Trophic ecology of Atlantic seabob shrimp *Xiphopenaeus kroyeri*: Intertidal benthic microalgae support the subtidal food web off Suriname

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ABSTRACT

A combination of stomach content analyses and dual stable isotope analyses was used to reveal the trophic ecology of Atlantic seabob shrimp *Xiphopenaeus kroyeri* off the coast of Suriname. This coastal penaeid shrimp species has a rather omnivorous diet, feeding opportunistically on both animal prey and primary food sources. The species is a predator of hyperbenthic crustaceans, including copepods, amphipods and the luciferid shrimp *Lucifer faxoni*, which are mainly preyed upon during daytime, when these prey typically reside near the seabed. Benthic microalgae (BM) from intertidal mudflats and offshore sedimentary organic matter (SOM) were important primary food sources. Due to their depleted ^{13}C values, coastal sedimentary and suspended organic matter, and carbon from riverine and mangrove-derived detritus were not incorporated by *X. kroyeri*. An ontogenetic diet shift was observed from postlavae to juveniles and adults. Adult *X. kroyeri* were located higher in the food chain, mainly preying on larger benthic organisms. Intertidal BM were an important food source for all life stages of *X. kroyeri*, contributing up to 64% to the overall diet based on a Bayesian mixing model. Because *X. kroyeri* is the main epibenthic organism found at high densities in nearshore waters up to 30 m depth, the species plays a crucial role in transferring energy from low trophic level prey and primary food sources up to higher levels in the food chain. Our results indicate that primary production on intertidal mudflats, through BM, forms an important energy source for the subtidal turbid-water food web in muddy tropical coasts. Conservation of intertidal areas and their associated mangrove systems will therefore likely benefit coastal shrimp production and fisheries in tropical ecosystems.

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1. Introduction

River-influenced muddy shorelines with mangrove systems represent a major biome in the tropics, characterizing more than 75% of the world's coastline between 25°N and 25°S (Flemming, 2002). The adjacent shelf waters often constitute productive environments related to the input of organic matter and nutrients from various sources (Bouillon and Connolly, 2009). River runoff and litter fall from mangrove forests provide terrestrial detritus (Robertson and Alongi, 1995), while riverine nutrient input invokes a high phytoplankton production in the offshore zone adjacent to the turbid nearshore waters (e.g. Smith and Demaster, 1996). Deposition of riverine sediments can create extensive bare intertidal mudflats (e.g. Augustinus, 2004), allowing for a significant primary production of benthic microalgae (MacIntyre et al., 1996).

Penaeid shrimps (Decapoda: Penaeoidea) are a major component of the benthos occupying soft-bottom habitats of tropical shelves (Alongi, 1989; Longhurst and Pauly, 1987). Their exploitation by industrial and artisanal fisheries worldwide, with an annual catch of ca. 1.3 million tons, provides income and employment for hundreds of thousands of fishers (Banks and Macfadyen, 2011). Penaeid shrimps are also known to play a key role in coastal food webs (e.g. Abarca-Arenas et al., 2007). They are low trophic level

consumers, feeding on detritus, plant material and small benthic animals (Dall et al., 1990). On the other side, penaeid shrimps pass energy to the higher trophic levels as they are heavily preyed upon by demersal fishes (e.g. Salini et al., 1994), including commercially important fish species (Manickchand-Heileman et al., 1998).

Atlantic seabob *Xiphopenaeus kroyeri* is a rather small penaeid shrimp, widely distributed in the Western Atlantic, from North Carolina (USA) through the Gulf of Mexico and Caribbean Sea to Southern Brazil (Holthuis, 1980). Adult *X. kroyeri* populations live in estuarine and shallow nearshore waters, characterized by fine substrates (Freire et al., 2011; Costa et al., 2007). This in contrast to other penaeid shrimps in the region (mainly *Penaeus sp.*), which are typically found further offshore (Villegas and Dragovich, 1984). *Xiphopenaeus kroyeri* can be very abundant, and locally constitutes the single dominant epifaunal organism up to ca. 30 m depth (e.g. Willems et al., 2015; Guéguen, 2000). This makes it an accessible resource for coastal fisheries, being one of the main target species for artisanal fisheries in southern Brazil (Silva et al., 2013; Branco, 2005). In recent decades commercial shrimp trawling has shown increasing interest in *X. kroyeri*, as *Penaeus sp.* stocks further offshore have been largely overexploited (e.g. Chin-A-Lin and IJspol, 2000). This caused a considerable increase in global landings of *X. kroyeri* from ca. 11.000 t in 1990 to nearly 50.000 t in 2013, making it one of the top ten most caught penaeid shrimps in the world (FAO, 2014; Silva et al., 2013).

Given its importance for fisheries, several aspects on the ecology (e.g. Simoes et al., 2010; Castilho et al., 2008; Costa et al., 2007), reproductive biology (e.g. Castilho et al., 2015; Heckler et al., 2013a), population dynamics (e.g. Heckler et al., 2013b; Castro et al., 2005), and population genetics (Gusmao et al., 2006, 2013) of *X. kroyeri* have already been studied. However, whereas this shrimp species is known to contribute to the diet of demersal coastal fishes (Camargo and Isaac, 2004), its general importance for higher trophic levels remains unassessed. Moreover, except for three studies that assessed the diet of *X. kroyeri* by means of stomach content analyses (Branco and Junior, 2001; Tararam et al., 1993; Cortés and Criales, 1990), little attention has been given to the trophic interactions between *X. kroyeri* and potential food sources in the environment. The three studies mentioned above show that the trophic spectrum of *X. kroyeri* exists of more than 30 different prey types, mainly benthic crustaceans. Dependent on the study, unidentifiable organic matter occurred in 13–100% of the analysed stomachs, which raises the question on the real primary food sources for *X. kroyeri*.

The currently available information does not allow to clearly understand the trophic ecology, and hence the ecological role of *X. kroyeri* in tropical coastal food webs. Many penaeid shrimps have complex life cycles, undertaking in-offshore migrations and changing habitats and food sources as they grow from postlarvae to adults (Stoner and Zimmerman, 1988). Understanding these ecological interactions is key in an ecosystem approach for fisheries (Cury et al., 2005). An increased knowledge on the species' trophic ecology may help predicting the potential effect of environmental changes on food availability, and on the subsequent recruitment success and yield for shrimp fisheries (e.g. Pinnegar et al., 2000).

The current study aimed to assess the trophic ecology of *X. kroyeri* on the inner continental shelf of Suriname, an area with muddy nearshore deposits and mangrove coasts, and strongly influenced by riverine input. The objectives were to reveal (1) which of the multiple potential food sources in the area are ingested and assimilated by *X. kroyeri,* and (2) whether food sources change or differ between postlarvae, juvenile and adult shrimps. To reveal basic dietary information on what prey are ingested, stomach content analyses were conducted on adult *X. kroyeri*. Stomach content analysis is an easy and straightforward method for diet

studies (Baker et al., 2014), and has been successfully applied to penaeid shrimp (Albertoni et al., 2003), including *X. kroyeri* (Branco and Junior, 2001). However, stomach analysis only provides a 'snapshot' of the diet. It does not allow identifying the food sources that are really assimilated in body tissue, nor allows revealing the origin of organic matter in the shrimp stomachs (Lin et al., 2007). Stomach content analyses were therefore complemented with stable isotope analyses (France, 1998). The combined analysis of the carbon (C) and nitrogen (N) stable isotopes (SI) has been successfully used to identify the dynamics of food webs, including the estimation of the trophic position of different ecosystem components and the identification of carbon sources fuelling coastal food webs (e.g. Boecklen et al., 2011; Peterson, 1999). Moreover, SI analysis allows for the identification of the food sources of postlarvae and juvenile *X. kroyeri*, which are too small for stomach content analysis. In this study, we compared the carbon (C) and nitrogen (N) SI composition of *X. kroyeri* adults, juveniles and postlarvae with the C-N composition of several potential food sources, including primary sources, such as sedimentary organic matter, suspended particulate organic matter, leaf litter and benthic microalgae, and secondary animal prey sources, *i.e.* macrobenthos, hyperbenthos and zooplankton.

