

Integrating stomach content and stable isotope analyses to elucidate the feeding habits of non-native sharptooth catfish *Clarias gariepinus*

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Abstract Sharptooth catfish *Clarias gariepinus* was introduced into the Eastern Cape Province, South Africa, in 1976 and there are concerns about its possible negative impacts on native biota. This study investigated its trophic impact by examining its feeding habits. Stomach content and stable isotope analyses were compared from three localities—the Great Fish River, Sundays River and Glen Melville Dam. Stomach content analysis indicated a catholic diet dominated by fish particularly in all localities. Spatially, however, the diets revealed differences based on the dominance of macrophytes that were only present in the rivers, and aquatic invertebrates that appeared more diverse within the Great Fish River compared to other localities. By contrast, stable isotopes revealed a more generalised feeding pattern with no clear dominance of particular prey. Stable isotopes further showed that the catfish was a complex predator, with large catfish being top predators whereas smaller size groups appeared to feed lower in the food chain. An ontogenetic shift in diet was evident, with small fish predominantly consuming aquatic invertebrates and shifting towards fish with increasing size. High dietary overlap suggests the potential risk associated catfish feeding, especially the

potential of piscivory by small catfish that are more likely to persist in shallow and marginal where endangered indigenous minnows occur. The alteration of environmental conditions, especially flow by inter-basin water transfer (IBWT) schemes, was inferred to have had a probable influence its invasion success. Occurrence of other invaders, which was facilitated by the IBWT together with the catfish, posits the risk of invasion meltdown within the study systems.

Keywords Catfish diet · Omnivory · Ontogenetic shift · Isotope mixing models

Introduction

Sharptooth catfish, *Clarias gariepinus*, is one of the most widely distributed fish species in Africa and some parts of the Middle East. It occurs naturally from Israel, Syria and southern Turkey in the north and throughout Africa to the Orange River in the south (Daget et al. 1984; Skelton 2001). *Clarias gariepinus* occurs in a variety of habitats that include rivers, swamps, natural lakes and man-made dams (Bruton 1978; Teugels 1986; Potts et al. 2008). In its natural range, it is an omnivore that feeds on fish, invertebrates, plant material, plankton, reptiles, and amphibians (Munro 1967; Bruton 1979a; Merron 1993; Winemiller and Kelso-Winemiller 1996; Yağın et al. 2001). The catfish is nonetheless regarded primarily as a piscivore

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that augments its diet with a wide range of prey items (Groenewald 1964; Willoughby and Tweddle 1978; Spataru et al. 1987). Its capacity for an amphibious lifestyle, due to its possession of an arborescent organ, makes it a hardy species that can access, and utilise, a variety of habitats (Cambray 2003a).

Several introductions of *C. gariepinus* out of its natural range have been reported and it is now established in Brazil, India and China (Cambray 2005; Vitule et al. 2006; Bhakta and Bandyopadhyay 2007; Khan and Panikkar 2009; Radhakrishnan et al. 2011). The impacts associated with the catfish in regions where it is introduced are related to its predatory nature (Vitule et al. 2008), its potential to compete with indigenous predators and potentially alter food webs (Khan and Panikkar 2009), and the risk of introgression with indigenous catfishes (Senanan et al. 2004; Peh 2010). In the Eastern Cape Province, South Africa, *C. gariepinus* was translocated from the Orange River into the Great Fish and Sundays Rivers through the Orange-Fish inter basin water transfer (IBWT) scheme in 1976 (Cambray and Jubb 1977; Laurenson and Hocutt 1986). There are also other populations in many rivers and dams in the Eastern Cape Province through angler introductions. The Eastern Cape region is characterised by a depauperate and mostly endemic ichthyofauna and there is concern over the spread and the potential negative impact of the catfish in the region (de Moor and Bruton 1988; Potts et al. 2008). The endemic minnows of the region such as the endangered Eastern Cape Rocky, *Sandelia biansii*, in Tyume River and the redbfin minnow, *Pseudobarbus asper*, in Gamtoos River occur mostly in marginal upstream habitats and rely on main channel pools for refuge in these intermittent rivers. These minnows have however disappeared or reduced in abundance following the spread and establishment of the catfish within the refuge pools (Cambray 2003a). There is recent concern about potential catfish impacts on populations of the goldie barb, *Barbus pallidus*, and the endangered Eastern Cape redbfin minnow, *Pseudobarbus afer*, due to its presence in the headwaters of the Sundays River where periodic invasions have been reported. The invasive impact on indigenous biota by the catfish in the mainstream sections of most Eastern Cape rivers may also be exacerbated by the alteration of flow regimes by the IBWT schemes. Alteration of abiotic conditions,

especially flow regimes, has been reported as a factor that contributes to the successful establishment of non-native invasive species while reducing the biotic resistance of indigenous fauna as they adjust to the new conditions (Baltz and Moyle 1993).

Cambray (2003a) highlighted the need for research and monitoring of catfish impacts in the region. It is therefore critical to understand its feeding habits. Stomach contents analysis is the traditional and most convenient way of addressing this objective but is problematic as it does not adequately consider spatial and temporal variation when drawing dietary inference (Pinnegar and Polunin 2000), and can underestimate the consumption of highly digestible material (Stapp 2002). Stable isotope analysis, in contrast, provides a relatively long-term and temporally integrated measurement of feeding relationships and diet preferences because it is less influenced by temporal bias (Vizzini et al. 2002). By using dual isotope tracers, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, the energy sources and trophic positions, respectively, of organisms can be inferred (DeNiro and Epstein 1981; Vander Zanden and Rasmussen 2001; Post 2002). However, differences in isotopic fractionation between the predator and its prey sources may complicate the interpretation of isotopic values (Gannes et al. 1997; Mill et al. 2007). In addition, the lack of species-specific fractionation turnover rates often obscures the inferences drawn from stable isotope analysis. Despite the limitations from either method, when combined, stomach contents and stable isotopes provide a robust and synthetic approach to analysing the trophic impact of invasive species such as *C. gariepinus*. This study examined the feeding habits of *C. gariepinus* in the Great Fish and Sundays Rivers. Stomach contents analysis and stable isotope analysis were compared for dietary composition from three localities—the Great Fish River, Sundays River and Glen Melville Dam. Dietary information provides an understanding of the community-wide impact of *C. gariepinus*. As a generalised predator, resource availability is unlikely to be limiting for catfish within invaded habitats. It was predicted that, at population level, catfish feeds from a wide prey range within the food webs of the invaded habitat. It was then hypothesised that, as an invader, catfish would exhibit non-specialised feeding habits and would show no variation in dietary composition among localities and size classes.

Materials and methods

Study area

The Great Fish and Sundays Rivers are major rivers in the Eastern Cape. The Great Fish River has a longitudinal axis of 650 km and a large catchment of 30,243 km². The Sundays River has a smaller catchment area of 20,792 km². The two rivers flow through an arid region with mean annual precipitation ranging from 350 to 600 mm. Much of the water comes from the Orange River system through the Orange-Fish tunnel into the Great Fish River from which it is diverted, through the Cookhouse tunnel, a secondary IBWT scheme, into the Sundays River. The flow regime within the two rivers was altered by the IBWT from seasonal flow to perennially flowing rivers with little seasonal variation (O'Keeffe and de Moor 1988). The Glen Melville Dam is part of the Great Fish River system from which it receives much of its water through a small, tertiary IBWT tunnel. The dam was constructed in 1992. The climate of the region is warm-temperate. The geology of the two basins comprise of a series of sedimentary strata including sandstones, tillite, marine shales and mudstones (O'Keeffe and de Moor 1988; Hattingh 1997). Conductivity was highest in the Sundays River (range 1,104–3,304 $\mu\text{S cm}^{-1}$) followed by the Great Fish (range 1,058–1,819 $\mu\text{S cm}^{-1}$) and lowest in the Glen Melville Dam (range 631–816 $\mu\text{S cm}^{-1}$). The pH was mostly alkaline and ranged between 8.6 and 9.2 within the Great Fish River, 7.1–8.6 within the Sundays River and 8.5–9.0 within the Glen Melville Dam. Water transparency is generally low in the Great Fish and Glen Melville Dam and ranged from 71 to 780 NTU (Nephelometric Turbidity Units) and 129–257 NTU, respectively, over the study period. The Sundays River, on the other hand, has relatively high water transparency that ranged from 5 to 46 NTU during this study.

