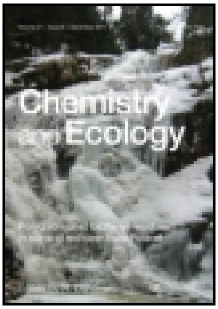

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PARTICULATE ORGANIC MATTER COMPOSITION IN A SEMI-ENCLOSED MARINE SYSTEM

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Spatial and temporal changes in the biochemical composition of particulate organic matter in a semi-enclosed marine system (Stagnone di Marsala, Mediterranean Sea) were studied, on a monthly basis, from January to December 1994, in order to assess nutritional value of suspended particles for benthic suspension feeders. According to previous findings, the study site displayed a strong oligotrophy. Chlorophyll-a accounted for a very low fraction of the total suspended matter pool (0.1%), whereas at least 75% of POC was of detrital/heterotrophic origin. POC:PON ratio values indicate that bacterioplankton biomass accounted for a significant fraction of the total POC pool, displaying values comparable to those of the phytoplankton biomass (phytoplankton to bacterial biomass ratio was about (1). Temporal and spatial changes in the biochemical composition of particulate organic matter were rather limited and related to its sources, the main of which is represented by detrital particles released by the *Posidonia oceanica* (L.) beds. The comparison between our results and those encountered in other coastal lagoons indicates that the low abundance of suspension-feeding organisms observed in the study area is related to the "quality depression" of particles due to the dilution of high quality compounds (*i.e.*, biopolymeric carbon) in a largely inorganic matrix. This result leads us to conclude that, to reach the same amount of high quality particulate food, a suspension feeder mollusc in the Marsala lagoon would need to filter a sea water volume around 3 times higher than in other Mediterranean coastal lagoons.

Keywords: POM; Carbohydrates; Proteins; Lipids; Mediterranean Sea; Lagoons

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INTRODUCTION

Particulate organic matter (POM) plays a crucial role in the biogeochemical cycling of carbon in marine ecosystems and represents an important food source for both planktonic and benthic organisms. POM is composed of non-living (detrital) organic material and living organisms, with a relative importance changes in relation with seasonal productivity patterns and environmental constraints and, finally, determine changes in the food availability of particles for consumers (Danovaro *et al.*, 2000).

In recent years, studies on the biochemical composition of particulate organic matter (POM) have been conducted in different marine systems, with the aim of assessing spatial and temporal changes in particle's nutritional value for suspension feeders. On this topic, some papers have been with POM elemental composition in terms of particulate organic carbon and nitrogen (Berg and Newell, 1986; Smaal and Haas, 1997). Other papers have assessed the protein, carbohydrate and lipid content of suspended particles and assumed their sum as the readily bioavailable fraction of particulate organic carbon (Navarro *et al.*, 1993; Navarro and Thompson, 1995; Danovaro and Fabiano, 1997; Grémare *et al.*, 1997; Sarà *et al.*, 1998). Studies on POM quantity and biochemical composition (in terms of proteins, carbohydrates and lipids) have been mostly conducted in the open sea and little information is actually available for Mediterranean coastal lagoons (Pusceddu, 1999).

Large phytoplankton, macrophytes and salt-marsh plant biomass, which production largely exceeds the heterotrophic consumption, characterise Mediterranean coastal lagoons (Newell, 1982). Nonetheless, only a minor fraction of this primary organic matter becomes directly available to consumers due to its refractory composition and, in most cases, it needs to be fragmented and processed by decomposers to become available for higher trophic levels (Hansen *et al.*, 1992).

In the present work, we illustrate spatial and seasonal changes in quantity and biochemical composition of suspended organic matter in the Stagnone di Marsala lagoon, a semi-enclosed marine system (SW Mediterranean Sea) characterised by strong hydrodynamic gradients. Our main aim was to investigate the possible role of some environmental constraints on the nutritional value of seston for benthic suspension feeders.

MATERIAL AND METHODS

Study Site

This study was carried out in the Stagnone di Marsala (hereafter Marsala lagoon) a semi-enclosed marine system characterised by two main communication channels with the open sea. A platform separates the rest of the basin from the open sea (Fig. 1). The basin is very shallow, with a depth ranging from 2 m along the eastern shore of the platform to 0.5 m in the western area. Depth increases to approximately 2.5 m in the southernmost area, close to the open sea. The northern channel is 450 m wide and characterised by occasional turbulent inputs of sea water. Sediments in the northern area display scant (low frequency) algal coverage (Calvo *et al.*, 1996). The hydrography of the central area is influenced by two little islands, which act as mechanical obstacles to the internal circulation of water and generate turbulent currents. Southernmost to this area a luxuriant *Posidonia oceanica* bed is present and influences water circulation and silting. The southern mouth (ca. 1450 m wide) is open to continuous sea water inflow and is characterised by internal tides. Water exchanges with the open sea are ensured by currents with mean speed of that in the southern mouth (on annual average $4.92 \pm 1.54\,\mathrm{cm\,s^{-1}}$) and are about two-fold higher than in the northern area ($2.34 \pm 0.87\,\mathrm{cm\,s^{-1}}$) (Mazzola and Sarà, 1995). Although the Marsala lagoon does not receive a supply of consistent continental input or significant tidal excursion, it exhibits typical ecological features of other Mediterranean coastal lagoons such as a benthic population "confinement" (*sensu* Guelorget and Perthuisot, 1983).

