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Alphonse Adite

Laboratoire d'Ecologie et de
Management des Ecosystèmes
Aquatiques (LEMEA),
Département de Zoologie,
Faculté des Sciences et
Techniques, Université
d'Abomey-Calavi, BP 526
Cotonou, Bénin

Hamidou Arame

Laboratoire d'Ecologie et de
Management des Ecosystèmes
Aquatiques (LEMEA),
Département de Zoologie,
Faculté des Sciences et
Techniques, Université
d'Abomey-Calavi, BP 526
Cotonou, Bénin

Edmond Sossoukpe

Laboratoire de Recherches sur
les Zones Humides (LRZH),
Département de Zoologie,
Faculté des Sciences et
Techniques, Université
d'Abomey-Calavi, BP 526
Cotonou, Bénin

Kayode Nambil Adjibade

Laboratoire d'Ecologie et de
Management des Ecosystèmes
Aquatiques (LEMEA),
Département de Zoologie,
Faculté des Sciences et
Techniques, Université
d'Abomey-Calavi, BP 526
Cotonou, Bénin

Correspondence

Alphonse Adite

Laboratoire d'Ecologie et de
Management des Ecosystèmes
Aquatiques (LEMEA),
Département de Zoologie,
Faculté des Sciences et
Techniques, Université
d'Abomey-Calavi, BP 526
Cotonou, Bénin

Comparative trophic ecology of two sympatric tilapia, *Oreochromis niloticus* (Linné, 1758) and *Sarotherodon melanotheron* (Rüppell, 1852) from Lake Toho, Southern Benin: Food competition and risk of species replacement

Alphonse Adite, Hamidou Arame, Edmond Sossoukpe and Kayode
Nambil Adjibade

Abstract

Knowledge on trophic ecology of coexisting invasive and native fishes is of great importance for fisheries management, species conservation, and ecosystem integrity. We investigated the feeding ecology of two tilapias, *Oreochromis niloticus*, exotic and invasive, and *Sarotherodon melanotheron*, native, in order to explore diet similarities and food competition between these two cichlids of Lake Toho (Southern Benin). Fish individuals were sampled bimonthly from May-December 2013 in all habitats. *Sarotherodon melanotheron* consumed about 107 food resources dominated by algae (86.88%) and detritus (7.87%). Likewise, *O. niloticus* ingested about 65 food resources dominated by algae (62.75%) and detritus (33.40%). *Sarotherodon melanotheron* exhibited a higher diet breadth (DB = 15.23), and the high diet similarity index ($\Theta_{jk}=0.83$) recorded indicated a high competition between the two cichlids. Further research on species behavior, hybridization and food competition are required to assess risks of native species replacement and the overall impacts of *O. niloticus* invasion.

Keywords: Alguivore, Competition, Hybridization, Invasive fish, Species replacement, Tilapiine Cichlids

1. Introduction

Knowledge on feeding ecology of coexisting invasive and native fish species is of great importance for conservation, fisheries management and ecological insight^[1, 2]. As reported by Huxel^[3] and Mooney & Cleland^[4], exotic and invasive species negatively affect native species by causing competition, niche displacement and hybridization. In particular, competition exerts high pressure on the communities and food web, and intensities vary according to species foraging abilities, food resource availabilities and species ecological status^[5, 6]. In addition, invasive species cause extinction of native taxa by modifying their evolutionary itinerary^[7].

In Benin, the Nile tilapia, *Oreochromis niloticus* (Pisces: Perciforme: Cichlidae) has been introduced through several aquaculture projects where the species was cultivated in net enclosures and floating cages installed in lakes (e.g: Lake Nokoué), lagoons (e.g: Porto-Novo Lagoon) and rivers (e.g: Sô River)^[8]. Likewise, the Nile tilapia was raised in conventional fish ponds and those built in swamps and wetlands located around lakes, lagoons and rivers^[9]. Also, to increase the national fish yields and productions, the Benin government has directly introduced thousands of *O. niloticus* fingerlings in many freshwater lakes such as Hlan, Cele, etc^[8, 10]. Due to the complexity of the Benin hydrological regime characterized by multiple interconnections between rivers and lakes from North to South^[11], *O. niloticus* has invaded almost all the Benin aquatic ecosystems, causing profound changes in the fish community structure^[7]. The introduction of this invasive alien species, though beneficial in short term to increase inland fish productions, constitutes an ecological disaster because appears to be an important threat for native species, mainly cichlids^[4, 12-13].

Particularly, in Southern Benin, the Nile tilapia has been accidentally introduced through

aquaculture in Lake Toho (10 km²), a Mono River floodplain lake where the species was well-established and numerically made about 19.56% of the fish community while a dominant coexisting native cichlid, the blackchin tilapia *Sarotherodon melanotheron* made about 68.46% [14-16]. In Benin, Lake Toho is one of the most productive water body where annual fish captures reached 603.60 metric tons dominated by cichlids that made about 92.53% of the total annual catches [17]. Tossavi [16] reported about twenty (20) species with Cichlidae, the most speciose family composed of six (6) species). Among cichlids, the native tilapia, *S. melanotheron* and the introduced invasive tilapia, *O. niloticus*, dominated Lake Toho fish community and numerically made 68.46% and 19.56%, respectively.

Notwithstanding the abundance and prominence of the invasive cichlid, *O. niloticus*, nothing is known about the

trophic ecology of Lake Toho fish community [18]. In particular, there is a gap of information on the feeding ecology of the two dominant cichlids [19], *O. niloticus*, an exotic species, accidentally introduced in Lake Toho [8], and *S. melanotheron*, a dominant native species. Investigation on the feeding ecology is important to document resource utilization, diet similarities and niche partitioning between the two sympatric tilapias and impacts of the non-native species [20, 21].

The current study aims to compare the feeding ecology of the invasive Nile tilapia, *O. niloticus* and the native tilapiine cichlid, *S. melanotheron*, in order to better document diet composition, resource exploitation, niche overlapping, food competition, and the impacts of the introduction of *O. niloticus* (Fig 1a) on dominant native tilapia, *S. melanotheron* (Fig 1b) and on Lake Toho fish community.



Fig 1: Photo (a) *Oreochromis niloticus* et (b) *Sarotherodon melanotheron*

2. Material and Methods

2.1. Study region

Lake Toho (6°36'0" N; 1°46'60" E) is a floodplain lake of the Mono River located in Southeast Benin at an altitude of 64 meters and covers about 10 km² during the dry season and 15 km² during the flooding. This freshwater lake receives water from the Mono River (also from Adiko & Akpatohoun streams), and withdraws its water in the Sazoé River during the high-water season [22]. Lake Toho showed a sub-equatorial climate comprising two (2) wet seasons (April - July; mid-September - October) with a peak usually recorded in June, and two (2) dry seasons (December - March; August - mid-September) [22]. Annual mean rainfall reached 1307.3 mm and ambient temperatures varied between 20.74°C and 33.6°C.

The plant community at Lake Toho is composed of floating species such as *Nymphaea lotus*, *Ipomoea aquatica*, *Brachiaria mutica* and *Echinochloa pyramidalis*, *Pistia stratiotes*, *Ceratophyllum demersum* and *Azolla africana* which were sometimes mixed with *Cyperus papyrus* and *Typha australis*. Plant species such as *Adansonia digitata*, *Saccharum officinalis*, *Elaeis guineensis*, *Tectona grandis* and *Imperata cylindrica* are common in the adjacent terrestrial habitats [16].

Artisanal and highly commercial multi-species fisheries dominated by cichlids, mainly *O. niloticus* and *S. melanotheron*, occurred in Lake Toho where a crowded fish market was settled.

