Pergamon

Continental Shelf Research, Vol. 15, No. 11/12, pp. 1453–1469, 1995

0278-4343/95 $9.50 + 0.00

0278-4343(94)00088-3

A three-year time series of elemental and biochemical composition of organic matter in subtidal sandy sediments of the Ligurian Sea (northwestern Mediterranean)

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(*Received* 13 *August* 1993; *in revised form* 18 *July* 1994; *accepted* 14 *September* 1994)

Abstract—Variations in organic matter composition and microphytobenthic biomass were examined in the surface sandy sediments at a water depth of 10 m in the Gulf of Marconi (NW Mediterranean Sea) over a three year period. Seasonal changes in elemental (organic C and total N) and biochemical (lipids, proteins, carbohydrates) composition of sediment organic matter as well as Chl *a* were assessed in order to provide information about the origin and fate of sedimentary organic matter, the contribution of microphytobenthic biomass, seasonal and interannual variations of food quantity and quality, and factors related to food availability. Data obtained in this three-year study revealed that organic matter determined with a muffle furnace is clearly an overestimate of the organic content of the sediment and is thus of little significance for benthic ecologists studying community dynamics in relation to food availability. Labile organic matter, utilized to estimate the food potentially available for benthic consumers, accounted for only a small percentage (on average less than 10%) of total organic C. The highest labile fraction was observed in spring, whereas minima were recorded in winter. Analysis of elemental and biochemical composition of organic matter showed an inverse relationship between amount of organic matter and its potential availability to consumers; small quantities of high-quality organic matter were replaced by large quantities of refractory material. The labile portion was mostly microphytobenthic (65% of the labile carbon). Protein:carbohydrate ratios were low and confirmed the role of proteins as a potentially limiting factor for consumers. Significant differences in nutritional quality of the sediment organic matter were observed from year to year, changes due to the increase in specific labile compound content.

INTRODUCTION

Quality and quantity of organic matter in surface sediments have been considered of primary importance in determining the amounts of material potentially available to consumer organisms, thus affecting community structure and benthic metabolism (Buchanan and Longbottom, 1970; Graf *et al.*, 1983; Grant and Hargrave, 1987; Thompson and Nichols, 1988; Graf, 1989). However, in recent years the nutritional importance of sediment organic matter, considered as potential food for sediment-ingesting organisms, has become controversial. Indeed, the gross measure of total organic matter content in sediments tells very little about its availability to consumers (Calow, 1975; Hanson, 1980; Newell and Field, 1983; Bianchi and Levinton, 1984). Food

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availability is related to the biochemical composition of the organic matter which, in turn, depends upon its origin (Tenore and Hanson, 1980).

Organic matter in the marine environment is composed of labile and refractory compounds. Simple sugars, fatty acids and proteins that are rapidly mineralized have been used to assess the labile portion of organic matter (Daumas *et al.*, 1983; Fichez, 1991a; Danovaro *et al.*, 1993). Conversely, the refractory matter, which consists of substances like humic and fulvic acids and complex carbohydrates, is characterized by lower degradation rates (Handa *et al.*, 1972; Robinson *et al.*, 1982; Sargent *et al.*, 1983; Wilson *et al.*, 1986; Buscail *et al.*, 1990; Biddanda and Riemann, 1991).

Although no clear universally accepted definition of methodology exists to assess the labile fraction in organic matter, specific labile compounds have been used to estimate the nutritional value of the sediment (Buchanan and Longbottom, 1970) and to discriminate between readily biodegradable compounds and those which are non-biodegradable (Liu, 1976). George (1964) tried to estimate the fraction of organic matter available to the polychaete *Cirriformia tentaculata* by treating sediment organic matter with enzymes such as lipases, proteinases and glucosidases. The sum of carbohydrate, protein and lipid carbon obtained from this treatment was referred to as the biopolymeric fraction (BPF, *sensu* Fichez, 1991b). The BPF was used to estimate the potential fraction readily available for sediment-ingesting organisms.

However, of all the studies which analyse the total organic carbon content in marine sediments as a measure of food available to consumers (e.g. Chester *et al.*, 1983; Romankevich, 1984; Kelly and Nixon, 1984; Basford and Eleftheriou, 1988; Ishikawa, 1989; Weston, 1990), few have documented the biochemical composition of organic matter in sediments (Johnson, 1977; Meyer-Reil, 1983; Graf and Meyer-Reil, 1985; Khripounoff *et al.*, 1985; Fabiano and Danovaro, 1994). Moreover, very little is known about seasonal variations in the specific biochemical composition of sediment organic matter (Ansell *et al.*, 1972; Sargent *et al.*, 1983), and studies longer than one year are practically nil (Mayer and Rice, 1992).

Microphytobenthos is a substantial food source for benthic invertebrates, which range from protozoans to meio- and macrofauna (Montagna *et al.*, 1983; Plante-Cuny, 1984; Bianchi and Levinton, 1984; Plante-Cuny *et al.*, 1986). Therefore, it is important to know the photosynthetic pigment concentration (measured as Chl *a*) to assess the amount of food available to higher trophic levels and its potential contribution to the bulk of organic carbon.

In this paper, the elemental and biochemical composition of sediment organic matter and the related role of microalgae have been examined during a three-year period in a subtidal sandy station to provide new insight on: (1) quantitative information on the amount of labile organic compounds used as a measure of food potentially available to benthic consumers; (2) the origin and fate of labile compounds and the contribution of microphytobenthic biomass; and (3) seasonal and interannual variations of food quality and factors related to food availability.

