Temporal variability in the Abra alba community
determined by global and local events

Gert Van Hoey a,b,⁎, Magda Vincx b, Steven Degraer b

a Netherlands Institute of Ecology, Centre for Estuarine and Marine Ecology, Korringsweg 7, P.O. Box 140, 4400 AC Yerseke, The Netherlands
b Ghent University (UGent), Biology Department, Marine Biology Section, Sterre Campus, Krijgslaan 281-S8, B-9000 Gent, Belgium

Received 29 September 2006; accepted 27 February 2007
Available online 19 March 2007

Abstract

Macrobenthic communities in temperate, shallow coastal waters are characterised by strong seasonal and year-to-year variations in community characteristics. These temporal variations were investigated in the Abra alba community on the Belgian Continental Shelf over a period of nine years (1995–2003). During this period, the community did not show a cyclic pattern, but a shift between the years 1995–1997 and 1999–2003 that was possibly triggered by changes in the hydroclimatic state of the North Sea and was reflected by a small shift of the dominant species in the A. alba community. In the years 1995–1997, the temporal pattern was dominated by strong year-to-year differences, coinciding with different successive events (strong recruitment, sedimentological changes, cold winters). Therefore, these years were characterised as the unstable period. Such events may affect the macrobenthic density, diversity and species composition. The mass recruitment of S. subtruncata may have been responsible for an initial 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 in the winter of 1996. After those events, the A. alba community needed time to recover (1996–1998). The recovery was possibly retarded by a slow amelioration of the habitat conditions, unsuccessful recruitment and the occurrence of a cold winter. This period was followed by some years in which the seasonal dynamics in the community exceeded the lower year-to-year variability and therefore these years were characterised as the stable period. The seasonal dynamics in the study were characterised by high macrobenthic densities and diversity in spring and summer, followed by declines in the autumn-winter period. The conclusion is that mainly local factors were responsible for the short-term variations within the community, whereas global events (hydroclimatic, cold and mild conditions) caused the long-term changes.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Ecosystem disturbance; Temporal variability; Hydroclimatic shift; Benthos; Abra alba community; Coastal zone; Belgian Continental Shelf

1. 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 constantly changing (Arntz and Rumohr, 1986; Dörjes et al., 1986). These changes are primarily influenced by seasonality (Buchanan et al., 1974, 1986; Eagle, 1975; Rosenberg, 1976; Rachor and Gerlach, 1978; Glémarec, 1979; Bonsdorff and Österman, 1985; Dörjes et al., 1986;
Anderlini and Wear, 1992), altering the seawater temperature and primary production. The macrobenthic seasonal pattern in temperate seas is characterised by density maxima at the end of summer and early autumn and density minima at the end of winter and early spring (Ibanez and Dauvin, 1988).

Besides the yearly repeated and thus predictable cycle of seasonality, shallow coastal water macrobenthos shows a large year-to-year variability (Rees and Walker, 1983; Arntz and Rumohr, 1986; Essink and Beukema, 1986; Ibanez and Dauvin, 1988; Beukema et al., 1993; Seys et al., 1994; Fromentin et al., 1997; Ghertsos et al., 2000; Desroy and Retière, 2001). Unpredictability of weather conditions (e.g. cold winters, heavy storms) (Dörjes et al., 1986; Fromentin and Ibanez, 1994), variations in current direction or velocity (Arntz and Rumohr, 1986; Dewarumez et al., 1994), variations in temperature and primary production. The macrobenthic community in shallow soft-bottom sediments in the southern North Sea (Van Hoey et al., 2004, 2005) are characterised by a large seasonal and inter-annual variability (Fromentin et al., 1997; Thiébaut et al., 1997; Desroy et al., 2002; Beukema, 1986; Ibanez and Dauvin, 1988; Beukema et al., 1988; Thiébaut et al., 1997; Desroy et al., 1993; Seys et al., 1994; Fromentin et al., 1997; Ghertsos et al., 2000; Desroy and Retière, 2001). The most important species of this community is the ecologically most important and diverse macrobenthos within the macrobenthos. The detection of such influences is of primary importance because they 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-year sampling period (1995–2003) at one station on the Belgian Continental Shelf. 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, 2005). The most important species of this community are *A. alba*, *Fabulina fabula*, *Lanice conchilega*, *Nephtys hombergii* and *Pectinaria koreni* (Pyrgiel et al., 1988; Thiébaut et al., 1997; Desroy et al., 2002; Van Hoey et al., 2005) and the community descriptors are characterised by a large seasonal and inter-annual variability (Fromentin et al., 1997; Thiébaut et al., 1997).

