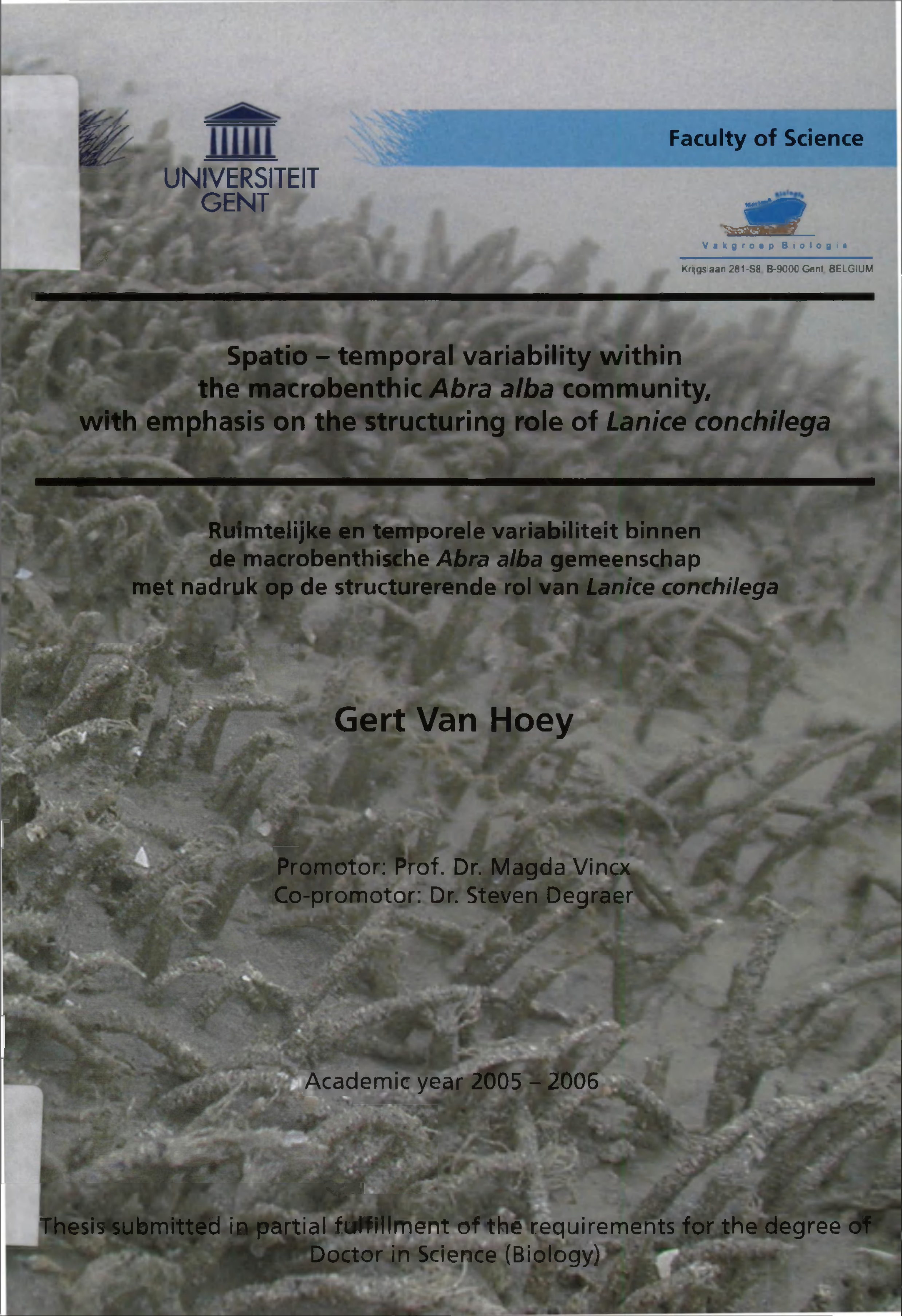

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Spatio – temporal variability within the macrobenthic *Abra alba* community, with emphasis on the structuring role of *Lanice conchilega*

Ruimtelijke en temporele variabiliteit binnen de macrobenthische *Abra alba* gemeenschap met nadruk op de structurerende rol van *Lanice conchilega*

Gert Van Hoey

Promotor: Prof. Dr. Magda Vincx
Co-promotor: Dr. Steven Degraer

Academic year 2005 – 2006

Thesis submitted in partial fulfillment of the requirements for the degree of
Doctor in Science (Biology)

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Foto: Vincent Zintzen

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TABLE OF CONTENTS

CHAPTER 6: 117

The impact of *Lanice conchilega* on the soft-bottom benthic ecosystem in the North Sea

DANKWOORD

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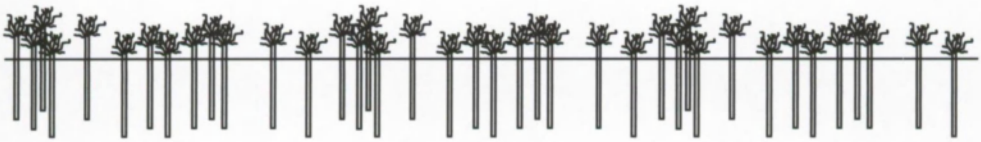
Summary -

samenvatting



Summary

The Belgian Continental Shelf (BCS) is situated in the southernmost part of the North Sea and is characterized by a high geomorphological and sedimentological diversity in soft – bottom habitats. The combinations of the ecological and the socio-economic values of the BCS cause conflicts between both interests. Initiatives are being taken by the scientific community to optimize the integration of the ecological value of the BCS with those of the different user functions, like shipping, dredging, sand and gravel extraction, fishing and tourism. The government has made a start with the implementation of Marine Protected Areas into the law (framework law of 20/01/1999): proposals for such areas have been made and are under investigation. In the mean time, it is important to provide the policy makers with a scientific basis for the development of a sustainable management plan for the natural resources of the BCS. This study focuses on the macrobenthic component of the ecosystem. This component was considered to be suitable to characterize and monitor the marine ecosystem because of its size (macroscopic), its relative immobility and its direct link with the sediment and with the processes that occur immediately above the seabed. This study aimed to investigate the macrobenthic community structure on the BCS, the spatial and temporal variability within the ecologically most important macrobenthic community (*Abra alba* community) and the importance and population dynamics of an ecologically important species (the sand mason, *Lanice conchilega*) within this community. Based on the information of a part of the marine ecosystem (macrobenthos), some remarks on the conservation of ecologically important areas or species on the BCS can be formulated.

In **Chapter 2**, the different macrobenthic communities and their distribution on the BCS were characterized based on a large number of samples gathered between 1994 and 2000. These samples cover a diverse range of habitats: from the sandy beaches to the open sea, from the gullies between the sandbanks to the tops of the sandbanks, and from clay to coarse sandy sediments. To investigate the large-scale spatial distribution of the macrobenthos of the BCS, the data of 728 samples were combined and analysed. By means of several multivariate techniques, ten sample groups were distinguished. Each sample group is found in a particular physico-chemical environment and has a specific species composition. Four sample groups are differing drastically, both in habitat and species composition, and are considered to represent four macrobenthic communities: (1) the muddy fine sand *Abra alba – Mysella bidentata* community (further called the *Abra alba* community) is characterized by high densities and diversity, (2) the *Nephtys cirrosa* community occurs in well-sorted sandy sediments and is characterized by low densities and diversity, (3) very low densities and diversity typify the *Ophelia limacina – Glycera lapidum* community, which is found in coarse sandy sediments and (4) the *Eurydice pulchra – Scolelepis squamata* community is typical for the upper intertidal zone of sandy beaches. Of course these macrobenthic communities are not isolated from each other, but are linked through six transitional species assemblages. The transition between the *A. alba – M. bidentata* community and the *N. cirrosa* community, is characterized by a reduction in the mud content and is dominated by *Magelona johnstoni*. The transition between the *N. cirrosa* and the *O. limacina – G.*

lapidum community is distinctive by decreasing densities and coincides with a gradual transition between medium to coarse sandy sediments. From the *N. cirrosa* to the *E. pulchra – S. squamata* community, transitional species assemblages related to the transition from the subtidal to the intertidal environment, were found. Each community or transitional species assemblages was found over a specific range along the onshore – offshore gradient, four types can be discerned: (1) almost restricted to the near-shore area, but possible further distribution, (2) distributed over the full onshore – offshore gradient, (3) restricted to the near-shore area, and (4) restricted to the sandy beach environment. The diversity pattern on the BCS follows this division, with species rich and poor assemblages in the near shore area to only species poor assemblages more offshore. The distribution and diversity patterns are linked to the habitat type, discerned by median grain size and mud content.

The small – to large scale geographical pattern within the ecologically most important macrobenthic community (*A. alba* community) of the BCS was investigated in **Chapter 3**. The *A. alba* community is widely spread in the coastal zone of the English Channel and the Southern Bight of the North Sea. The community is located on shallow, muddy fine sands. Its spatial distribution is characterized by a number of isolated patches (Atlantic French, British and German coast) and one large continuous distribution area (northern France up to the Netherlands). The aim of this study was to investigate the geographical patterns within the macrobenthic *A. alba* community at different scales: the community's full distribution range (i.e. large scale, > 1000 km) and a selected area with a continuous distribution of the *A. alba* community (i.e. small scale, 200 km) in relation to structuring environmental variables. Therefore, an analysis of newly collected samples along the Belgian coastal zone was combined with available information on the *A. alba* community throughout its distribution range. Although the community structure shows a high similarity across the full distribution range of the *A. alba* community, large- as well as small-scale changes in community composition were observed. The BCS should be considered as a major transition from the rich southern to the relatively poorer northern distribution area of the *A. alba* community. At a large scale (i.e. full distribution range), the differences in community structure are expected to result from (1) the specific hydrodynamic conditions in the English Channel (Atlantic ocean waters) and the Southern Bight of the North Sea, with a consequent differential connectivity between the different areas and (2) the climatological and related faunal shift from temperate (English Channel) to boreal conditions (German Bight). At a small scale (i.e. within the continuous distribution area), differences in structural and functional community aspects may result from geographic differences in (1) detrital food availability, related to riverine input and pelagic productivity, along and across the coastline and (2) the amount of suspended matter, impoverishing the *A. alba* community when excessively available.

The study in **Chapter 4** outlines the seasonal and year-to-year variations in the *A. alba* community. This variation is typical for macrobenthic communities in temperate, shallow coastal waters and is investigated in the *A. alba* community on the BCS 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 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 and species richness in spring and summer, with a decline in autumn towards the end of the winter. Although this cycle differed quantitatively from year-to-year, the general features were 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, on the cyclic seasonal patterns in the marine ecosystem and on the ability of the community to recover.

In **Chapter 5**, the population dynamics, recruitment and persistence of the *L. conchilega* populations in subtidal soft – bottom sediments along the Belgian coastline are described. An intensive sampling campaign (monthly - biweekly from April until August), the discrimination of different benthic stages and cohort analysis of the adult population enabled the discrimination of trends in recruitment patterns of *L. conchilega*. Three recruitment periods were defined based on the occurrence of peaks of aulophore larvae in the water column and peaks of recently settled individuals in the benthos: (1) spring recruitment period (April – July), (2) summer recruitment period (July – September), and (3) autumn recruitment period (September – November). The spring recruitment period was the most intense and was characterized by high densities of recently settled individuals and juveniles. These high densities resulted in an adult population, which consisted of different cohorts and which was characterized by a high turn over. The summer and autumn recruitments were less intense and did not occur at every station or in every year. Spatial and temporal variations in timing and intensity of settlement and recruitment were observed and described. Results indicate that *L. conchilega* is an opportunistic species, characterized by a long pelagic phase, high settlement of larvae and a high turn over in the adult population. Due to this recruitment strategy and the preferential settling of the larvae in adult patches, the studied *L. conchilega* population was able to maintain high abundances in moderately stable patches.

The tube building polychaete *L. conchilega* has a wide distribution and can form dense aggregations. Unfortunately, the effects of *L. conchilega* on the surrounding benthic community have received little attention, especially in subtidal areas. Therefore, the effects of the presence of *L. conchilega* on the abundance, species richness, diversity and species composition of the North Sea benthos in relation to sedimentology and depth were evaluated in **Chapter 6**. The results show that *L. conchilega* does have an effect on the benthic density and species richness in soft-bottom sediments. The density of the benthic species increased and was significantly (positively) correlated with the density of *L. conchilega*. Furthermore, the species richness increased with increasing density of *L. conchilega*. This trend was, however, not consistent: the number of species no longer increased or even decreased after reaching a certain density of *L. conchilega* (> 500 ind/m²). The same overall pattern was detected concerning the expected number of species. The N_1 - diversity index showed similar or slightly higher values in *L. conchilega* patches compared to patches without *L. conchilega*. The effects on density and diversity were most pronounced in shallow fine sands, which are the preferred habitat of *L. conchilega,* and less in deep fine sands. The changes in benthic characteristics result from the alterations of the habitat by *L. conchilega* (hydrodynamics, sediment stability, improved oxygen) and the complex interactions between the benthic organisms and the biogenic structures consisting of *L. conchilega* tubes. A lot of benthic species can profit from the creation, modification and maintenance of that habitat by *L. conchilega*, which results in an increased density and species richness in *L. conchilega* patches compared to the surrounding soft-bottom sediments. Finally, the results indicated that *L. conchilega* has an effect on the benthos present in a particular habitat, rather than forming its own association.

Samenvatting

Het Belgische Continentaal Plat (BCP) is gelegen in de zuidelijke bocht van de Noordzee en wordt gekarakteriseerd door een hoge geomorfologische en sedimentologische habitat-diversiteit (zachte substraten). De combinatie van de ecologische and socio – economische waarden van het BCP veroorzaakt conflicten tussen beide interesses. Wetenschappers nemen initiatieven om de integratie van de ecologische waarde van het BCP met deze van de verschillende gebruikers (scheepvaart, baggeren, zand en gravel extractie, visserij en toerisme) te optimaliseren. De overheid is gestart met de implementatie van Mariene Beschermde Gebieden in de wetgeving (wet van 20/01/1999): voorstellen voor zulke gebieden zijn gemaakt of worden onderzocht. In de tussentijd is het belangrijk om de beleidsmensen te voorzien van wetenschappelijke kennis om de ontwikkeling van een duurzaam beheerplan voor de natuurlijke rijkdommen van het BCP mogelijk te maken. De huidige studie richt zich op de macrobenthische component van het ecosysteem. Omwille van de grootte van het macrobenthos (macroscopisch), de relatieve immobiliteit en de directe link met het sediment en de processen direct boven de zeebodem, is deze component uitermate geschikt voor de karakterisering en opvolging van het mariene ecosysteem. Derhalve beoogde deze studie het onderzoek naar de macrobenthische gemeenschappen op het BCP, de ruimtelijke en temporele variabiliteit binnen de ecologische meest waardevolle macrobenthische gemeenschap (*Abra alba* gemeenschap) en het belang en de populatie dynamiek van een ecologisch belangrijke soort (schelpkokerworm, *Lanice conchilega*) binnen deze gemeenschap. Gebaseerd op deze kennis over een belangrijk deel van het mariene ecosysteem (macrobenthos), werden opmerkingen geformuleerd met betrekking tot het behoud van ecologisch waardevolle gebieden of soorten op het BCP.

In **Hoofdstuk 2** werden de verschillende macrobenthische gemeenschappen en hun verspreiding op het BCP gekarakteriseerd, gebaseerd op een groot aantal stalen genomen tussen 1994 en 2000. Deze stalen waren afkomstig van verschillende habitats: van zandstranden tot de open zee, van de geulen tussen de zandbanken tot de toppen van deze banken en van klei tot grof zandige sedimenten. Om de macrobenthische gemeenschappen op het BCP te onderzoeken werden alle data van de 728 stalen gecombineerd en geanalyseerd. Door middel van verschillende multivariate technieken werden tien groepen van stalen onderscheiden. Elke groep werd gevonden in een specifiek fysico-chemische omgeving en had een specifieke soortensamenstelling. Vier groepen verschilden drastisch van elkaar, zowel in habitat als soortensamenstelling en worden verondersteld vier macrobenthische gemeenschappen te vertegenwoordigen: (1) de *Abra alba – Mysella bidentata* gemeenschap (verder genoemd als *Abra alba* gemeenschap), welke is gekarakteriseerd door hoge densiteiten en diversiteit en werd gevonden in slibberig fijn zand, (2) de *Nephtys cirrosa* gemeenschap voorkomend in goed gesorteerd zand en gekarakteriseerd door lage densiteiten en diversiteit, (3) zeer lage densiteiten en diversiteit typeerden de *Ophelia limacina – Glycera lapidum* gemeenschap, welke werd gevonden in grof zanderige sedimenten, en (4) de *Eurydice pulchra – Scolelepis squamata* community was typisch voor het bovenste deel van de subtidale zone van zandstranden. Deze macrobenthische gemeenschappen waren niet geïsoleerd van elkaar, maar waren gelinkt door middel van zes overgangsgroepen. De transitie tussen de *A. alba – M. bidentata* community and de *N. cirrosa* gemeeenschap was gekarakteriseerd door een reductie in slib en werd gedomineerd door *Magelona johnstoni*. De transitie tussen de *N. cirrosa* gemeenschap en de *O. limacina – G. lapidum* gemeenschap was te onderscheiden door een daling in de densiteiten tesamen met een graduele transitie tussen medium en grof zanderige sedimenten. Van de *N. cirrosa* gemeenschap naar de *E. pulchra – S. squamata* gemeenschap werden overgangsgroepen gevonden, die gerelateerd waren met de transitie van een subtidale naar een intertidale omgeving. Elke gemeenschap of overgangsgroep werd gevonden over een specifieke range langsheen de onshore – offshore gradiënt: vier types konden onderscheiden worden: (1) meestal beperkt tot de kust (2) verspreid over de volledige onshore – offshore gradiënt, (3) beperkt tot de kust en (4) beperkt tot het strand. De diversiteits patronen op het BCP volgen deze verdeling, met soortenrijke en -arme groepen in het kustgebied tot enkel soortenarme groepen verder van de kust. Men kan besluiten dat de verspreiding van de soorten en de diversiteitspatronen gelinkt zijn met het habitat type, en dan vooral mer de mediane korrelgrootte en het slibgehalte in het sediment.

De klein- tot grootschalige geografische patronen binnen de ecologisch meest belangrijke macrobenthische gemeenschap (*A. alba* gemeenschap) van het BCP werd onderzocht in **Hoofdstuk 3**. De *A. alba* gemeenschap is wijd verspreid in de kustzones van het Engels kanaal en de Zuidelijke bocht van de Noordzee. Deze gemeenschap kan aangetroffen worden in ondiepe, slibrijke, fijnzanderige sedimenten. Diens ruimtelijke verspreiding is verdeeld over een aantal lokaal geïsoleerde gebieden (Atlantische kust van Frankrijk, Britse en Duitse kust) en één groot continu verspreidingsgebied (van het noorden van Frankrijk tot Nederland). De doelstelling van de huidige studie was de geografische patronen binnen de macrobenthische *A. alba* gemeenschap te bestuderen op verschillende ruimtelijke schalen: op het niveau van de volledige verspreiding (grootschalig) van de gemeenschap en op het niveau van een geselecteerd gebied gekenmerkt door een continue verspreiding van de *A. alba* gemeenschap (kleinschalig) in relatie tot structurerende omgevingsvariabelen. Met dit doel werden de analyses van recent verzameld materiaal langsheen de Belgische kust gecombineerd met de beschikbare informatie over de *A. alba* gemeenschap langsheen zijn volledige verspreidingsgradiënt. Alhoewel de gemeenschapsstructuur een hoge similariteit vertoont langsheen zijn volledige verspreidingsgradiënt, werden zowel groot- als kleinschalige veranderingen in de gemeenschapssamenstelling geobserveerd. Het BCP kan beschouwd worden als een transitie van het rijke zuidelijke naar het relatief armere noordelijke verspreidingsgebied van de *A. alba* gemeenschap. De verschillen in de gemeenschapsstructuur langsheen de volledige verspreidingsgradiënt (grootschalig) worden verondersteld het gevolg te zijn van (1) de specifieke hydrodynamische condities in het Engels kanaal (Atlantisch oceaanwater) en in de Zuidelijke Bocht van de Noordzee, met verschillende verbindingen tussen de gebieden als gevolg, en (2) de klimatologische en daaraan gerelateerde faunale verschuivingen van gematigde (Engels kanaal) naar boreale condities (Duitse bocht). De verschillen in structurele en functionele gemeenschapsaspecten op een kleine schaal (binnen de continue verspreidinszone) zijn het resultaat van geografische verschillen in (1) aanvoer van detritus, gerelateerd aan de aanvoer vanuit rivieren en de pelagische productiviteit langsheen de kustlijn en (2) de hoeveelheid gesuspendeerd materiaal, dewelke de *A. alba* gemeenschap verarmt bij overmatige aanwezigheid.

De studie in **Hoofdstuk 4** schetst de seizoenale en interannuele variaties binnen de *A. alba* gemeenschap. Deze variaties zijn typisch voor macrobenthische gemeenschappen in gematigde, ondiepe kustgebieden en werden onderzocht binnen de *A. alba* gemeenschap op het BCP gedurende negen jaar (1995 - 2003). De gemeenschap heeft de neiging om terug te keren naar zijn originele staat gedurende de onderzoeksperiode, maar het bereikt dit punt niet. Dit kan gerelateerd worden aan de vervanging van *Spisula subtruncata* door *Donax vittatus* als dominante bivalve achter 1997 en mogelijks als resultaat van de klimatische verandering in 1998. De opsplitsing van de studie periode in een onstabiele (1995 - 1997) en stabiele periode (1999 – 2003) valt samen met het jaar 1998. Een zeer sterke rekrutering van de tweekleppige *S. subtruncata* (biologische oorzaak), temperatuurfluctuaties en een sterke toename van het slibgehalte (fysische oorzaken) waren verantwoordelijk voor een verschuiving in de gemeenschapsstructuur gedurende de onstabiele periode. Deze oorzaken hadden een effect op de macrobenthische densiteit, diversiteit en soortensamenstelling. De zeer sterke rekrutering van *S. subtruncata* veroorzaakte een daling van de densiteit en diversiteit van het macrobenthos, terwijl de toename van het slibgehalte verantwoordelijk was voor een ineenstorting van de soortenrijkdom en macrobenthische densiteiten. De koude winter periode was hoogstwaarschijnlijk verantwoordelijk voor het trage herstel van de *A. alba* gemeenschap achter deze verstoringen. De onstabiele periode werd gevolgd door een aantal jaren van hogere stabiliteit (1999-2003), gekarakteriseerd door een cyclisch seizoenaal patroon waarin de kokerbouwende borstelworm *L. conchilega* domineerde. Het algemeen seizoenaal patroon in de huidige studie werd gekarakteriseerd door hoge macrobenthische densiteiten en soortenrijkdommen in de lente en zomer, met een daling gedurende de herfst naar het einde van de winter toe. Hoewel deze cycli kwantitatief verschilden tussen de jaren, werden de algemene patronen herhaald doorheen de stabiele periode. De dominantie van *L. conchilega* gedurende de stabiele periode kan een positieve invloed gehad hebben op het benthos door zijn habitat- structurerende kenmerken. Deze studie toont aan dat natuurlijke oorzaken een drastische impact kunnen hebben op de normale jaarlijkse variatie, het cyclisch seizoenaal patroon en de snelheid van herstel van het mariene ecosysteem.

Hoofdstuk 5 bestaat uit een beschrijving van de populatiedynamica, recrutering en persistentie van de *L. conchilega* populaties in subtidale zachte substraten langsheen de Belgische kust. De combinatie van een intensieve staalnamestrategie (maandelijkse – tweewekelijks van April tot Augustus), het onderscheiden van verschillende benthische stadia en een cohortanalyse van de adulte populatie laat toe om de trends in de rekruteringspatronen van *L. conchilega* te onderscheiden. Drie rekruteringsperiodes werden afgebakend gebaseerd op het voorkomen van densiteitspieken van de aulophora larven in de water kolom en pieken van recent gesettelde individuen in het benthos: (1) lenterekruteringsperiode (April – Juli), (2) zomerrekruteringsperiode (Juli – September), en (3) herfstrekruteringsperiode (September – November). De lenterekruteringsperiode was de meest intense en werd gekarakteriseerd door hoge densiteiten van recent gesettelde individuen en juvenielen. Deze hoge densiteiten resulteerden in een adulte populatie, welke bestond uit verschillende cohorten en welke gekarakteriseerd werden door een hoge turn - over. De zomer- en herfst rekrutering waren minder intens en kwamen niet voor op elk station of in elk jaar. Ruimtelijke en temporele variaties in timing en intensiteit van de rekrutering werden waargenomen en beschreven. De resultaten tonen aan dat *L. conchilega* een opportunistische soort is, gekarakteriseerd door een langdurige pelagische fase, hoge setteling van larven en een hoge - turn over in de adulte populatie. Door deze rekruteringsstrategie en de voorkeur van de larven om te settelen in adulte populaties, kunnen de *L. conchilega* populaties hoge dichtheden behouden op dezelfde locatie.

Lanice conchilega heeft een zeer wijde verspreiding en kan zeer dense aggregaties vormen. Helaas zijn de effecten van *L. conchilega* op de omringende benthische gemeenschap onvoldoende bestudeerd, zeker in subtidale gebieden. Daarom worden de effecten van de aanwezigheid van *L. conchilega* op de dichtheid, soortenrijkdom, diversiteit en soortensamenstelling van het Noordzee benthos geëvalueerd in relatie tot de sedimentologie en diepte (**Hoofdstuk 6**). De resultaten tonen dat *L. conchilega* wel degelijk een effect heeft op de benthische densiteit en soortenrijkdom in zachte substraten. De densiteiten van de benthische soorten stijgen en zijn significant (positief) gecorreleerd met de densiteit van *L. conchilega*. Bovendien stijgt de soortenrijkdom met toenemende densiteit van *L. conchilega*. Deze trend was echter niet rechtlijnig: het aantal soorten steeg niet langer of daalde zelfs na het bereiken van een zeker dichtheid van *L. conchilega* (> 500 ind/m^2). Hetzelfde patroon werd gedetecteerd aangaande het aantal verwachtte soorten (ES(50)). De N_1 – diversiteit toonde gelijkaardige of licht gestegen waarden bij de aanwezigheid van *L. conchilega* ten opzichte van zijn afwezigheid. De effecten op de densiteit en diversiteit kwamen het sterkst naar voren in ondiepe fijnzanderige sedimenten, welke het optimale habitat zijn voor *L. conchilega,* en het minst in diepe fijnzanderige sedimenten. De veranderingen in de benthische karakteristieken waren het gevolg van de veranderingen die *L. conchilega* aanbracht in zijn habitat (hydrodynamica, sediment stabiliteit, verhoogde zuurstofconcentraties) en de complexe interacties tussen de benthische organismen en de biogene structuren bestaande uit *L. conchilega* kokers. Heel wat benthische soorten kunnen profiteren van de creatie, modificatie en het behoud van het habitat door *L. conchilega*, wat dan weer resulteert in een verhoging van de densiteit en soortenrijkdom in *L. conchilega* populaties ten opzichte van de omgevende zachte substraten. Ten slotte tonen de resultaten aan dat *L. conchilega* een effect heeft op het benthos aanwezig in een bepaald habitat, eerder dan dat er een eigen soortenassociatie wordt gevormd.

Chapter 1

General introduction

General introduction

The socio-economical activities on the Belgian Continental Shelf

The Belgian Continental Shelf (BCS) (3600 km²) is situated in the southernmost part of the North Sea. The shallow BCS (maximum depth 46 m) is mainly characterized by the presence of several sandbank systems, which can be grouped into four entities: (1) Coastal banks, parallel to the coastline, (2) Flemish Banks, about 10-30 km offshore of the western Belgian coast, (3) Zeeland Banks, some 15 – 30 km offshore of the eastern Belgian coast, and (4) Hinderbanks, about 35 - 60 km offshore (Degraer et al., 1999). Those sandbanks on the BCS originated from sedimentation around hard sediment structures in the lower strata during the Pleistoceen / Holoceen. This occurs in different phases depending on the hydrodynamic circumstances and the supply of sediments. The current hydrodynamic pattern on the BCS is characterized by flood-dominated currents heading towards the northeast along the coast, while the offshore area is controlled by ebb-dominated currents pointing towards the southwest (Vlaeminck et al, 1989). Besides those currents, the northeastern coastal area is also influenced by the turbidity plume of the Westerscheldt and Rhine/Meuse (Lacroix *et al.*, 2004). Due to these physico – chemical characteristics, a high geomorphological and sedimentological diversity in soft – bottom habitats is found on the BCS, despite its small coverage on the North Sea shelf (< 0.5%).

The BCS is also a zone of intense human activity, like shipping, dredging, sand and gravel extraction, fishing (mainly beam – trawl), tourism and in the near future the construction of windmill farms (Maes et al., 2000). Some of the busiest shipping routes in the world cross the southern North Sea. As a result, the ecosystem is threatened by oil pollution, which may range from small, occasional oil stains to huge oil spills caused by shipping accidents (Kingston, 1992; Dauvin, 1998; observations MUMM). Sand and gravel extraction and dredging involve moving material from one place to another and thus physical disturbance for the benthic ecosystem (Kaplan et al, 1973; Kenny & Rees, 1996; Van Dalfsen et al., 2000). Extracted sand and gravel is used in the construction industry and dredging is carried out in order to maintain the maritime access routes to the Belgian coastal ports and to stabilize the depth of the coastal ports. The physical effects and the possible contamination caused by the dumping of dredged material should not be underestimated (Poiner & Kennedy, 1984; Harvey et al., 1998). Furthermore, an intensive fishery takes place having a major impact on all levels of the ecosystem. Biotopes and species disappear because the seabed is disturbed, species are fished to near-extinction, undersized fish are thrown back and eaten by scavengers and birds, and mammals get caught in fishing nets (Lindeboom & de Groot, 1998; Groenewold & Fonds, 2000). The construction of windmill farms at sea increased in popularity in recent years to obtain electricity of renewable energy sources (ICES BEWG report 2005). In addition to the industries in the coastal area and the economic activities carried out at sea, tourism and recreation also form an important social and economic activity (Gheskiere et al, 2005). The Belgian coast is a great tourist attraction for both Belgian and foreign visitors. For an integrated coastal zone and marine management, it is important to harmonize the socio - economical impacts with the natural values of the marine environment, which normally leads in many ways to conflict situations.

Nature conservation

The ecological value of soft-sediment habitats, which characterizes the BCS, has been ignored in the past and lots of these habitats are undervalued in the public opinion (Degraer, 1999). Because of this ecological value of parts of the Belgian Continental Shelf (Maertens et al., 1990; Devos, 1990; Offringa et al., 1995; Degraer et al., 1999; Seys et al., 2002), combined with increasing anthropogenic pressure on the marine ecosystem in the last decades, the governmental interest in the marine environment has increased and has led to an increased funding of scientific research and the implementation of Marine protected areas (MPA) into the law. The implementation of an MPA in the Belgian Law was facilitated by the framework law of 20 January 1999 on the protection of the marine environment in the marine areas under Belgian jurisdiction (BS 12 March 1999; as amended) and the Royal Decree of 21 December 2001 concerning the species conservation in the marine areas under Belgian jurisdiction (BS 14 February 2002) (Cliquet et al., 2004; Maes and Cliquet, 2005). 'Marine protected area' in the law is a general term and includes several categories: marine reserves, species protected areas (Bird directive), special areas of conservation (Habitat directive), closed areas and buffer zones, and each of them has separate types of uses (Maes et al., 2005). The development of marine protected areas in Belgian marine waters has a complicated history. Firstly, the Coastal bank area between the Belgian – French border and Oostende, which extends 3 nautical miles from the baseline and at maximum 6 m below MLLWS, is designated as a Ramsar site ("Wetlands of international importance"), but without protection measures (Maes et al., 2005). Recently, proposals were made to include parts of the Coastal bank area as Habitat or Bird Directive Area. These two European directives are framed in the NATURA 2000 Network, which is designed to guarantee the conservation of a minimum level of biodiversity in Europe (Maes et al., 2005). The types of habitat that have priority in the Habitat Directive (92/43/EEG) include, amongst others, sand banks with only a shallow covering of seawater (rarely more than 20 m below MLLWS). Next to the proposal of designating the Coastal Bank area (Trapegeer – Stroombank area) as a Special Area of Conservation under the Habitat Directive, a small area on the Vlakte van de Raan is recently proposed in this context (policy report Vande Lanotte). Three marine areas were recently proposed as Special Protected Areas under the Bird Directive (79/409/EEC) along our coast (policy report Vande Lanotte), namely: (1) an area on the west coast (off Koksijde and De Panne), from the low water line up to 6 nautical mile (NM) (part of the Coastal Bank area), (2) an area on the mid-coast (Middelkerke – Bredene), from the low water line up to 6 NM in the western part and between 1.5 and 6 NM from the coast in the eastern part of the area, and (3) an area enclosing the front part of the harbor of Zeebrugge. Implementation of the European Bird Directive implies taking protection measures for the sea and coastal areas where birds are living, so that they can continue to exist and reproduce in these places (Maes et al., 2005). The Habitat Directive and Bird Directive are recently implemented in the Federal legislation by the decree of 21

October 1997 concerning nature conservation and the natural environment, BS 10 January 1998, as amended by the Decree of 19 July 2002, BS 31 August 2002 (Cliquet et al., 2004; Maes and Cliquet, 2005), but none of the proposed areas in the framework of those directives are designated, although recently proposed in a Royal Decree (14 October 2005). A proposal for the establishment of marine reserves, where all activities will be prohibited (except commercial fisheries, shipping and military activities) is difficult to obtain due to pressure from different economic sectors. The establishment of such marine reserves is currently in an investigation phase (policy report Vande Lanotte). Two areas were indicated, more precisely the Coastal bank area and the subtidal part of the 'Bay of Heist'; only the last one was recently designated by the Royal Decree of 7 October 2005. It is also investigated if ecologically important wrecks on the seabed could be designated as small marine protected areas. Contrary to the Federal Government, the Flemish Government has designated several areas (e.g. parts of Belgium's beaches) of land within the region of Flanders as Special areas of Conservation under the Habitats Directive or as special protected areas under the Birds Directive. These differences in the rate of recognition of protected areas between the Flemish and the Federal Government are caused by the division of the authority in the case of the Belgian Coast and Sea. The Belgian Coast, including the beaches, falls under the authority of the Flemish Government, whereas the territorial sea falls under the authority of the Federal Government. This makes it difficult and complex to build up integrated nature reserves along our coast, for example the subtidal extension of the Nature reserve of the Bay of Heist.

Since no marine reserves or other Marine Protected areas are yet designated for the Belgian marine area, it is useful to broaden the knowledge on where the most important (or most valuable) marine areas for the different ecosystem components are located. Seys (2001), Seys *et al.* (2002) and Haelters et al. (2004) have already undertaken an investigation on marine avifauna, and three important bird areas have been identified (see above, Bird Directive areas). This type of information is not yet available for other ecosystem components. The project BWZee (2004-2006, financed by the Federal Science Policy) will produce a full-coverage biological valuation map ([1]) for the Belgian Continental Shelf, mainly considering macrobenthos and seabirds, but also epi – and hyperbenthos. A first attempt to make a biological valuation map was done by Gheerardyn (2002) and was based on functional and structural biodiversity and the distribution of rare and important macrobenthic species. This biological valuation map was expanded in the GAUFRE project (Maes et al., 2005) (Figure 1). The map to be produced by the BWZee project will give a more integrated picture of the ecologically valuable areas on the BCS.

Furthermore, a lot of additional biological information is needed to form the baseline for the scientific arguments for protection and management of the marine ecosystem. Next to information on the occurrence of species and biodiversity in an area, which were the basic criteria for designation of ecologically valuable areas, the processes (spatial and temporal variability, occurrence of ecologically important species) in the marine ecosystem have to be studied as well. Due to the existence of different faunal components within a marine ecosystem (microbenthos, meiobenthos, macrobenthos,

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[1] A biological valuation map is a national marine biological map showing relative ecological significance values, with the values defined in terms of preservation of biodiversity (BWZee – project).

epibenthos, hyperbenthos, plankton, birds and marine mammals) and the interaction between those faunal components, the selection of one component is justified to perform detailed analyses. This knowledge can later be combined and integrated in the knowledge of the entire marine ecosystem.

