Chapter 3

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

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), differences in 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.

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

Nowadays, human activities are considered to be the primary causes 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 Dewarumez, 1980; Kingston and Rachor, 1982; Prygiel et al., 1988; Duineveld et al., 1991; Dewarumez 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; Thiébaut et al., 1997; Dauvin, 1998; Degraer et al., 1999; Rees et al., 1999; Dauvin, 2000; Ghertsos 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 *A. 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 *A. 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 (Dewarumez 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; Arntz and Rumohr, 1986; Essink and Beukema, 1986; Beukema et al., 1993; Turner et al., 1995). The most important species are *A. alba*, *Fabulina fabula*, *Lanice conchilega*, *Nephtys hombergii* and *Pectinaria koreni* (Prygiel et al., 1988; Desroy et al., 2002; Van Hoey et al., 2004).

The *A. 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; Thiébaut et al., 1997;

Rees et al., 1999; Ghertsos 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 (Holtmann 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 *A. alba* community characteristics, because (1) it is the central part of the continuous distribution area, (2) the community has a 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 out-flows, human pressure) influence the area.

The aim of this study is to investigate the geographical patterns (structural and functional level) within the macrobenthic *A. 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.

Materials and Methods

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.

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 *Abra 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 nine years period (Figure 1). The mid coastal area and the southwestern coastal area were sampled during the full nine 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.
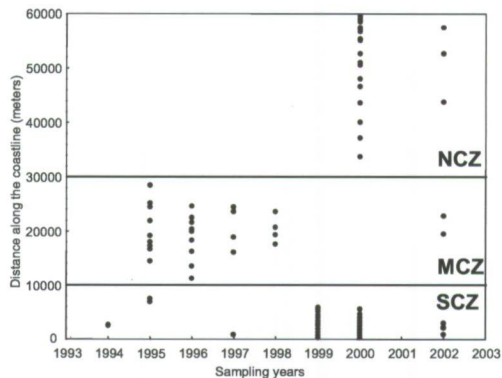

Figure 1. The sampling years in function of the distance along the coast (meters)

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.

Data analysis

Mapping

The map of the BCS is rotated (angle α, parallel with the coastline) to investigate the distribution gradient of the *A.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 are recalculated by $x' = x \cos α + y \sin α$; the y-coordinates are recalculated by $y' = -x \sin α + y \cos α$. The recalculated x-coordinates (x') now show the distance along the coastline (0m: French-Belgian border, 65000m: Dutch-Belgian border), while the recalculated y-coordinates (y') show the distance from the coastline (transformed into nautical miles, 0-38 miles).

Diversity

The different diversity patterns within the *A. 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 exponentiated form of the Shannon-Wiener index (ExpH') (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. ExpH' is most affected by species in the middle of the species rank sequence, whereas 1/Simpson is primarily a measure of dominance (Whittaker, 1972).

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).

Table 1. Feeding-classes and their abbreviations (Holtmann et al., 1996; Fauchald and Jumars, 1979; Hartman-Schröder, 1996) and the mobility classes and their abbreviations (Hartmann –Schröder, 1996; Hayward and Ryland, 1995).

| Feeding classes		Mobility - classes	
Abbreviation	Description	Abbreviation	Description
D	Deposit feeder	S	Non-tube building sedentary species
DF	Deposit feeder +	M	Mobile species
	filter feeder	T	Tube-building sedentary species
P	Predator		
O	Omnivoor		
F	Filter feeder		

