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Diet breadth variation and trophic plasticity behavior of the African bonytongue *Heterotis niloticus* (Cuvier, 1829) in the Sô River-Lake Hlan aquatic system (Benin, West Africa): Implications for species conservation and aquaculture development

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ABSTRACT

The African bonytongue, *Heterotis niloticus* (Pisces: Osteoglossidae), is an omnivore foraging mainly on aquatic insects, microcrustacea, seeds and detritus. We examined the diet breadth and the trophic plasticity behavior of this species (1461 specimens) in the Sô River and Lake Hlan water system located in the southern Benin (West Africa). Overall, the mean diet breadths of the two populations of *Heterotis* from both habitats were not significantly ($p \geq 0.05$) different and were not associated with seasons. However, in Lake Hlan, mean diet breadths tended to increase with size ($r = 0.81$) and gut length ($r = 0.82$) indicating that bonytongues ingest a broader range of food resources as they grow. In both habitats, the positive correlation of both standard length (Log SL) and gut length (Log GL) with the volumetric proportions of detritus and with the volumetric proportions of seeds suggests that the consumption of these two food resources increased with the size of *Heterotis* and with the development of the digestive tract. Likewise, the negative correlation of both (Log SL) and (Log GL) with the volumetric proportions of aquatic insects and with the volumetric proportions of microcrustacea suggests that the consumption of these two food categories decreased as the size and the gut length of *Heterotis* increased. The differences in the consumption of microcrustacea (13.77% in Lake Hlan versus 2.63% in Sô River) and mollusks (0.73% in Lake Hlan versus 4.91% in Sô River) evidenced that *Heterotis* shifts his trophic structure according to resource availability in the habitat. This foraging behavior suggests a degree of trophic plasticity in *Heterotis*. The specialized morphological structure of *Heterotis*, mainly the presence of a relatively high number of gill rakers (42 - 94 rakers on the first branchial arch) during its whole life, allowing sieving of zooplankton and other microcrustacea, and the presence of the gizzard favored this trophic plasticity. The broader diet breadth coupled with the trophic plasticity behavior is probably an advantage because it enables *Heterotis* not only to colonize and to adapt to unstable and changing aquatic habitats, but also to invade and to well-establish in various ecosystems, such as freshwater lakes, swamps, inundated plains, streams, rivers and fish farming ponds. As a result, the wider diet breadths and the trophic plasticity behavior depicted are useful eco-ethological tool for the conservation and the aquaculture development of *H. niloticus*.

Keywords: African Bonytongues; Aquaculture;

Conservation; Diet Breadth; Foraging Behavior; Gill Raker; Omnivore; Trophic Plasticity

1. INTRODUCTION

The Osteoglossiformes are highly specialized teleostean fishes of the Osteoglossomorpha super order with species almost wholly confined to tropical freshwater systems [1-3]. Among them, *Heterotis niloticus* (Osteoglossidae) is the only species of bonytongue occurring in Africa freshwater systems [4-6]. Indeed, *Heterotis* is widely distributed in the Nilo-Soudanian region and the Congo region of Central Africa and occurs in rivers such as Senegal, Gambia, Niger, Nile, Volta, Oueme, Lake Tchad, and others natural lakes and wetlands [7-9]. Moreover, *Heterotis* has been introduced in many lakes and aquaculture centers (e.g. lake Kossou and Ayame in Ivory coast, Lake Nyong in Cameroon) [6,10].

In Benin, *Heterotis niloticus* is widely distributed in rivers and inundated plains (Niger, Oueme, Zou, Sô, Mono, Couffo etc.), and freshwater lakes (Toho-Todougba, Nokoue, Hlan, Toho, lagoon of Porto-Novo, Azilli, Nakava, Cele, Codo etc.) [11-13]. The species is intensively exploited by both commercial and subsistence fishermen, and therefore, constitutes an important species for artisanal fisheries. Annual capture of *Heterotis* reached 742 tons and valued about $1,485,000 [13].

Heterotis has been characterized as a microphage or detritivore [14-16]. Recent studies [13] reveal that the African bonytongue is an omnivore foraging mainly on detritus, seeds, microcrustacea and aquatic insects.

The ability of a fish species to exploit a broad range of food resources (high diet breadth) or low range of food resources (weak diet breadth) may result from a specialized morphological structure (e.g. dental morphology, body form, number and structure of gill raker, intestine length etc.). For example the African pike, *Hepsetus*, a top carnivorous species [12] with high-developed teeth exhibits a very low diet breadth. On the contrary, *Clarias gariepinus*, a predator-omnivore species with less developed dental structure but with a relatively high number of small gill raker forages on a relatively high number of food resources, thus exhibiting a high diet breadth [14].

In addition to the morphological structure, the spatial and seasonal variation in the availability of food resources may greatly affect the food ingested and diet breadth, leading species to exhibit a trophic plasticity. Because *Heterotis* colonizes many natural aquatic systems ranging from rivers, streams to natural lakes and swamps [17], knowledge on diet breadth and trophic plasticity would give a better insight into the trophic structure dynamic, an important tool and baseline information to conserve, manage and restore fish resources in their habitat and to develop aquaculture technologies [18,19]. Given the spatial and seasonal variation of the food resources availability, it is important to well document the diet breadth variation and the trophic plasticity to explore the species feeding strategies.

