CHAPTER 2

TEMPORAL CHANGES WITHIN THE *LANICE CONCHILEGA* COMMUNITY (NORTH SEA, BELGIAN COAST)

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ABSTRACT

The macrobenthos of shallow coastal habitats is subject to a variety of physical and biological disturbances, varying in frequency and intensity, as well on a temporal and spatial scale. Consequently, the macrobenthic parameters (species composition, abundances, etc.) are continuously changing. To evaluate the ecological value of the *Lanice conchilega* community, knowledge on its temporal variation is indispensable. Furthermore, because of the possibility of recolonization by means of recruitment via the planktonic stages of many macrobenthic species, knowledge on the period of recruitment of the species allows to decrease the negative impact of the planned coastal defence works. The macrobenthic temporal variation and recruitment was studied in two stations over a 2.5 yr study period (April '95 – October '97). From Spring till Summer '95, a general amelioration of the community's condition was attributed to the recruitment of, at least, the dominant species. Though the polychaete *Notomastus latericeus*, the bivalves *Abra alba* and *Tellina fabula*, and the gastropod *Hinia reticulata* showed no recruitment, recruitment of all other dominant species was detected. Recruitment of the polychaetes mainly occurred between April and August '95, while amphipode and bivalve recruitments were observed between July and October '95. An overwhelming recruitment of *Spisula subtruncata* with densities up to 150000 ind m^{-2}, taking place in August '95, possibly caused a general decrease of the number of species per sample (N_0) and the density of all dominant polychaete species in one or both stations after August '95. A new deterioration of the community between January and March '96, only observed in one station, was attributed to the drastic increase of the sediment's mud content of the station (from 5 to 30 %), negatively affecting the macrobenthos of the *L. conchilega* community usually found in a fine sandy sediment with low mud concentrations. In contrary to 1995, no successful recruitments were observed in 1996 nor 1997, illustrating the large year-to-year within the success of recruitment of the macrobenthos. It is thus extremely important to be aware of the natural variability or 'potentials' of a macrobenthic community in order to evaluate its ecological importance.

INTRODUCTION

The macrobenthic communities of shallow coastal waters are subject to a variety of physical and biological disturbances which vary in frequency and intensity, as well on a temporal and spatial scale (Turner *et al.*, 1995). Consequently, the communities' parameters (species composition, dominant species, abundances, etc.) are continuously changing (Arntz and Rumohr, 1986; Dörjes *et al.*, 1986). In temperate regions, these changes are primarily influenced by the seasonality (Bonsdorff and Österman, 1985; Dörjes *et al.*, 1986; Ibanez and Dauvin, 1988; Anderlini and Wear, 1992; Seys *et al.*, 1994), altering the sea water temperature, light intensity, and, consequently, the primary production within the water column (Moll, 1998). Due to this seasonality, a strong response within the time of recruitment, mortality and production of macrobenthic populations is a well-known phenomenon (Beukema, 1974; Arntz and Rumohr, 1986; Herman *et al.*, in press).

In contrary to the yearly repeating cycle of (physical) seasonality, the shallow coastal water macrobenthos shows a large year-to-year variation (Arntz and Rumohr, 1986; Essink and Beukema, 1986; Beukema *et al.*, 1993; Turner *et al.*, 1995). Weather conditions are greatly influencing the success of recruitment, mortality and production of the composing macrobenthic species (Dörjes *et al.*, 1986; Meire *et al.*, 1994) and are thus constantly altering the density, biomass and, consequently, the biological interactions of the composing species of a macrobenthic community. As the biological interactions, on their turn will also influence the community's parameters (Dörjes *et al.*, 1986; Meire *et al.*, 1994; Herman *et al.*, in press), by, e.g., predation, competition for food and space, and inhibition of recruitment, highly variable macrobenthic community parameters are expected, even in the natural, undisturbed situation. The natural variation within the macrobenthic communities should help to explain issues fundamental to ecology, but also for the conservation and management of marine benthic habitats (Turner *et al.*, 1995).

Because of beach erosion along the western Belgian coast, coastal defence works on the western Coastal Banks may be necessary. To diminish the ecological damage to the Coastal Banks, an area of international importance for waterfowl (Kuijken, 1972), e.g. the common scoter (*Melanitta nigra*) (Maertens *et al.*, 1988; Devos, 1990; Maertens *et al.*, 1990) a study of the macrobenthos in the area, to be directly affected by the works, has been set up. Next to the study of the spatial distribution of the macrobenthic communities (Chapters 1 and 3) and the population dynamics of the bivalve *Spisula subtruncata* (Chapter 4), the project also concentrates on the temporal variation of the *Lanice conchilega* community, the ecologically most important and diverse macrobenthic community of the western Coastal Banks. Furthermore, because of the possibility of recolonization by means of recruitment via the planktonic life stages of many macrobenthic species (Dauvin, 1990; Feller *et al.*, 1992), knowledge on the period of recruitment of the community's species allows to decrease the negative impact of the coastal defence works. If damage to the *L. conchilega* community occurs before the period of major recruitment, a fairly quick recovery of the community can be expected (Arntz and Rumohr, 1986). The study thus aims at (1) the description of the temporal variation within the community over a 2.5 yr period and (2) the identification of the periods of recruitment of the dominant species.