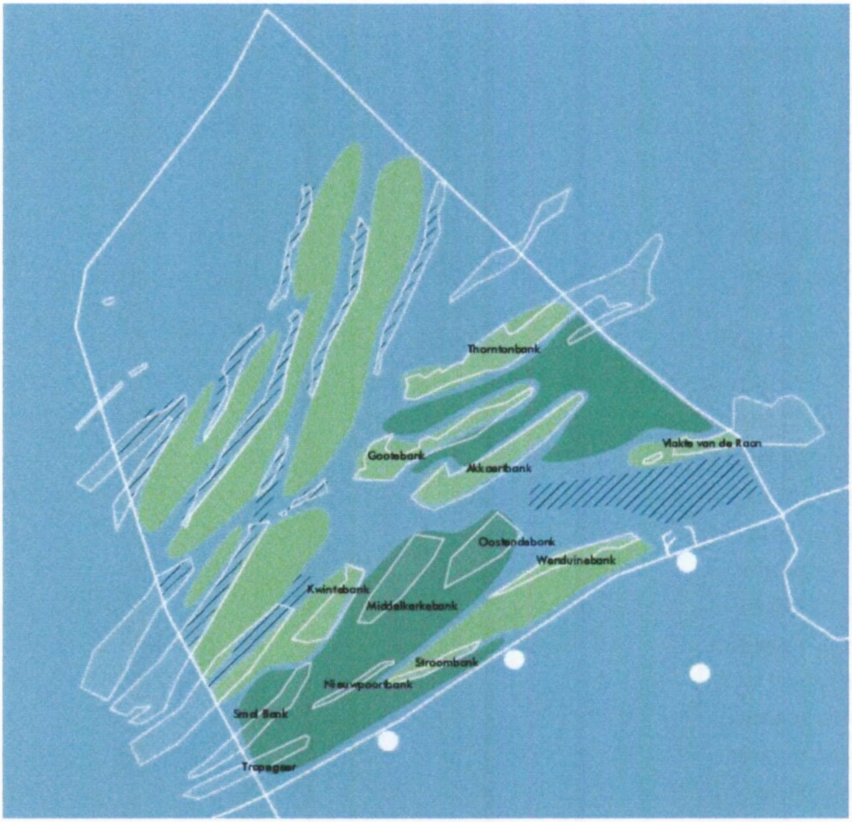


Figure 1. Start of ecological evaluation of the Belgian Continental Shelf. Ecologically very valuable (dark green), ecologically valuable (light green) and ecologically less valuable (cross – hatched) (Gheerardyn, 2002; Maes et al., 2005).

Macrobenthos as a representative part of the ecoystem

One of the most important components in the marine benthic ecosystem is the macrobenthos (all animals living in the sea bottom and being retained on a 1 mm sieve). It mainly includes polychaetes, bivalves, echinoderms and amphipods. The macrobenthos is suitable for characterizing and monitoring the marine ecosystem because of its size (macroscopic), its relative immobility and its direct link with the sediment and the conditions above the sediment (Gray, 1974; Creutzberg et al., 1984; Buchanan, 1984; Snelgrove & Butman, 1994). Macrobenthos plays an important role in the marine food web and is characterized by a high diversity of feeding types. Benthic organisms are the main food source for a lot of fishes (permanently residing or passing by the seabed) and for overwintering sea –birds, like the common scoter (Durinck et al., 1993; Degraer et al., 1999). Macrobenthos in soft sediments also plays an important role in the degradation of organic matter produced in the pelagic zone, and in the process of benthic nutrient regeneration, which affect primary production by supplying nutrients directly and by enhancing rates of pelagic recycling (Grall & Chauvaud, 2002). According to Gray et al. (1990), benthic organisms can be used as indicators for pollution levels and water quality in certain areas. Polychaetes, an important group within the macrobenthos, are amongst the most tolerant marine organisms to stressors (e.g. low oxygen, organic contamination of sediment and sewage pollution). As macrobenthos can integrate environmental changes in the benthic environment and is a highly cost effective parameter concerning sampling, the investigation of this faunal group is of significant interest for environmental surveillance. It is in fact the main component of biological trend monitoring programs aimed at evaluating the status of benthic ecosystems (Rees et al., 2002).

Communities, key – species, indicators

As discussed above, the macrobenthos is an important component in the ecosystem and is suitable for evaluating the state of the ecosystem. Therefore, the present study will focus on the macrobenthos of the Belgian Continental Shelf. Although a lot of separated studies on temporal and spatial distribution of macrobenthos in parts of the BCS have been undertaken, up till now, no general overview was made. Consequently, the present study aimed at providing a general overview of the patterns within the macrobenthos on the BCS based on those separated studies and newly collected data. It is of vital importance to visualize and summarize this huge amount of data and observations to give structured baseline information for nature conservation or future scientific research topics. In this context, terms as community, indicators, key species or ecologically important species have appeared. In the next paragraph, these terms will be explained and linked to possible uses in nature conservation, before the detailed objectives of this study will be outlined.

The term community is widely used, and most definitions of communities include the idea of a collection of species found in a particular place (physical habitat); some ecologists found that these species must interact in some significant way to be considered as community members (Morin, 1999). One of the basic definitions of the community concept is the following: "a community is a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment and separable from other groups by means of an ecological survey (Mills, 1969). So, a community can be found in a particular habitat and is characterized by typical community parameters (diversity, density, species composition, trophic structure), which summarize its characteristics. The knowledge on community ecology can be used to address some problems in nature. Overexploitation of fish is an example, because it causes changes in the abundance of other species, resources or predators and thus changes in the food web. Therefore, it is difficult for a heavily fished species that relied on the resources of that heavily exploited food web to subsequently recover from overexploitation (Morin, 1999). Another example is the problem of invasive species, which can lead to changes in the community structure or the exclusion of some original community members. A solution can be to introduce and reestablish a key fragment of the naturally occurring food web that was missing during the initial introduction and subsequent population expansion of the invader. As a result, there can be a biologically control on the introduction of such invasive species (Morin, 1999). In other words, a detailed knowledge on the community structure (structural and functional) and its spatial and temporal variability is needed to be able to make statements about changes or recovery.

A time and money saving strategy in the follow - up of the changes in a community or ecosystem is the use of indicators, key species or ecologically important species. These species concepts have the aim to reduce complex data into a simplified form, but have different definitions, with different accents on the concept. An indicator species is an indicator of the state of the local environment which it occupies. It should be easily sampled and it changes should be a reflection of the changes in the biodiversity (Feral, 1999). A key species is defined as a species that plays an important ecological role in determining the overall structure and dynamic relationships within a biotic community (Mills et al., 1993; Piraino et al., 2002). In the literature this key species concept is often confused with the keystone species concept. However, to the keystone species concept a more narrow definition is given: a keystone species is defined as a strongly interacting species whose top-down effect on species diversity and competition is large relative to its biomass dominance within a functional group (Piraino et al., 2002; Davic, 2003). Nevertheless, habitat structuring capacities, important feeding interactions and/or high densities of some macrobenthic species can be characteristics, giving an impression of the importance of a species in the community (ecologically important species). Therefore, this concept is closely related to the key species concept and many species can be named key species or ecologically important species because they are important prey items, competitors, habitat modifiers, engineers, hosts, processors, etc., or they are dominant within their environment. The search for ecologically important species within a community or ecosystem is important, as well as a fundamental knowledge on its function, life cycle and population dynamics. This detailed knowledge on macrobenthic species is fragmentary and should be supplemented with recent data (Warwick & George, 1980; Bhaud, 1988; Smith, 1989; Mathivat en Cazaux, 1991; Marcano & Bhaud, 1995; Lambert et al., 1996; Olivier et al., 1996; Thiébaut, 1996; Thiébaut et al., 1996; Desroy et al., 1997; Frashetti et al., 1997; Olive et al., 1997; Degraer, 1999; Van Hoey, 1999).

Therefore, the present study aimed to investigate the macrobenthic community structure on the BCS, focusing on the spatial and temporal variability within the most important macrobenthic community and investigating the importance and population dynamics of an ecologically important species within this community. The current knowledge about these topics is described in the next paragraph.

Current knowledge

Previous knowledge on macrobenthic community structure on the BCS dated from the beginning of the '80's (Govaere et al., 1980; Vanosmael et al., 1982). These authors distinguished three zones on the BCS: a coastal zone with a set of species– and abundance poor communities, a species– and abundance rich transition zone, and a species rich and abundance poor open sea zone. A more detailed macrobenthic community analysis on the western coastal banks was done by Degraer et al.

(1999) in 1994, with distinction of five coherent communities (1) the *Barnea candida* community, (2) a community characterized by the presence of *Mytilus edulis* spat, (3) the *Lanice conchilega* community, (4) the *Nephtys cirrosa – Echinocardium cordatum* community and (5) the *N. cirrosa community*, closely related to the latter. Only the *L. conchilega* community belongs to the diverse transition zone described by Govaere et al. (1980). The other four communities seem to be part of the heterogeneous, species-poor coastal zone associations. The study of Govaere et al. (1980) was based on only 74 sites, of which most were situated in the coastal zone, and the study of Degraer et al. (1999) only handled a small part of the BCS (Western Coastal Banks). Therefore, a more detailed macrobenthic community analysis for the BCS imposed itself. Data on the spatial and temporal variability within the different communities were mostly lacking, except for the communities in the western Coastal Bank area (Degraer, 1999). Detailed information on ecologically important species is only present for *Spisula subtruncata* (Degraer et al., submitted), the most abundant bivalve of the Coastal Banks and an important food item for the common scoter *Melanitta nigra* (Leopold, 1993, 1995).

New investigations

To fill these information gaps, this PhD study focused on the macrobenthic community structure on the BCS, the spatial and temporal variability within the most important macrobenthic community and the importance and population dynamics of an ecologically important species within this community.

Firstly, the different macrobenthic communities on the BCS were characterized and their distribution patterns discussed (**Chapter 2**). These analyses were possible because, since 1994, numerous separated studies focusing on the description of the temporal and spatial distribution of the macrobenthos in certain areas have been undertaken. Yet, a clear classification and comparison between the different outcomes of the studies was difficult and therefore all data were gathered into a database and reanalyzed in order to define the different macrobenthic communities. Due to the importance of having detailed knowledge on community diversity and differences within a single habitat, one important macrobenthic community was selected for detailed spatial and temporal analyses. In this study, the macrobenthic *Abra alba* community was selected, because it was already characterized as one of the most important soft-bottom macrobenthic communities along the coastal areas of the English Channel and Southern Bight of the North Sea (Fromentin et al., 1997). A detailed knowledge on the spatial and temporal variability of this community was already gathered in France (Fromentin et al., 1996; Sanvicente-Anorve et al., 1996; Dauvin, 1998, 2000; Ghertsos et al., 2000, 2001; Desroy et al., 2002; Sanvicente-Anorve et al., 2002; Dauvin et al., 2004), but was, until recently, lacking at the BCS.

Therefore, the geographical patterns (structural and functional level) within the macrobenthic *A. alba* community were studied at different scales in relation to structuring environmental variables: (a) the community's distribution range in the English channel and North Sea (i.e. large scale), (b) a selected area with a continuous distribution of the *A. alba* community (i.e. small scale) (**Chapter 3**).

As macrobenthic communities are known to show large temporal variations, both within and between years (Eagle, 1975; Rees & Walker, 1983; Bonsdorff & Österman, 1985; Arntz & Rumohr, 1986; Buchanan et al., 1986; Essink & Beukema, 1986; Ibanez & Dauvin, 1988; Beukema et al., 1993; Turner et al., 1995; Fromentin et al., 1997; Ghertsos et al., 2000; Desroy & Retière, 2001), the temporal variation of the community structure of the *A. alba* community was studied over a nine year period (**Chapter 4**). Knowledge on the temporal variation is necessary to enable objective evaluation of the effects of anthropogenic influences versus the natural dynamics of the macrobenthos.
When focusing on the *A. alba* community, it becomes clear that the tube building polychaete *Lanice conchilega* is an ecologically important species because it creates favourable conditions for other macrobenthic species (Zühlke et al., 1998; Zühlke, 2001), because (1) the tubes provide a settlement surface for larval and postlarval benthic organisms (Qian, 1999), (2) there is an improved oxygen supply in the sediments surrounding *L. conchilega* tubes (Zühlke, 2001) and (3) *L. conchilega* beds provide a refuge from predation (Woodin, 1978). *Lanice conchilega* is a common species in intertidal and shallow subtidal soft – bottom sediments and can reach densities of thousands individuals per m^2. Until now, the species distribution and temporal variability of *L. conchilega* were mainly investigated on intertidal sandflats (Heuers et al., 1998; Zühlke, 1998; Petersen & Exo, 1999; Ropert & Dauvin, 2000; Strasser & Pieloth, 2001; Zühlke et al., 2001; Callaway, 2003) and less in subtidal environments (Buhr & Winter, 1977). The description of its ontogenetic development and life cycle is mostly done (Ziegelmeier, 1952; Kessler, 1963; Buhr & Winter, 1977; Forster & Graf, 1995; Nicolaidou, 2003), just like the characteristics of the planktonic aulophore stage (Bhaud, 1988; Bhaud & Cazaux, 1990; Marcano & Bhaud, 1995). However, the information on the ecological aspects concerning its life-cycle and population dynamics in subtidal soft – bottom sediments is lacking. Therefore, the population dynamics of *L. conchilega*, with attention to the links between the larval phase (aulophore larvae) and the settlement and recruitment in shallow subtidal soft – bottom sediments on the BCS was studied in **Chapter 5**. The ecological importance of *L. conchilega* has already been shown in intertidal environments, where the species diversity and abundance were higher among tube aggregations compared to the surroundings (Zühlke, 2001). Nevertheless, the effects of *L. conchilega* on the macrobenthos in other parts of its distribution area are still unknown and therefore investigated in **Chapter 6**. Therein, the influence of *L. conchilega* on the macrobenthos in soft-bottom sediments of the North Sea is discussed.

The detailed knowledge on the macrobenthic community structure on the BCS, the spatial and temporal variability within the *Abra alba* community and the structuring function of *Lanice conchilega* adds to the scientific knowledge indispensable for managing this ecosystem and for monitoring changes which could affect it. Based on this information, a time and money saving strategy can be set up for monitoring this ecosystem. Based on knowledge on the natural variability within a community or within populations of an ecologically important species, possible influences of anthropogenic disturbance can be evaluated.

Thesis outline

Two parts of this thesis have already been published in the international literature and the remaining parts are submitted or will be submitted for publication soon. For that reason the outline and output of the chapters is almost exactly like the published or submitted papers. Each chapter is also intended to be an autonomous part, which can be read separately from other chapters. Inevitably, there may be some overlap between the introductions and material and methods of the different chapters. Cited literature is generalized and listed at the end of the thesis.

Chapter 2 "Macrobenthic community structure of soft – bottom sediments at the Belgian Continental Shelf" has the following aims: (1) to characterize the different macrobenthic communities on the Belgian Continental Shelf on the basis of their species composition, abundance, species richness and their habitat preferences (e.g. sedimentology and bathymetry); (2) to compare the macrobenthic community structure with similar communities in other parts of the North Sea; (3) to understand the relationships between those communities; and (4) to investigate the spatial distribution of the communities, with special attention to their diversity patterns along the BCS. This investigation is based on data collected within the framework of several studies between 1994 and 2000 (see acknowledgements).
This chapter has been published as Van Hoey, G., Degraer, S. and Vincx, M. (2004) Macrobenthic community structure of soft – bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science*: 59: 599-613

Chapter 3 "Small– to large-scale geographical patterns within the macrobenthic *Abra alba* community" investigate the geographical patterns (structural and functional level) within the macrobenthic *Abra alba* community at different scales: the community's distribution range in the English Channel and North Sea (i.e. large scale) and a selected area with a continuous distribution of the *A. alba* community (i.e. small scale) in relation to structuring environmental variables. The data for this study originate from several studies collected between 1994 and 2003 (see acknowledgements).
This chapter has been published as Van Hoey, G., Vincx, M. and Degraer, S. (2005) Small – to large-scale geographical patterns within the macrobenthic *Abra alba* community. *Estuarine, Coastal and Shelf Science*: 64: 751-763

Chapter 4 "Long-term variability in the *Abra alba* community: importance of physical and biological causes" evaluate changes in community characteristics (density, diversity and species composition) of the *Abra alba* community over a nine year period at one stations on the Belgian Continental Shelf in view of detecting causes of major biological changes. This investigation is based on data collected within the framework of different research projects between 1994 and 1999 (see acknowledgements) and newly collected data within this PhD - project (2002 – 2003).

This chapter is submitted to *Journal of Sea Research* as Van Hoey, G., Vincx, M. and Degraer, S. Long-term variability in the *Abra alba* community: importance of physical and biological causes.

Chapter 5 "Population dynamics of subtidal *Lanice conchilega* (Pallas, 1766) populations at the Belgian Continental Shelf" aims to disentangle the population dynamics of a subtidal *L. conchilega* population through observation of the larval phase (aulophore larvae), benthic settling and the adult population structure on three sits in the coastal area of the Belgian Continental Shelf (BCS) during a 1.5 year period (March 2002 – September 2003). The data for this study originate from newly collected information (March 2002 - September 2003).
This chapter will be submitted as Van Hoey, G., Vincx, M. and Degraer, S. Population dynamics of subtidal *Lanice conchilega* (Pallas, 1766) populations at the Belgian Continental Shelf.

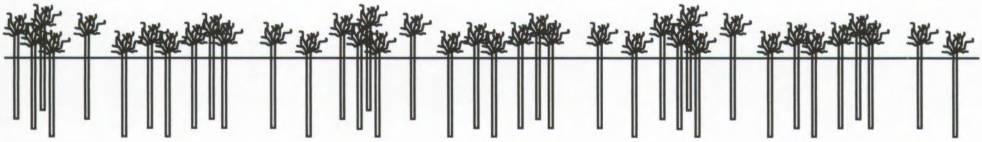
Chapter 6 "The impact of *Lanice conchilega* on the soft-bottom benthic ecosystem in the North Sea" investigates the effects of the presence of *L. conchilega* on the abundance, species richness, diversity and species composition of the North Sea benthos in relation to depth and sedimentology. This study is based on data gathered by the ICES Benthos Ecology Working Group for the North Sea Benthos Survey of 2000.
This chapter will be submitted as Van Hoey, G., Vincx, M. and Degraer, S. The impact of *Lanice conchilega* on the soft-bottom benthic ecosystem in the North Sea.

In the general discussion and conclusions (**Chapter 7**), key issues and considerations are deduced from the main results of the different chapters.

All the data used and collected in the framework of this PhD were gathered into the database 'Macrodat' and can (partially) be consulted via VLIZ (Flanders Marine Institute) or by contacting Gert Van Hoey (g.vanhoey@UGent.be) or Steven Degraer (steven.degraer@UGent.be).

Chapter 2

Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf



Paper published as

Van Hoey, G., Degraer, S. and Vincx, M. (2004)
Macrobenthic community structure of soft-bottm sediments at the Belgian Continental Shelf
Estuarine, Coastal and Shelf Science 59: 599-613

Abstract

Within the frame of different research projects, a large number of sites at the Belgian Continental Shelf (BCS) were sampled for the macrobenthos between 1994 and 2000. These samples cover a diverse range of habitats: from the sandy beaches to the open sea, from the gullies between the sandbanks to the tops of the sandbanks, and from clay to coarse sandy sediments. To investigate the large-scale spatial distribution of the macrobenthos of the Belgian Continental Shelf, the data of all these research projects - 728 samples - were combined and analysed. By means of several multivariate techniques, ten sample groups with similar macrobenthic assemblage structure were distinguished. Each sample group is found in a particular physico-chemical environment and has a specific species composition. Four sample groups are differing drastically, both in habitat and species composition, and are considered to represent four macrobenthic communities: (1) the muddy fine sand *Abra alba – Mysella bidentata* community is characterized by high densities and diversity, (2) the *Nephtys cirrosa* community occurs in well-sorted sandy sediments and is characterized by low densities and diversity, (3) very low densities and diversity typify the *Ophelia limacina – Glycera lapidum* community, which is found in coarse sandy sediments and (4) the *Eurydice pulchra – Scolelepis squamata* community is typical for the upper intertidal zone of sandy beaches. Of course these macrobenthic communities are not isolated from each other, but are linked through six transitional species assemblages. The transition between the *A. alba – M. bidentata* community and the *N. cirrosa* community, is characterized by a reduction in the mud content and is dominated by *Magelona johnstoni*. The transition between the *N. cirrosa* and the *O. limacina – G. lapidum* community is distinctive by decreasing densities and coincides with a gradual transition between medium to coarse sandy sediments. From the *N. cirrosa* to the *E. pulchra – S. squamata* community, transitional species assemblages related to the transition from the subtidal to the intertidal environment, were found. Each community or transitional species assemblages was found over a specific range along the onshore – offshore gradient, four types can be discerned: (1) almost restricted to the near-shore area, but possible further distribution, (2) distributed over the full onshore – offshore gradient, (3) restricted to the near-shore area and (4) restricted to the sandy beach environment. The diversity pattern on the BCS follows this dividing, with species rich and poor assemblages in the near shore area to only species poor assemblages more offshore. The distribution and diversity patterns are linked to the habitat type, discerned by median grain size and mud content.

Keywords
Macrobenthos, community structure, sandy sediments, Belgian Continental Shelf

Introduction

Different soft-sediment, macrobenthic assemblages were distinguished within the Southern Bight of the North Sea and the English Channel (e.g. Glémarec, 1973; Kingston and Rachor, 1982; Duineveld et al., 1991; Künitzer et al., 1992; Holtmann et al., 1996; Olivier et al., 1996; Dauvin 1998, Degraer et al., 1999(a); Dauvin, 2000; Ghertsos et al., 2000, 2001; Desroy et al., 2002; Sanvicente-Anorve et al., 2002). The distribution of these macrobenthic communities is highly correlated with the type of sediment, which is related to a wider set of environmental conditions, such as current speed and organic content of the sediment (Gray, 1974; Creutzberg et al., 1984; Buchanan, 1984; Snelgrove and Butman, 1994). At the Belgian Continental Shelf (BCS) characterized by a highly variable and diverse topography, with strongly differing environmental conditions (Degraer et al., 1999a), a wide range of macrobenthic assemblages might thus be expected. Because of the important ecological function of the macrobenthos within the marine ecosystem function, knowledge on the macrobenthic diversity patterns is indispensable to identify priority areas for conservation and for the adjustment of human activities in the marine zone, among other (Costello, 1998).

Early descriptions (1970-1982) of the macrobenthos on the BCS discerned between three zones: a coastal zone with a set of species and abundance poor communities, a species and abundance rich transition zone, and a species rich and abundance poor open sea zone (Govaere et al., 1980; Vanosmael et al., 1982). Although numerous recent data on the macrobenthos of the BCS are available, generalized and updated information on the macrobenthic assemblages and their distribution patterns is lacking. Since 1994, numerous studies focused on the description of the temporal and spatial distribution of the macrobenthos of the BCS (including sandy beaches) are undertaken.

Yet, a clear classification and comparison between the different macrobenthic assemblages described in the different studies is very difficult. To generalize and update the knowledge on the spatial distribution of the macrobenthic assemblages, all macrobenthos data from the Belgian Continental Shelf, collected during the period 1994-2000 (728 samples), were gathered into a database and reanalyzed.

The aims of this paper are (1) to characterize the different macrobenthic communities on the Belgian Continental Shelf on the basis of their species composition, abundance, species richness and their habitat preferences (e.g. sedimentology and bathymetry); (2) to compare the macrobenthic community structure with similar communities in other parts of the North Sea; (3) to understand the relationships between these communities; (4) to investigate the spatial distribution of the communities, with special attention to their diversity patterns along the BCS.

Material and methods

Study area

The study area covers the full Belgian Continental Shelf (BCS) (2600 km²) situated in the southern part of the North Sea and covers less than 0,5 % of the North Sea shelf. The BCS is mainly characterized by the presence of several sandbank systems (Figure 1): (1) Coastal Banks, parallel to the coastline, (2) Flemish Banks, about 10-30 km offshore of the western Belgian coast, (3) Zeeland Banks, some 15-30 km offshore of the eastern Belgian coast, and (4) Hinderbanks, about 35-60 km offshore (Degraer, 1999). Because of the presence of these sandbank systems a high geomorphological and sedimentological diversity is found (Degraer et al., 1999a).

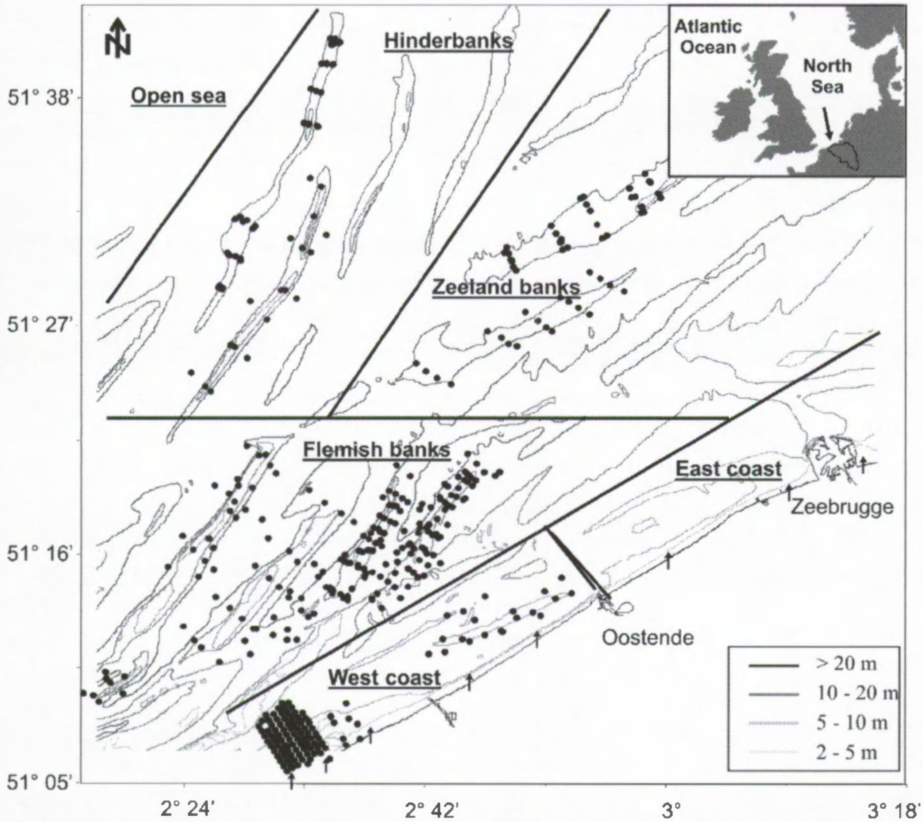


Figure 1. Geographic distribution of the sampling sites investigated for their macrobenthos between 1994 and 2000. Closed circles: subtidal sampling sites; arrows: intertidal sampling transects.

Next to these sandbank systems, the BCS also comprises 65 km of sandy beaches. According to the morphodynamic classification scheme of sandy beaches (Masselink and Short, 1993; Short, 1996), all beaches are classified as low tide bar/rip or ultra-dissipative beaches: tidal range, 4.5 – 5 m; median grain size: 199 – 352 µm; modal breaker height and period: 0.5m and 3s, respectively; width intertidal zone, 200 - 400m (Degraer et al., 2003).

Data origin

Within the framework of several studies, a total of 728 macrobenthos samples (443 sampling sites) were collected at the BCS between 1994 and 2000. Most samples were gathered in late Winter (52 %) or early Autumn (42 %). Because the data were gathered within the framework of different research projects, the sampling sites are unevenly distributed throughout the area (Figure 1). The Flemish Banks and, especially, the western part of the Coastal Banks were intensively studied, while no samples from the open sea zone and the eastern part of the Coastal Banks are available. Samples from the Zeeland - and the Hinder banks are concentrated on the sandbanks, while only few samples were situated in the gullies.

Generally, subtidal samples were taken with a Van Veen grab (sampling surface area: 0.1 m²) and sieved alive over a 1 mm mesh-sized sieve. Sandy beach samples were collected by excavating sediment enclosed by a frame (sampling surface area: 0.1026 m²) to a depth of ca. 0.15 m (Elliott et al., 1996) and sieved alive over a 1 mm mesh-sized sieve. All species were identified to species level if possible.

Water depth at each sampling station was recorded in situ and standardized to the mean low water spring level (MLWS). The grain size distribution of a subsample was measured with a LS Coulter particle size analyzer: median grain size and mud content (volume percentage < 64 µm) were used as granulometric parameters.

All species densities and environmental data (water depth, median grain size and mud content) were incorporated in a Microsoft Access database (MACRODAT) and yielded an original set of 254 taxa, of which 192 macrobenthic species. After exclusion of species that were not sampled quantitatively (e.g. hyperbenthic and extremely rare taxa) and lumping taxa, because of inconsistent identification throughout the different studies (e.g. genus level: *Bathyporeia*, *Ensis*, and *Harmothoe*; family level: Cirratulidae and Capitellidae), a set of 156 taxa (140 species) was used for multivariate analyses. These taxa are further referred to as species.

Community analysis

The community structure was investigated by several multivariate techniques: Group-averaging cluster analysis based on the Bray-Curtis similarity (Clifford and Stephenson, 1975), Detrended Correspondence Analyses (DCA) (Hill and Gauch, 1980) and Two-Way Indicator Species Analysis or TWINSPAN (Hill, 1979; Gauch and Whittaker, 1981), based on a dataset with 728 samples and 156 taxa. The cutlevels for TWINSPAN are chosen in such a way that all the cutlevels contain the same number of values, except the first cutlevel which contains all zero values, and the two last cutlevels which contain an equal number of values that is only the half of that of the other cutlevels (to give a little extra weight to the abundant taxa). TWINSPAN was performed on the non-transformed dataset (cutlevels: 7.9, 9, 17, 39, 100 and 225 ind/m²), while the abundance data were fourth root transformed prior to the cluster analysis and DCA. The results of these techniques were compared to distinguish between groups of biologically similar samples. Indicator species for each of these groups were identified through Indicator Species Analysis (IndVal) and their statistical significance was tested by a Monte Carlo Test (Dufrêne and Legendre, 1997).

The sample groups, resulting from the multivariate analyses, were characterized by means of their taxa composition, abundance, species richness and physical habitat (median grain size, mud content and bathymetry). The multivariate analyses and the description of the species assemblages are based on the dataset, which exist of 156 taxa, only species richness is based on a dataset with the presence of the real macrobenthic species (141 species), without different stages for one species.

Results

General characterization of the macrobenthos

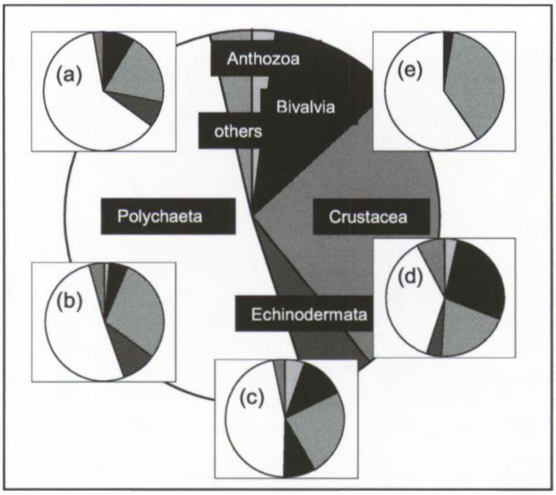


Figure 2. Relative abundance at higher taxonomic levels at the BCS (large pie diagram), (a) the Hinderbanks, (b) Zeeland Banks, (c) Flemish Banks, (d) Coastal Banks and (e) sandy beach (small pie diagrams).

With 83 species (43% of the macrobenthic species), are the polychaetes the most diverse taxon. Crustaceans comprised 65 species (34%), molluscs 32 species (16%), echinoderms 9 species (5%) and 5 species (3%) were anthozoans, nemertineans or pycnogonids. The species with the highest frequency of occurrence were the polychaetes *Nephtys cirrosa* (present in 71% of the samples), *Spiophanes bombyx* (40 %) and *Scoloplos armiger* (40 %).

The total macrobenthic abundance ranged between 8 and 149179 ind/m² (average: 1643 ind/m²). The sites with the highest abundance of macrofauna were situated on the western part of the Coastal Banks. Macrobenthic abundances were dominated by polychaetes, bivalves or crustaceans, depending on the area considered (figure 2). Bivalves (mainly *Spisula subtruncata, Abra alba* and *Mysella bidentata*) and polychaetes dominated the fauna of the Coastal Banks, but the dominance of polychaetes increased towards the more offshore bank areas, whereas the relative abundance of the bivalves decreased. Crustaceans and polychaetes were dominant on the sandy beaches.
Species richness ranged from 1 to 53 spp./0.1m² (average: 11 spp./0.1m²).

General distribution patterns

The distribution of the macrobenthic species richness and abundance along the onshore-offshore gradient follows a highly variable pattern, with species and abundance poor stations along the full gradient and species and abundance rich stations restricted to the coastal zone (< 15 miles offshore) (Figure 3). However, the trendlines both show a unimodal distribution, with peak values at about 3 nautical miles decreasing both offshore and towards the sandy beaches.

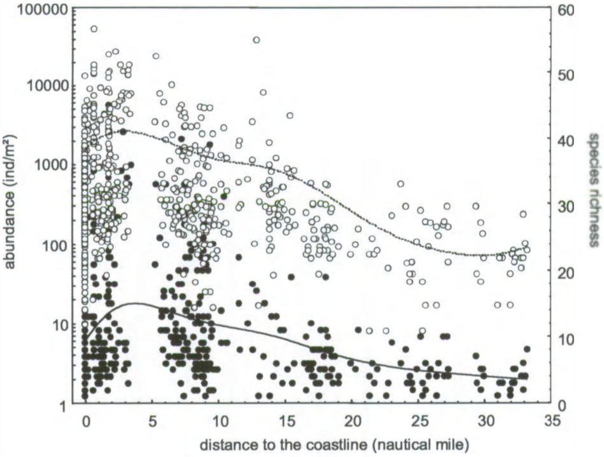


Figure 3. The species richness (species/sample) and abundance (ind/m²) distribution across the onshore – offshore gradient at the BCS. Trend lines set using Least squares methods. Species richness: black points, solid trend line; Abundance: open points, dotted trend line.

The species richness and abundance are highly correlated (Spearman rank: $p < 0.05$) with the sediment's mud content and median grain size. A high species richness (> 15 spp. sample-1) and abundance (> 2000 ind/m²) was mainly found in fine to medium sandy sediments (median grain size: < 300 μm) with a relatively high mud content (> 3 %) (Figure 4). Coarser sediments and/or low mud contents generally yielded species- and abundance-poor samples. Sediments characterized by coarser sediments with a high mud content were not encountered at the BCS. High densities generally corresponded with a high species richness (Spearman rank correlation: R = 0.756; p< 0.05), explaining the similar distribution patterns of species richness and abundance.

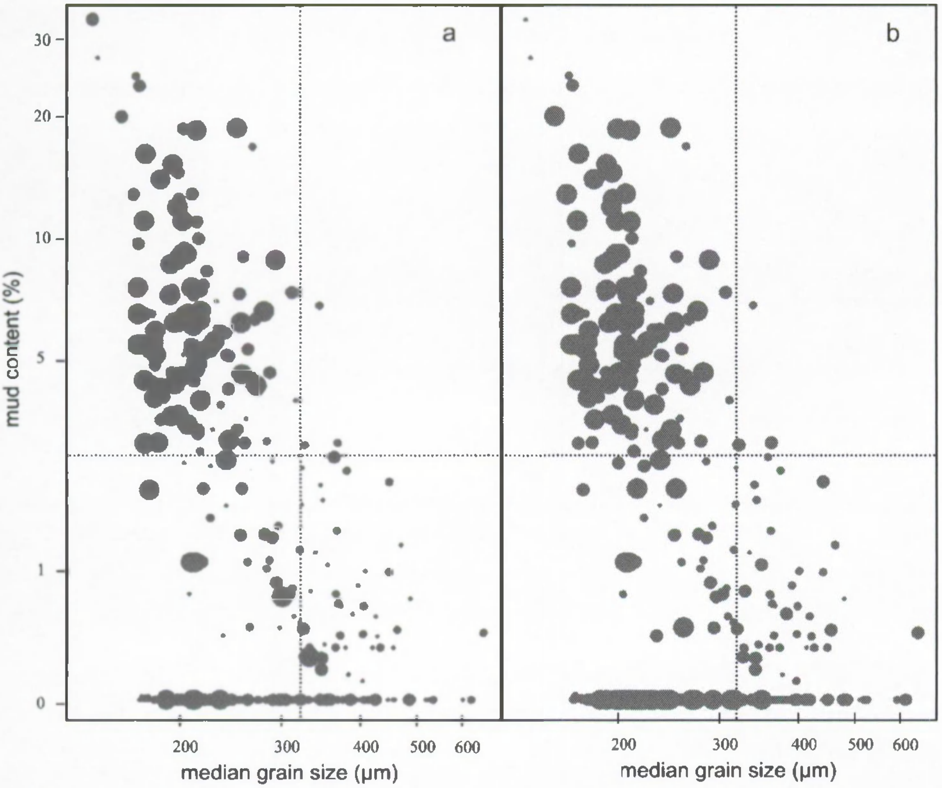


Figure 4. The species richness (N_0) and abundance (ind/m²) in relation to the sedimentolgical characteristics (median grain size and mud content). (a) Species richness (species/sample) • < 10; ● 10-15; ● 15-30; ● 30-55. (b) Abundance (ind/m²): • < 150; ● 150-500; ● 500-2000; ● > 2000.