2.2. Sampling locations and fish samplings

Fish individuals were sampled bimonthly in Lake Toho from May-December 2013 at two (2) fishing locations, namely Tohonou and Kpinnou villages. At each location, fish samplings were made in the aquatic vegetation habitat and in the open water habitat. At each sampling sites, physicochemical measurements showed depths ranging between 210-395 cm, transparencies between 46-90 cm and

water temperatures between 23.2°C - 29.6 °C. Dissolved oxygen concentrations varied from 3.2 mg/l to 7.4 mg/l, pHs from 4.3 to 7.4 and water salinity was nearly 0.2g/l.

Oreochromis niloticus and *S. melanotheron* collections were performed every two weeks (2 times a month) with a gill net (50 m x 1.30 m, 50 mm-mesh) and a seine (4.20 m-length, 2 m – width, 5 mm-mesh). Seines were used in the aquatic vegetation habitat and at each sampling location, ten rounds of seining were performed. Gill nets were set for 12 hours at the open water habitat [23]. In addition, at each location, samplings were done from fishermen catches and all size categories were sampled [24]. Combined fish samples from seining, gill netting and those from fishermen captures were gathered, identified, measured, weighted and preserved in 10% formalin. Species identification was based on references such as Van Thielen *et al.* [25], Leveque *et al.* [26]. All the fish samples were shipped to the “Laboratoire d’Ecologie et de Management des Ecosystèmes Aquatiques, Faculté des Sciences et Techniques, Université d’Abomey-Calavi”, and removed from the formalin after 2-3 days. Fishes were then sorted by habitat type and sampling period, and preserved in 70% ethanol to make easier dietary analysis [27].

2.3. Stomach content Analysis

After collections, each individual of the two targeted tilapiine cichlids, *O. niloticus* and *S. melanotheron* was measured for total length (TL) and standard length (SL) to the nearest 0.1 mm with an ichthyometer and weighed to the nearest 0.1g with an electronic balance (Philips). The fish individuals were then dissected, and the digestive tract was removed and measured as the distance from the distal end to the anus [28, 29]. The stomach was then opened and food resources were removed and spread on a glass slide for examination first under a binocular to identify macroscopic food resources. Water was added to facilitate separation and identification of small food items. To identify algae, a few drops of water containing fine

prey items from stomach contents were examined under a photonic microscope [30]. Prey items were identified to the lowest possible taxonomic level using the reference of Needham&Needham [30]. The identified food items were then 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. The food items belonging to a given category were gathered into a single sample for volumetric estimates.

2.4. Data Analysis

For both cichlids, *O. niloticus* and *S. melanotheron*, the estimated volume of each food item was recorded on Excel and SPSS software spreadsheet. The proportional volumetric consumption of each food resources was then computed as follows [31]:

$$P_i = \frac{(V_i)}{V_t} * 100$$

where p_i is the proportional volumetric consumption of food item i in the diet, v_i is the total volume of the food item i in n stomachs, V_t is the total volume of food ingested by n stomachs, n is the total number of stomachs examined ($n=517$ for *O. niloticus*; $n=607$ for *S. melanotheron*). Volumetric proportion variations of diet between the two tilapia were depicted with one-way ANOVA that were performed using Morgan *et al.*[32] SPSS computer program. To depict ontogenetic diet shifts, proportional consumptions of each food resource ingested were computed for different size categories. Niche breadth was calculated following Simpson [33].

$$\text{Niche breadth (NB)} = 1 / \sum_{i=1}^n P_i^2$$

where p_i is the proportion of food resources i in the diet, and n is the total number of food items in the diet. NB ranges from 1, when only one prey item is used, to n , when all preys are ingested in equal proportions. The matrices of computed niche breadth were submitted to one-way analysis of variance using SPSS computer program [32]. Diet similarities and ontogenetic diet shift were explored using Pianka's [34] niche overlap index (\mathcal{O}_{jk}) computed as follows:

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

where \mathcal{O}_{jk} is the dietary overlap between species j and species k , p_{ij} is the proportion of resource i used by species j , p_{ik} is the proportion of resource i used by species k , and n is the number of resource categories utilized by the species.

3. Results

3.1. Diet composition and volumetric percentages

The dietary analysis of 607 stomachs of *S. melanotheron* from Lake Toho indicated that this tilapiine cichlid consumed about 107 food resources dominated by algae (86.88%) and detritus (7.87%) (Table 1, Fig 2). Ingested algae comprised about 90 genera including green algae (53.09%) dominated by *Scenedesmus* (10.58%), *Microspora* (8.70%), *Staurodesmus* (8.19%), *Zygnema* (7.70%) and *Botryococcus* (4.18%); blue-

green algae (21.86%) dominated by *Coelophaerium* (11.10%) and *Phormidium* (4.03%); diatoms (10.26%) dominated by *Melosira* (5.85%), *Navicula* (1.98%) and *Synedra* (1.45%) and desmids (2.21%). Minor food resources consumed by *S. melanotheron* were substrate particles (1.54%), miscellaneous invertebrates (1.46%), protozoans (0.29%), Rotifera (0.01%), Crustacean (0.01%) along with some undetermined food items (1.30%) (Table 1).

Compared to the native tilapia *S. melanotheron*, *O. niloticus* ingested relatively less food resources in Lake Toho. Indeed, the analysis of 517 stomach contents of the Nile tilapia from Lake Toho indicated that this invasive cichlid consumed about 65 food items dominated by algae (62.75%), detritus (33.40%) and sand particles (2.03%) (Table 2, Fig 3). Consumed algae comprised about 56 genera and included green algae (41.04%) dominated by *Scenedesmus* (8.58%), *Zygnema* (12.36%), *Botryococcus* (9.57%) and *Pandorina* (4.21%); blue-green algae (4.30%) comprising *Polycystis* (1.60%) and *Coelophaerium* (0.77%); diatoms (13.34%) dominated by *Melosira* (9.01%), *Navicula* (2.74%) and *Synedra* (1.35%); desmids (4.07%) dominated by *Golacium* (2.03%). Minor food resources ingested by *O. niloticus* were protozoans (0.03%), Rotifera (*Brachionus*) (0.01%), miscellaneous invertebrates (0.66%), flowers (0.17%), insects (0.03%) and undetermined food resources (0.69%) (Table 1).

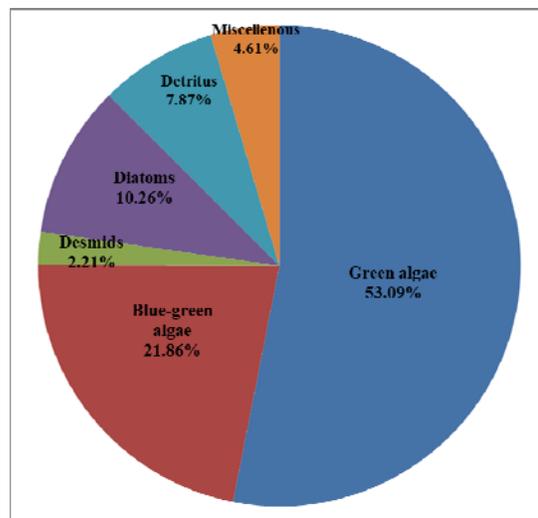


Fig 2: Volumetric percentages (%) of food items consumed by *Sarotherodon melanotheron* (n=607) from Lake Toho, South-Benin.

