

Seasonal and spatial changes in the sediment organic matter of a semi-enclosed marine system (W-Mediterranean Sea)

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Abstract

The composition of sediment organic matter and the related role of microphytobenthic biomass have been investigated during one-year in a semi-enclosed marine system (Marsala lagoon, Mediterranean Sea). Monthly samples from June 1993 to May 1994 were analysed for carbohydrate, protein, lipid, photosynthetic pigment and total organic matter.

The three main biochemical classes of organic compounds (i.e. carbohydrates, proteins and lipids) showed higher concentrations than reported in the literature. However, photosynthetic pigment was quite low, compared to other enclosed marine basins or Mediterranean coastal lagoons. As a result, the contribution of primary organic carbon to the sedimentary biopolymeric fraction of organic matter was low (on average 2.2%), indicating that most of the sedimentary organic matter in the study area originated from sources other than micro-algae. The sedimentary organic matter, dominated by carbohydrates (on average 51.2%) followed by proteins (39.0%) and lipids (9.8%), as well as the low protein to carbohydrate ratio, indicate the presence of large amounts of non-living and/or aged organic matter. Comparing data on spatial distribution of sedimentary and suspended organic matter, the dynamic balance of resuspension vs. sedimentation along a north-south axis is invoked as one major factor affecting the distribution and composition of the main classes of organic compounds. The macroalgal and vascular plant coverage is suggested to be another major factor affecting both amounts and composition of sedimentary organic matter. The northern area, characterised by partially unvegetated sediments, showed higher amounts of proteins, whilst moving southward and approaching a luxuriant *Posidonia oceanica* reef, carbohydrates became more important relative to proteins. As only the biopolymeric fraction of sediment organic matter showed significant seasonal changes, the quantity of sediment OM behaves as an emerging property. By contrast, OM quality is strictly connected to algal coverage as well as to episodic inputs of primary organic matter from deposited phytoplankton and/or microphytobenthos. The uncoupling between large amounts and relatively low nutritional value of sedimentary OM suggests that this particular environment behaves as a detrital 'trap'.

Introduction

Quantity and quality of organic matter in surface sediments are recognised as major factors affecting benthic fauna dynamics and metabolism (Graf et al., 1983; Grant & Hargrave, 1987). The gross measure of total organic matter content in sediment furnishes only scant information on its actual availability to consumers (Newell & Field, 1983; Bianchi & Levinton, 1984). In recent years much attention has been paid

to the nutritional value of sediment organic matter, assessed by its biochemical composition (Fabiano et al., 1995). A universally accepted methodology to assess the labile fraction of sedimentary organic matter does not exist. Total organic matter (as determined by combustion) is generally an overestimate of food available for consumers, mainly because various inorganic compounds may be oxidised at about 500 °C (Bretschko & Leichtfried, 1987). The determination of carbohydrate, lipid and protein carbon could be suitable



to estimate the fraction potentially available to sediment ingesting organisms (Fichez, 1991). Although this approach is not free of interpretation problems, it has been widely used (Fabiano & Danovaro, 1994; Fabiano et al., 1995; Danovaro, 1996).

Microphytobenthos can be a major food source for benthic fauna ranging from small protozoa to meio- and macrofauna (Montagna et al., 1983; Bianchi & Levinton, 1984; Plante et al., 1986). Despite methodological problems in assessing the actual microphytobenthic chlorophyll-*a* (MacIntyre et al., 1996), the determination of photosynthetic pigments is fundamental to assess the amount of food available to higher trophic levels and its contribution to organic carbon.

In shallow coastal systems, the biomass of benthic algae may exceed that of overlying phytoplankton (MacIntyre et al., 1996). Sediment resuspension, mainly driven by wind (Alpine & Cloern, 1992; Millet & Cecchi, 1992; Arfi & Bouvy, 1995), may contribute to such sediment-water exchange. Since microphytobenthos generally represents a limited fraction of sedimentary organic matter, the ecological role of resuspension in affecting plankton ecology is more evident in highly detrital systems. Hopkinson (1985) showed that resuspension can control the relative amounts of organic carbon as well as the sites and rates of organic matter degradation in the benthos and the water column. This appears even more important in coastal systems, where resuspension in shallows with wind forcing is frequent (Pusceddu et al., 1997a).

In shallow coastal ponds, sounds and coastal lagoons, the high spatial and temporal variability of physical variables (i.e. temperature, salinity, turbidity) may result in unpredictable changes of food resources for consumers (Pusceddu et al., 1997a, b). Such variability is responsible for an uncoupling between primary and secondary production (Newell, 1982).

In this paper the composition of the sediment organic matter and the microphytobenthic biomass are studied during one year in a semi-enclosed marine system. Our aims were: (1) to assess the origin and fate of labile organic compounds and the contribution of microphytobenthic biomass; (2) to quantify labile organic compounds usable as food by benthic consumers; (3) to focus on the role of some environmental constraints as major factors affecting seasonal and spatial variations of sedimentary food quality.

