



Isotopic diversity and niche patterns reveal contrasting resource use among co-occurring non-native fishes within a flow-altered African river system

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Abstract Classic and contemporary trophic ecology-based studies have shown that most non-native freshwater fish species (NNS) that integrate into novel environments have the potential to influence the recipient ecosystems' structure and function. However, the interspecific trophic interactions amongst co-occurring NNS within invaded systems remain poorly studied. Here, we used carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope analyses to examine general fish trophic diversity patterns (native and non-native fishes) and to explore trophic niche patterns amongst co-occurring NNS within a flow-modified river system, the Great Fish River (South Africa). The system was characterised by isotopic variation, which revealed spatial differences in trophic complexity from uninvaded headwater tributaries to invaded mainstem and downstream sections.

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Two of the invaded sections, the upper mainstem of the Great Fish River (UGFR) and the Koonap River, had low isotopic overlaps between NNS and the native fish assemblages. Furthermore, co-occurring NNS in these two invaded sections had variable isotopic niche sizes and low interspecific isotopic niche overlaps, suggesting the potential for trophic differentiation. By comparison, there was evidence of high resource use patterns among NNS within the lower mainstem section of the Great Fish River (LGFR), which likely reflected trophic plasticity. Overall, results of this study provided evidence of both trophic niche differentiation (UGFR and Koonap River) and niche overlap (LGFR) as probable mechanisms of co-occurrences of the non-native fishes within different invaded sections of the Great Fish River system, and underscores the difficulties associated with predicting their trophic impacts.

Keywords Inter-basin water transfer · Fish assemblages · Stable isotopes · Great Fish River · Trophic niche overlap

Introduction

Biological invasions and habitat degradation have been shown to potentially threaten community structure and function of freshwater ecosystems (Collen et al. 2014; Comte et al. 2016). Several empirical studies have provided insights on invasion impacts

in a wide range of freshwater ecosystems, including those invaded by keystone non-native species (Ligtvoet et al. 1991; Johnson et al. 2006; Ficetola et al. 2007; De Vanna et al. 2011), characterised by high local endemism and low invasion resistance (Tedesco et al. 2012; Collen et al. 2014; Weyl et al. 2014; Jordaan et al. 2020) and subject to high habitat-related anthropogenic modifications (Laurenson and Hocutt 1986; Ruhi et al. 2016; Liu et al. 2017). Whilst many of these studies have focused on impacts of one or few non-native species, there is increasing attention on the occurrence of multiple non-native invaders (e.g. Jackson 2015; Pyšek et al. 2020; Guareschi et al. 2021) whose net impacts are poorly known. Understanding how multiple non-native species integrate and impact the invaded freshwater environments is, thus, crucial for managing species invasions in these ecosystems (Comte et al. 2016). One way to understand such impacts is by exploring trophic and food web patterns of the invaded ecosystems (Copp et al. 2017).

From a trophic ecology perspective, non-native species have been shown to disrupt community structure and function either directly through predation and competition (e.g. Kadye and Booth 2012; Bašić et al. 2019; Rogosch and Olden 2020; Murphy et al. 2021) or indirectly by negatively influencing ecological aspects such as habitat associations and the behaviours of native taxa (e.g. Vander Zanden and Rasmussen 1999; Kadye et al. 2020), which may negatively influence aspects of native biota's life-history attributes such as growth and reproduction (e.g. Britton et al. 2010a; de Araújo et al. 2022). Both classic and contemporary research on the influence of non-native taxa on the trophic structure and function of recipient ecosystems has been largely instrumental in unravelling invasion impacts. Examples of this research include studies on the ecosystem-wide food web dynamics following the localised extirpations of native fauna by non-native piscivores in lentic habitats (Witte et al. 1992; Vander Zanden et al. 2003; Downing et al. 2012), the competitive interactions between native and non-native species (Byres 2002; Martin et al. 2010; Britton et al. 2018), interspecific and synergistic interactions among non-native species within invaded habitats (Britton et al. 2010b; Jackson et al. 2012), and the trophic cascade-induced dynamics, such as changes in primary production and algal biomass due to heavy predation on grazing

invertebrates by non-native salmonids and high nutrient cycling by invasive crustaceans in lotic habitats (Crowl et al. 1992; Flecker and Townsend 1994; Nyström et al. 2001; Herbst et al. 2009).

Recently, there have been increasing concerns on the co-occurrence of multiple non-native species and their potential impacts on recipient freshwater ecosystems' trophic dynamics (Johnson et al. 2009; Jackson and Britton 2013; Sagouis et al. 2015; Liu et al. 2018). Specifically, there is concern on the interactions among non-native invaders, which could potentially result in either complementary, additive and facilitative effects on the structure and function of food webs in invaded systems (Jackson et al. 2014; Jackson 2015). This is because multiple invasive species occurring in sympatry can have broader ecological impacts due to their likelihood of occupying different trophic levels within the food webs of the invaded communities (Johnson et al. 2009; Jackson and Britton 2013). Similarly, non-native species with high diet plasticity and/or broad trophic niches, such as opportunistic omnivorous and generalist predators, could also prey on native organisms across multiple trophic levels resulting in unpredictable impacts within the invaded communities (Jackson and Britton 2013; Liu et al. 2018). Other studies have shown potential synergistic impacts among invaders. Examples include the high predation and subsequent biomass reduction of predatory invertebrates by non-native bluegill *Lepomis macrochirus*, facilitating the establishment of non-native bullfrog *Lithobates catesbeiana* due to enhanced survival of their tadpoles (Adams et al. 2003), and the predation by non-native crayfish *Orconectes rusticus* on native snails (*Physa* and *Lymnaea* spp.), which potentially facilitated the establishment of non-native snail *Bellamya chinensis* due to reduced competitive interactions between the native and non-native snails (Johnson et al. 2009). Despite the emerging evidence of the impacts of multiple invasions (Jackson and Britton 2013; Sagouis et al. 2015), the broad nature of interspecific trophic interactions amongst co-occurring non-native species outside their native ranges is uncertain as these interactions are likely to be context-dependent (Jackson 2015). For example, there have been reports of different interspecific interactions, ranging from weak amensal and commensal interactions (Griffen et al. 2008; Johnson et al. 2009) to strong interactions, such as overt predation and competition impacts (Liu et al.

2018) and non-native species facilitating each other's establishment (Hohenadler et al. 2018). Therefore, understanding these complex interactions could assist to mitigate the impacts of co-occurring multiple non-native species on native communities (Liu et al. 2018; Balzani et al. 2020).

Stable isotopes have become an important tool to examine community trophic or food web structures (Layman et al. 2007, 2012), and in assessing the ecological impacts of anthropogenic environmental changes (Cucherousset et al. 2012a; Alp and Cucherousset 2022). Specifically, because they provide temporally-integrated assessment of consumer diet (Hershey et al. 2017), stable isotope analyses (SIA) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) can be used to assess the energy sources and trophic positions of organisms, respectively (Post 2002; Anderson and Cabana 2007; Vander Zanden et al. 2016). Thus, they can be used to trace energy flow from basal sources (primary producers and detrital sources) through primary to secondary and tertiary consumers (Hershey et al. 2017; Layman et al. 2012). Consequently, stable isotope analyses have been extensively used to evaluate biological invasions-related trophic ecology of aquatic organisms in freshwater ecosystems (Vander Zanden and Fetzer 2007; Jackson et al. 2020), including the assessment of trophic interactions between co-occurring native and non-native fishes (Pennock et al. 2021; Top-Karakuş et al. 2021) and broad trophic impacts of these introductions on recipient communities (Vander Zanden and Rasmussen 1999; Kadye and Booth 2012; Cucherousset et al. 2012a; Fink and Harrod 2013; Jackson and Britton 2013; Bašić et al. 2019). In addition to providing robust estimates of trophic interrelationships, applications of SIA have recently been extended to provide quantitative assessments of stable isotope-based trophic and functional diversity indices, which facilitate comparisons of food webs among different ecosystems (Layman et al. 2007; Cucherousset and Villéger 2015; Rigolet et al. 2015; De Cáceres et al. 2019). Besides the general applications of these diversity indices to assess the community structure and functioning of freshwater ecosystems (Comte et al. 2016; Frossard et al. 2020), they have also been used to evaluate the role of anthropogenic disturbances, including the impacts of biological invasions within these ecosystems (Cucherousset and Villéger 2015; Jackson et al. 2020).

