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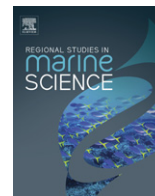48 PUBLICATIONS   1,287 CITATIONS

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Distribution patterns of the demersal fish fauna on the inner continental shelf of Suriname

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HIGHLIGHTS

- First study on the demersal fish community structure of the inner shelf of Suriname.
- A spatial shift from a *coastal* to an *offshore* species assemblage around the 30 m isobath.
- Demersal fish distribution related to sediment characteristics and *Xiphopenaeus kroyeri* density.
- The estuarine-like nearshore waters have a nursery function for demersal fishes.

ARTICLE INFO

ABSTRACT

This study aimed to characterise the spatio-temporal patterns of the demersal fish community in the shallow (<40 m) inner shelf waters of Suriname, based on (bi)monthly data for the period February 2012–April 2013. From 148 demersal trawl samples, distributed over 15 locations, 98 fish species were identified. *Stellifer rastrifer*, *Amphiarius rugispinis* and *Cynoscion jamaicensis* represented 50 % of the catches. Cluster analysis revealed three species assemblages, occurring in a nearshore–offshore depth gradient. A *coastal* fish assemblage occurred in the shallow turbid waters, characterised by muddy sediments with relatively high organic carbon content. A *transition* assemblage around 27 m water depth marked the shift towards a very different *offshore* fish assemblage on the deepest sampling locations (34 m), which were characterised by coarser sediments, with clear overlying waters. The *coastal assemblage* represented the 'sciaenid community' of tropical shelves, dominated by Sciaenidae and Ariidae. The *offshore assemblage* had a significantly lower fish density and diversity, and contained representatives of fish families typical for deeper tropical shelves, such as Paralichthyidae, Triglidae and Lutjanidae. The shift between the *coastal* and *offshore* fish assemblage was the most important feature of the demersal fish community, and coincided with a transition between two principal ecosystems: a coastal, river influenced system fuelled by detritus versus an open shelf system based on primary production. Whereas pelagic fishes are known to gain in importance on the open shelf, demersal fishes thrived in the coastal ecosystem, together with a potentially important epibenthic food source, the Atlantic seabob shrimp *Xiphopenaeus kroyeri*. In Suriname, large demersal (mainly sciaenid) fishes are the main fisheries resource for the artisanal fleet in the nearshore waters below 20 m depth. Because juveniles of commercially important fishes were abundant in our *coastal* trawl catches, we suggest the shallow nearshore waters have a main nursery function.

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1. Introduction

Coastal and shelf ecosystems worldwide provide nursery habitats for commercial fish species, coastal protection, water purification, carbon sequestration and recreational opportunities (Barbier et al., 2011). Biological production in shelf seas supports over 90% of global fish catches (Pauly et al., 2002), and coastal fisheries
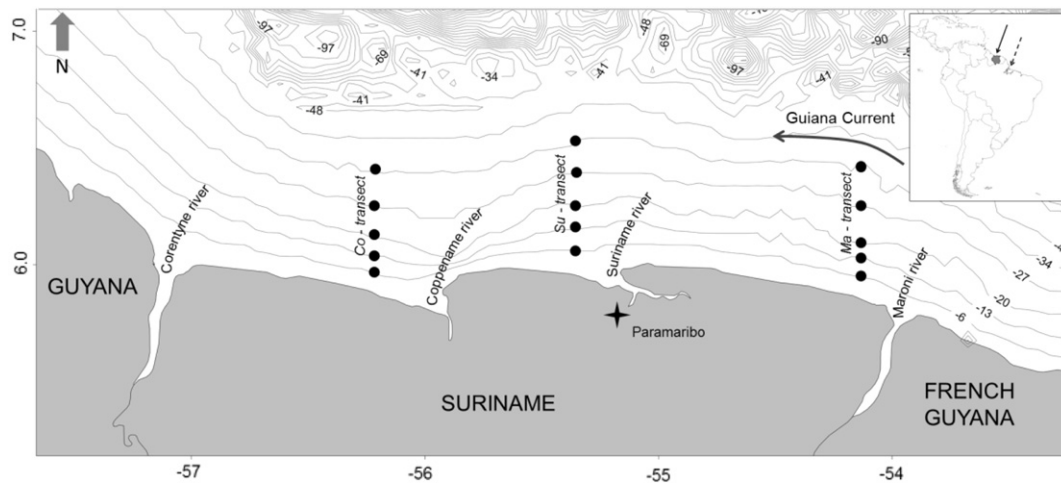
Fig. 1. Map of the inner Suriname Shelf with indication of the major river estuaries and the direction of the Guiana Current. Dots represent the sampling sites at 5 depths (6, 13, 20, 27, 34 m) in each of 3 transects: Co-transect in the west, Su-transect in the middle, Ma-transect in the east. Inset indicates the location of Suriname (solid arrow) and the Amazon River estuary in Brazil (dashed arrow).

generate income, employment and food security for millions of people (UNEP, 2011). While fisheries management has relied on individual fish stock assessments for decades, there is a growing consensus within the Ecosystem Approach to Fisheries (EAF) to consider the ecosystem-wide effects of fishing for a proper management of natural resources (Beddington et al., 2007; Garcia et al., 2003). Because an EAF recognises the complexity of ecosystem structure and functioning, basic understanding on the occurrence of the different life stages of exploited species and the interactions among them is essential, as well as understanding their relationship with the environment (e.g. Pikitch et al., 2004).

The current study was conducted on the continental shelf of Suriname, located in the Guianan Ecoregion of the North Brazil Shelf (Spalding et al., 2007). The productive coastal waters are highly influenced by heavy river runoff, notably from the Amazon River (Cadée, 1975; Smith and Demaster, 1996), and support extensive artisanal and industrial coastal fisheries (Miloslavich et al., 2011). In Suriname, the shallow nearshore waters below 20 m depth support about 70% of the total landings. These are mainly caught by artisanal small-scale fisheries, which use gillnets and fyke nets to catch sciaenid fishes (Perciformes: Sciaenidae) and Atlantic seabob shrimp *Xiphopenaeus kroyeri*. Somewhat deeper on the shelf, industrial bottom trawl fisheries targeting *X. kroyeri* are allowed between 18 and 30 m depth, while trawling for other demersal species like larger penaeid shrimps and finfish is only allowed from 30 m depth onwards (Bhagwandin, 2012).

Despite the socio-economic importance of fisheries on the inner Suriname Shelf, little information is available on the ecology and distribution of the demersal fish fauna. Early surveys were mainly taxonomic (e.g. Boeseman, 1948) or aimed at identifying fisheries resources (Aizawa et al., 1983). Charlier and Babb-Echteld (1994) report on the distribution of shrimp and fishes on the inner shelf based on the latest demersal trawl survey in Suriname (1993–1994). They mention a decrease in demersal finfish yield beyond 30 m, with the bulk of the biomass of commercial species occurring in less than 20 m depth. Because no environmental data were collected during this survey, the ecological interpretation for understanding the distribution patterns was not possible. In the wider Guianan Ecoregion, e.g. in Guyana (Lowe-McConnell, 1962), French-Guiana (Durand, 1959; Guéguen, 2000; Vendeville and Baudrier, 2006) and between the Orinoco and Maroni River (Bianchi, 1992), differences between a coastal and a more offshore (deeper shelf) fish assemblage were found, mainly related to differences in sediment characteristics.

