ICES Journal of Marine Science, 60: 120–131. 2002
doi:10.1006/jmsc.2002.1333

Macrobenthic resources of the shallow soft-bottom sediments in the eastern English Channel and southern North Sea

N. Desroy, C. Warembourg, J. M. Dewarumez, and
J. C. Dauvin

Desroy, N., Warembourg, C., Dewarumez, J. M., and Dauvin, J. C. 2003. Macrobenthic resources of the shallow soft-bottom sediments in the eastern English Channel and southern North Sea. – ICES Journal of Marine Science, 60: 120–131.

To obtain a baseline for future comparisons and to assist in the conservation of marine biodiversity, the distribution patterns and faunal composition of shallow (0–15 m depth) macrobenthic assemblages were studied along the French coast of the eastern English Channel and southern North Sea from two surveys conducted in 1998 and 2000. A total of 227 sites were sampled from Cap d'Ailly to the Belgian border, from which a total of 167 species were collected. Species richness, abundance and biomass were all increased in the vicinity of outflows from harbours, major bays and estuaries. Three principal macrobenthic assemblages were defined: (i) an *Ophelia borealis* medium to fine sand assemblage; (ii) a muddy heterogeneous sediment assemblage; and (iii) an *Abra alba* muddy fine sand assemblage. The *Abra alba* assemblage covered approximately 80% of the seabed in the survey area. Sediment characteristics and a latitudinal gradient accounted for a significant proportion of the observed variability in assemblage distribution patterns. In the eastern English Channel, the distribution patterns of species diversity, abundance and biomass values were most continuous, whereas in the southern North Sea a more heterogenous distribution was observed.

Keywords: *Abra alba* assemblage, eastern English Channel, macrobenthic resources, monitoting.

Received 10 July 2002; accepted 21 October 2002.

N. Desroy, J. M. Dewarumez and J. C. Dauvin: Station Marine de Wimereux, CNRS UMR 8013 ELICO, 28 Avenue Foch, BP 80, 62930 Wimereux, France. E-mail: Nicolas.Desroy@univ-lille1.fr. C. Warembourg: CEROV, Station Zoologique, BP 28, 06230 Villefranche-sur-Mer, France.

Introduction

Approaches to the study of marine biodiversity include the identification of spatial patterns via surveying and mapping, the description of these patterns, and the study of their relationships with, for example, ecosystem function and production (Costello, 1998). Well-informed decisions about possible uses are easier to make if information about the resource and changes over time are available. This descriptive information remains an important tool, as underlined by the Rio Convention on Biological Diversity, in the process of identifying areas of conservation importance and in providing an empirical basis for the classification of marine biotopes (Costello, 1998). However, the importance of monitoring the marine environment on large spatial scales, in order to better manage the marine habitats and resources, has only recently been recognized, especially in areas where biodiversity may be affected by human activities, such as in coastal zones. This recent awareness is paradoxical as coastal areas often support large concentrations of people, significant marine biodiversity resources, and have a higher probability of being exposed to perturbations than the open sea. Ideally, the biological components of coastal areas should be known in order to assess the consequences of man-made impacts (Bachelet *et al.*, 1996). However, Snelgrove (1999) emphasized that although soft-sediment habitats are common in coastal areas throughout the world, only a small proportion of the macrobenthos has been described, despite being considered a good bioindicator (Dauvin,

1054–3139/03/020120+12 $30.00/0

1993). Furthermore, shallow subtidal assemblages, samplable only during high tide, are often excluded from sampling areas and remain to a large extent unknown.

One of the few areas for which the macrobenthos is relatively well known is the English Channel. On the French coast of the eastern English Channel, the distribution of macrobenthic fauna has been described by Cabioch and Glaçon (1975, 1977) and Davoult *et al.* (1988). More recently, benthic diversity data for the eastern part of the Channel, collected in the 1970s, has been re-evaluated by Sanvicente-Anorve *et al.* (1996). Five main sub-tidal soft sediment communities were identified (Cabioch and Glaçon, 1975, 1977; Souplet and Dewarumez, 1980): the *Abra alba–Pectinaria koreni* assemblage associated with muddy fine sands (replaced by the *Donax vittatus–Abra alba–Macoma balthica* assemblage near the shoreline); the *Ophelia borealis* assemblage associated with fine to medium sands; the *Amphioxus lanceolatus* assemblage associated with coarse sands; the pebbly and gravelly assemblage; and the muddy heterogeneous sediment assemblage. These studies complete the research efforts along the Belgian coasts, in the southern Bight of the North Sea (Govaere *et al.*, 1980; Vermeulen & Govaere, 1983). In French waters, benthic ecologists have mainly focused their efforts on describing and interpreting variability in the benthic fauna over large spatial scales and over offshore sediments. To our knowledge, few studies have been conducted on the assemblages associated with the soft bottom sediments of very shallow areas (less than 15 m depth). Data often result from previous qualitative studies carried out with dredges, or from localized impact studies such as the Dunkirk industrial area (Dewarumez, 1979), which may be followed by a time-series of data collections (Dewarumez *et al.*, 1986; Ghertsos *et al.*, 2000). The present survey aims to provide an insight into the composition and distribution of benthic assemblages located in very shallow areas along the French coast of the eastern English Channel and southern North Sea. An important challenge of this work was the choice of a spatial observation scale that would be appropriate to adequately describe benthic assemblage structure and the distribution of the dominant species (Thrush, 1991; Luczak, 1996). Although there is no single correct scale, Armonies (2001) concluded from a study of the dispersal of the American jacknife, *Ensis directus*, that benthic assemblages should be sampled at a spatial scale similar to the dispersal capabilities of the dominant taxa. In the eastern English Channel, between the Seine river and the Cap Gris-Nez, the dispersion in the coastal water is often limited seaward by a coastal front located between 3 and 5 miles of the coasts (Brylinski *et al.*, 1991). The coastal water is characterized as a transfer pathway from the English Channel to the North Sea. In order to encompass the dispersal capabilities of the most dominant macrobenthic species in the study area, sampling was conducted over a spatial area of approximately 160 × 5 km.

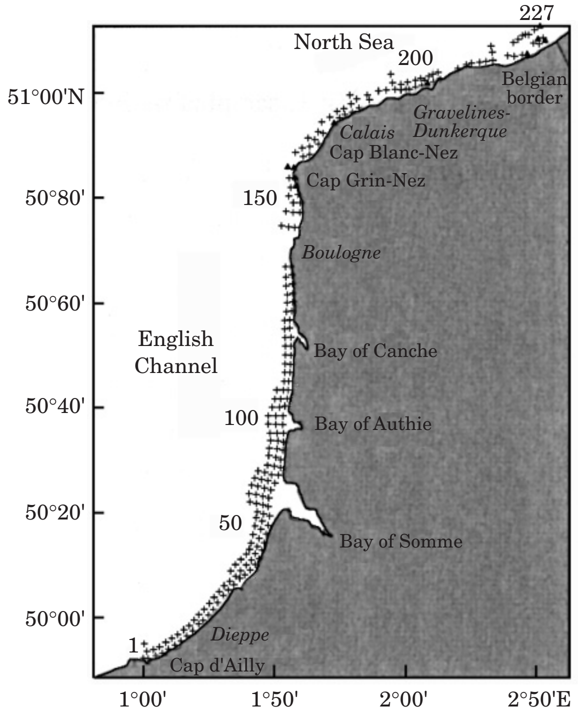

Figure 1. Location of benthic sampling stations (1 to 227); +: sampled station; ▲: hard substrate stations impossible to sample with a grab.

