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Distribution patterns and habitat associations of *Sandelia bainsii* (Teleostei: Anabantidae), a highly threatened narrow-range endemic freshwater fish

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Abstract

Sandelia bainsii is a range-restricted and highly threatened freshwater fish endemic to South Africa. Recent genetic evidence suggests that this species comprises three allopatrically distributed lineages that have been informally designated as *Sandelia* sp. "Kowie," *Sandelia* sp. "Keiskamma" and *Sandelia* sp. "Buffalo." As these lineages have only been recently identified and are likely to face a high risk of extinction because of restricted distributions, there is a critical need for generating ecological information to guide conservation prioritisation. The present study compared the historical and current distribution patterns, together with the habitat associations of *Sandelia* sp. "Kowie" in the Koonap and Kat rivers, tributaries of the Great Fish River. This study indicated that this lineage has been extirpated from one of the three localities in the Koonap River where it was historically abundant. In the Kat River, the current distribution of *Sandelia* sp. "Kowie" was comparable to its historical range, but its future persistence is threatened by the presence of non-native piscivores, instream physical barriers and potential future exploration for shale gas and infrastructure development in the Karoo Basin. A generalised hurdle negative binomial model revealed that although this lineage's probability of occurrence was high in habitats with boulder and sand substrates, and low conductivity, habitat characteristics were poor predictors of its abundance. Thus, it was postulated that the current range of this lineage probably represents the only available habitats for the persistence of different life stages for this taxon. Alternatively, the observed patterns may suggest the possibility of a shift in habitat associations, possibly for optimum utilisation of the remaining refugia within this river system. Immediate conservation measures should focus on preventing the spread on non-native invasive fishes, whereas future studies should evaluate the impacts of population fragmentation and identify appropriate intervention measures to maintain this lineage's long-term adaptive potential.

KEYWORDS

abundance, Anabantidae, distribution, ecology, fresh water, non-native fishes

1 | INTRODUCTION

Understanding ecological relationships of endangered fish species is important for identifying effective conservation measures that are appropriate for mitigating further losses (Arthington *et al*., 2016; He *et al*., 2018). For freshwater fishes in streams and rivers, these relationships are generally defined by abiotic and biotic factors that act simultaneously at different spatial and temporal scales (Cooke *et al*., 2012; Jackson *et al*., 2001). Abiotic factors include habitat characteristics, both at micro- (*e.g*., substratum type, depth and flow) and macro-scales (*e.g*., stream size, order and landscape characteristics), which influence distribution, refuge and resource utilisation (Butler *et al*., 2014; Chakona & Swartz, 2012; Dawson & Koster, 2018; Hong *et al*., 2017; Santos *et al*., 2018), and physical–chemical factors [*e.g*., dissolved oxygen (DO), pH and temperature], which directly or indirectly impose physiological limits to fish survival (Arthington *et al*., 2016; Carrizo *et al*., 2017; Dudgeon *et al*., 2006). Biotic factors include intra- and interspecific interactions that influence the persistence of both individual species and communities (Butler & Wooden, 2012; Crow *et al*., 2010; Hammerschlag *et al*., 2019). For endangered freshwater fish species, this basic ecological information is essential to identify areas that can be targeted for conservation interventions and for protection to promote persistence and recovery of populations (Januchowski-Hartley *et al*., 2016; Knaepkens *et al*., 2004; Lintermans, 2013).

Sandelia bainsii (Castelnau 1861), commonly known as the Eastern Cape rocky, is an endangered freshwater fish that occurs in a few river systems in the Amathole-Winterberg and the southern temperate freshwater ecoregions, in South Africa, where it has been a long-standing flagship species for conservation of aquatic biodiversity (Cambray, 1996, 1997a). Despite its endangered status, which has been largely informed by the studies performed over two decades ago (Cambray, 1996; Mayekiso, 1986; Mayekiso & Hecht, 1988), there is little information on the current status of this species. Knowledge of the ecological factors that influence its current distribution and abundance patterns is also lacking. Historical collection records indicate that *S. bainsii* had patchily distributed populations, which increased the susceptibility of this species to human impacts including alterations in land-use patterns, changes in water quality and availability, altered flow regimes and loss of critical habitat (Cambray, 1996; Cambray, 2007; Chakona *et al*., 2018a; Laurenson & Hocutt, 1986). Previous ecological studies have described this species as stenotopic, occurring in habitats that are dominated by coarse substrates, such as boulders in slow-flowing pools (Mayekiso, 1986; Mayekiso & Hecht, 1988, 1990). Although its interspecific interactions with other fishes have been underexplored, previous studies have inferred that the introduction of piscivores such as the sharptooth catfish *Clarias gariepinus* (Burchell 1822), largemouth bass *Micropterus salmoides* (Lacepède, 1802) and smallmouth bass *Micropterus dolomieu* (Lacepède, 1802) have led to a considerable decline in the distribution range and population sizes of *S. bainsii* (Cambray, 2007).

A recent molecular study revealed that *S. bainsii* comprises three divergent and allopatrically distributed lineages, such as *Sandelia* sp. "Kowie," *Sandelia* sp. "Keiskamma" and *Sandelia* sp. "Buffalo," each with a much narrower distribution than the species as currently described (Chakona *et al*., 2020). The most recent IUCN red list assessment highlighted that these lineages face an elevated risk of extinction because of the highly fragmented nature of the remnant populations coupled with multiple human impacts (Chakona *et al*., 2018a). As with many newly described species or recently identified lineages, the absence of relevant information on ecology, distribution patterns and population status hampers the implementation of effective conservation management strategies (Chakona *et al*., 2018b). The identification of three lineages within *S. bainsii* raises the need to evaluate and provide more accurate information on their geographic ranges and to investigate the ecological factors associated with their distribution patterns. There are serious conservation concerns because of growing evidence for possible localised extirpation and ongoing decline for some of the populations (Chakona *et al*., 2018b). The recent discovery of shale gas and potential future exploration and the associated infrastructure development in the Karoo basin adds to the existing threats to the unique biodiversity of the region (Holness *et al*., 2016; Netshishivhe, 2014; Todd *et al*., 2016). The area that has been mapped for potential shale gas exploration encompasses the Great Fish River system, which includes one of South Africa's National Freshwater Ecosystem Priority Areas (NFEPA) containing one of the remnant populations of *Sandelia* sp. "Kowie" (Chakona *et al*., 2020; Nel *et al*., 2011). The potential shale gas exploration adds to the uncertainty regarding the conservation of this lineage.

The first objective of the present study was to determine the current distribution of *Sandelia* sp. "Kowie" in the Great River system based on the recent surveys (2009–2017) and comparing this to historical distribution patterns based on the data collected between 1961 and 2005. The second objective was to determine the ecological factors that influence the lineage's spatial patterns of distribution and abundance, particularly focusing on habitat associations and interspecific interactions within the Kat River, a major tributary of the Great Fish River system. The Kat River was chosen because it is a critical NFEPA sanctuary for remnant populations of *Sandelia* sp. "Kowie," and yet it is under threat from the potential shale gas exploration and infrastructure development in the Karoo basin.

2 | MATERIALS AND METHODS

Permission for this research was granted by Eastern Cape's Department of Economic Development and Environmental Affairs through permit numbers CRO190/16CR. The care and handling of animals complied with South Africa's ethics and animal welfare laws.

