

Sediment structural properties mediating dominant feeding types patterns in soft-bottom macrobenthos of the Northern Adriatic Sea

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Abstract

In sediments sampled in Northern Adriatic Sea invertebrate benthic macrofauna was examined in comparison with both substratum bulk parameters (average grain size, sorting, total organic matter content) and attributes of grain size classes (specific organic matter content of dimensional fractions). The aims were: 1) to determine whether variations of community overall parameters (total spatial density, number of taxa) and in numerically dominant feeding types (deposit-feeders and suspension-feeders) patterns were related to changes in sediment general properties; 2) to evaluate whether the observed patterns of abundance for deposit- and filter-feeders had more valid correlates in specific properties of substratum dimensional fractions.

Number of taxa and animal spatial density resulted conventionally related to substratum bulk parameters while feeding types patterns in comparison with sediment total organic matter content exhibited a reciprocal negative effect; only when both feeding types and sediment structure were resolved to their specific attributes in terms of prevalence of tubicolous taxa among deposit-feeders and organic matter richness of single dimensional fractions, the analysis emphasized patterns unequally affected by specific size fractions abundance and organic matter content: deposit feeders demonstrated to be related to the presence in the substrate of intermediate grain size classes necessary for tube-building. Those intermediate fractions proved to be more adequate descriptors than average grain size or other overall sediment parameters per se of relations actually established between feeding types and the complex nature of bottom sediments.

Our results emphasize that for Northern Adriatic Sea benthic communities, sediment organic matter content may represent a factor of minor importance in comparison with other substrate attributes, for which it may be necessary a detailed analysis of sediment structure. Thus, we concluded that the complexity of soft-bottom communities may defy any simple paradigm relating macrobenthic patterns to any single sediment bulk attribute, and we propose a shift in focus towards an higher resolution of both functional groups in macrobenthic associations (as already suggested in other investigations) and of substratum structural description.

Introduction

Factors affecting animal distribution in nature still represent a critical issue in ecological research. In marine environments, analyses of soft-bottom benthic macroinfauna usually assume substratum structural and environmental properties as correlates of observed community patterns (Long & Lewis, 1987; Service & Feller, 1992; Platell & Potter, 1996). Since Thor-

son's (1957) generalizing concept of 'parallel level-bottom communities', the relationship between the distribution of infaunal invertebrates and the sediments which they inhabit has been interpreted as: 1) a cause-effect trophic relation (Sanders, 1958; Bloom et al., 1972; Lopez & Levington, 1987; Bianchi et al., 1986; Eleftheriou & Bansomford, 1989); 2) a substrate-mediated amensalistic interaction between feeding types (deposit- and filter-feeders: Rhoads &

Young, 1970; Rhoads 1974; Jaramillo et al., 1984; Weinberg, 1984; Wilson, 1981, 1991); 3) a spurious correlation biased by the indirect dependence between sediment characteristics and hydrodynamic factors, the latter actually influencing animal assemblages (Jumars et al., 1981; Fresi et al., 1983; Jumars & Nowell, 1984a, 1984b; Eckman, 1987; Snelgrove & Butman, 1994 for a review). In recent years, it has become evident that such relationship results from combined interactions among biotic (microbial activity, organic matter content, competition, predation, bioturbation, amensalism, larval settlement dynamics) and abiotic factors (grain size, hydrodynamics and chemistry of water-sediment interface layers), together with specific processes of sediment transport, resuspension and accumulation (Warwick & Uncles, 1980; Gray, 1981; Butman, 1987; Snelgrove & Butman, 1994; Hall, 1994). A strong support to these assumptions comes from the rich body of literature available on the benthic environment of northwestern Adriatic Sea: the basin geomorphological features (geology, position, shape, mean depth: Buljan & Zore-Armanda, 1976) together with the significant seasonal variation of salinity, temperature, currents, and sedimentary load induced by the Po River outflow and the discharge of a number of river mouths and coastal lagoons (Buljan & Zore-Armanda, 1976; Franco & Michelato, 1992) appear to exert an effective influence both on sediment biotic and abiotic structural features and on benthic communities patterns (e.g. Gamulin-Brida, 1967; Bedulli et al., 1983; Parisi et al., 1985; Ambrogi et al., 1989; Ambrogi et al., 1990).

Scarce efforts have been made to analyze soft-bottom macrobenthic communities (particularly in Northern Adriatic) in comparison not only with sediment overall features but also with the attributes of dimensional fractions (e.g. Ishikawa, 1989; Grebmejer et al., 1989), albeit mean particle size and total organic matter content have demonstrated to be 'super parameters' (in Gray, 1974, 1981; Fresi et al., 1983; Cocito et al., 1990; Snelgrove & Butman, 1994, *sensu* Jansson, 1967), sometimes inadequate in describing actual relationships between faunal assemblages and substratum.

