Diversity of benthic macrofauna in the eastern English Channel: comparison among and within communities

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Abstract. The diversity of benthic macrofaunal assemblages in the eastern English Channel is described
from 707 samples collected with a Rallier-du-Baty dredge during 1971–1975. Four assemblages were
primarily defined by means of multivariate data analyses and clustering methods: the '*Abra alba* com-
munity', the '*Ophelia borealis* community', the 'pebbles community' and a 'mixed assemblage' of the
first three communities. Spatial heterogeneity of these communities is significantly correlated with sedi-
mentary characteristics, although local variability appears to be controlled by both physical and biological
processes. Ecological diversity of these communities was analysed considering species richness (S), the
Shannon diversity index (H'), and rank-frequency diagrammes (RFD). These analyses were performed
at two spatial scales: for a single sample, and for a 'site' of 10 pooled samples. Thus, several sites were
chosen in order to compare diversity patterns and species quantitative structure among and within the
communities. The greatest species richness was recorded for the pebbles (57–69) and the *A. alba* (63–
79) communities. In the former, high values may be due to the complexity of microhabitats and the large
flux of food related to strong currents. In the latter, both organic matter and terrestrial inputs associated
with the mud favour the presence of deposit-feeder organisms. No clear trend was observed among and
within the community sites in terms of the species quantitative structure. Thus, convex RFD shapes were
observed in three assemblages: the 'mixed assemblage' (offshore site), the *A. alba* (North Sea), and the
pebbles (Normandy coast). 'Sigmoid' shapes were observed in the pebbles (Dover Strait) and *A. alba*
(English coast) communities. Presumably, these shapes can be caused by the combined action of phys-
ical (strong currents, substrate stability, mud content in the sediments) and biological factors (co-occur-
rence of species from different communities, strong species recruitment, relative dominance of carnivorous
species).

Key words: benthos, community structure, diversity, English Channel, spatial scales

Introduction

Oceans cover ~70% of the Earth's surface and, in consequence, marine sediments
represent the largest ecosystem in the world. In turn, benthic macrofauna usually
constitutes the dominant biomass of the marine bottom system, and at the phylum
level this group represents the most diverse assemblage on Earth (Snelgrove 1998).

But what determines the variety of organisms inhabiting together in a natural environment? MacArthur and MacArthur (1961) were the first to formulate the relationship between the structure of a community and the complexity of the habitat. More recently, Hicks (1980) and Stoner and Lewis (1985) have reaffirmed this idea for aquatic ecosystems. A global estimation of macrofaunal species ranges from 500,000 to 10,000,000 (Grassle and Maciolek 1992; May 1993), although as most of these species are undescribed, diversity patterns are poorly understood.

Ecologically, bottom macrofauna plays an important role in ecosystem processes, such as nutrient cycling, pollutant metabolism, secondary production, food webs, burial and dispersion (Snelgrove 1998). Based on several studies, Parker (1975) summarised the importance of studying benthic communities as follows: i) to determine the stability of aquatic environments through the study of the diversity and abundance of infaunal species, ii) knowledge of food chains is necessary for an adequate management of coastal waters and to maintain the normal level of biological production, iii) changes in dominant species can be used to detect environmental disturbance, caused by either natural or human perturbations, iv) knowledge of bottom community meio and megafauna composition is very important in managing commercial sea food production, and finally v) knowledge of species composition could help solve ecological problems related to ancient benthic communities. Thus, the community is the level of organization most popular for impact and conservation studies, since its structure reflects integrated environmental conditions over a period of time (Warwick 1993; Angermeier and Winston 1999).

In the European seas, the English Channel represents an interesting transition zone between the temperate and boreal regions. In the last decades, this Channel has been heavily impacted by anthropogenic activities, such as civil works, modifications of ports and bays, nuclear power plants, oil spills, and the use of antifouling paints (Cabioch et al. 1980; Clique and Lepetit 1987; Dauvin 1997; Michel and Averty 1999). Hence, scientific knowledge is needed to propose adequate measures to improve its conservation.

A first attempt in the study of benthic communities in the English Channel was conducted by Holme (1966), who analysed 311 samples on a grid covering the whole Channel. In the eastern Channel and southern part of the North Sea, most studies referring to benthic communities have focused on some restricted areas, especially coastal waters (Cabioch and Glaçon 1975, 1977; Souplet et al. 1980; Prygiel et al. 1988), and bottom biodiversity in the whole area has scarcely been studied. In our previous work (Sanvicente-Añorve et al. 1996) an attempt was made to explain the role of hydro-sedimentary processes as possible causes of large scale diversity patterns in this region, independently of species identity. Rees et al. (1999) compared the benthic diversity in the English Channel with the fauna from the North and Celtic Seas at several study sites. Other studies have dealt with the species richness of a particular benthic group (Dauvin et al. 1996; Dauvin 1999).