Sampling and Chemical Analyses

Samples of superficial water (0.5 m) were collected monthly from January to December 1994, using 10 l Niskin bottles, at 10 stations located along a north-south transect (Fig. 1). For analyses of total

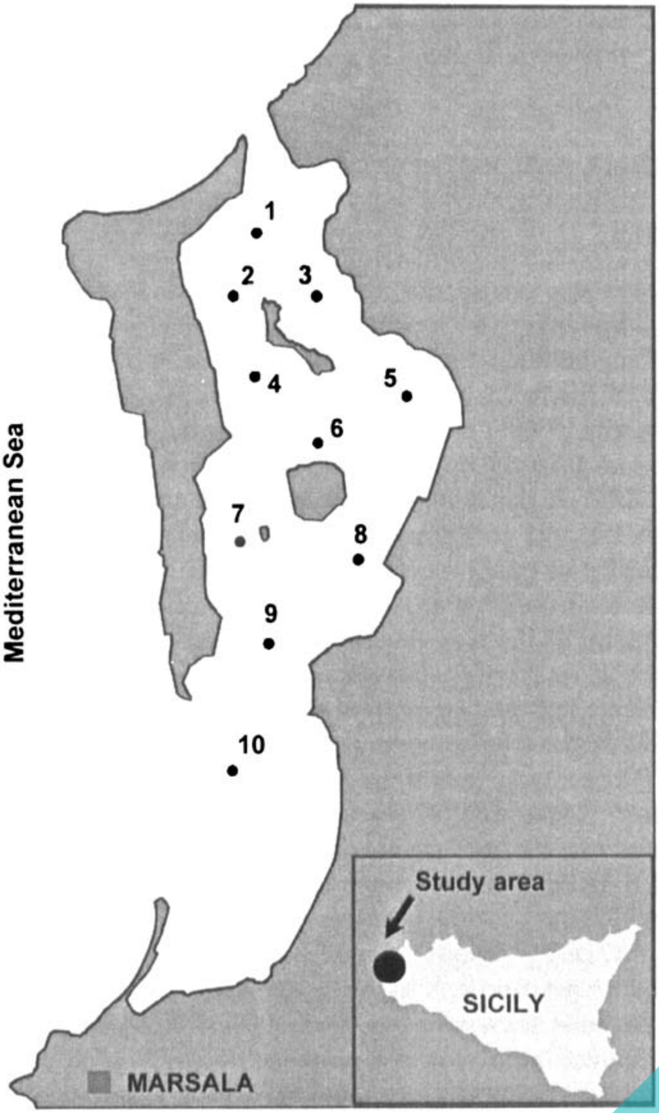


FIGURE 1 The study area and sampling station location.

suspended matter (TSM), phytopigments (chlorophyll-a and phaeopigments), carbohydrate, protein and lipid concentrations, aliquots (0.1 – 1.0 l) of water samples were filtered under gentle vacuum to

Whatman GF/F glass-fibre filters (0.8 μm nominal pore size). Water temperature and salinity were measured at each station using an automatic probe.

To determine total suspended matter concentrations, filters were weighed after desiccation (60°C, 24 h) using a Mettler M3 balance (accuracy ± 1 μg). The inorganic fraction (ISM) of total suspended matter was calculated as the weight of the material remaining after combustion at 500°C for 4 hours and reported as $mg\,l^{-1}$.

Phytopigments were extracted with 90% acetone and chlorophyll-a (Chl-a) analysis was carried out according to Lorenzen and Jeffrey (1980). Phaeopigments (Phaeo) were determined after acidification with 0.1N hydrochloric acid.

Particulate organic carbon (POC) and nitrogen (PON) were determined with a Perkin-Elmer CHN Elemental Analyser (Model 2400), after removal of carbonates under hydrochloric acid vapour (Hickel, 1984; Iseki *et al.*, 1987). Acetanilide was used as standard.

Particulate carbohydrates (CHO) were determined according to Dubois *et al.* (1956). D (+) glucose was used as the standard. Particulate proteins (PRT) were determined according to Hartree (1972), using bovine serum albumin as the standard. Particulate lipids (LIP) were extracted according to Bligh and Dyer (1959) and analysis was performed by carbonisation according to Marsh and Weinstein (1966). Tripalmitine was used as the standard.

Carbon equivalents of particulate lipids, carbohydrates and proteins were calculated using 0.75, 0.40 and 0.49 $\mu gC\,\mu g^{-1}$ as conversion factors, respectively and the biopolymeric fraction of particulate organic carbon (BPC) was defined as the sum of carbohydrate, protein and lipid carbon (Fabiano and Pusceddu, 1998).