2. Materials and methods

2.1. Study area

The study was conducted on the inner Suriname Shelf (54–57 °W, 6–7 °N, Fig. 1), situated in the Guianan Ecoregion of the North Brazil Shelf Province (Spalding et al., 2007). The area is characterized by a wide and gently sloping continental shelve and is profoundly influenced by the turbid freshwater discharge from the Amazon River (Heileman, 2008). Amazon water is carried northwest to the Suriname coast by the North Brazil Current and its extension, the Guiana Current (Hellweger and Gordon, 2002; Johns et al., 1998). Amazon-borne sediments with a mud-content (<63 μm) of 95–100% and a total organic carbon content (TOC) of 1% dominate the inner shelf deposits up to 20 m depth (Willems et al., 2015; Augustinus, 2004; Eisma et al., 1991). Mud resuspension by tides and currents causes turbid nearshore waters, with total suspended matter concentrations up to 150 g m^{-3}. Beyond the 20 m depth contour, coarser sediments (median grain size >300 μm; TOC <0.5%) gradually become more dominant and water turbidity decreases (Willems et al., 2015). The combination of increased irradiance and coastal nutrient input allows for a high offshore primary production between 20 and 50 km from the coast (Cadée, 1975). Most rainfall in Suriname, and peak discharge of both the Amazon and local rivers, occurs between December and July (Hu et al., 2004; Amatali, 1993). Typical values of salinity and surface temperature of the coastal waters measure around 35 and 28 °C, respectively (Willems et al., 2015).

2.2. Sample collection

Xiphopenaeus kroyeri (both for stomach content and SI analyses) and potential food sources (for SI analyses) were sampled during three different campaigns on board FV *Neptune 6*. Adult *X. kroyeri* and three potential food sources were collected on two surveys in April and July 2012, at six locations across the inner Suriname Shelf (6 and 20 m depth, three transects near the outflow of the Coppename, Suriname and Maroni River) (see Willems et al., 2015) (Fig. 1). Additionally, a full depth gradient was sampled in February 2014 near the outflow of the Suriname River (SU03, 10, 17 and 24), to collect different *X. kroyeri* life stages (adults, juveniles and postlarvae), and the other potential food sources. As well in
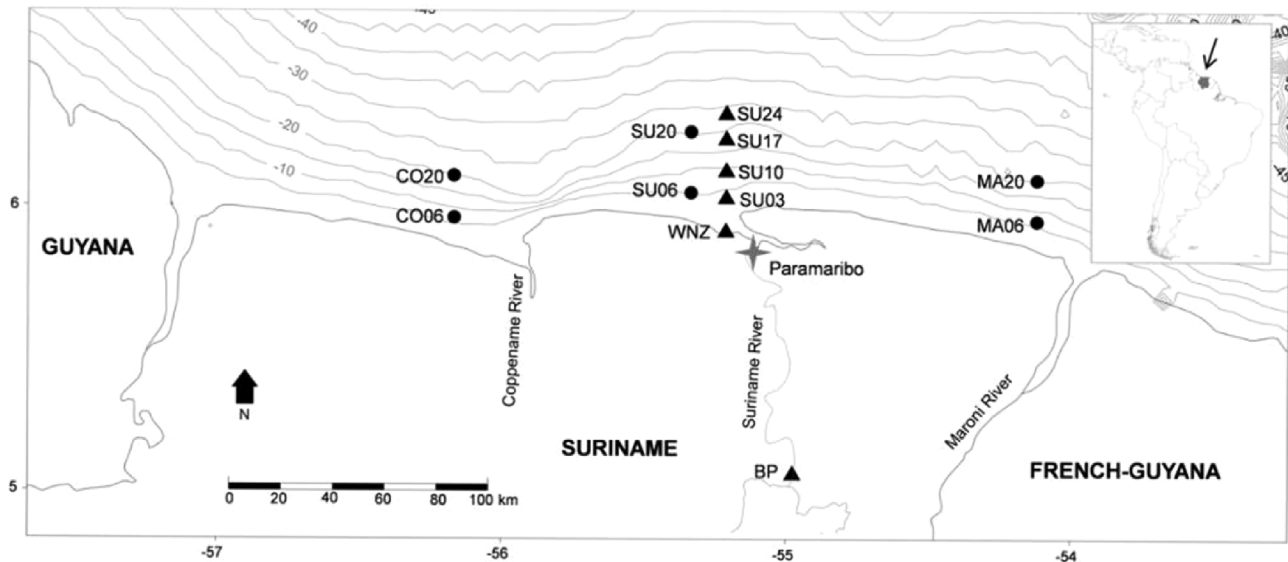
Fig. 1. Map of the study area with indication of the sampling locations. Circles indicate 2012-samples, triangles 2014-samples. Numbers in the sample station codes denote approximate water depth. WNZ and BP are land-based locations sampled for potential intertidal and terrestrial food sources.

February 2014, two land based locations (WNZ and BP) were sampled for potential intertidal and terrestrial food sources (Fig. 1). Table 1 gives an overview of the different samples taken at each location.

Xiphopenaeus kroyeri adults (both for stomach content and SI analyses) were sampled using a small demersal shrimp otter trawl (2.6 m door spread; 45 mm codend mesh size). Individuals were considered adult when the petasma was fused (males) (Fransozo et al., 2011) or when the carapace length (including rostrum) exceeded 33 mm (females) (de Campos et al., 2009). Individuals for stomach content analyses were preserved in a buffered 4% formaldehyde solution on board, while samples for SI analyses were immediately frozen (−20 °C).

A hyperbenthic sledge (1 mm mesh size) was used to sample juvenile and postlarval stages of *X. kroyeri,* and to collect potential hyperbenthic food sources (both for SI analysis). The entire hyperbenthic sample was immediately stored frozen (−20 °C) on board until further processing.

