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Ontogenetic, seasonal, and spatial variation in the diet of *Heterotis niloticus* (Osteoglossiformes: Osteoglossidae) in the Sô River and Lake Hlan, Benin, West Africa

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Synopsis

The African bonytongue, *Heterotis niloticus* (Osteoglossidae), is an important fisheries and aquaculture species in West Africa. This species has frequently been characterized either as an omnivore, insectivore or detritivore, the latter, in part, because of its benthic feeding habitats and possession of a gizzard (thick-walled pyloric stomach). We examined diets of two populations of *H. niloticus* in the Sô River in southern Benin. A population from the river channel and seasonally flooded marginal plains was dominated by juvenile and subadult size classes. Adults size classes were common in a second population from Lake Hlan, a natural lake in the river floodplain located upstream from the channel study region. *Heterotis* of all sizes consumed a variety of food resources, ranging from aquatic invertebrates to small seeds. Aquatic invertebrates composed a large proportion of the diets of juveniles, and adults consumed a mixture of aquatic invertebrates, seeds, and detritus. Seasonal dietary variation was observed in both populations, and diet breadth was not significantly different between populations. Aquatic invertebrates remained significant in diets of larger size classes; diets of fish between 100 and 200 mm began to include seeds and detritus, with a marked increase in the volumetric proportion of detritus in diets of fish between 300 and 400 mm in Lake Hlan and between 500–600 mm in the river. Relative gut length was inversely related to body size, which supports the notion that *Heterotis* is an omnivore and not a specialized detritivore. The thick-walled gizzard of *Heterotis*, which generally contained sand, probably aids digestion of seed coats. Because *Heterotis* consume mostly invertebrates and grass seeds in shallow waters of seasonal aquatic habitats and lakes in the river floodplain, foraging success and fishery production should be strongly dependent on the annual flood pulse.

Introduction

In spite of their great evolutionary and fishery significance, the bonytongue fishes of the family Osteoglossidae (Osteoglossiformes) generally have not received extensive study. All six of the known bonytongue species inhabit tropical lowland rivers, lakes, and wetlands (*Heterotis niloticus* (Cuvier, 1829) in Africa, *Arapaima gigas* (Schinz, 1822) and *Osteoglossum* spp. in the Amazon Basin, and *Scleropages* spp. in Southeast Asia, the East Indies, and northeastern Australia). All bonytongues practice some form of parental care, ranging from nest guarding (*Heterotis* and *Arapaima*) to mouth brooding (*Osteoglossum* and *Scleropages*). *Heterotis niloticus*, the only species of bonytongue

(Osteoglossidae) in Africa (Greenwood 1973, Moreau 1982, Li & Wilson 1996), occurs in rivers of West Africa, the Nilo-Sudanian region and the Congo region of Central Africa (Aubenton 1955, Daget 1957, Leveque et al. 1990), and has been introduced in many lakes and aquaculture centers (e.g., Lake Kossou in Ivory Coast, Lake Nyong in Cameroon) (Moreau 1974, Depiere & Vivien 1977). The African bonytongue has been characterized as microphagous (Lowe-McConnell 1975, 1987) and feeding on variable amounts of plant material, including seeds, and benthic and water-column invertebrates (Fagade & Olaniyan 1973, Lowe-McConnell 1975, Lauzanne 1976, Hickley & Bayley 1987). In contrast, bonytongues from other tropical regions are piscivorous (*Arapaima gigas*) or are generalized carnivores that feed on fishes and a variety of terrestrial vertebrates and invertebrates (*Osteoglossum* and *Scleropages* spp.) (Goulding 1980, Rainboth 1996, Allen et al. 2002).

In Benin, *H. niloticus* is an important fishery resource and is exploited intensively by both commercial and subsistence fishers. The species is most common in freshwater habitats in southern Benin (Van Thielen et al. 1987, Adite & Van Thielen, 1995), especially the Ouémé, Sô, Mono, Couffo and Zou rivers, and lakes Nokoue, Hlan, Toho and Toho-Todougba. Annual capture of *H. niloticus* in Benin has been estimated at 742 tons valued at US $1 485 000 (Benin Direction des Pêches, Cotonou, 1996). Given the bonytongue's great ecological and economic importance in West and Central Africa (Moreau 1982), more information is needed on natural feeding habitats and nutritional requirements of the species in order to inform both fisheries management and development of aquaculture technology. The present study investigated the feeding ecology of *H. niloticus* in the Sô River and Lake Hlan, a large lake in the river's floodplain, in Benin, West Africa, with emphasis on dietary variation associated with ontogeny, seasonality, and habitat.