MATERIALS AND METHODS

STUDY AREA

The western Coastal Banks are a geomorphogically diverse shallow marine habitat, extending from the Belgian – French border eastwards to Oostende and from the mean low water level to a depth of about 8 m (Figure 1). The two areas investigated include a complex of sandbanks separated from the beach by a gully (area 1) an a subtidal extension of the beach, with sandbanks and tidal gullies (area 2). The sediments are composed of fine to coarse sand (Chapter 3). The mean wave height in the area is 0.5 m with a maximum of 3.5 m (Anonymous, 1998). During the sampling period the average monthly temperature of the seawater ranged from 0.5 to 21°C, with the lowest temperatures in January – February gradually increasing till August (unpublished data, Coastal Waterways Division).

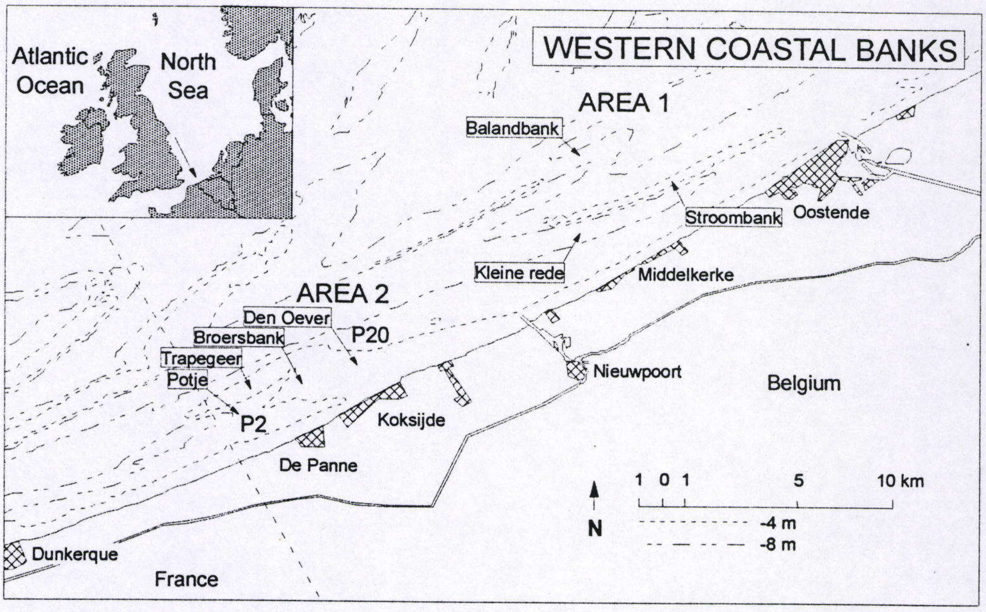

Figure 1. Geographical presentation of the western Coastal Banks, including area 1 and area 2, with indication of the two sampling sites (P2 and P20) for the study of the temporal variation within the *Lanice conchilega* community.

SAMPLING

Two stations (P2 and P20) were selected to study the temporal variation of the *Lanice conchilega* community on the western Coastal Banks (Figure 1). At each station, five Van Veen grabs (sampling surface area: 0.1026 m^2) were taken on 16 occasions: monthly between April '95 and April '96 and seasonally from April '96 till October '97. After fixation, with an 8 % formaldehyde – seawater solution, the samples were washed over two sieves with a 0.5- and 1 mm mesh size. The same samples were used to investigate the population dynamics of *Spisula subtruncata* within the *L. conchilega* community (Chapter 4). The residuals were preserved in an 8 % formaldehyde – seawater solution and stained with Bengal rose. From each macrobenthic sample, a subsample for sediment analysis was gathered.

DATA ANALYSIS

After the identification of all macrobenthic organisms up to the species level, the abundances were standardized to the number of individuals per square meter (ind m^{-2}). To investigate the gradual changes within the macrobenthos of the two stations during the sampling period, the dataset is subjected to a classification technique, Two-Way INdicator SPecies ANalysis (TWINSPAN) (Hill, 1979) and, after fourth root transformation of the densities, to an ordination technique, Correspondence Analysis (CA) (Ter Braak, 1988). The relation between two variables is studied by means of the non-parametric Spearman rank correlation (Conover, 1971).

RESULTS

PHYSICAL ENVIRONMENT

The fine sandy sediment of station P2 had a relatively constant median grain size of about 215 µm; the median grain size of station P20 showed a clear decrease between December ’95 and March ’96 (Figure 2). This major decrease in P20 coincided with an increase of the mud concentration of the sediment, with 5 % till December ’95, up to 30 % in March ’96, to decrease again to about 5 % after March ’96. The mud concentration in P2 was never higher than 6 %.

