INTRODUCTION

Mangrove forests are often considered to be highly productive tropical ecosystems (Clough 1992). There is, however, still a lot of uncertainty on the fate of the large amounts of leaf litter produced by these systems. The ‘outwelling hypothesis’, stating that large amounts of mangrove detritus are exported to the aquatic near-shore environment (reviewed by Lee 1995), where they enhance or sustain secondary productivity, has been the subject of much debate. Based on gut-content analysis of mangrove-inhabiting fauna, Odum & Heald (1975) stated that the major energy flow in these ecosystems occurs via the incorporation of microbially enriched mangrove detritus into secondary producers, which in turn support higher trophic levels. Although an appealing hypothesis, considering the high productivity of these trees compared to other primary producers such as phytoplankton and microphytobenthos (Robertson et al. 1992, Alongi 1994, Gattuso et al. 1998), a number of recent studies have led to the conclusion that the importance of these other primary producers which have a higher nutritional value due to
their higher nitrogen content, may have been underestimated (Stoner & Zimmerman 1988, Ambler et al. 1994, Newell et al. 1995, Primavera 1996, Marguillier et al. 1997, Loneragan et al. 1997, France 1998). Similar conclusions have been obtained in a variety of other estuarine systems (e.g. Sullivan & Moncreiff 1990, Deegan & Garrit 1997). Others, on the other hand, have concluded that mangrove detrital material constitutes an important food source for many aquatic organisms, yet only on a limited spatial scale, with phytoplankton becoming the primary carbon source in nearby coastal waters (Rodelli et al. 1984).

Suspension-feeding copepods often form the bulk of the zooplankton in estuarine ecosystems. Although results are contradictory, several experiments have shown convincing evidence that, besides being size-selective feeders, these organisms are capable of discriminating between live and dead algae (DeMott 1988, 1995 and references therein). Most of these results were obtained in laboratory experiments where copepods were offered only pairs of different particles, and DeMott (1995) stresses that these may be misleading or irrelevant to understanding copepod feeding selectivity under natural conditions. Estuarine zooplankton, however, are often considered to be indiscriminate, non-selective feeders (e.g. Hummel et al. 1988, Turner & Tester 1989). Considering the potentially important role of zooplankton as a trophic link between primary producers and higher trophic levels, which include many commercially important species, it is surprising that most stable isotope studies in mangrove ecosystems have not incorporated zooplankton analysis (Rodelli et al. 1984, Fleming et al. 1990, Newell et al. 1995) or have been limited to a relatively small number of measurements (Stoner & Zimmerman 1988, Ambler et al. 1994, Dittel et al. 1997, Marguillier et al. 1997) and did not include a thorough discussion of the possible carbon sources for zooplankton. As Robertson et al. (1992) noted, the relative importance of mangrove carbon and other sources to zooplankton nutrition in these ecosystems thus remains largely unknown.

Analysis of the natural abundance of carbon and nitrogen stable isotopes provides a powerful method to trace sources and transfer of organic matter through foodwebs (Peterson & Fry 1987), provided that different primary producers have a distinct isotopic signature, and based on the assumptions that fractionation of $^{13}$C between an organism and its diet is small or negligible (0 to 1‰; DeNiro & Epstein 1978), and that organisms are enriched in $^{15}$N relative to their diet by an average of 2.6 (Owens 1987) to 3.4‰ (Minagawa & Wada 1984). These fractionation values should be treated with some caution, as there is some recent evidence for differences in $^{15}$N enrichment depending on the nitrogen content of an organism’s diet (Fantle et al. 1999). Elemental and stable isotope analysis has been used in a large number of studies to determine the spatial and/or temporal distribution of different sources of organic matter (allochthonous detritus and local phytoplankton) in suspended matter and sediments of estuarine systems (e.g. Cifuentes et al. 1996, Ogawa & Ogura 1997, Middelburg & Nieuwenhuize 1998, Hel- lings et al. 1999). The majority of these studies focus on temperate ecosystems, but several authors have used this approach to characterise suspended organic matter sources in tropical mangrove ecosystems (Rezende et al. 1990, Hemminga et al. 1994, Cifuentes et al. 1996, Dehairs et al. 2000). These studies have shown that suspended organic matter in these systems is comprised of a highly variable proportion of terrestrial detritus and algae (and seagrasses when present), and that substantial spatial, seasonal, and tidal variations in the $\delta^{13}$C signal of suspended matter may occur. Such variations should be taken into account when suspended matter $\delta^{13}$C data are used in food web analysis (Goering et al. 1990, Cifuentes et al. 1996), but this aspect is still neglected in many studies. Large seasonal and spatial variations have also been observed in zooplankton $\delta^{13}$C and $\delta^{15}$N, both in marine and coastal environments (Fry & Wainright 1991, Malej et al. 1993, Wainwright & Fry 1994, Zohary et al. 1994 and references therein) and freshwater ecosystems (Toda & Wada 1990, Yoshioka et al. 1990), with variability generally being larger in freshwater ecosystems (Zohary et al. 1994).

In this study, we wanted to gain insight into the sources of organic matter present in the suspended material in an estuarine mangrove ecosystem located near the mouth of the Gautami Godavari, Andhra Pradesh, India, by measuring elemental (C:N) and stable carbon-isotope ratios in suspended particulate organic matter (SPOM), collected at monthly intervals between January 1995 and August 1996 at 13 different locations, representing different environmental conditions. In addition, we wanted to assess whether the use of stable carbon- and nitrogen-isotope ratios could provide evidence for selective or non-selective feeding of zooplankton on different components of suspended matter. These data would also provide some baseline information on the spatio-temporal variability of suspended matter and zooplankton isotope ratios, which could be useful for further studies on the trophic dynamics in this ecosystem.

