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Spatial variability and dynamics of macrobenthos in a Mediterranean delta front area: The role of physical processes

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Abstract

Benthic communities in delta fronts are subject to burial risk because of high riverine sediment discharges and to substrate instability due to deposition of fine sediments at shallow depths. This study examines the spatial distribution of macroinfauna in the subaqueous deltaic depositions of a small river in the eastern Mediterranean (the Spercheios river, Maliakos Gulf, Aegean Sea) in relation to environmental variables in the water column and sediment. Samples were taken at eight stations in January, May, August and November 2000. From late winter to spring enhanced phytoplanktonic biomass, elevated suspended load and poorly sorted sediments showed a simultaneous influence of riverine discharges and hydrodynamics on the benthic system. In contrast, from summer to autumn oligotrophy in the water column and low hydrodynamic regime were observed. Total abundance, biomass and numbers of benthic species were positively correlated with distance from the river but negatively correlated with suspended inorganic particles and sediment skewness. Species from different functional groups, ranging from surface-living opportunists to burrowers and predators, coexisted at each station. However, suspension feeders were numerically suppressed near the river mouth. Non-parametric multivariate regressions showed that the variance in the species data was explained by environmental variables to a level ranging from 53 to 69%. This indicated a strong link between the macrofauna and the delta front environment. The variables used as measures of hydrodynamics and turbidity (i.e. sediment skewness and sorting, suspended material and transparency) displayed great explanatory power. The results of the present study show that the distribution of species is related to fluctuations in hydrodynamic regime that influence substrate characteristics. The study also demonstrates that sediment discharges of small temperate rivers can determine species composition in the delta front and have a detrimental impact on the community at short distances from river outflows.

Keywords: Deltaic deposits; Macrofauna; Multivariate regression; Impact; Mediterranean
Regional terms: Greece; Aegean Sea; Maliakos Gulf

1. Introduction

Deltas form where sediment input from rivers exceeds sediment removed by waves and tidal currents. Climate, elevation, vegetation and geomorphology of the catchment area as well as the hydrodynamic regime

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at the coast where rivers discharge influence considerably deltaic progradation to the sea and subaqueous sedimentation. In terms of global sediment budgets to the ocean, sediment fluxes from small (drainage basins $<10^4$ km^2) mountainous rivers, i.e. draining mountainous areas and having their catchments adjacent to marine basins, range from 90 to 4 150 t km^{-2}, values some four times higher than fluxes from major world rivers (Milliman and Syvitski, 1992). Although small rivers drain only about 20% of the land area, they number in the many thousands, thus raising the concern not only about their contribution to fluvial discharges to the sea but also for their impact on biological communities. This concern is based on evidence that increased terrestrial sediment deposition in the coastal zone caused by changes in the land use in the catchment areas of small rivers (i.e. deforestation, intensive agriculture and urbanization) are detrimental to the biodiversity and ecological value of estuarine and coastal habitats (GESAMP, 1994; Thrush et al., 2004).

Europe is generally regarded as having the lowest sediment flux to the sea (Milliman, 2001). However, high annual yields, usually exceeding 1000 t km^{-2}, have been reported for the short rivers draining the Alps and Caucasus mountains south to the Mediterranean and the Black Sea, respectively (Milliman and Syvitski, 1992). Such yields have also been measured in small rivers of Oceania and western South America and are among the highest in the world. Sediment discharge rates in south European rivers usually peak within a few days after heavy rainfall during autumn and winter and sudden snow melt during early spring (Milliman, 2001). It has been shown that fluvial sediments discharged in the Mediterranean Sea are dispersed in extensive river plumes forming bottom nepheloid layers with high concentrations of suspended material (Poulos et al., 1996b and literature cited therein). However, estimating the amount of fluvial sediments delivered along narrow shelves associated with active margins, as in southern Europe, can be complicated by episodic events (e.g. flash floods and earthquakes) and / or the escape of the sediment to deeper basins (Milliman and Syvitski, 1992). Therefore, despite the elevated yields and bedloads, Holocene deltaic accumulation rates at the foreset beds of mountainous European Mediterranean rivers are relatively low and range between 3 and 6 m over the last 7000 years (Poulos et al., 1996a). These values are similar to those reported by Stanley (1988) for the Nile subaqueous delta (after the Aswan dam construction). However, these rates are about 30 to 200 times lower than those of major world rivers that discharge their sediments into passive margins and act as point sources for sediment influx, such as the Amazon and Mississipi (Milliman and Syvitski, 1992).

In intertidal deltaic systems, even low terrigenous sedimentation can alter the geochemical and nutritional characteristics of the sediments and hence the composition and potential for recovery (Cummings et al., 2003) and post-settlement behavior of the macrofauna (Cummings and Thrush, 2004). Accordingly, studies at a community level support evidence that intertidal benthic communities respond to thin terrigenous deposits (Lohrer et al., 2004). On the other hand, studies in the subtidal deltaic deposits of major rivers, such as the Amazon and Changjiang, have shown that species richness and trophic diversity of benthos are functions of the intensity of natural disturbance caused by sediment discharges, and hence the distance from the river mouth and the season, and resuspension (Rhoads et al., 1985; Aller and Aller, 1986; Aller and Stupakoff, 1996).

Three areas can be distinguished with respect to sedimentary shelf processes from the river mouth to the outer shelf: the delta front area, the plume area, and the shelf area outside the river influence (see conceptual model by Rhoads et al., 1985). In the delta front area, benthic organisms are subject to burial risk and sediment instability due to the high concentrations of suspended particles discharged from the river, the fine-grained sedimentary environment and the small depth. As a result, the macrofaunal community is poor and mainly consists of small early colonising species, as well as large burrowing species that are scarce but persistent. In the plume area, as well as in the delta front area after periods of low discharges, higher standing stocks of benthic populations are found, as they take advantage of the high nutrient inputs, consisting of a mosaic of species (early colonisers and more persistent species). In the outer shelf region, although sedimentation and resuspension are reduced, the low food inputs to benthos result in low benthic standing stocks. Field studies (Alongi et al., 1992; Wijsman et al., 1999) have provided supporting evidence that sedimentary processes in coastal areas influenced by smaller rivers are also related to the distance from riverine sources. However, benthic community structure in the subtidal deltaic depositions of small mountainous rivers is usually examined from the perspective of eutrophication impact, food inputs and biotic interactions (Albertelli et al., 1998; Moodley et al., 1998; Simonini et al., 2004) rather than the impact of physical processes on the sedimentary environment, such as riverine sedimentation and resuspension (Mancinelli et al., 1998).

Deltas in the eastern Mediterranean are small compared with those of the large river systems of the world. They are, however, well-developed, especially when formed in shallow, protected and tectonically stable receiving embayments, such as those in the northern Aegean Sea, where the high sediment yield and microtidal regime allow the dominance of fluviatile over marine-induced transport processes (Poulos et al., 1993, 1996a). This study examines the species composition and distribution of macroinfauna in the subtidal deltaic depositions of a small mountainous river in relation to distance from sources of riverine sediment inputs and to environmental variables in the water column and the sediment in a coastal area in the Aegean Sea (Maliakos Gulf, Greece). Maliakos is a shallow semi-enclosed embayment which receives terrestrial fine-grained sediment and inorganic inputs after heavy rainfall, especially from late autumn to spring. This, coupled with the anticlockwise water mass circulation, results in a highly turbid but well-mixed water column throughout the year, enhanced phytoplanktonic biomass in late winter, consistently high organic carbon levels in the sediment and fluctuating depositional and hydrodynamic regimes. Simultaneous studies on the dynamics of macrofauna body size in this delta front area demonstrated that community size structure is influenced by distance from the river mouth (Akoumianaki et al., 2006). In the present study, the environmental variables chosen for the analysis are those that can be recorded on spatial and temporal scales in relation to the fluctuations of riverine discharges and that are likely to be related to macrofauna species distribution. The influence of fluvial sediments on community structure was assessed by taking into account distance of each station from three different (in terms of water management and sediment yield) points of riverine sediment discharges, fed by the same catchment area. This also allowed weighing the influence of small rivers on sedimentary processes and benthic response with respect to the conceptual model of Rhoads et al. (1985). Because delta front ecosystems occur at the lower end of catchment areas, such areas are appropriate monitoring locations for the detection of human impacts within catchments and from land-based activities. Predictions can thus be made on the response of macroinfauna to the complex deltaic environment in terms of species diversity and functional role in the biogeochemical cycles.

2. Materials and methods

2.1. Study site

The study was conducted in 2000 in the inner Maliakos Gulf (38°45′N; 22°31′E), a 91.5 km^2 semi-enclosed shallow (25 m maximum depth) marine protected area that receives the discharges of the Spercheios river, a small mountainous river draining an area of 1664 km^2. The inner Maliakos communicates with the Aegean Sea through the outer Maliakos Gulf (Fig. 1a, b). Mean annual freshwater discharge rate from the main mouth of the Spercheios river at the ‘birdfoot’ delta (Fig. 1c, point 1) is 68 m s^{-1} and approximately 805 t km^{-2} of sediment are annually exported to the sea (Poulos et al., 1996b). The construction in 1958 of a spillway discharging north of the Spercheios river mouth had in 2000 led to the propagation of 0.94 km^2 of land into the gulf (Fig. 1, point 2), while irrigation for agricultural purposes has decelerated the propagation of the previously active ‘birdfoot’ delta. Sediments are also discharged from a small tributary of the Spercheios river in the southern part of the inner Maliakos Gulf (Fig. 1, point 3). Mean annual precipitation during the years 1990 – 1999 reached 535 mm but it was only 285 mm in 2000, the year of the present study (Local Meterological station, Greek Ministry of the Environment). Maximum and mean tidal range in the area is 90 and 31 cm, respectively. The Maliakos Gulf is aligned with the dominant wind direction in the region, which is from the west and the northwest, thus causing the anticlockwise circulation pattern (Fig. 1b), the homogenisation of the water column throughout the year and the fast turnover of the water masses that results in a seawater salinity range close to that of the open sea, which is above 38 (Christou et al., 1995).

