

Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter

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ABSTRACT: Mangrove epifaunal communities have access to various carbon and nitrogen sources and we hypothesized that the degree of material exchange with the aquatic environment might influence the overall use of different substrates by intertidal communities. Therefore, we analyzed C and N stable isotope ratios in primary producers, sediments and 245 samples of epifauna hand-collected from 5 sites in India, Sri Lanka and Kenya (representing estuarine, lagoonal and basin-type mangrove forests). Several patterns emerged from this data set. First, epifaunal communities used a range of available food substrates at all sites studied, including mangrove-derived organic matter, local microphytobenthos and micro-epiflora, as well as imported C and N from the aquatic environment (i.e. phytoplankton- and/or seagrass-derived organic matter). Secondly, our data indicate that at sites with significant inputs of aquatic sources, use of mangrove carbon is rather limited on a community basis, whereas in systems with less material exchange with adjacent waters, the relative importance of mangroves is higher. Thus, despite the unquestionable impact some epifaunal species may have on leaf litter dynamics, the dependency of the invertebrate community as a whole on mangrove litter is not ubiquitously large and varies according to the availability of local versus tidally imported sources. Precise quantification of the relative importance of different substrates with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ is, however, not always straightforward due to the multitude of available sources and the overlap in source stable isotope signatures. Micro-epiflora on mangroves trees were remarkably depleted in ^{15}N in all systems ($\delta^{15}\text{N}$ between -8.2 and -2.4 ‰) and thus form an example where $\delta^{15}\text{N}$ is a useful source indicator, as low $\delta^{15}\text{N}$ values of several gastropod species indicated substantial feeding on such epiflora.

KEY WORDS: Sesarmid crab · Mollusk · Intertidal · Invertebrate · Foodweb · Stable isotope · Carbon · Nitrogen

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INTRODUCTION

Mangrove forests are often a prominent feature of the coastline in the tropics and subtropics, and are increasingly being exploited by humans. A thorough understanding of the ecological functioning and of their interactions with adjacent ecosystems is important in providing a scientific basis for the management and/or restoration of mangroves. Many aspects of car-

bon dynamics in mangrove and adjacent ecosystems are still far from understood (e.g. Bouillon et al. 2004), and in view of the various settings in which mangrove forests may occur, it is imperative to obtain data from a range of contrasting mangrove ecosystems rather than generalizing conclusions from any particular site (e.g. Ewel et al. 1998).

Invertebrate communities in intertidal mangrove forests have access to a variety of carbon and nitrogen

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sources: local inputs from mangroves as litterfall or as part of the sediment organic matter pool, microphytobenthos, a variety of epiflora and tidally imported sources such as phytoplankton- or seagrass-derived organic matter. The removal of large amounts of leaf litter by crabs observed in some systems (see Lee 1998) and the fact that some other well-studied mangrove invertebrates (e.g. the gastropod *Terebralia palustris*) have been observed to feed extensively on mangrove leaves (e.g. Fratini et al. 2000) has nourished the still prevalent view that 'the great majority of the mangrove macrobenthos relies directly on the high production of the mangroves themselves, consuming either leaf litter or detritus composed of decaying leaves' (e.g. Fratini et al. 2000, Ashton 2002). The observation that a significant proportion of leaf production is efficiently removed and/or consumed by some epifaunal species (e.g. Ólafsson et al. 2002) in some mangrove systems, is not necessarily contradictory to the idea that mangrove epifaunal communities as a whole may not depend primarily on mangrove production as a direct food source. Recent results from stable isotope studies (e.g. Christensen et al. 2001, Bouillon et al. 2002, Hsieh et al. 2002) indeed suggest that only a limited number of species may rely substantially on mangrove carbon and that a range of other carbon sources are used by the invertebrate community. Nevertheless, the degree to which such results can be generalized is not known. In particular, mangroves occur in highly variable geomorphological settings, which greatly influence the availability of potential C and N sources: where tidal exchange is significant, marine/estuarine sources such as phytoplankton- or seagrass-derived organic matter can be imported, but in low tidal amplitude settings, mangroves are the dominant source of carbon available in the sedimentary pool (Bouillon et al. 2003).

The use of stable isotopes as tracers of the origin and assimilation of organic matter by faunal communities has become widespread, and is based on the assumptions that (1) different sources (may) have different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, and (2) assimilation by con-

sumers results in little fractionation in the case of ^{13}C (i.e. consumer $\delta^{13}\text{C}$ values are close to those of their diet, with a slight enrichment typically between 0 and 2‰), and somewhat higher for ^{15}N (a value of ~3‰ is often cited, but the actual degree of fractionation varies as a function of taxonomy, food quality and environmental factors, see e.g. Vanderklift & Ponsard 2003 for a recent review).

We hypothesized that the dependency of the epifaunal community on mangrove-derived organic matter would vary across different environmental settings and that such differences would be related to the relative availability of different potential sources. Therefore, we compared data on resource utilization patterns (as evident from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses) of a variety of epifaunal species from a number of contrasting mangrove sites (Table 1): (1) a seaward exposed site and a more inland protected site with adjacent seagrass beds in Gazi Bay (Kenya), (2) 1 site in the Coringa Wildlife Sanctuary (CWS), a large estuarine mangrove system without nearby seagrass beds in the Godavari delta (Andhra Pradesh, India), and (3) 2 small mangrove sites along the coast of Sri Lanka: the basin forest of Galle and the lagoonal forest in Pambala. Whereas the sites in India and Kenya experience medium or high tidal amplitudes (spring tidal range of ~2 and 3.2 m, respectively), the sites in Sri Lanka are both characterized by a low tidal amplitude (typically ≤ 0.20 m). We supplemented these data sets with a compilation of relevant literature data in an attempt to look for general patterns in the origin of the carbon assimilated by different epifaunal groups across different mangrove ecosystems.

MATERIALS AND METHODS

Description of study areas. Gazi Bay, Kenya: Gazi Bay (39° 30' E, 4° 22' S) is a shallow, tropical coastal water system, located ~50 km south of Mombasa (Fig. 1a,b). The total area of the bay is approximately

Table 1. Overview of the main characteristics of the study sites. CWS: Coringa Wildlife Sanctuary, Andhra Pradesh

Site	Forest type or setting	Dominant vegetation	Tidal range (m)	Adjacent seagrass beds?
Gazi Bay (Kenya)				
Upstream site	Estuarine	Mixed: <i>Rhizophora mucronata</i> , <i>Avicennia marina</i> , <i>Ceriops tagal</i>	~3.2	Yes
Seaward site	Estuarine	Dominated by <i>Sonneratia alba</i>	~3.2	Yes
CWS (India)	Estuarine	Mixed: <i>Avicennia officinalis</i> , <i>A. alba</i> , <i>Excoecaria agallocha</i>	~2	No
Galle (Sri Lanka)	Basin	Dominated by <i>Rhizophora apiculata</i>	≤ 0.20	No
Pambala (Sri Lanka)	Lagoonal (fringe)	Dominated by <i>R. apiculata</i>	≤ 0.20	Yes