Data collection

Sampling was conducted monthly from October 2009 to April 2010 and bimonthly from May 2010 to December 2010. All samples for stable isotope analysis were collected during the summer period from October 2009 to April 2010 in all localities. Samples of catfish and its potential prey were collected at 11 sites from each of the two rivers and three sites

from Glen Melville Dam (Fig. 1). Fish were captured using gill nets and fyke nets in the Great Fish and Sundays Rivers, and longlines in the Glen Melville Dam. A fleet of six multifilament gill nets were used in pools deeper than 1 m at each site. Each gill net measured 30 m and comprised of three 10 m panels of mesh size 50, 75 and 100 mm. Six double-ended fyke nets were used in shallow pools and riffles <1 m deep at each site. Each fyke net had an 8 m guiding net and a first ring diameter of 55 cm with a 10 mm mesh size. Longlines were constructed of polyethylene rope with 1 m nylon snoods and circle hooks. Hooks were baited with chicken livers. The nets and long lines were set from the surface overnight (16–07 h).

Captured fish from the different gears were measured to the nearest 1 mm, sacrificed by pithing and dissected. The stomachs were removed and stored in 10% formalin. In the laboratory, the contents of each stomach were removed and prey were sorted, counted and weighed to the nearest 0.001 g. Prey was identified to the lowest taxon possible.

Samples of muscle tissue were collected from fish for stable isotope analysis. Aquatic invertebrates were sampled using a hand-held scoop net. Epilithic algae were scraped from substrates, while filamentous algae, macrophytes and other visible organic matter were handpicked. Samples for stable isotope analysis were kept in ice in the field.

Stomach contents analysis

Cumulative prey curves (Smale 2005) were constructed to determine whether the number of stomachs sampled was adequate to describe the number of potential prey items in the diet. Dietary composition was assessed using percent by weight and by frequency of occurrence (Hyslop 1980) defined as:

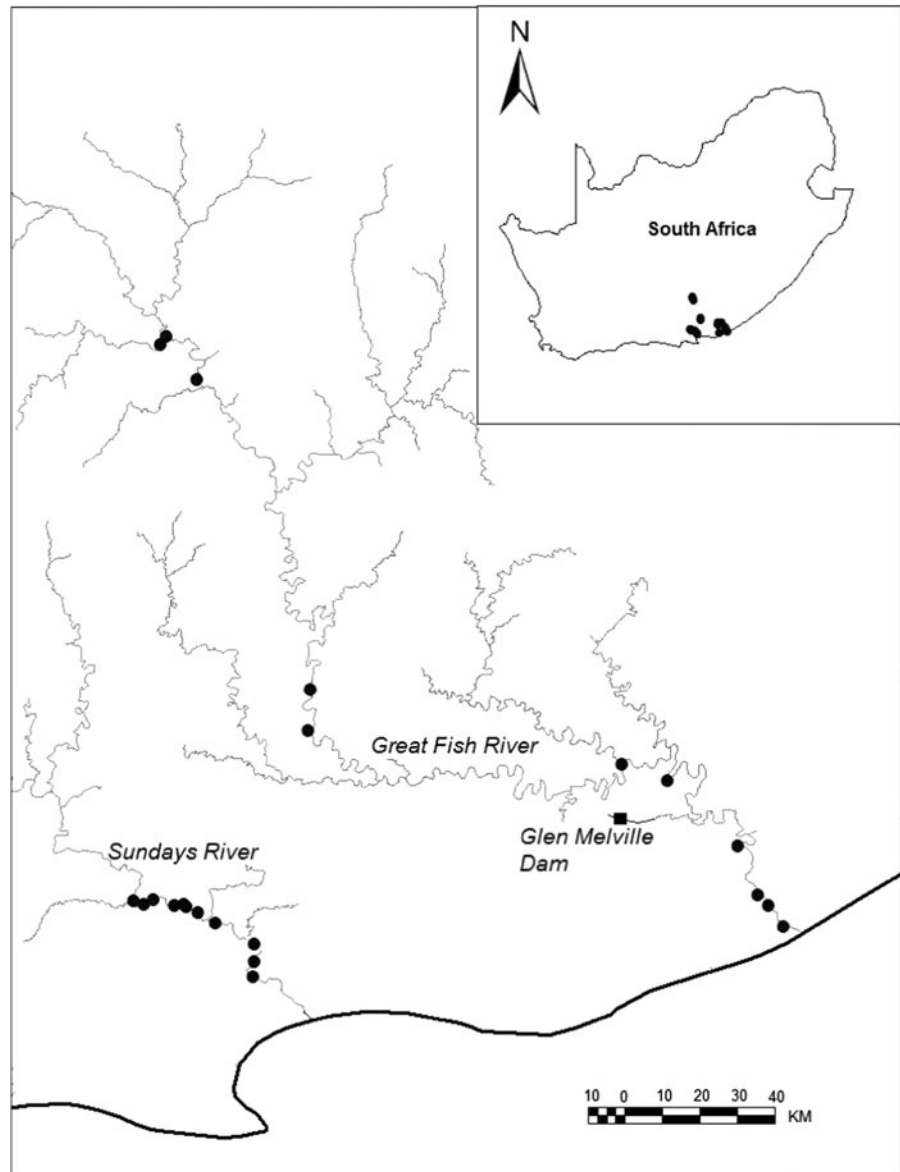
$$\%W_i = \frac{W_i}{\sum_{i=1}^t W_i} \times 100,$$

where % W_i is the percentage weight of prey i , W_i is the total wet weight of prey item i from a total of t prey items, and

$$\%F_i = \frac{F_i}{\sum_{i=1}^t F_i} \times 100,$$

where % F_i is the percentage frequency of occurrence of prey item i , where $F_i = \frac{n_i}{\sum_{i=1}^t n_i}$, where F_i is the

Fig. 1 Map of the study area of the Eastern Cape, South Africa, showing sites of fish collections with the Sundays River, Great Fish River and Glen Melville Dam, South Africa



frequency of item i from the stomachs containing prey item i , and n_i , the total number of stomachs examined.

To facilitate dietary comparison, catfish were categorised into three length classes, which were <25, 25–50 and >50 cm. Prey items from each fish were assessed by modifying the above equations as:

$$\%W_{ij} = \frac{W_{ij}}{\sum_{i=1}^t W_{ij}} \times 100,$$

where $\%W_{ij}$ is the percentage weight of prey i in stomach j , W_{ij} is the wet weight of prey category i in stomach j , and

$$\%F_{ij} = \frac{F_{ij}}{\sum_{i=1}^t F_{ij}} \times 100,$$

where $\%F_{ij}$ is the percentage frequency of prey i in stomach j , and F_{ij} is the frequency of prey category i in stomach j .

Prey items were allocated to diet categories as follows: all fish prey, aquatic invertebrates, terrestrial insects, aquatic macrophytes, filamentous algae and phytoplankton. Prey categories based on $\%W_{ij}$ and $\%F_{ij}$ were analysed using multivariate analysis of variance (MANOVA) to compare localities (L) and

size classes nested within localities [$L(S)$]. MANOVA was followed by linear discriminant analysis (LDA) using a stepwise procedure to determine the most important prey categories responsible for the differences in catfish diets among the different water bodies. The discrimination power among significant variables was compared using Partial Wilks' λ , with smaller values indicating higher discrimination power. Prey data were arcsine transformed prior to the analyses. Box's M test was used to test the homogeneity of variance–covariance matrices while multivariate normality was tested using a multivariate version of Shapiro-Wilks' test.

