Carbon and Nitrogen Stable Isotope Ratios of Subtidal Benthic Invertebrates in an Estuarine Mangrove Ecosystem (Andhra Pradesh, India)

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In order to assess the relative trophic importance of mangrove litterfall and aquatic primary production in the mangrove creeks of the Coringa Wildlife Sanctuary (Andhra Pradesh, India) and the adjacent semi-enclosed Kakinada Bay, carbon and nitrogen stable isotope ratios were determined in a variety of benthic invertebrate species collected at 22 sites during the pre-monsoon period (May–June) of 1997 and 1999. $\delta^{13}\text{C}$ values showed little interspecific variation at any given location, but there was a distinct spatial gradient in consumer $\delta^{13}\text{C}$ values of about 7‰, with more depleted values in the mangrove creeks (-23.6 ± 0.6 ‰), and gradually increasing in the mangrove outlets (-21.5 ± 0.9 ‰), a relatively restricted zone in the south-eastern part of Kakinada Bay adjacent to the mangroves (-18.8 ± 0.8 ‰), and the central and northern part of the Bay (-16.7 ± 1.4 ‰) which opens into the Bay of Bengal. This gradient is much larger than that observed during a previous study in suspended organic matter (maximum about 2.7‰) and during this study in sediment organic matter (about 1.5–2.5‰). The observed carbon stable isotope ratios thus suggest a marked selectivity of the benthic invertebrate community for pelagic and benthic microalgal food sources and indicate that mangrove-derived and other terrestrial carbon is not a significant food source for benthic invertebrate communities in this ecosystem during the pre-monsoon period. Furthermore, $\delta^{13}\text{C}$ values of sediment organic matter (SOM) suggest that terrestrial carbon is not a major contributor to the SOM-pool in this ecosystem. Evidence for seaward migration of Penaeid prawns was provided by some individuals caught in the North Bay which displayed low $\delta^{13}\text{C}$ values of characteristic of fauna found in the mangrove creeks or outlets. Nitrogen stable isotope ratios were found to be a useful indicator of trophic level, even though there remained some overlap between $\delta^{15}\text{N}$ values of presumed low and higher trophic levels. Benthic invertebrates showed a $\delta^{15}\text{N}$ gradient of about 3.2‰ between the mangrove creeks and the Central and North Bay whereas sediment $\delta^{15}\text{N}$ values showed a smaller spatial gradient of about 1.6‰. This gradient which is hypothesized to reflect differences in inorganic nitrogen sources and availability.

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Introduction

The degree of 'outwelling' of mangrove carbon to adjacent aquatic environments depends to a large degree on the geomorphology and tidal characteristics of the ecosystem (Lee, 1995, 1999a). If mangrove-derived material is exported to the aquatic environment, either as dissolved or particulate organic carbon, the question arises whether it forms a substantial contribution in sustaining the pelagic and benthic foodwebs, and to what geographical extent (Robertson *et al.*, 1992). The possibly limited importance of mangrove detritus in sustaining nearshore

communities has previously been suggested based on mass-balance restrictions (e.g. Li & Lee, 1998). Wafar *et al.* (1997), for instance, compared the phytoplankton productivity in a western Indian mangrove estuary with the potential contribution of mangrove carbon, and concluded that mangrove production is mainly important for the microbial food web, but not for the particulate. Daniel and Robertson (1990) found a positive correlation between the amount of mangrove macrodetritus and epibenthos biomass and density in an Australian mangrove estuary, but stressed that different factors such as reduction of predation, increased food availability and increased living space, may explain this pattern. In contrast, Lee (1999b)

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found no positive effect of mangrove detritus enrichment on benthic faunal biomass and even found a decrease in species diversity.

Stable isotope analysis offers one of the possible approaches to study the incorporation of different carbon sources into foodwebs on the condition that there is a sufficiently large difference in the isotopic composition of the different primary carbon sources (terrestrial material, phytoplankton, benthic microalgae), and have been used to study benthic foodwebs in a variety of ecosystems (e.g. Dauby, 1990; Riera *et al.*, 1999; Yoshii *et al.*, 1999; Lepoint *et al.*, 2000). Several stable isotope studies (e.g. Rodelli *et al.*, 1984; Newell *et al.*, 1995; Loneragan *et al.*, 1997; Marguillier *et al.*, 1997; Dehairs *et al.*, 2000; Bouillon *et al.*, 2000) have recently been carried out in mangrove ecosystems and have substantially increased the knowledge on mangrove foodwebs since the publication of the work of Odum and Heald (1975). The general conclusion resulting from many of these studies concerning the benthic communities in the aquatic environment adjacent to mangrove forests is that mangrove carbon is only used in a very restricted zone in and near mangrove forests but that its role is rapidly taken over by phytoplankton, even though mangrove detritus was present in suspended and sediment organic matter (Rodelli *et al.*, 1984; Zieman *et al.*, 1984; Fleming *et al.*, 1990). One major drawback of the latter studies is that they based their conclusions on the distribution of $\delta^{13}\text{C}$ values in invertebrates when compared to the $\delta^{13}\text{C}$ of mangrove leaves and typical marine phytoplankton, but did not take into account the possibility of $\delta^{13}\text{C}$ -depleted phytoplankton in the mangrove creeks and near-mangrove aquatic environment (e.g. Dehairs *et al.*, 2000; Bouillon *et al.*, 2000) due to a ^{13}C -depleted DIC-pool (dissolved inorganic carbon). This mechanism can even cause an overlap in the $\delta^{13}\text{C}$ signal of these two sources and could make the interpretation of consumer stable isotope data difficult if not carefully considered.