Statistical Analyses

Temporal and spatial changes were investigated by means of analysis of variance (ANOVA; Underwood, 1997) with time (month) and space (station) as sources of variation. When a significant difference ($p < 0.05$) for the main effect was observed, means were analysed by a Tukey's multiple comparison test to determine the differences between sampling stations and months. Data were transformed, only when necessary, to meet the assumptions of the parametric statistics.

RESULTS

Physical Measurements and Total Suspended Matter

Temperature and salinity showed a clear seasonal trend (Fig. 2a). The minimum temperature was observed in December ($12.4 \pm 0.2°C$), while the maximum was measured in August ($27.6 \pm 0.5°C$). The minimum value of salinity was recorded in February (35.5 ± 1.35), while the maximum was measured in September (42.50 ± 1.66). The seasonal pattern of wind velocity (Fig. 2b) was characterised by two main peaks in April and December. Prevailing winds came from the north-western sector.

Total suspended matter (TSM) concentrations were fairly high (ranging from 1.6 to $49.0\, mg\, l^{-1}$) and did not display clear temporal changes. By contrast, TSM concentrations decreased significantly

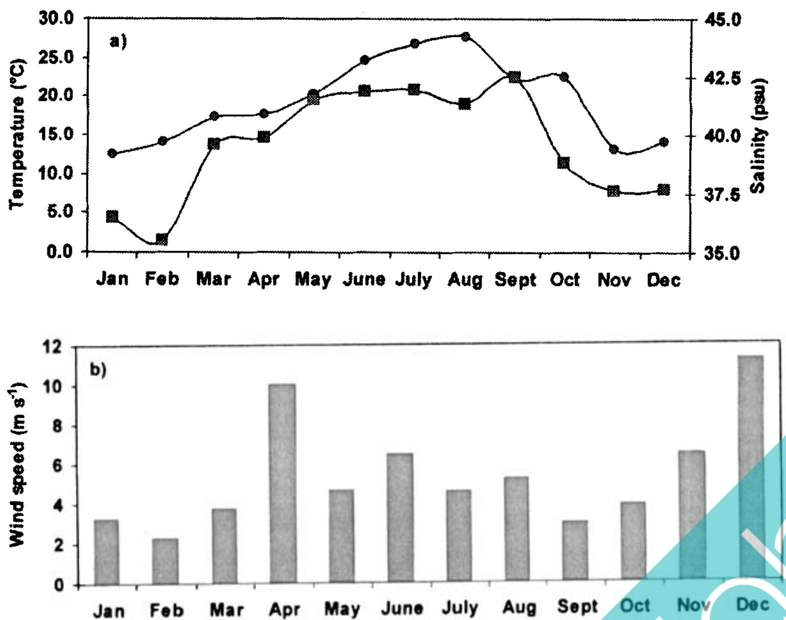


FIGURE 2 (a) Temperature (filled circles) and salinity (filled squares) seasonal patterns in the Marsala lagoon during 1994. Reported are values averaged between the 10 stations. (b) Seasonal pattern of wind speed in the Marsala lagoon during 1994. Data have been kindly provided by ITAV (Airport of Birgi).

from the northern to the southern stations (Fig. 3). TSM was dominated by its inorganic fraction (annual average 2.9 mg l^{-1}) that accounted for approximately 60% of TSM.

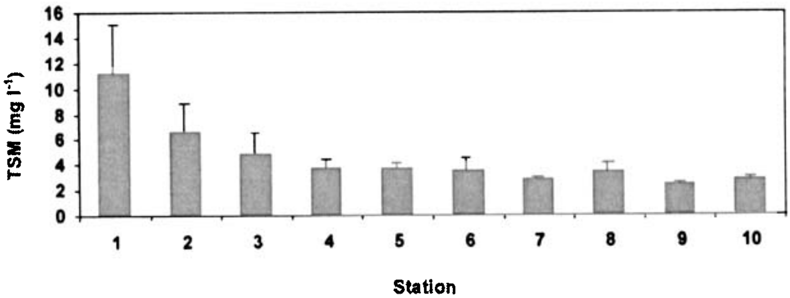


FIGURE 3 Spatial distribution of total suspended matter concentrations. Reported are annual averaged values. Bars indicate standard error.

