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Fate of mangrove organic matter along a subtropical estuary: small-scale exportation and contribution to the food of crab communities

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ABSTRACT: The export of mangrove primary production to adjacent habitats has long been regarded as playing a significant role in estuarine food webs. In the Logan River Estuary, a subtropical estuary situated in the southern part of Moreton Bay in Queensland, Australia, we used the fatty acid markers approach to investigate this export and its contribution to the estuarine food web, compared to other sources. During summer and autumn of 2004, 4 stations were sampled along a salinity gradient. Surface sediment samples were collected, using pre-cut syringes, in the mangrove forest of each station and in the adjacent tidal flats. Individuals of dominant crab species were also collected from the mangrove forests. Seasonal differences in fatty acid compositions of the surface sediments within the mangrove forests and along the adjacent banks were recorded, indicating that organic matter inputs varied between summer and autumn. Results also showed that mangrove production was accumulated at the surface sediments in some parts of the estuary during autumn and consequently was not exported to the tidal flat. The fatty acid composition of crab species present in the mangrove showed obvious differences between the grapsid and the ocypodid crabs collected from the estuary. These differences most likely reflect the distinctive feeding strategies of the crab groups, although there was some indication of species-specific biosynthesis/accumulation of certain polyunsaturated fatty acids. The grapsid of this study, *Parasesarma erythodactyla*, in addition to being more dependent on mangrove leaves than the ocypodid crabs, is shown to potentially feed on fungal biomass.

KEY WORDS: Mangrove · Estuary · Fatty acids · Surface sediment · Ocypodid · Grapsid · Food web

INTRODUCTION

Mangroves are among the most important habitats in tropical and subtropical estuaries in terms of primary production (Alongi 1998). The exportation of this primary production to adjacent habitats as leaves, detritus and dissolved organic matter is one of the most important topics of interest to ecologists, as this production has long been regarded as playing a significant role in estuarine and coastal food webs (Odum & Heald 1975, Twilley 1988). The contribution of mangrove production to coastal food webs varies, however, with the diversity and the physical structure of the mangrove forest (Chong et al. 1990, Vance et al. 1996, Nagelkerken & van der Velde 2004) as well as with the tidal activity (Twilley 1985). Moreover, results from several recent studies suggest a weaker direct trophic role for mangroves in nearshore environments (e.g. Meziane & Tsuchiya 2000, Lee 2004). For instance, Lee (2004) suggests in a comprehensive study that prawn catch in tropical nearshore environments is strongly influenced by the extent of intertidal areas and organic matter availability as represented by tidal amplitude, rather than relative mangrove abundance. In addition, within the mangrove forests, a large proportion of the leaf-litter, as has been shown in some tropical Aus-

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tralian mangroves, is not exported but recycled by resident crabs (Robertson & Daniel 1989, Robertson et al. 1992) with little chance of this organic matter being transported significantly towards adjacent habitats through these organisms. Indeed, Guest et al. (2004) showed, using stable ($\delta^{13}C$) isotope signature of crabs as an indicator of carbon source, that carbon movement between 2 adjacent habitats (mangroves and salt marshes) in a subtropical estuary was spatially restricted to a scale of several metres (<30 m). However, in the Indo-Pacific region, many organisms migrate into inundated mangroves at high tide to feed (Nagelkerken & Van der velde 2004) and, therefore, a substantial part of the mangrove productivity sequestered by herbivorous crabs might be exported from mangrove ecosystems as a result of tidal migration of predatory fish feeding on these crabs (Sheaves & Molony 2000). Nevertheless, the scale of this transfer of mangrove production cannot be estimated without a full understanding of the diet of the invertebrates living in the mangrove ecosystem.

Feeding habits and the position each crab species occupies in the food web are of great importance to understanding the ecology of mangroves (Dahdouh-Guebas et al. 1999). Ocypodid and grapsid crabs are the predominant organisms of the macrofauna in many mangrove ecosystems (Crane 1975, Macintosh 1988). The ocypodid crabs, with wider habitat preferences than those of the grapsids (which are usually limited to vegetated areas), are thought to be deposit-feeders and therefore rely more on sediment microorganisms for their nutritional needs (Dye & Lasiak 1986, Meziane et al. 2002). However, these opportunistic species have also been reported to supplement their diets by ingesting vascular plants detritus and macroalgae (Meziane & Tsuchiya 2000, 2002, Hsieh et al. 2002). Grapsid crabs from mangrove habitats have been described as being either grazers or shredder-detritivores dependent on mangrove biomass (Lee 1998). However, recent studies suggest more varied feeding strategies of sesarmid crabs (e.g. *Parasesarma erythodactyla*) that include scraping surface sediment (Skov & Hartwell 2002, Guest et al. 2004). The feeding activity of crabs is affected by seasonal change and consequently may influence the fate of the organic matter differently throughout the year (Mia et al. 2001). Therefore, at the time of low crab activity, most litter is decomposed by microbial action or is transported by tides to adjacent habitats. On this basis, a higher percentage of the litter produced in the mangrove during winter may be available for export than at other times of the year (Mfilinge et al. 2005).

The approach of using fatty acid as biomarkers has been successfully employed in the last few decades to discriminate between various types of organic matter sources in marine ecosystems, by investigating their potential contributions to sediment organic matter pools (Volkman et al. 1980, Budge & Parrish 1998, Meziane & Tsuchiya 2002) and by following their fate in the food web (Meziane et al. 1997, Howell et al. 2003). The current frequent use of this approach to diverse marine habitats and organisms has enabled the establishment of a reliable list of fatty acid markers, although the assignment of identified biomarkers to original sources can sometimes be ambiguous because of multiple potential sources (Cook et al. 2004). This ambiguity, however, can to a large extent be remedied by taking advantage, in the sampling strategy, of seasonal and spatial changes in fatty acid 'signals' (Meziane & Tsuchiya 2000). Ecological interpretation of the fatty acid compositions of sediment samples and macroinvertebrates can be considered at 2 levels. Firstly, using the entire profile of fatty acids as a fingerprint (Bossio & Scow 1998) and, secondly, focusing on particular compounds that can be traced to a specific food source in order to estimate its contribution to the diet (Meziane & Tsuchiya 2000, Cook et al. 2004).

The aims of the present study, using the fatty acid biomarkers approach, were as follows: (1) to identify seasonal changes in the composition of mangrove forests' sediment and in their adjacent intertidal flat in order to assess the scale of mangrove organic matter exportation along an estuary; (2) to assess the contribution of the mangrove organic matter in the diet of the dominant crab species; and (3) to identify other sources contributing to the organic matter pool in the sediments of the mangrove forest and the adjacent tidal flats as well as to the diet of the dominant crabs.

MATERIALS AND METHODS

Study site and sampling strategy. The estuary of Logan River (27° 45' S, 153° 25' E; Fig. 1) is situated ~40 km southeast of Brisbane (Queensland, Australia). The Logan River Estuary (LRE) forms part of southern Moreton Bay, an enclosed water body with direct communication with the Coral Sea at only a few locations. The study area ranged from the passage of Jumpinpin to about 10 km westward, with the river running off in the southern part of the Moreton Bay, where it is sheltered from the Pacific Ocean by the sandy North and South Stradbrooke Islands. The mangrove forest is well developed along the shore and dominated by *Avicennia marina* (Forsk.). Other species present in the estuary are *Aegiceras corniculatum*, *Bruguiera gymnorrhiza*, *Rhizophora stylosa* and *Ceriops australis*. The annual mean air temperature is 22.9°C, the highest monthly mean occurs in January (30.5°C), and the

lowest in July (13.1°C). The precipitation peaks at a mean of 188 mm mo^{-1} during the rainy season (December to February) and is at its lowest during spring (50 mm mo^{-1}; September to November).

We selected 4 sampling stations in the estuary, along a salinity gradient. Each station, accessible only by small boats, was chosen to be in a riverine mangrove area adjacent to a tidal flat. Stn 1 has a much narrower tidal flat compared to the other stations. From the most 'upstream' station to Jumpinpin, salinity during low tide varied from 27 to 31‰ in summer and from 31 to 34‰ in autumn. The mangrove forest structure consists mainly of mixed trees of the 5 species mentioned above. *Avicennia marina* is the dominant species in every station.

The sampling of surface sediments and crabs species was carried out on 2 occasions: during summer (January) and autumn (April) of 2004. In the mangrove forest (Mangrove Sites: MS), surface sediment was sampled at Stns 1, 2, 3 and 4. At Stn 1, because of the absence of a distinctive tidal flat, sediment samples were collected within the forest but on the border of the narrow bank.

Stn 2 was not sampled in summer as this station was added during the autumnal sampling. An additional and similar sampling was done at the surface sediment of the adjacent intertidal flat at Stns 2 (autumn only), 3 and 4 (Intertidal Sites: IS). At each station, 3 replicates of surface sediment were collected using pre-cut syringes (internal diameter of 1.8 cm, 1 cm depth) after being randomly selected inside a 1 m^2 quadrate positioned within the sites. Distance between MS and IS varied between 10 (Stn 2) and 15 m (Stns 3 and 4).

