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# 1 **Relative growth of invasive and indigenous tilapiine cichlid fishes** 2 **in Tanzania**

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19 Non-native species have been widely distributed across Africa for the enhancement of capture  
20 fisheries, but it can be unclear what benefits in terms of fisheries production the non-native  
21 species bring compared to native species. Here we compared the relative growth rate of  
22 sympatric populations of non-native *Oreochromis niloticus* (Nile tilapia) to native  
23 *Oreochromis jipe* (Jipe tilapia) in three waterbodies in northern Tanzania. Using scale  
24 increments as a proxy for growth, we found that *O. niloticus* had a high growth rate relative to  
25 *O. jipe*, with the highest *O. niloticus* growth rates being observed in Nyumba ya Mungu  
26 reservoir. These results help to explain why *O. niloticus* may be a superior competitor to native  
27 species in some circumstances. However, further introductions of this non-native species  
28 should be undertaken with caution given potential for negative ecological impacts on  
29 threatened indigenous tilapia species.

30

31

32 **Keywords:** aquaculture, growth, fisheries, *Oreochromis*, tilapia

33 Non-native invasive species are largely considered to have superior traits relative to their  
34 indigenous counterparts, enabling their establishment and success in invaded ranges.  
35 Characteristics associated with invasion success in fish include fast growth, broad  
36 environmental tolerances and high fecundity (Kolar and Lodge 2002; Moyle and Marchetti  
37 2006). These advantageous traits have been studied alongside environmental characters of the  
38 habitat to both evaluate impacts of non-native species, as well as predict future invasions (Copp  
39 et al. 2009; Marr et al. 2017). In some circumstances, non-native species outcompete  
40 established indigenous species for limited resources, such as food, breeding habitat and shelter  
41 (Bøhn et al. 2008). However, while competition is often inferred based on abundance trends,  
42 or shared patterns of resource use, often there is little evidence of the relative performance of  
43 non-native and native species where they co-occur.

44

45 One indicator of the relative fitness of sympatric species is growth. In fish, growth can be  
46 measured using a range of methods including quantifying the deposition of calcified layers on  
47 otoliths, vertebrae and scales (Cheung et al. 2007; Martin et al. 2012). Higher growth rates are  
48 considered advantageous as they enable individuals to reach reproductive age quicker, with  
49 less time spent at the more vulnerable juvenile life stage (Sutherland 1996). Furthermore in  
50 female fish, body size is directly related to egg output potential and therefore larger body sizes  
51 can enhance reproductive output (Barneche et al. 2018). Large body size may also pose an  
52 advantage for males in competition for spawning territories. Taken together, this evidence  
53 suggests that comparisons of growth rates of sympatric species with similar life history  
54 strategies can indicate relative competitive performance (Chifamba and Videler 2014).

55

56 *Oreochromis niloticus* (Nile tilapia (Linnaeus 1758)) is native to northern Africa, including the  
57 Nile and Niger river systems (Trewavas 1983). In Tanzania, the species is naturally distributed  
58 only in the Lake Tanganyika catchment (Shechonge et al. 2019a), but over recent decades the  
59 species has been widely distributed across the country (Shechonge et al. 2019b). Such  
60 introductions have been both deliberate to promote capture fisheries, and accidental following  
61 escapes from aquaculture facilities. Where *O. niloticus* is present in Tanzania, it typically co-  
62 occurs with indigenous tilapiine species (Bradbeer et al. 2019; Shechonge et al. 2019b).  
63 However, the fundamental ecological characteristics of populations of *O. niloticus* relative to  
64 those of native species in sympatric environments are largely unknown, including fisheries-  
65 related traits such as growth rates.

