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A case study of mollusc and polychaete soft-bottom assemblages submitted to sedimentary instability in the Mediterranean Sea

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Abstract

In the Strait of Messina (Sicily, Central Mediterranean Sea) strong tidal currents, very irregular hydrological regime and related solid load, and local seismic activity cause sediment instability; this area represents therefore a case-study of a naturally disturbed soft-bottom environment. In this paper, mollusc and polychaete assemblages of the northern part of the Strait were described. Composition, community structure, eco-ethological features, trophic guilds and sediment-type relationships were studied in 64 stations sampled located between 3.5 and 50 m depth in October 1992 by means of a Van Veen grab. A total of 131 species (65 molluscs and 66 polychaetes) were identified. A dense population of the tubicolous polychaete *Ditrupa arietina* was recognized, together with the occurrence of other species tied to a high sedimentation rate, such as *Corbula gibba* and *Tellina distorta*, as well as widespread, mud-tolerant species (*e.g. Chone* spp., *Hyalinoecia tubicola*). Diversity (H′) showed a peak at intermediate depths (10/20 m) and a clear decrease beyond this depth, corresponding to the *Ditrupa* core population. Multivariate comparison between sediment features and community composition throughout the bathymetric gradient showed a narrow ecocline between two environments subjected to opposite hydrodynamic constraints. In the shallower zone, a wide typology of trophic-ethological guilds was related to community patchiness, in contrast to a greater functional uniformity of the deeper assemblage, dominated by sessile, semi-infaunal suspension feeders. A possible role played by a phase of increased rainfall to increase bottom instability, locally emphasized by a previous human activity, is also discussed.

Problem

Many data are to date available on the ecological factors that control composition and distribution of soft-bottom communities, including abiotic interactions of hydrodynamic forces, suspended particulate matter and depositional processes (Gray 1974; Ibanez *et al.* 1993; Paiva 2001), as well as biotic factors such as food supply and larval recruitment (Woodin 1976; Eckman 1979, 1983; Savidge & Taghon 1988; Giangrande *et al.* 1994; Olafsson *et al.* 1994). However, some authors highlighted difficulties in establishing close relationships with single environmental factors (Cabioch 1968; Warwick & Uncles 1980; Snelgrove & Butman 1994; Seiderer & Newell 1999; Newell *et al.* 2001).

In this context, the occurrence of physical disturbance events on the benthic boundary layer represents a further unpredictable constraint, whose role in controlling the benthic community structure has been pointed out by various authors (Holme & Wilson 1985; Hall 1994; Snelgrove & Butman 1994). Although particularly investigated with regard to anthropogenic causes (López-Jamar

& Mejuto 1988; Newell *et al.* 1998; Chou *et al.* 2004), physical disturbance includes a wide typology of natural processes which impact on the benthic environment (strong tidal currents, intermittent storm-generated and seasonal wind waves, bioturbation) and may determine a rapid sediment movement and re-suspension, especially in intertidal and subtidal sedimentary environments. The resulting sediment instability, as a function of its intensity and recurrence, leads to a state of non-equilibrium in benthic communities and, directly or indirectly, affects the functionality of the whole biota. On a regional scale, as occurs in a wide part of the Mediterranean Sea, other geological and climatic factors may determine a steep sea floor slope and a highly irregular regime of torrents (episodic, rapidly moving waters), representing different sources of diffused bottom instability. In this respect, the blooming of some opportunistic species is a local event causally related to such a disturbed environment (*e.g.* Grassle & Grassle 1974; Grémare *et al.* 1998b) and the study of functional groups (*i.e.* trophic guilds, motility, preferential location with respect to the sediment) should be pursued to obtain a further insight into the response of the biota to the above-cited constraints (Pearson & Rosenberg 1978; Padilla & Allen 2000; Pearson 2001).

In the present paper the authors discuss the structural and functional response of the most representative benthic faunal taxa (molluscs and polychaetes) to the sedimentary constraints in an area of the Strait of Messina (central Mediterranean), which is characterized by a naturally disturbed soft-bottom environment and by different sources of anthropogenic impact.

Study Area, Material and Methods

The Strait of Messina separates Italy from the Isle of Sicily, thus connecting the western and eastern Mediterranean basins. The Strait is an area of tectonic activity, characterized by the absence of a continental shelf and by a rough sea-floor morphology, culminating in a narrow submarine sill (Barrier 1987; Colantoni 1987). Irregular solid load inputs are mainly due to seasonal torrents ('fiumare'), characterized by strong and violent flood periods (Amore *et al.* 1995). The occurrence of turbidity currents, triggered off by earthquakes, is also documented (Colantoni 1987). The hydrodynamic regime is dominated by strong tidal currents, reaching more than 300 cm·s^{-1} in speed, which are directly responsible for sediment transport, at least down to 300 m (Colantoni 1995; Mosetti 1995). Water mass energy rapidly decreases northwards from the sill, thus determining a moderate input of fine sediments in the Tyrrhenian basin. The investigated coastal area is located in the northern part of the Strait, and extends for about 2.5 km^2 along 2 km of

coastline, N-NE exposed, with a prevalent coastal drift NE–SE oriented. Moderately higher temperature and lower salinity indicate a prevalence of Tyrrhenian waters compared to Ionian waters, prevalent in the median zone of the Strait (De Domenico *et al.* 1995). The sampled area is scarcely populated and impacted, except for a pipeline operating since early 1980.

Data collection

The sampling plan included a set of stations located along nine transects spaced 200 m apart, with sampling sites at 3.5, 5, 7.5, 10, 20, 30, 40 and 50 m depth (Fig. 1). A total of 64 stations were sampled in October 1992, by a 70 l modified Van Veen grab with a sampling surface of 0.25 m^2. A ROV survey was also carried out in order to observe sea bottom features including the occurrence of sea-grass beds. A total of 0.5 l was collected from the upper layer of each sample for particle-size determination. Sand and gravel percentage fractions were determined by sieving dry samples, using a mesh ASTM-USA size series, whereas silt and clay contents were evaluated by the Buchanan & Kain (1971) column dispersion method. Particle-size quantitative data together with the most descriptive dispersion indices including mean grain size (Mz$_\Phi$, Udden-Wentworth scale), sorting grade (σ classes, Folk & Friedman), and skewness index (Sk, Inman & Folk), were investigated by means of multiple non-parametric Spearman's rank correlation (ρ) to test collinear distributions of sedimentary variables matching the depth gradient. Given the skewed, non normally distributed frequency of most biological populations (*e.g.* Sokal & Rohlf 1995), the same statistic was also employed to highlight which among the most abundant and recurrent species best match the grain-size factors, viewed as a super-parameter (Jansson 1967; Fresi *et al.* 1983).