Similarly, a recent study on the epibenthic (invertebrate) communities of the inner Suriname Shelf (Willems et al., 2015) showed a nearshore–offshore transition in species assemblages, linked to a gradient in sediment characteristics. In the nearshore waters with muddy Amazon-borne sediments, low epibenthic diversity was encountered, though *Xiphopenaeus kroyeri* reached high densities. Beyond 30 m depth, on coarser sediments, *X. kroyeri* was absent and epibenthic diversity was higher.

In the current study, we investigated the structure and dynamics of the demersal fish community of the inner Suriname Shelf area, which was sampled simultaneously with this epibenthos. The main objective was to provide an ecological context for the demersal fish populations on the inner Suriname Shelf. This was done by identifying species assemblages, their spatio-temporal distribution patterns and by linking their occurrence with both abiotic and biotic environmental parameters. This study is the first in 20 years to provide fisheries-independent information on the occurrence of demersal fish species and length-specific abundances. We compared our results with the knowledge on the fish fauna of the wider Guianan Ecoregion, and discuss how our findings can contribute to an ecosystem approach to fisheries management in Suriname.

2. Materials and methods

2.1. Study area

The Suriname Shelf (54–57°W, 6–7°N, Fig. 1) is situated in the Guianan Ecoregion of the North Brazil Shelf Province (Spalding et al., 2007). The area is characterised by wide, smoothly sloping continental shelves, macrotides and upwelling along the shelf edge, and is profoundly influenced by the turbid freshwater discharge from the Amazon River (Heileman, 2008), which is carried to the coast of Suriname by the North Brazil Current and its extension, the Guiana Current (Hellweger and Gordon, 2002; Johns et al., 1998). Shelf waters in the region can generally be characterised by three major zones parallel to the coast (Cadée, 1975; Lowe-McConnell, 1962; Smith and Demaster, 1996). The *brown* nearshore 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 input and decreased turbidity creates a productive zone with high chlorophyll concentrations, termed the *green water zone*. Offshore from this zone irradiance

Table 1
Overview of date and season of each sampling campaign (more details on abiotic parameter measurements in Willems et al. (2015)).

Nr	Date	Season
1	17/02–22/02/2012	Rainy
2	24/03–29/03/2012	Rainy
3	20/04–25/04/2012	Rainy
4	22/05–29/05/2012	Rainy
5	30/06–04/07/2012	Dry
6	21/07–26/07/2012	Dry
7	29/09–04/10/2012	Dry
8	27/11–01/12/2012	Dry
9[a]	29/01–03/02/2013	Dry
10[b]	10/04–15/04/2013	Rainy

[a] Missing data for location Ma06.
[b] Missing data for location Ma34.

further increases, while nutrients become limited for primary production, causing *blue waters*. Most rainfall in Suriname, and peak discharge of both the Amazon and local rivers, occurs between December and July (Amatali, 1993; Hu et al., 2004). From August to November, the combination of drier weather and a weaker Guiana Current causes less input of (Amazon) river discharges in the nearshore waters of Suriname. This is also a period with reduced northeast trade winds causing calm and warmer sea surface waters (Amatali, 1993; Augustinus, 2004).

2.2. Sampling and data origin

Data originated from 10 trawl surveys for epibenthos and demersal fish conducted between February 2012 and April 2013 (see Willems et al., 2015). Fifteen locations on the inner shelf were sampled onboard Neptune-6, a 25-m long commercial outrigger trawler used in the Suriname Atlantic seabob shrimp *Xiphopenaeus kroyeri* trawling fleet. 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 epibenthos and demersal fish. All loctions were sampled monthly for the first 6 months and bi-monthly later on (Table 1). Sampling locations were situated along three North–South transects positioned near the westward directed outflow of the Coppename (Co), Suriname (Su) and Maroni (Ma) rivers (Fig. 1). Each transect consisted of five locations along a depth gradient (6, 13, 20, 27 and 34 m depth). At each location, the net was towed 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. Upon retrieval of the trawl, all fishes were sorted from the catch, identified and measured to the nearest cm (total length for finfish, disc width for rays). Species identification was based on Aizawa et al. (1983), Cervigón et al. (1993) and Léopold (2005). Fish names followed Eschmeyer (2015) and higher classification was according to Nelson (2006).

For each trawl sample, water clarity (*Secchi*-depth) and subsurface (5 m depth) total suspended matter (SS-TSM) was measured. Due to logistic problems, CTD-data on water salinity, temperature and depth were only gathered for the first six campaigns. During three campaigns (February, April and May 2012) bottom sediment samples were collected with a Van Veen grab to assess sediment characteristics, including median grain size of the sand fraction (63–2000 μm; MEDSAND), mud-content (<63 μm; MUD) and total organic carbon content (TOC). These *in-situ* environmental data were complemented by remote-sensing values on surface total suspended matter concentrations (SF-TSM), chlorophyll a concentrations (CHL) and sea surface temperature (SST) from the

satellite-borne sensor MODIS on the polar-orbiting Aqua satellite (OBPG, 2014; Bailey et al., 2010). Land rainfall and river discharge data for Maroni River and Amazon River were available from the Suriname Meteorological Service and the Environmental Research Laboratory (ORE-HYBAM, 2014), respectively. Detailed data on the spatio-temporal distribution patterns in the epibenthos, the detailed description of the abiotic parameters, and more details on the density of *Xiphopenaeus kroyeri*, the most abundant epibenthic species in the study area, are presented in Willems et al. (2015). In the current study, these data are used as explanatory environmental variables, hence their collection and analysis is not further described here.

2.3. Data analysis

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 m^3 s^{-1}). As such, the campaigns in February, March, April and May 2012 were considered as *rainy* (Table 1). The five following campaigns were *dry* while the last campaign (April 2013) was again *rainy*.

Pelagic fish species (following FishBase) (Froese and Pauly, 2014) in the samples were excluded from all analyses as they were not sampled quantitatively with the demersal otter trawl. Fish abundance data were standardised, and expressed as numbers per surface unit (1000 m^2). For the most abundant demersal fish species, length-frequency distributions (LFD) were explored graphically and compared to the *common length*, i.e. the size at which fish specimens are commonly caught or marketed according to FishBase (Froese and Pauly, 2014). For every sample, species richness (S), total density (N) and Shannon diversity index (H′) was calculated on the full demersal fish species matrix (excluding pelagic species) using the DIVERSE function in PRIMER v6 (Clarke and Gorley, 2006).

Multivariate analyses were performed on fourth-root transformed fish abundance data using the Bray-Curtis similarity index with further exclusion of rare demersal fish species (occurring in <3% of the samples) to reduce the influence of highly abundant and rare fish species, respectively. Distance-based linear models (DistLM) using BEST selection and BIC criterion were used to relate patterns in species composition and abundance to environmental variables (Anderson et al., 2008). Environmental data were normalised and collinearity among all variables was examined using Spearman rank correlation coefficients prior to the DistLM analyses. For linearly dependent variables ($|r| \geq 0.8$) only one variable was retained in the analyses. Depth, MUD, *Secchi*-depth, rainfall and total epibenthic density were excluded from the DistLM analyses due to collinearity with respectively TOC (first three), Maroni discharge and density of *Xiphopenaeus kroyeri*. As such CHL, SF-TSM, SS-TSM, SST, Maroni discharge, Amazon discharge, MEDSAND, TOC and (fourth-root transformed) density of *X. kroyeri* were included in the analyses. 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).