Schoener's (1970) index of overlap was used to assess the diet similarity between length classes using wet weight. The index was calculated as: $\alpha_{jk} = 1 - 0.5 \sum_{i=1}^t |p_{ij} - p_{ik}|$ where p_{ij} is the proportion of prey item i in length class j , and p_{ik} is the proportion of prey item i in length class k . In this index, α ranges from 0 to 1 that corresponds to zero to complete dietary overlap, respectively. Mantel tests (Bahou et al. 2007) were conducted to test the interspecific overlap between length classes based on the proportion of wet weight of prey items.

Stable isotope analysis

Samples from the field were thawed and dried to a constant weight at 60°C in an oven before being ground into a fine powder. Dry 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. Samples were analysed using a Europa Scientific INTEGRA isotope ratio mass spectrometer at the IsoEnvironmental Lab, Grahamstown. Stable isotope ratios, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were obtained in parts per thousand (‰) relative to Vienna Pee Dee Belemnite and atmospheric nitrogen standards, respectively, according to the formula:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000,$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

Nested MANOVA models, with explanatory variables similar to those used for prey data, were used to compare the differences in catfish isotope values among localities and size classes. The relationship between ontogeny and catfish isotope values was further analysed using linear regressions for both ${}^{13}\text{C}$ and ${}^{15}\text{N}$.

The K-Nearest Neighbour Distance (KNNND) randomisation tests (Rosing et al. 1998; Lubetkin and Simenstad 2004) were conducted to evaluate differences in isotopic composition of the different prey categories. Prey categories that were not significantly different were pooled to reduce trophic redundancy. A Bayesian isotopic mixing model, *SIAR* (Stable Isotope Analysis in R, Parnell et al. 2010), was then used to determine proportional contributions of different prey groups as catfish food sources. The *SIAR* model uses a Markov Chain Monte Carlo simulation using a Dirichlet distribution to produce simulations of plausible values of dietary proportions of sources based on the consumer and potential prey item data. The resulting probability density distributions, with the mean proportion together with the 25, 75 and 95% credibility intervals (the Bayesian analogue of a confidence interval), were used to compare contributions of different source groups. Isotopic fractionation factors were calculated based on Hobson and Welch (1992). The fractionation values for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, were 3.6 and 0.4 in the Great Fish River, 2.7 and 0.6 in the Sundays River and 3.1 and 0.3 in the Glen Melville Dam. Spearman rank correlations were done to test the relationship between the estimated proportions of fish and aquatic invertebrates prey with those prey weight obtained from stomach contents. Spearman correlations were used instead of Pearson correlations because the data did not fit the assumptions of a parametric correlation analysis.

All analyses were conducted in *R* (R Development Core Team 2011). The following libraries were used; *ecodist* for Mantel tests, *mvoutlier* for multivariate outliers, *mvnrmtest* for multivariate normality and *siar v4.1.1* for the isotope mixing model.

Results

A total of 147 stomachs were analysed from which 67 (46%), were empty. The majority of the empty stomachs were of catfish sampled in winter. Of the remaining 80 stomachs, 35, 23 and 22 were from the Great Fish River, Glen Melville Dam and Sundays River respectively. Cumulative prey curves described a general asymptotic relationship for all locations. Therefore, the stomach contents were considered sufficient to describe both trophic diversity and the main prey items of the catfish. Analysis of the stomach

contents revealed total of 32 prey items belonging to five taxonomic groups. These were fish, aquatic invertebrates, terrestrial insects, zooplankton and plant matter (Table 1). Among the taxonomic groups, aquatic invertebrates were the most diverse with 20 families belonging to eight orders. These were Ephemeroptera ($n = 3$), Trichoptera ($n = 2$), Hemiptera ($n = 4$), Odonata ($n = 2$), Diptera ($n = 3$),

Lepidoptera ($n = 1$), Decapoda ($n = 2$) and Mollusca ($n = 3$). Fish were the most abundant diet by weight, contributing 53.8, 43.1 and 37.5% for Great Fish, Sundays River and Glen Melville Dam catfish, respectively. Fish were also the most frequently consumed prey in these three locations. Three indigenous fish species, goldie barb *Barbus pallidus*, Mozambique tilapia *Oreochromis mossambicus* and

Table 1 Dietary composition by percentage weight (% W) and percentage frequency of occurrence (% F) for sharptooth catfish, *Clarias gariepinus*, sampled in the Great Fish, the Sundays River and Glen Melville Dam, South Africa

			Great Fish		Sundays		Glen Melville	
			% W	% F	% W	% F	% W	% F
Fish	Unidentified		53.76	46.15	43.13	23.53	37.49	52.17
	Indigenous	<i>Barbus pallidus</i>	–	–	6.05	2.94	–	–
		<i>Oreochromis mossambicus</i>	5.69	2.56	–	–	–	–
		<i>Labeo umbratus</i>	–	–	–	–	26.26	26.09
	Non-native	<i>Labeobarbus aeneus</i>	6.78	2.56	–	–	4.99	4.35
Aquatic invertebrates	Ephemeroptera	Baetidae	0.46	10.26	0.34	5.88	–	–
		Leptophlebiidae	<0.10	<0.10	–	–	–	–
		Trycorythidae	0.18	2.56	–	–	–	–
	Trichoptera	Hydropsychidae	0.31	17.95	1.13	5.88	–	–
		Sericostomatidae	<0.10	<0.10	0.73	2.94	–	–
	Hemiptera	Belostomatidae	<0.10	2.56	0.23	2.94	<0.10	8.70
		Corixidae	<0.10	5.13	–	–	<0.10	13.04
		Naucoridae	<0.10	2.56	–	–	–	–
		Notonectidae	0.26	5.13	–	–	–	–
	Odonata	Libellulidae	0.17	10.26	0.48	5.88	–	–
		Coenagrionidae	<0.10	5.13	0.48	8.82	–	–
	Diptera	Ceratopogonidae	<0.10	2.56	–	–	–	–
		Chironomidae	<0.10	10.26	<0.10	2.94	<0.10	26.09
		Simuliidae	<0.10	5.13	–	–	–	–
	Lepidoptera	Pyralidae	0.40	7.69	–	–	–	–
	Decapoda	Crab	4.96	12.82	0.39	2.94	–	–
		Atyidae	–	–	<0.10	2.94	–	–
	Mollusca	Ancylidae	<0.10	2.56	–	–	–	–
		Physidae	<0.10	2.56	–	–	–	–
		Corbiculidae	<0.10	12.82	–	–	–	–
Terrestrial insects			5.98	38.46	3.21	11.76	3.74	47.83
Zooplankton			–	–	–	–	<0.10	26.09
Algae			2.59	<0.10	0.70	2.94	4.35	21.74
Phytoplankton			–	–	–	–	9.32	47.83
Macrophytes			14.45	30.76	42.07	20.59	–	–
Detritus			3.43	12.82	1.01	5.88	13.31	43.48
Gravel			0.33	5.13	–	–	0.50	4.35

Dashes (–) = not sampled

moggeel *Labeo umbratus*, and non-indigenous small-mouth yellowfish *Labeobarbus aeneus*, were among the identified fish prey. Among the aquatic invertebrates, crabs were the most abundant diet by weight and occurrence, contributing 4.9 and 12.8% respectively in the Great Fish River (Table 1). By comparison, hydropsychid caddisflies were the most abundant diet by weight and occurrence, contributing 1.1 and 5.9% respectively for catfish in the Sundays River. Aquatic invertebrates were generally less important by weight for catfish diets in Glen Melville Dam. Nevertheless, chironomids and corixids were the most frequently consumed invertebrates in the dam (Table 1). Among the plant matter prey, phytoplankton and algae were more abundant in the diets of Glen Melville Dam catfish. Macrophytes were only abundant in the diet of the Sundays River catfish. Terrestrial insects were consumed from all locations (Table 1).

