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Structure and diversity of shallow soft-bottom benthic macrofauna in the Gulf of Lions (NW Mediterranean)

Céline Labrune · Antoine Grémare ·
Jean-Michel Amouroux · Rafael Sardá ·
João Gil · Sergi Taboada

Abstract Samples of soft-sediment macrobenthos from 92 sites between 10 and 50 m depth were used to assess (1) the main soft-bottom macrofauna communities in the Gulf of Lions, (2) the different components of the diversity of benthic macrofauna in this area, and (3) the relevance of the use of major taxonomic groups as surrogates for the analysis of the structure and diversity of total macrofauna. Three main communities were identified by cluster analysis and associated procedures. These communities corresponded well to the assemblages recently identified on the basis of polychaete composition. The α-diversity indices were in accordance with those reported for similar communities in the Mediterranean. Conversely, the β-diversity value was higher than the few other data available in the literature for marine soft-bottom macrofauna. The total number of species in the studied area estimated by the "total species accumulation curve" (TS) method was 2,319, which was only 10% higher than the number obtained by extrapolation of the species–area curve. The similarity matrix based on polychaetes correlated best with the one based on total macrofauna. Polychaetes and crustaceans were also the best surrogates of total macrofauna when assessing α-diversity (except in the case of Δ*). Conversely, molluscs were the best surrogates of total macrofauna β-diversity. Our results show that the choice of an optimal surrogate for total benthic macrofauna depends on the characteristic of the benthic macrofauna to be studied. Moreover, this choice is also dependent on the environment to be studied.

Keywords Macrobenthos · Community structure · Surrogates · Diversity · Gulf of Lions

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C. Labrune · J.-M. Amouroux
UPMC Univ Paris 06, UMR7621, Laboratoire d'Océanographie
Biologique de Banyuls, 66650 Banyuls-sur-Mer, France

C. Labrune (✉) · J.-M. Amouroux
CNRS, UMR7621, Laboratoire d'Océanographie Biologique de
Banyuls, 66650 Banyuls-sur-Mer, France
e-mail: labrune@obs-banyuls.fr

A. Grémare
Station Biologique d'Arcachon, UMR 5085,
Université Bordeaux 1 – CNRS, 2 rue du Professeur Jolyet,
33120 Arcachon, France

R. Sardá · J. Gil · S. Taboada
Centre d'Estudis Avançats de Blanes, CSIC,
Carrer d'acces a la Cala Sant Francesc, 14,
17300, Blanes, Girona, Spain

Introduction

Biodiversity is commonly defined as the variety of life (Gaston and Spicer 1998) from the genomic to the eco-system scale. There are thus many ways to measure biodiversity and there is no single scale in which it should be measured (Levin 1992). As far as spatial scales and species diversity are concerned, this led to the classic distinction between α (i.e., the diversity of species occurring at a single site) and γ (i.e., the diversity of species occurring at the regional scale) diversity (Whittaker 1960). The α-diversity accounts both for species richness and dominance (number of species per site). Many indices accounting for different proportions of these two parameters have been proposed to assess α-diversity (e.g., Shannon and Weaver 1949; Pielou 1966; Hurlbert 1971). The main difficulty in assessing γ-diversity is related to

insufficient sampling. Several estimators (e.g., Chao 1984; Grassle and Maciolek 1992; Karakassis 1995; Gray et al. 1997) as well as several extrapolation techniques (e.g., Ugland et al. 2003, 2005) have been proposed to infer the true number of species present in a given area. However, this problem is far from being solved yet. At last β-diversity corresponds to the turnover of species along a gradient (or between communities). It is thus of different dimensional character from α and γ-diversity; β-diversity is most often assessed through the ratio between γ-and average α-diversity (Whittaker 1972). Measures of β-diversity are clearly needed to enhance our understanding of the structure of ecosystems, which could have important implications in conservation planning (Levin 1992; Kunin 1997).

In recent years, evaluating the consequences of changes in marine biodiversity due to human activities has become a priority. It is currently agreed that this priority is seriously compromised by inadequate knowledge of the patterns and the basic processes that control the biodiversity in the sea (National Research Council 1995). Soft substrates cover the vast majority of the bottom of the world's ocean. Assessing their biodiversity is thus of special importance. This assessment is however complicated by the difficulty in sampling and sharply delineating habitats in these systems.

Benthic macrofauna corresponds to organisms larger than 1 mm in size inhabiting marine bottoms. The analysis of macrofauna is essential for assessing diversity patterns in marine soft-bottoms. Soft-bottom macrofauna is structured in communities (groups of tightly associated species), which are largely controlled by abiotic factors (e.g., depth, granulometry). In marine soft-bottoms, disturbance has been shown to initiate a secondary succession process (Pearson and Rosenberg 1978), which is among other things characterized by important changes in the diversity of macrofauna (Rygg 1985; Rosenberg et al. 1987; Bellan and Bourcier 1990; Josefson et al. 1993; Bourcier 1996; Sardá et al. 2000, 2001). Studying the diversity of soft-bottom macrofauna is thus also of interest in assessing the level of disturbance experienced by marine habitats (Warwick 1988; Olsgard et al. 1997; Dauvin et al. 2003).

