KOEDOE - African Protected Area Conservation and Science
ISSN: (Online) 2071-0771, (Print) 0075-6458

River hydrology mediates fish invasions in Addo Elephant National Park, South Africa

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Dates:
Received: 11 Dec. 2023
Accepted: 06 Apr. 2024
Published: 20 May 2024

How to cite this article:
Woodford, D.J., South, J., Mofu, L. & Pegg, J., 2024, 'River hydrology mediates fish invasions in Addo Elephant National Park, South Africa', *Koedoe* 66(1), a1806. https://doi.org/10.4102/koedoe.v66i1.1806

Invasive freshwater fish can often have severe negative effects on native fishes in river systems. The interactions between hydrology and habitat variability can mediate the speed and success of individual invasions and the consequent impact on biodiversity. The rivers within Addo Elephant National Park (AENP) in the Eastern Cape, South Africa experience cyclical droughts and wet periods and as a result are naturally episodic. These rivers were recently invaded by three non-native species, the invasive largemouth bass (*Micropterus salmoides*) as well as the extralimital sharptooth catfish (*Clarias gariepinus*) and Mozambique tilapia (*Oreochromis mossambicus*). Monitoring of key sampling sites along two rivers over a 12-year period that included two major droughts revealed unexpected patterns in the spread of these species and their interactions with native fishes. On the Coerney River, *C. gariepinus* repeatedly invaded and was extirpated from a seasonal reach of the river, wherein *O. mossambicus* was only occasionally captured. On the Wit River, two apparently independent introductions of *M. salmoides* in the lower and upper reaches of the river resulted in patchy habitat occupancy over the course of 12 years. While *C. gariepinus* regularly co-occurred with native species, *M. salmoides* appeared to locally extirpate the endangered Eastern Cape redfin (*Pseudobarbus afer*). During drought, both species persisted in close but disconnected pools, suggesting that the episodic hydrology and geomorphology of these rivers may offer temporary predation refugia for native species during drought.

Conservation implications: Drought in episodic rivers can mitigate against the impact and spread of freshwater invasions within protected areas. Effects of drying on invasion corridors and spatial interactions with native species should be taken into consideration when managing such invasions. Severe droughts also offer an opportunity to actively control invasive species when they are confined to accessible drought refugia within the protected area.

Keywords: biological invasions; freshwater fishes; drought; dewatering; river connectivity; intermittent rivers; invasion corridors; predatory exclusion.

Introduction

Freshwater fishes are considered the most threatened group of vertebrate species on the planet, having higher extinction rates than any other group in the past century (Burkhead 2012; Cooke, Paukert & Hogan 2012). Major threats facing these species include habitat destruction, the overexploitation of water resources (Arthington et al. 2016; Cooke et al. 2012), as well as non-native invasive species, which can have catastrophic impacts on native fish assemblages (Bacher et al. 2023; Milardi et al. 2019). While marine fish species are increasingly the focus of targeted conservation through the promulgation and enforcement of marine protected areas (Edgar et al. 2014), freshwater fishes do not generally receive the same targeted protection inside terrestrial protected areas such as national parks, provincial and municipal nature reserves (Abraham & Kelkar 2012; Lawrence et al. 2011). A notable exception is Addo Elephant National Park (AENP) in South Africa where, unlike most terrestrial protected areas, the river systems were specifically included in the conservation planning during the park's expansion (Roux et al. 2002), although that has not exempted them from anthropogenic threats. Freshwater fishes inside terrestrial protected areas are particularly vulnerable to fish invasions because these areas do not necessarily protect habitats from invasion from upstream or downstream of the park's borders (Adams et al. 2015; Ellender, Weyl & Swartz 2016). In South Africa, non-native and translocated fishes have been recorded in 9 of the 13 National Parks with freshwater ichthyofauna (Russell 2011). Moreover, because recreational fishing is often a popular and promoted activity in and around protected areas,

Note: Additional supporting information may be found in the online version of this article as Online Appendix 1.

human interactions with these protected areas can actually increase the risk of detrimental introductions (South et al. 2023; Syslo, Guy & Koel 2016; Weyl et al. 2015). The spread of popular angling species such as black bass (*Micropterus* spp.) has had a particularly negative impact on native stream fish communities worldwide (Jackson 2002; Leunda 2010; Maezono et al. 2005) and in South Africa in particular (Ellender & Weyl 2014). Largemouth bass, *Micropterus salmoides* (Lacépède 1802) and smallmouth bass, *Micropterus dolomieu* (Lacépède 1802) have both managed to penetrate into protected areas within South Africa such as the Cederberg Wilderness Area and Groendal Nature Reserve, where they have driven population declines and extirpations of native fishes, primarily by depredation (Ellender et al. 2016; van der Walt et al. 2016).

Climate shifts are predicted to lead to more stochastic weather patterns, resulting in more extreme hydrological events such as droughts and severe flooding (Lennox et al. 2019). These changes are likely to affect both native and invasive species range distributions, especially in South African freshwaters characterised by Mediterranean climates (Broom, Weyl & South 2023; van Wilgen et al. 2022). Hydrological alterations will increase or decrease available aquatic habitat and connectivity dynamics, which will inevitably mediate or facilitate invasion processes (Guareschi & South 2024; Rahel & Olden 2008; van Wilgen et al. 2022; Winder, Jassby & Mac Nally 2011).

