UNIVERSITEIT ANTWERPEN

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Macrozoobenthos and waterbirds in the estuarine environment: spatio-temporal patterns at different scales

(Macrozoöbenthos en watervogels in het Schelde-estuarium ruimtelijke en temporele patronen)

Proefschrift voorgelegd tot het behalen van de graad van
doctor in de wetenschappen aan de
Universitaire Instelling Antwerpen te verdedigen door

Tom YSEBAERT

Promotor: Prof. Dr. P. Meire

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... Being neither sea nor land, with most of the organisms hidden inside the sediment and tedious to extract, with no inviting place to sit down and reflect for a while, the sediments between the tidemarks and the turbid tidal waters attracted few scientists. Indeed, by all standards, tidal flat ecologists appear somewhat backward: they have neither ship nor diving gear at their disposal, but walk out in rubber boots with a spade in one hand and a bucket in the other as if to collect potatoes; and when they come back from their field work, they are besmeared all over with sticky mud and yet confess they love it ...

K. Reise, Tidal Flat Ecology, 1985

Dank aan allen die hebben bijgedragen tot de realisatie van dit proefschrift.

Contents

Chapter one

General introduction and outline

Introduction

Coastal and estuarine ecosystems represent the vast biomes that join continental lands and oceanic islands with their surrounding seas. Although estuaries can be considered as transition zones or ecotones between the freshwater and marine habitats, many of their most important physical and biological attributes are not transitional, but unique.

Estuaries form only a small part of the total land area. For example, the several estuaries along Britain's coastal zone make up only 2.3% of the total area of British land (DAVIDSON et al. 1991). The total estuarine habitat of the North Sea shores and Atlantic seaboard (from mid-Norway at 60°N to southern Portugal at 37°N) is estimated at *c.* 1.895.000 ha (DAVIDSON et al. 1991). The area of British estuaries amounts to approximately 28%, the Wadden Sea between The Netherlands, Germany and Denmark 39.5 %, and the Delta area in southwest Netherlands 3.8%. The Belgian contribution to the estuarine habitat is estimated at 0.1%.

Human pressure and impact on estuaries is very high, as most of the urbanization is concentrated in the coastal zone. On the other hand, it is recognized that estuaries have unique functional and structural biodiversity values. Therefore, these ecosystems are particularly important for integrating sound ecological management with sustainable economics.

This chapter provides the definition and description of an estuary, and then gives a brief introduction to general features of the estuarine environment, revealing the importance of macrobenthos within estuaries, and the importance of estuaries for waterbirds. The major human impacts on estuaries are presented, after which the principles of integrated water management and ecosystem management are defined in view of the management of these unique ecosystems. Finally, the aim and outline of the present study are given.

What is an estuary?

Coastlines are transient on the geological time scale. The precise physical location of estuaries and other coastal landforms is substantially dependent on sea level and is constantly changing. Present-day estuaries are geologically ephemeral coastal features. They were formed during the last interglacial stage when, between 15000 and approximately 5000 years ago, the sea level rose 120 m to the present level (DAY et al. 1989).

There are many ways in which estuaries have been defined, but by their very nature as places of transition between land, sea and fresh water, no simple definition readily fits all types of estuarine systems. DAY et al. (1989) describe estuaries as a continuum of types ranging from entirely marine-influenced systems, such as lagoons formed behind wave-generated sand of shingle bars, to deltas created by river processes. In between lagoons and deltas lie estuarine lagoons, estuaries, and estuarine deltas, representing a mixture and gradation of the two extreme coastal environments. Perhaps the most quoted definition of an estuary in the scientific literature is given by PRITCHARD (1967):

« An estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage. »

Certainly one of the most characteristic attributes of most coastal areas and estuaries is the action of the tide[1], which is not mentioned in Pritchard's definition. In an attempt to address this limitation, FAIRBRIDGE (1980) gave a more comprehensive definition of an estuary:

« An estuary is an inlet of the sea reaching into a river valley as far as the upper limit of tidal rise, usually being divisible into three sectors: (a) a marine or lower estuary, in free connection with the open sea ; (b) a middle estuary subject to strong salt and fresh water mixing ; and (c) an upper or fluvial estuary, characterized by fresh water but subject to daily tidal action. The limits between these sectors are variable, and subject to constant changes in the river discharge. »

While most estuarine biologists have used Pritchard's definition of estuaries, recent studies in tidal freshwater regions of estuaries have suggested that the definition of Fairbridge is more suitable (McLUSKY 1999). Pritchard's landward boundary is the chemical one: where the chlorinity falls below 0.001% and the ratios of the major dissolved ions change significantly from their values in sea water. Fairbridge's landward boundary is physical: the upstream limit of a measurable tide. For some estuaries the difference is trivial, but for others the upper limit of the "Fairbridge estuary" can be tens of kilometers landward of the "Pritchard estuary" upper limit, which is certainly the case for the Schelde estuary. Nowadays, it is recognized that freshwater tidal reaches are part of the estuarine system. Following the Venice symposium (1958), via PRITCHARD (1967) and FAIRBRIDGE (1980), to MEIRE & VINCX (1993), we can now define estuarine regions as per Table 1.1 (McLUSKY 1993, 1999).

Estuary types include fjords, rias, coastal plain estuaries, lagoon or bar-built estuaries, embayments, etc. This thesis deals with coastal plain estuaries, sometimes called 'drowned river valley estuaries'. Maximum depths in these inlets are generally less than 30 m and the central channel is often sinuous. Extensive mudflats and marshes often occur and the estuary is usually floored by varying thickness of recent sediment, often mud in the upper reaches, but becoming increasingly sandy towards the mouth.

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[1] Latin *aestus* : heat, boiling, tide

Table 1.1. Classification of estuarine divisions (McLUSKY 1993, 1999).

Division	Tidal	Salinity (psu)	Venice system
River	Non-tidal	< 0.5	Limnetic
Head	The highest point to which tides reach		
Tidal fresh	Tidal	< 0.5	Limnetic
Upper	Tidal	0.5 – 5	Oligohaline
Inner	Tidal	5 – 18	Mesohaline
Middle	Tidal	18 – 25	Polyhaline
Lower	Tidal	25 – 30	Polyhaline
Mouth	Tidal	> 30	Euhaline

Estuaries that link freshwater and marine ecosystems represent perhaps the most obvious landscape boundary in aquatic ecology. Despite their intimate connection with freshwaters, however, estuaries are commonly studied as part of the marine sciences, and there has been little interaction among freshwater and estuarine researchers. As a consequence, the upper, freshwater tidal parts of estuaries are often neglected in both marine and freshwater ecological studies (e.g. ODUM 1988).

The estuarine environment

General characteristics and ecosystem functions

Estuaries are the main transition zones between the freshwater of the land and the salt water of the oceans. They concentrate waters from very large land surfaces into relatively small areas. Estuaries, in general, are shallow, open and dynamic systems. The small volume of water per m^2 of sediment surface, the presence of intertidal flats and very shallow subtidal areas, and the generally well-mixed nature of the water column, are physical conditions that intensify the exchange of matter and energy between the water column and the sediment system (intense benthic-pelagic coupling, HEIP et al. 1995). As so, estuaries support important ecosystem functions: biogeochemical cycling and movement of nutrients, purification of air and water, mitigation of floods, maintenance of biodiversity, etc. (DAILY et al. 1997; DE GROOT 1997; MEIRE et al. 1998). A world wide estimation of the economic value of the ecosystem functions (services and goods) pointed out the important contribution of wetlands and estuaries to these functions (COSTANZA et al. 1997).

Perhaps the most distinctive feature that contrasts estuaries from other biomes is the nature and variability of the physicochemical forces that influence these ecosystems. Within small geographic regions, many estuaries experience widely varying conditions of temperature, salinity, concentrations of a wide variety of chemicals, and plant and animal densities, much of which is mediated by water movement over relatively short time scales (MCLUSKY 1989; DAY et al. 1989).

Estuaries consist of a complex mixture of many different habitat types. These habitats do not exist in isolation, but rather have physical, chemical and biological links between them, for example in their hydrology, in sediment transport, in the transfer of nutrients and in the way mobile species move between them both seasonally and during single tidal cycles. Even small estuaries are typically composed of a mosaic of between four and nine major habitat types (subtidal, intertidal mudflats, intertidal sandflats, marshes, shingles, rocky shores, lagoons, sand-dunes and grazing marshes/coastal grassland) (DAVIDSON et al. 1991). Within these broad categories of habitats, a diverse array of smaller habitat forms exist along a vertical gradient going from the deep subtidal up to the upper shore and along a longitudinal gradient going from the marine zone, over the brackish zone to the freshwater tidal zone. Most characteristic habitats of estuaries are tidal flats and marshes. Tidal flats are important components of macro- and mesotidal estuaries and coastal systems all over the world. They are complex macromorphological structures, shaped in close relation to hydrodynamic factors in the estuary. A single tidal flat can consist of a series of habitats ranging from small sand dunes and mega-ripples to extensive flat muddy areas and may be inhabited by very different biological communities.

Despite the many different habitat types, the relatively large and unpredictable variations in salinity (physiological stress) and water movement (physical stress) tend to limit the number of animal and plant species capable of adapting to these rigorous conditions (MCLUSKY 1989; DAY et al. 1989). As a result, in general fewer species live in estuaries than in either the freshwater rivers above the tidal limit or the truly marine habitats outside estuaries. However, it has been suggested that despite low taxonomical diversity estuarine ecosystems have high functional diversity (COSTANZA et al. 1993).

Although estuaries generally contain relatively few species, the abundance and biomass of organisms is usually very high. Estuaries and coastal marine ecosystems are also cited among the most productive biomes of the world, and serve as important life-support systems also for human beings (DAY et al. 1989; COSTANZA et al. 1993). Other highly productive systems, such as coral reefs and tropical rain forests, differ greatly in how their productivity is achieved. Reefs and tropical rain forests efficiently recycle the limited resource of materials through a very diverse ecosystem. In contrast the low diversity estuarine ecosystems achieve their very high productivities through the continuous arrival of new supplies of nutrients.

Being open systems, estuaries also serve as important connections between rivers and the sea for many anadromous (ocean dwelling but spawning in estuaries and rivers) and catadromous (freshwater dwelling but spawning in seawater) species. Estuaries are important nursery grounds for several (commercial) fish and crustacean species, as they find plenty of food and shelter in the shallow subtidal and intertidal zones. Especially marshes are important feeding and spawning areas (e.g. CATTRIJSSE et al. 1997).

Macrobenthos

Macrobenthos is a central element of estuarine ecosystems and plays a key role in benthic and pelagic food chains, being an important food resource for epibenthic crustaceans, fish and birds.

Humans harvest many species of shellfish and crustaceans. According to their size, benthic organisms are classified as micro-, meio- and macrobenthos. Macrobenthos are commonly defined as organisms retained on a 1000 μm mesh size, although they are sometimes defined as organisms retained on either a 500 or 300 μm mesh. Macrobenthos is composed of Mollusca, Polychaeta, Echinodermata, Crustacea and a few other groups.

Macrobenthos plays an important role in benthic remineralisation processes (HERMAN et al. 1999), both directly as an important component of the system, and indirectly through its structuring effect on the sediment community. The presence of (macro)benthic organisms may largely affect sediment transport processes, by influencing the physical stability and erodability of natural cohesive sediments (e.g. LUCKENBACK 1986; MOURITSEN et al. 1998; PATERSON & BLACK 1999).

Similar to all ecological communities, intertidal and shallow subtidal soft-sediment communities are influenced by a variety of physical and biological processes that operate over different space and time scales. Physiological stresses can be particularly important in highly fluctuating environments such as estuaries in general, and intertidal habitats in particular. Figure 1.1 gives a schematic representation of the main environmental variables that are involved in structuring macrobenthic communities. River run-off and tidal action will determine to a large extent the chemical and physical characteristics of estuaries. The presence of macrobenthic species and assemblages in estuaries depends on their tolerance for different salinities (BOESCH 1977; WOLFF 1983; HOLLAND et al. 1987), as well as a suite of other physical factors that could affect their physiology, such as temperature and oxygen and the degree of immersion/emersion arising from the tidal regime (REISE 1985; PETERSON 1991). The major physical factors thought to influence distributions of macrobenthos in soft-sediment habitats are sediments (e.g. GRAY 1974; RHOADS 1974; MEIRE et al. 1994), nutrients and food supply (both quantitative as qualitative) (e.g. PEARSON & ROSENBERG 1978, 1987; DAUWE et al. 1998; HERMAN et al. 1999, *in press*) and hydrodynamic processes (NOWELL & JUMARS 1984; WARWICK et al. 1991; HALL 1994; SNELGROVE & BUTMAN 1994). Hydrodynamic variables such as current velocity, bed shear stress, and wind-wave activity have been recognized as influencing larval settlement and post-settlement transport (e.g. GRANT 1983; COMITTO et al. 1995), availability of particulate food resources (e.g. WARWICK & UNCLES 1980) as well as the stability of the substratum by mobilising bed material, including macrofauna (e.g. WARWICK et al. 1991; BELL et al. 1997). Food availability, especially the role of primary productivity, either through the phytoplankton or the micro-phytobenthos, may be the prime limiting factor for benthic biomass (HERMAN et al. 1999, *in press*).

Benthic populations are also, to a certain extend, controlled by biotic interactions, such as predation and inter- and intraspecific competition (PETERSON 1979; REISE 1985; reviews in WILSON 1991, OLAFSSON et al. 1994). The relative importance of processes determining the spatial-temporal distribution of macrofaunal species may depend on the scale considered (SCHNEIDER 1994;

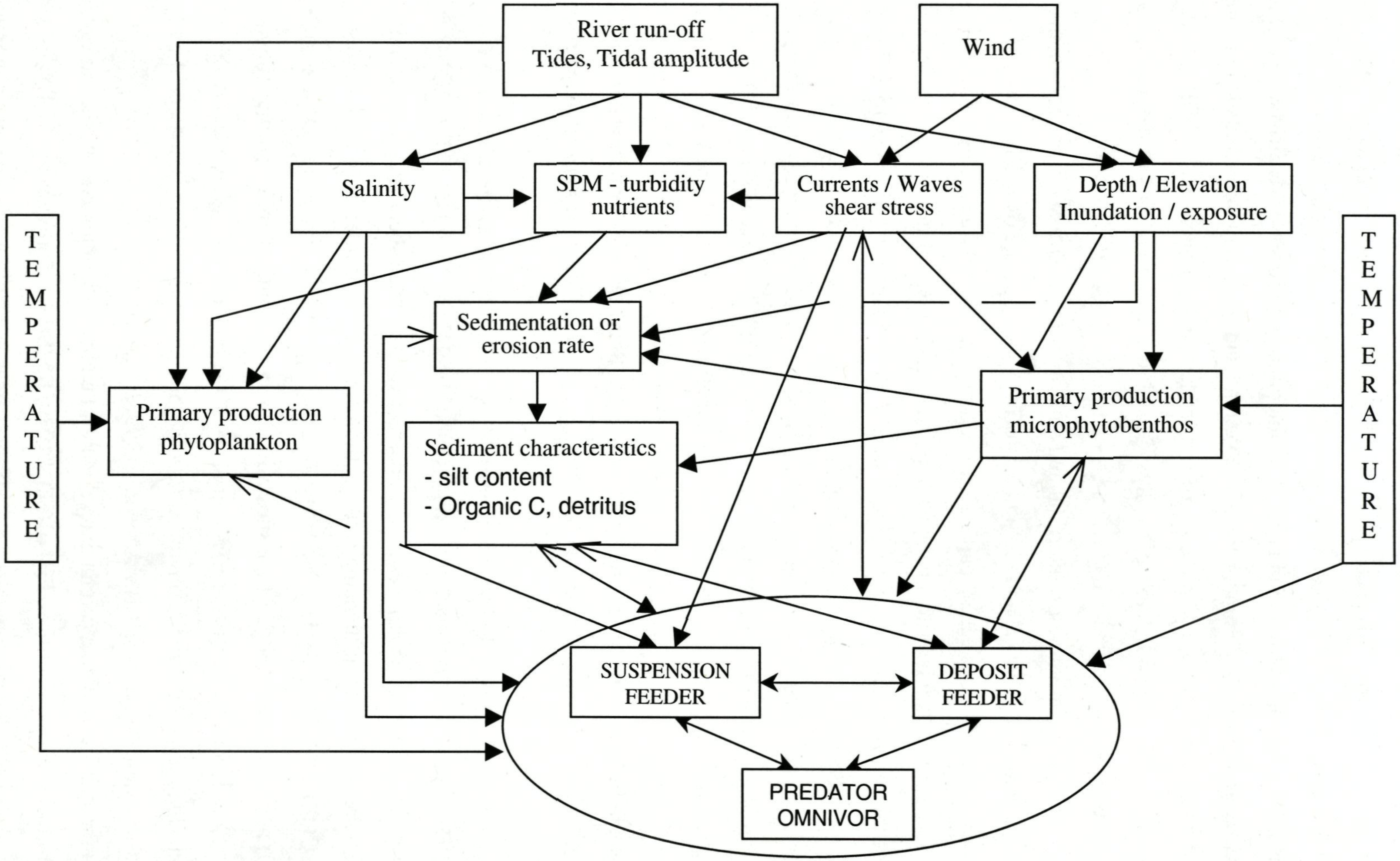


Figure 1.1. A schematic representation of the major environmental variables and their role in structuring macrobenthic communities in the estuarine environment.

THRUSH et al. 1999). Biological interactions and life history strategies are thought to operate within constraints imposed by large-scale physical factors, but will regulate local patterns of benthic community succession and structure (ZAJAC & WHITLATCH 1985; OLAFFSON et al. 1994; LEGENDRE et al. 1997, THRUSH et al. 1997).

Macrobenthic communities are good indicators of biotic integrity and reflect the present state of the estuarine ecosystem. Macrobenthos is often used in monitoring programmes as ecological bioindicator for possible changes in the system. As a consequence, a lot of studies have investigated the structure of macrobenthic communities in relation to the abiotic environment, coupling the dominance patterns (e.g. ABC method, WARWICK 1986) or functional life-history characteristics (e.g. trophic structure) (PEARSON & ROSENBERG 1978, BOESCH & ROSENBERG 1981, RAKOCINSKI et al. 1997; GASTON et al. 1998) of the macrobenthos to human impacts.

Waterbirds

Birds benefit from the high level of primary and secondary productivity of estuaries, and for many waterbird species estuaries are of vital importance for one or more stages of their life cycle. Most significant in temperate estuaries are the large numbers and variety of species of migrant and wintering waterbirds (waders and wildfowl), that depend on the abundant biomass of estuarine producers and consumers as a food supply for winter survival and for further migration to more southerly wintering grounds (PIENKOWSKI & EVANS 1984; PIERSMA 1987, 1994; SMIT & PIERSMA 1989; DAVIDSON et al. 1991; ENS et al. 1994; BEINTEMA & VAN VESSEM 1999). Within the East Atlantic Flyway (SMIT & PIERSMA 1989), the annual migration route of populations of waders and waterfowl between the breeding and wintering quarters, including the stopover areas, the Delta area (SW Netherlands), the Wadden Sea and several British estuaries are very important either as a refueling site (in spring and autumn), or as a wintering site. This immediately stresses the international importance of tidal areas such as the Schelde estuary.

Estuarine waterbirds feed mainly on three classes of food: plants, invertebrates and fish. Therefore, they can be classified into three functional groups: herbivores, benthivores, and piscivores. Macrobenthos is the main food source for benthivores such as waders and diving ducks. Herbivores depend mainly on the presence of suitable marshes. Therefore, distribution patterns of waterbird species are to a great extent related to the distribution of their food (EVANS et al. 1984; MEIRE et al. 1989; DAVIDSON et al. 1991).

Waterbirds are a significant link between estuaries and human society. Being situated high in the estuarine foodweb, waterbirds are important consumers and will react on changes or human impacts in the water system (e.g. MEIRE et al. 1989; DAVIDSON et al. 1991). This, and because the general public is sensitive to birds, waterbirds are widely used as an important indicator and tool to protect wetland habitats (KUSHLAN 1993; MOSER et al., 1993; SCOTT & ROSE, 1996). It is widely accepted that the number of waterbirds using a wetland site is a good indicator of that site's biological importance. Several international agreements and conventions on the protection and conservation of habitats in general and wetlands in particular rely to a great extent on the occurrence of (water)bird populations. Perhaps the best known convention for the conservation of wetlands is the Ramsar Convention (Convention of Wetlands of International Importance Especially as Waterfowl Habitat, Ramsar 1971, Paris Protocol 1982, Regina Amendments 1987) (MATTHEWS 1993; DAVIS 1994).

Humans and estuaries

Humans have lived in or near coastal zones and estuaries for tens of thousands of years. Especially the increasing industrialisation and urbanisation over the last 200 years have affected great changes to many formerly rural estuaries and shores. It is estimated that nowadays 67% of the global population lives on the coast or within 60 km of the coast and the percentage is still increasing (HAMMOND 1992). Within 30 years this population will be doubled (NORSE 1994). Furthermore, many of the largest cities in the world, where population growth rates are highest, are near the coast. Urban centres have developed along with their consequent port infrastructures, coastal manipulation, waste disposal, and commercial and recreational use of resources. This has led to considerable habitat loss, degradation and fragmentation in the coastal zone (GRAY 1997).

Estuaries are subject to a wide array of human impacts, the most important of which are: land-claim, coastal protection, sea defence and barrage schemes, urbanisation, industrial, port and related economic developments, shipping, waste discharge, pollution with toxic substances, global climate change, fisheries, species introductions and invasions, tourism and marine litter. As a consequence of the increased discharge of organic wastes, many European estuaries were virtually dead by the early and middle part of the 20th century (McLUSKY 1999). Along with the discharge of waste destruction of the estuarine habitat through land-claim schemes has in some cases removed over 90% of the natural habitat (DAVIDSON et al. 1991). Many of the estuaries of Europe have been drastically changed by construction works (land-claim and flood protection). One clear trend in European estuaries has been the modernization of shipping practices, resulting in more and deeper dredging of the channels or construction of deeper-water harbours. Examples of both practices can be seen all over Europe.

Human influences on estuarine biodiversity are reflected in both acute and chronic effects over various temporal and spatial scales, that ultimately lead to broad-scale loss of productive habitats and altered or impaired community structure and function.

More details on the threats to coastal and estuarine systems are reviewed by e.g. DAY et al. (1989), DAVIDSON et al. (1991), SUCHANEK (1994), GRAY (1997) and McLUSKY (1999).

Integrated water management and ecosystem management

We should manage so as not to deny future generations
the opportunities and resources we enjoy today

The negative impact of human activities and the widespread deterioration of estuarine habitats clearly point out the need of a sound estuarine management. In recent years, sustainability has become an explicitly stated goal of natural resource management (e.g. CAIRNS 1997, 1999). In practice, however, management approaches have often focused on maximizing short-term yield and economic gain rather than long-term sustainability (CHRISTENSEN et al. 1996). Management practices often failed as a result of (1) insufficient or inappropriate information, both about the state of the ecosystem and also about the impact of human activities (economic and non-economic), (2) insufficient coordination between different levels and sectors of administration, and (3) insufficient participation and consultation of the relevant stakeholders and their policies. Sectoral management solutions will not produce long-term solutions. Especially in complex ecosystems such as the coastal zone and estuaries, which are influenced by a myriad of interrelated driving forces and pressures including geomorphological, hydrological, socio-economic, administrative, institutional and cultural systems, with processes operating over a variety of space and time scales, attempts to manage these ecosystems sustainable will fail unless they consider concurrently the entirety of the many systems that have a significant influence on the dynamics of the coastal zones and estuaries.

Several management concepts and strategies have been worked out to bring the principles of sustainability and wise use into practice. Only "integrated" approaches taking into consideration all the characteristics and processes that typify and change estuarine ecosystems have any chance of securing a sustainable future. In the coastal zone such approaches are known under the common name of ICM, ICZM or ICMM (Integrated Coastal Management, Integrated Coastal Zone Mangement or Integrated Coastal and Marine Management) (e.g. CICIN-SAIN & KNECHT 1998; DONE & REICHELT 1998). But estuaries not only are an important part of the coastal zone, they also form the connection between the river basin and the coastal sea. Within river basins, the concept of "integrated water management" (IWM) or "integrated catchment management" was developed, analoguous to the ICM concept. Integrated water management is the coordinated and integrated development, management and restoration of water-systems in such a way that it fulfills the quality objectives for both the ecosystem and the human use functions without endangering the multifunctional use of future generations. The formulation of objectives and the resulting weighing of functions and land use must depend on a thorough knowledge of the functioning of the water-system and its natural limits.

Both ICM and IWM require integration of all relevant policy areas, sectors, and levels of administration, but also integration of science and knowledge and how to apply these in sound management strategies. Ecosystem management can contribute to the integration required in IWM and ICM through the compilation of scientific knowledge of the functioning of the system and the translation of this knowledge into different management options and strategies. Ecosystem management is management driven by explicit goals, executed by policies, protocols and practices, and made adaptable by monitoring and research on our best understanding of the ecological interactions and processes necessary to sustain ecosystem composition, structure and function (CHRISTENSEN et al. 1996). Ecosystem management involves aspects of both basic and applied ecology, biology and other natural sciences and, more importantly, the application of scientific principles to the management of natural resources.

Since estuarine ecosystems are dynamic and showing large spatial, seasonal and inter-annual variations, which are not at the moment predictable from ecological theory as it stands, an extensive, coherent and systematic approach to the observation of the changing state of ecosystems is necessary. This implies well designed long-term monitoring, the development of sound (predictive) ecological models and a multidisciplinary approach. Identifying how the effects of ecological/environmental processes change with variation in spatial and temporal scale is one of the most important issues facing ecologists (THRUSH et al. 1999).

