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Original Article

Food habits, ecomorphological patterns and niche breadth of the squeaker, *Synodontis schall* (Pisces: Siluriformes: Mochokidae) from Niger River in Northern Benin

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Abstract: The squeaker, *Synodontis schall* dominates the Mochokid fish sub-community in Niger River in Northern Benin and shows a great economic and commercial importance. The diet of *S. schall* has been analysed to evaluate the food habit and resource utilization in this regional River. Fish samplings were made monthly from February 2015 to July 2016 using unbaited longlines and traps, seines and experimental gillnets. The results indicated that *S. schall* is an omnivore foraging in benthic and pelagic habitats with diet dominated by aquatic insects (34.32%), sand particles (18.768%), macrophytes (13.415%), seeds (8.549%), roots (8.319%), detritus (5.344%), mollusks (1.204%) and phytoplankton (0.6255%). The omnivore food habit depicted was also shown by the ecomorphological analysis mainly the relative gut length (GL/SL) varying between 0.8 and 5. The species showed high diet flexibility with high niche breadth ranging between 1.86 and 5.74. *Synodontis schall* exhibited an ontogenetic diet shift that was also confirmed by Pianka's diet overlap indexes ranging between $Ø_{jk}$=0.54-0.93. The conservation and the sustainable fisheries exploitation of *S. schall* require the reinforcement of fishing regulation, habitat protection and ecosystem follow-up.

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Introduction

Knowledge on diet composition and food habits of fishes is important for habitat protection, species conservation, fisheries management and fish culture (Rosecchi and Nouaze, 1987; Adite et al., 2007; Kone et al., 2007). Furthermore, dietary analysis gives a better understanding of how food resources are shared and constitutes a basic tool for assessing trophic structure and fish's capability to adapt to environmental changes (Rosecchi and Nouaze, 1985; Hajisamae et al., 2003; Adité et al., 2006; Berté et al., 2008). In West Africa, catfishes are represented by 124 species, 24 genera and 8 families among which the family of Mochokidae made about 48 species (Paugy et al., 2004). Among Mochokids, *Synodontis* is the most diverse genus comprising about 36 species (Paugy and Roberts, 2004) with *S. schall*, the most widespread and dominant species that occurs in most African rivers such as Senegal, Gambia, Volta, Tchad, and Niger (Paugy et al., 2003). In Niger River, Paugy and Levêque (2004) reported 28 species for the genus *Synodontis*, with *S. schall*, the dominant and the most tolerant species to adverse environmental conditions (Lowe-McConnell, 1987).

In some African water bodies, *S. schall* is described as an omnivore feeding on macro-invertebrates, macrophytes and detritus (Willoughby 1974; Hickley and Bailey, 1987; Ofori-Danson, 1992). The species reproduces all seasons with peaks in wet and flood periods. In Niger River in Benin, to date, there is a gap of information on the feeding patterns of *S. schall* and no published work is available on its trophic ecology.

In Benin, *S. schall* dominated the Mochokid sub-community in many rivers and streams such as Oueme, Okpara, Zou, Sô, Hlan, Tove, Mono, and Niger (Lalèyè et al., 2004; Montchowui et al., 2007; Djidohokpin et al., 2017; Hazoume et al., 2017; Sidi Imorou et al., 2019). In Niger River in Northern Benin, Arame et al. (2019) reported only the genus *Synodontis* comprising fourteen valid species, with

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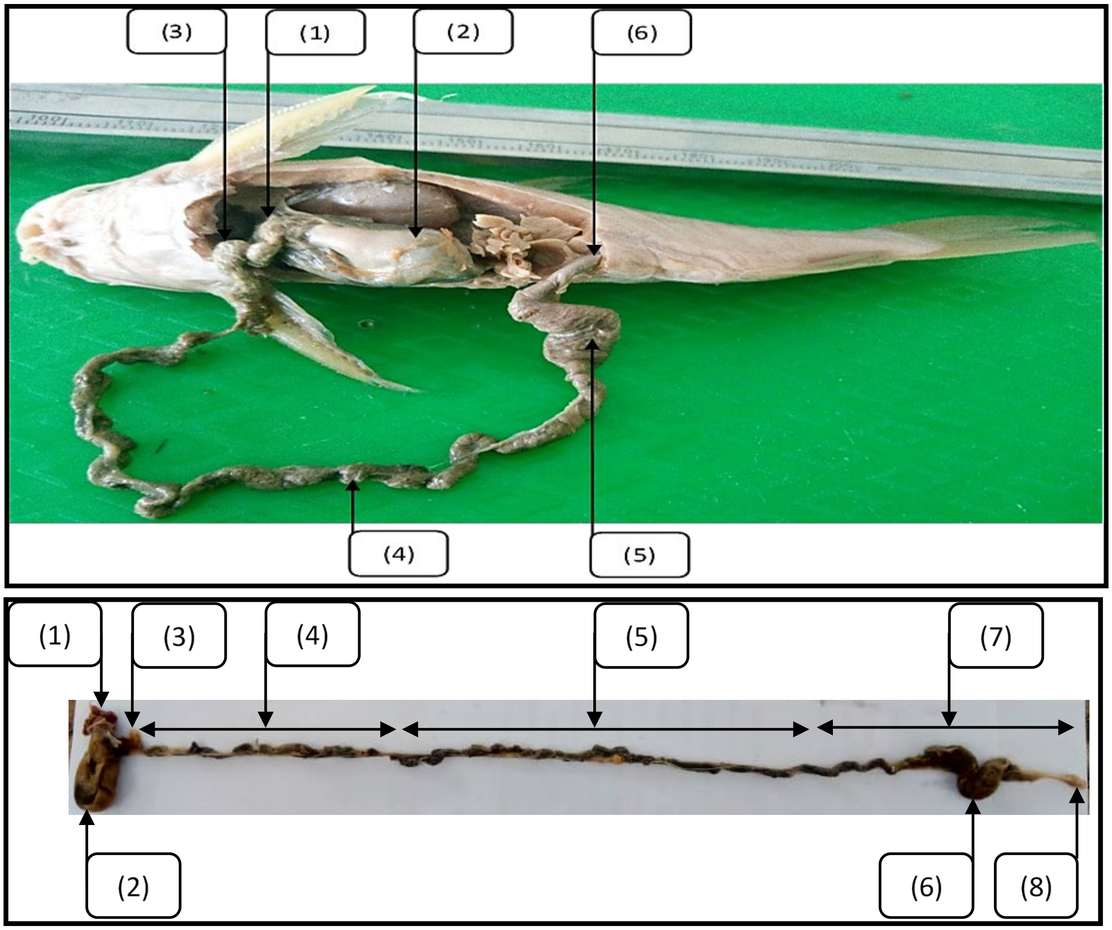