We collected 3 individuals from all 6 crab species along the estuary. Ocypodid species were selected based on their dominance in the sampled station (see Table 1), established by surveying their activities at low tide. At Stn 1, *Uca vocans* were collected in summer and autumn in MS. In autumn, *Australoplax tridentata* was also collected at Stn 1 within the mangrove (MS). At Stn 2, individuals of *Uca bellator minima* were collected in MS only. At Stns 3 and 4 *Australoplax tridentata* was found in abundance and collected in both seasons. In summer *Heloecius cordiformis* was also collected at Stns 3 and 4. However, because of a sharp decrease in abundances observed in autumn, this species was not sampled during this season. In addition to these ocypodid crabs collected within the mangrove, the grapsid *Parasesarma erythodactyla* was sampled at Stn 4, in autumn where it was especially abundant

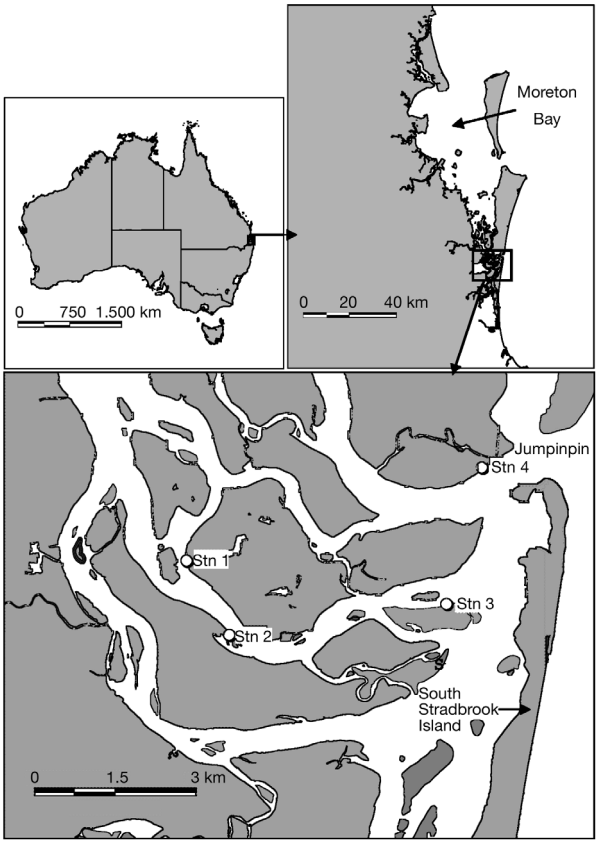

Fig. 1. Moreton Bay and the location of the study sites in the Logan River Estuary (LRE)

(Table 1). In summer, no individuals were collected at the intertidal site of Stn 2. All the surface sediment samples and the crab individuals were stored at –20°C until lipid analysis, which occurred within a couple of weeks.

Fatty acid analysis. The full volume of surface sediment contained in the sampling syringes (n = 3) and the hepatopancreas tissues of the crabs were used for the lipid analysis. The hepatopancreas, which is full of

Table 1. Crab species sampled at the 4 stations in the Logan River Estuary (LRE) in January (summer) and April (autumn) 2004. Short forms of species names are given in parentheses. –: no data

Stn	Summer	Autumn
1	*Uca vocans* (Uv)	*Uca vocans* (Uv) *Australoplax tridentata* (At)
2	–	*Uca bellator minima* (Ub)
3	*Heloecius cordiformis* (Hc) *Australoplax tridentata* (At)	*Parasesarma erythodactyla* (Pe) *Australoplax tridentata* (At)
4	*Heloecius cordiformis* (Hc) *Australoplax tridentata* (At)	*Australoplax tridentata* (At)

Table 2. Fatty acid (FA) composition (% of total FAs) of surface sediments sampled in January (summer) and April (autumn) 2004 at the 4 stations in the intertidal sites (IS) and mangrove sites (MS) along the LRE. Values are mean ± SD. n.i.: not identified; LCFAs: long chain fatty acids

FA	Summer					Autumn						
	Stn 1-MS	Stn 3-IS	Stn 3-MS	Stn 4-IS	Stn 4-MS	Stn 1-MS	Stn 2-IS	Stn 2-MS	Stn 3-IS	Stn3-MS	Stn 4-IS	Stn 4-MS
Saturated												
12:0	0.6 ± 0.6	0.7 ± 0.4	0.3 ± 0.3	0.1 ± 0.3	0.4 ± 0.4	0.9 ± 0.5	0.7 ± 0.7	0.4 ± 0.4	0.4 ± 0.1	0.6 ± 0.3	1.1 ± 0.8	1.3 ± 0.8
13:0	0.8 ± 0.4	1.6 ± 1.7	0.3 ± 0.3	0.2 ± 0.3	0.3 ± 0.3	1.2 ± 0.2	1.4 ± 0.8	0.6 ± 0.2	1.3 ± 0.7	1.7 ± 0.2	1.9 ± 0.9	2.2 ± 1.0
14:0	4.7 ± 0.6	3.1 ± 1.7	3.9 ± 0.6	4.2 ± 0.8	3.6 ± 1.5	6.0 ± 0.2	3.6 ± 0.0	5.0 ± 0.8	3.0 ± 0.8	3.7 ± 2.1	6.8 ± 2.1	5.3 ± 1.9
15:0	2.6 ± 1.3	1.9 ± 1.5	3.8 ± 0.3	3.0 ± 0.9	3.3 ± 1.5	6.7 ± 0.3	4.3 ± 1.2	3.7 ± 1.9	2.5 ± 1.0	5.1 ± 3.5	0.9 ± 0.2	2.8 ± 0.3
16:0	30.3 ± 3.5	30.1 ± 3.3	26.4 ± 3.3	27.3 ± 2.4	24.7 ± 3.3	24.0 ± 1.2	26.3 ± 1.2	26.0 ± 2.5	26.4 ± 2.2	23.7 ± 2.1	35.3 ± 1.04	22.4 ± 1.9
17:0	0.0 ± 0.0	0.7 ± 0.4	1.3 ± 0.1	1.1 ± 0.1	1.2 ± 0.6	2.2 ± 0.1	1.8 ± 0.4	1.6 ± 0.6	1.4 ± 0.3	1.6 ± 0.5	0.3 ± 0.3	0.9 ± 0.1
18:0	5.2 ± 0.8	6.0 ± 0.5	3.9 ± 1.6	3.7 ± 0.8	6.2 ± 2.3	3.3 ± 0.2	7.3 ± 0.4	4.4 ± 1.0	7.8 ± 2.1	8.7 ± 4.7	4.3 ± 0.4	6.4 ± 3.2
20:0	0.2 ± 0.3	0.3 ± 0.2	0.3 ± 0.2	0.2 ± 0.2	0.7 ± 0.3	0.3 ± 0.2	0.4 ± 0.3	0.5 ± 0.4	0.6 ± 0.2	0.9 ± 0.2	1.5 ± 0.4	0.8 ± 0.2
22:0	0.4 ± 0.7	0.9 ± 1.1	1.3 ± 0.0	1.0 ± 0.4	1.8 ± 1.2	1.4 ± 0.1	1.0 ± 0.7	1.5 ± 0.5	1.4 ± 0.7	1.7 ± 0.2	1.8 ± 0.4	2.4 ± 0.8
24:0	2.0 ± 0.8	1.7 ± 0.7	2.3 ± 0.6	4.0 ± 1.6	4.4 ± 2.9	3.2 ± 1.7	1.7 ± 0.5	2.3 ± 1.5	1.4 ± 0.5	7.9 ± 3.2	0.7 ± 0.2	8.8 ± 3.1
26:0	0.7 ± 0.7	0.3 ± 0.3	0.8 ± 0.6	1.0 ± 1.0	1.2 ± 1.1	1.0 ± 0.9	0.2 ± 0.3	0.5 ± 0.4	0.0 ± 0.0	0.9 ± 0.3	0.0 ± 0.0	3.4 ± 1.5
28:0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.9	0.1 ± 0.2	0.4 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0. ± 00.0	0.0 ± 0.0
Sum%	47.3 ± 2.3	47.3 ± 2.7	44.9 ± 2.5	45.9 ± 1.7	48.1 ± 5.7	50.3 ± 4.3	48.7 ± 2.3	46.6 ± 2.7	46.3 ± 2.3	56.6 ± 2.1	54.7 ± 2.7	56.7 ± 0.8
Branched												
15:0 iso	0.7 ± 0.4	0.3 ± 0.4	0.8 ± 0.3	0.5 ± 0.6	1.2 ± 0.7	1.6 ± 0.3	1.0 ± 0.0	0.9 ± 0.2	0.6 ± 0.7	1.2 ± 0.9	0.0 ± 0.0	1.1 ± 0.2
17:0 iso	0.7 ± 0.3	0.3 ± 0.2	0.3 ± 0.2	0.7 ± 0.2	0.4 ± 0.3	0.4 ± 0.3	0.7 ± 0.1	0.9 ± 0.1	0.5 ± 0.0	0.4 ± 0.3	0.5 ± 0.3	0.2 ± 0.2
17:0 ant	0.7 ± 0.3	0.9 ± 0.3	0.9 ± 0.1	0.8 ± 0.1	1.1 ± 0.5	0.9 ± 0.6	1.4 ± 0.2	1.2 ± 0.0	1.3 ± 0.2	1.7 ± 0.4	0.7 ± 0.1	1.3 ± 0.2
Sum%	2.1 ± 0.7	1.5 ± 0.8	2.0 ± 0.1	1.9 ± 0.4	2.7 ± 1.3	2.9 ± 0.9	3.1 ± 0.1	3.0 ± 0.1	1.8 ± 0.1	3.3 ± 0.8	1.2 ± 0.3	2.5 ± 0.5
Monounsaturated												
14:1	1.1 ± 0.5	0.9 ± 0.5	1.2 ± 0.6	0.7 ± 0.6	1.1 ± 0.8	1.3 ± 0.9	1.4 ± 0.1	1.5 ± 0.2	0.9 ± 0.4	1.3 ± 0.9	0.2 ± 0.2	1.8 ± 0.1
15:1	0.3 ± 0.3	0.3 ± 0.2	0.6 ± 0.3	0.1 ± 0.2	0.2 ± 0.3	0.5 ± 0.4	0.7 ± 0.1	0.6 ± 0.1	0.2 ± 0.3	1.1 ± 0.4	0.1 ± 0.2	0.7 ± 0.0
16:1ω7	26.0 ± 5.3	26.8 ± 4.1	26.2 ± 4.2	27.3 ± 1.6	21.7 ± 0.5	20.6 ± 1.5	19.4 ± 1.4	17.8 ± 1.6	23.8 ± 2.9	13.4 ± 2.4	22.8 ± 1.4	14.6 ± 1.7
16:1ω9	0.8 ± 0.1	0.6 ± 0.1	2.1 ± 2.2	1.1 ± 0.8	2.1 ± 1.6	1.2 ± 0.1	1.4 ± 0.1	1.5 ± 0.6	0.9 ± 0.5	2.0 ± 1.3	0.4 ± 0.0	2.5 ± 0.2
16:1	0.4 ± 0.4	0.5 ± 0.4	0.8 ± 0.3	0.7 ± 0.2	0.4 ± 0.5	0.9 ± 0.3	1.1 ± 0.1	1.1 ± 0.1	0.5 ± 0.1	0.6 ± 0.8	0.3 ± 0.2	0.7 ± 0.0
18:1ω9	7.7 ± 1.2	7.5 ± 0.8	5.0 ± 2.0	6.6 ± 3.0	5.5 ± 1.8	4.4 ± 0.2	4.6 ± 0.6	4.1 ± 0.7	5.0 ± 2.0	5.1 ± 1.7	3.0 ± 0.3	4.8 ± 1.4
18:1ω7	2.5 ± 0.2	2.3 ± 0.5	2.6 ± 0.6	2.4 ± 0.4	2.7 ± 0.6	2.6 ± 0.3	2.9 ± 0.6	2.9 ± 0.2	2.6 ± 0.7	2.9 ± 0.4	1.7 ± 0.2	2.6 ± 0.4
22:1	0.4 ± 0.4	0.1 ± 0.2	0.1 ± 0.2	0.2 ± 0.2	0.4 ± 0.7	0.0 ± 0.0	0.2 ± 0.3	0.3 ± 0.2	0.4 ± 0.0	0.3 ± 0.5	0.0 ± 0.0	0.1 ± 0.1
24:1	0.3 ± 0.3	0.6 ± 0.4	1.2 ± 0.8	0.7 ± 0.6	1.1 ± 0.8	1.6 ± 0.2	0.9 ± 0.2	0.4 ± 0.4	0.9 ± 0.4	0.3 ± 0.4	0.3 ± 0.2	1.7 ± 1.4
Sum%	39.6 ± 3.8	39.7 ± 3.0	39.8 ± 1.0	39.6 ± 3.2	35.2 ± 2.8	33.2 ± 0.5	32.6 ± 2.3	30.2 ± 0.7	34.5 ± 0.2	27.0 ± 1.2	28.8 ± 2.1	29.4 ± 2.1
Polyunsaturated												
16:2	0.7 ± 0.3	0.6 ± 0.1	0.8 ± 0.2	1.3 ± 0.5	1.0 ± 0.4	1.2 ± 0.3	1.1 ± 0.1	1.3 ± 0.5	1.2 ± 0.2	0.6 ± 0.2	1.2 ± 0.6	0.1 ± 0.2
18:2ω6	1.5 ± 0.2	1.6 ± 0.3	1.3 ± 0.2	1.6 ± 0.3	1.2 ± 0.3	1.2 ± 0.1	1.2 ± 0.3	1.7 ± 0.4	1.2 ± 0.2	1.5 ± 0.2	1.0 ± 0.1	1.5 ± 0.4
18:3ω6	0.9 ± 0.6	0.3 ± 0.2	0.4 ± 0.1	0.6 ± 0.1	0.4 ± 0.3	0.2 ± 0.2	0.2 ± 0.2	0.4 ± 0.1	0.5 ± 0.1	0.8 ± 0.4	0.5 ± 0.4	0.0 ± 0.0
18:3ω3	0.6 ± 0.1	0.7 ± 0.6	1.3 ± 0.4	0.8 ± 0.6	0.9 ± 0.6	0.5 ± 0.3	0.5 ± 0.7	1.8 ± 0.6	0.5 ± 0.4	0.9 ± 0.5	0.2 ± 0.2	1.4 ± 0.4
20:3ω6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 0.7	0.0 ± 0.0
20:2	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.3	0.1 ± 0.2
20:4ω6	2.6 ± 0.6	2.1 ± 0.8	3.1 ± 0.9	2.9 ± 0.4	3.3 ± 0.9	3.0 ± 0.4	2.9 ± 0.6	3.3 ± 0.1	3.1 ± 0.4	1.6 ± 0.8	1.6 ± 0.7	1.7 ± 0.0
20:5ω3	3.3 ± 0.6	3.1 ± 0.5	3.6 ± 1.0	4.7 ± 2.5	4.4 ± 1.4	4.6 ± 1.6	4.7 ± 1.2	5.6 ± 0.4	4.5 ± 1.2	4.1 ± 4.4	4.5 ± 1.2	1.4 ± 0.6
22:6ω3	0.1 ± 0.2	0.2 ± 0.3	0.1 ± 0.2	0.2 ± 0.3	0.4 ± 0.4	0.3 ± 0.4	0.2 ± 0.3	0.9 ± 0.1	0.1 ± 0.2	0.0 ± 0.0	1.2 ± 0.9	0.0 ± 0.0
Sum%	9.7 ± 1.9	8.7 ± 0.9	10.7 ± 2.1	12.2 ± 3.5	11.6 ± 2.3	11.0 ± 3.2	10.8 ± 3.2	15.1 ± 1.4	10.9 ± 2.1	9.5 ± 4.4	11.3 ± 1.0	6.3 ± 0.7
Sum n.i. %	1.3 ± 1.1	2.8 ± 1.4	2.5 ± 2.4	0.5 ± 0.4	3.1 ± 2.8	2.9 ± 2.2	4.9 ± 5.0	5.2 ± 3.0	5.0 ± 0.8	1.2 ± 1.2	4.0 ± 2.6	5.1 ± 0.9
Total%	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
18:2ω+ +18:3ω3	62.0 ± 0.2	2.3 ± 0.8	2.6 ± 0.4	2.4 ± 0.4	2.1 ± 0.6	1.6 ± 0.4	1.7 ± 1.1	3.4 ± 1.3	1.6 ± 0.2	2.4 ± 0.9	1.2 ± 0.4	2.9 ± 0.8
16:ω7/ 16:0	0.9 ± 0.1	0.9 ± 0.1	1.0 ± 0.2	1.0 ± 0.1	0.9 ± 0.1	0.9 ± 0.1	0.7 ± 0.0	0.7 ± 0.1	0.9 ± 0.1	0.7 ± 0.1	0.7 ± 0.3	0.7 ± 0.1
LCFAs	2.6 ± 1.5	2.0 ± 0.9	3.6 ± 2.1	5.1 ± 2.2	6.0 ± 3.7	4.2 ± 3.0	1.9 ± 0.9	2.8 ± 2.3	1.4 ± 0.7	8.9 ± 5.2	0.7 ± 0.0	12.2 ± 5.6

