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Slippery customers for conservation: Distribution and decline of anguillid eels in South Africa

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Abstract

1. Four anguillid eel species occur in the western Indian Ocean rivers of Africa: *Anguilla bengalensis*, *Anguilla bicolor*, *Anguilla marmorata* and *Anguilla mossambica*. These catadromous fishes face multiple stressors, including habitat alteration and deterioration, barriers to migration, pollution and the adverse impacts of alien species, but knowledge of eel species occurrence, abundance and ecology in Africa remains poor.
2. This study investigated the present and historical distribution of anguillid eels and the potential associated drivers of declines at the southern extremities of their ranges in South Africa. Data analysed included sampling conducted in KwaZulu–Natal and Eastern Cape between 2015 and 2020, and secondary data extracted from databases, museums and local management agencies.
3. The median extent of inland penetration increased as follows: 22 km for *A. bicolor*, 29 km for *A. marmorata*, 94 km for *A. bengalensis* and 293 km for *A. mossambica*. The median altitude followed a similar pattern.
4. Extent of occurrence analyses were carried out at the regional level in KwaZulu–Natal. The sampling data on present distribution (2015–2020), compared with historical data, suggests declines in the extents of occurrence of the four eel species in KwaZulu–Natal, ranging between 31 and 48% in the last 30 years and between 35 and 82% since the 1950s.
5. With increasing human threats in the region, especially from watercourse modification and water abstraction, further declines for these species are expected. Conservation measures recommended include the maintenance or restoration of the ecological connectivity of important rivers and the implementation of freshwater protected areas. Although eels are at present not widely exploited in South Africa, there is a need for fisheries regulations to manage sustainable commercial exploitation.

† Deceased.

KEYWORDS
dams, extent of occurrence analysis, river connectivity, southern Africa, threat to migratory species, water resource management

1 | INTRODUCTION

Anguillid eels (*Anguilla* spp.) are internationally important flagship conservation species, representing long-distance diadromous migrant taxa (Righton et al., 2012; Jacoby et al., 2015). Four anguillid eel species occur and undertake catadromous migrations in the Western Indian Ocean region: the African longfin eel *Anguilla mossambica*, the Indian mottled eel *Anguilla bengalensis*, the giant mottled eel *Anguilla marmorata* and the shortfin eel *Anguilla bicolor* (Hanzen et al., 2019). Anguillid eels are the only long-distance catadromous species to inhabit southern African freshwater systems, making them particularly vulnerable to growing human threats such as disruption of river connectivity, habitat loss and pollution (O'Brien et al., 2019). Similar to temperate anguillid eel species, such as *Anguilla anguilla* and *Anguilla rostrata*, which have become threatened because of significant decreases in abundance (Lecomte-Finiger, 2003; Castonguay & Durif, 2015), anguillid eels found in the Western Indian Ocean region (hereafter 'African anguillid eels') face increasing pressures, but unfortunately their conservation and population status are poorly understood, and they lack formal protection (Jacoby et al., 2015). Evidence of population declines has been reported on the island of Réunion (Valade, Hoarau & Bonnefoy, 2018), the only nation in the western Indian Ocean that has developed a conservation plan for their anguillid eels.

Whereas *A. mossambica* is endemic to Africa, the other species have broader distribution ranges across the northern and western Indian Ocean. *Anguilla marmorata* has been listed as Least Concern by the International Union for Conservation of Nature (IUCN) because of its widespread distribution and lack of evidence of population declines or other major threats (Pike et al., 2020a). *Anguilla bengalensis* and *A. bicolor* are listed as Near Threatened mainly because of constriction of their distribution ranges (Pike et al., 2020b; Pike et al., 2020c). The conservation status of the African endemic *A. mossambica* is listed as Near Threatened because of declines in its distribution range (Pike et al., 2020d).

South Africa's water resource management policies are considered to be among the best on the continent (O'Brien et al., 2019). Although innovative, these policies have not been broadly implemented, and issues such as fish migration, environmental flows and maintaining river connectivity are generally not incorporated in water resource management plans (O'Brien et al., 2019). Owing to the many present and increasing human threats (including pressure to meet increasing industrial, mining, agricultural and domestic water demands), most rivers in South Africa are heavily modified and exhibit reduced ecological functionality (Van Deventer et al., 2018; Evans et al., 2022). The estuaries in South Africa are also poorly conserved. The majority of temporarily open/closed estuaries in KwaZulu–Natal now exhibit extended periods of mouth closure (Scharler et al., 2020), probably because of excessive water abstraction. For example, the low numbers of anguillid eels observed in the St Lucia Basin has been attributed to impaired ecological connectivity within the freshwater system and to the sea (Desai et al., 2021). Indeed, extended estuary mouth closure can affect the movement and life cycle of many fish species and can potentially impede their breeding or recruitment (Bate, Whitfield & Forbes, 2011). As anguillid eels are migratory, widespread and occur across the highly diversified South African landscape, data on their distribution could provide valuable information on ecological connectivity that could inform integrated water resource management in the region.

Anguillid eels have received relatively little attention in the Western Indian Ocean region, including South Africa, and knowledge of their historical and present distributions is sparse (Righton et al., 2021). Consequently, this study aimed to (i) review the present and historical distribution ranges of the four anguillid eel species occurring in South Africa; (ii) assess changes in their distribution ranges in areas where sampling has been adequate; and (iii) evaluate catchment level drivers of distribution of the African endemic anguillid eel, *A. mossambica*. The results of the study may be used to inform the development of conservation priorities for anguillid eel species in South Africa.

2 | METHODS

In South Africa, anguillid eels are found in the south- and east-flowing drainages of the Cape Fold, Amatolo-Winterberg Highlands, Southern Temperate Highveld and Zambezian Lowveld aquatic ecoregions (Skelton, 2001; Abell et al., 2008). Freshwater habitats in the region range from short coastal streams to large river basins and have a diverse range of fish communities that include many endemic species.

2.1 | Historical and contemporary secondary data collection

Existing distribution data for *A. bengalensis*, *A. bicolor*, *A. marmorata* and *A. mossambica* in South Africa were extracted from several sources: (i) the Atlas of Southern African Freshwater Fishes (Scott et al., 2006); (ii) the Global Biodiversity Information Facility (GBIF, 2019a; GBIF, 2019b; GBIF, 2019c; GBIF, 2019d); (iii) the Freshwater Biodiversity Information System (fbis.org); and (iv) records of historical catches and recent survey data from provincial wildlife management bodies including Ezemvelo KZN Wildlife, Mpumalanga Parks Board and CapeNature. Additional distribution records obtained from researchers and consultants were included when photographic evidence confirming the species' identification was available. Occurrence data from Mozambique and Swaziland were included for the Pongolo, Incomati and Limpopo catchments, the upper reaches of which are in South Africa. The databases used are regarded as the best available sources because the data originate principally from reputable national research organizations, such as the South African Institute for Aquatic Biodiversity and its predecessors.

2.2 | Study areas

KwaZulu–Natal Province was chosen for the regional scale study of changes in eel distribution range because all four species of eel occurring in South Africa have historically occurred in sympatry there (Skelton, 2001). In addition, the availability of spatial coverage data for historical and present eel distribution ranges supported analyses.