Figure 1. (above) Internal organs and (below) structure of the digestive tract of *Synodontis schall* from Niger River in Northern Benin (1, Esophagus; 2, Stomach; 3, Cardiac stomach; 4 (above), Intestine; 4 (below), Anterior intestine; 5 (above), Rectum; 5 (below), Medium intestine; 6 (above), Anal orifice; 6 (below), Rectum; 7, Posterior intestine; 8, Anal orifice).

S. schall, the most abundant species making numerically 74.50% of the Mochokid fish assemblages (Arame et al., 2020). Despite the abundance and fisheries importance of *S. schall* that is intensively exploited in Niger River in Benin, nothing is known about the feeding ecology and resource utilizations. Successful fisheries management and fish culture require knowledge on trophic ecology of the target species. The current research aims to study the diet composition and feeding habits of *S. schall* in Niger River in Bénin.

Materials and Methods

Study area: The research area is the Niger River in Northern Benin around Malanville township. This region is located between 11°52'05″N and 3°22′59″E at an altitude of 200 m, and extended on about 3,016 km². The Niger River is a regional running water that stands as a frontier between the two neighbor countries, Benin and Niger Republics. In Benin, the three tributaries, Mékrou, Sota and Alibori of Niger River caused severe inundations with a peak flood reaching 275 Km^2 that boosted a high fish productivity (Welcomme, 1985; Moritz et al., 2006; Adjovi, 2006; Adite et al., 2017). The Niger River valley shows sandy-clayish and ferruginous soils showing plant communities comprising rooted, floating and submerged vegetation. A multi species artisanal fisheries occurred on floodplains, pools, river channels and involved many ethnic groups (Hauber, 2011; Arame et al., 2019; Adjibade et al., 2019).

Collection sites: Four stations were selected on Niger River for the sampling of the fish species (Arame et al., 2020): (1) Tounga village located at 11°52'216"N, 3°23'907"E constitutes a highly degraded site, (2) Behind Dry Port, situated at 11°52'216"N, 3°23'907"E, is also degraded, (3) Money village, located at 11°52'987"N, 3°20'819"E, is a less degraded site, and (4) Gaya village, less degraded, is located at 11°52'675"N, 3°25'329"E in the river at Niger Republic side.

Mochokid fish collections: Fish samplings were performed monthly from February 2015 to July 2016 in aquatic vegetation and in open water habitats at the four stations. Unbaited longlines and traps, seines and experimental gillnets were used for the samplings. Collection procedures follow Adite et al. (2013). Mochokid samplings were also performed from fishermen artisanal catches on the basis of 1/3 of species abundance when the abundance exceeded 50 individuals. All individuals were retained for the sample when the abundance is less than 50 for a given species (Kakpo, 2011; Okpeicha, 2011). The fishes were then identified in situ based on Van Thielen et al. (1987) and Levêque and Paugy (2006). Identified fishes were preserved in 10% formalin and transported to Laboratoire d'Ecologie et de Management des Ecosystèmes Aquatiques (LEMEA), at the Faculty of Sciences and Technics, in the University of Abomey-Calavi. In the laboratory, fish individuals were transferred into 70% ethanol to facilitate biological observations. http://www.fishbase.org (Froese and Pauly, 2018) were used to confirm fish species.

Dietary analysis: After sampling, each individual was measured for total length (TL) and standard length (SL) to the nearest 0.1 mm with an ichtyometer, and weighed to the nearest 0.01 g with an electronic balance (CAMRY 0.1 g / 500 g; AWS). Each individual was then dissected and the gut was removed and measured (Adite et al., 2007; Gbaguidi et al., 2016). The stomach was then opened and food resources were removed and spread on a glass slide for examination first under a binocular to identify macroscopic foods items. Then, a photonic microscope was used to identify fine food resources and algae (Adite et al., 2017). References such as Needham and Needham (1962), Bourrelly (1985, 1990) and Tachet et al. (2010) were used to identify prey items at the lowest possible taxonomic level. The volume (V) of each food resource identified from the 1505 stomach dissected was estimated by water displacement following Adite and Winemiller (1997).

