Chapter 4
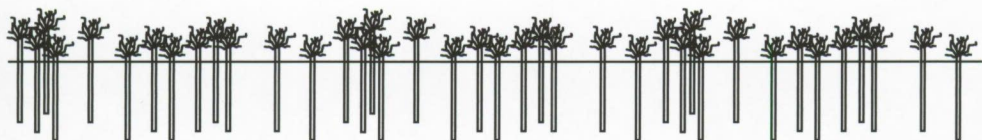
Long – term variability in the *Abra alba* community: importance of physical and biological causes

Abstract

The macrobenthic communities in temperate, shallow coastal waters are characterized by strong seasonal and year-to-year variations in community characteristics. These patterns are investigated in the *Abra alba* community on the Belgian Continental Shelf during nine years (1995 – 2003). During this investigation period, the community tended to return to its orginal state, but it never reached this point. This can be related to the replacement of *Spisula subtruncata* by *Donax vittatus* as dominant bivalve after 1997, and possibly as a result of the climatic shift of 1998. The devision of the study period in an unstable (1995-1997) and a more stable period (1999-2003) coincide with the year 1998. Different causes are believed to be responsible for shifts in the community structure during the unstable period, such as mass recruitment of the bivalve *Spisula subtruncata* (biological cause) and some direct physical causes, like a strong increase of the mud content and temperature fluctuations. All these causes have an effect on the macrobenthic density, diversity and species composition. The mass recruitment of *S. subtruncata* caused a decrease in the density and diversity of the macrobenthos, whereas the increase of mud content was responsible for a crash of the species richness and macrobenthic density. The cold winter could have been responsible for the slow recovery of the *A. alba* community after those disturbances. The unstable period was followed by a few years of higher stability (1999 – 2003), characterized by a cyclic seasonal pattern and the dominance of the tube building polychaete *Lanice conchilega*. The overall seasonal pattern in the study at hand was characterized by high macrobenthic densities in spring and summer, with a decline in autumn towards the end of the winter. Although this cycle differed quantitatively from year-to-ear, the general features have been repeated throughout the stable period. The dominance of *L. conchilega* during the stable period probably had a positive influence on the benthos, due to its habitat structuring characteristics. This study indicates that natural causes could have a drastic impact on the normal year-to-year variability and cyclic seasonal patterns in the marine ecosystem and its ability to recover.

Keywords

Introduction

The macrobenthic communities of shallow coastal waters are subject to a variety of physical and biological disturbances which vary in frequency and intensity, both on a temporal and spatial scale (Turner et al., 1995). Consequently, the community parameters (e.g. species composition, abundance and diversity) are continuously changing (Arntz & Rumohr, 1986; Dörjes et al., 1986). These changes are primarily influenced by seasonality (Buchanan et al., 1974; Eagle, 1975; Rosenberg, 1976; Rachor & Gerlach, 1978; Glémarec, 1979; Bonsdorff & Österman, 1985; Buchanan et al., 1986; Dörjes et al., 1986; Anderlini & Wear, 1992), altering the sea water temperature and primary production. The macrobenthic seasonal pattern in temperate seas is characterized by density maxima at the end of summer and early autumn and density minima at the end of winter and early spring (Ibanez & Dauvin, 1988).

Next to the yearly repeated and thus predictable cycle of seasonality, shallow coastal water macrobenthos shows a large year-to-year variability (Rees & Walker, 1983; Arntz & Rumohr, 1986; Essink & Beukema, 1986; Ibanez & Dauvin, 1988; Beukema et al., 1993; Seys et al., 1994; Fromentin et al., 1997; Ghertsos et al., 2000; Desroy & Retière, 2001). Unpredictability of weather conditions (e.g. cold winters, heavy storms) (Dörjes et al., 1986; Fromentin & Ibanez, 1994), variations in current direction or velocity (Arntz & Rumohr, 1986; Dewarumez et al., 1993) and gradual environmental changes like eutrophication and pollution (Beukema & Cadée, 1986) are physico-chemical processes that can cause shifts in the community parameters. Next to this physical variability, biological variability (Arntz & Rumohr, 1986; Dörjes et al., 1986) such as year-to-year differences in seasonal reproduction, predation, species competition for food and space or inhibition of recruitment (Essink & Beukema, 1986; Desroy & Retière, 2001) can be responsible for a high variability within the macrobenthos. The overall dominance of a species may have a negative effect on other species as a result of competition for space and food, or can exert a positive influence because of the creation of a favourable habitat (Zühlke et al., 1998; Zühlke, 2001). The detection of such influences is of primary importance because these often alter the conditions of the system in an apparently unpredictable way.

Seasonality and year-to-year variation in relation to biological and physical disturbances were investigated within the *Abra alba* community over a nine years sampling period (1995-2003). The *A. alba* community represents the ecologically most important and diverse macrobenthic community in shallow, soft-bottom sediments in the Southern North Sea (Van Hoey et al., 2004; Van Hoey et al., 2005). The most important species of this community are *A. alba, Fabulina fabula, Lanice conchilega, Nephtys hombergii* and *Pectinaria koreni* (Prygiel et al., 1988; Desroy et al., 2002; Van Hoey et al., 2005) and the community descriptors are characterized by a large seasonal and inter-annual variability (Fromentin et al., 1997; Thiébaut et al., 1997).

