Organic matter exchange and cycling in mangrove ecosystems: Recent insights from stable isotope studies

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Abstract

Mangrove ecosystems are highly productive tropical coastal ecosystems which have a potentially high impact on the carbon budget of the tropical and global coastal zone. The carbon dynamics in mangrove ecosystems has been the subject of numerous studies during the past decades, but we are still far from having an integrated view of the overall ecosystem functioning in terms of organic matter processing. The application of recent analytical techniques has produced a wealth of new information but has also indicated the gaps in our knowledge on organic matter cycling in these ecosystems. This paper provides an overview of our current understanding of organic matter dynamics in mangrove ecosystems, and reviews data based on stable isotope analyses, on (i) the delineation of carbon sources in different organic matter pools, (ii) utilization patterns of organic carbon by microbial and faunal communities, and (iii) organic matter exchange between mangroves and adjacent ecosystems. Although the use of stable isotopes has a number of limitations and has not always been able to unambiguously assess source contributions, it has been invaluable in refuting some long-standing paradwigms, and has shown that source characterization is crucial in order to better estimate organic matter budgets in these dynamic ecosystems. Future studies on process rates or flux measurements should therefore ideally be combined with a variety of chemical tracers to determine the source of the organic matter considered.
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1. Introduction

Mangrove forests have long been proposed to play an important role in the carbon balance of tropical coastal ecosystems. Jennerjahn and Ittekkot (2002) have estimated that inputs from mangrove forests could account for 11% of the total input of terrestrial carbon into the ocean and 15% of the total carbon accumulating in modern marine sediments. Similarly, Dittmar et al. (2006) estimated that mangroves contribute ~10% of the terrestrial dissolved organic carbon (DOC) exported to the ocean globally, despite their small area relative to other habitats. Recent upscaling of water-air CO_2 fluxes measured in (a limited number of) surface waters adjacent to mangroves suggests that mineralization of organic matter and subsequent CO_2 emission from the water column could also represent a significant source

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of CO_2 in the overall oceanic CO_2 budget (Borges et al., 2005). Despite the expected uncertainties associated with such global estimates, at the very least these numbers indicate a potentially large role of mangrove carbon in the coastal zone, and highlight the importance of understanding mangrove ecosystem C dynamics to better constrain global oceanic C budgets.

Mangrove ecosystems can attain high levels of primary production. Odum and Heald (1975) first proposed that mangrove litterfall provides a trophic subsidy in adjacent coastal waters (the 'outwelling hypothesis'), via a detritus–based foodweb whereby mangrove litter is converted into more palatable microbial biomass, which in turn acts as the dominant food source for higher trophic levels. In view of the economic importance of fisheries in mangrove systems and adjacent waters, such a trophic dependency is a much–publicised function of mangrove systems and an important argument for their conservation. The majority of studies, however, have found that mangrove organic matter is exported and incorporated into coastal foodwebs only to a very limited extent (Lee, 1995). A small number of studies have reported more extensive export and use of mangrove carbon and other nutrients in particular locations (e.g. Dittmar et al., 2001). The variability in findings is highlighted by stable isotope evidence for a very limited contribution of mangrove carbon to penaeid prawns in northern Australia (Lone-ragan et al., 1997), but a much greater apparent contribution in Malaysia (Chong et al., 2001).

Existing estimates of net primary productivity and mineralization in mangrove systems are probably underestimates due to methodological problems or uncertainties (Alongi, 2005). Recent direct measure-ments of rates of photosynthesis suggest that previous estimates of net primary production (based mostly on litter fall rates) might be significantly underestimated (Clough et al., 1997), with litterfall representing an average of ~30% of net canopy production (Alongi et al., 2005). Similarly, care should be taken when upscaling mineralization data. Carbon dioxide release from sediments, a common proxy for mineralization, is significantly lower than depth–integrated rates of mineralization, suggesting that part of the CO_2 produced may be released by porewater drainage (Alongi, 2005; Bouillon et al., 2007a).

Clearly, there remains a large degree of uncertainty about the overall fate of mangrove production, its importance in the oceanic C budget, and the role of allochthonous organic matter. In order to better constrain estimates on the role of mangroves, we need to critically review available data and take into account the uncertain-ties associated with many components of organic matter

cycling in mangrove systems. Novel analytical techni-ques and approaches applied in mangrove–related studies in recent years have exposed some of the knowledge gaps. In this review, we first introduce some theoretical aspects underlying the application of stable isotope analysis in mangrove systems and summarise the variability in isotope signatures in mangrove tissues and other relevant primary producers. The remainder of the review synthesises the new insights on organic matter cycling in mangrove ecosystems based on stable isotope analyses, focussing on (i) utilization of organic matter by faunal communities, (ii) exchange of organic matter between mangroves and adjacent habitats, and (iii) the fate of exported mangrove–derived organic matter.

2. Applying stable isotope techniques in mangrove systems

Analysis of natural abundance isotope ratios as indicators of the origin of organic matter and of trophic interactions is based upon three important assumptions:

(1) differences (may) exist in the stable isotope signatures of different primary producers;
(2) these differences are maintained or altered in a sufficiently predictable way during degradation processes; and
(3) consistent and predictable changes in the isotopic signatures occur during transfer to higher trophic levels.

2.1. Variability in isotope ratios in mangroves and other primary producers

$\delta^{13}C$ values can be used to distinguish among photosynthetic pathway types (e.g. O'Leary, 1981), with terrestrial C_3 and C_4 plants showing non–over-lapping $\delta^{13}C$ distributions, and plants using the CAM (Crassulacean Acid Metabolism) pathway showing intermediate $\delta^{13}C$ signatures which may overlap with those of C_3 or C_4 plants. In C_3 plants (such as man-groves) the major components of the overall fraction-ation are (1) the differential diffusion rates of CO_2 through the stomata, and (2) the fractionation by ribulose biphosphate carboxylase/oxygenase (Rubisco), the ini-tial enzyme of C_3–photosynthesis. According to Farqu-har et al. (1989), overall discrimination in C_3 plants can be described by:

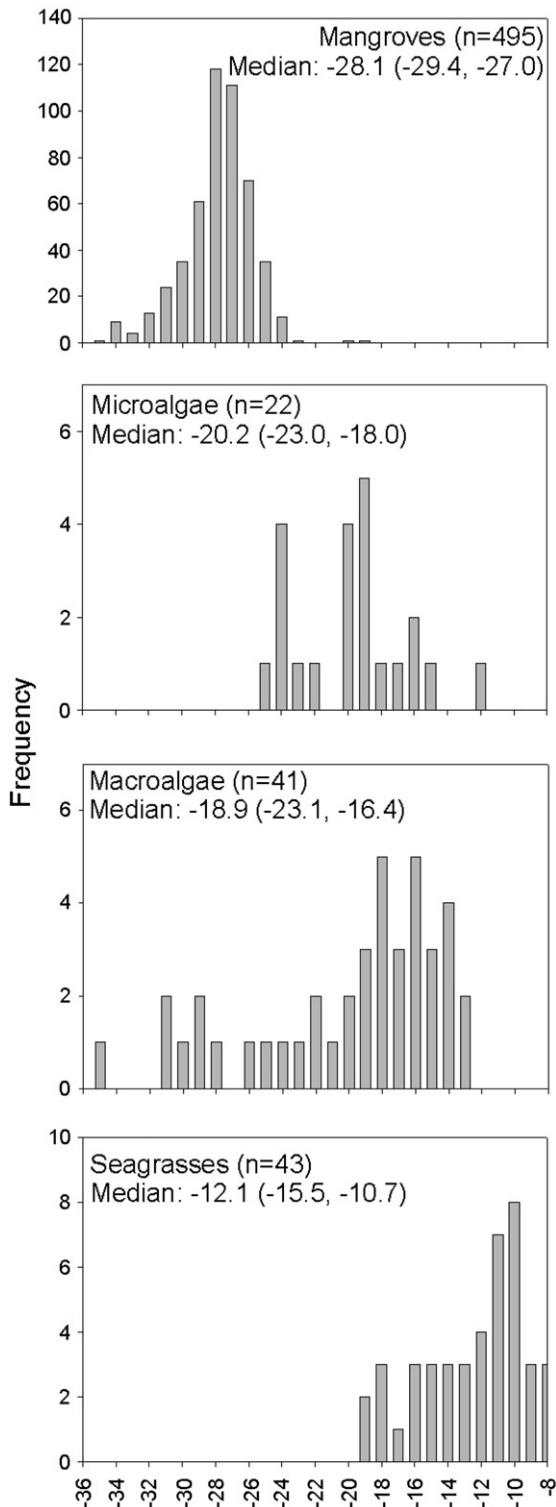$$\Delta = a + (b - a) * \left(\frac{c_i}{c_a} \right) \qquad (1)$$

Fig. 1. Compilation of literature $\delta^{13}C$ data on mangrove leaves, micro- and macroalgae, and seagrasses from seagrass beds adjacent to mangrove forests. Median $\delta^{13}C$ values are given on each plot. Values between brackets are the 25th and 75th percentiles. Data sources available on request.

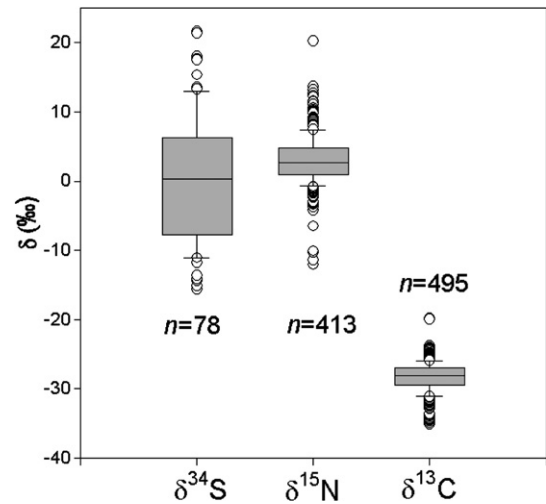Fig. 2. Boxplot of a compilation of literature $\delta^{34}S$, $\delta^{15}N$ and $\delta^{13}C$ data on mangrove leaf tissues, illustrating the relative variability of the three isotope tracers. Data sources available on request.

where Δ is the overall carbon isotope discrimination by the leaf (in ‰), a: the fractionation due to diffusion across the stomata (∼4.4‰, constant), b: the net fractionation caused by carboxylation (∼27‰, constant); and c_i and c_a are the internal (intercellular) and external (ambient) partial pressure of CO_2, respectively. If the leaf stomata are relatively closed, then c_i tends towards zero and Δ therefore tends towards 4.4‰ (=a). If, on the other extreme, stomatal limitations are minimal, $c_i=c_a$ and Δ approaches 27‰ (=b). As c_i/c_a values are typically between 0.4 and 0.8, the Δ range is about 13–22‰, and assuming a $\delta^{13}C$ of atmospheric CO_2 of − 7.8‰, this leads to typical $\delta^{13}C$ values for C_3 plants ranging between −24 and −30‰. Leaf $\delta^{13}C$ values thus reflect the long–term physiological activity of the leaf, and show a rather wide range for mangroves (between −35.1 and −21.9‰, Figs. 1 and 2). Several studies have examined the effect of environmental conditions such as salinity, nutrient status, growth form, and humidity on mangrove $\delta^{13}C$ values, both in the natural environment (e.g., Kao and Chang, 1998; McKee et al., 2002) and under culture conditions (e.g., Farquhar et al., 1982; Ish-Shalom-Gordon et al., 1992; Lin and Sternberg, 1992a; Kao et al., 2001). The possible role of variations in source (i.e. CO_2) $\delta^{13}C$ values has not been examined, although it is plausible that such variations occur in certain dense mangrove stands. Several laboratory and field studies have reported that increased salinity decreases stomatal conductance and thus leads to a more enriched $\delta^{13}C$ (e.g., Medina and Francisco, 1997; Lin and Sternberg, 1992b; Kao et al., 2001), but the relationship is not necessarily linear (Ish-

Shalom-Gordon et al., 1992). Due to salinity stress and/ or nutrient limitation effects, dwarf or stunted forms of mangroves typically show distinctly more enriched $\delta^{13}C$ values relative to their tall conspecifics (e.g., Lin and Sternberg, 1992b; McKee et al., 2002). The relationship between stable isotope signatures of mangroves and environmental factors is clearly quite complex but nevertheless holds potential for inferring longer-term changes in environmental conditions recorded in mangrove tree rings (e.g., Verheyden et al., 2004) or in the sedimentary record (e.g., Smallwood et al., 2003; Wooller et al., 2003a).

