Chemistry and Ecology

Pelagic-benthic coupling in a subtidal system of the North-Western Mediterranean

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Suspended particulate matter, zooplankton, and macrobenthos dynamics were investigated in a shallow area of the Ligurian Sea (north-west Mediterranean) characterized by wide temporal variability over an annual cycle. As indicated by multivariate analyses, the seasonal dynamics can be summarized as follows: (1) a late winter–early spring phytoplankton bloom followed by high zooplankton and macrobenthos densities during the spring months; (2) low-quality particulate suspended matter in summer, and an increase in the importance of zooplankton taxa with a wide range of feeding strategies, a decrease in macrofaunal abundance, and an increase in deposit-feeders and predators; and (3) a second phytoplankton bloom in autumn, followed by an increase in copepod density and a low macrofaunal abundance. In conclusion, pelagic and benthic communities in the coastal area of the Ligurian Sea mainly seem to be controlled bottom-up. Our results suggest that the quality of the particulate organic matter may play an important role in determining the temporal changes of both plankton and benthic assemblages, while the direct influence of other environmental features (such as sediment grain size) is relevant only for some macrobenthic taxa (e.g. crustaceans).

Keywords: Particulate organic matter; Phytoplankton; Zooplankton; Macrofauna; Coastal system; North-west Mediterranean

1.   Introduction

It is well known that the distribution of benthic communities varies in response to a complex array of variables. Of these, it has been demonstrated that the quality of the pelagic food supply plays an important role in the structure, abundance, and biomass of the benthic communities, especially in oligotrophic areas [1–4]. The quality and quantity of organic matter that sinks to the bottom depend on the intensity of the primary production of the water column [5] and on the grazing rate of planktonic heterotrophs. Zooplankton consume part of the particulate organic matter (POM) in the water column but contribute to the organic-matter flux to the sea floor with carcasses and faecal-pellet production [6]. Finally, benthic suspension-feeders harvest particulate food material from the surrounding water, thereby coupling the pelagic and benthic

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environments. This is particularly true in shallow, coastal waters, where benthic assemblages reflect seasonal fluctuations in the quality and quantity of the food supply [7, 8]. Previous studies carried out at coastal sites in the oligotrophic Ligurian Sea have recognized that such seasonal changes may have profound implications for the population dynamics of the keystone species of the soft-bottom communities. The bivalve *Spisula subtruncata*, for instance, exhibits different growth and production rates as a result of differences in food quality and quantity, and its ability to couple the recruitment of larvae with phytoplankton bloom is also affected [9, 10]. Moreover, Covazzi Harriague *et al.* [11] observed that the seasonal variations of the Ligurian Sea coastal macrobenthonic communities were related to the trophic sources available in the sediment; in fact, deposit-feeders dominated when sediments were quantitatively rich, while the major suspension-feeders dominated when particulate matter showed a high quality.

Within the framework of a multidisciplinary investigation on the structure and temporal evolution of the soft-bottom communities in a shallow station in the Ligurian Sea [1, 9, 10, 12–17], the present study investigated the seasonal fluctuations in zooplankton and macrobenthos assemblages and the composition of the POM in a shallow area over a 1-yr period in order to analyse the role of the POM and/or environmental features in structuring the faunal communities.

2. Materials and methods

2.1 *Study area and sampling*

The sampling was carried out monthly at a coastal station (10 m depth) in the Marconi Gulf (Ligurian Sea, Italy; figure 1), between February 1991 and February 1992 (fortnightly in April and May). The samples were always collected in the morning (starting between 9.00 and 10.00 am). A GPS was used to localize the sampling station. The study site was located
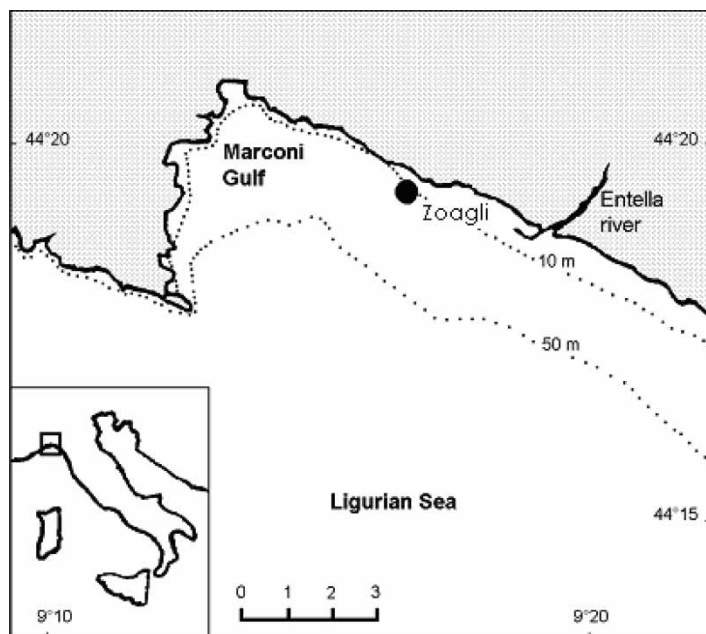

Figure 1. Study site.

in a high-energy area (exposed to wave action) characterized by well-oxygenated sediment (RPD: exceeding 19 cm throughout the year [5]) and by a lack of benthic macrophytes with the exception of occasional tufts of *Cymodocea nodosa* [18].

