

Food Habits and Diet Relationship in the Redbelly Tilapia (*Tilapia zillii*) and Guenther's Mouthbrooder (*Chromidotilapia guntheri*) from an Abandoned Gold Mine Reservoir, Southwestern Nigeria

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Abstract

The food and feeding habits of the redbelly Tilapia (*Tilapia zillii*) and Guenther's mouthbrooder (*Chromidotilapia guntheri*) was investigated in an abandoned gold mine reservoir at Igun from June 2013 to May 2014. Using a cast net and gill-net fishing gears, 370 fish individuals were caught and their stomach contents were analysed by using the frequency of occurrence and numerical methods. *Tilapia zillii* comprised 53.78% (199 individuals) while *Chromidotilapia guntheri* covered up the remaining percentage (46.22%) which is made up of 171 individuals. Food items in the stomachs of *T. zillii* individuals predominantly consisted of detritus, mud, and algae (77.97%) while those in *C. guntheri* individuals mostly consisted fish remains, detritus and algae (81.67%). *T. zillii* exploited more food items (23 of 27) as compared to *C. guntheri* (17 of 27). The Schoener's index value for the species was 0.65. This study showed that *T. zillii* and *C. guntheri* exhibited benthopelagic exploitation and are mainly herbivorous and omnivorous respectively based on the food items observed in the stomach contents of these species. The fish species fed on related food items as confirmed by Schoener's overlap index (0.65), suggesting that there was overlap in the dietary requirements of the two species. This index value, however, was probably not an indication of competition for food between these two species because they exploited abundant food sources.

Keywords: competition; diet overlap; fishes; freshwater; food items; food preference

Introduction

Interactions and inter-relationships are evident among fishes of a community during their search for food. Some species prey on other organisms or are being preyed upon, thereby forming a food chain or web (Valeila, 1991). This signifies the transfer of energy from one trophic level to another. It is also observed that fish species sometimes compete for food. Diet overlap among fish species or among size classes of a single species has been calculated in several studies to help explain community structure or to clarify competitive relationships (Zaret and Rand, 1971; Keast, 1978; Wallace Jr, 1981). Among the several measures of diet used in overlap indexes, the Horn (1966) and Schoener (1970) indexes give values from 0 (no overlap) to 1 (complete overlap) and measure the overlap between two species. Overlap in the other indexes is generally considered to be biologically significant when the value exceeds 0.60

(Zaret and Rand, 1971; Mathur, 1977). (Hurlbert, 1978) rejected certain overlap indexes as not appropriate because the overlap index values are dependent on the proportion of food in a category for one species when that category is not utilized by the other species. In addition, all measures of overlap that do not consider resource availability are poor measures, although the (Schoener, 1970) index is considered to be adequate in the absence of resource availability data (Hurlbert, 1978).

Many biologists invoke competitive exclusion to explain the niche separation of sympatric species. The "competitive exclusion principle" states that if two non-interbreeding populations occupying the same ecological niche are sympatric, one will ultimately exclude the other (Hutchinson, 1965). Therefore, sympatric species that differ in any aspect of their niche are said to owe their "character divergence" to competition in the past. Lindström and Nilsson (1962) reported that competition as the interaction between fish species or individuals adversely

affects survival or individual growth within populations.

Fishes have responded to various biotic and abiotic factors that control their feeding habits or patterns, through a number of characters and strategies. Therefore, fishes feed on different kinds of food ranging from plants, decayed plants and animals, detritus, insects, eggs of other fishes, mud deposits, mollusc, worms, crabs, algae, plankton and other small fishes (Adesulu and Sydenham, 2007). Habitat plays a large part in the feeding behaviour of fishes. Within the habitat exists, spectrums of good to poor feeding sites, which will be reflected by the spatial distribution of animals seeking to maximize food intake (Wafkowski and Thorpe, 1979). The most important factor that affects the feeding habit of fishes is the availability of food (Sirois and Boisclair, 1995). This is why fishes are highly selective in their feeding system despite the abundance of food (Komolafe, 1984).

