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Seasonal Diet Shift of the Most Important Fish Species in a Sahelo-Soudanian Reservoir (Burkina Faso)

[1]Adama Ouéda, [1]Wendengoudi Guenda, [2]Allassane Ouattara, [2]Germain Gourène, [3]Bernard Hugueny and [1]Gustave B. Kabré
[1]Laboratoire de Biologie et Ecologie Animale, UFR/SVT, Université de Ouagadougou, 03 BP 7021 Ouagadougou 03, Burkina Faso
[2]Laboratoire d'Environnement et de Biologie Aquatique, UFR/SGE, Université d'Abobo-Adjamé, 02 BP 801 Abidjan 02, Côte d'Ivoire
[3]IRD, Laboratoire d'écologie des Hydrosystèmes Fluviaux, Université Lyon 1, France

Abstract: Fish diet, feeding patterns and trophic interactions were studied according to season in a Sahelo-Soudanian man-made lake (Loumbila, Burkina Faso). Some food resources (zooplankton and benthic fauna) were also sampled. An examination of 425 non-empty stomachs belonging to 6 species showed that *Auchenoglanis occidentalis*, *Clarias anguillaris* and *Schilbe intermedius* varied their diets and feeding strategies from one season to another. These species adapt their feeding strategies to the seasonal food availability. The three other species (*Brycinus nurse*, *Oreochromis niloticus* and *Tilapia zillii*) showed constant specialisation in the same prey items. Diets overlaps were low during the wet season and Resource Breadths more or less higher. Thus diminution in food availability in the dry season appears to induce shortage of resources used by individuals and by whole populations, leading to an increased likelihood of competition between species. The changes in fishes feeding patterns within the year are an adaptive response to change in food availability and allow fish communities to make better use of available resources.

Key words: West Africa, Sahelo-soudanian reservoir, fish diet, feeding, diet overlap

INTRODUCTION

Seasonality in hydrology is a prominent aspect of pattern in tropical freshwater habitats, having major consequences on population, community and ecosystem processes (Junk *et al*., 1989). With regards to fish trophic ecology, hydrological seasonality is generally mirrored by seasonal changes in abundance, availability and accessibility of major food sources (Prejs and Prejs, 1987; Winemiller, 1990; Perga *et al*., 2005). In the case of seasonally fluctuating resource abundances, two outcomes can be expected. First, during the season of low abundance resource, diet breadth should increase in order to reduce intraspecific competition (Svanback and Persson, 2004) and/or diet overlap should decrease to reduce interspecific competition (Zaret and Rand, 1971; Pusey and Bradshaw, 1996). Secondly, if all resources do not decrease uniformly, fish species would be expected to forage according to the Optimal Foraging Theory (MacArthur and Pianka, 1966; Emlen, 1966; Charnov, 1976) by exploiting the seasonally most profitable resources, inducing seasonal diet shift. The few studies conducted so far on tropical freshwater fish communities provided mixed results. Some (Zaret and Rand, 1971) reported higher interspecific diet overlap during the period of low food abundance, but others did not (Prejs and Prejs, 1987). Moreover within the same system seasonal patterns of diet overlap may differ according to the regime of the species (Esteves and Galetti, 1995). The absence of a general pattern suggests that seasonal changes in trophic dynamics are not fully explained by feeding strategies aimed

Corresponding Author: Adama Ouéda, 12 BP 170 Ouagadougou 12, Burkina Faso Tel: (226) 76 41 45 09

to reduce competition and that feeding opportunism may be an important underlying factor (Prejs and Prejs, 1987). As most of the relevant studies were conducted within the neotropics, seasonal variations in resource use and trophic interactions within fish communities are not yet well documented for West African freshwater fishes. The aim of this study is to investigate seasonal changes in diet of the most abundant species within a reservoir in Burkina Faso (Africa) that is subject to seasonal variations in water level. In such systems, seasonal fluctuations in food resources availability are known to occur. Low densities of benthos and aquatic insect density were observed during the dry season in comparison with wet season (Kabré *et al*., 2002). In addition, in the wet season, flooding of riparian vegetation brings fish in contact with supplementary food resources such as vegetal and terrestrial insects carried into the reservoir by flow (Payne, 1986). Higher abundances of zooplankton were observed during the wet season (Ouéda *et al*., 2007). According to Winemiller and Jepsen (1998), lake shortage leading to high fish densities in dry season would lead to high piscivory. Besides documenting seasonal patterns of diet breath and diet overlap we studied how seasonal diet shifts could be accounted for by seasonal changes in the availability of major food resources. In particular we expected to observe the following diet shifts from dry to wet season: reduction of piscivory and more consumption of zooplankton and benthos. During high water level we could also expect omnivory to be higher as allochthonous and littoral carbon sources are more diversified.