MATERIALS AND METHODS

Study area. The study site (Fig. 1) comprises the area between Kakinada Bay and the Gautami Godavari branch of the Godavari, the second largest
Bouillon et al.: Sources of SPOM and selective feeding by zooplankton

river in India, and is located in the southeastern state of Andhra Pradesh (between 16°43' and 17°00' N, and 82°15' and 82°22' E). The Godavari has a mean annual discharge of $1.1 \cdot 10^{11}$ m$^3$, of which 93 to 96% occurs during the wet monsoon, and it is recognized 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 is dominated by mangrove forests and tidal mudflats, the most abundant species being *Avicennia marina*, *A. officinalis*, *Excoecaria agallocha*, *Sonneratia apetala*, *Rhizophora mucronata* and *R. apiculata* (Azariah et al. 1992, Satyanarayana 1997). The shallow Kakinada Bay (depth at high tide ranging from 3 to 8 m), which covers approximately 150 km$^2$, opens into the sea on its northern side, and is bordered along most of its eastern length by a narrow sand bar, which experienced a breakthrough along its southern end after the November 1996 cyclone. Tides are semidiurnal, and tidal amplitude in the Bay varies between 2.3 and 4.5 m (Sreenivas 1998), but is less in the mangrove-covered areas.

The town of Kakinada (population ~500 000), which hosts a large fishing harbour and several fertiliser factories, is located on the west side of Kakinada Bay. The whole area serves as an important fishing area for the local community, as well as for the collection of crabs, prawn ‘seed’ (mainly *Penaeus monodon* and *P. indicus*), and firewood. Due to increased human pressure (sewage, aquaculture ponds) and pollution, the area has witnessed a significant decline in biodiversity during the last 40 yr (Chandra Mohan et al. 1997).

In general, 4 seasons can be distinguished in the area, although substantial year-to-year variations in this pattern can be observed: (1) a cool and dry season from December to February; (2) a hot and relatively dry period from March to June; (3) abundant rains during the hot Southwest monsoon (July to September), when almost freshwater conditions prevail in the whole area; (4) a cooler transitional period during which estuarine and marine conditions are re-established in the Bay and mangrove creeks (October to November).

During the period of this study, however, a bimodal rainfall distribution was noticed, with highest rainfall occurring in May 1996 and November 1996.

**Sample collection and preparation.** During the period from January 1995 to August 1996, zooplankton samples were collected at 4 different locations, representing different environmental and hydrological settings (Fig. 1): Kakinada North Bay (K$_2$), at the mouth of Coringa (C$_1$), central Gaderu (G$_3$), and at the mouth of the Gautami Godavari (G$_6$). Suspended matter was collected at approximately monthly intervals at these 9 additional locations. As it was impossible to collect all samples at the same tidal elevation, we examined the tidal variability of $\delta^{13}$C$_{SPOM}$ at 1 station (G$_3$) during a 24 h period in November 1995.

Zooplankton samples were collected by towing a 120 µm plankton net equipped with a calibrated TSK flow meter at its opening. Material for stable isotope analysis was kept in a cool box on board, and transported to the field laboratory, where it was washed and dried at 60°C for 24 h. Subsamples were fixed on board in 5% formaldehyde for quantitative studies and identification as discussed in Chandra Mohan et al. (1997) and Sreenivas (1998). Samples were ground to a fine powder, and subsamples for $\delta^{13}$C analysis were washed with diluted HCl to remove carbonates, and redried. Subsamples for $\delta^{15}$N analysis did not receive this acid treatment, as this has been reported.

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**Fig. 1.** Map of study area, showing major waterways and sampling locations (●). Dark areas represent main mangrove-covered areas.
to affect δ15N values (Goering et al. 1990; Bunn et al. 1995). SPOM samples were obtained by collecting approx. 250 ml of subsurface water, which was kept in a cool box during transport, and was later filtered on pre-combusted glass-fibre filters (Whatman GF/F). Filters were then dried at 60°C for 24 h and decalcified under acid vapour. Due to their low nitrogen content, no SPOM δ15N measurements could be made. Salinity data are to be found in Murthy (1997) and Sreenivas (1998).

**Measurement of elemental and stable isotope ratios.** Most data on elemental (C:N) ratios of SPOM were taken from Dehairs et al. (2000). Some additional measurements were made using a Carlo Erba NA-1500 Elemental Analyser. Samples for stable isotope analysis were combusted in the same instrument, and the resulting gases (CO2 and N2) were separated by cryopurification using a Finnigan Mat CT-NT Trapping box (for CO2), or with a manual extraction line (for CO2 and N2). 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 (Coplen 1996) and atmospheric N2 for nitrogen, as δ values, defined as:

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

where \( R = ^{13}\text{C} \) or \( ^{15}\text{N} \), and \( X = ^{13}\text{C}/^{12}\text{C} \) or \( ^{15}\text{N}/^{14}\text{N} \). The normal working standard for carbon was CO2 produced from carrara marble, and atmospheric N2 was used as the working standard for nitrogen. The standard deviation of 10 aliquots of the same sample was lower than 0.17 and 0.2‰ for \( \delta^{13}\text{C} \) and \( \delta^{15}\text{N} \), respectively.

**RESULTS**

**Elemental and stable carbon-isotope composition of suspended matter**

SPOM δ13C values varied overall between −30.94 and −19.18‰, but average values per location ranged from a minimum of −25.51 (at C1 and C2) to −22.73‰ (at K3) (Table 1).

