Small- to large-scale geographical patterns within the macrobenthic *Abra alba* community

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**Abstract**

The *Abra alba* community is widely spread in the coastal zone of the English Channel and the Southern Bight of the North Sea. The community is located on shallow, fine muddy sands. Its spatial distribution can be broken up into a number of isolated patches (Atlantic French, British and German coast) and one large continuous distribution area (northern France up to the Netherlands). The aim of this study is to investigate the geographical patterns within the macrobenthic *A. alba* community at different scales: the community’s full distribution range (i.e. large scale) and a selected area with a continuous distribution of the *A. alba* community (i.e. small scale) in relation to structuring environmental variables. Therefore, an analysis of newly collected samples along the Belgian coastal zone was combined with available information on the *A. alba* community throughout its distribution range. Although the community structure shows a high similarity across the full distribution range of the *A. alba* community, large- as well as small-scale changes in community composition were observed: the Belgian Continental Shelf (BCS) should be considered as a major transition from the rich southern to the relatively poorer northern distribution area of the *A. alba* community. At a large scale (i.e. full distribution range), the differences in community structure are expected to result from (1) the specific hydrodynamic conditions in the English Channel (Atlantic ocean waters) and the Southern Bight of the North Sea, with a consequent differential connectivity between the different areas and (2) the climatological and related faunal shift from temperate (English Channel) to boreal conditions (German Bight). At a small scale (i.e. within the continuous distribution area), structural and functional community aspects may result from geographic differences in (1) detrital food availability, related to riverine input and pelagic productivity, along and across the coastline and (2) the amount of suspended matter, impoverishing the *A. alba* community when excessively available.

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**Keywords:** *Abra alba* community; large-scale; small-scale patterns; diversity; English Channel; Southern Bight of the North Sea

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**1. Introduction**

Nowadays, human activities are considered to be the primary cause of changes to marine biological diversity (biodiversity), especially in coastal areas. The present rate of habitat degradation in marine ecosystems is alarming (Gray, 1997; Snelgrove et al., 1997), and conservation of biodiversity is of critical importance. There is also an increasing concern amongst managers and policy-makers about the potential effects of biodiversity loss on the ‘functioning’ of ecological systems, in particular the goods and services, which they provide (Daily, 1997). There are indications that biodiversity can have significant effects on ecosystem processes, although these effects tend to be mediated through functional traits, rather than species richness per se (Raffaelli et al., 2003). The measurement and assessment of biodiversity however depend on spatial scale, and a comparison of only a few sites between areas is insufficient (Ellingsen, 2001). A detailed knowledge of community diversity and
differences within a single habitat type is needed to differentiate among habitats (Ellingsen, 2001) and to investigate its naturalness.

One of the ecologically most important soft-sediment macrobenthic communities along the coastal areas of the English Channel and Southern Bight of the North Sea is the *Abra alba* community, which is characterized by a high diversity, abundance and biomass and typically occurs in muddy fine sandy sediments (Jones, 1950; Glémarec, 1973; Cabioch and Glaçon, 1975; Souplet and Dewarumex, 1980; Kingston and Rachor, 1982; Prygiel et al., 1988; Duineveld et al., 1991; Dewarumex et al., 1992; Künitzer et al., 1992; Fromentin et al., 1996; Holtmann et al., 1996; Olivier et al., 1996; Sanvicente-Anorve et al., 1996; Fromentin et al., 1997; Thièbaut et al., 1997; Dauvin, 1998; Degraer et al., 1999; Rees et al., 1999; Dauvin, 2000; Konstantinos et al., 2000, 2001; Budd, 2002; Desroy et al., 2002; Sanvicente-Anorve et al., 2002; Dauvin et al., 2004; Van Hoey et al., 2004). This type of habitat typically occurs in low energy zones nearby the coast (Larsonneur et al., 1982).

Several descriptions of the *Abra alba* community in the European seas were made in the past three quarters of a century. From a limited assemblage of species described by Petersen (1911, 1913, 1918), to different specific traits of the *A. alba* community at different places have lead to several adopted characterizations of the community: 'Echinocardium cordatum—Venus gallina' community (Ford, 1923), 'boreal offshore muddy sand association' (Jones, 1950), 'A. alba community (Stripp, 1969), associations ‘P’ and ‘M’ (Eagle, 1973, 1975), etc.

