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INVASIVE SPECIES II

Niche complementarity between an alien predator and native omnivorous fish in the Wilge River, South Africa

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Abstract A major challenge in biological invasions is to predict community susceptibility to invasion. This study investigated trophic interrelationships between an alien predator, largemouth bass (*Micropterus salmoides*), and native omnivores, sharptooth catfish (*Clarias gariepinus*) and largescale yellowfish (*Labeobarbus marequensis*), in an invaded aquatic system to elucidate factors that might have aided their successful establishment. It tested the hypothesis that *M. salmoides* is able to co-exist with the two native omnivores by either utilising a previously vacant food niche or through niche complementarity. Gut content and stable isotope analyses were used to determine trophic interactions. There was no evidence that *M. salmoides* was utilising a previously vacant food niche but instead it occupied a restricted and specialised niche within a broad niche space utilised by the native omnivores. Differences in niche space and size have resulted in minimal niche overlaps that imply niche complementarity. The introduction of *M. salmoides* raises concerns about increases in predation pressure in the system. This, however, is difficult to ascertain because of complexities in measuring long-term trends in predator demands, abundance and community compensation mechanisms. There is a need for long-term monitoring of community structure, especially small-sized prey species that are vulnerable to increased predation pressure.

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Introduction

Alien predatory fish species have been introduced worldwide to enhance recreational and sport fishing (Cambray, 2003; Eby et al., 2006; Arlinghaus & Cooke, 2009) and to boost fisheries (Pringle, 2005). Despite the positive socio-economic values derived from these introductions, these fish have also been implicated in adversely altering community structure and functioning in areas of introduction (Cambray,

2003; Cowx et al., 2010; Britton & Orsi, 2012; Ellender & Weyl, 2014). They affect communities through the replacement of native predators, competition for food and space, increased consumption of prey, prey extirpation, increased top-down control, alteration of food web structures, changes in habitat coupling as well as overall ecosystem-level effects (see Eby et al., 2006 for a review of impacts of alien predatory fish).

Research on biological invasions has grown remarkably over the past few decades, yet predicting community susceptibility to invasion remains a major challenge (Sih et al., 2010). Two prominent concepts that have been put forward to explain the successful establishment of invasive species are the availability of vacant niches (Elton, 1958) or highly developed competitive abilities (Simberloff, 1982). The first concept suggests that introduced species utilise unexploited resources and this may facilitate successful establishment (e.g. Mack, 1996; Levine & D'Antonio, 1999; Shea & Chesson, 2002; Jackson & Britton, 2014). The second tenet proposes that introduced species out-compete and displace native species for resources such as habitat, food and breeding space (e.g. Blanchet et al., 2007; Zengeya & Marshall, 2007; Bøhn et al., 2008; Hasegawa, 2016; Taabu-Munyaho et al., 2016). The study of trophic resource partitioning in invaded aquatic systems can be a good way to characterise the long-term implications of non-native fish introductions and elucidate factors that might aid in their successful establishment (Vander Zanden et al., 2004; Gozlan et al., 2010; Sih et al., 2010; Britton et al., 2011; Juncos et al., 2015; Pereira et al., 2015; Comte et al., 2016).

This study therefore investigated trophic interrelationships between an alien predator fish, largemouth bass *Micropterus salmoides* (Lacepède, 1802) and two native facultative omnivores [sharptooth catfish, *Clarias gariepinus* (Burchell, 1822) and largescale yellowfish, *Labeobarbus marequensis* (Smith, 1841)] in the Wilge River, South Africa. It evaluated the hypothesis that *M. salmoides* was able to establish and is able to co-exist with the two native omnivores because it is either utilising a previously vacant food niche or co-existence is achieved through patterns of minimal diet overlap. *Micropterus salmoides* is native to river systems in eastern North America from the Great Lakes to the Gulf Coast (Page & Burr, 2011) but it has been widely introduced worldwide for sport

fishing (Froese & Pauly, 2016). The species was introduced into South Africa in 1928 (de Moor & Bruton, 1988) and it has established in most river catchments throughout the country. Several factors might have contributed to its establishment and including (1) a sustained and wide spread stocking for sport fishing throughout the country, initially by government agencies and later by angling societies and private individuals, (2) availability of suitable receiving environments—the species has managed to colonise most upland systems which have a similar climate to its native range, and (3) highly developed aggressive feeding strategies—*M. salmoides* is an aggressive predator that has had a major impact on small-sized native species in recipient systems (Ellender et al., 2011; Ellender & Weyl, 2014; Ellender et al., 2014; Kimberg et al., 2014). It is largely piscivorous, but is also known to consume a variety of animal prey such as aquatic insects, frogs, crabs and small mammals (Weyl et al., 2010; Wasserman et al., 2011).