Other potential food sources that were collected for SI analysis on the different surveys included (Table 1; Fig. 1):

- Macrobenthos; sampled with a Van Veen grab (0.1 m^2), and obtained by on board sieving of the sediment on a 1 mm mesh sieve;
- Zooplankton; collected by towing a bongo net (200 μm mesh size) in the upper water column;
- Leaf litter; picked out (2—5 leaves) from the trawl catches when present, and further collected from intertidal mud flats at location WNZ;
- Sedimentary Organic Matter (SOM); sampled by scraping off the top 5 mm of seabed sediment samples collected with a Van Veen grab;
- Suspended Particulate Organic Matter (sPOM); seawater sampled at 5 m water depth with a Niskin-bottle; sPOM obtained by filtering 0.3—1 l of seawater onto Whatman GF/F glass-fiber filters;
- Riverine sPOM; river water collected upstream the Suriname River at location BP; riverine sPOM similarly obtained by filtering river water onto Whatman GF/F glass-fiber filters;
- Benthic microalgae (BM); sampled on a coastal mudflat at location WNZ following an adapted method proposed by Couch (1989) by scraping off the top layer of intertidal mud in the field

Table 1
Overview of sample collection for SI analysis. XK = *Xiphopenaeus kroyeri* (AD = adult; JV = juvenile; PL = postlarva), SOM = sedimentary organic matter, sPOM = suspended particulate organic matter, LL = leaf litter; MB = macrobenthos, HB = hyperbenthos, ZP = zooplankton, BM = benthic microalgae.

Area	Station	Coordinates		Description	April 2012	July 2012	February 2014
		°N	°W				
Brokopondo	BP	5.06	54.98	riverine			sPOM
Weg naar Zee	WNZ	5.91	55.21	intertidal			LL, BM
Maroni estuary	MA06	5.95	54.12	coastal	XK-AD, SOM, sPOM, LL	XK-AD[b], sPOM, LL	
	MA20	6.15	54.12	coastal	XK-AD, SOM, sPOM, LL	XK-AD[b], sPOM, LL	
Coppename estuary	CO06	5.96	56.17	coastal	XK-AD, SOM, sPOM, LL	XK-AD[b], sPOM, LL	
	CO20	6.06	56.17	coastal	XK-AD, SOM, sPOM, LL	XK-AD[b], sPOM, LL	
Suriname estuary	SU06	6.13	55.34	coastal	XK-AD, SOM, sPOM, LL	XK-AD[b], sPOM, LL	
	SU20	6.26	55.34	coastal	XK-AD, SOM, sPOM, LL	XK-AD[b], sPOM, LL	
	SU03	6.03	55.21	coastal			XK-AD, SOM, sPOM, MB, HB, ZP
	SU10	6.16	55.21	coastal			XK-AD, MB, HB, ZP
	SU17	6.23	55.21	coastal			XK-AD[b], XK-JV, XK-PL, MB, HB, ZP
	SU24	6.30	55.21	offshore[a]			XK-AD[b], SOM, sPOM, MB, HB, ZP

[a] Offshore abiotic conditions dominate from >20 m depth onwards (Willems et al., 2015b).
[b] Samples for both SI analysis and stomach analysis.

and spreading this out in plastic trays for transportation to the lab.

All potential food sources (except for BM) were immediately frozen at −20 °C upon collection, which is a widely accepted preservation method (Barrow et al., 2008; Kaehler and Pakhomov, 2001; Bosley and Wainright, 1999).

2.3. Lab analyses

2.3.1. Stomach content analysis

Stomach content analyses were conducted on 120 adult *X. kroyeri* by randomly selecting 10 individuals from the six July 2012 hauls and 30 individuals from two February 2014 hauls (SU03 and SU10 yielded too few individuals). Carapace length was measured with a calliper to the nearest mm before the stomach was removed by a latero-dorsal cut in the carapace. Stomach content was suspended in a Petri dish with distilled water and all food items in the stomach were identified using a binocular microscope to the lowest taxonomic level possible. The 'points method' was used to assign a relative volumetric contribution (%) to each prey type in the stomachs (Williams, 1981; Hyslop, 1980; Hynes, 1950).

2.3.2. Stable isotope analysis

SI analyses were performed on the different life stages of *X. kroyeri* and the sampled potential food sources. The frozen samples of adult *X. kroyeri*, as well as the hyperbenthos, macro-benthos and zooplankton samples, were thawed and subsequently sorted using a binocular microscope (within 2 h to avoid label leakage; e. g Moens et al., 1999). Postlarvae of *X. kroyeri* were identified from the hyperbenthos samples using the keys by Cook (1964) and Lins-Oliveira and Lhomme (1993). Individuals of *X. kroyeri* >25 mm total length, but still lacking adult characteristics were considered juvenile (Cook, 1964). Juvenile and postlarval *X. kroyeri* were only encountered in sufficient densities in the SU17-sample.

Potential food sources for *X. kroyeri* from the hyperbenthos samples included amphipods, copepods, chaetognaths, fish larvae, brachyuran zoeae, *Acetes sp.* and *Lucifer faxoni* (the latter discriminated as they were highly abundant species) Potential macro-benthos food sources were sorted to the taxonomic level of sipunculids, polychaetes, bivalves, amphipods and brachyurans. From the zooplankton samples only copepods were retained as potential food source. Only the samples in which a certain taxonomic group (or food source) was found to be highly abundant were selected for further processing.

After sorting, bivalve shells and exoskeletons of *X. kroyeri* and *Acetes sp.* were removed to obtain carbonate-free muscle tissue (Mateo et al., 2008). Next, all samples were rinsed with Milli-Q water and dried for 24 h at 60 °C. Peeling was not feasible for smaller taxa. Therefore, the presence of carbonates was assessed with the 'champagne test' (Jaschinski et al., 2008): brachyurans and brachyuran zoeae were acidified by adding diluted HCl (4%) to the dried sample until bubbling ceased. For adult *X. kroyeri*, tissue of three individuals was used per sample, while for smaller organisms up to 50 individuals (from a single sample) were pooled to obtain enough material for SI analysis.

Leaf litter and SOM samples, and sPOM filters were thawed, rinsed with Milli-Q water and dried for 24 h at 60 °C. Inorganic carbon was removed from the SOM and leaf litter samples by adding diluted HCl (4%) to the dried sample until bubbling ceased (Fernandes and Krull, 2008; Carabel et al., 2006). sPOM filters were treated with HCl fumes (40%) for 5 h (Lorrain et al., 2003).

The trays with intertidal surface sediment were covered with a thin layer of *in situ* collected seawater and illuminated to allow the migration of benthic microalgae (BM) onto microscopic slides that were placed on top of the sediment with a lens tissue underneath the slide to avoid contamination with sediment. After 24 h, the slides were removed and washed with filtered seawater, which was then filtered onto Whatman GF/F filters to retain BM. The filters were subsequently rinsed with Milli-Q water and dried for 24 h at 60 °C (Couch, 1989).

All dry samples were grounded (except for GF/F filters) with mortar and pestle to homogeneous powder. From each sample, three aliquots (1.5 mg animal tissue, 3.8 mg leaf litter, 60 mg SOM, whole filters for sPOM and BM) were placed into tin (or silver in case of acidified samples) capsules (8 × 5 mm; Elemental Microanalysis). For the 2012 sPOM samples only single replicate GF/F filters were available. Multiwell plates containing all capsules were shipped to UC Davis Stable Isotope Facility (USA) for dual SI analyses (C, N) by means of a continuous flow isotope ratio mass spectrometer (Europa Integra). SI ratios are expressed as δ values where $\delta X = (R_{sample}/R_{standard}−1) \times 1000$ with X = ^{13}C or ^{15}N and R = ^{13}C/^{12}C or ^{15}N/^{14}N. Standard reference materials for C and N measurements are carbon in the Vienna Pee Dee Belemnite and atmospheric nitrogen (Peterson and Fry, 1987), respectively. δ^{13}C and δ^{15}N values were measured to 0.01‰ precision.