lipid reserve may fill much of the body cavity of crabs (Burggren & McMahon 1988), as is the case in the species of this study, and the fatty acids' (FAs) composition is directly affected by diet, which is not the case in other tissues such as gills and muscles (Styrishave et al. 2000). Hepatopancreas tissues will be hereafter be referred to as 'tissues'.

Samples were processed following a slightly modified version of Bligh & Dyer (1959). Lipids were extracted by homogenization for 2 min followed by ultrasonication for 20 min with a mixture of distilled water:methanol:chloroform (1:2:1, 20 cm^3, v:v:v). The addition of distilled water:chloroform mixture (5:5 cm^3, v:v) formed an aqueous-organic 2-layer

system. The lipids migrated into the lower chloroform phase and separation was enhanced by centrifugation (2000 rpm, 650 × *g*). The filtrate was concentrated by rotary evaporation and made up to 2 ml. These lipid extracts were dried under nitrogen and then saponified under reflux (2 h, 100°C) with a 2 mol dm^{-3} NaOH solution in methanol and distilled water (2:1, v:v). Saponification and methylation were carried out according to Meziane et al. (2002) in order to obtain total FAs. FA methyl esters (FAMEs) were purified by high performance thin-layer chromatography technique (HPTLC) using plates coated with silicagel. The developing solvent was a mixture of hexane/diethyl ether/acetic acid (8:2:0.1). Bands containing FAMEs were scraped and collected in a mixture of chloroform/methanol (2:1, v/v) at 40°C for 60 min. FAMEs were then isolated in the same solution until analysis by gas chromatography.

The FAMEs were separated and quantified by gas chromatography (Varian, 3800) equipped with a flame ionization detector. Separation was performed with a Supelco OMEGAWAX capillary column (30 m × 0.32 mm internal diameter, 0.25 µm film thickness) with hydrogen as carrier gas. After injection at 60°C, the oven temperature was raised to 150°C at a rate of 40°C min^{-1}, then to 240°C at 3°C min^{-1}, and finally held constant for 30 min. Flame ionization was held at 240°C. Most FAMEs peaks were identified by comparing their retention times with those of authentic standards (Supelco). For some samples, peaks of FAs were identified with gas chromatograph (GC)-mass spectrometry. The analytical precision for samples was generally <5% for major components of FAMEs.

FAs are designated as X:YωZ, where X is the number of carbon atoms, Y is the number of double bonds and Z is the position of the ultimate double bond from the terminal methyl group.

Data analysis. The software PRIMER was used for multivariate analysis (Clarke & Warwick 2001). The data matrices (composition of FAs of sediments samples or crab species) were used to create triangular similarity matrices, based on the Bray-Curtis similarity coefficient, followed by non-metric multidimensional scaling (MDS). No transformation was performed on the data. Using the same triangular matrices, cluster analyses were also performed. Differences between stations or crab species were tested using a 1-way analysis of similarity (ANOSIM). The test statistic was computed under 5000 permutations. Unidentified FAs were not used in these analyses.

Student's *t*-tests and 1-way analysis of variance (ANOVA) were used to test for differences in the percentage of individual FAs or a group of FAs between surface sediment and crab samples. Probabilities (p) of <0.05 were considered to be significant.

RESULTS

FAs in surface sediment

The FA composition of surface sediments sampled is summarised in Table 2. A statistically significant difference was found between the profiles of FAs of the samples collected in summer and those collected in autumn (ANOSIM, R = 0.119, $p < 0.01$). A similar analysis on the effect of site also showed a significant difference between MS and IS (ANOSIM, R = 0.14, $p < 0.001$). These seasonal and type of site groups are also well identified in the MDS analysis despite some overlapping (Fig. 2).

