

Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey

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Abstract

Ninety-two stations (10, 20, 30, 40 and 50 m depth) located on 21 inshore–offshore transects between the French–Spanish border and the mouth of the Rhône River were sampled during the 1998 Fall. Their polychaete fauna was analyzed to: (1) describe the distribution pattern of polychaete assemblages at the scale of the whole Gulf of Lions, (2) identify the relationships between these assemblages and the main environmental parameters, (3) establish a link between these assemblages and the benthic communities already described for Northwestern Mediterranean, and (4) assess recent historical changes in trends in densities and α diversity between assemblages. Three polychaete assemblages were identified using cluster analysis and associated procedures. These assemblages were tightly associated with depth and sediment granulometry as indicated by the concordance between their spatial distributions and the sedimentary map of the Gulf of Lions. Assemblage I contained most of the 10 and 20 m deep stations and was associated with littoral fine sands. Assemblage I was found all over the Gulf of Lions and was characterized by high abundance and high biomass due to the presence of large numbers of the serpulid *Ditrupa arietina*. Assemblage II was mostly composed of 30 m deep stations and was associated with littoral sandy mud. Assemblage II was dominated by the lumbrinerid *Lumbrineris latreilli*. It was composed of two sub-assemblages (IIa and IIb) in relation with sediment granulometry. Sub-assemblage IIb was associated with finer sediment than sub-assemblage IIa. Sub-assemblage IIa was only found in the Southern part of the Gulf of Lions, whereas sub-assemblage IIb was mostly found in the Northern part of the Gulf of Lions. This pattern is probably indicative of the sedimentation of fine particles originating from the Rhône River at intermediate depth as suggested by: (1) the sedimentary map of the Gulf of Lions, and (2) the outputs of recent models of sediment transport in the Gulf of Lions. Assemblage III was composed of 40 and 50 m deep stations; it was associated with terrigenous coastal mud and found all over Gulf of Lions. Assemblage III was dominated by the sternaspid *Sternaspis scutata*. These three assemblages were tightly related with the benthic communities already described independently by Picard [Picard, J., 1965. Recherches qualitatives sur les biocénoses marines des substrats meubles dragables de la région marseillaise. Recueil des Travaux de la Station Marine d'Endoume 52, 1–160] and Guille [Guille, A., 1971b. Bionomie benthique du plateau continental de la côte catalane française. II – Les communautés de la macrofaune. Vie et Milieu 21, 149–280] based on samples collected along the Provençal and the French Catalan rocky coasts, respectively. Unfortunately, no quantitative data were available to compare the α -diversity of the three newly defined assemblages with historical data collected by these two authors. We therefore compared our diversity measurements with the data collected by Desbruyères et al. [Desbruyères, D., Guille, A., Ramos, J.M., 1972/73. Bionomie du plateau continental de la côte catalane espagnole. Vie et Milieu 23, 335–363] in the Bay of Rosas (Spanish Catalan coast). Due to differences in the sampling effort between the two studies, this comparison was restricted to trends between assemblages. Our results show maximal densities and minimal α -diversity in the Littoral Fine Sand assemblage, which was not the case in Desbruyères et al. [Desbruyères, D., Guille, A., Ramos, J. M., 1972/73. Bionomie du plateau continental de la côte catalane espagnole. Vie et Milieu 23, 335–363]. Major temporal changes obviously reflect the increases of *Ditrupa arietina* (in the Littoral Fine Sands assemblage), and to a lesser extent *Lumbrineris latreilli* (in the Littoral Sandy Mud assemblage).
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1. Introduction

The Mediterranean Sea apparently includes 4–18% (depending on considered taxa) of the known world macroscopic marine species (Bianchi and Mori, 2000). It is probably one of the best-studied seas in the world. This is especially true for its Western Basin, which has been extensively studied due to the proximity of several long-established Spanish, French and Italian marine laboratories. Basic knowledge is still however lacking for some biological compartments and/or areas. This is for example the case for the composition of macrobenthos in the Gulf of Lions. Although many investigations have been performed on macrobenthos in this area (e.g., Picard, 1965; Guille, 1971b; Massé, 1972; Bellan and Bourcier, 1984; Grémare et al., 1998a,b), most quantitative studies have been conducted over very restricted areas (e.g., Guille, 1971a; Bellan and Bourcier, 1984; Grémare et al., 1998a,b). The benthic bionomy of the Gulf of Lions has for example been described based on samples collected on the Provençal and Catalan coasts (Picard, 1965; Guille, 1971b). These areas are located respectively at the Southwest and Northeast ends of the Gulf of Lions; their coastline is mostly rocky and entailed by a complex set of Capes and Bays. Conversely, the study of the composition of macrobenthos in the central part of the Gulf of Lions has been largely neglected even though: (1) this area is by far the largest of the Gulf, and (2) it presents distinct geomorphologic features (i.e., a sandy coast without indentation).

The descriptions of benthic bionomy along the Catalan and Provençal coasts have been carried out independently, which resulted in two distinct classifications of benthic communities in Northwest Mediterranean. For the lower infralittoral and the upper circalittoral, Picard (1965) identified along the Provençal coast: (1) the Well Sorted Fine Sands community associated with fine sands, (2) the Coastal Detritic and the Muddy Detritic communities associated with muddy sands containing shell debris and (3) the Terrigenous Costal Mud community associated with pure mud. Conversely, Guille (1971b) identified five benthic communities along the Catalan coast, namely: (1) the *Spisula subtruncata* community associated with fine sands, (2) the *Nephtys hombergii* community associated with muddy sands, (3) the *Scoloplos armiger* community associated with sandy mud, (4) the *Nucula sulcata* community associated with pure mud, and (5) the *Venus ovata* community associated with heterogeneous mud. There is thus a strong heterogeneity between these two classifications. In this context, there is a clear need to (1) better describe macrobenthic communities at the scale of the whole Gulf of Lions (and especially to consider its central part), and (2) establish a correspondence between the two classifications initially proposed by Picard (1965) and Guille (1971b).

This need is reinforced by the fact that some major changes in the composition of the Gulf of Lions soft-bottom benthic macrofauna have been recently observed (Grémare et al., 1998a,b). These changes have affected dominant taxa of shallow macrobenthic communities. In the sandy bottoms of the Catalan coast, they corresponded to a dramatic increase of the serpulid polychaete *Ditrupea arietina*. In the sandy mud

of the Bay of Banyuls-sur-Mer, they corresponded: (1) to the disappearance of the polychaete *Scoloplos armiger*, and (2) to the strong decline of the genus *Notomastus*. There is also some indirect evidence suggesting that the increase of *Ditrupea arietina* has affected the whole portion of coast between Barcelona and the mouth of the Rhône River (Grémare et al., 1998a). However, there is currently no direct information on the geographic extent and the magnitude of this phenomenon.

Polychaetes are one of the most characteristic groups of soft-bottom benthic communities (Knox, 1977) and one of the richest invertebrate benthic taxon with regard to species number (Arvanitidis et al., 2002). This group often dominates benthic macrofauna (e.g., Grémare et al., 1998a), and has been shown to constitute a good surrogate for describing the distribution of macrobenthic communities (Olsford and Somerfield, 2000) at least when it is the dominant component of macrofauna (Mackie et al., 2005).

In this context, the aims of the present study were (1) to describe the distribution pattern of polychaete assemblages at the scale of the whole Gulf of Lions, (2) to identify the relationships between these assemblages and the main environmental parameters, (3) to establish a link between these assemblages and the benthic communities already described for Northwestern Mediterranean, and (4) to assess recent historical changes in trends in densities and α -diversity between assemblages.

2. Material and methods

2.1. Collection and processing of benthic samples

Benthic samples were collected between September 19 and 29, 1998 on the N.O. Georges Petit along the portion of coast between the French-Spanish border and the mouth of the Rhône River (Fig. 1). This section of coast spans about 110 km from South to North and 140 km from West to East. Sampling sites were located on 21 inshore–offshore transects. Most (i.e., 16) transects were sampled at 10, 20, 30, 40 and 50 m depth. Due to technical constraints, transect F was not sampled at 30 m depth and transects O, P, Q, S and U were only sampled at 10, 20 and 30 m depth. Sediment samples were collected using a 0.1 m² van Veen grab. At each site, three grabs were taken for the analysis of benthic macrofauna, and one for granulometric and organic content analyses. Macrofauna samples were immediately sieved on a 1 mm mesh and the fauna retained was fixed in 5% formalin. At the laboratory, samples were sorted and polychaetes were separated from the remaining fauna. Polychaetes were later identified to the lowest practical taxonomic level and counted. Unidentified taxa were only taken into account when they could not be mistaken for other identified taxa. Data analyses were carried out on data pooled over the three replicated sampling units (Ellingsen, 2001). Individual species biomass was determined as wet weight to avoid destruction of the collected material except for *Ditrupea arietina* where the regression $DW = e^{-8.695} MAL^{2.872}$ ($N = 345$, $R^2 = 0.958$, where MAL is the Total Major Axis Length expressed in mm) was used (Medernach et al., 2000). Data were converted to dry weight