The analysis of benthic soft-bottom communities involves long and tedious sorting and identifying procedures (Warwick 1993; Roberts et al. 1998). Two main approaches have been proposed to overcome these difficulties. Taxonomic sufficiency consists in identifying macrofauna at a higher taxonomic level than species and has proved to be efficient in assessing the effects of major disturbances (Warwick 1988, 1993; Warwick and Clarke 1993; Somerfield and Clarke 1995; Gomez Gesteira et al. 2003). Another approach consists in conducting identifications to the species level but only on a restricted number

of major taxonomic groups, which are then used as surrogates for total macrofauna (Olsgard et al. 2003; Giangrande et al. 2005). This latter procedure has been most often carried out on polychaetes and molluscs (Belan 2004; Giangrande et al. 2005; Mackie et al. 2005). It aims not only on assessing the effect of disturbance on soft-bottom sediments (Bellan et al. 1988; Gesteira and Dauvin 2000; Belan 2004; Giangrande et al. 2005) but also on assessing the diversity of those bottoms (Olsgard et al. 2003; Mackie et al. 2005). Polychaetes have been shown to constitute a good surrogate for describing species richness (Olsgard et al. 2003) or even the distribution of macrobenthic communities along gradients in disturbed areas (Olsgard and Somerfield 2000). However, the use of surrogates for total macrofauna remains still questionable as several components of the same ecosystem may for example reflect different environmental gradients (Karakassis et al. 2006).

Labrune et al. (2006b, 2007) have recently carried out a detailed analysis of the structure and diversity of polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on an extensive set of 92 sampling sites. Although the Gulf of Lions is one of the best-sampled marine areas within the Mediterranean Sea, these authors pinpointed the lack of sound data regarding the composition and diversity of its soft-bottom marine fauna.
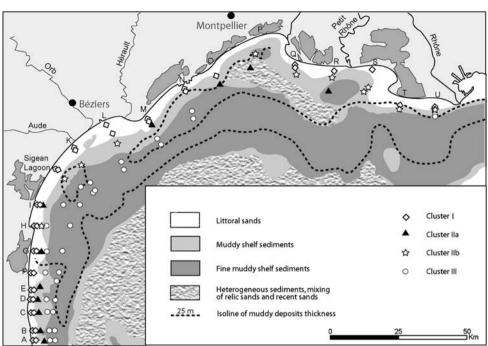
The present study is based on the same set of sampling sites, but considers total macrofauna through two complementary approaches. Considered first is a descriptive approach, which aims at describing benthic macrofauna communities in the Gulf of Lions and the different components of diversity in this area. Such a regional scale data set will provide a first valid reference for the structure and diversity of soft-bottom macrofauna in the Gulf of Lions. Second, a comparative approach aims at relating the results derived from the analysis of total macrofauna with those derived from the analysis of each major taxonomic group. This second approach deals with the possible use of major taxonomic groups as surrogates for the analysis of the structure and diversity of total macrofauna.

Materials and methods

Collection and processing of sediment samples

Benthic samples were collected in September to October 1998 on N.O. "Georges Petit" along the coast between the Spanish-French 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 (A–U). Most transects were sampled at 10, 20, 30, 40 and 50 m depth. Transects O, P, Q, S and U were only sampled at 10, 20 and

Fig. 1 Sedimentary map of the Gulf of Lions (after Aloisi et al. 1973) with location of the 92 sites and the spatial distribution of the four main clusters and sub-clusters identified on the basis of the composition of the benthic macrofauna. Letters *A* to *U* correspond to the 21 transects

30 m depth. Sediment samples were collected with a 0.1 m^2 *Van Veen* grab. At each site, three grabs were taken for the analysis of benthic macrofauna. Macrofauna samples were immediately sieved on a 1 mm mesh and the retained fauna were fixed in 5% formalin. Samples were sorted and macrofauna were later identified to the lowest practical taxonomic level and counted. The unidentified species were only taken into account when they could not be mistaken for other identified species. Macrofauna analyses were carried out on data pooled over the three replicated sampling units (Ellingsen 2001). Granulometric analysis was conducted on fresh sediment using a Malvern® Mastersizer 2000 laser microgranulometer. Organic carbon was measured after acidification (HCl 1 N) of freeze-dried sediment using a CHN Perkin Elmer® 2400 analyzer.

Data analysis

The frequency distributions of species range within major taxonomic groups were compared using Kolmogorov–Smirnov tests. Correlations between standardized similarity matrices of each major taxonomic group and of total macrofauna were tested for significance using Mantel tests. Macrofauna communities were determined through cluster analysis based on macrofauna composition (abundance square-root transformed data, Bray-Curtis similarity, average link grouping). This technique is appropriate for delineating groups of sites with distinct community structure and has proved useful in a number of ecological studies over the last three decades (Clarke and Warwick

2001). This analysis was carried out using the PRIMER® computer software. The average proportion of silt-clay particles (<63 µm) and organic carbon contents of the clusters were compared using Kruskal–Wallis ANOVAs. The average contributions of each major taxonomic group to species richness of the total macrofauna within each cluster were qualitatively compared. The species most responsible for similarity within clusters and dissimilarities between clusters were assessed using the SIMPER procedure of the PRIMER® package. The significance of the correlations between macrofauna composition and abiotic parameters (i.e., depth, percentage of silt-clay and organic carbon contents) were assessed by Mantel tests.

We used the same α-diversity indices as Labrune et al. (2006b), namely: species richness (*S*), Shannon-Wiener index (*H*′(log$_2$)), Pielou's evenness (*J*′), and average taxonomic distinctness (Δ*). These four indices were computed using the PRIMER® package. The average values of these indices within each cluster were compared using Kruskal–Wallis ANOVAs. The relationships between species richness of total macrofauna and of major taxonomic groups were assessed using stepwise (forward) multiple linear regression models, both for individual clusters and for the whole data set. Simple linear regression models were used for the three other α-diversity indices.