Variation in availability of the food resources greatly affects fish feeding patterns over time and space, and such patterns often are particularly strong in systems with seasonal hydrological regimes where seasonal availability of marginal habitats and allochthonous resources may affect fish diets (Winemiller 1989, 1990, 1991, Danson-Ofori 1992, Garcia-Berthou & Moreno-Amich 2000, Winemiller & Kelso-Winemiller 2003). In addition, ontogenetic diet shifts (size-related patterns of feeding) are a major feature of fish ecology (e.g., Winemiller 1989, Garcia-Berthou 1999, Garcia-Berthou & Moreno-Amich 2000, Claessen et al. 2002, Koen Alonso et al. 2002, Barbarino Duque & Winemiller 2003, Gill & Morgan 2003). Larvae of most freshwater fishes consume tiny animals, especially microcrustacea and other forms of zooplankton, which yields relatively narrow diet breadth (Adriaens et al. 2001). As they grow, early fish life stages may ingest progressively larger and more diverse food items while maintaining or increasing feeding efficiency (Adriaens et al. 2001, Steingrimsson & Gislason 2002). Most detritivorous fishes develop morphological and behavioral adaptations that allow efficient ingestion, digestion, and assimilation of refractory organic matter in detritus (Bowen 1983). The gizzard (muscular, thick-walled pyloric stomach) and pyloric caecae (blind pouches) of the gut of *H. niloticus* are examples of such adaptations (Moreau 1982).

Methods

Study region

The study region was a reach in the lower Sô River in southern Benin (6°34.97 N; 2°23.75 E) and Lake Hlan (6°56.88 N; 2°19.48 E) located in the river's floodplain. The Sô River flows into Lake Nokoue, a large estuarine system that also receives waters from the Ouémé River, the largest in Benin. The regional climate is sub-equatorial with two wet seasons (April–July, mid-September–October) and two dry seasons (December–March, August–mid-September). Annual rainfall during 2002 was 1167.2 mm (Service de la Metéorologie Nationale, Agence pour la Securité de Navigation Aerienne, 2003) and highest monthly rainfall (438.8 mm) was during June (Figure 1). The Sô River flows southward about 70 km, with floodplains covering about 1000 km^2 (Van Thielen et al. 1987). The river receives water via a connection with the larger Ouémé River. Hydrology of most rivers in southern Benin depends on the rainfall in the north. Sô River flooding influences the physical and chemical features (e.g., water level, conductivity) of floodplain lakes, including Lake Hlan.

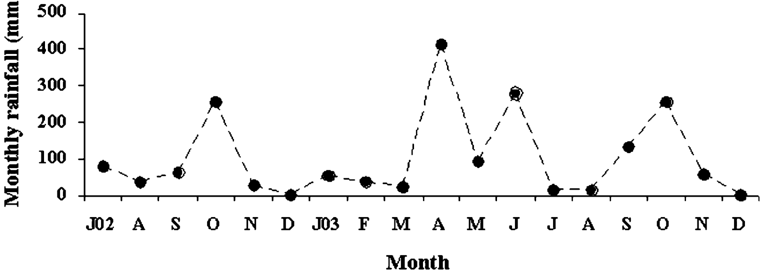

Figure 1. Monthly rainfall in the study region (Cotonou, Benin) during the study period (Source: ASECNA Cotonou).

At each survey site, information was recorded for habitat type, water quality, aquatic vegetation, substrate, terrestrial vegetation, utilization of adjacent lands and wetlands, and evidence of pollution. Water depth was measured using a graduated rope, temperature was measured with a thermometer to the nearest 0.1°C, turbidity was measured with a Secchi disk, pH was measured with a pH meter, dissolved oxygen was measured by a DO meter, conductivity and TDS (total dissolved solid) were measured with a conductivity meter (Table 1). Average monthly values for physico-chemical variables are reported in Table 1. The dominant floating vegetation in areas fringing the channel is *Ecchornia crassipes* (Poaceae). Introduction of this plant 20 years ago was followed by changes in water quality, reduction in fish production, and impeded boat navigation. Other common aquatic plants are *Pistia stratiotes* (Araceae) and *Ipomea aquatica* (Convolvulaceae), and riparian forests are dominated by a palm (*Elaies guinensis*). *Heterotis niloticus* is the principal species captured from the river channel and flooded marginal plains by resident and migratory fishers during the flooding period.

Table 1. Comparison of mean values (± 1 standard deviation) of environmental variables at the Sô River and Lake Hlan survey sites.

	Sô River	Lake Hlan
Depth (m)	4.21 (2.10)	2.50 (1.28)
Temperature (°C)	28.6 (2.2)	27.6 (1.8)
pH	5.4 (0.6)	5.3 (0.2)
Dissolved oxygen (mgl^{-1})	1.30 (1.29)	1.69 (1.13)
Conductivity (μs cm^{-1})	99.4 (3.1)	97.0 (5.5)
Total dissolved solids (mg l^{-1})	46.7 (5.4)	47.0 (2.8)
Nitrate (mg l^{-1})	0.0002 (0.0015)	0.0002 (0.001)
Secchi depth (cm)	40.3 (28.2)	88.1 (25.2)
Iron (mg l^{-1})	1.04 (0.66)	0.67 (0.26)