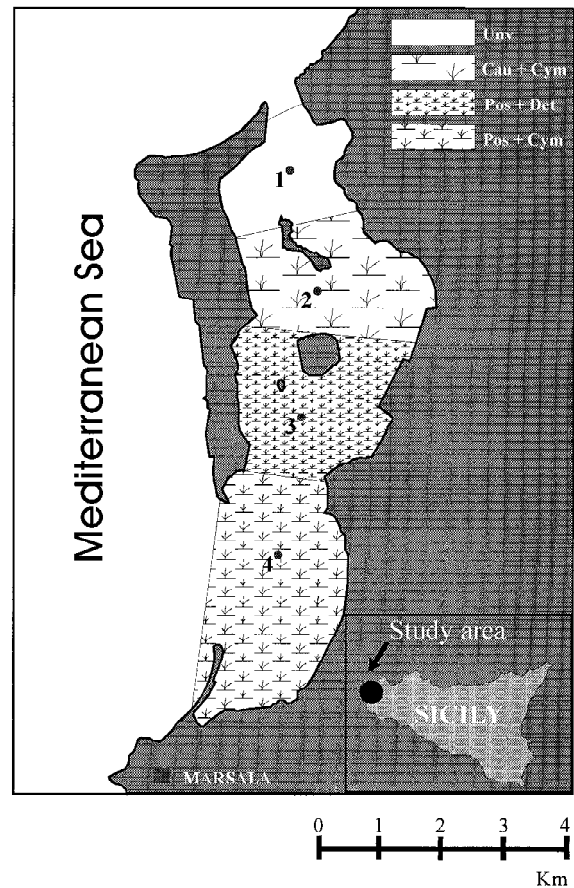


Figure 1. The study site and sampling stations. Illustrated in a very schematic way is also the spatial distribution of different algal and vascular plant coverage types (Unv = unvegetated; Cym = *Cymodocea nodosa*; Cau = *Caulerpa prolifera*; Pos = *Posidonia oceanica*; Det = detritus of *Posidonia*).

Description of the study site

The study was carried out in a semi-enclosed marine system (Marsala lagoon), characterised by two channels with the sea. A platform separates the rest of the basin from the open sea (Figure 1). The basin is shallow, depth ranging from 2 m along the eastern shore of the platform to 0.50 m in the western area. Depth increases to about 2.5 m in the southernmost area, close to the sea. The northern channel is 450 m wide with occasional turbulent inputs of sea-water. Here, sediments are characterised by reduced algal coverage. The southern mouth, 1450 m wide, is open to a continuous sea water inflow and characterised by internal tides. The hydrography of the central area is influenced by two little islands, which act as mechanical obstacles to water circulation and gener-

ate turbulent currents. Southernmost to this area is a luxuriant *Posidonia oceanica* reef, influencing water circulation and silting. No continental inputs are present. Water exchanges with the open sea are ensured by currents with mean speed between $4.92 \pm 1.54 \text{ cm s}^{-1}$ in the south and $2.34 \pm 0.87 \text{ cm s}^{-1}$ in the north.

Material and methods

Sampling

Monthly sediment samples were collected by Scuba diving between June 1993 and May 1994 at four stations (Figure 1). Three replicate cores per station and period were collected randomly from three quadrats (20 cm length, 400 cm² surface area) belonging to a larger quadrat (1 m²). Sediments were cored by inserting PVC tubes (i.d. 4.7 cm). Samples were brought back to the laboratory and processed within four hours. The top 0–1 cm of each core, used for analyses of carbohydrates, proteins, lipids and photosynthetic pigments was immediately frozen at -20°C and stored until analysis. Temperature and salinity were measured *in situ* using a Hydrolab multiprobe. The meteorological station of Birgi Airport (Trapani) provided data on wind speed and direction.

Chemical analyses and data analysis

Sediment was treated with 10% hydrochloric acid to remove carbonates (Buchanan, 1971). Total organic matter (OM) of three dried subsamples was determined as the difference between the dry weight (80°C , 24 h) of the sediment and the residue left after combustion at 450°C for 2 h (Parker, 1983).

After sonication in deionized water, total lipids (LIP) were extracted by direct elution with chloroform-methanol according to Bligh & Dyer (1959) and Marsh & Weinstein (1966). Data are reported in tripalmitine equivalents. Protein (PRT) analyses of three replicates were conducted following extraction with NaOH (0.5M, 4h) and were determined according to Hartree (1972), modified by Rice (1982) to compensate for phenol interference and expressed as bovine serum albumin (BSA) equivalents. Carbohydrates (CHO) of three replicate samples were analysed according to Gerchacov & Hatcher (1972) and expressed as glucose equivalents. The assay, which reacts with reducing saccharides (Table 2), is based on the same principle as the widely used method of

Dubois et al. (1956), but it is specific for carbohydrate in sediments. The soluble fraction of the sedimentary carbohydrate pool was determined according to Fabiano et al. (in press).

For each analysis, blanks used sediments that had been precombusted at 450°C for 2 h. Lipid, carbohydrate and protein were converted into carbon equivalents using 0.75, 0.40 and 0.49 gC g⁻¹ conversion factors, respectively (Fabiano & Pusceddu, 1998). The biopolymeric carbon fraction (C-BPF) was defined as the sum of carbohydrate, protein and lipid carbon (Fabiano et al., 1995).

Analyses of chlorophyll *a* (Chl*a*) and phaeopigments (Phaeo) were carried out according to Lorenzen & Jeffrey (1980). Pigments were extracted with 90% acetone (24 h in the dark at 4°C). After centrifugation, the supernatant was used to determine functional Chl*a* and acidified with 0.1 N HCl to estimate the amounts of phaeopigments (Plante-Cuny, 1974). Chloroplastic pigment equivalents (CPE) were calculated as sum of chlorophyll *a* and phaeopigment concentrations.