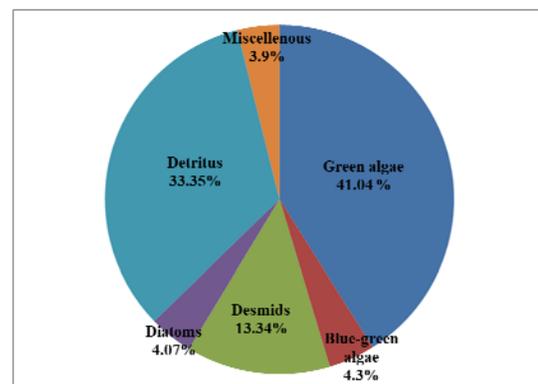


Fig 3: Volumetric percentages (%) of food items consumed by *Oreochromis niloticus* (n=517) from Lake Toho, South-Benin.

Table 1: Volumetric and occurrence percentages (%) of food items consumed by *Sarotherodon melanothron* (N = 607) from Lake Toho.

| Food categories | Food items | Volumetric percentages (%) | occurrence (Number) | Percentage occurrence (%) |
|--------------------------|-----------------------|----------------------------|---------------------|---------------------------|
| Blue-green algae | <i>Anabaena</i> | 0.361 | 11 | 1.812 |
| | <i>Aphanocapsa</i> | 1.886 | 30 | 4.942 |
| | <i>Coelohaerium</i> | 11.097 | 41 | 6.755 |
| | <i>Gelophaerium</i> | 0.008 | 3 | 0.494 |
| | <i>Glomotrichia</i> | 0.120 | 1 | 0.165 |
| | <i>Merismopedia</i> | 1.182 | 1 | 0.165 |
| | <i>Microcoleus</i> | 0.001 | 1 | 0.165 |
| | <i>Nostoc</i> | 1.418 | 7 | 1.153 |
| | <i>Phormidium</i> | 4.028 | 52 | 8.567 |
| | <i>Polysystis</i> | 1.717 | 21 | 3.460 |
| | <i>Raphidiopsis</i> | 0.120 | 2 | 0.329 |
| | <i>Tetrapedia</i> | 0.004 | 1 | 0.165 |
| | <i>Rivularia</i> | 0.012 | 5 | 0.824 |
| <i>Uronem</i> | 0.000 | 1 | 0.165 | |
| Green algae | <i>Ankistrodesmus</i> | 0.435 | 21 | 3.460 |
| | <i>Binuclearia</i> | 0.002 | 1 | 0.165 |
| | <i>Boryococcus</i> | 0.027 | 8 | 1.318 |
| | <i>Botryococcus</i> | 4.185 | 151 | 24.876 |
| | <i>Cladophora</i> | 0.001 | 1 | 0.165 |
| | <i>Coelastrum</i> | 0.001 | 1 | 0.165 |
| | <i>Cosmarium</i> | 0.001 | 1 | 0.165 |
| | <i>Characium</i> | 0.005 | 1 | 0.165 |
| | <i>Chodatella</i> | 0.120 | 1 | 0.165 |
| | <i>Cladophora</i> | 0.001 | 1 | 0.165 |
| | <i>Coelastrum</i> | 0.007 | 1 | 0.165 |
| | <i>Crucigenia</i> | 0.093 | 27 | 4.448 |
| | <i>Gosmarium</i> | 0.225 | 26 | 4.283 |
| | <i>Microspora</i> | 8.702 | 6 | 0.988 |
| | <i>Mesotaenium</i> | 0.107 | 10 | 1.647 |
| | <i>Oedogonium</i> | 0.370 | 10 | 1.647 |
| | <i>Pandorina</i> | 0.899 | 79 | 13.015 |
| | <i>Pediastrum</i> | 1.049 | 38 | 6.260 |
| | <i>Pleurotaenium</i> | 0.346 | 31 | 5.107 |
| | <i>Protococcus</i> | 0.631 | 14 | 2.306 |
| | <i>Phymatodocis</i> | 0.001 | 1 | 0.165 |
| | <i>Rhizochrysis</i> | 0.001 | 1 | 0.165 |
| | <i>Selenastrum</i> | 0.000 | 1 | 0.165 |
| | <i>Scenedesmus</i> | 10.582 | 355 | 58.484 |
| | <i>Staurodesmus</i> | 8.194 | 62 | 10.214 |
| | <i>Stigeoclonium</i> | 0.005 | 3 | 0.494 |
| | <i>Synechocystis</i> | 0.001 | 1 | 0.165 |
| | <i>Stephanoporus</i> | 0.002 | 1 | 0.165 |
| | <i>Tetraedron</i> | 0.012 | 4 | 0.659 |
| | <i>Tetraspora</i> | 1.128 | 26 | 4.283 |
| | <i>Tetrastrum</i> | 0.011 | 3 | 0.494 |
| | <i>Tribonema</i> | 0.142 | 7 | 1.153 |
| | <i>Trypicum</i> | 0.122 | 2 | 0.329 |
| <i>Typicum</i> | 0.002 | 2 | 0.329 | |
| <i>Ulothrix</i> | 0.051 | 3 | 0.494 | |
| Indetermined green algae | 7.925 | 281 | 46.293 | |
| <i>Zygnema</i> | 7.702 | 324 | 53.377 | |
| Desmids | <i>Desmidium</i> | 0.000 | 1 | 0.165 |
| | <i>Denticula</i> | 0.124 | 3 | 0.494 |
| | <i>Closterium</i> | 0.112 | 13 | 2.142 |
| | <i>Cosmarium</i> | 0.586 | 5 | 0.824 |
| | <i>Cymatopleura</i> | 0.002 | 1 | 0.165 |
| | <i>Ryptonas erosa</i> | 0.001 | 1 | 0.165 |
| | <i>Gonatozygon</i> | 0.001 | 1 | 0.165 |
| | <i>Genicularia</i> | 0.001 | 1 | 0.165 |
| | <i>Golacium</i> | 0.040 | 19 | 3.130 |
| | <i>Goniochloris</i> | 0.002 | 1 | 0.165 |
| | <i>Lepocinclis</i> | 0.001 | 1 | 0.165 |
| | <i>Micrasteria</i> | 0.060 | 1 | 0.165 |
| | <i>Netrium</i> | 0.007 | 1 | 0.165 |
| | <i>Nitzschia</i> | 0.119 | 1 | 0.165 |