Lake Hlan is located near Kpomey village (Sehoue County) about 80 km from the Atlantic coast. Well known as '*Heterotis* Lake', Lake Hlan is one of relatively few lakes in Benin that do not receive extremely heavy fishery exploitation, and this is due to strong local traditions that regulate fishing methods and effort. Seasonal flooding strongly influences reproduction and recruitment of *H. niloticus*. Areas sampled in Lake Hlan tended to be shallower than those surveyed in the Sô River (Table 1). Lake Hlan also was more transparent with lower iron concentrations relative to the river. All other measured environmental variables were similar (Table 1). Dominant floating plants in Lake Hlan were *Pistia stratiotes* (Araceae), *Azolla africana*, *Nymphaea lotus* (Nymphaeaceae), *Nymphaea maculatus* (Nymphaeaceae), *Ecchornia crassipes*, *Echinochloa pyramides* (Poaceae) and some submerged plants such as *Ceratophyllum demersum* (Ceratophyllaceae) and *Utricularia inflexa* (Lantibulariaceae). Some floating grasses, such as *Cyperus difformis* (Cyperaceae), covered important areas of the lake and hindered fishing activities. Nevertheless, these grasses provide important habitat for many fishes.

Fish collection

From July 2002 to December 2003, we collected bonytongues from both vegetation and open water habitats at four sites in the Sô River and Lake Hlan. At each site, we captured fish with two fishing gears in order to obtain representative samples of all size classes in the local population.

Surveys were conducted with assistance from commercial fishermen from each area. Because different techniques were used in the two study areas, catch-per-unit-area data are not comparable. Nonetheless, the surveys were designed to capture a sample that reflected the relative size distribution of the population within floodplain and lake habitats containing patches of dense vegetation interspersed with open water areas. Bonytongues are not typically captured in deep-water habitats in either of these areas.

In the Sô River, surveys were conducted along a longitudinal reach that included the villages 'Ahome-Blon', 'Ahome-Lokpo', 'Zoungome', and 'Kinto'. Three survey trips were made during each season (wet, high-water, dry), but fishing effort was greater during the dry season when many bonytongues leave the area for upstream reaches. Vegetation was sampled by encircling an area of approximately 225 m^2 (monthly mean) at four different locations with a seine net (10-mm mesh). After each area was enclosed, the net was incrementally drawn into a tighter circle, and vegetation and fish were removed. Fish were captured from patches of open water with cast nets (50–80 mm mesh). Mean monthly fishing effort in the Sô River was approximately 24 h for each of the methods.

In Lake Hlan, fishes were captured with traps (50-mm opening) and gillnets (20 × 2 m with 60-mm mesh). An average of 60 traps were set per month within each of four survey areas that were located in the shallow northwestern and central regions of the lake. Traps were set near bonytongue nests excavated within dense vegetation. Traps were placed in narrow channels created by the fish for passage to and from the nest. Gillnet surveys were made throughout the lake on a monthly basis. Mean monthly fishing effort was 48 h for traps as well as gillnets. To minimize loss of stomach contents via digestion, fish were removed from gillnets and traps each hour.

We measured fish specimens 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 (following Moreau 1982). Stomachs were preserved in 5% formalin and transported to the laboratory of the Department of Zoology and Genetics of the University of Abomey–Calavi. Preserved stomachs were removed from the formalin and preserved in 75% ethanol.

Dietary analysis

Preserved stomachs were opened and all food items were removed and spread on a glass slide for examination under a dissecting microscope. Water was added to facilitate separation of small items. To identify phytoplankton, a few drops of water containing fine particulate matter from stomach contents were examined under a compound microscope. Food items were identified to the lowest possible taxonomic level using Needham & Needham (1962) for aquatic invertebrates and algae. After identification, food items were separated and blotted on a paper towel to remove excess moisture. The volume of each food category from an individual stomach was estimated by water displacement using an appropriately sized graduated cylinder. Individual food items or particles belonging to a given category were gathered into a single sample for volumetric estimates. Volumes of small items (<0.002 ml) were estimated by spreading the material on a glass slide then estimating by visual inspection the approximate volume of the material by comparison with a 0.01 ml drop of water delivered with a pipet onto a clean glass slide (e.g., a food item having a volume approximately one quarter of the volume of the 0.01 ml water droplet was recorded as 0.0025 ml).

Data analysis

Volumes recorded for each diet category were summed across individual consumers within 100-mm size categories (yielding total volume consumed by a given size class). Diet breadth was calculated following Simpson's (1949) niche breadth formula (Krebs 1989)

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

where p_i is the proportion of food item i in the diet, an 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. Dietary overlap was calculated using Pianka's (1973) overlap index (∅):

$$\varnothing_{jk} = \sum_{i=1}^{n} p_{ij}p_{ik} / \left(\sum_{i=1}^{n} p_{ij}^2 \cdot \sum_{i=1}^{n} p_{ik}^2 \right)^{1/2}$$

where $\varnothing_{\mathrm{jk}}$ is 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 resource i used by species k, and n is the number of resource categories utilized. Habitat, seasonal, and size effects on volumetric proportions and values of indices were compared with 3-way analysis of variances (ANOVA) using STATISTICA (2000, Statsoft, Tulsa, Oklahoma, USA) software. Relationships between gut length or relative gut length and standard length or body weight were examined using linear regression analysis.

