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Litter dynamics and particulate organic matter outwelling from a subtropical mangrove in Okinawa Island, South Japan

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Abstract

Litter dynamics and outwelling of particulate organic matter (POM) was investigated in a subtropical mangrove (Okinawa Island, South Japan) in order to quantify the impact of mangrove POM on adjacent intertidal sediments. A distinct seasonal pattern was found with maximum litter fall during the autumn season, and minimum during winter. Total litter production between sites did not differ significantly. Tall mangroves (average 7 m) did not show any higher contribution to the litter production than short mangroves (average 4 m). The mean annual litter production was 12.95 ± 2.95 t ha^{-1} (dry weight) with leaf fall contributing more than 70% of the total litter production. Analysis of fatty acids (FAs) in the surface sediments of an adjacent mud flat and sand flat during the winter, spring and autumn seasons indicated that outwelling of POM from the mangrove ecosystem occurs. However, it is spatially restricted to within 300 m from the mangrove forest. The magnitude of the outwelling increased during spring and autumn consistent with the increase in the total litter production. Despite the presence of mangrove-derived organic matter in the estuarine surface sediments, autochthonous sources of organic matter, green macroalgae (*Ulva pertusa* and *Enteromorpha intestinalis*), diatoms and bacteria are the main contributors of sedimentary organic matter and ω3 and ω6 PUFAs than mangrove-derived (POM) during winter and spring. While the contribution of mangrove-derived POM to sedimentary organic matter is limited to the autumn season.
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1. Introduction

Litter fall is an important index of potential carbon transport to coastal ecosystems (Twilley et al., 1997) and a valuable indicator of mangrove productivity (Clough, 1992). The amount of litter produced in the mangrove forest directly affects the outwelling of particulate organic matter (POM) between mangrove forests and adjacent marine habitats. Unlike tropical mangroves, subtropical mangroves of southern Japan are subjected to drastic changes in weather. In particular, low temperatures are present during the winter season and sometimes fall below 14 °C in Okinawa Island (Mfilinge et al., 2002). Given this wide temperature range, there is little quantitative information of a comparative nature available for the effect of temperature and other climatic factors on mangrove outwelling and its impact on sedimentary organic matter. Low temperatures result in slowing important ecological processes such as litter production (Tam et al., 1998) and turnover, detritus decomposition, and activity of leaf eating crabs.

Direct grazing by crabs substantially reduces export of leaf litter by tidal transport and accelerates its

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breakdown (Robertson, 1986, 1991). Reduced crab activity in winter slows down the leaf breakdown process (Mia et al., 2001). Therefore, at that time, most litter decomposes by microbial action or is transported by tides to adjacent habitats. On this basis, it was assumed that the small amount of litter produced in the mangrove during winter might be available for export. Winters in Oura Bay estuary (Okinawa) are also associated with development of small blooms of green macroalgae *Ulva pertusa* and *Enteromorpha intestinalis*, which disappear by the end of spring (personal observation). The annual occurrence of these green macroalgal blooms in intertidal flats of Okinawa Island during winter–spring months is common and probably supplements organic matter in the intertidal flat surface sediments. Although mangrove and algal blooms may contribute substantially to the input of organic matter, the relative importance of these sources may vary temporally and spatially.

Little attention has been paid, however, to the role of autochthonous green macroalgal production in subtropical estuaries, and no study has attempted to assess the relative importance of mangrove and algal material, during months of minimum mangrove production in the subtropical mangroves (Mokolensang and Tokuyama, 1998; Tam et al., 1998). We assumed that the contribution of autochthonous sources of organic matter such as green macroalgae to marine sediments within the estuary might be substantial next to the mangrove-derived organic matter. Other seasonal events, like rainfall, are thought to contribute to the export of organic matter from mangroves (Dittmar et al., 2001).

The first aim of the present study is to detail seasonal changes in mangrove litter fall in relation to seasonal climatic factors (wind speed, temperature and rainfall), which may directly affect litter production and outwelling of POM from mangroves. The second aim is to examine, using fatty acid biomarkers, whether there is outwelling of particulate organic matter from the mangrove forest to adjacent intertidal flats during winter, a season which is particularly associated with low litter production, low rainfall, low temperature, low wind speed and low crab activity in the mangroves, factors which may give rise to temporal fluctuations and probably variations in the abundance and composition of organic matter in the estuary.

We compared concentrations of fatty acids (FAs) biomarkers of organic sources in the surface sediments during winter with FA in the surface sediments during spring and autumn. Further, we assess the impact of mangrove POM and autochthonous sources of organic matter in particular green macroalgae on sedimentary organic matter. Since polyunsaturated fatty acids (PUFAs) are labile in nature (Smith et al., 1983) our sampling strategy was carefully chosen to follow important ecological events; peak of the green macroalgal blooms which accompany low mangrove litter production during winter, onset of bloom decay during spring, and peak of mangrove litter fall during autumn, a non-bloom season.

2. Materials and methods

2.1. Study area

The study was carried out at Oura Bay estuary located in the northern part of Okinawa Island (26°N, 128°E: Fig. 1) in southern Japan. The mangrove forest structure consists of mixed stands of *Bruguiera gymnorrhiza*, *Kandelia candel* and *Rhizophora stylosa*, covering an area of approximately 10 ha at the mouth of Oura River, and serves as a natural reserve of significant importance to species of crabs, fish and water birds (Mfilinge et al., 2002). Stands of *B. gymnorrhiza* dominate the mangrove forest.

The forest is situated in an enclosed bay and the effects of wave action are relatively small. The tidal range is 2 m and the mangrove forest is frequently inundated by tides. The sediment surface in the mangroves varies from hard to soft mud, comprising mainly clay-like particles. An adjacent intertidal flat, up to 300 m from the mangroves comprises mainly soft mud, with a salinity range of 20–32‰, and from 400 m to 600 m (near the subtidal zone) the flat comprises fine sand sediments, with a salinity range of 27–38‰.

The river outflow is high during the rainfall season (May–July) and during the typhoon peak season (July–October), and it is low during winter (November–January) and spring (February–April). The annual mean air temperature is 22.9 °C, the highest monthly mean occurs in July (28 °C), and the lowest monthly mean occurs in January (14 °C) (Mfilinge et al., 2002). The annual precipitation peaks at a mean of 218 mm month^{-1} during the rainy season (May–July) and is at its lowest during the dry season (October–November) and winter through spring, mean 116 mm month^{-1} (Mfilinge et al., 2002).

Mangrove-derived POM is the dominant allochthonous source of organic matter to the estuary (Meziane and Tsuchiya, 2000). The abundance and quality of this organic matter is likely to vary temporally in response to climatic changes, especially temperature, rainfall and wind speed. Blooms of green macroalgae and probably phytoplankton appear in the estuary during winter and die off during spring, when both air and sediment temperature increases.