Hierarchical cluster analysis of the total identified FAs of the sediment samples separated the LRE sites into 3 groups at the 80% similarity level (Fig. 3). Cluster I separated the samples collected in autumn at MS3 and MS4 from other samples at the 74% similarity level. Cluster II separated surface sediments of IS4

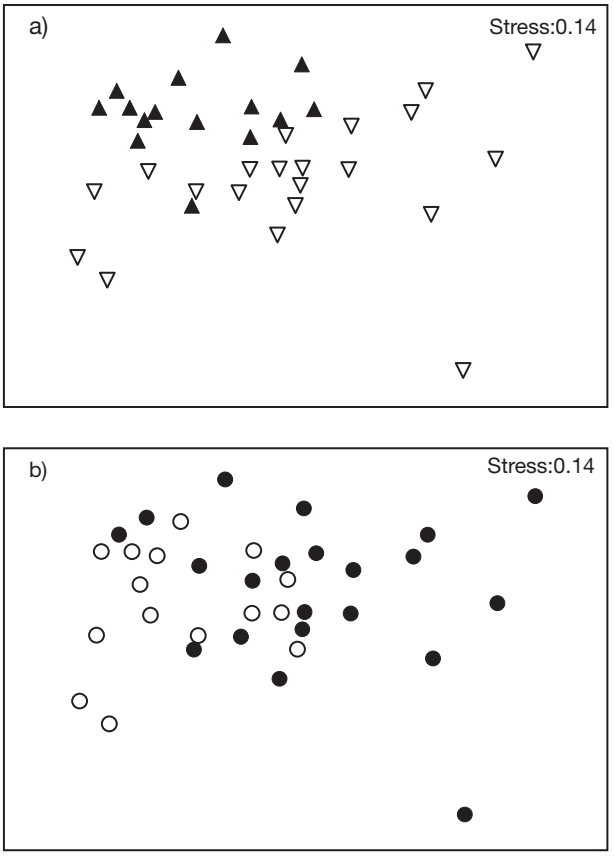

Fig. 2. MDS ordination of Bray-Curtis similarities for each sediment sample collected at study sites (IS and MS) along the LRE in January and April 2004. (a) The MDS with superimposed symbols for the season (summer: ▲; autumn: ▽) and (b) the same MDS but with superimposed symbols for sampling sites (MS: ●; IS: ○)

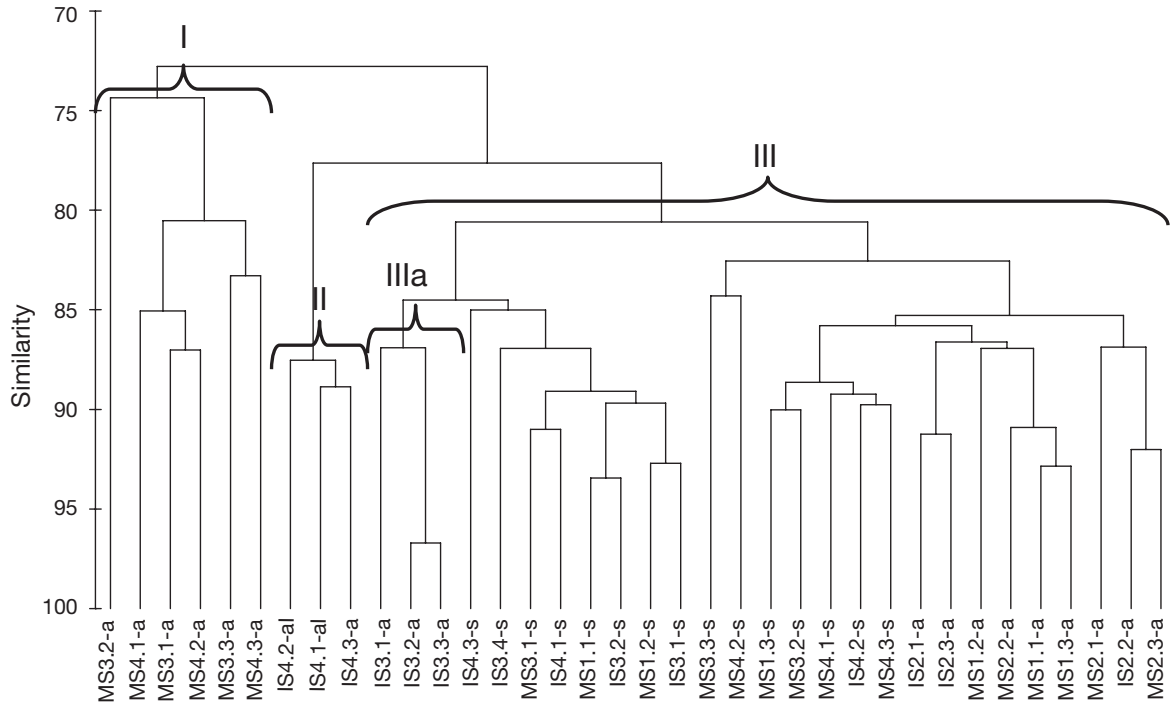

Fig. 3. Classification of surface sediment samples collected at study sites (IS and MS) along the LRE in January and April 2004. The label of each sample consists of 3 codes. The first code is the site (IS and MS); the second code is the replicate number; the final code is the season (s: summer; a: autumn)

sampled in autumn at the 77% of similarity. Within Cluster III, made up with all the rest of surface sediment samples, the samples collected in autumn from IS3 are well distinguished (IIIa).

About 35 individual FAs were originally identified in the surface sediment samples. At all stations, independent of the seasons, the ubiquitous 16:0 (24.9 ± 3.2 to 32.0 ± 6.4% of total FAs) and the monounsaturated 16:1ω7 (14.6 ± 2.5 to 26.7 ± 4.6% of total FAs) were the 2 most abundant FAs in the surface sediment samples. The monounsaturated 18:1ω9 is third in importance, with percentage values ranging between 3.0 ± 0.3 and 7.7 ± 1.2%.

The markers of bacteria, the vaccenic acid (18:1ω7) and the sum of branched 15:0 and 17:0 (iso and anteiso) FAs, were detected in all stations and with their contribution to the total of FAs between 1.7 ± 0.3 and 2.9 ± 0.8% (18:1ω7) and between 1.2 ± 0.3 and 3.3 ± 0.8% (branched 15:0+17:0). Seasonal comparison shows, independently of stations, that contributions of branched 15:0+17:0 were significantly higher in surface sediment collected in autumn than those collected in summer (*t*-test; $p < 0.006$) whereas there was no significant difference in the contribution of 18:1ω7 (*t*-test; $p > 0.05$). However, in each season, both groups of bacterial markers were not significantly different when analysed according to the type of sites (*t*-test; $p > 0.05$).

The eicosapentaenoic acid (20:5ω3), a marker of diatoms, was detected in each station and in both seasons. Its relative contribution was between 1.8 ± 0.8 and 5.6 ± 4.6% of total FAs. No clear trend could be observed along the estuary transect. Indeed, seasonal comparisons of sites showed no significant differences on the contribution of this FA in the sediment samples (*t*-tests, $p > 0.05$). However, the values of the ratio 16:1ω7/16:0, also an indicator of microalgal input, were higher in sediment samples collected in summer than those collected in autumn (*t*-test; $p < 0.001$).

The long chain FAs (LCFAs, >24:0), typical markers of mangroves (vascular plants) in an estuarine ecosystem, were detected in all sediment samples in both seasons. A seasonal comparison of the relative contribution of these markers in surface sediment shows no statistical difference (*t*-test; $p > 0.05$). Nevertheless, irrespective of the season, a significant difference was found for these compounds when comparing LCFAs of sediment samples collected in IS to those collected in MS (ANOVA, $p < 0.03$). Direct comparison of mangrove and intertidal sites at each station was only possible at Stns 3 and 4 (both seasons) and Stn 2 (autumn only) and significant differences between the sites were recorded only at Stns 3 and 4 in autumn (*t*-test; $p < 0.03$).

Table 3. FA composition (% of total FAs) of crab hepatopancreas sampled in January (summer) and April (autumn) 2004 at the 4 stations along the LRE. Values are means± SD. Uv, Hc, At, Ub, Pe: see Table 1 for full species' name