Results

Population structure and habitat use

Bonytongue population structure was different in the river channel and lake. Of 908 specimens collected from Lake Hlan, 36.5% were juveniles (< 300 mm SL) captured mostly during the high-water season, 17.8% were subadults (300–500 mm SL), and 45.7% were adults (> 500 mm SL). In Lake Hlan, aquatic vegetation was used as nesting and nursery habitat. Nests, including those with or without larvae, were common during the spawning season (wet and high-water seasons). Of 553 specimens collected from the Sô River, 35.1% were juveniles (<300 mm SL), 60.2% were subadults (300–500 mm SL) and 4.7% were adults (> 500 mm SL). More bonytongues were captured

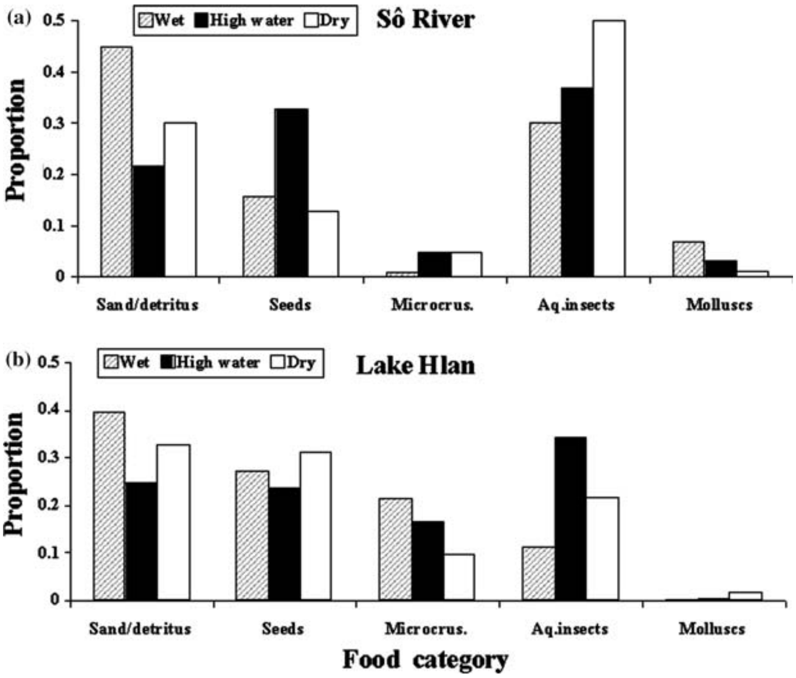

Figure 2. Seasonal trends in volumetric proportions of dominant food resources consumed by *Heterotis niloticus* (volumetric proportions based on all 1 461 specimens) from the Sô River (a) and Lake Hlan (b) (Microscru. = microcrustacea, Aq. insects = aquatic insects).

in the river/floodplain during the high-water season (October–November) and early dry season (falling-water period in December). No nests were observed or reported as observed by local fishermen within river or floodplain habitats during the study.

Diet composition

In both Lake Hlan and Sô River, the diet of *H. niloticus* contained a variety of benthic food resources. The principal food items recorded were detritus and substrate particles, hard seeds, aquatic insects, microcrustacea, and mollusks (Tables 2, 3 and Figure 2). Aquatic insects were mostly immature stages of Diptera (Chironomidae, Ceratopogonidae, Syrphidae, Tipulidae, Empididae), Ephemeroptera, Hemiptera, Odonata, Heteroptera, and Plecoptera plus mostly adult stages of Coleoptera (Dryopidae, *Cybister*, Helodidae, *Thermonectus*). Chironomid larvae dominated diets in both Lake Hlan and the river. Odonata and Ephemeroptera nymphs tended to be more common in diets of fish from Lake Hlan, and Coleoptera were consumed in greater proportions by fish from the Sô River. Gastropod mollusks (Limnidae, Planorbiidae, Hydrobiidae, Physidae) were more abundant in diets of fish from the river. Proportional consumption of sand/detritus, seeds, and aggregated aquatic insects were approximately the same for fish from the two habitats.

Microcrustacea consumed by bonytongues were mostly Cladocera (mainly Daphnidae), Ostracoda (*Cypridopsis*), Copepoda (mainly *Cyclop*s and *Diaptomus*), Amphipoda, and Eubranchipoda. In general cladocerans were the most important microcrustaceans in both habitats. Water mites (Hydracharidae) generally were consumed in low numbers, but were common in diets of subadults in Lake Hlan. Minor diet items were plant tissues (including flowers and fruits), terrestrial insects (Coleoptera, Hymenoptera, Megaloptera), chitin fragments, nematode worms, invertebrate eggs, Rotifera (*Testudinella*, *Asplanchna*, *Chromogaster*, *Brachionus*, *Euchlanis*, *Keratella*), and various algae taxa such as diatoms (*Raphoneis*, *Pleurosigma*, *Synedra*, *Nitzschia*, *Gomphonema*, *Melosira*, *Tabellaria*, *Asterinella*, *Navicula*), cyanobacteria

Table 2. Matrix of food categories consumed by size intervals (expressed as percent volumes of categories based on the total volume consumed by a given size class) of *Heterotis niloticus* at Lake Hlan (size intervals; SL = Standard Length).