66

67 Here, we report a study comparing the relative growth of non-native *O. niloticus* to native  
68 *Oreochromis jipe* (Jipe tilapia (Lowe 1955)), a large bodied species endemic to the Pangani  
69 catchment that partially supports multiple artisanal fisheries in the region (Shechonge et al.  
70 2019b). When first described, this taxon was believed to represent a complex of three closely-  
71 related morphologically similar species, with *O. jipe* and *O. girigan* occupying different niches  
72 within Lake Jipe and *O. pangani* occupying the main Pangani river (Lowe 1955). These  
73 populations have not been studied in depth since and have not generally been distinguished as  
74 separate taxa by subsequent workers. Instead, they are now treated as a single species (Seegers  
75 et al. 2003; Fricke et al. 2019), and we followed this approach by assigning all studies  
76 populations to *O. jipe*. However, further research may support original species-level  
77 designation of Lowe (1955). We sampled fishers catches from three locations: Lake Kumba  
78 (4.806°S, 38.621°E, altitude 367m), Nyumba ya Mungu reservoir (3.612°S, 37.459°E, altitude  
79 519m) and the Pangani Falls reservoir (5.347°S, 38.645°E, altitude 191m) in August 2015  
80 (Figure 1). Lake Kumba is a natural lake with a surface area of 0.5km<sup>2</sup>, and a maximum depth  
81 of 7 metres. The Nyumba-ya-Mungu reservoir was formed when the Pangani river was  
82 dammed in 1965, and has a maximum surface area of 180km<sup>2</sup> and a maximum depth of  
83 approximately 45 metres (Petr et al. 1975; Bailey 1996). The Pangani Falls reservoir was  
84 formed when the Pangani river was dammed in 1994, and has a surface area of 0.5km<sup>2</sup> and a  
85 maximum depth of 10 metres (Anderson et al. 2006).

86 All sampled fishes were identified to species, individually labelled, and stored in 70% ethanol  
87 (Table 1). To assess growth rates, we followed the scale measurement method of Martin et al.  
88 (2012) that has been validated in experimental trials as a technique for quantifying recent  
89 growth of tilapiine cichlids. For each specimen, three scales were removed from the area  
90 superior to the lateral line and posterior to the head. Scales were then placed onto a microscope  
91 slide, treated with glycerol and covered with a glass coverslip. Images with a superimposed  
92 scale bar were taken using a M205C microscope (Leica, Wetzlar, Germany). Image files were  
93 loaded into tpsDIG 2.2 (Rohlf 2015) and from each scale, five measurements were recorded,  
94 namely the scale total width (longest distance across the scale; Figure 2a) and four separate  
95 “increment size” measurements of the distance between the first and fifth circuli on primary  
96 radii viewed from the anterior field of the scale (Figure 2b). From these measurements we  
97 calculated a mean scale width, and the mean increment size of the individual. Scale total width  
98 was employed as a covariate of increment size, alongside the factor variables species and  
99 sampling site, in an analysis of covariance in R version 3.6.0 (R Core Team 2019). Size-

100 standardised increment size (hereafter termed “relative growth”) was compared using marginal  
101 means and pairwise *post-hoc* Tukey’s tests in the emmeans package (Lenth et al. 2018).

102

103 We first observed a positive dependence of scale total width on increment size ( $F_{1,142} = 138.53$ ,  
104  $P < 0.001$ ), and after accounting for this covariation we interpret differences in increment size  
105 among populations as differences in growth rates. We observed an overall difference in growth  
106 rates among tilapia species from the different water bodies ( $F_{2,142} = 57.55$ ,  $P < 0.001$ ), and we  
107 observed that overall *O. niloticus* had a greater growth rate than *O. jipe* ( $F_{1,142} = 30.49$ ,  $P <$   
108  $0.001$ ). However, the extent of the differences in growth rates between the two species varied  
109 among locations ( $F_{2,142} = 12.72$ ,  $P < 0.001$ ; Figure 3). The clearest difference between the  
110 species was at Nyumba ya Mungu, where *O. niloticus* grew significantly faster than *O. jipe* ( $t$   
111  $= -7.303$ ,  $P < 0.001$ ). However, there were no significant growth differences between the  
112 species at either Lake Kumba ( $t = -0.946$ ,  $P = 0.346$ ) or the Pangani falls reservoir ( $t = -1.427$ ,  
113  $P = 0.156$ ). When comparing growth rates of *O. niloticus* between the water bodies, we found  
114 fish at Nyumba ya Mungu grew faster than those at Pangani falls ( $t = -4.710$ ,  $P < 0.001$ ) and  
115 Lake Kumba ( $t = -11.629$ ,  $P < 0.001$ ), while fish at Pangani falls also grew significantly faster  
116 than Lake Kumba ( $t = 5.625$ ,  $P < 0.001$ ). Similarly we found that *O. jipe* grew significantly  
117 faster at Nyumba ya Mungu than Lake Kumba ( $t = -2.876$ ,  $P = 0.013$ ), but there were no  
118 significant differences in *O. jipe* growth rates between the Pangani Falls and either Nyumba ya  
119 Mungu ( $t = 0.245$ ,  $P = 0.967$ ) or Lake Kumba ( $t = 2.364$ ,  $P = 0.051$ ).