In this study, carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates and sediments were analysed at a wide variety of locations in an estuarine mangrove ecosystem in Andhra Pradesh (India) and baseline information of primary producer stable isotope ratios was used from previous studies in this area (Dehairs *et al.*, 2000; Bouillon *et al.*, 2000, 2001), in an effort to determine whether mangrove carbon was assimilated by benthic fauna in different zones of this ecosystem. In addition, whether the spatial trend in $\delta^{15}\text{N}$ values reported earlier (Dehairs *et al.*, 2001) would be confirmed and could be related to sewage inputs (e.g. McKinney *et al.*,

1999; Risk & Erdman, 2000), or to other processes was assessed.

Study area

The sampling sites (Figures 1 and 2) are located in the area between Kakinada Bay and the Gautami branch of the Godavari, the second largest river in India, and are located in the Southeastern state of Andhra Pradesh (between 82°15' and 82°22'E, 16°43' and 17°00'N). The Godavari has a mean annual discharge of 11.1×10^{14} l, of which 93–96% occurs during the wet monsoon season, and is listed as one of the largest POC (particulate organic carbon) transporting rivers in the world (Gupta *et al.*, 1997). The Gautami Godavari opens into the Bay of Bengal, but has several branches into Kakinada Bay, the largest and most important being Coringa (total length of 26 km) and Gaderu (total length of 11 km). The area between the river and Bay is dominated by extensive mangrove forests and tidal mudflats. The shallow Kakinada Bay (depth ranging from 3 to 8 m at high tide) which covers approximately 150 km², opens into the Bay of Bengal on its northern side, and is bordered along most of its eastern length by a narrow sand bar (Figure 1). Tides are semidiurnal, and tidal amplitude in the Bay is around 0.5 to 2 m. Monsoon rainfall in the area usually occurs between July and September, and causes near-freshwater conditions in the southern part of the study area during this period. Estuarine conditions re-establish thereafter, and aquatic primary production increases towards the pre-monsoon period (April–June), during which turbidity reaches its lowest values in the entire region.

Benthic fauna in this area has witnessed a significant decrease in species diversity over the last 50 years, presumably due to the increased human pressure in Kakinada, a large city which currently hosts about 400 000 inhabitants and is located on the western shore of Kakinada Bay. The Bay and creeks are important fishing areas and in addition, molluscs are harvested on a large scale for lime production.

Materials and methods

Sample collection and preparation

For benthic invertebrates, samples were taken along a linear transect from the mouth of Coringa Creek to the tip of Hope Island in the northern part of Kakinada Bay in June 1997 (open circles on Figure 1), and a variety of other sites were sampled in May–June 1999 (full circles). Sediment samples were taken

FIGURE 1. Location of the study area and sampling locations. Darkest areas represent the major mangrove-covered regions. Ma: mangrove creek stations, Mo: mangrove creek outlet stations, SEb: South-east Bay stations, CNb: Central and North Bay stations. Open circles indicate sampling locations of the June 1997 survey, black circles the May-June 1999 sampling location. Station Mo2 (in grey) was sampled during both surveys.

during surveys in July 1995 throughout the area (see Figure 2). Benthic fauna and sediments were collected using a dredge and Van Veen grab, and were kept in a cool box on board. After transportation to the field laboratory, all faunal samples were washed and dried at 60 °C for at least 24 h. Samples were later ground to a fine powder, and subsamples for $\delta^{13}\text{C}$ analysis were washed with dilute HCl to remove possible carbonates, and were redried. Subsamples for $\delta^{15}\text{N}$ analysis did not receive this treatment as this has been reported to affect $\delta^{15}\text{N}$ values (Goering *et al.*, 1990; Bunn *et al.*, 1995; Pinnegar & Polunin, 1999).

Measurement of stable isotope and elemental ratios

Samples for stable isotope analysis were combusted in a Carlo Erba NA-1500 Elemental Analyser and the resulting gases (CO_2 and N_2) were cryogenically separated in a manual extraction line. Stable isotope ratios were then determined on a Delta E Finnigan Mat isotope ratio mass spectrometer and are expressed relative to the conventional standards, i.e. PDB limestone for carbon (Coplen, 1996) and atmospheric N_2 for nitrogen (Mariotti, 1983) as δ values, defined as:

FIGURE 2. Spatial distribution of (a) $\delta^{13}\text{C}$ values, (b) $\delta^{15}\text{N}$ values, and (c) elemental ratios in the Coringa-Kakinada estuarine ecosystem.

TABLE 1. Average $\delta^{13}\text{C}$ values (expressed in ‰) of all invertebrates sampled at each of the sampling locations. Also indicated are the standard deviation on the mean $\delta^{13}\text{C}$, the number of samples, and the minimum and maximum $\delta^{13}\text{C}$ at each location

Location	Average $\delta^{13}\text{C}$	Minimum $\delta^{13}\text{C}$	Maximum $\delta^{13}\text{C}$
Ma1	-23.6 ± 0.2 (3)	-23.8	-23.3
Ma2	-23.6 ± 0.7 (8)	-24.7	-22.4
Mo1	-21.8 ± 0.9 (8)	-23.1	-20.5
Mo2	-21.5 ± 1.0 (10)	-23.0	-19.9
Mo3	-21.1 ± 0.9 (3)	-21.6	-20.0
Mo4	-21.5 ± 0.8 (14)	-22.5	-19.7
Mo5	-20.5 ; -20.2	—	—
SEb1	-18.4 ± 0.7 (8)	-19.6	-17.8
SEb2	-18.6 ± 1.0 (10)	-20.2	-16.2
SEb3	-19.0 ± 0.6 (10)	-20.1	-18.0
CNb1*	-17.1 ± 0.9 (10)	-18.7	-15.9
CNb2	-16.3 ± 1.9 (7)	-17.9	-13.2
CNb3	-16.5 ± 1.0 (4)	-17.3	-15.3
CNb4	-16.2 ± 0.5 (10)	-17.3	-15.7
CNb5	-16.3 ± 1.2 (14)	-18.0	-14.4
CNb6	-16.4 ± 0.6 (4)	-17.0	-15.6
CNb7*	-15.1 (1)	—	—
CNb8	-16.7 ± 1.0 (7)	-18.2	-15.4
CNb9	-18.4 ; -17.7	—	—
CNb10	-16.6 ± 1.2 (7)	-18.9	-15.1
CNb11	-15.9 ± 1.2 (5)	-16.9	-13.8
CNb12	-17.1 ± 1.5 (7)	-19.2	-14.9

