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Primary Carbon Sources for Juvenile Penaeid Shrimps in a Mangrove-Fringed Bay of Inhaca Island, Mozambique: A Dual Carbon and Nitrogen Isotope Analysis

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Abstract— A study to estimate the relative importance of mangrove primary carbon and nitrogen sources to five commercial penaeid shrimps species was done at Saco da Inhaca, a non-estuarine mangrove-fringed bay on Inhaca Island, southern Mozambique. Carbon and nitrogen stable isotope ratios were determined in a variety of primary producers (mangroves, epiphytes, phytoplankton and seagrasses), sediments and in five penaeid shrimp species (*Penaeus (Fenneropenaeus) indicus, P. japonicus, P. semisulcatus, Metapenaeus monoceros* and *M. stebbingi*), collected within the bay in different habitats and during two different periods. The penaeid shrimps showed $\partial^{13}C$ values ranging from –13 to –19 ‰, (average of –15.6 ± 0.4 ‰, n=19) which is highly enriched compared to the mean value for mangrove leaves (average -27.6± 3.6 ‰, n=3) which varied from –20 to –32‰. The results shows that some shrimps may derive their carbon either from detritus, plankton remains or from benthic organisms. Overall, the carbon isotopic signal shifted as the shrimps got bigger, suggesting a change of diet with growth. No significant differences were found between $\partial^{15}N$ isotope values among the shrimps studied, indicating that they may belong in the same trophic position (except *P. semisulcatus*, which occupies a higher level). There is some evidence that sampling period influences the carbon isotope ratios for sediment and shrimps.

INTRODUCTION

Mangroves and adjacent coastal habitats are considered to be important nursery areas for shrimps and fish, including some commercially important penaeid shrimp species (Robertson and Blaber, 1992). Mangroves offer juvenile shrimps shelter against predation (Boesch and Turner, 1984), providing food directly or indirectly through the carbon fixed in the leaves as well as by retaining the newly migrated stages by lateral trapping (Wolanski and Ridd, 1986; Chong, 1995; Chong et al., 1996). Litterfall is thought to support the detritus food webs in the mangroves and adjacent coastal waters (Odum and Heald, 1972; Mathias, 1978) although the importance of its support has probably been overestimated (Lee, 1995; Bouillon et al., 2002a).

Several studies have examined the potential significance of mangrove detritus as a food source for shrimps. Methods like stomach content analysis and isotope ratio analysis have been widely used for trophic relationship studies (Chong and Sasekumar, 1981; Rodelli et al., 1984; Primavera, 1996; Chong et al., 2001; Bouillon et al., 2002b). Stomach content examination requires a good taxonomic knowledge of the consumed organisms, but what is observed in the stomach contents may not necessarily be assimilated (Bruce & Brian, 1987; Créach et al., 1997). In this regard, isotope

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analysis allows a better discrimination since it estimates the assimilated carbon by a given species (Rodelli et al., 1984; Bruce & Brian, 1987).

Chong & Sasekumar (1981) and Stoner & Zimmerman (1988) have examined shrimp stomach contents and reported the occurrence of different amounts of identifiable mangrove detritus, animals and benthic algae remains, and this has led to classifying the shrimps either as detritivorous, carnivorous or herbivorous. Rodelli et al. (1984) reported that several juvenile shrimp species collected within mangrove creeks in Malaysia derived their tissue carbon from mangroves. Chong et al. (2001) and Mohan et al. (1997) suggested that some *P. merguiensis* species of shrimp inhabiting the upper Matang estuaries in Malaysia and *F. indicus* post-larvae in the Godavari, India derive some of their carbon from mangroves. On the contrary, studies by Zieman et al. (1984), Newell et al. (1995), Primavera, (1996) and Bouillon et al. (2002b) have shown that mangrove systems do not make a major contribution to coastal food webs and have reported that penaeid shrimps derive their organic carbon from benthic algae, epiphytic algae or plankton.

The contrasting results found in the literature concerning primary carbon sources for penaeid shrimps emphasises the need for more research on this aspect. This work is part of a broader study to understand mangrove and shrimp connectivity for management issues in Mozambique. Questions such as which penaied species enter mangrove forest, how far they enter, and how much of the forest they occupy, have been answered by Rönnbäck, et al. (2002). These answers have given rise to a subsequent question: Why do penaied shrimps enter mangrove forests? Is it for protection against predation or is it because of food supplied by mangroves? The refuge from predation offered by mangroves to two penaeid shrimp species through the structural complexity of the roots (pneumatophore density), substrate type and turbidity has been investigated in the laboratory at Inhaca (Macia et al., 2003). This study addresses questions concerning the provision of food by mangroves to penaeid shrimps. The food availability hypothesis is tested by comparing the different primary carbon sources in the area with the assimilated carbon found in shrimps.

