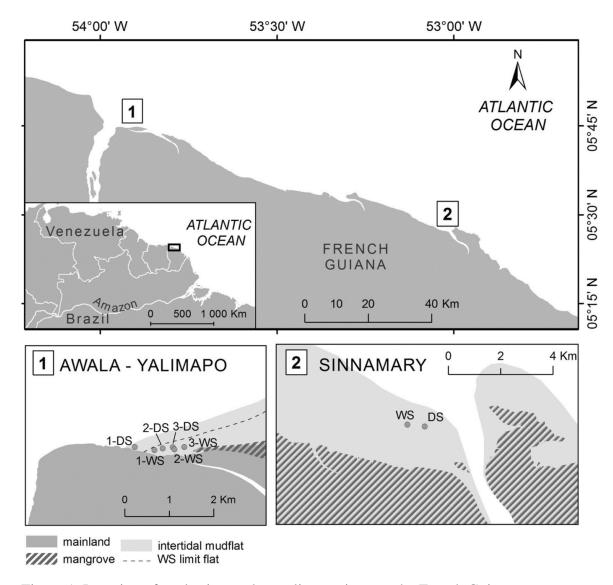


Figure 1. Location of study sites and sampling stations on the French Guiana coast

# Sampling strategy

At each of the sampling stations, triplicate meiofauna samples (0-2 cm) were taken using a 30 cm long plastic corer with an inner diameter of 15 cm. In order to analyse the vertical distribution of the meiofauna, samples were then subdivided into three different layers of the sediment column: 0-0.5 cm, 0.5-1.0 cm and 1.0-2.0 cm, then immediately reserved in 70% ethanol for later meiofauna investigation. Other subsamples were taken for the analysis of biomass of chlorophyll a (chl a), concentration of organic matter (OM), water content (WCO) and granulometry. Samples for granulometry analysis were fixed with formaldehyde (final concentration 4 %) and stored at ambient temperature. Pore water samples for the analysis of

salinity and nutrient concentrations were extracted with the help of Rhizon samplers (Rhizosphere Research Products Netherlands) method (Seeberg-Elverfeldt et al., 2005). Salinity was measured *in situ* using a refractometer (Atago S-10; Japan). All the samples for nutrient (except for silicates which samples were preserved at 4 °C), chlorophyll a, OM and WCO analyses were frozen and kept in dark upon the further processing in the laboratory.

# Meiofauna analysis and environmental parameters

Meiobenthic organisms were extracted by rinsing the sediment samples consecutively over 1000-μm and 50-μm sieves. The fraction retained on the 50-μm sieve were classified to the major groups and enumerated under a binocular loupe (Leica, WILD M3Z). From each replicate, 200 individuals of nematodes were randomly handpicked then transferred to anhydrous glycerol and mounted on slides for identification to species level (ZEISS, Axioskop 2). To investigate the trophic structure of the nematodes, four feeding guilds were assigned basing on nematode buccal morphology: absent of fine tubular - selective deposit feeders (1A), large but unarmed - non-selective deposit feeders (1B), with scraping tooth or teeth - epigrowth feeders (2A) and buccal cavity with large jaws – omnivores-carnivores (2B) (Wieser, 1953, 1960). The infaunal densities in the 0-0.5 cm, 0.5-1.0 cm, 1.0-2.0 cm layers were converted to ind.10 cm<sup>-2</sup>.

Chlorophyll *a* biomass (μg chl *a* g<sup>-1</sup> dry weight sediment) was estimated by a fluorometer (640 nm, Turner TD 700, Turner Design; USA) following the method of Lorenzen (1966). The percentage of organic matter in the sediment was measured according to Wollast (1989) (weight loss after incineration). Water content (WCO) of the sediment was obtained by calculating the percentage of weight loss after complete evaporation (60 °C, 24h) in total mass of the wet sediment (Nguyen et al, 2017). The grain size of the sediment was classified by a Malvern Mastersizer 2000 (Malvern Instruments Ltd, Worcs; UK) and expressed in particle size distribution D50 and percentage of the silt and clay (<63 μm). The nutrients in pore water (NH<sub>4</sub><sup>+</sup>, NO<sub>2</sub><sup>-</sup>, NO<sub>3</sub><sup>-</sup>, PO<sub>4</sub><sup>3-</sup> and Si(OH)<sub>4</sub> concentrations) were determined using an autoanalyzer (Seal Analytical, GmbH Nordertedt, Germany) equipped with an XY-2 sampler according to Aminot and Kérouel (2007).

# Data analysis

To assess the variation of meiofaunal abundance subjected to the spatio-temporal changes along the vertical distribution, differences in total meiofaunal densities were compared by three-way PERMANOVA (factors: station, season and layer) (software: PRIMER 6). To evaluate the differences in community structures as well as in habitat characteristics, PERMANOVA were also conducted for data of meiofaunal community structure, nematode community structures, nematode trophic structure and environmental variables. The design of this test included three different fixed factors: station, season and layer. Resemblance matrix of the infaunal densities was calculated using Bray-Curtis coefficients, meiofaunal densities were square root transformed to improve assessment of rare and common taxa on community structure. All environmental variables were normalized prior to analysis to handle measurements with different units and scale. The interaction of station, season and layer gave the information of the vertical profile changing with regard to different stations in different seasons. The a posteriori pairwise tests were performed when there was significantly different in the main test of PERMANOVA. Due to the restricted number of possible permutations in pairwise tests, pvalues were obtained from Monte Carlo permutation test. The similarity in nematode profiles was then compared by CLUSTER and SIMPROF (Similarity Profile Analysis) based on the Bray Curtis similarity matrix (PRIMER 6). To explore the multivariate relationship between meiofauna and environmental variables, a Redundancy Analysis (RDA) was used. The most significant explanatory variables contributing to meiofaunal distribution were chosen from the automatic forward selection (p < 0.05, Monte Carlo permutation test). Data of species abundance were square-root transformed while environmental data were automatically centered and standardized by the CANOCO software (CANOCO, version 4.5 for Window).

#### **Results**

# Sediment properties

Permutation multivariate analysis of all environmental variables together showed significant variation in different stations and sediment layers in two seasons (Table 1). Characteristics of sediments of Sinnamary significantly distinguished from the sediments of Awala in both seasons. All stations exhibited significant differences in sediment properties and biochemical composition between layers, except for Awa1 in the DS (PERMANOVA, pair wise test).

The sediment in Awala was mostly consistuted of fine sandy silt (mud content > 85%, D50 < 12  $\mu$ m). In contrast, Sinnamary had lower mud content (36%-74%) and samples contained larger particles (D50<sub>max</sub> = 142  $\pm$  1  $\mu$ m) (Table 2). Pore water salinity significantly differed between stations as well as between seasons (PERMANOVA, p = 0.001), but it did not differ between layers (PERMANOVA, p > 0.05). The salinity in Sinnamary ranged from 8.00-9.33%

(WS) to 15.00-15.67‰ (DS) and was significantly lower than in the stations of Awala in both seasons (PERMANOVA, p < 0.05). In addition, during WS there were no significant differences between Awa1, Awa2 and Awa3 while during DS, salinity reached the highest level in Awa3 (49.17‰  $\pm$  9.41), followed by Awa2 (43.00‰  $\pm$  3.28) and both were significantly higher than Awa1 (29.33-32.67‰) (Table 2). The percentage of OM was higher in the top layer in all stations in both seasons but did not significantly differamong stations during the WS (PERMANOVA, p > 0.05). In the DS, OM significantly increased in the first two layers at Sinnamary, which were double to almost triple the value of OM recorded in the third layer in Sinnamary and in the three stations in Awala (PERMANOVA, p < 0.05).

Table 1. Main comparison tests (three-way PERMANOVA) on different habitats (based on environmental variables) and changes in community structure (based on meiofaunal density, nematode density and feeding guild classification) in two seasons.

	Df	SS	MS	Pseudo-F	P(perm)
Environmental variable					
Station	3	216.69	72.229	38.169	0.001
Season	1	79.146	79.146	41.825	0.001
Layer	2	101.3	50.649	26.765	0.001
Station*Season	3	111.83	37.276	19.699	0.001
Station*Layer	6	62.857	10.476	5.5361	0.001
Season*Layer	2	33.331	16.666	8.807	0.001
Station*Season*Layer	6	85.022	14.17	7.4883	0.001
Meiofauna					
Station	3	18748	6249.3	58.776	0.001
Season	1	10111	10111	95.098	0.001
Layer	2	8833.7	4416.8	41.542	0.001
Station*Season	3	9225.9	3075.3	28.924	0.001
Station*Layer	6	4981.2	830.19	7.8082	0.001
Season*Layer	2	5369.6	2684.8	25.251	0.001
Station*Season*Layer	6	3173.2	528.87	4.9742	0.001
Nematode					
Station	3	45536	15179	61.289	0.001
Season	1	11028	11028	44.531	0.001
Layer	2	12045	6022.4	24.317	0.001
Station*Season	3	19712	6570.6	26.531	0.001
Station*Layer	6	8176.7	1362.8	5.5027	0.001
Season*Layer	2	3553.2	1776.6	7.1737	0.001
Station*Season*Layer	6	6395.7	1066	4.3042	0.001
Feeding type					
Station	3	18189	6063	58.354	0.001
Season	1	6995.4	6995.4	67.328	0.001
Layer	2	6151.3	3075.7	29.602	0.001
Station*Season	3	10309	3436.5	33.075	0.001
Station*Layer	6	5255.4	875.91	8.4303	0.001
Season*Layer	2	3923.5	1961.7	18.881	0.001
Station*Season*Layer	6	4118.3	686.39	6.6062	0.001
Station	3	18189	6063	58.354	0.001

Table 2. Environmental characteristics (mean of three replicates) of four stations in two seasons along French Guiana coast. L1: 0-0.5 cm, L2: 0.5-1 cm, L3: 1-2 cm. WS= Wet Season, DS= Dry season. Awa= Awala, Sinna= Sinnamary.

Sample	Label (In graphs)	Layer	Salinity (‰)	Chla (µg/g)	OM (%)	Mud content (%)	D50 (μm)	WCO (%)	NO <sub>3</sub> (μmol/L)	NO <sub>2</sub> (μmol/L)	NH <sub>4</sub> (µmol/L)	PO <sub>4</sub> (µmol/L)	SiOH (µmol/L)
SinnaWS	1-3	L1	9.33	22.25	6.49	62.10	14.96	52.63	0.94	0.30	21.80	0.95	76.73
	4-6	L2	8.33	4.48	5.45	72.41	20.51	55.00	0.11	0.48	19.27	0.99	138.36
	7-9	L3	8.00	2.14	4.81	58.92	26.70	57.14	0.68	0.89	67.46	1.82	236.67
Awa1WS	10-12	L1	18.00	85.31	8.91	90.96	9.30	62.50	3.26	0.54	9.93	2.22	78.46
	13-15	L2	13.33	14.04	6.27	96.68	8.49	66.67	1.15	0.17	33.04	1.06	87.47
	16-18	L3	12.67	7.50	5.31	97.54	7.17	61.11	0.82	0.48	65.84	1.10	90.22
Awa2WS	19-21	L1	13.00	82.31	7.46	86.63	10.33	63.16	0.05	0.18	19.78	1.69	46.47
	22-24	L2	11.67	10.61	5.45	96.60	7.51	63.16	0.00	0.55	16.82	2.03	81.81
	25-27	L3	11.33	3.64	5.01	96.47	6.89	55.56	0.00	0.57	17.87	1.82	102.48
Awa3WS	28-30	L1	16.00	89.00	7.98	85.32	10.72	57.89	0.93	0.24	20.69	2.93	69.98
	31-33	L2	13.67	12.14	5.53	96.79	7.53	55.00	1.18	0.84	21.27	4.07	65.42
	34-36	L3	14.00	2.43	5.21	97.95	7.07	60.00	0.13	3.52	21.17	16.10	74.91
SinnaDS	37-39	L1	15.67	11.84	16.46	46.00	81.28	82.39	6.72	0.71	23.06	0.76	93.78
	40-42	L2	15.00	6.95	11.35	36.13	142.25	72.67	1.30	0.32	23.93	0.80	101.45
	43-45	L3	15.67	4.51	6.18	74.61	13.68	60.10	0.56	0.19	27.97	0.68	104.52
Awa1DS	46-48	L1	32.67	8.31	5.29	94.83	8.36	60.43	6.94	2.58	91.17	2.48	86.83
	49-51	L2	29.33	5.30	5.43	95.16	8.22	57.61	2.28	0.60	170.80	0.98	113.45
	52-54	L3	32.17	4.99	5.30	96.86	7.44	56.76	3.69	0.31	208.11	1.36	121.34
Awa2DS	55-57	L1	41.00	45.05	7.38	88.31	11.68	70.97	0.46	1.01	12.12	2.82	54.17
	58-60	L2	41.33	17.43	6.19	96.45	7.25	59.02	0.00	2.37	10.53	2.30	45.82
	61-63	L3	43.17	11.77	5.88	87.68	9.93	55.91	0.00	5.89	13.19	6.82	55.30
Awa3DS	64-66	L1	43.83	44.67	6.53	95.57	8.20	59.55	5.43	0.62	21.00	3.49	42.97
	67-69	L2	43.00	14.58	5.55	98.60	7.17	57.30	1.17	5.02	20.34	8.59	69.83
	70-72	L3	49.17	12.67	5.50	98.00	7.27	56.48	1.63	1.39	91.36	4.96	111.99

WCO was highest at the top layer of SinnaDS (82.39%  $\pm 0.02$ ) and the lowest values were also found at the same layer in SinnaWS (52.63%  $\pm 0.01$ ). In Awala, the WCO ranged from 55.00-66.67% in the WS and from 55.00-70.97% in the DS and no significant differences were observed between seasons or stations and among layers

Pore water nutrients including nitrate, nitrite, ammonium, phosphate and silicate also varied significantly with station x season x layer interaction (Table 1, PERMANOVA, p < 0.05). Nitrate was mostly concentrated on the top layer with higher values observed in the DS (0.46  $\pm$  0.61 - 6.94  $\pm$  7.19  $\mu$ mol.L $^{-1}$ ) compared to the WS (0.05  $\pm$  0.04 - 3.26  $\pm$  4.62  $\mu$ mol.L $^{-1}$ ). Particularly, the depletion of NO<sub>3</sub> was observed at Awa2 for all layers in both seasons. In contrast, nitrite increased with depth during the WS except for Awa1 and during the DS at Awa2, Awa3. Higher concentration of NO<sub>2</sub> occurred in Awa1, Awa2 and Awa3 (0.31  $\pm$  0.08 - 5.89  $\pm$  2.66  $\mu$ mol.L $^{-1}$ ), while lower value was found in Sinnamary (0.19  $\pm$  0.02 - 0.32  $\pm$  0.03  $\mu$ mol.L $^{-1}$ ) during the DS. Additionally, the highest values of ammonium were found at Awa1DS (91.17  $\pm$  53.00 - 208.11  $\pm$  79.00  $\mu$ mol.L $^{-1}$ ) while in both seasons, Awa2 exhibited the lowest NH<sub>4</sub> concentration (10.53  $\pm$  0.2 - 19.78  $\pm$  3.57  $\mu$ mol.L $^{-1}$ ). Phosphate ranged from 0.60  $\pm$  0.18 (SinnaDS) to 16.10  $\pm$ 3.33  $\mu$ mol.L $^{-1}$  (Awa3WS) with the highest concentration observed in the most consolidated station, i.e. Awa3. Sinnamari showed the lowest value, followed by Awa1 and Awa2. The amount of silicate in the sediment was relatively abundant (42.69  $\pm$  0.58 - 236.67  $\pm$  37.24  $\mu$ mol.L $^{-1}$ ) and increased with depth in both seasons.