In most systems that *M. salmoides* has become established in South Africa, there is lack of a comparative top fish predator(s) and instead these systems are inhabited by facultative omnivores. This case is true for the Wilge River where before the introduction of *M. salmoides*, fish communities were likely controlled by large-sized omnivores (*C. gariepinus* and *L. marequensis*) as the top predators. These fish species consume a wide variety of prey (such as fish, insects, snails, clams, crabs, algae and macrophytes) and their diet varies in relation to food availability, different environments, season and the presence or absence of competing fish species and predators (Skelton, 2001; Marshall, 2011). The broad and versatile food niche among the two omnivores is likely to lead to low food resource overlap with *M. salmoides*. This study was therefore designed to assess whether *M. salmoides* is able to co-exist with the native omnivore species because it is either utilising a vacant niche or through niche complementarity. The euryphagous feeding pattern of native omnivorous species versus the more stenophagous nature of *M. salmoides* may minimise niche overlaps and allows for co-existence. In addition, a euryphagous feeding strategy may allow for the native omnivore species to shift resources and ultimately alter their trophic position in response to fluctuations in resource

availability and/or potential competition for food with *M. salmoides*.

Materials and methods

Study sites and sampling

Study sites were located on the Wilge River, a major perennial tributary of the Olifants River, which originates in the Highveld grasslands of the Mpumalanga and Gauteng Provinces in South Africa (Fig. 1). The catchment area of the Wilge River is about 4,400 km² and the area receives summer rainfall with mean annual precipitation of 670 mm (Schulze et al., 1997; Schultz & Watson, 2002). The vegetation ranges from Highveld grasslands in the upper reaches of the catchment to sub-tropical woodland eco-region in the lower reaches (Mucina & Rutherford, 2006).

The river flows through the Waterberg quartzite and conglomerate geological formation where it has incised a deep narrow valley and the river profile is characterised by a series of staggered rapids and runs that are interspersed by deeper and wider pools (EMF, 2009). Fish were sampled at six sites (Fig. 1) between October 2013 and September 2014 during periods of high flow (October–March) and low flow (June–September) using a variety of sampling techniques. Shallow reaches (< 1.35 m) were sampled using an electrofisher (Samus Special Electronics, Warsaw, Poland), while large and deep channels were sampled using three fleets of gill nets as well as angling.

The fish fauna in the Wilge River system is composed of 20 fish species, four of which are alien [common carp *Cyprinus carpio* Linnaeus, 1758; mosquito fish *Gambusia affinis* (Baird & Girard, 1853); small mouth yellowfish *Labeobarbus aeneus* (Burchell, 1822) and *M. salmoides*] (Table 1).
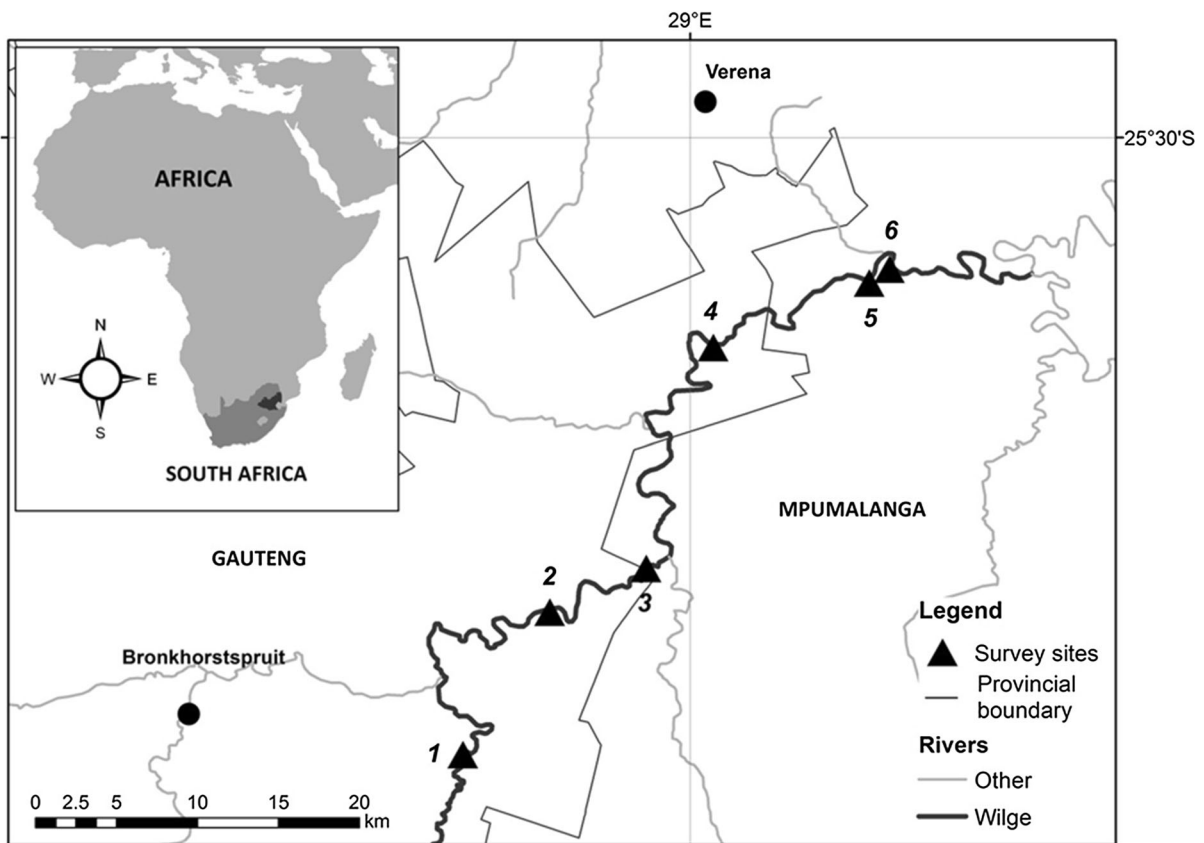