Suspended matter was, on average, more enriched in 13C at the bay stations, although significant overlap occurred (Fig. 2, Table 1). Contrary to the expectation that this enrichment would increase along a linear gradient towards the bay opening, i.e. from Stn K4 via K2 to K1, the reverse pattern was observed (average δ13C values = K1: −23.55‰; K2: −23.33‰; K4: −22.83‰), and most 13C-enhanced values (−22.73‰) were observed at K3. Using a paired t-test, this enrichment of K4 relative to K1 was significant (p = 0.041; \( \alpha = 0.05 \)), although the average difference was relatively small (0.72‰). A paired t-test revealed that K2, K3, and K4 differed significantly from all Coringa, Gaderu and Gautami Godavari stations (p < 0.043; \( \alpha = 0.05 \)), but SPOM from the northernmost station (K1) was found to differ only from the 3 Coringa stations and the Gaderu stations G2 (p = 0.018; \( \alpha = 0.05 \)), G3 (p = 0.004; \( \alpha = 0.05 \)) and G4 (p = 0.006; \( \alpha = 0.05 \)). Most depleted average δ13CSPOM values were observed in the 3 Coringa stations, which all had an average value of −25.5‰ (Table 1, Fig. 2). In Gaderu, suspended matter was found to be most depleted in 13C in the central station (G3: −25.21‰), and became more enriched both towards Kakinada Bay (G2: −24.86‰; G3: −23.98‰) and towards the Gautami Godavari opening (G4: −25.12‰; G5: −24.32‰) (Table 1, Fig. 2).

<table>
<thead>
<tr>
<th>Stn</th>
<th>( \delta^{13}\text{C} \pm 1 \text{ SD} )</th>
<th>Min. ( \delta^{13}\text{C} )</th>
<th>Max. ( \delta^{13}\text{C} )</th>
<th>C:N ± 1 SD</th>
<th>Min. C:N</th>
<th>Max. C:N</th>
<th>Salinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>K1</td>
<td>−23.55 ± 1.25 (n = 16)</td>
<td>−25.97</td>
<td>−20.82</td>
<td>9.98 ± 4.88 (n = 15)</td>
<td>5.4</td>
<td>23.6</td>
<td>28.5</td>
</tr>
<tr>
<td>K2</td>
<td>−23.33 ± 1.25 (n = 17)</td>
<td>−25.75</td>
<td>−21.71</td>
<td>8.52 ± 2.44 (n = 17)</td>
<td>5.8</td>
<td>14.0</td>
<td>27.3</td>
</tr>
<tr>
<td>K3</td>
<td>−22.73 ± 2.15 (n = 16)</td>
<td>−26.30</td>
<td>−19.18</td>
<td>8.26 ± 2.44 (n = 15)</td>
<td>5.0</td>
<td>13.5</td>
<td>23.5</td>
</tr>
<tr>
<td>K4</td>
<td>−22.83 ± 1.52 (n = 17)</td>
<td>−26.43</td>
<td>−20.68</td>
<td>8.49 ± 3.21 (n = 15)</td>
<td>4.8</td>
<td>17.3</td>
<td>25.8</td>
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<td>C1</td>
<td>−25.51 ± 1.53 (n = 13)</td>
<td>−28.81</td>
<td>−23.66</td>
<td>11.94 ± 8.79 (n = 13)</td>
<td>5.6</td>
<td>32.7</td>
<td>10.6</td>
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<td>C2</td>
<td>−25.51 ± 0.86 (n = 13)</td>
<td>−26.59</td>
<td>−23.71</td>
<td>12.74 ± 11.18 (n = 12)</td>
<td>5.1</td>
<td>38.0</td>
<td>6.5</td>
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<td>C3</td>
<td>−25.50 ± 1.13 (n = 13)</td>
<td>−26.83</td>
<td>−23.39</td>
<td>13.41 ± 12.18 (n = 11)</td>
<td>6.2</td>
<td>42.4</td>
<td>4.2</td>
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<tr>
<td>G1</td>
<td>−23.98 ± 1.23 (n = 16)</td>
<td>−26.41</td>
<td>−22.00</td>
<td>9.29 ± 3.45 (n = 15)</td>
<td>6.0</td>
<td>20.5</td>
<td>18.8</td>
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<td>G2</td>
<td>−24.86 ± 1.85 (n = 16)</td>
<td>−30.94</td>
<td>−23.15</td>
<td>8.71 ± 2.86 (n = 15)</td>
<td>5.0</td>
<td>15.2</td>
<td>17.5</td>
</tr>
<tr>
<td>G3</td>
<td>−25.21 ± 1.58 (n = 18)</td>
<td>−29.48</td>
<td>−23.22</td>
<td>8.29 ± 2.46 (n = 15)</td>
<td>5.7</td>
<td>13.2</td>
<td>17.6</td>
</tr>
<tr>
<td>G4</td>
<td>−25.12 ± 1.64 (n = 16)</td>
<td>−29.05</td>
<td>−23.22</td>
<td>8.67 ± 3.89 (n = 15)</td>
<td>6.3</td>
<td>20.5</td>
<td>15.3</td>
</tr>
<tr>
<td>G5</td>
<td>−24.32 ± 1.65 (n = 16)</td>
<td>−27.05</td>
<td>−20.95</td>
<td>10.08 ± 5.61 (n = 15)</td>
<td>3.9</td>
<td>27.8</td>
<td>16.3</td>
</tr>
<tr>
<td>G6</td>
<td>−24.65 ± 1.31 (n = 17)</td>
<td>−27.52</td>
<td>−22.31</td>
<td>9.23 ± 3.42 (n = 15)</td>
<td>5.4</td>
<td>17.2</td>
<td>15.6</td>
</tr>
</tbody>
</table>

Table 1. Average (±1 SD), minimum and maximum stable carbon-isotope ratios (δ13C, ‰) and elemental (C:N) ratios of suspended particulate organic matter (SPOM), and average salinity (‰) at different sampling locations in the Gautami Godavari estuarine region. Abbreviations of sampling locations as in Fig. 1. Numbers in parentheses: number of samples analysed. Most C:N ratios from Dehairs et al. (2000), salinity data from Murthy (1997)
Fig. 2. Average stable carbon-isotope ratios (‰) of suspended particulate organic matter (SPOM), collected at different locations in the Gautami Godavari estuarine region between January 1995 and July 1996. Error bars = ±1 SD. Sampling locations (ordinate) are shown in Fig. 1.