MACROBENTHOS: GENERAL

In August ’95, an the overwhelming recruitment of *Spisula subtruncata* occurred, with an average density up to 50000 (P20) and 150000 ind m^{-2} (P20) (Chapter 4). In order to understand the pattern of other macrobenthic temporal variation, macrobenthic density is given without incorporation of *S. subtruncata*, recruited in August ’95 (Figure 3). The ‘macrobenthic’ density peaked between June and August ’95, with densities up to about 5000 ind m^{-2} in both stations. After August ’95, the density steeply decreased to reach a density of 1000 ind m^{-2} in January ’96. After January ’96, the density never exceeded 1000 ind m^{-2} and no clear density peaks were found.

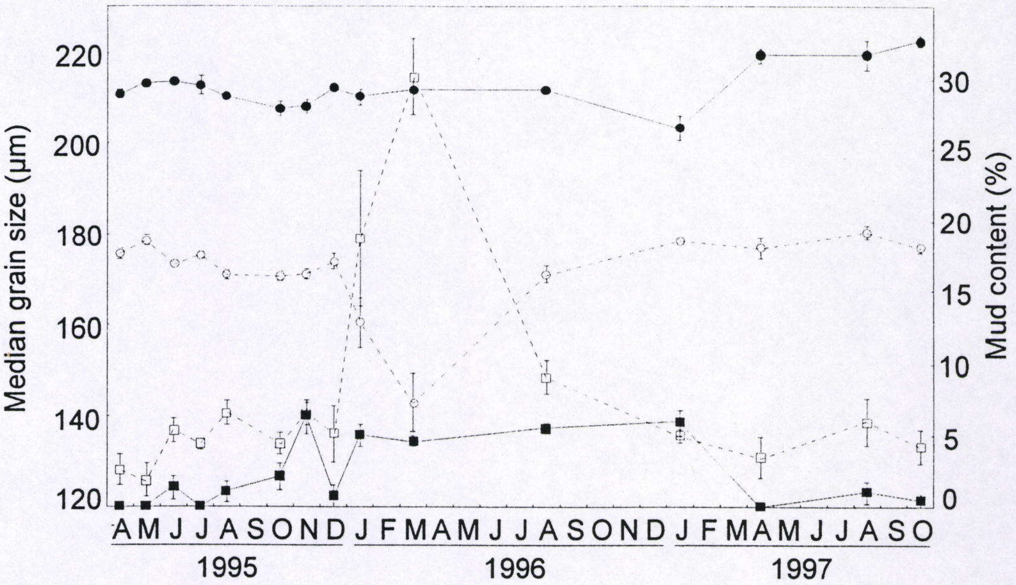

Figure 2. The temporal variation of the median grain size (P2, ●; P20, ○) and the mud content (0 – 63 µm) (P2, ■; P20, □) within both sampling sites, with indication of the standard error.

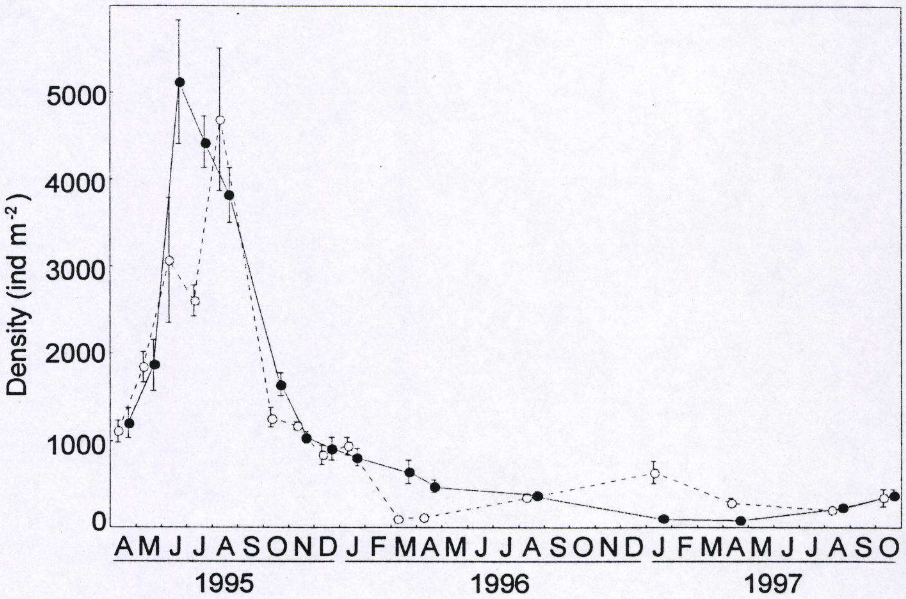

Figure 3. The temporal variation of the macrobenthic density (± standard error), with exclusion of the bivalve *Spisula subtruncata*, within both sampling sites: P2, ●; P20, ○.

Between April and August '95, the number of species per sample (N_0) increased from 20 to 32 and 38 species, in P2 and P20, respectively (Figure 4). After August' 95, N_0 of both stations decreased to less than 15 species from March '96 on. Except for April '96 (P20), N_0 continued to decrease till April '97 (P2: 6 spp.; P20: 3 spp.), after which N_0 increased again to 12 – 13 species. The Shannon-Wiener diversity index (H') was maximal between April and July '95 (P2: 2.2; P20: 2.6). A steep decrease of H' (to about 0.3) in both stations occurred between July and August '95. Whereas in P2, H' fluctuated between 0.2 and 1 from August '95 on, H' of P20 increased again after January '96 to a level of about 1.8.