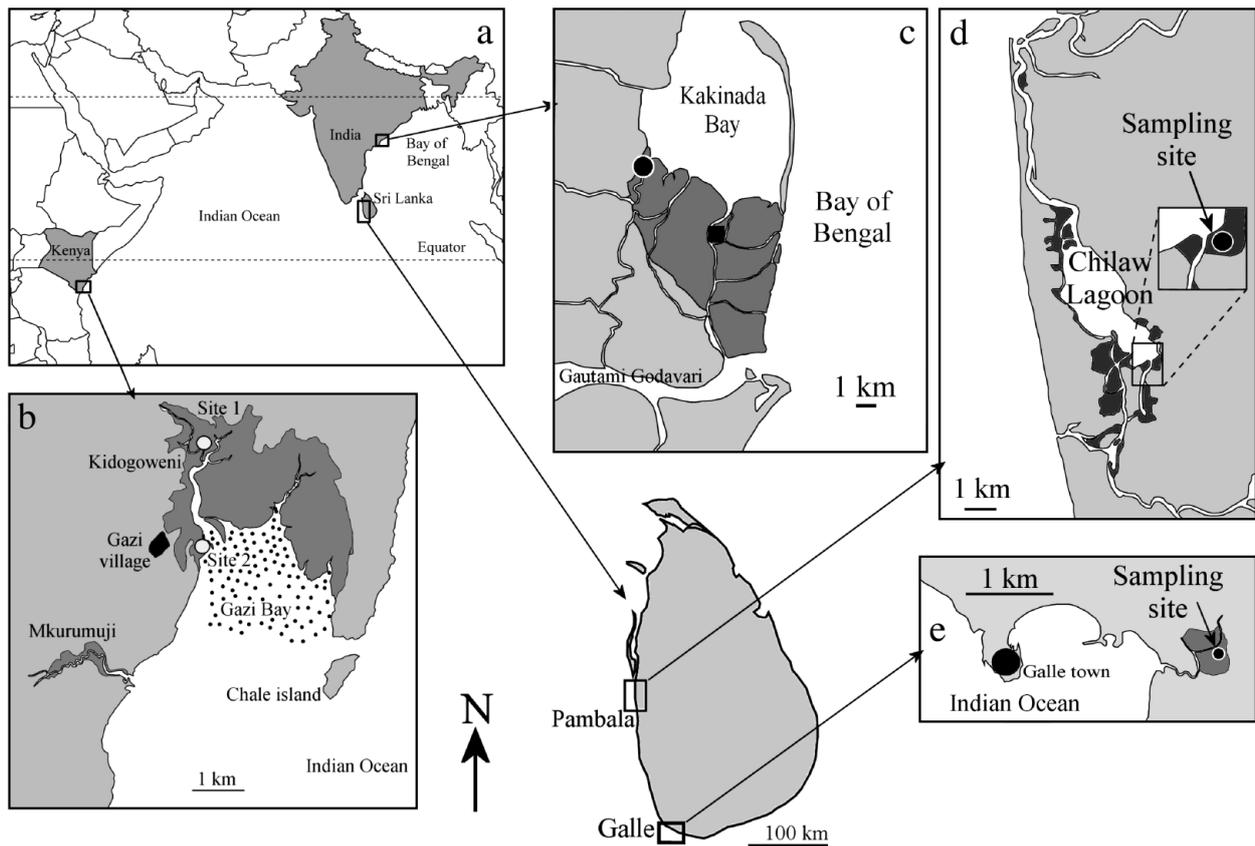


Fig. 1. Geographical location of the different sampling sites. (a) Overview, and location of (b) the 2 sampling sites in Gazi Bay, Kenya, (c) the sampling areas in the Coringa Wildlife Sanctuary, India, and (d,e) the sampling sites in Galle and Pambala, Sri Lanka, respectively. Note that the black square in (c) indicates the areas where similar data were collected and presented in Bouillon et al. (2002). The darkest areas represent the main mangrove-covered regions and the dotted area in (b) shows the location of the main seagrass beds. See Table 1 for an overview of the main site characteristics

10 km², with an additional 6 to 7 km² covered by mangroves, mostly *Rhizophora mucronata*, *Sonneratia alba*, *Ceriops tagal*, *Bruguiera gymnorhiza*, *Avicennia marina* and *Xylocarpus granatum*. The bay itself harbors large areas (~70% of the total area) of often dense seagrass beds, which are dominated by *Thalassodendron ciliatum* (Coppejans et al. 1992). The bay is open to the Indian Ocean through a relatively wide and shallow entrance in the south. Besides a few tidal creeks without freshwater inputs, the upper region of the bay receives freshwater from the Kidogoweni river, which cuts through the mangroves. Spring tidal range in Gazi Bay is reported to be 3.2 m (Kitheka 1997). Two intertidal sites were selected for the sampling of flora, sediments and invertebrates in July 2003: (Site 1) a mixed forest site located upstream along Kidogoweni creek, where vegetation consisted of *R. mucronata*, *A. marina*, *C. tagal* and a few *X. granatum*, and (Site 2) a seaward site predominantly vegetated by *S. alba* with some *R. mucronata* and *A. marina*, which bordered the edge of the bay and is, therefore, more likely to be influenced by seagrass inputs (Fig. 1).

Coringa Wildlife Sanctuary, Andhra Pradesh, India:

The Coringa Wildlife Sanctuary (CWS, between 82° 15' and 82° 22' E, 16° 43' and 17° 00' N, Fig. 1a,c) is part of the mangrove-covered area between Kakinada bay and the Gautami branch of the Godavari river (Fig. 1a,c). The CWS is dominated by mangrove forests (covering ~150 km²) and tidal mudflats, the most abundant mangrove species being *Avicennia marina*, *Avicennia officinalis*, *Excoecaria agallocha*, *Sonneratia apetala*, *Rhizophora mucronata* and *Rhizophora apiculata* (Satyanarayana et al. 2002). Seagrass beds are absent from the areas adjacent to the mangroves. Tides are semidiurnal and spring tidal amplitude in the bay is ~2 m. Samples of vegetation, sediments and epifauna were collected in May and June 2001 in the northwestern part of the CWS, in an intertidal area dominated by *A. officinalis*, *A. marina* and *E. agallocha* along Matlapalem creek (Fig. 1a,c).

Galle, Sri Lanka: The mangroves in Galle, southwest Sri Lanka (06° 01' N to 8° 14' E) cover an area of about 1.5 km² and can be classified as a basin forest (sensu Lugo & Snedaker 1974) (Fig. 1e). The forest is located

approximately 600 m from the Indian Ocean shoreline and is traversed by 2 rivers, the Thalpe Ela and its tributary, the Galu Ganga. The forest at Galle is further characterized by a very irregular topography due to the burrowing activity of the mud lobster *Thalassina anomala*, and large patches of the forest are permanently inundated. This site experiences very low to no tidal influence and hence, limited exchange of organic material with adjacent environments, except during exceptionally high water levels in the river. The majority of samples for Galle were collected in an area predominantly vegetated by *Rhizophora apiculata* in March 2002 (dry season). Some initial samples were collected earlier in February–March 2000; and some stable isotope data on vegetation and sediments were available from a previous study (Bouillon et al. 2003).