The aim of this study is to investigate changes in community characteristics (density, diversity and species composition) of the *A. alba* community over a nine years period at one station on the Belgian Continental Shelf in view of detecting causes of major biological changes.

Materials and Methods

Sampling site

The sampling site is situated at the western Coastal Bank area on the Belgian Continental Shelf (BCS) (Van Hoey et al., 2005). The western Coastal Banks form a geomorphologically diverse, soft sedimented shallow marine habitat, extending from the Belgian – French border eastward to Oostende. The sampling site (51° 9.06' N; 2° 32.43' E), at about 9 meter depth, is located near the slope of a sandbank (Den Oever), which consists mostly of fine sandy sediments. This sandbank lies parallel to the Belgian coastline, offshore of the city of Koksijde.

Data origin

The data gathered at the sampling site were collected within the framework of different research projects. During nine years (from 1995 to 2003) the study site was sampled on 48 occasions. These occasions were not evenly distributed over this period: monthly between April 1995 and April 1996 (11 occasions), seasonally from April 1996 till October 1997 (5 occasions), on 8 occasions between March 1999 and October 1999 and monthly (September-April) or biweekly (May-August) between March 2002 and September 2003 (24 occasions).

At each occasion, three Van Veen grabs were collected and sieved after fixation (8% formaldehyde–seawater solution) over a 1 mm mesh-sized sieve. The grain size distribution of a sub sample of each Van Veen grab was measured with a LS Coulter particle size analyser: 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. genera: *Ensis, Harmothoë, Eteone, Pseudocuma, Gammarus* and family: Cirratulidae), a set of 73 taxa (further referred to as species) was used for biological analyses.

Data Analysis

Multivariate analysis

To investigate the gradual multivariate changes within the *Abra alba* community at the sampling site during the nine years period, the dataset on macrobenthic densities was subjected to several multivariate techniques, after fourth root transformation: (1) group-averaging cluster analysis based on the Bray-Curtis similarity (Clifford & Stephenson, 1975), (2) TWINSPAN (Two-Way Indicator Species Analysis) (Hill, 1979) and (3) ordination by non-metric MDS (Multidimensional scaling) (PRIMER 5.2.9). A comparison between the different outcomes of the analyses was done to distinguish between biologically similar groups in time and thus temporal trends. Permutation based hypothesis testing

(ANOSIM), an analogue of univariate ANOVA, was used to test for differences between the multivariate groups.

Univariate analysis

The trends in the *A. alba* community were characterized by means of their species composition, density, diversity and physical habitat (i.e. median grain size and mud content). The univariate measures of diversity were species richness (S) and the exponential form of the Shannon-Wiener index (exp H': N_1) (Whittaker, 1972; Hill, 1973; Magurran, 1988), all calculated with PRIMER 5.2.9. The patterns within these commonly used diversity indices were evaluated regarding their response to different types of disturbances (biological and physical). The correlation between patterns was studied by means of the non-parametric Spearman rank correlation (Conover, 1971).
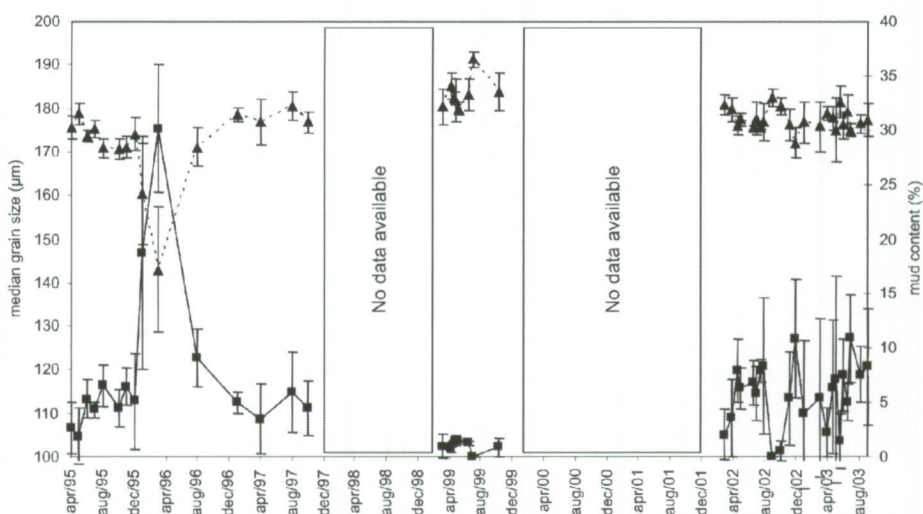
Results

Environmental change

Figure 1. Changes within median grain size (μm) (triangle, dotted line) and mud fraction (%) (square, black line) distribution over the nine years period (average per sampling occasion ± standard deviation).

