



Spatio-temporal distribution patterns of the epibenthic community in the coastal waters of Suriname



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ABSTRACT

This study aimed to characterize the spatio-temporal patterns of the epibenthic community in the coastal waters of Suriname. Data were collected on a (bi)monthly basis in 2012–2013 at 15 locations in the shallow (< 40 m) coastal area, revealing three spatially distinct species assemblages, related to clear gradients in some environmental parameters. A species-poor *coastal assemblage* was discerned within the muddy, turbid-water zone (6–20 m depth), dominated by Atlantic seabob shrimp *Xiphopenaeus kroyeri* (Crustacea: Penaeoidea). Near the 30 m isobath, sediments were much coarser (median grain size on average $345 \pm 103 \mu\text{m}$ vs. $128 \pm 53 \mu\text{m}$ in the *coastal assemblage*) and water transparency was much higher (on average $7.6 \pm 3.5 \text{ m}$ vs. $2.4 \pm 2.1 \text{ m}$ in the *coastal assemblage*). In this zone, a diverse *offshore assemblage* was found, characterized by brittle stars (mainly *Ophioderma brevispina* and *Ophiolepis elegans*) and a variety of crabs, sea stars and hermit crabs. In between both zones, a *transition assemblage* was noted, with epibenthic species typically found in either the *coastal* or *offshore* assemblages, but mainly characterized by the absence of *X. kroyeri*. Although the epibenthic community was primarily structured in an on-offshore gradient related to depth, sediment grain size and sediment total organic carbon content, a longitudinal (west-east) gradient was apparent as well. The zones in the eastern part of the Suriname coastal shelf seemed to be more widely stretched along the on-offshore gradient. Although clear seasonal differences were noted in the environmental characteristics (e.g. *dry* vs. *rainy* season), this was not reflected in the epibenthic community structure. *X. kroyeri* reached very high densities (up to 1383 ind 1000 m⁻²) in the shallow coastal waters of Suriname. As *X. kroyeri* is increasingly exploited throughout its range, the current study provides the ecological context for its presence and abundance, which is crucial for an ecosystem approach and the sustainable management of this commercially important species and its habitat.

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1. Introduction

Continental shelves cover only about 7% of the seabed surface (Snelgrove, 1999), yet their significance in terms of marine biodiversity and ecosystem goods and services can hardly be over-estimated. Biological production in shelf seas supports over 90% of global fish catches (Pauly et al., 2002). Other benefits of coastal and shelf ecosystems include the provision of nursery habitats for

commercial species, coastal protection, water purification, carbon sequestration and tourism (Barbier et al., 2011). de Groot et al. (2012) estimated the global value of the ecosystem services provided by marine coastal biomes (coral reefs, coastal wetlands and coastal systems) to be > 13 times higher than the value of all other marine and terrestrial biomes combined. Coastal and shelf ecosystems require proper management measures to assure sustainable use of their natural resources and to maintain their ecosystem services (Barbier et al., 2011). To develop effective conservation strategies, basic knowledge on the structure and functioning of the coastal ecosystem is pivotal (Reiss et al., 2010).

The present study was conducted on the continental shelf of Suriname in South-America, an area influenced by Amazon River runoff (Hellweger and Gordon, 2002), causing muddy coasts (Eisma et al., 1991) and productive shelf waters (Smith and Demaster, 1996).

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Suriname's coastal waters support extensive artisanal and industrial fisheries (Bhagwandin, 2012), and other economic activities (notably near-shore oil exploitation) are expected to develop in the near future. Benthic fauna is commonly used in monitoring programs to study the impact of anthropogenic activities and to assess the health of coastal systems (Bilyard, 1987). Up till now, the ecological knowledge on the benthic communities of the Suriname Shelf is limited. Some taxonomic studies have been conducted prior to 1975 (e.g. Holthuis, 1959; Logan, 1990), while later work mainly consisted of fisheries-related trawl surveys (e.g. Aizawa et al., 1983; Charlier and Babb-Echteld, 1994). Quantitative ecological research on benthic communities thus far only comprised one study in the intertidal area (Swennen et al., 1982) and scattered information from environmental impact assessments for oil exploration (e.g. ESC, 2011). As such, this is the first study describing the benthic community structure along the inner continental shelf of Suriname.

Due to the unstable nature of mud deposits in the nearshore waters below 20 m depth (Eisma et al., 1991; Augustinus, 2004), densities

of macrobenthic infauna are expected to be very low in the shallow parts of the Suriname Shelf (Aller and Aller, 1986, 2004). Therefore, we focused on the epibenthos living on and near the sea bottom, which is known to dominate the benthic fauna in tropical soft-bottom habitats (Alongi, 1989). Information on the epibenthos is relevant for fisheries management as well, as epibenthic species are either exploited directly (e.g. crabs and shrimps) or serve as primary food source for commercially important demersal fishes (e.g. Salini et al., 1994).

The aim of this study was to characterize the epibenthic communities in the shallow (< 40 m) continental shelf of Suriname by gathering data on species composition, abundance, biomass and biodiversity, and to investigate the spatio-temporal distribution patterns in the epibenthic community in relation to some environmental factors.

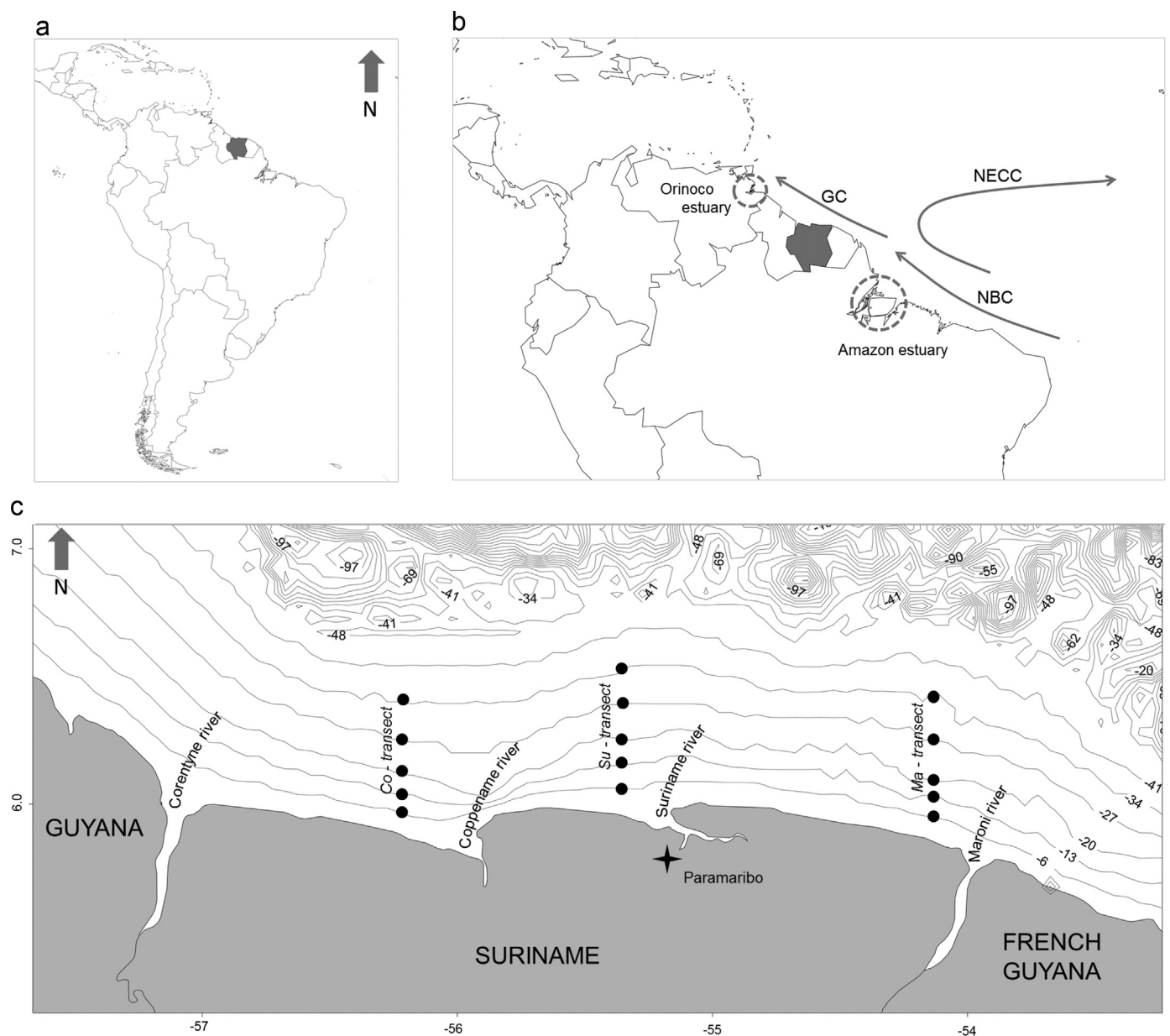


Fig. 1. (a) Location of Suriname (shaded in gray). (b) Indication of the Amazon and Orinoco estuary (dashed circles) and the major ocean currents. NBC= North Brazil Current; GC=Guyana Current; NECC=North Equatorial Counter Current. (c) Map of the inner Suriname continental shelf with indication of the major estuaries. Dots represent the sampling sites at 5 depths (6, 13, 20, 27, 34 m) along three transects: Co-transect in the west, Su-transect in the middle, Ma-transect in the east.

Table 1

Overview of available environmental data for each campaign. STD=salinity/temperature/depth, SECCHI=Secchi-depth, SS-TSM=sub-surface total suspended matter, TOC=sediment total organic carbon, MEDSAND=median grain size of sediment sand fraction, MUD=sediment mud content, CHL=Chlorophyll a, SF-TSM=surface total suspended matter, SST=sea surface temperature.

Nr	Begin	End	Season	Epi	STD	SECCHI	SS-TSM	TOC	MEDSAND	MUD	CHL**	SF-TSM**	SST**
1	17/02/2012	22/02/2012	rainy	X	X	X	X	X	X	X	X	X	X
2	24/03/2012	29/03/2012	rainy	X	X	X	X	–	–	–	X	X	X
3	20/04/2012	25/04/2012	rainy	X	X	X	X	X	X	X	X	X	X
4	22/05/2012	29/05/2012	rainy	X	X	X	X	X	X	X	X	X	X
5	30/06/2012	4/07/2012	dry	X	X	X	X	–	–	–	X	X	X
6	21/07/2012	26/07/2012	dry	X	X	X	X	–	–	–	X	X	X
7	29/09/2012	4/10/2012	dry	X	–	X	X	–	–	–	X	X	X
8	27/11/2012	1/12/2012	dry	X	–	X	X	–	–	–	X	X	X
9	29/01/2013	3/02/2013	dry	X*	–	X	X	–	–	–	X	X	X
10	10/04/2013	15/04/2013	rainy	X*	–	X	X	–	–	–	X	X	X

* missing data for Ma06 (campaign 9) and Ma34 (campaign 10)

** data originating from remote sensing (MODIS-satellite)

2. Materials and methods

2.1. Study area

The study was conducted on the continental shelf of Suriname (54–57°W, 6–7°N, Fig. 1), part of the Guianan Ecoregion of the North Brazil Shelf, and situated between the estuarine outflows of the Amazon and Orinoco Rivers (Spalding et al., 2007). The area is characterized by wide, smoothly sloping continental shelves, macrotides and upwelling along the shelf edge, and is profoundly influenced by the freshwater discharge from the Amazon River (Heileman, 2008). The Amazon River discharges on average 5330 km³ yr⁻¹ freshwater into the Atlantic Ocean (Dai and Trenberth, 2002), with peak flows around June and low flows around November (Lentz & Limeburner, 1995). Amazon water is carried northwest by the North Brazil Current (NBC; e.g. Johns et al., 1998) and continues along the Guiana coasts with the Guiana Current (GC; Hellweger and Gordon, 2002). Furthermore, the NBC typically deviates to the east for several months between July and December, feeding into the North-Equatorial Counter-Current (NECC) (Richardson et al., 1994). The NBC-retroflexion causes a periodical reduction in the intensity of the GC (Hellweger and Gordon, 2002). Low discharge and weakening of the GC causes a reduced arrival of Amazon water to the coast of Suriname in the second half of the year.