Fig. 1 The location of sampling sites along the Wilge River, South Africa. The sampled river reach was 77 km in length and stretched from the east of Bronkhorstspruit to the southeast of Verena. Sites are numbered in a downstream direction (1 = upper reaches, 6 = lower reaches)

Table 1 The mean trophic positions (with standard deviations in brackets) of fish species found in the Wilge River system, South Africa

Trophic position	Trophic level	Species
Top predators	4.3 (0.3)	*Micropterus salmoides*
	4.2 (1.2)	*Labeobarbus marequensis*
Mid-level predators and omnivores	3.9 (0.4)	*Clarias gariepinus*
	3.7 (0.2)	*Amphilius uranoscopus*
	3.6 (0.1)	*Enteromius neefi*
	3.6 (0.1)	*Chiloglanis pretoriae*
	3.4 (0.6)	*Labeobarbus polylepis*
	3.1 (0.4)	*Labeobarbus aeneus**
	3.1 (0.2)	*Gambusia affinis**
	3.1 (0.0)	*Cyprinus carpio**
	3.1 (0.2)	*Pseudocrenilabrus philander*
	3.0 (0.2)	*Enteromius anoplus*
Omnivores, herbivores and detritivores	2.9 (0.3)	*Marcusenius macrolepidotus*
	2.9 (0.2)	*Enteromius unitaeniatus*
	2.9 (0.1)	*Mesobola brevianalis*
	2.8 (0.4)	*Labeo umbratus**
	2.8 (0.1)	*Tilapia sparrmanii*
	2.6 (0.1)	*Enteromius trimaculatus*
	2.5 (0.1)	*Enteromius paludinosus*
	2.4 (0.2)	*Labeo rosae**

Data from Kleynhans et al. (2007), Deacon & Kotze (2009), Rashleigh et al. (2009) and this study. Alien species are indicated in bold and species with an asterisk were not sampled and their trophic levels were obtained from the literature (Froese & Pauly 2016)

Preliminary food web analysis showed that only two species (*C. gariepinus* and *L. marequensis*) had potential trophic overlap with *M. salmoides*. Therefore, for brevity, the other 17 species were excluded from the analysis. To account for spatial and temporal variability in isotopic values among the six sampling sites, diet comparisons were restricted to samples collected from (1) the same season (2) sites where *M. salmoides* was sampled and (3) sites where the isotope signatures for each of the three fish species were not statistical different. Three sites (sites 1, 4, 6) met these criteria. In addition, the analysis was restricted to samples collected during high flow because low flow samples were depauperate for any conclusive analysis.

Determination of diet and trophic interactions

Gut content (GC) and stable isotope (SI) analyses were used to determine diet and trophic interactions between *M. salmoides* and native fish species in the Wilge River. These two complimentary methods are increasingly being used concurrently to characterise changes in the structure and flow of energy in aquatic food webs related to non-native fish introductions (Zengeya et al., 2011; Kadye & Booth, 2012). Using