Species assemblages: macrobenthic structure, habitat preferences and distribution

Based on the multivariate analyses, ten sample groups were distinguished (Figure 5). Because each of these groups is composed of samples with a similar species composition, the groups are further referred to as 'species assemblages' (SA). The first DCA axis (Eigenvalue: 0.645) was negatively correlated with the sampled sites' depth and mud content (respectively correlation factors are –0.395 and –0.490); while the second DCA axis (Eigenvalue: 0.215) was positively correlated with the sediment's median grain size (correlation factor is 0.379).

Based on their position in the DCA plot, two types of species assemblages were identified. Type I species assemblages are situated at the edges of the multivariate biological gradients: SA1 and SA10 (ordination axis 1) and SA4 and SA6 (ordination axis 2). Type II species assemblages are positioned in between Type I species assemblages: SA2, SA3, SA5, SA7, SA8, and SA9.

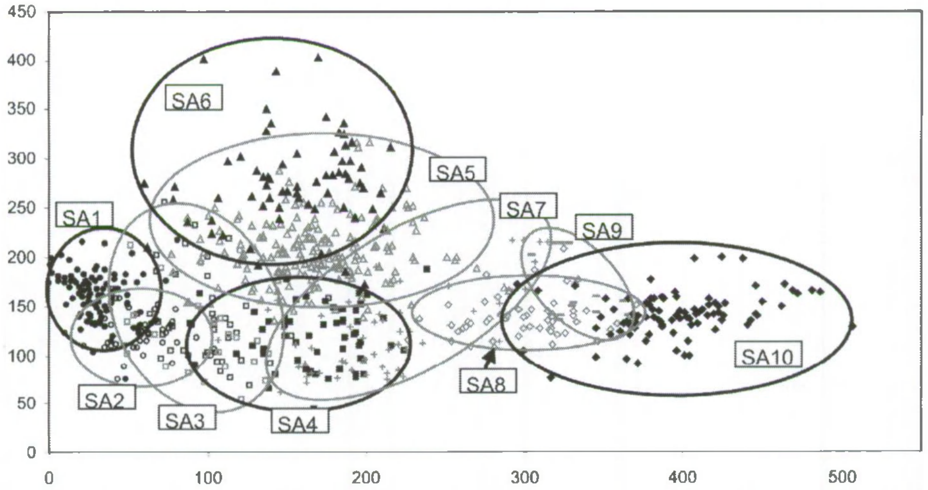


Figure 5. DCA ordination plot along the first two axes. The discrimination between sample groups is based on TWINSPAN, Cluster analysis and DCA. Position of the sample groups (species associations) is indicated by the ellipses. ●, SA1; ○, SA2; □, SA3; ■, SA4; Δ , SA5; ▲, SA6; +, SA7; ◊, SA8; -, SA9; ♦ , SA10.

Type I species assemblages (Table 1)

SA1 is characterized by the highest species richness (30 spp./sample) and macrobenthic abundance (6432 ind/m^2). Especially the bivalve *Spisula subtruncata* reached very high abundance (2943 ind/m^2), followed by several polychaete, bivalve and amphipod species with average abundance of more than 200 ind/m^2. Eight species were significantly (Monte Carlo permutation test: $p < 0.05$) indicative for SA1, all of which had an indicator value (IV) of at least 50. Three of these indicative species were found in high abundance: the bivalves *Abra alba* (514 ind/m^2) and *Mysella bidentata* (419 ind/m^2) and the amphipod *Pariambus typicus* (435 ind/m^2). Numerous species (e.g. the polychaetes *Sthenelais boa*, *Owenia fusiformis*, and *Pectinaria koreni*, the bivalve *Mya truncata*, and the amphipod *Ampelisca brevicornis*) were exclusively found within this species assemblage. SA1 is found in fine sandy sediments (median grain size: 219 µm), with a relatively high mud content (6 %), at an average depth of 13 m below MLWS.

SA4 has a rather low species richness (7 spp./sample) and abundance (402 ind/m^2). Except for the polychaete *Magelona johnstoni* (105 ind/m^2), all species had an abundance less than 100 ind/m^2. Only two species were significantly indicative for SA4: the polychaetes *Scolelepis bonnieri* and *Nephtys cirrosa*. Yet, both species had rather low indicator values (IV: 20 and 13, respectively). Only *Nephtys cirrosa* occurred in a relatively high abundance (84 ind/m^2). SA4 inhabits well-sorted fine to medium sandy sediments (median grain size: 274 µm), with low mud contents (< 1%), at an average depth of 12 m below MLWS.

A low species richness (5 spp./sample) and abundance (190 ind./m^2) is characteristic for SA6. All species occurred in low densities (maximum 32 ind./m^2). Two species are significantly indicative: the polychaetes *Ophelia limacina* (IV: 28) and *Glycera lapidum* (IV: 26), and with a respectively abundance of 17 and 9 ind. m-2. SA6 is found in medium sandy sediments (median grain size: 409 µm), with a low mud content (< 1%), at an average depth of 15 m below MLWS.

SA10 is characterized by a very low species richness (5 spp./sample), but relatively high abundance (983 ind/m²). Three species had an abundance of more than 200 ind/m²: the amphipod *Bathyporeia spp.* (357 ind/m²), the polychaete *Scolelepis squamata* (343 ind/m²) and the isopod *Eurydice pulchra* (218 ind/m²). All other species were found in abundances of maximum 21 ind/m². *Eurydice pulchra* (IV: 54) and *Scolelepis squamata* (IV: 44) were significantly indicative. SA10 inhabits pure (mud content: < 1%), fine to medium sandy sediments (median grain size: 248 µm) at the upper intertidal zone of the sandy beaches (4 m above MLWS).

Type II species assemblages (Table 1)

As suggested by the position of the Type II species assemblages in the DCA plot, these species assemblages are representing a gradual biological shift between the different Type I species assemblages.

SA2 and SA3 represent a transition in between the SA1 and SA4: a gradual decrease in macrobenthic abundance (SA2: 2746 ind/m²; SA3: 2017 ind/m²) and species richness (SA2: 18 spp./sample; SA3: 13 spp/sample) is observed. Comparing the list of the ten most abundant species, a gradual shift in taxa composition is found: SA2 has five dominant taxa in common with SA1 and only one with SA4, while SA3 has four dominant taxa in common with SA1 and no less than six taxa with SA4. SA2 and SA3 have four dominant species in common. SA2 and SA3 are characterized each by one species with high densities: post-larval and juvenile *Spisula* (SA2) and *Magelona johstoni* (SA3). SA2 is found in fine sandy sediments (median grain size: 208 µm) similar as SA1, while SA3 occurs in fine to medium sandy sediments (median grain size: 268 µm) similar as SA4. SA2 and SA3 show a gradual decrease in mud content between SA1 and SA4 (4 and 2 %, respectively). The depth range of both species associations falls within the range of 8 and 14 m below MLWS.

SA5 is found in between SA4 and SA6. This species assemblage has a similar species richness as both SA4 and SA6 (N0: 8 spp./sample), while its average macrobenthic abundance (304 ind/m²) was found between that of SA4 and SA6. SA5 had seven abundant taxa in common with SA4 and five with SA6. SA5 is found in medium sandy sediments (median grain size: 333 µm) with a low mud content (< 1%) at a depth of 16 m below MLWS.

In between SA4 and SA10, the gradual transition is represented by a complex of three species assemblages (SA7-SA9). SA7 had five abundant taxa in common with SA4 and only two with SA10, while both SA8 and SA9 had a abundant taxa composition similar to SA10 (7 and 6 spp. in common, respectively) rather than to SA4 (1 and 2 spp. in common, respectively). The species richness and abundance of all three species assemblages ranged between 5 and 8 spp./sample and 101 and 482 ind/m², respectively. The depth ranges from 2 below MLWS (SA7) to 2 m above MLWS (SA8-SA9). The three species assemblages are found in fine sandy sediments (median grain size: 219 – 243 µm) with a low mud content (< 1 %).

Table 1. Characterization of the species assemblage (environment: median grain size (µm), mud content (%), and depth (m); macrobenthos: species richness (N_0 and N_1), abundance (macrobenthic abundance and species-specific abundance of the 10 most abundant species per species assemblage, ind./m²), and indicator species-specific values (*: higher indicator value in another SA)). Species association: typology

	SA 1		SA 2		SA 3		SA 4		SA 5	
Environmental parameters:										
median grain size	219,24		208,28		267,85		274,02		333,07	
mud content	5,79		4,32		1,89		0,37		0,19	
depth	-12,56		-7,9		-13,93		-11,82		-16,07	
Macrobenthic variables:										
Diversity										
N_0	31		19		14		7		8	
N_1	11,008		5,678		6,476		4,754		4,979	
Densities										
mean densities	6432		2746		2017		402		304	
density top 10	*Spisula subtruncata*	2943	*Spisula subtruncata*	1637	*Magelona mirabilis*	1263	*Magelona mirabilis*	105	*Nepthys cirrosa*	60
	Scoloplos armiger	524	*Magelona mirabilis*	427	*Micropthalmus similis*	116	*Nephtys cirrosa*	84	*Urothoe brevicornis*	40
	Abra alba	514	*Spio filicornis*	130	*Scoloplos armiger*	102	*Bathyporeia* spp.	78	*Bathyporeia* spp.	33
	Pariambus typicus	435	*Fabulina fabula*	76	*Spiophanes bombyx*	71	*Urothoe poseidonis*	22	*Ophiura* spp. juv.	27
	Mysella bidentata	419	*Lanice conchilega* juv	64	*Nephtys cirrosa*	60	*Ophiura* spp. juv.	19	*Spiophanes bombyx*	27
	Magelona mirabilis	406	*Nephtys hombergii*	47	*Fabulina fabula*	48	*Scoloplos armiger*	15	*Scoloplos armiger*	24
	Lanice conchilega	273	*Lanice conchilega*	32	*Bathyporeia* spp.	27	*Scolelepis bonneri*	10	*Hesionura elongata*	12
	Capitellidae spp.	265	*Spiophanes bombyx*	31	*Urothoe poseidonis*	26	*Nephtys* spp. juv.	8	*Ophelia limacina*	9
	Spiophanes bombyx	232	*Ensis* spp.	30	*Spisula subtruncata*	21	*Hesionura elongata*	8	*Spio filicornis*	8
	Eumida sanguinea	214	*Mysella bidentata*	24	*Nephtys* spp. juv.	20	*Urothoe brevicornis*	8	*Nephtys* spp. juv.	5
Indicator species										
	Abra alba	64	*Spisula subtruncata*	46	*Magelona mirabilis*	16*	*Scolelepis bonneri*	20	*Urothoe brevicornis*	31
	Anaitides mucosa	53	*Nephtys hombergi*	29	*Scoloplos armiger*	15*	*Nephtys cirrosa*	13*	*Nephtys cirrosa*	14*
	Sthenelais boa	53	*Sigalion mathildae*	21	*Spiophanes bombyx*	13*			*Ophelia limacina*	14*
	Cirratulidae spp.	51	*Lanice conchilega*	21*	*Nephtys cirrosa*	12*				
	Owenia fusiformis	51								
	Mysella bidentata	51								
	Pariambus typicus	51								
	Pectinaria koreni	50								
Species assemblage										
	Type I SA *Abra alba - Mysella bidentata* community		Type II SA		Type II SA		Type I SA *Nephtys cirrosa* community		Type II SA	

	SA 6		SA 7		SA 8		SA 9		SA 10	
Environmental parameters:										
median grain size	409,05		218,91		242,64		230,15		248,44	
mud content	0,25		0,04		0,05		0		0,01	
depth	-15,32		-2,12		2,01		2,4		3,8	
Macrobenthic variables:										
Diversity										
N_0	6		5		8		5		5	
N_1	3,968		2,912		4,523		3,395		2,505	
Densities										
mean densities	190		135		482		101		983	
density top 10	*Hesionura elongata*	32	*Nephtys cirrosa*	66	*Capitellidae* spp.	126	*Bathyporeia* spp.	48	*Bathyporeia* spp.	357
	Nepthys cirrosa	32	*Bathyporeia* spp.	15	*Spio filicornis*	61	*Nepthys cirrosa*	19	*Scolelepis squamata*	343
	Ophelia limacina	17	*Urothoe poseidonis*	11	*Pygospio elegans*	59	*Scolelepis squamata*	15	*Eurydice pulchra*	218
	Ophiura spp. juv.	10	*Magelona mirabilis*	5	*Eteone longa*	49	*Spio filicornis*	5	*Psammodrilus balanoides*	21
	Glycera lapidum	9	*Spio filicornis*	5	*Scolelepis squamata*	39	*Eurydice pulchra*	4	*Eteone longa*	10
	Oligochaeta spp.	9	*Spisula subtruncata*	3	*Bathyporeia* spp.	37	*Pygospio elegans*	3	*Eurydice affinis*	10
	Echinocyamus pusilus	6	*Scoloplos armiger*	3	*nt-Calanoide Copepoda*	34	*Eteone longa*	2	*Pygospio elegans*	5
	Actinaria spp.	6	*Portumnes latipes*	3	*Hesionura arenaria*	14	*Hesionura arenaria*	2	*Capitellidae* spp.	5
	Ophiura spp.	6	*Capitellidae* spp.	3	*Psammodrilus balanoides*	14	*Polydora* spp.	2	*Hesionura arenaria*	4
	Urothoe brevicornis	5	*Nepthys hombergii*	3	*Cumopsis goodsiri*	14	*Cumopsis goodsiri*	1	*Ophelia rathkei*	4
Indicator species										
	Ophelia limacina	28	*Nephtys cirrosa*	15	*Pygospio elegans*	32	*Scolelepis squamata*	26*	*Eurydice pulchra*	54
	Glycera lapidum	26	*Portumnes latipes*	15	*Cumopsis goodsiri*	32	*Bathyporeia* spp.	11	*Scolelepis squamata*	44
					Eteone longa	27	*Nephtys cirrosa*	10*		
Species assemblage										
	Type I SA *Ophelia limacina-Glycera lapidum* community		Type II SA		Type II SA		Type II SA		Type I SA *Eurydice pulchra-Scolelepis squamata* community	

Geograpical distribution

Each species assemblage was found over a specific range along the onshore – offshore gradient (Figure 6). Four distribution types can be identified. The distribution of a first type (SA1 – SA3) ranged from 0 to 15 nautical miles and showed a nearshore average distribution (4 miles). A second type (S4 – SA6) was found across the full onshore – offshore gradient (range: 34 miles), with a species assemblage dependent average distribution, increasing from SA4 to SA6 (9 – 20 miles). A third type (SA7) showed a strictly nearshore distribution (0 – 3 mile). Finally, SA8 – SA10 were restricted to the coastline (i.e. sandy beaches).

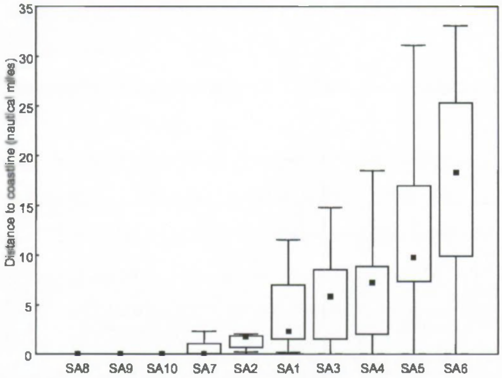


Figure 6. The onshore – offshore distribution of the ten species assemblages. Median distance (▪) + Percentiles (25% - 75%) (Boxes) and Non - Outlier range (Min – Max) (Whiskers).

Discussion

Communities and transitions

The term community is widely used and most definitions of communities include the idea of a collection of species found in a particular place (physical habitat); other ecologists found that these species must interact in some significant way to be considered as community members (Morin, 1999). One of the basic studies on the community concept in marine biology is from Mills (1969). He compared several definitions both in plant and animal biology and the discussion resulted in a final definition: "a community is a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment and separable from other groups by means of an ecological survey". Recently, Morin (1999) gave a good overview of the different approaches to delineate communities: (1) physically, by discrete habitat boundaries, (2) taxonomically, by the identify of a dominant indicator species, (3) interactively, by the existence of strong interactions among species or, (4) statistically, by patterns of assemblages among species.

Based on Morin's (1999) first (habitat boundaries) and fourth (statistical assemblages) approach to distinguish between communities, the four Type I species assemblages (SA1, SA4, SA6 and SA10) can be considered as communities because of (1) their extreme position along the habitat gradients (depth, mud content and median grain size) (figure 7) and, consequently, (2) the absence of overlap between the habitat of each species assemblages, based on the results of the multivariate analyses. The relationship between recurring groups of soft-bottom animals and certain sediment types and depth zones, was first described by Petersen (1914). Jones (1950) put forward an alternative classification of species groupings based on sediment and depth characteristics, followed by several other authors (e.g. Thorson, 1957; Kingston and Rachor, 1982; Duineveld et al., 1991, Heip and Craeymeersch, 1995; Degraer et al., 1999a).

Although these communities are found in a particular habitat (sedimentology and depth) and characterized by typical community parameters (diversity, density and species composition), the physical and biological boundaries of these four macrobenthic communities are not strict. Many ecological studies already demonstrated the unimodal distribution of species along environmental gradients. Following this approach, the discrimination of communities, defined as the collection of organisms occurring in the same environment, is a merely arbitrary abstraction of biological gradients: gradual transitions between different communities exist (Gray, 1981). Gradual biological and physical transitions between the four macrobenthic communities of this study are represented by the Type II species assemblages (further called: transitional species assemblages) (figure 7). These species assemblages are characterized by the occurrence of species of both related communities but in lower densities. Some of the transitional species associations are also characterized by typical species, such as *Magelona johnstoni* in SA3.

The macrobenthic communities of soft-bottom sediments at the BCS

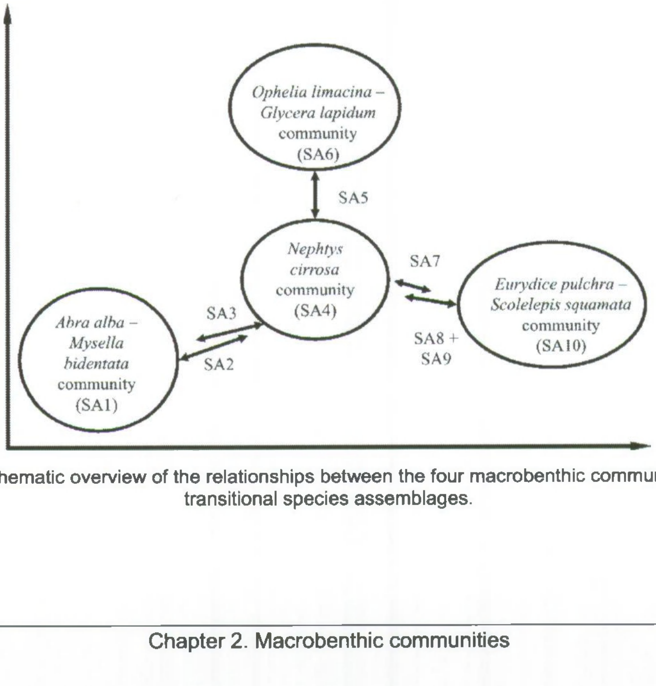


Figure 7. Schematic overview of the relationships between the four macrobenthic communities and the transitional species assemblages.

Four of the ten species associations (Type I species assemblages) thus differ drastically, both in habitat and species composition, and are considered to represent four macrobenthic communities. Based on their discriminating indicator species these communities are further referred to as the subtidal *Abra alba - Mysella bidentata* community (SA1), the *Nephtys cirrosa* community (SA4), the *Ophelia limacina - Glycera lapidum* community (SA6) and the intertidal *Eurydice pulchra - Scolelepis squamata* community (SA10) (Figure 7).

The Abra alba – Mysella bidentata community (SA1)

The *A. alba – M. bidentata* community seems to be of exceptional ecological importance: (1) high macrobenthic abundance (6432 ind/m²) and diversity (31 spp./sample), (2) high number of bivalves (e.g. *Spisula subtruncata* and *A. alba*) possibly serving as an important food resource for sea ducks or demersal fishes (Degraer, 1999), (3) numerous unique species for the Belgian Continental Shelf (e.g. *Ampelisca brevicornis*, *Owenia fusiformis*, *Sthenelais boa*, *Pectinaria koreni* and *Mya truncata*), and (4) the occurrence of habitat structuring species, such as *Lanice conchilega* (273 ind./m²) (Buhr and Winter, 1976; Dauvin, 2000; Ropert and Dauvin, 2000; Ropert and Goulletquer, 2000). This community is found in near shore shallow muddy sands (median grain size: 219 µm and mud content: 6%).

Because of its similar habitat preferences, macrobenthic abundance (2500 ind/m²) and diversity (18 spp./0.1m²) and the abundant occurrence of *A. alba* (139 ind/m²) and *L. conchilega* (228 ind/m²), the community should be regarded as a synonym for the *L. conchilega* community, as found and described by Degraer et al. (1999a) at the Belgian Coastal Banks.

A very similar *A. alba* community was described from areas South (French North-Atlantic and English Channel coast: Souplet and Dewarumez, 1980, Prygiel et al., 1988; Olivier et al., 1996; Dauvin 1998, 2000; Ghertsos et al., 2000, 2001; Desroy et al., 2002) and North (Dutch and German coast: Glémarec, 1973; Kingston and Rachor, 1982; Duineveld et al., 1991; Künitzer et al., 1992; Holtmann et al., 1996) of the BCS and is typically patchy distributed in shallow, nearshore waters (Jones, 1950; Cabioch and Glaçon, 1975). The average densities (5080 ind/m²) diversity (33 spp./0.1m²) and species composition (*L. conchilega, A. alba, Spiophanes bombyx*) of the *A. alba* community along the Northern French Coast (Calais) are similar to the *A. alba – M. bidentata* community of the BCS (Fromantin et al., 1996; Desroy et al., 2002), but the total number of species increased further to the south (from + 150 (Gravelines) to 300 à 400 (Pierre Noire)) (Fromantin et al., 1997). Compared to the BCS, the *A. alba* community along the Dutch coast is characterized by lower densities (average: 2556 ind/m²) and diversity (14 spp./0.1m²) (Holtmann et al., 1996).

Compared with biological classifications provided in literature, the *A. alba – M. bidentata* community belongs to the 'boreal offshore muddy sand association', which is equivalent to Petersen's *Echinocardium - Amphiura filiformis* communities (Jones, 1950).

The Nephtys cirrosa community (SA4)

The diversity (7 spp./sample) and abundance (402 ind/m²) in the *Nephtys cirrosa* community are low, which is typical for well-sorted mobile sands, and mostly characterized by mobile polychaetes (e.g. *N. cirrosa*) and crustaceans (e.g. *Bathyporeia* spp.).

Because of the large niche width of *N. cirrosa* (eurytopic species) (Rainer, 1991), this polychaete species is found in several transitional species associations (SA3, SA5, and SA7; average abundance: about 60 ind/m²), explaining its low indicator value (IV: 14), as well as the large overlap of the community with several transitional species assemblages. The *N. cirrosa* community takes a central place within the overall macrobenthic community structure of the BCS: all transitions between the communities pass by the *N. cirrosa* community.

At the Belgian Coastal Banks, Degraer et al. (1999a) described a *N. cirrosa* community and a *N. cirrosa – Echinocardium cordatum* community, which are characterized by a moderate abundance of *N. cirrosa* (respectively 93 and 70 ind/m²) and a low diversity (respectively 5 and 8 spp./0.1m²). Because of the similar physical habitat both communities were later lumped to the *N. cirrosa* community s.l. (Degraer, 1999).

Within adjacent areas, a species assemblage dominated by *N. cirrosa* (86 ind/m²) and *Bathyporeia* spp. (52 ind/m²) (Holtmann et al., 1996), characteristic for well-sorted sandy sediments with low mud content, is described by many authors (Curras et al., 1991; Duineveld, et al., 1991; Künitzer et al., 1992; Holtmann et al., 1996; Bachelet et al., 1996). Most probably the *N. cirrosa* community of this study should be regarded as part of or as synonym of the species assemblages occurring in well-sorted sandy sediments.

Jones (1950) included this community in the 'Boreal offshore sand association' – equivalent to Petersen's *Venus* communities.

The Ophelia limacina – Glycera lapidum community (SA6)

The *O. limacina – G. lapidum* community, with a very low diversity (6 spp./sample) and abundance (190 ind/m²), occurred in medium to coarse sandy sediments. Also the presence of shell fragments in the sediment is an important characteristic (Govaere et al., 1980). *G. lapidum* is typical for coarse sandy sediments, while *O. limacina* can also be found in low abundances in fine to medium sand, with very low mud content (Govaere, 1978; Hartmann-Schröder, 1996).

Interstitial polychaetes, such as *Hesionura elongata* (32 ind/m²), were also found, but most probably the abundance of these species is strongly underestimated in this study: former descriptions of this community revealed high abundances (up to 800 ind/m²) of interstitial polychaetes (Govaere, 1978). This might be explained by differences within the post-sampling treatment used by both authors compared to this study: sieving after fixation (Govaere, 1978) versus sieving alive (this study), allowing the interstitial polychaetes to escape actively through the sieve. Interstitial polychaetes become abundant at a median grain size of more than 300 µm (Willems et al., 1982).

The habitat characteristics (median grain size: 456 µm), diversity (4 spp./sample) and abundance (177 ind/m²) of the '*Mytilus edulis*' community (Degraer et al., 1999a) is similar to the *O. limacina – G. lapidum* community. The former community was characterized by the presence of juvenile *M. edulis* (the '*M. edulis*' community), but this juvenile bivalve may perform strong seasonal fluctuations in density. The juvenile individuals can attach to the coarse sediment particles, but when they grow, the chance of being washed out increases.

The *Venus fasciata* community is typically found in medium to coarse sandy sediments in the English Channel, well subdivided into various facies, and characterized by species such as *Travesia forbesi*, *Lumbrineris latreilli* and *N. cirrosa* (Cabioch, 1968). The facies '*Ophelia borealis* community' (syn. *O. limacina* community) is typically found in medium to coarse sediments mixed with gravel or shell fragments of the coastal sandbanks along the Normandy and Southern North Sea coasts at a depth of more than 10 m (Holtmann et al., 1996, Sanvicente-Anorve et al., 2002). A low number of species (26) (Souplet and Dewarumez, 1980) and abundance is typical for this community (Cabioch, 1968, Cabioch and Glaçon, 1977, Dewarumez et al., 1990). The low values may be explained by the harsh conditions at sandbanks in the Southern North Sea: according to Vanosmael et al. (1982), the top of these sandbanks as well as the ripples are continuously broken down and rebuilt by strong hydrodynamic forces. Hence, sessile tube-building polychaetes only represent a small number of individuals, whereas the dominant species are composed of mobile, burrowing organisms (Whiters and Thorp, 1978).

According to Jones (1950) this community is also included in the 'Boreal offshore sand association' – equivalent to Petersen's *Venus* communities.

The Eurydice pulchra – Scolelepis squamata community (SA10)

The *E. pulchra – S. squamata* community is exclusively found at the upper intertidal zone of Belgian sandy beaches and is characterized by a low diversity (5 spp./sample) and moderate abundances (983 ind/m²), mainly of *E. pulchra*, *S. squamata* and *Bathyporeia* spp.

Bathyporeia spp. and *E. pulchra* are found to be abundant on many European beaches (Eleftheriou and McIntyre, 1976, Degraer et al., 1999b), while *S. squamata* is also an abundant species on many Atlantic beaches (Souza and Gianuca, 1995; Eleftheriou and McIntyre, 1976; McDermott, 1987). Parallel communities, in which species might be replaced by (functionally) similar species, can be found within the upper intertidal zone of many sandy beaches worldwide (McLachlan and Jaramillo, 1995).

Special communities

Next to these four macrobenthic communities Degraer et al. (1999a) found an extremely rare (only one station) macrobenthic community in outcropping tertiary clay layers nearby Oostende, which he defined as the *Barnea candida* community. This rather diverse (species richness: 10 spp./sample) community occurs in a muddy (median grain size: 14 µm), shallow (8 m) sediment, containing high numbers of the bivalve *B. candida* (117 ind/m²). Recent sampling surveys confirmed the existence of this community in the gully Kleine Rede nearby Oostende.

Although being present at the BCS, gravel beds were not sampled qualitatively nor quantitatively for their macrobenthos, because of a lack of good sampling gear for this habitat (f.i. Hamon grab). Some accidental samples within this habitat revealed the presence of a very specific fauna (e.g. sponges and sea spiders) (pers. obs.). The macrobenthos of gravel and boulder beds is characterized by a specific set of species that differs drastically from the surrounding sandy environment, but rather shows similarities with the macrofauna of rocky substrates (Kenny et al., 1996; De Grave, 1999; Newell et al., 2001).

Temporal effects

Macrobenthic communities in temperate regions are subjected to a large year-to-year variability of the community structure (Turner et al., 1995). Temporal variability within the *A. alba – M. bidentata*, *N. cirrosa* and *O. limacina – G. lapidum* communities at the Western Coastal Banks was studied by Degraer (1999). They concluded that temporal variability in community parameters are prominent, but community shifts were not detected. As long as the main habitat characteristics do not change drastically, the basic composition and the distribution (including natural variability, such as seasonality) of the respective communities will remain stable over long periods of time (Govaere et al., 1980; Turner et al., 1995; Degraer, 1999). Temporal variability should thus be considered as being subordinate to spatial variation and the existence of six relatively stable macrobenthic communities at the BCS can be confirmed.

Only one dramatic temporal event, linked to the recruitment of *Spisula subtruncata*, was discerned in this study. In case of a (very) successful recruitment (e.g. August 1995), a surficial layer of 1 to 2 cm of post-larval *S. subtruncata* possibly caused an increased mortality of several other macrobenthic species and thus altered the general community structure (Degraer, 1999). This phenomenon is probably reflected within the species composition of SA2, which should be considered as a temporally impoverished *A. alba – M. bidentata* community.

Geographical distribution

Unlike the relationship between the macrobenthic distribution and the physical habitat (Gray, 1974; Creutzberg et al., 1984; Buchanan, 1984; Snelgrove and Butman, 1994), the macrobenthic geographical distribution across the onshore-offshore gradient is poorly documented. Yet, this geographical distribution is of utmost importance from a national and international legislation perspective, in which distance from the shore (e.g. 3-miles and 12-miles zone) is used to set limits for fisheries (Maes et al., 2000). Detailed knowledge on the macrobenthic geographical distribution will contribute to a well deliberated use of the marine environment.

A first attempt to document the macrobenthos along the onshore-offshore gradient of the BCS is given by Govaere et al. (1980), discriminating between three zones: (1) a coastal zone with a set of species- and density-poor communities, (2) a species- and density-rich transition zone, and (3) a species-rich and density-poor open sea zone. Yet, because this study was based on only 74 sites, of which most were situated in the coastal zone and did not include the different sandbanksystems nor the sandy beaches, it was doubted whether the distinction between three zones provided a detailed and reliable view on the macrobenthic distribution at the BCS. A more complex macrobenthic distribution can be expected and was indicated through several consequent studies (Vanosmael et al., 1982; Willems et al., 1982; Degraer et al., 1999a, 1999b, 2003).

Because of (1) the increase of the number of samples taken into account and (2) the widespread distribution of these samples, compared to Govaere et al. (1980), a more detailed view on the onshore-offshore diversity, abundance and community structure patterns is attained through this study. This distribution has to be considered as being very scattered: although a weak correlation between the zones of Govaere et al. (1980) and distribution patterns of this study was found, both cannot unambiguously be linked. Contrary to Govaere et al. (1980), the (subtidal) coastal area of the BCS cannot be characterized solely by species and abundance poor communities: a wide variety from macrobenthos poor to rich stations was encountered in the coastal zone, including the stations with the highest species richness and densities (i.e. *A. alba – M. bidentata* community). The high macrobenthic diversity of the coastal zone is further illustrated by the presence of all subtidal species assemblages, distinguished in this study. Analogous to the benthic characterization of the transition zone (Govaere et al., 1980), a set of highly species- and density-rich stations and assemblages (e.g. *A. alba – M. bidentata* community) was found in between 5 and 15 miles offshore. Nevertheless, also macrobenthos poor stations and assemblages (e.g. *N. cirrosa* community) were encountered. Finally, the characterization of the open sea zone (> 15 miles offshore) as a species rich and density poor area, is contradicted by this study: a typically low density, but also a low species richness, was found. All assemblages found in this zone (i.e. *N. cirrosa* and *O. limacina – G. lapidum* community) have a low species richness and density. This study further demonstrated the existence of a typical intertidal community, with a low species richness but high density, which were not distinguished by Govaere et al. (1980).

The highly complex and diverse geomorphological environment of the subtidal part of the BCS (covered with sandbanks) can explain the rather scattered macrobenthic distribution. Within sandbank areas, even within some tens of meters, completely different types of sediment can be encountered (Gray, 1974; Vlaeminck et al., 1989; Degraer et al., 1999a). Because of the high correlation between the macrobenthos (species richness, density and species assemblages) and the physical environment (sediment mud content and median grain size, this study), this small-scale physical variability thus explains the large benthic variability along the onshore-offshore gradient. Yet, irrespective of the rather scattered benthic distribution an onshore-offshore gradient was detected: the variability at the species richness, macrobenthic density and species assemblage level is decreasing towards the open sea. These macrobenthic distribution patterns on a larger scale are more influenced by ebb-dominated currents (Sanvicente-Anorve et al., 1996). Flood-dominated currents heading towards the northeast along the coast occur onshore, while the offshore area is controlled by ebb-dominated currents pointing towards the southwest (Vlaeminck et al., 1989). The irregular and patchy distribution of sediments in the coastal zone (Ruddick et al., 1998), combined with its diverse topography, creates a wealth in habitats and thus supports a high capacity for various species assemblages, explaining the high benthic variability in the onshore zone. In contrast, sediments in the offshore area are generally coarse, due to strong currents and have a very low mud content (Ruddick et al., 1998). These sediments are inhabited by only relatively few species and density poor assemblages, explaining the low benthic variability in the offshore area. The local diversity in all these different habitats are strongly influenced by recruitment effects, species interactions or environmental perturbations including those attributable to human activity in the different areas (Dewarumez et al., 1992; Heip et al., 1992).

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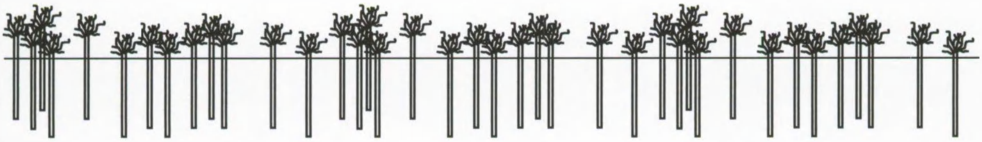
Chapter 3

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



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Abstract

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

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

Introduction

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

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

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

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

The *A. alba* community is found in the English Channel and Southern Bight of the North Sea, mostly in bays, estuaries and in a narrow zone along the coastline (Fromentin et al., 1997; Thiébaut et al., 1997;

Rees et al., 1999; Ghertsos et al., 2000; Desroy et al., 2002; Dauvin et al., 2004). However, there is one large continuous distribution area of the *A. alba* community: the coastal area, from Cap Griz-Nez (France) over Belgium north to the Dutch coast (Vanosmael et al., 1982; Vermeulen and Govaere, 1983; Prygiel et al., 1988; Fromentin et al., 1997; Desroy et al., 2002). In this continuous area gradual changes of the species composition, abundance and diversity within the *A. alba* community, related to the changing environment, are documented (Holtmann et al., 1996; Fromentin et al., 1996, 1997; Desroy et al., 2002; Van Hoey et al., 2004).

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

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

Materials and Methods

Study area

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

Data origin

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

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

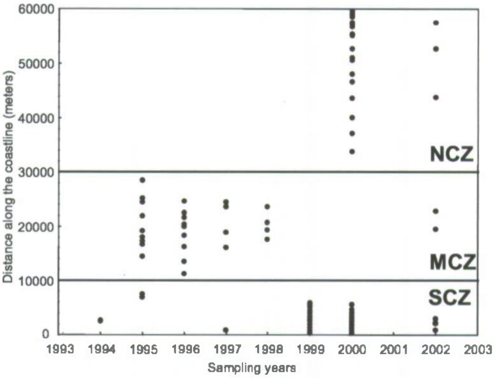

Figure 1. The sampling years in function of the distance along the coast (meters)

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

Data analysis

Mapping

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

Diversity

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

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

Functional diversity

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

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

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

Results

Distribution of the *Abra alba* community at the BCS

The *A. alba* community was found in muddy, fine sandy sediments with an average median grain size of 227 µm (+ 47 µm (SD)). The sediment composition was characterized by the dominance of the fine sand fraction (average: 49% - Figure 2a) combined with a low, though significant, mud fraction (9%: clay and silt) and coarse sand fraction had much lower contributions (9% and <5% respectively). The community could be found at depths between 4 m and 29 m (average depth of 15 m).