Microphytobenthic carbon was calculated by converting Chl*a* concentrations to carbon content (C-Chl*a*), using a conversion factor of 40 (De Jonge, 1980).

Data relative to macroalgal and vascular plants coverage were obtained from Calvo et al., 1996 and Scilipoti (1997).

Temporal and spatial fluctuations were assessed by two-way analysis of variance (ANOVA) with time (months) and space (stations) as sources of variation.

Results

Environmental variables

Temperature and salinity did not vary significantly between stations and showed a marked seasonality (Figure 2). Temperature values ranged between 12.1°C (Station 2, January 1994) and 27.7°C (Stations 2 and 4, August 1993). Salinity values ranged between 34.5 (Station 2, February 1994) and 43.8 (Station 1, September 1993). Temperature and salinity were positively correlated ($r = 0.78$; $n = 48$).

The seasonal pattern of wind velocity (Figure 3a) was characterized by two periods of high values, autumn-spring and summer. On an annual basis, winds came mainly from the 2nd and 4th quadrant (Figure 3b). Calm conditions occurred only in 20% of the study period.

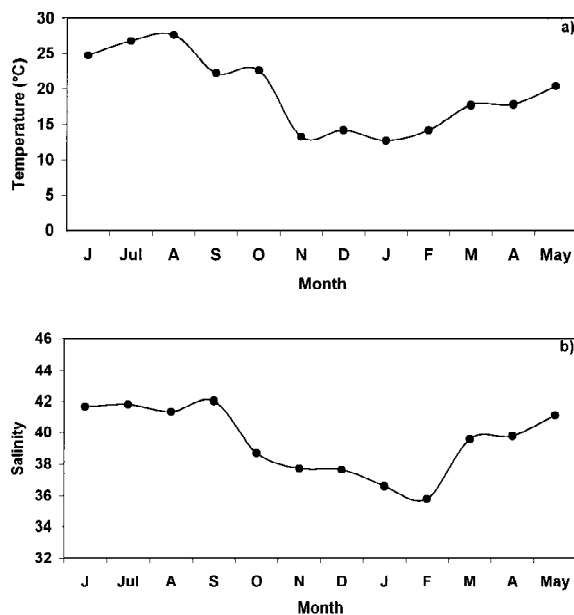


Figure 2. Seasonal changes of (a) temperature and (b) salinity in the Marsala lagoon during the study period. Data reported are averages of the four sampling stations.

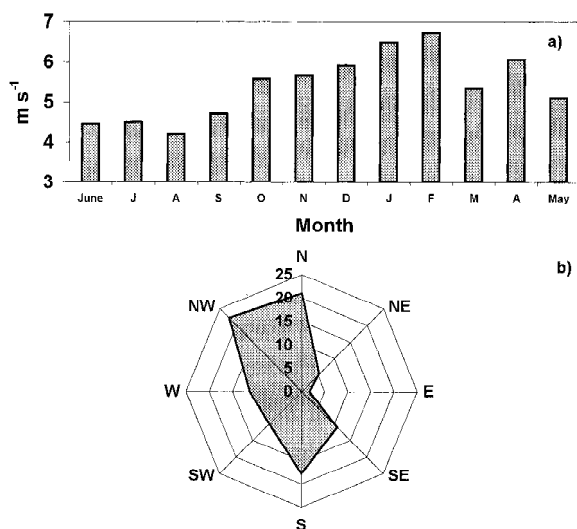


Figure 3. Seasonal changes (monthly averaged) of wind velocity (a, m s^{-1}) and annual average of wind direction frequency (b, %) in the Marsala lagoon.

Sediment organic matter content

Total organic matter (TOM) content varied seasonally. Highest concentrations occurred in November 1993 at Stations 1, 2 and 3 (526.4 ± 422.7 and 234.0 ± 131.6 and $269.3 \pm 123.7 \text{ mg g}^{-1}$, respectively), whilst at Station 4, where seasonality was less evident, the

highest concentration was measured in August 1993 ($136.5 \pm 64.0 \text{ mg g}^{-1}$). Lowest organic contents were measured in January 1994 in Stations 1, 2, and 3 (51.7 ± 44.9 , 101.0 ± 70.8 and $92.5 \pm 48.0 \text{ mg g}^{-1}$, respectively) and in November 1993 in Station 4 ($76.8 \pm 36.0 \text{ mg g}^{-1}$).

Biochemical composition of sediment organic matter

An ANOVA on biochemical composition of sediment organic matter and microphytobenthic biomass is summarised in Table 1. Carbohydrate, lipid and C-BPF temporal patterns showed strong seasonality, whilst protein concentrations did not vary significantly among seasons (Figure 4). The four stations had no significant differences in protein and carbohydrate content of sediments, whilst their contribution to C-BPF varied seasonally.

Sedimentary carbohydrate ranged between 0.76 mg g^{-1} (Station 2, January 1994) and 70.53 mg g^{-1} (Station 2, April 1994). Soluble carbohydrates accounted for 8.3% (range 0.3–26.7%) of the total carbohydrate pool. Proteins ranged between 2.16 mg g^{-1} (Station 2, January 1994) and 12.1 mg g^{-1} (Station 4, August 1993). Lipids ranged between 0.26 mg g^{-1} (Station 1, March 1994) and 4.47 mg g^{-1} (Station 3, June 1993). The biopolymeric fraction of sedimentary organic carbon (C-BPF) varied seasonally. Three main periods of C-BPF accumulation were detected (Figure 4): June–July 1993 (range from 4.05 to 21.05 mgC g^{-1}), November–December 1993 (range from 3.34 to 22.24 mgC g^{-1}) and April–March 1994 (range from 2.51 to 36.16 mgC g^{-1}).