The study was carried out in a small mangrove-fringed bay at Inhaca Island in Mozambique (with several different closely connected habitats). The five species of penaeid shrimps considered showed characteristic distributions within the bay (Rönnbäck et al., 2002; Macia, unpublished). Stable isotope analyses of carbon and nitrogen were used to investigate the contribution of mangroves, seagrasses, epiphytes, plankton and sediment to the food web of five juvenile penaeid species occurring in the area.

MATERIALS AND METHODS

Study area

Saco da Inhaca, located in the southern part of Inhaca Island, Mozambique, is a small, semi-enclosed bay with a total area of 60 ha. It is fringed by mangrove forest, where *Avicennia marina* is the most dominant species (Kalk, 1969; de Boer, 2002b). According to Macnae & Kalk (1962) and de Boer (2002) the most extensive mangrove thickets (between the fringe and the outer *A. marina*) in this area are made up of *Ceriops tagal* and *Bruguiera gymnorrhiza*, with *Rhizophora mucronata* lining the banks of creeks and canals. *Lumnitzera racemosa* is less common and forms a very small spot in the upper part of the high waters limit. The total mangrove area in the southern bay of Inhaca (Saco) is about 209 ha (de Boer, 2000a). Adjacent to the mangrove forest, extended intertidal sand- and mud-flats are connected to seagrass meadows, making this bay a unique assemblage of closely connected environments that offer shelter and food to a diverse fauna (de Boer et al., 2001; Rönnbäck et al., 2002; Macia et al., 2003; Macia, unpublished data). The exposed intertidal area of Saco da Inhaca has already been described with respect to the presence of substrate type and macrophytes (Kalk, 1969; Bandeira 1991; de Boer, 2000a) (Fig. 1).

Sampling collection and laboratory processing

Sampling was conducted at four main locations within the bay: (1) the intertidal sand flats adjacent to the mangrove fringe; (2) the intertidal mud-flats

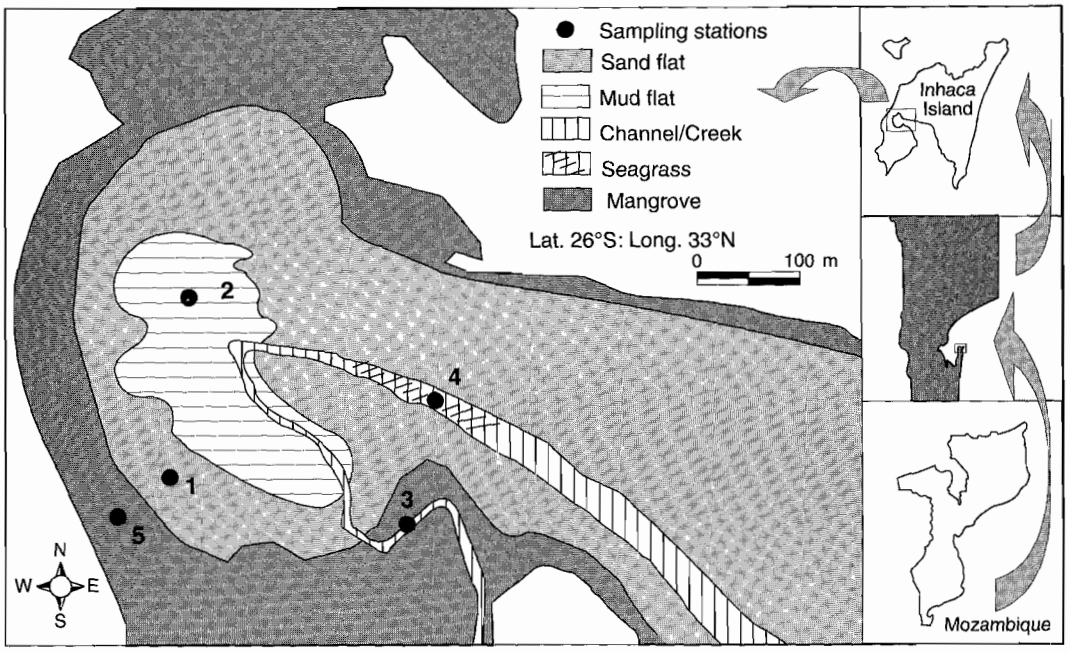

Fig. 1. Map of Inhaca Island showing the Saco Bay and the sampling sites

in the central part of the Saco (characterized by a relatively high percentage of fine sediment); (3) the creek in a mangrove-fringed (*R. mucronata* and *A. marina*) subtidal channel; (4) seagrass meadows (characterised by the occurrence of *Cymodocea serrulata Thalassodendron ciliatum* and *Halodule wrightii*) located in the subtidal channel bank and (5) mangrove forest (Fig. 1).

