

# Food sources of tropical thalassinidean shrimps: a stable-isotope study

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**ABSTRACT:** Carbon and nitrogen stable isotopes were used to determine the main food sources of the 4 tropical Caribbean thalassinidean shrimps *Glypturus acanthochirus*, *Corallianassa longiventris*, *Axiopsis serratifrons* and *Neocallichirus grandimana*. By using the isotopic signatures of 5 to 6 potential food items, the signatures of the shrimps were modelled to determine feasible combinations of these sources. For *G. acanthochirus*, microalgae mats on the sediment surface, dominated by cyanobacteria and to a lesser degree by diatoms, were the most important food item. *C. longiventris* and *A. serratifrons* (2 isotopically almost identical species which both capture drifting plant debris) relied mainly on the detrital leaves of the dominant seagrasses *Thalassia testudinum* and *Syringodium filiforme* (and also on drifting brown algae). The wall lining of *C. longiventris*' burrows also had some relevance as a dietary source. The diet of *N. grandimana* was less clear: no combination of potential food sources sampled could model this shrimp's isotopic signature. For this species, the smallest organic particles in the ambient sediment around the burrows, together with the burrow wall lining, may serve as a nitrogen source; the main carbon source of this species remains unknown. For the 3 species with conclusive diets, the low organic content of tropical littoral sediments may help explain their predominant reliance on more nutritious food sources foraged from the sediment surface. With regard to nutrition, the subsurface areas of the burrows function only as places where food is processed rather than acquired.

**KEY WORDS:** Burrowing mud shrimp nutrition · Callianassid · *Glypturus acanthochirus* · *Corallianassa longiventris* · *Axiopsis serratifrons* · *Neocallichirus grandimana* · Isosource · Mixing model

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## INTRODUCTION

Thalassinidean shrimps are a globally distributed group of 2 to 20 cm long decapods (Dworschak 2000) living in various types of marine sediments in which they construct extensive permanent burrows which they never leave. The shrimps may reach high population densities of up to several hundreds m<sup>-2</sup> (Dumbauld et al. 1996, McPhee & Skilleter 2002), and can exert significant influence on their biotope due to constant reworking and resuspension of the sediment (Branch & Pringle 1987, Berkenbusch & Rowden 2003). Their burrowing habits are related to feeding, shelter and reproductive behaviour (Atkinson & Taylor 1988). Within the

thalassinidean shrimps, different feeding groups exist. Architectural features of the burrows together with behavioural and morphological traits of the shrimps have been used to assign the species to 1 of the 3 general trophic modes, suspension feeding, deposit feeding and scavenging (Nickell & Atkinson 1995).

Identifying the major sources of nutrition for such dominant consumers is crucial to our understanding of nutrient cycling processes in sediment ecosystems. Gut-content analyses usually fail to provide this information because the ingested material is mixed with very fine sediment and triturated beyond identification by the crustacean gastric mill (Evans et al. 1990, Hart et al. 2003). Moreover, food items may be digested

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with different efficiencies, distorting their real dietary importance (Pinn et al. 1998). Ethological studies are hindered by experimental constraints and because the animals perform several tasks simultaneously; the actual ingestion of food items can rarely be observed. Nonetheless, the source of nutrition can be determined by stable isotope analysis: assimilated food items are distinguishable by the variable content of their stable isotopes, and an isotopic equilibrium prevails between a consumer and its food source (Peterson 1999). The stable isotopes of carbon and nitrogen are most commonly used to infer such nutritional relationships, whereby the ratios of  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  reflect the members' distinct signatures. In situations where more than 2 food items are used by a consumer, mathematical mixing models are available to calculate their individual contributions to the consumer's signature (Fry & Sherr 1984, Phillips 2001, Melville & Connolly 2003).

By analysing stable carbon isotopes in a South African estuary, the habitat of *Callianassa kraussi*, phytoplankton has been determined as the shrimp's main carbon source instead of the assumed freshwater macrophyte detritus (Schlacher & Woolridge 1996). Boon et al. (1997) used C and N stable isotopes to determine different sources of plant detritus as food of the 2 Australian deposit feeders *Biffarius arenosus* and *Trypaea australiensis*—their most important source of detrital carbon and nitrogen was a mixture of seagrasses, epiphytes and macroalgae. For *Calliax jonesi* and *Neocallichirus* (as *Callianassa*) *rathbunae*, 2 deposit-feeding Caribbean thalassinids, benthic microflora turned out to be their primary dietary carbon source rather than the expected seagrass leaves (Murphy & Kremer 1992). Herein, we studied 4 other thalassinidean shrimps commonly populating Caribbean sediments.

*Glypturus acanthochirus* Stimpson is a sublittoral species occurring in fine sediment bottoms from Florida (USA) to the Gulf of Mexico and throughout the Caribbean. Its burrows are characterised at the surface by large mounds and funnels, with avalanches of sediment sliding from the mounds into the funnels. This species permanently processes large volumes of sediment (Dworschak & Ott 1993) and can therefore be assigned to the deposit-feeding species potentially exploiting organic matter in surface or subsurface sediments.

*Corallianassa longiventris* (A. Milne-Edwards) inhabits sand bottoms adjacent to seagrass stands of South Florida and the Caribbean. Members of the genus *Corallianassa* frequently capture drifting seagrass and algae (Suchanek 1983, Manning 1987, Dworschak & Ott 1993, Abed-Navandi 2000); consumed either fresh or after partial decomposition, this may comprise their nutritional basis (Griffis & Suchanek 1991).

*Axiopsis serratifrons* (A. Milne-Edwards) has a wide pantropical distribution and occurs in back-reef environments (Kensley 1980, Manning & Chace 1990, Lemaitre & Ramos 1992), where it populates subtidal sands heavily interspersed with coral rubble. This species displays a debris-capturing behaviour similar to that of *Corallianassa* spp., perhaps also for nutritional purposes (Kensley 1980, Rodrigues 1983).