Data analysis: The estimated volume (V) and counts of each identified food item were recorded on Excel software spreadsheet and the proportional volumetric consumption (%V) of each food item was computed using the formula (Adite and Winemiller, 1997):

$$\%V = \frac{Vi}{Vt} \times 100$$

Where, %V is the proportional volumetric consumption of food item i in the diet, V_i is the total volume of the food item i in n stomachs, V_t is the total volume of food resource ingested by n stomachs, and n is the total number of stomachs dissected. The volumetric proportions of each food item consumed were calculated for different size classes to examine ontogenetic diet shifts. The analysis of variances (ANOVA) was run with SPSS software (Morgan et al., 2001) to assess spatial and seasonal variations in diet. Empty stomach indexes (Ce) were computed as the ratio of number of empty stomachs to total number of stomachs examined:

$$Ce = \frac{N_i}{N_t} \times 100$$

Where, Ce is the coefficient of emptiness, N_i is the number of empty stomachs and N_t is the total number of stomachs examined. The following formula of Bahou et al. (2007) was used to estimate the occurrence frequency (OF) of each food resource in the diet:

$$OF = \frac{J_i}{N_t} \times 100$$

Where, J_i is the number of stomachs containing prey item i and N_t is the total number of non-empty stomachs. According to Sorbe (1972), the prey is classified "accidental", "secondary" and "preferential" when OF<10%, OF between 10 and 50% and OF>50%, respectively. Diet breadth (DB) was computed following Simpson (1949):

$$\text{Diet breadth (DB)} = 1 \Big/ \sum_{i=1}^{n} P_i^2$$

Where, *Pi* is the proportion of food resource *i* in the diet and n is the total number of food items in the diet. In general, the DB ranges from 1 (when only one food resource is ingested), to n in case all food resources

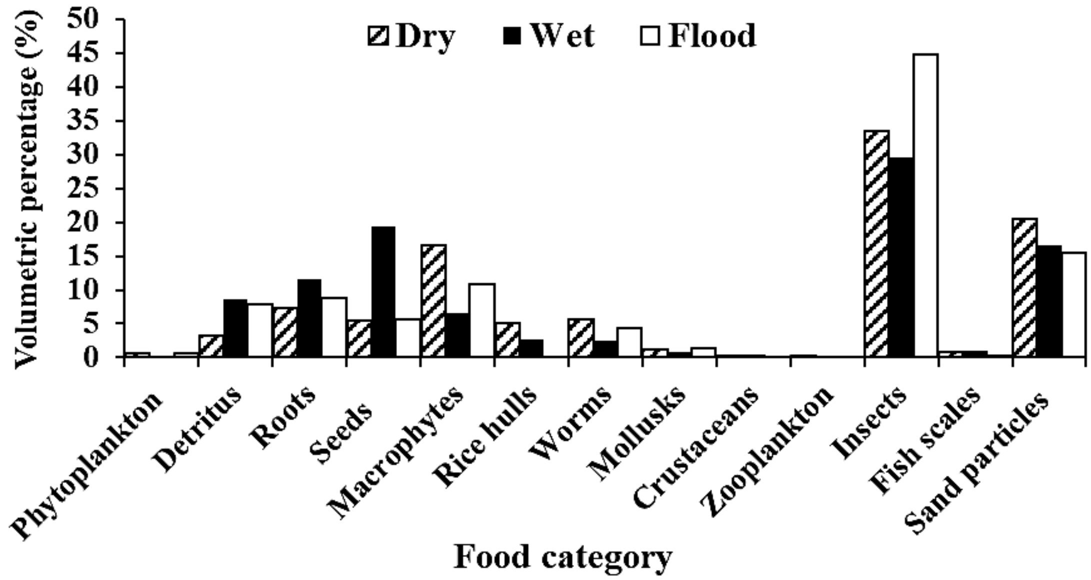

Figure 2. Seasonal variations of food resources consumed by *Synodontis schall* in Niger River in Northern Benin.

are ingested in equal proportions. The values of DB were submitted to ANOVA using SPSS software version 21 (Morgan et al., 2001) to show the variation among life stage. Pianka's diet overlap index ($Ø_{jk}$) (1976) was computed between fish size classes to examine diet similarities and ontogenetic diet shift:

$$Ø_{jk} = \frac{\sum_{i=1}^{n} P_{ij} P_{ik}}{\sqrt{\sum_{i=1}^{n} P_{ij}^2 \times \sum_{i=1}^{n} P_{ik}^2}}$$

Where, $Ø_{jk}$ is the Pianka's dietary overlap between species *j* and species *k*, P_{ij} is the proportion of resource *i* used by species *j*, P_{ik} is the proportion of food item i used by species *k* and n is the number of food resource ingested. The eco-morphological analysis of the diet was evaluated using the linear regressions between gut length (GL) and body weight (W) and between gut length (GL) and standard length (SL). Likewise, the ratio (GL/SL) was computed as a measure of relative gut length and compared to published reference ratios 0.8 to 5 for omnivores (Al-Hussaini, 1947; Kapoor et al., 1975). Also, the eco-morphological patterns were examined to document the food habit of *S. schall*.

Results

The digestive tract of *S. schall*: The morphology of digestive tract showed a thick-walled esophagus followed by a well-developed fork-like shape stomach, an intestine (anterior, medium and posterior), a rectum and an anal orifice (Fig. 1). The pyloric caecum is absent.

Diet composition: In Niger River, *S. schall* foraged mainly in pelagic and benthic habitats where the species consumed about 221 food resources dominated by aquatic insects (34.32%), sand particles (18.768%), macrophytes (13.415%), seeds (8.549%), roots (8.319%), detritus (5.344%), worms (4.735%) and rice hulls (3.681%), aggregating 97.131% of the stomach content (Table 1). Minor preys were mollusks (1.204%), fish scals (0.796%), crustacean (0.161%), zooplankton (0.083%) and phytoplankton (0.6255%) (Table 1).