The *Abra alba* community is dominated by species having a pelagic larval phase and shows important annual changes in the pattern of recruitment of the dominant species (Dewarumex et al., 1986). Consequently, it is characterized by short lived and fast growing species with a strong seasonal reproduction and by a high year-to-year variability (Gray et al., 1980; Armtz and Rumohr, 1986; Essink and Beukema, 1986; Beukema et al., 1993; Turner et al., 1995). The most important species are *A. alba*, *Fabulina fabula*, *Lanicce conchilega*, *Nephtys hombergii* and *Pectinaria koreni* (Prygiel et al., 1988; Desroy et al., 2002; Van Hoey et al., 2004).

The *Abra alba* community is found in the English Channel and Southern Bight of the North Sea, mostly in bays, estuaries and in a narrow zone along the coastline (Fromentin et al., 1997; Thièbaut et al., 1997; Rees et al., 1999; Konstantinos et al., 2000; Desroy et al., 2002; Dauvin et al., 2004). However, there is one large continuous distribution area of the *A. alba* community: the coastal area, from Cap Griz-Nez (France) over Belgium north to the Dutch coast (Vanosmael et al., 1982; Vermeulen and Govaere, 1983; Prygiel et al., 1988; Fromentin et al., 1997; Desroy et al., 2002). In this continuous area gradual changes of the species composition, abundance and diversity within the *A. alba* community, related to the changing environment, are documented (Holmann et al., 1996; Fromentin et al., 1996, 1997; Desroy et al., 2002; Van Hoey et al., 2004).

The Belgian part of this continuous area is very suitable for investigating small-scale spatial changes within the *Abra alba* community characteristics, because (1) it is the central part of the continuous distribution area, (2) the community has an aberrant distribution pattern along the Belgian coast compared to the other areas, (3) a large dataset is available, and (4) a lot of environmental factors (hydro-sedimentology, river outflows, human pressure) influence the area.

The aim of this study is to investigate the geographical patterns (structural and functional level) within the macrobenthic *Abra alba* community at different scales: the community’s distribution range in the English Channel and North Sea (i.e. large scale) and a selected area with a continuous distribution of the *A. alba* community (i.e. small scale) in relation to structuring environmental variables. This information will form a baseline for future comparisons and it will be contribute to a well-considered conservation of marine biodiversity in the coastal areas.

2. Materials and methods

2.1. Study area

The study area covers the full Belgian Continental Shelf (BCS) (2600 km²) situated in the Southern Bight of the North Sea. The BCS is characterized by the presence of several sandbank systems: (1) Coastal Banks, parallel to the coastline, (2) Flemish Banks, about 10–30 km offshore of the western Belgian coast, (3) Zeeland Banks, some 15–30 km offshore of the eastern Belgian coast, and (4) Hinder banks, about 35–60 km offshore (Degraer et al., 1999). Because of the presence of these sandbank systems a high geomorphologic and sedimentological diversity is found (Degraer et al., 1999). The physical, chemical and biological characteristics of the BCS are responsible for a gradient from turbulent, nutrient rich inshore-waters to more transparent and less productive offshore-waters.

2.2. Data origin

Within the framework of several studies a total of 1161 macrobenthos samples were collected at the BCS between 1994 and 2003. After analyzing this dataset with different multivariate methods (Twinspan, ordination, Cluster-analysis), as described in Van Hoey et al. (2004), 204 samples belonging to the same species assemblage, catalogued as the *Abra alba—Mysella bidentata* community (further called the *A. alba* community), were selected for this study. A species
assemblage was considered to represent a community because of (1) their extreme position along the habitat gradient (depth, mud content and median grain size) and, consequently, (2) the absence of overlap between the habitat of each species assemblage, based on the results of the multivariate analyses (Van Hoey et al., 2004). This community description is based on two approaches to delineate communities (Morin, 1999): (1) physically, by discrete habitat boundaries, and (2) statistically, by patterns of assemblages among species. The discrimination of communities however is a merely arbitrary abstraction of biological gradients: gradual transitions between macrobenthic communities exist (Gray, 1981). Even within a single habitat type there are small differences (Ellingsen, 2001), as will be investigated in this study for the A. alba community. The set of 204 samples (120 stations) retained by multivariate analyses were accepted as representative for the A. alba community. To avoid outbalancing of stations that were sampled more than once between 1994 and 2003 (i.e. temporal series), these stations were represented by one randomly selected sample. The final reduced dataset, used for all analyses, thus contains information of 120 samples from 120 different stations distributed along the Belgian Coast and sampled over a 9-year period (Fig. 1). The mid-coastal area and the southwestern coastal area were sampled during the full 9 years, whereas the northeastern coastal area was only recently sampled (2000–2003).

