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

3

4

5 SJ Bradbeer^{1,2*}, BP Ngatunga³, GF Turner⁴, and MJ Genner^{1*}

6

7 *1 School of Biological Sciences, Life Sciences Building, 24 Tyndall Avenue, University of*
8 *Bristol, Bristol, BS8 1TQ, United Kingdom*

9 *2 School of Biology, Miall Building, University of Leeds, Leeds, LS2 9JT, United Kingdom.*

10 *2 Tanzania Fisheries Research Institute (TAFIRI), PO. Box 9750, Dar es Salaam, Tanzania.*

11 *3 Department of Aquatic Sciences and Fisheries, University of Dar es Salaam, P.O. Box*
12 *35064, Dar es Salaam, Tanzania.*

13 *4 School of Natural Sciences, Bangor University, Bangor, Gwynedd, LL57 2UW, United*
14 *Kingdom.*

15

16 *Corresponding author, email: bssjb@leeds.ac.uk.*

17

18 **Abstract**

19

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

31

32

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

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

45

46 One indicator of fitness among sympatric species is growth. In fish, growth can be measuring
47 using a range of methods including quantifying the deposition of calcified structures on the
48 anterior of scale circuli (Cheung et al. 2007; Martin et al. 2012). Higher individual growth
49 rates are considered advantageous across populations as they enable those individuals to
50 reach reproductive age quicker, with less time spent at a more vulnerable juvenile life stage
51 (Sutherland 1996). Furthermore, in female fish body size is directly related to egg output
52 potential, therefore larger body sizes can enhance reproductive output (Barneche et al. 2018).
53 Greater body size may pose an advantage for males in competition for spawning territories.
54 Thus, comparing growth rates of species can also acts as an indication of potential relative
55 competitiveness (Chifamba and Videler 2014).

56

57 *Oreochromis niloticus* (Nile tilapia (Linnaeus 1758)) is native to much of northern Africa,
58 including the Nile and Niger systems (Trewavas 1983). In Tanzania, the species is naturally
59 distributed only in the Lake Tanganyika catchment (Shechonge et al. 2019a), but due to
60 favourable characteristics, such as potential for rapid growth and broad habitat tolerances, it
61 has been widely distributed to non-native habitats across the country (Shechonge et al.
62 2019b). Such introductions have largely been deliberate, to promote capture fisheries, but it is
63 also possible accidental escapes have occurred from aquaculture facilities in the country.
64 Where *O. niloticus* is present in Tanzania, it typically co-occurs with indigenous tilapiine
65 species (Bradbeer et al. 2019; Shechonge et al. 2019b). However, the fundamental ecological
66 characteristics of populations of *O. niloticus* relative to those of native species are typically
67 unknown, including the relative performance of fisheries-related traits such as growth rates.

68

69 Here, we report a study comparing the relative growth of introduced *O. niloticus* to
 70 indigenous *Oreochromis jipe* (Jipe tilapia (Lowe 1955)), a large bodied species endemic to
 71 the Pangani catchment that partially supports multiple artisanal fisheries in the region
 72 (Shechonge et al. 2019b). When first described, this ‘species’ was believed to represent a
 73 complex of three closely-related morphologically similar species, *O. jipe* and *O. girigan*
 74 occupying different niches within Lake Jipe and *O. pangani* within the river (Lowe 1955),
 75 but these have not been studied in depth since and have generally not been distinguished by
 76 subsequent workers and are now treated as a single species (Seegers et al. 2003; Fricke et al.
 77 2019). We sampled fisher’s catches from three locations, namely Lake Kumba (5°1.92’ S,
 78 38°32.88’ E), Nyumba ya Mungu reservoir (3°36.72’ S, 37°27.54’ E) and the Pangani Falls
 79 reservoir (5°20.82’ S, 38°38.7’ E) in August 2015 (Figure 1). All fishes were identified to
 80 species, individually labelled, and stored in 70% ethanol. To assess growth rates, we followed
 81 the method of Martin et al. (2012) that has been validated as a method of comparing recent
 82 growth of tilapiine cichlid fishes in experimental trials. For each specimen, three scales were
 83 removed from the area superior to the lateral line and posterior to the head. Scales were then
 84 placed onto a microscope slide, treating with glycerol and covered with a glass coverslip.
 85 Images with a superimposed scale bar were taken using a M205C microscope (Leica,
 86 Wetzlar, Germany). Image files were loaded into tpsDIG 2.2 (Rohlf 2015) and from each
 87 scale, five measurements were recorded, namely the scale total width (longest distance across
 88 the scale; Figure 2a) and four separate “increment size” measurements of the distance
 89 between the first and fifth circuli on primary radii viewed from the anterior field of the scale
 90 (Figure 2b). From these measurements we calculated a mean scale width of the individual,
 91 and the mean increment size of the individual.