2.2. Sampling strategy

A litter fall study was conducted in order to quantify the amount of litter falling on sediments and assess its impact on adjacent intertidal flat surface sediments in

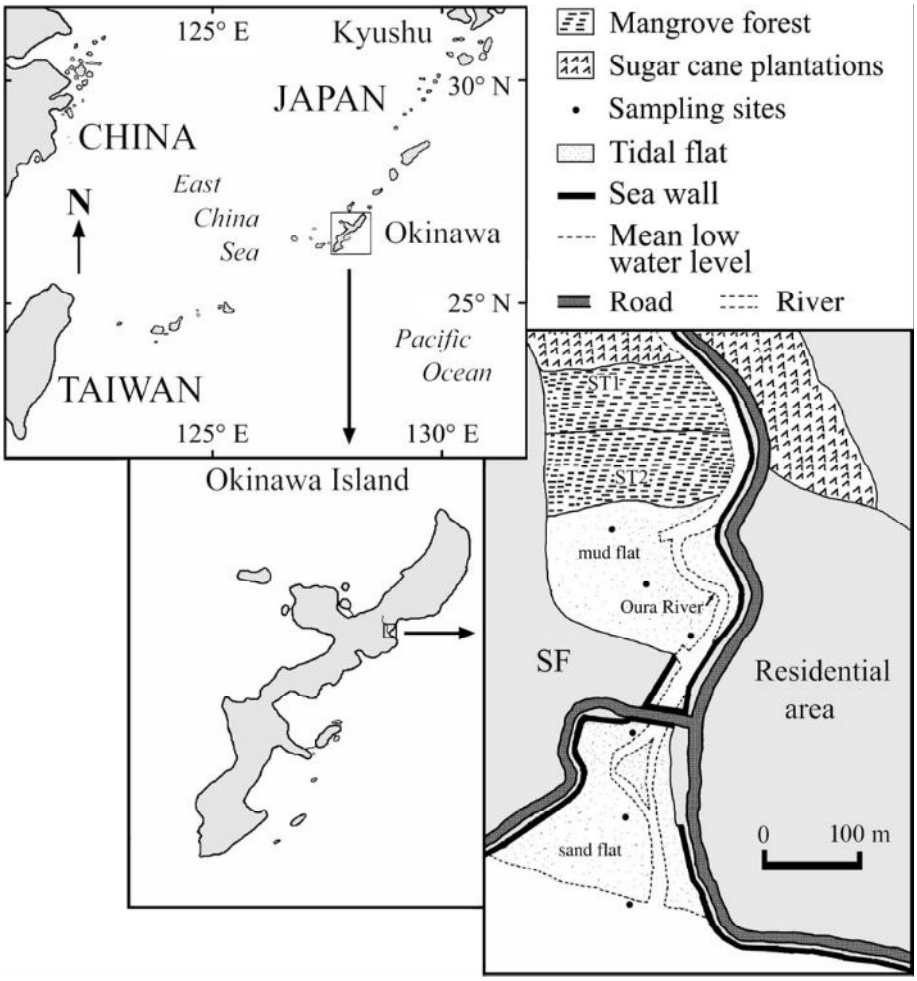


Fig. 1. Map of Okinawa Island and the location of the study sites in the Oura Bay mangrove forest and sampling transect in mud and sand flats.

Oura Bay estuary. To address spatial variability in litter production within the mangrove, comparison between sites was made, one in the high intertidal mangroves (ST1) and another in the low intertidal mangroves (ST2). The two sites differ in tree heights. The ST1 trees are taller (4–8 m, average 7 m) than the ST2 (2–5 m, average 4 m) stands. Litter traps (50 × 50 cm) each made of nylon net of 1 mm aperture, were suspended under mangrove trees, making sure that they were above the maximum tide height and at a position which ensured maximum catch of litter. Seven such traps were randomly distributed at each site, making a total sampling area of 3.5 m^2. The sampling area (3.5 m^2) was greater than that used in previous studies e.g. 1.8 m^2 (Woodroffe, 1985), and therefore was considered sufficient for this mangrove forest. Litter fall was collected monthly for 13 consecutive months from May 2000 to May 2001.

The collected litter samples were separated into leaves, stipules, flowers, fruits, twigs and trash (unidentified material), then dried in a hot air rapid drying oven at 80 °C for two days. Next, samples were put in desiccators and allowed to reach room temperature, then weighed. Weather conditions (wind speed, temperature and rainfall) were monitored throughout the sampling period. These data were obtained from a nearby weather station in Nago city Okinawa, located ~6 km from the estuary.

To examine whether outwelling of POM from mangroves occurs and whether it contributes substantially to organic matter in adjacent intertidal flats, we collected surface sediment samples along a transect line from the mud tidal flat to the end of the sand flat. Temporal variability was addressed by collecting sediment samples around ecological events that were perceived as the primary mechanisms of temporal variability; during winter (end of December, mid and end of January), associated with low mangrove production and high macroalgae production; during spring (mid and end of March, and beginning of April), associated with the bloom decay; and during autumn (end of August, mid and end of September), associated with the highest leaf litter production, enhanced by typhoon storms. We sampled these events in order to

evaluate the importance of mangrove POM in changing the quality of organic matter and to determine whether this variability is reflected in the adjacent intertidal flat sediments.

Surface sediments were carefully collected by scraping the topmost surface sediments 0–2 mm using a metal spatula with sharp edges, at six sites situated 100 m apart along a transect line from the mangroves to the subtidal region (Fig. 1). At each site, sediment samples were collected at three locations about 25 m^2 surrounding the site (located randomly 3–10 m apart perpendicular to the transect line on each side). Mangrove surface sediments and leaves of *Bruguiera gymnorrhiza* were collected from the high intertidal, low intertidal and along the riverbank during winter. Thalli of green macroalgae *Enteromorpha intestinalis* and *Ulva pertusa* were collected on the adjacent flat and within mangroves. The collected samples were stored at −20 °C and lipid analysis was done as soon as possible. A subsample of the surface sediments was dried at 60 °C to constant weight, a temperature that would not drastically change the nutrient status of the sediments. The dried sediments were used for C, N and P analysis and for determination of water content ($n = 3$).

2.3. Sample analysis

Prior to C and N analysis, 1 g of sediment for each sample was treated with a 20-ml solution of 1 N HCl to remove carbonates (for details see Yamamuro and Kayanne, 1995). Total organic C and N contents of the sediment samples were measured in a Shimadzu high sensitivity CN analyzer, model Sumigraph NC-80. Total P content was measured spectrophotometrically by the ascorbic acid method (Strickland and Parsons, 1972), after digestion of the sediments in a mixture of concentrated sulfuric acid and nitric acid (Greenburg et al., 1995). Three replicates were measured for each sample.

For lipid analysis, mangrove leaves and thalli of *Enteromorpha intestinalis* and *Ulva pertusa* were chopped into small pieces and milled in a miller. Then subsamples of 4 g and 2 g (wet weight) of the milled mangrove leaves and algal thalli, respectively, and 4 g (wet weight) of sediments were used for lipid analyses. The remaining subsamples of the milled leaves (4 g) and algal material (4 g) were dried at 80 °C to constant weight and used to determine water content ($n = 3$).