The samples were taken with a Van Veen grab (sampling surface area: 0.1 m²) and sieved alive over a 1 mm mesh-sized sieve. Water depth at each sampling station was recorded in situ and standardized to the mean low water spring level (MLWS) using the M2 reduction model (Coastal Waterways Division, Flemish Community). The grain size distribution of a sub-sample was measured with a LS Coulter particle size analyzer: median grain size of the fraction 2–850 μm and mud content (volume percentage <64 μm) were used as granulometric variables.

After exclusion of species that were not sampled quantitatively (e.g. hyperbenthic and extremely rare taxa) and lumping taxa, because of inconsistent identification throughout the different studies (e.g. genus level: Bathyporeia, Ensis, Spio and Harmothoe; family level: Cirratulidae), a set of 104 taxa (further referred to as species) was used for biological analyses.

2.3. Data analysis

2.3.1. Mapping

The map of the BCS is rotated (angle α, parallel with the coastline) to investigate the distribution gradient of the Abra alba community on the BCS on all the figures. The original calibration (UTM: Easting (m) between 451408 and 520000 and Northing (m) between 5659860 and 5728240) of the map was transformed as follows: the x-coordinates were recalculated by \( x' = x \cos \alpha + y \sin \alpha \); the y-coordinates were recalculated by \( y' = -x \sin \alpha + y \cos \alpha \). The recalculated x-coordinates (\( x' \)) now show the distance along the coastline (0 m, French–Belgian border; 65000 m, Dutch–Belgian border), while the recalculated y-coordinates (\( y' \)) show the distance from the coastline (transformed into nautical miles, 0–38 miles).

2.3.2. Diversity

The different diversity patterns within the Abra alba community were investigated by interpreting the k-dominance plots (Patil and Taillie, 1977; Lambshead et al., 1983) and species-area plots (Connor and McCoy, 1979).

Univariate measures of diversity were species richness (\( S \)), the exponential form of the Shannon–Wiener index (\( \exp H' \)) (log base 2) and the reciprocal of Simpson’s index (1/Simpson) (Whittaker, 1972; Magurran, 1988). Hill (1973) labeled these diversity measures \( N_0, N_1 \) and \( N_2 \), respectively. \( S \) is the number of all species regardless of abundance, \( \exp H' \) is most affected by species in the middle of the species rank sequence, whereas 1/Simpson is primarily a measure of dominance (Whittaker, 1972).

2.3.3. Functional diversity

Functional diversity along the distribution gradients was examined by comparing distribution patterns of feeding guilds (obligatory deposit feeders, facultative deposit-filter feeders, obligatory filter feeders, predators and omnivores) and mobility classes (non tube-building sedentary, tube-building sedentary and mobile species) of the species (Table 1).

![Fig. 1. The sampling years in function of the distance along the coast (meters).](image)
3. Results

3.1. Distribution of the Abra alba community at the BCS

The Abra alba community was found in muddy, fine sandy sediments with an average median grain size of 227 μm (±47 μm (SD)). The sediment composition was characterized by the dominance of the fine sand fraction (average 49%, Fig. 2a) combined with a low, though significant, mud fraction (9% clay and silt) and coarse sand fraction had much lower contributions (<5%).