MATERIALS AND METHODS

Study Site

The study was carried out in Loumbila Lake (12° 29'34'' N, 01° 24'05'' W) located at 20 km from Ouagadougou (Burkina Faso) (Fig. 1). Loumbila Lake is one of the most important shallow reservoirs in Burkina Faso. It is a man-made lake with 1500 ha maximum area and 6.6 m maximum depth. Lake water quantity and surface area vary greatly from one season to another. During our study, water volume varied from 4.57 millions m^3 (minimum in the dry season) to 22.88 millions m^3 (maximum in the wet season). This is essentially due to high social demands (drinking water and irrigation) and climatic effects (evaporation: 8.5 mm day^{-1}). Actually, Loumbila is located in the North

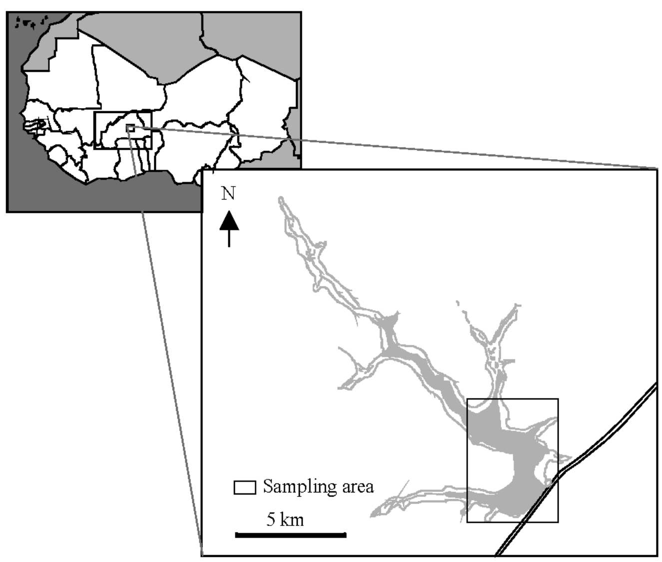

Fig. 1: Location of the study site in Burkina Faso (West Africa)

Soudanian climatic zone. The rainfall is uneven and may show great contrast from one year to another. The mean pluviometry for the ten previous years (1996 to 2005) was 706.8 mm year^{-1}. The dry season lasts from November to May and the wet season from June to October. On the lakeshore, socio-economic activities are essentially agriculture, ranching, fishing and trading. Fishing and market gardening which are directly associated with the lake, are the most important activities.

Stomach Collection and Data Analyses

Baijot *et al.* (1994) distinguish 26 species in the Loumbila reservoir. Among the species identified as dominant in Burkina Faso lakes by Baijot *et al.* (1994), we selected those that reached the highest occurrence in Loumbila Lake during the period of study in order to analyse diet variation between dry and wet seasons. Selected species were *Auchenoglanis occidentalis* (Valenciennes, 1840); *Brycinus nurse* (Rüppell, 1832); *Clarias anguillaris* (Linnaeus, 1758); *Oreochromis niloticus* (Linnaeus, 1758); *Schilbe intermedius* (Rüppell, 1832) and *Tilapia zillii* (Gervais, 1848).

Fish were collected monthly between May 2004 and April 2005 using gillnets. Each specimen was measured (Standard Length) and weighted and stomachs were removed and preserved in 5% formalin. Food items in each stomach were counted and weighted following identification. Prey items eaten by studied species were classified as follows. Fishes were separated into two categories according to life stage: alevins (Ale) and fish (Fsh). Insects were split into four categories: *Chironomidae larva* (Chi), *Chaoboridae larva* (Cha), Other Larva (OL) and flying and mature insects (Ins). Vegetal matter was grouped in two categories: seeds (See) and vegetal (Veg). The other prey items were: Araneidae (Ara), detritus (Det), mud (Mud), fish scales (Scl), shrimps (Shr) and zooplankton (Zpn). For the two Cichlidae (*O. niloticus* and *T. zillii*) the term Vegetal was used to designate both algae and macrophytes.

To discuss the variations on feeding strategy of each fish species within the season, the Costello method modified by Amundsen *et al.* (1996) was used. This analysis is based on a graphical representation (Amundsen *et al.*, 1996) and allows exploration of ingested food type data in relation with feeding strategies, as well as intra-individual and inter-individual variations in niche utilisation. Prey weights were used to compute the prey-specific abundance.