Aim of the present study

The general aim of the present study is to contribute to a better understanding of the environmental variability of estuarine soft-sediment ecosystems. Generating this understanding will lead to better predictions of future change to ecological systems, which is a prerequisite for improving conservation and management strategies.

The study is concentrated on ***macrobenthos*** and ***waterbirds*** in the Schelde estuary. Macrobenthos is an important component of estuarine ecosystems. The evaluation of effects of human induced changes will likely involve an analysis of possible responses of the benthos. Waterbirds are good indicators of environmental changes because of their position at the top of the food web. Waterbirds are widely used in monitoring programmes as an indicator of the value of wetland habitats.

The specific aims are therefore:

1. to describe spatio-temporal patterns in occurrence of soft-sediment macrobenthos in the Schelde estuary, with emphasis on the relation between macrobenthos and their environment at different scales;
2. to compare the spatial distribution of intertidal macrobenthos in the Schelde estuary with that of other NW-European estuaries (Oosterschelde and Ems estuary);

3. to statistically model and predict distribution patterns of macrobenthic species occurrence in the Schelde estuary;
4. to describe and evaluate the value of the Schelde estuary as wetland habitat for waterbird communities along the estuarine salinity gradient.

Outline of the thesis

This thesis is focused on the role of abiotic environmental variables (environmental constraints) in structuring macrobenthic communities in an estuarine environment. Data from different, mainly monitoring studies, that describe patterns and gradients in space and time, are used to get insight into the spatial and temporal variability of macrobenthos and to reveal how this variability can be explained by the environment.

The structure of macrobenthic communities is usually described using a variety of techniques. These range from a separate analysis of individual populations, typically focusing on the more abundant species or those species considered to be ecologically important, over an analysis of functional groups (e.g. trophic groups) and several univariate summary statistics (diversity measures, domiance curves), to multivariate techniques that consider species data, sample data and eventually environmental variables simultaneously (JONGMAN et al. 1995; LEGENDRE & LEGENDRE 1998). As no single method addresses all aspects of community structure, a combination of methods is also used in this study. Some of these methods are also applied to study the waterbird communities.

The **first part** considers spatio-temporal patterns in macrobenthic species and communities along the estuarine salinity gradient. A first paper (***chapter 2***) deals with the zonation of intertidal macrobenthos (diversity, abundance, biomass and species distributions) along the estuarine salinity gradient of the Schelde estuary. This paper is based on a sampling of 50 intertidal locations from the mouth of the Schelde estuary up to the freshwater tidal zone.

A second paper (***chapter 3***) describes the spatial distribution patterns of macrobenthos on an estuarine macro- and meso-scale, in relation to the predominant estuarine environmental variables salinity, depth, current velocity and sediment characteristics. Indicator species, trophic structure and community structure are defined along the estuarine gradients through multivariate analysis. For this purpose, a very large data set of 3112 samples was constructed, based on data collected by different institutes in the period 1980-1997.

A third paper (***chapter 4***) deals with the spatial and temporal variation in macrobenthic species composition, species assemblages and functional diversity along the salinity gradient in the Schelde estuary. The analysis involves the identification of the factors controlling the observed spatial and temporal patterns of variability in the macrobenthic communities. The study was carried out at five locations in the Schelde estuary, which were sampled monthly during a two-year period (1993-1994). Spatial analysis included regional (among salinity zones) and local (muddy versus sandy) sampling locations.

The **second part** compares the intertidal benthic communities of the Schelde estuary with benthic communities of other NW-European estuaries. In a first paper (***chapter 5***) a comparison is made between the Westerschelde and the Oosterschelde. In the Westerschelde the normal estuarine gradient from a brackish to a marine tidal system is found, whereas in the Oosterschelde major coastal engineering works have profoundly changed the character of the area, turning the system into a coastal basin without salinity gradient and a low turbidity. The intertidal macrofauna of both estuaries was studied in 1987 and the macrobenthic distribution and community structure in relation to the prevailing environmental factors was analysed by means of multivariate analyses.

In a second paper (***chapter 6***) a comparison is made with the Ems estuary, which is, like the Schelde estuary, an estuarine ecosystem with still a complete salinity gradient, including a freshwater tidal zone, of more or less the same latitude but with a different degree of antropogenic stress. Based on a large dataset, collected in the period 1980-1990, the spatial occurrence of macrobenthic species and communities, and the faunal change along the salinity gradient, including the freshwater tidal zone, was analysed.

In the **third part**, more detailed observations on the macrobenthic distribution patterns in the mesohaline part of the estuary are described. A first paper (***chapter 7***) deals with the subtidal macrofauna of the Beneden Zeeschelde. The macrobenthos of the subtidal, mesohaline zone of the Schelde estuary (Belgium) was sampled in October 1996 and 1997 at 54 and 73 sampling locations respectively. The results are compared with the species diversity along the complete Schelde salinity gradient and with data from 1952 (LELOUP & KONIETZKO 1956). Possible effects on benthic communities of dredging operations and other anthropogenic influences, like the occurrence of hard substrates within the sediment are discussed.

In a second paper (***chapter 8***) the variations in zoobenthos and microphytobenthos (algal biomass) occurrence between spring (April) and autumn (September) are investigated in relation to environmental characteristics of cohesive sediments, based on a sampling of ten locations on three mudflats in the intertidal mesohaline part of the Schelde estuary. Not only macrobenthos (> 1000 μm), but also the smaller fraction of the zoobenthos (sieved through 500 and 250 μm mesh size), as well as the vertical distribution of the benthos in the sediment are considered.

The **fourth part** deals with the development of statistical models to predict macrobenthic species response to (changes in) environmental conditions in estuarine ecosystems. In ***chapter 9*** so-called response curves and surfaces are fitted through mathematical relations obtained by logistic regression. Based on the associations between the probability of occurrence of estuarine macrobenthic species and abiotic environmental variables, predictions of macrobenthic species distributions are generated. The same data as in chapter 2 were used.

The **fifth part** describes estuarine gradients at a higher trophic level, namely by looking at the distribution patterns of waterbirds along the estuarine salinity gradient of the Schelde estuary (***chapter 10***). The relation of the observed diversity and community patterns with the functional and habitat diversity of the Schelde estuary as well as the effect of recent conservation measures to preserve this habitat are discussed.

The chapters of this thesis are prepared as individual publications, some of which have already been published in international journals, others accepted or (to be) submitted (see table of contents). This approach leads inevitably to some overlap between the chapters, especially concerning materials and methods and parts of the introductions and discussions. A description of the Schelde estuary is summarized hereafter, and hence can be skipped by the reader in each chapter. Several reports form the basis of the work presented here and are listed separately.

Study area: The Schelde estuary

Geographical situation

The river Schelde is a lowland-river, which takes its rise in the northern part of France (St. Quentin) and flows into the North Sea near Vlissingen (The Netherlands). The total catchment area is approx. 21.86 10^3 km^2 (Figure 1.2). The total length of the river is 355 km, the fall over the total river length is at most 100 meters. Approximately ten million people live in the total Schelde river basin.

The estuary of the river Schelde extends from the mouth at Vlissingen (km 0) till Gent (km 160), where the tidal movement is stopped by a complex of sluices (Figure 1.3). The major tributaries of the estuary are the Rupel, the Durme and the Dender.

The Schelde estuary is the only remaining true estuary of southwest Netherlands. Major coastal engineering works, mainly for flood protection, have profoundly changed the character of the other estuarine branches. Some estuaries (e.g. Krammer, Haringvliet) have become freshwater lakes, while others have become non-tidal brackish (Veerse Meer) or saline (Grevelingen) areas. The Oosterschelde was partly closed from the sea by a storm surge barrier, but the cut off of freshwater inflow turned the area into a marine tidal bay (SMAAL & NIENHUIS 1992, NIENHUIS & SMAAL 1994).

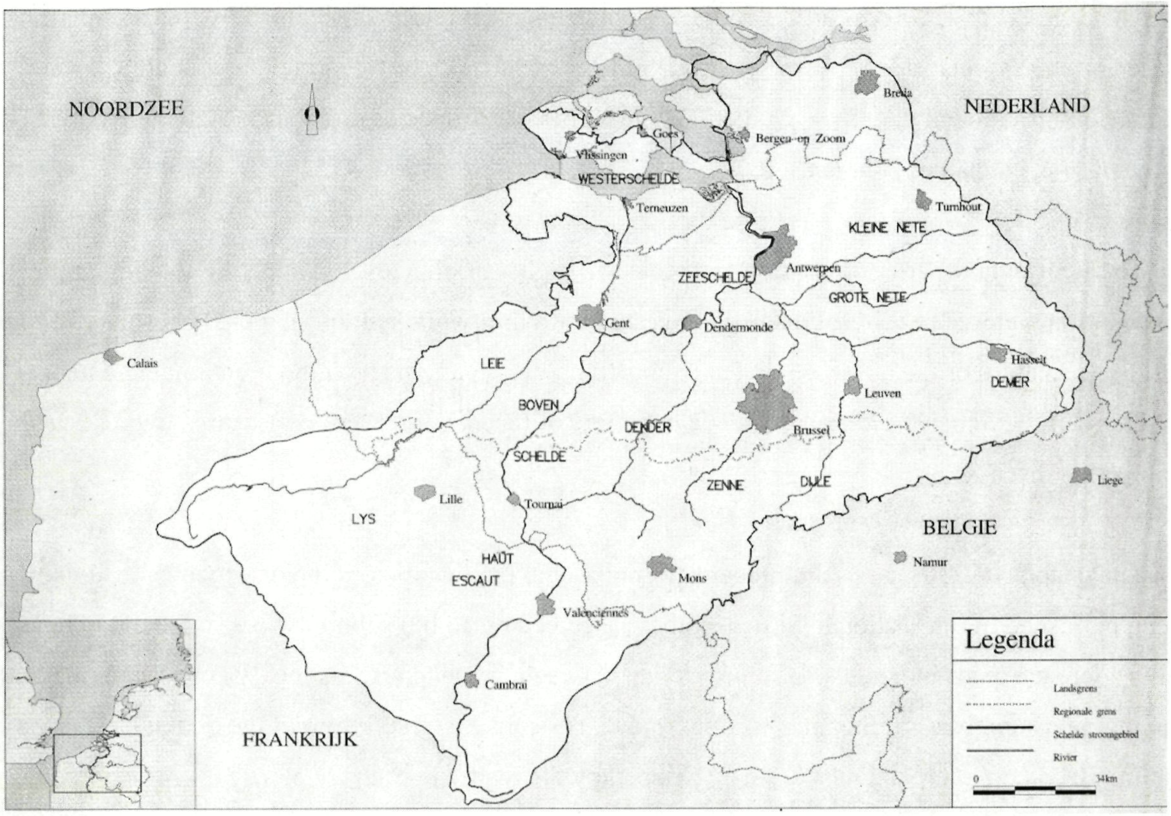


Figure 1.2. The catchment area of the river Schelde

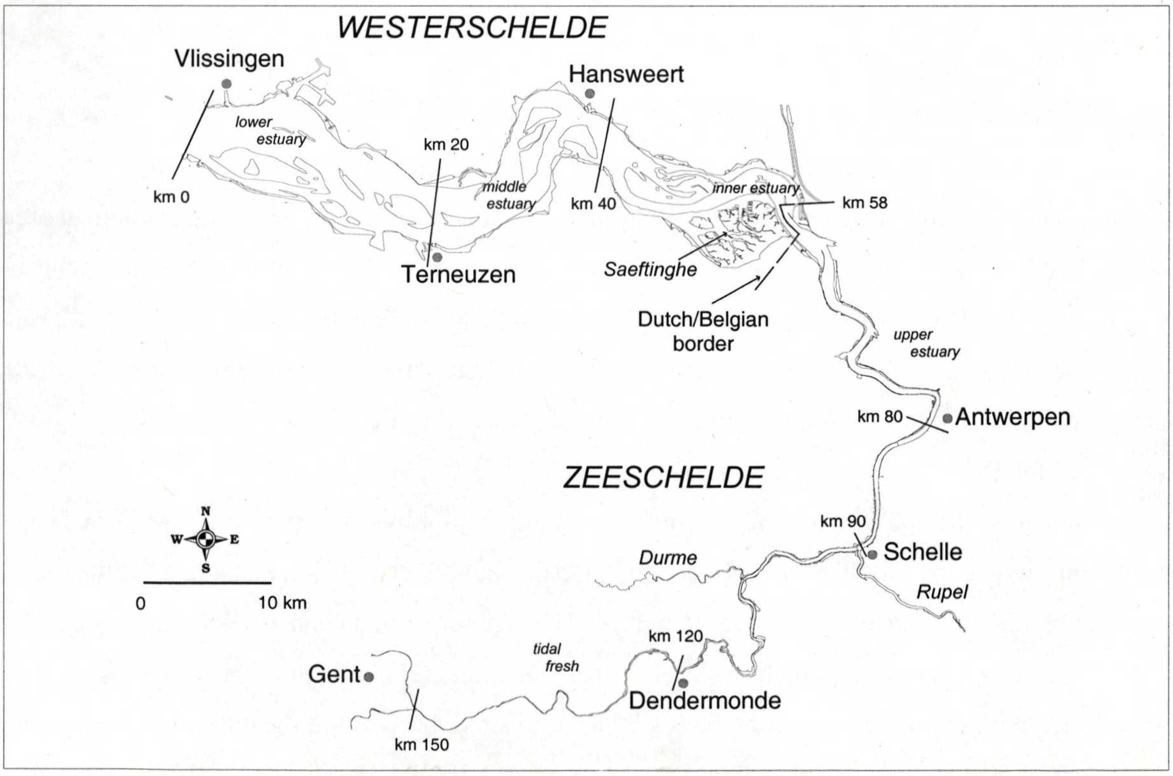


Figure 1.3. Map of the Schelde estuary

The Zeeschelde (105 km), the Belgian freshwater tidal and upper/inner part of the estuary, is characterized by a single ebb/flood channel, bordered by relatively small mudflats and marshes (28% of total surface). The surface of the Zeeschelde amounts to 44 km². Human activities are mainly concentrated in the Zeeschelde, where agglomerations and industries are located close to the river banks. The intertidal zone is often absent (e.g. quays, wharfs) or very narrow. Upstream of Dendermonde, the estuary is almost completely canalized (HOFFMANN & MEIRE 1997). The Zeeschelde is sometimes further subdivided into the 'Beneden Zeeschelde' between the Dutch/Belgian border and Antwerpen and the 'Boven Zeeschelde' between Antwerpen and Gent.

The middle and lower estuary, called the Westerschelde (58 km), is a well mixed region characterised by a complex morphology with flood and ebb channels surrounding several large intertidal flats and salt marshes. The surface of the Westerschelde amounts to 310 km², with the intertidal area covering 35%. The average channel depth is approximately 15-20 m. In the lower and middle estuary a multiple channel equilibrium exist.

Freshwater flow and tidal influence

The mean river discharge at Schelle (90 km from the mouth), amounted to 104 $m^3.s^{-1}$. Being a typical rain-fed river, river discharge varies among seasons. During winter, the mean river discharge amounts to 180 $m^3.s^{-1}$, with exceptional values up to 600 $m^3.s^{-1}$. Average summer values decrease to 60 $m^3.s^{-1}$, with minimal values down to 20 $m^3.s^{-1}$ (BAEYENS et al. 1998).

The residence time of the water ranges from one to three months, depending on the river discharge (SOETAERT & HERMAN 1995). Only the most seaward region has a residence time of 10-15 days.

Due to the funnel-shaped morphology of the estuary, the mean vertical tidal range is maximal in the freshwater tidal reaches (maximum tidal range at Schelle: 5.33 m, CLAESSENS 1988). In Vlissingen the mean vertical tidal range is 3.80 m, near the Dutch-Belgian border 4.94 m, in Antwerpen 5.19 m and in Gent 2.0 m. The ratio between the duration of rising and falling tide decreases from 0.88 at Vlissingen to 0.75 at Schelle and 0.39 at Gent.

The maximum tidal velocity at the mouth is about 0.9 $m\ s^{-1}$, in the Beneden Zeeschelde 1.1 $m\ s^{-1}$ and between Antwerpen and the Rupel 1.2 to 1.3 $m\ s^{-1}$ (BAEYENS et al. 1998).

Salinity

The longitudinal salinity profile of the Schelde estuary is primarily determined by the magnitude of the river discharge (Fig. 1.4), with the transition between fresh and salt water being particularly smooth. The estuary is well-mixed (except during peak discharges), which means that vertical salinity gradients are small or negligible.

A polyhaline zone stretches out from the river mouth (km 0) to the vicinity of Hansweert (km 40). Between Hansweert and the Dutch-Belgian border (km 58) a mesohaline zone is located. The section between the border and the vicinity of Antwerpen (km 80) is characterized by a steep salinity gradient.

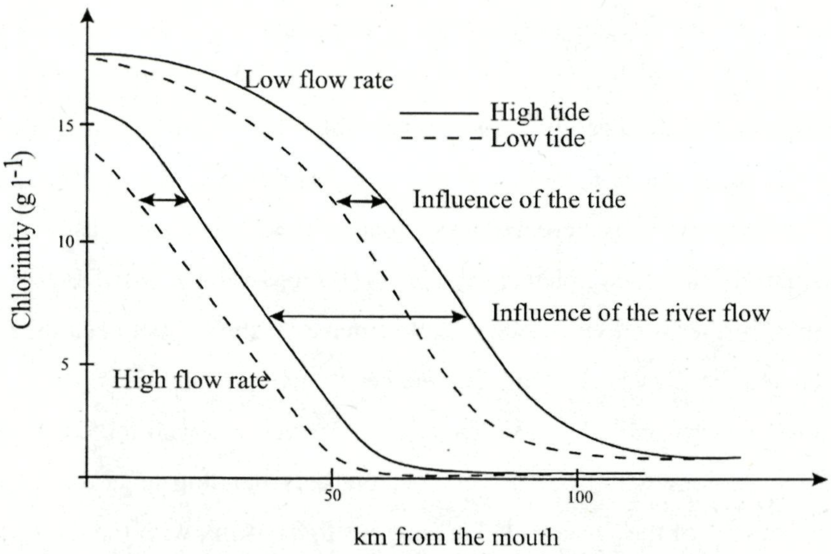


Figure 1.4. The influence of river flow and tide on the salinity profile (after Baeyens et al. 1998).

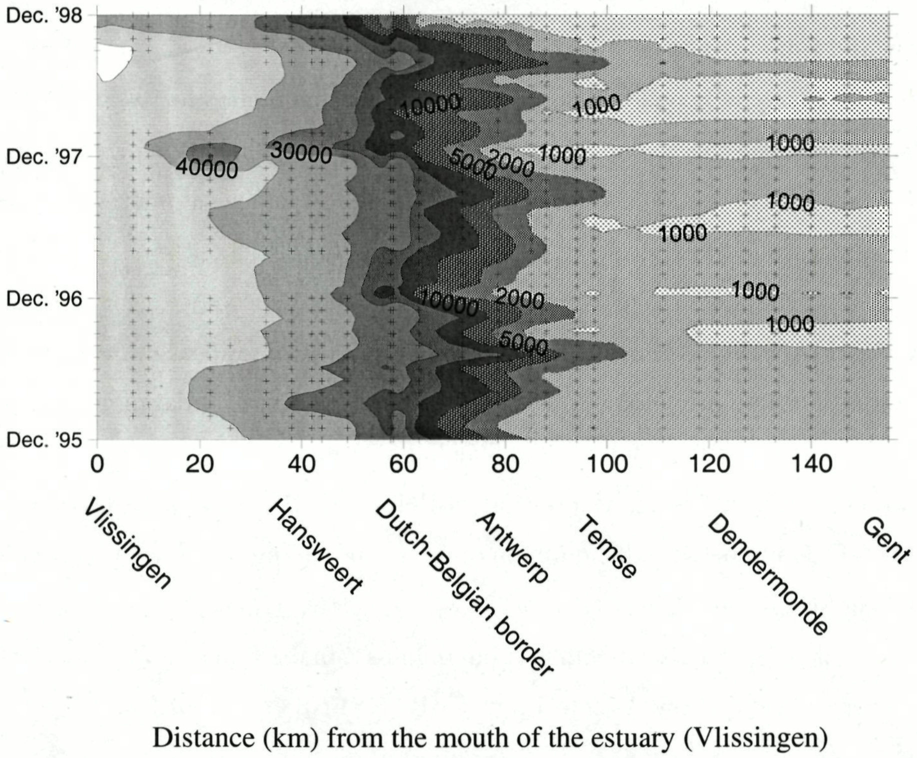


Figure 1.5. Spatio-temporal variation in specific conductivity (μS cm^{-1}) in the Schelde estuary in the period 1996-1998 (after Van Damme et al. 1999).

The zone between Antwerpen and the Rupel is an oligohaline zone. The fluvial estuary, upstream from the Rupel (km 90), is the fresh water tidal zone.

The spatio-temporal evolution in salt content is very sensitive to the seasonal change in river discharge and to a lesser extent to the fortnight tidal oscillation, which is of smaller amplitude. Salinity-shifts over a distance of 20 km are normal between seasons, as indicated by the changes in specific conductivity along the estuary in the period 1996-1998 (Fig. 1.5).

Maximum turbidity zone

Temperate, well-mixed, tidal estuaries are generally characterised by the presence of a maximum turbidity zone (MTZ) in the region of low salinity. The MTZ consists of an area where a large amount of cohesive sediments are accumulated and where these sediments are continually deposited and resuspended by the tidal flow. The distribution of suspended matter is influenced by a range of interrelated processes (e.g. temperature and biological activity, fresh water discharge and salinity, hydrodynamic conditions and turbulence, mineralogical composition, chemical conditions, aggregation and flocculation). In the Schelde estuary the turbidity maximum is situated at about 110 km from the mouth during dry periods and at about 50 km during wet periods (WOLLAST & MARIJNS 1981). Two maximum turbidity zones might be observed, one at the freshwater/seawater interface, and a second one originating from tidal asymmetry. More details on the MTZ can be found in BAEYENS et al. (1998), FETTWEIS et al. (1998) and HERMAN & HEIP (1999a,b).

The combination of favourable hydrodynamic conditions, several fine suspended matter sources, and the flocculation process, led in the salinity zone 2-10 psu to a bottom sediment that contains locally a high percentage of fine material (fine sand to mud, sometimes even a non-compacted, mobile hyperpycnal or fluid mud layer) (BAEYENS et al. 1998). Bottom sediments of the Westerschelde consist of sand (coarse, medium-coarse and medium-fine) except on the tidal flats.

Water quality

Due to high input of allochthonous organic matter and nutrients in the upper and freshwater tidal estuary, microbial activities are intense and oxygen depletion occurs frequently. Under unfavourable conditions, i.e. high temperatures and low river flows, the entire upper estuary could be anoxic in the late seventies (VAN DAMME et al. 1995). Because of ongoing wastewater treatment, dissolved oxygen concentrations increased during the eighties, and this improvement continues in the 1990's (VAN DAMME et al. 1995; VAN ECK et al. 1998). However, oxygen conditions are still low in the upper estuary, especially during summer (Figure 1.6). Oxygen conditions improve considerably towards the Dutch/Belgian border, and in the Westerschelde the water column becomes fully oxygenated.

Still an important source of pollution remains, as the city of Brussel still discharges untreated wastewater through the Zenne and Rupel in the Schelde estuary. In 2000 a first wastewater treatment plant will come into operation, a second one is tendered.

The huge amount of respiration suggests a heterotrophic system (HEIP et al. 1995). Indeed, annual gross bacterial production exceeds net primary production, even in the marine part, although differences there become rather small (GOOSEN et al. 1995, 1999)

The improvement in water quality resulted in a first recovery of fish live in the Zeeschelde, mainly near the Dutch/Belgian border (e.g. MAES et al. 1998a, 1998b).

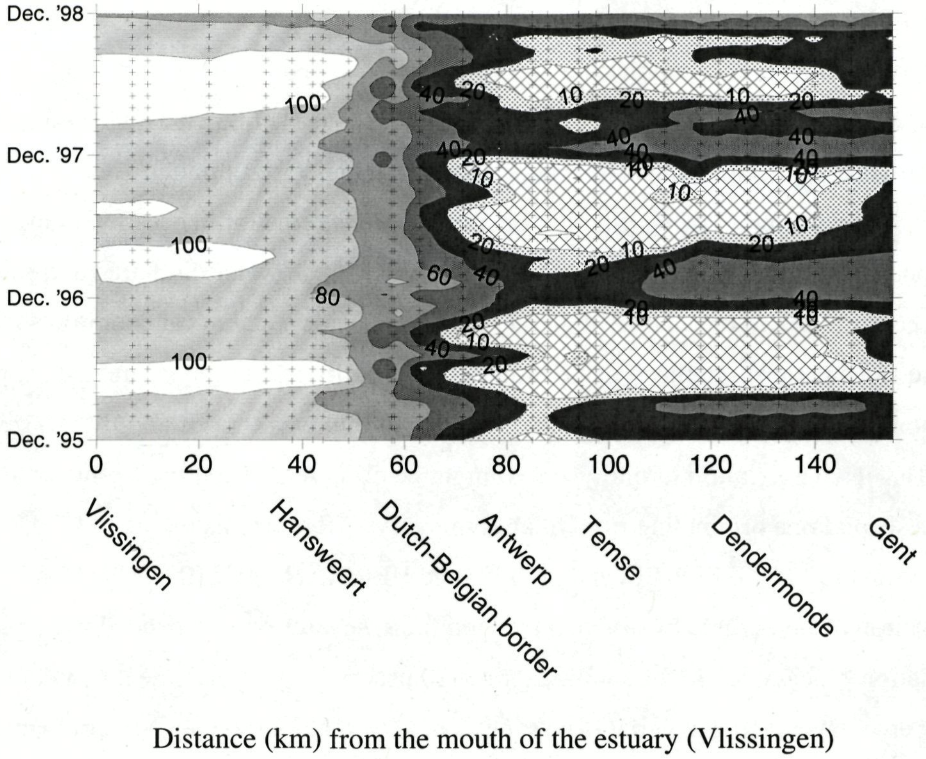


Figure 1.6. Spatio-temporal variation in percentage of oxygen saturation in the Schelde estuary in the period 1996-1998 (after Van Damme et al. 1999).

