



ORIGINAL ARTICLE

Nutritional ecology of thalassinidean shrimps constructing burrows with debris chambers: The distribution and use of macronutrients and micronutrients

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Abstract

Four different approaches were combined to determine the nutritional relevance of debris chambers in the burrows of two thalassinidean shrimps: (1) the natural abundance of carbon and nitrogen stable isotopes in potential food sources, (2) their nutritional value based on the content and composition of essential nutrients, (3) a dual labelling experiment with shrimp in aquaria employing ¹⁵N- and ¹³C-labelled seagrass debris and (4) ration estimates using the acquisition rate of plant debris by the shrimps. The results of the four approaches confirmed the use of plant debris as a food source. Based on the natural abundance of stable isotopes, *Corallianassa longiventris* apparently relies on the chamber content and the burrow wall as sources of carbon and nitrogen, whereas *Pestarella tyrrhena* probably relies on ambient debris and on benthic foraminiferans and microphytobenthos in the surface sediment. *Corallianassa longiventris* obtains its essential nutrients predominantly from chamber debris and to a lesser extent from its burrow wall, *P. tyrrhena* from chamber debris, the burrow wall and the surface sediment. Among the essential nutrients, those amino acids commonly deficient to deposit feeders were particularly enriched in the burrow environments of the two shrimps. Highly unsaturated fatty acids (HUFAs) were lacking in all of *C. longiventris* potential food sources; this species may either be able to synthesize them de novo from linolic acid or may use another unknown source. For *P. tyrrhena*, surface sediment and chamber debris represent potential HUFA sources. The most probable thiamine and β -carotene supplier for *C. longiventris* is the chamber debris, for *P. tyrrhena* again the surface sediment. In both species, the rate of debris introduction into the burrow is sufficient to meet the nutritional demand.

Key words: Burrow chambers, Crustacea, deposit feeding, essential nutrients, stable isotopes, Thalassinidea, thalassinidean nutrition

Introduction

Mud shrimps (Crustacea: Decapoda: Thalassinidea) are among the most common, but also the most commonly overlooked, macro-infauna organisms in estuarine and marine sediments (Dworschak 2000). Occurring in high densities with large and complex burrows, they can play a prominent role as ecosystem engineers (Berkenbusch & Rowden 2003; Bird 2003) in regulating the characteristics of these important habitats.

There is evidence that thalassinidean bioturbation is closely linked to nutritional aspects. Their feeding on small organic particles prompted scientists to partition them into suspension feeders (MacGinitie

1930; Dworschak 1987) and deposit feeders (MacGinitie 1934; Pohl 1946; Witbaard & Duineveld 1989; Stamhuis et al. 1996, 1998a,b).

The analysis of burrow architecture (Dworschak 1983; Griffis & Suchanek 1991; Nickell & Atkinson 1995) yields further features that help classify thalassinidean feeding. Interestingly, several species, all of them described as deposit feeders, construct burrow chambers that are filled with sediment and organic fragments of different size and decomposition stage. Such reports exist for *Axiopsis serratifrons*, *Axius serratus*, *Sergio mirim*, *Callianassa truncata*, *Pestarella tyrrhena*, *Calocaris macandreae*, *Corallianassa longiventris*, *Glypturus acanthochirus*, *Glypturus*

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laurae, *Upogebia affinis* and *Upogebia pusilla* (Buchanan 1963; Rodrigues 1966; Shinn 1968; Braithwaite & Talbot 1972; Ott et al. 1976; Nash et al. 1984; de Vaugelas 1984; Suchanek 1985; Griffis & Suchanek 1991; Dworschak & Ott 1993; Dworschak 2001). Two sources of the debris in the chambers have been discussed: several authors report an active capture and introduction of plant debris by *Corallianassa* spp., *Axiopsis serratifrons* (Suchanek 1985; Manning 1987; Dworschak & Ott 1993; Abed-Navandi 2000), *Neaxius acanthus* (Abed-Navandi & Dworschak, pers. obs.) and, in the case of *Calocaris macandreae*, of scavenged macrofauna from the sediment surface (Buchanan 1963; Nash et al. 1984) into the burrow. An alternative source for such debris aggregations is debris that is already embedded in the sediment and encountered during digging.

The function of these debris chambers remains unclear: a “dump hypothesis” proposes a depository for substrate that physically interferes with irrigation or burrowing processes. Other explanations include passive, water-current controlled aggregation (Yager et al. 1993; Huettel et al. 1996) in funnel-shaped burrow openings at the surface, or a mining encounter. Dumping in debris chambers is thought to be an alternative to ejection via the burrow opening, which would increase the shrimp’s risk of predation or might block the burrow (Farrow 1971; Tudhope & Scoffin 1984; Nickell & Atkinson 1995). Alternatively, the obtained material may be utilized to construct the burrows, as plant fragments are sometimes found in the wall lining.

A “hoard hypothesis”, which implies a caching behaviour for a nutritional purpose, has also been postulated (Buchanan 1963; Braithwaite & Talbot 1972; Frey & Howard 1975; Ott et al. 1976; Nash et al. 1984; Suchanek 1985; Griffis & Suchanek 1991). This hypothesis may be refined into either a “pantry model” or a “fermenter model”: (1) In the pantry model, organic debris is obtained during times of surplus and simply stored for later consumption. Such a “pantry” would organically enrich the subtropical and tropical carbonate sediments usually inhabited by chamber-building shrimp (Griffis & Suchanek 1991). These sands exhibit very low organic carbon values (typically <0.4% organic carbon content; Thomassin & Cauwet 1985; Williams et al. 1985; Miyajima et al. 1998). Such habitats therefore have a relatively low overall food availability for shrimps. (2) The fermenter model implies a microbial gardening on the imported organic debris. The ability of thalassinideans to impact their surrounding sediment micro- and meiofauna communities (Branch & Pringle 1987; Dobbs & Guckert 1988; Bird et al. 2000;

Dworschak 2001) indicates microbial gardens in mud shrimp burrows (Griffis & Suchanek 1991). Such gardening could exploit the biosynthetic capabilities of micro-organisms and improve the nutritional quality of the introduced debris beyond that of other potential food sources.

This study tested the “hoard hypotheses” by answering the following questions for the thalassinideans *Corallianassa longiventris* (A. Milne-Edwards, 1870) and *Pestarella* (formerly *Callianassa*) *tyrrhena* (Petagna, 1792):

1. Does the nutritional value of the chamber debris differ from other potential food sources? One factor that determines nutritional value is the amount of essential nutrients in the food. The debris must meet the crustacean-specific dietary requirement for fatty acids, amino acids, vitamins and carotenoids (D’Abramo et al. 1997). This was examined by comparing the content of essential fatty acids (EFAs), essential amino acids (EAAs), thiamine and β -carotene in potential food sources of two chamber-building thalassinideans. The potential food sources considered were the sand from the surface and the deep ambient sand near the burrows, the plant debris around the burrows, the burrow wall lining and the debris present in the chambers.
2. On which food sources do chamber-building mud shrimps rely? The natural carbon and nitrogen stable isotope signatures of the potential food sources were used to detect the dietary source of the two mud shrimps in situ and in a laboratory environment. The rationales of this method are (a) that assimilated food items are distinguishable by their variable content of stable isotopes and (b) that an isotopic equilibrium prevails between a consumer and its food source (Peterson 1999).
3. Is the introduced debris assimilated by the shrimps? A drawback of the natural abundance method is that dietary relationships are deduced based merely on the resemblance of isotopic compositions and that distinctly different signatures of potential sources and their consumers do not always exist. We therefore employed a laboratory approach with artificially ^{13}C - and ^{15}N -labelled seagrass debris to test for an actual assimilation of this material by the shrimps.
4. Does the quantity of debris acquired by the shrimp meet its dietary need? The amount of debris obtained by the mud shrimps was estimated and its nutrient content related to the dietary demands of comparable shrimp.