Samples were extracted in three replicates following a slightly modified version of the method of Bligh and 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 two-layer system. The lipids migrated into the lower chloroform phase and the separation was enhanced by centrifugation (2000 rpm). The extracted lipids were filtered through a glass funnel lined with a pre-combusted GF/C filter, which removed any fine sediments or particulate matter (Wilson et al., 2001). The filtrate was concentrated by rotary evaporation and made up to 2 ml.

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 done according to Meziane et al. (2002) in order to obtain total fatty acids. Methyl ester fatty acids (FAMEs) were purified by high performance thin-layer chromatography technique (HPTLC) using Merck plates coated with silica gel (Darmstadt, Germany). The solvents used for developing were a mixture of hexane/diethyl ether/acetic acid (70:30:1). 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. For all samples, a second plate was prepared in order to estimate the proportion of FAMEs in the total lipids (Yamashiro et al., 1999). After drying, the plate was scanned using a flatbed scanner (Epson GT-9000) and Adobe Photoshop software (Adobe systems). The resulting image file was imported into NIH image version 6, to estimate the relative contribution of the fatty acids, as a proportion of total lipid, by integrating the chromatogram.

The FAMEs were separated and quantified by gas chromatography (GC 14.B, Shimadzu) equipped with a flame ionization detector. Separation was performed with an FFAP-polar capillary column (30 m × 0.32 mm internal diameter, 0.25 μm film thickness) with hydrogen as a 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 230 °C at 3 °C min^{-1}, and finally held constant for 30 min. The flame ionization was held at 240 °C. Most FAME peaks were identified by comparing their retention times with those of authentic standards (Supelco Inc.). For some samples, peaks of FA were identified with a GC-mass spectrometry.

Fatty acids are designated as $X{:}Y\omega Z$, where X is the no. of carbon atoms, Y is the no. of double bonds and Z is the position of the ultimate double bond from the terminal methyl group. Because of their structural diversity and high biological specificity (Parkes, 1987), FAs can be used as biomarkers to identify sources and fate of organic matter in marine environments (Harvey, 1994). For example, fatty acids with greater than 24 carbon atoms are synthesized mostly by vascular plants (Volkman et al., 1980), and consequently have been used as vascular plant markers in sediments and animal tissues (LeBlanc et al., 1989; Meziane and Tsuchiya, 2002; Meziane et al., 2002).

The branched chain 15:0 and 17:0, *iso* and *anteiso* fatty acids, and the monounsaturated fatty acid (MUFA) 18:1ω7, are generally considered to be predominantly synthesized by bacterial communities (Jeffries, 1972; Volkman et al., 1980). These bacterial fatty acids (BFAs) are therefore used as biomarkers of bacteria (Parkes, 1987). Polyunsaturated fatty acids (PUFAs) 18:2ω6, 18:3ω3 and 18:3ω6 have been used as markers of green macroalgae (Napolitano et al., 1997; Meziane and Tsuchiya, 2000); and the PUFA 20:5ω3 has been strongly detected in diatoms (Pond et al., 1998) and used as a diatom marker in marine habitats (Currie and Johns, 1988; Canuel et al., 1995; Meziane and Tsuchiya, 2000).

2.4. Statistical analyses

One-way ANOVA was used to evaluate differences in total litter fall rate and its components among the 13 sampling months and four seasons. Any significant seasonal or month effects were further examined using Fisher's protected least significant difference (PLSD) test. Paired *t*-test was used to examine differences in the total litter fall rates between the two sites in the mangrove forest. A multifactorial correlation analysis was used to examine relationships between climate, litter fall, FA markers and concentrations of N, P and the C ratio. The absolute concentrations of fatty acid markers for vascular plants, green macroalgae, bacteria, diatoms, dinoflagellates, total microalgae and ω3 and ω6 PUFAs present in the sediments were compared using MANOVA. Seasons (three levels) and sites (six levels) were entered as fixed factors. Fisher's PLSD was used as a post hoc test to assess any significant seasonal or distance effects. All statistical analyses were performed using Stat View 5 software (SAS Institute Inc.). For all tests a criterion of $p < 0.05$ was used to determine statistical significance.

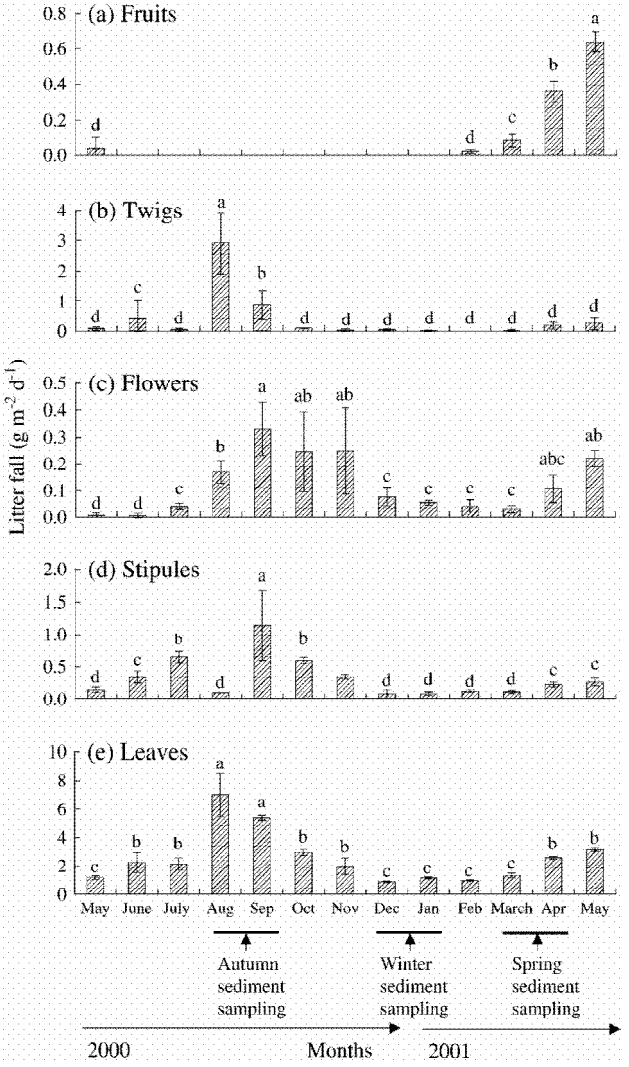


Fig. 2. Monthly variations in the daily fall rate of litter components from May 2000 to May 2001. Lower case letters indicate post hoc Fisher's protected least significant difference (PLSD) results for differences between months. Bars with different letters are significantly different. Values are means (±SD).

3. Results

3.1. Litter fall

There was no significant difference in the mean litter fall rates between the two sites ($p = 0.43$), no significant site main effect on litter fall rates of leaves, stipules, flowers and fruits between the two sites and data from the two sites were pooled in all further analyses (e.g. Figs. 2–4). The mean annual litter fall in the mangrove forest was 12.95 ± 2.95 t ha^{-1}. A highly significant difference in the litter fall rates was found among months (ANOVA, $p < 0.0001$) (Fig. 2). Highest litter fall rates occurred in August and September while lowest rates occurred in December–March. Leaves were the most important contributors in the total litter fall, (>70%), with annual mean rate of 9.09 ± 1.8 t ha^{-1}, followed by twigs 1.44 ± 0.2 t ha^{-1}, stipules 1.21 ± 0.3 t ha^{-1}, flowers 0.41 ± 0.1 t ha^{-1} and fruits 0.15 ± 0.8 t ha^{-1}.

