Biological invasion: evidence from a tropical reservoir (Eleiyele, South West Nigeria)

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Abstract

The encroachment of freshwater territories by invasive species is a global issue with its associated co-existence, displacement and facilitation of native species. The blackchin tilapia, *Sarotherodon melanotheron* is one of the most successful biological invasive species. Data on its apparent ecological consequences on native species are rare in Nigerian inland waters. Based on stomach contents analyses, diets, feeding strategies, and dietary niche breadths of two sympatric invasive *S. melanotheron* and native Nile tilapia *Oreochromis niloticus* populations in a tropical domestic water supply were assessed for possible convergence. Both species exhibited generalist feeding strategies subsisting mostly on algae but fish eggs and larvae were conspicuous preys of *S. melanotheron*. Dietary niche of *S. melanotheron* was wider than that of *O. niloticus*. Dietary niche overlap was high and significant between these sympatric species. These findings imply that competitive feeding interactions-including predations on vulnerable early life stages may potentially promote invasion success of *S. melanotheron* in Eleiyele Reservoir.

Keywords: stomach contents, diet, feeding strategies, niches, cichlids, Eleiyele Reservoir

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Introduction

Invasive species represent an emerging variable of concern in Nigerian inland waters, to their inhabitants—ultimately to man. As invasive floral pervasively contributes to the loss of functionality within these ecosystems, numerous invasive fish species are becoming well established either through useful or unintended introductions by man. Biological invaders are destructive to the structure and function of native species, communities, and ecosystems (Gurevitch and Padilla, 2004; Clavero and Garcı´a-Berthou 2005; Davis 2009; Kocovsky *et al* 2011; Van Kessel *et al* 2016). Invasive species often outcompete native species for resource use (food, nurseries ground, and habitats) not only because of their broader environmental tolerances, multiple spawning within seasons, effective feeding strategies but also due to their concealment from parasites and predators that modulate their population sizes in their native range (Mills *et al* 2004; Townsend 1996; Kennard *et al* 2005; Ahmad *et al* 2010; Kalogianni *et al* 2019).

One of the most successful invasive species in freshwater habitats with high negative ecological impacts is the Blackchin tilapia *Sarotherodon melanotheron* (Ruppel 1852) a cichlid fish principally inhabiting estuaries and lagoons. This species, tagged West African Lagoon Tilapiine supports significant fisheries in lagoons (Eyeson 1979). Its home range often extends into proximate freshwaters through flooding by rains (International Institute Rural Reconstruction (IIRR) *et al* 2001) via cage and pond culture. A flooding event on 31 August 1980 accidentally released specimens of *S. melanotheron* from experimental ponds into adjoining Awba Reservoir in University of Ibadan, south western Nigeria (Omoniyi and Agbon 2008); a habitat where the species is now abundant and ubiquitous possibly due to prolific breeding, wide environmental tolerance coupled with trophic plasticity (Molnar 2008). The species has since extended its non-native range into adjoining waters including drainages and ditches. Interconnections of river basins through canals expedite the dispersal of invasive fish species to novel habitats (Van der Velde *et al* 2006; Simberloff 2013).

Despite the socio-economic importance (food fish, aquaria, baitfish, control of aquatic weeds and insects *et cetera*), *S. melanotheron* is considered highly invasive and potential pest beyond the native range (United Nation 2010; Froese and Paul 2021). Thriving populations of invasive *S. melanotheron* caused a drastic reduction of aquatic vegetation due to overgrazing (Courtenay *et al* 1974); exceeded native species at competition for food, habitat with spawning ground (Dial and Wainright, 1983); and reduced biodiversity (Molnar 2008).

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All inherently linked to the trophic plasticity, adaptability, hardy nature coupled with multiple spawning within season that characterize this species.

There is a dearth of putative data on biological invasion of Nigerian waters. This study was prompted by our observation over a duration of seven years; and recently (2019) through the Ichthyofauna survey of Eleiyele Reservoir on the explosion in population of *S. melanotheron* corresponding with a decrease in the population of the Nile tilapia *Oreochromis niloticus* (a prominent component of the Ichythofauna of Eleiyele reservoir (Akinyemie *et al* 1986) and the frequently most abundant species in inland waters of Nigeria. Since resources use is a fundamental ecological interaction, we hypothesized that the sympatric emerging abundance of *S. melanotheron* is inimical to other species through resource use. Little or no studies have correlated patterns of resource use between *S. melanotheron* and *O. niloticus* although several reports on their feeding habits are copious (Abubakar 1997; Anene 2005; Oso *et al* 2006). We estimated and compared the composition of diets, feeding strategies, dietary niche breadths and overlaps between the invasive *S. melanotheron* and functionally similar native Nile tilapia, *O. niloticus* inhabiting Eleiyele Reservoir. Knowledge of diets of invasive species is critical to understand its ecology and to predict its effect on native species.