MATERIALS AND METHODS

Study site

The study area is located at 10 m depth in the Gulf of Marconi, Ligurian Sea (northwestern Mediterranean Sea, Fig. 1). This area has been investigated intensively

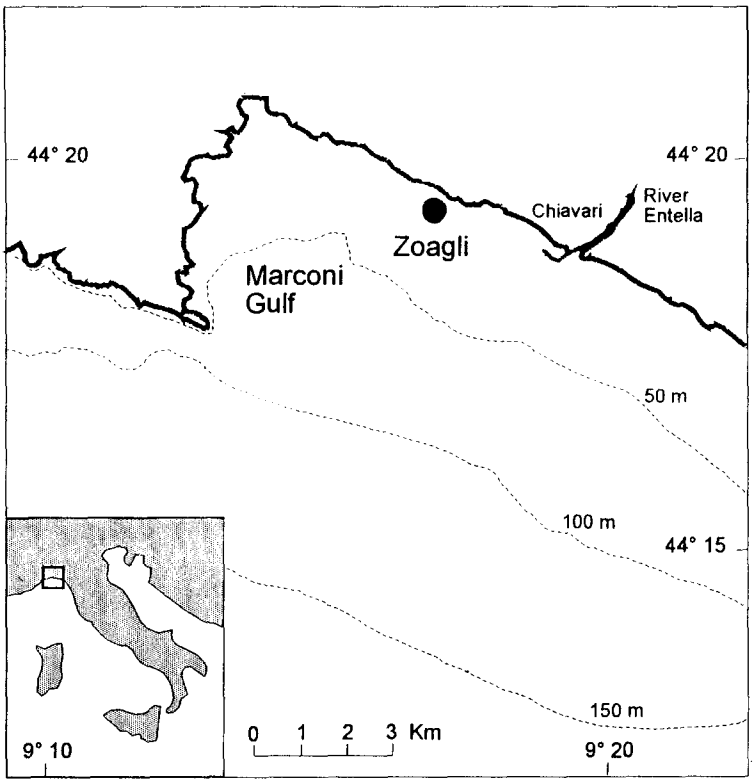

Fig. 1. The sampling station in the Gulf of Marconi, Ligurian Sea (northwestern Mediterranean Sea).

over the past 10 years. Seasonal cycles of phytoplankton dynamics, production and benthic–pelagic coupling have previously been described (Cattaneo and Fabiano, 1982; Fabiano, 1984; Albertelli and Fabiano, 1990; Bavestrello *et al.*, 1991). The macrofauna was dominated by suspension-feeders, among which the bivalve *Spisula subtruncata* (Da Costa) was particularly abundant in spring, while deposit-feeding polychaetes were dominant in autumn–winter (Albertelli *et al.*, 1992). This station is exposed to wave action and is characterized by relatively high current speeds 50 cm above the sediments (2.5–8.0 cm s^{-1}). Redox Potential Discontinuity depth (RPD) exceeded 12.0 cm throughout the year. Grain size in the top 4 cm of the sediments (modal size between 125 μm and 225 μm) did not show significant seasonal changes (Danovaro, 1993). Porosity in the top 2 cm of sediment ranged between 27% (October 1991) and 35% (January 1991; Danovaro, 1993).

Sampling

A series of sediment samples was collected monthly by Scuba diving between February 1990 and February 1993. Three cores per sampling period were taken randomly from three quadrats (20 cm length, 400 cm^2 surface area) belonging to a larger quadrat (1 m^2 surface area). Sediment cores were obtained by inserting PVC tubes (i.d. 4.7 cm, three replicates) into the sediments. The samples were brought back to the laboratory and

processed within 3 h of collection. The surface sediment layer (0–4 cm) of each core that was used for the analyses of organic carbon and nitrogen, lipids, proteins, carbohydrates and chlorophylous pigments was immediately frozen at −20°C. Temperature and salinity were measured *in situ* on a monthly basis using a CTD (Aanderaa Instruments, mod. 2975).

Composition of sedimentary organic matter

Sediment organic matter. Sediment was treated with 10% hydrochloric acid to remove carbonates that could interfere with organic-matter assessment (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).

Organic carbon and nitrogen. Total organic carbon (OC) and nitrogen (ON) were measured on four replicates using a Carlo Erba CHN Analyzer (mod. EA 1108) after acidification with 0.1 N HCl in Ag tins. The HCl treatment removed carbonates, allowing the remaining organic carbon and nitrogen to be measured directly. Cyclohexanone-2, 4-dinitrophenylhydrazone was used as a standard for C and N (Hedges and Stern, 1983).

Lipids. After sonication in distilled water, total lipids (LIP) were extracted by direct elution with chloroform and methanol (Danovaro and Fabiano, 1990). Sediment analyses of three replicates were conducted using methods outlined by Bligh and Dyer (1959) and by Marsh and Weinstein (1966). Various techniques are applicable for lipid analysis (Barnes and Blackstock, 1973; Moal *et al.*, 1985), but the method of Marsh and Weinstein (1966) was selected because of its sensitivity and capability to detect a wide range of lipid compounds. Data are reported as tripalmitine equivalents.

Proteins. Protein (PRT) analyses of three replicates were conducted following extraction with NaOH (0.5 M, 4 h) and were determined according to Hartree (1972) modified by Rice (1982) to compensate for phenol interference and expressed as albumin equivalents. There are other effective methods for protein determination (Bradford, 1976; Mayer *et al.*, 1986), however, this method was chosen due to its ease and high sensitivity. To further investigate the nature of organic nitrogen, protein concentrations were converted to organic nitrogen (N-PRT) by using the conversion factor 6.25 and expressed as percentages of ON (N-PRT:ON).

