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Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests

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Abstract In contrast to the large number of studies on the trophic significance of mangrove primary production to the aquatic foodweb, there have been few attempts to provide an overview of the relative importance of different primary carbon sources to invertebrates in the intertidal mangrove habitats. We determined carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in sediments, primary producers, and 22 invertebrate species from an intertidal mangrove forest located along the southeast coast of India in order to determine the contribution of mangrove leaf litter and other carbon sources to the invertebrate community. Organic matter in sediments under the mangrove vegetation was characterized by relatively high $\delta^{13}\text{C}$ values and low C:N ratios, indicating that mangrove-derived organic matter was not the principal source and that imported phytodetritus from the mangrove creeks and adjacent bay significantly contributed to the sediment organic matter pool. Invertebrates were found to display a wide range of $\delta^{13}\text{C}$ values, most being 3–11‰ enriched relative to the average mangrove leaf signal. The pulmonate gastropod *Onchidium* sp. showed unusually low $\delta^{15}\text{N}$ values ($-5.6 \pm 0.9\text{‰}$), but further work is needed to adequately explain these data. A compilation of stable isotope data from various sources indicates that significant assimilation of mangrove-derived carbon is only detectable in a limited number of species, and suggests that local and imported algal sources are a major source of carbon for benthic invertebrate commu-

nities in intertidal mangrove forests. These results provide new insights into carbon utilization patterns in vegetated tropical intertidal habitats and show a striking similarity with results from temperate salt marsh ecosystems where local plant production has often been found to contribute little to intertidal foodwebs.

Keywords Carbon · Intertidal foodwebs · Sediment · Trophic relations

Introduction

Tropical mangrove forests can attain high net primary production rates (Clough 1992), and although there remains some uncertainty about the fate of the leaf litter and its role in sustaining adjacent aquatic secondary production, it has become clear that this role has been overestimated in the past (e.g. Lee 1995, 1999; Bouillon et al. 2000, 2001; Dehairs et al. 2000). For the macro-invertebrate fauna inhabiting the intertidal regions, however, most studies assume or conclude that mangroves are the dominant primary producers sustaining these communities (e.g. Camilleri 1992), which are usually dominated – both in terms of numbers and biomass – by brachyuran crabs and gastropods (e.g. Sasekumar 1974; Wells 1984). Few studies have attempted to provide an overall evaluation of different primary carbon sources to the intertidal mangrove invertebrate community, despite the potential importance of these faunal communities in ecosystem carbon dynamics (Robertson et al. 1992) and as food sources for foraging fish during high tide (Sasekumar et al. 1984; Wilson 1989; Sheaves and Molony 2000). Stable isotope analysis can offer valuable insights into the relative importance of different primary producers, but such studies have only rarely been done on mangrove-inhabiting invertebrates (Rodelli et al. 1984; Newell et al. 1995), or have been limited to a specific invertebrate species (Slim et al. 1997; France 1998). The stable isotope approach is based on the assumptions that (1) different primary producers (can)

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have different $\delta^{13}\text{C}$ values because of different photosynthetic pathways or different inorganic carbon sources, and (2) a consistent degree of fractionation occurs between the isotopic signal of the diet and that of the consumer. For $\delta^{13}\text{C}$, a small or negligible enrichment of on average 0–1‰ has been found to occur (DeNiro and Epstein 1978). For $\delta^{15}\text{N}$, a higher fractionation of on average 2.6‰ (Owens 1987) to 3.4‰ (Minagawa and Wada 1984) is usually assumed, but the actual degree of fractionation may vary considerably, and several processes have been found to result in deviations from this general pattern (e.g. Scrimgeour et al. 1995).

Sesarmid crabs are known to have a high impact on leaf litter dynamics as they can remove a large amount of leaf litter from the sediment surface and carry it into their burrows (e.g. Twilley et al. 1997; Lee 1998). On the other hand, it appears that many sesarmids are more likely to be omnivores than strict herbivores (Dahdouh-Guebas et al. 1999). Ocypodid crabs from mangrove forests such as *Uca* spp. have been considered as either bacteria feeders (e.g. Dye and Lasiak 1986, 1987) or microalgal (including cyanobacteria) feeders (Rodelli et al. 1984; France 1998), and even less is known about the feeding habits of mangrove-dwelling gastropods which are often referred to as 'deposit-feeders' (Plaziat 1984), with little information on their selectivity for mangrove detritus or algal food sources (e.g. Yipp 1980; Rodelli et al. 1984).