both methods allows for a better estimate of the average diet for a fish as the two methods can reflect different times when the fish fed. Gut content analysis provides a snap shot of ingested food items within a short time frame (hours to days), while SI provides a longer time-averaged estimate (days to months) of food assimilated by a fish (Gearing, 1991). Subtle patterns of niche complementarity are not always apparent when the two methods are used in isolation (e.g. see Zengeya et al., 2011). Gut content analysis is constrained by difficulties in quantifying and identifying food items, differential digestive rates of ingested material, not all digested material is assimilated and large samples sizes over a long time period are required in order to give an accurate estimation of niche breadth (Hyslop, 1980). In turn, stable isotope analysis also has limitations to its application such as variations in species-specific nitrogen isotope fractionation according to food source and dietary nitrogen content, while carbon isotope ratios are dependent on metabolic pathways, season and geographical regions (Vanderklift & Ponsard, 2003; Fry, 2006; Finlay & Kendall, 2007; Marshall et al., 2007). Therefore in this study, gut content analysis was used to identify possible food items and the observed food

matrix was then used to calibrate the stable isotope mixing models. Stable isotope data were then used to differentiate food niches among fish species in terms of space, size and degree of overlap.

Stomach content analysis

Stomach contents were analysed using the modified methods of Platter & Potter (2001) and Zengeya & Marshall (2007). In brief, individual stomach contents were suspended in 100 ml of water and examined under a microscope. The contribution of each food category in each gut was estimated by evenly spreading all contents from each gut in a graduated petri dish and converting the surface area occupied by each ingested item to a percentage for each food category. Ingested items were identified to the lowest possible taxonomic level and then further pooled into broader taxonomic categories (such as sediments, detritus, algae, plant matter, zooplankton, macroinvertebrates, insects and fish) for quantitative estimates.

Stable isotope analysis

The samples required to delineate the food web structure in the river system were collected from the environment based on food items that were identified in the gut contents. These included insects, tadpoles and crustaceans (i.e. freshwater crabs, clams and shrimps) that were collected using the kick-net method on all available substrates at each site. Terrestrial and aquatic plant material, detritus and algae were collected by hand, while zooplankton was collected using a plankton drag net. Fish caudal muscle, plant and invertebrate samples were oven-dried at 70°C for 12 h after which samples were ground to a fine powder using a mortar and pestle. Lipid extraction was done with 2:1 Chloroform–Ethanol until the solution reached a pre-determined state (Søreide et al., 2006). Inorganic carbons (i.e. $CaCO_3$) were removed from all invertebrate and plant samples with 1 mol HCL (Søreide et al., 2006). Samples were then re-dried for 12 h before aliquots of approximately 0.6–0.7 mg (1–1.2 mg for plant samples) were weighed into tin capsules that were pre-cleaned in toluene. Isotopic analysis was done on a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by ThermoFischer, Bremen, Germany),

housed at the Stable Isotope Laboratory, Mammal Research Institute (MRI), University of Pretoria, Pretoria, South Africa.

A laboratory running standard (Merck Gel: $\delta^{13}C = -20.57‰$, $\delta^{15}N = 6.8‰$, C% = 43.83, N% = 14.64) and blank sample were run after every 12 samples. The standards were Vienna Pee Dee Belemnite limestone for δ13C (Craig, 1957) and atmospheric nitrogen for δ15N (Ehleringer & Rundel, 1989). Results were expressed in delta notation using a permil scale using the standard equation:

$$\delta X(‰) = \left[(R_{sample} - R_{standard})/R_{standard} - 1 \right] \times 1000,$$

where $X = {}^{15}N$ or ${}^{13}C$ and R represents ${}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$, respectively. Analytical precision was $< 0.08‰$ for $\delta^{13}C$ and $< 0.13‰$ for $\delta^{15}N$.

Statistical analysis

A modified Costello method (Amundsen et al., 1996, modified from Costello, 1990) was used to calculate the contribution of each food item to the diet of each species. This index uses the frequency of occurrence and prey-specific abundance of each food item to give a two-dimensional representation of prey importance (dominant to rare) and feeding strategy (specialist to generalist). Frequency of occurrence ($F\%$) is expressed as percentage of the total number of investigated fish containing specific food item in that period and prey-specific abundance ($A\%$) is the sum of the stomach proportions that contained a particular prey type, divided by the total number of stomachs that contained the specific prey item. A one-way analysis of similarly (ANOSIM) based on a Bray–Curtis similarity matrix was then used to test for diet differences among species.