*One low $\delta^{13}\text{C}$ value measured for a Penaeid prawn was excluded (see discussion).

$$\delta R = [(X_{\text{sample}} - X_{\text{standard}}) / X_{\text{standard}}] \times 10^3 \text{ [‰]}$$

where $R = ^{13}\text{C}$ or ^{15}N , and $X = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The normal working standard for carbon was CO_2 produced from Carrara marble, and high-purity tank

N_2 was used as the working standard for nitrogen. Internal reference materials used were ammonium sulphate (IAEA-N1, IAEA-N2) and ammonium nitrate (IAEA-NO3) for $\delta^{15}\text{N}$, and sucrose (IAEA-C6) and polyethylene (IAEA-CH-7) for $\delta^{13}\text{C}$. Standard

FIGURE 3. Average $\delta^{13}\text{C}$ of (a) suspended particulate organic matter (SPOM, data from Bouillon *et al.*, 2000) and (b) sediment organic matter, and (c) $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ plot for mangrove litter and benthic invertebrates collected in the mangrove creeks (Ma), mangrove outlets (Mo), South-east Bay (SEb), and Central and North Bay (CNb). Open symbols refer to species presumed to occupy a low trophic level, black symbols refer to species of higher trophic levels, and '+' indicate species of unknown trophic level from all zones. Two penaeid prawns collected in the North Bay with distinctly low $\delta^{13}\text{C}$ values (see discussion) are shown as grey circles. Data on mangrove litter are from Bouillon *et al.* (2001). Error bars indicate 1 SD.

deviations on ten aliquots of the same sample were lower than 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Nitrogen stable isotope ratios of sediments were determined with a continuous-flow IRMS system (Micromass Optima coupled to a Carlo Erba CNS Analyser) with an analytical precision of $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$. Elemental (C, N) analysis of sediment organic matter was performed by combusting pre-weighed and HCl-treated sediment samples in a Carlo Erba NA-1500 Elemental Analyser, similar to the method described by Nieuwenhuize *et al.* (1994).

Results

Sediments

Sediment organic matter had $\delta^{13}\text{C}$ values between -24.2 and -17.8‰ , with overall averages of $-21.3 \pm 1.0\text{‰}$ ($n=5$, mangrove creeks), $-20.2 \pm 1.1\text{‰}$ ($n=4$, mangrove outlets), $-19.7 \pm 0.4\text{‰}$ ($n=3$, South-east Bay) and $-19.7 \pm 1.2\text{‰}$ ($n=19$, Central and North Bay) [Figure 2(a)]. In the Bay,

FIGURE 4. $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ plot for (a) *Typhlocarcinus* sp., (b) *Tellina* spp., and (c) *Paphia undulata* sampled at different locations throughout the study area (see Figure 1 for location of stations).

however, the three most depleted values (all $< -21\text{‰}$) were observed near the outfall of Kakinada Canal draining the sewage systems of Kakinada town,

and in a northeastern direction from that point [Figure 2(a)]. $\delta^{15}\text{N}$ values of sediments [Figure 2(b)] also showed a spatial gradient, with relatively low values in the mangrove creeks ($+4.4 \pm 0.8\text{‰}$, $n=4$), but higher values in the mangrove outlets ($+5.1 \pm 0.8\text{‰}$, $n=3$), South-east Bay ($+6.4\text{‰}$, $n=1$) and the rest of the Bay ($+6.0 \pm 0.3\text{‰}$, $n=16$). Organic carbon content of all samples was relatively low ($0.40 - 1.42\%$ dry weight), and C/N ratios varied between 8.5 and 13.5 with no apparent differences between regions, although some Bay stations showed remarkably low values (8.5, 9.2, 9.8) compared to other Bay stations [average 12.0 ± 0.7 , $n=10$, Figure 2(c)].

Benthic invertebrates

Overall, $\delta^{13}\text{C}$ values of benthic invertebrates (see Appendix I) ranged between -24.7‰ (for an individual of the bivalve *Tellina* sp. 1 at Ma 2) and -13.2‰ (for an individual of the crab *Typhlocarcinus* sp. at CNb 2), while $\delta^{15}\text{N}$ values ranged from $+4.1\text{‰}$ (for *Tellina* sp. 2 at CNb 4) to $+14.5\text{‰}$ (for a *Metapenaeus monoceras* at CNb 1).

Stable carbon isotope ratios for different species sampled at a particular location were usually quite consistent and, with only three exceptions, showed a range of less than 4‰ . Thus, average $\delta^{13}\text{C}$ values of all invertebrates at a given location were calculated and were found to be similar in spatially adjacent locations, allowing us to distinguish different zones on the basis of invertebrate $\delta^{13}\text{C}$ values (Table 1). Stations were thus characterized as Mangrove creek locations (Ma, average $\delta^{13}\text{C}$ values around -23.5‰), Mangrove outlets (Mo, average $\delta^{13}\text{C}$ values around -21.5‰), South-east Bay stations (SEb, average $\delta^{13}\text{C}$ values around -18.5‰), and Central and North Bay stations (CNb, average $\delta^{13}\text{C}$ values around -16.5‰). Stations for which only one or two data were available (i.e. Mo5, CNb7, CNb9) were included in the group most adjacent to them geographically. In general, there appears to be a shift in benthic invertebrate $\delta^{13}\text{C}$ values of about 7‰ between the mangrove creeks and the North & Central Bay regions [Figure 3(c)]. Two Penaeid prawns caught in the North Bay, however, were very depleted in ^{13}C [$\delta^{13}\text{C} = -22.7$ and -21.5‰ , see Figure 3(c)] relative to other invertebrates from this zone, and their carbon isotopic signature was similar to that of organisms found in the mangrove creeks or outlets. Their $\delta^{13}\text{C}$ data were consequently not used in calculations of station-averaged $\delta^{13}\text{C}$ values (see above).

