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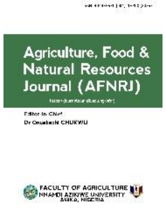

Review Article

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Mozambique Tilapia *Oreochromis mossambicus* (Peters 1852) and the threat from Oreochromis niloticus (Linnaeus 1758) in South Africa: A review

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ABSTRACT

This review provides background knowledge of *O. mossambicus* conservation genetics studies and the invasive potential of *O. niloticus*. The detailed aspects of 1) the species biology, taxonomy, geographic distribution, beneficial traits, and its conservation status; (2) *O. niloticus* biology and invasive potential; and, (3) the threat posed by *O. niloticus* in South Africa. The *O. mossambicus* is a deep-bodied, yellowish or dull greenish colour with weak bands. An omnivorous fish of the genus *Oreochromis*, tribe Oreochromini that can weigh up to 1.1 kg and globally used for aquaclture. They are indigenous to south Africa that can thrive in fresh, brackish, and seawater, with valued traits of tolerance to salinity, cold temperatures and drought. They are classified as “Vulnerable” on the IUCN Red List because of hybridization with *O. niloticus* and need to be conserved. *Oreochromis niloticus* can attain approximately 60 cm (standard length), 4.3 kg in weight, and are often aggressive competitors that out-compete other species for spawning and breeding grounds if these are limited. These attributes inherently predisposed *O. niloticus* as an invasive species. Introduced into South Africa, for aquaculture and its escape from farms, leads to hybridization with native *O. mossambicus*. Most reports of hybridisation and introgression are from the Limpopo river system in northern South Africa with few data from other regions. Secondly, previous works do not reflect whole genome diversity with low comparability among nuclear DNA markers. This article suggested a SNP based molecular approach with robust sampling in assessing introgressive hybridization of *O. niloticus* into *O. mossambicus* in South Africa.

KEYWORDS: *Conservation, Invasive threats, Orochromis, SNP, South Africa*

INTRODUCTION

Mozambique tilapia *Oreochromis mossambicus* is a deep-bodied fish indigenous from southern Africa and used worldwide in aquaculture (Trewavas, 1983). It has a yellowish or dull greenish colour with weak bands, the adult can weigh up to 1.1 kg and has a life span of up to 11 years (Frimodt, 1995; Luna, 2012). These characteristics can be influenced by environmental and breeding pressures operating on wild or cultured populations (Froese & Pauly, 2020). They are omnivorous with broad diets ranging from detritus, aquatic vegetation, single-celled algae, small invertebrates, fish fry, and rooted plants which allows them to survive in a variety of

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habitats (Trewavas, 1983). They are maternal mouthbrooders, exhibiting high parental care with the ability to spawn many broods over a long reproductive season, giving them high potential fecundity (Popma & Masser, 1999; Russell *et al*., 2012). They develop dominance social hierarchies and engage in a lek-breeding system, where males compete for resources such as food, mates, and territories. Dominance and social status determine the reproductive success of males within the lek (Barata, *et al*., 2008). The natural distribution of this species is in the southeastern coastal rivers of Southern Africa (Bills, 2019). They occur in diverse water bodies with a preference for still and slow-moving waters, such as in confined reservoirs, lagoons, and rivers. Their primary habitat is freshwater but some can thrive in brackish waters, and even in hypersaline environments with temperatures above seawater (Ford *et al.*,2019; Froese & Pauly, 2020).

Mozambique tilapia is an excellent candidate for aquaculture farming. They can be fed with both animal and plant-based food, and they have high meat quality that is appreciated on the market. The females can spawn 500 eggs every two weeks and can withstand extreme temperatures and saline conditions (Ford *et al.*, 2019; Skelton, 2001). Despite these features, growth of *O. mossambicus* is 40% slower than *O. niloticus* in South Africa, which makes the latter economically more viable for aquaculture (DAFF, 2018). The preferential utilisation of *O. niloticus* or its hybrids for aquaculture outside its natural range, such as in Southern Africa, comes with a cost. *Oreochromis niloticus* individuals can escape from aquaculture farms into the wild and threaten populations of indigenous species (Bills, 2019; Hallerman & Hilsdorf, 2014). *Oreochromis niloticus* grow bigger faster and are more aggressive than the native *O. mossambicus*, qualities that make them a successful invasive species (Stauffer *et al*., 2022; Zengeya *et al.*, 2011, 2013). Furthermore, these two species hybridizewith a report suggesting that pure native *O. mossambicus* might be disappearing in the Limpopo River as well as in the Zambezi River (Bills, 2019). *Oreochromis niloticus* is also an invasive threat to other *Oreochromis* species such as *O. andersonii*, *O. macrochir*, and *O. mortimeri* in rivers and lakes of Southern Africa (Deines *et al.*, 2014; Tweddle, 2010; Stauffer *et al*., 2022).