The current knowledge of benthic community structure and diversity patterns in this region is still limited. This study intends firstly, to identify the main benthic assemblages in the entire eastern English Channel, and secondly, to compare the distribution of the diversity patterns among and within communities. For these purposes, the database of the RCP (Recherche Coopérative sur Programme) Benthos de la Manche Research Programme (Cabioch 1984), the largest benthic database available for the Channel, was employed.

Materials and methods

Study area and sampling strategy

The studied area includes the eastern part of the English Channel, from the meridian crossing Hastings up to the French-Belgian border. Benthic and granulometric data were collected simultaneously during the oceanographic cruises for the RCP Benthos de la Manche Research Programme conducted in the summers of 1971 through 1975 (Cabioch 1984). A total of 707 stations was sampled in the study area, with no replications. A sampling grid was established considering sedimentary heterogeneity. Thus, sampling density was ~2 over 10 km^2 in the western part, and from 5 to 40 samples in the eastern part (Figure 1). Sampling was carried out onboard the R/V 'Pluteus II'. Bottom samples were taken with 3–5 min circular tows, using a standard 45 cm diameter and 1 mm mesh size Rallier-du-Baty dredge at each sampling location. The macrofauna was sorted from a 30 l sediment sample sieved through a 2 mm mesh size sieve. Individuals were quantified and identified to the lowest possible taxon by the scientific staff of the RCP Programme. In spite of this dredge being critized with respect to quantitative analyses, information on relative abundance obtained with it is considered reliable (Eleftheriou and Holme 1984; Sanvicente-Añorve and Leprêtre 1995).

The study area is characterised by a macrotidal regime. The tidal currents alternate and are essentially parallel to the coast: northwards at flood and southwards at ebb. Because of the tidal residual and the dominant southwesterly winds, the residual circulation drifts northeastwards. The greatest surface speed measured at spring tide exceeds three knots in the centre of the Dover Strait, and the currents are weaker in the bays and off the Somme River (S.H.O.M. 1968; Pingree and Maddock 1977). According to Vinchon et al. (1993), bottom currents decrease by 20–30% offshore, and more still in coastal areas, due to the interference of swell currents. These hydrodynamic features determine sediment distribution. Progressive weakening of the currents results in deposits of decreasing grain size. Finer deposits are concentrated in low energy zones, and rocky seabeds are found in the Dover Strait. Sand bodies and sand sheets are well developed both to the northeast and the southwest of Dover
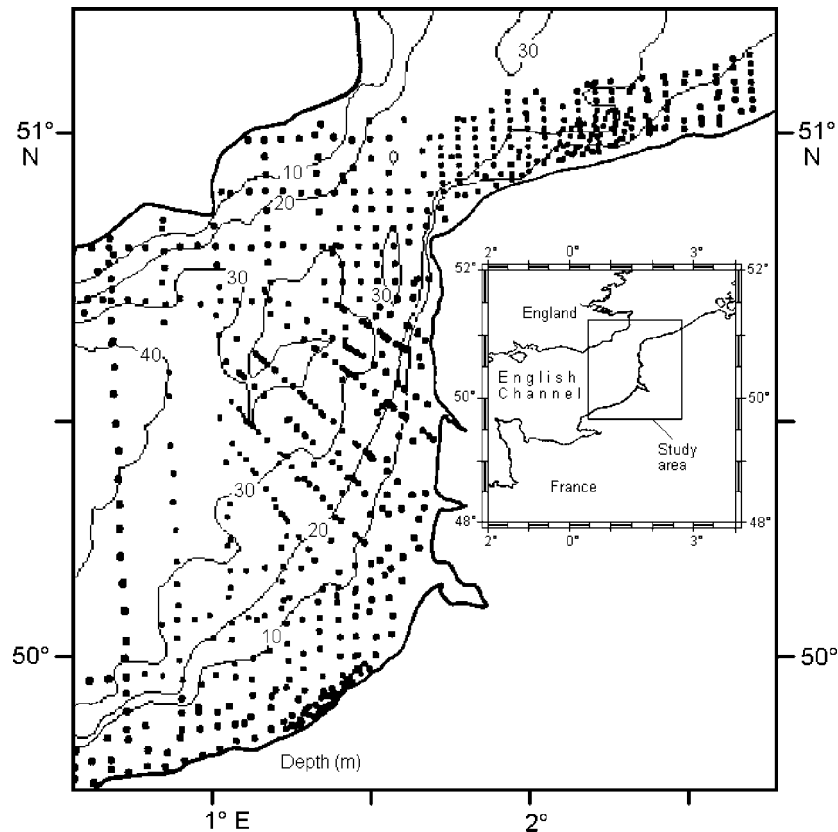
Figure 1. Study area and location of the 707 oceanographic stations.