Pambala, Sri Lanka: Pambala-Chilaw lagoon is situated in western Sri Lanka (07° 35' N, 79° 47' E) and is similarly characterized as a low tidal amplitude system (tidal range not exceeding 0.2 m, F. Dahdouh-Guebas pers. obs.), with ~3.5 km² of fringing mangroves (Fig. 1d). Surface water salinity in the lagoon varies strongly, between 0 and 55. All samples from Pambala were collected in a *Rhizophora mucronata*-dominated area in March 2002, but some previous data on vegetation and sediments were available (Bouillon et al. 2003).

In conclusion, the different sampling sites represent a variety of geomorphological settings (summarized in Table 1): (1) Pambala (Sri Lanka) as an example of a low tidal amplitude lagoon with fringing mangroves, (2) Galle (Sri Lanka) being a basin forest with insignificant tidal influence, (3) the CWS (India) as an example of a large estuarine mangrove forest with significant tidal influence but without seagrass inputs, and (4) 2 sites in the smaller estuarine system of Gazi Bay (Kenya), 1 of which is located in the interior part of the forest, the other site near the forest fringe and, therefore, more exposed to inputs from the extensive seagrass beds in the bay. The strongest tidal influence is experienced at Gazi Bay, Kenya.

Table 2. Overview of stable isotope data (average \pm 1 SD) for flora, sediments and epifauna from Gazi Bay, Kenya (Sites 1 and 2, see Fig. 1b)

	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
Site 1 (upstream site)			
Flora			
<i>Avicennia marina</i>	-31.2 \pm 0.9	3.0 \pm 0.8	4
<i>Ceriops tagal</i>	-29.4 \pm 0.9	0.1 \pm 1.3	4
<i>Xylocarpus granatum</i>	-27.7 \pm 0.4	-0.7 \pm 0.6	4
<i>Rhizophora mucronata</i>	-29.0 \pm 0.6	0.0 \pm 0.7	4
Microphytobenthos	-22.1 / -22.1	1.8 / 1.9	2
Micro-epiflora	-24.2	-2.4	1 (pooled)
Sediments			
Surface sediments	-25.2 \pm 0.0	2.1 \pm 1.2	3
All sediment layers, up to 10 cm	-25.2 \pm 0.2	2.7 \pm 0.9	15
Mollusks			
<i>Cerithidea decollata</i>	-21.6 \pm 0.8	4.7 \pm 1.2	7
<i>Isoognomon ephippium</i>	-22.8 \pm 1.0	4.8 \pm 0.3	5
<i>Littoraria scabra</i>	-25.2 \pm 1.3	1.7 \pm 0.3	3
<i>Trapezium</i> cfr. <i>sublaevigatum</i>	-23.0 \pm 0.2	4.9 \pm 0.1	3
<i>Cassidula labrella</i>	-23.5 \pm 0.6	5.6 \pm 0.1	4
<i>Onchidium</i> spp.	-23.7 \pm 1.5	1.7 \pm 0.6	5
<i>Saccostrea cucullata</i>	-23.7	4.8	1
<i>Terebralia palustris</i>	-26.1 \pm 0.9	3.5 \pm 1.1	8
Brachyuran crabs			
<i>Epixanthus dentatus</i>	-22.6 / -20.8	7.0 / 7.1	2
<i>Eurycarcinus natalensis</i>	-21.2 / -21.4	6.6 / 7.2	2
<i>Metopograpsus thukuhar</i>	-21.0 / -21.0	6.9 / 7.2	2
<i>Neosarmatium smithi</i>	-30.3	5.5	1
<i>Perisesarma guttatum</i>	-23.3 \pm 0.9	4.2 \pm 0.7	5
<i>Perisesarma</i> spp.	-22.1 \pm 0.3	4.0 \pm 0.3	5
<i>Uca chlorophthalmus</i>	-21.1 \pm 0.7	3.2 \pm 0.8	5
<i>Uca urvillei</i>	-20.8 \pm 0.8	4.1 \pm 0.7	6
Site 2 (seaward site)			
Flora			
<i>Avicennia marina</i>	-30.4 \pm 1.3	3.3 \pm 0.4	4
<i>Sonneratia alba</i>	-27.0 \pm 0.8	2.2 \pm 1.0	4
<i>Rhizophora mucronata</i>	-29.8 \pm 0.8	-0.5 \pm 2.2	4
Sediments			
Surface sediments	-23.0 \pm 0.9	1.7 \pm 0.8	3
All sediment layers, up to 10 cm	-23.8 \pm 0.9	2.1 \pm 0.4	11
Mollusks			
<i>Neritina</i> spp.	-17.9	4.2	1
<i>Littoraria scabra</i>	-23.5 \pm 1.0	1.1 \pm 1.4	7
<i>Crassostrea cucullata</i>	-18.4 \pm 0.6	5.1 \pm 0.6	5
<i>Terebralia palustris</i>	-22.9 \pm 0.8	4.5 \pm 0.5	6
<i>Clypeomorus</i> spp.	-19.0 \pm 0.7	5.1 \pm 0.4	5
Brachyuran crabs			
<i>Uca lactea annulipes</i>	-16.4 \pm 0.3	2.2 \pm 1.1	6
<i>Uca urvillei</i>	-16.6 \pm 1.2	3.0 \pm 1.0	5
<i>Perisesarma guttatum</i> (adults)	-20.1 \pm 0.5	4.9 \pm 0.5	5
<i>Perisesarma guttatum</i> (juveniles)	-19.1	5.2	1
<i>Metopograpsus thukuhar</i>	-20.5 \pm 2.2	5.5 \pm 0.2	3
<i>Thalamita crenata</i>	-25.4	3.0	1
<i>Sarmatium crassum</i>	-23.6	4.4	1
<i>Macrophthalmus depressus</i>	-16.4 \pm 0.2	2.6 \pm 0.5	5
Miscellaneous taxa			
<i>Tedania digitata</i>	-18.5 \pm 1.3	4.9 \pm 1.8	4
Barnacles (unidentified)	-18.3 \pm 0.7	7.2 \pm 0.4	3
<i>Clibanarius</i> spp.	-22.8 / -21.2	4.9 / 2.8	2