Five species of shrimp (*F. indicus*, *P. japonicus*, *P. semisulcatus*, *M. monoceros* and *M. stebbingi*), sediment (for associated carbon sources), mangrove leaves, epiphytic algae, seagrass and plankton samples were collected in December 2000 and October 2001 at the different sampling sites within the bay, including sites in the interior of the mangrove forest. Shrimps were collected by means of a beam net towed by a small boat (with an outboard engine) and by hand using a dip net. Mangrove leaves were picked by hand from the trees as well as the seagrass meadows. Bottom sediment was collected using five small plastic tubes (3 cm x 1cm), introduced into the sediment to a depth of 0.5 cm in each of the defined sampling habitats (Fig. 1). Plankton (seston) samples were collected by simultaneously towing three different mesh size nets (plankton nets: 60 µm, 125 µm and 330 µm). Epiphytic algae were removed by hand from mangrove pneumatophores and placed in plastic bags. All samples were immediately stored in a cool box with ice and transported to the Inhaca Island Marine Biological Station, where they were kept in a deep freezer for two days before being transported to the ecology laboratory at the Department of Biological Sciences, Eduardo Mondlane University in Maputo for analysis. The epiphytic algae were cleaned in a container with distilled water before being frozen in order to remove attached sediment and any scraped mangrove bark.

Plankton samples were decanted for 24 hours after removing all debris. The excess water was removed and the remainder oven-dried at 70 ° C for seven days. The dried plankton samples were ground to a fine powder using a pestle and mortar and treated with 1M HCl for 1.5 hours to remove carbonates. They were then rinsed three times with distilled water before freeze-drying for 24 hours. All collected sediments were oven-dried at 70 °C for six days, ground to fine powder and then sieved through a fine mesh and treated with 1 M HCl for 1.5 hours. The samples were rinsed three times with distilled water, dried and weighed for analysis.

Mangrove leaves, seagrasses (free of epiphytes) and epiphytes were cleaned and rinsed with distilled water prior to desiccation at 70 °C for six days then ground to a fine powder and passed through a fine-mesh size.

The shrimps were identified and their carapace length (CL) measured. Their midguts were removed from the abdominal muscle tissue prior to dissection, during which shrimp shell was also removed. Shrimp samples were grouped in sizes according to shrimp availability in the catches. The muscle was rinsed with distilled water and oven-dried at 70 °C for six days. Dried shrimps were ground into a fine powder, which was placed in plastic bags. All dried samples of primary producers, sediments and shrimp samples were processed in the Archaeometry Laboratory, Archaeology Department of the University of Cape Town for stable carbon and nitrogen isotope analysis. Samples were combusted in sealed Vycor tubes at 800 °C and the resulting gases (CO_2 and N_2) were separated and dried by cryopurification. Stable isotope ratios were measured using a Finnigan Mat 252 isotope ratio mass spectrometer. Ratios were expressed in relation to conventional standards, using the following equation (Craig, 1975):

$$\partial A = [(X \text{ sample} - X \text{ standard}) / X \text{ standard}] \times 1000$$

where A= ^{13}C ‰ or ^{15}N ‰ and X=$^{13}C/^{12}C$ or $^{15}N/^{14}N$ and the standards being PeeDee Belmmite (PDB) for carbon and atmospheric air for nitrogen. The precision of the analyser was 0.2‰.

Data analysis

Statistical analysis was used to test the hypothesis that all penaeid shrimp species use the same source of carbon in different habitats and that carbon sources found in different habitats are similar. Statistical Kruskall–Wallis non-parametric tests were performed to compare carbon and nitrogen signals among the sources, including sediment, the shrimp species within and between the different habitats.