The sediment type at the sampling site throughout the whole period could be characterised as muddy, fine sandy sediment (Figure 1). Median grain size varied between 170 and 180 μm for most of the sampling dates, except for two sampling periods. The first period was characterized by a strong decline in the median grain size in January and March 1996, with respective median grain sizes of 160 μm and 143 μm. A second anomaly was the slightly higher median grain size in 1999, varying between 180 and 190 μm. The mud content varied between 0 and 10% for most of the sampling

dates, again with two exceptions: a strong increase of the mud content in January and March 1996 (19 and 30% mud) and the constantly lower mud content in 1999 (+1% on average).

The monthly average air temperature at the study site was lowest in winter of 1995 - 1996 (1.5°C-2.6°C) and 1996 - 1997 (2.2°C - 0°C), while in other years the temperature reached a minimum of 4.0°C to 5.0°C (KMI: Royal Meteorological Institute of Belgium). In the summers of 1995 and 1997, a maximum monthly average temperature of more than 20.0°C was reached, whereas in other years the temperature varied between 16.5°C and 19.0°C.

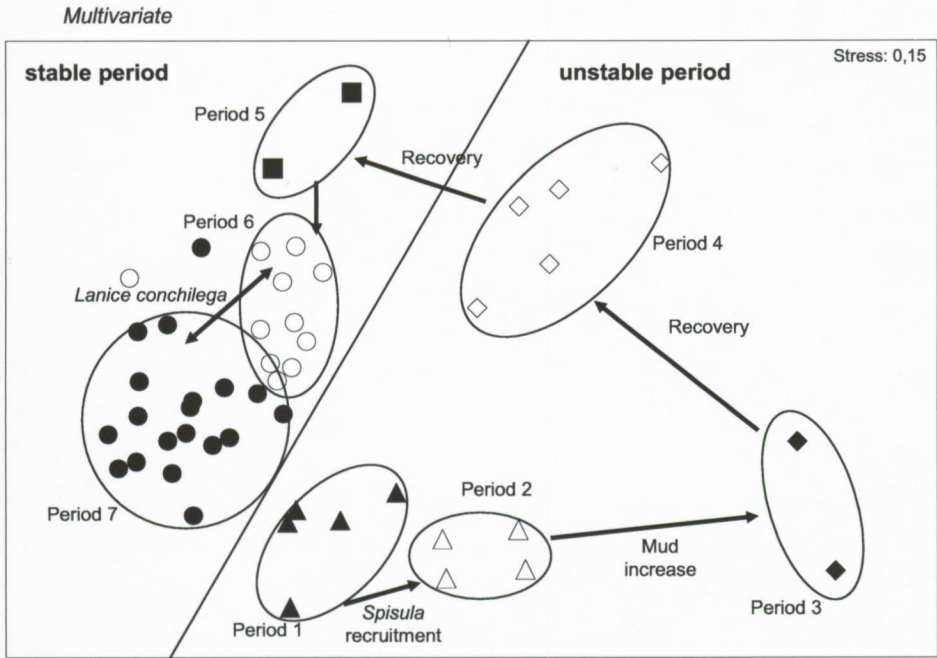## Community structure analysis

Multivariate

Figure 2. MDS–plot (Multidimensional scaling) of the samples, with indication of the seven periods: 1) Black triangle: April 1995 – August 1995, 2) open triangle: October 1995 – January 1996, 3) black rhombus: March – April 1996, 4) open rhombus: August 1996 – October 1997, 5) black square: March – April 1999, 6) open circle: autumn – winter samples of 1999, 2002 and 2003, and 7) closed circle: spring – summer samples of 1999, 2002 and 2003. The causes which were responsible for the changes are indicated.

Different multivariate techniques (summarizing MDS shown in figure 2) revealed a clear pattern of macrobenthic temporal variation. First, a major distinction between the period April 1995 - October 1997 (period 1-4) and the period March 1999 – September 2003 (period 5-7) was detected. The discriminating species responsible for this division was *Donax vittatus* (TWINSPAN indicator for period 1999-2003).

Within the period April 1995 - October 1997, four sub-periods could be distinguished: April 1995 to August 1995 (period 1), October 1995 – January 1995 (period 2), March and April 1996 (period 3) and August 1996 to October 1997 (period 4). These periods all reflect a gradual, though dramatic shift in

species composition from 1995 to 1997. Due to the high variability between the years this period will further be referred to as the unstable period.

During the period March 1999 – September 2003 the following periods could be distinguished: autumn - winter samples (September-April) of 1999-2003 (period 6) and spring - summer samples (May-August) of 1999-2003 (period 7). Only March – April 1999 (period 5) was slightly deviating from this general seasonal pattern. Due to fact that the subdivisions were a reflection of seasonality and due to the stability over the different years, the period March 1999 – September 2003 will further be referred to as the stable period.

The seven periods explained 85% of the multivariate variability within the dataset (ANOSIM: p = 0.0001) and all periods were significantly different from each other (ANOSIM: p = max. 0.0048).