Seasonal variations of diet: Figure 2 shows volumetric percentage (%) of preys consumed by *S. schall* according to seasons. The results of the food preys ingested showed significant (P<0.05) seasonal variations for insects ($F_{2,1502}$=5.855, P=0.003), seeds ($F_{2,1502}$=19.865, P=0.001), roots ($F_{2,1502}$=18.029, P=0.001), detritus ($F_{2,1502}$=16.24, P=0.001), phytoplankton ($F_{2,1502}$=11.875, P=0.001), zooplankton ($F_{2,1502}$=15.142, P=0.001), macrophytes ($F_{2,1502}$=5.466, P=0.004). Indeed, the highest volumetric percentage of insects (44.67%) ingested was recorded during flood while those of seeds (19.34%), roots (11.63%) and detritus (8.57%) were

Table 1. Volumetric, occurrence and numeric percentages of prey items ingested by Synodontis schall from Niger River in Northern Benin.

	Prey category	Prey / family/genus / species	Volumetric Percentage (%V)	Number (N)	Numeric percentage (%N)
Phytoplankton	Blue algae	Cyanophyceae	**0.096**	**435**	5.226
	Green algae	Chlorophyceae	0.181	942	11.318
		Trebouxiophyce	0.004	22	0.264
		Ulvophyceae	0.002	11	0.132
	Desmids	Eustigmatophyceae	0.002	14	0.168
		Zygnematophyceae	0.004	21	0.252
	Diatoma	Bacillariophyceae	0.22	1098	13.192
		Coscinodiscophyceae	0.051	179	2.151
		Mediophyceae	0.032	174	2.091
	Undetermined	Unidentified phytoplankton	0.034	314	3.773
Total phytoplankton			**0.6255**	**1765**	**38.568**
Zooplankton	Branchiopoda	Cladocerans	0.014	3	0.036
		Copepods	0.032	4	0.048
	Rotifera	Brachionidae	0.038	2	0.024
Total zooplankton			**0.083**	**9**	**0.108**
Worms		Nematoda	3.138	433	5.202
		Annelides oligochaetes	1.571	20	0.240
		Glossiphoniidae	0.026	2	0.024
Total worms			**4.735**	**455**	**5.467**
Insects	Ephemeroptera	Leptohyphidae	0.189	3	0.036
		Ephemerellidae	0.039	4	0.048
		Heptageniidae	0.124	3	0.036
		Baetidae	0.131	4	0.048
		Hydroptilidae	0.112	2	0.024
		Siphlonuridae	0.112	2	0.024
	Plecoptera	Pachygronthidae	0.004	2	0.024
		Leuctra geniculata	0.025	1	0.012
	Odonata	Libellulidae	1.128	53	0.637
		Lestidae	0.175	4	0.048
		Coenagrionidae	0.25	10	0.120
		Calopterygidae	0.112	3	0.036
		Aeshnidae	0.1	2	0.024
	Heteroptera	Tettigoniidae	0.05	1	0.012
		Notonectidae	0.037	1	0.012
		Pleidae	0.05	2	0.024
	Coleoptera	Aphodidae	0.006	1	0.012
		Copridae	0.149	1	0.012
		Coenagrionidae	0.093	2	0.024
		Curculionidae	0.301	13	0.156
		Dytiscidae	0.137	4	0.048
		Elmidae	0.398	7	0.084
		Elminthidae	0.121	3	0.036
		Ecnomidae	0.003	2	0.024
		Hydraenidae	0.243	10	0.120
		Hydrochidae	0.065	7	0.084
		Hydrophilidae	6.731	250	3.004
		Hydroporinae	0.162	4	0.048
		Noteridae	0.1	1	0.012
		Pleidae	0.1	1	0.012
		Psephenidae	0.025	1	0.012
	Tricoptera	Agupetidae	0.056	1	0.012
		Philopotamidae	0.137	5	0.060
		Sericostomatidae	0.028	5	0.060
		Helicopsychidae	0.025	1	0.012

Table 1. Continued.

	Prey category	Prey / family/genus / species	Volumetric Percentage (%V)	Number (N)	Numeric percentage (%N)
Insects		Hydroptidae	0.003	3	0.036
		Hydropsychidae	4.051	310	3.725
		Lepidostomatidae	0.152	6	0.072
		Limnephilidae	0.025	2	0.024
		Glossosomatidae	0.03	8	0.096
		Polycentropodidae	0.165	2	0.024
	Diptera	Chironomidae	9.918	621	7.461
		Ceratopogonidae	1.388	60	0.721
		Dasyheleinae	1.196	52	0.625
		Chaoboridae	0.065	3	0.036
		Psychodidae	0.006	3	0.036
	Insects parts		3.812	179	2.151
	Indetermine insects	Unidentified insects	1.994	204	2.451
Total insects			**34.32**	**1869**	**22.456**
Total mollusks	Mollusks	Sphaeriidae	**1.204**	**41**	0.493
Crustacean		Branchipodidae	0.001	2	0.024
		Platyischnopidae	0.008	2	0.024
		Candonidae	0.106	2	0.024
		Gammaridae	0.047	1	0.012
Total crustaceans			**0.161**	**7**	**0.577**
Fish scales		Fish scales	**0.796**	**59**	**0.709**
Roots		Roots	**8.319**	**361**	**4.337**
Seeds		Seeds	**8.549**	**170**	**2.043**
Machrophytes		Machrophytes	**13.415**	**172**	**2.067**
Rice hull		Rice hull	**3.681**	**84**	**1.009**
Detritus		Detritus	**5.344**	**748**	**8.987**
Sand particles		Sand	**18.768**	**1138**	**13.673**
Total			**100%**	**8323**	**100%**

recorded during the wet period. Also, the highest volumetric percentage of phytoplankton (0.73%) and zooplankton (0.14%) consumed were recorded during the dry season. Nevertheless, there were no significant (P>0.05) seasonal dietary variations for mollusks ($F_{2,1502}$=0.055, P=0.946), rice hulls ($F_{2,1502}$=0.510, P=0.477), worms ($F_{2,1502}$=0.275, P=0.760), crustaceans ($F_{2,1502}$=2.613, P=0.074), sand particles ($F_{2,1502}$=0.963, P=0.382) and fish scales ($F_{2,1502}$=2.527, P=0.080) (Fig. 2).