The community could be found at depths between 4 m and 29 m (average depth of 15 m). These sedimentological characteristics and the associated Abra alba community could be found in the sandbank gullies along the whole Belgian coastal zone, with a more offshore distribution towards the northeast (Fig. 3). South of Nieuwpoort, the community was found close to the coastline, especially in the Westdiep and Potje gullies as well as on two spots in the Smalbank gully (the southwestern coastal zone; hereafter abbreviated as SCZ). The mid-coastal zone (hereafter abbreviated as MCZ) contained stations situated in the gully between the Middelkerke bank and Kwintebank, as well as stations on the southwestern part of the Middelkerke bank. More to the northeast (the northeastern coastal zone; hereafter abbreviated as NCZ), the community had a more offshore distribution along the gullies of the ‘Wenduine bank’ and the ‘Akkaert bank’ and at the north of the ‘Vlakte van de Raan’. The A. alba community was not detected beyond the 14-mile zone on the BCS. The community was also found at five stations nearby the coastline at the northeast of Nieuwpoort (around the Stroombank and at the border of the gully of Zeebrugge).

On the BCS the Abra alba community was characterized by an abundance fluctuating between 129 and 26697 ind/m² (average of 4727 ind/m²) and a species richness fluctuating between 9 and 52 sp./0.1 m² (average of 28 sp./0.1 m²). There were no species spanning the whole sampling area (Fig. 2b). Only eight species (Spiophanes bombyx, Nephtys hombergii, Phyllodoce mucosa, A. alba, Scoloplos armiger, Mysella bidentata and Fabulina fabula) were represented in more than 75% of the samples, with S. bombyx the most commonly found (91% of the samples). Conversely, 66 species, or 54% of the total number of species (122), were restricted to less than 10% of the samples, with 18 species restricted to one site. These 18 species were excluded from further analysis, as described above.

3.2. Geographical patterns in community structure at the BCS

3.2.1. Sedimentological characteristics

The average median grain size was highest at the MCZ (249 ±38 μm (SD)) compared to the SCZ (219 ±43 μm) and the NCZ (222 ±45 μm) (Fig. 4a). In the SCZ the median grain size range was situated between 150 and 350 μm, in the MCZ between 200 and 300 μm and in the NCZ between 220 and 260 μm.
350 µm and in the NCZ between 150 and 300 (with one exception).

The highest average value in the mud content (Fig. 4a) was found in the NCZ (14 ± 10.8%), followed by 8 ± 4.6% in the SCZ and 5 ± 7% in the MCZ. For the fine sand fraction an opposite trend was found, with a significant decrease (Spearman rank, \( p = 0.000153 \)) towards the northeast (Fig. 4a), with the lowest average value in the NCZ (42 ± 13.6%), 46 ± 15.3% in the MCZ and 54 ± 14.7% in SCZ.
3.2.2. Biological characteristics

3.2.2.1. Multivariate analysis. Multivariate analysis (detrended correspondence analyses, DCA) clearly visualizes the differences in community organization along the gradient, with minor overlap between the areas SCZ, MCZ and NCZ (Fig. 5).

3.2.2.2. Abundance, higher taxa, species dominance. The macrobenthic density across the three zones was highest in SCZ (average of 5181 ind/m²) and NCZ (5941 ind/m²), with a drop in MCZ (average of 3010 ind/m²) (Fig. 4b). The variation in macrobenthic density is higher in the SCZ and NCZ, than in the MCZ.

In SCZ, molluscs and annelids were equally dominant in the macrobenthos (Fig. 4b). The molluscs, mainly bivalves, strongly decline (Spearman rank, \( p=0.000006 \)) in relative abundance towards the northeast, while annelids (mainly polychaetes) strongly increase (Spearman rank, \( p=0.01 \)) in dominance. This was also visible in the list of the ten most abundant species (Table 2), where bivalves were missing in the NCZ.