Species were classified as 'low' or 'higher' trophic level species when data on their trophic status were available. Thus, all bivalves, the gastropod *Cerithidea*

cingulata, the brachiopod *Lingula* sp., and the deposit-feeding crabs *Dorippe facchino*, *Macrophthalmus* sp., and *Typhlocarcinus* sp. were initially grouped as low trophic level species, and all penaeid prawns, the predatory or scavenging gastropods *Babylonia spirata*, *Volema cochlidium*, *Murex trapa*, *Thais lacera* and *Nassarius* spp., the crabs *Leucosia* sp., *Charybdis* sp., *Portunus sanguinolentus*, and *Phyllira* sp., and the polychaete *Diopatra neapolitana* were considered to occupy higher trophic levels. The bivalves *Meretrix meretrix* and *Pinctada radiata*, however, were then re-classified as 'unknown' trophic level species based on their intermediate $\delta^{15}\text{N}$ values (see discussion). All other species were considered to occupy an unknown trophic level. According to this classification, it appeared that higher trophic levels showed, on average, higher $\delta^{15}\text{N}$ values (by 2.1 to 3.8‰), and that there was also a marked spatial $\delta^{15}\text{N}$ gradient between the mangrove creeks and the Central and North Bay of about 3.2‰ which could be observed in both low and high trophic levels [Figure 3(c)].

Discussion

Sediments

Sediment organic matter showed a shift in $\delta^{13}\text{C}$ values between the mangrove creeks (-21.3‰) and the South-east and North Bay, where a zone of maximum $\delta^{13}\text{C}$ values between -17.8 and -19.1‰ can be found in the centre of the Bay [Figure 2(a)]. In the Bay, most depleted values ($< -21\text{‰}$) can be found in the region where satellite data indicate the plume of the Kakinada Canal, and are thus thought to be a reflection of larger inputs of ^{13}C -depleted terrestrial or sewage material. The magnitude of the overall $\delta^{13}\text{C}$ gradient is only slightly smaller than that found in suspended organic matter, but suspended matter was found to be on average about $3-4\text{‰}$ more ^{13}C -depleted than sediment organic matter (Bouillon *et al.*, 2000) [Figure 3(a-c)]. Such a discrepancy between suspended matter and sediment $\delta^{13}\text{C}$ values has also been found by Middelburg *et al.* (1998) in the Scheldt Estuary, with sediment $\delta^{13}\text{C}$ being enriched relative to the suspended matter in the upper estuary, but depleted in the lower estuary. C/N ratios of sediments in this study [Figure 2(c)] are also higher than the average values found in suspended matter (between 8.5 and 10, see Dehaire *et al.*, 2000). These results indicate first of all that mangrove-derived carbon (with an average $\delta^{13}\text{C}$ of -28.7‰ , Bouillon *et al.*, 2001) and other terrestrial carbon sources ($\sim -26.5\text{‰}$, e.g. Hellings *et al.*, 1999), do not appear to contribute substantially to the sediment organic

matter pool of the mangrove creeks and adjacent Bay. Furthermore, the discrepancy in C/N ratios and $\delta^{13}\text{C}$ values between suspended and sediment organic matter indicate different relative contributions of carbon sources in these two pools. However, while the higher C/N ratios in sediments would suggest a larger contribution by terrestrial sources, the higher $\delta^{13}\text{C}$ values in SOM indicate the opposite. A marked spatial shift of about 1.6‰ can also be observed in the sedimentary $\delta^{15}\text{N}$ record [Figure 2(b)], and will be discussed in conjunction with the parallel shift in consumer $\delta^{15}\text{N}$ values below.

$\delta^{13}\text{C}$ values of benthic invertebrates: importance of different primary producers

The overall distribution of $\delta^{13}\text{C}$ values for benthic invertebrates collected in this survey [Table 1, Appendix I and Figure 3(c)] shows that, considering a trophic enrichment of ~1‰, benthic invertebrates in the South-eastern, Central and Northern part of Kakindada Bay did not rely substantially on mangrove (-28.7‰ , Bouillon *et al.*, 2001) or other terrestrial carbon sources ($\sim -26.5\text{‰}$, e.g. Hellings *et al.*, 1999) during the study period. In fact, the $\delta^{13}\text{C}$ values of benthic invertebrates in these areas are typical for a marine, phytoplankton-based benthic food web, and some of the more ^{13}C -enriched values ($> -15\text{‰}$) also suggest some input of ^{13}C -enriched carbon sources, such as benthic microalgae (France, 1995). We have no direct measurements of the isotopic signature of these algae from the Bay or Creek bottoms due to the practical difficulties in sampling them in this environment, but benthic microalgae from the intertidal mangrove flats in this area have been found to have an isotopic signature of around -17.3‰ ($\delta^{13}\text{C}$) and between $+0.5$ and $+4.5\text{‰}$ ($\delta^{15}\text{N}$) (Bouillon *et al.*, 2001), whereas SPOM from the adjacent waters during the pre-monsoon period typically has $\delta^{13}\text{C}$ values of -23 to -20‰ (Bouillon *et al.*, 2000). Benthic microalgae have been found to occur throughout the study area (C. Kalavati, unpublished data), despite the high turbidity levels which may be encountered.