A cluster analysis with SIMPROF tests (significance level 1%) was conducted to investigate the fish community structure (Clarke and Gorley, 2006). The significance level was set more stringent given the multiple testing inherent in this hierarchical approach as suggested in Clarke et al. (2008). Next, a SIMPER analysis (cut-off 90%) was performed to determine the species that characterised each species assemblage as identified by the cluster analysis. Assemblages were further characterised in terms of average density (N) and diversity (species richness S, Shannon diversity
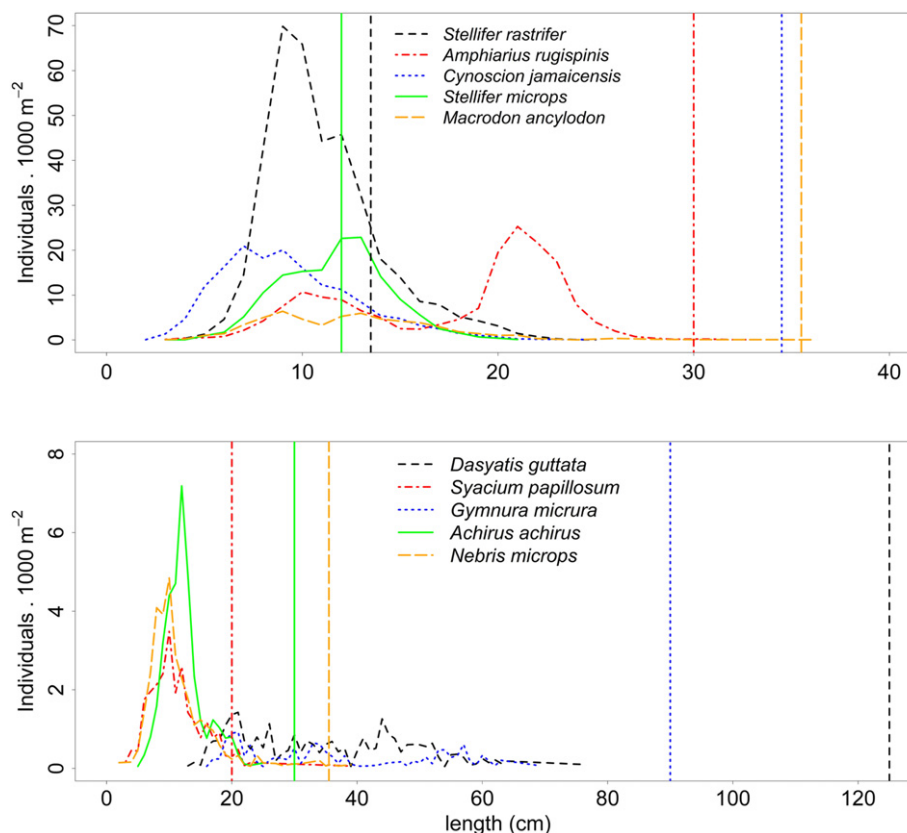
Fig. 2. Length-frequency distributions of the 10 most abundant fish species. Vertical lines indicate the reported *common lengths* for each species (based on FishBase). Note the different axis scales on both plots to account for variation in fish abundance and length.

index H′), and the most relevant (DistLM-based) environmental variables. Significant differences in these univariate parameters between assemblages 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 when significant differences were found. Monte Carlo corrections were applied when too few (<100) permutations could be calculated (Anderson and Robinson, 2003). Further, species richness (with the inclusion of rare demersal species) was compared among assemblages by means of species-accumulation curves (e.g. Gotelli and Colwell, 2001) with random permutation of the samples. Environmental characteristics of the assemblages were visualised by overlaying the most important parameters (based on DistLM) as vectors on a non-metric multi-dimensional scaling (nMDS) plot of the samples using multiple correlation (Clarke and Gorley, 2006).

Within-assemblage patterns in species composition and abundance were 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 species abundance data for all samples per identified cluster. Finally, within-assemblage 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. General characterisation of the fish community

From the 148 otter trawl samples, 18 892 fishes were collected and 98 fish taxa were identified, most of them to species level and hereafter referred to as species (Table 2). Fish species belonged to 47 families and 14 orders with Perciformes (46 species) and Siluriformes (13 species) being dominant. Thirteen pelagic fish species were excluded from all further analyses (Table 2). Samples contained between 3 and 24 demersal fish species with an average of $11.4 \pm$ SD 4.1 species per sample. Total fish density at the sampling stations averaged 9.7 ± 8.5 ind. 1000 m^{-2}, and ranged from 0.7 to 62.1 ind. 1000 m^{-2}. Ten species accounted for 83% of all fishes caught, while the three most abundant species, *Stellifer rastrifer*, *Amphiarius rugispinis* and *Cynoscion jamaicensis* accounted for 50% of the catches. These three species, together with *Dasyatis guttata*, *Macrodon ancylodon* and *Stellifer microps* were also prevalent most consistently, occurring in more than half of the samples. Many species were rare: 13 species were found in a single sample, while 28 species occurred in less than 3% of the samples (Table 2).

The most abundant fish species generally had unimodal length-frequency distributions (LFD), with a peak between 7 and 15 cm total length. *Amphiarius rugispinis* showed a bimodal distribution, while length (disc width) of the two abundant ray species *Gymnura micrura* and *D. guttata* spanned a large range (Fig. 2). When comparing the LFD with literature data, the reported *common length* matched with the peak of the LFD only in the small sciaenid *Stellifer microps*. All other species were smaller than the *common length*, notably the stingrays *D. guttata* and *G. micrura* (Fig. 2).

Table 2
List of fish taxa identified from the trawl samples. n = total number of specimens collected in 148 trawl samples.