2.1 | Study species

S. bainsii, as currently described, has a range that spans across seven river systems – Kowie, Great Fish, Keiskamma, Buffalo, Gxulu, Igoda and Nahoon rivers – in the Eastern Cape Province of South Africa (Skelton, 2001). Nonetheless, recent evidence from a DNA-based study using mitochondrial 16S sequences revealed the existence of three allopatrically distributed lineages within *S. bainsii* (Chakona *et al*., 2020, Appendix 1). These lineages have been informally referred to as *Sandelia* sp. "Kowie," which occurs in the Kowie and Great Fish river systems, *Sandelia* sp. "Keiskamma," which is currently only known from the Keiskamma River system, and *Sandelia* sp. "Buffalo," which occurs in the Igoda and Buffalo river systems (Chakona *et al*., 2020).

The present study focused on *Sandelia* sp. "Kowie" within the Great Fish River system. Evidence from surveys conducted by the authors in 2014, 2015 and 2016 indicated that the Kat River potentially harbours the strongest remaining population of *Sandelia* sp. "Kowie" as some localities where the Eastern Cape rocky was previously recorded in the Kowie River system and the Koonap River (Great Fish River system) were heavily degraded because of pollution and complete water abstraction. A better understanding of the distribution and ecology of this lineage in the Great Fish River system is thus crucial to inform the implementation of science-based conservation and management decisions.

2.2 | Study area

Within the Great Fish River system, *Sandelia* sp. "Kowie" is only known from two of its tributaries, the Koonap and Kat rivers (Figure 1), that drain the southern slopes of the Winterberg Mountains. The Eastern Cape rocky has never been recorded from the mainstem sections of the Great Fish River. The Kat River and Koonap River catchments have warm-temperate climate, with air temperatures ranging between 20°C and 35°C in summer (October to March) and from 0°C to 20°C in winter (April to September) (Hoare *et al*., 2006). Rainfall is unevenly distributed within these catchments and ranges from 400 to 800 mm. The region is regarded as sub-humid to semi-arid and receives approximately 75% of the annual rainfall between October/November and February/March (Hoare *et al*., 2006). Consequently, flow is highly seasonal, with many of the streams being ephemeral, whereas the major tributaries recede into a series of isolated pools during the dry season. Instream habitats and flow have been variously altered because of construction of weirs and dams, agricultural activities and invasion of the catchments by non-native plants, particularly black wattle *Acacia mearnsii* De Wild. Non-native fishes have also been introduced into the Kat River Dam located in the upper section of the Kat River and the lower sections of the Kat and Koonap rivers (Kadye & Booth, 2020; Laurenson & Hocutt, 1986).

2.3 | Data collection

This study used data from three time periods: 1961–2005 (historical), 2009–2011 and 2017 (current), with a total of 118 sites. Surveys were conducted using multiple sampling gears, including seine nets

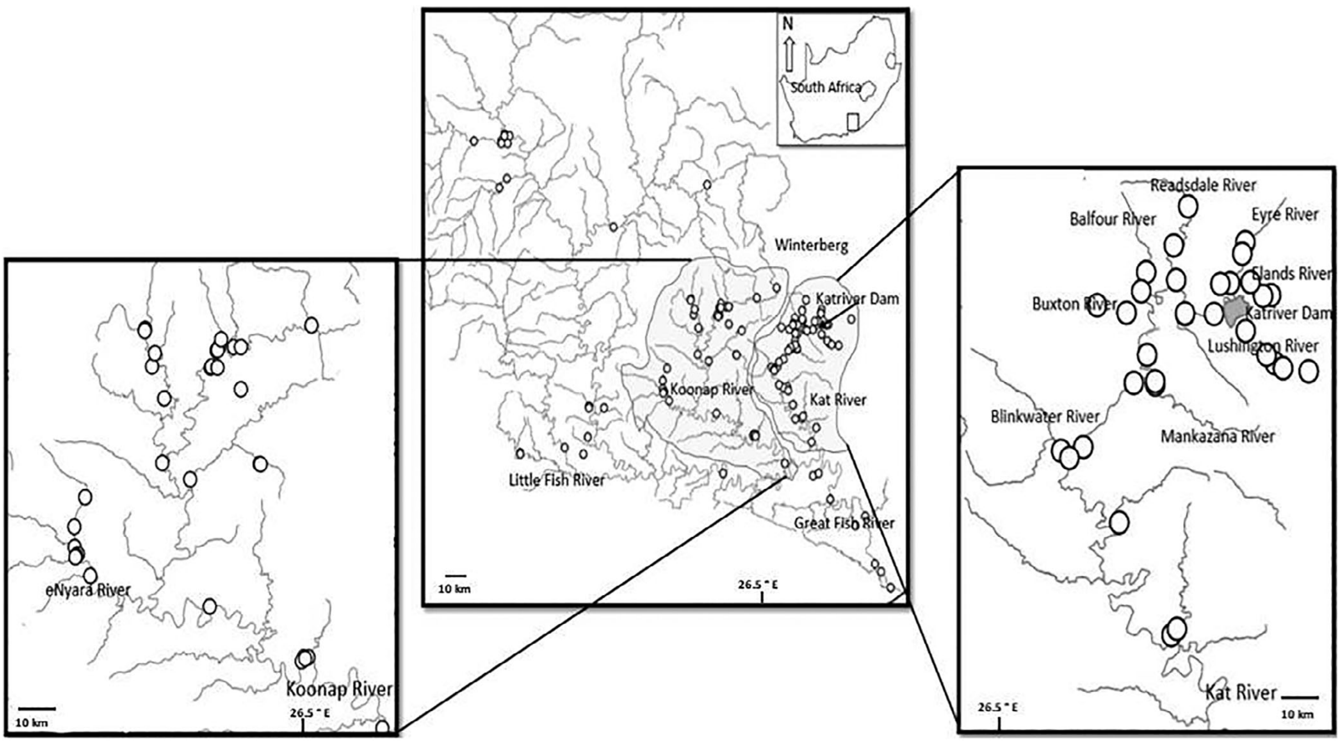

FIGURE 1 Map of the Great Fish River system (centre pane) showing all sampled localities (open circles). Right and left panes show the two major tributaries of the system, the Kat and Koonap rivers and their tributaries

(a 3 m length × 3 mm mesh size net and a 30 m length × 8 mm mesh size net), fyke nets (8 m long net × ring diameter of 55 cm × a 10 mm mesh size) and electrofishing (SAMUS-725MP powered by a 12 V battery with a standardised frequency of 90 Hz and sampling duration of approximately 15 min per site), to cover all available habitats at each site. The sampling gears varied across sites depending on the stream size and depth. Electrofishing was the most used capture method, covering 80% of the sampled sites. Seine and fyke nets were used at sites with deep pools (0.5 m). Four fyke nets per site were set in the evening and collected the next morning, with a soak time of approximately 12 h. Fish sampled were identified using keys in Skelton (2001), and fishes were returned to the collection sites alive.

Water temperature (°C), conductivity (μS cm^{-1}), total dissolved solids (TDS) (ppm) and pH were measured once per site using a HANNA HI 98129 Combo meter, turbidity [nephelometric turbidity units (NTU)] was measured using a HANNA HI 98703 turbidity meter (HANNA Instruments, Woonsocket, Rhode Island) and DO (mg l^{-1}) was measured using the OxyGuard probe (OxyGuard International, Farum, Denmark). To evaluate microhabitat characteristics for each site, 7–10 transects were set across the sampled area, perpendicular to the direction of flow to measure the width, depth, length and substrate composition. Three depth measurements (two on the near banks and one at the centre of transect) were taken along each transect using a graduated pole. The substratum type was also characterised at these three points for each transect. Substratum types were qualitatively assessed and classified following a modified Wentworth (1922) scale as silt (<0.05 cm), sand (0.05–2 cm), gravel (2–10 cm), cobble (10–30 cm), boulder (30–50 cm) and bedrock (>50 cm) (Cummins, 1962). Substratum types were expressed as proportions (%) of the total sampled points. The presence or absence of vegetation was also noted along the banks of each transect and was expressed as a proportion of sampled points at each site.