Levins' index of Resource Breadth (R_B) was used to analyse dietary breadth variation among the seasons (Reinthal, 1990):

$$R_B = 1 / \sum_{i=1}^{n} p_{xi}^2$$

where, p_{xi} is the proportions (percentage weight) of food item i in the diet of species x and n is the total number of resources used. To express the degree of variability in resource breadth between individuals of the same species we calculated the Standard Deviation (SD) of the individuals' R_B. The Wilcoxon paired test allowed us to test differences between Species R_B, the mean of individuals' R_B and the standard deviation of individuals' R_B obtained in the dry season to those of the wet season.

To compute diet overlap between species, Schoener's index α that varies between 0 and 1 (cases of lack of diet overlap to case of total overlap) was used:

$$\alpha = 1 - 0,5\left(\sum_{i=1}^{n} \left|p_{xi} - p_{yi}\right|\right)$$

where, p_{xi} and p_{yi} are, respectively the proportions (percentage weight) of food item i in the diet of species x and y. n is the total number of resources used. Food similarity is biologically significant when α is higher than 0.6 (Wallace, 1981).

To test differences in size structures between dry season specimens and those of wet season, we have used the Mann-Whitney U-test. For species for which individual sizes are significantly different according to season, we have secondly, after diet analyse, run the test to check difference between individuals with season-specific prey in their gut and those without this prey. This second analysis was run to check if a seasonal specialisation in a clearly defined prey item may be ascribable to the differences in size structure.

Food Availability

The study of stomach contents is complimented by an analysis of food availability by sampling zooplankton and benthos which are two of the main food items in freshwater fish diets. During the whole year, plankton samples were collected every 14 days by doing horizontal tows over a distance of 540 m with conical nitex plankton net of 100 μm mesh size. Samples were taken each time at two different depths (0.3 and 1 m) preserved in 5% formalin and analysed under an inverted microscope. After identification, individuals were counted in order to infer zooplankton density. The benthos was sampled with an Eckman grab every 14 days during three and two months, respectively in dry and wet seasons. In the dry season, samples were taken from open water (20 m to the lakeshore). In the wet season, after the flood, samples were taken from two stations, the first in open water and the second in the flooded vegetation (20 m to the lakeshore).

RESULTS

Feeding Strategy

The stomach contents of 425 individuals belonging to the six above-listed species were analysed. Characteristics of fish samples (minimum and maximum Standard Length, number of non-empty stomachs examined and percentage of empty stomachs per species and season) are given in Table 1. It appears that for all species, the percentage of empty stomachs was significantly lower in the wet season (Wilcoxon test, $n = 12$, $p<0.05$). Highest decreases of the percentages of empty stomach were observed for *S. intermedius*, *B. nurse* and *C. anguillaris*.

Figure 2 shows the evolution of feeding strategy of fish species, depending on seasons, according to the Costello method. In the dry season, resource use among individuals of *A. occidentalis* varied greatly: some individuals relied on Chironomidae larva whereas the majority of individuals fed on vegetal or detritus. In the wet season, this species was more specialized in Chironomidae larva, but the amount of zooplankton in its diet also increased.

Seeds were the main item in the diet of *B. nurse* during both dry and wet seasons. Nevertheless, this species increased its consumption of mature insects in the wet season.

Table 1: Standard Length (SL), number of non-empty stomachs analysed (NES) and percentage of empty stomachs (%EE) per season

	Dry season			Wet season			p-values*	
Species	SL (mm)	NES	EE (%)	SL (mm)	NES	EE (%)	BS	SSP
A. occidentalis	66-190	32	31.91	110-240	36	16.28	**0.0205**	0.1163
B. nurse	40-150	35	43.55	50-135	30	16.67	0.8953	-
C. anguillaris	135-475	23	41.03	125-300	28	15.15	0.3585	-
O. niloticus	55-152	69	32.35	55-155	37	22.92	0.5508	-
S. intermedius	75-170	23	59.65	85-160	30	11.76	**0.0174**	0.7758
T. zillii	44-115	41	25.45	65-120	41	12.77	**0.0007**	0.3034

*p-values for Mann-Whitney U-test; BS: Comparison between season; SSP: Comparison based on the season-specific prey. Significant values are showed in bold characters