The present study aims to investigate the variation of the diet breadth in relation to space and season and the trophic plasticity behavior in order to better document the trophic structure dynamic in the Sô River and Lake Hlan system.

2. MATERIAL AND METHODS

2.1. Study Locations

Field surveys were conducted at two locations in southern Benin (**Figure 1**): a reach of the lower Sô River (6˚34.97 N; 2˚23.75 E) and Lake Hlan (6˚56.88 N; 2˚19.48 E). This region has a sub-equatorial climate with two wet seasons (April to July; mid-September to October) and two dry seasons (November to mid-March; August to mid-September). Annual rainfall recorded for 2002 was 1167.2 mm [20], and the highest monthly rainfall during the investigation was 438.8 mm for June 2002. The Sô River is a secondary channel of the lower Oueme River and flows southward, parallel with the Oueme, approximately 100 km through a floodplain covering approximately 1000 km^2 [12]. Hydrology of rivers in southern Benin is strongly influenced by seasonal rainfall in the northern region. During the peak flood season (October-November), water from the Oueme and Sô rivers covers extensive floodplains. Habitat parameters were characterized at each sampling site (water quality, aquatic vegetation, substrate, riparian vegetation, and land use).

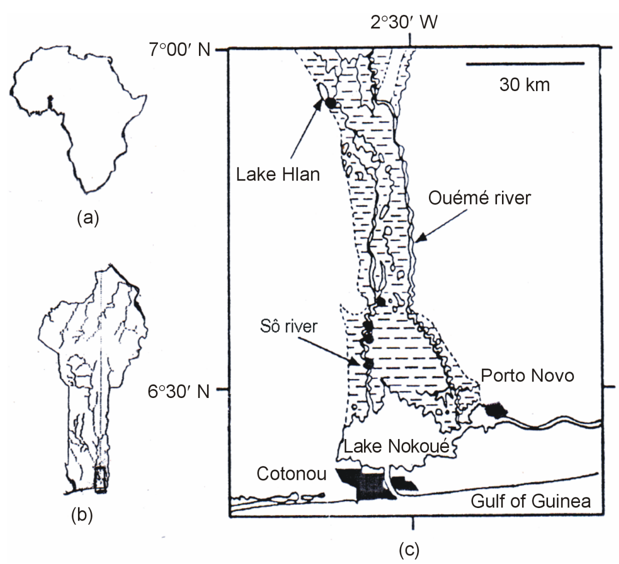

Figure 1. Map showing Benin in Africa (a), the study region in southern Benin (b) and the sampling sites (dots) in Sô River floodplain (villages Ahome-Gblon, Ahome-Lokpo Zoungome, Kinto) and Lake Hlan from South to North, respectively.

Water depth was measured using a calibrated rope. Temperature and dissolved oxygen were measured to the 0.1˚C and 0.1 $mg \cdot l^{-1}$ respectively with a digital oxythermometer. Turbidity was measured to the nearest millimeter with a secchi disk. pH was measured to the nearest 0.1 with a portable pH meter. Salinity, total dissolved solids (TDS) and conductivity were measured to the nearest 1, 0.1 and 0.1 $mg \cdot l^{-1}$ respectively with a conductivity meter. Nitrites and total iron were measured to the nearest 0.01 $mg \cdot l^{-1}$ via titration with Merck reagents. During the study period, water depth in the main river channel averaged 421.2 (±210.1 SD) cm and turbidity averaged 40.3 (±28.2) cm. Dissolved oxygen ranged between 0.4 and 4.5 mg/l (9% - 77% saturation). Most other physical and chemical features revealed less variation; mean water temperature during the study was 28.6 (±2.2)˚C, pH averaged 5.4 (±0.6), electric conductivity averaged 99.45 (±3.1) µs/cm, and average total dissolved solid (TDS) was 46.75 (±5.38) mg/l. Nitrite and total iron concentrations averaged 0.002 (±0.0015) mg/l and 1.04 (±0.66) mg/l, respectively. The dominant floating macrophytes on the Sô River are *Eicchornia crassipes*, a species that invaded the system about 25 years ago. Other common aquatic plants were *Pistia stratiotes* (Aracea) and *Ipomea aquatica* (Convolvulaceae). Palms (*Elaies guinensis*) were the dominant riparian trees.