Little is known about the nutritional ecology of *Neocallichirus grandimana* (Gibbes), a species with an amphi-American distribution in Florida, the Gulf of Mexico, the Caribbean and Pacific Colombia (Lemaitre & Ramos 1992), where it occurs in intertidal beach sands. Passively vented feeding on plankton and/or sedimentary organic matter may be concluded based on its occurrence in a continuously wave-swept habitat. For *Callichirus major* (Say), another Atlantic species occurring in a similar habitat, the same food sources were proposed by Rodrigues (1983).

The role of the wall lining in thalassinidean burrows is not clear. Many species construct it of very fine sediment and mucus secreted by specialised glands (Dworschak 1998), also plant fragments are sometimes incorporated (Griffis & Suchanek 1991). Aerobic conditions (Dworschak 1983, Bird et al. 2000) and an organic matter content that exceed values in the surrounding sediment (Vaugelas & Buscail 1990) make the wall into a place of high microbial activity (Bird et al. 2000). A nutritional role of the lining can be inferred because the wall material is in close contact with the shrimp's mouthparts during construction and reconstruction works (D. Abed-Navandi pers. obs.). Herein, we also considered the burrow walls, where present, as potential food sources.

The objective of this study was to identify the major food source of these 4 thalassinidean species by comparing their carbon and nitrogen stable isotope signatures with those of potential food items.

## MATERIALS AND METHODS

**Study sites.** Sampling was carried out in April 1997 at 4 sites in the Tobacco Reef section of the Belize Barrier Reef (Fig. 1): (1) Twin Cays in 'Cassiopea Cove'; (2) at the lagoonside of South Water Cay; (3, 4) at Carrie Bow Cay on (3) the reefside and (4) the lagoonside near the 'North End Sand Bar'.

**Shrimp. *Glypturus acanthochirus*:** At the study site, its habitat is in Cassiopea Cove at the north end of the main mangrove channel of Twin Cays. The density of funnels (reflecting shrimp density) was up to 5 funnels  $\text{m}^{-2}$ . The burrows consist of branches leading from the surface to the main gallery, a vertical spiral shaft and several blind tunnels; the burrow wall is smooth and

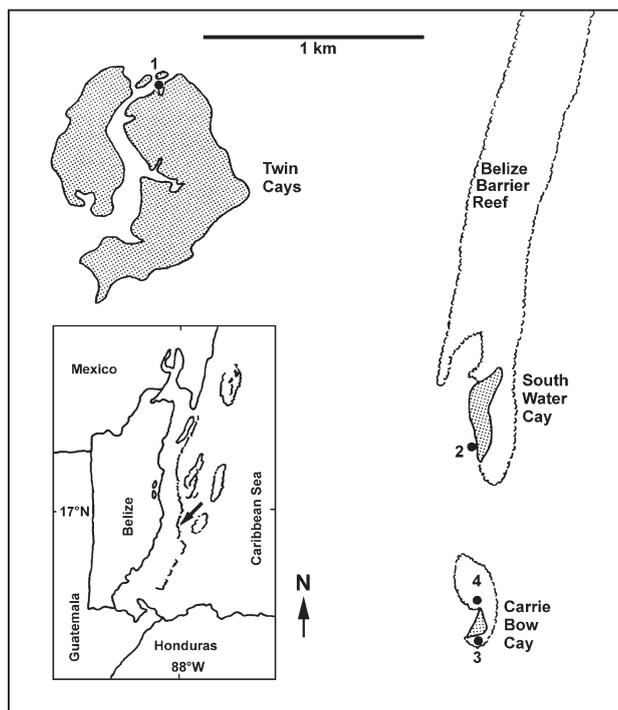


Fig. 1. Map of the study sites (modified from Dworschak & Ott 1993)

lined (Dworschak & Ott 1993). Shrimp were captured with weighted line traps (Vaugelas 1985); 14 traps over a period of 17 d yielded 7 shrimp.

There were 2 types of microalgal mats growing on the sediment surface around the burrow openings, a dark green mat dominated by the cyanobacteria genera *Oscillatoria*, *Spirulina*, *Beggiatoa* and *Leucothrix*, and a brown mat formed by pennate diatoms.

***Corallianassa longiventris*:** At the study site, this species was found on the lagoonside and reefside of Carrie Bow Cay. The burrow openings comprise 1 or 2 simple round holes, which are frequently closed by the shrimp. The burrow layout is a 1 to 2 m deep 'U' (Suchanek 1983), with chambers branching off that are either filled with coarse sediment or seagrass debris. The burrow wall is smooth, lined, and darker than the surrounding sediment.

Shrimp were baited to the surface with seagrass leaves, which they tried to pull into the burrow. Retreat was then blocked and the shrimp were carefully dug out.

***Axiopsis serratifrons*:** In Belize, these shrimp inhabit the back-reef of Carrie Bow Cay. Their burrow openings are characterised by holes surrounded by rubble. The simple, oblique burrows reach sediment depths of 30 cm and consist of a series of chambers, sometimes loosely filled with seagrass debris. No burrow wall is present for this species. The capture of *A. serratifrons*

was difficult. Only 2 specimens were caught by means of bait and digging or spearing; attempts to obtain more specimens using traps or poison failed.

***Neocallichirus grandimana*:** Its habitat at the study site is the intertidal and shallow subtidal sand at the lagoonside of South Water Cay. The burrow openings vary in appearance from simple round holes to small funnels or mounds with a density of up to 36 funnels  $m^{-2}$ . The burrow shape is simple, leading to a sediment depth of 36 cm. The burrow is only partially lined with dark brown sediments as opposed to the whitish surrounding sediment (Dworschak & Ott 1993); these thalassinideans were sampled with a yabby pump.

Microscopic examination of the meiobenthic community in the surface sediment showed diatoms, turbellarians and harpacticoid copepods dominating, while at 20 cm sediment depth harpacticoid copepods, oligochaetes, and stilbonematid nematodes were most abundant; the meiofauna in the burrow wall consisted almost solely of unidentified small pink nematodes.