The feeding of freshwater fish has been extensively investigated in West Africa particularly in Ghana (Blay, 1985) and Nigeria. In Nigeria, studies have been performed in Lake Kainji (Imevbore and Bakare, 1970; Arawomo, 1976; Olatunde, 1979); in upper Ogun River (Adebisi, 1981); in Lagos and Lekki Lagoons (Fagade, 1971; Fagade and Olaniyan, 1973) and in a number of rivers in the Niger Delta area (Brown, 1985; Tetsola, 1988; Odum, 1992). Recent works on food and feeding of fish include the work of Oboh *et al.* (2003) on twenty-three fish species from River Jamieson, a tributary of Benin River. Oribhabor and Ogbeibu (2012) on twenty-five species of fish in Buguma Creek, Niger Delta, Nigeria; Ekpo *et al.* (2014) seventeen fish species from Qua Iboe River estuary, Akwa Ibom State; and Abdul *et al.* (2016) on 8 species of fish including *Tilapia zillii* from Ogun estuary, Ogun State (all in Nigeria). Information on the feeding habits of fish species will aid the study of trophic relationships (Bajot and Moreau, 1997). Stomach content analyses have long been used to assess diet composition and assign trophic level in marine organisms (Hyslop 1980; Cortés 1999). Quantitative analyses of stomach contents provide an important tool to understand and elucidate predator-prey interactions (Cortés, 1997; Dávalos and González, 2003), feeding behaviour patterns (Preciado *et al.*, 2006), and ontogenetic shifts (Armstrong *et al.*, 1996). In addition, estimation of prey abundance, the frequency of occurrence, weight and relative importance of food items can provide critical ecological information (Joyce *et al.*, 2002; Ibáñez *et*

al., 2004).

Tilapias are mainly herbivorous, with flexible and opportunistic feeding habits (Trewavas, 1982). The success of *Tilapia* in Nigeria freshwaters probably depended on a wide diverse feeding regime (Fagade, 1971; Abayomi *et al.*, 2005). Every organic organism, plants, and mineral matters small enough to pass through the oesophagus are found in the gut of *Tilapia* fishes (Bowen, 1982). The dominant plant composition of *Tilapia* food is made up of phytoplankton, filamentous algae, and fine sediment rich in both diatoms and bacteria while the animal part is more of zooplankton (Olaleye, 1980; Adesulu, 1981).

There is no adequate work on the food and feeding behaviour, including diet composition of *T. zillii* and *C. guntheri* in habitats that are highly polluted e.g., abandoned gold mine reservoir of Igun, South-Western Nigeria (Lawal and Komolafe 2012). In this study, we examined the feeding and diet habits of the redbelly tilapia (*Tilapia zillii*) and Guenther's mouthbrooder (*Chromidotilapia guntheri*) from the gold mine reservoir. These two species were studied because of their ecological role and abundance in the reservoir.

Materials and Methods

Study area

This study was carried out in an abandoned gold mining reservoir at Igun, Southwestern Nigeria. Igun is a small village where the inhabitants are predominantly farmers. The study area lies within the equatorial rainforest vegetation belt where the climate is hot and humid in most months of the year. The catchment area of Igun gold mine reservoirs extends from Longitude 004°40'9.5''-004°40'40''E and from Latitude 07°31'20.2''-07°31'54.9''N (Fig. 1). The Nigerian Mining Company impounded three streams (Oika, Eleripon, and Osun) to make the reservoirs in 1941. Reservoirs 1, 2, and 3 were covered with rooted aquatic macrophytes, which disallowed the use of gill net. Reservoir 4 was being used by the community for core services and was partly covered by aquatic macrophytes while reservoir 6 had been overgrown with higher plants. All the above reasons made reservoirs 1, 2, 3, 4, and 6 not inappropriate for fish sampling in the course of this research. Hence, fish were sampled only in reservoir 5.