| | | | | |
|----------------|---------------------------|-------|-----|--------|
| | <i>Penium</i> | 0.002 | 2 | 0.329 |
| | <i>Peridinium cinetum</i> | 0.001 | 1 | 0.165 |
| | <i>Spirotaenia</i> | 0.005 | 2 | 0.329 |
| | <i>Phacus</i> | 0.903 | 101 | 16.639 |
| | <i>Truchemonas</i> | 0.119 | 1 | 0.165 |
| | Indetermined desmids | 0.124 | 3 | 0.494 |
| Diatoms | <i>Diatoma</i> | 0.016 | 5 | 0.824 |
| | <i>Atiheyia</i> | 0.002 | 1 | 0.165 |
| | <i>Chaetoceros</i> | 0.358 | 19 | 3.130 |
| | <i>Cyclotella</i> | 0.219 | 18 | 2.965 |
| | <i>Diploneisovalis</i> | 0.012 | 1 | 0.165 |
| | <i>Amphoroovalis</i> | 0.049 | 2 | 0.329 |
| | <i>Cymbela</i> | 0.016 | 5 | 0.824 |
| | <i>Eunotia</i> | 0.023 | 13 | 2.142 |
| | <i>Frustulia</i> | 0.227 | 2 | 0.329 |
| | <i>Gyrosigma</i> | 0.001 | 1 | 0.165 |
| | <i>Melosira</i> | 5.853 | 369 | 60.791 |
| | <i>Navicula</i> | 1.979 | 165 | 27.183 |
| | <i>Nitzschia</i> | 0.006 | 4 | 0.659 |
| | <i>Pinnularia</i> | 0.005 | 3 | 0.494 |
| | <i>Stauroneis</i> | 0.005 | 2 | 0.329 |
| | <i>Stephanodiscus</i> | 0.011 | 5 | 0.824 |
| | <i>Synedra</i> | 1.447 | 73 | 12.026 |
| | Indetermined diatoms | 0.028 | 15 | 2.471 |
| Protozoans | <i>Lacrymaria</i> | 0.008 | 3 | 0.494 |
| | <i>Acanthocys</i> | 0.001 | 1 | 0.165 |
| | <i>Actinophys</i> | 0.166 | 8 | 1.318 |
| | <i>Vampyrella</i> | 0.002 | 1 | 0.165 |
| | Indetermined protozoans | 0.113 | 1 | 0.165 |
| Rotifera | <i>Cromogaster</i> | 0.001 | 0 | 0.000 |
| | <i>Euchlanis</i> | 0.002 | 0 | 0.000 |
| | <i>Gastropus</i> | 0.001 | 1 | 0.165 |
| | <i>Keratella</i> | 0.002 | 2 | 0.329 |
| | <i>Synchecta</i> | 0.001 | 1 | 0.165 |
| | Indetermined rotifera | 0.001 | 1 | 0.165 |
| Crustacean | <i>Gamarus</i> | 0.004 | 1 | 0.165 |
| | Microcrustacean | 0.002 | 1 | 0.165 |
| Invertebrates | Bristle-worm | 0.237 | 1 | 0.165 |
| | <i>placobdella</i> | 0.001 | 1 | 0.165 |
| | Nematode Worm | 0.361 | 43 | 7.084 |
| | <i>Elama</i> | 0.001 | 1 | 0.165 |
| | Gemules and spicules | 0.860 | 57 | 9.390 |
| Detritus | Detritus | 7.872 | 301 | 49.588 |
| Sand particles | Sand particles | 1.537 | 111 | 18.287 |
| Indetermined | Indetermined | 1.312 | 112 | 18.451 |

Table 2: Volumetric and occurrence percentages (%) of food items consumed by *Oreochromis niloticus* (N = 517) from Lake Toho, South-Benin.

| Food categories | Food items | Volumetric percentages (%) | occurrence (Number) | Percentage occurrence (%) |
|------------------|-------------------------------|----------------------------|---------------------|---------------------------|
| Blue green algae | <i>Anabaena</i> | 0.03 | 2 | 0.39 |
| | <i>Aphanocapsa</i> | 0.74 | 30 | 5.80 |
| | <i>Coelophaerium</i> | 0.78 | 21 | 4.06 |
| | <i>Merismopedia</i> | 0.17 | 15 | 2.90 |
| | <i>Phormidium</i> | 0.39 | 6 | 1.16 |
| | <i>Polycystis</i> | 1.60 | 43 | 8.32 |
| | <i>Tetrapedia</i> | 0.42 | 6 | 1.16 |
| | <i>Microchaete</i> | 0.02 | 0 | 0.00 |
| | Indetermined blue-green algae | 0.03 | 3 | 0.58 |
| | <i>Rivularia</i> | 0.14 | 9 | 1.74 |
| Green algae | <i>Binuclearia eriensis</i> | 0.02 | 2 | 0.39 |
| | <i>Botryococcus</i> | 9.57 | 197 | 38.10 |
| | <i>Cosmarium caudranum</i> | 0.11 | 3 | 0.58 |
| | <i>Cladophora holsatica</i> | 0.03 | 2 | 0.39 |
| | <i>Coelastrum</i> | 0.03 | 2 | 0.39 |
| | <i>Crucigenia</i> | 0.48 | 29 | 5.61 |
| | <i>Gosmarium</i> | 0.09 | 1 | 0.19 |
| | <i>Mesotaenium</i> | 0.02 | 3 | 0.58 |

| | | | | |
|----------------------|--------------------------|-------|-------|-------|
| | <i>Oedogonium</i> | 0.34 | 2 | 0.39 |
| | <i>Pandorina</i> | 4.21 | 129 | 24.95 |
| | <i>Pedistrum</i> | 0.20 | 0 | 0.00 |
| | <i>Pleurotaenium</i> | 0.01 | 2 | 0.39 |
| | <i>Protococcus</i> | 0.13 | 6 | 1.16 |
| | <i>Scenedesmus</i> | 8.58 | 173 | 33.46 |
| | <i>Staurodesmus</i> | 0.01 | 1 | 0.19 |
| | <i>Stigeoclonium</i> | 0.64 | 10 | 1.93 |
| | <i>Tetraspora</i> | 0.68 | 14 | 2.71 |
| | <i>Uronema</i> | 0.19 | 14 | 2.71 |
| | <i>Tribonema</i> | 0.18 | 2 | 0.39 |
| | Indetermined green algae | 3.16 | 36 | 6.96 |
| <i>Zygnema</i> | 12.36 | 306 | 59.19 | |
| Desmids | <i>Euglena viridis</i> | 0.03 | 2 | 0.39 |
| | <i>Aphora avalis</i> | 0.17 | 1 | 0.19 |
| | <i>Sphaeroeca</i> | 0.02 | 1 | 0.19 |
| | <i>Amphora</i> | 0.00 | 1 | 0.19 |
| | <i>Gniochloris</i> | 0.18 | 2 | 0.39 |
| | <i>Cosmarium</i> | 0.38 | 4 | 0.77 |
| | <i>Genicularia</i> | 0.03 | 3 | 0.58 |
| | <i>Golacium</i> | 2.03 | 72 | 13.93 |
| | <i>Lepocinclis</i> | 0.07 | 4 | 0.77 |
| | <i>Netrium</i> | 0.01 | 2 | 0.39 |
| | <i>Peridium</i> | 0.17 | 1 | 0.19 |
| | <i>Phacus</i> | 0.96 | 122 | 23.60 |
| | Indetermined desmids | 0.02 | 3 | 0.58 |
| Diatoms | <i>Diatoma</i> | 0.01 | 1 | 0.19 |
| | <i>Cyclotella</i> | 0.11 | 7 | 1.35 |
| | <i>Eunotia</i> | 0.01 | 2 | 0.39 |
| | <i>Frustulia</i> | 0.00 | 1 | 0.19 |
| | <i>Melosira</i> | 9.01 | 229 | 44.29 |
| | <i>Navicula</i> | 2.74 | 130 | 25.15 |
| | <i>Pinnularia</i> | 0.04 | 5 | 0.97 |
| | <i>Stauroneis</i> | 0.04 | 0 | 0.00 |
| | <i>Stephanodiscus</i> | 0.02 | 0 | 0.00 |
| <i>Synedra</i> | 1.35 | 56 | 10.83 | |
| Indetermined diatoms | 0.02 | 2 | 0.39 | |
| Rotifera | <i>Brachionus</i> | 0.01 | 1 | 0.19 |
| Flower | Flower | 0.17 | 1 | 0.19 |
| Protozoans | <i>Amoeba</i> | 0.01 | 1 | 0.19 |
| | <i>Lacrymaria</i> | 0.16 | 13 | 2.51 |
| | <i>CLH Melana</i> | 0.07 | 1 | 0.19 |
| | <i>Mytilia</i> | 0.05 | 3 | 0.58 |
| Invertebrates | Nematod worms | 0.04 | 5 | 0.97 |
| | Gemules and spicules | 0.62 | 14 | 2.71 |
| Insects | Insects | 0.03 | 1 | 0.19 |
| Detritus | Detritus | 33.35 | 474 | 91.68 |
| Sand particles | Sand particles | 2.04 | 70 | 13.54 |
| Indetermined items | Indetermined items | 0.69 | 12 | 2.32 |