**Food items.** Individual, 'most probable' food items were sampled after assigning the shrimp to a trophic mode using the scheme of Nickell & Atkinson (1995). For those species with a burrow wall lining, this material was also treated as a potential food source. At least 2 replicates of at least 2 g wet weight were collected of each food item (see Table 1); plant data represent composite samples of more than 20 different blades.

Sediment samples from around the burrows of *Glypturus acanthochirus*, *Neocallichirus grandimana* and *Corallianassa longiventris* were obtained by means of a boxcorer (Hertweck 1974). Burrow wall lining was sampled with a spatula after carefully digging away the upper portion of the burrows; surface sediment of South Water Cay was collected with a spoon. The resuspendable particle fraction of the sediment surrounding the burrows of *N. grandimana* at 20 cm depth was washed out with seawater in a bucket, after which it was decanted and concentrated by filtering (Whatman GF/F, 0.7  $\mu m$ ); this fraction was mainly composed of particles  $<32 \mu m$ .

At Cassiopeia Cove, consolidated green and brown mats were lifted from the slopes of the burrow funnels using a spatula, after which they were transferred to a sampling tube. In the laboratory, adhering fine particles were carefully separated from the matrix using a thin spatula and forceps; any remaining traces of fine sediment were considered as integral parts of these food items.

Green seagrass leaves were cut off living stands of *Thalassia testudinum* Banks ex König and *Syringodium filiforme* Kützing at Carrie Bow Cay. The stands nearest to the shrimps burrows were sampled. Floating debris of seagrass and the brown algae *Dictyota* sp.

was collected by hand near the burrows of *Corallianassa longiventris* and *Axiopsis serratifrons*. *Rhizophora mangle* Linnaeus leaves were cut at the main channel in Twin Cays, and detrital leaves were collected from the sediment surface close to the burrows of *Glypturus acanthochirus* in Cassiopea Cove. During the study period, no stranding event of pelagic *Sargassum* sp. was observed at the study site and therefore no samples were taken; data acquired later at Twin Cays (Wooller et al. 2003) were considered for the interpretation of the results.

Plankton was collected by towing a 47 µm plankton net for 10 min at the lagoonside of South Water Cays. The plankton was then concentrated on a 0.7 µm filter (Whatman GF/F).

**Analytical procedures and sample preparation.** Immediately after collection, muscle tissue was dissected from abdomina and claws of the shrimps; all plant parts were rinsed with distilled water. Thereafter, all samples were frozen (−18°C) and later dried in an oven at 60°C to constant weight (24 h). After transport to the laboratory, samples were ground to a fine powder in a ball mill (Retsch MM2). Shrimp tissue samples were cooled in order to facilitate the grinding procedure.

Samples were then weighed into tin capsules, decalcified with 5 N HCl following an *in situ* decalcification procedure (Nieuwenhuize et al. 1994), and subjected to  $\delta^{13}\text{C}/\delta^{15}\text{N}$  and C/N analysis using continuous-flow gas isotope ratio mass spectrometry (CF-IRMS).

The elemental analyser (EA 1110, CE Instruments) was interfaced with a ConFlo II device (Finnigan MAT) to the gas-isotope ratio-mass spectrometer (Delta<sup>+</sup>, Finnigan MAT). The  $^{13}\text{C}$  and  $^{15}\text{N}$  abundances were calculated and expressed as

$$\delta^{13}\text{C} [\text{‰ vs. V-PDB}] = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (1)$$

$$\delta^{15}\text{N} [\text{‰ vs. at-air}] = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (2)$$

where R is the ratio of  $^{13}\text{C}:^{12}\text{C}$  and  $^{15}\text{N}:^{14}\text{N}$ , respectively.

The standard deviation of repeated measurements of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of a laboratory standard was 0.10‰ versus V-PDB and 0.15‰ versus at-air, respectively. These abundances are calculated in relation to the certified reference materials Vienna Pee Dee Belemnite-limestone (V-PDB) and atmospheric dinitrogen (at-air).

**Food-source modelling and statistics.** A mixing model was applied because no single item closely matched the signature of the consumers. With more potential sources than stable isotopes analysed for each thalassinidean shrimp, no single solution could be calculated in a model. To delineate individual contributions within the 5 or 6 food sources per shrimp, models were computed using the Isosource routine developed by Phillips & Gregg (2003). This method examines all

possible combinations of each source contribution (0 to 100%) in 1% increments. Combinations that delivered the observed consumer's isotopic signature within a small tolerance range were considered to be feasible solutions, from which the trimmed 1 to 99 percentile range of source contributions (rather than the mean) is presented as histograms (Phillips & Gregg 2003).

As  $^{15}\text{N}$  isotopic enrichment by food consumption is around 2.5‰ in herbivorous/detritivorous consumers rather than the 3 to 4‰ reported for carnivorous consumers (Vander Zanden & Rasmussen 2001), 2.5‰ was subtracted from the shrimps'  $\delta^{15}\text{N}$  values before isosource analysis. No adjustments of the shrimps'  $\delta^{13}\text{C}$  signatures were made, because only a negligible isotopic fraction is involved during assimilation of dietary carbon (Fry & Sherr 1984).

One-way ANOVA (post hoc Tukey-HSD test) was carried out with the shrimps' isotope data at a level of significance of  $\alpha < 0.05$ . Prior to analysis, data were tested for normal distribution (Kolmogorov-Smirnov test). Statistical analyses were performed with SPSS 8.0 software (SPSS).