Comparisons of catfish diets showed significant differences among localities based on both prey weight (MANOVA $F_{12,132} = 3.72$, $P < 0.01$) and occurrence (MANOVA $F_{12,132} = 5.27$, $P < 0.01$) (Table 2). Significant size class differences were

also noted based on prey occurrence (MANOVA $F_{30,266} = 3.72$, $P = 0.01$) but not prey weight. The discrimination among localities was highly significant based on both prey weight (Wilks' $\lambda = 0.57$, $F_{12,142} = 3.83$, $P < 0.01$) and prey occurrence (Wilks' $\lambda = 0.57$, $F_{12,142} = 5.12$, $P < 0.01$). The ordination biplots showed the separation along the first LDA of catfish diets from Glen Melville Dam with those from the rivers (Fig. 2). Based on prey weight, the second LDA axis showed wide variation in the diets of catfish from the Great Fish River compared to those within the Sundays River. Partial Wilks' λ indicates that macrophytes and aquatic invertebrates contributed most to the discrimination among localities (Table 3). Macrophytes were absent within the Glen Melville dam and were therefore not recorded in catfish diets from this locality (Fig. 3). The proportion of aquatic invertebrates in catfish diets were significantly different both among localities based on both prey weight (ANOVA $F_{2,71} = 4.80$, $P = 0.01$) and prey occurrence (ANOVA $F_{2,71} = 3.58$, $P = 0.03$) for the different size classes (nested ANOVA $P < 0.01$) based on both prey weight and occurrence (Table 2). Aquatic invertebrates were the dominant

Table 2 MANOVA and ANOVA results for spatial differences in prey weight and occurrence in sharptooth catfish, *Clarias gariepinus*, diets

MANOVA	Variable	Weight				Occurrence			
		df	Wilks' λ	F	P	df	Wilks' λ	F	P
	L	12,132	0.56	3.72	<0.01	12,132	0.46	5.27	<0.01
	L(S)	30,266	0.57	1.36	0.11	30,266	0.48	1.81	0.01
ANOVA		df	MS	F	P	df	MS	F	P
Fish	L	2,71	0.46	1.28	0.28	2,71	0.09	0.37	0.69
	L(S)	5,71	0.75	2.08	0.08	5,71	0.67	2.79	0.02
Aquatic invertebrates	L	2,71	1.08	4.80	0.01	2,71	0.64	3.58	0.03
	L(S)	5,71	0.90	4.03	<0.01	5,71	0.85	4.78	<0.01
Terrestrial insects	L	2,71	0.19	2.38	0.10	2,71	0.10	1.51	0.23
	L(S)	5,71	0.05	0.61	0.69	5,71	0.07	1.04	0.40
Macrophytes	L	2,71	0.56	2.79	0.07	2,71	0.56	3.22	0.05
	L(S)	5,71	0.19	0.96	0.45	5,71	0.19	1.11	0.36
Phytoplankton	L	2,71	0.25	6.11	<0.01	2,71	0.26	19.54	<0.01
	L(S)	5,71	0.01	0.21	0.96	5,71	0.02	1.32	0.26
Algae	L	2,71	0.01	0.10	0.91	2,71	0.01	0.19	0.82
	L(S)	5,71	0.02	0.45	0.81	5,71	0.01	0.37	0.87

Fish were sampled in the Great Fish, the Sundays River and Glen Melville Dam, South Africa. Results are presented by location, L, and Site within Location, L(S)

prey group for the smaller size catfish (<25 cm) especially within the Sundays River (Fig. 2). In addition, catfish exhibited significant differences in the proportion of phytoplankton among localities based on both weight and occurrence (ANOVA $P < 0.01$), reflecting the differences between the rivers and the Glen Melville Dam (Table 2; Fig. 3).

There was no evidence of differences among the localities in the proportions of fish prey, which was the most abundant dietary item. However, a discernible

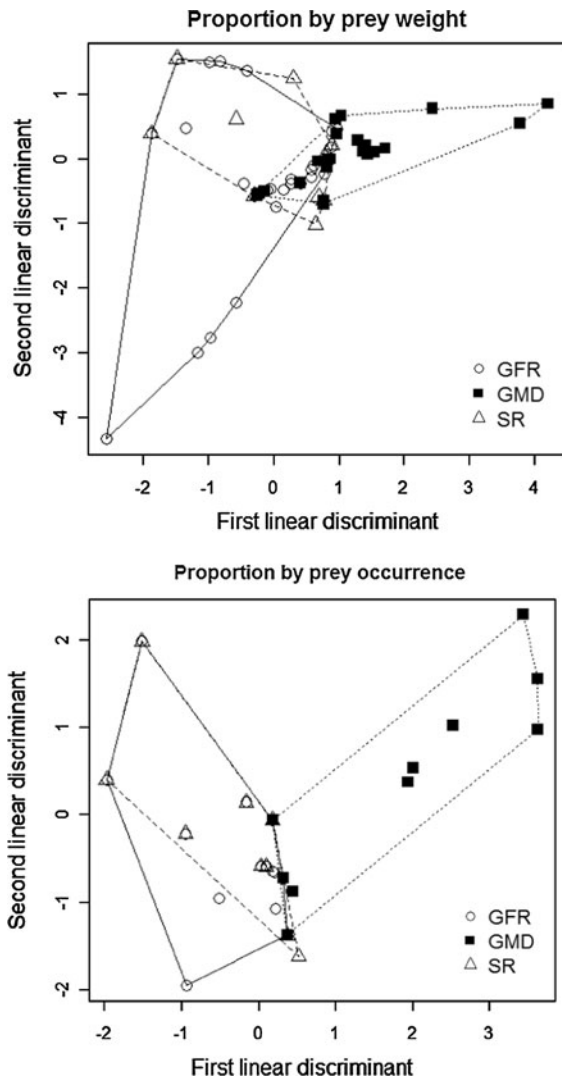


Fig. 2 Linear discriminant analysis plot of diets of sharptooth catfish, *Clarias gariepinus*, based on prey weight and occurrence. Fish were sampled at the Great Fish River (GFR), Sundays River (SR) and Glen Melville Dam (GMD), South Africa. Convex hulls have been included for each sampling locality

increase in the proportion of fish prey with size was observed based on prey weight, which indicated an ontogenetic shift. Despite the observed ontogenetic shift, there were no significant differences among all size classes within the different localities (nested ANOVA $P > 0.05$) (Table 2). This was supported by the analyses dietary overlap using Schoener's index which showed values >0.4 with significant overlap (Mantel tests, $P < 0.05$) for all pairwise comparisons in all localities. Significant ontogenetic differences were nonetheless noted for the catfish size classes based on prey occurrence (nested ANOVA $F_{5,72} = 2.79$, $P = 0.02$).