Human impacts

Despite the Schelde estuary is the only estuary left with a free connection to the North Sea in the Delta area of southwestern Netherlands, preserving its unique salinity gradient, human activities have had tremendous impact on the Schelde ecosystem.

In the past 200 years 150 km^2 of tidal area were lost due to land reclamation. The last decade still between 13-16% of the total surface of the Schelde estuary was lost, which was mainly due to loss in intertidal area. Until recently, the Schelde estuary (Westerschelde) was mainly seen as the maritime access to the harbour of Antwerpen. The harbour of Antwerpen, one of the biggest in Europe, is still expanding. Most of this industrialisation occurs in the surrounding valley, but in the last decade also harbour expansion was realised within the estuary itself. Two container terminals were built near the Dutch/Belgian border, and a new tidal container dock is planned.

To guarantee a minimum depth for the ships to enter the harbour of Antwerpen, hugh amounts need to be dredged (yearly average 10-12*10^6 m^3). To improve the access to the harbour, a further deepening program has been proposed, which will increase the dredging activities by more than 50 %. The deepening of the estuary altered the surface distribution of channel bottom, shallow water areas, sandbanks, mudflats en tidal marshes. Side channels shrinked. Flats became more streamlined and their edges steepened by erosion (VROON et al. 1997).

Besides the huge amounts of nutrients and organic carbon that are discharged into the estuary, also elevated concentrations of micropollutants such as heavy metals, PAHs, PCBs and organochlorine pesticides are observed, both in the water column as in the sediments (e.g. VAN ECK & DE ROOIJ 1993; VAN ZOEST & VAN ECK 1993; ZWOLSMAN & VAN ECK 1993; BAEYENS et al. 1998; VAN ECK et al. 1998; ZWOLSMAN 1999)

As a consequence of not being closed of from the sea, safety constructions (dikes) were built along the whole estuary. Along the Zeeschelde the SIGMA-plan is still ongoing (GRARE 1998).

Habitats at present

Table 1.2 gives the surface of the intertidal (tidal flats and marshes) and the subtidal zone along the Schelde estuary. Tidal flat surface was by far the largest in the Westerschelde, and area 3 is also characterized by the presence of the marsh of Saeftinghe, one of the largest brackish marshes in NW-Europe. In the Zeeschelde a relatively large surface of freshwater tidal marshes is present, which is on a European scale a very rare habitat.

1ha=0,01km2

Table 1.2. Surface area (ha) of the intertidal zone (tidal flats and marshes) and subtidal zone in the different areas along the Schelde estuary. Areas 1-3: Westerschelde. Areas 4-6: Zeeschelde.

Area	Classification	Tidal flats	Marsh	Subtidal	TOTAL
1	lower/middle (polyhaline)	2898	51	10195	13144
2	Middle/inner (poly/mesohaline)	2456	76	6564	9069
3	Inner (α-mesohaline)	3020	2383	3342	8745
4	Inner/upper (β-meso/oligohaline)	514	181	2005	2700
5	upper/tidal fresh (oligohaline/limnetic)	196	297	948	1441
6	Tidal fresh (limnetic)	9,5	30,5	250	290
TOTAL	whole estuary	9093,5	3018,5	23304	35389

8374 2510 20101

84 25 200

Management in the Schelde estuary

As in many other European estuaries, water quality in the Schelde estuary was already bad in the early fifties (VAN MEEL 1958), and in the sixties and seventies the situation deteriorated further. Without exaggeration, it can be stated that the Zeeschelde and its major tributaries were merely an open sewer in the sixties and early seventies. Growing awareness of environmental problems prompted legislation in The Netherlands and Belgium, aiming to reduce the industrial and domestic waste water discharges. As a result, the water quality of the Schelde estuary started to improve (VAN DAMME et al. 1995; VAN ECK et al. 1998). Despite this growing awareness for a better water quality, management in the Schelde estuary was mainly dictated by the economic development of the port of Antwerpen and by the safety considerations. Also management was mainly sectoral, with no real coordination between the different member states of the Schelde basin.

It is only recently that it is recognized that ecological recovery of the estuary must be achieved in the framework of integrated water management (International Schelde Symposium 1991, 1995, 1998). At the moment, both Belgium (Flanders) and The Netherlands are working together on a Long Term Vision for the Schelde estuary. Several management plans are in concept (e.g. VAN DEN BERGH et al. 1999), and scientific research is being incorporated within the ideas of integrated water management. For instance, ideas are being worked out to integrate both the safety considerations as the structural and functional biodiversity of the estuarine ecosystem (e.g. controlled inundation areas as protection against flooding can be designed in such a way that these areas also function as real intertidal areas with a daily tidal rhythm). The OMES project (Onderzoek Milieu-Effecten Sigmaplan), a multi-disciplinary research project, aims at building an ecosystem model for the Schelde estuary, in which the different management strategies can be evaluated (MEIRE et al. 1997).

Further reading

The Schelde estuary is one of the most extensively studied and well-documeted estuaries in NW Europe. General descriptions of the Schelde estuary have been published by e.g. SAEIJS (1977), HEIP (1988, 1989), WOLLAST (1988), BAEYENS et al. (1998) and VAN DAMME et al. (1999, subm.). In MEIRE & VINCX (1993), HEIP & HERMAN (1995) and HERMAN & HEIP (1999) many papers deal with morphological, physical, chemical and ecological aspects of the Schelde estuary.

Chapter two

The benthic macrofauna along the estuarine gradient of the Schelde estuary

T. Ysebaert, P.M. Meire, D. Maes and J. Buijs

Abstract

The intertidal benthic macrofauna of the Schelde estuary (The Netherlands and Belgium) was sampled in late autumn of 1990 at 50 stations along the whole salinity gradient (between Vlissingen and Dendermonde), including the freshwater tidal part. All stations were situated in sheltered areas with a relatively muddy sediment.

Species richness, diversity and total biomass of the benthic macrofauna decreased along the salinity gradient from Vlissingen to Dendermonde, while total density showed no clear trend. Especially the oligohaline and freshwater tidal part of the Schelde estuary was characterised by a very impoverished benthic community, composed only of Oligochaeta. No other species (freshwater, marine or brackish) was observed in this part of the estuary. The marine part had a more diverse macrozoobenthos structure than that of the brackish part. Species found only in the marine zone are *Cerastoderma edule*, *Tharyx marioni*, *Eteone longa*, *Nephtys hombergii* and *Capitella capitata*. In the brackish part of the estuary, *Corophium volutator* was a typical, dominant species. However, a lot of the dominant species were common in both the marine and brackish part of the Schelde estuary (e.g. *Heteromastus filiformis*, *Pygospio elegans*, *Nereis diversicolor*, *Macoma balthica*).

The observed gradient in species composition and dominance is compared with some other European estuaries. The marine and brackish part of the Schelde estuary is quite similar to other European estuaries. The freshwater tidal part, however, was more impoverished.

Introduction

Estuaries and the nearby coastal zones are characterised by steep gradients in chemical, physical and biological features. However, many studies have been restricted to small parts of these gradients and are mainly focussed on the marine or brackish part of the estuary. In most ecological studies on estuarine ecosystems, research on the tidal freshwater environments, which are essential parts of an estuary, has been neglected. ODUM (1998) attributed this phenomenon to the fact that limnologists ignored tidal freshwater environments because of the presence of oceanic tidal influence, and marine ecologists neglected these areas because they contain freshwater and are inhabited primarily by freshwater organisms.

This study deals with the occurrence of macrozoobenthos along the whole estuarine gradient in the Schelde estuary, including the freshwater tidal part. The tidal part of the river Schelde represents one of the few remaining European estuaries that are characterised by a natural salinity gradient from salt water, over brackish water to freshwater. As such, the Schelde estuary has a unique ecological value. Unfortunately, this estuary is also one of the most polluted estuaries, due to large industrial, agricultural and domestic waste effluents (WOLLAST 1988; LUDIKHUIZE 1989; HUPKES 1990; VAN ECK et al. 1991). Also extensive dredging activities and expanding harbour activities have a large morphological impact on the Schelde ecosystem (CLAESSENS et al. 1991; PIETERS et al. 1991).

Freshwater and marine benthic macrofauna have been identified as a suitable ecological group for monitoring and detecting the effects of stress and pollution (PEARSON & ROSENBERG 1978; BAYNE et al. 1988; GRAY 1989) and community structure of estuarine macrobenthos has been used as an indication of water and sediment quality (WARWICK 1986; WARWICK et al. 1987; AUSTEN et al. 1989; HARREL & HALL 1991). A survey of the benthic community along the Schelde estuary may therefore not only give valuable information on the ecological diversity along the whole estuarine gradient, but also on the present pollution status of the estuary. The objectives of this study were to characterise the intertidal benthic communities along the whole estuarine gradient of the Schelde estuary.

Materials and methods

Study area

The river Schelde has its source in Saint-Quentin (France) and it flows into the North Sea after 350 km. The influence of the tide is perceptible up to Gent (Belgium), where it is stemmed by a weir. The total length of the Schelde estuary between Gent and Vlissingen is 160 km (Figure 2.1). The width is about 50 m at Dendermonde, 250 m at Temse, 500 m at Antwerpen and 4.5 km at Vlissingen. The maximal width is 7.8 km. The mean tidal range increases from 3.8 m at Vlissingen, 4.5 m at Hansweert and 4.9 m at Antwerpen, to a maximum of 5.2 m at Kruibeke; it diminishes more upstream to about 2 m near Gent.

Upstream the Dutch/Belgian border, the upper estuary (called Zeeschelde) is characterised by a more or less single tideway. Brackish water and freshwater tidal marshes and mudflats are situated along the dikes. However, the width of the intertidal area is generally less than a few tens of meters. Only at a few locations there are larger mudflats and marshes. Downstream the Dutch/Belgian border,

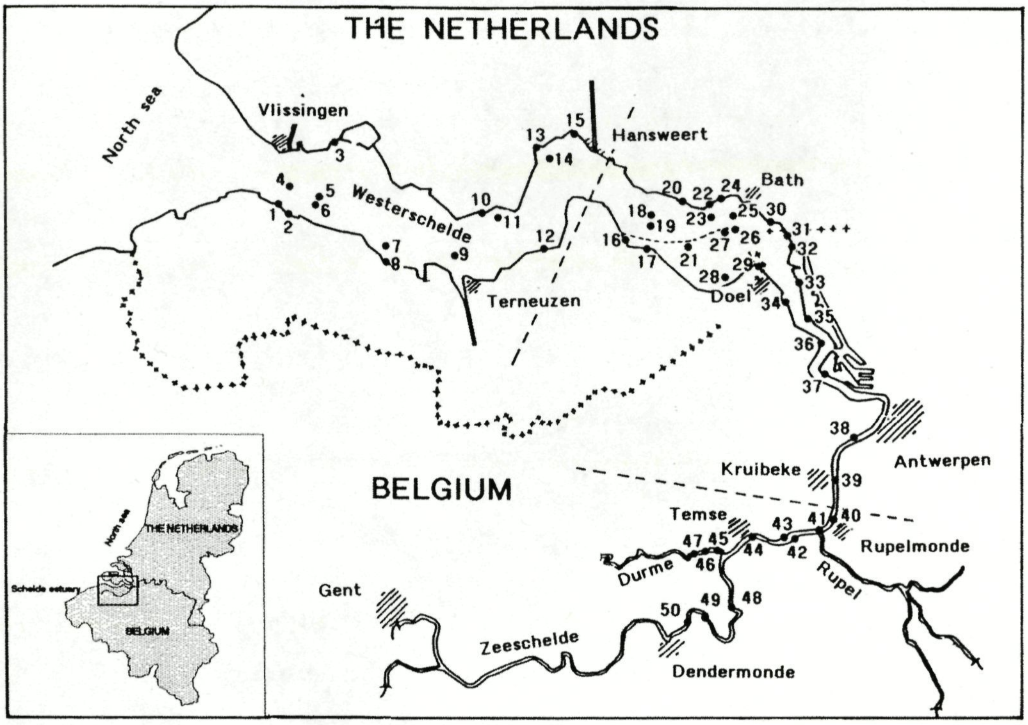


Figure 2.1. The Schelde estuary with the locations of the sampling stations (1-50).

the more or less single tideway changes into a wide bed, characterised by large intertidal sand flats with meandering channels and gullies, the so-called Westerschelde (Figure 2.1). Brackish water and saltwater marshes and mudflats are situated at the outer edges, often several hundreds of meters wide.

The sediment of the Schelde estuary ranges from sandy to clayish, depending on hydrodynamic forces and sediment discharges (OENEMA et al. 1988). In the channels and gullies as well as on the sand flats, the sediment is mainly sandy. In the more sheltered areas the sediment is muddy. Sandy sediment is found far upstream in the estuary. Mud characterises the sediment of the freshwater intertidal area.

The freshwater input of the Schelde amounts on average 100 m^3 s^{-1}. Seasonal fluctuations in drainage range from high values during winter (average 180 m^3 s^{-1}, maximum 500-600 m^3 s^{-1}) to low values during summer (average 50 m^3 s^{-1}, minimum 10 m^3 s^{-1} or less). Quantitatively, the river discharge of 5*10^6 m^3 per tide is negligible compared to the mean tidal flood volume of 1100*10^6 m^3 per tide near Vlissingen. This results in a very well mixed estuary with a relatively large transition zone from salt to freshwater, as reflected in the chlorinity gradient (Figure 2.2). The chlorinity decreases from *c.* 16.6 g Cl$^-$ l^{-1} near Vlissingen to *c.* 4.5 g Cl$^-$ l^{-1} at the Belgian-Dutch border; near the tributary Rupel the water becomes fresh (< 0.3 g Cl$^-$ l^{-1}). Generally spoken, the whole estuary can be divided into three main zones: a marine (polyhaline) zone between Vlissingen and Hansweert, a brackish (mesohaline and oligohaline) zone between Hansweert and the tributary Rupel, and a freshwater zone (limnetic zone) more upstream. Seasonal and annual fluctuations in chlorinity may be large, especially in the brackish zone (variations up to 10 g Cl$^-$ l^{-1} occur on a single location). The

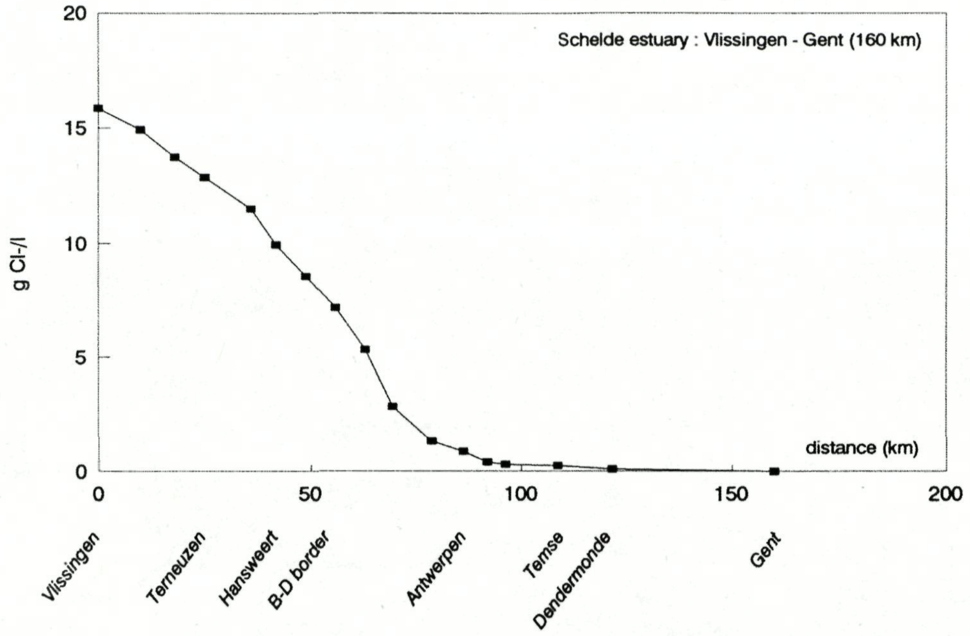


Figure 2.2. Mean annual chlorinity gradient in the Schelde estuary.

water column is well mixed because of the tidal movement; the vertical chlorinity gradient is less than 0.2%.

The Schelde estuary is heavily contaminated with heavy metals and organic micropollutants and experiences a huge organic matter input. The concentrations of PCBs, PAHs and cadmium are high in the freshwater and brackish part of the estuary. Most of the pollutants behave conservatively and concentrations generally decrease when salinity increases, as a result of the mixing of riverine and marine particulates (VAN ZOEST & VAN ECK 1990; VAN ECK et al. 1991). The large organic matter load causes oxygen depletion in the Schelde river and in the upper estuary. The upper estuary is often anoxic, especially in the summer period (ANONYMOUS 1990; VAN ECK et al. 1991). These (near-) anoxic conditions may prevail as far as the Dutch-Belgian border. Table 2.1 gives some physical and chemical characteristics of the water column along the whole estuarine gradient.

Sampling and laboratory analysis

The macrozoobenthos was sampled in the autumn of 1990 (September/October) at 50 sampling stations situated between Vlissingen and Dendermonde (Figure 2.1). All stations were situated in the intertidal zone, especially in sedimentation areas, at approx. 1.5 m above mean low water. On each station 15 small cores (diameter 4.5 cm) were taken to a mean depth of 25 cm and 5 large cores (diameter 15 cm) to a mean depth of 40 cm. The large cores were sieved in the field through a 3 mm mesh. All benthic samples were preserved in 4% neutralised formalin. Samples for sediment analysis were taken using a PVC core of 6.7 cm diameter to a depth of 10 cm. 6-8 cores taken per station, were mixed and preserved in a refrigerator at 4°C.

In the laboratory the samples of the small cores were sieved through a 1 mm mesh and sorted after

Table 2.1. Physical characteristics and water quality parameters (annual average of 1990 with standard errors) along the whole estuarine gradient at Vlissingen (1), Terneuzen (2), Hansweert (3), Dutch-Belgian border (4), Kruibeke (5), Temse (6), Dendermonde (7) and Melle (8). Data from 'Rijksinstituut voor Integraal Zoetwaterbeheer en Afvalwaterzuivering' (station 1–4: c. 12 observations per year), and 'Ministerie van Volksgezondheid en Leefmilieu, Instituut voor Hygiëne en Epidemiologie' (station 5–8: c. 5 observations per year).

Location	1	2	3	4	5	6	7	8
Distance (km)	160	137	124	111	78	63	40	6
Tidal range (m)	3.8	4.2	4.5	4.9	5.2	5.1	3.7	2.0
Width (m)	5000	5500	4300	2500	350	250	100	50
Chlorinity (g Cl^{-} $^{-1}$)	17.8 ± 0.1	14.9 ± 0.3	11.3 ± 0.4	6.0 ± 0.5	0.8 ± 0.4	0.4 ± 0.2	0.2 ± 0.1	0.1 ± 0.01
O_2 Water (mg^{-1})	8.9 ± 0.3	8.5 ± 0.3	8.1 ± 0.3	3.9 ± 0.5	1.2 ± 0.7	1.3 ± 0.8	1.3 ± 1.1	1.4 ± 0.7
BOD_5 Water (mg^{-1})	0.7 ± 0.2	0.9 ± 0.3	0.6 ± 0.2	2.6 ± 0.3	3.7 ± 0.5	6.8 ± 1.5	8.0 ± 1.8	6.4 ± 0.6
$NH4^+$ (mg N^{-1})	0.09 ± 0.01	0.14 ± 0.02	0.14 ± 0.05	0.83 ± 0.20	5.97 ± 1.66	7.66 ± 2.13	9.84 ± 2.99	11.3 ± 3.56
$NO2^-$ (mg N^{-1})	0.03 ± 0.01	0.05 ± 0.01	0.07 ± 0.01	0.15 ± 0.02	0.1 ± 0.05	0.1 ± 0.06	0.14 ± 0.10	0.21 ± 0.13
$NO3^-$ (mg N^{-1})	0.88 ± 0.15	1.58 ± 0.21	2.89 ± 0.31	4.56 ± 0.35	1.70 ± 1.05	1.34 ± 1.08	3.51 ± 1.42	2.23 ± 1.26
o-PO4 (mg P^{-1})	0.11 ± 0.02	0.19 ± 0.01	0.26 ± 0.01	0.35 ± 0.02	0.85 ± 0.16	1.23 ± 0.35	1.54 ± 0.37	1.95 ± 0.49

staining with 0.02% Rose Bengal. The organisms were identified to species level, except in the genera *Spio* and *Polydora*, in *Nemertini* and in *Oligochaeta*, and counted. The large cores were only used for estimation of density and biomass of large and deep living species (*e.g. Arenicola marina, Mya arenaria).* The ash-free dry weight (AFDW) biomass was measured by drying all specimens at 105°C for 12 h and ashing at 500°C. Surface sediment characteristics (median particle size, mud content (fraction < 63 μm), organic matter and pH) at all stations were determined by standard methods.

Water quality characteristics were obtained from fixed locations near the sampling stations (data from 'Rijkswaterstaat' (Dutch part) and IHE (Belgian part) (See Table 2.1)

Data analysis

Data were first organised into a samples by species matrix. Species diversity was measured using the Shannon-Wiener function H' (PIELOU 1996). All statistics were performed with the statistical package SYSTAT (WILKINSON 1990). Abiotic and biotic characteristics along the longitudinal gradient were fitted with a smoothing line, using the option LOWESS of the SYSTAT package. It smoothes by running along the X values and finding predicted values from a weighted average of nearby Y values.

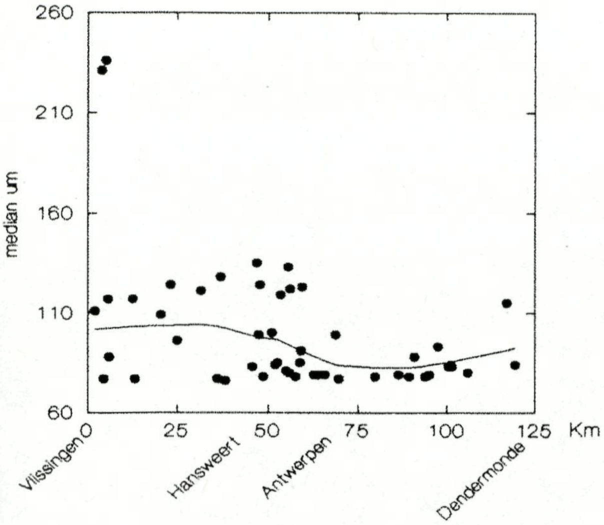


Figure 2.3. Median particle size of sediment (μm) at the sampling stations.

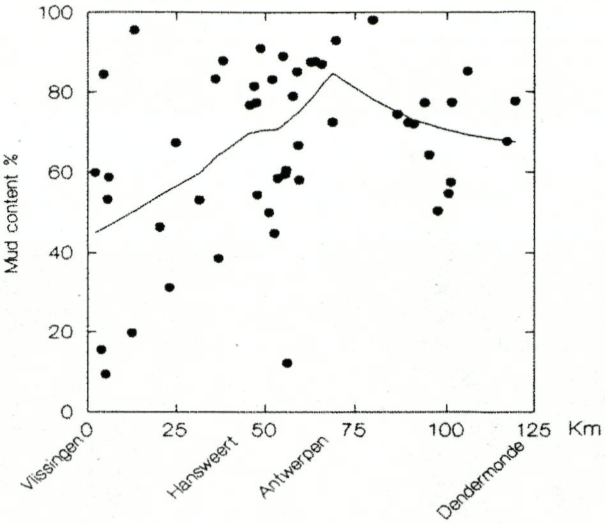


Figure 2.4. Mud content (fraction < 65 μm) of sediment at the sampling stations.

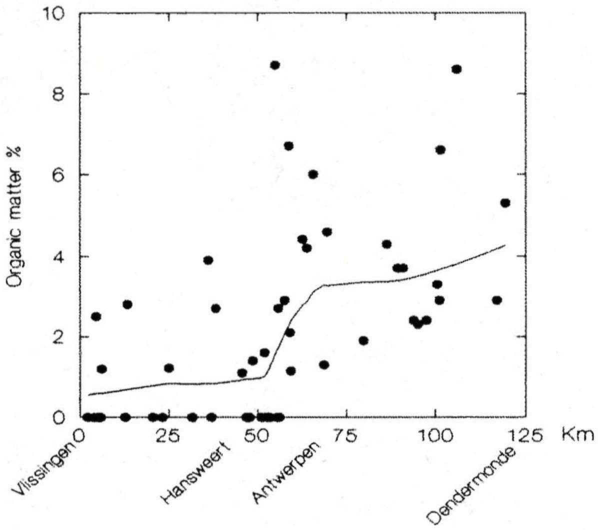


Figure 2.5. Organic matter content (%) of sediment at the sampling stations.

Sorensen's index (SORENSEN 1948) of similarity was calculated to compare overlap of species between each pair of subareas using the formula

$$S = \frac{2C}{A+B}$$

where C is the number of species common to both subareas, and A and B are the number of species occurring in each subarea.

The between-subarea similarity matrix was then projected as a series of curves plotted for subareas ordered along an environmental (*i.e.* salinity) gradient, the so-called coenocline similarity projection (CSP, see BOESCH 1977). The subareas were defined by the longitudinal salinity gradient and consist of 4 to 6 stations.

Table 2.2. List of observed macrobenthic species and their frequency of occurrence (%) in the sampling locations. Trophic position: DF = Deposit Feeders; FF = Filter Feeders; O = Omnivores; P = Predators.