2.4. Data analyses

2.4.1. Stomach content data

From the stomach content analyses, the dietary composition for adult *X. kroyeri* was assessed by calculating frequency of occurrence (%FO) and volumetric abundance (%V) indices for all food items found in the stomachs (Hyslop, 1980):

$$\%FO_i = (N_i/N) \times 100$$

$$\%V = \left(\sum S_i \Big/ \sum S_a \right) \times 100$$

with N_i the number of stomachs containing prey type *i* and N the total number of non-empty stomachs, S_i the relative volumetric contribution of prey type *i* to the stomach content, and ΣS_a the total volumetric stomach content of all stomachs together (Amundsen et al., 1996).

Data on the proportional prey composition in each stomach were square-root transformed to reduce the influence of abundant prey types before calculating the resemblance matrices based on Bray − Curtis similarity index. The 2012-data (Table 1) were used to test for spatial differences in the adult diet with a one-way PERMANOVA (Permutational ANOVA; Anderson et al., 2008) for the factor 'area' (Coppename *vs.* Suriname *vs.* Maroni area; 20 stomachs for each area), with 'depth' as a random factor. Temporal differences in the adult diet were based on the 'Suriname area' data (Table 1) and tested with a one-way Permanova for the factor 'sampling date' (July 2012 (20 stomachs) *vs.* February 2014 (60 stomachs)). In case of significant effects, the contribution of the different prey types was investigated with one-way SIMPER analyses for the respective factors.

2.4.2. Stable isotope data

Average (±SD) SI composition of the different *X. kroyeri* life stages and the potential food sources were visualized by means of C-N biplots.

To test for spatial and temporal differences in the C and N SI composition of adult *X. kroyeri,* Euclidean distance similarity matrices were calculated from the δ^{13}C and δ^{15}N adult datasets. Spatial differences in C and N SI composition of adult *X. kroyeri* were tested on the 2012-data, using one-way PERMANOVA for the factor

'area' (CO *vs.* SU *vs.* MA area; n = 12 per area), with 'depth' as a random factor. Temporal differences in adult C and N SI composition were based on the 'Suriname area' data, using one-way PERMANOVA for the factor 'sampling date' (April 2012 (n = 6) *vs.* July 2012 (n = 6) *vs.* February 2014 (n = 12)).

To test for differences in C and N SI composition between the different life stages of *X. kroyeri,* Euclidean distance similarity matrices were calculated from the bivariate δ^{13}C and δ^{15}N datasets for all processed *X. kroyeri.* One-way PERMANOVA tests were performed using the factor 'life stage' (adult (n = 48) *vs.* Juvenile (n = 5) *vs.* Postlarvae (n = 6)). In each PERMANOVA analysis, the main test was followed by pairwise tests in case of signicant effects.

Bayesian stable isotope mixing models (Parnell et al., 2010) were further applied to estimate the likely contribution of each food source to the diet of *X. kroyeri* adults, juveniles and postlarvae, using SIAR v4 (stable isotope analysis in R). As input in the models, only a limited number of the potential food sources were used. A first selection criterion was based on the fact that the carbon isotope signal of a consumer closely resembles its food sources (Kohn, 1999), with only a small fractionation per trophic level (Post, 2002). Therefore, the potential food sources that deviated too much in δ^{13}C values from *X. kroyeri,* were omitted from the models as they obviously did not support any life stage of *X. kroyeri.* Secondly, functionally similar food sources with overlapping isotopic compositions were grouped (Phillips et al., 2005). As such, all animal food sources (*i.e.* the hyperbenthos, macrobenthos and zooplankton taxa) were analysed with a group-averaging hierarchical cluster analysis with SIMPROF tests (significance level 5%), based on the Euclidean distance resemblance matrix of their δ^{13}C and δ^{15}N values. Finally, correlations between the retained food sources were tested prior to running the models, as SIAR cannot differentiate between correlated (Pearson's r > 0.8) sources (Carreon-Palau et al., 2013; Parnell et al., 2010). Concentration dependence was incorporated in the SIAR models to account for differences in C-N ratios among food sources (Phillips and Koch, 2002). Mean ($\pm$SD) trophic enrichment factors of 0.4 $\pm$ 1.3 for δ^{13}C and 3.4 $\pm$ 1 for δ^{15}N were used (Post, 2002).

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. PERMANOVA-tests were conducted with unrestricted permutation of raw data in case of single-factor designs, and Monte Carlo corrections were applied when too few (<100) permutations could be calculated (Anderson and Robinson, 2003). In most cases, values are given as averages together with their standard deviation (SD), while contribution estimates in the mixed models are given as 95% credibility intervals.

3. Results

3.1. Stomach analyses

Carapace length of the analysed shrimp was on average 20.3 $\pm$ SD 3.0 mm, and ranged from 11 to 27 mm. Of the 120 analysed stomachs, three were empty. A total of 25 prey types were identified (Table 2). More than 50% of the prey types were relatively rare (%FO <10%). The most recurring prey types were organic detritus, sediment, copepods and unidentified crustaceans. Organic detritus accounted for ca. 50% of the diet in terms of volume, followed by Crustacea (sum $\approx$ 30%), plant material and sediment (6 and 7%, respectively) (Fig. 2).

Dietary composition of *X. kroyeri* did not differ significantly among the three sampled areas (Pseudo-F = 2.9; p = 0.14). On the other hand, a significant temporal effect was observed (Pseudo-F = 14.0; p = 0.0001), with an increased contribution of plant

Table 2
Frequency of occurrence (%FO) and volumetric contribution (%V) of the prey types in the diet of *Xiphopenaeus kroyeri*, based on 120 adult stomachs.

Prey type	%FO	%V
Organic detritus	100	48.6
Crustacea		
Unidentified sp.	63.3	12.5
Copepoda sp.	76.1	9.4
Amphipoda sp.	27.4	3.9
Lucifer faxoni	24.8	2.7
Ostracoda sp.	19.7	1.0
Acetes sp.	1.7	0.1
Cladocera sp.	1.7	0.1
Mysida sp./mysis larva	1.7	0.1
Xiphopenaeus kroyeri postlarva	0.9	0.03
Brachyura sp. Zoea larva	0.9	0.03
Sediment	83.8	7.4
Plant material	36.8	5.9
Sponge spicules	51.3	2.8
Diatomea sp.	29.1	1.4
Polychaeta sp.	17.1	1.2
Plastic fibres	12.8	0.7
Bryozoa sp.	4.3	0.6
Foraminifera sp.	9.4	0.5
Rotifera sp.	5.1	0.3
Radiolaria sp.	6.0	0.3
Insecta sp.	2.6	0.3
Bivalvia sp.	5.1	0.2
Pisces sp. Larva	1.7	0.1
Hydrozoa sp.	2.6	0.1

material and sediment in the 2012 samples, while Crustacea were more important in the 2014 samples (Fig. 2).

3.2. Stable isotope analyses

3.2.1. SI composition of Xiphopenaeus kroyeri

No spatial differences among areas were observed in neither δ^{13}C nor δ^{15}N of adult *X. kroyeri* (Pseudo-F = 1.9; p = 0.15 and Pseudo-F = 3.0; p = 0.06, respectively). δ^{13}C did not differ between sampling dates either (Pseudo-F = 1.2; p = 0.33), but δ^{15}N did (Pseudo-F = 14.5; p = 0.0001). Whereas adult *X. kroyeri* did not differ in δ^{15}N between the two 2012-surveys, both had a significantly higher δ^{15}N (avg. 11.2 $\pm$ 0.4‰) compared to the 2014-survey (avg. 10.3 $\pm$ 0.4‰) (pairwise tests, p < 0.01).