There was a significant correlation between total litter fall rates and wind speed ($r = 0.899$, $p < 0.0001$) and temperature ($r = 0.644$, $p < 0.0174$). Total litter fall did not correlate significantly with rainfall ($r = 0.525$, $p < 0.0655$). Wind speed, especially during typhoon season (from August to October), had the strongest effect on litter fall. A sharp increase in litter fall rate occurred in May 2001, when exceptionally, during that month the island was hit by a typhoon and resulted in the elevation of litter fall from 1.634 g m^{-2} day^{-1} in May 2000 to 4.51 g m^2 day^{-1} in May 2001 (Fig. 3a,b).

Data on litter fall rates were grouped into seasons as follows: (May–July) summer, associated with rainfall

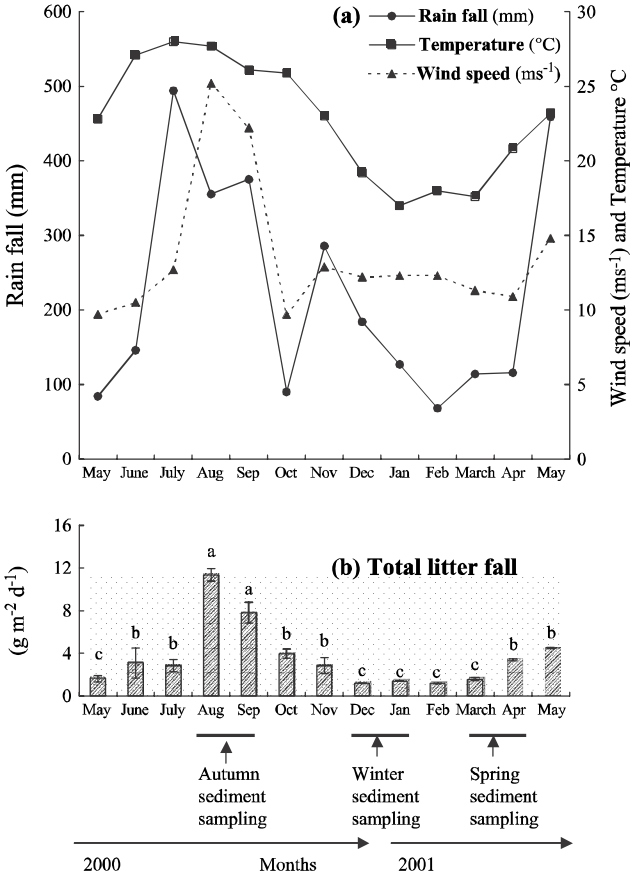


Fig. 3. Total litter fall rates (g m^{-2} dy^{-1}) and climatic factors; wind speed (m s^{-1}), temperature (°C) and rainfall (mm), from May 2000 to May 2001. Lower case letters for the total litter fall data indicate post hoc Fisher's protected least significant difference (PLSD) results. Bars with different letters are significantly different. Values for total litter fall rate are means (±SD).

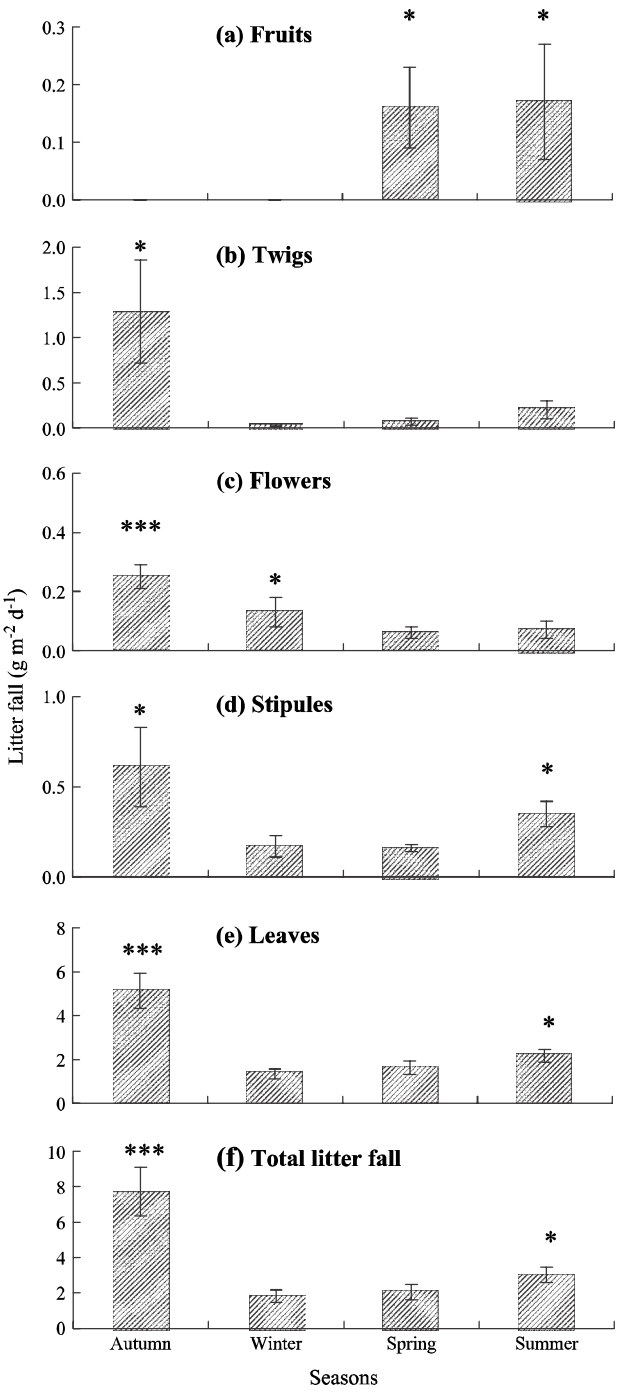


Fig. 4. Seasonal variations of total litter fall rates (g m^{-2} dy^{-1}) and its components. Asterisks signify post hoc Fisher's protected least significant difference (PLSD) results and indicate significant differences among seasons; *$p < 0.05$; ***$p < 0.001$. Values are means (±SD).

and beginning of the typhoon season; (August–October) autumn, associated with typhoon storms; (November–January) winter; and (February–April) spring. There was a significant seasonal effect due to one season, autumn, on litter fall rates ($p < 0.001$) and its components (leaves, stipules, flowers, fruits and twigs) (Fig. 4). During that season, total leaves, flowers and twigs were the highest compared to the three other seasons. Stipules were also significantly higher during autumn, but did not differ from the summer season. Fruits were significantly higher during spring and summer, and were not found during autumn and winter (Fig. 4a). There were no other statistical differences among the other seasons for leaves, stipules, flowers and twigs.