2.2. Sampling design

Samples were taken at eight stations during four cruises covering the seasonal range of discharge conditions: peak discharge in January (J), falling discharge in May (M), low discharge in August (A) and rising discharge in November (N) (Fig. 1, Table 1). To examine spatial changes in environmental variables and the community, stations spanned the northern and southern parts of the inner Maliakos Gulf, providing a measure of the influence of water mass circulation and local processes along the delta front area. Guidelines for the position of the stations with respect to distance from the main river mouth (point 1 in Fig. 1c) were obtained from previous knowledge on bathymetry and spread of buoyant plumes (Poulos et al., 1996b) as well as density range of plankton organisms along the inner and outer Maliakos Gulf (Christou et al., 1995), according to which a zone of high turbidity and impacted plankton communities occurs between 1 and 2 km away from the main river mouth, i.e. point 1.

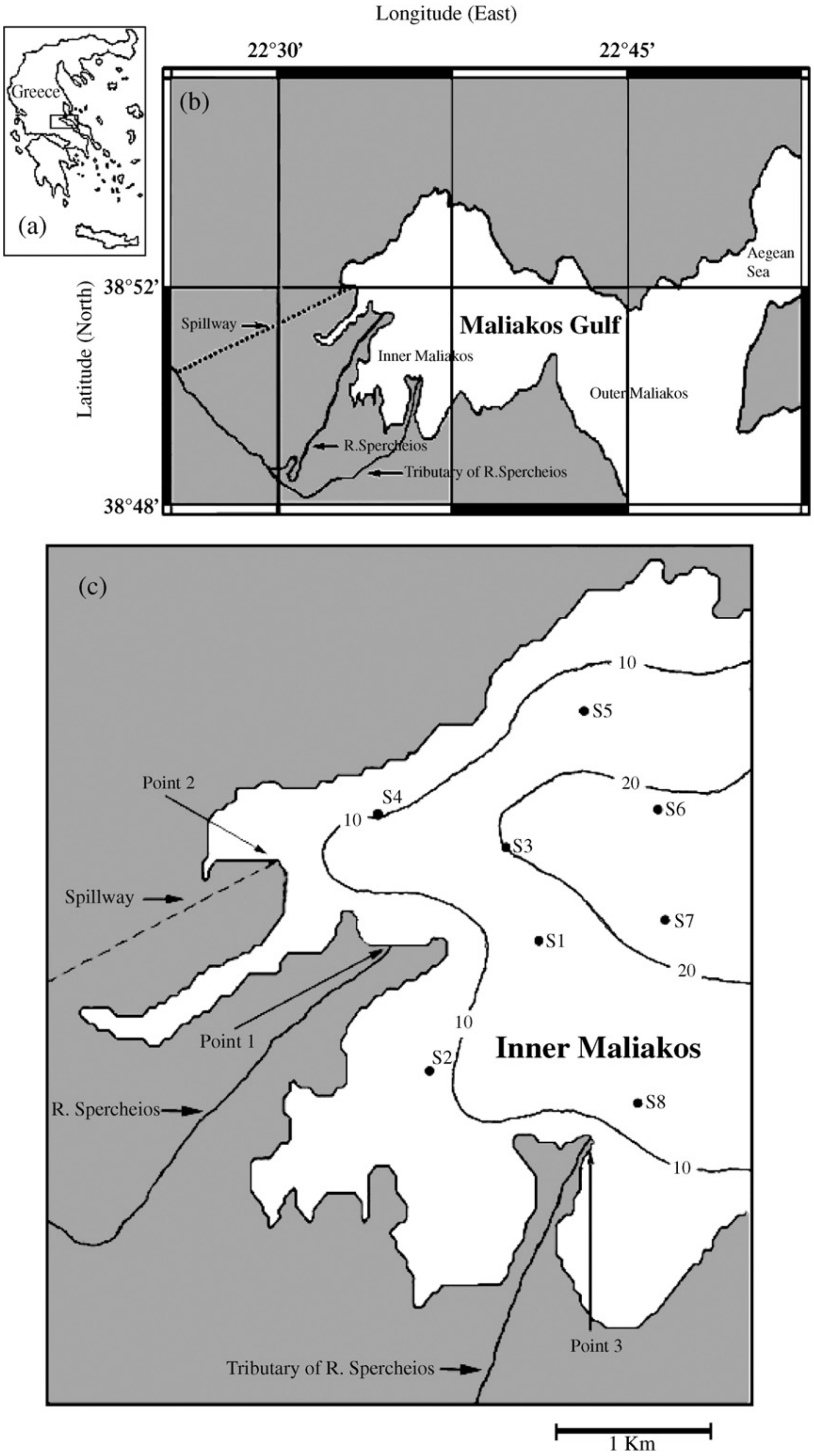


Fig. 1. Study site and sampling stations. (a) Map of Greece showing the position of Maliakos Gulf on the west coast of the Aegean Sea. (b) Maliakos Gulf, showing the inner semi-enclosed part that receives the discharges of the Spercheios river, its recently constructed spillway and its tributary on the innermost western and south coast, and the outer part that communicates with the Aegean Sea. (c) Bathymetry of the inner Maliakos Gulf indicating (circles) the location of the sampling stations (S1 to S8), the mouth of the Spercheios river (point 1), its spillway on the north-east coast (point 2), and its tributary on the southern coast (point 3).

Table 1
Water column and sediment characteristics at all sampling times and stations

Station	D1 (km)	D2 (km)	D3 (km)	Depth (m)	Time	Water column						Sediment		
						Temperature (°C)		Salinity (psu)		Secchi (m)	dO$_2$ (ml l^{-1})	md (μm)	σ (phi)	sk (phi)
						SNL	BNL	SNL	BNL		BNL			
S1	1.0	2.8	1.5	17.5	J	13.0	13.4	36.5	37.2	4.0	4.0	11	1.80	0.43
					M	22.2	18.9	37.0	37.3	2.0	4.0	11	1.07	0.30
					A	25.7	25.1	35.7	36.3	3.0	4.8	14	1.51	0.05
					N	17.6	17.7	36.6	36.7	5.0	4.4	10	0.84	0.42
S2	1.0	3.5	1.5	7.5	J	12.9	13.3	36.7	36.9	6.0	4.5	12	1.81	0.28
					M	22.7	21.1	36.6	37.1	1.2	4.1	15	1.60	0.15
					A	25.8	25.0	35.5	36.4	2.7	4.8	12	1.10	−0.12
					N	17.2	17.6	36.5	36.7	1.8	3.0	6	0.80	−0.11
S3	1.0	2.0	2.5	20	J	12.8	13.4	36.4	37.3	3.8	4.2	11	1.74	0.36
					M	22.9	18.0	36.7	37.5	3.0	4.4	12	1.24	0.05
					A	26.5	24.9	36.1	36.4	7.3	4.4	13	1.43	−0.03
					N	17.0	17.5	36.1	36.6	4.5	4.4	10	1.41	0.00
S4	1.0	0.8	3.0	10.5	J	12.7	13.3	36.3	37.2	3.5	3.7	11	1.72	0.31
					M	22.0	19.5	37.3	37.8	0.5	4.1	11	0.93	0.28
					A	26.6	24.7	35.9	36.5	0.5	4.2	11	0.86	0.33
					N	17.7	17.9	36.7	36.7	4.5	4.5	5	1.46	0.62
S5	2.0	1.8	3.5	16	J	12.8	13.3	36.6	37.2	2.0	3.2	11	1.88	0.34
					M	21.7	18.9	36.7	37.1	2.5	4.0	11	1.05	0.23
					A	25.9	24.4	35.1	36.5	7.0	4.4	12	1.39	0.04
					N	17.7	17.5	36.7	36.7	3.4	3.8	6	0.86	−0.03
S6	2.0	2.5	2.5	22	J	12.9	13.4	36.4	37.2	4.0	4.3	12	1.98	0.39
					M	21.3	16.3	36.1	37.8	3.0	3.9	12	1.17	0.17
					A	26.0	25.0	36.5	36.4	13.2	4.8	12	1.29	0.05
					N	17.3	17.7	36.3	36.7	5.0	4.5	7	1.50	–0.06
S7	2.0	2.7	1.5	22	J	12.8	13.4	36.7	37.2	4.5	4.0	11	2.10	0.41
					M	21.5	17.6	35.8	37.6	1.5	4.2	11	0.91	0.33
					A	26.1	23.5	36.2	36.9	2.7	4.7	13	1.49	0.06
					N	17.5	17.8	36.6	36.7	1.8	4.5	6	0.99	−0.16
S8	2.0	3.5	0.5	12	J	12.7	13.4	36.8	37.4	3.5	4.1	15	1.90	0.04
					M	23.4	18.3	35.3	37.0	1.5	4.2	13	1.25	0.24
					A	25.9	25.9	35.8	35.9	3.1	4.8	12	1.11	0.18
					N	17.4	17.8	36.3	36.7	4.8	4.2	6	0.32	0.00

Variable abbreviations as in Material and methods.

