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Using a head-start conservation intervention to boost spawning numbers of the endangered Clanwilliam sandfish

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Abstract

Freshwater ecosystems are the most threatened on Earth, with many species facing extinction. The Clanwilliam sandfish (*Labeo seeberi*) is South Africa's most threatened migratory freshwater fish and is endemic to the Olifants–Doring River system in the Cape Fold Ecoregion. Non-native fish predation and river desiccation have caused a recruitment bottleneck, severely compromising juvenile survival and resulting in a declining population of aging sandfish. The Saving Sandfish Project launched an emergency head-start intervention in 2020 to reduce extinction risk. We (1) rescued juvenile sandfish from drying pools in a key spawning tributary (the Biedouw River); (2) relocated them to 6 off-stream reservoirs; and (3) released reservoir-reared sandfish back into their natal river once large enough to evade non-native fish predation. Here, we estimate survival in the reservoir environment, evaluate return rates relative to wild run size, and assess the probability of return based on conditions at release. Between 2020 and 2022, we stocked 33,391 juvenile sandfish into the 6 reservoirs. After 1 year, the estimated survival rate at one reservoir was 0.679 (range based on 95% CI: 0.385–0.973). Release and return results are presented only for the first (2020) rescue cohort. In 2021, we released 1277 sandfish from 2 reservoirs into the Biedouw River, comprising 16.6% of the 2020 rescue cohort. Mean size at release was 169 mm (SE 0.6) total length. Of those released, 994 were PIT-tagged. A total of 77 PIT-tagged sandfish were recorded during the 2022 spawning migration—a return rate of 7.7% of tagged releases in the first year of returns. Size of fish and distance from the Doring River at release were significant predictors of return probability, with larger fish released further from the Doring experiencing a higher probability of return. This program serves as a model for the conservation of freshwater fish where there is an imminent and high risk of extinction.

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KEYWORDS
desiccation, endangered species, endemic species, fish rescue, head-start, migratory freshwater fish, non-native species, PIT tag, recruitment bottleneck, South Africa

1 | INTRODUCTION

Freshwater ecosystems hold a disproportionate percentage of Earth's vertebrate biodiversity (Hughes, 2021; Strayer & Dudgeon, 2010), yet they are the most threatened ecosystems on the planet (Grooten & Almond, 2018). Since 1970, populations of freshwater vertebrates have declined by 83% (Almond et al., 2022)—more than twice the rate of their terrestrial and marine counterparts (McRae et al., 2017). Major global threats to freshwater fishes include non-native species introductions, declining water flows, and habitat fragmentation (Dudgeon, 2019; Dudgeon et al., 2006). The last of these is especially problematic for migratory fish (Dudgeon, 2019), which declined by 76% between 1970 and 2016 (Deinet et al., 2020).

In South Africa, freshwater fish are the most threatened vertebrate group (Skowno et al., 2019); two-thirds of endemic species are listed as vulnerable, endangered, or critically endangered (Chakona et al., 2022; Skowno et al., 2019). There is an urgent need to prioritize the conservation of freshwater fish in South Africa to safeguard vulnerable species and the ecosystems they inhabit. Various approaches have been used to conserve freshwater fishes in South Africa and Lesotho, including habitat rehabilitation, non-native species removal, and conservation translocations (Appendix S1). Conservation translocations have historically involved wild-to-wild translocations and the creation of "refuge" populations in off-stream impoundments.

"Head-starting" is an alternative translocation approach that involves rescuing and captive-rearing early-stage individuals to a later life stage and then returning them to the wild (Alberts, 2007). This intervention is commonly used to conserve threatened reptiles and amphibians (Sainsbury et al., 2021a, 2021b, 2021c; Smith et al., 2020) to increase survival beyond vulnerable life stages, but is less well documented in the management of freshwater fishes, and is largely limited to salmonids (e.g., Beebe et al., 2021; Lopez Arriaza et al., 2017; but see Healy et al., 2022 for a non-salmonid example). Here, we present initial results from the implementation of a head-start program piloted for the most threatened migratory freshwater fish in South Africa, the Clanwilliam sandfish (*Labeo seeberi*).

The sandfish is a large-bodied cyprinid that grows to 600 mm total length (TL) and is endemic to the Olifants–Doring River system (ODRS) in the Cape Fold Ecoregion of South Africa (Figure 1). Its sub-terminal mouth allows it to feed on organic matter in soft sediments and graze algae from rocks (Skelton, 2001). Adults over-summer in isolated pools in the mainstem Doring River and undertake annual spawning migrations into its tributaries at the beginning of spring (Skelton, 2001). In addition to the migratory populations, some non-migratory populations persist in the permanent headwater reaches of several tributaries. Owing to their variable life cycle and dependence on large, connected river systems, sandfish act as an umbrella species (Noss, 1990).

Sandfish were once widespread throughout the ODRS (Gaigher, 1973, 1978), but have not been recorded in the Olifants River mainstem and tributaries in recent decades, likely due to predation by non-native fishes and the construction of large instream dam walls (>7 m high) that block spawning migrations (Jordaan et al., 2017). Presently, remaining sandfish persist in the Doring River system in fragmented and declining populations (Cerrilla et al., 2022; Jordaan et al., 2017).