Carbohydrates were the dominant class among labile organic compounds (on annual average, 51.2% of labile OM), followed by proteins (39.0%) and lipids (9.8%). The carbohydrate contribution to the labile OM pool was higher at Stations 3 and 4 (52.5% and 59.6%, respectively), whereas proteins increased in relative importance (36.9% and 31.1%) at Stations 1 and 2 (44.9 and 43.1%, respectively). On annual basis, lipid contribution to labile OM ranged between 8.4% (Station 1) and 10.7% (Station 3).

Microphytobenthic biomass

Average annual chlorophyll *a* concentration in the study area was $3.1 \mu\text{g g}^{-1}$. ANOVA results did not show significant seasonal or spatial changes. However, September 1993 and February–March 1994 appeared to be accumulation periods (Figure 5). Highest concentration of chloroplastic pigments (CPE) was meas-

Table 1. Analysis of variance results for the measured parameters. (*) = $P < 0.05$; (**) = $P < 0.01$; (***) = $P < 0.001$; Ns = not significant difference, $P > 0.05$

Variable	Source of variation	df	F	P-value
Lipids	months	11	1.991	Ns
	station	2	4.785	0.019(**)
Proteins	months	11	1.281	Ns
	station	2	0.388	Ns
Carbohydrates	months	11	3.780	0.004(**)
	station	2	1.202	Ns
Carbon of the biopolymeric fraction	months	11	3.227	0.009(**)
	station	2	1.487	Ns
chlorophyll <i>a</i>	months	11	0.851	Ns
	station	2	1.233	Ns
Phaeopigments	months	11	1.000	Ns
	station	2	0.136	Ns
Chlorplastic pigment equivalents	months	11	0.881	Ns
	station	2	0.310	Ns
% Proteins	months	11	4.436	0.001(***)
	station	2	1.823	Ns
% Carbohydrates	months	11	4.695	0.001(***)
	station	2	1.247	Ns
% Lipids	months	11	1.712	Ns
	station	2	0.075	Ns
Protein to carbohydrate ratio	months	11	1.867	Ns
	station	2	1.941	Ns

Table 2. Comparison of lipid, protein and carbohydrate concentrations from different areas. If unspecified, data are relative to the top 1-cm layer of sediments

Area	Water depth (m)	Lipids mg g ⁻¹	Proteins mg g ⁻¹	Carbohydrates mg g ⁻¹	Authors
Baltic Sea	18	nd	3.8–7.7	0.4–4.0	Meyer-Reil, 1983
Adriatic Sea	15–40	0.03–0.3	0.5–4.0	0.1–0.9	Fabiano, unpubl. data
W-Mediterranean	10–20	0.01–0.66	0.5–2.6	0.9–4.2	Fichez, 1991
Ross Sea	36–223	0.2	1.9	5.3	Fabiano et al., in press
Gulf of Gascogne Atlantic Ocean	2100	0.22	1.85	2.44	Khripounoff et al., 1985
Tyrrhenian Sea	20–60	0.01–0.02	0.3–1.7	0.3–1.9	Fabiano & Danovaro, 1994 (*)
Ligurian Sea	4	0.08–1.07	0.05–1.62	0.28–3.59	Danovaro et al., 1994
(<i>Posidonia</i> reef)					
Mactan Philippines	3	nd	0.5–1.3	0.7–1.6	Graf & Meyer-Reil, 1985 (**)
E-Mediterranean	100–2400	0.05–0.19	0.07–0.16	1.2–2.4	Danovaro et al., 1993 (***)
Ligurian Sea	10	0.06–0.23	0.02–0.04	0.18–0.58	Danovaro, 1993
Cretan Sea	40–1540	0.03–0.69	0.2–3.0	0.25–7.9	Tselepides et al., 1996
Marsala lagoon	~1	0.3–4.5	2.2–12.1	0.8–70.5	This study

(*) Average of 0–10 cm. (**) Data reported in mg cm⁻³; sediment layer not available. (***) Average of 0–15 cm.