The present study, as part of a wider programme of ecological investigations in the Northern Adriatic Sea (Italy), focuses on relationships between sediment and two infaunal feeding types (or guilds, *sensu* Root, 1967; Hawkins & McMahon, 1989) numerically dominating the macrobenthic community from three sites in the Po River Delta area. Several criti-

cisms have been moved, in the past, to the functional group approach: it may fail to give complete faunistic investigations of macrobenthos and may result too 'general', neglecting differences between individual species characteristics beside their trophic status (Dayton & Oliver, 1980; Levin, 1982; Weinberg, 1984); on the other hand, its effectiveness has been fully recognized in clarifying interactions between environmental factors and community structure, reduced into a simplified set of units (Gagnon & Haedrich, 1991; Simberloff & Dayan, 1991), and in revealing patterns not attributable simply to species abundances (Porras et al., 1996). Our study represents an attempt to make explicit underlying relationships between community patterns (in terms of variations of feeding types relative abundances) and substratum, shifting the focus from a) general trophic distinction among functional groups to specific tube-building activity of trophic groups dominant taxa; b) sediment overall parameters (grain size, sorting, total organic matter content) to specific attributes of dimensional fractions.

Materials and methods

From April 1995 to January 1996 three sites in Northern Adriatic Sea (site 1: 44°44.25' N, 12°27.65' E; depth: 23 m; 2: 45°08.96' N, 12°23.21' E, 26 m; 3: 45°14.75' N, 12°46.06' E, 30 m; Figure 1) were sampled for macrobenthos and sediments, using a Reineck box-corer (170 cm²) to a depth of 7 cm. Every 90 d five replicate cores per station were taken: the number of replicates and the total surface area sampled (850 cm²), in comparison with other investigations which adopted a trophic-group approach (n° replicates/total surface area in cm²: 1/200: Palacin et al., 1991; 8/145: Service & Feller, 1992; 3/104: Ambrogi et al., 1993; 10/160, 5/220: Meire et al., 1994) were judged adequate in providing effective estimates of numerically dominant species densities. Sites 1 and 2 were both situated inside the influence area of the Po River Delta and of some other rivers originating from the Alpine regions, although site 2 location was the closest to the coast (distances: site 1: 7.13 nautical miles, site 2: 4.28). Site 3 was located 23.51 nautical miles offshore, in an area scarcely influenced by the hydrographic system of the mainland.

For every sample were determined:

1) frequency distribution of grain size diameters (GSD): wet sieving was performed with distilled water on graded series of standard sieves suited to the inter-

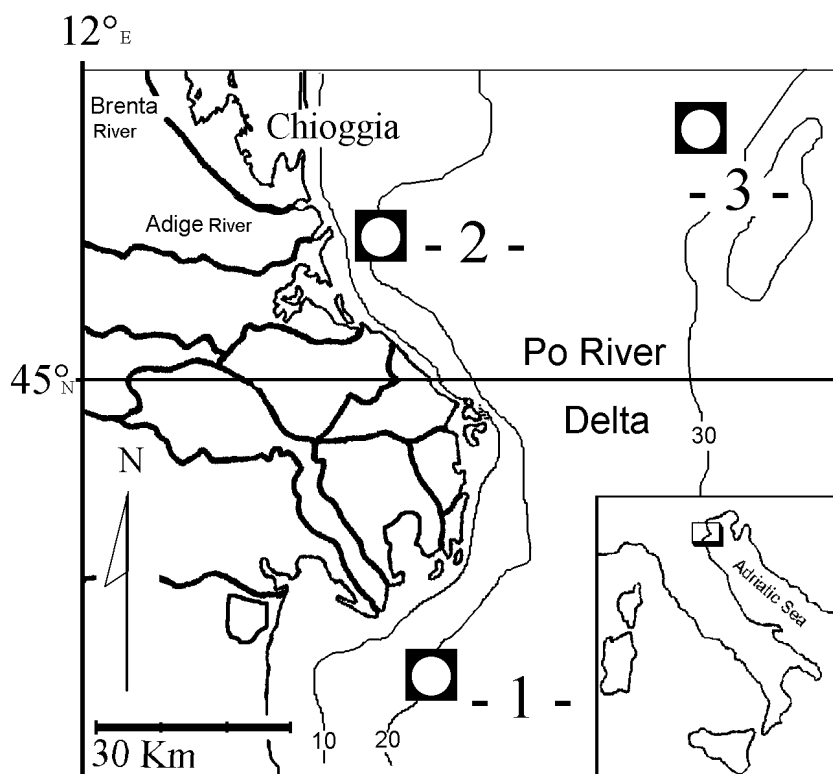


Figure 1. The Po River Delta: location of sampling points for sediment and benthic organisms.

vals of the Wentworth scale (ϕ units: -1.585 ; -0.585 ; 0.415 ; 1.415 ; 2.415 ; 3.415 ; 4.988 ; Mudroch & Bourbonniere, 1994, after Krumbein & Pettijohn, 1938). To avoid losses of organic matter, the finest fraction was oven-dried (60°C) till complete water evaporation. Every class was dried (60°C , 96 h) and weighed. Grain size frequency was expressed as percentage of the sample total dry weight (DW). The nomenclature used for sediment types is after Folk, 1974, while Shannon – Weaver informational index ($H' = -\sum \text{Pi} \log_2 \text{Pi}$) was chosen as a coefficient of substratum structure complexity (after Gray, 1974; Whitlatch, 1981): it resulted to be more sensitive than other parameters, such as $\text{QD}\phi$ or $\text{Sk}_d\phi$, for skewed or bimodal distributions (Folk, 1974, in Buchanan, 1984);

