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Stable isotope analyses and demographic responses counter prospects of planktivory by *Caridina* (Decapoda: Atyidae) in Lake Victoria

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Abstract *Caridina nilotica*, a freshwater atyid prawn, is a vital component of the Lake Victoria ecosystem. Despite its important role in the food web leading to Nile perch, the diet of *Caridina* is not well understood. *Caridina* freshly collected from the inshore littoral and offshore plankton of Lake Victoria were cultured individually under laboratory conditions on (A) decomposing hydrophytes, (B) living hydrophytes, (C) planktonic algae, (D) zooplankton and (E) 35-μm filtered lake water (a 'starvation' control). Inter-moult intervals (IMI, days), size-standardized moult intervals (MI, days mm^{-1}), per moult growth increments (PMI, mm) and survivorship (%) were monitored daily for up to 5 weeks. Significant effects of both food type and shrimp source on MI were revealed by ANOVA. MI increased progressively from treatment A to D, and was shorter in offshore than littoral shrimps. Food influence on IMI was confirmed by ANCOVA. PMI values were close to the limits of detection, but were generally in line with MI responses. PMI values were marginal in treatments A and B, and negligible or negative in treatments D and especially E. Survivorship values, although confounded by non-dietary factors, were generally consistent with dietary influences on MI, although values obtained for treatment E were inconsistently high for true starvation. Disparate responses between inshore and offshore shrimps hint at possible ecotypic differentiation, or perhaps the existence of cryptic species. Stable isotope analyses (SIA, $\delta^{13}C$ and $\delta^{15}N$ signatures) of cultured shrimps were further consistent with their utilization of food type A but not D. SIA signatures of feral shrimps maintained in situ in enclosure bags with three separate potential fresh hydrophyte food sources (*Vossia cuspidata*, *Cyperus papyrus,* and *Eichhornia crassipes*) reflected *Caridina*'s probable dietary reliance on decomposed organic matter with accompanying bacterial exudates. Collections of feral shrimps from various locations yielded parallel SIA results. No support for zooplanktivory by shrimps occupying either inshore littoral/benthic or offshore planktonic habitats is provided by the $\delta^{15}N$ signatures obtained from our data, which support *Caridina*'s primary role as a detritivore.

Keywords Detritivory · Trophic role · African Great Lakes · Perturbed ecosystem · Aquatic macroinvertebrate

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Introduction

Recent discoveries of substantial planktonic populations of *Caridina nilotica* (Roux) (Crustacea: Decapoda) in tropical Lake Victoria (Ignatow et al. 1996; Lehman et al. 1996; Mbahinzireki et al. 1998) have elicited proposals that these offshore populations of a shrimp generally regarded as an epibenthic detritivore (Fryer 1960) may function as facultative 'planktivores', 'consumers of living planktonic algae and other suspended particles', 'invertebrate planktivores', or 'zooplanktivores' (Ignatow et al. 1996; Lehman et al. 1996). This prospect is difficult to reconcile with the specialized functional feeding morphology and mechanism observed in *Caridina africana* and *C. nilotica* (Fryer 1960). These small atyid shrimps use brush chelae on pereiopods 1 and 2 to brush and comb fine particles off solid surfaces (lake bottom or submerged hydrophytes); the scrapings and sweepings collected on/by the brush chelae are removed by maxillipeds 1, and transferred to the maxillae, and subsequently ingested. Fryer accordingly described them as "mi-

crophagous chelate raptatory feeders". Prospects of filter feeding on phytoplankton or the raptorial capture of active zooplankton accordingly seem both structurally and functionally implausible in *Caridina.* However, equally unexpected findings have been made for other taxa. For instance the amphipod *Gammarus*, widely if not ubiquitously perceived to feed exclusively as a benthic shredder, was recently discovered to assume the role of a pelagic zooplanktivore at night in Rocky Mountain lakes in Canada (Wilhelm and Schindler 1999). Among purportedly detritivorous freshwater crayfish, the dependence of juveniles on invertebrate prey is increasingly recognized (Momot 1995 and other references in Parkyn et al. 2001). In view of *Caridina*'s unquestionable major significance in the contemporary Lake Victoria ecosystem (Branstrator et al. 1996; Lehman et al. 1996; Mbahinzireki et al. 1998), some assessment of its ability to utilize various diets was explored experimentally. Our objective was accordingly to evaluate the diet of this shrimp in Lake Victoria, and thereby examine prospects of its (zoo)planktivory.