When comparing the lists of the ten most common species (Table 2), a shift in species composition from southwest to northeast could be observed. There were only four species (Spiophanes bombyx, Nephthyis hombergii, Scoloplos armiger and Phyllodoce mucosa) in common in the top ten species list of the three areas, which were present in more than 80% (SCZ and MCZ) or 90% (NCZ) of the samples within each area. Additionally, the SCZ had another four dominant species (Abra alba, Cirratulidae spp., Mysella bidentata and Fabulina fabula) in common with MCZ. These species were also present in NCZ but in much lower abundances. MCZ had only one other species (Actinaria spp.) in common with NCZ. The tube building polychaete Lanice conchilega was present in almost all samples at SCZ (Table 2). NCZ was also characterized by five dominant species, which were not common in the other areas (Eteone longa, Pariambus typicus, Eumida sanguinea, Owenia fusiformis and Pectinaria koreni). In terms of species composition, SCZ showed more similarity with MCZ and NCZ differs from the SCZ and MCZ.

3.2.2.3. Diversity. The species dominance curve identified NCZ to be strongly different from the two other zones (Fig. 6a), indicating a lower diversity and a strong dominance of one species, in this case Spiophanes bombyx. The species dominance plots for the two other zones were more or less similar, with a similar ranking of species contribution to the abundance. The species area plots (Fig. 6b) of the NCZ and MCZ were similar, whereas the plot of the SCZ was clearly different, indicating higher species richness for the same sampling area.

The number of species per sample (\( N_0 \)) was highest at SCZ (31 spp./0.1 m²), compared to the NCZ and MCZ with respectively 24 and 25 spp./0.1 m² (Fig. 7a). \( N_1 \) and \( N_2 \) both follow the same pattern, with a decline (Spearman rank: \( p<0.01 \) for both) towards the NCZ, especially in the most northeastern part of it, caused by strong species dominance in this area (Fig. 7b). \( N_1 \) was highest in the SCZ (average 11.8) and lowest in the NCZ (average 7.3), with an intermediate value at the MCZ (average 9.7). \( N_2 \) was also highest in the SCZ (average 7.5) and lowest in the NCZ (average 4.6), with an intermediate value at the MCZ (average 6.3).

3.2.2.4. Functional biodiversity. The obligatory deposit feeders were the dominating feeding guild in the NCZ (61%), followed by predators (16%) (Fig. 8a,b). The obligatory deposit and filter feeders as well as the facultative deposit-filter feeders were almost equally dominating in the SCZ and MCZ, with respectively 38% and 37% for obligatory deposit feeders, 21% and 26% for obligatory filter feeders and 28% and 17% for facultative deposit-filter feeders.

In the NCZ there was a strong dominance of tube-building sedentary polychaetes (61%), such as Spiophanes bombyx, Owenia fusiformis, Lanice conchilega and Pectinaria koreni (Fig. 7b). This mobility class was less represented in the MCZ (17%), where the mobile species were dominating (46%). In the SCZ the non tube-building sedentary polychaetes formed the dominating group (44%).

3.2.2.5. Habitat heterogeneity. Within the habitat of the Abra alba community at the three zones on the BCS there was no correlation between community structure (macrobenthic species richness and density) and granulometry (sediment median grain size and mud content) (Spearman \( R: p>0.1 \)) (Fig. 9).

4. Discussion

The Abra alba community forms a well-established faunal unity in coastal areas of the North Sea (Dewarummez et al., 1986), where it is mostly found in
<table>
<thead>
<tr>
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<th>Belgian coast</th>
<th>Dutch coast</th>
<th>German coast</th>
<th>English coast</th>
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<td>SMith-McIntyre grab (0.1 m)</td>
<td>SCZ</td>
<td>81</td>
<td>61</td>
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<td></td>
<td>Rivière de Morlaix</td>
<td>Smith-McIntyre grab (0.1 m)</td>
<td>MCZ</td>
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<td>32</td>
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<td></td>
<td>Baie de Seine</td>
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<td>Gravelines</td>
<td>SMith-McIntyre grab (0.1 m)</td>
<td>English channel</td>
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<td>194</td>
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</table>