Several studies have identified and assessed the threat of hybridization and introgression of *O. niloticus* genes into *O. mossambicus* in Southern Africa. Non-molecular approaches based on morphological identification by qualified taxonomists were used to spot hybrids in the Limpopo river system of South Africa (Stauffer *et al.*, 2022; van der Bank & Deacon, 2007; van der Waal & Bills, 2000; Zengeya *et al.*, 2017). However, for a valid assessment of invasive species both morphology and molecular examination are required. The molecular approach remains the best in identifying and assessing hybrids, though it becomes more insightful when combined with adequate morphological identifications. Molecular tools such as allozymes, mitochondrial DNA (mtDNA), Simple sequence repeats (SSR) and Amplified fragment-length polymorphism (AFLP) have been applied to study introgression of *O. niloticus* genes into *O. mossambicus* in southern Africa (D'Amato *et al*., 2007; Deines *et al*., 2014; Firmat *et al*., 2013; Moralee *et al.*, 2000, Mashaphu *et al.*, 2024; Mojekwu *et al.*, 2021; Simbine & Hilsdorf, 2014). Nonetheless, the majority of these studies are from the northern part of South Africa (Limpopo system) with no baseline reference for the highly variable mtDNA control region and whole genome diversity.

This write up provides a review of: (1) *O. mossambicus* biology, taxonomy, geographic distribution, beneficial traits for aquaculture and its conservation status; (2) *O. niloticus* biology and invasive potential; and, (3) the threat posed by *O. niloticus* in South Africa.

Classification

Oreochromis is part of the large Oreochromini tribe, which comprises 43 recognised species, all endemic to Africa and the Middle East region (Fricke *et al*., 2020). The genus *Oreochromis* (maternal mouth-brooders) was formerly considered to be part of the Tilapiini tribe, together with *Sarotherodon* (bi-parental or paternal mouth-brooders) and *Tilapia* (substrate breeders) (McAndrew, 2000) However, mtDNA studies showed that this concept of Tilapiini was paraphyletic (Klett & Meyer, 2002; Nagl *et al*., 2001). A revised classification of African cichlids previously recognised as "Tilapia" (Dunz & Schliewen, 2013) grouped *Oreochromis* and *Sarotherodon* with eight other genera in the tribe Oreochromini. The genus *Oreochromis* includes several species utilised globally for aquaculture, including *O. mossambicus*, which is valued for its tolerance for a wide range of salinity, cold temperatures and drought (Ford *et al.*, 2019; Froese & Pauly, 2020).

Oreochromis mossambicus, commonly known as Blue Kurper in South Africa, was originally described from the lower Zambezi river in Mozambique, as *Chromis* (*Tilapia*) *mossambicus* . Later this species was identified as belonging to the genus *Oreochromis* (El-Sayed, 2020; Froese & Pauly, 2020)This classification was based on characters distinguishing *Oreochromis* from *Sarotherodon* and *Tilapia*. These characters include scales of belly smaller than flank scales, well developed genital papilla, the weight of ripe testes relative to body weight, and maternal mouth-brooding (El-Sayed, 2020)Prior phylogenetic studies of tilapiines included limited taxonomic coverage and gave conflicting results on relationships within *Oreochromis* (Klett & Meyer, 2002; Nagl *et al*., 2001). These studies included between four and seven species of *Oreochromis* and relied heavily on mtDNA markers, although some did include limited data from the nuclear genome (Dunz & Schliewen, 2013; Matschiner *et al.*, 2017; Schwarzer *et al.*, 2009). *Oreochromis* was grouped with other mouthbrooding lineages in Oreochromini (Dunz & Schliewen, 2013). The relationships and factors facilitating diversification within *Oreochromis* remain ambiguous. There is evidence that adaptation to increased salinity and temperature occurred multiple times within the phylogeny of *Oreochromis*, and of a single adaptation to soda lake conditions (Ford *et al.*, 2019). Furthermore, reconstruction of phenotypic characters indicated that secondary sexual characteristics such as extended jaw and genital tassel are not correlated but evolved independently in multiple clades. This suggests that these characters are not useful for taxonomic diagnosis of *Oreochromis* (Ford *et al.*, 2019).