Addo Elephant National Park is a protected area situated in the Eastern Cape province of South Africa. It was surveyed in 2007 by a Rhodes University research team to assess its fish diversity, and to determine the presence, distribution and threats posed by non-native fishes (Weyl, Booth & Traas 2008). The surveys focused on the Sundays River and its tributaries, which drain several sections of the park. The catchment was found to contain a number of non-native fish species, including invasive *M. salmoides*, which was introduced into the lower Wit River by anglers in 1972 (Weyl et al. 2010b), and two extralimital species: the sharptooth catfish *Clarias gariepinus* (Burchell 1822) and the Mozambique tilapia *Oreochromis mossambicus* (Peters 1852), which had been introduced to the Sundays catchment via an inter-basin water transfer scheme originating from the Orange River (Cambray & Jubb 1977; Weyl et al. 2008). The *C. gariepinus* population within AENP tributaries was confined to a single disconnected pool on the Coerney River and was manually eradicated by the survey team in 2007 (Weyl et al. 2010a), whereas *O. mossambicus* was only found in Darlington Dam on the Sundays River mainstem, in the Darlington section of AENP (Weyl et al. 2008). Both of these species have access to an invasion corridor into the Coerney River via an irrigation canal network that releases Sundays River water directly into the stream downstream of the national park border (Ellender, Woodford & Weyl 2015). *Micropterus salmoides* was not found within the borders of AENP, having been restricted from upstream movement into the park by an artificial causeway (Weyl et al. 2008, 2010b).

The end of a protracted drought in 2011, which saw several tributaries flow for the first time since the 2007 survey, prompted a research team from the National Research Foundation – South African Institute for Aquatic Biodiversity (NRF-SAIAB) to start a new long-term monitoring programme on two major tributaries of the Sundays inside AENP to track ongoing and potential new invasions of the park by non-native fishes. This article summarises the major outcomes of the subsequent fish surveys that were conducted between 2012 and 2019, compares them to the 2007 fish distributions, and explores how the hydrology of the surveyed rivers contributed to or mitigated against the spread and potential impacts of these invasive species on the native fish community.

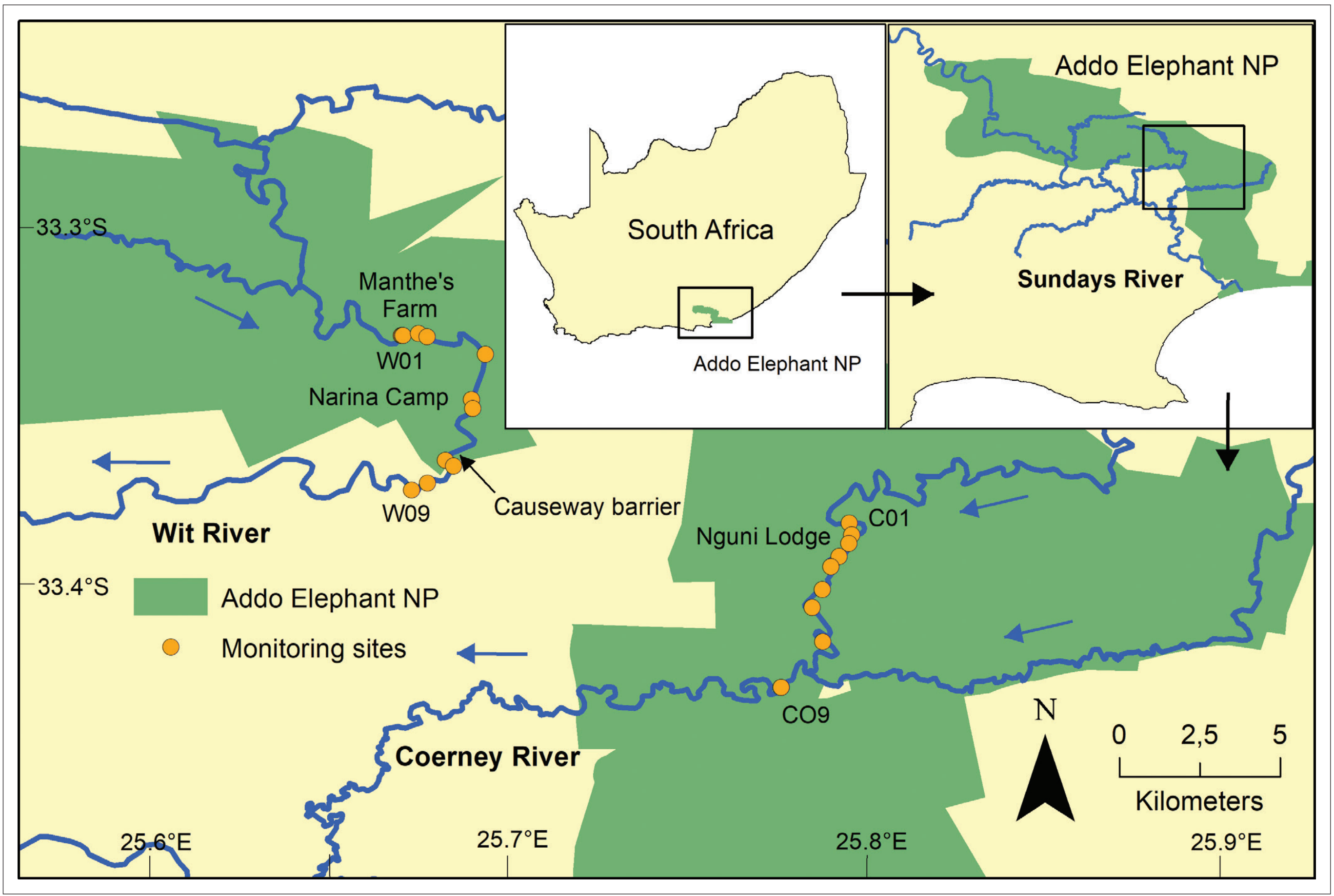
Research methods and design

Study system

Addo Elephant National Park, located at east of the city of Gqeberha in the Eastern Cape province of South Africa, is comprised of a patchwork of semi-contiguous national and former provincial nature reserves (e.g. the historic Zuurberg Nature Reserve) and formerly privately owned farmland that was brought together to maximise its capacity to preserve critical habitats and biodiversity unique to the region (Roux et al. 2002). The park straddles the mesic aquatic ecoregions of the southern folded mountains and the south-eastern coast belt (Nel et al. 2011), receiving a mean annual rainfall of 300 mm a year, although years with far lower precipitation are common (Hillmer & Bate 1990). This irregular rainfall means that the streams draining the park, all being tributaries of the Sundays River (Figure 1), are highly seasonal and often episodic in nature, with significant portions of their length drying and re-wetting in response to supra-annual and multi-year droughts and subsequent floods. The El Niño-Southern Oscillation (ENSO) global climate event of 2015–2017 caused unusually dry weather in the southern regions of South Africa, culminating in severe droughts along the southern coastal areas (Mahlalela et al. 2020; Wolski et al. 2021), with that drought lingering for several additional years in the Eastern Cape. Drought conditions were preceded by a brief wet period in 2011–2014, where two tributaries of the Sundays, the Wit and Coerney rivers, became reconnected with the Sundays River mainstem for the first time since 2007, when the initial fish survey was conducted (Weyl et al. 2008, 2010a). This study tracks changes in fish communities within the park that span both droughts and the intervening wet period from September 2007 to August 2019.