The objectives of the study were: (i) to estimate abundance and biomass of shallow water communities in order to obtain baseline data for future comparisons and to assist in the conservation of marine biodiversity; (ii) to describe the structure and spatial distribution of macrobenthic assemblages and their dominant species; and (iii) to identify the main environmental factors determining the distribution patterns.

Study area

The area investigated (49°92′–51°12′N 0°99′–2°51′E, Figure 1) was restricted as far as possible to water depths of less than 15 m, and extended from the Cap d'Ailly in the eastern English Channel to the Belgian border in the southern North Sea.

In the eastern English Channel, tidal current strengths increase from 1.5 to 3 knots from the south to the northeast as the narrower part of the Dover Strait is approached (Davoult *et al.*, 1988). Flow velocity decreases in the southern North Sea where it does not exceed 2 knots (Davoult *et al.*, 1988). Variations in the speed of the tidal current create a sedimentary gradient (Larsonneur *et al.*, 1982): pebbles and gravels dominate in the open sea, whereas coastal areas are dominated by large homogeneous sand banks and associated channel systems. Hard substrata and mudflats are restricted to such areas as capes, bays and harbours. In those areas of shoreline (<10 m depth) where there is a regular morphology, tidal currents decrease and wave action becomes comparatively more important (Cabioch and Glaçon, 1977). Sediments located in low energy environments (5–7 m depth) frequently consist of fine particles; a discontinuous border between muddy and fine sands is also typically observed.

The water quality of the sampling area is largely influenced by two main estuaries, namely the Seine estuary to the southwest, and the Scheldt delta to the northeast. Depending on the direction, intensity and duration of the wind, the plume of both rivers can reach the Cap Gris-Nez/Cap Blanc-Nez zone and modify the water salinity up to 2–3 miles offshore (Cabioch and Glaçon, 1975). Other smaller rivers (i.e. Somme, Authie, Canche, Liane, Aa and Yser) and runoff from sea cliffs contribute to a decrease in the salinity of the coastal waters. Although the outflows from these sources are relatively low, they may be locally significant at low tide. In the southern North Sea, water quality is also influenced by large industrial complexes surrounding Calais and Dunkerque harbours. A large variety of manufacturing industries, primarily metallurgical, chemical and petrochemical, are responsible for the input of a range of contaminants of varying significance (Dewarumez and Davoult, 1997). In contrast, the area from Dieppe to the Canche estuary is free from major industrialization, although water quality may be impacted by contaminants discharged from the Seine river.

Material and methods

The distribution of macrofauna was established from two surveys conducted in March 1998 and April 2000 (Figure 1). In March 1998, 142 sites were sampled between the cap d'Ailly and Boulogne harbour, and in April 2000, 85 sites were sampled between Boulogne harbour and the Belgian border, providing a total of 227 sites for the two surveys. Samples were collected at this time in order to describe the status of macrofauna prior to the spring recruitment. Samples were collected along transects spaced at 1 nmi intervals along the length of the study area. Between 2 to 4 samples, spaced at 1 nmi intervals, were collected from each transect.

At each site, two sediment samples for macrobenthos analysis were collected using a $0.25\ m^2$ Hamon grab (Dauvin, 1979). A large grab and mesh sieve (see below) were used as the aim of the study was not to quantify local biodiversity precisely but to define benthic assemblages and the distribution of adult benthic organisms. The recommendation of Ellingsen (2001) to sample a $5 \times 0.1\ m^2$ surface area was followed in order to obtain a meaningful measure of local biodiversity. Sub-samples of sediment were taken from additional grab samples and subsequently analysed for grain size distribution (wet sieving) and organic matter content (loss of weight of dry sediment at 600°C during 6 h). Replicates were collected from within a 50 m range of each site, using DGPS position-fixing.

The depth of sediment in the jaw of the grab provided an indication of the sample volume. Very small samples (i.e. less than about 5 cm depth) were discarded. The contents of the grabs were gently sieved on site through a 2-mm circular mesh sieve. The retained material was preserved for analysis in 5% buffered formaldehyde with added Rose Bengal. A visual description of the sediment type was recorded, along with the depth of the water column, and the location and times at which the sample was collected. The macrofauna was identified to the lowest possible taxon and enumerated. The biomass of each taxon was determined as g of AFDW $0.5\ m^{-2}$ (loss of weight of dry organisms after 6 h at 520°C).

Data analysis

Species diversity was calculated at each site using the Shannon–Wiener function, $H'Log_2$ (Shannon & Weaver, 1963) and Pielou's index of evenness, R (Pielou, 1975). Relationships between biological characteristics (total biomass and densities of main macrobenthic species) versus sediment parameters (median grain size and organic matter content) were tested using Spearman's rank correlation coefficient (Scherrer, 1984).

The affinity of assemblages both among species and sites were established from the stations × species matrix using factorial correspondence analysis (FCA) (Benzecri, 1973). Species occurring at fewer than five sites (i.e. 2.3%), and stations without macrofauna were omitted in data analysis procedures. Data were transformed logarithmically [$\log_{10}$ (species count + 1)] prior to analysis. From their coordinates on the axes of the FCA, station groupings were identified using the hierarchical clustering method of Ward (1963). To determine the important species of each station group, constancy [$C_{ij} = (n_{ij}/n_j) \times 100$] and fidelity [$F_{ij} = (C_{ij}/\Sigma_{j=1}^{k} C_{ij}) \times 100$] indices were calculated, where n_{ij} is the number of occurrences of species i in the station group j, and n_j is the number of stations in station group j, where j = 1 to k. Characteristic species were categorized as being constant (C>50%), common (50%>C>25%), elective (F<90%), or preferent (90%>F<66.7%) (Retière, 1979). This method was used by Cabioch and Glaçon (1975, 1977) and Davoult *et al.* (1988) to describe patterns of distribution in the benthic fauna of the eastern English Channel. It was chosen in preference to the indicative value process, which combines abundance and frequency of species for characterizing site groups (Dufrêne and Legendre, 1997), to facilitate comparison with previous studies.

Results

It was only possible to collect quantitative samples at 217 of the 227 sites as 10 stations were located over rocky substratum. The large sandbanks found in the study area, especially along the southern North Sea coast, reduce the depth of the water column substantially so that approximately 70% of sampled sites were at a low tide depth of <10 m, with approximately 90% of sites at a depth of <15 m.

Sediments

The distribution of superficial sediments was relatively homogenous throughout the study area; 80% of the sampling stations were associated with finer sediments, i.e. muds and medium to fine sands of particle sizes less than 0.5 mm (Figure 2a). Sediments distributed near the bays of Somme, Authie and Canche, and from Dunkerque harbour to the Belgian border, had a high proportion of fine sands, i.e. median particle sizes of <0.2 mm. Coarser sediments, with a gravel fraction exceeding 50%, were found at only a few stations located along the capes of Gris-Nez and Ailly. As a consequence of strong tidal currents, the organic matter content of sediments was very low, ranging from 0 to 2.03%.