The aim of this study was to investigate temporal (seasonal and year-to-year) changes in community characteristics (density, diversity and species composition) of the *A. alba* community, and to detect causes of these major biological changes.

2. Material and methods

2.1. 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 m 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 village of Koksijde.

2.2. Data origin

The data gathered at the sampling site were collected within the framework of different research projects. For nine years (from 1995 to 2003), the study site was sampled on 48 occasions. These occasions were not evenly distributed over the investigated period: monthly between April 1995 and April 1996 (11 occasions), seasonally from April 1996 to 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 sampling, 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 of species to genera or family level, because of inconsistent identification throughout the different studies (e.g. genera: *Ensis*, *Harmothoe*, *Eteone*, *Spio Pseudocuma*, *Gammarus* and family: *Cirratulidae*), a set of 73 taxa (further referred to as species) was used for biological analyses.

2.3. Data analysis

2.3.1. Multivariate analysis

To investigate the gradual changes within the *Abra alba* community at the sampling site over the nine-year 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 and 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.

2.3.2. Univariate analysis

The trends in the *A. alba* community were characterised 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': N1) (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).

3. Results

3.1. Environmental change

The sediment type at the sampling site throughout the period could be characterised as muddy, fine sand (Fig. 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 characterised by a strong decline in the median grain size in January and March 1996, with median grain sizes of 160 μm and 143 μm, respectively. 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 the 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) (Fig. 1). 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.

Fig. 3. Density distribution (ind m⁻², logarithmic scale) over the various years in (a) the unstable period and (b) the stable period 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 (black circle). Possible causes of the changes are indicated.

Fig. 4. Species richness (species per 0.1 m²) over the various years in (a) the unstable period and (b) the stable period 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 (black circle). Possible causes of the changes are indicated.
3.2. Community structure analysis

3.2.1. Multivariate analysis
Different multivariate techniques (summarising MDS shown in Fig. 2) revealed a clear pattern of macrobenthic temporal variation. First, a major distinction was detected between the period April 1995 – October 1997 (period 1 – 4) and the period March 1999 – September 2003 (period 5 – 7). The discriminating species responsible for this division was Donax vittatus (TWINSPAN indicator for period 1999 – 2003). Within the period April 1995 – October 1997, four subperiods 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: March – April 1999 (period 5), 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 deviated slightly from this general seasonal pattern. Because 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).

3.2.2. Univariate temporal changes: unstable period

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

The species richness (20 to 35 species per 0.1 m$^2$) and the N1 diversity index (11.6 – 14) reached their highest values in period 1 (Figs. 4 and 5). At the moment of the S. subtruncata recruitment (August 1995), the species richness was still high, whereas the N1 diversity index crashed spectacularly (N1: 1.3). In period 2, the species richness declined towards 17 species per 0.1 m$^2$, which is comparable to those of the years 1999, 2002 and 2003. The N1 diversity index remained low (N1: 1.3 – 1.9). The species richness crashed in period 3 (March – April 1996), with 151 and 115 ind m$^{-2}$, whereas the N1 index was around 6 and comparable to the same period in other years. During period 4, the species richness (7 – 12 species per 0.1 m$^2$) and the N1 index (N1: 4.9 – 7.4) remained very low compared to the same periods in other years.

b. Species dominance
During the unstable period, drastic changes in the species dominance of the 25 most abundant species in the Abra alba community were detected (Fig. 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 m\(^{-2}\)) during and after the *S. subtruncata* recruitment, than in the other years (<20 ind m\(^{-2}\)). The abundances of *Ensis* species, *Mysella bidentata* and Oligochaeta species did not change noticeably during this period. Most changes in species dominance occurred in period 3, when only five out of 25 abundant species were present in very low densities (Nepthys hombergii, Spio species, *M. bidentata*, *S. subtruncata* and Oligochaeta species). During the years 1996 – 1997 (period 4) a slow recovery of the original species dominance of the *A. alba* community was observed. *Spisula subtruncata*, *N. hombergii* and *Spio* species were the dominant species in lower densities compared to other years. Otherwise dominant species, such as *L. conchilega* and *F. fabula* did not re-occur instantly, but only did so from April 1997 and October 1997, respectively; *M. johnstoni* re-occurred instantly in low abundance.