Chl a biomass was significantly more concentrated in the surface layer compared to the other two layers (PERMANOVA, p < 0.05). During the WS, the biomass of chl a in Sinnamary was significantly lower than in Awala in all layers. During the DS, chl a biomass decreased drastically in the surface in all stations but increased slightly in the deeper parts of Sinna, Awa2 and Awa3. At Awa1, the significant reduction of chl a was observed in all three layers, marking Awa1 the lowest in chl a biomass, followed by Sinna, Awa3 and Awa2 (PERMANOVA, p < 0.05)

Meiofaunal diversity, community composition and vertical profile of abundance

A total of twelve major meiobenthic groups were found. Nematoda was the most abundant (from 57 to 99%), followed by Copepoda and Ostracoda (Fig. 2). Turbellaria, Kinorhyncha, and Oligochaeta occurred mainly in Sinnamary with less than 5% of total meiofaunal abundance in each replicate. Polychaeta, Acari, Foraminifera, Nemartine, Gastropoda and small bivalves were poorly presented, with relative abundance lower than 0.42% whatever the sites.

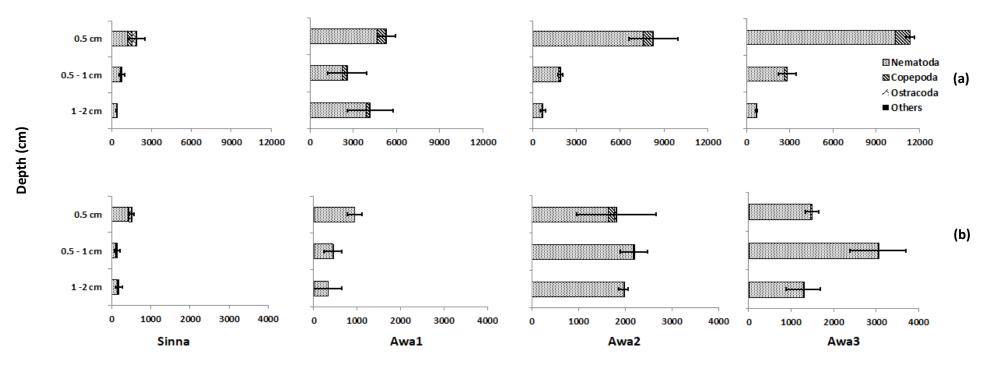


Figure 2. Vertical density profiles of the meiofauna (ind.10cm<sup>-2</sup>) in sediment column from four stations in wet (a) and dry (b) seasons. Others included Turbellaria, Kinorhyncha, Polychaeta, Oligochaeta, Acari, Nemartine, Foraminifera, small Bivalve and Gastropoda.

The composition of meiofaunal communities were significantly influenced by the location, season and by their position in the sediment column, as well as by the interaction among these three factors (three-way PERMANOVA, Table 3). The pair wise tests revealed that significant differences in community composition were more profound between habitats (Sinnamary vs. Awala) and between seasons (WS vs. DS) (t > 7, p(MC) < 0.001) compared to the variation among layers (t < 4, p(MC) < 0.05). Besides the dominance of the nematodes, Sinnamary was characterized with higher densities of ostracods, kinorhynchs and oligochaetes in comparison to the stations in Awala. The three stations in Awala were highly dominated by nematodes then followed by the copepods. The community composition in the WS was significantly different from the DS. Among layers, significant differences were obtained between three layers in two more consolidated muddy stations (Awa2 and Awa3) in the WS while there were no statistical differences in the fluid mud stations (Sinna, Awa1) in the WS. Particularly, all stations in the DS from the low to high tidal elevation exhibited no significant differences between three layers deeper layers.

Meiofaunal abundance was statistically different under the effect of Station x Season x Layer (PERMANOVA, p < 0.05; Table 3). In the WS, significant higher meiofaunal abundance was observed in the upper layer (0.0-0.5 cm) at Awa2 and Awa3 (pair wise test, p < 0.05) while there were no significant differences among layers at Sinna and Awa1. In the DS, meiofauna remarkably decreased in the first layer of all stations but did not significantly change in the two deeper layers at Awa1, Awa2 and Awa3. In Sinnamary, remarkable decrease of meiofauna abundance was only observed at two upper layers. No statistical differences in meiofauna abundances among three layers in all stations in the DS (pair wise test, p > 0.05).

# Nematode assemblages and trophic structure

A total of 23 nematode species belonging to 21 genera of 14 families was recorded. Five species accounted for over 90.3% of the French Guiana nematode assemblages: *Pseudochromadora galeata* (56%), *Metachromadora chandleri* (17%), *Halomonhystera* sp. 1 (10%), *Pseudochromadora incubans* (5%) and *Leptolaimoides* sp. 1 (3%) (data not show). Fourteen species with relative abundance lower than 0.8% were considered as rare species. Among the most dominant species, no *Metachromadora chandleri* was found in Sinnamary and *Pseudochromadora incubans* mostly occurred in the DS (data not show). Furthermore, nematode community structure was significantly different according to the results of similarity profile analysis (SIMPROF, p < 0.05).

Table 3. Main comparison test and post hoc tests (three-way PERMANOVA) for differences in total meiofaunal abundance.

Main test		SS	df	MS	F	р
Stat	ion	5.8668	3	1.9556	79.88	*
Seas	son	3.3916	1	3.3916	138.53	*
Lay	er	3.2671	2	1.6336	66.72	*
Stat	ion*Season	1.9967	3	0.6656	27.19	*
Stat	ion*Layer	0.4776	6	0.0796	3.25	*
	son*Layer	0.8082	2	0.4041	16.51	*
	ion*Season*Layer	1.6367	6	0.2728	11.14	*

Pairwise		Station (Season)	Season (Station)	Season (Layer)
	0-0.5 cm	Sinna (WS>DS)	WS (Sinna <awa1<awa2<awa3)< td=""><td>-</td></awa1<awa2<awa3)<>	-
		Awa1 (WS>DS)	DS (Sinna=Awa1=Awa2=Awa3)	-
		Awa2 (WS>DS)		-
		Awa3 (WS>DS)		-
	0.5-1 cm	Sinna (WS>DS)	WS (Sinna=Awa1=Awa2=Awa3)	-
		Awa1 (WS>DS)	DS (Sinna =Awa1 <awa2=awa3)< td=""><td>-</td></awa2=awa3)<>	-
		Awa2 (WS=DS)		-
		Awa3 (WS=DS)		-
	1-2 cm	Sinna (WS=DS)	WS (Sinna=Awa2=Awa3 <awa1)< td=""><td>-</td></awa1)<>	-
		Awa1 (WS>DS)	DS (Sinna=Awa1=Awa2=Awa3)	-
		Awa2 (WS=DS)		-
		Awa3 (WS=DS)		-
	Sinna	-	-	WS (L1=L2=L3)
		-	-	DS (L1=L2=L3)
	Awa1	-	-	WS (L1=L2=L3)
		-	-	DS (L1=L2=L3)
	Awa2	-	-	WS (L1>L2>L3)
		-	-	DS (L1=L2=L3)
	Awa3	-	-	WS (L1>L2>L3)
		=	-	DS (L1=L2=L3)

\*p<0.05; L1: 0-0.5 cm, L2: 0.5-1 cm, L3: 1-2 cm. > significantly higher, < significantly lower, = not significant difference at 5%

The assemblages found in the highly reworked sediment (fluid mud) habitat (SinnaWS, Sinna DS, Awa1DS) were clearly segregated from the ones occurring in other more stable, consolidated stations (CLUSTER, p < 0.05) (Fig. 3). Within these two big groups, nematode communities were then significantly subdivided into seven subcategories reflecting remarkable differences in seasonality (WS versus DS) and habitats (estuarine-Sinnamary versus seafront mudflats-Awala). Nonetheless, vertical profile (layers) was not clearly separated between two deeper layers. Cluster 1 consisted of all nematode assemblages inhabiting the top layer in Awala during the WS while cluster 2 was dominated by the nematode communities collected from second layer of Awa2WS, Awa2DS and Awa3WS. Cluster 3 was the mixture of nematode communities from two deeper layers in Awa1WS and Awa3DS with some from the third layer in Awa2DS.

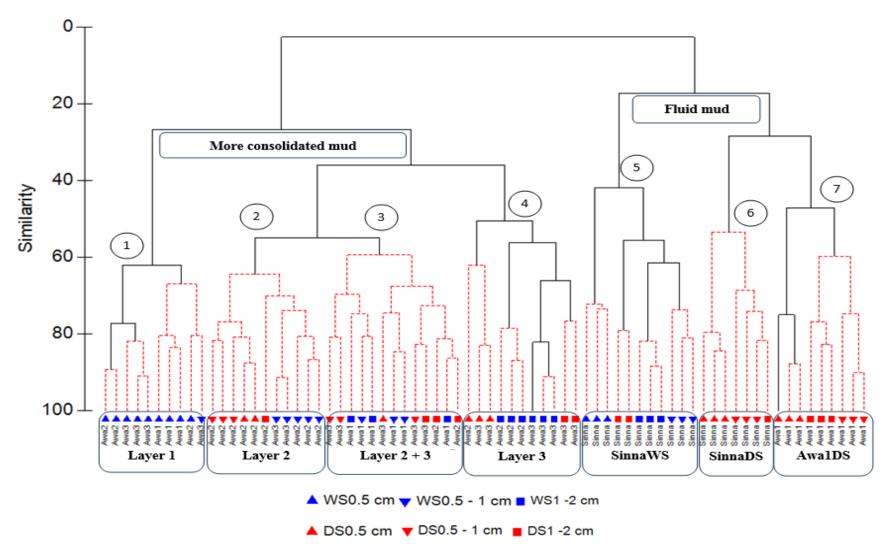


Figure 3. Cluster analysis of the nematode community composition along 3 layers of four stations from two seasons. Black lines indicate nematode profiles show significant differences, red dash-lines indicate clusters that are not significantly different (SIMPROF analysis, the threshold for p is at 0.05)

Cluster 4 presented nematode assemblages from the third layer of Awa2WS, Awa3WS and Awa3DS and was the last subcategory within consolidated muddy habitat. In regard to high reworked sediment habitat (fluid mud), the three remaining subgroups were segregated basing on habitat and seasonal differences inferring the lesser influence of vertical variation compared to nematodes found in consolidated mud habitat. Cluster 5, 6, 7 represented nematode communities of SinnaWS, SinnaDS (estuarine mudflat) and Awa1DS (seafront mudflat) respectively. In addition, all samples from both habitats showed considerable differences in species composition between wet and dry seasons except for the communities at second layer at Awa2. In both seasons, nematode composition of Awa1 in the first layer was significantly segregated while there were no differences between two deeper layers.

Nematode trophic structure was significantly affected by the interaction of Station x Season x Layer (three-way PERMANOVA, Table 3). In Awa2 and Awa3, Epistrate feeders (2A in Fig. 4) dominated all the depths in both seasons, while in Awa1 this group was only abundant in the WS and decreased significantly in the DS. In Sinna, reduction of the 2A was observed towards the deeper layers in both seasons, which consequently induced an increasing relative abundance of selective deposit feeders (1A) in layer two and layer three. Non-selective deposit feeders (1B) were the major component in trophic structure of Awa1 in the DS. In contrast, this feeding type decreased in the dry season in Awa3 with reduction towards the deeper layers but tends to increase in Awa3 in the WS, particularly in the upper layer. The omnivores/predators (2B) presented minor abundance in all layers among stations in two seasons.

# Meiofauna in relation to environmental variables

The distribution pattern of meiofauna community was teased out by RDA (Redundancy Analysis) ordination plot (Fig. 5). The triplot displayed the major patterns in the meiofaunal data with respect to the environmental variables, in which (a) the first axis explained 65.1% of the meiofaunal distribution variation and corresponded to chl a biomass (p = 0.002) (Fig. 5) and (b) the second axis (3.7%) roughly corresponded to mud content (p = 0.002), pore water salinity (p = 0.012) and NO<sub>2</sub> concentration (p = 0.034). In total, chl a biomass, mud content, pore water salinity and NO<sub>2</sub> explained 49%, 8%, 5% and 3% of the variation in the meiofaunal data respectively (Lambda A, Table 4).

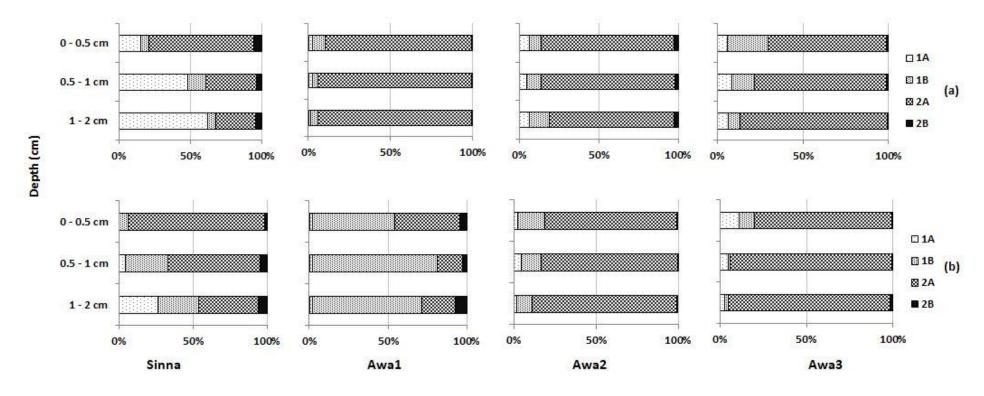


Figure 4. Vertical profile of nematode trophic composition in four stations in two seasons.

(a) – wet season, (b) - dry season, (1A) – selective deposit feeders, (1B) non-selective deposit feeders, (2A) – epistrate feeders, (2B) – omnivores/predators

Nematodes, copepods, turbellarians and polychaetes increased proportionally with the biomass of chl a while the distribution of ostracods and kinorhynchs were confined by lower salinity and nitrite concentration together with lessened mud content in the sediment composition (Multiple regression analysis, p < 0.05). The vertical zonation of meiofauna in the WS was presented along the gradient of chl a (first axis) with the upper layer mostly aggregating more on the upper-right quadrant of the ordination graph while two deeper layers concentrated on the left of the ordination graph. In Awala, the other two deeper layers showed no significant differences and distributed closed to each other. In the DS, meiofaunal vertical differences were defined along the second axis with the distribution of communities in the top to third layer following an increasing gradient of salinity and nitrite. Exceptionally, the highly aggregated scattering of samples at Awa1DS reflected high similarity among all three layers.

Table 4. Conditional effects obtained from the summary of forward selection – Explanation to species compositions of meiofauna and nematode. Table showed the environmental variables in the order of their contribution. Significant value obtained with p < 0.05, LambdaA was the percentage of species composition variation explained by particular environmental variable together with additional variances.