All living Mollusca and Polychaeta specimens (more than 90% of total fauna) retained by a 1-mm mesh sieve were identified to species level, and the abundance of each species was recorded. Decapod and peracarid crustaceans, as well as echinoderms occurred with very scanty and disperse counts; these taxa were not considered in the present study.

Data analysis

Individual density (no./0.25 m^2) and number of species (S) together with two weighted structural indices, Shannon–Weiner diversity (H′) and Pielou's evenness (J), were estimated along the depth gradient (Pielou 1975; Magurran 1991; Lande 1996; Clarke & Warwick 2001). Samples were aggregated every four depths units and minimum, maximum and mean values of the structural indices were
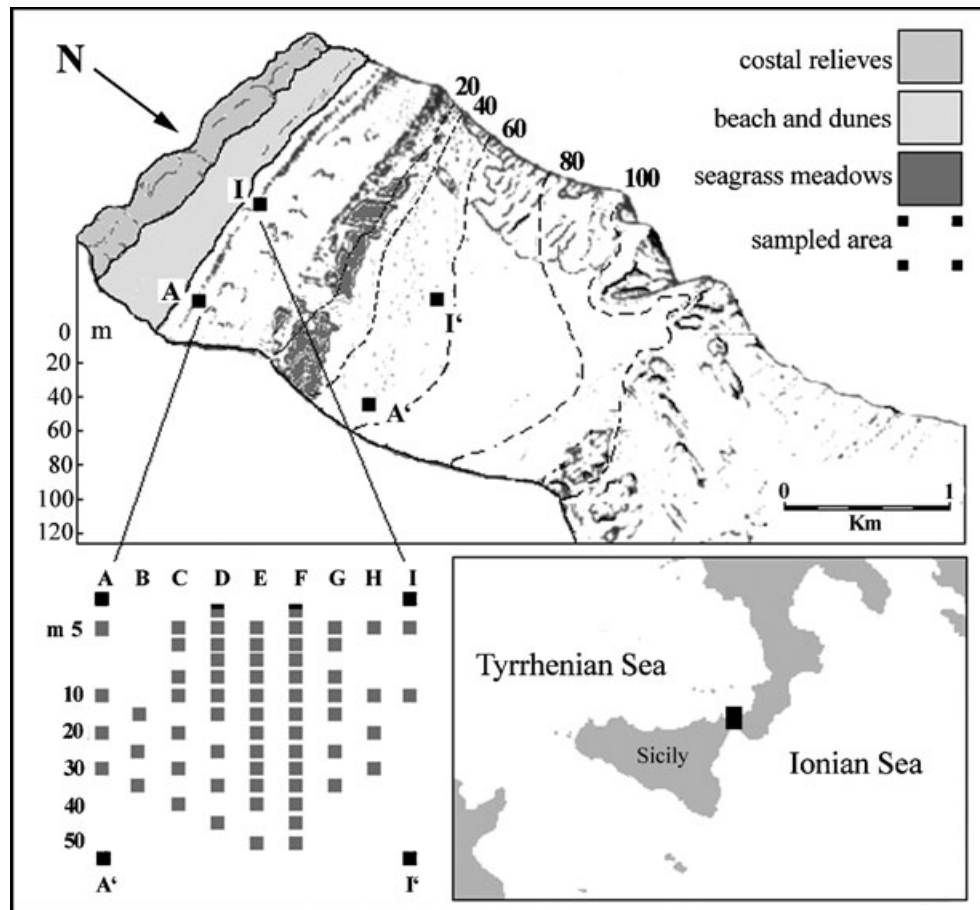
Fig. 1. Study area and sample's location. The geographic area and investigated site (black arrow) are shown at the bottom; the general sampling grid is also shown (grey checks): letters from 'A' to 'I' indicate the transects according to depths. A section of the local topography is displayed above as regarding both the continental shoreline and the main sea bottom features (Department of Animal Biology and Marine Ecology, Messina University, unpublished data).

then calculated. In order to investigate similarities/dissimilarities of the assemblages, the Bray–Curtis similarity coefficient (square root transformed data) was employed (Bray & Curtis 1957). Given the extremely impoverished macrofauna, 10 of the collected samples were considered as outliers and subsequently were removed from the analysis. Cluster analysis (group average linkage), MDS ordinations, two-way nested ANOSIM test and similarity percentage analysis (SIMPER) (all included in the PRIMER v5 package) were also applied (Field *et al.* 1982; Clarke 1993; Clarke & Warwick 2001). *K*-dominance curves have also been plotted in order to evaluate the distribution pattern of individuals among all ranked species at different sedimentary conditions.

Functional composition of the studied communities was carried out by analysing the patterns of trophic guilds and eco-ethological adaptations, such as motility and location with respect to the sediment surface (Jumars & Fauchald 1977; Fauchald & Jumars 1979; Pearson 2001).

The identified feeding guilds included the following categories: (a) carnivores (macrophages predators, including parasites); (b) herbivores (macrophages and grazers); (c) omnivores (macrophages, non-selective eaters); (d) surface detritus feeders (microphages, with selective feeding on organic detritus at the sediment surface); (e) subsurface deposit feeders (microphages, with selective or non-selective feeding on detritus below the sediment surface); (f) filter feeders (microphages, with active or passive feeding on suspended particulate matter). The following eco-ethological categories were identified: (i) epifauna (fauna standing or moving at the surface or in the first millimetres of the sediment); (ii) semi-infauna (fauna standing or moving with almost 2/3 of the body permanently buried into the sediment); (iii) infauna (fauna standing or moving totally and permanently buried into the sediment); (iv) motile (actively moving species); (v) discretely motile (species with limited motility only); (vi) sessile (species fixed to the substrate).

Species' abundance values were aggregated into the previously presented functional categories per sample and their percentages were subsequently incorporated in the MDS ordination analysis.

Results

The benthic environment

ROV observations showed some important bottom features, including main sedimentary structures and sea grass bed distributions. In particular, ripples, mega-ripples and dunes, were widely distributed at the shallower depths, while, in the deeper zone, the sediment surface appeared covered by a 'fluff' layer, some centimetres thick. A patchy *Cymodocea nodosa* meadow was also recorded in depths ranging from 12 to 22 m, except over a buried pipeline.