3.2. Frequency of occurrence

This dietary index refers to the number or percentage (%) of fish individuals that have ingested a specific food item. In Lake Toho, the 107 food resources recorded in the stomachs of *S. melanotheron* showed various frequencies of occurrence ranging between 0.165% and 60.79%. The lowest diet percentage occurrences (<1.00%: 6.07 stomachs) were recorded for 70 food items dominated by algae such as *Coelastrum*, *Cosmarium*, *Tetrapedia*, *Synechocystis*, *Glocotrichia*, *Characium*, *Chodatella*, *Desmidium*, *Nitzschia*, *Gastropus* etc. (Table 1). Moderate frequencies between 1% and 10% were recorded for 26 foods items among which *Phormidium*, *Coelophaerium*, *Pediastrum*, *Pleurotaenium*, *Aphanocapsa*, *Tetraspora*, *Crucigenia*, *Gosmarium*, *Ankistrodesmus*, *Polycystis*, *Cyclotella*, *Protococcus* and nematod worms. The highest frequencies of occurrence ($\geq 10\%$: 61 stomachs) were recorded for food resources such

as *Melosira* (60.79%), *Scenedesmus* (58.48%), *Zygnema* (53.38%), detritus (49.59%), *Navicula* (27.18%), *Botryococcus* (24.88%), sand particles (18.29%), *Phacus* (16.64%), *Pandorina* (13.02%), *Synedra* (12.03%) and *Staurodesmus* (10.21%) (Table 1).

Also, the 65 food resources identified in the stomachs of *O. niloticus* showed frequencies of occurrence varying between 0.19% and 91.68%. The lowest frequencies of occurrence (<1.00%: 5 stomachs) were recorded for 39 food resources dominated by algae such as *Gosmarium*, *Staurodesmus*, *Sphaeroeca*, *Aphora*, *Peridium*, *Diatoma*, *Frustulia*, *Brachionus*, *Anabaena*, *Coelastrum*, *Euglena*, *Cosmarium*, *Pinnularia*; flowers, nematod worms, and insects (Table). About 14 food items comprising *Phormidium*, *Tetrapedia*, *Protococcus*, *Cyclotella*, *Rivularia*, *Stigeoclonium*, *Lacrymaria*, *Tetraspora*, *Uronema*, *Merismopedia*, *Coelophaerium*, *Crucigenia*, *Aphanocapsa* and *Polycystis*

occurred between 1% and 10% stomachs of *O. niloticus*. The highest frequencies of occurrence ($\geq 10\%$: 61 stomachs) were recorded for detritus (91.68%), and algae such *Zygnema* (59.19%), *Melosira* (44.29%), *Botryococcus* (38.1%), *Scenedesmus* (33.46%), *Navicula* (25.15%), *Pandorina* (24.95%), *Phacus* (23.6%), *Golacium*, (13.93%), sand particles (13.54%) and *Synedra* (10.83%) (Table 2).

3.3. Diet breadth

In Lake Toho, *S. melanotheron* showed a high diet breadth (DB = 15.23) indicating that this tilapia cichlid ingested a large spectrum of food resources. Ontogenetically, diet breadth ranged between (DB = 4.48) for 175mm-SL (160-190mm) and (DB = 14.25) for SL<40mm. In general, the regression equation between standard length and the

corresponding diet breadth indicated that diet DB decreased as SL increased (Table 3):

Diet breadth (DB) = -12.90 (Standard length) -0.048; $r=0.76$
 Also, with 65 food items ingested, *O. niloticus*, showed a relatively high diet breadth (DB = 6.39), indicating that this invasive alien tilapia consumed a relatively broad range of food resources, but less than that of *S. melanotheron*. Ontogenetically, the diet breadth of *O. niloticus* ranged between (DB = 4.90) for 55mm-SL (40-70mm) and (DB = 8.76) for SL<40mm. Though not significant ($P>0.05$), the regression equation between standard length and diet breadth gave a negative slope $b = -0.011$ indicating that diet DB decreased as SL increased (Table 4):
 Diet breadth (DB) = -0.011(Standard length) + 7.72; $r=0.38$

Table 3: Diet breadth (DB) by size category of *Sarotherodon melanotheron* (n=607) from Lake Toho, South-Benin.

| Standard length class intervals (SL-mm) | <40 | 40-70 | 70-100 | 100-130 | 130-160 | 160-190 |
|---|-------|-------|--------|---------|---------|---------|
| Number of individuals | 382 | 77 | 82 | 54 | 11 | 1 |
| Diet breadth (DB) | 14.25 | 7.00 | 7.74 | 7.96 | 6.61 | 4.48 |

Table 4: Diet breadth (DB) by size category of *Oreochromis niloticus* (n=517) from Lake Toho, South-Benin.

| Standard length class intervals (SL-mm) | <40 | 40-70 | 70-100 | 100-130 | 130-160 | 160-190 |
|---|------|-------|--------|---------|---------|---------|
| Number of individuals | 81 | 345 | 51 | 23 | 11 | 6 |
| Diet breadth (DB) | 8.76 | 4.90 | 8.15 | 5.48 | 6.14 | 6.10 |

3.4. Diet overlaps (O_{jk}) and ontogenetic diet Shifts

Pianka's^[34] diet overlap (O_{jk}) among different size categories of *S. melanotheron* was relatively high, averaged $O_{jk} = 0.69 \pm 0.26$ and ranged between $O_{jk} = 0.44$ for the pairing SL class "<40 mm x 40-70 mm" and $O_{jk} = 0.98$ for the pairing SL "40-70mm x 100-130mm" (Table 5). Also, the results indicated that adjacent size classes tended to exhibit higher diet overlaps than distant pairings involving distant size class categories. This pattern suggested an ontogenetic diet shift indicated by the relatively higher ingestion of food resources such as detritus, sand particles and some algae such as *Botryococcus*, *Scenedesmus*, *Phacus*, *Melosira* by the higher size of *S. melanotheron*.

Likewise, *O. niloticus* exhibited relatively high diet overlaps averaging $O_{jk} = 0.81 \pm 0.18$. Ontogenetically, diet overlaps (O_{jk}) among different size categories of *O. niloticus* varied between $O_{jk} = 0.21$ (SL classes "<40 mm x 40-70 mm") and $O_{jk} = 0.93$ (SL classes "40-70mm x 100-130mm") (Table 6). Like *S. melanotheron*, adjacent size class categories tended to exhibit higher diet overlaps than pairings involving distant size class categories. This trend of diet overlaps suggested an ontogenetic diet shift indicated by the relatively high consumption of food items such as detritus, sand particles and some algae such as *Pandorina*, *Botryococcus*, *Scenedesmus*, *Zygnema*, *Melosira* and *Navicula* by higher sizes of *O. niloticus*.