	Meiofauna				Nematode				
Variable	LambdaA	P	F	Variable	LambdaA	P	F		
Chla	0.49	0.002	67.27	Chla	0.4	0.002	46.07		
Mud content	0.08	0.002	13.44	Mud content	0.06	0.006	7.67		
Salinity	0.05	0.012	7.45	$NO_2$	0.03	0.03	4.31		
$NO_2$	0.03	0.034	5.65	Salinity	0.02	0.078	2.9		
Si	0.01	0.138	2.94	D50	0.01	0.272	1.32		
$PO_4$	0.01	0.168	2.36	$PO_4$	0.01	0.238	1.39		
D50	0.01	0.426	1.28	$NO_3$	0.01	0.224	1.38		
$NO_3$	0	0.364	1.11	OM	0.01	0.254	1.3		
OM	0.01	0.56	0.54	WCO	0.01	0.226	1.39		
WCO	0	0.41	1.15	$NH_4$	0	0.478	0.67		
$NH_4$	0.01	0.558	0.55	Si	0.01	0.736	0.27		

Meanwhile, the horizontal zonation was clearly defined by the mud content, salinity and concentration of nitrite, resulting in two distinctive habitats, estuarine (Sinnamary) vs. bare seafront mudflat (Awala). The seasonal effect was not only correlated with chl a biomass, by shaping communities in the WS rightwards compared to the DS; but also significantly related to the variation of salinity and nitrite concentration (WS distributed on the upper part of the graph and DS was below).

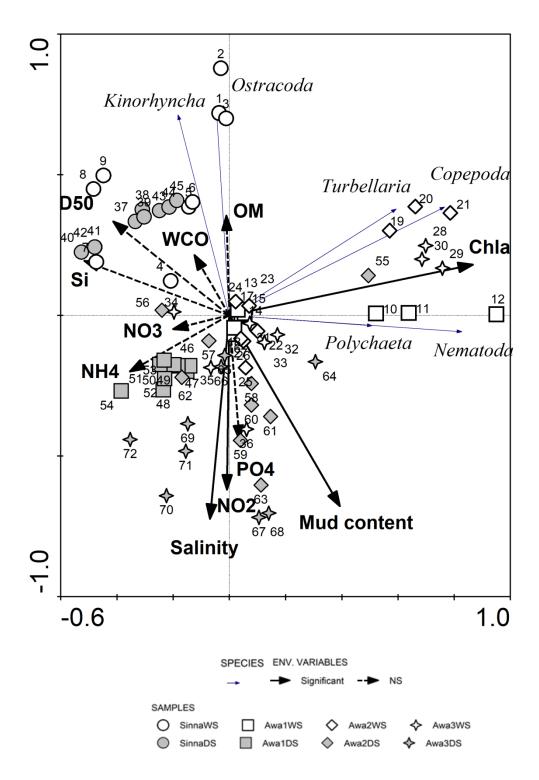


Figure 5. RDA triplots (stations. species and environmental factors) based on meiofaunal communities and measured environmental variables. The number of 1-9 indicating samples taken in SinnaWS. 10-18: Awa1WS. 19-27: Awa2WS. 28-36: Awa3WS. 37-45: SinnaDS. 46-54: Awa1DS. 55-63: Awa2DS. 64-72: Awa3DS; (see details in table 2)

In the same way, the correlation between environmental variables and nematode composition was evaluated by another RDA, in which chl a biomass, mud content and nitrite were also the main factors explaining 40%, 6% and 3%, respectively, of the variance in nematode distribution (LambdaA, table 4). In detail, axis 1 explained 52.9% of total variation in nematode distribution and was correlated to chl a biomass (p = 0.002) while axis 2 correlating to mud content (p = 0.006) and nitrite concentration (p = 0.03) controlled only 3.1% of the variance. Nevertheless, contrary to the results of meiofauna, high frequency of *Pseudochromadora incubans* and substantial decrease in chl a biomass in Awa1DS had grouped this station together with SinnaDS and SinnaWS in the upper-left quadrant of the graph (Fig. 6, left).

In Awala, high abundance of nematode communities from the top layer in the WS dominated the upper-right quadrant, corresponding to the high biomass of the primary food source - chl a. Samples in two deeper layers of Awa1, Awa2 and Awa3 during the WS were aggregated close to axis 2 in the lower-right quadrant. Communities in deeper layers were all characterized with lower chl a biomass and lower abundance of nematode. In the DS, nematode communities in Awa2 and Awa3 occupied both lower quadrants. However, the vertical zonation was not well defined for communities in the DS. Additionally, nematode communities from fluid mud with lower nitrite concentration was distinctively segregated from the more consolidated muddy stations. Shannon's diversity index (H') ranged between 0.8 and 1.8, with higher diversities in SinnaWS and Awa1DS despite their nematode densities were significantly lower compared to the other stations (Fig. 6, right).

Besides, Spearman's rank correlation analysis showed significant, positive correlations between all four feeding types and chl a biomass, with the strongest correlation with epistrate feeders (2A) (r = 0.73). Selective deposit feeders (1A) had a strongest correlation with omnivores/predators (2B) (r = 0.62) compared to the other groups while the non-selective deposit feeders (1B) were significantly correlated with the 2A (r = 0.69) (Fig. 6, left).

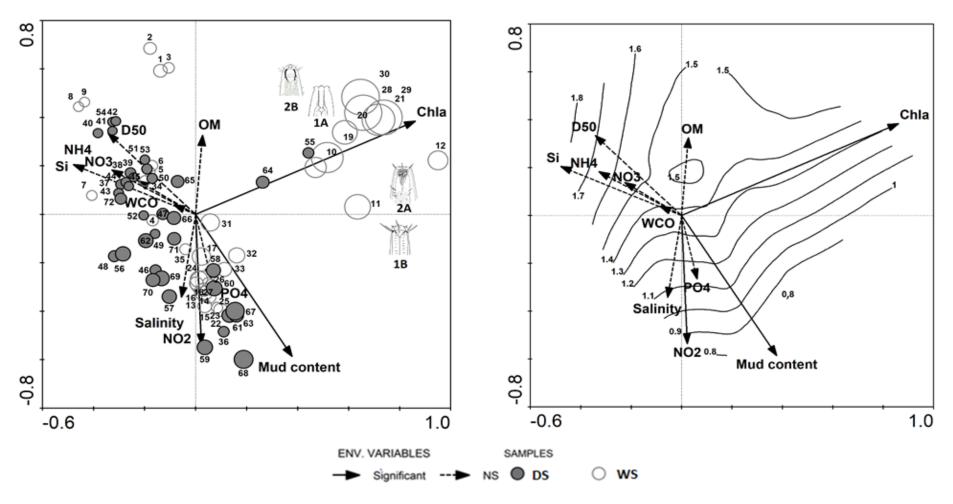


Figure 6. Distribution of total nematode density and its associated diversity index (H'). Attribute plots from the RDA of nematode assemblage under constrained environmental variables with the size of circle (left diagram) illustrating the variation in nematode density and the value related to each contour line (right diagram) showing the Shannon Weiner index. The number of 1-9 indicating samples taken in SinnaWS. 10-18: Awa1WS. 19-27: Awa2WS. 28-36: Awa3WS. 37-45: SinnaDS. 46-54: Awa1DS. 55-63: Awa2DS. 64-72: Awa3DS; (see details in table 1)

#### **Discussion**

Extremely high meiofauna abundance in extremely high dynamic ecosystem

Physical disturbance is a primary factor influencing the structure and composition of marine benthic communities (Hall, 1994). Reduction in diversity and biomass was observed in communities subjected to a high frequency of disturbance (Schratzberger and Warwick, 1998; Cowie et al., 2000). Therefore, it was reasonable to assume the extreme morphodynamics of French Guiana mudflats would negatively shape its associated infauna according to its unique conditions, especially, when meiofaunal diversity, particularly nematode species richness, was indeed absolutely lower in comparison to other mudflat habitats. On the contrary, notwithstanding their highly dynamic systems, French Guiana mudflats possessed much higher meiofauna abundance than the any productive tropical coastal habitats such as Indian coast (Ansari and Parulekar, 1993), Caribbean mangrove (Pusceddu et al., 2014) and Vietnamese tidal creek (Xuan et al., 2007). This result conformed to the studies of Dupuy et al. (2015), which also described the pattern of high meiofaunal densities with mainly structured by nematodes and copepods (>95%) in regional scale along Amazonian coast.

The predominance of meiofauna (mostly nematodes) in French Guiana mudflats could probably be related to its high resilience capacity to sediment disturbance (Alongi, 1987; Johnson et al., 2007) and more importantly, the French Guiana mudflats seemed to provide "unlimited" food source for this infauna group (Dupuy et al., 2015). Elsewhere, meiofauna also successfully inhabited other extreme habitats with most were opportunistic species, which abundantly colonizing the substrates by relatively short generation time and capability of producing numerous offspring (Coull and Bell, 1979, Zeppilli et al., 2017). However, lacking a pelagic dispersal stage for rapid spreading of the species was believed as the main cause for retarding rapid meiofaunal colonization (Coull and Bell, 1979). Nonetheless, since meiofauna could be easily suspended and transported by means of even weak currents (Boeckner et al., 2009), the minor disturbance imposed by nutrient-rich currents and waves in French Guiana mudflats, therefore, would bring great benefits to meiofaunal dispersal and proliferation. Sherman and Coull (1980) also pointed out that nematodes could rapidly adapt to the sediment disturbance, whereas such impact could cause mortality in other groups, particularly foraminiferans. Therefore, the high instability of the French Guiana sediment appears to be the most logical explanation for the predominance of nematode contrasting to the occurrence in very few number, or even absence of many other groups, including foraminifera.

In addition, ovoviviparous reproduction was observed in three nematode species, *Halomonhystera* sp.1, *Pseudochromadora incubans* and *Rhabditis (Rhabditoides) inermiformis*. This particular brood protection mechanism was recognized as an important adaptation of parents securing the survival and development of their brood when the environment was in extreme conditions such as sulphide-rich toxic sediments (Van Gaever et al., 2006) or dramatic decrease of temperature (Gerlach and Schrage, 1971). It is worth highlighting that ovoviviparity is only reported for a few marine nematode species (Gourbault and Vincx, 1990), therefore the unique numerous ovovivirous representatives thriving in French Guiana mudflats may suggest an addition to the meiofaunal successful recruitment strategies in such dynamic ecosystems.

#### Vertical zonation

In our study, distinctive segregations within meiofaunal communities were observed from micro- (cm) (vertical profile) to mesoscale (>300 m) (gradient of consolidated mud), and between different habitats (macroscale). A clear stratification of community structure in Sinnamary and Awa1 has rejected our hypothesis that high frequent sediment reworking habitat would be less influenced by vertical zonation. In fact, although there were no significant differences in vertical distribution of total meiofaunal abundance in these two stations, particular meiofauna organisms dominantly inhabited the first layer such as epistrate feeder nematodes, copepods, ostracods, kinorhynchs, etc... compared to mostly nematodes found towards the depths. This fine-scale vertical species-specific distribution was also obtained in the study of Joint et al. (1982), which suggests that different species may occupy particular spatial niches within the sediment column. Buffan-Dubau and Carman (2000) highlighted that midday low tide feeding peak detected in intertidal mudflat ostracods and harpacticoid copepods were coincident with peaks in microalgal biomass. The vertical zonation, therefore, could be characterized by meiofaunal interspecific differences in exploitation of food source, which reflects the variation in functional responses of meiofauna community (Pace and Carman, 1996).

Meanwhile, in consolidated muddy stations (Awa2, Awa3), the vertical zonation was a persistent pattern during the WS for both meiofaunal abundance and species composition. An approximate 80% of total meiofauna was confined in the first layer where plenty of the primary food source aggregated (biofilm). Contrastingly, meiofaunal density and diversity decreased drastically in the deeper layers. This vertical distribution of meiofauna was significantly

correlated with chl a biomass in the sediment, with high densities of diatom feeder nematodes (epistrate feeders) and copepods in the chl a-rich layer. Similar pattern has been obtained in many studies (eg. Pinckney and Sandulli, 1990; Ansari and Parulekar, 1993; El-Serehy et al., 2015). Pinckney et al. (2003) emphasised the tight coupling between meiofauna and microalgae in the upper few millimetres of estuarine sediments, inferring the pivotal role of microphytobenthos in characterising the vertical profiles of meiofaunal community structure. However, during the DS, no such vertical distribution pattern was observed. Meiofauna abundance sharply declined in the upper layer but stayed remain, and even slightly increased in the deeper layers in consolidated muddy stations, while the density decreased in all three layers in fluid muddy stations.

#### Horizontal variation

The horizontal distribution patterns of meiofauna were characterized by habitat differences and intertidal zonation. Meiofauna assemblages in estuarine habitat were more diverse but less abundant than seafront mudflat. Significant differences in meiofauna distribution between these two environments were well explained by the variation of chl a biomass, interstitial salinity and mud content. Among the most abundant species, the marine nematode Metachromadora chandleri (Guilini et al., 2016) was strictly distributed in Awala, where was not exposed to riverine discharge and possessed higher pore water salinity. Distinctive habitat selection also observed in the case of Pseudochromadora galeata and Pseudochromadora incubans. The Pseudochromadora galeata widely spread over the bare mudflats in front of the pioneer Avicennia mangrove in Awala, while Pseudochromadora incubans was dominant in the Sinnamary sediment, which is closely associated with the nearby Rhizophora mangle mangrove. These distribution patterns coincided with their habitat description in the studies of Gourbault and Vincx (1990) and Verschelde et al. (2006). Particularly, Pseudochromadora incubans seems to be an endemic species of Amazonian coast as their specific locations were all found in the Atlantic coast and island of northern South America so far (Gourbault and Vincx, 1990; Venekey et al., 2010). The peak of its density was obtained during the DS with the most individual concentrated in the seaward fringe stations, even in Awala, where it rarely occurred in the WS. However, it was not clear whether this species opportunistically proliferated by the new-brought detritus from the mangrove or it was passively transported from their close by origin mangrove habitat. The hydrodynamically passive recruitment processes were known to dominate such likewise habitats (Palmer, 1988).

In addition, the tidal regimes also sharply characterized the horizontal distribution of meiofauna. The high frequent sediment reworking stations, Sinnamary and Awa1, located in low tide zone, while more consolidated muddy stations, Awa2 and Awa3, respectively represented mid and high tide zone. During the WS, despite similar chl a biomass was obtained in all stations in Awala, the total meiofauna abundance decreased from high-elevated station towards low tide region. Moreover, this declining pattern was not well explained by all measured environmental parameters (Table 4, Fig. 5), thereby suggesting the effect of other interference. Reise (1985) demonstrated the impacts of macrofauna and fish predation on meiofauna as an important interaction in structuring infauna distribution. Numerous epibenthic feeders such as shore crabs, shrimp and gobies actively forage on meiofauna at high tide (Reise, 1985; Aarino, 2001). Especially, majority of meiofauna in the muddy environment occur in the top two centimetres of sediment (Steyaert et al., 2003; Kotwicki et al., 2005), making them easily accessible to predators (El-Serehy et al., 2015). In French Guiana mudflats, relative high frequency of occurrence of three epibenthic fish were observed. While the Highfin goby Gobionellus oceanicus tends to inhabit low tide soft mud area, the two four-eyed fish, Anableps anableps and A. microlepis, undertake regular intertidal migrations and forage according to tidal rhythm (Brenner and Krumme, 2006). The meiofaunal community in low tide zone, therefore, was most susceptible to these natant predations, resulted in the lowest density in the two upper layers compared to higher tidal zones.