Suriname has a humid-tropical climate, with mean temperatures between 26.2 and 28.2 °C, and an annual rainfall between 1450 and 3000 mm (Amatali, 1993). The climate is influenced by the Inter-Tropical Convergence Zone (ITCZ) which passes over the country twice a year, creating two major seasons. The dry season lasts from August to November and the rainy season from December to July, the latter interrupted by a drier period (“short dry season”) in February–April. (Amatali, 1993). The seasonality in rainfall determines the amount of freshwater discharged into the coastal waters from four rivers (on average 152 km³ yr⁻¹ in total, Amatali, 1993). These rivers enter the Suriname coast via estuaries and are, from Guyana to French Guyana (west to east), the Corantyne, Coppename, Suriname and Maroni River, respectively. Shelf waters in the region can generally be characterized by three major zones parallel to the coast (Cadée 1975; Lowe-McConnell, 1962; Smith and Demaster, 1996). The brown inshore waters have a high turbidity and low salinity due to suspension of the muddy deposits and freshwater input of both the Amazon and main local rivers. Between 20 and 50 km offshore the combination of riverine nutrient inputs and decreased turbidity creates a productive zone with high chlorophyll concentrations, termed the green water zone. Offshore from this zone, irradiance further increases, but nutrients become limited for primary production. This is the blue water zone,

which stretches offshore to the continental slope.

2.2. Sampling and data origin

Data originated from 10 trawl surveys for epibenthos and demersal fish conducted between February 2012 and April 2013. Samples were collected at 15 locations situated on 3 transects positioned near the westward directed outflow of the Coppename (Co), Suriname (Su) and Maroni (Ma) River (Fig. 1). Each transect consisted of 5 locations along a depth gradient (6, 13, 20, 27 and 34 m depth). Sampling was done onboard Neptune-6, a 25-m long commercial outrigger trawler of the Suriname seabob shrimp (*Xiphopenaeus kroyeri*) trawling fleet (Heiploeg Suriname). A small otter trawl at the stern of the vessel (the ‘try-net’: 4.3 m horizontal spread; 45 mm stretched cod end mesh size) was used for sampling. This gear type was chosen because it is known to operate well on the often muddy seabed, and it has proven efficient in catching shrimp (so presumably as well other epibenthos).

During each sampling campaign, one trawl sample was collected at each station by towing the trawl for 40 min in westward direction at a speed of approximately 2.5 knots. Sampling time, start and stop coordinates and sampling depth were noted to enable a correct conversion towards sampled surface units. All stations were sampled monthly for the first 6 months and bi-monthly later on (Table 1). Two samples could not be taken due to drift sein fisheries on the spot (Ma06, January 2013) and technical problems (Ma34, April 2013).

Epibenthos was sorted from the catch and frozen (–20 °C) onboard. In the lab, organisms were identified to species or higher taxon level, counted and weighted (wet weight; 0.1 g precision). Species identification was based on, among others, Holthuis (1959), Walenkamp (1976), Takeda and Okutani (1983) and Cervigón et al. (1993). Fish was also retained from the catches, but reported on elsewhere (Willems et al., Submitted for publication).

Several *in-situ* environmental parameters were determined per location (Table 1). Water salinity, temperature and depth were measured with a CTD (SAIV SD200), but data were not recorded for the last 4 campaigns due to technical problems. Water clarity was measured with a Secchi-disk. Sub-surface total suspended matter concentrations (SS-TSM) were measured from water collected at 5 m depth with a Niskin bottle, filtered on pre-washed, pre-weighted GF/F filters and stored at –20 °C. Filters were subsequently dried in the lab (48 h at 70 °C) and re-weighted (0.0001 g precision) to calculate SS-TSM.

A Van Veen grab was used to collect sediment samples on three campaigns (February, April and May 2012). A sediment subsample was dried in the lab (48 h at 70 °C), and analyzed for total organic carbon content (TOC) and grain size composition. For the latter a

Malvern Mastersizer 2000G hydro version 5.40 (Malvern, 1999) was used to calculate mud percentage ($< 63 \mu\text{m}$; MUD) and median grain size of the sand fraction (63–2000 μm ; MEDSAND).

The above mentioned environmental data were complemented by remote sensing data from the satellite-borne sensor MODIS on the polar-orbiting Aqua satellite (OBPG, 2014; Bailey et al., 2010), including surface total suspended matter concentrations (SF-TSM), chlorophyll *a* concentrations (CHL) and sea surface temperature (SST) (Nechad et al., 2010). MODIS values (spatial resolution of approximately 1x1 km) with the best spatial and temporal accordance with *in-situ* sampling were used (see Vanhellemont et al., 2011), Vanhellemont and Ruddick, 2011 for an extensive explanation on the use of this technology).

Rainfall data at 65 land-based stations in Suriname were obtained from the Suriname Meteorological Service. River discharge data for Maroni River (measured at Langa Tabiki, Suriname) and Amazon River (measured at Obidos, Brazil) were available from the Environmental Research Laboratory (ORE-HYBAM, 2014).

2.3. Data analyses

Sampling campaigns were considered to occur either in the

rainy or dry season based on real-time river outflow data of Maroni River with a cut-off at the mid-range discharge value (2960 $\text{m}^3 \text{s}^{-1}$). As such, the four campaigns in February to May 2012 were considered as *rainy*. The five following campaigns were *dry* while the last campaign (April 2013) was again *rainy* (Table 1, Fig. 3).

Spatial and temporal variability in environmental variables was tested with a three-way Permanova (Anderson et al., 2008) on an Euclidean distance resemblance matrix with the factors 'depth', 'transect' and 'season'. Sediment parameters were only measured in the *rainy* season and hence only tested for 'depth' and 'transect'. In case of significant effects, pairwise tests were conducted to test for differences within factors. *P*-values were drawn from Monte Carlo (MC) permutations when the number of possible permutations was restricted (< 100) (Anderson and Robinson, 2003). Correlations between rainfall and river discharge were tested with Pearson product moment correlations after the data appeared normally distributed (Shapiro–Wilk normality test; $p > 0.05$).

Epibenthos data were standardized and expressed as numbers and biomass per surface unit (1000 m^2). Multivariate analyses were performed on fourth-root transformed epibenthos abundance data using the Bray–Curtis similarity index with exclusion of

Table 2
List of epibenthic taxa identified from the trawl samples.

CRUSTACEA		
Decapoda - Penaeoidea		
<i>Penaeus brasiliensis</i> Latreille, 1817		
<i>Penaeus notialis</i> Pérez Farfante, 1967 *		
<i>Penaeus subtilis</i> Pérez Farfante, 1967		
<i>Penaeus schmitti</i> Burkenroad, 1936		
<i>Sicyonia typica</i> Boeck, 1864 *		
<i>Sycionia</i> sp. H. Milne Edwards, 1830 *		
<i>Xiphopenaeus kroyeri</i> Heller, 1862		
Decapoda - Anomura		
<i>Clibanarius foresti</i> Holthuis, 1959		
<i>Dardanus fucosus</i> Biffar & Provenzano, 1972		
<i>Ostraconotus spatulipes</i> A. Milne-Edwards, 1880 * §		
Paguroidea sp. 1 Latreille, 1802 *		
Paguroidea sp. 2 Latreille, 1802 *		
<i>Petrochirus diogenes</i> Linnaeus, 1758		
<i>Porcellana sayana</i> Leach, 1820		
Decapoda - Brachyura		
<i>Acanthilia intermedia</i> Miers, 1886 *		
<i>Achelous spinimanus</i> Latreille, 1819 *		
Brachyura sp. 1 Linnaeus, 1758 *		
Brachyura sp. 2 Linnaeus, 1758 *		
<i>Calappa nitida</i> Holthuis, 1958		
<i>Calappa sulcata</i> Rathbun, 1898		
<i>Callinectes bocourti</i> A. Milne-Edwards, 1879		
<i>Callinectes danae</i> Smith, 1869 *		
<i>Callinectes ornatus</i> Ordway, 1863		
<i>Collodes inermis</i> A. Milne-Edwards, 1878 *		
<i>Hepatus gronovii</i> Holthuis, 1959		
<i>Hepatus pudibundus</i> Herbst, 1785 *		
<i>Hepatus scaber</i> Holthuis, 1959 *		
<i>Hypoconcha arcuata</i> Stimpson, 1858 *		
<i>Iliacantha liodactylus</i> Rathbun, 1898 *		
<i>Lupella forceps</i> Fabricius, 1793		
<i>Moreiradromia antillensis</i> Stimpson, 1858 *		
<i>Paradasygius tuberculatus</i> de Castro, 1949		
<i>Persephona lichtensteinii</i> Leach, 1817		
<i>Podochela riisei</i> Stimpson, 1860		
<i>Portunus gibbesii</i> Stimpson, 1859		
<i>Stenorhynchus seticornis</i> Herbst, 1788		
Decapoda - Caridea		
<i>Exhippolysmata oplophoroides</i> Holthuis, 1948		
<i>Nematopalaemon schmitti</i> Holthuis, 1950		
Stomatopoda		
<i>Squilla empusa</i> Say, 1818		
<i>Squilla lijdingi</i> Holthuis, 1959		
<i>Squilla rugosa</i> Bigelow, 1893 *		
ECHINODERMATA		
Asteroidea		
<i>Astropecten americanus</i> Verrill, 1880 *		
<i>Astropecten brasiliensis</i> Müller & Troschel, 1842		
<i>Astropecten marginatus</i> Gray, 1840		
<i>Echinaster guyanensis</i> A.M. Clark, 1987		
<i>Luidia alternata</i> Say, 1825		
<i>Luidia clathrata</i> Say, 1825		
<i>Luidia senegalensis</i> Lamarck, 1816		
Ophiuroidea		
<i>Astrophyton muricatum</i> Lamarck, 1816 §		
<i>Ophioderma brevispina</i> Say, 1825 §		
<i>Ophiopsis elegans</i> Lütken, 1859 §		
Crinoidea		
<i>Tropiometra carinata</i> Lamarck, 1816 * §		
Echinoidea		
<i>Euclidaris tribuloides</i> Lamarck, 1816 * §		
<i>Hygrosoma petersii</i> A. Agassiz, 1880 *		
Holothuroidea		
Holothuroidea sp. *		
MOLLUSCA		
Bivalvia		
<i>Adrana gloriosa</i> A. Adams, 1856 *		
<i>Aequipecten lineolaris</i> Lamarck, 1819 *		
<i>Amygdalum politum</i> Verrill & Smith, 1880 *		
<i>Anadara notabilis</i> Röding, 1798		
<i>Arcinella arcinella</i> Linnaeus, 1767 *		
<i>Argopecten gibbus</i> Linnaeus, 1758 §		
<i>Argopecten nucleus</i> Born, 1778 §		
Bivalvia sp. 1 Linnaeus, 1758 *		
<i>Dallocardia muricata</i> Linnaeus, 1758 * §		
<i>Euvola chazaliei</i> Dautzenberg, 1900 *		
<i>Modiolus squamosus</i> Beaufort, 1967 §		
Pinnidae sp. 1 Leach, 1819 *		
<i>Trachycardium isocardia</i> Linnaeus, 1758 *		
Cephalopoda		
Cephalopoda sp. Cuvier, 1795		
<i>Doryteuthis pleii</i> Blainville, 1823 *		
<i>Doryteuthis surinamensis</i> Voss, 1974		
Octopodidae sp. 1 d'Orbigny, 1839 *		
Octopodidae sp. 2 d'Orbigny, 1839 *		
Gastropoda		
<i>Conus compressus</i> G.B. Sowerby II, 1866 *		
<i>Distorsio clathrata</i> Lamarck, 1816		
<i>Fusinus ansatus</i> Gmelin, 1791 *		
Gastropoda sp. 1 Cuvier, 1795 *		
Gastropoda sp. 2 Cuvier, 1795 *		
<i>Marsupina bufo</i> Bruguière, 1792		
<i>Murex</i> sp. 1 Linnaeus, 1758 *		
<i>Murex</i> sp. 2 Linnaeus, 1758 *		
<i>Phyllonotus pomum</i> Gmelin, 1791 *		
<i>Pugilina morio</i> Linnaeus, 1758 §		
<i>Terebra taurina</i> Lightfoot, 1786 *		
<i>Tonna galea</i> Linnaeus, 1758		
<i>Turritella variegata</i> Linnaeus, 1758 * §		
CNIDARIA		
Anthozoa		
Anthozoa sp. Ehrenberg, 1834		
<i>Renilla muelleri</i> Kölliker, 1872 §		
<i>Virgularia</i> sp. Lamarck, 1816 *		
PORIFERA		
Porifera sp. Grant, 1836 *		
ANNELIDA		
Polychaeta sp. 1 Grube, 1850 *		
TUNICATA		
Asciacea		
Asciacea sp. Nielsen, 1995 *		