Survey sites

Field work to follow up the Rhodes University surveys of 2007 commenced in October 2012, with subsequent field trips in February 2014, November 2014, March 2015 and September 2019. The large gap between the 2015 and 2019 field trips was caused by logistic and personnel constraints at NRF-SAIAB preventing the mounting of additional trips,



Note: Blue arrows denote direction of stream flow. The furthest upstream site on the Wit (W01) is located within the formerly private property referred to as Manthe's Farm, while the furthest downstream site (W09) is located outside the National Park. Narina Camp is located approximately halfway along the river between the uppermost site and the border of the park, and the precise location of the causeway that acted as an historical bass barrier near the park boundary is indicated with a black arrow. The furthest upstream site on the Coerney River (C01) is located immediately upstream of the Nguni Lodge.

FIGURE 1: Map of the study reaches visited between 2007 and 2019 and their monitoring sites located both within and outside the Addo Elephant National Park on two episodic tributaries of the Sundays River, namely the Wit River and the Coerney River (Eastern Cape province, South Africa).

which were considered low priority as the sustained drought experienced across the region during this time meant the majority of the river sites being monitored were completely dry. While three tributaries were initially chosen for the monitoring programme, namely the Wit, Coerney and Uie Rivers, the Uie has been excluded from this study as too few sites were consistently revisited over the 12-year period. In contrast, nine sites on each of the Wit and Coerney rivers were consistently revisited by the research team between 2012 and 2019 (Figure 1), allowing long-term patterns of fish species occupancy of these sites to be evaluated.

Field sampling

Fish collection protocols varied between each trip in terms of the sampling gear and effort employed, but two main sampling techniques were consistently used across the surveys, namely electrofishing and the deployment of fyke nets. Electrofishing was conducted in single passes through wadeable habitats, using a SAMUS 725G (Electro Fisher Company, Bialystok, Poland) backpack electrofisher (max output 400 V, 0.3 ms pulsed DC current at 90 Hz), following Ellender et al. (2015). Fyke nets consisted of twin trap fyke nets and single trap elver nets, each with a 0.5 m mouth diameter. Fyke and elver nets were placed in pools near potential fish cover in the afternoon and retrieved the following morning, representing one net-night of sampling effort. In addition, one fleet of multisized mesh monofilament gill nets was deployed opportunistically at the two deepest pool sites on the Coerney River in 2012, being set and retrieved at the same time as the fyke nets, although this sampling method was discontinued for the rest of the project. All captured fish were identified to species and measured to the nearest millimetre before native fish were returned to the stream. All non-native fish were euthanised and collected per the stipulations of the sampling permit.

Data analysis

The hydrological cycle of wetting and drying on the Coerney River was assessed using aerial photography accessed using the historical imagery tool in Google Earth. Sampling sites (generally designated as stream reaches immediately above and below a river causeway) were characterised as either dry or wet, based on the presence or absence of visible surface water. The proportion of the nine sampling sites containing water was thus calculated. Slope at a given sampling site was calculated as the change in vertical height over a 1 km longitudinal transect following the river channel, with the site placed in the centre of the transect. The distance between each site and the nearest fish invasion point (an irrigation canal outflow outside the national park) was calculated along a shapefile of the Coerney River using the Network Analyst tool in ArcGIS version 10.8.2. The presence of overhanging marginal vegetation, as well as visually obstructing cliffs and gullies prevented application of these hydrological analyses to the Wit River.

To explore the relative effects of introduced fish, habitat and hydrology on community dynamics, catch-per-unit-effort (CPUE) data from the various sampling techniques conducted on the river over the 12-year period were converted to mean standardised catch (MSC) data using the multi-gear mean standardisation method of Gibson-Reinemer et al. (2017), which employed the following equation to convert CPUE to MSC:

$$MSC_{ij} = \frac{C_{ij}/e}{\overline{TC}/e} \quad \text{[Eqn 1]}$$

where:

- MSC_{ij} is the mean standardised catch of species i in site visit j,
- C_{ij}/e is the CPUE for a particular sampling gear in that site visit,
- and $\overline{TC}/e$ is the mean total CPUE across all sites for that sampling gear over a particular sampling event.

We summed MSC data from all sampling gears deployed at each site per visit to generate non-biased relative abundance data for key native and non-native fishes along the Coerney and Wit rivers across the 12-year monitoring period.

All analysis was completed in R v. 4.0.2 (22 June 2020). Linear models were implemented via the 'car' package, to test for relationships between: (1) *C. gariepinus* MSC and distance to source, (2) *Pseudobarbus afer* MSC and distance to nearest refuge in the Coerney River. A Wilcoxon rank-sum test was used to determine whether non-native fish presence influenced native fish relative abundance in the Wit River and Coerney River separately. Fish community assemblages and associations regarding invasion status, i.e. communities containing only native fish, those containing extralimital species (*C. gariepinus* and *O. mossambicus*) and those containing invasive *M. salmoides*, were visualised using non-metric multidimensional scaling (nMDS) ordination via 'vegan' (Oksanen et al. 2019). The community data matrix was compiled using the MSC values from all surveys, using only wetted sites which had fish present. Environmental data were categorical factors relating to invasion status. Community data were square-root transformed and Wisconsin double standardisation was applied (*vegan::metaMDS*). Ordination stress was used to assess whether a two-dimensional ordination biplot was suitable to represent community data variation. Stress values < 0.15 were considered appropriate (Cousins, Kennard & Ebner 2017). A one-way PERMANOVA using Bray–Curtis non-metric similarity and 999 permutations was then used to test for significant effects of environmental variables on fish species abundance, after assessing for homogeneity of variances via *vegan::betadisper*. An ANOSIM was also completed to determine similarity of fish assemblage between sites with different invasion status. Finally, after calculating the mean distance between the three fish assemblages, we performed a SIMPER analysis via *vegan::simper* with 999 permutations to determine the most influential species separating each assemblage from the other. A SIMPER analysis performs pairwise comparisons of groups to determine average contribution of each species to the average overall Bray-Curtis dissimilarity. A species with a high average SIMPER value would indicate that the species has a high contribution to the difference between a particular pair within the three groups.