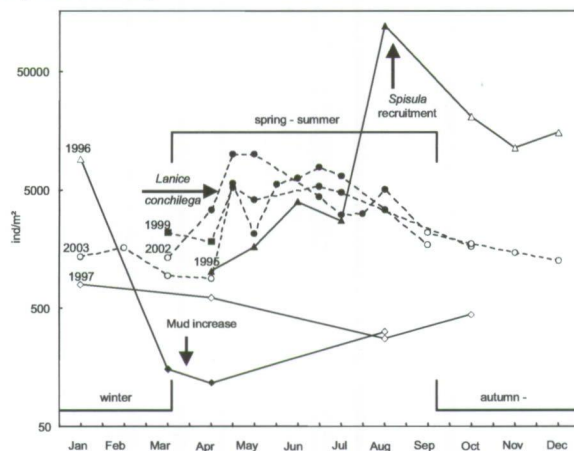*Univariate temporal changes: unstable period*

Density and diversity

Figure 3. Density distribution (ind/m², log transformed) over the different years visualised on a year axis, with indication of the seven periods: period 1 (black triangle); period 2 (open triangle); period 3 (black rhombus); period 4 (open rhombus); period 5 (black square); period 6 (open circle); period 7 (closed circle). The causes which were responsible for the changes are indicated.

In period 1 (April – August 1995) the highest macrobenthic density (120239 ind/m²), caused by an overwhelming recruitment of *Spisula subtruncata* was detected (Figure 3). Afterwards (period 2) the density remained high (20801 and 9066 ind/m²), due to the high densities of *S. subtruncata*, whereas the density of the other macrobenthic species was much lower (1250 – 818 ind/m²). The lowest densities were found in period 3 (March - April 1996), with 151 and 115 ind/m² respectively. During period 4 (August 1996 - October 1997) the density remained low (<1000ind/m²) compared to the same periods in other years.

The species richness (20 to 35 species/0.1m²) and the N_1 diversity index (11.6 - 14) reached their highest values in period 1 (Figures 4 and 5). At the moment of the *S. subtruncata* recruitment (August 1995), the species richness was still high, whereas the N_1 diversity index crashed spectacularly (N_1: 1.3). In period 2 the species richness declined towards 17 species/0.1m², which is comparable to those of the years 1999, 2002 and 2003. The N_1 diversity index remained low (N_1: 1.3 – 1.9). The

species richness crashed in period 3 to 8 – 7 species/0.1m², whereas the N_1 index was around 6 and comparable with the same period in other years. During period 4 the species richness (7 - 12 species/0.1m²) and the N_1 index (N_1: 4.9 – 7.4) remained very low compared to the same periods in other years.
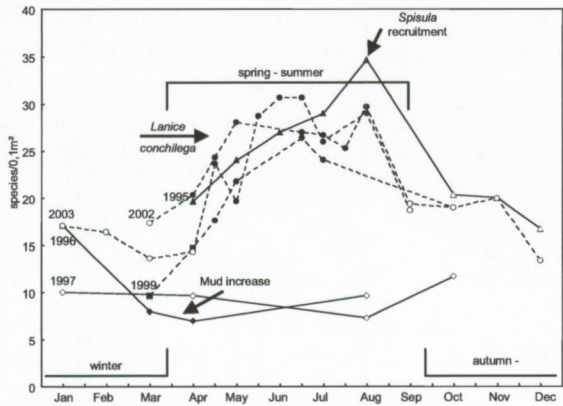

Figure 4. Species richness (species/0.1m²) over the different years visualised on a year axis, with indication of the seven periods: period 1 (black triangle); period 2(open triangle); period 3 (black rhombus); period 4 (open rhombus); period 5 (black square); period 6 (open circle); period 7 (closed circle). The causes which were responsible for the changes are indicated.

Figure 5. N_1- index over the different years visualised one a year axis, with indication of the seven periods: period 1 (black triangle); period 2(open triangle); period 3 (black rhombus); period 4 (open rhombus); period 5 (black square); period 6 (open circle); period 7 (closed circle). The causes which were responsible for the changes are indicated.
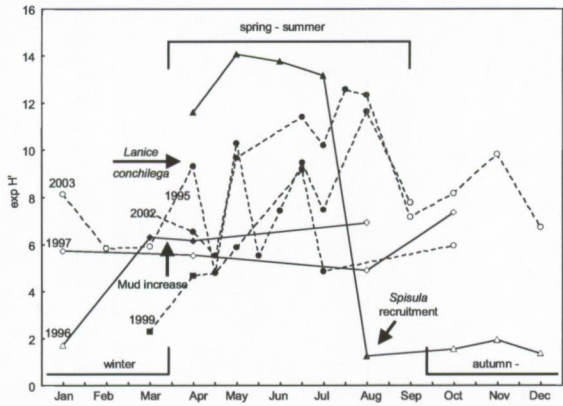
Species composition

During the unstable period, drastic changes in the species composition of the 25 most abundant species in the *Abra alba* community were detected (Figure 6). Before August 1995 most of the 25 dominant species (23) were present, without any one species being dominant (period 1). Changes were observed after the mass recruitment of *S. subtruncata* (period 2): the densities of numerous abundant species decreased (*Magelona johnstoni, Fabulina fabula, Spiophanes bombyx, A. alba* and *Lanice conchilega*). The scavenger *Hinia reticulata* was the only species found in higher densities (>