2.4 | Data analysis

To compare whether there were any changes between the historical and current distribution of *Sandelia* sp. "Kowie," data from 14 sites were used for pair-wise comparisons (Figure 2). These data, which were based on historical locality records and recent survey records, were presented in the form of N matched pairs of binomial data indicating whether this lineage was recorded as present (1) or absent (0) for each ith pair of historical (Y_{i1}) and current (Y_{i2}) distribution. The data were summarised in a 2 × 2 contingency table with each n_{jk}, for$j$, k = 0,1 corresponding to the number of locality pairs (Y_{i1}, Y_{i2}) with outcomes $Y_{i1} = j$ and $Y_{i2} = k$, respectively. To evaluate whether there were significant changes in the historic and current distributions of *Sandelia* sp. "Kowie," McNemar's χ^2 test was used to compare the discordant pairs (McNemar, 1947). This was evaluated under the null hypothesis that the marginal probabilities for Y_{i1} (p_1) and Y_{i2} (p_{+1}) are the same (*i.e.*, $H_0 : p_1 = p_{+1}$).

To assess the ecological factors influencing *Sandelia* sp. "Kowie" in the Kat River, first, the distribution of this lineage was evaluated in relation to other species, including both native and non-native fishes and the associated environmental variables from 36 sites. This was carried out using a non-metric multidimensional scaling (NMDS) that was performed based on a binomial distance matrix for the fish data. Species data were presented as $n \times p$ (sample × species) data matrix, where species data were based on presence/absence. Environmental data were presented as $n \times q$ (sample × environmental variable) data matrix. Before the analysis, each environmental variable was

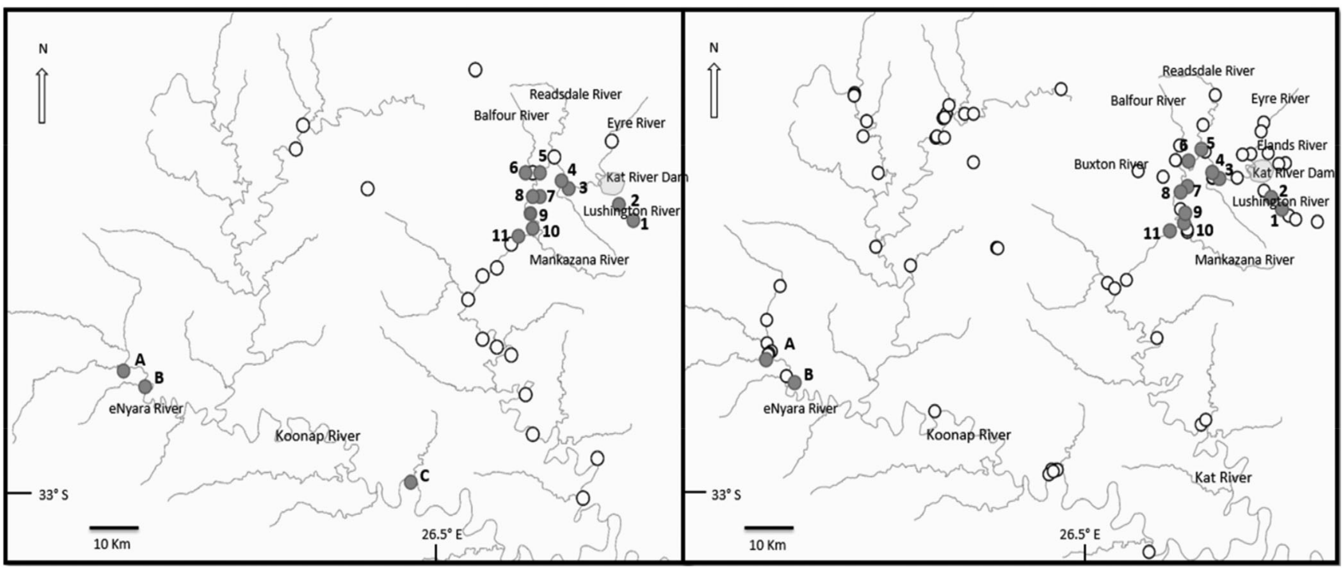

FIGURE 2 Map of all sampled sites (open circles) and sites where *Sandelia* sp. "Kowie" was present (grey circles) in the Kat and Koonap rivers in the Great Fish River system. Left pane shows the historical records (1961–2005), and right pane shows the current records from the recent surveys (2009–2017)

standardised using *z*-scores. Predictor variables were standardised to allow comparisons of predictor variables that were measured in different units (Quinn & Keough, 2002). The environmental and habitat variables were further pre-screened for multicollinearity by comparing the variance inflation factors (VIFs) that were based on a generalised linear regression model; variables with VIF < 5 were retained. The NMDS was performed using the function *meta-MDS* in the *vegan* package (Oksanen *et al*., 2019) using the R statistical software (R Development Core Team, 2019). To visualise the joint fish distribution patterns and the environmental variables, a biplot was created using the function *envfit* in the *vegan* package. The statistical significance of the environmental variables was evaluated based on randomisation permutation tests (×1000).

Second, the relationship between *Sandelia* sp. "Kowie" abundance and environmental variables was evaluated using general linear models (GLMs). Fish abundances were based on electrofishing data from 30 sites. Because of the patchy distribution of *S. bainsii*, these data were characterised by many zero count observations. Therefore, four GLMs were developed to assess the relationship between fish abundance and environmental variables: Poisson, negative binomial (NB), zero-inflated negative binomial (ZINB) and hurdle negative binomial (HNB) (Cameron & Trivedi, 1998; Mullahy, 1986) (see Appendix 2 for model specifications). Poisson regression is conceptualised as a count model, with the Poisson distribution being assumed to have equal mean and variance (Greene, 2005; O'Hara & Kotze, 2010). Violation of this assumption indicates over-dispersion which affects the standard errors of the model parameters. Consequently, modifications of the Poisson model are necessary to cater for the violations of the underlying distribution. NB is often appropriate to cater for over-dispersion by allowing the variance to be greater than the mean and by accommodating the heterogeneity within the count data (O'Hara & Kotze, 2010; Yau *et al*., 2003). Nonetheless, the NB distribution may be inadequate when there are excess zeros in the observed data. Consequently, the ZINB and HNB models are both designed to deal with high occurrence of zeros with a NB distribution in the observed data (Mullahy, 1986; Saffari *et al*., 2012).

A ZINB model assumes that the zero observations are because of both structural and sampling designs (Saffari & Robiah, 2011). For example, within the known geographic range of *Sandelia* sp. "Kowie," this lineage may be naturally absent from some sampling sites, leading to many zero observations (structural zeros). On the contrary, at all sites where *Sandelia* sp. "Kowie" is likely to occur, this lineage may not be captured, leading to binomial distribution with both zero (sampling zeros) and non-zero observations. In comparison, a HNB model assumes that all zero observations are structural, whereas the non-zero observations, which are due to the sampling design, follow a truncated NB distribution (Loeys *et al*., 2012). For example, within the known distribution range of *Sandelia* sp. "Kowie," sites where this lineage is naturally absent will have zero observations (structural zeros), whereas sites with this lineage will have positive observations that may follow an NB distribution. To select the model that best fitted the data, AIC was used to evaluate the goodness-of-fit of each model based on the log-likelihood functions of the data. In addition, multi-model inference was conducted from a fully saturated model with all environmental variables to select the best predictor variables for the candidate model (Bolker *et al*., 2009). The most parsimonious model was selected based on the lowest Akaike weight (Burnham & Anderson, 2004). Multi-model inference was conducted in R using the package *MuMIn* (Barton, 2019).

