Interactive comment on “Small scale variability of geomorphological settings influences mangrove-derived organic matter export in a tropical bay” by Geraldina Signa et al.

Anonymous Referee #1

Received and published: 22 September 2016

Comments

The authors of this paper have investigated changes in mangrove outwelling to seagrass beds and coral reefs over seasons in Gazi Bay, Kenya. Mangrove forests are highly productive-ecosystems and have important implications for the exchange of organic material in the tropical coastal seascape. They have combined more traditional analyses (isotopes) with modern techniques (fatty acids) to explain the source contributions and spatial distribution of organic material across the bay. In addition they also investigated how physical factors such as tidal exchanges, river runoff and season may affect the exchange of organic material between different habitats.

The authors state they have found significant differences in transport of organic material from mangrove forest creeks to adjacent systems. This was primarily due to river runoff and tidal transport. However the river runoff creek was influenced strongly by the rainy season. Interestingly the authors found that macroalgae also had a contribution to organic material, this ecosystem is often ignored in the tropical seascape.

The paper is of an interesting subject with new techniques applied. There is a dearth of data regarding the outwelling of mangroves with physical factors taken into account especially with respect to connectivity. It is quite well written and structured. The abstract and introduction are well done and flow nicely. There are minor comments on these sections. I admire the authors for doing such a through job on this study, they have tried to expand our understanding using new techniques in addition they must have worked very hard. It is not easy to complete fieldwork over two seasons and fatty acids are very labor intensive. However, I have some concerns regarding the methodology, results and major concerns (section 4.2) regarding the discussion.

Methodology

No statistics were used to compare the isotopes sources. This makes it difficult to understand the patterns in the data the authors state. The changes the authors saw in the organic material sources did not seem statistically significant nor could was it shown in the figures. A statistical test would resolve this.

R: We agree with the reviewer that statistical tests were needed to support our results and discussion. Consequently, we have performed permutational multivariate ANOVA (PERMANOVA) both on d^{13}C and C/N values of organic matter sources and on the outputs of the Bayesian models (lower and upper limit of the credibility intervals, mode and mean). In both cases, the outcomes of the analysis highlighted that the patterns described in the text were significant, hence the main message of the manuscript was unchanged. PERMANOVA on the Bayesian mixing models will be showed in a new (now Table 1).

Results

The figures depicting the results are numerous and difficult to understand. Several of the tables/figures could go into the supplementary section (even though there is already data in this section), other figures need to be edited for clarity and others could be drastically improved by a different method of illustrating them. Several issues in the discussion may be due to the difficulty in understanding the figures. In addition I and I think others would find it easier if at some points the authors specified which creek applied to transects A and B, it was annoying to keep on referring to the methodology to understand which was which.

R: We thank the reviewer for his/her constructive comments. Consequently, we have made several changes in tables and figures (described in more detail below). Moreover, throughout the manuscript, we refer to the creek name, together with the transect letter.

For example, section 3.1.2, line 7- I am not sure if “often” is the correct word to use. They seemed to be almost always overlapping.

R: We have changed "often" with "overall". P. 9 L. 2

Table 1 and 2 could go in the supplementary material. Table 1 especially should be in the supplementary material.

R: Both Table 1 and 2 are in supplementary materials (Suppl. 1 and 2).

Figure 1 is badly drawn. The labels for the ecosystems do not seem to correspond to where the ecosystems are although I understand that the authors found it difficult to place them on the actual systems. The map looks amateurish.

R: We have changed Figure 1 to improve clarity. The names of the stations have been placed in the right position. “Creek” and “river” have been added to the watercourse names. Moreover, we have drawn both coastline and transects.

Figure 2 is a very difficult figure to understand at first glance. For example if mangrove leaves are a source (symbol is a cross) then why are they not deceasing in size similar to the other sources? In addition the symbols decreasing in size do not help comprehension of the figure. This information may be better shown in a table.

R: We agree with the reviewer 1 that Figure 2 is not clear as it was drawn in the previous draft. Nevertheless, we think it is more appropriated to keep a figure for representing isotopic and elemental data, rather than drawing a table, because the scatter plot draws together both variables and allows to see reciprocal trends at a first glance. Hence, we have changed the figure to make it clearer and more understandable. The sources from the different stations have been drawn in different colors instead of different size. There is only one symbol for mangrove leaves (the black cross) because they were collected only in the mangrove stations, as we will specify in the manuscript.

Figure 4 and 5. Could this be done better as a percentage column graph? From my comments on the discussion, I found it difficult to see the patterns the authors stated were there.

R: Figures 4 and 5 represent the probability distributions that a certain source contribute to the two abiotic compartments studied: SOM and SPOM. Hence, it is important to show the entire credibility interval, indicating both the modes and the upper and lower limits of the 95% credibility interval. Anyway, we agree with the reviewer that the patterns described in the text are not always evident from the figures. To address this issue, we have performed a statistical analysis (PERMANOVA) and changed the whole paragraph to make clearer the description of the patterns.

Figure 6, should either be deleted, put into a table or put into the supplementary material.

R: Figure 6 has been deleted.

Discussion

In the first section (4.1) of the discussion the authors state (pg 11 Line 2-5) that the depleted 13C in seagrasses and macroalgae could be due to the different physical settings of the two creeks. The depleted 13C in seagrasses and macroalgae is also referred to in the results but I cannot see how this can be inferred by the associated figure. The explanation is plausible but I cannot see the evidence from the data the authors refer to. It would be easier to understand if this figure (fig.2) was represented in a table.

R: We agree with the reviewer that figure 2 is not clear enough. Now we have modified the figure to make it clearer, and the trends described in the text have been also changed to be more intelligible. In the right panels (transect B corresponding to Kinondo creek), $\delta^{13}C$ values of macroalgae and seagrasses from the mangrove stations (black diamonds and circle respectively) are more negative (macroalgae ~ -25‰; seagrasses ~ -20‰) than those represented in the left panels (macroalgae ~ -20‰; seagrasses ~ -15‰). Moreover, PERMANOVA confirmed that these differences were significant.

Section 4.2 states that mangrove derived material from Kinondo Creek greatly contributed to the sedimentary pool and moving seaward decreased its contribution until dropping steeply in the coral reef. This is true for fatty acids (fig. 7) but I cannot see from the isotopes (fig. 4 and 5) how the authors came to this conclusion. In transect B (Kinondo Creek), mangrove derived material does contribute to the sediment although I would not state it contributed the most nor does it decrease from mangrove forests to seagrass beds, at some points it increased its contribution! However the authors are correct in that its contribution steeply drops off at the coral reef. The authors also state that the transect A, due to the influx of freshwater the export of mangrove derived material is further and indicates a significant contribution to the whole bay. Again this explanation is plausible and the authors place their explanation well within the known literature. But if Figure 4 and 5, which are suppose to represent this pattern, they do not show this. Considering that the authors state that there is a difference between the creeks, I cannot see a statistical significant difference between the two transects from the figures. However their explanation is plausible and I wonder if the wrong data is being shown? The fatty acids do confirm the authors explanation, not the isotopes.

R: Thanks to the reviewer's comment, we have revised the whole isotopic dataset and actually there were a few typos: mean $\delta^{13}C$ (± ds) of macroalgae from the intertidal area along transect A (-20.08 ± 0.66 ‰ instead of -20.63 ± 1.41 ‰) and along transect B (-21.79 ± 1.44 ‰ instead of -20.12 ± 0.89 ‰) and the mean $\delta^{13}C$ (± ds) of seagrasses from the mangrove area along transect B (-20.23 ± 1.74 ‰ instead of -19.34 ± 2.83 ‰). Nevertheless, the patterns of the contribution of organic matter sources to SOM and SPOM did not change significantly. We agree with the reviewer that the patterns described in the text are not striking from figures 4 and 5. Hence, we have run PERMANOVA to test for differences among seasons, transects and stations and results highlighted significant differences in all cases. Pair-wise tests among stations were always significant too. Moreover, we have modified this paragraph, softening the discussion about mixing models outcomes and focusing more on fatty acid results.

Section 4.2 (pg 12, lines 7-9), the authors should include a line or two regarding seasonal changes in litter fall. Avicennia sp. in Brazil will lose their leaves only directly between seasons whilst Rhizophora sp. have leaf fall continuously over the seasons.

R: We are grateful to the reviewer for this interesting comment. We have added a few lines on the seasonal variability in litterfall in Gazi Bay. P. 14 L. 5-7

All other comments for the discussion are minor.

Minor comments

Pg 2, line 20. Hemminga et al. 1994 is a eminent paper but not a recent one.

R: We have removed Hemminga et al. 1994.

Line 26. Wave power is not the correct word to use here.

R: We have changed "wave power" with "wave action". P. 2 L. 27

Pg 3, line 6-10. Nitrogen isotopes are also used and should be mentioned here.

R: d^{15}N is a powerful tool to identify diet and trophic levels of consumers in natural ecosystems, rather than to trace organic matter sources. This is because tracing organic nitrogen food sources is complicated by trophic enrichment, and then it is rarely used to this end. Consequently, we think that mentioning nitrogen stable isotopes here would be misleading.

Line 23, A reference should be given for rainfall magnitude.

R: We have added a reference. P. 3 L. 25

Pg 4, line 19. What is the depth of the coral reef?

R: We have added this information. P. 4 L. 24

Line 23. “unless low groundwater discharge” please re-write for clarity.

R: We have rephrased the sentence to improve clarity. P. 4 L. 27

Line 24. What are the high flow rates?

R: We have added this information. P. 5 L. 2

Line 27. “ones” is not a scientific word.

R: We have changed "ones" with "flows”. P. 5 L. 5

Pg 5, line 2 “one” not a scientific word.

R: We have rephrased the sentence to remove the word "one". P. 5 L. 5-8

Line 8. “ones” not a scientific word.

R: We have rephrased the sentence to remove the word "ones". P. 5 L. 12-15

Line 14. How much volume of sediment was collected in the cores?

R: The cores were approximately half-filled but only the first 5 cm were used for the analysis, as specified in the text. P. 6 L. 2-3

Line 15. How were the seagrass leaves and macroalgae sampled, plucked?

R: We agree that the sentence was not clear. We did not collect the leaves, but the whole shoots (seagrass) and thalli (macroalgae). Hence, we have changed the sentence to specify this. P. 5 L. 21-23

Line 18. How were the samples kept cool and dark before arrival?

R: We have added "in a cool box". P. 5 L. 25

Line 27. What type of micro mill was it?

R: We have added the model of the micro mill. P. 6 L. 8; 11

Pg 6, line 6. The equation could be presented much more clearly.

R: The equation has been centered in the page and spaces will be inserted to improve clarity and readability. P. 6 L. 15

Line 10. I cannot understand what you did from this sentence.

R: A more detailed description of the lipid extraction method has been provided. P. 6 L. 17-23

Line 25. Why did you not also look at terrestrial sources, two lines in the introduction should provide some justification for not using terrestrial sources.

R: Mangroves are the dominant terrestrial sources in the area as highlighted by previous research, but agricultural runoff from the sugar plantations surrounding the forest might also flow into the watercourses. We have specified both information: the former in the Introduction section (P. 4 L.11) and the latter in the Materials and methods section (P. 5 L.2-3). Moreover, we have also taken into account the potential contribution of agricultural runoff through the fatty acid approach, as suggested by reviewer 2.

Pg 11, line 19. Do you mean the transects when you state “stations”.

R: We agree that the sentence was not clear because we meant stations, not transects. Now we have changed the sentence to clarify our point of discussion. P. 13 L. 8-12

Pg 12, line 21. When was the timing of the other studies?

R: The timing of sampling is not specified in Bouillon et al (2007). In contrast, Hemminga et al (1994) sampled at both ebb and flood tide. The spatial gradient of the SPOM d^{13}C found by Hemminga et al (1994) at ebb tide was similar to that found in this study. Hence, we mentioned only Hemminga et al 1994 highlighting the comparable trend. P. 14 L. 19-20

Line 22-25. I find this line confusing and had to read it several times to understand what the authors were meaning.

R: We agree with the reviewer that the sentence was confusing. Now we have changed the sentence as follows: “Despite the buffering role of seagrass beds in preventing a direct connection between mangrove and oceanic waters, we infer that high mangrove export coupled with high rate of water exchange at spring ebb tide has favoured the outwelling of suspended mangrove material up to the coral reef inner area”. P. 14 L. 22-25

Interactive comment on “Small scale variability of geomorphological settings influences mangrove-derived organic matter export in a tropical bay” by Geraldina Signa et al.

T. Meziane (Referee)
meziane@mnhn.fr
Received and published: 28 September 2016

General comments:
This paper deals with the fate of the mangrove derived organic matter in relation with local geomorphological differences. Using elemental, isotopic and Fatty acids markers, the authors emphasize the combined role of the tide and the riverine water runoff in the distribution of the Mangrove organic matter. This paper is the latest of a long series of studies that characterised OM in Gazi Bay. The “plus” of this paper is the recording of FAs data and the fact that two seasons were sampled. Therefore, the main finding of this paper is the seasonal differences in term of export, which help to better understand the OM dynamic in the Bay; the combined control of tide and runoff is not something exceptional as this is a general feature of estuarine mangrove and this must have been anticipated.

R: We agree that the combined effect of runoff and tide, together with rainfall and wave action is a general feature of tropical estuarine systems. Indeed, this point was already mentioned in the previous version of the manuscript. Now we have strengthened further this point. P. 2 L. 26 - P. 3 L. 6

The paper is well written and organised with however overstretching use of the fatty acid method.
I have several concern, some I share with the other reviewer, I already read the comments, such as the statistical issues.

R: Following the reviewer’s comments, we have dampened the use of the fatty acid approach (see specific comments below). As for the statistical analysis we have carried out permutational analysis of variance (PERMANOVA) to test for spatio-temporal differences in isotopic and elemental signatures of organic matter sources and in their contribution to SOM and SPOM, using the outcomes of the Bayesian mixing models (lower and upper limit of the credibility intervals, mode and mean) as variables.

My main concern is on the manner how fatty acids were ascribed to sources is this study. The Fatty acid markers method, have evolved quiet a lot in the recent years. The use of FAs in a qualitative, at best semi-quantitative, manner (%) need some precautions when it comes to comparing them in living tissues and to extrapolate these relative contributions to “non living” matter in the environment. The conservative feature of these markers do not apply in sediment or POM and most of the fatty acids, at least most of those used in this study, cannot be ascribed solely to one particular source. It is probably not necessary to analyse microorganisms such as Bacteria but it would have been suitable to look at the composition of microalgae and terrestrial sources that can be brought by water draining. Indeed, relating 20:5w3 to red algae is not a good assumption when this FA is readily present in diatoms and/or other brown algae who seem to be dominant in this bay. The question is the big amount of brown algae (+ diatoms) with low % can be of less impact than red macroalgae with high % of 20:5w3 but low biomass? Also, 18:3w3 is also found in large amounts if terrestrial leaves and is more labile than LCFAs in sediments. 18:2w6 is very common in wastes and agriculture waters and we don’t have indication about these possibilities in the Method’s section. Also there in no indication about the seasonal changes that may affect the composition of sources which certainly can moderate here or there their relative contributions at the surface sediments as well as in the SPOM. A better knowledge on available sources and how their productions are impacted by seasonal patterns would have render this spatially restricted study to be less speculative in term on fatty acids evidences.