Material and methods

Corallianassa longiventris is distributed in the west Atlantic from Bermuda to Brazil (Pernambuco) and is common in 0–10 m in backreef sediments near seagrass beds in the Caribbean (Biffar 1971; Markham & McDermott 1980; Dworschak 1992; Melo 1999). Recently, Sakai (1999) synonymized the genus *Corallianassa* with *Glypturus*. Some aspects of this revision, however, are the subject of active debate and here we follow Manning & Felder (1991).

The burrow openings are one to two simple round holes that are frequently closed by the animal. The burrow layout is a deep “U” that can reach sediment depths of 2 m (Suchanek 1983). At two or three positions, blind tunnels branch off and form chambers; these chambers may be filled with coarse sediment and plant debris. The burrow wall is smooth, lined and darker than the surrounding sediment.

Pestarella tyrrhena is distributed in the east Atlantic from the southern North Sea to Guinea and is the most common callianassid shrimp in the Mediterranean (Ngoc-Ho 2003). It inhabits intertidal and shallow subtidal zones, and the burrow openings are sand funnels and mounds around exhalant openings. The burrows extend to a sand depth of 62 cm and consist of a “U” with one shaft leading to the surface and below a main shaft consisting of a series of enlarged chambers. Several chambers filled with plant debris and coarse sediment branch off. The burrow walls are usually better oxidized than the sediment surface between burrows and sometimes contain plant fragments (Dworschak 2001).

In situ studies

Study sites. *Corallianassa longiventris* was observed in Bermuda, at St. George’s, west of Cooper’s Island Nature Reserve (32°21’13”N 64°39’36”W). The habitat of the shrimp is exposed to Atlantic waves from the southeast; the animals live in 2–4 m water depth in poorly sorted silty carbonate sand interspersed with coral rubble. Seaward of the shrimp’s habitat, stands of the seagrasses *Halodule bermudensis*, *Syringodium filiforme* and *Thalassia testudinum* exist. *Pestarella tyrrhena* was studied in the Adriatic Sea at Lido di Carabinieri (45°40’48”N 13°26’00”E), a wave-protected tidal flat in front of the camp site Punta Spin near Grado, Italy. Here, its habitat is the lower intertidal and subtidal where a dense meadow of *Cymodocea nodosa* covers large areas around the burrows. The sediment is a well-sorted fine silicate sand, with abundant interstitial foraminiferans and diatoms (Koller, pers. obs.).

Estimation of passive debris supply to *C. longiventris* and *P. tyrrhena*. Four tubular debris traps were dug flush into the sediment close to the shrimps’ burrow openings; the dimensions of the traps were scaled to average-sized animals (83 mm diameter for *C. longiventris*; 46 mm for *P. tyrrhena*). Traps were deployed on 4 days for 24 h. Thereafter, the debris was sorted; only organic debris manipulable by the shrimps (>1 mm) was retained, dried at 60°C, weighed and the amount expressed as mg dry weight (dw).

Video surveillance of debris intake by *C. longiventris*. Openings with shrimps present were selected, and their debris intake recorded in January, May and October 2001 with an infrared camera (Deep Diving Services and Investigations Inc., Zäziwil, Switzerland) S-60H/60E and infrared light mounted on a tripod. The system was connected with a 40 m cable to a Sony Video Walkman GV-S50E containing Hi8 tapes. Eleven shrimps were recorded for a total of 24.75 h. The caught debris was identified, measured from the television screen and the amount estimated as mg dw.

Sampling of *C. longiventris* and *P. tyrrhena* burrows. Burrows of *C. longiventris* were sampled with SCUBA and an air lift suction device with 5 cm diameter operated by independent SCUBA tanks. The surrounding sediment was carefully siphoned off to a depth of 1 m, the respective parts of the burrow were excavated and transferred into sampling vials with spoons. *Pestarella tyrrhena* burrows were sampled during spring low tides when access from land was possible. Parts of the burrows were excavated and sampled with spoons and spatulas. From both burrow types, five sample categories were collected: (1) surface sediment (to a depth of 3 mm) within 10 cm of the openings, (2) ambient sediment >2 cm away from burrow walls (below 10 cm sediment depth), (3) ambient debris, i.e. degraded plant fragments either from the surface around *C. longiventris* openings or embedded in the sediment within 20 cm of *P. tyrrhena* burrows, (4) chamber debris, taken from opened burrow chambers and (5) the burrow wall, i.e. the 1 mm thick sediment layer lining the burrows. From each sample category at least 20 ml was collected, stored at –5°C and later transferred to the laboratory. This material was then processed and analysed for carbon and nitrogen stable isotopes and the nutritional value parameters stated below. Animals were caught either inside their burrows during excavation, by using a bait pump, or by luring them to the surface and cutting off their retreat.

Dual labelling experiments in laboratory-held shrimp

Animals were transported to Vienna and were maintained in narrow aquaria with the following dimensions (inner height \times breadth \times width): *C. longiventris* 80 \times 28 \times 3.2 cm, *P. tyrrhena* 62 \times 28 \times 3.2 cm, filled to a height of 65 and 50 cm, respectively, with the corresponding ambient sediment. Recirculating systems consisting of eight aquaria connected to a 60 l filter pool with a pump and a 7 l overhead tank that gravity fed the individual aquaria were used. The flow rate through each aquarium was kept at 0.5–1.0 l min⁻¹. Artificial seawater was utilized (hw Sea Salt professional, Wiegandt) at a salinity of 35; the water temperature ranged from 23 to 26°C. The sediment was allowed to settle for several days before the animals were introduced and began to construct burrows. The aquaria were covered with black plastic sheeting in order to prevent extensive algal growth on the glass. The experiment was performed several months after the animals had successfully established their burrows and had moulted repeatedly. During this period, no food was provided externally.

Labelling of seagrass. Shoots of the seagrasses were collected near the shrimps' burrows, cleared of epiphytes and dead parts, and exposed to dim sunlight in a 10 l aquarium containing filtered seawater (Whatman GF/C). ¹⁵NH₄¹⁵NO₃ and NaH¹³CO₃ (Sigma) were added to final concentrations of 100 and 500 μ M, respectively, for 5 days. Thereafter, the plants were rinsed 10 times with seawater and dried at 60°C. This procedure yielded seagrass debris with stable isotope signatures of 23,566‰ δ^{15} N and 327‰ δ^{13} C.

Labelled debris was offered to *C. longiventris* (n = 3) and *P. tyrrhena* (n = 2) close to their burrow openings. The shrimps introduced the debris into their burrows within several hours. After 140 days the aquaria were sampled. The aquaria were drained, turned over and opened, the shrimps were captured, and the sediments collected from the sand surface, ambient sediment, burrow wall and chamber bottom. Aquaria where no debris was provided served as controls. Samples were then subjected to carbon and nitrogen stable isotope analysis by continuous flow gas isotope ratio mass spectrometry (CF-IRMS), as described below.