Particle-size analysis (Fig. 2A and B) showed that the whole area was characterized by a prevalence of moderately to poorly sorted fine sands. Up to 20 m depth, a minor fraction of gravels or silt, varying from 2 to 15%, was recorded. A moderate sorting grade (σ mean value 0.70) characterized these shallower sediments up to 10 m. They had a mean grain size from −0.02 to about 3.00 Φ and prevalent negative values of the skewness. At the zones deeper than 15 m the silt content progressively increased (20/30%), showing Mz_Φ values ranging between 3 and more than 4 Φ (very fine sands to silt/clay), a poor sorting grade ($\sigma = 0.87$ on average), and prevalent positive scores of Sk. Such marked differences between shallower and deeper samples occurred within a depth of five meters. Silt and sand contents, Mz_Φ and Sk values *versus* depth (Spearman correlation coefficient ρ: 0.85, −0.79, 0.82, 0.77 respectively, P < 0.001) indicated a prevalence of erosive processes above 15/20 m depth and a sediment deposition regime below 20/25 m. In contrast, σ values indicated poorly or moderately sorted sediments along the whole bathymetric range (0.40, P < 0.01), poorly correlated with the other parameters (gravels, e: 0.12, P > 3%; silt/clay, 0.51, P < 0.01) except for sands percentage (−0.68, P < 0.01), thus indicating an irregular deposition regime, with a moderate reduction of particle sorting grade in deeper samples. Highly negative correlated fractions were sands *versus* silt/clay (−0.89, P < 0.001); sand content also decreased with respect to both Sk (−0.72, P < 0.001), whilst silt/clay was positively related to Sk (0.81, P < 0.001).

Mollusc and polychaete communities

A total of 131 species were identified: 65 species of molluscs (1042 individuals) and 66 species of polychaetes
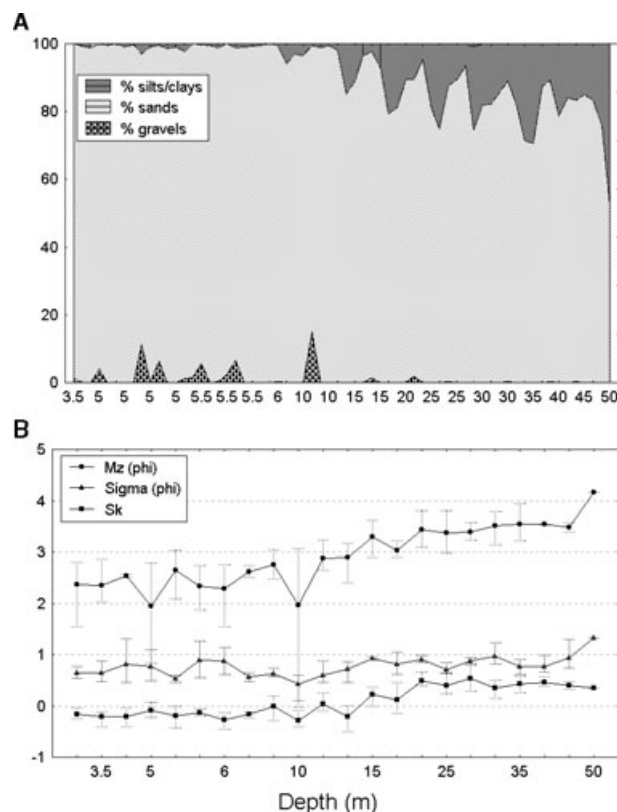
Fig. 2. Sedimentary characterization of the investigated area. A: Bathymetric distribution of the three main particle-size classes, estimated as relative percentage for each sampling station. Sand fractions are almost ubiquitous, progressively decreasing beside 10/15 m; the shallow zone shows the scattered presence of coarsest fractions (cobbles and gravels), whereas mud content sharply increases deeper than 15 m. B: Linear trends (three-sample point aggregated, interval bars displayed as minimum, maximum and mean values) of some grain-size indices, well describing the two different sedimentary environments (explained in the text); isobaths of 10/15 m represent the narrow strip of changing processes.

(10,148 individuals). Molluscs were absent at nine stations, whereas polychaetes were absent at ten stations. Polychaetes had 10 fold higher abundance than molluscs. The majority of the species (92) were characteristic of well-defined sub-tidal communities; 32 species were widely distributed (*e.g.* Bellan-Santini *et al.* 1994 and cited references). Seven species are reported in the literature as indicators of high sedimentation rates. As regards this latter group, the free-living tusk-shaped serpulid *Ditrupa arietina* was found in high densities, reaching more than 500 ind./0.25 m^2 (mean value 53.3, maximum standard deviation 116.23).

In shallower zones, mollusc density showed a clear prevalence compared to polychaetes, which dominated the sediments of the deeper waters. *Donax venustus*, *Nassarius mutabilis*, *Chamelea gallina*, *Glycera alba*, *G. gigantea* and

Sigalion mathildae were the species that preferentially occurred within 20 m depth, while other euritopic, mud-tolerant species, such as the polychaetes *Ditrupa arietina*, *Aponuphis bilineata bilineata* and *A. brementi*, *Chloeia venusta*, species of the genus *Chone*, *Euclymene oerstedi*, *Eunice vittata*, *Marphysa bellii*, *Nematonereis unicornis*, *Phyllodoce lineata*, *Spiophanes kroyeri kroyeri*, *Sthenelais boa*, and the molluscs *Hynia limata*, *Pitar rudis*, *Tellina distorta*, *Timoclea ovata* and *Turritella communis*, were prevalent in the deeper zones. *D. arietina*, showed the highest density between 35 and 45 m, about 10 m deeper than its previous records from the north Mediterranean (Grémare *et al.* 1998a,b). Moreover, the onuphid *Hyalinoecia tubicola*, the nephtid *Nephtys hombergii* and the corbulid *Corbula gibba* were distributed on both bathymetric zones, occurring at depths greater than 20 m. Some of the previously cited taxa were more or less correlated to the amount of sands (*D. venustus*, $\rho = 0.46$, P < 0.001; *S. mathildae*, 0.40, P < 0.01; *D. arietina*, −0.70; *Aponuphis* spp., −0.63; *Chone* spp., −0.54; *T. distorta*, −0.53; *C. venusta*, −0.48, all P < 0.001; *H. tubicola*, −0.40, P < 0.01) and, conversely, to silt/clay percentages or to related Mz_Φ values (*D. venustus*, $\rho = -0.44$ and −0.48, respectively; *D. arietina*, 0.75 for both; *Aponuphis* spp., 0.61 and 0.62; *Chone* spp., 0.59 and 0.54; *T. distorta*, 0.55 and 0.60; *C. venusta*, 0.52 and 0.50, all P < 0.001; *H. tubicola*, 0.46, P < 0.001 and 0.41, P < 0.01).

Community structure analyses

The trends of the main structural indices (mean values) showed some degree of progressive community change, according to the two different sedimentary environments (Fig. 3). Density of individuals (no./m^2) was mildly low (<100 ind./0.25 m^2) up to 20 m, showed a maximum at 35/40 m (*Ditrupa* core population) and decreased deeper. Species number (S) was low in the shallow zone, and moderately high in the deeper zone, with a slight reduction beyond 30 m. Equitability (J) was high up to 15/20 m, whilst it becomes lower between 20/40 m due to the rapid increase of some species (*D. arietina* in particular). All indices are summarized by H′ diversity, which showed low values at the shallower site (4/6 m), with a peak at intermediate depths (10/20 m) and a clear decrease deeper. At 45/50 m depth we observed an increase of diversity and evenness in agreement with the decline of *Ditrupa* population.