Table 5: Matrix of diet overlaps (O_{jk}) of *Sarotherodon melanothron* (N=607) by size (Standard length) category from Lake Toho, Southern Benin

| Standard length class intervals (mm) | <40 | 40-70 | 70-100 | 100-130 | 130-160 | 160-190 |
|--------------------------------------|-----|-------|--------|---------|---------|---------|
| <40 | 1 | 0.44 | 0.46 | 0.56 | 0.60 | 0.46 |
| 40-70 | | 1 | 0.94 | 0.98 | 0.92 | 0.80 |
| 70-100 | | | 1 | 0.89 | 0.89 | 0.74 |
| 100-130 | | | | 1 | 0.88 | 0.82 |
| 130-160 | | | | | 1 | 0.04 |
| 160-190 | | | | | | 1 |

Table 6: Matrix of diet overlaps (O_{jk}) of *Oreochromis niloticus* (N=517) by size (Standard length) category from Lake Toho, Southern Benin

| Standard length class intervals (mm) | <40 | 40-70 | 70-100 | 100-130 | 130-160 | 160-190 |
|--------------------------------------|-----|-------|--------|---------|---------|---------|
| <40 | 1 | 0.90 | 0.93 | 0.93 | 0.89 | 0.82 |
| 40-70 | | 1 | 0.91 | 0.70 | 0.90 | 0.77 |
| 70-100 | | | 1 | 0.90 | 0.89 | 0.74 |
| 100-130 | | | | 1 | 0.21 | 0.73 |
| 130-160 | | | | | 1 | 0.90 |
| 160-190 | | | | | | 1 |

4. Discussion

4.1. Food habits and niche breadth

Sarotherodon melanotheron is the foremost native tilapia cichlid of great economic and commercial importance, and occur abundantly in most inland water fisheries of Benin^[35].

Also, the invasive tilapia, *O. niloticus*, is the only exotic fish species that has been introduced in some Benin freshwater lakes and in aquaculture^[9]. The current investigation on the trophic ecology indicated that in Lake Toho, *S. melanotheron* is a phytoplanktivore foraging

mainly on algae (90 genera) and detritus that corresponded to volumetric percentages of about 86.88% and 7.87%, respectively. Preferential phytoplankton recorded in the diet were green algae (53.09%) dominated by *Scenedesmus*, *Microspora*, *Staurodesmus*, *Zygnema*, *Botryococcus* and blue-green algae (21.86%) dominated by *Coelopharium* and *Phormidium*. Also, diatoms significantly contributed to the diet and made about 10.26% of the stomach contents. Similar food habits were reported by Ofori-Danson and Kumi [36] in Sakumo Lagoon (Ghana) and by Ndimele [37] in Ologe Lagoon (Nigeria) where algae dominated the diet of *S. melanotheron*. However, unlike *S. melanotheron* from Ologe Lagoon [37], protozoans (*Lacrymaria*, *Acanthocycs*, *Actinophys*), Crustacean (*Gammarus*, microcrustacean), rotifera (*Cromogaster*, *Euchlanis*, *Gastropus*, *Keratella*, *Synchecta*), invertebrates (Bristle-worm, *placobdella*, Nematode Worm, *Elanna*) and detritus were ingested by *S. melanotheron* from Lake Toho.

Likewise, the invasive alien species, *O. niloticus* displayed similar phytoplanktivorous food habit that included about 62.75% of phytoplankton, mainly green algae (41.04%) dominated by *Scenedesmus*, *Zygnema*, *Botryococcus* and *Pandorina*; blue-green algae (4.30%) comprising *Polycistis* and *Coelopharium*; diatoms (13.34%) dominated by *Melosira*, *Navicula* and *Synedra*, and desmids (4.07%) dominated by *Golacium*. These findings agreed with those reported by Mukankomeje *et al.* [38] in Lake Muhazi (Rwanda), Jihulya [1] in Lake Victoria (Tanzania), Otieno *et al.* [2] in Lake Naivasha (Kenya) and Assefa and Getahun [39] in Lake Hayq of Ethiopia where the Nile tilapia foraged preferentially on various type of algae. However, in contrast with Lake Toho, *O. niloticus* from the Barra Bonita reservoir in Brazil ingested less algae (4.90%), but incorporated more detritus (56.8%) than those of Lake Toho along with various microcrustacean, aquatic insect and macroinvertebrate species that were absent in the stomachs of *O. niloticus* from Lake Toho [40]. According to Gbaguidi *et al.* [30], this trophic specialization (alguivore) of the two tilapiine cichlids, probably results from anatomical structures, mainly the presence of numerous lower gill-rakers, 19-25 and 12-20 for *S. melanotheron* and *O. niloticus*, respectively, that facilitated the filtering of numerous phytoplankton species.

Also, the results indicated that *O. niloticus* ingested more detritus (volumetric percentage: 33.34%; frequency occurrence: 91.68%) than the native tilapia, *S. melanotheron* that consumed less detritus (volumetric percentage: 7.8%; frequency occurrence: 49.59%). These findings agreed with those reported by Ofori-Danson and Kumi [36] in Sakumo Lagoon of Ghana and Ayoade & Ikulala [41] in Eleiyeye Lake of Southwestern Nigeria where *S. melanotheron* ingested about 5.3% and 7.41% of detritus, respectively. Also, like in Lake Toho, detritus were prominent in the stomachs of *O. niloticus* from the Barra Bonita reservoir of Brazil where volumetric proportion and frequency of occurrence reached 56.8% and 91.6%, respectively [40]. The relatively high consumption and utilization of detritus by *O. niloticus*, and at lower degree by *S. melanotheron*, is probably the result of morphological and behavioral adaptations of these tilapiine cichlids. Indeed, as reported by Dabbadie [42], both cichlids possess numerous bicuspid teeth capable to break down detritus for hydrolyse, to reject tuff and non-nutritional resistant items (sand particles, sediments) and to select only nutritional material [23]. In addition, the high ingestion of detritus by *O. niloticus* could be an adaptation of the species

to successfully dwell in poor-nutrient habitats. Indeed, as detritus are highly available in most inland waters, the Nile tilapia takes advantage of this food resource to satisfy its nutritional needs. This capacity to exploit and to utilize a high quantity of detritus explains why *O. niloticus* colonizes a wide range of freshwater habitats regardless of less availability of preferred food items (phytoplankton) [42]. In Lake Hlan (South-Benin), similar feeding trend was recorded for the bonytongue species, *Heterotis niloticus* (Osteoglossidae) that fed on about 50.37% of combined sand particles/detritus and exhibiting a high trophic plasticity that allow this osteoglossid to invade all type of freshwater habitat [23].

This study indicated that both species exploited and utilized efficiently the food resources of Lake Toho and shared almost the same ecological niche. However, the native species, *S. melanotheron*, have exploited more food resources (107 food items recorded) than the alien cichlids, *O. niloticus* that have ingested 65 food items. As a result, in Lake Toho, *S. melanotheron* covered a higher ecological niche (Diet breadth = 15.23) compared to the introduced tilapia, *O. niloticus* exhibiting a reduced DB = 6.10. Probably, as the Nile tilapia concentrated more on detritus, it is obvious that this invasive species would collect less phytoplankton compared to its congener *S. melanotheron* that consumed less detritus (7.87%), but in turn, foraged more on algae (90 genera).

4.2. Diet similarities and food competition

The current dietary analysis of *S. melanotheron* and *O. niloticus* from Lake Toho indicated that these two cichlids displayed a high diet similarity. Except detritus, the two fishes failed to show any significant ($P > 0.05$) variations in the volumetric proportion of ingested foods. The computed F values along with degree of freedom and p values was $F_{1,10} = 0.357$, $p = 0.564$ for blue-green algae, $F_{1,10} = 2.081$, $p = 0.180$ for green algae; $F_{1,10} = 2.832$, $p = 0.123$ for desmids; $F_{1,10} = 1.170$, $p = 0.305$ for diatoms; $F_{1,10} = 1.424$, $p = 0.260$ for invertebrates; $F_{1,10} = 2.383$, $p = 0.154$ for protozoans; $F_{1,10} = 1.487$, $p = 0.251$ rotifers and $F_{1,10} = 1.052$, $p = 0.329$ for sand particles.