Both δ^{13}C and δ^{15}N differed significantly among *X. kroyeri* life stages (Pseudo-F = 54.3; p = 0.0001 and Pseudo-F = 44.4; p = 0.0001, respectively). All lifestages differed significantly in δ^{13}C. δ^{15}N values of adult *X. kroyeri* were significantly higher than both postlarvae and juveniles, but the latter two did not differ in δ^{15}N (pairwise tests, p < 0.01) (Table 3; Fig. 3).

3.2.2. SI composition of the potential food sources

The C-N SI composition of 21 potential food sources, including 8 primary sources and 13 animal prey taxa were identified (Table 3). Riverine sPOM and intertidal and coastal leaf litter showed low δ^{13}C values below −27‰, while coastal sPOM, offshore sPOM and coastal SOM had overlapping δ^{13}C values between −20 and −25‰. The primary sources that were less depleted in ^{13}C were BM (−16.2‰) and offshore SOM (−12‰) (Table 3; Fig. 3).

δ^{13}C values of hyperbenthos, macrobenthos and zooplankton prey taxa ranged from −20 to −16.3‰ (Table 3; Fig. 3). Cluster analysis distinguished two main groups with overlapping isotope signals, further classified as 'prey group 1' (hyperbenthic and planktonic copepods, bivalves, brachyurans, brachyuran zoeae, *Lucifer faxoni* and macrobenthic amphipods) and 'prey group 2' (hyperbenthic amphipods, sipunculids, fish larvae, chaetognaths, *Acetes sp.* and polychaetes) (Fig. 4).
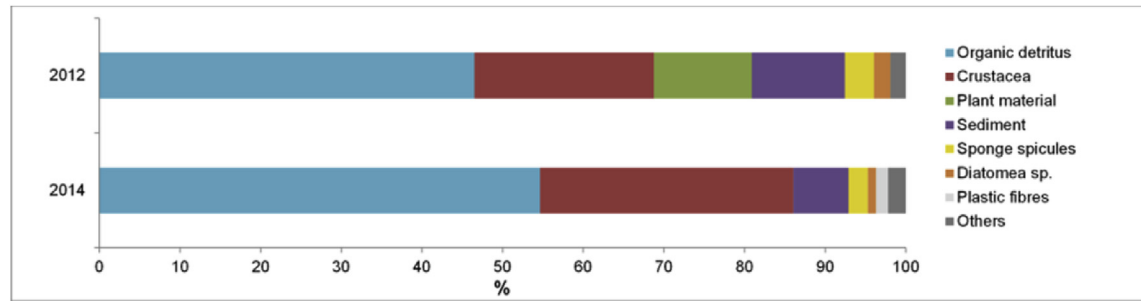
Fig. 2. Volumetric contribution (%V) of each prey type in stomachs of *Xiphopenaeus kroyeri* from the 'Suriname area' in 2012 and 2014. All crustaceans grouped and prey types with low contribution (<1%) lumped as 'Others'.

Table 3
Average (±SD) carbon and nitrogen SI composition and C-N ratios for different life stages of *Xiphopenaeus kroyeri* and their potential food sources.

Group/species	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C-N	n
Xiphopenaeus kroyeri				
Adult	-14.7 ± 0.2	10.8 ± 0.5	3.2 ± 0.0	48
Juvenile	-15.0 ± 0.2	9.5 ± 0.1	3.3 ± 0.1	5
Postlarvae	-15.7 ± 0.2	9.3 ± 0.2	3.5 ± 0.0	6
SOM				
coastal	-23.0 ± 1.2	6.2 ± 0.8	5.9 ± 0.7	21
offshore	-12.0 ± 0.2	5.4 ± 0.0	10.2 ± 0.2	3
sPOM				
Riverine	-33.1 ± 0.2	3.8 ± 0.2	8.5 ± 0.1	3
Coastal	-22.6 ± 1.4	5.2 ± 2.2	4.2 ± 1.5	15
Offshore	-22.7 ± 0.0	2.9 ± 0.8	5.2 ± 0.2	3
Leaf litter				
Intertidal	-27.0 ± 0.1	3.3 ± 0.0	27.6 ± 0.5	3
Coastal	-29.2 ± 1.9	6.5 ± 2.4	26.8 ± 11.2	24
Benthic microalgae				
Intertidal	-16.2 ± 0.1	6.5 ± 0.1	7.6 ± 0.2	3
Prey group 1				
Hyperbenthos				
Copepods	-19.0 ± 0.6	7.1 ± 0.4	4.5 ± 0.1	3
Lucifer faxoni	-20.0 ± 0.6	5.8 ± 0.1	7.4 ± 0.7	3
Brachyuran zoeae	-18.0 ± 0.9	5.2 ± 1.2	5.5 ± 0.5	3
Macrobenthos				
Amphipods	-17.7 ± 0.3	6.8 ± 0.1	7.6 ± 0.4	2
Bivalves	-18.2 ± 0.6	7.7 ± 0.4	4.6 ± 0.2	3
Brachyurans	-17.4 ± 0.2	7.0 ± 0.2	5.1 ± 0.2	3
Zooplankton				
Copepods	-18.3 ± 0.4	6.6 ± 0.6	4.5 ± 0.2	3
Prey group 2				
hyperbenthos				
Amphipods	-17.2 ± 0.5	8.2 ± 0.7	6.4 ± 0.5	3
Acetes sp.	-16.3 ± 0.0	9.3 ± 0.0	3.8 ± 0.0	3
Chaetognaths	-16.9 ± 0.1	9.1 ± 0.1	4.4 ± 0.0	3
Fish larvae	-17.2 ± 0.3	9.7 ± 0.2	3.8 ± 0.1	3
Macrobenthos				
Polychaetes	-17.4 ± 0.1	9.9 ± 0.0	4.6 ± 0.1	3
Sipunculids	-16.7 ± 1.3	8.7 ± 0.6	3.6 ± 0.2	3

3.2.3. SIAR mixing models

Except for BM and offshore SOM, the other primary sources were not considered to be food sources for any life stage of *X. kroyeri* (all $\delta^{13}C > -15.7$‰) because of their depleted $\delta^{13}C$ values below −20‰. As such, only four food sources were retained for the SIAR models: BM, offshore SOM, and prey groups 1 and 2 (Fig. 5). None of these were significantly correlated (Pearsons r < 0.8).

SI mixing models (Fig. 6) showed a rather similar diet for *X. kroyeri* postlarvae and juveniles, characterized by a contribution of BM between 4 and 64% (95% credibility interval), while prey group 1 and prey group 2 contributed 1–53%, and the contribution of offshore SOM ranged from 7 to 19%. The diet of adult *X. kroyeri* was characterized by high contributions of prey group 2 (28–50%)

and BM (23–49%), followed by offshore SOM (18–20%), and prey group 1 (0–15%) (Fig. 6).