Therefore, stations S1, S2, S3 and S4 were located 1 km away from point 1 at depths ranging from 7.5 to 20 m and stations S5, S6, S7 and S8 were set at 2 km from point 1 at depths ranging from 12 to 22 m (Fig. 1c). The influence of discharges from points 2 and 3 (Fig. 1) was weighed by measuring the distance of each station from these points.

2.3. Environmental variables

Vertical profiles of salinity (in Practical Salinity Units) and temperature (°C) in the water column were obtained using a Seabird CTD while transparency depth (m) was measured with a 20 cm Secchi disk. Seawater samples for the analysis of suspended material and chloroplastic pigments were taken at the surface and the bottom nepheloid layers (SNL and BNL, respectively) and filtered on GF/F filters within 3 h of sampling. Only the BNL was sampled for dissolved oxygen analysis. Triplicate quantitative benthic samples were taken with a Ponar grab (sampling area: 0.05 m^2, penetration depth: 15 cm). A cut-off syringe core (2.9 cm i.d., 8 cm length) subsample was taken from each grab for the determination of sediment biochemical parameters, i.e. total organic carbon (TOC), and chloroplastic pigments at 2–cm intervals (0–2 cm, 2–4 cm and 4–6 cm sediment depth). Particle size analysis was based on subsamples taken from a fourth grab sample at each station.

All filters and sediment core subsamples were immediately frozen and stored at – 22 °C for subsequent laboratory analysis. Sediment biochemical parameters were measured using freeze-dried homogenized aliquots. The concentrations of dissolved oxygen (dO_2), suspended particulate inorganic material (PIM) and particulate organic material (POM) were analysed as in Parsons et al. (1984). Chlorophyll-a (Chl-a) and its degradation products, i.e. phaeopigments (Pheo), from filters and sediment samples were extracted with 90% acetone and determined fluorometrically according to Yentsch and Menzel (1963). TOC was estimated as in Nelson and Sommers (1975). Median grain size (md), sorting coefficient (σ) and skewness (sk) were determined according to Buchanan (1984).

2.4. Macrofauna

After syringe core subsampling, the remainder of the sediment from each replicate (area: 0.047 m^2) was sieved through a 0.5 mm mesh and the residue was immediately fixed in 4% formaldehyde. The organisms retained were sorted, enumerated and identified to species level. The species from all major taxa were classified to functional groups according to (1) their food acquisition mode (surface (S) or subsurface (B) deposit feeders, suspension feeders (F), omnivorous (O) and carnivorous (C) feeders), (2) their motility (mobile (A) or discretely motile (D), i.e. capable of moving between feeding sessions, and sedentary (S)), and (3) their living position in the sediment layer and relation with the substrate (tubicolous burrowers (T) or not (X) and for bivalves, bysally attached (BA) or unattached (UA) in permanent or temporary burrows). This classification was based on the ecological literature for families, genera or species (Woodin, 1976; Fauchald and Jumars, 1979; Holdich and Jones, 1983; Kamermans, 1994; Levinton, 1982) as well as on specific systematic keys for the Mediterranean Sea. The species were also classified in three groups with respect to their time of appearance in the succession process, temporal and spatial persistence as well as rates of population growth and decline, following Rhoads et al. (1978), i.e. (a) Group-1 or first-order opportunistic species (pioneering species that reach high abundances within short periods of time in disturbed sediments and decline in the absence of further disturbance), (b) Group-3 or equilibrium species (species that may also appear early and maintain constant and persistent but relatively low populations), and (c) Group-2 or second-order opportunistic species (intermediates between Groups-1 and -3 modes of colonisation). Additional information for the present classification was taken from the review by Borja et al. (2000) assuming that similar species are eliminated, or significantly reduced, after any major environmental disturbance.

2.5. Statistical analysis

All analyses were completed at the level of replicate unit ($n=3$) at each station. Total community variables, i.e. abundance m^{-2} and numbers of species 0.047 m^{-2} (hereafter referred as 0.05 m^{-2}), were compared among stations using ANOVA, preceded by Cochran's test for homogeneity of variances and followed by a posteriori Student–Newman–Keuls (SNK) tests. The Pearson product moment correlation coefficients were also calculated between abundance and species numbers, and the environmental variables.

Multivariate analyses were carried out using species of macrofauna that exceeded 4 individuals per sampling period (corresponding to an average density of 3 ind m^{-2}) so as to remove very rare species. Only the environmental variables in the BNL were used because of the high significant correlation coefficients between levels in the BNL and SNL. Temperature and salinity were not included in the analyses owing to their negligible spatial variability. Only the TOC and chloroplastic pigments equivalent (CPE: Chl-a+Pheo) concentrations in the top 2 cm of sediment were used in the statistical analyses, as they were significantly spatially variable ($p<0.05$) as opposed to those of the subsurface layers, which did not vary significantly. The distance of each station from the main sources of terrigenous sediment input to the inner Maliakos (i.e. points 1, 2 and 3 in Fig. 1, corresponding to D1, D2, D3) was used to account for unmeasured gradients in sedimentation.

Non-parametric multivariate multiple regression (McArdle and Anderson, 2001) was applied to analyse the relationship between species data and environmental variables at each sampling time. p–values were obtained using 9999 permutations of the raw data and the estimates of the analyses were obtained using the program DISTLM (courtesy of M.J. Anderson, University of Auckland, New Zealand). Non-metric multidimensional scaling (nMDS) was carried out to visualize patterns in species abundances at each sampling period. Then, projection biplots were drawn onto these MDS axes to examine their relationship with species abundances and environmental variables using the MultivEcol package (freely available from Brian McArdle's website: http://www.stat.auckland.ac.nz/people.php) with the R statistical program (Ihaka and Gentleman, 1996). All multivariate analyses were based on Bray–Curtis distance measure. Species abundances were not transformed prior to these analyses because of the patchy distribution of most taxa.

3. Results

3.1. Environmental variability

The physical and chemical properties of the water column and the sediment in the delta front of the Maliakos Gulf are summarised in Table 1. Distance from point 2 (D2) ranged from 0.8 to 3.5 km and distance from point 3 (D3) ranged from 0.5 to 3.5 km. Salinity ranged from 35.1 (S5, August) to 37.3 (S4, May) in the SNL and from 35.9 (S8, August) to 37.8 (S4, S6, May) in the BNL, being slightly higher in the near-bottom than in the surface layer. Mean Secchi disk transparency depth along the delta front was 1.9±0.9 m in January, 3.9 m in August and November and 4.9±4.1 m in May, decreasing from summer towards winter and spring. Dissolved oxygen at the BNL ranged from 3.0 to 4.8 ml l^{-1} and was highest in August at all stations except S4.

The foreset beds of the inner Maliakos Gulf were characterised by silty sediments (5<md<15 μm). Finer