Lake Hlan is located near Kpomey village (Sehoue City) about 80 km from the Atlantic coast. Locally known as "the Bonytongue Lake", Lake Hlan receives comparatively low exploitation owing to local enforcement of traditional fishing regulations. Lake Hlan has a lower average depth (250.3 ± 128.5 cm) than the study reach on the Sô River. The annual flood was very low in Lake Hlan during 2002 (maximum water depth = 340 cm), but occurred normally during 2003 (maximum water depth = 670 cm). Dissolved oxygen ranged from 0.1 mg/l (25.47% of saturation) to 4.8 mg/l (79%). Water transparency averaged 88.1 (±25.2) cm, mean water temperature was 27.60 (±1.80)˚C, mean pH was 5.3 (±0.20), average conductivity was 97.0 (±5.5) µs/cm, and mean total dissolved solid (TDS) was 47.0 (± 2.85) mg/l. Nitrites and total iron concentration were low and averaged 0.002 (±0.001) mg/l and 0.67 (±0.26) mg/l, respectively. Floating grasses, such as *Cyperus difformis* (Cyperaceae), cover large areas of the lake and hinder fishing activities. Wind-driven movement of grass mats sometimes damages fishing gear. These grasses also provide habitat for many aquatic organisms, including small fishes. Water hyacinth is present in Lake Hlan, but at low biomass compared to most areas of the river channel. Other common floating macrophytes in Lake Hlan were *Pistia stratiotes*, *Azolla africana*, *Nymphaea lotus* and *N. maculatus* (Nymphaeacea), *Eicchornia crassipes*, *Echinochloa pyramides* (Poacee). Submerged plants included *Ceratophyllum demersum* (Ceratophyllaceae) and *Utricularia inflexa* (Lantibulariaceae).

2.2. Fish Sample Collection

Bonytongue specimens were collected monthly from both aquatic vegetation and open water at four sites in the Sô River and Lake Hlan during eighteen (18) months. At each site, fish individuals were captured with two fishing gears in order to obtain representative samples of all size classes in the local population. In the Sô River, surveys were conducted along a longitudinal reach. Patches of vegetation were encircled with a net (2-m high, 10-mm mesh), and vegetation and fish were removed. Open water areas of the river were sampled with a cast net (50 - 80 mm mesh). In Lake Hlan, fish were collected with traps (80 mm long; 50 mm opening), gill nets (20 m × 2 m, 60-mm bar mesh), and hooks. Local fishermen were enlisted to set traps in vegetation close to the openings of active nests. All captured size classes were retained for analysis. Adult size classes were rare at Sô River survey sites, and monthly sampling effort was continued until collection effort yielded samples that reflected population structure.

Each specimen of *Heterotis* was measured for standard (SL) and total length (TL) to the nearest 0.1 mm with a graduated measuring board and weighed to the nearest 0.1 g with an electronic balance. Specimens were dissected, and each alimentary canal was removed and its length was measured as the distance from the distal end of one of the two pyloric caecae to the anus (Moreau; 1982). Stomachs were preserved in 5% formalin and transported to the laboratory of the Department of Zoology & Genetics of the University of Abomey-Calavi. Preserved stomachs were removed from the formalin and placed in 75% ethanol for preservation.

2.3. Stomach Content Analysis

The ethanol-preserved stomachs were opened and all preys were removed and spread on a glass slide for examination under a dissecting microscope. Water was added to facilitate separation of small items. A sub-sample of the contents was examined under a compound microscope to identify phytoplankton. Food items were identified to the lowest possibly taxonomic level using Needham and Needham (1962) [21] for aquatic invertebrates, zooplankton, and phytoplankton. After identification, food items were separated and blotted on a paper towel to remove excess moisture. The volume of each food category was estimated by water displacement using an appropriately sized graduated cylinder. Volumes of small items (<0.002 ml) were estimated by spreading the material on a glass slide then visually estimating the collective volume by comparison with a sample of known volume

[22].

2.4. Data Analysis

Food items ingested by the different sizes classes of *H. niloticus* were aggregated by category, and volumetric proportions of these new aggregate categories were summed.

Volumetric proportions of each food item ingested by *H. niloticus* were computed following the formula:

$$p_i = \left(\sum_{i=1}^{n} \text{vi}\right) \Big/ \text{Vt}$$

where p_i is the proportion of food item i in the diet, n is the number of stomachs, vi is the volume of food item i in a single stomach, Vt is the total volume of food ingested by n stomachs (in this study, n = 1461 stomachs).

Diet breadth was calculated following Simpson's (1949) diet breadth formula (Krebs, 1989) [23,24]:

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

where p_i is the proportion of food item i in the diet, and n is the total number of food items in the diet. B ranges from 1, when only one resource is used, to n, when all resources are consumed in equal proportions. Seasonal and size differences in volumetric proportions and values of indices were compared with analysis of variances (ANOVA) using SPSS software package [25]. Ecomorphological relationships were examined using linear regression analysis between standard length/gut length and the main food items and between standard length/gut length and the diet breadth.