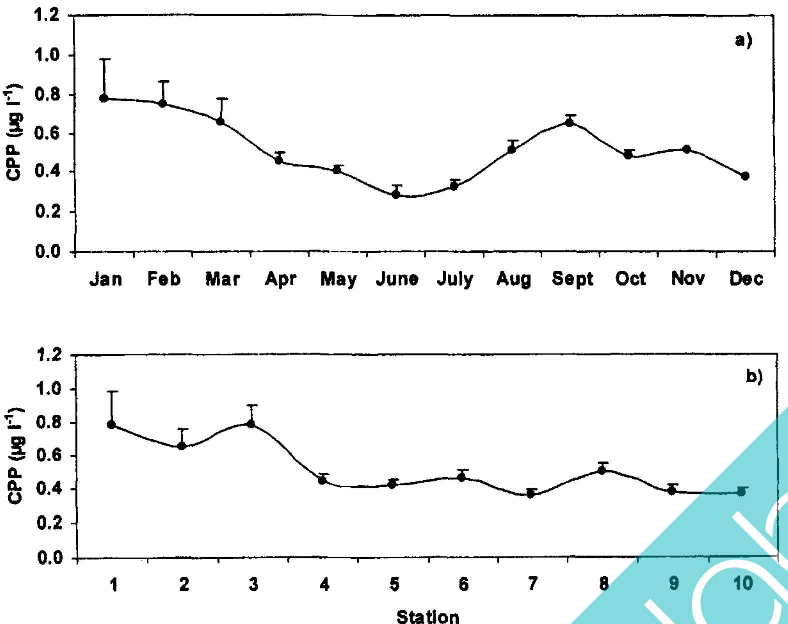
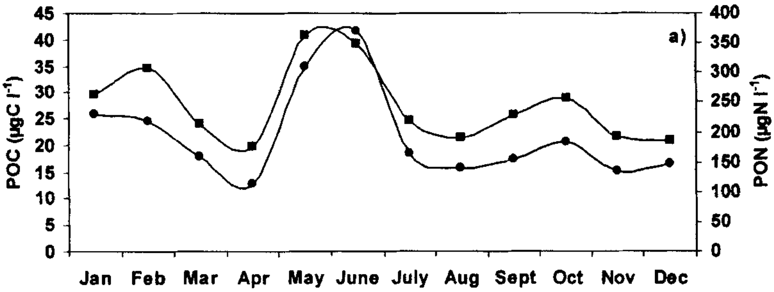


FIGURE 4 Seasonal (a) and spatial (b) changes in suspended chlorophaeopigments (CPP, as sum of chlorophyll-a and phaeopigments) in the Marsala lagoon during 1994. Bars indicate standard error.



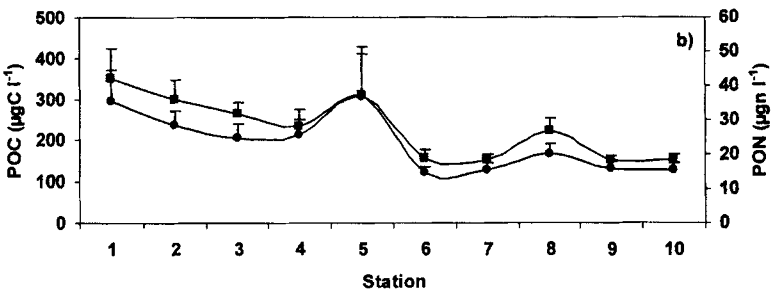


FIGURE 5 Seasonal (a) and spatial (b) changes in particulate organic carbon (POC, filled circles) and nitrogen (PON, filled squares) in the Marsala lagoon during 1994. Bars indicate standard error.

Chloroplastic Pigments

Chlorophyll-a (Chl-a) concentrations (annual average 0.4 µg l^{-1}) ranged from 0.02 to 2.0 µg l^{-1}. Phaeopigment (Phaeo) concentrations (annual average 0.1 µg l^{-1}) ranged from 0.01 to 0.7 µg l^{-1} and represented, on an annual average basis, 25% of the total pigment concentration. Chlorophyll-a and phaeopigments were significantly correlated ($r_s = 0.98$, $P = 0.00$, $n = 120$). The concentration of chloro-phaeopigments (CPP, as sum of Chl-a and Phaeo) displayed significant ($P < 0.05$) temporal and spatial changes (Figs. 4a – b). Significant peaks occurred in January (on average 0.8 µg l^{-1}) and resulted in an accumulation during the first three months of the year. Values decreased until June and then increased in September (average 0.6 µg l^{-1}). CPP concentrations showed their highest values at stations 1 and 3 (average 0.8 µg l^{-1}) and their lowest values in the southern basin (minimum at stations 7 and 10, average 0.4 µg l^{-1}).

Particulate Organic Carbon and Nitrogen

Particulate organic carbon and nitrogen concentrations ranged from 33 to 1288 $\mu g\,C\,l^{-1}$ and 5.3 $\mu g\,N\,l^{-1}$ to 131 $\mu g\,N\,l^{-1}$ respectively. POC and PON concentrations were significantly correlated ($r_s = 0.92$; $p < 0.05$) and showed a decreasing pattern from the northern to the southern stations (Fig. 5a), with the exception of station 5, where concentrations reached an annual average of 307 $\mu g\,C\,l^{-1}$ and 37 $\mu g\,N\,l^{-1}$. POC and PON concentrations (Fig. 5b) showed three main accumulation periods in January–February, May–June and September–October.