The Biedouw River, a seasonal tributary of the Doring River, is one of the few known tributaries where sandfish still undertake annual spawning migrations (Figure 1). Non-native smallmouth bass (*Micropterus dolomieu*), spotted bass (*M. punctulatus*), and bluegill sunfish (*Lepomis macrochirus*), as well as extralimital banded tilapia (*Tilapia sparrmanii*), co-occur with adult and juvenile sandfish in the lower reaches of the Biedouw River during spring and early summer. As these non-natives are well-established throughout the Doring River mainstem, it is suspected that they re-invade the seasonal Biedouw River each year when flows return. After hatching, young sandfish suffer significant predation from the North American centrarchids. The predatory impacts of black bass species on indigenous fishes in the ODRS are well documented (Cerrilla et al., 2022; Paxton et al., 2002; van der Walt et al., 2016; Weyl et al., 2014; Woodford et al., 2005), with smaller-bodied species and juveniles of larger species (<100–200 mm TL) mostly unable to coexist with bass (Cerrilla et al., 2022; van der Walt et al., 2016; Weyl et al., 2013).

Observations over several spawning seasons have shown that young sandfish that evade predation by non-native fish in the Biedouw River eventually succumb to river desiccation. The Biedouw River is a seasonally flowing system that historically held water through summer

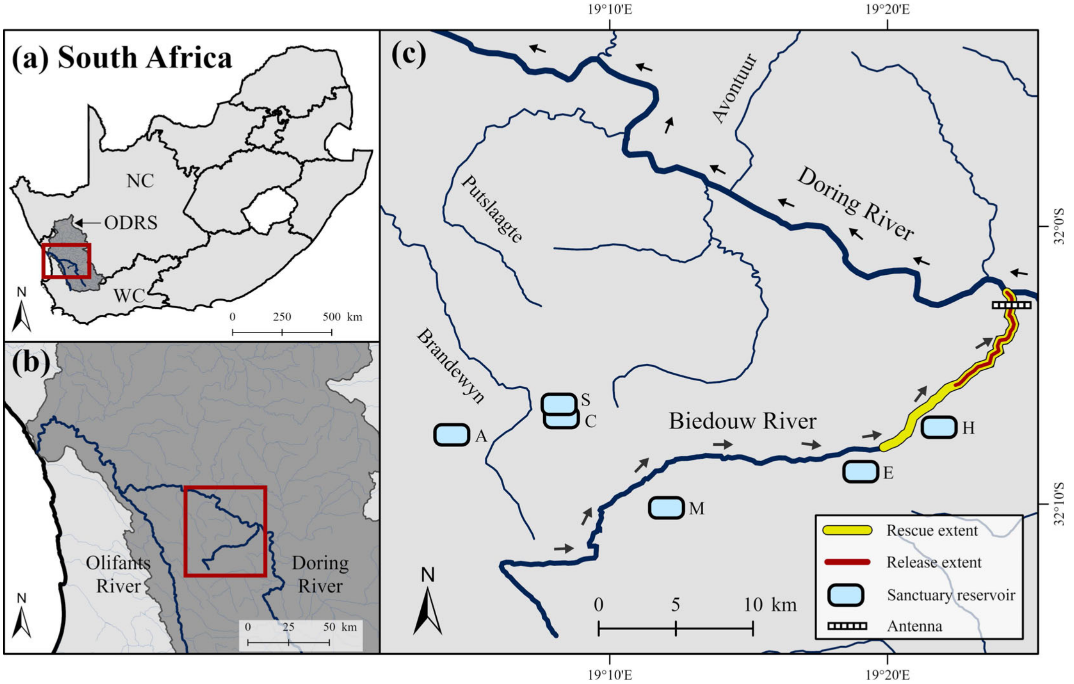

FIGURE 1 Map of study area: (a) South Africa with provinces outlined, (b) Olifants and Doring Rivers, and (c) Biedouw River and surrounding area. A, Alpha Excelsior Reservoir; C, Clay Reservoir; E, Enjo Reservoir; H, Hartsbesluit Reservoir; M, Mertenhof Reservoir; NC, Northern Cape; ODRS, Olifants–Doring River system; S, Syfer Reservoir; WC, Western Cape. In 2020, Clay (C), Mertenhof (M), and Enjo (E) Reservoirs were stocked, but sandfish were only released from Mertenhof (M) and Enjo (E) Reservoirs in 2021. The remaining reservoirs were stocked in 2021 and 2022.

in isolated pools, creating nursery habitat for indigenous fish. However, the prolific spread of thirsty non-native plant species in the catchment and water over-abstraction for agricultural purposes have over time caused the lower 15 km of the river, where sandfish spawn and juveniles develop, to dry up completely by mid-summer. This results in mass stranding and the loss of tens of thousands of juvenile sandfish. Moreover, young sandfish that reach the Doring River mainstem before flow ceases in the Biedouw River face predation from the larger bass that reside there. It is thus suspected that few young sandfish survive the juvenile phase.

The sandfish population in the Doring River mainstem mostly comprises large adults, with few subadults and no juveniles detected during recent surveys (Paxton et al., 2016). Without intervention, the species is in danger of extinction. In 2020, the Saving Sandfish Project (SSP), a collective of NGOs, government organizations, landowners, and students, launched a head-start intervention as an emergency measure to augment the wild population by increasing recruitment, thus safeguarding the species in the short term. We rescued juvenile sandfish from the drying Biedouw River, relocated them to off-stream sanctuary reservoirs, and returned them to the river once they had grown to at least 100 mm TL, minimizing their vulnerability to predatory non-native fish. Here, we present findings from the first cycle of this intervention. Specifically, our objectives were to (1) estimate 1 year post-stocking survival in one reservoir; (2) estimate wild run size; (3) evaluate return rates of tagged head-started fish and their relative contribution to run size; and (4) assess the probability of return based on several conditions at the time of release.