### 3.2.3. Univariate temporal changes: stable period

#### a. Density and diversity

The highest densities for the period March–April were reached in 1999 (period 5), with 2165 and 1832 ind m\(^{-2}\),
respectively (Fig. 3). For 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 m\(^{-2}\)), declining in autumn towards the end of the winter (from 2127 ind m\(^{-2}\) to 872 ind m\(^{-2}\)). The density peak was observed in spring (10011 ind m\(^{-2}\) in 1999, 5299 ind m\(^{-2}\) in 2002) or early summer (7825 ind m\(^{-2}\) in 2003).

In period 5, the species richness (10 – 14 species per 0.1 m\(^{2}\)) and \(N_1\) diversity index (2.3 and 4.7) were low, compared to other years (Figs. 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 per 0.1 m\(^{2}\)) followed by a decline in autumn to winter (20 – 14 species per 0.1 m\(^{2}\)). The \(N_1\) index varied strongly (between 4.8 and 12.6) during the spring – summer period of 1999, 2002 and 2003 (period 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 winter.

b. Species dominance

Period 5 was characterised by a strong dominance of Spio species and M. johnstoni, which remained dominant along with F. fabula and L. conchilega during the stable period (Fig. 6). 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, which strongly recruited during every spring (highest in 2002). Many species, such as 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, such as the amphipods Periuloculides longimanus, Leucothoe incisa and the cumacean Pseudocuma species, were mainly found when L. conchilega was present. Other abundant species (Spio species, 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, whose 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, such as Pectinaria koreni and Nephtys hombergii, were almost continuously present during the sample period in less fluctuating densities.

4. Discussion

The Abra alba community at the study site on the Belgian Continental Shelf was characterised by strong seasonal and year-to-year variations during the period investigated. The year-to-year differences dominated the temporal pattern during the first years (1995 – 1997), coinciding with different biological and physical events (strong recruitment, sedimentological changes, cold winters) and, therefore, those years were characterised as the unstable period. From 1999 onwards (1999 – 2003) seasonal dynamics in the community exceeded the lower year-to-year variability and therefore those years were characterised as the stable period. Although during the stable period the community structure was similar to that found in 1995, it never reached exactly the same state during the observed period. Such a continuous pattern, or with a slight indication of a cyclic pattern, within the A. alba community, was also detected in other areas (Bay of Morlaix, Bay of Seine, Gravelines) (Fromentin et al., 1997) and related to more or less rapid and abrupt successions of different groups of species (Eagle, 1975; Rees and Walker, 1983; Dewarumez et al., 1986; Gentil et al., 1986; Daunin et al., 1993; Olivier et al., 1996; Fromentin et al., 1996, 1997; Dauvin, 1998, 2000; Ghertsos et al., 2000). In the literature, a cyclic pattern of seven to eight years, triggered by a cyclic pattern of cold and mild winters is recorded. This pattern is generally clearer in the northern assemblages due to the higher amplitude of variations of temperature (Rees and Walker, 1983; Fromentin et al., 1997). Such conclusions for the A. alba community at our study site cannot be made, based on only nine years of observation and the occurrence of one cold winter period (1996 and 1997). What was observed during our investigation period was a shift in the community structure between the unstable and stable period. This shift coincided with the regime shift in the North Sea observed in 1998 (Kröncke et al., 1998; Reid et al., 1998, 2001; Weijerman et al., 2005), which was related to changes in the hydroclimatic state of the North Sea caused by changes in the North Atlantic Oscillation. This resulted in an increase in sea surface temperature, changes in sediment structure and food availability (Reid and Edwards, 2001). Such a shift may be of minor importance in coastal areas already characterised by high food availability, 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 *A. alba* community during the observed period was the replacement of *Spisula subtruncata* by *Donax vittatus* after 1998 as the dominant bivalve. *D. vittatus* is characterised as a warm-temperate species (Kröncke et al., 2001) and its dominance is possibly linked to the regime shift in 1998 or maybe an effect of global warming and the northward migration of warm-temperate species (Reid and Edwards, 2001). A small shift in the dominant species, possibly triggered by changes in the hydroclimatic state of the North Sea, may have been responsible for the non-cyclic temporal pattern of the *A. alba* community at our study site. Besides this global event, some local biological and physical events were observed that may have been responsible for the observed year-to-year variability within the *A. alba* community at our study site. These events taken place very shortly after each other, probably contributing to the strong year-to-year variability within the *A. alba* community, characterised by drastic changes in macrobenthic density, diversity and species composition.