Biochemical Composition of POM

Particulate protein concentrations (annual average 191 $\mu g\,C\,l^{-1}$) showed significant spatial and temporal changes ($P < 0.05$) (Figs. 6a–b). Peaks appeared in January–February (average 283 $\mu g\,C\,l^{-1}$)

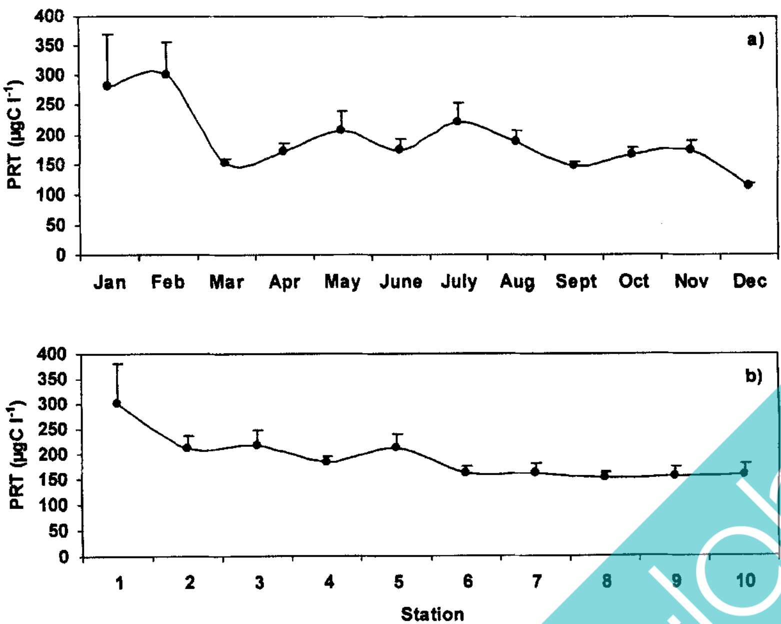


FIGURE 6 Seasonal (a) and spatial (b) changes in particulate protein concentrations in the Marsala lagoon during 1994. Bars indicate standard error.

and in July (221 μg C l^{-1}). The highest concentrations were observed in the northern area (maximum 299 μg C l^{-1} at station 1), with concentrations decreasing continuously from the northern to the southern area (mean value between stations 6 and 11, 161 μg C l^{-1}). Particulate carbohydrate concentrations (on annual average 27.1 μg C l^{-1}) did not display significant spatial changes (Fig. 7a), although concentrations decreased from station 1 to station 4 (from 42 to 16 μg C l^{-1}, respectively), increasing once again until station 10 (37 μg C l^{-1}). Carbohydrate concentrations fluctuated widely and displayed significant seasonal changes (Fig. 7b). Particulate lipid concentrations (annual average 138 μg C l^{-1}) did not display significant spatial changes (Fig. 8a), whereas significant seasonal changes were observed (Fig. 8b) and a significant peak occurred in July (274 μg C l^{-1}).

Biopolymeric carbon concentrations (BPC, annual average 355 μg C l^{-1}) did not show significant spatial changes (Fig. 9a), while significant seasonal changes were observed (Fig. 9b), with maximum values in February, July and November (average 446 μg C l^{-1}, 535 μg C l^{-1} and 339 μg C l^{-1} respectively).

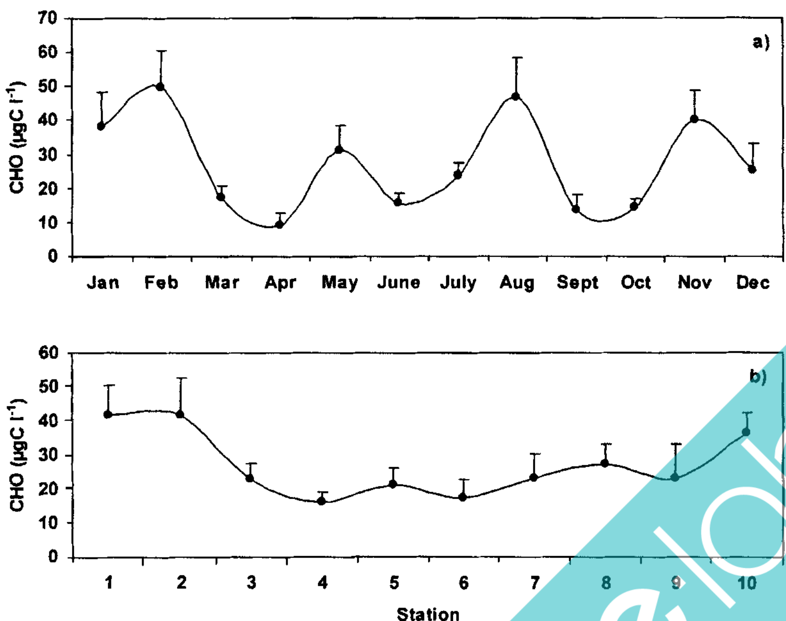


FIGURE 7 Seasonal (a) and spatial (b) changes in particulate carbohydrate concentrations in the Marsala lagoon during 1994. Bars indicate standard error.