Carbohydrates. Carbohydrates (CHO) of three replicate samples were analysed according to Gerchakov and Hatcher (1972) and expressed as glucose equivalents. The assay, which reacts with reducing saccharides, which is based on the same principle as the widely used method of Dubois *et al.* (1956) however it has been modified for carbohydrate assessment in sediments. The reported methods were similar to those used for the study of suspended particular organic matter in a similar environment (Fabiano *et al.*, 1984; Danovaro, 1993). For each biochemical analysis, blanks were performed using sediments that had been precombusted at 450°C for 2 h. All these methods are described in detail in Danovaro and Fabiano (1990).

Carbohydrate, protein and lipid were converted into carbon equivalents using conver-

sion factors (according to Fabiano *et al.*, 1993) 0.40, 0.49 and 0.70 for CHO, PRT and LIP, respectively.

Accuracy was tested against prepared standards and the deviations from the true standard values were expressed as coefficients of variation (CV%). CV ($n = 4$) calculated on the basis of the standard used were 0.5 and 0.9% for OC and ON respectively, 7.8 for LIP, 6.0 for CHO and 6.6% for PRT.

Photosynthetic pigments

Analyses of Chl *a* and phaeopigments were carried out according to Lorenzen and Jeffrey (1980). Pigments were extracted with 90% acetone (24 h in the dark at 4°C). After centrifugation, the supernatant was used to determine the functional Chl *a* and acidified with 0.1 N HCl to estimate the amount of phaeopigments (Plante-Cuny, 1974). Microphytobenthic carbon was calculated by converting Chl *a* concentrations to carbon content (C–Chl *a*) using a conversion factor or 40 (De Jonge, 1980).

Data analysis

Least-squares regression was applied to the data set to relate organic carbon and nitrogen to lipids, proteins, carbohydrates and other sedimentary factors (Draper and Smith, 1981). These analyses were carried out using the Statgraphics (1989) programme. Analyses of variance (ANOVA) were carried out to test for seasonal differences in physico-chemical factors using time as repeated measure (Statistical Analysis System-SAS, 1984). Ordination techniques (Principal Component Analysis, PCA and Multidimensional Scaling, MDS) were performed in order to detect which parameters behave similarly. These analyses were carried out using the PRIMER Programme (Plymouth Marine Laboratory).

RESULTS

Temperature and salinity

At the sediment–water interface the lowest temperatures were recorded in February (under 13.0°C), while temperatures above 20°C were observed between June and October. The highest temperature measured was 29.3°C in August 1992 (Fig. 2). Salinity

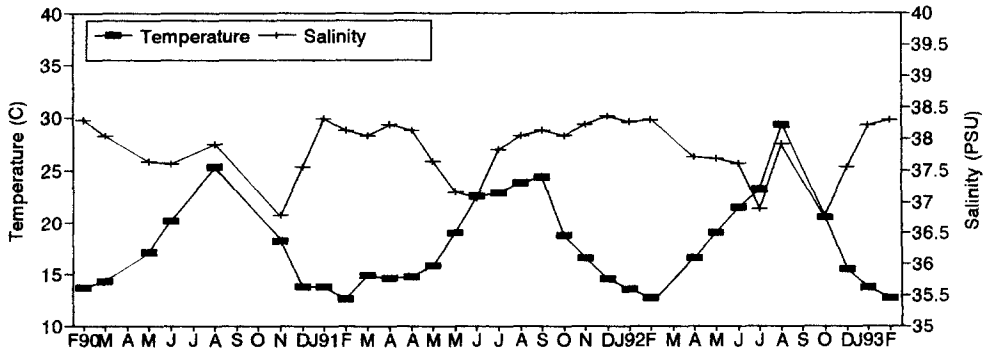

Fig. 2. Seasonal variations in temperature (°C) at the sediment–water interface.

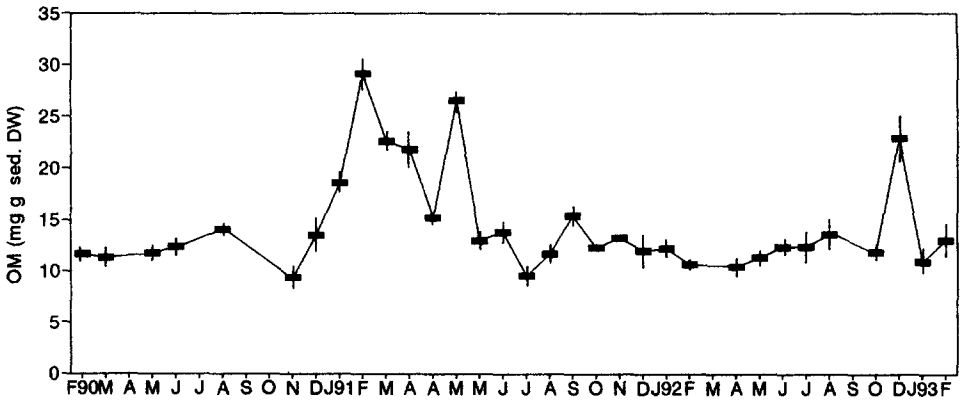

Fig. 3. Temporal trend of total organic matter concentrations (OM) in the surface sediments (0–4 cm). Data are expressed as mg g^{-1} of sediment dry weight (standard deviations are indicated).

ranged between 36.80 and 38.35% (November 1990 and October 1992, respectively; Fig. 2).

Elemental and biochemical composition of organic matter

Sediment organic matter (OM, Fig. 3) ranged between 9.36 ± 0.09 (November 1990) and 29.13 ± 0.04 mg g^{-1} of sediment dry weight (February 1991). Total sediment organic carbon (OC) exhibited clear seasonality characterized by highest values in winter (1.99 ± 0.07, 2.29 ± 0.57 and 2.90 ± 0.06 mg g^{-1} of sediment dry weight in February 1991, December 1991 and January 1993, respectively) followed by other high values in spring [2.21 ± 0.14 and 2.18 ± 0.03 mg g^{-1} of sediment dry weight, in April 1991 and April 1992, respectively; Fig. 4(a)].