Species name	Code	Occurrence
Annelida		
Anaitides mucosa (P)	ANAI MUCO	2
Arenicola marina (DF)	AREN MARI	14
Capitella capitata (DF)	CAPI CAPI	20
Eteone longa (P)	ETEO LONG	38
Heteromastus filiformis (DF)	HETE FILI	58
Nephtys caeca (P/O)	NEPH CAEC	2
Nephtys hombergii (P/O)	NEPH HOMB	22
Nereis diversicolor (O)	NERE DIVE	62
Nereis succinea (O)	NERE SUCC	10
Oligochaeta (DF)	OLIG	84
Polydora spec. (DF)	POLY SPEC	32
Pygospio elegans (DF)	PYGO ELEG	58
Scolelepis squamata (U)	SCOL SQUA	2
Scoloplos armiger (DF)	SCOL ARMI	6
Spio spec. (DF)	SPIO SPEC	18
Tharyx marioni (DF)	THAR MARI	24
Mollusca		
Cerastoderma edule (FF)	CERA EDUL	34
Ensis minor (FF)	ENSI MINO	12
Hydrobia ulvae (DF)	HYDR ULVA	26
Macoma balthica (DF)	MACO BALT	62
Mya arenaria (FF)	MYA AREN	12
Mysella bidentata (FF)	MYSE BIDE	6
Mytilus edulis (FF)	MYTI EDUL	2
Retusa obtusa (P)	RETU OBTU	2
Scrobicularia plana (DF)	SCRO PLAN	32
Tellina fabula (DF)	TELL FABU	4
Arthropoda		
Bathyporeia pilosa (DF)	BATH PILO	10
Carcinus maenas (O)	CARC MAEN	4
Corophium arenarium (DF)	CORO AREN	10
Corophium volutator (DF)	CORO VOLU	30
Crangon crangon (P)	CRAN CRAN	18
Cyathura carinatha (U)	CYAT CARI	10
Gastrosaccus spinifer P)	GAST SPIN	2
Sphaeroma rugicauda (DF)	SPHA RUGI	2
Nemertini		
Nemertini spec. (P)	NEME SPEC	6

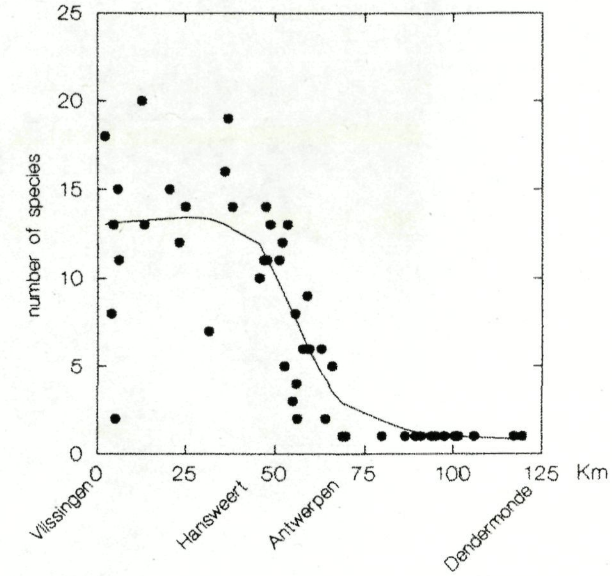


Figure 2.6. Number of species per sampling station.

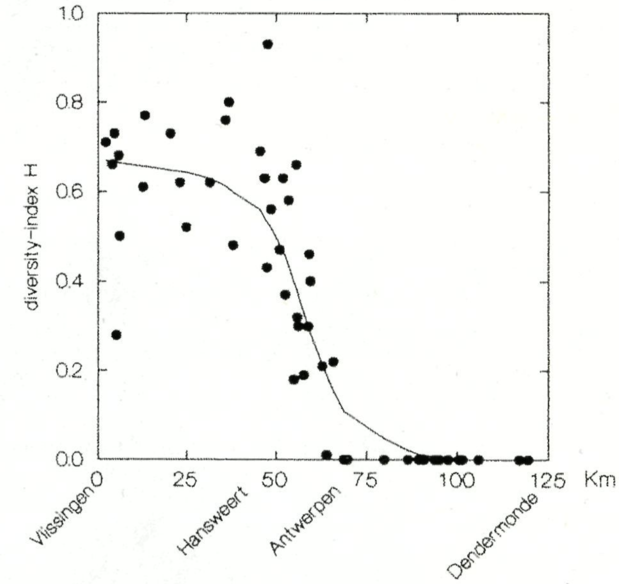


Figure 2.7. Species diversity (Shannon-Wiener function H') per sampling station.

Numerical classification (TWINSPAN, *see* HILL 1979), based on species abundance, was used to assess multispecies patterns. Only species that were observed in five or more stations were used for the analysis. Two stations (3 and 36) were not used in the analysis. All absolute abundances were transformed by x = log (x+1). Cut levels used in the TWINSPAN analyses were : 1.00, 2.00, 3.00, 4.00, 5.00, and 6.00.

Table 2.3. Correlation coefficients (Spearman's rank) between some environmental variables and biotic characteristics (N = 50). * = $p < 0.01$; ** = $p < 0.005$; NS = not significant.

Environmental variable	Species	Density	Biomass	H'
Water chlorinity	.85 **	.19 NS	.58 **	.66 **
Water oxygen content	.86 **	.21 NS	.61 **	.69 **
Water BOD	-.86 **	-.18 NS	-.60 **	-.62 **
Median grain size	.25 NS	-.18 NS	-.08 NS	.22 NS
Organic matter	-.54 **	.01 NS	-.21 NS	-.43 *
Fraction <63 µm	-.14 NS	.01 NS	.04 NS	-.18 NS

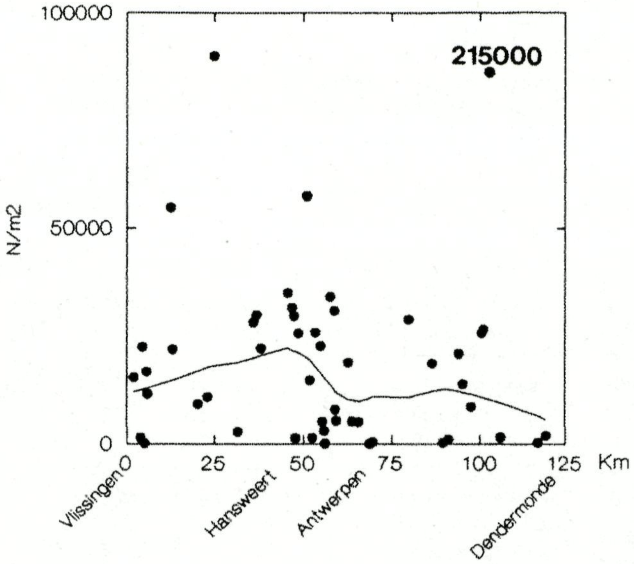


Figure 2.8. Mean total population density (Nm^{-2}) per sampling station.

Results

Sediment characteristics

The dominant sediment type throughout the intertidal zone of the Schelde estuary, sampled in this study, was muddy sand (median grain size between 75-125µm). The variation in median grain size of the stations was more pronounced in the marine part (Figure 2.3). Two stations (3 and 4) in the mouth of the estuary had a much coarser sediment with a median grain size of approx. 235µm. The mud content of the sediment was highly variable, especially in the marine part (Figure 2.4). Highest values occurred in the brackish part and remained relatively high in the freshwater tidal part.

The organic matter content showed also large variation, but a clear increasing trend towards the freshwater tidal part was observed (Figure 2.5). It is stressed again that especially sedimentation areas were chosen for this study (see Materials and Methods).

Benthic fauna

Diversity

Of the 35 species observed, almost 50% were annelids, 28% molluscs and 23% arthropods (Table 2.2). Taking the thropic structure into account, 23% of the observed number of species were predators, 14% filter feeders, and 6% omnivores; the remaining and dominant part (57%) were deposit feeders. Oligochaeta were present at almost every station. The annelids *Nereis diversicolor, Heteromastus filiformis* and *Pygospio elegans* and the mollusc *Macoma balthica* were also very common (>50%). Seven species were observed only once.

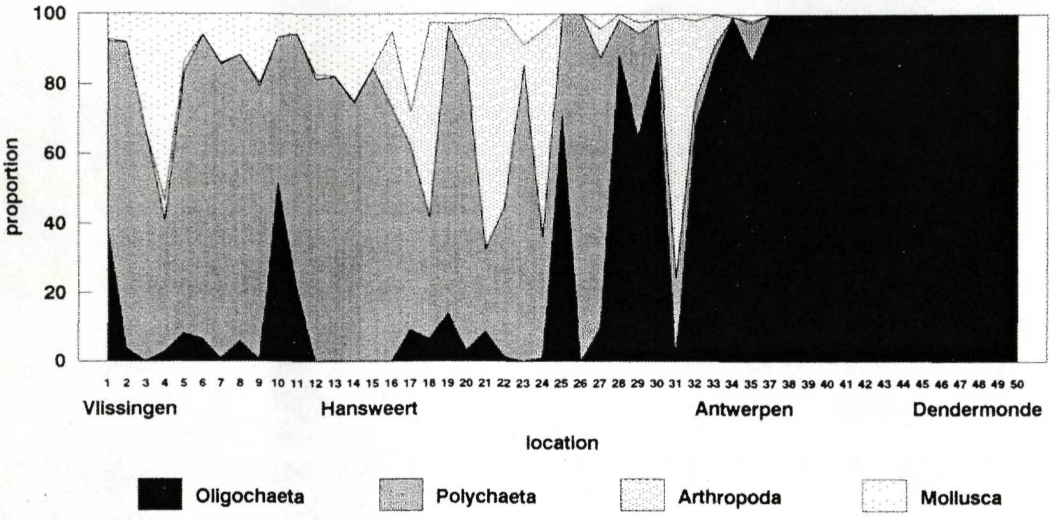


Figure 2.9. Contribution (%) of the different taxa to the total density at each sampling station.

The number of species and the diversity H' showed a significant positive correlation with chlorinity and oxygen content, and a significant negative correlation with BOD. To a less extent the number of species also showed a correlation with organic matter (Table 2.3). The number of species at each station along the longitudinal gradient between Vlissingen and Dendermonde is shown in Figure 2.6.

The mean number of species per sampling station remained relatively constant up to Hansweert, but clearly declined in the brackish zone. Upstream of Antwerpen, only *Oligochaeta* occurred. The same pattern was shown by the diversity index H' (Figure 2.7). At one station (36) no benthic invertebrates were observed.

Population density

The mean total population density (± SE) of all sampling stations was 21000 ± 4600 ind m^{-2}, ranging from 0 ind m^{-2} (station 36) to a maximum density of 2.16*10^{5} ind m^{-2} (station 47). Six stations had densities less than 1000 ind m^{-2}. Densities were mainly determined by annelids (84% of the total density), especially Oligochaeta (56% of the annelids), *Pygospio elegans* (22%) and *Heteromastus filiformis* (12%). To a lesser extent arthropods, notably *Corophium volutator* (90% of the arthropods) and molluscs, notably *Cerastoderma edule* (48% of the molluscs), *Hydrobia ulvae* (21%) and *Macoma balthica* (16%) also contributed to the total densities. Deposit feeders were dominant in all sampling stations and represented 95% of the total density.

The total density along the longitudinal gradient between Vlissingen and Dendermonde is summarised in Figure 2.8. A large variation was observed with no clear trend along the estuarine gradient; high and low density values were randomly distributed. Density did not significantly correlate with the measured abiotic characteristics (Table 2.3). At station 47 a very high density of Oligochaeta was found (2.16*10^{5} ind m^{-2}). However, the relative contribution to the density of the

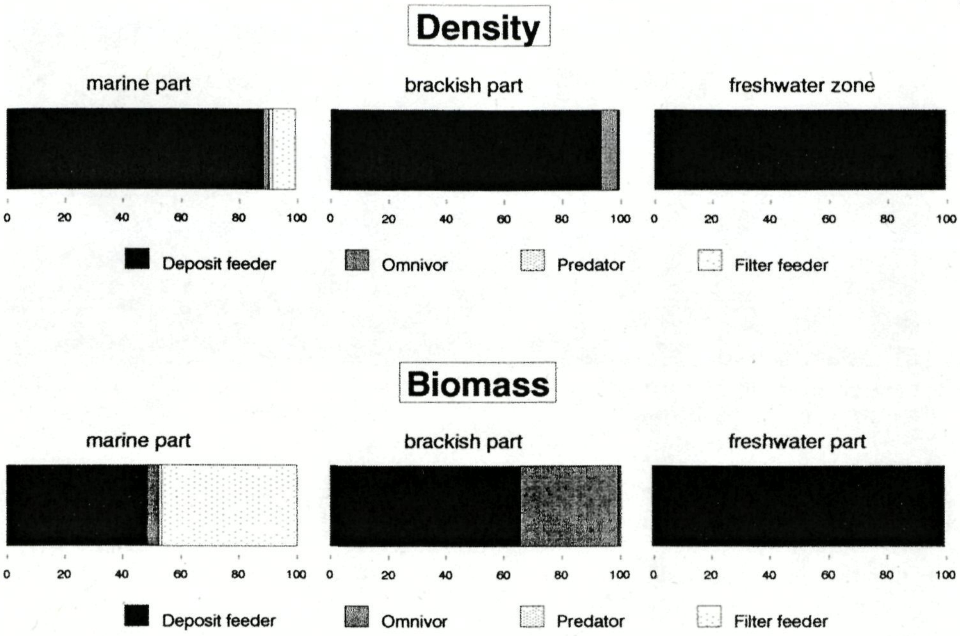


Figure 2.10. Contribution (%) of the different trophic groups to total population density and biomass in the marine, brackish and freshwater part of the Schelde estuary.

different taxa changed markedly from the marine zone, over the brackish zone to the oligohaline-freshwater zone (Figure 2.9). Between Vlissingen and Hansweert, *i.e.* in the marine zone, the macrobenthic densities were mainly determined by dense populations of Polychaeta and to a lesser extent by Mollusca. Between Hansweert and Antwerpen (brackish zone) both Polychaeta and Anthropoda contributed to the macrobenthic densities; at some sampling stations Oligochaeta tended to predominate. Upstream of Antwerpen (oligohaline-freshwater zone) only Oligochaeta were present. Deposit feeders contributed mostly to the density in all three zones along the gradient, although the filter feeder *Cerastoderma edule* in the marine zone and the omnivore *Nereis diversicolor* in the brackish zone were also relatively important (Figure 2.10).

Biomass

The mean total biomass (± SE) of all sampling stations was 21 ± 4.5g AFDW m^{-2}, ranging between 0.0031 and 153.1 g AFDW m^{-2}. Contrary to the population density, biomass was not only determined by annelids (54% of the total biomass), but also by molluscs (44%), due to their high individual biomass. Dominant annelids were *Heteromastus filiformis* (52% of the annelids), *Oligochaeta* (18%) and *Nereis diversicolor (*18%), whereas *Cerastoderma edule* was the dominant mollusc (75% of the molluscs). The latter contributed by far the most to the mean total biomass of the whole study area. The dominant arthropod is *Corophium volutator* (73% of the arthropods).

The total biomass along the longitudinal gradient between Vlissingen and Dendermonde is summarised in Figure 2.11. On the average, there was a gradient from high biomass in the marine and brackish zone to low biomass in the oligohaline-freshwater zone, with a sharp decline at the Dutch-

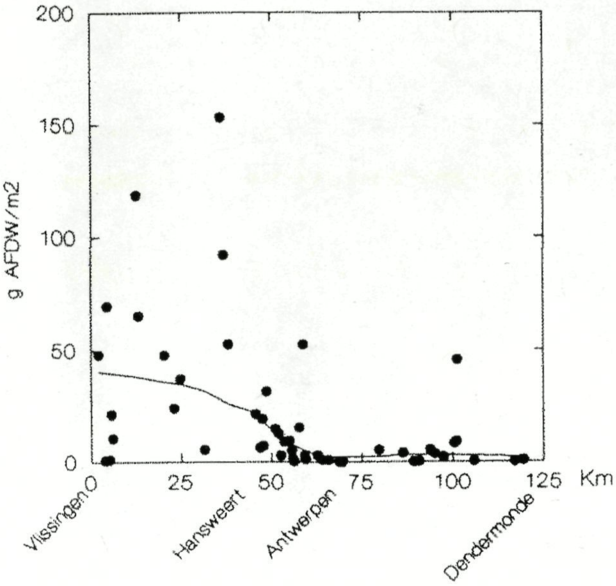


Figure 2.11. Mean total biomass (g AFDW/m^2) per sampling station.

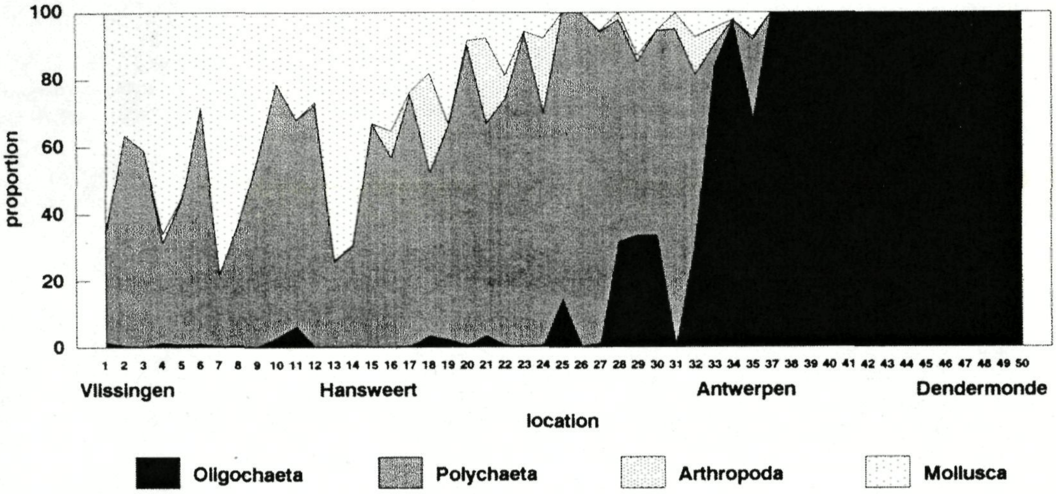


Figure 2.12. Contribution (%) of the different taxa to the total biomass at each sampling station.

Belgian border. Biomass was significantly correlated with all water quality characteristics. No correlations were found with the sediment characteristics. Only at station 47 a relatively high biomass was found (*c.* 50 g AFDW m^{-2}), due to the very high density of Oligochaeta. As with the density, the relative contribution to the biomass of the different taxa changed markedly from the marine zone, over the brackish zone to the oligohaline-freshwater zone (Figure 2.12). Between Vlissingen and Hansweert (marine zone) Mollusca and Polychaeta contributed mostly to the biomass. Between Hansweert and Antwerpen (brackish zone) Polychaeta tended to predominate; Oligochaeta already dominated at some sampling stations (Figure 2.12). Upstream of Antwerpen, Oligochaeta were dominant. Contrary to the density, there was a clear gradient in the trophic position of the organisms contributing most to the biomass (Figure 2.10). Filter feeders, notably *Cerastoderma edule*, and deposit feeders dominated in the marine zone. The brackish zone was dominated by omnivores,

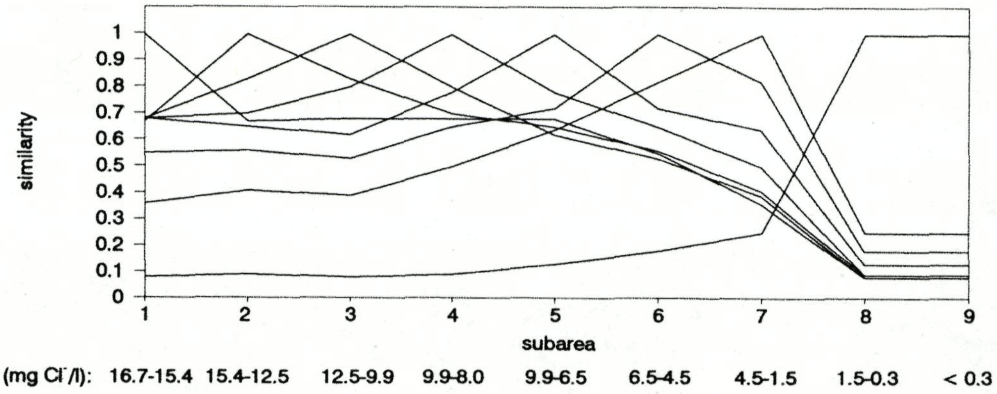
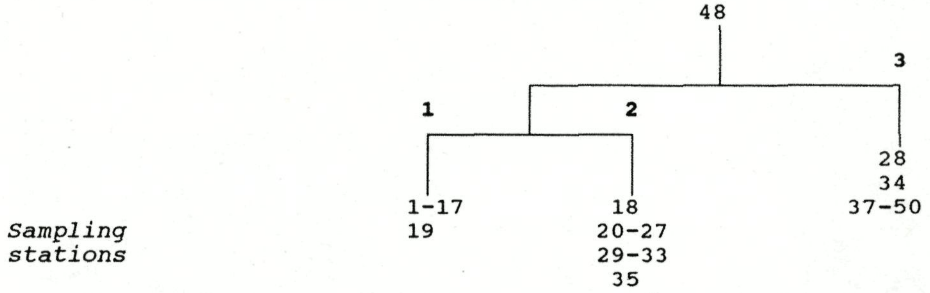


Figure 2.13. Coenocline similarity projections of qualitative similarity (Sorensen's index) along the estuarine gradient. Nine subareas of 4 to 6 sampling stations each are distinguished. Chlorinity range of subareas is indicated.



	1	2	3
Number of taxa	33	22	3
Mean total density *N/m2* *min./max.*	22384 ± 5801 126 - 89883	18527 ± 4002 93 - 57343	23093 ± 1235 31 - 216387
Mean total biomass *g AFDW/m2* *min./max.*	45.4 ± 19.2 0.8 - 153.1	11.1 ± 3.5 0.1 - 52.4	5.5 ± 2.6 0 - 45.5

Figure 2.14. Characterisation of the different station groups, distinguished by a TWINSPAN analysis.

especially *Nereis diversicolor*, and deposit feeders, whereas in the freshwater part only deposit feeders occurred.

Change along the estuarine gradient

The coenocline similarity projections showed a more or less gradual and continual change in assemblage along the estuarine gradient (Figure 2.13). The rate of change in the benthic coenocline of the Schelde estuary was by far the greatest between subarea 7 and 8. Between other subareas, this change was much less pronounced. From this figure it is clear that especially towards the oligohaline zone, the benthic community abruptly changed.

Community structure

Cluster analysis of all stations produced three station groups (Figure 2.14). The first group (group

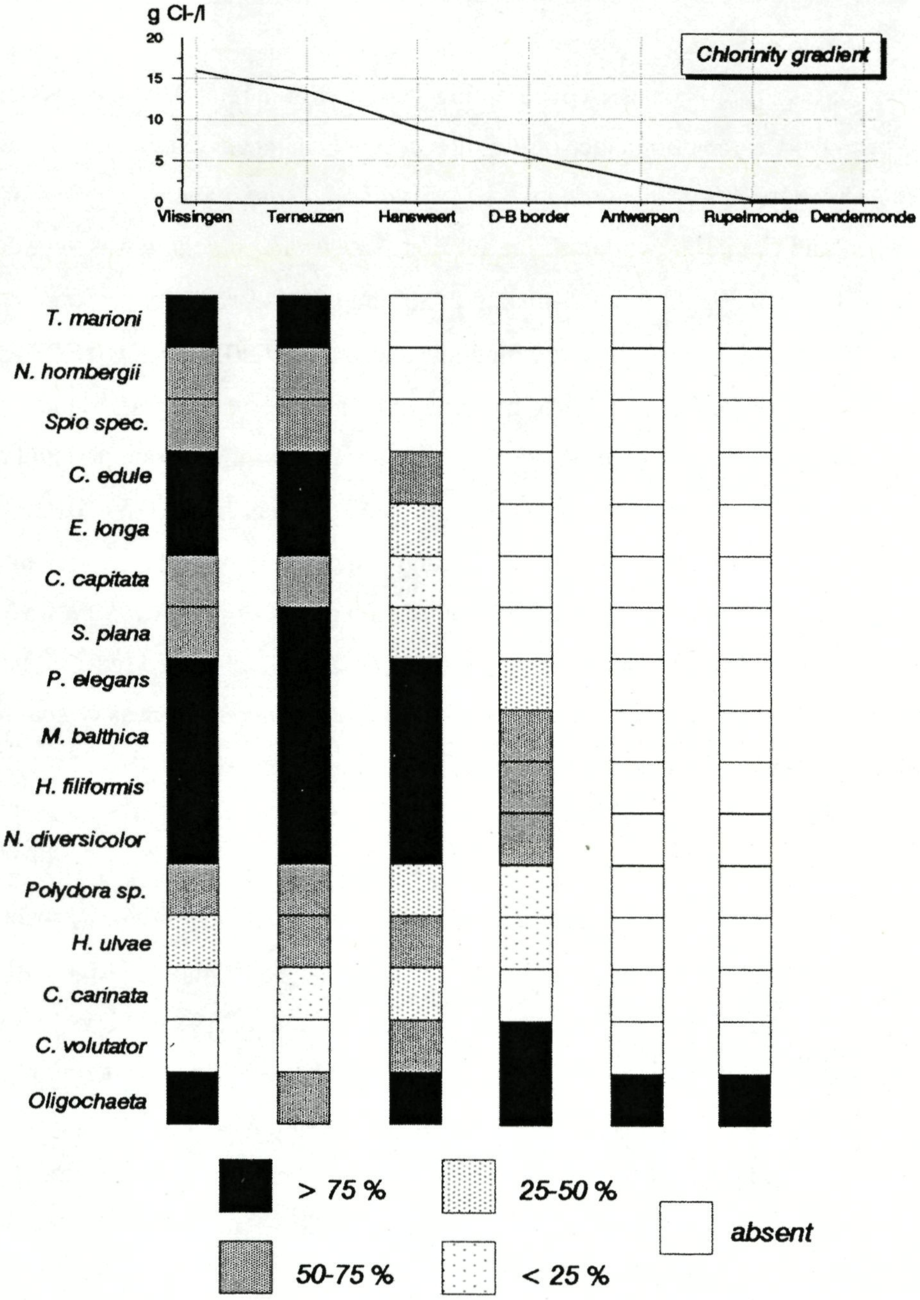


Figure 2.15. Distribution and average constancy of the most dominant species in six subareas along the salinity gradient.