A Bayesian mixing model SIAR V4.0 for Stable Isotope Analysis in R (Parnell et al., 2010) was used to estimate the relative contributions of food sources to fish diet. The SIAR model was calibrated using food sources that were grouped into broader taxonomic categories based on a k-Nearest Neighbour analysis (Rosing et al., 1998), namely seston, detritus, aquatic macrophytes, crustaceans, insects, molluscs and vertebrates. Raw fish isotopic values were corrected for trophic enrichment prior to analysis, using values calculated following the approach

proposed by Hobson & Welch (1992). In brief, trophic enrichment for a given food web can be estimated in cases where the diet of a particular consumer is well known. In this study, we used the river sardine *Mesobola brevianalis* (Boulenger, 1908) and bulldog *Marcusenius macrolepidotus* (Peters, 1852) that were found to be insectivores in a parallel on-going study to calculate the step-wise enrichment of carbon and nitrogen from insects to fish muscle. The trophic enrichment factors obtained from the two species were further compared to other consumer–prey relationships within the food web to obtain a food web average of 3.39 ± 0.08‰ for nitrogen and 0.1 ± 0.1‰ for carbon. Concentration dependence (Phillips & Koch, 2002) was also included into the model to take into account the different digestibility of food sources in the omnivorous diet of *C. gariepinus* and *L. marequensis.* The trophic structure of the fish fauna found in the river was determined using the equation:

$$TP = \left(\frac{N_{consumer} - N_{baseline}}{3.39}\right) + 2,$$

where 3.39 is the trophic enrichment factor and $N_{baseline}$ was the δ15 N of freshwater clams, a filter-feeding mollusc ($\delta^{13}C = -28.23 \pm 1.88‰$, δ15 N = 10.70 ± 0.64‰). Non-parametric Kruskal–Wallis, followed by a Mann–Whitney pairwise post hoc test (Zar, 1996), was used to test for differences in the mean stable isotope ratios for δ15 N and δ13C among fish species because isotopic data departed from normality and homogeneity of variance.

Sample size-corrected standard ellipse areas (SEAc) in the R package *Stable Isotope Ellipses in R* (SIBER) (Jackson et al., 2011) were used to estimate niche size and trophic overlap among the three fish species. The niche space utilised by a species is often delineated by a convex hull drawn around the most extreme outliers in a given isotope bi-plot (Layman et al., 2007). This inherently makes it susceptible to changes in sample size, as a convex hull area is likely to increase with increasing sample size. To counteract this sample size effect, Jackson et al. (2011) proposed the use of standard ellipse areas (SEA) which are constructed using variance and covariance of the isotope bi-plot to contain only 40% of the data, which represents the core isotopic niche that is not affected by sample size. The resultant SEA is then corrected to

minimise bias caused by small sample sizes (SEAc) using the following correction factor:

$$SEAc = SEA \times [(n-1)/(n-2)].$$

Results

Gut content

A total of 55 specimens of *M. salmoides* and the two native omnivores (*L. marequensis* and *C. gariepinus*) were collected for gut contents analysis (Fig. 2). The average proportion of empty stomachs among the three species was 21.4% but this varied considerably from low values in *C. gariepinus* (10%) and *M.*
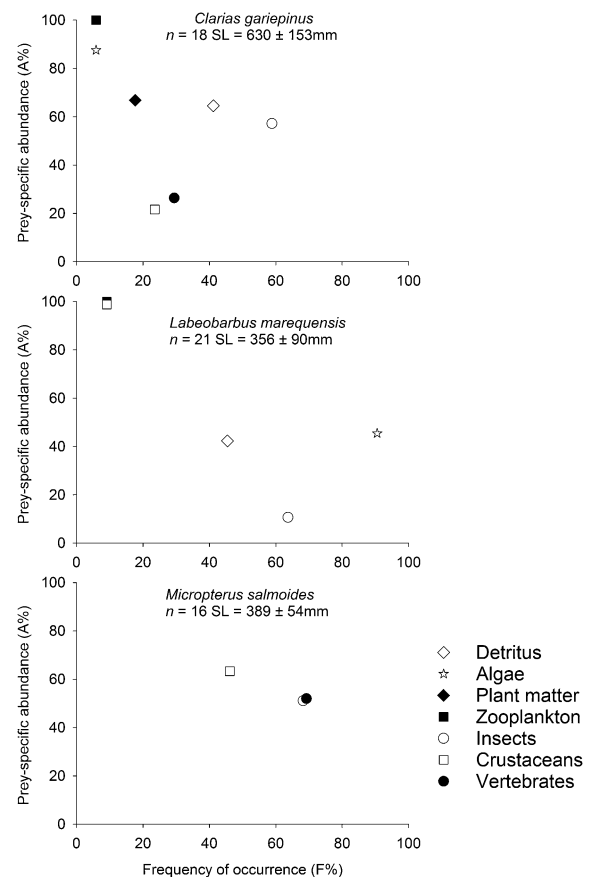