This study focused on the Great Fish River system in South Africa. In addition to hosting multiple non-native fishes, this river system is characterised by modified mainstem habitats due to an inter-basin water transfer scheme (IBWT) that connects the Orange River (the donor system) with the Great Fish River (Laurenson and Hocutt 1986; Kadye and Booth 2013; Mpopetsi and Kadye 2023). The presence of a flow-modified mainstem section, along with tributaries with near-natural flow regimes, have created spatially variable habitats that likely have implications on the structural and functional interrelationships of fish taxa within the Great Fish River system. Despite the spatial variability in the structural nature of these habitats, non-native fishes have established within both the flow-modified mainstem and the unmodified sections of the major tributaries (Kadye and Booth 2013; Sifundza et al. 2021). This raises the need to understand the ecological dynamics associated with these invasions in the different habitats of this river system. Whilst previous research on species-environment relationships revealed that the non-native species assemblage was characterised by taxa with high environmental tolerance, an indication of propensity towards niche opportunism (Kadye and Booth 2020), there is little information regarding the trophic niche patterns of these species. To fill this gap knowledge, this study employed SIA-based approaches as proxy for trophic ecology. Therefore, the primary objectives of this study were to (1) describe the isotopic patterns of the Great Fish River system food web across its broad spatial scale, (2) elucidate the isotopic diversity patterns of non-native and native fishes within the invaded sections and (3) to evaluate the isotopic niche patterns and probable interspecific interactions of non-native fishes to determine whether trophic niche patterns were the likely drivers of non-native fishes' proliferation within this river system. Due to the likely preponderance of niche opportunism shown by species-environment relationships (e.g. Kadye and Booth 2020), it was, firstly, hypothesised that non-native fishes would exhibit consistent isotopic diversity patterns that would reflect broad resource use patterns compared to native fishes. Secondly, because of the high likelihood of exploiting broad range of trophic resources, as it has been demonstrated elsewhere (e.g. De Santis et al. 2022), it was hypothesised that the non-native fish species would exhibit high

interspecific trophic niche overlap that would likely reflect trophic niche generalisation.

Materials and methods

Data collection and sample preparation

Sampling was done to collect carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope data in the Great Fish River mainstem, and its major two tributaries, the Koonap and Kat rivers (Fig. 1a). In total, 67 sites were sampled, with each site being sampled once. In the Great Fish River, sampling was conducted during summer from October 2009 to April 2010 in the flow-altered mainstem, and October 2014–March 2015 in its headwater section. In the Koonap and Kat rivers, sampling was done in October 2018–March 2019. Samples for stable isotope analysis were collected from fishes (Table 1) and all potential prey that included macroinvertebrates and basal sources (Supplementary material 1). Several sampling methods, including electrofishing, fyke netting, gill netting, hand netting and seine netting were used to capture fish from both the tributaries and the mainstem sections of the Great Fish River. For electrofishing, a 12 V battery-powered SAMUS backpack electrofisher in combination with a

stop net (4 mm mesh net) were used to sample shallow rocky habitats in the headwaters where neither seine nor fyke nets were efficient. Stunned fish were collected with a hand net. A stop net, secured to the streambed, was used downstream to block electrocuted fish that were missed by hand netting. To standardise the sampling effort, a multiple (three) pass electrofishing was conducted for a maximum of 15 min per site. Marginal and shallow habitats (<1 m), in headwaters and tributaries, were sampled using an 8 m long seine net with 4 mm mesh size. Two to four seine hauls (average of three) were performed at each site where seine netting was conducted. The seine net was deployed at a distance (the distance varied with river channel size) parallel to the shore and was then rapidly pulled onto the shore. Mainstem sites were sampled using experimental gill nets, fyke nets (single and double ended) and the seine net. Experimental gill nets were 30 m long with three 10 m panels of mesh sizes of 50, 75 and 100 mm. Fyke nets had an 8 m guiding net and a first ring diameter of 55 cm and a 10 mm mesh size. Experimental gill- and fyke-nets were deployed overnight, from late afternoon/evening to morning, with an average soak time of 14 h. Captured fish were identified to species following Skelton (2001) and other regional literature in line with the recent taxonomic changes in some taxa (e.g.,

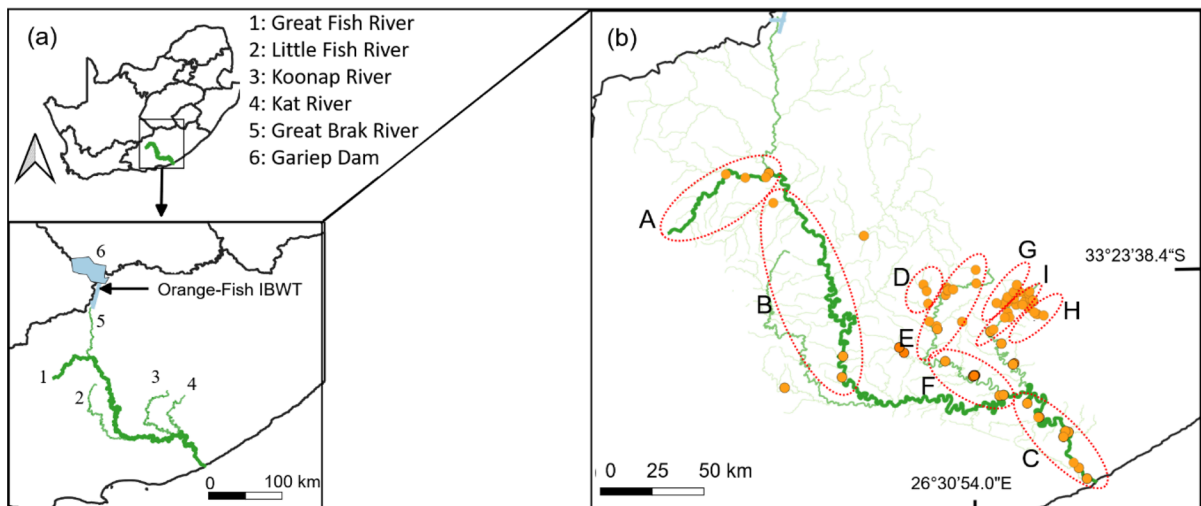


Fig. 1 **a** The Great Fish River system and its major tributaries; **b** study system was delineated into nine sections (A–I) based on the presence or absence of non-native species. Red ellipses indicate the nine sections; **A** The Great Fish River headwaters; **B** the upper Great Fish River (UGFR); **C** The lower Great Fish

River (LGFR), **D** The Koonap River headwater tributaries, **E** the Koonap River upper mainstem, **F** The lower Koonap River, **G**, **H** the Kat River headwater tributaries and **I** the Kat River upper mainstem section

Table 1 Native and non-native fish species samples (in ‰ ± standard deviation) used for stable isotope analyses in the present study

Sample	Stable isotope	Great Fish			Koonap			Kat		
		(A)	(B)*	(C)*	(D)	(E)	(F)*	(G)	(H)	(I)
Native fish species	$\delta^{13}\text{C}$	-	-	-23.5 ± 0.3 (3)	-	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	+18.4 ± 0.4 (3)	-	-	-	-	-	-
<i>Anguilla marmorata</i>	$\delta^{13}\text{C}$	-	-25.0 ± 1.1 (4)	-25.8 ± 1.6 (3)	-	-	-	-	-	-
	$\delta^{15}\text{N}$	-	+14.9 ± 0.8 (4)	+16.1 ± 4.2 (3)	-	-	-	-	-	-
<i>Anguilla mossambica</i>	$\delta^{13}\text{C}$	-26.5 ± 0.8 (6)	-	-	-21.5 ± 0.6 (18)	-24.9 ± 0.8 (20)	-20.1 ± 0.6 (31)	-24.1 ± 1.4 (32)	-19.4 ± 1.2 (26)	-22.0 ± 1.2 (50)
	$\delta^{15}\text{N}$	+12.2 ± 0.4 (6)	-	-	+11.2 ± 0.6 (18)	+12.0 ± 0.6 (20)	+9.9 ± 0.3 (31)	+11.5 ± 1.6 (32)	+9.1 ± 0.4 (26)	+12.6 ± 0.4 (50)
<i>Enteromius mandelai</i>	$\delta^{13}\text{C}$	-	-	-30.0 ± 0.5 (9)	-	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	+18.3 ± 0.4 (9)	-	-	-	-	-	-
<i>Gilchristella aestuaria</i>	$\delta^{13}\text{C}$	-	-	-24.9 ± 2.0 (12)	-	-	-	-	-	-20.1 ± 1.3 (30)
	$\delta^{15}\text{N}$	-	-	+14.4 ± 1.2 (12)	-	-	-	-	-	+12.4 ± 1.0 (30)
<i>Glossogobius callidus</i>	$\delta^{13}\text{C}$	-	-28.2 ± 1.9 (11)	-27.4 ± 3.6 (20)	-	-	-25.3 ± 1.2 (22)	-	-	-
	$\delta^{15}\text{N}$	-	+11.6 ± 0.6 (11)	+14.4 ± 2.7 (20)	-	-	+12.8 ± 0.7 (22)	-	-	-
<i>Labeo umbratus</i>	$\delta^{13}\text{C}$	-	-	-26.2 ± 6.2 (6)	-	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	+15.6 ± 2.0 (6)	-	-	-	-	-	-
<i>Mugil cephalus</i>	$\delta^{13}\text{C}$	-	-	-26.8 ± 3.4 (2)	-	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	+18.2 ± 1.5 (2)	-	-	-	-	-	-

Table 1 (continued)