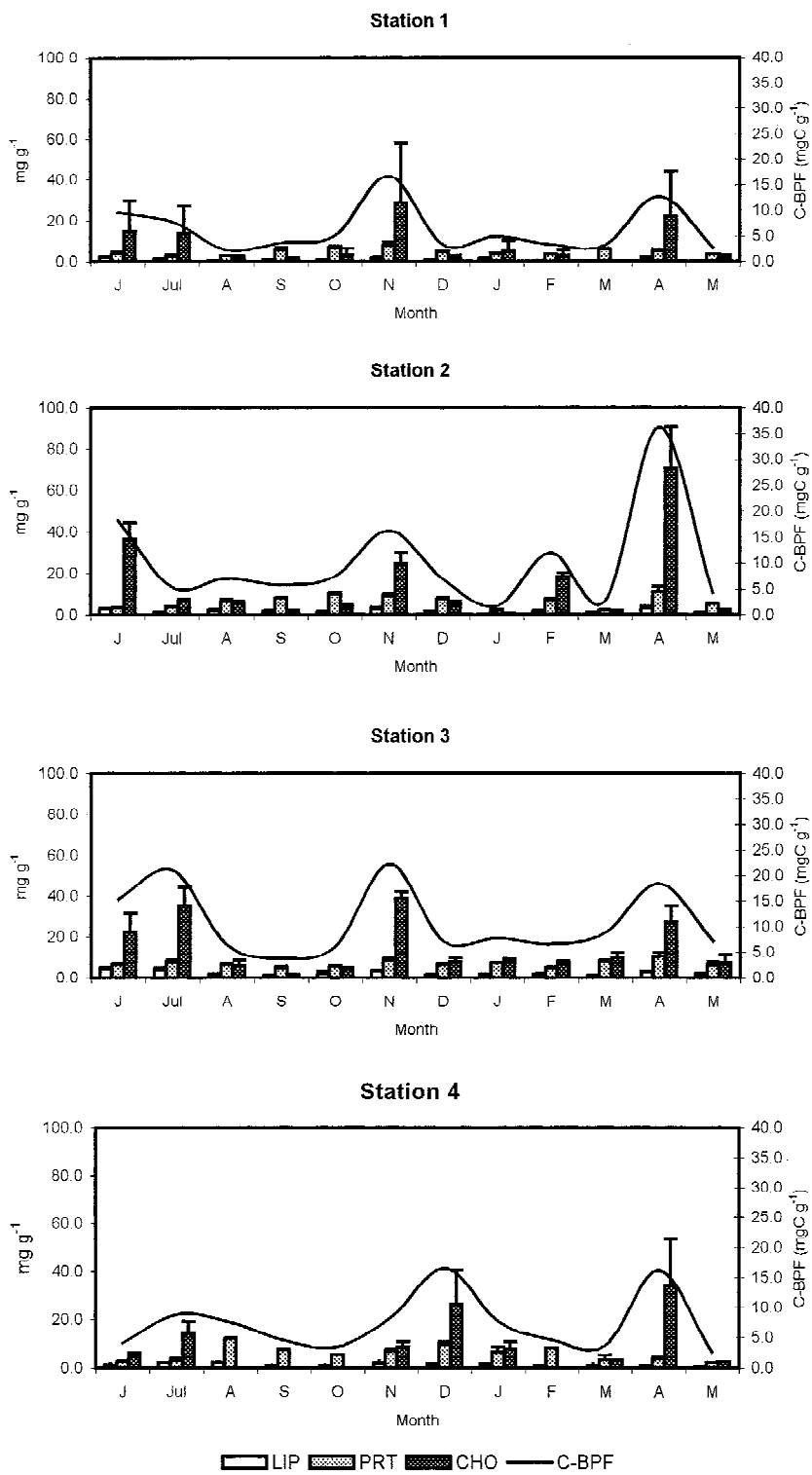


Figure 4. Seasonal changes in sedimentary lipid (mg g⁻¹), protein (mg g⁻¹), carbohydrate (mg g⁻¹) and C-BPF (mg C g⁻¹) concentrations in the four sampled stations in the Marsala lagoon.