RESULTS

Primary producers and sediment

Mangrove leaves showed a wide range of $\partial^{13}C$ ratios between the different tree species (–32.8 to –20.0 ‰). They were among the most depleted values found in the study period. Similarly, the epiphytic algae showed low values (Table 1). Two species of mangrove trees had comparable values, while senescent *C. tagal* leaves had more enriched $\partial^{13}C$ isotope as well as ^{15}N values (Table 1). The average $\partial^{13}C$ and $\partial^{15}N$ ratios were -27.6 ± 3.7‰, (n=3) and 1.8 ± 1.2 ‰, (n=3) respectively. Epiphytic algae from *A. marina* pneumatophores were very depleted in ^{13}C with a mean value of -32.9 ± 0.5 ‰ (n=3). However, the mean $\partial^{15}N$ of 2.4 ± 0.4 ‰ (n=3) was much higher than the mean mangrove value for this isotope (Table 1).

Plankton (seston) samples for $\partial^{13}C$ and $\partial^{15}N$ isotope ratios ranged from -21.1 to -19.8 ‰ and from 3.4 to 3.8 ‰, respectively, with isotopes average for each of –20.5 ± 0.3 ‰ (n=3) and 3.6 ± 0.2 ‰ (n=3). The sediment collected in December 2000 showed $\partial^{13}C$ and $\partial^{15}N$ values between –24.7 and –21.9 ‰ and between 1.0 and 0.7 ‰ respectively while for sediment collected during October 2001 the ranges were from –26.9 to –18.0 ‰ and from 1.2 to 1.9 ‰ respectively. Sediments from the mangrove forest and creek were more highly depleted in carbon than the remaining sampled habitats (Table 1). Mud sediment collected in December 2000 was on average more depleted in ^{13}C ($\partial^{13}C$ = -23.3±1.4, n=2) than sediment collect from the same area in October 2001 ($\partial^{13}C$ =21.3±2.1, n=4).

In general, sediment carbon values were more enriched in relation to all primary producers except the seagrasses. Kruskall–Wallis ANOVA showed significant differences between carbon signatures among the potential sources (mangroves, epiphytic algae, plankton) including sediment [H (9, N = 19) = 17.44737, p = 0.0422] but did not indicate any significant differences in the nitrogen values among the sources [H (9, N = 19) = 15,89025, p = 0.069].

Table 1. Carbon and Nitrogen stable isotope ratios for penaeid shrimps, plankton, mangroves, seagrass, epiphyte and sediment collected inside the Saco Bay, Inhaca

Species/Sources (no. of shrimps, tows or leaves used)/n+		Site	$\partial^{13}C$	$\partial^{15}N$
A. December 2000				
	Size (CL-mm)			
Metapenaeus monoceros (22)/4	5–10	Mud flat	-19.7 ± 0.6	5.4 ± 0.5
Fenneropenaeus indicus (31)/5	4–10	Mudflat	-19.9 ± 0.3	5.9 ± 0.3
Metapenaeus stebbingi (15)/3	2–4	Mudflat	-16.1 ± 0.4	5.0 ± 0.4
M. stebbingi (21)/ 2	5–10	Sand flat	-14.5 ± 0.5	6.4 ± 1.2
Penaeus japonicus (22)/3	4–7	Sand flat	-16.8 ± 0.5	5.5 ± 0.3
Penaeus semisulcatus (4)/ -	12	Seagrass	-13.7	5.1
P. semisulcatus (6)/ -	16	Seagrass	-16.7	11.8
Plankton (seston)	**Mesh Size**			
Plankton I (3)/3	60 µm	60µm	-19.8 ± 0.2	3.8 ± 0.2
Plankton II (3)/3	125 µm	125µm	-21.1 ± 0.3	3.6 ± 0.3
Plankton III (3)/3	330 µm	330µm	-20.4 ± 0.2	3.4 ± 0.5
	(All sizes)	–	-20.4 ± 0.3	3.6 ± 0.2
Mangrove leaves	**Status**			
Rhizophora (6)/3	Green		-32.8 ± 1.0	0.5 ± 0.4
Avicennia (6)/3	Green		-30.1 ± 0.8	0.8 ± 0.4
Ceriops (6)/3	Senescent		-20.0 ± 1.0	4.1 ± 0.4
	Mean		-27.6 ± 3.7	1.8 ± 1.2
Epiphytic algae -/2	Green	Pneumatophore	-32.9 ± 0.5	2.4 ± 0.4
Seagrass (6)/2	Green	Seagrass	-11.9 ± 0.4	-0.8 ± 0.2
Sediment samples (5)/3		–	-21.9 ± 0.5	0.7 ± 0.6
Sediment under Mangrove (5)/3	–	Mudflat	-24.7 ± 0.5	1.0 ± 0.3
B. October 2001				
	Size (CL-mm)			
Metapenaeus monoceros (31)/3	5–10	Creek	17.6 ± 0.7	5.96± 0.3
Penaeus indicus (23)/3	5–7	Creek	-17.7 ± 0.4	5.6 ± 0.3
M. monoceros (9)/-	4	Mudflat	-14.8	5.9
M. monoceros (10)/-	6	Mudflat	-14.7	5.74
M. monoceros (5)/-	10–14	Mudflat	-13.9-	6.09
M. monoceros (5)/-	8	Sandflat	-15.7	5.75
M. monoceros (3)/-	15	Sandflat	-16.2	6.50
Metapenaeus stebbingii (9)/-	4	Mudflat	-15.1	5.80
M. stebbingii (8)/-	12–13	Mudflat	-13.7	6.05
Penaeus japonicus (14)/-	4	Mud flat	-14.2	6.09
P. japonicus (12)/ 3	7–13	Mud flat	-13.7 ± 0.4	6.0 ± 0.2
P. japonicus (16)/2	4–6-	Sand flat	-16.0 ± 0.6	5.9 ± 0.2
		Mud flat	-18.0 ± 0.2	1.9 ± 0.3
Sediment samples (15)/3		Sand flat	-18.5 ± 0.3	1.4 ± 0.3
		Creek	-26.9 ± 1.5	1.2 ± 0.8
Sediment under mangrove (5)/3	–	–	-21.9 ± 0.5	2.7 ± 0.1