All 18 major catchments in KwaZulu–Natal flow eastward into the Indian Ocean, and it is the only province in South Africa that is not considered to be water-scarce (Rivers-Moore, Goodman & Nkosi, 2007). Human demand for water has resulted in the construction of numerous dammed impoundments and inter-basin transfer schemes (Mantel, Rivers-Moore & Ramulifho, 2017). These, together with direct water abstraction from the rivers for agriculture, have resulted in altered water and sediment budgets and catchment degradation, and the loss of river connectivity (Rivers-Moore, Goodman & Nel, 2011). For instance, in 2007, only nine of the rivers in KwaZulu–Natal longer than 100 km remained free-flowing from source to sea: 35% of rivers >100 km in the province (Rivers-Moore, Goodman & Nkosi, 2007). Typically, human impacts increase down the river continuum, and headwaters in KwaZulu–Natal are in a better ecological state than the lowland reaches (Agboola, Downs & O'Brien, 2019). Indeed, estuaries in KwaZulu–Natal are becoming degraded because of lower freshwater inputs and increased pollution (Scharler et al., 2020). About 19% of the estuaries in KwaZulu–Natal are in poor condition (Whitfield & Baliwe, 2013). The resulting prolonged closures of the estuaries are affecting their biodiversity (Scharler et al., 2020) and the life cycles of species that depend on connectivity between freshwater and marine ecosystems.

The Keiskamma River catchment (2,580 km^2), Eastern Cape Province, was chosen for the assessment of environmental variables affecting eel distribution at a catchment scale because of its relatively natural state. The Keiskamma originates in the Amatola Mountains and runs through a relatively undeveloped region. Although there are dams in the upper reaches and small weirs in the main stem and tributaries, most of the catchment is considered accessible to anguillid eel species throughout the year (G. O'Brien, pers. obs.). The Keiskamma catchment is one of the larger catchments in the Eastern Cape (Grothmann et al., 2017), with a human population of about 100,000 people and without major cities or industries. Its estuary is permanently open and is considered to be in a fair state (Whitfield & Baliwe, 2013).

2.3 | Sampling

In total, 188 sites were sampled in KwaZulu–Natal between 2015 and mid 2020 (Supplementary Information, Table S1 and Figure S1). Comprehensive fishing surveys were designed for fish community assessments and included the use of overnight fyke nets, electrofishing, gill nets and seine nets (Desai, 2018; Dlamini, 2019; Hanzen, 2019; Mashaphu, 2019; Evans et al., 2022; Supplementary Information, Table S1). These sites were sampled several times during the study period. In addition, rapid assessment surveys were carried out using electrofishing and seine nets only (see River Health Programme and River Eco-Monitoring Programme, Supplementary Information, Table S1; Evans et al., 2022).

The Keiskamma River catchment (Supplementary Information, Figure S2) was sampled for yellow and silver phase eels using commercial fyke nets, each consisting of a single central leader ~7 m long, with two or three internal funnels, 23 mm mesh and an opening height of ~70 cm (T&L Netmaking, Mooroolbark, Australia). Nets were set in the afternoon and retrieved the next morning, standardizing the sampling effort. Survey sites were chosen based on the distance from the sea and elevation to give broad coverage across the catchment. Time and budget constraints restricted the Keiskamma River sampling to a survey between 21 February 2018 and 2 March 2018. At each sampling site, habitat data were recorded based on a minimum of five transects to evaluate flow, depth and substrate. In addition, water temperature, electrical conductivity, pH and total dissolved solids were measured (Hannah HI991300, Woonsocket, USA).

Captured eels were identified to species according to Ege (1939) with the amendments of Réveillac et al. (2009) and released at their capture location. The anal–dorsal fin ratio, colouration pattern (for adults) and tail pigmentation (for juveniles) were used to distinguish the four eel species. All relevant site data were recorded: geographical coordinates (Garmin Etrex 10, Garmin, Olathe, USA), date of sampling, species captured and photographs of the individuals captured.

2.4 | Data processing and analyses

All location data were mapped using the QGIS Geographic Information System (QGIS 3.12, 2018). Altitude was calculated for each point by extracting the value from the 30 m digital elevation model of South Africa from Shuttle Radar Topography Mission supplied by the South African National Space Agency, courtesy of the USA Geological Survey.

The extent of occurrence (EOO), used by the IUCN Standards and Petitions Committee (2019) to assess the conservation status of species, was used in this study to measure changes in distribution of eel species in South Africa. The EOO, based on a minimum convex polygon generated from species records, can potentially under- or over-estimate the true extent of eel species: it has been designed primarily for species not restricted to a linear habitat, such as a river (IUCN Standards and Petitions Committee, 2019). As anguillid eels are marine spawned and have to use the entire stretch of the river downstream of their occurrence location, the EOO approach was modified to incorporate recorded maximum inland penetration using quaternary catchments. This approach is more ecologically relevant than using only the minimum convex polygon. The EOO was calculated for each eel species at the KwaZulu–Natal regional scale using QGIS 3.12.

All statistical analyses of the catchment scale data were carried out using R version 4.1 (R Core Team, 2021), with statistical significance set at $P < 0.05$. To understand the variables driving the presence of eels at the catchment scale, non-metric multidimensional scaling (NMDS; Groenen & Velden, 2017) as well as permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017), were conducted using the VEGAN package for R (Oksanen et al., 2018). Before analyses, all of the variables were normalized to reduce the disparity between the magnitude of the scales for respective variables and the sites grouped based on the detection of

