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Research Article

The diet of an invasive crayfish, *Cherax quadricarinatus* (Von Martens, 1868), in Lake Kariba, inferred using stomach content and stable isotope analyses

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Abstract

The diet of an invasive crayfish, *Cherax quadricarinatus* (Von Martens 1868), in Lake Kariba, was investigated using stomach content analysis (SCA) and stable isotope analysis (SIA). The frequency of occurrence of macrophytes and detritus ranged between 63.6–97.1% and 20–45.5%, respectively, and the index of relative importance ranked these as the two most important food items across all size classes. Significant differences in the ranking of fish, macroinvertebrates and crayfish were found between size classes 29–37.9, 38–46.9 and 47–55.9 mm. Stomach content analysis showed 16% of crayfish stomachs were empty. Feeding intensity differed significantly between size classes and ranged from 3.46 to 5.21. Stable isotope analysis was done by comparing $\delta^{13}C$, $\delta^{15}N$ and C/N ratios in crayfish muscle and potential dietary items in the lake. Macrophytes were the most dominant food item (57%), followed by macroinvertebrates (20%), then detritus, and finally fish and crayfish. Stable isotope analysis revealed that all crayfish size classes analysed were in the same trophic level. Nevertheless, while SCA showed high dietary overlap among all crayfish size classes (>65%), SIA showed that small crayfish (< 28.9mm) had limited overlap with large crayfish (> 56mm), with the former showing a higher proportion of macroinvertebrates in their diet. In Lake Kariba, *C. quadricarinatus* predominantly feeds on macrophytes, macro-invertebrates and detritus, which may bring about nutrient cycle alterations in the lake. Littoral habitat changes caused by the feeding characteristics of *C. quadricarinatus* might also lead to competition with, and eventual displacement of, some native littoral fishes in this lake.

Key words: detritus, dietary shift, omnivorous, stomach content analysis

Introduction

The deliberate and unintentional introduction of many aquatic invasive species has often led to adverse effects on ecosystems (Lodge et al. 2006). Unintentional introductions of alien species into natural water systems often occur when they escape from water-based production systems (Howard 2004; Padilla and Williams 2004). Invasive aquatic species can threaten biodiversity through predation, competition and possible introduction of new diseases (Barki et al. 2006). Interaction between native and introduced species can also lead to structural and functional changes in ecosystems due to changes in trophic structure (Wong et al. 2003; Edgerton et al. 2007; Sousa et al. 2012). Some invasive species, however, have been reported to have positive effects in environments where they increased biodiversity and supported food webs (Griffith et al. 1994; Davis 2011). In other cases, indigenous species have also offered resistance to known invasive species (Kimbro et al. 2013; Dorn and Hafsadi 2016).

The differing conclusions from past invasion biology studies demonstrates that predicting the impacts of invasive species is not easy without base-line investigations (Dalosto et al. 2015). Past studies have identified native species richness, vacant niches, absence of natural predators/enemies and competitive abilities of resident species (Elton 1958; Herbolt and Moyle 1986; Mack et al. 2000) as key biotic factors that have caused some ecosystems to be vulnerable to invasion. Other studies have identified local climate, nutrient levels and habitat modifications as key physical factors (Moyle and Light 1996; Rejmanek 2000). While an investigation into all possible factors is not always possible, an understanding of the feeding ecology of invasive species can be important in assessing the risk they might pose for indigenous biota and ecosystems (Chucholl 2012).

Stomach content analysis (SCA) is a useful tool in analysing the diet of animals at a given time (Whitmore et al. 2000; Parkyn et al. 2001; Hollows et al. 2002). Differences in digestion rates of food items and their assimilation can, however, give misleading indications of the importance of various dietary items (Hyslop 1980). As such, some studies now couple SCA with stable isotope analysis (Hollows et al. 2002), which is useful in analysing the long term diet of animals by indicating which food items were assimilated after ingestion (Jussila et al. 2015) and can consequently help our understanding of the possible threats posed by invasive species (Bodey et al. 2011). Thus SCA can give an indication of the short term consumption of diet items, while stable isotope analysis (SIA) can give an indication of the assimilation of dietary items (Junger and Planas 1994).

The redclaw crayfish *Cherax quadricarinatus* (Von Martens, 1868) is native to northern Australia and Papua New Guinea (Austin 1996). It is an invasive crayfish species which has established feral populations in several tropical and subtropical countries (Jones 2011). *Cherax quadricarinatus* is able to grow fast under a wide range of water quality conditions and is known to have an omnivorous diet (Holdich 2002; Snovsky and Galil 2011). The species was initially introduced into Zambia from South Africa for aquaculture purposes (Thys van den Audenaerde 1994), from where it escaped into Lake Kariba (Phiri 2009). A study by Nakayama et al. (2010) showed that in 2008 *C. quadricarinatus* was already present in the Bumi Basin of Lake Kariba, and it has since spread to other parts of the lake, such as the Sanyati Basin in Zimbabwe (Marufu et al. 2014).