Sediment organic nitrogen (ON) generally increased from winter to spring (ranging from 0.15 ± 0.02 and 0.32 ± 0.03 mg $g^{-1}$of sediment dry weight in December 1991 and February 1992, respectively) with a minimum (0.14 ± 0.02 mg g^{-1} of sediment dry weight) in December 1991 [Fig. 4(b)].

Carbon:nitrogen (C:N, w:w) ratio of the organic matter in the bottom sediments showed significant seasonal fluctuations [Fig. 4(c); Table 1]. Maxima were recorded in December 1990 (C:N = 11.3), December 1991 (C:N = 13.3) and January 1993 (C:N = 10.2). Minima were observed in spring: March 1990 (C:N = 6.6), May 1991 (C:N = 6.0) and June 1992 (C:N = 6.4).

Concentrations of the three main biochemical components of the organic matter (i.e. carbohydrates, proteins and lipids) are shown in Fig. 5(a)–(c) [for carbohydrates (CHO), proteins (PRT) and lipids (LIP), respectively]. Carbohydrate content in surface sediments showed the lowest value in November 1991 (128.9 ± 11.0 μg g^{-1} of sediment dry weight), whereas two peaks were clearly recorded in April 1991 and April 1992 (515.9 ± 28.4 and 669.0 ± 89.5 μg g^{-1} of sediment dry weight, respectively).

A similar trend was shown by protein concentrations, which peaked in the same months (45.10 ± 4.4 and 66.9 ± 2.2 μg g^{-1} of sediment dry weight, in April 1991 and April 1992, respectively).

Maximum lipid content was observed in November 1991 (214.1 ± 43.7 μg g^{-1} of

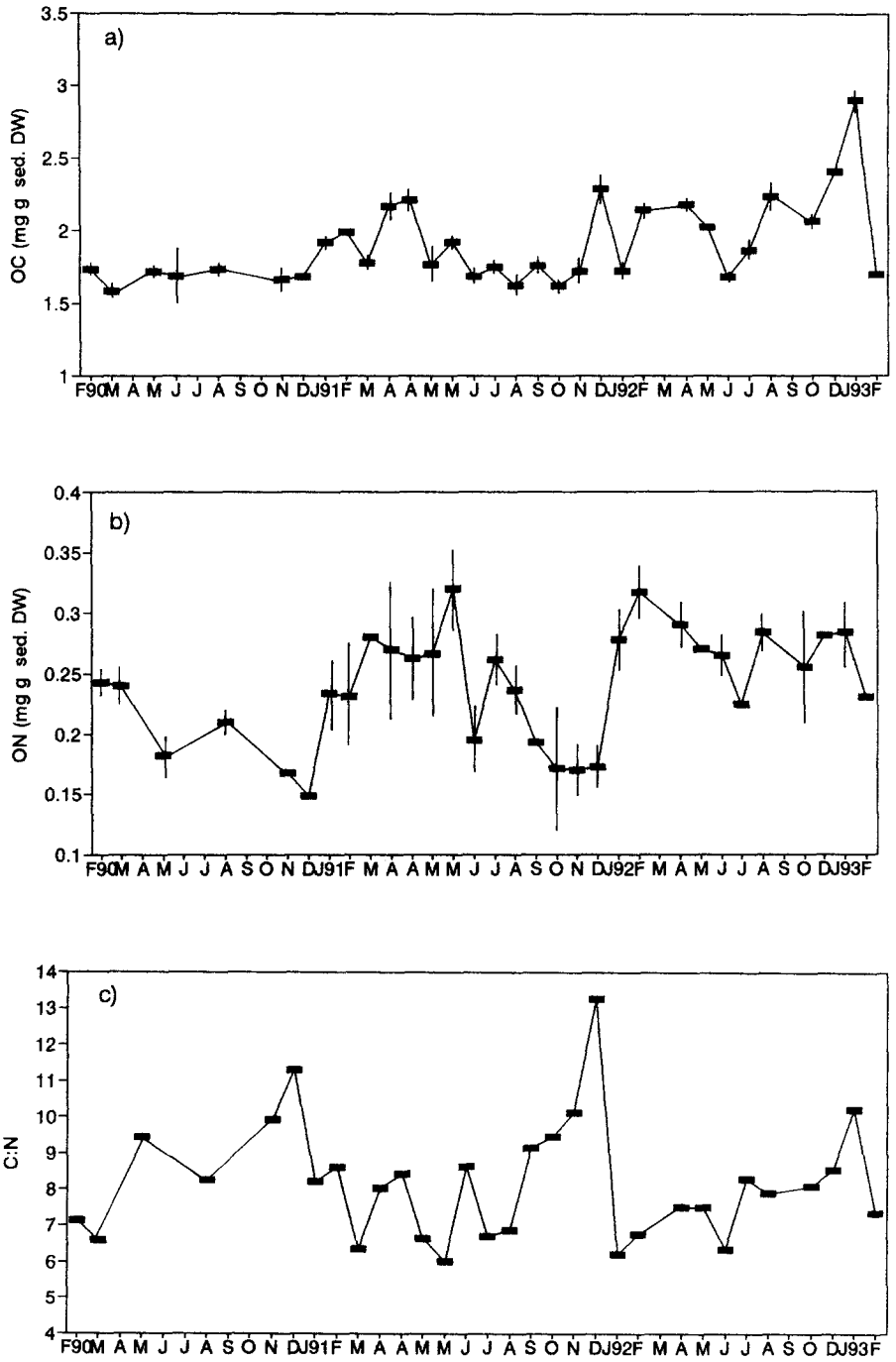

Fig. 4. Elemental composition of organic matter. Illustrated are: (a) total organic carbon (OC); (b) total organic nitrogen (ON); (c) C:N ratio (standard deviations are indicated).