Strait. The inter-bank zones are composed of mixed sediments, including pebbles, gravel and sand (Larsonneur et al. 1982).

Data analysis

To determine the spatial distribution and structure of the benthic assemblages, two multivariate techniques were applied: 1) Correspondence analysis (CA) on the contingency table crossing samples and species, and 2) hierarchical classification of the axes from the CA that accounted for more than 60% of the total variance. Dendrograms were constructed using the Euclidean Dissimilarity Index and the Ward agglomerative method (Jambu 1978; Juan 1982; Volle 1985). Groups were defined at a cut level of 60% similarity in these dendrograms, and then plotted onto the station grid map. These methods were applied to the presence–absence data and to the quantitative data. A total of 347 species was identified. Species present in five or fewer stations

were excluded from the analyses. Thus, only 247 species from the 707 oceanographic stations were analysed.

Species diversity was mathematically characterised by:

i) species richness (S) and Shannon–Weaver diversity index (H'), calculated as:

$$H' = -\sum_{n=1}^{S} \frac{N_i}{N} \log_2 \frac{N_i}{N}$$

where S = total number of species, N = total abundance of organisms, and N_i = abundance of ith species (Shannon and Weaver 1963; Pielou 1975).

ii) species distribution represented by a rank-frequency diagramme (RFD), ranking the species in a decreasing order of abundance. The abscissa is the rank of the species, and the ordinate is the frequency (or percentage of abundance). Frequency and ranks are expressed on logarithmic scales. Statistically, this procedure is equivalent to a classical retrocumulative frequency function (Magurran 1983), after permutation of both axes (Frontier 1976, 1985).

The shape of a RFD describes three stages:

Stage 1: Curves are steep and show an inflection (so-called 'sigmoid'): diversity is low.

Stage 2: Curves are convex: diversity is high.

Stage 3: The curve is essentially linear in its left part and represents an intermediate stage of diversity.

In plankton communities, these three stages have been recognised by Frontier (1976) as different ecosystem maturation stages. Stage 1 corresponds to pioneer communities or communities under environmental pressure, stage 2 corresponds to mature communities, and stage 3 to the final stage of succession. Similar observations have been made by Warwick and Ruswahyuni (1987) and Warwick and Clarke (1995) on benthic communities.

The diversity measures and the quantitative structure of the communities were defined on two scales: that of a single sample, and that of a 'site', which included 10 combined samples. 'Mean' and 'global' parameters were calculated at each site (or section). 'Mean' parameters correspond to the arithmetic mean of the diversity values of each sample, representing the single sample scale. 'Global' parameters represent the 'site' scale and are calculated by adding samples. The RFD are drawn for each scale:

Mean RFD: The frequency mean of each rank is calculated independently of the species identity. The result is a mean shape characterising the community at a single sample scale. This method eliminates the sampling bias within the sample groups.

Global RFD: The numerical abundance of the species in all samples is added before constructing the diagramme. The resulting shape describes the diversity at a 'site' scale.

Differences between mean and global parameters represent the differences between the two observational spatial scales.

The importance of this type of diagrammes resides in the fact that it is possible to visualise the two essential components of diversity simultaneously: species richness (in the x-axis) and equitability (in the shape). Futhermore, Kobayashi (1981) has emphasised the importance of species spatial distribution as a third component, which can be detected in differences between the mean and global shapes.

According to Davoult (1992), 10 samples are enough to visualise the structure of a community and to detect differences in species composition at the scales of a 'site' and a 'single sample'. In this study, the 10 samples used to examine each community were spatially adjacent to each other, and were chosen according to the results of both qualitative and quantitative analyses, as is shown below.