3) includes the stations 37-50, together with stations 28 and 34, and represents the whole freshwater tidal part and the most upstream situated brackish part (oligohaline zone). This community was characterised by a very impoverished benthic fauna with only one taxon dominating, namely Oligochaeta. Oligochaeta were very abundant, resulting in a mean density that was comparable to that of the other two groups, but with a significantly lower mean biomass. In a further division, the remaining stations were separated into group 1, with the marine stations 1-17 and 19, and group 2 with the brackish water stations 18, 20-27, 29-33 and 35.

The total number of observed species as well as the mean number of species per sampling station was clearly higher in group 1 as compared to group 2. The mean biomass was significantly higher in group 1 as compared to group 2.

Group 1 (the marine group) consisted of sampling stations with a relatively species rich benthic fauna. Molluscs as well as the dominance of the filter feeders characterised this community (see above). Characteristic species of this group were *Cerastoderma edule, Tharyx marioni, Eteone longa, Nephtys hombergii* and *Capitella capitata* (Figure 2.15). *Cerastoderma edule* was very common with a mean density of 1.34 ± $0.39*10^3$ ind m^{-2} (max: $5.2*10^3$ ind m^{-2}). *Cerastoderma edule* contributed most to the total biomass of the marine part with a mean biomass of 20.3 ± 7.3 g AFDW m^{-2} (max: 96g AFDW m^{-2}). *Cerastoderma edule* penetrated the estuary up to the brackish part, but here only young brood occurred. *Tharyx marioni* was also a very common species of the marine part and did not occur upstream from Hansweert. The mean density in the marine zone was 1.37 ± $0.57*10^3$ ind m^{-2} (max: $8.0*10^3$ ind m^{-2}). *Eteone longa* was another very common species, but also penetrated into the brackish part. The densities were always lower than 300 ind m^{-2}. *Capitella capitata* was a common species in the marine part. In the brackish part this species was only observed twice. The densities did not exceed more than 550 ind m^{-2} and biomass was low. *Nephtys hombergii* was typical for the marine part but the observed densities were low, not exceeding 250 ind m^{-2}.

Group 2 (brackish group) sampling stations had a less species-rich benthic fauna with a typical dominance of *Corophium volutator*. It is the only important species that was found in the brackish part of the estuary and not in the marine part (Figure 2.15). *Corophium volutator* contributed substantially to the total density having a mean density of 7.0 ± $2.9*10^3$ ind m^{-2} (max: $40*10^3$ ind m^{-2}). The biomass on some stations was relatively high, with a maximum of 3.7 g AFDW m^{-2}.

Several species are common to both group 1 and group 2, and were very abundant, notably *Heteromastus filiformis, Nereis diversicolor, Pygospio elegans* and *Macoma balthica* (Figure 2.15). *Heteromastus filiformis* was one of the most common species in this study, penetrating the estuary up to Antwerpen. Mean (*c.* $4.0*10^3$ ind m^{-2}) and maximum (*c.* $15.5*10^3$ ind m^{-2}) densities in the marine and brackish zone were comparable.

Heteromastus filiformis contributed considerably to the total biomass. On some locations the biomass was > 30 g AFDW m^{-2}. *Nereis diversicolor* was the most important omnivore in the Schelde estuary, and was found up to Antwerpen. Especially in the brackish zone, high densities (mean 1096 ± 455 ind m^{-2}; max: $7.0*10^3$ ind m^{-2}) are reached. In this zone, the contribution of *Nereis diversicolor* to the total biomass was quite important, with a maximum biomass of 50 g AFDW m^{-2}. In the marine zone, densities were much lower (mean: 482 ± 126 ind m^{-2}; max: 1718 ind m^{-2}).

Pygospio elegans was a very common species of both the marine and the brackish zone, penetrating the estuary up to Antwerpen. It contributed substantially to the total density with a mean density in the marine zone of 9.5 ± $3.7*10^3$ ind m^{-2} (max: $56.6*10^3$ ind m^{-2}) and in the brackish zone of 2.2 ± $0.9*10^3$ ind m^{-2} (max: $21.5*10^3$ ind m^{-2}). The maximum biomass was 5 g AFDW m^{-2}, but on most stations the biomass did not exceed 1 g AFDW m^{-2}.

Macoma balthica was the most common mollusc in the Schelde estuary. This species occurred upstream to Antwerpen. The mean density amounts 285 ± 61 ind m^{-2} (max: 1048 ind m^{-2}) in the marine zone and 199 ± 45 ind m^{-2} (max: 545 ind m^{-2}) in the brackish zone. *M. balthica* contributed substantially to the total biomass and the maximum biomass was 11.2 g AFDW m^{-2}.

Some species like *Polydora* spec. and *Hydrobia ulvae* were also common in both the marine and brackish part, but were less abundant than the species mentioned above. Polydora spec. was a relatively common species, penetrating the estuary up to the Dutch-Belgian border. It was most abundant in the marine zone (mean 1.84 ± 0.75*10^3 ind m^{-2}; max: 9.2*10^3 ind m^{-2}). In the brackish zone, densities did not exceed 1000 ind m^{-2}. The observed biomass was very low. *Hydrobia ulvae* was a common species in the marine and brackish zone, although less common near the mouth of the estuary. Mean density was much higher in the marine zone (535 ± 221 ind m^{-2} ; max: 3311 ind m^{-2}), as compared to the brackish zone (63 ± 32 ind m^{-2}; max: 461 ind m^{-2}). The biomass was relatively low.

As illustrated already by the direct gradient analysis, it can be concluded from the cluster analysis that the stations are separated in groups closely linked with the salinity gradient of the Schelde estuary. However, since many dominant species (*Heteromastus filiformis, Pygospio elegans, Nereis diversicolor, Macoma balthica*) were common in both the marine and brackish part, the distinguished groups are likely to be variants of one community type, rather than that a clear distinction into two totally different benthic communities can be made.

The macrozoobenthos of the marine part had a more complex structure than that of the brackish part, which was a more impoverished form. However, due to the presence of the filter feeder *Cerastoderma edule* in the marine part, the trophic structure differed clearly between the marine and brackish part of the Schelde estuary.

Discussion

This study is the first on the Schelde estuary investigating the macrozoobenthos along the whole estuarine gradient, including the freshwater tidal part. Previous studies on the macrozoobenthos of the Schelde estuary dealt only with the marine and brackish part of the estuary, but found the same gradient, as presented here (VERMEULEN & GOVAERE 1983; MEIRE et al. 1991, YSEBAERT & MEIRE 1991). However, in these studies other benthic communities, besides the one described here, were distinguished. The difference is due to sampling exclusively in the intertidal zone in this study, particularly in the most sheltered areas of the estuary with relatively muddy sediment with a low dynamic nature. The sampling stations in VERMEULEN & GOVAERE (1983) and YSEBAERT &

MEIRE (1991) covered a wide range of habitats, including the sublittoral zone. These studies clearly demonstrated the important role of sediment characteristics in determining the environmental conditions of the benthic habitat (see also GRAY 1974; RHOADS 1974). The community types described in this study are by far the most common in the intertidal zone of the Schelde estuary. Another important intertidal community, dominated by very mobile species like *Bathyporeia* spec., *Haustorius arenarius* and *Eurydice pulchra*, was observed on places with a highly dynamic nature, and therefore with a much coarser sediment ('megaripples', see YSEBAERT & MEIRE 1991). This community was not observed in this study but is found on some parts of the sand banks and mudflats, mainly in the brackish part of the estuary.

Distribution of the intertidal macrozoobenthic species in the Schelde estuary seems to be mainly controlled by salinity. The observed species distribution follows the classical concepts of species response to salinity gradients (REMANE & SCHLIEPER 1958; REMANE 1971), except that the reduction of species was more acute and that a lag occurred in the increase in number of species from the oligohaline to the freshwater tidal zone of the Schelde estuary.

The observed gradient in species composition and dominance in the marine and brackish part of the Schelde estuary is comparable with other European estuaries like the Ems, Weser, Elbe, Loire and Forth (WOLFF 1973; MICHAELIS 1983. ROBINEAU & MARCHAND 1984; ROBINEAU 1987; McLUSKY 1987). Many similarities, especially in the marine part, can be demonstrated, but on the other hand every estuary has its own physical and therefore ecological characteristics (see also MEIRE et al. 1991; WARWICK et al. 1991). For instance, how far a marine species is able to penetrate into an estuary largely depends on the amount and variability of the freshwater discharge, relative to the tidal inflow of sea water.

The macrozoobenthos of the oligohaline and freshwater tidal part of the Schelde estuary, characterised by the presence of only Oligochaeta, is at present quite different from some other European estuaries. However, as compared to the marine and brackish parts of estuaries, less data on the occurrence of benthic invertebrates in the freshwater tidal parts of estuaries is available. The oligohaline zone, which is both a physical and a biological buffer, is in estuaries like Weser, Elbe and Loire also characterised by the lowest species richness. Contrary to the Schelde estuary, however, in these estuaries also other species, both real freshwater species (*e.g.* insect larvae) and marine/brackish water species (*e.g. Corophium lacustre)*, occur (MICHAELIS 1983; ROBINEAU 1987; HAESLOOP 1990).

In the real freshwater tidal parts of the Ems, Weser and Elbe estuaries an increase in freshwater species richness had been found. Besides various Oligochaeta species, also molluscs (*e.g. Potamopyrgus jenkinsi, Pisidium* spp.), insect lavae (*e.g.* chironomids) and crustaceans (*e.g. Gammarus* spp.) are observed (DÖRJES & REINECK 1981; RHODE 1982; HAESLOOP 1990). However, compared to the marine part of these estuaries, species richness is still very low. In the Weser estuary a special situation occurs since the freshwater tidal part is suffering from an anthropogenic increase in salinity, coming from industries more upstream. Therefore, no real distinction can be made between the brackish and freshwater part of the Weser estuary since also a lot of brackish water species are observed in the freshwater part, besides the normal fresh water species (HAESLOOP 1990). However, the above mentioned studies did not find the same species richness as described for the former freshwater tidal area Biesbosch (WOLFF 1973) and for the Elbe estuary (CASPERS 1948). In the latter, CASPERS observed more than 30 species, of which 8 Oligochaeta (*e.g. Limnodrilus hoffmeisteri* and *Tubifex tubifex*), larvae of 10 chironomids, 8 molluscs (*e.g. Pisidium* and *Sphaerium*) 3 gastropods and 4 crustacaens (*e.g. Gammarus zaddachi* and *Neomysis integer*). This is however still much lower as compared to the marine part of estuaries. In the North-American estuaries the oligohaline and freshwater tidal parts are also characterised by a relatively low species richness, with Oligochaeta and chironomids, and to a lesser extent amphipods and molluscs, as the dominating species (SIMPSON et al. 1986; ODUM et al. 1988; DIAZ 1989).

The impact of pollution on estuarine ecosystems is particularly difficult to assess because of a high degree of natural biological variability (in time and space), due to the highly dynamic nature of the estuarine physical environment (see also MEIRE et al. 1991). Therefore, it is very difficult to separate pollution effects from natural variation in these benthic communities or to determine the impact of pollution on benthic communities.

Especially in the Schelde estuary it is very difficult to relate the distribution patterns of the macrozoobenthos to anthropogenic stress, since concentrations of most pollutants are following the same gradient as the salinity. There is, however, evidence that the benthic fauna in the freshwater tidal zone and the upstream part of the brackish zone (the oligohaline zone) is suffering from the pollutants entering the estuary. In the Schelde estuary the reduction of species is extremely acute and more severe than predicted by Remane's model. Over a very large stretch only a very uniform benthic community, existing of Oligochaeta, was found. Unfortunately, no historical data exist on the benthic fauna of the freshwater tidal part of the Schelde estuary before the heavy industrialisation and urbanisation. Other evidence for impact of pollution on the structure of the benthic community is the observation that some euryhaline (*e.g. Nereis diversicolor*) or brackish water (*e.g. Corophium volutator*) species don't enter the Schelde as far as in other estuaries. Also the lack of some typically brackish water species (*e.g. Streblospio shrubsolii*) can probably be attributed to pollution.

Based on these observations it seems that the Schelde estuary is suffering more severe from pollution than many other European estuaries. The way how pollution is responsible for this impoverishment, is at this moment not yet unraveled. The lack of oxygen in both water and sediment, which appears very often in the freshwater tidal zone of the estuary as a consequence of the very high inputs of organic matter and nutrients, is probably a main cause. Interaction between sediment contaminants (organic and inorganic micropollutants) and benthic organisms is not yet well understood, but sublethal effects on the benthic fauna are expected.

Finally, not only pollution is threatening freshwater tidal parts of European and North-American estuaries. Some authors mention impacts of canalisation and dredging on the freshwater tidal ecosystem in general, and more particularly on the benthic fauna (ROBINEAU & MARCHAND 1984; HAESLOOP 1990).

Acknowledgements

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Chapter three

Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW-Europe

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Abstract

In literature, few macrobenthic studies have dealt with the two major gradients in estuarine benthic habitats: the salinity gradient along the estuary (longitudinal) and the gradients from high intertidal to deep subtidal sites (vertical gradient). In this broad-scale study, a large data set (3112 samples) of the Schelde estuary allowed us to thoroughly analyze these both gradients, and relate macrobenthic species distributions and community structure to the predominant environmental variables (salinity, depth, current velocities and sediment characteristics). An univariate analysis clearly revealed distinct gradients in diversity, abundance, and biomass along the vertical and longitudinal gradient. In general, highest diversity and biomass were observed in the intertidal, polyhaline zone and decreased with decreasing salinity. Abundance did not show clear trends. Spring abundance and biomass were much lower as compared to autumn values. In all salinity regions, very low values for all measures were observed in all subtidal depth strata.

Abundance was in all salinity regions dominated by both surface and sub-surface deposit feeders. Clear gradients in the biomass of the different feeding guilds were observed in the intertidal zone. Suspension feeders dominated in the polyhaline zone and showed a significant decrease with decreasing salinity. A same trend was observed for surface deposit feeders and sub-surface deposit feeders had significantly higher biomass values in the polyhaline zone as compared to the mesohaline zone. Omnivores showed an opposite trend, with a significantly higher biomass in the β-mesohaline zone.

The different multivariate analyses showed a strong relationship between the macrobenthic assemblages and the predominant forces (gradients) in the Schelde estuary. A first gradient was related to depth, which reflected also the hydrodynamic conditions. A second gradient was clearly related to salinity and confirms the observations from the univariate analysis. Sediment characteristics appeared to be more correlated with depth and current velocities, but correlation was rather weak. The different assemblages are further described terms of indicator species and abiotic characteristics.

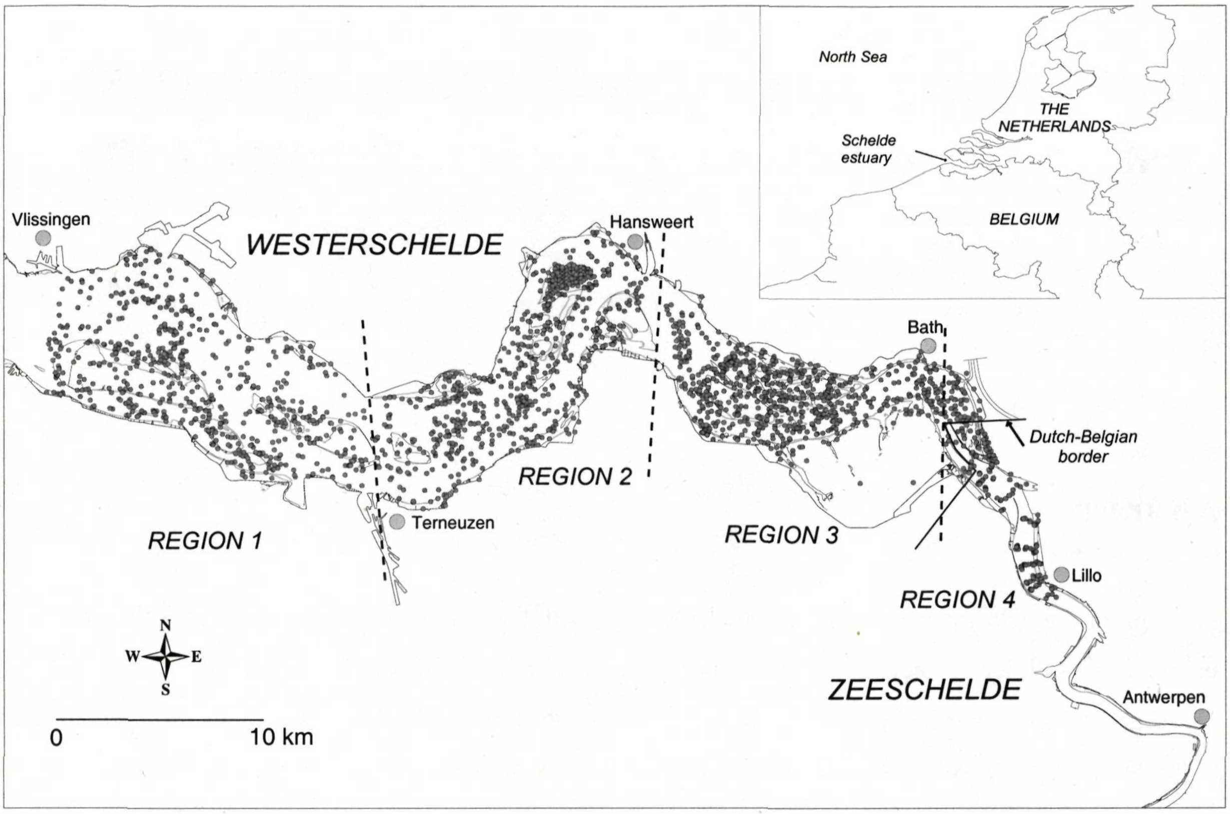


Figure 3.1. Map of the Schelde estuary (polyhaline and mesohaline zone) with indication of the sampling locations and the four salinity regions.

Introduction

Macrobenthos is an important component of estuarine ecosystems and plays an important role in the system dynamics (structure and function) of estuaries (HERMAN et al. 1999). It is a central element of estuarine food webs, being an important food resource for crustaceans, fish and birds (DAY et al. 1989). Humans also harvest many species of shellfish and crustaceans.

Estuaries are transitional environments between rivers and the sea, characterized by widely varying and often unpredictable hydrological, morphological and chemical conditions and gradients (DAY et al. 1989). Estuarine organisms are often restricted to particular sections of environmental gradients, resulting in well developed zonation patterns. The spatial heterogeneity of macrobenthos across the estuarine gradient is mostly described in relation to salinity and sediment composition (e.g. SANDERS et al. 1965; CARRIKER 1967; WOLFF 1973; GRAY 1974; BEUKEMA 1976; BOESCH 1977; MICHAELIS 1983; HOLLAND et al. 1987; MEIRE et al. 1994; SCHLACHER & WOOLDRIDGE 1996; MANNINO & MONTAGNA 1997; YSEBAERT et al. 1993,1998a). WARWICK & UNCLES (1980) and WARWICK et al. (1991) pointed out the relative importance of dynamic processes themselves, and the static factors resulting from them, in determining the community structure of macrobenthos.

Other studies emphasize the importance of hydrodynamical conditions such as current velocity and bed shear stress for the transport of sediment, food and juvenile macrofauna (WARWICK & UNCLES 1980; GRANT 1983; BUTMAN 1987; SNELGROVE & BUTMAN 1994). Recent studies also consider hydrodynamic factors affecting the stability of the sediment by mobilising bed material, including macrofauna (HALL 1994; BELL et al. 1997; GRANT et al. 1997).

Knowledge on the spatial distribution patterns of macrobenthos along estuarine gradients might help to identify the linkages between species distributions and ecological processes and therefore to gain insight into the functioning of estuarine ecosystems (see e.g. THRUSH et al. 1999), which is essential for a sound implementation of integrated estuarine management. However, in their review HEIP et al. (1995) concluded that, because of a biased sampling strategy, few studies dealt with the two major gradients in macrotidal, estuarine benthic habitats, the salinity gradient of the estuary and the gradient from high intertidal to deep subtidal sites.

The macrotidal Schelde estuary is one of the longest estuaries in NW-Europe. It is a turbid, nutrient-rich, heterotrophic ecosystem (HEIP et al. 1995; SOETAERT & HERMAN 1995a) which is under permanent stress due to a high load of urban, industrial and agricultural waste (VAN ECK & DE ROOIJ 1993). Being an important shipping channel to the harbour of Antwerpen, the estuary is extensively dredged (8–12*10^6 m^3 per year at present). This has resulted in several changes in the morphology of the estuary (VROON et al. 1997). Future plans of a further deepening of the estuary will increase the dredging activities by more than 50%. To evaluate the impacts of the dredging activities, the macrobenthos has been monitored extensively during the last decade, resulting in a large amount of data. The present paper describes the spatial distribution patterns of macrobenthos on an estuarine meso- and macro-scale, in relation to the predominant estuarine environmental variables salinity, depth, current velocity and sediment characteristics. Indicator species, trophic structure and community structure are defined along the prevalent estuarine gradients. The dataset presented here will be used further to model and predict macrobenthic species response to (changes in) environmental conditions in estuarine ecosystems (YSEBAERT et al. subm.).

Materials and methods

Study area

The Schelde estuary, a macrotidal, nutrient-rich, heterotrophic sytem, measures 160 km from the mouth near Vlissingen (The Netherlands) to Gent (Belgium) and is one of the longest estuaries in NW-Europe with still a complete salinity gradient. The study area is limited to the Westerschelde (Dutch part) and a small part of the Zeeschelde (Belgian part) near the Dutch-Belgian border (Figure 3.1), comprising the complete polyhaline and mesohaline zone of the estuary. The mean tidal range increases from 3.8 m at Vlissingen to 5.0 m near the border. The river discharge varies from 20 m^3s^{-1} during summer to 400 m^3s^{-1} during winter, with a mean annual average of 105 m^3s^{-1}. The residence time of the water in the estuary ranges from one to three months, depending on the river discharge (SOETAERT & HERMAN 1995b). Only the most seaward region has a residence time of about 10-15 days.

The lower and middle estuary, the Westerschelde (55 km), is a well mixed region characterised by a complex morphology with flood and ebb channels surrounding several large intertidal mud- and sandflats. The surface of the Westerschelde amounts to 310 km², with the intertidal area covering 35%. The average channel depth is approximately 15-20 m. Upstream the Dutch/Belgian border the estuary is characterized by a single channel. The turbidity maximum is situated near Antwerpen but moves over a quite large distance, mainly as a result of tidal action and river run off (WOLLAST & PETERS 1978; BAEYENS et al. 1998; FETTWEIS et al. 1998). Also in this zone of the estuary oxygen concentration decreases rapidly, mainly due to the heavy loading with nutrients and allochtonous organic material, causing high microbial activity (e.g. GOOSEN et al. 1995, 1999). For more details on the ecological and physicochemical properties of the estuary see MEIRE & VINCX (1993), HEIP & HERMAN (1995), BAEYENS et al. (1998), HERMAN & HEIP (1999) and VAN DAMME et al. (1999; subm.).

Macrobenthos database

An extensive data set on macrobenthos is available for the Schelde estuary. A total of 3112 macrobenthos samples, mainly within the framework of monitoring programmes, were collected in the study area by different institutes in the period 1978-1997. By far most data were collected and analysed by two institutes, namely the Centre for Estuarine and Coastal Ecology NIOO-CEMO (e.g. CRAEYMEERSCH et al. 1996; BRUMMELHUIS et al. 1997; CRAEYMEERSCH 1999) and the Institute of Nature Conservation (before that at the University of Gent) (e.g. YSEBAERT & MEIRE 1991, 1998; DE NEVE et al. 1998), mainly in co-operation with the National Institute for Marine and Coastal Management (RWS-RIKZ). 90% of the samples were collected from 1990 onwards. 54% were taken in autumn (September-October), 32% in spring (March-April-May). Most sampling locations (68%) were sampled only once, but several locations were sampled two to five times in the sampling period considered, and a few were sampled more frequently within a long term programme.

Different collecting methods were used, but in general multiple sediment cores were used for sampling the intertidal zone, and Van Veen grab or Reineck box corer for the subtidal zone. All samples regard the macrobenthos, these are all animals retained on a sieve with mesh size 1 mm. For more details on the sampling methods and the design of the monitoring programmes see MEIRE et al. (1991), YSEBAERT et al. (1993) and CRAEYMEERSCH (1999).

Abiotic variables

For each sample the following abiotic environmental variables were added to the macrobenthos database: depth/elevation, salinity, current velocities (maximum ebb and flood current velocities), sediment characteristics (median grain size and mud content). At subtidal stations depth was recorded at the time of sampling. The elevation of the intertidal stations was measured directly in the field or from a Geographical Information System, storing all bathymetric data in the area. For 2874 samples (92%) depth was added in the database. Depth is expressed in m NAP (NAP, Dutch Ordnance level, similar to Mean Sea Level).