Materials and Methods

Study area

Eleiyele Reservoir (Figure 1) is located in Ibadan Oyo State Nigeria (7°23'49"N, 3°52'2"E). The reservoir has a surface area of 152.76 ha and a storage capacity of 1,550 million gallons. Eleiyele Reservoir supports thriving artisanal fisheries in Ibadan although it was established primarily for the provision of potable water supply. It was constructed in 1939 by the Water Corporation of the old Western Region to supply water to Ibadan city by damming of the River Ona. The fisheries of Eleiyele Reservoir are controlled by the Department of Fisheries through the Ministry of Agriculture and Natural Resources, Oyo State Nigeria.

Sampling and data collection

Random samples of *Orecochromis niloticus* (Plate 1a) and *Sarotherodon melanotheron* (Plate 1b) were purchased monthly from fishermen at Eleiyele Reservoir for eight months (January – August, 2019). The fishermen use diverse fishing gears including drag nets, hook and lines, bottom-set gillnets, and bottom-set traps for fishing. Samples were conveyed in a cooler containing ice to the Hydrobiology and Fisheries Laboratory, Zoology Department, the University of Ibadan where they were preserved by deep freezing.

Biometric data

After identification according to standard guides (Idodo-Umeh 2003; Froese and Pauly 2019), the total lengths of specimens were measured (cm) on a fish measuring board and weighed (g) on an electric balance (Portable Electronic Laboratory Scale: B30003T).

Stomach content data

Gastrointestinal tracts for individuals of the species were removed after dissection; the stomach regions were cut off (the degree of stomach fullness was rated on a binary scale: stomachs with food and empty stomachs and recorded) and preserved in formalin solution (5%) to halt further decomposition prior to analysis of stomach contents.

Feeding intensity

Stomach conditions were categorized by visual inspection as either empty stomachs or stomachs with food. Based on these criteria, the proportion of the population with food representing the feeding intensity of the populations for each of the species; was calculated using the Vacuity Index (VI) (Hureau 1969):

$$\mathrm{VI} = \frac{E_s}{T_s} \times 100$$

where E_S = number of empty stomach samples, T_S = total number of stomach samples. The intensity of feeding as described by the VI is interpreted as: edacious species ($0 \leq \mathrm{VI} < 20$); relatively edacious species ($20 \leq \mathrm{VI} < 40$); moderate feeder ($40 \leq \mathrm{VI} < 60$), relatively (abstemious $60 \leq \mathrm{VI} < 80$); abstemious ($80 \leq \mathrm{VI} < 100$).

Diet compositions

Volumes of the stomach were determined by water displacement in a measuring cylinder (25 ml). The modification of Jones (1968) was adopted to enumerate food items: clumped contents of excised stomachs were mixed with 10 ml tap water in a petri dish; stirred and identified according to standard guides. Algae were identified according to (Prescott 1979) under the microscope at a magnification of × 100. Identified Identified stomach contents of animal origins were easily counted using a hand lens or microscope. Several stomach contents could not be identified to the species levels because they were at varying stages of digestion. Food items were initially grouped as animal and plant matter before subdivided into broad categories (zooplankton, fish, crustaceans, gastropods, algae, macrophytes, insects, and detritus).