Results and discussion

Benthic assemblages

Four benthic assemblages were identified in the eastern English Channel using the CA and cluster analyses. According to their species composition, three of these assemblages were designated as 'muddy fine sand with the *Abra alba* community', 'clean medium fine sand with an *Ophelia borealis* community', and a 'pebbles community'. These communities have been previously recognised in some restricted areas of the Channel and southern bight of the North Sea (Cabioch and Glaçon 1975, 1977; Souplet et al. 1980; Prygiel et al. 1988). The fourth faunistic complex corresponds to a 'mixed assemblage' of the above three communities, dominated in some sections by species belonging to the *Amphioxus lanceolatus* community (Cabioch and Glaçon 1977). Temporal stability of the spatial distribution of the benthic structures of this data set was demonstrated by Sanvicente-Añorve and Leprêtre (1995), who showed that all spatial groups were composed of samples collected in different years.

Results of both the qualitative and quantitative analyses were similar (Figure 2a, b). The main differences reside in the location of the boundaries between the assemblages. Moore (1974) pointed out that in studies made on a large spatial scale, little information is gained by using quantitative instead of qualitative data. In our study, the area occupied by both the *A. alba* and *O. borealis* assemblages in the qualitative analysis coincides with the sand distribution pattern described by Larsonneur et al. (1982). Some spatially localised community sections, like the sandbanks in the Channel, the inner English and French shelves, the Dover Strait and the Normandy coast, were associated with the same group by both analyses. Thus, these sections might be considered good representatives of their respective communities. In contrast, the analyses showed that the area near the French-Belgian border has been associated with different communities (Figure 2a, b). All these sections were chosen to establish their species quantitative structure. The boundaries observed in this work do not ex-
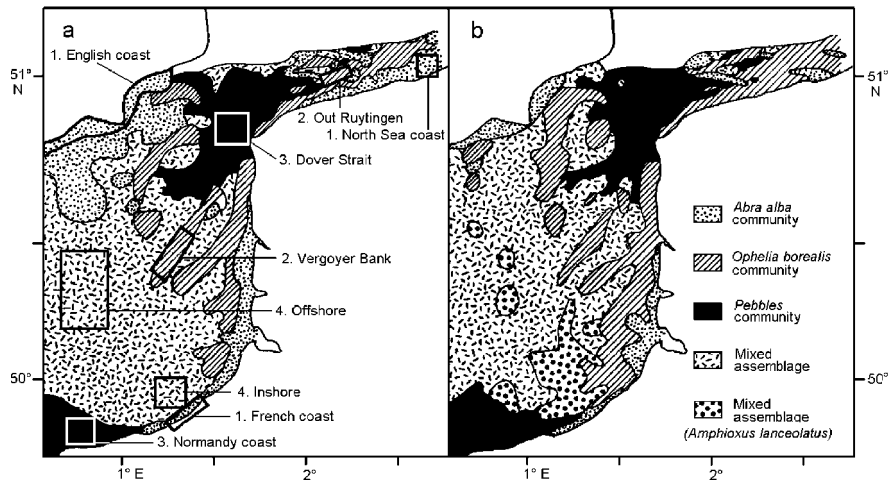
Figure 2. Spatial distribution of the benthic assemblages in the eastern English Channel. a) Results of the qualitative analysis and locations of the study sites of the communities. b) Results of the quantitative analysis.

actly correspond to those determined by Cabioch and Glaçon (1975, 1977) in studies made in a smaller geographic area. Hence, true boundaries between communities are difficult to define at this large geographic scale. Nevertheless, the results herein presented provide an idea of the spatial distribution of the benthic communities in the eastern English Channel.

The *A. alba* community appears distributed along the coast at depths of 10 m or less. These are weak-current areas where fine sand (70–90%) and mud (1–12%) constitute the bulk of the sediment (Prygiel et al. 1988). This community is very common in the northwestern European seas. In the English Channel, it is limited to the shallow waters of bays and estuaries, usually well separated from other bottom types (Chardy and Dauvin 1992). Three sections were examined in the study area: the English, French, and North Sea coasts (Figure 2a). The dominant species along English and French coasts was the deposit feeder bivalve *A. alba*, but the associated species groups were different (Table 1). Cabioch and Glaçon (1975) and Dewarumez et al. (1992) have also described these differences. In the North Sea coast, two of the dominant species of this community, *Nephtys cirrosa* and *Spiophanes bombyx*, are also representatives of the *O. borealis* community, as Prygiel et al. (1988) previously observed.

The *O. borealis* community was found in coastal areas deeper than 10 m, over the sandbanks in fine to coarse grains. Sandbanks are interesting ecological habitats: they can be considered 'islands' because of the differences with the surrounding fauna (Vanosmael et al. 1982). In our study area, the *O. borealis* community is well represented in the Southern North Sea and near the Normandy coast, as was recorded by Vanosmael et al. (1982) and Cabioch and Glaçon (1977). Two sections were chosen

Table 1. Species occupying the first eight ranks of abundance in each community site. R = species abundance rank, % A = percentage of total abundance.