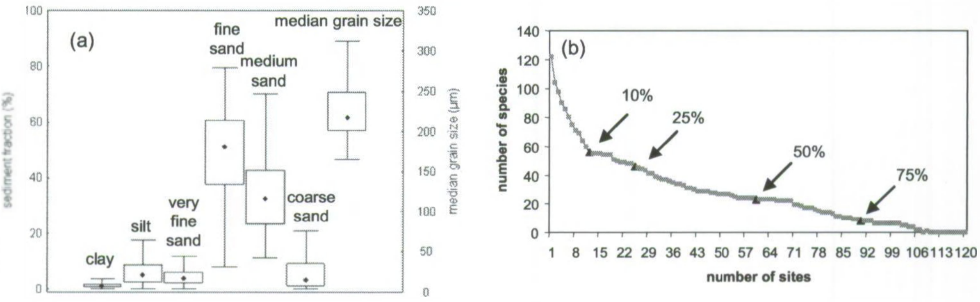

Figure 2. a) The sediment fraction (left) and the median grain size (right) of the *Abra alba* community. Median (symbol) + percentiles (25% -75%) (Boxes) and Non-Outlier range (Min – Max) (Whiskers). b) Distribution of species range size, which is the number of stations occupied by a species out of a total of 120 sites, with indication of the points representing 10, 25, 50 and 75% of the total stations.

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

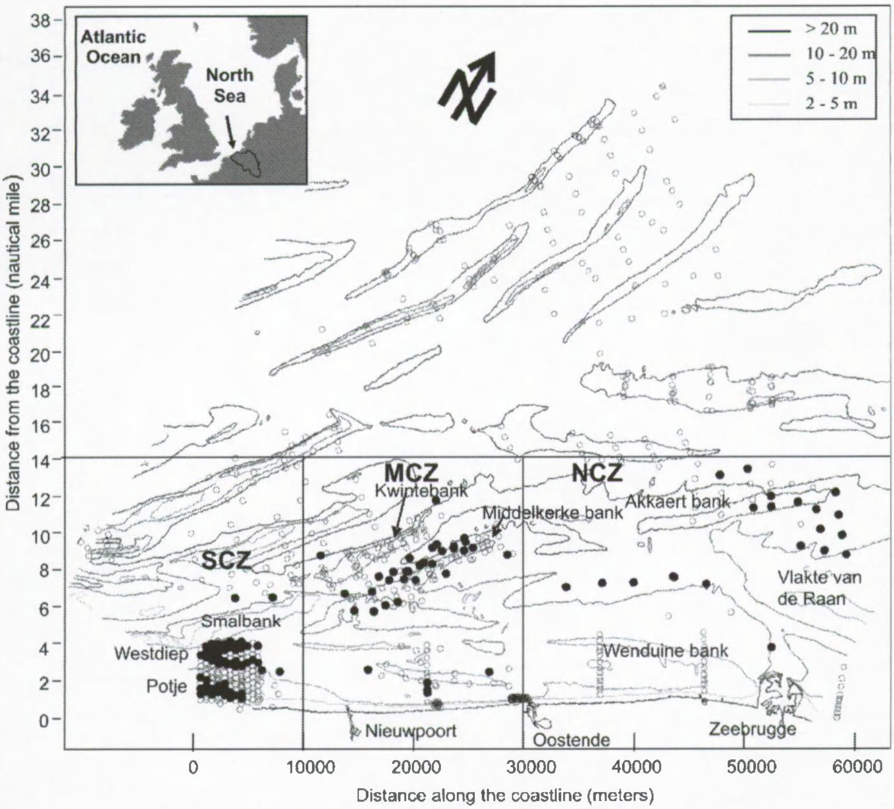

Figure 3. Northeastern spatial distribution gradient of the *Abra alba* community on the Belgian Continental Shelf with indication of the different zones. Black dots (stations where this community is present), open dots (absence of this community).

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

Geographical patterns in community structure at the BCS

Sedimentological characteristics

The average median grain size was highest at the MCZ (249 µm ± 38 (SD)) compared to the SCZ (219 µm ± 43) and the NCZ (222 µm ± 45) (Figure 5a). In the SCZ the median grain size range was situated between 150 and 350 µm, in the MCZ between 200 and 350 µm and in the NCZ between 150 and 300 (with one exception).

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

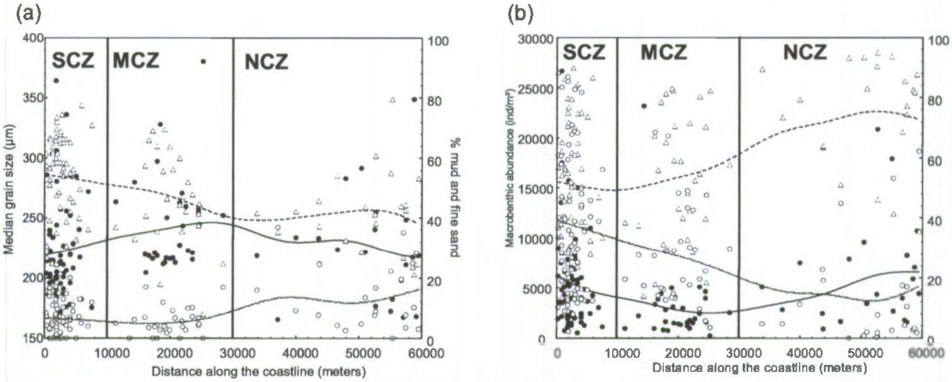

Figure 4. (a) Median grain size (black points, black line), mud (open points; dotted trend line) and fine sand (open triangles; interrupted black trend line) fraction within the *Abra alba* community in relation to the distance along the coastline, with indication of the three zones. (b) Macrobenthic abundance (black points, black line), percentage of Annelida (open triangles; interrupted black trend line) and percentage of Mollusca (open points; dotted trend line) in relation to the distance along the coastline, with indication of the three zones.

Biological characteristics

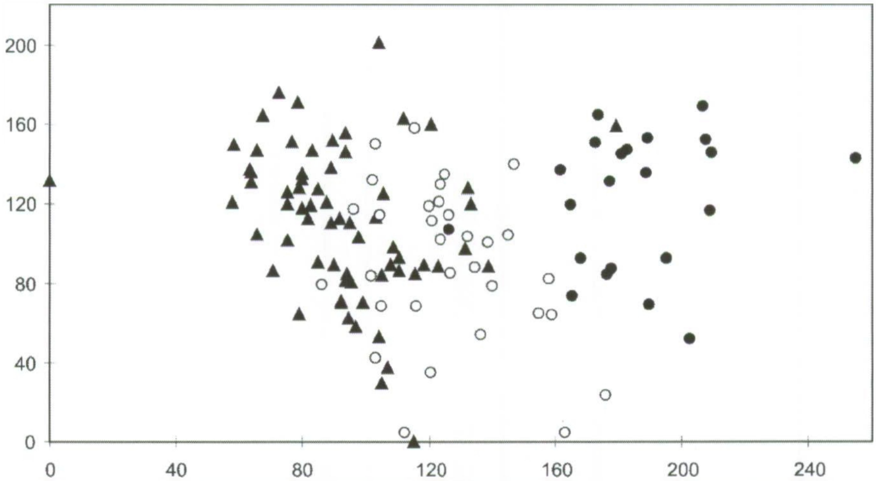

Figure 5. DCA ordination plot along the first two axes. The discrimination of the three zones (triangle: SCZ; open points: MCZ; black points: NCZ) is made.

Multivariate analysis

Multivariate analysis (Detrended Correspondence analyses, DCA) clearly visualizes the differences in community organization along the gradient, with minor overlap between the areas SCZ, MCZ and NCZ (Figure 5).

Abundance, higher taxa, species dominance

The macrobenthic density across the three zones was highest in SCZ (average of 5181 ind/m^2) and NCZ (5941 ind/m^2), with a drop in MCZ (average of 3010 ind/m^2) (Figure 4b). The variation in macrobenthic density is higher in the SCZ and NCZ, than in the MCZ.

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

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

Diversity

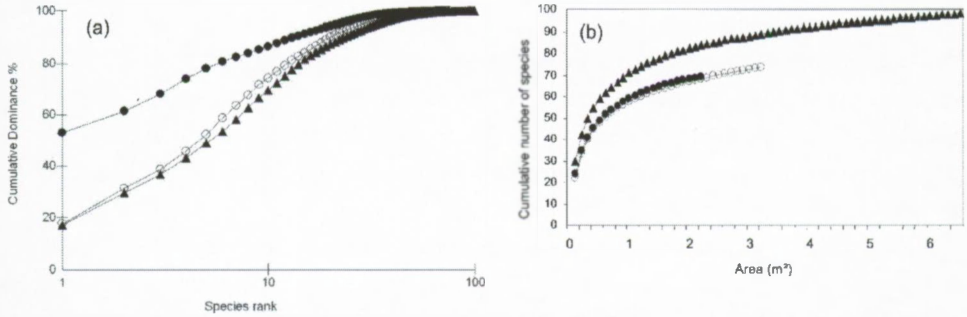

Figure 6. (a) species dominance plot at the three zones (SCZ: black triangle; MCZ: open circles; NCZ: black points) (b) species area plot for the three zones (similar symbols as (a))

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

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

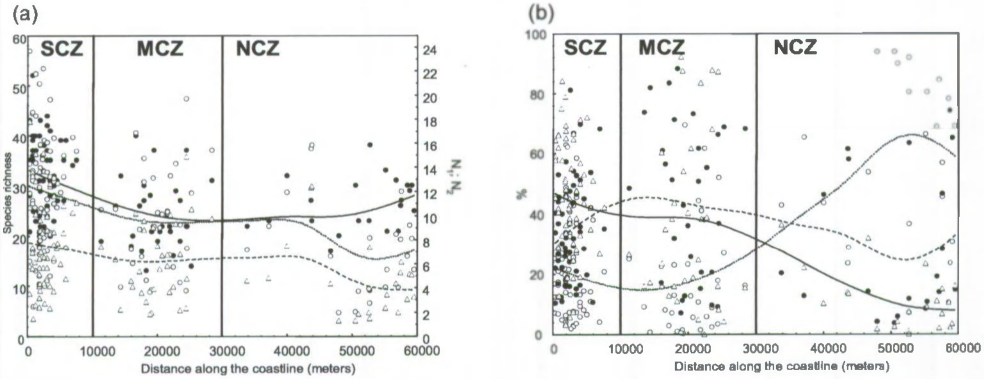

Figure 7. (a) The distribution of the different diversity indices in relation to the distance along the coastline: Species richness: N_0, black circles, solid trend line; Exponentiation form of H': N_1, open circles, dotted trend line; the reciprocal of the Simpson's index: N_2, open triangles, interrupted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

Functional biodiversity

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

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

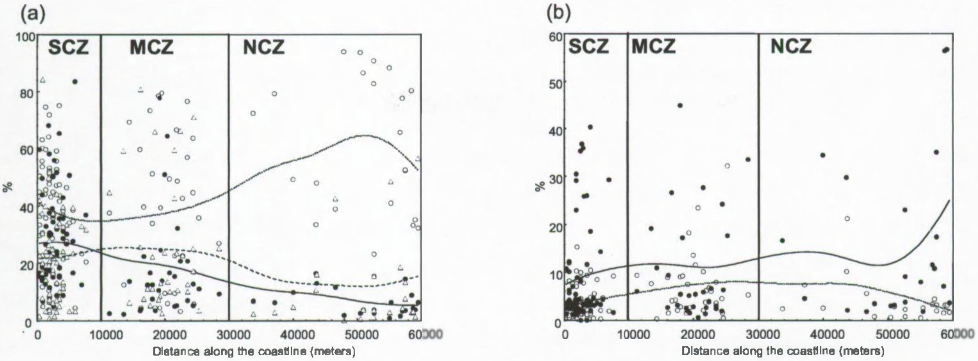

Figure 8. (a) The distribution of the relative abundance of different feeding guilds: facultative deposit – filter feeders (DF): open triangles, interrupted black trend line; obligatory filter feeders (F): black circles, solid trend line; obligatory deposit feeders (D): open circles, dotted trend line.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

Habitat heterogeneity

Within the habitat of the *A. alba* community at the three zones on the BCS there was no correlation between community structure (macrobenthic species richness and density) and granulometry (sediment median grain size and mud content) (Spearman R: $p>0.1$) (Figure 9).

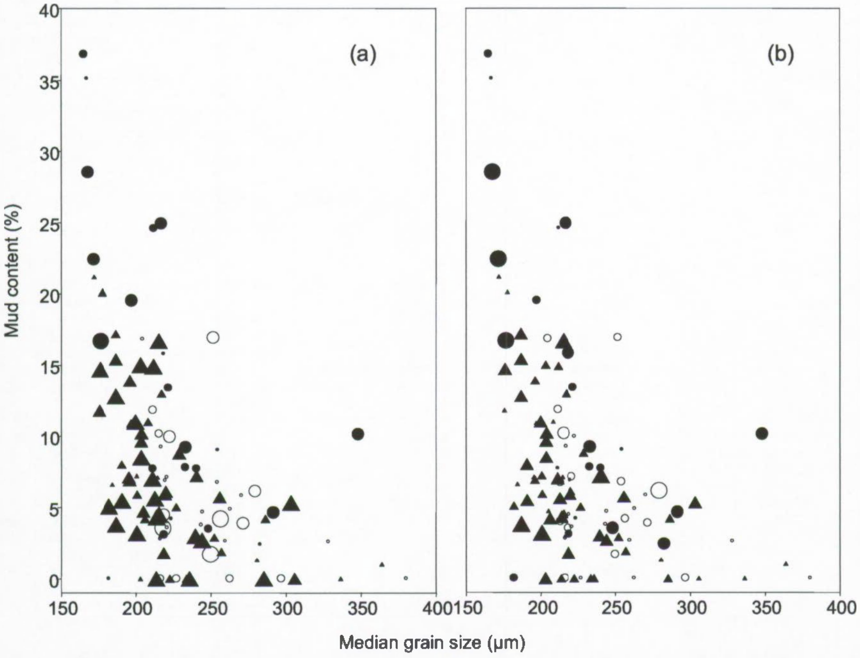

Figure 9. The species richness (N_0) and abundance (ind/m²) in relation to the sedimentological characteristics (median grain size (μm) and mud content (%)), with indication of the three zones: SCZ: black triangles; MCZ: open circles; NCZ; black circles. (a) Species richness (species/0.1m²): •∘▴ 9-23;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

Discussion

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

The largest continuous distribution area of the *A. alba* community is situated along the northeastern coast of France (Gravelines) over Belgium north to the Dutch coast (Kingston & Rachor, 1982; Vanosmael et al., 1982; Vermeulen & Govaere, 1983; Prygiel et al., 1988; Holtmann et al., 1996; Fromentin et al., 1997; Desroy et al., 2002; Van Hoey et al., 2004). Next to this continuous distribution

Tabel 2. Overview of the community parameters (abundance, diversity ([1], species top 10), sedimentology and sampling method of different areas in the English Channel and Southern North Sea, where the *Abra alba* community occurs. Species in bold occur in the top 10 of the three zones on the BCS. The underlined species are present in both the SCZ and MCZ; the species in brackets are present in both the MCZ and the NCZ.

	French coast				Belgian coast			Dutch coast	German coast	English coast
	Pierre Noire	**Rivière de Morlaix**	**Baie de Seine**	**Gravelines**	**SCZ**	**MCZ**	**NCZ**			**English channel**
Sampling method	Smith-McIntyre grab (0.1m^2)				Van Veen Grab (0.1m^2)					Rallier-du-Baty dredge
No of samples	117	77	38	81	61	32	22	194	14	10
Type of area	Isolated	Isolated	Isolated	One continuous area					Isolated	Isolated
Median grain size (µm)	148-184	77-122	80-120	100 - 150	219 ± 43	249 ± 38	222 ± 45	196.7 ± 54.8	Muddy fine sand	Muddy fine sand
Mud content(%)					8 ± 6	5 ± 4	14 ± 11	7.2 ± 12		
Depth(m)	17	10	10.5	10	11.5	17.7	10.8	12 ± 4.5	13-45	<10
Density (ind/m^2)	7545 ± 1641	3320 ± 402	5380 ± 848	5080 ± 1965	5181 ± 4542	3010 ± 3909	5941 ± 5254	2556 ± 3458	3828	6304
Total no of sp.	420	308	130	154	118	89	85		83	79
Diversity (No)				32	31 ± 8	24 ± 7	25 ± 6	14 ± 7	37	
Diversity (Shannon - Wiener)	3.8	2.9	3.2	2.4	2.4	2.17	1.83	1.84	2.2	2.1 ± 0.46
Species top 10 based on	% of total abundance	% of total abundance	% of total abundance	% of total abundance	Mean abundance	Mean abundance	Mean abundance	Mean abundance	Mean abundance	% of total abundance
Species top 10 (Ind/m^2)	*Ampelisca armoricana*	*Chaetozone setosa*	*Owenia fusiformis*	*Lanice conchilega*	Abra alba	*Mysella bidentata*	**Spiophanes bombyx**	*Spisula subtruncata*	*Nucula nitidosa*	*Abra alba*
	Ampelisca sarsi	*Melinna palmata*	*Acrocnida brachiata*	*Abra alba*	**Spiophanes bombyx**	[Actiniaria sp.]	**Nephtys hombergii**	*Magelona johnstoni*	*Spiophanes bombyx*	*Nucula nitidosa*
	Polydora pulchra	*Polydora pulchra*	*Pectinaria koreni*	*Spiophanes bombyx*	*Lanice conchilega*	***Phyllodoce mucosa***	***Phyllodoce mucosa***	*Spiophanes bombyx*	*Ophiura albida*	*Melinna palmata*
	Spio decoratus	*Nephtys hombergii*	*Mysella bidentata*	*Fabulina fabula*	Cirratulidae sp.	***Nephtys hombergii***	***Scoloplos armiger***	*Urothoe poseidonis*	*Mysella bidentata*	*Mysella bidentata*
	Paradoneis armata	*Mediomastus fragilis*	*Aphelochaeta marioni*	*Eumida sanguinea*	*Mysella bidentata*	*Abra alba*	*Eteone longa*	*Macoma balthica*	*Nephtys hombergii*	*Notomastus latericeus*
	Chaetozone setosa	*Aphelochaeta marioni*	*Abra alba*	*Phyllodoce mucosa*	***Nephtys hombergii***	*Fabulina fabula*	*Pariambus typicus*	*Fabulina fabula*	*Phoronis sp.*	*Nephtys hombergii*
	Marphysa bellii	*Euclymene oerstedii*	*Cultellus pellucidus*	*Nephtys hombergii*	***Scoloplos armiger***	***Scoloplos armiger***	*Eumida sanguinea*	*Mysella bidentata*	*Ophiura ophiura*	*Euclymene oerstedii*
	Urothoe pulchella	*Lanice conchilega*	*Pholoe minuta*	*Pectinaria koreni*	***Phyllodoce mucosa***	***Spiophanes bombyx***	*Owenia fusiformis*	*Scoloplos armiger*	*Scoloplos armiger*	*Magelona alleni*
	Aricidea fragilis	*Thyasira flexuosa*	*Magelona mirabilis*	*Notomastus latericeus*	*Fabulina fabula*	*Capitella capitata*	[*Actiniaria* sp.]	*Nepthys hombergii*	*Abra alba*	
	Nephtys hombergii	*Abra alba*	*Nephtys hombergii*	*Macoma balthica*	Oligochaeta spp.	Cirratulidae spp.	*Pectinaria koreni*	*Nepthys cirrosa*	*Pectinaria koreni*	
Literature	Fromentin *et al.*, 1997	Fromentin *et al.*, 1997	Fromentin *et al.*, 1997	Fromentin *et al.*, 1997; Dewarumez *et al.*, 1992				Holtmann *et al.*, 1996	Salzwedel *et al.*, 1985	Sanvicente-Anorve *et al.*, 2002

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

area, there are a lot of isolated distribution areas in the English Channel, such as the Bay of Morlaix with two small (6 and 2 km²) spots, respectively Pierre Noire and Rivière de Morlaix, the Bay of the Seine (Cabioch and Glaçon, 1975; Souplet and Dewarumez, 1980; Fromentin et al., 1997; Thiébaut et al., 1997), some bays (Eagle, 1975; Rees & Walker, 1983) and coastal areas nearby the U.K. coast (St- Andrews and Aberdeenshire, Cumberland coast, South-West England and some locations in the Irish Sea) (Rees et al., 1999; Sanvicente-Anorve, 2002) and a small area in the German Bight of the North Sea, seaward of the rivers Elbe and Weser (area of 1000km²) (Stripp, 1969; Kingston and Rachor, 1982; Salzwedel et al., 1985). The *A. alba* community is further present along the Atlantic coast of France, Spain and Portugal, and in the Mediterranean Sea. Yet, the community structure within these areas falls out the scope of this study.

Geographical patterns in community structure

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

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

There is a clear pattern in the diversity between the different sites: total number of species, species richness (N_0) and Shannon index (h') decrease towards the northeast. The total number of species (420 sp.) and the Shannon index (3.8) are highest at the Pierre Noire site (Fromentin et al., 1997) and decrease towards the NCZ (total number of species: 85 spp., N_0: 25 spp./0.1m², h': 1.8 (this study)) and Dutch coast (N_0: 14 spp./0.1m²; h': 1.8 (Holtmann et al., 1996)), where they displayed the lowest values. At the isolated places along the German and southern English coast, the Shannon index (respectively 2.2 and 2.1) and total number of species (respectively 83 spp. and 79 spp.) are comparable with those of the SCZ and MCZ. In the study of Rees et al. (1999), the *A. alba* community in inshore muddy fine sand at some places along the E and W coast of the U.K. is characterized by a species richness of 25 spp./0.1m².

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

Although the community structure shows a high similarity across the full distribution range of the *A. alba* community, changes in community composition were observed: the BCS should be considered as a major transition from the rich southern to the relatively poorer northern distribution area of the *A. alba* community. In this transition zone, the *A. alba* community was on a structural level characterized by, high variation in abundance, high species richness (31 spp./0.1 m²) and high diversity (N_1: 11.8; N_2: 7.5) in the SCZ, while the MCZ was characterized by low variation in abundance, low species richness (24 spp./0.1 m²), and lower diversity (N_1: 9.7; N_2: 6.3) and the NCZ by high abundance variation, low species richness (25 spp./0.1 m²) and the lowest diversity (N_1: 7.3; N_2: 4.6). On a functional level, there was no strong feeding guild and mobility class dominance in the SCZ; they were all more or less equal represented. Obligatory deposit feeders and tube – building sedentary species dominate the NCZ, while the MCZ shows intermediate values for feeding guilds and a dominance of mobile species.

Structuring environmental variables

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

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

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

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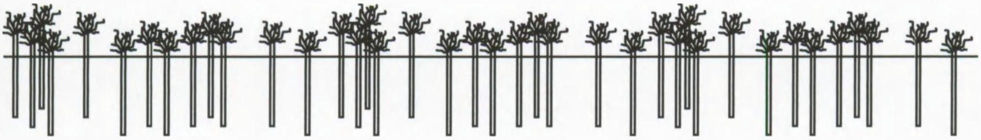
Chapter 4

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



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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

Ecosystem disturbance, temporal variability, benthos, *Abra alba* community, coastal zone, Belgian Continental Shelf

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

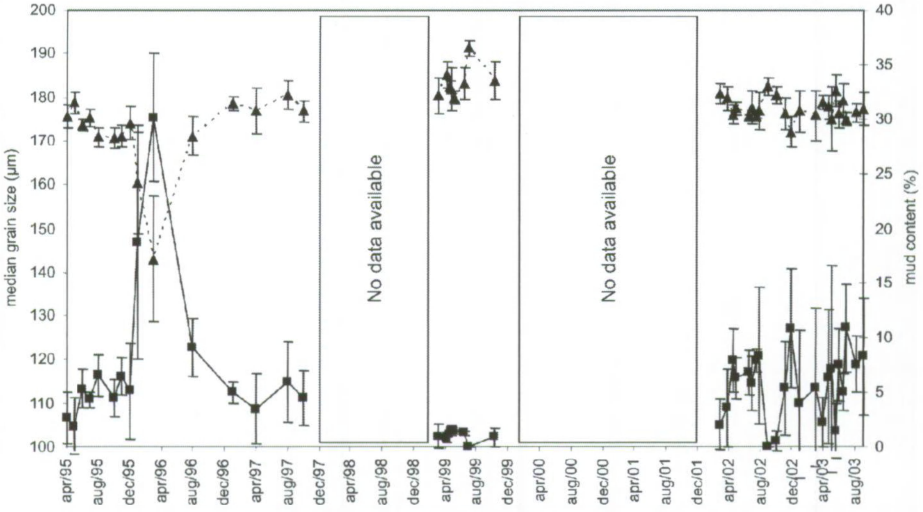

Figure 1. Changes within median grain size (µm) (triangle, dotted line) and mud fraction (%) (square, black line) distribution over the nine years period (average per sampling occasion ± standard deviation).

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

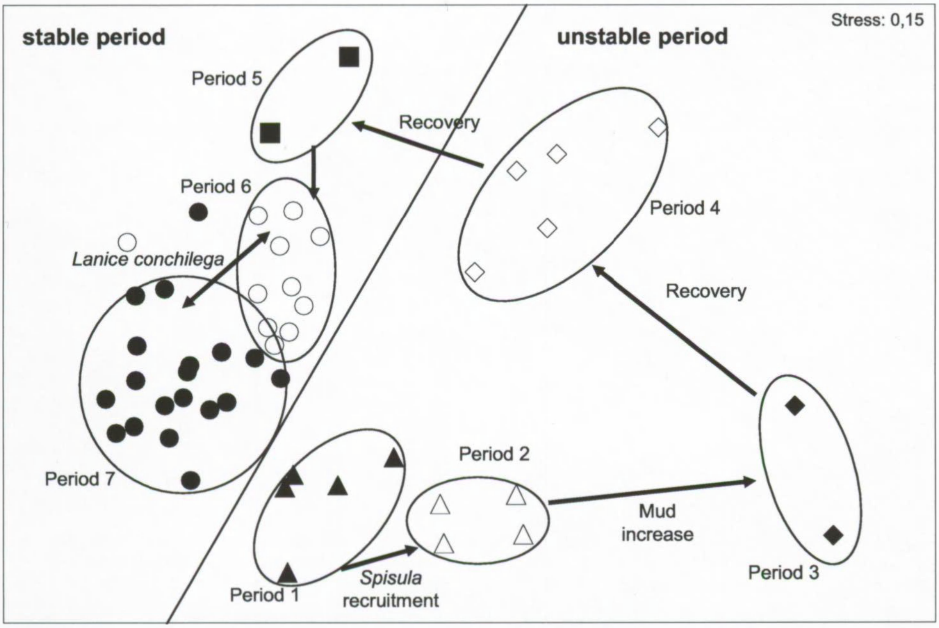

Figure 2. MDS–plot (Multidimensional scaling) of the samples, with indication of the seven periods: 1) Black triangle: April 1995 – August 1995, 2) open triangle: October 1995 – January 1996, 3) black rhombus: March – April 1996, 4) open rhombus: August 1996 – October 1997, 5) black square: March – April 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

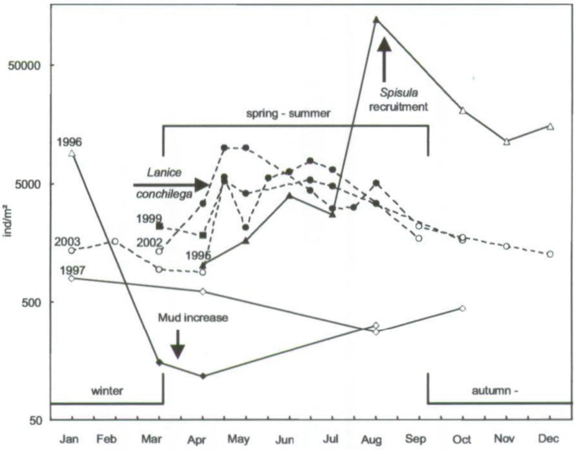

Figure 3. Density distribution (ind/m², log transformed) over the different years visualised on a year axis, with indication of the seven periods: period 1 (black triangle); period 2 (open triangle); period 3 (black rhombus); period 4 (open rhombus); period 5 (black square); period 6 (open circle); period 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.

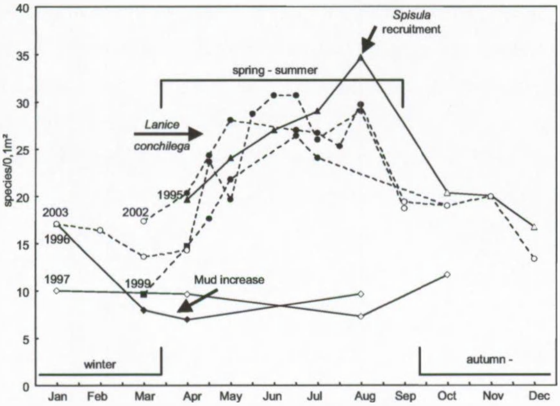

Figure 4. Species richness (species/0.1m²) over the different years visualised on a year axis, with indication of the seven periods: period 1 (black triangle); period 2(open triangle); period 3 (black rhombus); period 4 (open rhombus); period 5 (black square); period 6 (open circle); period 7 (closed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

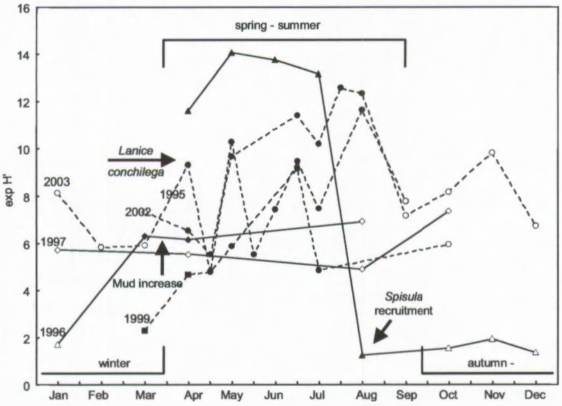

Figure 5. N_1- index over the different years visualised one a year axis, with indication of the seven periods: period 1 (black triangle); period 2(open triangle); period 3 (black rhombus); period 4 (open rhombus); period 5 (black square); period 6 (open circle); period 7 (closed circle). The causes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

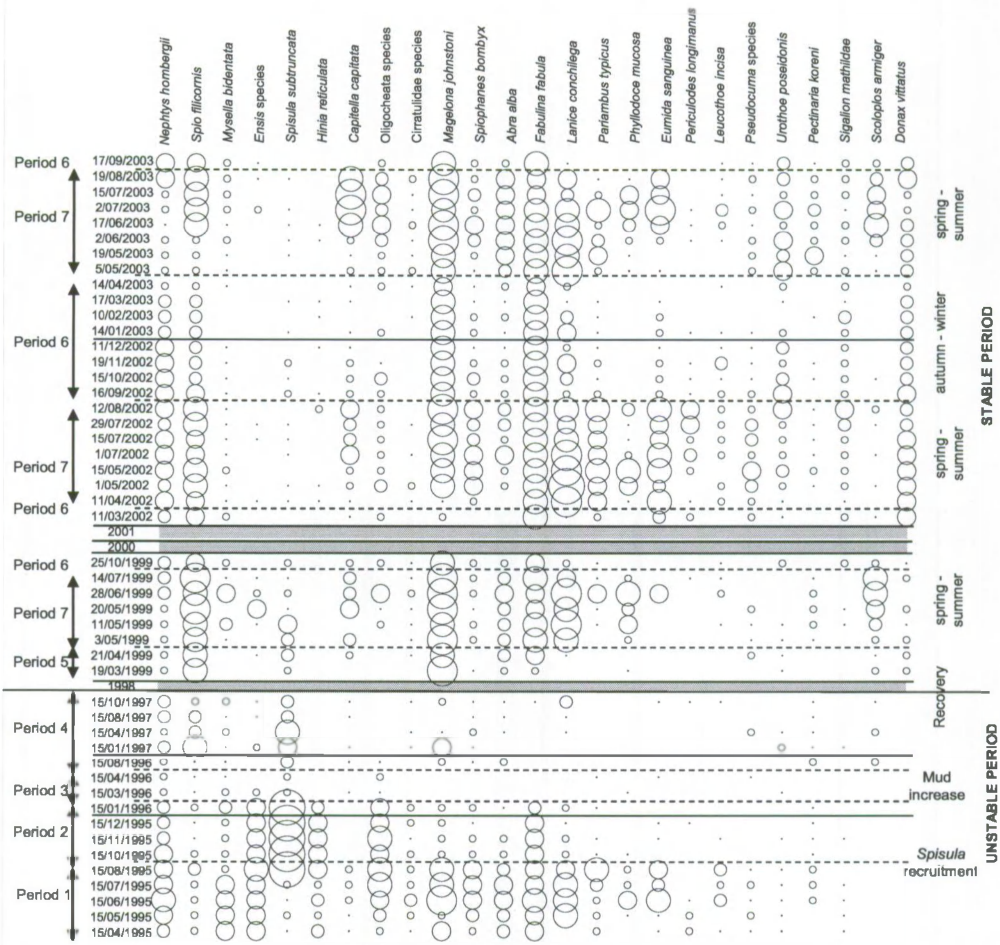

Figure 6. Density distribution of the 25 most abundant species in the *Abra alba* community, with indication of the different periods and the major causes responsible for the changes. The different density classes, with increasing size, are: 0 (no symbol); 1-10 ind/m² (•); 10 -50 ind/m² (o); 50-100 ind/m² (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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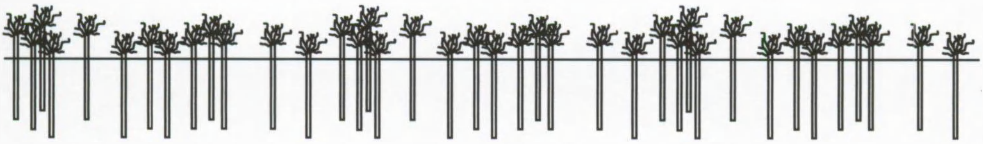
Chapter 5

Population – dynamics of subtidal *Lanice* conchilega (Pallas, 1766) populations at the Belgian Continental Shelf



Paper to be submitted as

Van Hoey, G., Vincx, M. & Degraer, S.
Population – dynamics of subtidal *Lanice conchilega* (Pallas, 1766) populations
at the Belgian Continental Shelf

Abstract

The paper at hand describes population dynamics, recruitment and persistence of the *Lanice conchilega* populations in subtidal soft – bottom sediments along the Belgian coastline. An intensive sampling campaign (monthly – biweekly from March 2002 untill September 2003), the discrimination of different benthic stages and cohort analysis of the adult population enabled the discrimination of trends in recruitment patterns of *L. conchilega*. Three recruitment periods were defined based on the occurrence of peaks of aulophore larvae in the water column and peaks of recently settled individuals in the benthos: (1) spring recruitment period (April – July), (2) summer recruitment period (July – September), and (3) autumn recruitment period (September – November). The spring recruitment period was the most intense and was characterized by high densities of recently settled individuals and juveniles. These high densities resulted in an adult population, which consisted of different cohorts and which was characterized by a high turn over. The summer and autumn recruitments were less intense and did not occur at every station or in every year. Spatial and temporal variations in timing and intensity of settlement and recruitment were observed and described. Results indicate that *L. conchilega* is an opportunistic species, characterized by a long pelagic phase, high settlement of larvae and a high turn over in the adult population. Due to this recruitment strategy and the preferential settling of the larvae in adult patches, the studied *L. conchilega* population was able to maintain high abundances in moderately stable patches.

Keywords
Lanice conchilega, population-dynamics, life-cycle, aulophora larvae, growth, Belgian Continental Shelf

Introduction

Lanice conchilega (Pallas, 1766), a tube-building terebellid polychaete, is a wide-spread species commonly encountered in European intertidal and shallow subtidal sands (< 100m), where it reaches densities of up to several thousands of individuals per m² (Buhr & Winter, 1976; Ropert & Dauvin, 2000; Callaway, 2003). The tubes of adult *L. conchilega*, made from cemented sand grains and shell breccia, have a diameter of about 0.5 cm and are up to 65 cm in length (Ziegelmeier, 1952). The anterior end of the tube protrudes above the sediment surface by 1 - 4 cm and is crowned with a sand-fringe. *Lanice conchilega* prefers surface deposit feeding when occurring in low densities and switches to suspension feeding in the case of high densities (Buhr & Winter, 1977). The species is of high ecological importance since (1) its dense populations affect sediment properties (Jones & Jago, 1993) and oxygen transport (Forster & Graf, 1995), (2) it alters the composition of benthic communities (Zühlke, 2001), and (3) it is an important food item for birds and fish (Petersen & Exo, 1999).

