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Conserving Freshwater Biodiversity in an African Subtropical Wetland: South Africa's Lower Phongolo River and Floodplain

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Abstract

Freshwater biodiversity is under constant threat from a range of anthropogenic stressors. Using South Africa's Phongolo River and floodplain (PRF) as a study case, the aim of this chapter is to provide an overview of the conservation and management of freshwater biodiversity in a highly diverse subtropical ecosystem. The PRF is the largest floodplain system in South Africa which is severely threatened by irregularly controlled flood releases from a large upstream dam, prolonged drought, deteriorating water quality, organic pollutants and the increasing dependence of the local communities. Based on a decade of survey of the PRF conducted from 2010 to 2020, this chapter highlights the current diversity of aquatic organisms (invertebrates, fishes, frogs and their parasitic fauna), followed by an overview of their biological and physical stressors. The current challenges in the management of the aquatic biodiversity of this region and a way forward to conservation strategies are also addressed in this chapter.

Keywords: conservation, aquatic organisms, biological stressors, physical stressors, management

1. Introduction

The Phongolo River (PR) originates in the South African Mpumalanga Province from where it flows first eastwards, before turning north through the Ubombo mountain ranges in South Africa's northern KwaZulu-Natal (KZN) [1]. The lower Phongolo River and associated floodplain (PRF) starts from where the river exits a gorge in the Ubombo mountains, which is known as the Pongolapoort, for approximately 80 km downstream to the confluence of the PR and Usuthu River (UR) at the South Africa/Mozambique border [2] (**Figure 1**). The PRF is about 10,000 increasing to 13,000 ha in full inundation and is characterised by its permanent and

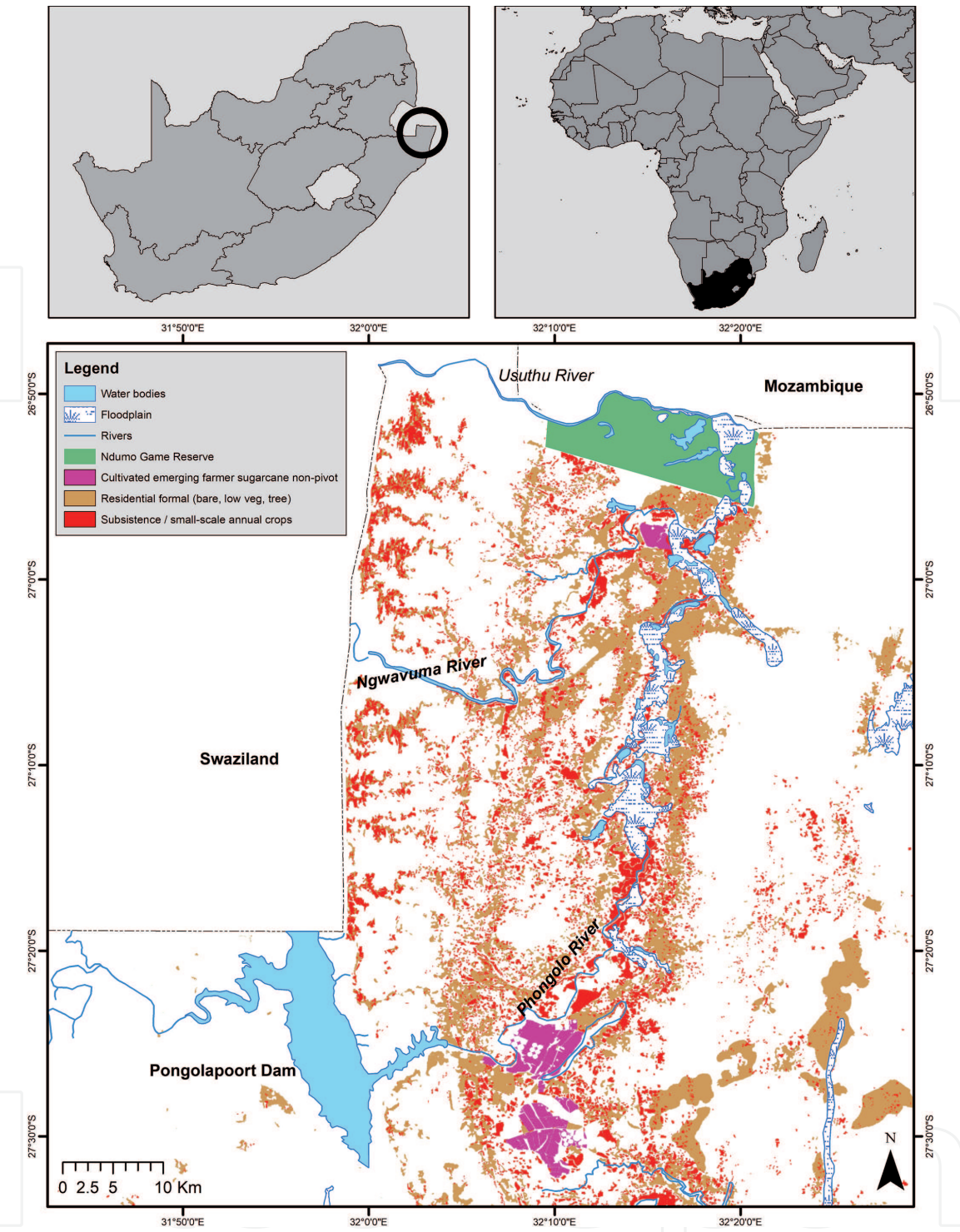


Figure 1.
Map of the Pongolapoort dam, the lower Phongolo River and its associated floodplain in North-Eastern South Africa.

temporary floodplain depressions (from here on further referred to as pans) that have either permanent, intermitted or no connectivity with the river. Natural flow regime determines the heterogeneity of the floodplain habitats. Pans that are river-fed function as spawning and breeding sites and as foraging areas for migratory species. The temporary pans are also known to harbour endemic species, therefore presenting a unique diversity. The connection between the river and floodplain also enables the exchange of organic matter, nutrients and aquatic vegetation. Thus, the flood pulse plays a key role in the health of the river ecosystem and productivity of the wetlands. The PRF constitutes one of the largest and the most biodiverse floodplain systems in South Africa.

The previously mentioned gorge (Pongolapoort) in the Ubombo mountains provided the perfect structural position for the building of a dam and therefore it was no surprise that the building of a dam in the PR (**Figure 2A, B**), with the main aim to supply irrigation water for sugarcane and cotton crops, was commissioned in the 1960s. The Pongolapoort Dam (also referred to as the Jozini Dam) was completed in 1973, and although research on its possible effect on the PRF started before the completion of the dam, there have been continuous concerns over the past almost 50 years about the real impact thereof on the PRF. In order to mitigate the dam's impacts on the ecological integrity of and ecosystem services provided by the floodplain, a controlled flood release regime was developed to simulate natural flooding [3]; however, this was never fully implemented [1, 4]. The fragile ecosystem of the PRF has also, over the past 40 years, been further impacted by extreme climatic events such as a cyclone (1984) and severe droughts (1981–1983 and 2016–2020) [1].

The only officially protected section of the PRF lays within the 102 km² Ndumo Game Reserve (NGR) that was proclaimed in 1924 (**Figure 1**). In 1997, the game reserve was also declared a Ramsar site under the Wetlands of International Importance convention [2]. In addition to the PR and UR sections that fall inside the reserve, the NGR also provides protection to five distinct wetland types ranging between fresh, brackish and saline and permanent and intermittent rivers, lakes, pools and riparian/gallery forests. One of the largest water bodies and also the only naturally saline lake (approximately 5000 $\mu\text{S}\cdot\text{cm}^{-1}$) within NGR is Lake Nyamithi (183.4 ha) (**Figure 2C**). Nyamithi receives water largely from the PR through the annually controlled flood release from the Pongolapoort Dam, through rainfall during the wet season (summer) from its own small catchment and natural floods from the UR. Although the reserve is almost 100 years old, very little has been accomplished in terms of research since the reserve's establishment, and it is unknown whether the water that NGR receives is of a quality and quantity to support and protect this biodiversity hotspot.

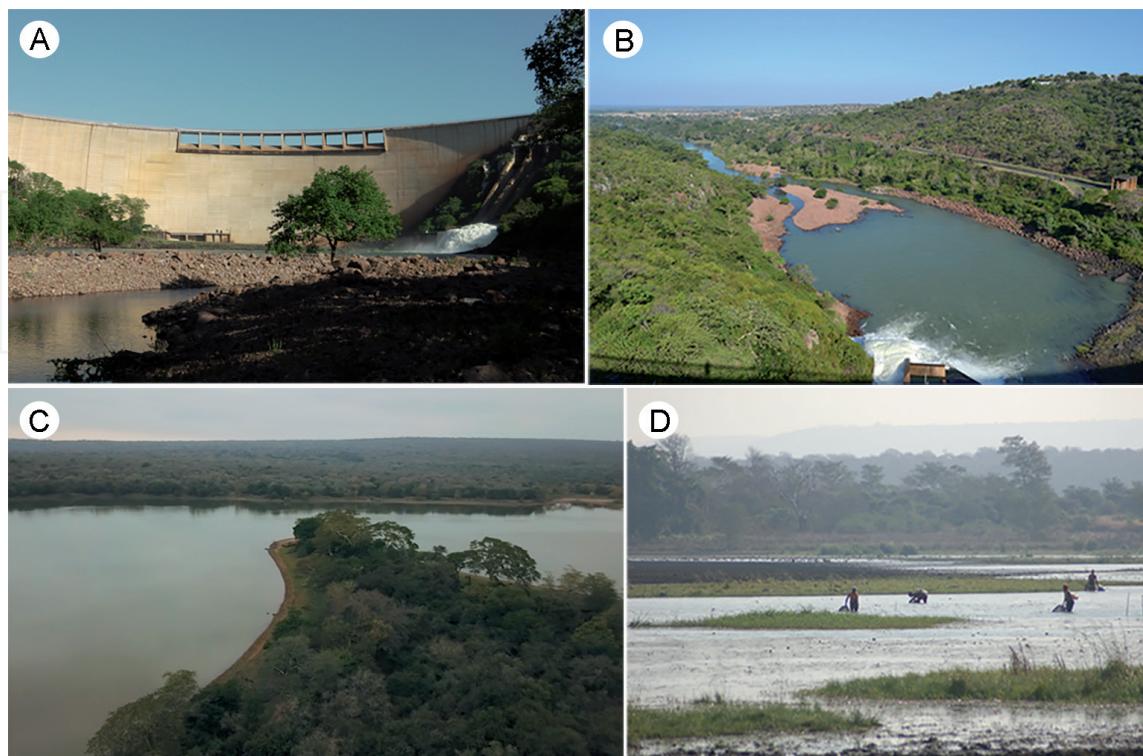


Figure 2.
(A) View of the dam wall from the Phongolo River; (B) downstream view from the dam wall; (C) Lake Nyamithi and (D) example of activity of people directly dependent on the floodplains for cultural and provisioning ecosystem services.



Figure 3. View of the Phongolo River flowing North with Ndumo Game Reserve (NGR): protected site on the left (western) side, and invaded areas used for agriculture on the right (eastern) side.