Biological Description of Mozambique tilapia (*Oreochromis mossambicus)*

The Native *O. mossambicus* is deep-bodied and laterally compressed with long dorsal fins and spines (Table 1). Adult males have pointed duckbill-like snout with enlarged jaws and concave upper profile (Froese & Pauly, 2020; Lamboj, 2004; Mashaphu *et al.,* 2024 Skelton, 2001. Breeding males are black with simple or shallow distal notch genital papillae while females and non-breeding males are silvery with mid-lateral blotches (Luna, 2012; Trewavas, 1983). The males grow larger than the females commonly to a length of approximately 35 cm (14 in) with 1.1 kg the maximum published weight (Frimodt, 1995; Luna, 2012).

Oreochromis mossambicus is considered as a freshwater fish but also thrives in brackish estuaries and coastal lakes with high fecundity (Froese & Pauly, 2020; Gupta & Acosta, 2004; Trewavas, 1983). They easily adapt to extreme environmental conditions, feeding mostly on phytoplankton and algae, while some feed on zooplanktons, earthworms, shrimps, and aquatic macrophytes (Lamboj, 2004; Skelton, 2001). The natural thermal environment for *Oreochromis mossambicus* typically ranges from 17 to 35°C, but can extend to 42°C depending on salinity tolerance (Chervinski, 1982; Ford *et al.*, 2019; Froese & Pauly, 2020; Philippart & Ruwet, 1982). They can reach sexual maturity at 15 cm (standard length) within three months, weighing 60 to 100 g (Allen *et al*., 2002; Popma & Masser, 1999).

Oreochromis mossambicus are sexually dimorphic, and prolific spawners, with the males mating with multiple female partners, and the female caring for the eggs and larvae (maternal mouthbrooders). In a season, females can spawn several times and carry multiple broods (Skelton,2001). Males compete for breeding grounds during the breeding season, with the largest male using sounds and urinary odours to exhibit territorial dominance to females and other males, allowing the female to lay their eggs in his nest (Barata *et al.,* 2008). The male releases milt on his nest and the female gulps the milt to fertilise her eggs. The female takes the fertilised eggs in her mouth to a different territory for about 20 to 22 days, providing protection and thereby increasing the survival rates of eggs and fry (James & Bruton, 1992). Reproductive form and spawning frequency in most species are largely controlled by temperature, and this is the case as well for *O. mossambicus*. In regions with a year-round stable temperature above 24°C, there are steady spawnings, with thresholds reported between 18°C and 25°C in some species (Webb & Maughan, 2007). Fecundity reflects female body size; a large female produces more and larger broods, while stunted, early maturing females produce fewer broods (James & Bruton, 1992).

Geographical distribution: original and present

The natural distribution of *O. mossambicus* ranges across the east flowing rivers of Southern Africa, from the lower Zambezi River system to the Bushmans River, in the Eastern Cape Province of South Africa. Populations introduced for recreational fishing occur further west in the Eastern and Western Cape provinces of South Africa and also in Namibia (Figure 1; Nico & Neilson, 2017; Pullin *et al*.,1997; Skelton, 2001; Zengeya *et al.,* 2015). This is one of six *Oreochromis* species occuring naturally in Southern Africa (Skelton, 2001).

Oreochromis mossambicus is introduced worldwide for aquaculture, as an ornamental fish and to some extent as a biological control agent to control insects and aquatic weeds (Ranathunge et al., 2021; Sunarto *et al.,* 2022). Today, it occurs on five continents, with wild populations established in many countries (De Silva *et al.,* 2004; Russell *et al*., 2012). Currently, the Global Biodiversity Information Facility (https://www.gbif.org) holds 6,542 recorded occurrences of *O. mossambicus* in more than 50 countries. As of June 2020, these records (with coordinates) were based mainly on preserved specimens (3,861) and human observations (2,406), while the remaining records were based on living specimens (4), machine observation (1), material samples (29), other observations (5) and other unknown categories (236). *Oreochromis mossambicus* has the highest number of records in Mozambique (1,940), followed by South Africa with 1,394 recorded occurrences (GBIF, 2020). Other countries of occurrence include Australia, Belgium, Brazil, Botswana, China, Congo, Democratic Republic of Congo, Costa Rica, Cuba, Côte d'Ivoire, Dominican Republic, Egypt, Ethiopia, Eswatini, French Polynesia, Ghana, Germany, Guatemala, Guam, Guadeloupe, Haiti, Hong Kong, India, Indonesia, Israel, Japan, Kenya, Madagascar, Malawi, Mozambique, Myanmar, Malaysia, Mexico, Namibia, Philippines, Papua New Guinea, Puerto Rico, Seychelles, Singapore, Sri Lanka, Solomon Island, South Africa, Taiwan, Tanzania, Thailand, Timor Leste, United States, Vietnam, Zimbabwe and Zambia (GBIF, 2020).