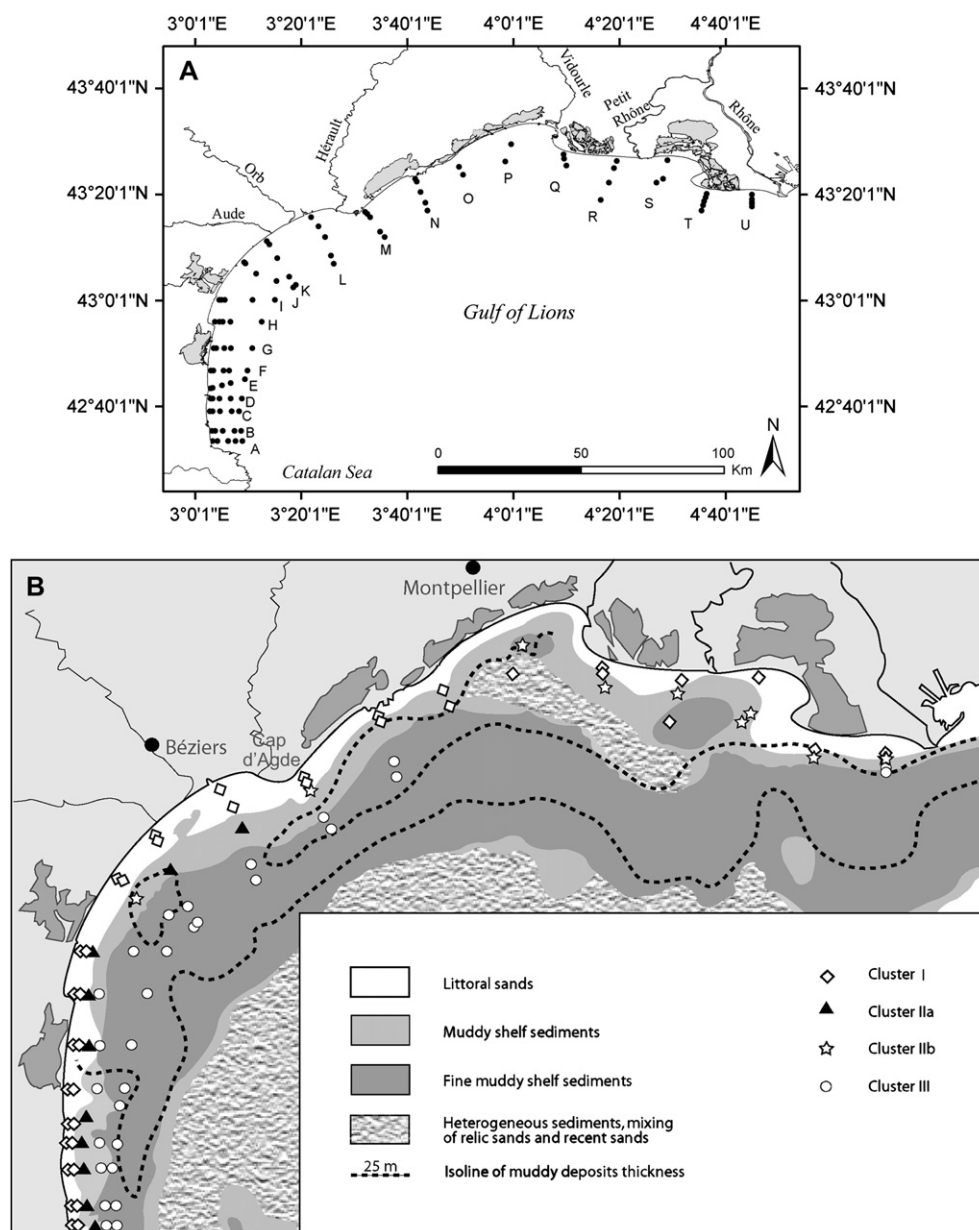


Fig. 1. Location of the 92 sites sampled during the present study (A), and spatial distribution of the four main clusters and sub-clusters identified based on the analysis of polychaete fauna over the sedimentary map drawn by Aloisi et al. (1973) (B).

using a conversion factor of 17.6% proposed for polychaetes by Rumohr et al. (1987) and pooled for four trophic groups: suspension-feeders, mixed, deposit-feeders, and carnivores/omnivores. Granulometric analysis was conducted on fresh sediment using a Malvern® Mastersizer 2000 laser microgranulometer. Organic carbon was measured after acidification (HCl 1N) of freeze-dried sediment using a CHN Perkin Elmer® 2400 analyzer.

2.2. Data analysis

Polychaete assemblages were elucidated by cluster analysis based on the faunal composition (all 173 identified taxa, Bray–Curtis similarity, average link grouping). Abundances

were square-root transformed to limit the influence of the most dominant taxa. The taxa most responsible for similarities within each cluster of stations on one hand, and for dissimilarities between clusters of stations on the other hand were identified using the SIMPER procedure. All these analyses were carried out using the PRIMER® computer software. The relationships between polychaete distribution and environmental parameters were first assessed by testing for significant correlation between the similarity matrices of polychaete abundance and (1) depth, (2) silt-clay content and (3) organic carbon using Mantel tests. We also mapped the clusters of the sampled stations over the sedimentary map of the Gulf of Lions drawn by Aloisi et al. (1973). Several diversity and dominance indices were computed for each sampled stations.

These included the number of taxa (S), the inverse of Berger Parker dominance measure ($1/BP$, Berger and Parker, 1970), and the Shannon–Wiener diversity index ($H' \log_2$). The mean values of these indices and of total abundances were compared between clusters of stations using Kruskal–Wallis non parametric ANOVAs.

2.3. Classification of polychaete assemblages

The correspondence between clusters of stations determined during the present study and the classification proposed by Guille (1971b) was first assessed using two non parametric MDS based on polychaete compositions recorded: (1) during the present study, and (2) by Guille (1971a) in the *Spisula subtruncata*, *Nephtys hombergii*, *Scoloplos armiger* and *Nucula sulcata* communities. These analyses were carried out at the lowest taxonomic level, on square-root transformed abundance data and using the Bray–Curtis similarity index. Two distinct MDS were carried out because rare taxa were not listed by Guille (1971a). Characteristic taxa of a given cluster were defined as the taxa present in one cluster and presenting less than two individuals in each of the other clusters. The lists of these taxa were compared with those established by Picard (1965) and Guille (1971b). The lists of dominant taxa in each cluster were then compared with the lists of dominant taxa in the communities defined by Picard (1965) and Guille (1971b). We also compared the proportions of fines (particles <40 µm in size) measured during the present study with those measured by Guille (1971b).

3. Results

3.1. Cluster identification

We identified a total of 16,884 polychaetes belonging to 173 taxa (Appendix A). Out of these 173 taxa, 33 were singletons (taxa represented by only one individual) and 40 were

unique (taxa occurring at only one single station). The three most dominant taxa were *Ditrupa arietina* (overall dominance of 43.4%), *Lumbrineris latreilli* (overall dominance of 15.7%) and *Owenia fusiformis* (overall dominance of 8.4%). Other taxa individually accounted for less than 3.2% of total abundance.

Based on a 25% similarity level, the quantitative cluster analysis showed the existence of three main clusters with the exception of the affinities of stations T10, U10 (very low number of taxa) (Fig. 2). Cluster I stations were mostly shallow and associated with littoral sands (Fig. 1). However, stations O30, P30 and R30 also belonged to this cluster. These stations were located in or near the area of deep heterogeneous sandy sediments located off Montpellier. Cluster II consisted mainly in 30 m deep stations and could be separated into two main sub-clusters (IIa and IIb). Cluster IIa stations were only found South of Cap d'Agde. Conversely, cluster IIb stations were mostly found in the Northern part of the studied area, with the exception of station J30. All 40 and 50 m deep stations (except E40) belonged to cluster III.

3.2. Similarities and dissimilarities in taxa composition within and between clusters

The taxa, which contributed most to similarity within cluster I were *Ditrupa arietina*, *Owenia fusiformis*, *Chone dumeri*, *Aponuphis bilineata*, *Glycera unicornis* and *Nephtys hombergii* (Table 1A). *Lumbrineris latreilli*, *Scoletoma impatiens*, *D. arietina*, *Goniada* spp., *Lumbrineris gracilis* and *Laonice bahusiensis* contributed most for similarity within cluster IIa. *Lumbrineris latreilli*, *Notomastus* sp. and *Sternaspis scutata* contributed most for similarity within cluster IIb. The taxa most responsible for similarity within cluster III were *S. scutata*, *L. latreilli*, *Nephtys incisa*, *Heteromastus filiformis*, *Scoletoma emandibulata mabiti*, *G. unicornis* and *Ninoe armoricana*. The contributions of taxa to dissimilarities between clusters are presented in Table 1B. The transition

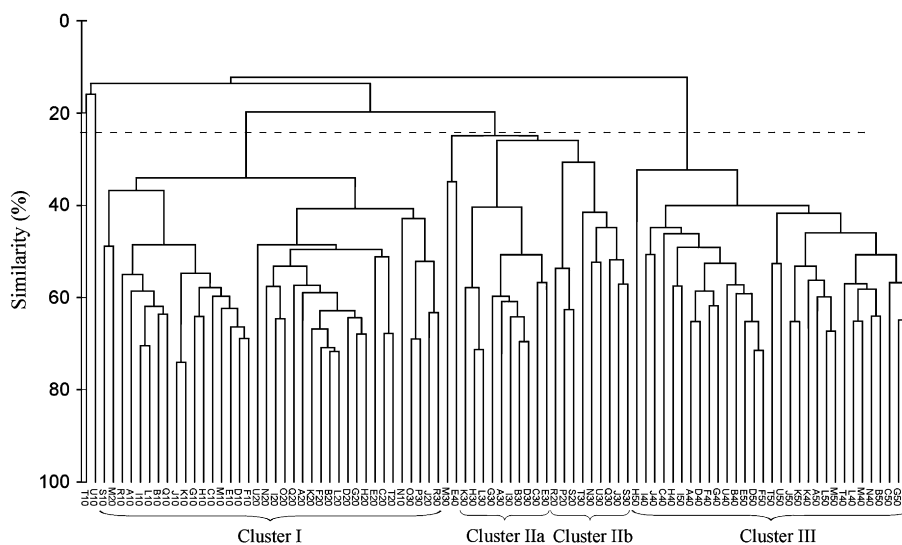


Fig. 2. Cluster analysis of polychaete fauna.