Frequency of occurrence in diet: The analysis of the occurrence frequencies (OF) of the food resources revealed that phytoplankton was ingested by all 1505 individuals collected with an occurrence frequency OF=100% indicating that, though of reduced volumetric percentage (0.6255%), phytoplankton appeared to be the preferential prey. Also, insects, sand particles and detritus with a huge aggregated volumetric percentage (Vp=58.42%), displayed a high OF estimated at 73.53, 59.19 and 59.11%, respectively, that classified them as preferential preys (Table 2). The secondary preys consumed were worms, roots, zooplankton, seeds and macrophytes that were common in some stomachs with moderate OF ranging between 12.04 and 35.74% (Table 2). The accidental preys, rice hulls, fish scales, mollusks, and crustaceans ingested by *S. schall* occurred just in few stomachs with reduced OF varying between 0.55 and 6.66%.

Diet according to life stages: The ontogenetic analysis of the diet indicated that preys such as roots (59.63%), insects (16.75%) and sand particles (15.30%) dominated the stomach of juveniles. In addition, macrophytes (15.97%) and rice hulls (9.23%) consistently occurred in the stomach of sub-adults, and insects (38.56%) relatively dominated the diet of adults (Table 3). Overall, the three life stages tended to consume more roots, insects and sand

Table 2. Occurrence frequencies of prey consumed by *Synodontis schall* from Niger River in Northern Benin.

Prey categories	Occurrence frequency (%)	Food importance
Phytoplankton	100.00	Preferential prey
Insects	73.53	Preferential prey
Detritus	59.11	Preferential prey
Sand particules	59.19	Preferential prey
Zooplankton	17.51	Secondary prey
Worms	35.74	Secondary prey
Seeds	13.15	Secondary prey
Machrophytes	12.04	Secondary prey
Roots	28.92	Secondary prey
Crustaceans	0.55	Accidental prey
Mollusks	3.25	Accidental prey
Fish scales	4.68	Accidental prey
Rice hulls	6.66	Accidental prey

Table 3. Ontogenetic variations of preys consumed (volumetric percentage) by *Synodontis schall* from Niger River in Northern Benin.

	Volumetric percentage (%V)		
Prey categories	**Juveniles (TL < 5)**	**Sub-adults (5 ≤ TL < 8)**	**Adults (TL ≥ 8)**
Phytoplankton	0.5504	0.6008	0.6332
Detritus	0.0612	3.2259	5.6091
Roots	59.633	11.937	7.4895
Seeds	-	6.8155	8.9774
Macrophytes	-	15.9743	12.912
Rice hulls	6.1162	9.2315	2.4342
Worms	1.5291	3.4191	3.1153
Mollusks	-	-	1.3559
Crustaceans	-	-	0.1976
Zooplankton	0.0738	0.0032	0.0388
Insects	16.7458	25.1464	38.5602
Fish scales	-	0.9225	0.7717
Sand particles	15.2905	22.7238	17.9051
Total	**100%**	**100%**	**100%**

particles. The presence of sand in a high volumetric percentage indicated that *S. schall* is a benthic feeder. Macrophytes occurred only in the diet of sub-adults and adults probably because their digestive tracts were more developed than those of juveniles. The food items consumed by different life stages of *S. schall* showed significant (P<0.001) variations for insects ($F_{2,1502}$=26.943, P=0.001), roots ($F_{2,1502}$=4.607, P=0.001), rice hulls ($F_{2,1502}$=2.5393, P=0.001), worms ($F_{2,1502}$=4.055, P=0.001), macrophytes ($F_{2,1502}$=23.24, P=0.001), seeds ($F_{2,1502}$=21.370, P=0.001), detritus ($F_{2,1502}$=47.711, P=0.001). However, there were no significant (P>0.05) ontogenetic variations in the consumption of mollusks ($F_{2,1502}$=1.147, P=0.273), crustaceans ($F_{2,1502}$=0.114, P=0.758) and fish scales ($F_{2,1502}$=0.29363, P=0.932), phytoplankton ($F_{2,1502}$=0.00127, P=0.129), zooplankton ($F_{2,1502}$=0.708, P=0.136) and sand particles ($F_{2,1502}$=9.482, P=0.29).

Empty stomachs: For this study, 1505 stomachs of *S. schall* were examined and 243 of them were empty (Table 4). In general, the coefficient of emptiness varied with seasons and life stages and ranged between 5.88 and 23.47%. Empty stomachs were higher in adults and averaged 19.08±4.57% whereas relatively lower percentages were recorded among sub-adults (mean: 11.22±4.65%). In contrast, almost all juveniles exhibited full stomachs and only one individual was empty. Also, significant seasonal variations of empty stomachs were recorded during the study. Indeed, higher values were recorded during the wet and flood periods where the coefficient of

Table 4. Seasonal variations of empty stomachs of *Synodontis schall* from Niger River in Northern Benin.

Life stage	Flood			Dry			Wet			Total		
	Nt	Ne	Ec (%)	Nt	Ne	Ec (%)	Nt	Ne	Ec (%)	Nt	Ne	Ec (%)
Juveniles<5 mm	-	-	-	5	1	20	-	-	-	5	1	20
Sub-adults [5-8 mm]	14	2	14.3	252	34	13.49	17	1	5.88	283	37	13.07
Adults≥8 mm	247	48	19.4	774	111	14.34	196	46	23.47	1217	205	16.84
Total	**261**	**50**	**19.2**	**1031**	**146**	**14.16**	**213**	**47**	**22.07**	**1505**	**243**	**16.15**

Nt=Total number of stomachs, Ne= number of empty stomachs, Ec (%) = Coefficient of emptiness

Table 5. Matrix of diet overlaps (Øjk) by life stage category of *Synodontis schall* from Niger River in Northern Benin.

