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► To cite this version:

Jérôme Jourde, Christine Dupuy, Hien T Nguyen, David Mizrahi, Nyls de Pracontal, et al.. Low Benthic Macrofauna Diversity in Dynamic, Tropical Tidal Mudflats: Migrating Banks on Guiana's Coast, South America. *Estuaries and Coasts*, 2017, 10.1007/s12237-016-0205-y . hal-01428844

HAL Id: hal-01428844

<https://hal.science/hal-01428844v1>

Submitted on 6 Jan 2017

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1 **Low benthic macrofauna diversity in dynamic, tropical tidal mudflats: migrating banks**
2 **on Guiana's coast, South America**

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19 **Abstract**

20 In tropical South America, the mudflats of the Amazonian coast are unique because of their
21 large size and unrivaled migration dynamics. On Guiana's coast, macrofaunal communities
22 are believed to be well-adapted to these dynamic conditions. In this study, the benthic
23 macrofauna was sampled in April 2012 in the Awala-Yalimapo region of western French
24 Guiana and at two sites in Suriname, Warappa Kreek and Bigi Pan, These sites are found 800,
25 920, and 1,140 km from the Amazon delta, respectively. The richness, diversity, and densities
26 of the macrofaunal communities in these mudflats are here described for the first time. Only
27 38 OTU were recorded, among which two species were common and widely distributed: the
28 tanaid crustacean *Halmyrapseudes spaansi* and the polychaete *Sigambra grubii*; the former
29 represented 84% of all individuals collected, with densities reaching up to 73,000 individuals.
30 m⁻². Most of the OTU consisted of relatively small individuals (< 10 mm in length). The very
31 low richness and diversity and the small sizes of the organisms are likely linked to the
32 instability and softness of the substrate on these mudflats. This study suggests that the
33 differences in macrofaunal community composition among sites could be due to the migration
34 stage of banks rather than the distance from the Amazon Delta and associated effects of river
35 discharge.

36 **Keywords:** Amazon influence, tropical mudflats, soft-bottom macrobenthos, communities,
37 dynamic habitat.

38

39 **Introduction**

40 The mudflats of the Amazonian coast in South America are unique because of their size and
41 dynamics. The coastline between the Amazon and Orinoco Rivers (ca. 1,500 km long), often
42 referred to as the "Guianan Coast," is considered the muddiest in the world because of the
43 large flow of suspended sediment from the Amazon River ($754 \text{ Mt y}^{-1} \pm 9\%$; Martinez et al.
44 2009). The fluid mud is transported along the Guianan coast in a series of large migrating
45 mudbanks resulting from complex interaction among waves, tides, wind and coastal currents.
46 The physical dynamics of these mudbanks have been studied extensively in French Guiana
47 (Augustinus 1978; Eisma et al. 1991; Allison et al. 2000; Allison and Lee 2004; Baltzer et al.
48 2004; Gratiot et al. 2007; Anthony et al. 2010). These migrating mudflats, at least 15 in all,
49 each 10–60 km long, 20–30 km wide (126,000 km² area) and thickness up to 5 m, travel > 1
50 km y⁻¹ from Brazil to eastern Venezuela (Gardel and Gratiot 2005). The mudflats are
51 associated with space- and time-varying depositional ‘bank’ phases and erosional ‘inter-bank’
52 phases, which lead to either rapid settlement or destruction of mangroves, depending on the
53 level of accretion or erosion of the intertidal fringe. The specific characteristics of each
54 sedimentary area depend on the tidal range and swells. These induce strong sedimentation
55 rates of homogeneous fluid mud, often several meters thick, while tides induce repeated
56 sedimentation of several centimetres, depending on sediment availability (Gensac et al. 2015).

57 Although the dynamics of mudbanks along the Guianan coast have been studied
58 extensively in recent years, data on infaunal biodiversity, community structure, and thus food
59 web function is lacking for this highly dynamic and unstable environment. Macrofauna,
60 sometimes defined as metazoans retained by a sieve with a 1-mm square mesh opening (Mare
61 1942; Bachelet 1990), is usually a major component of the total biomass and plays a central
62 role in the functioning of these ecosystems (Gray and Elliot 2009). Surprisingly, only two
63 studies on macrofaunal biodiversity and abundance have been conducted in this region over
64 the last 30 years. The first provided data on the main OTU occurring along Suriname's coast,
65 but lacked species-level identification for many organisms (Swennen et al. 1982). The second
66 study was conducted in the Kaw Estuary in French Guiana, but had only a limited number of
67 sampling stations (Clavier 1999). Despite these shortcomings, both studies found low

68 macrofaunal diversity and the dominance of very few taxa such as tanaidaceans, although
69 densities were highly variable depending on the habitat sampled. However, a recent study on
70 the structure of meiofauna in French Guiana and Suriname mudflats indicates a very
71 productive zone with a thick biofilm of microphytobenthos and prokaryotes (up to 1 mm
72 thick. Gensac et al. 2015), coupled with a high abundance and biomass of meiofauna, mainly
73 dominated by nematodes (Dupuy et al. 2015). Local sediment granulometry and organic
74 matter content appeared to drive the size structure and functional characteristics of nematodes.
75 Despite the high instability of mudflats in this region, chlorophyll *a*, biomass and meiofauna
76 abundance always tend to be higher than in other areas such as temperate European or tropical
77 Australian and Vietnamese mudflats (Dupuy et al. 2015). Consequently, the question arises if
78 this biofilm could be essential in food web function through direct trophic links with the
79 macrofauna, and thus support a rich benthic community.

80 In the present study, sediment characteristics, and richness, diversity, and density of
81 the benthic macrofaunal communities are documented at three sites along the coast of French
82 Guiana and Suriname. It is hypothesized that differences in these characteristics are
83 determined by the relative distance from the Amazon Delta, the sediment source for these
84 coastal mudbanks. It is also postulated that because of the highly dynamic nature of
85 mudbanks, richness and diversity of macrofaunal benthic communities will differ from other
86 tropical or temperate mudflats. Biometric measures (individual size/length) of macrofaunal
87 organisms are documented in this study based on the premise that highly dynamic conditions
88 along the Guianan coast limit the occurrence of large-bodied macrofaunal species.
89 Consequently, it is expected that findings of the present study will support the theory of a
90 complex diversity-stability relationship, in which high environmental variability results in
91 fewer species and greater evenness (Lehmann-Ziebarth and Ives 2006).

92

93 **Methods**

94 **Study sites**

95 The study was conducted at one site in the Awala-Yalimapo region of western French Guiana,
96 near the mouth of the Maroni River (05°44'44"N; 53°55'36"W), and at two sites in Suriname,
97 Warappa Kreek, Commewijne district (05°59'33"N; 54°55'50"W) and Bigi Pan, Nickerie
98 District (05°59'09"N; 56°53'03"W), near the mouth of the Corentyne River (Fig. 1). The sites

99 are located 800, 920 and 1,140 km, respectively, from the Amazon Delta. Tides at all three
100 sites are semidiurnal with a range of 0.8–2.9 m. The Awala site was at the leading edge of a
101 mudbank composed of very fluid mud, and below a bare sandy beach. The site was adjacent
102 to an area with young mangrove trees on somewhat consolidated mud. The Bigi Pan and
103 Warappa sites were closer to the trailing edges of two different mudbanks and characterized
104 by an erosive area (consolidated muds with micro-cliffs) crowded with dead trees lying in the
105 mud, situated below a sandy shore that was partially colonized by adult mangrove trees.
106 Sampling stations were below this erosive area.