Ethical considerations

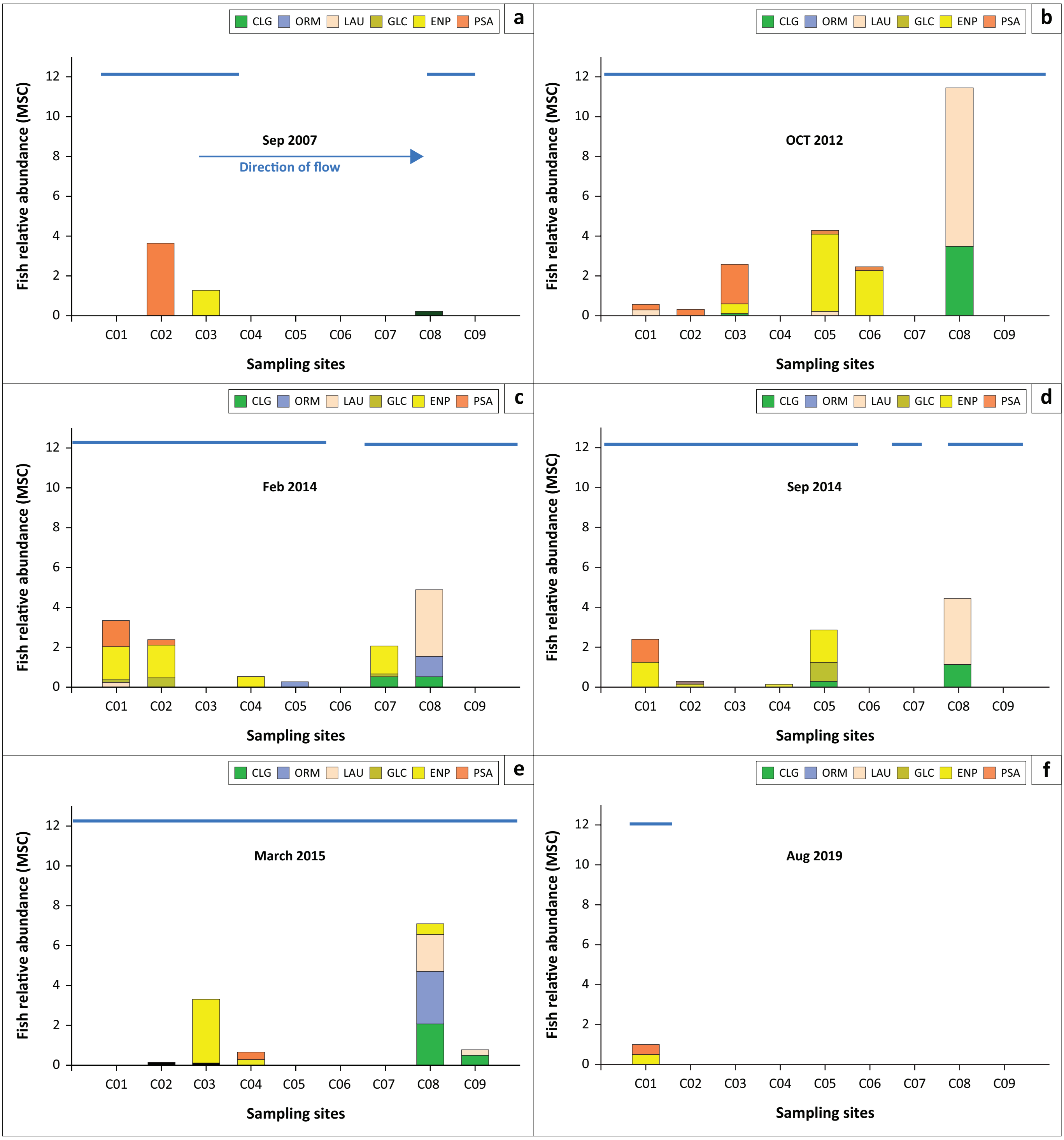
Ethical clearance to conduct this study was obtained from the National Research Foundation, South African Institute for Aquatic Biodiversity Animal Ethics Committee (2011/02).

Results

A total of eight species of freshwater fish were captured over the period of study, including one catadromous species (*Anguilla mossambica*), three native primary freshwater species (*Enteromius pallidus*, *P. afer* and *Labeo umbratus*), one native secondary freshwater species (*Glossogobius callidus*) and three non-native species (*C. gariepinus*, *O. mossambicus* and *M. salmoides*). The eel *A. mossambica* and the bass *M. salmoides* were only encountered in the Wit River, while the native mudfish *L. umbratus* and non-native tilapia *O. mossambicus* were only recorded in the Coerney River.