* = rare species (occurring in $< 3\%$ of the samples)

§ = no previous record for Suriname was found

rare species (occurring in < 3% of the samples; Table 2), to reduce the influence of highly abundant and rare species, respectively.

Distance-based linear models (DistLM) based on BEST selection and BIC criterion were used to relate patterns in species composition and abundance to the nine calculated environmental variables: CHL, SF-TSM, SS-TSM, SST, Maroni discharge, Amazon discharge, Secchi-depth, MEDSAND, and TOC. As sediment was only three times sampled, averages per location were calculated from these campaigns and used for the missing months (this approach was validated by a DistLM analysis with only the three campaigns, giving similar results as the full DistLM analysis). Environmental data were normalized and collinearity among variables was examined using Spearman rank correlation coefficients prior to the DistLM analyses. For linear dependent variables ($|r| \geq 0.8$) only one variable was retained in the analysis. As such, depth, rainfall and MUD were excluded from the analyses, due to collinearity with TOC, Maroni discharge and TOC, respectively.

In a next step, cluster analyses with SIMPROF tests (1% significance level) were performed to investigate the epibenthic community structure, based on Bray–Curtis similarity index for the fourth root transformed species abundance matrix. The significance level was set more stringent given the multiple testing inherent in this hierarchical approach as suggested in Clarke et al. (2008). Following, a SIMPER analysis (cut-off 90%) was performed to specify the discriminating species within the observed clusters. The clusters were further characterized in terms of density (N), biomass (B), species richness (S), Shannon Wiener diversity (H') and Pielou's evenness (J'), and in terms of the relevant (DistLM-based) environmental variables. Significant differences in these univariate parameters between cluster groups were tested through one-way PerMANOVA analyses, based on the Euclidean distance resemblance matrix with unrestricted permutation of raw data (Anderson et al., 2008) and through pairwise tests. Monte Carlo (MC) corrections were applied when too few (< 100) permutations could be calculated (Anderson and Robinson, 2003).

Within-cluster patterns in species composition and abundance were further investigated for small-scale spatial and temporal patterns, using a three-way PerMANOVA design with the factors 'depth', 'transect' and 'season'. These analyses were based on a Bray–Curtis similarity index constructed of fourth-root transformed epibenthos abundance data for all samples per cluster. Finally, within-cluster variation in the univariate parameters was tested using a similar three-way PerMANOVA design based on an Euclidean distance resemblance matrix. All data analyses were performed in R v.3.0.1 (R Core Team, 2013) and in PRIMER v.6.1.13 with PerMANOVA add-on software (Anderson et al., 2008; Clarke and Gorley, 2006). A significance level of $p=0.05$ was used in all tests. Throughout the text, averages are always given together with their standard deviation (SD).

3. Results

3.1. Environmental characterization

3.1.1. Spatial variability

Most water parameters were significantly influenced by the factor 'depth' (Appendix A1, Fig. 2), corresponding with an inshore-offshore gradient. Chlorophyll *a* concentrations (CHL) steadily decreased from the 6m-locations (average $5.2 \pm \text{SD } 2.1 \text{ mg m}^{-3}$) towards the 34m-locations ($1.6 \pm 1.4 \text{ mg m}^{-3}$) and differed significantly between most depths (pairwise tests), except between 13 and 20 m (pseudo- $F=24.2$, $p=0.0001$). Similarly, sub-surface total suspended matter concentrations (SS-TSM) decreased from $99.0 \pm 53.7 \text{ g m}^{-3}$ at 6 m-depths to $36.0 \pm 11.3 \text{ g m}^{-3}$ at 34 m-depths (Pseudo- $F=27.9$; $p=0.0001$), and also most pairwise tests

for the factor 'depth' were significant. On the contrary, sea surface temperatures (SST) were significantly higher at the 6 m-locations ($28.7 \pm 1.2 \text{ }^\circ\text{C}$) compared to the 20, 27 and 34 m locations together (avg. $27.8 \pm 1.0 \text{ }^\circ\text{C}$) (pseudo- $F=3.1$; $p=0.0188$) and separately (pairwise tests).

The parameters Secchi-depth and surface total suspended matter concentration (SF-TSM) were significantly influenced by the interaction factor 'depth x transect' (Appendix A1, Fig. 2). Per transect, the 6m-locations had significantly lower Secchi-depths compared to the 34 m-locations (Pseudo- $F=3.5$; $p=0.001$), while in the Su-transect Secchi-depth was significantly lower than in the Co-transect (at 6 m-depth) and the Ma-transect (at all other depths, pairwise tests). On the contrary, SF-TSM was significantly higher at the 6 m-locations compared to the 34 m-locations in all transects (Pseudo- $F=2.2$; $p=0.0301$), with some local differences between the three transects (pairwise tests). For salinity (avg. 34.9 ± 0.9 , measured at 5 m below water surface) no significant spatial differences were noted.

Also, the three sediment characteristics were significantly influenced by the factor 'depth' and showed a clear inshore-offshore gradient (Appendix A1; Fig. 2). The sand fraction (MEDSAND) increased from the 6 m-locations ($90.8 \pm 1.8 \text{ } \mu\text{m}$) towards the 34 m-locations ($318.1 \pm 105.8 \text{ } \mu\text{m}$) (Pseudo- $F=6.0$; $p=0.0056$). In the pairwise tests, significant differences in MEDSAND were mainly noted between the 34 m-locations and most other locations except the 27 m-locations. On the contrary, high MUD values were noted at all 6 m-, 13 m- and 20 m-locations (avg. $96.8 \pm 5.9\%$), which were significantly different from the lower values at the 27 m- and 34 m-locations (avg. $38.9 \pm 18.7\%$) in the pairwise tests.

For total organic carbon content of the sediment (TOC), a significant interaction 'depth x transect' was detected as well (Pseudo- $F=4.4$; $p=0.0072$) (Appendix A1, Fig. 2). In the Ma-transect, a steady decrease with depth was observed from 1.5% at 6 m-depth to 0.3% at 34 m-depth, with the main pairwise differences noted between the 6 m-location and the other depths. In both the Su- and Co-transect, a sudden significant drop in TOC was observed near the 34 m and 27 m-locations, respectively, compared to the shallower locations (pairwise tests).

3.1.2. Seasonal variability

In 2012, most land rainfall was noted between January and August (on average $221 \pm 53 \text{ mm}$). The period September 2012–January 2013 was much drier with an average rainfall of $60 \pm 28 \text{ mm}$, after which the rainfall increased again (Fig. 3).

The average monthly Maroni River discharge largely followed this rainfall pattern with a peak-discharge over $5000 \text{ m}^3 \text{ s}^{-1}$ in April 2012 and a minimum flow of $126 \text{ m}^3 \text{ s}^{-1}$ in November 2012. The correlation was stronger when taking into account a one-month time lag between rainfall and Maroni discharge (Pearson $r=0.73$; $p=0.002$). Also, a similar discharge pattern was noted for the Amazon River (Pearson $r=0.81$; $p=0.0001$), with a peak flow in July 2012 and a minimum flow in November 2012. The peak volume discharged by the Amazon River was about $260,000 \text{ m}^3 \text{ s}^{-1}$, nearly 50 times the Maroni peak-discharge volume (Fig. 3).

CHL, SS-TSM and SST were significantly influenced by the factor 'season' but not by any interaction term (Appendix A1). In the rainy season, all locations were characterized by significantly higher CHL ($3.7 \pm 2.2 \text{ mg m}^{-3}$ vs. $3.0 \pm 1.7 \text{ mg m}^{-3}$ in the dry season) (Pseudo- $F=7.9$; $p=0.0056$). Also, SS-TSM was higher in the rainy season ($60.6 \pm 36.7 \text{ g m}^{-3}$ vs. $46.5 \pm 32.9 \text{ g m}^{-3}$) (Pseudo- $F=8.6$; $p=0.0035$). On the other hand, SST was significantly higher in the dry season ($28.3 \pm 1.2 \text{ }^\circ\text{C}$) than in the rainy season ($27.9 \pm 1.0 \text{ }^\circ\text{C}$; Pseudo- $F=4.1$; $p=0.0443$). Elevated SST-values preceded low river discharge (Pearson $r=-0.80$; $p=0.0003$ for SST and one month time-lag Maroni discharge).