107 **Sampling strategy**

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

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

120 For each nearshore station, six replicate sediment samples were haphazardly collected,
121 avoiding trampling the area, with a plastic corer (15-cm internal diameter) to a depth of 20
122 cm. For the intertidal transect at Warappa, a metal vacuum corer with a 10-cm internal
123 diameter was used, and two cores were combined into one sample. There were six of these
124 combined samples per station (Bocher et al. 2007). Sampling from a boat or on foot yields
125 identical estimates (Kraan et al. 2007). All samples were sieved through a 0.5-mm mesh and
126 organisms retained on the sieve were fixed in 70% ethanol.

127 **Sediment characteristics**

128 At every station, a sediment sample was taken to a maximum depth of 4–5 cm to evaluate
129 grain size. The sediment grain size was characterized using a Malvern Mastersizer 2000

130 (Malvern Instruments Ltd, U.K.) (size range: 0.02–2000 μm). Results were computed using
131 Gradistat version 4.0 software and expressed as percentages of different grain size classes and
132 geometric mean grain size. The different size classes given by Gradistat were grouped into
133 four main categories: silt and clay ($< 63 \mu\text{m}$), fine sand ($63 \mu\text{m}$ – $250 \mu\text{m}$), medium sand (250
134 μm – $500 \mu\text{m}$) and coarse sand ($500 \mu\text{m}$ – $2000 \mu\text{m}$).

135 **Macrofaunal sorting and species identification**

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

153 **Statistical analyses**

154 One-way analysis of variance (ANOVA) and post-hoc Dunn's multiple comparison tests were
155 performed on geometric mean grain size among sites (Awala, Bigi Pan, Warappa nearshore
156 stations and Warappa offshore transect). Normality of the data was evaluated using a Shapiro-
157 Wilk test. Taxonomic richness (S), density (N) and Shannon diversity index (H') data were
158 not normally distributed (Shapiro-Wilk test: $P < 0.05$), so Kruskal-Wallis one-way ANOVA
159 on ranks was used to test for differences in each variable (S, N and H') among sites.
160 Subsequently, post-hoc Dunn's pairwise multiple comparison tests were performed for the
161 three variables to allow a comparison among sites.

162 Community statistical analyses were performed using Primer 6 software (Clarke and
163 Gorley 2006). Hierarchical clustering and multidimensional scaling (MDS) of the stations
164 were obtained from a Bray-Curtis similarity matrix computed with fourth root-transformed
165 species densities. The SIMPROF routine ('SIMilarity PROFile' permutation tests) was used
166 to identify genuine clusters (at a 5% significance level) to better define groups of stations
167 using hierarchical clustering. The SIMPER routine (SIMilarity PERcentages) was performed
168 to answer the questions of which OTU structured the clusters (90% cutoff for low
169 contributions) and which contributed to dissimilarity. It was considered that a "good"
170 discriminating OTU shows a ratio of dissimilarity to standard deviation between clusters
171 $(Diss/SD) > 1.5$ (Wildsmith et al. 2009).

172

173 **Results**

174 **Sediment characteristics**

175 No obvious granulometric gradient was detected among the three study sites based on their
176 distance from the Amazon Delta. The intertidal substrate was devoid of macro-vegetation and
177 was mostly comprised of fine silt and clay (Table 1; ESM 1) at every site. Thus, mud
178 accounted for > 99% of the total sediment in all nearshore stations of Awala and Warappa. In
179 Bigi Pan, sand accounted for almost 10% (B1, B5 and B6), with mud content ranging between
180 89.3 and 98.6%. On the Warappa transect, at stations W1 to W6, sand percentages were
181 higher, reaching almost 25% at the most remote station (W1). Transect stations closest to the
182 coast (W7 and W8) had a similar mud content to nearshore stations. Mean grain size was
183 consistently < 10 μm for all nearshore stations (Table 1). Values differed significantly among
184 sites (one-way ANOVA, $F = 17.236$, $df = 3$, $P < 0.001$). Post-hoc Dunn's multiple
185 comparison tests indicated that the mean grain size for Warappa transect stations was
186 significantly different from Awala and Warappa nearshore stations ($P < 0.05$), but not from
187 Bigi Pan ($P > 0.05$).

188 **Richness**

189 Thirty-eight OTUs were identified across the three study sites (Table 2), 16 at Awala, 28 at
190 Warappa (22 offshore, 11 nearshore) and 14 at Bigi Pan. Among these OTU, 50% were
191 identified to the species level and another 18% to genus. Among the 38 OTU, 7 were
192 Crustacea, 13 Polychaeta and 13 Mollusca. Two species showed an occurrence > 50% and

193 were widely distributed among sites (Table 2): the tanaid *Halmyrapseudes spaansi* was
194 present at every station and the polychaete *Sigambra grubii* was recorded at 76% of the
195 stations, including 100% of the nearshore stations. Other OTU found at the three sites were
196 the tanaid *Discapseudes surinamensis* (Crustacea: Tanaidacea), the bivalve *Macoma*
197 *constricta* (Mollusca: Bivalva) and nemerteans. Ten OTU were recorded at two sites and 22
198 were sampled at only one station (three in Awala, 16 in Warappa and three in Bigi Pan), out
199 of which 12 were encountered at only one station (Table 2) and 13 along the Warappa
200 transect. The highfin goby *Gobionellus oceanicus* was the only fish species found residing in
201 mud during low tide, where it inhabits U-shaped burrows (Puyo 1949 in Pezold 2004;
202 Lefrançois, University of La Rochelle, pers. com.). This species was mainly recorded at
203 Awala, but was also found at Warappa. Larvae of long-legged flies (Dolichopodidae) were
204 found in Awala and at all Bigi Pan stations.

205 Mean taxonomic richness differed significantly among sites (Kruskal-Wallis one-way
206 ANOVA on ranks, $H = 14.201$, $df = 3$, $P = 0.003$). However, a post-hoc Dunn's multiple
207 comparison test showed that mean taxonomic richness differed significantly only between
208 Bigi Pan and both Warappa groups ($P < 0.05$). At the site scale, total richness by station was
209 3–11 OTU in Awala (Table 2), and mean richness (Fig. 2A) ranged from 1.3 (A2) to 5.8 OTU
210 (A5). At Warappa stations, total richness ranged from 2 to 11 OTU. Whereas 6–11 OTU were
211 recorded at transect stations, total richness was lower at nearshore stations with 2–7 OTU
212 (Table 2). This difference, however, was not supported by mean richness, which ranged from
213 2.5 to 3.0 OTU per station for the whole site (Fig. 2A) (post-hoc Dunn's pairwise multiple
214 comparison test between Warappa transect and nearshore stations: $P > 0.05$). At Bigi Pan,
215 total and mean richness (7–9 OTU and 4.0–5.2 OTU, respectively) were homogenous and
216 among the highest recorded in the present study.