3. RESULTS

3.1. Prey Ingested

In both Lake Hlan and Sô River, *H. niloticus* consumed a variety of benthic and pelagic prey resources dominated by detritus and sand particles, hard seeds, aquatic insects, microcrustacea and mollusks (**Tables 1-6**). Aquatic insects were mostly immature stages of Diptera (Chironomidae, Ceratopogonidae, Syrphidae, Tipulidae, Empididae), Ephemeroptera, Coleoptera (Dryopidae, *Cybister*, Helodidae, *Thermonectus*), Hemiptera, Odonata, Heteroptera, and Plecoptera. Among aquatic insects, chironomid larvae dominated diets in both Lake Hlan and Sô River with volumetric proportions varying from 5.98% to 39.57% (mean = 17.15%), and from 0% to 38.94% (mean = 21.08%), respectively. Ephemeroptera (means = 4.80% in Lake Hlan vs 0.05% in Sô River) were more common in diets of Lake Hlan fish, whereas Coleoptera (means = 1.67% in Lake Hlan vs 7.56% in Sô River) were more abundant in Sô river fish diets. Microcrustacea were mostly Cladoceran (mainly Daphnidae), Ostracoda (*Cypridopsis*), Copepoda (mainly *Cyclops* and *Diaptomus*), Amphipoda, and Eubranchipoda. In general cladocerans were the most important microcrustaceans in both habitats. Water mites (Hydracharidae) generally were consumed in low proportions, but were common in diets of subadults in Lake Hlan. Gastropod mollusks (Limnidae, Planorbiidae, Hydrobiidae, Physidae) were more abundant in diets of fish from Sô River. Minor diet items were plant tissues (including flowers and fruits), terrestrial insects (Coleoptera, Hymenoptera, Megaloptera), chitin fragments, nematode worms, invertebrate eggs, Rotifera

Table 1. Matrix of food categories consumed by size class of *Heterotis niloticus* captured in Lake Hlan during the wet season.

Prey categories	*Heterotis* size class (SL)							
	<100	200	300	400	500	600	700	800
Sands	-	-	-	21.43	18.78	50.52	26.13	36.86
Detritus	-	-	-	-	3.74	14.40	6.49	14.48
Algae	-	-	-	-	0.036	0.34	0.06	-
Plants	-	-	-	-	-	-	-	-
Seeds	-	-	-	74.29	25.48	19.95	30.74	15.26
Rotifer	-	-	-	-	-	0.82	0.06	-
Microcrustacea	-	-	-	-	37.68	3.05	24.39	22.66
Invertebrate eggs	-	-	-	-	-	0.38	0.11	-
Aquatic insects	-	-	-	4.29	13.55	9.26	11.35	10.64
Terrestrials arthropods		-	-	-	0.24	0.02	0.11	-
Hydracharids	-	-	-	-	0.24	0.39	0.04	0.08
Worms	-	-	-	-	0.12	0.47	0.46	-
Molluscs	-	-	-	-	0.12	0.016	0.07	0.01

Table 2. Matrix of food categories consumed by size class of *Heterotis niloticus* captured in Lake Hlan during the high-water season.

Prey categories	***Heterotis* size class (SL)**							
	<100	**200**	**300**	**400**	**500**	**600**	**700**	**800**
Sands	10.28	10.18	13.00	20.53	22.93	23.54	25.68	30.66
Detritus	1.03	0.96	5.52	5.32	7.00	10.16	8.55	6.51
Algae	-	-	-	0.03	-	0.02	0.03	-
Plants	-	2.13	0.08	-	0.05	0.20	0.23	-
Seeds	-	5.62	17.72	33.08	36.65	37.64	35.33	25.42
Rotifer	-	-	-	-	-	0.22	0.08	-
Microcrustacea	13.87	26.69	23.22	10.47	11.55	1.27	11.27	17.68
Invertebrate eggs	10.28	3.43	0.88	-	-	-	-	-
Aquatic insects	64.44	49.95	38.69	30.57	21.78	28.55	18.45	19.38
Terrestrials arthropods	-	-	-	-	-	-	-	-
Hydracharids	0.10	0.70	0.52	0.01	0.01	0.03	0.03	0.35
Worms	-	-	-	-	-	-	0.04	-
Molluscs	-	0.34	0.34	-	0.03	0.63	0.28	-

Table 3. Matrix of food categories consumed by size class of *Heterotis niloticus* captured in Lake Hlan during the dry season.

Prey categories	***Heterotis* size class (SL)**							
	<100	**200**	**300**	**400**	**500**	**600**	**700**	**800**
Sands	-	-	37.12	29.23	23.58	27.38	23.17	22.88
Detritus	-	-	9.97	3.01	3.75	6.34	6.68	11.76
Algae	-	-	0.02	0.01	-	0.01	0.01	0.01
Plants	-	-	11.84	0.56	4.76	0.94	0.73	1.16
Seeds	-	-	24.39	34.40	32.45	24.89	34.68	25.42
Rotifer	-	-	0.02	-	-	-	-	-
Microcrustacea	-	-	3.24	6.84	4.20	11.24	17.28	3.65
Invertebrate eggs	-	-	-	0.43	-	-	-	-
Aquatic insects	-	-	12.46	23.14	30.42	24.28	16.23	31.61
Terrestrials arthropods	-	-	0.05	0.03	0.03	0.24	-	-
Hydracharids	-	-	0.04	-	0.03	-	-	-
Worms	-	-	-	0.17	-	-	-	-
Molluscs	-	-	0.86	2.17	0.78	4.68	1.22	3.57

Table 4. Matrix of food categories consumed by size class of *Heterotis niloticus* captured in the Sô river during the wet season.