+'n' indicates the number of replicates used to calculate the mean ± SE; /- indicates no replicates.

Shrimps

Juvenile shrimps exhibited a wide range of carbon isotope ratios (Table 1). The shrimp community could be separated into two basic groups: *M. stebbingi, P. japonicus* and *P. semisulcatus* on sand substrate and seagrass (–17‰ to –13‰) and *M. monoceros, F. indicus* on mudflats/mangroves creek (–20 ‰ to –17‰). In general, the variability for nitrogen isotope ratios was lower for all shrimp species. However, large sized (CL=16 mm) *P. semisulcatus* showed much higher $\partial^{15}N$ values in comparison to all other species.

Kruskall–Wallis ANOVAs showed that carbon ratios differed significantly between shrimp species[H (3, N = 18) = 13.228, p = 0.0041], but that nitrogen did not [H (3, N = 18) = 4.365, p = 0.2246]. Different species occupying the same habitat seem to derive their carbon from the same source (Table 1). No statistical differences were found between *F. indicus* and *M. monoceros*, caught on the mud flat [H (1, N = 8) = 0.084, p = 0.771] and *M. stebbingi* and *P. japonicus* caught on the sand flat [H (1, N = 8) = 0.083, p = 0.773]. *Fenneropenaeus indicus* and *M. monoceros* showed the most depleted ^{13}C signatures while *M. monoceros* exhibited a variety of isotope values among the habitats (–13.9 to –19.7 ‰) (Table 1).

The dual plot of $\partial^{13}C$ and $\partial^{15}N$ isotope ratios (Fig. 2) shows that the carbon signatures of the shrimps are generally very different from those of the primary producers, especially mangrove leaves and epiphytic algae on pneumatophores. However, *F. indicus* and *M. monoceros* have carbon isotope ratios close to that of plankton (seston) and senescent *C. tagal* leaves, as well as close to some sediment organic matter. The remaining three species had carbon signatures between the seagrasses and the plankton. Some specimens of *P. semisulcatus, P. japonicus* and larger *M. monoceros* had carbon signatures close to those of seagrasses, although somewhat more depleted.

DISCUSSION

Mangroves mean $\partial^{13}C$ ratio values (-27.6‰) were very close to the mean values reported in other studies and locations, e.g. –27.4 to –28.3 ‰ (Rodelli et al., 1984; Hemminga et al., 1994; Newell et al., 1995; Primavera, 1996; Loneragan et al., 1997). However, carbon values for senescent *C. tagal* were very much enriched (–20‰) compared to these reported by Loneragan et al. (1997) in Australia, e.g. –27 ‰ for both the dry and the wet seasons. They were, however, closer to the values reported by Hemminga et al. (1994), (–24.1 ‰) in Kenya and Skov (pers. com.), (–22.1 ‰) in Zanzibar, Tanzania. *Ceriops tagal*, together with *B. gymnorrhiza*, comprise the most extensive mangrove thicket in the area. Therefore, its contribution in terms of litterfall in the area may probably be significant. It is important to note that during the collection period *C. tagal* was the only species with yellow senescent leaves. Except for C. *tagal* nitrogen isotope ratios