Seasonal incursions of extralimital species in the Coerney River

Clarias gariepinus was recorded at least at one site along the Coerney River in all but the final field survey, conducted in 2019. This represented two separate invasions (occurring before 2007 and again before 2012), which were both followed by extirpations from the river, the former being deliberately conducted by the Rhodes survey team, and the latter being the natural result of drought (although the site of the 2007 removal activities subsequently dried up as well). The river had almost completely dried up in the years leading up to the 2019 survey, with only a single site at the upper end of the survey reach still containing water (Figure 2). Across the overall sampling period, *C. gariepinus* abundance was significantly negatively predicted by distance from source (t = - 3.63, p < 0.01; Online Appendix 1, Figure S1A), the source being the irrigation canal outflow connecting the Coerney River to water from the Sundays mainstem. In contrast to *C. gariepinus*, the extralimital *O. mossambicus* was only recorded at three site visits between the 2014 and 2015 surveys, indicating a casual occurrence within the stream during the time of surface flow connectivity. Other species



Note: Horizontal blue line at the top of each graph represents extent of surface water across surveyed sites at the time of sampling. CLG, extralimital *Clarias* gariepinus; ORM, extralimital *Oreochromis* mossambicus; LAU, native *Labeo* umbratus; GLC, native *Glossogobius* callidus; ENP, native *Enteromius* pallidus; PSA, native *Pseudobarbus* afer; MSC, mean standardised catch.

FIGURE 2: Change in fish community structure (relative abundance represented as mean standardised catch - MSC) along the seasonally episodic monitored segment of the Coerney River between 2007 and 2019 (sequenced from furthest upstream, C01, to furthest downstream, C09, as indicated by blue flow direction arrow).

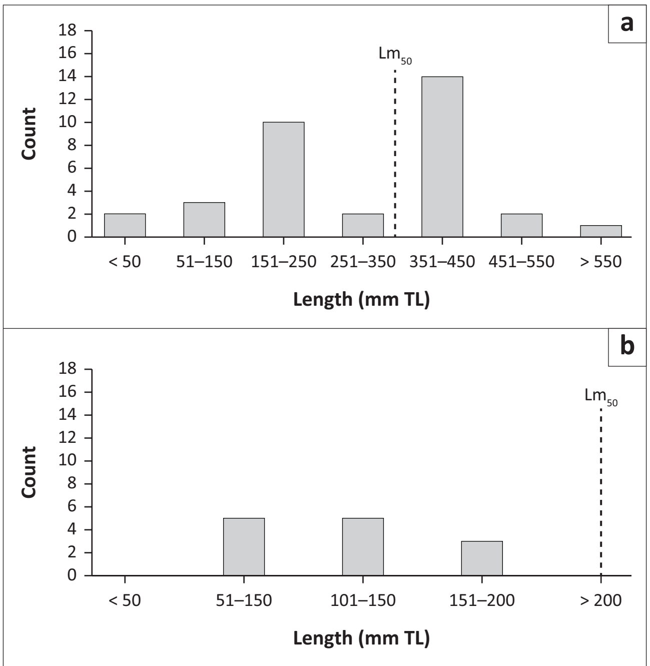
captured in the river included the native cyprinids *E. pallidus*, *P. afer* and *L. umbratus*, with the former two (small minnow species) being more abundant in the upstream sites and the latter (a large mudfish) being more common in the lower reaches throughout the study period (Figure 2). The relative abundance of the endangered Eastern Cape redfin *P. afer* in particular was significantly negatively predicted by increasing downstream distance from the uppermost site (t = -2.07, p < 0.05, Online Appendix 1, Figure S1B), which never completely dried throughout the survey period and was considered a permanent drought refuge. In addition, the freshwater goby *G. callidus* was recorded at low abundances throughout the surveyed segment of the Coerney in all surveys except the final survey in 2019. Of the *C. gariepinus* specimens captured between 2012 and 2019, exactly half (17 individuals) were larger than the length at 50% maturity previously recorded for the species in South Africa (Bruton 1979), although only one specimen reached the modal length for spawning migrant adults (> 550 mm) recorded in that study (Figure 3). In addition to the records on the Coerney River, *C. gariepinus* was recorded for the first time in the Wit River upstream of Slagboom Dam in 2012, but this was downstream of the park boundary and the bass-barrier causeway, and the species was not recaptured in subsequent Wit River surveys up to 2019.

Bass invasions in the Wit River

Following the return of continuous surface flows to the monitored section of the Wit River in 2011, *M. salmoides* was recorded at two localities along the Wit River; a specimen was collected immediately below the causeway outside the AENP boundary that had previously been identified as the invasion barrier, while another specimen was recorded for the first time 6.5 km further upstream on a segment of river recently acquired by the park from private ownership (locally known as 'Manthe's Farm'). This second record, taken from a sequence of long, deep pools, was the first confirmed record of the invasive species inside the park and suggested that the entire length of the river between these two sites could now be considered to be invaded. However, subsequent surveys revealed a patchy, low-abundance presence of *M. salmoides* within the park, with single individuals being captured downstream of Manthe's Farm sporadically at different monitoring sites over the next four surveys. The Manthe's Farm pool complex was one of the few reaches to still retain surface water by the final survey in 2019, where small juvenile *M. salmoides* were found to be persisting in disconnected surface pools, with the benthic goby *G. callidus* the only other fish species present in the same pools. No other specimens were found inside the national park's borders, including all other accessible refuge pools containing surface waters. Throughout the monitoring period of 2012–2014, not a single adult bass was collected (Figure 3), although the presence of very small juveniles (< 100 mm TL) in the 2019 survey indicated that some successful spawning had occurred within the invaded reach over the monitoring period.

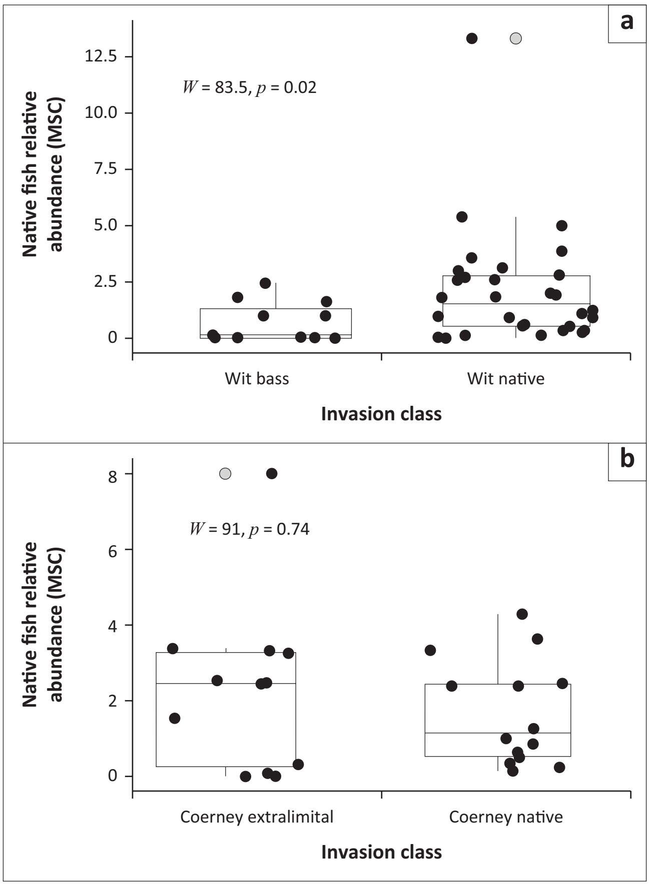
Relative impacts of non-native fish on native communities