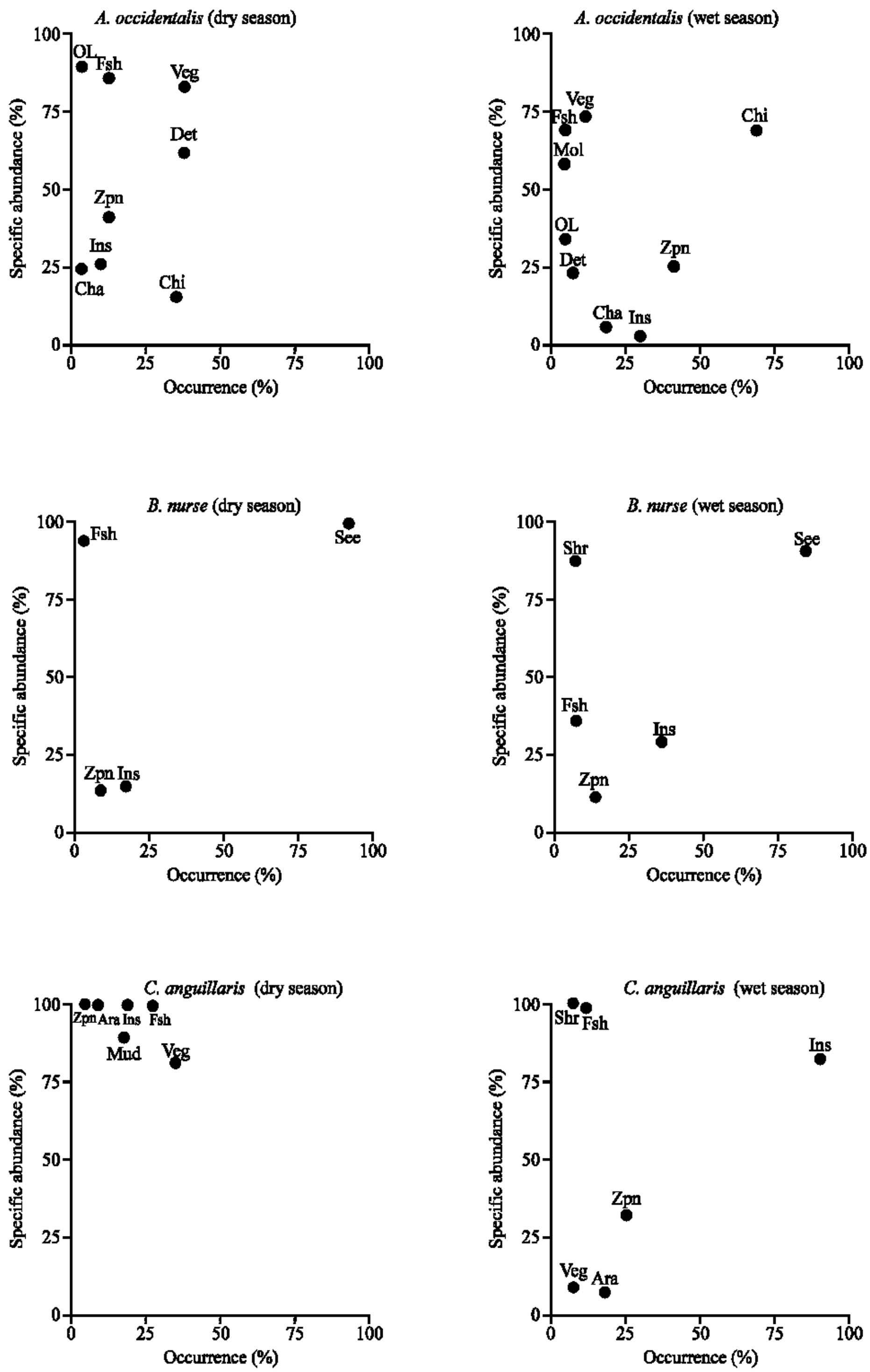

Fig. 2: Continued

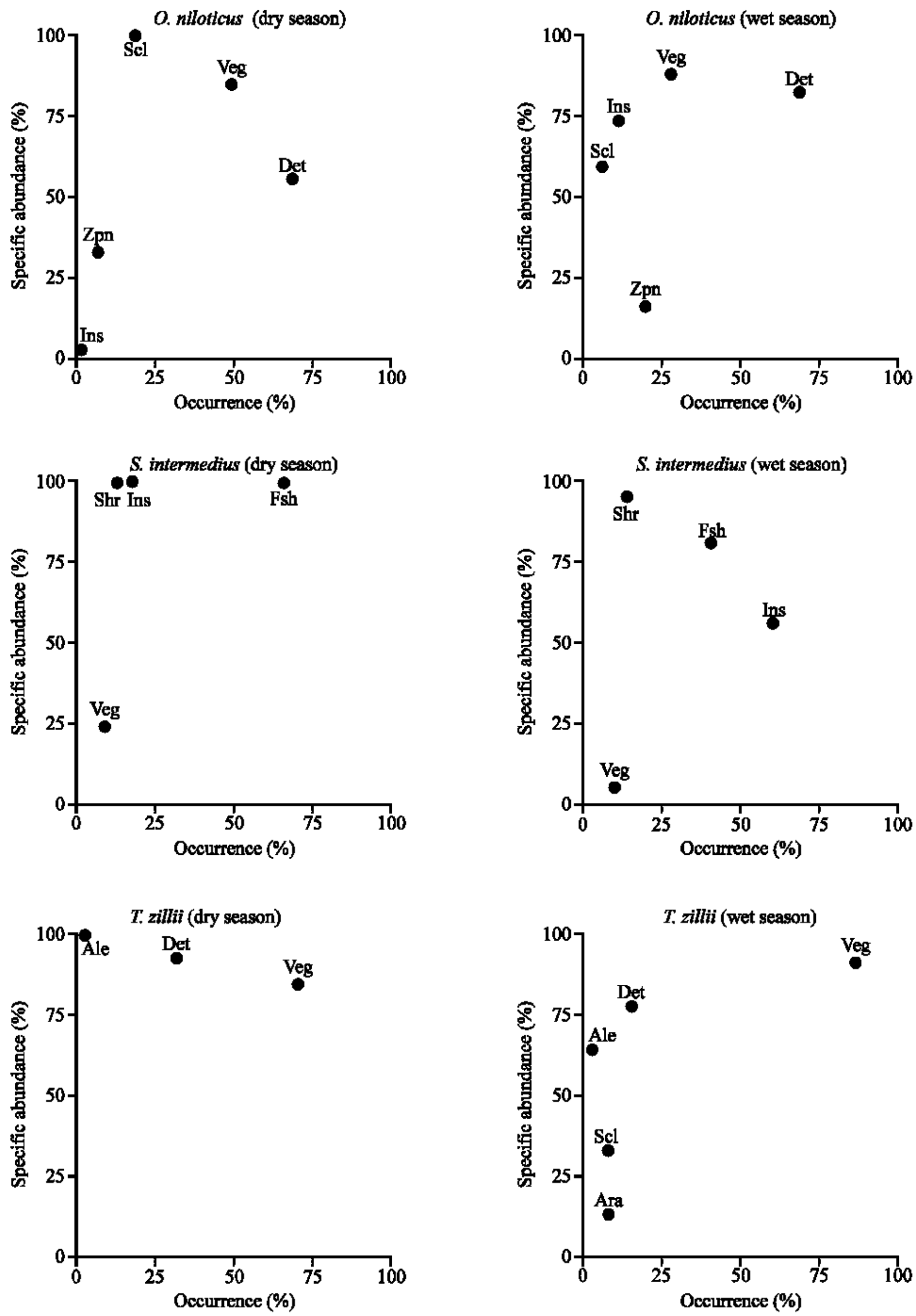

Fig. 2: Feeding strategy diagrams. Prey importance and niche contribution of some fish species in the dry and wet seasons. Specific abundance against frequency of occurrence of food items. Prey identification code: Ale: Alevins, Ara: Araneidae, Cha: Chaoboridae larva, Chi: Chironomids larva, Det: Detritus, Fsh: Fish, Ins: Mature insects, Mud: Mud, OL: Other larva, Scl: Scales, See: Seeds, Shr: Shrimp, Veg: Vegetal, Zpn: Zooplankton

The six food items in the diet of *C. anguillaris* in the dry season are plotted in the upper left corner of the graph. This indicates great variability in resource use between individuals of this species (High between-phenotype component to niche width) in this season. *C. anguillaris* population was then divided into subpopulations, each specialised on a different food resource (mainly vegetal, fish, insects or mud). In the wet season, *C. anguillaris* showed clear specialisation in mature insects and a slight increase of zooplankton in its gut content.

Detritus and vegetal items were the main food of *O. niloticus* in the dry season. In the wet season, this species increased its specialisation and consumption of detritus at the expense of vegetal items.