This enrichment compared to G3 is significant (paired t-test) in G1 (p = 0.0077; α = 0.05) and G5 (p = 0.012; α = 0.05). At the Gautami Godavari station (G6), suspended matter had an average δ13C of –24.65‰.

Seasonal variations in SPOM δ13C values (i.e. the range of δ13C values observed) at each location were larger than the average differences in SPOM δ13C between different locations. An apparent depletion in 13C can be observed during the transitional and dry season (between October and February), and is most pronounced in the Coringa and Gaderu stations (Fig. 3, Table 2).

Overall, C:N ratios of suspended matter ranged from 3.9 to 42.4; but average values for all stations were between 8.3 (at G3 and K3) and 13.4 (at C3) (Table 1, Fig. 4). Suspended matter samples with C:N ratios higher than 12 are often considered to be indicative of containing mainly terrestrial detritus (Faganeli et al. 1988, Cifuentes et al. 1996). As shown in Fig. 4 (dotted line), these have an average δ13C value of –25.93‰, which is within the range of values reported for typical terrestrial C3-plants (Peterson & Fry 1987). The bulk of samples with lower C:N ratios (including all but 4 of the Kakinada Bay and Gautami Godavari samples) are enriched in 13C relative to this detrital signal, but about 23% of all samples, the majority of which come from Coringa and Gaderu, are depleted in 13C (Fig. 4).

During the tidal cycle recorded at Gaderu Stn G3 in November 1995, δ13CSPOM varied between –26.51 and –28.30‰, and was well correlated with salinity fluctuations (R² = 0.62; p = 0.012), with low δ13CSPOM values occurring at lower salinity (low-tide period) (Fig. 5).

Table 2. Seasonal variations in suspended matter δ13C (‰) at the different sampling locations. *Data from Dehairs et al. (2000). Abbreviations of sampling locations as in Fig. 1. nd: not determined.
Stable carbon- and nitrogen-isotope composition of zooplankton

The overall range of $\delta^{13}C$ values for zooplankton (–30.13 to –16.45‰) was larger than the range of $\delta^{13}C_{SPOM}$ values from the same locations (–29.48 to –21.71‰; Tables 1 & 3). Zooplankton were most enriched in $^{13}C$ in Kakinada Bay (Stn K2, average $\delta^{13}C_{ZP} =$ –21.02‰), but exhibited the largest range at this station (–28.19 to –16.45‰). The average zooplankton $\delta^{13}C$ at the 4 sampling locations followed the same trend in $^{13}C$-depletion as the suspended matter from these stations (i.e. $K_2 > G_6 > G_3 > C_1$), but the $\delta^{13}C$ gradient was more pronounced in the zooplankton, caus-
As observed for SPOM, most depleted values were usually observed between the middle of the monsoon period (i.e. September) and the middle of the dry season (i.e. February) (Fig. 7), and the range of $\delta^{15}N$ values observed at each station was larger than the average spatial differences (Table 3).

Zooplankton $\delta^{15}N$ values exhibited much less seasonal variation than the $\delta^{13}C_{ZP}$ variations (Table 3). Due to the small sample sizes, it was impossible to analyse the $\delta^{15}N$ of all samples, which makes it difficult to detect any clear seasonal trend in zooplankton $\delta^{15}N$. Based on these data, however, it seems that Coringa zooplankton were lower in $\delta^{15}N$ (+4.76 and +5.22‰, n = 2) than that at the 3 other stations, which were relatively similar in their average $\delta^{15}N$ values (average $\delta^{15}N = +7.46$‰ at G3, +7.92‰ at K2, and +8.42‰ at G6). Due to the small amount of concurrent data from different stations, we were unable to detect any statistically significant spatial differences in $\delta^{15}N$.

**DISCUSSION**

**Sources of organic matter in SPOM**

Because of the high turbidity in the study area, aquatic macrophytes and seagrasses are virtually absent (Dehairs et al. 2000). The 3 main local primary producers to be considered are thus mangroves, phytoplankton, and benthic microalgae, of which the latter 2 are generally quantitatively much less important in turbid estuarine mangrove ecosystems (Roberston et al. 1992). In addition, some terrestrial detritus from outside the area, carried by the Gautami Godavari and

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Table 3. Average ($\pm$1 SD), minimum and maximum $\delta^{13}C$ and $\delta^{15}N$ (‰) of zooplankton (ZP), collected at different locations in the Gautami Godavari estuarine region. Some of the zooplankton $\delta^{13}C$ data were taken from Dehairs et al. (2000). Abbreviations of sampling locations as in Fig. 1