Introductions of alien crayfish have been associated with decreases in vegetation, detritus, macroinvertebrates and displacement of benthic fish (Feminella and Resh 1989; Guan and Wiles 1997; Sala et al. 2000; Kreps et al. 2015). In terms of feeding ecology, SIA has shown that the invasive crayfish *Orconectes rusticus* caused a change in the trophic structure of some lakes by reducing the abundance of benthic macroinvertebrates and small fishes (Kreps et al. 2015). Another study showed that the crayfish *Procambarus clarkii* has a preference for particular macrophytes in their diet, causing their reduction due to overgrazing (Gherardi and Barbaresi 2007). However, the potential effects of *C. quadricarinatus* are not well understood in tropical Africa owing to limited studies of the species in the wild and the inexistence of freshwater crayfish species native to the continent. Therefore, the potential effects of *C. quadricarinatus* on native biota in Africa should be accorded research priority.

The current study was conducted to provide the first assessment of the diet of the invasive *Cherax quadricarinatus* in the Sanyati Basin of Lake Kariba, Zimbabwe, using a combination of stomach content and stable isotope analyses. Investigating the diet and potential trophic changes caused by an invasive species like *C. quadricarinatus* may help provide evidence for, and give impetus to, conservation of indigenous fauna (Mohanty et al. 2016).

Material and methods

Study area

The study was done on the northern shore of the Sanyati Basin of Lake Kariba, Zimbabwe (Figure 1). Lake Kariba is a man-made lake shared between Zimbabwe and Zambia that was built in 1956 for hydroelectric power generation. It has five basins, namely Mlibizi, Binga, Sengwa, Bumi and Sanyati (Cronberg 1997). The Lake Kariba catchment area is semi-arid with annual mean temperatures, rainfall and evaporation of 26 °C, 766 mm and 1700 mm, respectively. The dominant macrophytes found in the Sanyati Basin include *Eichhornia crassipes, Ceratophyllum demersum*, *Lagarosiphon ilicifolius*, *Ludwigia stolonifera, Najas pectinata*, *Panicum repens, Potamogeton octandrus*, *Potamogeton pectinatus, Pistia stratiotes, Salvinia molesta*, and *Vallisneria aethiopica* (Phiri 2010). Forty five species of fish have been recorded in Lake Kariba (Marshall 2006) and all of them are, at a given time of their life cycle, associated with the littoral zone of the lake (Phiri and Mhlanga 2014). The main fish families found in the lake include Cichlidae, Cyprinadae, Claridae, Characidae, Momyridae and Alestidae (Phiri and Mhlanga 2014).

Crayfish sampling

Crayfish were sampled between July and October 2012 from nine sites along the northern shoreline of