The main food item of *S. intermedius* in the dry season was fish. Indeed, the majority of individuals showed specialisation in fish while the others were specialised in insects or shrimps. This species switched its diet in the wet season. It greatly increased its consumption of mature insects and reduced its consumption of fish.

In both the dry and the wet season, vegetal items were the main food in the diet of *T. zillii*. However, in the dry season, there much greater variability in resources use between individuals. While more than half of the population is specialised in vegetal items some individuals were specialised in detritus and the other in alevins. In wet season, nearly all individuals are specialised in vegetal items despite the increased number of prey items in the diet of *T. zillii*.

The last columns of Table 1 show p-values of Mann-Whitney U-tests of between-season contrasts in length and feeding specialisation. *A. occidentalis*, *S. intermedius* and *T. zillii* individuals show significantly higher Standard Length in the wet season. For those species, there was however no difference in size structures between individuals with the season-specific prey in their stomach and those without this prey. This means that prey consumption is not size dependant (Chironomids for *A. occidentalis*, fish for *S. intermedius* and vegetal for *T. zillii*). For example, *S. intermedius* specialisation in fish in the dry season was not ascribable to individual sizes (Mann-Whitney test, $n = 53$, $p>0.05$; individuals with fish in their gut vs. individuals without fish in their gut content).