3 | RESULTS

Sandelia sp. "Kowie" was present at 13 of 14 historical sites (Figure 2), with the one non-detection site located in the Koonap River. It was also captured at two additional sites that were not historically surveyed in the Kat River (see Supporting Information in Supplementary S1 for the complete 2017 survey data). Although the comparison of the historical and current distribution patterns revealed no significant differences (McNemar's χ^2_1, $P = 1.00$), the absence of *Sandelia* sp. "Kowie" from one site in the Koonap River represents a 33% reduction in the lineage's range as it was historically known from only three sites in this river. At the two sites where it was present, *Sandelia* sp. "Kowie" co-occurred with the non-native *Tilapia sparrmanii* Smith 1840 in the Koonap River (Table 1). The other species that were recorded from the Koonap River were *Labeo umbratus* (Smith 1841) and two non-native species *Labeobarbus aeneus* (Burchell 1822) and *C. gariepinus*.

In the Kat River, fishes were captured at 29 sites during the recent survey. These sites were characterised by a wide variation in conductivity (33–1618 μS cm^{-1}), TDS (19–990 ppm), pH (7.8–10.7), water temperature (20.1–30.7°C), DO (3.2–14.6 mg l^{-1}) and water clarity (8.36–720 NTU). Similarly, substratum composition was variable among sites (Table 2).

The NMDS ordination indicated a fair goodness-of-fit (stress value = 0.09), with five environmental variables being significant (randomisation permutation tests, $P < 0.05$) in explaining the spatial patterns in the distribution of fishes (Figure 3). The NMDS axis 1 showed that in the upper section of the Kat River, *Sandelia* sp. "Kowie" co-occurred with one native fish species, *Enteromius anoplus* (Weber 1897), at sites that were at high altitude. In particular, these two species co-occurred in one headwater tributary, the Lushington River, above Kat River Dam. By comparison, in the middle section that comprised the greater portion of the mainstem, this lineage co-occurred with two native fish species, *L. umbratus* and *Glossogobius callidus* (Smith 1937), at sites that were wider and deeper. *Sandelia* sp. "Kowie" was absent at sites that had the non-native species, *L. aeneus*, *C. gariepinus* and *T. sparrmanii* (Figure 3). Sites with these non-native fish species were characterised by high conductivity, and these were within the lower sections of the Kat River catchment.

Comparison of the GLMs using AIC showed that the HNB (AIC = 84.4) was a better fitting model than the Poisson (AIC = 410.9), NB (AIC = 146.7) and ZINB (AIC = 96.9) models (Table 3). Consequently, the HNB model was used to evaluate the relationship between *Sandelia* sp. "Kowie" and environmental factors. The hurdle

TABLE 1 Fish species collected during the most recent survey at sites where *Sandelia* sp. "Kowie" historically occurred in the Great Fish River

		Kat River											Koonap River		
Species	**Common name**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**A**	**B**	**C**
Anguilla mossambica	Longfin eel	×	×	×	×	×	×	×	✓	×	×	×	×	✓	×
Enteromius anoplus	Chubbyhead barb	×	×	✓	✓	✓	✓	✓	✓	✓	×	✓	✓	×	✓
Labeobarbus aeneus[a]	Smallmouth yellowfish	×	×	×	×	×	×	×	×	×	×	×	×	×	✓
Labeo umbratus	Moggel	×	×	×	×	×	×	×	×	✓	✓	×	×	✓	✓
Clarias gariepinus[a]	Sharptooth catfish	×	×	×	×	×	×	×	×	×	×	×	×	×	✓
Tilapia sparrmanii[a]	Banded tilapia	×	×	×	×	×	×	×	×	×	×	×	✓	✓	×
Sandelia bainsii	Eastern Cape rocky	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	×
Glossogobius callidus	River goby	×	×	×	✓	×	×	×	✓	✓	✓	✓	×	×	×

Note: The numbers 1–11 and letters A–C represent sites where this lineage occurred in the Kat and Koonap river catchments, respectively. The symbol ✓ represents the presence, and × represents the absence.
[a]Non-native fish species.

part of this model showed that the contrasts for all parameters were significant ($P < 0.05$) (Table 4). In general, the probability of occurrence of *Sandelia* sp. "Kowie" was high in habitats with boulder and sand substratum and low conductivity. On the contrary, the NB part of the model showed that the contrasts for all environmental variables were not significant ($P > 0.05$) in explaining the relationship between *Sandelia* sp. "Kowie" abundance and environmental factors (Table 4). This indicated that despite the wide variability in environmental variables, none of the environmental factors were important predictors for the abundance of *Sandelia* sp. "Kowie" in the Kat River.

4 | DISCUSSION

The present study confirmed that the current patchy distribution pattern of *Sandelia* sp. "Kowie" was consistent with historical records. This is because despite fine-scale geographic sampling in the Great Fish River system, this lineage was captured at the localities only where it was historically recorded in both the Koonap and the Kat rivers. The underlying causes of the contemporary patchy distribution between the Koonap and Kat rivers populations of this lineage are unclear because there are no historical records of the occurrence of the Eastern Cape rocky in the mainstem Great Fish River or lower sections of the Koonap and the Kat rivers. A possible explanation is that this lineage was once present in these river sections but became locally extinct possibly as a result of natural factors or human impacts. The contemporary patchy distribution pattern of the Eastern Cape rocky suggests that it may have limited dispersal capabilities and, thus, faces a high risk of extinction because of reduced ability to restore locally extirpated populations through natural recolonisation.

Over the past five decades, the habitats for different lineages of *S. bainsii* experienced substantial changes, including alteration in flow regimes, degradation, increased pollution and invasion by non-native and extralimital fish species (Cambray, 1996; Kadye & Booth, 2013; Laurenson & Hocutt, 1986; Mayekiso & Hecht, 1988). These modifications resulted in substantial changes in the distribution ranges of *S. bainsii* and other endemic fish species, resulting in their listing under highly threatened categories of the IUCN (Cambray, 1996, 2007; Chakona, 2018; Chakona *et al*., 2018a). The present study represents the most recent comprehensive survey of the known historical ranges of one lineage of the Eastern Cape rocky, *Sandelia* sp. "Kowie" in the Great Fish River system, to provide fine-scale geographic distribution and ecological attributes in this system and compared with its historical distribution patterns. The present study confirmed that, consistent with the historical data, this lineage has a disjunct distribution in the Great Fish River system. There are two isolated populations, one in the Koonap River catchment and another in the Kat River catchment. Historical data indicate that, within the Koonap River catchment, this lineage was recorded at three localities, Edgehill Farm, Berkeley Farm and Hebert's Hope Farm. The present study recorded a localised extirpation of this lineage from Edgehill Farm as the pools where this species was previously recorded were dry at the time of sampling. Thus, sampling was conducted at a weir immediately upstream of this locality where only one native fish species, *L. umbratus*, was recorded. At this site, the other species that were present included the extra-limital *L. aeneus* and *C. gariepinus*. Despite historical records indicating that this species was abundant at both Berkeley and Herbert's Hope farms, only a few individuals were captured during recent surveys. Possible stressors that could have resulted in the substantial decline in population sizes of *Sandelia* sp. "Kowie" at these localities could be sewage effluent discharge from two towns located upstream of these localities and invasion by *T. sparrmannii* which was found to be highly abundant at these localities. There is high concern over Koonap River population of *Sandelia* sp. "Kowie" because Cambray (2007) considered this isolated population to be unviable in the long term. Without active intervention, long-term persistence of this population in the Koonap River catchment is highly uncertain.