Order Family	Species	n	Order Family	Species	n
Albuliformes			Sciaenidae (cont.)	*Lonchurus elegans*	89
Albulidae	*Albula vulpes*[b]	1		*Lonchurus lanceolatus*	58
Anguilliformes				*Macrodon ancylodon*	841
Muraenesocidae	*Cynoponticus savanna*	10		*Menticirrhus americanus*	56
Nettastomatidae	*Hoplunnis sp.*[a]	16		*Micropogonias furnieri*	19
Ophichthidae	*Ophichthus cylindroideus*[a]	1		*Nebris microps*	440
Aulopiformes				*Paralonchurus brasiliensis*	203
Synodontidae	*Saurida caribbaea*	41		*Plagioscion auratus*[a]	4
	Synodus foetens	32		*Stellifer microps*	2094
	Trachinocephalus myops[a]	1		*Stellifer rastrifer*	5451
Batrachoidiformes			Scombridae	*Scomberomorus brasiliensis*[b]	1
Batrachoididae	*Batrachoides surinamensis*	23	Serranidae	*Diplectrum formosum*	22
	Porichthys plectrodon[a]	2		*Diplectrum radiale*	67
Carcharhiniformes			Sparidae	*Calamus penna*[a]	1
Triakidae	*Mustelus higmani*	9	Stromateidae	*Peprilus paru*	27
Clupeiformes			Trichiuridae	*Trichiurus lepturus*[b]	71
Clupeidae	*Harengula jaguana*	59	**Pleuronectiformes**		
Engraulidae	*Anchoa spinifer*[b]	132	Achiridae	*Achirus achirus*	480
	Anchovia surinamensis[b]	8		*Apionichthys dumerili*	55
	Anchoviella lepidentostole[b]	25	Bothidae	*Bothus ocellatus*[a]	3
	Pterengraulis atherinoides[b]	10	Cynoglossidae	*Symphurus plagusia*	133
Pristigasteridae	*Odontognathus mucronatus*[b]	247	Paralichthyidae	*Syacium papillosum*	347
	Pellona flavipinnis[b]	39	**Rajiformes**		
Lophiiformes			Dasyatidae	*Dasyatis americana*[a]	3
Ogcocephalidae	*Ogcocephalus sp.*	19		*Dasyatis geijskesi*	35
Perciformes				*Dasyatis guttata*	390
Carangidae	*Caranx hippos*[b]	2	Gymnuridae	*Gymnura micrura*	190
	Chloroscombrus chrysurus[b]	54	Myliobatidae	*Rhinoptera bonasus*[a]	1
	Oligoplites saliens[a]	1	Rhinobatidae	*Rhinobatos percellens*[a]	5
	Selene brownii	42	Urotrygonidae	*Urotrygon microphthalmum*	77
	Selene vomer	13	**Scorpaeniformes**		
	Trachinotus cayennensis[a]	6	Dactylopteridae	*Dactylopterus volitans*	13
	Carangidae sp.[b]	3	Scorpaenidae	*Scorpaena sp.*	11
Centropomidae	*Centropomus ensiferus*	15	Triglidae	*Prionotus punctatus*	282
	Centropomus parallelus[a]	1	**Siluriformes**		
Ephippidae	*Chaetodipterus faber*	26	Ariidae	*Amphiarius phrygiatus*[a]	55
Gerreidae	*Diapterus auratus*[a]	2		*Amphiarius rugispinis*	2540
Gobiidae	*Gobionellus oceanicus*[a]	1		*Aspistor quadriscutis*	115
Haemulidae	*Conodon nobilis*[a]	6		*Bagre bagre*	56
	Genyatremus luteus	5		*Notarius grandicassis*	18
	Haemulon boschmae	66		*Sciades couma*[a]	1
	Orthopristis ruber	136		*Sciades herzbergii*[a]	2
	Pomadasys corvinaeformis	12		*Sciades parkeri*	4
Lutjanidae	*Lutjanus jocu*[a]	1		*Sciades passany*[a]	3
	Lutjanus purpureus[a]	1		*Sciades proops*[a]	3
	Lutjanus synagris	73	Aspredinidae	*Aspredo aspredo*[a]	7
Mullidae	*Upeneus parvus*	29	Auchenipteridae	*Pseudauchenipterus nodosus*[a]	2
Polynemidae	*Polydactylus oligodon*	14	**Tetraodontiformes**		
	Polydactylus virginicus[a]	2	Diodontidae	*Chilomycterus antillarum*	6
Priacanthidae	*Priacanthus arenatus*	16	Monacanthidae	*Stephanolepis hispidus*[a]	6
Sciaenidae	*Ctenosciaena gracilicirrhus*	344	Ostraciidae	*Acanthostracion quadricornis*	5
	Cynoscion jamaicensis	2340	Tetraodontidae	*Colomesus psittacus*	123
	Cynoscion microlepidotus	5		*Lagocephalus laevigatus*[b]	3
	Cynoscion virescens	276		*Sphoeroides testudineus*	9
	Isopisthus parvipinnis[a]	1	**Torpediniformes**		
	Larimus breviceps	233	Narcinidae	*Narcine bancoftii*	64

[a] Rare (present in <3% of samples).
[b] Pelagic species (according to FishBase).

3.2. Environmental influence and fish assemblage structure

Based on the defined criteria (demersal and present in >3% of all samples), 58 of the 98 fish species were retained for multivariate analyses (Table 2).

The linear combination of environmental variables that best explained the variation in the multivariate data cloud included MED-SAND (37%), TOC (49%), SS-TSM (9%) and density of *Xiphopenaeus kroyeri* (45%) (marginal tests). When fitted together, these variables explained 37% of the total variation in the fish community structure (DistLM BEST—BIC).

Hierarchical clustering of the samples revealed three main clusters. A first cluster split off at ca. 10% similarity, containing mainly

34 m-samples and as such termed the *offshore assemblage* (Fig. 3). At a 30% similarity level, the other two clusters and two outliers were discerned. The largest cluster mainly grouped samples from the 6, 13 and 20 m depth zones, and is further referred to as the *coastal assemblage*. A smaller cluster with mainly 27 m-samples can be regarded as the *transition assemblage* (Figs. 3 and 4).

3.3. Characterisation of the assemblages

One-way SIMPER analysis showed that the *coastal assemblage* had an average similarity of 51%, and mainly consisted of sciaenid fishes (Perciformes: Sciaenidae) including *Stellifer rastrifer*, *S. microps*, *Cynoscion jamaicensis* and *Macrodon ancylodon*. The
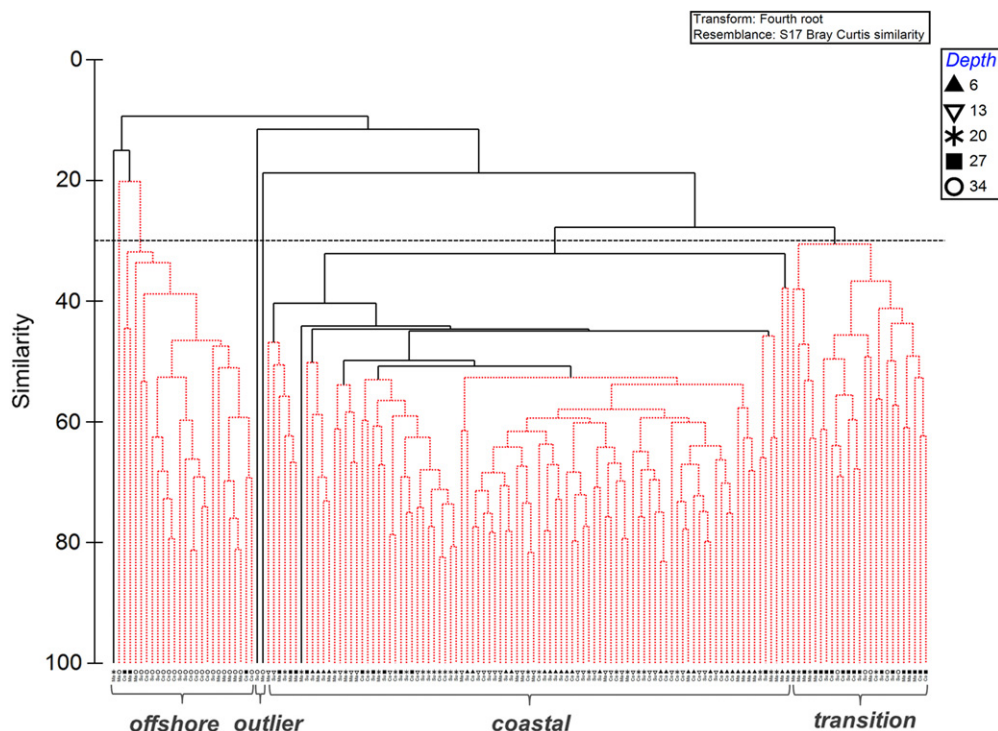
Fig. 3. Group-averaging cluster analysis based on Bray-Curtis resemblance matrix of fourth-root-transformed species abundance data in all fish samples. Significant clusters (SIMPROF test 1% significance level) are indicated by the coloured (red) lines. Samples are labelled with depth (symbol) and transect (Ma = Marowijne transect; Su = Suriname transect; Co = Coppename transect). The dashed line indicates the 30% similarity level. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
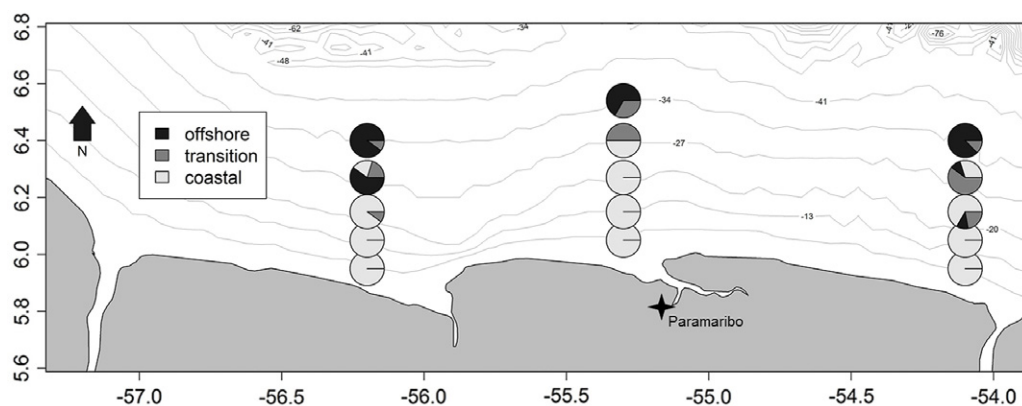