The relative contributions of each food item in the stomach contents were quantified by using three primary indices (Hyslop 1980): percentages Numerical (N), Frequency of occurrence (F), and Volumetric (V) methods- based on simple proportions. N is the number of a food item as a percentage of the total number of that food item. F is the total number of occurrences of a food item as a percentage of the total number of stomachs. V is the volume of a food item as a percentage of the total volume of all food items. Dietary compositions of the

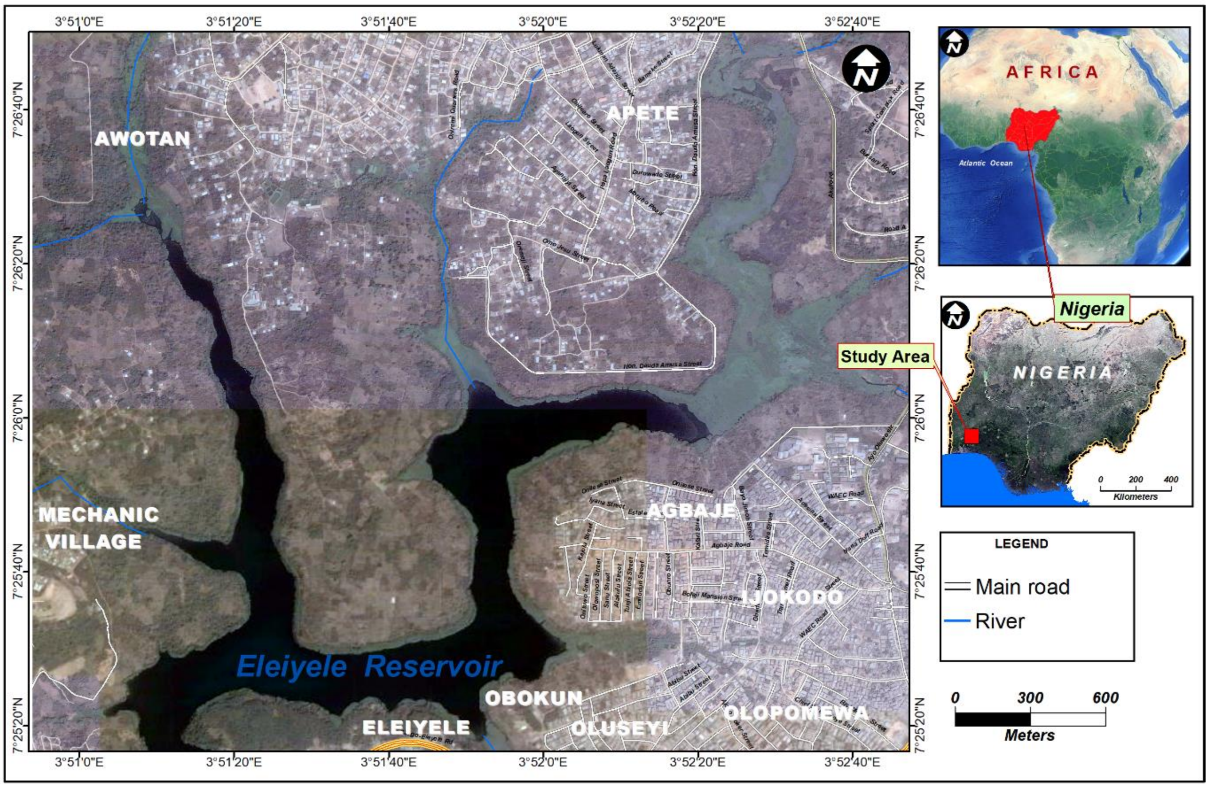


Figure 1: Map of Ibadan showing Eleiyele Reservoir with insert of Maps of Africa and Nigeria

Plate 1a: The Nile Tilapia, *Oreochromis niloticus* from Eleiyele Reservoir

Plate 1b: The Blackchin Tilapia, *Sarotherodon melanotheron* from Eleyeile Reservoir

sympatric species were interpreted using the Index of relative importance (IRI) (Pinkas *et al* 1971) expressed as %IRI = F (V + N). Sand grains, organic debris, and unidentified stomach contents were excluded from diet data.

Feeding strategy

Feeding strategists of both species were evaluated using the graphical method Amundsen *et al.* (1996); a modification of Costello's (1990) graphical method. This approach involves two-dimensional plots of identified food items pooled into taxonomic categories are plotted against the frequency of occurrence (proportions). Prey-specific abundance (P) measures the proportion of food items based on bulk (volume); it was calculated as:

$$\%P = \frac{\sum S_i}{\sum S_{ti}} \times 100$$

Where S_i = volume of food item i in the stomach while S_{ti} = overall volume of stomach contents in only those individuals with food item i in the stomachs. Food items were pooled in taxonomic categories (zooplankton, fish, crustaceans, gastropods, algae, macrophytes, insects, and detritus. Feeding strategies for the species are depicted along the vertical axis: a dichotomy of either specialization (upper limits) or generalization (lower limits). The linear vector (axis): lower left to the upper right depicts the importance of every prey category. Points in the upper right represent a dominant prey item and points in the lower left display rare prey items.