3.2. Fatty acids in mangrove leaves, mangrove sediments and green macroalgae

The predominant fatty acid in the mangrove leaves of *Bruguiera gymnorrhiza*, the mangrove sediments and dead filaments of *Enteromorpha intestinalis* and *Ulva pertusa* were saturated fatty acids (SAFAs), of which the most commonly detected was 16:0 (Table 1). Long chain fatty acids (LCFAs), markers of vascular plants, were detected only in *B. gymnorrhiza* leaves and the mangrove sediments. The polyunsaturated fatty acids (PUFAs), in particular 18:2ω6 and 18:3ω3, markers of

Table 1
Fatty acid concentrations (μg g^{-1} dry weight) in yellow leaves of *Bruguiera gymnorrhiza*, mangrove surface sediments and thalli of *Enteromorpha intestinalis* and *Ulva pertusa*

Fatty acids	Yellow leaves	Mangrove sediments	*E. interstinalis*	*U. pertusa*
16:0	6125.1 ± 214.4	44.7 ± 4.2	5066.4 ± 174.8	3686.1 ± 364.6
18:0	1175.6 ± 262.9	7.3 ± 0.3	12.0 ± 20.8	283.8 ± 5.4
15:0 *iso*	33.7 ± 7.40	4.2 ± 0.9	–	–
15:0 *anteiso*	–	3.6 ± 0.7	–	–
15:0	36.5 ± 11.8	1.8 ± 0.3	56.6 ± 16.4	77.7 ± 1.4
16:1ω9	20.1 ± 28.4	20.3 ± 2.4	31.4 ± 27.2	429.6 ± 312.8
16:1ω7	–	2.2 ± 0.2	301.2 ± 260.9	369.0 ± 36.9
17:0 *iso*	–	2.4 ± 0.4	151.8 ± 27.5	211.7 ± 2.0
17:0 *anteiso*	23.5 ± 30.6	1.7 ± 0.4	144.0 ± 18.8	41.2 ± 1.8
16:2ω4	–	0.9 ± 0.1	–	–
17:0	229.0 ± 38.5	1.5 ± 0.2	–	8.9 ± 15.5
17:1	–	1.8 ± 0.3	223.7 ± 2.3	377.2 ± 3.8
18:1ω9	310.2 ± 6.8	9.5 ± 0.4	2288.4 ± 41.9	210.1 ± 8.7
18:1ω7	76.3 ± 47.4	7.7 ± 0.2	–	280.2 ± 9.7
18:2ω6	298.6 ± 226.8	5.5 ± 0.1	936.4 ± 11.9	400.7 ± 5.5
18:3ω6	39.9 ± 12.7	0.8 ± 0.0	175.4 ± 3.9	–
18:3ω3	51.3 ± 7.7	1.0 ± 0.0	2034.3 ± 22.6	2171.0 ± 31.1
18:4ω3	120.2 ± 119.4	0.8 ± 0.0	651.0 ± 11.6	525.3 ± 12.1
20:1ω9	–	0.5 ± 0.2	11.4 ± 19.8	33.9 ± 3.6
20:1ω7	–	0.6 ± 0.1	–	–
20:2	92.1 ± 57.3	0.8 ± 0.0	–	–
20:3ω6	–	0.5 ± 0.0	–	–
20:4ω6	53 ± 4.6	2.0 ± 0.1	117.5 ± 4.6	52.1 ± 2.8
20:4ω3	33 ± 4.1	–	57.4 ± 3.2	69.7 ± 3.9
20:5ω3	–	7.5 ± 3.3	197.5 ± 8.5	88.3 ± 3.4
22:1ω9	70.0 ± 56.6	–	–	–
22:2	92.9 ± 7.8	–	–	–
22:4ω3	128.3 ± 40.8	1.5 ± 0.0	66.8 ± 3.7	–
22:5ω6	–	0.7 ± 0.2	52.8 ± 5.6	–
22:5ω3	29.0 ± 1.3	0.6 ± 0.1	341.6 ± 20.9	102.1 ± 3.6
24:0	269.0 ± 79.0	15.8 ± 0.2	–	68.5 ± 3.3
22:6ω3	78.1 ± 14.1	0.8 ± 0.0	–	–
24:1	35.5 ± 1.6	–	–	–
26:0	166.9 ± 3.5	13.4 ± 0.4	–	–
28:0	75.1 ± 20.9	1.3 ± 0.1	–	–
30:0	341.6 ± 133.6	17.7 ± 1.0	–	–
32:0	154.1 ± 46.5	1.4 ± 0.1	–	–
Σ Saturated FAs (SAFAs)	9906.1 ± 1146.3*	128.9 ± 12.4*	5413.0 ± 243.6*	4571.2 ± 411.9*
Σ Monounsaturated FAs (MUFAs)	588.8 ± 249.3*	42.6 ± 3.8*	2856.1 ± 352.1*	1700.0 ± 375.5*
Σ Polyunsaturated FAs (PUFAs)	1016.4 ± 496.5*	23.3 ± 4.1*	4630.6 ± 96.4*	3409.1 ± 62.3*
Σ Odd branched FAs (BrFAs)	57.2 ± 38.0	11.8 ± 2.4	295.9 ± 46.2	252.8 ± 3.
Σ Long chain FAs (LCFAs)	737.7 ± 204.6	33.8 ± 1.6	–	–
Σ Bacterial FAs (BFAs)	57.9 ± 38.4	15.3 ± 2.5	295.9 ± 46.2	255.5 ± 3.9
Σ Essential FAs (EFAs) ω3 & ω6	831.3 ± 431.5	21.6 ± 4.0	4630.6 ± 96.4	3409.1 ± 62.3
Σ Green macroalgae biomarkers	389.8 ± 247.2	7.2 ± 0.2	3146.1 ± 38.4	2571.7 ± 36.6
Σ Diatom biomarkers	–	7.5 ± 3.3	197.5 ± 8.5	88.3 ± 3.4
Σ Dinoflagellate biomarkers	198.3 ± 133.5	1.7 ± 0.0	651.0 ± 11.6	525.3 ± 12.1
Σ Microalgae biomarkers	198.3 ± 133.5	9.1 ± 3.4	848.4 ± 20.1	613.6 ± 15.4
Σ Fatty acids (FAs) μg g^{-1} dry weight	11 800.5 ± 827.7	222.6 ± 0.7	14 412.0 ± 195.8	10 573.4 ± 328.8

Values are (means ± SD); $n = 3$; – non-detected or traces; *includes fatty acids not indicated in this table.

green macroalgae, were detected abundantly in the filaments of *E. intestinalis* and *U. pertusa*, total markers in each species were 3146.1 and 2571.7 μg g^{-1} dry weight, respectively. The total FAs in plants and mangrove surface sediments were higher than in the intertidal surface sediments. Total FAs concentration in the intertidal surface sediments was the highest in spring (Fig. 5g).