217 **Densities and diversities**

218 Considering all OTU values by station, individual densities (\pm SD) ranged widely from $72 \pm$
219 56 ind. m^{-2} at A2, up to $31,000 \pm 27,000 \text{ ind. m}^{-2}$ at B3 (Fig. 2B), which contributed to the
220 significant differences recorded among sites (Kruskal-Wallis one-way ANOVA on ranks, $H =$
221 20.072 , $df = 3$, $P < 0.001$). A post-hoc test identified differences among Bigi Pan and both
222 Awala and Warappa transect stations, as well as between Warappa nearshore and transect
223 stations ($P > 0.05$), but not between Warappa nearshore stations and Awala ($P > 0.05$).

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

232 In this study, only three species represented > 1% of the total of individuals counted
233 per station: *Halmyrapseudes spaansi* (84.5%), *Sigambra grubii* (7.9%) and *Discapseudes*
234 *surinamensis* (5.3%). Each of the remaining OTU accounted for < 0.4% of all individuals
235 counted.

236 Taxonomic diversity (Shannon index H'), which reflects taxonomic richness and the
237 relative densities of the OTU, differed among stations within sites, ranging from twofold in
238 Bigi Pan up to tenfold in Awala. Thus, mean $H' \pm SD$ ranged from 0.17 ± 0.41 to 1.74 ± 0.30
239 (Fig. 2C).

240 **Size of macrobenthic organisms**

241 An important common characteristic of the macrobenthic community in intertidal mudflats of
242 the Guianas coast was the small size of most individuals. Among the three most common
243 OTU, no individuals were > 13 mm long. Mean length ($\pm SD$) of *H. spaansi* was 3.8 ± 1.0
244 mm (1.7–8.6 mm, $n = 653$), 7.8 ± 2.8 mm (2.5–12.9 mm, $n = 146$) for *D. surinamensis* and
245 6.6 ± 1.7 mm (2.1–13.0 mm, $n = 40$) for the polychaete *S. grubii*. The shell length (greatest
246 antero-posterior length) of all bivalves was 2.1 to 8.4 mm, with the exception of *Macoma*
247 *constricta* (11.2 ± 5.1 mm, ($n = 6$) and *Tagelus plebeius*, with two individuals with a shell
248 length of 11.9 and 12.7 mm. The most common gastropods, *Assimineea succinea* and
249 *Cylichnella bidentata*, had a mean shell height ($\pm SD$) of 1.3 ± 0.3 mm ($n = 54$) and of $2.1 \pm$
250 0.4 mm ($n = 15$), respectively. Few annelids exceeded 20 mm. The largest organisms was the
251 fish, *G. oceanicus*, with a mean length of 14.3 ± 5.1 mm ($n = 28$), and maximum length of
252 32.9 mm.

253 **Macrofaunal assemblages**

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

264 The main OTU contributing to similarity within site clusters are shown in Table 3
265 (SIMPER results). The tanaid *Halmyrapseudes spaansi* appeared to be the main contributor,
266 especially at nearshore stations in Warappa and Bigi Pan. The polychaete *Sigambra grubii*
267 characterized nearshore assemblages (A, B, Wn). Moreover, these two species were
268 responsible for > 90% of the similarity within the Wn cluster. The remaining OTU in Table 3
269 were typical of different clusters. Thus, the gastropod *Assimineia succinea*, the fish
270 *Gobionellus oceanicus* and polychaete *Streblospio gynobranchiata* distinguished cluster A.
271 Cluster B was distinguished by the tanaid *Discapseudes surinamensis*, the capitellid
272 polychaete *Heteromastus* sp. and the Dolichopodidae insect family. The offshore cluster (Wo)
273 was typified by an unidentified lumbrinerid polychaete (cf. *Abyssoninoe* sp. likely to be an
274 undescribed species, Carrera-Parra, El Colegio de la Frontera Sur, pers. com.), the gastropod
275 *Cylichnella bidentata*, the polychaetes *Alitta* sp., *Mediomastus* sp. and an unidentified orbiniid
276 polychaete (cf. *Scoloplos* sp.).

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

286 The OTU mainly responsible for similarities within clusters were the main OTU
287 allowing discrimination among clusters (Table 4). However, distinguishing OTU could be
288 split into two categories: ‘typical’ OTU, mainly, if not exclusively, recorded from one cluster
289 (e.g., *A. succinea*, *Alitta* sp., *C. bidentata*, *D. surinamensis*, Dolichopodidae, *G. oceanicus*,
290 *Heteromastus* sp., Lumbrineridae; ESM 3) and ‘ubiquitous’ OTU (e.g., *H. spaansi*), widely
291 distributed throughout the study area and whose contributions to dissimilarities were likely
292 due to differences in their distribution (densities and density variability) among stations
293 within clusters (ESM 3). Thus, *S. grubii* was both a ‘typical’ species and a ‘ubiquitous’
294 species in the nearshore clusters.

295

296 **Discussion**

297 The 1,500-km coast between the Amazon and Orinoco River deltas is a unique system,
298 comprised of an array of migrating, shifting mudbanks (Anthony et al. 2010). The biological
299 communities in these mudflats are poorly known. Previous studies dealing with intertidal
300 macrofaunal communities in Suriname (Swennen et al. 1982) and French Guiana (Clavier
301 1999) were restricted to a few mudflat sites and limited in taxonomic resolution, focusing
302 only on major taxa. The present study was thus constrained by the lack of previous taxonomic
303 work in the region, given the few available studies and the nature of the substrate compared to
304 the east coast of the Amazon estuary (Kober and Barlein 2006; Braga et al. 2011; Venturini et
305 al. 2011; Botter-Carvalho et al. 2014). It is thus likely that some individuals sampled belong
306 to undescribed species (e.g., within the Lumbrineridae). Among the 19 identified species in
307 the present study, 14 were previously recorded from the Brazilian coast east of the Amazon
308 Estuary, whereas 13 had been previously observed in the Caribbean Basin. Only one species,
309 the tanaid *Discapseudes surinamensis*, has never been previously collected outside the study
310 area (Bacescu and Gutu 1975).