Sample	Stable isotope	Great Fish		Koonap			Kat		
		(A)	(B)*	(C)*	(D)	(E)	(F)*	(G)	(H) (I)
<i>Oreochromis mossambicus</i>	$\delta^{13}\text{C}$	-	-	-23.1 ± 2.3 (14)	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	$+12.1 \pm 2.4$ (14)	-	-	-	-	-
<i>Planiliza macrolepis</i>	$\delta^{13}\text{C}$	-	-	-31.6 ± 0.0 (1)	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	$+17.9 \pm 0.0$ (1)	-	-	-	-	-
<i>Pomadasys commersonii</i>	$\delta^{13}\text{C}$	-	-	-23.1 ± 0.0 (1)	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	$+16.7 \pm 0.0$ (1)	-	-	-	-	-
<i>Psammogobius knysnaensis</i>	$\delta^{13}\text{C}$	-	-	-23.4 ± 0.5 (3)	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	$+16.6 \pm 0.2$ (3)	-	-	-	-	-
<i>Pseudomyxus capensis</i>	$\delta^{13}\text{C}$	-	-	-25.8 ± 3.0 (14)	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	$+16.0 \pm 1.4$ (14)	-	-	-	-	-
<i>Redigobius dewaalli</i>	$\delta^{13}\text{C}$	-	-	-24.6 ± 0.4 (3)	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	$+16.7 \pm 0.3$ (3)	-	-	-	-	-
<i>Rhabdosargus holubi</i>	$\delta^{13}\text{C}$	-	-	-23.8 ± 2.0 (5)	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	$+17.2 \pm 1.0$ (5)	-	-	-	-	-
<i>Sandelia bainsii</i>	$\delta^{13}\text{C}$	-	-	-	-	-	-	-	-18.1 ± 0.4 (5)
	$\delta^{15}\text{N}$	-	-	-	-	-	-	-	$+9.5 \pm 0.2$ (5)
									-20.4 ± 0.8 (7)
									$+12.9 \pm 0.4$ (7)

Table 1 (continued)

Sample	Stable isotope	Great Fish		Koonap			Kat			
		(A)	(B)*	(C)*	(D)	(E)	(F)*	(G)	(H)	(I)
Non-native fish species	$\delta^{13}\text{C}$	-	-22.7 ± 0.0 (4)	-24.0 ± 1.3 (8)	-	-	-24.7 ± 0.6 (2)	-	-	-
	$\delta^{15}\text{N}$	-	$+13.9 \pm 0.0$ (4)	$+13.9 \pm 2.3$ (8)	-	-	$+14.0 \pm 0.1$ (2)	-	-	-
<i>Clarias gariepinus</i>	$\delta^{13}\text{C}$	-	-23.1 ± 0.7 (9)	-25.9 ± 2.5 (28)	-	-	-24.9 ± 0.0 (1)	-	-	-
	$\delta^{15}\text{N}$	-	$+13.5 \pm 0.8$ (9)	$+15.8 \pm 2.0$ (28)	-	-	$+14.0 \pm 0.0$ (1)	-	-	-
<i>Gambusia affinis</i>	$\delta^{13}\text{C}$	-	-	-23.7 ± 0.6 (14)	-	-	-	-	-	-
	$\delta^{15}\text{N}$	-	-	$+14.4 \pm 1.0$ (14)	-	-	-	-	-	-
<i>Labeobarbus aeneus</i>	$\delta^{13}\text{C}$	-	-25.1 ± 1.2 (36)	-26.9 ± 2.6 (17)	-	-	-	-	-	-
	$\delta^{15}\text{N}$	-	$+13.3 \pm 0.9$ (36)	$+14.5 \pm 1.2$ (17)	-	-	-	-	-	-
<i>Labeo capensis</i>	$\delta^{13}\text{C}$	-	-26.7 ± 0.0 (4)	-27.0 ± 1.1 (3)	-	-	-	-	-	-
	$\delta^{15}\text{N}$	-	$+12.9 \pm 0.0$ (4)	$+13.2 \pm 0.4$ (3)	-	-	-	-	-	-
<i>Tilapia sparmanii</i>	$\delta^{13}\text{C}$	-	-	-27.8 ± 1.4 (6)	-	-	-26.0 ± 0.9 (20)	-	-	-
	$\delta^{15}\text{N}$	-	-	$+15.0 \pm 0.9$ (6)	-	-	$+15.1 \pm 0.7$ (20)	-	-	-

(A) = Great Fish River headwater section, (B)* = upper Great Fish River mainstem section, (C)* = lower Great Fish River mainstem section, (D) = the Koonap River headwater, (E) = Koonap River upper mainstem, (F)* = Koonap River lower mainstem, (G and H) = Kat River tributaries and (I) = upper mainstem. Numbers in brackets indicate sample sizes for each species within each section

*Indicate invaded sections

Kambikambi et al. 2021). A sample of a maximum of 15 individuals (across species) per site was euthanised by a lethal dose of clove oil after which a small piece of the dorsal muscle tissue was taken using a clean scalpel blade for stable isotope analysis, and the samples were transferred to Eppendorf tubes for storage. For *Sandelia bainsii*, which is endangered, a small tissue was taken at the tip of the anal fin using a clean pair of scissors.

Macroinvertebrates were collected from instream substratum and submerged vegetation. In flowing habitats, stream substrates were disturbed by kick sampling, two minutes per sample, and the dislodged animals were collected using a 250 µm hand-held scoop net positioned downstream of flow. The net was then progressively moved upstream to catch dislodged macroinvertebrate samples. In vegetated and slow-flowing habitats, macroinvertebrates were captured by sweeping the scoop net for 2 min. Captured macroinvertebrate samples were then rinsed with clean water and then transferred into a collection tray for sorting. Coarse particulate matter (CPOM), which included C₃ and C₄ plants and other large organic matter debris, was either handpicked or dislodging from the substratum and filtered through a hand-held net. Fine particulate organic matter (FPOM) was collected by filtering 25 L of stream water through a 100 µm net. Epilithic algae was scrapped from coarse substratum (boulders and bedrock) with a scalpel blade and rinsed with distilled water. Free-floating filamentous algae, macrophytes and other organic matter were collected by hand, rinsed and transferred into collection bottles. For basal and macroinvertebrate, three samplings were performed for each taxon at each site. The three samples were then combined to form one sample for that site, and this was then used for stable isotope analysis. All samples for stable isotope analysis were kept on ice in the field and transported to the laboratory, Rhodes University, Makhanda, South Africa, for further processing. For macroinvertebrates, a reference sample (of every taxon collected at each site) was also collected and stored in 70% ethanol, and this was later used in conjunction with frozen samples to confirm the collected samples' identification in the laboratory.

At the laboratory, sample of macroinvertebrates were thawed, sorted and identified to either family, genus or species level using a dissecting microscope (Labomed CZM4, Labomed, USA) and regional

identification guides (Day et al. 2001a, b; Day and De Moor 2002a, b; Day et al. 2002; Gerber and Gerber 2002). All samples were oven-dried at 60 °C for 48–72 h after which they were ground into a fine homogenous powder, using a mortar and pestle. The sample material was weighed (1 ± 0.05 mg for animal tissue and 3 ± 0.5 mg for plant tissue) and packed into 8×5 mm tin capsules. Stable isotope analysis was done at the Rhodes University and the University of Pretoria, South Africa. At Rhodes University, stable isotope analysis of carbon and nitrogen was performed using a Europa Scientific INTEGRA isotope ratio mass spectrometer at the IsoEnvironmental Lab, Makhanda. At the University of Pretoria, the isotopic analysis was done on a Flash SEA 1112 series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via ConFlo IV system (ThermoFischer, Bremen, Germany). Stable isotope ratios are reported in the δ notation in per mil units (‰) using the following formula:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where X is ¹³C or ¹⁵N and R is the corresponding ratio ¹³C/¹²C or ¹⁵N/¹⁴N. The R_{standard} values are based on Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}\text{C}$ and atmospheric N₂ for $\delta^{15}\text{N}$. Analytical precision was evaluated using the following calibrated laboratory standards: Merck Gel ($\delta^{13}\text{C} = -20.3 \pm 0.1\text{‰}$, $\delta^{15}\text{N} = +7.9 \pm 0.1\text{‰}$), DL-Valine ($\delta^{13}\text{C} = -10.6 \pm 0.1\text{‰}$, $\delta^{15}\text{N} = +6.2 \pm 0.1\text{‰}$), and Casein ($\delta^{13}\text{C} = -27.0 \pm 0.1\text{‰}$, $\delta^{15}\text{N} = +5.9 \pm 0.1\text{‰}$). Laboratory standards were calibrated using the following reference material: IAEA-CH-3 (cellulose), IAEA-CH-6 (sucrose), IAEA-CH-7 (polyethylene 241 foil), IAEA N-1 & IAEA N-2 (ammonium sulphate) and IAEA NO-3 (potassium nitrate). Sample precision based on standard deviation of repeated measurements of laboratory standards was 0.1‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. To address potential $\delta^{13}\text{C}$ lipid-content bias, fish tissue stable isotope values were mathematically normalised based on C/N ratio following Post et al. (2007).