**Sampling method**
- Smith-McIntyre grab (0.1 m)
- Van Veen Grab (0.1 m)
- Rallier-du-Baty dredge

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<th>No of samples</th>
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<th>81</th>
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<th>22</th>
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<tr>
<td>Median grain size (µm)</td>
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<td>77–122</td>
<td>80–120</td>
<td>100–150</td>
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<td>100</td>
<td>150</td>
<td>200</td>
<td>300</td>
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<td>2</td>
<td>5</td>
<td>8</td>
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<td>11.5</td>
<td>17.7</td>
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<tr>
<td>Density (ind/m²)</td>
<td>745 ± 164</td>
<td>3520 ± 402</td>
<td>5080 ± 1964</td>
<td>5118 ± 5452</td>
<td>3010 ± 3909</td>
<td>5941 ± 5254</td>
<td>2556 ± 3458</td>
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<td>Species top 10 based on abundance</td>
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<td>Chaetozone setosa</td>
<td>Abra alba</td>
<td>Spiophanes bombyx</td>
<td>[Actiniaria sp.]</td>
<td>Mysella bidentata</td>
<td>Spio decoratus</td>
<td>Fabulina fabula</td>
<td>Pariambus armiger</td>
<td>Fabulina fabula</td>
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<td>745</td>
<td>5080</td>
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<td>5118</td>
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**Literature**
- Fromentin et al., 1997
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- Fromentin et al., 1997
- Dewarumez et al., 1992
- Holtmann et al., 1996
- Salzwedel et al., 1985
- Sanvicente-Anorve et al., 2002

**Table 2**
Overview of the community parameters (abundance, diversity, species top 10), sedimentology and sampling method of different areas in the English Channel and Southern North Sea, where the *Abra alba* community occurs. Species in bold occur in the top 10 of the three zones on the BCS. The underlined species are present in both the SCZ and MCZ; the species in brackets are present in both the MCZ and the NCZ.
bays, estuaries and in a narrow zone along the coastline, mostly between 0 and 10 m depth (Souplet and Dewarumez, 1980; Konstantinos et al., 2000) and thus strongly influenced by terrestrial organic matter inputs (Sanvicente-Anorve et al., 2002).

The largest continuous distribution area of the Abra alba community is situated along the northeastern coast of France (Gravelines) over Belgium north to the Dutch coast (Kingston and Rachor, 1982; Vanosmael et al., 1982; Vermeulen and Govaere, 1983; Prygiel et al., 1988; Holtmann et al., 1996; Fromentin et al., 1997; Desroy et al., 2002; Van Hoey et al., 2004). Next to this continuous distribution area, there are a lot of isolated distribution areas in the English Channel, such as the Bay of Morlaix with two small (6 and 2 km²) spots, respectively Pierre Noire and Rivière de Morlaix, the Bay of the Seine (Cabiocq and Glaçon, 1975; Souplet and Dewarumez, 1980; Fromentin et al., 1997; Thièbaut et al., 1997), some bays (Eagle, 1975; Rees and Walker, 1983) and coastal areas near the UK coast (St Andrews and Aberdeen, Cumberland coast, South-West England and some locations in the Irish Sea) (Rees et al., 1999; Sanvicente-Anorve, 2002) and a small area in the German Bight of the North Sea, seaward of the rivers Elbe and Weser (area of 1000 km²) (Stripp, 1969; Kingston and Rachor, 1982; Salzwedel et al., 1985). The A. alba community is further present along the Atlantic coast of France, Spain and Portugal, and in the Mediterranean Sea. Yet, the community structure within these areas falls out the scope of this study.

### 4.1. Geographical patterns in community structure

Although the community’s habitat is characterized by fine, muddy sands throughout its distribution range (Table 2), it is clear that minor differences in
sedimentological characteristics occur (Salzwedel et al., 1985; Holtmann et al., 1995; Fromentin et al., 1997; Sanvicente-Anorve et al., 2002). The *Abra alba* community is mostly found at depths of 0–20 m; the deepest are found along the German coast (45 m) (Salzwedel et al., 1985), MCZ (18 m) and the Pierre Noire site (17 m) (Fromentin et al., 1997).

The highest mean abundance was found at the Pierre Noire area (7545 ind/m²) (Fromentin et al., 1997) and the lowest at the Dutch coast (2556 ind/m²) (Holtmann et al., 1996) (Table 2). Abundance, however, is a strongly varying community parameter, depending on meteorological conditions (wind) and currents, which can induce unpredictable year-to-year changes in the abundance of some species. Moreover, new recruits are able to form patches of high abundances after a disturbance (Desroy et al., 2002). High variations in abundance characterize most areas only the Bay of the Seine shows a great temporal stability in abundances, due to the high larval retention capacity of the bay (Thiébaut et al., 1992, 1996).