120

121 The key results of this study are that *O. niloticus* had higher growth relative to the indigenous  
122 *O. jipe*, but also that extent of differences varied among locations. Such differences may have  
123 multiple explanations. Since *Oreochromis* can respond rapidly to selection on body size traits  
124 (Hulata et al. 1986), and recent work has identified significant genetic differences in neutral  
125 markers among the three sampled *O. niloticus* populations (Shechonge et al. 2019a), then  
126 genetic variation may underpin growth differences among the populations of both species. This  
127 may reflect historic selection from aquaculture prior to being introduced, or perhaps fisheries-  
128 induced evolution (Heino et al. 2015). Alternatively, the different sampled environments may  
129 differentially favour the species, with conditions within the Nyumba ya Mungu reservoir  
130 particularly well suited to the growth of *O. niloticus* relative to *O. jipe* present. It is unknown  
131 to what extent these species use different niches within each of the sampled environments. To  
132 fully understand the underlying reasons for the differences in growth rates between and within  
133 species would require more detailed study of growth rates in common-garden conditions, in

134 addition to an improved understanding of the relative differences among populations in habitat,  
135 diet and levels of fisheries exploitation.

136

137 Although our analysis of scale increments suggest higher growth for *O. niloticus* than *O. jipe*,  
138 to compare fisheries productivity, other relevant phenotypic characters need to be assessed  
139 including maximum length, age of maturity and food conversion rate. Higher individual growth  
140 rate need not always translate into greater rate of total fish biomass production, which is likely  
141 to be more relevant for small-scale fishery yields. Whether the differences we observed will  
142 have relevance for ecological interactions between the species is also unclear. It is possible that  
143 a faster growth rate may be advantageous for the non-native *O. niloticus* when competing with  
144 *O. jipe* for limited resources, including food, breeding space or shelter from predators. This is  
145 potentially of concern given the Critically Endangered IUCN red list status of the *O. jipe*, linked  
146 to its narrow geographic range and overall decreasing population trajectory (Bayona and  
147 Hanssens 2006). In Lake Kariba, *O. niloticus* has been shown to possess faster growth rate than  
148 indigenous *Oreochromis mortimeri* (Trevawas, 1966; Chifamba and Videler 2014). This,  
149 coupled with evidence of a rapid population expansion of *O. niloticus* matching a decline in *O.*  
150 *mortimeri* from the late 1990s onwards (Chifamba 2006), and evidence of overlapping resource  
151 use patterns (Mhlanga 2000), suggestss strong potential for *O. niloticus* to outcompete  
152 indigenous species. Equivalent monitoring of the abundance changes, resource use patterns and  
153 detailed analyses of life history parameters of both native and non-native tilapia populations in  
154 invaded habitats are needed to understand the full effects of introduced tilapia species across  
155 East Africa.

156

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161

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233



234 Table 1. Number and average standard length ( $\pm$  standard deviation) of *O. niloticus* and *O. jipe*  
235 sampled from the three study locations.