Benthic microalgal production in mangrove forests is often low due to light limitation and/or inhibition by soluble tannins (e.g. Alongi 1994), but they have been found to be an important component of foodwebs in other intertidal ecosystems such as salt marshes (e.g. Sullivan and Moncreiff 1990; Currin et al. 1995; Page 1997), and several authors have suggested that their potential role in mangrove ecosystems deserves further

study (e.g. Micheli 1993; Newell et al. 1995). The potential trophic importance of imported organic matter such as phytoplankton from creeks (Bouillon et al., unpublished data) has also not been investigated. In an attempt to evaluate the importance of different primary producers to mangrove-inhabiting fauna, we analysed carbon and nitrogen stable isotope ratios of 23 species of invertebrates from a mangrove forest on the east coast of India, near the mouth of the Gautami Godavari River, along with sediments and primary producers.

Materials and methods

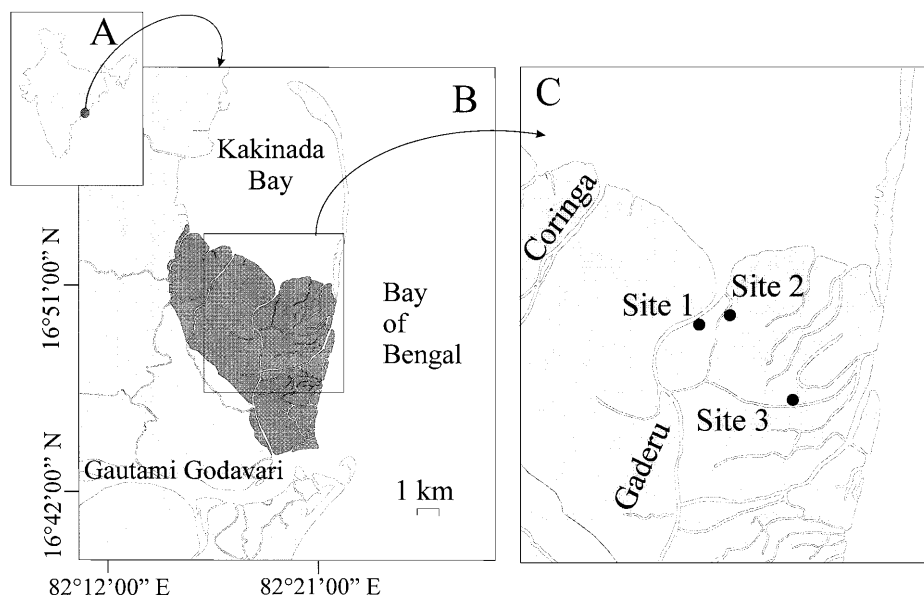
Study area

Samples were collected in the Coringa Wildlife Sanctuary (Fig. 1), which is part of the mangrove-covered area between Kakinada Bay and the Gautami branch of the Godavari (between 82°15' and 82°22' E, 16°43' and 17°00' N). The Godavari is India's second largest river and opens into the Bay of Bengal in the south-eastern state of Andhra Pradesh. The Gautami Godavari also has several branches into Kakinada Bay, the most important of these being Coringa and Gaderu. The sanctuary is dominated by mangrove forests and tidal mudflats, the most abundant mangrove species being *Avicennia marina*, *A. officinalis*, *Excoecaria agallocha*, *Sonneratia apetala*, *Rhizophora mucronata* and *R. apiculata*. Tides are semidiurnal and tidal amplitude in the bay is about 0.5–2 m. Samples were collected at three sites within the sanctuary, located along the Gaderu creek and one of its side creeks (Fig. 1) during a 2-week period in November and December 1999, but some mangrove leaf samples were collected in June 1999 at several other sites in the sanctuary. At all three sites, vegetation is dominated by *A. officinalis* and *E. agallocha*, but site 3 was near to a patch of non-mangrove species, *Suaeda maritima* and *S. monoica*.

Sample collection and preparation

All samples of vegetation, surface sediments and fauna were collected by hand, while benthic microalgae were obtained by gently

Fig. 1 Location of the sampling sites. Darkest areas in panel B indicate the most important mangrove-covered areas



scraping them off the sediment where they formed a conspicuous layer. All faunal samples were kept in a cool box, transported to the field laboratory, washed and dried at 60°C for at least 48 h. For the smaller *Uca* spp. and *Metaplex* spp., the gut and intestinal system were first removed and muscle tissue of the body was used; for larger crab species muscle tissue was taken from the chelae. For the small *Assimineea* sp. four individuals were pooled as one sample. These tissues were ground to a fine powder, and subsamples for $\delta^{13}\text{C}$ and elemental (C:N) analysis were treated with dilute HCl to remove possible carbonates and redried. As this treatment has been reported to affect $\delta^{15}\text{N}$ values (Bunn et al. 1995), subsamples for $\delta^{15}\text{N}$ analysis were not acidified.