2 | METHODS

The Biedouw River (Figure 1) is located in an ecotone between the Fynbos and Succulent Karoo biomes (SANBI, 2018) in South Africa's Western Cape Province. Mean annual rainfall is 234 mm, of which 187 mm falls in "winter" (April–September) and only 43 mm falls in "summer" (October–March; South African Weather Service).

2.1 | Establishment of sanctuary reservoirs

Between March 2019 and May 2022, we eradicated non-native fish from 5 off-stream reservoirs in the Doring catchment (Figure 1). Prior to removal, we set fyke nets ($n = 4$–7) overnight in each reservoir to determine the species present. The reservoirs were either drained, treated with the piscicide rotenone, or both (Appendix S2). Following removal, we resurveyed each reservoir with overnight fyke nets and conducted visual inspections to assess eradication efficacy. A 6th reservoir (Alpha Excelsior) was not drained or treated because it contained only native Clanwilliam yellowfish (*Labeobarbus seeberi*).

2.2 | Rescues

Following sandfish spawning migrations in 2020, 2021, and 2022, we rescued juvenile sandfish from the Biedouw River in November of each year (Figure 2). The 2021 rescue season extended into March 2022. Rescuers used seine nets to collect sandfish from shallow pools located in the lower 15 km of the Biedouw River where young sandfish were observed. Seine net passes were continued in each pool until fewer than 10 sandfish were caught in 3 consecutive passes. We transported rescued sandfish to the reservoirs in 25-L buckets fitted with oxygen pumps. During the 2021/22 and 2022 rescue seasons, we measured a subsample of rescued fish from a subset of source pools prior to relocation. Each subsample consisted of 30–55 sandfish per source pool to minimize the number of fish subjected to handling, while allowing a representative length distribution to be obtained. In one case, where only 10 individuals were rescued from a source pool, all 10 were measured. The subset of source pools spanned the spatial range of rescue locations over the entire duration of the 2021/22 and 2022 rescue seasons.

It is important to note that we report the methods and results corresponding to the first 3 rescue seasons to demonstrate the scope of the intervention. However, the

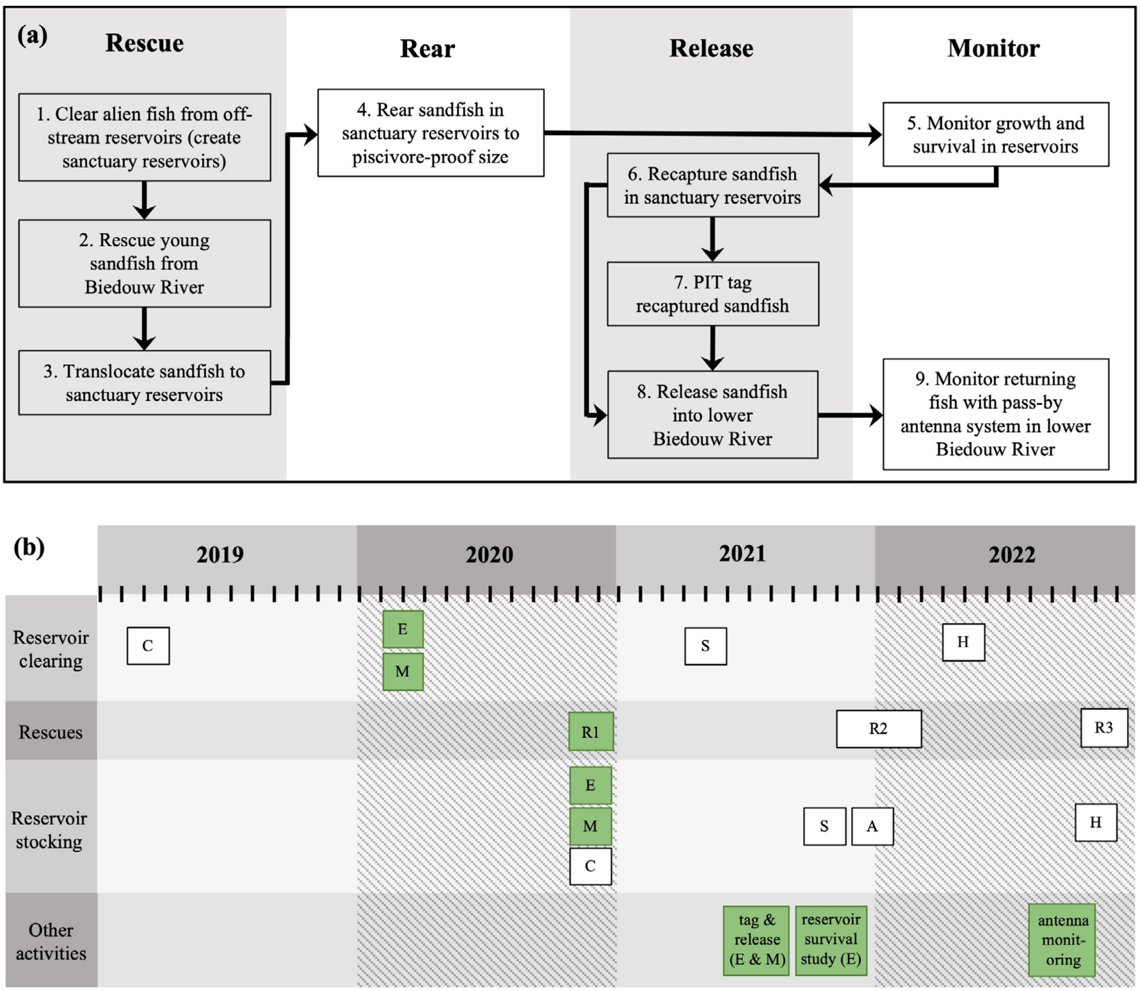

FIGURE 2 (a) Flowchart and (b) timeline of events throughout head-start intervention. A, Alpha Excelsior Reservoir; C, Clay Reservoir; E, Enjo Reservoir; H, Hartsbesluit Reservoir; M, Mertenhof Reservoir; R1, R2, and R3, rescues 1–3; S, Syfer Reservoir. The events related to Enjo (E) and Mertenhof (M) Reservoirs, which contain the only fish which underwent a full rescue–rear–release–return cycle between 2020 and 2022, are highlighted in green. A full timeline of events is available in Appendix S3.

results of releases and returns are reported only for the first rescue season's cohort (i.e., sandfish that were rescued in 2020, released in 2021, and returned to the Biedouw in 2022), as this cohort alone has completed a full rescue–rear–release–return cycle.