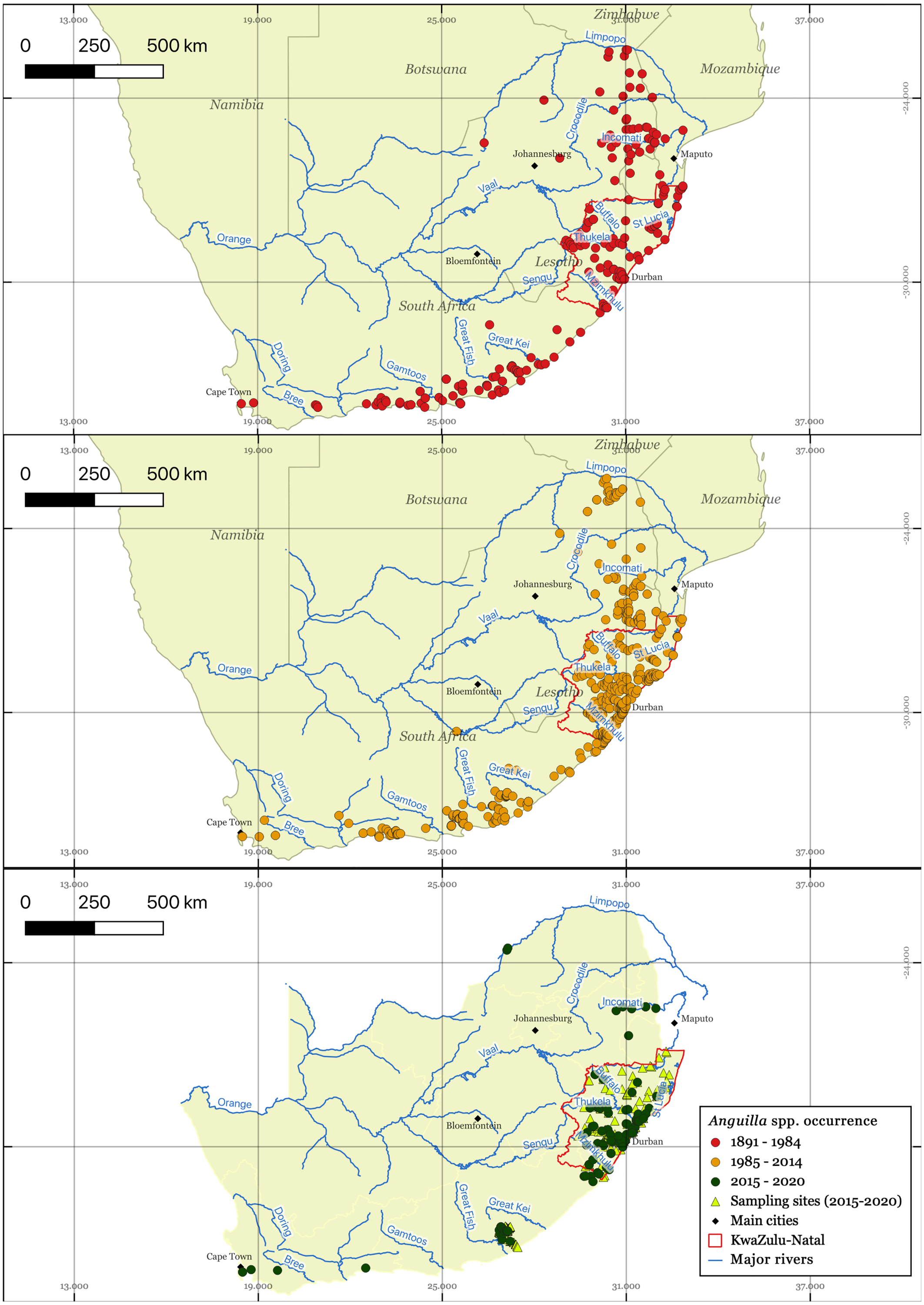

FIGURE 1 Occurrence points collected for the four African eel species in South Africa between 1891 and 2020. The map also includes data points from Swaziland and Mozambique for catchments whose upper reaches are in South Africa. Sampling sites for the present study are also shown

A. mossambica, i.e. sites where they were detected and those where they were not detected, hereafter referred to as 'site groups'. A resemblance matrix was constructed using the *vegdist* function in VEGAN based on Euclidean distance. Non-metric multidimensional scaling was performed on the resemblance matrix using the *metaMDS* function in VEGAN. Dispersion between the site groups was calculated using the *betadisper* function in VEGAN and permutation-based tests of the homogeneity of multivariate dispersion between the site groups (PERMDISP) were evaluated using the *permtest* function in VEGAN. Permutational multivariate analysis of variance to evaluate the centroid position and multivariate dispersion between the site groups was evaluated using the *adonis* function in VEGAN. A similarity percentages (SIMPER) analysis was performed to identify the environmental variables that contributed most to the dissimilarity between site groups using the *simper* function in VEGAN.

3 | RESULTS

3.1 | National scale

In total, 1,202 historical records and present occurrence points for the four eel species in southern Africa between 1891 and June 2020 were collated (Figure 1). *Anguilla mossambica* had the highest number of records, representing 76.4% (n = 918) of all the observations, followed by *A. marmorata* (n = 202, 16.8%), *A. bengalensis* (n = 61, 5.1%) and *A. bicolor* with only 21 observations (1.7%). Most of the data collected were from South Africa (n = 1,119; representing 93.7% of all the data), followed by Swaziland (n = 73; 6.1%) and Mozambique (n = 3; 0.2%). In South Africa, KwaZulu–Natal was the most data-rich province (n = 533; 44.3%), followed by the Eastern Cape (n = 412; 34.3%; Figure 1). These numbers potentially represent a difference in sampling effort rather than a difference in species distribution or abundance. Only anecdotal data were available for the Gauteng (n = 1) and North West (n = 1) regions. One eel was recorded in the Free State where all rivers flow to the Atlantic Ocean, but it is believed that the specimen might have been translocated or moved between tributaries of the neighbouring catchments. No eels were recorded in the Northern Cape, where all rivers also empty to the Atlantic Ocean.

Based on all species records, the four species had different longitudinal (Kruskal–Wallis, $P < 0.001$) and altitudinal distributions (Kruskal–Wallis, $P < 0.001$; Figure 2). Pairwise comparisons showed that *A. bicolor* and *A. marmorata* used similar habitats in terms of altitude (Mann–Whitney U, $P = 0.251$) with medians of 30 and 49.5 m.a.s.l. However, *A. marmorata* was observed at much higher altitudes with a maximum of 1,022 m.a.s.l. compared with 577 m.a.s.l. for *A. bicolor*. In terms of inland penetration, *A. marmorata* and *A. bicolor* exhibited similar medians (Mann–Whitney U, $P = 0.084$) of 29 and 22 km from the sea, respectively, but maximum distances of 693 and 218 km from the sea, respectively. The other eel species occupied habitats at different altitudes (Kruskal–Wallis, $P < 0.0001$ when all species were compared) and longitudinal ranges (Kruskal–Wallis, $P < 0.0001$ when all species were compared), with *A. mossambica* exhibiting the largest range with a maximum of 1,776 m.a.s.l. (median = 250 m.a.s.l.) and 1,828 km (median = 94 km) away from the sea, against a maximum of 1,424 m.a.s.l. (median = 632 m.a.s.l.) and 866 km (median = 293 km) away from the sea for *A. bengalensis*.

3.2 | Regional scale: KwaZulu–Natal

In total, 533 eel records were collated, or sampled, from 1957 to June 2020 in KwaZulu–Natal (*A. mossambica* 370 records, *A. marmorata* 109 records, *A. bengalensis* 44 records, *A. bicolor* 10 records). Based on the entire time series, these records occurred across 30 catchments, with the Thukela having 28.9% of all records (n = 154), followed by the uMngeni with 11.1% (n = 59). The

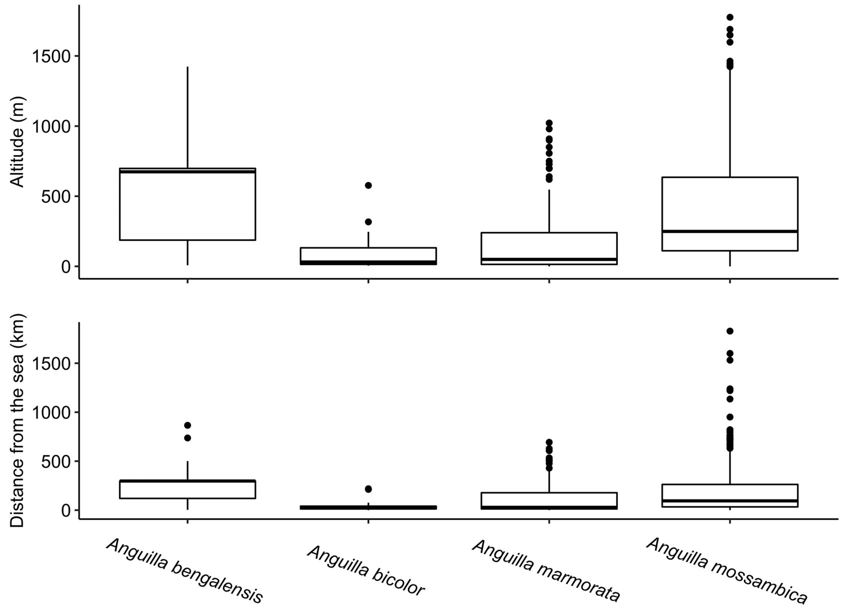

FIGURE 2 Longitudinal (distance from the sea) and altitudinal (above sea level) distribution of the four African eel species, *Anguilla bengalensis*, *Anguilla bicolor*, *Anguilla marmorata* and *Anguilla mossambica* in South Africa. The boxplot represents the lower (25%) and upper quartile (75%), the black line represents the median, the whisker represents the minimum and maximum while the dots represent outliers

remaining catchments all had fewer than 35 records, each representing <10% of the data collected. Only three catchments held the four African eel species: the Mhlatuze, the Mfolozi and the most northern quaternary catchment, including small seasonal streams or large coastal lakes such as Kosi Bay.