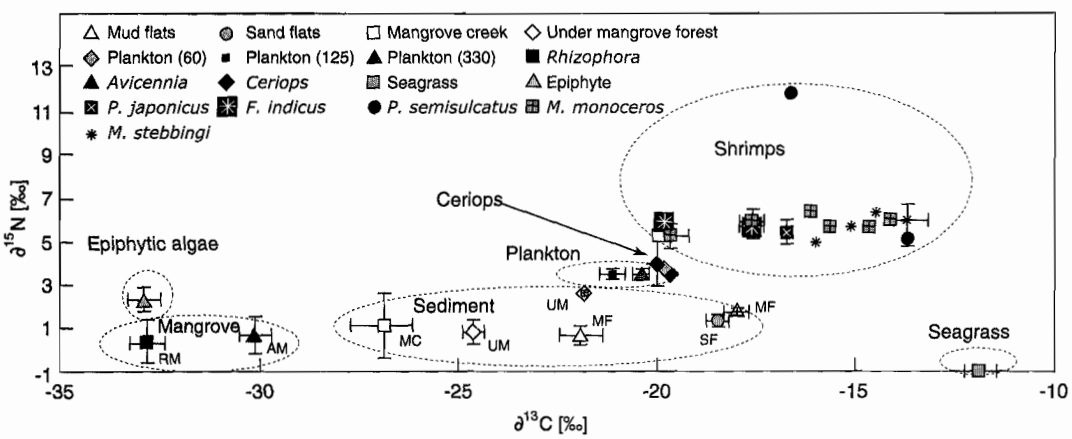

Fig. 2. Plot of ∂C13 and ∂N15 for different primary producers, plankton (seston), sediment and penaeid shrimps collected at Saco da Inhaca, Mozambique. Error bars indicate SE. (n = 2–6)

for mangrove leaves were generally lower compared to those from studies performed at other geographic locations, especially those in Africa and Asia (see Rodelli et al., 1984; Newell et al., 1995; Primavera, 1996; Mohan et al., 1997; Chong et al., 2001). However, according to Fry et al. (2000) mangrove leaf nitrogen isotope values are extremely variable, ranging from –10 to 10 ‰.

Epiphytic algae on the mangrove pneumatophores exhibited a very depleted $\partial^{13}C$ rate, but close to the $\partial^{13}C$ of the mangroves, indicating that the sources of inorganic carbon may be similar to those of the mangroves. However, this is not consistent with the $\partial^{15}N$ values, which were on average higher than the mangrove $\partial^{15}N$ values.

Sediment carbon signatures were different between some habitats and between the sampling periods, suggesting temporal and spatial changes in carbon signal of the producers. Mean sediment carbon values in creeks and under mangrove forest areas reflect the presence of large amounts of mangrove detrital carbon when compared to sand and mud sediment, which exhibit more enriched ratios. The sediment organic matter under the mangrove vegetation had $\partial^{13}C$ less depleted compared to the $\partial^{13}C$ ratios found in some other studies (Rodelli et al., 1984; Primavera, 1996; Chong et al., 2001) especially in October 2001, but were very similar to those reported by Bouillon et al. (2002a), who obtained an average carbon signature of -21.8‰ in an estuarine mangrove sediment in India. There is a clear gradient of enrichment of $\partial^{13}C$ as we move from the mangrove areas to the seagrass habitat.

In the mud and sandflats the $\partial^{13}C$ values were very similar and much more enriched compared to mangrove $\partial^{13}C$. This result emphasises the low mangrove detritus influence in the carbon pool of these habitats. Bouillon et al. (2002b) also found a discrepancy between the sediment organic matter in the creeks and adjacent Bay in an Indian estuarine mangrove and that of mangrove-derived carbon. Despite the uncertainty regarding *C. tagal* carbon contribution in the area, its carbon signal reveals it to be a potential direct source of carbon for shrimps. Its carbon signature is about –1 ‰ more depleted in comparison to some *F. indicus* and *M. monoceros* captured in the area. However, information concerning its contribution to the carbon budget of the system requires further investigation.

The nitrogen signatures reported in sediment samples were very depleted. It should be noted that all the sediments analysed in this study are exposed for long periods during low tides. This may allow some of the primary producers occurring in the sediment to utilise atmospheric nitrogen, which, in turn, contributes to depletion of the isotopic signal, as suggested by Flemming et al. (1990).