311 The present study allowed identification of two distinct communities whose
312 differences depend on the level in the intertidal (mean high water vs mean medium and low
313 water) rather than the distance from the Amazon estuary as originally hypothesized. The
314 nearshore communities of the three sites fit partially with descriptions already reported by
315 Clavier (1999) and Swennen et al. (1982), as tanaid species are highly abundant and dominant
316 taxa. Thus, *Halmyrapseudes spaansi* and *D. surinamensis* reached densities of up to 73,000
317 ind. m⁻² and 8,000 ind. m⁻², respectively, in the present study. Both previous studies reported

318 dominance of tanaids at most of the sampling sites, i.e., up to 67,000 ind. m⁻² in the Kaw
319 Estuary, French Guiana, although the species was not identified (Clavier 1999), and mean
320 abundances of 16,000 ind. m⁻² for *H. spaansi* and 20,500 ind. m⁻² for *D. surinamensis* in a
321 coastal lagoon near Krofajapasi, Suriname (Swennen et al. 1982). *Halmyrapseudes spaansi*
322 and *S. grubii*, which are widely distributed in the studied area, were the main species in
323 nearshore communities in the present study. *Sigambra grubii* is common along the coast of
324 Brazil in different soft bottom habitats (Lana et al. 1997; Venturini et al. 2011; Braga et al.
325 2011; Botter-Carvalho et al. 2014). This ubiquitous species seems enough of a generalist to
326 exploit the highly unstable mudflats of the coast of Guiana. These two dominant species can
327 locally make up > 90% of the observed densities (Warappa), although *S. grubii* seems to be
328 typical of nearshore communities as it was almost completely absent from the offshore
329 intertidal community at Warappa. This dominance by a very few species and the low
330 taxonomic richness, explain the low Shannon diversity indices values for the nearshore
331 macrofaunal communities here reported. Furthermore, each site appeared to have its own
332 characteristic density ratios between the two dominant species as well as a characteristic
333 OTU. Indeed, the singularity of the Warappa nearshore community was precisely in the huge
334 contribution of *H. spaansi* and *S. grubii* to the exclusion of most other OTU, whereas Awala
335 and Bigi Pan were more diverse and differed in their site-specific OTU. These local
336 differences cannot be explained by sediment characteristics, as there was no obvious gradient
337 at mean high water among the sites. Consequently, as reported by Dupuy et al. (2015) for
338 meiofauna, differences in macrofaunal assemblages are mainly attributed to local conditions,
339 especially the migration stage of banks, at the scale examined in the present study. The Awala
340 stations were located at the leading edge of a mudbank, characterized by very fluid mud, and
341 were close to a mangrove colonization area, whereas stations at Bigi Pan and Warappa were
342 closer to the trailing edges of two mudbanks characterized by an erosive regime and mature
343 mangrove trees. A complex interaction of local physical factors could explain the differences
344 in macrofaunal benthic assemblages among sites, but unfortunately, it was not possible to
345 measure these characteristics, except for sediment grain size.

346 The mid- and lower tidal level community at Warappa was not described by Swennen
347 et al. (1982) and Clavier (1999), and thus appears to be unknown prior to this study. This
348 sparse, but diverse community comprises > 50% of all macrobenthic OTU recorded (22 out of
349 38), with more than half found to be site-specific (13). *Halmyrapseudes spaansi* was present,
350 but in low densities, and, *S. grubii* almost absent. A lumbrinerid (cf. *Abyssoninoe* sp.),

351 together with *Alitta* sp. and the gastropod *Cylichnella bidentata* dominate this community.
352 Sediment granulometric composition may also partially explain the difference in taxonomic
353 faunal composition between nearshore and offshore stations. Most notably, the offshore
354 sediments at Warappa had a higher proportion of coarse sand. Another possible explanation
355 for the differences between the offshore and nearshore stations might be a higher nutrient
356 supply inshore due to the proximity of sources of estuarine and mangrove leaf decomposition.
357 The subtidal extent of the offshore community at Warappa is unknown.

358 Low diversity seems to be a major feature of bare intertidal mudflats. Previous studies
359 on tropical mudflats showed that 10–32% of the species account for 80 or 95% of the
360 individuals reported (Vargas 1987; Wolff et al. 1993; Dittmann 1995). In the present study, *H.*
361 *spaansi* constituted 84% of all individuals sampled. Thus, tanaids *H. spaansi*, widely
362 distributed, *D. surinamensis*, locally very abundant, and probably the tanaid
363 *Monokalliapseudes guianae* that prefers estuarine conditions (Drumm et al. 2015), clearly
364 constitute the major component of the macrobenthic communities along the 1,500 km-length
365 of Guiana's coast. A fourth tanaid species, *Discapseudes holthuisi*, described from Suriname
366 by Bacescu and Gutu (1975), was not recorded in the present study. Tanaids might occupy the
367 same ecological niche and importance as the well-studied amphipod *Corophium volutator* in
368 temperate systems. In bare mudflats of the Bay of Fundy and Europe, *C. volutator* can occur
369 at densities of 10,000s ind. m⁻² (Hawkins 1985, Murdoch et al. 1986, Peer et al. 1986, Møller
370 and Riisgård 2006). Like corophids (Meadows and Reid 1966, Peer et al. 1986, Møller and
371 Riisgård 2006), tanaids live in burrows (Bacescu and Gutu 1975) and are believed to be
372 surface deposit-feeders that mostly feed on biofilms they collect by scraping the mud surface
373 with their long appendages.

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

384 widespread gastropod *Hydrobia ulvae*, considered the most common deposit-feeder in
385 European intertidal mudflat communities (Newell 1979), where they can reach several
386 thousands of individuals per m² (Dekker 1989; Bocher et al. 2007).

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

395 The highfin goby, *Gobionellus oceanicus*, was present in most Awala samples. Like
396 insect larvae, fishes are not usually included in studies of benthic macrofaunal communities
397 since they are mobile, and not necessarily well sampled by benthic cores. This estuarine
398 resident (Andrade-Tubino et al. 2008) is widely distributed from the state of Virginia in the
399 United States to southern Brazil, and occurs in soft bottoms along coasts and estuaries
400 (Robins et al. 1999). At low tide, *G. oceanicus* individuals remain in water-filled burrows (U-
401 shaped in Awala) that they excavate in the mud (Puyo 1949 in Pezold 2004; Lefrançois,
402 University of La Rochelle, pers. com.). In the present study, this fish species was patchily
403 distributed at low tide, but sometimes reached densities up to 50 ind. m⁻². The individuals
404 collected were < 33 mm in length and were likely juvenile that depend on this habitat during
405 early, nursery stages (Wyanski and Targett 2000; Gomes and Bonecker 2014; Gomes et al.
406 2014). Although the species is considered to be a detritivore (Vasconcelos Filho et al. 2003),
407 there is evidence from field observations and stomach contents that it can also feed on tanaids
408 (Lefrançois, unpublished results). Thus, densities of the benthic goby could either be related
409 to the importance of the surface biofilm as a food source or/and to high densities of tanaids as
410 an abundant food source.

411 The highly dynamic conditions of the intertidal mudflats of the Guianas, related to the
412 high variability of environmental factors (e.g., high physical forcing, and large variable
413 freshwater input), should limit settlement success and the adaptive capacities especially of
414 large-sized species in very soft mobile mud. A previous study on the meiofauna at the same
415 sites documented a very high abundance of these small organisms, especially nematodes,

416 which was higher than that reported in other areas worldwide (Dupuy et al. 2015). However,
417 the production of these mudflat ecosystems is expected to be very high and largely subject to
418 export. Based on the results of the present study, future research should focus on the resilience
419 capacity, via shifts in functional benthic groups due to adaptation or resistance to local stress
420 conditions, especially strong physical instability, of all community components of the mudflat
421 ecosystem.

422

423 **Acknowledgments**

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

430

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581 Gobiidae) from western North Atlantic estuaries, with notes on early life history.
582 *Bulletin of Marine Science* 67: 709–728.
- 583
- 584

585

586 **List of Table Captions**

587

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

590 **Table 2** Densities (ind. m⁻²) of each OTU for the 25 stations (coded by letters) sampled in
591 April 2012 in French Guiana and Suriname. Total number of OTU per station and per site (in
592 Warappa, values in brackets refer to the number of OTU for transect and nearshore stations,
593 respectively). Total occurrences (Occ.) (percentage of stations where the OTU were present)
594 for each OTU over the whole study area are also given.