Prey categories	***Heterotis* size class (SL)**							
	<100	**200**	**300**	**400**	**500**	**600**	**700**	**800**
Sands	-	-	38.43	43.19	49.13	32.84	46.87	-
Detritus	-	-	0.30	1.73	-	10.82	3.50	-
Algae	-	-	-	-	-	2.09	-	-
Plants	-	-	4.85	0.90	0.18	1.93	1.23	-
Seeds	-	-	26.39	12.29	4.62	27.42	8.41	-
Rotifer	-	-	-	-	-	-	-	-
Microcrustacea	-	-	-	2.06	-	0.54	-	-
Invertebrate eggs	-	-	-	-	-	3.91	-	-
Aquatic insects	-	-	28.57	35.54	23.75	9.66	39.77	-
Terrestrials arthropods	-	-	-	-	-	-	-	-
Hydracharids	-	-	0.03	-	-	0.04	0.04	-
Worms	-	-	-	-	-	0.16	-	-
Molluscs	-	-	1.43	2.23	11.59	0.18	-	-

Table 5. Matrix of food categories consumed by size class of *Heterotis niloticus* captured in the Sô river during the high-water season.

Prey categories	*Heterotis* size class (SL)							
	<100	200	300	400	500	600	700	800
Sands	-	-	30.57	17.32	16.70	-	77.12	43.30
Detritus	-	-	3.33	0.89	0.48	-	-	-
Algae	-	-	0.06	-	-	-	-	-
Plants	-	-	5.96	1.80	-	-	-	-
Seeds	-	-	18.99	36.10	50.71	-	8.60	25.77
Rotifer	-	-	0.09	-	-	-	-	-
Microcrustacea	-	-	0.86	8.35	5.46	-	2.38	-
Invertebrate eggs	-	-	-	0.24	-	-	-	-
Aquatic insects	-	-	32.45	31.48	26.65	-	11.83	30.93
Terrestrials arthropods	-	-	-	-	-	-	-	-
Hydracharids	-	-	0.03	-	-	-	0.03	-
Worms	-	-	0.06	-	-	-	-	-
Molluscs	-	-	7.61	4.50	-	-	-	-

Table 6. Matrix of food categories consumed by size class of *Heterotis niloticus* captured in the Sô river during the dry season.

Prey categories	*Heterotis* size class (SL)							
	<100	200	300	400	500	600	700	800
Sands	-	48.88	25.79	27.17	18.59	-	-	-
Detritus	-	0.42	2.91	3.42	2.93	-	-	-
Algae	-	-	-	-	-	-	-	-
Plants	-	-	1.35	1.57	-	-	-	-
Seeds	-	22.91	13.61	12.24	19.93	-	-	-
Rotifer	-	-	-	-	-	-	-	-
Microcrustacea	-	0.42	4.63	5.04	8.80	-	-	-
Invertebrate eggs	-	-	-	0.13	-	-	-	-
Aquatic insects	-	27.37	50.41	49.57	47.79	-	-	-
Terrestrials arthropods	-	-	-	-	-	-	-	-
Hydracharids	-	-	0.03	-	-	-	-	-
Worms	-	-	-	-	-	-	-	-
Molluscs	-	-	1.27	0.86	1.96	-	-	-

(*Testudinella*, *Asplanchna*, *Chromogaster*, *Brachionus*, *Euchlanis*, *Keratella*), and various algae taxa such as diatoms (*Raphoneis*, *Pleurosigma*, *Synedra*, *Nitzschia*, *Gomphonema*, *Melosira*, *Tabellaria*, *Asterinella*, *Navicula*), cyanobacteria (*Polycistis*, *Protococcus*, *Phormidium*, *Coelosphaerium*, *Nostoc*, *Oscillatoria*, *Merismopodia*), green algae (*Rhizodonium*, *Botyococcus*, *Ulothrix* sp, *Richterella*, *Spirogyra*, *Coelastrum*) and desmids (*Gonatozygon*, *Closterium*).

One-way ANOVA revealed significant between-habitat differences in consumed volumetric proportions of some of the dominant food resources. Among aquatic invertebrates, significant differences were found between proportions consumed in the two habitats for Odonata niads ($P < 0.01$), item that was more common in diets of fish individuals from Lake Hlan, as well as Coleoptera ($P < 0.05$) and mollusks ($P < 0.05$) groups that were consumed in greater proportions by individuals from the Sô River. Most of the Coleoptera in stomachs were adults. Volumetric proportions of aggregated microcrustaceans (Ostracoda, Cladocera, Copepoda, Eubranchipoda, Amphipoda) consumed by *Heterotis* differed in diets of fishes from the two habitats ($P < 0.05$), with higher proportions associated with individuals from Lake Hlan. Proportional consumption of sand and detritus, seeds, and aggregated aquatic insects did not differ significantly ($P \geq 0.05$) between the two habitats. With regard to seasons, in Lake Hlan, proportional consumption of aquatic insects was greater during the high-water season and those of sand & detritus and microcrustacea was greater during the wet season (**Tables 1** and **2**). Also, in Lake Hlan, proportional consumption of seeds tended to be greater during the dry season (**Table 3**). In the Sô River, proportional consumption of sand and detritus was greater during the wet season and proportional consumption of seeds was greater during the high-water season (**Tables 4** and **5**). Also, in the Sô River, the volumetric proportion of aquatic insects ingested by bonytongues was greater during the dry season when inundated plain is shrinking and aquatic insects become more concentrated and more available for *Heterotis* (**Table 6**).