Prey category	*Heterotis* size class (mm SL)							
	<100	200	300	400	500	600	700	800
Sand	10.28	10.18	7.16	26.69	22.98	29.37	25.18	31.19
Detritus	1.03	0.96	–	−3.47	4.65	9.87	7.58	10.74
Algae	–	–	21.87	0.02	0.02	0.09	0.03	–
Plants	–	1.73	4.41	0.39	3.05	0.44	0.30	0.27
Seeds	–	5.62	20.18	35.71	33.01	30.87	34.02	21.58
Rotifer	–	0.001	0.01	–	–	0.27	0.06	–
Microcrustacea	13.87	27.07	15.87	7.48	9.12	4.41	16.04	16.32
Invertebrate eggs	10.28	3.43	0.56	0.30	–	0.07	0.03	–
Chironomid larvae	39.57	26.14	15.40	11.58	16.84	13.47	5.98	8.20
Other diptera larvae	1.23	0.76	0.83	1.54	0.97	1.49	1.55	1.45
Ephemeroptera nymphs	11.31	17.51	3.40	1.53	2.42	–	0.88	1.33
Coleoptera larvae	–	0.74	2.62	2.85	1.46	1.14	2.21	2.34
Odonata nymphs	8.22	1.70	2.92	4.20	2.20	3.69	1.39	3.09
Other aq. insects	4.11	3.11	3.88	2.59	2.68	3.02	4.12	2.49
Terrestrial arthropods	–	–	0.02	–	0.04	0.05	0.01	–
Hydracharids	0.10	0.70	0.34	0.01	0.04	0.03	0.03	0.17
Worms	–	–	–	0.12	0.01	0.09	0.14	–
Molluscs	–	0.35	0.53	1.53	0.51	1.65	0.45	0.83
Diet breadth	2.19	2.96	4.87	3.78	4.10	4.08	4.23	4.60
Number of individuals	9	322	89	73	73	74	232	36

Table 3. Matrix of food categories consumed by size intervals of *Heterotis niloticus* at River Sô.

Prey category	*Heterotis* size class (mm SL)						
	200	300	400	500	600	700	800
Sand	32.28	23.91	23.78	18.72	32.84	64.72	43.30
Detritus	3.06	2.30	2.24	1.26	10.82	1.44	–
Algae	0.05		–	–	–	2.09	–
Plants	5.40	1.02	1.46	0.01	1.93	0.50	–
Seeds	19.35	20.71	22.62	38.66	27.24	8.52	25.77
Rotifer	0.08	0.01	–		–	–	–
Microcrustacea	0.82	3.20	6.19	6.32	0.54	1.40	–
Invertebrate eggs	–	0.02	0.18	–	3.1	–	–
Chironomid larvae	13.13	38.94	34.75	28.64	–	1.17	30.93
Other diptera larvae	0.13	0.38	0.43	0.28	1.55	0.14	–
Ephemeroptera nymphs	–	0.16	0.15	0.02	–	–	–
Coleoptera larvae	17.25	5.44	2.59	2.25	4.25	21.13	–
Odonata nymphs	–	0.20	1.00	0.80	–	0.72	–
Other aq. insects	1.47	1.82	2.05	1.44	3.86	0.14	–
Terrestrial arthropods	–	0.01	–	–	–	–	–
Hydracharids	0.03	0.03	–	–	0.04	0.04	–
Worms	0.05	0.02	–		–	0.15	–
Molluscs	6.9	1.84	2.55	1.61 11.59	0.07	–	
Diet breadth	3.96	3.10	3.56	3.33	4.58	2.08	2.86
Number of individuals	14	180	222	111	19	6	1

Percentages calculated the same as in Table 2; fish <200 mm Standard Length were not collected.

Table 4. Percentage of empty stomachs recorded from *Heterotis niloticus* during wet, high-water and dry seasons at Lake Hlan and the Sô River.

Size classes (mm)	Wet	High-water	Dry
Lake Hlan			
<100	–	0 (9)	–
200	–	4.3 (322)	–
300	–	0 (64)	4.0 (25)
400	33.3 (3)	0 (13)	10.5 (57)
500	12.5 (8)	0 (11)	0 (54)
600	21.4 (28)	0 (27)	15.8 (19)
700	7.3 (82)	4.8 (103)	10.6 (47)
800	5.6 (18)	16.7 (12)	0 (6)
Sô River			
200	–	14.3 (14)	–
300	0 (5)	7.5 (173)	50.0 (2)
400	0 (12)	4.9 (102)	2.8 (108)
500	0 (4)	0 (17)	0 (90)
600	0 (4)	–	0 (15)
700	0 (4)	0 (2)	–
800	–	0 (1)	–

Number of individuals from each size class appears in parenthesis.