Distribution of the *Abra alba* community at the BCS

The *A. 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% - Figure 2a) combined with a low, though significant, mud fraction (9%: clay and silt) and coarse sand fraction had much lower contributions (9% and <5% respectively). The community could be found at depths between 4 m and 29 m (average depth of 15 m).
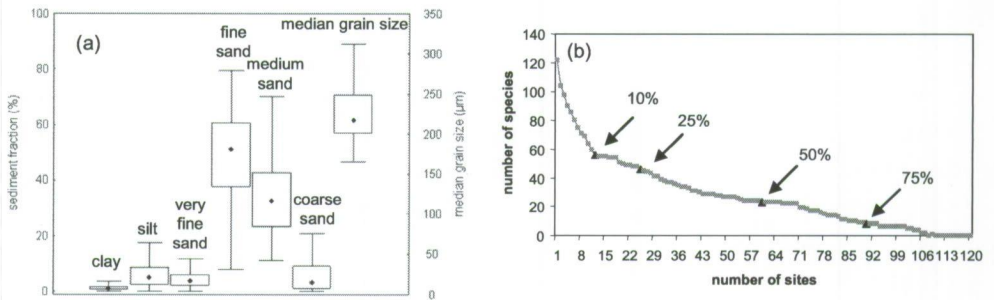
Figure 2. a) The sediment fraction (left) and the median grain size (right) of the *Abra alba* community. Median (symbol) + percentiles (25% -75%) (Boxes) and Non-Outlier range (Min – Max) (Whiskers). b) Distribution of species range size, which is the number of stations occupied by a species out of a total of 120 sites, with indication of the points representing 10, 25, 50 and 75% of the total stations.

These sedimentological characteristics and the associated *A. alba* community could be found in the sandbank gullies along the whole Belgian coastal zone, with a more offshore distribution towards the northeast (Figure 3). Southwest 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-miles 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).
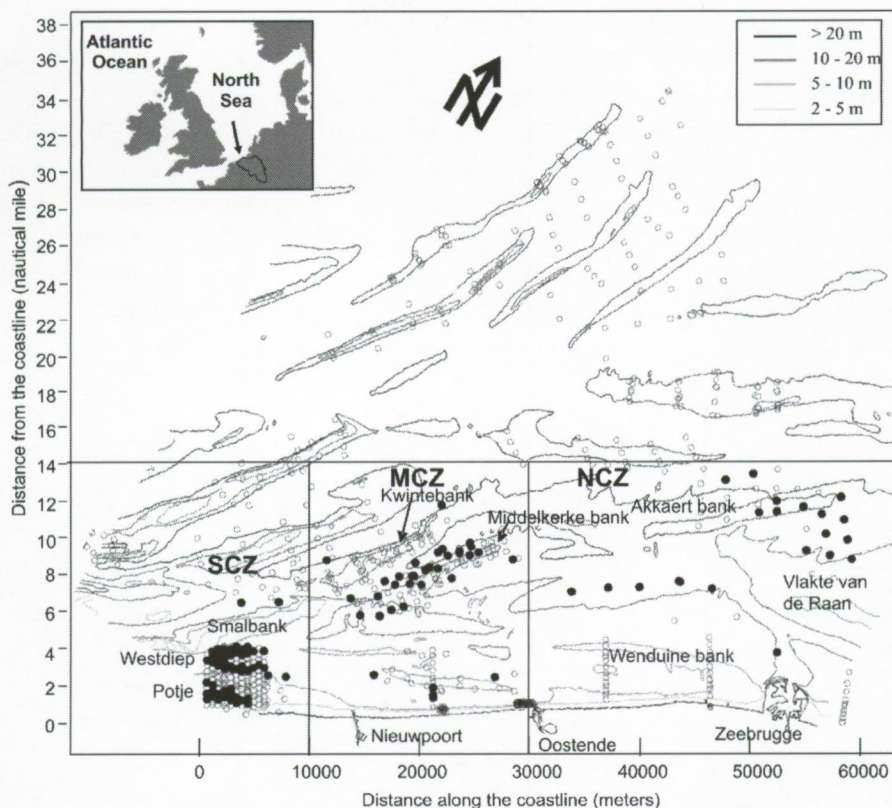
Figure 3. Northeastern spatial distribution gradient of the *Abra alba* community on the Belgian Continental Shelf with indication of the different zones. Black dots (stations where this community is present), open dots (absence of this community).