Fig. 2 The prey-specific abundances (A%) and frequency of occurrence (F%) of food items in the diet of two native omnivores (*Labeobarbus marequensis* and *Clarias gariepinus*) and the alien piscivore *Micropterus salmoides* in the Wilge River, South Africa. n = sample size, SL = standard length ± standard deviation

salmoides (11.8%) to 42.1% in *L. marequensis*. They were no significant differences in prey-specific abundance (Global R = 0.12, $P > 0.05$) but the frequency of food items among the three species was significantly different (Global R = 0.15, $P < 0.05$). Pairwise comparisons indicate that the significant difference ($P < 0.05$) was only between *M. salmoides* and *C. gariepinus* and not among any other species cross-comparisons. *Clarias gariepinus* had a broad diet that consisted of various foods items such as detritus, algae, plant matter, zooplankton, insects, crustaceans (crabs, clams and shrimps) and vertebrates (frogs and fish) (Fig. 2). The most abundant food items were zooplankton (A = 100%, F = 7%), algae (A = 88%, F = 6%) and plant materials (A = 67%, F = 18%) but these were only observed in a few stomachs. Detritus (A = 65%, F = 42%) and insects (A = 57%, F = 59%) were relatively abundant and were frequently observed in most individuals. Crustacean (A = 22%, F = 24%) and vertebrate prey (A = 26%, F = 29%) were the least abundant and were only observed in a few stomachs.

Labeo marequensis also had a broad diet that consisted of detritus, algae, zooplankton, insects and crustaceans (Fig. 2). The most abundant foods were zooplankton (A = 100%, F = 9%) and crustaceans (A = 99%, F = 9%) but these only occurred in few stomachs. Algae (A = 45%, F = 90%) and detritus (A = 42%, F = 45%) were relatively abundant and occurred in most stomach, while insects (A = 11%, F = 64%) were frequent but not abundant. In contrast, *M. salmoides* consumed only animal prey that consisted of insects (A = 51%, F = 68%), crustaceans (A = 63%, F = 46%) and vertebrates (A = 52%, F = 69%) that were all abundant and occurred frequently in all the examined stomachs (Fig. 2).

Stable isotopes

The results from the SIAR mixing model were similar with results from gut content analysis and indicated significant differences (Global R = 0.12, $P < 0.05$) in diet of *M. salmoides* and *C. gariepinus* but not among any other species cross-comparisons. *Clarias gariepinus* was omnivorous with a broad diet composed of plant and animal prey, while *M. salmoides* and *L. marequensis* were carnivorous and consumed largely crustaceans and vertebrates (Fig. 3). There were significant differences (Kruskal–Wallis $\chi^2 = 10.23$,
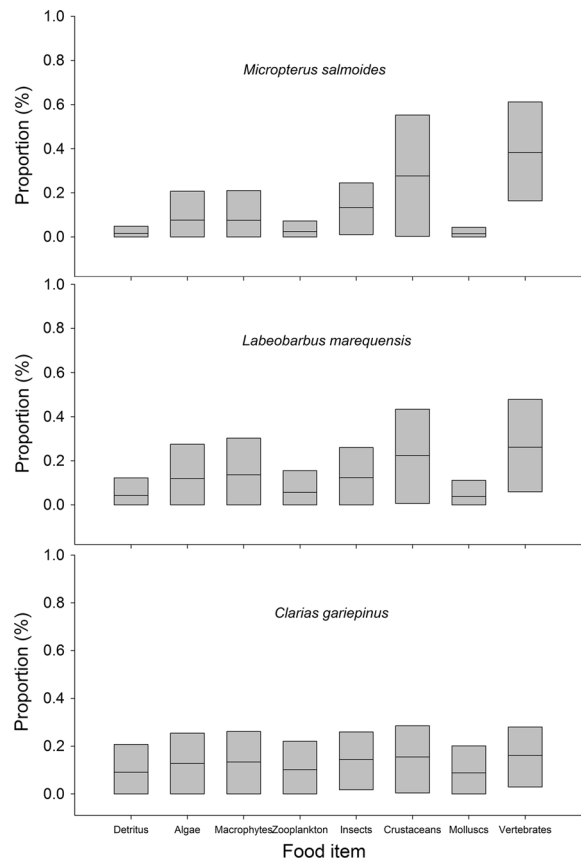