## RESULTS

### Shrimp stable-isotope signatures

Within the 4 species of shrimp, *Axiopsis serratifrons* and *Corallianassa longiventris* showed neither significantly different  $\delta^{13}\text{C}$  ( $-9.60 \pm 0.28$  and  $-9.80 \pm 0.28$ ‰, respectively,  $p > 0.05$ ) nor  $\delta^{15}\text{N}$  signatures ( $2.69 \pm 0.52$  and  $2.98 \pm 0.30$ ‰, respectively,  $p > 0.05$ ), whereas *Glypturus acanthochirus* and *Neocallichirus grandimana* differed significantly from the former 2 ( $\delta^{13}\text{C}$ :  $-11.73 \pm 0.24$  and  $-12.01 \pm 0.44$ ‰,  $p < 0.05$ ;  $\delta^{15}\text{N}$ :  $1.12 \pm 0.10$  and  $3.67 \pm 0.30$ ‰,  $p < 0.05$ , respectively) (Fig. 2). Differences between *G. acanthochirus* and *N. grandimana* were not significant for  $\delta^{13}\text{C}$  ( $p > 0.05$ ), while their  $\delta^{15}\text{N}$  values differed significantly ( $p < 0.05$ ). The shrimps' isotope data followed a normal distribution (Kolmogorov-Smirnov test,  $p > 0.05$ ).

### Composition of possible food sources

#### $\delta^{13}\text{C}$

Among the 18 possible food sources at the 4 sites, the detrital *Rhizophora mangle* leaves were most depleted with regard to  $^{13}\text{C}$  ( $-28.60 \pm 0.25$ ‰), while the green leaves of *Syringodium filiformis* were most enriched ( $-4.77 \pm 0.35$ ‰) (Table 1). Detrital leaves of both seagrasses showed a weak tendency towards depletion compared to the green leaves.

$\delta^{15}\text{N}$

With regard to  $\delta^{15}\text{N}$ , all samples showed a tendency to strong depletion; the surface-sediment organic matter was strongest depleted ( $-3.18 \pm 0.14\text{‰}$ ), while plankton was most enriched ( $3.07 \pm 0.46\text{‰}$ ) (Table 1).

Carbon and nitrogen contents

The lowest carbon contents among all food sources were found in deep sediments at South Water Cay, while fresh *Rhizophora mangle* leaves showed the highest values. Nitrogen contents of burrow walls of *Corallianassa longiventris* exhibited the lowest values, while the plankton reached the highest levels (Table 1). C/N ratios ranged from  $6.90 \pm 0.94$  for plankton to  $88.43 \pm 3.76$  for detrital *R. mangle* leaves (Table 1).

Food-source analysis

The plot of possible food items from *Glypturus acanthochirus*' habitat at Twin Cays (Fig. 3) shows a close proximity of the shrimp's carbon and nitrogen isotopic signatures to both types of microalgal mats. Compared

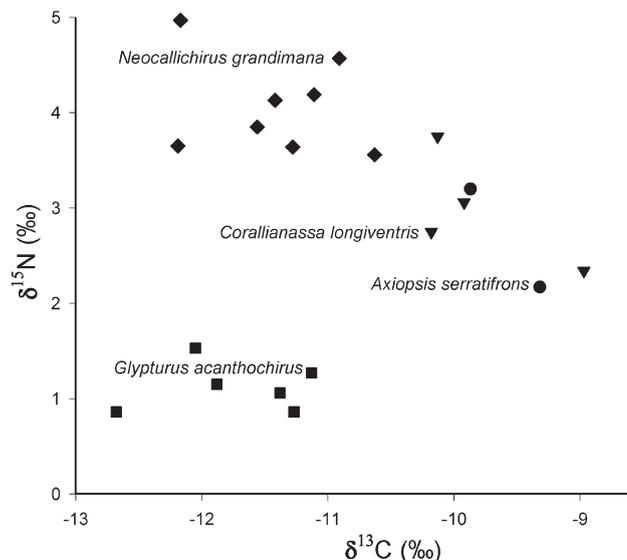


Fig. 2. *Axiopsis serratifrons*, *Corallianassa longiventris*, *Glypturus acanthochirus* and *Neocallichirus grandimana*. Carbon and nitrogen isotope signatures

with the shrimp's signature, the deep sediment and burrow wall showed moderate depletion of  $^{13}\text{C}$  (difference  $-2.3$  to  $-3.9\text{‰}$ ), while green and detrital *Rhizophora mangle* leaves were very strongly depleted in  $^{13}\text{C}$  (mean difference to the shrimp is  $-16.1\text{‰}$ ).

Table 1. *Glypturus acanthochirus*, *Corallianassa longiventris*/*Axiopsis serratifrons* and *Neocallichirus grandimana*. Carbon and nitrogen stable isotope signatures (mean  $\pm$  SE) of thalassinidean shrimps, C, N contents and C/N ratios of food sources at sampling