The proximity to water has always been an important factor that governs the distribution of rural communities. The human population that is directly or indirectly dependent on the PRF has grown over the past 40 years from 30,000 to a projected 400,000 in 2020 [5, 6]. The majority of the people dwelling the floodplain live in very poor conditions, being directly dependent on the floodplain. The water is used for both humans and livestock existence as well as for other goods from the floodplain such as fish (**Figure 2D**), fruits, reeds, thatch grass and firewood. The indirect dependence on the PRF is shown by the increase of agricultural lands that were once covered by natural vegetation (**Figure 3**). Practices of subsistence agriculture in the PRF introduced fertilisers and chemicals into the area, decreasing water quality and aquatic biodiversity. This together with alterations in the natural flow regime that was brought about by the construction of the dam, including irregular flood releases, prolonged droughts, deteriorating water quality, and organic pollutants, all severely threaten the functioning and biodiversity of the PRF.

Therefore, the aim of this chapter is to provide information on the current status of the freshwater diversity of the PRF comprising invertebrates, fishes, frogs and their parasitic fauna as well as their biological and physical stressors. Furthermore, the challenges and a way forward in managing the aquatic biodiversity of the PRF and proposed research to inform management and conservation strategies will be addressed herein. This chapter is based on the results of a decade (2010–2020) of research on the PRF led by the North-West University's Water Research Group (WRG).

2. Biodiversity of aquatic organisms from the lower Phongolo River and associated floodplains

2.1 Diversity of aquatic invertebrates

Aquatic invertebrates are invertebrates that require aquatic habitats to complete either one, several or all of their life stages in the aquatic environment [7]. Many terrestrial insects have a larval aquatic life stage including dragonflies and damselflies (Odonata), mosquitoes and flies (Diptera) and mayflies (Ephemeroptera) [8–10] and are therefore considered aquatic invertebrates in their larval phase. Truly aquatic or 'permanent' aquatic invertebrates complete all of their life stages in the aquatic environment and include zooplankton such as water fleas (Cladocera), micro-crustaceans (Copepoda) and fairy shrimp (Anostraca) as well as larger macroinvertebrates such as freshwater snails (Mollusca) and crabs (Potamonautidae).

[10–12]. Aquatic invertebrates are present in most freshwater ecosystems and respond rapidly to a broad range of physical and chemical environmental conditions such as changes in habitat condition or water chemistry [7, 13]. They are also quite immobile, particularly those that complete all their life cycles in water, and are constantly in contact with both bottom sediments and the water column [14]. Aquatic invertebrates are also in the unique position to act as the transitional link between lower level producers (including diatoms and algae) that they feed on and higher level consumers (including larger invertebrates, fish and birds) that feed on them [15–17]. For these reasons, aquatic invertebrates are ideal indicators of change in the aquatic environment and ecosystem health, particularly in lotic habitats, and have been used as such in various ecological assessments (e.g. [13, 18, 19]).

Aquatic biodiversity research in the PRF has been undertaken since the late 1960s, but it was not until 2012 that aquatic invertebrates were also included in ecological assessments of the region (see [2, 20, 21]). As part of these assessments, aquatic invertebrates were collected from the PR as well as many floodplain and temporary pans, both within and outside NGR. Approximately 131 taxa of aquatic invertebrates from 70 families have been identified from the river, while 117 taxa from 49 families and 109 taxa from 54 families have been collected from the floodplain and temporary pans, respectively (e.g. **Figure 4**). Many of the aquatic invertebrates collected from the river and floodplain pans both within and outside NGR include sensitive biota [7] such as riffle beetles (Elmidae), brush-legged mayflies (Oligoneuriidae), caseless caddisflies (Philopotamidae) and spiny crawlers (Teloganodidae).

Lake Nyamithi forms an important part of the assessment of the aquatic invertebrates of the PRF. This lake is quite unique as it is a large naturally saline lake and the only permanent wetland-type ecosystem located within the NGR [3, 22]. Due to its permanence, this habitat acts as a refuge to many of the aquatic and (semi-)

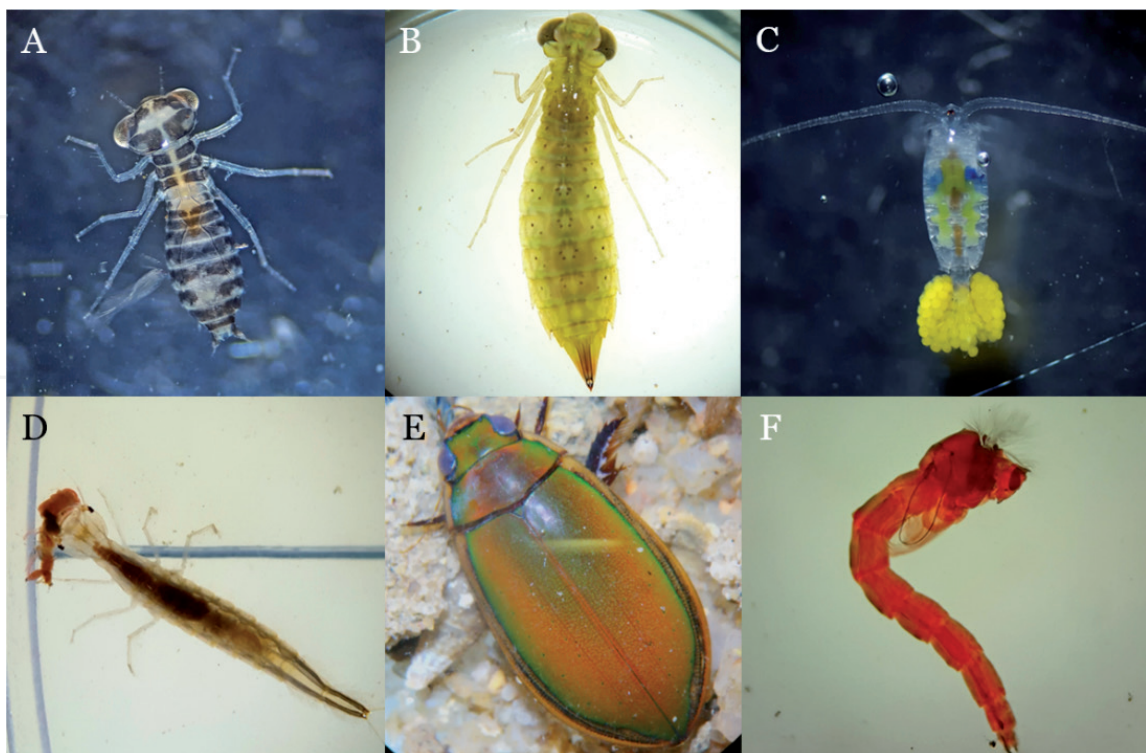


Figure 4.
Examples of aquatic invertebrates found in the lower Phongolo ecosystem. (A) Young dragonfly nymph (Aeshnidae); (B) mature dragonfly nymph (Aeshnidae); (C) female micro-crustacean with eggs (Cyclopoida); (D) larval predaceous diving beetle (Dytiscidae) feeding on a bloodworm (Chironomidae); (E) adult Dytiscidae beetle and (F) pupal stage of Chironomidae.

terrestrial biota of the region during the dry season when many of the pans dry out [2]. Even though it is naturally saline, the diversity and abundance of aquatic invertebrates found in this ecosystem (108 taxa from 47 families) is comparable to that found in the river and floodplain and temporary pans. Overall, the diversity of aquatic invertebrates in the PRF is greater than that of comparable lowland river (see [23, 24]), pan (see [25]) and saline lake (see [26]) ecosystems. These findings further demonstrate that the PRF is a biodiversity hotspot for aquatic invertebrates and of great ecological importance.

Worryingly, aquatic invertebrate assessments of this ecosystem have also indicated the possibility that the anthropogenic disturbances taking place outside NGR has a negative impact on the ecological integrity of the aquatic habitats of the PRF. Although biodiversity has generally been found to be greater in the river and pans located within NGR compared to outside the reserve, the river section that flows through the reserve is clearly not well protected given the types and abundances of certain aquatic invertebrates found. Several pollutant-tolerant taxa [7] such as the sharp-spined bladder snail, *Physa acuta*, and aquatic earthworms, Lumbriculidae, were found to be some of the most abundant taxa in the river inside NGR. Research found these types of taxa, particularly snails of the genus *Physa*, to flourish in systems that are nutrient enriched [27] suggesting that this may be the case for the PR. Additional stressors also include the invasive quilted melania snail, *Tarebia granifera*, which is distributed throughout the PR and is discussed further in Section 3.1.

Many of the pans outside the reserve are also threatened by anthropogenic stressors since they are utilised by local communities as a source of domestic and agricultural water and for subsistence fishing [2, 28, 29] all of which affects the integrity of pans. Ndumo Game Reserve therefore acts as a refuge for aquatic invertebrates of the PRF. This can be observed by the much higher number of invertebrate families that are present exclusively within NGR compared to outside (19 inside vs. 4 outside). Additionally, those invertebrate families present in high abundance in pans outside the reserve, namely rat-tailed maggots (Syrphidae), biting midges (Ceratopogonidae) and crane flies (Tipulidae) are known to be more tolerant of eutrophication and other forms of pollution [7] further demonstrating how these wetlands are being negatively affected.

2.2 Diversity of freshwater fishes

Fish have been regarded as one of the world's most important natural resources as they provide animal protein to billions of people annually, especially in developing countries [30]. Furthermore, fish also play an important role in freshwater ecosystem ecology where they can control prey such as zooplankton or be prey themselves for other reptiles, fish, mammals or birds. Fish communities within the PR and its associated floodplain wetlands are one of the most diverse found in South Africa [31] (see **Figure 5**). There have been 46 species recorded in this region from 12 different families (**Table 1**). Of these 46 species, *Oreochromis mossambicus* (Mozambique tilapia) (**Figure 5D**) is listed on the IUCN Redlist as a vulnerable species [40]. The South African Threatened or Protected Species List (TOPS) from 2013 [41] also included the *O. mossambicus* as a protected species in South Africa placing restrictions on its utilisation. This listing of *O. mossambicus* is due to the threat of hybridisation with the alien cichlid *Oreochromis niloticus* (Nile tilapia) [42] that could lead to a loss in genetic integrity. To date *O. niloticus* has not been recorded from the PRF thus making the *O. mossambicus* population from this region potentially one of only a few remaining genetically pure *O. mossambicus* populations left, although this needs confirmation through genetic studies. One of the unique fish species found in the PRF

is the annual killifish, *Notobranchius orthonotus* (spotted killifish). This fish species is found in the temporary pans, specifically within NGR, as it is able to withstand drying through dormant eggs that are deposited in the sediment [43].