Fig. 3 The proportion (% of isotopic value) of possible food sources utilised by two native omnivores (*Labeobarbus marequensis* and *Clarias gariepinus*) and the alien piscivore *Micropterus salmoides* from the Wilge River, South Africa. Boxes represent low and high 95% confidence intervals around the median (solid line)

df = 2, $P < 0.05$) in δ^{15}N values among the three species (Fig. 4). Mann–Whitney post hoc tests indicated no significant differences in δ^{15}N values between *C. gariepinus* (median = 16.92‰) and *L. marequensis* (15.47‰) but the two species were significantly different ($P < 0.05$) from *M. salmoides* (18.51‰). In contrast, the median δ^{13}C values of *M. salmoides* (− 21.59‰), *L. marequensis* (− 21.85‰) and *C. gariepinus* (− 22.91‰) were similar (Kruskal–Wallis $\chi^2 = 5.09$, df = 2, $P > 0.08$) (Fig. 4). All three species showed no ontogenic changes in diet for δ^{15}N [*L. marequensis* (mean TL = 344.05 ± 105.22; $r^2 = 0.01$; $P > 0.05$), *C. gariepinus* (mean TL = 630.4 ± 152.9; $r^2 = 0.10$; $P > 0.05$) and *M. salmoides* (mean TL = 389.3 ± 53.7; $r^2 = 0.01$; $P > 0.05$)] and for
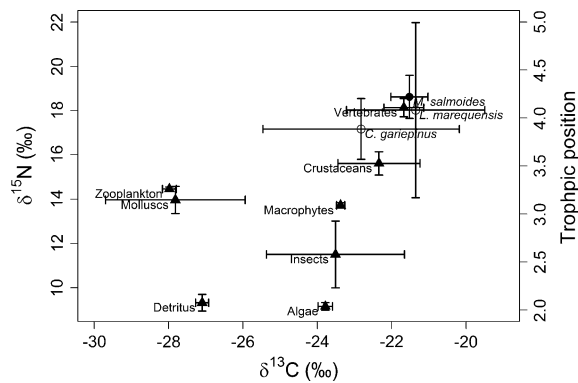
Fig. 4 Trophic positions, mean carbon (δ13C) and nitrogen (δ15C) values of two native omnivores (*Labeobarbus marequensis* and *Clarias gariepinus*) and the alien piscivore *Micropterus salmoides* in the Wilge River, South Africa. Error bars indicate standard deviations, (open circle) = native species, (filled circle) = introduced species and (filled triangle) = possible food sources
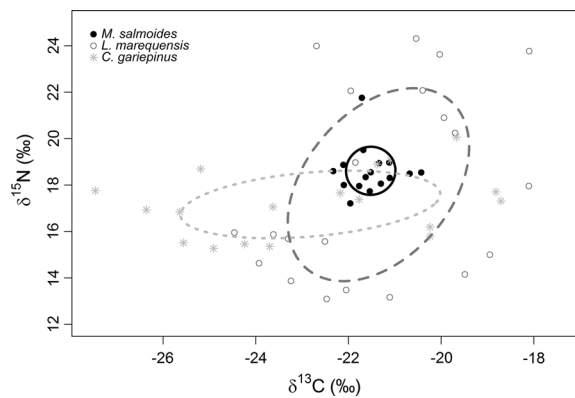

Fig. 5 Estimates of niche size and trophic overlap derived from size-corrected standard ellipse areas (SEAc) of two native omnivores *Labeobarbus marequensis* (dark grey lines) and *Clarias gariepinus* (light grey) and the alien piscivore *Micropterus salmoides* (black) from the Wilge River, South Africa

δ13C [*L. marequensis* ($r^2 = 0.01$; $P > 0.05$), *C. gariepinus* ($r^2 = 0.14$; $P > 0.05$) and *M. salmoides* ($r^2 = 0.05$; $P > 0.05$)]. There were statistically significant differences (SIBER: $P < 0.05$) in niche size (SEAc) among the three species. *Labeobarbus marequensis* had the largest niche (SEAc = 23.54), which was almost twice the size of *C. gariepinus* (SEAc = 12.19) (Fig. 5). In contrast, *M. salmoides* had the smallest niche size (SEAc = 1.73). The most pronounced trophic overlap was between *L. marequensis* and *C. gariepinus* (20.31%), while *M.*

salmoides had a small overlap (< 7%) with any of the two native species.

The trophic levels of all the 20 fish species that are known to occur in the system was composed of three categories: top predators (TP ≥ 4), mid-level predators and omnivores (TP = 3–3.9) and herbivores and detritivores (TP < 3) (Table 1). *Clarias gariepinus* (3.9) was categorised as a mid-level predator and omnivore, while *L. marequensis* (4.2) and *M. salmoides* (4.3) were top predators.