R: We are very grateful to the reviewer for the stimulating comments. Now we have softened the use of many FA tracers, using much more caution than in the previous version of the manuscript. In particular, now we have treated 18:3 n3 as a combined marker of mangroves and seagrasses and 18:2 n6 as a combined tracer of seagrasses and agricultural runoff from the sugar plantations diffused around the bay (we have also added this information also in the Method's section). In addition, for both fatty acids, we have taken into account the potential lability due to decomposition as a discussion point for explaining their low relative abundance in SOM and SPOM. As for 20:5 n3, SIMPER results highlighted high 20:5 n3 content in red algae, and not in brown algae, hence, we have treated this FA as a combined tracer of diatoms and red algae. Moreover, as suggested by the reviewer 1, we have discussed the seasonal variability of mangrove litterfall to explain the seasonal patterns recorded in this study. Seasonal and spatial variability was detected also in bacterial biomarker and has been discussed in the manuscript.

Other comments
Introduction P4L10 : typo : approaches

R: The typo has been corrected.

P4L2 : it is important de say if it is a qualitative or quantitative contribution

R: We have rephrased the sentence pointing out that the contribution of dominant primary producers to sedimentary and suspended particulate organic matter pools was assessed based on quantitative (isotope mixing models) and semi-quantitative (fatty acid profiles) approaches. P. 4 L. 13-16

M&M : P 6 L18: Here and the entire paper, including tables and figures; the terminology of saturated Fatty acids is not properly defined : the is one “0” to much 23:0 instead of 23:00 and so on for all the paper.

R: We have corrected the FA nomenclature through the paper.

P7 L4: I am puzzled by the transformation arcsine square root because % data are “transformed “ (total 100%) which means that they have to be used as it is.

R: Proportional fatty acid (percentage of total FAME) data require transformation to meet the assumption of multivariate normality (Budge et al. 2006). The arcsine square root transformation is commonly used for proportional fatty acid data (e.g. Iverson, 2009; Thiemann et al., 2011; Raymond et al., 2014).

Budge, Suzanne M., Sara J. Iverson, and Heather N. Koopman. "Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation." Marine Mammal Science 22.4 (2006): 759-801.

Iverson, Sara J. "Tracing aquatic food webs using fatty acids: from qualitative indicators to quantitative determination." Lipids in Aquatic Ecosystems. Springer New York, 2009. 281-308.

Thiemann, Gregory W., et al. "Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore." Oikos 120.10 (2011): 1469-1478.

Raymond, Wendel W., Alexander T. Lowe, and Aaron WE Galloway. "Degradation state of algal diets affects fatty acid composition but not size of red urchin gonads." Marine Ecology Progress Series 509 (2014): 213-225.

P7 L10 : using SIMPER to identify potential FAs is somehow wrong , SIMPER give you what are the FA that contribute the most to the similarity . A small contribution of a “specific” FA, say a Branched one for Bacteria, would be a enough to trace the OM and still, will not show up in the best five of the primer analysis. This practice adds confusion on the data that are % but discussed in a quantitative manner.

R: SIMPER is a common routine to identify fatty acids that contribute to similarity within groups and dissimilarity between groups. We agree with the reviewer that this approach can be misleading in some cases. However, in this study, we used SIMPER only to identify the main fatty acids that characterized the primary producers sampled in the area (accordingly to Kelly and Scheibling, 2012). Then, the identified FAs were used as indicators of specific primary producer-derived organic matter in the abiotic compartments, assuming that the relative abundance of specific FA indicators in sedimentary or suspended organic matter will be proportional to the contribution of the correspondent primary producer.
The contribution of other potential organic matter sources to SOM and SPOM, as Bacteria, was assessed using the biomarkers published in literature.
To clarify better the aims and the results of this statistical approach, we have specified better the objectives of the SIMPER analysis highlighting that this approach is used to identify the FAs that contributed more to the similarity within and dissimilarity between primary producer groups (Clarke and Warwick, 2001). Moreover, we have specified that these FAs are used only as indicators of specific primary producer-derived organic matter for sedimentary and suspended particulate material characterisation, together with those reported in current literature (P. 7 L. 27 – P. 8 L. 3). To add clarity to these information, we have included also the dissimilarities between groups in the table (Suppl. 1).

Kelly, Jennifer R., and Robert E. Scheibling. "Fatty acids as dietary tracers in benthic food webs." Marine Ecology Progress Series 446 (2012): 1-22.

Clarke K.R., Warwick R.M. "Change in marine communities: an approach to statistical analysis and interpretation." Plymouth, UK: Primer-E (2001).

Results :
P7 L15to L21: all comparisons need to be tested statistically

R: All comparisons have been tested through permutational analysis of variance (PERMANOVA).

P8 L5 the Bayesian model (SIAR) is may be not needed to see the contributions of the sources since there is no fractionation to correct.

R: Bayesian models are valid tools to assess the contribution of sources to consumers (in this case SOM and SPOM) even regardless of fractionation value. In this study, we analysed the contribution of organic matter sources to sediment and particulate compartment assuming that their isotopic compositions remained unchanged after their incorporation in SOM and SPOM accordingly to Gonneea et al. (2004). Now have specified this in the manuscript. P. 7 L. 18-20.

P9 : L 25: Using 18:2w6+18:3w3 as tracers of seagrasses in zone full of mangrove is very risky.

R: We agree and now we were much more cautious in using FAs as tracers of primary producers. The whole paragraph has been rephrased, considering 18:3 n3 as a tracer of both seagrasses and mangroves, 18:2 n6 as a tracer of both seagrasses and agricultural runoff and 20:5 n3 as a tracer of both diatoms and red macroalgae. P. 11 L. 1-10

Discussion :
P10 L26 : In this paragraph it will be useful to discuss possible ocean inputs (seaward station)

R: The influence of oceanic input in the seaward station, in terms of influence of oceanic dissolved inorganic carbon on the carbon isotopic signature of primary producers, was discussed in the subsequent sentence P. 12 L. 14-18. In particular, we stated that “A similar enrichment was already observed in Gazi Bay and other tropical areas (Hemminga et al., 1994; Lugendo et al., 2007) and mirrors changes in d^{13}C$_{DIC}$ (Alongi, 2014; Maher et al., 2013). d^{13}C$_{DIC}$ is typically more negative close to mangroves as a result of the intense localized mineralization of mangrove detritus (Bouillon et al., 2007) and increases seaward due to the increased contribution of oceanic DIC, whose d^{13}C is typically around 0‰ (Bouillon et al., 2008)”. If necessary, further details will be added.

P13 L4-L5 : Speculative.

R: We will remove this sentence.

P4L15 : 16:1w7/16:0 is certainly not an indicator of dino/diatoms and , 20:5w3/22ww3 is a diatom/dino marker (not the opposite) . Another reason to not ascribed 20:5w3 to red algae.

R: We thank the reviewer for pointing out this mistake. Now we have corrected it and changed the sentence giving more importance to 20:5 n3/22:6 n3 as a diatom/dinoflagellate marker. We have decided to eliminate the mention to 16:1w7/16:0 because there was not a univocal pattern. P. 16 l. 2-4

P14 L25 : it is very speculative to relate a relative increase of bacterial FA (compare to what ?) to an increase bacterial activity , at best it may show an increase in biomass but only if to compare the same site, for instance between season.

R: We are grateful to the reviewer for this comment. We will change "greater benthic mineralization" with "high bacterial biomass". p. 16 L. 10-12

Figure 1 : the limit of the mangrove forest is not obvious in the map, please write Mkurumunji RIVER

R: We agree that Figure 1 was not clear, as it was pointing out also by reviewer 1.
Then we have changed it to improve clarity. The names of the stations have been placed in the right position. “Creek” and “river” have been added to the watercourse names. Moreover, we have drawn the transects and the coastline to improve the identification of the limits of the mangrove forest.

Fig 7 and 8 : besides all my comments on the use of markers, here I would like to emphasize that Branched and 18:1w7 are surely tracers of bacteria, but one should complete the other and must not any more be added as it was done 20 years ago . there are many papers that show discrepancy between these two type of markers.

R: We have modified figures 7 and 8 (now 6 and 7) showing individually the two bacterial markers (branched and 18:1 n7) . Moreover, following previous comments of the reviewer, also 18:3 n3 and 18:2 n6 have been indicated individually.

Small-scale variability of geomorphological settings influences mangrove-derived organic matter export in a tropical bay

Eliminato: Small scale

Geraldina Signa[a,*], Antonio Mazzola[a], James Kairo[b], Salvatrice Vizzini[a]

[a] Department of Earth and Marine Sciences, University of Palermo, CoNISMa, via Archirafi 18, Palermo, Italy
[b] Kenya Marine and Fisheries Research Institute, PO Box 81651, Mombasa, Kenya

Correspondence to: Geraldina Signa (geraldina.signa@unipa.it)

Abstract

Organic matter (OM) exchanges between adjacent habitats affect the dynamics and functioning of coastal systems, as well as the role of the different primary producers as energy and nutrient sources in food webs. Elemental (C, N, C:N) and isotope ($\delta^{13}C$) signatures and fatty acid (FA) profiles were used to assess the influence of geomorphological setting in two climatic seasons on the export and fate of mangrove OM across a tidally influenced tropical area, Gazi Bay (Kenya). The main results indicate that tidal transport, along with riverine runoff, play a significant role in the distribution of mangrove organic matter. In particular, a marked spatial variability in the export of organic matter from mangroves to adjacent habitats was due to the different settings of the creeks flowing into the bay. Kinondo Creek acted as a mangrove retention site, where export of mangrove material was limited to the contiguous intertidal area, while Kidogoweni Creek acted as a "flow-through" system, from which mangrove material spread into the bay, especially in the rainy season. This pattern was evident from the isotopic signature of primary producers, which were more ^{13}C-depleted in the Kinondo Creek and nearby, due to the lower dilution of the dissolved inorganic carbon (DIC) pool, typically depleted as an effect of intense mangrove mineralization. Despite the trapping efficiency of the seagrass canopy, suspended particulate OM showed the important contribution of mangroves across the whole bay, up to the coral reef, as an effect of the strong ebb tide. Overall, mixing model outcomes indicated a widespread mixed contribution of both allochthonous and autochthonous OM sources across Gazi Bay. Moreover, FAs indicated a notable contribution of brown

Eliminato: DIC

Eliminato: and FA profiles

macroalgae and bacteria in both sediment and suspended pools. These results suggest that ecological connectivity in Gazi Bay is strongly influenced by geomorphological setting, which may have far-reaching consequences for the functioning of the whole ecosystem and the local food webs.

Eliminato: particulate

1 Introduction

Mangrove forests are known to be among the most productive ecosystems worldwide, with a crucial role in the carbon budget (Alongi, 2014; Dittmar et al., 2006; Kristensen et al., 2008). Indeed, mangroves sequester large amounts of carbon deriving from two main pathways: atmospheric carbon fixation contributing to high aboveground and belowground biomass and carbon input from adjacent terrestrial and marine systems (Alongi, 2014). However, a considerably large amount of mangrove-derived carbon in the form of leaves, particulate detritus and dissolved organic and inorganic matter is exported to adjoining ecosystems, subsidising coastal waters and influencing nutrient biogeochemical cycling (Dittmar et al., 2006; Duarte and Cebrián, 1996).

The long-standing scientific debate regarding the fate of the high mangrove productivity has led to various theories and paradigms. With the “outwelling hypothesis”, Odum and Heald (1972) first suggested that leaf detritus exported from mangrove forests would represent an important trophic source contributing to secondary production in adjacent offshore areas. While a few studies confirmed this hypothesis (Dittmar et al., 2001; Lugendo et al., 2007), others reported limited evidence that exported mangrove detritus subsidises offshore food webs (Lee, 1995). More recently, a tight interlinkage between mangroves and adjacent seagrasses has been found in many geographical areas (Bouillon et al., 2003, 2007; Gillis et al., 2014; Kennedy et al., 2004), leading to the "inwelling hypothesis”, whereby the tidal import of seagrass litter to mangrove forests and its contribution to the carbon budget would be also significant (Bouillon et al., 2003; Walton et al., 2014).

According to the “environmental setting hypothesis” (Twilley, 1985), geomorphological features and hydrology are the most important abiotic factors affecting the exchange of mangrove material across ecosystem boundaries (Adame and Lovelock, 2011; Lee, 1999). In particular, the combined control of river discharge (magnitude and frequency), tidal amplitude, rainfall, and wave action is reported to influence the exchange of material across boundaries in estuarine mangrove systems. Tropical rivers are

Eliminato: magnitude and frequency

Eliminato: power

Eliminato: are

Eliminato: all

Eliminato: of

one of the main vectors of carbon from terrestrial to coastal areas (Bouillon and Connolly, 2009), especially when the flushing rate is amplified by high rainfall (Dittmar et al., 2001). Otherwise, low rainfall and freshwater runoff have been related to reduced mangrove outwelling (Walton et al., 2014). Tidal amplitude, frequency and direction (flood *vs.* ebb tide) influence cross-habitat connectivity in the tropical coastal seascape, through bidirectional movements of water and nekton across wide spatial scales (Adame and Lovelock, 2011).

Bulk elemental composition (C, N and C:N ratio) and carbon stable isotope (SI) signature ($\delta^{13}C$) are widely used to trace organic matter origin and fate in coastal systems (*e.g.*, Bouillon et al., 2003; Vizzini and Mazzola, 2008; Walton et al., 2014). This is because C:N ratio and $\delta^{13}C$ composition of the different organic matter sources contributing to sedimentary and suspended particulate pools are often markedly distinct (Bouillon et al., 2008; Lamb et al., 2006). Nevertheless, this dual approach has a number of constraints, such as the lowering effect of decomposition on C:N ratio (Bosire et al., 2005; Dunn et al., 2008; Kennedy et al., 2004) or the potential overlapping of basal source isotopic signatures (Fry and Sherr, 1989), which may complicate inferences in coastal areas where autochthonous and allochthonous materials mix. The simultaneous use of other complementary tracers, such as fatty acids (FAs), may significantly improve the determination of OM sources in aquatic systems (Alfaro et al., 2006; Dunn et al., 2008) and their trophic pathways, both detrital and grazing pathways, in complex systems (Kelly and Scheibling, 2012). Indeed, FAs are particularly well-suited to distinguishing among a wide range of organic matter sources (*i.e.*, dinoflagellates, diatoms, mangroves, macroalgae, seagrasses, bacteria) because of their high biological specificity and their structural and trophic stability (Kelly and Scheibling, 2012; Meziane et al., 2006).