Resource Breadth

Results for the Levin index of Resource Breadth (R_B) (Table 2) show that, except for *T. zillii*, the studied fish species increased their dietary breadth from the dry season to the wet season, to varying degrees. However, the Wilcoxon test reveals that this seasonal variation was not significant ($n = 12$, $p>0.05$). Higher increases in R_B are observed for *C. anguillaris* and *S. intermedius*. The average of individual R_B increased slightly in the wet season for all species. The Standard Deviation for all species individuals' R_B is lower in the dry season and higher in the wet season. Those seasonal variations (for Individuals' R_B and SD) are significant according to the Wilcoxon test ($n = 12$, $p<0.05$).

Diet Overlap Between Species

Based on Schoener's α index (Table 3), the six studied fish species can be divided into three groups in the dry season. The first group includes species that fed mainly on vegetal and detritus: *A. occidentalis*, *O. niloticus* and *T. zillii*. The second group is composed by *C. anguillaris* and

Table 2: Resource Breadth (Levins' index: R_B) and its variability between individuals (Mean and Standard deviation: SD) of the seven fish species according to season

	Seasons	Ao	Bn	Ca	On	Si	Tz	p-value*
Species R_B	Dry season	2.26	1.03	1.42	1.94	1.35	1.95	0.17
	Wet season	2.38	1.29	2.13	2.43	2.06	1.43	
Mean of individuals R_B	Dry season	1.25	1.07	1.06	1.12	1.00	1.03	**0.02**
	Wet season	1.37	1.24	1.20	1.17	1.09	1.08	
SD of individuals R_B	Dry season	0.44	0.19	0.22	0.25	0.02	0.17	**0.02**
	Wet season	0.53	0.45	0.33	0.33	0.20	0.27	

*p-values for the Wilcoxon test, significant values are showed in bold characters. Ao = *Auchenoglanis occidentalis*, Bn = *Brycinus nurse*, Ca = *Clarias anguillaris*, On = *Oreochromis niloticus*, Si = *Schilbe intermedius* and Tz = *Tilapia zillii*

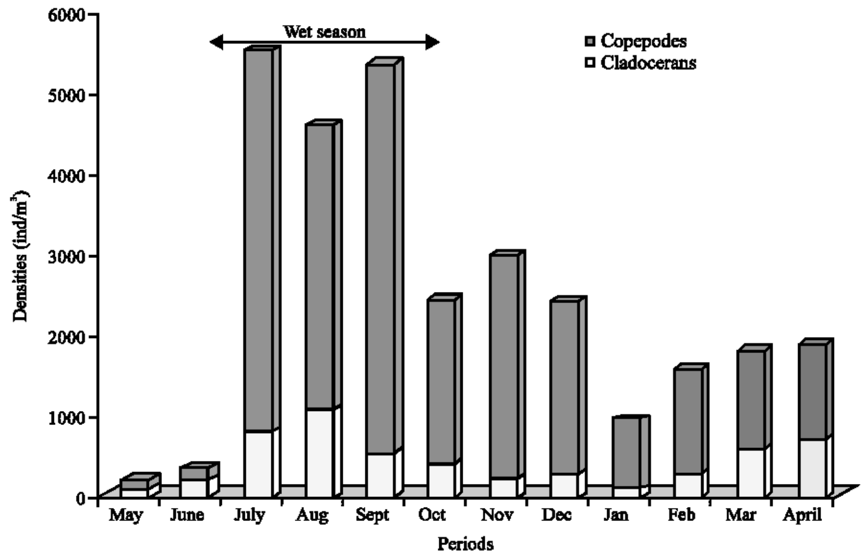

Fig. 3: Mean densities (number of individuals m^{-3}) of zooplankton taxa (Crustaceans) in Loumbila Lake during the study period

Table 3: Diet overlap (Shoener's index: α) among fish species in dry and wet season

	Dry season					Wet season				
Species	Ao	Bn	Ca	On	Si	Ao	Bn	Ca	On	Si
Bn	0.02					0.03				
Ca	0.24	0.01				0.05	0.11			
On	**0.80**	0.00	0.14			0.08	0.10	0.13		
Si	0.10	0.01	**0.84**	0.01		0.04	0.11	**0.87**	0.13	
Tz	**0.74**	0.00	0.14	**0.90**	0.01	0.05	0.00	0.01	0.42	0.01

Significant overlaps (Wallace, 1981) are show in bold characters. Ao = *Auchenoglanis occidentalis*, Bn = *Brycinus nurse*, Ca = *Clarias anguillaris*, On = *Oreochromis niloticus*, Si = *Schilbe intermedius* and Tz = *Tilapia zillii*

S. intermedius that fed mainly on fish and mature insects (flying adults). *B. nurse* fed on seeds, forming the last group. In the wet season, only the couple *C. anguillaris* and *S. intermedius* showed significant values of α. The mean diet overlap is higher during the dry season than during the wet season (0.264 vs. 0.143).