Across all catchments, 183 sites were sampled between 2015 and 2020 and 143 individuals were collected (*A. mossambica*, $n = 77$; *A. marmorata*, $n = 42$; *A. bengalensis*, $n = 23$; and *A. bicolor*, $n = 1$). Additional occurrence data ($n = 36$) were provided by local researchers and consultants, as well as extracted from online databases and the local wildlife management agency (Ezemvelo KZN Wildlife) for the same period. These contemporary data comprised one-third of all existing occurrence data for eels in KwaZulu–Natal. Most of these data were collected from two catchments – the Thukela with 45% of observations ($n = 91$), followed by the uMngeni ($n = 17$) with 9.5% of all recent observations.

Eels were found in 17 of the 18 major catchments sampled in KwaZulu–Natal between 2015 and 2020. None of the catchments were found to have all four species. Both *A. marmorata* and *A. mossambica* were found to be spread across the major and minor catchments of KwaZulu–Natal. *Anguilla bicolor* and *A. bengalensis* were restricted to three (aMatigulu, $n = 1$; Mfolozi, $n = 2$; and Mhlatuze, $n = 2$) and two catchments (Thukela, $n = 18$ and Mfolozi, $n = 1$), respectively.

The extent of occurrence of the four eel species was calculated for the recent sampling data (2015–2020) and compared with historical records. Compared with the previous 30 years (1985–2014), a decline of 80% in the EOO was observed for *A. bengalensis*, 47% for *A. mossambica*, 48% for *A. bicolor* and 31% for *A. marmorata*. When compared with the full time series, a decline in the EOO of 82% was observed for *A. bengalensis*, 75% for *A. bicolor*, 50% for *A. mossambica* and 35% for *A. marmorata*.

Anguilla bengalensis, the species with the highest apparent decrease in its EOO, was found in only two catchments in KwaZulu–Natal over the period 2015–2020, the Thukela and the Mfolozi (Figure 3), and so appears to have undergone a strong reduction in its distributional range in the north and south of KwaZulu–Natal. *Anguilla bicolor* is a species that is associated with coastal areas and may have been lost from large parts of its range since the 1950s as it has only been found in the Matigulu, Mfolozi and Mlalazi catchments in recent years (Figure 4). *Anguilla marmorata* has been recorded in most of the major catchments of KwaZulu–Natal, including the Mtamvuna, Umlazi, Umgeni, Thukela, Matigulu, Mhlatuze, Mfolozi and Hluhluwe, but also seems to have undergone a strong range reduction in the north and south of the province (Figure 5). *Anguilla mossambica*, although also suffering an apparent decline in its EOO, especially from the upper reaches of the Thukela,

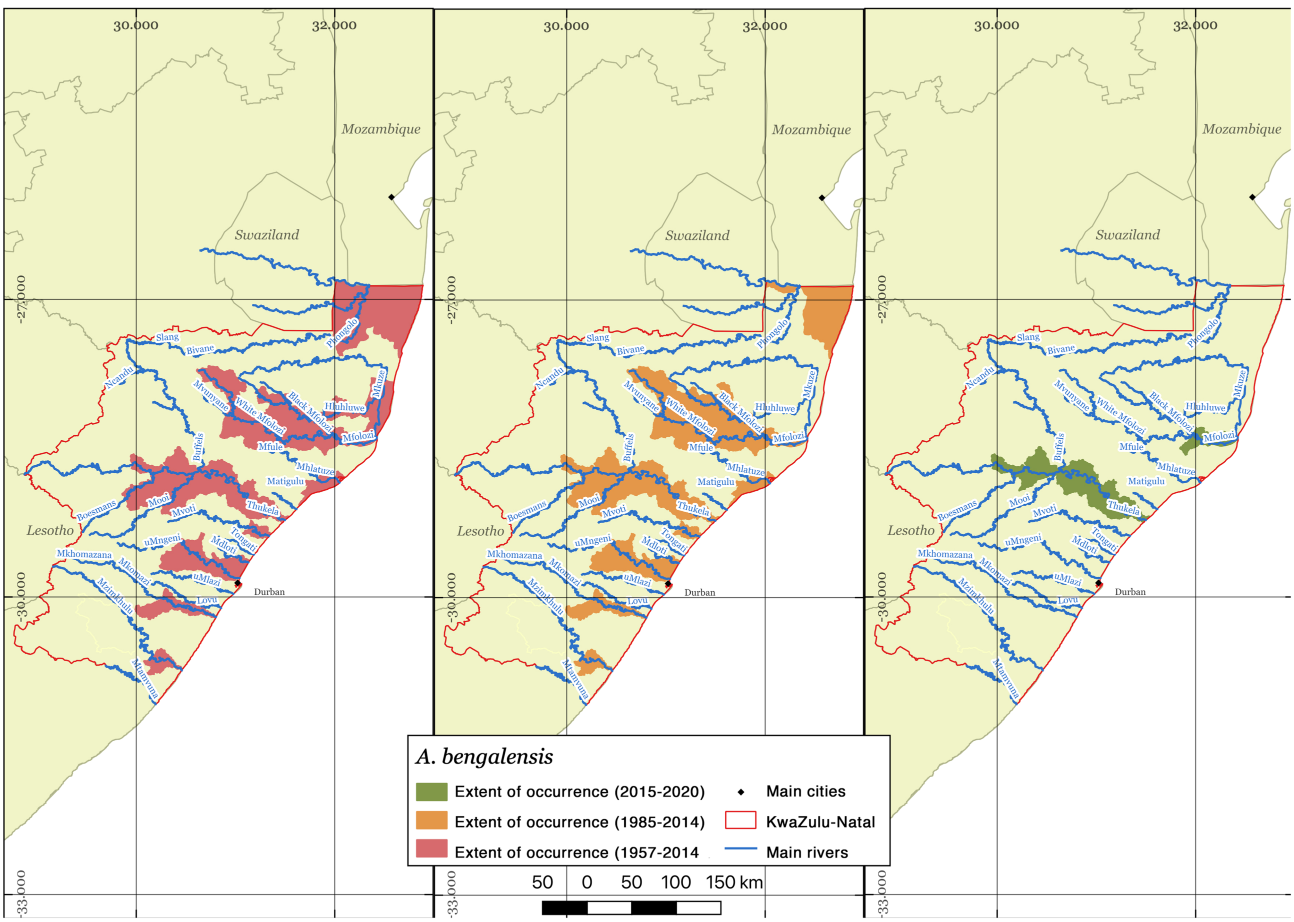

FIGURE 3 Changes in the extent of occurrence of *A. bengalensis* in KwaZulu–Natal