Of the 21 fish species collected during this study, seven species were non-native and constituted 33% of the total richness (Table 4). Within the Great Fish River and Sundays River, the anguillid eel, *Anguilla marmorata* and the Cape moony *Monodactylus falciformis*, respectively, were the most enriched native fish species in $\delta^{15}\text{N}$ with values of $18.4\text{‰} \pm 0.4$ and $22.4\text{‰} \pm 1.8$. The $\delta^{15}\text{N}$ varied widely for the native fish species within the Great Fish River (range $13.9\text{--}18.4\text{‰}$) compared to those within the Sundays River (range $15.6\text{--}19.7\text{‰}$). Similarly, non-native fish species exhibited a wide range in $\delta^{15}\text{N}$ within the Great Fish River where they varied by 2.7‰ compared to those within the Sundays River that varied by 2.3‰ . By contrast, $\delta^{13}\text{C}$ for indigenous species varied widely within the Sundays River (range -34.0 to -23.3‰) compared to those within the Great Fish River (range -31.7 to -23.1‰). The $\delta^{13}\text{C}$ for non-native fish nonetheless varied widely within the Great Fish River than the Sundays River. Within the Glen Melville Dam, only one indigenous fish species *Labeo umbratus* was collected. *Labeo umbratus* was depleted in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ compared to the non-native fish species within the dam (Table 4). Among the non-fish prey collected within the study localities were the aquatic invertebrates that were more depleted in $\delta^{13}\text{C}$ but more enriched in $\delta^{15}\text{N}$ in the Sundays River compared to the other locations. Algae were more enriched in $\delta^{13}\text{C}$ and more depleted in $\delta^{15}\text{N}$ in the Glen Melville Dam compared to other locations (Fig. 4).

The stable isotope values of the catfish showed variation among size classes, with the large catfish (>50 cm) being more enriched in $\delta^{15}\text{N}$ in all localities (Fig. 4). This observation was supported by a significant positive linear relationship for $\delta^{15}\text{N}$ and total length in all localities (Fig. 5). This indicates

Table 3 Significance of prey categories in stepwise linear discriminant analysis based on proportion by weight and occurrence sharp-tooth catfish, *Clarias gariepinus*, diets

Prey category	Weight				Occurrence			
	Wilks' λ	Partial Wilks' λ	F	P	Wilks' λ	Partial Wilks' λ	F	P
Algae	0.62	0.92	3.21	0.05	0.52	0.95	2.03	0.14
Aquatic invertebrates	0.71	0.80	8.85	<0.01	0.59	0.83	7.46	<0.01
Fish	0.66	0.86	5.65	0.01	0.56	0.86	5.62	0.01
Macrophytes	0.73	0.79	9.62	<0.01	0.60	0.81	8.26	<0.01
Phytoplankton	0.57	1.00	0.01	0.99	0.53	0.92	3.29	0.04
Terrestrial insects	0.69	0.82	7.55	<0.01	0.52	0.94	2.22	0.12

Fish were sampled in the Great Fish, the Sundays River and Glen Melville Dam, South Africa

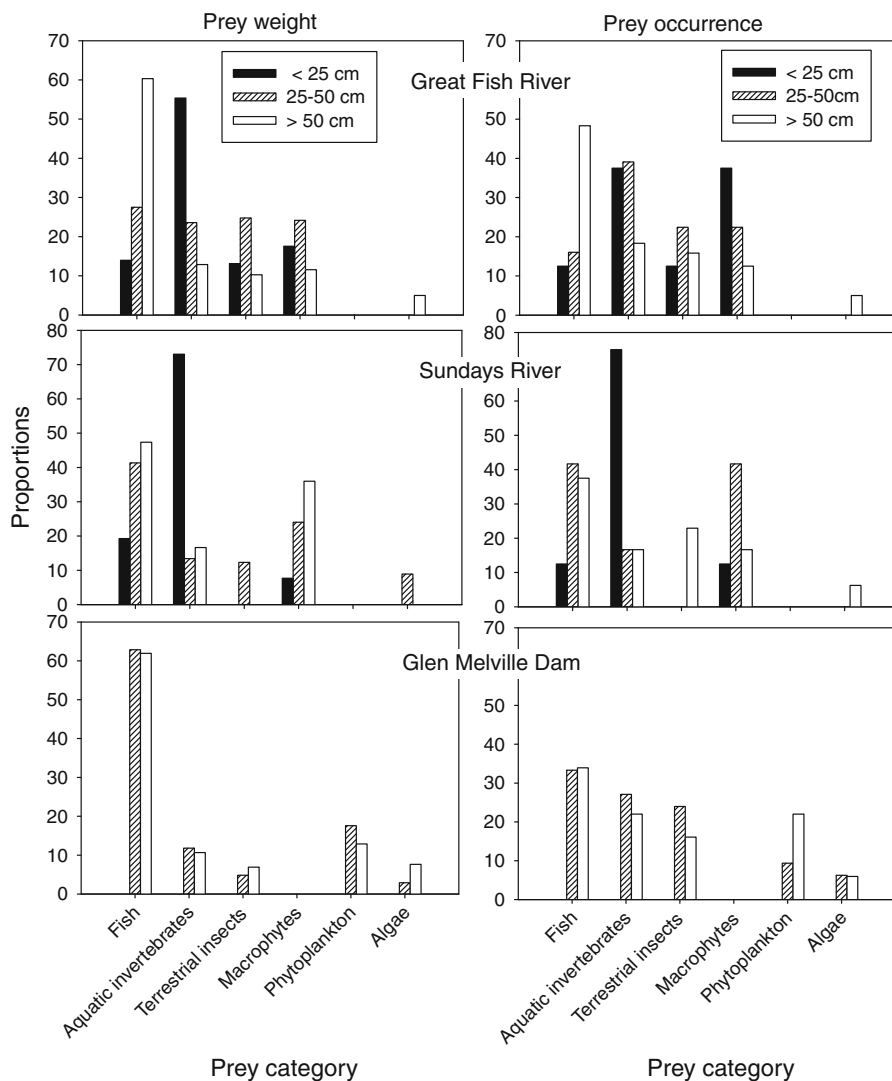


Fig. 3 Diet comparisons among locations and size classes for sharp-tooth catfish, *Clarias gariepinus*, sampled at the Great Fish River, Sundays River and Glen Melville Dam, South Africa

Table 4 Carbon and nitrogen stable isotope values for fish collected in the Great Fish River, Sundays River and Glen Melville Dam, South Africa

Species	Great Fish River		Sundays River		Glen Melville Dam	
	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$
<i>Anguilla marmorata</i>	-23.4 ± 0.3	18.4 ± 0.4	-23.2 ± 0.0	18.7 ± 0.0	–	–
<i>Anguilla mossambica</i>	-25.5 ± 1.4	16.1 ± 2.8	-29.1 ± 1.3	19.5 ± 1.8	–	–
<i>Barbus pallidus</i>	–	–	-28.8 ± 1.1	18.4 ± 0.9	–	–
<i>Clarias gariepinus</i> *	-25.7 ± 2.4	15.9 ± 1.7	-27.5 ± 1.8	18.4 ± 1.9	-26.4 ± 0.4	18.9 ± 0.5
<i>Cyprinus carpio</i> *	-24.4 ± 1.6	15.7 ± 1.5	-30.0 ± 1.4	17.8 ± 1.6	-24.6 ± 0.8	16.7 ± 0.5
<i>Gambusia affinis</i> *	-23.3 ± 0.2	15.2 ± 1.0	–	–	–	–
<i>Gilchristella aestuaria</i>	-30.0 ± 0.5	18.3 ± 0.4	-30.3 ± 0.7	17.7 ± 1.1	–	–
<i>Glossogobius callidus</i>	-27.7 ± 2.3	15.8 ± 1.8	-28.8 ± 1.2	18.4 ± 0.5	–	–
<i>Labeo capensis</i> *	-26.9 ± 0.9	13.2 ± 0.4	–	–	–	–
<i>Labeo umbratus</i>	-28.7 ± 2.0	13.9 ± 2.4	–	–	-24.7 ± 0.8	18.2 ± 0.5
<i>Labeobarbus aeneus</i> *	-25.8 ± 2.0	13.7 ± 1.2	–	–	-26.8 ± 1.2	15.8 ± 1.1
<i>Liza macrolepis</i>	-31.6 ± 0.0	17.9 ± 0.0	–	–	–	–
<i>Monodactylus falciformis</i>	-26.8 ± 3.4	18.2 ± 1.5	-30.6 ± 1.8	19.7 ± 0.9	–	–
<i>Mugil cephalus</i>	-31.7 ± 1.3	16.9 ± 1.4	-34.0 ± 0.0	15.6 ± 0.0	–	–
<i>Myxus capensis</i>	-26.2 ± 3.2	16.7 ± 0.6	-30.1 ± 2.3	18.0 ± 0.9	–	–
<i>Oreochromis mossambicus</i> #	-28.5 ± 0.0	16.8 ± 0.0	-28.3 ± 2.6	16.1 ± 1.2	–	–
<i>Pomadasys commersonii</i>	-23.1 ± 0.0	16.7 ± 0.0	–	–	–	–
<i>Psammogobius knysnaensis</i>	-23.4 ± 0.5	16.6 ± 0.2	–	–	–	–
<i>Redigobius dewaali</i>	-24.6 ± 0.4	16.7 ± 0.3	–	–	–	–
<i>Rhabdosargus holubi</i>	-23.8 ± 2.0	17.2 ± 1.0	-28.9 ± 0.0	16.1 ± 0.0	–	–
<i>Tilapia sparrmanii</i> *	-27.8 ± 1.3	15.0 ± 0.9	-29.3 ± 1.1	16.3 ± 1.5	–	–