The surface salinity and temperature were measured with an AANDERAA Mod. 2975 probe and the transparency with a Secchi disk. The water samples were collected using a Niskin bottle. Two litres of water were filtered with Millipore HA filters (0.45 μm porosity) for the chlorophyll *a* determinations. Subsamples of 1 l of water were filtered with pre-ashed (450 °C, 2 h) Whatman GF/C filters (0.45 μm porosity) to determine the total suspended matter, particulate organic carbon (POC), particulate organic nitrogen (PON), particulate protein, particulate lipid, and particulate carbohydrate determinations (from two to three replicates for each analysis). Five litres of water were collected and fixed with buffered formalin (4% final concentration) for the phytoplankton determination.

The zooplankton samples were collected vertically from the bottom to the surface of the water column (10 m in depth) using a Nansen net (200 μm mesh, Φ30 cm), and preserved in 4% buffered formalin–sea water.

The sediment samples were collected with a PVC core (Φ = 3.7 cm) for the analysis of the sediment texture and total organic matter content. The macrofauna samples were collected by scuba divers, using a suction device [19]. Five to eight replicate samples (each replicate sample 0.1 m^2, 20 cm in depth) were collected randomly each time, using a net with a 1-mm mesh size. The samples were fixed in 10% buffered formalin–sea water.

2.2 *Particulate matter and phytoplankton analyses*

The total suspended matter (TSM) was estimated using the gravimetric method: filters (previously weighed) were placed in a drying oven at 60 °C for 6 h and then weighed on a Mettler H54AR ($d = 0.01$ mg) scale. The TSM was calculated as the difference of the total weight and filter weight [20]. The particulate carbon and nitrogen (POC and PON, respectively) were estimated using an elemental analyser (CHN Carlo Erba mod. 1106): cyclohexanon 2,4 dinitrophenylhydrazone was used as standard. The particulate lipid (LIP) extraction was made according to Bligh and Dyer [21] and the dosage according to Marsh and Weinstein [22]. The particulate proteins (PRT) were estimated according to Hartree [23], [24], with bovine albumin as standard (Boeringer 6 MBH). The particulate carbohydrate concentration (CHO) was measured according to the colorimetric method of Dubois *et al.* [25]. The POM was determined as the sum of the particulate proteins, lipids, and carbohydrates. Pigment concentrations were established using the spectrophotometric method [20], following the SCOR-UNESCO formula. The carbon equivalents of the chlorophyll *a* concentrations were obtained using 40 as a conversion factor [26]. The phytoplankton composition was analysed after sedimentation using a Uthermöl microscope to assess the contribution of diatoms and dinoflagellates.

2.3 *Zooplankton analyses*

All the taxa were sorted and counted in the laboratory, separating organisms longer than 5 mm which are considered 'macroplankton' and are not taken into account in this work. Copepods, which were the main component of the mesozooplankton, were classified down to genera. Identifications and counts were made in aliquots containing no fewer than 100 copepods [27]. The total mesozooplankton dry weight was determined by placing the samples in an oven at 60 °C for 16 h [28] and then weighing the residue on a Mettler H54AR ($d = 0.01$ mg) Scale. The biomass (dry weight) of the total sample and the abundance of the organisms (number) were calculated in terms of filtered water volume (m^3).

2.4 *Sediment and macrofauna analyses*

The grain-size analysis was performed using the sieving technique. The mean particle diameter $(M) = (P_{75} + P_{25})/2$, and sorting coefficient $(SC) = (P_{75}/P_{25})^{1/2}$ where P_{75} and P_{25} were determined from the cumulative curve by reading the diameter value which corresponded to 75% and 25%, respectively, on the curve [29].

The total sedimentary organic-matter (TOM) content was determined by burning the organic matter in a muffle furnace (550 °C for 4 h) and weighing the residue with a Mettler H54 AR Scale (accuracy = 0.01 mg) [30].

The macrofaunal organisms were determined to species level. After identification, the biomass was determined. The calcium carbonate exoskeletons of molluscs and echinoderms were eliminated using hydrochloric acid (10%). The flesh of the molluscs and echinoderms, and the specimens of the other taxa were placed in a drying oven at 60 °C for 24 h to obtain their dry weight (DW) (Mettler H54AR ($d = 0.01$ mg) Scale). To obtain the ash weight (AW), samples were placed in a muffle furnace at 550 °C for 4 h and then weighed. The ash-free dry weight (AFDW) was calculated as follows: DW − AW. The abundances of the different trophic groups, separated according to the literature [31–35], were estimated.

2.5 *Statistical analyses*

Spearman rank correlation analyses were performed. Shannon-Wiener diversity (H', log base 2) and evenness (J) and multivariate analysis were performed using a PRIMER 6β programme package (Plymouth Marine Laboratory). A PCA analysis was performed on the normalized data of the total suspended matter, the biochemical composition of the POM (proteins, lipids, and carbohydrates), and chlorophyll *a*. Cluster analyses were performed on the fourth-root transformed square data of the zooplankton abundance and on the presence/absence of the transformed data of the macrobenthos density. A similarity percentage analysis (SIMPER) was used to analyse the species contribution to the similarity between samples [36].

3. **Results**

3.1 *Environmental parameters*

The data of the environmental parameters are reported in table 1. The surface temperature showed a seasonal pattern with the minimum value in winter (12.3 °C, February 1991) and the maximum in summer (25.5 °C, July). The surface salinity ranged from 37.1 PSU (June) to 39.0 PSU (March). Transparency was at its maximum value (bottom) for 60% of the sampling period (especially during spring and summer), while the minimum value (5.5 m), was observed during December. The monthly rainfall ranged between 1.8 mm (December) and 293.0 mm (October).