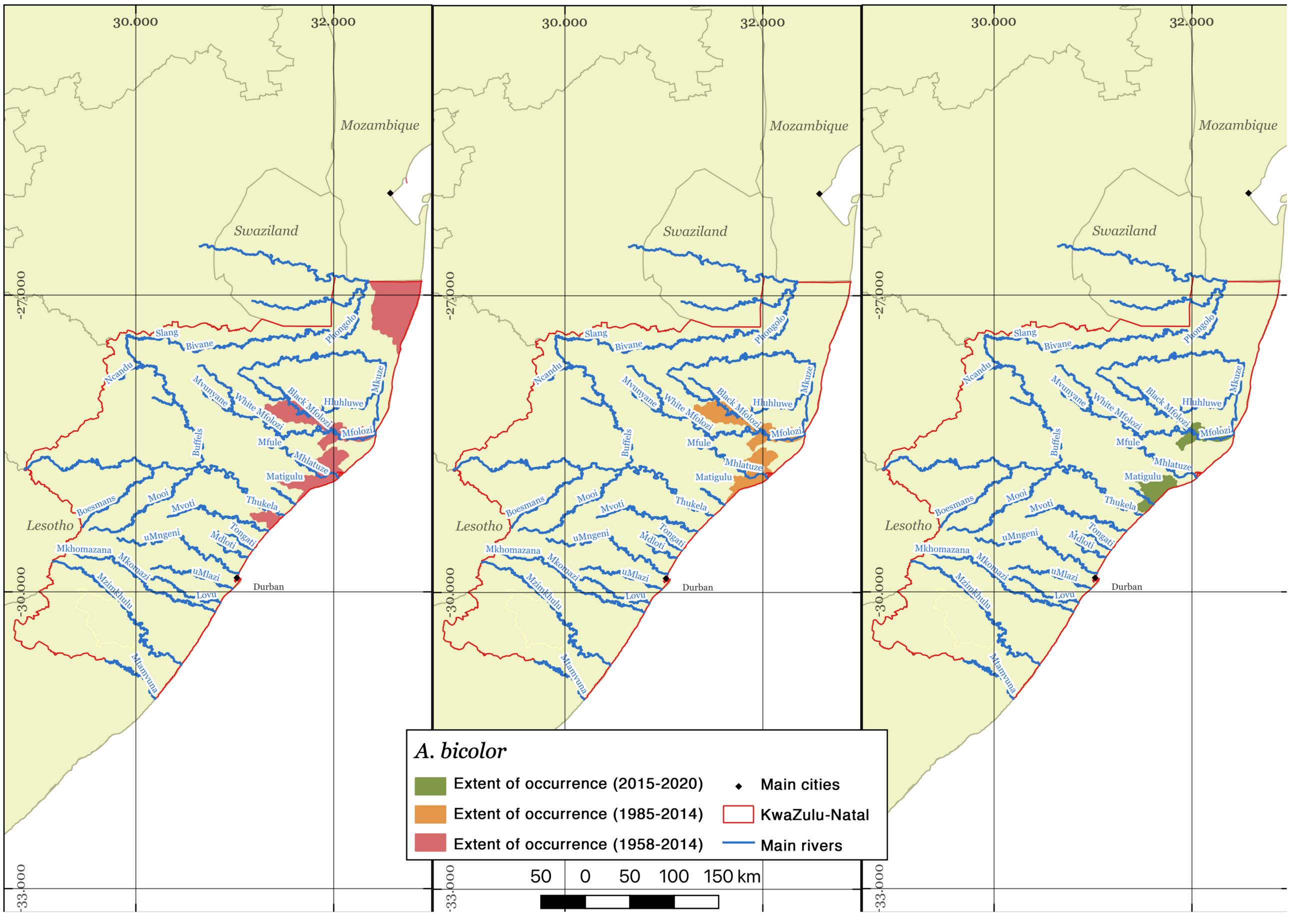

FIGURE 4 Changes in the extent of occurrence of *A. bicolor* in KwaZulu–Natal

as well as most of the Phongolo and Mfolozi systems, remains in most catchments of KwaZulu–Natal (Figure 6). Although Figures 3–6 emphasize the distribution of eels in the larger catchments of KwaZulu–Natal, eels were present in numerous small coastal streams (Supplementary Information, Table S1).

3.3 | Catchment scale

Despite the 75 net-nights sampling effort, relatively few eels were collected in the Keiskamma River: 17 *A. mossambica* and four *A. marmorata*. *Anguilla mossambica* occurred in the headwater and middle reaches, ranging from 130 to 816 m.a.s.l. and from 72 to 244 km from the sea (Supplementary Information, Figure S2). *Anguilla marmorata* were recorded at a single site in the middle reaches of the catchment, at an altitude of 274 m.a.s.l., 250 km from the sea.

The NMDS plot of the environmental variables showed that the sites where *A. mossambica* was detected lay entirely in the *n*-dimensional space of the sites where the species was not detected (Figure 7). The stress for the NMDS plot was 0.107, indicating that the plot is a good representation of the data with a low probability of misinterpreting groupings. The PERMDISP found a significant difference in multivariate dispersion between the site groups (F = 6.511, d.f. = 1, number of permutations = 999, P = 0.014). However, the PERMANOVA showed no significant differences between the site group centroids (F = 0.781, d.f. = 1, number of permutations = 9999, P = 0. 964). The SIMPER analysis showed that the differences between the site groups were based on small contributions by all the variables included in the analyses. Therefore, it was difficult to distinguish between sites where *A. mossambica* was detected and those where the species was not detected based on the environmental variables used in the study.

4 | DISCUSSION

This study is the first to evaluate changes in the distribution of anguillid eels in the Western Indian Ocean region of Africa, in particular southern Africa. From a conservation viewpoint, this study has characterized and highlighted declines in the distributions of all four southern African eel species in KwaZulu–Natal.

Limited data are available to evaluate the distribution and drivers of changes in eel distribution in Africa compared with eel species occurring at higher latitudes (Righton et al., 2021). For comparison, a search on the GBIF returned over 300,000 records for the European eel *A. anguilla* (GBIF, 2022a), over 9,000 for the American eel