Lanice conchilega has a complex life cycle that includes separate larval (planktonic), juvenile and adult phases. The planktonic larval stage of *L. conchilega* was termed aulophore by Kessler (1963) and is characterized by the presence of a transparent tube, which is used as a floating device. The aulophore looks like a juvenile individual, but has a number of larval characteristics (Bhaud & Cazaux, 1990). The aulophore stage succeeds an intermediate benthic stage (1 - 2 days), which in turn follows a short-lived planktonic trochophore and metatrochophore phase (5 days) (Bhaud, 1988; Marcano & Bhaud, 1995). Since aulophore larvae spend up to 60 days in the plankton, they have the ability to disperse over large distances, depending on the hydrodynamical regime. According to Heuers et al. (1998), settling aulophores prefer tubes of adult *L. conchilega*, shell fragments or other hard epibenthic structures. During the settlement of aulophore larvae, the tentacles glue the anterior end of the larval tube to the substratum and extend the width and length of the tube by gathering sediment particles (Heimler, 1981). A *L. conchilega* individual grows and stabilizes its tube into the sediment during its benthic life, but maintains the capability to re-establish its tube after being washed out (Nicolaidou, 2003). Even though the life span of this species is estimated to be 1-2 years (Beukema *et al.*, 1978) or up to 3 years (Ropert & Dauvin, 2000), there is no information on the age at maturity. A lot of processes can affect the duration of each stage and the transition between stages (e.g. the availability of food, intra- and interspecific competition for space and food, mortality due to factors such as predation and physiological stress (e.g. intolerable temperatures, salinities or oxygen concentrations), disease or parasites (Eckman, 1996)).

A lot of studies have described the planktonic larval phase of *L. conchilega* (Bhaud, 1988; Belgrano et al., 1990; Bhaud & Cazaux, 1990; McHugh, 1993; Marcano & Bhaud, 1995), but fewer investigations studied the benthic settling and population structure (e.g. intertidal studies of Ropert & Dauvin, 2000 and Callaway, 2003). Up till now, none of the studies about *L. conchilega* combined information on the planktonic and benthic stages.

The present study aims to disentangle the population dynamics of a subtidal *L. conchilega* population through observation of the larval phase (aulophore larvae), benthic settling and the adult population structure on three sites in the coastal area of the Belgian Continental Shelf (BCS) during a 1.5 year period (March 2002 – September 2003). The main research questions are the following: (1) How strong are the turnover and the spatial and temporal variability within a *L. conchilega* population, and (2) Is there temporal stability of the patch locations of *L. conchilega* in subtidal environments?

Materials and Methods

Study area

Three sampling stations in the Belgian coastal zone, which is a part of the Southern Bight of the North Sea (Figure 1), were investigated concerning the population dynamics of *Lanice conchilega*. Station O1 (51° 28.16'; 3° 09.11') is situated in the northeastern coastal zone (NCZ), north of the 'Vlakte van de Raan', whereas WK1 (51° 09.13'; 2° 37.25') and WK2 (51° 09.13'; 2° 32.72') are situated in the southwestern coastal zone (SWZ), in the 'westdiep' gully at the slopes of the Broersbank and Smalbank, respectively (Van Hoey et al., 2005). The three stations are situated at a depth below MLWS of 14 m for station O1, 15 m for station WK2 and 12 m for station WK1. The coastal zone of the BCS is characterized by turbulent, nutrient rich inshore-waters and a dominance of muddy sands. The NCZ is further strongly influenced by the Westerschelde estuary (Van Hoey *et al.*, 2005).

Figure 1. Map of the Belgian Continental Shelf with the location of the three stations (WK1, WK2 and O1).

Data origin

The three stations were sampled monthly (September – April) or biweekly (May-August) during the period March 2002 - September 2003. Such a frequent sampling is seldomly found in population dynamical studies (Thompson and Schaffner, 2001 and the study at hand), but is usually monthly or bimonthly (Garcia-Arberas & Rallo, 2002; Roubah & Scaps, 2003; Garcia-Arberas & Rallo, 2004; Plyushceva et al., 2004; Kevrekidis, 2005). At every sampling occasion and at every sampling station, macrobenthos and plankton samples were taken. There are, however, some gaps in the sampling period due to logistic problems.

The plankton samples were taken with a trawl plankton net with a net aperture of 1 m diameter and a mesh size of 200 µm. Sampling the entire water column and especially the part nearby the bottom was ensured by taking the plankton net down, holding it passively during a period of 1 (in plankton bloom periods) to 2 minutes nearby the bottom and then pulling it up. After cleaning the net, the plankton was sieved on a 200 µm mesh sieve and fixed in a 4% formaldehyde seawater solution. The sampled water volume was calculated using the following equation: water volume filtered (m^3) = pi X $(0.5m)^2$ * the sampling distance in meter. The sampling distance was measured by an electronic flow meter, which was fitted in the net aperture.

In the lab, the aulophore larvae of *L. conchilega* were counted by taking subsamples of 10 ml out of a fixed volume (depending on the size of the sample) that was continuously homogenized. This procedure was repeated until a volume was reached, that contained minimally 100 aulophore larvae (Thiébaut et al., 1992). Afterwards, the amount of aulophore larvae was standardized to numbers per m^3. Aulophore larvae were recognized by a slimy, transparent tube and a morphological organization clearly marked by numerous segments (Bhaud, 1988).

The macrobenthic samples were taken with a Van Veen grab (sampling surface area: 0.1026 m^2) and sieved after fixation (with 8% formaldehyde seawater solution) over a 1 and 0.5 mm sieve. The amount of *L. conchilega* individuals retained on these two sieves was combined in the final dataset. On each sampling occasion and location three replicate samples were taken.

While processing the benthos samples, a distinction was made between the following developmental phases of *L. conchilega*: (1) recently settled individuals (morphological features similar to aulophore larvae, without transparent tube); (2) juveniles (recently settled individuals with prolongation of the abdomen, building a small tube); (3) young adults (*L. conchilega* individuals with a tube diameter < 1 mm); (4) adults (*L. conchilega* individuals with a tube diameter > 1 mm, therefore not mature) and (5) tubes with intact sand fringes (Figure 2). No discrimination between mature and immature individuals was made. Counting tube tops with intact sand fringes has been previously used to estimate the densities of *L. conchilega* (Ropert & Dauvin, 2000; Strasser & Pieloth, 2001; Callaway, 2003; Van Hoey et al., submitted).

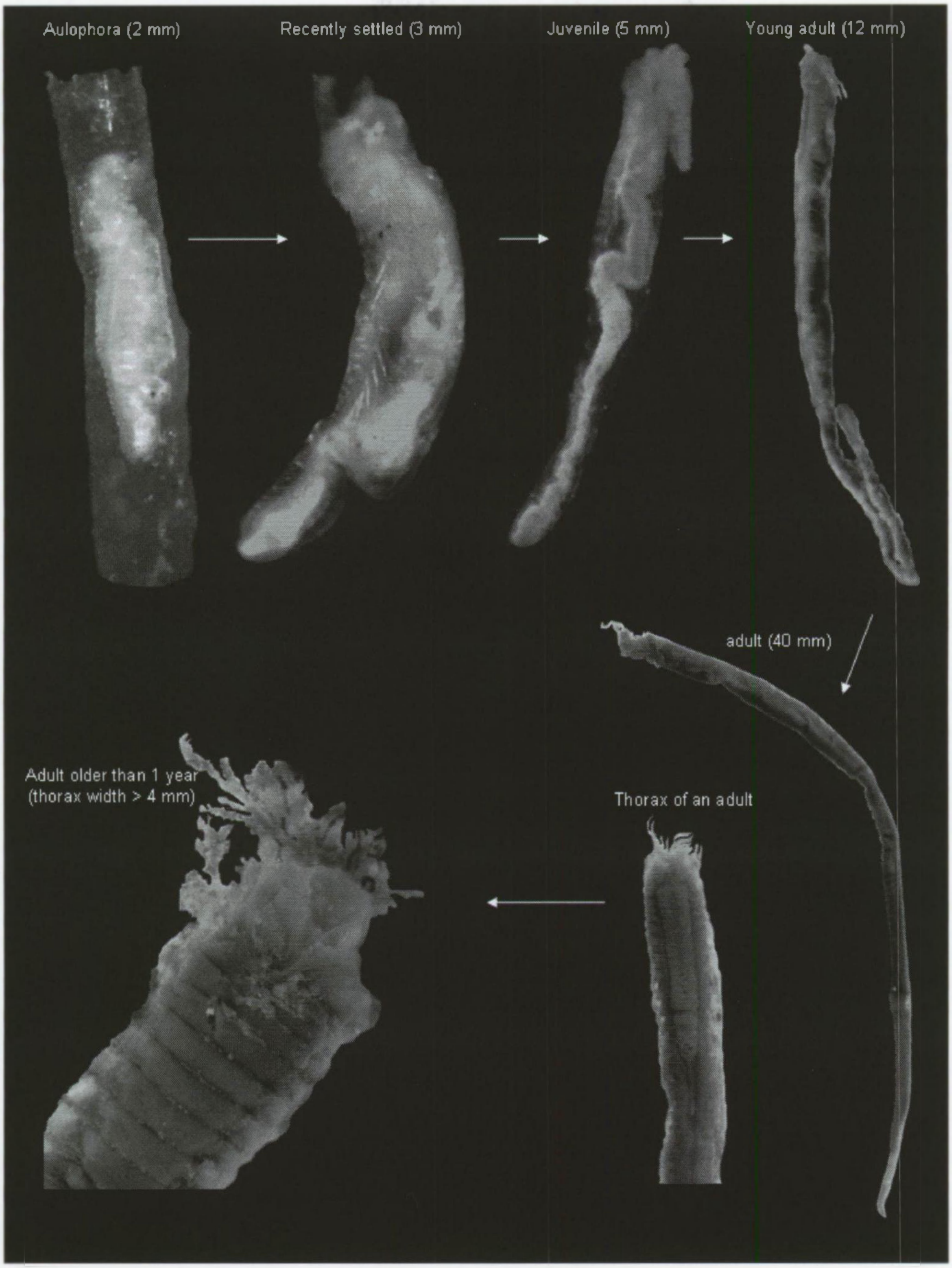


Figure 2. Picture of the different developmental phases of *L. conchilega*

Data analysis

Buhr (1976) and Ropert & Dauvin (2000) used the internal diameter of the *Lanice* tube as a proxy for biomass, whereas Callaway (2003) found a significant correlation between the width of the tubes and the thorax width. The use of partial size measurements is highly extended in studies on the population dynamics of polychaetes in order to estimate biomass and production (Garcia-Arberas & Rallo, 2002). The diameter of the tube was measured by introducing a cone-shaped stainless steel gauge into the opening of the tube. The diameter of the instrument varied from 0 to 5 mm with steps of 0.01 mm. The relationship between the individual ash free dry weight, assessed firstly by drying for 4 hours by 110°C (Dry weight) and then burning at 550°C for 4 hours (Ash weight), and the inner diameter of the sand tube was linearly shaped and expressed as:

$$\mathrm{Sqrt(AFDW)} = 0.0612^{*}\ \mathrm{diameter} - 0.0366 \quad (N = 61;\ r^2 = 0.9186,\ p < 0.001)$$

with D the inner diameter of the sand tube (mm) and W the ash free dry weight (g) (Figure 3).

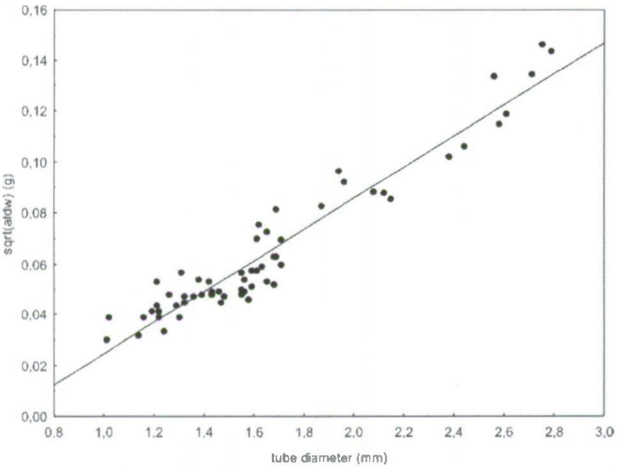


Figure 3. The relationship between the individual ash free dry weight (mg) and the inner diameter of the sand tube (mm).

The tubes were subjected to diameter measurements and were classified into 0.1 mm classes. In order to detect and separate cohorts, the length-frequency distributions were subjected to modal analysis with the help of the software NORMSEP (Tomlinson, 1971), which is based on the means detected in the analysis of the histograms with the Bhattacharya method (Bhattacharya, 1967). This method splits composite length-frequency distributions into separate normal distributions. The normal components (mean, theoretical number per group, standard deviation) of frequency size distributions were identified for each date with an adequate number of individuals. The means of the normal distributions for all sampling dates were then linked to trace the modal length progression of the cohorts. The growth rates were estimated as the differences in mean tube width values of the individuals of identified cohorts between successive samplings. The secondary production was calculated by means of the weight increment method, which estimates the production as the increment of biomass from one sampling date to the next for each cohort separately, and for the whole sampling period (Crisp, 1984). All these analyses were done with the program FISAT II (FAO-ICLARM Fish Stock Assessment Tools).

Results

Environmental data

The stations O1, WK2 and WK1 were characterized by fine muddy sand, with an average median grain size of 197 ± 39.4 (SD), 196 ± 5 (SD) and 177 ± 2.4 (SD) µm, respectively, and an average mud content of 17.9 ± 12.47 (SD), 7.12 ± 3.28 (SD) and 5.7 ± 4.75 (SD) % (Figure 4). The median grain size was quite stable at stations WK1 and WK2, whereas at station O1, there were considerable fluctuations including three periods of lower median grain size (July - August 2002; May – July 2003 and after August 2003). These oscillations were caused by increases in the mud content during July – August 2002 (17 and 21%) and during May – July 2003 and after August 2003 (above 20%, up to 47.6%).

The water temperature at the three stations reached its highest values in August 2002 and 2003 (19.1 °C - 20.0 °C and 21.2 °C - 22.0 °C) and the lowest values in February 2003 (4.3 °C - 4.4 °C). The temperature increase after the winter of 2002-2003 was detected much faster at station WK2 (March - April 2003: 7.2 – 10.6 °C) compared to station O1 (March - April 2003: 6.0 – 9.6 °C).

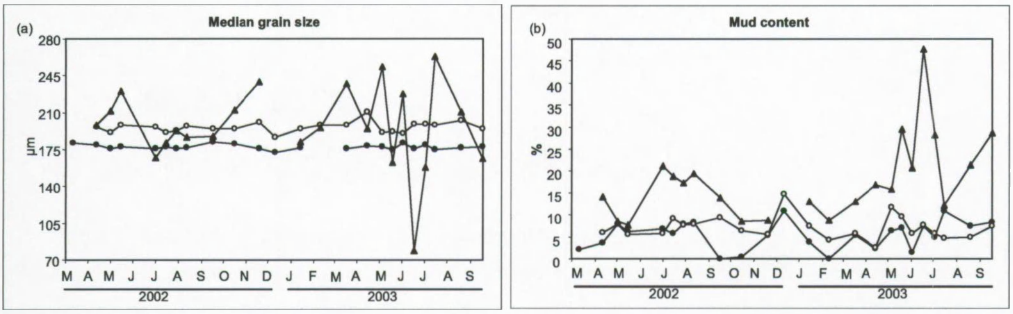


Figure 4. Distribution of the median grain size (a) and mud content (b) during the sampling period at the three stations (station WK1: black points; Station WK2: open points; Station O1: black triangle).

Life cycle and demography

Periods of recruitment

General pattern

In this section, the general recruitment pattern of *L.* conchilega is described based on the observations of 2002. Three peaks in the density of aulophore larvae could be observed: (1) a peak of very high densities in early May (O1: 859 ind/m^3; WK2: 437 ind/m^3), (2) a very small peak at the end of July (O1: 62 ind/m^3; WK2: 41 ind/m^3), and (3) a small peak in autumn (September – October) (Figure 5). During winter, aulophore larvae were scarcely found (< 2 ind/m^3). The three peaks in the planktonic density of aulophore larvae (spring, summer, autumn) were also detected in the benthos samples, in which the different successive stages (recently settled, juvenile, young adults and adults) followed each other in their density peaks (Figure 6). The three periods, in which increased densities of aulophore larvae and benthic stages were found, will further be referred to as (1) spring recruitment period (April – July), (2) summer recruitment period (July - September) and (3) the autumn recruitment period (September – November).

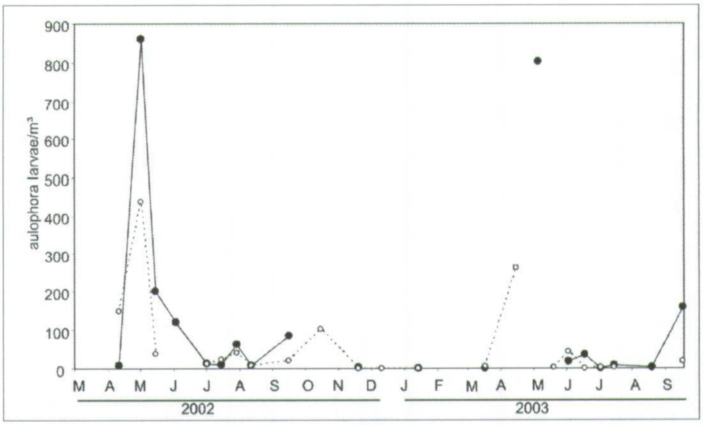


Figure 5. Density distribution of the aulophore larvae in the water column at station WK2 (open points, dotted line) and station O1 (black points, black line).

During the spring recruitment period, the settling phase of *L. conchilega* (recently settled individuals) was found from April 2002 onwards at the three stations and reached its highest densities in early May (1855 ind/m^2 at station O1, 2651 ind/m^2 at station WK2, 5292 ind/m^2 at station WK1). Hereafter, early July, the densities declined to < 10 ind/m^2 at stations WK2 and WK1, and to 64 ind/m^2 at station O1. The older stages of *L. conchilega* (juvenile and young adult) showed a similar pattern, though with a time lag of about two weeks. Juveniles and young adults from the spring recruitment were found until half of July, but this pattern was not clearly defined due to the partial overlap with the summer recruitment period. Due to the spring recruitment, the adult densities started to increase from half of May – June 2002 and reached their highest densities in early July (2495 ind/m^2 at station O1, 1439 ind/m^2 at station WK2, 1059 ind/m^2 at station WK1).

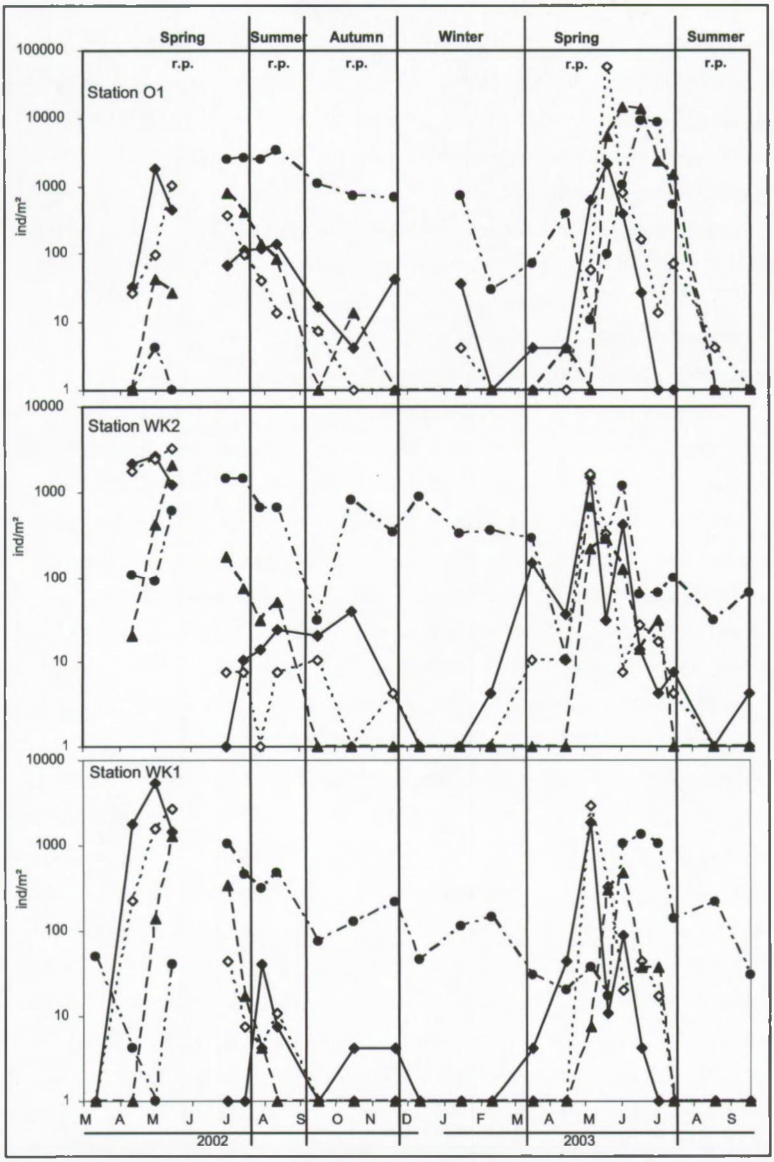


Figure 6. Density distribution of the different benthic stages of *Lanice conchilega* for the three stations: recently settled individuals (black rhombus, black line), juvenile individuals (open rhombus, dotted line), young adults (black triangle, interrupted line), adults (black points, interrupted – dotted line). Sampling points with a time lag of more than one month were not connected. (r.p.: recruitment period)

During the summer recruitment period, an increase of the density of recently settled individuals could be found from half of July until August (64 – 136 ind/m² at station O1, 10 – 22 ind/m² at station WK2 and 39 – 6 ind/m² at station WK1). The densities of the juveniles and young adults decreased at the three stations or remained stable at low densities (± 10 ind/m²). The adult densities remained high at station O1 (to 3434 ind/m²) or but decreased at stations WK2 (to 650 ind/m²) and WK1 (to 478 ind/m²) during the summer period.

During the autumn recruitment period, a small density increase of recently settled individuals was detected at stations O1 (42 ind/m²) and WK2 (40 ind/m²), in some cases followed by small peaks of successive stages. At station WK1, only low densities (3 ind/m²) of recently settled individuals were found, but no following successive stages and therefore no autumn recruitment.

During the winter, recently settled (max 36 ind/m² at station O1) and juvenile individuals (3 ind/m²) were scarce. In autumn-winter, the densities of adult individuals declined (1105 - 72 ind/m² at station O1, 794 - 284 ind/m² at station WK2, 215 - 30 ind/m² at station WK1).

Spatial and temporal variability

Within this generally observed recruitment pattern of *L. conchilega*, spatial differences in timing and intensity, and year-to-year variations were detected. On a small spatial scale (stations WK2 and WK1 - hundred of meters), the same recruitment patterns were observed, except for the absence of a successful autumn recruitment (at station WK1) and differences in intensity of the density peaks (e.g. density of recently settled individuals in May: 5293 ind/m² at station WK1 and 2652 ind/m² at station WK2). On a larger spatial scale (stations WK2 - WK1 and O1 - kilometres), differences in timing and intensity were observed. In 2003, a time lag of about two weeks was observed in the recruitment pattern between station O1 and stations WK2 - WK1 and the density peaks of recently settled individuals (< 100 ind/m² at station O1, > 1000 ind/m² at stations WK2 - WK1) and aulophore larvae (149 ind/m³ at station WK2, 7 ind/m³ at station O1) were already higher in April 2002 at stations WK2 – WK1 compared to station O1.

Next to spatial differences between stations WK2, WK1 and O1, a temporal difference was observed between the two investigated years (2002 and 2003). The most obvious temporal difference between the two years concerned the recruitment intensity. For stations WK2 – WK1, the densities of the *L. conchilega* stages (e.g. total density half May at station WK2: 640 ind/m² in 2003 and 6608 ind/m² in 2002), were lower in the spring recruitment period of 2003 than in 2002, resulting in lower adult densities in 2003 compared to 2002 (e.g. adult density for station WK2 in the beginning of July: 66 ind/m² in 2003, 1440 ind/m² in 2002). The inverse pattern was observed at station O1, with lower densities of the benthic stages of *L. conchilega* in 2002 (1030 ind/m²) compared to 2003 (juveniles, 57017 ind/m²). The spring recruitment at station O1 in 2003 was not successful, due to the disappearance of adult *L. conchilega* individuals in the summer. In 2003, no summer recruitment period was detected for the three stations (density of recently settled individuals <10 ind/m²).

Adult population structure

The size frequency histograms clearly show that small individuals (Ø 1 – 1.5 mm) were only found during the period April – October, which indicates a long period of recruitment (Figure 7). During the winter period (November – March), no obvious new recruitment was detected and the size frequency distribution remained rather stable. During the prolonged recruitment period, the densities of the small individuals decreased in time. In June – July, the majority of the large individuals (Ø > 3 mm) disappeared, and older solitary individual (Ø > 4 mm) were only occasionally found.

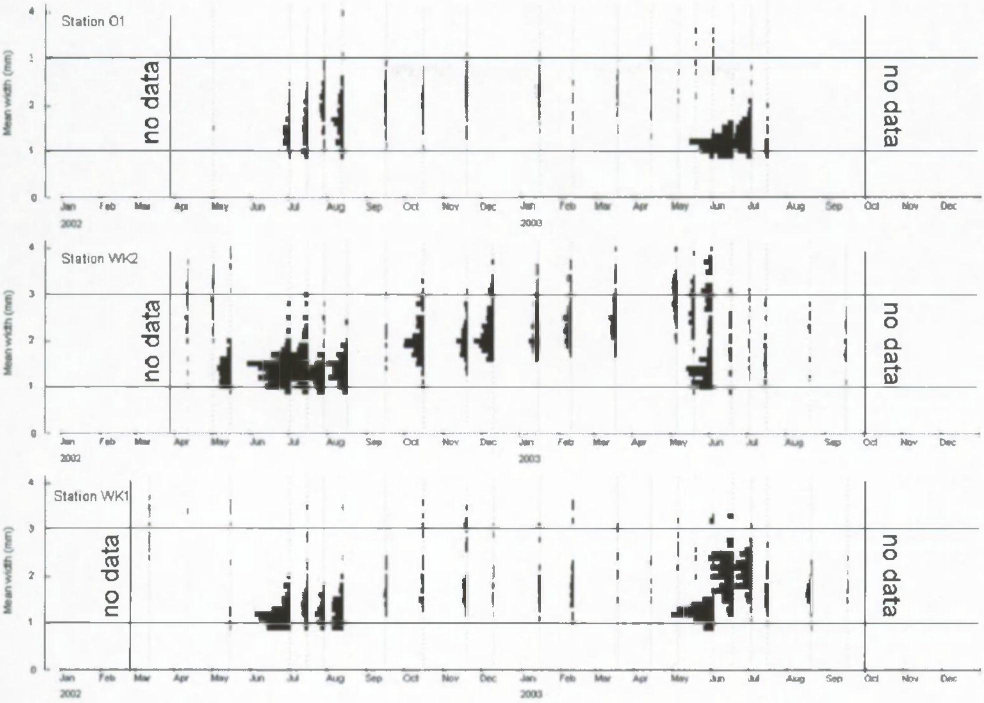


Figure 7. Size-frequency distribution of the adult *Lanice conchilega* individuals for the three stations

Cohorts

Based on the size frequency distributions, different cohorts were objectively distinguished using the Bhattacharya method and were afterwards validated by NORMSEP (see Material and Methods) (Figure 8). A cohort is defined as the individuals originating from a well outlined recruitment moment. In the present study, almost on every sampling date, a new cohort could be distinguished, which was due to the constant presence of *L. conchilega* individuals of the smaller size classes during April - October. Based on the presence and abundance of aulophore larvae and recently settled stages of *L. conchilega*, three periods of recruitment were defined. The different identified cohorts were lumped into groups representing the individuals originating from the respective recruitment periods. The cohort – groups reflect the growth and population structure of the individuals originating from a certain recruitment period.

New cohorts were detected from April until October, with small differences between the three stations; no new cohorts were observed during winter (Figure 8). At station WK2, some cohorts originating from 2001 could be defined. The spring cohort – group contained different cohorts appearing from April until July and disappeared within the same year or in the following year. The cohorts, which disappeared within the same year, reached a maximum tube width of 3 mm, whereas the survivors of the winter period reached a maximum tube width of up to 3.5 mm. The summer cohort – group consisted of 1 or 2 cohorts originating from August – September, and disappeared in the following year.

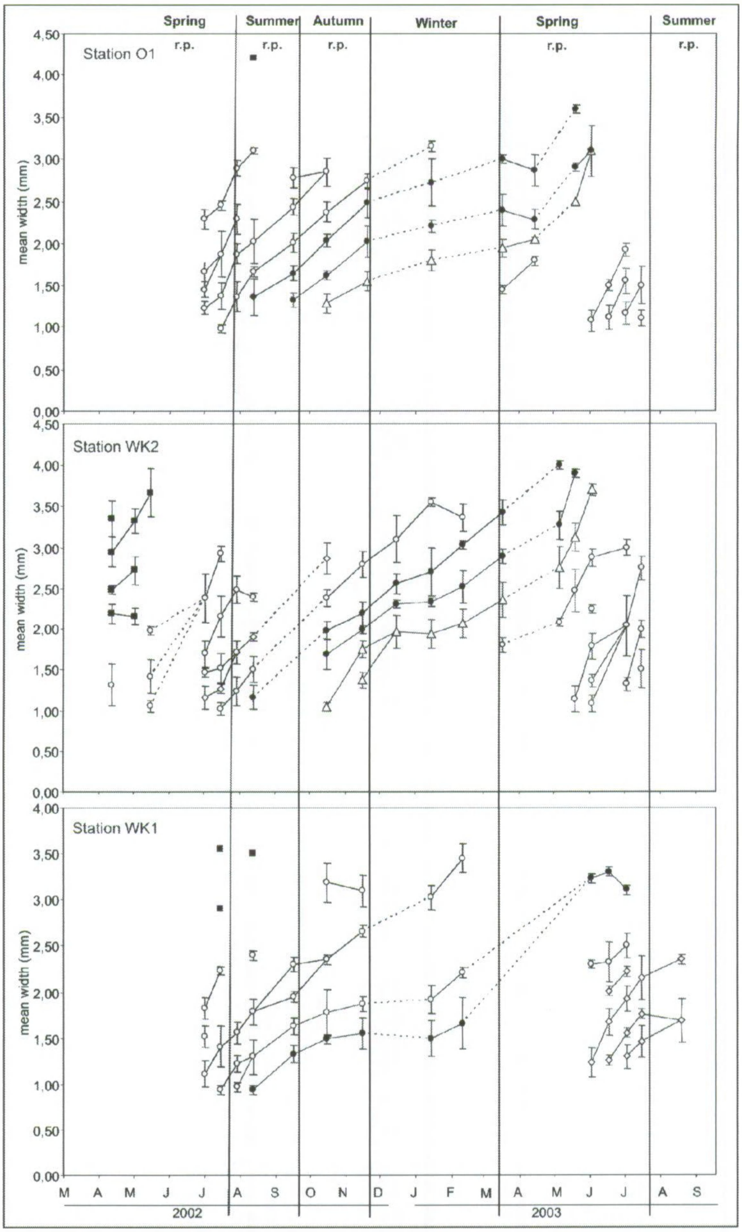


Figure 8. Variations of the mean tube width (in mm) of each *Lanice conchilega* cohort differentiated by Bhattacharya and validated by NORMSEP during the sampling period for the three stations with indication of the recruitment periods (r.p.). Cohorts of 2001 (black square); cohorts of the spring recruitment period (open points); cohorts of the summer recruitment period (black points); cohorts of the autumn recruitment period (open triangles). Sampling points with a time lag of more than one month were connected with a dotted line.

Finally, the autumn cohort – group, originating from October – November, survived until spring of the following year. The individuals of the summer and autumn cohorts reached a maximum tube width of

3.5 to 4 mm. Mean widths were sometimes characterised by a relatively large standard deviations, due to the overlap between some cohorts.

Population size

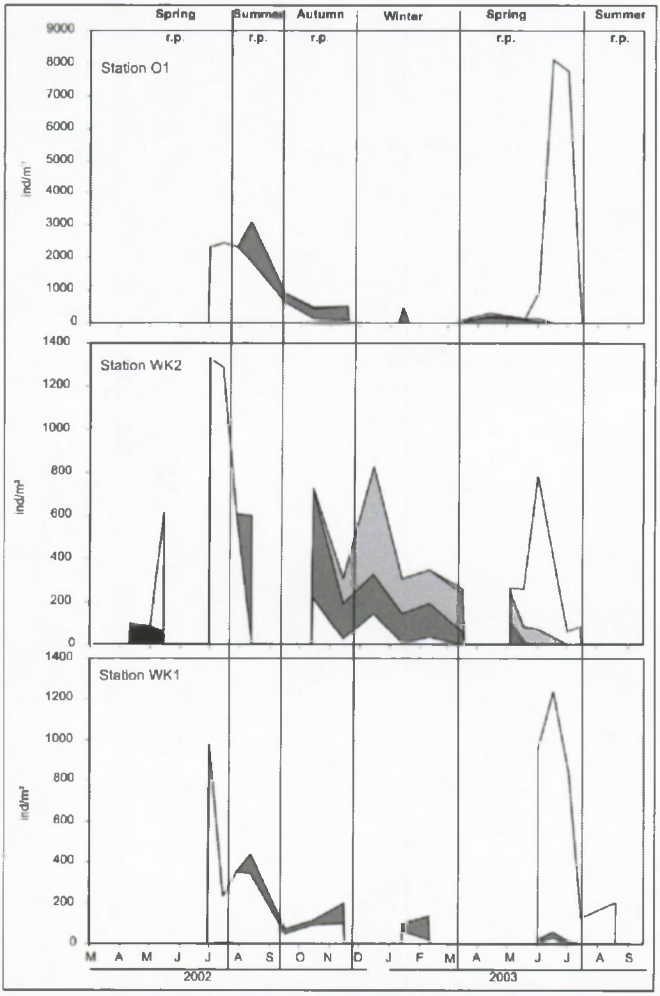


Figure 9. *Lanice conchilega* adult population structure (density of each cohort - group originating from a defined recruitment period) during the study period for the three stations with indication of the recruitment periods (r.p.). Population of 2001 (black), spring recruitment (white), summer recruitment (grey), autumn recruitment (light grey). Sampling points with a time lag of more than one month were connected with a dotted line.

At station WK2 only, a population originating from 2001 was still represented in relatively high densities (+ 100 ind/m²) in May 2002 (Figure 9). During the period of investigation, two major density peaks (June – July 2002 and 2003), consisting of individuals of the spring cohort – group, were observed. After the peak, the densities decreased rapidly. The abundant presence of individuals from the summer cohort – group resulted in a second peak in August 2002 at the stations. The overwintering population of *L. conchilega* mainly consisted of individuals from the spring or summer cohort - group, whereas at station WK2, the densities of the individuals from the autumn cohort – group were similar to those of the other cohort – groups during winter. Generally, the spring cohort – group formed not always the dominant group in the population of the following year, despite its high densities after the spring recruitment.