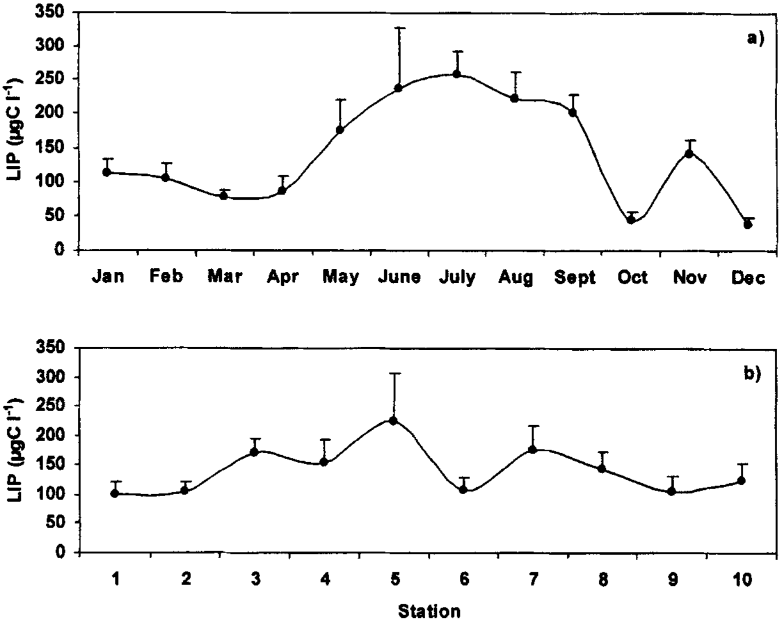


FIGURE 8 Seasonal (a) and spatial (b) changes in particulate lipid concentrations in the Marsala lagoon during 1994. Bars indicate standard error.

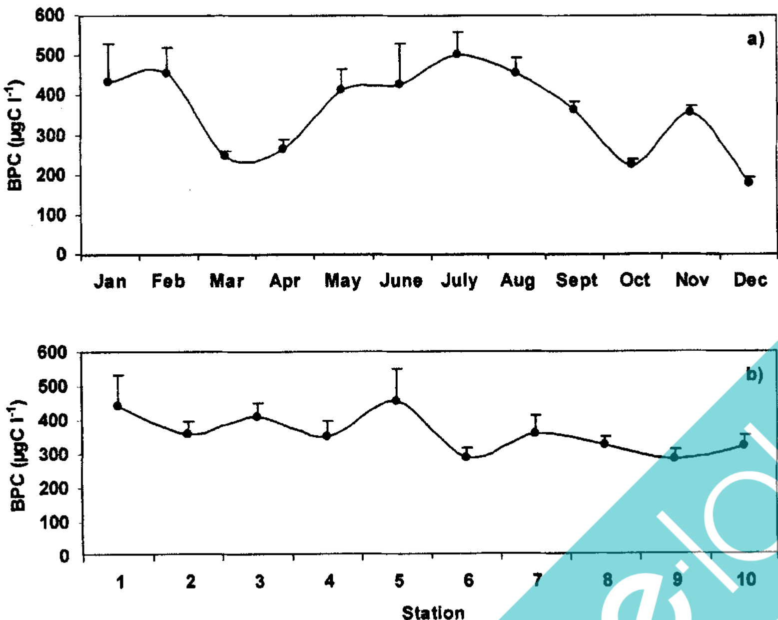


FIGURE 9 Seasonal (a) and spatial (b) changes in biopolymeric carbon concentrations in the Marsala lagoon during 1994. Bars indicate standard error.

DISCUSSION

Environmental Constraints on Spatial Distribution of POM

Although no continental inputs or significant tidal excursion are present, the study site exhibits features typical of other Mediterranean coastal lagoons, with wind-induced water dynamics as the major forcing factor (Pusceddu, 1999; Sarà *et al.*, 1999; Fabiano *et al.*, 1998). Previous studies have shown that in the study area, a southward decreasing pattern of hydrodynamic conditions is concurrent with the increase in water depth (Pusceddu *et al.*, 1997). The northern area, continuously exposed to wind stress, was characterised by very large amounts of total suspended matter. Carper and Bachman (1984) have calculated the theoretical critical wind speed required for inducing particle resuspension and established a threshold value of $4\,m\,s^{-1}$ above which significant resuspension effects may occur. In the entire study area, wind speed often exceeded $5\,m\,s^{-1}$ throughout the year (see Fig. 2b). This, together with the very shallow depth (0.5 m), suggests that, in the northern area of the Marsala lagoon, wind-induced sediment resuspension may be invoked as a principal factor influencing the quantity of suspended matter. We observed a strong dominance of the inorganic fraction as seston (accounting for 60% of TSM). Such results stress the possible role of frequent wind-induced sediment resuspension and possibly of lateral advection in controlling the actual amount of suspended particles (Arfi and Bouvy, 1995; Arfi *et al.*, 1993). Moving southward, TSM concentrations decreased approximately two-fold and were mirrored by POC concentrations, which decreased approximately about 3 times moving from station 1 and approaching station 7, where a large meadow of the marine phanerogame *Posidonia oceanica* (L.) was present. Such spatial pattern is in good agreement with previous studies indicating that seagrass meadows can act as mechanical barriers to seston lateral drifting, also enhancing particles sink (Ward *et al.*, 1984; Pirc and Wollemweber, 1988). Accordingly, in a previous study, Pusceddu *et al.* (1999) found, in the northern area of the Marsala lagoon, total organic matter content in the sediments gradually increasing towards the *P. oceanica* meadow.