4. Discussion

4.1. Trophic ecology of Xiphopenaeus kroyeri

The stomach content and stable isotope analyses pointed out that *X. kroyeri* has an omnivorous diet, feeding on both small benthic animals and primary food sources. Little spatio-temporal variation was observed in the diet of *X. kroyeri*, but an ontogenetic shift was apparent.

4.1.1. Spatio-temporal patterns in the diet of Xiphopenaeus kroyeri

Both stomach content analyses and the C-N SI composition indicated that adult *X. kroyeri* had a consistent diet across the study area, with no significant spatial differences. Willems et al. (2015) showed that the inner Suriname Shelf <20 m depth is characterized by a uniform, muddy seabed habitat with a single coastal epibenthic community. This suggests that probably little spatial variation will be present in the available food sources as well. On the other hand, some slight temporal patterns were observed. The 2012 stomachs contained relatively more plant material than the 2014 samples, possibly related to the higher availability of terrestrial plant material at the end of the long rainy season in July 2012 (Amatali, 1993). This suggests an opportunistic ingestion of food sources, which are readily available in the environment, as has been found for other penaeid shrimps as well (e.g. Nunes et al., 1997). The opportunistic feeding behaviour might also be the reason for the somewhat higher $\delta^{15}N$ signals of the 2012 versus 2014 SI composition of adult *X. kroyeri*. This difference, however, could also be caused by a general upward shift in $\delta^{15}N$ of (part of) the food web due to a temporal shift in primary producer $\delta^{15}N$. The lack of clear spatio-temporal patterns in the SI composition of adult *X. kroyeri* was supported by the stomach content analyses. This justifies the lumping of the SI composition data in the SIAR mixing models, independent of the spatial and temporal spread of the data.

In these mixing models, the widely-used trophic fractionation factors calculated by Post (2002) were used. Trophic fractionation is known to depend on a number of factors, including taxonomic group, the type of tissue and the SI composition value itself, with most variation occurring in the N-isotope (e.g. Caut et al., 2009; Vanderklift and Ponsard, 2003). Nevertheless, when rerunning the SIAR mixing models with two alternative scenarios for $\delta^{15}N$ fractionation (i.e. 2.4 ± 1 and 4.4 ± 1), the estimated contributions of the different food sources to *X. kroyeri* postlarvae, juveniles and adults were almost identical to the original model (with $\delta^{15}N$ fractionation of 3.4 ± 1).
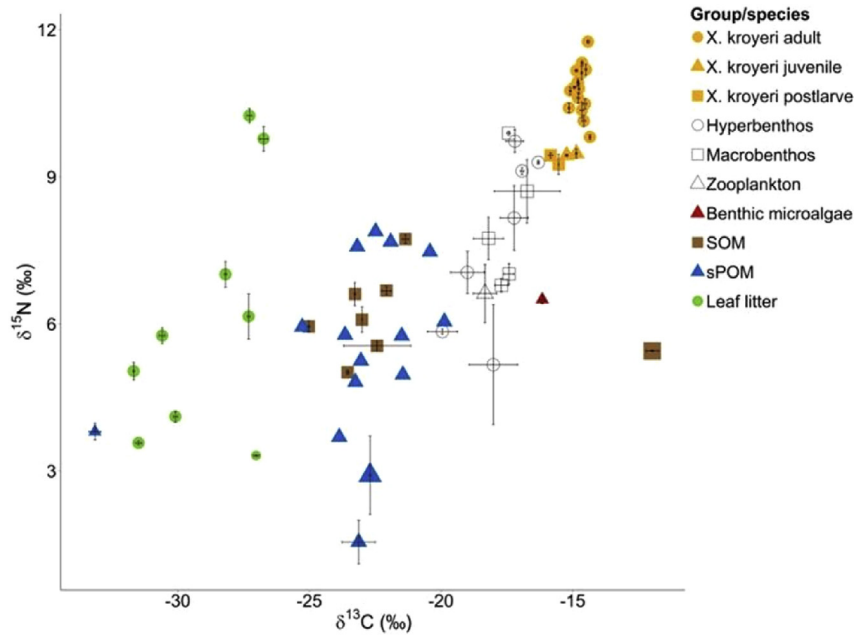
Fig. 3. C-N biplot representing average (±SD) values of carbon and nitrogen stable isotopes for different life stages of *Xiphopenaeus kroyeri* and their potential food sources. For the primary food sources, symbols of riverine/intertidal samples are plotted slightly smaller and offshore samples somewhat larger.
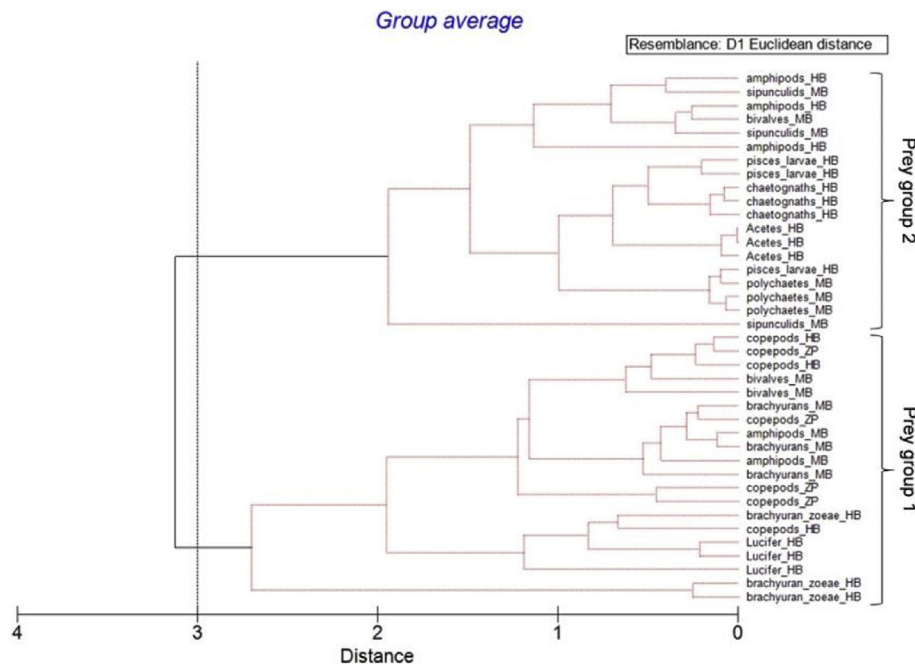

Fig. 4. Group-averaging cluster analysis of the Euclidean distance resemblance matrix based on the carbon and nitrogen stable isotope composition of macrobenthos (MB), hyperbenthos (HB) and zooplankton (ZP) food sources. Significant clusters (SIMPROF test 5% significance level) are indicated by the coloured (red) lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1.2. Ontogenetic diet shift