100 ind/m²) during and after the *S. subtruncata* recruitment, than in the other years (less than 20 ind/m²). The abundances of *Ensis* species, *Mysella bidentata* and Oligochaeta species did not change noticeably during this period. Most changes in species composition occurred in period 3, when only five out of 25 abundant species were present in very low densities (*Nepthys hombergii, Spio filicornis, M. bidentata, S. subtruncata* and Oligochaeta species). During the years 1996 – 1997 (period 4) a slow recovery of the original species composition of the *A. alba* community could be seen. *Spisula subtruncata, N. hombergii* and *S. filicornis* were the dominant species but were found in lower densities compared to other years. Otherwise dominant species, like *L. conchilega* and *F. fabula* did not reoccur instantly, but only did so from April 1997 and October 1997 respectively; *M. johnstoni* reoccurred instantly in low abundance.
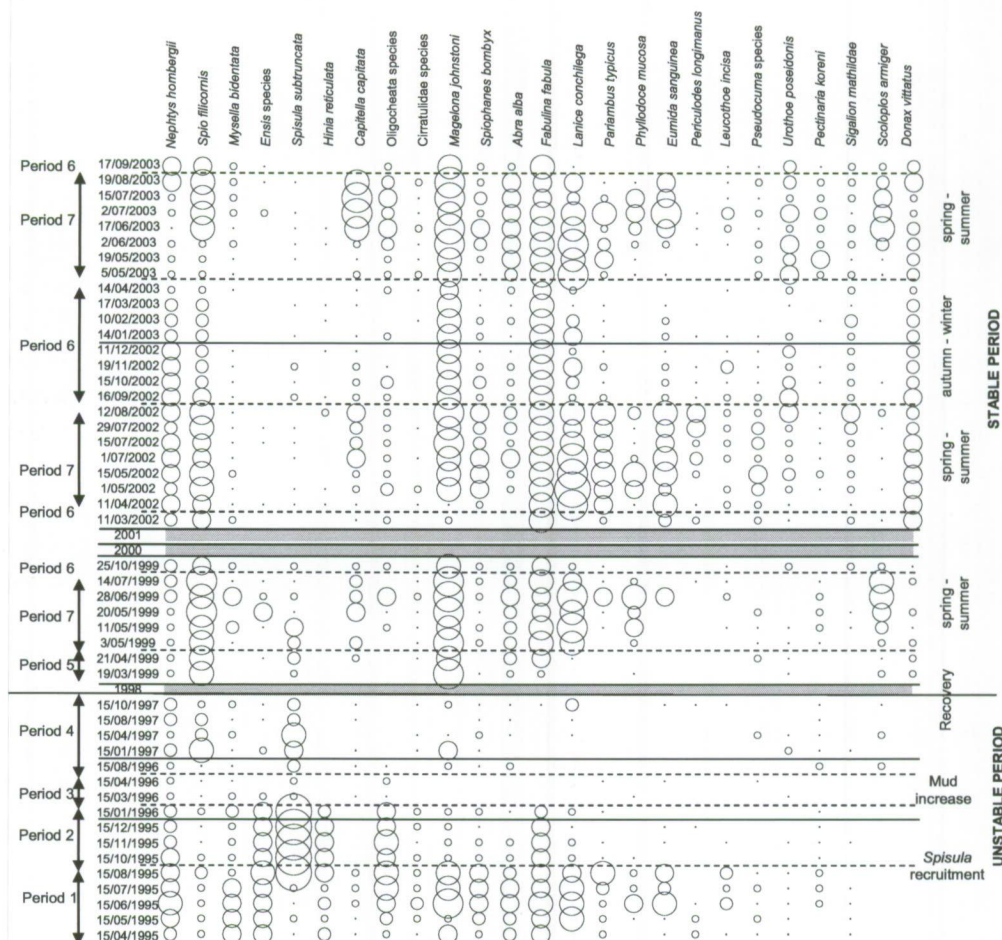

Figure 6. Density distribution of the 25 most abundant species in the *Abra alba* community, with indication of the different periods and the major causes responsible for the changes. The different density classes, with increasing size, are: 0 (no symbol); 1-10 ind/m² (●); 10 -50 ind/m² (o); 50-100 ind/m² (O); 100-250 ind/m² (O); 250-1000 ind/m² (O); 1000-5000 ind/m² (O); > 5000 ind/m² (O). Grey bars indicate periods without sampling occasions.

Univariate temporal changes: stable period

Density and diversity

The highest densities for the period March-April (period 5) were reached in the year 1999, with respectively 2165 and 1832 ind/m² (Figure 3). For the years 1999, 2002 and 2003 (periods 6 – 7) the variability between years was low with a similar pattern of high densities in spring and summer (2120 - 10011 ind/m²), declining in autumn towards the end of the winter (from 2127 ind/m² to 872 ind/m²). The density peak was observed in spring (10011 ind/m² in 1999, 5299 ind/m² in 2002) or early of summer (7825 ind/m² in 2003).