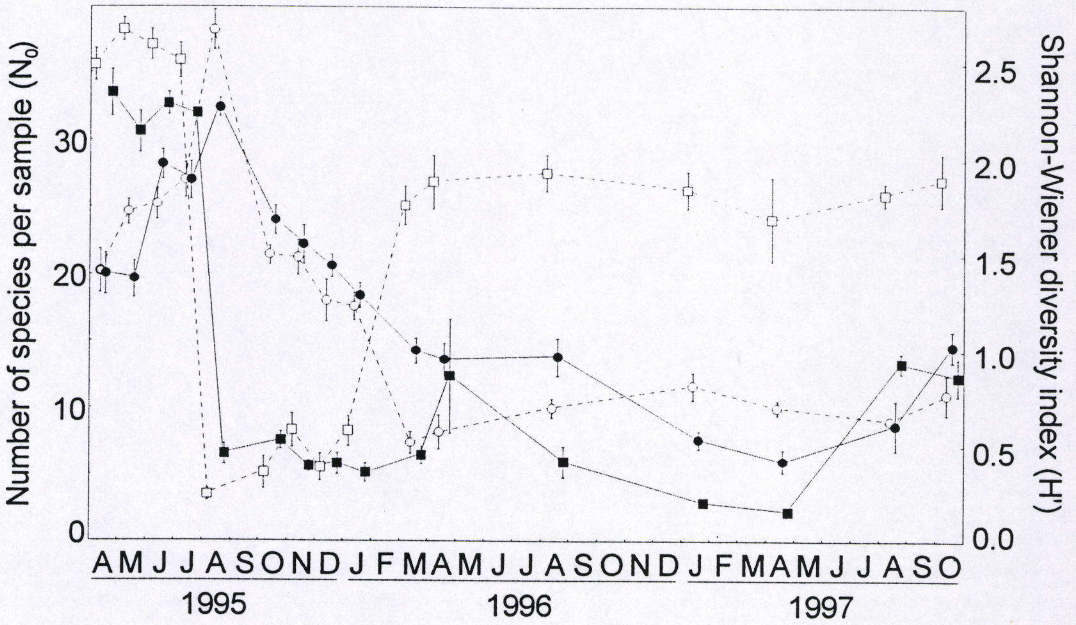

Figure 4. The temporal variation of the number of species per sample (N_0) and the Shannon-Wiener diversity index (H') (± standard error) within both sampling sites: N_0: P2, ●; P20, ○. H': P2, ■; P20, □.

RECRUITMENT

The temporal variation of the macrobenthic density, the number of species per sample (N_0), and the Shannon-Wiener diversity index (H'), changed most during the first year of the study. Therefore, the next part of the results will focus on the sampling period April '95 – April '96 by the investigation of the temporal variation of the abundances of the most dominant species, since after April '96 densities became too low.

Considering the most abundant polychaete species (Figure 5), an increase of the species' densities within the 0.5 mm fraction is found between April (*Nephtys hombergii*) and July (*Spio filicornis*). Except for *Spiophanes bombyx*, all species were about absent in the 0.5 mm fraction between October and April. No individuals of *Notomastus latericeus* were found in the 0.5 mm fraction. Except for *S. filicornis*, an increasing density within the 1 mm fraction, in one or both of the stations (P2 and P20), occurred together with or just after the appearance of small individuals (0.5 mm fraction). In the case of *Lanice conchilega*, where a discrimination between juvenile (smaller than 1 cm) and adult individuals is made within the

1 mm fraction, a drastically increasing density within the 0.5 mm fraction and juvenile individuals coincides in May, while an increase of the adults' density is found in June, and this in both stations.