Measurement of elemental and stable isotope ratios

Elemental ratios (C:N) of sediment were determined with a Carlo Erba NA-1500 Elemental Analyser. Sediment and biotic samples for stable isotope analysis were similarly combusted, and the resulting gases (CO_2 and N_2) were separated by cryopurification using a manual extraction line. Stable isotope ratios were then measured on a Delta E Finnigan Mat isotope ratio mass spectrometer, and are expressed relative to the conventional standards, i.e. PDB limestone for carbon and atmospheric air for nitrogen, as δ values, defined as:

$$\delta R = \left[\frac{X_{\text{sample}} - X_{\text{standard}}}{X_{\text{standard}}} \right] \times 10^3 [\text{permil}] \quad (1)$$

where $R = ^{13}\text{C}$ or ^{15}N , and $X = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Internal reference materials used were ammonium sulphate (IAEA-N1, IAEA-N2) and ammonium nitrate (IAEA-NO-3) for ^{15}N , and sucrose (IAEA-C6) and polyethylene (IAEA-CH-7) for ^{13}C . The standard deviation on 10 aliquots of the same sample was lower than 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Results

Primary producers and sediments

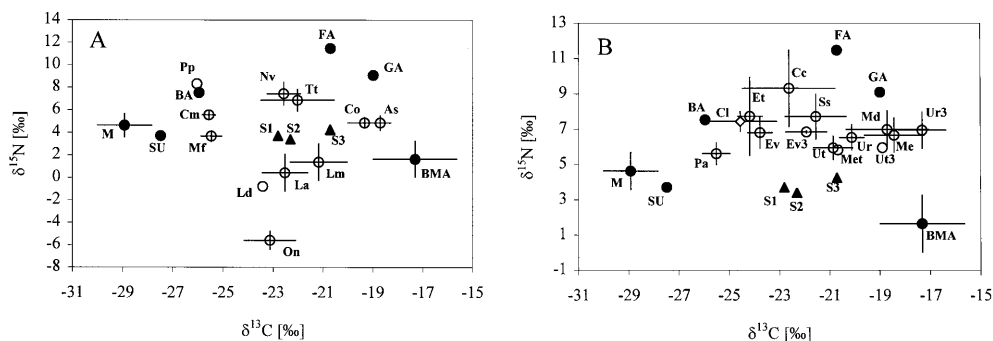
Leaves of *Avicennia officinalis* and *Excoecaria agallocha* showed an average $\delta^{13}\text{C}$ of -27.9‰ ($n=5$), close to the overall value for mangrove leaves from this area ($-28.6 \pm 1.4\text{‰}$, $n=17$). Nitrogen stable isotope ratios for these leaves averaged $+4.1\text{‰}$ ($n=5$), close to the average of $+4.6 \pm 1.1\text{‰}$ ($n=12$) for the area (Fig. 2A). *Suaeda* sp. showed similar values of -27.5‰ and $+3.7\text{‰}$ for carbon and nitrogen, respectively. Carbon stable isotope ratios of benthic microalgae scraped off the sediment were much more enriched, averaging $-17.3 \pm 1.7\text{‰}$ ($n=5$), but $\delta^{15}\text{N}$ values were lower than those for mangroves ($\delta^{15}\text{N} = +1.7 \pm 1.7\text{‰}$, $n=5$) (Fig. 2A). Three different mac-

roalgae which were found only in very small quantities at site 1 had the highest $\delta^{15}\text{N}$ values of all primary producers sampled ($+7.5\text{‰}$ for red algae, $+9.1\text{‰}$ for green algae, and $+11.5\text{‰}$ for filamentous algae on *Avicennia* pneumatophores), but had intermediate $\delta^{13}\text{C}$ values of -26.0‰ , -20.0‰ , and -20.9‰ respectively. Sediments under the mangrove vegetation had a low organic carbon content (0.8–1.2%), low C:N ratios (7.0–8.5), and a carbon isotope composition ($\delta^{13}\text{C} = -22.8$ to -20.7‰ , Fig. 2A) enriched by 6–8‰ relative to the dominant vegetation.

Stable isotope composition of invertebrates

Overall, invertebrates exhibited a remarkably wide range of values, between -26.9 and -16.6‰ for $\delta^{13}\text{C}$ and between -6.6 and $+12.3\text{‰}$ for $\delta^{15}\text{N}$ (Fig. 2A, B), and all invertebrates showed average $\delta^{13}\text{C}$ values at least 3‰ enriched relative to the mangrove $\delta^{13}\text{C}$ signal. Most depleted $\delta^{13}\text{C}$ values were found in the gastropods *Melampus fasciatus* ($\delta^{13}\text{C} = -25.5 \pm 0.4$, $n=6$), *Cassidula mustelina* ($\delta^{13}\text{C} = -25.4$ and -25.8 , $n=2$), and *Pythia plicata* ($\delta^{13}\text{C} = -25.2$ and -26.9 , $n=2$) and in the sesarimid *Par-*