More depleted values were found in the mangrove outlets ($-21.5 \pm 0.9\text{‰}$, $n=37$) and creeks ($-23.6 \pm 0.6\text{‰}$, $n=11$). However, phytoplankton $\delta^{13}\text{C}$ values in this dynamic ecosystem have been suggested to be spatially and seasonally variable (Dehairs *et al.*, 2000; Bouillon *et al.*, 2000; Bouillon & Dehairs, 2000) and are thought to exhibit a $\delta^{13}\text{C}$ gradient between the mangrove creeks (depleted values) and the North Bay (enriched values). The magnitude of the $\delta^{13}\text{C}$ gradient observed in benthic invertebrates ($\sim 7\text{‰}$) is much larger than that ob-

served in suspended organic matter ($\sim 2.5\text{‰}$) or sediment organic matter ($\sim 1.5\text{‰}$) but is quite similar to the average difference in zooplankton $\delta^{13}\text{C}$ between the mouth of Coringa (see Figure 1) and the North Bay ($\sim 6\text{‰}$, Bouillon *et al.*, 2000). Benthic invertebrates in the mangrove creeks and outlets were observed to be more ^{13}C -depleted relative to the sediment organic matter, whereas those in the South-east, Central and North Bay were enriched relative to the sediment organic carbon pool. In contrast, compared to the average $\delta^{13}\text{C}$ values for suspended organic matter (Bouillon *et al.*, 2000), benthic invertebrates were enriched at all locations, although markedly more so in the Bay environment than in the mangrove creeks [Figure 3(a–c)].

The magnitude of the observed $\delta^{13}\text{C}$ gradient in benthic invertebrates and a comparison with $\delta^{13}\text{C}$ data of suspended and sediment organic matter thus indicate a marked selectivity for pelagic and benthic microalgal carbon sources. Phytoplankton and benthic microalgae are expected to exhibit a larger $\delta^{13}\text{C}$ gradient because of a more ^{13}C -depleted DIC-pool (dissolved inorganic carbon) in and near the mangrove creeks, where bacterial respiration of ^{13}C -depleted vascular plant material will result in a dilution of the DIC-pool with isotopically light CO_2 (e.g. Marguillier *et al.*, 1997; Bouillon *et al.*, 2000; S. Bouillon, unpublished data). It is also conceivable that there are spatial differences in the importance of carbon sources, i.e. mangrove carbon (and other terrestrial sources) could be more important in the mangrove creeks yet be fully replaced by algal sources towards the marine end, in which case we would also expect to find a gradient of increasing $\delta^{13}\text{C}$ values towards the northern Bay. However, the discrepancy between benthic invertebrate $\delta^{13}\text{C}$ values and the mangrove $\delta^{13}\text{C}$ signature [Figure 3(c)] and the fact that phytoplankton $\delta^{13}\text{C}$ values are expected to be more ^{13}C -depleted in the mangrove creeks relative to marine phytoplankton and thus presumably overlap with the $\delta^{13}\text{C}$ values observed in benthic invertebrates, suggest that this is not the case. A similar steeper gradient in clam $\delta^{13}\text{C}$ values compared to suspended matter $\delta^{13}\text{C}$ was found by Canuel *et al.* (1995) in San Francisco Bay, and was also interpreted as selectivity for phytoplanktonic sources. It thus appears that during the pre-monsoon period, when turbidity is least and the numerical abundance of phytoplankton is at a maximum, pelagic and benthic microalgal sources are the dominant primary producers sustaining the benthic community in this ecosystem. Whether this situation is representative of other seasons remains to be determined.

When comparing $\delta^{13}\text{C}$ data from the Central and North Bay and the mangrove regions, it appears that the two $\delta^{13}\text{C}$ distributions are entirely non-overlapping, except for two rather negative values (-21.5 and -22.7‰) found in the North Bay [Figure 3(c), shown as grey-filled circles]. These two negative values were found in 2 species of penaeid prawns (*Penaeus merguensis* and *Metapenaeus monoceros*, respectively), i.e. mobile species which are expected to migrate during this season from the mangrove creeks towards the marine environment. Thus, as the tissues of these organisms require some time to equilibrate with the isotopically distinct new diet (Riera *et al.*, 2000), these low values are hypothesized to indicate that these individuals had only recently migrated from the mangrove regions (e.g. *Macrobrachium rosenbergii* collected at Coringa mouth was found to have a $\delta^{13}\text{C}$ of about -21‰) to the North Bay, whereas some other Penaeids captured in the North Bay (including other individuals of the same species) had 'normal' values of -15 to -17‰ . The use of carbon stable isotopes as a tracer of shrimp migration has been reported earlier (e.g. Fry, 1983; Riera *et al.*, 2000). The $\delta^{15}\text{N}$ values of these two specimens were among the highest and lowest recorded in this study [Figure 3(c), Appendix I]. Large variations in penaeid $\delta^{15}\text{N}$ values have been reported earlier (Riera *et al.*, 2000), and we currently do not have a convincing explanation for this.

Finally, some common species were sampled at different sites, and examples of the spatial variability in their stable isotopic signatures are given in Figure 4. These data show three quite different patterns and thus indicate that species-specific differences in relative contributions of carbon sources also occur. For *Typhlocarcinus* sp. [Figure 4(a)], the general trend of Figure 3(c) is confirmed, i.e. an enrichment in ^{13}C and ^{15}N is found when going from the mangrove creeks to the Central and North Bay but in addition, the Central and North Bay data also display some variability, suggesting that *Typhlocarcinus* sp. feeds in a highly selective way. For *Tellina* spp. [Figure 4(b)], the $\delta^{13}\text{C}$ trend is also confirmed, but the specimens from station CNb 4, near the outfall of Kakinada Canal, are depleted in ^{15}N relative to the expected pattern. For *Paphia undulata* [Figure 4(c)], no data are available for Ma or Mo stations, but it can be seen that within the Central and North Bay, substantial differences in $\delta^{15}\text{N}$ values are observed whereas $\delta^{13}\text{C}$ values of SEb and CNb stations are relatively uniform, suggesting less selective feeding.