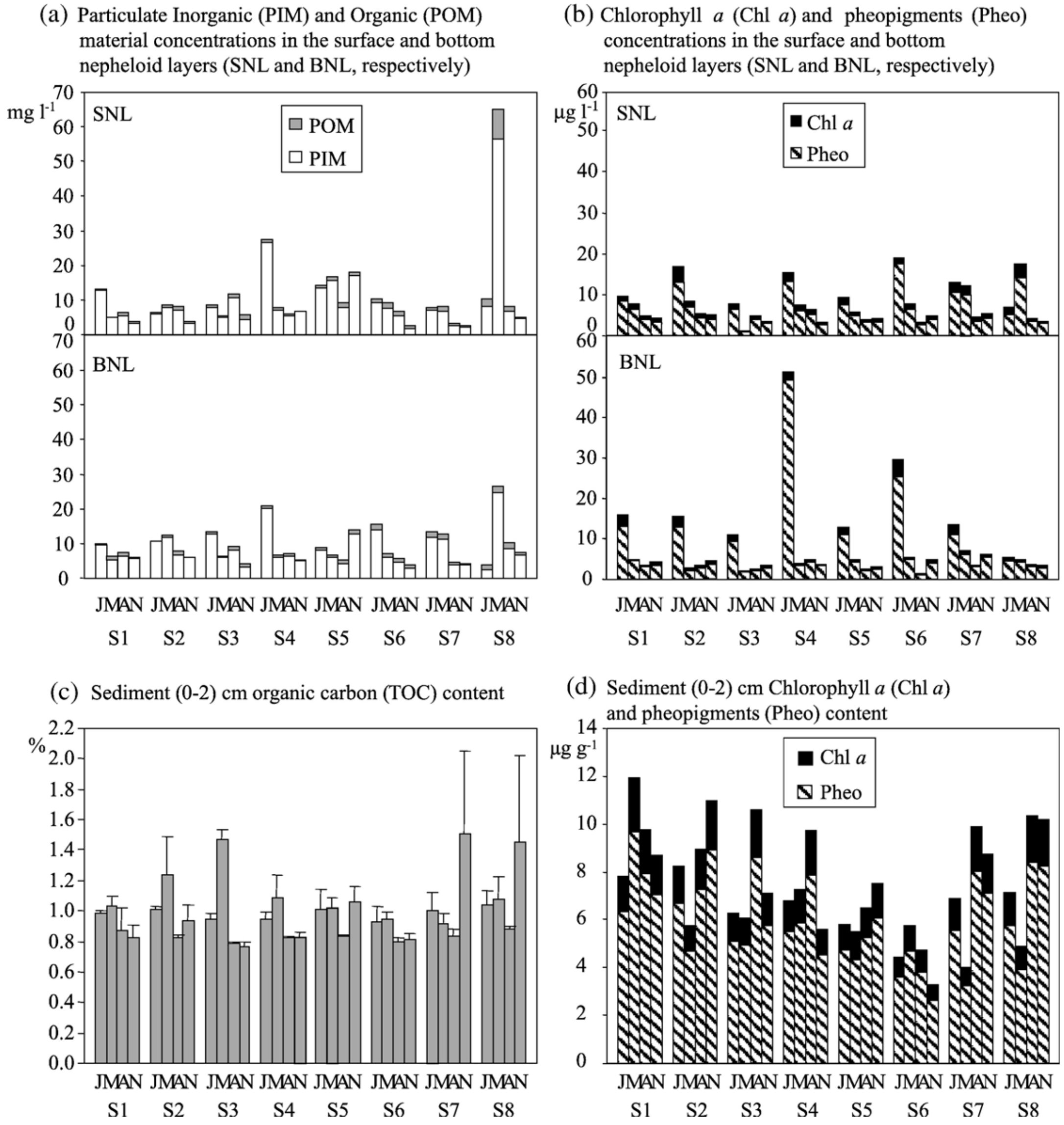


Fig. 2. Seasonal variation in the composition of suspended particulate and sedimentary material at the eight stations in the inner Maliakos. (a) Particulate inorganic (PIM) and organic material (POM) in the surface and bottom nepheloid layer (SNL and BNL, respectively). (b) Chlorophyll-a (Chl-a) and pheopigment (Pheo) concentrations in the surface and bottom nepheloid layer (SNL and BNL, respectively). (c) % TOC content (+1 standard error) in the upper 2 cm of sediment. (d) Sediment chlorophyll-a (Chl-a) and pheopigment (Pheo) concentration in the upper 2 cm of the sediment.

grains persisted in November ($md < 10$ μm) while coarser grain size in the remainder of sampling times coincided with higher sorting coefficients. In particular, poorly sorted sediments were observed at all stations except S7 in January, S4 in May and S4 and S7 in August, while in November only the stations S3, S4, S6 had poor sediment sorting ($\sigma > 1.0$ phi) (Table 1). Sediment skewness (sk) ranged from -0.16 (coarse skewness) to 0.62 (very fine skewness). sk was positively correlated with clay fraction only in January ($r = 0.8$, $p < 0.05$), revealing high deposition of fine material at all stations except S8. In contrast, symmetrical distribution of sediment grains ($sk \sim 0$) was observed at the deeper stations in August, i.e. S1, S3, S5, S6 and S7, and at S3, S5, S6 and S8 in November.

The concentrations of particulate material and pigments in the water column and the sediment are given in Fig. 2. PIM concentrations varied from 1.9 mg l^{-1} (S1, November) to 56.4 mg l^{-1} (S8, May) in the SNL and from 2.6 mg l^{-1} (S8, January) to 24.8 mg l^{-1} (S8, May) in the BNL, thus notably increasing near the mouth of the small tributary in spring (point 3) (Fig. 2a). POM concentrations did not exceed 8.8 mg l^{-1} in the SNL (S8, May) and 1.9 mg l^{-1} (S8 in May) in the BNL, accounting for 1.4% (S4, November, SNL) – 35% (S8, January, BNL) of total suspended particulate material (Fig. 2a). Chl-a concentrations in the water column ranged from 0.1 to 5.9 μg l^{-1} and exceeded 3 μg l^{-1} at stations S1 (BNL), S2 (SNL, BNL) and S6 (BNL) in January and at S8 (SNL) in May (Fig. 2b). CPE levels (i.e. Chl-a + Pheo) in the BNL in January were 1.5 to 38 times higher than those observed in the remainder of sampling times (Fig. 2b). Generally, CPE accounted for less than 5% of POM, at all stations and sampling times, except S1 and S2 in January (8% in SNL and BNL). No consistent spatial or temporal trend was observed in the levels of sedimentary TOC (0.77 – 1.51%) while mean Chl-a levels in the top 2 cm of the sediment ranged from 0.66 μg g^{-1} (S6, November) to 2.26 μg g^{-1} (S1, May) (Fig. 2c and d, respectively).

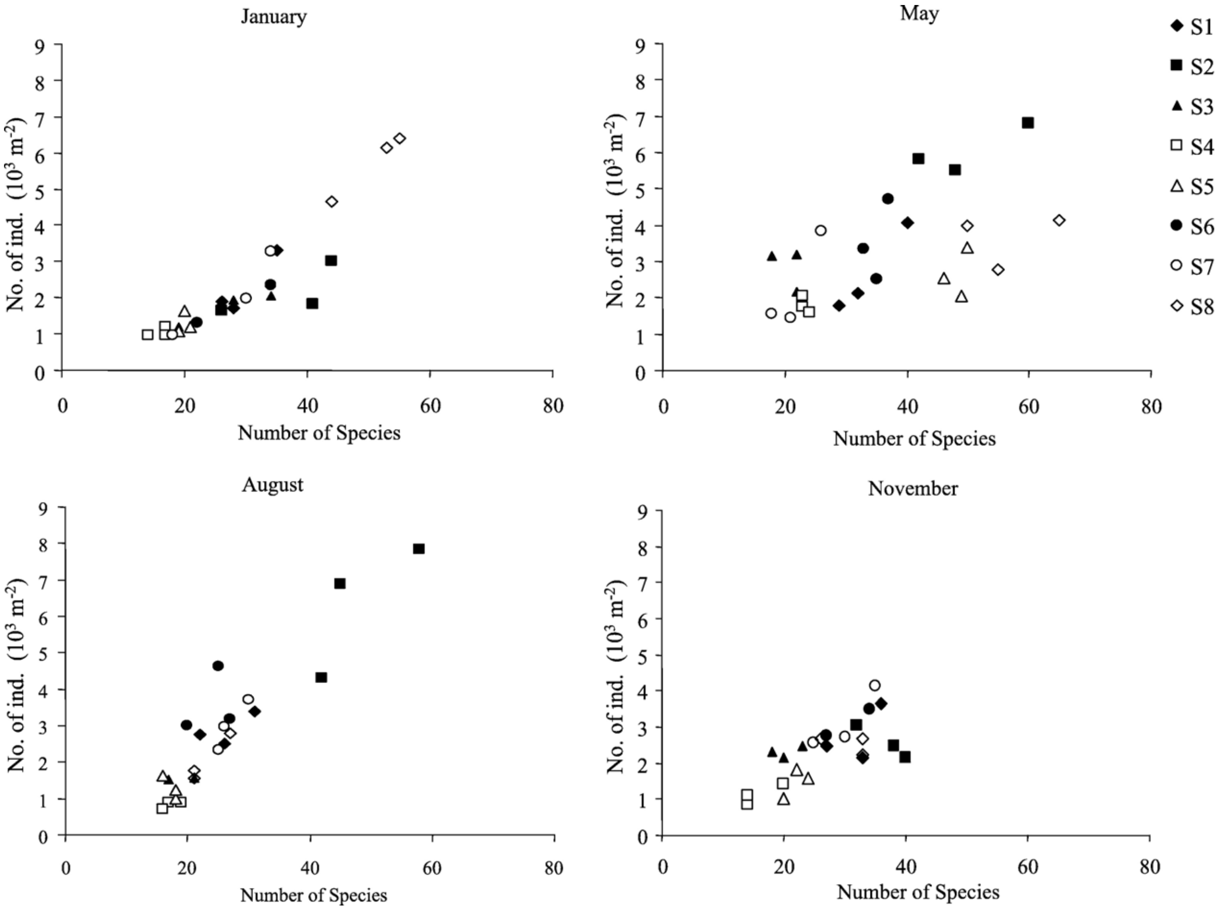


Fig. 3. Relation between number of ind m^{-2} and number of species 0.05 m^{-2} at each sampling time at the eight stations in the inner Maliakos Gulf.

Table 2
Results of one-way analyses of variance and SNK tests examining the effect of station on abundance and number of species

Sampling time	$F_{7,\,16}{}^{p}$	SNK tests
		Abundance
January	12.5***	S1 = S2 = S3 = S4 = S5 = S6 = S7 > S8
May	2.8*	S1 = S3 = S4 = S5 = S6 = S7 = S8 < S2
August	13.9***	S1 = S3 = S4 = S5 < S6 = S7 = S8 < S2
November	3.8**	S4 = S5 < S1 = S2 = S3 = S7 = S8 < S6
		Number of Species
January	8.56***	S4 = S5 < S1 = S2 = S3 = S6 = S7 < S8
May	12.8***	S3 = S4 = S7 < S1 = S6 < S2 = S5 = S8
August	18.4***	S1 = S3 = S4 = S5 = S6 = S7 = S8 < S2
November	6.5***	S4 = S3 = S5 < S1 = S2 = S6 = S7 = S8

* $p<0.05$; ** $p<0.01$; *** $p<0.001$.

3.2. Macrofaunal abundance, species numbers and species composition

Average macrofaunal abundance varied between 840 and 6 346 ind m^{-2}, both values recorded in August (Fig. 3), with molluscs and polychaetes comprising more than 60% of the total numbers of individuals. Numbers of species per ponar grab sample (i.e. 0.05 m^{-2}) ranged from 14 (S4, January) to 65 (S2, May) (Fig. 3) and were also dominated by polychaetes and molluscs. Abundance strongly correlated with species numbers at all sampling times ($r>0.61$, $p<0.001$, df = 24). The a posteriori SNK tests revealed different groups of stations (homogeneous at $p \geq 0.05$) depending on the community variable tested (i.e. abundance and species numbers) (Table 2). However, stations S4 and S5 consistently displayed the lowest abundance and diversity in the delta front area, although these were not significantly lower in January. In addition, the maximum levels of abundance and species numbers were recorded at stations S2, S8 and S6, although not always at the same sampling time.