Fig. 2 a Plot of $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ for different primary producers, sediments, and gastropods collected in the intertidal mangrove forest of the Coringa Wildlife Sanctuary (data available on request). (n) Number of individuals/samples, error bars indicate 1 SD. *As* *Assimineea* sp. (6), *BA* brown macroalgae (1), *BMA* benthic microalgae (5), *Cm* *Cassidula mustelina* (2), *Co* *Cerithidea obtusa* (6), *FA* filamentous algae (1), *GA* green macroalgae (1), *La* *Littoraria articulata* (5), *Ld* *Littoraria delicatula* (2), *Lm* *Littoraria melanostoma* (6), *M* mangrove leaves (17), *Mf* *Melampus fasciatus* (6), *Nv* *Neritina violacea* (6), *On* *Onchidium* sp. (7), *Pp* *Pithia plicata* (2), *S* sediment, *SU* *Suaeda* spp. (1), *Tt* *Telescopium telescopium*. Numbers refer to sampling sites, if not from sites 1 or 2. **b** Plot of $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ for different primary producers, sediments, and crustaceans collected in the intertidal mangrove forest of the Coringa Wildlife Sanctuary (data available on request). (n) Number of individuals/samples, error bars indicate 1 SD. *BA* Brown macroalgae (1), *BMA* benthic microalgae (5), *Cc* *Cardisoma carnifex* (8), *Cl* *Clibanarius longitarsis* (6), *Et* *Episesarma tetragonum* (6), *Ev* *E. versicolor* (5 at site 1, 3 at site 3), *FA* filamentous algae (1), *GA* green macroalgae (1), *M* mangrove leaves (17), *Md* *Metaplex distinctus* (9), *Me* *M. elegans* (12), *Met* *Metopograpsus messor* (1), *S* sediment, *Pa* *Parasesarma asperum* (5), *Ss* *Scylla serrata* (7), *Su* *Suaeda* spp. (1), *Ur* *Uca rosea* (3 at each site), *Ut* *U. triangularis bengali* (7 at site 1, 1 at site 3). Numbers refer to sampling sites, if not from site 1 or 2



asesarma asperum ($\delta^{13}\text{C} = -25.5 \pm 0.6$, $n=5$) (Fig. 2A, B). The omnivorous sesarmids *Episesarma versicolor* and *E. tetragonum* were characterized by more enriched $\delta^{13}\text{C}$ values (-24.2 to -21.9‰ , Fig. 2B), the latter showing highly variable $\delta^{15}\text{N}$ values ($+4.9$ to $+10.1\text{‰}$). Two other large brachyurans, *Cardisoma carnifex* and *Scylla serrata*, had $\delta^{13}\text{C}$ values within the same range, but *C. carnifex* had markedly higher $\delta^{15}\text{N}$ values ($+9.3 \pm 2.2\text{‰}$, $n=8$). $\delta^{13}\text{C}$ values comparable to those of the sediment organic matter were found in the surface grazing gastropods *Telescopium telescopium* ($\delta^{13}\text{C} = -22.0 \pm 1.5$, $n=6$) and *Neritina violacea* ($\delta^{13}\text{C} = -22.6 \pm 0.7$, $n=6$). A large number of invertebrate species had $\delta^{13}\text{C}$ values in between those of the sediment organic matter and benthic microalgae, including the fiddler crabs *Uca rosea* ($-20.1 \pm 0.5\text{‰}$, $n=3$, at site 1, -17.3 ± 1.0 , $n=3$, at site 3) and *U. triangularis* (-20.9 ± 0.8 , $n=7$, at site 1 and -18.9‰ ($n=1$) at site 3), the grapsids *Metaplexis distinctus* (-18.7 ± 1.7 , $n=9$) and *M. elegans* (-18.4 ± 1.1 , $n=12$), and the gastropods *Cerithidea obtusa* (-19.3 ± 0.7 , $n=6$) and *Assimineia* sp. (-18.7 ± 0.5 , $n=6$).

Unusually depleted $\delta^{15}\text{N}$ values ($-5.6 \pm 0.9\text{‰}$, $n=7$) were found in the pulmonate gastropod *Onchidium* sp., and three species of the genus *Littoraria* showed relatively low $\delta^{15}\text{N}$ values between -1.7‰ and $+2.6\text{‰}$. No differences were found between the isotopic signatures of specimens collected at site 1 or site 2, but some species which were collected at both site 1 and site 3 (*E. versicolor*, *U. rosea*, and *U. triangularis*) were enriched in ^{13}C at site 3 (Fig. 2B).