Although some native species were occasionally captured together with the bass, their relative abundances were significantly lower than that of native fish recorded at sites where bass were absent ($W = 83.5$; $p = 0.017$; Figure 4a). The impact of bass on the endangered minnow *P. afer* was particularly notable at the Manthe's Farm pools in 2019, where *P. afer* were found together with *G. callidus* in an isolated refuge pool only 100 m away from another isolated pool that contained *M. salmoides* and *G. callidus*. In contrast to *M. salmoides*, *C. gariepinus* and *O. mossambicus* were regularly caught together with native species in often



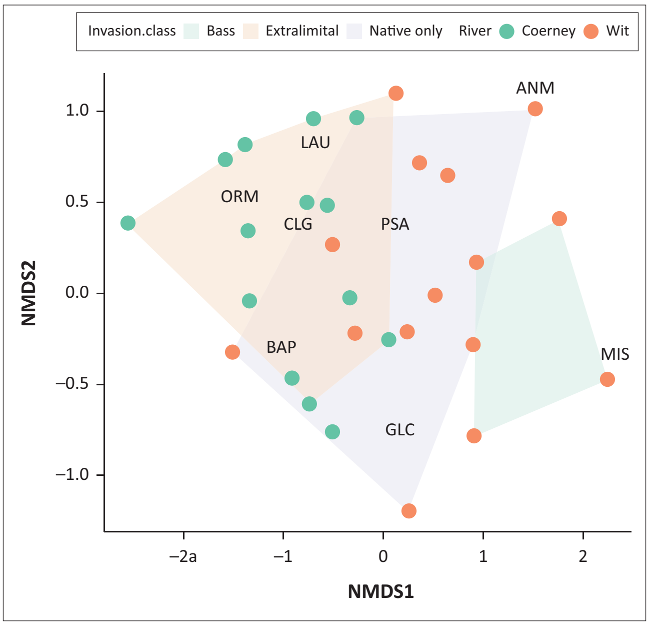
TL, total length.

FIGURE 3: Length frequency distributions (TL) of (a) *Clarias gariepinus* captured in the Coerney River and (b) *Micropterus salmoides* captured in the Wit River between 2012 and 2019. Length at 50% maturity (Lm_{50}) for *C. gariepinus* and *M. salmoides* in southern Africa are derived from Bruton (1979) and Taylor and Weyl (2017), respectively.



MSC, mean standardised catch.

FIGURE 4: Box plots showing relative abundance (MSC) of native fishes (a) on the Wit River, comparing sites with bass present versus only native species present and (b) on the Coerney River, comparing sites with extralimital species present versus only native species present. Wilcoxon rank sum statistics represent significance of the difference in mean native fish abundances between invasion classes on each river.



Note: Three letter species codes represent the ordination centroid for each species.
ORM, extra-limital *Oreochromis mossambicus*; CLG, extralimital *Clarias gariepinus*; LAU, native *Labeo umbratus*; ENP, native *Enteromius pallidus*; PSA, native *Pseudobarbus afer*; GLC, native *Glossogobius callidus*; ANM, native *Anguilla mossambica*; MIS, invasive *Micropterus salmoides*.

FIGURE 5: Non-metric multidimensional scaling plot of variation in fish communities at sites sampled in the Wit and Coerney Rivers between 2007 and 2019. Communities are classified as native only, containing invasive bass, and containing extralimital species (*O. mossambicus, C. gariepinus*) not native to the Sundays River system, and the relative overlap in species composition between these invasion classes is represented by convex hulls.

high abundances, which is reflected in the overlap of the respective community convex hulls produced by the nMDS (Figure 5), as well as a lack of significant difference in native fish relative abundance between sites containing and not containing extralimital species ($W = 91$; $p = 0.738$; Figure 4b).

The ordination stress was 0.10 and therefore appropriate to display on a two-dimensional scale and thus provides an acceptable representation of the fish assemblage. The PERMANOVA showed that invasion class contributed to 17% of the variance in fish assemblage ($R^2 = 0.17$, $F_{64,66} = 6.94$, $p < 0.001$; Figure 5), and the ANOSIM reflected a weak but significant similarity between fish found in sites with different invasion status (ANOSIM R: 0.4542, $p = 0.001$; Figure 5). Although the nMDS visualisation of fish assemblage revealed substantial overlap in overall species composition between the native and extralimital communities, there was significant separation between the sites containing only native fish and those containing invasive bass. SIMPER analysis of the contributions of individual species to the separation between the 'native only' and 'bass' assemblages revealed a particular negative impact of bass on the two native minnows, as variation in the relative abundance of *E. pallidus*, *P. afer* and *M. salmoides* together contributed 74.6% of total difference between the communities (see Online Appendix 1, Table S1).

The sites where the native and extralimital communities did not overlap were mostly the lower reaches of the Coerney, as *C. gariepinus* abundances were higher at sites closer to the invasion source (the canal outflow downstream) than at sites further upstream (Online Appendix 1, Figure 1-A1). These distribution patterns indicate the slow upstream penetration of the river by the introduced extralimital species during periods of surface flow connectivity, followed by their retreat outside the park during the subsequent drought (Figure 2). As neither *C. gariepinus* nor *O. mossambicus* ever penetrated as far upstream as the permanently wetted site at the uppermost extent of the monitoring reach (C01; Figure 1, Figure 2), neither species ever became trapped together with native species in this spatially constrained drought refugium.