Analytical techniques

Fatty acids. Lipids were extracted from a 1 g dried sample by elution with chloroform/methanol (Bligh & Dyer 1959) after 20 min ultrasonication (Branson, USA), converted into methyl esters (FAMES) and

analysed with gas chromatography using an Auto-System gas chromatographer (Perkin Elmer, Vienna, Austria) equipped with a split/splitless capillary injector. FAMES were separated by a 30 m \times 0.25 mm ID fused silica column (RTx-2330) and detected with a flame ionization detector whose temperature was set at 250°C; the analytical precision was <5% (standard deviation). Total fatty acids (TFA) and fatty acids essential to Crustacea (EFA) were expressed as mg g(dw)⁻¹ or as their percentage proportion of TFAs, and the ratio of non-essential fatty acids (NEFA) to EFA was calculated (NEFA/EFA). Linolic acid (C18:2n6), arachidonic acid (20:4n6), linolenic acid (C:18:3n3), eicosapentaenoic acid (EPA; C20:5n3) and docosahexaenoic acid (DHA; C22:6n3) were considered as EFAs (D'Abramo et al. 1997).

Amino acids. Amino acids were quantified from a 0.5 g dried sample after acid hydrolysis (6 N HCl, 110°C, 24 h) and derivatization with *o*-phthalaldehyde by high-performance liquid chromatography (HPLC) with fluorescence detection (Lindroth & Mopper 1979). A precision of 3–5% (standard deviation) was typical for the individual amino acids. Total amino acid (TAA) yields were expressed as μ M g(dw)⁻¹; amino acids essential to crustaceans (EAA) were expressed as their percentage proportion of TAA. In order to show a potential enrichment of EAA, the ratio of non-essential amino acids (NEAA) to EAA was calculated (NEAA/EAA). Histidine, threonine, arginine, methionine, valine, phenylalanine, isoleucine, leucine and lysine were considered as essential (D'Abramo et al. 1997). Tryptophane was not analysed due to technical limitations.

β -carotene. The β -carotene content was determined with reversed phase HPLC from the extracts produced for fatty acid analysis (Barua 2001). The analytical system consisted of a 1-7100 pump, L-7400 detector, D-7000 Interface module and a 250 \times 4.5 μ m LiCrospher 100RP-18 column (Merck, Vienna, Austria). Methanol/dichloromethane (85:15 v/v) was used as the mobile phase, the flow rate was 0.8 ml min⁻¹, and the detection wavelength was set at 295/450 nm. Extracted lipids were dissolved in hexane, diluted and evaporated until dry under vacuum, resolved in the mobile phase and injected. The β -carotene content was expressed as μ g g(dw)⁻¹.

Thiamine. Σ thiamine (thiamine and its phosphates) was determined by an HPLC fluorimetric thiochrome method with post-column derivatization according to Kimura & Itokawa (1983). For extract preparation, 0.5 g dried samples were autoclaved

with 0.1 M H₂SO₄ at 120°C (1 bar, 15 min). After adjusting the pH to 7 using 0.1 M NaOH, the samples were centrifuged at 3500 rpm for 5 min. They were then filtered and immediately analysed; wavelengths of 375 and 450 nm were used for excitation and emission, respectively. Values were expressed as $\mu\text{g g(dw)}^{-1}$.

Stable isotope analysis. Frozen animal tissue and food items were dried in an oven at 60°C for 12 h. After transport to the laboratory, samples were ground to a fine powder in a ball mill (Retsch MM2, Vienna, Austria). Shrimp tissue samples were cooled in order to facilitate the grinding procedure. Samples were then decalcified with 5 N HCl, dried again at 60°C, weighed into tin capsules and subjected to $\delta^{13}\text{C}$ / $\delta^{15}\text{N}$ and carbon/nitrogen analysis using CF-IRMS. The elemental analyser (EA 1110, CE Instruments, Milan, Italy) was interfaced with a ConFlo II device (Finnigan MAT, Bremen, Germany) to the gas isotope ratio mass spectrometer (Delta⁺, Finnigan MAT). The ¹³C and ¹⁵N abundances were calculated and expressed as follows:

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

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

where R is the ratio of ¹³C:¹²C and ¹⁵N:¹⁴N. 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, where V-PDB is the abundance referred to the certified reference materials Vienna Pee Dee Belemnite-Limestone and at-air is atmospheric dinitrogen.

Food source modelling. A mixing model was applied in natural abundance situations where no single item closely matched the signature of the consumer. With more potential sources than stable isotopes analysed, no unique solution could be calculated in a model. To delineate individual contributions within the four to five food sources, models were computed using the Isosource routine (Phillips & Gregg 2003). This method examined all possible combinations of each source contribution (0–100%) 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 1–99 percentile range of source contributions (rather than the mean) was reported in histograms (Phillips & Gregg 2003).

As ¹⁵N isotopic enrichment after feeding is about 2.5‰ in herbivorous/detritivorous consumers, rather than the 3–4‰ reported for carnivorous mammalian consumers (Vander Zanden & Rasmussen 2001;

Vanderklift & Ponsard 2003), this value was subtracted from the shrimps' $\delta^{15}\text{N}$ values before the Isosource calculations. No adjustments of the animals' $\delta^{13}\text{C}$ signatures were made because only negligible isotopic fractionation occurs during the assimilation of dietary carbon (Fry & Sherr 1984).

Statistics. One-way ANOVA (post-hoc Tukey-HSD test) was carried out with the essential nutrients data; the isotope data in the labelling experiment were analysed for significant differences using Student's t-tests. Prior to the analysis, data were tested for normal distribution (Kolmogorov–Smirnov test) and where necessary were log-transformed. Unless stated otherwise means ± 1 standard error are reported. Statistical analyses were performed at a significance level of $\alpha < 0.05$ with SPSS 8.0 software.

Results

Debris catching

Debris traps deployed in the habitat of *C. longiventris* caught 375 ± 85 mg (dw) debris in 24 h. Debris consisted of fragments of seagrass leaves, *Sargassum natans*, unidentified red and brown algae, terrestrial plants and polychaete tubes (listed in order of frequency). Sediment and portunid crabs occasionally present were not included in the dw calculation of debris.

Video surveillance of active animals showed that *C. longiventris* caught 55 ± 33 mg (dw) debris h⁻¹ and the shrimps were active during daylight and darkness. Based on the estimated time the shrimps actually spend at the surface catching debris (10%, Abed-Navandi & Dworschak, pers. obs.), the daily catch rate was 132 mg (dw) debris. A comparison of surface activity corrected catch rates of the traps with those of the shrimps themselves indicated a 2.8-fold enhancement of the catch rate due to the shrimps' activity.

In the habitat of *P. tyrrhena*, an average of 135 ± 60 mg (dw) debris was caught in the traps in 24 h; this material consisted of seagrass and terrestrial plant fragments.

Nutritional quality

Debris sampled from the chambers of both shrimps consisted of small plant fragments and coarse sediment. Ambient debris embedded in the sediment consisted mainly of seagrass leaves and rhizomes.