Gazi Bay in Kenya is a tropical area characterised by high cross-habitat contiguity. The bay is fringed by a dense mangrove forest and the seabed covered with seagrass beds mixed with patchy macroalgae. Two tidal creeks, of which only one receives riverine freshwater input, intersect the mangrove forest. Rainfall seasonality exerts a marked influence on runoff magnitude (Kitheka, 1997). Earlier studies in Gazi Bay reported a marked outwelling of mangrove-derived material up to the adjacent seagrass beds (Bouillon et al., 2007; Hemminga et al., 1994) and also a reversed inwelling of seagrass material that contributes to a tight linkage between these two contiguous habitats (Hemminga et al., 1994). In contrast, adjacent coral

Formattato: Tipo di carattere: Corsivo

Codice campo modificato

Formattato: Tipo di carattere: Corsivo

Formattato: Tipo di carattere: Corsivo

Eliminato: organic

reefs have been found to be fairly isolated from the inshore habitat (Hemminga et al., 1994). However, previous investigations were limited to only a few parts of the bay or only one climatic season, and were conducted exclusively through a qualitative analysis of stable isotopes. Moreover, only tidal pumping was considered as the main driver of outwelling and inter-habitat connectivity. In contrast, the role of small-scale variability in the geomorphology of the bay, in terms of tidal creek length, depth and freshwater runoff on mangrove export and cross-habitat organic matter exchange, has never been assessed. Given the importance and ecological implications of mangrove export along the river-bay-coral reef-open sea *continuum*, a higher spatial resolution, combined with a conjoint analytical approach and a quantitative data elaboration, provides more detailed and complete quantitative information.

The main goal of this study was to assess the fate of mangrove-derived organic matter in Gazi Bay, the dominant terrestrial source in the area (Bouillon et al., 2007; Neukermans et al., 2008), in relation to the small-scale variability of geomorphological settings, using combined elemental, isotopic and fatty acid analyses. In particular, following a preliminary characterization of primary producers, sediment (SOM) and suspended particulate organic matter (SPOM), we estimated the contribution of dominant primary producers to SOM and SPOM pools based on quantitative (isotope mixing models) and semi-quantitative (fatty acid profiles) approaches. This allowed to assess the export of mangrove-derived organic matter towards adjacent habitats in relation to the different geomorphological settings of the bay in the two main climatic seasons, dry and rainy.

2 Materials and methods

2.1 Study area and sample collection

Gazi Bay (4°25'S; 39°30'E) is a ~10 km^2 shallow semi-enclosed marine ecosystem on the southern Kenyan coast (Fig. 1). In the northern part it is fringed by a ~6 km^2 mangrove forest, while in the southern part it is sheltered from the Indian Ocean by shallow coral reefs (max depth: 10 m). Kidogoweni and Kinondo tidal creeks flow through the mangrove forest into the upper part of the bay. Kinondo Creek is shorter and shallower than Kidogoweni (2500 m long and 1-2 m deep *vs*. 4500 m long and 2-3 m deep) and lacks direct freshwater input, except for limited groundwater seepage (Kitheka et al., 1996). Kidogoweni Creek receives freshwater input from the semiperennial Kidogoweni River. A third

Formattato: Tipo di carattere: Corsivo

Eliminato: a

Eliminato: approach

Eliminato: es

Eliminato: assessed

Eliminato: :

Eliminato: a)

Eliminato: ; b) similarity of profilethe quantitative (isotope mixing models) and semi-quantitative (fatty acids) contribution of dominant primary producers to sedimentary and suspended particulate organic matter pools

Eliminato:

Eliminato: 5

Eliminato: unless

Eliminato: low

Eliminato: discharge

freshwater input, the Mkurumuji River, discharges into the southern part of the bay with high flow rates (max flow: 16.7 m^{3} s^{-1}; Kitheka et al., 1996). Sugar plantations are diffuse in the area surrounding the whole bay, hence their runoff might flow into the watercourses. The tide is semidiurnal, ranging from 0.5 m at neap tide to 4.0 m at high spring tide (Kitheka et al., 1996). Tidal currents are faster in the creeks than in the southern part of the bay and ebb flows are stronger than flood flows (Kitheka, 1997). Two main climatic seasons and a bimodal rainfall distribution characterise the area: a distinct dry season (January– February) is followed by two rainy seasons: the first is long and intense (April–August) and the second is shorter and weaker (October-November).

The dominant mangrove species along the creek fringes at Gazi bay are *Rhizophora mucronata, Ceriops tagal, Sonneratia alba* and *Avicennia marina* (Hemminga et al., 1994; Neukermans et al., 2008). Seagrass beds mixed with macroalgae cover both the creeks and the bay up to the seaward mouth (Githaiga et al., 2016). *Thalassodendron ciliatum, Cymodocea serrulata, C. rotundata* and *Enalhus acoroides* are among the most abundant seagrass species, while *Sargassum binderi, Dictyota cervicornis, Turbinaria conoides*, and *Gracilaria corticata* and *Hypnea cornuta* are among the most abundant brown and red macroalgae respectively.

Sampling was carried out in February and July 2009, during the dry and rainy seasons respectively, in four stations: mangrove forest (M), intertidal area (IA), seagrass bed (SB) and coral reef (CR), situated along two land-to-sea transects, corresponding to the two tidal creek mouths: Kidogoweni (A) and Kinondo (B) (Fig. 1). In both seasons, sampling was carried out at spring tides. At each station, three replicates of surface water and sediment were collected using 5*l* bottles and hand corers (length: 20 cm; inner diameter: 4 cm) respectively. The most abundant organic matter sources (senescent yellow mangrove leaves, seagrass shoots and macroalgae thalli) were collected by hand at each station, except for mangrove leaves, which were sampled only in the mangrove stations. Zooplankton were captured towing a net (335 µm mesh) for 15 minutes at constant speed in each station. All samples were kept cool and dark in a cool box upon arrival at the laboratory.

2.2 Laboratory activities and analytical procedures

Eliminato: i.e.

Formattato: Non Apice / Pedice

Eliminato: (

Eliminato: rivers and the creeks

Eliminato: ones

Eliminato: a

Eliminato: rainy season

Eliminato: a

Eliminato: one

Eliminato: season

Eliminato: the

Eliminato: brown macroalgae

Eliminato: species

Eliminato: the red ones

Eliminato: leaves

Eliminato: e

Eliminato: .

Eliminato: leaves which

Eliminato: collected

Surface water was pre-filtered using a 200 µm net and then filtered onto precombusted (450°C, 4 h) Whatman GF/F filters to collect suspended particulate organic matter (SPOM). The first centimetres (~5 cm) of sediment cores were sliced, homogenized and subsampled for subsequent analysis of sedimentary organic matter (SOM). After species identification, mangrove and seagrass leaves and macroalgae were quickly rinsed to remove any extraneous material, and, when present, epiphytes were scraped. Zooplankton samples were sorted under a stereo microscope (10 to 40×). Subsamples for elemental and isotopic analyses were dried at 60°C to constant weight and ground to a fine powder using a micro-mill (Retsch MM200). Filters and sediments for carbon stable isotope analysis were drop-by-drop acidified (HCl, 2 N) to remove carbonates, washed and dried again. Subsamples for fatty acid analysis were frozen (-80°C), freeze-dried (ALPHA 1-4 LD plus, Martin-Christ) and ground into a powder using a micro-mill (Retsch MM200). Ground samples were kept at -80 °C until analysis.

An elemental analyser (Thermo Flash EA 1112) was used for the determination of total carbon and nitrogen, and connected to an isotope ratio mass spectrometer (Thermo Delta Plus XP) for $\delta^{13}C$ analysis. $\delta^{13}C$ was expressed in relation to PeeDee Belemnite international standard, and defined as:

$$\delta^{13}C = [(R_{sample} / R_{standard}) - 1] \times 10^3$$

where R is the $^{13}C/^{12}C$ ratio. Analytical precision based on the standard deviation of replicates of internal standards (International Atomic Energy Agency IAEA-CH-6) was 0.2 ‰.

Lipids were extracted from suspended particulate organic matter collected in filters, surface sediment and primary producers using a distilled water/methanol/chloroform solvent mixture (1:2:1 v/v/v) with 0.01% BHT (butylated hydroxyl toluene) to prevent lipid oxidation, following a modified version of the Bligh and Dyer (1959) method. Samples with the extracting mixture were sonicated to extract lipids and then centrifuged to separate the lipid phase from the aqueous phase. Afterwards, the lipid extract was subjected to acid-catalysed transesterification with methanolic hydrogen chloride to obtain fatty acids (FAs). FAs were then analysed as methyl esters (FAME) by gas chromatography (GC-2010, Shimadzu) equipped with a BPX-70 capillary column (30 m length; 0.25 mm ID; 0.25 µm film thickness) and with a flame ionization detector (FID). Peaks were identified using retention times from mixed commercial standards (37FAME and BAME from Supelco; BR1 and QUALFISH from Larodan). For quantification, tricosanoic acid (C23:0) was used as internal standard. Individual FAs were expressed as percentage of total FAs.

Formattato: Allineato al centro

Eliminato: ,

Eliminato: ,

Eliminato: the

Eliminato: from the various matrices

Eliminato: aqueous and the

Eliminato: lipid phases

Eliminato: A 0.01% solution of butylated hydroxyl toluene (BHT) was added to prevent lipid oxidation. L

Eliminato: :00

2.3 Data analysis

Differences in the elemental and isotopic signatures of primary producers (mangroves, red and brown macroalgae, seagrasses) were tested through permutational multivariate analysis of variance (PERMANOVA; PRIMER-E Ltd., Plymouth, UK) carried out on the Euclidean distance matrix calculated from C:N and δ^{13}C datasets. The following experimental design was used, including the following three orthogonal fixed factors: Season (2 levels: dry season and rainy season), Transect (2 levels: A and B) and Station (4 levels: mangrove forest, intertidal area, seagrass beds and coral reef).

Bayesian mixing models were run 5 times on δ^{13}C data using the software package SIAR (Stable Isotope Analysis in R) (Parnell et al., 2010) to estimate the contribution of each organic matter source to sedimentary and suspended particulate organic matter. Bayesian models circumvent the limitations of classical qualitative approaches, by including in the models the high degree of variability and uncertainty inherent of ecological systems (Parnell et al., 2010). The dominant organic matter sources in the area, namely mangroves, macroalgae and seagrasses were chosen as end-members for sedimentary organic matter. Oceanic SPOM was not included in the model as a proxy of phytoplankton because of the small proportion of phytoplankton biomass within the POM pool in Gazi Bay (Bouillon et al., 2007). Mangroves, macroalgae, seagrasses and zooplankton were chosen as end-members for suspended particulate organic matter. No trophic enrichment factor was included in the models, assuming that the isotopic composition of the organic matter sources did not change following their incorporation into SOM and SPOM (Gonneea et al., 2004). PERMANOVA was carried out on the Euclidean distance matrix calculated from the Bayesian mixing model outcomes (mode, mean, upper and lower limits of the 95th credibility interval, 5 replicates) of each source using the same experimental design as for the elemental and isotopic signatures.

PERMANOVA was also performed to examine differences in FA profile between species within primary producer groups (mangroves, red and brown macroalgae, seagrasses) and among primary producer groups. FAs were resembled using Bray Curtis similarity after arcsine square root function transformation. The analysis of percentage similarity (SIMPER) was used on untransformed data to identify the FAs that contributed more to the similarity within and dissimilarity between primary producer

Eliminato: and elemental …ignatures of primary producers (mangroves, red and brown macroalgae, seagrasses) were tested through permutational multivariate analysis of variance (PERMANOVA; PRIMER-E Ltd., Plymouth, UK) performed…arried out on the Euclidean distance matrix calculated from C:N and δ^{13}C and C/N ...

Formattato: Inglese (Stati Uniti)

Eliminato: First, we assessed the differences among primary producers at each level of the interaction season x transect. Then, in both dry and rainy season and in each station, we tested the δ^{13}C variability of each primary producer between transects. ¶

Eliminato: ies…and uncertaintyies…which are ...

Eliminato: . No trophic enrichment factor was included in the models… The dominant organic matter sources in the area, namely M ...

Eliminato: (Mang)… macroalgae (Alg) …nd seagrasses (Seag) ...

Eliminato: were chosen as end-members for sedimentary ...

Eliminato: (Mang)

Eliminato:

Eliminato: (Alg)… seagrasses (Seag)…and zooplankton ...

Formattato ...

Eliminato: s

Formattato: Colore carattere: Automatico

Eliminato:

Eliminato: d

Formattato: Colore carattere: Automatico

Formattato ...

Eliminato: , to encompass the whole variability associated ...

Eliminato: The following three fixed factors-experimental ...

Formattato ...

Eliminato: Multivariate analysis

Eliminato: species

Eliminato: on primary producer FA data

Eliminato: using Primer 6 & Permanova packages ...

Eliminato: and permutational multivariate analysis of ...

Formattato ...

Eliminato: which

Formattato: Non Evidenziato

groups (Clarke and Warwick, 2001). Therefore, these FAs were used as indicators of specific primary producer-derived organic matter for sedimentary and suspended particulate material, together with those reported in current literature.

3 Results

3.1 Isotopic and elemental tracers

3.1.1 Primary producers, sedimentary and suspended particulate organic matter

Mangrove leaves showed the most depleted δ^{13}C signatures and the highest C:N ratios of all organic matter sources in both transects and seasons (Fig. 2; PERMANOVA: $p < 0.05$). Macroalgae, followed by seagrasses, presented significantly higher δ^{13}C than mangroves, and the values increased progressively moving from the mangroves towards the sea. This trend was especially marked along transect B, where also wider δ^{13}C ranges were observed, compared to those recorded along transect A. In addition, both macroalgae and seagrasses from the landward stations (M, IA) were significantly more ^{13}C-depleted in transect B than in transect A (PERMANOVA: $p < 0.05$ and < 0.01 for macroalgae and seagrasses respectively). Differently, isotopic and elemental values of zooplankton were more homogeneous at both spatial and temporal scales (PERMANOVA: $p > 0.05$).