Table 1A

Contribution and cumulative contribution of the species the most responsible for similarity within clusters based on square root transformed species abundances according to the SIMPER analysis

	Species	Contribution (%)	Cumulative contribution (%)
Cluster I	<i>Ditrupa arietina</i>	24.29	24.29
	<i>Owenia fusiformis</i>	15.43	39.72
	<i>Chone duneri</i>	7.28	46.99
	<i>Aponuphis bilineata</i>	7.15	54.14
	<i>Glycera unicornis</i>	7.00	61.15
	<i>Nephtys hombergii</i>	6.36	67.50
Cluster IIa	<i>Lumbrineris latreilli</i>	22.60	22.60
	<i>Scoletoma impatiens</i>	11.88	34.48
	<i>Ditrupa arietina</i>	9.88	44.36
	<i>Goniada</i> spp.	8.90	53.26
	<i>Lumbrineris gracilis</i>	7.48	60.74
	<i>Laonice bahusiensis</i>	5.01	65.75
Cluster IIb	<i>Lumbrineris latreilli</i>	47.29	47.29
	<i>Notomastus</i> sp.	15.57	62.86
	<i>Sternaspis scutata</i>	8.44	71.30
	<i>Glycera unicornis</i>	5.62	76.91
Cluster III	<i>Sternaspis scutata</i>	18.72	18.72
	<i>Lumbrineris latreilli</i>	16.27	34.99
	<i>Nephtys incisa</i>	11.75	46.74
	<i>Heteromastus filiformis</i>	6.59	53.33
	<i>Scoletoma emandibulata mabiti</i>	5.82	59.14
	<i>Glycera unicornis</i>	5.19	64.34

between clusters I and IIa mostly corresponded to the decrease in the average abundance of *D. arietina* and *O. fusiformis* and to the increase of *L. latreilli*, *Goniada* spp. and *L. gracilis*. The transition between clusters IIa and IIb mostly corresponded to the decrease in the average abundance of *D. arietina*, *L. latreilli*, *L. gracilis*, *Goniada* spp. and *S. impatiens*. The

transition between clusters IIb and III mostly corresponded to the decrease of *L. latreilli*, *G. unicornis* and *Notomastus* sp., to the increase of *N. incisa*, *S. scutata*, *H. filiformis* and *S. emandibulata mabiti*.

3.3. Cluster main characteristics

Average densities of polychaete fauna significantly differed between clusters (Kruskal–Wallis ANOVA, $P < 0.001$) (Fig. 3). Average density tended to decrease between clusters I and III. It was maximal and most variable in cluster I due to the presence of high densities of *Ditrupa arietina* at some stations. The average number of taxa also significantly differed between clusters (Kruskal–Wallis ANOVA, $P = 0.014$). This number was minimal for cluster IIb (12.9) and relatively close for the three other clusters (20.4, 18.8 and 18.2 for clusters I, IIa and III, respectively). 1/BP significantly differed between clusters and tended to increase between clusters I and III (Kruskal–Wallis ANOVA, $P < 0.001$ in both cases). This pattern reflected the dominance of: (1) *D. arietina* in cluster I, and (2) *Lumbrineris latreilli* in cluster IIa. H' also significantly differed between clusters (Kruskal–Wallis ANOVA, $P < 0.001$). It was between 2.3 for cluster I and 3.4 for cluster III. Suspension-feeders were dominant in clusters I and IIa (95% and 35% of total biomass, respectively), whereas in clusters IIb and III carnivorous (58 and 62% of total biomass, respectively) and deposit-feeders (41 and 38% of total biomass, respectively) were clearly dominant.

3.4. Relationships between clusters and environmental variables

The average cumulated granulometric curves and organic carbon contents within each cluster are presented in Fig. 4.

Table 1B

Contribution and average abundance of species responsible for most of the dissimilarities between clusters, based on square-root transformed abundances according to the SIMPER analysis

1st cluster	2nd cluster	Species	Av. Abundance 1st cluster	Av. Abundance 2nd cluster	Cumulative contribution (%)
I	IIa	<i>Ditrupa arietina</i>	616.45	99.67	10.36
		<i>Owenia fusiformis</i>	233.20	1.33	18.75
		<i>Lumbrineris latreilli</i>	21.45	171.33	25.52
		<i>Goniada</i> spp.	1.67	36.00	29.24
		<i>Lumbrineris gracilis</i>	0.00	30.33	32.66
IIa	IIb	<i>Ditrupa arietina</i>	99.67	2.22	8.25
		<i>Lumbrineris latreilli</i>	171.33	91.11	14.85
		<i>Lumbrineris gracilis</i>	30.33	0.37	19.87
		<i>Goniada</i> spp.	36.00	2.59	24.84
		<i>Scoletoma impatiens</i>	34.00	6.30	29.54
IIb	III	<i>Lumbrineris latreilli</i>	91.11	40.86	7.48
		<i>Nephtys incisa</i>	0.00	10.22	12.33
		<i>Sternaspis scutata</i>	6.30	24.62	16.86
		<i>Heteromastus filiformis</i>	2.96	11.72	20.69
		<i>Glycera unicornis</i>	11.11	5.91	24.20
		<i>Notomastus</i> sp.	11.48	3.23	27.53
		<i>Scoletoma emandibulata mabiti</i>	20.00	0.00	30.76

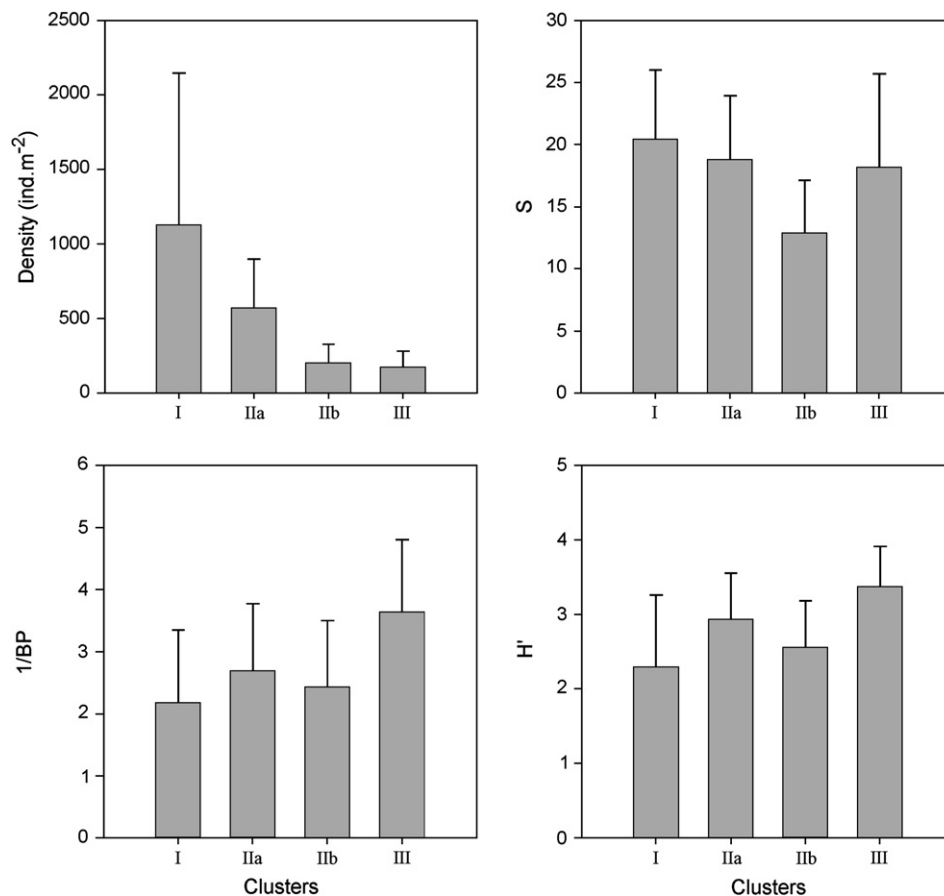


Fig. 3. Mean density, number of taxa (S), inverse of Berger Parker dominance index (1/BP), and Shannon-Wiener index (H') in the four main clusters and sub-clusters identified based on the analysis of polychaete fauna.