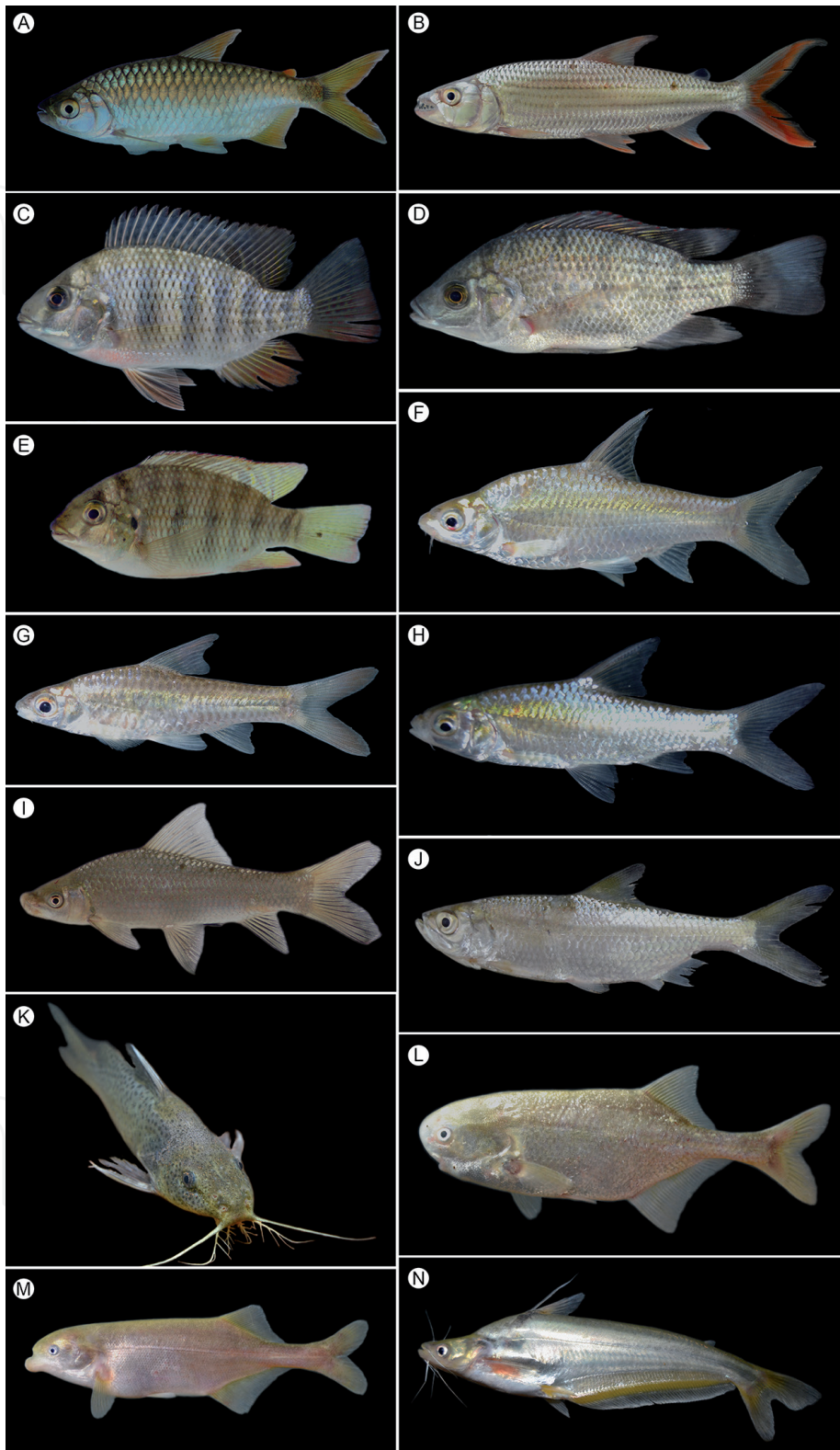


Figure 5. Selection of fishes collected from the lower Phongolo River and floodplain: (A) *Brycinus imberi* (max. length 19.8 cm); (B) *Hydrocynus vittatus* (max. Length 105 cm); (C) *Coptodon rendalli* (max. length 45 cm); (D) *Oreochromis mossambicus* (max. length 39 cm); (E) *Tilapia sparrmanii* (max. length 23.5 cm); (F) *Enteromius afrohamiltoni* (max. length 17.5 cm); (G) *Enteromius annectens* (max. length 7.5 cm); (H) *Enteromius paludinosus* (max. length 15 cm); (I) *Labeo rosae* (max. length 40 cm); (J) *Megalops cyprinoides* (common length 30–45 cm); (K) *Synodontis zambezensis* (max. length 43 cm); (L) *Petrocephalus wesselsi* (max. length 11.4 cm); (M) *Marcusenius macrolepidotus* (max. length 32 cm); (N) *Schilbe intermedius* (max. length 50 cm). Data on maximum length extracted from [32].

Species	1974–1976	1983	1984	1993–1994	2012–2014	2016–2019
Alestidae						
<i>Brycinus imberi</i> (<i>B. lateralis</i>)	x	x	x	x	x	x
<i>Hydrocynus vittatus</i>	x	x	x	x	x	x
<i>Micralestes acutidens</i>	x	x	x	x	x	x
Anguillidae						
<i>Anguilla bengalensis labiata</i> (<i>A. nebulosa</i>)	x	x		x	x	x
<i>Anguilla bicolor bicolor</i>	x	x		x	x	
<i>Anguilla marmorata</i>	x	x		x	x	x
<i>Anguilla mossambica</i>	x		x	x	x	
Cichlidae						
<i>Coptodon rendalli</i> (<i>Tilapia rendalli</i>)	x	x	x	x	x	x
<i>Oreochromis mossambicus</i>	x	x	x	x	x	x
<i>Oreochromis placidus</i>					x	
<i>Pseudocrenilabrus philander</i>	x	x	x	x	x	x
<i>Tilapia sparrmanii</i>	x	x	x	x	x	x
Clariidae						
<i>Clarias gariepinus</i>	x	x	x	x	x	x
<i>Clarias ngamensis</i>	x	x	x	x		
Cyprinidae						
<i>Enteromius afrohamiltoni</i>	x	x	x	x	x	x
<i>Enteromius annectens</i>	x	x	x	x	x	x
<i>Enteromius pallidus</i>				x	x	
<i>Enteromius paludinosus</i>	x	x	x	x	x	x
<i>Enteromius radiatus</i>	x	x	x	x	x	x
<i>Enteromius toppini</i>	x	x	x	x	x	x
<i>Enteromius trimaculatus</i>	x	x	x	x	x	x
<i>Enteromius unitaeniatus</i>				x	x	
<i>Enteromius viviparus</i>	x	x	x	x		x
<i>Cyprinus carpio</i> *				x	x	x
<i>Labeo congoro</i>	x	x	x	x		x
<i>Labeo cylindricus</i>	x	x	x	x	x	x
<i>Labeo molybdinus</i>	x	x	x	x	x	
<i>Labeo rosae</i>	x	x	x	x	x	x
<i>Labeobarbus marequensis</i>	x	x				x
<i>Engraulicypris brevianalis</i>	x	x	x	x		x
<i>Opsaridium peringueyi</i> (<i>zambezensis</i>)				x		
Cyprinodontidae						
<i>Nothobranchius orthonotus</i>	x			x	x	x

Species	1974–1976	1983	1984	1993–1994	2012–2014	2016–2019
Gobiidae						
<i>Awaous aeneofuscus</i>				x	x	x
<i>Glossogobius callidus</i>				x	x	x
<i>Glossogobius giuris</i>	x	x	x	x	x	x
<i>Redigobius dewaali</i>	x	x	x	x	x	
Megalopidae						
<i>Megalops cyprinoides</i>				x	x	
Mochokidae						
<i>Chiloglanis paratus</i>	x		x	x	x	x
<i>Chiloglanis swierstrai</i>	x	x	x	x	x	x
<i>Synodontis zambezensis</i>	x	x	x	x	x	x
Mormyridae						
<i>Marcusenius macrolepidotus</i>	x	x	x	x	x	x
<i>Petrocephalus wesselsi</i> (<i>P. catostoma</i>)	x	x	x	x	x	x
Schilbeidae						
<i>Schilbe intermedius</i>	x	x	x	x	x	x
Sparidae						
<i>Acanthopagrus berda</i>						x
Syngnathidae						
<i>Microphis fluviatilis</i>				x		
Total no. of species	35	32	30	42	37	35
<i>*Invasive species.</i>						

Table 1.
Comparative species list of the fishes collected from the lower Phongolo River and floodplain (data from [2, 33–39], and the present study).

Research on the fish community have been extensive since the 1970s during the construction of the Pongolapoort Dam. Fish surveys were completed in various decades from the 1970s to the most recent surveys from 2016 to 2019 (**Table 1**). The species diversity found from the 1970s to the current surveys show variation, potentially due to fluctuating rainfall, the flooding regime and management of flood releases from Pongolapoort Dam. Of the 46 expected species, only the intensive surveys of [34–39] came close to sample all of the expected species (42 species collected), highlighting how the species diversity varies depending on many different physical and biological aspects. Interestingly, a total of 43 species (one more than the number recorded during the intensive surveys in the 1990s) were recorded by the WRG research teams between 2012 and 2019.

The occurrence and diversity of fish in the floodplains are driven by their dependence on receiving enough water during the summer rainfall season. Often the dominance of cichlids (*O. mossambicus* and *Coptodon rendalli* [redbreast tilapia]) occur during periods of lower flows while a more equal distribution of species and biomass are present during higher flow periods [3, 33]. The success of the cichlids during lower flow periods are attributed to its resilience to survive in systems with higher electrical conductivity. Furthermore, of the various important fish species in the system, these are the only species able to spawn without increased flow and flow

velocity triggering spawning events [3]. Smit et al. [2] indicated that two species [*Labeobarbus marequensis* (large-scale yellowfish) and *Engraulicypris brevianalis* (river sardine)] were potentially locally extinct, especially as the *Lb. marequensis* were not sampled during the 1990s and 2012–2014 surveys (**Table 1**). However, both these species were collected during the recent (2016–2019) surveys showing the resilience of the fishes and the system. There were eight species not collected during 2016–2019, which were collected during 2012–2014 (see **Table 1**), that might be the result of the extreme drought during the latter surveys. Furthermore, as no flood releases from the Pongolapoort Dam have been possible during this drought (since 2016), it is unlikely that these species are extinct from the PR, but should return from refugee areas in the Usuthu and Maputo Rivers once increased flows and flood releases occur.

The fish community in the PRF are important both ecological and economically. Firstly, many of the fish found in the PRF represent the southernmost distribution range of these species, making the system very important for biodiversity conservation. Secondly, the fish from the floodplain wetlands are extensively utilised (third most popular animal protein [44]) as a major source of protein by the local communities. Heeg and Breen [3] estimated that 400 tonnes of fish was harvested every year. The main fish species identified for consumption were *O. mossambicus* (**Figure 5D**), *C. rendalli* (**Figure 5C**), *Glossogobius giuris* (tank goby), and *Glossogobius callidus* (river goby). These species are also important fodder fish for *Hydrocynus vittatus* (tigerfish, **Figure 2B**), a popular recreational angling species in the PRF as well as in the Pongolapoort Dam [2, 45]. Thirdly, the fish communities are a crucial link in the food chain within the floodplain wetlands and especially in Lake Nyamithi where the abundances of fish serve as food sources to the unique and extremely diverse water bird community [2].

The 2012–2014 study [2] on the PRF investigated the Present Ecological State (PES), using the Fish Response Assessment Index. The results indicated that the fish community was in a seriously modified ecological state (Ecological Category of D/E); indicating an extensive or serious loss of natural habitat, biota and basic ecosystem functioning. This impacted state was especially evident downstream of the Pongolapoort Dam where high flow velocities are experienced during flood releases. The major threats to the fish communities were identified as physical impacts (unseasonal flood releases, poor water quality, water abstraction), over utilisation of fish from floodplains outside NGR, and biological threats (invasive species) [2].