# Seasonal effects

Strong effects of seasonality resulted in altering both vertical and horizontal zonation meiofauna assemblages in the DS were recorded in our study. The seasonal pattern was generally explained by the reduction of chl a biomass, elevated interstitial salinity and relatively higher nitrite concentration within the sediments in the DS. These parameters played a key role on separating the more diverse WS assemblages from the DS ones (Fig. 5). High density of nematodes commonly found in a wide range of salinity, even in the hypersaline condition (>40%), suggesting minor influence of this variable on this group. In contrast, dramatically decrease of other meiofauna such as copepods, turbellarians and kinorhynchs in the DS inferred their sensitivity to seasonal change of salinity in the sediment. Heip et al. (1988) also showed that nematodes were more tolerant than copepods to environmental differences. Meanwhile, chl a biomass merely explained for the declining trend of meiofauna in the surface layer. In the deeper layers, this infauna remained abundantly regardless of the low value of the chl a biomass. The chl a biomass significantly reduced in the surface layer during the DS despite the highly

resembled value of pore water nutrients compared to the WS. Exceptionally, higher nitrite concentrations were found in deeper layers at the two more elevated stations in Awala. As the production of nitrification process, which requires aerobic conditions to oxidize ammonium to nitrite the later to nitrate (Niels et al., 2004), the occurrence of nitrite in deeper sediment layers indicated a wider range of oxygenated zone in these stations. This would be probable explanation for the deeper distribution of meiofauna in Awa2, Awa3 during the DS as oxygen availability can sharply regulate the vertical distribution of meiofauna (Joint et al, 1982; Shirayama, 1984). However, the low value of direct measured environmental variables contributing to total explanation of meiofauna distribution patterns in multivariable ordination analyses suggested other factors should be included in the analyses in order to get a comprehensive elucidation.

McLachlan (1977) conferred that meiofauna remains mainly in conditions where oxygen is plentiful, but also escape from unfavourable conditions such as desiccation, disturbance and predation pressure by vertical migration to deeper sediment layers (Johnson et al., 2007; Braeckman et al., 2011; Giere, 2013). In our study, it was true that with substantially reduced precipitation in the DS, the higher the tide zones are, the more meiofauna would be subjected to desiccation. And more importantly, given by largely increase of epibenthic feeders during the DS, strong impacts of higher predation pressure and its associated disturbance induced by predatory activity on the meiofauna would be expected. Every year, thousands of the semipalmated sandpipers Calidris pusilla turn the French Guiana mudflats into intensively feeding ground during their winter migration (Boyé et al., 2009). Although the favourite prey item for these small shorebirds mostly regarded the tainadaceans, a macrofauna crustacean dominantly inhabits French Guiana mudflats (Bacescu and Gutu, 1975; Nguyen et al., 2017), the high occurrence of microphytobenthos (100%) and sometimes, meiofauna, in their diet were observed (Gerwing et al., 2016). This indicated that whether by directed consumption or "bycatch" ingestion, the intensive predatory activity of this shorebird would also drastically decrease the biofilm biomass in the surface layer and simultaneously stimulate the downward refugee mode of meiofauna in the sediment column. Such patterns have been observed elsewhere in the many studies (Sutherland et al., 2000 Jonhson et al., 2007; Jardine et al., 2015) So, together with the natant predation pressure already discussed above (see sestion 4.3.), the effects of predatory could better explained the variation in horizontal and vertical profiles of meiofauna compared to other direct measured parameters.

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## CHAPTER 4

TROPHIC LINKAGES AND CONCEPTUAL MODEL

OF INTERTIDAL FOOD WEB IN THE

FRENCH GUIANA MUDFLATS

Feeding relationships are fundamental to understand biological interaction. Generally, the identification of animal diet is important for understanding their basic ecology, characterizing trophic interactions, and predicting community-level consequences of biotic and abiotic change. Nonetheless, in the intertidal mudflats, direct observation of feeding is impractical or impossible, especially for the benthic compartments. Therefore, in this chapter, the biochemical tracer method basing on stable isotope will be applied to get insight into the trophic structures of the ecological communities inhabiting the highly dynamic French Guiana mudflats as this method potentially provide less biased and longer-term dietary information.

As mentioned above, the coastal line of French Guiana is influenced by fluid mud coming from Amazon River. Sediment is transported in west-northwest direction and forms huge mud banks along the coastline from Amazon River mouth to Orinoco River. With alternative phases of accretion and erosion induced by the combination of currents, waves and winds, the coastline is characterized by unstable and continuously changing conditions. Despite mud banks instability, French Guiana mudflats support a vigorous development of microphytobenthos biofilm (MPB) in surficial sediment with a very high-biomass and a low-diversity. MPB supports various communities: an exceptionally high abundance of meiofauna, a remarkably low diversity but relatively high abundance of deposit feeding benthic macrofauna, and a very high abundance and diversity of many species of patrimonial migrating shorebirds, local waterbirds and fish.

This chapter aimed to better understand the functioning of those tropical mudflats in French Guiana by 1) describing, with isotopic analysis, the food web in two contrasted mudflats (estuarine and coastal) in French Guiana over two main seasons (dry and wet) and 2) evaluating the dependence of different components of the food web to MPB as a main food source. The  $\partial^{15}N$  and  $\partial^{13}C$  signatures indicated a direct trophic transfer of MPB to higher trophic levels and a strong marine influence for both mudflats during both seasons.

### PAPER 5

# ECOLOGICAL FUNCTIONING OF THE BENTHIC COMMUNITIES IN THE VIEW OF TROPHIC LINKAGES

# Spatio-temporal trophic significance of the biofilm in intertidal mudflats of French Guiana

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In preparation for Marine ecology progress series

#### Introduction

Among the diversity of coastal ecosystems, intertidal flats represent a key system known as one of the most productive on earth (Walker and Mossa 1982) providing many ecological function, at least in temperate areas (e.g. primary production, nursery for fish, feeding area for birds...) (Dupuy et al. 2015). Indeed, ecological functioning of tropical mudflats remains ignored by scientists. The coast located between the Amazon and Orinoco Rivers (1,500 km) is considered as the muddiest in the world because of the large flow of suspended sediment discharged from the Amazon and carried along the coast via the Atlantic current (754 M t/year  $\pm$  9%; Martinez et al. 2009). These particular habitats found locally differ from temperate mudflats notably in the Guiana's coast, where they show high instability, unique in the world (Anthony et al. 2010). More fluid than in temperate systems, the mud is transported by a complex interplay between waves, tides, wind and coastal currents forming a series of huge mud banks. These "migrating mudflats" move over at least one km per year and stretch over at least 15 units of 10-60 km long and 20-30 km wide (126 000 km²) over the total 330 km of the French Guianas coast. The mud bank can extend down to 9 m depth, and 5% of its surface is located within the intertidal domain, imposing geomorphological dynamics leading to rapid shoreline changes and fast alternations of facies types. In temperate coastal zones, research on intertidal mudflats productivity has established their central role because of their capacity to enrich the adjacent terrestrial and marine zones through biological (export by mobile consumers such as birds and fish) (Bocher et al. 2014; Carpentier et al., 2014) and physical pathways (waves, wavegenerated and estuarine currents and tides; Allison et al. 2000). At the opposite, in subtropical and tropical estuarine areas, research has mainly focused on mangroves (Faunce and Serafy 2006; Nagelkerken et al. 2008), expected to provide many ecological functions, while the role of adjacent intertidal mudflats has been ignored even if they often represent larger areas and constitute the necessary substrate for mangrove growth after sediment consolidation. Hence, studying of the functioning of these intertidal mudflats appears fundamental in tropical context

and is challenging for ecologists in bringing new knowledge and testing the current paradigm developed in temperate areas. Only few data on biodiversity, benthic community structure, and food web functioning of tropical banks are available and dynamics of biological communities associated with these highly unstable environments are still exploratory. The food web in intertidal bare mudflats and by extension the trophic role of this habitat for transient species (notably fish and birds) is particularly well studied in Europe (Leguerrier et al. 2007; Pascal et al. 2009; Ubertini et al. 2012). According to these studies, 35 to 70 % of matter consumed by the benthic meio-macrofauna was microphytobenthos (hereafter called MPB), the major primary resource of the ecosystem. In opposite, few bacterial matters were flowing through the benthic food web, only 3 to 6 % of bacteria production being grazed (Pascal et al. 2009). By comparison, the few studies on French Guiana intertidal mudflats highlighted a thicker (of 200 um scale), high-biomass, but low-diversity biofilm of MPB and prokaryotes, coupled with a higher abundance and biomass of meiofauna and a remarkably low diversity but relatively high abundance of deposit feeding benthic macrofauna (Dupuy et al., 2015; Nguyen et al. 2017). Simultaneously, a very high abundance and diversity of many species of migrating shorebirds, local water birds and fish, including commercially exploited species was also foundr the French Guiana mudflats (Guéguen, 2000).

Among intertidal bare mudflats food web major compartments, MPB is the major primary producer. It is mainly controlled by light and temperature under temperate climate (Denis et al. 2012) and facing the extreme conditions, cells are able to regulate their photosynthesis by behavioral (migration) or physiological mechanisms to avoid photoinhibition damages (Cartaxana et al., 2011). It is likely that temperature and light conditions are much more constraining in tropical climates and strongly influence the composition and behavior of MPB biofilm components. Associated meiofauna (40 µm–1 mm length) constitutes an inconspicuous component of the benthic fauna, and may provide generally the most abundant and diverse taxa in marine sediments. Meiofauna may control MPB (Montagna et al., 1995) and can be important prey for macrofauna such as fish and infauna (Gee 1989). But, relatively little is known about meiofauna role (Alongi, 1989) and even less in tropical systems. Macrofauna (> 1 mm length) is usually a major part of the total biomass of temperate mudflats and has a central role in the functioning of these ecosystems (Gray and Elliot, 2009; Nguyen et al., 2017). Interestingly, the extreme poverty of this compartment in the Atlantic Amazonian coast (Jourde et al. 2017, Nguyen et al., 2017) appears as one of the main difference with temperate systems and has to be particularly explored notably through the food web approach. If polychaetes appear to be the most diverse group, mean densities of taxa vary from 1 ind. m<sup>-2</sup> for many groups or species to 24,000 ind. m<sup>-2</sup> for the mudshrimp *Halmyrapseudes spaansi* (Jourde et al .2017, Nguyen et al. 2017). In addition, individuals collected are mostly of small size (i.e. below 1 cm; Nguyen et al. 2017). The studies in temperate zones suggest also the importance of intertidal mudflats in the lifecycle of numerous fish species (e.g. Laffaille et al. 1998; Morrisson et al. 2002; Almeida 2003; Carpentier et al. 2014) notably as nursery areas but also as feeding areas for others at their adult stage, able to feed on macrofauna or more rarely, being potential biofilm grazers. In French Guiana, preliminary investigations on common fish species living in or- on mudflats, like four-eyed fish (Anableps microlepis) and highfin goby (Gobionellus oceanicus), showed that their stomach were often filled with mud, suggesting their grazing capacities. Finally, at the top of the food web, previous research (Laguna Lacueva et al. 2012) demonstrated that numerous shorebirds species were specialized on intertidal mudflat habitats during the nonbreeding period (van de Kam et al. 2004). They commonly feed on macrofaunal benthic prey (Colwell 2010), while small-size shorebirds may also ingest biofilm (Kuwae et al. 2012). Despite recent decline of some species as Semipalmated Sandpiper (Calidris pusilla) (Morrison et al. 2012), migrating and wintering birds remains very important along the Guianas coast (Laguna Lacueva et al. 2012).

In this context, this study aimed to reveal for the first time the functioning of the tropical bare mudflats along Guianas coast by 1) describing, with tool of isotopic analysis, the food web in two contrasted mudflats (estuarine and coastal) in French Guiana over two main seasons (dry and wet seasons), 2) evaluating the dependence of different levels of consumers of the food web to MPB (and associated meiofauna) as a food source and, finally 3) discussing on the role of the mudflat and their potential ecological functions for fish and shorebirds.

#### **Material and Methods**

#### Sampling 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). According to Plaziat and Augustinus (2004), the evolution of mudbanks in Awala-Yalimapo has been characterized by a gradual overall west-ward 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). At 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 two main periods: from January to July, i.e. wet season and from August to the end of December, i.e. dry season. Four contexts (2 seasons x 2 sites) were therefore considered for the food web organization studies, hereafter called AWS (Awala wet season), ADS (Awala dry season), SWS (Sinnamary wet season) and SDS (Sinnamary dry season).

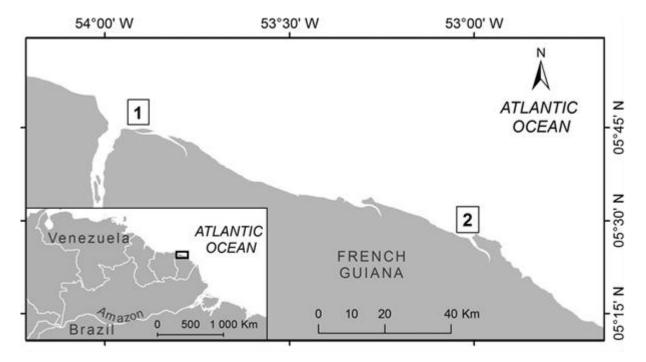


Figure 1. Location of the sampling sites in French Guyana during both wet and dry season in 2014, site 1 being Awala and site 2 being Sinnamary

#### Sampling design

Except for shorebirds sampled in Awala in 2011, all samples were collected in 2014 in the mudflats intertidal area during the wet season (WS, May–June) and late in the dry season (DS, November–December) in both Awala and Sinnamary (Figure 1). For each context, mudflat was considered and investigated as a whole to collect most abundant taxa, which could have a role in the food web functioning of the mudflats (Table 1). The main source, the biofilm of MPB,

was collected in all stations and all seasons (except in SWS). The upper-layer (approx. 500  $\mu$ m) of sediment was collected at low tide, and immediately brought back to the laboratory. After sieving through a 500  $\mu$ m mesh to remove macrofauna, the sediment was homogenized by thoroughly mixing and was spread as a plane layer in 4 cm deep plastic trays and maintain under natural light rhythm. On the top of sediment, 2 nylon nets (200  $\mu$ m and 60  $\mu$ m) were placed on the sediment. These nets allow migration of the majority of diatoms on the surface and permit the separation of MPB from the sediment. The harvest of the MPB took place at the time corresponding to the low tide in the field. The top of nylon net (60  $\mu$ m) was recuperated and scraped to recover the MPB, and then freezed at -20°C. In AWS, filamentous green algae were collected by hand in the surface of the sediment. To explore terrestrial and by extension freshwater sources influence, we opted to collect mangroves tree leaves belonging to three species in the mangrove along the Sinnamary river estuary.

Meiofauna was sampled with a core (15 cm diameter) to a depth of 2 cm. At the laboratory, sediment was sieving through a 50 µm mesh and samples were preserved in 70% ethanol. Major groups of meiofauna were selected: nematoda, ostracoda, copepoda. For nematoda, between 300 to 700 individuals of nematodes per sample for isotope analysis, were randomly handpicked for identification of species. Macrofauna was sampled with a core (15 cm diameter) to a depth of 20 cm. At the laboratory, sediment was sieving through a 500 µm mesh and samples were preserved in 70% ethanol. Tanaidacea and polychaeta were handpicked for identification of species. Resident fish (highfin goby) were collected by hand in their burrow at low tide while four-eyed fish were caught with hand net or beach-seine at high tide. Juveniles from other species were randomly caught with hand net and pushnet at high tide. Larger individuals were caught with gill nets of various mesh sizes, beach-seine and fishing rod. Small individuals were identified and preserved in 70% ethanol before to be dissected to collect muscle. A biopsy was carried out on large individuals for further analysis on muscle. Shorebirds were caught in mistnets on high tide roosts during non-moonlit nights from October to December 2011. Whole blood was sampled from randomly selected birds, after which the birds were immediately released. The stable isotope analyses were performed on less than 300 µL of whole blood. Blood was extracted from the wing vein and kept in 75% ethanol.