On the BCS the *A. 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 spp./0.1m² (average of 28 spp./0.1m²). There were no species spanning the whole sampling area (Figure 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 higher.

Geographical patterns in community structure at the BCS

Sedimentological characteristics

The average median grain size was highest at the MCZ (249 μm ± 38 (SD)) compared to the SCZ (219 μm ± 43) and the NCZ (222 μm ± 45) (Figure 5a). In the SCZ the median grain size range was

situated between 150 and 350 µm, in the MCZ between 200 and 350 µm and in the NCZ between 150 and 300 (with one exception).

The highest average value in the mud content (Figure 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 (Figure 4a), with the lowest average value in the NCZ (42% ± 13.6%), 46% (± 15.3%) in the MCZ and 54% (± 14.7%) in SCZ.
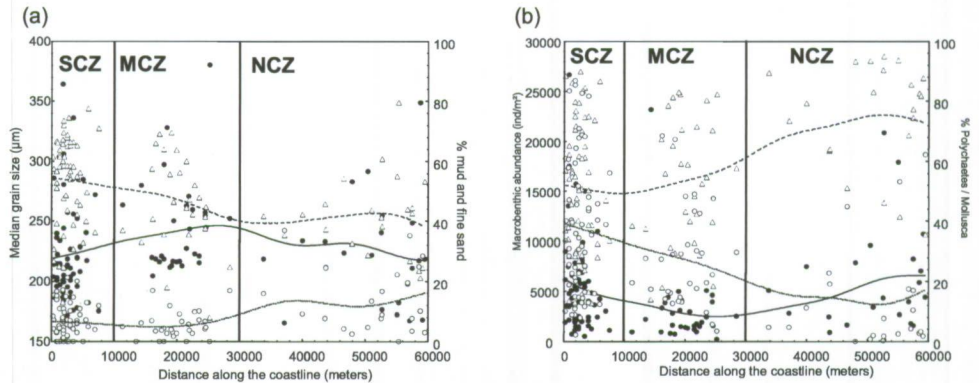
Figure 4. (a) Median grain size (black points, black line), mud (open points; dotted trend line) and fine sand (open triangles; interrupted black trend line) fraction within the *Abra alba* community in relation to the distance along the coastline, with indication of the three zones. (b) Macrobenthic abundance (black points, black line), percentage of Annelida (open triangles; interrupted black trend line) and percentage of Mollusca (open points; dotted trend line) in relation to the distance along the coastline, with indication of the three zones.

Biological characteristics
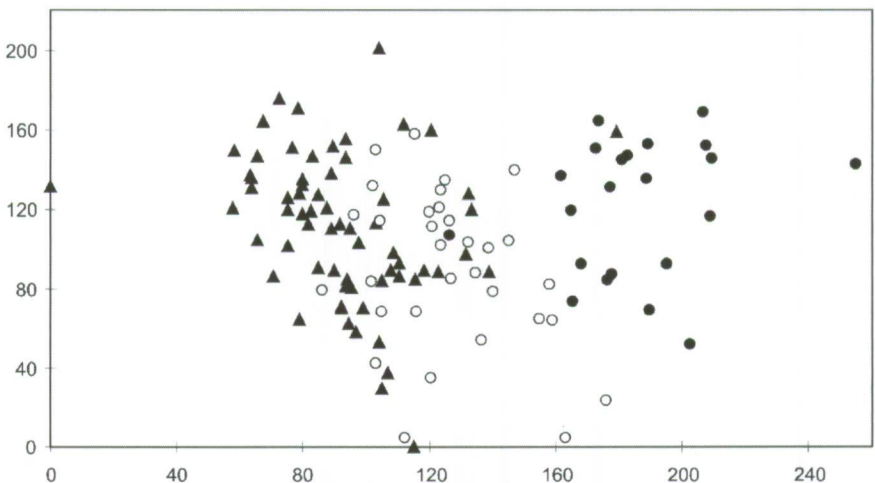
Figure 5. DCA ordination plot along the first two axes. The discrimination of the three zones (triangle: SCZ; open points: MCZ; black points: NCZ) is made.