The species richness (10 - 14 species/0.1m²) and N_1 diversity index (2.3 and 4.7) was low in period 5, compared to other years (Figures 4 and 5). The species richness differed strongly between spring – summer (period 6) and autumn – winter (period 7), with an increase from spring to summer (17 – 31 species/0.1m²) followed by a decline in autumn to winter (20 – 14 species/0.1m²). The N_1 index varied strongly during the spring – summer period of 1999, 2002 and 2003 (period 6) between 4.8 and 12.6, with the lowest values (4.8 - 5.5) in early May and the highest (11.6 - 12.3) in August. In autumn and winter 2002 - 2003 (period 7) the N_1 values fluctuated between 9.8 and 5.8, with a decline towards the end of the winter.

Species composition

Period 5 was characterised by a strong dominance of *S. filicornis* and *M. johnstoni*, which remained dominant along with *F. fabula* and *L. conchilega* during the stable period. The stable period was characterised by high densities of the dominant species during spring – summer (period 7), with a decline in autumn – winter (period 6). This pattern was clearly observed for *L. conchilega*, strongly recruiting during every spring (highest in 2002). A lot of species, like *Pariambus typicus, Phyllodoce mucosa* and *Eumida sanguinea* appeared after the *L. conchilega* recruitment and their densities were closely correlated to the density of *L. conchilega* (Spearman rank: p < 0.01). Some crustaceans, like *Perioculodes longimanus, Leucothoe incisa* and *Pseudocuma* species were mainly found when *L. conchilega* was present. Other abundant species (*S. filicornis, C. capitata, F. fabula* and *M. johnstoni*) also reached their highest densities during spring – summer, due to recruitment. A decline in their density occurred in autumn – winter, except for *F. fabula*, for which the density remained high. Two species, *Scoloplos armiger* and *D. vittatus*, were only found in the stable period. *Donax vittatus* was detected for the first time in March 1999 and replaced *S. subtruncata* as relatively large bivalve in 2002 – 2003, whereas *S. armiger* reached its highest densities in 1999 and 2003.

Some common species in the *A. alba* community, as *Pectinaria koreni* and *Nephtys hombergii,* were almost continuously present during the sample period in less fluctuating densities.

Discussion

The *Abra alba* community at our study site showed strong year-to-year differences in its characteristics. The period of investigation can be divided into (1) an unstable period, after a high *Spisula subtruncata* recruitment in August 1995, characterized by low abundances and diversity (1996-1997), and (2) a stable period with a yearly repeated seasonal cycle and a dominance of *Lanice conchilega* (1999-2003). Although during the stable period the community tends to return to its original state (early 1995), it never reaches this point during the observed period. Such continuous pattern within the *A. alba* community was also detected in other areas (Bay of Morlaix, Bay of Seine) or with an indication of a cyclic pattern (Gravelines) (Fromentin et al., 1997). Those observed patterns in the year-to-year variability within the *A. alba* community at different sites (the bay of Morlaix, the bay of the Seine, Gravelines, Liverpool bay) were characterised by more or less rapid and abrupt successions of different groups of species (Eagle, 1975; Rees & Walker, 1983; Dewarumez et al., 1986; Gentil et al., 1986; Dauvin et al., 1993; Olivier et al., 1996; Fromentin et al., 1997; Dauvin, 1998 & 2000; Ghertsos et al., 2000). The temporal patterns of those species can be different from one site to another and species common to two or more sites can show different temporal patterns between sites (Fromentin et al., 1997). In literature, a cyclic pattern of seven to eight years, triggered by a cyclic pattern of cold and mild winters is recorded, which is generally clearer in the northern assemblages due to the higher amplitude of variations of temperature (Rees & Walker, 1983; Fromentin et al., 1997). Those studies demonstrate that temporal fluctuations within the *A. alba* community were greatly regulated by local factors, but were probably also influenced by at least one mesoscale climatic event; the alternation of cold and mild conditions (Fromentin et al., 1996; Fromentin et al., 1997).

During our study period, some causes of temporal variability (strong species recruitment, mud content increase, temperature variability) were observed. These are considered to be responsible for the instability and a higher year-to-year variability during the unstable period compared to the stable period, which showed a clearly repeated seasonal cycle. The shift between the unstable and stable period also coincides with the observed climatic shift in 1998 (Reid et al., 1998; Reid & Edwards, 2001), which was caused by a new, dramatic inflow of Atlantic water masses, causing an increase in primary production. This shift may be of minor importance in coastal areas already characterized by a high primary production, but some temperate and warm-temperate species can react to changes in sea-surface-temperature and changes in food availability (Kröncke et al, 2001). One of the remarkable changes in the species composition of the community during the observed period is the replacement of *Spisula subtruncata* by *Donax vittatus* after 1998 as the dominant bivalve. *Donax vittatus* is characterised as a warm-temperate species (Kröncke et al., 2001) and its appearance is possibly linked to the climatic shift in 1998.

Unstable period: year-to-year variability due to biological and physical causes

Recruitment, competition, changes in the mud content and probably also the occurrence of a cold winter, all had a drastic impact on the *A. alba* community during the unstable period. Those causes

comprise both physical (current direction or velocity, weather conditions and changes in sedimentology) and biological components (species competition, recruitment differences and predation), taking into account that a lot of the biological causes are triggered by underlying physical conditions (e.g. recruitment is influenced by currents, see next paragraph). Compared to the importance of biotic interactions in structuring stable communities, unstable communities tend to be mainly structured by physical causes (Fromentin et al., 1996).