$\delta^{15}\text{N}$ values of sediments and benthic invertebrates

When species in each zone were grouped according to their assumed or known trophic status (with a distinc-

tion made between 'low' or 'higher' trophic levels), it appeared that higher trophic levels showed on average higher $\delta^{15}\text{N}$ values (by 2.1 to 3.8‰), and that there was also a marked spatial $\delta^{15}\text{N}$ gradient between the mangrove creeks and the Central and North Bay of about 3.2‰ which could be observed in both low and higher trophic levels [Figure 3(c)]. By comparing the $\delta^{15}\text{N}$ values of species of unknown trophic status with the average $\delta^{15}\text{N}$ values of species of known low or high trophic level from that zone, we can tentatively classify *Oratosquilla* sp. and *Harpisquilla* sp. as 'higher' trophic level species, whereas *Meretrix meretrix* and *Acaudina molpaidoides* had intermediate $\delta^{15}\text{N}$ values. For *Meretrix meretrix* this is confirmed by gut content analysis which indicated the presence of animal tissues (C. Kalavati, unpublished data). For the bivalve *Pinctada radiata* and the sponge *Tetilla dactyloidea*, however, insufficient data are available to assess its trophic status. Overall, the $\delta^{15}\text{N}$ signature appears to be a useful indicator of trophic level, if the local baseline $\delta^{15}\text{N}$ values are taken into account. However, in each of the zones, there remained some overlap in the $\delta^{15}\text{N}$ signatures of the two proposed trophic levels. The degree of ^{15}N -enrichment between two trophic levels and the mechanisms causing it are still not yet fully understood (Ponsard & Averbuch, 1999) and the enrichment factor has been found to be quite variable (e.g. Adams & Sterner, 2000), but is assumed to be on average about 2.6 to 3.4‰ (Owens, 1987; Minagawa & Wada, 1984).

The spatial $\delta^{15}\text{N}$ gradient could also be noticed in the sediment organic matter [Figure 2(b)], but was less pronounced with a difference of about 1.6‰ between the mangrove creeks and the Central and North Bay. Contrary to our expectations, the distribution of sedimentary $\delta^{15}\text{N}$ values was relatively uniform throughout the Bay and was not indicative of major sewage impact from the Kakinada Canal [Figure 2(c)]. Such a $\delta^{15}\text{N}$ gradient was also noted in this area in zooplankton (Bouillon *et al.*, 2000) and fish (S. Bouillon, unpublished data). Thus, whereas low trophic level species in the mangrove creeks had $\delta^{15}\text{N}$ values about 1.5‰ higher than sediment organic matter, this difference increased to almost 3‰ in the Central and North Bay. Several factors may be responsible for this $\delta^{15}\text{N}$ trend, which is ultimately related to $\delta^{15}\text{N}$ differences in primary producers. First, the source nitrogen for the primary producers in the different regions may have a variable $\delta^{15}\text{N}$ signal. For example, NO_3^- from sewage waste has been found to have significantly higher $\delta^{15}\text{N}$ values than other NO_3^- sources (Heaton, 1986; Macko & Ostrom, 1994), and thus ecosystem $\delta^{15}\text{N}$ has been found to increase with the degree of urbanization of

the watershed (e.g. Fry, 1999; McClelland *et al.*, 1997; McClelland & Valiela, 1998). Risk and Erdmann (2000) found higher $\delta^{15}\text{N}$ values in invertebrates in sewage-impacted coral reef invertebrates than in non-impacted reef invertebrates. On the other hand, sewage effluent organic matter has been found to have low $\delta^{15}\text{N}$ values (e.g. Sweeney & Kaplan, 1980; Macko & Ostrom, 1994) causing invertebrates to exhibit lower $\delta^{15}\text{N}$ values in the vicinity of sewage outfalls than in nearby unpolluted marine locations (e.g. Rogers, 1999; Thornton & McManus, 1994; Tucker *et al.*, 1999). Several bivalves collected near to the outfall of Kakinada Canal (station CNb4) did show relatively low $\delta^{15}\text{N}$ values compared to other low trophic level species in the Bay [Figure 4(b), Appendix I], but their high $\delta^{13}\text{C}$ values ($\sim -17\text{‰}$) are not indicative of direct utilization of sewage-derived matter.

Secondly, the load and the phytoplankton demand for these nutrients (NO_3^- and NH_4^+) is an important factor controlling primary producer $\delta^{15}\text{N}$ values. It has been shown that $\delta^{15}\text{N}$ values of particulate (and sediment) organic matter increase as NO_3^- concentrations decrease, either along a spatial gradient or during the course of a phytoplankton bloom, and this is due to the selective assimilation of $^{14}\text{NO}_3^-$ resulting in an isotopically heavier DIN pool and subsequently newly produced biomass (see Altabet & Francois, 1994 and references therein), and a similar situation holds for NH_4^+ assimilation (Cifuentes *et al.*, 1988). Thus, spatial and seasonal variations in the DIN concentration and speciation will affect primary producer $\delta^{15}\text{N}$ values and these will in turn be reflected in consumer tissue isotopic composition. Another process which has been shown to increase $\delta^{15}\text{N}$ values locally or seasonally is denitrification, which causes an enrichment in the residual DIN pool, and subsequently in all ecosystem compartments (e.g. Mariotti *et al.*, 1984).

In the study area, ammonium concentrations (AV Raman, unpublished data) have been found to be highest (average values of 0.6, 1.3, 8.9 and 13.1 μM for the North Bay, South Bay, Gaderu and Coringa, respectively) during the monsoon period (July–September), and afterwards decrease until values of $<0.1 \mu\text{M}$ are reached by the end of the pre-monsoon period (i.e. the sampling period). Thus, it appears that NH_4^+ consumption depletes the NH_4^+ pool and this should lead to an enrichment of the remaining pool in ^{15}N . In a similar way, there is a spatial gradient with NH_4^+ generally being a more important constituent of the DIN pool in the mangrove creeks and outlets, and nitrate taking over this role in the Bay waters. As Cifuentes *et al.* (1988) mention that no NO_3^- uptake

by phytoplankton takes place as long as the NH_4^+ concentration remains $>2 \mu\text{M}$, for the present study this would imply that NO_3^- uptake only occurs towards the end of the pre-monsoon period, for the whole area. We thus hypothesize that uptake by DIN, imported via the mangrove creeks and other freshwater sources, enriches the remaining DIN pool in the Bay and results in the observed $\delta^{15}\text{N}$ gradient in sediments and consumers.