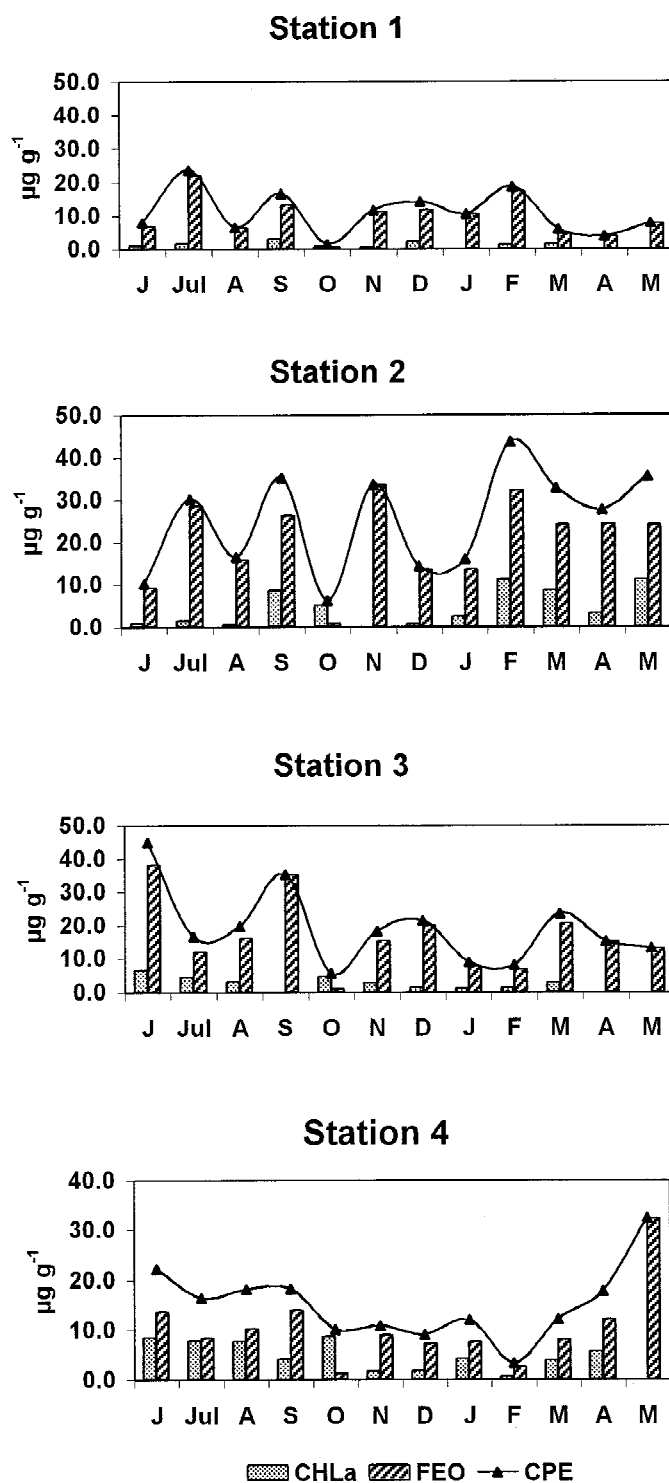


Figure 5. Seasonal changes in sedimentary chlorophyll *a*, phaeopigments and CPE concentrations (expressed as $\mu\text{g g}^{-1}$) in the four sampled stations in the Marsala lagoon.

ured in Station 2 ($43.7 \mu\text{g g}^{-1}$ in February 1994). *Chla* carbon accounted for a negligible fraction of C-BPF (on average 2.2%). Phaeopigment was always higher than active chlorophyll-*a* and ranged from 0.6 to $38.3 \mu\text{g g}^{-1}$.

Discussion

Origin and biochemical composition of sedimentary OM

The photosynthetically produced organic matter (i.e. CPE) in aquatic environments may represent the main food source for benthic communities (McIntyre et al., 1996). The chlorophyll *a* and CPE concentrations reported here were low compared to other enclosed basins or Mediterranean lagoons, indicating that this system, although extremely rich in organic detritus, receives low inputs of primary organic matter from micro-algae. In particular, chlorophyll *a* concentrations (annual average $3.1 \mu\text{g g}^{-1}$) were comparable to those reported in oligotrophic sites such as the Ligurian Sea and the Gulf of Fos (Plante et al., 1986; Fabiano et al. 1995). Moreover, the contribution of primary organic carbon to the sedimentary biopolymeric fraction of organic matter, calculated assuming a conversion factor of $40 \mu\text{gC } \mu\text{g CHLa}^{-1}$ (De Jonge, 1980), was 30 times lower than in the oligotrophic Ligurian Sea (Fabiano et al., 1995). The use of a C:CHLa ratio of 40 could introduce an error. Yet, even if the ratio should vary from about 10 to 100, the contribution of primary organic carbon to sedimentary biopolymeric fraction of organic matter would still remain low (0.6 and 5.6%, using 10 and 100 as conversion factors, respectively). Nevertheless, as turnover rates of living microphytobenthos and detritus might not be comparable, the contribution of microphytobenthos to sedimentary organic carbon could be higher than estimate. But the lack of a significant correlation between sediment organic matter composition and phytopigment content suggests that most sedimentary organic matter originated from sources other than micro-algae.

Microphytobenthos is a suitable food source for benthic deposit-feeders (Miller et al., 1996). However, the mere measurement of chlorophyll *a* does not quantify the fraction available to benthic consumers and does not discriminate between labile and refractory detritus. In this regard, the biochemical composition of sedimentary organic matter has recently been

used to gather information on the origin, quality and availability of deposited material (Danovaro et al., 1993; Fabiano et al., 1995; Danovaro, 1996).

In Marsala lagoon, the three main classes of organic compounds showed the highest concentrations ever reported in the literature (Table 2). The composition of the sedimentary organic detritus showed a dominance of carbohydrates (on average 51.2%) followed by proteins (39.0%) and lipids (9.8%). The dominance of carbohydrates over proteins is characteristic of highly oligotrophic or detritic (such as the deep-sea) environments (Danovaro et al., 1993). In these environments, indeed, the utilisation of labile compounds results in a highly refractory composition of sedimentary organic material. In the highly oligotrophic Cretan Sea (N-E Mediterranean), Tselepidis et al. (1996) reported that soluble carbohydrates (measured using the same procedure) represented less than 6% of total carbohydrate content. By contrast, coastal Antarctic sediments are dominated by soluble compounds that account for about 98% of total carbohydrate (Fabiano et al., in press). In our study soluble sedimentary carbohydrates accounted (on average) for 8.3% of total sedimentary carbohydrate, indicating the presence of refractory and structural carbohydrates.

Organic nitrogen (i.e. protein) is widely considered as the major limiting factor for deposit-feeders. Protein concentrations in sediments of Marsala lagoon were very high, even when compared with extremely productive areas such as the coastal Baltic Sea (Meyer-Reil, 1983). However, protein accounted for less than 40% of sedimentary biopolymeric carbon. Thus, although large amounts of detrital organic matter were present in Marsala lagoon, this detritus was of relatively low nutritional quality.

A low protein to carbohydrate ratio (PRT:CHO) suggests the presence of aged organic matter (Danovaro et al., 1993) and a role of proteins as a potentially limiting factor for benthic consumers (Fabiano et al., 1995). This ratio ranges from lower than 0.1 in oligotrophic deep-sea sediments (500–2400 m depth in the Eastern Mediterranean Sea, Danovaro et al., 1993) to higher than 10 in coastal antarctic sediments (Pusceddu, 1997). No significant seasonal or spatial changes were found in PRT:CHO ratio in our study area. For most of the study period, the ratio remained below 1.0, whereas it reached 6.9 in September 1993, corresponding with the highest primary organic matter concentration (in terms of CPE). This confirms that the sediments of the lagoon were characterised by a large amount of aged and/or non-living organic matter.