2.3 | Survival rate in reservoir environment

To evaluate the suitability of the reservoir environment as rearing habitat for juvenile sandfish, we estimated the survival rate of translocated fish in Enjo Reservoir 1 year after initial stocking, which took place in October–November 2020. Survival was inferred based on known stocking numbers and estimated abundance 1 year after stocking.

First, we estimated the population size of sandfish in Enjo Reservoir in November 2021 using the Lincoln–Peterson index (LPI), which uses a mark/recapture sampling design. The LPI requires 3 values to estimate population size (M): n_1 (the number of animals caught, marked, and released in the first sample at time 1), m_2 (the number of marked animals present in the second sample at time 2), and n_2 (the total number of animals caught in the second sample at time 2; Pine et al., 2003; Equation 1; Table 1).

$$M = \frac{n_1 n_2}{m_2} \quad (1)$$

The 95% confidence intervals around the abundance estimate were calculated with the *ciPetersen* function from the R package *recapr* (Tyers, 2021), using the normal approximation.

Over the course of 2 tagging sessions on October 8 and November 6, 2021, we tagged 100 individuals (n_1) in Enjo Reservoir with 12 mm Biomark APT12 passive integrated transponder (PIT) tags. Tags were injected into the body cavity, posterior to the pelvic fins and offset from the midventral line. Fish tagged for mark/recapture study ranged in size between 159 and 218 mm. We allowed 3 weeks to pass after the second tagging session to ensure tagged fish mixed randomly back into the population. We then used fyke nets to collect the second sample (n_2) from Enjo Reservoir on November 28, 2021, and used the LPI to calculate population size (M).

The LPI assumes that the population is closed (i.e., that no immigration, emigration, births, or deaths occur between marking and recapture). We treated the Enjo Reservoir population of sandfish as a closed population as immigration and emigration could not have occurred (the reservoir is land-locked and isolated from all water courses), and no births took place (verified by lack of spawning activity and larval fish). While some deaths may have occurred between tagging and sampling, they were likely minimal due to the short intervening time period. Nevertheless, the violation of this assumption may have biased the population estimate (M) and results should therefore be interpreted with caution. Tagging of rescued juveniles upon initial stocking and subsequent monitoring under an open population model was not possible due to the small size of juveniles during stocking (23–143 mm, mean of 54 ± 1.5 SE), which precluded safe tagging.

The estimated population size in November 2021 (M) allows us to estimate 1-year survival if we also know the number of fish potentially available for capture during the sampling event. During October–November 2020, 1815 juvenile sandfish were stocked into Enjo Reservoir

TABLE 1 Elements of mark–recapture study and survival estimate from Enjo Reservoir using the Lincoln–Peterson index ($M = \frac{n_1 n_2}{m_2}$; Pine et al., 2003) and estimated abundance in November 2021.

Time period	Variable name	Description	Value
Oct–Nov 2020	-	Initial stocking of rescued sandfish into Enjo Reservoir	1815 fish
Jun–Sep 2021	-	Removal of sandfish from Enjo Reservoir for release into the wild	−588 fish
Oct 2021	-	Maximum number of fish potentially available for recapture in November 2021, that is, initial population size (stocking number: 1815) minus amount removed in Jun–Sep 2021 (588)	1227 fish
Oct 8 and Nov 6, 2021	n_1	Number of sandfish caught, marked, and released at time 1	100 fish
Nov 28, 2021	n_2	Number of sandfish in sample at time 2	150 fish
Nov 28, 2021	m_2	Number of marked sandfish in sample at time 2	18 fish

(initial population size). During June–September 2021, 588 of these were recaptured from Enjo Reservoir and released into the Biedouw River. The remainder (1227) is the maximum number of known stocked fish that could potentially be available for capture during the November 2021 sampling event. The estimated survival rate was inferred by dividing the estimated abundance derived from the LPI (*M*) by 1227. The range of survival rates was calculated by dividing the upper and lower bounds of the 95% confidence intervals by this same value.

2.4 | Release of sanctuary-reared sandfish

Between June and September 2021, we recaptured 1-year-old sandfish from Enjo and Mertenhof Reservoirs using fyke nets and released them back into the Biedouw River. Sandfish were not released from Clay Reservoir in 2021 due to staffing and timing constraints that made the longer transport time challenging. We PIT-tagged 988 fish 150 mm TL and larger to monitor survival and return rates (George et al., 2009). A total of 243 fish (all from Mertenhof Reservoir) measuring less than 150 mm were released without a tag to minimize handling and tagging stress to smaller fish, which are more vulnerable to predation. Five fish measuring 142–149 mm were tagged and released prior to the implementation of this size limit. Several fish ($n = 34$) were released without a tag due to shortage of tags in one tagging session ($n = 6$), accidental escape into the river prior to tagging ($n = 16$), or the presence of injuries or deformities ($n = 12$). All tagged fish were measured to enable monitoring of growth rate if sampled again in the future. One additional tagged fish escaped prior to being measured.