Food source	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C (%)	N (%)	C/N
<b><i>Glypturus acanthochirus</i></b> (6)	$-11.73 \pm 0.24$	$1.12 \pm 0.10$			
Green <i>Rhizophora mangle</i> leaves (2)	$-26.98 \pm 0.09$	$0.73 \pm 0.67$	$46.33 \pm 1.97$	$0.65 \pm 0.03$	$71.42 \pm 0.60$
Detrital <i>Rhizophora mangle</i> leaves (2)	$-28.60 \pm 0.25$	$-0.67 \pm 0.21$	$44.12 \pm 1.52$	$0.50 \pm 0.04$	$88.43 \pm 3.76$
Cyanobacteria mat (4)	$-12.06 \pm 0.30$	$-0.39 \pm 0.80$	$6.99 \pm 0.90$	$0.96 \pm 0.12$	$7.31 \pm 0.24$
Diatom mat (4)	$-12.83 \pm 0.30$	$-0.75 \pm 0.49$	$4.71 \pm 0.54$	$0.51 \pm 0.06$	$9.32 \pm 0.48$
Deep sediment (2)	$-14.05 \pm 0.27$	$-0.12 \pm 0.03$	$2.88 \pm 0.77$	$0.31 \pm 0.07$	$9.14 \pm 0.46$
Burrow wall (5)	$-15.64 \pm 0.10$	$-0.62 \pm 0.13$	$2.14 \pm 0.21$	$0.23 \pm 0.02$	$9.46 \pm 0.37$
<b><i>Corallianassa longiventris</i></b> (4)	$-9.80 \pm 0.28$	$2.98 \pm 0.30$			
<b><i>Axiopsis serratifrons</i></b> (2)	$-9.60 \pm 0.28$	$2.69 \pm 0.52$			
Green <i>Syringodium filiforme</i> leaves (2)	$-4.77 \pm 0.35$	$1.00 \pm 0.55$	$26.86 \pm 1.69$	$1.35 \pm 0.09$	$19.86 \pm 0.04$
Detrital <i>Syringodium filiforme</i> leaves (2)	$-6.76 \pm 0.13$	$0.28 \pm 0.36$	$17.76 \pm 1.73$	$0.84 \pm 0.23$	$22.12 \pm 3.90$
Green <i>Thalassia testudinum</i> leaves (2)	$-6.34 \pm 0.06$	$2.97 \pm 0.12$	$28.67 \pm 2.46$	$1.42 \pm 0.09$	$20.17 \pm 0.49$
Detrital <i>Thalassia testudinum</i> leaves (2)	$-7.71 \pm 0.02$	$1.05 \pm 0.23$	$16.12 \pm 0.41$	$0.54 \pm 0.01$	$29.91 \pm 0.15$
<i>Dictyota</i> sp. (2)	$-13.95 \pm 0.06$	$1.90 \pm 0.11$	$13.55 \pm 0.76$	$0.86 \pm 0.12$	$15.97 \pm 1.37$
Pelagic <i>Sargassum</i> sp. <sup>a</sup> (1)	$-14.10$	$2.04$	nd	nd	
Burrow wall of <i>C. longiventris</i> (3)	$-16.08 \pm 1.45$	$-1.46 \pm 0.92$	$0.95 \pm 0.62$	$0.08 \pm 0.04$	$10.59 \pm 1.70$
<b><i>Neocallichirus grandimana</i></b> (8)	$-11.41 \pm 0.18$	$4.07 \pm 0.13$			
Plankton (3)	$-15.66 \pm 0.48$	$3.07 \pm 0.46$	$17.90 \pm 3.49$	$2.86 \pm 1.00$	$6.90 \pm 0.94$
Surface sediment (2)	$-17.47 \pm 0.00$	$-3.18 \pm 0.14$	$0.74 \pm 0.12$	$0.11 \pm 0.00$	$6.98 \pm 1.02$
Deep sediment (2)	$-19.76 \pm 2.83$	$-0.73 \pm 0.26$	$0.57 \pm 0.01$	$0.11 \pm 0.02$	$5.32 \pm 1.01$
Resuspended sediment fraction (2)	$-18.11 \pm 0.00$	$1.25 \pm 0.05$	$3.24 \pm 0.15$	$0.32 \pm 0.01$	$10.13 \pm 0.80$
Burrow wall (3)	$-15.93 \pm 1.18$	$1.43 \pm 1.47$	$1.87 \pm 0.54$	$0.25 \pm 0.14$	$9.58 \pm 2.25$

<sup>a</sup>Data from Twin Cays/Belize (Wooller et al. 2003)

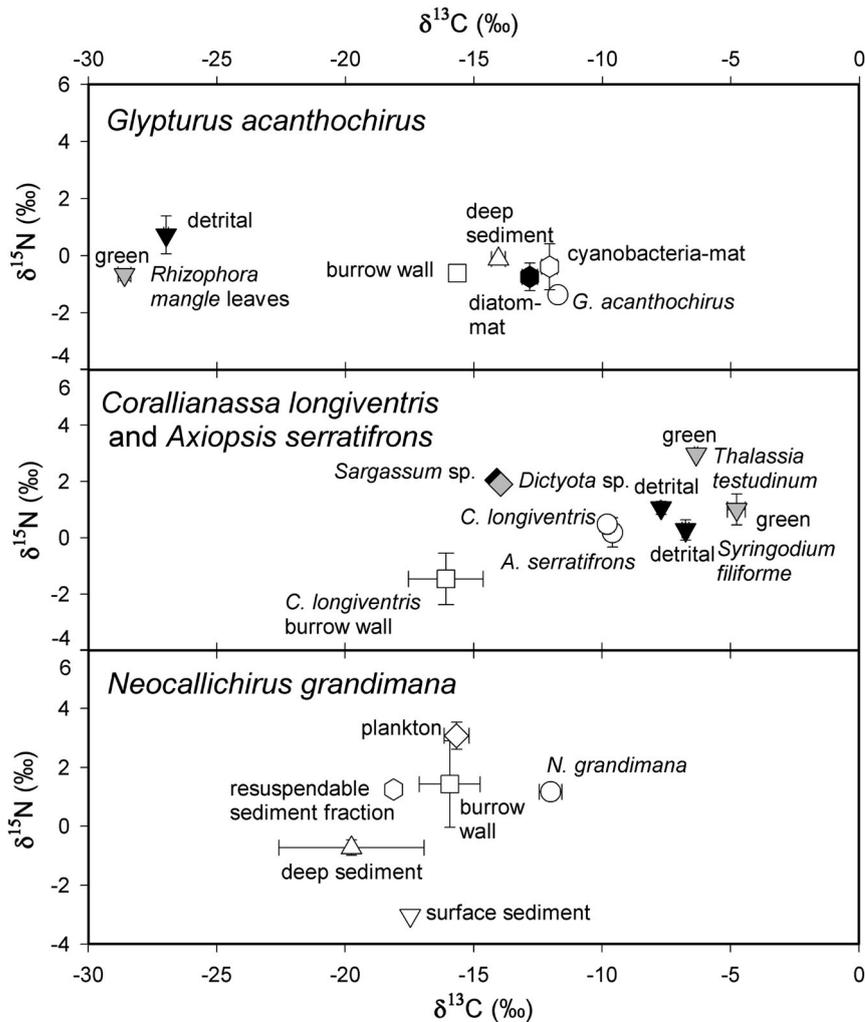


Fig. 3. *Glypturus acanthochirus*, *Corallianassa longiventris*/*Axiopsis serratifrons* and *Neocallichirus grandimana*. Habitat plots of mean ( $\pm$ SE)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of the thalassinidean shrimps and their potential food sources. Shrimps' nitrogen content corrected for trophic enrichment