Biological causes: recruitment and competition

It can be suggested that the yearly variability in the community structure is partly influenced by variation in the larvae and species transport with the prevailing currents and winds. The *A. alba* community at the Belgian Continental shelf belongs to the fine sand *A. alba* community spreading from the coast of Calais, over Belgium to the Netherlands (Van Hoey et al., 2005). This area is characterized by frequent changes of wind- and current direction (Trentesaux et al., 1994). Hence, changes in the larval transport between the English Channel and the southern part of the North Sea are common (Fromentin et al., 1997), inducing an important spatial heterogeneity in the recruitment (Dewarumez et al., 1993), and eventually leading to variation in adult population size (Feller et al., 1992). Although the exchange of larvae between neighbouring sites is very important, secondary settlement or recruit emigration cannot be ignored when hydrodynamics are particularly intense (Desroy & Retière, 2001). Furthermore, recruit densities also depend on the biological interactions in the sediment (predation, spatial and trophic competition, bioturbation). Finally, not every species recruits every year, nor is the recruitment always successful or of the same intensity.

A pattern of moderate recruitment followed by low post-settlement mortality of recruits should be most frequent, but massive recruitment followed by high mortality rates do occur (Desroy & Retière, 2001). At our sampling site, massive recruitment events followed by a high post-settlement mortality is most pronounced in the case of *S. subtruncata* and *L. conchilega*. However, species, like *Fabulina fabula*, *Nephtys hombergii* and *Donax vittatus*, show a rather moderate recruitment and a more or less constant adult population. *Nephtys hombergii*, for example, is known as a conservative species with litte variation in abundance (Buchanan et al., 1974).

According to the study of Fromentin et al. (1996), the intensity of the recruitment has more influence on the community structure than the identity of the dominant species. An abundant and dominant species may have a negative effect on other species as a result of competition for space and food, as is probably the case for *S. subtruncata* in the present study. The highly variable recruitment of this species (Fraschetti et al., 1997; Degraer et al., submitted), being extremely successful in August 1995, caused a steep decrease of the N_1 – diversity index in the present study. Due to the presence of high numbers of recruits of *S. subtruncata,* covering the sediment with a one centimeter thick layer (Degraer et al., submitted), a strong competition for space and food with a consequent decrease in density of other species might be hypothesized. Indeed, successful recruitment events can induce biological alterations in the habitat, which may lead to changes in the overall community structure (Turner et al., 1995). Because of the high post-settlement mortality of *S. subtruncata* between August and October (increasing the quantity of decomposing organisms) scavengers, like the gastropod *Hinia*

reticulata may have been attracted to the increasing food resource. There are also other examples of species which could have a negative influence on other species (e.g. deposit feeding organisms, like *Abra alba* and *Pectinaria koreni*), reducing the stability of the habitat and prevented the settlement of other spat due to their bioturbating feeding activities (Rhoads & Young, 1970; Eagle, 1975). In contrast with species having negative impacts, the dominance of a species, like *L. conchilega* can exert a positive impact because of the creation of a favourable habitat (Zühlke et al., 1998; Zühlke, 2001), as observed during the stable period (see the discussion section about the stable period).

Physical causes: mud content, temperature

Direct physical causes, like changes in sedimentology, can trigger drastic changes in the community structure, as seen in January - April 1996 when the mud content increased from 5 to 30%. This period was characterised by a remarkable decrease of the species richness and macrobenthic density (N_1 was not affected). An ephemeral increase of the sediment's mud content can be expected in wintertime, when stronger hydrodynamical forces (e.g. winter storms) increase the suspended mud concentration in the water column and settlement of the fine material during hydrodynamically calm periods is possible (Geo et al., 1994). The increase of the fine materials in the sediment might then negatively affect the macrobenthos of the *A. alba* community, usually occurring in a fine sandy sediment with low mud concentrations (Van Hoey et al., 2005). A lot of species, especially filter feeding organisms, cannot survive when covered by a mud layer (Shackley & Collins, 1984). As a result the densities of *S. subtruncata* and a lot of other species drastically decreased. Furthermore, in March '96, a high number of recently dead or dying *Ensis* was found on top of the sediment. Because of the high biomass of decomposing bivalves (*S. subtruncata* and *Ensis*), the oxygen level in the sediment decreased and an almost completely anoxic sediment with a strong rotting smell was found at that station in March '96 (pers. obs.). After March '96, the sediment's mud concentration slowly returned to its original level of about 5%, but, compared to the 7-8 cm thick oxygenated top-layer of the sediment before January '96, the oxygenated level was never more than 2 cm after March '96 (pers. obs.). The conditions for the *A. alba* community only started to ameliorate again after April '96, when recruits of several species started to invade the sampling location.