Zooplankton and Benthos Distribution

Zooplankton community in the Loumbila reservoir is represented by Rotifers (17 species), Cladocerans (7 species), Copepods (2 species) and Macrozooplankton (*Chaoborus* larva, cnidarians and alevin). Zooplankton individuals observed in fish diets are mainly Cladocerans and Copepods. Figure 3 shows the distribution of those groups during the study time. Copepods and Cladocerans densities were higher in the wet season, precisely in July, August and September (4400 to 5000 individuals m^{-3}). Medium densities (2000 to 3000 individuals m^{-3}) were found in October, November and December.

The benthic fauna of Loumbila reservoir is mainly constituted by Dipterans larva, principally by Chironomidae larva (93.5%). Chaoboridae, Ceratopogonidae, Oligocheta, Trichoptera and Ephemeroptera are present at low densities. In the dry season, benthos density is 877.78 individuals m^{-2} (20 m from the lake shoreline). In the wet season, this density is 573.33 individuals m^{-2} in open water and reaches value of 1876.67 individuals m^{-2} in flooded shore vegetation (20 m from the shoreline).

DISCUSSION

In the wet season, low percentages of empty stomachs were observed indicating that in this season, food was more accessible for fishes. The flooding of shore vegetation represents an additional food source for phytophages during this season whereas the stock of available food is increased by terrestrial food items (insects and detritus) that flow into the reservoir. Moreover, our results showed that zooplankton and benthos were more abundant during the wet season. According to Ouéda *et al.* (2007), the abundance of zooplankton in the wet season can be linked to the seasonal inflow water to the reservoir. Indeed, water arriving in the reservoir brings a great quantity of nutrients into the reservoir. High abundance of insects in the wet season is explained by high availability and diversity of habitat and food. So, we can conclude that, in Loumbila Lake, trophic resources are more diversified and more available for fish species in the wet season than in the dry season.

We found that in Loumbila Lake *A. occidentalis* is mainly omnivorous but with strong insectivorous tendency. *B. nurse* is a seed consumer. *S. intermedius* is omnivorous like *C. anguillaris*, but with a piscivorous tendency. *O. niloticus* and *T. zillii* are phytophages. Theses observations are in accordance with the conclusions of Lauzanne (1988) and Paugy and Lévêque (1999) regarding the diet composition of the above-mentioned species.

A. occidentalis, *C. anguillaris* and *S. intermedius* shifted their diet between the dry and wet seasons. *A. occidentalis* and *C. anguillaris* became more specialised (respectively in chironomids larva and mature insects) while *S. intermedius* switched from fish to insects. In reality, this species is euryphagous (Adebisi, 1981) but can exhibit well marked piscivorous habits when predation pressure on the available fish prey is very low. *C. anguillaris* is omnivorous (Paugy and Lévêque, 1999), as it is an adaptive generalist predator, like *A. occidentalis* and *S. intermedius*. These three species forage according to the Optimal Foraging Theory, which predicts that the more profitable prey type is always included in the predator diet while the less profitable (i.e., alternative) prey type is included only if the density of the more profitable prey type falls below a critical threshold (Emlen, 1966; MacArthur and Pianka, 1966; Charnov, 1976). The generalist feeding strategy is then favoured when food density is low or constantly fluctuating. Diet shifts were consistent with the seasonal variation in zooplankton, benthos and insects abundance. Species consume more insects, benthic invertebrates or zooplankton when those preys were more abundant. In accordance with these results, Prejs and Prejs (1987) have shown that most fish species in a Venezuelan savanna fed predominantly on invertebrates during wet season and most of them switched to alternative foods following the drastic decline in invertebrate availability towards the end of the dry season. As reported by Pusey and Bradshaw (1996), despite such changes, most seasonal variations occurred more by changes in the relative contributions of a small core group of prey rather than the ingestion of novel prey.

The three other species (*B. nurse*, *O. niloticus* and *T. zillii*) are specialised in the same way in both seasons, though they did show minor seasonal variations in their diets. *O. niloticus* and *T. zillii* are primary consumers, specialised respectively in detritus and in vegetal matter. These observations on *T. zillii* feeding habits contrast with those of Spataru (1978) who found seasonal variations for this species. According to this researcher the diet of *T. zillii* in Lake Kinneret was mainly represented by zooplankton during summer and autumn. In winter and spring, pupae of Chironomidae and other aquatic insects take the place of zooplankton. *B. nurse* is generally reported as omnivore and its food and feeding habits appear to be variable depending on habitat conditions (Paugy and Lévêque, 1999). However, *B. nurse* in Loumbila Lake is specialised in seed. Nevertheless, its secondary prey item (Insects) becomes more important in wet season.