Sampling and analytical techniques. At all sites, samples of epifauna and flora were taken from a 20 m by 20 m area in order to avoid spatial variations in producer stable isotope signatures (e.g. Fry et al. 2000). Although our sampling design does not, therefore, consider potential spatial and seasonal variations in the foodweb structure within sites, this should not limit our conclusions (see 'Discussion'). Sampling efforts were concentrated on those intertidal species (mainly mollusks and brachyuran crabs) that were numerically abundant in the area and, therefore, likely to play an important role in the overall processing of organic matter. Samples of vegetation and epifauna were collected by hand, while benthic microalgae were obtained by gently scraping them off the sediment where they formed a conspicuous layer; this was only the case in Gazi Bay, although previous data were available from the CWS. Mangrove leaf samples were picked from different trees to avoid any bias in the resulting isotope signatures. Typically, only surface sediments were collected, but for the 2 sites in Gazi, sediment cores were taken in the framework of another study and partitioned into 0–1, 1–2, 2–4 and 4–10 cm layers. 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 some of the smaller crab species (e.g. *Uca* spp., smaller sesarmids) 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 mollusks, tissues were removed from their shell and analyzed whole. All samples were ground to a fine powder and sub-samples for $\delta^{13}\text{C}$ subsequently acidified with dilute (5%) HCl before analysis to remove carbonates (except those of mangrove tissues). Sediment total organic carbon (TOC) and total nitrogen (TN) were determined by combusting pre-weighed samples in a ThermoFinnigan Flash1112 elemental analyzer. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of flora, fauna and sediments was performed with the aforementioned elemental analyzer, coupled to a ThermoFinnigan delta + XL via a Conflo III interface, with a typical reproducibility of $\pm 0.15\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The samples from the CWS, however, were all measured on a dual inlet Finnigan Mat delta E off-line after cryogenic purification of the CO_2 or N_2 , with a reproducibility of 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. All stable isotope ratios are expressed relative to the conventional standards (VPDB limestone and atmospheric N_2) as δ values (‰), defined as:

$$\delta^{13}\text{C} = \frac{X_{\text{sample}} - X_{\text{standard}}}{X_{\text{standard}}} \times 10^3$$

where $X = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ in the case of $\delta^{15}\text{N}$.

RESULTS

Sedimentary organic matter

Sediment at the upstream Gazi site had $\delta^{13}\text{C}$ values ($-25.2 \pm 0.2\text{‰}$) somewhat more enriched than mangrove leaf tissues and showed relatively high TOC/TN ratios (16.0 ± 1.3 atom, Fig. 2). At the seaward site, however, $\delta^{13}\text{C}$ values of sediments were higher and more variable, particularly in the surface layers (the latter on average $-23.0 \pm 0.9\text{‰}$). Sediments in Galle and Pambala showed consistently low $\delta^{13}\text{C}$ values (-27.8 ± 1.1 and $-27.5 \pm 0.9\text{‰}$, respectively), high concentrations of organic carbon and high TOC/TN ratios (Fig. 2). Sediments in the CWS showed the highest $\delta^{13}\text{C}$ values and had low TOC and TOC/TN ratios (Fig. 2).

Primary producer stable isotope signatures

Different mangrove species from the 2 sites in Gazi all showed typical $\delta^{13}\text{C}$ signatures, with averages ranging between -27.0 and -31.2‰ (Table 2, Fig. 3). The 3 mangrove species collected in the CWS had $\delta^{13}\text{C}$ values similar to those found previously in the area (see Bouillon et al. 2002), but 2 species had markedly higher $\delta^{15}\text{N}$ values (*Avicennia marina*: $+8.9\text{‰}$ and *Excoecaria agallocha*: $+8.8 \pm 0.3\text{‰}$, Table 3, Fig. 3). Mangrove leaf tissues from Pambala all showed rather

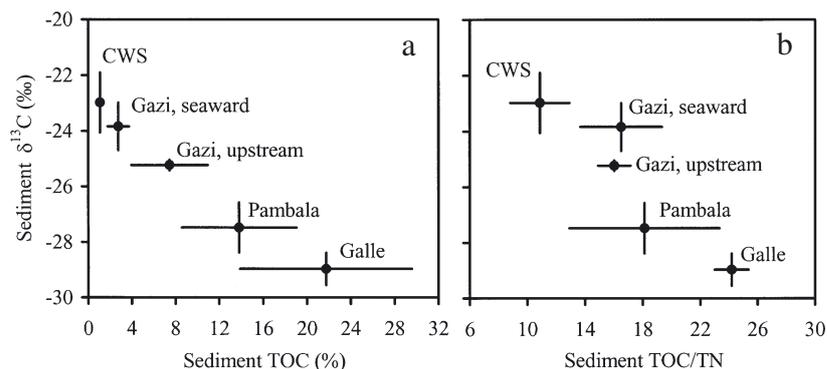


Fig. 2. Relationship between (a) sedimentary total organic carbon content (TOC) and $\delta^{13}\text{C}$ of sediment organic carbon, and (b) sediment TOC/TN (total nitrogen) ratios (atom) and $\delta^{13}\text{C}$ of sediment organic carbon, for the different systems/sites studied. Note that some additional data for Galle and Pambala, and all TOC and TOC/TN data for the CWS (Coringa Wildlife Sanctuary) were taken from Bouillon et al. (2003)