$\delta^{13}C$ values can vary among mangrove tissue types, but as yet no consistent patterns in variation have emerged. Ellison et al. (1996) found no significant differences between leaves, branches, and twigs of *Rhizophora mangle*, but cable roots and small rootlets were all significantly enriched in ^{13}C relative to leaf material. Ish-Shalom-Gordon et al. (1992) found little or no consistent difference in $\delta^{13}C$ of leaves and stems in their experimental study for *Avicennia germinans*, and Boon et al. (1997) also found no significant differences between *Avicennia marina* leaves and branches, while pneumatophores were on some occasions significantly depleted in ^{13}C relative to leaves (by up to 3.1‰). Lee et al. (2001) found twigs and bark tissue of *Kandelia candel* and *Aegiceras corniculatum* to be slightly depleted (by <2‰) relative to leaf tissues. Similarly, Muzuka and Shunula (2005) found no consistent patterns in $\delta^{13}C$ and $\delta^{15}N$ differences between roots, leaves, flowers and fruits of various mangroves.

Isotope analysis of food webs often uses isotopes of nitrogen and/or sulfur along with carbon. Variability in mangrove $\delta^{15}N$ and, particularly, $\delta^{34}S$ values is more pronounced than for $\delta^{13}C$ (Fig. 2). This variability in $\delta^{15}N$ and $\delta^{34}S$ often occurs over short distances, with differences of up to 10‰ for N (e.g., Fry et al., 2000) and 29‰ for S (e.g., Okada and Sasaki, 1998) occurring among sites within a single estuary. Such differences may result from variation in the source values and/or in differences in fractionation during uptake (Fry et al., 2000). One of the important drivers of source variability for N is pollution from urban sewage or agriculture, and $\delta^{15}N$ values for mangroves have been used to map the extent of influence of sewage N (McClelland and Valiela, 1998; Fry et al., 2000; Costanzo et al., 2001; Jones et al., 2001, see also Wooller et al., 2003b). For $\delta^{34}S$, technical difficulties have led to low replication in earlier studies, reducing the rigour of conclusions (e.g., Newell et al., 1995; Loneragan et al., 1997; Wiedemeyer, 1997). Improved survey designs providing a better measure of spatial variability in S isotopes of

mangroves have increased the usefulness of $\delta^{34}S$ (e.g., Hsieh et al., 2002; Benstead et al., 2006). In general, the typically large differences in average sulfur isotope signatures between mangroves and other primary producers in estuaries mean that they will prove useful in distinguishing the importance of different primary producers to food webs, despite the relatively high variability (Connolly et al., 2004).

In the aquatic environment, the substrate for algal photosynthesis is dissolved carbon dioxide or bicarbonate. $\delta^{13}C$ values for DIC $(=CO_2 + H_2CO_3 + HCO_3^- + CO_3^{2-})$ approach 0‰ if there is an equilibrium with CO_2 from the atmosphere (e.g. in an open ocean environment), but several processes may alter the $\delta^{13}C$ of the DIC pool: (1) autotrophic production in the water column causes the residual DIC pool to become enriched in ^{13}C, due to the preferential fixation of ^{12}C during photosynthesis; (2) the diffusive efflux of CO_2 to the atmosphere causes the residual DIC pool to be enriched in ^{13}C, as 'lighter' CO_2 diffuses at a faster rate; (3) the dissolution or precipitation of $CaCO_3$ influences the overall $\delta^{13}C$ DIC, as carbonates usually have enriched $\delta^{13}C$ values compared to the DIC pool; and (4) mineralization processes result in the addition of ^{13}C–depleted CO_2 as the $\delta^{13}C$ of respired CO_2 will be similar to that of the organic substrate. Besides these variations in the $\delta^{13}C$ composition of the substrate for photosynthesis, a variety of factors influence the degree of fractionation between the substrate and the biomass formed, including the availability of DIC, growth rate limiting factors such as nutrients or light, temperature, species, and the size and dimensions of the cells. Thus, the carbon stable isotope composition of algae can show large variations, being generally in the range of −17 to −23‰ for marine phytoplankton, but significantly more ^{13}C–depleted in estuarine and freshwater environments. Benthic microalgae in marine waters are typically enriched in ^{13}C relative to phytoplankton by an average of ∼5‰ (France, 1995). This difference is thought to be a result of the thicker boundary layer experienced by benthic algae (MacLeod and Barton, 1998), causing more diffusion–limitation of CO_2 and thus a decrease in overall fractionation. Our compilation of $\delta^{13}C$ values for benthic algae include epiphytic and edaphic algae, and shows that the algae generally are enriched relative to mangroves (Fig. 1). Cyanobacteria data are pooled with those for benthic microalgae, but the few available data suggest that cyanobacteria typically show the most enriched $\delta^{13}C$ values (e.g., Al-Zaidan et al., 2006). The amount of $\delta^{15}N$ data on algae is more limited, and there is no indication that values are sufficiently different to be of general use as an additional source indicator. In

some cases, however, epiphytes show markedly depleted δ^{15}N (e.g. -8 to -6‰, Bouillon et al., 2004c), and these can be reflected in consumer δ^{15}N as was suggested for *Onchidium* sp. and various species of *Littoraria* (Christensen et al., 2001; Bouillon et al., 2004c).

Seagrasses adjacent to mangroves can be imported into tidal creeks and into the intertidal forest, and thus represent another potential source of carbon in mangroves. Seagrass δ^{13}C values vary considerably but are typically enriched relative to other estuarine producers, with most values between -16 and -12‰ (Hemminga and Mateo, 1996). Seagrasses adjacent to mangrove forests show remarkable variability in δ^{13}C over short distances (Fig. 1), with more depleted values close to the mangroves, steadily becoming more enriched with distance towards the sea (e.g. a range of almost 10‰ over <4 km distance found by Hemminga et al. (1994) and Marguillier et al. (1997), see also Lin et al. (1991) and France and Holmquist (1997)). This trend probably reflects parallel changes in the δ^{13}C of the DIC pool, being more negative close to mangroves where mineralization supplements the DIC pool with ^{13}C-depleted CO_2. As discussed later, such a trend is also expected for phytoplankton and benthic microalgae, although no direct measurements on microalgae have been made because of the difficulties in obtaining pure samples for analysis.