Similarity, the clustering (Fig. 4) emphasized the separation of macrofaunal assemblages into two groups, which match the two different bathymetric levels previously highlighted. At 30% similarity it was possible to distinguish all samples down to 20 m depth, separated into four main clusters (groups I, II, III, VII) plus four small clusters (two stations only, groups IV, V, VI, VIII) and four single shallow stations. In addition, a cluster grouped almost all samples below 25 m together (group IX), which, at a higher similarity level (35%) may be divided in two further sub-groups according to overlapping depth levels: from 20 to 35 m and from 25 to 50 m. This second cluster includes virtually the deeper assemblages and shows greater homogeneity among samples. The computation of the related MDS (Fig. 5) is a good representation of the community pattern; the superimposition of the identified groups confirms the agreement of the established assemblages to the two different sedimentary environments, although the comparison is not easily interpreted at more than 30% similarity level. Moreover, by superimposing the silt/clay contents in turn on the MDS plot, a clear gradient of particle-size sediment composition of the samples emerges. The assemblages established within 4 to 20 m
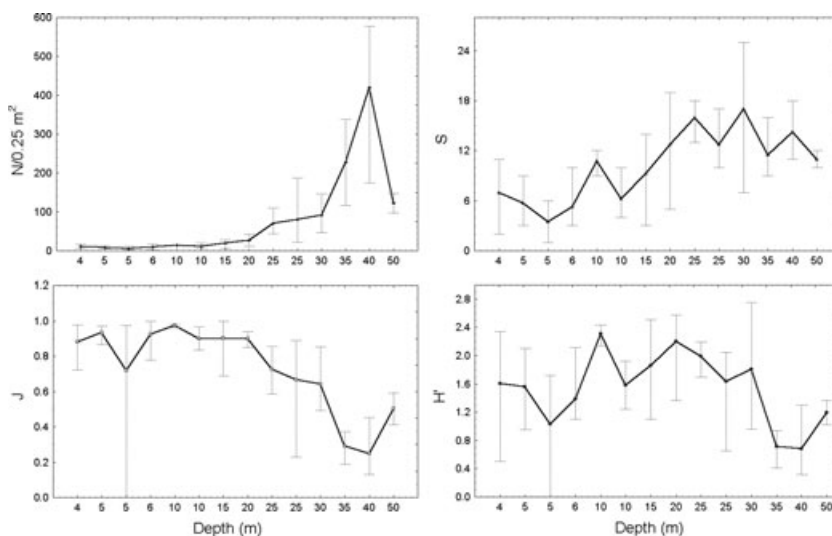
Fig. 3. Aggregated broken-line plots of the main biotic structural indices according to the bathymetry. Similar sample depths are aggregated every four units; interval bars (minimum/maximum values) are also indicated.
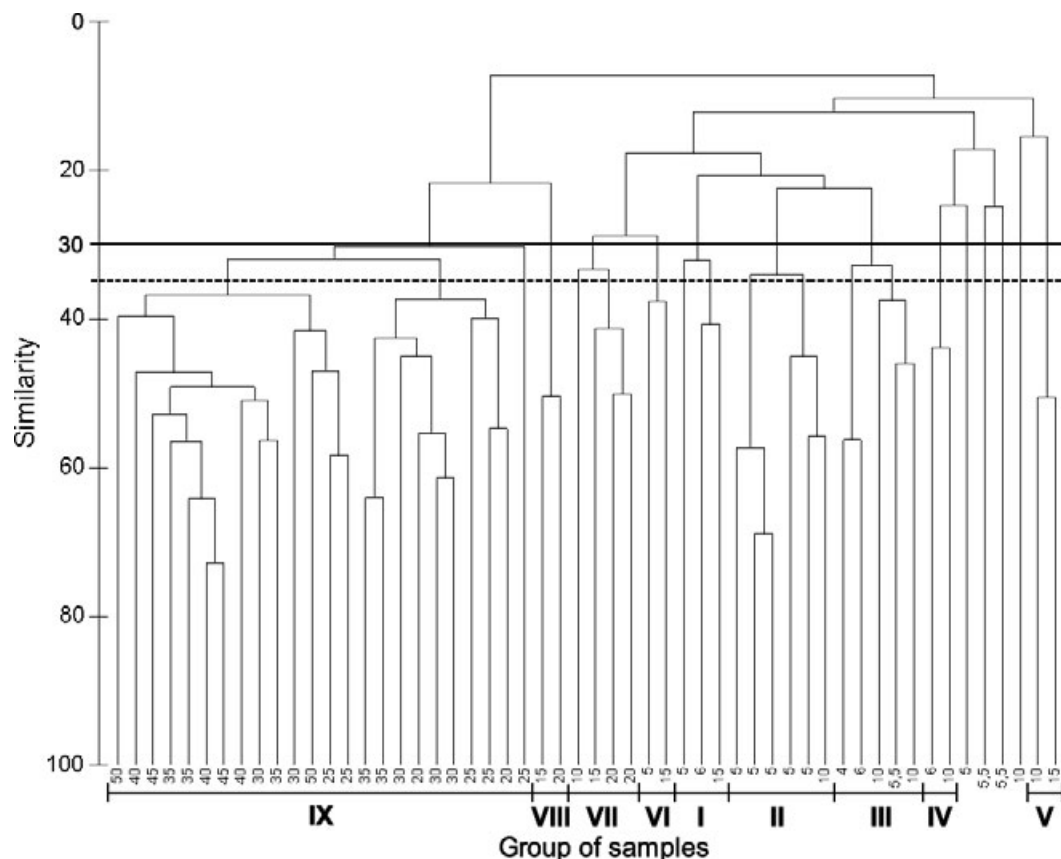
Fig. 4. Cluster plot of the 54 out of 64 quantitative samples, indicated as depths. Five main groups are identified at 30% (continuous line), plus other small clusters or single stations; at 35% level (dashed line) other sub-clusters are highlighted according to depth.
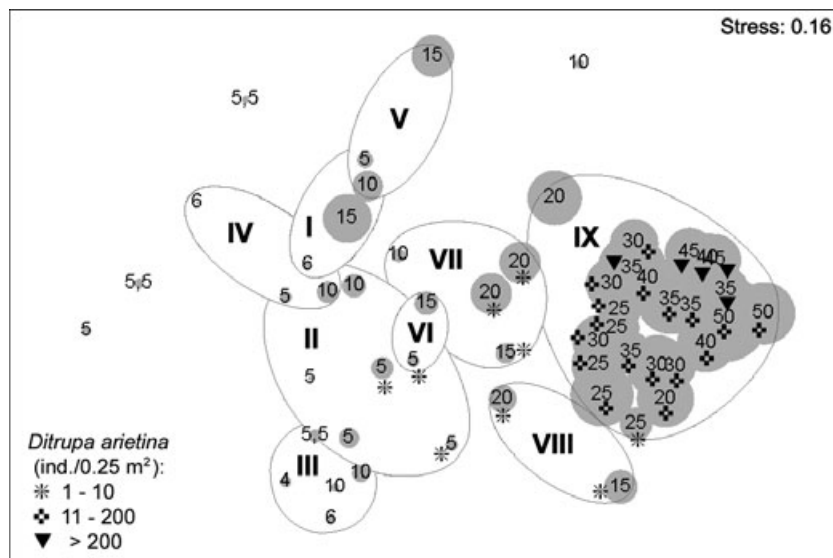
Fig. 5. Non-metrical multi-dimensional scaling of the investigated communities with superimposed clusters at 30% of similarity. Circles refer to the silt/clay percentage values (not transformed). Numbers inside the circles indicate the sample depth (m). Abundance classes of the serpulid *Ditrupa arietina* are also superimposed. The clear separation between the shallower, high-energy and fluctuating environment and the deeper, more uniform depositional zone is shown.