The Pearson correlation coefficient (r) between pairs of total community variables and environmental variables showed that their relationships largely depended on the sampling time (Table 3). The concentrations of suspended particulate inorganic material (PIM) showed consistently negative correlation with the community. On the other hand, granulometric characteristics were found to be correlated with the community at all times, with md and σ displaying positive correlations and sk negative with abundance and species numbers. Distance from the spillway, D2, had a strong positive relation with abundance and numbers of species in January while at the same sampling time the community displayed a negative correlation with the distance from the small tributary, D3. This is partly in accordance with the results of SNK comparisons that showed the significantly lower levels of species numbers at stations S4 and S5, i.e. the stations closer at the spillway mouth. CPE concentrations in the BNL showed significant correlations with both total community variables in January and November but these were low. Dissolved O_2 (dO2) did not significantly correlate with the community at any of the sampling times (Table 3).

Of the 203 species recorded, 133 were present in January, 117 in May, 113 in August and 103 in November. Regarding the most dominant species (i.e. exceeding 200 ind m^{-2} in at least one of the stations), those that belonged to Group-2 were present in very high densities when they peaked but exhibited high spatial (e.g. *Lumbrineris latreilli*, *Mysella bidentata*, *Corbula gibba*, *Levinsenia gracilis*)

Table 3
Pearson correlation coefficients, r, among total abundance m^{-2}, number of species 0.05 m^{-2} and the environmental variables in the BNL in the water column and in the 0–2 cm layer in the sediment at each sampling time (n = 24 for each time)

Environmental variables	January		May		August		November	
	Abundance	Species	Abundance	Species	Abundance	Species	Abundance	Species
CPE in BNL (CPEw)	−0.49*	−0.46*	ns	ns	ns	ns	0.53**	0.45*
Particulate inorganics in BNL(PIM)	−0.76***	−0.67***	ns	ns	ns	ns	−0.43*	ns
Particulate organics in BNL (POM)	ns	ns	ns	ns	ns	ns	ns	ns
Water transparency (Secchi)	ns	ns	ns	ns	ns	ns	ns	ns
Dissolved oxygen (dO_2)	ns	ns	ns	ns	ns	ns	ns	ns
Median grain size (md)	0.85***	0.70***	0.70*	0.50*	ns	ns	ns	ns
Sediment sorting (σ)	ns	ns	0.71***	0.48*	ns	ns	ns	0.43*
Sediment skewness (sk)	−0.75**	−0.65***	ns	ns	−0.61**	−0.57**	ns	−0.48*
Sediment Organic Carbon (TOC)	ns	ns	ns	ns	ns	ns	ns	ns
Sediment CPE (CPEs)	ns	ns	ns	ns	ns	ns	ns	ns
Distance from river mouth (D1)	ns	ns	ns	ns	ns	ns	ns	ns
Distance from spillway (D2)	0.70***	0.63***	0.48*	0.49*	0.54**	0.52**	0.55**	0.75***
Distance from tributary (D3)	−0.75**	−0.67**	ns	ns	ns	−0.45**	ns	−0.58**

n.s. $p>0.050$; *$p<0.050$; **$p<0.010$; ***$p<0.001$.

and / or temporal variability (e.g *Pseudoleiocapitella fauveli*, Oligochaeta, *Corrophium runcicorne*, *Ampelisca* sp.) (Table 4, Fig. 4). On the other hand, species belonging to Group-3, such as *Hyala vitrea*, *Nephtys hystricis* and *Maera schmidti*, were ubiquitous and persistent but displayed lower densities than the Group-2 species (Table 4, Fig. 4). However, *Lepton nitidum* occasionally peaked, exceeding the densities of Group-2 species. The community was also dominated by surface deposit feeding bivalves such as species of the genera *Abra*, *Tellina* and *Nucula* as well as by infaunal burrowing amphipods that exhibited remarkable variation. Generally, the most abundant taxa comprised actively mobile species, excluding *Phoronis psamophila*, *Corbula gibba* and *Terebellides stroemi*, while carnivory and omnivory coexisted with suspension feeding, surface and burrowing deposit feeding (Table 4). Group-1 species were either very rare or absent.

3.3. Multivariate analysis

Non-parametric multivariate regressions (McArdle and Anderson, 2001) were significant at all times ($p<0.05$) and showed that the variance of the species data could be explained by different environmental variables at each sampling time to a level ranging from 52.66% in January to 68.64% in August (Table 5). The variable that explained the greatest amount of variation was median grain size in January (i.e. md, 23.94%), Secchi transparency depth in May (i.e. Secchi, 12.3%), distance from the spillway in August (i.e. D2, 16.53%) and chloroplastic pigments equivalent concentrations in the BNL in November (i.e. CPEw, 15.32%), (Table 5a). Interestingly, distance from the river mouth (D1), the tributary (D3) or the spillway (D2) contained a considerable proportion of the information at all sampling times, explaining 11.39 to 17.74% of the species variation, when considered individually (Table 5a). Moreover, sediment skewness alone explained 8.27 to 23.32% of the species variation at all times. Other variables, such as PIM and md closely followed, explaining more than 10% of the species variation, when considered individually, while dO_2 explained a significant amount of the species variation only in August. TOC and CPEs did not have a significant relation with the species data when considered singly in any of the sampling times.

Table 4
List of dominant taxa exceeding 200 individuals m^{-2} in at least one of the stations at each sampling time

Species	Functional classification		Number of individuals m^{-2}			
	T, M, BS	Colonization pattern	January	May	August	November
Aricidea claudiae	B, A, T	Group 2	93 ± 124	67 ± 108		
Lumbrineris latreilli	O, A, X	Group 2 or 3	414 ± 203	101 ± 140	156 ± 247	70 ± 108
Nephtys hystricis	C, A, X	Group 3		210 ± 33	118 ± 50	
Levinsenia gracilis	B, A,T	Group 2		208 ± 102		
Oligochaeta	B, A, T	Group 1 or 2		32 ± 234		
Pseudoleiocapitella fauveli	B, A,T	Group 2	115 ± 234			
Sternaspis scutata	B, A, X	Group 2	71 ± 58	129 ± 34		
Terebellides stroemi	S, D, T	Group 3			44 ± 164	
Phoronis psamophila	F, SD, T	Group 3	201 ± 132		92 ± 115	
Lepton nitidum	F, A, NB	Group 3		202 ± 183	98 ± 194	53 ± 268
Mysella bidentata	F, A , NB	Group 2	95 ± 59	389 ± 44	494 ± 74	345 ± 78
Corbula gibba	F, D, BA	Group 2		344 ± 119	122 ± 47	142 ± 49
Abra prismatica	B, A, UN	Group 2			85 ± 234	
Tellina compressa	B, A, UN	Group 3			39 ± 283	
Nucula turgida	B, A, UN	Group 3				88 ± 81
Turitella communis	F, A, X	Group 3				58 ± 134
Hyala vitrea	C, A, X	Group 3	193 ± 74	182 ± 52	310 ± 71	323 ± 43
Maera shmidtii	F, A, T	Group 3			27 ± 283	
Ampelisca sp.	F, A, T	Group 1 or 2		78 ± 78	138 ± 81	121 ± 79
Leptocheirus mariae	F, A, T	Group 2				65 ± 164
Corrophium runcicorne	F, A, T	Group 2	386 ± 281			
Harpinia crenulata	F, A, T	Group 2			48 ± 261	
Apseudes l. mediterranea	S / F, A, X	Group 2			141 ± 101	103 ± 109

Functional classification and average abundance m^{-2} (± CV%, coefficient of variation) of the eight stations are given. Trophic mode (T): S = surface deposit feeder; B = subsurface deposit feeder; F = suspension feeder; O = omnivorous; C = carnivorous. Motility (M): A = actively mobile; D = discretely motile; SD = sedentary. Burrowing strategy (BS): T = tube-forming; X = non tube-forming; NB = nested within the burrows of other species; BA = bysally attached to grains; UN = unattached. Colonization pattern (sensu Rhoads et al., 1978): Group 1 = first order opportunists; Group 2 = second order opportunists; Group 3 = equilibrium species.