δ^{13}C of sedimentary organic matter ($\delta^{13}C_{SOM}$) increased drastically along the land-to-sea transects (Fig. 3-a). $\delta^{13}C_{SOM}$ of the landward stations (M, IA) was lower overall in transect B than in A, while it was more homogenous in the other stations and showed a marked increase in the coral reefs (CR). Sedimentary C:N ratio (C:N_{SOM}) also showed a marked spatial pattern in the bay, decreasing steadily from mangroves (M) to coral reefs (CR) (Fig. 3-b). A striking seasonal difference was observed in the mangrove station of transect A, where the lowest value (10.2) was recorded in the rainy season and the highest (21.5) in the dry. Unlike SOM, $\delta^{13}C_{SPOM}$ and C:N_{SPOM} were overall more homogeneous among stations (Fig. 3-c,d) except for the highest values recorded in the samples collected in seagrass beds (SB).

3.1.2 Mixing models

Bayesian mixing model outcomes provided the ranges of possible contributions (95th percentile intervals) of organic matter sources to sedimentary (SOM) and suspended particulate (SPOM) organic matter. The

Eliminato: could be used as
Formattato: Non Evidenziato
Formattato: Non Evidenziato
Formattato: Non Evidenziato
Eliminato: in
Eliminato: characterisation
Formattato: Non Evidenziato
Formattato: Non Evidenziato
Formattato: SpazioDopo: 0 pt
Eliminato: . more
Eliminato: ly
Eliminato: than along A
Eliminato: were observed
Eliminato: showed
Eliminato: the most
Eliminato: ^{13}C
Eliminato: ,
Eliminato: as well as a wider δ^{13}C range,
Eliminato: compared with
Eliminato: Fig. 2
Eliminato: In
Eliminato: contrast
Eliminato: I
Eliminato: zooplankton
Eliminato: , as confirmed by hence statistics
Eliminato: did not highlighted any significant differences

outputs of the models are expressed as probability distributions and, although the percentile intervals were wide and overall overlapped, indicating a potential contribution of multiple sources and a non-negligible level of uncertainty in some cases, their validity is assured because they incorporate error terms (Parnell et al., 2010). Overall, the contribution of mangroves to SOM was high in the whole bay up to the seagrass beds, while it decreased sharply in coral reefs (Fig. 4). In more detail, at multivariate level, the mangrove contribution to SOM was significantly different between stations in both seasons and transects (Tab. 1). Indeed, along the transect B, in correspondence of the Kinondo tidal creek, the credibility intervals were particularly wide in both seasons (DS: 11.2-71.4%; RS: 10.7-69.1%) and tended to narrow going seaward. Moreover, the mode values slightly decreased from the mangrove stand (M) up to seagrass beds (SB) (DS: 40.7– 37.9%; RS: 40.1-36.8%), except for the peak (48.3%) recorded in the intertidal area (IA) in the rainy season. In contrast, along the transect A, in correspondence of the Kidogoweni tidal creek, both mode values and the credibility intervals showed a slight but significant decrease, more evident in the rainy season than in the dry, and credibility intervals were overall narrower than in the other transect. The contribution of macroalgae and seagrasses to SOM was also significantly different between stations in both seasons and transects (Tab. 1). Credibility intervals were rather wide, and mode values were overall comparable except in coral reefs, where they were higher than in the other stations in all cases (except for the low values of macroalgae in the dry season in transect A).

The contribution of mangrove-derived organic matter to SPOM was important in Gazi Bay up to the coral reefs (Fig. 5), without any relevant seasonal pattern. Along transect A, the mangrove contribution was significantly higher than that of the other sources in the seagrass beds (range: 15.5-73.8%) and then diminished in CR, becoming comparable to the other sources. Along transect B, mangrove contribution was fairly important in all stations, with a peak in IA (13.7-82.9%).

3.2 Fatty acids

3.2.1 Primary producers

The different species of primary producers within each group (mangroves, brown and red macroalgae, seagrasses) showed no significant differences in their FA profiles between seasons, transects, and stations (PERMANOVA: p > 0.05). In contrast, there were significant differences among primary producer groups

Eliminato: ¶
A…lthough the percentile intervals were wide and often overall overlapped, … indicating a potential contribution of multiple sources and a non-negligible level of uncertainty in some cases, …their validity is assured because they incorporate error terms (Parnell et al., 2010). o

Eliminato: Tab. 1; …ig. 4). In more detail, at multivariate level, the mangrove contribution to SOM was significantly different between stations in both seasons and transects (Tab. 1). Indeed, along the transect B, in correspondence of the Kinondo tidal creek, the credibility intervals were particularly wide in both seasons (DS: 11.2-71.4%; RS: 10.7-69.1%) and tended to narrow going seaward. Moreover, in the mangrove station (M) within Kinondo stand (transect B), t…he mode values slightly decreased were overall comparable

Eliminato: higher

Eliminato: , while

Eliminato: In the dry season,

Eliminato: the credibility intervals mangrove contribution to SOM waswere particularly wide in both season higher in the mangrove station (M), especially in transect B (DS: 11.2-71.410.8-74.4%; RS: 10.7-69.1%)), and tended to narrow going seaward

Eliminato: while

Eliminato: in…long the transect A, in correspondence of the Kidoi…oweni tidal stand…reek, both mode values and the credibility intervals showed a slight but significant decrease along the transect (A)

Eliminato: in the rainy season it was higher in mangrove, intertidal and seagrass bed stations along transect A and in the former two in transect B.

Eliminato: generally …omparable except in coral reefs, where where their influence was more important …hey were higher than in the other stations overall …n both …ll transects

Eliminato: peak …n the dry season inalong

Eliminato: in the dry season

Eliminato: within the bay …range?

Eliminato: 1…-74…3.5

Eliminato: in both seasons

Eliminato: 9…-83…2.8

Eliminato: seagrasses,

Spostato (inserimento) [1]

Eliminato: Indeed

based on their FA profile (PERMANOVA: df = 3; MS: 15076; p < 0.001). All pairwise comparisons were also highly significant (p < 0.001). Thus, the data of each species within each group were combined (see Suppl. 1).

Saturated fatty acids (SFAs) were particularly abundant in mangroves and brown and red macroalgae, due to the contribution of 16:0 and 14:0 FAs. Long chain fatty acids (LCFAs), typical biomarkers of mangroves (Kelly and Scheibling, 2012; Meziane et al., 2006), were particularly abundant in mangrove leaves. Polyunsaturated fatty acids (PUFAs) consisted almost exclusively of 18:2 n6 and 18:3 n3 FAs in seagrasses and mangroves, and 20:5 n3 in red macroalgae, while 18:4 n3, 20:4 n6 and 20:2 n6 were also abundant in brown macroalgae, consistent with the literature (Kelly and Scheibling 2012 and references therein). Among monounsaturated fatty acids (MUFAs), overall 18:1 n9, followed by 16:1 n7, were the most abundant in all primary producers. SIMPER analysis revealed that mangroves differed from the other primary producers mainly in having a higher contribution of LCFAs (see Suppl. 2). Seagrasses and mangroves were distinguished also by 18:3 n3 and 18:2 n6, which contributed more to the seagrass than to the mangrove within-group similarity. Together with the ubiquitous 16:0 and 14:0, 20:5 n3 contributed most to the red macroalgae within-group similarity and to the between-group dissimilarity with the other groups. Likewise, 18:1 n9, 18:4 n3, 20:4 n6 and 20:2 n6 characterised brown macroalgae, but only 18:1 n9, 18:4 n3 and 20:4 n6 contributed most to the dissimilarity with the other primary producers.

3.2.2 Sedimentary and suspended particulate organic matter

Forty and thirty-five individual fatty acids were identified respectively in sedimentary and suspended particulate organic matter. They included i) straight- and branched-chain saturated FAs (SFAs) dominated by 16:0, 18:0 and long chain fatty acids (LCFAs), ii) monounsaturated fatty acids (MUFAs), mainly constituted by 16:1 n7, 18:1 n7 and 18:1 n9, iii) polyunsaturated fatty acids (PUFAs) with a high contribution of 18:2 n6, 20:5 n3 and 22:4 n6, iv) cyclopropyl (CY) FAs, and v) hydroxyl (OH) FAs (see Suppl. 3 and 4).

The contribution of LCFAs to SOM was markedly high in the mangrove stands at the Kinondo mouth (transect B), comprising up to 40% of the total FAs, and progressively decreased toward coral reefs (Fig. 6). In contrast, at the Kidogoweni mouth (transect A), LCFAs were between approximately 5 and 10%

Eliminato: ok???

Eliminato: were further elaborated as the above groups

Eliminato: Tab. 1

Eliminato:

Eliminato: :00

Eliminato: :00

Spostato in su [1]: Indeed, there were significant differences among primary producer groups based on their FA profile (PERMANOVA: df = 3; MS: 15076; p < 0.001). All pairwise comparisons were also highly significant (p < 0.001).

Eliminato: ¶
Primary producer groups were well separated in the multivariate ordination (Fig. 6), with mangroves and seagrasses in the left part of the plot, and brown and red macroalgae in the right part.

Eliminato: (

Eliminato: Tab. 2).

Eliminato: was abundant

Eliminato: in

Eliminato: e

Eliminato: ,

Eliminato: in

Eliminato: :00

Eliminato: :00

Eliminato: s

Eliminato: ementary material

Eliminato: of

Eliminato: 7

Eliminato: in

within the mangrove stand and increased in the adjacent habitats (IA, SB), especially in the rainy season. Relative contributions of 18:3 n3, which can be ascribed to both seagrass and mangrove contribution (Alfaro et al., 2006; Meziane et al., 2006) was rather limited in the whole bay or even null within seagrass beds in the rainy season. 18:2 n6, which has been often considered a seagrass indicator in tropical systems (Kelly and Scheibling, 2012 and references therein), and is also a tracer of agriculture-derived organic matter (Meziane and Tsuchiya, 2002), showed fairly low and comparable relative contributions in the whole bay. Indicators of brown macroalgae (18:1 n9, 18:4 n3 and 20:4 n6) resulted relatively more abundant (5-10%) than 20:5 n3, which is usually considered tracer of diatoms (Alfaro et al., 2006; Bachok et al., 2003; Meziane et al., 2006), and also of red macroalgae (Kelly and Scheibling, 2012; results of the present study). It should be mentioned that combined indicators of brown macroalgae and 20:5 n3 showed a similar spatial trend, that is progressively increasing toward the coral reef along transect B and slightly higher in M and CR than in the other stations along transect A (Fig. 6). The relative contribution of bacterial fatty acids, BaFAs, branched 15:0 and 17:0, and 18:1 n7 (Kelly and Scheibling 2012 and reference therein) was notable in the whole bay. In particular, 18:1 n7 was relatively more abundant than branched FAs and, as a general trend, both were higher in IA and SB than in the other stations.

FA profiles of suspended particulate organic matter were also characterised by a large contribution of LCFAs and BaFAs (Fig. 7). In the dry season, they showed a similar spatial trend in both transects, with increasing proportions from mangrove stands to seagrass beds, followed by a decrease in coral reefs. In contrast, in the rainy season these FAs tended to decrease seaward. Mean contribution of brown macroalgae was also notable and overall similar across the bay especially in the dry season. The contribution of 20:1 and 22:1, biomarkers of zooplankton (Alfaro et al., 2006; Bachok et al., 2003), was also fairly uniform in the whole bay. 18:3 n3, 18:2 n6 and 20:5 n3 showed the lowest relative contribution to suspended particulate FA profile and were fairly homogenous in Gazi Bay, except for a few peaks; 18:3 n3 was null in IA and SB (rainy season-transect B); 18:2 n6 peaked in M (dry season-transect B); 20:5 n3 peaked in IA (rainy season-transect A).

4 Discussion

4.1 Organic matter sources

Formattato
Eliminato: (
Formattato
Eliminato: but
Eliminato: is
Eliminato: also common in
Formattato
Eliminato: e
Formattato
Eliminato: wastewaters
Formattato
Formattato
Formattato
Eliminato: relative contributions …airly low and
Formattato
Eliminato: and 18:3 n3), b
Formattato
Eliminato: l
Formattato
Eliminato: biomass
Formattato
Eliminato: and
Formattato
Eliminato: a
Formattato
Eliminato: biomarker
Formattato
Eliminato: current SIMPER
Formattato
Formattato
Eliminato: in each transect and season
Eliminato: and red macroalgae (20:5 n3) biomarkers were
Eliminato:
Eliminato:
Eliminato: slightly greater in IA and SB than in mangrove
Formattato
Eliminato: 8…. In the dry season, they showed a similar
Eliminato: ice
Eliminato: and red macroalgae- and seagrass-derived
Eliminato: s
Eliminato: ….18:3 n3 was null in IA and SB (rainy season

Elemental and isotopic signatures of mangrove leaves were consistent with documented data from Gazi Bay (Hemminga et al., 1994; Rao et al., 1994) and other mangrove forests (Kristensen et al. 2008). The high C:N ratio of leaves (overall, between 100 and 200) is attributable to their senescent status, due to resorption of nitrogen by the mangrove tree during leaf senescence (Woitchik et al., 1997). After the leaf drops onto the soil, consistent nitrogen enrichment *versus* carbon occurs during decomposition, as a result of a number of physical and chemical transformations (litter breakdown by benthic organisms and microbial remineralization; Bosire et al., 2005). These processes explain why the C:N ratio of mangrove sediments was one order of magnitude lower than that of recently fallen senescent leaves, consistent with the literature (Davis et al., 2003; Dunn et al., 2008; Woitchik et al., 1997).

Mangrove leaves showed low carbon isotopic signatures characteristic of C_3 vegetation (Bouillon et al., 2008), while both macroalgae and seagrasses were ^{13}C enriched compared to mangroves, and variable along the land-to-sea transects. Indeed, marked gradients were observed, with the most depleted values in the landward station close to mangrove forest, especially in the Kinondo mouth, and the most enriched ones in the seaward station. A similar enrichment was already observed in Gazi Bay and other tropical areas (Hemminga et al., 1994; Lugendo et al., 2007) and mirrors changes in $\delta^{13}C_{DIC}$ (Alongi, 2014; Maher et al., 2013). $\delta^{13}C_{DIC}$ is typically more negative close to mangroves as a result of the intense localized mineralization of mangrove detritus (Bouillon et al., 2007) and increases seaward due to the higher contribution of oceanic DIC, whose $\delta^{13}C$ is typically around 0‰ (Bouillon et al., 2008). The among-creek variability, with both macroalgae and seagrasses noticeably more ^{13}C depleted in Kinondo Creek than in Kidogoweni, may be due to many factors, but the different settings of the two creeks must account for most of this variability. In particular, the lack of fresh water in Kinondo, coupled with its lower water volume, suggests that terrestrial and mangrove-derived DIC export is less effective when driven by tidal pumping only. Consequently, macrophytes are supposed to use a more depleted DIC in this area than in the other. The higher salinity (Kitheka et al., 1996) and lower $\delta^{13}C_{DIC}$ in Kinondo waters (Bouillon et al., 2007) support this hypothesis.