Table 1: Comparisons of *O. mossambicus* and *O. niloticus* characters

S/n	Characters	*O. mossambicus*	*O. niloticus*
1	Dorsal spines	15 - 18	15 - 18
2	Dorsal soft rays	10-13	11 - 13
3	Anal spines	3	3
4	Anal soft rays	7 - 12	9 - 11
5	Vertebrae	28 - 31	30 - 32
6	Lower gill-rakers	14-20	27 - 33
7	Adult males	Enlarged jaws, Pharyngeal teeth very fine, long blade, simple genital papilla or with a shallow distal notch, caudal fin not densely scaled. Breeding male black with white lower parts of the head and red margins to dorsal and caudal fins	Jaws not greatly enlarged, Pharyngeal with firm teeth, genital papilla short, conical and not tassellated, striped caudal fins, dark margin of the dorsal fin Breeding males with red flush to head, lower body, dorsal fin and caudal fins
8	Females	Silvery with 2-5 mid-lateral blotches	Brownish, silvery/white beneath with around 10 thin vertical bars
9	Caudal fin colouration	Orange or red tinge. No stripes on caudal or tail fins.	Regular vertical stripes throughout the depth of the caudal fin, tail fin marked with numerous thin vertical stripes
10	Head and body form	Large head and deep-bodied	Small head and large-bodied

Source: Froese & Pauly, 2020

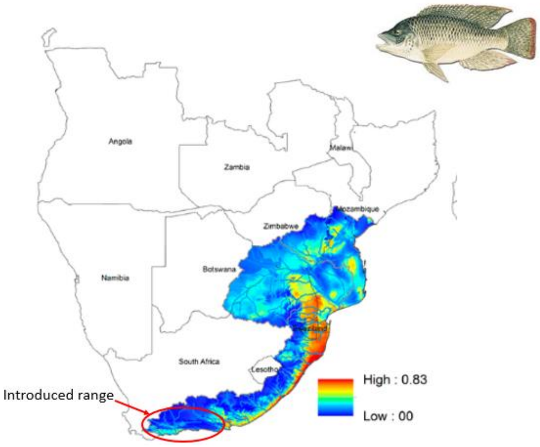

Figure 1 Potential distribution of *O. mossambicus* in Southern Africa (Zengeya *et al.*, 2015)

Importance of *Oreochromis Mossambicus* as a resource

Oreochromis mossambicus, has several qualities that are important for aquaculture. These include high fecundity, high salinity tolerance, the ability to adapt to extreme environmental conditions, the ability to utilise plant and animal nutrients for growth, high meat quality, with good market acceptance and potential to develop value-added fish products (Mashaphu *et al.*, 2024).

Salinity tolerance

Oreochromis mossambicus is one of the most euryhaline species, being able to adapt from freshwater to seawater and hypersaline environments, with a reported salinity tolerance range of 10% to 180% of seawater (Gardell *et al*., 2014; Jaspe & Caipang, 2011; Lorenzi & Schlenk, 2014; Sardella *et al.*, 2008). This species reproduces better in a brackish environment (~15.2%) compared to freshwater, and is able to reproduce in more saline environments such as seawater (El-Sayed, 2006; Ford *et al*., 2019; Uchida *et al.*, 2000). This trait is valued and should be preserved in aquaculture and stocks as it is used to produce hybrids with fast growth and high salinity tolerance. These populations also serve as a good model for studies of teleost osmoregulation (Copatti & Baldisserotto, 2021; King & Brian, 2017; Wong *et al.*, 2016).