Postlarvae, juveniles and adults of *X. kroyeri* had a different SI composition, indicating an ontogenetic shift in the diet. Postlarvae and juveniles (δ^{15}N = 9.3 and 9.5‰) were situated lower in the food chain than adults (δ^{15}N = 10.8‰). Comparing the SI mixing models for the three life stages, a shift was observed towards the adult stage from lower to higher trophic level prey organisms, as judged from the δ^{15}N values of the prey (Post, 2002). Prey group 2 organisms (δ^{15}N ≈ 9‰) such as chaetognaths, fish larvae and *Acetes*

sp. were probably either too large or too mobile to be preyed upon by postlarval and juvenile *X. kroyeri*. Both life stages mainly fed on smaller prey from prey group 1 (δ^{15}N ≈ 6.5‰), such as bivalves, copepods and *Lucifer faxoni*. Furthermore, the contribution of offshore SOM was highest in adult *X. kroyeri*. This supports the fact that, like in other penaeid shrimps (Dall et al., 1990), adult *X. kroyeri* live further offshore while younger life stages reside more in very shallow nearshore waters (Oliveira, 1991).
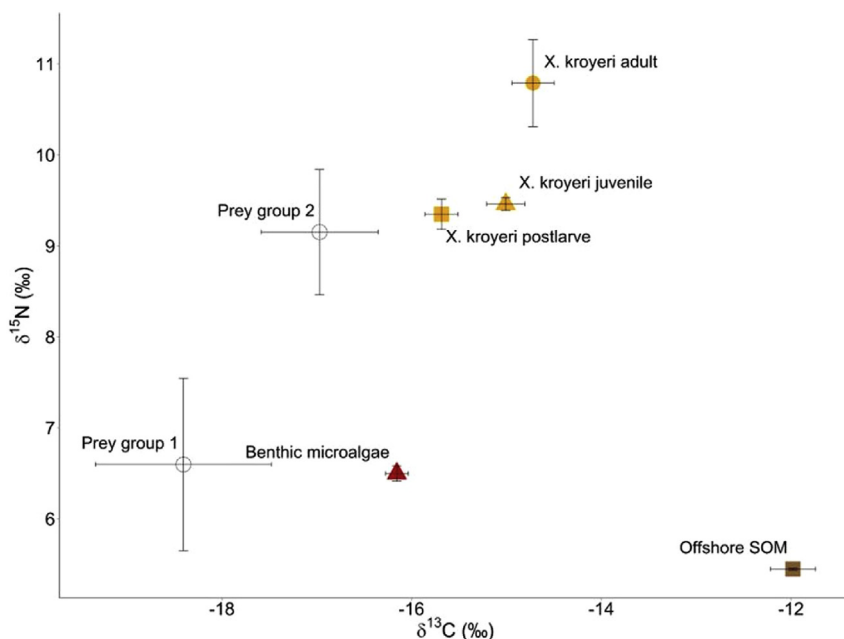
Fig. 5. C–N biplot representing average (±SD) values of carbon and nitrogen stable isotopes for different life stages of *Xiphopenaeus kroyeri* and the potential food sources retained in the SI mixing models.
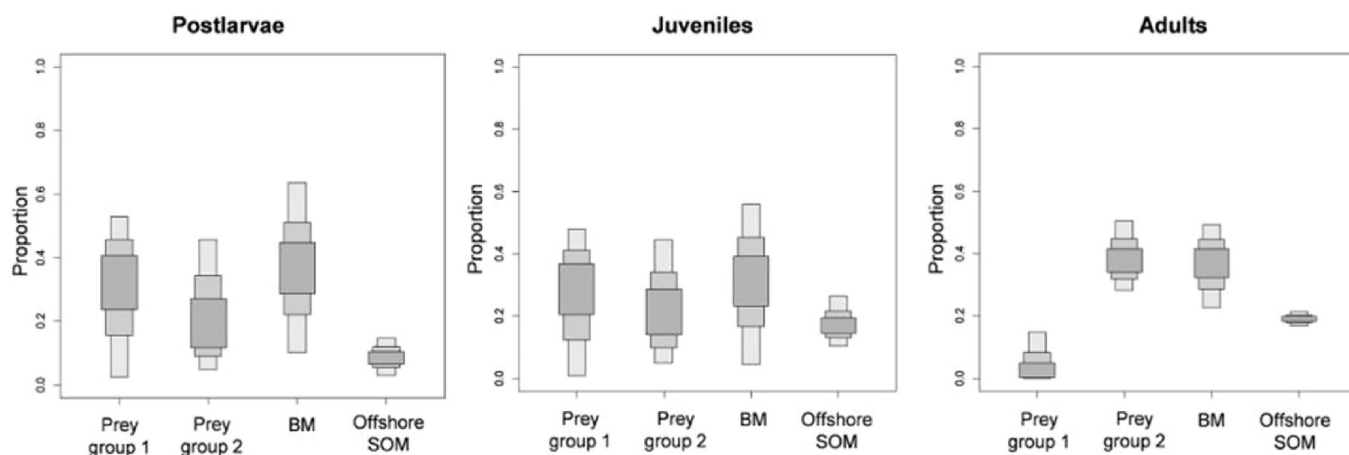
Fig. 6. Modelled contribution of the potential food sources to the diet of postlarvae, juvenile and adult *Xiphopenaeus kroyeri*, based on the SIAR stable isotope mixing models. Boxes in different gray shading denote 95% (light), 75% and 50% (darker) credibility intervals.

4.1.3. Xiphopenaeus kroyeri as omnivorous feeder

Based on the findings of Branco and Junior (2001), *X. kroyeri* has been classified as a secondary consumer, and more specifically as a carnivore animal (Corbisier et al., 2006). The current study is the first to reveal its role as a true primary consumer as well. Therefore, we suggest to classify the species as omnivorous rather than carnivorous, feeding on both benthic animals and primary food sources.

4.1.3.1. Xiphopenaeus kroyeri as predator.
Both stomach content and SI analyses confirmed the trophic importance of animal prey in the diet of *X. kroyeri*. The fact that penaeid shrimp feed on small fauna is well-known (e.g. Dall et al., 1990; Chong and Sasekumar, 1981). However, penaeid shrimps are typically feeding on infauna (e.g. polychaetes and bivalves), as they search for food by probing the bottom with their pereopods (Dall et al., 1990). Cortés and Criales (1990) also found bivalve and polychaete remains as the

dominant prey of adult *X. kroyeri* off Colombia. In contrast, bivalves were rarely found in the stomachs we analysed from Suriname. Polychaetes did occur in 17% of the adult stomachs, but they do not necessarily belong to the infauna (e.g. Wildish et al., 1992). Generally, infauna is expected to be scarce on the inner Suriname Shelf, due to the instability of the muddy nearshore (<20 m depth) sediments (Willems et al., 2015; Aller and Aller, 2004).

In our study, SI mixing models estimated >50% contributions for animal sources (prey group 1 and 2), while crustaceans represented nearly 30% of the stomach contents of *X. kroyeri* by volume. Tararam et al. (1993) also noted 'unidentified crustaceans' as the main food source for *X. kroyeri*, and Branco and Junior (2001) identified gammarid amphipods as a main food source (38% by volume) of adult *X. kroyeri* along the Brazil Coast. Among the crustaceans, we found copepods and the luciferid shrimp *Lucifer faxoni* as important animal food sources, occurring in 76 respectively 25% of the analysed adult stomachs. Based on the length of the antennas (pers.

Observation), the majority of the copepods in the stomachs were considered as planktonic (calanoid and cyclopoid) species, while *L. faxoni* is a pelagic species (Teodoro et al., 2012). This raises the question on how and when these organisms were preyed upon, knowing that *X. kroyeri* (like other penaeids) normally reside near the sea bottom. Penn (1984) found that penaeid shrimps from clear waters burrow during the day and only emerge for feeding at night, while such an activity pattern was not seen in turbid waters, where little or no light reaches the bottom. Mauchline et al. (1998) noted that many planktonic copepods reside close to the bottom during the day to avoid predation in the pelagic realm. Similarly, *L. faxoni* is associated with the sea bottom during day time (Teodoro et al., 2012; Woodmansee, 1966). The turbid nearshore waters of the inner Suriname Shelf might allow for *X. kroyeri* to be active around the clock (Freire et al., 2011), feeding preferably during daytime while many of these planktonic animals are associated with the seabed. Overall, our results indicated that *X. kroyeri* may be considered as a predator of hyperbenthic organisms, i.e. animals that live close to the seabed in the lower meter of the water column.