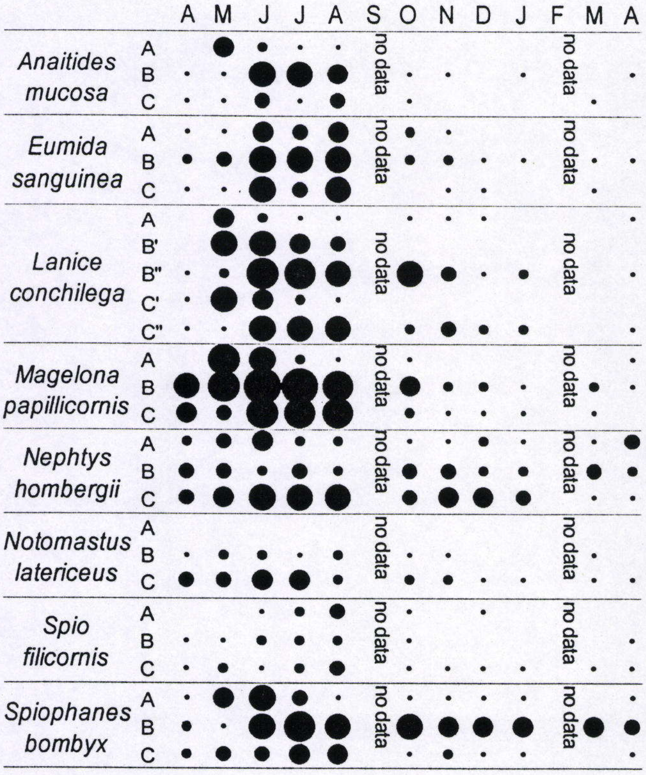

Figure 5. The temporal variation of the density of the eight most dominant polychaetes, within the 0.5 mm fraction of station P2 (A) and the 1 mm fraction of the stations P2 (B) and P20 (C).· , 1 – 20 ind m^{-2}; •, 21 – 50 ind m^{-2}; ●, 51 – 100 ind m^{-2};●, 101 – 200 ind m^{-2}; ●, 201 – 500 ind m^{-2}; ●, 501 – 1000 ind m^{-2}; ●, > 1000 ind m^{-2}.

Considering the dominant amphipods and molluscs (Figure 6), an increasing density within the 0.5 mm fraction, coinciding with or followed by an increasing density within the 1 mm fraction, is observed for both amphipods, *Pariambus typicus* and *Urothoe poseidonis* and for only one bivalve, *Ensis* sp. and this in July – August. All other molluscs were not encountered in the 0.5 mm fraction. Still, an increase of the density of the bivalve *Spisula subtruncata* (August) and the gastropod *Hinia reticulata* (October) within the 1 mm fraction is observed. In contrary to *S. subtruncata*, all individuals of *H. reticulata* had a height of at least 0.5 cm, most of them being larger than 1 cm.

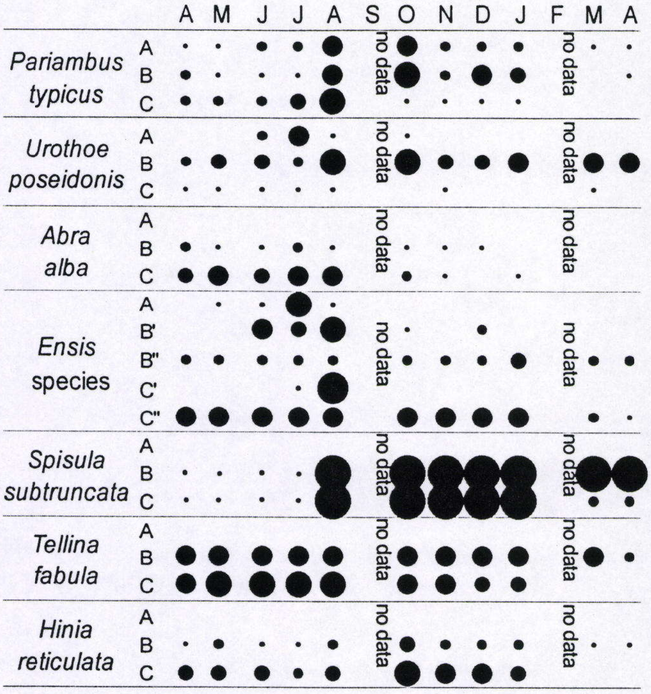

Figure 6. The temporal variation of the density of the seven most dominant amphipodes and gastropodes, within the 0.5 mm fraction of station P2 (A) and the 1 mm fraction of the stations P2 (B) and P20 (C).· , 1 – 20 ind m^{-2}; •, 21 – 50 ind m^{-2}; ●, 51 – 100 ind m^{-2}; ●, 101 – 200 ind m^{-2}; ●, 201 – 500 ind m^{-2}; ●, 501 – 1000 ind m^{-2}; ●, > 1000 ind m^{-2}.

Unlike the polychaetes *Eumida sanguinea*, *Lanice conchilega*, *Magelona papillicornis*, and *Spio filicornis*, the amphipod *Pariambus typicus*, and the bivalves *Spisula subtruncata* and *Tellina fabula*, other species were unevenly distributed over both stations (Figures 5 and 6). The polychaetes *Anaitides mucosa* and *Spiophanes bombyx*, and the amphipod *Urothoe poseidonis* showed a clear preference for station P2. Station P20 accounted for the highest densities of the polychaetes *Nephtys hombergii* and *Notomastus latericeus* and the molluscs *Abra alba*, *Ensis* sp., and *Hinia reticulata*. Furthermore, except for *S. bombyx* in P2 and *N. hombergii* in both stations, all polychaete species showed a drastic density decrease within the 1 mm fraction in both stations after August. A drastic density decrease of the amphipods and molluscs (1 mm fraction) was observed after August (*P. typicus* and *A. alba*) and after January (*Ensis* sp., *S. subtruncata*, *T. fabula* and *H. reticulata*) in P20, while in P2, only the density of *P. typicus* steeply decreased after January

TEMPORAL COMMUNITY CHANGES

By means of multivariate techniques (TWINSPAN and CA), the macrobenthic temporal variation within both stations during the whole sampling campaign is investigated. For station P2, the TWINSPAN revealed a clear temporal pattern with a major distinction (first level) between April '95 – March '96 (group 1) and April '96 – October '97 (group 2). On the second level, a distinction between April – August '95 (group 1A) and October '95 – March '96 (group 1B) and between April '96 – April '97 (group 2A) and August – October '97 (group 2B) is made. Station P20 grossly followed the same pattern: (1) April '95 – January '96 (group 1) and March '96 – October '97 (group 2) (first level) and (2) May – August '95 (group 1A), April '95 together with October '95 – January '96 (group 1B), March – April '96 (group 2A), and August '96 – October '97 (group 2B). 94 % (P2) and 96 % (P20) of the replicates of each month were grouped together, indicating that all replicates are representative for their respective month. In both stations, especially group 1 has a number of indicator species, while group 2 is characterized by the absence of indicator species (Table 1).