Cold tolerance

Oreochromis mossambicus is the only *Oreochromis* species that exhibits high tolerance to salinity change and high thermal tolerance in both fresh and seawater (Ampaw, 2022; Al Amoudi *et al.*, 1996; Sardella *et al.*, 2008; King & Brian, 2017). Their survival can even be improved at lower temperatures in water with higher salinity than in freshwater. They can survive at temperatures between 8º and 42º C, with an optimal temperature range of 28 to 30°C for growth and reproduction (El-Sayed *et al.*, 2023; Sardella *et al.*, 2008; Shipton & Britz, 2007). However, they can breed in waters above 20º C throughout the year. In South Africa, large adults have been recorded to survive temperatures as low as 9°C to 11°C in brackish waters (, Harrison & Whitfield, 2006; Sun *et al*., 1992; Wu *et al*., 1998; Whitfield, 2005).

Drought tolerance

Unlike most species, *O. mossambicus* can continue to reproduce in warmer months under these conditions. They show early maturation at small sizes (9–10 cm) during these stressful conditions (Hutchison *et al*., 2011). They also survive within a wide pH range from acidic (pH 3.7) to alkaline (pH 10.0) environments (Popma & Masser, 1999), with fatality limits being pH 3.4 for acidic conditions and pH 11 for alkaline conditions (Webb & Maughan, 2007). This species can withstand up to 14 mg N/l levels of nitrogen concentration and ammonia stress of 3 mg N/l without any significant effect on growth. It can also tolerate oxygen levels as low as 20% saturation with 0.1 ppm (0.1 mg/L) dissolved oxygen (Russell *et al.*, 2012; Webb & Maughan, 2007). Being a facultative air-breather, it survives a low level of oxygen by gulping air thereby supplementing oxygen requirements (Senguttuvan & Sivakumar, 2002). They survive low water level during drought periods by their ability to aestivate in wet river sands, with several eyewitness accounts, reporting their emergence from dry sand, or fish being found alive at depths of 0.3 to 3.0 m below the surface (Donnelley, 1978; Minshull, 2008; van der Waal, 1997). These traits are essential for their survival in extreme conditions, and can be utilized in aquaculture production.

Recreational activities

Recreational fishers provide reasonable economic advantage by their expenditure on many things including fishing tackle, boats, licenses, travel, and accommodation (Pita *et al.*,2018). Though, these values could be influenced by pollution impact leading to fish death (Burnett *et al.*, 2024).

South Africa has broader recreational fishing sector estimated to be ZAR 32.6 billion (~USD 2.2 billion) per annum (Potts *et al.,* 2022). The coastline is vast with varying recreational fishing activities that have not been concisely quantified around the coast. Nevertheless, the economic contributions of the recreational sector is known to be significant and relates to other associated downstream industries aside direct fishing activity. The main recreational sectors include: Recreational diving for west coast and natal rock lobsterRecreational hoop nets for west coast rock lobster (257 tonnes allocated for 2009/10, Recreational diving – spearfishing,), Ski-boat (small harbours and beach launches) – linefish species including tuna, and Rod and line (beaches and estuaries) (Stats SA, 2009).

In South Africa *O. mossambicus* are further used not only for recreational fishing, but as a trophy species (https://www.farmersweekly.co.za). For instance, Red coloured strains of *O. mossambicus* are sought as ornamental fish in the aquarium industry.

Conservation Status and Threats

Oreochromis mossambicus is classified as "Vulnerable" on the IUCN Red List because of hybridization with *O. niloticus* and also due to hybridization with five closely related indigenous species (Bills, 2019). Introduced Nile tilapia *Oreochromis niloticus* (Linnaeus 1758) are considered a major threat to endemic freshwater fishes of South Africa (Blackburn *et al.,* 2011; Ellender & Weyl, 2014; Stauffer *et al*., 2022; Tweddle *et al*., 2009). The importation of vertebrate species in South Africa has been happening for a long time (Picker & Griffiths, 2017; van Rensburg *et al*., 2011). Freshwater fishes were brought into the country from the 1700s, with the authorities in that period permitting these introductions without much concern over the ecological implications to native biodiversity (Ellender & Weyl, 2014). *Oreochromis niloticus* was introduced to South Africa in 1955 and has been evaluated as one of several invasive freshwater fishes that have had a massive impact on South Africa aquatic communities (Marr *et al*., 2017). Optimal water temperatures of 28°C to 30°C make *O. niloticus* suitable for aquaculture in Limpopo, Mpumalanga, North West, northern coastal areas of KZN, northern Gauteng and Eastern Cape province of South Africa (DAFF, 2018). The majority of registered Tilapia farms for both *O. mossambicus* and *O. niloticus* production are situated in these provinces (DAFF, 2018). Hence, the escape of *Oreochromis* from farms into the wild could be detrimental throughout the native distribution of *O. mossambicus.*