	Communities																
	A. alba						O. borealis				Pebbles				Mixed assemblage			
	English coast		French coast		North Sea coast		Out Ruytingen		Vergoyer		Normady coast		Dover Strait		Offshore		Inshore	
	R	%A	R	%A	R	%A	R	%A	R	%A	R	%A	R	%A	R	%A	R	%A
A. alba	1	51.9	1	62.7	4	4.7							fc					
Am. lanceolatus																		
B. elegans							8	3.5	3	6.2								
B. guilliamsoniana							6	4.6	5	5.2								
Buccinum undatum											8	2.9						
Diastylis bradyi									6	3.2								
Echinocardium cordatum			5	2.7														
Echynocyamus pusillus													3	1.7	2	14.3	2	8.2
Ensis arcuatus					5	5.2												
Ensis sp.																	5	3.2
Euclymene oerstedii	7	2.1																
Galathea intermedia													5	1.3				
Gari tellinella															7	4.1		
Gastrosaccus spinifer							2	15.1	2	9.9								
Glycera trydactyla			7	1.4														
Glycymeris glycymeris															8	4.1		
Harmothoe extenuata													8	0.3				
Laevicardium crassum															5	5.1	4	4.3
Lanice conchilega			2	10.2														
Lepidopleurus asellus													7	0.4				
Lumbrineris latreilli																	6	2.5
Magelona alleni	8	1.7																
Melinna palmata	3	3.7																

Species	Abundance data (rank / %)
Mysella bidentata	4 3.7
N. cirrosa	6 2.3 · 1 9.7 · 1 40.7 · 4 5.6
N. hombergii	7 5.1
N. longosetosa	3 12.8
Notomastus latericeus	5 3.2 · 4 4.3
Nucella lapillus	5 6.0
Nucula turgida	2 19.2
O. borealis	5 4.6 · 8 2.4
Op. fragilis	6 5.4 · 1 80.8 · 1 16.2
Ophiura albida	2 2.9
Owenia fusiformis	2 8.2
Pagurus bernhardus	7 4.6 · 2 17.5
Pandulus montagui	8 3.8 · 4 6.8
Pectinaria koreni	3 5.8
Pilumnus hirtellus	6 0.6
Pisidia longicornis	1 19.4 · 2 7.7
Polynoe scolopendrina	7 3.5
Psammechinus miliaris	3 10.3 · 4 1.6 · 3 10.8 · 8 2.1
Spatangus purpureus	
S. bombyx	1 41.9
Sp. elliptica	4 7.0
S. ovalis	8 1.0
Sthenelais boa	6 1.7 · 7 2.1
Urothoe poseidonis	6 5.1 · 3 6.0

to study this community, the Vergoyer and the Out Ruytingen banks (Figure 2a). Common species in both sections were the polychaete *N. cirrosa* and the crustaceans *Gastrosaccus spinifer*, *Bathyporeia elegans* and *B. guilliamsoniana*. The dominant species were *N. cirrosa* in the Out Ruytingen Bank, and *S. bombyx* in the Vergoyer Bank (Table 1).

The pebbles community was located in the strong-current areas of the Dover Strait and off the Normandy coast. Pebbles constitute more than 80% of the weight of the sediment. In the Strait, high organic matter fluxes favour the dominance of suspension feeders, especially sessile epifauna and *Ophiothrix fragilis* (Davoult and Gounin 1995). Sites to study this community were located in the Normandy coast and in the Dover Strait (Figure 2a). In the former, the community was numerically dominated by carnivores, especially the crustaceans *Pisidia longicornis* and *Pagurus bernhardus*. The Dover Strait section represents a typical facies of the community (Davoult 1990), and the most abundant species was *Op. fragilis* (Table 1).

The 'mixed assemblage' was located in areas with gravel and coarse sand, and without mud (Figure 2a, b). Some species in this assemblage are found in the *Am. lanceolatus* community (Table 1), a faunistic group previously described by Cabioch and Glaçon (1977) in coastal areas off Dieppe, France. Nevertheless, the occurrence of the ophiuroid *Op. fragilis* and the mollusc *Ensis arcuatus*, represents a drift towards other communities. The sites chosen to examine this assemblage were inshore and offshore waters over gravel sediment (Figure 2a). In the inshore waters, the main species corresponded to the typical representatives of the *Am. lanceolatus* community. In the deeper waters, species of the pebbles community such as *Op. fragilis* and *Psammechinus miliaris* were the most abundant (Table 1).