β-diversity was computed as the ratio between the regional (γ) and the average local ᾱ-diversity (Whittaker 1972). Cumulative curves of β_w were computed based on randomly generated subsets of sampling sites (Ellingsen 2001, 2002). These computations were carried out for: (1) total macrofauna and each major taxonomic group, and (2)

for the whole data set and each cluster separately. Cumulative β_w curves were generated using specially programmed Matlab® routines.

We used the same estimators as Labrune et al. (2006b) to assess the true numbers of species within each cluster: S_{obs}, Chao$_1$, Chao$_2$ and ICE. S_{obs} is the total number of species recorded in the whole data set. Cumulative curves of these indices were established by randomly generating subsets of sampling sites increasing in size. This procedure (50 randomizations) was carried out using the EstimateS freeware (Colwell 1997). Both Chao's and ICE estimators were used on homogeneous subsets of samples as recommended by Foggo et al. (2003a, 2003b) and Magurran (2004). We used two extrapolation methods to infer γ-diversity (i.e., the total number of species in the whole studied area): (1) the extrapolation of the species accumulation curve, and (2) the "total species-accumulation curve" (TS). This latter method has been recently introduced by Ugland et al. (2003). It consists in constructing a regression of the average number of species in all combinations of, respectively, one, two, three and four predefined subsets of sites versus the logarithm of the cumulative number of samples in each of these combinations. This regression is then extrapolated to the whole surface of the studied area. According to Ugland et al. (2003, 2005), the TS method provides more realistic estimates of total species richness than the usual estimators, which result in important underestimations. Labrune et al. (2006b) recently argued that the TS method provides more accurate results when subsets of sites do not correspond to macrofauna communities/assemblages. The rationale for that is that the whole studied area does not necessarily contain more communities than the ones already identified. During the present study, we therefore used the TS method based on four geographical sub-areas (area 1 = transect A to E, area 2 = transect F to J, area 3 = transect K to P, area 4 = transect Q to U). For both estimation methods, the total surface area of the studied area was estimated as 2921 km^2 and the surface area represented by one sampling unit was considered to be 0.3 m^2 (i.e., the true sampled surface area at each site).

Results

A total of 26,999 individuals belonging to 425 species were identified during the present study, including 173 species of polychaetes, 133 species of crustaceans, 86 species of molluscs and 15 species of echinoderms. Of the ten most abundant species, six were polychaetes, three were molluscs and one was a crustacean. The most dominant species was the serpulid *Ditrupa arietina*, which accounted for 27.3% of total macrofauna abundance. The oweniid *Owenia fusiformis* accounted for 9.8% and the turritellid

Turitella communis for 6.4% of the total macrofauna abundance. The two most widespread species were *Lumbrineris latreilli* and Tanaidacae ind., which were present at 79 and 80 sites, respectively. The ranges of the other most abundant species were much more restricted (i.e., 43, 40 and 42 sites for *D. arietina, O. fusiformis* and *T. communis*, respectively) and 119 species were singletons. Species range distribution curves for each major taxonomic group are shown in Fig. 2. Although polychaetes, crustaceans and molluscs featured a quite similar general pattern (i.e., right skewed distributions), the frequency distributions of species range significantly differed among major taxonomic groups (Kolmogorov-Smirnov tests, $P < 0.01$, except for crustaceans and molluscs for which $P > 0.05$). This pattern was less clear for echinoderms due to a lower number of species. Polychaetes and crustaceans had both 40 species present at only one site, while molluscs and echinoderms had 29 and 4, respectively. Polychaetes had 25 species present at more than 20 sites versus 13 for molluscs, 12 for crustaceans and 6 species for echinoderms, respectively.
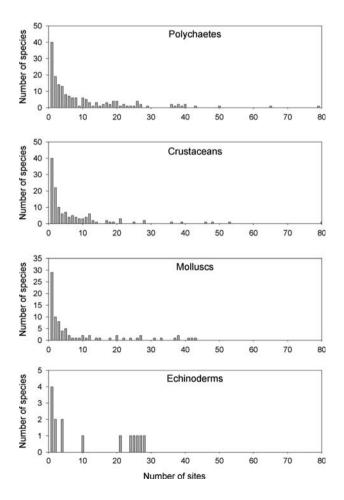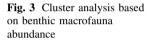

Fig. 2 Distributions of species ranges for the four major taxonomic groups

Cluster definition and composition

Total macrofauna composition correlated most tightly with the composition of polychaetes (Mantel test, $\rho = 0.927$, $P < 0.001$), followed by molluscs, echinoderms and crustaceans (Mantel tests, $\rho = 0.700$, 0.682 and 0.596, respectively, with $P < 0.001$ in all cases). The results of the cluster analysis based on total macrofauna composition are presented in Fig. 3.

Three main clusters were identified based on a 25% similarity level. The first cluster mainly grouped sites in 10 and 20 m depth (except T10 and U10, which both featured extremely low species richness). The second cluster mainly grouped sites 30 m depth and could be divided into two sub-clusters as already proposed by Labrune et al. (2007) for polychaetes. The third cluster grouped all sites in 40 and 50 m depth except E40, which was more similar to the sites of cluster II. The locations of sites belonging to the

four clusters and sub-clusters, identified based on macrofauna composition, are shown in Fig. 1.