Eliminato: stands

Eliminato: transect B

Eliminato: as well as

Eliminato: parallel

Eliminato: increased

4.2 Export of mangrove organic matter

Mangrove-derived organic matter contributed greatly to the sedimentary pool at Kinondo Creek and the adjacent intertidal area, as revealed the great abundance of long chain fatty acids (LCFAs). Moving seaward, mangrove contribution progressively decreased along the land-sea transect and dropped steeply in the coral reef in both seasons, consistent with Hemminga et al. (1994). This pattern was less evident from isotope mixing models than that observed from FA data. Moreover, in the rainy season, the most likely mangrove contribution to SOM (mode) was higher in the intertidal area adjacent to mangrove forest and then decreased seaward. This pattern suggests that mangrove area at the Kinondo mouth acted as a retention site where mangrove organic carbon tends to accumulate into sediments. In contrast, freshwater discharge from the Kidogoweni Creek seemed to enhance the export of mangrove material, which contributed to the sediment pool relatively more in both the intertidal and seagrass bed areas than in the mangrove stands as revealed by the higher relative abundance of LCFAs in both IA and SB stations, especially in the rainy season. In addition to the efficient suspended particle trapping by the seagrass canopy (Hemminga and Duarte, 2008), a certain influence of the Mkurumuji River to the organic matter pool of the seagrass bed area cannot be excluded. Indeed, the Mkurumuji River is characterised by high water flows in the south-western part of the bay peaking at 16.7 m^3 s^{-1} during the rainy season (Kitheka et al., 1996) and a large catchment area covered by dense C$_4$ vegetation and fewer mangrove trees (Bouillon et al., 2007). The combined highest δ^{13}C and C:N values of SPOM found in the seagrass beds in the rainy season corroborate this assumption, since C$_4$ plants have higher δ^{13}C and C:N ratio than mangroves (Lamb et al., 2006). This may also have affected mixing model outcomes, which revealed a lower mangrove contribution to both SOM and SPOM in these stations, contrarily to FA results.

The among-site variability observed in Gazi Bay is consistent with the pattern recently described by Adame and Lovelock (2011): mangroves dominated by tidal pumping, like the Kinondo stand, are characterised by bidirectional flows that favour retention of autochthonous material and tight interlinkage between mangroves and adjacent seagrass beds. Higher retention of autochthonous organic matter within a mangrove forest has also been reported in arid mangrove systems in the Arabian Gulf with almost no freshwater input (Walton et al., 2014). On the other hand, riverine mangroves, like the Kidogoweni stand, are dominated by unidirectional flows that favour outwelling (Adame and Lovelock, 2011).

Eliminato: by isotope mixing models and

Eliminato: progressively

Eliminato: significantly

Eliminato: due to efficient suspended particle trapping by the seagrass canopy (Hemminga and Duarte, 2008),

Eliminato: , as . particularly evident from the progressive decreasing trend of LCFA relative contribution to SOM along the land-sea transect at both seasons. Although

Eliminato: PERMANOVA tests on the isotope mixing model outcomes highlighted also significant differences of the mangrove contribution among stations in both seasons.

Eliminato: less markedly, the isotope mixing model outcomes confirm th

Eliminato: is

Eliminato: , as

Eliminato: from the decreasing trend of the credibility interval upper limits along the transect and confirmed by the significant differences among stations highlighted by PERMANOVA tests

Eliminato: Only at

Eliminato: mangrove contribution

Eliminato: slightly

Eliminato: stands

Eliminato: ing

Eliminato: up to 50% to

Eliminato: the

Eliminato: ,

Eliminato: mixing models and confirmed by

Eliminato: within the bay

Eliminato:

Eliminato: A

Eliminato: s

The different dominant vegetation in Kidogoweni and Kinondo creeks (*Avicennia marina vs. Rhizophora mucronata;* Neukermans et al. 2008) may also affect the magnitude of organic matter export from mangrove forest. Higher export from forests dominated by *Avicennia* sp., compared to those dominated by *Rhizophora* sp., has been observed in Brazil and related to different detritus decomposition rates (Lacerda et al., 1995). Moreover, the differing seasonal patterns recorded in Gazi Bay for *A. marina* and *R. mucronata* litterfall corroborate further this point: *A. marina* litterfall is higher in the rainy season than in the dry (Ochieng and Erftemeijer, 2002), while *R. mucronata* litterfall is the opposite (Slim et al., 1996). Indeed, the sediment C:N ratio in the Kidogoweni stand was almost twofold higher in the dry season than in the rainy (20.8 ± 0.6 *vs.* 11.6 ± 1.3). Given that δ^{13}C was constant across time, we may infer a greater contribution of decomposed mangrove litterfall to the sediment in the rainy season. Indeed, decomposition processes are known to reduce the C:N ratio, but not δ^{13}C (Bosire et al., 2005; Dunn et al., 2008), and are enhanced by a greater supply of nutrients through freshwater flooding during rainfall (Woitchik et al., 1997). In contrast, sediment C:N ratio in the Kinondo stand was almost constant across the seasons, as effect of the lower seasonal variability in freshwater flooding.

Contrarily to sediments, mangrove-derived organic matter was recorded in suspended particulate organic matter throughout the whole bay up to the coral reefs, as indicated by the outcomes of mixing models, C:N ratio and LCFA relative abundances. This contrasts with previous findings that indicated a limited contribution of mangrove material to the SPOM pool in the southern part of Gazi Bay (Bouillon et al., 2007) and may be due to the timing of sampling, which was carried out mostly during ebb tide. This is confirmed by the similar δ^{13}C spatial trend found at ebb tide by Hemminga et al., (1994). Strong downstream ebb currents have been shown to enhance mangrove detritus export and the displacement of mangrove and seagrass waters toward coral reefs (Kitheka, 1997). Despite the buffering role of seagrass beds in preventing a direct connection between mangrove and oceanic waters, we infer that high mangrove export coupled with high rate of water exchange at spring ebb tide has favoured the outwelling of suspended mangrove material up to the coral reef inner area. The high peaks of mangrove contribution and LCFA relative abundances recorded in the intertidal area adjacent to the Kinondo mouth, especially in the rainy season, reflects the sediment patterns and confirm its role as a retention site for mangrove-derived organic matter.

Eliminato: ian

Eliminato: forests

Eliminato: the higher litterfall of

Eliminato: in Gazi Bay

Eliminato: compared

Eliminato: to the

Eliminato: season

Eliminato: coupled

Eliminato: with the opposite seasonal trend of

Eliminato: strengthen this argument

Eliminato: This is plausible also because

Eliminato: in the Kinondo stand was constant across seasons, while

Eliminato: it

Eliminato: differences

Eliminato:

Eliminato: (

Eliminato: the

Eliminato: link

Eliminato: the

Eliminato: a

Eliminato: the

Eliminato: did not impede

Eliminato: reaching

Eliminato: the

Eliminato: of the Kinondo mouth

Eliminato: of

4.3 Contribution of other primary producers to the sediment and suspended particulate pool

Mixing model results revealed a widespread contribution of seagrasses and macroalgae to both sediment and suspended particulate organic matter pools. In particular, the macroalgae contribution was slightly higher than that of seagrasses within the bay and similar or lower in the coral reef. This pattern was overall confirmed by fatty acid results, although caution is needed in interpreting FA findings because biomarkers of primary producers cannot be ascribed solely to one source, as showed by SIMPER results. For instance, both 18:3 n3 and 18:2 n6 are combined biomarkers of seagrasses and mangroves (Kelly and Scheibling, 2012; Meziane et al., 2006), and 18:2 n6 is also tracer of agriculture-derived organic matter (Meziane and Tsuchiya, 2002). Hence, their role as seagrass biomarkers in sediment and particulate compartments must be interpreted with caution and may also be limited because their higher lability than LCFAs during decomposition (Mfilinge et al., 2003). Consequently, the higher 18:2 n6 abundance in SPOM than in SOM suggests the potential influence of agricultural runoff from the sugar plantations surrounding the bay.

With their wide distribution and high productivity as well as their ecological function for marine fauna (e.g. Heck et al. 2008, Gillis et al. 2014), the importance of seagrasses in providing marked carbon input to adjacent and even distant habitats has been widely described. However, relatively few data are available on the productivity and contribution of macroalgae to the carbon budget. Moreover, macroalgae are seldom end-members in mixing models, despite studies on the important trophic and budgeting role of macroalgae associated with mangroves (Koch and Madden, 2001), seagrasses (Heck et al., 2008) and coral reefs (Wernberg et al., 2006). A large quantity of drifting macroalgae, especially *Sargassum* sp., is transported passively by tides in Gazi Bay (pers. obs.; Coppejans et al. 1992) and may account for the large and widespread contribution of brown macroalgae to sediment and, in particular, to the suspended particulate organic matter pool, as revealed by detection of specific fatty acid biomarkers (18:1 n9 + 18:4 n3 + 20:4 n6).

Red macroalgae seemed contributing less than brown macroalgae to the Gazi Bay organic matter pool and it is reasonable because different abundance and biomass of these macroalgae groups were recorded in the area (Coppejans et al., 1992). Nevertheless, caution should be used in dealing with 20:5 n3, because

Formattato
Formattato
Eliminato: need caution
Formattato
Eliminato: s
Eliminato: (
Eliminato: Fatty acids confirmed the spread of seagrass an
Formattato
Eliminato: waters
Formattato
Formattato
Eliminato: the former, seagrass and
Formattato
Eliminato: al
Eliminato: wastes
Formattato
Eliminato: the latter;
Formattato
Formattato
Formattato
Eliminato: , h
Formattato
Formattato
Formattato
Eliminato: needs
Formattato
Eliminato: also
Formattato
Formattato
Formattato
Formattato
Formattato
Eliminato:
Eliminato: ¶
Eliminato: -
Eliminato: the
Eliminato: macroalgal
Formattato
Formattato

it is highly abundant also in diatoms (Alfaro et al., 2006; Bachok et al., 2003; Meziane et al., 2006). Moreover, FA ratio 20:5 n-3/22:6 n-3, marker of diatom/dinoflagellate organic matter, was >1 in SOM and <1 in SPOM samples, indicating that local production of benthic and pelagic microalgae is an important part of sediment and suspended particulate organic matter respectively (Alfaro et al., 2006).

In contrast, FAs were clear and unambiguous in revealing the marked importance of bacterial-derived organic matter (branched FAs and 18:1 n7) in both sediment and suspended particulate pools, indicating a central role for bacteria as mineralizers of organic detritus in Gazi Bay. Cyclopropyl (CY) and hydroxyl (OH) fatty acids have been ascribed to gram-negative bacteria (Kaur et al., 2005) and were also found in both compartments. The abundance of bacteria is not surprising, as they are able to process most of the energy and nutrients in tropical systems (Alongi, 1994). The higher percentage of bacterial biomarkers within the bay suggests a high bacterial biomass in the intertidal and seagrass bed sediments and water column. This is consistent with a previous study carried out in Gazi Bay using δ^{13}C analysis of bacteria-specific PLFAs (phospholipid fatty acids), which found that mangrove carbon was a significant source for bacteria mineralization in the adjacent seagrass beds (Bouillon et al. 2004). Although branched FAs and 18:1 n7 are ascribed to both anaerobic and aerobic bacteria (Kaur et al., 2005; Meziane et al., 2006), the similar spatial patterns indicate similar response to the environmental conditions of Gazi Bay. As previously found by Meziane et al., (2006) in a subtropical Australian estuary, both markers are probably linked to anaerobic conditions due to high litter accumulation coupled with high temperature. Furthermore, the peaks of 18:1 n7 recorded in the dry season out of the Kinondo mouth are likely the result of the retention feature of the area. Indeed, a higher increase of 18:1 n7 than branched FAs was observed after 40 days of decomposition of *Rhizophora apiculate* leaves (Rajendran and Kathiresan, 2000), co-genus species of *R. mucronata*, the most abundant species living along the Kinondo creek.

5. Conclusion

Using elemental and SI signatures, together with FA profiles, this study showed that small-scale variability in the environmental settings of the mangrove forest has a crucial role in influencing the export of mangrove-derived organic matter to adjacent habitats. In Gazi Bay, the short and shallow Kinondo Creek lacks significant freshwater input and, being influenced by tidal pumping only, acted as a retention

Formattato ...

Codice campo modificato

Eliminato: ¶

Eliminato: ¶

Eliminato: are also

Eliminato: ,

Eliminato: s…of diatoms and ...

Formattato: Colore carattere: Automatico

Eliminato: s, 16:1n-7/16:0 and

Eliminato: /diatom

Eliminato: respectively (Alfaro et al., 2006)

Formattato ...

Formattato: Colore carattere: Automatico

Formattato: Colore carattere: Automatico

Eliminato: were …as >1 in lower than established thresholds (1.6 and 1 respectively; Alfaro et al. 2006) in all SOM and <1 in SPOM samples, … suggesting …ndicating dinoflagellate dominance. Although …hat local production of benthic and pelagic and benthic …icroalgae may be …s an important part of sediment and suspended particulate pools…rganic matter respectively (Alfaro et al., 2006), the low relative abundance of 22:6n3 (SOM: 0.9 ± 0.6%; SPOM: 1.3 ± 0.8%) indicated a negligible role. ...

Eliminato: ¶
In contrast, FAs were clear and unambiguous in revealing the marked relative abundance…mportance …of bacterial-derived organic matter biomarkers …branched FAs and 18:1 n7) was particularly important …n both sediment and suspended particulate pools, indicating a central role for bacteria as mineralizers of organic detritus in Gazi Bay. Cyclopropyl (CY) and hydroxyl (OH) fatty acids have been ascribed to gram-negative bacteria (Kaur et al., 2005) and were also found in both compartments. The abundance of bacteria is not surprising, as they are able to process most of the energy and nutrients in tropical systems (Alongi, 1994). ...

Formattato: Colore carattere: Automatico

Eliminato: benthic mineralization

Formattato ...

Eliminato: The high percentage of bacterial biomarkers in ...

Formattato ...

Eliminato: , confirming the higher trapping ability of this ...