Food ingested by *Caridina* is macerated into totally unrecognizable remains by its gastric mill, precluding direct dietary analysis of stomach contents (Fryer 1960; Lehman et al. 1996; R.C. Hart, personal observations). Dietary evaluation was accordingly assessed from demographic responses (moulting rate, growth, and survival) of shrimps exposed to different types of potential food during experiments extending over a total of 6 weeks. Comparative responses were determined for animals derived from inshore littoral and offshore pelagic stocks. In addition, stable isotope analyses (SIA) were undertaken for both feral and laboratory-held shrimps. SIA is a powerful analytical tool, increasingly used in aquatic ecosystems to identify food sources of particular consumers (Hamilton et al. 1992; Mihuc and Toetz 1994; Kikuchi and Wada 1996; Brandstrator et al. 2000; Grey et al. 2001), and/or to evaluate food web structure or elemental fluxes (Fry and Sherr 1984; Peterson and Fry 1987; Fry 1991; Beaudoin et al. 2001). We determined both $\delta^{13}C$ and $\delta^{15}N$, which respectively reflect food source and trophic level. As $\delta^{13}C$ fractionates only slightly between food and consumer, consumers retain $\delta^{13}C$ values similar to those of their dietary items. In contrast, $\delta^{15}N$ fractionates progressively as food moves between successive consumers; accordingly, the $\delta^{15}N$ value of an organism relates to its trophic level (Peterson and Fry 1987). Ultimately, the isotopic signature of the consumer depends on the isotopic signatures of its food.

Materials and methods

This study focused on *Caridina nilotica* from the Napoleon Gulf region of northern Lake Victoria in Uganda. Dietary experiments were made for 'offshore' shrimps collected in vertical plankton hauls from 60 m depth in pelagic waters near Bugaia Island (00°03.25′S, 33°17.0′E) on 3 November 1998, and for 'inshore' shrimps dip-netted from littoral vegetation at Jinja Pier (00°25.0′N, 33°12.5′E) over the subsequent week. Ten individuals of approximately comparable size (95% CI for orbital carapace length =3.24–3.35 mm, range =2.0–4.6 mm) from each source were cultured under each of five different food treatments (A–E below). Shrimps were maintained individually in 250-ml plastic jars of 35 μm-filtered lake water, replaced completely every 2 or 3 days along with appropriate food freshly collected from the lake in the proximity of Jinja Pier. Food treatments were: (A) Decomposing hydrophyte material, hereafter referred to as benthic floc, with several large fragments per jar; (B) Living hydrophytes, mostly water hyacinth (*Eichhornia crassipes*), with several root masses and small leaves per jar; (C) <153 to >35 μm planktonic algae concentrate added to tinge each jar a faint green colour; (D) >153 μm zooplankton concentrate from roughly 75 l of lake water per jar; (E) 35 μm-filtered lake water, intended as a 'starvation' treatment.

Jars were examined every day for moulted exuviae, which were removed for carapace length (CL, mm) and sex determination wherever possible according to the presence or absence of the appendix masculina on the 2nd pleopod. In the absence of a measuring eyepiece, CL was measured against a finely divided precision ruler at ×10. Absolute inter-moult intervals (IMI, days), per moult change in CL, and percentage survival, were determined from individual moulting schedules recorded over 35 days from a starting population of 100 shrimps. For ANOVA, moult intervals were size-normalized to provide a relative moult interval (MI = IMI/CL, days mm^{-1}). This direct normalization was justified by the observed linear increase in IMI with CL (Hart 2001). The experiment was run in a cool, shady laboratory, subjected to natural thermal and light variations, in which water temperature varied between roughly 25°C and 27°C (see Hart 2001). Statistical analyses were undertaken with Minitab Version 12.1 (ANOVA), and Statistica 5.1 (ANCOVA). For ANCOVA, absolute IMI values for food treatments A–E were compared using size as the covariate, with Tukey's HSD test used for post-hoc multiple comparisons.

Stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) were measured using standard procedures (see Campbell et al. 2003). Values were determined for: (1) sub-samples of shrimps cultured on the different food types A–E listed above and most of these food types (A–D) themselves; (2) shrimps and their food sources held in situ in enclosure bags; and (3) feral shrimps collected from various lake sites. The short-term in situ bag enclosure experiment (2 above) was used to determine (a) the dietary importance to *Caridina* of various potential hydrophyte foods, and (b) any temporal changes in stable isotope values of *Caridina* on exposure to these different food sources. Three types of fresh hydrophyte material were tested: water hyacinth (*E. crassipes*), hippo grass (*Vossia cuspidata*), and papyrus (*Cyperus papyrus*). All were obtained from adjoining stands of these hydrophytes on the shoreline at Jinja Pier. Roughly equal amounts (a handful) of each food type was added separately to two replicate enclosure bags (roughly 0.5 mm mesh aperture and capacity of 1 l) which were sealed after adding 15 live adult or near-adult *Caridina*, concurrently collected near the above-mentioned *V. cuspidata* stand. Bags were submerged approximately 1 m underwater in shade and away from the shoreline near the Jinja Pier and sub-sampled on day 1 (1 December 1998), day 12 and day 19. Enclosure bags were retrieved individually, and sub-samples of *Caridina* and hydrophyte material were quickly removed before re-suspending the bag in situ. Other additional potential food sources sampled included: (a) phytoplankton, collected with a 53 μm plankton net in the water column adjacent to the enclosures; (b) detritus from inside the bag; and (c) 'bag floc'—sedimentary floc settled on and attached to the bag exterior during the incubation period.