General description of fauna

A total of 167 taxa were identified and consisted of 83 polychaetes (49.7% of the fauna), 35 crustaceans (20.9%), 29 molluscs (17.4%), 8 echinoderms (4.8%) and 12 in the category "diverse" (i.e. anthozoans, nemerteans, sipunculids and cephalochordates) (7.2%). In terms of the numbers of individuals, polychaetes accounted for 68.3% of all specimens recorded. Other groups were less numerous: molluscs constituted 18.6% of the total individuals, crustaceans 8.1%, echinoderms 4.0% and "diverse" 1.0% (Table 1).

The total abundance and species richness recorded from the grab samples was variable throughout the survey area. Abundance ranged from 0 to 1130 ind. 0.5 m^{-2} with a mean of 114.8 ind. 0.5 m^{-2} (s.d. 27.4; Table 1). Similarly, the species richness showed variation from a maximum of 28 species at station 55, to 0 at 3 stations. The average taxonomic diversity was 11.1 (s.d. 6.4). Values for biomass also showed considerable variations, from 0 to a maximum of 310.2 g AFDW 0.5 m^{-2} at station 68. The average for the survey area was 7 g AFDW.0.5 m^{-2} (s.d. 24.4). Most of the biomass was accounted for by molluscs and echinoderms and, to a lesser extent, by polychaetes. Total biomass was negatively correlated with both median particle size and the gravel and sand/gravel fraction, and positively correlated with the silt and clay fraction (Table 2).

Spatial distribution patterns of species richness, abundance and biomass are given in Figure 2b–d. The demographic parameters were distributed more homogenously and continuously in the eastern English Channel, from Cap d'Ailly to Cap Gris-Nez, than in the southern North Sea, where three main patches were identified: at the entrance to Calais and Dunkerque harbours and near to the Belgian border. Greatest species richness, abundance and biomass values were generally located near the main bays (i.e. Somme, Authie and Canche) and close to the Belgian border, at sites characterized by a range of small median particle sizes (<0.5 mm) and by freshwater outflows. Shannon diversity and evenness indices summarize the above observations: to the south of Cap Gris-Nez, values were homogeneously distributed, whereas to the east the distribution was patchier. Diversity values ranging from 3.0 to a maximum of 3.85, and evenness values greater than 0.8, characterized 21.2% and 30.1% of the sites respectively, all of which were situated in the vicinity of freshwater outflows.

Spatial distribution of dominant species and characteristic taxa of fine sediment assemblages

Correlation analysis suggested that the predominant influence on the structure of the benthic populations in the study area is the proportion of gravel and sand/gravel mixtures in the sediment. These factors were significantly correlated with the distribution of eight of the ten highest ranked species (Table 2). Variation in median particle size also exerted an influence, albeit to a lesser degree. However, it is recognized that these are not independent variables but are inter-correlated to a certain degree. Despite statistically significant relationships between the distributions of some dominant species and organic matter content, we do not attach much ecological significance to these because of the generally very low amounts of organic matter encountered.

The spatial distribution of the dominant taxa in the survey area is illustrated in Figure 3. In agreement with the above results, the frequency of occurrence and abundance of these species were greater to the south of Cap Gris-Nez than to the east. Three main patterns can be identified: (i) taxa associated with fine sediments influenced by freshwater outflows (*Macoma balthica* – Figure 3f); (ii) taxa associated with muddy sediments (*Abra alba* – Figure 3e); and (iii) taxa associated with sandy sediments (*Nepthys cirrosa* – Figure 3a; *Donax vittatus* – Figure 3d; *Magelona johnstoni* – Figure 3c; *Ophelia borealis* – Figure 3b).

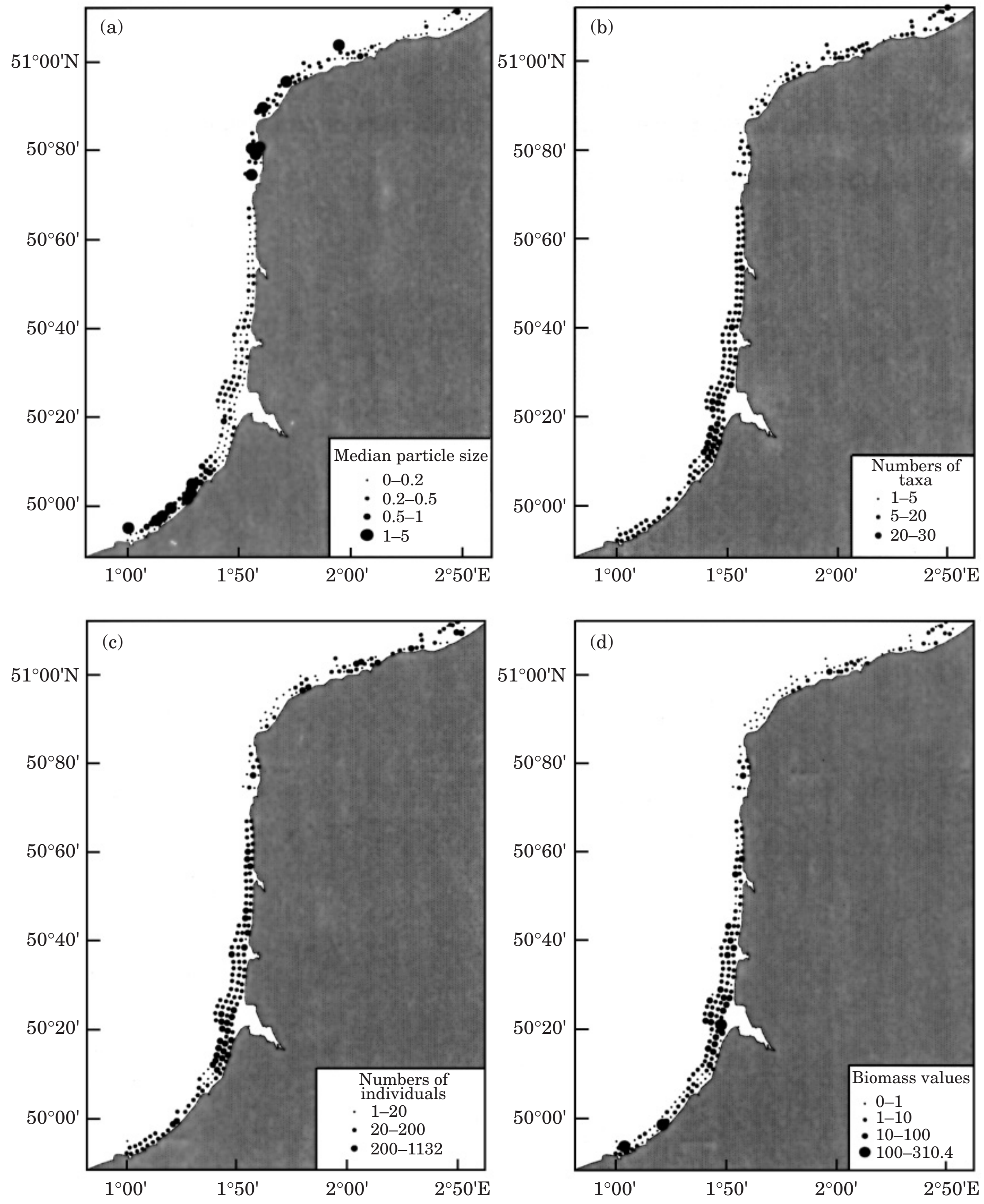

Figure 2. Distribution patterns of (a) median particle size, (b) numbers of taxa, and (c) abundances (No 0.5 m^{-2}) and (d) biomass (g AFDW 0.5 m^{-2}).