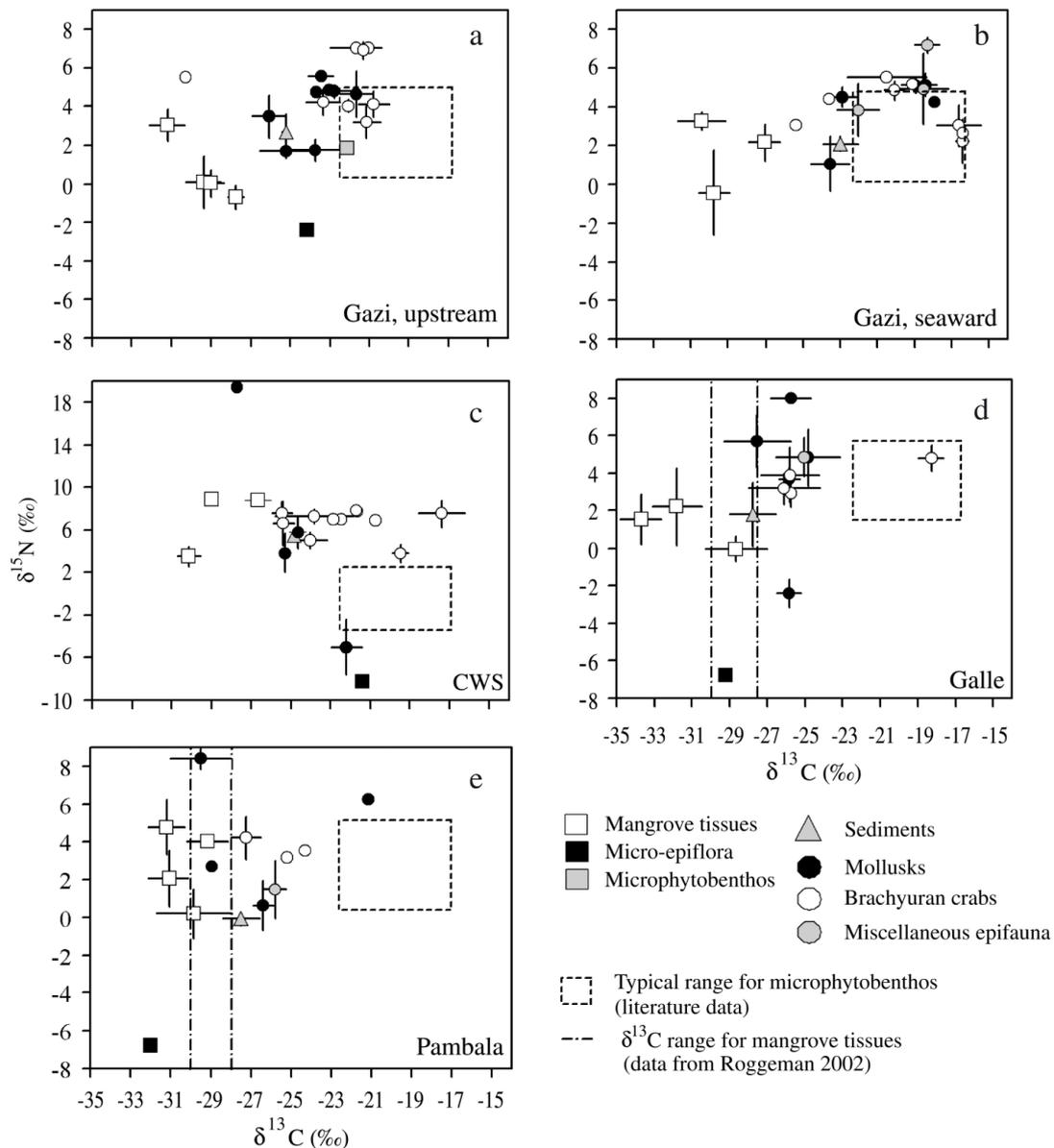


Fig. 3. Plot of $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ for epifauna from the 5 study sites. (a) Upstream site along Kidogoweni creek (Gazi Bay, Kenya), (b) the seaward site (Gazi Bay, Kenya), (c) Coringa Wildlife Sanctuary, India, (d) Galle, Sri Lanka and (e) Pambala lagoon, Sri Lanka. Note the different scale of the y-axis in (c). See Table 1 for site characteristics

low $\delta^{13}\text{C}$ values, with averages ranging between -29.2 and -31.2 ‰ for various mangrove species (Table 4, Fig. 3). The most depleted $\delta^{13}\text{C}$ values for mangrove tissues, consistently lower than -30 ‰, were found in *Rhizophora apiculata* and *Bruguiera gymnorrhiza* from Galle (Table 4, Fig. 3). *E. agallocha*, however, which mostly grows at slightly elevated patches in this area, had $\delta^{13}\text{C}$ values in the usual range, averaging -28.6 ‰. In contrast to mangrove tissues, micro-epiflora growing on mangrove stems (the composition of which was not studied) showed consistently low $\delta^{15}\text{N}$ values in all areas studied: -8.2 ‰ in the CWS, -6.8 ‰ in both Galle

and Pambala, and -2.4 ‰ in Gazi. $\delta^{13}\text{C}$ values for these epiphytes were highly variable: -21.4 ‰ in the CWS, -24.2 ‰ in Gazi, -29.2 ‰ in Galle and -32.0 ‰ in Pambala (Tables 2 to 4, Fig. 3). It should be noted that all data of micro-epiflora were gathered on pooled samples and we have no indications of the variability in isotope signatures of this source. Due to difficulties in sampling, we only have data for microphytobenthos from the upstream site in Gazi ($\delta^{13}\text{C}$: -22.0 ‰, $\delta^{15}\text{N}$: $+1.8$ ‰), but previous data from the CWS were available ($\delta^{13}\text{C}$: -17.3 ± 1.7 ‰, $\delta^{15}\text{N}$: $+1.7 \pm 1.7$ ‰, see Bouillon et al. 2002).

Table 3. Overview of stable isotope data (average ± 1 SD) for flora, sediments and epifauna from the Coringa Wildlife Sanctuary, Andhra Pradesh, India. Note that additional data from this area (but different localities within the CWS) can be found in Bouillon et al. (2002)

	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
Flora			
<i>Avicennia marina</i>	-29.0	8.9	1 (pooled)
<i>Avicennia officinalis</i>	-30.1 \pm 0.6	3.5 \pm 0.9	4
<i>Excoecaria agallocha</i>	-26.6 \pm 0.6	8.8 \pm 0.3	5
Micro-epiflora	-21.4	-8.2	1 (pooled)
Sediments			
Surface sediment	-24.9	5.6	1 (pooled)
Mollusks			
<i>Pythia plicata</i>	-25.3 \pm 0.3	3.8 \pm 1.8	4
<i>Onchidium</i> spp.	-22.2 \pm 0.8	-5.0 \pm 2.6	4
<i>Teridionidae</i> spp.	-24.6 \pm 0.4	5.8 \pm 1.5	5
<i>Polymesoda bengalensis</i>	-27.7	19.5	1
Brachyuran crabs			
<i>Episesarma versicolor</i>	-25.4 \pm 0.5	6.6 \pm 2.1	4
<i>Perisesarma bengalensis</i> (adults)	-25.4 \pm 0.5	7.6 \pm 1.1	6
<i>Perisesarma bengalensis</i> (juveniles)	-24.0 \pm 0.8	5.0 \pm 0.7	6
<i>Parasesarma asperum</i>	-23.8 \pm 2.0	7.3 \pm 0.7	4
<i>Parasesarma plicatum</i>	-19.5 \pm 0.4	3.8 \pm 0.8	4
<i>Metaplex distinctus</i>	-22.5 / -22.9	7.0 / 7.0	2
<i>Uca rosea</i>	-20.7	6.9	1
<i>Uca triangularis</i>	-21.7 / -21.7	7.8 / 7.8	2
<i>Uca urvillei</i>	-17.4 \pm 1.1	7.6 \pm 1.3	4

Consumer stable isotope signatures

Invertebrates from both sites in Gazi showed quite diverse stable isotope signatures, ranging overall between -30.3 and -16.4‰ for $\delta^{13}\text{C}$, and between 1.1 and 7.2‰ for $\delta^{15}\text{N}$ (Table 2, Fig. 3). However, $\delta^{13}\text{C}$ values were typically higher at the seaward site (Fig. 3). Our $\delta^{13}\text{C}$ data on mangrove sesarmids are

highly variable both within and between different systems (overall range: -30.3 to -18.9‰, with a fairly even distribution between these extremes). In the CWS, for example (Table 3, Fig. 3), average $\delta^{13}\text{C}$ values for sesarmids were -25.4‰ (adult *Perisesarma bengalensis* and *Episesarma versicolor*), -24.0 (juvenile *P. bengalensis*), -23.8‰ (*Parasesarma asperum*), and -19.5‰ (juvenile *Parasesarma plicatum*). As previously noted for this area (Bouillon et al. 2002), ocyppodid crabs (3 *Uca* spp.) and *Metaplex distinctus* were found at the more enriched end of the $\delta^{13}\text{C}$ range, and mollusks showed a diverse $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ pattern (Table 3, Fig. 3). With the exception of *Uca lactea annulipes*, invertebrates from Galle all showed relatively uniform $\delta^{13}\text{C}$ values (Table 4, Fig. 3), with averages between -27.5 and -24.8‰. However, $\delta^{15}\text{N}$ values ranged more widely, with unusually low values for *Pythia plicata* (-2.4 \pm 0.7‰) and high values for the 2 bivalves examined (i.e. *Polymesoda* spp. and an unidentified oyster, 5.7 \pm 1.4 and 8.0 \pm 0.2‰, Table 4, Fig. 3). Invertebrates from Pambala, with the exception of *Cerithidea cingulata*, similarly showed a fairly narrow range of $\delta^{13}\text{C}$ signatures, with averages between -28.5 and -24.3‰ (Table 4, Fig. 3). As in Galle, the filter-feeding *Polymesoda* spp. showed distinctly higher $\delta^{15}\text{N}$ values (8.4 \pm 0.5‰) compared to other invertebrates (0.6 to 6.2‰).