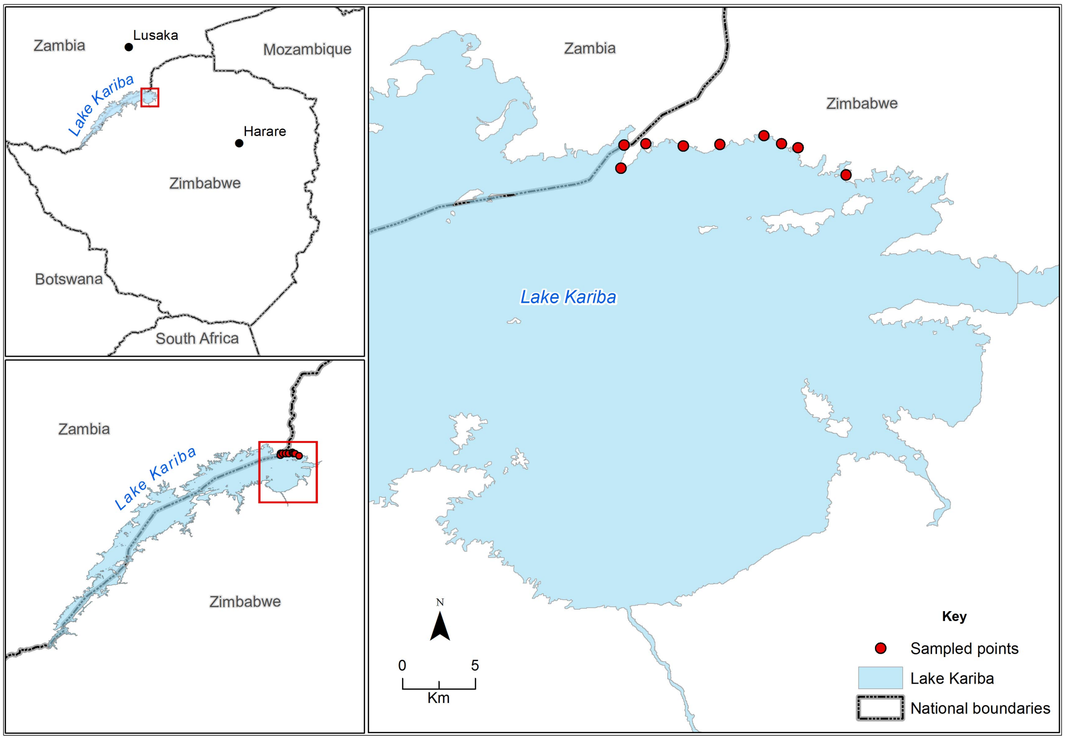

Figure 1. Location of the study sites in the Sanyati Basin of Lake Kariba, Zimbabwe (for details see Supplementary Table S1).

the Sanyati Basin (Figure 1), using opera house trap nets (rectangular frame: 70 × 30 cm, mesh: 3 mm). Five trap nets were laid 10 m apart at each site in the evening and removed the following morning. Crayfish caught were transferred to sampling buckets and immediately transported to the laboratory where they were killed by freezing. Crayfish carapace length and mass were measured and crayfish were sorted into different size classes (< 28.9 mm, 29–37.9 mm, 38–46.9 mm, 47–55.9 mm and > 56 mm).

Stomach content analysis

A total of 161 redclaw crayfish were caught for stomach content analysis (< 28.9 (n = 11), 29–37.9 (n = 30), 38–46.9 (n = 71), 47–55.9 (n = 34) and > 56 mm (n = 15)). The whole and empty stomach wet mass of each crayfish was measured. Stomach contents were identified using a dissection microscope and food particles were divided into different categories: macrophytes, detritus, fish, macroinvertebrates, crayfish and unidentified. The numbers and approximate volume of the various food categories were recorded by emptying the contents into a petri dish and adding 100 ml of water per gram of stomach contents, according to Zengeya and Marshall (2007). Dietary items were identified and separated within the petri dish and, after counting them, their percentage volume was approximated visually.

Gut content analysis used both quantitative and qualitative methods modified from Hynes (1950) and Hyslop (1980). The Frequency of occurrence (Fp) (Hyslop 1980) was calculated as:

$$Fp = Nsj \times (100/NS),$$

where Nsj is the number of stomachs containing prey item j, and NS is the number of stomachs containing food. The Index of relative importance (IRI) (Pinkas et al. 1971), which allows prey items to be ranked according to their importance (Hart et al. 2002), was calculated as:

$$IRI_j = (\%V_j + \%N_j) \times \%Fp_j,$$

where %Vj is the percentage volume of diet item j, %Nj is the percentage number of prey item j and %Fpj is the percentage frequency of occurrence of prey item j. The values were then standardised following Hansson (1998) by presenting the IRI as %IRI. The Gastro-somatic index (GI), which is a measure of feeding intensity, was calculated for each individual in accordance with Baskar et al. (2012), using the formula:

$$GI = SW/W \times 100,$$

where SW indicates stomach weight and W is the total weight of crayfish. The Vacuity index (VI), which is the proportion (%) of the number of empty stomachs relative to the total number of stomachs analysed, was calculated using the formula:

$$VI = (ES \times 100) / TS,$$

where ES is the number of empty stomachs and TS is the number of stomachs analysed. This index gives an estimate of voracity of predatory/omnivorous crayfish. The more voracious the crayfish in question, the lower the percentage of empty stomachs present.

Stable isotope sample collection

Crayfish (n = 44: size class < 28.9 mm, n = 5; 29–37.9 mm, n = 7; 38–46.9 mm, n = 5; 47–55.9 mm, n = 8 and > 56 mm, n = 19) were caught using opera house traps on a separate occasion in April 2014 for SIA. Potential dietary items (n = 3–20) at each site were collected within a 30 m radius from where traps were laid. These included detritus (rotting organic matter at the bottom of the water, e.g. small twigs, leaves), fish (*Oreochromis niloticus*), macroinvertebrates (Notonectidae, *Caridina nilotica*, Chlorolestidae) and macrophytes (*Lagorasiphon major, Pistia stratiotes*, *Eichhornia crassipes, Potamogeton pectinatus*, *Salvinia molesta* and *Vallisneria aethiopica*). A seine net (50 m length, 5 mm mesh size) was used to catch fish, and macroinvertebrates were collected using a nylon hand net (500 µm mesh size, 30 × 30 cm dimension). Macrophytes and detritus were collected by hand at each site. Zooplankton was collected using a zooplankton net (40 cm diameter, 63 µm mesh size). All samples were placed in separate labelled ziplock bags. For stable isotope analysis, crayfish and fish muscle were used.