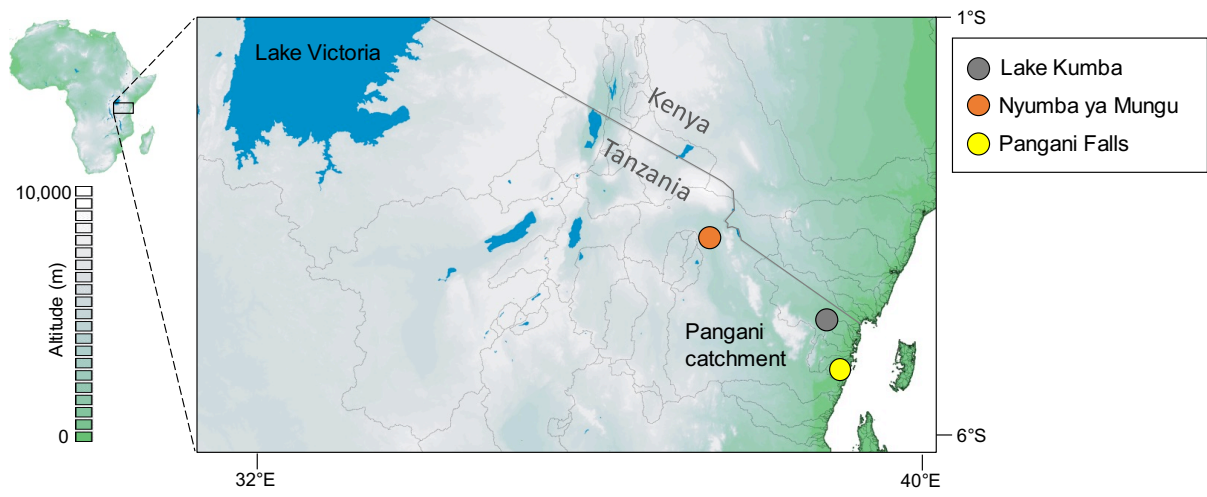
236

	Lake Kumba		Nyumba ya Mungu		Pangani Falls	
	n	SL $\pm$ SD	n	SL $\pm$ SD	n	SL $\pm$ SD
<i>O. niloticus</i>	71	10.88 $\pm$ 2.59	15	12.97 $\pm$ 4.58	26	6.51 $\pm$ 0.96
<i>O. jipe</i>	13	9.41 $\pm$ 1.31	18	11.80 $\pm$ 3.33	6	5.66 $\pm$ 0.65

237

238

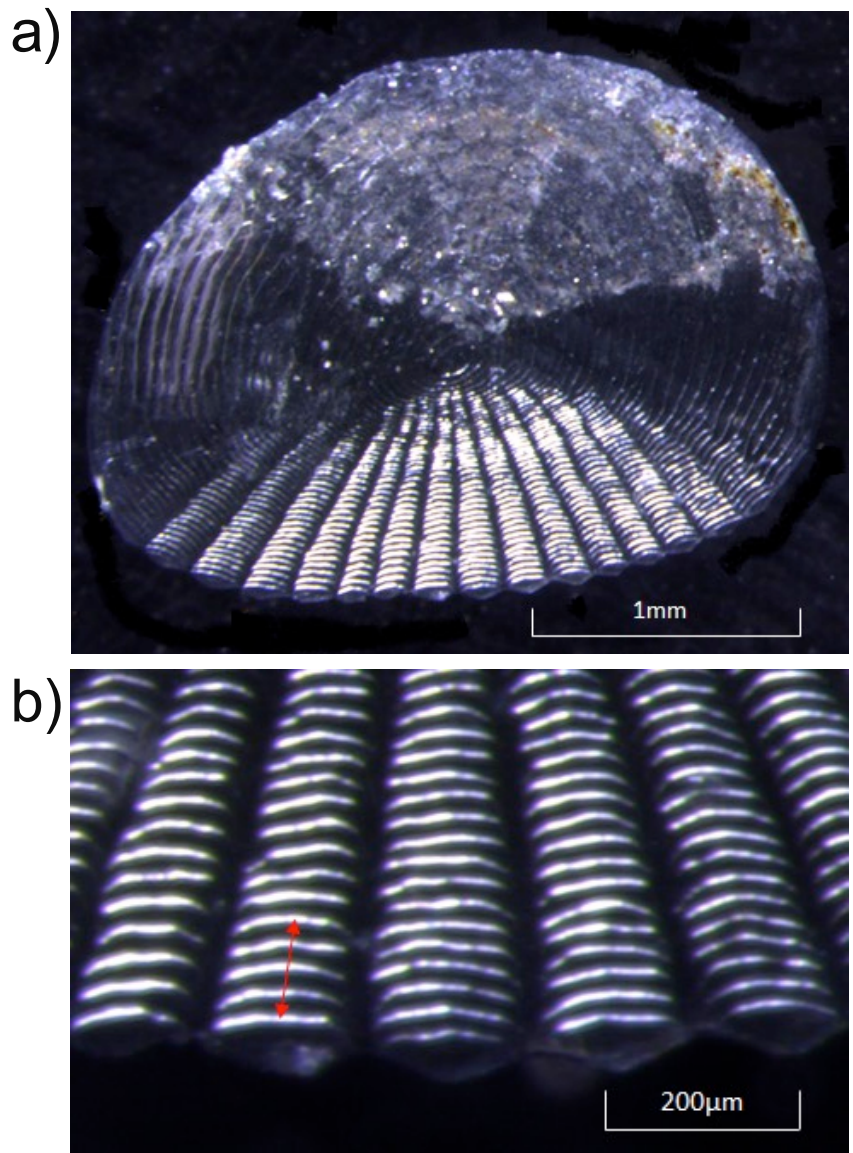
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241 Figure 1. Sampling sites for sympatric Nile tilapia and Jipe tilapia in August 2015.