(*Polycistis*, *Protococcus*, *Phormidium*, *Coelosphaerium*, *Nostoc*, *Oscillatoria*, *Merismopodia*), green algae (*Rhizodonium*, *Botyoccocus*, *Ulothrix* sp, *Richterella*, *Spirogyra*, *Coelastrum*) and desmids (*Gonatozygon*, *Closterium*).

Three-way ANOVA (2 habitats, 3 seasons, 3 size classes) revealed significant ($p < 0.05$) interaction between season and size for dietary proportional volumes of detritus, seeds, and aquatic insects. Significant interaction between habitat (lake versus river) and season was revealed for proportional volumes of detritus, seeds, aquatic insects, and mollusks. A significant habitat effect (without interactions with other independent variables) was revealed for microcrustacea, with more consumed in Lake Hlan than river sites. A significant 3-way interaction was obtained for proportional volumes of seeds and aquatic insects in the diet.

In Lake Hlan, proportional consumption of aquatic insects was greater during the high-water season (Figure 2). In the Sô River, proportionally more aquatic insects were consumed during the dry season (Figure 2). Consumption of sand tended to be greater during the wet season when river water began to invade floodplains, and proportional consumption of seeds tended to be higher during the high-water season (Figure 2).

Empty stomachs

In Lake Hlan, the incidence of empty stomachs (Table 4) was significantly associated with season ($F = 4.20$, df = 2.12, $p < 0.05$), with a higher percentage recorded during the wet season. Season did not significantly affect the percentage of empty stomachs in the sample of river fish. Percentages of empty stomachs were low and comparable between Lake Hlan fish during the high-water and dry seasons and Sô River fish during all periods (Table 4).

Diet breadth

Diet breadth of fish in both habitats was not significantly associated with season. For Lake Hlan fish, seasonal means (±1 SD) for diet breadth were 3.37 (±1.05) (wet), 3.62 (±0.70) (high-water), and 4.18 (±0.31) (dry). Diet breadth means for river fish were 3.27 (±0.78) (wet), 3.01 (±0.96) (high-water), and 2.95 (±0.18) (dry). Although overall mean diet breadth was slighter higher for Lake Hlan fish, this difference was not statistically significant. Mean diet breadth in Lake Hlan tended to increase from <100 to 300 mm SL (Table 1, $r = 0.07$) indicating bonytongues consume a broader range of food resources as they grow. This pattern was not apparent for river fish (Table 2, $r = -0.30$), however low sample sizes for the 700 and 800 mm size classes likely resulted in underestimates of diet breadth.

Ontogenetic diet shifts

The smallest specimen measured 74 mm SL (85 mm TL, W = 5 g) and the largest specimen was 765 mm SL (836 mm TL, W = 5838 g). Diet similarity based on volumetric proportions of fine-resolution categories (e.g., ordinal level taxa) among different size classes (Tables 2 and 3) was high ($\varnothing_{jk} > 0.45$) within both habitats (Table 5). Highest mean dietary overlap among size classes occurred during the dry season in both habitats, although a seasonal trend was extremely weak in the river population (Table 6). Adjacent size classes tended to have higher diet similarity than distant pairings involving distant size classes (Table 5), an indication of ontogenetic progression of feeding habits.

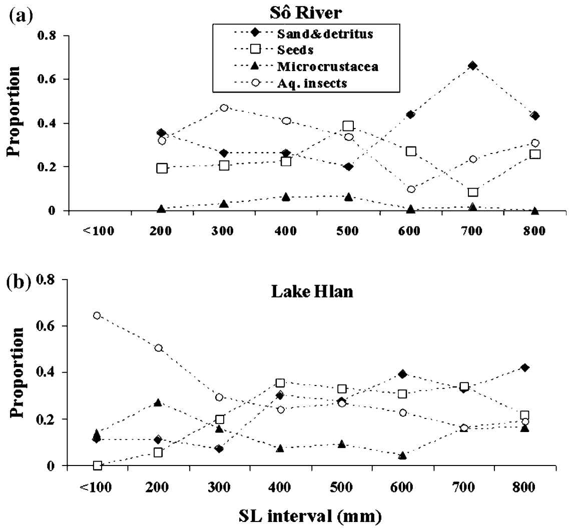

Figure 3. Volumetric proportions of dominant food resource categories consumed by size classes of *Heterotis niloticus* from the Sô River (a) and Lake Hlan (b).