Stable isotope sample processing

All plant material (macrophytes, detritus), crayfish, fish, zooplankton and macroinvertebrate samples were placed in aluminium foil envelopes and oven dried at 60 °C for 72 hours. The dried samples of macroinvertebrates, crayfish and fish muscle, and plant material were further ground to a fine homogeneous powder using a mortar and pestle. Aliquots of approximately 0.6 to 0.7 mg (animals) and 1.0 to 1.2 mg (plant material) were weighed into tin capsules that were pre-cleaned in toluene.

Stable isotope analysis was carried out using a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (Thermo Fischer, Bremen, Germany), housed at the Stable Isotope Laboratory, University of Pretoria. Merck Gel ($\delta^{13}C$ = −20.57‰, $\delta^{15}N$ = 6.8‰, C% = 43.83, N% = 14.64) standards and blank samples were run after every 12 unknown samples. All results were expressed as parts per thousand (‰) delta values ($\delta^{15}N$ or $\delta^{13}C$) referenced to atmospheric nitrogen for $\delta^{15}N$ (Ehleringer and Rundel 1989) and Vienna Pee-Dee Belemnite for $\delta^{13}C$ (Craig 1957). Average analytical precision was < 0.15‰ for $\delta^{13}C$ and < 0.1‰ for $\delta^{15}N$.

The trophic positions of redclaw crayfish in different size classes were estimated following McCutchan et al. (2003) whereby:

$$\text{Trophic position} = 2 + (^{15}N\ \text{consumer} - {}^{15}N\ \text{zooplankton}) / 3.4$$

where $\delta^{15}N$ consumer is the measured consumer $\delta^{15}N$ for which the trophic position needs to be estimated, $\delta^{15}N$ zooplankton is the average $\delta^{15}N$ of the primary consumer and 3.4 is the trophic fractionation for $\delta^{15}N$ (McCutchan et al. 2003). Level 2 was attributed empirically to zooplankton following Dalu et al. (2016).

Data analysis

Stomach content analysis

The stomach content and indices data followed an ordinal rating so rank correlation coefficients were used to test the null hypothesis of different prey rankings in different crayfish size classes, against the alternative that prey rankings were similar (Martin et al. 1996). The relative % IRI rankings for prey categories were thus compared using Spearman's rank correlation coefficient. A non-parametric Kruskal Wallis test was carried out to test the differences in mean GI of redclaw crayfish in different size classes. All statistical analyses were performed using Systat 12.10 (Systat 2007).

Stable isotope analysis

Crayfish $\delta^{13}C$, $\delta^{15}N$ and C/N ratio values per size class were compared by means of a one-way analysis of variance (ANOVA) using Systat 12.10 (Systat 2007). Pearson correlations were used to determine the relationships among crayfish length, weight, $\delta^{13}C$, and $\delta^{15}N$ in crayfish muscle tissues. A Bayesian mixing model SIAR V4.0 for Stable Isotope Analysis in R (Parnell et al. 2010) was used to assess the proportions of different food sources (fish, macroinvertebrates, macrophytes, zooplankton, crayfish, detritus) on the diet of redclaw crayfish in different size classes. We grouped together some taxa due to similar isotopic values, i.e. macroinvertebrates + zooplankton, and fish + redclaw crayfish.

Table 1. Occurrence of the six categories of food items recorded in the stomachs of *Cherax quadricarinatus* from the Sanyati basin of Lake Kariba. F_p – Frequency of occurrence, IRI – index of relative importance, macroinvert – macroinvertebrates, unident – unidentified.

Size class	Food item					
	Macrophytes	Detritus	Fish	Macroinvert	Crayfish	Unident
< 28.9 mm						
Volume (%)	87.5	12.1	0.0	0.4	0.0	0.0
Fp (%)	90.0	20.0	0.0	10.0	0.0	0.0
IRI	15327	606	0.0	95	0.0	0.0
%IRI	95.60	3.80	0.00	0.60	0.00	0.00
Vacuity index (%)	9.1					
29–37.9 mm						
Volume (%)	69.0	29.7	0.8	0.4	0.0	0.1
Fp (%)	97.1	32.4	11.8	5.9	2.9	0.0
IRI	14331.96	1811.16	121.54	30.68	6.96	0
%IRI	87.91	11.11	0.75	0.19	0.04	0.00
Vacuity index	19.1					
38–46.9 mm						
Volume (%)	61.1	35.9	2.2	0.2	0.0	0.6
Fp (%)	86.8	52.8	7.5	5.7	0.0	7.6
IRI	11961.04	4361.28	66.75	29.64	0	55.48
%IRI	72.60	26.47	0.41	0.18	0.00	0.34
Vacuity index	10.0					
47–55.9 mm						
Volume (%)	62.0	36.4	1.4	0.1	0.0	0.1
Fp (%)	84.6	53.9	11.5	7.7	0.0	3.9
IRI	11065.68	4322.78	124.2	49.28	0	0.39
%IRI	71.11	27.78	0.80	0.32	0.00	0.00
Vacuity index	21.2					
>56 mm						
Volume (%)	57.2	42.8	0.0	0.0	0.0	0.0
Fp (%)	63.6	45.5	0.0	0.0	9.1	0.0
IRI	6608.04	3462.55	0	0	60.97	0
%IRI	65.22	34.18	0.00	0.00	0.60	0.00
Vacuity index	26.7					