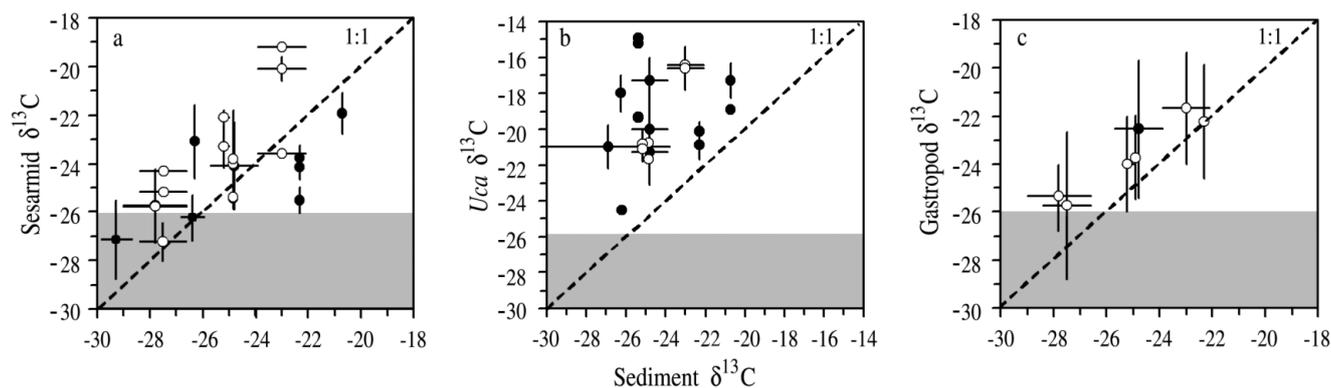


Fig. 4. Relationship between surface sediment $\delta^{13}\text{C}$ values and those recorded in various species of (a) Sesarminae, (b) *Uca* spp. and (c) gastropods (data from all species at a specific site were pooled for c). Data were compiled from the 5 sites mentioned in this study and additional literature data (data sources available on request). ●: literature data; ○: data from this study. Grey shaded areas show typical range of values for mangrove-derived organic matter. Literature data taken from Fry (1984), Rodelli et al. (1984), France (1998), Thimdee et al. (2001), Bouillon et al. (2002) and Hsieh et al. (2002)

Table 4. Overview of stable isotope data (average ± 1 SD) for flora, sediments, particulate organic carbon (POC) and epifauna from Pambala and Galle, Sri Lanka

	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
Pambala, Sri Lanka			
Flora			
<i>Avicennia officinalis</i>	-29.9 ± 1.8	0.2 ± 1.3	5
<i>Bruguiera gymnorrhiza</i>	-31.1 ± 1.0	2.1 ± 1.5	4
<i>Rhizophora apiculata</i>	-29.2 ± 1.0	4.0 ± 0.7	5
<i>Rhizophora mucronata</i>	-31.2 ± 0.9	4.8 ± 1.5	15
Micro-epiflora	-32.0	-6.8	1 (pooled)
Sediments			
Surface sediments	-27.5 ± 0.9	-0.1 ± 0.3	18 (4 for $\delta^{15}\text{N}$)
Mollusks			
<i>Pythia plicata</i>	-26.4 ± 0.5	0.6 ± 1.3	4
<i>Cassidula mustelina</i>	$-28.0 / -29.0$	$2.7 / 2.7$	2
<i>Cerithidea cingulata</i>	$-21.3 / -21.0$	$6.2 / 6.3$	2
<i>Polymesoda</i> spp.	-29.5 ± 1.5	8.4 ± 0.5	3
Brachyuran crabs			
<i>Episesarma tetragonum</i>	-25.2	3.2	1
<i>Perisesarma dussumieri</i>	-27.3 ± 0.8	4.2 ± 1.2	6
<i>Pseudosesarma crassimanum</i>	-24.3	3.5	1
Miscellaneous			
Isopoda (unidentified)	-25.8 ± 0.6	1.5 ± 1.6	4
Galle, Sri Lanka			
Flora			
<i>Rhizophora apiculata</i>	-31.8 ± 1.3	2.2 ± 5.0	13 (7 for $\delta^{15}\text{N}$)
<i>Excoecaria agallocha</i>	-28.6 ± 1.6	0.0 ± 0.7	8 (6 for $\delta^{15}\text{N}$)
<i>Bruguiera gymnorrhiza</i>	-33.7 ± 1.1	1.5 ± 1.3	9 (7 for $\delta^{15}\text{N}$)
Micro-epiflora	-29.2	-6.8	1 (pooled)
Sediments and POC			
Surface sediments	-27.8 ± 1.2	1.8 ± 1.7	17 (15 for $\delta^{15}\text{N}$)
POC	-26.9 ± 1.3	6.8 ± 2.6	6
Mollusks			
<i>Terebralia palustris</i>	-24.8 ± 1.7	4.8 ± 1.5	10
<i>Cassidula mustelina</i>	-25.8 ± 0.6	3.7 ± 0.6	6
<i>Pythia plicata</i>	-25.8 ± 0.6	-2.4 ± 0.7	6
<i>Polymesoda</i> spp.	-27.5 ± 1.8	5.7 ± 1.4	6
Unidentified oyster	-25.7 ± 1.1	8.0 ± 0.2	5
Brachyuran crabs			
<i>Perisesarma dussumieri</i>	-25.8 ± 1.5	3.9 ± 1.5	6
<i>Perisesarma bengalensis</i>	-25.7 ± 0.1	2.9 ± 0.7	3
<i>Uca lactea annulipes</i>	-18.3 ± 0.7	4.8 ± 0.7	5
Miscellaneous			
<i>Clibanarius</i> spp.	-25.0 ± 1.5	4.9 ± 1.0	5

DISCUSSION

Differences in sedimentary organic matter origin

The different sites in this study represent different geomorphological settings (i.e. estuarine, lagoonal and basin forests, sensu Lugo & Snedaker 1974) with varying tidal amplitude and, therefore, the relative importance of local vascular plant material and aquatic organic matter sources to the sedimentary pool varies significantly (Fig. 2). It has previously been shown (Bouillon et al. 2003) that for the majority of systems, these parameters

reflect the balance between local inputs from mangroves (high TOC, high TOC/TN and low $\delta^{13}\text{C}$) and inputs from the water column (low TOC, low TOC/TN and higher but variable $\delta^{13}\text{C}$). Thus, our data show that both the fringing lagoonal mangroves in Pambala and the basin forest of Galle are 'retention' sites, where mangrove carbon accumulates and dominates the sedimentary organic matter pool. For the CWS and Gazi, however, a balance exists between local mangrove inputs and tidally imported organic matter (see also Hemminga et al. 1994, Slim et al. 1996). Moreover, the data from the seaward site in Gazi show that seagrass inputs (with $\delta^{13}\text{C}$ values in the area between -19.7 and -10.7% , Hemminga et al. 1994, authors' unpubl. data) are more important at this location than at the upstream sampling site.