Concluding remarks

Overall, our results indicate a strong selectivity of the benthic invertebrate community for local algal sources and a limited trophic dependancy on mangrove or other terrestrial carbon sources. In contrast to the wide range of resources used by intertidal invertebrates (Bouillon *et al.*, 2001), benthic fauna in the subtidal regions appear to show much less diversity in their carbon sources, as evidenced by the relative uniformity of $\delta^{13}\text{C}$ values at each location. The stable isotopic composition of sediments furthermore suggest that burial of mangrove and terrestrial carbon in sediments is limited in this particular system. Besides the evidence provided by stable isotopes (e.g. Newell *et al.*, 1995; Dehairs *et al.*, 2000; this study), several authors have recently questioned the importance of mangrove-derived carbon to estuarine or nearshore aquatic secondary production based on mass-balance considerations. Wafar *et al.* (1997) estimated that the total potential C-flux of mangroves in a western Indian estuary was only 37% of the measured average phytoplankton C production, and this number dropped to 3–4% in terms of N and P. Similarly, Li and Lee (1998) estimated mangrove carbon to contribute only 1.8% to the total available carbon pool in Deep Bay, China. Using the litter fall measurements made by Dehairs *et al.* (2000) (weighted average of 1.2 g C/m²/day) and phytoplankton primary production rates (from 1.1 to 3.3 g C/m²/day when assuming a depth of 1.5 m with photosynthetic activity, AV Raman, unpublished data), it becomes clear that the potential contribution of mangrove carbon to the system is much less than that from phytoplankton (by a factor of ~ 5), considering the relative surface areas of aquatic and mangrove habitats. It should be stressed that this is a very rough estimate which did not take into account e.g. the fact that part of the litter fall will be stored, consumed, and respired in the intertidal areas, and that a major part of the mangrove C-flux might be in the form of DOC (see Lee, 1995) or be directed towards the Bay of Bengal on the eastern edge of the forest. It also does not include potential contributions from benthic microalgae and

from other terrestrial sources (e.g. via the Kakinada Canal, and from the Gautami Godavari), and thus no doubt overestimates the potential contribution made by mangrove litterfall.

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APPENDIX I. Carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, expressed in‰) of benthic invertebrates collected in the Coringa-Kakinada Bay complex, during pre-monsoon season in 1997 (indicated by *) and 1999

Location	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
Ma 1	<i>Diopatra neapolitana</i>	– 23.8	+10.4	1
	<i>Meretrix meretrix</i>	– 23.6, – 23.3	+8.1, +10.4	2
Ma 2	<i>Diopatra neapolitana</i>	– 23.9	+9.5	1
	<i>Macrophthalmus</i> sp.	– 22.4	+5.1	1
	<i>Typhlocarcinus</i> sp.	– 23.8	+4.7	1
	<i>Tellina</i> sp. 1	– 23.8 ± 0.7	+6.2 ± 0.8	5
Mo 1	<i>Tellina</i> sp. 1	– 21.1	+7.6	1
	<i>Typhlocarcinus</i> sp.	– 22.4 ± 0.7	+6.7 ± 0.3	5
	<i>Cerithidea cingulata</i>	– 21.1, – 20.5	+10.8, +10.2	2
Mo 2	<i>Diopatra neapolitana</i> *	– 21.2	+9.0	1
	<i>Dorippe facchino</i>	– 21.7 ± 1.5	+6.4 ± 0.5	4
	<i>Macrophthalmus</i> sp.	– 22.2, – 21.9	+4.7, +5.2	2
	<i>Macrobrachium rosenbergii</i>	– 21.5, – 20.9	+10.3, +10.6	2
	<i>Metapenaeus dobsoni</i>	– 20.3	+9.4	1
Mo 3	<i>Typhlocarcinus</i> sp.*	– 20.0	+6.9	1
	<i>Anadara granosa</i> *	– 21.6	+8.0	1
	<i>Macoma</i> sp.*	– 21.6	+8.5	1
Mo 4	<i>Cerithidea cingulata</i>	– 21.2 – 19.7	+9.1, +8.4	2
	<i>Dorippe facchino</i>	– 21.3, – 20.8	+8.9, +6.9	2
	<i>Penaeus merguensis</i>	– 21.1 ± 0.6	+9.5 ± 1.1	3
	<i>Tellina</i> sp. 1	– 22.1 ± 0.2	+8.0 ± 0.4	6
Mo 5	<i>Placuna placenta</i>	– 20.5, – 20.2	+8.7, +9.1	2