Length classes	Juveniles (TL<5)	Sub-adults (5≤TL<8)	Adults (TL≥8)
Juveniles (TL<5)	1	0.54	0.66
Sub-adults (5≤ TL< 8)		1	0.93
Adults (TL≥8)			1

Table 6. Diet Breadth (DB) variations by life stage of *Synodontis schall* from Niger River in Northern Benin.

	Length Classes (TS, cm)			
Seasons	Juveniles (TL<5)	Sub-adults (5≤TL<8)	Adults (TL≥8)	Total
Wet	-	4.44	5.22	5.32
Flood	-	1.86	4.42	4.22
Dry	2.46	5.74	4.34	4.84
Total	**2.46**	**5**	**4.45**	**4.93**

Table 7. Spearman correlation coefficients between standard length (SL)/gut length (GL) and the volumetric percentages of food resources consumed by *Synodontis schall* from Niger River in Northern Benin.

Prey categories	SL				GL			
	r	a (slope)	*b*	*P*-value	r	a (slope)	*b*	*P*-value
Phytoplankton	0.3162	23.1	10.30	0.842	0.3162	191	17.2091	0.374
Detritus	0.4472	3.506	10.2936	0.066	0.3317**	14.628	17.3040	0.0001
Roots	0.3162	0.88	10.3166	0.645	0.5477	7.437	17.3239	0.036
Seeds	0.4472	1.52	10.2873	0.090	0.3464**	7.150	17.3174	0.0001
Macrophytes	0.8944**	2.9363	10.2479	0.001	0.6325	4.104	17.3472	0.01
Rice hulls	-0.8367**	-8.63	10.4	0.001	-0.4899**	-28.732	17.6907	<0.001
Worms	-0.3873	-0.32	10.3353	0.876	-0.3162	-1.001	1.4751	0.793
Mollusks	0.3162	5.684	10.318	0.141	0.3162	3.610	17.4564	0.615
Crustaceans	-0.3162	-3.12	10.3	0.799	-0.3162	-11.08	17.4687	0.626
Zooplankton	0.3162	6.667	10.3025	0.175	0.4000**	44.790	17.2657	0.0001
Insects	0.5000**	3.8133	10.0679	<0.0001	0.5916**	10.621	16.7272	<0.0001
Fish scales	0.3464	1.627	10.3293	0.831	0.3162	4.81	17.4567	0.735
Sand particles	0.4472*	2.569	102291	0.050	-0.3606	-1.280	17.5163	0.608

* : Correlation is significant at P=0.05 level, **: Correlation is significant at P=0.01 level.

emptiness reached 22.07 and 19.20%, respectively, whereas that of dry season was relatively low with a value of 14.16% (Table 4).

Pianka's diet overlaps and ontogenetic diet shifts: Overall, diet overlaps between size classes of *S. schall* ranged from $Ø_{jk}$=0.54 (pairing "Juvenile X Sub-adults") to $Ø_{jk}$=0.93 (pairing "Sub-adult X Adults") and averaged $Ø_{jk}$=0.71±0.20 indicating relatively high diet similarities among different life stage categories. Nevertheless, the reduced $Ø_{jk}$=0.54 and $Ø_{jk}$ =0.66 recorded respectively between "Juvenile" and "Sub-adults" and between "Juvenile" and "adults" indicated an ontogenetic diet shift (Table 5).

Diet breadth: In Niger River in Benin, *S. Schall* consumed a wide range of food resources reaching 221 food items classified in 13 foods categories (phytoplankton, detritus, roots, seeds, macrophytes, rice hulls, worms, mollusks, crustacean, zooplankton, insects, fish scales, and sand particles). Consequently, a high diet breadth (DB=4.93) was recorded for the