FA	Summer					Autumn					
	Uv- Stn 1	Hc-Stn 3	At-Stn 3	Hc-Stn 4	At-Stn 4	Uv-Stn 1	At-Stn 1	Ub-Stn 2	Pe-Stn3	At-Stn 3	At-Stn 4
Saturated											
14:0	3.9 ± 0.3	2.9 ± 0.4	3.6 ± 0.6	2.6 ± 0.8	4.7 ± 1.4	2.7 ± 1.5	3.5 ± 0.9	5.4 ± 0.9	2.9 ± 0.7	4.1 ± 1.8	3.5 ± 0.5
15:0	1.2 ± 0.4	1.7 ± 0.4	1.8 ± 0.2	1.3 ± 0.4	2.2 ± 0.2	1.9 ± 0.9	1.2 ± 0.2	2.0 ± 0.6	1.1 ± 0.3	2.2 ± 0.6	2.2 ± 0.9
16:0	32.6 ± 1.6	29.9 ± 1.6	31.3 ± 3.1	31.6 ± 2.2	31.4 ± 2.0	21.4 ± 2.5	28.8 ± 3.2	28.1 ± 2.2	17.6 ± 3.7	30.0 ± 3.7	28.3 ± 3.1
17:0	4.0 ± 0.4	2.8 ± 1.0	3.4 ± 0.1	4.2 ± 1.7	1.5 ± 0.6	2.3 ± 0.7	3.8 ± 2.8	4.2 ± 2.7	0.9 ± 0.1	2.2 ± 0.4	2.5 ± 0.2
18:0	7.1 ± 0.9	3.6 ± 1.1	4.9 ± 0.8	4.4 ± 0.9	4.6 ± 1.6	6.3 ± 2.4	7.3 ± 1.5	4.2 ± 1.7	9.9 ± 2.2	6.5 ± 1.1	5.0 ± 1.5
20:0	0.5 ± 0.2	0.3 ± 0.2	0.3 ± 0.2	0.2 ± 0.2	0.0 ± 0.0	0.7 ± 0.2	0.6 ± 0.2	0.6 ± 0.2	1.0 ± 0.6	0.4 ± 0.1	0.5 ± 0.1
22:0	0.6 ± 0.4	0.6 ± 0.2	0.5 ± 0.1	0.6 ± 0.3	0.6 ± 0.3	0.9 ± 0.1	1.0 ± 0.7	0.9 ± 0.3	1.4 ± 0.4	0.6 ± 0.1	0.7 ± 0.2
24:0	0.5 ± 0.1	0.0 ± 0.0	0.2 ± 0.2	0.4 ± 0.2	0.0 ± 0.0	0.1 ± 0.2	0.4 ± 0.3	0.4 ± 0.3	0.3 ± 0.2	0.0 ± 0.0	0.1 ± 0.2
Sum%	50.3 ± 2.2	41.7 ± 2.5	46.1 ± 3.2	45.4 ± 2.7	45.2 ± 1.7	36.3 ± 1.7	46.6 ± 6.6	45.8 ± 4.3	35.3 ± 2.3	46.1 ± 4.9	42.7 ± 1.5
Branched											
15:0 iso	0.7 ± 0.3	0.8 ± 0.2	1.1 ± 0.3	0.5 ± 0.2	0.8 ± 0.2	0.12 ± 0.2	0.0 ± 0.0	0.2 ± 0.3	0.0 ± 0.0	0.6 ± 0.2	1.1 ± 0.6
15:0 ant	0.4 ± 0.3	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.6
17:0 iso	0.4 ± 0.3	0.4 ± 0.4	1.1 ± 0.6	0.5 ± 0.2	0.4 ± 0.3	0.7 ± 0.1	0.1 ± 0.2	1.3 ± 0.7	0.0 ± 0.0	0.9 ± 0.3	0.6 ± 0.2
17:0 ant	0.5 ± 0.1	0.3 ± 0.3	0.5 ± 0.4	0.4 ± 0.1	0.8 ± 0.2	0.7 ± 0.6	0.6 ± 0.5	0.3 ± 0.6	0.0 ± 0.0	0.8 ± 0.5	0.7 ± 0.2
Sum%	1.9 ± 1.1	1.7 ± 1.0	2.7 ± 0.5	1.4 ± 0.3	1.9 ± 0.7	1.5 ± 0.8	0.7 ± 0.6	1.8 ± 0.3	0.0 ± 0.0	2.3 ± 0.7	2.7 ± 1.6
Monounsaturated											
14:1	0.0 ± 0.0	0.7 ± 0.6	1.4 ± 0.4	1.1 ± 0.5	1.5 ± 0.5	0.5 ± 0.1	0.3 ± 0.3	0.5 ± 0.5	0.3 ± 0.2	1.0 ± 0.3	0.4 ± 0.6
15:1	0.1 ± 0.2	0.3 ± 0.3	0.8 ± 0.1	0.6 ± 0.2	0.8 ± 0.2	0.2 ± 0.2	0.1 ± 0.2	0.0 ± 0.0	0.1 ± 0.2	0.6 ± 0.1	0.7 ± 0.3
16:1ω7	14.4 ± 0.5	17.4 ± 1.3	14.0 ± 1.9	14.6 ± 4.0	15.4 ± 2.3	9.5 ± 1.6	14.9 ± 3.3	14.6 ± 0.7	4.5 ± 1.9	16.7 ± 1.0	14.1 ± 2.9
16:1ω9	0.6 ± 0.2	1.5 ± 0.4	2.0 ± 0.6	2.0 ± 1.2	2.2 ± 0.3	0.4 ± 0.3	0.4 ± 0.0	0.7 ± 0.1	0.4 ± 0.0	1.1 ± 0.2	2.3 ± 1.1
17:1	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.1 ± 0.2	0.0 ± 0.0	0.6 ± 1.1	0.0 ± 0.0	0.6 ± 0.6	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 0.8
18:1ω9	4.6 ± 0.5	4.9 ± 1.4	3.8 ± 0.6	4.1 ± 0.5	6.0 ± 3.0	3.7 ± 0.7	4.4 ± 1.4	3.3 ± 0.7	16.8 ± 3.4	3.7 ± 0.8	4.3 ± 1.1
18:1ω7	3.8 ± 0.2	4.2 ± 1.0	5.6 ± 0.8	5.0 ± 1.3	4.4 ± 0.2	3.1 ± 0.1	3.5 ± 0.6	2.4 ± 0.5	5.4 ± 1.1	4.7 ± 1.1	4.9 ± 0.8
22:1	0.6 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.5 ± 0.1	0.0 ± 0.0	0.5 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.1
24:1	0.4 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.3	0.2 ± 0.3	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
Sum%	24.6 ± 1.1	29.0 ± 1.9	27.9 ± 4.6	27.9 ± 1.4	30.2 ± 3.6	18.6 ± 2.0	24.1 ± 2.9	22.7 ± 2.0	27.7 ± 1.4	27.9 ± 1.4	27.8 ± 2.1
Polyunsaturated											
16:2	1.8 ± 0.5	1.1 ± 0.2	1.6 ± 0.1	1.2 ± 0.2	1.2 ± 0.5	2.1 ± 0.8	1.2 ± 0.3	2.9 ± 2.1	1.3 ± 0.3	1.7 ± 0.2	1.4 ± 0.2
18:2ω6	3.3 ± 0.2	2.0 ± 0.1	2.2 ± 0.7	2.3 ± 0.2	2.3 ± 0.5	3.4 ± 0.7	2.1 ± 0.1	1.9 ± 0.5	10.9 ± 0.8	1.9 ± 0.1	2.3 ± 0.6
18:3ω6	0.5 ± 0.1	0.6 ± 0.1	0.5 ± 0.2	0.6 ± 0.2	0.3 ± 0.3	0.5 ± 0.1	0.3 ± 0.3	0.8 ± 0.3	1.1 ± 0.2	0.3 ± 0.3	1.0 ± 0.9
18:3ω3	2.8 ± 0.3	1.2 ± 0.3	1.6 ± 0.6	1.8 ± 0.2	1.6 ± 0.3	1.6 ± 0.3	1.6 ± 0.1	1.3 ± 0.6	3.3 ± 1.5	1.3 ± 0.1	1.0 ± 0.7
20:2	0.3 ± 0.0	0.1 ± 0.2	0.1 ± 0.2	0.3 ± 0.0	0.0 ± 0.0	0.6 ± 0.1	0.3 ± 0.3	0.0 ± 0.0	0.7 ± 0.2	0.1 ± 0.2	0.4 ± 0.1
20:4ω6	4.8 ± 1.6	5.5 ± 0.6	3.5 ± 0.5	4.4 ± 0.9	3.5 ± 1.5	11.2 ± 0.8	5.3 ± 1.0	5.1 ± 1.4	8.2 ± 1.8	4.4 ± 0.9	4.7 ± 0.6
20:5ω3	5.0 ± 1.4	10.2 ± 1.5	8.2 ± 3.0	7.7 ± 0.9	7.4 ± 2.2	11.1 ± 1.0	11.3 ± 2.6	10.8 ± 0.7	5.5 ± 1.9	8.3 ± 2.4	8.5 ± 1.4
22:2	0.0 ± 0.0	0.1 ± 0.2	0.3 ± 0.3	0.4 ± 0.1	0.3 ± 0.3	1.7 ± 1.9	0.6 ± 0.0	0.5 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3
22:5 ω6	0.4 ± 0.3	0.7 ± 0.1	0.5 ± 0.1	0.4 ± 0.0	0.3 ± 0.2	1.2 ± 0.3	0.7 ± 0.3	0.6 ± 0.1	0.3 ± 0.3	0.4 ± 0.3	0.6 ± 0.1
22:5 ω3	0.1 ± 0.2	0.3 ± 0.2	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.7 ± 0.2	0.4 ± 0.3	0.2 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.1
22:6 ω3	1.5 ± 0.8	2.7 ± 0.2	1.6 ± 0.4	1.9 ± 0.3	1.8 ± 1.0	6.0 ± 0.7	2.3 ± 0.7	2.2 ± 0.7	1.5 ± 0.4	1.7 ± 0.5	2.0 ± 0.6
Sum%	20.5 ± 4.2	24.5 ± 1.6	20.0 ± 5.0	21.2 ± 0.3	18.7 ± 5.1	40.1 ± 2.5	26.2 ± 4.1	26.2 ± 3.5	32.7 ± 5.6	20.1 ± 4.2	22.4 ± 3.2
Sum n.i.%	2.7 ± 1.1	3.0 ± 1.1	3.3 ± 0.6	4.1 ± 1.7	4.0 ± 1.2	3.5 ± 1.8	2.4 ± 1.5	3.4 ± 0.9	4.3 ± 1.0	3.7 ± 1.5	4.4 ± 1.0
Total%	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
18:2ω6 +18:3ω3	6.1 ± 0.5	3.2 ± 0.3	3.7 ± 0.9	4.2 ± 0.1	3.9 ± 0.3	5.0 ± 0.9	3.7 ± 0.2	3.2 ± 0.1	14.2 ± 2.3	3.2 ± 0.1	3.4 ± 1.7
16:ω7/16:0	0.4 ± 0.0	0.6 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.0	0.4 ± 0.0	0.5 ± 0.0	0.5 ± 0.1	0.3 ± 0.0	0.6 ± 0.1	0.5 ± 0.1
LCFAs	0.5 ± 0.1	0.0 ± 0.0	0.2 ± 0.2	0.4 ± 0.2	0.0 ± 0.0	0.1 ± 0.2	0.4 ± 0.3	0.4 ± 0.3	0.3 ± 0.2	0.0 ± 0.0	0.1 ± 0.2

The total contribution of the 2 other dominant FAs found in mangroves leaves, the polyunsaturated 18:2ω6 and 18:3ω3 did not exceed 3.5% in the surface sediments of the estuary. There was no significant difference between MS and IS (*t*-test; $p > 0.05$) with the exception in autumn of Stn 2 (*t*-test; $p < 0.01$) and Stn 4 (*t*-test; $p < 0.04$).