There were clear differences in sediment granulometry between clusters with a gradient from coarser to finer sediments between clusters I and III and a clear difference between clusters IIa and IIb as well. The proportion of silt-clay significantly differed between clusters (Kruskal–Wallis ANOVA, $P < 0.001$). Sediments mostly consisted in fine sands in cluster I, muddy sands

in cluster IIa, sandy mud in cluster IIb and fine mud in cluster III. Organic carbon contents also significantly differed between clusters (Kruskal–Wallis ANOVA, $P < 0.001$). It correlated positively with silt-clay content ($\rho = 0.94$, $P < 0.001$). Organic carbon contents were lower in clusters I and IIa and higher in clusters IIb and III. There were positive correlations between

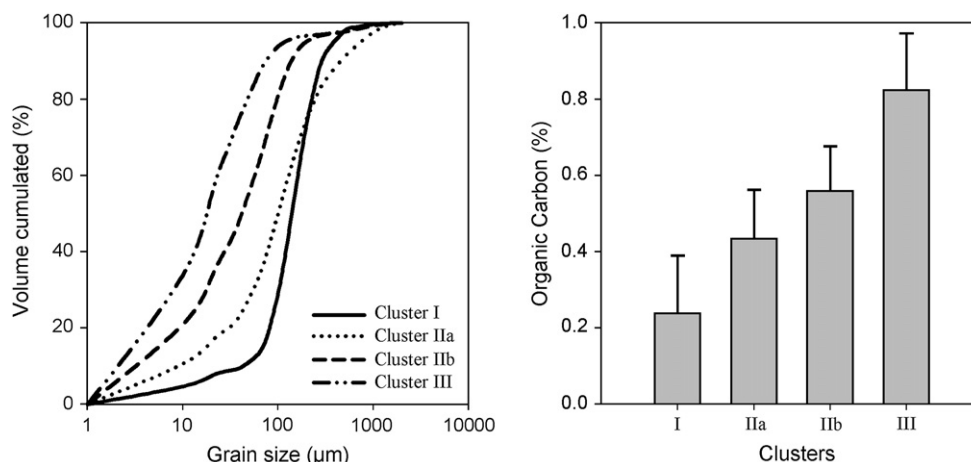


Fig. 4. Mean cumulated granulometric curves (A) and organic carbon contents (B) in surface sediments in the four main clusters and sub-clusters identified based on polychaete fauna. Vertical bars are standard deviations.

polychaete fauna composition and depth ($\rho = 0.765$, $P < 0.001$), % of silt-clay ($\rho = 0.726$, $P < 0.001$), and organic carbon content ($\rho = 0.681$, $P < 0.001$).

3.5. Assessment of recent historical changes

The results of the non parametric MDS based on the polychaete compositions recorded during the present study and by Guille (1971a) in the *Spisula subtruncata*, *Nephtys hombergii*, *Scoloplos armiger* and *Nucula sulcata* communities are presented in Fig. 5. Communities and clusters both featured an overall similar pattern characterized by a transition from the *S. subtruncata* to the *N. sulcata* communities, and from cluster I to cluster III, respectively. However, this transition was much more continuous during the present study than in Guille (1971a) where there was a clear shift between the *S. subtruncata* (fine sands) and the *N. hombergii* communities (muddy sands). This complicated the establishment of a correspondence between our clusters and the communities identified by Guille (1971b). We found 27 characteristic taxa in cluster I including *Magelona mirabilis*, *Spiophanes bombyx* and *Sigalion mathildae*. We found eight characteristic taxa in cluster IIa including *Laonice bahusiensis*, *Ampharete* sp. and *Chone acustica*. We only found one characteristic taxa (*Websterinereis glauca*), which was represented by only two individuals in cluster IIb. We found 31 characteristic taxa in cluster III including *Nephtys incisa*, *Ninoe armoricana* and *Paraprionospio* cf. *pinnata*. The 10 most dominant taxa in each cluster are listed in Table 2.

4. Discussion

4.1. Correspondence between the polychaete assemblages identified during the present study and the classification of benthic communities proposed by Picard (1965) and Guille (1971b)

Comparisons of depth range, main sediment granulometric characteristics (Table 3) and polychaete fauna composition

(Table 2) showed that cluster I was closely related to both the *Spisula subtruncata* and the *Nephtys hombergii* communities (Guille, 1971b), and to the Well Sorted Fine Sands community (Picard, 1965). The only major discrepancy in terms of fauna composition was the high abundance of *Ditrupa arietina* during the present study, whereas this species was not even mentioned by Picard (1965) and Guille (1971b). *Ditrupa arietina* has drastically increased in the Gulf of Lions during the last 40 years or so (Grémare et al., 1998a,b) and is known to feature an unstable population dynamics (Medernach et al., 2000) probably in relation with climatic oscillators (Labrune et al., personal observation). Changes in its abundance should thus not necessarily interfere with the definition of assemblages. Based on this rationale, we propose that cluster I should be named Littoral Fine Sands assemblage (LFS) (Table 4).

Polychaete fauna in clusters IIa and IIb were both intermediate between the *Nephtys hombergii* and the *Scoloplos armiger* communities (Guille, 1971b), but clearly closer to the later one (Table 2). Polychaete fauna in these two clusters were both largely similar with the Coastal Detritic and the Muddy Detritic communities (Picard, 1965) as well. Picard (1965) described the Coastal Detritic sediment as heterogeneous with mud and shells debris, which does not match with sediment textures in cluster IIa and IIb, which did not show marked heterogeneity and did not contain shell debris (Table 3). Conversely, the Muddy Detritic community corresponds to the silt zones under the influence of terrestrial inputs from rivers (Picard, 1965), which is consistent with our results since stations of cluster IIb were mainly located within the North of the studied area (i.e., under the influence of the Rhône River). Clusters IIa and IIb were indeed the only ones tightly related with particular geographical areas of the Gulf of Lions (i.e., the South for cluster IIa and the North for cluster IIb). They thus both can be considered as intermediate between the assemblages associated with fine sands on one side, and mud on the other side. Based on this rationale, we propose to group clusters IIa and IIb in a single assemblage named Littoral Sandy Mud (LSM) (Table 4).

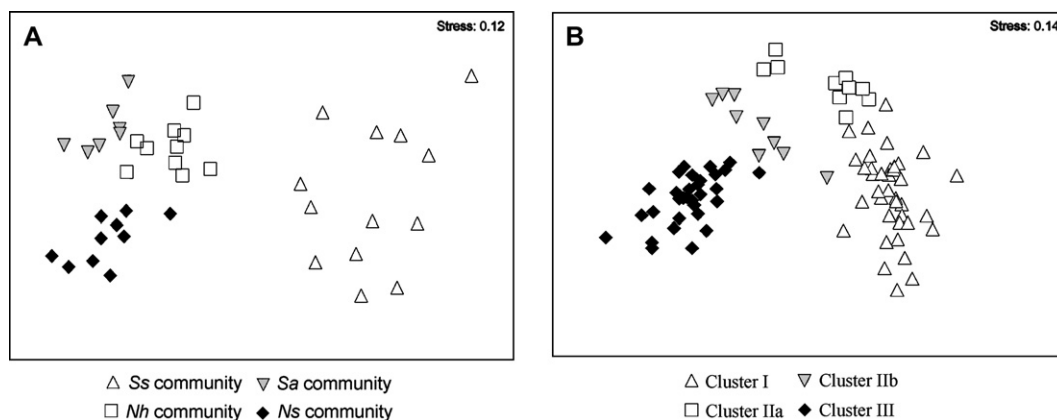


Fig. 5. (A) Non-metric MDS analysis of polychaete fauna on the samples identified by Guille (1971a). Symbols correspond to the four communities: the *Spisula subtruncata* (Ss), the *Nephtys hombergii* (Nh), the *Scoloplos armiger* (Sa) and the *Nucula sulcata* (Ns) community. (B) Non-metric MDS analysis of polychaete fauna on the samples identified during the present study. Symbols correspond to the four main clusters and sub-clusters identified during the present study.