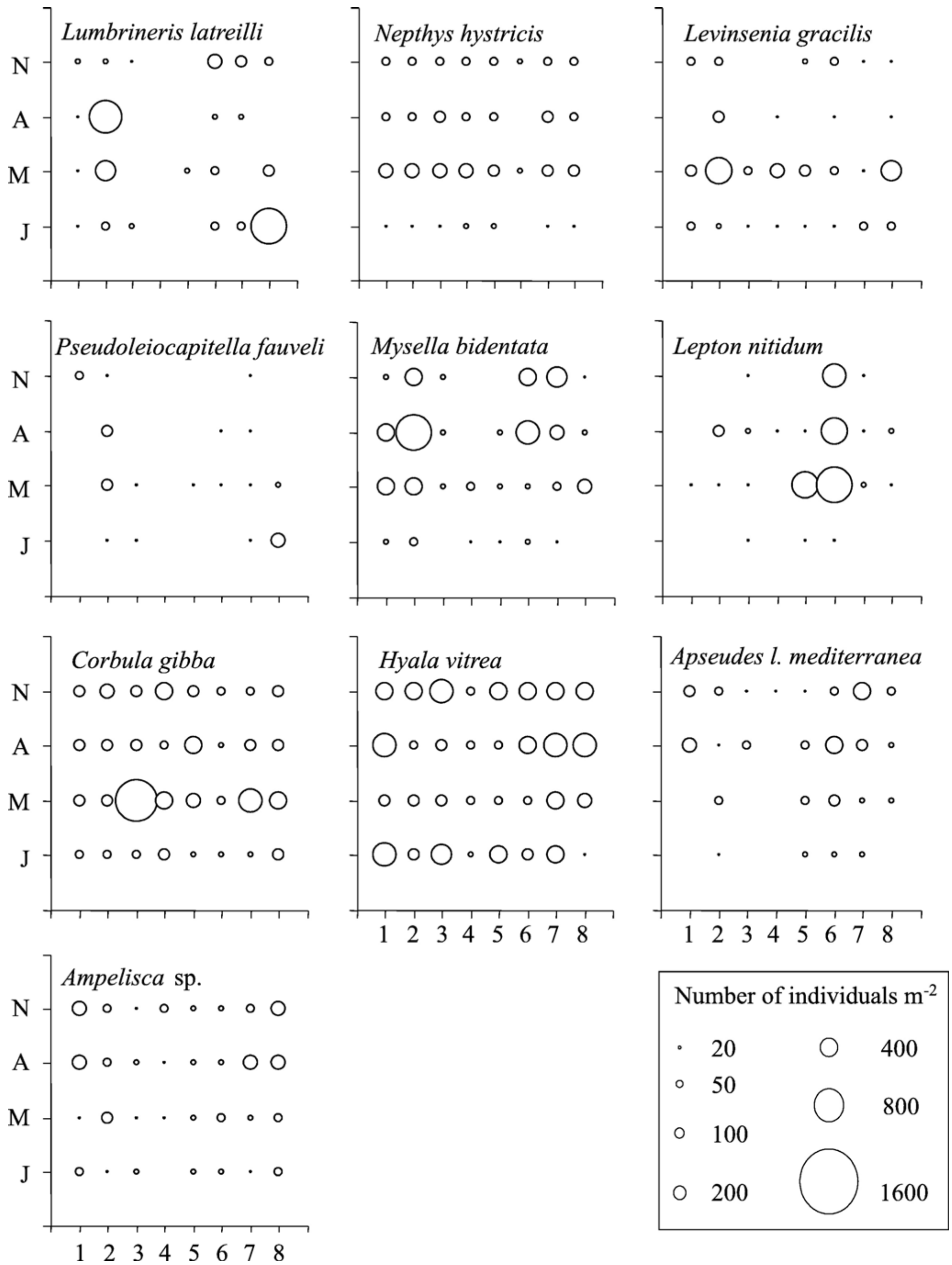


Fig. 4. Distribution of selected dominant macrobenthic species at the eight stations in the inner Maliakos Gulf at each sampling time. J = January; M = May; A = August; N = November.

A sequential model was also built using the forward-selection procedure with the conditional tests (i.e. fitting each variable one at a time, depending on the variables that are already included in the model). This regression model showed that most of the variables added significantly to the ability to explain species data variation during the study (Table 5b). The contribution of distance from the river mouth (D1) and the tributary (D3), the CPEs and TOC were never significant in explaining the spatial variation in species data at any sampling time, when fitted sequentially. In the case of D3, this is partly due to the high negative correlation with D2 (r = −0.8).

The MDS ordination plots of stations showed high spatial heterogeneity in community composition along

Table 5
Results of non-parametric multiple regression of multivariate species data on individual environmental variables for (a) each variable taken individually (ignoring other variables) and (b) forward-selection of variables, where amount explained by each variable added to model is conditional on variables already in the model (i.e. those variables listed above it)

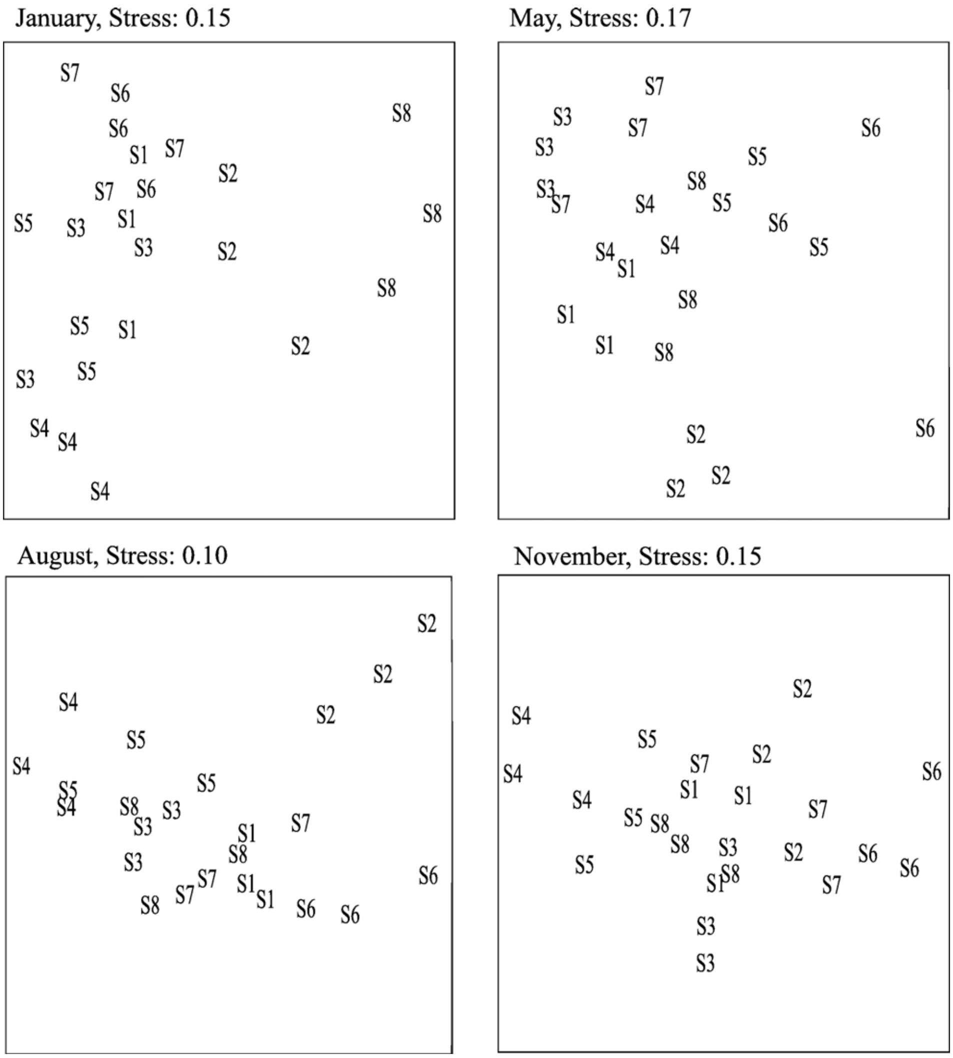
January				May				August				November			
Variable	Var (%)	F	Cum. (%)	Variable	Var (%)	F	Cum. (%)	Variable	Var (%)	F	Cum. (%)	Variable	Var (%)	F	Cum. (%)
(a) Variables considered individually				(a) Variables considered individually				(a) Variables considered individually				(a) Variables considered individually			
md	23.94	6.92***		Secchi	12.30	3.09**		D2	16.53	4.35***		CPEw	15.32	3.98***	
sk	23.32	6.68***		σ	12.11	3.03**		sk	15.04	3.89**		D2	15.06	3.90***	
D3	17.64	4.71***		D1	12.04	3.01**		D3	11.39	2.83*		sk	13.99	3.58**	
D2	15.05	3.89***		D3	12.02	3.01**		md	11.37	2.82*		D3	10.94	2.70**	
PIM	14.42	3.71***		md	10.00	2.44*		σ	11.10	2.74*		PIM	10.7	2.64*	
σ	11.05	2.73**		D2	9.54	2.32*		Secchi	10.96	2.71*		md	8.91	2.15*	
CPEw	9.95	2.43*		CPEw	8.35	2.00*		dO$_2$	8.63	2.08*		σ	8.35	2.00*	
D1	9.15	2.22*		sk	8.27	1.98*		CPEw	6.55	1.54^{ns}		POM	8.24	1.98*	
POM	8.08	1.93*		PIM	8.13	1.95*		CPEs	5.61	1.31^{ns}		D1	7.29	1.73ns	
dO$_2$	7.53	1.79^{ns}		POM	7.72	1.84^{ns}		POM	5.49	1.28^{ns}		dO$_2$	6.12	1.44^{ns}	
Secchi	6.27	1.47^{ns}		TOC	5.19	1.21^{ns}		D1	5.48	1.28^{ns}		CPEs	5.85	1.37^{ns}	
CPEs	4.79	1.11^{ns}		dO$_2$	4.71	1.09^{ns}		PIM	4.37	1.01^{ns}		Secchi	4.5	1.04^{ns}	
TOC	3.9	0.89^{ns}		CPEs	4.08	0.94^{ns}		TOC	1.49	0.33^{ns}		TOC	3.44	0.79^{ns}	
(b) Variables fitted sequentially				(b) Variables fitted sequentially				(b) Variables fitted sequentially				(b) Variables fitted sequentially			
md	23.94	6.92***	23.94	Secchi	12.30	3.09**	12.30	D2	16.53	4.35***	16.53	CPEw	15.32	3.98***	15.32
sk	12.07	3.96***	36.01	σ	12.20	3.52***	24.50	σ	13.87	5.43***	30.40	sk	12.3	3.99***	27.62
PIM	6.08	2.09*	42.09	CPEw	11.51	3.62**	36.01	Secchi	10.94	3.16**	41.34	D2	10.83	3.08***	38.45
CPEw	5.60	2.03*	47.68	md	11.35	5.05***	47.36	sk	10.18	3.26**	51.52	PIM	9.12	3.31***	47.57
D2	4.98	1.89*	52.66	sk	10.43	4.71***	57.79	CPEw	8.54	3.85**	60.06	md	8.11	3.29***	55.68
CPEs	3.61	1.40^{ns}	56.27	POM	3.97	1.88^{ns}	61.76	dO$_2$	4.41	2.11*	64.47	POM	5.97	2.65**	61.65
Secchi	2.93	1.15^{ns}	59.21	D1	3.49	1.72^{ns}	65.25	md	4.17	2.12*	68.64	Secchi	3.95	1.84*	65.60
TOC	2.01	0.78^{ns}	61.22	CPEs	3.53	1.84^{ns}	68.78	CPEs	1.59	0.80^{ns}	70.23	CPEs	2.68	1.27ns	68.28
D1	1.99	0.76^{ns}	63.21	TOC	1.58	0.81^{ns}	70.36	TOC	1.14	0.56^{ns}	71.37	TOC	2.17	1.01ns	70.45
dO$_2$	0.02	0.01^{ns}	63.23	dO$_2$	0.93	0.46^{ns}	71.29	D1	0.37	0.15^{ns}	71.74	dO$_2$	0.05	0.02ns	70.50
σ	1.55	0.48^{ns}	64.78	D3	0.72	0.36^{ns}	72.01	PIM	0.02	0.01^{ns}	71.76	D3	0.04	0.01ns	70.54
D3	0.00	0.00^{ns}	64.78	D2	2.20	0.98^{ns}	74.21	D3	0.00	0.00^{ns}	71.76	D1	0.01	0.00ns	70.55
POM	0.00	0.00^{ns}	64.78	PIM	0.00	0.00^{ns}	74.21	POM	0.00	0.00^{ns}	71.76	σ	0.00	0.00^{ns}	70.55