$\delta^{15}\text{N}$  values ranged from  $-0.75$  to  $1.12\text{‰}$ , with *Glypturus acanthochirus* as the lowest member after  $-2.5\text{‰}$  fractionation correction, and the detrital *Rhizophora mangle* leaves as the highest. Modelling of the shrimp's isotope values yielded highly different distributions of feasible source contributions (Fig. 4). Cyanobacteria mats contributed the most (52 to 97%), followed by diatom mats (0 to 46%). Deep sediment and the burrow wall ranked lower (0 to 16 and 0 to 8%, respectively), while both types of *R. mangle* leaves ranked lowest, with 0 to 1% contribution to the shrimp's signature.

The *Corallianassa longiventris*/*Axiopsis serratifrons* habitat plot (Fig. 3) depicted the 2 isotopically almost identical species in the middle of a polygon of their

food sources, none of which bore close resemblance to the  $\delta^{13}\text{C}$  values of the shrimps (Fig. 3). The food item with the closest  $\delta^{13}\text{C}$  was detrital leaves of both seagrasses, followed by their green leaves, then the brown algae *Dictyota* sp. and *Sargassum* sp. (with almost equal signatures). In the case of *C. longiventris*, the burrow wall was next in rank.

Based on the  $\delta^{15}\text{N}$  signatures, the detrital and green *Syringodium filiformis* leaves and also the detrital leaves of *Thalassia testudinum* were closest to the fractionation-corrected value of the shrimp.

Modelling of the *Corallianassa longiventris* isotopic signature gave different contribution ranges for the 6 food sources: detrital leaves of *Thalassia testudinum* contributed most (0 to 62%), followed by detrital and green *Syringodium filiformis* leaves, with 0 to 49 and 0 to 43%, respectively (Fig. 5). The organic matter in the burrow wall accounted for 13 to 38%, while green leaves of *T. testudinum* and the brown algae contributed least to the shrimp's signature (0 to 28 and 0 to 27%, respectively).

For *Axiopsis serratifrons*, different source contributions were computed from the signatures of its 5 potential food items. The highest range was attained by the detrital leaves of *Syringodium filiformis* (57 to 69% contribution), followed by the brown algae (28 to 34%), detrital *Thalassia testudinum* leaves (0 to 14%) and green leaves of both seagrasses (*S. filiformis* 0 to 6% and *T. testudinum* 0 to 2% contribution) (Fig. 6).

*Neocallichirus grandimana* at South Water Cay was by far the most enriched in  $^{13}\text{C}$  compared with its potential food items sampled from this site, with plankton and the burrow wall showing the least  $\delta^{13}\text{C}$  differences ( $-3.7$  and  $-3.9\text{‰}$ , respectively) to the potential consumer. The  $\delta^{15}\text{N}$  values ranged from  $-3.18$  to  $3.67\text{‰}$ , with the surface sediment the most depleted and *N. grandimana* showing the most enriched values. After the  $-2.5\text{‰}$  fractionation correction, both the resuspended sediment fraction and the burrow wall most resembled the  $\delta^{15}\text{N}$  signature of *N. grandimana* (Fig. 3). Due to the lack of components with more positive  $\delta^{13}\text{C}$  values, no feasible mixing solution could be modelled for this species.

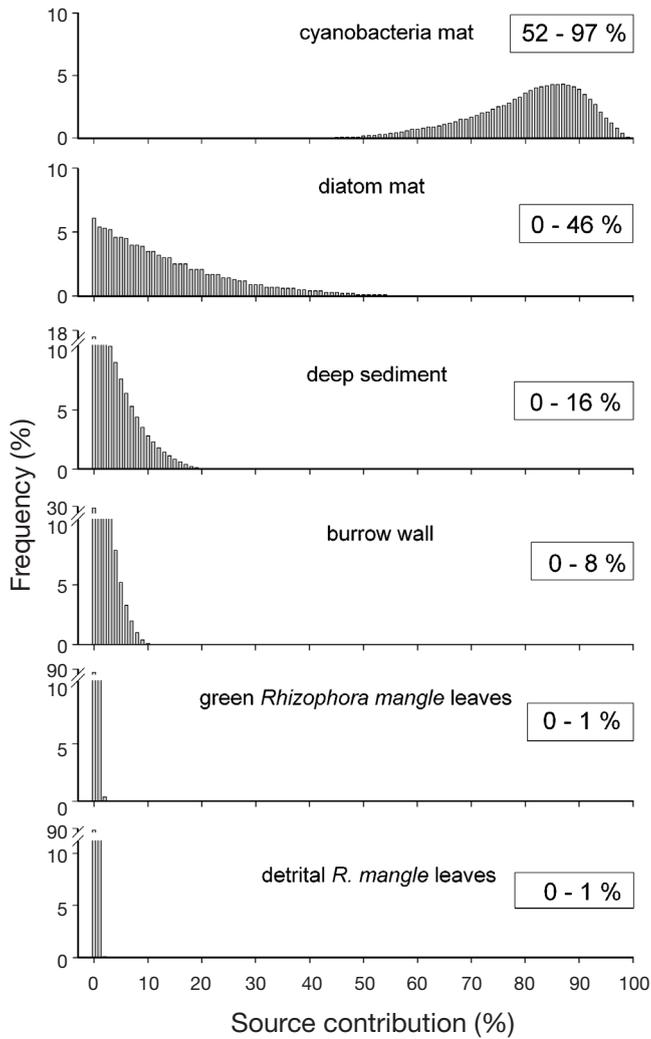


Fig. 4. *Glypturus acanthochirus*. Feasible contributions of 6 food sources to the shrimp's isotopic signatures after correction for  $^{15}\text{N}$  trophic enrichment. Values in boxes: 1 to 99 percentile range of source contributions