Role of macroalgal and vascular-plants detritus on the quality of sedimentary OM

Marsala lagoon is a typical semi-enclosed system characterised by an absence of chemical-physical gradients towards the open sea (Pusceddu et al., 1997a). It is characterised by a southward gradient of algal coverage, associated with decreasing resuspension and turbulent water. Previous studies (Pusceddu et al., 1997a, b; Sarà et al., 1995) demonstrated that wind forcing is the major factor controlling spatial distribution and composition of suspended particles. Owing to the depth profile of the basin, turbulent water is present in the northern area (dominance of resuspended particles), whilst sedimentation prevails at the *Posidonia oceanica* reef (southern area).

In the north (Station 1), highly turbulent water affects the possibility for algae to colonise the sediments. Only occasionally, low-density mats of the seagrass *Cymodocea nodosa* and of the algae *Caulerpa prolifera* appear. Accordingly, the lowest amounts of sediment organic matter (in terms of C-BPF), with co-dominance of proteins and carbohydrates, were found at Station 1. Approaching the central area (Station 2), *Cymodocea nodosa* becomes dominant, gradually substituted by a *Posidonia oceanica* reef towards Station 3. Here, suspended particulate matter decreases, owing to the presence of the reef mechanical barrier and increase in sinking velocity of particles (Pusceddu et al., 1997a). As a consequence, at Station 2 and 3, C-BPF concentrations in the sediments are 1.7 times those at Station 1. Moving from Station 1 to 2 and 3, the contribution of carbohydrates to C-BPF increases from 47% to about 52% while protein decreases from 45% to 37%. The carbohydrate content of the sediment at Stations 2 and 3 is composed of *Posidonia* fragments rich in structural carbohydrates (Danovaro, 1996). Since their gross composition is highly refractory (Lawrence et al., 1989), a large fraction of organic matter accumulated at the south of our study site may not be available for benthic consumers. Kenworthy & Thayer (1984) showed by *in situ* experiments that from 50 to 60% of organic carbon of seagrass leaves was lost within 170d. Thus, although *Posidonia* reefs provide much organic detritus to the sediments, only a small fraction (i.e. proteins, soluble carbohydrates and free amino acids; Pirc & Wollemweber, 1988) may be available to benthic consumers.

A confirmation of this pattern in availability of sediment organic matter to benthic consumers (sug-

gested by the increasing carbohydrate contribution to the C-BPF) comes from the isotopic composition of particulate organic carbon (Mazzola et al., submitted). POC isotopic composition increased from the north ($\delta^{13}\text{C} = -21\text{‰}$; phytoplankton origin, Fry, 1984) to the south ($\delta^{13}\text{C} = -13.7\text{‰}$, macroalgae and vascular plant origin, Mann, 1988). Such enrichment in $\delta^{13}\text{C}$ values has also been found in the study area (Sarà, *pers. com.*) varying from -17.5 to -15.0 and to -11.0‰ in open sea, in a tidal exposed site (north) and in a sheltered site (south), respectively. These results, combined with those by Pusceddu et al. (1997a), who found sedimentation to increase southwards, suggest the balance of wind-induced resuspension vs. seagrass-induced sedimentation as a major factor in accumulation/exportation of sediment organic matter.

Sarà et al. (1995), studying short-term changes in biochemical composition (i.e. proteins, carbohydrates and lipids) of particulate matter in Marsala lagoon, found particulate protein to prevail in the north and particulate carbohydrate in the south. This confirms that in the north, where sediments lack algal or vascular plant coverage, resuspended material is dominated by small protein-rich particles, probably linked to phytoplankton (Fabiano et al., 1994) or resuspended microphytobenthos (McIntyre et al., 1996; Pusceddu et al., 1997a). Moreover, according to Mayer et al. (1993), resuspension generally results in a high proportion of low-density protein-rich particles with nutritional value to suspension feeders (Muschenheim, 1987a, b). By contrast, in the south, characterised by *Posidonia oceanica* detritus, larger and, consequently highly refractory, particles dominate. Such conditions are mirrored by amounts of sedimentary detritus (in terms of C-BPF) and biochemical composition of sedimentary OM, which show the highest protein contribution to C-BPF in the north and the highest carbohydrate contribution in the south (Figure 6).

Conclusions

The low-definition temporal and spatial scales of sampling (2 km \times 12 months) did not allow identifying short-term variations in the processes that lead to changes in sedimentary carbon composition. However, the lack of significant seasonal changes in the biochemical variables investigated suggests that Marsala lagoon is a 'pulsing' environment in which no clear temporal primary production pattern can be identified. In 'true' Mediterranean lagoons (Alpine & Clo-