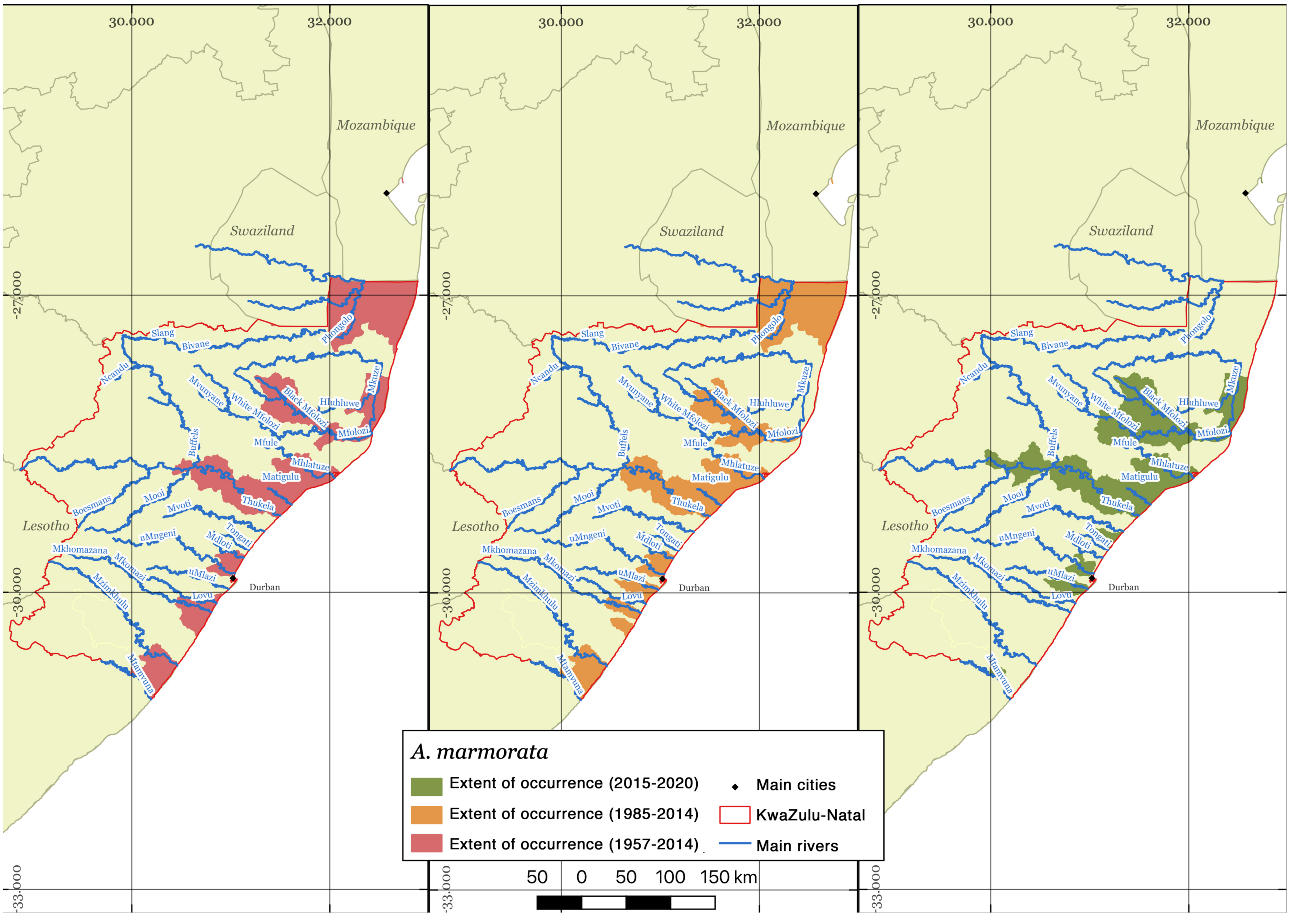

FIGURE 5 Changes in the extent of occurrence of *A. marmorata* in KwaZulu–Natal

A. rostrata (GBIF, 2022b), over 6,000 for the Japanese eel *Anguilla japonica* (GBIF, 2022c) and over 4,000 for the Australian long-finned eel *Anguilla reinhardtii* (GBIF, 2022d), with records starting in the eighteenth century for all these species.

In South Africa, there seems to be a general indifference to riverine fish migrations despite their essential role in maintaining healthy, sustainable ecosystems (O'Brien et al., 2019). The low research effort is a consequence of the country's relatively small number of freshwater fish researchers, a lack of directed funding for surveys of fish range distribution and, until recently, a lack of a historical repository for fish distribution data in the country. Moreover, the long and complex life history of anguillid eels and their elusive habits make them 'slippery' species to study. The present low economic value of eels in the region, with virtually no established fisheries known for any eel species, compounds the problem (Hanzen et al., 2019). However, this could change in the near future as international interest and investment in these eel species for ranching is growing (Gollock et al., 2018). Although no official reports were made to the UN Food and Agriculture Organization, east Asian customs authorities have reported the export of live glass eels originating from Madagascar and Mauritius in the past 10 years (Crook & Nakamura, 2013; Gollock et al., 2018; Kaifu et al., 2019). A market for *A. bicolor* and *A. marmorata* exists in other countries, including Malaysia, Indonesia, the Philippines and East Asia, and *A. bengalensis* is also traded throughout the Indian peninsula (Kaifu et al., 2019).

Eels are difficult to identify to species level based on morphological characteristics alone (Watanabe, Aoyama & Tsukamoto, 2004; Aoyama, 2009; Hanzen et al., 2020). Some of the data on present and historical distributions are likely to have been for misidentified species. Indeed, Balon (1975) reported the impossibility of separating *A. mossambica* and *A. bengalensis* in Lake Kariba in the 1970s. The use of DNA barcoding by Hanzen et al. (2020) for identifying African eel species has been successful and is recommended for future research in the region. Ideally, determining the changes in distribution and abundance of a species should use a fixed effort survey over time, but details of the extent of sampling effort are not available for the historical data in this study. Therefore, the estimates of the reduction in EOO require caution but are the best available. Despite intensive surveying for eels in KwaZulu–Natal between 2015 and 2020, the distribution of the four anguillid eel species was markedly reduced when compared with previous time periods, whereas the opposite pattern would be expected if contemporary sampling had been more intensive than in previous time periods.

Well-studied eel species, such as *A. anguilla* and *A. japonica*, are threatened by many stressors and have been listed by the IUCN (Pike,