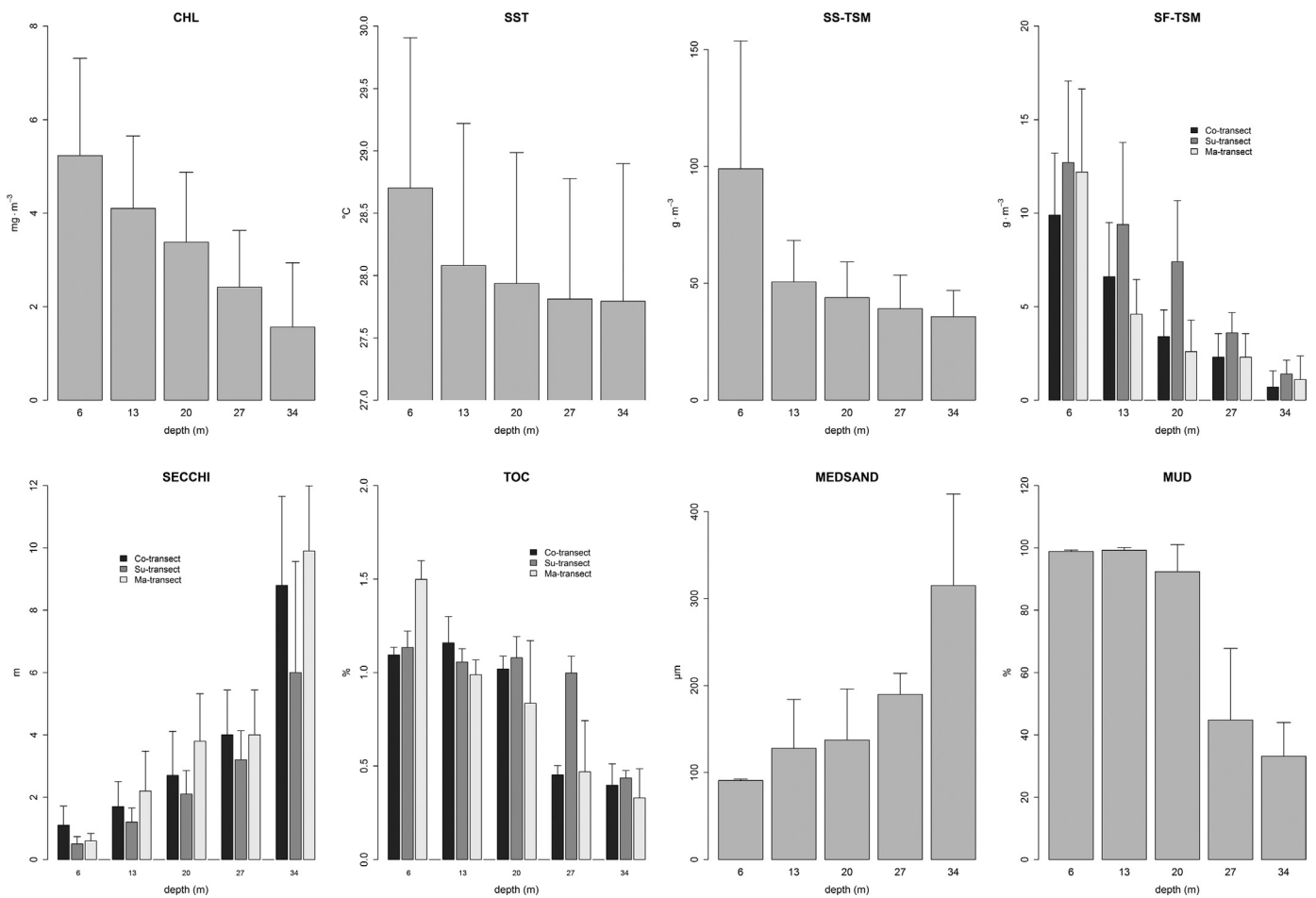


Fig. 2. Barplots (average + SD) of water and sediment parameters. CHL=remote sensing chlorophyll *a* values; SST=remote sensing sea surface temperature; SS-TSM=*in situ* measured sub-surface total suspended matter; SF-TSM=remote sensing surface total suspended matter; SECCHI=*in situ* measured Secchi-depth; TOC=total organic carbon content; MEDSAND=median grain size of sand fraction; MUD=sediment mud content; (the latter three derived from *in situ* bottom-grab samples).

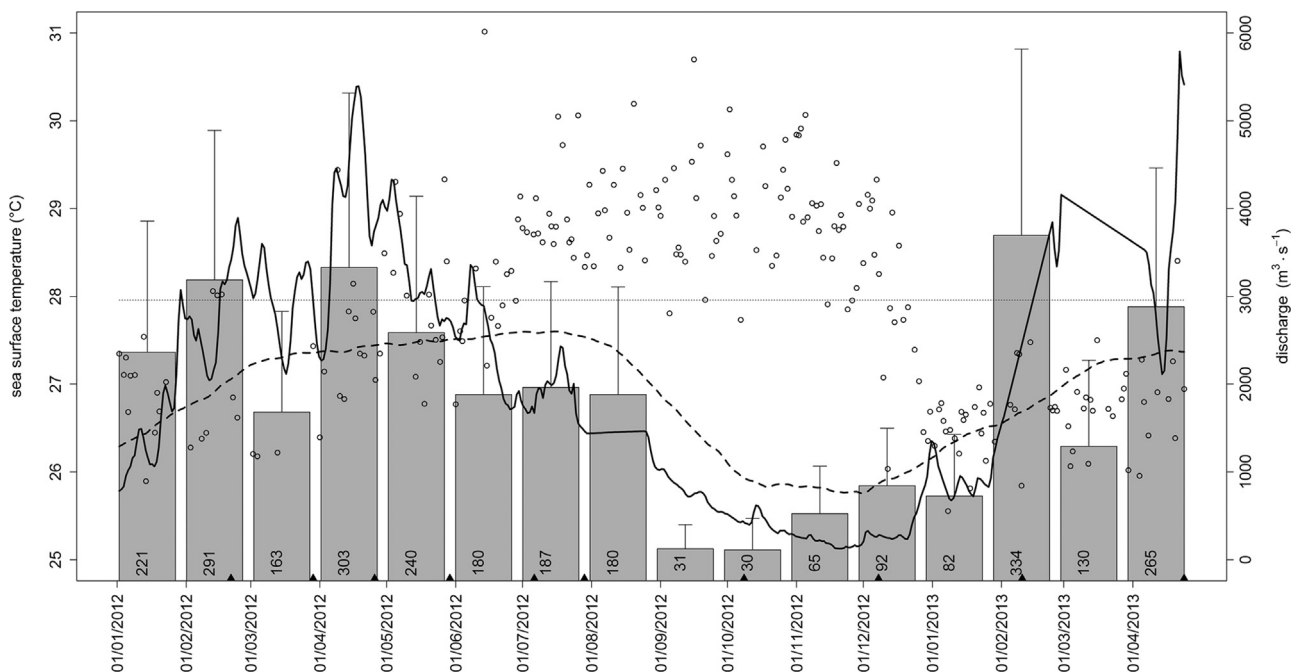


Fig. 3. Rainfall, sea surface temperature and river discharge over time during the study. Bars: average (+SD) monthly rainfall at 62 land-based stations in Suriname; vertical numbers at bar-base denote average rainfall in mm; black triangles indicate sampling campaigns. Open dots: remote sensing sea surface temperature, averaged over 15 sampling locations (left axis). Solid line: daily discharge of Maroni River measured at Langa Tabiki (right axis); the horizontal dashed line indicates the cut-off Maroni discharge value between dry and rainy season. Dashed line: daily discharge of Amazon river measured at Obidos (Brazil) (right axis); discharge values for Amazon have been divided by 100 for visualization purposes.

For the parameters SF-TSM, Secchi-depth and salinity no significant 'seasonal' effect was observed. Sediment parameters were only measured in the rainy season and could not be tested for 'seasonal' interactions.

3.2. Epibenthos characterization

3.2.1. General

From the 148 bottom-trawl samples, 92 epibenthic taxa, further referred to as species, were identified. Crustaceans were the most abundant group with 41 species, followed by molluscs (31 species) and echinoderms (14 species). Three cnidarians, a polychaete, a tunicate and a sponge (Porifera) completed the list (Table 2). Samples contained between 1 and 31 epibenthic species with on average 6.6 ± 4.7 species per sample. Density ranged from 0.2 to 1392 ind 1000 m⁻², wet weight biomass from 0.8 to 6675 g 1000 m⁻². Overall, Atlantic seabob shrimp *X. kroyeri* was the dominant species, accounting for $61 \pm 43\%$ of the total density and occurring in 70% of all samples. Other abundant species (occurring in 50–60% of the samples) were brown shrimp *Penaeus subtilis* ($9 \pm 20\%$), soft coral *Renilla muelleri* ($7 \pm 17\%$), brittle star *Ophioderma brevispina* ($7 \pm 19\%$) and blue swimming crab *Callinectes ornatus* ($2 \pm 6\%$). Many species were rare: 25 species only occurred in one sample, while 64 species were found in <5% of the samples.

Demersal fishes were abundant in the trawl catches, with

Stellifer rastifer, *Amphiarius rugispinis* and *Cynoscion jamaicensis* being the most dominant species by number. A description of the demersal fish community based on this survey can be found in Willems et al. (Submitted for publication).

3.2.2 Delineation of epibenthic assemblages

After omitting rare species (occurring in <3% of the samples), 44 of the 92 epibenthic species were retained for further analyses. Hierarchical clustering of the samples discriminated 6 outliers and three main cluster groups at the 28% similarity level (Fig. 4). The largest cluster contained nearly all samples located at the 6, 13 and 20 m-depths, supplemented with most of the 27 m-samples of the Ma-transect. This cluster is further referred to as the coastal assemblage. A second large cluster is called the transition assemblage, containing the remaining samples at 27 m-depth of the Co- and Su-transects and the 34 m-depth samples of Ma-transect. The third cluster (i.e. the offshore assemblage) contained the 34 m-samples of the Co- and Su-transects (Figs. 4 and 5).

3.2.3. Spatio-temporal patterns in the epibenthic assemblages

Overall, no temporal differences in epibenthic species composition and abundance were observed in either the coastal or the transition assemblage. Only within the coastal assemblage a significant effect for the factor 'season' was noted for Pielou's evenness index *J'* (Pseudo-*F*=5.0; *p*=0.03), being higher in the rainy season. Secondly, a significant 'transect x season'-interaction was found for