2.3 Diversity of anurans

Amphibians are a diverse group that have adapted to a variety of habitats throughout the world. According to Frost [46], there are more than 8,203 known amphibian species globally, with more than 178 species in southern Africa. In recent decades, amphibians have suffered sudden, high mortality rates with many species becoming extinct [47, 48]. Although many factors contribute to this decline in amphibian populations, the most significant cause is habitat loss and fragmentation through anthropogenic disturbances. Paradoxically, the realisation that frog numbers are in decline sparked a renewed interest in amphibian biodiversity studies. The use of modern molecular and bioacoustic techniques and increased scientific surveys in remote areas, have resulted in new species being discovered and described frequently. Since 1985, the total number of globally recognised species has increased by over 60% [48–51].

In terms of amphibian diversity at a global scale, South Africa is currently ranked as the 27th country with the highest known species richness [52]. Within South Africa, the highest amphibian diversity can be found in the eastern part of the country and in particular, the province of KZN [53]. This province is an

essential refuge for several endangered and endemic species. However, environmental stress, due to anthropogenic activities, poses a severe threat to the survival of amphibians, with safe havens becoming more critical for the conservation of amphibian species richness in South Africa. Currently, there are 71 different anuran species (excluding subspecies) in KZN; these account for 40% of the total frog diversity that occur in southern Africa [50, 54]. Northern KZN or Zululand has two humid, subtropical regions, namely, the Maputaland and the KZN coastal area. These areas are transition zones between tropical and temperate climates, characterised by high anuran species richness (see **Figure 6**) [52, 53, 55, 56].



Figure 6.
Frogs of the lower Phongolo river and floodplain. (A) Arthroleptis stenodactylus; (B) Leptopelis mossambicus; (C) Breviceps adspersus; (D) B. mossambicus; (E) Poyntonophrynus fenoulheti; (F) Schismaderma carens; (G) Sclerophrys garmani; (H) Scl. gutturalis; (I) Scl. pusilla (J) Hemisus marmoratus; (K) Afrixalus aureus; (L) Afr. delicatus; (M) Afr. fornasini; (N) Hyperolius argus; (O) Hyp. marmoratus; (P) Hyperolius poweri; (Q) Hyp. pusillus; (R) Hyp. tuberilinguis; (S) Kassina senegalensis; (T) Phlyctimantis maculatus; (U) Phrynomantis bifasciatus; (V) Phrynobatrachus acridoides; (W) Phry. mababiensis; (X) Phry. natalensis; (Y) Xenopus laevis; (Z) X. muelleri; (AA) Hildebrandtia ornata; (BB) Ptychadena anchietae; (CC) Pty. mossambica; (DD) Pty. nilotica; (EE) Pty. oxyrynchus; (FF) Pty. porosissima; (GG) Amietia delalandii; (HH) Cacosternum boetgeri; (II) Pyxicephalus edulis; (JJ) Strongylopus fasciatus; (KK) Tomopterna adiasola; (LL) T. krugensis; (MM) T. natalensis and (NN) Chiromantis xerampelina. Photos not to scale.

According to Du Preez and Carruthers [50], frogs inhabit almost every environment and habitat on the subcontinent. However, even though frogs are found in a variety of habitats, most species are specific to the particular habitat in which they are able to survive and more importantly, reproduce. Because of this specialisation many frog species are vulnerable to changing habitats and are directly affected by environmental disturbances [57].

The PRF is an area recognised as a biodiversity hotspot for amphibians, offering a great diversity of habitats suitable for amphibians ranging from big rivers, streams, pans, pools, swamps, marshland, rain-filled depressions and terrestrial habitats [58]. Currently, this selection of habitats caters for the 41 species known from the area (**Figure 6**) [59]. Furthermore, as a result of the survey work conducted during the current project the previously unknown Ndumo rain frog (*Breviceps passmorei*) (**Figure 7**) was discovered and described, the common name referring to the type locality [60].

Amphibians are a sensitive group, especially to rapidly changing environments, with many species only adapted to survive in specific habitat types. To gain a better perspective of how additional stressors such as habitat loss and fragmentation affect amphibians within the PRF in comparison to historical data, the current study undertook an extensive survey using both active and passive sampling techniques. While most anuran species are nocturnal, some species have prolonged breeding seasons whereas others are explosive breeders and are only active following rainfall events. Due to the unpredictability of weather and breeding activity, certain species are often overlooked during traditional active biodiversity surveys. Furthermore, each frog species has unique vocalisation calls serving as a valuable identification aid. In the current project, passive acoustic monitoring (PAM) was utilised in the NGR, with automated recorders were set up at two selected wetlands and set to record from 18:00 till 5:00 the following morning for 13 months. Findings, in combination with active sampling, were used to monitor biodiversity and breeding activity of frog species associated with the selected endorheic habitats.

In the current study, 83% (34/41) of the expected frog species were recorded based on the 75 years (1929–2004) of historical data. In the NGR alone, a total of 32 frog species were recorded, stressing the importance and value of natural protected areas and how they support not only specific species but whole communities. These results indicate that even though there are significant global amphibian declines, areas such as the NGR still provide a haven and refugia for frog species to flourish in, and should remain protected at all costs.



Figure 7.
The Ndumo rain frog (Breviceps passmorei).

Results from PAM indicated that the peak breeding season for the majority of the species, with 79% (15/19) calling males recorded, was in the southern hemisphere summer between December 2013 and January 2014. Of the 19 species of frogs recorded the hourly calling activity and intensity differed among species, with only four species, namely, *Sclerophrys pusilla*, *Phlyctimantis maculatus*, *Phrynobatrachus mababiensis* and *Phrynomantis bifasciatus* were recorded reaching an average call intensity of 5/5 (**Figure 8**). These findings are indicative of explosive breeders, with a high calling intensity for only a few weeks a year in correlation with rainfall patterns. Six species were recorded calling in all 12-h slots, namely, *Chiromantis xerampelina*, *Hemisus marmoratus*, *Hyperolius marmoratus*, *Phly. maculatus*, *Kassina senegalensis* and *Phry. mababiensis*. Furthermore, four species (*Afrixalus aureus*, *Afr. delicatus*, *Hyp. marmoratus* and *K. senegalensis*) call intensity and thus breeding activity peaked between 18:00 and 00:00, and for six species, (*Scl. pusilla*, *Phry. mababiensis*, *Phry. natalensis*, *Phryn. bifasciatus*, *Ptychadena anchietae* and *Pty. mossambica*) call intensity peaked between 00:00 and 5:00 (**Figure 8**).

As mentioned previously, the PRF area experienced a massive influx of people over the past four decades that resulted in a transformation of the landscape and fragmentation of natural habitats. These alterations place enormous pressures on the environment. Furthermore, the introduction of the invasive redclaw crayfish (*Cherax quadricarinatus*) (see Section 3.1) poses a severe risk to tadpole population density and should be considered high priority threat to biodiversity. However, the

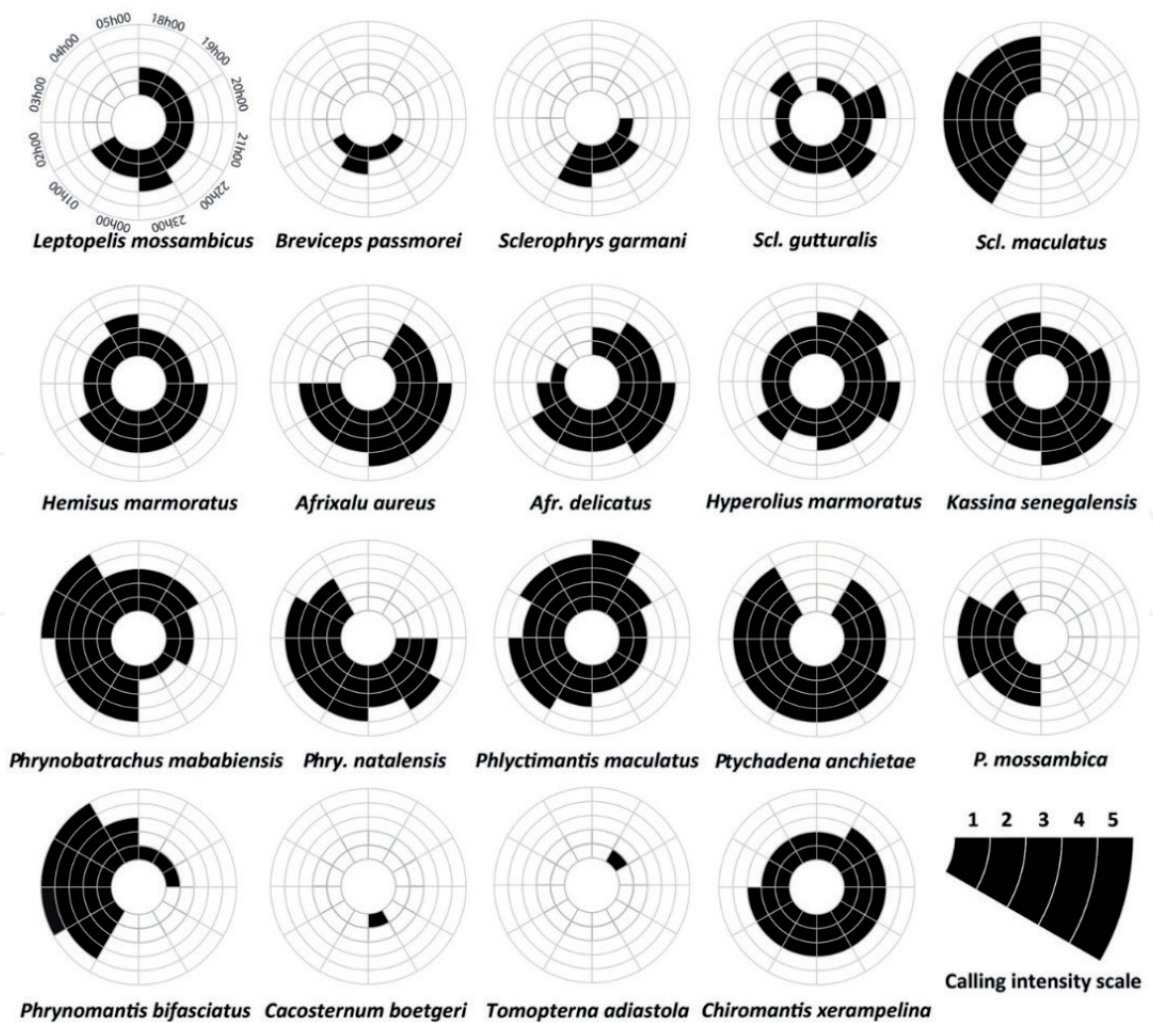


Figure 8. The average hourly activity and intensity of male frog species. Displayed are the data on the average calling activity and intensity of each frog species recorded by the song metre for the first 10 min of each hour (18:00 to and including 05:00). The scale bar represents the hourly calling intensity.

use of educational posters and the field guide to the frogs of Zululand [59] helped inform and educate local communities on the importance of conserving the environment for future generations.

2.4 Diversity of parasites of aquatic organisms

Parasites constitute a fundamental component of the global biodiversity, accounting for one third of the species on Earth, playing a key role in ecosystem functioning by regulating host population density and abundance, and being an integral part of food webs. However, parasites are still a neglected component in biodiversity surveys [61, 62]. Parasite inventories can provide knowledge to the comprehension of life cycles, pathological impacts, and evolution of host-parasite systems in aquatic environment [63].