Origin and Composition of Particulate Organic Matter

Little difference in phytoplankton biomass (in terms of chlorophyll-a concentrations) is observed when our results are compared with those previously reported for the same area (Magazzù, 1982; Giani *et al.*, 1995) or with those encountered in the adjacent open sea (Carrada *et al.*, 1996). The study area can be defined oligotrophic as Chl-a concentrations were on annual average $< 1.0\,\mu g\,l^{-1}$. Throughout the study period, Chl-a represented almost consistently the largest fraction of chlorophaeopigments (on average 75%), indicating the constant presence of photosynthetically active phytoplankton. Nevertheless, phytoplankton biomass accounted for a very low fraction of the total suspended matter pool (on annual average about 0.1%). Assuming an average Chl-a carbon content of $54\,\mu g\,C\,l^{-1}$ (Nival *et al.*, 1972), chloroplastic pigments accounted for an annual average of approximately 13% of POC. The use of a C:Chl-a ratio of 54 could certainly introduce an error and, moreover, since respective turnover rates of living phytoplankton and detritus might not be comparable, the contribution of phytoplankton to POC could be higher than the estimate. But, even if the C:Chl-a ratio should vary from about 10 to more than 100, the contribution of primary organic carbon (as Chl-a) to POC would remain below the threshold of 25%. Therefore, our results indicate that at least 75% of POC in the study site was unaccounted for by primary organic matter (even with the inclusion of degraded pigments) and was, thus, assumed to be of detrital (non-living) and/or of heterotrophic origin. This result is consistent with literature data reporting the dominance of bacterioplankton in oligotrophic systems, where bacterial biomass can represent up to 70% of the entire POC pool (Danovaro *et al.*, 2000).

In natural aquatic environments characterised by the dominance of phytoplanktonic biomass, POC:PON ratio values ranges generally from about 4 to 11 (Valiela, 1984). As we found POC:PON ratios ranging from 4.9 to 10.9 (annual average 6.9) a contribution of primary organic matter to POC higher than that observed should be expected in the present study and/or other sources of organic nitrogen could be responsible for the relatively low POC:PON ratio values. As the C:N ratio for bacteria ranges from 3.5 to 5.0 (Lee and Fuhrman, 1983), a possible explanation for this discrepancy could be found in the large bacterioplankton biomass reported for the study area (Genovese, 1969). Additional data (Manini E., pers. comm.) indicate that in the Marsala lagoon bacterial biomass (on average $50\,\mu g\,C\,l^{-1}$) can be of the same magnitude as phytoplankton biomass. The POC:PON ratio values were lowest in the northern area (stations 1–3, on annual average 6.5), where the maximum concentrations of Chl-a were also observed. Moving southward, the ratio increased to about 7.3 (stations 4, 5 and 7) increasing to 8.1 at station 10. From such a spatial pattern we can infer that the low POC:PON ratio values in the northern area, characterised by strong and persistent wind-induced sediment resuspension (as also indicated by the dominance of tycoplanktonic cells and harpacticoid copepods (Campolmi *et al.*, 1997), were probably related to the presence of living phytoplankton or re-suspended microphytobenthos cells (Mazzola *et al.*, 1998). In this regard, Demers *et al.* (1987) in a shallow estuarine environment observed a large increase in chlorophyll-a, phaeopigment and POC concentrations each time the wind reached a velocity of $4\,m\,s^{-1}$, which is consistent with the present study.

Temporal changes in the biochemical composition of particulate organic matter in the Marsala lagoon were rather limited (Fig. 10a). The POM biochemical composition in the Marsala lagoon did not display clear spatial patterns (Fig. 10b), with the exception of an increasing contribution of carbohydrates and lipids whilst approaching the central and southern regions of the study area (stations 3–8). These areas are characterised by large meadows of *Posidonia oceanica*, displaying standing crop values close to the highest ever reported for the entire Mediterranean (Buia *et al.*, 1992; Mazzella *et al.*, 1995). Such areas were indeed characterised by particulate lipid concentrations that, accounting for 26% of POM, were up to twice higher than in the northern area. An increasing contribution of lipids in particulate organic matter deriving from *P. oceanica* beds has been reported also by Danovaro *et al.* (1998) in the Ligurian Sea, who concluded that high concentrations of particulate lipids are typical of the sediment-water interface of such systems (Danovaro and Fabiano, 1997). Our results together with data reported in previous studies (Mazzola *et al.*, 1999) indicate that the composition of particulate organic matter in the study area is deeply related with its sources, the main of which is