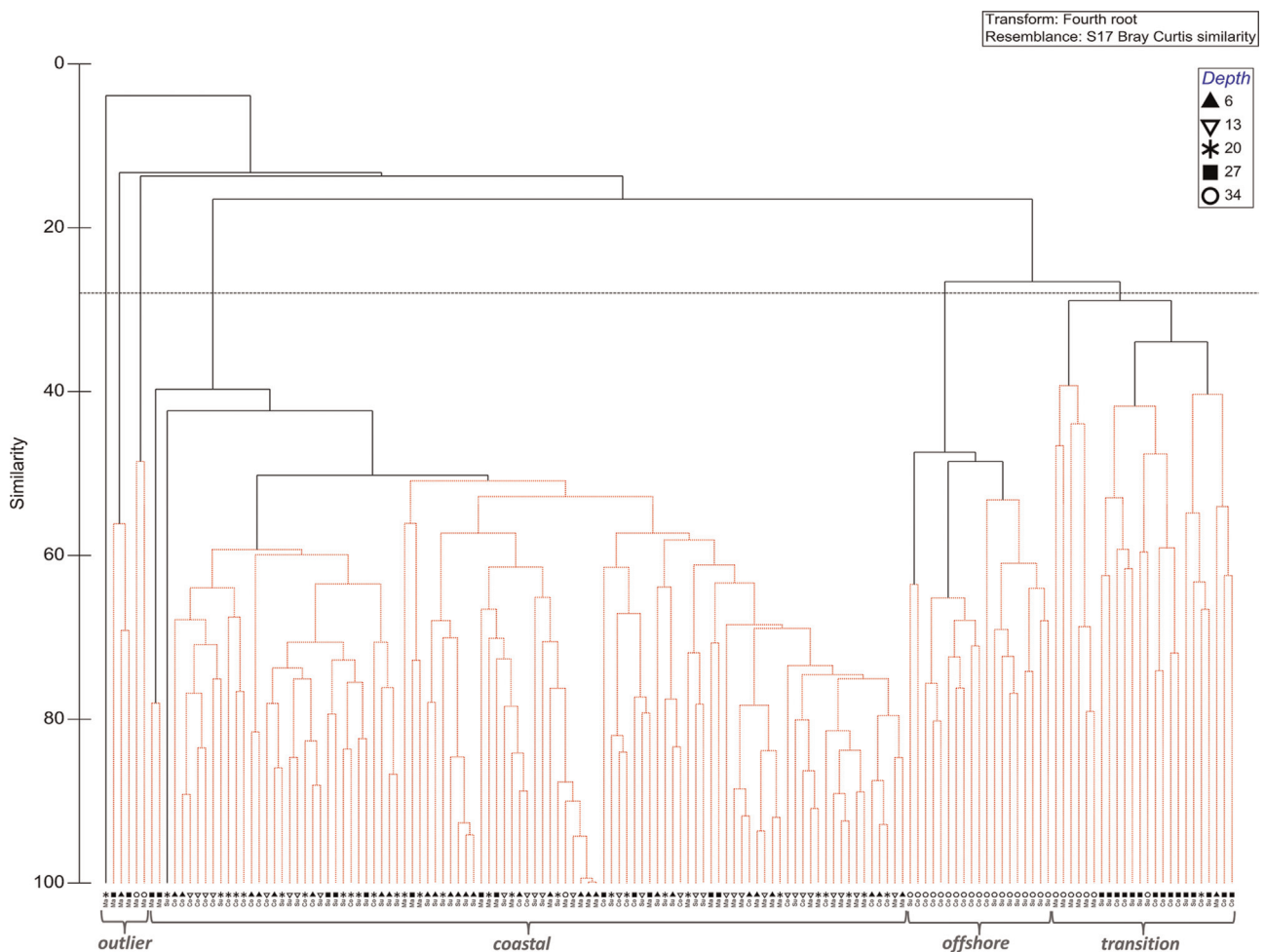


Fig. 4. Group-averaging cluster analysis based on Bray–Curtis resemblance matrix of fourth-root-transformed species abundance data in all epibenthos samples. Significant clusters (SIMPROF test, 1% significance level) are indicated by the colored (red) lines. Samples are labeled with depth (symbol) and transect (Co=Coppename; Su=Suriname; Ma=Marowijne transect). Assemblages are identified at the 28% similarity level (dashed line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

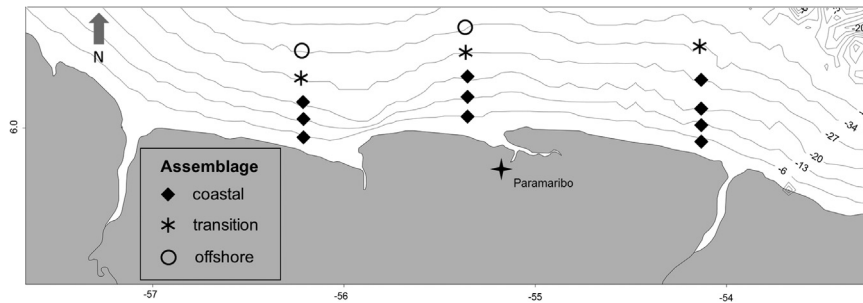


Fig. 5. Map of the study area with the three epibenthic assemblages plotted at the 15 locations, sampled along 5 parallel depths (6, 13, 20, 27, 34 m) and 3 longitudinal transects (Co-transect in the west, Su-transect in the middle, Ma-transect in the east).

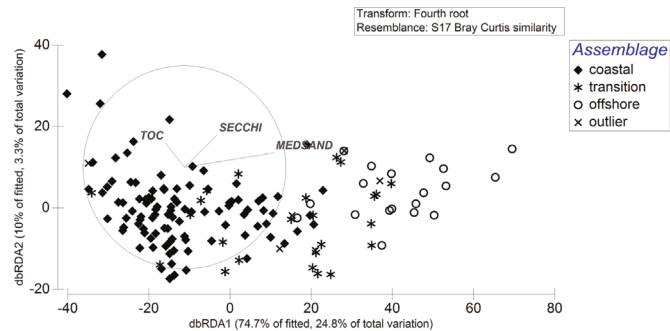


Fig. 6. Distance-based redundancy analysis (dbRDA) plot of all epibenthic samples (fourth-root transformed density values; Bray–Curtis similarity) and 9 environmental predictor variables. Symbols represent species assemblages delineated from hierarchical clustering (28% similarity level). The three variables selected to fit the best model in DistLM are overlaid as vectors using multiple correlation. TOC = sediment total organic carbon; SECCHI = Secchi-depth; MEDSAND = median grain size of the sand fraction.

Shannon diversity index H' (Pseudo- $F=3.8$; $p=0.03$), which was higher in the *rainy* season in the Co-transect (Appendix B2). In the *offshore* assemblage, species composition and abundance differed between the *dry* and *rainy* season (Pseudo- $F=2.1$; $p=0.03$), but no differences in diversity indices were observed.

As shown above, mainly spatial differences were noted in the epibenthic community. The linear combination of environmental variables that best explained the variation in the multivariate data cloud included TOC (21%), MEDSAND (20%) and Secchi-depth (16%). When fitted together (DistLM BEST - BIC; $p=0.0001$), these variables explained 27% of the total variation in the epibenthic community structure (Fig. 6).

Significant differences were observed between the three assemblages for total epibenthic density (Pseudo- $F=5.5$; $p=0.0087$), biomass (Pseudo- $F=5.6$; $p=0.0089$), species richness (Pseudo- $F=89.1$; $p=0.0001$), Shannon diversity (Pseudo- $F=149.9$; $p=0.0001$) and Pielou's evenness (Pseudo- $F=43.6$; $p=0.0001$). Pairwise comparisons revealed that epibenthic density and biomass in the *coastal* assemblage attained significantly higher values (on average 2–3 times higher) than the *transition* and *offshore* assemblages (Fig. 7, Table 3). Species richness differed significantly among all assemblages (pairwise tests; $p < 0.01$) and gradually increased from the *coastal* assemblage (4.8 ± 2.6) to the *offshore* assemblages (14.6 ± 4.1). Also, Pielou's evenness and Shannon diversity indices were significantly lower in the *coastal* assemblage.

Similarly, significant differences were observed between the three assemblages for the three environmental parameters that explained most of the variance in the data, namely TOC (Pseudo- $F=57.9$; $p=0.0001$), MEDSAND (Pseudo- $F=106.0$; $p=0.0001$) and Secchi-depth (Pseudo- $F=40.9$; $p=0.0001$). Pairwise comparisons further revealed that the *coastal* assemblage had significantly higher TOC, lower MEDSAND and lower Secchi-depth compared to

the other two assemblages (Fig. 7, Table 3).

One-way SIMPER analyses revealed that the *coastal* assemblage was dominated by seabob shrimp *X. kroyeri*, contributing 74% to within-group similarity (Table 3, Fig. 8). Other characterizing species were brown shrimp *Penaeus subtilis*, soft coral *Renilla muelleri* and blue swimming crab *Callinectes ornatus*. The latter three species together with hermit crab *Clibanarius foresti* were the most important species contributing to within-group similarity in the *transition* assemblage. The *offshore* assemblage was characterized by brittle stars *Ophioderma brevispina* and *Ophiolepis elegans*, and starfish *Luidia clathrata* and *Luidia senegalensis* as important contributors to within-group similarity.

Although three epibenthic assemblages were discerned, each assemblage grouped several significant sample clusters based on SIMPROF tests (Fig. 4). This variation was reflected in some spatial differences in species composition and abundance within each assemblage (Appendix A2). A significant 'depth x transect' interaction occurred in the *coastal* assemblage (Pseudo- $F=1.8$; $p=0.006$). Pairwise tests revealed significant differences between depths in each transect, and between transects at each depth (pairwise tests, $p < 0.05$). SIMPER results indicated a decreasing dominance of *X. kroyeri* with depth and from east (Ma-transect) to west (Co-transect) in the *coastal* assemblage. Within the *transition* assemblage a significant effect of the factor 'transect' was found (Pseudo- $F=3.3$; $p=0.0002$) with the Ma-transect being significantly different from the Su- and Co-transects (pairwise tests, $p < 0.01$). In the *transition* assemblage, the number of species contributing to within-group similarity increased from east to west. Within the *offshore* assemblage, species composition and abundance differed significantly between the Co-transect and the Su-transect (Pseudo- $F=7.9$; $p=0.0002$), with epibenthic biomass being significantly higher in the Co-transect than in the Su-transect (Pseudo- $F=5.8$; $p=0.0222$). SIMPER results also revealed a slightly different species composition in both offshore locations. For example, arrow crab *Stenorhynchus seticornis* was abundant in the offshore Co-location, while this species was nearly absent from the Su-transect.

Furthermore, within-cluster differences in S , H' and J' occurred. Within the *coastal* assemblage, S increased significantly from 6 m to 27 m-depth locations (Pseudo- $F=8.4$; $p=0.0005$, significant differences, except between 20 and 27 m). On the other hand, a significant decrease in S was noted from the Co-transect to the Ma-transect (Pseudo- $F=12.0$; $p=0.0001$). A similar pattern was seen for H' ('depth x transect'-interaction; Pseudo- $F=2.4$; $p=0.0425$). Within the *transition* assemblage, a significant effect of 'transect' was found for S and J' (resp. Pseudo- $F=5.0$; $p=0.0208$ and Pseudo- $F=11.2$; $p=0.0008$), with the Ma-transect having significantly lower S and higher J' compared to the Co- and Su-transects.