Ordination of stations

The area sampled was notable for the number of "rare" species encountered, in that 99 species were recorded at less than five stations. These rare species were excluded from further analysis. As a result, a faunal data set of 204 sites × 68 species was used as input to the FCA. The first six axes of the FCA accounted for only 34.7% of the total inertia. Hierarchical classification, performed while taking into account the inertia of all axes, separated the

Table 1. Mean abundance (ind. $0.5\,m^{-2}$) and biomass (g AFDW $0.5\,m^{-2}$) (± s.d.) of the main zoological taxa.

	Polychaetes	Molluscs	Echinoderms	Crustaceans	"Diverse"	Total
Abundance	78.4 ± 144.6	21.4 ± 44.4	4.6 ± 18.8	0.64 ± 3.4	0.6 ± 0.1	114.8 ± 27.4
Biomass	0.50 ± 0.92	3.46 ± 21.34	2.84 ± 12.26	0.18 ± 0.82	0.006 ± 0.028	6.98 ± 24.38

Table 2. Spearman rank correlation coefficients for total biomass and main macrobenthic species abundance vs. sediment parameters. Significance levels: $^*p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

	Median particle size	% gravel (≥2 mm)	% sand/gravel (≥500 μm)	% silt/clay (<63 μm)	% organic matter
Magelona johnstoni	−0.537***	−0.364***	−0.470***	0.128	−0.152*
Nephtys cirrosa	−0.124	−0.230***	−0.239***	−0.224**	−0.251***
Cirratulus cirratus	−0.034	−0.039	−0.035	−0.05	−0.094
Tellina fabula	−0.565***	−0.337***	−0.424***	0.284***	−0.018
Donax vittatus	−0.411***	−0.203**	−0.355***	−0.072	−0.191**
Echinocardium cordatum	−0.244***	−0.276***	−0.259***	0.119	−0.059
Scoloplos armiger	−0.108	−0.154*	−0.140*	0.030	−0.026
Notomastus latericeus	0.063	0.275***	0.210**	0.160*	−0.196**
Urothoe brevicornis	0.111	−0.022	0.016	−0.234***	−0.115
Sigalion mathildae	−0.462***	−0.215**	−0.322***	0.056	−0.122
Total biomass	−0.288***	−0.140*	−0.224**	0.146*	−0.098

more ill-defined site groups, which suggests a degree ofcontinuity in the structure of the assemblage types (Figure 4). Contiguous groups contained common, dominant taxa, reflecting the high level of similarity at which they are linked. The classification of stations resulted in one major unity (Group "G"=163 sites), which accounted for approximately 80% of all stations, five small Groups ("A"=2 sites; "B"=9 sites; "C"=5 sites; "D"=4 sites; and "F"=20 sites), and an isolated site not associated with any other cluster ("E"=station 222). Excluding Group E, the distribution of classes was found to be significantly correlated with sediment distribution (Spearman rank correlation: $P<0.05$), as shown in Figure 5.

Group A sites are associated with the most oligospecific assemblage, as only five taxa in low densities were identified (Table 3). The assemblage, typified by *Mactra corallina* and *Ensis arcuatus*, occurred in medium to fine sands located off Cap Blanc-Nez and in the southeastern region of the Bay of Somme (Figure 5). Molluscs in this group were responsible for 98% of the total biomass (3.482 g AFDW $0.5\,m^{-2}$). The Group B assemblage is also mainly located near to Cap Blanc-Nez, a region where tidal currents can be locally enhanced. Associated with heterogeneous sands, the fauna of this group (18 species) is characterized by *Gastrosaccus spinifer* and dominated by typical inhabitants of mobile sandy sediments, such as *Nephtys cirrosa* and *Ophelia borealis*. As a result of the low abundance of species associated with this group, biomass values are correspondingly low (0.346 g AFDW). Group C stations are associated with various deposits ranging from fine to coarse sands, and were occasionally enriched by heterogeneous particles (shells or gravel), as indicated by the presence of *Sagartia troglodytes* and *Malmgrenia arenicolae*, which were among the five top ranked species. This assemblage of 10 species is spatially limited to those sand banks adjacent to Cap Blanc-Nez and to the southern region of the Bay of Somme. The Group D assemblage, associated with Group E by way of a similar species composition, occurs at a few sites in the south-eastern Bay of Somme and off Dunkerque Harbour, and is characterized by muddy heterogeneous sands found in the channels separating the sandbanks. Of the 32 species recorded, *Crepidula fornicata*, *Abra alba*, and *Sagartia troglodytes* were the most abundant. This assemblage group could be interpreted as transitional as it also comprises fauna that are characteristic of pebbles and muddy fine sediments. Group F (90 species), typified by *Notomastus latericeus* (elective – constant), is located along the coast of Cap d'Ailly, adjacent to Boulogne and Dunkerque harbours, and near to the Belgian border where it progressively replaces the Group D assemblage. The dominant species of Group F show an affinity for muddy fine sands (*Notomastus latericeus*, *Abra alba*, *Ensis directus* and *Tellina fabula*) and heterogeneous sediments (attested by the occasional presence of *Sthenelais boa*). Group G stations occur in medium to fine sands that are sometimes enriched with silt/clay, as indicated by the presence of *Magelona johnstoni*,