2.2. Changes in stable isotope signatures during senescence and degradation

Relatively few data are available on the effects of senescence and degradation on the δ^{13}C signature of mangrove tissues. Rao et al. (1994) noted little difference (<1‰) between fresh and senescent leaves for five species of Kenyan mangroves, but for four other species, senescent leaves were markedly depleted (by 1.3– 2.6‰) relative to fresh ones. No marked differences were observed between green and senescent leaves by Schwamborn et al. (2002) and Kieckbusch et al. (2004), and the direction and magnitude of the difference between green and yellow leaves for two species in the study of Lee (2000) was opposite. Kao et al. (2002) and Wooller et al. (2003a) demonstrated that δ^{13}C of *K. candel* and *R. mangle* were not significantly altered during senescence. Several degradation experiments have demonstrated that changes in the δ^{13}C signatures during decomposition are either insignificant (Zieman et al., 1984; Dehairs et al., 2000; Wooller et al., 2003a; Werry and Lee, 2005) or very small, i.e. typically < ~1.5‰ (Primavera, 1996; France,

1998; Fourqurean and Schrlau, 2003). From the few data available, there are no indications that floating leaves collected in creeks or offshore are different from fresh leaves (Rodelli et al., 1984; Schwamborn et al., 2002). This lack of effect of decomposition on mangrove isotopes is consistent with results from decomposition studies of other producers (Ehleringer et al., 2000). Nevertheless, even in sites where litter is expected to be the sole input, the sediment organic matter pool in mangrove forests is consistently enriched in ^{13}C relative to the litter (e.g., Lallier-Vergès et al., 1998), probably because of an increase in microbial and fungal residues (Ehleringer et al., 2000).

Shifts in the isotopic signature of decomposing mangrove litter are probably dependent on the type, diversity and abundance of microbial decomposers colonising the organic matter.

Similarly, experimental work has indicated that changes in δ^{15}N are either small (e.g., Fourqurean and Schrlau, 2003; Wooller et al., 2003a; Werry and Lee, 2005), or insignificant (e.g., Dehairs et al., 2000). Werry and Lee (2005) noted, however, much more significant depletion of ^{15}N of shredded mangrove leaf litter material in the faeces of the sesarmine crab *Parasesarma erythrodactyla*, and attributed this change to the higher density of colonising microbes compared to whole leaf litter. Since changes in δ^{15}N are mainly due to the microbial immobilization or new N (Caraco et al., 1998), the magnitude and direction of δ^{15}N changes will depend on a range of factors such as the inorganic N-substrate, the importance of N_2 fixation (e.g., Woitchik et al., 1997), the δ^{15}N of the added N, and the degree of fractionation during immobilization. Changes in the stable isotopic signature of mangrove litter through macrofaunal processing and microbial decomposition, if significant, will have strong implications for using these signatures as tracers for energy flow.

2.3. Changes in stable isotope signatures during assimilation

Fractionation during assimilation by consumers typically enriches δ^{13}C values by 0–1‰, although the full range of enrichment values found in aquatic systems may vary between -2.1 and $+2.8$‰ (Vander Zanden and Rasmussen, 2001; McCutchan et al., 2003). Fractionation for δ^{15}N is larger, with enrichment often around 2.7 to 3.4‰ but with a full range between -0.7 and $+9.2$‰. Sulfur fractionation is smaller even than for C (McCutchan et al., 2003). In aquatic ecosystems, the degree of fractionation for C and N appears to be more variable for invertebrates than for fish, laboratory results are more variable than field estimates, and trophic

fractionation in herbivores is more variable than in carnivores (Vander Zanden and Rasmussen, 2001). Caution is therefore required when using average literature values for fractionation to calculate the trophic position of consumers or to adjust mean consumer values in preparation for analysis with mixing models. Rigorous tests on how natural (e.g. salinity) and anthropogenic (e.g. pollution) environmental variations may affect fractionation in consumers are needed to validate the application of stable isotope analysis in particular environmental settings.

2.4. Analysis of isotope data using mixing models

Stable isotope data are often used to determine the contribution of different primary sources to consumers in a food web. Two-source mixing models have been frequently used in the form:

$$\delta^{13}C_{consumer} = (X_A.\delta^{13}C_A + X_B.\delta^{13}C_B) + \Delta \qquad (2)$$

where $\delta^{13}C_A$ and $\delta^{13}C_B$ are the carbon isotope composition of dietary source A and B, respectively, X_A and X_B are the proportion of source A and B to the consumers diet ($0 < X_A, X_B < 1$), and Δ is the fractionation associated with a trophic level transfer. The application of such a model becomes problematic when the isotopic difference between the two sources is small or when the variability in $\delta^{13}C$ values of a single source is high (Lee, 2005), even where models incorporating variance are used (Phillips and Gregg, 2001). Moreover, it is essential that correct $\delta^{13}C$ values are assigned to each source, which has not been the case in many mangrove studies (see below). When multiple stable isotope ratios are analysed (e.g. $\delta^{13}C$ and $\delta^{15}N$, or $\delta^{13}C$ and $\delta^{34}S$), it is possible to use this additional information to derive the contribution of three different food sources to a consumer's diet. Theoretically speaking, the number of producer sources that can be resolved in a multiple isotope ratio analysis deploying n elements is n+1. $\delta^{34}S$ is more useful as a second element than $\delta^{15}N$, because of the large degree of fractionation of ^{15}N during trophic transfer, the sensitivity of $\delta^{15}N$ to local conditions (such as urban pollutants), and the small differences among producers in their $\delta^{15}N$ signatures (Connolly et al., 2004). A problem with 3-source mixing models using multiple elements is that they provide unreliable estimates of contributions where food sources contain different proportions of the elements. In mangrove systems, for example, consumers can be expected to assimilate a higher proportion of N (and S) from animal than from

plant sources. This is illustrated in Fig. 3, where the relative contributions of three hypothetical sources (using realistic input values of mangroves, sediment organic matter, and benthic microalgae) for a given consumer are shown as 0, 25, 50, 75, and 100% isolines - the effect of differences in the C and N content of the different sources is that the isolines are curvilinear rather than straight, and hence, that not taking these differences into account result in a severe bias in the estimated source contributions (Phillips and Koch, 2001).