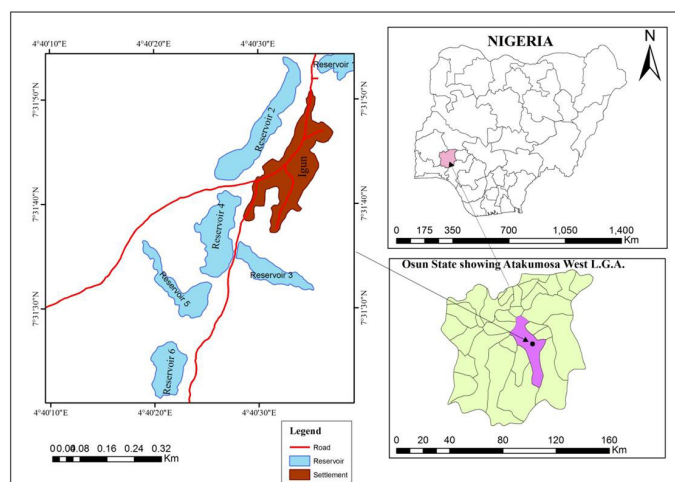


Fig. 1. Map of Nigeria showing abandoned gold mine reservoirs at Igun village

Fish sampling

Samples of fish were collected from reservoir 5 (Fig. 2) from 9 AM-12 PM on every sampling day, each month from June 2013 to May 2014. Cast net (with a mesh size of 2.5 cm) and traps, made from *Eremospatha* sp. with entrances in the form of a funnel and with non-return valves, were used to collect fish samples under contract with the local artisanal fishermen. The traps were baited with ripe palm fruits and set under sedges. This ensured that actively feeding fish were caught. All the fish samples were brought into the laboratory in an ice chest covered with ice for preservation. Standard identification keys (Paugy *et al.*, 2003; Adesulu, 2007) were used to identify fish species. Fish biometric data such as the total length (cm), standard length, and body mass (g) of individual fish from the samples were measured and recorded. Fish lengths were measured to the nearest 0.1 cm while and weight measured to the nearest 0.1 g using Denward balance Scale, Serial No. 9512. Each fish specimen was smitten open from the anus to the pectoral fin and the stomach carefully removed. Each stomach was then preserved in 4% formalin solution in a well-labelled sample bottle for identification. The contents of each stomach were carefully removed into a petri-dish for observation using a compound microscope.

The analysis of the stomach contents was carried using frequency of occurrence and numerical methods (Hyslop, 1980; Costa *et al.*, 1992). The frequency of occurrence is the number of stomachs of a species in which each type of food item occurred and expressed as a percentage of the total number of stomachs of that species examined, in order to determine the proportion of the fish population that fed on a particular food item (Hynes, 1950). In the numerical

method, the number of each food item was expressed as the percentage of the total number of food items found the stomach.

Schoener's overlap index (C)

The Schoener (1970) overlap index was used to establish dietary affinity between the 2 species. Based on a review of dietary overlap measures (Cailliet and Barry, 1979; Linton *et al.*, 1981), the index was chosen because it was found to measure overlap accurately over most of the range of potential overlap. The incorporation of resource availability into an overlap index would enhance measurement of overlap if technical and theoretical problems were overcome. When resource availability data are absent, the Schoener index is one of the least objectionable indexes available (Wallace Jr, 1981). Schoener's index, C_{xy} , between species x and y was calculated as:

$$C_{xy} = 1 - 1/2 \left(\sum_{i=1}^n |P_{x,i} - P_{y,i}| \right)$$

where $P_{x,i}$ and $P_{y,i}$ are the frequencies (or proportions) of species x and y respectively in category i . The index ranges from 0 which indicates no dietary overlap to a maximum overlap of 1 when all prey items are found in equal proportions. Diets of different species can normally be regarded as significantly different when the overlap index value is below 0.6 (Zaret and Rand, 1971; Wallace Jr, 1981). Cartes and Sardà (1989) took index values ≤ 0.8 to be indicative of significant differences because the dietary overlap considered in their work was between different size classes of the same species in the same habitat.