Station P2			
Group 1A	Group 1B	Group 2A	Group 2B
Magelona papillicornis *Tellina fabula* *Notomastus latericeus*		---	
Magelona papillicornis	*Spisula subtruncata*	*Urothoe poseidonis*	*Spio filicornis* *Eumida sanguinea*
Station P20			
Group 1A	Group 1B	Group 2A	Group 2B
Tellina fabula		---	
Lanice conchilega (juv.) *Notomastus latericeus* *Anaitides mucosa* *Abra alba* *Magelona papillicornis*	---	Oligochaeta	*Nephtys hombergii* *Spio filicornis* *Nephtys* sp. (juv.)

Table 1. Overview of the indicator species of all groups, retrieved by TWINSPAN analyses of both stations.

The ordination figure of the CA (Figure 7) clearly separates both stations and no overlap between the two stations is observed. Within both stations, a gradual transition from April '95 till April '96 along the second axis (Eigenvalue: 0.198) is found. A first relatively important change along the second ordination axis is found between July and August '95 (① and ④). Furthermore, a major change along the first ordination axis (Eigenvalue: 0.232), being very drastic in P20, occurred between April and August '96 (② and ⑤). In P2, from August '96 on, a gradual transition till October '97 along the second axis is detected (③). After August '96, a movement towards the original macrobenthic situation is found in P20 (⑥). A negative correlation (Spearman rank correlation: $p < 0.000001$) between the first axis and the number of species per sample (N_0) and the macrobenthic density is found. The standard error on the replicates ordination scores increased from April '95 till October '97.