Diversity patterns

Quantitative structure of the communities' sections
The A. alba *community*. The RFD shapes of the three sections studied were quite different. In English waters, the mean RFD shape of the 10 samples was linear and the global shape was sigmoid (Figure 3). This difference represents a change in the community quantitative structure at both spatial scales, which is caused by a high dominance of the first two ranking species (Table 1) and by permutations of other common species over the individual samples. For the French coast, the shapes of both RFD were linear (Figure 3), and H' values were relatively low (Table 2). According to Dewarumez et al. (1990) this is a very rare kind of shape for benthic communities. The shapes of the mean and global RFD for the North Sea coast were convex (Figure 3), indicating an even quantitative distribution of species at the two perception scales. H' values were high (2.7–4.1, mean = 3.4). Numerically, this section was very poor (Table 2). Since the dominant species was the carnivore *N. cirrosa*, it seems that the demographic distribution was partially controlled by species interactions.
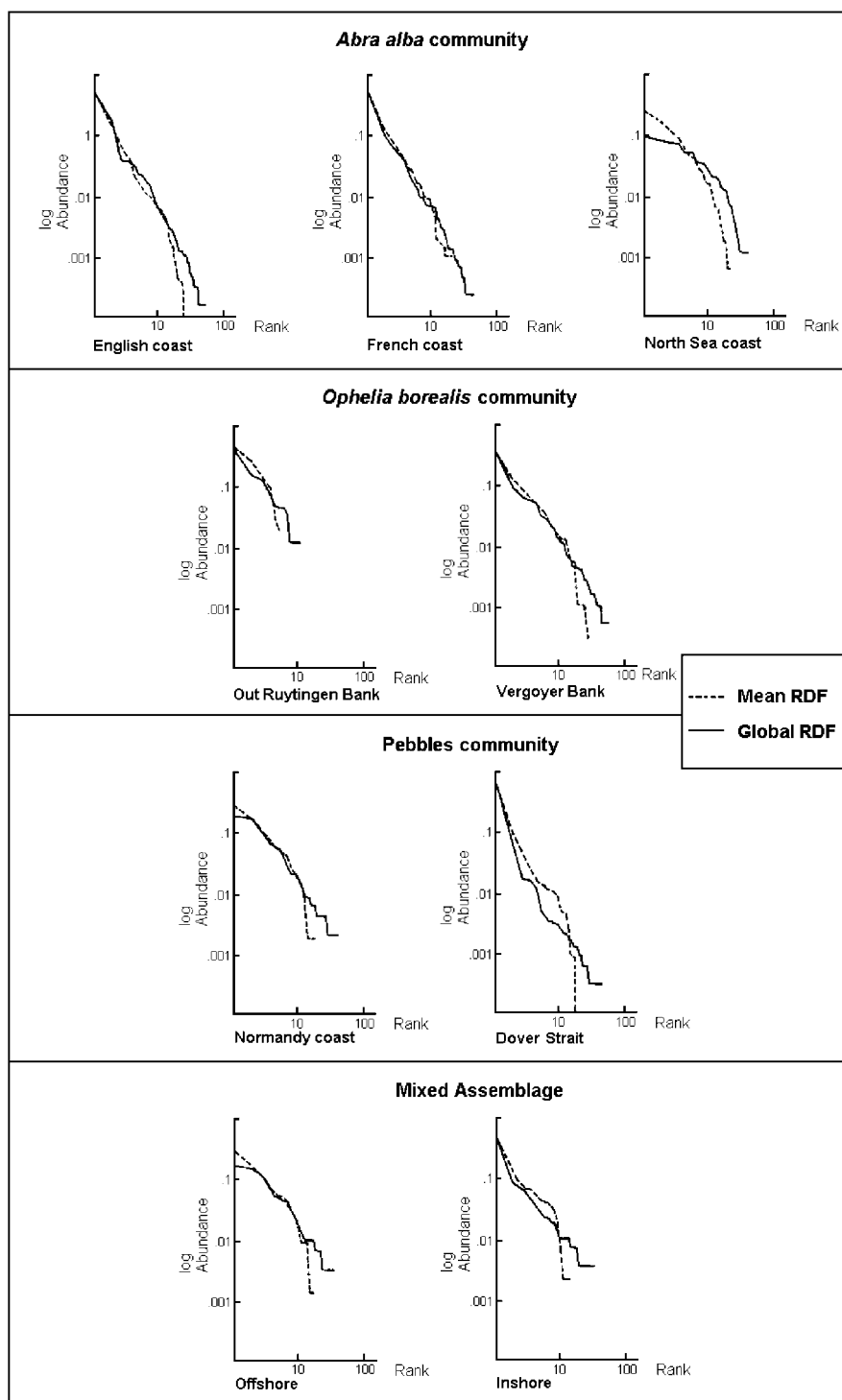
Figure 3. Mean and global RFD of the four benthic assemblages and their respective study sites.