Fig. 4. Map of the fish species assemblages as identified by cluster analysis. Each pie represents the allocation of the different fish samples collected at a station ($n = 9$ or 10) to an assemblage. Two outlier samples are not considered.

catfish *Amphiarius rugispinis* (Siluriformes: Ariidae) was also characteristic for the *coastal assemblage* (Table 3). With 61 demersal fish species identified, the *coastal assemblage* was the most diverse. The *offshore assemblage* was characterised by less (i.e. 39), and very different species, with *Syacium papillosum* (Pleuronectiformes: Paralichthyidae), *Dasyatis guttata* (Rajiformes: Dasyatidae) and *Prionotus punctatus* (Scorpaeniformes: Triglidae) being the most important contributors to the average within-group similarity of 42%. The transition assemblage was a less well-defined species assemblage with the lowest average similarity (38%). It was characterised by a mix of 49 *coastal* and *offshore* species, although still dominated by Sciaenidae (Table 3, Fig. 5).

Significant differences between the three assemblages were observed for total fish density (Pseudo-F = 11.0; $p = 0.0001$), species richness (Pseudo-F = 37.7; $p = 0.0001$) and Shannon diversity (Pseudo-F = 47.7; $p = 0.0001$). Fish density (N) in the *coastal assemblage* was significantly higher than in the

transition and *offshore assemblage*. Species richness (S) significantly decreased from *coastal* to *offshore*, while Shannon diversity (H′) was significantly lower in the *offshore* compared to the *coastal* and *transition assemblage* (pairwise tests; Table 3; Fig. 6). Correcting for sampling effort, the species-accumulation curve for each assemblage also showed the lowest diversity of demersal fishes in the *offshore assemblage* (Fig. 7).

Fish assemblages also differed in environmental parameters: Depth (Pseudo-F = 69.4; $p = 0.0001$), MEDSAND (Pseudo-F = 68,5; $p = 0.0001$), TOC (Pseudo-F = 131.0; $p = 0.0001$) and SS-TSM (Pseudo-F = 8.3; $p = 0.001$). Pairwise comparisons revealed a significant *coastal* to *offshore* increase in depth and MEDSAND, while TOC showed the opposite trend. SS-TSM was significantly higher in the *coastal assemblage* compared to the other assemblages. *Xiphopenaeus kroyeri* was absent from the offshore assemblage, whereas densities did not differ between the *coastal* and *transition assemblage* (pairwise tests; Fig. 6). The influence of
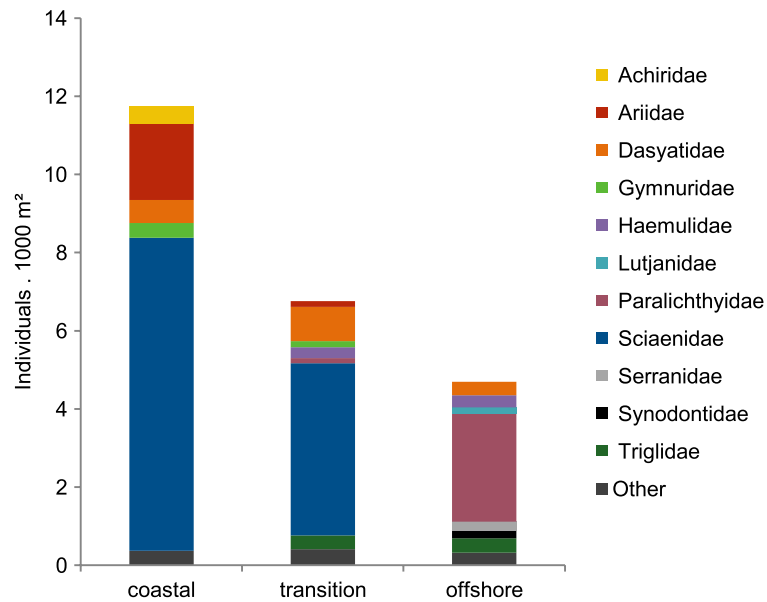
Fig. 5. Barplots showing average fish density per assemblage broken down in the main contributing fish families.
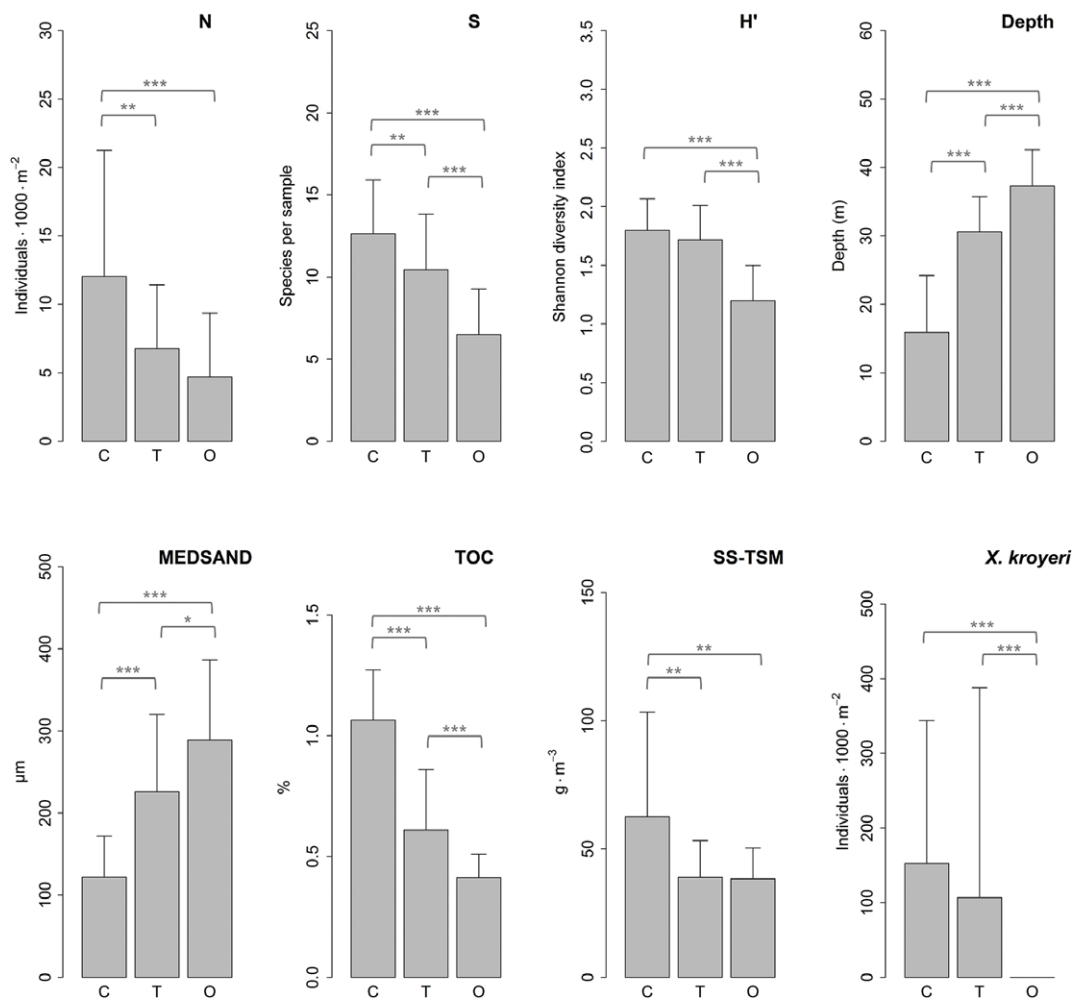