Data analysis

To describe the food web patterns, the study system was firstly delineated into different sections based on the presence or absence of non-native fish species,

and with each section being made up of multiple sites (Fig. 1b, Table 1). Thus, the river system was delineated into the following nine sections. (A) The Great Fish River headwaters, which comprised an uninhabited section where one native species occurred. (B) The upper Great Fish River (UGFR), which comprised an invaded upper section of the mainstem. This section had two native and four non-native fishes. (C) The lower Great Fish River (LGFR) that constituted the invaded lower reaches of the mainstem was characterised by both primary freshwater and estuarine-dependent fishes. This section was invaded by six non-native fishes and had 14 native species. (D) The Koonap River headwater tributaries and (E) the Koonap River upper mainstem that were both uninhabited and had one native species. (F) The lower Koonap River where two native fishes and three non-native fishes occurred. Only the uninhabited sections of the Kat River were sampled. This was because the invaded portion of the Kat River comprised sections that were either dominated by silviculture (due to citrus plantations) or heavily polluted by sewage, specifically the section downstream of the Fort Beaufort town. Therefore, the sampled sections of the Kat River included (G) the headwater tributaries where one native species occurred, (H) the headwater tributary where two native fishes occurred, and (I) the upper mainstem section where three native fishes occurred. (Fig. 1b, Table 1).

To elucidate the trophic diversity patterns of non-native and native fish assemblages within the invaded sections, isotopic diversity indices were computed following Cucherousset and Villéger (2015) and Rigolet et al. (2015). Because the sampled isotope data varied both spatially and temporally, the food webs were likely influenced by differences in the stable isotope values for basal sources (e.g., Cucherousset and Villéger 2015). To circumvent this, prior to the computing of diversity indices, stable isotope data were first standardised to z-scores to normalise the effect of baselines following Fry and Davis (2015), and the resultant values were then scaled. The scaling procedure does not affect the distribution of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, but instead transforms the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ multidimensional δ -space so that each isotopic axis is scaled to the same range of 0–1 (Cucherousset and Villéger 2015). Thus, the isotopic diversity indices were computed using standardised isotopic data

pooled from the three invaded sections, the upper (UGFR) and lower (LGFR) Great Fish River mainstem sections, and the lower Koonap River. During the computation of diversity metrics, stable isotope values were weighed by species relative abundance based on the appropriate catch per unit effort (CPUE) for each section. The isotopic diversity indices were computed as;

1. Isotopic richness (IRic), which provides a quantitative estimate of the isotopic space for the whole community or assemblage. Low IRic values (close to 0) may indicate low functional diversity, possibly due to species loss, limited use of resources and low buffering from disturbances, whereas high IRic values (close to 1) may indicate high use of the trophic space.
2. Isotopic divergence (IDiv), which describes how the isotopic space is occupied based on the degree of isotopic spacing by community members. Low IDiv values (close to 0) likely reflects a community characterised by trophic generalists, whereas high IDiv values (close to 1) likely indicates a high degree of trophic specialisation for the community.
3. Isotopic dispersion (IDis), which reflects the extent to which community members differ in their stable isotope values. Low IDis values (close to 0) indicates that community members have similar stable isotope values, whereas high IDis values (close to 1) reflect dissimilar stable isotope values.
4. Isotopic uniqueness (IUni), which indicate the degree of isotopic dissimilarity among community members. Low IUni values (close to 0) indicate that most of the weight belongs to isotopically similar organisms, whereas high IUni values (close to 1) indicate that most of the organisms are isolated in the stable isotope space.

In addition, isotope overlap between the non-native and native fish assemblages was evaluated based on isotopic nestedness (INes), which provides a quantitative estimate of the degree to which one group or community is a subset of the other (Cucherousset and Villéger 2015). Low INes value indicates no isotopic overlap, whereas high nestedness, which is consistent with high isotopic overlap, reflects that one group is a subset of the other.

Lastly, to evaluate the trophic niche patterns and interspecific interactions of non-native fishes, a Bayesian isotope niche analysis was conducted following Swanson et al. (2015). This was based on a two-pronged approach. Firstly, the isotope niche size for each non-native species was computed based on the joint probability distributions of scaled (0–1) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, resulting in probability distributions ($\alpha=95\%$) that reflect the most plausible isotopic trophic niche sizes from a multi-dimensional isotopic-space. This was expressed as: $P(Y \in N_R)$, where Y is the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data matrix for a particular species and N_R is the probable isotopic niche region for a particular species. Secondly, interspecific interactions between two species were determined based on the extent of isotopic niche overlap as: $O_B^A = P(Y_A \in N_R(B))$, where O_B^A is the probability of species A overlapping onto the isotopic niche of species B (Swanson et al. 2015). The isotope niche overlaps were based on Bayesian posterior distributions (posterior means and 95% credible intervals) and were estimated based on Monte Carlo simulations with 1000 iterations. All statistical analyses were performed using *R* software program version 4.2.2 (R Development Core Team 2022). Isotopic diversity indices were computed using published *R* code provided by Cucherousset and Villéger (2015). Isotopic niche patterns were computed using the *R* package *nicheROVER* (Lysy et al. 2021).

Results

Isotopic variation

The Great Fish River system exhibited spatial variation in its isotopic values from the headwaters and tributaries to the lower section, which appeared consistent with food web complexity (Table 2). Specifically, the Great Fish River mainstem was mostly distinguished by an upstream to downstream differences in the ranges of $\delta^{15}\text{N}$, which were small in the headwater section ($\delta^{15}\text{N} = +6.9$ to $+12.2\text{‰}$), intermediate in the UGFR ($\delta^{15}\text{N} = +4.8$ to $+14.9\text{‰}$) and large in the LGFR ($\delta^{15}\text{N} = +0.8$ to $+18.4\text{‰}$). Similarly, the Koonap River's isotopic values were distinguished by $\delta^{15}\text{N}$ ranges, which were smaller in the tributaries ($\delta^{15}\text{N} = +1.6$ to $+11.2\text{‰}$) and the upper section ($\delta^{15}\text{N} = -0.4$ to $+12.0\text{‰}$) than the lower section

($\delta^{15}\text{N} = +1.8$ to $+15.1\text{‰}$). In comparison, the Kat River isotopic values were mostly distinguished by a large breadth in $\delta^{13}\text{C}$ values together with upstream to downstream differences in $\delta^{15}\text{N}$ ranges. Specifically, there was a wide breadth in $\delta^{13}\text{C}$ for macroinvertebrates in the headwater tributaries, whereas the macroinvertebrates in the mainstem section had both wide $\delta^{13}\text{C}$ breadth and high $\delta^{15}\text{N}$ range.

Within the invaded UGFR section, non-native fishes were distinguished by intermediate $\delta^{15}\text{N}$ values compared to the two native fishes, *L. umbratus* that had the lowest ($\delta^{15}\text{N} = +11.6\text{‰}$) and *A. mossambica* that had the highest ($\delta^{15}\text{N} = +14.9\text{‰}$) values (Table 1). Furthermore, non-native fishes had a wider breadth in $\delta^{13}\text{C}$ values (-26.7 to -22.6‰) compared to those in either the LGFR (-26.9 to -23.7‰) or the lower Koonap River (-26.1 to -24.7‰). By comparison, within the invaded LGFR, the non-native fishes generally had lower $\delta^{15}\text{N}$ values than most native fishes. In contrast, within the invaded lower Koonap, all non-native fishes were distinguished by higher $\delta^{15}\text{N}$ values than native fishes (Table 1).

Isotopic diversity patterns of non-native and native fishes

In the UGFR, the non-native and native fish assemblages differed in their isotopic diversity patterns, which also showed no overlap ($\text{INes}=0$) between the two groups (Fig. 2a). Specifically, non-native fishes were mostly distinguished by high isotopic divergence ($\text{IDiv}=0.8$) and isotopic dispersion ($\text{IDis}=0.7$) compared to native species ($\text{IDiv}=0.4$; $\text{IDis}=0.5$) (Table 3). This showed that the non-native fishes were characterised by dissimilar isotopic values, and likely comprised species that were characterised by trophic specialisation. By comparison, native fishes were mostly distinguished by high isotopic uniqueness ($\text{IUni}=0.7$), indicating that these species had different stable isotope values, reflecting different resource utilisation patterns, which was likely consistent with trophic differentiation. In the LGFR, non-native and native fishes were characterised by high isotopic nestedness ($\text{INes}=0.9$), which depicted high isotopic diversity overlap (Fig. 2b). The non-native fish assemblage's isotopic diversity, which appeared to be a subset of the native fish assemblage's isotopic diversity, was distinguished by low isotopic richness ($\text{IRic}=0.0$) compared to native species ($\text{IRic}=0.3$).