* Non-native fish in all localities

Non-native within the Sundays River

ontogenetic differences within the food web with large catfish occupying higher trophic levels whereas the medium and small catfish appeared to feed lower in the food chain. By contrast, catfish exhibited a significant negative relationship between $\delta^{13}\text{C}$ and total length indicating that large catfish were depleted in $\delta^{13}\text{C}$ compared to small catfish. An exception was for Sundays River catfish that did not exhibit a linear relationship between $\delta^{13}\text{C}$ and total length. Catfish, however, exhibited significant differences in the dual stable isotope values (MANOVA $F_{4,120} = 13.7$, $P < 0.001$) among localities. There was also evidence of size class differences in the dual isotope values (nested MANOVA $F_{12,120} = 4.6$, $P < 0.001$) within the different localities.

The KNND randomisation tests showed that the broad prey categories were statistically different. An exception was for the basal food sources of algae, macrophytes, CPOM and phytoplankton, and these

sources were pooled as plant matter for analysis in SIAR. The SIAR mixing models indicate that the catfish diets were diverse among all size classes (Fig. 6). In contrast to stomach content analysis, the SIAR model showed no clear dominance of particular prey items. However, the SIAR estimates showed a discernible increase in indigenous fish prey and decrease in aquatic invertebrates prey with increasing catfish size, partially corroborating with those observed from stomach content analysis. In particular, small catfish appeared to have high estimates of aquatic invertebrates whereas big catfish had high estimates of fish prey in all localities. Spearman's rank correlations nonetheless showed no significant relationship ($P > 0.05$) between prey proportions of fish and aquatic invertebrates from the SIAR model and those obtained using stomach contents analysis. This indicates that although the two methods were complementary the overall patterns in the estimates of prey

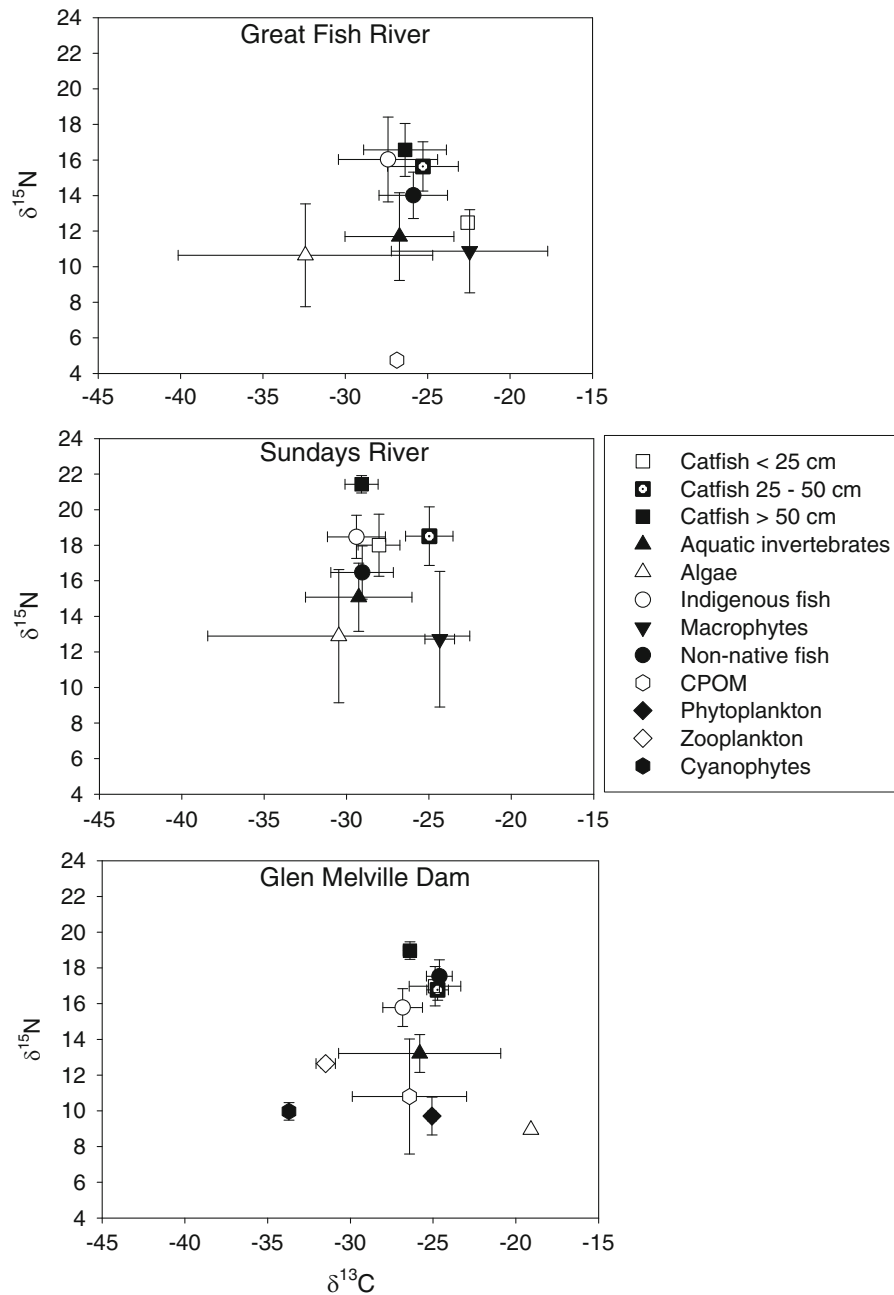


Fig. 4 Stable isotope biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean $\text{‰} \pm$ standard deviation) for the different size classes of sharptooth catfish *Clarias gariepinus* and its consumed food