Discussion

Primary producers and sediments

The $\delta^{13}\text{C}$ values found for mangrove leaves are typical for terrestrial C_3 -plants and are within the range reported for leaves of various mangrove species by others (e.g. Rao et al. 1994; Newell et al. 1995; Loneragan et al. 1997; Marguillier et al. 1997). The $\delta^{13}\text{C}$ signature of the benthic microalgae ($-17.3 \pm 1.7\text{‰}$) was very different from the mangrove leaves and similar to that reported earlier for benthic algae from mangroves and other intertidal ecosystems (e.g. Newell et al. 1995 and references therein; Dittel et al. 1997; Page 1997; Lee 2000; Wainright et al. 2000). Although a more appropriate technique than the one used has been described to collect these algae (e.g. Couch 1989), this was found to result in insufficient material in our study. However, the close correspondence of our $\delta^{13}\text{C}$ data to values reported in the literature and with the most enriched $\delta^{13}\text{C}$ data for invertebrates allows us to conclude that our results for microalgae are likely to be valid. A large discrepancy was observed between the $\delta^{13}\text{C}$ values of mangrove leaves (average -28.6‰ , Fig. 2A) and the underlying sediment (-22.8‰ at site 1 to -20.7‰ at site 3, Fig. 2A). Such an enrichment in ^{13}C in mangrove sediments has been reported in earlier studies (e.g. Rodelli et al. 1984; Stoner

and Zimmerman 1988; Hemminga et al. 1994; Dittel et al. 1997; Lallier-Verges et al. 1998; Machiwa 1999), although the discrepancy was usually less pronounced than that found in this study. This enrichment, in combination with the low organic carbon content and low C/N ratios found in sediments in this area, indicates substantial inputs of suspended matter from the mangrove creeks and adjacent bay (Bouillon et al., unpublished data). Suspended particulate organic matter in these creeks and in the adjacent bay has been found to have a highly variable $\delta^{13}\text{C}$ (between -19.2 and -30.9‰ in the study area, see Bouillon et al. 2000) and was estimated to contain a large contribution by phytoplankton (Bouillon and Dehairs 2000; Dehairs et al. 2000). There are thus three major types of primary carbon sources available for invertebrates on the sediment surface: mangrove litter, imported plant detritus, and microphytobenthos.

Macro-invertebrates

Only a limited number of species showed evidence for significant assimilation of mangrove-derived carbon. The gastropods *Melampus fasciatus*, *Cassidula mustelina*, and *Pythia plicata* had some of the most depleted $\delta^{13}\text{C}$ values encountered in this study (averages between -26‰ and -25‰ , Fig. 2A), and these data suggest that mangrove-derived carbon and sediment organic matter could contribute in roughly equal proportions to their diet, although the large differences in their $\delta^{15}\text{N}$ signature suggest that their trophic position may be more complex. Sesarmid crabs are often a dominant feature of mangrove invertebrate communities, and although most experimental studies on their feeding habits only include mangrove leaf material (e.g. Steinke et al. 1993; Kwok and Lee 1995), several authors have suggested that they exploit a wider range of food sources under natural conditions (e.g. Micheli 1993; Lee 1997). The three sesarmids sampled in the Coringa area were the most ^{13}C -depleted brachyurans in this study (Fig. 2B). Of these, *Parasesarma asperum* had the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 2A), but the discrepancy with the mangrove $\delta^{13}\text{C}$ signature (about 3.2‰) indicates that other sources also contributed to its diet. Feeding off the sediment surface has been noted frequently in several sesarmid species (e.g. Micheli 1993; M. Skov, personal communication), including *P. asperum* (personal observation), and we hypothesize that the $\delta^{13}\text{C}$ data for this species reflect extensive use of this source as a food source. The wide range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values found in *Episesarma tetragonum* and *E. versicolor* and the large difference of their $\delta^{13}\text{C}$ values and the mangrove $\delta^{13}\text{C}$ signature (on average 4.6 – 6.8‰ , Fig. 2B) suggest a heterogeneous and mixed diet which included mangrove litter to some extent but not as the major food source. Their higher $\delta^{15}\text{N}$ values compared to *P. asperum* indicate that other invertebrates or carrion contributed to their diet. The low N content of mangrove leaves has led several authors to suggest that these can not be sufficient to meet the ses-

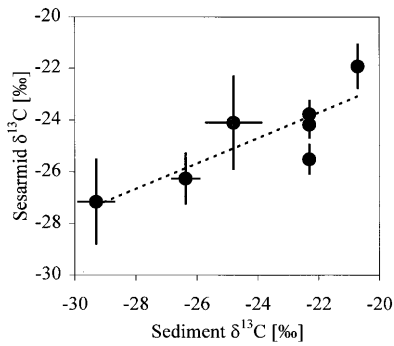


Fig. 3 Relationship between $\delta^{13}\text{C}$ values of sediment organic matter and those of different species of sesarmid crabs ($R^2=0.71$, $P<0.02$). *Black symbols* This study, *grey symbols* data from Rodelli et al. (1984). Sediment data for Galle (Sri Lanka) were taken from Bouillon et al. (unpublished data). *Error bars* indicate 1 SD. Data available on request