## DISCUSSION

### Stable isotope signatures

A comparison of the plant signatures with published values for the same species and states of decomposition shows accordance in  $\delta^{13}\text{C}$  values for *Syringodium filiformis* (Hemminga & Mateo 1996) and for *Rhizophora mangle* leaves (Zieman et al. 1984, Fry & Smith 2002). The values recorded in the green *Thalassia testudinum* leaves resemble the most enriched signatures reported for this species (Stoner & Waite 1991, Murphy & Kremer 1992, Hemminga & Mateo 1996). The  $\delta^{15}\text{N}$  values measured for the seagrasses are in accordance with those of previous studies (Zieman et al. 1984, Wooller et al. 2003), those of *R. mangle* reconfirm

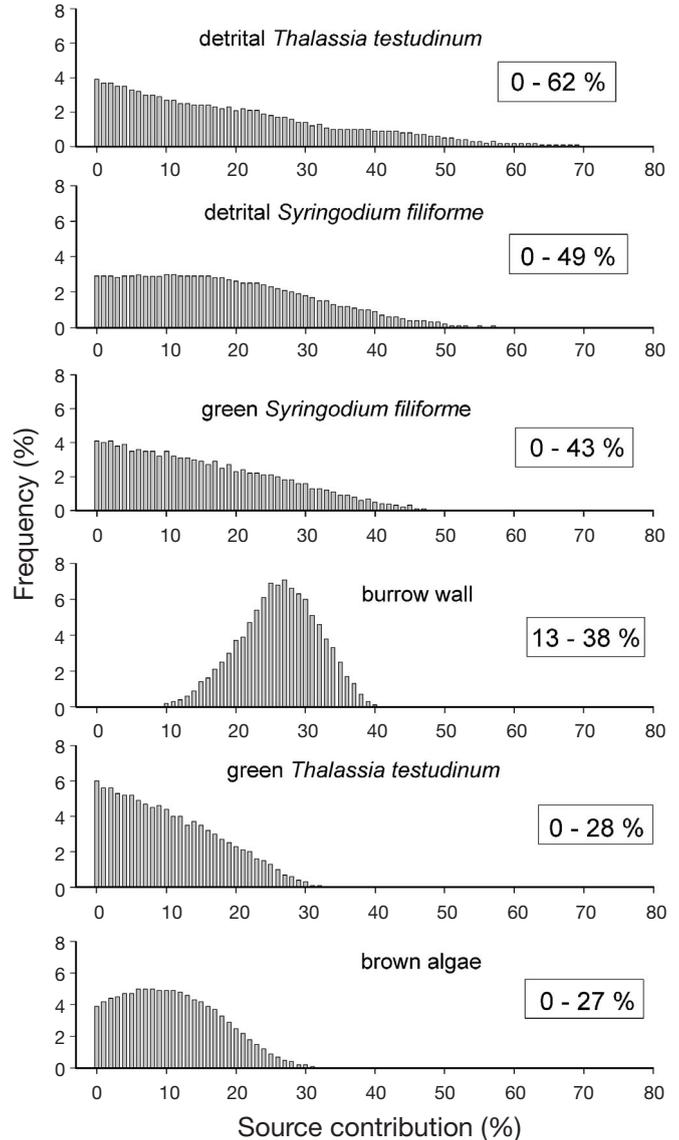


Fig. 5. *Corallianassa longiventris*. Feasible contributions of 6 food sources to the shrimp's isotopic signatures after correction for  $^{15}\text{N}$  trophic enrichment. Values in boxes: 1 to 99 percentile range of source contributions

values of McKee et al. (2002) and Wooller et al. (2003). The plants' C/N values are similar to the ratios measured by Atkinson & Smith (1983).

### Food sources of the shrimps

Carbon and nitrogen stable isotope analyses, together with the mixing models, were helpful in determining the food sources of the 4 thalassinidean species.

The mixing model revealed the major nutritional role of the microalgae mats on the sediments around the burrow openings of *Glypturus acanthochirus*. The

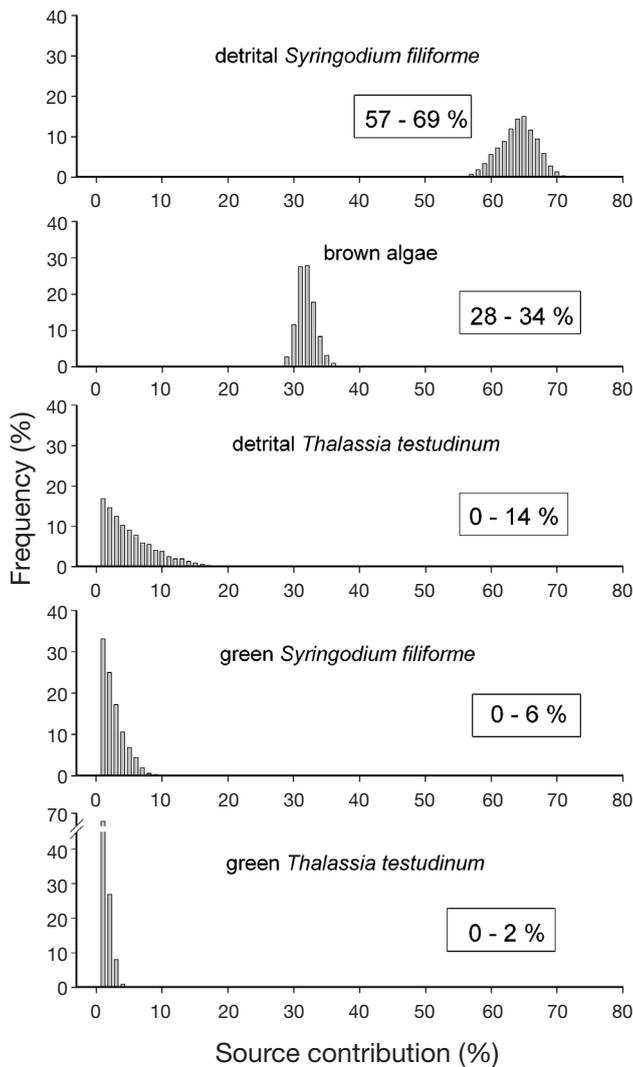


Fig. 6. *Axiopsis serratifrons*. Feasible contributions of 5 food sources to the shrimp's isotopic signatures after correction for  $^{15}\text{N}$  trophic enrichment. Values in boxes: 1 to 99 percentile range of source contributions