Table 2 Mean values (in ‰) of carbon and nitrogen stable isotopes and range values (in parentheses) for basal sources, macroinvertebrates and native and non-native fishes within the Great Fish River headwater section (A), upper Great Fish River mainstem section (B)*, lower Great Fish River mainstem section (C)*, the Koonap River headwater (D), upper (E) and lower (F)* mainstem, and the Kat River tributaries (G and H) and upper mainstem (I)

	Great Fish River			Koonap River			Kat River		
	(A)	(B)*	(C)*	(D)	(E)	(F)*	(G)	(H)	(I)
Basal	$\delta^{13}\text{C}$ (-27.5, -23.5)	-29.8 (-41.3, -23.8)	-23.9 (-28.5, -14.9)	-21.4 (-26.2, 17.2)	-26.1 (-29.0, -21.7)	-24.4 (-26.5, -21.5)	-26.3 (-30.1, -21.2)	-15.7 (-24.8, -9.7)	-20.7 (-27.6, -12.5)
	$\delta^{15}\text{N}$ (+6.9, +10.6)	+8.7 (+4.8, +10.6)	+7.1 (+0.8, +13.9)	+4.2 (+1.6, +5.6)	+4.5 (-0.4, +7.7)	+6.2 (+1.8, +8.9)	+5.0 (+3.0, +7.0)	+3.4 (+1.7, +4.6)	+6.2 (+3.2, +10.5)
Invertebrates	$\delta^{13}\text{C}$ (-29.5, -24.2)	-26.1 (-29.8, -23.2)	-26.0 (-29.3, -14.4)	-23.9 (-25.8, -22.4)	-27.7 (-29.4, -24.6)	-24.1 (-29.5, 19.9)	-24.3 (-27.1, -18.7)	-23.6 (-28.4, -18.1)	-23.1 (-25.9, -19.2)
	$\delta^{15}\text{N}$ (+7.8, +10.8)	+10.0 (+8.6, +11.1)	+12.0 (+8.7, +16.0)	+5.5 (+3.2, +6.5)	+8.0 (+5.9, +8.7)	+8.7 (+5.5, +12.8)	+6.6 (+5.4, +8.0)	+5.7 (+3.4, +7.3)	+9.3 (+6.7, +11.9)
Native fish	$\delta^{13}\text{C}$ (-26.5, -26.5)	-26.6 (-28.2, -25.0)	-25.7 (-31.6, -23.1)	-21.5 (-21.5, -21.5)	-24.9 (-24.9, -24.9)	-22.7 (-25.3, -20.1)	-24.1 (-24.1, -24.1)	-18.7 (-19.4, -18.1)	-20.8 (-22.0, -20.1)
	$\delta^{15}\text{N}$ (+12.2, +12.2)	+13.2 (+11.6, +14.9)	+16.3 (+12.1, +18.4)	+11.2 (+11.2, +11.2)	+12.0 (+12.0, +12.0)	+11.3 (+9.9, +12.8)	+11.5 (+11.5, +11.5)	+9.3 (+9.1, +9.5)	+12.7 (+12.4, +12.9)
Non-native fish	$\delta^{13}\text{C}$	-24.4 (-26.7, -22.7)	-25.9 (-27.8, -23.7)			-25.2 (-26.1, -24.7)			
	$\delta^{15}\text{N}$	+13.4 (+12.9, +13.9)	+14.5 (+13.2, +15.8)			+14.4 (+14.0, +15.1)			

*Indicate invaded sections. Taxonomic composition for basal sources and macroinvertebrates for each section is given in Supplementary material 1, while species composition for fishes is reflected on Table 1

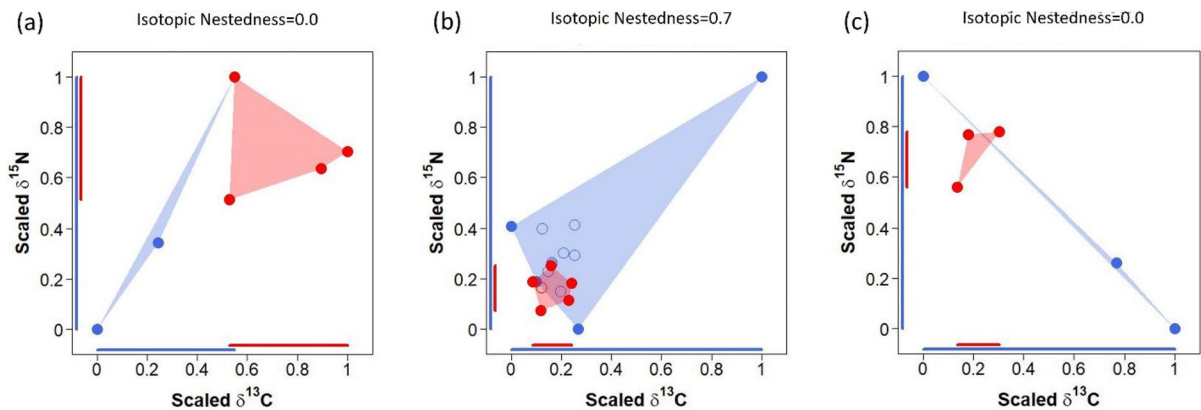


Fig. 2 Isotopic diversity overlap metrics between native (blue) and non-native (red) fish species of the three communities within the Great Fish River system; the upper Great Fish River (UGFR) mainstem (**a**), the lower Great Fish River (LGFR)

mainstem (**b**) and the Koonap River (**c**) Isotopic overlap metric, isotopic nestedness (INes), computed from scaled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, is reflected on top of each plot

Table 3 Isotopic niche variability of native and non-native fishes based on isotopic diversity indices (IDIs) and the isotopic overlap metric, isotopic nestedness (INes)

Locality	Community	<i>n</i>	Scaled $\delta^{13}\text{C}$ range	Scaled $\delta^{15}\text{N}$ range	IRic	IDiv	IDis	IUni	INes
UGFR*	Assemblage	7	1.0	1.0	0.3	0.8	0.4	0.3	0.0
	Native	3	0.5	1.0	0.0	0.4	0.5	0.7	
	Non-native	4	0.5	0.5	0.1	0.8	0.7	0.6	
LGFR	Assemblage	20	1.0	1.0	0.3	0.8	0.1	0.1	0.7
	Native	14	1.0	1.0	0.3	0.7	0.2	0.1	
	Non-native	6	0.1	0.2	0.0	0.8	0.7	0.7	
Koonap	Assemblage	6	1.0	1.0	0.2	0.8	0.7	0.8	0.0
	Native	3*	1.0	1.0	0.0	0.8	0.7	0.5	
	Non-native	3	0.2	0.2	0.0	0.8	0.8	0.8	

Values are scaled to range between 0 and 1

n, number of species; IRic, isotopic richness; IDiv, isotopic divergence; IDis, isotopic dispersion; IUni, isotopic uniqueness. UGFR and LGFR refer to upper Great Fish River and lower Great Fish River mainstem sections, respectively

*Two populations of *Enteromius mandelai* were used to allow for computation of IDIs within the UGFR

However, non-native species had higher values for other isotopic diversity metrics (i.e., IDiv, IDis and IUni) compared to native species, likely indicating broader resource utilisation pattern among the non-native species. In the Koonap River, although the non-native and native fish assemblages exhibited low isotopic diversity overlap (Fig. 2c), most of their isotopic diversity metrics were comparable (Table 3). Specifically, the two groups were characterised by high isotopic divergence (IDiv=0.8) and isotopic dispersion (IDis > 0.7). This suggested that although these two groups had species that exhibited different

resource patterns, as shown by lack of isotopic diversity overlap, trophic resource utilisation was likely driven by trophic specialisation in both groups.

Isotopic niche patterns and interspecific interactions of non-native fishes

In the UGFR, non-native fishes had variable isotopic niche sizes that ranged from the largest for *L. aeneus* (scaled niche size (NS)= $0.33 \pm 0.06\text{‰}^2$), followed by *C. gariepinus* (NS= $0.15 \pm 0.06\text{‰}^2$) to small for *L. capensis* (NS= $0.03 \pm 0.01\text{‰}^2$) and *C.*

carpio ($NS=0.02\pm0.00\%o^2$) (Fig. 3a). In general, most pairwise comparisons revealed low isotopic niche overlaps (mean overlap <20%) (Fig. 4), which showed the likelihood of trophic niche differentiation among these non-native species. Nevertheless, exceptions were shown by the high probabilities of isotopic niche overlaps for *C. gariepinus* onto the isotopic niche of *L. aeneus* (mean overlap=53.24%, 95% CI=16.0–90.0%) and *L. capensis* onto the isotopic niche of *L. aeneus* (mean overlap=80.23%, 95% CI 32.0–100%). In the LGFR, three non-native species, *C. carpio*, *C. gariepinus* and *L. aeneus* had relatively large niche sizes (NS range= 0.33 ± 0.06 – $0.48\pm0.18\%o^2$) compared to those of *T. sparrmanii*, *G. affinis* and *L. capensis*, which had smaller isotopic niche sizes (NS range= 0.05 ± 0.04 – $0.18\pm0.08\%o^2$) (Fig. 3b). Pairwise comparisons revealed moderate to high probabilities of isotopic niche overlaps (mean overlap >50%) for 10 of the 30 non-native fishes' pairings (Fig. 5). In addition, *C. gariepinus* and *L. aeneus* had high probabilities of isotopic niche overlaps (mean overlap >60%) with most non-native species, indicating that these two species were likely dietary generalists in this section. Similarly, *G. affinis*