Discussion

Drying-wetting regimes of riverine systems have been overlooked in invasion science but may be both a barrier and facilitator to invasive species spread (Guareschi & South 2024). This case study in ANEP exemplifies the complex dynamics, which are predicted to become more common in this region (van Wilgen et al. 2022). The two major droughts over the research period of 2007–2019 resulted in its tributary streams becoming disconnected and, in some instances, almost completely dry apart from key deep water refugia for much of this 12-year period. Freshwater fish native to these systems appear to have utilised these drought refugia effectively to resist the effects of dewatering and displayed resilient population growth in the form of rapid expansion of range and abundance in the re-wetted reaches during the rainy periods (2012–2015). Non-native fishes showed contrasting responses to drought and re-wetting over the same period. *Clarias gariepinus* expanded their range upstream into the Coerney River from the invasion point (the Sundays River irrigation network, which served as an invasion corridor providing a steady source propagule pressure; Ellender et al. 2014; Woodford et al. 2013) during periods of surface flow connectivity.

When drought returned after 2015, however, *C. gariepinus* retreated downstream and outside the park's boundaries. *Clarias gariepinus* had previously been identified as a potentially damaging invader in Eastern Cape headwater streams, with an ecological impact on native communities that is yet to be fully understood (Ellender et al. 2014). Extralimital *C. gariepinus* in the Sundays River have highly plastic feeding niches that overlap with native species, suggesting the potential for competitive interference in confined headwater habitats, especially those constrained by low flows (Kadye & Booth 2012, 2013). Moreover, *C. gariepinus* have been shown to be more efficient and aggressive predators compared to native competitors such as *G. callidus* (Alexander et al. 2014), reinforcing the potential for competitive exclusion. Nonetheless, the large proportion of small, juvenile catfish captured throughout the monitoring period suggests that the Coerney River merely functioned as opportunistic spawning and nursery habitat, compared to the Sundays River mainstem, where populations have long been fully established (Kadye & Booth 2013). The naturally episodic hydrology of the Coerney River primarily acted to mitigate against the overall progression of the catfish invasion, rather than enhance the potential negative impact of *C. gariepinus* on native fishes trapped together in disconnected drought refugia. If future *C. gariepinus* invasions following the return of flows manage to penetrate as far upstream as critical refuge pools such as the large pool above the Nguni Lodge (C01), this potential threat will need to be re-evaluated. It is nonetheless noteworthy that neither extralimital species appeared to have a measurable negative impact on native fishes in the Coerney River throughout the study, compared to the negative associations with North American bass observed on the Wit River. While international studies comparing the relative impact of extralimital versus extra-regional invaders on native aquatic communities are scarce, Magoulick (2014) found that introduced extra-regional alien freshwater crayfish had a higher impact potential in invaded river ecosystems compared to extralimital crayfish species because of differences in their functional traits that may reduce biotic resistance to extra-regional species.

The unexpected capture of *C. gariepinus* below the barrier causeway on the Wit River, but upstream of the Slagboom Dam, which had previously served as the barrier to upstream dispersal for the species (Weyl et al. 2008), suggests that a new independent human-mediated introduction had occurred between 2007 and 2012. This introduction was likely made into the Slagboom Dam reservoir by anglers, who are widely believed to facilitate such introductions in the Western and Eastern Cape provinces (Weyl et al. 2016) and is a cause for concern. While *C. gariepinus* did not appear to penetrate above the concrete causeway into AENP during the study period, it is not clear that such a minor barrier, which is known to be effective for blocking upstream bass invasions (van der Walt et al. 2016), would necessarily prevent the upstream migration of *C. gariepinus*. It is recommended that the presence of catfish in the lower Wit River be closely monitored once flows return to the region.

In contrast to the potential ecological impacts of *C. gariepinus*, *M. salmoides* has a well-established record of negative impacts in South African rivers (Ellender & Weyl 2014) and was expected to pose a major threat to fish communities in the Wit River after its presumed deliberate introduction into the upper reaches of AENP, inside the former privately held Manthe's Farm section. A positive finding of this study is that no native fish previously found to occur in these tributaries (Russell 1998; Weyl et al. 2008) were missing from our catches, indicating that no complete extirpations have taken place following the introduction of bass. While *M. salmoides* did appear to deplete native fish communities in pools where it occurred, it was nonetheless constrained in its distribution throughout the survey period. Bass were generally captured close to their introduction points in the Slagboom reservoir and the Manthe's Farm pools, with a few notable exceptions where the species was caught in the vicinity of Narina Camp (near the middle of the study reach) and above the original (prior to 2012) causeway barrier outside the park in 2015, respectively, 4 km and 6.5 km downstream of the presumed upper introduction point. Subsequent to these temporary range expansions, the drought and associated dewatering of all but a few critical refugia appears to have mitigated against the establishment and further spread of these non-native populations. The minimum recorded length at 50% maturity (Lm_{50}) for introduced *M. salmoides* is above 200 mm TL, with South African populations ranging from 232 mm to 254 mm (Taylor &Weyl 2017). All bass collected throughout the study were juveniles, with the largest recorded being 184 mm TL. This may have mediated the overall ecological impact of the bass invasion, because despite there being clear evidence for successful reproduction in the Manthe's Farm pools, the initial point of invasion, the population throughout the Wit River was dominated by juveniles, and could be considered to still be in the lag phase of population growth and spread (*sensu* Crooks 2005). In this way, the drought of 2016–2019 was instrumental in preventing the bass invasion from exiting the lag phase and likely restricted the invasive population's overall impact on the fish community.