The dominant mean sediment particle diameter (table 1) over the period was the fine sand fraction, with the exception of the first sampling of May, when the mean particle diameter was much higher (1.2 mm), probably due to a long stormy period before the sampling. Sediments were, in general, moderately well or moderately sorted for the entire sampling period (table 1). In general, the total sedimentary organic matter content displayed a decreasing pattern from February 1991 to February 1992 (table 1). The highest values were observed from February to April 1991 (on average 23.8 ± 2.9 mg g^{-1}). The total organic matter was significantly

Table 1. Environmental parameters on each sampling date.

Date	Surface temperature (°C)	Salinity (PSU)	Rain (mm)	Wind speed (km h^{-1})	Current speed (cm s^{-1})	M (mm)	SC	TOM (mg g^{-1} sed.)
20 Feb 1991	12.3	38.1	27.6	7.4	n.d	0.21	0.68	28.0
21 Mar 1991	14.5	39.0	96.2	7.7	4.7	0.24	0.73	22.0
08 Apr 1991	15.0	38.2	37.1	7.6	8.0	n.d	n.d	22.0
22 Apr 1991	14.5	38.2	37.1	7.6	n.d	0.22	0.69	23.0
8 May 91	15.0	37.6	69.9	7.1	n.d	1.15	0.55	12.0
29 May 1991	18.3	37.2	69.9	7.1	n.d	0.22	0.71	14.0
28 Jun 1991	22.8	37.1	39.2	7.7	5.5	0.22	0.68	10.0
18 Jul 1991	25.5	37.8	20.2	7.1	5.4	0.27	0.76	12.0
1 Aug 1991	24.8	38.0	98.6	8.1	3.9	0.23	0.71	16.0
5 Sep 1991	24.5	38.1	67.6	9.1	3.0	0.16	0.70	13.0
31 Oct 1991	14.6	38.0	293.0	6.8	6.6	0.23	0.74	14.0
30 Nov 1991	12.6	37.2	90.4	7.3	2.5	0.27	0.74	12.0
23 Dec 1991	12.7	38.2	1.8	8.7	7.1	0.20	0.67	9.0
7 Jan 1992	13.0	38.3	37.6	8.0	4.2	0.24	0.76	9.0
24 Feb 1992	12.5	38.7	72.2	7.9	n.d	0.29	0.67	7.0
Avg	17.0	38.0	70.6	7.7	5.1	0.30	0.70	14.9
S.E.	4.4	9.8	18.2	2.0	1.3	0.08	0.18	3.8

Rain = monthly precipitation; Wind speed = Mean monthly speed of the wind; M = mean particle diameter; SC = sorting coefficient; TOM = total organic matter; Avg = average value; S.E. = standard error; n.d. = not determined.

correlated to the POC and PON ($r = 0.64$ and 0.54 for POC and PON, respectively; $P < 0.05$; $n = 15$).

3.2 *Particulate organic matter*

We utilized the PCA analysis of the particulate-organic-matter data to characterize and find similarities between the samplings. The two axes of the PCA analysis explained 74.6% of the annual fluctuations in the organic-matter composition (figure 2). An increasing particulate-matter lability gradient was observed along pc1. The spring samplings showed the highest suspended matter quality, while the lowest was observed at the end of summer and at the beginning of winter. The notable lability of the organic matter during the spring season (March–May) was indicated by the highest PRT:CHO ratio values (on average 3.3), considered as an indicator of the quality of the POM, by the highest POM:TSM ratio values (on average 5.8), utilized as a measure of the potentially available seston fraction of food (Danovaro and Fabiano, 1997), and by the POM composition (proteins were on average c. 51% and lipids c. 31%). The chlorophyll a concentrations mainly associated with the pc2 axis of the PCA plot were chosen as an indicator of freshly produced organic matter. The major phytoplankton bloom was observed on 20 February 1991 (concentration of chlorophyll a : $2.5 \, \mu g \, l^{-1}$). Slight increases were also observed on 29 May 1991 ($1.4 \, \mu g \, l^{-1}$), 30 November 1991 ($1.3 \, \mu g \, l^{-1}$), and 24 February 1992 ($1.7 \, \mu g \, l^{-1}$).

The phytoplankton population was principally composed of diatoms for most of the year (table 2). Dinoflagellates were dominant only during the spring–summer period (May–August), representing on average 79%.