Findings from the recent surveys indicated that in the Kat River catchment, the population of *Sandelia* sp. "Kowie" appeared to be more stable, as the present distribution patterns were comparable to historical records. The Kat River catchment has been designated as sanctuary area under the NFEPA because of the presence of the

TABLE 2 Physical–chemical variables and substrate types of all sampled sites where fishes were captured in the Kat River

River	Alt (m)	Temp (°C)	Cond (μS)	pH	TDS (ppm)	Turb (NTU)	DO (mg L^{-1})	M.dep (cm)	M.wid (m)	%Bd	%Bl	%Sn	%Sl	%Cl	%Gr	%V
Kat	948	22.3	43	9.31	24	17.2	8.2	13.7	2.9	0.0	6.7	0.0	0.0	93.3	0.0	36.7
	892	24.1	33	7.83	19	19.2	6.4	22.3	2.5	40.0	16.7	0.0	43.3	0.0	0.0	46.7
	872	30.2	86	8.06	41	55.8	7.0	24.1	3.0	15.0	51.7	0.0	6.7	10.0	16.7	28.3
	850	23.5	150	8.19	86	26.9	7.4	29.8	6.9	40.0	10.0	3.3	46.7	0.0	0.0	36.7
	846	24.1	65	8.08	39	25.9	6.8	27.8	4.2	13.3	76.7	0.0	0.0	3.3	6.7	93.3
	841	24.3	82	9.13	48	33.2	7.5	19.2	3.7	30.0	36.7	0.0	26.7	6.7	0.0	50.0
	820	24.2	161	8.66	94	40.4	7.8	41.9	6.7	0.0	36.7	6.7	36.7	20.0	0.0	23.3
	807	26	186	9.19	109	43.3	7.6	18.4	3.0	3.3	53.3	10.0	26.7	0.0	6.7	6.7
	793	28.5	216	8.42	127	28.9	5.5	33.2	6.8	3.3	6.7	10.0	40.0	23.3	16.7	6.7
	777	27.4	380	8.38	223	8.35	6.5	37.0	2.7	10.0	0.0	0.0	0.0	0.0	90.0	76.7
	773	23.4	60	9.74	34	29.1	7.8	15.9	5.7	3.3	96.7	0.0	0.0	0.0	0.0	16.7
	762	26.3	202	9.24	123	22.9	10.5	29.2	3.3	6.7	20.0	3.3	0.0	53.3	16.7	3.3
	754	26.3	106	8.5	62	29.3	7.4	16.4	3.3	10.0	50.0	0.0	26.7	6.7	6.7	30.0
	688	26.3	97	8.92	57	18.7	7.8	28.6	7.6	56.7	10.0	0.0	26.7	0.0	6.7	23.3
	663	23.7	156	8.44	90	118	8.1	15.3	3.1	6.7	53.3	3.3	16.7	0.0	20.0	26.7
	659	20.1	134	10.71	77	10.6	9.9	29.7	7.4	86.7	3.3	0.0	0.0	10.0	0.0	16.7
	639	22.9	129	9.67	76	70.3	8.0	30.3	8.1	100.0	0.0	0.0	0.0	0.0	0.0	41.7
	637	24.2	130	8.7	76	69.9	8.0	41.7	5.7	93.3	6.7	0.0	0.0	0.0	0.0	20.0
	631	26.2	94	8.57	55	146	7.8	27.2	5.3	0.0	0.0	30.0	33.3	0.0	36.7	70.0
	609	25.1	132	8.68	77	64.1	8.3	32.6	8.7	0.0	66.7	0.0	6.7	0.0	26.7	36.7
	598	28.3	98	9.72	57	58.5	8.0	25.0	4.6	56.7	0.0	3.3	10.0	6.7	23.3	56.7
	577	25	110	8.35	64	272	8.2	24.2	6.8	0.0	70.0	0.0	6.7	0.0	23.3	53.3
	546	23.4	118	9.22	69	275	7.2	83.2	21.5	0.0	0.0	30.0	33.3	0.0	36.7	23.3
	540	25.6	121	9.1	71	31.8	8.1	86.3	12.3	58.3	8.3	0.0	0.0	33.3	12.5	0.0
	512	27.3	130	8.12	74	518	7.2	44.2	4.0	6.7	56.7	0.0	0.0	0.0	36.7	16.7
	473	23.2	185	9.37	109	720	7.5	31.4	8.7	0.0	23.3	0.0	16.7	60.0	0.0	23.3
	464	29	185	9.32	109	699	7.0	36.4	10.3	0.0	26.7	0.0	63.3	0.0	10.0	60.0
	314	30.7	1678	9.84	990	8.72	14.6	35.2	4.0	100.0	0.0	0.0	0.0	0.0	0.0	100.0
	312	24.5	383	9.4	227	51.2	3.2	36.2	4.2	83.3	0.0	0.0	3.3	13.3	0.0	60.0

Note: Physical–chemical and habitat variables are abbreviated as follows: Alt: altitude; Bd: bedrock; Bl: boulder; Cl: cobble; Cond: conductivity; DO: dissolved oxygen; Gr: gravel; M.dep: mean depth; M.wid: mean width; Sl: silt; Sn: sand; TDS: total dissolved solids; Temp: temperature; Turb: turbidity; V: vegetation.

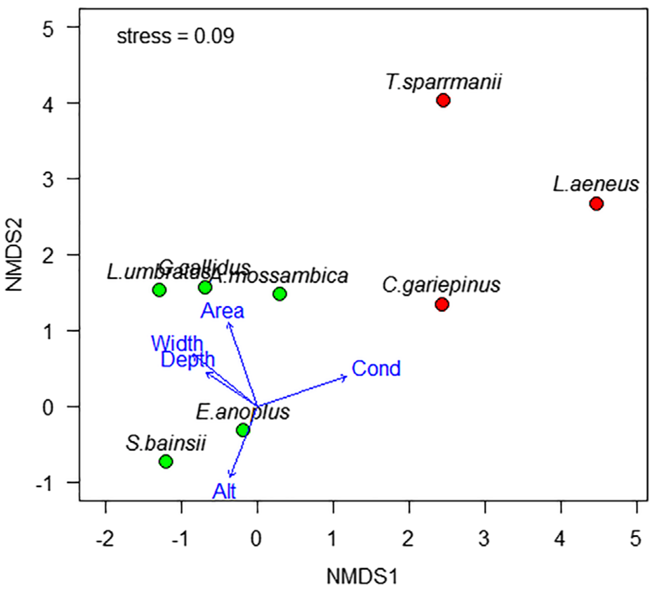

FIGURE 3 Non-metric multidimensional scaling (NMDS) ordination showing the spatial patterns of distribution of *Sandelia* sp. "Kowie" together with both native (green circles) and non-native (red circles) fishes in the Kat River

TABLE 3 Comparison of models for *Sandelia* sp. "Kowie" abundance in the Kat River