There is a clear pattern in the diversity between the different sites: total number of species, species richness
(N₀) and Shannon index (N₁) decrease towards the northeast. The total number of species (420 sp.) and the Shannon index (3.8) are highest at the Pierre Noire site (Fromentin et al., 1997) and decrease towards the NCZ (total number of species, 85 sp.; N₀, 25 spp./0.1 m²; N₁, 1.8 (this study)) and Dutch coast (N₀, 14 spp./0.1 m²; N₁, 1.8 (Holtmann et al., 1996)), where they displayed the lowest values. At isolated places along the German and southern English coast, the Shannon index (respectively 2.2 and 2.1) and total number of species (respectively 83 spp. and 79 spp.) are comparable with those of the SCZ and MCZ. In the study of Rees et al. (1999), the Abra alba community in inshore muddy fine sand at some places along the east and west coasts of the UK is characterized by a species richness of 25 spp./0.1 m².

The most common species in all areas were Abra alba, Nephtys hombergii and Spiophanes bombyx. Furthermore, the dominant species in each area belong to polychaetes or bivalves; this is opposite to the Pierre Noire area (in the Bay of Morlaix), where amphipods (Ampelisca sp.) dominate (Fromentin et al., 1997). Numerous species are consistently found in the 10 most common species of the continuous distribution area from the Gravelines over Belgium north to the Dutch coast. Along the southern coast of the UK (in the English Channel) the A. alba community was dominated by A. alba, Nucula nitidosa, Pectinaria koreni, Ophitura albida and Echinocardium cordatum (Rees and Walker, 1983; Budd, 2002; Sanvicente-Anorve et al., 2002). The dominant species in the A. alba community along the east and west coast of the UK were Chamelea gallina, Amphiprila filiformis, N. nitidosa, S. bombyx and A. alba (Rees et al., 1999). The species composition of the A. alba community along the German coast, also referred to as the N. nitidosa association (Salzwedel et al., 1985), shows a high similarity with the continuous distribution area of the A. alba community.

Although the community structure shows a high similarity across the full distribution range of the Abra alba community, changes in community composition were observed: the BCS should be considered as a major transition from the rich southern to the relatively poorer northern distribution area of the A. alba community. In this transition zone, the A. alba community on a structural level was characterized by high variation in abundance, high species richness (31 sp./0.1 m²) and high diversity (N₁, 11.8; N₂, 7.5) in the SCZ, while the MCZ was characterized by low variation in abundance, low species richness (24 sp./0.1 m²), and lower diversity (N₁, 9.7; N₂, 6.3) and the NCZ by high abundance variation, low species richness (25 sp./0.1 m²) and the lowest diversity (N₁, 7.3; N₂, 4.6). On a functional level, there was no strong feeding guild and mobility class dominance in the SCZ; they were all more or less equal represented. Obligatory deposit feeders and tube-building sedentary species dominate the NCZ, while the MCZ shows intermediate values for feeding guilds and a dominance of mobile species.

4.2. Structuring environmental variables

Large-scale spatial patterns in community characteristics largely result from differences in hydro-sedimentary processes (natural or anthropogenic) (Creutzberg et al., 1984; Heip et al., 1992). The Abra alba community within its southern distribution areas (Bays of Morlaix and Seine) is mainly influenced by flood-dominated currents from the Atlantic Ocean, while mainly ebb-dominated currents influence the northern areas (the continuous distribution area and German Bight) (Vlaeminck et al., 1989; Grochowski et al., 1993; Lanckneus et al., 1994; Trentesaux et al., 1994). Since hydrodynamic conditions play an important role in the exchange of planktonic larvae (Eckman, 1983; Devarumpet et al., 1993; Luczak et al., 1993), only little (larval) contact between the isolated southern and UK distribution areas on the one hand and the continuous and German distribution areas on the other hand might be expected. The hydrological isolation might partly explain the differences in community structure observed at a large scale. Moreover, the transition from temperate to boreal conditions in the English Channel might further strengthen the differences in community structure, mainly the species composition, between the southern and northern distribution areas (Sanvicente-Anorve et al., 2002). Because of (1) the obvious strong exchange between populations within the A. alba community and (2) the similar climatological conditions within its continuous distribution area, the differences in community structure here within cannot solely be explained by differences in hydrological or climatological conditions; other factors should play a structuring role.