According to several studies (Adebisi, 1981; Paugy and Lévêque, 1999; Kouamélan *et al.*, 2000), fish species (generally piscivorous) often show ontogenetic diet shifts. However, according to the Mann-Whitney U-test results, for all species, the seasonal diet shifts observed in Loumbila Lake are not related to differences in individual sizes.

Observed seasonal diet shifts are generally consistent with changes in the availability of major food resources. Zooplankton, benthos and insects occurred more frequently in diet during the wet season as expected. However, only *S. intermedius* feeding strategies are compliant with Winemiller and Jepsen's (1998) hypothesis that piscivory should be higher and omnivory lower during the dry season. Those of *C. anguillaris* and *A. occidentalis* are mot consistent with this hypothesis. Actually, *C. anguillaris* as *A. occidentalis* shifted from omnivorous diets (dry season) to ones that are insectivorous. Perga *et al*. (2005) using isotope analyses have also showed some exceptions to Winemiller and Jepsen's hypothesis on floodplain food webs.

As shown by the increase of the values of Resource Breadth and the greater variability in Resource Breadth between individuals observed in the wet season, fish species had more extended trophic niches (excepted *T. zillii*: low R_B in wet season) and displayed more plastic feeding behaviours in the wet season at the population scale and between individuals. These changes, which are related to resource availability, are adaptive as they allow the individuals to survive in conditions that would otherwise be disadvantageous (Paugy and Lévêque, 1999). According to Svanback and Persson (2004), the increase in resource breath would be indicative of increasing intraspecific competition. Such competition would lead a higher proportion of individuals to include secondary food items in their diets.

In Loumbila Lake, because fish are able to capitalize on the boom of aquatic production and more diverse food resources associated with flood (Balcombe *et al*., 2005), prey abundance in the wet season allows each individual to substantially diversify its gut content (higher individual R_B) and degree of specialisation (higher SD). This in turn also enables species to develop feeding patterns that differ more between species (except for *C. anguillaris* and *S. intermedius*) according to their ability to efficiently use other food resources.

The highest diet overlap between species is observed during the season with the lowest food abundance (dry season). The most likely explanation is that the dry season has a less diversified array of food resources so there less opportunity for resource partitioning (Matthews, 1998). Actually this pattern is mainly due to the quite high occurrence of detritus and vegetal matter in the diet of *A. occidentalis* during the dry season, leading to a high overlap with the diet of the two Cichlidae. Similar increases in diet similarity with a diminishing resource base were documented by some tropical fish researchers like Prejs and Prejs (1987) and Jepsen *et al*. (1997). As showed by Pusey and Bradshaw (1996) diet overlaps were high in the dry season because of a lack of niche segregation, due to the structural monotony in dry season habitat. Like Esteves and Galetti (1995), we noticed that while the herbivorous and detritivorous species showed higher overlap during the dry season, omnivorous species (*S. intermedius* and *C. anguillaris*) conversely tend to have their highest overlap in the wet season, though they show high overlap even in the dry season. According to Pusey and Bradshaw (1996) and Matthews (1998) higher diet overlap may be an indicator of competition only if resource availability is low. Therefore, in the Loumbila Lake context (high food abundance in the wet season), we can assume that in the dry season, there was probably competition between *A. occidentalis*, *O. niloticus* and *T. zillii*, pair by pair, due to the reduction of resource abundance.

The observed diet of fish species in a given place and time results from a complex interplay between resource availability, species feeding plasticity and strategies to avoid intra and inter-specific competition. This study shows that the main fish species of Loumbila Lake use most resources available for them and seasonal diet shifts reflected in part seasonal food availability. These variations in species diets are usually illustrated by variations in the frequency or quantity of items consumed. However, some prey (Insects and Zooplankton) were specific to the wet season. We found weak evidence supporting the hypothesis that piscivory should increase and omnivory decrease during the low water season. We noticed that the amplitude and pattern of diet shifts varied between species, probably reflecting the constraints imposed by their trophic status, as specialized species are less likely to display diet shift. Finally our results are not consistent with hypotheses that under low resource abundance/availability resource breadth may increase and/or diet overlap may decrease to reduce intra and inter-specific competition. If strategies for avoiding competition occur they are subtle and probably blurred by the seasonal changes in resources availability. Within Loumbila reservoir strong interspecific competition is more likely to occur during the dry season because food resources are depleted and diet overlap between species is high due to less diversified resources. While highly plausible and consistent with previous studies this result should be confirmed by including all the species of the assemblage, not only the most abundant ones.

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