depth because of the high-energy environment and the occurrence of the *Cymodocea nodosa* seagrass patches, shows a highly variable spread and is responsible for such

a level of dissimilarity. On the other hand, the transition from the shallower to deeper stations is in accordance with the presence of several opportunistic, mud-tolerant

and widespread species. The correlation between community density and increasing depth is caused by the very high density of the serpulid *Ditrupa arietina*, which is not, however, the only species responsible for the observed clustering. In fact, the superimposition of relative abundances (standardized by sample total) on the MDS highlighted other species restricted to the deeper stations (IX group), such as *Aponuphis b. bilineata*, *Chloeia venusta*, *Chone acustica* and *C. arenicola*, *Hinia limata*, *Nematonereis unicornis*, *Phyllodoce lineata*, *Pitar rudis*, *Spiophanes kroyeri kroyeri*, *Sthenelais boa*, *Tellina distorta*, *Timoclea ovata* and *Turritella communis*, most of which are typical of muddy or sandy-muddy bottoms. The calculation of the index of multivariate dispersion (IMD), to estimate the sample-point dispersion under high disturbance conditions (Warwick & Clarke 1993) at the two bathymetric ranges of 0–20 and 20–50 m, showed notably diverse values of dispersion (1.252 and 0.460 respectively) and a consequent high IMD (0.793). This index thus quantifies the high variability of the shallower environment and the higher cenotic homogeneity of the deeper one.

A further validation of the role played by depth was given by the two-way nested ANOSIM test, performed for all samples in order to evaluate the effect of sites rather than transects on the total variance. Transects, defined *a priori*, represent a possible geographic variability source, occurring east-westward along the shoreline, whilst site samplings should summarize the variability due to the bathymetric/sedimentary gradient. The two-way test confirms that the factor 'site' is more important than the 'transect' one; in fact the former significantly differs (P-level 0.3% with a global R of 0.73), in contrast with the latter, showing no statistical discrimination (p-level 17.7%, R = 0.062).

To evaluate the contribution of each species to the total (dis)similarity through the similarity percentage analysis (SIMPER), the whole assemblage has been divided into two main bathymetric levels (Tables 1 and 2). The shallower zone (from 4 to 20 m), showed a low similarity (average S' 16.2%). The polychaete *Sigalion mathildae*, the molluscs *Nassarius mutabilis* and *Donax venustus* reach a cumulative percentage of 66.3%, but only the former is a

Table 1. Similarity percentage analysis (SIMPER S'$_{av.}$) within mollusc and polychaete assemblages at two depth ranges. Cut off for low contribution: 90%.

species – depth range	Av.ab. on $1m^2$	S'$_{av.}$	S'$_{av.}$/SD	cont.%	cum. %
group 1 (≤20 m)		16.22			
Sigalion mathildae	1.56	7.28	0.84*	44.88	44.88
Nassarius mutabilis	0.84	1.98	0.42	12.23	57.11
Donax venustus	0.75	1.50	0.32	9.22	66.33
Ditrupa arietina	0.97	0.80	0.24	4.90	71.24
Hyalinoecia tubicola	1.00	0.63	0.23	3.91	75.15
Glycera alba	0.19	0.38	0.17	2.37	77.52
Phylo ligustica	0.25	0.35	0.17	2.17	79.69
Tellina nitida	0.53	0.34	0.20	2.11	81.80
Nephtys hombergii	0.31	0.31	0.20	1.88	83.68
Acantocardia tuberculata	0.28	0.30	0.21	1.87	85.55
Glycera unicornis	0.22	0.19	0.14	1.16	86.71
Onuphis eremita	0.25	0.18	0.10	1.08	87.79
Scolaricia typica	0.22	0.17	0.11	1.06	88.86
Notomastus aberans	0.16	0.14	0.11	0.87	89.73
Chone duneri	0.31	0.14	0.14	0.84	90.57
group 2 (>20 m)		38.34			
Ditrupa arietina	136.68	21.21	2.18**	55.32	55.32
Hyalinoecia tubicola	2.91	3.09	1.05*	8.07	63.39
Chloeia venusta	2.68	2.29	0.87*	5.97	69.36
Aponuphis brementi	3.41	2.22	0.82*	5.80	75.16
Chone duneri	3.00	1.70	0.51	4.42	79.58
Marphysa bellii	1.32	1.47	0.68	3.85	83.42
Tellina distorta	3.41	1.18	0.52	3.07	86.50
Nematonereis unicornis	0.59	0.52	0.36	1.34	87.84
Sigalion mathildae	0.77	0.46	0.36	1.19	89.04
Chone arenicola	1.59	0.39	0.29	1.02	90.05

Av.ab., average abundance (no.ind./m²); S'$_{av.}$, total and partial average similarity; cont.%, percentage contribution of each species to the group similarity; cum.%, cumulative percentage contribution to group similarity; SD, standard deviation. Highly significant and significant species in determining the intra-group S' are signed by ** and *, respectively.