Model	Log-likelihood	*df*	AIC
Poisson	−197	8	410.9
Negative binomial	−59	14	146.7
Zero-inflated negative binomial	−31	17	96.9
Hurdle negative binomial	−25	17	84.4

highly threatened *S. bainsii* (Nel *et al*., 2011). In addition to the role of declared protected areas such as national parks in conserving freshwater fishes (Russell, 2011), these NFEPAs are important support tools that are envisaged to contribute towards achieving the conservation goals enshrined in the National Environment Management Biodiversity Act (NEMBA) through identification and designation of areas of high biodiversity and ecological significance across South Africa (Nel *et al*., 2011). Any activities that have detrimental impacts on biodiversity, such as the introduction of non-native species and habitat alteration, are prohibited within protected areas and in ecosystems with threatened species. Nonetheless, the Kat River catchment poses a conservation challenge because the flow regime has been altered by construction of several instream impoundments along the course of the rivers, including the Kat River Dam, which is the largest impoundment in the catchment and is located in the upper sections of Kat River. At least four extralimital and invasive species such as *C. gariepinus*, *L. aeneus*, *Cyprinus carpio* Linnaeus 1758 and *M. salmoides* were recorded in Kat River Dam (Potts *et al*., 2008). This poses a threat to the remnant populations of *Sandelia* sp. "Kowie" that occur both above and below the dam. The invasive piscivores *C. gariepinus* and *M. salmoides* have been implicated as some of the key causes for the decline in distribution range and population size of *S. bainsii* (Cambray, 2000, 2007; Mayekiso, 1986; Mayekiso & Hecht, 1988). Elsewhere, these species have also impacted native fishes, such as the possible localised extirpation of native species because of the invasion of *C. gariepinus* within the mainstems of the Great Fish and Sundays rivers (Kadye & Booth, 2012; 2013) and the negative influence on the distribution and abundance of native and endemic fishes because of predation by *Micropterus* species in the Cape Fold ecoregion (Shelton *et al*., 2008; Van Der Walt *et al*., 2016). Therefore, there are serious concerns about the long-term persistence of the population of *Sandelia* sp. "Kowie" in the Lushington River which flows into Kat River Dam, as there are no barriers to prevent invasion by the non-native fishes from the dam. There is also a risk that if these species escape from the dam, they are likely to establish on the deep pools below the dam, which sustain the largest remaining population of this lineage in the mainstem section of the Kat River.

Previous studies considered the Eastern Cape rocky to be stenotopic, being frequently associated with coarse substratum and in pools with slow-flowing water (Mayekiso, 1986; Mayekiso & Hecht, 1988, 1990). The present study found that although *Sandelia* sp. "Kowie" likely occurred in habitats with low conductivity and high DO, which were characteristic of the headwaters, there were no specific association of this lineage's abundance and any of the measured environmental and habitat variables in the Kat River. The lack of specific habitat and abundance relationship is likely to be the main reason that has facilitated persistence of this species in a highly altered landscape in the Kat River catchment. In general, several studies have reported that endangered fishes often exhibit clear habitat requirements for different aspects of their life history, including feeding, refuge and spawning (Knaepkens *et al*., 2004; Olden *et al*., 2010; Wong *et al*., 2018). Although the loss of critical habitats for endangered species often leads to both range reduction and decline in population sizes (Januchowski-Hartley *et al*., 2016; Lintermans, 2013), these species usually exhibit clear habitat affinities, which are often identifiable and prioritised for conservation to mitigate further losses. In contrast, in the Kat River, *Sandelia* sp. "Kowie" was found in varying densities with no clear predictor habitat variables for its abundance. Because species-specific habitat requirements generally vary depending on life stages and interspecific interactions (Rosenfeld & Hatfield, 2006; Schumann *et al*., 2017), this study postulates that the entire portion of the Kat River system inhabited by this lineage probably represents the only available habitats for the persistence of different life stages of this species. *S. bainsii* is reported as requiring habitats with slow-flowing pools, which provide refuge for adults, and coarse substratum types for spawning and refuge for juveniles (Cambray, 1997b). In addition, this species is known to be a territorial nest guarder, which suggests that it requires relatively clear water habitats. Alternatively, if this remnant population is resilient, the observed patterns suggest the possibility of a shift in habitat associations for optimum utilisation of the remaining refugia within this river system. Nonetheless, both the scenarios raise concerns about the future persistence of this

TABLE 4 Parameter estimates, standard errors (S.E.) and the associated *P*-values for hurdle negative binomial (HNB) model for the abundance of *Sandelia* sp. "Kowie" in the Kat River

	Estimate	S.E.	*z*-value	*P*-value
Hurdle				
Intercept	13.71	2.17	6.32	<0.001
Conductivity	22.35	4.60	4.86	<0.001
Dissolved oxygen	−6.19	1.11	−5.57	<0.001
Mean depth	−3.08	0.54	−5.70	<0.001
Area	2.58	0.31	8.40	<0.001
Boulders	0.77	0.34	2.30	0.021
Sand	18.78	4.62	4.07	<0.001
Gravel	−8.76	1.59	−5.50	<0.001
Negative binomial				
Intercept	−348.08	109,982.26	−0.003	0.997
Conductivity	−899.3	290,273.64	−0.003	0.998
Dissolved oxygen	133.48	72,860.05	0.002	0.999
Mean depth	280.18	91,570.6	0.003	0.998
Area	−49.28	26,700.98	−0.002	0.999
Boulders	63.82	33,349.76	0.002	0.998
Sand	−1271.39	1,765,597.43	−0.001	0.999
Gravel	164.39	353,499.65	0.000	1.000

population in the event that the available habitats are sub-optimal for the long-term maintenance of a viable population size. This risk is further heightened by the possibility of range expansion by non-native fishes that occur in certain sections of the river.

A surprising observation was the absence of *S. bainsii* "Kowie" from the Elands and Eyre rivers that flow into Kat River Dam, despite these rivers having ideal habitat and this species occurring in the Lushington River which also flows into the Kat River Dam. This suggests that this species could potentially have limited dispersal capabilities, which increases its susceptibility to localised impacts and reduces the possibilities of rescuing populations that become locally extirpated. The limited dispersal abilities could be inferred from some aspects of this species' biology, including its reproductive behaviour. This species is generally known to have specific habitat requirements for spawning, which include deep pools with course substratum (Cambray, 1997b). In addition to its low fecundity compared to other anabantids (Mayekiso & Hecht, 1990), this species requires nesting areas where males are involved in brood caring (Cambray, 1997b).

In addition to the high possibility of invasion by invasive piscivores, remnant populations of *S. bainsii* in the Kat River catchment are highly fragmented because of the presence of several weirs along the profile of the river. Studies have shown that small isolated populations face a greater risk of extinction because of the possible loss of genetic diversity as a result of genetic drift and inbreeding (Coleman *et al*., 2018; Fitzpatrick *et al*., 2016; Frankham *et al*., 2014; Jang *et al*., 2017). There is a need for dedicated studies that focus on population genetic and riverscape genetic analyses to explore the consequences of population fragmentation on genetic diversity of *S. bainsii* "Kowie." This information will help guide conservation actions such as genetic rescue through regular translocations of individuals among remnant populations to maintain the species' long-term adaptive potential, as recommended for the Macquarie perch *Macquaria australasica* in Australia (Pavlova *et al*., 2017).

5 | CONCLUSION

Within the Great Fish River system, *Sandelia* sp. "Kowie" population is disjunctly distributed, occurring in two tributaries, the Koonap and Kat rivers. Connectivity between these sub-populations appears to be limited because of anthropogenic factors, such as the occurrence of non-native fishes and habitat alterations, particularly in the downstream sections of these tributaries. In addition, there are further concerns that include hydrological modifications of the system and the proposed shale gas exploration. For example, studies in the Kat River catchment have suggested that there are approximately three weirs per kilometre, and that the lower catchment had approximately 25 weirs (Farolfi & Abrams, 2005). This is likely to negatively impact on population mixing and genetic diversity of this population. On the contrary, the proposed shale gas fracking adds to the uncertainty because of the possibilities of habitat loss, water contamination and altered flow regimes (Holness *et al*., 2016). The recent discovery of the anchor worm parasite *Lernaea cyprinacea* Linnaeus 1758, a non-native copepod, in *S. bainsii* within the region (Chakona *et al*., 2019) further adds to the ongoing challenges in conserving this threatened species. Therefore, the lineages of *S. bainsii* remain fragile and require additional studies to ascertain the extent of the negative factors within the catchment. These studies include an assessment of the genetic diversity and population viability.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Arthington, A. H., Dulvy, N. K., Gladstone, W., & Winfield, I. J. (2016). Fish conservation in freshwater and marine realms: status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*, 838–857.