The average cumulated granulometric curves and organic carbon contents within each cluster are shown in Fig. 4. There were marked differences in sediment granulometry among 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 mean proportions of silt-clay significantly differed among clusters (Kruskal–Wallis ANOVA, $P < 0.001$). Sediments mostly consisted of fine sands in cluster I, muddy sands in cluster IIa, sandy mud in cluster IIb and fine mud in cluster III. Mean organic carbon contents significantly differed among clusters (Kruskal–Wallis ANOVA, $P < 0.001$) and correlated positively with silt-clay contents ($r = 0.94$, $P < 0.001$). Organic carbon contents were lower in clusters I and IIa and higher in clusters IIb and III. There were significant correlations between macrofauna composition and depth (Mantel

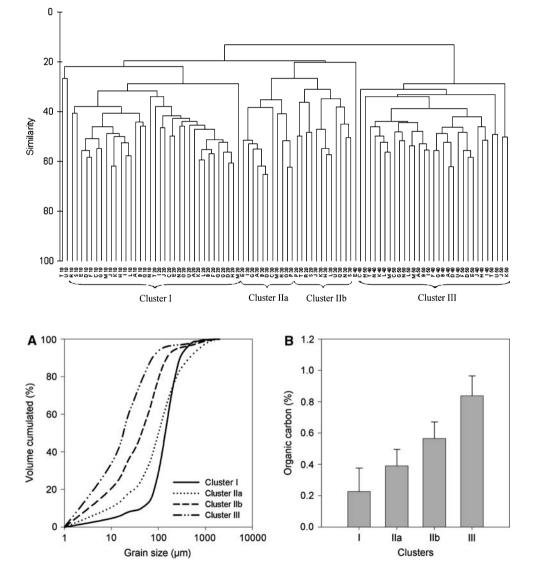Fig. 3 Cluster analysis based on benthic macrofauna abundance

Fig. 4 Average cumulated granulometric curves (**a**), and organic carbon contents (**b**) of surface sediments in the four main clusters and sub-clusters identified on the basis of total macrofauna composition. *Vertical bars* are standard deviations
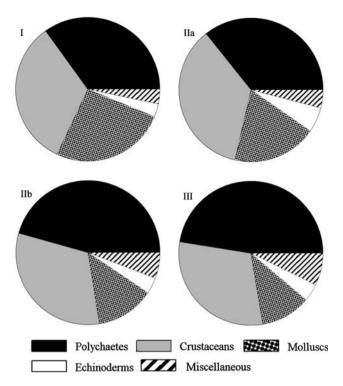
Fig. 5 Contributions of the four major taxonomic groups to the species richness of the total macrofauna within the four main clusters and sub-clusters identified on the basis of total macrofauna composition

test, $\rho = 0.788$, $P < 0.001$), percentage of silt-clay (Mantel test, $\rho = 0.735$, $P < 0.001$), and organic carbon content (Mantel tests, $\rho = 0.706$, $P < 0.001$).

Polychaetes and crustaceans were the two major taxonomic groups contributing most to total macrofauna species richness (Fig. 5). The relative contributions of each major taxonomic group to total species richness within each cluster are shown in Fig. 5. The contribution of polychaetes tended to increase from cluster I to cluster III. Crustaceans and molluscs showed an opposite trend. The contribution of echinoderms was maximal in cluster IIa.

Contributions and cumulative contributions of the ten species most responsible for similarities within each cluster are shown in Table 1. Polychaetes accounted for seven, five, four and six of these ten species in clusters I, IIa, IIb and III, respectively. Species most responsible for dissimilarities between clusters are listed in Table 2.

Different components of macrofauna diversity

Average values and standard deviations of the four indices of α-diversity of total macrofauna within each cluster are shown in Fig. 6. All indices featured significant differences among clusters (Kruskal–Wallis ANOVAs, $P < 0.001$ in all cases). Mean species richness was higher in clusters I

Table 1 Contributions and cumulative contributions of the species most responsible for similarity within each cluster identified on the basis of total macrofauna composition
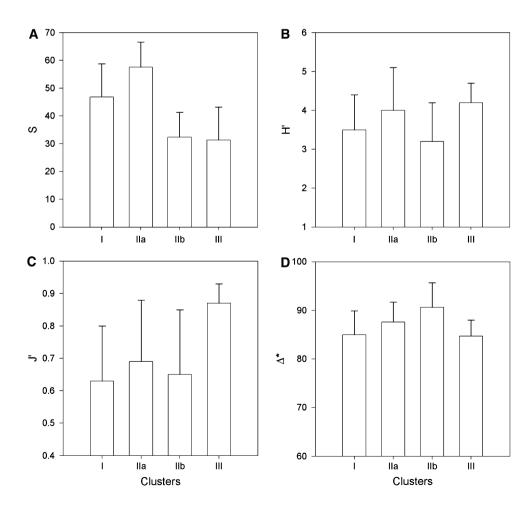
	Species	Contribution (%)	Cumulative contribution (%)
Cluster I	*Ditrupa arietina*	12.90	12.90
	Owenia fusiformis	10.48	23.38
	Tanaidacae ind.	5.89	29.26
	Spisula subtruncata	5.33	34.59
	Chone duneri	5.09	39.68
	Nephtys hombergii	4.35	44.03
	Glycera unicornis	4.28	48.31
	Aponuphis bilineata	3.98	52.29
	Corbula gibba	2.58	54.88
	Lumbrineris latreilli	2.48	57.36
Cluster IIa	*Ditrupa arietina*	10.31	10.31
	Lumbrineris latreilli	7.44	17.75
	Tanaidacae ind.	6.45	24.20
	Goniada spp.	4.76	28.97
	Aponuphis bilineata.	4.75	33.71
	Tellina pulchella	3.79	37.51
	Scoletoma impatiens	3.56	41.06
	Nucula nitidosa	3.45	44.51
	Phaxas pellucidus	3.29	47.80
	Amphiura chiajei	2.57	50.37
Cluster IIb	*Lumbrineris latreilli*	20.21	20.21
	Turitella communis.	20.11	40.32
	Tanaidacae ind.	6.62	46.94
	Notomastus sp.	6.01	52.95
	Amphiura chiajei	4.09	57.04
	Ampelica typica	4.07	61.11
	Scoletoma impatiens	2.52	63.63
	Nucula nitidosa	2.51	66.15
	Ampelisca diadema	2.43	68.58
	Aspidosiphon muelleri	2.05	70.63
Cluster III	*Sternaspis scutata*	12.70	12.70
	Lumbrineris latreilli	11.09	23.79
	Nephtys incisa	7.78	31.57
	Tanaidacae ind.	6.84	38.40
	Heteromastus filiformis	4.45	42.86
	Scoletoma emandibula mabiti	4.02	46.87
	Labidoplax digitata	3.95	50.83
	Glycera unicornis	3.61	54.43
	Ampelisca diadema	3.33	57.76
	Goneplax rhomboides	3.00	60.76