exhibited high probability of overlap onto the isotopic niche of *C. carpio* (mean overlap=97.84%, 95% CI 84–100%), *C. gariepinus* (mean overlap=84.73%, 95% CI 62–98%) and *L. aeneus* (mean overlap=76.99%, 95% CI 49–96%). In comparison, most species had low probabilities of isotopic niche overlap (mean overlap <20%) with both *G. affinis* and *L. capensis* (Fig. 5). Within the Koonap River, all three non-native species had small isotopic niche sizes ($NS<0.1\%o^2$), with *T. sparrmanii* having the largest ($NS=0.08\pm0.02\%o^2$) of the three (Fig. 3c). Most pairwise comparisons revealed low to moderate isotopic niche overlaps (mean overlap=34.35–37.91%), indicating propensity for niche differentiation amongst species (Fig. 6). These included the overlaps of *C. carpio* onto the isotopic niche of *T. sparrmanii* (mean overlap=34.35%, 95% CI 1–93%) and *C. gariepinus* onto the isotopic niche of *C. carpio* (mean overlap=37.91%, 95% CI 1–97%). Nevertheless, there was a moderately high probability of isotopic niche overlap by *C. gariepinus* onto the isotopic niche of *T. sparrmanii* (mean overlap=58.73%, 95% CI 2–100%).

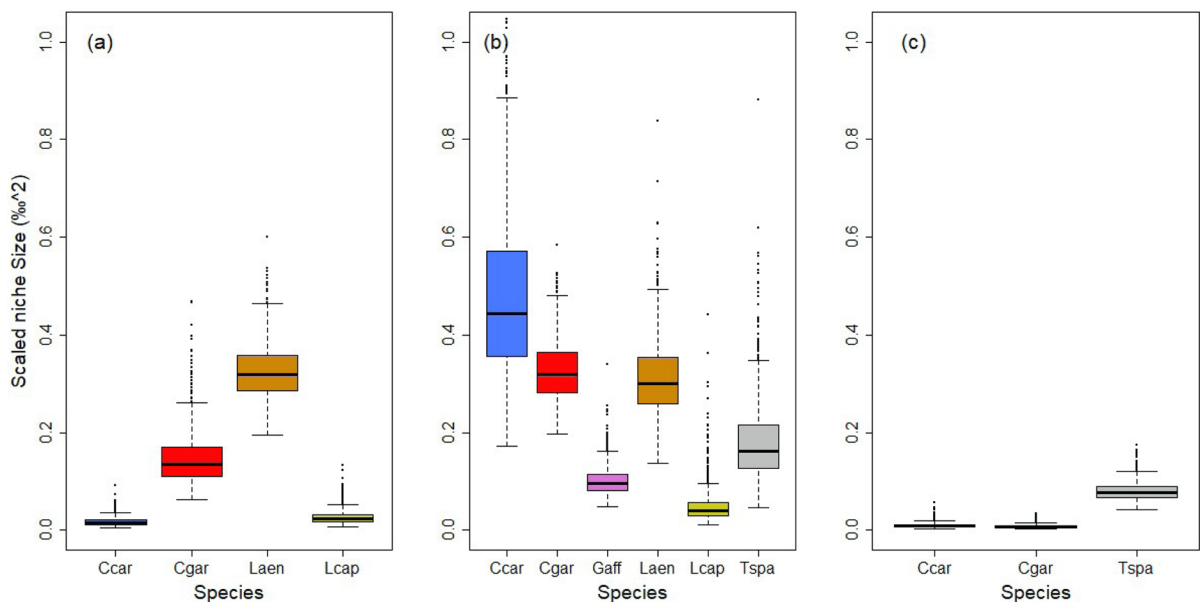


Fig. 3 Isotopic niche sizes (in $\%o^2$) for non-native fishes within the three invaded sections of the Great Fish River system, the upper (a) and the lower (b) Great Fish River mainstem sections and the Koonap River (c). Niche sizes were computed based on the joint probability distributions of $\delta^{13}C$ and $\delta^{15}N$

values, scaled to range between 0 and 1. Species are colour coded consistently across the three sections and are abbreviated as: Ccar, *Cyprinus carpio*, Cgar, *Clarias gariepinus*, Gaff, *Gambusia affinis*, Laen, *Labeobarbus aeneus*, Lcap, *Labeo capensis*; Tspa, *Tilapia sparrmanii*

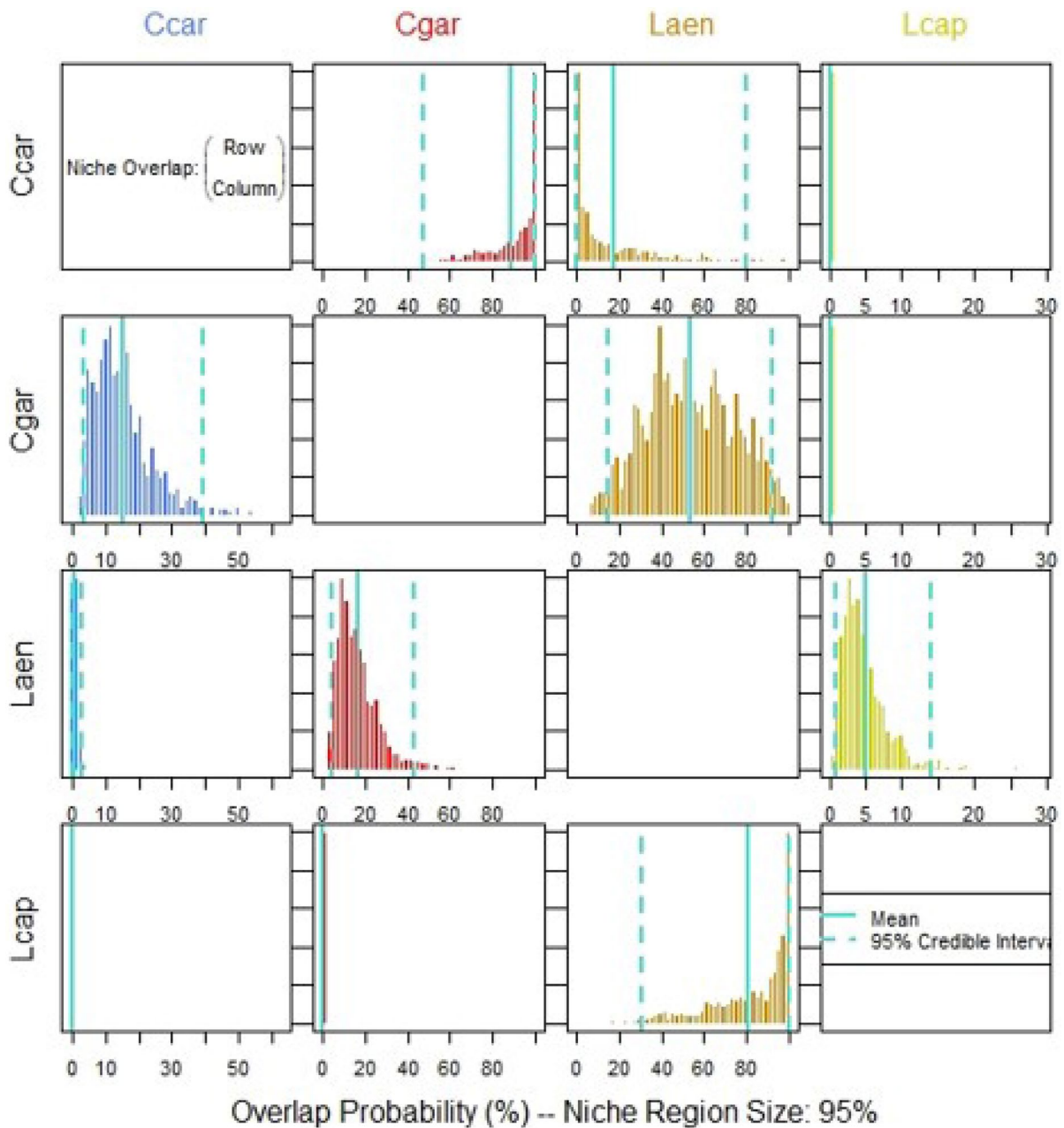


Fig. 4 Mean niche overlap probabilities (%) of the non-native species within the upper Great Fish River (UGFR). The overlap metric is directional, such that it represents the probability that an individual from a species (row) will overlap onto the isotope niche of the other species (column). The niche size

(niche region) was defined as the 95% credibility intervals of isotopic space. Species are abbreviated as *Ccar*, *Cyprinus carpio*; *Cgar*, *Clarias gariepinus*; *Laen*, *Labeobarbus aeneus*; *Lcap*, *Labeo capensis*