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 (Figure 5).

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) (Figure 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 (Figure 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 (*S. bombyx, N. hombergii, S. armiger* and *P. 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 (*A. alba*, Cirratulidae spp., *M. bidentata* and *F. 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.
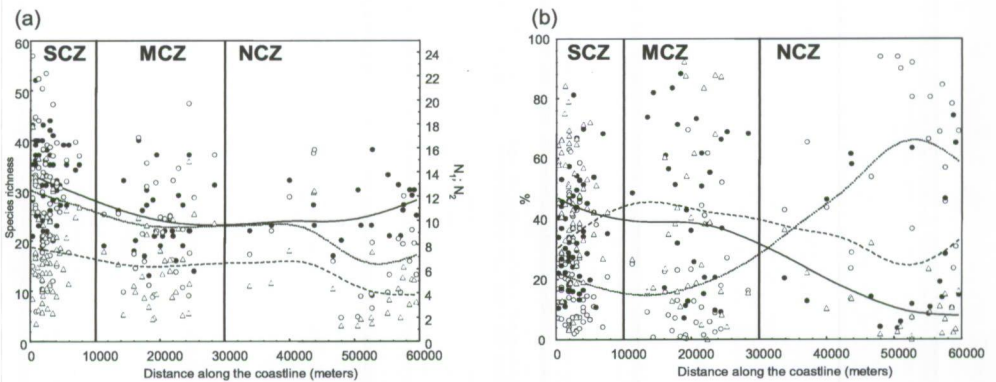
Diversity
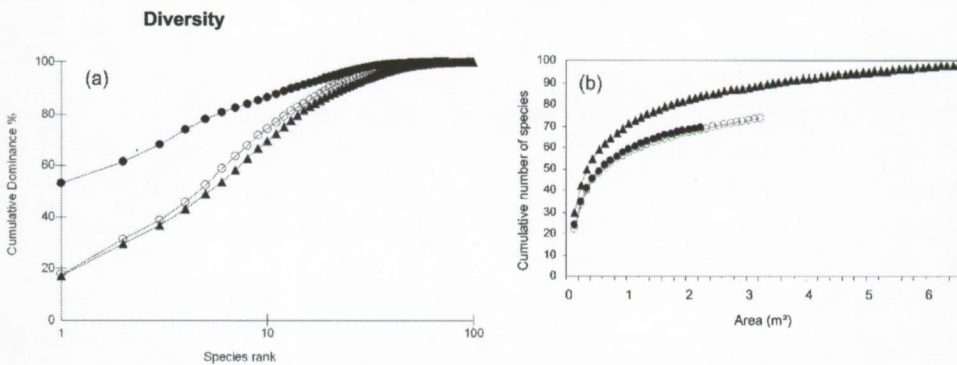
Figure 6. (a) species dominance plot at the three zones (SCZ: black triangle; MCZ: open circles; NCZ: black points) (b) species area plot for the three zones (similar symbols as (a))

The species dominance curve identified NCZ to be strongly different from the two other zones (Figure 6a), indicating a lower diversity and a strong dominance of one species, in this case *S. 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 (Figure 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./0.1m²), compared to the NCZ and MCZ with respectively 24 and 25 spp./0.1m² (Figure 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 (Figure 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 of 6.3).
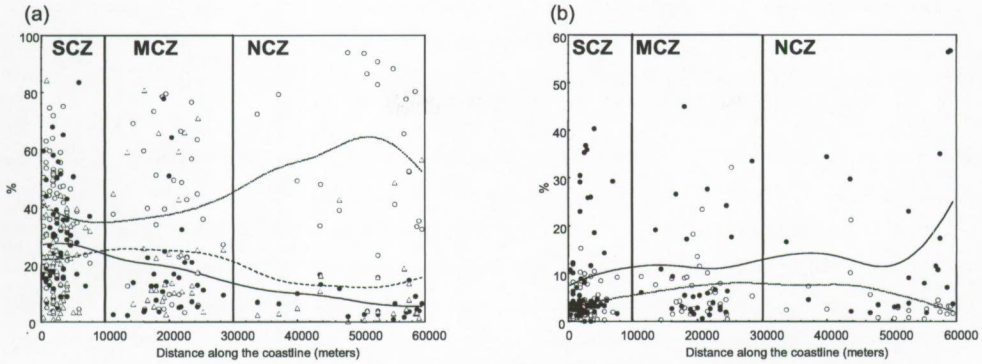