Salinity was estimated for each sampling location using a 2Dh-hydrodynamic model SCALDIS400 (LIEVENSE 1994) with a spatial resolution of 400 meter. The model calculations are based on values for mean tidal conditions with a yearly averaged discharge, giving an average salinity value. The advantage of using the SCALDIS400 model is that a high spatial resolution is obtained but the estimates are not seasonally defined. Therefore also monthly to fortnightly measurements at nine stations along the Westerschelde were used to represent the temporal variation in salinity, but at a much coarser spatial resolution than model salinity. For each sample the temporal salinity was determined as the average salinity of the three months previous to the date of sampling. Estimates obtained from model simulations are called 'model salinities', whereas the values derived from field observations are called 'temporal salinities'.

Current velocities (maximum ebb and flood current velocities in $m.s^{-1}$) for each sampling location were estimated with the SCALDIS100 model (DEKKER et al. 1994) for mean tidal conditions, with a spatial resolution of 100 meter. For 3037 samples current velocity estimates were available.

Samples for sediment grain size analysis (by laser diffraction technique) were collected during several campaigns. For 1502 and 1386 samples (48 % and 45%) median grain size and mud content (volume % < 63 μm) values were added to the database respectively.

Data analysis

All macrobenthic abundance data were transformed to $numbers.m^{-2}$ ($ind.m^{-2}$), and biomass data to g Ash Free Dry $Weight.m^{-2}$ (g $AFDW.m^{-2}$). Most species were determined at species level. *Bathyporeia, Ensis, Microphthalmus, Nemertea, Oligochaeta, Ophelia, Polydora, Spio, and Spisula* were lumped as the determination level differed among studies. Each species was classified into feeding groups based on the food source (e.g. FAUCHALD & JUMARS 1979; BARNES 1982). Trophic groups included surface deposit feeders, sub-surface deposit feeders, suspension feeders, omnivores and predators. Species feeding by more than one mode were classified by their most common feeding mechanism.

The longitudinal (model salinity) gradient of the study area was categorized into four salinity regions: lower estuary (region 1: Vlissingen-Terneuzen); middle estuary (region 2: Terneuzen-Hansweert); inner estuary (region 3: Hansweert-Bath); inner/upper estuary (region 4: Bath-Lillo)

Table 3.1. Average (± standard deviation) and minimum-maximum model and temporal salinity of the sampling occasions in each salinity region (see text for further explanation).

Salinity region	1	2	3	4
Model salinity				
Average	29.23 ± 1.36	23.96 ± 1.52	16.52 ± 2.04	8.93 ± 1.41
min.-max.	26.21 – 31.61	20.33 – 27.35	10.20 – 20.33	5.69 – 13.38
Temporal salinity				
Average	27.56 ± 2.71	20.36 ± 4.50	14.22 ± 5..32	9.78 ± 3.04
min.-max.	16.96 – 32.39	8.38 – 26.87	1.86 – 21.55	1.15 – 15.18
N	722	959	956	475

(Figure 3.1). In salinity regions 1-3 the proportion of samples collected in spring was similar (33-44%), whereas in salinity region 4 only 15% of the samples were collected in spring. The vertical (depth) gradient was divided into four depth strata: the intertidal or littoral zone and three strata in the subtidal (undeep 2-5m beneath NAP; deep 5-8m beneath NAP; channel > 8m beneath NAP). Comparisons among depth categories and sediment characteristics and current velocities were examined with ANOVA on log-transformed data. The relations between environmental variables were further examined by Spearman rank correlations. The general trends in diversity, abundance, biomass and trophic structure of the macrobenthos along the longitudinal and vertical gradients were examined with a Two-way ANOVA on log-transformed data. A spring-autumn comparison was made for the intertidal zone.

Numerical classification and ordination (based on log transformed data) were used to analyze community structure and its relationship to matching environmental data (FIELD et al. 1982). Only species observed in more than 15 samples were included in the analyses and all higher taxa, except Oligochaeta and Nemertea, were excluded, resulting in 58 macrobenthic species. Separate analyses were performed for the data set without sediment data (n=2612) and the data set with sediment data (n=1243), hereafter called data set A and data set B. The samples were classified into clusters (both for abundance and biomass data) using the classification program Two-Way Indicator Species Analysis - TWINSPAN (HILL 1979).

Multivariate ordination techniques were used to investigate, for the dataset with sediment data and the dataset without sediment data separately, the variation in the species data set and the relationship between species composition and the measured environmental variables. As the gradient length in standard deviation (SD) units, determined in a preliminary detrended correspondence analysis (DCA; with detrending by segments), did exceed 4 SD, a strong unimodal response was considered and therefore Canonical Correspondence Analysis (CCA) was applied (JONGMAN et al. 1995; TER BRAAK 1994; TER BRAAK & SMILAUER 1998). As the macrobenthos data were sampled in different seasons, it is likely that there is seasonal variation in the biological assemblage and the

Table 3.2. Average ± Standard Deviation for median grain size (μm), mud content (% < 63 μm), maximum ebb and flood current velocities (m/s) for each depth stratum.

	Median grain size	Mud content	Max ebb	Mab flood
Depth stratum				
1 (intertidal)	139.1 ± 69.1 *n=922*	22.9 ± 23.1 *n=888*	0.42 ± 0.19 *n=1481*	0.39 ± 0.23 *n=1481*
2 (undeep subtidal)	192.9 ± 84.8 *n=173*	13.5 ± 21.6 *n=150*	0.74 ± 0.25 *n=471*	0.79 ± 0.27 *n=471*
3 (deep subtidal)	202.7 ± 87.2 *n=143*	14.0 ± 21.9 *n=116*	0.83 ± 0.22 *n=429*	0.88 ± 0.26 *n=429*
4 (channel)	218.2 ± 91.9 *n=264*	10.5 ± 18.4 *n=232*	0.97 ± 0.23 *n=656*	1.00 ± 0.27 *n=656*

environment. This seasonal variation was not the prime research question. Therefore, a partial CCA was applied, with the different months representing covariables (TER BRAAK 1988; TER BRAAK & VERDONSCHOT 1995; TER BRAAK & SMILAUER 1998). Forward selection of environmental variables was used to identify and rank their importance for determining the species composition (TER BRAAK & VERDONSCHOT 1995; TER BRAAK & SMILAUER 1998). In the first step of this method, all environmental variables are ranked on the basis of the fit for each separate variable (marginal effects). At the end of the first step of the forward selection the best variable is selected. Hereafter, all remaining environmental variables are ranked on the basis of the fit that each separate variable gives in conjunction with the variable(s) already selected (conditional effects). The statistical significance of the effect of each variable and the significance of the first canonical eigenvalue and of the sum of all eigenvalues was tested with Monte Carlo permutation tests (199 unrestricted permutations, p<0.05).

Results

Characterization of the abiotic environment

Average model salinity varied between 5.7 and 31.6 for the whole study area. Salinity regions 1 and 2 belonged to the polyhaline zone, salinity regions 3 and 4 to the α- and β-mesohaline zone respectively (Table 3.1). Based on temporal salinity, region 2 could be considered as a poly-/mesohaline transition zone, whereas salinity region 4 could be considered as a meso-/oligohaline transition zone. Both salinity measures were strongly correlated (r= 0.86; p<0.01; n=3112).

There was a significant difference between depth strata for median grain size (ANOVA, F=56; p<0.001) and mud content (ANOVA, F=53; p<0.001), with a clear trend of coarser sediments with less silt content from the intertidal to the deep subtidal and channel (Table 3.2), which was also demonstrated by the significant positive correlation between depth and median grain size (r= 0.46;

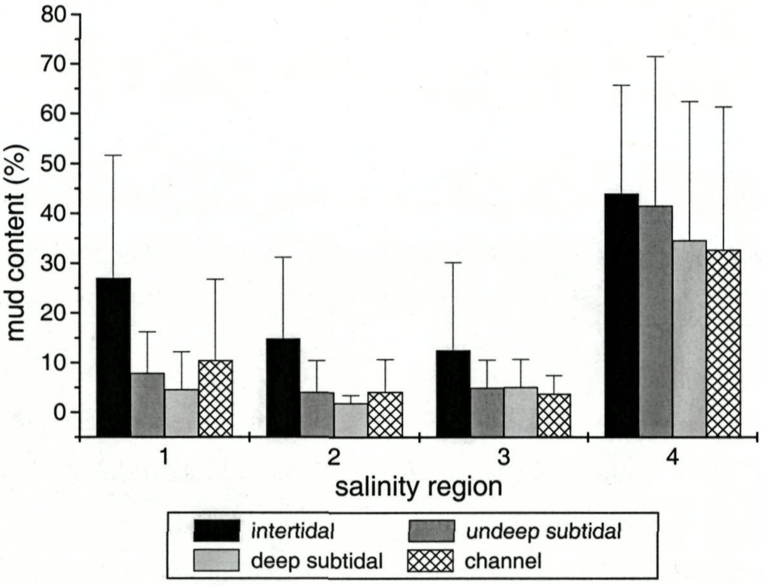


Figure 3.2. Mean mud content (± SD) observed in each depth stratum per salinity region. For the division of salinity regions: see text and Figure 3.1. (salinity regions 1&2: polyhaline zone; salinity regions 3&4: mesohaline zone).

$p<0.01$; n=1436) and the significant negative correlation between depth and mud content (r= -0.39; $p<0.01$; n=1326). This rather weak correlation could be explained by the fact that this trend was not consistent within each salinity region (Figure 3.2). In salinity regions 1-3 mud content was significantly higher in the intertidal zone as compared to all subtidal strata, but overall means were relatively low. In comparison, in salinity region 4 much higher mud contents were observed in all depth strata, but here differences between depth strata were relatively small, with only a weak trend towards coarser sediments with increasing depth.

Significantly higher current velocities, both under ebb and flood conditions, were observed in the subtidal strata as compared to the intertidal zone (ANOVA, F=815 (ebb) and F=789 (flood), $p<0.001$), which was also demonstrated by the highly significant correlation between depth and maximal ebb current velocities (r= 0.76; $p<0.01$; n=2827) and maximal flood current velocities (r= 0.75; $p<0.01$; n=2827). This pattern is consistent within each salinity region. A significant, but rather weak, correlation was observed between current velocities and median grain size (r=.44; $p<0.01$; n=1455) and mud content (r=-.38; $p<0.01$; n=1340) respectively, indicating coarser sediments with lower mud contents with higher current velocities. Finally, a strong negative correlation was observed between median grain size and mud content (r=-.84; n=1386).

General characteristics of macrobenthos

Macrofauna species richness (number of species, N_0) in a single sample varied between 0 and 25 species. In 202 samples (6.5 %) no macrobenthic animals were found. Most samples (51 %) had less then 5 species and in 28 % of the samples between 5 and 10 species were observed. The most

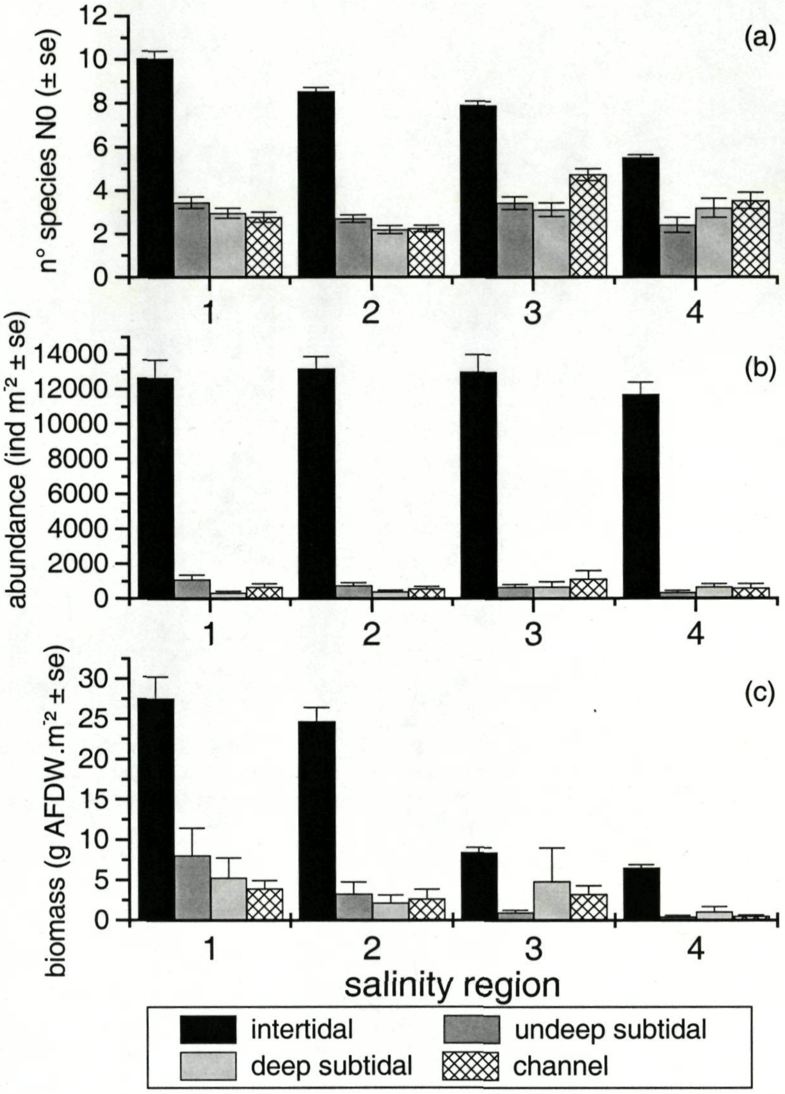


Figure 3.3. Mean number of species, mean abundance (ind m^{-2}) and mean biomass (g AFDW m^{-2}) observed along the longitudinal (salinity regions) and vertical gradient (depth strata) in the Schelde estuary. For the division of salinity regions: see text and Figure 3.1. (salinity regions 1&2: polyhaline zone; salinity regions 3&4: mesohaline zone).

common species were *Heteromastus filiformis*, observed in 58% of the samples, *Macoma balthica* (41%), *Pygospio elegans* (36%), *Bathyporeia spp.* (30%), *Nereis diversicolor* (26%) and *Hydrobia ulvae* (25%). Other species occurred in less than 20 % of the samples.

Total abundance varied between 0 and 225.568 ind.m^{-2}. In about half the samples abundance was less than 1000 ind.m^{-2} and in about one third, abundance varied between 1000 and 10.000 ind.m^{-2}. The three most abundant macrofauna taxa were Polychaeta, Mollusca and Crustacea.

Total biomass varied between 0 and 466,5 g AFDW.m^{-2}. In about half the samples biomass was less than 1 g AFDW.m^{-2} and in about one third biomass varied between 1 and 10 g AFDW.m^{-2}.

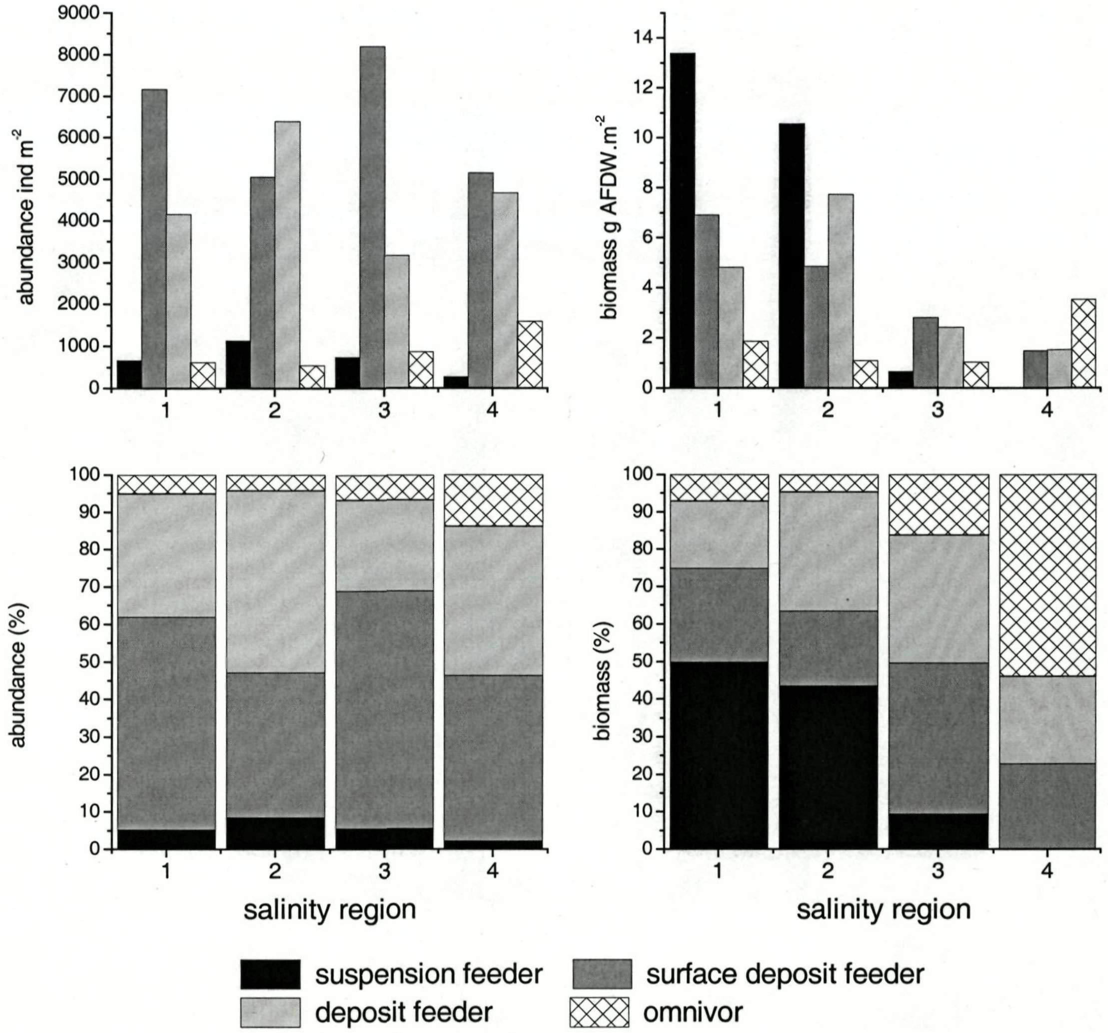


Figure 3.4. Absolute and relative dominance (abundance and biomass) of the different feeding guilds in the intertidal (littoral) zone of each salinity region. For the division of salinity regions: see text and Figure 3.1. (salinity regions 1&2: polyhaline zone; salinity regions 3&4: mesohaline zone).

General trends along longitudinal (salinity) and vertical (depth) gradients

As the ratio spring:autumn samples was more or less similar within each salinity region, except for salinity region 4 where relatively more autumn samples occurred, trends were based on all available data. The mean number of species (N0) per sample was significantly different between the salinity regions (Two-way ANOVA, F=15.5; p<0.0001) and the depth strata (Two-way ANOVA, F=499; p<0.0001), with also a significant interaction term salinity*depth (Two-way ANOVA, F=14; p<0.001). In the intertidal zone a clear decrease in N0 from the polyhaline zone towards the mesohaline zone was observed (Figure 3.3). In each salinity region a significantly higher number of species (per sample) was observed in the intertidal zone as compared to the subtidal zone. In the subtidal zone the average number of species observed per sample did not show a clear trend and was more or less similar within each salinity region and within each depth stratum.

Intertidal macrofauna total abundance was similar between salinity regions, but gave both an overall (Two-way ANOVA, F=762; p<0.0001), as for each salinity region separately, significant difference with depth, showing a significant higher abundance for the intertidal zone as compared to the subtidal strata (Figure 3.3). Within the subtidal strata, no significant difference was observed.

Macrofauna total biomass showed both a significant difference between salinity regions (Two-way ANOVA, F=21; p<0.0001) and depth strata (Two-way ANOVA, F=439; p<0.0001), with also a significant interaction term salinity*depth (Two-way ANOVA, F=7; p<0.001). Highest biomass values were observed in the highest salinity regions (polyhaline zone) and the intertidal zone (Figure 3.3). Within the subtidal strata, no significant difference was observed.

Trophic structure of the macrobentos

In the intertidal zone, abundance was in all salinity regions dominated by surface deposit feeders and deposit feeders showing no clear trends (Figure 3.4). Abundance of suspension feeders was low. Omnivore/predator abundance was low in the salinity regions 1-3, but increased significantly in salinity region 4 (ANOVA F=121.3, p<0.001).

Clear gradients in the biomass of the different feeding guilds were observed in the intertidal zone (Figure 3.4). Suspension feeders dominated in the polyhaline zone and showed a significant decrease with decreasing salinity (ANOVA F=30.2, p<0.0001). A same trend was observed for surface deposit feeders (ANOVA F=22.9, p<0.0001) and deposit feeders had significantly higher biomass values in the polyhaline zone as compared to the mesohaline zone (ANOVA F=65.2, p<0.0001). Omnivores showed an opposite trend, with a significantly higher biomass in the β-mesohaline zone (ANOVA F=51.6, p<0.0001); in salinity region 4 omnivores were the dominant group. Salinity region 3 acted as an intermediate region with here surface deposit and deposit feeders dominating the biomass.

In the subtidal zone abundance was also dominated by surface deposit feeders and deposit feeders in all salinity regions (44-85%), whereas biomass was dominated by suspension feeders. This was in all salinity regions due to the presence of high biomass values of suspension feeders in only a few samples. In the polyhaline zone the suspension feeders were mainly *Ensis* and *Spisula*, whereas in the α-mesohaline zone a few samples in *Mytilus* banks were responsible for this dominance. In salinity region 4 a few samples with oysters were responsible for this dominance (YSEBAERT et al., in press).

Seasonal variations in the intertidal zone

In the intertidal zone mean number of species per sample, mean total abundance and mean total biomass were in general significantly higher in autumn as compared to spring in all salinity regions (Table 3.3). The five most dominant species in each salinity region, both in terms of abundance and biomass, are presented in Figure 3.5. In salinity region 1 abundance was dominated in both seasons by the surface deposit feeders (SDF) *P. elegans* and *Tharyx marioni* and the sub-surface deposit feeder (SSDF) *H. filiformis*. Biomass in spring was more evenly distributed among several species, whereas

Table 3.3. Mean number of species per sample, mean total abundance (ind m^{-2}) and mean total biomass (g AFDW m^{-2}) in spring (March-May) and autumn (August-October) per salinity region in the intertidal zone of the Schelde estuary (means ± standard error). For salinity regions: see table 3.1 and Figure 3.1.

Salinity region	1		2		3		4	
Intertidal zone	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn
N° of species	8.57 ± 0.55	10.90 ± 0.48	8.12 ± 0.62	8.95 ± 0.31	6.59 ± 0.28	8.36 ± 0.27	4.18 ± 0.35	5.78 ± 0.14
Total abundance	7833 ± 1171	16139±1658	8205 ± 642	16682±1340	6378 ± 764	15766 ± 1559	5325 ± 997	12614 ± 838
Total biomass	14.50 ± 1.88	34.48 ± 4.68	20.39 ± 2.07	31.32 ± 3.60	4.99 ± 0.73	8.90 ± 0.92	4.97 ± 0.79	6.06 ± 0.44
N	97	135	169	218	147	249	33	214

in autumn the suspension feeder (SF) *Cerastoderma edule* dominated. In salinity region 2 abundance was dominated by *H. filiformis* and *P. elegans*, and to a lesser extent by the grazer *H. ulvae*. For biomass, most dominant species in both seasons was *C. edule*, but also *H. filiformis,* the SDF *M. balthica*, the SF *Mya arenaria* (autumn) and the SSDF *Arenicola marina* (spring) contributed substantially to the biomass. In salinity region 3 abundance was dominated by *P. elegans* and *H. filiformis*, with in autumn also the SDF *Corophium volutator* predominantly present. In spring biomass was dominated by *M. balthica*, the omnivore *N. diversicolor* and *H. filiformis*, whereas in autumn the dominance of *H. fili*formis became more pronounced. In salinity region 4 abundance was dominated by *C. volutator*, *H. filiformis and N. diversicolor* in both seasons. Biomass was dominated by *N. diversicolor*, with in autumn also *H. filiformis and C. volutator* predominantly present.

The relatively large differences in abundance and biomass between spring and autumn for most macrobenthic species could only be partially attributed to a difference in occurrence (presence), since most species were present in the same proportion in both seasons. Largest differences in occurrence between both seasons were observed for *C. edule* and for the species of salinity region 4 (*M. balthica*, *H. filiformis*, and *C. volutator*).