#### Isotope analysis

Concerning animals, muscle tissues have been extracted when possible (i.e. for large individuals, > 1 cm) whereas entire animals were taken into account when they were large

enough, allowing a mid to long-term view of the diet (about one month). For shorebirds, the entire blood sample was used (plasma + cells) and provided an indication on the diet according to an integrated signal over a time window of at least 20 days as described for the Dunlin *Calidris alpina* by Ogden (2004).

Both vegetal and animal samples were then freeze-dried (i.e. Fischer Scientific ® – Alpha 1-2 LD *plus*) during 24h and grounded into a fine and homogeneous powder using a ball mill (i.e. Retsch ® MM 200). The nitrogen and carbon isotopic compositions in different sampled organisms were determined using EA- IRMS (Isoprime, Micromass, UK). The carbon and nitrogen isotope ratios are expressed in the delta notation  $\delta^{13}$ C and  $\delta^{15}$ N, where:  $\delta X = [(R_{Reference}/R_{Sample})-1] \times 1000$ , where  $X = \delta^{13}$ C or  $\delta^{15}$ N and R is the ratio  $\delta^{13}$ C:  $\delta^{12}$ C or  $\delta^{15}$ N in the sample and in the reference material. Results are referred to Vienna Pee Dee Belemnite (VPDB) for C and to atmospheric nitrogen for N and expressed in units of ‰ ± standard deviation (sd).

#### Data analysis

To estimate contributions for several dietary sources to the diet of consumers including meifoauna, macrofauna and vertebrates components, we adopted Bayesian stable-isotope mixing models (stable isotope analyses in R: SIAR; Parnell et al., 2010, Parnell et al. 2013), which allows the inclusion of isotopic signatures from food web components, elemental concentrations and trophic enrichment factors (TEF) together with the uncertainly of these values within the model. Since TEF were not known for all predator prey relationships, we used theoretical values from literature. TEF were set to  $1 \pm 0.1$  % and  $2.4 \pm 0.1$  % for carbon and nitrogen respectively according to Zanden and Rasmussen (2001) between primary producers and first consumers and to 1  $\pm$  0.1 % and 3.4  $\pm$  0.1 % between first consumers and their potential predators (trophic level >1) (De Niro and Epstein, 1978). The tolerance of 0.1 ‰ was chosen according to Phillips and Gregg (2003) recommendations. By extension, models dealing with "intermediate consumers" suspected to consume both primary producers and primary consumers were parameterized with both TEF values according to the source considered. Additionally, after assumptions verification (normality of residues and homoscedasticity verified by Shapiro-Wilk and Bartlett tests respectively, p<0.05), a two-way ANOVA was performed on SIAR issues to explore the relative influence of terrestrial-freshwater and mudflat sources on mudflat meiofauna.

#### **Results**

#### Mudflat food web general pattern

A total of 38 taxa were sampled during the two seasons in the two sites including three different sources (MPB, green algae and leaves from 3 species of mangroves), benthic meiofauna (undetermined copepoda, undetermined ostracoda and 4 species of nematods: *Halomonhystera* sp., *Pseudochromadora* sp., *Metachromadora* sp., *Sphaerolaimus* sp.), benthic macrofauna (tanaidacaea: *Halmyrapseudes spaansi*, *3 polychaeta*: *Nephtys sp.*, *Alitta sp. and Sigambra sp.*), resident species of fish (2 species), transient species of fish (17 species for which stages were specified, i.e. juveniles, subadult or adult) and foraging shorebirds (3 species) (Table 1).

Despite species diversity sampling varied significantly among contexts (site x season), notably for secondary and tertiary consumers (Table 1 and Fig. 2), food web organization followed similar patterns whatever the season or the site investigated.

MPB, according to contexts, appeared the most enriched source in C and ranged from -14.32  $\pm$  0.07 to -17.16  $\pm$  0.04 ‰ in  $\delta^{13}$ C (in ADS and SDS, respectively) and from 4.49  $\pm$  0.50 to 5.65  $\pm$  0.32 ‰ in  $\delta^{15}$ N (in AWS and ADS, respectively). At the opposite, the mangroves leaves (in SWS) appeared largely C depleted (-28.94  $\pm$  0.60 ‰ in mean  $\delta^{13}$ C) and was used as a proxy of terrestrial-freshwater sources influence. As their isotopic ratios were similar (Figure 2), they were grouped as "mangroves leaves" for further analysis. Finally, green algae had similar  $\delta^{13}$ C ratio to MPB (-17.06 ‰) but was more  $\delta^{15}$ N depleted (3.00 ‰).

According to the  $\delta^{13}$ C ratios of sources, consumers are *a priori* largely distributed and could be grouped as i) terrestrial-freshwater sources dependent, ii) influenced by both terrestrial-freshwater sources and MPB (+ green algae), iii) MPB strictly dependent, iv) influenced by a mix of MPB and probably additional marine sources (not sampled) (Figure 2). Most of taxa appeared to be influenced or dependent from MPB (totally or partially included in green parallelepipeds, Figure 2), probably secondary by green algae (more  $\delta^{15}$ N depleted than MPB (3.00 % (only one replicate) and 4.49 ± 0.50 % for green algae and MPB, respectively, in AWS)) and according to contexts, terrestrial-freshwater source (Figure 2). Since green algae and MPB had similar isotopic signature and were sampled together within mudflat, they could be considered as "mudflat sources" (see below). Terrestrial-freshwater influence seemed to concern all taxa being more C-depleted than MPB: few fish in SWS, most fish in AWS and SDS, almost all taxa including fish, meio- and macrofauna in ADS.

Table 1. List of species sampled in mudflat at two seasons in 2014 (except for shorebirds sampled in 2011) and used to study the food web of two sites from French Guyana. Numbers of replicates were given for each site and each season. Stage of fish was provided when they were not adult (i.e. juvenile or subadult). NA= no samples.

Common name	Scientific name	n AWS	n SWS	n SDS	n ADS
Sources					
Microphytobenthos		4	NA	3	3
green algae		1	NA	NA	NA
Mangrove leaves sp. 1	Laguncularia racemosa	NA	3	NA	NA
Mangrove leaves sp. 2	Rhizophora mangle	NA	3	NA	NA
Mangrove leaves sp. 3	Avicennia germinans	NA	3	NA	NA
Benthic meiofauna					
Halomonhystera sp.	Halomonhystera sp.	3	2	1	3
Pseudochromadora sp.	Pseudochromadora sp.	NA	1	1	NA
Metachromadora sp.	Metachromadora sp.	3	NA	NA	3
Sphaerolaimus sp.	Sphaerolaimus sp.	3	3	NA	2
Ostracoda		4	3	3	3
Copepoda		3	3	1	3
Benthic macrofauna					
Polychaeta					
Nephtys sp.	Nephtys sp.	1	NA	NA	NA
Alitta sp.	Alitta sp.	1	NA	NA	NA
Sigambra sp.	Sigambra sp.	1	NA	NA	NA
Crustacea					
Tanaidacea	Halmyrapseudes spaansi	6	8	NA	NA
<u>Fish</u>					
Resident					
Highfin goby	Gobionellus oceanicus	12	17	14	12
Four-eyed fish	Anableps microlepis	19	5	2	14
Clupeiforms					
Engraulidae sp. juv.		NA	NA	11	5
Scaled herring juv.	Harengula jaguana	3	NA	NA	1

Wingfin anchauvy	Pterengraulis atherinoides	3	NA	1	2
Catfish					
Coumassi catfish	Sciades couma	NA	NA	3	NA
Crucifix sea catfish	Sciades proops	NA	4	4	3
Madamango sea		6	4	NA	NIA
catfish	Cathorops spixii	0	4	NA	NA
Pleuronectiforms					
Duskycheek		NA	1	11	NA
tonguefish juv.	Symphurus plagusia	NA	1	11	NA
Longtailsole	Apionichtys dumerili	1	NA	NA	NA
Puffers					
Banded puffer juv.	Colomesus psittacus	4	8	8	11
Checkered puffer juv.	Sphoeroides testudineus	3	NA	4	NA
Other					
Acoupa weakfish juv.	Cynoscion acoupa	3	NA	11	25
Acoupa weakfish		2	1	1	NA
subadult	Cynoscion acoupa	2	1	1	NA.
Tarpon	Megalops atlanticus	NA	1	4	NA
Mullet juv.		3	1	1	NA
Rake stardrum	Stellifer rastrifer	3	1	NA	NA
	Centropomus				
Common snook	undecimalis	1	NA	NA	NA
Fat snook	Centropomus parallelus	1	NA	NA	NA
Swordspine snook	Centropomus ensiferus	1	NA	NA	NA
<b>Shorebirds</b>					
Least sandpiper	Calidris minutilla	NA	NA	NA	9
Semipalmated					
sandpiper	Calidris pusilla	NA	NA	NA	74
	Charadrius				
Semipalmated plover	semipalmatus	NA	NA	NA	7

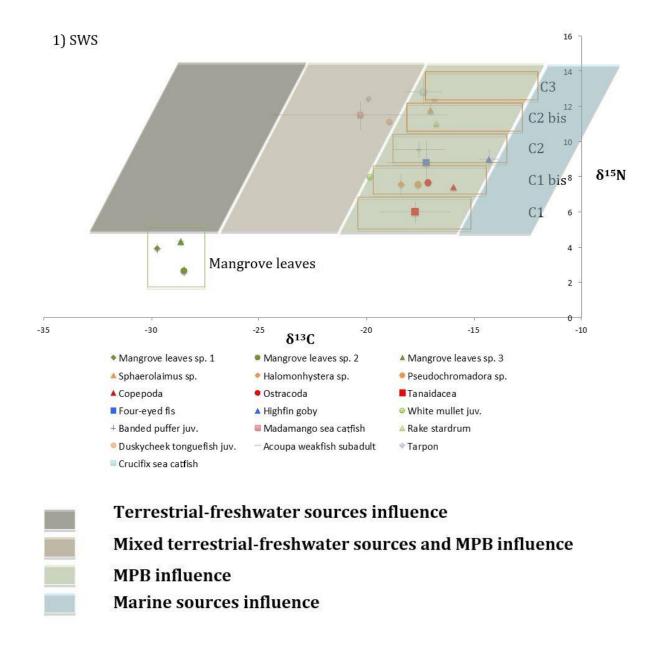


Figure 2(1):  $\delta^{15}$ N vs  $\delta^{13}$ C (mean  $\pm$  SD) for the potential food sources and consumers sampled in 2014 in four contexts, i.e. 1) Sinnamary during wet season (SWS), 2) Awala during wet season (AWS), 3) Sinnamary during dry season (SDS) and 4) Awala during dry season (ADS). Blood isotopic ratio for three species of shorebirds sampled in 2011 were added to ADS. See table 1 for numbers of replicates. Theoretical influences of primary producers (MPB, green algae and mangrove leaves) are represented by coloured parallelepipeds.

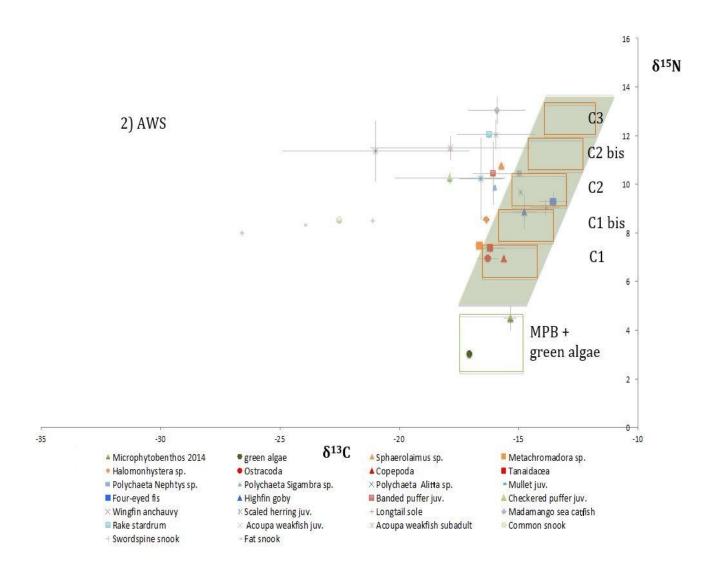


Figure 2(2):  $\delta^{15}N$  vs  $\delta^{13}C$  (mean  $\pm$  SD) for the potential food sources and consumers sampled in 2014 in four contexts, i.e. 1) Sinnamary during wet season (SWS), 2) Awala during wet season (AWS), 3) Sinnamary during dry season (SDS) and 4) Awala during dry season (ADS). Blood isotopic ratio for three species of shorebirds sampled in 2011 were added to ADS. See table 1 for numbers of replicates. Theoretical influences of primary producers (MPB, green algae and mangrove leaves) are represented by coloured parallelepipeds.

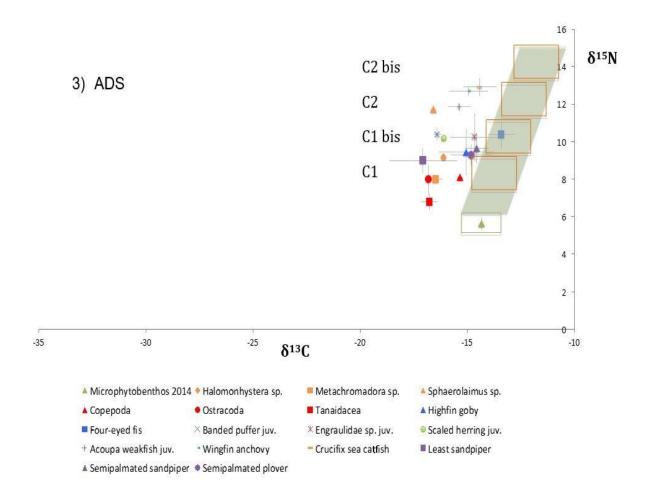


Figure 2(3):  $\delta^{15}N$  vs  $\delta^{13}C$  (mean  $\pm$  SD) for the potential food sources and consumers sampled in 2014 in four contexts, i.e. 1) Sinnamary during wet season (SWS), 2) Awala during wet season (AWS), 3) Sinnamary during dry season (SDS) and 4) Awala during dry season (ADS). Blood isotopic ratio for three species of shorebirds sampled in 2011 were added to ADS. See table 1 for numbers of replicates. Theoretical influences of primary producers (MPB, green algae and mangrove leaves) are represented by coloured parallelepipeds.

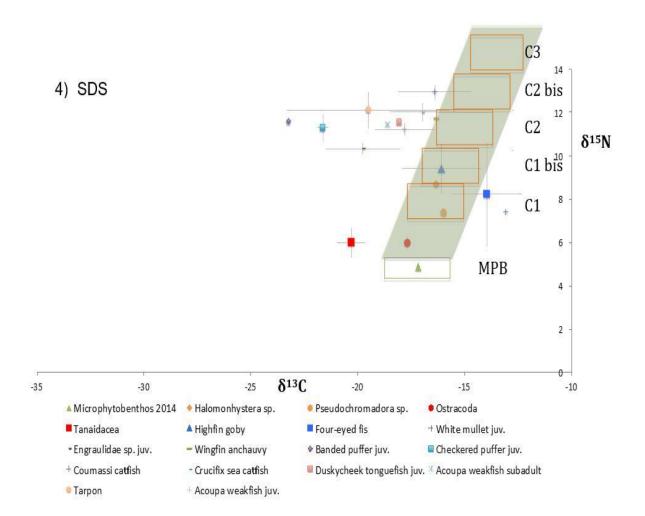


Figure 2(4):  $\delta^{15}N$  vs  $\delta^{13}C$  (mean  $\pm$  SD) for the potential food sources and consumers sampled in 2014 in four contexts, i.e. 1) Sinnamary during wet season (SWS), 2) Awala during wet season (AWS), 3) Sinnamary during dry season (SDS) and 4) Awala during dry season (ADS). Blood isotopic ratio for three species of shorebirds sampled in 2011 were added to ADS. See table 1 for numbers of replicates. Theoretical influences of primary producers (MPB, green algae and mangrove leaves) are represented by coloured parallelepipeds.