armids' N demand (e.g. Micheli 1993; Kwok and Lee 1995; Lee 1997), and our data confirm that other sources can constitute an important contribution to the diet of sesarmids. When combining our data with those from the literature (Rodelli et al. 1984) and some data on *Chironanthes* sp. from a Sri Lankan mangrove (S. Bouillon, unpublished data), a significant correlation between the $\delta^{13}\text{C}$ of sediment organic matter and of sesarmids (Fig. 3) is apparent, confirming the contribution of sediment organic matter in the diet of some sesarmids. *Cardisoma carnifex* stable isotope ratios (Fig. 2B) suggest an even more omnivorous and heterogeneous diet with only a minor contribution of assimilated mangrove leaf litter, contrary to previous reports of a mainly herbivorous diet (Micheli et al. 1991; Dahdouh-Guebas et al. 1999).

Two surface-grazing gastropods, *Telescopium telescopium* and *Neritina violacea*, had $\delta^{13}\text{C}$ values slightly enriched relative to that of the sediment on which they were found to forage (Fig. 2A) and their $\delta^{15}\text{N}$ signatures ($+6.9\pm 1.0\text{‰}$ and $+7.5\pm 1.1\text{‰}$, respectively) were higher by about 3.2–3.7‰ relative to this substrate. Our data suggest that these species feed rather indiscriminately on sediment organic matter, which in turn comprised mainly deposited phytoplankton/detritus (Bouillon et al., unpublished data). The pulmonate gastropod *Onchidium* sp. also had $\delta^{13}\text{C}$ values ($-23.1\pm 1.1\text{‰}$, $n=7$) close to that of the sediment it was usually found on (-22.8‰), but it exhibited remarkably low $\delta^{15}\text{N}$ values ($-5.6\pm 0.9\text{‰}$). The fact that no other invertebrates in this survey displayed such low $\delta^{15}\text{N}$ values renders unlikely the possibility that we have overlooked a very $\delta^{15}\text{N}$ -depleted food source. Such low $\delta^{15}\text{N}$ values have, to our knowledge, so far only been reported for organisms with endosymbiotic chemoautotrophic bacteria from hydrothermal vent systems, 'cold seeps' and reducing sediments (e.g. Fisher 1990; Conway et al. 1994), and have been attributed to either the utilization of NH_4^+ by the endosymbionts, non-limitation of inorganic N allowing maximal fractionation, or nitrogen fixation (see Conway et al. 1994). Clearly, fur-

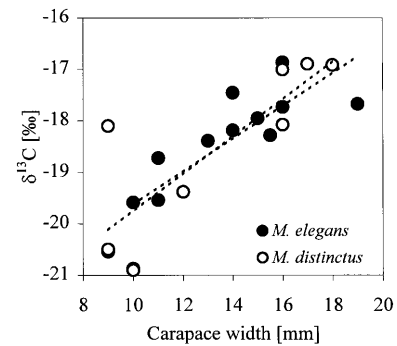


Fig. 4 Relationship between the carbon stable isotopic composition ($\delta^{13}\text{C}$, expressed in ‰) and carapace width (mm) for *Metaplex distinctus* (open circles, $R^2=0.70$, $P<0.01$) and *M. elegans* (black circles, $R^2=0.66$, $P<0.01$)

ther work is needed to clarify the mechanism leading to the very low $\delta^{15}\text{N}$ values in *Onchidium* sp.

A large number of surface grazers and deposit feeders had $\delta^{13}\text{C}$ signatures intermediate between those of sediment organic carbon and benthic microalgae, reflecting different degrees of selectivity for the latter and indicating little or no assimilation of mangrove carbon. These include the abundant gastropods *Assiminea* sp. and *Cerithidea obtusa*, for which $\delta^{13}\text{C}$ data indicate selective assimilation or ingestion of benthic microalgae. Consistent with this hypothesis, their $\delta^{15}\text{N}$ values ($+4.8\pm 0.7\text{‰}$ and $+4.9\pm 0.5\text{‰}$, respectively) were higher by about 3‰ than those of benthic microalgae (Fig. 2A), suggesting that bacteria were not important trophic intermediates. The two species of fiddler crabs (*Uca tringularis* and *U. rosea*) and the grapsids *Metaplex elegans* and *M. distinctus* collected in this study had significantly more enriched $\delta^{13}\text{C}$ values than the sesarmids, *S. serrata* or *C. carnifex* (Fig. 2B). Although there continues to be some ambiguity on the importance of different food sources for fiddler crabs, our data confirm results from previous stable isotope studies (e.g. Rodelli et al. 1984; France 1998) that at least some species select for microphytobenthos such as diatoms and cyanobacteria. For both *Metaplex* species, $\delta^{13}\text{C}$ values increased with increasing carapace width, indicating a higher selectivity for benthic microalgae in larger individuals (Fig. 4). Similar to the findings of France (1998), no such ontogenetic shift was found for fiddler crabs, or for any other of the invertebrates sampled. Only one specimen of *Metopograpsus messor* was sampled in this study, and although it is not possible to draw definite conclusions on its diet, it clearly does not rely heavily on mangrove carbon, and its isotopic composition is consistent with extensive feeding on littorinids in this genus (Reid 1986b), although others have found a large contribution of mangrove leaves and macroalgae in the diet of *Metopograpsus* sp. (Dahdouh-Guebas et al. 1999).