An abundant species may have a negative effect on other species as a result of competition for space and food, as was probably the case for *S. subtruncata* in the present study. The highly variable recruitment of this species (Fraschetti et al., 1997), being extremely successful in August 1995, caused a steep decrease of the *N*$_1$ — diversity index and changes in the species composition. Due to the presence of high numbers of recruits of *S. subtruncata*, covering the sediment with a one-cm thick layer (Degraer, pers. obs.), a strong competition for space and food with a consequent decrease in density of other species was observed (i.e. in this study for example *Magelona johnstonii*, *Lanice conchilega*, *Spio spp.*). In contrast, some species, e.g. scavengers (the gastropod *Hinia reticulata* in this study), were attracted to the increasing food resource due to the high post-settlement mortality of *S. subtruncata* between August and October. Indeed, successful recruitment events can induce biological alterations in the habitat that may lead to changes in the overall community structure (Turner et al., 1995), as was observed in the present study. However, the statement of the study of Fromentin et al. (1996) that the intensity of the recruitment has more influence on the community structure than on the identity of the dominant species was not confirmed by the present results. Some species have a negative influence on other species (e.g. *S. subtruncata* in the present study and species such as *A. alba* and *Pectinaria koreni*, due to their bioturbating feeding activities) (Rhoads and Young, 1970), while other species such as *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 further).

This biological impact on the *A. alba* community was immediately followed by changes in the sedimentology in January – March 1996, when the mud content increased from 5 to 30%. An ephemeral increase of the sediment’s mud content can be expected in winter, 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 (Gao et al., 1994). The increase of fine materials in the sediment might then negatively affect the macrobenthos of the *A. alba* community, which usually lives in fine sandy sediment with low mud concentrations (Van Hoey et al., 2005). Many species, especially filter feeding organisms, cannot survive when covered by a mud layer (Shackley and Collins, 1984). As a result, the densities of *S. subtruncata* and many other species drastically decreased, with a consequent decrease in species richness and macrobenthic density. Furthermore, in March 1996, a large 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 1996 (pers. obs.). The crash in species richness and density in spring 1996 will have been due to the high mud content and low oxygen level in the sediment.

The recovery of the *A. alba* community after these events took at least 2 years and this period was characterised by low densities, species richness and diversity. The slow recovery may have been linked to the slow amelioration of the habitat conditions, unsuccessful recruitment and the occurrence of a cold winter. The mud concentration of the sediment slowly returned to its original level of about 5% after March 1996, but, compared to the 7–8 cm thick oxygenated top-layer of the sediment before January 1996, the
oxygenated level was never more than 2 cm after March 1996 until 1997 (pers. obs.). During this recovery period there was no sign of successful recruitment. However, the recruitment success and intensity depends on various factors such as the prevailing currents (Dewarumé et al., 1993; Trentesaux et al., 1994; Fromentin et al., 1997) and the biological interactions in the sediment (predation, spatial and trophic competition, bioturbation) (Desroy and Retière, 2001). Temperature is known to significantly impact recruitment and persistence of the population, especially at higher latitudes where the amplitude of the temperature variability is larger (Fromentin et al., 1997). Cold winters reduce the survival of species and result in reduced diversity compared to warm winters (Buchanan et al., 1978; Buchanan and Moore, 1986). Temperature also affects the timing of spawning, settlement and growth of the young stages. During the present study, low temperatures were found in the winters of 1996 and 1997 (air temperature of 1.5° and 0 °C). Similarly, low temperatures were also observed along the French coast in that period, causing changes in the community structure (Fromentin and Ibanez, 1994; Fromentin et al., 1997; Woehrling et al., 2005). This indicates that the occurrence of cold and mild winters acts on a wide scale, as also confirmed in the study of Beukema et al. (1996). It is concluded that these facts were responsible for the delayed recovery of the benthos at our study site.