Eliminato: FA profiles,

site where mangrove material accumulated in the forest sediment and the contiguous intertidal area. In contrast, the longer and deeper Kidogoweni Creek, receiving high freshwater input especially in the rainy season, contributed to the export of mangrove material to seagrass beds within the bay. Suspended particulate organic matter revealed a greater contribution of mangrove material up to the coral reefs during ebb tide and confirmed the patterns highlighted for sediments. Moreover, the riverine efflux of the Mkurumuji River, which flows into the southern side of the bay, seemed to contribute more to the suspended particulate pool with C_4 vegetal material. In addition, a notable importance of brown macroalgae-derived material across the bay was detected, probably due to the high biomass of drifting *Sargassum binderi*. Fatty acids were particularly well suited to detecting the great bacterial biomass in both the sedimentary and suspended particulate organic matter, suggesting a central role for bacteria as mineralizers of organic detritus in Gazi Bay. These findings confirm the importance of taking into account geomorphological settings and seasonal variability when addressing the question of organic matter export from mangroves in tropical systems. Given the major influence that organic matter exchange across ecosystem boundaries has on organic matter availability and consumption by fauna in trophic webs, future research should be focused on understanding how this small-scale spatial variability may affect trophic dynamics. Further, future research needs to investigate changes in marine productivity with changes in land use activities within and adjacent to Gazi Bay, including mining, seaweed farming, and large-scale sugar plantation.

Eliminato: ,

Eliminato: with almost no influence from the creek settings

Eliminato: Instead

Eliminato: . In particular, brown macroalgae seemed to be the most important,

Eliminato: b

Acknowledgement

This work was financially supported by the Research Grant "Luigi e Francesca Brusarosco 2008" (Luigi e Francesca Brusarosco Association – Research centre Space, University of Milano – Italian Association of Ecology S.It.E) and by the Flagship Project "RITMARE – Italian Research for the Sea" funded by the Italian Ministry of Education, University and Research. Special thanks to Dr J. Bosire for providing facilities and logistical support during the study. We are also grateful to the people of Gazi who assisted in the fields and to the staff of KMFRI for support during laboratory activities.

References

Adame, M. and Lovelock, C.: Carbon and nutrient exchange of mangrove forests with the coastal ocean, Hydrobiologia, 663(1), 23–50, doi:10.1007/s10750-010-0554-7, 2011.

Alfaro, A. C., Thomas, F., Sergent, L. and Duxbury, M.: Identification of trophic interactions within an estuarine food web (northern New Zealand) using fatty acid biomarkers and stable isotopes, Estuar. Coast. Shelf Sci., 70(1–2), 271–286, doi:10.1016/j.ecss.2006.06.017, 2006.

Alongi, D. M.: The role of bacteria in nutrient recycling in tropical mangrove and other coastal benthic ecosystems, Hydrobiologia, 285(1–3), 19–32, doi:10.1007/bf00005650, 1994.

Alongi, D. M.: Carbon Cycling and Storage in Mangrove Forests, Ann. Rev. Mar. Sci., 6(1), 195–219, doi:10.1146/annurev-marine-010213-135020, 2014.

Bachok, Z., Mfilinge, P. L. and Tsuchiya, M.: The diet of the mud clam *Geloina coaxans* (Mollusca, Bivalvia) as indicated by fatty acid markers in a subtropical mangrove forest of Okinawa, Japan, J. Exp. Mar. Bio. Ecol., 292(2), 187–197, doi:10.1016/S0022-0981(03)00160-6, 2003.

Bligh, E. G. and Dyer, W. J.: A rapid method of total lipid extraction and purification, Can. J. Biochem. Physiol., 37, 911–917, doi:10.1139/o59-099, 1959.

Bosire, J. O., Dahdouh-Guebas, F., Kairo, J. G., Kazungu, J., Dehairs, F. and Koedam, N.: Litter degradation and CN dynamics in reforested mangrove plantations at Gazi Bay, Kenya, Biol. Conserv., 126(2), 287–295, doi:10.1016/j.biocon.2005.06.007, 2005.

Bouillon, S. and Connolly, R. M.: Carbon Exchange Among Tropical Coastal Ecosystems, in Ecological Connectivity among Tropical Coastal Ecosystems, pp. 45–70., 2009.

Bouillon, S., Dahdouh-Guebas, F., Rao, A., Koedam, N. and Dehairs, F.: Sources of organic carbon in mangrove sediments: variability and possible ecological implications, Hydrobiologia, 495(1–3), 33–39, doi:10.1023/A:1025411506526, 2003.

Bouillon, S., Moens, T. and Dehairs, F.: Carbon sources supporting benthic mineralization in mangrove and adjacent seagrass sediments (Gazi Bay, Kenya), Biogeosciences, 1(1), 71–78, doi:10.5194/bg-1-71-2004, 2004.

Formattato: Inglese (Stati Uniti)

Formattato: Tipo di carattere: Corsivo, Inglese (Stati Uniti)

Formattato: Inglese (Stati Uniti)

Bouillon, S., Dehairs, F., Velimirov, B., Abril, G. and Borges, A. V.: Dynamics of organic and inorganic carbon across contiguous mangrove and seagrass systems (Gazi Bay, Kenya), J. Geophys. Res., 112(G2), doi:G0201810.1029/2006jg000325, 2007.

Bouillon, S., Connolly, R. M. and Lee, S. Y.: Organic matter exchange and cycling in mangrove ecosystems: Recent insights from stable isotope studies, J. Sea Res., 59(1–2), 44–58, doi:10.1016/j.seares.2007.05.001, 2008.

Clarke, K. and Warwick, R.: Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation., 2nd ed., PRIMER-E Ltd, Plymouth., 2001.

Coppejans, E., Beeckman, H. and De Wit, M.: The seagrass and associated macroalgal vegetation of Gazi Bay (Kenya), Hydrobiologia, 247(1–3), 59–75, doi:10.1007/bf00008205, 1992.

Davis, S. E., Corronado-Molina, C., Childers, D. L. and Day, J. W.: Temporally dependent C, N, and P dynamics associated with the decay of *Rhizophora mangle* L. leaf litter in oligotrophic mangrove wetlands of the Southern Everglades, Aquat. Bot., 75(3), 199–215, doi:10.1016/S0304-3770(02)00176-6, 2003.

Dittmar, T., Lara, R. J. and Kattner, G.: River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters, Mar. Chem., 73(3–4), 253–271, doi:10.1016/S0304-4203(00)00110-9, 2001.

Dittmar, T., Hertkorn, N., Kattner, G. and Lara, R. J.: Mangroves, a major source of dissolved organic carbon to the oceans, Global Biogeochem. Cycles, 20(1), 1–7, doi:10.1029/2005GB002570, 2006.

Duarte, C. M. and Cebrián, J.: The fate of marine autotrophic production, Limnol. Oceanogr., 41(8), 1758–1766, doi:10.4319/lo.1996.41.8.1758, 1996.

Dunn, R. J. K., Welsh, D., Teasdale, P. R., Lee, S. Y., Lemckert, C. J. and Meziane, T.: Investigating the distribution and sources of organic matter in surface sediment of Coombabah Lake (Australia) using elemental, isotopic and fatty acid biomarkers, Cont. Shelf Res., 28(18), 2535–2549, doi:10.1016/j.csr.2008.04.009, 2008.

Formattato: Tipo di carattere: Corsivo, Inglese (Stati Uniti)

Formattato: Inglese (Stati Uniti)

Fry, B. and Sherr, E. B.: δ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems, in Stable Isotopes in Ecological Research, edited by P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, pp. 196–229, Springer-Verlag, New York., 1989.

Gillis, L. G., Ziegler, A. D., van Oevelen, D., Cathalot, C., Herman, P. M. J., Wolters, J. W. and Bouma, T. J.: Tiny Is Mighty: Seagrass Beds Have a Large Role in the Export of Organic Material in the Tropical Coastal Zone, PLoS One, 9(11), e111847, doi:10.1371/journal.pone.0111847, 2014.

Githaiga, M. N., Gilpin, L., Kairo, J. G. and Huxham, M.: Biomass and productivity of seagrasses in Africa, Bot. Mar., 59(2–3), doi:10.1515/bot-2015-0075, 2016.

Gonneea, M. E., Paytan, A. and Herrera-Silveira, J. A.: Tracing organic matter sources and carbon burial in mangrove sediments over the past 160 years, Estuar. Coast. Shelf Sci., 61(2), 211–227, doi:10.1016/j.ecss.2004.04.015, 2004.

Heck, K. L., Carruthers, T. J. B., Duarte, C. M., Hughes, A. R., Kendrick, G., Orth, R. J. and Williams, S. W.: Trophic Transfers from Seagrass Meadows Subsidize Diverse Marine and Terrestrial Consumers, Ecosystems, 11(7), 1198–1210, doi:10.1007/s10021-008-9155-y, 2008.

Hemminga, M. A. and Duarte, A. C.: Seagrass Ecology., 2008.

Hemminga, M. A., Slim, F. J., Kazungu, J., Ganssen, G. M., Nieuwenhuize, J. and Kruyt, N. M.: Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral-reefs (Gazi Bay, Kenya), Mar. Ecol. Prog. Ser., 106(3), 291–301, doi:10.3354/meps106291, 1994.

Kaur, A., Chaudhary, A., Kaur, A., Choudhary, R. and Kaushik, R.: Phospholipid fatty acid-A bioindicator of environment monitoring and assessment in soil ecosystem, Curr. Sci., 89(7), 1103–1112, 2005.

Kelly, J. R. and Scheibling, R. E.: Fatty acids as dietary tracers in benthic food webs, Mar. Ecol. Prog. Ser., 446, 1–22, doi:10.3354/meps09559, 2012.

Kennedy, H., Gacia, E., Kennedy, D. P., Papadimitriou, S. and Duarte, C. M.: Organic carbon sources to SE Asian coastal sediments, Estuar. Coast. Shelf Sci., 60(1), 59–68, doi:10.1016/j.ecss.2003.11.019,

Formattato: Tipo di carattere: Symbol, Inglese (Stati Uniti)

Formattato: Inglese (Stati Uniti), Apice

Formattato: Inglese (Stati Uniti)

2004.

Kitheka, J. U.: Coastal tidally-driven circulation and the role of water exchange in the linkage between tropical coastal ecosystems, Estuar. Coast. Shelf Sci., 45(2), 177–187, doi:10.1006/ecss.1996.0189, 1997.

Kitheka, J. U., Ohowa, B. O., Mwashote, B. M., Shimbira, W. S., Mwaluma, J. M. and Kazungu, J. M.: Water circulation dynamics, water column nutrients and plankton productivity in a well-flushed tropical bay in Kenya, J. Sea Res., 35(4), 257–268, doi:10.1016/S1385-1101(96)90753-4, 1996.

Koch, M. S. and Madden, C. J.: Patterns of primary production and nutrient availability in a Bahamas lagoon with fringing mangroves, Mar. Ecol. Prog. Ser., 219(1998), 109–119, doi:10.3354/meps219109, 2001.

Kristensen, E., Bouillon, S., Dittmar, T. and Marchand, C.: Organic carbon dynamics in mangrove ecosystems: A review, Aquat. Bot., 89(2), 201–219, doi:10.1016/j.aquabot.2007.12.005, 2008.

Lacerda, L. D., Ittekkot, V. and Patchineelam, S. R.: Biogeochemistry of Mangrove Soil Organic Matter : a Comparison Between *Rhizophora* and *Avicennia* Soils in South-eastern Brazil, Estuar. Coast. Shelf Sci., 40, 713–720, doi:DOI: 10.1006/ecss.1995.0048, 1995.

Lamb, A. L., Wilson, G. P. and Leng, M. J.: A review of coastal palaeoclimate and relative sea-level reconstructions using δ^{13}C and C/N ratios in organic material, Earth-Science Rev., 75(1–4), 29–57, doi:10.1016/j.earscirev.2005.10.003, 2006.

Lee, S. Y.: Mangrove outwelling - a review, Hydrobiologia, 295(1–3), 203–212, doi:10.1007/BF00029127, 1995.

Lee, S. Y.: Tropical mangrove ecology: Physical and biotic factors influencing ecosystem structure and function, Aust. J. Ecol., 24(4), 355–366, doi:10.1046/j.1442-9993.1999.00984.x, 1999.

Lugendo, B. R., Nagelkerken, I., Kruitwagen, G., van der Velde, G. and Mgaya, Y. D.: Relative importance of mangroves as feeding habitats for fishes: a comparison between mangrove habitats with different settings, Bull. Mar. Sci., 80, 497–512, 2007.

Formattato: Tipo di carattere: Corsivo, Inglese (Stati Uniti)

Formattato: Inglese (Stati Uniti)

Formattato: Tipo di carattere: Corsivo, Inglese (Stati Uniti)

Formattato: Inglese (Stati Uniti)

Formattato: Inglese (Stati Uniti), Apice

Formattato: Inglese (Stati Uniti)

Maher, D. T., Santos, I. R., Golsby-Smith, L., Gleeson, J. and Eyre, B. D.: Groundwater-derived dissolved inorganic and organic carbon exports from a mangrove tidal creek: The missing mangrove carbon sink?, Limnol. Oceanogr., 58(2), 475–488, doi:10.4319/lo.2013.58.2.0475, 2013.

Meziane, T. and Tsuchiya, M.: Organic matter in a subtropical mangrove-estuary subjected to wastewater discharge: Origin and utilisation by two macrozoobenthic species, J. Sea Res., 47(1), 1–11, doi:http://dx.doi.org/10.1016/S1385-1101(01)00092-2, 2002.

Meziane, T., D'Agata, F. and Lee, S. Y.: Fate of mangrove organic matter along a subtropical estuary: small-scale exportation and contribution to the food of crab communities, Mar. Ecol. Prog. Ser., 312, 15–27, doi:10.3354/meps312015, 2006.

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

Neukermans, G., Dahdouh-Guebas, F., Kairo, J. G. and Koedam, N.: Mangrove species and stand mapping in Gazi bay (Kenya) using Quickbird satellite imagery, J. Spat. Sci., 53(1), 75–86, doi:10.1080/14498596.2008.9635137, 2008.

Ochieng, C. A. and Erftemeijer, P. L.: Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya, Trees - Struct. Funct., 16(2–3), 167–171, doi:10.1007/s00468-001-0146-2, 2002.

Odum, W. E. and Heald, E. J.: Trophic Analyses of an Estuarine Mangrove Community, Bull. Mar. Sci., 22, 671–738, 1972.

Parnell, A. C., Inger, R., Bearhop, S. and Jackson, A. L.: Source partitioning using stable isotopes: coping with too much variation., PLoS One, 5(3), e9672, doi:10.1371/journal.pone.0009672, 2010.

Rajendran, N. and Kathiresan, K.: Biochemical Changes in Decomposing Leaves of Mangroves, Chem. Ecol., 17(2), 91–102, doi:10.1080/02757540008037664, 2000.

Rao, R. G., Woitchik, A. F., Goeyens, L., Vanriet, A., Kazungu, J. and Dehairs, F.: Carbon, nitrogen contents and stable carbon-isotope abundance in mangrove leaves from an east-african coastal lagoon

Formattato: Tipo di carattere: Corsivo, Inglese (Stati Uniti)

Formattato: Inglese (Stati Uniti)

(Kenya), Aquat. Bot., 47(2), 175–183, doi:10.1016/0304-3770(94)90012-4, 1994.