3.3. Distribution of FA biomarkers in surface sediments

All FA markers were significantly higher in the mud flat (100–300 m from mangrove) than in the sand flat (400–600 m from mangrove). There was a significant difference in the absolute concentrations of FA biomarkers of organic sources detected in the surface

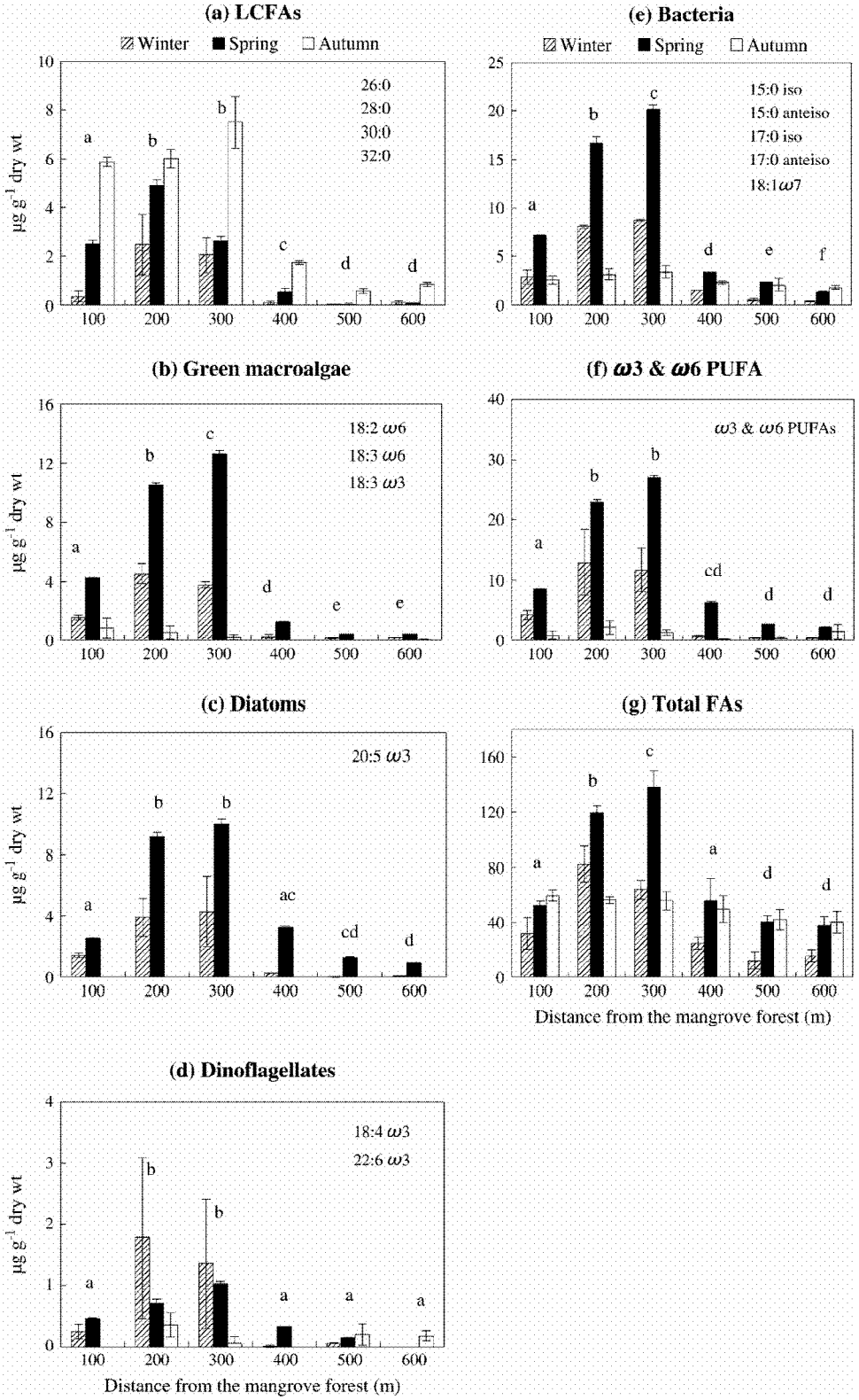


Fig. 5. Comparison of the contribution of fatty acid biomarkers of organic sources and total fatty acids (FAs) in the estuarine surface sediments during winter, spring and autumn seasons. Lower case letters signify post hoc Fisher's protected least significant difference (PLSD) results and indicate significant differences between distances. Bars with different letters are significantly different. Values are means (±SD).

sediments among the three seasons (winter, spring and autumn) (MANOVA, Pillai's trace, $p < 0.0001$) and sites (MANOVA, Pillai's trace, $p < 0.0001$). Statistical analysis also indicated a significant interaction between season and site (ANOVA, $p < 0.0001$) (Fig. 5), which indicated that both season and distance from the mangrove forest affect the concentration of FA biomarkers of organic sources in the surface sediments. Further, ANOVA test indicated significant differences in the concentration of LCFAs, and all fatty acid markers of organic sources and ω3 and ω6 PUFAs, with distance from the mangrove forest ($p < 0.001$) (Fig. 5a). All fatty acid markers differed significantly among seasons (LCFAs $p < 0.0001$; green macroalgae $p < 0.0001$; diatoms $p < 0.0001$; BFAs $p < 0.0001$; ω3 and ω6 PUFAs $p < 0.0001$) except fatty acid markers of dinoflagellates ($p = 0.3571$), 18:4ω3 and 22:6ω3 (Napolitano et al., 1997; Carrie et al., 1998) (Fig. 5e). Fatty acid markers that differed significantly among the three seasons were therefore potentially useful in assessing the outwelling of POM from mangroves and the autochthonous sources of organic matter in the estuarine intertidal sediments.

3.4. Carbon, nitrogen and phosphorus in the surface sediments

There were significant differences in the mean concentrations of N, P and the C:N ratios of the surface sediments among seasons and sites, with a significant interaction between the two factors (ANOVA, $p < 0.0001$). There were significantly higher N and P concentrations and significantly lower C:N ratios in the surface sediments during spring than during winter and autumn (ANOVA, $p < 0.0001$). Highest N and P concentrations were restricted to 300 m from the mangrove forest; the concentrations declined sharply 400–600 m away from the mangroves (Fig. 6).