Consumption of different primary food sources by mangrove epifauna

Before discussing the differences in C and N sources for epifaunal communities between different sites, we will first briefly examine the major primary organic matter sources for the 2 dominant groups of epifauna, i.e. brachyuran crabs and mollusks, at the different sites studied.

Brachyuran crabs

Brachyuran crabs and mollusks are typically the dominant groups of mangrove epifauna and can attain very high densities (e.g. Ashton & Macintosh 2002). Their role in nutrient cycling (Lee 1998) and in sediment biogeochemistry, via bioturbation, is therefore considered to be large. Even though the focus of most studies has been on the effect of sesarmid crabs on leaf litter dynamics (e.g. Ashton 2002), several studies have stressed that different groups of mangrove crabs display a wide range of feeding preferences. Although for several of the larger species $\delta^{13}\text{C}$ values were on average within $\sim 4\%$ of those of mangrove tissues (which indicates substantial inputs from mangrove litter, albeit with some contributions of other dietary sources), several species showed consistently

high $\delta^{13}\text{C}$ values tending towards those typical of microphytobenthos (e.g. *Perisesarma* spp. from Gazi: -20.1 ± 0.5 and $-22.1 \pm 0.3\text{‰}$, *Parasesarma plicatum* from the CWS: $-19.5 \pm 0.4\text{‰}$). Thus, although some mangrove sesarmids undoubtedly rely substantially on mangrove carbon, this is clearly very species-specific. Secondly, when comparing sesarmid $\delta^{13}\text{C}$ data from all the sites studied here and with the inclusion of literature data, we find (despite the species-specific variation) a good overall correlation between the isotope signature in sedimentary organic carbon and that in sesarmids (Fig. 4a, Spearman rank correlation test: $p = 0.0057$, $R^2 = 0.37$). The latter confirms the idea that many sesarmids may spend more time feeding on the sediment surface than actively searching for fallen leaves (Skov & Hartnoll 2002) and indicates that the C and N source for this group of epifauna will partially depend on the geomorphological settings of the system, as the latter is a primary determinant of the origin of sedimentary organic matter (Bouillon et al. 2003). Such a correlation with sediment $\delta^{13}\text{C}$ values is not significant (Spearman rank correlation test: $p = 0.349$, $R^2 = 0.06$) for the second major group of brachyurans found in mangroves, ocypodid crabs (mostly *Uca* spp. and *Macrophthalmus* spp., see Tables 2 to 4). Ocypodid crabs are typical deposit feeders which forage on the sediment surface. Stable isotope data presented earlier (e.g. Rodelli et al. 1984, Marguillier et al. 1997, France 1998, Hsieh et al. 2002) and in this study consistently show high $\delta^{13}\text{C}$ values, ranging between -24.5 and -12.5‰ , with an average of $-18.9 \pm 2.3\text{‰}$, and with a distribution markedly different from that of sesarmids. These data indicate a clear selectivity for ^{13}C -enriched carbon sources such as microphytobenthos. Among the other brachyuran crab taxa associated with mangroves, *Eurycarcinus natalensis*, *Epixanthus dentatus* and *Metopograpsus thukuhar* from Gazi Bay clustered close together and their stable isotope signatures (high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, Table 2) are suggestive of little direct inputs from mangroves and of significant predation on lower trophic levels, consistent with literature data (e.g. Dahdouh-Guebas et al. 1999).

Mollusks

Most of the scarce, previously published stable isotope data for bivalves from intertidal mangrove habitats (Rodelli et al. 1984) point towards microalgal food sources, but the data presented here show a more diverse pattern. Both the *Polymesoda* spp. (sampled in the CWS, Galle and Pambala) and the unidentified oyster from Galle show consistently low $\delta^{13}\text{C}$ signatures, close to those of mangrove tissues. However, this resemblance does not necessarily indicate a strong

reliance on mangrove carbon, as aquatic microalgal production may be similarly depleted in ^{13}C due to low $\delta^{13}\text{C}$ values in the dissolved inorganic carbon (DIC) pool (e.g. surface water $\delta^{13}\text{C}_{\text{DIC}}$ values in Galle ranged between -14.2 and -7.8‰ , authors' unpubl. data, whereas typical seawater values are close to 0‰). The data in Table 4 (see also Fig. 3) also show that these bivalves were consistently enriched in ^{15}N compared to most other consumers in the ecosystem, despite similar $\delta^{13}\text{C}$ values. For Galle, the only site with significant permanently inundated sites, suspended organic matter was similarly enriched in ^{15}N compared to sediment organic matter. Thus, the situation for these bivalve species remains somewhat unclear, with strong contributions from either mangrove-derived material (after microbial processing in the water column, which can result in higher $\delta^{15}\text{N}$ values, e.g. see De Brabandere et al. 2002) or from aquatic primary production. A special group of bivalves are wood-boring species such as the Teredinidae (which were sampled in the CWS), known to harbor symbiotic cellulolytic bacteria capable of N_2 -fixation. Our $\delta^{13}\text{C}$ data of Teredinidae ($-24.6 \pm 0.4\text{‰}$) are consistent with *Avicennia* wood ($\delta^{13}\text{C}$: -25.7‰) being the major C source, but the $\delta^{15}\text{N}$ signatures of the Teredinidae ($+5.8 \pm 0.5$) are only slightly higher than those of the log ($\delta^{15}\text{N}$: $+5.1\text{‰}$) in which they were collected, indeed suggesting an additional input of N_2 -fixation to the N-requirements of these bivalves. Another bivalve from dead mangrove wood in Gazi, *Trapezium* cfr. *sublaevigatum* (which does not have such a symbiotic relationship), showed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values markedly more distant from those of mangroves (Table 2, Fig. 3), suggesting additional inputs from aquatic C and N sources.

Two previous studies have found unexpectedly low $\delta^{15}\text{N}$ values in some mangrove mollusks (Christensen et al. 2001, Bouillon et al. 2002) and similar data were obtained here, i.e. for *Pythia plicata* from Galle, *Onchidium* spp. from the CWS and to a lesser extent from Gazi, and for *Littoraria scabra* from Gazi (see Tables 2 to 4, Fig. 3), all of which are species typically found grazing on mangrove roots or stems. The unusually low $\delta^{15}\text{N}$ values found here in micro-epiflora ($\delta^{15}\text{N} = -6.8\text{‰}$ in both Pambala and Galle, $\delta^{15}\text{N} = -8.2\text{‰}$ in the CWS, -2.4‰ in Gazi Bay) offer a convincing explanation for these consumer $\delta^{15}\text{N}$ values and indicate a significant input of N from such a source. The $\delta^{15}\text{N}$ values of the epiflora are likely to reflect the importance of atmospheric nitrogen (from precipitation and/or through N_2 -fixation) as their N source (see e.g. Hietz et al. 1999 for vascular epiphytes). It is worth noting that some other gastropods often found in large numbers on mangrove stems, such as *Cerithidea obtusa* (found in the CWS, see Table 3) or *C. decollata* (found in Gazi, see Table 2) do not show evidence of extensive feeding

on ^{15}N -depleted epiflora, but as these species are also found on the sediment surface, the isotope data suggest that these are more likely to feed on sediment organic matter and microphytobenthos. In conclusion, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ patterns (Fig. 3) indicate a diverse range of feeding preferences for mangrove-inhabiting mollusks.