92

93 Scale total width was employed as a covariate of increment size, alongside the factors
 94 Species and Sampling Site, in an analysis of covariance in R 3.6.0 (R Core Team 2019), with
 95 size-standardised increment size (hereafter termed “relative growth”) compared using
 96 marginal means and *post-hoc* pairs tests in the emmeans package (Lenth et al. 2018). After
 97 accounting for the significant positive associations of scale total width on increment size
 98 ($F_{1,142} = 138.53$, $P < 0.001$), there were significant overall differences among sites in
 99 increment size ($F_{2,142} = 57.55$, $P < 0.001$), and *O. niloticus* had a relatively greater increment
 100 size than *O. jipe* ($F_{1,142} = 30.49$, $P < 0.001$). However, the extent of the difference differed
 101 significantly among locations ($F_{2,142} = 12.72$, $P < 0.001$; Figure 3). Pairwise *post-hoc* Tukey’s

tests confirmed a significantly greater growth of *O. niloticus* relative to *O. jipe* at Nyumba ya Mungu ($t = -7.303$, $P < 0.001$), but no significant differences between the species at either Lake Kumba ($t = -0.946$, $P = 0.346$) or the Pangani falls ($t = -1.427$, $P = 0.156$). Pairwise *post-hoc* Tukey's tests confirmed *O. niloticus* has a significant higher growth rate at Nyumba ya Mungu than Pangani falls ($t = -4.710$, $P < 0.001$) and Lake Kumba ($t = -11.629$, $P < 0.001$), while it also grew faster at Pangani falls than Lake Kumba ($t = 5.625$, $P < 0.001$). Pairwise *post-hoc* tests showed that *O. jipe* grew faster at Nyumba ya Mungu than Lake Kumba ($t = -2.876$, $P = 0.013$), but there were no significant differences in growth rates between the Pangani Falls population and either Nyumba ya Mungu ($t = 0.245$, $P = 0.967$) or Lake Kumba ($t = 2.364$, $P = 0.051$).

The key results of this study are that *O. niloticus* demonstrates faster growth relative to the indigenous *O. jipe*, but also that extent of differences varies among locations. Such differences may have multiple explanations. Since *Oreochromis* can respond rapidly to selection on body size traits (Hulata et al. 1986), and recent work has identified significant genetic differences in neutral markers among the three sampled *O. niloticus* populations (Shechonge et al. 2019a), then genetic variation may underpin growth differences among the populations of both species. This may reflect historic selection from impoundments or aquaculture facilities prior to being introduced, or fisheries-induced evolution (Heino et al. 2015). Alternatively, the different sampled environments may differentially favour the species, with conditions within the Nyumba ya Mungu reservoir particularly well suited to growth of *O. niloticus* relative to *O. jipe*. It is unknown to what extent these species use different niches within each of the sampled environments. To fully understand the underlying reasons for the differences in growth rates between and within species would require more detailed study of growth rates in common-garden conditions, in addition to an improved understanding of the relative differences among populations in habitat, diet and levels of fisheries exploitation.

Although our analysis of scale increments is suggestive of more rapid growth of *O. niloticus* than *O. jipe* in some circumstances, other phenotypic characters relevant to fisheries need to be assessed, including maximum length, age of maturity and food conversion rate. Higher individual growth rate need not translate into greater rate of total fish biomass production which is likely to be more relevant for small-scale fishery yields. Whether the observed differences will have relevance for ecological interactions between the species is also unclear.

It is possible that a faster growth rate for the non-native *O. niloticus* may be advantageous when competing with *O. jipe* for limited resources, including food, breeding space or shelter from predators. This is potentially of concern given the Critically Endangered IUCN red list status of the *O. jipe*, linked to its narrow geographic range and overall decreasing population trajectory (Bayona and Hanssens 2006). In Lake Kariba, *O. niloticus* has been shown to possess faster growth rate than indigenous *Oreochromis mortimeri* (Trevawas, 1966; Chifamba and Videler 2014). This, coupled with evidence of a rapid population expansion of *O. niloticus* matching a decline in *O. mortimeri* from the late 1990s onwards (Chifamba 2006), and evidence of overlapping resource use patterns (Mhlanga 2000), is suggestive of the potential for *O. niloticus* to outcompete indigenous species. Equivalent monitoring of the abundance changes, resource use patterns and detailed analyses of life history parameters of *O. niloticus* and sympatric indigenous tilapia would help to understand the full effects of introductions of *O. niloticus* across East Africa.

Acknowledgements - The work was funded by Royal Society-Leverhulme Trust Africa Awards AA100023 and AA130107. We thank the Tanzania Commission for Science and Technology (COSTECH) for research permits, and staff of the Tanzania Fisheries Research Institute for contributions to fieldwork.