4.2. Stable period: seasonal patterns

During the years 1999 – 2003, relatively stable seasonal patterns were observed. 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 and Dauvin, 1988). The seasonal pattern in our study (1999 – 2003) was characterised by high densities in spring (5000 – 10000 ind m⁻²) and summer (2734 – 7825 ind m⁻²), with a decline in autumn towards the end of the winter (from 2127 ind m⁻² to 872 ind m⁻²). Although this cycle varied 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, and (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 and 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 and Österman, 1985). Yet, even though the macrobenthic environmental conditions (e.g. temperature, sediment organic matter content, planktonic production and hydrodynamics) improve 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 was also a strong seasonal fluctuation of the species richness and diversity (N₁), with the highest values in summer (S: 25 – 35; N₁: 7.5 – 14) and the lowest in winter (S: 13 – 20; N₁: 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: Phyllodoce mucosa, Gattyana cirrosa, Notomastus latericeus, and some crustacean species). However, an effect of the sampling method could have played a role as well. In summer, there was 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 increased in summer, which consequently may have given 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 N₁ index, which is primarily affected by species in the middle of the species rank sequence, was caused by a set of species which became alternately dominant (Buchanan et al., 1978). A dominance of a wide set of species, such as in April – July 1995, leads to a high N₁ index. When one species, such as Lanice conchilega in May 2002 and 2003, strongly dominated a drop in the N₁ index occurred, whereas the species richness increased. This tube-building polychaete was a dominating species during the stable period and probably had a positive effect on the community structure, because this species creates positive conditions for other macrobenthic species (Zühlke et al., 1998; Zühlke, 2001; Callaway, 2006). Therefore, it is possible that the occurrence and density of some species within the A. alba community was influenced by the L. conchilega tube aggregations. The distribution patterns and occurrences of some species, such as Pariambus typicus, Eumida sanguinea,
P. mucosa, Periculodes longimanus, Leucothoe incisa and Pseudocuma species in the present study, were significantly correlated with the density of L. conchilega. So, L. conchilega could have had a positive influence on the A. alba community characteristics during the stable period, due to its habitat-structuring capacity.

5. Conclusion

Some successive events (high Spisula subtruncata recruitment, increase of mud content, cold winter) may be responsible for the variability in the temporal pattern of the Abra alba community 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. After those events, the A. alba community needed time to recover (1996 – 1998). This recovery was possibly slowed down by a slow amelioration of the habitat conditions, unsuccessful recruitment and the occurrence of a cold winter. This period was followed by some years of more stability, characterised by the dominance of L. conchilega and by cyclic seasonal patterns. During the investigated period, the community did not show a cyclic pattern, but rather a shift between the unstable and stable period, possibly triggered by changes in the hydroclimatic state of the North Sea. This shift was reflected by a small shift of the dominant species in the A. alba community. It is concluded that mainly local factors (recruitment differences, sedimentological changes) were responsible for the short-term variations within the community, while global events (hydroclimatic, cold and mild conditions) caused the long-term variability.

Acknowledgements

The major part of the data were obtained through different research projects: (1) ‘Structural and Functional Biodiversity of North Sea ecosystems’ funded by the Belgian Federal Science Policy Office (Belgium; project number: MN/DD40), (2) ‘Ecological adjustment of a coastal defence project’ funded by AMINAL (Flemish administration responsible for environment, nature, land and water management, department Nature; project number: AN/1995/nr3) and AWK (the Administration of Waterways and Coast, Flemish Government; dossier number: 97190). The first author acknowledges a grant from the Institute for the Promotion of Innovation through Science and Technology in Flanders (IWT, Flemish Government). We wish to thank everybody who assisted in collecting and analysing the macrobenthos samples (all people of the Marine Biology Section), the sedimentological samples (e.g. Danielle Schram) and who made improvements to earlier drafts (Sofie Vandendriessche). We also want to thank the crew of RV ‘Zeeleeuw’ for their assistance during the sampling campaigns.

References