Classification and indicator species

The clusters distinguished only reveal the large-scale estuarine patterns. Up to five levels of the TWINSPAN classification are summarized in Table 3.4 and 3.5 for data set B on abundance and biomass data respectively. Further divisions were not considered. The classification based on abundance and biomass data resulted in similar divisions. Especially clusters 2, 7 and 8 were very similar, with 77-94% of the samples mutually observed. The division of clusters 3-6 was slightly different when based on abundance or biomass data respectively, with several samples interchanged among clusters of the two classifications. However, abiotic characterization and indicator species of

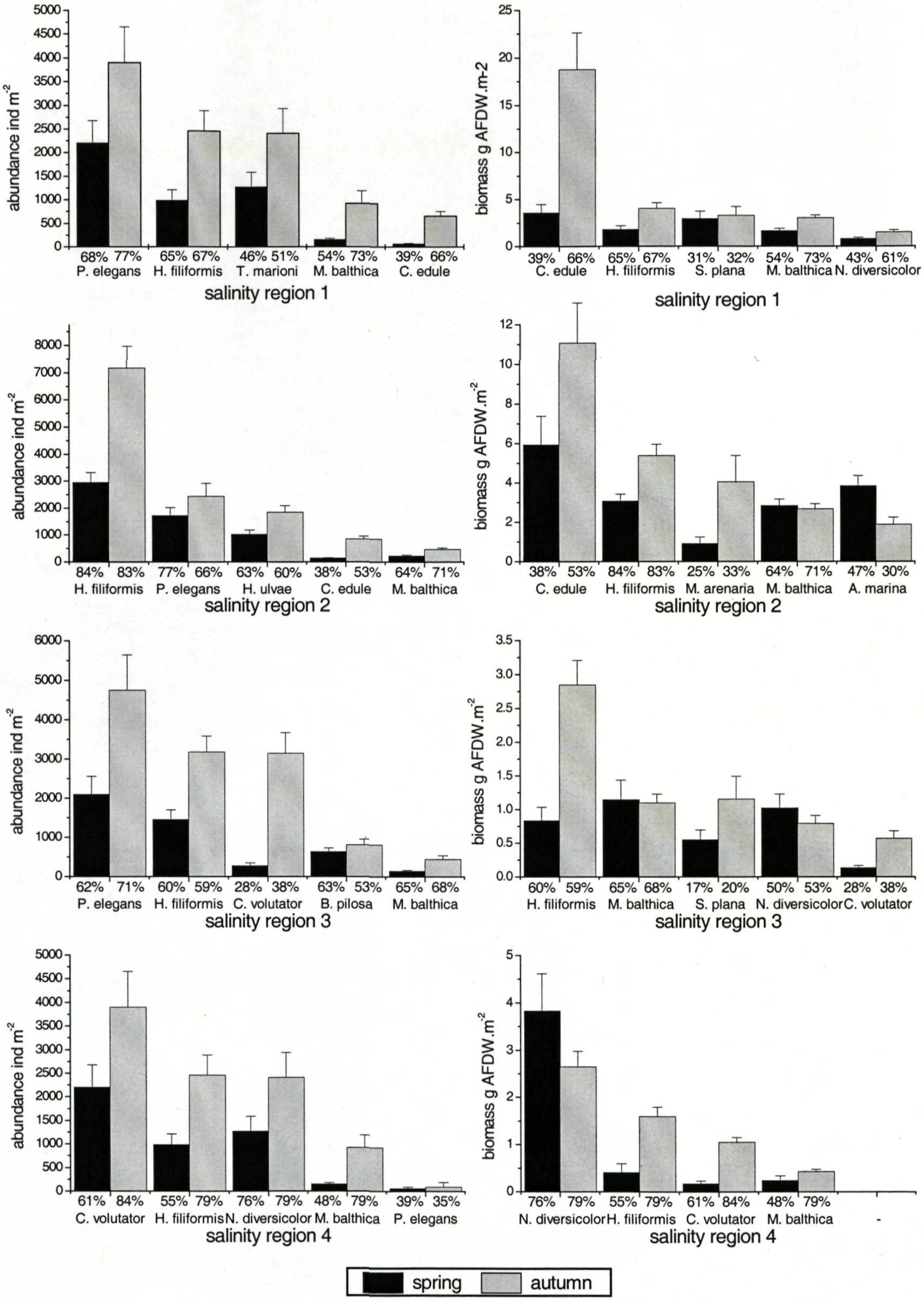
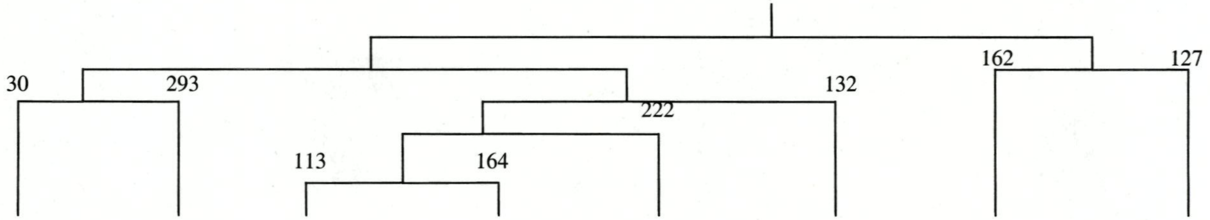


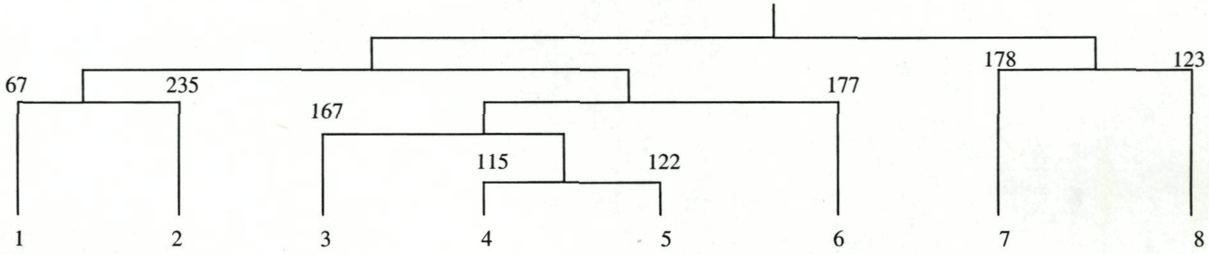
Figure 3.5. Abundance (ind m^{-2} ± se) and biomass (g AFDW m^{-2} ± se) in spring (March-May) and autumn (August-October) of the five most dominant macrobenthic species in the intertidal (littoral) zone of each salinity region. For the division of salinity regions: see text and Figure 3.1. (salinity regions 1&2: polyhaline zone; salinity regions 3&4: mesohaline zone).

Table 3.4. Dendrogram representing the TWINSPAN classification based on macrofauna abundance (data set B, n=1243). For each cluster mean ± SD of the environmental variables model salinity (psu), depth (m), maximum ebb and maximum flood current velocity ($m.s^{-1}$), median grain size (µm) and mud content (%) is given. Mean diversity (N0), mean abundance ($ind.m^{-2}$) and mean biomass ($g\ AFDW.m^{-2}$) per cluster are given (mean ± SE). For each cluster mean abundance of the most important macrobenthic species is given, together with its occurrence (% present) in that cluster. Boldfaced numbers represent the main data set structure.



	1	2	4	3	5	6	7	8
Salinity	7.8 ± 3.8	11.0 ± 4.4	20.1 ± 5.1	21.9 ± 3.4	21.3 ± 4.4	18.8 ± 5.7	22.6 ± 5.2	16.4 ± 4.3
Depth	8.4 ± 4.4	0.7 ± 4.9	0.7 ± 4.7	0.4 ± 2.6	1.2 ± 4.1	5.0 ± 6.2	9.7 ± 5.6	5.1 ± 5.5
Max. ebb	0.90 ± 0.22	0.44 ± 0.28	0.39 ± 0.18	0.47 ± 0.10	0.51 ± 0.20	0.71 ± 0.24	0.86 ± 0.26	0.81 ± 0.29
Max. flood	0.81 ± 0.23	0.38 ± 0.30	0.37 ± 0.22	0.30 ± 0.14	0.45 ± 0.26	0.69 ± 0.32	0.93 ± 0.26	0.87 ± 0.30
Median	83 ± 85	95 ± 61	112 ± 48	134 ± 59	179 ± 51	222 ± 59	227 ± 75	213 ± 45
Mud content	52 ± 24	40 ± 23	23 ± 19	21 ± 17	7 ± 7	6 ± 8	4 ± 7	3 ± 4
Mean N0	6.7 ± 3.9	5.7 ± 2.6	13.4 ± 3.5	9.4 ± 2.5	7.8 ± 3.5	4.2 ± 2.7	5.8 ± 4.3	3.0 ± 2.0
Mean density	2114 ± 3582	9899 ± 10398	29609 ± 29065	21680 ± 17530	5682 ± 6233	1012 ± 1765	768 ± 2535	597 ± 1197
Mean biomass	0.98 ± 1.67	6.6 ± 9.9	41.5 ± 55.8	37.3 ± 38.9	10.7 ± 22.9	1.76 ± 5.76	1.05 ± 3.32	0.20 ± 0.35
Density								
Poly lige	**1333 / 80%**	-	-	-	-	-	-	-
Oligochaeta	215 / 83%	**1834 / 96%**	1101 / 48%	23 / 7%	132 / 22%	11 / 4%	3 / 6%	0.2 / 2%
Nere dive	0.3 / 3%	**1299 / 72%**	**868 / 84%**	87 / 34%	80 / 34%	4 / 10%	0.01 / 1%	0.01 / 1%
Coro volu	77 / 60%	**3669 / 78%**	**3712 / 61%**	60 / 12%	100 / 14%	0.4 / 2%	2.6 / 2%	0.2 / 1%
Pygo eleg	9 / 33%	573 / 35%	**10240 / 96%**	1650 / 77%	1486 / 78%	45 / 23%	1 / 4%	0.5 / 3%
Eteo long	0.3 / 3%	8 / 10%	**489 / 74%**	48 / 34%	54 / 41%	13 / 14%	3 / 17%	0.1 / 2%
Maco balt	0.3 / 3%	337 / 74%	**1029 / 95%**	444 / 87%	233 / 75%	22 / 23%	3 / 17%	0.6 / 4%
Nere succ	63 / 70%	9 / 9%	171 / 44%	**685 / 84%**	17 / 15%	2 / 3%	1 / 3%	0.3 / 3%
Hete fili	209 / 63%	1652 / 71%	6318 / 96%	**13673 / 98%**	1740 / 86%	146 / 83%	20 / 35%	3 / 6%
Hydr ulva	-	18 / 22%	925 / 77%	**1777 / 87%**	523 / 59%	44 / 19%	0.3 / 6%	2 / 4%
Bath spec.	5 / 7%	92 / 11%	119 / 18%	170 / 25%	**634 / 65%**	**526 / 60%**	21 / 25%	**453 / 87%**
Spio spec.	-	-	4 / 13%	15 / 4%	30 / 15%	4 / 8%	**245 / 60%**	3 / 6%
Neph cirr	-	-	0.7 / 1%	0.15 / 1%	1.3 / 3%	5 / 8%	**30 / 51%**	0.5 / 1%
Other species	*Coro lacu* *Coro insi*	*Mana aest*	*Cera edul* *Thar mari* *Poly spec* *Scro plan*	*Cera edul* *Thar mari* *Mya aren*	*Scol armi*		*Gast spin* *Ensi spec*	*Haus aren* *Eury pulc*

Table 3.5. Dendrogram representing the TWINSPAN classification based on macrofauna biomass (data set B, n=1243). For each cluster mean ± SD of the environmental variables model salinity (psu), depth (m), maximum ebb and maximum flood current velocity ($m.s^{-1}$), median grain size (µm) and mud content (%) is given. Mean diversity (N0), mean abundance ($ind.m^{-2}$) and mean biomass ($g\ AFDW.m^{-2}$) per cluster are given (mean ± SE). For each cluster mean biomass of the most important macrobenthic species is given, together with its occurrence (% present) in that cluster. Boldfaced numbers represent the main data set structure.



		1	2	3	4	5	6	7	8
Salinity		9.1 ± 5.3	10.6 ± 3.8	21.4 ± 4.8	22.7 ± 1.4	20.6 ± 5.7	19.7 ± 5.0	21.8 ± 5.5	16.4 ± 4.7
Depth		7.9 ± 4.4	-0.7 ± 2.3	0.3 ± 3.3	-0.1 ± 0.7	2.5 ± 5.8	4.0 ± 6.3	9.9 ± 5.6	4.3 ± 4.9
Max. ebb		0.86 ± 0.26	0.39 ± 0.24	0.41 ± 0.14	0.49 ± 0.09	0.54 ± 0.23	0.66 ± 0.23	0.87 ± 0.27	0.77 ± 0.28
Max. flood		0.77 ± 0.27	0.32 ± 0.27	0.31 ± 0.15	0.31 ± 0.14	0.53 ± 0.29	0.60 ± 0.32	0.93 ± 0.28	0.82 ± 0.29
Median		97 ± 91	93 ± 54	112 ± 47	162 ± 58	170 ± 59	213 ± 60	223 ± 63	213 ± 45
Mud content		45 ± 27	41 ± 21	24 ± 19	14 ± 13	11 ± 14	6 ± 9	4 ± 7	3 ± 4
Mean N0		4.4 ± 3.5	5.9 ± 2.1	12.7 ± 3.4	8.7 ± 2.2	7.7 ± 3.6	5.4 ± 3.6	5.7 ± 4.2	2.7 ± 1.6
Mean density		1058 ± 2575	11882 ± 10455	32529 ± 26281	12853 ± 9913	6718 ± 7318	1693 ± 2204	560 ± 1330	601 ± 1100
Mean biomass		0.48 ± 1.21	6.6 ± 5.7	50.8 ± 54.0	24.3 ± 16.8	9.1 ± 23.6	3.47 ± 10.34	1.68 ± 14.04	0.21 ± 0.32
Biomass									
Poly lige	*39*	**0.11 / 39%**	-	-	-	-	-	-	-
Coro volu	*65*	0.009 / 39%	**1.12 / 87%**	0.29 / 40%	0.009 / 11%	0.065 / 10%	0.0005 / 3%	0.00007 / 1%	0.00001 / 1%
Oligochaeta	*58*	0.005 / 87%	**0.23 / 84%**	0.08 / 30%	0.004 / 3%	0.008 / 25%	0.003 / 5%	0.0004 / 6%	0.0004 / 2%
Nere dive	*45*	0.001 / 3%	**3.39 / 87%**	2.36 / 72%	0.53 / 23%	0.27 / 30%	0.07 / 15%	0.00001/ 1%	-
Cera edul	*66*	-	0.0001 / 1%	**14.77 / 86%**	2.25 / 53%	2.18 / 33%	0.11 / 16%	0.0004 / 14%	0. 0001 / 1%
Mya aren	*64*	0.001 / 4%	0.003 / 6%	**6.35 / 75%**	1.09 / 48%	0.02 / 18%	0.0002 / 2%	0.00002 / 1%	-
Pygo eleg	*56*	0.0003 / 19%	0.06 / 36%	**0.55 / 92%**	0.06 / 72%	0.20 / 71%	0.03 / 45%	0.0003 / 4%	0.00004 / 2%
Scro plan	*48*	0.004 / 1%	0.02 / 2%	**4.26 / 60%**	1.05 / 15%	0.004 / 2%	-	0.0001 / 1%	-
Hydr ulva	*48*	-	0.01 / 22%	**0.59 / 77%**	**0.32 / 87%**	0.11 / 59%	0.02 / 19%	0.0001 / 6%	0.0002 / 4%
Maco balt	*41*	0.006 / 7%	0.42 / 81%	**4.80 / 95%**	**3.66 / 86%**	1.88 / 77%	0.36 / 34%	0.015 / 17%	0.003 / 3%
Hete fili	*46*	0.05 / 55%	1.31 / 71%	**9.23 / 96%**	**6.34 / 100%**	1.75 / 84%	0.31 / 82%	0.03 / 34%	0.01 / 14%
Aren mari	*59*	-	-	1.26 / 34%	**8.17 / 75%**	0.37 / 11%	0.50 / 8%	-	-
Bath spec.	*16*	0.007 / 18%	0.02 / 8%	0.03 / 17%	0.05 / 46%	**0.14 / 48%**	**0.11 / 60%**	0.004 / 12%	**0.07 / 87%**
Spio spec.	*41*	-	-	0.002 / 10%	0.0008 / 3%	0.006 / 17%	0.003 / 14%	**0.03 / 56%**	0.0003 / 2%
Neph cirr	*40*	-	-	-	0.006 / 2%	0.003 / 3%	0.012 / 5%	**0.13 / 48%**	0.004 / 2%
Ensis spec.	*33*	-	-	0.15 / 1%	-	-	-	**1.13 / 33%**	-
Haus aren	*31*	-	-	-	-	-	0.0004 / 1%	0.001 / 6%	**0.05 / 31%**

Table 3.6. Results of canonical correspondence analysis (CCA) for macrobenthic assemblages from data set A (sediment data excluded, n = 2612) and data set B (n = 1243), for abundance and biomass data respectively. Given are the eigenvalues of the first and second canonical axis. The percentage variance of the species data and the percentage variance of the species-environment relation explained by the axes is given cumulatively. Both the first canonical eigenvalue as the sum of all canonical eigenvalues were statistically significant by Monte Carlo permutation test (p=0.005).

	Axis 1	*Axis 2*		*Axis 1*	*Axis 2*
Abundance data (dataset A)			Abundance data (dataset B)		
Eigenvalue CCA	0.34	0.20	Eigenvalue CCA	0.40	0.24
% variance of species data	3.5	5.6	% variance of species data	5.2	8.2
Species – environment relation	51.2	81.3	Species – environment relation	42.5	67.6
Correlation of environmental variables with axes			Correlation of envirOnmental variables with axes		
Model salinity	0.42	-0.62	Model salinity	0.40	-0.70
Temporal salinity	0.50	-0.50	Temporal salinity	0.40	-0.50
Depth	0.62	0.27	Depth	0.68	0.32
Maximum ebb current velocity	0.62	0.36	Maximum ebb current velocity	0.62	0.26
Maximum flood current velocity	0.66	0.36	Maximum flood current velocity	0.66	0.36
			Median grain size	0.57	-0.02
			Mud content	0.48	0.18

	Axis 1	*Axis 2*		*Axis 1*	*Axis 2*
Biomass data (dataset A)			Biomass data (dataset B)		
Eigenvalue CCA	0.51	0.29	Eigenvalue CCA	0.29	0.14
% variance of species data	3.1	4.8	% variance of species data	2.1	3.1
Species – environment relation	50.3	79.4	Species – environment relation	55.6	82.1
Correlation of envirOnmental variables with axes			Correlation of envirOnmental variables with axes		
Model salinity	0.29	-0.66	Model salinity	-0.70	0.13
Temporal salinity	0.36	-0.52	Temporal salinity	-0.56	-0.01
Depth	0.77	0.21	Depth	-0.14	0.29
Maximum ebb current velocity	0.67	0.04	Maximum ebb current velocity	-0.20	0.22
Maximum flood current velocity	0.70	0.07	Maximum flood current velocity	-0.14	0.38
			Median grain size	-0.31	0.14
			Mud content	0.35	-0.11

all biomass clusters were similar to the abundance clusters, but the contributions of the individual species, as indicated by the indicator values, differed.

In a first division two clusters (7-8) were separated, both characterized by high current velocities, a high median grain size and low mud content. Samples of cluster 7 were mainly situated in the subtidal (95% of the samples), polyhaline zone, but this community occurred up to the mesohaline zone. Abundance and biomass were low, with indicator species *Spio* spp. and *Nephtys cirrosa*. Cluster 8 was situated more in the mesohaline zone, with 60% of the samples observed subtidally. Cluster 8 had the lowest diversity, abundance and biomass of all clusters. Indicator species was *Bathyporeia* spp.

The remaining samples were then further separated in two clusters (clusters 1-2), representing mainly the β-mesohaline zone (salinity region 4), and four clusters (clusters 3-6) representing mainly the polyhaline and α-mesohaline zone (salinity regions 1-3). Clusters 1 and 2 (with approx. 95% and

85% of the samples from salinity region 4) were separated into a characteristic subtidal cluster with high current velocities (cluster 1) and an intertidal cluster with low current velocities (cluster 2). Both clusters had high mud contents. Cluster 1 had more samples in the biomass classification, with also 35 samples of abundance cluster 2 included, which were separated from the 30 samples in a next division. Indicator species of cluster 1 was *Polydora ligerica*. Other characteristic species for this cluster were several amphipods such as *Corophium lacustre* and *Pleusymtes glaber*, and Oligochaeta. Mean biomass was low. Cluster 2 had a relatively high abundance and indicator species were *C. volutator*, Oligochaeta and *N. diversicolor*, the latter having the highest contribution to the biomass.

The communities revealing from clusters 5 and 6 could be considered as transitional between the low diversity clusters 7-8 and the high diversity clusters 3-4. In both clusters a relatively high proportion of winter and spring samples was observed. Samples of cluster 6 were found in all salinity regions, in the subtidal as well as in the intertidal zone. Abiotic characterization of this cluster resembled cluster 8; only mean current velocities were somewhat lower. Abundance was relatively low. As for cluster 8, the indicator species was *Bathyporeia* spp., but in this cluster also a higher occurrence and higher densities of some characteristic species from clusters 3-4 were observed (e.g. *H. filiformis*). Cluster 5 was mainly found in the intertidal zone of both the polyhaline and α-mesohaline zone, and was characterized by intermediate current velocities and fine/medium sands with a low mud content. Biomass cluster 5 had much less samples as abundance cluster 5. Abundance and biomass was much lower as compared to cluster 4, but the occurrence of several species was similar (e.g. *P. elegans, M. balthica, H. filiformis*). As for cluster 6, the indicator species of cluster 5 was *Bathyporeia* spp., but this species only marginally contributed to the total biomass.

Cluster 3 and 4 were intertidal clusters (>92%), characterized by low current velocities, and by fine sand sediments with a relatively high mud content. Biomass cluster 3 contained a lot of samples of abundance cluster 4. The clusters represented the macrobenthic communities with the highest diversity, abundance and biomass. Cluster 3 had the highest mean diversity, with the indicator species for abundance being *P. elegans*, whereas bivalves contributed most to the biomass, with the suspension feeder *C. edule* having the largest contribution. Indicator species for cluster 4 differed, with *H. filiformis* contributing most to abundance. Biomass in this cluster was mainly dominated by the sub-surface deposit feeders *Arenicola marina* and *H. filiformis*. This cluster was also characterized by a higher proportion of spring and winter samples as compared to cluster 3.

Ordination and relation with the abiotic environmental variables

The results of the different CCA ordinations are summarized in Table 3.6. Ordination biplots are presented for the abundance data sets A and B respectively (Figures 3.6a-3.7). Seasonal changes, by adding sampling month as covariables in the CCA, appeared of no importance in explaining the main differences in species composition in both analyses. The relation between the ordination axes and the environmental variables were similar for all data sets. The first axis was strongly correlated with

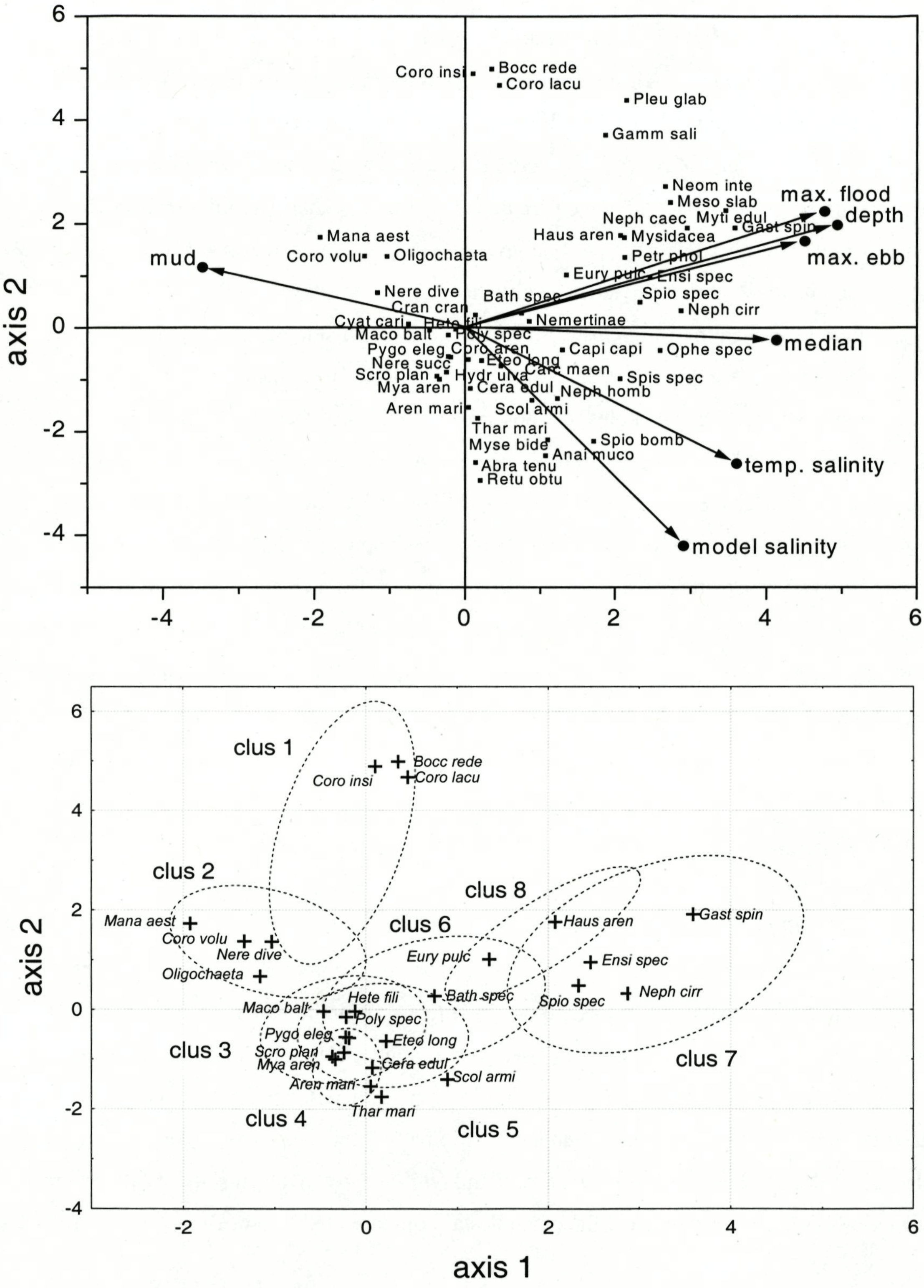


Figure 3.6. Canonical Correspondence Analysis (CCA) ordination biplots based on the analysis of abundance data of dataset B (with sediment data, n= 1243). The top figure shows the species distributions in relation to environmental variables (max. ebb and max. flood = maximum ebb and flood current velocity; mud = mud content; median = median grain size; temp. salinity = temporal salinity). The orthogonal projection of a species point onto an environmental arrow represents the approximate center of the species distribution along that particular environmental gradient. The bottom figure shows the 75 percent confidence regions of the sample scores for each cluster. For results on the CCA analysis see Table 3.6. For abbreviation of the macrobenthic species names: see Appendix).