3.2. Spatial and Seasonal Variation of Diet Breadth

In spite of the significant differences ($P < 0.05$) in microcrustacea consumption between *Heterotis* populations from Lake Hlan and Sô River, which was not the case for detritus & sand, seeds, and aquatic insects, these two habitats failed to show any significant ($P < 0.05$) differences in the diet breadth. Mean diet breadth for Lake Hlan and Sô River was 3.71 (range = 2.19 - 4.87) and 3.35 (range = 2.08 - 4.58), respectively (**Tables 7** and **8**). Likewise, the diet breadths of *Heterotis* population from both habitats, Lake Hlan and Sô River were not significantly ($P \geq 0.05$) associated with seasons. In Lake Hlan, diet breadths varied from 1.67 to 4.18 (mean = 3.37) during the wet season, from 2.19 to 4.38 (mean = 3.62) during the high-water season and from 3.78 to 4.66 (mean = 4.18) during the dry season. In the Sô river, diet breadths varied from 2.59 to 4.58 (mean = 3.27) during the wet season, from 1.61 to 4.38 (mean = 3.01) during the high-water season and from 2.92 to 3.96 (mean = 2.95) during the dry season (**Tables 7** and **8**).

3.3. Ecomorphological Correlates

To explore the ecomorphological patterns of the trophic structure of *Heterotis*, the volumetric proportion of each main food resource consumed (detritus, seeds, microcrustacea, aquatic insects) were plotted against the standard length (SL) and the gut length (GL). Logarithm transformation of SL and GL was used to reduce skew in the dataset. In both habitats, the linear regression equations showed that Log (SL) and Log (GL) were positively correlated with the volumetric proportion of detritus and with the volumetric proportion of seeds (**Table 9**). On the contrary, the standard length (Log SL) and the gut length (Log GL) were negatively correlated with the volumetric proportion of aquatic insects and with the volumetric proportion of microcrustacea (**Table 9**). However, in Lake Hlan, the coefficients of correlation tended to be higher than those of the Sô River (**Table 9**).

In Lake Hlan, the scatter plot and the linear regression equations (**Figures 2** and **3**) showed that the diet breadth was positively correlated ($P < 0.05$) with the standard length ($r = 0.81$) and the gut length ($r = 0.82$). On the contrary, in the Sô River, the diet breadth was negatively correlated (but not significant) with the standard length ($r = -0.39$) and the gut length ($r = -0.37$) (**Figures 2** and **3**). As results, the computed coefficient of correlations indicated that DB in Lake Hlan exhibited similar trends with SL ($r = 0.81$) and GL ($r = 0.82$). The same pattern was recorded in Sô River with $r = -0.39$ and $r = -0.37$ for the regression of DB with SL and GL, respectively.

Table 7. Diet breadth (DB) by size class of *Heterotis niloticus* captured in Lake Hlan.

Season	*Heterotis* size class (SL)							
	<100	200	300	400	500	600	700	800
Wet	-	-	-	1.67	3.81	3.07	4.18	4.12
High-Water	2.19	2.98	3.92	3.86	3.96	3.61	4.08	4.32
Dry	-	-	4.20	3.78	3.86	4.66	4.26	4.29
Total DB	2.19	2.96	4.87	3.78	4.10	4.08	4.23	4.60
N˚ Individuals	9	322	89	73	73	74	232	36

Table 8. Diet breadth (DB) by size class of *Heterotis niloticus* captured in the Sô River.

Season	*Heterotis* size class (SL)							
	<100	200	300	400	500	600	700	800
Wet	-	-	3.32	3.02	2.86	4.58	2.59	-
High-Water	-	-	4.08	3.72	2.78	-	1.61	2.86
Dry	-	3.96	2.92	2.95	3.21	-	-	-
Total DB	-	3.96	3.10	3.56	3.33	4.58	2.08	2.86
N˚ Individuals	-	14	180	222	111	19	6	1

Table 9. Matrix of coefficient of correlation (r), slope and intercept for the regression between the volumetric proportion of the main foods resources (detritus, seeds, microcrustacea, aquatic insects) and the morphological features (standard length, gut length) of *Heterotis niloticus* captured in lake Hlan and in the Sô River. Logarithmic transformation of standard length (SL) and gut length (GL) was considered for the regression. N = number of SL size classes.

Regressions	Lake Hlan (N = 8)			Sô River (N = 7)		
	Slope	r	Intercept	Slope	r	Intercept
Detritus – Log (SL)	37.39	0.84	−71.14	37.39	0.51	−62.13
Detritus – Log (GL)	40.03	0.84	−81.33	45.97	0.57	−89.48
Seeds – Log (SL)	36.69	0.82	−71.85	3.13	0.07	14.95
Seeds – Log (GL)	41.31	0.86	−87.28	0.49	0.01	21.92
Microcrustacean – Log (SL)	−7.82	−0.35	33.90	−2.30	−0.18	8.75
Microcrustacean– Log (GL)	−10.12	−0.41	40.68	−0.92	−0.30	5.04
Aquatic insects – Log (SL)	−53.01	−0.96	168.04	−28.12	−0.49	105.79
Aquatic insects – Log (GL)	−57.93	−0.97	185.61	−84.15	−0.94	265.3