<table>
<thead>
<tr>
<th>Sampling Location</th>
<th>$\delta^{13}C_{ZP}$</th>
<th>$\delta^{15}N_{ZP}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kakinada Bay</td>
<td>$-21.02 \pm 3.21$ (n = 19)</td>
<td>$+7.92 \pm 1.42$ (n = 12)</td>
</tr>
<tr>
<td>Coringa</td>
<td>$-25.85 \pm 2.99$ (n = 9)</td>
<td>$+4.99 \pm 0.33$ (n = 2)</td>
</tr>
<tr>
<td>Gaderu</td>
<td>$-24.25 \pm 2.82$ (n = 14)</td>
<td>$+7.46 \pm 0.86$ (n = 4)</td>
</tr>
<tr>
<td>Gautami Godavari</td>
<td>$-22.03 \pm 2.40$ (n = 13)</td>
<td>$+8.42 \pm 1.17$ (n = 4)</td>
</tr>
</tbody>
</table>

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*Fig. 5. Salinity ($S$), elemental composition ($N$, %) and stable carbon-isotope composition ($\delta^{13}C$, ‰) of suspended particulate organic matter collected during a 24 h period at the central Gaderu station (G3) on 16/17 November 1995. Arrows pointing upwards: high tides; arrow pointing downwards: low tide.*

*Fig. 6. Average zooplankton $\delta^{13}C$ (‰) vs average SPOM $\delta^{13}C$ (in ‰) for different locations. Only concurrently collected samples were used to construct this figure. Error bars = ±1 SD; dotted line represents $\delta^{13}C$ for the zooplankton food source assuming fractionation of 1‰.*
entering Coringa and Gaderu, can be expected to contribute to the suspended organic matter load. Leaves of 7 out of 19 mangrove species occurring in the area showed an average $\delta^{13}C$ signal of $-29.02 \pm 1.11\%$ (Dehairs et al. 2000, S. Bouillon unpubl. data), which is consistent with literature data on these and other mangrove species (Rodelli et al. 1984, Zieman et al. 1984, Stoner & Zimmerman 1988, Rezende et al. 1990, Hemminga et al. 1994, Rao et al. 1994, Cifuentes et al. 1996, Primavera 1996, Marguillier et al. 1997, France 1998), and which is a typical $\delta^{13}C$-signature for terrestrial C3-plants. Factors reported to influence mangrove leaf $\delta^{13}C$ include their water-use efficiency, salinity, and ambient humidity (Farquhar et al. 1982, Lin & Sternberg 1992, Kao & Chang 1998). Loneragan et al. (1997) found no seasonal differences in mangrove leaf $\delta^{13}C$. Several authors have found no significant changes in the $\delta^{13}C$ signal of mangrove leaves during decomposition (Zieman et al. 1984, Dehairs et al. 2000), so that we may assume that mangrove detritus exported into the water column also exhibits a carbon-isotope signal in the same range as the measured $\delta^{13}C$ values for mangrove leaves. Although fresh mangrove leaves are reported to have C:N ratios ranging between 20 and 78 (average around 50), this ratio increases 2- to 3-fold during senescence due to re-absorption of 60 to 70% of the nitrogen by the plants (Rao et al. 1994, Jennerjahn & Ittekot 1997). During subsequent decomposition and bacterial colonization, however, nitrogen enrichment occurs through nitrogen fixation (Woitchik et al. 1997) and immobilization, both on the forest floor (Twilley et al. 1992) and in the water column (Cifuentes et al. 1996). These processes result in much lower C:N ratios for mangrove detritus. According to Cifuentes et al. (1996), suspended mangrove detritus (defined as suspended matter having a carbon-to-chlorophyll a ratio higher than 100) has an average C:N ratio of 12.1, whereas other investigators report C:N ratios of 24 to 51 after 45 d of decomposition for *Excoecaria agallocha* and *Avicennia marina*, respectively (Dehairs et al. 2000), and C:N ratios approaching 24 after about 100 d decomposition for *A. marina*, *A. corniculatum* and *Kandelia candel* (Tam et al. 1990).

Because of the practical difficulties in obtaining phytoplankton samples free from terrestrial detritus, no $\delta^{13}C$ data specifically for phytoplankton are available. It is generally accepted, however, that marine phytoplankton from tropical regions shows a $\delta^{13}C$ signal between $-18$ and $-22\%$ (Fontugne & Duplessy 1981, Goericke & Fry 1994), whereas estuarine and freshwater phytoplankton may be more depleted in $^{13}C$ due to the uptake of isotopically light DIC resulting from the bacterial respiration of terrestrial organic matter (Mook & Tan 1991, Hellings et al. 1999). Phytoplankton C:N ratios are reported to range typically from 6.6 to 8.7 (Redfield et al. 1963, Holligan et al. 1984).

Due to light limitation and inhibition by soluble tannins, benthic microalgal production in mangrove
forests is usually very low (Alongi 1994 and references therein). In the following discussion, only phytoplankton and terrestrial (including mangrove) detritus will be considered as major components of SPOM.