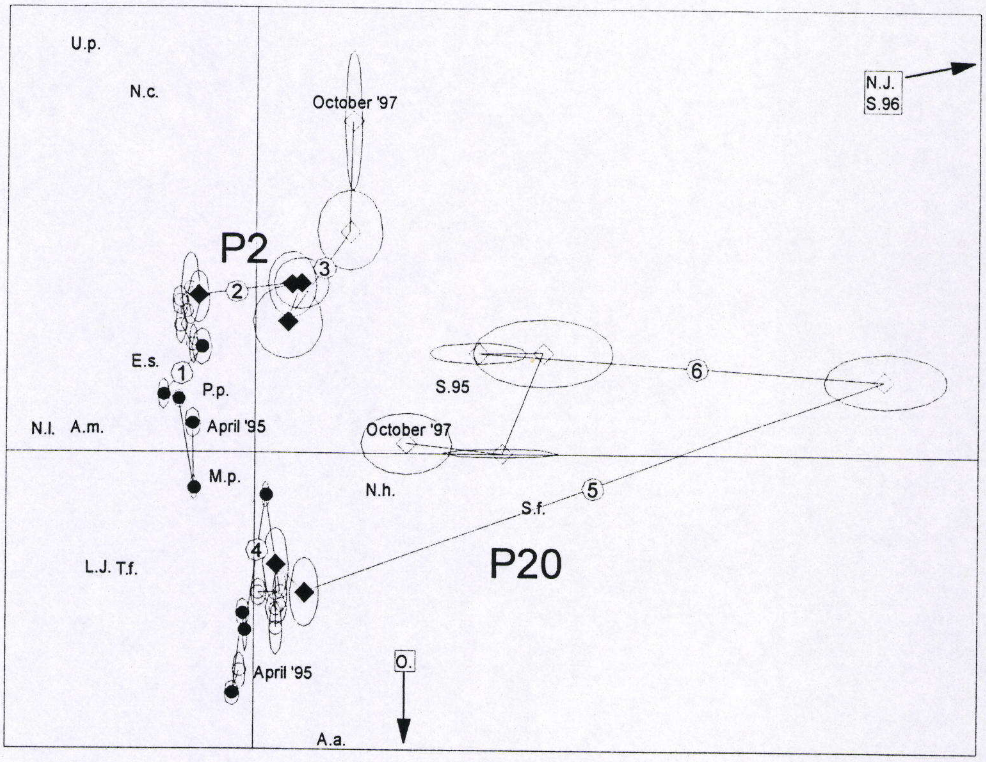

Figure 7. Correspondence Analysis (CA) plot (X-axis: first CA axis and Y-axis: second CA axis), including all samples of both sampling sites (P2 and P20). The temporal changes per sampling site (from April '95 till October '97) are represented by the centroids of all samples of each month ± standard error ellips. The TWINSPAN groups for both stations are: P2: ●, April ' – August '95; O, October '95 – March '96; ♦, April '96 – April '97; ◊, August '97 – October '97 and P20: ●, May '95 – August '95; O, April '95 and October '95 – January '96; ♦, March '96 – April '96; ◊, August '96 – October 97. The situation of the TWINSPAN indicator species: A.a., *Abra alba*; A.m., *Anaitides mucosa*; E.s., *Eumida sanguinea*; M.p., *Magelona papillicornis*; L.J., juvenile *Lanice conchilega*; N.c., *Nephtys cirrosa*; N.h., *Nephtys hombergii*; N.J., juvenile *Nephtys* spp.; N.l., *Notomastus latericeus*; O., Oligochaeta; P.p., *Polydora pulchra*; S.95, *Spisula subtruncata*, cohort '95 (Chapter 4); S.96, *Spisula subtruncata*, cohort '96 (Chapter 4); S.f., *Spio filicornis*; T.f., *Tellina fabula*; U.p., *Urothoe poseidonis*.

Most of the TWINSPAN indicator species are situated on the negative side of the first ordination axis, together with the first 11 sampling months (April '95 – April '96) of both stations. A distinction between both stations is made by means of *Urothoe poseidonis* and *Nephtys cirrosa* in P2, while *Abra alba* and Oligochaeta are typically found in P20. The major change between April and August '96 in P20 is explained by the appearance of juvenile *Nephtys* sp. and *Spisula subtruncata*, cohort '96.

DISCUSSION

As the macrobenthos of the two investigated stations belongs to the *Lanice conchilega* community in 1994 and 1997, typically occurring in area 2 of the western Coastal Banks (Chapter 3), only minor temporal changes within the macrobenthos were expected. Yet, in contrary to the expected stability of the stations' macrobenthos, temporal changes were obvious during this study. Considering the temporal variation of the macrobenthic density and the number of species per sample and the similarities between samples, depicted by TWINSPAN and CA, a large year-to-year variability of the community's parameters is observed, as already demonstrated for a variety of macrobenthic communities in temperate regions (Arntz and Rumohr, 1986; Essink and Beukema, 1986; Beukema *et al.*, 1993; Turner *et al.*, 1995). Two different periods can be distincted within the 2.5 yr study period: (1) April '95 till April '96 and (2) April '96 till October '97.

During the first period an increase of the density and N_0 from April '95 till August '95 (Spring and Summer), followed by a decrease of both variables till April '96 (Autumn and Winter), was found. This general amelioration of the community's condition can be attributed to the recruitment of, at least, most of the dominant species. As a recruitment is indicated by the appearance of a large number of small, juvenile individuals, recruitments can be traced by means of an investigation of the temporal variation of the species' densities (increasing at a recruitment) and by the appearance of the species in the 0.5 mm fraction (small individuals) (Feller *et al.*, 1992). Considering the dominant species of the *L. conchilega* community, recruitment took place from April till August, with specifical recruitment peaks. Although the polychaetes' recruitments generally took place between April and August (as demonstrated by the density increase within the 0.5 and 1 mm fraction), four recuitment patterns of polychaete species could be recognized. A first type (*N. latericeus*) showed no recruitment in 1995. A prolonged recruitment, from April till August (second type) was typical for *N. hombergii.* The recruitment of *Anaitides mucosa*, *L. conchilega*, *Magelona papillicornis*, and *S. bombyx* took place in May – June (third type), while the fourth type showed a recruitment mainly in June – August (*Eumida sanguinea* and *S. filicornis*). Considering the period of recruitment of the amphipods and the molluscs, four types were discriminated. No recruitment is detected for *Abra alba*, *Tellina fabula*, and *H. reticulata* (see below) (type 1). A recruitment took place in July for *U. poseidonis* and *Ensis* sp. (type 2). A huge recruitment of *S. subtruncata* took place in August (type 3). *Pariambus typicus* showed a recruitment in August – October (type 4). A period of recruitment of the macrobenthos, starting in early Spring and ending at the end of the Summer or early Autumn, has already been demonstrated in other marine ecosystems (Dörjes *et al.*, 1986; Ibanez and Dauvin, 1988;

Dauvin, 1990) and 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) ameliorate from early Spring on (Dauvin, 1990), the settlement of planktonic larvae does not occur at the same time for the different species (Feller *et al.*, 1992).