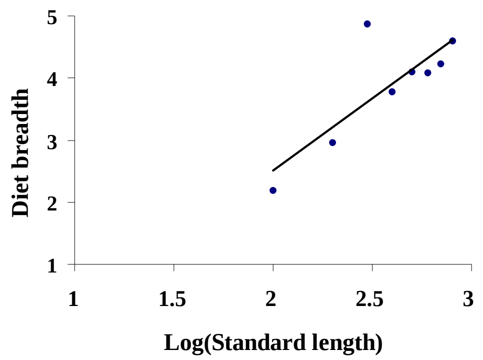

Figure 2. Relationships between diet breadth (DB) and standard length (SL) of *Heterotis niloticus* captured in Lake Hlan. DB is positively correlated with Log (SL). Regression equation is: DB = 2.33*Log (SL) - 2.15; r = 0.81; N = 8.

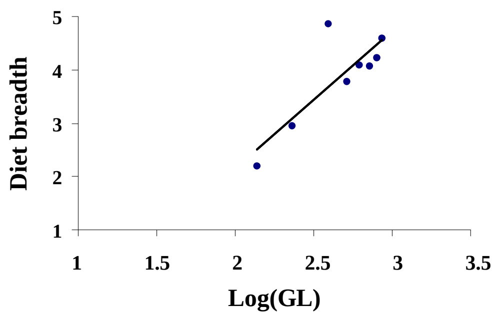

Figure 3. Relationships between diet breadth (DB) and gut length (GL) of *Heterotis niloticus* collected in Lake Hlan. DB is positively correlated with Log (GL). Regression equation is: DB = 2.56*Log (GL) - 2.97; r^2 = 0.82; N = 8.

4. DISCUSSIONS

4.1. Diet Breadth Trends

Because Lake Hlan is a relatively more stable aquatic ecosystem with the presence and the persistence of swamp habitats throughout all the seasons, facilitating permanent colonization and availability of food resources [13], we expect to obtain higher diet breadth in this habitat compared to Sô River. The Sô river, a less stable habitat, although periodically flooded (3 - 4 months) should exhibit a relatively low food resource availability during much time of the year (dry season: 8 - 9 months) and consequently *Heterotis* population from the Sô river should exhibit a low diet breadth. This was not the case. Mean diet breadths were nearly the same regardless of habitats. This result suggest that, probably, when a main food resource (detritus, seeds, microcrustacea, aquatic insects) availability is low in an habitat (e.g. zooplankton in the Sô River, mollusks in Lake Hlan), *Heterotis* adjust his foraging efficiency on the available resources to maintain the diet breadth at a top level in order to satisfy their food and nutritional needs.

In term of biodiversity conservation, this trophic pattern is an advantage for species survival and conservation in natural habitats, and may explain why *Heterotis* is widely distributed in the numerous freshwater systems of Benin. In captivity (aquaculture), the broader diet breadth and this trophic adaptation of *Heterotis* may facilitate the efficient exploitation of the different levels (detritus, zooplankton, insects) of the trophic chain in the fish ponds [17,18].

In both habitats, diet breadth was not associated with season. However, in the Sô River, the relative low diet breadth of the dry season compared to that of the wet and high water seasons is probably due to the low food resource availability during the dry season when the river is not flooded and is reduced to the main channel. In Lake Hlan, the progressive increase of the diet breadth from wet to dry season is probably due to a progressive colonization (multiplication) of food resources which have become concentrated and more available during the dry season, as water volume is depleted.

The lack of association of the diet breadth with habitats on one hand, and with seasons on the second, suggests that, despite the differences in food resources availability between habitats or throughout seasons, *Heterotis* manage to adjust his diet (volumetric proportion of food items ingested) in order to maintain nearly the same diet breadth. This prey consumption adjustment and foraging strategy are possible because of *Heterotis* omnivore diet habit and its specialized morphological structure [7].

4.2. Ecomorphological Patterns

In both habitats, the positive correlation of both standard length Log (SL) and gut length Log (GL) with the volumetric proportions of detritus and seeds suggests that the consumption of these two food resources increased with the size of *Heterotis* and the development of the digestive tract (Danson-Ofori, 1992; Koen Alonso, 2002) [26,27]. At the early age (<100 mm), the digestive tract of *Heterotis* is less developed to digest detritus and seeds with hard coats. As the development of the digestive system is initiated with a functional gizzard, *Heterotis* begin to progressively ingest detritus and seeds. Indeed, the digestive apparatus of *Heterotis* comprises a gizzard, a thick – walled muscular chamber that facilitates the digestion of refractory organic matter such as plants detritus, hard seeds, carapace and shell (Bowen, 1983; Adite *et al*., 2005) [13,28]. Likewise, the negative correlation of both standard length Log (SL) and gut length Log (GL) with the volumetric proportions of aquatic insects and with those of microcrustacea suggests that the consumption of this two food categories decreased as the sizes and the gut length of *Heterotis* increased. In general, small fish individuals with less developed digestive system forage heavily on live food such as microcrustacea, insect larva and nymphs (Garcia-Berthou, 1999; Garcia-Berthou and Moreno-Amich, 2000) [29,30]. However, as digestive tract becomes well developed, *Heterotis* takes advantage to other available resources such as detritus and seeds to rapidly satisfy his high protein and energetic requirements (Steingrimsson and Gislason, 2002) [31]. The low negative correlations of standard length and gut length with microcrustacea compared to those with aquatic insects were probably due to the presence of gill rakers (42 - 94 rakers on the first branchial arch) (Moreau, 1982) during the whole life of *Heterotis*, which facilitate sieving of zooplankton and other microcrustacea regardless of age or size (Adite *et al*., 2006) [8,32]. For example, a 605 mm specimen, collected from Lake Hlan have consumed 100% (volume = 3 ml) of microcrustacea, mainly cladoceran and copepod.