Figure 7. (a) The distribution of the different diversity indices in relation to the distance along the coastline: Species richness: N_0, black circles, solid trend line; Exponentiation form of H': N_1, open circles, dotted trend line; the reciprocal of the Simpson's index: N_2, open triangles, interrupted black trend line.
(b) The relative abundance of the different mobility classes: sedentary species (S): black points, black trend line; mobile species (M): open triangles, interrupted black trend line; tube-building species (T): open circles, dotted trend line.

Functional biodiversity

The obligatory deposit feeders were the dominating feeding guild in the NCZ (61%), followed by predators (16%) (Figure 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 *S. bombyx, O. fusiformis, L. conchilega* and *P. koreni* (Figure 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%).

Figure 8. (a) The distribution of the relative abundance of different feeding guilds: facultative deposit – filter feeders (DF): open triangles, interrupted black trend line; obligatory filter feeders (F): black circles, solid trend line; obligatory deposit feeders (D): open circles, dotted trend line. (b) The distribution of the relative abundance of different feeding guilds: predators (P): black circles, black trend line; and omnivores (O): open circles, dotted trend line

Habitat heterogeneity

Within the habitat of the *A. 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) (Figure 9).
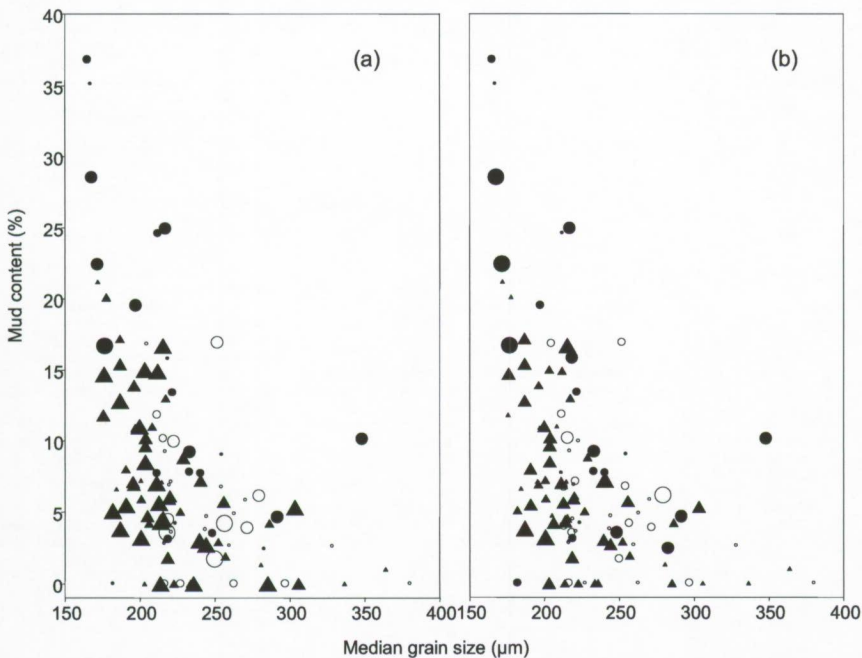
Figure 9. The species richness (N_0) and abundance (ind/m²) in relation to the sedimentological characteristics (median grain size (μm) and mud content (%)), with indication of the three zones: SCZ: black triangles; MCZ: open circles; NCZ: black circles. (a) Species richness (species/0.1m²): •○▲ 9-23; •○▲ 23-29; ●○▲ 29-36; ●○▲ 36-53, (b) Abundance (ind/m²): •○▲ < 2000; •○▲ 2000-5000; ●○▲ 5000-10000; ●○▲ 10000-27000.