Ectoparasites live on the surface of hosts, while endoparasites live internally [64]. The life cycle of parasites can be direct (monoxenous), requiring only one host to be completed, or indirect (heteroxenous), requiring one or more intermediate hosts to be completed [65]. A definitive (or final) host is the one in which the parasite is sexually mature; while the intermediate host is the one required for the development of parasitic stages without reaching sexual maturity. Paratenic or transport hosts are the ones in which parasites do not develop further but remain alive and infective [64]. Parasites exhibit variable degrees of host specificity, with some infecting only a single species or related species (specialists), and some infecting many unrelated species (generalists) [66].

A myriad of metazoan parasitic groups is found in aquatic organisms, including Protista, Myxozoa, Platyhelminthes [Monogenea, Trematoda (subclasses Aspidogastrea and Digenea), Cestoda], Acanthocephala, Nematoda and Crustacea. Some species infecting aquatic organisms present zoonotic potential, such as certain digeneans, cestodes and nematodes. All parasitic groups have species that can harm aquatic hosts, especially when present at high intensity of infections that normally occurs in aquaculture scenarios or in the case of invasive parasites.

Parasites that naturally occur in wild fish normally do not cause negative impacts on host populations. The opposite is usually true as a high diversity of parasites in freshwater fishes in natural conditions are used as indicators of a healthy and functional ecosystem [67]. Moreover, parasites are very sensitive to environmental alterations such as pollutants, providing relevant information about the quality of a given system. Some parasites have been identified as sentinels for chemical pollution because these organisms can accumulate chemicals at a higher level compared to their hosts [68, 69]. Monogeneans ectoparasites are in direct contact with the environment, thus more sensitive to changes in water parameters. Studies on monogeneans of fishes as biomarkers have been conducted under different approaches, such as effects of high concentrations of effluents, hydrological cycle of floodplain areas, heavy metal concentrations, trophic concentrations of reservoirs, and prevalence and abundance in lotic and lentic environments of a river basin ([70] and references therein).

Research on freshwater fish parasites in the PRF is relatively new and still scant. Before the present study the only fish parasites recorded from the PR were two monogenean species by Price et al. [71] from the gills of *Tilapia sparrmanii* and *Enteromius trimaculatus*, respectively (see [72]). Svitin et al. [73] studied the diversity of camallanid nematodes from two catfishes, providing novel information on their morphology and genetic data; Hoogendoorn et al. [74] studied the diversity of digenean metacercariae (Diplostomidae) and also provided novel information on the morphology and genetic data of these parasites from freshwater fishes; Smit et al. [75] recorded for the first time trypanosomes in freshwater fish and in their leech vectors from this region, providing morphological and molecular characterisation

of the haemoparasites; and recently, Schaeffner et al. [76] described a new cestode species from *S. zambezensis*. Information on the abovementioned records are shown in **Table 2** and some of the fish parasites are shown in **Figure 9**.

Parasite species	Locality	Host species	Reference
Trypanosomatida			
<i>Trypanosoma mukasai</i>	PR (NGR)	<i>Clarias gariepinus</i> , <i>Coptodon rendalli</i> , <i>Oreochromis mossambicus</i> , <i>Synodontis zambezensis</i>	[75]
Monogenea			
<i>Characidotrema auritum</i>	PR	<i>Brycinus imberi</i>	[77]
<i>Pseudodactylogyus anguillae</i>	PR (NGR)	<i>Anguilla marmorata</i>	[78]
<i>Cichlidogyrus papernastrema</i>	PR	<i>Tilapia sparrmanii</i>	[71]
<i>Dactylogyus myersi</i>	PR,	<i>Enteromius trimaculatus</i>	[71]
<i>Macrogyrodactylus clarii</i>	KP (NGR),	<i>C. gariepinus</i>	[79]
<i>Macrogyrodactylus congolensis</i>	UR (NGR)	<i>C. gariepinus</i>	[79]
<i>Macrogyrodactylus karibae</i>	KP, UR (NGR)	<i>C. gariepinus</i>	[79]
<i>Quadriacanthus</i> sp. 1	LN, KP, PR (NGR)	<i>C. gariepinus</i>	Present study
<i>Quadriacanthus</i> sp. 2	LN, KP, PR (NGR)	<i>C. gariepinus</i>	Present study
Digenea			
<i>Diplostomum</i> sp.	PR (NGR)	<i>S. zambezensis</i>	[74]
<i>Diplostomum</i> sp. 14	PR (NGR)	<i>Anguilla bengalensis labiata</i> , <i>O. mossambicus</i> , <i>S. zambezensis</i>	[74]
Cestoda			
<i>Barsonella lafoni</i>	LN	<i>C. gariepinus</i>	Present study
<i>Tetracampos ciliotheca</i>	LN, PR	<i>C. gariepinus</i>	Present study
<i>Wenyonia gracilis</i>	PR (NGR)	<i>S. zambezensis</i>	[76]
Nematoda			
<i>Paracamallanus cyathopharynx</i>	NL	<i>C. gariepinus</i>	[73]
<i>Procamallanus pseudolaeviconchus</i>	NL	<i>C. gariepinus</i>	[73]
<i>Spirocamallanus daleneae</i>	PR	<i>S. zambezensis</i>	[73]
Hirudinea			
<i>Batrachobdelloides tricarinata</i>	PR (NGR)	<i>C. gariepinus</i> , <i>S. zambezensis</i>	[75]
Abbreviations: KP—KuShokwe Pan; LN—Lake Nyamithi; NGR—Ndumo Game Reserve; PR—Phongolo River; UR—Usuthu River.			

Table 2.
Diversity of freshwater fish parasites naturally occurring in the lower Phongolo River and floodplain.

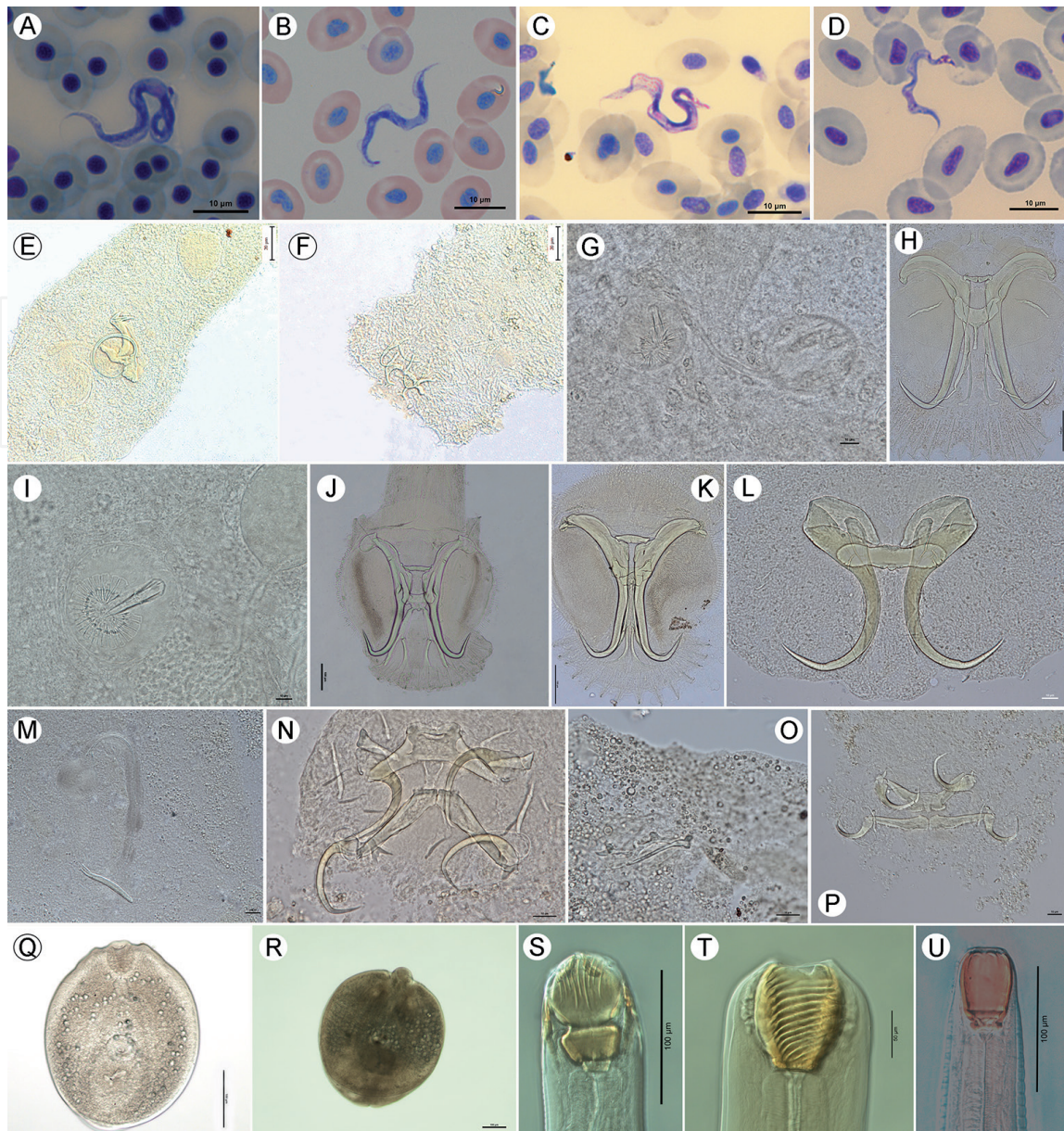


Figure 9.
Photomicrographs of some helminth parasites from freshwater fishes from the Phongolo River and floodplain. *Trypanosoma mukasai* from: (A) *Clarias gariepinus*; (B) *Coptodon rendalli*; (C) *Oreochromis mossambicus*; (D) *Synodontis zambezensis*. *Characidotrema auritum* (Monogenea: Dactylogyridae) from *Brycinus imberi*: (E) male copulatory complex (MCO); (F) haptor. *Macrogyrodactylus clarii* from *C. gariepinus*: (G) MCO; (H) haptor. *Macrogyrodactylus congolensis* from *C. gariepinus*: (I) MCO and (J) haptor. *Macrogyrodactylus karibae* from *C. gariepinus*: (K) haptor; *Pseudodactylogyrus anguillae* from *Anguilla marmorata*: (L) haptor; (M) MCO. *Quadriacanthus sp. 1* from *C. gariepinus*: (N) haptor; (O) MCO. *Quadriacanthus sp. 2* from *C. gariepinus*: (P) haptor. *Diplostomum sp. 14* from *O. mossambicus*: (Q) total view. *Diplostomum sp.* from *S. zambezensis*: (R) total view. *Paracamallanus cyathopharynx* from *C. gariepinus*: (S) anterior end with detail of buccal capsule. *Spirocamallanus daleneae* from *S. zambezensis*: (T) anterior end with detail of buccal capsule. *Procammallanus pseudolaeviconchus* from *C. gariepinus*: (U) anterior end with detail of buccal capsule.

Amphibians are well suited hosts for parasites, as most parasites rely on aquatic infective stages for transmission and reproduction, much in the same way that amphibians depend on extended exposure to aquatic systems for reproduction and their life history. This in turn increases the host–parasite contact rates. Frogs serve as host for most parasite groups including protozoans, monogeneans, digeneans, cestodes, acanthocephalans, nematodes and mites [50]. Furthermore, frogs are often infected with metacercaria where the frog serve as an intermediate host for a definitive reptile or bird host. However, parasites of frogs and other ectotherms have co-evolved over a long period of time and although these parasites are still true parasites per

definition, they seldom inflict adverse effects on their hosts, as compared to endo-therm hosts [80, 81]. Parasites that have thus far been encountered in frogs from the PRF are presented in **Table 3**. Additionally, parasites reflect their host species’ environmental interactions, revealing feeding behaviour, geographical ranges and social systems [87]. Blood parasites present good examples of these interaction based on their various transmission strategies, such as via consumption of an infected interme-diate host or directly from a blood feeding vector. Frogs from the PRF were shown to harbour a number of protozoan blood parasites ranging from intracellular apicom-plexan parasites to extracellular euglenozoan flagellates (see **Figure 10**) [85, 88].