Barton, K. (2019) MuMIn: Multi-Model Inference. R Package Version 1.43.6. https://CRAN.R-project.org/package=MuMIn. 2019, doi: citeulike:11961261.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*, 127–135.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding aic and bic in model selection. *Sociological Methods and Research*, *33*, 261–304.

Butler, G. L., & Wooden, I. J. (2012). Dietary habits of a large, long-lived endangered Australian Percichthyid, the eastern freshwater cod *Maccullochella ikei*. *Endangered Species Research*, *16*, 199–209.

Butler, G. L., Rowland, S. J., Baverstock, P. R., & Brooks, L. (2014). Movement patterns and habitat selection of the endangered eastern freshwater cod *Maccullochella ikei* in the Mann River, Australia. *Endangered Species Research*, *23*, 35–49.

Cambray, J. A. (1996). Threatened fishes of the world: *Sandelia bainsii* Castelnau, 1861 (Anabantidae). *Environmental Biology of Fishes*, *45*, 150–150.

Cambray, J. A. (1997a). Captive breeding and sanctuaries for the endangered African anabantid *Sandelia bainsii*, the eastern cape rocky. *Aquarium Sciences and Conservation*, *1*, 159–168.

Cambray, J. A. (1997b). The spawning behaviour of the endangered eastern cape rocky, *Sandelia bainsii* (Anabantidae), in South Africa. *Environmental Biology of Fishes*, *49*, 293–306.

Cambray, J. A. (2000). Community involvement and the eastern cape rocky, (*Sandelia bainsii*, Pisces, Anabantidae) from the perspective of a researcher. *South African Journal of Wildlife Research*, *30*, 114–117.

Cambray, J. A. (2007) Sandelia bainsii. The IUCN Red List of Threatened Species 2007: E.T19889A9107020.

Cameron, A. C., & Trivedi, P. K. (1998). *Regression analysis of count data. Econometric society monograph no.30*. New York, NY: Cambridge University Press.

Carrizo, S. F., Jähnig, S. C., Bremerich, V., Freyhof, J., Harrison, I., He, F., … Darwall, W. (2017). Freshwater megafauna: flagships for freshwater biodiversity under threat. *Bioscience*, *67*, 919–927.

Chakona, A., Gouws, G., Kadye, W. T., Mpopetsi, P., & Skelton, P. (2020). Probing hidden diversity to enhance conservation of the endangered narrow-range endemic Eastern Cape rocky, *Sandelia bainsii* (Castelnau, 1861). *Koedoe*, *62*(1), a1627. https://doi.org/10.4102/koedoe.v62i1.1627.

Chakona, A. (2018) Pseudobarbus trevelyani. The IUCN Red List of Threatened Species 2018. E.T2573A100159948 8235.

Chakona, A., & Swartz, E. R. (2012). Contrasting habitat associations of imperilled endemic stream fishes from a global biodiversity hot spot. *BMC Ecology*, *12*, 1–12.

Chakona, A., Sifundza, D. & Kadye, W. T. (2018a) Sandelia bainsii. The IUCN Red List of Threatened Species 2018: E.T19889A99447325.

Chakona, A., Rennie, C., & Kadye, W. (2019). First record of *Lernaea cyprinacea* (Copepoda: Lernaeidae) on an imperilled endemic anabantid, *Sandelia bainsii* (Teleostei: Anabantidae), from the eastern Cape Province, South Africa. *African Journal of Aquatic Science*, *44*, 183–187.

Chakona, G., Swartz, E. R., & Chakona, A. (2018b). The status and distribution of a newly identified endemic galaxiid in the eastern cape fold ecoregion, of South Africa. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*, 55–67.

Coleman, R., Gauffre, B., Pavlova, A., Beheregaray, L., Kearns, J., Lyon, J., … Sunnucks, P. (2018). Artificial barriers prevent genetic recovery of small isolated populations of a low-mobility freshwater fish. *Heredity*, *120*, 515–532.

Cooke, S. J., Paukert, C., & Hogan, Z. (2012). Endangered river fish: factors hindering conservation and restoration. *Endangered Species Research*, *17*, 179–191.

Crow, S., Closs, G., Waters, J., Booker, D., & Wallis, G. (2010). Niche partitioning and the effect of interspecific competition on microhabitat use by two sympatric galaxiid stream fishes. *Freshwater Biology*, *55*, 967–982.

Cummins, K. W. (1962). An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *The American Midland Naturalist*, *67*, 477–504.

Dawson, D. R., & Koster, W. M. (2018). Habitat use and movements of Australian grayling (*Prototroctes maraena*) in a Victorian coastal stream. *Marine and Freshwater Research*, *69*, 1259–1267.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., … Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, *81*, 163–182.

Farolfi, S. & Abrams, M. (2005) *Water uses and their socio-economic impact in the Kat river catchment: a report based on primary data*. Wate Research Commision Project number K5/1496. CIRAD-TERA.

Fitzpatrick, S. W., Gerberich, J. C., Angeloni, L. M., Bailey, L. L., Broder, E. D., Torres-Dowdall, J., … Chris Funk, W. (2016). Gene flow from an adaptively divergent source causes rescue through genetic and demographic factors in two wild populations of Trinidadian guppies. *Evolutionary Applications*, *9*, 879–891.

Frankham, R., Bradshaw, C. J. A., & Brook, B. W. (2014). Genetics in conservation management: revised recommendations for the 50/500 rules, red list criteria and population viability analyses. *Biological Conservation*, *170*, 56–63.

Greene, W. (2005). Functional form and heterogeneity in models for count data. *Foundations and Trends in Econometrics*, *1*, 113–218.

Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., … Cooke, S. J. (2019). Ecosystem function and services of aquatic predators in the anthropocene. *Trends in Ecology and Evolution*, *34*, 369–383.

He, F., Bremerich, V., Zarfl, C., Geldmann, J., Langhans, S. D., David, J. N. W., … Jähnig, S. C. (2018). Freshwater megafauna diversity: patterns, status and threats. *Diversity and Distributions*, *24*, 1395–1404.

Hoare, D. B., Mucina, L., Rutherford, M., Vlok, J. H., Euston-Brown, D., Palmer, A., et al. (2006). Albany thicket biome. *Strelitzia*, *19*, 540–567.

Holness, S., Driver, A., Todd, S., Snaddon, K., Hamer, M., Raimondo, D., et al. (2016). Biodiversity and ecological impacts: Landscape processes, ecosystems and species. In R. Scholes, P. Lochner, G. Schreiner, L. Snyman-Van der Walt, & M. de Jager (Eds.), *Shale gas development in the Central Karoo: A scientific assessment of the opportunities and risks*. Pretoria: CSIR. http://seasgd.csir.co.za.

Hong, Y. K., Sung, H. C., Ko, M. H., Kim, K. S., & Bang, I. C. (2017). Distribution status and habitat characteristics of the endangered freshwater fish, *Microphysogobio rapidus* (Cyprinidae). *Animal Cells and Systems*, *21*, 286–293.

Jackson, D. A., Peres-Neto, P. R., & Olden, J. D. (2001). What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 157–170.