Niche breadths and overlap

Frequency of occurrence (F) of identified stomach contents was used to compute the Levine dietary breadth (Levine 1968) and the Schoener dietary overlap (Schoener 1974) index for these sympatric species (Levine 1968) and in the reservoir. Levine dietary breadth, L:

$$\mathrm{L} = \left(\sum_{i=1}^{n} p_i^2\right)^{-1}$$

where pi represents the proportions, out of all those items, used by i that consists of the i stomach contents and n is the number of stomach contents.

The Schoener dietary overlap (α) is defined as:

$$\alpha = 1 - 0.5 \sum_{i=1}^{n} (px_i - py_i)$$

Where α is the similarity between diets of species x and y, px_i is the proportion of food category $_i$ in the diet of species x, and py_i is the proportion of food category $_i$ in the diet of species y. The values of Schoener dietary overlap index ranges from 0 (no overlap) to 1 (complete over-lap). Values > 0.6 is considered biologically significant (Wallace 1981).

Statistical analysis

Primary (percentages number, frequency of occurrence and volume) and composite (index of relative importance) dietary indices were analyzed using Microsoft Excel (2013). Two sample t-test assuming unequal variances were used to compare the sizes (total lengths (cm)) between the two species using Microsoft Excel (2013). Plots of feeding strategies were plotted in the same software. Non-parametric Mann-Whitney U test was performed in R programming language to test if there was significant difference in the calculated Levin Dietary breadths (continuous data) based on the different food categories identified in the stomachs of the independent categories (two sympatric species). In order to report the differences between groups as median, the distributions of the dependent variable (niche breadth) were visualized as histograms for the species using ggplot2 (Wickham 2016), an add-on package in R environment. Alpha was at set 0.05.

Results

Biometric characteristics, Vacuity indices and feeding habits

Mean fish total length of the examined eighty-six specimens (n= 86) of each species were significantly different at 0.05 level of significance ($t(169) = -11.92$), df = 169, $p < 0.05$) (Table 1). The Nile tilapia, *Oreochromis niloticus* had empty stomachs more frequently than invasive *S. melanotheron* in Eleiyele Reservoir, as showed by Vacuity Index (VI) values (Table 2): the former is relatively abstemious feeder, while the latter is an edacious species in the reservoir. The spectral of food items consumed by these species suggest both species exhibit omnivorous feeding habits (Table 2).

Overall, *O. niloticus* subsists on 40.12% animal matter and 59.88% plant matter. The diet of *S. melanotheron* consisted of 50.52% animal matter and 49.48 % of plant matter. All are based on indices of relative importance. Fish eggs and larvae are conspicuous preys of *S. melanotheron* indicating its potential predatory tendencies.

Dietary feeding strategy, niche and overlap

The Nile tilapia *Oreochromis niloticus*, and the blackchin tilapia, *Sarotherodon melanotheron* are generalists feeder subsisting mostly on algae in Eleiyele Reservoir (Figure 2). Niche breadths for these sympatric species were almost identical in Eleiyele Reservoir (Figure 3). *Oreochromis niloticus* has a narrower dietary breadth (L = 3.47) than *S. melanotheron* (L = 4.25) which was not significantly different (W = 29, p-value = 0.79) in Eleiyele Reservoir. Schoener index of dietary overlap value, 0.91, indicate significant dietary overlap between invasive *S. melanotheron* and *O. niloticus* in the reservoir.

Table 1: Summary of the mean, standard deviation (SD), minimum and maximum total lengths (cm) and body weight of the Nile tilapia, *Oreochromis niloticus* and *Sarotherodon melanothron* inhabiting Eleiyele Reservoir

	Oreochromis niloticus (n = 86)				*Sarotherodon melanotheron* (n = 86)			
Parameters	x̄ ± SD	Min	Max	95% CI	x̄ ± sd	Min	Max	95% CI
Total length (cm)	15.44± 2.63**	11.9	21.6	14.88,16.01	20.38 ± 2.8**	14.9	26.4	19.78, 20.97
Body weight (g)	87.40 ± 47.54	32.7	201.6	75.90, 98.91	165.3 ± 63.6	71.3	394.8	147.52, 111.74