Comparative stable isotope values of feral *Caridina* from different sites were also determined, using shrimps collected from: (1) separate stands of *Eichhornia crassipes*; (2) *C. papyrus* stands; and from two open water sites—firstly (3) from the middle of Jinja Bay in proximity to Jinja Pier where the enclosure experiments were run; and (4) from offshore Bugaia. All field samples were collected between October and December in 1998. Shrimps were held in clean water for some hours to allow gut evacuation before drying. Food and shrimp samples were dried in an oven at 60°C. Published stable isotope data for particulate organic matter (Ramlal

2002) and benthic sludge (Talbot and Laerdal 2000) from Lake Victoria were included for comparative purposes.

Results

Demography

Moult frequency

IMI increased directly with CL (Fig. 1; P=0.000, df=22, 230 in one-way ANOVA) across all treatments and records combined. Size-normalization effectively removed this influence, and MI was accordingly used as the response measure for most subsequent analyses. MI was virtually independent of size (Fig. 2; P=0.394), and was significantly influenced only by food type and shrimp origin (Tables 1, 2). MI was also independent of sex (P=0.551), although this may be an artefact of bias introduced by the male predominance (74%) of experimental material. Overall, food effects were highly significant (Table 1), and MI increased progressively from treatments A to E (respectively 1.705, 1.836, 1.908, 1.945 and 2.113, for n=72, 41, 50, 50 and 40). Offshore shrimps were somewhat larger on average than inshore animals

Table 1 General Linear Model ANOVA of factors influencing relative moult interval and survival of *Caridina* under laboratory conditions

	df	*F*	*P*
Moult interval			
Origin	1	20.82	0.000
Food	4	9.71	0.000
Sex	1	0.36	0.551
Food × Origin	4	1.74	0.141
Sex × Origin	1	0.50	0.479
Sex × Food	4	0.29	0.887
Survival			
Origin	1	40.58	0.000
Food	4	19.41	0.000
Food × Origin	4	7.57	0.000

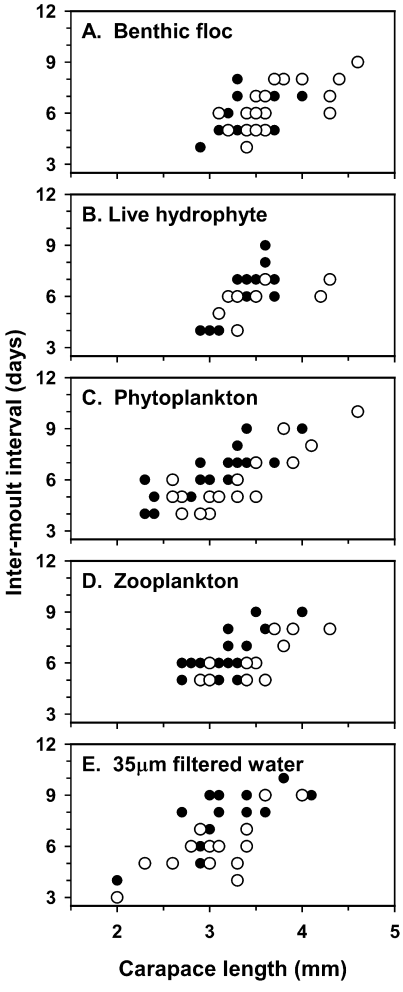

Fig. 1 Inter-moult intervals in relation to shrimp size under different food treatments (**A–E**) for inshore (*filled circles*) and offshore (*clear circles*) shrimps

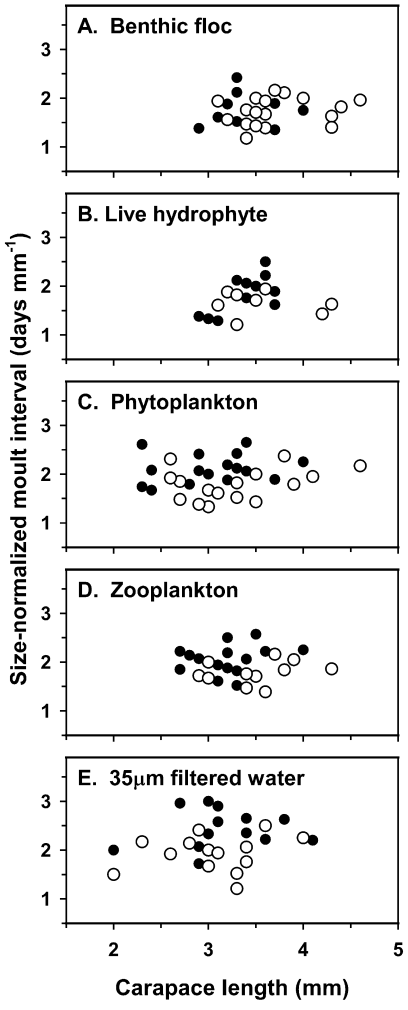

Fig. 2 Size-normalized moult intervals in relation to shrimp size under different food treatments (**A–E**) for inshore (*filled circles*) and offshore (*clear circles*) shrimps