Amino acids. In both species, significantly higher amounts of TAAs were found in ambient debris, while ambient and surface sediments exhibited the lowest values (Tables I and II). For *P. tyrrhena*,

Table I. Total amount and composition of amino acids, fatty acids, thiamine and β -carotene of food sources of *Corallianassa longiventris* (mean \pm standard error; n in parentheses).

	Surface sediment	Ambient sediment	Ambient debris	Burrow wall	Chamber debris
Amino acids	(2)	(3)	(3)	(2)	(3)
Total amino acids ($\mu\text{M g}^{-1}$)	13.45 \pm 0.96 ^a	13.47 \pm 8.41 ^a	623.90 \pm 17.16 ^b	25.71 \pm 2.74 ^a	63.76 \pm 30.62 ^a
NEAA/EAA	1.92 \pm 1.36	2.99 \pm 0.54	3.14 \pm 0.28	4.35 \pm 0.34	2.19 \pm 0.50
EAA (% of total)					
Histidine	nd	0.66 \pm 0.33	1.71 \pm 0.40	0.57 \pm 0.57	3.99 \pm 2.58
Threonine	nd	3.34 \pm 3.34	0.41 \pm 0.41	nd	0.32 \pm 0.32
Arginine	7.92 \pm 3.80	3.43 \pm 1.84	6.36 \pm 0.47	3.27 \pm 2.29	5.83 \pm 2.62
Methionine	0.80 \pm 0.80	0.42 \pm 0.42	1.10 \pm 0.17	1.53 \pm 1.53	1.57 \pm 0.61
Valine	3.62 \pm 0.93	1.50 \pm 0.75	2.21 \pm 0.48	1.54 \pm 0.36	2.27 \pm 0.23
Phenylalanine	2.92 \pm 0.52	2.09 \pm 1.06	1.85 \pm 0.96	9.68 \pm 3.57	3.94 \pm 1.64
Isoleucine	6.15 \pm 3.60	1.95 \pm 1.02	2.59 \pm 0.58	0.81 \pm 0.81	4.79 \pm 1.31
Leucine	14.48 \pm 8.19	3.79 \pm 1.89	4.46 \pm 1.96	1.37 \pm 1.37	5.17 \pm 0.23
Lysine	nd	nd	4.20 \pm 2.14	nd	5.11 \pm 3.28
Fatty acids	(4)	(3)	(2)	(6)	(4)
TFA (mg g^{-1})	0.20 \pm 0.02 ^{a,b}	0.19 \pm 0.02 ^a	1.57 \pm 0.04 ^d	0.33 \pm 0.03 ^{b,c}	0.40 \pm 0.04 ^c
NEFA/EFA	3.5 \pm 0.1	3.8 \pm 1.0	3.8 \pm 0.9	3.8 \pm 0.3	4.5 \pm 0.5
EFA (% of total)					
C18:2n6	10.9 \pm 0.3	11.4 \pm 2.5	11.4 \pm 1.6	10.8 \pm 0.4	9.6 \pm 0.6
C18:3n3	11.5 \pm 0.0	9.9 \pm 1.5	10.0 \pm 2.2	10.3 \pm 0.5	8.9 \pm 1.2
C20:5n3	nd	1.4 \pm 1.4	nd	nd	nd
C22:6n3	nd	nd	nd	nd	nd
Thiamine ($\mu\text{g g}^{-1}$)	0.08 \pm 0.03 (3) ^a	0.06 \pm 0.01 (3) ^a	0.47 \pm 0.28 (3) ^{a,b}	0.72 \pm 0.18 (3) ^{c,b}	3.00 \pm 1.33 (3) ^c
β -carotene ($\mu\text{g g}^{-1}$)	0.68 \pm 0.27 (3) ^{a,b,c}	0.12 \pm 0.05 (3) ^a	1.53 \pm 0.24 (2) ^c	0.22 \pm 0.10 (3) ^{a,b}	0.98 \pm 0.08 (3) ^{b,c}

nd, not detected; NEAA, non-essential amino acids; EAA, essential amino acids; TFA, total fatty acids; NEFA, non-essential fatty acids; EFA, essential fatty acids.

Different superscript letters indicate significant differences at $P < 0.05$.

Table II. Total amount and composition of amino acids, fatty acids, thiamine and β -carotene of food sources of *Pestarella tyrrhena* (mean \pm standard error; n in parentheses).

	Surface sediment	Ambient sediment	Ambient debris	Burrow wall	Chamber debris
Amino acids		(2)	(2)	(2)	(2)
Total amino acids ($\mu\text{M g}^{-1}$)	na	7.14 \pm 0.24 ^a	138.08 \pm 81.90 ^b	60.45 \pm 2.38 ^{a,b}	36.87 \pm 13.67 ^{a,b}
NEAA/EAA	na	0.66 \pm 0.06	0.85 \pm 0.03	0.87 \pm 0.02	0.84 \pm 0.06
EAA (% of total)					
Histidine	na	nd ^a	2.61 \pm 0.11 ^b	3.77 \pm 0.05 ^c	2.49 \pm 0.11 ^b
Threonine	na	10.96 \pm 1.07	5.80 \pm 0.18	7.98 \pm 2.55	5.66 \pm 0.30
Arginine	na	7.65 \pm 1.35	13.29 \pm 3.63	14.88 \pm 0.78	13.47 \pm 2.19
Methionine	na	nd	2.31 \pm 1.33	0.41 \pm 0.03	1.39 \pm 0.15
Valine	na	4.38 \pm 0.17 ^a	6.72 \pm 0.64 ^b	5.99 \pm 0.17 ^b	5.62 \pm 0.08 ^{a,b}
Phenylalanine	na	10.42 \pm 4.81	7.56 \pm 0.52	7.12 \pm 0.39	7.55 \pm 1.02
Isoleucine	na	5.68 \pm 2.00	5.06 \pm 0.82	4.09 \pm 0.22	4.29 \pm 0.32
Leucine	na	13.80 \pm 1.40	9.49 \pm 2.10	7.52 \pm 0.41	8.69 \pm 0.76
Lysine	na	7.49 \pm 1.44 ^b	1.18 \pm 0.06 ^a	1.74 \pm 0.04 ^a	5.17 \pm 1.39 ^b
Fatty acids	(4)	(3)	(2)	(6)	(4)
TFA (mg g^{-1})	0.11 \pm 0.00 ^a	0.11 \pm 0.01 ^a	0.32 \pm 0.03 ^{a,b}	0.54 \pm 0.14 ^b	0.22 \pm 0.04 ^{a,b}
NEFA/EFA	9.5 \pm 1.2 ^{a,b}	18.9 \pm 4.0 ^{a,b}	4.5 \pm 1.1 ^a	39.9 \pm 11.9 ^b	9.9 \pm 3.3 ^{a,b}
EFA (% of total)					
C18:2n6	nd	3.2 \pm 2.0	8.4 \pm 3.0	0.1 \pm 0.1	4.8 \pm 4.2
C18:3n3	nd	nd	6.6 \pm 3.3	nd	nd
C20:5n3	9.6 \pm 1.1	nd	3.5 \pm 2.0	nd	nd
C22:6n3	nd ^a	2.3 \pm 1.1 ^{a,b}	1.7 \pm 1.1 ^{a,b}	3.2 \pm 1.3 ^{a,b}	6.6 \pm 1.1 ^b
Thiamine ($\mu\text{g g}^{-1}$)	3.33 \pm 0.33 (3) ^b	0.69 \pm 0.31 (3) ^a	1.32 \pm 0.34 (3) ^a	0.70 \pm 0.30 (3) ^a	0.74 \pm 0.26 (3) ^a
β -carotene ($\mu\text{g g}^{-1}$)	0.55 \pm 0.21 (3) ^{a,b}	0.16 \pm 0.08 (3) ^a	1.74 \pm 0.46 (3) ^b	0.64 \pm 0.23 (4) ^{a,b}	0.78 \pm 0.19 (3) ^{a,b}

na, data not available; nd, not detected; NEAA, non-essential amino acids; EAA, essential amino acids; TFA, total fatty acids; NEFA, non-essential fatty acids; EFA, essential fatty acids.