Jang, J., Kim, J., Kang, J., Baek, S., Wang, J., Lee, H., … HJ, L. (2017). Genetic diversity and genetic structure of the endangered Manchurian trout, *Brachymystax lenok tsinlingensis*, at its southern range margin: conservation implications for future restoration. *Conservation Genetics*, *18*, 1023–1036.

Januchowski-Hartley, S. R., Holtz, L. A., Martinuzzi, S., Mcintyre, P. B., Radeloff, V. C., & Pracheil, B. M. (2016). Future land use threats to range-restricted fish species in the United States. *Diversity and Distributions*, *22*, 663–671.

Kadye, W. T., & Booth, A. J. (2012). Integrating stomach content and stable isotope analyses to elucidate the feeding habits of non-native sharptooth catfish *Clarias gariepinus*. *Biological Invasions*, *14*, 779–795.

Kadye, W. T., & Booth, A. J. (2013). An invader within an altered landscape: one catfish, two rivers and an interbasin water transfer scheme. *River Research and Applications*, *29*, 1131–1146.

Kadye, W. T., & Booth, A. J. (2020). Environmental niche patterns of native and non-native fishes within an invaded african river system. *Journal of Fish Biology*, *96*(5), 1267–1277. https://doi.org/10.1111/jfb.13988.

Knaepkens, G., Bruyndoncx, L., Coeck, J., & Eens, M. (2004). Spawning habitat enhancement in the european bullhead (*Cottus gobio*), an endangered freshwater fish in degraded lowland rivers. *Biodiversity and Conservation*, *13*, 2443–2452.

Laurenson, L. B. J., & Hocutt, C. H. (1986). Colonisation theory and invasive biota: the great fish river, a case history. *Environmental Monitoring and Assessment*, *6*, 71–90.

Lintermans, M. (2013). A review of on-ground recovery actions for threatened freshwater fish in Australia. *Marine and Freshwater Research*, *64*, 775–791.

Loeys, T., Moerkerke, B., de Smet, O., & Buysse, A. (2012). The analysis of zero-inflated count data: beyond zero-inflated poisson regression. *British Journal of Mathematical and Statistical Psychology*, *65*, 163–180.

Mayekiso, M. (1986) Some aspect of the ecology of the eastern cape rocky, *Sandelia bainsii* (Pisces: Anabantidae) in the Tyume River, eastern cape, South Africa. MSc thesis, Rhodes University.

Mayekiso, M., & Hecht, T. (1988). Conservation status of the anabantid fish *Sandelia bainsii* in the Tyume River, South Africa. *South African Journal of Wildlife Research*, *18*, 101–108.

Mayekiso, M., & Hecht, T. (1990). The feeding and reproductive biology of a south African anabantid fish, *Sandelia bainsii*. *Revue d'Hydrobiologie Tropicale*, *23*, 219–230.

McNemar, Q. (1947). Note on the sampling error of the difference between correlated proportions or percentages. *Psychometrika*, *12*, 153–157.

Mullahy, J. (1986). Specification and testing of some modified count data models. *Journal of Econometrics*, *33*, 341–365.

Nel, J., Driver, A., Strydom, W., Maherry, A., Petersen, C., Hill, L., Roux, D., Nienaber, S., Van Deventer, H., Swartz, E., et al. (2011) *Atlas of freshwater ecosystem priority areas in South Africa: maps to support sustainable development of water resources*. Water Research Commission report no. TT 500/1, Water Research Commission, Pretoria, South Africa.

Netshishivhe, S. (2014) The Karoo fracking scenario: can development and environmental wellbeing coexist, or must one of them prevail? *AISA Policy Brief*, No 109.

O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, *1*, 118–122.

Oksanen, A. J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P. R., Hara, R. B. O., Simpson, G. L., Solymos, P., et al. (2019) Vegan: community ecology package. R Package Version 2.5-4. 2019.

Olden, J. D., Kennard, M. J., Leprieur, F., Tedesco, P. A., Winemiller, K. O., & García-Berthou, E. (2010). Conservation biogeography of freshwater fishes: recent progress and future challenges. *Diversity and Distributions*, *16*, 496–513.

Pavlova, A., Beheregaray, L. B., Coleman, R., Gilligan, D., Harrisson, K. A., Ingram, B. A., … Sunnucks, P. (2017). Severe consequences of habitat fragmentation on genetic diversity of an endangered Australian freshwater fish: a call for assisted gene flow. *Evolutionary Applications*, *10*, 531–550.

Potts, W. M., Hecht, T., & Andrew, T. G. (2008). Does reservoir trophic status influence the feeding and growth of the sharptooth catfish, *Clarias gariepinus* (Teleostei: Clariidae)? *African Journal of Aquatic Science*, *32*, 149–156.

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

R Development Core Team. (2019). *R: A language and environment for statistical computing*. Vienna: R Development Core Team.

Rosenfeld, J. S., & Hatfield, T. (2006). Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 683–698.

Russell, I. A. (2011). Conservation status and distribution of freshwater fishes in south African national parks. *African Zoology*, *46*, 117–132.

Saffari, S. E., & Robiah, A. (2011). Zero-inflated negative binomial regression model with right censoring count data. *Journal of Materials Science and Engineering B*, *1*, 551–554.

Saffari, S. E., Adnan, R., & Greene, W. (2012). Hurdle negative binomial regression model with right censored count data. *Statistical and Operations Research Transactions*, *36*, 181–194.

Santos, J. M., Rivaes, R., Boavida, I., & Branco, P. (2018). Structural microhabitat use by endemic cyprinids in a Mediterranean-Type River:

implications for restoration practices. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*, 26–36.

Schumann, D. A., Hoback, W. W., Koupal, K. D., Schoenebeck, C. W., Schainost, S. C., & Wilson, T. L. (2017). Experimental analysis of reintroduction strategies to conserve the vulnerable plains topminnow *Fundulus sciadicus* in Nebraska. *Endangered Species Research*, *34*, 349–355.

Shelton, J. M., Day, J. A., & Griffiths, C. L. (2008). Influence of largemouth bass, *Micropterus salmoides*, on abundance and habitat selection of cape galaxias, *Galaxias zebratus*, in a mountain stream in the cape floristic region, South Africa. *African Journal of Aquatic Science*, *33*, 201–210.

Skelton, P. H. (2001). *A complete guide to the freshwater fishes of southern Africa* (2nd ed.). Cape Town: Struik.

Todd, S. W., Hoffman, M. T., Henschel, J. R., Cardoso, A. W., Brooks, M., & Underhill, L. G. (2016). The potential impacts of fracking on biodiversity of the Karoo basin, South Africa. In J. Glazewski & S. Esterhuyse (Eds.), *Hydraulic fracturing in the Karoo: Critical legal and environmental perspectives* (pp. 278–301). Cape Town: Juta.

Van Der Walt, J. A., Weyl, O. L. F., Woodford, D. J., & Radloff, F. G. T. (2016). Spatial extent and consequences of black bass (*Micropterus* spp.) invasion in a cape floristic region river basin. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*, 736–748.

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology*, *30*, 377–392.

Wong, L. S. C., Lynch, T. P., Barrett, N. S., Wright, J. T., Green, M. A., & Flynn, D. J. H. (2018). Local densities and habitat preference of the critically endangered spotted handfish (*Brachionichthys hirsutus*): large scale field trial of GPS parameterised underwater visual census and diver attached camera. *PLoS One*, *13*, e0205040.

Yau, K. K. W., Wang, K., & Lee, A. H. (2003). Zero-inflated negative binomial mixed regression modeling of over-dispersed count data with extra zeros. *Biometrical Journal*, *45*, 437–452.

SUPPORTING INFORMATION

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

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