2) organic matter content, as loss of DW of every defaunated grain size class after ignition (450°C , 6 h; in Rosa et al., 1994, modified from Buchanan, 1984, to avoid volatilization of carbonates). Total organic matter content (TOM) was calculated as percentage of sample total DW, organic matter frequency distribution among size fractions as percentage of total organic matter content in each grain size fraction (OMD), and

organic matter content of each grain size class (OMF) as DW percentage of every fraction;

3) macrofauna: living organisms >0.5 mm retained during sediment wet sieving were separated from inorganic particles and fixed in ca 5% buffered formalin. All organisms were counted and identified according to the available literature to the lowest taxonomic level necessary for trophic strategy determination. Polychaeta species were grouped into feeding types according to Emson (1977), Fauchald & Jumars (1979), Gambi & Giangrande (1985), and Gambi (1989). Four large trophic categories were determined: Suspension feeders (SF), carnivores (C: including carnivores and omnivores), surface deposit feeders (SDF) and sub-surface deposit feeders (BDF). A further distinction was performed according to Woodin (1976), between non-tubicolous, mobile deposit-feeders (M) and tubebuilders of varying trophic type (T). Due to the high correlation found between SDF and BDF ($r > 0.947$, $p < 0.0001$, 10 d.f.), for further analysis they were grouped into a single feeding type (DF).

Total spatial density (n. individuals/ m^2) was calculated for each feeding type and for the whole benthic

Table 1. List of taxa found: FG: functional groups, according to Woodin, 1976; FT: feeding types. Asterisks indicate qualitative data of taxa presence according to Soyer's (1970) classification. (***) = abundant, presence in samples > 50%; xxx = constant, presence between 25 and 50%; xx = accidental, presence < 25%.

	FG	FT	Site 1	Site 2	Site 3
GASTROPODA					
<i>Hinia incrassata</i> (Mull.)	M	C		xxx	
<i>Turritella communis</i> (Risso)	M	SDF	xx	xx	xx
<i>Fusinus rostratus</i> (Olivi)	M	C			xx
<i>Cylichna cylindracea</i> (Pennant)	M	C		xx	
BIVALVIA					
<i>Ruditapes</i> sp.		S F	***	***	***
<i>Tellina pulchella</i> (L.)		S F			***
<i>Acanthocardia aculeata</i> (L.)		S F			***
<i>Venus verrucosa</i> (L.)		S F			xxx
POLYCHAETA					
<i>Hyalinoecia</i> sp.	T	SDF			xx
<i>Hyalinoecia tubicola</i> (Muller)	T	SDF			xxx
<i>Lumbrineris fragilis</i> (Muller)	M	C			xxx
<i>Lumbrineris</i> sp.	M	C			xx
<i>Maldane sarsi</i> (Malmgren)	T	BDF	***	***	***
<i>Melinna palmata</i> (Gruben)	T	SDF	***		***
<i>Nephtys hystericis</i> (McIntosh)	M	C	***	***	***
<i>Owenia fusiformis</i> (Delle Chiaje)	T	SDF	***	***	
<i>Sternaspis scutata</i> (Renier)	M	BDF		***	***
<i>Tharyx multibranchiis</i> (Grube)	T	SF		***	
<i>Tharyx</i> sp.	T	SDF			xx
CRUSTACEA					
<i>Gammarus insensibilis</i> (Stock)	M	SD F		***	xx
<i>Dyastilis</i> sp.	M	SDF		xx	
<i>Caprella</i> sp.	M	C		xx	
<i>Corophium</i> sp.	T	S F		xx	
<i>Liocarcinus arcuatus</i> (Leach)	M	C	xx		
ECHINODERMATA					
<i>Ophiura texturata</i> (Lamarck)	M	SDF			***
<i>Ophiura</i> sp.	M	SDF		xx	
SIPUNCULA					
<i>Sipunculus</i> sp.		C	xx	xx	***

community, Quantitative Trophic Dominance (QTD) was determined as percentage of individuals belonging to a given feeding type (Boudouresque, 1971), while species number (S) was utilized as an index of species richness (Magurran, 1988). Highly motile epifauna (crabs, amphipods, cumaceans, and echinoderms) together with 'accidental' taxa (*sensu* Soyer, 1970; Table 1) were included only in species number and total spatial density calculations.

For parametric statistical analysis, all percentages were normalized as $x = \arcsin \sqrt{P/100}$. Where transformation failed to meet the assumptions of nor-

mality of error terms and homogeneity of variance (Cochran's test), nonparametric 1-WAY ANOVA by ranks (Kruskal – Wallis ANOVA, KW in the text) was performed.

Results

Characteristics of bottom sediments

Grain size analysis demonstrated a scarce influence of seasonality on GSD (KW among seasons, site

Table 2. Summary of sedimentary parameters (means, SE in brackets: TOM, total organic matter content; H' , sorting index.; OMF, organic content of specific fractions) for the three sites in the four seasons (Sp: spring; Su: summer; fa: fall; Wi: winter). Grain size classes are expressed in ϕ units; for OMF values standard errors are not shown.