Addo Elephant National Park represents a unique protected area for freshwater fishes in that its native species have evolved to cope with naturally variable hydrology and thus the potential for more stochastic rainfall and prolonged drought cycles driven by climate change (Lennox et al. 2019) is less likely to directly affect the conservation of these species. Prolonged drought does, however, have the potential to both mitigate the spread of invasive fishes at large spatial (whole tributaries) and temporal scales (multi-year droughts), while conversely mediating or enhancing ecological impact in the short term at different spatial scales (i.e. between and within confined surface water refugia for the period of their isolation from the rest of the river). Drought has been observed to mediate the impact of invasive fish on native freshwater fish in Australia, where seasonal dewatering not only limited the upstream penetration of invasive predatory trout but also enabled vulnerable native galaxiid fish to become spatially separated from the trout in disconnected pools within the drying river channel (Closs & Lake 1996). Human-mediated dewatering also appeared to create temporary predation refugia for galaxiids in trout-invaded streams in Otago, New Zealand (Leprieur et al. 2006). In the case of *M. salmoides* in this study, dewatering appeared to spatially segregate bass from the other fishes in the stream, although deep pools containing bass clearly became hostile environments for the native species, with *P. afer* in particular only found in the same pool as bass in the very first survey of the Manthe's Farm pools in which bass were detected. Bass are able to exert high predatory impact on small minnows because of their ecomorphology, which is better adapted to simplified habitats and pursuit hunting compared with native predator species (Khosa et al. 2021; Luger et al. 2020). The severe impact of bass on the minnows *P. afer* and *E. pallidus*, relative to the goby *G. callidus*, may be a result of differences in evolved predator-avoidance behaviour, as *P. afer* displayed disproportionate vulnerability to bass predation in open water during crepuscular hunting hours in rivers, relative to their vulnerability to the native benthic predator *A. mossambica* (Ellender et al. 2018). This variation in behavioural traits is a likely reason why the more cryptic benthic gobies were able to co-occur with bass, even in confined drought refuge pools.

Conclusion

The long-term monitoring of freshwater fish invasions in AENP indicates that non-native fish, in particular the invasive bass *M. salmoides*, pose a credible threat to fish biodiversity within the park's borders. Proactive management of these invasive species is thus required going forward, as is minimising the risk of future invasions within the park. A key goal of SANParks as a national institution is to 'restore or promote hydrological connectivity' within its national parks (Roux et al. 2023), although headwater tributaries in AENP do not hold as high a priority for such proactive management compared to lowland rivers in flagship parks like Kruger National Park, where the active removal of dispersal barriers such as causeways and weirs is being pursued. Present barriers to dispersal in AENP, like the causeway on the Wit River, continue to provide a positive service to the conservation of freshwater fishes inside the park, and should be preserved and potentially enhanced, if doing so would further guard the park from upstream fish invasions in the future. Barriers to dispersal are increasingly being recognised as a critical tool in managing aquatic invasions worldwide, and the creation or enhancement of physical barriers has seen positive conservation outcomes (70% – 100% upstream exclusion of invasive fauna) for invaded rivers across North America, Australasia and Europe (Jones et al. 2023).

When considering how to address the ongoing presence of non-native species inside Addo Elephant National Park, this study shows that *M. salmoides* poses a far more significant long-term threat to freshwater fish conservation relative to the extralimital *C. gariepinus* and *O. mossambicus*. It should therefore be a priority for continual monitoring and population control operations to be conducted in regions of the park where bass have established. While the 2016–2019 drought had a significant limiting effect on the ongoing invasion, it was unable to extirpate the species in the same way extralimital species were excluded from the Coerney River in that time, and thus future interventions by SANParks and conservation partners are likely to be necessary to limit the impact of bass on the native ichthyofauna. Populations of *Micropterus* sp. have been successfully removed from South African streams using the piscicide rotenone (Weyl et al. 2014) and through manual removal (van der Walt et al. 2019), with the latter technique also seeing success in population control (although not eradication) within a lake in Japan, where behavioural vulnerabilities such as nest making and guarding were exploited to remove breeding fish (Fujimoto et al. 2021). Manual removal is preferable to piscicides within protected areas, especially in small streams where vulnerable native fish co-occur with the invader. Within AENP, bass and other non-native fish are likely to be easiest to remove during severe droughts, where their populations are confined to small, easy to access drought refugia. Regional downscaled climate models suggest southern Africa will receive less rainfall overall in the coming century (van Wilgen et al. 2022) indicating that more large droughts are likely to occur affecting the rivers of AENP and that fish will have to adapt to longer and more severe dewatering events. The native fishes' rapid recovery and expansion from isolated pools following the return of surface flow in this study suggests an evolved adaptation to the natural intermittency of the Sundays River's tributaries that should grant them resilience against these future hydrological disturbances. Nonetheless, this resilience could be compromised if they are forced into prolonged contact with non-native predators within a shrinking number of wetted refugia. It is thus recommended that future droughts on the scale of the 2016–2019 drought be taken as opportunities to conduct renewed fish surveys, and that refugia found to contain non-native fish be fished to depletion to maximise the possibility of eradicating these fish from within the park's borders.

Acknowledgements

This research was performed with the support of the NRF-SAIAB Research Platform. The authors would like to acknowledge the intellectual and material contributions of the late Professor Olaf Weyl, who was a mentor to us all over the duration of the AENP monitoring programme. The authors are thankful for SANParks support from Jessyca Domingo and Portia Chake. Jonathan Levin is thanked for additional statistical support.

Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

D.J.W. developed the monitoring programme that was the basis for this study and is responsible for the aims and scope of the article, as well as compiling the primary field dataset. D.J.W., J.S., L.M., and J.P. all contributed directly to field data collection. J.S. performed all statistical analyses. D.J.W. took the lead in writing the article, with editorial input from all authors.

Funding information

Funding for this research was provided by the NRF-SAIAB Institutional Support system, the DSI/NRF Centre for Invasion Biology, the Water Research Commission (Project K5/2039) and the DSI/NRF SARChI Chair in Inland Fisheries and Freshwater Ecology (UID 110507). DJW acknowledges financial support from the DSI/NRF incentive fund for rated researchers (Grant No. 103581); LM was supported by the DSI/NRF Professional Development Programme (Grant No. 101039).

Data availability

The primary data for this study are available to download from Figshare.com. DOI: 10.6084/m9.figshare.25495306

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