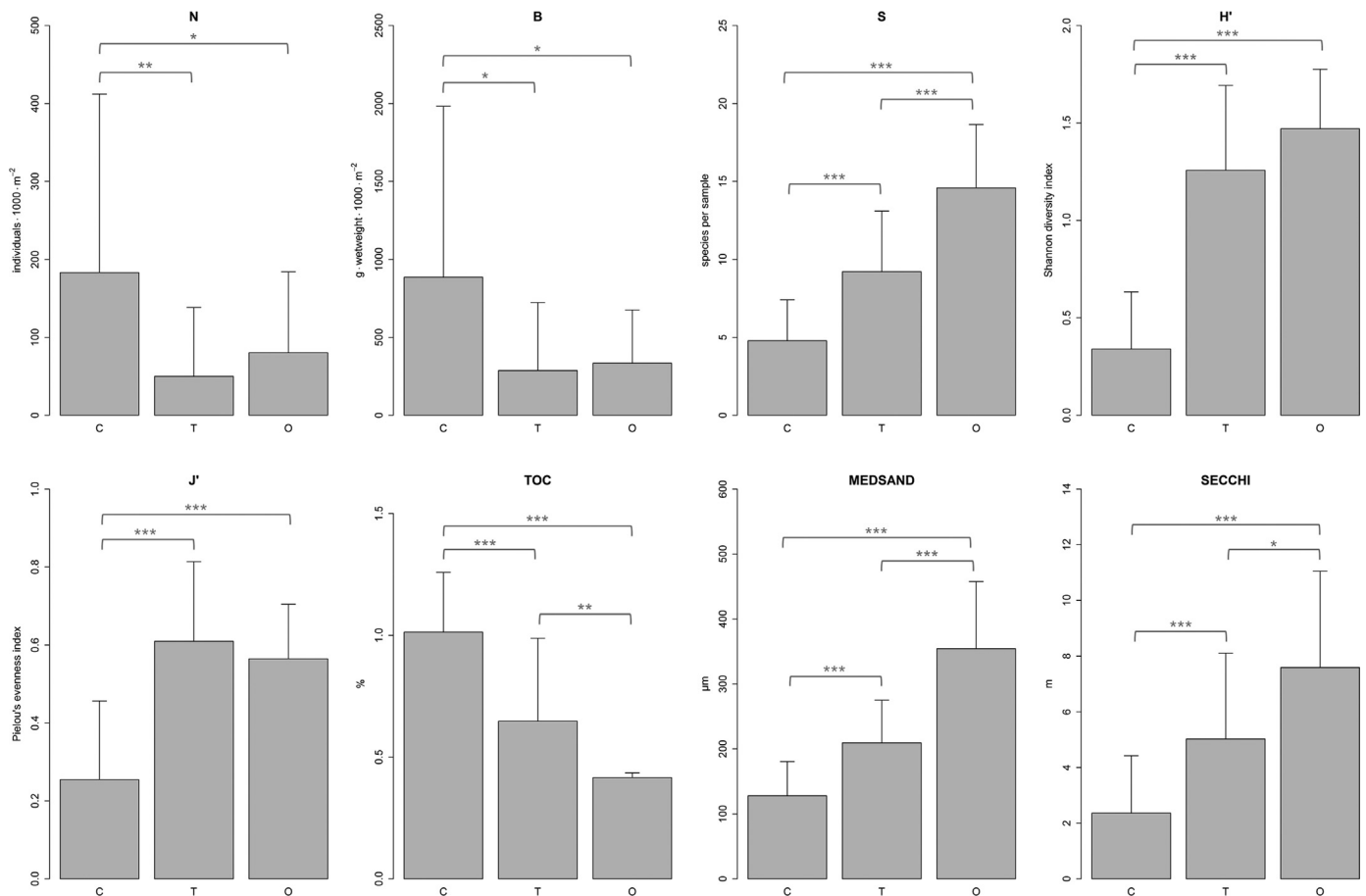


Fig. 7. Barplots showing main characteristics of the three assemblages (C=coastal, T=transition, O=offshore assemblages) as defined by cluster analysis (averages+SD). N=density, B=biomass, S=species richness, H'=Shannon-diversity, J'=Pielou's evenness, TOC=sediment total organic carbon, MEDSAND=median grain size of sand fraction, SECCHI=Secchi-depth. Significant differences between assemblages as defined by Permanova are indicated (*p=0.01–0.05, **p=0.001–0.01, ***p < 0.001).

Table 3

Characterization of the three species assemblages defined by cluster analysis, showing average 'within group' similarity based on one-way SIMPER analysis of fourth-root transformed abundance data. Species accounting for 90% cumulative contributing of the 'within group' similarity are listed along with their contribution (Contrib%). Also the average (± SD) per assemblage for a number of univariate parameters is given. TOC: sediment total organic carbon, MEDSAND: median grain size of the sand fraction, SECCHI: Secchi-depth.

Coastal assemblage		Transition assemblage		Offshore assemblage	
(avg. sim.=54.4%)		(avg. sim.=36.6%)		(avg. sim.=54.4%)	
Species	Contrib%	Species	Contrib%	Species	Contrib%
<i>Xiphopenaeus kroyeri</i>	73.5	<i>Penaeus subtilis</i>	21.3	<i>Ophioderma brevispina</i>	21.5
<i>Penaeus subtilis</i>	9.9	<i>Renilla muelleri</i>	18.8	<i>Ophiolepis elegans</i>	13.6
<i>Renilla muelleri</i>	5	<i>Clibanarius foresti</i>	11.3	<i>Luidia clathrata</i>	9.5
<i>Callinectes ornatus</i>	4.9	<i>Callinectes ornatus</i>	8.5	<i>Luidia senegalensis</i>	8.1
		<i>Luidia senegalensis</i>	8.4	<i>Dardanus fucusus</i>	6.6
		<i>Dardanus fucusus</i>	5.9	<i>Portunus gibbesii</i>	5.6
		<i>Doryteuthis surinamensis</i>	4.5	<i>Argopecten gibbus</i>	5
		<i>Paradasygius tuberculatus</i>	4.5	<i>Clibanarius foresti</i>	4.7
		<i>Porcellana sayana</i>	3.8	<i>Stenorhynchus seticornis</i>	4
		<i>Anthozoa sp.</i>	2.1	<i>Renilla muelleri</i>	3.2
		<i>Marsupina bufo</i>	2.1	<i>Callinectes ornatus</i>	3.1
				<i>Doryteuthis surinamensis</i>	2.5
				<i>Astropecten brasiliensis</i>	2.2
				<i>Echinaster guyanensis</i>	2.2
N samples	99		24		19
Density (ind 1000 m⁻²)	183 ± 229		50 ± 88		80 ± 104
WW Biomass (g 1000 m⁻²)	885 ± 1098		293.1 ± 432.4		335 ± 341
Species richness S	4.8 ± 2.6		9.2 ± 3.9		14.6 ± 4.1
Shannon diversity H'	0.3 ± 0.3		1.3 ± 0.4		1.5 ± 0.3
Pielou's evenness J'	0.3 ± 0.2		0.6 ± 0.2		0.6 ± 0.1
TOC (%)	1 ± 0.3		0.7 ± 0.3		0.4 ± 0.02
MEDSAND (µm)	128 ± 53		209 ± 66		345 ± 103
SECCHI (m)	2.4 ± 2.1		5 ± 3.1		7.6 ± 3.5

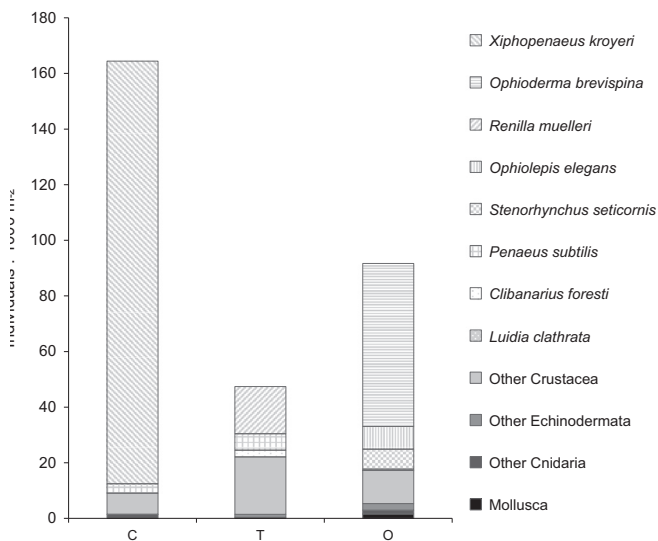


Fig. 8. Average epibenthic density per assemblage with indication of the most important species (> 10% SIMPER contribution). Average densities for all other species are given per taxonomic group. C=coastal, T=transition, O=offshore assemblage.

4. Discussion

The current study describes the epibenthic community structure in the coastal waters of Suriname. In total, 92 epibenthic species were identified from the trawl samples, mainly crustaceans and molluscs. Although the mesh size of our trawl gear was rather large for an epibenthic survey, we did capture the species to be expected within the area (e.g. Holthuis, 1959; Takeda and Okutani, 1983) and found 14 species with no previous reference for Suriname. Epibenthic organisms play an important role in tropical soft-bottom ecosystems (e.g. Robertson et al., 1992), and are the only benthic invertebrates in areas where the seabed is too unstable to support infauna (Aller and Aller, 1986). Although the epibenthic species of the Suriname Shelf are generally known, they have never been quantified or described in their ecological context. Knowledge on the spatio-temporal distribution in relation with the environment is crucial to understand the functioning of the coastal ecosystem, and forms the ecological basis for a sustainable management (Reiss et al., 2010).

4.1. Spatial patterns

The epibenthic community in the Suriname coastal system was largely structured by spatial differences in the environment. Both sediment and water parameters showed a clear inshore to offshore gradient. Up to the 20 m-depth contour, muddy deposits dominated, while further offshore, at higher depths, sediment grain size became coarser. Mud predominantly originates from the Amazon River, which provides an enormous flux of suspended matter into the ocean each year (Salisbury et al., 2011). From the river mouth, mud migrates both in suspension and in the form of mudbanks along the coast in a northwest direction, creating a dynamic 'mud belt' in the intertidal and shallow subtidal zone of the Guianas (Anthony et al., 2010). In Suriname this 'mud belt' is restricted to the area below the 20 m-isobath, beyond which it gradually mixes with coarser sediments of the outer shelf (Augustinus, 2004; Eisma et al., 1991).

The term community usually indicates a group of species occurring in a particular place or physical habitat (Mills, 1969). Based on the definitions to delineate biological communities given by Morin (1999), a single epibenthic coastal species assemblage could be discerned in the muddy coastal environment, overall

dominated by Atlantic seabob shrimp *X. kroyeri*, an *r*-selected, fast growing and mobile species (Branco et al., 1994). This Penaeid shrimp is known to prefer fine substrates (Freire et al., 2011) and to complete its life cycle in estuarine and coastal environments (e.g. Dall et al., 1990). Furthermore, the coastal assemblage was species-poor with on average < 5 species per sample. Environmental stress in the coastal environment is naturally high (Elliott and Quintino, 2007): deposition and resuspension of fine sediments by tides and currents cause turbid waters and unstable seabeds, and salinity highly varies due to extensive river runoff (Nittroer and Demaster, 1996). Only few epibenthic and other species can cope with such conditions. In general, tropical shelves under severe river-influences show reduced epifaunal and infaunal populations (Aller and Aller, 2004).

Although the infauna of the Suriname Shelf has been poorly studied, a few studies confirm low densities of macrobenthic animals in the nearshore muddy sediments. Whereas densities of Tanaidacea (Arthropoda: Crustacea) up to 6000 ind m⁻² were observed on the higher intertidal mudbanks, total infauna density decreased to 245 ind m⁻² in the lower, more unstable mudbanks (Swennen et al., 1982). In the shallow subtidal area (up to ca. 20 m depth) macrobenthic densities were even lower (around 40 ind m⁻²), with the dominant taxa being Magelonidae (Annelida: Polychaeta), Marginellidae (Mollusca: Gastropoda) and Tanaidacea (ESC, 2011). Rather than by macro- or meio-infauna, benthic communities on tropical river-influenced shelves are dominated by bacteria, accounting for > 95 % of the total benthic biomass (Aller et al., 2010; Aller and Stupakoff, 1996). Moreover, Aller and Blair (2006) showed that bacteria efficiently mineralize organic carbon within the Amazon-borne mud, resulting in low sediment total organic carbon values. As such, the high bacterial biomass may explain the low total organic carbon values of 1% we observed, which is remarkably low for an area with high sediment deposition rates (e.g. Aller, 1998).