Table 1. *Summary of analyses of variance of organic carbon (OC), organic nitrogen (ON), C:N ratio, proteins (PRT), carbohydrates (CHO), protein:carbohydrate ratio (PRT:CHO). Significance levels*: *0.05 > p > 0.01; **0.01 > p > 0.001; ns p > 0.5

Parameter		F ratio	Significance
Chl *a*	Season	4.56	*
	Year	6.32	**
OC	Season	3.22	*
	Year	1.01	ns
ON	Season	1.37	ns
	Year	0.87	ns
C:N	Season	3.80	*
	Year	2.25	ns
PRT	Season	2.26	ns
	Year	5.20	**
CHO	Season	1.58	ns
	Year	3.18	*
PRT:CHO	Season	0.86	ns
	Year	1.12	ns

sediment dry weight), whereas a second peak was observed in April 1991 (144.8 ± 38.6 μg g^{-1} of sediment dry weight). The peak recorded in April 1992 (117.2 ± 0.6 μg g^{-1} of sediment dry weight) is less significant statistically, though it was the maximum in 1992–1993.

N–PRT accounted for 2.32% on average of total organic nitrogen, and ranged from 0.91% (March 1991) to 4.40% of PON (December 1991; Table 2).

Since carbohydrate concentrations always exceed protein content, the PRT:CHO ratio showed little change ranging between 0.07 (September 1991) and 0.27 (June 1992). The highest values were generally recorded in late spring–summer, with the exception of November–December 1991 (Table 2).

The sum of carbohydrate, protein and lipid carbon was referred to as the biopolymeric fraction (C-BPF, *sensu* Fichez, 1991b) and utilized to estimate the fraction potentially available for benthic consumers (Table 3). C-BPF usually accounted for a small percentage of organic carbon (OC, on average 9.5%). Maximal C-BPF values were generally recorded in spring (14.1 and 17.8% of OC, respectively, in April 1991 and April 1992).

Photosynthetic pigments

Microphytobenthic biomass measured as Chl *a* in the uppermost 1 cm sediment layer (from February 1990 to January 1992) ranged from 1.95 ± 0.23 (August 1990) to 3.96 ± 0.89 (July 1991) μg g^{-1} of sediment dry weight. Chlorophyll *a* concentrations showed strong seasonal variations as indicated by an increasing trend in the period under investigation. Phaeopigment concentrations were characterized by a marked peak in July 1991 (4.12 ± 0.80 μg g^{-1} sediment dry weight), whereas the minimum was recorded in August 1990 (1.92 ± 0.12 μg g^{-1} sediment dry weight). C–Chl *a* accounted for a small percentage of OC (ranging between 4.4 and 9.0%, on average 6.12%) but accounted for

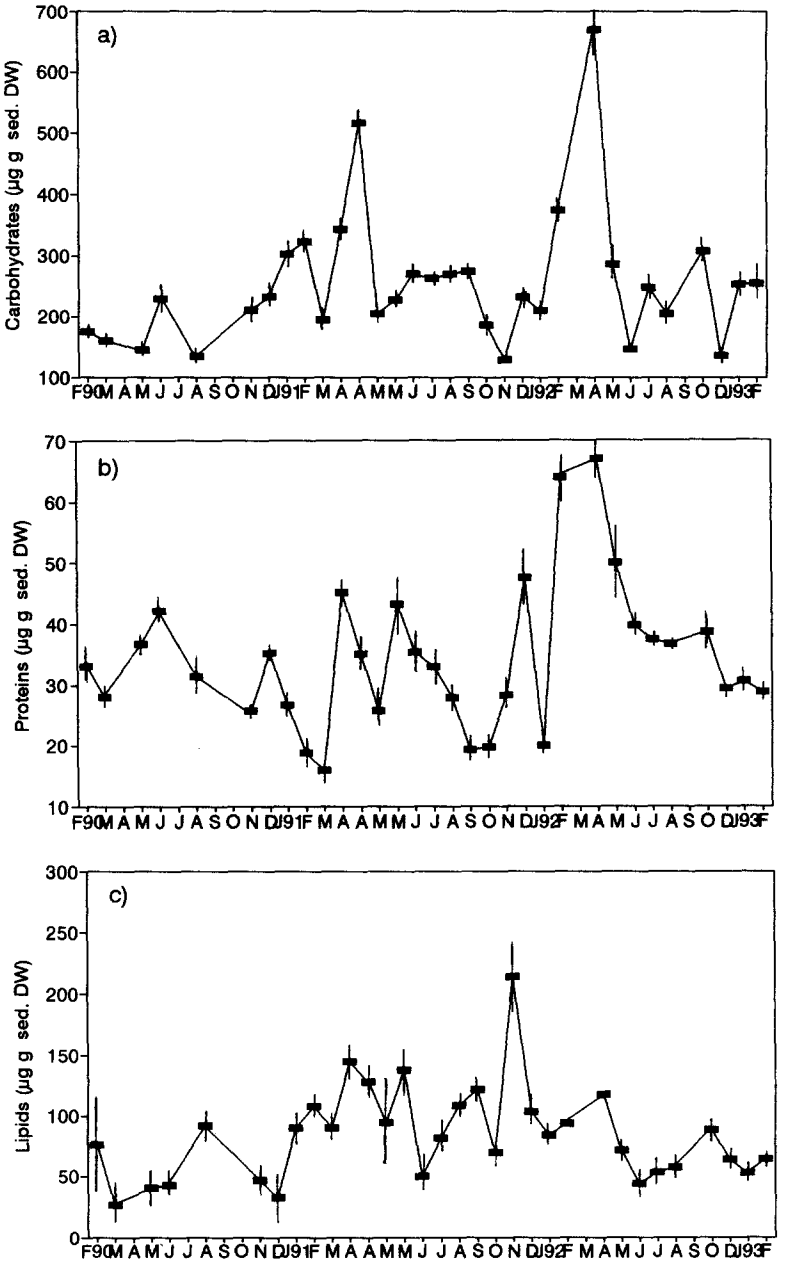

Fig. 5. Seasonal variations of the concentrations of main biochemical components of the organic matter ($\mu g\, g^{-1}$ of sediment dry weight): carbohydrates (glucose equivalents) (a); proteins (albumin equivalents) (b); and lipids (tripalmitine equivalents) (c).