Another approach that has recently gained popularity is the IsoSource model (Phillips and Gregg, 2003), a technique that constrains the possible contribution by different sources when the number of sources is too large to find a unique solution (see also Phillips et al., 2005). IsoSource has proven informative in studies of mangrove contributions to food webs (Melville and Connolly, 2005; Benstead et al., 2006), but the approach still suffers from a number of limitations. For example, variability in the degree of trophic fractionation is not taken into account, and the concentration-dependent adjustment in the two-source model (Phillips and Koch, 2001) is not available in IsoSource. These shortcomings would normally result in a range of solutions that is conservative (i.e. too narrow), and biased towards those sources with low concentrations of N (or S).
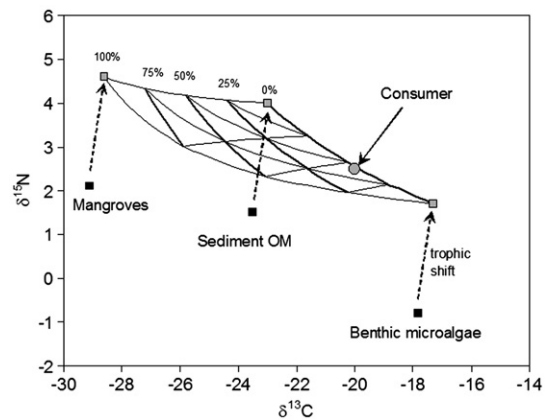

Fig. 3. Contribution of thre different sources (representative data given for mangroves, sediment organic matter, and microphytobenthos) to the diet of a consumer (represented by the grey circle), using a concentration−dependent 3−source mixing model (Phillips and Koch, 2001). The original $\delta^{13}C$ and $\delta^{15}N$ signatures for the sources (black squares) have been corrected for fractionation associated with a trophic shift (grey squares). Isolines represent the relative contribution (in steps of 25%) of the three sources to a consumers' diet. In the example consumer, the contribution of mangroves, sediment organic matter and microphytbenthos are 2, 42, and 56%, respectively.

3. Cycling within the mangrove forest: role of benthic fauna

Whereas a large number of studies have dealt with the trophic subsidy for consumers in aquatic environments adjacent to mangrove systems, less attention has been paid to foodweb structure in intertidal mangrove faunal communities, and their potential importance as prey items for mobile fauna (see Sheaves and Molony, 2000). Despite the fact that these communities have more direct access to mangroves as a food source, a number of recent studies have indicated that mangrove invertebrates show a much more diverse pattern of resource utilization than previously expected (e.g., Thimdee et al., 2001, 2004; Bouillon et al., 2002b). The degree to which they rely on mangrove-derived C also varies across mangrove systems, with a higher reliance in 'closed' systems where more of the mangrove production is retained and where there is less exchange of material with adjacent systems (Bouillon et al., 2002a, 2004c). A number of stable isotope studies have focussed on specific species or groups of fauna, and are largely consistent with these conclusions (e.g. *Uca* spp.: France, 1998; *Littoraria* spp.: Christensen et al., 2001; Lee et al., 2001; *Terebralia palustris*: Slim et al., 1997; *Aratus pisonii*: Lacerda et al., 1991). Despite the potentially large-scale movement of organic matter, evidence is emerging that many invertebrates have a small home-range and derive most of their diet from locally available food sources (Guest et al., 2006). This has been illustrated by the small-scale changes in stable isotope signatures (and hence, carbon sources used by invertebrates) in the vicinity of habitat boundaries (Guest and Connolly, 2004; Guest et al., 2004).

Allochthonous carbon and local production by benthic microalgae appear to be important food sources for a wide variety of invertebrate species, including those typically considered as important in leaf litter processing. Very few mangrove animal species have been examined for their overall food resources, and our knowledge is biased by the neglect of whole groups of fauna, in particular most groups of infauna and meiofauna. The diversity in resource utilization for the entire community is almost certainly underestimated, and the overall role of consumers in the processing of different organic matter sources is still far from clear.

An example of the complexities of carbon cycling is provided by a sacoglossan, *Elysia* sp. nov., common in shallow tidal pools under *Avicennia* spp. in Andhra Pradesh, India. Sacoglossans are herbivorous marine opisthobranchs (sea slugs) which feed mainly on green

or red algae, but an often-encountered phenomenon in this group is the occurrence of kleptoplasty, i.e. the intercellular retention of chloroplasts obtained from the algae. These chloroplasts often remain functional for prolonged periods (up to 10 months, Rumpho et al., 2000) and presumably provide part of the carbon requirements of the host. Our data on *Elysia* sp. nov. show unusually depleted $\delta^{13}C$ signatures (between −43.3 and −35.2 ‰ in different seasons and sites, Fig. 4) previously unrecorded in any kleptoplastidic or other algae-invertebrate symbiosis (see Raven et al., 2001). We hypothesize that strong internal recycling of CO_2, i.e. the fixation of host-respired CO_2 by the functional kleptoplastids, in combination with a ^{13}C-depleted external DIC pool, could be responsible for the observed $\delta^{13}C$ values. Although these appear to be the first isotope data on sacoglossans with kleptoplasty from mangroves, other species are known to occur in these systems, e.g. *E. bangtawaensis* from Thailand (Swennen, 1997) and *E. australis* in Moreton Bay, eastern Australia (Davie, 1998).

Such highly specialized symbiotic relationships are probably more widespread than is often assumed. Lucinid bivalves are known to host sulfur-oxidizing bacteria, have been found in a number of reducing environments such as mangrove sediments (Lebata and Primavera, 2001), and show $\delta^{13}C$ signatures around −32 to −28‰ and $\delta^{15}N$ values ranging between −11 and +4‰ (Fig. 4), which is consistent with a strong contribution by their symbionts. The significance of such trophic interactions in tropical mangrove sediments
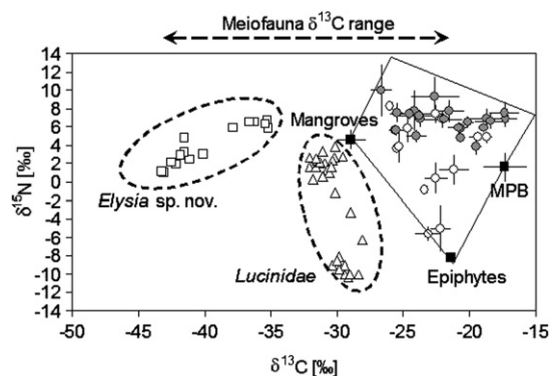