Differences in C and N utilization between contrasting mangrove systems

In a previous study, we found no evidence for a dominant role of mangroves in sustaining epifaunal invertebrate communities (Bouillon et al. 2002). However, as these data came from an estuarine system where tidally imported organic matter was found to dominate the sediment pool, we hypothesized that such a situation may not be representative for other types of mangrove systems, in particular for those where exchange of material with the aquatic environment is limited due to low tidal action.

The data gathered in this study provide a first test of this hypothesis. First, as noted above, we found that the origin of sedimentary organic matter at least partially determines the overall dependency of sesarmid crabs on different primary sources (Fig. 4a), despite the obvious fact that different species have different feeding specializations. In Fig. 4c, data for all gastropod species are presented per site with data from this study, as well as those given in Rodelli et al. (1984) and Bouillon et al. (2002). Again, despite their varying feeding specializations (some being selective for epiflora, microphytobenthos or mangrove litter, see 'Mollusks' above), an analogous pattern as that found for sesarmids shows up for gastropods, i.e. a markedly lower direct use of mangrove carbon in estuarine forest types where inputs from the aquatic environment are significant (Spearman rank correlation test for the relationship between sediment and gastropod $\delta^{13}\text{C}$: $p = 0.029$, $R^2 = 0.86$). It is worth mentioning that the slope of the relationship between $\delta^{13}\text{C}$ of consumers and sediments is markedly different for sesarmids (slope of ~ -0.56) and gastropods (slope of ~ 1.0).

The same conclusions are also evident when comparing the panels in Fig. 3: much of the species data for the low-amplitude sites in Sri Lanka cluster quite closely together in the range expected for species that assimilate significant mangrove-derived organic matter (from the sediment pool); for the upstream site in Gazi and for the CWS the data are more scattered; and at the seaward site in Gazi, a clear trend towards much more enriched values is evident. However, for both Pambala and Galle, our $\delta^{13}\text{C}$ values for most mangrove tree species are rather low. Roggeman (2002) analyzed *Rhizophora*

mucronata leaves from both areas during the same sampling period and found typically higher $\delta^{13}\text{C}$ values, ranging between -29 and -25‰ . A clear relationship with tree age (as measured by the circumference of the tree crown or the height of the tree) was found, with younger trees showing more negative $\delta^{13}\text{C}$ values (between -32 and -30‰). A generally more enriched $\delta^{13}\text{C}$ signature for mangrove leaf tissues at both Galle and Pambala would be consistent with indications from sedimentary TOC and TOC/TN data that the organic matter pool is derived primarily from mangrove tissues, and the sediment $\delta^{13}\text{C}$ signatures ($-27.5 \pm 0.9\text{‰}$ in Pambala, $-27.8 \pm 1.2\text{‰}$ in Galle) are indeed closer to the data from Roggeman (2002). In this interpretation, the trophic dependency of epifauna on mangroves in both Galle and Pambala would overall be large, and likely to occur both directly through feeding on mangrove leaves and indirectly through feeding on sediment organic matter (which is strongly enriched in N compared to senescent mangrove leaves, e.g. see Skov & Hartnoll 2002). Finally, it should be mentioned that our sampling design did not accommodate potential seasonal and/or spatial variations in the foodweb structure within sites. However, even if such variations were present, we do not see any arguments to conclude that these would interfere with the general patterns observed in Figs. 3 & 4.

Results of litter removal experiments and stable isotope analyses: how compatible are they?

The idea that much of the mangrove litter produced is removed and/or consumed by mangrove epifauna (at least in the Indo-Pacific, McIvor & Smith 1995 and even there not in all forest zones alike or depending on the tidal stage, see Slim et al. 1997 and Ólafsson et al. 2002) seems to contrast with the stable isotope results presented and compiled in this study. They demonstrate that, from a community perspective, only a limited number of species rely substantially and directly on mangrove carbon, and that, when available, a range of other sources are used by the invertebrate community. There are several points which can be raised to reconcile these 2 superficially contrasting viewpoints. First, the fact that a large proportion of the leaf litter is removed and/or consumed by the local crab fauna does not necessarily imply that mangrove leaves are the dominant item in their diet, as the population of sesarmids may consume even more of 'something else'. In this respect, the study of Skov & Hartnoll (2002) is particularly enlightening, as their field observations clearly demonstrate that sesarmids spend considerably more time feeding off the sediment surface than collecting or eating leaves. Even though this does not necessarily imply that more sediment organic mat-

ter is assimilated than mangrove leaves, it does indicate the importance of deposit feeding. Evidently, the sources of organic matter present in the sediment and the degree of selectivity with which sesarmids feed on it (both of which may be highly variable) will further determine which carbon sources contribute to their diet and in which proportions. Secondly, much of the work on the trophic significance of different sources in mangrove ecosystems has focussed on a limited number of invertebrate groups or species, notably sesarmids and a disproportionate number of studies on *Terebralia palustris* (e.g. Slim et al. 1997). From a community perspective, however, this may severely bias our view of the importance of mangrove litter, as the often diverse invertebrate community apparently displays a wide variety of feeding specializations.

Lastly, it should also be noted that in view of the significant differences in elemental ratios between different food sources available to intertidal consumers (e.g. mangrove leaves have a very low N content, microphytobenthos is much richer in N, etc.), the contributions of C and N from any dietary source are not necessarily equal, but likely to be proportional to the C/N ratios of the substrates. The latter implies that the dependency in invertebrate communities on mangrove-derived N will generally be less than their dependency on mangrove-derived C.

CONCLUSIONS

Our data strongly suggest that where multiple C and N sources are available, intertidal mangrove epifaunal communities exploit all available food resources with clear and consistent differences in utilization patterns between different taxa or species. Secondly, we have shown a strong influence of the relative inputs of local and tidally imported carbon sources (as reflected in sedimentary $\delta^{13}\text{C}$ values) on the relative importance of mangrove carbon to several groups of epifauna. This variability shows strong similarities to the variable contribution of different carbon sources to sedimentary microbial communities observed across various mangrove sites (Bouillon et al. 2004).

Although $\delta^{15}\text{N}$ was a poor source indicator except for micro-epiflora, which showed consistently low $\delta^{15}\text{N}$ values in all sites (-2.4 to -8.2%), we can expect that the importance of mangroves as a N source for invertebrates is less than for C, due to the low N content of mangrove-derived organic matter. Finally, it is worth pointing out that the areal extent of 'closed' mangrove systems (i.e. in which mangroves appear to provide most of the carbon fuelling epifaunal and microbial communities) is rather limited on a global scale, as the largest mangrove-covered areas are found in estuarine and deltaic systems.

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