Fractionation factors of $\delta^{15}N$ 2.9 ± 0.32 and $\delta^{13}C$ 1.3 ±0.35 were used for fish and crayfish muscle samples, $\delta^{15}N$ 2.1 ± 0.21 and $\delta^{13}C$ 0.3 ± 0.14 for macroinvertebrate and zooplankton samples, and $\delta^{15}N$ 2.3 ± 0.28 and $\delta^{13}C$ 0.4 ± 0.17 for all macrophytes (McCutchan et al. 2003).

The Stable Isotope Bayesian Ellipses in R (SIBER) model in SIAR was used to analyse the isotopic niche breadth and overlap among redclaw crayfish using $\delta^{13}C$ and $\delta^{15}N$ values (Layman et al. 2007). Convex hull areas and ellipses represent the calculated isotopic niche breadths and widths for all individuals, as described by Jackson et al. (2011). The corrected Standard Ellipse Area (SEAc) measures the degree of niche overlap (%), with an absolute limit of 100% indicating complete overlap, which can then be used as a quantitative measure of dietary similarity between populations (see Layman et al. 2007; Jackson et al. 2011). Values > 0.6 indicate ecologically significant dietary overlap and potentially direct resource competition (Parnell et al. 2010).

Results

Stomach content analysis

Macrophytes and detritus occured in the diet of all crayfish size classes, with their frequency of occurrence (Fp) ranging between 63.6–97.1% and 20–45.5%, respectively (Table 1). Cannibalism was detected, with frequencies of occurrence between 0–9.1%. The frequency of occurrence of unidentified food material in the different size classes ranged between 0–7.6%.

The index of relative importance indicated that macrophytes and detritus were the most important crayfish diet items across all size classes (Table 1). There were, however, significant differences in the ranking of diet items, particularly between size class 47–55.9 mm and both classes 29–37.9 mm and 38–46.9 mm (Table 2).

There was a general increase in feeding intensity with increased size of crayfish, although a slight decline was observed in the 38–46.9 mm size class

Table 2. Spearman's Rank correlation results of the % Index of relative importance of the dietary items in the different size classes of *C. quadricarinatus* from Lake Kariba. Area shaded grey highlights *p*-values and bold indicates significant differences at $p < 0.05$.

Size class	< 28.9 mm	29–37.9 mm	38–46.9 mm	47–55.9 mm	> 56 mm
< 28.9 mm	1.00	0.05	0.12	0.05	0.09
29–37.9 mm	0.82	1.00	**0.04**	**0.00**	0.12
38–46.9 mm	0.70	0.83	1.00	**0.00**	0.23
47–55.9 mm	0.82	0.94	0.94	1.00	0.23
> 56 mm	0.74	0.70	0.58	0.58	1.00

Table 3. Gastro-somatic index (GI) (± standard deviation) of different size classes of *Cherax quadricarinatus* in Lake Kariba.

Size class (mm)	Total stomach weight (g)	Mean stomach weight (g)	GI
< 28.9	10.48	0.95±0.42	3.46±1.92
29–37.9	63.61	1.55±0.47	5.14±1.26
38–46.9	143.34	2.38±0.73	4.92±1.14
47–55.9	140.16	4.25±1.19	5.19±1.44
> 56	80.15	5.34±2.26	5.21±1.72

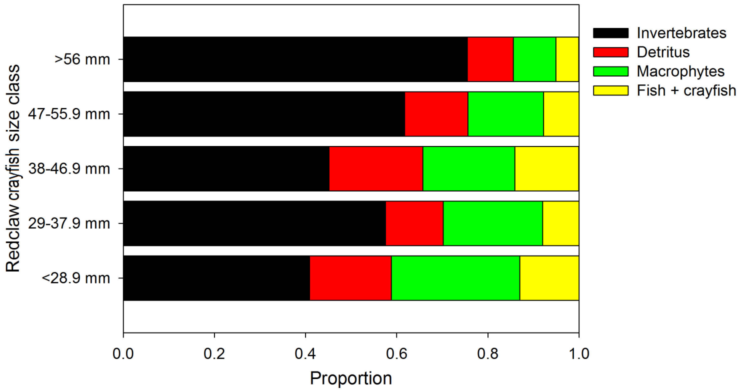

Figure 2. Food source proportions of different size classes of redclaw crayfish in Sanyati Basin, Lake Kariba, revealed by SIAR-model.