Table 2 Relative moult interval (*MI*) values (days) obtained in laboratory experiments, categorised by food treatment and shrimp origin (In, inshore, Off, offshore)

Treatment	Origin	Mean MI±95% CI	Median MI	*n*
A. Benthic Floc	In	1.73±0.083	1.75	35
A. Benthic Floc	Off	1.68±0.084	1.71	37
B. Hydrophytes	In	1.89±0.099	1.88	30
B. Hydrophytes	Off	1.68±0.141	1.71	11
C. Phytoplankton	In	2.07±0.103	2.06	26
C. Phytoplankton	Off	1.72±0.135	1.67	23
D. Zooplankton	In	2.03±0.092	2.06	31
D. Zooplankton	Off	1.80±0.116	1.84	19
E. Starvation	In	2.31±0.174	2.33	21
E. Starvation	Off	1.89±0.158	1.94	19

Table 3 Analysis of covariance statistics and post hoc multiple comparisons for food effects on moulting intervals

Sample population	*df* Effect, Error	*F*	*P*		
ANCOVA—Summary of effects					
Overall	4, 247	14.136	<0.0000		
Inshore	4, 138	19.224	<0.0000		
Offshore	4, 103	3.021	0.021		
Homogeneity of variance tests					
	Variable	Hartley *F*-max	Cochran *C*	Bartlett χ^2	*P*
Overall	Moult Interval	2.909	0.326	23.110	0.0001
Inshore		3.386	0.321	14.027	0.007
Offshore		3.930	0.329	7.924	0.094
Overall	Carapace length	3.477	0.348	22.256	0.0002
Inshore		5.615	0.394	30.510	<0.0000
Offshore		2.127	0.314	4.532	0.339
Tukey's HSD test					
Overall	A–E				0.017
		C–E			0.021
Inshore	A–E				<0.0000
		B–E			0.001
			C–E		0.0008
				D–E	0.0138

(with 95% CL ranges of 3.29–3.47 vs 3.17–3.29). Despite this, offshore shrimps moulted significantly faster than inshore animals overall (MI =1.75±0.053, *n*=144 vs 1.98±0.054, *n*=109), and this distinction was maintained across all food treatments (Table 2).

The food treatment effect was confirmed by ANCOVA, overall and for inshore and offshore shrimps separately (Table 3). However, post hoc multiple comparisons revealed overall significant differences only between treatments A to E, and A and C. For inshore shrimps, all food treatments differed individually from E, but not from each other, while no significant differences existed for the offshore population (Table 3). Homogeneity of variance was invalidated only in respect of CL for the offshore fraction (Table 3).

Size change—increments and decrements

Most size changes were too slight to quantify adequately. However, apparent trends were consistent with observed patterns in moult frequency (see above): size increases were marginal in treatments A and B, and absent or even slightly negative in treatments D and especially E.

Survivorship

Survival was influenced by food type, shrimp source, and their interaction (Table 1). Over the full duration of the experiment (35 days) overall survival was nearly 40%, but varied from 70% to 10% between treatments. Treatment rankings (A >D >B >C >E) were consistent with those shown in the MI responses, apart from treatment D. Higher overall survival was recorded for inshore than offshore shrimps (48% vs 28%). Survival rates and moulting persistence of shrimps in treatment E were inconsistently high for a genuine starvation treatment.

Stable isotope signatures

The δ^{13}C values of laboratory-held *Caridina* varied between –16.9‰ and –18.9‰, while δ^{15}N varied from 4.4‰ to 7.3 ‰ in all experimental food treatments (Table 4). These laboratory stable isotope values fall within the range of those obtained for feral *Caridina* from Bugaia and Napoleon Gulf (Table 5). The measured substrate values from the laboratory experiment have much lighter δ^{13}C values (–27.6‰ to –27.0‰) than the

Table 4 Average ±SD of stable isotope values (‰) for samples from the laboratory and in situ field enclosure experiments. The number of samples (*n*) indicated for $\delta^{13}C$ values are the same as for $\delta^{15}N$ values. Values for samples ≤2 are shown individually, without standard deviations. Alphabetical prefixes correspond to the laboratory treatments listed in the text and Table 2