595 **Table 3** Average percent similarities within clusters and percent OTU contribution to the
596 average similarities within clusters identified in the study area in April 2012 (A: Awala. B:
597 Bigi Pan. Wo: Warappa offshore. Wn: Warappa nearshore – SIMPER: OTU contribution
598 cutoff > 90%). For outliers A2 and W7, individual frequencies within stations are shown
599 (cutoff > 90% of total abundance within each station). Letters in parenthesis indicate the
600 faunal group to which the individual OTU belongs (P: polychaetes; T: tanaids; G: gastropods;
601 F: fishes and I: insects).

602 **Table 4** Ratios of dissimilarity to standard deviation (Diss. /SD) and the percent contributions
603 of various OTU to dissimilarities (Contrib %) between clusters identified in the study area in
604 April 2012 (A: Awala. B: Bigi Pan. Wo: Warappa offshore. Wn: Warappa nearshore). Only
605 OTU detected by SIMPER as good discriminating OTU (Diss/SD > 1.5; Wildsmith et al.
606 2009) are presented. Highest contributions (> 10%) are in bold face. Letters in parenthesis as
607 in Table 3.

608

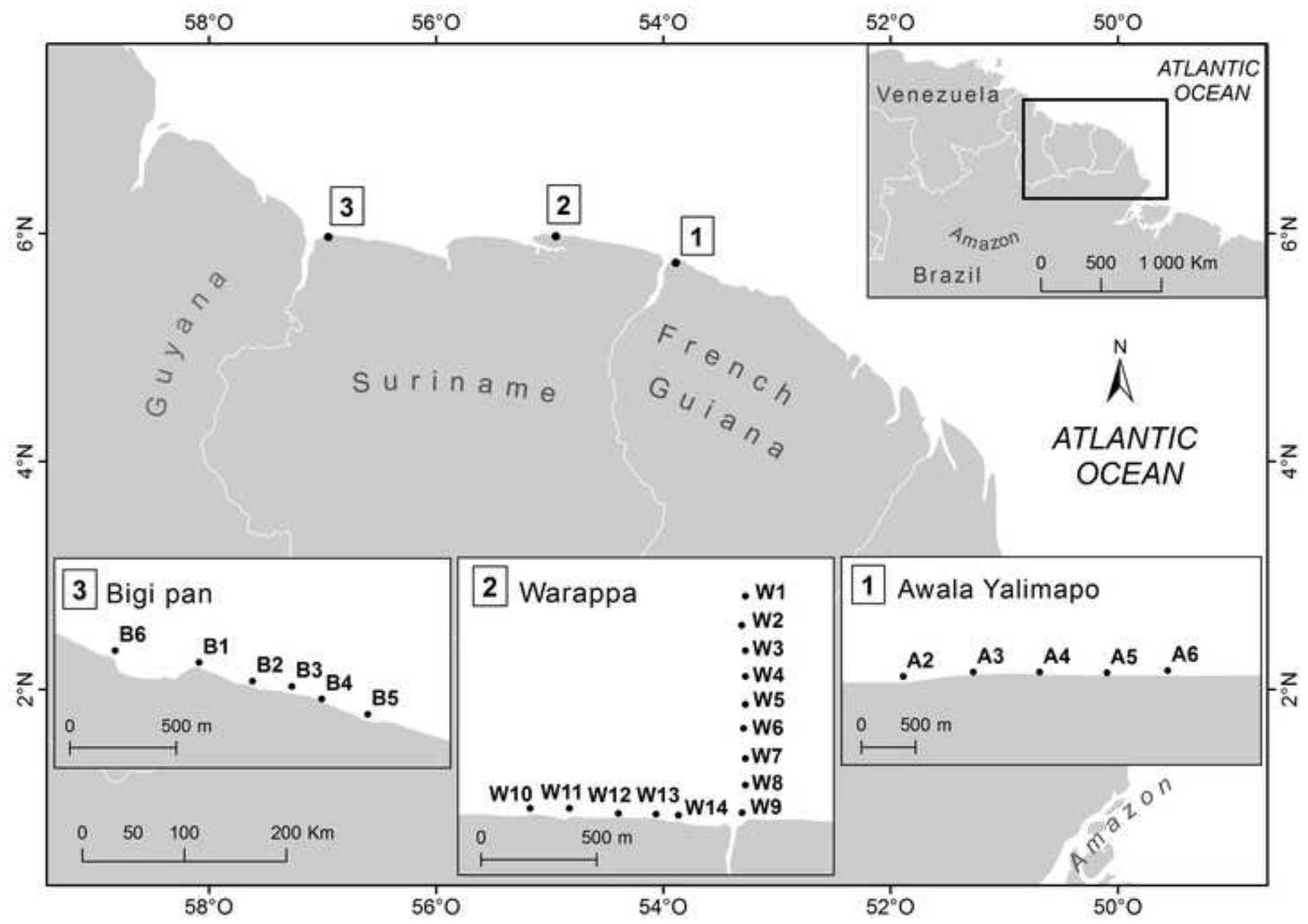
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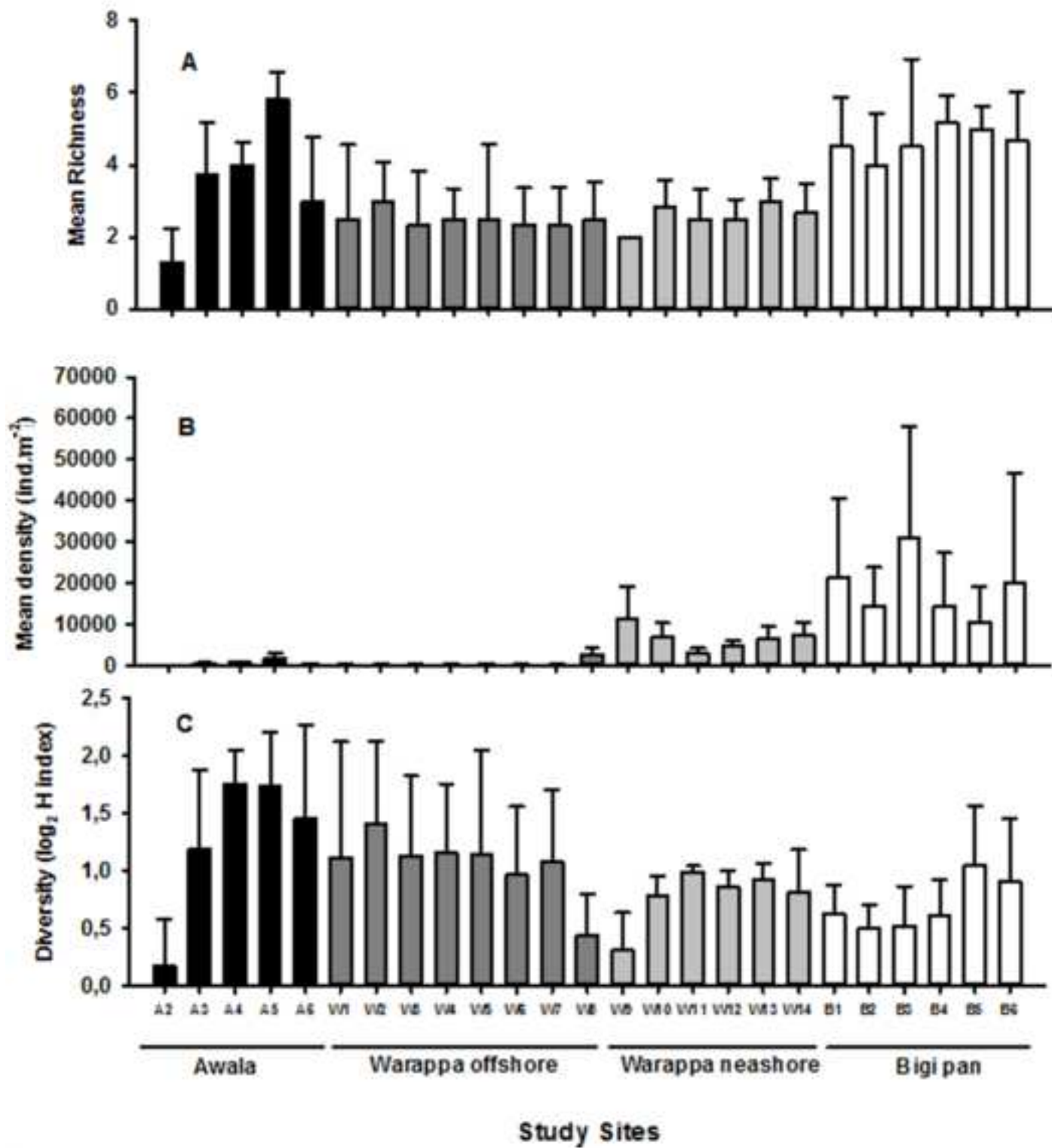
610 **List of figure captions**