The Invasive Potential of *Oreochromis niloticus*

Biological Description of Nile Tilapia (Oreochromis niloticus)

Oreochromis niloticus appears to be one of the most commonly farmed and studied species, and that justifies their remarkable contributions to the world production of *Oreochromis*. *Oreochromis niloticus* is an ecological microphage, known to feed selectively on phytoplankton and algae (Getabu, 1994; ; Zengeya *et al*., 2011; Zengeya & Marshall, 2007). It can adapt to freshwater and brackish water, at optimal temperatures between 28°C to 42°C, (Teichert-Coddington *et al.*, 1997). *Oreochromis niloticus* can attain approximately 60 cm (standard length), 4.3kg in weight and longevity of up to 10 years (GISD, 2020). This species is characterised by its fast growth rate, early sexual maturity (5 to 6 months), high degree of parental care, ability to spawn multiple broods in a season and high fecundity associated with its large body size (Handago *et al*., 2024; Mbewea *et al*., 2023; Ojuok *et al*., 2007). Large males are often aggressive competitors that out-compete other species for spawning and breeding grounds if these are limited (Lowe-McConnell, 2000). These attributes inherently predisposed *O. niloticus* as an invasive species, after escape from farms, adversely affecting native fish species by competing for food and space (Shuai *et al.*, 2023; ; Stauffer *et al*., 2022; Zengeya *et al*., 2011, 2013).

Distribution of Oreochromis niloticus (native and potential invasive range)

Oreochromis niloticus is native to north, west and central Africa; area extending along the Nile from below Albert Nile to the delta; Jebel Marra; Lake Chad basin and the rivers Niger, Benue, Volta, Gambia and Senegal (Figure 2). This has been introduced worldwide with reports from up to 104 countries and islands (http://www.fishbase.org/). There are also records of *O. niloticus* distribution from more than 50 countries with 6,697 records in the Global Biodiversity Information Facility (https://www.gbif.org).

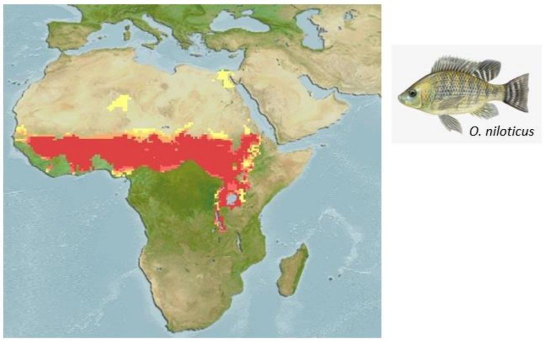

Figure 2 Native range of *O. niloticus* indicated with red colour (http://www.fishbase.org)

Red indicates native ranges while yellow colour is introduced populations of O. niloticus

Invasive potential in Southern Africa

Oreochromis niloticus was first introduced into South Africa in the 1950s with introductions in the Cape Flats area of Cape Town, Western Cape, and KwaZulu-Natal Province (Froese and Pauly, 2020). Additional introductions were made in the 1980s, for aquaculture, in KwaZulu-Natal and the Zambezi river system (Bills, 2019; Hallerman & Hilsdorf, 2014 ; Schwank, 1995; Skelton, 2001). In the 1990s and 2000s, this species was found in the Incomati river, upper Limpopo and lower Limpopo River, likely due to escape during the great flood of 2000. It has been widely distributed to almost all eastern rivers in South Africa and Mozambique where it is established and introgressing (van der Waal & Bills, 2000; Weyl, 2008; Arthur *et al*., 2010) (Figure 3). They have been widely introduced across Southern Africa for aquaculture purposes with feral populations now established in many river catchments within the sub-region (Skelton, 2001; Stauffer *et al*., 2022; Weyl, 2008; Zengeya & Marshall, 2007).