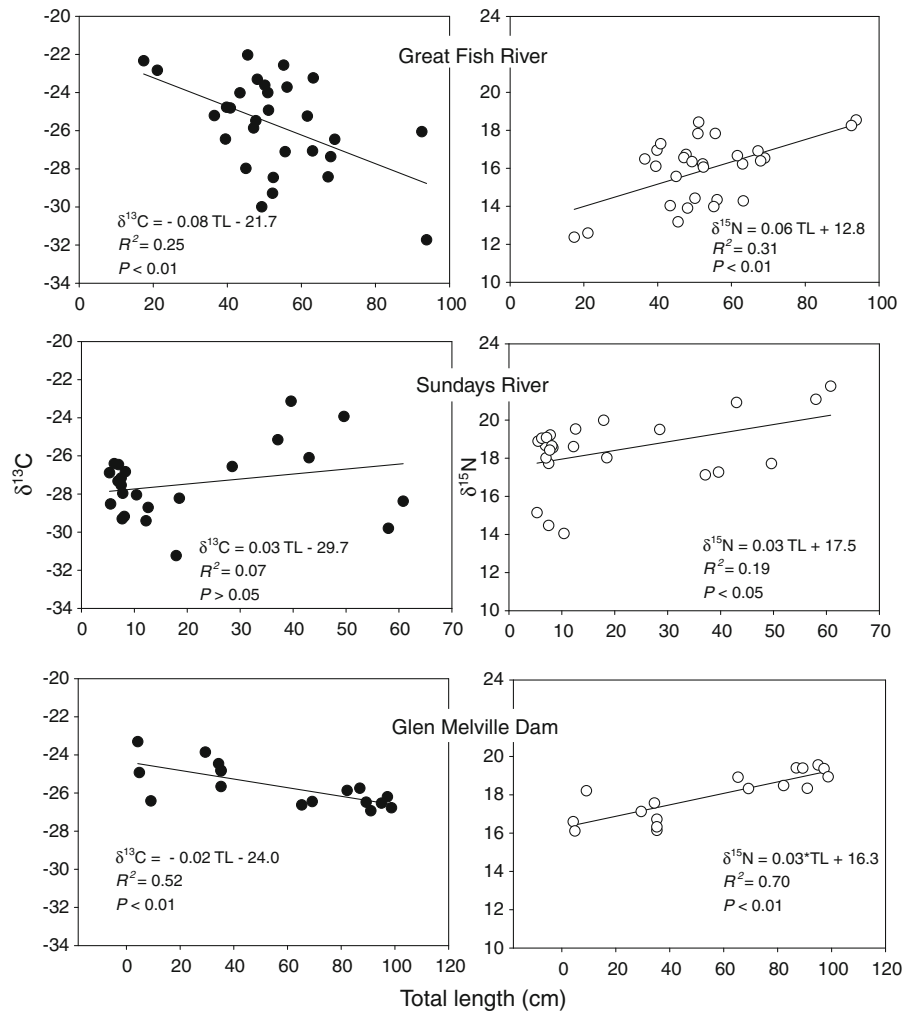
items. Samples were collected from the Great Fish River, Sundays River and Glen Melville Dam, South Africa

contributions were different. Estimates of basal food sources appeared to be high for small (<25 cm) and medium size catfish (25–50 cm) compared to large catfish (>50 cm).

Discussion

Understanding the predation impact associated with generalised predators such as *Clarias gariepinus* is a

Fig. 5 The relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ against total length for sharptooth catfish, *Clarias gariepinus*, sampled from the Great Fish River, Sundays River and Glen Melville Dam, South Africa



crucial step towards the assessment of the risks associated with their introductions. Freshwater ecosystems are considered biogeographic islands with specific species pools and limited dispersion from adjacent systems (Oberdorff et al. 1997; Leprieur et al. 2009). As such, freshwater ecosystems, especially rivers, are considered unsaturated with species and more likely to be invaded because their ecological space is less densely packed and characterised by low interspecific competition (Leprieur et al. 2009). Therefore, the establishment of invasive predators in many freshwater ecosystems has the potential of accelerating the risk of species loss and local extinctions (Chapman et al. 1996; Leprieur et al. 2006). Invasion risk and species loss is likely to be high in developing and species rich countries where research is still lagging and impacts often go unnoticed

(Vitule et al. 2009). This study showed that fish formed the bulk of the catfish prey, which suggests the potential of a predation impact. The concern for such an impact is because the study systems are characterised by mostly endemic and species poor ichthyofauna. Among the fish prey were three indigenous species, goldie barb *Barbus pallidus* in the Sundays River, Mozambique tilapia *Oreochromis mossambicus* in the Great Fish River, and moggel *Labeo umbratus* from Glen Melville Dam. Goldie barb, which has a restricted distribution in most Eastern Cape rivers, including the Sundays, is reported to be threatened by the presence of catfish (de Moor and Bruton 1988; Skelton 2001). While the conservation status of the two other identified fish prey species is considered to be in the category of least concern, these species may be subjected to high predation pressure in

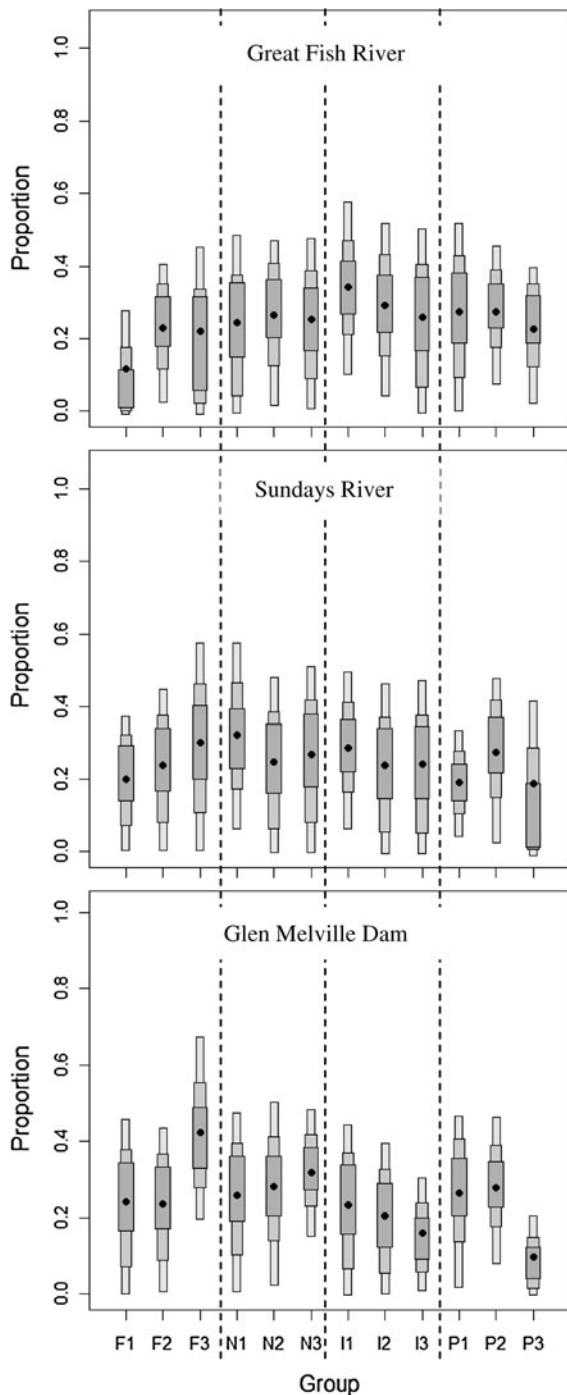


Fig. 6 Estimated percentage contributions (mean and 95% credibility intervals) of prey consumed by sharp-toothed catfish, *Clarias gariepinus*, derived from stable isotopes using SIAR from the Great Fish River, Sundays River and Glen Melville Dam, South Africa. Prey groups are abbreviated as *F* indigenous fish, *N* non-native fish, *I* aquatic invertebrates and *P* plant matter. Catfish size classes are given as 1 = <25 cm, 2 = 25–50 cm and 3 = >50 cm

less structured habitats where the catfish grow to bigger sizes such as in dams and wider and deeper riverine habitats especially of the Great Fish River. In Glen Melville Dam, Booth et al. (2010) reported that large catfish dominate the population and are both highly mobile and aggressive feeders.