In Kakinada Bay, suspended matter from Stns K2, K3, and K4 was significantly enriched in $^{13}$C relative to all mangrove waterway stations (paired $t$-test), but values were generally more depleted than those reported for typical tropical marine phytoplankton. Several C:N ratios for suspended matter at these stations were relatively high (i.e. between 9 and 17.3) compared to typical phytoplankton C:N ratios (6.6), which leads to the conclusion that a certain amount of terrestrial detritus is present at these locations. In view of the relative proximity to the mangrove waterways (e.g. about 4 km from K4 to the Coringa mouth: Fig. 1), it may be assumed that mangrove detritus constitutes at least a part of this terrestrial matter. Suspended matter $\delta^{13}$C values at these stations also exhibited a fairly wide range ($-21.71$ to $-25.75\%$ at K3, $-19.18$ to $-26.30\%$ at K3, and $-20.68$ to $-26.43\%$ at K4). This variability may have been caused simply by a variable contribution of terrestrial material to the local phytoplankton, but some samples which, judging from their low C:N ratios ($<7$) were dominated by phytoplankton, had $\delta^{13}$C values ranging between $-21.57$ and $-26.30\%$, indicating that phytoplankton at these stations may also exhibit variations in its $\delta^{13}$C signal, e.g. due to the uptake of isotopically-light DIC (e.g. Hellings et al. 1999), variability in growth rate (e.g. Fry & Wainright 1991, Burkhardt et al. 1999), or variability in ambient dissolved CO$_2$ concentrations (Hinga et al. 1994, Burkhardt et al. 1999). Suspended matter $\delta^{13}$C values from all Kakinada Bay stations showed only a minor seasonal pattern, although it is clear that all stations usually followed the same trend. Remarkably, the northernmost station (K1), which is located in the opening of the bay into the Bay of Bengal, exhibited the most depleted average $\delta^{13}$C$_{\text{SPOM}}$ value, indicating a larger terrestrial influence than the central bay stations. It is unclear, however, whether this is the result of circulation patterns in the bay (Sreenivas 1998), which could direct the water flowing out of the mangrove waterways along a clockwise route to the bay opening (K1), or because of a more direct influence by the Kakinada Canal (see Fig. 1), which opens into the western side of the bay on the south end of Kakinada town and carries substantial amounts of domestic waste. Satellite data show that the outflow of the Kakinada Canal is directed towards the bay opening, supporting the latter hypothesis. Either way, it seems that terrestrial detritus, presumably including mangrove-derived material, comprises a variable and detectable fraction of suspended matter in Kakinada Bay, several kilometres from the outlets of the mangrove creeks.

At all 3 Coringa stations, suspended matter had an average $\delta^{13}$C of $-25.5\%$, which was the lowest average value encountered in this study. Of all the sites considered, Coringa is clearly least influenced by the saline bay water, so the $\delta^{13}$C$_{\text{SPOM}}$ values at these stations (especially at C3 which had an average salinity of 4.15: Table 1) can be considered to be representative of the freshwater end-members of suspended matter $\delta^{13}$C.

In Gaderu, suspended matter exhibited the lowest average $\delta^{13}$C at the central G3 station, and it became more enriched in $\delta^{13}$C towards both its marine ends (Table 1, Fig. 2). This gradient may be caused by a combination of 2 factors, i.e. a lesser admixture of marine phytoplankton with terrestrial material from the outer stations towards G3, or a depletion in $\delta^{13}$C in local phytoplankton in the central Gaderu station compared to the other stations. Contrary to the expectation that C:N ratios would have been largest at G3 and lower towards the open water because of a possibly elevated contribution of mangrove detritus to suspended matter, the reverse pattern was observed (Table 1), suggesting that the observed trend in $\delta^{13}$C$_{\text{SPOM}}$ was not due solely to a larger contribution of terrestrial material. In addition, phytoplankton counts and chlorophyll measurements indicated that in Gaderu, phytoplankton was most abundant at G1 and diminished towards G1 and G3 (Rohini 1997). Thus, in Gaderu, a larger contribution of phytoplankton to suspended matter (at G3) was accompanied by more depleted $\delta^{13}$C$_{\text{SPOM}}$, suggesting that, on average, phytoplankton here may have been more $^{13}$C-depleted than the nearby bay phytoplankton.

If we consider $\delta^{13}$C$_{\text{SPOM}}$ data from all locations, it is clear that the stable carbon-isotope composition of suspended matter was very variable, and that seasonal variability was more pronounced than average spatial differences. Based on the wide range of C:N ratios encountered (3.9 to 42.4), part of this variation may have been caused by a variable contribution of terrestrial and autochthonous material to the total suspended organic matter load. However, the wide range of $\delta^{13}$C values (e.g. $-21.57\%$ at K4 to $-29.48\%$ at G3) in samples with low C:N ratios (C:N $<7$, suggesting a substantial phytoplankton contribution) suggests that there was some spatial and temporal variation in phytoplankton $\delta^{13}$C, which was suppressed or masked in samples where the terrestrial contribution was high. Especially for the mangrove creeks, we expect local phytoplankton to have been relatively depleted in $\delta^{13}$C, due to the uptake of isotopically light DIC, which results from the degradation of the large amounts of mangrove litter. In fact, a few preliminary $\delta^{13}$C$_{\text{DIC}}$ results from Coringa surface-water samples collected in February 1999 showed significant $^{13}$C-depletion of the DIC pool, with $\delta^{13}$C values between $-10.5\%$ at G3 and $-10.0\%$ at C1.
Furthermore, 2 relatively pure (visually assessed) phytoplankton samples (10 ≪ 50 µm) collected in Coringa at the same time as the samples assessed for δ13C-DOC showed a δ13C of −28.91‰ (at C7) and −26.87‰ (at C7), respectively, i.e. they were depleted in 13C relative to the average δ13CSPOM at these sites, and fell within the same range as δ13C values reported for mangrove leaves.

δ13C values of SPOM collected during a 24 h period at G3 in November 1995 showed substantial variations with the stage of the tide, with suspended matter being most depleted (−28.30‰) during low tide, and most enriched (−26.51‰) at high tide (Fig. 5). Similar observations in tidal mangrove ecosystems were made by Rezende et al. (1990), and tidal variations in δ13CSPOM at the same range as δ13CSPOM at these sites, and fell within the same range as δ13C values reported for mangrove leaves.