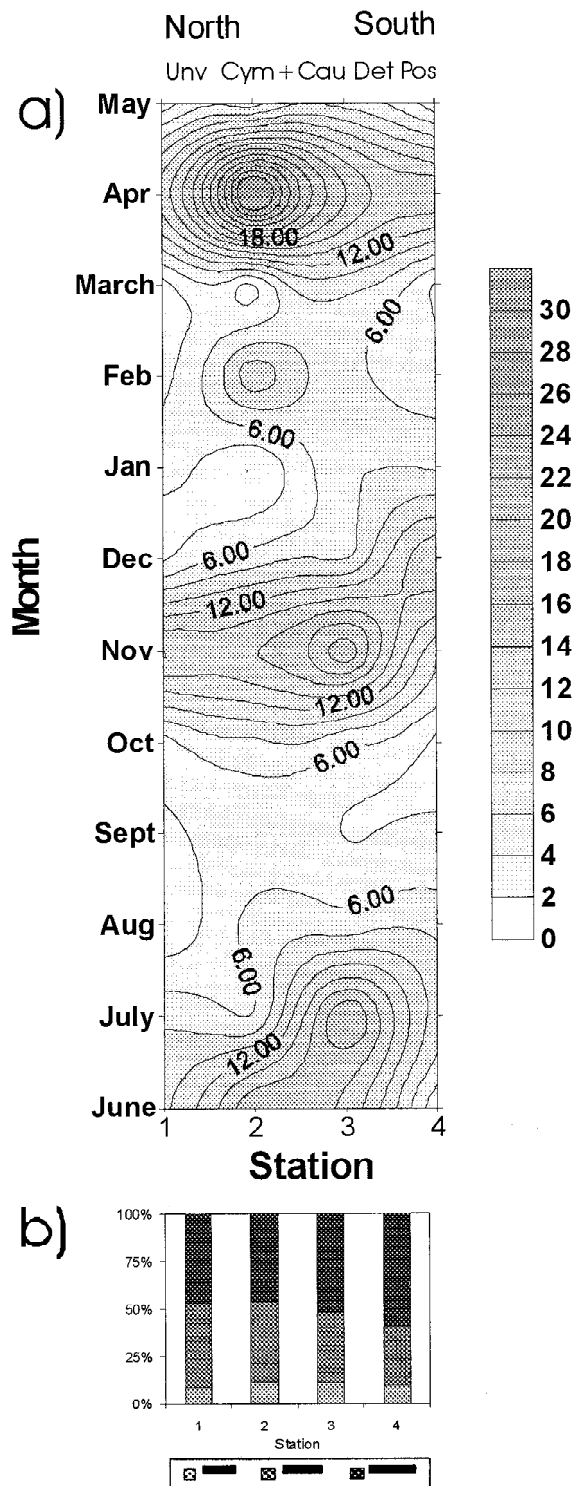


Figure 6. Seasonal and spatial changes of C-BPF concentrations (a, mg C g⁻¹) and biochemical composition of sedimentary organic matter (b, %) in the four sampled stations in relation to macroalgal and vascular plant coverage (Unv = unvegetated; Cym = *Cymodocea nodosa*; Cau = *Caulerpa prolifera*; Pos = *Posidonia oceanica*).

ern, 1991), several sources of 'environmental noise', like wind-induced sediment resuspension or rainfall drastically affect the seasonal pattern of phytoplankton standing stock (Millet & Cecchi, 1992). As an example Pusceddu et al. (1996), in a Sardinian coastal lagoon, demonstrated that the seasonal pattern of phytoplankton abundance was masked by episodic benthic diatom resuspension, induced by wind. In Marsala lagoon, only the biopolymeric fraction of sediment organic matter showed significant seasonal changes. Thus, we might infer that only sediment OM quantity behaves as an emerging property affected by seasonality. By contrast, sediment OM quality (i.e. availability) appears strictly connected to the degree of algal coverage as well as to episodic inputs of primary organic matter from phytoplankton and/or microphytobenthos.

As in other oligotrophic environments (in terms of phytopigment concentrations), we might expect a large fraction of autochthonous organic matter production to be rapidly canalised through the planktonic or microbial web. However, as indicated by the LOM:TOM ratio (LOM = labile organic matter, *sensu* Danovaro et al., 1993), most of the deposited OM is unaccounted for by labile organic compounds (Table 3). What is this other material is an open question. We can exclude that structural carbohydrates compose this fraction, as the Gerchacov & Hatcher protocol detects also chitin, cellulose and lignin. The difference between total organic matter and the sum of proteins, carbohydrates and lipids could be adsorbed to the mineral component of the sediment. It has been defined as COM (Complex Organic Matter, Fichez, 1991).

This uncoupling between the high amounts of sediment OM and its low nutritional value suggests that the environment behaves as a detrital 'trap' in which the gross primary production of macroalgae and seagrasses, not directly available to benthic consumers, tends to accumulate. Further studies (in progress) need to deal with the dynamics and secondary production of bacterial assemblages, to focus on the fate of the large detrital pool in the sediments.

Acknowledgements

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Table 3. Spatial changes in total organic matter (TOM) and labile organic compound concentrations in sediments of the Marsala lagoon. Reported are annual averages \pm SE. LOM (Labile Organic Matter) has been calculated as the sum of sedimentary lipids, proteins and carbohydrates (Danovaro et al., 1993)

Station	Lipids (mg g ⁻¹)	Proteins (mg g ⁻¹)	Carbohydrates (mg g ⁻¹)	LOM (mg g ⁻¹)	TOM (mg g ⁻¹)	LOM:TOM (%)
1	1.0 \pm 0.2	4.7 \pm 0.4	8.0 \pm 2.7	13.7 \pm 3.0	171.9 \pm 37.3	8.0
2	1.7 \pm 0.2	6.4 \pm 0.8	14.7 \pm 5.8	22.8 \pm 6.4	163.8 \pm 10.6	13.9
3	2.3 \pm 0.3	6.9 \pm 0.5	14.5 \pm 3.6	23.7 \pm 4.2	141.4 \pm 13.8	16.8
4	1.3 \pm 0.2	6.0 \pm 0.9	8.5 \pm 3.1	15.8 \pm 3.2	104.9 \pm 5.1	15.1

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