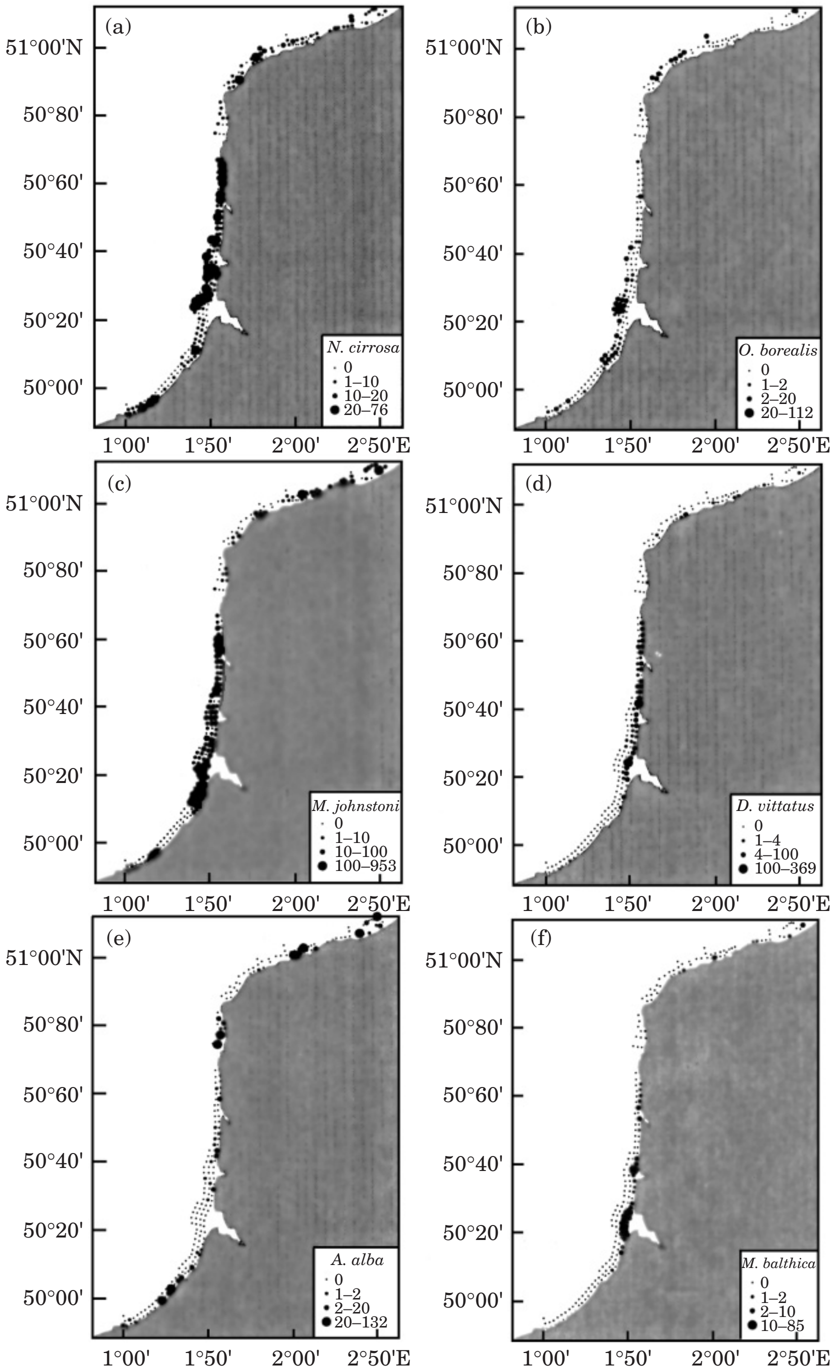

Figure 3. Distribution and abundances (ind. $0.5\,m^{-2}$) of (a) *Nephtys cirrosa*, (b) *Ophelia borealis*, (c) *Magelona johnstoni*, (d) *Donax vittatus*, (e) *Abra alba* and (f) *Macoma balthica* populations. Upper limits of each classes defined are excluded to intervals.

Nephtys cirrosa and *Donax vittatus*. The assemblage, characterized by the polychaetes *Magelona johnstoni* and *Sigalion mathildae* (constant – elective), accounted for 186 sites located from Cap d'Ailly to the Belgian border, and supported a greater diversity of species (133) as well as enhanced densities and biomass (average of 7.926 g

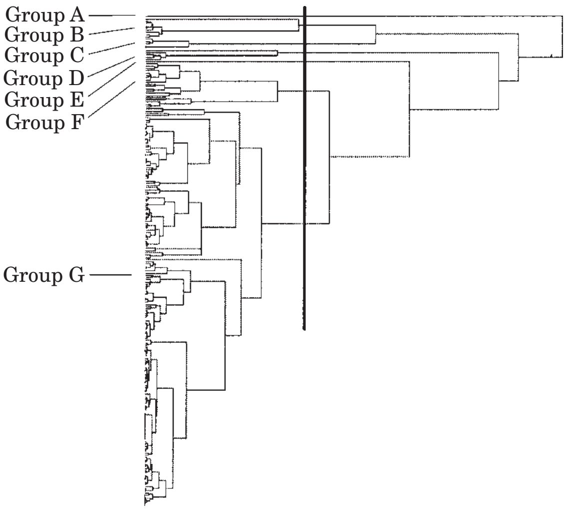

Figure 4. Dendrogram resulting from hierarchical ascendant classification of stations (Ward's method).

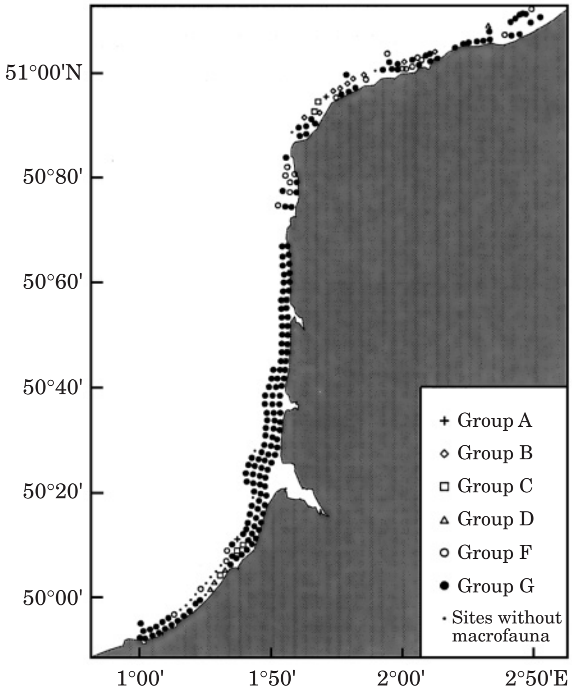

Figure 5. Spatial distribution of the faunal assemblages (Group E excluded) defined by FCA and hierarchical classification.

AFDW 0.5 m^{-2}). The fauna of Group G stations found in shallower areas was enriched by estuarine species, such as *Macoma balthica* and *Cardium edule*. Group G stations therefore comprised two subgroups, divided at a high similarity level, corresponding to coastal and offshore stations (Figure 4).

Discussion

The uniformity of the seabed environment along the French coast of the eastern English Channel and southern North Sea contrasts strongly with the heterogeneity reported in offshore sediments where various substrata are represented, such as pebbles, muddy heterogeneous sediments, fine to coarse sands, and muddy-fine sediments (Davoult *et al.*, 1988). As a consequence, about 80% of the shallow sites support a single benthic assemblage typified by species showing an affinity for sands or slightly muddy sands, such as *Magelona johnstoni* and *Nephtys cirrosa*. This well-known species association, used in the classification of biotopes by conservation workers, extends along the Belgian (Govaere *et al.*, 1980) up to the western Scheldt estuary (Vermeulen & Govaere, 1983).