and IIa than in clusters IIb and III. Changes in average H′ were more limited with higher values in clusters IIa and III and lower ones in clusters I and IIb. Average J′ were

Table 2 Contributions and average abundances of species responsible for most of the dissimilarities between clusters identified based on total macrofauna composition

First cluster	Second cluster	Species	Average abundance, first cluster	Average abundance, second cluster	Cumulative contribution (%)
I	IIa	*Ditrupa arietina*	497.19	638.18	5.66
		Owenia fusiformis	253.20	1.82	9.68
		Lumbrineris latreilli	17.29	119.09	12.12
		Tanaidacae ind.	49.90	118.18	14.39
		Spisula subtruncata	82.24	0.61	16.60
		Goniada sp.	0.00	36.67	18.56
IIa	IIb	*Ditrupa arietina*	638.18	1.67	7.59
		Turritella communis	6.36	434.73	13.08
		Tanaidacae ind.	118.18	33.06	15.87
		Aponuphis bilineata	36.97	0.28	18.16
		Lumbrineris latreilli	119.09	126.94	20.20
IIb	III	*Turitella communis*	434.73	7.74	8.91
		Lumbrineris latreilli	126.94	40.86	12.95
		Amphiura chiajei	25.83	1.61	15.36
		Sthenelais boa	4.72	24.62	17.63
		Ampelisca typica	22.78	2.26	19.82
		Ampelisca diadema	31.11	7.74	22.01

Fig. 6 Average species richness (**a**), Shannon index (**b**), Pielou evenness (**c**), and taxonomic distinctness (**d**) for the four main clusters and sub-clusters identified on the basis of total macrofauna composition. *Vertical lines* are standard deviations

almost similar in clusters I, IIa and IIb, and much higher in cluster III. Average Δ^* showed only limited changes among clusters with increasing values between clusters I and IIb and then decreasing ones between clusters IIb and III.

The main characteristics of the stepwise multiple regression models linking the species richness of major taxonomic groups and the species richness of total macrofauna are shown in Table 3. The combination of major taxa best accounting for the species richness of total macrofauna clearly differed between clusters. Overall species richness of crustaceans and polychaetes correlated best with species richness of total macrofauna. Molluscs were also always included in the best combination of major taxa, which conversely was not the case for echinoderms.

Relationships between the other α-diversity indices of each major taxonomic groups and total macrofauna are shown in Table 4. H′ and J′ of polychaetes correlated best

Table 3 Adjusted r^2 of the forward stepwise multiple regression models linking species richness of total macrofauna and of major taxonomic groups

	Variables and coefficients	Adjusted cumulated r^2
Cluster I ($N = 35$)	Cte $= -1.106$	
	Pol $= 1.084$	0.581
	Cru $= 1.052$	0.830
	Mol $= 0.938$	0.986
	Ech $= 1.266$	0.996
Cluster IIa ($N = 11$)	Cte $= 7.037$	0.614
	Cru $= 0.855$	0.773
	Mol $= 1.127$	0.994
	Pol $= 0.983$	
Cluster IIb ($N = 12$)	Cte $= -0.553$	
	Cru $= 1.320$	0.517
	Pol $= 1.200$	0.948
	Mol $= 0.741$	0.981
Cluster III ($N = 3$)	Cte $= 0.551$	
	Pol $= 1.076$	0.885
	Cru $= 0.929$	0.971
	Mol $= 1.049$	0.985
	Ech $= 1.068$	0.990
Whole area ($N = 92$)	Cte $= 0.453$	
	Cru $= 1.009$	0.623
	Pol $= 1.453$	0.889
	Mol $= 0.936$	0.986
	Ech $= 1.120$	0.994

Coefficients are provided both for individual clusters and for the whole data set. Probability threshold: 0.005

Cte contant, *Pol* polychaetes, *Cru* crustaceans, *Mol* molluscs, *Ech* echinoderms

with those of the total macrofauna within the whole studied area and within all clusters but IIb (where molluscs correlated better). Only the Δ^* of polychaetes in cluster I, of molluscs in the whole studied area and of echinoderms in cluster III correlated significantly with those of the total macrofauna. Determination coefficients were always less than 0.36, which was much lower than those recorded for the three other indices of α-diversity.