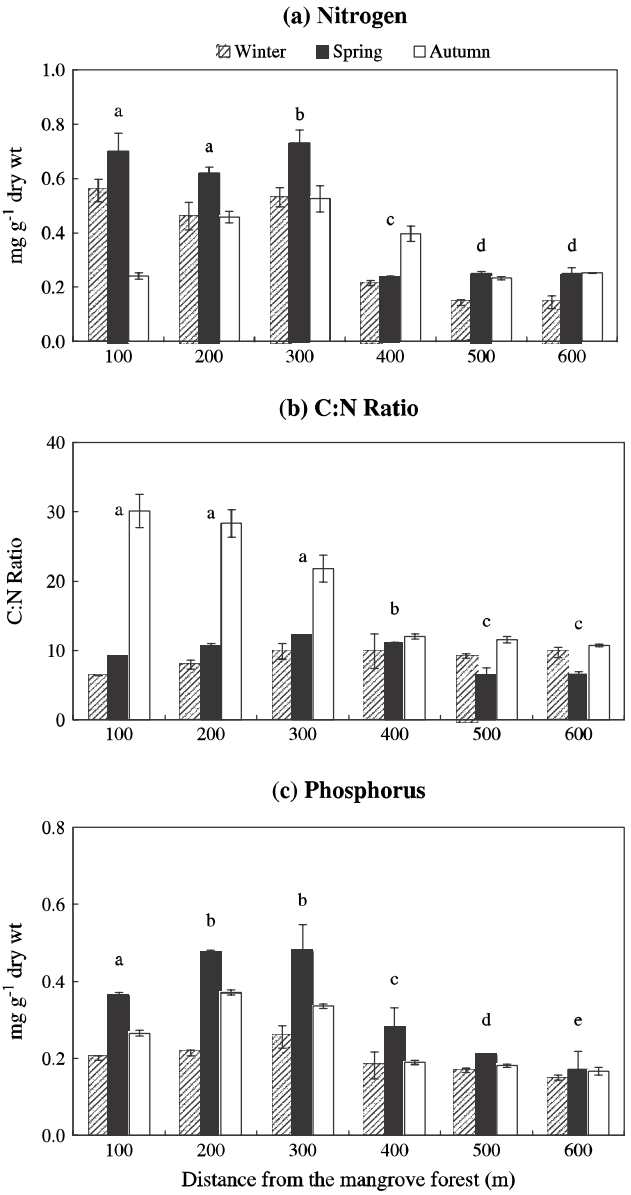


Fig. 6. Comparison of the concentrations of total nitrogen, C:N ratios and phosphorus in the estuarine surface sediments during winter, spring and autumn seasons. Lower case letters indicate post hoc Fisher's protected least significant difference (PLSD) results and signify significant differences between distances. Bars with different letters are significantly different. Values are means (±SD).

4. Discussion

4.1. Spatial and seasonal variations in litter fall

Spatial variations in litter fall rate have been related to specific growing conditions such as tidal inundations, water turnover (Wafar et al., 1997), soil salinity (Pool et al., 1975; Wium-Andersen and Christensen, 1978) and tree heights, with low litter fall rates in the short stands (Woodroffe, 1985). In contrast, there was no significant difference in litter fall rates between the two study sites in the present study, located in the upper intertidal (ST1) with tall trees (mean 7 m), and another site located in the lower intertidal (ST2) with short trees (mean 4 m). This was probably due to a small difference in average tree height between the two sites, and to a greater tidal inundation and more flushing with freshwater which may have improved the growing conditions (Wafar et al., 1997), resulting in increased leaf growth, senescence and consequently, litter production at ST2.

Mangrove litter production also varies seasonally (Woodroffe, 1982; Steinke and Ward, 1988; Lu and Lin, 1990). These variations have been previously reported as related to storm conditions (Pool et al., 1975; Goulter and Allaway, 1979; Woodroffe, 1982) and to rainfall (Tam et al., 1998). In the present study, the highest litter component fall rates, except fruits, were recorded during the autumn season, which could be attributed to

increased wind speed and rain during the typhoon storms. The lowest litter fall rate was recorded in winter due to reduced mangrove production and growth, as a result of decrease in average and minimum temperature of both air and soil (Clough, 1992).

The more frequent typhoons on the island during autumn could be the main reason for the slightly higher total annual litter fall rate, 12.95 t ha^{-1}, than reported from other subtropical studies: 8.8 t ha^{-1} in a *Bruguiera gymnorrhiza* community, Iriomote Island, Japan (Kishimoto et al., 1987); 8.61 t ha^{-1} in South Africa (Steinke and Charles, 1984); and 11.7 t ha^{-1} in a *Kandelia candel–Aegiceras corniculatum* mangrove community, Hong Kong, China (Tam et al., 1998). Of the litter components, leaf litter accounted for >70% of total annual litter, similar to other study findings (Steinke and Ward, 1988; Chale, 1996; Twilley et al., 1997).

4.2. Outwelling of particulate organic matter from mangroves

The detection of LCFAs, markers of vascular plants, in the surface sediments of Oura Bay estuary indicates that outwelling of POM from mangroves occurs in all seasons, and increases consistently with increases on litter falls. Nevertheless, it is the weakest in winter possibly due to the decline in total litter production, and it is the strongest in autumn (significantly higher LCFAs markers, Fisher's PLSD, $p < 0.001$) likely due to increased total litter production (Figs. 3–5a). The total litter production was also found to correlate more significantly with LCFAs ($r = 0.50$, $p < 0.0344$) than other markers of organic sources, and also with wind speed ($r = 0.899$, $p < 0.0001$), temperature ($r = 0.644$, $p < 0.0174$) and rainfall ($r = 0.525$, $p < 0.0655$), which suggested that, the temporal variability in the magnitude of organic matter outwelling from mangroves and its contribution into the intertidal surface sediments is mainly influenced by wind speed (accompanied with rainfall during typhoon storms) and temperature.

Furthermore, results show that the amount of POM derived from mangroves is mainly restricted to within 300 m from the mangrove forest, and further away the detection of LCFAs markers including other FAs declined drastically in all seasons (Fig. 5). This restriction in the flow of POM from the mangrove ecosystem may be related to the geomorphology of the tidal basin (Robertson et al., 1992; Lee, 1995). The tidal basin in Oura Bay is flat and wide just adjacent to the mangroves up to 300 m. Between 300 m and 400 m, the basin width is reduced to form a narrow deep channel passing under a bridge (Fig. 1). Just before this channel at the site located 300 m from the mangroves, is where most of the exported POM deposited likely due to reduced water velocity. Away from the bridge, the tidal basin receives very little POM from the mangrove forest (between stations 400 m and 600 m).

Previous studies have indicated that river dominated habitats are characterized by strong outwelling of POM from the mangrove forest (Woodroffe, 1992). The river channel in Oura was regulated by building concrete banks, which increased the width of the channel. The regulation of the riverbanks possibly resulted in the reduction of current velocity and probably its influence on outwelling of POM. However, the river is thought to cause strong outwelling of POM during the rainfall season when the channel floods, as previously noted by Meziane and Tsuchiya (2000). This indicates that outwelling is reduced when rainfall is low and that during the rainfall season the forest may receive some terrestrial inputs.

4.3. Importance of autochthonous POM to the tidal flats

Seaweed detritus is typically richer in nutrients than vascular plant detritus (Tenore et al., 1982). Mangrove detritus is characterized by high C:N ratios and poorer nutrients than algal detritus (Robertson, 1988; Mfilinge et al., 2002). High C:N ratios in the intertidal flats adjacent to mangroves have been related to increases of mangrove outwelling (Boto and Bunt, 1981). Likewise, in freshwater wetlands, Wetzel (1983) reported an increase in the C:N ratio due to input of a greater proportion of organic content from vascular plant material produced in the wetland and littoral marsh areas. This also suggests that a low C:N ratio would probably indicate a relative lower input of organic material from mangroves and/or a higher contribution of algal material.