The POC and PON showed a decreasing pattern with maximum values on 20 February 1991 and minimum values on 23 December 1991. Three small peaks were observed, corresponding to increases in chlorophyll a concentrations (table 2). Significant correlations between chlorophyll-a and POC ($r = 0.51$, $P < 0.05$, $n = 15$) and chlorophyll-a and PON ($r = 0.51$,
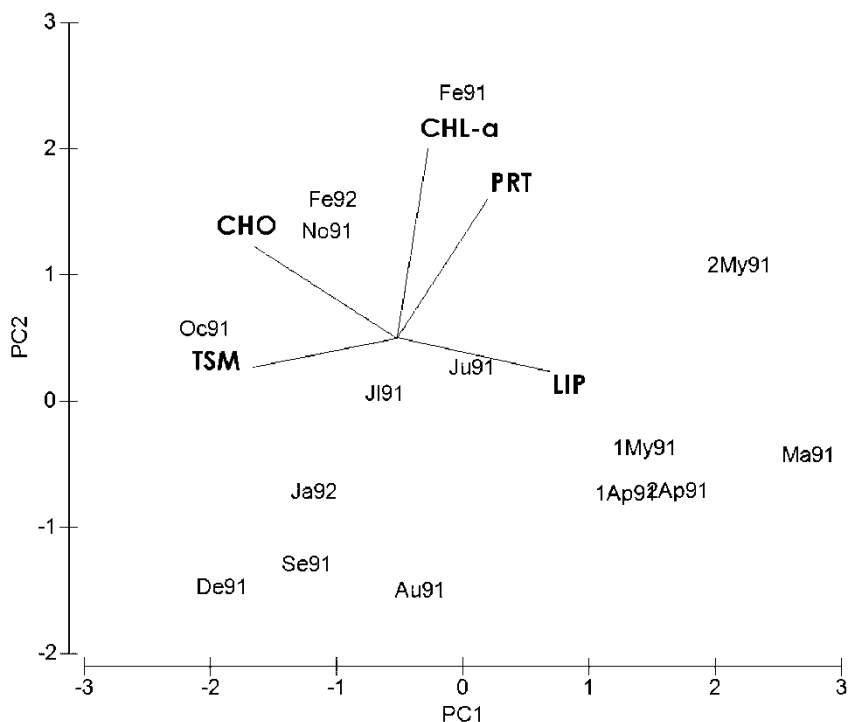
Figure 2. PCA analysis performed on the normalized data of the particulate organic matter components. Sampling dates are expressed as: Fe91 = 20 February 1991, Ma91 = 21 March 1991, 1Ap91 = 8 April 1991, 2Ap91 = 22 April 1991, 1My91 = 8 May 1991, 2My91 = 29 May 1991, Ju91 = 28 Jun 1991, Jl91 = 18 July 1991, Au91 = 01 August 1991, Se91 = 5 September 1991, Oc91 = 31 October 1991, No91 = 30 November 1991, De91 = 23 December 1991, Ja92 = 7 January 1992, Fe92 = 24 February 1992. TSM = total suspended matter; PRT = particulate proteins; LIP = particulate lipids; CHO = particulate carbohydrates; CHL − a = particulate chlorophyll *a*.

$P < 0.05, n = 15$) were noted, and the contribution of the chlorophyll *a* to the organic carbon pool ranged from 14.8% (28 June 1991) and 48.3% (24 February 1991; table 2).

3.3 *Zooplankton*

The data on the zooplankton composition and biomass are presented in table 2. We performed a cluster analysis on the zooplanktonic data but did not find any clear seasonal pattern (figure 3); the stations were mostly grouped according to Copepod dominance (on average, 76.2% of the total zooplankton abundance).

Although no significant seasonal fluctuations were observed, copepod dominance decreased strongly in summer when appendicularians and cladocerans dominated. The highest number of taxa (14) was observed in September, while the lowest number (3) was observed in February 1991, at the end of April, and at the beginning of May.

The copepod genera *Acartia*, *Paracalanus*, and *Centropages* were the most abundant during spring, while *Clausocalanus* was more abundant during the second half of the year. The copepod density was inversely correlated to the water temperature ($r = -0.56$; $P < 0.05$; $n = 15$) and directly correlated to the particulate nitrogen concentration ($r = 0.52$; $P < 0.05$; $n = 15$) and with the POM:TSM ratio ($r = 0.55$; $P < 0.05$; $n = 15$).

The zooplankton biomass ranged from 8.2 mg DW m^{-3} (24 February 1992) to 1.8 mg DW m^{-3} (1 August 1991; table 2). The copepod contribution to the total biomass was, on

Table 2. Pelagic parameters on each sampling date.

Date	TSM	CHL-a	PRT	LIP	CHO	POC	PON	POM: TSM	PRT: CHO	C-CHLa: POC	Dia	Din	Cop	App	Cni	Cla	TN	Total D	Total B
20 Feb 1991	3.9	2.5	94.1	38.1	56.2	242.2	28.2	4.8	1.7	40.5	82.0	11.0	772.5	20.0	–	–	3	825.8	5.2
21 Mar 1991	2.7	1.0	105.9	77.1	32.6	229.2	25.8	7.9	3.3	17.6	73.0	24.0	899.8	17.8	17.8	–	4	935.4	6.5
8 Apr 1991	4.3	1.1	81.1	69.1	34.8	203.0	20.2	4.3	2.3	20.7	n.d	n.d	288.4	4.8	26.4	–	4	319.7	3.3
22 Apr 1991	3.5	0.9	83.7	75.3	43.1	160.6	16.0	5.8	1.9	23.2	62.0	36.0	381.1	51.9	–	–	3	436.5	4.6
08 May 1991	4.2	1.0	114.2	54.3	24.4	162.3	20.0	4.6	4.7	24.2	n.d	n.d	150.3	11.3	–	–	3	163.1	2.9
29 May 1991	3.6	1.4	147.2	61.0	32.4	211.4	24.5	6.6	4.5	27.3	18.0	82.0	467.2	13.0	30.2	–	5	566.5	3.5
28 Jun 1991	5.0	0.7	125.5	53.0	59.4	200.5	23.3	4.8	2.1	14.8	19.0	73.0	80.5	3.8	–	–	5	94.3	3.3
18 Jul 1991	6.2	0.9	103.9	55.0	56.0	172.2	19.3	3.5	1.9	21.8	20.0	73.0	87.7	150.2	–	42.2	6	304.5	2.7
1 Aug 1991	5.6	0.6	72.5	47.0	32.7	135.3	12.7	2.7	2.2	17.7	8.0	86.0	99.7	119.5	8.2	51.1	9	296.7	1.8
5 Sep 1991	5.8	0.7	60.3	36.4	42.5	124.4	11.4	2.4	1.4	21.5	50.0	47.0	251.3	101.0	22.2	46.8	14	517.5	4.2
31 Oct 1991	6.1	1.2	84.8	32.4	70.8	114.9	14.2	3.1	1.2	40.0	85.0	12.0	270.6	44.9	2.2	–	6	418.7	3.9
30 Nov 1991	5.7	1.3	113.0	46.5	74.9	146.8	17.7	4.1	1.5	36.0	81.0	11.0	301.8	15.1	6.0	3.0	10	443.7	2.6
23 Dec 1991	5.2	0.6	24.3	37.8	64.2	60.2	8.2	2.4	0.4	42.5	47.0	34.0	276.7	8.3	2.8	–	6	298.9	3.2
7 Jan 1992	5.9	0.8	82.4	29.8	38.9	117.7	16.5	2.6	2.1	27.5	57.0	28.0	557.1	217.0	10.6	–	7	821.8	3.4
24 Feb 1992	6.1	1.7	111.9	40.8	59.3	141.8	13.2	3.5	1.9	48.3	94.0	4.0	264.2	24.4	–	10.9	7	313.0	8.2
Avg	4.9	1.1	93.7	50.2	48.1	161.5	18.1	4.2	2.2	28.2	53.5	40.1	343.3	53.5	8.4	30.8	6.1	450.4	3.9
S.E.	1.3	0.3	24.2	13.0	12.4	41.7	4.7	1.1	0.6	7.3	13.8	10.3	89.1	13.8	2.2	8.0	1.6	116.3	1.0