Figure 7 shows the β_w accumulation curves based on samples from the whole studied area. Corresponding β_w were: 10.4 for total macrofauna; 12.3, 10.7, 9.1 and 7.8 for crustaceans, molluscs, polychaetes and echinoderms, respectively. The pattern of β_w differed among clusters (Fig. 8). In cluster I, total macrofauna and molluscs featured the highest β_w, whereas the other major taxonomic groups all featured lower and quite similar β_w. In cluster IIa, total macrofauna featured the highest β_w and all major taxonomic groups featured lower and quite similar β_w. In cluster IIb, polychaetes featured the highest β_w followed by total macrofauna, whereas the three other dominant taxonomic groups featured much lower β_w. In cluster III, molluscs featured by far the highest β_w, followed by total macrofauna, polychaetes, crustaceans and echinoderms, which featured very similar β_w.

Cumulative curves of the estimators of total species richness within each cluster are shown in Fig. 9. Chao$_2$ and ICE always led to the highest estimates followed by Chao$_1$ and S_{obs}. None of the tested estimators reached an asymptote in any of the four clusters. Since the estimates of total species richness depend on sampling effort, they were compared between clusters for a standardized sampling effort (i.e., 11 sampling sites, which correspond to the number of sites in the smallest cluster). On this ground, cluster IIa featured the highest total species richness followed by clusters I, IIb and III.

The two estimates of total species number within the whole studied area are presented in Fig. 10. The extrapolation of the species accumulation resulted in an estimation of 2,082 species versus 2,319 species when using the TS method.

Discussion

Main soft-bottom macrofauna communities

The first quantitative descriptions of Mediterranean soft-bottom macrofauna have been carried out independently along the Provence and the French Catalan coasts, which has resulted in two distinct denominations for most communities (Picard 1965; Guille 1971). Since most communities have then been found elsewhere in the Mediterranean (Desbruyères et al. 1972; Gamulin-Brida

Table 4 Determination coefficients (r^2) of the simple linear regression models linking α-diversity indices for total macrofauna and for each major taxonomic group

H'	Cluster I (N = 35)	Cluster IIa (N = 11)	Cluster IIb (N = 12)	Cluster III (N = 31)	Whole area (N = 92)
Polychaetes	**0.83**	**0.84**	0.04	**0.72**	**0.67**
Crustaceans	0.07	0.02	0.03	**0.42**	0.04
Molluscs	0.00	0.01	**0.42**	**0.26**	0.00
Echinoderms	0.09	**0.45**	0.10	**0.23**	0.03
J'	Cluster I (N = 35)	Cluster IIa (N = 11)	Cluster IIb (N = 12)	Cluster III (N = 31)	Whole area (N = 92)
Polychaetes	**0.00**	**0.89**	0.00	**0.69**	**0.69**
Crustaceans	0.01	0.38	0.01	0.01	0.04
Molluscs	0.01	0.25	**0.54**	0.01	**0.05**
Echinoderms	0.00	**0.44**	0.29	0.18	**0.08**
Δ^*	Cluster I (N = 35)	Cluster IIa (N = 11)	Cluster IIb (N = 12)	Cluster III (N = 31)	Whole area (N = 92)
Polychaetes	**0.36**	0.06	0.04	0.01	0.02
Crustaceans	0.05	0.01	0.28	0.01	0.00
Molluscs	0.07	0.01	0.00	0.03	**0.05**
Echinoderms	0.03	0.02	0.01	**0.34**	0.00

Coefficients are provided both for individual clusters and for the whole data set. Significant positive correlations ($P < 0.05$) are in bold
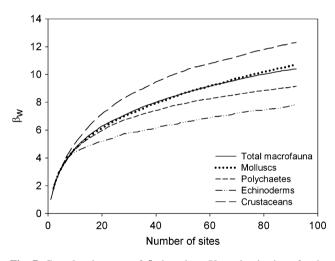

Fig. 7 Cumulated curves of β_w based on 50 randomizations for the four major taxonomic groups and total macrofauna in the whole studied area
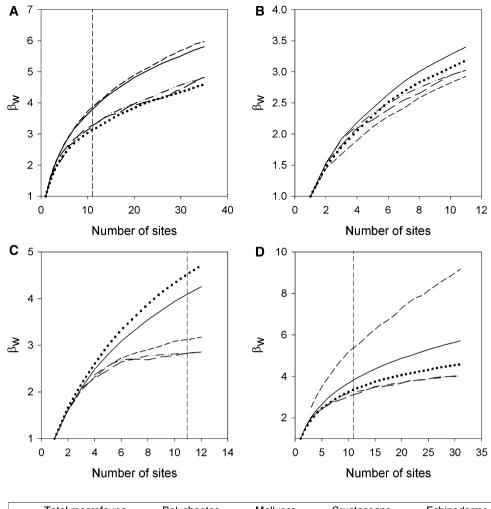
1974; Dounas and Koukouras 1992; Karakassis and Eleftheriou 1997; Tselepides et al. 2000) or even in other areas in the world (Probert and Grove 1998), this requires some clarification. During the present study, we identified four main clusters and sub-clusters, which were very similar to those reported based on the sole analysis of polychaete fauna (Labrune et al. 2007). Cluster I tightly corresponded to the littoral fine sands assemblage (LFS), clusters IIa and IIb to the littoral sandy mud assemblages (LSM, with a distinction between southern and northern part), and cluster III to the terrigeneous coastal mud assemblage (TCM). We

therefore propose that the terminology LSF/LSM/TCM should now be used to account for the three main communities of macrofauna in the littoral soft-bottoms of the Gulf of Lions.

Components of macrofaunal diversity

During the present study, species richness per site was between 10 and 76, H' between 0.74 and 5.14, and J' between 0.16 and 0.94. Great caution should be taken when comparing results of different studies due to possible heterogeneity in sampling strategies, gears and processing. Nevertheless, our results are coherent with those of Albertelli et al. (1999) who assessed α-diversity along a 5–135 m depth transect in the Ligurian Sea. At depths comparable to ours (i.e., 20 and 35 m), species richness ranged between 54 and 89, H' between 3.1 and 3.2, and J' between 0.7 and 0.8.