Besides changes in the sedimentology, climatic changes, like temperature variability and storms, can lead to irregularities and possibly also drastic changes in the benthic communities (Rachor & Gerlach, 1978; Dörjes et al., 1986; Rees & Walker, 1983, Fromentin et al., 1997). Temperature is known to significantly impact recruitment and persistence of the population, especially in the northern sites where the amplitude of the temperature variability is greater (Fromentin et al., 1997). The abundance of some species at Gravelines and at the Bay the Seine was correlated to the alternation of cold and mild years (Fromentin et al., 1996). Cold winters reduced the survival of species and result in reduced diversity compared to warm winters (Buchanan et al., 1978; Buchanan & Moore, 1986). Temperature also affects the timing of spawning, settlement and growth of the young stages (Bhaud, 1993). During the study at hand, low temperatures were found in the winter of 1996 and 1997 (air temperature of 1.5° and 0°C). Those low temperatures observed in those years at the Belgian Coast, were also

observed along the French coast (Woehrling et al., 2005). The cold winter of 1996 and especially those of 1997 could be responsible for the unsuccessful recruitment, causing a slow recovery within the *A. alba* community and thus low abundances, species richness and diversity in the period August 1996 – October 1997.

Stable period: seasonal patterns

During the years 1999 – 2003 stable seasonal patterns were observed in the present study. In North European seas, the macrobenthic populations generally show a cyclic seasonality in abundance, which is characterised by maxima at the end of summer and beginning of autumn and minima at the end of the winter and beginning of spring (Ibanez & Dauvin, 1988). The seasonal pattern in our study (1999 - 2003) is characterised by high densities in spring (5000 - 10000 ind/m²) and summer (2734 - 7825 ind/m²), with a decline in autumn towards the end of the winter (from 2127 ind/m² to 872 ind/m²). Although this cycle may differ quantitatively from year-to-year, the general features were repeated throughout the whole stable period. The underlying processes are the following (Beukema, 1974): (1) from spring to summer and autumn a net increase in density due to settlement of larvae and immigration, (2) from autumn to winter and spring a net loss due to the predominance of mortality and emigration. The period of recruitment, from early spring to the end of the summer or early autumn (Dörjes et al., 1986; Ibanez & Dauvin, 1988; Dauvin, 1990), is believed to be caused by an increased influx of organic matter to the sediment, due to an increased primary and secondary production within the plankton (Bonsdorff & Österman, 1985). Yet, even though the macrobenthic environmental conditions (e.g. temperature, sediment organic matter content, planktonic production and hydrodynamics) ameliorate from early spring onwards (Dauvin, 1990), the settlement of planktonic larvae does not occur at the same time for the different species (Feller et al., 1992): spring – summer is known to be the prime period for polychaete recruitment, while the main bivalve recruitment takes place in summer (Buchanan et al., 1986).

There is also a strong seasonal fluctuation of the species richness and diversity (N_1), with the highest values in summer (S: 25 - 35; N_1: 7.5 - 14) and the lowest in winter (S: 13 - 20; N_1: 2.3 - 9.8). Different processes can be responsible for this kind of variability, such as migration of species and/or the presence of a group of temporary species, which may be absent in winter (for winter-summer 2002 - 2003: *P. mucosa*, *Gattyana cirrosa*, *Notomastus latericeus*, and some crustacean species). However, an effect of the sampling method could play a role as well. In summer, there is not only an increase in the density of the dominants, but also of the temporary or rarer species. Thus, the chance to collect those rarer species increases in summer. This increased chance will consequently give a superficial impression of higher diversity (Buchanan et al., 1978). Most probably, a combination of these factors explains the seasonal diversity pattern in the present study.

The more fluctuating pattern in the N_1 index, which is primarily affected by species in the middle of the species rank sequence, is caused by a set of species which became alternately dominant (Buchanan et al., 1978). A dominance of a wide set of species, like in April – July 1995, leads to a high N_1 index. When one species, like *Lanice conchilega* in May 2002 and 2003 strongly dominated, a drop in the N_1

index occurred, whereas the species richness increased. This tube building polychaete is a dominating species during the stable period and could have a positive effect on the community structure, because this species creates positive conditions for other macrobenthic species (Zühlke et al, 1998; Zühlke, 2001). Therefore, it is possible that the occurrence and density of some species within the *A. alba* community were influenced by the *L. conchilega* tube aggregations. The distribution patterns and occurrences of some species, like *Pariambus typicus*, *Eumida sanguinea*, *P. mucosa*, *Periculodes longimanus*, *Leucothoe incisa* and *Pseudocuma* species in the present study are closely correlated to the density of *L. conchilega*, which did not have a negative influence on the densities of the other macrobenthic species or on the species richness. *Lanice conchilega* could have had a positive influence on the *A. alba* community characteristics during the stable period.

Conclusion

Several causes (high *Spisula subtruncata* recruitment, increase of mud content, cold winter) were responsible for the high variability in the *Abra alba* community characteristics during the unstable period (1995 - 1997). The mass recruitment of *S. subtruncata* caused a decrease in the density and diversity of the macrobenthos, whereas the increase of mud content was responsible for a crash of the species richness and macrobenthic density. The cold winter could have been responsible for the slow recovery of the *A. alba* community after those disturbances. This period was followed by some years of more stability, characterized by the dominance of *L. conchilega* and by cyclic seasonal patterns. It can be concluded that natural causes can have a drastic impact on the year-to-year variability and cyclic seasonal patterns normally observed in the macrobenthic *A. alba* community.

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