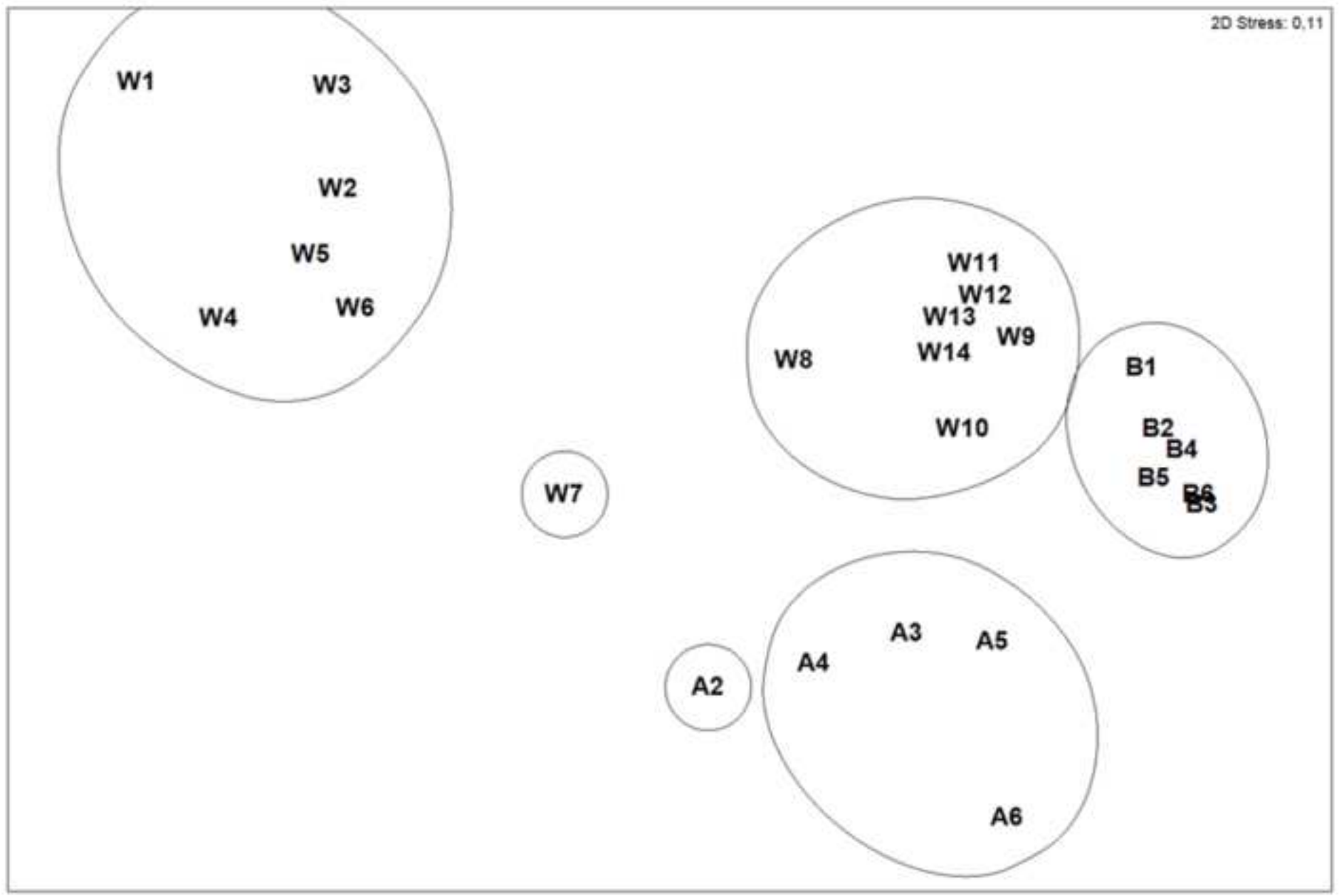
611 **Fig. 1** Map showing the study area and the location of the study sites sampled in French
612 Guiana and Suriname in April 2012, with locations of sampling stations at each study sites.

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

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







Study site	Station	Station coordinates		Sediment characteristics		
		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	
	B3	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	
	B5	56°53'03.0"W	5°59'09.9"N	8.6	91.2	
	B6	56°53'41.3"W	5°59'19.5"N	9.5	89.3	