These feral populations can cause the river systems to face reduced native fish abundance and extinction of indigenous congenerics by competitive exclusion and hybridization (Arthur *et al*., 2010 ; van der Waal & Bills, 2000; Zengeya *et al*., 2013, 2015). Hybridization readily occurs if they escape from farms (Weyl, 2008; Zengeya *et al.*, 2015). Previous genetic studies have found evidence of extensive hybridization between *O. mossambicus* and *O. niloticus* in the Limpopo River system (D'Amato *et al.*, 2007; Moralee *et al*., 2000). Populations of *O. mossambicus* along the South-East coast from Durban to Grahamstown and introduced populations along the southern Coast, near Port Elizabeth are expected to have little or no introgression from *O. niloticus* (Figure 1.3).

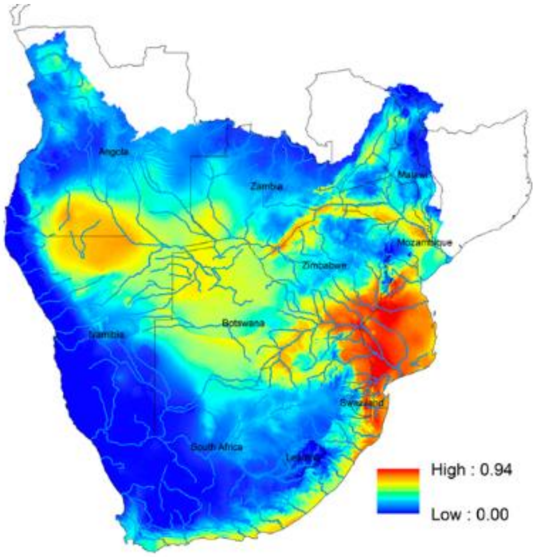

Figure 3 *O. niloticus* predicted invasive range in the river system of Southern Africa (Zengeya *et al.* 2015*)*

Assessing Invasive Threats (Hybridization) in South Africa by Molecular Approaches

South Africa is a signatory of the Convention on Biological Diversity and its Strategic Plan for Biodiversity 2011–2020 (UNEP, 2011), with an obligation to implement the Aichi Target Nine: to identify and manage pathways to control and prevent the establishment of invasive alien species (UNEP, 2011). In agreeing to this international obligation, the South African government promulgated the National Environmental Management: Biodiversity Act (Republic of South Africa, 2014) with its associated alien invasive species lists and regulations (the Republic of South Africa 2014; Wilson *et al.,* 2017). There has been an increasing demand to prevent further fish invasion but there are limited available resources for managing established invasions in freshwater ecosystems (Stauffer *et al*., 2022; Woodford *et al*., 2017). A risk assessment framework is usually used to assess the risk of importing a species into a country compared to the economic benefits. That is, whether the economic gain from importing such species outweighs its potential environmental impacts. National legislation, however, is intended to prevent the secondary spread of invasive alien fishes into wild areas (Ellender *et al*., 2014).

Several nonmolecular publications have assessed the introduction, invasiveness, and impacts of alien fishes, including *O. niloticus*, in South Africa (Blackburn *et al.*, 2011; Ellender *et al*., 2014; Ellender & Weyl, 2014; van Rensburg *et al.,* 2011; Stauffer *et al*., 2022; Zengeya *et al.,* 2017). The most substantial evidence for the expansion of *O. niloticus* hybridization with native *O. mossambicus* is from the Limpopo River system (van der Bank & Deacon, 2007; van der Waal & Bills, 2000; Weyl 2008). *Oreochromis niloticus* spread and extinction of non-hybrid *O. mossambicus* in Lower Limpopo was reported to be high (Tweddle & Wise, 2007; Weyl, 2008), although it was later shown not to be lower in the intermittently connected Changane tributary of the lower Limpopo (Firmat *et al*., 2013). The expansion of *O. niloticus* and the disappearance of *O. mossambicus* were also reported for some parts of the Upper Limpopo (Moralee *et al*., 2000; van der Bank & Deacon, 2007; van der Waal & Bills, 2000).

