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Relative growth of invasive and indigenous tilapiine cichlid fishes in Tanzania

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

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

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

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

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

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

All sampled fishes were identified to species, individually labelled, and stored in 70% ethanol (Table 1). To assess growth rates, we followed the scale measurement method of Martin et al. (2012) that has been validated in experimental trials as a technique for quantifying recent growth of tilapiine cichlids. For each specimen, three scales were removed from the area superior to the lateral line and posterior to the head. Scales were then placed onto a microscope slide, treated with glycerol and covered with a glass coverslip. Images with a superimposed scale bar were taken using a M205C microscope (Leica, Wetzlar, Germany). Image files were loaded into tpsDIG 2.2 (Rohlf 2015) and from each scale, five measurements were recorded, namely the scale total width (longest distance across the scale; Figure 2a) and four separate "increment size" measurements of the distance between the first and fifth circuli on primary radii viewed from the anterior field of the scale (Figure 2b). From these measurements we calculated a mean scale width, and the mean increment size of the individual. Scale total width was employed as a covariate of increment size, alongside the factor variables species and sampling site, in an analysis of covariance in R version 3.6.0 (R Core Team 2019).Sizestandardised increment size (hereafter termed "relative growth") was compared using marginal means and pairwise *post-hoc* Tukey's tests in the emmeans package (Lenth et al. 2018).

We first observed a positive dependence of scale total width on increment size ($F_{1,142} = 138.53$, $P < 0.001$), and after accounting for this covariation we interpret differences in increment size among populations as differences in growth rates. We observed an overall difference in growth rates among tilapia species from the different water bodies ($F_{2,142} = 57.55$, $P < 0.001$), and we observed that overall *O. niloticus* had a greater growth rate than *O. jipe* ($F_{1,142} = 30.49$, $P < 0.001$). However, the extent of the differences in growth rates between the two species varied among locations ($F_{2,142} = 12.72$, $P < 0.001$; Figure 3). The clearest difference between the species was at Nyumba ya Mungu, where *O. niloticus* grew significantly faster than *O. jipe* ($t = -7.303$, $P < 0.001$). However, there were no significant growth differences between the species at either Lake Kumba ($t = -0.946$, $P = 0.346$) or the Pangani falls reservoir ($t = -1.427$, $P = 0.156$). When comparing growth rates of *O. niloticus* between the water bodies, we found fish at Nyumba ya Mungu grew faster than those at Pangani falls ($t = -4.710$, $P < 0.001$) and Lake Kumba ($t = -11.629$, $P < 0.001$), while fish at Pangani falls also grew significantly faster than Lake Kumba ($t = 5.625$, $P < 0.001$). Similarly we found that *O. jipe* grew significantly faster at Nyumba ya Mungu than Lake Kumba ($t = -2.876$, $P = 0.013$), but there were no significant differences in *O. jipe* growth rates between the Pangani Falls 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* had higher growth relative to the indigenous *O. jipe*, but also that extent of differences varied 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 aquaculture prior to being introduced, or perhaps 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 the growth of *O. niloticus* relative to *O. jipe* present. 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 suggest higher growth for *O. niloticus* than *O. jipe*, to compare fisheries productivity, other relevant phenotypic characters need to be assessed including maximum length, age of maturity and food conversion rate. Higher individual growth rate need not always translate into greater rate of total fish biomass production, which is likely to be more relevant for small-scale fishery yields. Whether the differences we observed will have relevance for ecological interactions between the species is also unclear. It is possible that a faster growth rate may be advantageous for the non-native *O. niloticus* 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), suggestss strong 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 both native and non-native tilapia populations in invaded habitats are needed to understand the full effects of introduced tilapia species across East Africa.

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