An increase of organic matter input in the surface sediments of the Oura Bay intertidal flat was indicated by an increase in total FAs during spring (Fig. 5g). In particular, there was a high share of highly unsaturated FAs (three or more double bonds) in the FA composition of surface sediments in comparison to other seasons, an evidence of a high input of fresh algal detritus (Carrie et al., 1998). The absolute concentrations of FA markers of green macroalgae 18:2ω6, 18:3ω3 and 18:3ω6, diatoms 20:5ω3 and dinoflagellates 18:4ω3 and 22:6ω3 were higher in winter–spring than in the autumn season. The high concentrations in spring are likely due to the incorporation of decomposed macroalgal and microalgal material in the surface sediments (Fig. 5b–d) and were confirmed by the increase in N and P of these surface sediments (Fig. 6a,c). Therefore, the high concentration of algal markers and the low C:N ratio of the surface sediments coupled with a significantly low litter fall and significantly low LCFAs markers during winter and spring (Fisher's PLSD, $p < 0.001$), indicate that in these

seasons, autochthonous sources contributed more substantially to organic input than mangroves.

In autumn, the high C:N ratios on the surface sediments, and the high concentrations of LCFAs markers consistent with the increases in litter fall, suggest a greater input of vascular plant or organic material produced in the mangroves. This was also supported by a positive correlation between C:N ratios and total litter fall ($r = 0.696$, $p < 0.0013$), and between C:N ratio and LCFAs markers ($r = 0.808$, $p < 0.0001$) in the intertidal surface sediments. The lowest absolute concentrations of green macroalgae, dinoflagellates and the absence of diatom markers during autumn may indicate that the contribution of autochthonous sources of organic matter to intertidal surface sediments was not substantial.

Bacterial markers were more important in the fatty acid composition of the mud flat (100–300 m) and sand flat (400–600 m) surface sediments at each site during spring than in winter and autumn (Fisher's PLSD, $p < 0.001$) (Fig. 5e). Furthermore, these markers concentration was significantly (Fisher's PLSD, $p < 0.001$) lower in the sand surface than in the mud surface. This difference is probably due to higher nutrient input and organic matter quality in the mud flat and because of a lower specific surface, C influx and retention of C, N and P on sand sediments (Alongi, 1994).

The significant increase in bacterial markers during spring compared to winter and autumn likely indicates an increase in bacterial abundance in the sediments. The BFA markers were found to correlate more significantly with algal markers; green macroalgae ($r = 0.988$, $p < 0.0001$), diatoms ($r = 0.966$, $p < 0.0001$) and dinoflagellates ($r = 0.671$, $p < 0.0023$) than with LCFA markers ($r = 0.318$, $p < 0.1985$), and were negatively correlated with total litter fall ($r = -301$, $p < 0.2247$), which suggest that increase in bacteria was probably due to the presence of algal material rather than mangrove-derived POM. In another investigation, Alongi (1989) found that additions of exported mangrove detritus in near shore sediments did not affect bacterial densities and suggested that the exported litter was highly refractory and of poor nutritional quality. This suggests that poor nutritional quality of mangrove detritus does not stimulate bacterial colonization as much as algal matter does. Given the high nutrient content of seaweed and diatom detritus (Tenore et al., 1982), the significant increase in bacterial abundance in spring was likely due to the decomposition of benthic algae and their detritus.

4.4. Sources of ω3 and ω6 PUFAs

Green macroalgae contain higher concentrations of ω3 and ω6 PUFAs than mangrove leaves and mangrove sediments (Table 1) (Mfilinge et al., 2003). However, during decomposition algal material lose their PUFAs faster than vascular plants, and high levels of these acids in the sediments indicate high input of fresh algal detritus (Carrie et al., 1998). Litter fall rate increased during spring through autumn. But the low concentration of PUFAs in mangrove leaves, and the low concentration of these PUFAs in the surface sediments during autumn, a season associated with maximum litter fall and strong outwelling, and the elevated levels of these PUFAs during spring (seasonal peak of macroalgae degradation) suggest that a large proportions of the ω3 and ω6 PUFAs detected in the surface sediments originated from decomposing algal material rather than from mangrove-derived POM. This was also supported by a significant correlation between ω3 and ω6 PUFAs and algal markers; green macroalgae ($r = 0.986$, $p < 0.0001$), diatoms ($r = 0.989$, $p < 0.0001$), dinoflagellates ($r = 0.725$, $p < 0.0007$), and bacterial markers ($r = 0.983$, $p < 0.0001$). A negative correlation between ω3 and ω6 PUFAs and total litter fall ($r = -0.432$, $p < 0.0737$) suggested that mangrove detritus contribution to PUFAs in the surface sediments was probably not substantial.

Other studies indicate that invertebrates can affect sedimentary lipid distributions (Bradshaw et al., 1989, 1990) and may influence PUFA concentrations in surface sediments. Although the biomass of benthic invertebrates was not determined in this study, invertebrates such as fiddler crabs are known to appear abundantly and active on the surface sediments during spring, summer and autumn, and inactive during winter. Meziane et al. (2002) found that food pellets and feces of fiddler crabs contained lower amounts of ω3 and ω6 PUFAs than their surrounding surface sediments and concluded that the crabs foraging activities do not enrich the sediments with ω3 and ω6 PUFAs.

It is also important to point out that PUFAs are relatively labile (Smith et al., 1983), and their half-lives are of order of days in POM present in the water column and in deep oceanic detritus (Conte, 1989). In such a case a use of a lability index is recommended in order to reduce the multi-dimensional biomarker information into single quantitative measure of changes in organic matter lability (Conte et al., 2003). However, in coastal sediments, decomposing algal blooms and probably mangrove detritus, contain large amounts of high molecular weight humic material, which may protect lipids not enclosed within cellular structures e.g. diatoms (Harvey et al., 1983; Smith et al., 1983) and probably dinoflagellates. The structural lipids of these cells may remain unchanged when the cell was living and therefore can be easily extracted by lipophilic solvents (Smith et al., 1983).

A study by Mfilinge et al. (2003) indicated that a higher amount of PUFAs in decomposing *Bruguiera gymnorrhiza* was detected in the old detritus (8–18 weeks) than in the fresh detritus. Meziane and Tsuchiya

(2000) also indicated that blooms of diatoms were clearly indicated by a better contribution of their respective markers in the surface sediments during summer than winter. These two examples suggest that tracers can be used semi-quantitatively assuming that the lability affects all markers and therefore it is by nature comparable.

In conclusion, the data presented in this study suggest that outwelling of mangrove-derived POM varies seasonally and spatially in Oura Bay estuary. The seasonal variations in mangrove outwelling seem to be related to mangrove litter fall dynamics, and to climatic conditions, particularly wind speed and temperature. Of the exported material, a significant proportion ends up in the adjacent mud flat and a very small amount reaches the sand flat. Results further suggest that during winter and spring when mangrove litter production is the lowest, autochthonous sources of organic matter, particularly macroalgae, become the major sources of organic matter rather than mangrove POM in Oura Bay estuary. This seasonal variation in organic sources may have beneficial implications to macrozoobenthic communities and in the food webs, as animals, after an inactive winter, may take advantage of a higher quality detritus (macroalgae) and bacteria during spring.

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