Note. **p<0.01, CI = Confidence Interval, Min = minimum values, Max = maximum values

Table 2: Number of empty stomachs, Vacuity Indices (VI), diet composition by number (%N), frequency of diet occurrence (% F), diet composition by volume (%V), and index of relative importance expressed as a percent (IRI) of food items found in stomachs of native *Oreochromis niloticus* and invasive *Sarotherodon melanotheron* inhabiting Eleiyele Reservoir

	Oreochromis niloticus (n = 86)				*Sarotherodon melanotheron* (n = 86)			
Empty stomachs number	26				12			
Vacuity Index	32.2 %				14.0 %			
	%N	%F	%V	% IRI	%N	%F	%V	%IRI
Animal matter								
Zooplankton								
Protozoa								
Vorticella sp.	6.55	2.90	0.20	2.81	4.28	3.47	1.29	2.67
Peranema sp.	4.25	1.93	0.08	1.20	3.48	3.60	1.54	2.50
Monosiga sp.	2.65	3.29	0.12	1.31	4.01	5.09	1.03	3.55
Arcella sp.	5.49	4.26	0.20	3.47	3.01	1.86	1.03	1.04
Stenor sp.	7.17	3.87	0.24	4.11	6.75	5.09	2.31	4.38
Crustacea								
Cyclops	1.68	1.16	0.81	0.41	8.29	1.36	0.51	1.66
Unidentified	2.48	2.32	1.62	1.36	3.07	3.35	0.77	1.78
Copepods								
Unidentified	1.24	1.74	0.81	0.51	2.07	2.23	0.51	1.1
Cladocerans								
Unidentified Zooplankton	7.17	3.87	0.24	4.11	6.75	5.09	2.31	4.38
Fish								
Fish eggs					5.21	5.09	7.97	4.28
Fish scales	3.72	3.09	2.43	2.73				
Fish larvae					3.34	4.47	13.11	7.17
Insect								
Trichoptera	5.48	6.18	11.34	7.46	4.82	6.46	9.76	8.5
Hemiptera	1.24	1.93	4.45	1.58	1.40	2.11	3.08	1.31
Odonata	2.48	3.68	4.86	3.86	2.07	3.35	3.08	2.39
Diptera	2.83	3.29	3.64	3.05	1.47	2.61	2.83	1.55
Insect parts	2.57	1.55	4.05	1.47	1.27	1.36	3.08	0.82
Gastropod								
Physa sp.	1.68	0.77	0.81	0.28				
Gastrpod shells	3.01	4.26	10.52	1.20	1.40	1.99	3.60	1.10
Plant matter								
Phytoplankton	5.66	4.26	3.64	5.67	5.08	5.71	2.83	6.24
Zygnema sp.	6.28	2.06	3.24	5.54	4.41	4.71	2.57	4.55
Cladophora sp.	2.74	3.68	2.83	2.94	2.54	2.36	2.83	1.75
Microspora sp.	4.25	2.03	2.83	5.10	3.34	2.61	2.06	1.95
Spirogyra sp.	4.51	2.61	2.43	5.58	2.81	2.36	2.31	1.67
Chlorella sp.	3.54	3.58	2.43	5.62	3.41	3.72	1.54	2.55
Pediastrum sp.	2.83	3.29	2.02	2.29	4.14	3.35	1.29	2.52
Closterium sp	2.30	2.71	1.21	1.36	2.41	2.36	1.03	1.12

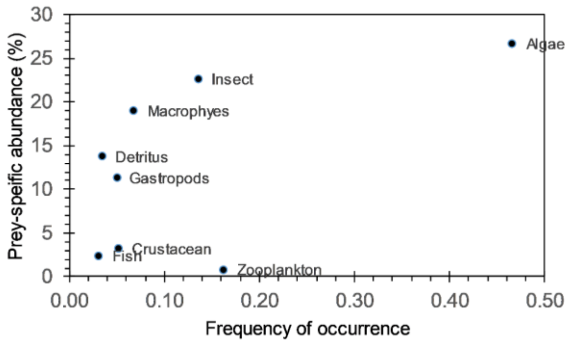
	Oscillatoria sp.	2.39	3.48	1.62	2.00	2.27	3.35	1.54	1.77
	Anabaena sp.	2.48	2.51	1.21	1.33	2.54	2.11	1.03	1.04
	Phormidium sp.	2.57	3.09	1.21	1.68	1.94	2.36	1.03	0.97
	Eugelena sp.	1.95	2.32	2.02	1.32	2.07	2.36	1.29	1.09
	Nostoc sp.	5.66	4.26	3.64	5.67	5.08	5.71	2.83	6.31
	Macrophytes								
	Leaves/branches	3.10	3.68	10.93	7.88	6.28	4.96	12.86	9.6
	Flower buds	3.63	3.09	8.09	5.20	3.21	3.60	5.66	4.41
Others									
	Detritus		3.48	4.76			3.85	4.83	