Fig. 6. Barplots showing main characteristics (averages + SD) of the 3 assemblages (C = *coastal*, T = *transition*, O = *offshore assemblages*). N = total fish density, S = species richness, H′ = Shannon-diversity, MEDSAND = median grain size of the sand faction, TOC = sediment total organic carbon, SS-TSM = sub-surface total suspended matter, *X. kroyeri* = density of Atlantic seabob shrimp *Xiphopenaeus kroyeri*. Significant differences between communities as defined by Permanova are indicated (*p = 0.01–0.05, **p = 0.001–0.01, ***$p < 0.001$).

Table 3
Characterisation of the three species assemblages as defined by hierarchical cluster analysis, showing average 'within-group' similarity based on one-way SIMPER analysis of fourth-root transformed abundance data. Species accounting for 90% cumulative contribution of the 'within group' similarity are listed along with their contribution (%) and average density (N; ind. 1000 m^{-2}). The average ($\pm$SD) per assemblage for a number of univariate parameters is also given. MEDSAND = median grain size of the sand faction, TOC = sediment total organic carbon, SS-TSM = sub-surface total suspended matter, *X. kroyeri* = density of Atlantic seabob shrimp *Xiphopenaeus kroyeri*.

Coastal assemblage (avg. sim. = 50.7)			Transition assemblage (avg. sim. = 38.5)			Offshore assemblage (avg. sim. = 41.6)		
Species	%	N	Species	%	N	Species	%	N
Stellifer rastrifer Rake stardrum	17	4.05	*Cynoscion jamaicensis* Jamaica weakfish	25.	1.43	*Syacium papillosum* Dusky flounder	39	2.76
Amphiarius rugispinis Softhead sea catfish	15	1.84	*Dasyatis guttata* Longnoze stingray	18.	0.88	*Dasyatis guttata* Longnoze stingray	18	0.35
Cynoscion jamaicensis Jamaica weakfish	10	1.33	*Ctenosciaena gracilicirrhus* Barbel drum	10.	0.96	*Prionotus punctatus* Bluewing searobin	18	0.37
Macrodon ancylodon King weakfish	9	0.55	*Prionotus punctatus* Bluewing searobin	9.1	0.35	*Lutjanus synagris* Lane snapper	7.3	0.16
Stellifer microps Smalleye stardrum	8	1.24	*Paralonchurus brasiliensis* Banded croaker	5.6	0.27	*Diplectrum radiale* Pond perch	5.4	0.18
Dasyatis guttata Longnoze stingray	7	0.53	*Stellifer microps* Smalleye stardrum	4.6	1.05	*Synodus foetens* Inshore lizardfish	3.9	0.07
Gymnura micrura Smooth butterfly ray	6.2	0.38	*Orthopristis ruber* Corocoro grunt	4.2	0.18			
Nebris microps Smalleye croaker	5.7	0.34	*Menticirrhus americanus* Southern kingcroaker	4.2	0.11			
Cynoscion virescens Green weakfish	5.1	0.19	*Larimus breviceps* Shorthead drum	3.6	0.24			
Achirus achirus Drab sole	4.9	0.38	*Symphurus plagusia* Duskycheek tonguefish	2.4	0.05			
Symphurus plagusia Duskycheek tonguefish	2.1	0.08	*Gymnura micrura* Smooth butterfly ray	2.2	0.15			
Urotrygon microphthalmum Smalleyed round stingray	1.4	0.17	*Stellifer rastrifer* Rake stardrum	1.7	0.16			
N samples	95			25			26	
Density (ind. 1000 m^{-2})	12.0 $\pm$ 9.2			6.8 $\pm$ 4.7			4.7 $\pm$ 4.7	
Species richness S	12.6 $\pm$ 3.3			10.4 $\pm$ 3.4			6.5 $\pm$ 2.8	
Shannon diversity H′	1.8 $\pm$ 0.3			1.7 $\pm$ 0.3			1.2 $\pm$ 0.3	
Depth (m)	15.9 $\pm$ 8.3			30.6 $\pm$ 5.1			37.3 $\pm$ 5.3	
MEDSAND (μm)	121.8 $\pm$ 50.2			225.7 $\pm$ 94.2			288.8 $\pm$ 97.9	
TOC (%)	1.1 $\pm$ 0.2			0.6 $\pm$ 0.3			0.4 $\pm$ 0.1	
SS-TSM (g m^{-3})	62.6 $\pm$ 40.7			38.9 $\pm$ 14.3			38.3 $\pm$ 12.0	
X. kroyeri (ind. 1000 m^{-2})	152.5 $\pm$ 191.4			106.8 $\pm$ 280.9			0.0 $\pm$ 0.0	

(DistLM-selected) environmental parameters on fish community structure was visualised by overlaying them as vectors in the nMDS plot (Fig. 8).

Looking at a more detailed level within each assemblage, no significant spatial or temporal patterns in species composition and abundance, total fish density, species richness or Shannon diversity were apparent in the *transition assemblage*. In the *coastal assemblage*, however, significant spatial (depth × transect interaction, Pseudo-F = 2.2; p = 0.0001) and temporal (season effect, Pseudo-F = 2.0; p = 0.0346) differences in species composition and abundance were observed (Annex 1). Pairwise tests in the depth × transect interaction revealed significant differences among depths in each transect, and among transects at most depths (pairwise tests; Annex 1). Two-way SIMPER analysis (depth × transect) revealed little spatial variation in the abundances of the typical *coastal* species, but tests of the univariate parameters showed significantly higher total fish density in the Co-transect (17.6 $\pm$ 11.8 ind. 1000 m^{-2}) compared to the Su- (9.7 $\pm$ 5.9 ind. 1000 m^{-2}) and Ma-transect (8.9 $\pm$ 6.3 ind. 1000 m^{-2}; Annex 2). No significant seasonal effects were found in any of the univariate parameters within the *coastal assemblage*, nor did one-way SIMPER reveal obvious differences in species composition between the *rainy* and *dry* season. Finally, within the *offshore assemblage* species composition and abundance differed between the *rainy* and *dry* season (Pseudo-F = 2.0; p = 0.0449), mainly caused by higher abundances in the *rainy* season (one-way SIMPER). Univariate tests also showed

a higher species richness in the *rainy* compared to the *dry* season (resp. 8.0 $\pm$ 3.4 *vs.* 5.4 $\pm$ 1.5 species per sample; Annex 2). No spatial patterns were found within the *offshore assemblage*.