Type:	*n*	*Caridina* $\delta^{13}C$	*n*	Substrate $\delta^{13}C$	*Caridina* δ^{15} N	Substrate $\delta^{15}N$
Laboratory experiment						
A. Benthic floc	2	–17.59, –17.37	1	–27.56	4.93, 5.66	1.25
B. Hydrophytes	2	–16.94, –17.69	1	–26.96	5.75, 7.28	1.91
C. Phytoplankton	2	–18.13, –18.92			4.35, 6.50	
D. Zooplankton	2	–17.32, –16.41			5.73, 5.96	
E. Starvation	2	–17.60, –17.57			5.30, 5.46	
Enclosure experiment						
V. cuspidata (day 1)	3	–18.37±0.12	6	–12.93±0.52	3.30±0.21	0.67±0.15
V. cuspidate (day 12)	1	–19.20	2	–12.70, –13.5	4.50	0.29, 0.97
V. cuspidata (day 19)	4	–17.77±0.24	4	–13.23±0.63	4.06±0.19	1.16±1.23
E. crassipes (day 1)	3	–18.70±0.43	3	–26.00±1.53	3.95±0.25	2.10±0.95
E. crassipes (day 12)	2	–18.11, –18.00	4	–26.06±1.34	3.21, 3.57	2.74±1.27
E. crassipes (day 19)	3	–17.80±0.36	4	–25.78±1.50	4.20±0.41	3.09±1.02
C. papyrus (day 1)	3	–20.60±1.44	8	–12.77±1.14	3.32±0.21	–0.17±0.41
C. papyrus (day 12)	2	–18.05, –19.32	6	–12.73±0.54	4.21, 4.89	0.85±0.95
C. papyrus (day 19)	2	–18.36, –18.40	6	–12.86±0.79	4.50, 4.64	1.91±1.07

Table 5 Average ±SD of stable isotope values for samples collected in the field, and the number of samples (*n*) analysed for both $\delta^{13}C$ and $\delta^{15}N$. Subscripts indicate published sources of data. Isotopic signature ranges of the POM samples are also indicated to reflect their wide variability in this food type

Type	*n*	$\delta^{13}C$ (‰)	δ^{15} N (‰)
Organic matter			
Phytoplankton	3	–19.54±0.20	4.3±0.8
'Bag Floc'	2	–19.33 to –18.95	2.7–3.2
Detritus	1	–26.26	5.36
Benthic sludge [a]	5	–20.4±0.42	–0.36±0.59
Nearshore POM [b]	23	–25.2±2.7 (–21.4 to –30.6)	4.5±2.7 (0.8–13)
Offshore POM [b]	30	–26.9±2.7 (–21.4 to –31.4)	7.8±4.2 (1.4–16.3)
Caridina			
Napoleon Gulf [c]	17	–18.77±1.03	4.63±0.82
Jinja Bay [c]	19	–21.37±2.46	3.32±0.93
Bugaia Island	3	–18.47±0.19	6.39±0.12
E. crassipes mat	3	–18.70±0.53	3.95±0.31
V. cuspidata stands	5	–18.19±0.44	3.50±0.50
C. papyrus stands	3	–20.60±1.76	3.32±0.26
Other invertebrates			
Nearshore zooplankton [c]	6	–17.63±0.84	7.18±0.30
Offshore zooplankton [c]	2	–20.39 to –20.64	7.73 to 7.85
Odonata [c]	5	–18.29±0.64	5.70±0.37
Ephemeroptera [c]	5	–18.87±0.19	2.62±0.35

[a] Talbot and Laerdal 2000
[b] Ramlal 2002
[c] Campbell et al. 2003

Caridina (–17.0 to –17.7‰; Table 4), ruling out the laboratory benthic floc and macrophyte foods (treatments A and B) as direct or immediate food sources to *Caridina*, despite the short MI values associated with these foods (Table 2).

During the field enclosure experiments, in which little variation was recorded in environmental parameters (Table 6), $\delta^{13}C$ signatures of *Caridina* (–17.8 to –20.6‰) remained consistently between the $\delta^{13}C$ extremes of the macrophytes (Fig. 3, Table 4), but became progressively heavier with time within each food type. The final *Caridina* $\delta^{13}C$ signatures (–17.8‰ to –18.4‰ on day 19) were comparable between food treatments, and were most similar to the $\delta^{13}C$ signature of benthic sludge, bag floc and phytoplankton (–20.4‰ to –19.3 ‰; Table 5). Mean $\delta^{13}C$ values for 'C-4' *C. papyrus* and *V. cuspidata* hydrophytes (–12.8‰ to –13.0 ‰) were much heavier than those of the 'C-3' *E. crassipes* (–26.0‰ to –25.8‰; Table 4, Fig. 3), in accordance with the different $\delta^{13}C$ signatures of 'C-3' and 'C-4' hydrophytes which derive from their distinct photosynthetic pathways which discriminate against ^{13}C differently (Hecky and Hesslein 1995). The $\delta^{15}N$ signatures of *Caridina* (3.2–4.9‰) did not vary greatly over time within or between hydrophyte foods (Table 4). The corresponding $\delta^{15}N$ values of hydrophyte material ranged more widely between –0.17‰ and 3.1 ‰ (Table 4). Despite some $\delta^{15}N$ enrichment between food and shrimp (3.24, 1.15 and

Table 6 Environmental parameters (means±SD) measured during the in situ enclosure experiments

Parameter	
Maximum depth (m)	1.30±0.20
Chlorophyll-a (μg l^{-1})	7.40±0.67
Temperature (°C)	26.47±0.67
Conductivity (μS cm^{-1})	98.28±0.63
pH	8.07±0.48