The three species of *Littoraria*, typically found on mangrove leaves and stems, exhibited a fairly wide

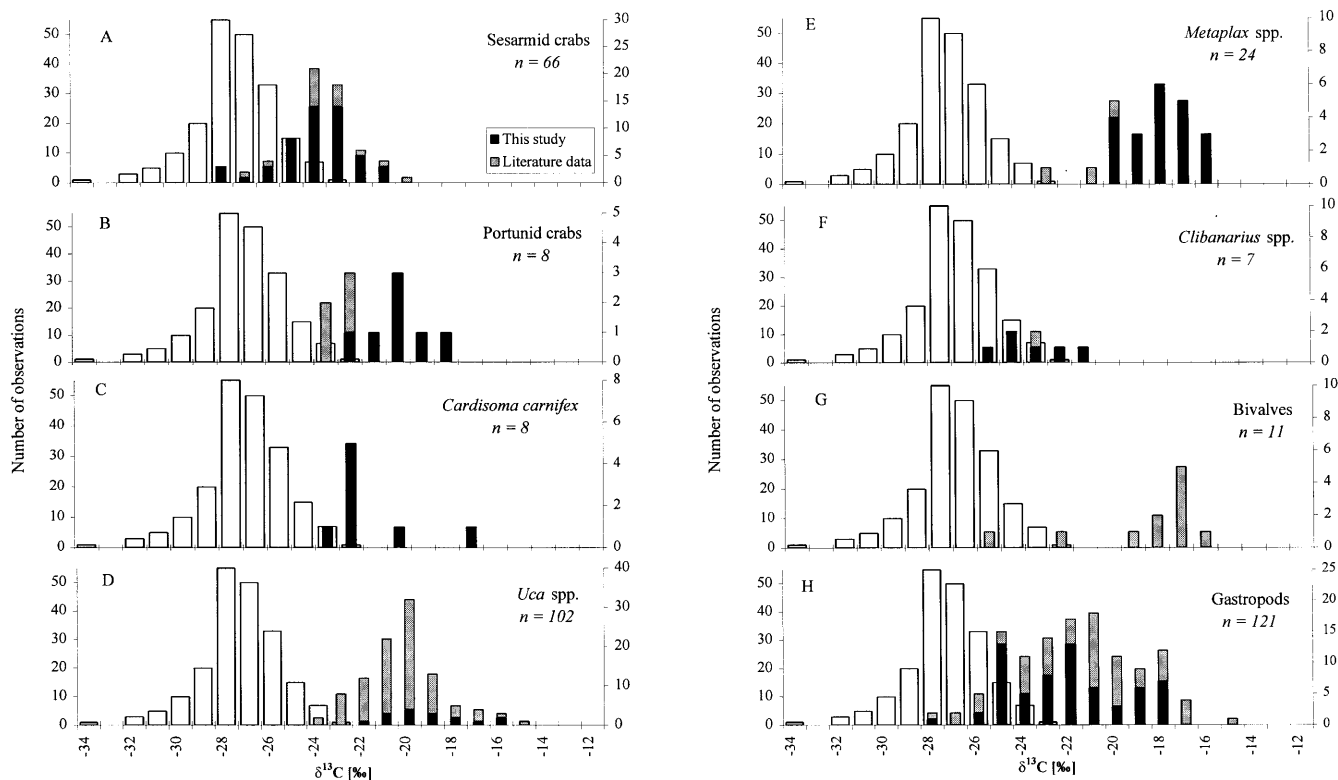


Fig. 5 Frequency distribution of $\delta^{13}\text{C}$ values of mangrove leaves (white columns, this study and literature data, $n=200$) and $\delta^{13}\text{C}$ values of different invertebrate groups from intertidal mangrove forests. Black bars correspond to data from this study, grey bars refer to published data. A Sesamid crabs, B portunid crabs, C *Cardisoma carnifex*, D *Uca* spp., E *Metaplex* spp., F *Clibanarius* sp., G bivalves, and H gastropods. n Number of data. Data available on request