The overall β_w value recorded in the present study was 10.4. To our knowledge, β_w values in the Mediterranean Sea are still lacking. However, our value can be compared with values reported for the North Sea (2.6 by Ellingsen 2001; 5.0 by Ellingsen 2002; 9.3 by Ellingsen and Gray 2002) and the Hong Kong waters (11.0 by Shin and Ellingsen 2004). Our β_w value is thus indicative of high β-diversity (Shin and Ellingsen 2004). The heterogeneity in the β_w values in the North Sea largely results from the diversity of sampled habitats (Ellingsen 2002). When computed for the different clusters, our β_w values were

Fig. 8 Cumulated curves of β_w based on 50 randomizations for the four major taxonomic groups and total macrofauna for cluster I (**a**), cluster IIa (**b**), cluster IIb (**c**) and cluster III (**d**). *Dashed lines* correspond to a standardized sampling effort of 11 sites

—— Total macrofauna ······ Polychaetes – – – Molluscs —·— Crustaceans — — Echinoderms

between 3.4 (cluster IIa) and 5.8 (cluster I), which was still higher than the value reported for a single North Sea habitat by Ellingsen (2001). Thus, irrespective of the heterogeneity of sampled habitats, our results suggest that β-diversity of soft-bottom macrofauna is higher in the Gulf of Lions than in the North Sea.

All three indices provided reasonably close estimates, although slightly higher for ICE and Chao$_2$ than for Chao$_1$. This result is in accordance with those of Foggo et al. (2003a), Magurran (2004) and Mackie et al. (2005). When standardized for sampling effort, these estimates were higher for cluster IIa than for clusters I, IIb and III, which differed from what was reported by Labrune et al. (2006b) based on the analysis of polychaete fauna (i.e., lower estimate for clusters IIa than for clusters IIb, I and III). It should be underlined that this discrepancy did not result from differences in the delimitation of clusters, since cluster III was also affected although its composition was exactly the same in both studies.

Overall, 425 species were recorded in the present study. The extrapolation of the species accumulation curve to the whole sampled area resulted in an estimation of an overall number of 2,082 species versus 2,319 for the TS method (Ugland et al. 2003). The difference between the results derived from these two approaches was low (i.e., about 10% of the TS value) as compared to the Norwegian continental shelf (about 78% of the TS value, Ugland et al. 2003). This probably reflects the higher homogeneity of the areas sampled in the present study. There are very few estimates of the overall number of species for soft-bottom macrofauna and these estimates are rather uncertain. Based on the comparison of estimates from the TS method with literature data on total macrofauna, Ugland et al. (2003) concluded that the TS method might provide appropriate estimates of total species numbers. Our estimate for the Gulf of Lions (2,319 species) is close to the one for the Hong Kong waters (2,254 species), but much smaller than the one for the Norwegian shelf (5,403 species; Ugland

Fig. 9 Estimates of the total number of species within each of the four main clusters and sub-clusters identified on the basis of total macrofauna composition. Estimators are S_{obs}, $Chao_1$, $Chao_2$ and ICE. *Plotted values* are means $\pm$SD of 50 estimates based on 50 randomizations. For clarity reasons, standard deviations are not shown
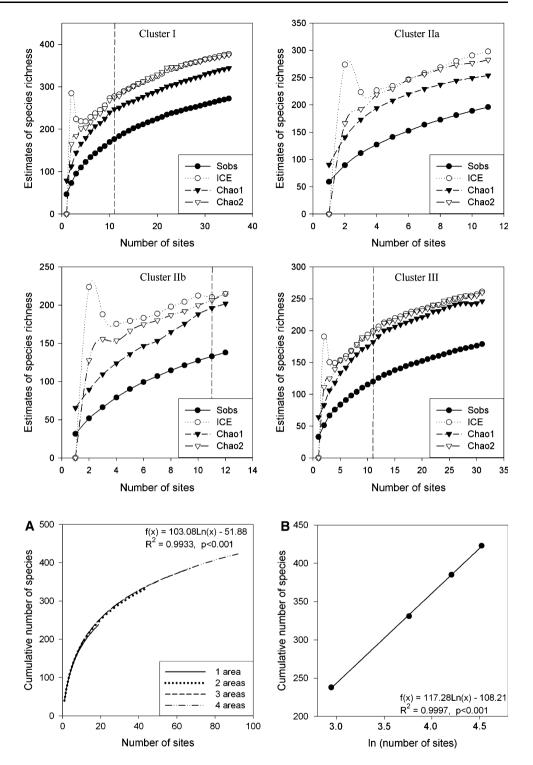

Fig. 10 Species accumulation curve for all combinations of one to four geographical sub-areas (**a**), and corresponding semi-logarithmic regression used for the estimation of true species richness (TS method; **b**). See text for details

et al. 2003). The sampled depth range in the Gulf of Lions was almost similar to that in Hong Kong waters (Shin and Ellingsen 2004) and much lower than the one sampled on the Norwegian continental shelf (Ellingsen and Gray 2002). Thus, in agreement with Shin and Ellingsen (2004), differences in depth range may be responsible for the discrepancies in the total number of species.

Use of major taxonomic groups as surrogates for total macrofauna

For all major taxonomic groups the similarity matrix based on abundances correlated significantly with that for the total macrofauna. This correlation was highest for polychaetes, lowest for crustaceans and intermediate for

molluscs and echinoderms. Similar results have already been reported for a set of North Sea sites (Olsgard and Somerfield 2000). The sequence reported by these authors was polychaetes > molluscs > crustaceans and no data were provided for echinoderms. The highest correlation found for polychaetes may have resulted partly from the fact that polychaetes represented the dominant group both in terms of abundance and species richness during the present study.