4. Discussion

4.1. Spatio-temporal patterns in the demersal fish community on the inner Suriname Shelf

The most apparent characteristic of the demersal fish community on the inner Suriname Shelf was a transition from a *coastal* to an *offshore* assemblage around 30 m depth, corresponding with an environmental shift from a shallow environment with muddy deposits rich in organic carbon and turbid overlying waters ('brown-water zone') towards the deeper shelf, which is characterised by coarser sediments and clear waters ('blue water zone'; (Lowe-McConnell, 1962)). This environmental shift has also been observed in Guyana (Lowe-McConnell, 1962) and French-Guiana (e.g. Vendeville and Baudrier, 2006), and is the main feature structuring demersal assemblages of fishes and invertebrates (up to 200 m depth) between the Orinoco and the Maroni River (Bianchi, 1992). Although the depth range of the current study was limited (6–34 m depth), we did observe a shift towards the offshore fish communities of the deeper shelf. Despite some smaller scale spatial and temporal variation within the *coastal* and *offshore* assemblage, the nearshore–offshore spatial gradient remained the most important feature of the demersal fish community.
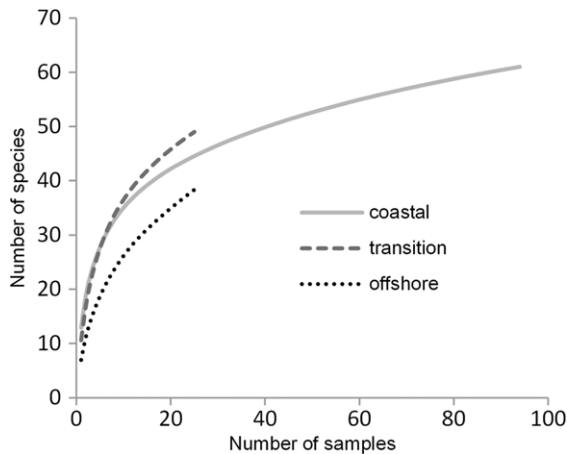
Fig. 7. Species accumulation curves showing the number of demersal fish species encountered in a number of randomly permutated samples.

Both the *coastal* and *offshore* assemblages represented typical fish assemblages that occur in similar habitats throughout the Guianan Ecoregion. Rather than a separate and well-defined assemblage, the *transition assemblage* had characteristics intermediate between the *coastal* and *offshore assemblage*, though it generally resembled the *coastal assemblage* in species composition. The *coastal assemblage* was present in the nearshore waters up to 20–27 m depth, and was dominated by drums and croakers (Sciaenidae), but also included catfishes (Ariidae) and stingrays (Dasyatidae, Gymnuridae). This assemblage clearly represents the 'sciaenid community' of tropical shelves, occurring on nearshore and estuarine muddy habitats with turbid waters, from the southern Caribbean to Cape Frio in Brazil (23°S), and in similar environments throughout the tropics (Longhurst and Pauly, 1987). Although most references for the occurrence of sciaenid communities in South-America come from Brazil (e.g. Bernardes Junior et al., 2011; Rocha and Rossi-Wongtschowski, 1998, and references in Rodrigues-Filho et al., 2015), sciaenids also dominated nearshore catches in trawl surveys off Guyana (Lowe-McConnell, 1962, 1966)

and French-Guiana (Durand, 1959; Guéguen, 2000; Vendeville and Baudrier, 2006). In Guyana, Lowe-McConnell (1966) identified two subsets of the sciaenid community. In the shallowest, turbid nearshore waters over very soft mud, which is in constant suspension and where large changes in salinity occur, sea catfishes (Ariidae) played an important role, while sciaenids became relatively more important when going deeper. In French-Guiana too, 11 of the 17 species of the Ariidae were only found below 10 m depth (Durand, 1959). Ariidae are known to prefer shallow and low saline estuarine waters and coastal lagoons (e.g. Yanezarancibia and Laradominguez, 1988). Our survey, with the shallowest sampling location around 6 m depth, probably missed a part of this habitat, and therefore we were not able to discriminate a separate catfish-dominated assemblage. We did, however, identify 10 species of Ariidae, some of them very abundant in the *coastal assemblage*.

At the 34 m stations, characterised by coarser sediments with low organic carbon content and rather clear overlying waters, an *offshore assemblage* was discerned, discriminated by the absence of Sciaenidae. Typical fish families in the *offshore* assemblage were Haemulidae, Lutjanidae, Synodontidae and Triglidae, with the dominant species being dusky flounder *Syacium papillosum* (Paralichthyidae). As such, the *offshore assemblage* contained representatives from two tropical western Atlantic fish communities as identified by Longhurst and Pauly (1987): the 'Sparid' (sea bream) community of (muddy) sands and the 'Lutjanid' (snapper) community of rocks, corals and coral sands. The substratum at the *offshore* sampling locations was sandy, explaining the occurrence of a Sparid community. Hard substrate in the form of relict (fossil) coral reefs is also known to occur deeper on the Suriname Shelf (Nota, 1967), also see Fig. 1, supporting the presence of a Lutjanid community as well.

Little temporal variation was detected in the fish community, despite clear seasonality in several environmental parameters during the study, e.g. elevated sub-surface total suspended matter and chlorophyll *a* concentrations during the *rainy* season (Willems et al., 2015). Seasonal patterns were however observed in older studies from Guyana (Lowe-McConnell, 1962) and French Guiana (Puyo, 1949), were a general inshore movement of demersal fishes
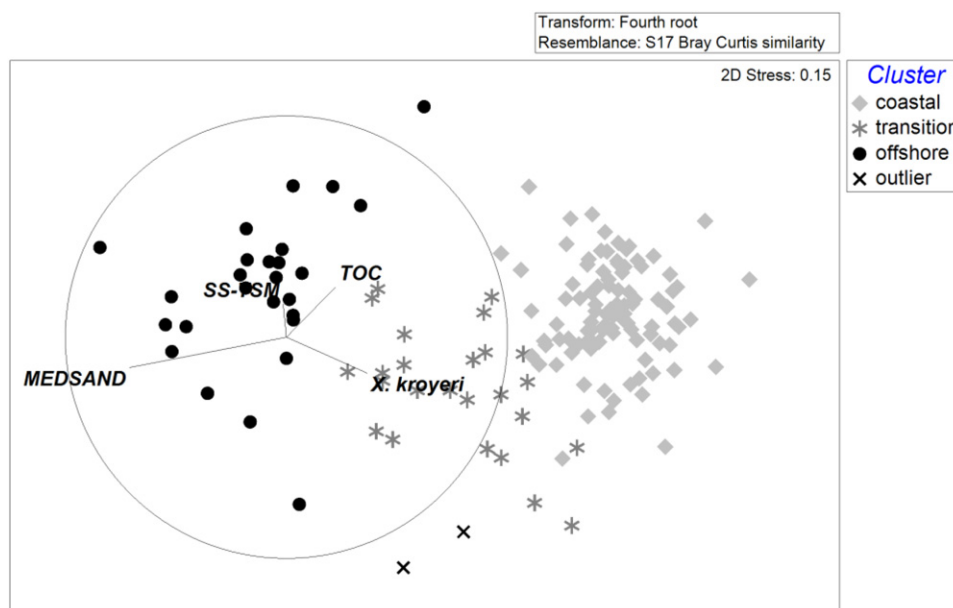

Fig. 8. Non-metric multidimensional scaling (nMDS) ordination plot based on Bray-Curtis resemblance matrix of fourth-root-transformed species abundance data of all fish samples. Each symbol represents one trawl sample. Symbols represent species assemblages delineated from hierarchical clustering. The four environmental variables selected to fit the best model in DistLM are overlaid as vectors using multiple correlation. TOC = sediment total organic carbon; MEDSAND = median grain size of the sand faction; SS-TSM = sub-surface total suspended matter; *X. kroyeri* = density of Atlantic seabob shrimp *Xiphopenaeus kroyeri*.

during the rainy season occurred, most likely related to spawning. On the other hand, Longhurst and Pauly (1987) suggest that within tropical coastal marine ecosystems, interannual changes in species composition and relative abundance are more important than seasonal changes. Further research should clarify to what extent seasonal patterns occur in the demersal fish assemblages on the Suriname Shelf, as insights on (spawning-related) migrations might be relevant for fisheries management.