Table

OTU	Awala					Warappa														Bigi Pan						Occ.
	A2	A3	A4	A5	A6	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10	W11	W12	W13	W14	B1	B2	B3	B4	B5	B6	%
Crustacean																										
<i>Halmyrapseudes spaansi</i>	18	206	54	242	18	10	49	59	10	69	69	20	2,255	10,951	5,538	1,846	3,136	4,462	5,296	19,185	13,190	27,957	13,297	7,966	16,846	100
<i>Discapseudes surinamensis</i>		9											10							1,084		2,428	215	1,873	2,688	28
Gnathiidae							20									18	27		9							16
Isopoda											10	10	10													12
Mysidacea			9																9							8
<i>Uca maracoani</i>																				54	9					8
<i>Callinectes bocourti</i>		9																								4
Polychaetes																										
<i>Sigambra grubii</i>	45	152	179	896	63							20	137	275	1,272	1,075	1,622	1,774	1,935	645	780	430	475	269	278	76
Lumbrineridae						10	10	59	108	69	20	10	10													32
<i>Heteromastus</i> sp.													10							45	54	45	116	63	45	28
<i>Mediomastus</i> sp.			27	36			10		10	20	167	29														28
<i>Alitta</i> sp.						20	29	20	10	29	10															24
Orbinidae						20	10	10		10																16
<i>Streblospio gynobranchiata</i>		9	188	18											9											16
<i>Phyllodoce</i> sp.																				36			18			8
Polychaeta							10				10															8
<i>Capitella</i> sp.					9																					4
Capitellidae												39														4
<i>Glycinde multicens</i>								10																		4
<i>Nephtys</i> sp.															9											4
Oligochaetes																										
Oligochaeta							10		39		10	29	10		18			18	9	9						36
Nemertea																										
Nemertea	9			9									10		9							9				20
Molluscs																										
Bivalves																										
<i>Macoma constricta</i>				9	9										9						18		9		9	24
<i>Mulinia cleryana</i>				36	18																	9		18	9	20
<i>Ennucula dalmasi</i>						49	20	10																		12
<i>Nuculana concentrica</i>							20		10																	8
<i>Eurytellina trinitatis</i>						10																				4
<i>Tagelus plebeius</i>																		27								4
Tellinidae																						9				4

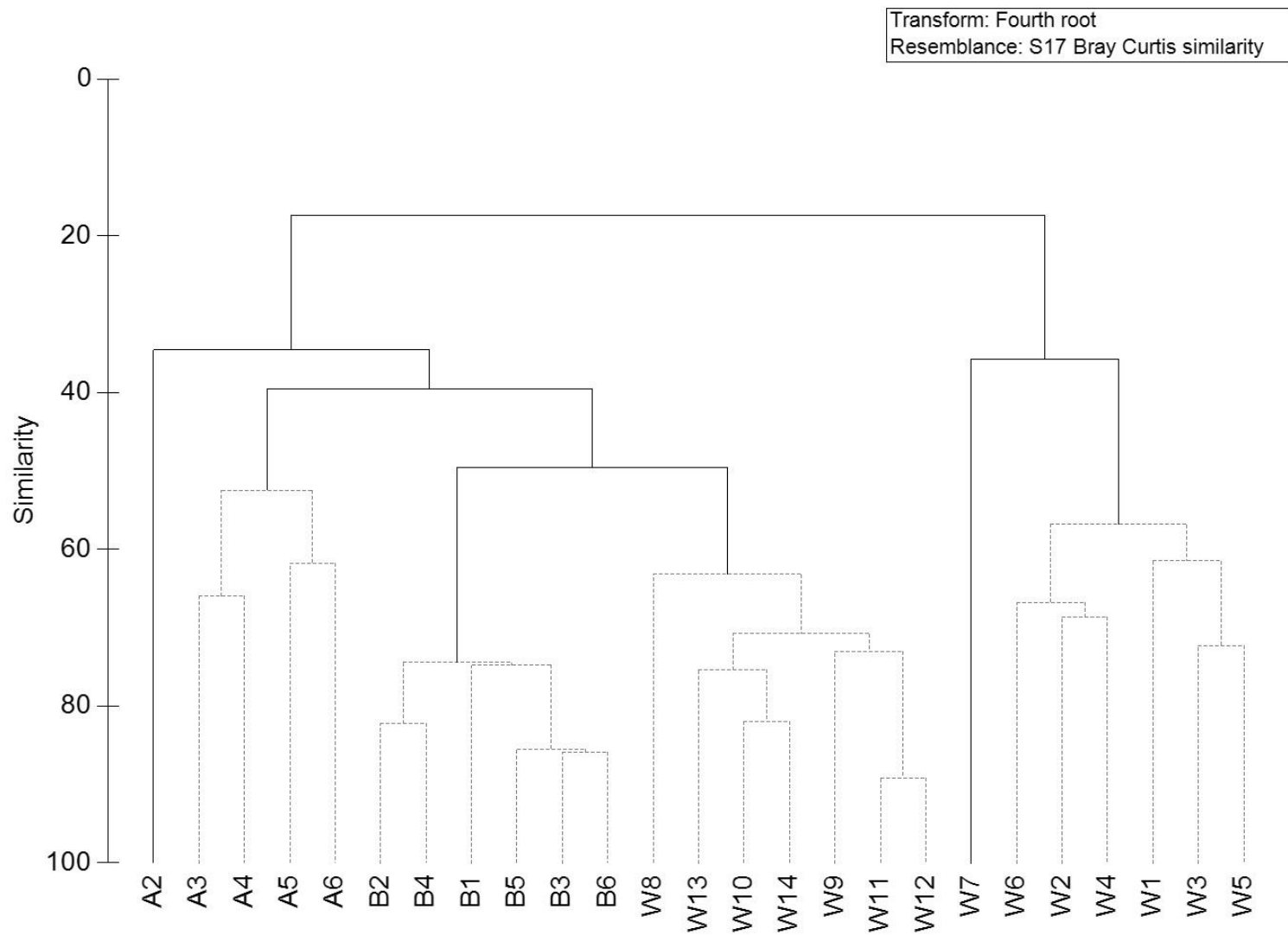
Stations	A	B	Wo	Wn	A2	W7
Average similarity (%)	56.2	77.2	60.5	70.6	-	-
<i>Halmyrapseudes spaansi</i> (T)	21.3	40.7	20.7	56.4	25.0	11.1
<i>Sigambra grubii</i> (P)	26.7	16.8		36.7	62.5	11.1
<i>Assimineia succinea</i> (G)	19.5					
<i>Gobionellus oceanicus</i> (F)	15.4					
<i>Streblospio gynobranchiata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