We used Welch's two-sample *t*-test (significance threshold .05; R package "stats" version 4.2.2; R Core Team, 2022) to evaluate potential differences in size at release between Enjo and Mertenhof Reservoirs.

2.5 | Monitoring of returning sandfish

Between August 25 and September 17, 2021, schools of large adult sandfish (~300–600 mm TL) migrated into the Biedouw River to spawn. During this time, we undertook 3 exhaustive visual surveys of the lower 15 km of the Biedouw River (the area occupied by migrating sandfish) to obtain an estimate of the size of the wild spawning migration. Pairs of researchers walked along the banks and counted the numbers of migrating sandfish in each pool. Sightings were cross-referenced with simultaneous sightings from other locations along the reach to ensure that each fish was counted only once. Surveys of this nature were possible because the pools were relatively shallow (<1 m in most cases) and narrow (7–16 m wide), the water was relatively clear, and there were very few instream visual obstructions (Appendix S4). Although reservoir-reared sandfish were released into the same area during this period, they were easily distinguishable from the wild fish by the large disparity in size between the 2 groups. Moreover, the vast majority of reservoir-reared fish were assumed to have left the Biedouw almost immediately after release, as very few were observed thereafter, and none were observed schooling with the wild adults.

In August 2022, prior to the spawning migration, we installed a 9-m-long solar-powered Biomark Litz Cord pass-by antenna system with an IS1001 data reader across the width of the channel in the Biedouw River, 900 m upstream from its confluence with the Doring River (Figure 1). The antenna, which was anchored to the streambed, passively detected and stored the unique identification number of any PIT-tagged sandfish moving up the river channel to a depth of 50 cm. A PIT tag was used to test the system throughout the study period to confirm that fish swimming close to the surface at various flow rates and maximum depths would be recorded. Additionally, we set fyke nets twice in September 2022 during the spawning migration and scanned each fish to test for the presence of a tag (Appendix S3).

To assess which factors might affect the probability of a fish returning 1 year after release, we used a generalized linear model (R package "stats" version 4.2.2; R Core Team, 2022) with a binomial distribution. The explanatory variables included in the original model were fish size at release (mm), distance of release site from the Doring River confluence (km), and release window (timing of release). The 7 release dates were grouped into 3 release windows based on their temporal proximity to one another: June 26 to June 27, August 30 to September 3, and September 12. We excluded source reservoir from the model to avoid multicollinearity with size at release since tagged fish from Mertenhof Reservoir were significantly smaller than those from Enjo Reservoir. We carried out model selection using iterative stepwise selection to a minimum adequate model. All variables with a *p*-value lower than .1 were removed from the model.

All work was carried out with permits from CapeNature (CN54-28-14847, CN54-28-14848, CN54-28-22956, CN54-28-19451, CN54-28-19450, CN54-28-19448, CN54 -28-19449) and ethical clearance from the University of Cape Town (2021/V8/CR/A). The Department of Water and Sanitation issued a general authorization for the reservoir rotenone treatments.

3 | RESULTS

3.1 | Establishment of sanctuary reservoirs

Pre-treatment surveys of sanctuary reservoirs indicated the presence of bluegill sunfish at Mertenhof, Clay, and Syfer Reservoirs, bluegill sunfish and common carp (*Cyprinus carpio*) at Enjo Reservoir, and bluegill sunfish and 8 adult sandfish at Hartsbesluit Reservoir. Dense aquatic vegetation at Hartsbesluit Reservoir prevented the use of a motorboat to access sandfish as they surfaced after initial rotenone exposure; therefore, we were unable to rescue and relocate the individuals during treatment. Post-treatment fyke net surveys revealed no fish remaining in any of the reservoirs.

3.2 | Rescues

Between 2020 and 2022, we rescued 33,391 juvenile sandfish—7699 during the 2020 season (translocated to Enjo, Mertenhof, and Clay Reservoirs; Table 2), 7396 during the 2021/22 season (as in 2020, with the addition of Syfer and Alpha Excelsior Reservoirs), and 18,296 during the 2022 season (translocated to Mertenhof, Syfer, Alpha Excelsior, and Hartsbesluit Reservoirs). The mortality rate of rescued sandfish (the proportion of sandfish that died during transport to reservoirs) during the 2021/22 and 2022 seasons was 0.7%. Rescued sandfish during the 2021/22 and 2022 seasons ranged in size from 23 to 143 mm TL, with a mean of 54 mm (SE 1.5) TL ($n = 511$).

3.3 | Survival rate in reservoir environment

Capture probabilities during the first and second sampling events at Enjo Reservoir are as follows: both events (0.022), first event but not second (0.098), second event but not first (0.158), and neither event (0.722). The LPI yielded an estimated population size (M) of 833 (95% CI [472, 1194]) sandfish at Enjo Reservoir in November 2021 (Table 1). Given the maximum number of fish available for capture (1227), this corresponds to an estimated survival rate of 0.679 (with a range of 0.385 to 0.973 given the lower and upper bounds of the 95% CI) 1 year after the initial stocking.

3.4 | Release of sanctuary-reared sandfish

Between June and September 2021, we released 1277 reservoir-reared sandfish from Enjo and Mertenhof Reservoirs into the Biedouw River (994 with PIT tags), comprising 16.6% of the 2020 rescue cohort. The number of fish released was constrained by limitations in funds and personnel.