The O. borealis *community*. Species richness and number of individuals in the Out Ruytingen Bank were the lowest for all the studied sections (Table 2). According to Cabioch and Glaçon (1977) and Dewarumez et al. (1990), these characteristics are common in the community. The low values may be a consequence of the dynamics of the banks in the Southern North Sea. According to Vanosmael et al. (1982), the top of these sandbanks as well as the ripples are continually broken down and rebuilt by strong currents. Sessile tube-building polychaetes represent a small number of individuals in these sandbank systems, whereas the dominant species are mobile quickly burrowing organisms such as *N. cirrosa*, which is able to tolerate strong physical disturbances of the sediment caused by the force of tidal currents. According to Whiters and Thorp (1978), the ability of some polychaetes and small crustaceans to rapidly burrow in the sediment after having been washed out is very important to remain in the system.

A different situation was observed in the Vergoyer Bank. The number of species (79) and individuals was high (Table 2). The shapes of both the mean and the global RFD were linear and sigmoid, respectively (Figure 3), and H' values fluctuated between 2.4 and 3.8. The sigmoid shape in the global diagramme is mainly due to the high abundance of *S. bombyx*. Strong recruitment of this species has also been noted by Sanvicente-Añorve (1991) and Dewarumez et al. (1992).

The pebbles community. The species richness and the number individuals in the pebbles community in the Normandy coast were relatively low (Table 2), although the quantitative structure of the species was evenly distributed at both perception scales (Figure 3). The five most abundant species (Table 1) were carnivorous, suggesting that species interactions may regulate the demographic structure in this site.

In the Dover Strait site, both shapes of the mean and global RFD were sigmoid (Figure 3), probably because of the strong dominance of the suspension-feeder *Op. fragilis*. The Shannon diversity index is low (Table 2), as was also observed by Migne and Davoult (1997). This community may show a stage 1 RFD for years, presumably because of the selection pressure from one or more environmental factors acting on the community, and maintain a low diversity (Dewarumez et al. 1990). According to these authors, anthropogenic actions, tidal currents and silt content of the sediment act directly on the species composition of this community.

The 'mixed assemblage'. Both sites with this assemblage had low values of species richness and numerical abundance (Table 2). One reason for these low values is that nutrients are low (Davoult and Gounin 1995) as a result of low flux currents (Salomon and Breton 1991). The role of food patches on biodiversity spatial patterns and population density has been discussed by Snelgrove et al. (1992). No species dominated in the offshore site, consequently, the shapes of both the mean and the global RFD were convex (Figure 3), and reflected an even species distribution and a high diversity. In the inshore site, the diagrammes were sigmoid (Figure 3), and the suspension-feeder *Am. lanceolatus* was the dominant species.

Table 2. Number of individuals, species richness, mean (± standard deviation) and global Shannon diversity values for each community site.

	Communities								
	A. alba			O. borealis		Pebbles		Mixed assemblage	
	English coast	French coast	North Sea coast	Out Ruytingen	Vergoyer	Normandy coast	Dover Strait	Offshore	Inshore
Number of individuals	6304	4353	848	86	1918	485	3386	315	281
Species richness	79	68	63	14	79	57	69	54	49
Mean (10 samples) Shannon index	2.1 ± 0.46	2.2 ± 0.35	3.4 ± 0.28	1.8 ± 0.27	3.1 ± 0.23	3.2 ± 0.21	1.7 ± 0.58	3.2 ± 0.26	2.6 ± 0.43
Global Shannon index	2.8	2.4	4.9	2.8	3.7	4.2	1.4	4.5	3.6