%Var: percentage of variance in species data explained by that variable; Cum%: cumulative percentage of variance explained. Variable abbreviations as in Table 3.

the delta front, both within and among stations (Fig. 5). Stations were not clearly ordered from the mouth of the main river (point 1) and the small tributary (point 3) to more distant areas, indicating that Bray–Curtis distance among assemblages in the ordination plot were not strongly correlated with distance on the map (compare Figs. 1 and 5). Nevertheless, replicates from the two stations with the smallest D2 (S4 and S5) tended to cluster in January and November, being clearly distinct from stations positioned more than 1.5 km away from riverine sources (points 1, 2 and 3 in Fig. 1) at both times, i.e. S6 and S7, as well as stations with high D2 i.e. S8 (January) and S2 (January and November). This is in agreement with the January and November sequential regression models that revealed a significant power of D2 in explaining community structure. In May, S2, S3, and S7, being distinct from each other, were clearly separated in ordination space from the remainder of the stations. Stations S4 and S6 were the most different sites in August and November.

Different environmental variables correlated with the MDS axes at each sampling time (Fig. 6). In January, the area near the small tributary mouth (S8) was associated with higher md as well as lower sk and PIM, the deepest stations, i.e. S6 and S7, were related to enhanced σ and POM, while S4, near the spillway mouth, was characterised by an increase in CPEw. The species *L. latreilli*, *P. fauveli*, *C. runcicorne*, *P. psamophila, A. prismatica* increased at S8. Greater abundances of *A. claudia* and *H. vitrea* were found at S6 and S7, while the species *S. scutata*, *Echinocardium cordatum* and *N. hystricis* increased at S4.

In May, S2 tended to have higher md and σ, while S3, S4 and S7 were associated with higher TOC but lower md. High CPEw and transparency characterised


January, Stress: 0.15

May, Stress: 0.17

August, Stress: 0.10

November, Stress: 0.15

Fig. 5. Non-metric MDS ordination of the taxa with average density >3 ind m^{-2} at each sampling time, separately, showing the replicates of the eight stations. Analyses were performed on Bray–Curtis dissimilarities of untransformed data.

areas away from the mouth of the Spercheios river and its small tributary, (points 1 and 3), such as S5 and S6. The species *L. latreilli* and *M. bidentata* increased at station S2. *C. gibba* increased at stations S3, S4 and S7. *N. hystricis* preferred S1 while suspension feeding amphipods (*L. mariae* and *M. schmidtii*), *T. stroemi* and *A. claudia* increased at S5, S6 and S7.

In August, σ, md, POM and Secchi increased at S1 and S6, while areas near the spillway mouth, (stations S4 and S5) were positively related to CPEw and PIM. S2 was found negatively associated with sk. The species *T. stroemi*, *L. nitidum*, *H. crenulata*, *A. latreilli mediterranea* and *H. vitrea* tended to increase at stations S1 and S6, while *C. gibba* and *N. hystricis* appeared to be abundant at S4 and S5. A large proportion of species such as *P. psamophila*, *A. prismatica*, *M. bidentata*, *P. fauveli, T. compressa* preferred station S2.

In November, stations away from the spillway mouth, such as S2, S6 and S7, were associated with elevated levels of CPEw and POM, while stations relatively near the spillway mouth (S4 and S5) were characterised by higher sk and PIM. The majority of species including *L. nitidum*, *L. maria*, *L. latreilli*, *M. schmidtii* and *M. bidentata* were more abundant at stations S2, S6 and S7. On the other hand, *C. gibba* and *N. hystricis* preferred S4 and S5. Species such as *L. gracilis*, *H. vitrea*, *N. turgida* and *A. latreilli mediterranea*, were not associated with any particular station.

Generally, species were found to be associated with different environmental variables at each sampling time. However, certain species always peaked at the same

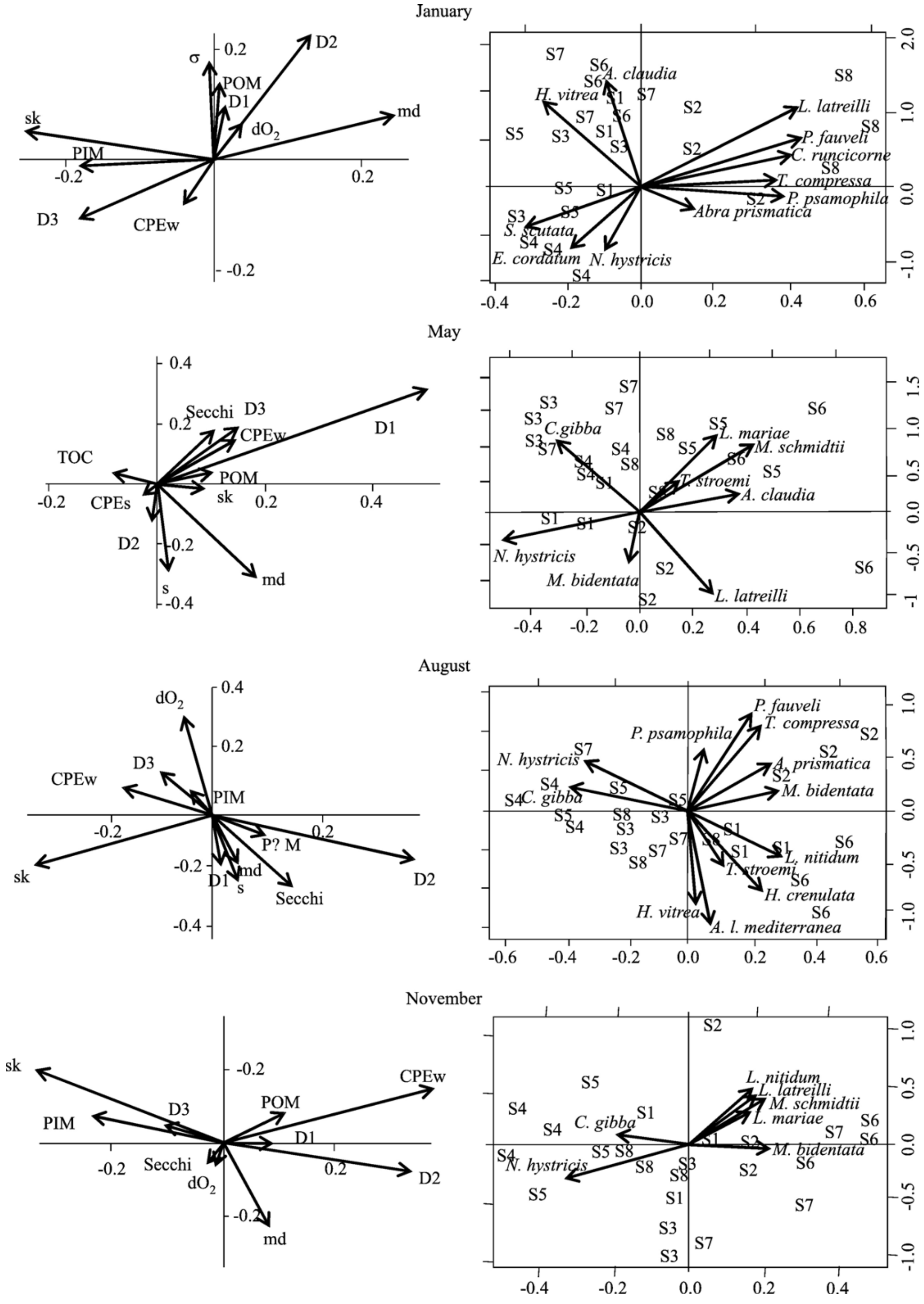


Fig. 6. Projection biplots of the environmental variables and individual taxa onto the non-metric MDS ordination plots of Fig. 5, based on Bray–Curtis dissimilarities of untransformed taxa abundances. Arrows indicate direction and relative magnitude of influence. Only variables and taxa with high projection are shown at each sampling time.

stations, such as *N. hystricis* and *C. gibba*, which usually peaked near the spillway mouth (S4). Moreover the biplots show that dominant suspension feeding bivalves and amphipods were negatively associated with high levels of PIM and sk.