(Table 3). Lowest feeding intensity was found in < 28.9 mm size class (GI = 3.46 ± 1.92) and the highest GI values were observed for the > 56 mm size class (GI = 5.21 ± 1.72; Table 3). There were significant differences (H = 12.63, df = 4, $p < 0.05$) in mean GI values of different crayfish size classes. Pairwise comparisons showed that only crayfish < 28.9 mm differed significantly (MannWhitney, $p < 0.05$) from the other size classes.

There were 26 empty stomachs, resulting in a vacuity index (VI) of 16.2%.

Stable isotope composition

SIAR model outputs showed that redclaw crayfish fed mostly on macrophytes (> 57%), followed by macroinvertebrates (~ 20%), across all size classes (Figure 2; Table S2). The contribution of macrophytes generally showed an increase with increasing size, while the rest of the basal food sources decreased with an increase in size class (Figure 2; Table S2).

The $\delta^{15}N$ ($F_{4,38} = 1.884$, $p = 0.133$) and $\delta^{13}C$ ($F_{4,38} = 1.411$, $p = 0.249$) values for redclaw crayfish were found to be similar across different size classes. Nevertheless, in the < 28.9 mm size class, crayfish had the most depleted $\delta^{15}N$ values, with animals in the > 56 mm having the most $\delta^{13}C$ enriched values (Figure 3). No significant correlations ($p > 0.05$) were observed for mass and carapace length *vs* $\delta^{13}C$ and $\delta^{15}N$, with all relationships being positive ($r < 0.25$).

For potential redclaw crayfish food sources, fish were both $\delta^{15}N$ and $\delta^{13}C$ enriched, in comparison to all other food sources (Figure 3). Based on their $\delta^{15}N$ values, basal food sources were distinct from those of consumers (Figure 3).

Trophic positions, isotopic niche breadth and overlaps

The trophic positions of redclaw crayfish highlighted that all size classes fall within the same trophic position level (2.61 to 2.87), with animals in the 29–37.9 mm size class occupying the highest position of 2.87 (Figure 4).

Stomach content analyses dietary overlap was high (> 65%) for all crayfish groups (Table 4). SIBER analysis using convex hull areas and standard ellipses revealed relatively small isotopic niche width among crayfish in the < 28.9 mm, 29–37.9 mm and

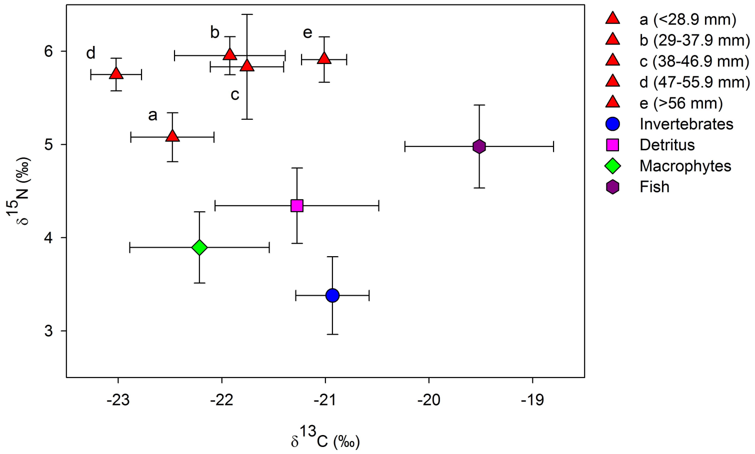

Figure 3. Mean (± standard deviation) $\delta^{13}C$ and $\delta^{15}N$ isotope signatures for redclaw crayfish different size classes and potential food sources in the Sanyati Basin, Lake Kariba. Letters refer to redclaw crayfish different size classes.

Table 4. Niche breadth overlaps for redclaw crayfish different size classes in the Sanyati Basin, Lake Kariba, calculated using stomach content analyses (shaded area) and SIBER analyses (unshaded area).

Size class	< 28.9 mm	29–37.9 mm	38–46.9 mm	47–55.9 mm	> 56 mm
< 28.9 mm	100.0	84.0	74.0	73.0	67.0
29–37.9 mm	17.6	100.0	84.0	84.0	70.0
38–46.9 mm	40.0	85.0	100.0	91.0	66.0
47–55.9 mm	41.1	76.3	75.3	100.0	71.0
> 56 mm	< 0.01	63.8	95.7	72.3	100.0