Site	Season	TOM (%)	H'	OMF (%)							ϕ units
				- 1.6	- 0.6	0.42	1.42	2.42	3.42	4.99	
1	Sp	6.70 (0.46)	0.07 (0.01)	6.05	16.90	21.00	16.44	31.26	15.29	6.59	
	Su	10.52 (0.77)	0.04 (0.01)	5.13	9.06	8.90	17.45	16.92	15.93	10.51	
	Fa	6.96 (0.23)	0.09 (0.01)	3.70	7.14	12.05	10.99	13.21	17.14	6.94	
	Wi	8.24 (0.23)	0.09 (0.02)	5.47	9.38	10.83	10.61	12.59	12.53	8.25	
2	Sp	3.64 (0.53)	0.25 (0.03)	16.62	42.58	50.07	43.84	35.52	4.33	3.43	
	Su	11.75 (0.18)	0.33 (0.02)	5.71	22.26	29.61	22.61	20.91	1.89	12.64	
	Fa	7.18 (1.34)	0.27 (0.04)	13.55	41.68	44.87	38.42	20.89	4.01	7.22	
	Wi	13.34 (2.11)	0.40 (0.03)	9.25	24.50	25.34	22.18	23.39	2.79	14.65	
3	SP	2.33 (0.31)	1.58 (0.02)	5.47	4.05	3.34	0.81	0.78	1.00	5.73	
	Su	2.16 (0.05)	1.03 (0.05)	2.17	2.62	2.19	1.27	0.44	1.10	7.03	
	Fa	2.95 (0.29)	1.46 (0.04)	2.96	2.31	2.42	1.71	0.83	1.15	6.72	
	Wi	3.25 (0.14)	1.48 (0.03)	2.68	2.82	3.26	1.38	1.00	1.74	8.21	

Table 3. Pearson product-moment correlation coefficients calculated between sediment parameters (GSD: grain size distribution among classes; OMD: organic content distribution among classes; OMF: organic content of specific fractions) for the three sites. * $p < 0.05$; ** $p < 0.001$.

Site		1			2			3		
		GSD	OMD	OMF	GSD	OMD	OMF	GSD	OMD	OMF
1	GSD	*								
	OMD	0.98**	*							
	OMF	0.37	0.38	*						
2	GSD	0.99**	0.99**	0.38*						
	OMD	0.99**	0.99**	0.40	0.99**	*				
	OMF	0.96**	0.95**	0.59	0.96**	0.96**	*			
3	GSD	-0.38	-0.30	0.39	-0.36	-0.31	-0.28	*		
	OMD	-0.40	-0.52	-0.23	-0.40	-0.44	-0.44	0.26	*	
	OMF	0.80*	0.74	0.18	0.79*	0.75	0.65	0.75	-0.20	*

1: $H=2.15$; site 2: $H=1.13$; site 3: $H=3.01$; differences were always NS; Figure 2): sites 1 and 2 were both characterized by well-sorted, silt-clay sediments (Table 2, Figure 2) dominated by the finest fraction ($\phi=4.99$, site 1: $98.89 \pm 0.22\%$; site 2: $91.51 \pm 1.61\%$, annual mean \pm SE). GSD of sediment from the two sites showed non-significant differences (KW: $H=3.21$, NS), even if site 2 showed higher values than site 1 for grain size $\phi=3.42$ (site 2: $7.82 \pm 1.56\%$, site 1: $0.39 \pm 0.18\%$, annual mean \pm SE). Site 3 was characterized by a significantly poor sorting (Table 2, Figure 2) and a different GSD from the other sites: the cumulative curve (Figure 2: silty-sand type) suggests a bimodal distribution, characterized by the preva-

lence of intermediate size classes ($0.42 \leq \phi \leq 2.42$: $58.58 \pm 2.87\%$, annual mean \pm SE) and a significant presence of the coarsest fractions ($\phi \leq -0.58$, $6.31 \pm 1.78\%$, annual mean \pm SE). Results of correlations among sediment parameters are given in Table 3. For site 1 and 2 significant relationships were found between GSD and OMD, while for site 3 no correlation occurred. TOM analysis evidenced significant variations among both sites and seasons (2-WAY ANOVA: among sites: $F=71.63$; among seasons: $F=13.89$; sites – seasons: $F=6.44$, $p < 0.001$); site 3 registered the lowest TOM (site 1: $8.1 \pm 1.00\%$; site 2: $8.98 \pm 2.54\%$; site 3: $2.67 \pm 0.29\%$: annual mean \pm SE; 1-WAY ANOVA, contrast analysis,