Table 2. Pairwise comparisons by means dissimilarity percentage (SIMPER, $\delta_{av.}$) between the two depth-groups of molluscs and polychaetes. Cut off for low contribution: 88%.

species	group 1 on lm^2 (Av.ab.)	group 2 on lm^2 (Av.ab.)	$\delta_{av.}$	$\delta_{av.}$/SD	cont.%	cum.%
groups 1 and 2			90.96			
Ditrupa arietina	0.97	136.68	23.50	1.92**	25.84	25.84
Hyalinoecia tubicola	1.00	2.91	3.57	1.26*	3.93	29.77
Aponuphis brementi	0.19	3.41	3.49	1.00*	3.84	33.61
Chone duneri	0.31	3.00	3.41	0.90*	3.75	37.36
Chloeia venusta	0.13	2.68	3.25	1.26*	3.57	40.93
Tellina distorta	0.06	3.41	2.77	0.86*	3.04	43.97
Sigalion mathildae	1.56	0.77	2.44	1.22*	2.68	46.65
Marphysa bellii	0.19	1.32	2.25	1.05*	2.47	49.12
Nassarius mutabilis	0.84	0.09	1.51	0.83*	1.66	50.78
Chone arenicola	0.03	1.59	1.50	0.63	1.65	52.43
Nematonereis unicornis	0.00	1.59	1.34	0.71	1.48	53.91
Donax venustus	0.75	0.00	1.33	0.65	1.46	55.36
Lumbrineris latreilli	0.13	0.73	1.21	0.66	1.33	56.70
Chone cf. *acustica*	0.25	0.73	1.12	0.49	1.24	57.93
Hinia limata	0.06	0.64	1.10	0.70	1.21	59.14
Aponuphis bilineata	0.00	0.64	1.08	0.55	1.18	60.33
Phyllodoce lineata	0.00	0.41	1.07	0.64	1.18	61.51
Pitar rudis	0.00	0.77	1.02	0.66	1.12	62.63
Tellina nitida	0.53	0.27	1.02	0.56	1.12	63.75
Sthenelais cf. *boa*	0.03	0.36	1.00	0.57	1.10	64.85
Eunice vittata	0.09	0.45	0.98	0.69	1.08	65.93
Glycera tridactyla	0.06	0.55	0.95	0.54	1.04	66.97
Tellina fabula	0.22	0.91	0.93	0.35	1.02	67.99
Spiophanes kroyeri kroyeri	0.00	0.77	0.89	0.51	0.98	68.97
Phylo ligustica	0.25	0.18	0.86	0.62	0.95	69.92
Turritella communis	0.00	0.55	0.85	0.42	0.93	70.84
Glycera alba	0.19	0.18	0.82	0.54	0.91	71.75
Euclymene oerstedi	0.00	0.55	0.81	0.59	0.89	72.64
Glycera unicornis	0.22	0.27	0.75	0.57	0.83	73.47
Timoclea ovata	0.00	0.41	0.74	0.52	0.81	74.28
Corbula gibba	0.19	0.27	0.71	0.52	0.78	75.07
Bela nebula	0.13	0.18	0.64	0.52	0.70	75.77
Plagiocardium papillosum	0.03	0.45	0.63	0.47	0.69	76.46
Acanthocardia tuberculata	0.28	0.05	0.63	0.54	0.69	77.16
Notomastus aberans	0.16	0.23	0.62	0.47	0.68	77.84
Nephtys hombergii	0.31	0.00	0.60	0.50	0.66	78.50
Placostegus tridentatus	0.03	0.32	0.59	0.49	0.65	79.15
Notocirrus scoticus	0.25	0.14	0.55	0.47	0.61	79.75
Spio multioculata	0.09	0.18	0.52	0.39	0.57	80.32
Lumbrineris emandibulata mabiti	0.13	0.18	0.51	0.46	0.56	80.87
Onuphis eremita	0.25	0.00	0.48	0.35	0.53	81.40
Naytiopsis granum	0.38	0.00	0.46	0.24	0.50	81.90
Scolaricia typica	0.22	0.00	0.46	0.35	0.50	82.40
Smaragdia viridis	0.25	0.09	0.44	0.32	0.48	82.89
Ensis ensis	0.06	0.09	0.38	0.29	0.42	83.30
Orbinia cuvieri	0.00	0.23	0.38	0.39	0.42	83.72
Mangelia smithi	0.00	0.18	0.37	0.31	0.41	84.12
Chamelea gallina	0.16	0.00	0.37	0.35	0.40	84.53
Glycera gigantea	0.22	0.00	0.36	0.30	0.39	84.92
Neverita josephinia	0.16	0.00	0.35	0.36	0.38	85.30
Leiochone clypeata	0.13	0.09	0.35	0.33	0.38	85.69
Abra prismatica	0.00	0.18	0.33	0.30	0.37	86.06
Goniada maculata	0.03	0.18	0.33	0.35	0.36	86.42
Pista sp.	0.00	0.14	0.33	0.39	0.36	86.78
Gouldia minima	0.00	0.18	0.30	0.31	0.33	87.10

species	group 1 on lm^2 (Av.ab.)	group 2 on lm^2 (Av.ab.)	$\delta_{av.}$	$\delta_{av.}$/SD	cont.%	cum.%
Lunatia macilenta	0.00	0.09	0.29	0.21	0.32	87.42
Mactra glauca	0.13	0.00	0.27	0.24	0.29	87.71
Dentalium inaequicostatum	0.06	0.09	0.27	0.33	0.29	88.01

Av.ab., average abundance (no.ind./m²) of species within the group; $\delta_{av.}$, total and partial average dissimilarity; cont.%, percentage contribution of each species to the inter-group dissimilarity; cum%, cumulative percentage contribution to the inter-group dissimilarity; SD, standard deviation. Highly significant and significant species in determining the inter-group δ are signed by ** and *, respectively.

good discriminating species as shown by the S′/SD ratio column (Clarke 1993; Clarke & Warwick 2001). The communities characterizing the deeper water (20 to 50 m) show a greater 'intra-group' similarity (average S′ 38.3%), mainly due to the serpulid *D. arietina* and, secondarily, to *Hyalinoecia tubicola*, *Chloeia venusta* and *Aponuphis brementi*, responsible together for more than 75% of cumulative similarity. In contrast, the comparison of this group with the first one shows a high dissimilarity percentage, which accounted for almost 91%. This fact supports the role played by the serpulid *D. arietina* as the main local discriminating species, reaching almost 26% of cumulative dissimilarity δ alone. Other significant species in determining the inter-group dissimilarity, are *H. tubicola*, *A. brementi*, *Chone duneri*, *C. venusta*, *Tellina distorta* and *Marphysa bellii*, prevailing in the deeper level, whilst *S. mathildae* and *N. mutabilis* are more representative of the shallower zone.
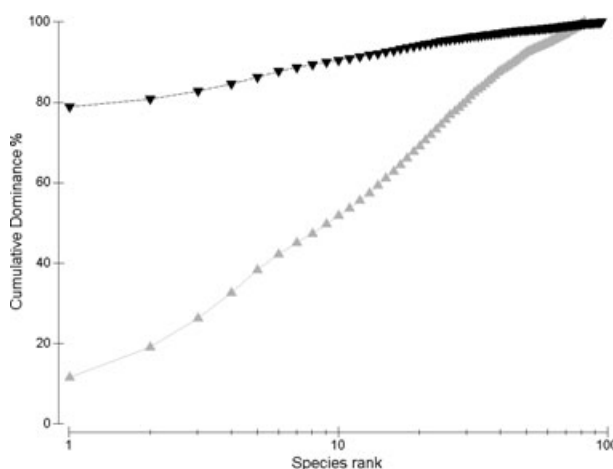

Fig. 6. *K*-dominance curves for the polychaete and mollusc macrofauna in the two identified depth ranges. Within the first 20 m (grey triangles) the biota shows a similar sigmoidal trend indicating a high number of species with a good distribution of population densities. From 20 to 50 m (black triangles), although a noticeable species richness, the *Ditrupa arietina* alone accounts for almost 80% of cumulative abundance, hence the 'flat-shaped' curve.