In spite of an overall good correlation between the compositions of total macrofauna and polychaete fauna, our results suggest that polychaetes do not always constitute a sound basis for classifying sites in areas of transition between sandy and muddy sediments. Out of the 92 sampled sites, 7 showed discrepancies in the classifications based on polychaete and total macrofauna composition. Most of these sites were located at the limit of areas characterized by different sediment granulometry (Labrune et al. 2007). K30 was located at the limit of the small area of muddy sediments off the Lagoon of Sigean and the River Aude, L30 was located off the mouth of the Hérault River; O30, P30 and R30 were located within and/or at the edge of the area of heterogeneous sediments off Montpellier (Aloisi et al. 1973). Discrepancies thus corresponded to the classification of sites in clusters characterized by a finer granulometry when using total macrofauna. The switch in the classification of H30, K30 and L30 from cluster IIa to IIb mainly resulted from high abundances of *Turitella communis*. The switch in the classification of O30, P30 and R30 resulted from the absence of *Spisula subtruncata* and high abundances of Tanaidacae ind. *Spisula subtruncata* is a suspension-feeder, which has long been known to be negatively affected by the increase of the proportion of fine particles within the sediment (Rhoads and Young 1970). On the contrary, most of the Tanaidacae and *Turitella communis* are known to prefer muddy substrates (Riedl 1983).

Overall species richness of crustaceans and polychaetes correlated best with species richness of total macrofauna. This is consistent with previous studies, which suggested that polychaetes as a whole (Olsgard and Somerfield 2000) or even a fraction of them (Olsgard et al. 2003) might be used as a surrogate for benthic macrofaunal species richness. Olsgard and Somerfield (2000) suggested that the correlation between indices computed for polychaetes and the total macrofauna were lower in pristine than in disturbed areas. Since the Gulf of Lions can be considered to be a non-perturbed area (Grémare et al. 1998; Rosenberg et al. 2003; Labrune et al. 2006a), our results support the use of polychaetes as a surrogate for the analysis of total macrobenthos species richness in soft-bottoms under moderate disturbance. They also highlight the fact that crustaceans are good surrogates as well for total macrobenthos species richness.

Olsgard and Somerfield (2000) also reported that H' of polychaetes correlated positively with those of total macrofauna. In the present study, polychaetes were the only major taxonomic group whose H' correlated positively with that of the total macrofauna when considering the whole sampled area. However, in the Gulf of Lions the significance of the relationship between H' and also J' values of polychaetes and the total macrofauna strongly differed between communities. Conversely, there was almost no significant correlation between the $\Delta*$ of major taxa and total macrofauna. This is in agreement with Karakassis et al. (2006) who also reported a lack of constancy in the correlation of $\Delta*$ obtained for all the studied components. In the present study, the scarcity of significant correlations recorded for $\Delta*$ probably resulted from the fact that this index is largely independent of species richness and dominance (Clarke and Warwick 1998). Overall, our results suggest that the relevance of using polychaetes as surrogates for the α-diversity of total macrofauna is highly dependent on the sampled cluster/communities. Therefore, this option should not be based on an a priori decision, but rather on the results of preliminary surveys (see Mackie et al. 2005, for the South Irish Sea) assessing at least the dominance patterns between and within major taxonomic groups.

There is also a crucial need to assess patterns of β-diversity among major taxonomic groups, which has only rarely been achieved in the marine environment. When considering the whole studied area, crustaceans featured the highest β_w, followed by molluscs, total macrofauna, polychaetes and echinoderms. This sequence is in good agreement with the few comparable data available for the marine environment. Crustaceans and molluscs both featured with high β_w in the North Sea (Ellingsen 2001, 2002; Ellingsen and Gray 2002) and in Hong Kong waters (Shin and Ellingsen 2004). Conversely, polychaetes showed low β_w values in all these studies, while data on echinoderms are scarcer (e.g., not provided in Shin and Ellingsen 2004) and more variable (e.g., Ellingsen 2001, 2002). High β_w are usually attributed to the dominance of species with low distribution range (Harrison et al. 1992; Ellingsen 2001, 2002). Our results showed that there were significant differences in the distribution ranges of the major taxonomic groups and that polychaetes had a higher number of species with a wide distribution range than other major taxonomic groups, which partly accounted for their low β_w. There were also marked differences in the ranking of β_w between the major taxonomic groups, depending on the considered cluster. Similar results have already been reported for distinct geographical areas both in the North Sea (Ellingsen and Gray 2002) and in Hong Kong waters (Shin and Ellingsen 2004). As for α-diversity indices, this suggests that the validity of a major taxonomic group as a surrogate

of total macrofauna is highly dependent on the considered environment. This confirms that a single taxonomic group cannot be taken to represent overall β-diversity (Ellingsen and Gray 2002).

Overall, our results show that the choice of a surrogate for total benthic macrofauna depends on the characteristic of the benthic macrofauna to be studied. Polychaetes clearly would constitute the best choice for an assessment of the overall composition of the soft-bottom macrofauna in the whole Gulf of Lions. In this particular case, polychaetes and crustaceans are also the best surrogates when assessing α-diversity (except in the case of Δ^*). Conversely, molluscs constituted the best surrogate of β-diversity. Moreover, the choice of an optimal surrogate also depends on the studied environment as shown by the important discrepancies between clusters reported in the present study.

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