Considering the large extent of the area we sampled ($\approx 800\ km^2$), the number of taxa recorded (167) is relatively low and cannot easily be compared with data from previous studies due to differences in sieve mesh size (1 or 2 mm), the sampling gear used (Rallier du Baty dredge, Smith–McIntyre or Hamon grabs) and the surface area sampled. The large number of taxa classified as "rare" although to some extent influenced by use of a larger (2 mm) sieve mesh, indicate that the majority of large animals in the sediments encountered in the study area are present in relatively low densities and are also patchily distributed. Moreover, the survey was conducted during the winter period, which is characterized by a low abundance of benthic fauna in the English Channel (Dauvin, 1984; Thiébaut *et al.*, 1997). The analysis of long-term data series for the *Abra alba* community on the southern North Sea, adjacent to Gravelines, also highlights the difference in species richness, abundance and biomass that exists between winter and summer as a consequence of pronounced seasonal fluctuations (Ghertsos *et al.*, 2000).

Species abundance varied along the coastal survey area; several sites were strongly dominated by a few species such as *Magelona johnstoni*, which represented more than 60% of the total abundance at some sites. Depending on meteorological conditions, and after any post-settlement mortality that may occur in response to physical and biological characteristics of the habitat, new recruits can form patches of high abundances, as observed for *Ensis directus* in the southern North Sea (Luczak, 1996). Variable currents and winds can induce unpredictable changes from year to year in the abundance and structure of macrobenthic assemblages in the southern part of the North Sea (Nihoul, 1975; Belgrano *et al.*, 1995). These stochastic dispersions differ from the larval retention reported in the Bay of Seine (Lagadeuc, 1992; Thiébaut *et al.*, 1992; Thiébaut *et al.*, 1994), which is responsible for the spatio-temporal persistence of the muddy–fine sand assemblage.

Table 3. Averaged density (ind. 0.5 m^{-2}, $\bar{y}$) of the top five ranked taxa and characteristic species (in bold; C: Constant; E: Elective; P: Preferent) for assemblage (E excepted) defined by FCA. Mean, maximal and minimal values for number of taxa, abundances, biomass, median particle sizes, depths are listed with habitat types.

	A	$\bar{y}$	B	$\bar{y}$	C	$\bar{y}$
	Gastrosaccus spinifer	4.4	*Nephtys cirrosa*	7.0	*Sagartia troglodytes*	3.4
	Ensis arcuatus (C, P)	1.0	***Gastrosaccus spinifer*** (C, P)	4.4	*Ophelia borealis*	2.0
	Mactra corallina (C, E)	0.4	*Ophelia borealis*	2.4	*Tellina tenuis*	0.4
	Processa canaliculata	0.4	*Magelona johnstoni*	1.4	*Nephtys cirrosa*	0.4
	Glycera gigantea	0.4	*Urothoe brevicornis*	0.8	*Malmrenia arenicolae*	0.4
Number of taxa	2.5 (2–3)		4.7 (3–7)		2.8 (1–5)	
Number of individuals	7.0 (3.0–11.0)		19.2 (7.0–51)		8.0 (2.0–23)	
Biomass (g AFDW 0.5 m^2)	3.482 (0.114–6.854)		0.346 (0.076–0.756)		0.260 (0.026–1.006)	
Median diameter (mm)	0.35 (0.26–0.44)		0.29 (0.13–0.39)		0.32 (0.29–0.38)	
Depth (m)	9.0 (5.0–13.0)		13.2 (2.5–21)		8.8 (5–17.8)	
Habitat type	Clean medium–fine sand		Mobile clean medium–fine sand ± heterogeneous particles		Coarse to fine sand	

	D	$\bar{y}$	F	$\bar{y}$	G	$\bar{y}$
	Crepidula fornicata	52.6	***Notomastus latericeus*** (C, P)	29.6	***Magelona johnstoni*** (C, P)	58.2
	Abra alba	12.0	*Abra alba*	21.8	*Nephtys cirrosa*	10.0
	Sagartia troglodytes (C, P)	10.4	*Ensis directus*	3.2	*Donax vittatus*	6.8
	Urothoe poseidonis	4.6	*Tellina fabula*	2.8	*Cirratulus cirratus*	6.8
	Polycarpa gracilis	4.6	*Heterocirrus alatus*	2.0	*Scoloplos armiger*	5.4
	Owenia fusiformis (C, P)	1.0			***Sigalion mathildae*** (C, E)	4.2
Number of taxa	11.7 (7–17)		13.3 (4–21)		12.5 (1–28)	
Number of individuals	113.4 (25.4–196.0)		92.4 (10.0–401.0)		135.6 (1.0–1130)	
Biomass (g AFDW 0.5 m^2)	4.128 (0.270–7.718)		4.428 (0.052–23.808)		8.606 (0.005–310.258)	
Median diameter (mm)	1.81 (0.19–4.50)		0.86 (0.11–2.63)		0.28 (0.11–2.44)	
Depth (m)	7.2 (5.0–14.0)		10.5 (3.4–19.7)		7.3 (0.5–21.5)	
Habitat type	Muddy heterogeneous sand		Stable lightly muddy medium–fine sand ± heterogeneous particles		Stable lightly muddy fine sand ± heterogeneous particles	

Table 4. Biomass values (g AFDW m $^{-2}$) recorded for *Abra alba* community in different location in the English Channel. Values, initially expressed in dry weight (DW) were conversed in AFDW from results reported by Ricciardi and Bourget (1998): AFDW = 0.75 × DW.

Study	Area	Biomass (g AFDW m $^{-2}$)
Davoult *et al.* (1988)	From Boulogne to Dunkerque	15.0–37.5
Dewarumez *et al.* (1992)	Gravelines	45.0–187.5
Thiébaut *et al.* (1997)	Bay of Seine (1986)	23.5
Thiébaut *et al.* (1997)	Bay of Seine (1987)	27.5
Thiébaut *et al.* (1997)	Bay of Seine (1988)	24.2
Thiébaut *et al.* (1997)	Bay of Seine (1991)	26.0
Dauvin (1998)	Pierre Noire	10.6
Dauvin (2000)	Morlaix river	10.9
Ghertsos *et al.* (2000)	Gravelines	52.5–3000
Govaere *et al.* (1980)	Belgian coasts	2.7
Our study	Eastern English Channel–southern North Sea	8.1

Relative proximity to inshore waters, outflows from bays, harbours and the Scheldt estuary were all factors that enhanced the structure of the benthic community along the French coast of the eastern English Channel and southern North Sea. Increases in species diversity, abundance and biomass may indicate an increased food supply at these locations, as recently reported by Rees *et al.* (1999) for macrobenthic assemblages along the UK coast. The disparity between benthic assemblages in the eastern English Channel and the southern North Sea is clearly demonstrated; species diversity, density and biomass values are greatest and their distribution patterns more continuous in the eastern English Channel from Cap d'Ailly to Cap Gris-Nez. Beyond Cap Gris-Nez, and despite the presence of a homogeneous habitat, a biological "fragmentation" is observed as three patches were identified. It is, however, surprising that samples collected in the first survey seem to be on the whole homogeneous, while those collected in the second do not. This tendency could reflect temporal or artifactual differences rather than spatial differences, but could also be related to a decreasing trend in biomass with latitude, as reported by Heip *et al.* (1992) for North Sea macrofauna. Organic matter content, although found to be influential in determining the distribution of the *Abra alba* assemblage in the eastern Bay of Seine (Thiébaut *et al.*, 1997), cannot be considered a significant parameter in our study area as the amounts recorded are very low.