Table 2

Ten most dominant species of each cluster identified during the present study and their importance in some communities identified by Guille (1971a,b) and Picard (1965). Ss, the *Spisula subtruncata* community; Nh, the *Nephtys hombergii* community; Sa, the *Scoloplos armiger* community; Ns, the *Nucula sulcata* community (Guille, 1971b). SFBC, the Well Sorted Fine Sands community; DC, the Coastal Detritic community; DE, the Muddy Detritic community; VTC, the Terrigenous Coastal Mud community (Picard, 1965). The number of asterisks corresponds to the degree of importance of the species in the corresponding communities

Dominant species in the present study	Species mentioned by Guille (1971b)		Species mentioned by Picard (1965)	
Cluster I	Ss	Nh	SFBC	
<i>Ditropa arietina</i>				
<i>Owenia fusiformis</i>	**	*		***
<i>Aponuphis bilineata</i>	*	***		
<i>Chone duneri</i>	*			
<i>Scoletoma impatiens</i>	**	***		**
<i>Lumbrineris latreilli</i>	**	*		**
<i>Glycera unicornis</i>	*	*		
<i>Nephtys hombergii</i>	**	***		***
<i>Magelona mirabilis</i>	****			***
<i>Galathowenia oculata</i>				
Cluster IIa	Nh	Sa	DC	DE
<i>Lumbrineris latreilli</i>	*	***	**	**
<i>Ditropa arietina</i>			****	*
<i>Goniada</i> spp.	*	**	*	
<i>Scoletoma impatiens</i>	***	***	**	**
<i>Lumbrineris gracilis</i>	*		**	
<i>Laonice bahusiensis</i>		***	*	
<i>Myriochele heeri</i>	*			
<i>Aponuphis bilineata</i>	***		**	**
<i>Macroclymene santanderensis</i>				
<i>Ampharete</i> sp.	*	**		
Cluster IIb	Nh	Sa	DC	DE
<i>Lumbrineris latreilli</i>	*	***	**	**
<i>Nephtys hombergii</i>	***	*	***	***
<i>Notomastus</i> sp.	*	***	**	**
<i>Glycera unicornis</i>	*	**	***	***
<i>Sternaspis scutata</i>		***	*	*
<i>Scoletoma impatiens</i>	***	***	**	**
<i>Galathowenia oculata</i>				
<i>Ampharete gracilis</i>				*** (grubei)
<i>Glycinde nordmanni</i>	*	*		
<i>Laonice bahusiensis</i>	*	**	*	
Cluster III	Ns		VTC	
<i>Lumbrineris latreilli</i>	*			
<i>Sternaspis scutata</i>	***		****	
<i>Heteromastus filiformis</i>	*			
<i>Nephtys incisa</i>	***		***	
<i>Scoletoma emandibulata mabiti</i>				
<i>Glycera unicornis</i>	***		***	
<i>Monticellina heterochaeta</i>				
<i>Levinsenia gracilis</i>				
<i>Ditropa arietina</i>				
<i>Terebellides stroemi</i>	***		***	

Polychaete fauna found in cluster III clearly corresponded to the *Nucula sulcata* and the Terrigenous Coastal Mud communities described by Guille (1971b) and Picard (1965), respectively (Table 4). Guille (1971b), and then Desbruyères et al. (1972/73) also identified a *Venus ovata* community which was restricted to the vicinity of the capes of the Catalan rocky coast and corresponded to heterogeneous sediment associated with strong hydrodynamics. This community could not correspond to cluster III since granulometry was homogeneous in this cluster (Table 3). Picard (1965) also reported that terrigenous coastal mud were pure mud, which is consistent with what was observed for cluster III. We therefore propose that cluster III should be named Terrigenous Coastal Mud assemblage (TCM) (Table 4). Picard (1965) found the Terrigenous Coastal Mud community only in the immediate vicinity of the West of the mouth of the Rhône River, which is directly affected by river inputs. However, as mentioned above, he mostly studied the Provençal coast, which is located East of the mouth of the Rhône River and less exposed to Rhône inputs. Our own results show that cluster III is present over the whole dilution area of the Rhône River and thus show the wide spatial repartition of TCM at the scale of the whole Gulf of Lions.

The polychaete fauna described during the present study were clearly related with those already described for other areas of the Mediterranean Sea (Gambi and Giangrande, 1986; Karakassis and Eleftheriou, 1997). This supports the similarity in deeper polychaete fauna between the Bay of Banyuls-sur-Mer and the continental shelf of Crete (Karakassis and Eleftheriou, 1997). The polychaete assemblages identified by Gambi and Giangrande (1986) were also tightly related to the ones described during the present study and to the terminology initially proposed by Picard (1965). For example 51% of the taxa found by Gambi and Giangrande (1986) were also collected during the present study. Gambi and Giangrande (1986) identified four polychaete assemblages corresponding respectively to the well-sorted fine sand, the enriched well-sorted fine sand, sandy mud and terrestrial coastal mud. The first two of these assemblages clearly correspond to LSF, the third one to LSM and the fourth one to TCM. Moreover, characteristic taxa were largely similar in both studies. This was also true, although to a lesser extent, when comparing the taxa associated with each type of substrates in the Gulf of Lions (present study) and along the coast of Greece (Simbora et al., 2000) including the shallow area of the continental shelf of Crete (Karakassis and Eleftheriou, 1997). According to Gambi and Giangrande (1986), the assemblages identified with polychaetes correspond to the communities based on the analysis of the whole macrofauna. It is thus interesting to mention that benthic communities similar to those initially proposed by Picard (1965) have been reported as well in other areas of the Mediterranean Sea such as the Adriatic (Gamulin-Brida, 1974). In this sense, our results thus support the existence of a general pattern of polychaete distribution in the Mediterranean Sea as already postulated by Gambi and Giangrande (1986) for the Tyrrhenian Sea.

Table 3

Depth range and main sediment granulometric characteristics of: (1) the clusters identified during the present study, and (2) the communities described by Picard (1965) and Guille (1971b)

Study	Cluster/ Community	Depth	Sediment granulometry
Present study	Cluster I	10 and 20 m	0–47% of fines
	Cluster IIa	30 m	11–62% of fines, homogeneous sediment
	Cluster IIb	20 and 30 m	37–62% of fines, homogeneous sediment
	Cluster III	40 and 50 m	36–92% of fines
Guille (1971b)	<i>Spisula subtruncata</i>	7–15 m	10–16% of fines
	<i>Nephtys hombergii</i>	22–24 m	31–55% of fines
	<i>Scoloplos armiger</i>	32–33 m	43–68% of fines
	<i>Nucula sulcata</i>	43–85 m	70–92% of fines
Picard (1965)	Well Sorted Fine Sands	3.5–20 m	Well sorted fine sand
	Coastal Detritic		Heterogeneous sediment with mud and shell debris
	Muddy Detritic		Silt zones under the influence of terrestrial inputs from rivers
	Terrigenous Coastal Mud		Pure mud

4.2. Relationships between polychaete assemblages and sediment characteristics

There were clear links between polychaete assemblages and both bathymetry and sediment granulometry. These last two parameters were themselves correlated due to a general decrease of hydrodynamism with depth. The analysis of polychaete fauna within the specific sediment structures, which did not fit the general trend of decreasing particle size with depth, suggests that fauna composition was probably more related to sediment granulometry than to depth per se as already suggested for the shallow area of the Crete continental shelf (Karakassis and Eleftheriou, 1997). Stations P20, R20 and S20, which were located off the mouths of the Vidourle and of the Petit Rhône Rivers, were for example the only 20 m deep stations belonging to LSM. These stations were all located in river prodeltas with muddy sediments (Aloisi et al.,

1976). In the same manner, J30 was the only 30 m deep station within the southern part of the Gulf of Lions belonging to sub-cluster IIb. This station was located within a small area of muddy sediments off the Lagoon of Sigean and the Aude River. Conversely, O30, P30 and R30 were the only 30 m deep stations belonging to LSF. P30 and O30 were located within and at the edge of the area of heterogeneous sediments reported by Aloisi et al. (1973) off Montpellier. The occurrence of LFS at station R30 suggests that the delimitation of this area should be partially revised. Overall, our results thus support the importance of sediment granulometry in structuring polychaete assemblages as already shown in the Mediterranean Sea (Fresi et al., 1983; Gambi and Giangrande, 1986; Nicolaidou and Papadopoulou, 1989; Simboura et al., 2000) and elsewhere (McKnight, 1969; Muniz and Pires, 2000; Probert et al., 2001; Díaz-Castañeda and Harris, 2004).

Both LFS and TCM were distributed over the whole studied area. Conversely, the 2 sub-clusters of LSM (IIa and IIb) were mostly located within its southern and northern part, respectively. The limit between the spatial distributions of these two clusters was off Cap d'Agde, which is in accordance with: (1) the observations of Aloisi et al. (1976) who reported an influence of the Rhône River deposits until the east of the Sète meridian, and (2) the modeling of the deposition of Rhône River outputs, which shows that deposition becomes maximal between 30 and 50 m depth as particles progress towards the West of the Gulf (Estournel, personal communication). This suggests that the discrepancy between the southern and the northern forms of LSM results from the impact of the Rhône River, which contributes for about 80% of total riverine inputs in the Gulf of Lions (Durrieu De Madron et al., 2000). Conversely, the Rhône River had no apparent effect on: (1) LFS because of strong hydrodynamism at shallow depth, and (2) TCM because this assemblage is associated with pure mud.