Slim, F. J., Gwada, P. M., Kodjo, M. and Hemminga, M. A.: Biomass and litterfall of *Ceriops tagal* and *Rhizophora mucronata* in the mangrove forest of Gazi Bay, Kenya, Mar. Freshw. Res., 47(8), 999–1007, doi:10.1071/mf9960999, 1996.

Twilley, R. R.: The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary, Estuar. Coast. Shelf Sci., 20(5), 543–557, doi:10.1016/0272-7714(85)90106-4, 1985.

Vizzini, S. and Mazzola, A.: The fate of organic matter sources in coastal environments: a comparison of three Mediterranean lagoons, Hydrobiologia, 611(1), 67–79, doi:10.1007/s10750-008-9458-1, 2008.

Walton, M., Al-Maslamani, I., Skov, M., Al-Shaikh, I., Al-Ansari, I., Kennedy, H. and Le Vay, L.: Outwelling from arid mangrove systems is sustained by inwelling of seagrass productivity, Mar. Ecol. Prog. Ser., 507, 125–137, doi:10.3354/meps10827, 2014.

Wernberg, T., Vanderklift, M. A., How, J. and Lavery, P. S.: Export of detached macroalgae from reefs to adjacent seagrass beds, Oecologia, 147(4), 692–701, doi:10.1007/s00442-005-0318-7, 2006.

Woitchik, A. F., Ohowa, B., Kazungu, J. M., Rao, R. G., Goeyens, L. and Dehairs, F.: Nitrogen enrichment during decomposition of mangrove leaf litter in an east African coastal lagoon (Kenya): Relative importance of biological nitrogen fixation, Biogeochemistry, 39(1), 15–35, 1997.

Formattato: Tipo di carattere: Corsivo, Inglese (Stati Uniti)

Formattato: Inglese (Stati Uniti)

Formattato: Tipo di carattere: Corsivo, Inglese (Stati Uniti)

Formattato: Inglese (Stati Uniti)

Tables

Table 1. Results of PERMANOVA main tests and pair-wise tests (9999 permutations) for organic matter source contribution to SOM (a) and SPOM (b). df: degree of freedom; MS: mean square; P(perm): permutational probability values.

a) SOM		**Mangroves**			**Macroalgae**			**Seagrasses**		
Main test										
Source of variation	**df**	**MS**	**Pseudo-F**	**P(perm)**	**MS**	**Pseudo-F**	**P(perm)**	**MS**	**Pseudo-F**	**P(perm)**
Season (se)	1	0.26	654.9	0.0001	0.12	461.7	0.0001	0.37	2058.9	0.0001
Transect (tr)	1	0.01	31.5	0.0001	0.25	956.4	0.0001	0.26	1487.1	0.0001
Station (st)	3	1.84	4653.0	0.0001	0.07	282.0	0.0001	1.51	8456.4	0.0001
se x tr	1	0.01	21.7	0.0001	0.24	938.7	0.0001	0.21	1151.8	0.0001
se x st	3	0.08	197.2	0.0001	0.08	302.6	0.0001	0.13	757.7	0.0001
tr x st	3	0.11	282.4	0.0001	0.26	1010.4	0.0001	0.20	1147.5	0.0001
se x tr x st	3	0.03	68.9	0.0001	0.15	594.9	0.0001	0.11	598.3	0.0001
Residual	64	0.00			0.00			0.00		
Total	79									

Pair-wise Tests: Term 'se x tr x st' for pairs of levels of factor 'station'

all the comparisons resulted significant at P(perm) < 0.01

b) SPOM		**Mangroves**			**Macroalgae**			**Seagrasses**			**Zooplankton**		
Main test													
Source of variation	**df**	**MS**	**Pseudo-F**	**P(perm)**	**MS**	**Pseudo-F**	**P(perm)**	**MS**	**Pseudo-F**	**P(perm)**	**MS**	**Pseudo-F**	**P(perm)**
Season (se)	1	0.01	107.6	0.0001	0.01	13.0	0.0007	0.04	146.5	0.0001	0.01	22.9	0.0001
Transect (tr)	1	0.04	522.1	0.0001	0.06	136.6	0.0001	0.09	348.0	0.0001	0.02	35.4	0.0001
Station (st)	3	0.51	5976.4	0.0001	0.02	41.9	0.0001	0.24	940.1	0.0001	0.18	367.4	0.0001
se x tr	1	0.24	2813.1	0.0001	0.02	36.9	0.0001	0.03	122.2	0.0001	0.05	96.6	0.0001
se x st	3	0.20	2372.4	0.0001	0.09	198.8	0.0001	0.05	180.9	0.0001	0.12	244.4	0.0001
tr x st	3	0.36	4204.5	0.0001	0.06	118.1	0.0001	0.13	531.3	0.0001	0.04	75.1	0.0001
se x tr x st	3	0.05	631.8	0.0001	0.02	50.9	0.0001	0.02	61.1	0.0001	0.01	26.6	0.0001
Residual	64	*0.00*			*0.00*			*0.00*			*0.00*		
Total	79												

Pair-wise Tests: Term 'se x tr x st' for pairs of levels of factor 'station'

all the comparisons resulted significant at P(perm) < 0.01 except for:

OM source	**Term**	**Stations**	**P(perm)**	**Stations**	**P(perm)**	**Stations**	**P(perm)**
Macroalgae	DS - A	IA vs.SB	< 0.05	*IA vs.CR*	n.s.	SB vs.CR	< 0.05
Seagrasses	RS - B	*M vs.CR*	n.s.				

Formattato
Formattato
Formattato
Formattato
Formattato
Tabella formattata
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Tabella formattata
Tabella formattata
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato
Formattato

Figures

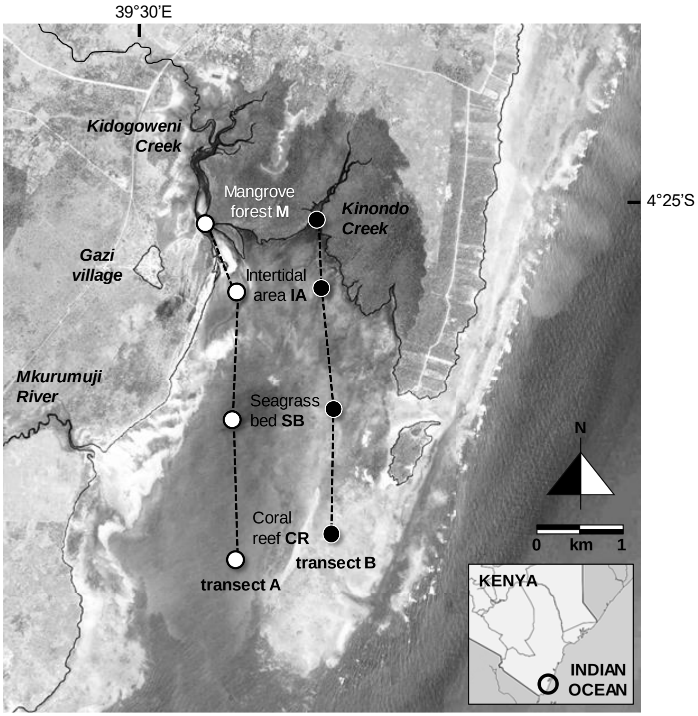


Figure 1. Gazi Bay. Sampling stations lying along two land-to-sea transects are shown: mangrove forest (M), intertidal area (IA), seagrass bed (SB), coral reef (CR). Transect A (white circles) is in correspondence with Kidogoweni Creek; transect B (black circles) is in correspondence with Kinondo Creek.

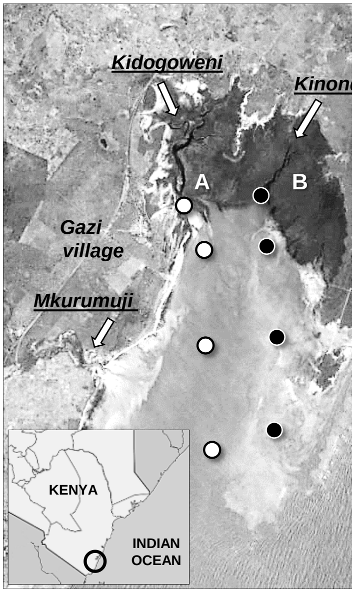
Eliminato:

Primary producer group	FAs	Averag abundance
Mangroves	16:00	38.2
average similarity: 81.7%	18:3 n3	18.4
	LCFAs (>22)	8.0
	18:1 n9	8.1
	18:2 n6	10.1
Seagrasses	18:3 n3	40.4
average similarity: 86.6%	18:2 n6	24.6
	16:00	18.7
Brown macroalgae	16:00	34.8
average similarity: 85.5%	18:1 n9	12.7
	18:4 n3	12.2
	14:00	10.8
	20:4 n6	7.0
	20:2 n6	5.3
Red macroalgae	16:00	59.6
average similarity: 86.4%	20.5 n3	15.5
	14:00	8.7

...

Eliminato: ¶

Eliminato:



Formattato: Inglese (Stati Uniti)

Eliminato: ¶

Formattato: Giustificato, Interlinea: 1.5 righe

Eliminato: ¶

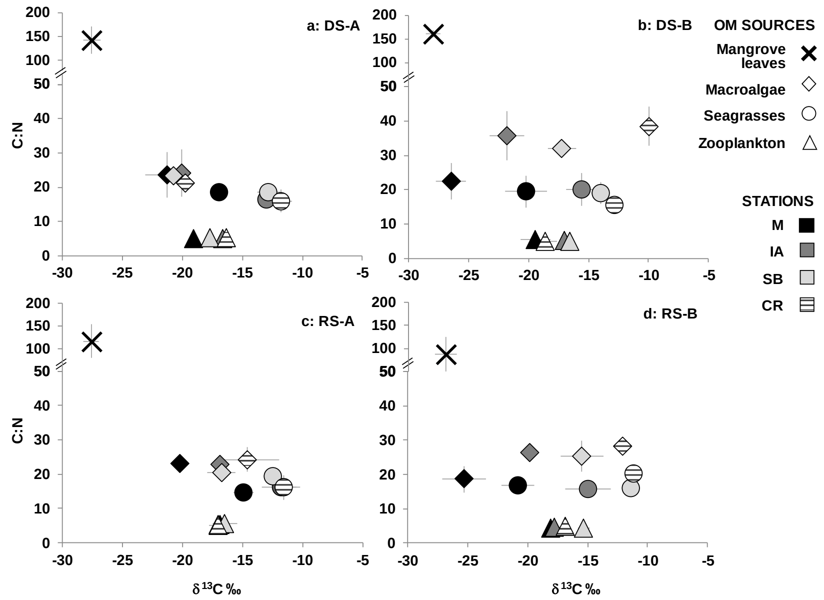
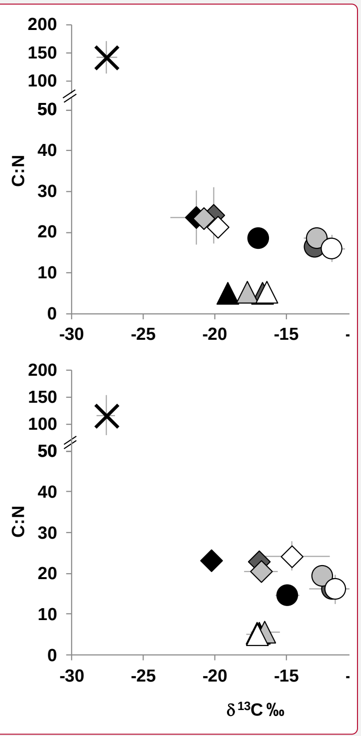


Figure 2. C:N ratio *versus* δ^{13}C (‰) of organic matter sources from the four sampling stations (mangrove forest M in black, intertidal area IA in dark grey, seagrass bed SB in light grey, coral reef CR in white) along transects A and B in dry (DS) and rainy seasons (RS). Mangroves (cross), macroalgae (diamond), seagrasses (circle) and zooplankton (triangle).

Eliminato: ¶



Eliminato:

Eliminato: M

Eliminato: I

Eliminato: A

Eliminato: S

Eliminato: B

Eliminato: C

Eliminato: R

Eliminato: (symbols with decreasing size from mangroves to intertidal areas, seagrass beds and coral reefs

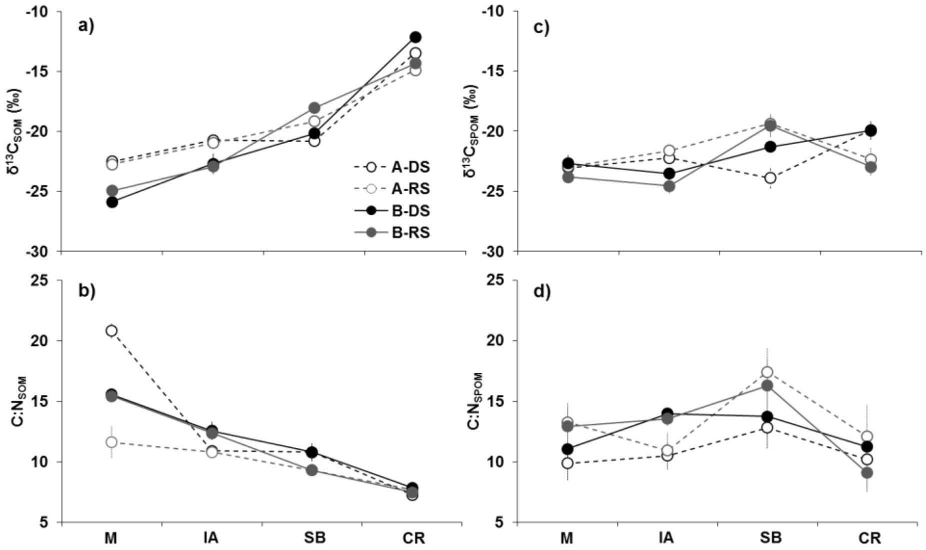


Figure 3. δ^{13}C (‰) and C:N ratio of sedimentary organic matter (SOM; a, b) and suspended particulate organic matter (SPOM; c, d) from the four sampling stations (mangrove forest M, intertidal area IA, seagrass bed SB, coral reef CR). Transects A and B are indicated with open and filled circles respectively. Dry (DS) and rainy seasons (RS) are indicated in black and grey circles respectively.