Biomass

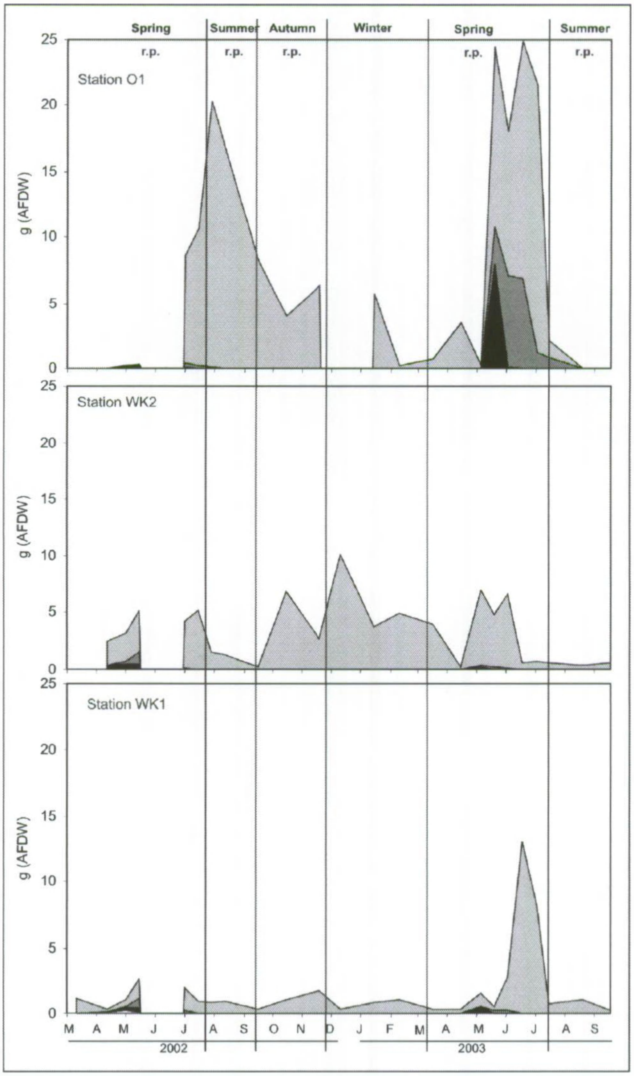


Figure 10. Biomass (g AFDW) pattern of the different benthic stages of *Lanice conchilega* for the three stations with indication of the different recruitment periods (r.p.): recently settled individuals (white), juvenile individuals (black), young adults (grey), adults (light grey). Sampling points with a time lag of more than one month were connected with a dotted line.

The biomass values (expressed as grams AFDW) at the three stations were primarily determined by a high relative contribution of adults in the population (Figure 10). During spring – summer, the high adult biomass resulted from high densities of small individuals, while the high autumn – winter biomass resulted from the presence of bigger individuals (in lower numbers). Only during the spring recruitment, other benthic stages were present in such high numbers that they significantly contributed to the total biomass. The highest biomass values were recorded at station O1 in the summer of 2002 (up to 20.3 g/m²) and in May-June 2003 (up to 24.9 g/m²). These peaks were caused by the high relative contribution of the adult biomass in the summer of 2002, of juveniles and adults in May 2003 and of young adults and adults in June 2003. At station WK2, biomass reached its highest values in July (5.1 g/m²) and in autumn – winter 2002-2003 (up to 10.1 g/m²), due to the high relative contribution of the adult population. At station WK1, the biomass values were low in 2002 (0.2 - 1.8 g/m²) compared to the other stations, due to the smaller adult population. In June 2003, high densities of adults originating from the spring recruitment of 2003 resulted in higher biomass values (maximum 13 g/m²).

Growth

Growth was more distinct at station WK2 (0.0178 mm/day) than at the two other stations (O1: 0.0154 mm/day; WK1: 0.0102 mm/day) (Table 1). The individuals of the spring cohort group were characterised by a relatively faster growth (0.0128 – 0.0191 mm/day), especially in 2003 (0.0118 – 0.0323 mm/day), than the individuals of the summer (0.0061 – 0.0123 mm/day) and autumn (0.0124 – 0.0155 mm/day) cohort groups. When comparing the spring cohorts, growth was faster in 2003 than in 2002 at stations O1 and WK2; values of WK1 were comparable between years.

Production

The total production during the 1.5 year study period was highest at station O1 (64.8 g/m²), followed by stations WK2 (28.2 g/m²) and WK1 (10.3 g/m²) (Table 1). The production was highest for the individuals of the spring cohort group (32.6 g/m² at station O1, 12.4 g/m² at station WK2, 3.3 g/m² at station WK1) compared to the individuals of the summer and autumn cohort group (7.9 – 1.3 g/m² at station O1, 6.8 – 4.5 g/m² at station WK2, 1.7 g/m² at station WK1). The production of the spring cohort group was lower in 2003 than in 2002, except for station WK1 (5.33 g/m²).

In 2002, annual secondary production of *L. conchilega* amounted to 38.34 g/m² at station O1, 22.13 g/m² at station WK2, and 5.00 g/m² at station WK1. The total biomass during this period at the three stations was respectively: 85.59 g/m², yielding a P/B ratio of 0.45 for station O1, 58.67 g/m², yielding a P/B ratio of 0.38 for station WK2, 13.54 g/m², yielding a P/B ratio of 0.37 for station WK1.

Table 1. Production, growth, biomass and P/B – ratio per cohort group during the 1.5 year study period

Station O1	production g/m^2	growth mm/day	biomass g AFDW /m^2	P/B
2001				
2002/1	32,6000	0,0164	58,9162	0,5533
2002/2	7,8620	0,0078	21,8444	0,3599
2002/3	1,3178	0,0124	4,8340	0,2726
2003/1	23,0413	0,0250	31,8544	0,7233
	total	average	total	
	64,8211	0,0154	117,4491	0,5519

Station WK 2	production g/m^2	growth mm/day	biomass g AFDW /m^2	P/B
2001	0,5132	0,0099	3,6583	0,1403
2002/1	12,3929	0,0191	20,9055	0,5928
2002/2	6,7741	0,0123	17,7583	0,3815
2002/3	4,5121	0,0155	16,7148	0,2699
2003/1	4,0352	0,0323	7,0037	0,5762
	total	average	total	
	28,2276	0,0178	66,0406	0,4274

Station WK 1	production g/m^2	growth mm/day	biomass g AFDW /m^2	P/B
2001				
2002/1	3,2937	0,0128	11,7363	0,2806
2002/2	1,6495	0,0061	1,4766	1,1172
2002/3				
2003/1	5,3288	0,0118	21,9255	0,2430
	total	average	total	
	10,2720	0,0102	35,1384	0,2923

Discussion

The family Terebellidae is characterized by a remarkable heterogeneity in terms of developmental strategies and larval ecology. *Lanice* (together with *Loimia*) is separated from other genera, which have a direct or mixed development. *Lanice* is characterized by two planktonic stages separated by a benthic larval stage, the second planktonic stage lasting much longer than the first and having morphological features similar to those of the juvenile worms (Bhaud, 1988; McHugh, 1993).

Because Thorson (1966) suggested that recruitment and early-life stages play an important role in bottom population dynamics, we made a detailed study about the recruitment patterns of *L. conchilega*. To this end, we detailedly discriminated between the first benthic stages (recently settled individuals, juveniles and young adults), based on a high sampling frequency. This enabled us to observe the settlement and recruitment patterns of *L. conchilega*. The detailed population structure of the subtidal *L. conchilega* patches was disentagled with the method of Bhattacharya and valided with NORMSEP. Due to the rather subjective way of this method, the obtained results of the population structure were handled and discussed with caution. Unfortunately, the patchiness of *L. conchilega*, especially in subtidal locations, makes it difficult to differentiate the trends in recruitment patterns of the successive sampling occasions. Nevertheless, we believe that the patterns of settling, recruitment and population structure of *L. conchilega* obtained and discussed in this paper provide a good estimate of the population dynamics of *L. conchilega* populations in fine muddy sands along the Belgian Coast.

Life cycle and demography

Fertilization

A step which was not directly investigated in this study, but which is important to address in closing the larval loop is the success of fertilization and larval production. Egg fertilization and larval production are controlled by both behavior (reproductive synchrony, aggregation or swarming) and the external physical environment (Eckmann, 1996). Reproductive synchrony in temperate regions, for example, is controlled by insolation, water temperature and stratification, with resultant effects on primary and secondary production. For sexually mature benthic organisms, a fertilization probability of 70-80% can be assumed if density exceeds several individuals per m² (as is the case for *L. conchilega* in this study). In the case of lower densities, a probability of 20% is expected (Eckman, 1996). The maximum fecundity of *L. conchilega* is estimated at 90000 - 160000 oocytes per individual of 125-150 µm (Bhaud, 1988; McHugh, 1993). Eckman (1996) mentioned that the degree of uncertainty about the fertilization is not of major importance, due to the increased losses in later stages (high rates of mortality of planktonic larvae) and the influences of advection on their fate.

Sexually mature males and females of *L. conchilega* can be found from April to the end of June according to Kessler (1963) in the German Bight. However, this period is probably longer along the Belgian coast, as larval release was detected until October in the present study.

Larval phase

After a short planktonic (trochophore and metatrochophore) and benthic phase (metamorphose I) of a few days, the second planktonic stage (the aulophore larva) stays in the water column for up to 60 days (Bhaud, 1988). In our study, aulophore larvae were found during almost the whole year (mainly March – November), with three peaks: one mean peak in spring and two smaller peaks in summer and autumn. The most important larval density peak (spring) coincided with the period of increase of temperature and primary production (April – May). The hypothesis that the timing of the occurrence of larvae and settling is linked to temperature and primary production is supported by the observations in the present study. The occurrences of aulophore larvae and the timing of settlement, together with the increases in temperature and primary production (pers. observation), were observed approximately one month later at station O1, compared to stations WK2 and WK1. Similarly, it can be hypothesized that the autumn peak of aulophore larvae coincided with an autumn plankton bloom, which regularly occurs in temperate regions (Rousseau, 2000). The increase in larval density in summer cannot be linked to such an event. The few larvae found in December – February were older aulophore stages (more than five tentacles; personal observation), indicating that there was no obvious new recruitment during winter. Normally, aulophore larvae have the ability to settle as soon as they have five tentacles, but older aulophore larvae were frequently found in the water column (Marcano & Bhaud, 1995), due to the resuspension ability of the larvae (Bhaud & Cazaux, 1990). In other studies, the aulophore larvae were also found during the whole year, with variations in the timing of periods with marked abundance (e.g. June – September in Arcachon and Roscoff; April – October in Plymouth; March – April + July in Helgoland) (Marcano & Bhaud, 1995).

The occurrence of planktonic larvae is related to temperature and primary production increases, but the distribution of the larvae in the southern Bight of the North Sea is also influenced by hydrodynamics (Belgrano et al., 1990) and, to a large extent, larval behavior (Bhaud, 2000). The position of the aulophore larvae in the water column depends on the secretion of a mucus trail, while the sinking rate depends on the behavior of the larvae, which can quickly loosen their connection with the mucus trail and secrete another one (Bhaud & Cazaux, 1990). The success of the settling of these planktonic larvae to the benthos is unpredictable, because the transition is complex and affected by many variables (Feller et al., 1992).

Periods of recruitment

Settlement is defined as the successful transition from the larval stage to benthic life, whereas the term recruitment represents the success of the life cycle, resulting in the appearance of new classes of adult individuals (Bhaud, 2000).

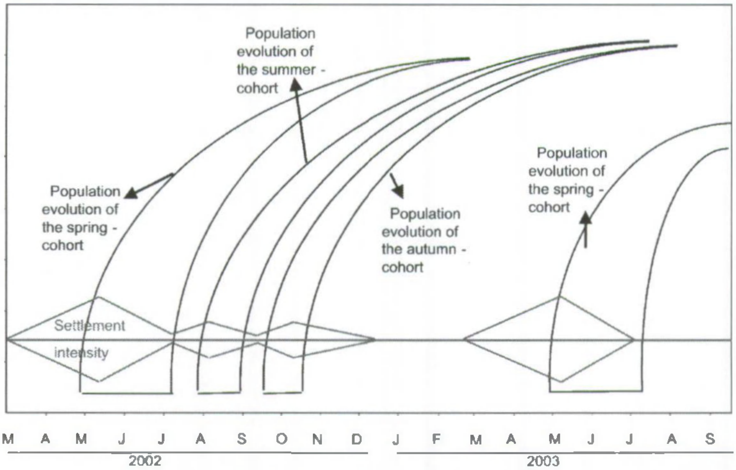


Figure 11. Schematic overview of the general trends in settlement and recruitment and evolution of the populations originating from the different recruitment periods.

General pattern of settlement and recruitment

In general, the settling of aulophore larvae was visible from March – April onwards, while recruitment was clearly visible from May - June onwards (cf. size frequency distributions). The settling and recruitment of *L. conchilega* can be situated continuously from March until November and can be divided into three periods (Figure 11). These three periods were defined based on the occurrence of peaks of aulophore larvae in the water column and peaks of recently settled individuals in the benthos. Consequently, following periods were distinguished: (1) spring recruitment period (April – July), (2) summer recruitment period (July – September), and (3) autumn recruitment period (September –

November). Each period was characterized by a peak in recently settled individuals, followed by recruitment to the adult population. The evolution of the adult population, consisting of different cohorts, was visualized in Figure 10. The transition from settling to final recruitment was investigated in the present study by distinguishing different developmental stages in the benthos (recently settled individuals, juveniles and young adults). These stages succeeded each other in time, with declining densities from the settling phases towards the adult population. The time lapse between settling and detection of the individuals in the adult population is not more than one month, as juveniles started to detach and re-settle in the sediment one month after attachment to adults (Callaway, 2003). This transition period was characterized by a high mortality (from 1000-s ind/m² to <1000 ind/m²). Cohort analysis indicates that the densities of the individuals of the small size classes (< 2 mm width) rapidly decreased in time and that they were replaced by high densities of newly recruited individuals by the time the following sampling occasion took place. This high mortality and turn over of individuals could mainly be due to competition for space and food, erosion, predation, mechanical damage, disease or other physiological stress (Eckman, 1996).

The three defined recruitment periods in the present study were characterized by variations in intensity and duration. The spring recruitment period was the most intense and prolonged recruitment period, with a lot of new cohorts resulting in high adult densities in the beginning of the summer. Some of the cohorts disappeared in the same year, without reaching the maximal tube width of older *L. conchilega* individuals. It is not clear if those individuals were sexually mature, because there is no information on the age of maturity of *L. conchilega*, but they could be responsible for new recruitment in the same year. Others survived the winter and were, together with the individuals from the summer and autumn recruitment period, responsible for the spring recruitment of the following year. The summer and autumn recruitment periods were less intense and could not always be detected in the adult population structure. It can be concluded that *L. conchilega* is characterized by a pattern of constant recruitment with one or more definite periods of acute increase. This pattern has already been reported for a lot of other polychaete species (e.g. Spionidae spp., *Hediste diversicolor, Capitella* spp) (Méndez et al., 1997; Bolam, 2004; Garcia-Arberas & Rallo, 2004). The population structure of *Hediste diversicolor*, for example, showed different cohorts, originating from a varying recruitment rate, and which were lumped into two periods (Garcia-Arberas & Rallo, 2002).

The continuous recruitment of *L. conchilega* in Belgian Coastal waters is characterized by a high turn over and population renewal, which result in the maintenance of high densities of *L. conchilega* during the year. This type of population renewal was not detected every year in the intertidal *L. conchilega* populations of the bay the Veys (France) to maintain the high adult densities (Ropert & Dauvin, 2000). In that particular case, the population renewal probably resulted from transfer of benthic populations from offshore towards the coast. Population renewal due to a significant recruitment was detected in the intertidal *L. conchilega* population at the sandflat 'Gröninger Plate', which was yearly (1998 – 2000) characterized by a high percentage of juvenile tubes (< 3 mm wide; adults 3 – 8 mm) in May – October (Zühlke, 2001).

Settlement supports temporal stability

The high adult densities are not only maintained due to the recruitment strategy; the settlement strategy plays a major role and determines the temporal stability of the *L. conchilega* patch locations. Epibenthic structures (adult tubes or tube like structures, shells) are needed for the settling and tube building of the *L. conchilega* larvae (Heuers et al, 1998; Callaway, 2003). The success of initial larval settlement, i.e. the number of recruits per adult tube, increases with the density of adult tubes (Heuers et al., 1998). Generally, settling in areas occupied by adult conspecifics increases the probability of adequate survival conditions in terms of food supply, predation pressure and abiotic environmental conditions (Pawlik, 1992). The main advantage for *L. conchilega* individuals attaching to adults is probably the secure anchorage in the sand, because settling directly in the sediment would subject individuals to a higher risk of passive dislodgement. In the present study and in the study of Callaway (2003), averages of 5 to 13 juveniles and a maximum of 72 individuals were found attached to single adult tubes. However, attachment of *L. conchilega* individuals to adults or hard substratum is not obligatory. Strasser & Pieloth (2001) showed that juveniles recolonized a sandflat that had experienced a collapse of the *L. conchilega* population and was devoid of adult tubes. Similarly, settling and recruitment were observed at station O1 in 2002, in spite of the absence of adult tubes. However, the settling and recruitment was more successful at station O1 in 2003, which could be due to the presence of adult tubes. It can be concluded that the presence of adult tubes enhances settling in existing *L. conchilega* patches, but new establishments are possible.

Spatial and temporal variability

Within this generally observed recruitment pattern of *L. conchilega*, spatial differences in timing and intensity, and year-to-year variations were detected. On a small spatial scale, differences in intensity were observed, but there were no significant differences in timing. On a larger spatial scale, however, differences in both intensity and timing were quite pronounced. In 2003, for example, there was a time lag in the recruitment of 2 weeks between station O1 and stations WK2 - WK1. This time lag on a large spatial scale was also observed in the timing of the plankton bloom, which was later at station O1 (pers. obs.). These differences between stations indicate that the larval presence and settling were not synchronized along the Belgian coast, but may mainly be influenced by variations in local factors, like temperature and primary production. Spatial and temporal differences in intensity could also be linked to differences in larval supply (Strasser & Pieloth, 2001). In the present study, the aulophore densities were similar in 2002 and 2003 at station O1 (± 800 ind/m^3), in spite of unequal recruitment success between the years. The density estimates of the aulophore larvae were based on one sample at each sampling occasion, without taking into account the possible short – term tidal (Belgrano et al., 1990) and spatial variability at those locations. Consequently, no conclusions can be formulated about the linkage between the recruitment variability and differences in larval supply.

Temporal differences in settling period of *L. conchilega* were observed in the present study (between 2002 and 2003 and between stations) and in the study of Callaway (2003) (April – May in 1998; May – June in 1999; June in 2000). The three recruitment periods discerned were not detected every year (e.g. summer recruitment period in 2003 at the three stations, autumn recruitment period at station WK1).

Differences in settling and recruitment success can explain part of differences in the adult density in the following year (Buchanan et al., 1986). The extensive adult population in spring 2003 at stations WK2 and WK1 is probably due to successful settling and recruitment in 2002. The recruitment success was lower in 2003, resulting in low adult densities at the end of the summer. The inverse pattern was detected at station O1, with an extremely high settling and recruitment in 2003 compared to 2002. Recruitment and settling, however, were not successful: the adult population completely crashed in August, probably due to a disturbance (e.g. beam – trawling and waves). Despite the lower settling and recruitment in 2002 at station O1, an adult population was present in high densities in 2003. This means that other factors, like natural (storms) or anthropogenic (beam –trawling) disturbances and post – settlement processes can influence the normal temporal pattern in coastal zones, which complicates making predictions on success of settlement and recruitment (Buchanan et al., 1986; Feller et al., 1992).

Life span

In the study of Ropert & Dauvin (2000), a cohort of juvenile individuals needed 17 to 24 months to integrate into a persistent adult population (tube width: 3.4 - 4.2 mm). In our study, the individuals already reached a tube width of 2 - 3 mm after a few months and a persistent adult population was not present (at least not in meaningful densities). Therefore, the life span of the *L. conchilega* individuals in the present study was estimated to be one year, with variations of a few months (individuals with a tube width of more than four mm were seldomly found). In the study of Ropert & Dauvin (2000), however, individuals with a tube width of more than two mm were estimated to be more than one year old. The smaller ones originated from the recruitment in June (samples in October) and in that particular study, *L. conchilega* reached a life-span of three years. In the Wadden Sea area, this species was estimated to live 1 – 2 years (Beukema et al., 1978). Although the differences in life-span between the different locations are considerable, they are commonly found for a lot of other species (Spionidae, *Perinereis cultrifera*) (Roubah & Scaps, 2003; Bolam, 2004).

Growth and production

In the present study, *L. conchilega* was characterized by a high growth rate (average of 0.0102 – 0.0178 mm/day), whereas its growth rate in the Bay the Veys was lower (0.0039 to 0.0053 mm/day) (Ropert, 1999). Most probably, the reduced food availability and feeding time in intertidal areas reduce the growth of *L. conchilega* compared to the subtidal areas. The growth is at its maximum after the integration of the juveniles into the population (Ropert, 1999; the present study). The increased food supply after the spring phytoplankton bloom might be responsible for the high growth rates and the fast development of the individuals to adults in the same year. The high productivity and biomass of *L. conchilega* is also linked to the high and almost constant food availability in the coastal zone of the BCS, which is characterized by turbulent, nutrient rich water and riverine input of the Westerscheldt and Yzer. Rees (1983) stated that spatial differences in production mainly depend on the food availability and quality. Therefore, it can be assumed that the constantly high supply of nutrients via the Westerscheldt caused for the high production and biomass values observed at station O1. Similarly, the P/B ratio was highest at station O1 (P/B: 0.55) compared to the two other stations (P/B: 0.43, 0.29), but was comparable with the P/B ratios obtained in the study of Ropert (1999) (P/B: 0.55, 0.36). These P/B ratio's deviate from the values expected for a short – living species. Normally, the productivity becomes more important when the life-span is shorter, resulting in higher P/B ratio's (Ménard et al., 1989). This is not the case for *L. conchilega*: the populations of *L. conchilega* (high turn over) do not correspond with a "classic" population.

Conclusion

This study underlined the opportunistic status of the tube - building polychaete *Lanice conchilega*, whose life – cycle is characterized by a long pelagic phase, mass benthic settling with high mortality, rapid growth and a high turn – over in the adult population. It is difficult to predict the adult population density in the long run, based on the settlement and recruitment success in a particular year, due to the high natural and anthropogenic disturbance in coastal areas. Nevertheless, due to the (almost continuous) high recruitment and the preferential settling of the aulophore larvae nearby *L. conchilega* tubes, a temporal stability of the location of the *L. conchilega* population was found, with varying density. Finally, we detected temporal and spatial variability in settling and recruitment patterns of *L. conchilega* along the Belgian Coast.

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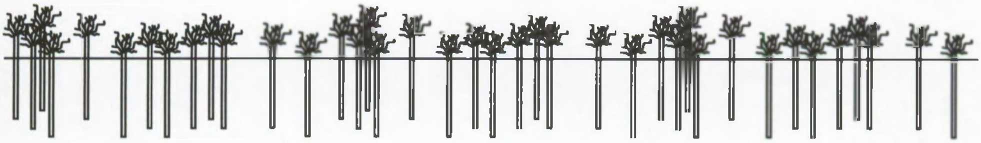
Chapter 6

The impact of *Lanice conchilega* on the soft-bottom benthic ecosystem in the North Sea



Paper to be submitted as

Van Hoey, G., Vincx, M. & Degraer, S.
The impact of *Lanice conchilega* on the soft-bottom benthic ecosystem in the North Sea

Abstract

The tube building polychaete *Lanice conchilega* has a wide distribution and can form dense aggregations. Unfortunately, the effects of *L. conchilega* on the surrounding benthic community have received little attention, especially in subtidal areas. Therefore, the effects of the presence of *L. conchilega* on the abundance, species richness, diversity and species composition of the North Sea benthos in relation to sedimentology and depth were evaluated in the present paper. The results show that *L. conchilega* does have an effect on the benthic density and species richness in soft-bottom sediments. The density of the benthic species increased and was significantly (positively) correlated with the density of *L. conchilega*. Furthermore, the species richness increased with increasing density of *L. conchilega*. This trend was, however, not consistent: the number of species no longer increased or even decreased after reaching a certain density of *L. conchilega* (> 500 ind/m²). The same overall pattern was detected concerning the expected number of species. The N_1 - diversity index showed similar or slightly higher values in *L. conchilega* patches compared to patches without *L. conchilega*. The effects on density and diversity were most pronounced in shallow fine sands, which are the preferred habitat of *L. conchilega*, and less in deep fine sands. The changes in benthic characteristics result from the alterations of the habitat by *L. conchilega* (hydrodynamics, sediment stability, improved oxygen) and the complex interactions between the benthic organisms and the biogenic structures consisting of *L. conchilega* tubes. A lot of benthic species can profit from the creation, modification and maintenance of that habitat by *L. conchilega*, which results in an increased density and species richness in *L. conchilega* patches compared to the surrounding soft-bottom sediments. Finally, the results indicated that *L. conchilega* has an effect on the benthos present in a particular habitat, rather than forming its own association.

Keywords
Lanice conchilega, diversity, associated species, soft-bottom sediments, North Sea

Introduction

Biogenic habitat structures play a major role in structuring the distribution pattern of benthic fauna by modifying the sediment (Eckman et al., 1981; Carey, 1987) and hydrodynamic parameters (Eckman 1983), or by changing interactions between species (Woodin, 1978). In some cases, those biogenic habitat structures could even be considered as 'biogenic reefs'. 'Biogenic reefs' were defined as rocky marine habitats or biological concretions that rise from the sea bed and were created by the animals themselves (Holt et al., 1998). The best know species forming 'biogenic reefs' and structuring the environment with possible effects on the benthic fauna are *Serpula vermicularis, Mytilus edulis, Sabellaria* species and *Modiolus modiolus* (Holt *et al.*, 1998).

Additionally, some other tube-building polychaetes provide considerable structures in the otherwise relatively unstructured soft-bottom sediments (Woodin, 1978; Zühlke et al., 1998; Zühlke, 2001; Bolam and Fernandes, 2002; Rees et al., 2005). An example of a structuring tube-forming polychaete is the sand mason, *Lanice conchilega*, which lives in a tube of sand or shell breccia attached to an inner thin organic layer. The tube itself is crowned with a sand-fringe, which protrudes 1 - 4 cm above the sediment surface (Ziegelmeier, 1952). This species can reach densities of several thousands of individuals per m² (Buhr and Winter, 1976; Ropert and Dauvin, 2000) and has the ability to influence the surrounding benthic populations (Zühlke et al., 1998; Zühlke, 2001). This ability is mainly due to the following factors: (1) the tubes provide a settlement surface for larval and postlarval benthic organisms (Qian, 1999), (2) there is an improved oxygen supply in the sediments surrounding *L. conchilega* tubes (Forster and Graf, 1995)), (3) the tubes affect the current velocities in the benthic boundary layer (Eckman et al., 1981; Heuers et al, 1998, Hild & Günther, 1999), (4) the tubes have a stabilizing effect on the sediment, and (5) the space between tubes can serve as a refuge from predation (Woodin, 1978). The presence of *L. conchilega* tube aggregations in an intertidal sandflat, for example, resulted in an increase in the species diversity and abundance compared to the surrounding sediment (Zühlke et al., 1998; Zühlke, 2001).

Lanice conchilega has an amphiboreal distribution, is found on all European coasts and colonizes a wide variety of intertidal and subtidal sediments down to about 1900m (Hartmann – Schröder, 1996; Ropert and Dauvin, 2000). Despite its wide distribution and the formation of sometimes dense aggregations, the effects of *L. conchilega* on the surrounding benthic community have received little attention, especially in subtidal areas. The interaction between *L. conchilega* and the benthos was only studied by Zühlke et al., 1998; Zühlke, 2001 and Dittmann (1999) on two sandflats of the East Frisian Waddensea (the Gröninger Plate and the Domumer Nacken) and included some experiments on the effect of artificial tubes on the benthos. Both studies concluded that the benthos in tidal flats has a temporary and optional association with the biogenic structures of *L. conchilega* and that the presence of such structures enriches the *Arenicola*-dominated sandflat associaton in abundance and species numbers due to a reduction of current velocity.

Under the guidance of the Benthos Ecology Working group of ICES, a large-scale benthos survey was performed in the subtidal of the North Sea in 2000 (Rees et al, 2002). The resulting dataset forms the basis of the description of the impact of *L. conchilega* on the soft-bottom benthic ecosystem in the North Sea. In other words, the present study aims to investigate the effects of the presence of *L. conchilega* on the abundance, species richness, diversity and species composition of the North Sea benthos. These effects of *L. conchilega* will be investigated in relation to depth and sedimentology, and the obtained results will be discussed in the light of the potential environmental and biological effects that *L. conchilega* may cause. Finally, the results will be linked to the arguments used to consider the biogenic structures formed by *L. conchilega* as 'biogenic reefs'.

Materials and Methods

Study area

The study area covers most of the English Channel and the North Sea (delimited by Norway and Denmark in the east, the UK in the west and Germany, the Netherlands, Belgium and northern France in the south). The North Sea (51° to 61° N, 3° W to 9° E) is divided into a number of loosely defined areas: a relatively shallow southern North Sea (Southern Bight and German Bight), the central North Sea (Doggerbank, Oysterground), the Northern North Sea, the Norwegian Trench and the Skaggerak, from which the last two areas are not included in the present study.

Data origin

Under the guidance of the Benthos Ecology Working group of ICES, a total of 2227 macrobenthic samples (1405 stations) were gathered in the North Sea and English Channel in the year 2000 – 2001. These data originate from various projects, including national monitoring surveys (Rees et al., 2002). Most of the sampling was done as agreed beforehand, i.e. collecting infauna (and slowly moving epifauna) with grabs of the Van Veen type (at least 2 grabs of 0.1m² at each station), and sieving alive over a 1 mm sieve. In spite of the initial agreement, some data contributors used other sampling devices, such as Hamon grab, box corer and Day grab. In order to enable detailed analyses on a uniform dataset, only samples, which were taken with a 0.1 m² Van Veen or Day grab and were sieved alive, were included in the present study (except in the description of the distribution of *L. conchilega* in the North Sea). This resulted in a final dataset of 1098 samples (comprising 513 different stations).

All data was incorporated into a database, and taxonomic inter-comparisons were performed (Rees et al, 2002). These data modifications were executed during several workshops of the ICES North Sea Benthos Study group. After taxonomic clearance, a dataset consisting of 717 taxa (further referred to as species) was obtained. The density of *L. conchilega* in the present study is based on individual counts, rather than tube counts.

The sedimentological characteristics of the different samples were coded according to sediment classes: (a) mud, (b) muddy sand, (c) fine to medium sand, (d) medium to coarse sand, (e) sand and gravel, and (f) mixed sediments (Report ICES CM 2004/E:05). Additionally, water depth at each sampling station was recorded. The different habitat types were distinguished by using the sediment classes. Based on the bathymetrical information, those sediment classes were each split up in shallow (< 70 meter) and deep (> 70 meter) (cf. Künitzer et al., 1992).

Data analysis

The effects of *L. conchilega* on the macrobenthos were investigated for every habitat type, in which the species was found and for which a representative amount of samples (> 100) was available (Figure 2). The following univariate indices were used to describe the macrobenthos (excluding *L. conchilega*) in each sample: (1) density N, (2) species richness S, expressed as number of species per sample (i.e. per $0.1m^2$), (3) the exponential form of the Shannon – Wiener index N_1 and (4) expected number of species (ES 50). All indices were calculated with the Primer 5.2.9 software package. The relations between benthic density, species richness, expected number of species or N_1 - diversity and the density of *L. conchilega* in the different habitats were observed and visualised based on different density classes of *L. conchilega*, and were statistically tested using Spearman rank correlations.

In order to identify species which are possibly associated with the presence of *L. conchilega*, three reductions and calculations of the species dataset were performed. Firstly, only species which were present in more than 5 samples per habitat type were selected, thereby excluding rare species. Secondly, an association degree (the percentage of occurrence of a species in samples with *L. conchilega* relative to the total presence of that species in all samples) was calculated. Species with an association degree of more than 50% (> 50% of all individuals were found in association with *L. conchilega*) were regarded as associated species. Thirdly, the level of the significance of association was calculated using a Mann – Whitney U test comparing densities of a certain species between *L. conchilega* samples and samples without *L. conchilega*. Finally, species from which the densities showed a positive correlation (Spearman Rank correlation) with the density of *L. conchilega* were retained. Non – parametric test were used because the assumptions for parametric test, even after transformation, were not fullfiled.

Results

Distribution pattern

Lanice conchilega was found in the entire North Sea and English Channel (Figure 1) (25% of the stations). In the central English Channel, *L. conchilega* was seldomly found (< 5% of the samples), whereas the species occurred frequently in the entire North Sea (42% of the samples). The areas with the highest frequency of occurrence and densities were the German Bight, the central part of the North Sea (Dogger Bank) and along the French, Belgian and Dutch coast. In the deeper northern part of the North Sea, *L. conchilega* was frequently found, but in low densities (< 100 ind/m^2), whereas in the western North Sea, *L. conchilega* was seldomly found.

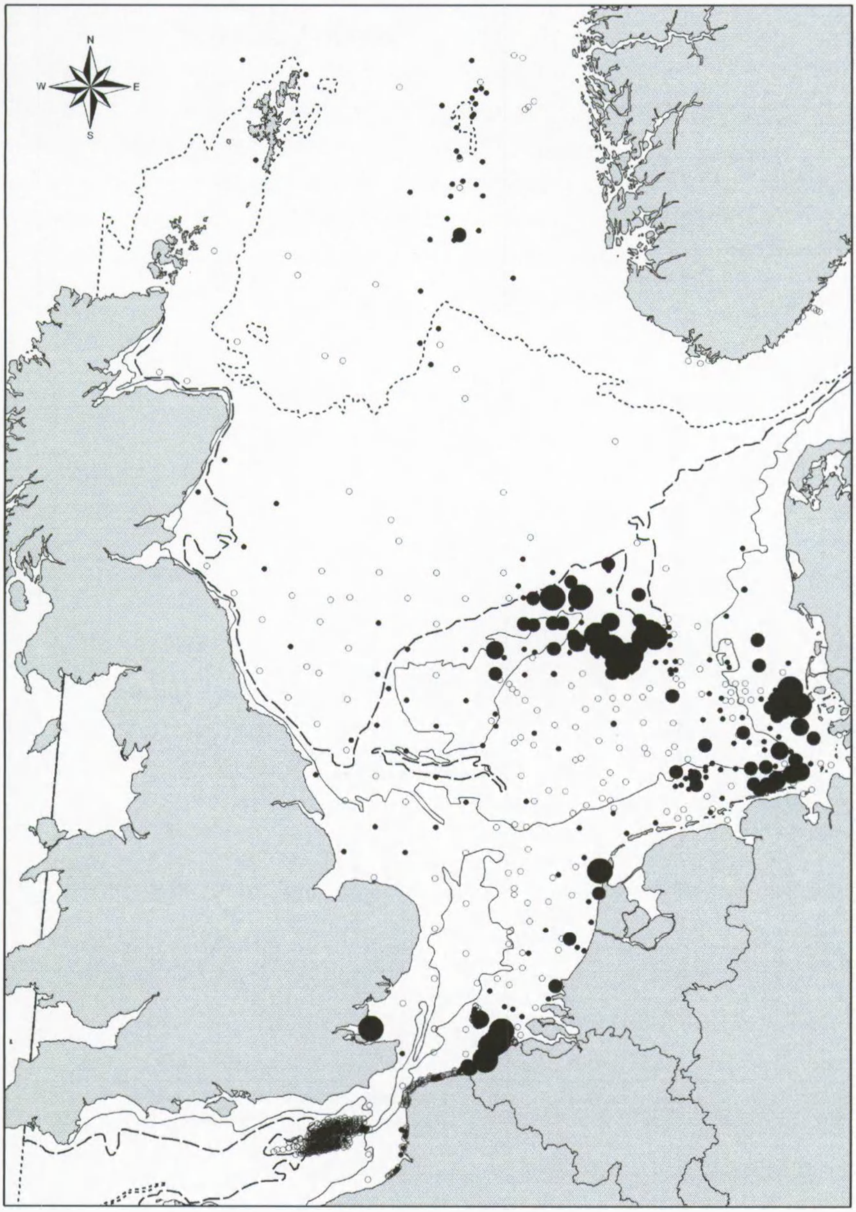


Figure 1. Density distribution of *L. conchilega* in the entire North Sea and English Channel. 0 ind/m^2: (○); 1-100 ind/m^2 (•); 100-500 ind/m^2 (●); 500-1000 ind/m^2 (●); > 1000 ind/m^2 (⬤)

Habitat preferences

Lanice conchilega was found in all soft-bottom sediment types in the North Sea; however, with differences in frequency of occurrence and average density between the habitat types discerned (Figure 2). No evaluation of the occurrence of *L. conchilega* in shallow mud, deep muddy sands and deep medium sands could be made, due to the low number of samples in these habitat types (< 30 samples). As for the other habitats, the highest percentages of occurrence (41 - 51 %) and highest densities (138 – 419 ind/m²) of *L. conchilega* in shallow areas were observed in muddy, fine and mixed sediments. In shallow medium and coarse sediments, the frequencies of occurrence (24 and 30%, respectively) and average densities (17 and 12 ind/m², respectively) were much lower. In deep muds and fine sands (> 70 meter), *L. conchilega* occurred frequently (53 and 45%, respectively), but in low average densities (32 and 14 ind/m², respectively). Although *L. conchilega* was found in all habitat types, for reasons of representativeness further detailed analyses were only done for habitats containing more than 100 samples (deep fine sand, shallow muddy sand, shallow fine sand and shallow medium sand).