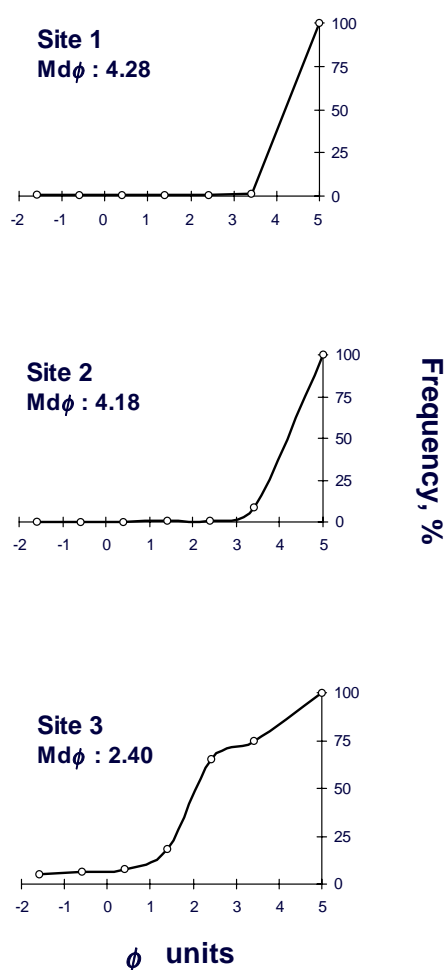


Figure 2. Sediment particle size analysis: cumulative curves and median particle diameters ($Md\phi$) of the three sites. Kruskal – Wallis ANOVA among sites: 1–2: N.S.; 1–3: $H=28.38$, $p < 0.0001$; 2–3: $H=26.11$, $p < 0.0001$.

Table 4. 2-Way ANOVA results from analysis of specific fractions parameters among sites and seasons. Only site-season effects (6 d.f.) are reported. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$.

ϕ	GSD	OMD	OMF
-1.58	5.08*	12.49***	1.64 NS
-0.58	7.08**	10.16***	2.83*
0.42	7.36**	6.14**	2.72*
1.42	16.65***	3.24*	6.00**
2.42	28.75***	0.95 NS	3.37*
3.42	4.64*	1.25 NS	3.30*
4.99	8.06***	2.14 NS	5.35*

$F=142.94$, $p < 0.0001$) and the lowest OMF values observed in all the fractions analyzed (Table 2, KW among annual means, $H=12.25$, $p < 0.005$); Site 2 differed from site 1 only for the significant higher OMF of the coarsest fractions ($\phi < -0.58$: KW: $H=10.096$, $p < 0.01$). In Table 4 the results of comparisons among site/seasons (2-WAY ANOVA) in every grain size fraction are shown. GSD showed great differences for the finest ($\phi=4.99$) and for intermediate fractions ($1.42 \leq \phi \leq 2.42$), on the other hand OMD differences among the finest classes ($\phi=4.99$), were found significant, while the coarsest fractions ($\phi \leq -0.58$) demonstrated to be particularly variable. OMF showed to be significantly different for all the considered fractions, with the exception of $\phi = -1.58$. Only fractions showing significant site/season effects were considered, and tested for correlation with feeding types patterns.

Characteristics of macrobenthos

A total of 1605 individuals, belonging to 27 taxa, were collected from the three sampling points. Of these, 12 taxa comprised over 98.43% of total animal abundance (Table 1, 'abundant' and 'constant' taxa). Site 3 showed the highest number of taxa (19) regarding sites 1 (8) and 2 (14). Among deposit-feeders, four species of tubicolous polychaeta – *Hyalinoecia tubicola* Muller, *Maldane sarsi* Malmgren, *Melinna palmata* Gruben, *Owenia fusiformis* Delle Chiaje – collectively outnumbered other groups in the three sites (Site 1: 66.7%; Site 2: 87.5%; Site 3: 96.9%: percentages of individuals total number). On site 1 and 2 *Ruditapes sp.* represented the dominant species among suspension-feeders (Site 1: 98.5%; Site 2: 97.6%), while on site 3 besides *Ruditapes sp.* (61.4%) also *Tellina pulchella* (15.38%) and *Acanthocardia aculeata* (13.23%) were recorded. SF dominated macrobenthic communities of coastal sites, while on site 3 DF prevailed (Table 1, 5). Analysis of general trends showed for animal spatial density a positive variation with sediment TOM ($R=0.626$, 10 d.f., $p < 0.05$), while a negative correlation was assessed with heterogeneity H' index ($R=-0.601$, 10 d.f., $p < 0.05$). Feeding types patterns showed for SF a positive relationship with TOM, whereas deposit-feeders were characterized by an inverse relation (Figure 3). Further comparisons of feeding types patterns to GSD and OMD among size fractions are reported in Table 6. Both trophic groups exhibited strong interactions with sediment parameters, although in some cases such relationships are inverse: DF were inversely related both to GSD and OMD of the