TSM = total suspended matter (mg$\,$l^{-1}); CHLa = particulate chlorophyll a(μg$\,$l^{-1}); PRT = particulate proteins (μg$\,$l^{-1}); LIP = particulate lipids (μg$\,$l^{-1}); CHO = particulate carbohydrates (μg$\,$l^{-1}); POC = particulate organic carbon (μg$\,$l^{-1}); PON = particulate organic nitrogen (μg$\,$l^{-1}); POM : TSM = particulate organic matter:total suspended matter ratio (%); PRT : CHO = protein:carbohydrate ratio; C-CHLa : POC = carbon of particulate chlorophyll a:organic carbon ratio (%); Dia = diatoms (%); Din = dinoflagellates (%); Cop = copepod density (ind. m^{-3}); App = appendicularian density (ind. m^{-3}); Cni = cnidaria density (ind. m^{-3}); Cla = cladocera density (ind. m^{-3}); TN = number of taxa; Total zooplankton density (D; ind. m^{-3}) and biomass (B; mg DW m^{-3}); DW = dry weight; Avg = average value; S.E. = standard error.

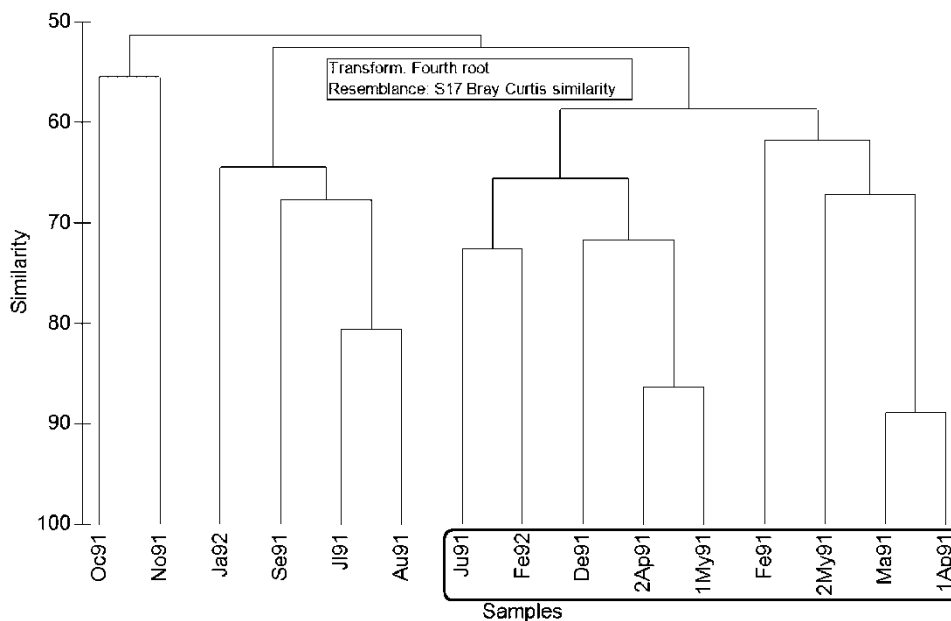*Pelagic–benthic coupling in a subtidal system*

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Figure 3.   Cluster analysis of fourth-root transformed data of the zooplankton density.

average, $32.6 \pm 8.4\%$. The copepod biomass was significantly correlated to the particulate carbon ($r = 0.60$; $P < 0.05$; $n = 15$), particulate nitrogen ($r = 0.63$; $P < 0.05$; $n = 15$), and POM:TSM ratio ($r = 0.65$; $P < 0.01$; $n = 15$).

3.4   *Macrofauna*

The macrofaunal data are reported in table 3. The macrofaunal abundance was generally low and showed a decreasing pattern from spring to winter. The number of species also followed a decreasing pattern from February to December 1991. Molluscs were a major taxon, representing *c*. 58% of the total macrofaunal density. The most abundant species was the bivalve *Spisula subtruncata* (da Costa), which represented 82.6% of the mollusc density and 48% of the total macrofaunal abundance. This bivalve showed two recruitment events (21 March 1991 and 29 May 1991), followed by a high juvenile mortality (Albertelli *et al.*, 1994b).