Fish <100 mm SL (all captured from Lake Hlan) fed primarily on microcrustacea, aquatic insects, and invertebrate eggs (Table 2). Aquatic insects and, to a lesser extent, microcrustacea remained significant in the diet of larger size classes even to lengths >700 mm (Figure 3). Adult Coleoptera

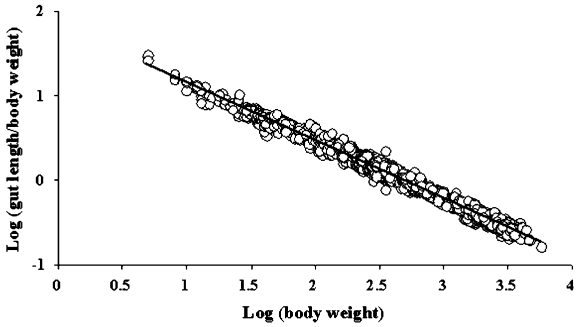

Figure 4. Scatter plot showing relationship between Log (gut length/body weight) and Log (body weight) of *Heterotis niloticus*. Regression equation, coefficient of determination, sample size, and significance are as follows: Log (GL/W) = -0.69 Log(W) + 1.85, $r^2 = 0.99$, n = 1 461, $p < 0.00001$ (GL = gut length, W = body weight).

Table 5. Matrix of diet overlaps for differents size intervals of *Heterotis niloticus* at Lake Hlan and the Sô River, respectively.

Size classes (mm)	Lake Hlan						
	200	300	400	500	600	700	800
<100	0.95	0.71	0.56	0.63	0.55	0.47	0.56
200		0.79	0.63	0.70	0.6	0.60	0.68
300			0.75	0.79	0.70	0.72	0.69
400				0.99	0.98	0.97	0.92
500					0.98	0.96	0.92
600						0.96	0.95
700							0.95
		Sô River					
		300	400	500	600	700	800
200		0.95	0.96	0.89	0.86	0.86	0.97
300			0.99	0.91	0.70	0.72	0.90
400				0.94	0.74	0.73	0.92
500					0.79	0.61	0.88
600						0.80	0.88
700							

and mollusks were only consumed by individuals >100 mm. Specimens <100 mm consumed low proportions of detritus (1%) and no seeds. Between 100 and 200 mm SL, the diet began to include seeds and detritus (Figure 3). A marked increase in the volumetric proportion of detritus in the diet occurred between 300–400 mm SL in Lake Hlan, and between 500–600 mm SL in the river (Figure 3).

Relative gut length

The ratio of gut length (GL) to body weight (W) was computed as a measure of relative gut length. Logarithmic transformations reduced skew in the dataset. Relative gut length (GL/W) ranged from 30 ($\log GL/W = 1.48$) to 0.16 ($\log GL/W = -0.79$) and was negatively correlated with body weight ($r^2 = 0.99$; $p < 0.0001$, $n = 1461$, Figure 4). Though weaker, the same trend was obtained for the ratio GL/SL ($r^2 = 0.22, p < 0.0001, n = 1461$). The linear relationship between GL and SL was calculated as $GL = 1.133 \cdot SL + 88.21$ ($r^2 = 0.90$, $p < 0.0001$, $n = 1461$); and the linear relationship between log(GL) and log(W) was $\log(GL) = 0.309 \cdot \log(GL) + 1.85$ ($r^2 = 0.93$, $p < 0.0001$, $n = 1461$).

Table 6. Mean diet overlaps with standard deviations (sd) for size intervals of *Heterotis niloticus* during wet, high-water and dry seasons at Lake Hlan and the Sô River.

Season	Lake Hlan		Sô River	
	Mean (SD)	Number of Pairings	Mean (SD)	Number of Pairings
Wet	0.75 (0.16)	10	0.88 (0.07)	10
High-water	0.81 (0.18)	28	0.78 (0.18)	10
Dry	0.93 (0.04)	15	0.90 (0.09)	6

Discussion

Subsistence and commercial fishers of the Sô River refer to the high and falling-water period as the ‘bonytongue season’, and about 94% of the fish captured, mostly juveniles and subadults, were taken during this period. The Sô River floods each year from September to mid-November, allowing juveniles and subadults to migrate to the floodplain to feed within a greatly expanded aquatic ecosystem. By providing abundant food resources and dense cover in the form of aquatic vegetation, the floodplain can be considered a nursery area that enhances growth and survival of early life stages. Almost all of the adults captured in this study were from Lake Hlan, a location where many active nests were encountered during the wet and high-water seasons. Bonytongue nests were not observed in the river study area during any of the survey periods, and local fishermen report that the species does not nest in that region. About 4% of individuals captured at the river floodplain site were larger than the minimum size of maturation as determined by examination of gonads among the 1461 specimens (authors' unpublished manuscript). This difference in population structure is unlikely to result from sampling bias associated with different fishing gears, because fishermen employ those fishing methods that most effectively capture bonytongues at their localities. In metapopulation terminology (Pulliam 1988), Lake Hlan appears to serve as a 'source habitat', and the river channel acts as a 'sink habitat' that receives large numbers of juvenile fish during the period when river floodwaters enter productive floodplains.

Welcomme (1975, 1979) stressed the importance of flooding regimes for fish production in tropical rivers. Seasonal flooding of nutrient-rich floodplain landscapes induces a burst of primary and secondary production (Junk et al. 1989). As water invades adjacent terrestrial vegetated habitat, terrestrial allochthonous resources also become available to fish. Seeds were an especially important food resource for subadult and adult bonytongues. At Lake Hlan, flooding of surrounding herbaceous vegetation forms large swamps, and the seeds of semiaquatic and terrestrial grasses provided a major food resource for this lacustrine bonytongue population. The proportion of aquatic insects in the diet increased during the dry season (Figure 2), and this pattern probably was the outcome of several months of aquatic insect recruitment during submergence of surrounding floodplains that allowed invertebrate stocks to build up (Blanco-Belmonte et al., 1998, Nessimian et al. 1998).