Also, the computed Pianka's [34] diet overlaps (O_{jk}) between *S. melanotheron* and *O. niloticus* gave a high diet similarity index $O_{jk} = 0.83$. Moreover, the matrix of diet overlaps (O_{jk}) between different life stages (small juveniles, large juveniles, subadults, adults) of *S. melanotheron* and *O. niloticus* showed high diet overlaps ranging between $O_{jk} = 0.65$ (Subadult ON x Adult SM), and $O_{jk} = 0.99$ (Adult ON x Subadult SM) (Table). In addition, the diet overlaps between the same life stage (example: Small juveniles ON x Small juveniles SM) of *S. melanotheron* and *O. niloticus* were always high and varied between $O_{jk} = 0.83$ and $O_{jk} = 0.93$. These findings suggest a high diet similarity between these two sympatric tilapiine cichlids. With respect to spatial and temporal variations of food resources, these diet overlappings could lead to a high food competition targeted to phytoplankton, their preferential food resources. Nevertheless, significant ($F_{1,10} = 8.555$, $p = 0.015$) variations in the proportional consumption of detritus was recorded between *S. melanotheron* and *O. niloticus*. Indeed, the native cichlid *S. melanotheron* incorporated a relatively reduced detritus (7.87%) in its diet whereas the exotic invasive cichlid, *O. niloticus*, consumed more detritus that reached 33.34% of the stomach content. This relatively high consumption of detritus by the non-native species is an advantage because will allow *O. niloticus* to positively cope with this competition in order to satisfy its nutritional needs

for intensive reproduction, higher specific growth rate and to increase the population size [21]. In contrast, the reduced exploitation and consumption of detritus by the native cichlids, *S. melanotheron*, is a disadvantage, especially in case of high competition on phytoplankton, which may cause a progressive decline of the blackchin tilapia population [6]. In a meantime, *O. niloticus* may continue to take advantage to detritus to stay prominent and to progressively replace the native cichlid, *S. melanotheron*, unless this latter develops a trophic or behavioral adaptation to better exploit detritus in order to deal with the food competition [6]. Nevertheless, the aggressive behavior displayed by the blackchin tilapia, *S. melanotheron* [43] could help to out-compete *O. niloticus*. However, as the Nile tilapia was well-established in Lake Toho, there is a need to evaluate the aggressive behavior of *S. melanotheron* and impacts on competition.

4.3. Impacts of non-native species: Risk of species replacement

The introduction of the invasive alien cichlid, *O. niloticus* in the Benin aquatic system and particularly in Lake Toho, though beneficial for aquaculture, probably constitutes an ecological disaster with regard to biodiversity conservation and ecosystem protection [44]. Once introduced, the exotic species might compete native species for resources such as nutrients, light, physical space or food to quickly proliferate and to become prominent and invasive [43]. Particularly, the study showed a high diet similarity ($O_{jk} = 0.83$) between *O. niloticus* and the native species, *S. melanotheron*, evidencing a high food competition between these two tilapias from Lake Toho. Such competition would modify the food webs components and structure and the dynamics of the fish population [42-43]. According to Huxel [3] and Mooney & Cleland [4] closely related species such as *O. niloticus* and *S. melanotheron* could hybridize to cause “genetic pollution” population decline, species replacement and extinction of native species [44-45]. To date, whether or not *O. niloticus* and *S. melanotheron* hybridize is uncertain. As reported by Li *et al.* [46], so far, there is no data showing that *O. niloticus* and *S. melanotheron* inter-breed in nature. Also, fisheries biologists have difficulty to create hybrids of these two tilapiine cichlids. More ecological surveys and spawning/hybridization experiments on the Nile tilapia and *S. melanotheron* are required to fill this gap of biological information.

In Benin, a similar case of species replacement (personal observation) has been recorded in Lake Cele (Center-Benin) [17], a floodplain lake of Oueme River where *O. niloticus* has been introduced to increase fish production and fish catches. After about three (3) years, the Nile tilapia has been well-established while the population of the native species, *Tilapia zilli*, has declined. Similar case of fish species extinction has been reported by IFC [5] in Uganda's Lake Victoria where more than 200 native fish species have been extinct through predation after the introduction of the non-native Nile Perch, *Lates niloticus*. In Lake Toho, the high exploitation and utilization of detritus by *O. niloticus* could boost the population size of this exotic species that could exert a high competition pressure on the blackchin tilapia, *S. melanotheron* and other related species, leading to species replacement.

5. Conclusion

The current investigation on the feeding ecology of the invasive alien tilapia, *O. niloticus*, and the native tilapia, *S. melanotheron* from Lake Toho (Southern Benin) give insight

on their diet composition, niche breadth and diet overlaps. Both species foraged intensively on algae. The invasive exotic tilapia, *O. niloticus*, ingested more detritus, but exhibited a lower niche breadth. The two tilapias displayed a high diet similarity that led to a high food competition, increasing the risk of species replacement targeted mainly to *S. melanotheron*. Lake management and species recovery decisions require further research on species behavior, hybridization and food competition in order to ascertain the replacement of native species and the overall impacts of *O. niloticus* invasion.

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7. References

- Jihulya NJ. Diet and Feeding ecology of Nile tilapia, *Oreochromis niloticus* and Nile Perch, *Lates niloticus* in protected and unprotected areas of Lake Victoria, Tanzania. International Journal of Scientific & Technology Research. 2014; 3(11):280-286.
- Otieno ON, Kitaka N, Njiru JM. Some aspects of the feeding ecology of Nile tilapia, *Oreochromis niloticus* in Lake Naivasha, Kenya. International Journal of Fisheries and Aquatic Studies. 2014; 2(2):01-08.
- Huxel GR. Rapid displacement of native species by invasive species: Effect of Hybridization. Biological Conservation. 1999; 89:143-152.
- Mooney H, Cleland E. The evolutionary impact of invasive species. Proceeding of the national academy of Sciences of the United state of America. Proceeding of the National Academy of Sciences, USA. 2001; 98(10):5446-5451.
- IFC. The Threat of Non-native Species to Biodiversity. www.ifc.org/ Biodiversity Guide, 2017.
- Ward AJW, Webster MM, Hart PJB. Intraspecific food competition in fishes. Fish and Fisheries. 2006; 7(4):231-261.
- Agostinho AA, Zalewski M. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Paraná River, Brazil. Hydrobiologia. 1994; 1979; 303:141-148.
- Adite A, Tossavi EC, Kakpo DBE. Biodiversity, length-weight patterns and condition factors of cichlid fishes (Perciformes: Cichlidae) in brackish water and freshwater lakes of the Mono River, Southern Benin, West Africa. International Journal of Fauna and Biological Studies. (in press), 2017.
- Arame H. Ecologie trophique comparée de *Oreochromis niloticus* (perciforme : Cichlidae) introduit dans le lac Toho (Sud-Bénin) et de *Sarotherodon melanotheron* (Perciforme : Cichlidae): Implications pour la conservation de l'ichtyofaune du Lac Toho. Master's thesis, Faculté des Sciences et Techniques, Université d'Abomey-Calavi, Abomey-Calavi, 2013, 63.
- Kakpo DBE. Biodiversité et exploitation des poissons du Bas-Mono: Implications pour la conservation et la gestion durable des ressources halieutiques. Master's thesis. FAST/UAC, Abomey-Calavi, Benin, 2011.