δ13CSPOM values were well correlated with salinity (R² = 0.62; p = 0.012) but not with C:N ratios (R² = 0.14). These suspended matter C:N ratios are within the same range as most other data reported from other mangrove ecosystems (e.g. Cifuentes et al. 1996), even though the salinity fluctuations they encountered (Δ sal. = 1.7) were much smaller than those recorded in our study (Δ sal. = 7.5). δ13CSPOM values were well correlated with salinity (R² = 0.62; p = 0.012) but not with C:N ratios (R² = 0.14). These suspended matter C:N ratios are within the same range as most other data reported from other mangrove ecosystems (e.g. Cifuentes et al. 1996).

Zooplankton δ13C and its relation to SPOM δ13C

Very little information exists on the trophic pathways associated with zooplankton in mangrove ecosystems, but Grindley (1984) suggested that the abundant particulate organic matter (i.e. detritus) in mangrove estuaries constitutes the major food source for zooplankton in these ecosystems, and similar conclusions have been made in temperate estuaries (e.g. Hummel et al. 1988). Camillieri & Ribi (1986) showed experimentally that several species of small crustaceans are able to survive when offered flakes formed from DOC (dissolved organic carbon) leached from Rhizophora spp. leaves. The species they investigated included some harpacticoid copepods and amphipods (i.e. benthic organisms), but no calanoid copepods, which usually form the bulk of the pelagic zooplankton in the study area (Chandra Mohan et al. 1997). Moreover, the fact that these organisms are able to survive on this food source does not imply that they would utilise it under natural conditions, when more nutritious algal material is also present.

Careful comparison of the zooplankton and suspended matter δ13C data revealed several patterns which suggest that zooplankton were not feeding indiscriminately on bulk suspended matter, but selected components of the SPOM, presumably phytoplankton, that had a more pronounced spatial and seasonal variability in δ13C than SPOM.

Firstly, the overall range of δ13C values for zooplankton (δ13CZP) collected at the 4 selected stations (−30.13 to −16.45‰) was much larger than the range of δ13CSPOM values from those locations (−29.48 to −21.71‰; Tables 1 & 3). If zooplankton were feeding indiscriminately on SPOM (and assuming a constant δ13C shift), the seasonal fluctuations of their δ13C values would have been of the same magnitude as those observed in SPOM. If, however, they were feeding selectively on either terrestrial detritus (which should have a fairly constant δ13C) or phytoplankton (which may have a more variable δ13C), the fluctuations of their δ13C signal should have been either smaller or larger than those of SPOM, respectively.

Secondly, the average zooplankton δ13C of the 4 sampling locations followed the same trend in 13C-depletion as did the suspended matter from these stations (i.e. K₂ > G₆ > G₃ > C₁), but the δ13C gradient was more pronounced in the zooplankton (Fig. 6), causing zooplankton to be on average enriched in 13C relative to the suspended matter at K₂ (by 1.80‰ when using only data from months when both parameters were measured), at G₆ (by 2.92‰) and at G₃ (by 0.07‰), but depleted at C₁ (by 0.10‰). If we assume a constant and small fractionation in 13C between zooplankton and their diet (1‰; DeNiro & Epstein 1978), this would suggest that at K₂ and G₆, zooplankton were feeding on a fraction enriched in 13C relative to the total suspended matter, but on a fraction that was 13C-depleted relative to SPOM at G₃ and C₁. Del Giorgio & France (1996) found from a compilation of literature data that there is a trend in the mean difference between δ13CZP and δ13CSPOM going from the open ocean (+2.7‰), coastal (+1.8‰) and estuarine (+0.8‰) ecosystems, to freshwater lakes, where zooplankton is depleted relative to SPOM by an average of 2.7‰. The most likely explanation for this trend is that zooplankton feeds selectively on phytoplankton which, in freshwater and sometimes in estuarine systems, is isotopically lighter than the total suspended matter (del Giorgio & France 1996).

A third argument for selectivity in zooplankton feeding comes from a comparison of the average difference in δ13CSPOM and the average difference in δ13CZP between different stations, as shown in Fig. 8. Although the spatial differences in δ13CSPOM are often significant (paired t-test), they are relatively small (0.3 to 2.1‰) compared to the difference in the zooplankton δ13C signal between these locations (1.4 to 6.0‰). If zooplankton would have been feeding indiscriminately on SPOM, these between-site differences would be expected to be of equal magnitude for both SPOM and zooplankton.

Although these data do not allow us to quantitatively determine the exact contribution of phytoplankton or terrestrial carbon to zooplankton nutrition, our results
clearly indicate that phytoplankton constitutes a more important carbon source for zooplankton, despite the high inputs of terrestrial (mangrove) carbon in the aquatic system.

**Possible mechanisms influencing spatio-temporal variations in SPOM and zooplankton δ¹³C**

The selective feeding of zooplankton on phytoplankton (discussed above) implies that the δ¹³CZP will provide us with a better parameter than δ¹³CSPOM for elucidating possible mechanisms influencing the stable carbon-isotope signal of the phytoplankton in the study area. Some important factors influencing the δ¹³C of phytoplankton have been found to include the δ¹³C of the DIC pool and the phytoplankton growth rate (e.g. Fry & Wainright 1991, Hellings et al. 1999). To our knowledge, no studies have previously attempted to analyse the seasonal variability of phytoplankton δ¹³C in tropical, monsoon-influenced estuaries.