Table 2. Sampling dates, total organic nitrogen (ON, $\mu g\ g^{-1}$ sediment dry weight), *protein concentrations* ($\mu g\ g^{-1}$ sediment dry weight), *protein–nitrogen content* (N–PRT, $\mu g\ g^{-1}$ sediment dry weight) *contribution of the protein–nitrogen to ON* (N–PRT:ON, %) *protein:-carbohydrate ratios* (PRT:CHO, *expressed as percentage*). *Standard deviations are indicated*

Sampling date	ON $\mu g\ g^{-1}$	PRT $\mu g\ g^{-1}$	N–PRT $\mu g\ g^{-1}$	N–PRT:ON (%)	PRT:CHO
19/02/90	242.6 ± 10.5	33.1 ± 3.5	5.3	2.18	0.19
21/03/90	239.8 ± 22.6	28.0 ± 0.8	4.5	1.87	0.18
03/05/90	182.1 ± 22.2	36.7 ± 1.1	5.9	3.22	0.25
13/06/90	nd	42.1 ± 0.9	6.7	nd	0.18
23/08/90	209.9 ± 7.8	31.4 ± 5.2	5.0	2.39	0.23
13/11/90	167.5 ± 3.1	25.7 ± 0.1	4.1	2.45	0.12
14/12/90	148.9 ± 11.9	35.1 ± 0.3	5.6	3.78	0.15
17/01/91	233.9 ± 40.0	26.7 ± 1.8	4.3	1.83	0.09
20/02/91	230.8 ± 50.0	18.8 ± 0.8	3.0	1.30	0.06
21/03/91	280.0 ± 33.1	15.9 ± 2.7	2.5	0.91	0.08
08/04/91	270.0 ± 80.0	45.1 ± 4.4	7.2	2.67	0.13
22/04/91	262.5 ± 40.0	35.1 ± 10.8	5.6	2.14	0.07
08/05/91	266.3 ± 150.0	25.7 ± 1.7	4.1	1.54	0.13
30/05/91	319.7 ± 40.0	43.2 ± 8.5	6.9	2.16	0.19
20/06/91	194.9 ± 30.0	35.4 ± 3.5	5.7	2.90	0.13
18/07/91	261.5 ± 30.0	32.9 ± 3.5	5.3	2.01	0.13
05/08/91	236.0 ± 30.0	27.8 ± 2.6	4.5	1.89	0.10
08/09/91	190.0 ± 13.2	19.3 ± 1.5	3.1	1.60	0.07
31/10/91	171.3 ± 90.0	19.7 ± 1.7	3.2	1.84	0.11
31/11/91	287.8 ± 30.0	28.2 ± 3.0	4.5	2.66	0.22
23/12/91	170.0 ± 20.0	47.5 ± 7.4	7.6	4.40	0.20
07/01/91	277.8 ± 30.0	20.0 ± 0.6	3.2	1.15	0.10
24/02/92	316.8 ± 31.2	64.0 ± 5.3	10.2	3.23	0.17
30/04/92	290.3 ± 19.6	66.9 ± 2.2	10.7	3.69	0.10
15/05/92	270.0 ± 36.0	49.9 ± 12.4	8.0	2.96	0.17
01/06/92	265.0 ± 16.4	39.7 ± 0.1	6.4	2.39	0.27
09/07/92	224.4 ± 39.6	37.3 ± 0.7	6.0	2.22	0.15
06/08/92	283.6 ± 23.2	36.5 ± 1.2	5.8	2.06	0.18
14/10/92	254.8 ± 55.7	38.5 ± 4.8	6.2	2.96	0.17
11/12/92	281.5 ± 18.5	29.3 ± 0.0	4.7	1.67	0.22
26/01/93	283.8 ± 32.0	30.6 ± 2.1	4.9	1.72	0.12
25/02/93	230.5 ± 20.1	28.8 ± 0.6	4.6	2.00	0.11

nd: not determined.

the dominant fraction of C–BPF (ranging between 35.6 in August 1991 and 94.8% in January 1992—on average 65.0%; Table 3).

As far as the ordination of data is concerned, no significative result was obtained and apparently no relation was found between sedimentary parameters.

DISCUSSION

Nature, origin and composition of sedimentary organic matter

Data obtained from this three-year study revealed that OM and OC were not significantly correlated. The combined percentage of organic carbon and nitrogen in the

Table 3. *Contribution of the different components to the standing stocks of total organic carbon. Sampling dates, total organic carbon* (OC, mg g^{-1} sediment dry weight), *labile organic carbon* (C–BPF, *as sum of lipid, carbohydrate and protein carbon equivalents*, $\mu gC\ g^{-1}$ sediment dry weight), *contribution of the labile organic carbon to the* OC (C–BPF:OC, %), *chlorophyll carbon content* (C–CHL = Chl *a* × 30; $\mu gC\ g^{-1}$ sediment dry weight, *De Jonge*, 1980) *and relative contribution to the total organic carbon* (C–CHL:OC, %) *and to the labile fraction* (C–CHL:C–BPF)