The *k*-dominance curves (Fig. 6) describe the distribution patterns of individuals among ranked species (Lambshead *et al.* 1983; Warwick 1993), thus stressing the different role of high density species with respect to the whole assemblage. In particular, the shallow assemblages (4 to 20 m) comprise a high number of taxa (82), whose cumulative dominance is well distributed among the species; this pattern is best fitted by a logistic curve. In contrast, the assemblages deeper than 20 m are characterized by the prevalence of the serpulid polychaete, which account for up to 80% of cumulative dominance alone (out of 95 total taxa); this pattern produces a typical 'flat' curve and is considered indicative of disturbance.

Trophic and eco-ethological features

As regards the eco-ethological and feeding habits (Figs 7 and 8), sessile forms (*sensu* Fauchald & Jumars 1979), most of which belong to filter/suspension feeders, are restricted to the deeper stations, while motile and discretely motile species showed a preferential distribution in the shallow/intermediate stations. Impoverishment of the infauna in the deeper sedimentary environment is observed. Macrophages/omnivores and microphages/surface detritus feeders displayed a different pattern, the former mainly distributed in the intermediate zone. Grazers/herbivores match with the limited patches of seagrass meadow. Finally, the clear decrease of both carnivorous and sub-surface trophic guilds in the deeper zone is noteworthy.

Discussion

In the studied area a narrow eco-coenocline (Attrill & Rundle 2002) settles from a sandy shallow bottom up to muddy deeper sands. The high biodiversity of the intermediate belt has been observed in other investigations in the Tyrrhenian Sea (Fresi *et al.* 1983; Gambi & Giangrande 1986), testifying to the increased spatial heterogeneity, and therefore the number of potential niches, due to mixed sediments along the ecocline.
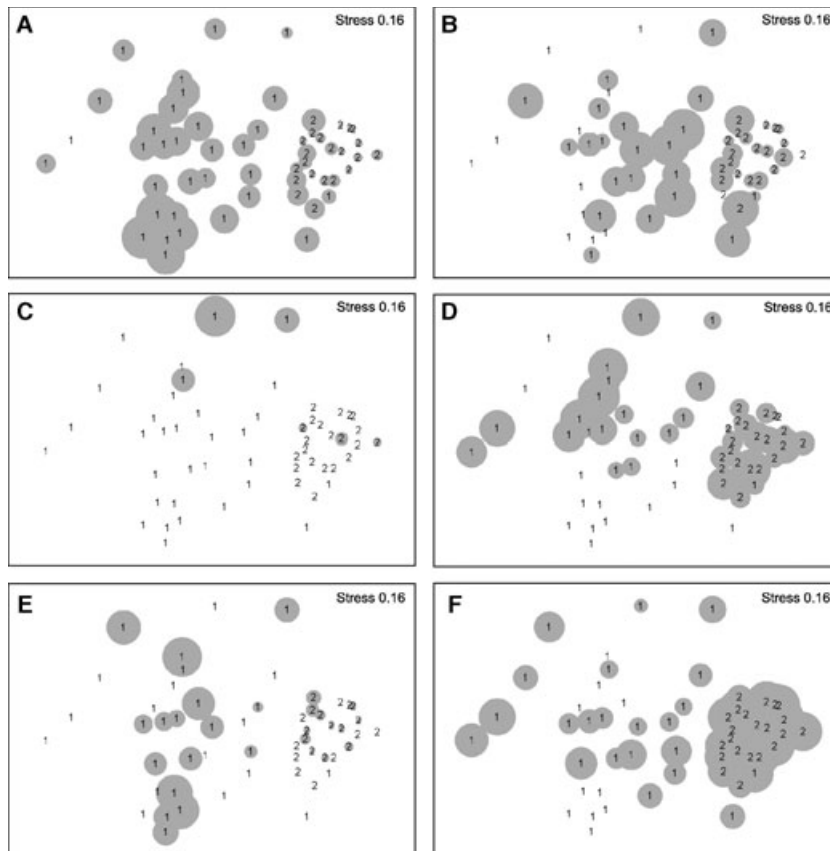
Fig. 7. MDS 2-d plots displaying the distribution patterns of the main identified functional groups. Circle sizes refer to the relative percentage of each functional group. Numbers inside the circles indicate the two bathimetric ranges (see Fig. 6). The differential deep distribution of both sessile and discretely motile semi-infauna is shown in comparison to the shallow/intermediate settlement of motile/discretely motile epifauna and infauna. Sessile epifauna and infauna are not shown, due to very low occurrence. A: Motile epifauna; B: motile infauna; C: motile semi-infauna; D: discretely motile semi-infauna; E: discretely motile infauna; F: sessile semi-infauna.
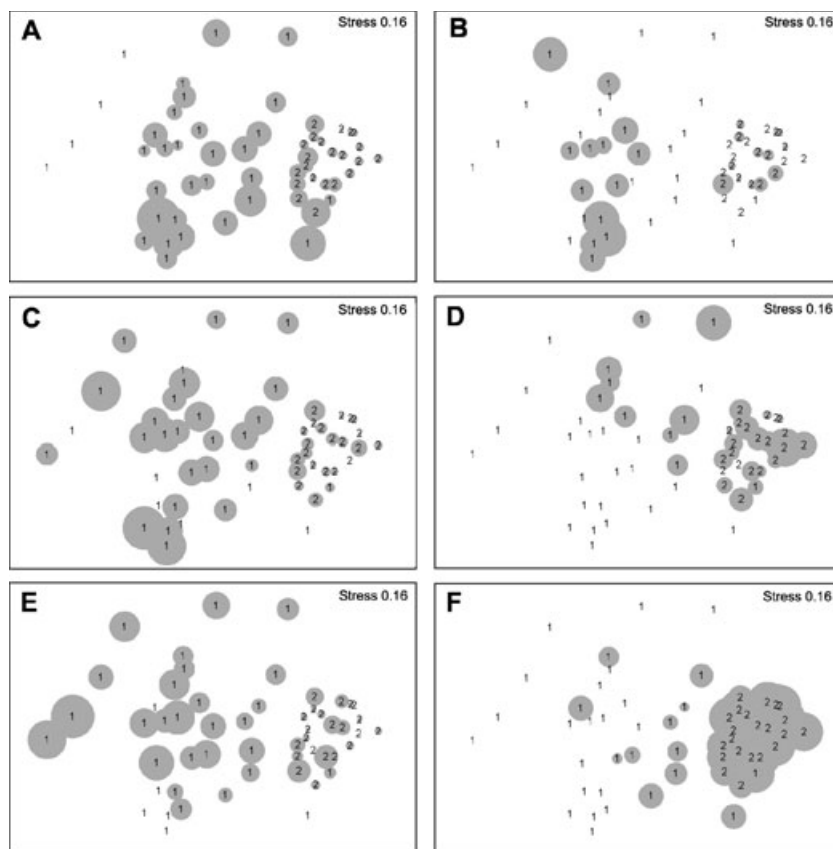
With respect to trophism and motility (Yonge 1928; Jorgensen 1966; Pearson & Rosenberg 1978; Fauchald & Jumars 1979; Maurer & Leathem 1981; Pearson 2001) two main patterns have been identified. In the shallow sublittoral bottoms, a wide range of trophic-ethological habits is associated with the community patchiness. In contrast, a greater functional uniformity exists in the deeper biotopes, dominated by sessile, semi-infaunal suspension-feeders.