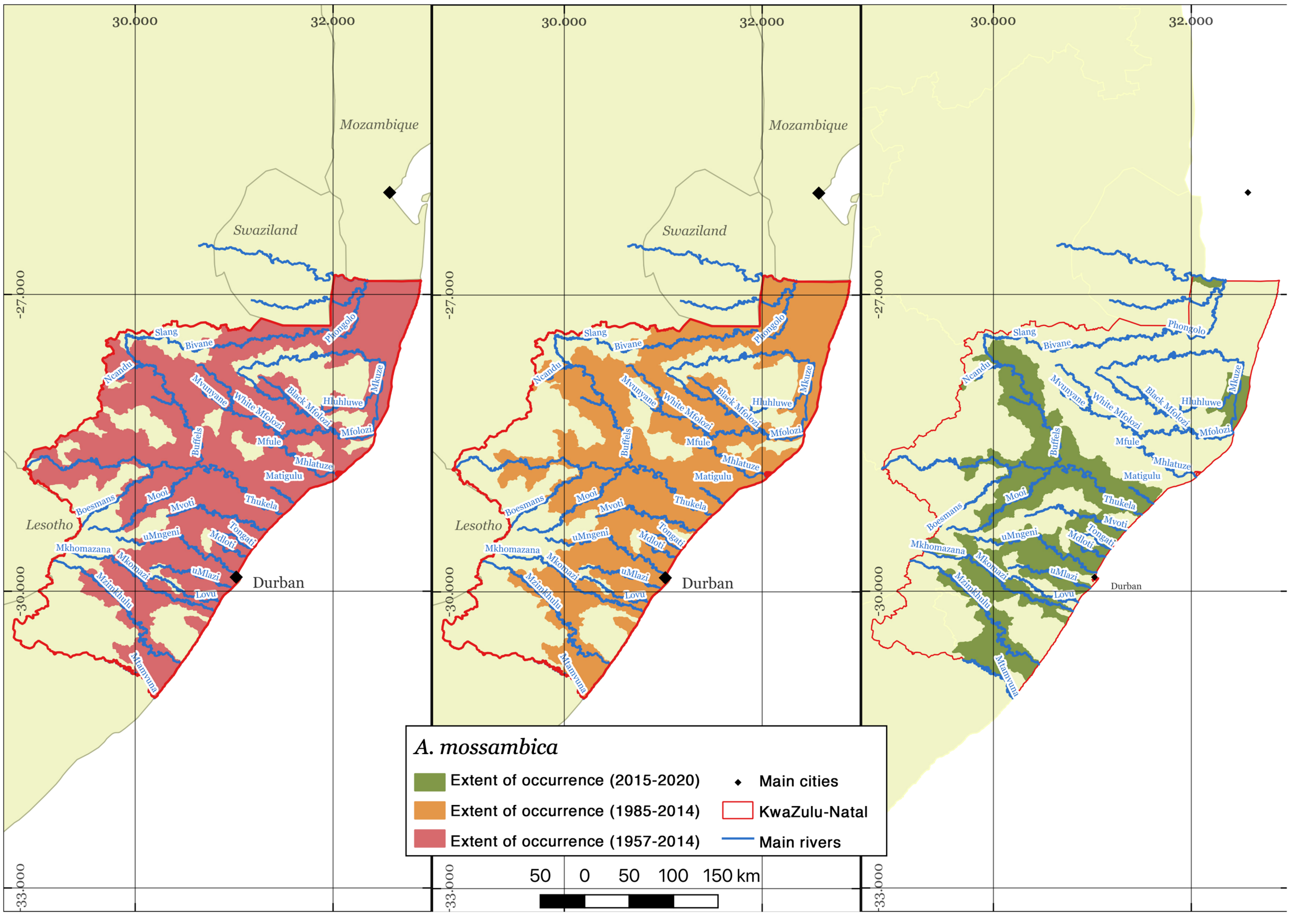

FIGURE 6 Changes in the extent of occurrence of *A. mossambica* in KwaZulu–Natal

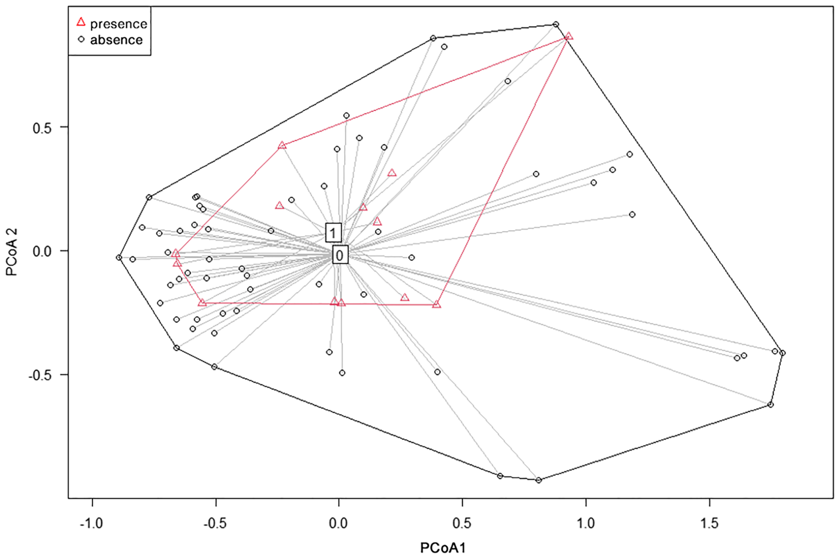

FIGURE 7 Convex hull plot for the non-metric multidimensional scaling results of the analysis of the environmental drivers for the presence and absence of *A. mossambica* in the Keiskamma River, Eastern Cape (stress = 0.107). The '0' indicates the centroid of the sites where *A. mossambica* was not detected while the '1' represents the centroid of the sites where *A. mossambica* was detected

Crook & Gollock, 2020e; Pike et al., 2020f) as Critically Endangered and Endangered, respectively. A decline of ~90% in numbers has been found in the recruitment of *A. anguilla* into European rivers since the 1980s and a 50% decline in both yellow and silver eel stages (Pike, Crook & Gollock, 2020e).

Given the declining abundance of *A. anguilla* and *A. japonica* and the increasing global demand for eels, conservation attention for eels in Africa needs to increase, particularly in light of the results of the present study. Added pressures are likely with potential increased exploitation of eel species in Africa. Available data for this evaluation are limited to southern Africa, including the comprehensive sampling in KwaZulu–Natal from 2015. *Anguilla bengalensis* and *A. bicolor* may now be restricted to a few rivers or even a few sites in KwaZulu–Natal. Indeed, although more than 180 KwaZulu–Natal sites were sampled in recent years, these species were only observed in four catchments, and *A. bicolor* was not detected after 2017. Although concerning, limited historical data and previous identification issues suggest that *A. bicolor* and *A. bengalensis* may be naturally less abundant in KwaZulu–Natal as it represents the southern limit of their distribution. *Anguilla bengalensis* was reported to be rare south of the Limpopo catchment (Bell-Cross & Minshull, 1988) and *A. mossambica* is considered to be the most common anguillid species in South Africa (Jubb, 1961; Scott et al., 2006). *Anguilla bicolor* is usually restricted to coastal areas in floodplains and wetlands – habitat types that were not well represented in this river-focused study. Eels were present in several small (<10 km) coastal streams (Supplementary Information, Table S1) and show the potential importance of these for eel production and conservation; we recommend that future eel surveys include the sampling of a wider range of coastal streams and lagoons in addition to the rivers in larger catchments.

Where eel species occur in sympatry and have similar niches, they may exhibit differences in local distribution or habitat use to minimize interspecific competition (Jellyman & Sykes, 2003). This phenomenon has been observed in the western Indian Ocean region, with *A. bicolor* commonly found in the lower reaches of freshwater systems below 300 m.a.s.l. in Madagascar (Kiener, 1963) and below 100 m.a.s.l. in Mayotte (Valade, Hoarau & Bonnefoy, 2018). A similar pattern was also found for *A. bicolor* in India (Shanmughan et al., 2022). In contrast, both *A. mossambica* and *A. bengalensis* are found far inland and at the highest altitudes. In Madagascar, *A. bengalensis* is known to inhabit altitudes higher than 900 m.a.s.l. (Kiener, 1963). *Anguilla mossambica* is a more generalist species and has been recorded along the entire length of catchments (Marshall, 2011). Similar trends were found here with *A. mossambica* using the entire catchment similarly to *A. bengalensis*, while *A. bicolor* and *A. mamorata* were normally found in the lower reaches of river systems. Inland penetration is also dependent on catchment morphology (Valade, Hoarau & Bonnefoy, 2018) but may also be explained by differing recruitment dynamics as different species reach the coast at different body sizes (Robinet et al., 2003; Hanzen et al., 2019). Range contraction, especially at the limit of species distribution, has been suggested to be associated with reduced recruitment (Jellyman, 2021).

The analyses of drivers affecting the distribution of *A. mossambica* in the Keiskamma River included the influence of habitat (depth, width, velocity and substrate), ecological connectivity and water quality on the presence of the species at the survey sites. The PERMANOVA analysis found no significant differences in environmental variables between sites where *A. mossambica* were recorded and those where the species was not detected. Explanations for this result include a possible low abundance of eels in the Keiskamma River, patchy population density of eels in the Keiskamma River, potential population depletion at the sites because of localized overfishing, poor detection probability of the sampling gear, insufficient sampling effort over a short period at each site, and weather events affecting the movement of eels in the sites. The catches of eels in the Keiskamma River were higher than those observed in surveys of KwaZulu–Natal rivers of a similar size (Hanzen, 2019). This suggests that the eel populations in the Keiskamma River are healthy, even though this river is towards the southern extremity of the distribution range of anguillid eels in Africa. Detection could be improved in future surveys by diversifying sampling methods; for example, by including environmental DNA techniques and by increasing sampling effort.

The Keiskamma River is largely a free-flowing river with two dams in the upper catchment. The presence of anguillid eels above large barriers is not uncommon, and they have been found upstream of the Howick Falls (111 m) in KwaZulu–Natal (Hanzen, 2019), Kariba Dam (128 m; Balon & Coche, 1974) and the Cahora Bassa Dam on the Zambezi (Skelton, 2001). Eel abundance has also been shown to decrease with distance from the sea (Halvorsen et al., 2020). A lack of river connectivity might impede the upstream migration of healthy numbers of eels, leading to lower numbers of maturing female silver eels going back to sea to spawn. Furthermore, insufficient spawning stock has been suggested as a reason for recruitment collapse (Jellyman, 2021). In addition, smaller obstacles such as weirs are sometimes overlooked as impediments to fish migration as they represent semi-permeable barriers, but these should be considered in river conservation and planning (Mantel, Rivers-Moore & Ramulifho, 2017). Barriers not only affect the hydrological connectivity of the river ecosystem but also alter thermal characteristics and sediment transport. Although the ecological dynamics of eel recruitment remain largely unknown in South Africa, they have been hypothesized to be linked to hydrological stimuli, coinciding with strong summer river flows (Bruton, Bok & Davies, 1987; Robinet et al., 2003). These natural changes in flow are likely to be compounded in strongly regulated systems, such as the uMngeni River in KwaZulu–Natal, where major obstacles and associated impacts are present in the lower reaches of the river. In addition, water resource developments in KwaZulu–Natal are relatively greater than in other regions of southern Africa (O'Brien et al., 2021), suggesting that the threats to the eel populations may be greater than in other areas.