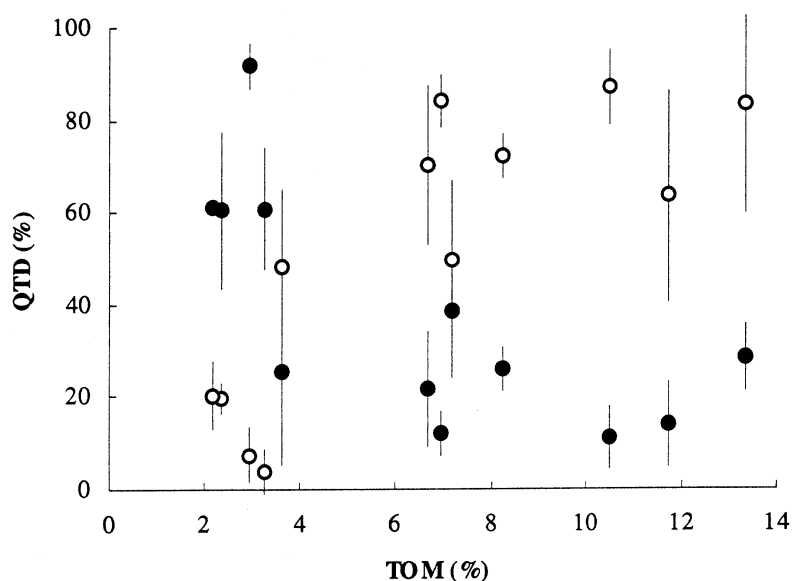


Figure 3. Relationships between feeding types QTD (% of total infaunal benthos: mean \pm 1 S.E.) and sediment total organic content, TOM. Suspension-feeders (\circ): $R=0.776$, 10 d.f., $p < 0.01$; deposit-feeders (\bullet): $R = -0.870$, 10 d.f., $p < 0.001$.

Table 5. Summary (means, SE in brackets) of community parameters (spatial density and QTD, Quantitative Trophic Dominance, of feeding types) among sites and seasons. SF: suspension feeders; DF: deposit feeders.

Site	Season	Spatial density (n.ind/m ²)		QTD			
				SF	(%)	DF	(%)
1	Sp	980.39	(245.69)	70.09	(17.41)	21.68	(12.51)
	Su	1823.53	(500.29)	86.94	(8.08)	10.92	(6.65)
	Fa	1803.92	(306.28)	84.14	(5.70)	11.99	(4.96)
	Wi	1196.08	(19.61)	72.22	(4.91)	26.11	(4.76)
2	Sp	960.78	(402.32)	47.86	(17.11)	25.71	(20.50)
	Su	2039.22	(98.04)	63.33	(22.73)	13.89	(9.00)
	Fa	1137.25	(103.75)	49.53	(17.15)	38.69	(14.58)
	Wi	901.96	(226.13)	83.33	(23.57)	28.21	(7.25)
3	Sp	745.10	(137.25)	19.77	(3.22)	60.38	(17.03)
	Su	803.92	(109.17)	20.42	(7.52)	60.83	(1.02)
	Fa	1156.86	(494.88)	7.41	(6.00)	91.61	(5.15)
	Wi	568.63	(215.69)	3.92	(4.80)	60.78	(13.21)

finest class ($\phi = 4.99$), while demonstrated to be positively correlated to GSD of coarse and intermediate size fractions ($\phi \leq 2.42$), but only to corresponding OMD of intermediate sizes ($0.42 \leq \phi \leq 0.42$); SF showed a behaviour towards OMD and GSD substantially opposite, as expected due to the inverse, rough correlation between DF and SF ($R = -0.643$, 10 d.f., $p < 0.05$). On the other hand, comparison of feeding types pat-

terns to OMF, showed for DF a negative relationship to OMF of intermediate classes ($0.42 \leq \phi \leq 0.42$; Figure 4), while SF relations were non-significant (max $R = 0.451$, 10 d.f., always NS).

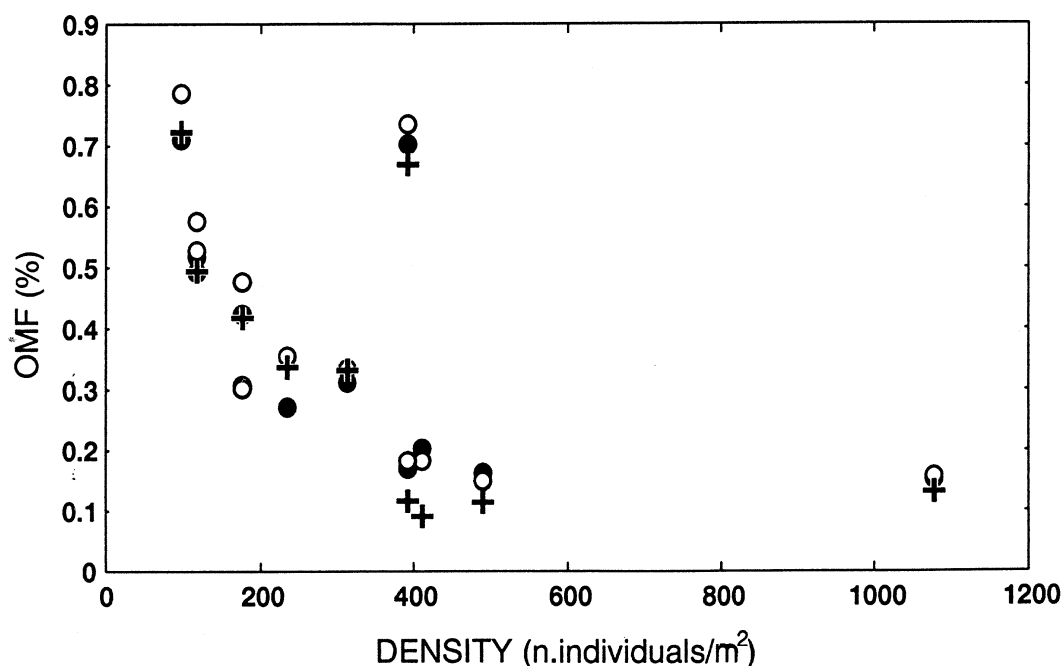


Figure 4. Relationships between variations in organic content of single fractions (OMF) and deposit-feeders density in sediment samples. $\phi=0.42$ (●): $R = -0.644$, $p < 0.05$; $\phi=1.42$ (○): $R = -0.676$, $p < 0.05$; $\phi=2.42$ (+): $R = -0.708$, $p < 0.01$.