Mean carbon isotopes values reported in some specimens of shrimp species (e.g. *F. indicus* and *M. monoceros*) in both study periods are very close to the sediment carbon signal, which supports the interpretation that these shrimps may obtain their carbon from detritus and are probably detritivores. This, however, contradicts Primavera's (1996) conclusion, disproving the widely held concept of detritivory in penaeid shrimps. According to Dall et al. (1990), penaeid shrimps are omnivorous, although they might show preference for animal food over detritus. It is important to note that despite the similarity between some sediment organic matter and some of the shrimp $\partial^{13}C$ signals (Table 1), not all the species examined in this study showed the same trend. Loneragan et al. (1997), found that primary carbon sources utilised by shrimp depend on their location within the Australian estuary studied. In our study, it is evident that this assumption is not always applicable. For example, some *M. monoceros* and *F. indicus* found in the creeks (Table 1B) have carbon signals more resemble the signal from mudflats and sandflats more closely than those from the creek areas.

It seems that smaller-sizes shrimp species have more depleted $\partial^{13}C$ values than larger-sized ones (see *M. monoceros*). However, a more consistent size–class analysis is required to better clarify this finding.

The results on shrimp carbon isotope signatures in different habitats around Saco da Inhaca show that, apart from senescent *C. tagal*, these mangroves do not seem to contribute very much to the shrimp food web, at least during the seasons when the study was conducted.

There is a strong indication that large amounts of carbon are probably derived from plankton and other benthic organisms. The nitrogen ratios in this

groups of carbon suppliers are more in-keeping with the levels reported in the shrimps, and they seem to be the most likely sources. Similar findings have been reported by other authors (Zieman et al., 1984; Stoner & Zimmerman, 1988; Primavera, 1996; Loneragan et al., 1997; Bouillon et al., 2002b) who showed that some penaeid shrimps did not obtain their carbon from mangroves, but from benthic algae, plankton, epiphytic algae or seagrasses. *Fenneropenaeus indicus* and *M. monoceros* may probably obtain their carbon from plankton or even from detritus and sediment-associated organisms, while the other species may derive their carbon from less evident, non-identified sources that might be associated with the sediment, most probably benthic microalgae, as reported by Zieman et al. (1984) and Stoner & Zimmerman (1988). According to the literature, carbon ratio values of benthic micro-algae are known to vary from -12 to -20 ‰ (Bouillon, 2003). Micro-algae are thus a possible carbon source for these shrimps. No attempts were however, made to isolate any benthic algae or bacteria in the sediment during this study. However, this author's recent unpublished data reveals that benthic micro-algae from the Saco da Inhaca area have $\partial^{13}C$ and $\partial^{15}N$ signatures of –19 and 6 ‰ respectively which shows that they might be a potential source of carbon and nitrogen for these crustaceans.

It is important to note that only one seagrass species was analysed in this study, although the seagrass meadows in the bay are composed of two to three species. According to Hemminga & Mateo (1996), values of carbon and nitrogen isotope ratios vary considerably between seagrass species. It might also be expected that the remaining seagrass species could have some influence on the shrimp carbon signal.

Isotopic evidence for mangroves being a carbon source for shrimps was only found in the sediment collected in the creeks and in the mangrove forest. Because samples representing shrimp catches from the mangrove forest habitat were insufficient for isotope analysis, no information on shrimp carbon signatures is available for this habitat. Nevertheless, shrimps captured in the creeks (the mangrove vicinities) did not reflect the $\partial^{13}C$ isotope ratios reported in the sediment analysis for this habitat.

Despite the small size of the bay, carbon distribution varied greatly in its various habitats, and differences in the carbon signal were also found for different species and shrimps sizes. This observation is substantiated by the wide range in isotope ratios (–19.9 to –13.7 ‰) for the shrimps captured in the bay, indicating possible assimilation of carbon from different sources. For example, *M. monoceros*, *M. stebbingi* and *P. japonicus* from mudflats, have similar signatures to *M. monoceros* and *P. japonicus* from sandflats and *F. indicus* and *M. monoceros* from creeks and from mudflats. This finding suggests an overlap in diet for some of the shrimp species, which may contribute to inter-specific competition for food. *Metapenaeus monoceros* was observed to be the species with the widest utilization of different carbon sources. It should be noted that *M. monoceros* is also widely distributed in different habitats around the Saco Bay (Macia, unpublished data). *Metapenaeus stebbingi*, *P. japonicus* and *P. semisulcatus* and some specimens of *M. monoceros* and *F. indicus* had carbon signatures between of those of plankton and seagrass. It appears that these shrimps may most probably derive their nitrogen from plankton rather than from mangroves and seagrass. One interesting aspect from the results is that the $\partial^{15}N$ values of all penaeid species collected in the different habitats and periods show fairly consistent signatures (Table 1), which may suggest that these penaeid shrimps belong to the same trophic level. However, the large-sized *P. semisulcatus* had high nitrogen values (11.8 ‰) compared to all other species, suggesting that it occupies a higher position.