Outputs from the Rhône River resulted in an increase in the proportion of fines and organic carbon contents of superficial sediments. A similar effect has already been reported for several other rivers (Jouanneau et al., 2002; Mucha et al., 2003; Giberto et al., 2004), including Mediterranean ones (Cardell et al., 1999; Simonini et al., 2004). Benthic macrofauna responds quickly to changes in organic matter availability, which constitutes a major driving force of secondary succession (Pearson and Rosenberg, 1978). Together with changes in granulometry, organic enrichment thus constitutes a mechanism by which rivers influence the composition of

Table 4

Correspondence between the communities identified by Guille (1971b) along the Catalan coast, the ones identified by Picard (1965) along the Provençal coast, and the communities identified during the present study between the French-Spanish border and the mouth of the Rhône River

Present study	Guille (1971b)	Picard (1965)	New terminology
Cluster I	<i>Spisula subtruncata</i> community <i>Nephtys hombergii</i> community	Well Sorted Fine Sands community	Littoral Fine Sands
Cluster IIa Cluster IIb	Between <i>Nephtys hombergii</i> and <i>Scoloplos armiger</i> community	Muddy Detritic community	Littoral Sandy Mud
Cluster III	<i>Nucula sulcata</i> community	Terrigenous Coastal Mud	Terrigenous Coastal Mud

marine benthic macrofauna. Such an effect has already been shown for several rivers (Fresi et al., 1983; Aller and Stupakoff, 1996; Mannino and Montagna, 1997; Simonini et al., 2004). However, there is no current consensus on the nature and magnitude of these effects, due to the occurrence of: (1) steep gradients in sediment characteristics around river mouths (Aloisi et al., 1976; Kennicutt et al., 1995; Aller and Stupakoff, 1996; Jouanneau et al., 1998; Roussiez et al., 2005), and (2) potential confounding factors such as pollutants, which are also preferentially carried out by rivers and negatively affect benthic macrofauna (Mucha et al., 2003).

One important result of the present study is that the effect of the Rhône River on benthic macrofauna is effective over a large spatial scale and is not restricted to its prodelta. Overall, stations of cluster IIa featured higher mean species richness than those of cluster IIb. Stations of cluster IIa were also much more dominated by suspension-feeders than those of cluster IIb. These two observations are consistent with the model of secondary succession proposed by Pearson and Rosenberg (1978), which postulates an increase in species richness and a switch from deposit- to suspension-feeders as organic matter availability decreases. In this sense our results support that, differences between clusters IIa and IIb may result from a moderate organic enrichment caused by the Rhône River. However, stations of cluster IIa also featured a higher mean abundance than those of cluster IIb, which does not fit with the model of Pearson and Rosenberg. This was mostly due to the decrease of the two most dominant species in cluster IIa: *Ditrupa arietina* and *Lumbrineris latreilli*.

4.3. Major taxa

Ditrupa arietina, *Owenia fusiformis*, *Lumbrineris latreilli* and *Sternaspis scutata* were the four taxa that contributed most to within cluster similarity. In addition, *D. arietina*, *O. fusiformis* and *L. latreilli* were by far the three most dominant taxa, and together accounted for 67.5% of total dominance. The ecological importance of these four taxa in the NW Mediterranean has already been put forward by several authors (Grémare et al., 1998a,b; Cardell et al., 1999; Sardá et al., 1999; Salen-Picard et al., 2003). *Ditrupa arietina* accounted for 43.4% of total polychaete dominance. This species was absent of the initial description of the composition of the benthic fauna of the Catalan Sea (Guille, 1971b). Grémare et al. (1998a) first showed the occurrence of extremely high abundance of *D. arietina* in the Bay of Banyuls-sur-Mer. Based on a compilation of several benthic surveys carried out off the French and the Spanish Catalan coasts between 1970 and 1998, Grémare et al. (1998b) suggested that the increase of this species on sandy bottoms was affecting the whole portion of coast between Barcelona and the mouth of the Rhône River. The main weakness of this study was the lack of synchronous sampling such as the one carried out during the present study. Our results show that *D. arietina* was present in high abundances at 20 of the 21 sampled transects. They thus clearly establish that the increase of *D. arietina* in the Gulf of Lions is a large scale process in spite of the instability of its population

dynamics (Medernach et al., 2000). Picard (1965) classified *D. arietina* as exclusively characteristic of the Coastal Detritic community. However, Grémare et al. (1998a,b) and then Medernach et al. (2000) showed that *D. arietina* was mostly associated with fine and muddy sands. The results of the present study support this later observation since *D. arietina* was mostly present in clusters I and II (mostly in sub-cluster IIa) and only rarely in cluster III (average abundance of 2 ind m⁻², present only at C40 but with high abundance).

Owenia fusiformis accounted for 15.7% of total polychaete dominance. *Owenia fusiformis* was long considered as a cosmopolitan species inhabiting a large variety of habitats (Snelgrove and Butman, 1994). Some recent works by Koh and Bhaud (2003) and Ford and Hutchings (2005) suggest that this is probably not the case and that this denomination may indeed corresponds to several species. Furthermore, Picard (1965) classified this species as characteristic of the Well Sorted Fine Sands community and many authors reported high abundances in Mediterranean sandy bottoms (e.g. Gambi and Giangrande, 1986; Somaschini, 1993). Literature data regarding the Catalan Sea and the Gulf of Lions support the importance of *O. fusiformis* in shallow sandy bottoms (Grémare et al., 1998a; Cardell et al., 1999; Sardá et al., 1999). During the present study, *O. fusiformis* showed a restricted depth range and was strongly associated with LFS. As for *Ditrupa arietina*, the population dynamics of this species appears to be rather unstable (Dauvin and Gillet, 1991; Pinedo et al., 2000) and is characterized by important differences in the spatial distribution of newly recruited juveniles and adult populations (Dauvin, 1992). In spite of such instability, this species appears to constitute a major component of polychaete fauna in the Gulf of Lions.

Lumbrineris latreilli accounted for 8.4% of total polychaete dominance. The presence of this species in the Gulf of Lions has already been reported by several authors (Romano, 1979; Salen-Picard, 1981; Bellan and Bourcier, 1984; Cardell et al., 1999; Salen-Picard and Arlhac, 2002; Salen-Picard et al., 2003). Bellan and Bourcier (1984) reported dominance up to 7%. They noticed that this species showed a wide ecological distribution, which is supported by the wide depth range recorded during the present study since *L. latreilli* is present in all identified assemblages. Salen-Picard (1981) reported high abundance of *L. latreilli* in the Gulf of Fos and noticed that its dominance tended to increase at the sites most disturbed by the construction of the Fos-sur-Mer industrial harbor. This result was supported by other observations carried out near the sewage output of the city of Marseilles, which suggested that the dominance of *L. latreilli* occasionally increases in moderately impacted areas (Romano, 1979; Bellan and Bourcier, 1984). However, the analysis of the dominance and the distribution of the other indicator species mentioned by Romano (1979) and Bellan and Bourcier (1984) in our data set suggests the absence of major disturbances in our sampled area. *Lumbrineris latreilli* thus appears to constitute a major component of the polychaete fauna in the Gulf of Lions, but should not necessarily be considered as indicative of large scale disturbance process.

Although *Sternaspis scutata* only accounted for 1.5% of total abundance, it should be considered as an important species, which contributed for 18.8% of similarities within cluster III and for 14.1% of the polychaete dominance in this cluster. *Sternaspis scutata* was considered as characteristic of the *Nucula sulcata* community by Guille (1971b) and as exclusively characteristic of the Terrigenous Coastal Mud community by Picard (1965). The presence of this species in the muddy bottoms of the Gulf of Lions has already been pointed out by several authors (Pérès and Picard, 1964; Pérès, 1967; Grémare et al., 1998a; Salen-Picard and Arlhac, 2002; Salen-Picard et al., 2003). Furthermore, in Northwest Spain, Lopez-Jamar (1982) named *Sternaspis scutata*-*Tharyx* (*Aphelochaeta*) *mari- oni* one of the benthic communities associated with in muddy bottoms. Even if little is known yet about the ecology of this species, we can confidently state that it is an important component of polychaete fauna in the muddy bottoms of the Gulf of Lions.

4.4. Diversity

One hundred and seventy-three taxa were recorded during the present study, which can be compared with the total of 884 polychaete species recently reported by (Arvanitidis

et al., 2002) for the whole Mediterranean Sea. Unfortunately, there was no reference data from the sampled area to compare with the values of our α diversity indices. For example, Guille's raw data (1971a) are no longer available, since he did not report rare taxa. We therefore decided to restrict such comparison with the data collected by Desbruyères et al. (1972/73) along the Spanish Catalan coast. According to Desbruyères et al. (1972/73), the benthic communities in this area are largely similar to those of the French Catalan coast, which are themselves closely related with the polychaete assemblages described in the present study (see above). Desbruyères et al. (1972/73) used the same sampling gear, and the same mesh size as ours. The main discrepancy between the two studies is the number of replicated samples, which was limited to 3 during the present study versus 5 for Desbruyères et al. (1972/73). Such a discrepancy does not preclude the comparison of the trends in abundance and diversity indices between assemblages. This required to establish a correspondence between the assemblages defined during the present study and those used by Desbruyères et al. (1972/73). We considered that: (1) LFS corresponded both to Desbruyères et al. (1972/73) Fine Sands and Muddy Sands communities, (2) LSM corresponded to Desbruyères et al. (1972/73) Littoral Sandy Mud community, and (3) TCM corresponded to