Molecular approaches based on Allozymes, mitochondria control region (mtDNA-CR), SSR and AFLP genotyping, have been used to detect and measure *O. niloticus* introgressive hybridization into *O. mossambicus* in Southern Africa (D'Amato *et al*., 2007; Deines *et al*., 2014; Firmat *et al*., 2013; Moralee *et al.*, 2000; Mashaphu *et al.,* 2024). The first detection of *O. niloticus* was in 1996 at the Upper Limpopo of South Africa (van der Bank & Deacon, 2007). Allozymes analyses following later collections in 1998 showed the existence of interspecific hybrids between *O. niloticus* and *O. mossambicus* (Moralee *et al.,* 2000). In early 2000, hybrids were discovered in dry pools beside the Limpopo River, alongside pure strains of each species (Moralee *et al*., 2000). Hybrids were confirmed in the upper Limpopo by D'Amato *et al*., 2007 using both mtDNA-CR and microsatellite genotyping. D'Amato *et al*., 2007 reported that specimens initially identified morphologically as *O. niloticus* or *O. mossambicus* were later found to be hybrids using microsatellite markers. D'Amato *et al*., 2007 sampled populations in areas of known introduction in the upper Limpopo with some samples from the Olifants River. The *O. niloticus* haplotypes recovered in the Upper Limpopo by D'Amato *et al*., 2007 differed from those in the lower Limpopo. These distinct O. *niloticus* haplotypes, are likely from separate introduction events in the upper (Tweddle & Wise, 2007) and lower Limpopo (Simbine & Hilsdorf, 2014). Firmat *et al*. (2013) provided more genetic insight for lower Limpopo *Oreochromis* populations using mtDNA and 423 AFLP loci. That study showed a low frequency of *O. niloticus* hybrids in the lower Limpopo system. They identified *O. mossambicus* with no indication of hybridization, particularly in the Changane tributary, which was in contrast to published approximations of the alarming rate of invasion and hybridization in this system (Stauffer *et al*., 2022; Tweddle & Wise, 2007; Weyl, 2008). The Firmat *et al*. (2013) study identified a promising refugial area for *O. mossambicus* in the upper Changane drainage and nearby wetlands.

Nevertheless, Most reports of hybridisation and introgression are from the Limpopo river system in northern South Africa with few data from other regions.

Secondly, previous works do not reflect whole genome diversity with low comparability among nuclear DNA markers.

Another issue confronting studies of species delimitation and hybridization among Oreochromis species is that there is no baseline reference for mtDNA sequences from indigenous populations (Mojekwu *et al.,* 2021; Muhala *et al*., 2024). Most available sequence data for Oreochromis are from hatchery stocks or introduced populations occurring outside the natural range of this genus. Species identification of these fish is based on phenotypic characters. However, farmed fish are hybridized for desirable aquaculture traits and subsequently, these populations carry genes from several Oreochromis species (Mojekwu *et al.,* 2021). The lack of a baseline from indigenous populations has confounded previous mtDNA based attempts to distinguish *O. niloticus* from *O. mossambicus* (Aquilino *et al*., 2011; Chen *et al*., 2015; Maranan *et al*., 2016; Pereira *et al.*, 2011; Muhala *et al*., 2024).

Recent study based on microsatellite data determined the genetic patterns of *O. mossambicus* populations in three regions of South Africa (Limpopo, Mpumalanga, and KwaZulu-Natal). They identified low genetic diversity within sample localities but significant differentiation among wild *O. mossambicus* populations in South Africa (Mashaphu *et al.,* 2024).

CONCLUSION AND RECOMMENDATIONS

The availability of *O. niloticus* and other Pseudocrenilabrine Cichlid genomes (Brawand *et al.,* 2014) opens new opportunities such as development of a gene-capture based exome SNP panel, based on *O. niloticus* and other Pseudocrenilabrine Cichlid reference genomes. Recent studies have identified species diagnostic SNPs for *O. niloticus* which have been used for detecting its introgression with other *Oreochromis* species (Ciezarek *et al*., 2022; Shechonge *et al.,* 2019). However, these studies are limited to East Africa river systems, does not capture *O. mossambicus* species and invasive effects of *O. niloticus* in South Africa river catchments.

We therefore recommend this tool as a reliable and replicable genome resource for a diversity of research questions, including measurement of invasive introgression of *O. niloticus* into indigenous *Oreochromis* species in South Africa. This will inform policy makers and suggest options for protecting natural genetic resources in vulnerable fishes like *O. mossambicus*.

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Authors Contribution:

Author TM conceived the research review, design, wrote the draft manuscript and made final corrections. TH participated in the design, technical assistance, profread and supervised the work. All authors finalized and approved the final version.

Ethics Committee Approval

N/A.

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