Table 6. Pearson product-moment correlation coefficients calculated between sediment parameters (GSD: grain size distribution among classes; OMD: organic content distribution among classes) and feeding types densities. * $P < 0.05$; ** $P < 0.01$.

ϕ units	GSD		OMD	
	DF	SF	DF	SF
-1.585	0.63*	-0.47	0.53	-0.49
-0.585	0.66*	-0.61*	0.53	-0.67*
0.415	0.77**	-0.65*	0.63*	-0.77**
1.415	0.70**	-0.59*	0.76**	-0.67*
2.415	0.68*	-0.62*	-	-
3.415	0.25	-0.86**	-	-
4.988	-0.65*	0.73**	-0.61*	0.74**

Discussion

The sampling method adopted in this study proved to be generally effective for the substrata structural analysis in marine environments: a very low variability of sediment parameters between replicas was detected, although macrobenthos data appeared much more variable, in spite of the number of replicas (5) sampled. Such variability could be, for some animal groups (especially infaunal), the expression of heterogeneous

spatial distributions, while for others (fast moving, epifaunal specimens) it could represent the effect of bias in the sampling technique (McIntyre et al., 1984). In this study, besides determinations of total animal density could have been underestimate, the relative percentages of infaunal feeding types shouldn't have been affected by the sampling method; yet the significant variability could actually represent the effect of a non-random spatial distribution of individuals in sediments (Vézina, 1988).

Three preeminent results emerged from data analysis:

1) fractions specific attributes, more than overall parameters (Md ϕ sorting coefficient H' , TOM) permitted an effective characterization of sediments of the three sampling sites; 2) co-occurring variations in community parameters (number of taxa, organism spatial density) and bulk substrate properties confirmed general animal-sediment relationships already recognized in literature; comparison of DF and SF trends evidenced a negative relationship, while analyses of relations between feeding types and sediment bulk features evidenced for deposits organic content, TOM, a negative effect on DF; 3) the analysis of relationships between characteristics of dominant taxa constituting DF and specific attributes of sediment fractions per-

mitted to relate animal distribution patterns to specific size availability in substratum: the requirement of appropriate grain sizes for tube-building activity more than sediment trophic value turned out as the prevailing determinant of DF patterns.

Site 1 and 2 showed similar cumulative curves (Figure 2), $Md\phi$, heterogeneity H' indexes and TOM. On the other hand, analysis of grain sizes features permitted a more effective characterization: site 2 significantly higher presence of organic matter in the coarsest classes suggested a dependence (probably due to its closeness to the littoral and/or to hydrodynamic factors) on coastal sources of organic detritus. Such hypothesis seems to be grounded by the constant presence on site 2 of *Gammarus insensibilis* Stock, a detritivorous amphipod widely distributed in seagrass and macrophyte meadows all over Europe (Stock, 1967). Only in the Mediterranean Sea it has been recorded in marine environments at depths greater than 15 m, characterized by a significant presence of alloctonous, coast-originated plant detritus (Sheader & Sheader, 1985). The low total organic content registered for site 3 was consistent with canonical marine sedimentation theories – sediment organic content decreases as the distance from the shore increases – and available literature on Northern Adriatic (Bortoluzzi et al., 1984) but the anomalous sorting H' index suggested peculiar bottom conditions. The sampling area probably occurred on pleistocenic emergences of organogenic deposits: such extraneous facies are common findings in Northern Adriatic Sea, and they are constituted by elements of coarse grain found in open sea areas, not in equilibrium with the sedimentation processes (Pigorini, 1969; Buljan & Zore-Armanda, 1976; Brambati et al., 1984). The cumulative curve and correlations reported in Table 3 give support to such an assumption: the absence of relation between GSD and OMD (and the significant correlation of GSD of site 1 and 2 with site 3 OMF) suggests for grain size partitioning among dimensional classes a weak relation to present depositional processes, deeply affected by Po River inputs of fine suspended particulate, which influence both OMD in sediments (Dal Cin, 1983; Bortoluzzi et al., 1984) and GSD in those areas (site 1 and 2) where deposits structure is not affected by anomalous facies.

Relationships between deposit bulk features and animal density or number of taxa (point 2) is well documented (Gray, 1974, 1981; Snelgrove & Butman, 1994 and literature cited); in general, sandy and heterogeneous sediments present higher species richness than

clayish, homogeneous fine sediments ('spatial heterogeneity' of sandy substrates, *sensu* Pianka, 1966; Sanders, 1968; cited in Boesch, 1973). Moreover, fine deposits – characterized by relevant TOM – determine trophically enriched bottom conditions which facilitate in macrobenthos higher densities than coarse sediments, poor in organic matter (Longbottom, 1970; Pearson & Rosenberg, 1978; Ishikawa, 1989, Snelgrove & Butman, 1994). Our results are consistent with these assumptions, and with evidences reported for Northern Adriatic Sea macrobenthos (Stefanon & Boldrin, 1982; Ambrogi et al., 1990). Benthic communities of the area demonstrate to be sensitive both to TOM in sediments (a positive relation which suggests that, even if the whole region receives important organic matter inputs from a number of sources, sediment enrichment has not yet reached a condition of trophic pollution: Pearson & Rosenberg, 1978), and to structural attributes ($Md\phi$, sorting coefficient H'): in our study the negative variations between sorting coefficient and animal density co-occurs with a positive increase of S, number of taxa. Site 3 showed on coarse sandy deposits a community characterized by a higher S and a lower spatial density than sites 1 and 2, where on fine sediments a less varied, but denser community established.