High concentrations of *X. kroyeri* are known to occur around 20 m depth on the Suriname Shelf, as the major seabob shrimp fishing grounds are located in this zone (Bhagwandin, 2012), known as the green water zone (Lowe-McConnell, 1962). In Guyana (Cadée 1975) and within the Amazon plume (Smith and Demaster, 1996), this zone coincided with a midshore peak in primary production, stimulated by increased irradiance due to flocculation of suspended matter from the surface layer. We also observed a shift from brown to greenish waters around the 20 m isobath on several sampling campaigns. Also, surface total suspended matter was lower than sub-surface suspended matter in this area, but no peak in primary production was measured. Most probably, chlorophyll *a* measurements were biased due to the high water turbidity (Dall'Olmo et al., 2005). Several authors already noted that real patterns in primary production in near-shore coastal areas may be masked when based on MODIS measurements (e.g. Santer and Schmechtig, 2000; Vantrepotte et al., 2013).

Epibenthic biodiversity (*S* and *H'*) gradually increased with depth. With depth and increasing distance from riverine input, environmental conditions became more stable and more beneficial for other benthic organisms, resulting in a completely different epibenthic species assemblage along the 34 m depth contour. While the coastal assemblage was dominated by the long-shore 'mud belt', more local environmental conditions prevailed in the offshore assemblage. The latter zone is characterized by lower organic carbon content in the sediment, coarser sediments and clear overlying waters with less chlorophyll *a* and less suspended matter. These conditions had a positive influence on the epibenthic biodiversity and abundance. With on average 15 epibenthic species per sample, the offshore assemblage was three times more diverse than the coastal assemblage. Also at lower latitudes (e.g. the North Sea) epibenthic diversity seems higher in deeper and more offshore areas (Callaway et al., 2002). van Hoey et al. (2004) showed that as a consequence of the

Table A1
Average (\pm SD) values of water and sediment parameters per depth, transect and season and results of three-way Permanova tests on Euclidean distance resemblance matrices with the factors 'depth', 'transect' and 'season'. CHL=remote sensing chlorophyll *a* values (in mg m^{-3}); SS-TSM=*in situ* measured sub-surface total suspended matter (in g m^{-3}); SF-TSM=remote sensing surface total suspended matter (in g m^{-3}); SST=remote sensing sea surface temperature (in $^{\circ}\text{C}$); SECCHI=*in situ* measured Secchi-depth (in m); TOC=total organic carbon content (in %); MEDSAND=median grain size of sand fraction (in μm); MUD=sediment mud content (in %); (the latter three derived from *in situ* bottom-grab samples).

Variable	Depth					Transect			Season		Main test		
	6	13	20	27	34	Co	Su	Ma	Dry	Rainy	Significant term	Pseudo-F	P
CHL	5.2 \pm 2.1	4.1 \pm 1.6	3.4 \pm 1.5	2.4 \pm 1.2	1.6 \pm 1.4	3.3 \pm 2.2	3.2 \pm 2.3	3.5 \pm 1.4	3.0 \pm 1.7	3.7 \pm 2.2	depth	24.2	0.0001
<i>Pairwise tests</i>		<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>
		depth	depth	–	6, 13	2.3	0.023	depth	depth	–	13, 34	6.4	0.0001
		depth	depth	–	6, 20	3.9	0.0002	depth	depth	–	20, 27	2.9	0.0045
		depth	depth	–	6, 27	6.5	0.0001	depth	depth	–	20, 34	4.8	0.0001
		depth	depth	–	6, 34	7.7	0.0001	depth	depth	–	27, 34	2.6	0.0122
		depth	depth	–	13, 27	4.8	0.0001						
SS-TSM	99.0 \pm 53.7	50.6 \pm 17.7	43.9 \pm 15.3	39.2 \pm 14.4	36.0 \pm 11.3	57.4 \pm 41.3	47.1 \pm 26.4	56.4 \pm 36.9	46.5 \pm 32.9	60.6 \pm 36.7	depth	27.9	0.0001
<i>Pairwise tests</i>		<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>
		depth	depth	–	6, 13	4.9	0.0001	depth	depth	–	13, 27	2.8	0.0074
		depth	depth	–	6, 20	5.6	0.0001	depth	depth	–	13, 34	3.7	0.0003
		depth	depth	–	6, 27	6.1	0.0001	depth	depth	–	20, 34	2.1	0.0396
		depth	depth	–	6, 34	6.4	0.0001						
SF-TSM	11.6 \pm 4.1	6.8 \pm 3.7	4.5 \pm 3.1	2.4 \pm 1.5	1.1 \pm 1.0	4.3 \pm 4.6	4.6 \pm 3.9	6.9 \pm 5.1	5.5 \pm 4.9	5.1 \pm 4.5	depth x transect	2.2	0.0301
<i>Pairwise tests</i>		<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>
		depth x transect	transect	Co	6, 13	2.4	0.0305	depth x transect	transect	Ma	13, 34	4.6	0.0007
		depth x transect	transect	Co	6, 20	5.7	0.0001	depth x transect	transect	Su	6, 20	2.9	0.0117
		depth x transect	transect	Co	6, 27	6.6	0.0001	depth x transect	transect	Su	6, 27	6.1	0.0002
		depth x transect	transect	Co	6, 34	8.4	0.0001	depth x transect	transect	Su	6, 34	7.7	0.0001
		depth x transect	transect	Co	13, 20	3.1	0.0078	depth x transect	transect	Su	13, 27	4	0.0006
		depth x transect	transect	Co	13, 27	4.1	0.0007	depth x transect	transect	Su	13, 34	5.6	0.0001
		depth x transect	transect	Co	13, 34	6	0.0001	depth x transect	transect	Su	20, 27	3.3	0.0045
		depth x transect	transect	Co	20, 34	5.3	0.0002	depth x transect	transect	Su	20, 34	5.4	0.0002
		depth x transect	transect	Co	27, 34	3.3	0.003	depth x transect	transect	Su	27, 34	5.1	0.0005
		depth x transect	transect	Ma	6, 13	5.1	0.0003	depth x transect	depth	13	Ma, Su	3.1226	0.0059
		depth x transect	transect	Ma	6, 20	6.5	0.0001	depth x transect	depth	20	Co, Su	3.4361	0.0049
		depth x transect	transect	Ma	6, 27	7.8	0.0001	depth x transect	depth	20	Ma, Su	3.9131	0.0017
		depth x transect	transect	Ma	6, 34	7.4	0.0001	depth x transect	depth	27	Co, Su	2.2888	0.0387
		depth x transect	transect	Ma	13, 20	2.4	0.0273	depth x transect	depth	27	Ma, Su	4.6121	0.0005
		depth x transect	transect	Ma	13, 27	4.7	0.0002						
SST	28.7 \pm 1.2	28.1 \pm 1.1	27.9 \pm 1.0	27.8 \pm 1.0	27.8 \pm 1.1	27.9 \pm 1.0	28.2 \pm 1.1	28.0 \pm 1.2	28.3 \pm 1.2	27.9 \pm 1.0	depth	3.1	0.0188
<i>Pairwise tests</i>		<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>
		depth	depth	–	6, 20	2.4	0.0191	depth	depth	–	6, 34	2.8	0.0081
		depth	depth	–	6, 27	2.9	0.0056						
SECCHI	0.8 \pm 0.5	1.7 \pm 1.0	2.9 \pm 1.4	4.7 \pm 2.1	8.3 \pm 3.3	4.8 \pm 3.7	3.7 \pm 3.2	2.6 \pm 2.5	3.7 \pm 3.4	3.6 \pm 3.1	depth x transect	3.5	0.001
<i>Pairwise tests</i>		<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>
		depth x transect	transect	Co	6, 20	3.1	0.0064	depth x transect	transect	Su	6, 13	4.3	0.0008
		depth x transect	transect	Co	6, 27	5.9	0.0002	depth x transect	transect	Su	6, 20	6.6	0.0002
		depth x transect	transect	Co	6, 34	7.9	0.0001	depth x transect	transect	Su	6, 27	8.6	0.0001
		depth x transect	transect	Co	13, 27	4.5	0.0006	depth x transect	transect	Su	6, 34	4.6	0.0001
		depth x transect	transect	Co	13, 34	7.2	0.0001	depth x transect	transect	Su	13, 20	3.3	0.0026
		depth x transect	transect	Co	20, 34	5.8	0.0002	depth x transect	transect	Su	13, 27	5.8	0.0001

Table A1 (continued)

Variable	Depth				Transect				Season			Main test		
	6	13	20	27	34	Co	Su	Ma	Dry	Rainy	Significant term	Pseudo-F	P	
		depth x transect	transect	Co	27, 34	4.6	0.0005	depth x transect	transect	Su	13, 34	4	0.0005	
		depth x transect	transect	Ma	6, 13	3.4	0.002	depth x transect	transect	Su	20, 27	2.7	0.014	
		depth x transect	transect	Ma	6, 20	5.9	0.0002	depth x transect	transect	Su	20, 34	3.2	0.0007	
		depth x transect	transect	Ma	6, 27	13.8	0.0001	depth x transect	transect	Su	27, 34	2.3	0.0157	
		depth x transect	transect	Ma	6, 34	16.3	0.0001	depth x transect	depth	6	Co, Ma	2.1465	0.049	
		depth x transect	transect	Ma	13, 20	2.5	0.0234	depth x transect	depth	6	Co, Su	3.0192	0.005	
		depth x transect	transect	Ma	13, 27	7.9	0.0001	depth x transect	depth	13	Ma, Su	2.1757	0.024	
		depth x transect	transect	Ma	13, 34	11.4	0.0001	depth x transect	depth	20	Ma, Su	3.0128	0.004	
		depth x transect	transect	Ma	20, 27	4.7	0.0009	depth x transect	depth	27	Co, Ma	4.7325	0.002	
		depth x transect	transect	Ma	20, 34	8.4	0.0002	depth x transect	depth	27	Ma, Su	7.1323	0.001	
		depth x transect	transect	Ma	27, 34	4.8	0.0002	depth x transect	depth	34	Ma, Su	3.154	0.009	
MEDSAND	90.8 ± 1.8	127.8 ± 56.8	137.4 ± 58.7	189.8 ± 24.3	318.1 ± 105.8	183.5 ± 48.8	151.7 ± 75.0	182.3 ± 144.2	173.3 ± 99.1	171.4 ± 99.4	depth	6	0.006	
<i>Pairwise tests</i>		<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	
		depth	depth	–	6, 27	19.7	0.0001	depth	depth	–	13, 34	2.6	0.0399	
		depth	depth	–	6, 34	3.9	0.0109	depth	depth	–	20, 34	2.6	0.0339	
MUD	98.9 ± 0.4	99.2 ± 0.9	92.4 ± 8.7	44.7 ± 23.0	33.7 ± 10.6	65.4 ± 34.1	73.7 ± 31.7	82.2 ± 24.7	73.3 ± 31.3	74.4 ± 30.8	depth	23.4	1.00E-04	
<i>Pairwise tests</i>		<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	
		depth	depth	–	6, 27	11.9	0.0002	depth	depth	–	13, 34	5.5	0.0034	
		depth	depth	–	6, 34	5.5	0.0032	depth	depth	–	20, 27	5.4	0.0019	
		depth	depth	–	13, 27	12	0.0001	depth	depth	–	20, 34	4.3	0.0049	
TOC	1.2 ± 0.2	1.1 ± 0.1	1.0 ± 0.1	0.6 ± 0.3	0.4 ± 0.0	0.8 ± 0.4	0.8 ± 0.3	0.9 ± 0.3	0.9 ± 0.3	0.9 ± 0.3	depth x transect	4.4	0.007	
<i>Pairwise tests</i>		<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	<i>Significant term</i>	<i>Factor</i>	<i>Level</i>	<i>Groups tested</i>	<i>t</i>	<i>P</i>	
		depth x transect	transect	Co	6, 27	14.9	0.0112	depth x transect	transect	Ma	13, 34	6.5	0.0226	
		depth x transect	transect	Co	6, 34	15.7	0.0121	depth x transect	transect	Su	6, 34	12.7	0.0112	
		depth x transect	transect	Co	13, 27	7.8	0.0189	depth x transect	transect	Su	13, 34	9.8	0.0108	
		depth x transect	transect	Co	13, 34	8.6	0.0113	depth x transect	transect	Su	20, 34	12.1	0.0108	
		depth x transect	transect	Co	20, 27	8.8	0.011	depth x transect	transect	Su	27, 34	7.3	0.0202	
		depth x transect	transect	Co	20, 34	9.7	0.0113	depth x transect	depth	6	Co, Ma	7.1091	0.0251	
		depth x transect	transect	Ma	6, 13	8.8	0.0095	depth x transect	depth	6	Ma, Su	5.8036	0.0341	
		depth x transect	transect	Ma	6, 27	5.8	0.0235	depth x transect	depth	27	Co, Su	7.1151	0.0224	