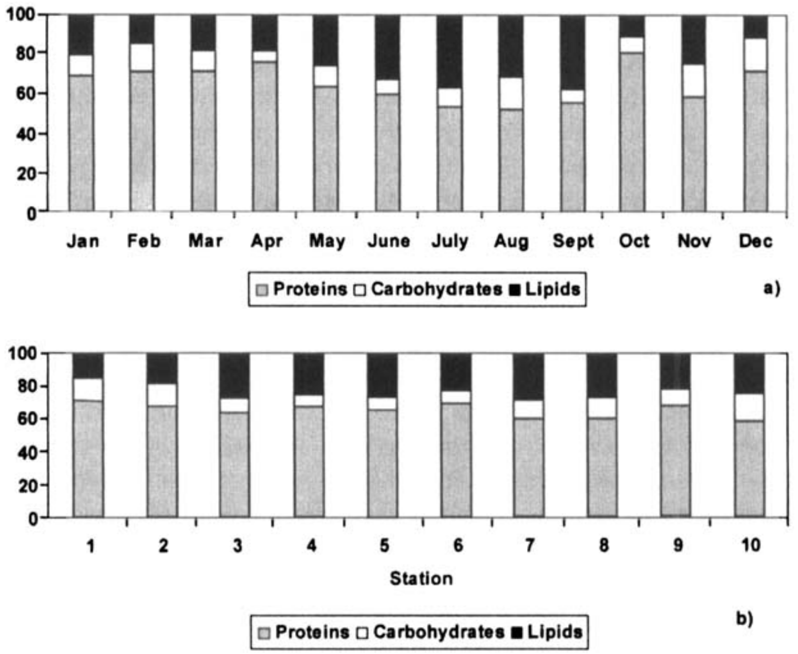


FIGURE 10 Seasonal (a) and spatial (b) changes in the biochemical composition of particulate organic matter in the Marsala lagoon during 1994.

represented by detrital particles released by the *Posidonia oceanica* (L.) beds.

Nutritional Value of Particulate Organic Matter

Analysis of both quality and quantity of POM revealed that the study area is controlled/affected by a wide and complex array of variables. The amount of particulate primary organic matter was rather low when compared to other coastal areas (Pusceddu, 1999). However, the biochemical composition of POM revealed the dominance of large amounts of readily available compounds (*i.e.*, proteins). Proteins, indeed, were almost constantly the dominant biochemical compound, accounting for about 66% of POM, followed by lipids (23%) and carbohydrates (11%). This was evident also from the protein to carbohydrate ratio values that, on average, were > 10. The dominance of particulate proteins over carbohydrates is a typical feature of highly productive areas and, indeed, proteins have been reported to dominate in coastal lagoons (Pusceddu *et al.*, 1996), estuarine systems (Navarro *et al.*, 1993; Sorokin *et al.*, 1996) and river impacted areas (Fabiano and Danovaro, 1994). Since high values of the protein to carbohydrate ratio indicate non-limiting conditions for the growth of benthic filter feeders (Danovaro and Fabiano, 1997), we could infer that particulate organic matter in the study area was characterised by a relatively high food quality. This hypothesis is in agreement with studies carried out in other Mediterranean lagoons. For instance, Pusceddu *et al.* (1996) reported that in the S. Gilla lagoon (Sardinia, Mediterranean Sea), high quality particles (*i.e.*, protein enriched) sustain very large populations of natural and cultured molluscs (such as *Tapes decussatus* and *Mytilus galloprovincialis*) and sedentary polychaetes (*Phicopomatus enigmaticus*). By contrast, in the Marsala lagoon the abundance and biomass of benthic suspension feeding molluscs is very limited (Chemello, R., pers. comm.). Such discrepancy could be due to three main factors: (1) the lower quantity of POM available in the Marsala lagoon when compared with other coastal lagoons; (2) the reduced primary (freshly generated) organic matter input to consumers; (3) the persistence of relatively huge amounts of refractory material.

In the Marsala lagoon, the contribution of phytoplankton to the bulk of particulate organic carbon was low (about 13%) as in other coastal lagoons, suggesting that other factors could be responsible for the almost complete absence of benthic filter feeding molluscs. The ratio of particulate organic matter (POM, as the sum of proteins, carbohydrates and lipids) to the total suspended matter (TSM) has been widely utilised as an indicator of the fraction of seston readily available for benthic suspension feeders (Navarro *et al.*, 1993; Danovaro and Fabiano, 1997). Our data indicate that in the Marsala lagoon this ratio (on annual average 19%) was up to 5 folds lower than in other coastal lagoons (average 50%; range 30–100%) where large populations of filter feeders are encountered (Pusceddu *et al.*, 1996; Navarro *et al.*, 1993). From this comparison we may conclude that, to obtain the same amount of high quality particulate food, a suspension feeder in the Marsala lagoon would need to filter a sea water volume about 3–5 times higher than in other coastal lagoons.

The low abundance of suspension-feeding organisms observed in the study area leads us to hypothesise that the nutritional advantage for these organisms, (*i.e.*, large amounts of readily available organic matter), is "depressed" by the dilution of labile organic particles in a largely inorganic matrix. A similar "quality depression" effect has been reported also in an open-sea area, in which POM nutritional value is constantly constrained by an "inorganic dilution effect" due to sediment resuspension events, which makes particulate food "available with difficulty" for suspension feeders (Sarà *et al.*, 1998).

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