A major distinction, considering the period of recruitment, is obvious between the Polychaeta, of which recuitment took place between April and August, and the Amphipoda and Bivalvia, recruting between July and October. Furthermore, while all polychaetes and amphipods had a recruitment in 1995, a recruitment of the bivalves was only observed for *Spisula subtruncata* and *Ensis* sp. The highly variable recruitment of *Spisula subtruncata* , being extremely succesful in August '95, has already been described for the western Coastal Banks (Chapter 4). As a consequence of the dominant presence of *S. subtruncata* in August '95, a steep decrease of the Shannon-Wiener diversity index (H'), in contrary to the high N_0, can be observed. Possibly because of drastically changing biological interactions due to the presence of large numbers of recruits of *S. subtruncata*, covering the sediment with a 1 cm thick layer (personal observation), this event may be responsible for the general decrease of N_0 and the density of all dominant polychaete species in one or both stations after August '95. Indeed, large 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 large post-settlement mortality of *S. subtruncata* between August and October, increasing the quantity of decomposing organisms, scavengers, as *Hinia reticulata*, may have been attracted to the increasing food resource. The consequent active immigration of *H. reticulata* in both stations may explain its increasing density of (large) individuals. Between January and March '96, another remarkable decrease of N_0 and macrobenthic density is found in P20. This new deterioration of the community coincided with a drastic increase of the sediment's mud concentration (from 5 to 30 %), only observed in P20. A temporary increase of the sediment's mud concentration can be expected in wintertime, when higher 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 (unpublished materials, Van Lancker). The increase of the fine materials in the sediment of P20 then negatively affects the macrobenthos of the *L. conchilega* community, usually occurring in a fine sandy sediment with low mud concentrations (Degraer *et al.*, in press a). Because the filter feeding bivalve, *Spisula subtruncata*, cannot survive in an environment with high mud concentrations (Shackley and Collins, 1984, Chapter 4), the drastic decrease of its density (from over 1000 to less than 50 ind m^{-2}) and, consequently, an increase of H' can be explained. Furthermore, in March '96, a high number of recently died and dying *Ensis* sp. were found on top of the sediment. Probably because of the high biomass of decomposing bivalves (*S. subtruncata* and *Ensis* sp.), the oxygen level in the sediment decreased and an almost completely anoxic sediment with a strong rotting smell, was found in P20 in March '96 (personal observation). After March '96, the sediment's mud concentration slowly returned to its original level of about 5 %, but, in contrary 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. The condition of the *L. conchilega* community in P20 started to ameliorate again after April '96, but never reached the original condition of the first year of the study period. In P2, where the mud concentrations were never higher than about 6 %, high densities of *S. subtruncata* (> 1000 ind m^{-2}) were present till October '97. Possibly, because of the continuing competition, the condition of the *L. conchilega* community in P2, continued to deteriorate gradually till April '97: no drastic changes were observed between October '95 and April '97. After April '97, a gradually increasing N_0 and macrobenthic density, indicating a slow recovery of the original *L. conchilega* community in P2, was observed.

The second period (April '96 till October '97) is characterized by a generally low macrobenthic density, with only a low number of species in both stations. Furthermore, a number of species typically found during the first period (P2: *Magelona papillicornis* and *Notomastus latericeus*; both stations: *Tellina fabula*) were absent during this second period. Because of this generally poor macrobenthic condition, a greater chance of finding a large variability within the macrobenthos of the five replicate samples of each month exists. This explains the larger standard error of the samples' average ordination score (CA) for each months of the second period.

During the second period, no obvious macrobenthic density increases were found, indicating a possible absence of successful recruitments of the species. Yet, during the periods of expected recruitment, being April '96 – August '96 and April '97 – August '97, no samples are available. Recruitment of some species, recruting in Spring (mainly polychaetes), may thus have been taken place, but, if so, these recruitments have not been successful as no obvious density increase was noticed in August '96, nor August '97. In contrary to 1995, no successful recruitments could thus be observed in 1996, nor 1997. Many authors already reported on a large year-to-year variability within the success of recruitment of macrobenthic species (Arntz and Rumohr, 1986; Essink and Beukema, 1986; Beukema *et al.*, 1993; Turner *et al.*, 1995), causing longer-term (e.g. more than one year) fluctuations of the populations. The population of *L. conchilega* in Liverpool Bay, for instance, is found to perform a cycle of six to seven years (Rees and Walker, 1983).

In P20, an increase of the density of juvenile *Nephtys* and *S. subtruncata* is found in August '96, causing its aberrant situation within the CA plot. Although recruitment of *S. subtruncata* is found in August '96, their density was much lower than in August '95 and no surviving individuals were detected after April '97 (Chapter 4).

Conclusion: seasonal fluctuations of the macrobenthic community's parameters are caused mainly by the settlement and post-settlement mortality of the composing species. Yet, the success of recruitment of different species differs from year to year and during some years significant recruitment (and post-settlement survival) can be absent as well. Although a large variability within the macrobenthos of the stations P2 and P20 between April '94 and October '97 is demonstrated, the macrobenthos of both stations still belonged to the *L. conchilega* community in October '97 (Chapter 3). As the detection of community stability does not require that a community remain unchanged, but rather that the observed change in structure is not larger than can normally be expected to occur given the natural temporal and spatial variability of the populations (Turner et al., 1995), the species composition and density is thus still typical for the *L. conchilega* community, even with the observed variability. However, even though the macrobenthos of both stations is part of the same community, not all species are evenly distributed over both stations: the different species are found in different absolute and relative abundances in both stations (no overlap in CA plot!). As demonstrated by Meire *et al.* (1994), many different combinations of dominant species are possible within each major habitat and which species actually do occur is probably mainly determined by differences in recruitment and subsequent biological interactions. The year-to-year variability in rates and, possibly, periods of recruitment (combining settlement and consequent survival) of the composing species of the *L. conchilega* community (as demonstrated above) may thus be responsible for the differing community parameters of both stations. It is thus extremely important to be aware of the natural variability or 'potentials' of a macrobenthic community in order to evaluate its ecological importance.