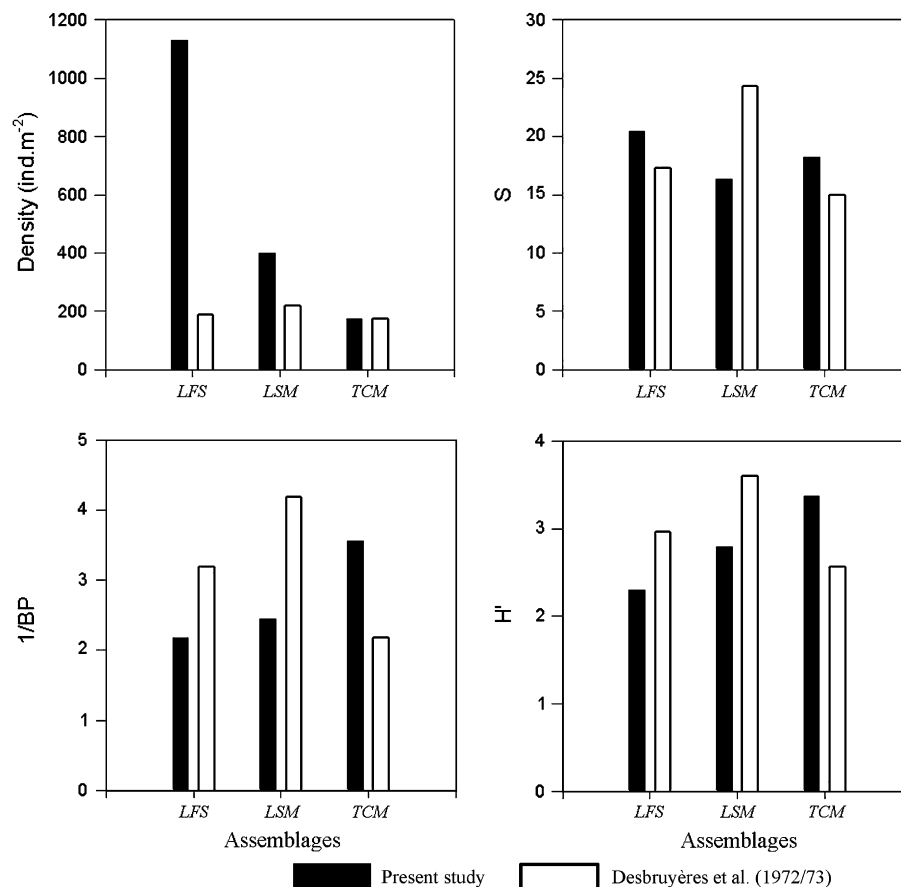


Fig. 6. Comparison between the trends of the diversity indices in the three assemblages identified during the present and the corresponding assemblages of the Spanish Catalan coast (Desbruyères et al., 1972/73). Indices that are compared are: Mean density, Number of taxa (S), inverse of Berger Parker dominance index (1/BP), and Shannon–Wiener index (H').

Desbruyères et al. (1972/73) Coastal Mud community. Although caution should be taken in comparing the two studies, there were apparent differences (Fig. 6). Densities tended to decrease from LFS to TCM during the present study, whereas they seemed maximal in LSM in Desbruyères et al. (1972/73). In LSF and TCM, the number of taxa seemed slightly higher during the present study than in Desbruyères et al. (1972/73). The inverse trend was observed for LSM. In LSF and LSM, dominance tended to be higher during the present study than in Desbruyères et al. (1972/73). The inverse trend was observed for TCM. Overall H' seemed higher in the present study for LSF and LSM and lower for TCM. Here again, discrepancies between the two studies were mainly due to dominant species. *Ditrupa arietina* was for example only reported as an accessory species by Desbruyères et al. (1972/73), whereas it was highly dominant during our study. Interestingly, high densities of this species have been recorded on several occasions along the Spanish Catalan coast (including the Bay of Rosas, Sardá personal observation) since 1990 (Grémare et al., 1998a; Sardá et al., 2001). This species is primarily associated with LFS where it accounts for low diversity and high dominance pattern. It is also present in LSM and thus contributes to lower diversity and higher dominance in this assemblage relative to TCM. The dominance of *Lumbrineris latreilli* in the LSM was also much higher during the present study than in Desbruyères et al. (1972/73) (32.9% and 10.6%, respectively). This species thus also contributed to lower diversity and higher dominance in this assemblage.

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Appendix A

List and average abundance per cluster (ind m^{-2}) of the 173 polychaete taxa identified during the present study

Taxa	I	IIa	IIb	III
<i>Aglaophamus</i> sp.	0.0	0.0	0.3	0.0
<i>Amage adspersa</i>	0.1	0.0	0.0	0.0
<i>Ampharete falcata</i>	0.0	0.0	0.0	0.4
<i>Ampharete finmarchica</i>	0.0	0.0	0.0	0.2
<i>Ampharete gracilis</i>	7.3	0.0	3.3	0.0
<i>Ampharete</i> sp.	0.0	15.3	0.0	0.0
<i>Amphiteis gunneri</i>	0.3	0.3	0.0	0.0
<i>Ancistrosyllis groenlandica</i>	0.0	0.0	0.0	1.0
<i>Anobothrus gracilis</i>	1.8	0.0	5.3	2.2
<i>Aonides oxycephala</i>	0.2	0.0	0.3	0.0
<i>Aphelochaeta filiformis</i>	0.1	0.0	0.0	0.0
<i>Tharyx marioni</i>	0.0	0.0	0.0	0.6

Appendix A (continued)

Taxa	I	IIa	IIb	III
<i>Aphelochaeta</i> sp.	0.5	0.0	0.0	0.3
<i>Chaetozone vivipara</i>	0.0	0.0	0.0	0.9
<i>Aphrodita aculeata</i>	0.0	0.0	0.0	0.1
<i>Aponuphis bilineata</i>	42.0	19.0	1.7	0.0
<i>Aponuphis brementi</i>	0.1	0.7	0.0	0.0
<i>Aricidea assimilis</i>	0.0	0.0	0.0	0.4
<i>Aricidea capensis bansei</i>	0.0	0.0	0.3	0.0
<i>Aricidea claudiae</i>	0.0	0.0	0.3	0.5
<i>Aricidea suecica</i>	0.2	0.0	0.0	0.0
<i>Caulleriella</i> sp.	0.0	1.3	0.0	0.0
<i>Chaetozone caputesocis</i>	0.0	0.0	0.0	0.1
<i>Chaetozone cf. setosa</i>	0.4	0.0	0.3	2.2
<i>Chone acustica</i>	0.1	13.3	0.3	0.0
<i>Chone duneri</i>	29.5	0.0	0.0	0.4
<i>Chone infundibuliformis</i>	0.0	0.0	0.0	0.6
<i>Cirriformia</i> sp.	1.8	0.0	2.7	0.0
<i>Cirrophorus</i> sp.	0.0	0.3	0.3	0.0
<i>Clymenura clypeata</i>	1.9	0.0	0.0	0.0
<i>Cossura</i> sp.	0.0	1.3	0.7	0.0
<i>Dasybranchus gajolae</i>	0.0	0.0	0.0	0.1
<i>Diplocirrus glaucus</i>	0.0	0.0	0.0	0.9
<i>Dipolydora caeca</i>	0.5	0.0	1.0	0.2
<i>Ditrupa arietina</i>	616.4	99.7	2.0	4.3
<i>Dorvillea rubrovittata</i>	0.1	0.0	0.0	0.0
<i>Drilonereis filum</i>	0.1	0.0	1.3	1.3
<i>Syllis parapar</i>	0.0	0.0	0.0	0.3
<i>Eteone foliosa</i>	0.7	0.0	1.7	0.0
<i>Eteone picta</i>	1.5	0.0	0.0	0.3
<i>Euchone rosea</i>	0.4	0.0	0.0	0.0
<i>Euclymene oerstedii</i>	1.5	0.0	2.7	0.0
<i>Euclymene robusta</i>	1.0	0.0	1.0	0.0
<i>Eumida sanguinea</i>	3.2	0.0	0.0	0.0
<i>Eunereis longissima</i>	0.0	0.0	0.3	0.8
<i>Eunice vittata</i>	4.6	0.3	0.7	0.0
<i>Euphrosine foliosa</i>	0.1	0.0	0.0	0.0
<i>Flabelligeridae</i> ind.	0.7	0.7	0.0	0.0
<i>Galathowenia oculata</i>	7.9	0.0	5.0	1.8
<i>Glycera alba</i>	0.0	0.0	0.0	1.4
<i>Glycera tridactyla</i>	0.0	0.0	0.0	0.1
<i>Glycera unicornis</i>	17.8	0.0	13.7	5.9
<i>Glycinde nordmanii</i>	3.0	0.0	3.3	0.4
<i>Goniada</i> spp.	1.7	36.0	4.7	1.0
<i>Gyptis</i> sp.	0.4	0.0	0.3	0.0
<i>Harmothoe antilopes</i>	0.0	0.0	0.0	0.1
<i>Harmothoe cf. areolata</i>	0.1	0.0	0.0	0.0
<i>Harmothoe gilchristi</i>	0.0	0.0	0.0	0.2
<i>Harmothoe goreensis</i>	0.0	0.0	0.0	0.2
<i>Heteromastus filiformis</i>	0.0	0.0	2.7	11.7
<i>Hydroides</i> sp.	1.2	0.0	0.0	0.0
<i>Jasmineira</i> sp.	2.1	6.0	0.0	0.0
<i>Psamathe fusca</i>	0.1	0.0	0.0	0.0
<i>Labioleanira yhleni</i>	0.0	3.7	0.0	3.3
<i>Laonice bahusiensis</i>	4.7	21.3	3.7	0.6
<i>Laonome salmacidis</i>	0.1	0.0	0.0	0.0
<i>Levinsonia gracilis</i>	0.1	0.0	0.3	4.4
<i>Lumbrineris coccinea</i>	0.0	0.7	0.0	0.0
<i>Lumbrineris gracilis</i>	0.0	30.3	0.3	0.6
<i>Lumbrineris latreilli</i>	21.4	171.3	91.0	40.9
<i>Lumbrineris nonatoi</i>	0.3	0.0	0.0	0.2
<i>Macroclymene santanderensis</i>	0.3	18.7	0.0	0.1
<i>Magelona alleni</i>	0.1	1.0	0.0	1.2
<i>Magelona minuta</i>	0.4	0.0	0.0	0.1
<i>Magelona mirabilis</i>	13.1	0.0	0.0	0.0
<i>Magelona wilsoni</i>	0.0	0.0	0.0	1.3