In South Africa, there are more than 4,000 formal dams with impoundments and more than 1,400 gauging weirs (O'Brien et al., 2019); these represent partial, temporary or complete barriers to fish migration. This situation is likely to worsen in the future as southern Africa has been described as the most vulnerable area to climate change in Africa (Intergovernmental Panel on Climate Change, 2007). New impoundments are being planned on largely free-flowing rivers in South Africa to address water security needs, including the Limpopo, Crocodile, Thukela, Umkomas, Mzimkulu and Mzimvubu (Hanzen et al., 2019). For example, future plans to dam the Thukela catchment will possibly lead to a flow reduction of between 16 and 44% from present flows (Lamberth, Drapeau & Branch, 2009).

In South Africa, the effects of climate change are likely to translate into increased inter-annual variability of rainfall, with extremely wet periods and more intense drought (Kusangaya et al., 2014). Temperatures will generally increase (Graham et al., 2011), and the eastern part of South Africa (i.e. KwaZulu–Natal) will probably see increased runoff or extreme rainfall events during the wet season. These will have impacts on the hydrological regimes in rivers but will also induce changes in the estuaries, and the frequency and duration of river mouth opening, particularly in KwaZulu–Natal, thereby affecting species that depend on connectivity between freshwater and marine environments, including anguillid eels.

5 | IMPLICATIONS FOR CONSERVATION

We raise concerns regarding the apparent decline in the distribution ranges of the four African eel species in the rivers of South Africa. With growing human threats exacerbated by increasing demand for both fish and water resources and the impact of global change, in parallel with poor regional management (O'Brien et al., 2019), it is naive to ignore the continued decline of the four southern African eel species. It is possible that two of the four species (*A. bicolor* and *A. bengalensis*) may be extirpated from South Africa in the coming decades.

In the Western Indian Ocean Region, only one nation, Réunion, has a conservation plan for anguillid eels (Valade, Hoarau & Bonnefoy, 2018). This includes measures to combat poaching, fisheries management, restoration of river connectivity and habitat quality, as well as improved governance. We recommend that similar conservation initiatives are proposed and implemented for rivers in South Africa to restore eel stocks in the country.

5.1 | Connectivity and fish passage

Although river connectivity is key to eel distribution, no more than 60 fish passage structures have been built in South Africa, and their effectiveness has not been assessed (O'Brien et al., 2019). None of the new impoundments under construction will be legally obliged to incorporate fish pass structures; solutions are available, however, and restoration of river connectivity has had a positive impact on eel abundance (Hitt, Eyler & Wofford, 2012). Fish passage structures have been shown to have varied effects, depending on their design and placement: nature-like fishways appear to have the greatest benefit for assisting the occurrence of European eel upstream of barriers (Tamario et al., 2019). Obstacles along the downstream pre-spawning migration route are another problem that the present study has not addressed but has been noted for temperate species (Jacoby et al., 2015), especially in areas where hydropower is well developed. Although it is advised to plan for fish passage in the early stages of designing new structures, there are low-cost solutions that can be fitted after construction. On small obstacles, such as culverts and channels, low-cost remediation solutions include the installation of ropes, baffles or floating ramps.

Where possible, river barriers that no longer have a use should be removed, as this permits rapid recolonization by eels (Hitt, Eyler & Wofford, 2012; Sun, Galib & Lucas, 2021). In this regard, the Kruger National Park in South Africa is taking the lead by removing all of the artificially constructed river barriers present in the park (Freitag-Ronaldson & Venter, 2008; Pollard, Du Toit & Biggs, 2011) for the benefit of all biota present. It is hoped that this conservation action will inspire others.

5.2 | Ecological flows

The increasing impairment of river–sea connectivity in South African rivers is a matter of concern. An increased duration of estuary mouth closure will have impacts on anguillid eels during their recruitment and escapement and could lead to local stock collapses. In the north of KwaZulu–Natal, studies have already highlighted the increasingly unsustainable use of the Mfolozi, Hluhluwe and Mkuze catchments (Whitfield & Taylor, 2009; Lawrie & Stretch, 2011). Concern has also been raised about the wellbeing of anguillid eels because of prolonged mouth closure in these catchments (Desai et al., 2021). Multiple stressors are responsible for this, including unsustainable water use, human land use changes, poor river and water management and increasingly prolonged droughts. A further example illustrating the need for ecologically sensitive river flow management is the case of the Thukela Marine Protected Area (MPA), which was declared in 2021. The Thukela MPA includes the estuarine portion of the Thukela catchment, as the river flows are indispensable to the wellbeing of the MPA (De Lecea & Cooper, 2016; Wade et al., 2021). Although the wellbeing of freshwater and marine environments is at stake, the ecological reserve (as provided by the National Water Act (Act 36 of 1998)) is yet to be implemented and enforced. Laws, methods and frameworks exist in South Africa, but their implementation is slow or completely lacking (Adams, 2014; Wade et al., 2021). The ecological reserve could and should be part of the conservation solution, but this requires stakeholder engagement (including the public) and solid governance, which is a challenge in South Africa (Wade et al., 2021).

5.3 | Fisheries and aquaculture

Although the threat of over-exploitation of anguillid eels is not yet a reality in South Africa, international interest in developing fisheries there is growing (Hanzen et al., 2019). With this in mind, local stakeholders should formulate precautionary fisheries regulations for the relevant species. Recommendations from the Global South include, for example, the closure of fishing reservoirs, village-level quotas and the monitoring of populations (Shanmughan et al., 2022). In Réunion, where there is a strong eel fishery tradition (Hanzen et al., 2019), all life stages are allowed to be harvested. Landings are regulated, however, depending on the species, time of the year and section of river (Valade, Hoarau & Bonnefoy, 2018). In contrast, eel fishing and trading are strictly prohibited in the Comores Islands (Valade, Hoarau & Bonnefoy, 2018). Although anguillid eels are not abundant in South Africa, the development of ranching aquaculture for these species has been investigated in the region. Such a development has been observed in Madagascar (Hanzen et al., 2019), although the venture appears to have failed. If such a fishery were allowed in South Africa, it would have to be strictly regulated and the wild population closely monitored.

5.4 | Research, monitoring and communication

There is a need for focused monitoring of African anguillid eels to improve the baseline data on their abundance and distribution range in the region. More detailed knowledge regarding the ecology and biology of these species is also urgently needed, especially concerning the increasing potential for their exploitation and trade, but also in the face of the many human stressors threatening their persistence and the sustainable use of the rivers they occupy. The future of rivers and anguillid eels in South Africa will also rely on integrated and collaborative research, combining the skills of mixing hydrologists, engineers, biologists and climate change experts. Moreover, better communication is needed with stakeholders regarding the conservation of flagship species such as anguillid eels and their habitats throughout southern Africa; programmes such as the African Swimways initiative (https://globalswimways.com/african-swimways/) can help with this.

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CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

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

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