Fig. 4. Plot of $\delta^{13}C$ and $\delta^{15}N$ signatures for typical mangrove primary producers (black squares), macro−epifauna (grey circles: brachyuran crabs, open circles: molluscs), *Elysia* sp. nov. (open squares), the lucinid bivalves *Anodontia edulenta* and *Austriella corrugata* (open triangles; S. Bouillon and J.H. Primavera, unpubl. data) and preliminary range of meiofauna $\delta^{13}C$ (T. Moens and S. Bouillon, unpubl. data). Data for primary producers and macro−epifauna were taken from Bouillon et al. (2002a).

should not be underestimated, as some lucinids are known to occur at very high local density (e.g. *Austriella* cf. *plicifera* in Moreton Bay, Queensland, Australia; S.Y. Lee, unpubl. data). Symbiotic relationships have been documented in meiofaunal taxa from a variety of coastal habitats, and mouthless species have recently been reported from mangrove systems (Kito and Aryuthaka, 2006). Some of these taxa collected from mangroves in Kenya have highly depleted $\delta^{13}C$ signatures, with values as low as −43‰ (T. Moens and S. Bouillon, unpubl. data). It thus appears that not only do many mangrove invertebrates rely extensively on algal sources rather than on mangrove litter, but that a wide range of organisms may show very specialized pathways of carbon and nitrogen acquisition through symbiotic relationships. To date, however, there are no data that give any indication of the importance of such trophic interactions. Given that isotope signatures of such symbioses can be quite distinct (Fig. 4), isotope approaches should be useful in revealing the importance of symbiotic relationships in mangrove systems. The trophic dependency of other mangrove macrofauna on these symbiotic species is largely unknown.

The unexpected diversity in patterns of resource utilization in mangrove systems can be considered a form of niche segregation: mangrove systems represent complex and highly dynamic environmental conditions, where faunal assemblages typically show distinct horizontal or vertical zonation, or where different species forage at different times (low/high tide, day/night). The ability of closely related species to use different food resources therefore likely represents an additional strategy to optimally exploit this environment.

Despite stable isotope evidence that macrofauna often utilize carbon from sources other than mangroves, other evidence demonstrates that removal and consumption of mangrove litter can represent a significant fraction of the overall litterfall, and thus an important trophic link. Key species involved in litter processing include sesarmid crabs (e.g., Lee, 1998), the ocypodid *Ucides cordatus* (up to ∼80% of annual litterfall, Nordhaus et al., 2006), and the molluscs *Terebralia palustris* (Slim et al., 1997) and *Melampus coffeus* (Proffitt and Devlin, 2005).

The apparently contradictory aspects of macrofauna trophodynamics are best understood by considering densities and carbon requirements of macrofauna. Even where algae are important and only a portion of the carbon requirements of macrofauna is derived from mangroves, the high consumer densities and rates of consumption mean that most or all of the leaf litter is turned over (Bouillon et al., 2004c). Furthermore, most emphasis in carbon budgets has to date been on conspicuous macrofauna such as crabs. If the entire community of epifauna and infauna is considered, the impact on organic matter cycling and litter dynamics could be overwhelming. In order to obtain a realistic estimate of this community role, data on faunal assemblage structure and secondary production coupled to information on resource utilization would be required - data that are entirely lacking for any mangrove system. Although the impact of fauna in current mangrove C budgets is often considered only in terms of direct herbivory or invoked to estimate the proportion of leaf litter retained within the system due to burial and/or consumption by sesarmid crabs, it is clear that future ecosystem budgets should attempt to re-evaluate the potential role of other resident, less conspicuous, fauna (e.g., in- and meiofauna).

4. Isotopes as tracers of movement of organic matter - import and export

Stable isotope ratios have been used in a large number of studies to infer the contribution of mangrove carbon and other potential sources to the sedimentary or suspended organic matter pool (e.g., Lacerda et al., 1986, 1995; Machiwa, 2000; Kuramoto and Minagawa, 2001; Thimdee et al., 2003). A major shortcoming of some studies is that variations in $\delta^{13}C_{POC}$ values have been related to the admixture of mangrove-derived carbon and 'marine' phytoplankton, whereby the latter is characterized by typical $\delta^{13}C$ values of ∼−20 to −18‰ (e.g., Rezende et al., 1990; Chong et al., 2001). This approach is an oversimplification since it assumes that phytoplankton within estuaries or mangrove creeks has a $\delta^{13}C$ signature similar to that of marine phytoplankton. This is unlikely, however, since mangrove creeks and estuaries typically have $\delta^{13}C$ signatures for DIC which are distinctly depleted in ^{13}C by 6–8‰ (Fig. 5), with a clear gradient towards the marine environment (Fig. 6). Primary producers in the water column can therefore be expected to show a similar depletion in ^{13}C relative to DIC as those in open marine environments, where $\delta^{13}C_{DIC}$ is typically around 0‰, as described for seagrasses in Section 2.1. (see also Fig. 6). The cause of the ^{13}C-depletion in the DIC pool in the water column may be dilution by a freshwater source (e.g. in estuaries) and/or the inputs of DIC from mineralization in the water column or in the intertidal sediments, whereby the excess DIC shows a strongly negative $\delta^{13}C$ signature, similar to that of its source (e.g. Bouillon et al., 2007b).
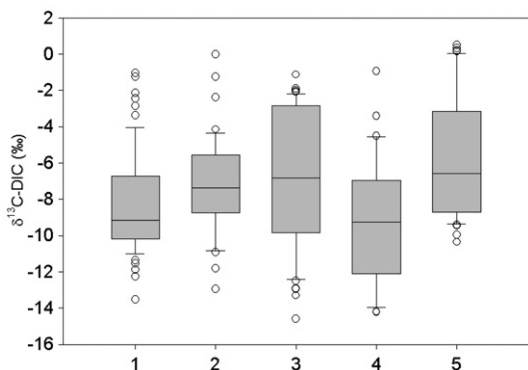
Fig. 5. Boxplot compilation of data on the $\delta^{13}C$ composition of dissolved inorganic carbon ($\delta^{13}C$−DIC) from a number of mangrove creeks. (1): Coringa Wildlife Sanctuary, India (Bouillon et al., 2003b and unpubl. data); (2): Tana delta, Kenya (Bouillon et al., 2007a); (3) mangrove creeks in Ca Mau, Vietnam (S. Bouillon and A.V. Borges, unpubl. data); (4) Gazi Bay, Kenya (Bouillon et al., 2007b); (5) Ras Dege, Tanzania (Bouillon et al., 2007c).