Size at release ranged from 111 to 214 mm TL, with a mean of 169 mm (SE 0.6) TL. Sandfish released from Enjo Reservoir and Mertenhof Reservoirs measured, on average, 184 mm (SE 0.5) TL ($n = 575$) and 156 mm (SE 0.5) TL ($n = 684$), respectively (Figure 3). There was a significant difference between the 2 reservoirs in size at release of all released fish ($t(1246.7) = 38.144$, $p < .05$) and in size at release of tagged fish ($t(984.34) = 29.34$, $p < .05$).

3.5 | Monitoring of returning sandfish

The 2021 visual surveys yielded an estimated run size of 180 adults. During the following year's spawning migration (August–September 2022), the antenna recorded 77 unique PIT tags (Table 2), representing a return rate of 7.7% of the 994 tagged fish released in 2021. Returning fish included Enjo-reared and Mertenhof-reared fish proportionately, with 7.7% of each reservoir's tagged releases forming part of the migration. As 283 sandfish were

TABLE 2 Numbers of sandfish belonging to the first head-start cohort that were rescued (2020), released (2021), and returned during the 2022 spawning migration.

		Release (2021)		
	Rescue (2020)	Tagged	Not tagged	Tagged returns (2022)
Enjo Reservoir	1815	567	21	44
Mertenhof Reservoir	4999	427	262	33
Clay Reservoir	885	0	0	0
Total	7699	994	283	77

Note: Sandfish were only released from Enjo and Mertenhof Reservoirs in 2021. They were not released from Clay Reservoir due to staffing and timing constraints that made the longer transport time impractical.

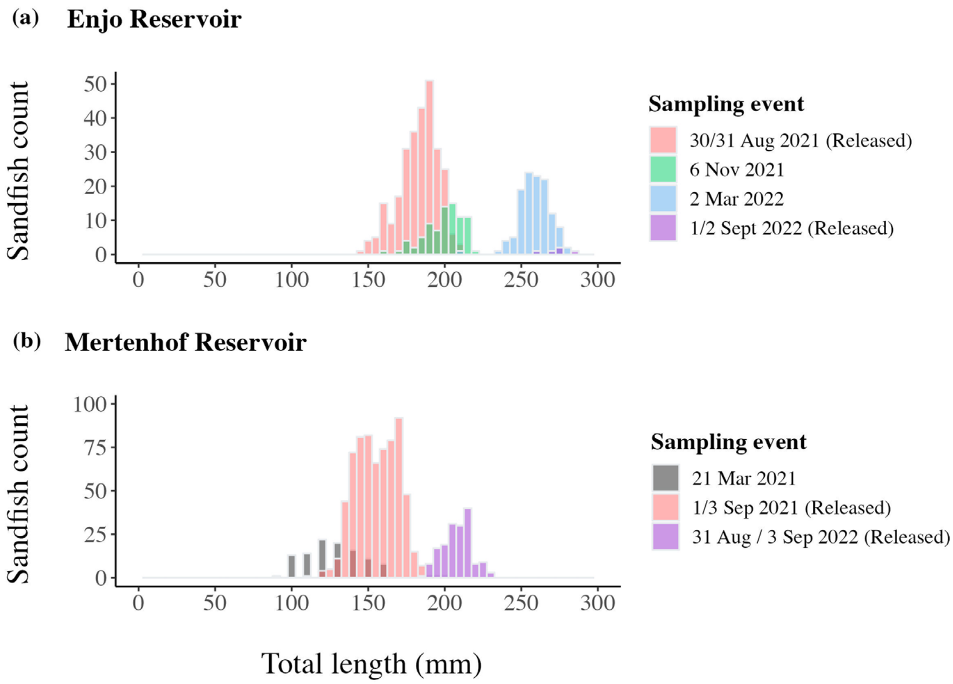

FIGURE 3 Size distribution of sandfish from the 2020 rescue cohort in (a) Enjo and (b) Mertenhof Reservoirs over time. Those labeled as '(Released)' were released into the Biedouw River during that sampling event. Similarly shaded histograms correspond to sampling events carried out during the same time period.

TABLE 3 Results of final generalized linear model examining predictors of sandfish return probability.

Response variable	Predictor variables	Coefficient (β)	Standard error	Odds ratio	95% confidence interval (lower bound, upper bound)	*p*-value
Sandfish return status (yes/no)	Intercept	−6.6333	1.6354	NA	NA	<.001***
	Total length (cm) at release	0.2107	0.0889	1.2345	0.0361, 0.3854	.0179*
	Distance (km) from Doring River	0.1804	0.0814	1.1977	0.0171, 0.3380	.0267*

*denotes $p < 0.05$. ***denotes $p < 0.001$.

released without a tag and detection probability is likely imperfect, this return rate is likely an underestimate.

Head-started sandfish that returned in 2022 measured 150–210 mm TL upon release in 2021, with a mean of 179 mm (SE 1.8) TL. A single 2-year-old tagged male released from Enjo Reservoir in September 2021 was recaptured in September 2022 using a fyke net. It had grown from 194 mm TL at release to 309 mm TL at recapture and was sexually mature (determined by observation of milt).

The final generalized linear model retained size at release and distance from the Doring River as significant predictors of return status (Table 3). Release window was not a significant predictor. All else being equal, larger fish had a higher likelihood of returning to the Biedouw River in 2022 than did smaller fish: For every additional centimeter in length at the time of release (2021), the likelihood of a fish returning to the Biedouw River in 2022 increased by approximately 23.45%. These results should be interpreted with caution, given that several hundred fish measuring less than 140 mm were released but not tagged, preventing their return status from being considered in the model.

Fish that were released further from the Doring River confluence were more likely to return the following year: For every additional kilometer in distance from the confluence at release, the likelihood of a fish returning increased by approximately 19.77%.