The analysis of the relationships among feeding types and deposits properties showed for filter-feeders a preference for silt-clayish, highly organic substrates, while deposit-feeders preferred sandy, poorly organic sediments. Although deposit-feeders preference for sandy sediments is well documented (e.g., Young & Rhoads, 1971; Nicolaidou & Papadopoulou, 1989), the negative relation (Figure 3) between them and organic matter in the substrate cannot be explained according to direct trophic interaction assumptions (Lopez & Levinton, 1987): organic matter positive variations in sediment seems to exert, instead of a direct improvement of deposit-feeders density, a negative effect on it. The inverse relation existing among intermediate fractions OMF ($0.42 \leq \phi \leq 0.42$) and DF density showed in Figure 4 supported the hypothesis that they could be affected by the properties of specific grain size classes. As a matter of fact the inverse relationship among deposit-feeders and intermediate fractions organic content excluded a trophic dependence or a selective preference for organic particles on a dimensional basis (Fenchel et al., 1975; Whitlatch, 1980, 1981). On the contrary, availability of specific grain size appeared to be crucial: the generalized dominance of tubicolous deposit-feeders in the three sites studied, but the domi-

nance on a community scale only on site 3 (Table 1 and 5), suggested that both their presence and density are mainly regulated by coarse fractions availability in the substrate (point 3). Laboratory studies have repeatedly demonstrated for tubicolous polychaeta a strong preference for intermediate granulometric fractions, for both adults (Wilson, 1952; Gray, 1967, 1971; Sendall et al., 1995), and larval stages (Gray, 1971; Scheltema 1974; Butman 1987 for a review). Moreover, the available information on the species collected in this survey reports effective grain size selection in tube-building activity (Fauchald & Jumars, 1979, and literature cited; in Gambi, 1989, for example, on *Owenia fusiformis* tubes are clearly recognizable highly sorted sediment particles), suggesting the presence of optimal fractions needed for tube-building as controlling factor both for larval settlement and/or for adults permanence in the substrate (Gray, 1974, 1981).

Because of the correlative nature of this study, results lead to non-conclusive statements regarding suspension-feeders pattern variations, i.e. if they were due to abiotic environmental factors or to amensalistic interactions with deposit-feeders. In fact, the strong correlation with OMD of the finest fractions ($\phi = 4.99$) showed on Table 6 can express both a dependance of SF on availability of organic matter in the finest class (which, in turn, relates SF to primary production in the water column: in fact a significant benthic-pelagic coupling have been demonstrated for Northern Adriatic Sea: Ott, 1992) or a negative effect exerted by DF on SF distribution: evidences are probably biased by the high covariation among sediment parameters. Yet, the general assumption of suspension-feeders preference for sandy bottoms (Jaramillo et al., 1984; Ishikawa, 1989; Snelgrove & Butman, 1994) and the negative trend in response to deposit-feeders increasing density observed in our study, suggests an indirect exclusion, a case of amensalism as Rhoads & Young (1970) and Rhoads (1974) had assumed, and which is recognizable in other investigations on feeding types patterns in the Po River Delta area (Bedulli et al., 1983; Ambrogi et al., 1989); moreover, available literature on sampled taxa natural history and biological cycles allowed to exclude that the observed variations in density of feeding types patterns (together with relationships between deposit-feeders and intermediate fractions attributes showed in Figure 4) were biased by seasonal recruitment: in this area, in fact, both SF and DF are characterized by almost synchronous late spring-summer peak densities, decreasing throughout summer and fall and reaching minimum

values in winter (Bedulli et al., 1983). The data thus suggest a sediment mediated interaction between feeding types in which specific substrate properties, and not trophic availability, act as the prevailing causative factor determining community patterns. The results of the present study indicate a different interpretation clue for the analysis of relationships between macrobenthic fauna and sediment: the recorded patterns for the benthic community, the effect and the importance of the different trophic groups proved to be linked not only to the overall characteristics of deposits analyzed, but also to the interaction between the properties of single granulometric fractions and the specific requests of each group of organisms. Analysis of benthic community patterns based on trophic groups, thus, require to consider not only the characteristics of individual taxa, as already stated by Brenchley (1981), Levin (1982) and Weinberg (1984), but also an advanced resolution of substrate attributes, regarding bottom sediments not only as undifferentiated homogeneous matrixes but also as composite, structured environments resulting from a combination of biotic and abiotic factors which indirectly reflect on fraction abundances and their organic richness. Such an approach, taking into account what a benthic organism actually needs and what actually encounters in nature, could offer a more biologically realistic assessment of effective influences of sediment on soft-bottom communities.

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