Discussion

The *Abra alba* community forms a well-established faunal unity in coastal areas of the North Sea (Dewarumez et al., 1986), where it is mostly found in bays, estuaries and in a narrow zone along the coastline, mostly between 0 and 10 m depth (Souplet & Dewarumez, 1980; Ghertsos et al., 2000) and thus strongly influenced by terrestrial organic matter inputs (Sanvicente-Anorve et al., 2002).

The largest continuous distribution area of the *A. alba* community is situated along the northeastern coast of France (Gravelines) over Belgium north to the Dutch coast (Kingston & Rachor, 1982; Vanosmael et al., 1982; Vermeulen & 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

Tabel 2. Overview of the community parameters (abundance, diversity ([1], 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.

	French coast				Belgian coast			Dutch coast	German coast	English coast
	Pierre Noire	Rivière de Morlaix	Baie de Seine	Gravelines	SCZ	MCZ	NCZ			English channel
Sampling method	Smith-McIntyre grab (0.1m²)				Van Veen Grab (0.1m²)					Rallier-du-Baty dredge
No of samples	117	77	38	81	61	32	22	194	14	10
Type of area	Isolated	Isolated	Isolated	One continuous area					Isolated	Isolated
Median grain size (µm)	148-184	77-122	80-120	100 - 150	219 ± 43	249 ± 38	222 ± 45	196.7 ± 54.8	Muddy fine sand	Muddy fine sand
Mud content(%)					8 ± 6	5 ± 4	14 ± 11	7.2 ± 12		
Depth(m)	17	10	10.5	10	11.5	17.7	10.8	12 ± 4.5	13-45	<10
Density (ind/m²)	7545 ± 1641	3320 ± 402	5380 ± 848	5080 ± 1965	5181 ± 4542	3010 ± 3909	5941 ± 5254	2556 ± 3458	3828	6304
Total no of sp.	420	308	130	154	118	89	85		83	79
Diversity (No)				32	31 ± 8	24 ± 7	25 ± 6	14 ± 7	37	
Diversity (Shannon - Wiener)	3.8	2.9	3.2	2.4	2.4	2.17	1.83	1.84	2.2	2.1 ± 0.46
Species top 10 based on	% of total abundance	% of total abundance	% of total abundance	% of total abundance	Mean abundance	Mean abundance	Mean abundance	Mean abundance	Mean abundance	% of total abundance
Species top 10 (ind/m²)	Ampelisca armoricana	Chaetozone setosa	Owenia fusiformis	Lanice conchilega	Abra alba	Mysella bidentata	Spiophanes bombyx	Spisula subtruncata	Nucula nitidosa	Abra alba
	Ampelisca sarsi	Melinna palmata	Acrocnida brachiata	Abra alba	Spiophanes bombyx	[Actiniaria sp.]	Nephtys hombergii	Magelona johnstoni	Spiophanes bombyx	Nucula nitidosa
	Polydora pulchra	Polydora pulchra	Pectinaria koreni	Spiophanes bombyx	Lanice conchilega	Phyllodoce mucosa	Phyllodoce mucosa	Spiophanes bombyx	Ophiura albida	Melinna palmata
	Spio decoratus	Nephtys hombergii	Mysella bidentata	Fabulina fabula	Cirratulidae sp.	Nephtys hombergii	Scoloplos armiger	Urothoe poseidonis	Mysella bidentata	Mysella bidentata
	Paradoneis armata	Mediomastus fragilis	Aphelochaeta marioni	Eumida sanguinea	Mysella bidentata	Abra alba	Eteone longa	Macoma balthica	Nephtys hombergii	Notomastus latericeus
	Chaetozone setosa	Aphelochaeta marioni	Abra alba	Phyllodoce mucosa	Nephtys hombergii	Fabulina fabula	Pariambus typicus	Fabulina fabula	Phoronis sp.	Nephtys hombergii
	Marphysa bellii	Euclymene oerstedii	Cultellus pellucidus	Nephtys hombergii	Scoloplos armiger	Scoloplos armiger	Eumida sanguinea	Mysella bidentata	Ophiura ophiura	Euclymene oerstedii
	Urothoe pulchella	Lanice conchilega	Pholoe minuta	Pectinaria koreni	Phyllodoce mucosa	Spiophanes bombyx	Owenia fusiformis	Scoloplos armiger	Scoloplos armiger	Magelona alleni
	Aricidea fragilis	Thyasira flexuosa	Magelona mirabilis	Notomastus latericeus	Fabulina fabula	[Actiniaria sp.]	Nephtys hombergii	Abra alba	
	Nephtys hombergii	Abra alba	Nephtys hombergii	Macoma balthica	Oligochaeta spp.	Cirratulidae spp.	Pectinaria koreni	Nepthys cirrosa	Pectinaria koreni	
Literature	Fromentin et al., 1997	Fromentin et al., 1997	Fromentin et al., 1997	Fromentin et al., 1997; Dewarumez et al., 1992				Holtmann et al., 1996	Salzwedel et al., 1985	Sanvicente-Anorve et al., 2002