The factorial correspondence analysis revealed six major site groups, which can be associated with three main assemblages. Rather than viewing these as discrete and isolated entities, they may be better viewed as noda along a continuum, as their faunal composition progressively varies with edaphic parameters and hydrodynamics. Despite local trends in accretion and erosion that are related to hydrological changes, the comparison with previous studies of spatial distributions (Cabioch and Glaçon, 1975, 1977; Davoult *et al.*, 1988) does not suggest drastic changes. Site Groups A, B and C, characterized by species showing an affinity for well-sorted medium to fine sands, were found to occur in sediments subjected to significant physical disturbance, such as would be caused by strong tidal streams and wave action. These species associations clearly ascribed to the *Ophelia borealis* assemblage defined by Thorson (1957) are also distributed on the southeast English coasts (Rees *et al.*, 1999). Due to (i) natural deposits of mud, (ii) erosion of cliffs and (iii) *Crepidula fornicata* colonies, the shells of which modify the flow regime at the sediment/water interface, sandy substrates are progressively colonized by species living on muddy heterogeneous sediments such as *Cirratulus cirratus* and *Sthenelais boa*. As a result, the muddy heterogeneous sediment assemblage (Group D sites) progressively replaced the *Ophelia borealis* assemblage. Group F sites, which including a few components of the muddy heterogeneous sediments (e.g. *Sthenelais boa*), progressively replaced the Group D assemblage. A common group of species that characterize slightly muddy sands or slightly mixed sediments (*Notomastus latericeus*, *Owenia fusiformis*, *Pectinaria koreni*, *Ophiura texturata*) links Group F and G sites, which are both comparable with the *Donax vittatus*–*Macoma balthica* form of the *Abra alba*–*Corbula gibba* assemblage (Cabioch and Glaçon, 1975). Although the biomass distribution pattern is highly heterogeneous due to local dominance of molluscs and echinoderms, the average biomass for the study area (4.03 ± 13.08 g AFDW 0.5 m $^{-2}$ for F and G assemblages) is respectively lower and higher to that reported in other areas in the Channel and along the Belgian coast (Table 4). The one exception is at Gravelines, where a very high biomass was observed in 1992 and 1994 as a result of mass recruitment of *Lanice conchilega* and *Ensis directus* (Luczak, 1996). Average biomass values of 0.77 g AFDW 0.5 m $^{-2}$ from Calais to the Belgian border compared to 5.30 g AFDW 0.5 m^{-2} from Cap d'Ailly to Boulogne harbour confirm the contrast in benthic productivity either side of the Dover strait.

On French coasts the increasing need for coastal zone observation, brought about by a desire to enhance environment quality and public health, has led to the development of national grid systems for water quality monitoring. These grids allow an examination of changes in chemical and biological parameters in the pelagic ecosystem in relation to natural or human influences. The data are valuable in increasing our knowledge of coastal areas, for example through their use in calibrating or validating models. However, data acquisition was until recently mainly focused on water column processes and not sufficiently on benthic environments. Studies of benthic communities are, nevertheless, essential for monitoring changes in biodiversity and initiating adaptive management measures in order to preserve the integrity of shallow areas and the species of commercial interest that they support may be preserved. In the North Sea, efforts to describe and interpret variability in the benthic fauna over large geographical areas are more developed (Eleftheriou and Basford, 1989; Kunitzer *et al.*, 1992; Duineveld and Van Noort, 1990; Jennings *et al.*, 1999). The potential benefits from studying shallow benthic communities over such a wide spatial scale are clearly demonstrated. Such data provide a valuable baseline for understanding changes in benthic communities and can act as a useful tool for environmental monitoring and conservation projects.

Acknowledgements

The authors would like to thank the crew of N/O "Côtes de la Manche" and S. Baudet, L. Dauvin, L. Denis, S. Gaillard, T. Ruellet, C. Six, S. Skibinski and E. Thiébaut for participating in the sea missions. C. Luczak is gratefully acknowledged for his help in statistical treatments. Authors are also grateful for comment and corrections on the manuscript made by H. L. Rees and address their special thanks to Dr Paul Eastwood for help in correcting the English text.

References

Armonies, W. 2001. What an introduced species can tell us about the spatial extension of benthic populations? Marine Ecology Progress Series, 209: 289–294.

Bachelet, G., De Montaudoin, X., and Dauvin, J. C. 1996. The quantitative distribution of subtidal macrozoobenthic assemblages in Arcachon bay in relation to environmental factors: a multivariate analysis. Estuarine, Coastal and Shelf Science, 42: 371–391.

Belgrano, A., Legendre, P., Dewarumez, J. M., and Frontier, S. 1995. Spatial structure and ecological variation of meroplankton on the Belgian-Dutch coast of the North Sea. Marine Ecology Progress Series, 128: 51–59.

Benzecri, J. P. 1973. L'analyse des données. Tome 2: L'analyse des correspondances. Dunod, Paris. 619 pp.

Brylinski, J. M., Brunet, C., Bentley, D., Thoumelin, G., and Hilde, D. 1991. Hydrography and phytoplankton biomass in the Eastern English Channel in spring 1992. Estuarine, Coastal and Shelf Science, 43: 507–519.

Cabioch, L., and Glaçon, R. 1975. Distribution des peuplements benthiques en Manche Orientale, de la Baie de Somme au Pas-de-Calais. Compte-Rendus de l'Académie des Sciences de Paris, 280: 491–494.

Cabioch, L., and Glaçon, R. 1977. Distribution des peuplements benthiques en Manche Orientale, du Cap d'Antifer à la Baie de Somme au Pas-de-Calais. Compte-Rendus de l'Académie des Sciences de Paris, 285: 209–212.

Costello, M. J. 1998. To know, research, manage and conserve marine biodiversity. Oceanis, 24: 25–49.

Dauvin, J. C. 1979. Recherches quantitatives sur le peuplement des sables fins de la Pierre Noire, baie de Morlaix et sur sa perturbation par les hydrocarbures de l'Amoco-Cadiz. PhD Thesis. Univ. Paris VI.

Dauvin, J. C. 1984. Dynamique d'écosystèmes macrobenthiques des fonds sédimentaires de la baie de Morlaix et leur perturbation par les hydrocarbures de l'Amoco-Cadiz. Thesis. Univ. Paris VI.

Dauvin, J. C. 1998. The fine sand *abra alba* community of the bay of Morlaix twenty years after the Amoco Cadiz oil spill. Marine Pollution Bulletin, 36: 669–676.

Dauvin, J. C. 1993. Le benthos: témoin des variations de l'environnement. Oceanis, 19(6): 25–53.

Dauvin, J. C. 2000. The muddy fine sand *Abra alba – Melinna palmata* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. Marine Pollution Bullentin, 40: 528–536.

Davoult, D., Dewarumez, J. M., Prygiel, J., and Richard, A. 1988. Carte des peuplements benthiques de la partie française de la mer du Nord. IFREMER/Région Nord, Pas-de-Calais. 30 pp.