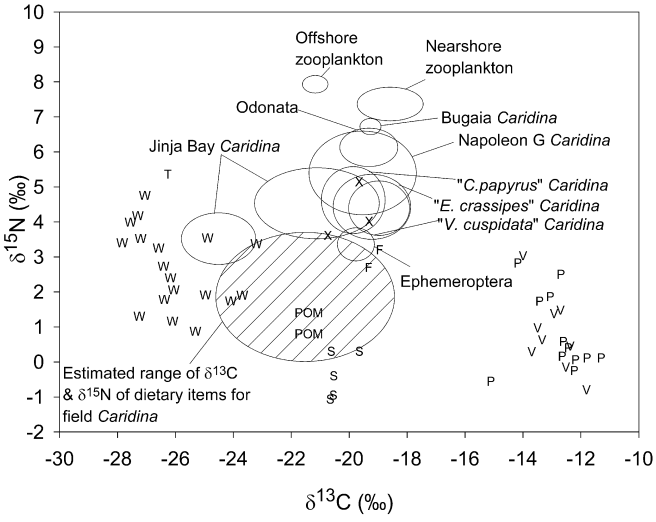

Fig. 3 The relationship between δ^{15}N and δ^{13}C for *Caridina* from the field bag enclosure experiments and field, and for organic matter and other invertebrates. Ranges of δ^{15}N and δ^{13}C values are indicated for different sets of *Caridina* from different field bag enclosures (*Cyperus papyrus*, *Eichhornia crassipes*, and *Vossia cuspidata*) and from different sites in the field. [*Eicchornia crassipes* (*W*), *C. papyrus* (*P*) and *V. cuspidata* (*V*) macrophyte material are indicated along with field phytoplankton (*X*), detritus (*T*) and bag floc (*F*), benthic sludge values (*S*) and the lowest POM δ^{15}N and highest POM δ^{13}C values (*POM*). The *hatched area* indicates the estimated range of stable isotope values of dietary items for field *Caridina*]

3.6‰ on average for *V. cuspidata*, *E. crassipes*, and *C. papyrus*) the wide corresponding disparities between δ^{13}C values of hydrophytes and shrimps clearly preclude these hydrophytes as sole food sources for *Caridina* (Fig. 3).

In contrast to the relatively uniform values reflected in the confined shrimps, signatures measured for feral animals collected from other sites showed wide variations; –18.2‰ to –21.4‰ in δ^{13}C and 3.3–6.4 in δ^{15}N (Table 5, Fig. 3). Zooplankton showed high mean δ^{15}N values (7.2–7.7‰) relative to all other biota, while δ^{15}N values for offshore zooplankton, POM and *Caridina* were higher than corresponding near-shore values (Table 5). Odonata and Ephemeroptera nymphs collected from nearshore macrophytes shared similar δ^{13}C values but differed in δ^{15}N values (5.7‰ vs 2.6‰; Table 5), although their δ^{15}N values bracketed most of the *Caridina* δ^{15}N values (Fig. 3).

Discussion

At the outset of this paper we drew attention to the difficulty of reconciling a filtering or raptorial planktivous feeding modality with the structural morphology of *Caridina*'s feeding appendages, and its functional feeding mechanism (Fryer 1960). The experimental demographic findings reported here generally support the reservations expressed. Moulting frequency, survivorship and growth responses on laboratory diets (A–E) were mostly poorer on planktonic than benthic food types. Consistently best performances were observed with benthic floc, although stable isotope signatures negate it as a direct food source. Living hydrophytes did not yield favourable results, but this may reflect our use of free-floating *E. crassipes* as the experimental food source rather than a more representative indigenous submerged-leaf hydrophyte with its attendant periphyton community. However, significant overall differences existed only between food treatments A and C (floc and algae), and A and E (floc and starvation).

Obviously, none of the laboratory diets was exclusive. Benthic floc often contained epiphytic growth, and bacterial films presumably developed on all container surfaces and organic substrates in the interval between successive food and medium replacements. The unexpectedly high survival rates and moulting persistence of 'starved' shrimps (treatment E) are plausibly attributable to their utilization of such bacterial films.

There are no clear distinctions in δ^{13}C and δ^{15}N values of *Caridina* from the different sites (Fig. 3). Instead, there is a gradual change from higher to lower isotopic values in *Caridina* between Bugaia Island offshore and near-shore animals from Jinja Bay (Fig. 3). Values determined for *Caridina* in the field enclosures (Table 4) were well within the ranges of the feral *Caridina* (Table 5). The estimated range of δ^{13}C and δ^{15}N values for *Caridina*'s dietary items indicated in Fig. 3 were calculated by applying conservative trophic fractionation values of 1.0‰ for δ^{13}C and 3.0‰ for δ^{15}N to the maximum and minimum stable isotope values recorded for *Caridina*. These fractionation values were derived for fish from Lake Victoria (Campbell et al. 2003), for which ranges of between 3.2‰ and 3.8‰ for δ^{15}N and from 0.8‰ to 1.1‰ for δ^{13}C were estimated. The mean isotopic values for POM, bag floc, macrophytes, and zooplankton do not conform to the predicted dietary isotopic values for *Caridina* (Tables 3, 4, Fig. 3). Only some of the δ^{15}N and δ^{13}C values for individual samples of benthic sludge, *E. crassipes*, and floc, and the lowest δ^{15}N and highest δ^{13}C values for POM (Table 5) lie within this region (Fig. 3). Also, the hypothesized region lies between the isotopic values of the C-3 and C-4 hydrophytes, suggesting *Caridina* might consume a mixture of those hydrophytes under some situations. However, the lack of feeding upon water hyacinth leaves in the laboratory and lack of correspondence in isotopic values between the hydrophyte material and *Caridina* in the field mesh bags