Date	OC mg g^{-1}	C–BPF $\mu gC\ g^{-1}$	C–BPF:OC (%)	C–CHL $\mu gC\ g^{-1}$	C–CHL:OC (%)	C–CHL:C–BPF (%)
19/02/90	1.73 ± 0.01	143.0	8.3	90.9	5.2	63.5
21/03/90	1.58 ± 0.01	97.5	6.2	82.9	5.2	85.0
03/05/90	1.72 ± 0.08	105.9	6.2	84.8	4.9	80.1
13/06/90	1.69 ± 0.44	144.4	8.6	79.9	4.7	55.3
23/08/90	1.73 ± 0.04	137.7	7.9	78.2	4.5	56.8
13/11/90	1.66 ± 0.13	131.8	7.9	94.7	5.7	71.8
14/12/90	1.68 ± 0.00	134.6	8.0	103.7	6.2	77.1
17/01/91	1.92 ± 0.03	201.3	10.5	85.7	4.5	42.6
20/02/91	1.99 ± 0.07	218.8	11.0	91.3	4.6	41.7
21/03/91	1.78 ± 0.08	153.0	8.6	93.5	5.3	61.1
08/04/91	2.17 ± 0.20	267.9	12.3	95.4	4.4	35.6
22/04/91	2.21 ± 0.14	311.3	14.1	131.6	6.0	42.3
08/05/91	1.77 ± 0.31	165.1	9.3	105.0	5.9	63.6
30/05/91	1.92 ± 0.03	215.8	11.2	105.2	5.5	48.8
20/06/91	1.69 ± 0.04	162.6	9.6	95.0	5.6	58.4
18/07/91	1.75 ± 0.02	182.7	10.4	158.4	9.0	86.7
05/08/91	1.62 ± 0.10	202.8	12.5	132.7	8.2	65.4
08/09/91	1.76 ± 0.06	210.2	11.9	140.0	7.9	66.6
31/10/91	1.62 ± 0.08	136.1	8.4	128.9	8.0	94.8
31/11/91	1.72 ± 0.16	226.0	13.1	105.2	8.2	62.8
23/12/91	2.29 ± 0.57	193.5	8.4	147.0	6.4	76.0
07/01/91	1.73 ± 0.04	156.7	9.1	148.6	8.6	94.8
24/02/92	2.14 ± 0.02	251.2	11.7	nd	nd	nd
30/04/92	2.18 ± 0.03	388.3	17.8	nd	nd	nd
15/05/92	2.03 ± 0.03	192.1	9.5	nd	nd	nd
01/06/92	1.68 ± 0.00	110.9	6.6	nd	nd	nd
09/07/92	1.86 ± 0.09	157.1	8.4	nd	nd	nd
06/08/92	2.24 ± 0.25	143.1	6.4	nd	nd	nd
14/10/92	2.07 ± 0.03	208.1	10.1	nd	nd	nd
11/12/92	2.41 ± 0.00	116.6	4.8	nd	nd	nd
26/01/93	2.90 ± 0.06	155.6	5.4	nd	nd	nd
25/02/93	1.70 ± 0.00	164.0	9.7	nd	nd	nd

nd = not determined.

sediments (0.22% of sediment dry weight) is much less then the organic material percentage estimated as OM (1.44% as determined by heating in a muffle furnace at 450°C). Such difference is likely to be partially due to O and H covalently bound to C and N in organic material, but in most cases it was likely to be due to H_2O hydrating inorganic material (Mook and Hoskin, 1982; Sargent *et al.*, 1983). For that reason OM is clearly an overestimate of the organic content of the sediment and is thus of little significance for benthic ecologists studying community dynamics in relation to food availability.

OC concentrations fall within the range of values reported for other coastal areas of the Mediterranean Sea (Buscail *et al.*, 1990; Fichez, 1991a; Danovaro, 1993 and tables

therein). C:N ratios were, on average, rather low when compared with other coastal areas of northwestern Mediterranean (Cocito *et al.*, 1990) indicating the recent origin of organic matter and the limited burial due to high fluid energy (Metzler and Smock, 1990; Zavattarelli, 1986).

From analysis of the biochemical composition of organic matter, the carbon content of the biopolymeric fraction (C–BPF, assumed to account for the labile and easily degradable fraction) accounts for about 10%, on average, of total organic carbon. These results, although based on a different approach, confirm the hypothesis by Mare (1942), substantiated by several authors (George, 1964; Hargrave, 1970; Tenore and Hanson, 1980; Yingst, 1976), that only 5–15% of sediment detritus is available at any one time as food for benthic consumers. The percentages reported here are higher than those reported by Fabiano and Danovaro (1994) from an estuarine and eutrophic environment (C–BPF = 3% of OC) but lower than those reported for a highly oligotrophic system such as marine caves (C–BPF more than 20% of OC; Fichez, 1991a) or for the extremely oligotrophic deep-sea sediments of the eastern Mediterranean (BPF from 14.1 to 38.3% and on average 23.1% of OM, Danovaro *et al.*, 1993). Although such differences may be due to large-scale geographical and geological differences or to different calculation methods, these results would suggest that moving from an eutrophic to an oligotrophic environment may cause an increase in the biopolymeric fraction and therefore enhance food quality.

The temporal analysis of organic matter composition in surface sediments also showed an inverse relationship between amounts of organic matter and its potential availability to consumers; low quantities of high-quality organic matter (in spring) were replaced by large quantities of refractory material (in winter). The lack of any relationship between ON and PRT content is consistent with the results obtained by Rice (1982), who demonstrated that nitrogen enrichment is not synonymous with protein enrichment. This result indicates that organic nitrogen detected analytically is the same as is sequestred in the non-living portion of the detrital complex (Rice, 1979; Tenore and Rice, 1980; Mayer *et al.*, 1986 and citations therein). Correlation of OC content and C:N ratio lead to a similar conclusion ($r = 0.45$ $n = 22$; $p < 0.05$) indicating that high amounts of organic carbon were related to an increase in the refractory fraction.