Dewarumez, J. M. 1979. Etude biologique d'Abra alba, Wood (mollusque lamellibranche) du littoral de la mer du Nord. PhD Thesis. Univ. Lille I.

Dewarumez, J. M., Quisthoudt, C., and Richard, A. 1986. Suivi pluriannuel du peuplement à Abra alba dans la partie méridionale de la mer du Nord (région de Dunkerque – France). Hydrobiologia, 142: 187–197.

Dewarumez, J. M., Davoult, D., Sanvicente-Anorve, L. E., and Frontier, S. 1992. Is the "muddy heterogenous sediment assemblage" an ecton between the pebbles commuity and the *Abra alba* community in the southern bight of the North Sea? Netherlands Journal of Sea Research, 30: 229–238.

Dewarumez, J. M., and Davoult, D. 1997. Les biocénoses macrobenthiques en Manche Orientale et mer du Nord. *In* Les biocénoses marines et littorales françaises des côtes atlantique, manche et mer du Nord, pp. 79–82. Ed. by J. C. Dauvin. Service du patrimoine naturel/IEGB/MNHN, Paris. 359 pp.

Dufrêne, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs, 67: 245–366.

Duineveld, G. C. A., and Van Noort, G. J. 1990. Geographical variation in the epifauna of the Southern North Sea and adjacent regions. ICES CM 1990/Moni: 9, 11 pp.

Eleftheriou, A., and Basford, D. J. 1989. The macrobenthic infauna of the offshore northern North Sea. ICES Journal Marine Biological Association of the United Kingdom, 69: 123–143.

Ellingsen, K. E. 2001. Biodiversity of a continental shelf soft-sediment macrobenthos community. Marine Ecology Progress Series, 218: 1–15.

Govaere, J. C. D., Van Damme, D., Heip, C., and De Coninck, L. A. P. 1980. Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring. Helgoländer Meeresuntersuchungen, 33: 507–521.

Ghertsos, K., Luczak, C., Dewarumez, J. M., and Dauvin, J. C. 2000. Influence of spatial scales of observation on temporal change in diversity and trophic structure of the fine-sand communities from the English Channel and the Southern North Sea. ICES Journal of Marine Science, 57: 1481–1487.

Heip, C., Basford, D., Craeymeersch, J. A., Dewarumez, J. M., Dörjes, J., De Wilde, P., Duineveld, G., Eleftheriou, A., Herman, P. M. J., Niermann, U., Kingston, P., Künitzer, A., Rumohr, H., Soetaert, K., and Soltwedel, T. 1992. Trends in biomass, density and diversity of North Sea macrofauna. ICES Journal of Marine Science, 49: 13–22.

Jennings, S., Lancaster, J., Woolmer, A., and Cotter, J. 1999. Distribution, diversity and abundance of epibenthic fauna in the North Sea. Journal of the Marine Association of the United Kingdom, 79: 385–399.

Kunitze, A., Basford, D., Craeyermeersch, J. A., Dewarumez, J. M., Dorjes, J., Duineveld, G. C. A., Eleftheriou, A., Heip, C., Herman, P., Kingston, P., Niermann, U., Rachor, E., Rumohr, H., and De Wilde, P. A. 1992. The benthic infauna of the North Sea: species distribution and assemblages. ICES Journal of Marine Science, 49: 127–143.

Lagadeuc, Y. 1992. Répartition verticale des larves de *Pectinaria koreni* en Baie de Seine Orientale: influence sur le transport et le recrutement. Oceanologica Acta, 15: 95–104.

Larsonneur, C., Bouysse, P., and Auffret, J. P. 1982. The superficial sediments of the English Channel and its western approaches. Sedimentology, 29: 8541–864.

Luczak, C. 1996. Dynamique du recrutement au sein du peuplement à Abra alba dans la baie sud de la mer du Nord: approche systémique. PhD Thesis. Univ. Lille I.

Nihoul, J. C. J. 1975. Mesoscale secondary flows and the dynamics of ecosystems in the Southern Bight of the North Sea. Mémoires de la Société Royale de Sciences de Liège, 7: 83–91.

Petersen, C. G. 1913. Valuation of the sea. The animal communities of the sea-bottom and their importance for marine zoogeography. Report of the Danish Biological station to the board of agriculture, 21: 1–42.

Pielou, E. C. 1975. Ecological diversity. Wiley-Interscience, New-York. 165 pp.

Rees, E. I. S., Pendle, M. A., Waldock, R., Limpenny, D. S., and Boyd, S. E. 1999. A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic seas. ICES Journal of Marine Science, 56: 228–246.

Retière, C. 1979. Contribution à la connaissance des peuplements benthiques du golfe Normano-Breton. Thesis, Univ. Rennes I.

Ricciardi, A., and Bourget, E. 1998. Weight-to-weight conversion factors for marine benthic macroinvertebrates. Marine Ecology Progress Series, 163: 245–251.

Sanvicente-Anorve, L., Leprêtre, A., and Davoult, D. 1996. Large-scale spatial pattern of the macrobenthic diversity in the eastern English Channel. Journal of the Marine Biological Association of the United Kingdom, 76: 153–160.

Shannon, C. E., and Weaver, W. 1963. The Mathematical Theory of Communication. University of Illinois Press, Urbana, Illinois. 117 pp.

Sherrer, B. 1984. Biostatistique. Gaëtan Morin, Chicoutimi, Québec. 850 pp.

Snelgrove, P. V. R. 1999. Getting to the bottom of marine biodiversity: sedimentary habitats. Ocean bottoms are the most widespread habitat on earth and support high biodiversity and key ecosystem services. BioScience, 49: 129–138.

Souplet, A., and Dewarumez, J. M. 1980. Les peuplements benthiques du littoral de la région de Dunkerque. Cahiers de Biologie Marine, 11: 23–39.

Thiébaut, E., Dauvin, J. C., and Lagadeuc, Y. 1992. Transport of *Owenia fusiformis* larvae (Annelida: Polychaeta) in the Bay of Seine. I. Vertical distribution in relation to water column stratification and ontogenic vertical migration. Marine Ecology Progress Series, 80: 29–39.

Thiébaut, E., Dauvin, J. C., and Lagadeuc, Y. 1994. Horizontal distribution and retention of *Owenia fusiformis* larvae (Annelida: Polychaeta) in the Bay of Seine. Journal of the Biological Association of the United Kingdom, 74: 129–142.

Thiébaut, E., Cabioch, L., Dauvin, J. C., Retière, C., and Gentil, F. 1997. Spatio-temporal persistence of the *Abra alba–Pectinaria koreni* muddy-fine sand community of the Eastern Bay of Seine. Journal of the Marine Biological Association of the United Kingdom, 77: 1165–1185.

Thorson, G. 1957. Bottom communities (sublittoral or shadow shelf). Geological Society of America, 67: 461–534.

Thrush, S. F. 1991. Spatial patterns in soft-bottom communities. Trends in Ecological Evolution, 6: 75–79.

Vermeulen, Y. M., and Govaere, J. C. R. 1983. Distribution of benthic macrfauna in the Western Scheldt estuary (The Nederlands). Cahiers de Biologie Marine, 24: 297–308.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. Journal of American Statistic Association, 58: 236–244.