Different superscript letters indicate significant differences at $P < 0.05$.

chamber debris and burrow walls showed significantly higher levels than ambient sediment (Table II). Values for the surface sediment associated with the burrows of this species are not available due to a sample storage failure.

The chamber debris of *C. longiventris* showed an improved NEAA/EAA ratio compared with ambient debris (2.19 ± 0.50 versus 3.14 ± 0.28); this difference, however, was not significant (Table I). Among the *P. tyrrhena* samples, no differences in NEAA/EAA ratios were observed. These samples consistently exhibited significantly higher proportions of EAA than those from *C. longiventris* burrows (mean NEAA/EAA ratios: 0.80 ± 0.05 versus 2.92 ± 0.43).

Among the individual EAAs, the fractions of histidine and valine were significantly lower in ambient sediment associated with *P. tyrrhena*, while lysine was significantly enriched there. The burrow wall lining exhibited significant histidine enrichment; the same was also true for lysine in the chamber debris of *P. tyrrhena*. In chamber debris from burrows of *C. longiventris*, the histidine and lysine proportions were high compared with the other categories, while the burrow wall lining showed elevated phenylalanine fractions. These differences, however, were not significant.

Fatty acids. Among the categories analysed from the *P. tyrrhena* habitat, the burrow wall showed significantly higher TFA levels, whereas for *C. longiventris* the ambient debris showed the highest values, followed by chamber debris and the burrow wall lining (Table I and II). The highest enrichment of EFAs occurred in the *P. tyrrhena* ambient debris, while the burrow wall exhibited very low EFA values.

No differences in enrichment were observed for *C. longiventris*.

Considering the individual EFAs, significant differences existed for DHA in *P. tyrrhena* burrows. In the surface sediment, no DHA was found, while in the chamber debris DHA accounted for 6.6% of the TFA. In *C. longiventris* burrows, no DHA and EPA were detected; arachidonic acid was not present in any of the samples from in and around burrows of either thalassinidean species.

Thiamine. The chamber debris of *C. longiventris* contained significantly higher thiamine concentrations than the burrow wall lining (Table I). At *P. tyrrhena* burrows, the surface sediment had significantly higher levels of this vitamin, while chamber debris levels were close to those recorded for ambient sediment (Table II).

β -carotene. The ambient debris samples from both species' habitat contained the significantly highest amounts of β -carotene, with the lowest values found in ambient sediments (Table I and II).

Stable isotope food source analysis

In situ burrows. The plot of the possible food items from *C. longiventris* burrows shows a close proximity of the animals' carbon and nitrogen isotopic signature with that of chamber debris and burrow wall (Figure 1). Compared with the shrimps' signature, both types of sediment showed depletion of ^{13}C , while the ambient debris was enriched in ^{13}C .

Modelling of the shrimps' isotope values yielded different distributions of feasible source contribu-

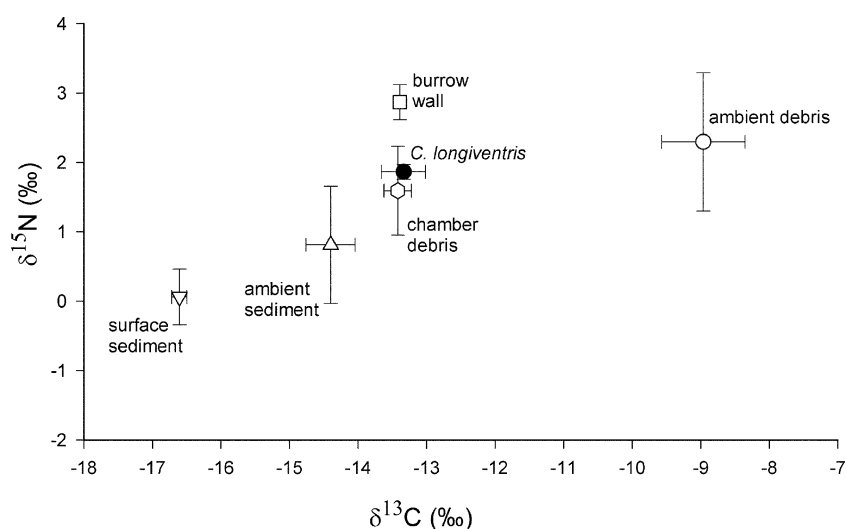


Figure 1. Habitat plots of mean (\pm standard error) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of *Corallianassa longiventris* and its potential food sources in situ. The shrimps' nitrogen values have been corrected for trophic enrichment.

tions (Figure 2). Chamber debris contributed most to the shrimps' signature (0–73%), followed by the burrow wall (21–46%). Ambient and surface sediment and the ambient debris ranked lower (0–42, 0–29 and 2–23%, respectively).

The *P. tyrrhena* habitat plot depicts the consumer to the right of its potential food sources, none of which bore resemblance to the signature of the shrimp (Figure 3). The closest was the ambient debris around the animals' burrows.

Labelling experiments in laboratory-held shrimp. Without seagrass, the $\delta^{13}\text{C}$ signature of *C. longiventris* was similar to that of its burrow wall and chamber bottom sediment (Figure 4). The Isosource modelling of *C. longiventris* carbon and nitrogen isotopic signature gave different contribution ranges: the burrow wall contributed most (48–66%), followed

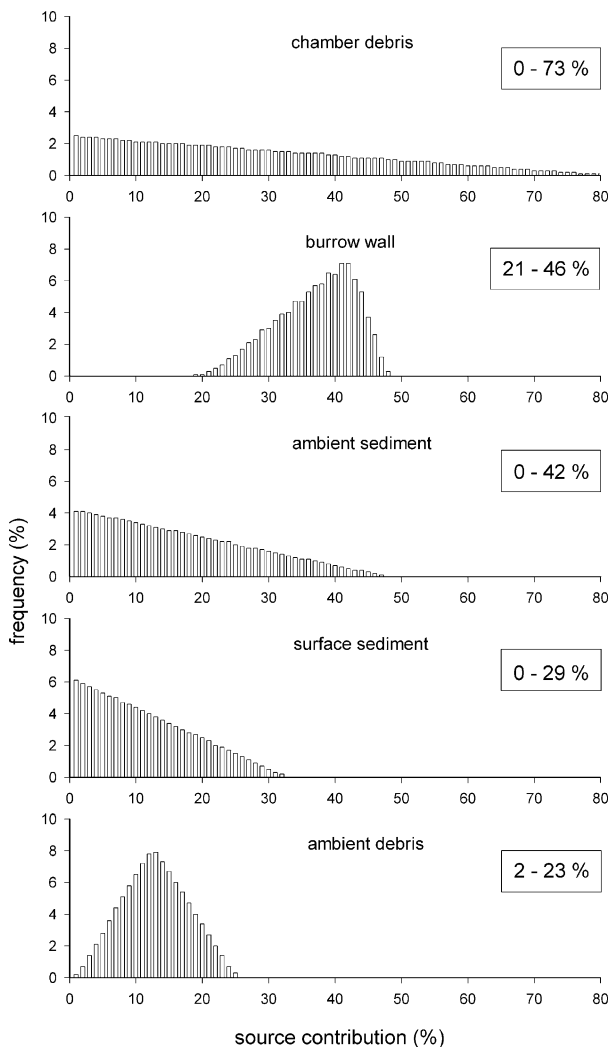


Figure 2. Histograms of the feasible contributions of five food sources delivering the signatures of *Corallianassa longiventris* in situ after correction for ^{15}N trophic enrichment. Values in boxes are the 1–99 percentile range of source contributions.