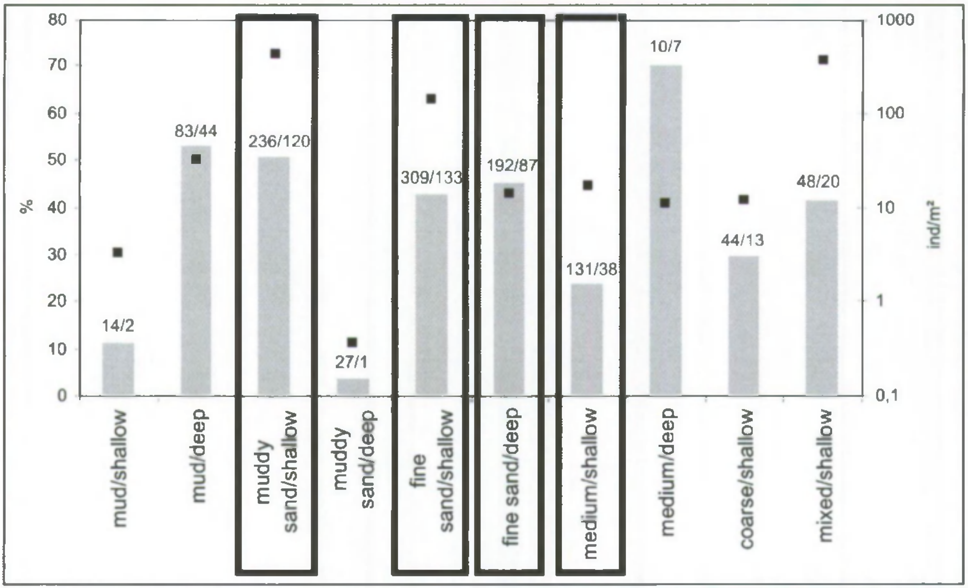


Figure 2. Percentage of occurrence and average density (ind/m²) of *Lanice conchilega* in the different discerned habitat types, with indication of the total amount of samples versus samples with *L. conchilega*. The four habitats, which were represented by more than 100 samples in the database, were encircled.

Effect of *Lanice conchilega* on the benthic characteristics

Presence / absence of Lanice conchilega

A highly significant difference ($p < 0.0001$) in benthic density and species richness (excluding *L. conchilega*) was found between *L. conchilega* samples and samples without *L. conchilega* in shallow muddy sands, fine sands and medium sands (Table 1). Those differences in density and species richness were significant in deep fine sands ($p = 0.0115$ and $p = 0.0027$). The N_1 – diversity index in *L. conchilega* samples differed significantly in shallow fine sands ($p < 0.0001$), medium sands ($p = 0.0012$) and deep fine sands ($p = 0.0225$). Only in shallow muddy sands, no significant differences were found ($p = 0.1299$). The ES (50) was only significantly different in shallow fine sands and medium sands.

Table 1. First, the differences tested in benthic density, species richness, N_1 – diversity and ES (50) by Mann – Whitney U test, between *Lanice conchilega* samples and samples without *L. conchilega* for the different habitats. Second, the Spearman rank correlation between the benthic density, species richness, N_1 – diversity and ES (50) and the density of *L. conchilega* for the different habitats. The number of observations (n) within each habitat where 236 for shallow muddy sand, 309 for shallow fine sand, 192 for deep fine sand and 131 for shallow medium sand.

	HABITATS	Mann - Whitney U- test	Spearman rank correlation	
			R	p
DENSITY	shallow muddy sand	$p < 0,0001$	0,45	$p < 0,0001$
	shallow fine sand	$p < 0,0001$	0,63	$p < 0,0001$
	deep fine sand	$p = 0,0115$	0,23	$p = 0,0013$
	shallow medium sand	$p < 0,0001$	0,39	$p < 0,0001$
SPECIES RICHNESS	shallow muddy sand	$p < 0,0001$	0,4	$p < 0,0001$
	shallow fine sand	$p < 0,0001$	0,65	$p < 0,0001$
	deep fine sand	$p = 0,0027$	0,27	$p = 0,0001$
	shallow medium sand	$p < 0,0001$	0,5	$p < 0,0001$
N_1	shallow muddy sand	p = 0,1299	0,08	p = 0,22
	shallow fine sand	$p < 0,0001$	0,39	$p < 0,0001$
	deep fine sand	$p = 0,0225$	0,158	$p = 0,028$
	shallow medium sand	$p = 0,0012$	0,36	$p < 0,0001$
ES (50)	shallow muddy sand	p = 0,07	0,08	p = 0,22
	shallow fine sand	$p < 0,0001$	0,39	$p < 0,0001$
	deep fine sand	p = 0,16	0,17	p = 0,17
	shallow medium sand	$p < 0,0001$	0,34	$p < 0,0001$

Correlation between benthic structure characteristics and density of Lanice conchilega

In the four habitats, the densities of the surrounding benthos increased with increasing density of *L. conchilega* (Figure 3a). The increasing trend of the density was comparable in the four habitats. The correlation between densities of the benthic fauna and the densities of *L. conchilega* was positive and significant in all habitats, was strongest in shallow fine sands (Spearman R: 0.63) and was lowest in deep fine sands (Spearman R: 0.23) (Table 1).

In shallow muddy sands, the species richness decreased when the density of *L. conchilega* exceeded 1000 ind/m², while in shallow fine sands, the species richness levelled of at 500 ind/m² of *L. conchilega* (Figure 3b). Although species richness differed strongly between habitats, a significant correlation was found between the species richness and the density of *L. conchilega* in all habitats, with the highest value in shallow fine sands (Spearman R: 0.65) and the lowest in deep fine sands (Spearman R: 0.27) (Table 1). In shallow muddy sands, the correlation was atypical: the species richness decreased with higher densities of *L. conchilega.*

The N_1- diversity index and its relation with *L. conchilega* density differed between the habitats (Figure 4a). In shallow muddy sands, the N_1- diversity index did not increased with the *L. conchilega* density and did not show a significant correlation (Spearman R: 0.07; p = 0.28) (Table 1), whereas a minor, through significant to very highly significant correlation was observed in the other three habitats. The strongest correlation was found in shallow fine sands (Spearman R: 0.39) (Table 1).

The trend in the ES(50) was comparable with that of the species richness (Figure 4b), with some small differences: (1) in shallow muddy sands and deep fine sand no increase and no significant correlation in ES(50) with the *L. conchilega* density was observed, (2) in shallow fine and medium sands an increase and a significant correlation (Spearman R: 0.39 – 0.36, respectively) was found, but the curve levelled of at 100 ind/m² in medium sands and slowly increased or even decreased in fine sands (Table 1).

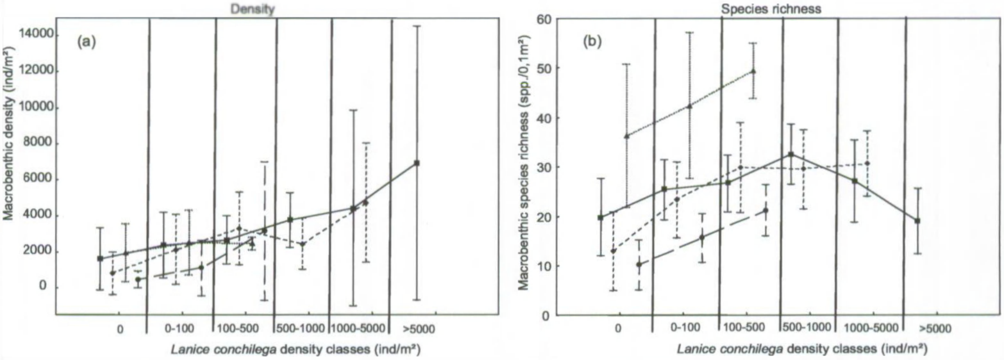


Figure 3. (a) The density (with exclusion of *Lanice conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation, and (b) the species richness (with exclusion of *L. conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation. Shallow muddy sand: square; shallow fine sand: rhombus; deep fine sand: triangle; shallow medium sand: circle.

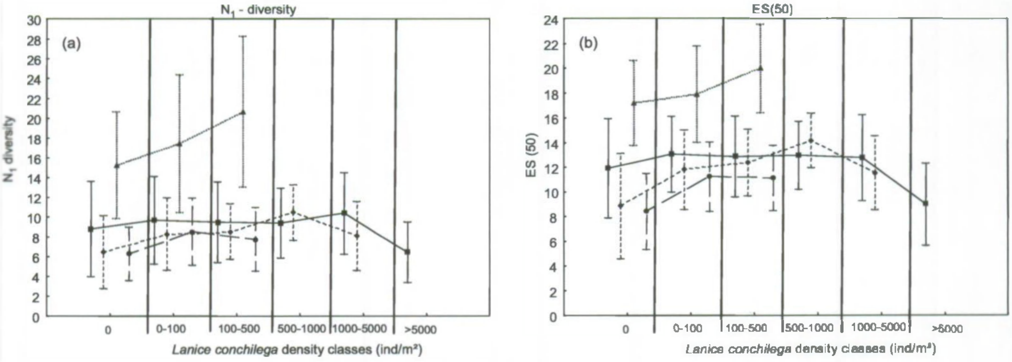


Figure 4. (a) The N_1-diversity (with exclusion of *Lanice conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation, and (b) the ES(50) (with exclusion of *L. conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation. Shallow muddy sand: square; shallow fine sand: rhombus; deep fine sand: triangle; shallow medium sand: circle.

Species associated with *L. conchilega*

Table 2. First, an overview of the percentage of the species associated with *Lanice conchilega* in relation to the total amount of species (with exclusion of the rare species) is given for the most important higher taxa within each habitat type. Secondly, the amount of associated species of *L. conchilega*, which where also the most frequent occurring species (found in most samples) for that habitat. Thirdly, the percentage of each discerned feeding type within each habitat for the group of samples which contain *L. conchilega* and samples whithout *L. conchilega.*

	shallow muddy sands			**shallow fine sands**		
Higher taxa	**# associated species**	**total # species**	**%**	**# associated species**	**total # species**	**%**
Anthozoa	1	1	100	1	1	100
Polychaeta	13	54	24	26	54	48
Bivalvia	6	22	27	10	19	53
Gastropoda	2	5	40	3	7	43
Amphipoda	4	16	25	12	20	60
Cumacea	2	9	22	3	8	38
Decapoda	1	5	20	5	6	83
Echinodermata	0	9	0	4	7	57
others	1	8	13	5	11	45
TOTAL	30	129	23	69	133	52
Most frequent occuring species	13	20	65	17	20	85
Feeding type	***Lanice* %**	**no *Lanice* %**		***Lanice* %**	**no *Lanice* %**	
I: suspension feeding	15	14		22	24	
II: surface deposit, facultative suspension and interface feeding	64	54		64	56	
III: subsurface deposit feeding, grazing	11	21		4	5	
IV: omnivore, predator, scavenger	9	8		8	10	
V: unknown	1	3		2	6	

	deep fine sands			**shallow medium sands**		
Higher taxa	**# associated species**	**total # species**	**%**	**# associated species**	**total # species**	**%**
Anthozoa	1	1	100	1	1	100
Polychaeta	1	107	1	7	32	22
Bivalvia	0	25	0	1	9	11
Gastropoda	0	7	0	0	1	0
Amphipoda	1	26	4	1	10	10
Cumacea	0	6	0	2	3	67
Decapoda	0	2	0	1	3	33
Echinodermata	0	6	0	0	3	0
others	0	12	0	3	3	100
TOTAL	3	192	2	16	65	25
Most frequent occuring species	1	20	5	1	20	5
Feeding type	***Lanice* %**	**no *Lanice* %**		***Lanice* %**	**no *Lanice* %**	
I: suspension feeding	9	8		5	6	
II: surface deposit, facultative suspension and interface feeding	76	77		72	47	
III: subsurface deposit feeding, grazing	4	5		6	12	
IV: omnivore, predator, scavenger	9	8		15	33	
V: unknown	2	2		2	2	

A species was identified as being associated with *L. conchilega* if the association degree was more than 50%, if the species density significantly differed between the samples with and without *L. conchilega* and if a positive correlation with the density of *L. conchilega* was found.

In shallow fine sands, 52 % of the species were positively associated with *L. conchilega*, whereas only 23 - 25% of the species were associated in shallow muddy and medium sands. In deep fine sands, only 3 out of 202 species showed an association with *L. conchilega*. In the first three habitats, associated species were found within each higher taxon, except for the Echinodermata. The percentage of associated species within each higher taxon was highest (> 40%) in shallow fine sands. Furthermore, most of the frequently occurring species within that habitat were associated with *L. conchilega* (85%). In shallow muddy sands, only 65% of those species were associated. In deep fine sands and shallow medium sands, the frequently occurring species were not associated with *L. conchilega*.

Differences in the relative abundance of each feeding type within a habitat were observed between samples containing *L. conchilega* and *L. conchilega* free areas (Table 2). In the shallow habitat types, surface deposit feeding was the dominant feeding type and was more dominant in samples containing *L. conchilega*. The dominance of subsurface deposit feeders decreased in *L. conchilega* samples, especially in shallow muddy and medium sands. The percentage of omnivorous and predatory species did not change strongly, except in shallow medium sands, where their dominance was reduced.

Discussion

Distribution

Lanice conchilega has a cosmopolitan distribution, as it is found from the Arctic to the Mediterranean, in the Arabian Gulf and the Pacifc, from the low water neap tide mark down to 1900 m (Hartmann–Schröder, 1996). In our survey, *L. conchilega* was found in the entire North Sea down to a depth of 180 meter (deepest record in the dataset was 380 meter). This tube–building polychaete is known to live mainly in sandy sediments from mud to coarse sand (Hartmann – Schröder, 1996), as was confirmed by the present study. Yet, shallow muddy and fine sands were strongly preferred: *Lanice conchilega* showed its highest frequencies of occurrence and densities in these sediments (more than 1000 individuals per m² compared to maximally 575 ind/m² in shallow medium sands). In the deeper habitats, *L.* conchilega was frequently encountered but only in low abundance (maximally 170 ind/m² in deep fine sand). Hence, it can be concluded that *L. conchilega* has a wide geographical distribution and a low habitat specialization (i.e. eurytopic species), leading to the absence of an obvious relationship between the distribution pattern of *L. conchilega* and the sediment type (cf. Buhr (1979), who assumed that the hydrodynamics are more important). Heuers et al. (1998) also found that the density of *L. conchilega* was related to hydrodynamics: patches of low density occurred in areas with low current velocities (10 cm/s), while patches of high densities were found in areas with high current velocities (20 cm/s). It was, however, not clear which aspect of the hydrodynamics was really relevant.

From the distribution map of *L. conchilega* (Figure 1), it can be deducted that the highest densities and percentages of occurrence were observed in the coastal areas of the North Sea (German Bight, French Belgian and Dutch coast) and in the central part of the North Sea (Dogger Bank). Those areas were already characterized as the zones with the highest primary production in the North Sea (McGlade, 2002, Peters et al., 2005). Besides physical factors (sediment type, flow regime), which mainly determine the distribution of a benthic species, the availability of food might also have a positive influence on the abundance of *L. conchilega*. However, for modeling the habitat preferences of *L. conchilega* based on several types of environmental variables (granulometrics, hydrodynamics, pigments, nutrients), only granulometric variables were selected in the final model (Willems et al., submitted).

Effect of *Lanice conchilega* on benthic characteristics

The results of the present study clearly show that *L. conchilega* has the potential to positively affect the benthos, as reflected in the significant and positive correlation between the benthic density and the density of *L. conchilega*. Furthermore, the species richness increased with increasing density of *L. conchilega*. This trend was however not consistent: the number of species no longer increased or even decreased after reaching a certain density of *L. conchilega* (> 500 ind/m²). The trend observed concerning the expected number of species indicates an enrichment of species in *L. conchilega* patches. The N_1 - diversity index, which takes into account species abundances and richness, showed similar or slightly higher values in *L. conchilega* patches compared to patches without *L. conchilega*. This diversity pattern implies that mainly species with low abundance contribute to the higher species richness in samples containing *L. conchilega*. Due to the higher density of a lot of species in *L. conchilega* patches, the chance to catch a certain species increases in those patches compared to the surroundings, which partly explains the increase of species richness in *L. conchilega* patches. The observed increases in species richness and abundances recorded in *L. conchilega* patches have also been discerned around the tubes of other polychaetes (Woodin, 1978; Luckenbach, 1986), in *L. conchilega* patches in intertidal areas (Zühlke et al., 1998; Zühlke, 2001) and even around artificial tubes (Zühlke et al., 1998; Dittmann, 1999).

The observed trends in density, species richness and diversity were most pronounced in shallow fine sands and were less pronounced in deep fine sands. The strong effect of *L. conchilega* in shallow fine sands indicates that the habitat structuring capacity of *L. conchilega* has an optimal effect in shallow fine sands. In deep fine sands, which were already characterized by a high benthic diversity and low densities of *L. conchilega*, the effect on benthic species was minimal. It is not kown if the effect on the benthos increases whit even higher densities of *L. conchilega*. It can be hypothesized that the habitat structuring effect of *L. conchilega* in deeper environments has a less optimal result, due to the lower environmental variability in such habitats; less species can profit from the improved conditions around *L. conchilega* tube aggregates. *Lanice conchilega* had an effect on the density of some benthic species in shallow muddy sands, but no real increases of the species richness and diversity were observed. On the contrary, very high densities of *L. conchilega* (> 1000 ind/m²) had a decreasing effect. In shallow medium sands, the effects of *L. conchilega* on benthic density and diversity were not strongly pronounced, but were present, due to the lower maximal densities of *L. conchilega*.

The patterns in density and species richness observed in the present study were in agreement with the results on the species composition. In the habitat where the effect of *L. conchilega* was most pronounced (shallow fine sands), most associated species were found, which belonged to different higher taxa. These associated species mostly belonged to the overall species–pool of a certain habitat, rather than being commensals of *L. conchilega*. It was thus demonstrated that *L. conchilega* has an effect on the benthos present in a particular habitat, rather than forming its own community (see also Zühlke et al, 1998, Dittmann, 1999). It seems that the effect of *L. conchilega* tubes on the benthic fauna is highly dependent on the native species present in the surrounding sands at any moment and on their susceptibility to tube effects. Therefore, it is logical that the species richness and diversity levelled off in some habitats: no new species for that habitat were attracted but *L. conchilega* rather affected the habitat quality, which led to increases of the densities of otherwise seldom species in that habitat.

It can be argued that underlying factors (e.g. food availability) determine the densities of *L. conchilega* and therefore also the densities of other benthic species. However, the results of the present study clearly show that *L. conchilega* has the potential to affect the surrounding benthic species. The effects of *L. conchilega* on the surrounding benthos result from alterations of some habitat characteristics (cf. other studies on effects of biogenic habitat structures). Changes in following environmental and biological characteristics were induced by the presence of *L. conchilega*: (1) hydrodynamics, (2) sediment modifications and (3) species interactions.

Effect of Lanice conchilega on hydrodynamics

High densities of *L. conchilega* can influence the hydrodynamics, as has been shown in flume experiments, in which dense assemblages of tubes significantly reduced the current velocity of the near-bottom flow and in which normal, laminar near-bottom flow was deflected around and across the assemblages (turbulence effect) (Heuers et al., 1998). The effect of *L. conchilega* on the benthic density and diversity in intertidal areas is partially attributed to those reductions of the current velocities around the tubes (Zühlke et al, 1998). It can be expected that *L. conchilega* tube aggregations also have an effect on the near-bottom flow in shallow coastal areas. These hydrodyamical changes could have an effect on the sedimentation of particles, detrital food and on the settling of larvae and benthic species.

It is known that *L. conchilega* tubes can provide a settlement surface for larval and post-larval benthic organisms (Qian, 1999). First, the increased settling rate could be caused by the reduction of the current speed and the turbulence around the tubes. These factors are responsible for the higher preference of settling of the *L. conchilega* aulophore larvae nearby adult tubes (Heuers et al., 1998, Callaway, 2003). Similarly, larvae of other benthic species can profit of the changes in hydrodynamics to settle within *L. conchilega* patches. Second, larvae can directly attach to *L. conchilega* tubes, which act as a hard substrate. Zühlke et al. (2001), for example, observed that individual *Mytilus edulis* attached to the *L. conchilega* tubes, but the tubes did not provide secure anchorage for *M. edulis* clumps.

Reduced currents do not only have an effect on larvae, but they also influence the sedimentation of particles and detritus. Sedimentation leading to elevation of the sediment surface occurs in high density patches of *L. conchilega* in intertidal as well as in subtidal areas (Heuers et al., 1998; Seys & Musschoot, 2001, Degraer et al., 2002). On the other hand, the accretion of fine and organic detritus between the tubes promotes the formation of a stable and productive sediment, suitable for both suspension and deposit feeders (Eagle, 1975). *Lanice conchilega* itself is a deposit feeder when occurring in low densities and switches to suspension feeding when present in high densities (cf. increased competition) (Buhr and Winter, 1976). In shallow muddy and fine sands, an increase of surface deposit feeders or facultative suspension feeders in *L. conchilega* patches was observed, probably profiting from the higher deposition rate of detrital organic matter between the tubes. On the other hand, suspension feeders were not found in increased percentage in *L. conchilega* patches, which could be caused by the competition with *L. conchilega*.

Effect of Lanice conchilega on sediment modifications

Other habitat changes resulting from the presence of tube aggregations include increased or decreased sediment stability (Eckman et al., 1981; Luckenbach, 1986). The effect of a tube dweller on the physical modifications of sediments depends on its density, spacing and on the length of the tubes (Rhoads & Boyer, 1982). The dense aggregations of *L. conchilega* cause sedimentation, leading to elevations of the sediment surface and to an increase of the bottom roughness. These processes indicate that dense aggregations cause a "skimming flow" (protecting the bed within the tube field from higher-energy turbulence, Morris, 1955) with reduced shear stress near the bottom (Heuers et al., 1998). High densities of *L. conchilega* probably create stability in the soft-bottom sediments, due to the reduced shear stress near the bottom. This stability could be a very important factor for the benthos to increase their survival in shallow coastal areas, which are characterized by a high environmental variability and a lot of disturbance. At low densities, animal tubes can create destabilization of sediments by scouring around single tubes (Luckenbach, 1986). This was recently observed nearby single tubes of *L. conchilega*, but they still act as bio-engineers, affecting their environment in a positive way (Callaway, 2006). The sediment stabilizing effect of tubes is also strongly influenced by the activity of other organisms, which can have a destabilizing effect (high bioturbation by depositfeeders) or can increase the stability (fecal pellets, sediment-binding exudates from surface-living bacteria and diatoms) (Rhoads & Boyer, 1982). It can be concluded that the presence and activities of both tube building species and surrounding benthic fauna play a role in the sediment stability, but that the effects are expected to be positive in the case of high density *L. conchilega* patches.

Tube building species are also known to control the pumping of water into and out of the bottom. Consequently, some species might benefit from an improved oxygen supply in the sediment surrounding *L. conchilega* tubes. Forster & Graf (1995) suggested that *L. conchilega* acts as a piston when moving in its tube, exchanging burrow water with the overlying water and providing oxygen to the adjacent sediment along the whole length of the tube.

In this way (by increasing the habitat stability and oxygen supply), *L. conchilega* alters the habitat characteristics and affects other organisms. Therefore, the species can be considered as an ecosystem engineer (Jones et al., 1994).

Effect of Lanice conchilega on species interactions

The interactions between benthic species and *L. conchilega* itself or its tubes can be important factors in explaining the effect of *L. conchilega* on the surrounding benthos. Some species were exclusively associated with *L. conchilega* tubes (e.g. *Harmothoe species*, *Eumida sanguinea, Eteone longa, Malmgreniella lunulata, Gammarus species* and *Microprotopus maculates*) in intertidal areas, while some were found in significantly higher abundances in *L. conchilega* aggregations (e.g. *Mya arenaria, Mytilus edulis* and *Phyllodoce mucosa*) (Zühlke et al., 1998, Zühlke, 2001). A lot of these exclusively associated species in intertidal areas were also found associated with *L. conchilega* in subtidal habitats, however not exclusively. No species is known to be commensal with *L. conchilega*, but numerous species do interact with *L. conchilega* and are therefore preferentially found in association with *L. conchilega*. A lot of species were observed in or attached to the tubes of *L. conchilega*: *Phyllodoce* spp., *Eumida sanguinea* and species of the family of the Polynoidae (like *Malmgreniella* and *Harmothoe* species) were generally found inside the tubes or among the ragged fringes (pers. obs.). Similarly, a lot of amphipods were found associated with *L. conchilega*, suggesting that feeding conditions might be facilitated among *L. conchilega* tubes for species that are at least partly epibenthic. Furthermore, a lot of surface deposit feeders can profit from the increased food supply, as mentioned higher. Other species, like epibenthic and infaunal predators, can profit from the abundant prey in *L. conchilega* patches. Epibenthic predatory species are recorded in association with *L. conchilega* (e.g. some Decapoda), and a lot of infaunal predatory species, like *Eteone longa* and *E. sanguinea* were found in higher numbers and frequencies in *L. conchilega* patches. These polychaetes probably prey on macrofauna but might also benefit from an enriched meiofauna, which can develop around tubes (Zühlke et al, 1998). Due to the presence of a lot of predatory species, tube aggregates are by no means perfect refuges from predation.

***Lanice conchilega* as 'biogenic reef'-builder?**

'Biogenic reefs' were defined as biological concretions that rise from the sea bed and were created by the animals themselves (Holt et al., 1998). In both intertidal and subtidal areas, *L. conchilega* accretions, which rise from the sea bed (10 – 40 cm), were found (pers. obs.). These reefs were formed by sediment trapping in dense aggregations of *L. conchilega* tubes, which is a different mechanism than in *Sabellaria alveolata* reefs (real concretions of animal tubes) (Holt et al., 1998). *Lanice conchilega* aggregations were characterized by a constant renewal of the population due to the high turn-over of *L. conchilega* (Van Hoey et al., in prep.). This is different from the real biogenic reef builders where the reef increases with settling juveniles on the older static structures. However, the biogenic structures of *L. conchilega* do affect the environment by increasing the habitat heterogeneity, which in turn affects the density and species richness of the surrounding benthos, even at low densities (few individuals per m²) of *L. conchilega*. Although, in many cases, it is probably more realistic to refer to these aggregations as *L. conchilega* beds rather than reefs, their characteristics and effects are, in some cases (rise from the sea bed at high densities), likely to be very similar to those of really protruding 'biogenic reefs'. Consequently, *L. conchilega* beds can be considered as important habitat structuring features in the soft – bottom sediments of the North Sea.

Conclusion

It can be concluded that *Lanice conchilega* has an effect on the benthic density and diversity in soft-bottom sediments. This effect is most pronounced in shallow fine sand, which is its preferred habitat. The changes in benthic characteristics result from the alterations of the habitat by *L. conchilega* (hydrodynamics, sediment stability, improved oxygen) and the complex interactions between the benthic organisms and the biogenic structures consisting of *L. conchilega* tubes. A lot of benthic species can profit from the creation, modification and maintenance of that habitat by *L. conchilega*, which results in an increased density and species richness in *L. conchilega* patches compared to the surrounding soft-bottom sediments. It was further demonstrated that *L. conchilega* only has an effect on the benthos present in a particular habitat, rather than forming its own association. Consequently, *L. conchilega* beds can be considered as important habitat structuring features in the soft – bottom sediments of the North Sea.

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Chapter 7

General discussion and conclusions

General discussion

As outlined in the general introduction, the combination of the ecological and the socio-economic values of the Belgian Continental Shelf (BCS) cause conflicts between both interests. Initiatives are being taken by the scientific community to optimize the integration of the ecological value of the BCS with those of the different user functions, like shipping, dredging, sand and gravel extraction, fishing and tourism (Maes et al, 2005). The government has made a start with the implementation of Marine Protected Areas into the law (framework law of 20/01/1999): proposals for such areas have been made (Royal Decree of 7 and 15 October) and are under investigation. In the meantime, it is important to provide the policy makers with a scientific basis for the development of a sustainable management plan for the natural resources of the BCS. To obtain this goal, information and knowledge is required. First, the structure and geographical distribution of marine fauna and flora in relation to the physico-chemical environment have to be investigated. Second, the natural ecological variability in space and time has to be outlined. Third, detailed knowledge on key species or ecologically important species will help to establish a time and money saving monitoring program.

Due to the complexity of the marine ecosystem, which consists of many components (microbenthos, meiobenthos, macrobenthos, hyperbenthos, epibenthos, plankton, birds, fishes and marine mammals), it is not possible to include all those components into one research. Therefore, this study focused on only one component, being the macrobenthos. Macrobenthic organisms are considered suitable to characterize and monitor the marine ecosystem because of their size (macroscopic), their relative immobility and their direct link with the sediment and with the processes that occur immediately above the seabed (see general introduction).

This study aimed to investigate the macrobenthic community structure on the BCS (Chapter 2), the spatial and temporal variability within the ecologically most important macrobenthic community (*Abra alba* community) (Chapters 3 – 4) and the importance and population dynamics of an ecologically important species (the sand mason, *Lanice conchilega*) within this community (Chapters 5 – 6). Based on the information of a part of the marine ecosystem (macrobenthos), some remarks on the conservation of ecologically important areas or species on the Belgian Continental Shelf can be formulated.

The macrobenthic community structure on the BCS

Out of an analysis of 728 macrobenthic samples, collected between 1994 and 2000 on the BCS and the intertidal beaches, four species associations were distinguished. Those species associations differed drastically, both in habitat and species composition, and were considered to represent four macrobenthic communities: (1) the *Abra alba – Mysella bidentata* community (further referred to as *Abra alba* community) is characterized by high densities and diversity and can be found in muddy fine sand; (2) the *Nephtys cirrosa* community occurs in well-sorted sandy sediments and is characterized by low densities and diversity; (3) the *Ophelia limacina – Glycera lapidum* community, which is found in coarse sands and is characterized by very low densities and diversity, and (4) the *Eurydice pulchra – Scolelepis squamata* community, which is typical for the upper intertidal zone of sandy beaches and is characterized by a very low diversity and relative high densities (Chapter 1). In more recent analyses (taking into account recently collected data), a fifth community, the *Macoma balthica* community was detected, which is typical for muddy sediments and is characterized by a low diversity and density (Degraer et al, 2003). Between the communities, gradual transitions in biological and physical characteristics exist, because communities are a merely arbitrary abstraction of gradients (Gray, 1981). Besides the communities in sandy sediments, an extremely rare (only one station) sixth macrobenthic community was detected in outcropping tertiary clay layers near Oostende, and was defined as the *Barnea candida* community (Degraer et al., 1999). Gravel beds on the BCS were recently sampled (2005), but the details on the macrobenthic fauna are not yet available. It can be expected that the community is characterized by a specific set of species that differs drastically from the surrounding sandy environment (Kenny and Rees, 1996; Newell et al., 2001). It can be concluded that the BCS (though being small) is characterized by a high variety of macrobenthic communities, each one being typical for one type of habitat. Some of these macrobenthic communities defined for the BCS were also found in similar habitats in the North Sea with comparable species composition. This is clearly demonstrated in the study about the large spatial variability of the *A. alba* community in the North Sea (Chapter 3). The different macrobenthic communities found on the BCS, based on the dataset of chapter 2, were the same when analysed in a broader dataset of the BCS and even in an analysis of the macrobenthic communities in the North Sea as done for the North Sea Benthos survey of 2000 (Rees et al., 2002).

The macrobenthic communities were only found in a very specific physical habitat (mainly determined by sedimentology) (Gray, 1974; Creutzberg et al., 1984; Buchanan, 1984; Snelgrove and Butman, 1994, Chapter 2), and their macrobenthic characteristics, like density and species richness were strongly linked to the conditions in that habitat (Figure 4, Chapter 2). The highest species richness (> 15 ind/m²) and densities (> 2000 ind/m²) were mainly found in fine to medium sandy sediments, with relatively high mud content (3-20%). The density and species richness declined with decreasing and increasing grain size. The associations between the macrobenthic characteristics or communities and their physical habitat lead to the possibility to predict the 'macrobenthic potential' of an area. This means that, based on physical information, a prediction can be made of the composition of the macrobenthos or macrobenthic community in an area. This way, a time- and cost effective evaluation of the spatial distribution of the communities can be performed and later confirmed by selective sampling. The description and demarcation of the macrobenthic communities on the BCS in this study can aid the further development of those time- and cost efficient, full-coverage methods, like predictive modeling or macrobenthic side-scan sonar interpretation (Degraer et al., 2002). Next to delivering basic scientific knowledge to improve other evaluation techniques, these results also provide a reflection of the ecological value of some communities.

Based on biodiversity criteria, the *A. alba* community is the most dense and diverse macrobenthic community on the BCS. Although low, the ecological value of the *N. cirrosa* community and the *O. limacina – G. lapidum* community, which were not so diverse, should not be ignored, as they are representative for a unique habitat system: the sandbanks. The species from these communities are adapted to the harsh conditions at the sandbanks (Vanosmael et al., 1982) and this habitat system is scarce in the North Sea, but characteristic for the BCS. The geographical distribution of these different macrobenthic communities did only weakly correspond with an onshore – offshore gradient, as was earlier hypothesized (Govaere et al., 1980). Some communities were distributed over the entire onshore – offshore gradient (the *N. cirrosa* and the *O. limacina – G. lapidum* community), whereas others were restricted to the near – shore (*A. alba* and *M. balthica* community) or to sandy beaches (the *E. pulchra – S. squamata* community). This geographical distribution is of utmost importance from a national and international legislation perspective, in which distance from the shore (e.g. 3 miles and 12 miles zones) is used to set limits for fisheries or the criteria of the Habitat Directive. The coastal zone (< 12 mile from the coastline) and especially the southwestern part is characterized by a wide variety of macrobenthic communities from species poor to rich, including the areas with the highest species richness and densities (i.e. *A. alba* community). The offshore area (> 12 mile) is characterized by low densities and lower diversity. The shallow coastal area can be put forward as an ecologically important area, characterized by a highly complex and diverse geomorphological environment, with associated macrobenthic communities. Of those macrobenthic communities, the *A. alba* community seems of exceptional ecological importance, not only due to the high densities and diversity, but also due to the presence of high numbers of bivalves (important food resource for higher trophic levels) (Chapter 2 – 3), numerous unique species and the presence of a habitat structuring species, i.e. *Lanice conchilega* (Chapter 6; Zühlke et al, 1998; Zühlke, 2001).

The *Abra alba* community

The objective of biodiversity monitoring is not only to determine what kind of species or communities inhabit a particular area, but also to detect any spatial or temporal change in the fauna or communities in addition to natural variability. Afterwards, any observed changes can be linked to the different causes (natural or anthropogenic). Macrobenthic communities are known to show a high variability, both within and between years (Rees & Walker, 1983; Essink & Beukema, 1986; Ibanez & Dauvin, 1988; Fromentin et al., 1997). The knowledge about the temporal variability, together with the spatial difference within one habitat provides information about the naturalness of the community. As already described, the *A. alba* community is an ecologically important macrobenthic community in soft-bottom sediments and was therefore selected for detailed spatial and temporal investigations on the BCS.

There is a clear decreasing pattern in the diversity (total number of species, species richness and the Shannon index) from the English Channel towards the northeast, which is confirmed by different individual studies along this transect (Dewarumez et al., 1992; Fromentin et al., 1997; Thiébaut et al., 1997; Dauvin, 1998; 2000). This is detailedly visualized in table 2 of chapter 3: the discussed trends in diversity parameters and species top 10 were confirmed by other studies along the gradient (Thiébaut et al., 1997; Dauvin, 1998; 2000). These spatial differences in the community characteristics within the *A. alba* community do not seem to be related with the slight differences in sedimentology (Chapter 3). At a large scale, the differences in the *A. alba* community structure are expected to result from (1) the specific hydrodynamic conditions in the English Channel and the Southern Bight of the North Sea, with a consequent differential connectivity between the different areas, and (2) the climatological and related faunal shifts from temperate (English Channel) to boreal conditions (German Bight). The *A. alba* community along the Belgian Coast can be considered as situated in a major transition zone between the rich southern area (English Channel, France) and the relatively poor northern distribution area (Dutch coast, German Bight) of the *A. alba* community. At a small scale, structural and functional community aspects may result from geographic differences in (1) detrital food availability, related to riverine input and pelagic productivity, along and across the coastline, and (2) the amount of suspended matter, impoverishing the *A. alba* community when excessively available. In the *A. alba* community along the Belgian coast, the lower diversity in the mid-coastal zone is most probably related to the decreased detrital food availability. The decrease in the northeastern coastal zone, on the other hand, is related to the high amount of suspended matter. In the northeastern coastal zone, there are indications of stress on the populations, reflected in (1) an increase in production, especially linked to eutrophication processes (high productivity of *L. conchilega*, Chapter 5), (2) reduction in diversity and increase of dominance by opportunistic species (*Spiophanes bombyx* was the dominant species, chapter 3), and (3) decreasing number of species and increasing number of individuals (zone characterized by a lower species richness and high densities, chapter 3) (Pearson and Rosenberg, 1978; Giangrande et al., 2005). The results indicate that the benthos in the northeastern coastal zone might be under pressure of anthropogenic influences, like eutrophication and pollution. Contrary to the rest of the BCS, the southwestern coastal zone (also referred to as Western Coastal Banks) is of higher ecological importance, due to the high diversity of habitats and related macrobenthic communities (Chapter 2), and also due to the presence of a highly structurally and functionally diverse *A. alba* community in this area (Chapter 3).