In Lake Hlan, mean diet breadth tended to increase with size ($r = 0.81$) and gut length ($r = 0.82$) indicating that bonytongues ingest a broader range of food resources as they grow (Winemiller, 1989) [22]. This patterns was not apparent for Sô River (**Figures 2** and **3**) because of the low sample size for the 700 mm SL (N = 6) size class and for the 800 mm SL (N = 1) size class, and probably led to an underestimate of diet breadth for these size classes in the Sô River.

4.3. Trophic Plasticity Behavior: Implications for Species Conservation and Aquaculture Development

When examining the volumetric proportion of the main food items (detritus, seeds, microcrustacea, aquatic insects) consumed by *Heterotis* in the two habitats, the microcrustacea ingested in the Sô River was significantly ($P < 0.05$) lower compared to that consumed by the population of Lake Hlan. The mean volumetric proportions of microcrustacea in Lake Hlan and Sô River were 13.77% (range: 4.41% - 27.07% for 600 mm SL and 200 mm SL size classes, respectively) and 2.63% (range: 0% - 6.32% for 800 mm SL and 500 mm SL size classes, respectively), respectively. This high gap in the consumption of microcrustacea between the two populations was probably due to the low availability of this food resource in the Sô River and may result from the differences in habitat characteristics: the Sô River is a lotic environment (running water) which undergoes a high disturbance during the flooding season creating a high turbidity. This disturbance may inhibit photosynthesis and consequently may reduce primary production (phytoplankton) and zooplankton proliferation.

In the Sô River, this low ingestion of microcrustacea was associated with a relatively high consumption of mollusks compared to Lake Hlan. Mean volumetric proportions of mollusks consumed in the Sô river and lake Hlan were 4.91% (range: 0% - 11.59%) and 0.73% (range: 0% - 1.65%), respectively. Therefore, the zooplanktinovore trend of *Heterotis* diet habit observed in Lake Hlan was not apparent in the Sô River, probably because of the low availability of zooplankton in this habitat. Likewise, the relatively high consumption of mollusks in the Sô River was not apparent in Lake Hlan where this food item is likely less available.

As a result, this foraging pattern suggests a degree of trophic plasticity in *Heterotis*, which may shift his trophic structure according to resource availability in the habitat [13,33]. This trophic plasticity behavior is favored by the specialized morphological structure of *Heterotis*, mainly the presence of a relatively high number of gill rakers (42 - 94 rakers on the first branchial arch) [7,8] during its whole life, allowing sieving of zooplankton and other microcrustacea, and the presence of the gizzard that facilitates the digestion of refractory organic matter such as mollusks with hard carapace [13,28]. Also, the omnivorous diet habit and the relatively high diet breadth resulting from this specialized morphological structure favored such trend of trophic plasticity in *Heterotis*.

In the Sô River, despite the relatively high availability of both seeds and aquatic insects resulting from their periodic invasion caused by the intrusion of flood water in the relatively dense adjacent vegetation, *Heterotis* did wider its consumption towards mollusks, source of animal protein. These foraging behavior suggest that this species take advantage to the available preys to probably maintain a balance diet and to satisfy energetic and protein requirements for rapid growth.

The trophic plasticity behavior, presently evidenced in *Heterotis*, is common in migratory species and in fish species inhabiting unstable habitats. For example, in lake Sibaya (South Africa), Bowen *et al*. (1982) [34] have reported a similar trend of trophic plasticity with *Tilapia mossambicca* (Cichlidae) whose diet changed from benthic detrital aggregate to periphyton while moving from a deep offshore water to shallow (0.5 m) littoral areas.

In addition to the broader diet breadths, the trophic plasticity behavior depicted is an advantage for the survival, the conservation and the aquaculture development of *Heterotis* because enable the species not only to colonize and to adapt to unstable and changing aquatic habitats, but also to invade and to well establish in many habitats with different features (physical characteristics; food availability, niche breadths and niche overlaps), such as freshwater lakes, swamps, inundated plains, streams, rivers and fish ponds capable of varying water level in order to stimulate gonad maturation and to insure reproduction success [32,35].

5. CONCLUSION

Currently, among the African freshwater fishes, *H. niloticus* is considered as an important key species under genetic, bio-ecology, fishery and aquaculture researches because of its large size, high growth rate, the omnivore food habit and its overexploitation in the highly degrading aquatic environment. The output of the present investigation on the diet composition, the diet breadth and the trophic plasticity gives valuable information for the conservation, the sustainable fisheries management and the farming development of this highly economic and commercial species.

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