11. Leveque C. Biodiversity dynamics and conservation: The freshwater fish of tropical Africa. Cambridge University Press, 1997.
12. Lowe-McConnell RH. Ecological studies in tropical fish communities. Cambridge University Press, Cambridge, 1987.
13. Fryer G, Iles TD. The cichlid fishes of the Great Lakes of Africa. Their biology and evolution. Edinburg, Olivier & Boyd, 1972.
14. Ahouansou Montcho S. Etude de l'écologie et de la production halieutique du lac Toho au Bénin. Mémoire de DESS, Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, Bénin, 2003, 88.
15. Ahouansou Montcho S, Laleye PA. Some aspects of biology of *Oreochromis niloticus* L. (Perciformes: Cichlidae) recently introduced in Lake Toho (Benin, West Africa). International Journal of Biology and Chemistry Science. 2008; 2(1):114-122.
16. Tossavi CE. Evolution de la biodiversité et de l'exploitation des poissons du lac Toho (Sud Bénin) : Implications pour la gestion durable des ressources halieutiques. Mémoire de Master, FAST/USA, 2012, 100.
17. Welcomme RL. Fisheries Ecology of Floodplain Rivers. London, Longman.
18. Ward JV, Tockner K, Schiemer F. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers Research and Management. 1999; 15:125-139.
19. Food preferences of the commercial fishes in the black Volta Lake. Volta Basin Restoration Project. University of Ghana, Technical Report. 1967; 22:1-8.
20. Woni D. Analyse du phytoplancton dans le régime alimentaire de *Sarotherodon galilaeus* (Linnaeus, 1758) dans le lac de barrage de Ziga. Mémoire de Master, Institut du Développement Rural, Université Polytechnique de Bobo-Dioulasso, Burkina Faso, 2014.
21. Fagade SO. The food and feeding habits of *Sarotherodon galilaeus* from a small lake. Archives Hydrobiology. 1982; 93:256-263.
22. Adite A. Diversity and management of mangrove fishes in the Benin coastal zone. Research Technical Report. International Foundation for Science-IFS, 2002, 26.
23. Adité A, Winemiller KO, Fiogbé ED. Ontogenetic, seasonal, and spatial variation in the diet of *Heterotis niloticus* (Osteoglossiformes: Osteoglossidae) in the Sô River and lakes Hlan, Benin, West Africa. Environmental Biology of Fishes. 2005; 73:367-378.
24. Okpéicha OS. Biodiversité et exploitation des poissons du barrage de la SUCOBE dans la commune de Savè au Bénin. Mémoire de Master Hydrobiologie Appliquée. FAST/UAC, 2011, 62.
25. Van Thielen R, Hounkpe C, Agon G, Dagba L. Guide de détermination des poissons et crustacés des lagunes et lacs du Bas Bénin. GTZ&Direction des Pêche, Cotonou, Bénin, 1987, 135.
26. Lévêque C, Paugy D, Teugels GG. Faune des poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest. Tome 2. Editions OSTORM/MRAC, Paris, 2004, 902.
27. Winemiller KO. Fish assemblages across a complex, tropical freshwater/marine ecotone. Environmental Biology of Fishes. 1992b; 3:29-50.
28. Winemiller KO, Kelso-Winemiller LC. Food habits of tilapine cichlids of the Upper Zambezi River and floodplains during the descending phase of the hydrological cycle. Journal of Fish Biology. 2003; 63:120-128.
29. Gbaguidi HMAG, Adite A, Abou Y. Trophic ecology and establishment of the silver catfish, *chrysiichthys nigrodigitatus* (Pisces: Siluriformes: Claroteidae) introduced in an artificial pond of Bénin. Journal of Fisheries and Aquatic Sciences. 2017; 12:42-53.
30. Gbaguidi HMAG, Adite A, Sossoukpe E. Feeding Ecology and Establishment of the Naturally-Colonized Freshwater Cichlid, *Sarotherodon galilaeus* (Pisces: Actinopterygii: Perciformes) from a Man-Made Lake, South-Benin, West Africa. Natural Resources. 2016; 7:337-355.
31. Adite A, Winemiller KO. Trophic ecology and ecomorphology of fish assemblages in coastal lakes of Benin. Ecoscience. 1997; 4:6-23.
32. Morgan GA, Grieggo OV, Gloekner GW. SPSS for Windows: An introduction to use and interpretation in Research, Lawrence Erlbaum associates, Publishers, Mahwah, New Jersey, 2001, 224.
33. Simpson EH. Measurement of diversity. Nature. 1949; 163:688.
34. Pianka ER. Evolutionary ecology. Fifth edition, HarperCollins College Publishers, 1994, 486.
35. Gbaguidi AS, Pfeifer V. Statistics of inland water fisheries : Year : 2008. Services Etudes et Statistiques, Projet Pêche Lagunaire, GTZ-GMBH, Direction des Pêches- Cotonou, Bénin, 2009, 145.
36. Ofori-Danson PK, Kumi GN. Food and Feeding Habit of *Sarotherodon melanotheron*, Rüppell, 1852 (Pisces: Cichlidae) in Sakumo Lagoon, Ghana. West African Journal of Applied Ecology. 2006; 10(1):9-18.
37. Ndimele PE, Kumolu-Johnson CA, Aladetohun NF, Ayorinde OA. Length-weight relationship, condition factor and dietary composition of *Sarotherodon melanotheron*, Rüppell, 1852 (Pisces: cichlidae) in Ologe Lagoon, Lagos, Nigeria. Agriculture and Biology Journal of North America. 2010; 1(4):584-590.
38. Mukankomeje R, Laviolette F, Descy JP. Régime alimentaire de Tilapia, *Oreochromis niloticus* du Lac Muhazi (Rwanda). Annales Limnology. 1994; 30(4):297-312.
39. Assefa WW, Getahun A. The food and feeding ecology of Nile tilapia, *Oreochromis niloticus*, in Lake Hayq, Ethiopia. International Journal of Fisheries and Aquatic Studies. 2015; 2(3):176-185.
40. Zaganini RL, Vidotto-Magnoni AP, Edmir Carvalho ED. Ontogenetic diet shifts of *Oreochromis niloticus* and *Tilapia rendalli* of the Barra Bonita reservoir (Tietê river, São Paulo State, Brazil). Acta Scientiarum. 2012; 34(3):255-262.
41. Ayoade AA, Ikulala AOO. Length – weight relationship, condition factor, and stomach contents of *Hemichromis bimaculatus*, *Sarotherodon melanotheron* and *Chromidotilapia guntheri* (Perciformes: Cichlidae) in Eleiyele Lake, Southwestern Nigeria. Revista de Biologia Tropical. 2007; 55(3-4):969-977.
42. Dabbadie L. L'alimentation du tilapia du Nil *Oreochromis niloticus*. Aquatro.cirad.fr/encyclopedie/especes_d_interet_aquacole/tilapia/l_alimentation_du_tilapia_du_nil. 2013.
43. Duponchelle F, Legendre M. *Oreochromis niloticus* (Cichlidae) in Lake Ayame, Côte d'Ivoire: Life history traits of strongly diminished population. Cybium. 2000;

24(2):161-172.

44. Anonyme. Les introductions d'espèces dans les milieux aquatiques continentaux en métropole. Enjeux, conséquences et recommandations. Séminaire, Ministère de l'environnement, GIP Hydrosystème, Paris (13-15/02/1996). Bulletin Français de la Pêche et de la Pisciculture. 1997, 344-345
45. Abari MA, Usman M, Yusuf K. Food and Feeding Habit of Nile Tilapia (*Oreochromis niloticus*) in Doma Dam, Nasarawa State, Nigeria. PAT. 2015; 11(1):67-74.
46. Lie SF, Yan Z, Wu-Jiang F, Wan-Qi C, Ying-Fang X. Possible reproductive isolation between two tilapiine genera and species: *O. niloticus* and *S. melanotheron*. Zoological Research. 2011; 32(5):521-527.