Comparison among and within the communities

Frontier (1985), in his review on the diversity in aquatic ecosystems, noted the extreme complexity of these systems and the fact that all systems are heterogeneous at different scales of observation. The results of this study confirm this concept since, on a large scale, a high heterogeneity of species assemblages was observed in the eastern English Channel and, on a smaller scale, no consistent pattern in diversity and species quantitative structure was observed within a community. Wiens (1989) established that physical factors are the main mechanisms controlling the distribution of organisms at large scales. Concerning bottom biodiversity in the Channel, Sanvicente-Añorve et al. (1996) stated that large scale spatial patterns of bottom biodiversity are independent of the spatial distribution of species assemblages. The main physical factors controlling diversity spatial patterns are the temperature gradient, depth, grain size, current velocity and hydro-sedimentary processes (Sanvicente-Añorve et al. 1996; Dauvin 1999; Rees et al. 1999). On a planetary scale, however, a high diversity has been observed over the apparently homogeneous habitats of deep-sea bottoms (Gage 1996). It seems that the food supply is the main factor controlling latitudinal gradients of species richness in the deep-sea benthos (Culver and Buzas 2000; Rex et al. 2000).

On a smaller scale, species associations appeared to be influenced by both biological and physical features, as has been mentioned by Hixon and Menge (1991), Snelgrove et al. (1992) and Gee and Warwick (1994). Thus, species richness in both the pebbles and the *A. alba* communities was high, compared with that recorded for the other communities (Table 2). The high species richness in the pebbles community may be due to the variety of microhabitats and the large flux of food (Davoult and Gounin 1995) associated with strong currents (Salomon and Breton 1991). In the *A. alba* community, organic matter and other terrestrial inputs related to the mud favour the development of the fauna, especially the deposit-feeders.

The Dover Strait pebbles community and the *A. alba* English coast community showed a stage 1 RFD (Figure 3), but the reason for this structure is different in the two communities. The strong currents in the Dover Strait constitute a permanent stress, which only a few species can tolerate and the community might show this structure for years (Dewarumez et al. 1990). On the English coast, the strong recruitment of some species leads to occasional changes in the quantitative structure.

Convex RFD shapes were observed in three assemblages: the *A. alba* community in the North Sea, the 'mixed assemblage' in offshore waters and the pebbles community in the Normandy coast (Figure 3). One of the causes of this structure was the co-occurrence of species from different communities. In the North Sea coast, the occurrence of *N. cirrosa* and *S. bombyx* represents a drift towards the *O. borealis* community. Also, the analysis of the sediment showed that the content of mud was lower than 1%. The species composition of the offshore water site (Table 1)

constitutes an interface between the pebbles and the *Am. lanceolatus* communities. In the Normandy coast, the low numerical abundance of the ophiuroid *Op. fragilis* results in a high diversity in the pebbles community. Another possible assumption that may explain the quantitative structure of this community is the high relative dominance of carnivorous species (>30%) in all three sections. Although numerical abundance is less appropriate than biomass for the characterisation of the dominance of a trophic group, these values reveal the importance of carnivorous species. This fact led us to infer that species interactions also have an important role in regulating the quantitative structure of these community sections.

Conclusions

Four main benthic assemblages at the spatial scale of the eastern English Channel were defined using the largest database available in the area. These results provide, for the first time, an idea of the spatial distribution of the benthic communities in the entire eastern English Channel. At this geographic scale, we think that the qualitative data alone are adequate for an efficient ecological survey and monitoring programme. However, at a smaller scale, changes in the species community structure are important keys in detecting environmental perturbations. Knowledge on the physical/biological complexity of this system is essential in the improvement or development of conservation programmes and monitoring strategies in the Channel.

The high heterogeneity of the four benthic assemblages in the eastern English Channel was primarily influenced by the nature of the sediment, and secondly by the velocity of bottom currents. These results indicate that physical factors are the main mechanisms controlling the distribution of bottom macrofauna at a large scale. On a smaller scale, no clear trend was observed for macrofauna diversity in the community sections analysed in this study. At this scale, species associations appeared to be influenced by both biological and physical features.

The diversity and the quantitative structure of the benthic communities were well described by the RFD method. Changes in this structure and permutations of species within the same structure, indicating a rearrangement of the community, can be directly visualised by the shape of the RFD. Low diversity communities may reflect habitat stress. Different RFD shapes in benthic communities can be interpreted as a result of different selection pressures. Hence, a sigmoid shape or stage 1 RFD indicates the presence of long or short term environmental stresses, such as high hydrodynamic flux (pebbles community) or species recruitment (*A. alba* community). A convex shape or stage 2 RFD may indicate a strong species interaction, leading to a dynamic stability of the number of individuals (North Sea *A. alba* community, offshore 'mixed assemblage'). The linear or stage 3 RFD (French coast *A. alba* community) is difficult to interpret. It might indicate mature communities with a lower stress than those in stage 1.

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