by the sediment from the chamber bottom with 0–49%. Ambient sediment and surface sediment contributed least to the animals' signature (0–28 and 2–7%; Figure 5).

After the 140 day handling of the labelled debris by the shrimps, only traces of debris were visible in the chambers. The components of this system gained different labels: the burrow wall reached highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, followed by the shrimp's tissue ($\delta^{13}\text{C}$: $7.70 \pm 2.60\text{‰}$; $\delta^{15}\text{N}$: $1143 \pm 146\text{‰}$) and by the sediments from the chamber bottom, the surface and the ambient bed (Figure 4; Table III). In all cases, more ^{15}N was gained than ^{13}C .

Pestarella tyrrhena also gained label from the introduced labelled debris (albeit less than in *C. longiventris*). Here, final values of $-1.10 \pm 0.32\text{‰}$ $\delta^{13}\text{C}$ and $961.68 \pm 6.84\text{‰}$ $\delta^{15}\text{N}$ were reached (Table III).

Discussion

Nutritional value of potential food sources

Amino acid composition. For *C. longiventris*, the relative enrichment of EAAs in the chamber debris over ambient debris signifies an enhancement of the amino acid nutritional value of debris tended by the shrimp (NEAA/EAA 2.2 versus 3.0). An even better amino acid composition was found in the surface sand. This category, however, represents a less accessible food source because this species does not process surface sand. The uniformly higher EAA proportions in the habitat of *P. tyrrhena* indicate a generally better supply of EAA to this species.

A striking feature among the individual EAAs is the enrichment of the basic amino acids histidine or lysine in sources tended by the shrimps (chamber debris of *C. longiventris*, burrow wall lining and chamber debris of *P. tyrrhena*). These amino acids are described (together with arginine, methionine and phenylalanine) as being most deficient in detritivores (Phillips 1984; Marsh et al. 1989; Dauwe et al. 1999), probably due to their strong adsorption to sedimentary material (Henrichs & Sugai 1993). Likewise, the dominance of the aromatic amino acid phenylalanine in the EAA profile of the burrow wall of *C. longiventris* corresponds to reports stating that detritivore growth rates are greatly influenced by the levels of this amino acid (Marsh et al. 1989). The percentage levels of these EAAs required in shrimp nutrition (D'Abramo et al. 1997) are only attained in either the chamber debris or the burrow wall linings.

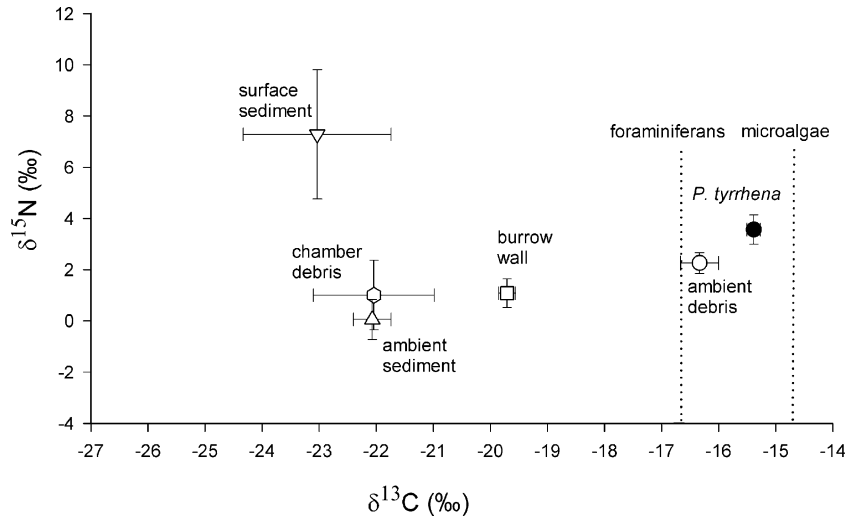


Figure 3. Habitat plots of mean (\pm standard error) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of *Pestarella tyrrhena* and its potential food sources in situ. Dotted lines show mean $\delta^{13}\text{C}$ values of benthic foraminiferans and microalgae. (Data after Currin et al. 1995, Stribling & Cornwell 1997, Moodley et al. 2000). The shrimps' nitrogen values have been corrected for trophic enrichment.

These differing profiles indicate the utilization of a mixture of food sources, resulting in amino acid complementarity (Phillips 1984).

Fatty acid composition. The high EFA percentages found in potential food sources of *C. longiventris* indicate a good supply of this nutrient group. Comparable analyses performed by Meziane et al. (2002) on intertidal surface sediments encountered 2.5 times lower EFA fractions.

Of these EFAs, however, only linolic and linolenic acid were present. The virtual absence of EPA and DHA is enigmatic, as these two highly unsaturated fatty acids (HUFAs) are indispensable for crustacean metabolism (D'Abramo et al. 1997). *Corallianassa longiventris* may either exploit a dietary HUFA source not accounted for in this study (perhaps animal tissue?) or, alternatively, it may be able to synthesize HUFAs via elongation and desaturation of the abundant linolenic acid.

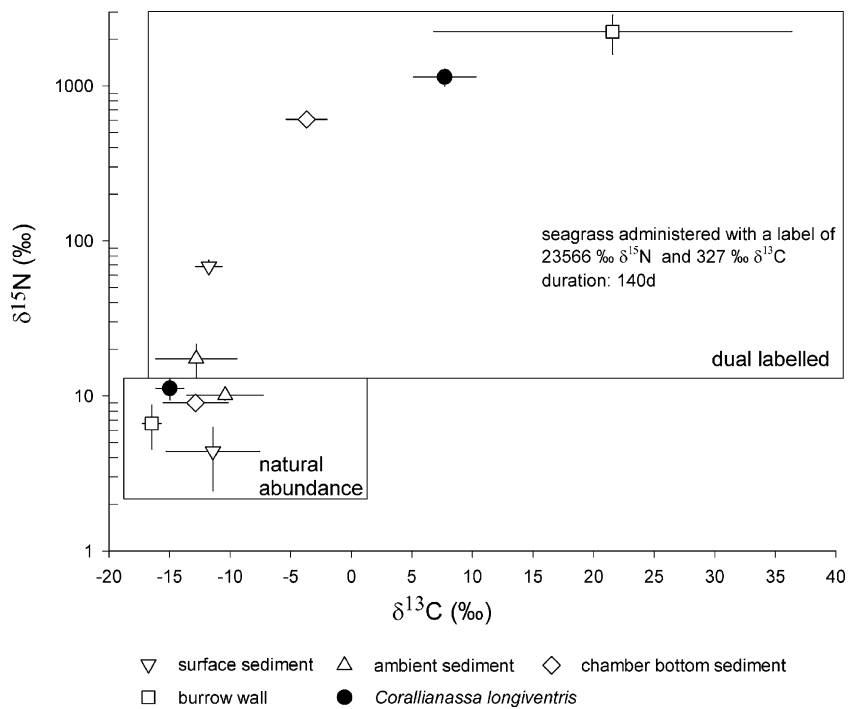


Figure 4. Dual labelling experiment in *Corallianassa longiventris* aquaria burrows. Habitat plots of mean (\pm standard error) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of *C. longiventris* and its potential food sources. The shrimps' nitrogen values have been corrected for trophic enrichment.