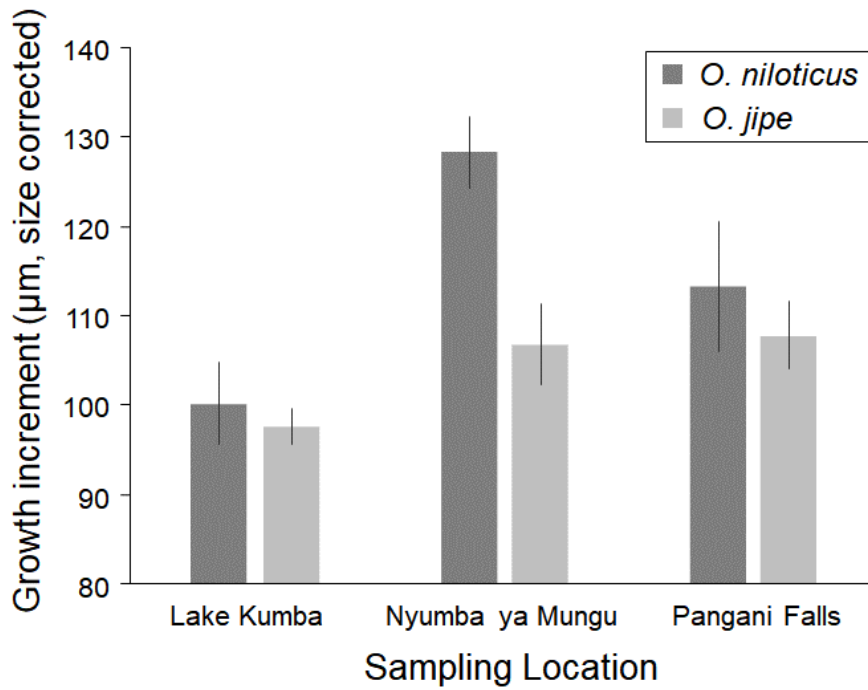
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246 Figure 2. Measurements were made of a) total scale width, and b) the distance between the first  
247 and fifth circuli (indicated by arrow) on a primary radius of the same scale.



248

249 Figure 3: Scale growth measurements (corrected for scale width) for *Oreochromis niloticus*  
 250 (dark grey) and *Oreochromis jipe* (light grey) at three sites, Lake Kumba, Nyumba ya Mungu  
 251 and Pangani Falls. Error bars represent 95% confidence intervals.

252