[1] In the original publication, the diversity in column one was expressed as N_1, when in fact, the values expressed the Shannon Wiener index. This is corrected in the PhD – text.

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 (Cabioch and Glaçon, 1975; Souplet and Dewarumez, 1980; Fromentin et al., 1997; Thiébaut et al., 1997), some bays (Eagle, 1975; Rees & Walker, 1983) and coastal areas nearby the U.K. coast (St- Andrews and Aberdeenshire, 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 1000km²) (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.

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 *A. alba* community is mostly found at depths of 0 to 20m; the deepest are found along the German coast (45m) (Salzwedel et al., 1985), MCZ (18m) and the Pierre Noire site (17m) (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 (N_0) and Shannon index (h') 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 spp., N_0: 25 spp./0.1m², h': 1.8 (this study)) and Dutch coast (N_0: 14 spp./0.1m²; h': 1.8 (Holtmann et al., 1996)), where they displayed the lowest values. At the 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 *A. alba* community in inshore muddy fine sand at some places along the E and W coast of the U.K. is characterized by a species richness of 25 spp./0.1m².

The most common species in all areas were *A. 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* spp.) 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 U.K. (in the English Channel) the *A. alba* community was dominated by *A. alba*, *Nucula nitidosa, Pectinaria koreni, Ophiura albida* and *Echinocardium cordatum* (Rees, 1983; Budd, 2002; Sanvicente- Anorve et al., 2002). The dominant species in the *A. alba* community along the E and W coast of the U.K. were *Chamelea gallina, Amphiura filiformis, Nucula 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 *Nucula 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 *A. 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 was on a structural level characterized by, high variation in abundance, high species richness (31 spp./0.1 m²) and high diversity (N_1: 11.8; N_2: 7.5) in the SCZ, while the MCZ was characterized by low variation in abundance, low species richness (24 spp./0.1 m²), and lower diversity (N_1: 9.7; N_2: 6.3) and the NCZ by high abundance variation, low species richness (25 spp./0.1 m²) and the lowest diversity (N_1: 7.3; N_2: 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.

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 *A. 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; Dewarumez et al., 1993; Luczak et al., 1993), only little (larval) contact between the isolated southern and U.K. 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 in its continuous distribution area, the differences in community structure here within cannot solely be explained by differences in the 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 *A. 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) (Cabioch & Glacon, 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 (Gravelines 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 *A. 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 Butmann (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 & 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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