Appendix A (continued)

Taxa	I	Ila	Ilb	III
<i>Malacoceros fuliginosus</i>	0.1	0.0	0.0	0.0
<i>Malmgreniella andreapolis</i>	0.0	0.0	0.0	1.0
<i>Malmgreniella darbouxi</i>	0.0	0.0	0.0	0.1
<i>Malmgreniella glabra</i>	0.0	0.0	0.0	1.6
<i>Malmgreniella lunulata</i>	0.1	0.0	0.0	0.0
<i>Marphysa</i> spp.	0.2	0.3	0.0	2.3
<i>Mediomastus fragilis</i>	2.2	0.0	15.3	0.1
<i>Melinna palmata</i>	4.1	3.0	0.0	0.0
<i>Microspio mecknikowianus</i>	0.1	0.3	0.0	0.0
<i>Monticellina</i> cf. <i>dorsobranchialis</i>	0.0	0.0	0.0	3.2
<i>Monticellina heterochaeta</i>	2.4	0.0	2.7	4.7
<i>Myriochele heeri</i>	0.4	20.7	0.3	0.0
<i>Neanthes irrorata</i>	0.0	0.0	0.0	0.1
<i>Nephtys cirrosa</i>	5.4	0.0	0.3	0.0
<i>Nephtys hombergii</i>	13.9	0.0	18.0	0.0
<i>Nephtys incisa</i>	0.0	0.0	0.0	10.2
<i>Nephtys kersivalensis</i>	0.0	0.0	0.0	3.2
<i>Nephtys</i> sp.	0.0	0.0	0.3	0.1
<i>Nereiphylla rubiginosa</i>	0.1	0.0	0.0	0.0
<i>Nereis</i> sp.	0.0	0.3	0.0	0.0
<i>Nicomache</i> sp.	0.0	0.3	0.0	0.0
<i>Ninoe armoricana</i>	0.0	0.0	0.0	2.8
<i>Notomastus</i> sp.	3.9	13.3	11.0	3.2
<i>Ophiodromus flexuosus</i>	0.4	0.0	0.0	0.0
<i>Orbinia bioreti</i>	0.0	0.3	0.0	0.0
<i>Orbinia cuvieri</i>	0.0	0.0	0.3	0.0
<i>Oriopsis armandi</i>	0.2	0.0	0.0	0.0
<i>Owenia fusiformis</i>	233.2	1.3	0.0	0.0
<i>Paraonis fulgens</i>	0.6	0.0	0.0	0.0
<i>Paradoneis lyra</i>	0.1	0.0	0.3	0.0
<i>Paralacydonia paradoxa</i>	0.2	3.3	0.3	0.0
<i>Paranaitis kosteriensis</i>	0.1	0.0	0.0	0.0
<i>Paraprionospio</i> cf. <i>pinnata</i>	0.0	0.3	0.0	2.4
<i>Pectinaria auricoma</i>	0.0	7.0	0.0	0.2
<i>Pectinaria belgica</i>	0.0	0.3	0.0	0.0
<i>Pectinaria koreni</i>	2.5	5.3	0.7	0.0
<i>Peresiella clymenoides</i>	0.0	0.0	0.0	0.8
<i>Pherusa flabellata</i>	0.4	0.0	0.0	0.0
<i>Phisidia aurea</i>	0.0	0.0	0.0	0.0
<i>Phyllodoce laminosa</i>	0.1	0.0	0.0	0.0
<i>Phyllodoce lineata</i>	1.8	0.0	1.0	0.1
<i>Phyllodoce mucosa</i>	0.1	0.0	0.0	0.0
<i>Pilargidae</i> ind.	0.0	0.0	0.0	0.1
<i>Pilargis verrucosa</i>	0.1	0.0	0.0	0.2
<i>Piromis eruca</i>	4.4	0.0	0.0	0.3
<i>Pista cristata</i>	1.4	1.3	1.0	0.0
<i>Pista unibranchia</i>	0.6	0.0	0.0	0.2
<i>Pistella lornensis</i>	0.0	0.0	0.0	0.8
<i>Poecilochaetus fauchaldi</i>	0.0	0.0	0.0	1.5
<i>Poecilochaetus serpens</i>	1.8	4.7	0.3	0.0
<i>Polycirrus plumosus</i>	0.0	0.0	0.0	0.1
<i>Polydora</i> sp.	0.3	0.3	1.0	0.0
<i>Polygordius</i> sp.	0.0	0.0	0.0	0.0
<i>Pomatoceros triqueter</i>	1.0	0.0	0.7	0.0
<i>Praxillella affinis</i>	1.0	0.0	0.3	0.2
<i>Praxillella gracilis</i>	0.0	0.0	0.0	0.2
<i>Praxillella lophoseta</i>	0.1	0.0	0.0	0.0
<i>Prionospio caspersi</i>	6.5	0.0	0.3	0.1
<i>Prionospio</i> cf. <i>multibranchiata</i>	0.0	0.0	0.0	1.1
<i>Prionospio cirrifer</i>	0.0	3.3	0.3	0.0
<i>Prionospio dubia</i>	0.0	0.0	0.0	2.0
<i>Prionospio elheresi</i>	0.0	2.0	0.0	0.1
<i>Prionospio fallax</i>	0.7	5.0	2.0	0.6
<i>Prionospio steenstrupi</i>	0.0	5.3	0.0	0.0

Appendix A (continued)

Taxa	I	Ila	Ilb	III
<i>Proclea graffi</i>	0.0	0.0	0.0	0.1
<i>Protodorrvillea kefersteini</i>	0.2	0.0	0.0	0.0
<i>Protula</i> sp.	0.2	0.0	0.0	0.0
<i>Pseudomystides limbata</i>	0.3	3.7	0.0	0.0
<i>Pseudopolydora paucibranchiata</i>	0.0	0.0	0.0	0.1
<i>Pseudopolydora</i> sp.	0.1	0.0	0.0	0.0
<i>Sabella</i> sp.	0.2	0.0	0.0	0.0
<i>Scalibregma inflatum</i>	1.1	0.0	1.3	0.0
<i>Scolecopsis cantabra</i>	0.0	0.0	0.3	0.0
<i>Scolecopsis tridentata</i>	0.1	0.0	0.0	0.2
<i>Scoletoma emandibula mabiti</i>	0.3	0.0	0.0	6.7
<i>Scoletoma fragilis</i>	0.0	0.0	0.0	0.2
<i>Scoletoma impatiens</i>	23.6	34.0	7.0	0.2
<i>Scoloplos armiger</i>	3.1	9.0	0.3	0.0
<i>Serpulidae</i> ind.	0.7	0.0	0.0	0.0
<i>Sigalion mathildae</i>	0.4	0.0	0.0	0.0
<i>Sigalion squamosus</i>	2.5	0.0	0.3	0.0
<i>Sphaerosyllis taylori</i>	0.1	0.0	0.0	0.0
<i>Spio filicornis</i>	1.7	0.3	0.0	0.0
<i>Spiochaetopterus costarum</i>	0.0	0.0	0.0	0.4
<i>Spiochaetopterus solitarius</i>	0.0	0.0	0.0	0.3
<i>Spiophanes bombyx</i>	4.5	0.7	0.7	0.0
<i>Spiophanes kroyeri</i>	0.2	0.7	0.0	0.2
<i>Sthenelais boa</i>	1.1	0.0	0.3	0.0
<i>Sternaspis scutata</i>	0.3	0.0	5.7	24.6
<i>Streblosoma bairdi</i>	0.3	0.0	0.0	0.0
<i>Syllidae</i> ind.	0.1	0.3	0.3	0.1
<i>Syllis garciai</i>	0.1	0.0	0.0	0.0
<i>Thelepus setosus</i>	3.6	0.0	0.0	0.0
<i>Terebellides stroemi</i>	0.4	2.7	0.0	3.3
<i>Timarete filigera</i>	1.5	0.0	1.0	0.0
<i>Trichobranchus glacialis</i>	0.1	0.0	0.0	0.0
<i>Websterinereis glauca</i>	0.0	0.0	0.7	0.0

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