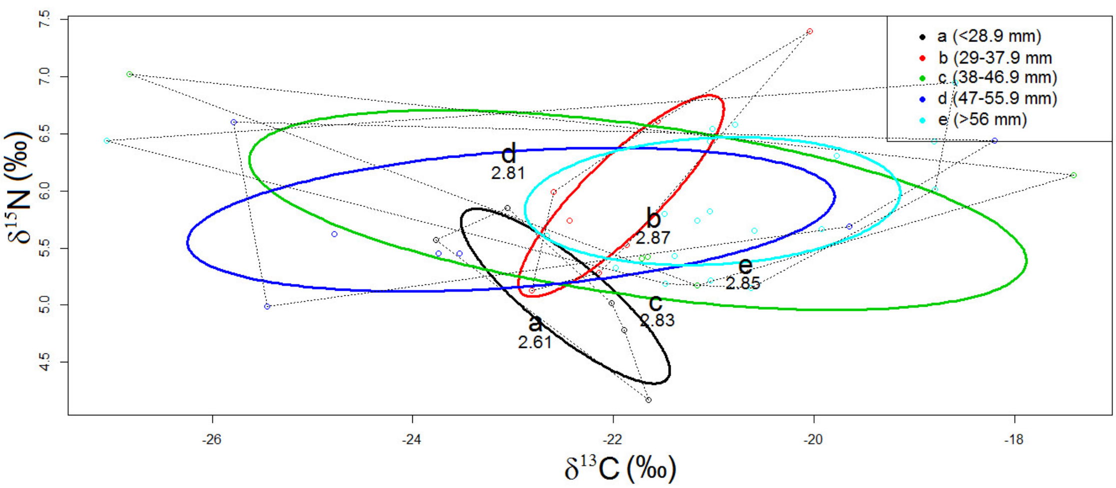

Figure 4. SIBER output $\delta^{13}C$ and $\delta^{15}N$ biplot of redclaw crayfish different size classes in the Sanyati Basin, Lake Kariba. Convex hulls areas (dotted lines) and ellipses (solid lines) represent the calculated isotopic feeding niche breadths and widths, respectively. Numbers represent trophic positions, whereas letters refer to redclaw crayfish size classes.

> 56 mm size classes, whereas large isotopic niche widths were observed for the 38–46.9 mm and 47–55.9 mm crayfish size classes (Figure 4, Table 4). Isotopic niche breadth overlap was high for most size classes comparisons (> 60%), except for the < 28.9 mm class, especially versus the > 56 mm class (Table 4).

Discussion

The main dietary components of redclaw crayfish recorded in the current study were macrophytes, macroinvertebrates and detritus, as revealed by both stable isotope and stomach content analyses. Omnivory was evident in this study, in agreement with studies in other aquatic ecosystems where redclaw crayfish has been classified as a polytrophic facultative omnivore (Holdich 2002; McPhee et al. 2004; Thompson et al. 2006; Saoud et al. 2013). The omnivorous nature of crayfish, as in other crustaceans, plays an important role in nutrient regulation in aquatic ecosystems (Lodge and Hill 1994; Buck et al. 2003).

The abundant macrophytes on the shores of Lake Kariba (Chikwenere et al. 1999; Phiri 2010) may explain why macrophytes and detritus main dietary items of the redclaw crayfish. This has also been observed for other species including *Orconectes rusticus* (Lodge and Lorman 1987), *Procambarus clarkii* (Harper et al. 2002) and *Orconectes limosus* (Vojkovska et al. 2014). Macroinvertebrates are strongly associated with aquatic vegetation in Lake Kariba (Phiri 2010), which may explain them being the second most important dietary item indicated by the stable isotope analysis.

Stomach content analysis identified small crayfish (< 28.9 mm) as the biggest influence on aquatic vegetation, whereas stable isotope analyses revealed that the large sized crayfish (> 56 mm) had a potential higher impact in the medium to long term. These differences might be explained by prey items being temporarily abundant (Gearing 1991): stable isotope analysis denotes a temporal integration of assimilated carbon and nitrogen from diet (Phillips and Gregg 2003), while stomach content analyses provides only a snapshot of the diet consumed. Regardless, this suggests that redclaw crayfish of all sizes are likely to have a significant impact on the abundance of aquatic vegetation in the lake, similar to the rusty crayfish *Orconectes rusticus* in Vilas County, Wisconsin (USA) (Baldridge and Lodge 2014). Other than causing impacts by directly reducing their abundance (Feminella and Resh 1989; Brown et al. 1990; Warner and Green 1995), the high consumption of macrophytes by crayfish might affect nutrient cycling (de Moor 2002), given that both macrophytes and detritus are important stores of nutrients in the shore zone of lakes (Pieczynska 1993).

Body size can influence fundamental biological processes, such as foraging (Preisser and Orrock 2012). As such, differences in body size may explain differences in feeding intensity (GI) between the various size classes found in the current study. Potential predators such as tigerfish (*Hydrocynus vittatus*) and catfish (*Clarias gariepinus*) in Lake Kariba can prey on crayfish (Tyser and Douthwaite 2014; Marufu et al. 2017), possibly inducing smaller crayfish to adopt predator avoidance mechanisms (Presser and Orrock 2012), that in turn cause reduced foraging activity.