As for the spatial variability, there is a clear trend towards higher δ¹³C values for zooplankton (and, to a lesser degree for SPOM) with increasing salinity, i.e. from more depleted δ¹³C values in the most freshwater parts (Coringa), and a gradual increase towards more estuarine (G₃, G₅) and near-marine (K₂) locations. As to the magnitude of this longitudinal δ¹³C gradient, it should be noted that, in view of the relatively small area considered, there was a remarkably high average difference in δ¹³CZP between the mouth of Coringa (C₁) and central Kakinada Bay (K₂) of about 6‰ (Table 3, Fig. 8). The phytoplankton δ¹³C difference between these stations might have been even larger, as we have no indication concerning the precise degree of selectivity in zooplankton feeding. This longitudinal gradient may be determined principally by an accompanying gradient in δ¹³CDIC, which might have been more negative in the mangrove sites due to the microbial respiration of the higher amounts of terrestrial POC available; but apart from an indication by the few δ¹³CDIC measurements made in Coringa (see above), we have no conclusive evidence for this so far. Bearing in mind possible effects of tidal amplitude and year-to-year variations in the climatic pattern on the stable carbon-isotope composition of SPOM, the following trends seem to be a general feature in the δ¹³CZP signal (Fig. 7): (1) During the pre-monsoon period (i.e. March–April to May–June), when salinity is high in the entire area and the suspended organic matter load is minimal (Dehairs et al. 2000), zooplankton is enriched in ¹³C relative to its average δ¹³C signal. The small amount of data from the first half of the monsoon period (July to August) seem to suggest that the δ¹³CZP remains high during this period (Fig. 7). (2) Minimal values of δ¹³CZP are observed between the middle of the monsoon period and the middle of the dry season (i.e. between September and February). The pre-monsoon period, during which most ¹³C-enriched zooplankton were observed (especially in Kakinada Bay) coincided with a period of increased phytoplankton abundance, presumably induced by the lower turbidity during this period (Rohini 1997). ¹³C-enrichment in SPOM or phytoplankton during periods of higher phytoplankton biomass or higher chlorophyll concentrations has been observed in several studies (e.g. Fry & Wainright 1991, Ogawa & Ogura 1997, Burkhardt et al. 1999), although there remains some discussion on the precise mechanisms causing this enrichment. It remains to be determined to what effect the high δ¹³CZP values encountered during pre-monsoon period are a reflection of increased phytoplankton growth rate, or a less negative δ¹³CZP caused by the lesser dilution of the DIC pool by ¹³C-depleted respired CO₂.

Minimum δ¹³C values were encountered between the second half of the monsoon period and the first half of the dry period (i.e. between September and February). We had expected lowest δ¹³C values to occur during the monsoon period (July to September), when the large amounts of terrestrial detritus released (Gupta et al. 1997) might have lowered the δ¹³CDIC signal because of increased microbial activity. Our data seem to suggest that the ¹³C-depletion of the DIC pool does not occur until some time after the initiation of the monsoon, and that this depletion may persist for several months after the freshwater inflow has almost ceased. The few measurements of δ¹³CDIC and δ¹³C of size-fractionated phytoplankton made in Coringa, which indicated significant ¹³C-depletion, were carried out in February, thus providing further evidence that this
period still experiences low δ13C values. More recent data on zooplankton isotope composition from this area also confirm this general pattern (S. Bouillon unpubl. data). Correlating our carbon-isotope data with salinity, POC load (Dehairs & Rao 1997), or oxygen concentrations (Sreenivas 1998) has not provided any clear relationships that might explain this depletion. One explanation might be that there is a certain time lag between the occurrence of high POC loads (i.e. when the monsoon period starts) and the build-up of a 13C-depleted DIC pool due to the microbial degradation of this material. After the freshwater inflow has again reached minimal values, further degradation of the deposited terrestrial material may explain the persistence of the low δ13C values encountered. A closer monitoring of δ13CpOM, δ13CZP, and especially δ13CDIC and phytoplankton growth rate should provide clearer insights into this.

**Zooplankton δ15N variability**

Zooplankton δ15N values exhibited much less seasonal variation compared to the δ15CZP variations (Table 3). Due to the small amount of δ15N data, it is difficult to detect any clear seasonal trend in zooplankton δ15N. Based on these few data however, it seems that Coringa zooplankton had lower δ15N values (+4.76 and +5.22‰, n = 2) than did zooplankton at the 3 other stations, which showed relatively similar average δ15N values (average δ15N = +7.46‰ at G3; +7.92‰ at K2; and +8.42‰ at G6). Because of the small amount of concurrent data from different stations, we were unable to detect any statistically significant spatial differences in δ15N, but it does appear that the estuarine and near-marine stations (G3 and K2) were more enriched in 15N than Gaderu and, especially, Coringa. It is well known that marine invertebrates, including zooplankton, are usually more 15N-enriched than freshwater invertebrates (e.g. France 1994), and this has been ascribed to the 15N-enriched inorganic N-pool that occurs under lower N-concentrations through the selective uptake of 14N by phytoplankton (e.g. Altabet & Francois 1994). In this study area, average nitrate concentrations in the northern Kakinada Bay (4.9 to 6.5 µmol l–1; Murthy 1997) were indeed lower than those found in Gaderu (6.6 to 15.0 µmol l–1) or Coringa (12.6 to 16.4 µmol l–1). The Gautami Godavari station (G6), however, had both a high average nitrate concentration (15.3 µmol l–1) and a high δ15N (+8.42‰). On the other hand, anthropogenic inputs of N (via wastewater) can significantly increase the δ15N in aquatic ecosystems (e.g. McClelland & Valiela 1998 and references therein), and in our case large amounts of domestic wastewater enter the Kakinada Bay via the Kakinada Canal (Fig. 1). Preliminary results from benthic invertebrates and fishes also show a clear enrichment in 15N between the mangrove areas and Kakinada Bay of about 2‰ (S. Bouillon unpubl. data), but further studies are needed to determine the factors responsible for this enrichment in 15N.

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