Spatially, the catfish diets broadly revealed differences in habitat types (lotic versus lentic) and dietary diversity (Great Fish River versus Sundays River). These differences were related to the dominance of certain prey, especially the macrophytes that were only abundant within the rivers, the aquatic invertebrates, such as crabs that formed the bulk of catfish diets, and other prey including fish that appeared to be more diverse in the Great Fish River compared to other localities. In many rivers of the Eastern Cape, the indigenous crab, *Potamonautes perlatus*, is considered threatened from predation by the catfish (de Moor and Bruton 1988). In comparison to stomach content analysis, stable isotope analysis suggests a more generalised feeding pattern, with no clear dominance of particular prey type, neither for particular habitat nor for size class. Stable isotope analysis further revealed that large catfish were top predators in all localities whereas smaller catfish occupied lower trophic levels. This suggests that, by utilising food from different trophic groups, the sharp-toothed catfish has a complex role as an invasive species in the aquatic food webs. Omnivory was also evident, based on the SIAR estimates, with all prey groups being observed in the diets of all size classes. Since stable isotope analysis for muscle tissue represents a temporal integration of carbon and nitrogen assimilated from diet (Phillips and Gregg 2003; McCutchan et al. 2003; Grey 2006), the stable isotope analysis suggest that the catfish feeds on a wide range of prey, including those that may be temporarily unavailable, over a long period. In contrast, stomach content analysis provides a “snapshot” of consumed diet depending upon the rate of digestion, with the observed indicating prey items that may be temporarily abundant (Gearing 1991). Furthermore, during this study, assessment of seasonal variation in prey consumption based on stomach content analysis was not feasible as most stomachs were empty in winter. However, the taxonomic resolution of stomach content analysis provided additional information that was not afforded by stable isotope analysis, such as the consumption of terrestrial insects. The two approaches were therefore complimentary in providing information on catfish feeding.

The observations on the catfish's feeding habits were consistent with other studies which show that its diets reflects the most common prey of suitable size in particular habitats (Groenewald 1964; Munro 1967; Bruton 1979b) and even changes in environmental conditions that influence prey availability (Willoughby and Tweddle 1978; Spataru et al. 1987). The catfish's ability to utilise a broad range of prey in different habitats suggests its dietary plasticity, which is considered one of the important character for its success to live in a wide range of habitats including those where forage fish are absent (Groenewald 1964), even in areas where it is introduced (Vitule et al. 2009; Radhakrishnan et al. 2011). In southern Brazil, the catfish has rapidly expanded its range into streams that have suffered habitat degradation where it is reported to prey on the native amphibian, *Leptodactylus ocellatus*, which is well adapted to habitat modification and disturbance (Vitule et al. 2008, 2009). The catfish's ability to feed across all trophic levels may present ecosystem impacts associated with homogenisation of biota. Khan and Panikkar (2009) showed that the non-native catfish exerts a negative predation impact on all fish prey, both indigenous and introduced, resulting in cascading positive impacts on insects and zoobenthos. Such trophic cascading may however be obscured and probably less evident because of the catfish's ability to prey on lower trophic level groups such as insects and zoobenthos. Morphologically, as the catfish grows, both its gape size and number of gill rakes increase, conferring more efficiency to filter feeding (Munro 1967). Therefore the trophic impacts of the catfish may be contrary to those of piscivorous invaders, such as different bass and trout species, that cause significant top-down effects within the invaded communities (Flecker and Townsend 1994; Gratwicke and Marshall 2001; Cambray 2003b; Nystrom and McIntosh 2003; Vander Zanden et al. 2004; Maezono et al. 2005).

In addition to its remarkable dietary plasticity, both stomach content analysis and stable isotope analysis showed an ontogenetic shift towards the preference to fish prey and a general decrease in the dominance of aquatic invertebrates with increasing catfish size. Similar ontogenetic shifts have been observed for the catfish. For instance, Munro (1967) showed the dominance of aquatic invertebrates, especially chironomid larvae and pupae, in juvenile catfish and the dominance of fish prey in large catfish in Lake McIlwaine, Rhodesia (Zimbabwe). Similarly,

Willoughby and Tweddle (1978) found a reduction in the importance of insect larvae in large catfish, as they preferred fish prey. Despite the observed ontogenetic shifts in this study, there was evidence of significant dietary overlap among the different size classes. This suggests that catfish of different size can persist on a wide range of prey. The implication of this overlap also suggests the risk associated with juvenile catfish, which are more likely to occur in shallow and marginal habitats such the intermittent pools and upstream habitats where indigenous minnows occur, and would exert predation pressure including piscivory. The catfish has been found to be piscivorous from a small size of about 16 cm (Willoughby and Tweddle 1978). Presently, there are no physical barriers that limit the dispersal and possible establishment of the catfish into the headwater streams of the Sundays River where the endangered redbfin minnow *Pseudobarbus afer* occurs. There is also a likelihood of invasion into the upper Koonap River, a tributary of the Great Fish River, in habitats with the indigenous chubbyhead minnow *Barbus anoplus*. The catfish already occurs in the lower sections of the Koonap River. Cambray (2003a) reported that the endangered endemic minnows, *Pseudobarbus asper* and *Sandelia bainsii*, have disappeared, presumably due to predation, in pools invaded by juvenile catfish in the Gamtoos and Tyume Rivers, respectively.

Moyle and Light (1996) reported that the alteration of hydrological regimes in the highly seasonal Mediterranean streams in California (USA) facilitated the establishment of non-native fish species. Altering the environmental conditions decreases the strength of biotic interactions among indigenous species, and reduces their populations, ultimately reducing their resistance while increasing the risk of predation and competition by invasive non-native species (Baltz and Moyle 1993; Moyle and Light 1996). A similar pattern can be inferred in the Great Fish and Sundays Rivers where IBWT schemes have altered flow regimes. Prior to the opening of the IBWT schemes, the natural flow was seasonal, with the rivers occurring as series of unconnected pools during the dry season, to which indigenous fauna was adapted (O'Keeffe and de Moor 1988). Presently, these rivers are characterised by perennial flow and low seasonality, with the catfish being widely distributed in these systems. In addition, a number of reservoirs within the study systems where catfish has established, such as the Glen Melville Dam,

may act as sources of the invasion, as has been noted elsewhere (e.g. Havel et al. 2005). Therefore, in addition to its dietary plasticity, the alteration of hydrological regimes in the study systems could potentially have had an influence in enhancing the invasion success of the invasive catfish. The IBWT schemes have also facilitated the translocation of other non-native species that were collected during this study. From an ecosystem perspective, the occurrence of other introduced species within the Great Fish and Sundays River has the potential to create invasion meltdown. Invasion meltdown is a phenomenon in which the joint impact of two or more species would be more severe than that of the single invaders (Simberloff and Von Holle 1999; Simberloff 2011). The meltdown could be associated with non-native species such as common carp, *Cyprinus carpio*, smallmouth yellowfish, *Labeobarbus aeneus* and mudfish, *Labeo capensis*. Common carp is renowned for altering habitats by uprooting macrophytes and disturbing bottom substrate, thereby directly affecting habitats for other species and influencing nutrient cycling (Miller and Crowl 2006). Homogenisation of habitats by common carp may lead to loss of alternative refugia for other species while resuspension of sediments may increase the vulnerability to catfish predation. Smallmouth yellowfish has recently established a breeding population in the Great Fish River (Weyl et al. 2009) whereas mudfish appears to be increasing in abundance. These two species are likely to compete with indigenous moggel *Labeo umbratus*. The invasive cichlids (*Tilapia sparrmanii* and *Oreochromis mossambicus*) are likely to have devastating impact in the lower reaches of the two rivers where they are more abundant.

To conclude, catfish diet reflected spatial differences in prey availability within the study localities. Dietary plasticity and omnivory, which was shown by both stomach content analysis and stable isotope analysis, suggest its remarkable ability to persist and cause negative predation impact within the invaded localities. The alteration of flow regimes by the IBWT schemes has had a probable influence of the invasion success of the catfish while the occurrence of other non-native invasive species posits the potential for invasion meltdown within the Great Fish and Sundays Rivers. There is also concern over the potential establishment of catfish populations within the

headwater streams inhabited by endangered indigenous minnows.

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