Redclaw crayfish was found to be cannibalistic, as reported by both SCA and SIA, and in agreement with other studies (Skurdal and Taugbol 2002; Westman et al. 2002). The percentage of occurrence of crayfish in the diet of the largest individuals (> 56 mm) was similar to the 12% found in the diet of *Cherax destructor* (Faragher 1983), but much higher than the 1% found for *Parastacoides tasmanicus tasmanicus* (Growns and Richardson 1988). Previous studies have suggested that cannibalism in crayfish results from adults feeding on newly hatched young or, alternatively, on recently moulted individuals (Corkum and Cronin 2004). That may explain why cannibalism was mostly found in the largest crayfish size class (> 56 mm) during the current study.

The occurrence of fish in the diet of crayfish has also been reported in other studies (Guan and Wiles 1998; Parkyn et al. 2001). Our findings of fish occurring in 0–12% of the crayfish diet are similar to those of Taylor and Soucek (2010), who found fish to constitute a low proportion (~ 12%) of crayfish diet. This suggests that crayfish probably do not have a direct impact on fish populations by predation. However, crayfish have been shown to displace indigenous fish due to competition for food and shelter (Guan and Wiles 1997). *Cherax quadricarinatus* in Lake Kariba may compete for resources with native herbivorous, insectivorous and detritivorous fishes, which requires further investigation. Crayfish might also affect fish populations in Lake Kariba by reducing macrophytes, which are used as fish spawning ground, and by feeding on the eggs of nest brooding fish, as is implicated by other studies (Dorn and Wojdak 2004; Haertel-Borer et al. 2004).

Crayfish possess chemosensory systems that allow them to move towards a food source and locate the desired items before using their chelae to catch and draw food to the mouth (Giri and Dunham 1999; Moore and Grills 1999). This may explain why mobile prey (fish, crayfish and, to some extent, macroinvertebrates) were found in smaller quantities during the current study (SCA in particular). Preying on fish and crayfish, which are very mobile, requires more energy than capturing macrophytes and detritus, which are easier to handle (Stenroth and Nystrom 2003; Gherardi et al. 2004; Arce et al. 2006).

Differing dietary overlap results were indicated by SCA and SIA. High dietary overlap values for SCA between different size classes are consistent with the findings of Ruokonen et al. (2012), who found no ontogenetic dietary shift in different crayfish sizes. On the other hand, using stable isotopes, we found low isotopic overlap (< 0.01%) between the smallest (< 28.9 mm) and largest (> 56 mm) sized crayfish, suggesting that the two might be feeding on different diets. The results from stable isotope analysis are consistent with other studies that showed that adult crayfish feed mainly on detritus and macrophytes, while juveniles feed more on insects (Lodge and Hill 1994; Nystrom 2002). These differences between SCA and SIA results may be due to the former only taking into account recently ingested food (Hyslop 1980) rather than the degree of assimilation of ingested food (Parkyn et al. 2001). The importance of soft bodied prey is usually underestimated using SCA since they are quickly assimilated (Polito et al. 2011). This may also explain why SIA indicated macroinvertebrates as the second most important dietary item after macrophytes, whereas SCA indicated this to be detritus. Despite these differences, both methods are highly complementary in understanding dietary shifts and trophic relationships (Polito et al. 2011; Davis et al. 2012).

The results from SIA in this study should be interpreted with caution, because possible limitations of our methodology are the assumption of constant fractionation rates and the potential lack of appropriateness of selected baseline organisms. In the future, fractionation factors similar to the ones used by Glon et al. (2016) should be calculated for the redclaw crayfish, using the main dietary food sources, i.e. macrophytes, macroinvertebrates, detritus and fish. Moreover, stable isotope analysis is not very robust if sample sizes are small (Syvaranta et al. 2013), indicating that future studies should also increase sample sizes. Nevertheless, our study provides empirical evidence of the redclaw crayfish diet through provision of potential food contribution and trophic interactions.

Due to its feeding characteristics, *C. quadricarinatus* has the potential to cause littoral habitat changes in Lake Kariba. Management strategies of this invasive species may include the identification and conservation of endemic predators such as tigerfish (Marufu et al. 2017). Local populations in the nearest town to Kariba include crayfish in their diets which may help in controlling future populations once commercial capture is promoted. Commercial fishing permits are now being given for crayfish, but the high operating costs and uncertainty over the actual stocks present in the lake results in few takers. Future studies on the redclaw crayfish in Lake Kariba should include crayfish stock assessments, population dynamic studies, further dietary studies and the identification of endemic predators to crayfish, in order to come up with recommendations on the most effective management strategies for this invader in the lake.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Location of the study sites in the Sanyati Basin of Lake Kariba, Zimbabwe.

Table S2. Results of stable isotope analysis in R of the food source proportions in redclaw crayfish diet.

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2018/Supplements/BIR_2018_Marufu_etal_SupplementaryTables.xlsx