Finally, only few taxa seem totally excluded from MPB influence (highly C-depleted species) concerning some fish like snooks (3 species) and longtail sole (all in AWS). These assumptions would be clarified with SIAR models (see below focuses on meiofauna and species suspected to consume MPB).

An overview of the organization of the trophic levels of consumers revealed 3 main theoretical categories (primary producers, first (C1) secondary (C2) and tertiary consumers (C3)), including for mains taxa, meio- and macrofauna for C1, a nematode (*Sphaerolaimus sp.*), polychaeta, clupeiforms and puffers for C2, catfishes and tarpon for C3. Furthermore, intermediate levels occurred between C1 and C2 (named C1bis, Figure 2), coinciding to taxa consuming probably both primary sources and C1 category (i.e. meiofauna). This concerned mainly highfin goby, four-eyed fish, white mullet, shorebirds and another species of nematode (*Halomonhystera sp.*). This had probably consequences for consumers of higher levels determining a potential C2bis level with species, which diet included C1bis species. These assumptions have to be confirmed with SIAR models (see below).

#### Focus on meiofauna

#### Fate of MPB and river influence on meiofauna

According to first exploration of food web organization, a SIAR model was performed for three of the four contexts (all contexts except SWS because MPB was not available) including 3 sources: MPB, green algae (sampled only in AWS but added in all models) and mangrove leaves (sampled only in SWS but added in all models). Note that green algae and mangrove leaves could have different isotopic signatures according to context, which for technical reasons has not been explored, and could lead to potential bias in estimations of relative proportions of different sources in consumer's diet. As stated above, mangrove leaves had a highly depleted  $\delta^{13}$ C ratio and was used as a proxy of terrestrial-freshwater sources influence. First consumers (C1) were copepoda, ostracoda and 3 species of nematoda when available in different context, the 4<sup>th</sup> species of nematoda, i.e. *Sphaerolaimus sp.* being clearly identified as secondary consumer (C2) (see 2.2 and figure 3) was excluded from models.

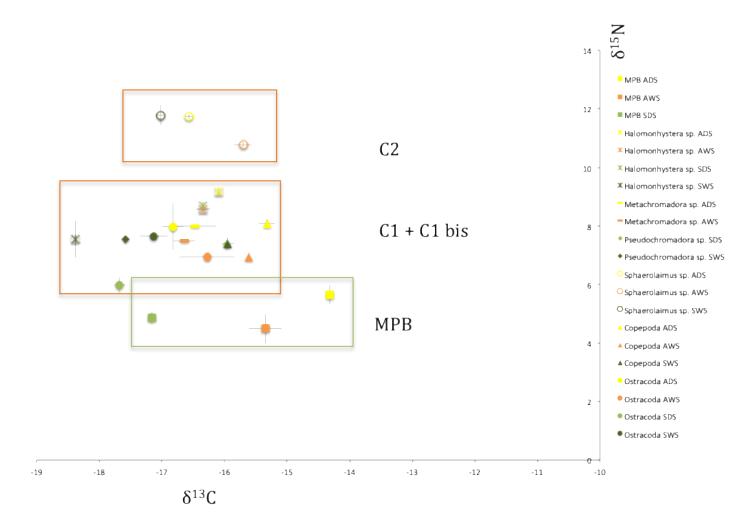


Figure 3.  $\delta^{15}N$  vs  $\delta^{13}C$  (mean  $\pm$  SD) for microphytobenthos and meiofauna in four contexts, i.e. Awala during dry season (ADS), Awala during wet season (AWS), Sinnamary during dry season (SDS) and Sinnamary during wet season (SWS). See table 1 for numbers of replicates.

Overall, MPB seems to enter in great proportion of the diet of most first consumers sampled except in SDS (Figure 3). According to SIAR models, proportion of MPB in the diet (compared to green algae and mangrove leaves) varied from  $50.15 \pm 16.74$  % (*Halomonhystera* sp.) to  $73.18 \pm 13.58$  % (copepoda) in ADS, from  $48.27 \pm 17.86$  % (*Halomonhystera* sp.) to  $66.25 \pm 16.17$  % (copepoda) in AWS and only from  $33.80 \pm 14.21$  % (Ostracoda) to  $35.72 \pm 18.87$  % (*Pseudochromadora sp.*) in SDS. There is no MPB data for SWS. Whatever the context, the proportion of MPB in the diet of C1 reached  $51.59 \pm 12.55$  %. Green algae appeared globally more  $\delta^{15}$ N depleted and seems to constitute a secondary food source reaching in mean  $32.00 \pm 9.35$  % all context included (except in SWS where no comparison with MPB could be made).

Finally, considering MPB and green algae as "mudflat sources" vs mangrove leaves as "terrestrial-freshwater source", mudflat sources counted for  $83.60 \pm 7.91$  % ( $82.53 \pm 11.35$  % if SWS context is added) in the diet of C1 whereas terrestrial-freshwater sources reached 16.40  $\pm$  7.91 %. As shown in figure 4, a site effect appeared on mean contribution of mudflat vs. terrestrial-freshwater sources. C1 from Awala (ADS + AWS) were less influenced by terrestrial-freshwater sources ( $14.69 \pm 4.04$  % and  $10.76 \pm 3.90$  % in ADS and AWS, respectively) than C1 from Sinnamary ( $26.21 \pm 9.09$  % and  $20.41 \pm 18.88$  % in SDS and SWS, respectively), while no significant effect was detected between wet and dry seasons (two-way ANOVA, F (1;15) = 5.601; p = 0,032 for site effect; F(1;15) = 1.717; p =0.210 for season effect; F(1;18) = 0.304; p = 0.589) for interaction).

#### Trophic levels of meiofauna taxa

Among the 4 species of nematodes in different contexts,  $\delta^{15}N$  isotopic ratios revealed different trophic levels: 2 species being C1 (*Pseudochromadora* sp. and *Metachromadora* sp.), *Halomonhystera* sp. being intermediate (C1 bis in SDS, ADS and AWS, C1 in SWS) and *Sphaerolaimus* sp. being C2 (Figure 3). Copepoda and ostracoda were all considered to the group of C1 ( $\delta^{15}N$ ) whatever the context. Moreover, they probably entered in the diet of the nematode *Halomonhystera* sp. with a mix of MPB (except in SWS), confirming its diet and explaining the intermediate trophic level of this species (C1bis). This was partly confirmed by SIAR models, which were performed only in ADS and AWS since only one replicate was available for *Halomonhystera* sp. in SDS and no MPB data was available in SWS). Indeed, a mix of primary producers (MPB represented  $16.18 \pm 12.32$  and  $17.09 \pm 11.77$  % of the diet of *Halomonhystera* sp. in ADS and AWS, respectively, copepoda  $24.87 \pm 12.76$  and  $21.76 \pm 12.29$  % and ostracoda  $31.05 \pm 12.44$  and  $30.11 \pm 13.65$  %.

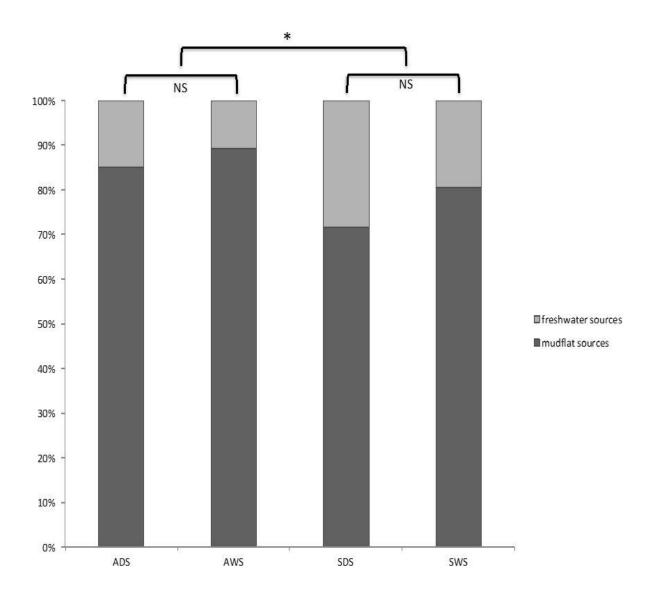


Figure 4. Comparison of cumulated percentages of contributions of mudflat sources (green algae and microphytobenthos) versus freshwater source (mangrove leaves) in the diet of meiofauna first consumers (C1) in different contexts (Awala during dry season (ADS), Awala during wet season (AWS), Sinnamary during dry season (SDS) and Sinnamary during wet season (SWS). Percentage data come from SIAR models executed for each context. C1 from meiofauna include copepoda, ostracoda and 3 species of nematoda (see table 1 for number). *Sphaerolaimus sp.* nematoda was excluded from analysis since it was secondary consumer (C2).

#### Tanaidacea, resident fish species and birds: main taxa suspected to consume MPB

A focus on food web organization implying the most abundant macrofauna species (tanaidacea *Halmyrapseudes spaansi*), resident fish (highfin goby and four-eyed fish) and three species of shorebirds seen foraging on mudflats was presented on Figure 5. According to their  $\delta^{15}N$  isotopic ratios, tanaidacea had the lowest trophic ratio among consumers and were classified as C1. Trophic enrichment factors between MPB  $\delta^{15}N$  and tanaidacae  $\delta^{15}N$ , varied between 1.1 (SDS and ADS) and 3 (AWS), indicating probable alternative sources, which was confirmed by their  $\delta^{13}C$  depleted ratios compared to  $\delta^{13}C$  MPB whatever the context (from -0.9 % in AWS to -3.1 % in SDS). Tanaidacea would be more or less influenced by terrestrial-freshwater sources as shown for meiofauna. Highfin goby, the three species of birds and four-eyed fish shared the same trophic level (C2).

Accordingly, SIAR models were performed on isotopic ratios from Tanaidacea as C1 in all contexts. Sources involved were MPB (all contexts except SWS), green algae (ratios from AWS extrapolated to all contexts) and mangroves leaves (ratios from SWS extrapolated to all contexts). MPB proportions in Tanaidacea diet varied greatly according to context, from 22.98  $\pm$  8.01 % in SDS to 72.89  $\pm$  13.70 % in AWS, reaching 47.10  $\pm$  5.30% in ADS. Terrestrial-freshwater's source influence (i.e. mangrove leaves) was always lower and varied from 11.5  $\pm$  2.98 % in AWS to 35.54  $\pm$  1.30 % in SDS. Remaining influence was attributed to the alternative mudflat source, green algae. Finally, mudflat sources counted from 64.46  $\pm$  5.14 % (SDS) to 88.5  $\pm$  12.39 % (ADS) to the diet of tanaidacea.

Additional SIAR models were performed to evaluate highfin goby and four-eyed fish in all contexts and on three species of birds only in ADS. Models integrated the same primary producers used for meiofauna and tanaidacea (i.e. MPB, green algae and mangroves leaves) to which were added other potential sources like ostracoda (all contexts), copepoda (all contexts except for SDS), 4 species of nematoda (according to their occurrence in different contexts) and tanaidacea (all contexts). As expected, all consumers are significantly dependent from MPB, green algae and excepted for least sandpiper (ADS) and foureyes in SDS, mangrove leaves never exceeded 10%. MPB entered in highfin goby diet in proportions varying from  $14.82 \pm 8.45 \%$  in SDS to  $36.91 \pm 14.42 \%$  in ADS  $(23.77 \pm 11.56 \%$  in mean) whereas terrestrial-freshwater sources (mangrove leaves) remained always below 4%  $(2.08 \pm 1.34\%)$ .

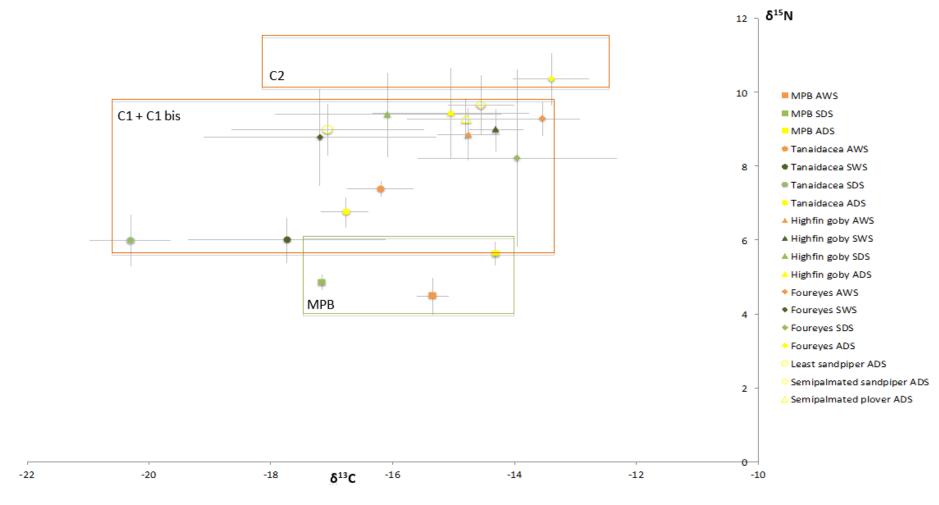


Figure 5.  $\delta^{15}N$  vs  $\delta^{13}C$  (mean  $\pm$  SD) for microphytobenthos and main fauna suspected to consume mpb (i.e. tanaidacea, highfin goby, foureyes and 3 species of shorebirds) in four contexts (i.e. Awala during dry season (ADS), Awala during wet season (AWS), Sinnamary during dry season (SDS) and Sinnamary during wet season (SWS). See table 1 for numbers of replicates.

Meiofauna occupied a great proportion of its diet (67.78  $\pm$  4.44 % in total) containing nematoda (47.38  $\pm$  3.20 %, 4 species), copepoda (16.50  $\pm$  5.10 %), ostracoda (12.02  $\pm$  2.89 %) and tanaidacea (9.03  $\pm$  4.51 %).

Concerning foureye, MPB accounted for a range comprised between  $14.82 \pm 8.45$  % (SDS) and  $32.24 \pm 10.14$  % (AWS)  $(25.39 \pm 9.29$  % in mean). Meiofauna largely dominated its diet (81.86  $\pm 2.55$ % in mean) and contained nematoda  $(42.52 \pm 1.86\%, 4 \text{ species})$ , copepoda  $(18.98 \pm 1.95\%)$ , ostracoda  $(11.35 \pm 2.75\%)$  and tanaidacea  $(9.10 \pm 4.99\%)$ .