References

- Barneche DR, Robertson DR, White CR, Marshall DJ. 2018. Fish reproductive-energy output increases disproportionately with body size. *Science* 360: 642-645.
- Bayona, JDR, Hanssens M. 2006. *Oreochromis jipe*. The IUCN Red List of Threatened Species 2006: e.T60628A12388450. <https://bit.ly/2Kag28O>. Downloaded on 01 August 2019.
- Bøhn T, Amundsen PA, Sparrow A. 2008. Competitive exclusion after invasion? *Biological Invasions* 10: 359-368.
- Bradbeer, SJ, Harrington, J, Watson, H, Warriach, A, Shechonge, A, Smith, A, Tamatamah, R, Ngatunga, BP, Turner GF, Genner MJ. 2019. Limited hybridization between introduced and Critically Endangered indigenous tilapia fishes in northern Tanzania. *Hydrobiologia*, 832: 257-268.
- Cheung CHY, Chaillé PM, Randall DJ, Gray JS, Au DWT. 2007. The use of scale increments as a means of indicating fish growth and growth impairments. *Aquaculture* 266: 102-

111.

Chifamba PC, Videler JJ. 2014. Growth rates of alien *Oreochromis niloticus* and indigenous *Oreochromis mortimeri* in Lake Kariba, Zimbabwe. *African Journal of Aquatic Science* 39: 167-176.

Chifamba PC. 2006. Spatial and historical changes of indigenous *O. mortimeri* following introduction of exotic *O. niloticus* in Lake Kariba. In: Odada EO, Olago DO, Ochala W, Ntiba N, Wandiga S, Gichuki N, Oyieke H (eds), 11th World Lakes Conference, Nairobi, Kenya, 31 October–4th November 2005, Proceedings Vol. II. Nairobi: Ministry of Water and Irrigation, Kenya, and International Lake Environment Committee. pp 500–504.

Copp G.H, Vilizzi L, Mumford J, Fenwick GV, Godard MJ, Gozlan RE. 2009. Calibration of FISK, an invasiveness screening tool for nonnative freshwater fishes. *Risk Analysis: An International Journal* 29: 457-467.

Fricke, R. Eschmeyer, W.N. and Van der Laan R. (eds) 2019. Eschmeyer's Catalog of Fishes: Genera, Species, References. Electronic version accessed 15 Aug 2019.

Heino M, Pauli BD, Dieckmann U. 2015. Fisheries-induced evolution. *Annual Review of Ecology, Evolution and Systematics* 46: 461-480.

Hulata G, Wohlfarth GW, Halevy A. 1986. Mass selection for growth rate in the Nile tilapia (*Oreochromis niloticus*). *Aquaculture* 57: 177-184.

Kolar CS, Lodge DM. 2002. Ecological predictions and risk assessment for alien fishes in North America. *Science* 298: 1233-1236.

Lenth R 2019. emmeans: estimated marginal means, aka least-squares means. *R Package version 1.4*. <http://CRAN.R-project.org/package=emmeans>

Marr SM, Ellender BR, Woodford DJ, Alexander ME, Wasserman RJ, Ivey P, Zengeya T, Weyl OL. 2017. Evaluating invasion risk for freshwater fishes in South Africa. *Bothalia-African Biodiversity and Conservation* 47: 1-10.

Martin, C.H. 2012. Weak disruptive selection and incomplete phenotypic divergence in two classic examples of sympatric speciation: Cameroon Crater lake cichlids. *The American Naturalist* 180: 90-109.

Mhlanga L. 2000. The diet of five cichlid fish species from Lake Kariba, Zimbabwe. *Transactions of the Zimbabwe Scientific Association* 74: 16-21.

Moyle PB, Marchetti MP. 2006. Predicting invasion success: freshwater fishes in California as a model. *BioScience* 56: 515-524.

Rohlf 2015 tpsDig, digitize landmarks and outlines, version 2.2. Department of Ecology and

204 Evolution, State University of New York at Stony Brook

205 Seegers L, de Vos LDG, Okeyo DO 2003 Annotated checklist of the freshwater fishes of

206 Kenya (excluding the lacustrine haplochromines from Lake Victoria). *Journal of East*

207 *African Natural History* 92: 11-47.

208 Shechonge A, Ngatunga BP, Tamatamah R, Bradbeer SJ, Sweke E, Smith A, Turner G.F.,

209 Genner MJ (2019a) Population genetics of Nile tilapia confirms the Lake Tanganyika

210 population as a unique genetic resource. *Environmental Biology of Fishes* 102: 1107-

211 1117

212 Shechonge A, Ngatunga BP, Bradbeer SJ, Day JJ, Freer JJ, Ford AGP, Kihedu J, Richmond

213 T, Mzighani S, Smith AM, Sweke EA, Tamatamah R, Tyers AM, Turner GF, Genner

214 MJ. 2019b. Widespread colonisation of Tanzania catchments by introduced

215 *Oreochromis tilapia* fishes: the legacy from decades of deliberate introduction.

216 *Hydrobiologia* 832: 235-253.

217 Sutherland WJ. 1996. From individual behaviour to population ecology. Oxford University

218 Press.

219 Trewavas, E., 1983. Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and

220 *Danakilia*. British Mus. Nat. Hist., London, UK.

221

222

223

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

226

	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

227

228

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

233

234

235

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

238

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