Discussion

This study assessed patterns of trophic partitioning between the alien piscivore *M. salmoides* and two native omnivore species in the Wilge River. We found no evidence that *M. salmoides* is utilising a vacant food niche but instead it occupied a restricted and specialised niche within a broad niche space that is utilised by the native omnivore species. The differences in niche size and the minimal trophic overlap between the native omnivores and *M. salmoides* imply that niche complementarity may have been achieved through differences in prey preferences and feeding behaviour. In most invaded systems, alien and native species with similar niches co-exist through niche differentiation along important niche axes such as diet or habitat (Goodenough, 2010; Schlaepfer et al., 2011). The niche space utilised by *M. salmoides* was entirely encompassed by that of *L. marequensis*, suggesting that the diet of *L. marequensis* entirely included that of *M. salmoides*, but was not limited to that of the latter. *Labeobarbus marequensis* is a facultative omnivore that feeds on a variety of food items that include detritus, algae, insects, crustaceans and small fish (Crass, 1964; Pienaar, 1978; Gaigher, 1979; Bell-Cross & Minshull, 1988; Skelton, 2001; Fouché & Gaigher, 2001; Fouché et al., 2003). This omnivorous feeding behaviour is well supported by results from this study, where *L. marequensis* had the largest niche space of the studied species, inferring a broad-based diet. The large proportion of empty stomachs, enriched δ15N values and a high trophic position imply that the diet of *L. marequensis* was dominated by animal prey and is similar to the diet of *M. salmoides*.

Similar to *L. marequensis*, *C. gariepinus* also had low niche overlaps with *M. salmoides*. *Clarias*

gariepinus and *M. salmoides* are both aggressive and highly mobile predators that feed on a wide range of vertebrate species (Skelton, 2001; Garcia-Berthou, 2002; Post, 2003; Jang et al., 2006; Booth et al., 2010; Kadye & Booth, 2012). However, the trophic overlap between the species is likely to be minimised by the generalist feeding behaviour of *C. gariepinus* and temporal difference in feeding behaviour. The large variation in δ^{13}C and large niche size (SEAc) of *C. gariepinus* indicates a euryphagous diet consisting of a wide range of food sources in contrast to the smaller niche size of *M. salmoides* that suggests a stenophagous diet predominantly composed of vertebrate prey. In addition, *M. salmoides* is a visual predator that utilises daylight to hunt prey (Crowl, 1989; Petit, 2001), while *C. gariepinus* is predominantly a nocturnal feeder (Bruton, 1979; Hogendoorn, 1981; Viveen et al., 1985) that uses sensitive barbels to locate prey in murky environments. These temporal differences in hunting activity might also have implications on prey selection, where *M. salmoides* might be more selective, while *C. gariepinus* might eat whatever is available.

The highlighted subtitle niche partitioning would likely reduce niche overlap especially as the three species have rather similar habitat affinities. The three species were caught in both fast-flowing (runs and rapids) and slow-flowing habitats such as deep pools. This is consistent with other comparative studies done elsewhere which consider the three species as eupotamonic (main stream) guild species (Gratwicke et al. 2003; Kimberg et al. 2014). However, detailed telemetry studies are still required to investigate the home range and habitat use, the temporal distribution and population connectivity among the three species.

Conservation implications

The establishment of alien predators often leads to one of two outcomes: either the native predators are extirpated or native and alien species co-exist, thus increasing the species richness (Pringle, 2005; Eby et al., 2006; Kishe-Machumu et al., 2012, 2015). The introduction of *M. salmoides*, in conjunction with three other alien species, has increased the number of omnivorous and predatory species by 40%, raising concerns about the potential increase in predation pressure impacts. However, this is difficult to ascertain because of complexities in measuring long-term trends in community absolute abundance, predator demands and community compensation mechanisms. However, the stenophagous diet of *M. salmoides* and its higher functional responses (resource up-take rate as a function of resource density) relative to the native predator species (Alexander et al., 2014) suggest an increased predation pressure to the system. Introduced predators that have higher functional responses relative to native predators tend to cause adverse ecological impacts in recipient systems (Bollache et al., 2008; Dick et al., 2013; Alexander et al., 2014). This assertion is supported by observed impacts of *M. salmoides* in other systems into which it has been introduced in southern Africa, where it has been implicated in the reduction in fish diversity and abundance of smaller-sized river minnows (Gratwicke & Marshall 2001; Weyl et al., 2010; Ellender et al., 2011. 2014; Kimberg et al., 2014). It is most likely that the impacts of *M. salmoides* will not manifest through the replacement of native predators/omnivores species but through increased consumption and extirpation of smaller-sized prey as observed elsewhere (Gratwicke & Marshall 2001; Gratwicke et al. 2003; Ellender et al., 2014; Kimberg et al., 2014). However, a major limitation with these studies is that they have not quantified and compared the niche utilised by *M. salmoides* and the native omnivore species to assess whether it the former is utilising a vacant niche or co-existence is achieved through niche complementarity. This study therefore provides baseline evidence that co-existence in the Wilge River is achieved through niche complementarity. There is, however, a need for further studies in the river system to monitor long-term trends in community absolute abundance and resource partitioning (e.g. food and habitat) to have a better understanding of the overall impacts of *M. salmoides* on community structure and functioning in the Wilge River.

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