4.1.3.2. Xiphopenaeus kroyeri as primary consumer.

Unidentified organic detritus occurred in all investigated adult stomachs, representing nearly 50% of the stomach content by volume. Moreover, based on the SI composition, *X. kroyeri* is situated lower in the food chain than could be expected from previous studies that were based on stomach content analyses alone. Overall, *X. kroyeri* occupies a trophic level between 2 and 3, as assumed by Villeger et al. (2008).

The SI analyses suggested that the primary sources mainly contributing to this unidentified organic detritus were BM and offshore SOM. Judging from their depleted $\delta^{13}C$ values, the other potential primary sources were considered as no real food sources for *X. kroyeri* in the study area. While plant material was encountered in 37% of the adult stomachs, decomposing leaf litter was most probably only ingested for the nutritional value of its associated bacterial biofilm (Gatune et al., 2012), or by more random feeding. Leaf litter mainly originated from mangroves, which are present all along the Suriname coastline (Latawiec et al., 2014). In contrast to earlier hypotheses (Odum and Heald, 1975), our findings support the theory that mangrove organic matter is only limitedly incorporated into coastal food webs (Chew et al., 2012; Fry and Ewel, 2003; Lee, 1995).

On the other hand, mangrove detritus may be an important contributor to the carbon pool of coastal SOM, which typically exists of a mixture of terrestrial detritus and marine primary production (Bouillon and Boschker, 2006). sPOM in turbid nearshore waters mainly contains suspended sediments (Vantrepotte et al., 2013), hence the depleted $\delta^{13}C$ values similar to coastal SOM (−25 to −20‰). In contrast, offshore SOM was more enriched in $\delta^{13}C$ (−12‰), making it a potential food source for *X. kroyeri*. It remains unclear which carbon sources caused the enriched signal of this offshore SOM. Most likely, however, the signal results from a high carbonate ($CaCO_3$) content in the offshore sediment, which was not completely removed by acidification with diluted HCl. Although little information is available on the marine sediments off Suriname, the zone beyond the inshore mudbelt is known to harbor fossil coral reefs, causing carbonate-rich sediments (Nota, 1967).

4.2. Intertidal mudflats provide trophic support for Xiphopenaeus kroyeri

BM from intertidal mudflats was the second primary food source that seemed to be directly ingested by *X. kroyeri*. Yokoyama et al. (2009) stated that penaeid shrimps indirectly depend on BM through their intermediate prey, while Newell et al. (1995) also identified BM as a direct food source for penaeid prawns. Based on observations of a golden-brown stained biofilm on the intertidal mudflats in the field (Consalvey et al., 2004) and a microscopic inspection in the lab, we characterized diatoms as the main component of BM in our study. Also, the $\delta^{13}C$ values of BM around −16‰ are within the range typically observed for benthic diatoms (e.g. Yokoyama et al., 2009; Newell et al., 1995). The regular encounter of diatoms in the stomachs of adult *X. kroyeri* (FO = 29%) provides additional support for BM as an important and direct food source, although diatoms may originate from the phytoplankton as well.

BM from intertidal mudflats was estimated to contribute up to 64% to the diet of juvenile and postlarval *X. kroyeri* in the mixing models. Postlarvae are known to reside in inshore shallow waters (Torrez, 2015; Oliveira, 1991) and might feed directly on BM when intertidal areas are inundated at high tide. Surprisingly, the mixing model for adult *X. kroyeri*, which live down to ca. 30 m depth (Willems et al., 2015), also estimated a contribution of BM up to 49% to their diet. Although very little is known on the life cycle and inshore-offshore migrations of *X. kroyeri* in the area, artisanal fisheries for *X. kroyeri* in estuaries suggest that adults periodically reside in inshore areas (Bhagwandin, 2012), where they can feed upon BM from the intertidal mudflats. This signal will be reflected in the SI composition of adult *X. kroyeri* caught more offshore, because the turnover of the SI composition in muscle tissue is low (e.g. Buchheister and Latour, 2010). On the other hand, several authors found that intertidal BM may support offshore production through tidal resuspension and outwelling of BM (e.g. Yoshino et al., 2012; Herman et al., 2000), which might be an important process on the inner Suriname Shelf as well.

Our study provided evidence for BM as a main carbon and energy source fuelling the coastal food web. The so-called detritus-based food web, typical for the turbid nearshore waters of the Guianan Ecoregion as suggested by Bianchi (1992), may also thrive on BM as important carbon source. We only sampled BM at a single time and location. Because isotopic signatures might vary in space and time, further research should include more extensive sampling of BM along the Suriname coast to confirm the general validity of our results. Further, the relative importance of BM versus *in situ* phytoplankton production (Chew et al., 2012), the significance of imported offshore phytoplankton production, and the trophic importance of bacterial communities associated with decomposing terrestrial and marine detritus (Gatune et al., 2012; Fry and Ewel, 2003), remains to be assessed in order to better understand the carbon flows, and the ecological role of *X. kroyeri* in the food webs off Suriname.

4.3. Management implications

The current study supports a growing evidence that the BM layer on (bare) intertidal mudflats subsidize secondary production in the subtidal water body (e.g. Yokoyama and Ishihi, 2007; Middelburg et al., 2000; Underwood and Kromkamp, 1999). On the inner Suriname Shelf, *X. kroyeri* seems to play a crucial role in this process. Being the single abundant epibenthic species up to 30 m depth, it acts as a vector for energy from intertidal primary production to subtidal secondary production. Furthermore, the species is known to be a prey for commercially important demersal fishes (Camargo and Isaac, 2004). While the general importance of *X. kroyeri* as a prey for higher trophic levels on the Suriname Shelf is still to be assessed, it can be stated that *X. kroyeri* passes energy from offshore sedimentary organic matter (SOM), intertidal benthic microalgae (BM) and small hyperbenthic prey up the food chain. Fisheries for *X. kroyeri* should therefore be carefully managed, as overexploitation of this key coastal species might lead to trophic

cascade effects, with negative consequences at higher trophic levels and the fisheries these higher organisms support.

Intertidal mudflats are an integral part of the dynamic nearshore environment of the tropical muddy coastline (e.g. Augustinus, 2004). Our study showed that primary production on these mudflats is at the basis of the subtidal food chains, in contrast to detritus from the mangrove forests that border them. Nevertheless, mangrove systems provide crucial services such as trapping sediment, reducing erosion and enhancing coastal accretion (Alongi, 2008), which in turn promote the formation of intertidal mudflats. Worldwide, intertidal areas are being lost by land-reclamation (McLusky and Elliott, 2004), and mangrove forests are being destroyed at a high rate (Blanco et al., 2012). The trophic importance of intertidal mudflats to offshore fisheries production provides an additional argument for the conservation of the tropical muddy coastlines and their associated mangrove systems.

Acknowledgements

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