The cluster and SIMPER analyses (figure 4) showed a grouping driven by the seasons: (1) the end of the winter–spring months (similarity 54%) were characterized by the highest densities and number of species and communities, composed principally of suspension feeders (figure 5); (2) in the summer months (similarity 51%), the density and species number were lower than in the springtime, and the importance of suspension-feeders was slightly lower; (3) the autumn–winter months (similarity 49%) were characterized by low densities and number of species, and an increase in the importance of deposit-feeders. Two samples, from 8 May 1991 and 30 November 1991, were faunistically different and could not be integrated into any single group.

The total macrofaunal abundance was significantly correlated to the suspended organic matter. It was directly correlated to the particulate lipids ($r = 0.69$; $P < 0.01$; $n = 15$) and to the indicators of organic-matter quality (PRT:CHO, $r = 0.68$; $P < 0.01$ and POM:TSM, $r = 0.84$; $P < 0.001$; $n = 15$), and was inversely correlated to the detrital component of the

Table 3. Macrobenthic density (D, ind. m^{-2}), biomass (B, mg AFDW m^{-2}), and species number (SN) on each sampling date.

Date	Polychaetes D	Polychaetes B	Crustaceans D	Crustaceans B	Molluscs D	Molluscs B	Echinoderms D	Echinoderms B	Others D	Others B	Total D	Total B	SN
20 Feb 1991	147.1	193.4	75.7	31.9	88.6	38.7	5.7	67.7	11.4	9.3	328.6	341.1	71
21 Mar 1991	100.0	137.1	94.0	39.4	1040.0	86.2	8.0	0.1	30.0	2858.1	1272.0	3121.0	54
8 Apr 1991	110.0	262.9	77.1	29.7	500.0	74.3	18.6	87.4	11.4	12.8	717.1	467.2	57
22 Apr 1991	145.7	184.9	78.6	49.1	110.0	57.3	30.0	63.0	14.3	18.2	378.6	372.4	57
8 May 91	26.7	131.3	310.0	90.1	0.0	0.0	18.3	161.5	5.0	1.0	360.0	383.9	30
29 May 91	93.8	178.5	131.3	36.9	1040.0	191.2	38.8	170.3	15.0	65.5	1318.8	642.4	58
28 Jun 1991	45.0	147.2	46.7	17.6	281.7	106.4	31.7	24.4	20.0	207.8	425.0	503.4	45
18 Jul 1991	60.0	90.7	67.1	290.5	134.3	200.1	15.7	66.1	11.4	26.1	288.6	673.5	52
1 Aug 1991	72.5	133.2	63.8	22.7	102.5	97.1	15.0	278.9	10.0	155.4	263.8	687.2	49
05 Sep 1991	57.1	291.5	32.9	26.0	114.3	87.1	14.3	150.7	10.0	69.8	228.6	625.0	35
31 Oct 1991	60.0	165.9	42.9	13.9	98.6	125.3	4.3	10.6	8.6	162.9	214.3	478.6	35
30 Nov 1991	41.4	261.7	42.9	21.6	15.7	8.1	18.6	513.2	4.3	221.7	122.9	1026.4	20
23 Dec 1991	57.1	39.9	17.1	5.9	44.3	114.4	5.7	51.9	5.7	5.7	130.0	217.7	33
7 Jan 1992	45.0	97.3	48.3	25.7	106.7	220.8	6.7	29.2	6.7	21.0	213.3	394.0	36
24 Feb 1992	31.3	113.3	47.5	11.2	56.3	74.8	27.5	357.5	27.5	8.1	190.0	564.9	28
Avg	72.8	161.9	78.4	47.5	248.9	98.8	17.3	135.5	12.8	256.2	430.1	699.9	44
S.E.	18.8	41.8	20.2	12.3	64.3	25.5	4.5	35.0	3.3	66.2	111.1	180.7	11.4

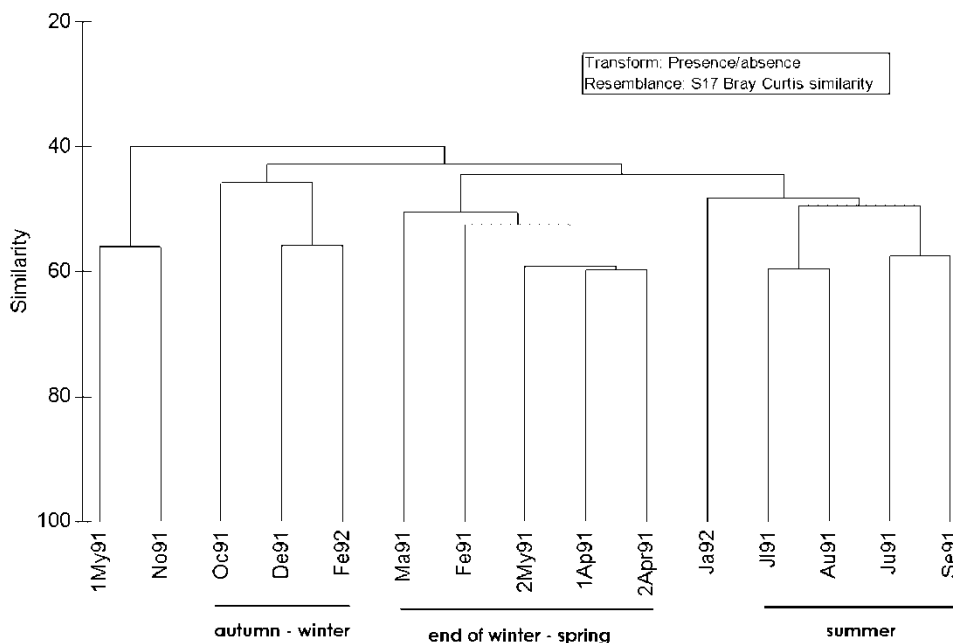D = density; AFDW = ash free dry weight; Avg = average value; S.E. = standard error.