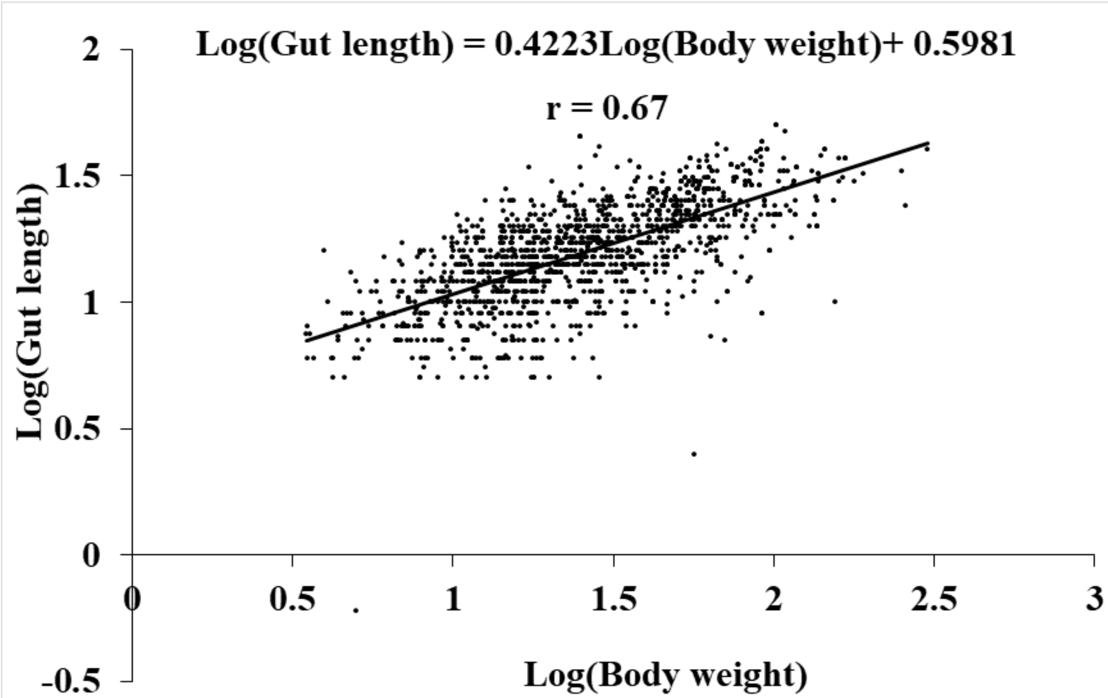

Figure 3. Relationship between Log (gut length) and Log (body weight) of *Synodontis schall* (N=1505) from Niger River in North-Benin.

whole population. Ontogenetically, the DB increased with fish sizes and ranged between DB=2.46 (juveniles and DB=5 (sub-adults) (Table 6). Also, the results showed seasonal variations in the diet breadth with a higher value (DB=5.32) recorded during the wet season whereas a relatively lower value (DB=4.22) was recorded during the flood period (Table 6).

Eco-morphological relationships: The diet of *S. schall* was evaluated by plotting the volumetric proportion of the food categories (phytoplankton, insects, crustaceans, fish scales, mollusks, zooplankton, worms, roots, seeds, detritus, macrophytes, rice hulls and sand particles) against standard length (SL) and gut length (GL) to explore ecomorphological correlates of food habits. The matrix of spearman correlation coefficients recorded indicated that SL was positively correlated with the volumetric proportions of insects (r=0.5000, P<0.01), macrophytes (r=0.8944, P<0.01), sand particles (r=0.4472, P≤0.05) and negatively correlated with rice hulls (r=-0.8367, P<0.01). Also, GL was positively correlated with detritus (r=0.3317, P<0.01), insects (r=0.5916, P<0.01), seeds (r=0.3464, P<0.01) and zooplankton (r=0.4000, P<0.01) and negatively correlated with rice hulls (r=-0.4899, P<0.01) (Table 7). In addition, the regressions between SL-GL and between W (weight)-GL were established to evaluate the ecomorphological trends. The regression equations were as follow: Log(GL)=1.0878Log(SL) +0.1146, r=0.6007 (Fig. 4); and Log (GL)=0.4223Log (W)+0.5981, r=0.6731 (Fig. 3). Both equations indicated that GL increased with SL and weight with significant (P<0.05) correlation coefficients. The ratio (GL/SL) was also computed as a measure of relative gut length and compared to published reference ratio (Kramer and Bryant, 1995). GL/SL varied from 0.12 (SL=5 cm) to 5 (SL=9 cm) with a mean of 1.69±0.56.

Discussions

Food and feeding patterns: The dietary analysis indicated that *S. schall* consumed a wide range of food resources (221 food items) dominated by eight prey categories such as insects (34.32%), sand particles (18.768%), macrophytes (13.415%), seeds (8.549%), roots (8.319%), detritus (5.344%), worms (4.735%) and rice hulls (3.681%) aggregating 97.131% of the stomach contents. This large food spectrum resulted from the presence of numerous developed mandibular teeth ranging between 24-39 and numerous gill rakers

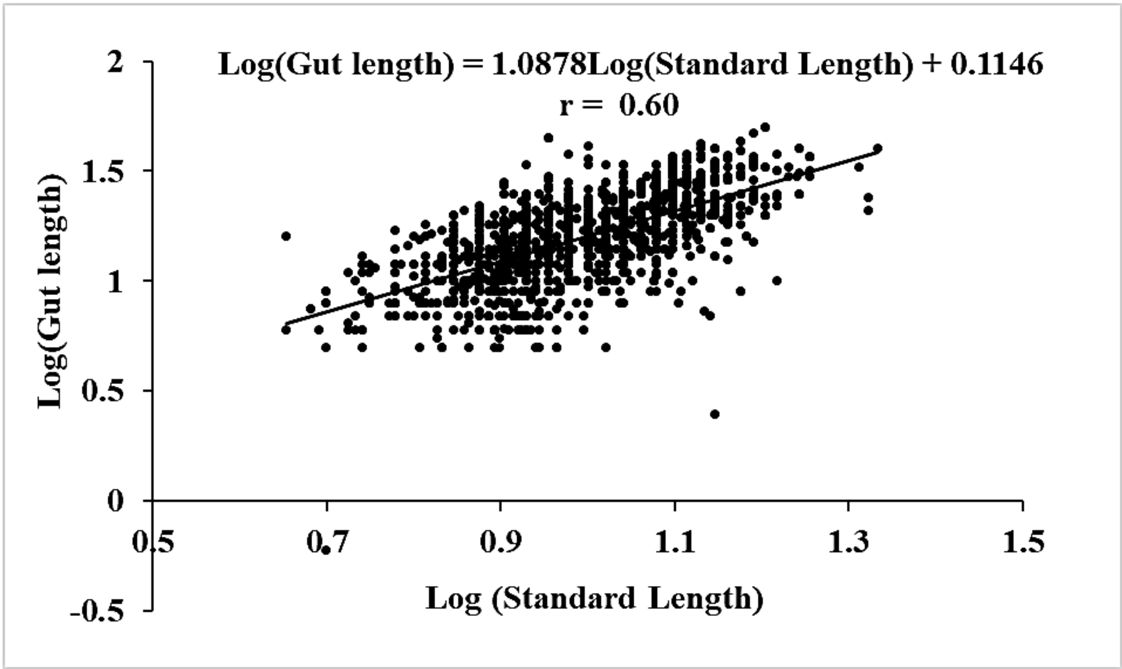

Figure 4. Relationship between Log (gut length) and Log (standard length) of Synodontis schall (N=1505) from Niger River in North-Benin.