APPENDIX I. *Continued*

Location	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
SEb 1	<i>Paphia undulata</i>	-18.0	+8.5	1
	<i>Placuna placenta</i>	-19.6, -19.2	+9.5, +9.3	2
	<i>Echiuroides</i> (unid.)	-17.8	+11.8	1
	<i>Thais lacera</i>	-17.9	+11.0	1
	<i>Metapenaeopsis stridulans</i>	-17.9, -18.2	+10.8, +4.8	2
	<i>Metapenaeus brevicornis</i>	-18.5	+10.8	1
SEb 2	<i>Paphia undulata</i>	-18.5	+7.7	1
	<i>Tellina</i> sp. 1	-18.8 $\pm$ 0.4	+8.4 $\pm$ 0.2	4
	<i>Tellina</i> sp. 2	-18.4	+9.3	1
	<i>Diplodonta</i> sp.	-20.2	+8.0	1
	<i>Macrophthalmus</i> sp.	-16.2	+6.5	1
	<i>Echiuroides</i> (unid.)	-19.0	+12.0	1
	<i>Metapenaeus brevicornis</i>	-18.2	+11.8	1
SEb 3	<i>Meretrix meretrix</i>	-19.6	+9.5	1
	<i>Tellina</i> sp. 1	-18.3	+8.4	1
	<i>Lingula</i> sp.	-20.1	+9.3	1
	<i>Anadara granosa</i>	-19.3, -19.2	+7.2, +6.1	2
	<i>Acaudina molpaidioides</i>	-18.5	+9.6	1
	<i>Diopatra neapolitana</i>	-19.4	+11.2	1
	<i>Oratosquilla</i> sp.	-18.1	+11.4	1
	<i>Volema cochlidium</i>	-18.0	+9.6	1
	<i>Penaeus merguiensis</i>	-19.2	+9.3	1
	<i>Paphia undulata</i>	-18.7	+12.9	1
	<i>Leucosia</i> sp.	-18.0	+11.4	1
	<i>Dorippe facchino</i>	-16.7	+10.7	1
CNb 1	<i>Nassarius olivaceus</i>	-17.5	+11.9	1
	<i>Portunus sanguinolentus</i>	-16.8	+12.9	1
	<i>Harpisquilla</i> sp.	-17.6	+7.8	1
	<i>Metapenaeopsis</i> sp.	-15.9	+13.4	1
	<i>Metapenaeus monoceros</i>	-22.7, -16.1	+14.5, +11.9	2
	<i>Charybdis</i> sp.	-17.0, -16.2	+11.4, +11.7	2
	<i>Paphia undulata</i>	-17.5	+12.0	1
	<i>Pinctada radiata</i>	-17.4	+11.6	1
	<i>Macrophthalmus</i> sp.	-17.9, -17.3	+9.5, +8.0	2
	<i>Typhlocarcinus</i> sp.	-14.6 $\pm$ 1.9	+9.8 $\pm$ 1.5	3
CNb 3	<i>Paphia undulata</i> *	-17.2	+8.1	1
	<i>Nassarius</i> sp.*	-15.3	+10.5	1
	<i>Murex trapa</i> *	-16.0	+9.9	1
	<i>Typhlocarcinus</i> sp.*	-17.3	+7.2	1
CNb 4	<i>Meretrix meretrix</i>	-16.0 $\pm$ 0.3	+9.8 $\pm$ 0.8	4
	<i>Tellina</i> sp. 2	-16.4 $\pm$ 0.5	+6.8 $\pm$ 1.6	6
CNb 5	<i>Paphia undulata</i>	-18.0, -16.9	+11.1, n.d.	2
	<i>Anadara granosa</i>	-17.3, -16.8	+10.0, +10.4	2
	<i>Charybdis</i> sp.	-17.1	+13.4	1
	<i>Macrophthalmus</i> sp.	-16.7, -15.5	+7.5, +5.9	2
	<i>Murex trapa</i>	-14.5, -14.4	+13.9, +13.9	2
	<i>Nassarius olivaceus</i>	-17.1, -16.9	+13.2, +12.0	2
CNb 6	<i>Typhlocarcinus</i> sp.	-15.5 $\pm$ 0.9	+10.7 $\pm$ 0.5	3
	<i>Paphia undulata</i> *	-16.6	+9.4	1
	<i>Anadara natalensis</i> *	-16.6	+8.3	1
	<i>Babylonia canaliculata</i> *	-15.6	+12.2	1
	<i>Typhlocarcinus</i> sp.*	-17.0	+8.9	1
CNb 7	<i>Penaeus merguiensis</i>	-21.5	+7.3	1
	<i>Parapenaeopsis stylifera</i>	-15.1	+12.6	1
CNb 8	<i>Paphia undulata</i> *	-16.4	+8.9	1
	<i>Typhlocarcinus</i> sp.*	-15.9	+8.3	1
	<i>Murex trapa</i> *	-15.4	+10.9	1
	<i>Anadara granosa</i> *	-17.1	+10.2	1
	<i>Meretrix meretrix</i> *	-18.2	+12.0	1

APPENDIX I. *Continued*

Location	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
CNb 8	<i>Nassarius</i> sp.*	-17.4	+11.1	1
	<i>Philyra</i> sp.*	-16.8	+8.3	1
CNb 9	<i>Paphia undulata</i>	-17.7	+9.9	1
	<i>Tetilla dactyloidea</i>	-18.4	+12.1	1
CNb 10	<i>Paphia undulata</i> *	-16.7	+9.6	1
	<i>Typhlocarcinus</i> sp.*	-18.9	+10.1	1
	<i>Murex trapa</i> *	-15.7	+11.3	1
	<i>Nassarius olivaceus</i> *	-17.0	+11.5	1
	<i>Nassarius</i> sp.*	-15.1	+10.9	1
	<i>Charybdis</i> sp.*	-16.5, -16.1	+9.6, +9.4	2
CNb 11	<i>Charybdis</i> sp.	-15.7	+13.0	1
	<i>Harpiosquilla</i> sp.	-16.2	+11.9	1
	<i>Murex trapa</i>	-16.7	+11.9	1
	<i>Tellina</i> sp. 2	-16.9	+8.0	1
	<i>Penaeus semisulcatus</i>	-13.8	+10.6	1
CNb 12	<i>Paphia undulata</i> *	-16.9	+8.7	1
	<i>Typhlocarcinus</i> sp.*	-19.2	+8.4	1
	<i>Nassarius olivaceus</i> *	-18.7	+10.9	1
	<i>Thais lacera</i> *	-14.9	+9.0	1
	<i>Macoma</i> sp.*	-17.1	+8.9	1
	<i>Siliqua albida</i> *	-16.5	+7.6	1
	<i>Harpiosquilla</i> sp.*	-16.1	+10.3	1