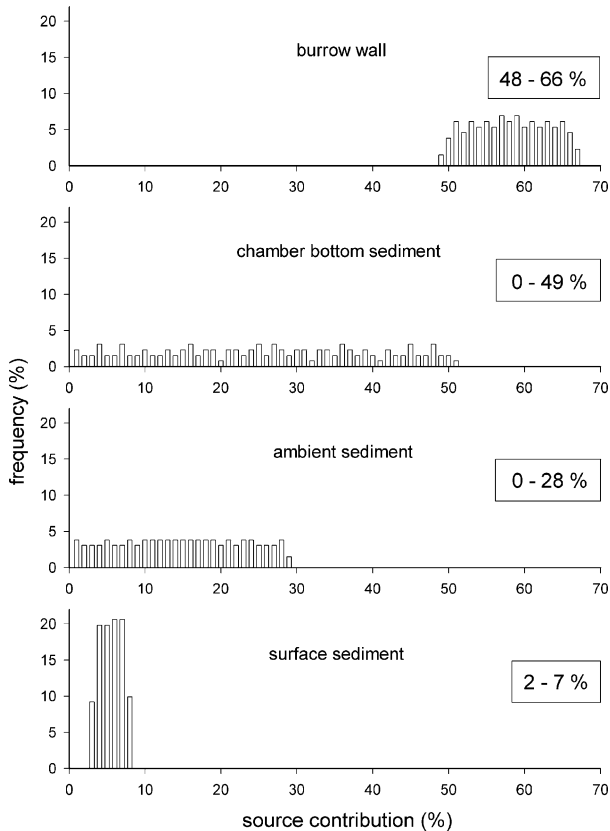


Figure 5. *Corallianassa longiventris* in aquaria burrows without seagrass. Histograms of the feasible contributions of the four potential food sources to the signature of *C. longiventris* after correction for ^{15}N trophic enrichment. Values in boxes are the 1–99 percentile range of source contributions.

This, however, has rarely been reported for crustaceans (Kanazawa et al. 1979; Ito & Simpson 1996).

Among the potential food sources of *P. tyrrhena*, the most complete EFA profile was present in ambient debris. The extremely low fractions present in the burrow wall lining make this category an improbable supplier of EFAs, but the high percentage of DHA in the chamber debris and of EPA in the surface sediments indicate a complementary dietary use of these sources. Epibenthic or settled pelagic diatoms may explain the enhanced EPA fraction in the surface sediment (Dunstan et al. 1994; Pond et al. 1998). This source is readily accessible for *P. tyrrhena*; sediment mounds around exhalant burrow openings are common, and intensive sediment-processing behaviour has been observed in the laboratory (Dworschak 1987, 2001).

The DHA in the chamber debris could either originate from flagellates or from relatively fresh seagrass, both of which are reported to be de novo DHA synthesizers (Phillips 1984; Kharlamenko

et al. 2001), or from metazoan tissue scavenged by *P. tyrrhena*.

Thiamine. For *C. longiventris*, ambient and surface sediment thiamine levels lay within the lower range of the data available for marine sediments (Niimi et al. 1997). The high levels encountered in the chamber debris and in the burrow wall may have been due to either bacteria or microalgae, both prominent producers of thiamine (Niimi et al. 1997; Pinto et al. 2003). *Corallianassa longiventris* probably utilizes chamber debris as a main thiamine supplier.

In the *P. tyrrhena* habitat, the very high values in the surface sediment are an interesting feature: they exceed the highest published values by three times (Niimi et al. 1997). Microalgae, probably microphytobenthic diatoms, may have been responsible for this peak value.

β -carotene. The β -carotene concentrations in the surface sediments of both species lay within the commonly observed range (Jeffrey 1974; Stauber & Jeffrey 1988). Microalgae and seagrass detritus are the probable sources of this micronutrient. The elevated content in the chamber debris of *C. longiventris* may be nutritionally significant because other potential sources – ambient sediment and burrow wall samples – exhibited less β -carotene. For *P. tyrrhena*, the surface sediment, the burrow wall lining and the chamber debris represented equivalent β -carotene sources.

Stable isotope analysis of the shrimps' food sources

The results obtained in situ for *C. longiventris* indicate a major reliance on chamber debris and on the burrow wall lining as sources of dietary carbon and nitrogen. Those shrimps living in the laboratory systems that were not supplied with debris apparently derived their nutrition from sources in the burrow wall lining and in the sediment of their empty chambers. Both situations underline the high nutritional relevance of the debris chambers and the burrow wall lining.

The nutritional source of *P. tyrrhena* is less clear. The ambient debris probably had some dietary relevance, whereas the surface sediment, ambient sediment, chamber debris and burrow wall lining made no significant contribution to the animals' carbon pool. Benthic diatoms and foraminiferans could have been carbon sources because their commonly encountered carbon signatures (Currin et al. 1995; Stribling & Cornwell 1997; Moodley et al. 2000) border the possible consumer's signatures (Figure 3). If this is the case, sorting and

Table III. Carbon and nitrogen stable isotope signatures of *Corallianassa longiventris* and *Pestarella tyrrhena*, carbon and nitrogen contents and carbon/nitrogen ratios of food sources in situ and in aquaria (mean \pm standard error, n in parentheses). "Natural abundance" refers to unlabelled samples.