unimodal distribution of species along environmental gradients, biological and physical boundaries of benthic communities are not strict and gradual shifts between communities exist. As such, the *transition assemblage* can be seen as a 'hybrid' assemblage, representing the shift between the *coastal* and the *offshore* epibenthic communities. This *transition assemblage* contained a mix of species of secondary importance in both other assemblages, but was mainly characterized by the absence of seabob shrimp *X. kroyeri*.

Next to a clear on-offshore gradient, also some differences could be noted going from west to east, both in environmental parameters and the epibenthic communities. In the *coastal assemblage*, species diversity increased from east to west, while the *offshore assemblage* in the west (Co-transect) was characterized by higher average epibenthic densities and biomasses compared to the Su-transect. Moreover, we could discern three clear epibenthic assemblages along both Co- and Su-transects, while in the east (Ma-transect) the *transition assemblage* was located deeper and no offshore assemblage could be delineated. This seems to be related to the bathymetry and geomorphology of the coastal shelf in Suriname. The zones in the east are wider compared to the more squeezed coastal shelf in the west, meaning that the *offshore assemblage* in the east will probably be located more offshore between the 40 and 50 m isobaths.

4.2. Temporal variability

As expected, peak outflow of the domestic rivers in Suriname coincided with peak Amazon discharge, at times of maximum supply of Amazon water to the coasts of the Guianas through the Guiana Current (Hellweger and Gordon, 2002). Elevated sub-surface total suspended matter and chlorophyll *a* indicated a clear river-influence during the rainy season (Smith and Demaster, 1996). However, seasonal fluctuations in the coastal environment did not affect species composition and abundance in the *coastal* or *transition assemblages*. In shallow waters under direct influence of river-runoff the water column is assumed to be fully mixed and to transfer warm and low saline surface water to the bottom (e.g. Pacanowski and Philander, 1981). Moreover, population dynamics of penaeid shrimps, like the dominant seabob shrimp *X. kroyeri*, are known to be related to seasonality in freshwater input (e.g. Galindo-Bect et al., 2000). Therefore, at least for the *coastal assemblage* we expected some seasonal influence on the epibenthos.

Most probably the benthos is more likely to respond to changes in bottom-water properties (Pires, 1992), while only (sub-)surface water parameters were available. On the other hand, Longhurst and Pauly (1987) suggested that interannual changes in species composition and relative abundance are more important than seasonal changes within tropical coastal marine ecosystems.

4.3. Implications for management

The fact that benthic communities respond to their environment is well known (e.g., Gray, 2002), and the present study largely confirms the results from epibenthic studies in neighboring French-Guyana (Durand, 1959; Guéguen, 2000; Le Loeuff and Cosel, 2000). Still, detailed *in-situ* information on benthic communities is needed as a sound basis for local marine management.

Commercial shrimp fisheries in Suriname shifted to shallower waters targeting *X. kroyeri* after the decline of more valuable deep-water species (*Penaeus* spp.). Also in other countries, *X. kroyeri* has become increasingly important as a fisheries resource in recent decades (FAO, 2014). The present study showed that the epibenthic community in the coastal waters of Suriname was structured by an environmental inshore to offshore gradient, and that *X. kroyeri* was highly abundant in muddy substrates, which harbor a species-poor epibenthic community without habitat-structuring species. In this environment, the physical impact of commercial shrimp outrigger trawls is expected to be low. Nevertheless, removing large quantities of *X. kroyeri* can impact the ecosystem by affecting an important link in the coastal food web (e.g. Abarca-Arenas et al., 2007). *X. kroyeri* feeds at a low trophic level, on benthic detritus, microalgae and crustaceans (Branco, 2005; Cortés and Criales, 1990; Kerkhove, 2014), while the species itself constitutes staple food for demersal fishes (Camargo and Isaac, 2004; Quilez, 2014). As such, populations of *X. kroyeri* are probably crucial for energy transfer within the coastal food web, as has been shown for other penaeid shrimp (Abarca-Arenas et al., 2007). Moreover, *X. kroyeri* was found to strongly contribute to the existence and maintenance of benthic communities in southeastern Brazil (Pires, 1992). Whereas this stabilizing role was seasonally taken over by the swimming crab *Portunus spinicarpus* in response to variation in water masses (Pires, 1992), it might be played year-round by *X. kroyeri* on the Suriname Shelf.

Because the benthic communities on the inner Suriname Shelf

Table A2

Results from three-way Permanova analyses of species composition and abundance within clusters (assemblages) using factors 'depth', 'transect' and 'season'. The analysis was based on a Bray-Curtis similarity index constructed of fourth-root transformed epibenthos abundance data of the stations classified within a cluster. Only significant results ($p < 0.05$) are shown.

Within-cluster pairwise tests of epibenthic species composition and abundance						
Assemblage	Significant term	Factor	Level	Groups tested	<i>t</i>	<i>P</i>
Coastal	depth x transect	transect	Co	6, 20	1.8232	0.0135
Coastal	depth x transect	transect	Co	6, 27	2.1138	0.0148
Coastal	depth x transect	transect	Co	13, 27	1.697	0.0183
Coastal	depth x transect	transect	Ma	6, 27	2.188	0.0055
Coastal	depth x transect	transect	Ma	13, 27	2.6091	0.0009
Coastal	depth x transect	transect	Ma	20, 27	1.7222	0.024
Coastal	depth x transect	transect	Su	6, 13	1.8153	0.0093
Coastal	depth x transect	transect	Su	6, 20	1.9347	0.0018
Coastal	depth x transect	depth	6	Co, Ma	2.2564	0.0035
Coastal	depth x transect	depth	6	Co, Su	3.1732	0.0002
Coastal	depth x transect	depth	6	Ma, Su	2.6221	0.0002
Coastal	depth x transect	depth	13	Co, Ma	2.4978	0.0006
Coastal	depth x transect	depth	13	Ma, Su	1.8611	0.0157
Coastal	depth x transect	depth	20	Co, Ma	2.0637	0.0053
Coastal	depth x transect	depth	20	Ma, Su	2.1537	0.002
Coastal	depth x transect	depth	27	Ma, Su	1.62	0.0317
Transition	transect	transect	–	Co, Ma	1.9024	0.0038
Transition	transect	transect	–	Ma, Su	2.185	0.0008

Table B2

Results from three-way Permanova analyses of species composition and abundance within clusters (assemblages) using factors 'depth', 'transect' and 'season'. The analysis was based on a Bray–Curtis similarity index constructed of fourth-root transformed epibenthos abundance data of the stations classified within a cluster. Only significant results ($p < 0.05$) are shown.

Within-cluster pairwise tests of univariate parameters							
Parameter	Assemblage	Significant term	Factor	Level	Groups tested	<i>t</i>	<i>P</i>
	Coastal	depth x transect	transect	Co	6, 27	4.0846	0.017
<i>H'</i>	Coastal	depth x transect	transect	Co	13, 27	3.1359	0.0137
<i>H'</i>	Coastal	depth x transect	transect	Su	6, 13	3.0132	0.0036
<i>H'</i>	Coastal	depth x transect	transect	Su	13, 20	2.7408	0.015
<i>H'</i>	Coastal	depth x transect	transect	Su	13, 27	3.8441	0.0021
<i>H'</i>	Coastal	depth x transect	depth	6	Ma, Su	2.6334	0.0195
<i>H'</i>	Coastal	depth x transect	depth	13	Co, Ma	2.7005	0.0136
<i>H'</i>	Coastal	depth x transect	depth	13	Co, Su	2.3157	0.0306
<i>H'</i>	Coastal	depth x transect	depth	27	Co, Su	22.196	0.0392
<i>H'</i>	Coastal	depth x transect	depth	27	Co, Ma	3.3046	0.0221
<i>H'</i>	Coastal	transect x season	season	rainy	Co, Ma	4.3618	0.0006
<i>H'</i>	Coastal	transect x season	season	rainy	Ma, Su	2.6654	0.0108
<i>H'</i>	Coastal	transect x season	transect	Co	dry, rainy	3.3433	0.006
<i>J'</i>	Coastal	season	season	–	dry, rainy	2.234	0.0346
<i>J'</i>	Transition	transect	transect	–	Co, Ma	2.2667	0.0403
<i>J'</i>	Transition	transect	transect	–	Co, Su	2.3128	0.0407
<i>J'</i>	Transition	transect	transect	–	Ma, Su	5.9968	0.0001
<i>S</i>	Coastal	depth	depth	–	6, 13	2.3238	0.0244
<i>S</i>	Coastal	depth	depth	–	6, 20	4.3931	0.0003
<i>S</i>	Coastal	depth	depth	–	6, 27	5.2934	0.0002
<i>S</i>	Coastal	depth	depth	–	13, 20	2.4913	0.0146
<i>S</i>	Coastal	depth	depth	–	13, 27	3.4549	0.0016
<i>S</i>	Coastal	transect	transect	–	Co, Ma	4.5813	0.0001
<i>S</i>	Coastal	transect	transect	–	Co, Su	2.5691	0.0178
<i>S</i>	Coastal	transect	transect	–	Ma, Su	2.4324	0.0176
<i>S</i>	Transition	transect	transect	–	Co, Ma	2.6557	0.0208
<i>S</i>	Transition	transect	transect	–	Ma, Su	3.4864	0.0052
<i>B</i>	Offshore	transect	transect	–	Co, Su	2.4047	0.027

were mainly spatially structured, with little temporal variation, spatial management measures are likely to be more effective than temporal restrictions. The current ban on all demersal trawl fisheries below 18 m depth indeed seems a valid management measure to ensure the integrity of the coastal food web and to protect demersal fish recruits (Willems et al., Submitted for publication). Still, indirect (trophic) effects of intensive *X. kroyeri* fisheries beyond 18 m depth might occur. Furthermore, the current study only considered adult *X. kroyeri*, while temporal patterns are likely to be important within the younger life stages (Torrez, 2015). Information on the life cycle and ecological role of *X. kroyeri* within the coastal food web of the Suriname Shelf is therefore needed to support an ecosystem-based fisheries management.

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Appendix

See appendix Table A1 and A2, Table B2.

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