FAs in crab tissues

The FAs identified in the tissues of crabs collected in the estuary are presented in Table 3**.** Hierarchical cluster analysis of the total identified FAs of the crabs separated the individuals into 3 groups at the 80% similarity level (Fig. 4). Cluster I separated the individuals of

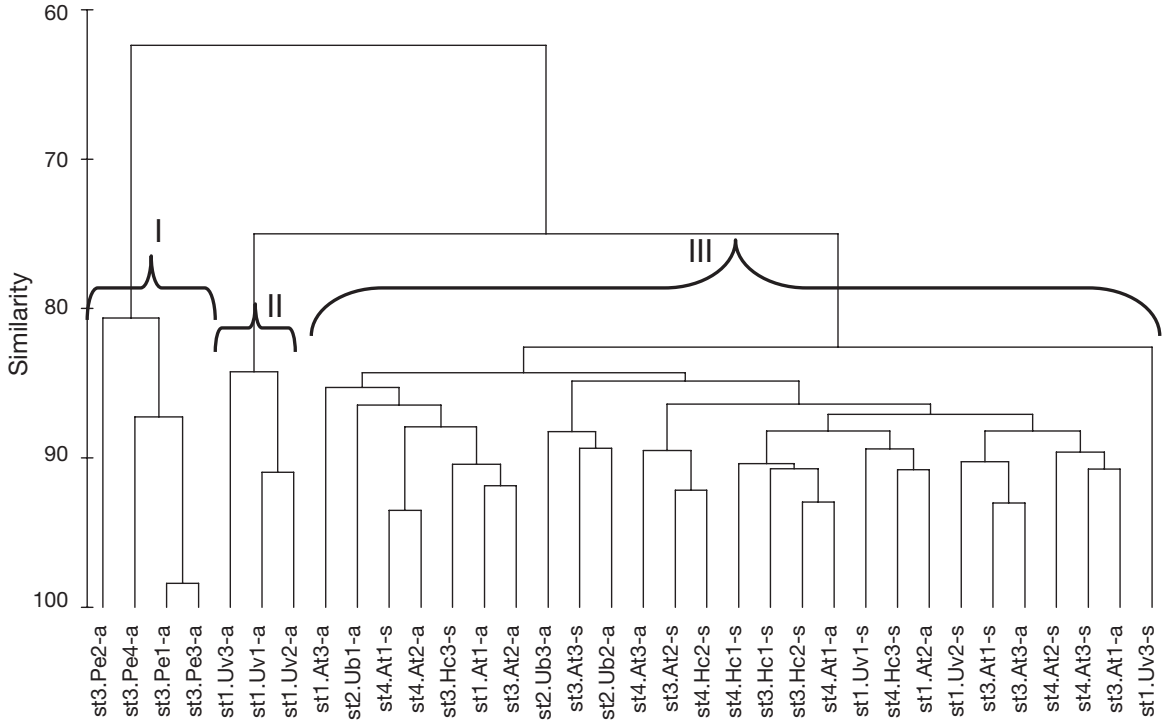

Fig. 4. Classification of crabs collected at the 4 study sites along the LRE in January and April 2004. The label of each sample consists of 3 codes. The first code is the station: st1 (Stn 1), st2 (Stn 2), st3 (Stn 3) and st4 (Stn 4); the second code is the species name (see Table 1 for abbreviations) and replicate number; the final code is the season (s: summer; a: autumn)

Parasesarma erythodactyla from other crab species at 62% similarity level. Cluster II separated individuals of *Uca vocans* sampled in autumn from the rest of the ocypodid crabs at 74% similarity and Cluster III was made up with all the other crabs.

The major saturated FA of all crabs was palmetic acid (16:0), representing 15.7 ± 1.6 to 32.5 ± 1.9% of total FAs. The FA 16:1ω7 dominated the monounsaturated group at 10.6 ± 3.3 to 17.4 ± 1.3% (18:1ω9 in the grapsid *Parasesarma erythodactyla*, 16.6 ± 4.3%) and 20:5ω3 dominated the polyunsaturated group at 5.0 ± 1.7 to 11.3 ± 2.6% (18:2ω6 in *P. erythodactyla*, 11.1 ± 0.5%). The relative contribution of total monounsaturated and total polyunsaturated in *P. erythodactyla* and in *Uca vocans* collected in summer were respectively in lower and higher proportions than in all other species (Table 3).

Bacterial markers, the branched FAs 15:0+17:0 and 18:1ω7, were detected in all species. There were no significant differences in either group of bacterial markers between species (ANOVA, $p > 0.05$).

The FA 20:5ω3 was detected in all species with contributions between 5.0 ± 1.7 and 11.3 ± 2.6% of total FAs. However, there were no significant differences between species (ANOVA, $p > 0.05$). The ratio 16:1ω7/16:0, as an indicator of diatoms input to the animal diets, was much lower in *Parasesarma erythodactyla* (0.253 ± 0.10) compared to all other crab species (0.445 ± 0.01 to 0.596 ± 0.08). Two other polyunsaturated FAs, 20:4ω6 and 22:6ω3, exhibited a higher contribution in *Uca vocans* collected in autumn in comparison to other sampled crab communities (ANOVA, $p < 0.05$).

The LCFAs, markers of mangroves, occurred only in small amounts (less than 0.7%) in the crabs and there were no significant differences between species (ANOVA $p > 0.05$). The contribution of 18:2ω6+18:3ω3 was significantly higher in *Parasesarma erythodactyla* (14.4 ± 2.3%) than all other sampled species ($p < 0.001$). Among the ocypodids, contributions of 18:2ω6+18:3ω3 in *Uca vocan*s individuals of both seasons were not different ($p > 0.05$) whereas these were significantly higher than all the other species ($p < 0.001$).

DISCUSSION

Mangrove exportation along LRE

Organic matter from vascular plants is indicated by LCFAs (Volkman et al. 1980), which can be traced in the seston (Canuel et al. 1995), sediment (LeBlanc et al. 1989) and animal tissues (Meziane & Tsuchiya 2000).

The leaves of *Avicennia marina*, the most abundant species in LRE, exhibit a contribution of more than 5% of LCFAs (T. Meziane & S. Y. Lee unpubl. data). In general, LCFAs were present in the surface sediment of all the sites within the mangroves and tidal flat along the entire transect. Because they are found in the waxy part of the leaf lipids, LCFAs can resist degradation for a longer period of time than the polyunsaturated FAs (Mfilinge et al. 2003). A large presence of these markers indicates that mangrove production was a major source of organic matter in this environment (Meziane & Tsuchiya 2000, Mfilinge et al. 2003) and therefore was a potential food source available to the detritivores and deposit feeders living in the LRE. However, in autumn, at the lower part of the estuary (Stns 3 and 4), hierarchical cluster analysis clearly distinguishes the sites MS3 and MS4 (Cluster I, Fig. 3), which exhibit the richest sediments in terms of LCFAs contributions, and the sites IS3 and IS4, with the lowest contribution of LCFAs, as 2 distinct groups (Clusters II and IIIa, Fig. 3). The very low contributions of LCFAs at IS3 and IS4 (less than 15 m from MS) strongly indicate a very spatially limited transfer of organic matter from the mangrove forest to the adjacent tidal flat in autumn.

In MS3 and MS4, the higher autumnal level of LCFAs compared to those recorded during summer is an indication of a higher rate of litter fall and/or an accumulation of the mangrove organic matter. A high contribution of LCFAs in the surface sediments within a mangrove forest was correlated to an increase of litter fall as a result of a high rainfall in a study in Okinawa, Japan (Mfilinge et al. 2005). Mackey & Smail (1995) showed that an *Avicennia marina* forest, also situated in Moreton Bay, exhibited higher litter fall rates during rainfall in summer, agreeing with the general positive correlation between rainfall and litter fall (Lee 1989). In LRE, the intensity of rainfall was much higher in January 2004 (237 mm mo^{-1}) than in April 2004 (62 mm mo^{-1}). Therefore this difference in rainfall may explain the limited exportation from the forest to the tidal flat in autumn and why, in parallel, lower rainfall most likely led to an accumulation of mangrove litter within the forest in MS3 and MS4, which exacerbated the seasonal reduced litter production (Mackey & Smail 1995).

The other dominant FAs in the composition of mangrove leaves from LRE were 18:2ω6 and 18:3ω3 (>20% in *Avicennia marina*, T. Meziane & S. Y. Lee unpubl. data). The total amount of these 2 FAs has been used as an indicator for the relative importance of terrestrial material in marine sediments (Budge & Parrish 1998). During decomposition, the FAs 18:2ω6 and 18:3ω3 tend to disappear more rapidly than saturated FAs (i.e. LCFAs) in the litter (Mfilinge et al. 2003) and in the sediment (Grossi et al. 2001). The FA 18:2ω6 can potentially also be produced by the fungi that colonise the leaves, and a phytoplanktonic origin has also been suggested for the FA 18:3ω3 in a temperate estuary (Napolitano et al. 1997). The possibility of a terrestrial origin of these markers also needs to be considered due to the presence of agricultural fields upstream of the studied zone that produce crops which are usually rich in 18:2ω6 (Napolitano et al. 1997, Meziane & Tsuchiya 2002). However, because of their dominance in the mangrove leaves and the prevalence of mangrove forest in the estuary, the origin of 18:2ω6 and 18:3ω3 found in the surface sediment of LRE during both seasons could be attributed primarily to mangrove leaf production, and/or the fungi colonising them, rather than from another terrestrial source.