Table

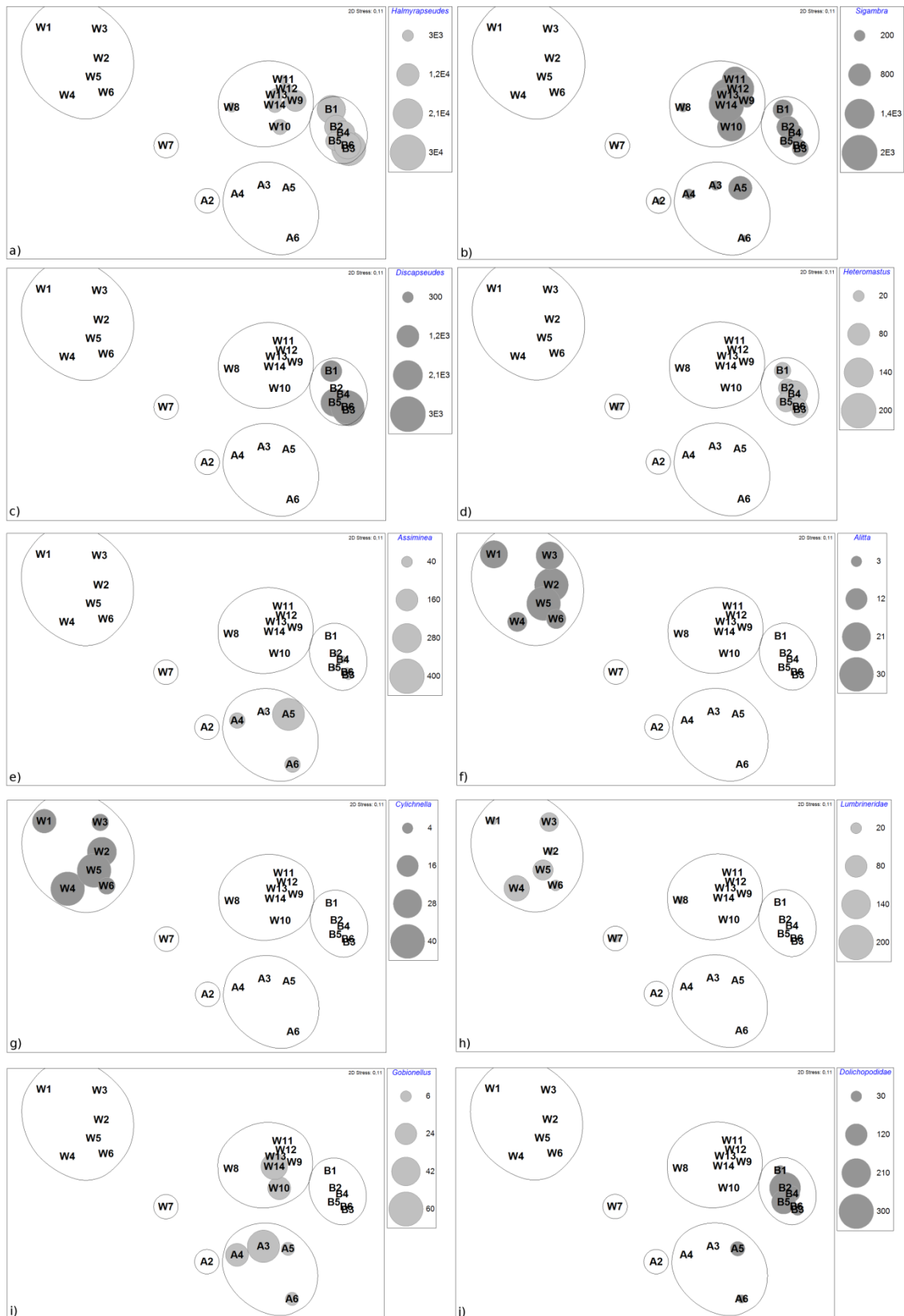
	A/B		A/Wo		A/Wn		B/Wo		B/Wn		Wo/Wn	
Average dissimilarity (%)	60.14		84.68		60.87		89.72		50.52		81.09	
	Diss/SD	Contrib%	Diss/SD	Contrib%	Diss/SD	Contrib%	Diss/SD	Contrib%	Diss/SD	Contrib%	Diss/SD	Contrib%
<i>Halmyrapseudes spaansi</i> (T)	5.6	24.6			2.9	20.8	8.7	19.2	2.1	11.9	3.7	19.6
<i>Sigambra grubii</i> (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
<i>Discapseudes surinamensis</i> (T)	2.0	14.4					2.0	11.0	2.0	19.2		
<i>Heteromastus</i> sp. (P)	7.0	8.5					8.1	6.1	7.8	10.6		
<i>Assiminea succinea</i> (G)			4.7	9.0	4.6	12.2	2.2	3.7	2.2	6.4		
<i>Alitta</i> sp. (P)			5.9	6.4			8.1	4.6			6.7	7.2
<i>Cylichnella bidentata</i> (G)			4.7	6.7			5.8	4.8			5.0	7.6
Lumbrineridae (P)			3.2	7.6			3.6	5.4			2.3	7.6
<i>Gobionellus oceanicus</i> (F)	3.7	6.5	3.3	6.7	1.7	7.1						
Dolichopodidae (I)							3.1	6.2	3.1	10.8		

ESM 1: Sediment granulometric fractions of the 25 stations sampled in French Guiana and Suriname in 2012. Additional data (organic matter (OM), chlorophyll *a* (per dry weight, DW, of sediment) and concentration of prokaryotes in the sediment), and matching stations to those in the present study in Dupuy et al. (2015) are both in bold face.

		Silt & Clay	Fine Sand	Medium Sand	Coarse Sand	OM	Chlorophyll <i>a</i>	Prokaryotes	Dupuy et al (2015)
		%	%	%	%	%	µg.g⁻¹ DW sed	Cells.mL⁻¹	
Awala	A2	100.0	0.0	0.0	0.0	-	-	-	
	A3	100.0	0.0	0.0	0.0	-	-	-	
	A4	99.9	0.1	0.0	0.0	6.0	18.8	2.5E+09	Awala StB
	A5	100.0	0.0	0.0	0.0	6.0	15.3	2.5E+09	Awala StC
	A6	100.0	0.0	0.0	0.0	-	-	-	
Warappa Kreek	W1	76.5	4.1	0.0	19.3	-	-	-	
	W2	80.3	4.8	0.0	14.8	-	-	-	
	W3	89.8	3.3	0.0	7.0	-	-	-	
	W4	78.3	2.1	0.0	19.6	-	-	-	
	W5	86.0	2.6	0.6	10.8	-	-	-	
	W6	81.9	2.5	0.0	15.7	-	-	-	
	W7	99.5	0.5	0.0	0.0	-	-	-	
	W8	97.4	2.6	0.0	0.0	-	-	-	
	W9	96.5	2.3	1.0	0.2	-	-	-	
	W10	99.7	0.3	0.0	0.0	6.2	8.6	2.8E+09	Warappa
	W11	99.8	0.2	0.0	0.0	-	-	-	
	W12	99.8	0.2	0.0	0.0	-	-	-	
	W13	98.6	1.1	0.3	0.0	-	-	-	
	W14	99.5	0.5	0.0	0.0	-	-	-	
Bigi Pan	B1	92.7	5.9	1.3	0.1	-	-	-	
	B2	96.4	2.6	0.9	0.2	-	-	-	
	B3	97.3	1.8	0.7	0.2	-	-	-	
	B4	98.6	1.4	0.0	0.0	-	-	-	
	B5	91.2	4.2	1.4	3.3	5.6	15.6	4.4E+09	Nickerie
	B6	89.3	3.4	0.6	6.7	-	-	-	



ESM 2: Dendrogram of hierarchical clustering compiled from fourth root-transformed densities of OTU based on Bray Curtis similarities of the 25 stations sampled in April 2012 in French Guiana and Suriname. Grey dotted clusters correspond to genuine clusters identified by the SIMPROF routine (A: Awala, B: Bigi Pan, W: Warappa).



ESM 3: Bubble plots of densities (ind. m⁻²) of the ten “good discriminating” OTU (see text) generated by the SIMPER routine on the ordination plot of the 25 stations sampled in April 2012 in French Guiana and Suriname (A: Awala. B: Bigi Pan. W: Warappa); OTU are ranked following Table 4; overlaid clusters indicated by black

lines (50% Bray-Curtis similarity level) correspond to genuine clusters defined by the SIMPROF routine (5% significance level).