Discussion

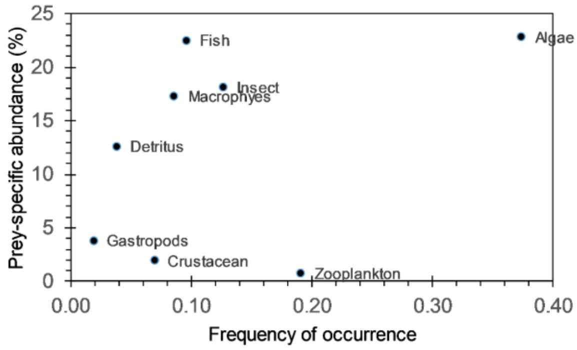
We found a high and biological significant dietary niche overlap between the invasive *Sarotherodon melanotheron* and indigenous *Oreochromis niloticus* inhabiting Eleiyele Reservoir. This proposes resource competition between these species in the reservoir. Coexistence, displacement or facilitation is the potential consequence of these interactions (Simberloff and von Holle 1999). Distinct generalists feeding strategies primarily on algae exhibited by both species clearly underscore interference feeding competition; this proscribes co-existence of these species on limited resources. Similar spectral of dietary items identified from stomach contents are portent indicator of interference feeding interactions. Interference feeding competition coupled with predations on vulnerable early life stages mostly eggs and larvae represent pathways of the negative ecological impacts of invasive *S. melanotheron* in Eleiyele Reservoir. These are ubiquitous traits of successful high aquatic biological invaders (Welcome 1984; Canonico *et al* 2005) that drive large impacts of invasive species in new habitats. Locally abundant and widespread invasive *S. melanotheron* could decimate the populations of native species in the reservoir due to predation and resource utilization.

Low natural flux in the abundance of food items that are associated with feeding strategies—morphological and behavioral—may also cause dietary niche overlap among sympatric species (Scarcity of preferred prey expedites competition for limited resources). Other variables including location in the water column, swimming propensity, similarity in feeding habits (feeding apparatus, type, and prey size) facilitate niche overlap among sympatric species (Medeiros and Arthington 2008). The spectral of food items consumed by these sympatric species indicate their ecological interactions (Knight and Rose 1994), and the potential availability of these resources in their habitat.

The dietary composition of *O. niloticus* and *S. melanothron* agree with previous studies on the food and feeding habits of these species. *Oreochromis niloticus* is an omnivore subsisting mainly on algae and plant materials (Oso *et al* 2006; Tesfaye *et al* 2020; Froese and



(a) *Oreochromis niloticus*



(b) *Sarotherodon melanotheron*

Figure 2: Amundsen feeding strategy diagram: prey-specific abundance plotted against frequency of different categories of native (a) *Oreochromis niloticus* (11.1- 21.6 cm, TL) and (b) invasive *Sarotherodon melanotheron* (14.9-26.4cm, TL) inhabiting Eleiyele Reservoir.

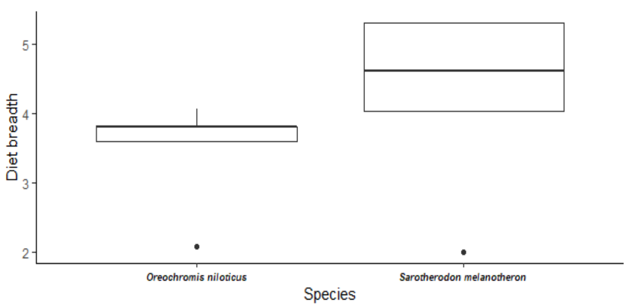


Figure 3: Box-plot of the Dietary niche breadths of native *Oreochromis niloticus* and invasive *Sarotherodon melanotheron* inhabiting Eleiyele Reservoir. Dietary breadths of these sympatric species are identical, and not significantly difference (Mann-Whitney U, W = 29, p-value = 0.79).