Fig. 2. Reservoir 5 at Igun showing (A) its view and the surrounding vegetation, (B) heaps of earth at the nearby mining site and, (C) miners at work processing gold with their locally made equipment

Statistical analysis

Data were analysed by the use of IBM SPSS Statistics for Windows, (Version 21.0). Descriptive statistics of fish biometric data were presented as means \pm standard errors of the mean. Statistical difference between a total number of fish individuals caught during the rainy and dry seasons for the species from Igun reservoir was analysed using unpaired t-test.

Results

A total of 370 fish individuals, made up of a family (Cichlidae) and two species were recorded in Igun reservoir during the study (Table 1). *T. zillii* was higher in number (53.78%) than *C. guntheri* (46.22%). There was no significant difference ($P < 0.05$) in the mean number of individuals caught during the rainy season (3.90 ± 1.46 and 12.29 ± 1.13 for *T. zillii* and *C. guntheri* respectively) to those caught in the dry season (17.00 ± 2.24 each for *T. zillii* and *C. guntheri*). The mean total- and standard lengths and weight were 16.00 ± 6.06 cm, 12.95 ± 4.83 cm and 123.7 ± 118.06 g for *T. zillii*; 13.04 ± 1.75 cm, 10.04 ± 1.42 cm, and 38.00 ± 16.45 g for *C. guntheri*. *T. zillii* fed on more food items (23 of 27) than *C. guntheri* (17 of 27) (Table 2). Table 3 reveals that the food of *T. zillii* showed variation in the dry and rainy seasons. A high proportion of algae, diatoms, insects, crustaceans and fish parts were fed upon during the rainy season (April to September) while mud, detritus and higher plants fragments complemented the diet during this period. In the dry season (October-March), *T. zillii* fed on algae, insects, detritus, higher plant fragments, and mud. *C. guntheri* had a slight variation in its food items in relation to the two seasons.

During the dry and rainy seasons, the species fed predominantly on higher plants fragments, fish remains, algae, detritus, and diatoms. The inclusion of insect remains in the dry season was the slight variation in the seasons.

Table 4 shows that both fed predominantly on algae (85.47% and 55.98% for *T. zillii* and *C. guntheri* respectively) by the percentage of the number of prey items observed. In addition, the second largest food items consumed by *C. guntheri* were diatom (32.40%). Other

food items of importance found in the stomach of *T. zillii* included fish parts (eggs and scales, 5.40%) and plants fragment (4.65%) while those in the stomach of *C. guntheri* included diatom (32.40%) and fish remains (6.72%). The diet of the fishes included both the blue-green and green algae, which were filamentous or unicellular. In *T. zillii*, *Closterium* sp. and *Oscillatoria* sp. were very prominent in its diet while *Microcystis* sp. and *Closterium* sp. were the major algae in the diet of *C. guntheri*. The three main diets of *T. zillii* were detritus, mud, and algae and constituted 77.97% of its total prey items (Fig. 3). In *C. guntheri*, fish remains, detritus, and algae were the main three contents of its stomach food item composition and these constituted 81.67% of the total food items (Fig. 4). The Schoener's overlap index value of 0.65 was obtained for the species in the reservoir, suggesting a dietary overlap between the species (Table 4).

Discussion

In the present study, *T. zillii* and *C. guntheri* fed on similar food items such as algae, insects, higher plant fragments, detritus, and diatoms. However, algae, higher plant fragments, and detritus were the only common food items fed upon by the species.

Other food items were fed upon at variance. A number of factors are attributable to changes in the feeding habits of fish species. Fryer and Iles (1972) and Jobling (1995) listed these factors as the size of the fish, sex, season, water temperature, habitat, and competition. Because of the feeding rhythm of *T. zillii*, the species have been variously classified as plankton feeders, higher plant and algae feeders or macrophagous as well as mudsuckers (Fagade, 1971; Brown and Colgan, 1984). According to (Spataru, 1978), adult *Tilapia zillii* are considered to be voracious herbivores, often decreasing plant density and changing the composition of native plants which can threaten many native aquatic organisms that depend on such plants for forage, protection, or spawning. In this study, *T. zillii* was largely herbivorous with its food similar to that in the report of Akintunde (1976) in Lake Kainji, Komolafe (1984) in Opa reservoir and Abdul et al. (2016) in Ogun estuary.