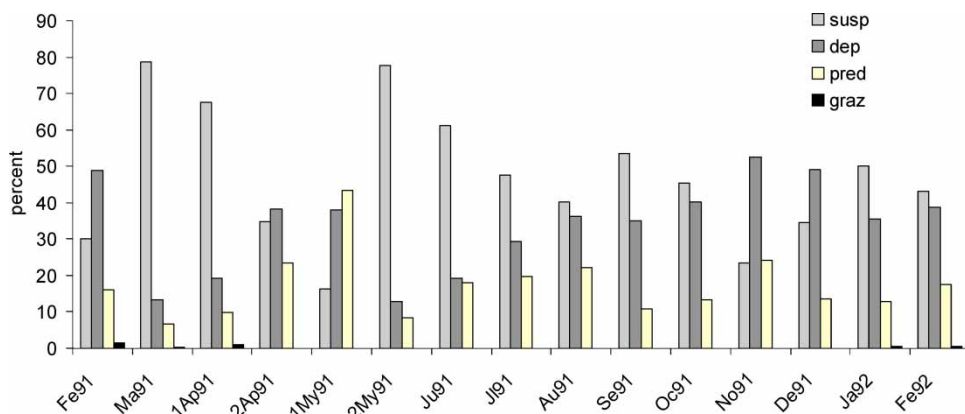Figure 4. Cluster analysis of presence/absence transformed data of macrofaunal density.

Figure 5. Trophic groups of the Zoagli macrofauna in percentages: suspension-feeders (susp), deposit-feeders (dep), predators (pred), and grazers (graz). Sampling dates as in figure 2.

organic matter (CHO, $r = -0.55$; $P < 0.05$; $n = 15$). The mollusc density was significantly correlated to the sorting coefficient ($r = 0.58$; $P < 0.05$), the polychaete density was significantly correlated to the total sedimentary organic-matter content ($r = 0.58$; $P < 0.05$; $n = 15$) and the crustacean density was significantly correlated to the mean grain size ($r = 0.92$; $P < 0.001$; $n = 15$).

Diversity and evenness (figure 6) showed a quite constant pattern (from July to February). Two decreases were observed, on 21 March 1991 and 29 May 1991, when *S. subtruncata* largely dominated.

The total macrofaunal biomass ranged from 217.7 mg AFDW m^{-2} (23 December 1991) to 3121.0 mg AFDW m^{-2} (21 March 1991; table 2). Molluscs represented *c.* 14% of the
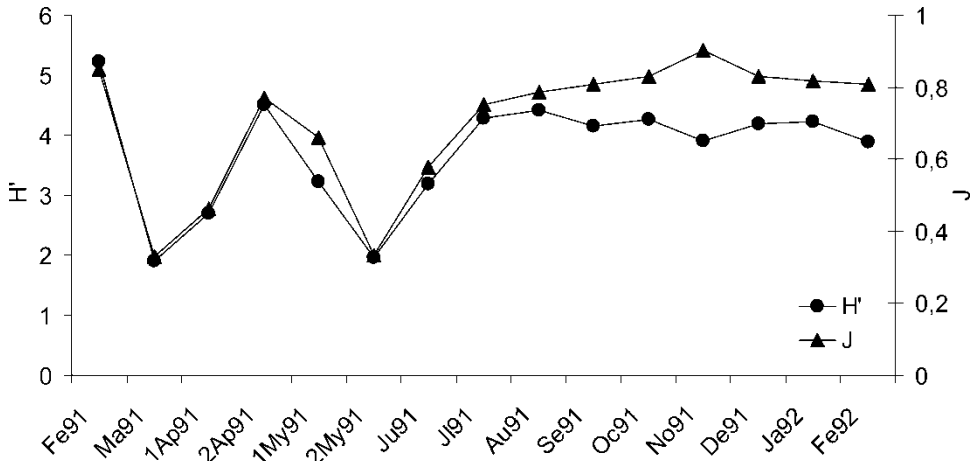
Figure 6.   Shannon–Wiener's Macrobenthic diversity (H′) and evenness (J). Sampling dates as in figure 2.

total biomass, on average 98.8 ± 25.5 mg AFDW m^{-2}. The *S. subtruncata* contribution to the mollusc biomass was 54.6%. Echinoderms (on average 135.5 ± 35.0 mg AFDW m^{-2}) represented 19% of the total biomass and crustaceans 7% (on average 47.5 ± 12.3 mg AFDW m^{-2}). The polychaete biomass, on average 161.9 ± 41.8 mg AFDW m^{-2}, represented 23% of the total. The largest proportion of the biomass (37%, on average 256.2 ± 66.2 mg m^{-2}) was made up of other organisms; *c*. 73% of this value corresponded to just one large Sipuncullida individual found in March (table 2). The major trophic guild groups (figure 6) represented were deposit feeders (on average $43.6 \pm 11.3\%$), predators (on average $27.4 \pm 7.1\%$), suspension feeders (on average $26 \pm 6.7\%$), and grazers (on average $0.04 \pm 0.01\%$).

The total macrofaunal biomass was significantly correlated to the food index (POM:TSM, $r = 0.61$; $P < 0.05$; $n = 15$).

4.   Discussion

The site studied was characterized by two main phytoplankton blooms typical of temperate areas (mainly due to diatoms), the first at the end of winter (February) and the second in autumn (November). Dinoflagellates were responsible for the chlorophyll *a* increase observed at the end of May. This increase was related to storms observed during April, which favoured the mixing of the shallow water column and therefore the resuspension of the nutrients recycled in the bottom layer. In addition, the increase in the rainfall in May could have enriched the water column with allochthonous inorganic nutrients via runoff from the Entella River.