varying between 40-44 (personal records) on the first branchial arch that could have favored this trophic flexibility (Paugy and Roberts, 2003). Minor food items were fish scales (0.80%), crustacean (0.16%) and zooplankton (0.08%) and none of them had a volumetric proportion more than 0.80%. The presence of fish scales may indicate that this species had tendency to lepidophag. This feeding pattern suggested that in Niger River in Benin, *S. schall* displayed an omnivorous feeding habit that was confirmed by the presence of balanced animal and plant matters in the stomach of *S. schall* (Dadebo et al., 2014; Admassu et al., 2015).

These findings agreed with those reported by Willoughby (1974) in Lake Kanji in Nigeria, by Yatabary (1983) in the Central Delta of Niger River and by Diomande et al. (2009) in the River-Lacustrine hydrosystem of Bia in Ivory Coast where *S. schall* foraged mainly on insect nymphs and larvae, fish eggs, detritus, zooplankton, benthos, dipteran larvae, animal fragments, fish scales, macrophytes and sediment. Likewise, in Oueme River in Benin, Laleye et al. (2006) reported identical food habits for *S. schall* that foraged mainly on macrophytes, algae, insect larvae, aquatic insects, crustacea, rotifera, molluscks, nematoda, fish eggs, fish scales and sand particles.

Ecomorphological patterns and food habits: The wide spectrum of food resources (221 foods items recorded) ingested by *S. shall* in Niger River suggested that this dominant Mochokid is an omnivore. This food trend depicted is consistent with the ecomorphology patterns of the species. Indeed, the mean relative gut length (ratio: GL/SL) fall in most omnivore ranges. These findings agreed with those reported by Al-Hussaini (1947) and Kapoor et al. (1975) where the relative gut length varied between 0.8 and 5 for omnivores while herbivore showed higher ratio ranging between 2 and 21. As reported by Dadebo et al. (2012), omnivore fishes forage both on plant and animal items and tend to have a moderate to short intestine with reduced relative gut length (GL/SL). In contrast, herbivore fishes exhibit long intestines with greater relative gut length (Al-Hussaini, 1947; Fryer and Iles, 1972; Kapoor et al., 1975).

Niche breadth, diet shift and trophic plasticity: This opportunistic feeding habit displayed by *S. schall* is the result of the high diet breadth (DB) varying between 1.86 and 5.74 that were computed from the 221 food items identified. The body morphology, the feeding behavior and the various ecological niches explored, greatly accounted for this wide spectrum of food ingested. Indeed, the ventrally positioned mouth of *S. schall* is adapted for benthic feeding. Also, the fact that *Synodontis* is able to swim in upside down position enables this genus to switch from benthic feeding to surface/pelagic feeding depending on the availability and emergence of some food items (Bishai and Gideiri, 1965; Sanyanga, 1998). Nevertheless, as *S. schall* grows and move to pelagic waters, this Mochokid is limited in foraging large prey because of its small mouth. However, its specialized teeth are suited to pick scales from other fishes in pelagic ecological niches (Fryer et al.,1955).

Although the proportional consumptions of the food items were not equally represented in the diet, the wide choice of foods available to *S. schall* suggested that when one prey was in reduced supply, the species could forage on another abundant and available prey. As reported by Mbadu (2011), this can be, not only an adaptation to reduce intraspecific competition among individuals in different classes of size, but also an indicator of trophic plasticity in *S. schall* which may shift its feeding structure according to prey availability (Adite et al., 2013; Gbaguidi et al., 2016).

The current study revealed ontogenetic diet shift of *S. schall*. Indeed, juvenile foraged preferentially on aquatic larvae (Chironomidae larva) while sub-adults and adults ingested mainly macrophytes in proportional consumptions of 15.97 and 12.912%, respectively. In contrast, in Oueme River, Laleye et al. (2006) reported *S. schall* juvenile foraging mainly on macrophytes that accounted for 59.65% of the stomach content while seeds, sand, roots, insects (diptera and coleoptera) were the dominant food items of sub-adults and adults. In Lake Chamo in Ethiopia, Dadebo et al. (2012) reported the same diet shift according to life stages. The differential development of the digestive tract and the trophic flexibility could have caused this ontogenetic diet shift in *S. schall.* Also, the study consistently showed high diet similarities between life stages indicated by a relatively high diet overlaps ranging between $Ø_{jk}$=0.54-0.93. However, the reduced diet overlaps between juveniles (TL<5 cm) and sub-adults (5≤TL<8 cm) confirmed the ontogenetic diet shift depicted (Adite et al., 2005). These results are consistent with those reported by Gbaguidi et al. (2016) with *Sarotherodon galilaeus* from a man-made Lake of Southern Benin.

Conclusion

This study documents the feeding ecology of *S. Shall*, the dominant Mochokid in Niger River in Benin. *Synodontis schall* is an omnivore foraging both in benthic and pelagic habitats and consuming mainly aquatic insects**,** macrophytes, sand particles, seeds, roots, detritus, worms, rice hulls, mollusks and phytoplankton that resulted in a large niche breadth and a high trophic plasticity. The omnivorous food habit was also shown by the ecomorphological analysis. The species exhibited an ontogenetic diet shift that was also indicated by Pianka's diet overlap. The reinforcement of fishing regulation, the protection of habitats and the permanent ecological follow-up of the river are required for the conservation and the sustainable exploitation of *S. schall*.

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