4.2. Link between demersal fish and epibenthos assemblages

The shift between *coastal* and *offshore* fish assemblages marks the transition between two principal ecosystems as identified by Bianchi (1992): a coastal, river influenced system fuelled by detritus and characterised by muddy deposits and turbid waters, versus an open shelf system with clear waters and coarser sediment which is based on primary production. This shift seems to have contrasting effects on the diversity of two important ecosystem components on the Suriname Shelf, namely epibenthos and demersal fish. The epibenthic community in the shallow nearshore waters is species poor, but characterised by high densities of Atlantic seabob shrimp *Xiphopenaeus kroyeri* (Willems et al., 2015). Except for this shrimp, the estuarine-like conditions in the shallow nearshore waters seem to be too harsh for most epibenthos species, due to rapid environmental changes (Elliott and Quintino, 2007). Average density of *X. kroyeri* formed one of the major structuring variables for the demersal fish community, and *X. kroyeri* might also constitute an important food source for demersal (sciaenid) fishes (e.g. Camargo and Isaac, 2004; Quilez, 2014). This can explain why both density and diversity of demersal fishes was highest in the nearshore waters (*coastal* and *transition* assemblage). The same pattern was noted in other studies from the Guianan Ecoregion (e.g. Bianchi, 1992; Lowe-McConnell, 1966).

Xiphopenaeus kroyeri was almost absent from the *offshore assemblage*, but overall epibenthos diversity increased when going offshore on the Suriname Shelf (Willems et al., 2015). A similar diversity pattern in the epibenthic community was noted in French Guiana (e.g. Le Loeuff and Cosel, 2000), but also in temperate areas like the North Sea (Callaway et al., 2002). On the contrary, the offshore demersal fish assemblage was characterised by a low diversity and density. Offshore areas are generally characterised by sandy deposits beyond the influence of coastal mud, leading to clearer waters and an increased abiotic stability (Elliott and Quintino, 2007). As such, these offshore areas become less important for demersal fishes. Indeed, Longhurst and Pauly (1987) showed that on tropical shelves, pelagic fishes become relatively more dominant when going offshore.

4.3. Considerations for fisheries management in Suriname

Several *coastal* fish species that were found to be abundant in our study, such as the sciaenids *Macrodon ancylodon*, *Cynoscion jamaicensis*, *Nebris microps* and *Cynoscion virescens,* are important target species (as adults) for artisanal gillnet fisheries in Suriname LVV (2013). Length-frequency distributions of these and other common species indicated that most fishes were considerably smaller than the common landing lengths (as reported in FishBase), suggesting we mainly caught juveniles. This confirms the role of the shallow, estuarine-like nearshore waters as nursery grounds for demersal fishes (Blaber, 2002; Blaber et al., 1995), much like the role of estuaries in temperate regions (Able, 2005). To further assess this nursery function, future surveys should include the shallowest (<6 m depth) waters, and use a trawl with a smaller cod end mesh size (e.g. 20 mm) to assess densities of the early life stages as well. Nevertheless, we can conclude that the current ban on industrial trawl fisheries below 18 m depth in Suriname is a valid management measure to protect commercial fish species, by allowing the young fishes to recruit to the adult stocks.

On the other hand, it seems a bit strange that we rarely caught larger, commercial sized sciaenids in our hauls, although they form a main target group in the coastal Suriname fishery. By using a small-sized shrimp trawl, the present study probably underestimated the abundance of larger, more mobile fishes, which are more efficiently sampled by larger trawls with a higher vertical opening (e.g. Wassenberg et al., 1997) and by gillnets, as used by the artisanal fishing fleet in Suriname. Therefore, our results on the densities of larger-sized fishes should be interpreted with care, as they might not have been sampled adequately by the gear used. Nevertheless, larger fishes might have effectively become scarcer due to an increased fishing pressure and the constant adult removal by coastal gillnet fisheries. Already in 1998 declining catch rates indicated that large demersal fishes were overfished (Charlier, 2000), while the number of fishing licences has not been reduced since (LVV, 2013).

From 18 m onwards, i.e. within the *transition* and (deeper) *coastal assemblage*, industrial trawling for *Xiphopenaeus kroyeri* with fine-meshed demersal shrimp trawls is allowed. This fishery has a considerable bycatch of small-sized fishes (Southall et al., 2011). The artisanal fisheries in river estuaries targeting *X. kroyeri* with fine-meshed fyke nets might produce considerable bycatches of non-target (sciaenid) fishes as well (LVV, 2013). Unfortunately, no detailed information on bycatches is currently available. Therefore, bycatch assessments are urgently needed to gain more insight in the impact of these fisheries on the populations of larger demersal (mainly sciaenid) fishes, being the most important fisheries resource in terms of landings and employment in Suriname (Bhagwandin, 2012).

The two stingrays *Dasyatis guttata* and *Gymnura micrura*, which were commonly noted in our surveys, were much smaller than the reported common landing sizes. Although they are not targeted by any fishery, these species are still commonly caught by the *X. kroyeri* trawl fisheries, despite the use of net adaptations (Willems et al., submitted). In general, elasmobranch populations are highly vulnerable to fishing mortality (Stevens et al., 2000). Besides affecting the length distribution of the more resilient species, fishing activity might have locally wiped out some critically endangered elasmobranchs, such as daggernose shark *Isogomphodon oxyrhynchus* and sawfishes *Pristis pristis and P. pectinata* (IUCN, 2015), which were caught off Guyana in the 1960s (Lowe-McConnell, 1962) but not observed in the present study. The impact of coastal fisheries on large sized-individuals of commercial and globally threatened elasmobranch species, which are crucial contributors to healthy fish populations (Birkeland and Dayton, 2005), should be properly assessed.

5. Conclusion

The most important feature of the demersal fish community of the Suriname Shelf was a spatial shift from a *coastal* to an *offshore* demersal fish species assemblage around the 30 m isobath, corresponding with an important habitat shift. No clear temporal patterns in species composition and abundance were found. In describing the species composition and structuring environmental factors of each assemblage, this paper provides insight in the ecology and distribution of several target species in the multi-species coastal fisheries of Suriname. The current ban on trawl fisheries in most of the nearshore area seems a valid management measure to ensure the nursery function of the nearshore waters. Still, the interaction between the different fishing fleets operating on the inner Suriname Shelf and their impact on commercial and potentially vulnerable species such as sharks and rays should further be assessed.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.rsma.2015.10.008.

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