Overall, the incidence of empty stomachs was low (0–15%), but *Heterotis* in Lake Hlan had a greater proportion of empty stomachs during the wet season, and this probably reflects reduced feeding by reproducing and nest-guarding adults. Season was not significantly associated with the proportion of empty stomachs in the sample of river fish. Again, most of the specimens collected from this habitat were juveniles and subadults (94%) that migrated from lakes, such as Lake Hlan, and possibly other permanent water bodies. Among Lake Hlan fish, highest diet overlap occurred during dry season, the period when adults dominated the lake population. In contrast, the Sô River population revealed no association between season and diet overlap, probably because these samples were always dominated by juveniles and subadults that consume many of same food resources.

The gut of *Heterotis* has a gizzard, a thick-walled, muscular chamber (Bowen 1983) that facilitates digestion of refractory organic matter such as plant detritus and seed coats. The gizzard is not well developed in small individuals (74–400 mm SL), and these individuals may have limited abilities to process detritus and seeds with hard coats. Small individuals consumed few beetles and other insects with a thick carapace, but fed heavily on softer larvae and nymphs. The structure of *Heterotis* gill rakers (42–94 rakers on the first branchial arch; see Moreau, 1982 for a description) probably facilitates sieving of zooplankton and other microcrustacea. Volumetric proportions of consumed microcrustacea (16.0%) and aquatic insects (16.6%) were high for the 600–700 mm size class in Lake Hlan. A 605-mm specimen collect from lake Hlan in October had consumed 100% (volume 3 ml) microcrustacea (mainly Cladodera and Copepoda). Overall, juvenile *Heterotis* in Lake Hlan had relatively narrow dietary breadth, and later ontogeny was associated with an increase in diet breadth and more pronounced omnivory. Tropical fishes that are trophic specialists demonstrate reduced diet breadth during ontogeny (e.g., Winemiller 1989), whereas trophic generalists tend to reveal the opposite trend (Winemiller & Kelso-Winemiller 2003), the latter trend being consistent with findings for *Heterotis*.

The relative gut length of *Heterotis* is consistent with our findings that support classification as an omnivore rather than a detritivore or strict invertebrate feeder. Kramer & Bryant (1995) examined the relationship between log(GL) and log(W) for fishes inhabiting a Central American stream. Their Figure 3 reported slopes of approximately 0.35–0.4 for carnivores, 0.4–0.68 for omnivores, and 0.58–0.68 for herbivores. Mean slope for log(GL) – log(W) relationship for *Heterotis* was 0.31 which aligns more with carnivores. The mean ratio for GL/SL for *Heterotis* ranged from 2.02 (74 mm SL, the smallest fish) to 0.98 (715 mm SL, among the largest). These ratios are lower than those reported by Paugy (1994) for African detritivorous fishes (mean = 7.2) but similar to those for omnivores (mean = 1.3). The main plant component in the diet of *Heterotis* was small seeds that have relative high density of energy and protein relative to most other plant parts, and which may be more similar to animal than plant tissue in terms of digestive properties.

In our study, most gizzards contained significant amounts of sand, which provides evidence that *Heterotis* feeds on the substrate. Given that the proportion of detritus consumed was relatively low, what are the principal food resources being selected, and what is the function of the gizzard? Seeds, an energy-dense food resource, were an important food resource for bonytongues regardless of location or season. Most of these seeds, which appeared to be from grasses and sedges, had hard seed coats. Thus, the gizzard probably is an adaptation for grinding through seed coats to facilitate digestion. Ingestion of sand, and its retention in the gizzard would increase abrasion (Bowen 1983). In contrast, seed-eating characid fishes of the Neotropics, such as *Brycon*, *Colossoma* and *Piaractus* species, lack a muscular gizzard and instead crush seeds that typically are larger than grass seeds using multicuspid oral teeth (Goulding 1980). Whether or not *Heterosis* facilitates seed dispersal, as has been suggested for large granivorous characids of the Neotropics (Goulding 1980, Horn 1997), is currently unknown.

Improved knowledge of fish feeding ecology is valuable for management of both wild and captive stocks. Wild stocks are members of river/floodplain food webs with dynamics that influence population abundance (Winemiller 1996). Ontogenetic dietary shifts are determined, in part, by seasonal and spatial variation in availability of resources required for growth and development of different size classes. Detailed information about dietary requirements also is essential for aquaculture. The African bonytongue appears to have large potential for fish farming in West Africa, and findings from the present study reveal that juveniles have different feeding habits than adults. *Heterotis* is not a specialized detritivore and probably requires food resources with significantly higher nutritional content than detritus, with grass seeds being particularly important in diets of fish in floodplain river systems.

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