Pauly 2021); *S. melanotheron* are phytoplankton feeders (El-Sayed 2020; Froese and Pauly 2021). These species feed majorly on primary production (phytoplankton, macrophytes, flower seeds, and buds); and form critical links between other consumers and primary production (Winemiller 1996). These species may impact primary production with trophic cascading effect in the food web via consumption and competition.

Foraging voracity, a measure of the rate resource use, is greater in *S. melanotheron* than *O. niloticus* as confirm by the present data based on vacuity index: the formal species is edacious feeder while the latter is abstemious feeder. An apparent consequence is competitive exclusion (Tilman 1982) where resources are depleted to unsustainable levels for *O. niloticus* and other native species in the reservoir. Several reports indicate that resource use is associated with invasion success; successful invasive species have a higher rate of resource consumption than native analogues (Dick *et al* 2013; McKnight *et al* 2016). Adaptive significance of efficient resource use includes fast growth and early reproductive maturity; these ensure their establishment and spread (Funk and Vitousek 2007).

Observed proportion of empty stomach for species correspond to an index of instantaneous energy balance (Boivin and Power 1990; Huey *et al* 2001; Arrington *et al* 2002)—either denotes positive energy balance characterized by frequent stomachs with food (edacious feeding as estimated by VI for *S. melanotheron* in this study); an attribute that ensures perpetual energy supply, a requisite for growth and reproduction or negative energy balance (*O. niloticus* is relatively edacious based on VI) where species stockpile energy from earlier feeding as input for metabolism (Huey *et al* 2001). Energy acquisition directly affects fitness; it is optimized by edacious feeding. This suggests that invasive *S. melanotheron*, besides its wider dietary niche compare to *O. niloticus*, represent a feral predator in Eleiyele Reservoir. Documented trophic plasticity and prolific reproductive strategy of *S. melanotheron* (Dial and Wainright 1983; Molnar 2008) suggest further pervasive colonization and aggravated competition with other species in the reservoir.

Previous studies have persistently showed native population declines—they are even extirpated—during successful biological invasion (Kumschick *et al* 2012; Blackburn *et al* 2014; Welcome 1984; Canonico *et al* 2005). *Sarotherodon melanotheron* now dominates the catches of local fishermen in Eleyele Reservoir. Previously abundant Nile tilapia, *O. niloticus,* especially during the 1980s (Akinyemi *et al* 1986), is now rare in the reservoir. Loss of biodiversity through decrease in abundance and eventual displacement of native species characterize biological invasion by *S. melanotheron* (Englund 2002; Ordoñez *et al* 2015; Cassemiro *et al* 2017; Pèlèbè *et al* 2021). Extensive ecological tolerance associated with environmental parameters of this reservoir drive the abundance of population of *S. melanotheron* in Eleyele Reservoir albeit not describe in this study.

It is apparent from the present data that fish eggs as diet of invasive *S. melanotheron* constitute ambiguities; it is inconsistent with prevailing records: *S. melanotheron* as well as *O. niloticus* achieve parental care through mouth brooding to aerate and protect their eggs in the mouth cavity (Speaker and Kishida 2000; Gómez-Márquez *et al* 2022). *S. melanotheron* may prey on the eggs of other fish species due to its associated feeding behaviour in the vegetation and detrital zones use for breeding and nestling space by most fish species. Campbell (1987) described carnivorous feeding habits of *S. melanotheron* on fish eggs, larvae and newly hatched fry of other reared species. Above all, only stomach contents were analysed in the present study.

Conclusion

The range expansion and population growth of the blackchin tilapia, *S. melanothron* is still ongoing in Eleiyele Reservoir. It is almost impossible to find the erstwhile abundant Nile tilapia, *O. niloticus* in the reservoir. Unchecked thriving population of the blackchin tilapia, *S. melanotheron* potentially impair population of the Nile tilapia, *O. nilotucs* in Eleyele Reservoir through competitive feeding interactions linked to similarity in their diet composition, feeding strategies and dietary niche breadths Loss of biodiversity thorough displacement of native species by *S. melanotheron* remain grave issue of concerns. *Oreochromis niloticus* may be displaced from its native home range in Eleyele reservoir.

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