Discussion

The Great Fish River system's isotopic values in both its mainstem and the tributaries were characterised by

longitudinal differences in food web structure, which were generally depicted by high $\delta^{15}\text{N}$ ranges in downstream sections compared to upstream and headwater sections. These patterns appeared to be congruent

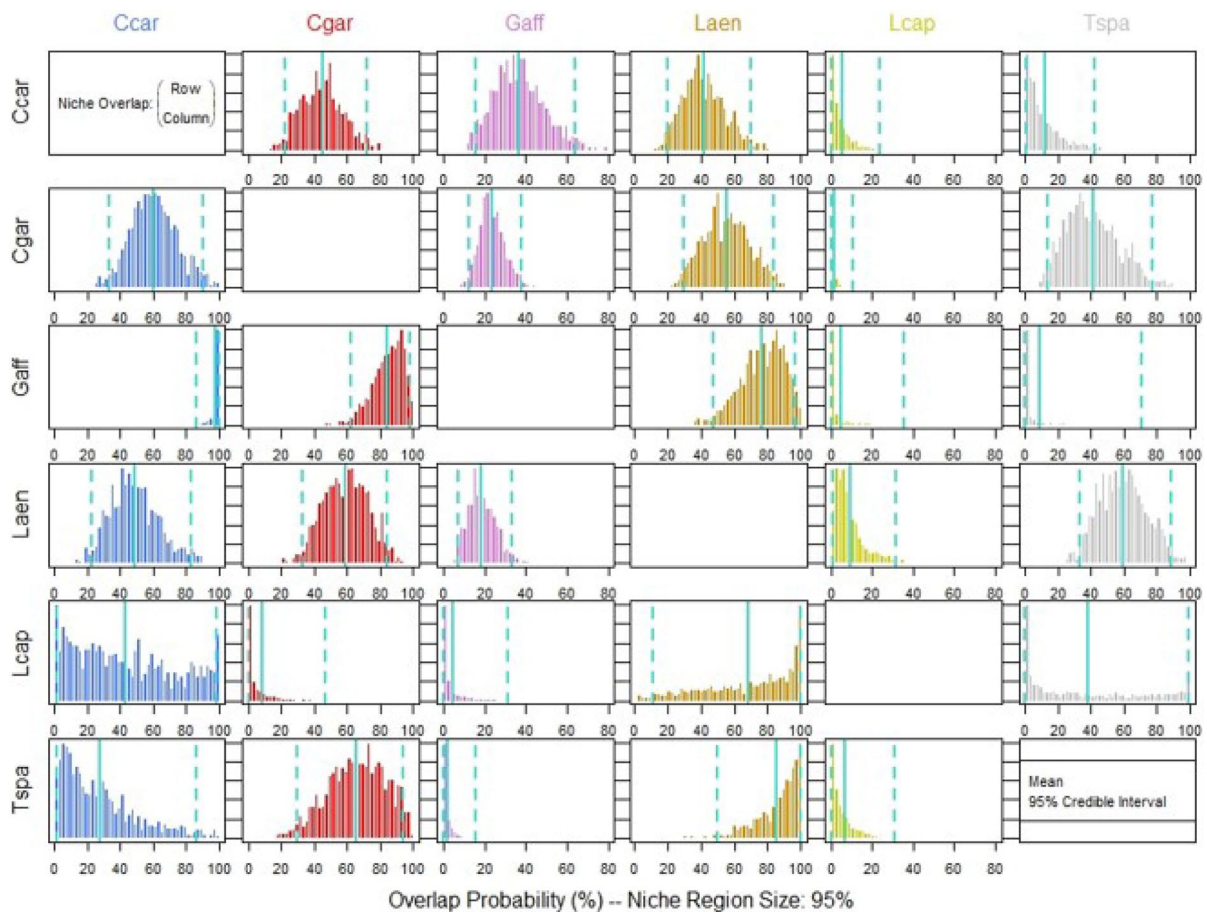


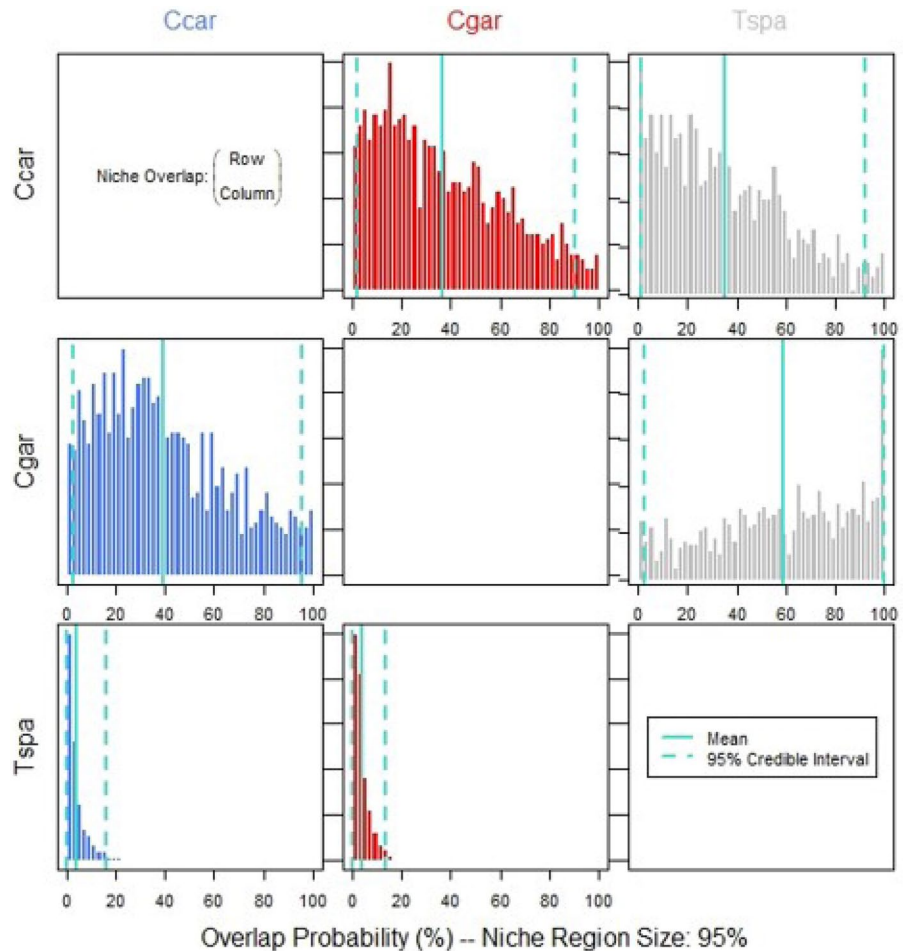
Fig. 5 Mean niche overlap probabilities (%) of the non-native species within the lower Great Fish River (LGFR). The overlap metric is directional, such that it represents the probability that an individual from a species (row) will overlap onto the isotopic niche of the other species (column). The niche size (niche

region) was defined as the 95% credibility intervals of isotopic space. Species are abbreviated as Ccar, *Cyprinus carpio*; Cgar, *Clarias gariepinus*; Gaff, *Gambusia affinis*; Laen, *Labeobarbus aeneus*; Lcap, *Labeo capensis*; Tspa, *Tilapia sparrmanii*

with the longitudinal shifts in food web properties, which are generally linked to aspects such as the structural changes in river size and geomorphometry, differences in productivity, and increases in habitat complexity and species richness along the river continuum (e.g. Vannote et al. 1980; Angermeier and Schlosser 1989; Romanuk et al. 2006; Sánchez-Hernández 2023). Similar to other studies elsewhere, which have shown spatial differences in food web characteristics in anthropogenically-modified river systems, including altered flow that influences energy transfer dynamics (e.g. Cross et al. 2013; Brauns et al. 2019) and in invaded systems where non-native fishes influence both trophic chain length and breadth (e.g. Pennock et al. 2021), this study revealed different

invasion patterns from a food web perspective. Specifically, relative to native fishes, the non-native species exhibited isotopic variations that ranged from intermediate $\delta^{15}\text{N}$ values and wide $\delta^{13}\text{C}$ breadth in the UGFR, low $\delta^{15}\text{N}$ values and narrow $\delta^{13}\text{C}$ breadth in the LGFR, and high $\delta^{15}\text{N}$ values but narrow $\delta^{13}\text{C}$ breadth in the Koonap River. Although the non-native fish assemblages exhibited variable isotopic diversity patterns that were broadly defined by low overlaps with native species in the UGFR and Koonap River and high isotopic diversity overlap in the LGFR, these non-native fishes were mostly characterised by comparable isotopic diversity metrics across the different sections. Thus, these broad patterns appeared to be consistent with our first hypothesis whereby

Fig. 6 Mean niche overlap probabilities (%) of the non-native species within the Koonap River. The overlap metric is directional, such that it represents the probability that an individual from a species (row) will overlap onto the isotope niche of the other species (column). The niche size (niche region) was defined as the 95% credibility intervals of isotopic space. Species are colour coded consistently across the three sections and are abbreviated as Ccar, *Cyprinus carpio*; Cgar, *Clarias gariepinus*; Tspa, *Tilapia sparrmanii*



we postulated consistent patterns that would reflect broad trophic resources utilisation patterns for the non-native fishes. On the other hand, the non-native fishes were characterised by low interspecific isotopic niche overlaps within the invaded UGFR and Koonap River. This posited the likelihood of isotopic niche differentiation among these non-native fishes, which appeared to be inconsistent with our second hypothesis. Nevertheless, in the LGFR, the non-native fishes were mostly characterised by high isotopic niche overlaps, a pattern that appeared to support the second hypothesis. These broad patterns suggest that both the trophic diversity and trophic niche patterns of non-native fishes were likely influenced by the nature of the invaded section, the intraspecific resource use patterns of the non-native species and their probable interactions with the native fish assemblage within the respective invaded sections.