range of $\delta^{13}\text{C}$ values (-24.7‰ to -20.5‰), but were all characterized by their low $\delta^{15}\text{N}$ values (-1.7‰ to $+2.6\text{‰}$, Fig. 2A). Although it has sometimes been suggested that *Littoraria* spp. feed on the hairs of *Avicennia* leaves, it is generally accepted that they graze the surface layers of trunks and roots where they feed on microepiphytes (Reid 1986a; Blanco and Cantera 1999). Our data support the latter hypothesis, as the $\delta^{13}\text{C}$ values are within the range of those reported for cyanobacterial crusts (Ziegler and Luttge 1998), and the low $\delta^{15}\text{N}$ values of *Littoraria* spp. suggest that the epiphytes are N_2 -fixing, as the process of nitrogen fixation has been reported to result in a fractionation of $0\text{--}4\text{‰}$ (Kohl and Shearer 1980) relative to atmospheric N_2 ($\delta^{15}\text{N}_{\text{air}}=0\text{‰}$, Mariotti 1983). Nitrogen fixation by such cyanobacterial crusts on mangrove stems has also been demonstrated in other studies (Sheridan 1991).

The predatory crab *Scylla serrata*, which feeds almost exclusively on animal matter (e.g. Williams 1978; Hill 1979; Jones 1984) is usually considered to be the top predator of the mangrove benthic community. Although its carbon isotope composition corresponds well with this hypothesis, its $\delta^{15}\text{N}$ values ($+7.7\pm 1.3\text{‰}$, $n=7$) are lower than might be expected from the $\delta^{15}\text{N}$ signatures of po-

tential prey items (Fig. 2B). A possible explanation could be that *Onchidium* sp., which exhibits very low $\delta^{15}\text{N}$ values around -5.6‰ , contributes to the diet of *S. serrata*. The fact that local fishermen collect *Onchidium* sp. as bait for the capture of *S. serrata* in the mangrove creeks provides circumstantial evidence for this hypothesis.

Finally, the anomuran *Clibanarius longitarsis* had variable but depleted $\delta^{13}\text{C}$ values consistent with its filter-feeding habit (Manjulatha and Babu 1991), as suspended matter in the mangrove creeks during the sampling season is relatively depleted in ^{13}C (Bouillon et al. 2000).

A broader perspective

A striking feature of Fig. 2A, B is the diversity in stable isotope signatures found in co-occurring mangrove invertebrates, indicating a fairly limited overlap in resource utilization. Overall, the data show that although mangrove carbon was assimilated by some invertebrate species (e.g. some gastropods and sesamid crabs), other sources formed a major part of these species' diet. For the majority of the species studied, freshly deposited phyto-detritus, benthic microalgae, and N_2 -fixing microepiphytes were found to be dominant carbon sources. The distribution of $\delta^{13}\text{C}$ data of some important mangrove-inhabiting invertebrate groups from this study and several published studies have been compiled in Fig. 5, whereby data for *Neosarmatium meinerti* and *N. smithi* from Gazi Bay (Kenya) and on *Chiromanthes* sp. and *Terebralia palustris* from Galle (Sri Lanka) have also been included (S. Bouillon, unpublished data). The distribution patterns of

invertebrate $\delta^{13}\text{C}$ values confirm that substantial amounts of mangrove carbon are assimilated only by a limited number of invertebrate groups (such as sesamid crabs, and some of the gastropods), but even in these cases there is only a limited overlap in the $\delta^{13}\text{C}$ distributions. The fairly large discrepancy found between the distribution of mangrove $\delta^{13}\text{C}$ values and other invertebrate groups (*Uca* spp., *Metaplex* spp., bivalves, most of the gastropod species) clearly demonstrates the important role of imported organic matter and microphytobenthos for the macro-invertebrate community in intertidal mangrove habitats. The overall average $\delta^{13}\text{C}$ value of all invertebrates is around -21.9‰ , that is 6.8‰ enriched relative to the average mangrove litter signature. These results show a remarkable similarity with those obtained in temperate salt marsh ecosystems, where a number of recent studies (Sullivan and Moncreiff 1990; Currin et al. 1995; France 1995; Créach et al. 1997; Page 1997; Riera et al. 1999) have demonstrated the trophic importance of imported phytoplankton and local microalgal sources. Although standing stocks of salt marsh vegetation are about an order of a magnitude lower than those of mangroves, their above-ground productivity is comparable (e.g. see Twilley et al. 1992; Middelburg et al. 1997). Mangrove ecosystems and saltmarshes have also been found to show analogous patterns of variability in the sources of organic carbon in surface sediments (Middelburg et al. 1997; Bouillon et al., unpublished data), which suggests that carbon pathways and utilization patterns in these two types of vegetated intertidal ecosystems may be quite similar. However, many aspects of mangrove intertidal foodwebs remain virtually unknown, e.g., there is as yet very little information on the carbon sources for many infaunal organisms, notably meiofauna, or on the role of microheterotrophs as trophic intermediates. Until more studies are undertaken in a variety of mangrove ecosystems, regional differences and the influence of the availability of carbon sources in structuring mangrove foodwebs also remain to be determined.

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