Considering the diversity of fishes and amphibians of the lower PRF, future studies on the diversity of their parasites can reveal unique ecological characteristics of the environment, more insights on the drivers of host–parasite relationships like

Parasite species	Locality	Host species	Reference
Protista			
<i>Dactylosoma kermiti</i>	PR (NGR)	<i>Ptychadena anchietae</i>	[82]
<i>Hepatozoon involucrum</i>	PR	<i>Hyperolius marmoratus</i>	[83]
<i>Hepatozoon ixoxo</i>	PR (NGR)	<i>Hemisus marmoratus</i> , <i>Sclerophrys garmani</i> , <i>Sclerophrys gutturalis</i> , <i>Sclerophrys pusilla</i> , <i>Ptychadena mossambica</i> , <i>Ptychadena nilotica</i>	[84, 85]
<i>Hepatozoon tenuis</i>	PR	<i>Afrixalus fornasini</i> , <i>Hyperolius argus</i> , <i>Hyp.</i> <i>marmoratus</i>	[83]
<i>Hepatozoon thori</i>	PR	<i>Hyp. argus</i> , <i>Hyp. marmoratus</i>	[83]
<i>Hepatozoon</i> sp.	PR (NGR)	<i>Ptychadena anchietae</i> ,	[85]
<i>Haemococcidia</i> sp.	PR (NGR)	<i>Pty. anchietae</i> , <i>Phrynobatrachus mababiensis</i>	[86]
<i>Trypanosoma</i> spp.	PR (NGR)	<i>Afr. fornasini</i> , <i>Hem. marmoratus</i> , <i>Hyp.</i> <i>argus</i> , <i>Hyp. marmoratus</i> , <i>Hyperolius</i> <i>tuberilinguis</i> , <i>Pty. anchietae</i> , <i>Pty.</i> <i>mossambica</i> , <i>Scl. gutturalis</i> , <i>Scl. pusilla</i>	[85]
Monogenea			
<i>Polystoma vernoni</i>	NGR	<i>Ptychadena oxyrhynchus</i>	Present study
<i>Protopolystoma orientalis</i>	NGR	<i>Xenopus muelleri</i>	Present study
Cestoda			
<i>Cephaloclamys</i> sp	NGR	<i>Xenopus muelleri</i>	Present study
Nematoda			
<i>Cosmocerca</i> sp.	NGR	<i>Kassina senegalensis</i>	Present study
<i>Cosmocerca</i> sp.	NGR	<i>Ptychadena anchietae</i>	Present study
<i>Cosmocerca</i> sp.	NGR	<i>Tomopterna tandyi</i>	Present study
<i>Aplectana</i> sp.	NGR	<i>Breviceps passmorei</i>	Present study
<i>Camallanus kaapstaadi</i>	PR (NGR)	<i>Xenopus mulleri</i>	Present study
<i>Batrachocamallanus xenopodis</i>	PR (NGR)	<i>Xenopus mulleri</i>	[73]
Abbreviations: NGR—Ndumo Game Reserve; PR—Phongolo River.			

Table 3.
Diversity of parasites occurring in frogs in the lower Phongolo River and floodplain.

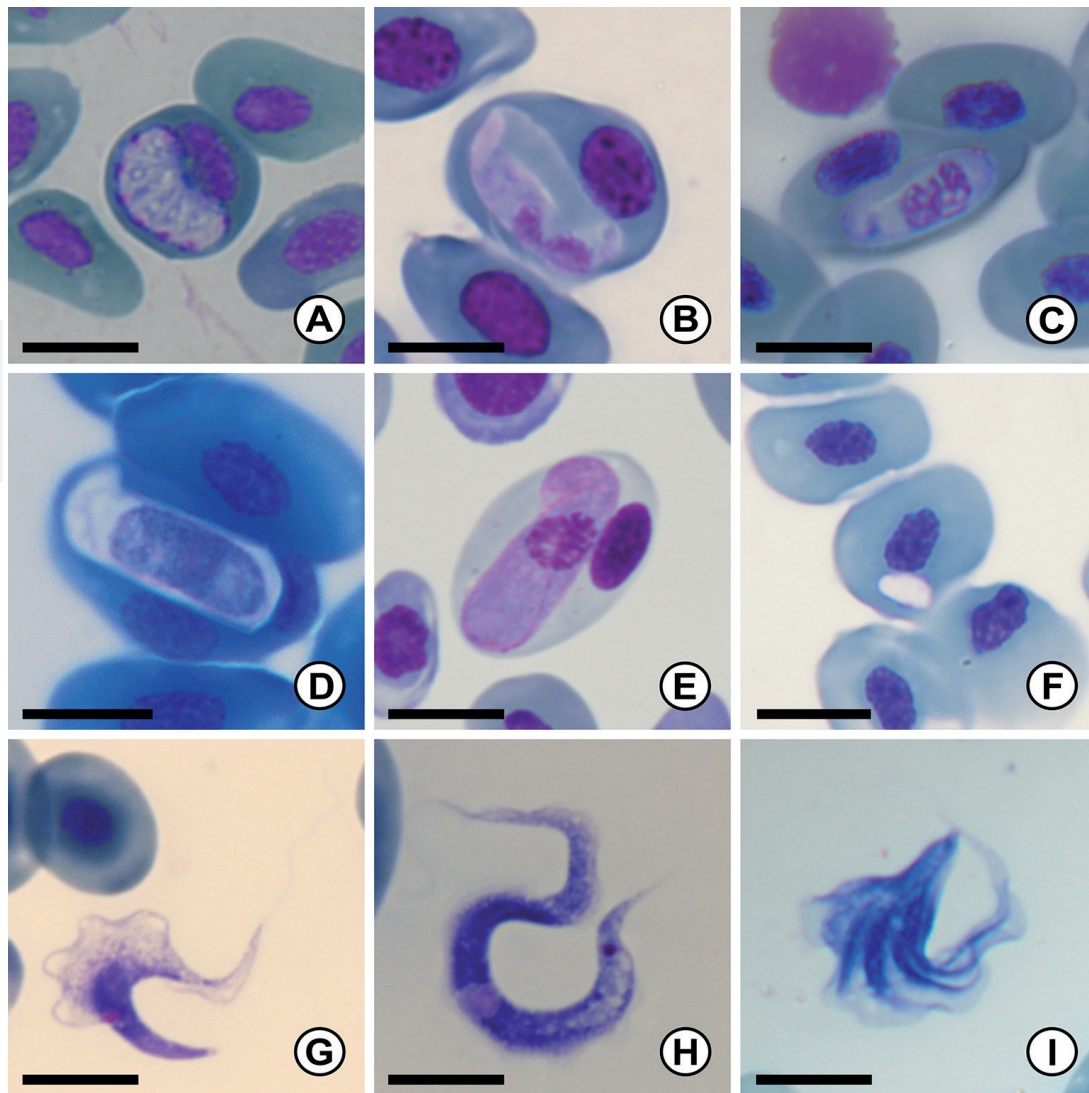


Figure 10. Photomicrographs of various frog blood parasites encountered in the Phongolo River and floodplain. (A) *Dactylosoma kermi* infecting *Ptychadena anchietae*; (B) *Hepatozoon involucrium* found infecting *Hyperolius marmoratus*; (C) *Hepatozoon ixoxo* infecting *Sclerophrys gutturalis*; (D) *Hepatozoon thori* infecting *Hyperolius argus*; (E) *Hepatozoon sp.* infecting *Pty. anchietae*; (F) *Haemococcidia sp.* infecting *Ptychadena anchietae*; (G) *Trypanosoma sp.* infecting *Pty. anchietae*; (H) *Trypanosoma sp.* infecting *Scl. gutturalis* and (I) *Trypanosoma sp.* infecting *Sclerophrys pusilla*. Scale bar 10 μ m.

patterns of host-specificity specially for monogeneans, as well as unravel parasite species that are still new to science, thus increasing the knowledge about the aquatic biodiversity of South Africa.

3. Biological and physical stressors of aquatic organisms from the lower Phongolo River and associated floodplains

3.1 Invasive and alien aquatic species

Aquatic organisms are intentionally moved and introduced through several pathways and occasionally their introduction is accidental. Natural introductions of alien species occur when dispersed beyond its natural distribution range with connectivity of two geographic regions during floods (pans, rivers and streams) or migration of species that host parasitic organisms. Human mediated introductions are more common and deliberate when introduced for breeding, ornamental and recreational purposes (angling) or as a food source (aquaculture). Meanwhile, accidental

introductions arise with escapes from captivity (aquaculture), uncontrolled releases of angling and ornamental species, inter-basin water transfer schemes, underlying contaminants or as stowaways on vessels and aquaria or farmed species [89–91].

Contaminants, pathogens or parasites accompanying introduced host species such as aquatic plants, molluscs, crustaceans and fish species are only noticed with increased infection, disease or mortality of the associated hosts. Often when an alien host is introduced it loses some of its native parasites (enemy release), however alien species may acquire native parasites and amplify transmission of pathogens or parasites of the native hosts (spillback). Alien host species can also 'dilute' transmission and infection of native pathogens and parasites (see [92, 93]). In contrast to this, parasites and pathogens that are co-introduced only infect the alien host and is co-invasive once it spills over to native biota (see [94] and references therein, [95]). Once alien species are introduced and established in the novel environment, they can become pests or threaten native biota and are then invasive or co-invasive (for parasites).

Alien or invasive species can impact aquatic ecosystem services and biological diversity through predation, parasitism, competition, hybridisation, habitat use and food web alterations [96, 97]. Livelihoods dependent on freshwater ecosystem and its resources can also be affected if aquatic diseases arise because of alien or invasive species, influencing marketability and commercial value for species used as a staple by local communities.

To date, eight invasive species have been recorded from the PRF (see **Table 4**). The first invasive to be recorded in the lower Phongolo was the common carp *Cyprinus carpio* in 1993 [34]. Apart from competing for resources, impact on water quality and threat to larval populations of macro-invertebrates, *C. carpio* is a known host to a variety of co-invasive parasites. The widespread Asian tapeworm *Schyzocotyle acheilognathi* and the anchor worm *Lernaea cyprinacea* has been co-introduced into the PRF with *C. carpio* and has spilled over to two native small barb species *Enteromius annectens* (broad-stripped barb) and *Enteromius bifrenatus* (hyphen barb), and to the vulnerable native *O. mossambicus*, respectively (see **Table 4**). The presence of these two co-invaders is concerning as infections with *S. acheilognathi* is associated with high infection intensities and pathology of the gut lumen, while *L. cyprinacea* cause haemorrhagic ulcers on the body surface of fish, leading to increased susceptibility to secondary infections [100 and references therein]. A recent study in the lower Phongolo also confirmed that the overall health state of fishes can be compromised when heavy infestations with *L. cyprinacea* occur [102]. This is of concern since *O. mossambicus* is a vulnerable native species and plays important economic and ecological roles in the PRF (see Section 2.2).