The lack of consistent and predictable trophic diversity and niche patterns for non-native fishes across the invaded sections in this study posits the likelihood of trophic plasticity, which is a common phenomenon related to environmental stochasticity, variation in prey availability and interspecific interactions coupled by niche opportunities that has been observed in other studies (Córdova-Tapia et al. 2015; Pennock et al. 2021). Trophic plasticity has been postulated to facilitate establishment of non-native species in freshwater ecosystems (e.g. Pettitt-Wade et al. 2015; Rolla et al. 2020) and to confer a strategy to minimise and/or avoid potential trophic competition (Jackson et al. 2012; Pelage et al. 2022).

In the UGFR and the Koonap River, the low isotopic diversity overlaps (low isotopic nestedness) between non-native and native species and the low isotopic niche overlaps amongst the non-native

species, suggest that trophic niche differentiation was a probable mechanism facilitating the proliferation of non-native species in these habitats. Specifically, the results of this study suggested the possibility of trophic niche specialisation due to high isotopic divergence and diversion for the non-native species, and the high isotopic uniqueness for the native species. Furthermore, despite large isotopic niche breadths, most non-native species generally showed low trophic niche overlaps, except for trophic generalists, such as *C. carpio* and *C. gariepinus* whose isotopic niche overlapped onto those of other non-native species. This appeared to be consistent with empirical studies elsewhere, which have also shown low isotopic overlaps to reflect trophic niche differentiation among non-native and native species (e.g. Zambrano et al. 2010; Zengeya et al. 2011; Córdova-Tapia et al. 2015; Tarkan et al. 2018; Top-Karakuş et al. 2021). The creation of permanent habitats in the UGFR, as a result of the IBWT, may have facilitated resources by potentially increasing biomass of primary production and that of lower trophic secondary production, such as benthic invertebrates, which in turn could have influenced trophic resource patterns of fishes in this section. For example, O’Keeffe and De Moor (1988) noted that following the creation of permanent flow in the Great Fish River, the system was characterised by a substantial shift towards the dominance of hydropsychid, chironomid and simuliid invertebrate species. These resources likely sustain the proliferation of rheophilic taxa of non-native species such as the benthivorous *L. capensis* and the generalist invertivorous *L. aeneus* probably through reduced interspecific interactions with *C. carpio*, and the generalist piscivore *C. gariepinus*. Alternatively, it is likely that the low native species richness of the UGFR and Koonap River may have presented vacant niches that were exploited by the different non-native fishes with minimum competitive interactions. This is because species depauperate environments are more likely to be susceptible to invasions due to high availability of vacant niches (Shea and Chesson 2002; Hierro et al. 2005; Leuven et al. 2009; Jeschke 2014).

While trophic niche differentiation is generally considered a common mechanism for coexistence among fishes (Mason et al. 2008; Pilger et al. 2010; Jackson and Britton 2013) and appeared to be most probable in the UGFR and Koonap River, this mechanism appeared less plausible in the LGFR. This is

because the non-native fish assemblage’s isotopic diversity largely overlapped with, and appeared to be a subset of, that of the native fish assemblage. Furthermore, these non-native fishes exhibited high isotopic niche overlaps. In contrast to native fishes, the relatively low non-native species’ isotopic diversity within the LGFR suggested less trophic complexity within this species group. While this contradicts other studies that have found non-native species to generally have high isotopic diversity (e.g. Sagouis et al. 2015; De Santis et al. 2022), findings of this study likely reflect the incipient nature of the trophic habits of the predominant non-native species, which mostly comprised generalist piscivores, such as *C. gariepinus* and species that likely occupied lower trophic levels, including benthivores and invertivores, such as *C. carpio*, *L. aeneus* and *T. sparrmanii*. On the other hand, the generally high isotopic diversity for the native fish assemblage may reflect high trophic complexity that characterises most downstream sections of large rivers, which is generally hypothesised to be maintained by weak consumer-resource interactions (Levin 2000; Kokkoris et al. 2002; Bellmore et al. 2015).

The occurrence of multiple non-native species with relatively low isotopic diversity but high isotopic niche overlap in the LGFR may suggest weak trophic interactions among these species within this invaded section. The establishment of multiple non-native species in this section, however, raises concern on their potential impact. This is because non-native species such as *C. gariepinus*, *C. carpio* and *L. aeneus*, which were found to be characterised by large isotope niche sizes, were likely to exert negative influences on the trophic dynamics of this system due to their foraging habits and possible facilitative interactions. For example, *C. carpio*, a global invader, is known to influence nutrient availability and to increase water turbidity (Zambrano et al. 2006; Parkos et al. 2011), which may confer an advantage to *C. gariepinus*, a generalist predator that does not require high visibility for foraging. Thus, there exists a concern about the potential synergistic impacts of these two species on aspects such as facilitated direct predation by *C. gariepinus* on small- to medium-sized native species, such as the round herring *Gilchristella aestuaria*, oval moony *Monodactylus falciformis* and *Pseudomyxus capensis*. Furthermore, there is potential indirect impacts through interspecific interference and

probable competitive interaction for benthic resources by non-native species such as *C. carpio* and *L. capensis*, and the invertivorous *L. aeneus* on species such as the native populations of *L. umbratus* that feeds on soft sediments and detritus, *P. macrolepis* that feeds on diatoms grubbed out of bottom sand and the *G. callidus* that feeds on bottom-living insects and small invertebrates.

General studies on trophic impacts by non-native fishes in lotic habitats have shown that they (non-native fishes) can influence food webs by either increasing the ecosystem's trophic ranges, such as when there is invasion by non-native top predators (Post and Takimoto 2007; Cucherousset et al. 2012b; Walsworth et al. 2013), expanding the food web sizes, such as when there is invasion by taxa that are located on the edges of the food webs (Sagouis et al. 2015) or shrinking of the food webs and/or compression of the isotopic niche (Vander Zanden and Rasmussen 1999; Walsworth et al. 2013), such as when there is invasion by generalist predators and/or when there is elimination of certain taxa. In this study, some of these aspects appeared to have been reflected as well. For example, the UGFR and the Koonap River appeared to typify food web expansion due to the addition of non-native species, with high $\delta^{15}\text{N}$ values, on the top or edges of the food webs. Specifically, in the UGFR, the food web appeared to show a wider breadth in carbon sources for the fishes, which was typified by non-native species such as *C. carpio* with high $\delta^{13}\text{C}$ value and *L. capensis* with low $\delta^{13}\text{C}$ value. In comparison, the Koonap River appeared to reflect an increase in its food web structure, as all the non-native fishes in this section (*C. carpio*, *C. gariepinus* and *T. sparmanii*) had higher $\delta^{15}\text{N}$ than native fishes.

In conclusion, the results of the present study suggested that isotopic diversity patterns likely reflected trophic niche differentiation among native and non-native fishes. In addition, isotopic niche patterns suggested that trophic niche differentiation was a probable mechanism associated with co-occurrence of different non-native fishes in some invaded sections. Nevertheless, these patterns appeared to vary across the different invaded sections. Specifically, the low isotopic diversity overlaps between native and non-native fishes and low isotopic niche overlap among most non-native fishes in the upper mainstem (UGFR) and invaded tributary (Koonap River) sections posits the likelihood of exploitation of vacant trophic niches by the invaders.

In comparison, weak trophic interactions among non-native species were likely responsible for their co-occurrence within the LGFR. The results of this study add to the body of knowledge that seeks to understand how non-native species integrate into disturbed ecosystems and the mechanisms facilitating these integrations.

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Author contributions PPM and WTK were involved in conceptualisation and designing of the study, data acquisition and analysis, as well as the final approval of the final version to be submitted for review. PPM interpreted data and led the writing of the manuscript. WTK critically evaluated manuscript for important intellectual content.

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Availability of data and materials Data analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose. The authors have no conflict of interest to declare pertaining to the contents of this article.

Ethical approval We also confirm that this study was conducted within the norms and regulations of animal welfare as required by the laws of the country. Ethical approval was granted by Rhodes University Animal Research Ethics Committee (Approval number: 2020–2822–4866). Sampling permission was granted by Eastern Cape's Department of Economic Development, Environmental Affairs and Tourism (Permit number: CRO 130/19CR).

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