4. Discussion

4.1. Physical processes in the Maliakos Gulf subtidal delta

The present study shows that a relatively high proportion of the variability in macrobenthic community composition in the inner Gulf (i.e. 53 to 69%) can be explained by the environmental variables in the water column and the sediment. This indicates a strong link between the chief characteristics of the delta front environment and the macrobenthic community. This link was time dependent, in terms of both the amount of variation explained and the environmental variables that display significant explanatory power. In particular, a higher proportion of species variation explained by the environmental variables was observed in August and November than in January and May. This coincided with an increase in the number of significant explanatory variables in August and November. In parallel, the explanatory power of variables that are evidently controlled by the riverine discharges such as CPE, PIM and POM concentrations in the water column, Secchi and gradients from the spillway mouth, increased in August and November. Moreover, the symmetrical grain size distributions and the well sorted sediments along the delta front in August and November reflected a lower hydrodynamic regime and thus a more stable sedimentary environment. Subsequently, the multivariate results indicate that a greater proportion of species variation can be predicted from the water column variables and the distance from the river in summer and autumn.

During the period of maximum riverine discharges, the effects of water column processes, such as sedimentation of phytodetrital or fine terrigenous particulate material, occur simultaneously with the effects of sediment resuspension and advection of sediments and other particles induced by near-bottom currents, whether they be driven by wind, tidal movements or thermohaline circulation. This lack of distinction between riverine and hydrodynamic effects on the sediments reduces the explanatory power of water column variables from winter to late spring. The explanatory power of water column variables increases in the absence of strong hydrodynamic effects, as in August and November.

4.2. Macrofauna community structure

Given the small depth and the very fine sedimentary environment of the study site, hydrodynamics can impose mild disturbance upon the species other than that induced by the deposition of terrigenous sediments. Such disturbance operates at a site-wide scale but is modified by local seabed topography and is manifested by transporting sediment and removing macrofauna that live close to the sediment surface as well as the recently settled juvenile stages (Rhoads et al., 1985; Turner et al., 1997; Norkko et al., 2002). At the same time, this facilitates the recovery of localised already disturbed patches through larval colonisation and post-settlement transport (Butman, 1987). This physical passive removal / transport process has been recognized to maintain high patchiness and species diversity in sandflats and estuaries (Emerson and Grant, 1991; Gunther, 1992; Turner et al., 1997). It is believed that the mosaic spatial distribution of most species as well as the lack of consistent spatial trends in the levels of sedimentary pigments in the study site can be attributed to such physical processes. This patchiness in combination with disturbance may also weaken the statistical link between macrofauna spatial structure and the delta front environmental characteristics.

The multivariate analyses suggest that the spatial structure of the community is largely determined by the ability of species to cope with their fluctuating sedimentary environment, most notably to maintain their position and population in a certain patch tolerating at the same time the deposition of fine material. This is supported by the high explanatory power of sorting coefficient and sediment skewness, especially in January and May. As a rule, the dominant Group-2 species did not peak at the same station and season, nor did they have a consistent relation with grain distribution variables during the study. As evidenced by the MDS biplots, this also holds true for the Group-3 bivalves and the carnivorous species, i.e. *N. hystricis* and *H. vitrea*. It is believed that the temporally variable patterns of species dominance, the mosaic of species abundances and the coexistence of amensal (sensu Young and Rhoads, 1971) trophic groups observed along the delta front emerged in response to the spatially and temporally variable intensity and frequency of resuspension events as well as of events associated with the removal and subsequent bedload transport of individuals.

The influence of high turbidity on diversity and function of benthic organisms is recognised to be detrimental or at least negative (GESAMP, 1994). Suspension feeders are the functional group most likely to be directly impacted by increased suspended sediment concentrations. They feed by extracting organic particles from the water column, so high concentrations of inedible suspended sediment particles can directly interfere with food intake by clogging filter-feeding structures, potentially affecting growth and condition of these animals. It has been experimentally shown that suspended material concentrations as high as 80 mg l^{-1} can increase mortality and hamper feeding itself not only of suspension feeding bivalves but also of burrowing deposit-feeding heart sea-urchins and tubicolous polychaetes (Nicholls et al., 2003). It is also well known that turbid waters reduce the ability of the microphytobenthos to photosynthesise and grow, thus indirectly affecting the deposit feeders and grazers in high depositional areas (Kromkamp et al., 1995). Evidently, the suspended material in the inner Maliakos rarely exceeds 40 mg l^{-1} during low land run-off and precipitation periods (Kormas et al., 1998; present study for levels in the SNL) and sedimentary chlorophyll-a values point to relatively high benthic microalgal biomass. Despite the relatively low amounts of suspended material, the negative relationships of macrofauna with the PIM levels, together with the fact that the majority of species are negatively associated with high PIM concentrations, imply that episodes or activities that increase terrigenous inputs will be detrimental for the macrobenthic community.

4.3. Comparison with other subtidal deltaic systems

There were certain similarities in species — genus composition between the inner Maliakos infralittoral community and the ‘coastal detritic’ (DC) and ‘terrigenous muds’ (VTC) communities described by Peres (1967), on the basis of substrate preferences. However, the inner Maliakos Gulf was characterised by the prevalence of highly motile predatory species, such as lumbrinerids and nephthyids, deposit-feeding species, such as paraonids, as well as burrowing suspension feeders such as ampeliscid amphipods and cumaceans, while suspension-feeding polychaetes and bivalves were suppressed near the spillway mouth. Selection for similar taxonomic and functional groups, i.e. highly mobile deposit-feeding and carnivorous groups which can function in the relatively unstable muddy sediments by maintaining a favourable position for feeding and avoidance of disturbances and predation, was also observed in the world’s major subaqueous deltaic systems (Rhoads et al., 1985; Aller and Aller, 1986; Aller and Stupakoff, 1996). In such systems, tube building is possible during periods of minimal disturbance and hydrodynamic stress offering an advantage because this further stabilises the sediment, facilitating colonisation and succession by mature community stages, and allows the fauna to benefit from the large amounts of organic matter entrained in the near-bottom water layer (Rhoads et al., 1978, 1985; Aller and Stupakoff, 1996).

In our case, the lower densities at the stations close to the spillway (S4 and S5) at all sampling times, and the high explanatory power of the distance from it (D2), denote that the Maliakos Gulf community is impacted by the terrigenous inputs. However, high abundances of tube-building and burrowing species as well as of certain bivalve species point to a relatively lower sedimentation regime and hydrodynamic disturbance than in the subtidal depositions of major world rivers. Similarly, in the continental shelf of the Po river (Adriatic Sea), lower levels of disturbance from riverine effluents and the energy regime allowed the same species of burrowing amphipods, bivalves and carnivorous species as in the inner Maliakos to dominate the macrofauna community (Moodley et al., 1998; Mancinelli et al., 1998; Simonini et al., 2004).

Most of the taxa in the study site were Group-2 types, indicating small size and rapid colonisation rates. Indeed, density and biomass trends of small individuals (i.e individual wet body mass <4 mg) in the inner Maliakos indicated that colonisation is a frequent phenomenon, with different taxa dominating in each season (Akoumianaki et al., 2006). In particular, individuals smaller than 0.25 mg, i.e. recently recruited, mainly comprised bivalve molluscs, polychaetes, amphipods and decapod larvae and were present more frequently and in higher numbers at sites at least 2 km away from points 1, 2 and 3 in all seasons, except summer, than near the river mouth during winter. In a similar way, macrofaunal size distributions and biomass estimates from the Amazon shelf indicated an annual turnover and high frequency of juvenile stages for most species, at all times except in peak discharge periods (Aller and Stupakoff, 1996).

The present study demonstrates that there is a link between the spatial distribution of macrobenthos and the environment of the delta front which is evident throughout the year. The benthic system is strongly influenced by hydrodynamics that provide the mechanism maintaining the mosaic species distributions. However, species composition, total abundance and diversity patterns are determined by levels of sediment deposition. The average levels of disturbance allow the fauna to recover and modify the deposits through tube building and burrowing, thus further influencing the sediment microtopography and biogeochemistry. Therefore, the monitoring of macrobenthic community in relation to the study of biogeochemical cycles in deltaic depositions is suggested so as to link changes in land use not only with the diversity and abundance of macrobenthos but also with element fluxes to the sediments. This appears essential in view of the growing evidence that land erosion and increasing deposition of fine sediment in estuaries are related to the rapid growth of human populations in coastal areas (GESAMP, 1994) and that even thin sediment depositions can have chronic effects on the function of these habitats (Lohrer et al., 2004). The present study offers an interpretation of the processes that shape the benthic communities in the deltaic depositions of small non-polluted temperate rivers and can be used as a baseline for the design of future monitoring of such systems.

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