Concentrations of the three components were usually lower than those reported in other estuarine areas or coastal areas, especially as far as lipids and proteins are concerned (Table 4). Biochemical composition of organic matter seems to be quite different from one coastal area to another, but is usually characterized by small amounts of total lipids and also by large quantities of proteins, which may exceed carbohydrate concentrations (Fabiano and Danovaro, 1994; Meyer-Reil, 1983; Sargent *et al.*, 1983). In the studied sediments, carbohydrates exceeded proteins and lipids in abundance. However, since CHO analysis involves acidification and partial hydrolysis of complex organic compounds and geopolymers able to react with various reagents (Cawet, 1981), carbohydrate content and the biopolymeric fraction may have been overestimated.

In the studied sediments, PRT:CHO ratios were low (on average 0.14) and comparable to those observed in bathyal sediments of the eastern Mediterranean (PRT:CHO = 0.09, Danovaro *et al.*, 1993) and lower than those reported from the Arno estuary (PRT:CHO = 0.3, Fabiano and Danovaro, 1994). Since proteins are more readily utilized than carbohydrates (Newell and Field, 1983) and are rapidly bound into refractory compounds, such low values would again confirm the role of labile proteins as a potentially limiting element for consumer growth in this area (Tenore *et al.*, 1984; Jumars and Wheatcroft, 1989).

Table 4. Comparison of lipid, protein and carbohydrate concentrations from different areas

Area	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)
Mactan Philippines		nd	0.5–1.3	0.7–1.6	Graf and Meyer-Reil (1985)
Gulf of Gascogne Atlantic Ocean	2100	0.22	1.85	2.44	Khripounoff *et al.* (1985)
Western Mediterranean	10–20	0.01–0.66	0.5–2.6	0.9–4.2	Fichez (1991a)
Ligurian Sea	10	0.06–0.23	0.02–0.04	0.18–0.58	Danovaro (1993)
Eastern Mediterranean	100–2400	0.05–0.19	0.07–0.16	1.2–2.4	Danovaro *et al.* (1993)
Prelo Ligurian Sea	4	0.08–1.07	0.05–1.62	0.28–3.59	Danovaro *et al.* (1994)
Tyrrhenian Sea	20–60	0.003–0.02	0.3–1.7	0.3–1.9	Fabiano and Danovaro (1994)

nd = not determined.

Algae are often important contributors to organic carbon and nitrogen pools (Mayer *et al.*, 1988). Chlorophyll *a* concentrations reported in our study are low and can be compared to those reported by Plante *et al.* (1986) in the Gulf of Fos (from 0.91 μg g^{-1} dry weight in March to 4.91 μg g^{-1} dry weight in September). Although the spectrophotometric method does not allow discrimination between phytoplanktonic and microphytobenthic chlorophylls, values reported here should be considered of microphytobenthic origin. In fact, during the study period, highest Chl *a* values were reported in April–May whereas phytoplankton blooms occurred always in late February (2–3 μg Chl *a* l^{-1}; Danovaro, 1993), and the sedimentation of senescent cells generally occurs in the week following the bloom (Graf *et al.*, 1983). For this reason, two months following, phytoplankton contribution to the sedimentary organic matter is negligible. As suggested by the high contribution of C–Chl *a* to the C–BPF (on average 64%, Table 4), labile organic carbon at the Zoagli station is mostly of microphytobenthic origin. Seasonal fluctuations of photosynthetic pigment concentrations would consequently be responsible for the changes in labile organic matter content of sediment thus providing indirect evidence of the real availability of the biopolymeric fraction. This result is in contrast to those reported by Mayer *et al.* (1985) and Mayer and Rice (1992) who presented evidence indicating that: (a) deposition of planktonic material was the major source of organic matter, and (b) the *in situ* algal production was not an important control of protein concentrations at this site.

Seasonal fluctuations

Differences in quantity and composition of sediment organic matter showed clear seasonality but were not directly related to temperature, salinity or grain size. That fluctuations of organic matter content and composition may be attributed mainly to an algal bloom that occurred in the spring is not a novel finding. Blooms were characterized

by high OC, C–Chl *a* concentrations with a high C–Chl contribution to C–BPF (Table 3). Conversely, heavy rains typical of winter were responsible for the large input of terrestrial material. Such fluctuations also affected C:N ratios, also characterized by a clear seasonality. C:N values above 12 were always recorded in the cold months due to terrestrial material brought to the sea by rainfall. During the microphytobenthic bloom, C:N values were relatively low (6.2–7.4).

Interannual variations in organic matter content and composition

The bulk of organic carbon does not appear to change significantly during the three years investigated. Conversely, significant differences were found for some specific biochemical classes and for photosynthetic pigments (Table 1). In particular, both CHO and LIP were significantly higher during the second year of sampling and were significantly correlated with Chl *a* content.

Although the ratios between the various biochemical compounds showed little change during the period studied, and the average percentage contribution of the C–BPF to OC remained relatively low (ranging from 7.9% in the first year to 11.1% in the third), the absolute amount of the biopolymeric fraction increased considerably, as a result of the increase in microphytobenthic biomass, from 1991 to 1993. Comparison with data collected during 1987–1988 (Fabiano, unpublished data) indicates that the earlier lower amounts of OM, proteins and lipids were significantly related to lower Chl *a* contents of the sediments. The reason for such an increasing trend is so far unknown.

Acknowledgement—We thank Prof. P. A. Jumars (Seattle) for criticisms, suggestions and for improving the paper.

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