Furthermore, three invasive freshwater snail species, a crayfish and its co-invasive parasite inhabits the waters of the lower Phongolo. The reticulate pond snail *Lymnaea columella*, *P. acuta* and *T. granifera* directly competes with and affect the distribution of three native freshwater snails species: the common pond snail *Lymnaea natalensis*, *Bulinus africanus* and the red-rimmed melania *Melanooides tuberculata* [2, 101, 103]. A single niche competitor, the invasive *C. quadricarinatus*, which escaped from aquaculture farms in Swaziland, was first recorded from the PRF in 2013 [99]. In addition to posing a threat through direct predation on tadpoles, habitat modification and the resident native Natal freshwater crab *Potamonautes sidneyi*, the *C. quadricarinatus* in the PRF also hosts a co-invasive temnocephalan *Diceratocephala boschmai* (see **Table 4**) [99]. To date, no spillover of this temnocephalan to native freshwater crab, shrimp and other branchiopods have been noted. However, it has been experimentally proven that one of three co-invasive temnocephalan species infecting invasive freshwater crayfish species in South Africa can utilise native freshwater crabs as a host [91]. Some of the invasive organisms mentioned are shown in **Figure 11**.

Species	Vector/pathway into RSA	Presence	Infection of native species	Reference
<i>Diceratocephala boschmai</i> (Platyhelminthes: Temnocephalida: Diceratocephalidae)	<i>Cherax quadricarthus</i> (crayfish) escapes from aquaculture farm in Swaziland [98]	LN	No record of spread to native freshwater crabs, shrimps and other Branchiopoda.	[99]
<i>Schyzocotyle acheilognathi</i> (Cestoda: Bothriocephalidae)	<i>Cyprinus carpio</i> (common carp)	LN, PR, P	<i>Enteromius annectens</i> ; <i>Enteromius bifrenatus</i>	[100]
<i>Lymnaea columella</i> (Gastropoda: Lymnaeidae)	Stowaway on aquarium plants	—	—	[2]
<i>Physa acuta</i> (Gastropoda: Physidae)	Stowaway on aquarium plants	LN, PR	—	[2, 101]
<i>Tarebia granifera</i> (Gastropoda: Thiarinae)	Stowaway on aquarium plants	LN, PR	—	[2, 101]
<i>Lernaea cyprinacea</i> (Arthropoda: Lernaeidae)	<i>Cyprinus carpio</i>	LN, PR	<i>Oreochromis mossambicus</i> ; <i>Coptodon rendalli</i>	[2, 102]
<i>Cherax quadricarinatus</i> (Arthropoda: Parastacidae)	Escape from aquaculture farm in Swaziland [98]	LN, PR, UR	—	[99]
<i>Cyprinus carpio</i> (Cypriniformes: Cyprinidae)	Recreational angling	Various sites in lower PR	—	[34]

Abbreviations: LN—Lake Nyamithi; PR—Phongolo River; P—Pumphouse; UR—Usuthu River.

Table 4.
Introduced aquatic species present in the lower Phongolo system.

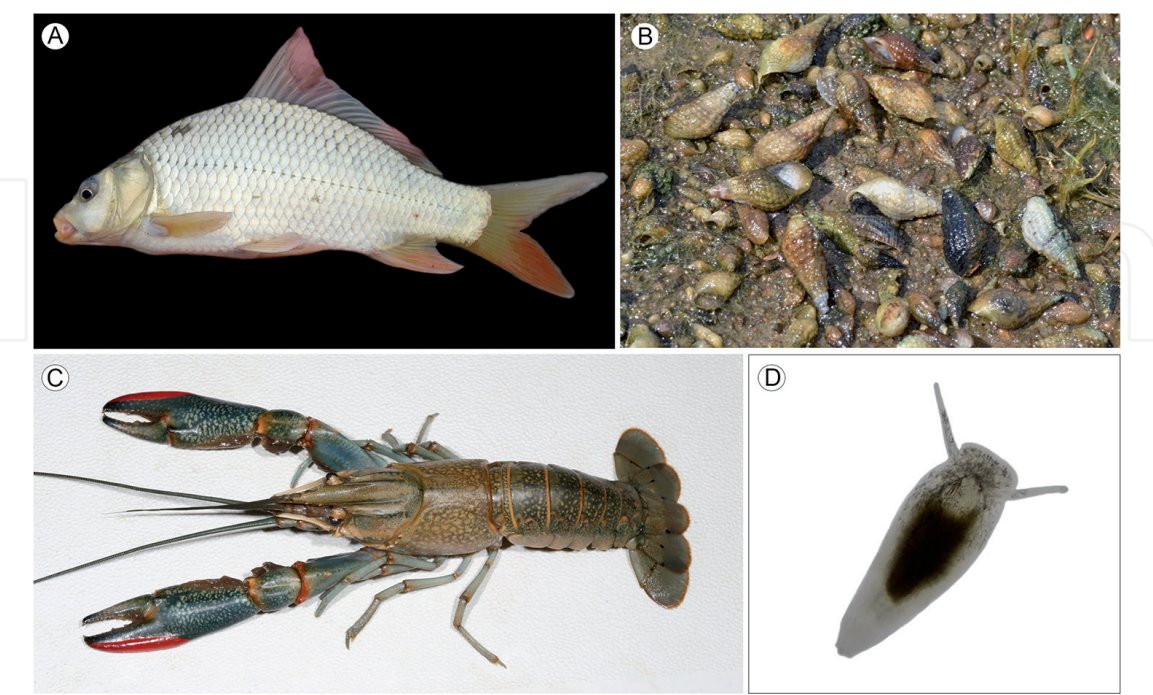


Figure 11.
Invasive species in the lower Phongolo River and floodplain: (A) *Cyprinus carpio* (Cypriniformes: Cyprinidae) (common length 31 cm); (B) *Tarebia granifera* (Gastropoda: Thiarinae); (C) *Cherax quadricarinatus* (Arthropoda: Parastacidae) (max. Length 35 cm) from Ndumo game reserve; (D) *Diceratocephala boschmai* (Platyhelminthes: Temnocephalida: Diceratocephalidae) (length 832–1500 μm) parasite from *C. quadricarinatus*. Information on length extracted from [32, 104, 105], respectively.

3.2 Physical and chemical stressors

The construction of the Pongolapoort Dam (Jozini Dam) in the early 1970s is arguably the greatest agent of change in the PRF. Following the construction of the dam, the downstream terrestrial physical and chemical template of the system was irrecoverably altered with a complicated interaction between the benefits and threats derived from the damming of the PR. Prior to the construction of the dam, the subsistence fisheries and agriculture practices were synchronised with the natural floods and their flooding and alluvial sediment deposit regimes of the floodplain pans [3]. Since its construction, there have been various 'flood release' strategies to simulate the natural floods in the floodplain with varying degrees of success [4]. Recently, Brown et al. [106] developed a set of holistic environmental flow recommendations that would supposedly meet the ecosystem and agricultural water requirements. However, these have yet to be evaluated since the region has been in the grip of a long-term drought that has negated water releases, other than base flows of $8 \text{ m}^3 \cdot \text{s}^{-1}$, since 2015 to the present [1].

As mentioned previously, the assurance of water resources and potential for sustained larger-scale agriculture resulted in exponential growth in the human population that is directly or indirectly dependent on the PRF. These communities are considered to be among southern Africa's poorest and traditionally highly dependent on harvesting natural resources. For these impoverished communities, living on or near the PRF allows them to maintain subsistence agricultural activities, provide for livestock, water collection for household usage, religious activities, a source of protein and sustenance through fishing and lastly the harvesting of plants such as water lilies, reeds and thatching grass [2, 5].

The conversion of natural land cover to agricultural landscapes is one of the main causes of environmental degradation and is a known driver of pollution of surface waters and subsequent loss of habitats and biodiversity [107]. Between 1955 and 2003, 40% of the natural floodplain vegetation was transformed into agricultural land [5]. The inadequate accessibility to water leads to further exploitation of the limited water resources of the region. Recent years have seen a marked increase in informally installed pumps along the length of the river, mostly used to irrigate the fields of the subsistence farmers. The water systems of the floodplain are further contaminated by oil and fuel leaks from the aforementioned pumps and washing of clothes. Waste dumping is common practice in South Africa and is not solely limited to urban areas, as is evident throughout the rural communities surrounding the floodplain and this poses significant risks to human and environmental health. Such practices even created waste management issues within the NRG.

The excessive reliance on the floodplain and its resources could be considered unsustainable and thus leads to significant biodiversity losses. Less than 10% of the entire floodplain is formally conserved in the NGR. Outside of the reserve, the riparian forests and vegetation are removed, being the wood used as fuel and the cleared areas for subsistence agriculture (see **Figure 3**). In 2008, the communities along the eastern boundary took down the 11 km long fence to gain access to 1000 hectares of the reserve for resources and establishing subsistence agriculture. As such, the only intact riparian zone is a 3-km stretch along the western bank of the active channel of the PR within the reserve.

The altered water releases, drought and increased pesticide use in the floodplain has resulted in increased chemical stressors being released into surface and groundwater of the system. Historically, the floodplain has been subjected to fluctuations in drought periods and flood inundation. As a consequence, highly saline conditions (total dissolved solids in excess of $5000 \text{ mg} \cdot \text{l}^{-1}$) have been reported in the floodplain pans that are prone to seepage of salts from the underlying marine cretaceous

geological structure [3]. The salinities subsequently decrease when the pans are flooded during the next flood event. Due to the prolonged drought from 2014 and the absence of flooding since 2016, there has been a steady increase in electrical conductivity and nutrients. However, these levels still seem very similar to the historical conductivity and nutrient concentrations [1]. It would thus seem that the system is highly resilient to altered flow conditions with large fluctuations in water quality.

Large-scale organic pesticide application has been in place on the PRF for many decades. Dichlorodiphenyltrichloroethane (DDT) has been used for malaria vector control since the 1930s [108]. Sereda and Meinhardt [109] studied the levels of pesticides in surface- and groundwater of water bodies of the PRF. They attributed the presence of pyrethroids (cypermethrin, λ -cyhalothrin and cyfluthrin), organophosphates (fenthion and fenitrothion) organochlorines (DDT and its metabolites—pp-DDD and pp-DDE) and carbamates (carbosulfan and carbofuran) to agricultural and malaria vector control applications. The first records of DDT in fish and other wildlife from the PRF were reported by [110]. Bouwman et al. [111] concluded that the high levels of DDT and its metabolites found in human serum and breast milk from the PRF could be attributed to a combination of consuming contaminated fish and direct exposure through spray drift.

Pesticide usage and subsequent spillage and run-off remain a major concern due to the numerous negative impacts on wildlife and ecosystems. Organochlorine pesticides (OCPs) are a group of pesticides which have been banned globally due to their persistence, attested by the quantifiable concentrations even though usage has been banned for over two decades, as well as consequent negative impacts on the environment [2, 112, 113]. Volschenk et al. [114] highlighted the renewed focus on quantifying OCPs in aquatic ecosystems in and around the floodplain. These chemicals accumulate throughout the food web and represent a significant threat to the aquatic diversity of the floodplain. The floodplain and its surrounding area are still classified as a malaria endemic area and as such has consistently been sprayed with DDT for the purpose of malaria vector control. General pesticide use has also increased due to increasing agriculture activities. Recently, [114] recorded a range of pesticides, including discontinued pesticides such as lindane in five of the most economically and ecologically important fish species of the floodplain. Contamination levels in the floodplain were lower than other regions across South Africa. They are however a reason for concern due to the risks posed to both humans and animals reliant on the floodplain, including important protected and red data listed species such as the Nile crocodile (*Crocodylus niloticus*), pelicans (*Pelecanus onocrotalus*) and Saddle billed storks (*Ephippiorhynchus senegalensis*). As anticipated, DDT and its metabolites were the dominant OCPs and were shown to magnify through the food chain. DDTs are associated with several harmful effects on fish, crocodile and bird populations across the world, including but not limited to reproductive impacts, endocrine disruptions, eggshell thinning and ensuing population declines. Importantly, as OCPs do not adhere to any type of border, conservation efforts that are implemented within the region should strive towards better management and increased public education.