Eliminato: s

Eliminato: s

Eliminato: s

Eliminato: s

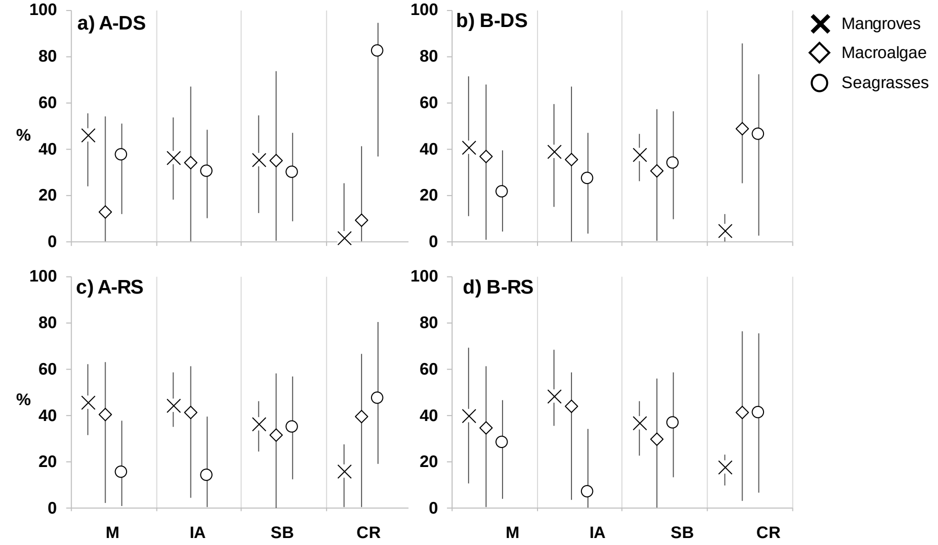
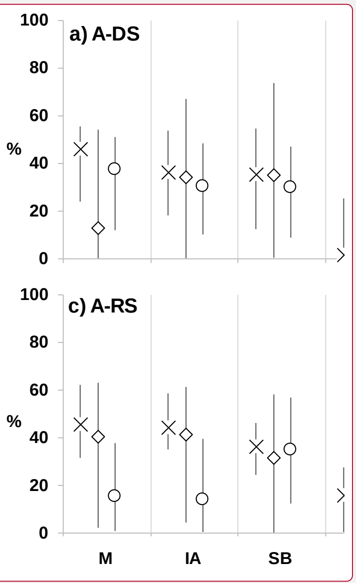
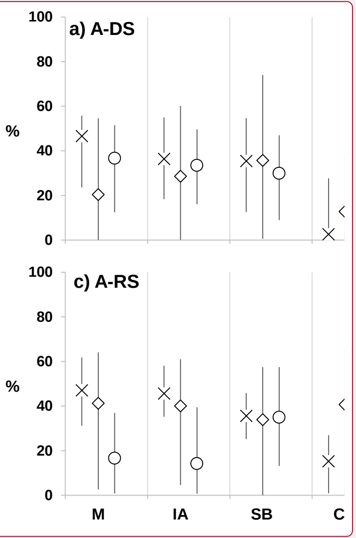


Figure 4. Organic matter source probability of contribution (mode ± 95th credibility interval) to SOM in the four sampling stations (mangrove forest M; intertidal area IA; seagrass bed SB; coral reef CR) along transects A and B in dry (DS) and rainy season (RS). Mangroves (cross), macroalgae (diamond) and seagrasses (circle).

Eliminato:



Eliminato:



Formattato: Allineato a sinistra

Formattato: Inglese (Stati Uniti)

Eliminato: s…M; intertidal areas…IA; seagrass beds…SB; coral reefs

...

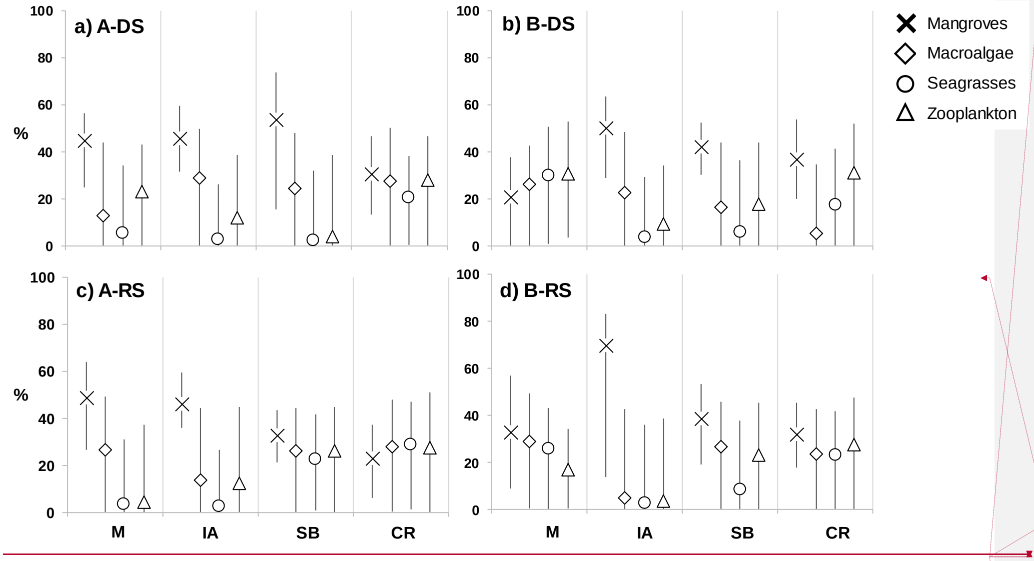
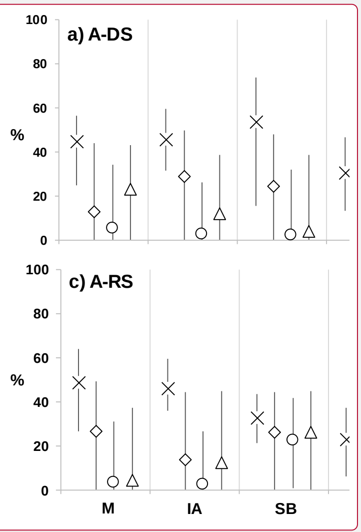
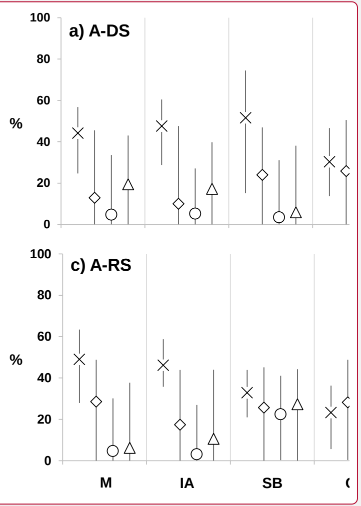


Figure 5. Organic matter source probability of contribution (mode ± 95th credibility interval) to SPOM in the four sampling stations (mangrove forest M; intertidal area IA; seagrass bed SB; coral reef CR) along transects A and B in dry (DS) and rainy season (RS). Mangroves (cross), macroalgae (diamond), seagrasses (circle) and zooplankton (triangle).



Eliminato:

Formattato: Allineato a sinistra



Eliminato:

Formattato: Inglese (Stati Uniti)

Eliminato: s…M; intertidal areas…IA; seagrass beds…SB; coral reefs

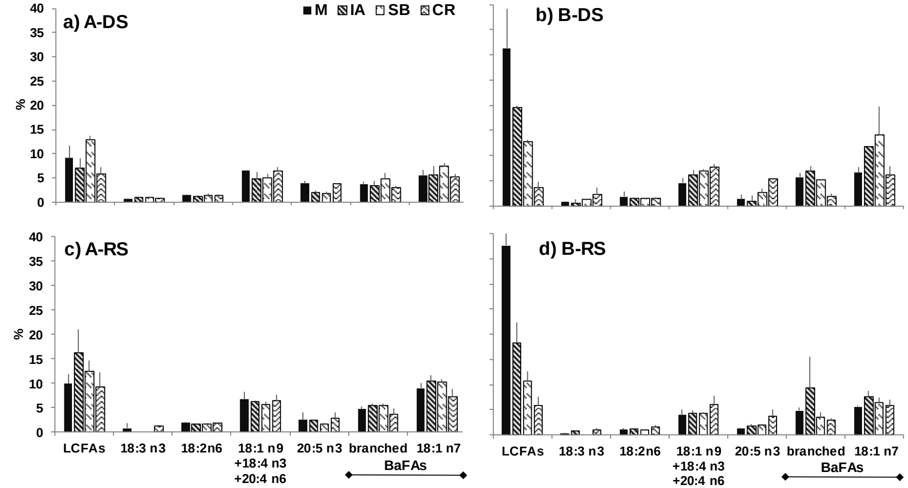
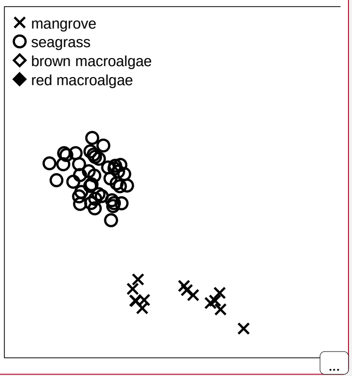
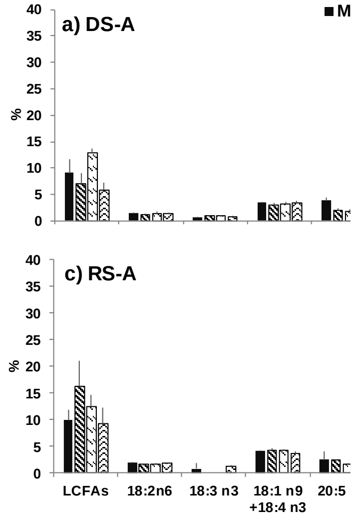


Figure 6. Mean (± s.d.) relative abundance of biomarker FAs (% of total FAs) in SOM. Selected biomarkers include: LCFAs, 18:3 n3 and 18:2 n6 for mangroves, 18:2 n6 and 18:3 n3 for seagrasses, 18:2 n6 for agricultural runoff, 18:1 n9 + 18:4 n3 + 20:4 n6 for brown macroalgae, 20:5 n3 for red macroalgae and diatoms, branched FAs and 18:1 n7 for bacteria.

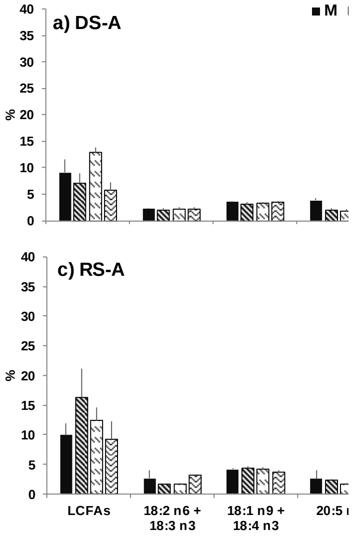
Eliminato:



Eliminato:



Eliminato:



Formattato: Inglese (Stati Uniti)

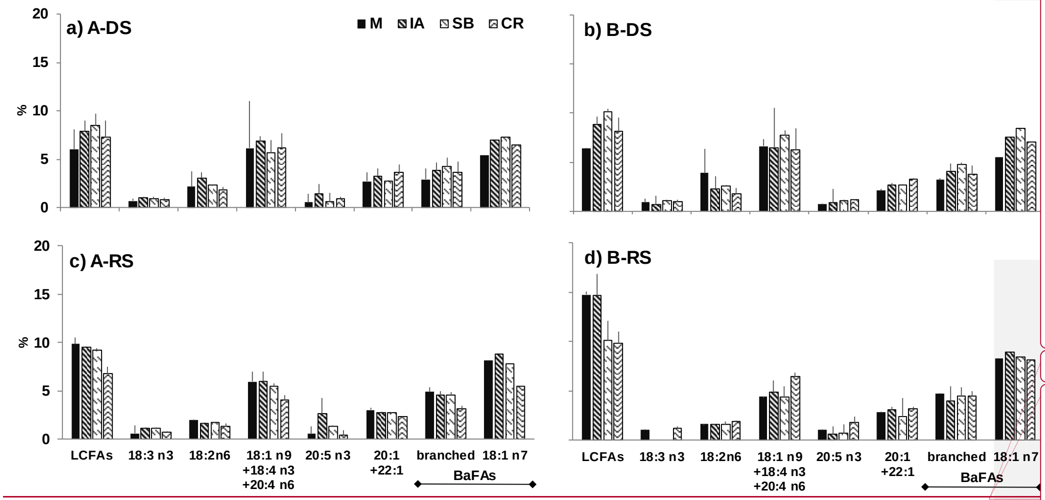
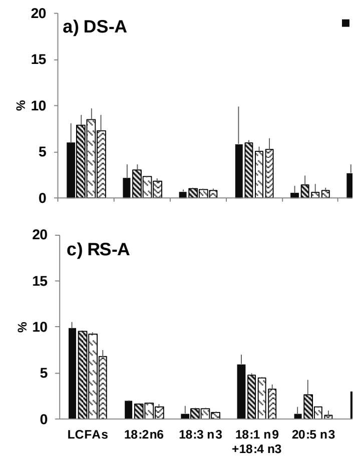
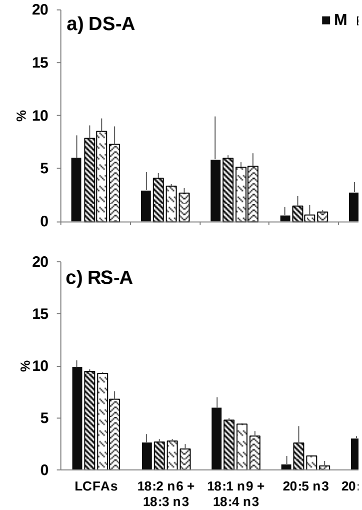


Figure 7. Mean (± s.d.) relative abundance of biomarker FAs (% of total FAs) in SOM. Selected biomarkers include: LCFAs, 18:3 n3 and 18:2 n6 for mangroves, 18:2 n6 and 18:3 n3 for seagrasses, 18:2 n6 for agricultural runoff, 18:1 n9 + 18:4 n3 + 20:4 n6 for brown macroalgae, 20:5 n3 for red macroalgae and diatoms, 20:1 + 22:1 for zooplankton, branched FAs and 18:1 n7 for bacteria.



Eliminato:

Formattato: Inglese (Stati Uniti)



Eliminato:

Eliminato: 18:2 n6 and

Eliminato: Figure 87. Mean (± s.d.) relative abundance of biomarker FAs (% of total FA) in SPOM. Selected biomarkers include: LCFAs for mangroves, 18:2 n6 + 18:3 n3 for seagrasses, 18:1 n9 + 18:4 n3 for brown macroalgae, 20:5 n3 for red macroalgae and branched + 18:1 n7 for bacteria.¶