4 | DISCUSSION

This head-start intervention is the first of its kind in South Africa (Appendix S1). With more than 33,000 juvenile sandfish rescued and 2820 released to date, it has the potential to be among the largest freshwater fish head-start programs ever documented for a non-salmonid.

Low mortality rates during the rescue indicate that our capture and transportation methods were appropriate for individuals of the rescued size classes. While there was a wide range of 1-year survival estimates at Enjo Reservoir based on the bounds of the calculated confidence intervals, the survival estimate based on the LPI estimate was relatively high (0.679). This may be attributed to the species' natural ability to survive in isolated lentic habitats during the summer months and their adaptation to extreme seasonal environments. The closely related *Labeo umbratus* and *L. capensis* are also known to thrive in impoundments (Gaigher, 1984; Potts et al., 2005; Skelton, 2001). It is important to note that the survival rate mentioned here was derived from a single reservoir; survival rates could vary between reservoirs due to differences in several factors, including the presence of predators (e.g., birds and terrapins), vulnerability to predation due to water clarity, the availability of food, and competition for resources due to different stocking densities. Similar mark–recapture studies should be carried out at the different reservoirs over the course of several years to assess factors impacting sandfish survival in reservoir environments in the long term.

After 1 year in the sanctuary reservoirs, most sandfish that were recaptured had reached sufficient size for release into the wild. However, sandfish released from Enjo Reservoir were significantly larger than those released from Mertenhof Reservoir. Differences in stocking density, available resources, and temperature may have accounted for this disparity; these factors should be monitored, and their relative impacts on sandfish growth rates assessed in the future.

None of the tagged fish measuring less than 150 mm returned in 2022, although the small sample size ($n = 5$) of <150 mm tagged releases prevents meaningful interpretation. While the model suggests that smaller fish have a slim chance of return, it is worth noting that very few fish under 150 mm TL were tagged, and therefore, the return status of over 240 fish smaller than 150 mm TL at release was not recorded by the antenna, nor incorporated into the model. This may have biased the model outputs; future efforts should therefore be made to tag and release several hundred sandfish measuring 100–150 mm TL to improve the model's accuracy and predictive power. This is especially important given that a significant proportion of fish fell within the range of 111–149 mm TL 1 year after stocking into reservoirs, comprising 19% of the Enjo and Mertenhof Reservoir releases in 2021. PIT tag detections in the coming years will shed better light on return probability, helping managers to establish the ideal lower size threshold at release to ensure maximum survival.

In creating sanctuary reservoirs, we removed 5 potential future sources of non-native fish invasion from the Biedouw catchment and the greater ODRS. While *Micropterus* spp. were intentionally introduced into the system between 1930 and 1950 to promote angling opportunities (Skelton, 2001), bluegill sunfish invaded the system after escaping from stocked off-stream reservoirs in the catchment (Harrison, 1963). Therefore, the removal of non-native species from such impoundments must be considered a conservation priority, especially in catchments where these species are not yet present in rivers, or where they have been eradicated from these rivers.

PIT tags are widely used in developed countries to monitor freshwater fish movement and survival (e.g., Dzul et al., 2021; Hewitt et al., 2010; Teixeira & Cortes, 2007). The successful translocation of PIT-tagged humpback chub (*Gila cypha*; Healy et al., 2022) and the large-scale tagging and stocking of captive-reared razorback suckers (*Xyrauchen texanus*; Cathcart et al., 2018; Dowling et al., 2013; Zelasko et al., 2010) within the Colorado River Basin provide some examples of the application of this technology in monitoring freshwater fish conservation efforts in the United States. However, few comparable studies have taken place in developing countries, and none have documented the use of PIT tags in monitoring freshwater fish in Africa (Burnett et al., 2021). To our knowledge, this is the first study to use PIT tags to monitor a freshwater fish conservation intervention in Africa. It thus serves as an important proof of concept to catalyze the use of this valuable and cost-effective technology for conservation purposes in developing countries.

The return of 77 PIT-tagged head-started sandfish to the Biedouw River suggests that this intervention can increase the survival of young sandfish into adulthood, effectively bypassing the recruitment bottleneck resulting from non-native fish predation and excessive water abstraction. The detection of 77 head-started sandfish is likely an underestimate of the true number of returning fish; it therefore represents at least a 43% increase in run size when compared with the 180 adult sandfish observed migrating in 2021. This comparison, however, should be interpreted with caution, given that detection probability likely varies between visual surveys and passive PIT tag detection. Despite this, the magnitude of the potential increase in run size is significant.

Importantly, the recapture of a sexually mature male suggests that returning males are capable of spawning 1 year after their release. Females of *L. umbratus* and *L. capensis* reach sexual maturity at 200–370 mm standard length (SL) and 240 mm SL, respectively (Gaigher, 1984; Skelton, 2001). If patterns of sexual maturity in sandfish mirror those of *L. umbratus* and *L. capensis*, returning head-started females may also have been sexually mature upon return to the Biedouw River. Future net sampling of returning individuals should be carried out to assess size at sexual maturity, which remains poorly studied.

The fate of the tagged head-started sandfish that were not recorded in 2022 is unknown. It is likely that natural predation accounts for some of these absences. Although PIT tag retention is typically high in fish (Hopko et al., 2010), tag loss may also account for some of the absent releases. Furthermore, imperfect detection probabilities, which are influenced by the orientation of the passing tag, electromagnetic interference from outside sources, and other factors (Burnett et al., 2013), may have resulted in an underestimation of returning tagged sandfish. However, the fact that most fish would have passed over the antenna at least twice during the migration (as they entered and then exited the tributary) gives us confidence that the majority of returning tagged fish were registered by the system.