Table 1. Relative abundance and seasonal distributions of *Tilapia zillii* and *Chromidotilapia guntheri* from the Igun gold mine reservoir

Fish species	Fish catch				% total catch by species	t	Sig. (2- tailed)
	Rainy season		Dry season				
	N	X \pm SE	N	X \pm SE			
<i>Tilapia zillii</i>	114	3.90 \pm 1.46	85	17.00 \pm 2.24	53.78	-0.28	0.79
<i>Chromidotilapia guntheri</i>	86	12.29 \pm 1.13	85	17.00 \pm 2.47	46.22	-1.92	0.08
Total	200		170		100		

Table 2. Biometric parameters of *Tilapia zillii* and *Chromidotilapia guntheri* sampled from Igun gold mine reservoir

parameter	<i>Tilapia zillii</i>		<i>Chromidotilapia guntheri</i>	
	Range	X \pm SD	Range	X \pm SD
Total length (cm)	9.1 – 27.7	16.00 \pm 6.06	9.7 – 16.8	13.04 \pm 1.75
Standard length (cm)	7.4 – 22.0	12.95 \pm 4.83	7.5 – 12.8	10.04 \pm 1.42
Weight (g)	13.0 – 375.0	123.7 \pm 118.06	13.0 – 84.0	38.00 \pm 16.45

Table 3. Seasonal variations in the diets of *Tilapia zillii* and *Chromidotilapia guntheri* from Igun gold mine reservoir

Prey category	<i>Tilapia zillii</i>		<i>Chromidotilapia guntheri</i>	
	Dry season	Rainy season	Dry season	Rainy season
Blue green algae				
<i>Oscillatoria sp</i>	+	+	+	+
<i>Microcystis sp</i>	-	+	+	-
<i>Phormidium sp</i>	+	+	-	-
<i>Spirulina sp</i>	+	+	-	-
<i>Lyngbya sp</i>	+	+	+	+
Green algae				
<i>Closterium sp</i>	+	+	+	+
<i>Spirogyra sp</i>	+	+	+	+
<i>Arscella sp</i>	+	+	+	+
<i>Euglena sp</i>	-	+	-	-
<i>Scenedesmus sp</i>	-	+	+	+
<i>Cosmarium sp</i>	+	+	-	-
<i>Hydrodictyon sp</i>	-	+	-	+
<i>Asplancha sp</i>	-	-	+	+
Diatom				
<i>Asterionella sp</i>	-	+	-	-
<i>Melosira sp</i>	-	+	-	-
<i>Navicular sp</i>	-	-	+	+
Rotifer				
<i>Keratella quadrata</i>	-	+	-	-
<i>Symecococcus sp</i>	+	-	-	-
Insect				
Insect remains	+	+	+	-
Crustaceans				
<i>Cladocerus sp</i>	-	+	-	-
Fish parts				
Eggs	-	+	-	-
Scales	+	+	-	-
Fish				
Fish remains	-	-	+	+
Others				
Higher plants fragments	+	+	+	+
Detritus	+	+	+	+
Mud	+	+	-	-
Unidentified	-	-	+	+

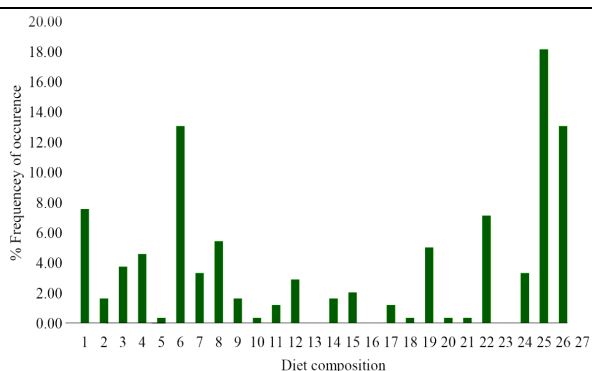


Fig. 3. Relative frequency of dietary composition of *Tilapia zillii* in Igun gold mine reservoir, Nigeria. Note: 1 – 13 = algae; 14 – 16 = diatom; 17 – 18 = rotifer; 19 = insect remains; 20 = crustaceans; 21 – 22 = fish parts; 23 = fish remains; 24 = plants fragment; 25 = detritus; 26 = mud; 27 = unspecified