Two groups of FAs, 18:1ω7 and branched 15:0+17:0, are commonly used to assess the bacterial contribution in the surface sediment (Carrie et al. 1998, Meziane & Tsuchiya 2002). The relative contribution of these markers shows that, throughout the entire transect, bacteria always contributed significantly to the pool of organic matter. The branched 15:0+17:0 have been ascribed to sulfate reducing bacteria (Canuel 2001, Pinturier-Geiss et al. 2002) whereas the monounsaturated 18:1ω7 has been assigned to bacteria living in anaerobic as well as in aerobic conditions (Edlund et al. 1986, Pinturier-Geiss et al. 2002). In surface sediments of LRE, both markers are more probably indicating anaerobic conditions. Indeed, these conditions are expected in summer, as higher temperatures would increase litter degradation rate, which in turn reduces the sediment (Fenchel et al. 1998). In autumn, surface sediments were probably even more reduced due to the accumulation of organic matter (mangrove detritus) that favours anaerobic metabolism and sediment reduction (Fenchel et al. 1998).

The polyunsaturated 20:5ω3 is commonly used to assess the importance of diatoms in aquatic environments (Canuel et al. 1995, Meziane & Tsuchiya 2000). As a general trend, the contribution of 20:5ω3 from the LRE in surface sediments along the estuary indicates that the input of benthic diatoms to the organic matter pool was similar in both sampled seasons. However, summer values of the ratio 16:1ω7/16:0, also indicative of diatoms input to the surface sediment (Mudge et al. 1998), were higher than those calculated in autumn. This may be due to a higher contribution in summer of planktonic diatoms to the pool of organic matter of the surface sediment. Indeed, a higher concentration in the water column of chl *a* was recorded in January (2.5 to 5 µg l^{-1}) than in April (1 to 2 µg l^{-1}), which is indicative of a better phytoplankton biomass.

Food sources of the crabs

Mangrove litter, predominantly composed of leaves during the sampling periods (Mackey & Smail 1995), seems to have not been assimilated by the ocypodid crabs or by *Parasesarma erythodactyla*, as indicated by the absence or weak contributions of LCFAs (<1%). However, the contributions of 18:2ω6+18:3ω3 in the FA composition of the crab tissues were higher (>3.2%). The discrepancy between LCFAs and 18:2ω6+18:3ω3, both markers of mangrove leaves in this habitat, can be due in part to the fungal biomass contributing to the amount of 18:2ω6 (see next paragraph). The discrepancy can also be explained by selective assimilation of the more desirable polyunsaturated FAs during the digestion process. Indirect evidence of selective assimilation has previously been reported in 3 species of ocypodids, including *Uca vocans* (Meziane et al. 2002) and *P. erythodactyla* (D. J. Hall et al. unpubl. data). These authors kept crabs in controlled conditions and fed them exclusively with *Avicennia marina* leaves. Preliminary data showed that LCFAs proportion in the tissues of *P. erythodactyla* were of the same level as the tissues of the field individuals of this present study (<1%), but were highly abundant in their feces (~10%), whereas 18:2ω6 and 18:3ω3 were present at the total concentration of 10% in the tissues, demonstrating that they were preferentially assimilated by the crabs.

Ingestion of fragmented mangroves leaves is possible for the ocypodid crabs as they have well-developed mandibles (Maitland 1990) and is established for many grapsids such as *Parasesarma erythodactyla* (Lee 1998, Guest et al. 2004). Indeed, this grapsid is the species that exhibits the highest contribution of 18:2ω6+18:3ω3 (up to 14.3%), which reflects the importance of mangrove organic matter in its food diet. However, the individuals of *P. erythodactyla* also exhibited a large content of 18:1ω9 in comparison to the other crabs. Combined high amounts of 18:2ω6 and 18:1ω9 is characteristic of some fungal strains (cf. Chen et al. 2001) and these FAs have been used as reliable markers of this microbial source in the terrestrial environment (Frostegård et al. 1996, Mikola & Setälä 1998, Chen et al. 2001). Therefore, a potential origin of 18:2ω6 and 18:1ω9 in *P. erythodactyla* would be the fungal biomass that develops at the surface and within the mangrove leaves and litter. There is no doubt that *P. erythodactyla* actively shreds mangrove leaf in the litter, but it is possible that this animal specifically seeks the microbial biomass (fungi, bacteria, diatoms) living on the surface and within the leaf tissues, rather than the mangrove organic matter, as a food source.

The amount of 20:5ω3 in ocypodid crab tissues suggests that diatoms were most likely a major food source in both seasons. In particular, a higher contribution of 20:5ω3 in *Uca vocans* in April indicates that this species assimilated more diatoms in autumn than during summer. Such a seasonal increase in the contribution of diatoms to the diet of *U. vocans* has previously been reported (Meziane & Tsuchiya 2000) but was in that case related to an identified summer bloom of the microphytobenthos. At Stn 1, no noticeable microphytobenthic bloom seemed to occur at the surface sediment in autumn (see above discussion paragraph on 20:5ω3 contribution in surface sediment). However, a better availability of this food source in the environment is emphasized by the fact that individuals of *Australoplax tridentata* sampled in autumn at Stn 1, showed a much higher contribution of the diatoms marker than their conspecifics from the other stations (*t*-tests, $p < 0.05$). Diatoms have been suggested to be a major food source for this ocypodid crab (Guest et al. 2004).

The contributions of 20:5ω3 to the tissues of the crab *Uca bellator minima* sampled in autumn and *Heloecius cordiformis* collected in summer indicate that these ocypodid species also rely on the microphytobenthic biomass for their diet. Individuals of the semaphore crab *Heloecius cordiformis* have been previously described as being primarily microphagous, as shown by the specialisation of its mouth parts (Maitland 1990).

In *Parasesarma erythodactyla*, the contribution of 20:5ω3 was significantly lower than in any other species except *Uca vocans* sampled in summer. Diatoms can be ingested incidentally during feeding on mangroves detritus (Mfilinge et al. 2003) or taken directly from the sediment (Guest et al. 2004). The lower input of microalgae to the diet of *P. erythodactyla* was confirmed by the calculated values of 16:1ω7/16:0, a diagnostic ratio for the contribution of diatoms (Copeman & Parrish 2003), which exhibited an average value of 0.3 that was lower than in all other species (~0.5).

The essential FA 22:6ω3 was significantly higher in the autumn *Uca vocans* individuals (6% of total FAs) than in all other crab populations (<3%). Since dinoflagellates, the usual source of this marker (Pond et al. 1998), were scarce in the surface sediments along LRE (<1%), it is unlikely that dinoflagellates are the major dietary source of 22:6ω3. The thraustochytrids, in which 22:6ω3 can contribute up to 40% of total FAs, are a much more plausible origin for this FA in crabs, as these microorganisms are known to colonise decaying mangrove leaves (Fan et al. 2001, Jiang et al. 2004). A significant contribution of mangroves leaves to the diet of *U. vocans* is supported by the high content of 18:2ω6+18:3ω3 in their tissues compared to the other ocypodid crabs studied.

A relatively high amount of the polyunsaturated 20:4ω6 was detected in all crab tissues collected in LRE. This FA has been assigned to different sources of

organic matter, as it has been found in large amounts in microalgae (Dunstan et al. 1994) and macroalgae (Graeve et al. 2002). Microalgae cannot be ruled out as a potential source of 20:4ω6 in LRE but macroalgae can be ignored as contributor of this FA, as there was no significant algal biomass in the mangrove and on the adjacent tidal flats (T. Meziane pers. obs.). Additionally, the potential main source of 20:4ω6 found at the surface sediment of LRE is most likely derived from protozoans and microeukaryotes that dwell in the sediment (Bell & Sargent 1985, Howell et al. 2003). Thus, these microorganisms could have been ingested by the crabs, which provided them with this essential FA. Surprisingly, the contribution of 20:4ω6 to *Parasesarma erythodactyla* was one of the highest in FA compositions of the crab populations collected at LRE. This species was less of a deposit feeder than the rest of the crabs. Therefore, as suggested by Copeman & Parrish (2003) for some other macroinvertebrates, the elevated level of 20:4ω6 in *P. erythodactyla* can also be related to an active metabolic conservation and retention in membranes rather than by simple dietary intakes.

Bacteria were one of the main components of the organic matter pool in the surface sediments. It was, therefore, not surprising to find that irrespective of season, bacteria contributed to the diet of all ocypodid species collected in LRE. The use of bacteria as a food source by ocypodid crabs has been reported previously (Dye & Lasiak 1986, Meziane et al. 2000, 2002, Takeda et al. 2004). Nevertheless, it has been suggested that the bacterial marker, 18:1ω7 can be formed *in vivo* by chain elongation of dietary 16:1ω7 in some marine invertebrates, including crabs (Styrishave et al. 2000, Stevens et al. 2004 and reference therein). However, as suggested by Stevens et al. (2004), in a benthic environment such as the tidal flats of the LRE, bacterial inputs, rather than possible chain elongation, is the most realistic scenario.

CONCLUSIONS

To conclude, the seasonal difference between FA compositions of the surface sediments in the mangrove forest of the LRE and in the adjacent bank was an indication of the variation in the sources of organic matter inputs from summer to autumn. In addition to this seasonal variation, MDS analysis of FA profiles exhibits a difference between the surface sediments of mangroves and their adjoining flats, which indicates a difference in terms of the source and transport of organic matter at a small spatial scale (less than 15 m). Further investigations of individual FA biomarkers revealed the sources of sediment organic matter in this aquatic habitat.