cyanobacteria-dominated mats, which represented the most important food source, also had a 50% higher carbon content than the mats dominated by diatoms (Table 1). Surprisingly, the mangrove leaves, although abundant around the burrows, did not play a role in *G. acanthochirus*' diet. One explanation may be that the shrimps had no access to this potential food items for some unknown reason. Alternatively, the high leaf C/N ratios (up to 88), which is obviously higher than the suggested maximum (C/N = 17) for sustainable invertebrate nutrition (Russell-Hunter 1970), may explain why they did not serve as food source. Similarly, mangrove forest-dwelling sesamid crabs prefer sediment detritus with C/N ratios below 20, rather than abundant mangrove leaves (Micheli 1993, Skov & Hartnoll

2002). The burrow wall and the deep sediment (other potential food items) were not relevant for *G. acanthochirus*.

*Corallianassa longiventris*' diet consisted mainly of the brown, detrital leaves of the seagrasses *Thalassia testudinum* and *Syringodium filiforme* drifting by their burrow openings. The green, fresh leaves of these 2 species contributed only minimally to the shrimp's diet directly: this material may either have been captured and subjected to ageing in the burrows' debris chambers, or may not have been captured at all in this stage. Detached green leaves of these seagrasses are strongly positively buoyant through gas canals in their tissue (Phillips & McRoy 1980); they gradually lose buoyancy during decomposition, which may more often bring brown leaves within the reach of the shrimp.

Stable isotope analysis revealed the burrow wall lining also to be an important food source. Its low C/N ratio (10.6) may provide good nutritional value for *Corallianassa longiventris* (Table 1). This possibly explains the greater importance of the burrow wall sediment as food for *C. longiventris* (13 to 38% contribution) than for *Glypturus acanthochirus* (0 to 8%), whose other food items showed C/N ratios well below the Russell-Hunter ratio of 17. Brown algae may be less important to *C. longiventris* than seagrass leaves because of their lower abundance and availability.

Most of the diet of *Axiopsis serratifrons* was comprised of detrital *Syringodium filiforme* leaves, followed by brown algae; green leaves of both seagrasses had the least nutritional importance. As in its 'behavioural sibling' *Corallianassa longiventris*, (same food-capture behaviour), the preferential assimilation of brown leaves may reflect either a poor efficiency in capturing green leaves directly, or their later consumption in a more decomposed state within the burrow. The most 'valuable' item based on the C/N ratio in the *A. serratifrons* diet was *Dictyota* sp. (Table 1); this possibly supplements the nitrogen fraction lacking in detrital *S. filiforme* leaves.

Similar to these 2 drift-collecting thalassinideans, a dietary reliance on drifting macroalgae has been reported for intertidal sea urchins, polychaetes and molluscs (Magnum & Cox 1971, Tutschulte & Connell 1988, Bustamante et al. 1995, Rodríguez 2003).

The most probable sources of nitrogen in the diet of *Neocallichirus grandimana* were the easily resuspendable fraction of the smallest particles in the sediment surrounding the burrows and the burrow wall lining. As suitable nitrogen source, a diet primarily based on plankton or sedimentary sources such as the surface sediment or the bulk sediment surrounding the burrow seems improbable.

With regard to carbon sources, the burrow wall lining and plankton contributed to this in part. However, a further, unknown, food item with a  $\delta^{13}\text{C}$  signature greater than  $-11.4\text{‰}$  must also have been assimilated by *Neocallichirus grandimana* to account for its carbon signature. Most probably, both dominant Caribbean seagrass species (signatures greater than  $-8\text{‰}$ ) were also of dietary relevance, and added to the shrimp's  $^{13}\text{C}$  isotope pool. How the shrimp obtains this seagrass carbon is not clear, since neither drift-capture behaviour nor seagrass-filled burrow chambers have been observed in this species.

### CONCLUSION

Stable isotope analysis proved to be a valuable tool in detecting of the food sources and feeding modes of the studied thalassinideans.

The nutritional mode of *Glypturus acanthochirus* as a deposit feeder was determined. Analogous to other conveyor-belt deposit feeders, sediment is continuously subduced from the surface, separated from food, and rejected at the surface by this species. Its diet is primarily derived from microalgae mats on the surface sediments, mainly formed by filamentous cyanobacteria of the genera *Oscillatoria*, *Spirulina*, *Beggiatoa* and *Leucothrix* and to a lesser extent by pennate diatoms.

The nutritional relevance of *Corallianassa longiventris* and *Axiopsis serratifrons* drift-capture behaviour was corroborated by our results: the species consume drifting plants caught at the surface openings of their burrows. Brown, detrital leaves of the seagrasses *Thalassia testudinum* and *Syringodium filiforme*, and to a minor degree brown algae, form the nutritional basis for both thalassinids. In the case of *C. longiventris*, the organic matter in the burrow wall sediment also comprises a minor part of its diet. For these 3 thalassinidean species, the low organic content of tropical littoral sediments (Miyajima et al. 1998) helps explain the reliance on food sources foraged mainly from the sediment surface. With regard to nutrition, the subsurface parts of the burrows function only as places where food is processed rather than acquired.

The food sources of *Neocallichirus grandimana* remain open. A preferential utilisation of its burrow wall sediments and the smallest particles in the sediments surrounding the burrows is indicated, at least as nitrogen sources.

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