indicate that relatively fresh hydrophyte material may not form a part of their preferred diet.

Based on similarities in $\delta^{13}C$ values, the laboratory experiments indicate that phytoplankton and zooplankton are potential food sources for *Caridina*. However, the $\delta^{15}N$ values of zooplankton are higher than that of its postulated consumer, negating this prospect. Were zooplankton to serve as a dietary item for *Caridina*, the shrimp should exhibit a $\delta^{15}N$ value at least 3–5‰ higher than that of zooplankton (Peterson and Fry 1987). In a paper addressing *Caridina*'s low-oxygen tolerance, Brandstrator and Mwebaza-Ndawula (1998) reach a corresponding conclusion, reporting (p 127) on the basis of unspecified $\delta^{15}N$ values obtained for *C. nilotica* from Lake Victoria that "these prawns feed low in the food chain and are not carnivores" (cf. Ignatow et al. 1996; Lehman et al. 1996). The intermediate position of *Caridina* between carnivorous Odonata and herbivorous Ephemeroptera (Fig. 3) further supports this conclusion.

Our experiments also reflect that alternative food items are important for *Caridina*. Firstly, the extended survival of 'starved' *Caridina* (treatment E) points to the likelihood of micro-organisms in their diet—perhaps bacterial films encrusting the container vessels. Secondly, the similarity of $\delta^{13}C$ in *Caridina* subjected to different feeding regimes, both in the laboratory and in the field enclosure experiments, also accords with this possibility. Thirdly, there is no single potential food item that lies within the estimated dietary range of $\delta^{13}C$ and $\delta^{15}N$ for *Caridina*. This indicates that either an important food source for *Caridina* has not been included or that *Caridina* consumes multiple food items in an opportunistic manner, resulting in an "average" isotopic signature which would lie between the isotopic values of the different items. Lastly, our stable nitrogen and carbon isotope values complement the results from the demographic study indicating that benthic sludge (and possibly the accompanying micro-organisms) is a better dietary source, while *Caridina* furthermore may feed upon benthic sludge material and related organic aggregrates "glued" together by bacterial exudates in nature (R.E. Hecky, personal observations). Along with our field and laboratory observations, we interpret our isotope signatures as arising from the indirect consumption of decomposed algal / hydrophyte detritus rather than direct consumption of living algae and hydrophytes.

Caridina in Lake Victoria may well feed on such large organic aggregates as well as decomposing colonial algae in offshore regions. In small aquaria, *Caridina* routinely swims up to 'embrace' and then devour sinking fish-food flakes (R.C. Hart, personal observations). In offshore regions of Lake Victoria, large floc particles are quite abundant and visible in the water column (R.E. Hecky, personal observations), and chelate-feeders could intercept and consume them (as noted above in aquaria). Analogous circumstances exist in Lake Tanganyika where *Caridina* swarms are found well offshore in pelagic situations with hundreds of meters to the nearest benthic surface (R.E. Hecky, personal observations). The seasonal thermocline may effectively provide a density-bounded "virtual" surface on which these flocs can concentrate. High resolution studies of *Caridina*'s vertical distribution could assist in evaluating the prospect of its feeding on this 'surface'. Subsequent disturbance or uplift of this thermocline will introduce these large floc particles into the upper mixed layer, where they may become accessible to pelagic *Caridina*. While *Caridina* does not feed directly on "fresh" POM which usually has very high $\delta^{15}N$ values and low $\delta^{13}C$ values (Table 5), the consistently heavier $\delta^{15}N$ values of POM, zooplankton and *Caridina* from offshore waters (Table 5) indicates a corresponding link between these biota and this organic matter in offshore regions. Decomposed organic matter may have $\delta^{15}N$ and $\delta^{13}C$ values depleted relative to living phytoplankton and suspended particulates (France and Schaepfer 2000). Given the predominance of *Caridina* in the contemporary food web of Lake Victoria, this deserves closer investigation as a potential food source.