The phytoplankton dynamics drove the seasonal fluctuations observed in the quality of the POM. Notwithstanding the moderate chlorophyll *a* contribution to the organic carbon pool, the correlation of chlorophyll *a* with both POC and PON suggested that both depended on phytoplankton biomass. The highest POM lability was observed after the spring bloom (March–May); in particular, the PCA analysis highlighted the lipid concentrations as the discriminating factor. These compounds, besides being part of the phytoplankton cells, could be related to the production of copepod eggs and to the spawning that generally occurs during the post-spring bloom and depends on the fresh food available to the copepods [37].

The highest organic-matter content in the sediments was observed in the late winter–early spring period, probably related to the phytoplankton bloom sinking. In fact, the total sedimentary organic content was correlated to the particulate carbon and nitrogen concentrations.

The trophic resources in the water column played an important role in the annual succession of zooplankton taxa, and the zooplankton biomasses also followed the typical seasonal cycle described for Ligurian coastal waters [38]. The coupling between food availability and zooplankton seasonal fluctuations in the shelf areas has already been reported [39, 40]. Herbivores responded rapidly to the diatom bloom. From the end of winter to spring, when diatoms dominated the bloom, and the water column was characterized by freshly generated organic matter and high food-index values (high POM:TSM ratio), the zooplankton was dominated by copepods such as the genera *Clausocalanus*, *Paracalanus*, and *Acartia*, which are known to be suspension-feeders and herbivores. These genera were replaced by the omnivore *Centropages* at the end of spring, when the organic matter was mainly detrital and/or composed of small phytoplankton (dinoflagellates). In summer, the predominance of omnivores in the zooplankton assemblage could be related to the dominance of the phytoplankton dinoflagellates and to the detrital condition of the particulate matter. It was principally composed of carbohydrates with a low nutritional value [41] and the highest quantity of total suspended matter, mainly terrigenous, also confirmed by Danovaro and Fabiano [5] in the interface water. Appendicularia and Cladocera, which were highly represented, are particularly well adapted to efficiently assimilating small particles [42].

The copepod density and biomass were also correlated to the food index (POM:TSM ratio), confirming the important role of the quality of the POM in limiting zooplanktonic abundance. On the contrary, notwithstanding the similar trend, no significant correlation was found between the total zooplankton biomass and the indicators of POM quality, probably due to the fact that the large mesozooplanktonic specimens were omnivores or carnivores and fed on resources other than particulate.

The seasonal fluctuations in the macrofaunal abundance seem to have been linked to the success of *Spisula subtruncata* recruitment, due to the huge number of juveniles of this species. However, we observed that the cluster analysis of the presence/absence transformed data (which dramatically reduced the weight of this bivalve on the other species) confirmed a grouping of the samplings based on seasonality [16]. In particular, the different composition observed at the beginning of May (lack of molluscs, decrease in the number of polychaetes, and increase in the number of crustaceans) seemed to be related to the coarser sediment found at that time, probably as the consequence of the late-spring storm period. In fact, the abundance of crustaceans was correlated to the mean grain size.

The good trophic condition of the water column in the spring months probably supported the high abundance and number of macrofaunal species, and explained the success of the massive settlement of the suspension-feeder bivalve *Spisula subtruncata* in March and at the end of May and the survival of juveniles. The evolution of juvenile settlement and the community abundance and species number followed the organic-matter cycle throughout the year. In the spring–summer period (figure 4), the community had a cyclical evolution starting with the two recruitments (March and end of May), and reaching maximum densities and minimum diversity. Both recruitments corresponded to the chlorophyll *a* increases of February and the end of May. However the rapidity of the response of the community and of the bivalves was different. The slowness observed in February was probably due to the low temperature of the water, unfavourable for the recruitment events [10]. However, the lack of competitors for the available food in May (no molluscs at the beginning of May) could explain the rapid response to the bloom. The settlement was followed by the post-recruitment period (beginning of April and June), critical for the survival of the juveniles. The mortality rate at the beginning of April was lower than in June (52 and 77%, respectively) probably due to the higher quality and quantity

of the food available in April, which could support a high number of juveniles. Moreover, from June, the importance of predators increased; thus, top-down and bottom-up controls could act synergetically. An increase in the importance of predators and deposit-feeders characterized the summer period. The relationship between macrofaunal density and the food supply in the water column was confirmed by the significant correlations found between abundance and particulate lipids and the indicators of organic-matter quality (POM:TSM and PRT:CHO). In contrast, the detrital fraction (CHO) was inversely correlated to the macrofaunal abundance. The community was dominated by suspension- and deposit-feeders, both depending on the production of food in the water column. However, the contribution of the microphytobenthos to the fluctuations in the quantity and quality of the sedimentary organic matter should be considered [17].

Furthermore, the total biomass seemed to be controlled bottom-up; in fact, it was significantly correlated to the food index. Macrofaunal suspension- and deposit-feeders were probably adapted to efficiently exploiting the scarce but high-quality material available. Beukema *et al.* [4] in the long-term study in the Wadden Sea found a direct control of macrobenthic biomass exerted by the phytoplankton abundance. The limitation was more evident in the functional groups that directly depend on algal food such as suspension- and deposit-feeders.

In conclusion, pelagic and benthic communities in the costal area of the Ligurian Sea mainly seem to be bottom-up controlled. The quality of the POM may shape the seasonal fluctuations of both assemblages, while the direct influence of the environmental features could be observed only on the macrobenthic assemblages (influence of mean grain size on crustaceans).

Acknowledgements

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