Although a relationship between small-scale habitat heterogeneity and community abundance and diversity could be expected, no such correlation was found at the BCS: habitat heterogeneity—as given by the sediment characteristics in this study—within each of the three zones was independent from community abundance and diversity. Thiébaut et al. (1997) also found sediment variables to be a poor predictor for the structure within the Abra alba community. Another structuring variable might be food availability: increases in species diversity, abundance and biomass can be correlated to an increased food supply to the system (Rees et al., 1999). Being dominated by detritivores, detritus is the major food resource for the A. alba community. The detrital food availability is mainly coupled to the hydrology and largely depends on planktonic primary and secondary production and/or terrestrial inputs (through riverine systems). At the BCS the offshore zone mass is typically
characterized by low productive and more transparent waters, whereas turbid, highly productive waters characterize the coastal zone (Lancelot et al., 1986). The high turbidity and productivity of the coastal zone mainly result from the strong terrestrial input of suspended matter and nutrients from the rivers Westerscheldt and Yzer. The turbidity plume of the Westerscheldt can, depending on the wind direction, intensity and duration, reach as far as the Cap Gris Nez (northern France) (Cabiöch and Glaçon, 1975), thus influencing the whole southern part of the continuous distribution area of the A. alba community. Smaller rivers, such as the Yzer, have lower riverine inputs in the coastal zone, but may be locally significant in structuring the A. alba community: higher diversity, abundance and biomass were observed in the vicinity of river outflows (Seine, Somme, Authie, Canche) (Desroy et al., 2002). The increased food availability in the coastal zone, due to riverine inputs of suspended matter and nutrients might thus be responsible for the high diversity and abundance of the A. alba community in the southern part of its continuous distribution area (Graveline north to SCZ) in contrast to the lower diversity and abundance in more offshore areas (e.g. MCZ).

Despite the general positive influence of river outflows on the Abra alba community, a clear decrease in diversity was observed in the NCZ, offshore of the Westerscheldt estuary. This decrease in diversity coincides with a functional community shift towards a dominance of deposit feeders, an increase in predators and the expense of filter feeders. It is hypothesized that this decrease in diversity and functional community shift might be due to the outflow of suspended matter from larger rivers being too high to support rich populations of filter feeding species, as already demonstrated by Snelgrove and Butman (1994). The excess in suspended matter input from the Westerscheldt might also explain the (near) absence of the A. alba community in the Belgian inshore waters south of the river mouth (Nieuwpoort–Zeebrugge; less than four nautical miles offshore). This area is dominated by the Macoma balthica community (less diverse), where A. alba is also present, but in much lower abundance (Van Hoey et al., 2004). More offshore the distribution of the A. alba community was limited by the occurrence of coarser sediments (due to strong offshore currents) in the gullies further than ten nautical miles to the southwest and 14 nautical miles to the northeast of the coastline (Van Hoey et al., 2004). Since the A. alba community along the Dutch and German coast is also confronted with large rivers, such as Rhine, Meuse, Elbe and Weser, it might also explain the relatively low diversity and abundance in the whole northern part of the continuous distribution area. Yet, also other factors, such as salinity and pollution can have an effect on the community structure in the proximity of a river (Thiébaut et al., 1997; Ysebaert et al., 2003). An inshore–offshore gradient of salinity can significantly affect the distribution of species, which are commonly considered to be stenohaline (Strickle and Diehl, 1987), but the absence of such species was (e.g. Echinoderms) not observed in this study. The study of Lacroix et al. (2004) confirms that the impact of the Westerscheldt on the salinity in the Belgian coastal area is minimal. Although pollution is known to impact the distribution of some species in the Westerscheldt (Ysebaert et al., 2003), such effects were not yet investigated further offshore.

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