From the weak mangrove carbon signature in the sediment, especially for the 2001 samples, it seems that the mangrove litterfall is either seasonal, the decomposition is fast, or there is a net export of litter. This suggests that there might be other sources of carbon or an important import of carbon from other sources with more enriched signatures, such as seagrass and plankton. According to de Boer et al. (2000) higher water velocities are reported at Saco Bay during ebb tides (0.70 m/s) than during flood tides (0.5 m/s), which may probably lead to a higher tendency for drainage of mangrove carbon than for its retention. Bouillon et al. (2002a) reported that the export of mangrove

carbon does not necessarily imply that a net export of organic matter occurs between the mangrove forest and the adjacent environment, as the amount of organic matter imported during high tide may exceed that of outwelling mangrove carbon.

According to Dehairs et al. (2000) the mangrove carbon contribution to an Indian estuarine system is less than, e.g., the phytoplankton contribution, by a factor of five, taking into account the relative surface area of the water column and the mangrove area. Saco da Inhaca is a very small bay with good light conditions for phytoplankton development and an average water depth of 1.5m (Macia, unpublished). De Boer (2000a) found that seagrasses production exceeded that of mangrove litter. However, the seagrass isotope signal reported in this study was less depleted than those of the consumers. It is not known, however, what type of signal is reflected in shrimp flesh if the carbon is coming from different sources of producers e.g. mangroves and seagrasses (the former enriched and the latter depleted). This is a question that needs to be addressed in future studies. Bouillon et al. (2002b) stated that other sources of depleted carbon, such as phytoplankton, in areas near mangroves, may overlap in signatures and confound the interpretation of the carbon signatures of consumers. Flemming et al. (1990), who studied mangrove detritus in an estuarine ecosystem in USA, reported that in areas where mangroves and seagrass communities are in close association, the relative contribution of detritus to the food web is difficult to determine.

The carbon signatures of *F. indicus* and *M. monoceros* collected in mud habitats in both study periods provide very strong evidence that the sampling time may have had a large influence on isotope ratios. Therefore, it seems that some care should be taken when comparing the results of isotope analysis from samples that have been taken during different seasons.

Despite the apparent lack of a direct supply of carbon from mangroves to shrimps, the role of Saco mangroves as a habitat for juvenile peanaeid shrimps and other fauna has been stressed by Rönnbäck et al. (2002) and Macia et al. (2003) and, for other locations worldwide, by several authors (Staples et al., 1985; Vance et al., 1990: Vance et al., 1996). Mangroves are complex ecosystems that have direct or indirect importance on the development of potential sources of carbon for the shrimps occurring in Saco Bay. In order to fully understand the carbon pathway in the mangrove ecosystems, more information is needed on carbon sources for many infaunal organisms feeding on mangroves, especially meiofauna, and on the microheterotrophs as trophic intermediates (Bouillon et al., 2002a). The fact that the isotope signatures of some shrimp species do not match any of the studied primary producers may also be because these shrimps are omnivorous and derive their carbon through carnivorous foraging as referred to by Gleason & Zimmerman (1984).

The results in this study contradict the expectations based on the current food hypothesis proposed to explain the mangrove–shrimp connectivity. However, further studies are required in order to precisely discriminate the contributors of carbon to some of the penaeid shrimps occurring at Saco da Inhaca. Emphasis should be placed on other potential sources of carbon such as benthic microalgae, benthic microfauna, seagrasses and the interior of the mangrove forest where species like *F. indicus* are very common (Rönnbäck et al., 2002). Shrimp sizes need to be taken into consideration in future studies in order to better understand the diet shift with regard to shrimp growth.

CONCLUSIONS

Overall, the results presented here suggest that there is no clear evidence that mangroves are the major carbon and nitrogen contributors for penaied shrimps occurring in the area. Plankton and organic matter from the sand- and mudflats appear to be the only sources for carbon and nitrogen in the penaeid shrimps studied. A gradual decrease in carbon isotopic ratio with increasing size was seen for all of the shrimp species, suggesting a diet shift to less dependence on primary carbon source as the shrimps grow.

All of the shrimp species appear to belong to the same trophic level, except the larger-sized *P. semisulcatus*, whose level seems to be higher. Season may have an influence on carbon isotope ratios, thus any comparisons between sites and seasons should be made with caution.

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