	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C (%)	N (%)	C/N
<i>C. longiventris</i>					
In situ – natural abundance					
<i>C. longiventris</i> (6)	-13.34 ± 0.30	4.36 ± 0.13			
Surface sediment (2)	-16.61 ± 0.06	0.06 ± 0.23	0.36 ± 0.01	0.07 ± 0.00	5.13 ± 0.05
Ambient sediment (2)	-14.40 ± 0.29	0.81 ± 0.69	0.39 ± 0.05	0.04 ± 0.01	11.43 ± 0.91
Ambient debris (2)	-8.96 ± 0.00	2.30 ± 0.70	23.98 ± 6.65	1.06 ± 0.04	23.24 ± 7.18
Burrow wall (2)	-13.39 ± 0.05	2.87 ± 0.15	1.19 ± 0.01	0.13 ± 0.00	9.02 ± 0.36
Chamber debris (2)	-13.36 ± 1.48	1.59 ± 0.45	2.52 ± 0.05	0.20 ± 0.02	12.48 ± 0.81
Aquarium – natural abundance					
<i>C. longiventris</i> (5)	-14.98 ± 1.05	11.19 ± 1.63			
Surface sediment (3)	-11.43 ± 3.84	4.38 ± 1.93	0.43 ± 0.20	0.03 ± 0.00	13.43 ± 4.87
Ambient sediment (3)	-10.42 ± 3.16	10.10 ± 1.01	0.61 ± 0.17	0.02 ± 0.01	38.65 ± 14.71
Burrow wall (2)	-17.27 ± 0.04	8.57 ± 1.54	1.41 ± 0.60	0.08 ± 0.02	17.12 ± 3.79
Chamber bottom sediment (3)	-12.86 ± 2.71	9.02 ± 0.69	0.90 ± 0.21	0.03 ± 0.00	28.40 ± 6.27
Aquarium – dual labelled					
<i>C. longiventris</i> (3)	7.70 ± 2.60	1143 ± 146			
Surface sediment (2)	-11.77 ± 1.09	68.41 ± 7.04	0.46 ± 0.00	0.03 ± 0.00	28.66 ± 1.40
Ambient sediment (4)	-15.87 ± 1.75	16.08 ± 5.22	0.40 ± 0.02	0.03 ± 0.01	17.05 ± 2.90
Burrow wall (3)	21.56 ± 14.80	2233 ± 637	2.96 ± 1.00	0.08 ± 0.01	39.03 ± 12.80
Chamber bottom sediment (3)	-3.68 ± 1.68	608 ± 51	0.73 ± 0.10	0.03 ± 0.00	26.30 ± 3.79
<i>P. tyrrhena</i>					
In situ – natural abundance					
<i>P. tyrrhena</i> (3)	-15.39 ± 0.09	6.07 ± 0.47			
Surface sediment (3)	-23.03 ± 1.06	7.29 ± 2.52	0.35 ± 0.11	0.04 ± 0.02	28.23 ± 0.82
Ambient sediment (3)	-22.16 ± 0.17	0.06 ± 0.45	0.32 ± 0.06	0.07 ± 0.03	7.51 ± 3.42
Ambient debris (3)	-17.14 ± 0.67	2.26 ± 0.23	1.94 ± 0.52	0.13 ± 0.07	21.89 ± 5.69
Burrow wall (3)	-19.71 ± 0.12	1.08 ± 0.46	1.60 ± 0.01	0.14 ± 0.02	12.29 ± 1.45
Chamber debris (3)	-22.04 ± 0.86	1.00 ± 1.11	1.85 ± 0.37	0.13 ± 0.02	14.03 ± 1.06
Aquarium – natural abundance					
<i>P. tyrrhena</i> (2)	-15.24 ± 2.33	8.35 ± 0.21			
Aquarium – dual labelled					
<i>P. tyrrhena</i> (2)	-1.10 ± 0.32	961.68 ± 6.84			

concentration mechanisms must allow the animals to effectively separate diatoms and foraminiferans from the bulk organic matter within the sediment. A resuspension feeding mode, as reported for other thalassinidean species, is a good candidate (e.g. Nickell & Atkinson 1995; Stamhuis et al. 1998b).

The assimilation of artificially labelled seagrass debris demonstrated a strong uptake of debris carbon and nitrogen for both shrimps. The distribution within the *C. longiventris* burrow shows that carbon and nitrogen from labelled debris was also present in the burrow wall and to a lesser extent in the sediments of the chamber bottom and the surface. The debris was either directly transferred to these localities by the shrimp or may have been deposited there as faecal material. Thalassinideans have repeatedly been observed incorporating their faecal rods into the burrow wall (de Vaugelas et al. 1986; authors' pers. obs). In either case, the burrow wall lining plays an important role.

Quantitative estimation of nutrient demand in the burrow environment

To answer the question of whether thalassinidean shrimps can cover their nutritional demands by consuming the acquired debris requires making several assumptions about food quality and quantity.

For protein, the most important nutrient to shrimp, a maintenance ration of $1.5 \text{ mg g (shrimp)}^{-1} \text{ day}^{-1}$ was established for *Litopenaeus vannamei* (Kureshy & Davis 2002). Based on a comparison of thalassinidean shrimp respiration rates (Felder 1979) with those of penaeid shrimps (Chen & Lai 1993), thalassinideans probably need about 28% of the ration required by penaeid shrimp (based on equal temperatures and body weights).

An average *C. longiventris* individual from the sampling site weighs 3.77 g, which translates into a protein maintenance demand of $1.58 \text{ mg shrimp}^{-1} \text{ day}^{-1}$. The average rate at which debris is obtained is 132 mg day^{-1} . Based on the debris protein

content of 90 mg g^{-1} ($624 \text{ } \mu\text{M}$ (amino acid) g^{-1}), the shrimps would be able to cover their daily demand for bulk protein 7.5-fold with the debris caught each day (assuming direct consumption without conversion into chamber debris). This margin of excess certainly decreases due to protein losses during decomposition processes. Furthermore, only the minimal rations have been considered; the rations consumed during maximum growth in shrimps are about 10 times the maintenance levels (Kureshy & Davis 2002).

The same calculations for an average *P. tyrrhena* of 0.9 g, with a maximum debris supply of 135 mg day^{-1} and a protein content of 20 mg g^{-1} ($138 \text{ } \mu\text{M}$ (amino acid) g^{-1}), indicate that this shrimp would be able to cover its daily needs for bulk protein 7.1-fold. This number may also decrease due to the same factors mentioned above for *C. longiventris*. In *P. tyrrhena*, this value may drop further because we used the maximum amount of debris supplied to the burrow for the estimation.

Conclusion

The stable isotope experiments provided evidence that mud shrimps use the seagrass debris accumulated in their burrow chambers as a nutritional source. This corroborates the “hoard hypothesis”. Seagrass carbon and nitrogen are also transferred to the burrow wall lining, indicating an additional nutritional relevance of this part of the burrow. In both thalassinidean species, the rate at which debris is acquired from the surface was sufficient to cover the demands for macronutrients. However, a mixture of food sources is utilized to cover different dietary needs.

The macronutrients (delivering the bulk carbon and nitrogen) of *C. longiventris* are mainly derived from the debris inside the chambers and the burrow wall, whereas in *P. tyrrhena* they may originate from the ambient debris and probably from benthic foraminiferans and microphytobenthos. The distribution pattern of essential nutrients supports a microbial gardening as proposed in the “fermenter model”: *C. longiventris* preferentially feeds on chamber debris and to a lesser extent on its burrow wall, whereas *P. tyrrhena* obtains its essential nutrients from chamber debris, the burrow wall and the surface sediment. Among the essential nutrients, the EAAs lysine, histidine and phenylalanine, which are commonly in deficient supply to deposit feeders, were enriched in the burrow environments of the two shrimps. The HUFAs DHA and EPA are lacking in all potential food sources of *C. longiventris*. This species may be able to synthesize them de novo from the PUFA linolenic acid or may use another source.

For *P. tyrrhena*, the surface sediment represents a potential source of EPA, whereas its DHA may be supplied from the chamber debris. The most probable thiamine supplier for *C. longiventris* is the chamber debris, whereas for *P. tyrrhena* the uppermost layer of the surface sediment appears to be important. The dietary β -carotene of *C. longiventris* may also be derived from chamber debris, while for *P. tyrrhena* no specific source of this micronutrient was indicated.

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