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LITERATURE CITED

Alongi DM (1998) Coastal ecosystem processes. CRC Press, Boca Raton, FL

Bell MV, Sargent JR (1985) Fatty acid analyses of phosphoglycerides from tissues of the clam *Chlamys islandica* (Muller) and the starfish *Ctenodiscus crispatus* (Retzius) from Balsfjorden, Northern Norway. J Exp Mar Biol Ecol 87:31–40

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:911–917

Bossio DA, Scow KM (1998) Impact of carbon and flooding on soil microbial communities: phospholipid FA profiles and substrate utiliszation patterns. Microb Ecol 35:265–278

Budge SM, Parrish CC (1998) Lipid biogeochemistry of plankton settling matter and sediments in Trinity Bay, Newfoundland. II. Fatty acids. Org Geochem 29:1547–1559

Burggren WW, McMahon BR (1988) Biology of the land crab. Oxford University Press, Oxford

Canuel EA (2001) Relations between river flow, primary production and fatty acid composition of particulate organic matter in San Francisco and Chesapeake Bays: a multivariate approach. Org Geochem 32:563–583

Canuel EA, Cloern JE, Ringelberg DB, Guckert JB, Rau GH (1995) Molecular and isotopic tracers used to examine sources of organic matter and its incorporation into the food webs on San Francisco Bay. Limnol Oceanogr 40: 67–81

Carrie RH, Mitchell L, Black KD (1998) Fatty acids in surface sediment at the Hebridean shelf edge, west of Scotland. Org Geochem 29:1583–1593

Chen J, Ferris H, Scow KM, Graham KJ (2001) Fatty acid composition and dynamics of selected fungal-feeding nematodes and Fungi. Comp Biochem Physiol B 130: 135–144

Chong VC, Sasekumar A, Leh MUC, D'Cruz R (1990) The fish and prawn communities of a Malaysian coastal mangrove system with comparisons to adjacent mud flats and inshore waters. Estuar Coast Shelf Sci 31:703–722

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth

Cook PLM, Revill AT, Clementson LA, Volkman JK (2004) Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary. III. Sources of organic matter. Mar Ecol Prog Ser 281:55–72

Copeman LA, Parrish CC (2003) Marine lipids in a cold coastal ecosystem: Gilbert Bay, Labrador. Mar Biol 143: 1213–1227

Crane J (1975) Fiddler crabs of the world. Ocypodidae: Genus *Uca*. Princeton University Press, Princeton, NJ

Dahdouh-Guebas F, Giuggioli M, Oluoch A, Vannini M, Cannicci S (1999) Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. Bull Mar Sci 64:291–297

Dunstan GA, Volkman JK, Barret SM, Leroi JM, Jeffrey SW (1994) Essential polyunsaturated fatty acids from 14 species of diatom (Bacillariophyceae). Phytochem (Oxford) 35:155–161

Dye AH, Lasiak TA (1986) Microbenthos, meiobenthos and fiddler crabs: trophic interactions in a tropical mangrove sediment. Mar Ecol Prog Ser 32:259–264

Edlund A, Nichols PD, Roffey R, White DC (1986) Extractable and lipopolysaccharide fatty acids and hydroxy acid profiles from *Desulphovibrio* species. Lipid Res 26:982–988

Fan KW, Chen F, Jones EBG, Vrijmoed LLP (2001) Eicosapentaenoic and docosahexaenoic acids production by and okara-utilising potential of thraustochtrids. J Indust Microbiol Biotech 27:199–202

Fenchel T, King GM, Blackburn N (1998) Bacterial biogeochemistry. The ecophysiology of mineral cycling. Elsevier, London

Frostegård A, Tunlid A, Baath E (1996) Changes in microbial community structure during long-term incubation in two soils experimentally contaminated with metals. Soil Biol Biochem 28:55–63

Graeve M, Kattner G, Wiencke C, Kartsen U (2002) Fatty acid composition of Arctic and Antarctic macroalgae: indicator of phylogenetic and trophic relationship. Mar Ecol Prog Ser 231:67–74

Grossi V, Blokker P, Damsté JSS (2001) Anaerobic biodegradation of lipids of the marine microalga *Nannochloropsis salina*. Org Geochem 32:795–808

Guest MA, Connolly RM, Loneragan NR (2004) Carbon movement and assimilation by invertebrates in estuarine habitats at a scale of metres. Mar Ecol Prog Ser 278:27–34

Howell KL, Pond DW, Billet DSM, Tyler PA (2003) Feeding ecology of deep-sea seastars (echinodermata: Asteroidea): a fatty acid biomarker approach. Mar Ecol Prog Ser 255: 193–206

Hsieh H, Chen C, Chen Y, Yang H (2002) Diversity of benthic organic matter flows through polychaetes and crabs in a mangrove estuary: $\delta^{13}C$ and $\delta^{34}S$ signals. Mar Ecol Prog Ser 227:145–155

Jiang Y, Fan KW, Wong RTY, Chen F (2004) Fatty acid composition and squalene content of the marine microalga *Schizochytrium mangrovei*. J Agric Food Chem 53: 1196–1200

LeBlanc CG, Bourbonniere RA, Schwarcz HP, Risk MJ (1989) Carbon isotopes and fatty acids analysis of the sediments of Negro Harbour, Nova Scotia, Canada. Estuar Coast Shelf Sci 28:261–276

Lee SY (1989) Litter production and turnover of the mangrove *Kandelia candel* (L.) Druce in a Hong Kong tidal shrimp pond. Estuar Coast Shelf Sci 29:75–87

Lee SY (1998) Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar Freshw Res 49:335–343

Lee SY (2004) Relationship between mangrove abundance and tropical prawn production: a re-evaluation. Mar Biol 145:943–950

Macintosh DJ (1988) The ecology and physiology of decapods of mangrove swamps. Symp Zool Soc Lond 59:315–341

Mackey AP, Smail G (1995) Spatial and temporal variation in litter fall of *Avicennia marina* (Forssk.) Vierh. in the Brisbane River, Queensland, Australia. Aquat Bot 52:133–142

Maitland DP (1990) Feeding mouthpart morphology in the semaphore crabs *Heloecius cordiformis* (Decapoda: Brachyura: Ocypodidae). Mar Biol 66:191–197

Meziane T, Tsuchiya M (2000) Fatty acids as tracers of organic matter in the sediment and food web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. Mar Ecol Prog Ser 200:49–57

Meziane T, Tsuchiya M (2002) Organic matter in a subtropical mangrove estuary subjected to wastewater discharge: origin and utilization by 2 macrozoobenthic species. J Sea Res 47:1–11

Meziane T, Bodineau L, Retière C, Thoumelin G (1997) The use of lipid markers to examine sources of organic matter and its incorporation into food web of the intertidal salt marsh-flat ecosystem, Mont Saint Michel Bay, France. J Sea Res 38(1):47–58

Meziane T, Sanabe MC, Tsuchiya M (2002) Role of fiddler crabs of a subtropical intertidal flat on the fate of sedimentary fatty acids. J Exp Mar Biol Ecol 270:191–201

Mfilinge PL, Meziane T, Bachok Z, Tsuchiya M (2003) Fatty acids in decomposition mangrove leaves: microbial activity, decay and nutritional quality. Mar Ecol Prog Ser 265: 97–105

Mfilinge PL, Meziane T, Bachok Z, Tsuchiya M (2005) Litter dynamics and particulate organic matter outwelling from a subtropical mangrove in Okinawa Island, South Japan. Estuar Coast Shelf Sci 60:301–313

Mia Y, Shokita S, Watanabe S (2001) Stomach content of 2 grapsid crabs, *Helice formosensis* and *Helice leachi*. Fish Sci 67:173–175

Mikola J, Setälä H (1998) No evidence of trophic cascades in an experimental microbial-based soil food web. Ecology 79:153–164

Mudge SE, East JA, Bebianno MJ, Barreira LA (1998) Fatty acids in the Ria Formosa Lagoon, Portugal. Org Geochem 29(4):963–977

Nagelkerken I, van der Velde G (2004) Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? Mar Ecol Prog Ser 274: 143–151

Napolitano GE, Pollero RJ, Gayoso AM (1997) Fatty acids as trophic markers of phytoplankton blooms in the Bahia Blanca estuary (Buenos Aires, Argentina) and Trinity Bay (Newfoundland, Canada). Biochem System Ecol 25: 739–755

Odum WE, Heald EJ (1975) The detritus based food web of an estuarine mangrove community. In Cronin LE (ed) Estuarine research. Academic Press, New York, p 265–286

Pinturier-Geiss L, Mejanelle L, Dale B, Karlsen DA (2002) Lipids as indicators of eutrophication in marine coastal sediments. J Microbiol Meth 48:239–57

Pond DW, Bell MV, Harris RP, Sargent JR (1998) Microplanktonic polyunsaturated fatty acid markers: a mesocosm trial. Estuar Coast Shelf Sci 46:61–67

Robertson AI, Daniel PA (1989) The influence of crabs on leaf litter processing in high intertidal mangrove forests of tropical Australia. Oecologia 78:191–198

Robertson AI, Alongi DM, Boto KG (1992) Food chains and carbon fluxes. In: Robertson AI, Alongi DM (eds) Tropical mangrove ecosystems. American Geophysical Union, Washington, DC, p 293–326

Sheaves M, Molony B (2000) Short-circuit in the mangrove food chain. Mar Ecol Prog Ser 199:97–109

Skov MW, Hartwell RG (2002) Paradoxical selective feeding on a low nutrient diet: Why do mangrove crabs eat leaves? Oecologia 131:1–7

Stevens CJ, Deibel D, Parrish CC (2004) Species-specific differences in lipid composition and omnivory indices in Arctic copepods collected in deep water during autumn (North Water Polynya). Mar Biol 144:905–915

Styrishave B, Faldborg Petersen M, Andersen O (2000) Influence of cadmium accumulation and dietary status on fatty acid composition in 2 colour forms of shore crabs, *Carcinus maenas*. Mar Biol 137:423–433

Takeda S, Poovachiranon S, Murai M (2004) Adaptations for feeding on rock surfaces and sandy sediment by the fiddler crabs (Brachyura: Ocypodidae) *Uca tetragonon* (Herbst, 1790) and *Uca vocans* (Linnaeus, 1758). Hydro-

biologia 528:87–97
Twilley RR (1985) The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. Estuar Coast Shelf Sci 20:543–557
Twilley RR (1988) Coupling of mangroves to the productivity of estuarine and coastal waters. In: Jansson BO (ed) Coastal-offshore ecosystems: Interactions 22, lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 155–180
Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Loneragen NR, Pendrey RC (1996) How far do prawns and fish move into mangroves? Distribution of juvenile Banana prawns *Penaeus merguiensis* and fish in a tropical mangrove forest in northern Australia. Mar Ecol Prog Ser 131: 115–124
Volkman JK, Johns RB, Gillan FT, Perry GJ (1980) Microbial lipids of an intertidal sediment. I. Fatty acids and hydrocarbons. Geochem Cosmochem Acta 44:1133–1143

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