Finally, as for fish, the 3 species of birds appeared to consume primary producers (MPB (26.58  $\pm$  14.77 %), green algae (14.91  $\pm$  6.77 %)), associated meiofauna (40.19  $\pm$  8.31 %) and tanaidacea (9.80  $\pm$  1.88 %) (Figure 6). The three species consumed similar % of nematoda, copepoda, ostracoda and tanaidacea. Differences were observed in MPB consumption, semipalmated sandpiper consuming in mean 2 to 3 times more MPB than the least sandpiper and the semipalmated plover, respectively. Contrarily, the semipalmated sandpiper appeared to consume two times less green algae than the two other species. Finally, terrestrial-freshwater influence (mangrove leaves) was almost absent in semipalmated sandpiper and semipalmated plover's diet (1.03  $\pm$  0.08 % and 3.24  $\pm$  2.88 %, respectively) and of greater importance for least sandpiper (15.67  $\pm$  4.14 %), indicating a probable differential use of feeding habitats.

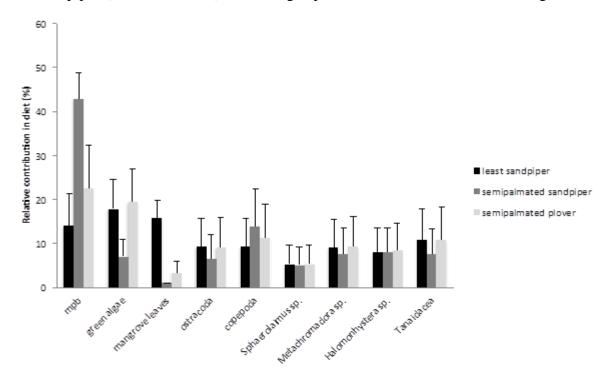


Figure 6. Relative mean  $(\pm SD)$  proportions of primary sources and associated meiofauna in the diet of three shorebirds species according to SIAR modelling

#### **Discussion**

This study aimed to describe trophic interaction between a variety of organisms sampled in this particular ecosystem of tropical mudflats. Despite apparently low resources, numerous species including highly mobile ones like fish and birds seem to exploit mudflats and succeed at low and high tides. This implied a huge pressure of consumption supported by the well-known high productivity of biofilm at the basis of the food web (Underwood and Kromkamp, 1999). In return, consumers have to support large and more or less unpredictable constraints like mudflat dynamic, temporary access due to daily tide cycle and seasonal freshwaters discharge variations due to frequent vicinity of estuaries (Blaber and Barletta, 2016). Isotopic ratios have the advantage to integrate several weeks of diet (Michener and Kaufman, 2007) and by extension potential daily switch in foraging areas when mudflat is not accessible; e.g. during low tide for transient fish and during high tide for shorebirds. This conducted us to perform seasonal investigations (wet vs. dry season) in two sites under *a priori* contrasted influence of terrestrial sources through freshwater discharge.

Main result was that mudflat resources (green algae and MPB in our study), had a major influence on food webs whatever the season or site. Fortunately, this distinction was possible since mudflat resources were highly C enriched compare to terrestrial ones (mangrove leaves). The use of green algae as source in models could have biased real contribution of MPB in food web since both sources shared similar  $\delta^{13}$ C ratio. Green algae developed mainly on upper consolidated mudflat areas and appeared less consumed by organisms like for instance shorebirds (Bocher, pers. obs.). Note that green algae had still been involved in food web study on Malaysian tropical mudflat (see Syaizwan et al. 2016) but without considering MPB for comparison. Interestingly, mudflat's green algae isotopic ratios in this study are comparable to our (4 and -20 ‰ in  $\delta^{13}$ C and  $\delta^{15}$ N respectively in Malaysia, 3 and -17 ‰ in French Guyana) and are described as main source of the mudflat's food web compared to mangrove tree.

As expected, Sinnamary's food web, the most estuarine site, was significantly more influenced by terrestrial-freshwater source (at least for meiofauna), whereas no seasonal effect was found. Freshwater inputs generate consequent fluxes of organic matter and nutrients, which is presumed to have a major role in the great productivity of mudflat ("outwelling" hypothesis from mangroves to offshore, see the review from Lee (1995)). Indeed, several studies have shown for instance that wet season have strong influence on the diversity and abundance of coastal fishes in tropical areas (Barletta et al., 2008; Pichler et al., 2016). During the wet season,

rainfall induces additionally fluxes of terrestrial nutrients, increases turbidity enhancing protection against predators, improving juveniles fish feeding and survival (e.g. Robins *et al.*, 2006). However, the "outwelling" hypothesis in tropical coastal systems is controversial since several recent studies, which have shown the main influence of MPB on tropical mudflat foodweb (Kruitwagen et al. 2010; Claudino et al. 2015; Lugendo et al. 2006; Kon et al. 2015), also measured negligible participation of riverine mangrove carbon in adjacent mudflat foodwebs. This concerned benthic macrofaunal communities (Kon et al., 2015) and above all the whole food web including fish (Lugendo et al., 2006; Kruitwagen et al., 2010, Claudino et al., 2015). Our results are more contrasted with apparent variable mangrove carbon influence even for resident first consumers as tanaidacea. This finally underlines that the relative origin of carbon sources driving food webs in these highly variable interface habitats could be more complex than expected and maybe site specific.

In temperate area, the benthic trophic network is supported by the primary production of the MPB which was the most important flow in the intertidal mudflat (Leguerrier et al. 2003) with 35 to 70 % of matter for benthic consumers (meio-macrofauna) coming from MPB (Pascal et al. 2009; Ubertini et al. 2012). The meiofauna had a small biomass, but constituted a very active compartment compared to the macrofauna (Leguerrier et al. 2003). Macrofauna is usually a major part of the total benthic biomass and has a central role in the functioning of these ecosystems (Gray and Elliot 2009, Ubertini et al. 2012). In French Guiana mudflats, the benthic trophic network seems supported too by the primary production of the MPB. Differences appeared: French Guiana mudflats possessed much higher meiofauna abundance (Dupuy et al. 2015; Nguyen et al. this thesis), extreme poverty of macrofauna (Nguyen et al. 2017; Jourde et al. 2017), tanaidacaea dominating the macrofauna compartment. Therefore, meiofauna exerted a high pressure on MPB (diet mainly based on MPB; > 60 %) but with probably no limitation of food source due to the very high biomass of MPB (Dupuy et al. 2015).

Among taxa expected to be highly dependant from MPB mudflats, meiofauna taxa were the most difficult to explore in terms of tropic relationships due to technical difficulties to identify and sort out the different species. This nevertheless led to a noteworthy understanding of the functioning of this community with unintended complexity. Indeed, taxa occupied almost all trophic levels, most of them being grazers, other had mixed diet including both primary producers and primary consumers while still others were predators (C2), sharing  $\delta^{15}$ N ratio of vertebrates like for instance shorebirds and resident fishes. This trophic niche partition was particularly clear for nematodes for which, specific trophic levels were consistent with diets

provided by the literature (Wieser 1953): *Pseudochromadora* sp. and *Metachromadora* sp. (C1) have the same feeding ecology and are classified as "epistrate feeder", *Halomonhystera* sp. (C1 and C1 bis) is "non selective deposit feeder", *Sphaerolaimus* sp. (C2) being "omnivore predator".

Mudflat resident fish were expected to consume biofilm. They were represented by highfin goby, the only species able to stay at low tide in burrows, and four-eyed fish, always observed in most shallow waters on the mudflat. As expected, both species were the most MPB dependant fish (but see also mullet) and were characterized by a low intermediate trophic level (between first and secondary consumers) with a mixed diet of MPB and associated meiofauna. Highfin goby was previously described as detritivore and primary consumer (Vasconcelos Filho et al. 2003), isotopic ratios permitted here to specify the role of mudflat in feeding ecology of this species. Specifically, according to its range of isotopic ratios, the more mobile four-eyed fish exhibited a more diversified diet than highfin goby. This could indicate that four-eyed fish is able to feed on more diverse organisms probably with marine origin according to its enriched  $\delta^{13}$ C ratio. This is confirmed by Kervath et al. (2001), who described opportunistic feeding behaviour observed in different habitats and including small food particles < 2mm in length (algae, "worms" and crustaceans) in muddy substrate whereas crustacean, bivalvia and microbenthos were consumed in sandy beach (2001). A similar species (Anableps anableps) is also known to consume mud only at neap tides, additional preys being insects, Grapsidae and intertidal red algae consumed in inundated mangroves and subtidal area according to the tidal cycle (Brenner and Krumme, 2007).

Among the 28 species of shorebirds present in French Guiana, the semipalmated sandpiper (Calidris pusilla) is by far the most abundant species representing half of the birds caught during an annual monitoring conducted in 2011 (Laguna Cueva et al, 2012, Morrisson et al; 2012). The least sandpiper (Calidris minutilla) is also an abundant species, as well as the semipalmated plover (Charadrius semipalmatus) among these 28 species (Laguna Cueva et al. 2012). These three species exceed 700 000 individuals at the early wintering period on the coast of Guyana. Since the catches are made on roost bordering the rice fields of Mana, it is impossible to know exactly the feeding areas of each species. The least sandpiper is the most commonly observed species foraging in growing mangroves (Bocher, pers. obs.), explaining its distinctly different signature from the other two species. The semipalmated sandpiper is known to have a diet based primarily on MPB or crustaceans Corophium volutator during its migratory stopover in the Bay of Fundy in Canada (Hamilton et al. 2006, Cheverie et al. 2014, Gerwing

et al. 2016). This species seems indeed able to feed preferentially on the microphytobenthos on the coast of Guyana with a substantial part of tanaïdacea; however, according to the results of the model, a good part of the prey seems coming from the meiofauna community. Nematods, ostracods and copepods are most likely absorbed indiscriminately when feeding from biolfilm by skimming method. The semipalmated plover diet has never been described and is not distinguishable from that of Semipalmated Sandpiper despite a different beak structure. The feeding niches of both species overlapped extensively considering they did not select prey among the most abundant benthic biomass.

Finally, this was among transient fish taxa that terrestrial-freshwater source had the strongest influence with several taxa being C-depleted. This dependence remains relatively low as stated in recent literature on fish sampled in mudflats (Lugendo et al. 2006, Kruitwagen et al. 2010, Claudino et al. 2015) and only 4 species appeared really independent from MPB, i.e. a benthic species (longtail sole) and the three species of snooks. These species are described as estuarine, two of them known to enter in rivers (longtail sole and fat snook, the most C-depleted species) (Planquette et al. 1996). They are predators, consuming young fish and/or crustaceans, and probably depend more on terrestrial-freshwater preys (not sampled) than other fish taxa investigated. Several fish taxa sampled in mudflat were found only as juveniles (6/17) confirming the role of nursery of mudflat often evoked in literature (e.g. Hindell and Jenkins 2004, Barletta and Blaber 2007). Adult fish sampled exhibited diversified trophic ecology including benthophagous species (e.g. catfishes, pleuronectiforms), pelagic predators (e.g. clupeiforms, tarpon, acoupa weakfish).

To conclude, this main influence of MPB presumes that most organisms, and even the most mobile of them like shorebirds or large fish species, are highly dependent from mudflat resources despite their temporary accessibility. As perspectives, the approach with natural stable isotopes is based on predictable difference between the isotopic composition of a predator and that of its preys. Using mixing model (SIAR), the approach can estimate the contribution of each potential food source to the diet of a predator. But unfortunately, it is impossible to provide quantitative fluxes between the predator and its preys. Further experiments need to be made to measure the fluxes between MPB/meiofauna/macrofauna/resident fish/ with enrichment stable isotopes experiments. Stable isotope enrichment of MPB and meiofauna/macrofauna (carbon 13 and nitrogen 15) will be done experimentally. Those enriched preys will be used to conduct grazing experiments in order to measure their ingestion rates.

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# CHAPTER 5

GENERAL DISCUSSION

GENERAL CONCLUSIONS

PERSPECTIVES

#### 1. Characteristics of the Guianas benthic communities

An important topic of the research presented in this thesis was to characterize the community structure and dynamics of the benthic infauna, focusing on meiofauna and macrofauna, in mudflat habitats along the Amazonian coast. Given the extreme morphodynamics of the mudflats, a pattern of low diversity but high density of small-sized organisms with more frequent occurrence of opportunistic species was observed from local scale (Chapter 3) to regional scale (Chapter 2). These results are coincide with the reviews of Rapport et al. (1985) and Schindler (1987), which suggested that reduction in diversity, change in size structure to small-sized species and dominance by opportunists were clear and almost universal changes of community structure induced by stress.

In the Guianas mudflats, the fluid mud, together with physical instability of sediment, surely caused a substantial perturbation to the settlement of the infauna, whereby benefited the smaller meiobenthic organisms (mainly epistrate-feeder nematodes) and disturbed the larger macrofauna in the sediment. Further, the highly turbid water, which can adversely influence many benthic animals such as suspension feeding bivalves (Thrust et al., 2004), would be another possible explanation for the scanty distribution of bivalves and gastropods in this area (Chapter 2, Paper 1). Overall, it resulted in very low diversity of macrofauna compared to other bare mudflat habitats (Wolff et al., 1993; Dittmann, 1995). Among total 39 operational taxonomic units found along the regional scale of the Guianas coast, only two species, the tanaid *Halmyrapseudes spaansi* and the polychaeta *Sigambra grubii*, were widely distributed with relatively high abundance.

Likewise, meiofauna, particularly nematode community, in Guianas mudflats was much less diverse than other mudflat habitats (Nicholas et al., 1991; Rzeznik-Orignac et al., 2003), however, its abundance was surprisingly high with mainly structured by nematodes and copepods (95%) (Chapter 2, Paper 2; Chapter 3, Paper 4). Other meiofaunal taxa presented in a few number, especially foraminifera rarely occurred in our samples. Debenay et al. (2002) also discerned the absence of foraminifera on the exposed mudflat, indicating that such unstable soft substrate was seemingly impossible for foraminiferans "to anchor". Conversely, in the sediment more consolidated, foraminifera started developing quickly in concomitant with the presence of the young *Avicennia* mangrove.

The predominance of the meiofauna are often related to its high resilience capacity to sediment disturbance (Alongi et al., 1987; Johnson et al., 2007), shorter lifespan and numerous offspring it can produce (Coull & Bell, 1979; Zeppilli et al., 2017). Interestingly, in this study, high number of the dominant nematodes exhibited ovoviviparity during their reproduction. This particular brood protection mechanism is only reported for a few marine nematodes and occurs just in extreme conditions (Gerlach & Schrage, 1971; Gaever et al., 2006) (Chapter 3, Paper 4). Moreover, the same protection mechanism is also observed in the most widely distributed macrofauna representative, the tanaid *Halmyrapseudes spaansi* and in the coastal fish community (e.g. high frequent occurrence of the viviparous fish *Anableps* spp.). The dominant occurrence of these opportunistic species thriving on the mudflats, therefore, infer an important adaptation of these particular mudflat species to such constantly changing environment. The capabilities of organisms inhabiting the unstable environments (e.g. hydrothermal vents), to develop diverse strategies to survive these stochastic variations have been also observed elsewhere (CAREX, 2011).

In addition, the effect of intensive environmental selection also resulted in the small-sized class of Guianas macrobenthic community (Chapter 2, Paper 1). The body size of the two most abundant species, which locally can account for more than 90% of total macrofauna density, rarely exceeded 10 mm (*Halmyrapseudes spaansi*: 3.8±1.0 mm; *Sigambra grubii*: 6.6±1.7 mm). Similar response of benthic community was recorded in Smith & Kukert (1996) that described high macrobenthic abundance, with very small deposit-feeding polychaetes dominating the community subjected to high rates of sedimentation in the entire Kane'Ohe Bay (Hawaii). Thus, the high prevalence of small organisms in a benthic community are possibly indicative of habitat instability (Schwinghamer, 1983).