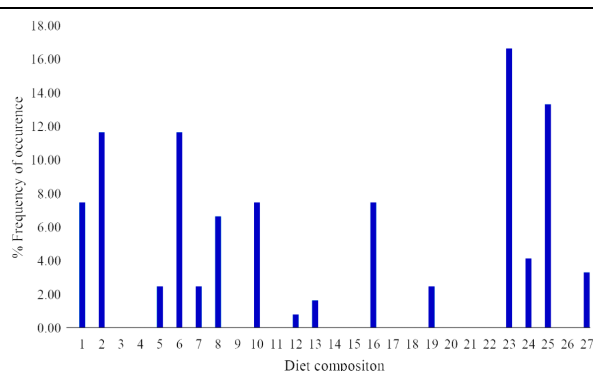


Fig. 4. Relative frequency of dietary composition of *Chromidotilapia guntheri* in Igun gold mine reservoir, Nigeria. Note: 1 – 13 = algae; 14 – 16 = diatom; 17 – 18 = rotifer; 19 = insect remains; 20 = crustaceans; 21 – 22 = fish parts; 23 = fish remains; 24 = plants fragment; 25 = detritus; 26 = mud; 27 = unspecified

Table 4. Prey items observed (N), percentage of prey items observed, (%N), frequency of occurrence (Fo), percentage occurrence (%O), and diet overlap indexes of *Tilapia zillii* and *Chromidotilapia guntheri* from Igun reservoir

Prey category	<i>Tilapia zillii</i>				<i>Chromidotilapia guntheri</i>				Cx,y
	N	%N	Fo	%O	N	%N	Fo	%O	
Blue green algae	4,283	46.22	43	18.22	377	37.81	26	21.67	0.65
<i>Oscillatoria sp</i>	2,884	31.12	18	7.63	281	28.18	9	5.7	
<i>Microcystis sp</i>	301	3.25	4	1.69	72	7.22	14	11.67	
<i>Phormidium sp</i>	902	9.73	9	3.81	-	0	-	0	
<i>Spirulina sp</i>	195	2.1	11	4.66	-	0	-	0	
<i>Lyngbya sp</i>	1	0.01	1	0.42	24	2.41	3	2.5	
Green algae	3,637	39.25	67	28.39	182	18.17	36	30	
<i>Closterium sp</i>	3,221	34.76	31	13.14	108	10.83	14	11.67	
<i>Spirogyra sp</i>	52	0.56	8	3.39	21	2.11	3	2.5	
<i>Arscella sp</i>	96	1.04	13	5.51	17	1.71	8	6.67	
<i>Euglena sp</i>	25	0.27	4	1.69	-	0	-	0	
<i>Scenedesmus sp</i>	1	1.01	1	0.42	24	2.41	9	7.5	
<i>Cosmarium sp</i>	90	0.97	3	1.27	-	0	-	0	
<i>Hydrodictyon sp</i>	152	1.64	7	2.97	1	0.1	1	0.83	
<i>Asplancha sp</i>	-	0	-	0	11	1.01	2	1.67	
Diatom	333	3.59	9	3.81	323	32.4	9	7.5	
<i>Asterionella sp</i>	82	0.88	4	1.69	-	0	-	0	
<i>Melosira sp</i>	251	2.71	5	2.12	-	0	-	0	
<i>Navicular sp</i>	-	0	-	0	323	32.4	9	7.5	
Rotifer	8	0.008	4	1.7	0	0	0	0	
<i>Keratella quadrata</i>	5	0.05	3	1.27	-	0	-	0	
<i>Synechococcus sp</i>	3	0.03	1	0.42	-	0	-	0	
Insect	24	0.26	12	5.09	12	1.2	3	2.5	
Insect remains	24	0.26	12	5.08	12	1.2	3	2.5	
Crustacean	1	0.01	1	0.42	0	0	0	0	
<i>Cladocerus sp</i>	1	0.01	1	0.42	-	0	-	0	
Fish part	550	5.94	18	7.63	0	0	0	0	
Eggs	500	5.4	1	0.42	-	0	-	0	
Scales	50	0.54	17	7.2	-	0	-	0	
Fish	0	0	0	0	67	6.72	20	16.67	
Fish remains	-	0	-	0	67	6.72	20	16.67	
Others	431	4.65	82	34.75	36	3.61	22	18.33	
Higher plant fragments	431	4.65	8	3.39	26	2.61	5	4.17	
Detritus	-	0	43	18.22	-	0	16	13.33	
Mud	-	0	31	13.14	-	0	-	0	
Unidentified	-	0	-	0	10	1	4	3.33	
Total	9,276	100	236	100	997	100	120	100	