Although $\delta^{13}C$ alone is thus often not sufficient to unambiguously estimate the contribution of various sources to the POC pool, its potential is much enhanced when used in combination with other tracers such as POC/PN ratios (Hemminga et al., 1994; Cifuentes et al., 1996; Bouillon and Dehairs, 2000; Gonneea et al., 2004), $\delta^{15}N$ (e.g., Cifuentes et al., 1996), POC/Chl-a ratios (Cifuentes et al., 1996) or biochemical tracers such as lignin-derived phenols (Dittmar et al., 2001). Nevertheless, considering that a multitude of sources with different signatures may be present and that other tracers such as POC/PN ratios and $\delta^{15}N$ may change substantially during degradation and microbial rework-
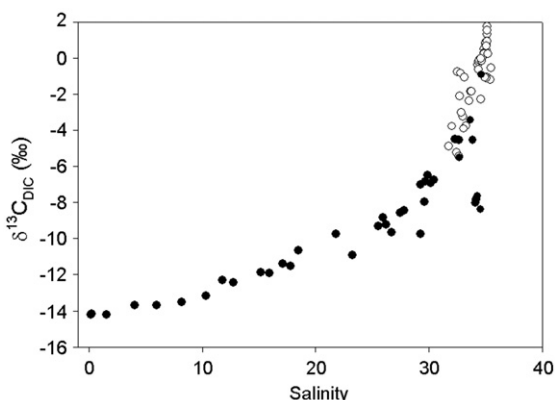
ing, the power of stable isotopes in delineating sources comes from being able to constrain the contribution of different sources (i.e. define upper and lower possible contributions), rather than enabling an exact quantification of the various inputs.

It has become clear that both local and imported sources can contribute to the sediment organic matter pool in intertidal mangrove sediments, and elemental and $\delta^{13}C$ data are generally consistent with a simple two-source mixing model whereby mangrove litter and suspended matter are taken as end-members (Bouillon et al., 2003a; see also Kristensen et al., submitted for publication ms). Riverine input of terrestrial carbon to mangrove systems is another aspect of carbon budgets yet to be adequately addressed. Recent results on the isotope composition of organic matter in mangrove systems with catchments supporting significant amounts of C4 vegetation highlight the potential importance of riverine-transported terrestrial material. In the Tana estuary and delta (northern Kenya), Bouillon et al. (2007a) found an important contribution of C4 material to riverine particulate and dissolved organic carbon (POC and DOC), as well as in intertidal sediments below the mangrove canopy. In contrast, porewater DOC from the same sampling locations had much more depleted $\delta^{13}C$ signatures reflecting a predominantly mangrove origin (Fig. 7). $\delta^{13}C$ data on bacterial markers from these samples (Bouillon and Boschker, 2006), however, indicate that bacteria derive their C from both C3 (i.e. mangrove) and C4 material in almost the same proportion as found in the sediment TOC pool. In the Betsiboka estuary (Madagascar), a similar high contribution of C4 material has been observed in both the water column POC and DOC, and in the intertidal
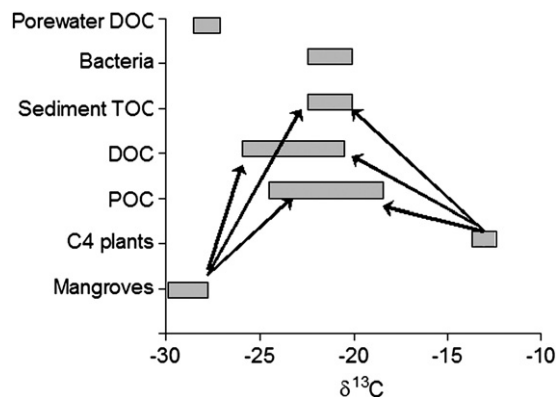

Fig. 6. Gradient of $\delta^{13}C_{DIC}$ along the salinity gradient in the Gazi Bay mangrove−seagrass ecosystem (data from Bouillon et al. (2007b)). Filled circles represents samples collected in the tidal mangrove creeks, open circles represent data from the seagrass beds.

Fig. 7. Range of $\delta^{13}C$ values found in different compartments in the Tana estuary and delta (data from Bouillon and Boschker (2006), Bouillon et al. (2007a)).

mangrove sediments (O. Ralison and S. Bouillon, unpubl. data). The importance of terrestrial matter from catchments dominated by C3 plants has not been revealed by C isotopes, since imported terrestrial material and local mangrove inputs are indistinguishable based on their δ^{13}C signatures. The highly efficient trapping of suspended matter in mangroves (e.g., Victor et al., 2004), and the evidence from C4 catchments, suggest that terrestrial material might also be an important C input in these systems, but complementary (molecular and isotopic) approaches will be needed to evaluate this. Dittmar et al. (2001), for example, used a combination of δ^{13}C and lignin-derived phenol signatures to estimate the contribution of terrestrial, marine, and mangrove-derived organic matter to the POC and DOC pool in a Brazilian mangrove estuary. Their data suggested high terrestrial contributions in the upper parts of the estuary, but a predominance of mangrove and marine organic matter in the creek water column. Another isotopic approach has been recommended by Raymond and Bauer (2001), who report that paired ^{14}C and ^{13}C measurements can potentially separate riverine and marine allochthonous sources of POC and DOC. Further development and application of such approaches in a range of systems will be required to obtain a more general view on the contribution and fate of different organic matter sources in mangrove systems. For example, recent data on the stable isotope composition of DOC in mangrove systems (see Bouillon et al., 2006, 2007c) indicate that the origin of DOC can be highly variable and quite distinct from that of POC. Given the high productivity of mangroves, their potential importance in the C budget of the coastal zone is high (Jennerjahn and Ittekkot, 2002; Dittmar et al., 2006), but our ability to quantify this role is currently limited.