On the other hand, in the Guianas mudflat, the small sized class can also be the results of high predation pressure of fish and shorebirds on the benthic community (Chapter 3, Paper 3). Given the predators intend to peak larger prey items as the obtained energy rises in direct proportion to the prey length and mass (Charnov, 1976), the smaller body size would help the organisms being less exposed to the predation. Particularly, by comparing the total length and maturity stage of three different tanaid species, smaller body size together with earlier maturity stage seemed to be important characteristics determining the more successful recruitment and development of *H. spaansi* compared to the other two larger species.

## 2. Factors structuring the benthic communities

In our study, benthic communities were found to be influenced by both abiotic and biotic factors. However, the changes in benthic community structure induced by biotic interactions were more prominent than the assemblage variations imposed by abiotic parameters. These observations, to a certain extent, conformed to the review of Wilson (1991), which emphasized the importance of biotic mechanisms such as predation and competition in structuring infauna communities while simultaneously argued the differences in physical environment seemed to offer little insight into the structure of marine soft-sediment communities.

First of all, the suprabundance of MPB (chl a biomass as proxy data) in the Guianas mudflats was responsible for the high abundance of meiofauna assemblages, by providing "unlimited" food sources for these animals. On the large scale, though MPB did not show correlation with density of the meiofauna, its important influence was clearly reflected in the community composition, in which the majority was comprised of epistrate-feeders (the MPB grazers) in any studied sites (Chapter 2, Paper 2). On the microscale (vertical zonation), meiofauna revealed its inevitable affinity for food as highly aggregated at the top layer (0.5 cm), where the MPB largely concentrated. Most of the copepods and ostracods aggregated in this layer. This tight coupling between meiofauna and MPB was also observed in the upper few millimeters of estuarine sediment (Pinckney et al., 2003), indicating a possible trophic pathway of meiofauna to higher trophic level predators, particularly the epibenthic feeding species (Chapter 3, Paper 4). In contrast, given the high amount of organic matter and MPB presenting in the sediment, the dynamics of community structure of macrofauna, represented by tanaid communities, was therefore not constrained by food source availability.

Instead, both spatial distribution (horizontal zonation) and seasonal variation of the tanaids as well as the meiofauna could be well explained in the light of predation interactions (Chapter 3, Papers 3, 4). The densities of the infauna communities decreased proportionally with the intensity of predation pressure. Two patterns were observed representing for the dynamics of infauna communities in wet and dry seasons. The first one linked the decline in the infauna abundance with the natant predators as the infauna increased from low towards higher tidal levels (Beukeman & Cadée, 1997; Dittmann, 2000), which was coincided with the intertidal foraging regimes of the coastal fish such as *Anableps anableps*, *A. microlepsis* and *Gobinellus oceanicus* (Brenner and Krumme, 2006). A slight difference between macrofauna and meiofauna was that after increasing the density towards mid-intertidal level, tanaids decreased

again in the high tide area. Similar results were obtained in Beukeman (1976) and Hertweck (1994), in which the decline of the infauna in high tidal zone was correlated to the effects of desiccation.

The second distribution paradigm involved the addition of new predators during the dry season - thousands of the migrating shorebirds *Calidris* spp. These sandpipers are well known intensively foraging on the mudflats during their wintering period along the Guianas coast (Boyé et al., 2009) as well as at their stopover mudflats in the Bay of Fundy (Hamilton et al., 2006; Cheverie et al., 2014). Particularly, results of stomach content analyses demonstrated the important role of the tanaids in Guianas mudflats as the favorite food for these small shorebirds (Bacescu and Gutu, 1975; Spaans, 1978, 1979). In our study, a sharp decline of infauna density, especially the tanaid *Halmyrapseudes spaansi*, in all stations was observed (Chapter 3, Paper 3). Given this species is not building tube during its life, the actively crawling to search for food and for mates (Mendoza, 1982) would make this tanaid more susceptible to such epibenthic predators, resulted in the drastic decrease of tanaid community in the more exposed areas during the foraging season of the *Calidris* spp.. Compared to other feeding area of these small shorebirds, the mudflats in the Bay of Fundy, the same declining tendency of benthic prey density was observed according to the sudden increase of these predators (Hamilton et al., 2006; Cheverie et al., 2014).

Meiofauna and MPB were also found in the diet breadth of these migrating shorebirds (Gerwing et al., 2016). However, the response of the meiofauna to this predation was more subtle (Chapter 3, Paper 4). During the dry season, meiofauna drastically decreased in the upper layer but remained abundantly as in the wet season in the deeper layers. The dominance of meiofauna, mainly nematodes, in two deeper layers despite their hypersaline condition (>40‰) eliminated the impact of the elevated pore water salinity on these organisms. This high resistance of nematodes compared to copepods to such environmental variables was already mentioned in Heip et al. (1988). Additionally, higher proportion of epistrate feeders presented in deeper layers (Paper 4, Fig.4) in spite of lower MPB biomass, contradicted its affinity for food observed in the wet season. In regard to this phenomenon, McLachlan (1977) elaborated the vertical migration to deeper sediment layers of meiofauna by its capacity to escape from unfavorable conditions such as desiccation and predation. Further, the same migrating pattern was observed in the wet season at the low tide zone, which was believed to be induced by natant predation. Therefore, different from tanaids, although being subjected to the same intensive

predation activities, the meiofauna assemblage still could maintain their relatively high density thanks to its permanent interstitial residence together with the downward refugee mode.

While such biotic interactions were largely responsible for the spatial and seasonal variation of infauna communities, the discrimination between benthic assemblages inhabiting different habitats (estuarine mudflat vs. bare seafront mudflat) was correlated to the two key abiotic factors, which were the percentage of mud content and the gradient of pore water salinity in the sediment. More benthic diversity was found in the estuarine mudflat Sinnamary, which was characterized with larger mean grain size, lower mud content and lower interstitial salinity. This habitat exhibited the highest density of tanaids and less abundance of meiofauna compared to the seafront mudflat Awala. Meanwhile, possessing higher salinity and fine mud composition, Awala was less diverse but extremely higher in meiofaunal density. Pattern of low diversity but high abundance of meiofauna was observed on a regional scale while the macrofauna, Tanaidacea, tended to be more predominant forward the more stable, consolidation part of the mudbanks. All studied sites at Sinnamary, Warappa and Bigi Pan were closer to the trailing edges, whereas Awala was at the leading edge of the mudbank. Nonetheless, the distribution of tanaids was highly patchy in all stations.

Apart from the common species that widely distributed in all studied mudflats, some specific habitat selection were observed for particular species. The marine nematode Metachromadora chandleri (Guilini et al., 2016) was strictly distributed in Awala, where was not exposed to riverine discharge and possessed higher pore water salinity. The nematode *Pseudochromadora* galeata widely spread over the bare mudflats in front of the pioneer Avicennia mangrove in Awala, while *Pseudochromadora incubans* was dominant in the Sinnamary sediment, which is closely associated with the nearby *Rhizophora mangle* mangrove. These distribution patterns coincided with their habitat description in the studies of Gourbault & Vincx (1990) and Verschelde et al. (2006). The peak of Pseudochromadora incubans density was obtained during the dry season with the most individual concentrated in the seaward fringe stations, even in Awala, where it rarely occurred in the wet season. Thus, a question is raised on whether this species opportunistically proliferated by the new-brought detritus from the mangrove or it was passively transported from their close by origin mangrove habitat. And last but not least, the high density of the new tanaid species Monokalliapseudes guianae (Drumm et al., 2015), which was strictly limited to the riverside waterfront mud during low tide in Sinnamary, suggesting its potential ecological role as an addition food source for many epibenthic feeders (fish) within this habitat.

## 3. Trophic linkage between benthic communities with coastal fish and shorebirds

The study presented in Paper 5 (Chapter 4) deals for the first time with the description of the trophic structures of benthic intertidal communities in the French Guiana mudflats. By using stable isotope ( $\delta^{13}$ C and  $\delta^{15}$ N) analyses, it was possible to identify the potential food sources and consumers, which revealed trophic pathways of MPB and infauna as the major carbon sources supporting the intertidal benthic food web. On a spatial mesoscale (~80 km), trophic interactions of benthic organisms seems to be relatively similar. However, the herbivorous compartment in the estuarine mudflat Sinnamary were more influenced by freshwater sources, which was assigned as mangrove leaves, than in the seafront mudflat Awala. Nonetheless, since these two intertidal communities show comparable trophic structures as it is displayed by the trophic continuum, these similar features therefore may be also reflected in other intertidal mudflats along the Guianas coast.

In this study, it was also observed that benthic food webs were conformed by a wide spectrum of feeding guilds such as epistrate feeders, non-selective deposit feeders, surface deposit feeders, predators. Interestingly, these results perfectly matched with the assumption guilds basing on the morphological description. The two nematode epistrate feeders were truly depending on the MPB, while the non-selective deposit *Halomonhystera* sp. possessed higher isotopic ratios as its diet breath contains wider range of food items which can be diatom, ciliates, detritus, bacteria,... (see Moens & Vincx, 1997). The stable isotopic composition of the predator Sphareolaimus sp. confirmed its feeding strategy clearly as secondary consumer. As its  $\delta^{15}$ N value was approximately 3% higher than the primary consumers, suggesting that Sphareolaimus sp. heavily fed on various type of this group, such as the epistrate feeder nematodes, ostracods and copepods. On the other hand, copepods were highly depending on the MPB by the great contribution of MPB to its diet. These results therefore disclosed the mechanism explaining for the tight coupling between meiofauna and MPB in the ecosystem. In contrast, the tanaids were not completely depending on MPB as their food source. Trophic enrichment factors between MPB  $\delta^{15}N$  and tanaidacae  $\delta^{15}N$ , varied between 1.1 and 3, indicating probable alternative sources. As this species is believed to be surface deposit feeder, a variety of food sources such as detritus, particle organic matter and bacteria might be also better to be taken into account (Yingst, 1976; Alfaro et al. 2006; Xu et al., 2018).

Using the dual isotope and multisource mixing models, we estimated the relative contributions of potential food sources to the top predator diet. The meiofauna together with MPB played an

important source of energy for fish and small shorebirds. Meiofauna entered the predator diet in great proportion, for instance in the case of the four-eyed Anableps spp., meiofauna contributed up to  $81.86 \pm 2.55\%$  to the fish diet. Unexpectedly, the tanaids only placed the third in the contribution to the predator diet, after meiofauna and MPB, despite the fact that they were found in the stomach contents of birds (Bacescu and Gutu, 1975) and fish (Nguyen T.H., unpublished data). Nonetheless, it is worth highlighting that our samples of the shorebirds were collected in late dry season, corresponding to the period of drastic decline of tanaids within the sediment (Chapter 3, Paper 3). Additionally, given the mean half-life for isotopic turnover in blood and muscle was rather fast (Hobson and Clark, 1992), there comes a question of whether there was a shift in food sources for these top predators after tanaid depleted or the tanaids do not have such crucial role in their diet as we expected? This dietary information therefore leaves open this issue to further investigation. Besides, a relative large uncover part in the diet of the shorebirds indicated a wider range of food items should be included. These results conformed to the study of Gerwing et al. (2016), but gave more details on the relative significance of each prey contributing to the diet of the birds.

The aims of this study were to describe the structure and dynamics of the intertidal benthic infauna in the Guianas mudflats and to define its functioning in such highly unstable tropical muddy environments. In order to achieve these objectives, the community structure of the benthic assemblages inhabiting the Guianas mudflats and its dynamics were thoroughly evaluated from local to regional scale. Interestingly, despite the extreme morphodynamics of the migrating mudflats, the infauna communities of the Guianas mudflats were characterized with remarkably high abundance with the predominance of small-sized opportunistic species.

However, the instability of the sediment, on the other hand, resulted in very low diversity of both macrofauna and meiofauna assemblages. A total of 39 operational taxonomic units of macrofauna was recorded while meiofauna was less diverse with the occurrence of 34 taxa. The tanaid *Halmyrapseudes spaansi* and the polychaeta *Sigambra grubii* are the two most abundant macrofauna species, which widely distributed along the Guianas coast. Likewise, the nematodes epistrate feeder *Pseudochromadora* spp. and non-deposit feeders *Halomonhystera* sp. were the principal components of meiofauna communities in every stations.

The distribution patterns of the infauna were both site-specific and seasonal variation. The assemblages in estuarine habitat were more diverse than in the bare mudflat habitat. And infauna abundances in the WS were always higher than in the DS. The benthic communities were found to be influenced by both abiotic and biotic factors. Nevertheless, the changes in benthic community structure induced by food source availability (chl a) and predation pressure were more prominent than the assemblage variations imposed by abiotic parameters.

By using stable isotope ( $\delta^{13}$ C and  $\delta^{15}$ N) analyses, trophic pathways of MPB and infauna as the major carbon sources supporting the intertidal benthic food web were revealed. Although the herbivorous compartment in the estuarine mudflat Sinnamary were more influenced by freshwater sources than in the seafront mudflat Awala, trophic interactions of benthic organisms seems to be relatively similar. The two intertidal communities show comparable trophic structures as it is displayed by the trophic continuum, these similar features therefore may be also reflected in other intertidal mudflats along the Guianas coast.

Particularly, the tight coupling between meiofauna and MPB was observed in both distribution patterns and trophic structures. The isotopic measurements of different intertidal compartments not only revealed the pivotal role of MPB on structuring meiofaunal coummunities, but also indicated the ecological importance of meiofauna as the main food source for epibenthic feeders (fish and birds). Meiofauna and MPB entered the diet of three coastal fish in great proportion, whereas the migrating shorebirds showed a wider diet breadth. The isotopic ratios were perfectly matched with the feeding guilds assigned by morphological features. However, the relative contribution of tanaids to the top epibenthic predators were surprisingly lower than expected.

"Look deep into nature, and then you will understand everything better."

Albert Einstein

Nowadays, the composition of species communities is changing rapidly through drivers such as habitat loss and climate change, with potentially serious consequences for the resilience of ecosystem functions on which human depend. For the first time, a relatively comprehensive picture of the benthic communities in the extremely unique mudflats along the Guianas coast was described. Given currently high rates of extinction, it is critical to be able to predict how ecosystems will respond to loss of species and consequent changes in community structure. Therefore, the descriptive results of this thesis give fundamental understanding of biodiversity as well as an initial insight into the ecosystem functioning of the Guianas mudflats.

Additionally, this thesis also represents a step further towards the knowledge about benthic communities, particularly the functioning of this infauna group within an entire intertidal food wed. By defining the links between species as well as the interaction between species and its surrounding conditions, we can predict the threats to species survival and the propagation of these threats throughout a system. For instance, in the case of Guianas mudflats, the highly unstable sediment can disturb the development of the large benthic organism. Therefore, unlike many other mudflat habitat, in order to reduce the risk of economic loss, it is maybe better not to invest into the bivalve shellfish farming.

Another prospect can relate to human health. It is well known that the alluvium produced by the natural erosion of the Amazonian soils is naturally enriched in mercury. Also, the run-off from gold mining activities is known to contribute to mercury pollution. Although the densities of the mollusc, which often reflect the higher degree of environmental contamination by heavy metals, are relatively low, a chance of heavy metal bioaccumulation through the benthic food chain is still high because of the tight benthic-pelagic coupling through intertidal food web. Therefore, further research on heavy metal should be conducted regarding to these trophic linkages since humans, as a final link in the food chain, are mostly affected. Thus, this thesis has also raised and contributed to our knowledge of some interesting ecological and management issues, of which the information derived from this thesis can pave the way to build up a powerful guide for environmental monitoring as well as ecosystem management.

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