This study is also in agreement with the study of Spataru (1978) and Olayemi (2000) who observed that *T. zillii* fed on whatever comes its way while searching for preferred food. According to their studies, its food consisted of algae, nematodes, arthropods, zooplankton, ostracods as well as chironomid larvae. Ifedayo (2006) had also reported *T. zillii* to feed on algae, higher plants, fish eggs and insect larvae in Osinmo reservoir. The species can, therefore, be said to have selectively fed on food items in the reservoir. The stomach contents of *C. guntheri* in Igun reservoir was dominated by fish, algae, diatoms, and insect remains. The food items were similar to food items recorded by Olayemi (2000) for *Hemichromis fasciatus* in Owalla reservoir. *C. guntheri* is an omnivore, feeding on whatever comes its way as observed in Owalla and Eko-Ende reservoirs by Taiwo (2008). The diatoms (*Asterionella sp* and *Melosira sp*) recorded for *T. zillii* in the rainy season was not found in the diet during the dry season while *Navicula sp* appeared both in the dry and rainy seasons in the diet of *C. guntheri*. The variety of food

items of *T. zillii* in this study was higher in number compared to the observations of (Walter, 2004; Abayomi et al., 2005) who reported plant materials and detritus for the species.

Since index values > 0.60 are indicators of dietary overlap (Zaret and Rand, 1971; Langton, 1982), this suggests that there is overlap in the diets of *T. zillii* and *C. guntheri* ($C_{xy} = 0.65$) from the gold mine reservoir. The feeding habits of fish had been found to overlap in some cases (Crozier, 1985; Yang and Livingstone, 1986). However, (Komolafe and Arawomo, 2011) reported no overlap in the feeding habits of *Clarias gariepinus* and *Parachanna obscura* in Osinmo reservoir. Since dietary overlap is dependent upon available resources (Keast, 1978), this diet overlap value might not be an indication of competition for food between these two species because they exploited abundant food sources (Ekpo et al., 2014). In spite of the high diet overlap value recorded (0.67 - 0.90) between Kamchatka flounder and arrowtooth flounder size

classes, (Yang and Livingstone, 1986) argued that there was probably no competition for food between these two species because they were exploiting abundant food sources.

There is fairly general agreement that studies of niche overlap (or equivalently, resource partitioning) are of interest because of their relevance to competition. According to (Schoener, 1974), the major purpose of resource partitioning studies is to analyse the limits interspecific competition places on the number of species that can stably coexist. A study by (Cody, 1974) which make extensive use of niche overlap data is essentially concerned with competition. In the article referred to above, Hurlbert (1978) suggests that niche overlap measures should serve "as a foundation for discussion of resource utilization strategies, competition, and species packing, and so on". It could also be argued that niche overlap is of interest in its own right, independent of any relationship to competition. Evolutionary forces (such as character displacement) and ecological forces (such as competitive exclusion) that determine observed overlap are directly related to competition, not niche overlap. An understanding of the reason for different levels of niche overlap in different communities will, therefore, requires that one understands both the competitive relationships between the species and the relationship between overlap and competition.

Conclusions

Exploitation of food resources differs between *T. zillii* and *C. guntheri*, with the different species exploiting separate levels of the available resources in the water column. This is a function of the food preferences when foraging during normal feeding activity.

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