Furthermore, as a migratory species, olfactory imprinting cues may be especially important in determining homing probability in subsequent years (George et al., 2009). While rescued sandfish spent their first 2–5 months in their natal river and were returned there upon release, little is known about sandfish natal philopatry and natural stray rates. While it is possible that captive rearing may lead to increased straying in migratory fish (Keefer & Caudill, 2014), more research into sandfish imprinting mechanisms and natural stray rates is needed to better contextualize the return rates. Future antenna-assisted monitoring of spawning migrations in the Biedouw River and neighboring tributaries will be especially telling in this regard.

Model outputs suggest that size of fish and distance from the Doring River confluence at release significantly impact return probability. Given the known size-selective impacts of *Micropterus* spp. on indigenous fish in the ODRS (e.g., Cerrilla et al., 2022; van der Walt et al., 2016; Weyl et al., 2013; Woodford et al., 2005), it is likely that predation of smaller fish post-release accounts for their lower predicted likelihood of return. The reason for the positive impact of distance from the Doring River at release on likelihood on return can only be hypothesized given the available data. It is assumed that sandfish released at a greater distance from the confluence spent a longer time in the Biedouw River before entering the larger Doring River. It is possible that longer exposure to the physicochemical characteristics of the Biedouw River positively influences the strength of olfactory imprinting to the natal river, thus increasing the likelihood of philopatric behavior in subsequent years. Another mechanism could be that fish that spent more time in the smaller and relatively safer Biedouw River prior to entering the Doring River were able to acclimate to wild conditions more gradually, thus increasing their likelihood of survival upon entering the Doring River. Research on the nature of imprinting mechanisms among sandfish and continued monitoring of return rates are necessary to ascertain the mechanisms behind the observed patterns. It is worth noting that an additional 1543 reservoir-reared tagged sandfish were released in 2022 and 2023, including fish measuring a larger range of sizes and release locations than those released in 2021. The logistic regression analysis should therefore be repeated once return data are available from the most recent releases, which will improve the model's sample size and predictive power and refine the outputs. Managers should use these outputs to guide future releases, prioritizing release sites that maximize return probability and setting a lower threshold for fish size at release.

While head-starting is designed to maintain population viability in the short term, future conservation efforts must address the underlying threats that inhibit natural recruitment (Beebe et al., 2021). Such efforts in the ODRS should focus on (1) increasing habitat availability for threatened endemic fishes by eradicating non-native fishes from critical riverine habitat and (2) increasing flows by removing thirsty non-native plants and improving water management practices in critical catchments. The latter is especially important, given the substantial predicted future increase in frequency and intensity of droughts in the Western Cape as a consequence of climate change (Naik & Abiodun, 2020).

The results presented here provide encouraging indications that this head-start program successfully increased the size of the Biedouw River spawning sandfish population 1 year post-release. Especially encouraging are the high rescue numbers, low mortality during translocation, high survival in Enjo Reservoir between 2020 and 2021, and the subsequent return of at least 77 head-started fish. These efforts should be continued to prevent sandfish extinction in the short term, and strategic river restoration interventions should be implemented to secure sandfish survival in the long term.

Future research and monitoring efforts should be directed toward (1) the continuation of monitoring of the Biedouw River annual spawning migration to better understand factors influencing survival and return rates of reservoir-reared sandfish; (2) the fyke net-assisted recapture of reservoir-reared sandfish during subsequent migrations to monitor growth rates in the wild; and (3) antenna-assisted monitoring in neighboring tributaries to investigate stray rates and natal philopatry. These data will allow managers to optimize the intervention toward the strategies that will most likely result in population augmentation in the long term.

Importantly, the head-start intervention piloted by the SSP can serve as a model for the conservation of threatened freshwater fishes elsewhere in Africa, particularly in its use as an emergency measure where imminent extinction is a distinct possibility.

AUTHOR CONTRIBUTIONS

Cecilia Cerrilla is the lead and corresponding author. She contributed substantially to the conception and design of the work; the acquisition, analysis, and interpretation of the data; and the writing of the manuscript. Charles L. Griffiths contributed to the interpretation of the data and the revision of the manuscript. Dean Impson, Martine S. Jordaan, and Leonard Flemming contributed substantially to the conception and design of the work and the revision of the manuscript. Mohammed Kajee contributed to the acquisition of the data, the production of the figures, and the revision of the manuscript. Bruce R. Paxton, Johannes A. van der Walt, and Thomas Otto Whitehead contributed substantially to the conception and design of the work, the acquisition of the data, and the revision of the manuscript. Jeremy M. Shelton contributed substantially to the conception and design of the work, the acquisition and interpretation of the data, the iterative drafting process, and the revision of the manuscript. All co-authors have given their final approval of the version to be published.

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CONFLICT OF INTEREST STATEMENT

I declare that there is no conflict of interest regarding the publication of this paper. I, corresponding author on behalf of all contributing authors, hereby declare that the information given in this disclosure is true and complete to the best of my knowledge and belief.

DATA AVAILABILITY STATEMENT

Data will be made available on the Freshwater Biodiversity Information System, which publishes all data to the Global Biodiversity Information Facility.

ETHICS STATEMENT

All work was carried out with permits from CapeNature (CN54-28-14,847, CN54-28-14,848, CN54-28-22,956, CN 54-28-19,451, CN54-28-19,450, CN54-28-19,448, CN54-28-19,449, and CN44-87-17,976) and ethical clearance from the University of Cape Town (2021/V8/CR/A). The Department of Water and Sanitation issued a general authorization for the rotenone treatments.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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