4. Conceptualising conservation approaches for the PRF

The previous sections explain the biodiversity and conservation importance of the PRF whilst also highlighting particular conservation challenges. In order to conserve this unique biodiversity, different conservation governance and/or management approaches exist. Therefore, this section briefly explains the different

approaches available in South Africa, for consideration in the Phongolo context. Although we explain the different approaches, we do not prescribe any specific approach. The entire suite of options needs to be considered to inform the design of a combined or hybridised tapestry of approaches, best suited to achieve the conservation objectives of the PRF. There is therefore no silver bullet or single solution when it comes to identifying conservation governance and management approaches. We frame our brief discussion around approaches and instruments already developed within the South African context more generally (for a more detailed discussion of these approaches and instruments see [115]). Three broad approaches are distinguished as illustrated by the three circles in **Figure 12**, namely: command- and control (CaC)-based, fiscal-/market-based and civil-based approaches. In relation to each approach, different so-called governance and management instruments are identified. Some of these instruments are considered hybridised instruments nesting between more than one approach, illustrated by the overlapping areas between the three circles numbered A, B, C and D.

The CaC approach includes those management instruments provided for by legal means. This is the most basic or classical approach centred on the understanding that the best way to control human behaviour is to enact laws and then enforce them—or the ‘stick approach’. In terms of conservation, South Africa has a complex legal framework (for a detailed discussion of the legal framework see [116, 117]) and a myriad of instruments covering strategic and project level decision making. Strategic level instruments inform decision making at a policy and planning level such as the National Biodiversity Framework, Bioregional Plans, Biodiversity Management Plans and the proclamation of different protected areas (PAs). An example of these with in the PRF, is the formally proclaimed NGR. At project level CaC-based instruments include the issuing of permits and/or prohibition notices for legally defined ‘restrictive activities’ in relation to listed ecosystems and species (threatened or alien invasive). The protection of species through CaC has obvious relevance to the wealth of biodiversity in the PRF, highlighted in previous sections. While the CaC arrangements are considered critical for any conservation regime, failures of CaC instruments are well documented in the literature [118, 119]. The strengths of CaC are that it provides a high level of certainty by defining for example boundaries of PAs and prescribing behaviour in relation to listed species and ecosystems. The weaknesses relate to the resources required and time it takes

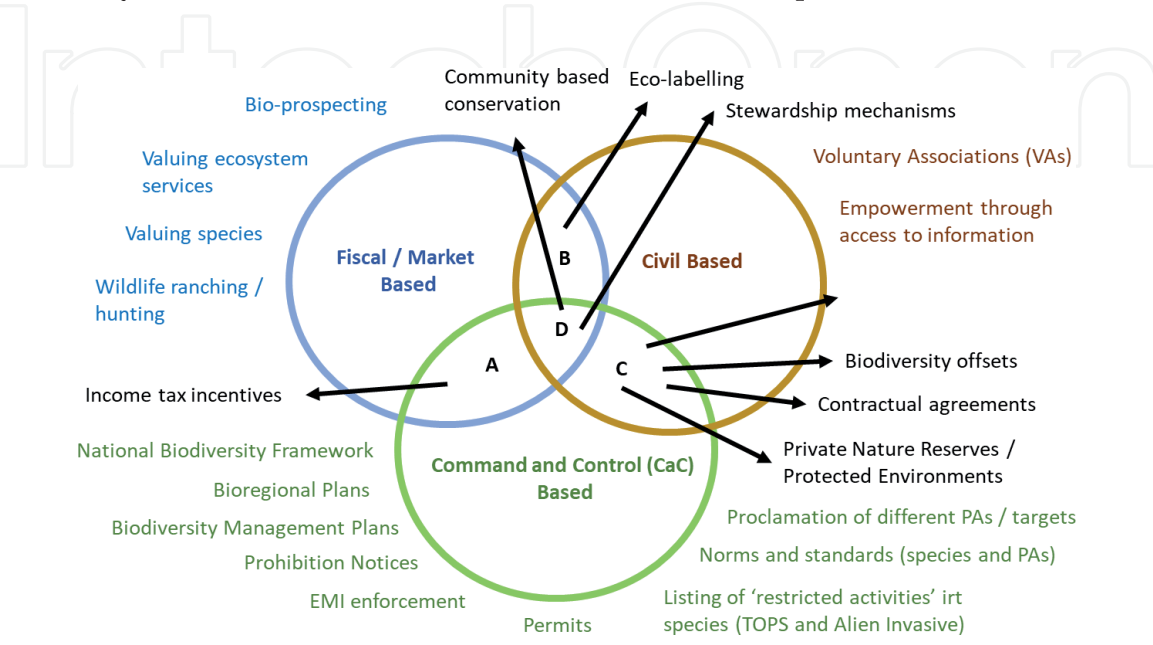


Figure 12.
Different conservation governance and management approaches within the south African context.

to ensure enforcement of these legal mechanisms. For this reason, additional approaches have emerged to supplement and support CaC arrangements such as fiscal- and civil-based approaches.

Fiscal-based approaches aim to use the market or price mechanism to change or incentivise certain behaviour, also sometimes referred to as the ‘carrot approach’. In the case of conservation this refers to valuing ecosystem services and/or species within a market-based economy to incentivise their protection. The wildlife and bioprospecting industries are typically integral to this market-based system. The strengths of market-based instruments are the instant effect it seems to have on behaviour, unlike CaC-based instruments. However, pricing ecosystems and species have been controversial, especially in relation to the trade in endangered species – ivory and rhino horn a case in point. Market-based instruments are not well developed in the PRF and South African in general. This is mainly due to the significant inherent challenges in commodifying ecosystems and wildlife [120].

Civil-based instruments centre around empowerment of civil society in order to affect behaviour. The need for civil-based instruments derives from the acknowledgement that governments alone cannot deliver on conservation goals and objectives. Civil-based instruments include opportunities for civil society to organise themselves through for example voluntary associations (VAs) and empowerment of civil society through access to information on for example conservation-related matters. The PRF is an example of a highly complex civil society context with a range of civil society actors such as tribal authorities, farming unions, water user associations, etc. The advantage for the study area is that civil society seems well organised and represented. However, the challenge is to achieve a common understanding and general agreement on the future of conservation in the area amidst the range of actors.

In an ever-changing complex world, it is also evident that many of the most effective management instruments do not fit neatly into a specific approach but rather are designed as so-called hybrid instruments. For example, income tax incentives for landowners promoting conservation on their land is a clear hybrid between CaC and market-based approaches—see ‘A’ in **Figure 12**. This is because the tax incentive is incorporated into law, but the incentive is market based. We are not aware of any example within the PRF where this instrument has been used. Furthermore, instruments such as eco-labelling aims to make certain products more appealing to civil society or consumers based on their environmental performance—see ‘B’ in **Figure 12**. The hybrid approaches between civil- and CaC-based approaches shown as ‘C’ in **Figure 12** have a high level of potential relevance to the study area. These include biodiversity management agreements or contractual agreements between private or communal landowners and the state. The conservation status of private or communal land can also be formalised through different kinds of protected areas such as Private Nature Reserves (PNRs) and Protected Environments [121]. An extension of the latter in recent years has been so-called community-based conservation (CBC) and conservation stewardship programmes that are considered the most integrated conservation instruments combining CaC, fiscal- and civil-based approaches—see ‘D’ in **Figure 12**. For example, the stewardship programme combines different levels of legal protection with money saving incentives and strong community involvement and ownership. Much research has been conducted on the success and failures of CBC generally, but also within the KZN Province, which could inform the future application within the study area (see [122–124]).

There are two guiding principles when considering these approaches, firstly the use of multiple approaches and instruments is preferred especially within

a complex and multi-faceted context such as the PRF. Multiple approaches also enhance the redundancy effect by ensuring multiple possible solutions for a range of conservation challenges. Secondly, hybrid approaches are preferred (as represented by A, B, C, and D in **Figure 12**) that aim to optimise and merge the strengths of different approaches into single instruments. Ultimately the design and selection of conservation approaches for the PRF will depend on the agreed context specific conservation goals and objectives.

5. Conclusions

It is clear from the information presented in the preceding sections that South Africa's PRF is, in terms of aquatic organisms, highly diverse and of national and international importance. However, the aquatic ecosystem of the PRF is also under extreme pressure from a vast array of human activities, ranging from broadscale influences such as climate change and associated extreme weather events to local-scale impacts such as pollutants, over utilisation and invasive species. Interestingly, the PRF ecosystem has also exhibited tremendous resilience in dealing with all these anthropogenic stressors. Despite more than 10-fold increase in the human population depending on the ecosystem services provided by the PRF, a 5-year ongoing below-rainfall period with no flood release from the Pongolapoort Dam and reduction in the size of the area under formal protection, there is currently no evidence that points towards a loss in species diversity. However, at least for fishes, Smit et al. [2] showed that although all species are still present, there has been a clear shift in the community structures and dominance. The main question for the PRF therefore still remains; how long, and especially in the light of the continued lack of flooding events and increasing human settlement and activities, can the socio-ecological system of the PRF stay resilient before complete collapse?

To answer this very important question, we propose that future research into this and similar systems in Africa and globally should follow the One Health approach. The One Health approach deals with a multidisciplinary and collaborative approach to ensure optimum health of humans, animals and the environment. The importance of, and need for, this approach has really come to the front during the Covid-19 pandemic of 2020 where the world was brought to a standstill due to a virus that originated from an animal (zoonotic disease). Therefore, studies on specifically environmental health are urgently required in order to gain a better understanding of the causes and consequences of anthropogenic activities, and how these in return have an impact on human health. Future research should thus aim at investigating the possible natural hazards associated with effects of climate change (i.e. droughts and floods), in combination with environmental pollutants, on the severely threatened aquatic ecosystem of the PRF. Specific research objectives should include:

- Determine the risk and possible impact of climate change on water quantity and quality, and food security.
- Identify different water quality governance approaches and instruments to ensure environmental conservation and human health protection amidst a changing climate.
- Identify dimension of vulnerability and characteristics of resilience that make local communities more, or less, susceptible to water-related disaster risks as a result of climate change.

- Monitoring the introduction and spread of invasive aquatic animals (both free-living and parasitic).
- Develop and validate holistic environmental flows to maintain and support ecosystem structure and functions.
- Develop and apply a risk assessment framework that integrates the ecological, human and wildlife factors to evaluate the socio-ecological consequences of climate change-induced changes in water quality and quantity.

Although the abovementioned recommendations are specifically proposed for the PRF, these research questions, aims and objectives are applicable to all threatened floodplain systems globally.

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Conflict of interest

The authors declare no conflict of interest.

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