In such a context, the feeding plasticity, as an adaptation to switch between suspension and deposit feeding, is suggested by literature data for *Ditrupa arietina* (Jordana *et al.* 2001a), *Corbula gibba* (Yonge 1946; Salen-Picard 1981) and species of the genus *Chone* (Giangrande 1989). Such a strategy would allow these species to exploit the suspended POM during peaks of fall-out from the upper levels (turbidity phases), as well as the deposited organic bulk in the phase of decreasing sediment deposition. This etho-physiological adaptation would also avoid secondary, negative phenomena such as covering and clogging the feeding/respiratory structures (Brenchley 1981). It may be hypothesized that after a strong turbidity event, the local establishment of high densities of suspension/surface detritus-feeders could prevent a successful recruitment of other more specialized

detritus-feeding species. Thus, a selective reduction of sub surface-deposit feeders may therefore occur at deeper levels (Rhoads & Young 1970; Wildish 1977; Long & Lewis 1987). Soft-bottom communities dominated by *D. arietina* are noteworthy for the oligotrophic Calabrian and Sicilian waters (Giacobbe & Parisi 1997). Climatic events (Grémare *et al.* 1998b) as well as anthropogenic disturbance (Sardà *et al.* 2000) have been correlated with such dramatic serpulid population increases. The ecological significance of *Ditrupa* as an indicator of sediment instability was first suggested by Picard (1965), who dealt with the so-called 'heterogeneous assemblages'. From a palaeo-ecological point of view, Di Geronimo (1984) and Di Geronimo & Robba (1989) considered *Ditrupa*-dominated communities as relevant to tectonic and/or climatic instability within Sicilian plio-pleistocene sedimentary basins. Recently, several field and laboratory investigations on this species have been carried out in the Mediterranean Sea, both from a synecological (Grémare *et al.* 1998b; Sardà *et al.* 1999, 2000) and auto-ecological view (Grémare *et al.* 1998a; Medernach & Grémare 1999; Jordana *et al.* 2000, 2001a,b; Medernach *et al.* 2000; Riisgard *et al.* 2002). A high temporal variability of population dynamics, an extended breeding period with a high reproductive effort, and good dispersal

Fig. 8. MDS 2-d plots displaying the distribution patterns of the trophic guilds. Circle sizes refer to the relative percentage of each feeding category. Numbers inside the circles indicate the two bathimetric ranges (see Fig. 6). According to the previous figure, plots show the dominance of suspension-feeder guilds, mainly due to *Ditrupa arietina*, *Chone* species and *Tellina distorta*, in the deeper level. Most of the omnivores, *i.e. Hyalinoecia tubicola*, are localized at the intermediate depths, whereas deposit-feeder guilds display a different preferential distribution. A: Macrophages, carnivore; B: macrophages, omnivores; C: macrophages, herbivores/grazers; D: microphages, surface detritus-feeders; E: microphages, sub-surface deposit-feeders; F: microphages, suspension/filter-feeders.

ability of the 6-week planktotrophic larvae allow the species to colonize rapidly after a phase of high sedimentation. Therefore, *D. arietina* shows evidence of a mixed strategy: it behaves as a good fast colonizer species during the pelagic or settlement stages, and as a competitive specialist during the adult benthic stage (Grassle & Grassle 1974).

The observed high density of *D. arietina* in the studied area may be a result of both climatic and anthropogenic factors. With regard to the former, the bloom observed in late 1992 could be related to high rainfall recorded in the winter of 1990 (Agnese *et al.* 2002). This hypothesis is supported by the high average size of the living tubes, the presence of noticeable tube growth constrictions and the occurrence of epibionts upon the largest specimens (Gambi & Jerace 1997), indicating an already existing mature population. The construction of some pipelines during the early 1980s (Department of Animal Biology and Marine Ecology, unpublished data) could be a local source of disturbance which had a significant impact on the destruction of the sea-grass bed. Such a disturbance would enhance the sliding of sediments from the upper zone towards the deeper one. This fact may confirm man-induced soft sediment displacement as an important

factor, which may also affect these serpulid demographic blooms. It is meaningful that further sampling carried out in the same area during 1993 to 1995 showed a noticeable reduction of *Ditrupa* density, whilst during a last cruise held in 1999 no evidence of past (death assemblages) or present (living tubes) *Ditrupa* populations was observed (Cosentino & Giacobbe, unpublished data). This fact confirms the transitory settlement of the dense serpulid populations.

On the other hand, it could be supposed that the high densities of *D. arietina* may stabilize the bottom surface at mesoscales, as documented for other tube-building species (Fager 1964; Gallagher *et al.* 1983; Luckenbach 1986; Bolam & Fernandes 2002). Such high densities might increase the environmental and coenotic complexity, providing a new substrate for the establishment of other species (Wilson 1976; Gambi 1986; Gambi & Jerace 1997).

Conclusions

In the studied area, a good correspondence exists between the different abiotic-sedimentary environments and the benthic communities, with a narrow cenocline between

the two assemblages. A good correspondence with respect to the trophic-ethological habits has also been clarified; the peculiar shortage of the infaunal deposit feeders in the deeper zone seems related to dominance of surface-detritus feeders and suspension feeders. Local demographic blooms of the serpulid *Ditrupa arietina*, together with some other eurytopic, mud-tolerant species, are related to unpredictable, natural or man-induced sediment displacement. In such a synecological study, the *D. arietina* 'mixed' strategy as a good colonizer during phases of higher variability, and as a discrete competitor in a recently stabilized and more predictable environment, has been better clarified. Its role as a key species in stabilizing the substrate and contributing to coenotic complexity in communities submitted to mean/high levels of sedimentary instability has been postulated.

Acknowledgements

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