The year-to-year variability within the *A. alba* community was characterized by a more or less rapid and abrupt succession of different groups of species (Eagle, 1975, Dauvin et al., 1993, Fromentin et al., 1997). The seasonal and year-to-year variability within the *A. alba* community in the present study was mainly triggered by differences in the recruitment of species (Chapter 4). Despite the differences in dominance of species during the sampling period (9 years), no shifts in species were observed, with exception of the replacement of *Spisula subtruncata* by *Donax vittatus* from 1999 onwards. This means that the *A. alba* community remains rather stable, taking into account the cyclic seasonal patterns, which were characterized by high densities and diversity in spring – summer, with a decline during autumn towards the end of the winter. During the sampling period, some events had a drastic impact on the *A. alba* community (Chapter 4), and disturbed the higher mentioned stability. Significant effects (mainly a decrease in diversity) were observed after an overwhelming recruitment of *S. subtruncata*, a mud increase and a cold winter period. By describing these events, the variability, including the present anthropogenic influences (like beam-trawling, dredging, eutrophication and pollution) was assessed. However, though the observed patterns for the investigated sampling area were clear, it is difficult to generalize with regard to the entire *A. alba* community on the BCS: the trends may be varying between neighboring sites, and local factors strongly determine the temporal pattern. Nevertheless, it can be concluded that there is year-to-year and seasonal variability within the

A. alba community, which can be enhanced by drastic changes due to different causes of natural or anthropogenic origin (the latter were not investigated in the present study).

Lanice conchilega

The tube–building species *Lanice conchilega* has a positive effect on the density and species richness of benthic species in subtidal soft–bottom sediments in the North Sea (Chapter 6) and in intertidal areas (Zühlke et al, 1998; Dittmann et al., 1999; Zühlke, 2001). Intertidal and subtidal studies showed that the associated benthos has a temporary and optional association with the tube aggregations and that the effect of *L. conchilega* largely depends on the benthic species present in the surrounding sediment at a certain time. The high amount of associated species in shallow fine sands supports the hypothesis that the whole benthos is affected, rather than specific species. However, species like *Eumida sanguinea*, *Malmgreniella* species, *Sagartia* species and some amphipod species had a more specific relation with *L. conchilega* (Zühlke et al, 1997; Chapter 6). It also has to be mentioned that the effect of *L. conchilega* on the surrounding benthos is not always linear. The density of the surrounding benthos tends to increase with increasing density of *L. conchilega*, but the species richness leveled off (e.g. shallow fine sand) or decreased (e.g. shallow muddy sand) when a certain density of *L. conchilega* was reached.

Temporal stability of Lanice conchilega populations

The *L. conchilega* tube aggregations were identified as short-lived structures (Zühlke, 2001), due to their natural dynamics and the opportunistic status of *L. conchilega*. The opportunistic status is confirmed by the present study in which the life–cycle of *L. conchilega* was characterized by a long pelagic phase (up to 60 days) and a prolonged period of benthic settling with high mortality and fast growth (Chapter 5). The population of *L. conchilega* is characterized by a high turn-over rate, but due to the high and continuous recruitment, preferentially in *L. conchilega* tube aggregations (Callaway, 2003), the areas of occurrence of *L. conchilega* were characterized by a certain temporal stability (semi-permanent). In the present study, two out of three stations showed a constant presence of an adult population, with fluctuating densities, whereas the third station did not yield a stable *L. conchilega* population (without any apparent cause). In the long-term temporal study of the *A. alba* community (Chapter 4), *L. conchilega* was observed for many years in the same area (1999 – 2003). Similarly, this temporal stability of the patch location of *L. conchilega* was detected in the study of Buhr and Winter (1978) over a period of ten years.

The temporal stability of each *L. conchilega* tube aggregation will inevitably be interrupted by strong physical disturbance, like a storm, a severe winter or anthropogenic disturbance such as beam trawling. After autumn and winter storms, huge amounts of *L. conchilega* tubes, swept out of the subtidal, can be found on the beach (pers. observation). The disappearance of *L. conchilega*, especially in intertidal areas, is probably due to its sensitivity to low temperatures in winter (Strasser & Pieloth, 2001). The effect of beam trawling on *L. conchilega* is still uncertain, but detailed investigations are in progress (pers. com. M. Rabaut). In conclusion, it can be stated that *L.*

conchilega, despite its opportunistic status, provides a certain temporal stability in soft – bottom sediments.

Ecosystem engineer

The fact that *L. conchilega* tube aggregations host a more diverse and abundant fauna is because of their effects on the habitat (Chapter 6): (1) tube aggregations influence the near-bottom currents (Heuers et al., 1998), which has an effect on sedimentation of particles and food, (2) the tubes act as a settling surface for other benthic species (Qian, 1999) (3) the *L. conchilega* tubes provide stability in the soft – bottom sediments (Luckenbach, 1986), (4) they provide an improved oxygen supply around the tubes (Forster and Graf, 1995), and (5) there are important species interactions between the species and the *L. conchilega* tubes (Zühlke et al., 1997, Chapter 6). Consequently, *L. conchilega* can be considered as an ecosystem engineer: this species physically creates, modifies or maintains a habitat (*sensu* Jones et al., 1994). Consequently, *L. conchilega* modifies the biodiversity, abundance and the distribution of large numbers of associated organisms (Jones et al., 1994). Those changes are due to alterations of the environment caused by the physical structures of *L. conchilega* (the tubes). Therefore, *L. conchilega* can be considered as a member of the group of autogenic engineers (Jones et al., 1994).

'Biogenic reefs'

The characteristics of *L. conchilega* as ecosystem engineer, together with the elevation of the sediment in case of high densities, enable *L. conchilega* to build 'biogenic reefs'. 'Biogenic reefs' are defined as rocky marine habitats or biological concretions that rise from the sea bed and were created by the animals themselves (Holt et al., 1998). The interpretation of this definition is not obvious, because a continuous gradient exists from non-reefs conditions (e.g. low densities of *L. conchilega*; scattered indivduals of *Sabellaria spinulosa* or *S. alveolata*; discontinuous beds of *Mytilus*) to reef conditions for many species (dense aggregations of *L. conchilega*; dens aggregations of *Modiolus, Mytilus* or *S. spinulosa* on mixed substrata). In literature, reefs of *S. alveolata, S. spinulosa, M. modiolus, M. edulis* and *Serpula vermicularis* are considered to be true biogenic reef communities (Holt et al., 1998) due to the formation of a solid, massive structure (accumulation of organisms), usually rising from the seabed, or at least forming a substantial, discrete community or habitat which is very different from the surrounding seabed.

Figure 1. Pictures of 'biogenic reefs' of *Lanice conchilega* on the beach of Boulogne (Fr.).

However, the formation of the *L. conchilega* reefs differs from the reefs formed by other species, like *S.alveolata*. This polychaete creates tubes of coarse sand grains cemented together into reefs consisting of fused hummocks (tubes radiate out from an initial settlement point) (Holt et al., 1998). *Lanice conchilega* on the other hand creates reefs by trapping sediment between the tubes, resulting in an elevation of the sediment. In most cases, the aggregations of *L. conchilega* do not substantially raise above the surrounding area, but they still provide structure in the sediment. However, accretions formed by *L. conchilega* were regularly found in the field (Figure 1). In Belgium and France, those patches were observed in the intertidal zone, nearby the low water line (Flemish nature reserve "Baai van Heist", nearby the harbour of Boulogne) or at the lee-side of runnels (beach of Zeebrugge). In the subtidal area, such patches were observed with side-scan sonar at the lee-side of sandbanks (e.g. Trapegeer). Detailed bathymetric measurements of the encountered *L. conchilega* 'mounds' were done on the beach of Zeebrugge, where elevations were measured of five to ten cm compared to the surrounding beach. The patches reached a diameter of 1 – 2 m across, with densities of up to 3600 ind/m² (Seys & Musschoot, 2001). The same observations were done in the "Baai van Heist", where the density of *L. conchilega* reached 2000 - 4000 ind/m² (pers. obs.). In the intertidal of the North Norfolk coast (U.K.), patches elevated up to 45 cm compared to the surrounding gravelly sediment were observed (Holt et al., 1998). Overwhelming settling of *L. conchilega* in soft-bottom sediments, whereby the tubes were cemented together and rose for a 20-30 cm above the surroundings, were also observed during the subtidal sampling campaigns of this study (June 2003 at station O1; summer 2002 at station O3), but these structures did not appear to be temporally stable.

Lanice conchilega provides one of the main habitat structures in intertidal and subtidal soft-bottom sediments, but was, for example in the U.K., not selected as 'biogenic reef' builder because it was unknown how seasonal / stable these features were. At present, it seems unlikely that they are sufficiently solid or change the environment enough to qualify as 'biogenic reefs' (Holt et al., 1998). However, results of the present study contradict that *L. conchilega* lacks the qualities of a true 'biogenic reef' builder. The *L. conchilega* patches showed a semi – permanent stability (chapter 5) and have an effect on the surroundings (benthos) at densities of only a few individuals per m² by altering the habitat (Chapter 6). They create ecological islands, which generally host a more diverse and abundant fauna. Therefore, it can be hypothesized that *L. conchilega* has the potential to form real 'biogenic reefs' under certain circumstances (elevation of the sediment at high densities), in which the characteristics and effects are similar to those of real protruding reefs. In many cases (low densities and scattered distribution), however, it is probably more realistic to refer to these aggregations as *L. conchilega* beds rather than reefs.

Key species/indicator

Lanice conchilega is clearly an ecologically important species (Chapter 5, 6, general discussion), due to its importance in the benthic community. However, the question remains if it is also a key species or even an indicator. *Lanice conchilega* can be fitted into the key species definition, because it plays an important ecological role in determining the overall structure and dynamic relationships within benthic communities (Mills et al., 1993; Piraino et al., 2002). The building capacity of this species adds complexity to the soft-bottom sediments (habitat heterogeneity), which in turn enhances the occurrence of other benthic species. *Lanice conchilega* can be considered as an indicator of biodiversity, due to the increased species richness within *L. conchilega* patches. However, it is not yet known if it is also an indicator for environmental changes.

Due to its recruitment strategy, *L. conchilega* is characterized as an opportunistic species in the present study (Chapter 5). However, there are differences in the response of *L. conchilega* to changes in the habitat compared to some other opportunistic species (e.g. *Capitella capitata,* species of the families Cirratulidae and Spionidae). Those species have the capability to directly proliferate after, for example, an increase in organic matter, to survive in polluted areas and to immediately colonize disturbed areas (Giangrande et al., 2005). *Lanice conchilega* can also profit from a certain increase in organic matter, but there are no records of early colonization of *L. conchilega* in recently disturbed or polluted areas. Further in the succession process, however, *L. conchilega* can become dominant, as observed after the Amoco Cadiz Oil Spill in the muddy fine sand *A. alba – Melinna palmata* community of the Bay of Morlaix (Dauvin, 1998, 2000). Furthermore, *L conchilega* is known to have a relatively low sensitivity to many physical and chemical influences (smothering, increase or decrease of suspended sediment, changes in flow rate, turbidity, hydrocarbon or heavy metal contamination, etc.) and is characterized by a high recoverability (MarLIN: Marine Life Information Network for Britain and Ireland). In the present study, some *L. conchilega* samples were found, in which the absence of a well-developed ragged fringe at the end indicated a disturbance event, probably beam-trawling (Appendix I). However, *L. conchilega* can quickly repair its tube and due to its recruitment strategy, it can recolonize disturbed areas. *Lanice conchilega* also retains the ability to re-establish itself in the sediment after being washed out (Ropert, 1999). Its low sensitivity and high recoverability enable this species to live in slightly disturbed conditions from anthropogenic or natural origin. Such conditions can be found in coastal areas, where *L. conchilega* structures the sediment and enhances the occurrence of other benthic species. In conclusion, it can be stated that *L. conchilega* is a key species in soft bottom sediments.

Nature conservation

As already discussed, some of the macrobenthic communities occurring on the Belgian Continental Shelf have specific features, especially the *A. alba* community with the key-species *L. conchilega*. Of the entire BCS, the coastal zone is considered to be the ecologically most important area due to the high diversity of macrobenthic communities, the presence of the diverse *A. alba* community (this study) and the importance of this zone for sea-birds (Haelters et al., 2004). Due to the suitability of this area for nature conservation and the conflict with the socio-economical interests, it would be useful to focus on an integrated coastal zone management. Preferably, some users or user-functions should be reduced or re-located to other locations. From a nature conservation perspective, parts of the coastal area have to be designated as Marine Protected Area to maintain the natural biological richness of the Belgian coastal area. The Western Coastal Banks, which are recently proposed as Habitat and Bird Directive area (Royal Decree of 14 October 2005), could be such an area. The Bird Directive as well as the Habitat Directive exclude and/or reduce some activities (e.g. wind mill parks, artificial islands or reefs, sand extraction, angling, shell fisheries, dumping of dredged material, mariculture, and industrial fishery in the three mile zone). These protection measures are beneficial initiatives, but are not sufficient from a nature conservation perspective, because the strongest anthropogenic influences (shipping, beam-trawling, dredging, eutrophication) are still allowed or insufficiently reduced in valuable / sensitive areas.

The disturbance caused by anthropogenic activities, especially beam - trawling, intensifies the high natural variability of the *A. alba* community in the coastal zone and therefore amplifies the stress on the benthic populations to such an extent that the natural balance of the ecosystem is seriously endangered. A higher stress on the *A. alba* community in the northeastern coastal zone may account for the decreased diversity and increased variability compared to the southwestern coastal zone (Western Coastal Banks), in spite of the same macrobenthic potential. Based on the calculation of the Biotic Coefficient (Borja et al., 2000), the state of the benthic ecosystem in the coastal area can be evaluated as impoverished to unbalanced (unpublished data). Therefore, it is recommended to create a Marine Protected Area to study the effects of anthropogenic activities and to conserve and rehabilitate the natural diversity in the ecologically valuable Western Coastal Banks. Of course, the establishment of such an MPA would not be the endpoint of the conservation measures. Although it is expected that an extensive protection would result in increased stability, which in turn would improve conditions for longer living species, the effects of such protection on the macrobenthos in the Western Coastal Banks are hard to predict. Especially the role and evolution of *L. conchilega* beds and reefs should be monitored in future research programs concerning MPA's at the Belgian Continental Shelf, because the results of the research presented in this PhD-thesis indicate that an increase in *L. conchilega* densities would be beneficial for the establishment of a diverse benthic fauna.

General conclusions

The major conclusions of the present study are:

- On the Belgian Continental Shelf (BCS) and sandy beaches, five macrobenthic communities can be delimited: (1) the *Abra alba – Mysella bidentata* community (the *A. alba* community), (2) the *Nephtys cirrosa* community, (3) the *Ophelia limacina – Glycera lapidum* community, (4) *Macoma balthica* community, and (5) the *Eurydice pulchra – Scolelepis squamtata* community.
- These macrobenthic communities are found in a specific physical habitat (mainly sedimentology).
- The *A. alba* community is considered to be of exceptional ecological importance due to its high macrobenthic density and diversity in the soft bottom sediments on the BCS.
- The *A. alba* community on the BCS forms a major transition from the rich southern to the relatively poorer northern distribution area of the *A. alba* community.
- The small-scale spatial variability within the *A. alba* community on the BCS seems to be related to the detrital food availability and amount of suspended matter.
- The *A. alba* community is characterized by a clear pattern of natural year-to-year and seasonal variability, which can be enhanced by drastic changes due to different biological and physical causes.
- The tube building species *Lanice conchilega* is a key species in the soft bottom sediments of the North Sea, due to its positive relation with the benthic density, diversity and numerous associated species.
- *Lanice conchilega* is classified as an opportunistic species, whose life cycle is characterized by a long pelagic phase, a prolonged period of benthic settling, a high turn-over rate and a rapid growth.
- Due to the high and almost constant recruitment (March – November), *L. conchilega* populations add stability to the soft bottom habitat (semi-permanent).
- From a nature conservation perspective, the Belgian Coastal zone is of ecological importance, especially the southwestern coastal zone, which was characterized by a high diversity of macrobenthic communities and a rich *Abra alba* community. Within this community, the key-species *L. conchilega* could be easily monitored and could give a reflection of the state of the macrobenthic community.

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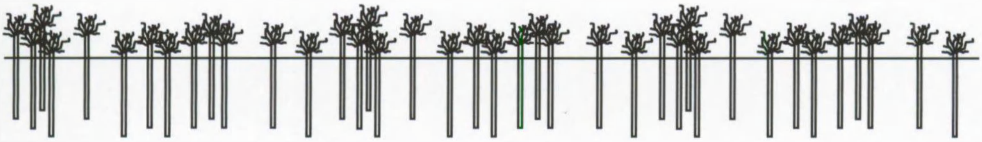
Appendix I

Abundance estimates of subtidal *Lanice conchilega* populations based on tube counts



Paper submitted as short communication

Van Hoey, G., Vincx, M. and Degraer, S.
Abundance estimates of subtidal *Lanice conchilega* populations based on tube counts
Helgoland Marine Research

Abstract

The tube building polychaete *Lanice conchilega* is a common and ecologically important species in intertidal and shallow subtidal sands. It builds a characteristic tube with ragged fringes and can retract rapidly into its tube to depths of more than 20 cm. Therefore, it is very difficult to sample *L. conchilega* individuals, especially with a Van Veen grab. Consequently, many studies used tube counts as estimates of real densities. This study reports on some aspects to be considered when using tube counts as a density estimate of *L. conchilega*, based on samples in intertidal and subtidal *L. conchilega* populations.

The accuracy of the density estimates, along with the depth-independency of the tube method, indicates that the tube method should be the prime method to estimate the density of *L. conchilega*. However, caution is needed when analyzing samples with fragile young individuals and samples from areas where temporary physical disturbance is likely to occur.

Keywords

Lanice conchilega, tube counts, Belgian Continental Shelf

Introduction

The tube building polychaete *Lanice conchilega* (Pallas, 1766) is a dominant species of European intertidal and shallow subtidal sands (Ropert, 1996; Van Hoey et al., 2004). The species is of high ecological importance since (1) its dense populations affect sediment properties (Jones and Jago, 1993) and oxygen transport (Forster and Graf, 1995), (2) it alters the composition of benthic communities (Zühlke, 2001), and (3) it is an important food item for birds and fish (Petersen and Exo, 1999). The species builds a very characteristic tube, made from cemented sand grains and shell breccia (Ziegelmeier, 1952). The top of the tube usually projects a few centimeters above the sediment and carries a ragged fringe. *L. conchilega* itself can grow up to a length of 30 cm, while its tube can reach a length of 65 cm (Ziegelmeier, 1952). When disturbed, it can rapidly retract into its tube to depths of more than 20 cm (Ziegelmeier, 1952; Dales, 1955). Consequently, it is very difficult to sample *L. conchilega* individuals with corers for intertidal sampling (Heuers et al., 1998; Petersen and Exo, 1999; Ropert and Dauvin, 2000; Strasser and Pieloth, 2001; Zühlke, 2001; Callaway, 2003) and certainly with a Hamon grab (Ropert and Dauvin, 2000) or a Van Veen grab in the case of subtidal populations (Buhr and Winter, 1977; this study). Generally, a Van Veen grab (50 to 70 kg, not loaded with extra weight), frequently used in macrobenthic studies, penetrates 10 to 15 cm into the sediment, depending on the type of substrate (Beukema, 1974). When using this sampling device, an underestimation of the real density by specimen counts could thus be expected.

Observations in the field and in fixed samples, however, indicated that unoccupied tubes are different from tubes occupied by *L. conchilega,* which can be discerned by the existence of a certain rigidity of the tube, caused by cement mucus produced by *L. conchilega*. Observations also suggested that the tube top with the fringe is destroyed shortly after the death of *L.conchilega* or the abandonment of the tube, although remains of the tubes can still be found in the sediment until several months later (Zühlke, 2001). Therefore, many studies use the number of tubes with a well developed ragged fringe and certain rigidity, as a reflection of the abundance of *L. conchilega* (Ropert and Dauvin, 2000; Strasser and Pieloth, 2001; Zühlke, 2001; Callaway, 2003).

This paper reports on some aspects to be considered when using tube counts as a density estimate of *Lanice conchilega*.

Materials and Methods

Due to the local abundance of *L. conchilega*, three subtidal sampling stations (O1, WK2 and WK1) in the coastal zone of the Belgian Continental Shelf (BCS) were selected for this study. All three stations were sampled monthly (September – April) or biweekly (May – August) during the period March 2002 – September 2003 (23 sampling occasions). The macrobenthic samples were taken with a Van Veen grab (0.1026 m²) on board of the research vessel 'Zeeleeuw'. The samples were fixed with an 8% formaldehyde-seawater solution and sieved over a 1 mm and 0.5 mm sieve. The samples were treated with care in order to avoid destruction of the *L. conchilega* tubes.

The volume of the sediment was recorded to estimate the sampling depth of the Van Veen grab for each sample. The grain size distribution of a sub sample from the Van Veen was determined with a LS Coulter particle size analyzer: median grain size of the fraction 2 - 850 µm and mud content (volume percentage < 64 µm) were used as granulometric variables.

A field study at the Flemish beach nature reserve " Baai van Heist" (Belgium) was set up to test the relationship between tube counts and number of *L. conchilega* individuals as a function of excavated depth. Cores (0.0031 m²) were inserted into the sand down to different depths (5, 10, 15, 20 and 30 cm). Three replicate samples were collected per depth and sieved over a 1 mm sieve.

In this study the *L. conchilega* individuals (further referred to as specimen counts) as well as the tubes with a well developed ragged fringe (further referred to as tube counts) were counted in the samples. These two methods can be used to estimate the real density of this polychaete at a certain place or time. Valid tube counts were based on the following criteria, irrespective of tube length: (1) tubes have a well developed ragged fringe at the end, (2) they have a good rigidity and (3) they are not filled with sand.

The non-parametric Mann-Whitney U test and median or Kruskal Wallis test was used to test for significant differences between tube and specimen counts at different depths and Spearman rank was used to trace correlations between variables.

Results

Field study

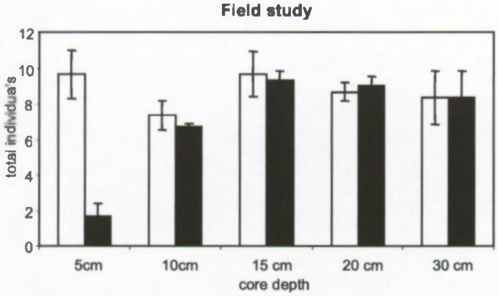


Figure 1. Differences between tube counts (white column) and specimen counts (black column) at different sampling depths, with indication of the standard error.

By digging out sampling cores down to different depths, a sampling depth dependent relationship between tube counts and specimen counts was found (Figure 1). At a depth of 5 cm, on average 82% less specimens than valid tubes were found (Mann-Whitney U test: p = 0.049). At a depth of 10 cm

(9% less specimens than valid tubes), no significant differences between the two counting methods were found (Mann-Whitney U test: p = 0.83). From 15 cm depth onwards, equal values for the two counting methods were found (Mann-Whitney U test: p = 0.66 (15 - 20 cm) and p = 1 (30 cm)), indicating a good estimate of the real density of *L. conchilega*. Counts of tubes with fringes were not depth dependent (Median test: p = 0.8925), whereas specimen counts were (Median test: p = 0.0469).

Abiotic variables

The median grain size of most of the samples varied between 150 and 250 µm, whereas the mud content varied mostly between 0 and 20% (muddy, fine sandy sediment) (Figure 2). There was no correlation between sampled volume and median grain size (Spearman rank: p = 0.9), whereas a positive, though low correlation was found between sampled volume and mud content (Spearman rank: p = 0.036).

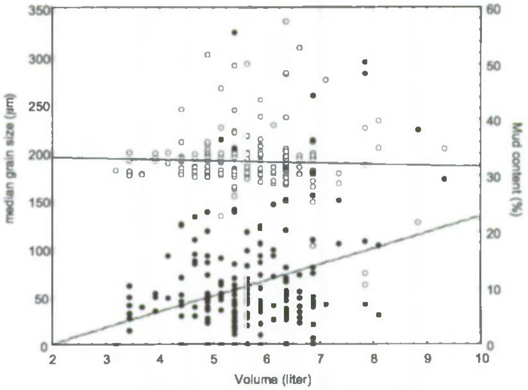


Figure 2. Median grain size (µm) (open circles, black trend line) and mud content (%) (black circles, dotted trend line) against sample volume (liter), with indication of a trend line.

The sampled volume was min. 3.19 and max. 9.33 liter and the variance between the different sampling stations was low (average volume of 5.97 liter ± 1.1 (SD) for station O1, 5.51 liter ± 0.93 for station WK2, 5.4 liter ± 0.92 for station WK1). The maximum volume of a Van Veen grab was about 15.05 liter at the maximal sampling depth of 18.5 cm. The volume range obtained for the three stations is in accordance with a sampling depth of the Van Veen grab varying between 5.5 (3.03 liter) to 12 cm (9.23 liter).

Valid tube counts versus specimen counts

More tubes than specimens were counted at most sampling occasions for the three separated stations (Figure 3). However, no correlation was found between the percentage differences between tube and specimen counts and the sampled volume (Spearman rank: p = 0.24) (Figure 4a). On a few sampling occasions there were more specimens than fringed tube counts. These sampling occasions were characterized by the absence of tubes with well developed fringes or by high densities of small tubes (spring – summer). A significant difference was found between the percentage differences between tube and specimen counts and the season of sampling (Kruskal Wallis test: p = 0.0121). Most occasions where less tube than specimen counts were found were in spring and summer (Figure 4b).

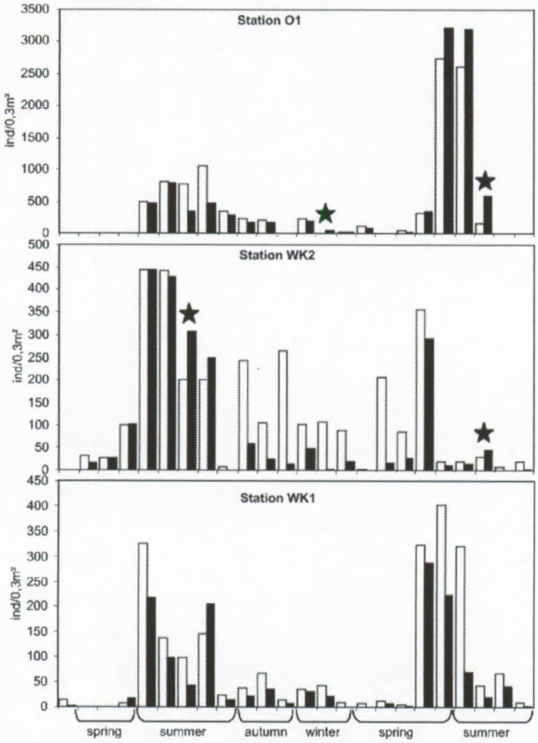


Figure 3. Differences between tube counts (white column) and specimen counts (black columns), expressed in ind/0.3m². The star indicates samples with absence of tubes with well developed fringes.

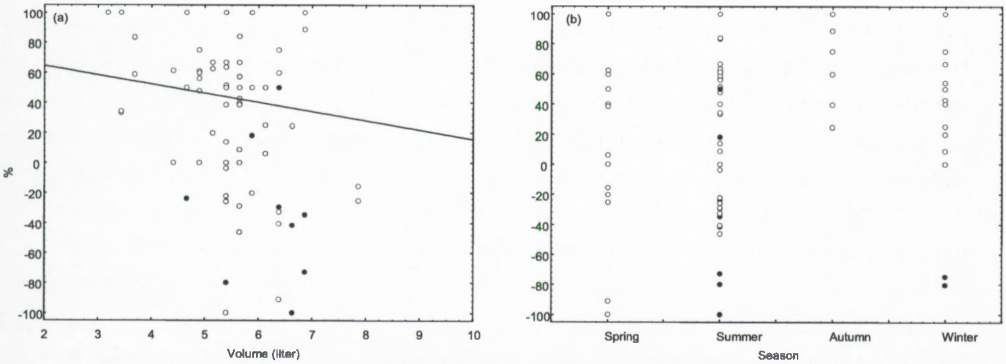


Figure 4. a) Scatter plot of sample volume against the percentage differences between tube and specimen counts (tubes – specimen/ max counted * 100). Black dots indicated samples characterized by the absence of tubes with well developed fringes. b) Scatter plot of the season against the percentage differences between tube and specimen counts. Black dots indicated samples characterized by the absence of tubes with well developed fringes.

Discussion

The intertidal field study at the beach of Heist showed that counting fringed tubes is a good method for estimating *Lanice conchilega* density. This is mainly due to the depth independency of the method, which is not the case for specimen counts. However, not every sampling method reaches adequate depths of at least 10 cm. In the case of sampling with a Van Veen grab, a strong underestimation of the real density is given by counts of larger worms, like *L. conchilega*, due to the low sampling efficiency (Beukema, 1974). Sampling efficiency is only high for species that live in the upper five centimeters of the bottom (Ursin, 1956; Lie and Pamatmat, 1965; Beukema, 1974). Additionally, the average sediment content of a Van Veen depends on the coarseness of the sediment: the grab penetrates relatively deep in both very fine (sand with a high proportion of mud) and very coarse sand, whereas relatively small volumes were obtained from fine sands that were free from mud or had low concentrations of mud (Beukema, 1974). In our study the sedimentology of the three stations is characterized by fine sands with a varying mud concentration (0 – 20% or more) and the sampled volume increased with increasing mud content. The average volume of the three stations corresponded with a Van Veen grab penetration depth of 5 to 12 cm. Although, a Van Veen grab, under ideal sampling conditions, makes a horizontal rather than a semicircular cut on a sandy substrate (Lie and Pamatmat, 1965), personal observations show that a semi-circular cut is not unusual at our sampling sites. Due to this characteristic shape of the Van Veen grab, *L. conchilega* tubes at the outside of the grab are sampled less efficiently, even when the Van Veen reaches its maximal sampling depth (18.5 cm). Therefore, it is advisable to use the tube tops with fringes, irrespective of tube length, as an estimate of the *L. conchilega* density, as was previously done in other studies (Ropert and Dauvin, 2000, Strasser and Pieloth, 2001; Zühlke, 2001; Callaway, 2003).

Strasser and Pieloth (2001) also found a strong linear correlation (Spearman rank $r=0.97$, $p<0.001$) between the number of tube top counts and living worms, although the tube counts slightly overestimated the number of animals present (trend line above the 1:1 ratio). This supports the idea that the shape of the tubes (U or – W type) is independent from the density (Strasser and Pieloth, 2001). Therefore, they proposed a correction factor of 0.73 to estimate real densities. However, in the case of high *L. conchilega* densities, this correction is too strong, whereas in low densities patches the correction factor is too weak. That is why a correction factor should be replaced by a regression equation depending on the *L. conchilega* abundance. Furthermore, since both methods in our field study rendered exactly the same density estimates at a sampling depth of 30 cm (Mann-Whitney U-test: $p = 1.000$), it can be expected that this number reflects the real density of *L. conchilega*. This conclusion confirms the one to one relationship between the number of fringed tubes and the real density of *L. conchilega*, at least in high density patches such as the ones at the beach of Heist. The one to one relationship in high density patches also supports the idea that the shape of *L. conchilega* tubes is indeed density dependent (less U- or W- shaped tubes).

Higher number of tubes compared to specimens was found on most occasions, as expected based on the sampling efficiency of a Van Veen grab. However, sometimes lower numbers of tubes than specimens were detected. Two hypotheses are suggested to explain these deviations from the general pattern. Firstly, in some cases this is most due to the absence of tubes with well developed fringes. The destruction of the tube fringe could be caused by previous disturbances, like beam-trawl fishery (sampling areas are characterized by a high beam-trawl frequency, personal observations) or even storm conditions (not the case on the discussed sampling dates). *Lanice conchilega* normally rebuilds its tube very quickly (within 48 hours), but the form of the fringes of the tubes can differ according to the water condition (Nicolaidou, 2003). In still water the fringe of the new tube was thinner and extended to all directions, while under a wave regime the individual branches were thicker and positioned perpendicularly to the direction of the waves. Secondly, tube tops of young adults (tube diameter between 1 and 1.5 mm) are more fragile and less developed (personal observations) and therefore more sensitive to destruction during sieving or sorting. This factor may explain the lower number of tubes during periods, characterized by high abundances of young individuals in the adult population (i.e. spring – summer).

Conclusion

The accuracy of the density estimates, along with the depth-independency of the tube method, indicates that the tube method should be the prime method to estimate the density of *Lanice conchilega*. However, caution is needed when analyzing samples with fragile young individuals and samples from areas where temporary physical disturbance is likely to occur.

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Appendix II

Publication list Gert Van Hoey

A 1 - Publications

Van Hoey, G., Degraer, S., Vincx, M., 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. Estuarine, Coastal and Shelf Science, 59, 599-613

Massin, C., Appeltans, W., Van Hoey, G., Degraer, S., Vincx, M., 2005. *Leptosynapta minuta* (Becher, 1906) (Echinodermata, Holothuroidea), a new species for Belgian marine waters. Belgian Journal of Zoology, 135 (1), 83-86

Van Hoey G., Vincx, M., Degraer, S., 2005. Small- to large scale geographical patterns within the macrobenthic *Abra alba* community. Estuarine, Coastal and Shelf Science, 64(4), 751-763

Van Hoey, G., Vincx, M., Degraer, S., submitted. Long-term variability in the *Abra alba* community: importance of physical and biological causes. Journal of Sea Research

Van Hoey, G., Vincx, M., Degraer, S., submitted. Abundance estimates of subtidal *Lanice conchilega* populations based on tube counts. Helgoland Marine Research

Willems, W., Goethals, P., Van den Eynde, D., Van Hoey, G., Van Lancker, V., Verfaille, E., Vincx, M., Degraer, S., submitted. Where is the worm? Predictive modelling of the habitat preferences of the tube-building polychaete *Lanice conchilega* (Pallas, 1766). Ecologal modelling

A 4 - Publications

Rees, H., Cochrane, S., Craeymeersch, J., de Kluijver, M., Degraer, S., Desroy, N., Dewarumez, J.-M., Duineveld, G., Essink, K., Hillewaert, H., Kilbride, R., Kröncke, I., Nehmer, P., Rachor, E., Reiss, H., Robertson, M., Rumohr, H., Vanden Berghe, E., Van Hoey, G., 2002. The North Sea Benthos Project: planning, management and objectives. *ICES, C.M. L(9)*, 1-10.

C 1 - Publications

Degraer, S., Van Lancker, V., Moerkerke, G., Van Hoey, G., Vincx, M., Jacobs, P., Henriet, J.P., 2002. Intensieve opvolging van de evolutie van een beschermd benthisch habitat (HABITAT): samenvatting van het onderzoek [Intensive evaluation of the evolution of a protected benthic habitat (HABITAT): summary of the research]. *Sustainable Management of the North Sea = Duurzaam Beheer van de Noordzee = Gestion Durable de la Mer du Nord.* DWTC/SSTC: Brussel, Belgium. 9 pp.

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Vincx, M., Bonne, W., Cattrijsse, A., Degraer, S., Dewicke, A., Steyaert, M., Vanaverbeke, J., Van Hoey, G., Stienen, E., Van Waeyenberge, J., Kuijken, E., Meire, P., Offringa, H., Seys, J., Volckaert, F., Gysels, E., Huyse, T., Zietara, M.S., Geets, A., Hellemans, B., 2002. Structural and functional biodiversity of North Sea ecosystems: species and their habitats as indicators for a sustainable development of the Belgian Continental Shelf = De structurele en functionele biodiversiteit van de Noordzee-ecosystemen, *in*: (2002). *Sustainable Management of the North Sea: presentation of research results, 21-22/01/2002. Sustainable Management of the North Sea = Duurzaam Beheer van de Noordzee = Gestion Durable de la Mer du Nord*

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Degraer, S., Van Lancker, V., Moerkerke, G., Van Hoey, G., Vincx, M., Jacobs, P., Henriet, J.P., 2002. Intensive evaluation of the evolution of a protected benthic habitat: HABITAT. Final report. Federal Office for Scientific, Technical and Cultural Affaire (OSTC). Ministry of the Flemish Community, Environment and Infrastructure. Department: Waterways and Marine Affairs Administration, Coastal Waterways, 124pp.

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