Stable isotope turnover due to growth, metabolic requirements and dietary shifts is an important factor in determining final isotopic signatures. Juvenile and larval stage of brown shrimp *Penaeus aztecus* and krill *Euphausia superba*, with high growth rates, have rapid isotopic turnover; turnover in adults is correspondingly slower (Fry and Arnold 1982; Frazer et al. 1997). However, growth rates observed for *Caridina* in Lake Victoria are rapid; moulting intervals range roughly between 2 days for small juveniles and 10 days for relatively large adults; shrimps reach maturity around 45 days after hatching (Hart 2001). The *Caridina* used in the field enclosures were generally large (sub-adult and adult), probably minimizing turnover rates, and resulting in correspondingly slow changes in stable isotope values during in situ enclosure confinements over 19 days. Even so, the mean $\delta^{15}N$ and $\delta^{13}C$ values of all *Caridina* in the enclosures changed over the period of the experiment, with the mean $\delta^{13}C$ value converging around –18.0‰ and the mean $\delta^{15}N$ value increasing by about 0.5‰. Assuming that benthic sludge is a primary dietary source for *Caridina* in the wild, the trophic enrichment appears to be roughly +1.0‰ to + 2.2 ‰ for $\delta^{13}C$ and + 3.7‰ to + 5.0 ‰ for $\delta^{15}N$. This compares well with other laboratory studies that found a difference of –0.9‰ to 1.1‰ for $\delta^{13}C$ in brown shrimp (Fry and Arnold 1982) and a difference of 0.3‰ to 2.0‰ for $\delta^{13}C$ and 0.8‰ to 4.4 ‰ for $\delta^{15}N$ in krill (Frazer et al. 1997).

Ontogenetic changes in diet are well known, as exemplified in transitions from herbivory to carnivory in many cyclopoid copepods (Santer 1993), progressive carnivory in an omnivorous mysid (Branstrator et al. 2000), and converse changes in freshwater crayfishes (Momot 1995; Parkyn et al. 2001). The shrimps used in our experiments were of generally comparable size within and between treatments (see Materials and methods), rendering equivalent ontogenetic switches to carnivory unlikely in the present case. While large berried females comprised 8.7, 10.5 and 11.3% of the post-larval catches in three replicate vertical hauls at Bugaia on 3 November

1998 when the present experimental stock was collected, offshore pelagic populations of *Caridina* in Lake Victoria are more generally dominated by juveniles (Lehman et al. 1996; Mbahinzireki et al. 1998). Accordingly, converse reversals from juvenile carnivory to adult detritivory, as recently recognized among freshwater crayfish (Momot 1995; Parkyn et al. 2001) may be of greater potential significance in *Caridina* in Lake Victoria. But this prospect must be tempered by recognition of surface-scraping as a ubiquitous feeding mechanism among *Caridina* of all sizes (R.C. Hart, personal observations), rather countering prospects of ontogenetic dietary shifts.

The consistent effect of shrimp source on the results (Table 1, Fig. 3) is contextually notable, particularly with regard to ecotypic variation, and perhaps even cryptic speciation. Fryer (1960) noted that "In Lake Victoria, and apparently in other African lakes, *C. nilotica* has given rise to a slender form with attenuated appendages which is misleadingly spoken of as an "open water" form and on which the varietal name *gracilipes* de Man has been bestowed. This appears to be an ecotype from deep water and to be without doubt benthic and not pelagic in habits. Its attenuated appendages are probably correlated with the presence of thick deposits of flocculent mud on the lake floor". The dietary inference of this observation is largely in line with our interpretation of the stable isotope and demographic data presented here. However, morphological variability among atyids is well known. Variability in major attributes of external morphology used in the taxonomic diagnosis of species of Atyidae, measured within a single population of *Paratya australiensis* by Smith and Williams (1980) led them to caution species diagnosis within the group. Although no comparable quantification of intra-specific variation exists for *C. nilotica*, impressions of inter-population variation in this species (R.C. Hart, personal observations) accord with Smith and Williams' interpretations, and lend credence to Fryer's rejection of sub-speciation. Conversely, while no estimates of distribution exist to support Fryer's resolute assertion of *C. nilotica*'s benthic existence in former times, Worthington (1931) reported planktonic shrimps, and Lehman et al. (1996) using underwater video found only 9% and 14% of the *C. nilotica* stock to be benthic by night and day, respectively, in modern Lake Victoria. Equivalent evidence is reported by Mbahinzireki et al. (1998). The apparent contrast between *Caridina*'s putatively former benthic existence (Fryer 1960) and its contemporary pelagic occurrence does accord with the increasing deep-water anoxia experienced in this progressively eutrophic lake (Hecky 1993), which may drive *C. nilotica* into a more planktonic existence in better oxygenated waters. Conversely, though, Branstrator and Mwebaza-Ndawula (1998) report its ability to tolerate low oxygen conditions, suggesting that this tolerance facilitates its deep-water refuge from oxygen-dependent Nile perch predators. Nonetheless, the striking difference reported here between demographic responses of inshore and offshore shrimps might be indicative of a more fundamental distinction—perhaps even the existence of cryptic species. Some re-appraisal of *Caridina nilotica* systematics in Lake Victoria (and elsewhere), perhaps using modern molecular techniques to compare inshore and offshore source stocks appears justified if not mandated.

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