In conclusion, the original focus on outwelling of mangrove carbon towards adjacent habitats has now been redirected, and recent results emphasize the role of imported organic matter in the intertidal zone (Bouillon et al., 2003a; Kennedy et al., 2004). This raises additional questions about the fate of the imported material, and a number of studies have already indicated that they contribute both to sustaining intertidal invertebrate communities (Bouillon et al., 2004c; Connolly et al., 2005) and to mineralization by sedimentary bacteria (Bouillon et al., 2004b, 2004d; Bouillon and Boschker, 2006). Stable isotopes are likely to play an important role in future studies of carbon sources and fluxes, but a number of alternative or complementary molecular approaches have recently been applied in mangrove systems: viz. lignin-derived phenols (Moran et al., 1991; Dittmar and Lara, 2001), carbohydrate composition (Marchand et al., 2005), amino acid and hexosamine profiles (Jennerjahn and Ittekkot, 1997), and biomarkers such as n-alkanes (Mead et al., 2005), triterpenols and sterols (Koch et al., 2003, 2005; Versteegh et al., 2004; Kim et al., 2005; Jaffé et al., 2006).

5. Fate of exported mangrove C: importance in adjacent foodwebs

Since the hypothesis that mangroves (partially) sustained aquatic foodwebs was first postulated, there have been numerous stable isotope studies (~ 40) of foodweb dynamics in and around mangroves. The original approach of Rodelli et al. (1984), of analysing carbon isotopes of consumers along a gradient from tidal mangrove creeks towards open marine waters, has been adopted in several later studies (e.g., Fleming et al., 1990; Newell et al., 1995; Lee, 2000; Chong et al., 2001; Bouillon et al., 2000, 2002b, 2004a). Rodelli et al. (1984) found a distinct gradient in consumer δ^{13}C values, with generally depleted δ^{13}C values in mangrove creek consumers, more enriched values offshore, and intermediate values in coastal inlets. End-members considered were mangroves (δ^{13}C ~ -27‰), marine phytoplankton (-22 to -20‰) and a variety of other algae (-22.5 to -14.8‰). Subsequent studies in other sites, however, detected only very limited contributions of mangrove carbon to offshore foodwebs (e.g., Loneragan et al., 1997; Lee, 2000; Macia, 2004).

Technical difficulties meant that these studies lacked measurements of phytoplankton δ^{13}C or δ^{13}C$_{DIC}$. As mentioned above, the gradient in consumer isotope values is likely to be confounded with an expected gradient in microalgal δ^{13}C from depleted in mangroves to enriched offshore, preventing these studies from quantifying mangrove contributions. In a study on the carbon sources for penaeid prawns, Chong et al. (2001), citing Hayase et al. (1999), actually provided some indirect evidence for the existence of ^{13}C-depleted phytoplankton in mangrove creeks. They noted that δ^{13}C values of total suspended organic matter showed a large spatial gradient between the mangrove creeks and the marine environment (-25.6 to -17.9‰, i.e. more than 8‰), whereas the estimated contribution of phytoplankton to the POC pool (based on Chl-a measurements) changed very little over the same gradient (from 17 to 25%), a discrepancy strongly indicating that phytoplankton in the creeks was significantly depleted in ^{13}C. The high estimate of

mangrove contribution to some species of penaeids by Chong et al. (2001) should therefore be reconsidered.

A number of approaches have been proposed to take the spatial variation in autotroph stable isotope signatures into account and to improve the utility of stable isotopes to assess the relative contribution of various sources. First, Fry and Smith (2002) proposed a mixing model to determine the relative contribution of mangroves and phytoplankton to filter-feeding barnacles along an estuarine gradient, and measured $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ of both mangroves and barnacles along the entire gradient. Since the resolving power of $\delta^{15}N$ is limited and $\delta^{13}C$ signatures of both primary sources overlap (i.e. along some parts of the gradient, $\delta^{13}C$ signatures for phytoplankton are expected to be similar), $\delta^{34}S$ was selected to calculate the contribution of both sources to the barnacle diet, based on a simple two-end mixing model. Although we commend their approach, Fry and Smith (2002) would have over-estimated mangrove contributions by not accounting for the higher S content in phytoplankton than mangroves (see Section 2.4.). Using indicative values of 1.05% and 0.31% for the S content of phytoplankton and mangroves (data from Ho et al. (2003) and Fry and Smith (2002), respectively), a re-evaluation of the data presented in Fry and Smith (2002) suggests that the estimated contribution by mangroves ranges between 9 and 17%, rather than between 30 and 58% as originally estimated. If such concentration effects can be taken into account, however, this sampling strategy offers a spatially-explicit approach to estimating the contribution of different sources along landscape gradients, and thus holds the potential to infer the effect of spatially varying environments on the resources that sustain faunal communities.

A second approach is to exploit the observed variation in stable isotope signatures of consumers and potential carbon sources rather than the absolute values. This approach assesses the degree of selectivity with which consumers exploit carbon sources, and eliminates the need for assumptions about isotope fractionation. Examples have been described in Bouillon et al. (2000, 2004a) to estimate the degree of selectivity of zooplankton and benthic invertebrates, respectively, based on the spatial and seasonal variations of $\delta^{13}C$ signatures of consumers, POC, and DIC. The approach has its own assumptions, most importantly that selectivity is similar either seasonally or spatially (see Bouillon et al., 2004a). Spatial analysis of variation in carbon and nitrogen isotopes has been further refined by Melville and Connolly (2003), who developed a two-element correlation test between consumer and source signatures, and

used it to indicate important sources for fish in a mangrove-lined bay.

Since most studies have potentially confounded a gradient in consumer $\delta^{13}C$ with a (usually unmeasured) gradient in phytoplankton $\delta^{13}C$, there is in our opinion currently no unambiguous evidence that mangrove carbon contributes substantially to faunal communities, either in tidal mangrove creeks or adjacent waters (see also Fry and Ewel, 2003). This does not imply that such a contribution is absent, but merely that existing data either suggest only a minimal role and a clear selectivity for alternative sources, or do not allow any unambiguous conclusions to be drawn. Future studies on these aspects are likely to benefit from careful sampling of all necessary components (i.e. including data on algal sources at varying spatial scales), and the incorporation of complementary tracers such as fatty acid markers (e.g., Alfaro et al., 2006; Hall et al., 2006).

Acknowledgements

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