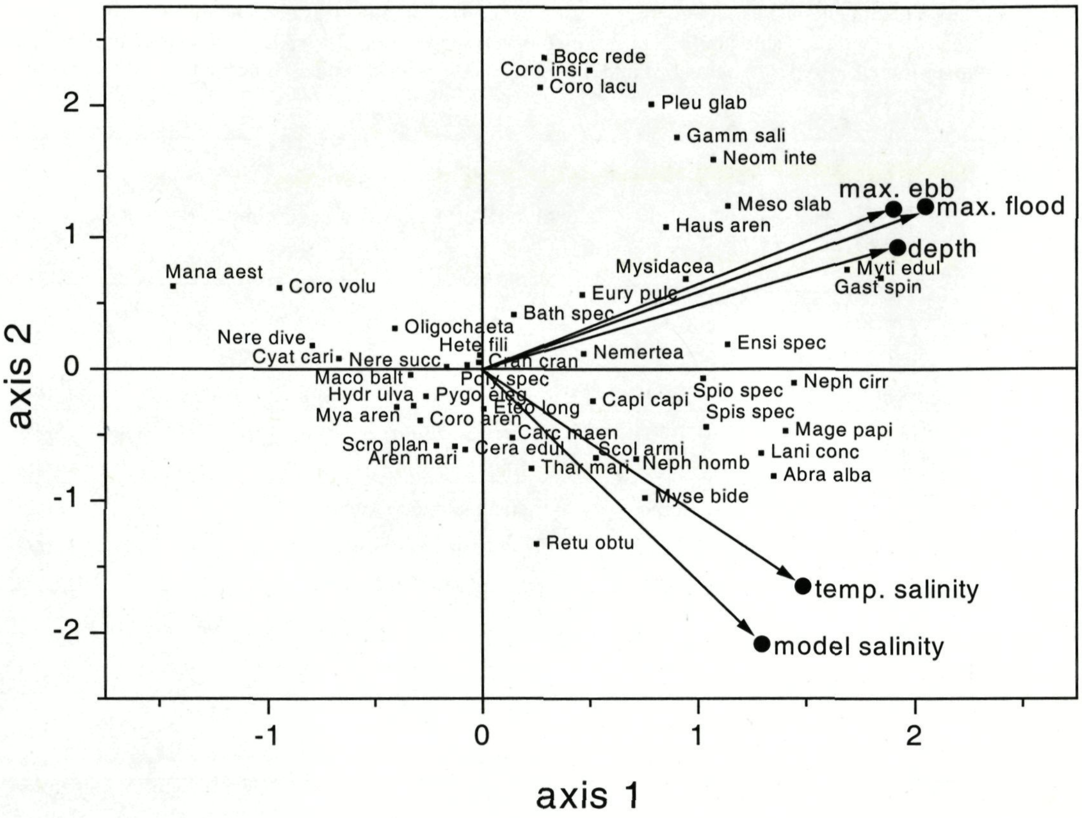


Figure 3.7. Canonical Correspondence Analysis (CCA) ordination biplot based on the analysis of abundance data of dataset A (without sediment data, n= 2612). The figure shows the species distributions in relation to environmental variables (max. ebb and max. flood = maximum ebb and flood current velocity; temp. salinity = temporal salinity). The orthogonal projection of a species point onto an environmental arrow represents the approximate center of the species distribution along that particular environmental gradient. For results on the CCA analysis see Table 3.6. For abbreviation of the macrobenthic species names: see Appendix).

depth, maximum flood and ebb current velocity. When sediment characteristics were included, these also correlated with the first axis, but correlation was less strong. The second axis represented the salinity gradient. Only in the CCA analysis with biomass data set B the opposite was observed, with salinity correlating with the first axis, and a weak correlation of max. flood current velocity and depth with the second axis. The third ordination axis (not presented) had very low eigenvalues in all analysis, and showed highest correlation with sediment characteristics (median grain size (r= -0.38) for abundance data and mud content (r=0.26) for biomass data respectively).

Forward selection on the abundance data sets A and B corroborated the correlations observed between ordination axes and environmental variables (Table 3.7). With each one variable as the only environmental variable (marginal effects), the highest eigenvalues were observed for depth and current velocity estimates, followed by the salinity estimates, but differences were relatively small. When included (data set B), lowest eigenvalues were observed for median grain size and mud content. Forward selection (conditional effects) showed that depth or current velocity and model salinity added most to the total fit. As depth was closely correlated with current velocities and temporal salinity with model salinity, the extra fit of these variables is less, because already large part of the effect of these

Table 3.7. Ranking environmental variables in importance by their marginal (left) and conditional (right) effects of the macrobenthos in data set A (sediment data excluded, n=2612) and data set B (n= 1243), as obtained by forward selection on the CCA. (λ_1 = fit = eigenvalue with variable j only; λ_a = additional fit = increase in eigenvalue; p = significance level of the effect, as obtained with a Monte Carlo permutation test under the null model with 199 random permutations). For results on the CCA analysis see Table 3.6.

Abundance data (data set A, n=2612)
Marginal effects (forward: step 1) | Conditional effects (forward: continued)

j	*variable*	λ_1	*p*	*j*	*variable*	λ_1	*p*
1	max. flood current velocity	.28	.005	1	max. flood current velocity	.28	.005
2	max. ebb current velocity	.25	.005	2	model salinity	.23 (.51)	.005
3	depth	.24	.005	3	depth	.08 (.59)	.005
4	model salinity	.23	.005	4	max. ebb current velocity	.04 (.63)	.005
5	temporal salinity	.23	.005	5	temporal salinity	.04 (.67)	.005

Abundance data (data set b, n=1243)
Marginal effects (forward: step 1) | Conditional effects (forward: continued)

j	*variable*	λ_1	*p*	*j*	*variable*	λ_1	*p*
1	depth	.31	.005	1	depth	.31	.005
2	max. flood current velocity	.28	.005	2	model salinity	.26 (.57)	.005
3	model salinity	.26	.005	3	median grain size	.15 (.72)	.005
4	temporal salinity	.25	.005	4	max. flood current velocity	.07 (.79)	.005
5	max. ebb current velocity	.25	.005	5	mud content	.05 (.84)	.005
6	median grain size	.24	.005	6	max. ebb current velocity	.05 (.89)	.005
7	mud content	.20	.005	7	temporal salinity	.04 (.93)	.005

variables was already explained. When included (data set B), median grain size added significantly to the total fit, but eigenvalue was lower than for depth and model salinity.

The position of the different macrobenthic species along the two axes was similar for the CCA analyses on abundance data of data set A and data set B respectively (Figures 3.6a-3.7). Species which were mainly observed in the subtidal zone, at high current velocities, were situated at the right side of the biplot (e.g. *Gastrosaccus spinifer, Haustorius arenarius, N. cirrosa, P. ligerica*), whereas species characteristic for the intertidal zone, observed at low current velocities, where observed at the left side of the biplot (e.g. *C. volutator, N. diversicolor, M. arenaria, H. ulvae*). Species characteristic for the polyhaline zone were mainly observed in the down right quadrant of the biplot (e.g. *Abra tenuis, Anaitides mucosa, T. marioni, Nephtys hombergii*). At the other end, characteristic species for the β-mesohaline zone were e.g. *C. volutator, Manaeyunkia aestuarina* and *P. ligerica*. The position of the different macrobenthos species in the biplot resembled the division in indicator species over the different clusters, as observed by superimposing the different clusters on the bipot (Figure 3.6b). The superimposed clusters on the CCA diagram showed to some extent overlap. Especially the clusters 3-6, which clustered at a higher dichotomy, largely overlap. The β-mesohaline clusters 1 and 2 clearly discriminated, and also the subtidal clusters 7 and 8 were separated from the other clusters.

Discussion

Trends along the longitudinal (salinity) and vertical (depth) gradient

In their review HEIP et al. (1995) concluded that, because of a biased sampling strategy, few macrobenthic studies dealt with the two major gradients in estuarine benthic habitats: the salinity gradient along the estuary (longitudinal) and the gradients from high intertidal to deep subtidal sites (vertical gradient). The large data set available for the Schelde estuary allowed us to thoroughly analyze these both gradients, and relate macrobenthic species distributions to the predominant environmental variables.

The univariate and multivariate analyses clearly demonstrated the role of both salinity and depth in relation to diversity, abundance and biomass of the macrobenthos. Many studies have demonstrated that salinity is a major factor affecting macrofauna species distributions and community structure within estuaries. The pattern of species richness and diversity declining with decreasing salinity is a recurring one in most estuaries (REMANE & SCHLIEPER 1971; BOESCH 1977; WOLFF 1983; DITTMER 1983; MICHAELIS 1983; MANNINO & MONTAGNA 1997) and our data support this. Not only mean number of species per sample decreased with decreasing salinity, but also total number of species decreased (see also YSEBAERT et al. 1993, 1998a, in press). In several estuaries also a trend from lower biomass in the upper estuarine regions to higher biomass in the more downstream regions was observed, e.g. Ems, Schelde and Elbe estuary (MEIRE et al. 1991; YSEBAERT et al. 1998a), James River Estuary (SCHAFFNER et al. 1987), Lavaca Bay, Texas (KALKE & MONTAGNA 1991), Chesapeake Bay (DAUER 1993). In our study the same trend was observed, although it was most pronounced in the intertidal zone, and less clear in the subtidal zone. In contrast to diversity and biomass, no clear trend in abundance was observed, similar to observations on 50 intertidal locations along the salinity gradient of the Schelde estuary (YSEBAERT et al. 1993). Other studies on the intertidal macrobenthos of the Schelde estuary, based on a much smaller sampling effort, revealed remarkable similar values for density and biomass (MEIRE et al. 1991; YSEBAERT et al. 1993, 1998a).

Only a few studies have dealt with the zonation of macrobenthos from high intertidal to deep subtidal sites (e.g. ELLIOT & TAYLOR 1989). Our study showed much higher values of diversity, abundance and biomass in the intertidal zone as compared to the subtidal zone. Especially in the subtidal channels of the Schelde estuary tidal current speeds and instability of the sediment clearly become the limiting factors, leading to very poor communities. In more shallow estuaries, such as James River Estuary (SCHAFFNER et al. 1987), subtidal macrobenthic biomass might reach high values.

HEIP et al. (1995) showed that on a system-wide scale, biomass values for complete benthic assemblages among estuaries are not very different, but that variability within an estuary is usually high. The mean biomass values found in this study are within the range described by HEIP et al. (1995).

The role of the abiotic environment

The different multivariate analyses, based on macrofauna abundance or biomass, and data sets with or without sediment characteristics included, confirmed the strong relationships between the macrobenthic assemblages and the predominant forces (gradients) in the Schelde estuary. CRAEYMEERSCH (1999), based on a more limited data set for the Westerschelde, derived similar results.

A first gradient is related to depth, which reflects also hydrodynamic conditions. This was clear from the ordinations, in which depth and current velocities were closely correlated with the first of the ordination axes. Therefore, it appeared that the vertical gradient, reflecting the hydrodynamical regime was dominant upon the salinity gradient. A second gradient (second axis in the ordination) was clearly related to salinity and confirms the observations from the univariate analysis.

Sediment characteristics appeared to be more correlated with depth and current velocities, but correlation was rather weak. It was apparent from the ordination analyses that sediment characteristics added less to the total fit of the model than depth/current velocities on the one hand and salinity on the other hand. However, median grain size still explained a significant part not yet explained by the two other main gradients. In a study on macrobenthic responses to natural and contaminant-related gradients in Northern Gulf of Mexico estuaries, RAKOCINSKI et al. (1997) showed three primary natural gradients in a CCA analysis: CCA axis 1 represented a predominant salinity gradient, CCA axis 2 a predominant depth gradient, and CCA axis 3 a gradient in sediment silt/clay content. RAKOCINSKI et al. (1997) did not include current velocities, and sampling stations were restricted to the subtidal zone, probably explaining why salinity was the most dominant gradient. WARWICK et al. (1991), investigating the intertidal macrobenthic community structure of six British estuaries, separated sites mainly along two axes, one determined by static variables (e.g. sediment grain size and organic content), and the other by dynamic variables (i.e. current velocities), but in this study the salinity range was restricted. In summary, therefore, the relative importance of the different gradients will differ among estuaries, depending on the local physical and physicochemical conditions. Also the scale at which studies are performed (e.g. subtidal *v* intertidal or the inclusion of the freshwater tidal zone into the survey) will influence the perception of their relative importance. Collinearity between environmental variables may also differ among estuaries or among zones within an estuary. For instance, in our study mean mud content appeared to be much higher in salinity region 4 (meso-/oligohaline) as compared to the higher salinity regions, whereas SCHLACHER & WOOLDRIDGE (1996) observed the opposite for the Gamtoos estuary in South-Africa.

Interactions between soft-sediment macro-invertebrates and their environment not only include responses to the physicochemical environment (tolerances), but also the effects of species that modify the substratum (biogenic habitat modifiers), as well as biological interactions, such as predation and competition, will determine the distribution of a certain species (WILSON 1991; OLAFSSON et al. 1994). Although biological interactions are thought to operate within the constraints imposed by large-scale physical factors (LEGENDRE et al. 1997; MCARDLE et al. 1997; THRUSH et al. 1997, 1999), more information is needed about the interaction of both physical and biological factors.

Macrobenthic assemblages

The macrobenthic assemblages, distinguished at a broad, estuarine scale, are related to gradients in the environmental conditions observed along the estuary. Similar macrobenthic assemblages were observed by CRAEYMEERSCH (1999), although our results provided additional information on the lower salinity zones of the estuary.

Some macrobenthic assemblages are typically related to the subtidal zone, where highest current velocities were observed. A first subtidal assemblage was mainly situated in the polyhaline zone, and occurred in medium sand sediments with a very low mud content. This assemblage was characterized by the polychaetes *Nepthys cirrosa* and *Spio* spp. *N. cirrosa* is known as a typical subtidal species, inhabiting sandy sediments (CLARK & HADERLIE 1960; WOLFF 1971). In this assemblage also often species were observed which belonged more to the hyperbenthos, such as the mysid *Gastrosaccus spinifer* (MEES et al. 1993, 1995). In a few samples high biomass values were observed of some bivalve species, such as *Ensis* and *Spisula*, but in general diversity, abundance and biomass were low for this assemblage.

A second subtidal assemblage was found mainly in the mesohaline zone, but this assemblage extended both into the polyhaline as into the oligohaline zone of the estuary. Diversity, abundance and biomass of the macrobenthos were very low. This assemblage was characterized by the very mobile amphipod *Bathyporeia spp.* This species is capable of very fast swimming and digging (CROKER 1967; NICOLAISEN & KANNEWORFF 1969; SAMEOTO 1969) and *Bathyporeia spp.*, like most Haustoriidae, is a typical, well adapted inhabitant of unstable, sandy sediments (BOUSFIELD 1970; KHAYRALLAH & JONES 1980) and exposed beaches with a lot of wave action (SHACKLEY 1981). Other characteristic species for this assemblage were the amphipod *Haustorius arenarius* and the isopod *Eurydice pulchra*. This assemblage was not only restricted to the subtidal zone, but extended into the intertidal zone.

A third subtidal community was clearly restricted to the most upstream part of the study area (β-meso-/oligohaline zone). Here, this zone being part of the turbidity maximum area of the estuary, high current velocities often coincided with a muddy or very fine sand bottom sediment. This assemblage was characterized by some typical 'genuine brackish water' species (WOLFF 1973; MICHAELIS et al. 1992), with indicator species being *Polydora ligerica* (YSEBAERT et al. in press). In samples, containing hard substrates such as stones and pieces of wood, a relatively species rich community was observed, with several amphipod species like *Corophium lacustre*, *Corophium insidiosum*, *and Pleusymtes glaber*. In very muddy sediments, only Oligochaeta and *H. filiformis* were observed.

In the intertidal zone assemblages were in the first place determined by salinity, and secondly by the sediment composition (see also YSEBAERT et al. 1993, 1998a). A first assemblage was found in the polyhaline zone of the estuary, extending to some extent into salinity region 3. Current velocities are much lower as compared to the subtidal assemblages (low dynamic areas), and sediments consist of very fine sand or mud. Diversity, abundance and biomass of the macrobenthos are much higher than in the other assemblages. Abundance of this assemblage is mainly determined by spionid (*P. elegans*) and capittelid species (*H. filiformis*). Biomass is mainly determined by bivalves, of which the suspension feeder *C. edule* is the most important. In the more sandy sediments of the polyhaline zone a second intertidal assemblage was observed, which was characterized by a high biomass of the sub-surface deposit feeder *A. marina*. This assemblage was only obvious from the biomass classification, as *A. marina* was observed only in very low densities. Diversity, abundance and biomass were lower, with another sub-surface deposit feeder, *H. filiformis*, dominating this assemblage numerically. Both polyhaline assemblages are also commonly observed in other estuaries and shallow coastal zones, such as the Wadden Sea (e.g. BEUKEMA 1976, 1981; DÖRJES et al. 1986).

A third intertidal assemblage is found in the mesohaline zone of the estuary, especially in salinity region 4. As for the first intertidal assemblage, this assemblage occurred in the low dynamic areas, characterized by sediments with a high mud content, but with a lower macrobenthos species diversity and biomass. Indicator species was *C. volutator*, this species being almost absent in the polyhaline zone of the estuary. *N. diversicolor* was the main species determining biomass in this assemblage. In this part of the estuary also Oligochaeta become a predominant part of the benthic community, a dominance which increase towards the oligohaline zone of the estuary (YSEBAERT et al., 1993), and which is also more pronounced in spring as compared to autumn (YSEBAERT et al. subm). The nearly absence of *C. volutator* from the polyhaline zone could be due to a negative effect of *C. edule* and especially *A. marina* (e.g. FLACH 1992, 1996), both very common in the polyhaline zone of the Schelde estuary. In the Wadden Sea a zonation pattern was observed with a *Corophium* zone in the muddy upper tidal flats and a zone dominated by *A. marina* and *C. edule* at the lower edges. In the Schelde estuary it rather appeared that this pattern was observed along the longitudinal salinity gradient.

A fourth assemblage could be considered as the intertidal extension of the second subtidal assemblage, characterized by the amphipod *Bathyporeia spp.* This assemblage is observed at intermediate current velocities in fine/medium sand sediments with a low mud content. Several species from the other assemblages were also observed in this assemblage, but at much lower densities. A characteristic polychaete of these sandy sediments in the polyhaline zone was *Scoloplos armiger*. In the most dynamic areas, sand flats characterized by pronounced megaripples, only a few mobile crustaceans were observed. This assemblage resembles the benthic communities that are found on exposed sand beaches with a pronounced wave action (SHACKLEY 1981; DEGRAER et al. 1999).

It should be emphasized that the previously described assemblages should not be considered as static, nor that the transition from one assemblage to another is abrupt. This was noticed from the large overlap in the clusters superimposed on the ordination diagrams. The exact extent and position of estuarine zones will differ between assemblages, seasons and years, but their persistent occurrence points to a real underlying structure in the distribution of biota of the estuarine eocystem at large (BULGER et al. 1993).

Trophic and functional structure

The search for a more meaningful measure of community response (e.g. to disturbance) led investigators to consider trophic ecology (feeding ecology) of macrobenthos (PEARSON & ROSENBERG 1978; BOESCH & ROSENBERG 1981; GASTON et al. 1998). Trophic ecology provides a functional approach to help clarify the complex community changes that occurs along estuarine gradients.

Based on field evidence, a relation between system-averaged macrobenthic biomass and pelagic primary productivity of shallow well-mixed estuarine systems was presented by HERMAN et al. (1999). Between 5 and 25% of the annual primary production is consumed by macrobenthos respiration. On a system-average basis, suspension feeders are often the dominant component (with respect to biomass) of estuarine benthic assemblages (HEIP et al. 1995). Also in the Schelde estuary, suspension feeders, mainly *C. edule*, dominate the macrobenthic biomass in the polyhaline zone. However, in the turbid Schelde estuary and other estuaries at the low productive end of this spectrum, suspension feeders are, both in absolute and relative terms, less dominant compared to estuaries with higher productivities (HERMAN et al. 1999). In the Schelde estuary light, rather than nutrients, is limiting primary production. The underwater light climate is better in the most seaward part (polyhaline zone) of the estuary, and one can conclude that the benthic (suspension feeder) biomass is, in general, following the trend of primary productivity in the system (HEIP et al. 1995).

HERMAN et al. (1999) showed that in the comparison of macrofauna biomass in different ecosystems, particularly the suspension feeders seem to constitute the most variable part. Indeed, suspension feeders appeared very patchy in the Schelde estuary, with 68 samples containing a suspension feeder biomass > 50 g AFDW m^{-2}, which was 66% of the total suspension feeder biomass observed. Their distribution, being dependent on pelagic food sources, within the polyhaline zone of the estuary will be mainly determined by the hydrodynamical conditions. In the subtidal zone, current speeds and instability of the sediment will prevent suspension feeders from settling down. Where conditions are favourable, such as on hard substrates (peat banks, stones), high biomass of for instance mussel spat (up to 455 g AFDW m^{-2}) can be observed (pers. observ.). In the intertidal zone, the distribution of suspension feeder will also be determined by the hydrodynamical conditions, but the positive relationship that have been suggested between the suspension feeders' biomass and current velocities might not be generally valid. Indeed, studies on an intertidal sand flat of the Westerschelde demonstrated that biomass of the suspension feeder *C. edule* was highest in the zone with lowest current velocities, probably depending on sinking material (HERMAN et al. 1999).

A higher primary production in the mesohaline zone of the estuary would probably lead to an increase in suspension feeder biomass. Especially *Mya arenaria*, a bivalve well adapted to mesohaline salinity conditions, would profit of such a situation. However, at the meso-/oligohaline transition zone, where salinity conditions show large, seasonal fluctuations, conditions will become unfavourable.

Deposit feeders are much more evenly distributed over space within an estuary, and their biomass is much less variable from one system to another than the biomass of suspension feeders (HERMAN et al. 1999). The Schelde estuary receives large quantities of allochtonous organic matter and nutrients, and it is supposed that there is no food limitation for deposit feeders, although also qualitative aspects should be taken into account (e.g. DAUWE 1999). On a large scale, the distribution of deposit feeders, together with their food, will be determined to a great extent by the hydrodynamical conditions. In the intertidal zone, deposit feeders, especially grazers and surface deposit feeders, also depend to a large extent on microphytobenthos production and, as this production is relatively constant over a broad range of environments, a relative constancy of the macrofauna groups dependent on this source may be expected (HERMAN et al. in press). In our study, deposit feeders were abundant along the complete salinity gradient. However, biomass of deposit feeders, especially the surface deposit feeders, was highest in the polyhaline zone (salinity region 1) and decreased with decreasing salinities. Several factors could explain this decrease. Firstly, assigning a species to one functional group is difficult as many estuarine macrobenthic species are flexible in their natural history and response to environmental conditions (high generalism). Many species of surface deposit feeders are known to be facultative suspension feeders (e.g. *M. balthica* (OLAFSSON 1986; KAMERMANS 1994) and 'interface' feeding spionid polychaetes (DAUER et al. 1981; TAGHON & GREENE 1992)). Therefore, surface deposit feeders in the polyhaline zone might profit from the higher phytoplankton primary production (high quality food source) in this part of the estuary, resulting in a higher biomass. Secondly, disturbance and stress increases towards the lower salinity zones, as a consequence of the highly varying salinity conditions here (physiological constraints). Additionally, a maximum turbidity zone is situated near the freshwater-seawater interface (oligohaline zone) and due to a high input of allochtonous organic matter and nutrients, microbial activity is pronounced in this region, resulting in oxygen depletion observed during several months a year, especially in summer (e.g. GOOSEN et al.

1999). This highly variable environment causes numerous, perhaps constant disturbances that might result in communities that seldom progress beyond early benthic-community succession. The macrobenthic species observed in this zone of the estuary are typically very mobile (e.g. the amphipod *C. volutator*), opportunistic (tubificid Oligochaeta, capitellid *H. filiformis*) or omnivorous (the nereid *N. diversicolor*), strategies which resemble the early response to 'succession after disturbance series' (RHOADS et al. 1978) or 'distance to pollution source series' (PEARSON & ROSENBERG 1978). In this zone of the estuary probably physical and physiological stress coincides with 'high loading' stress. On top of that, sediment contamination with metals and organic micropollutants is rather high, provoking additional stress (e.g. RAKOCINSKI et al. 1997). Unravelling the contribution and interaction of each of these multiple stressors is necessary in order to determine natural versus human induced disturbances.

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Appendix 3.1. List of the macrobenthic species mentioned in the text and figures, together with their abbrevations used. For each species the feeding type is given. SF = suspension feeder; SDF = surface deposit feeder; SSDF = sub-surface deposit feeder; O = omnivore; P = predator

Abbrevation	Species name	Feeding type
Anai muco	*Anaitides mucosa*	P
Abra tenu	*Abra tenuis*	SF
Aren mari	*Arenicola marina*	SSDF
Bath spp.	*Bathyporeia spp.*	SDF
Bocc rede	*Polydora ligerica*	SDF
Capi capi	*Capitella capitata*	SSDF
Carc maen	*Carcinus maenas*	O
Cera edul	*Cerastoderma edule*	SF
Coro aren	*Corophium arenarium*	SDF
Coro insi	*Corophium insidiosum*	SDF
Coro lacu	*Corophium lacustre*	SDF
Coro volu	*Corophium volutator*	SDF
Cran cran	*Crangon crangon*	P
Cyat cari	*Cyathura carinata*	P
Ensi spp.	*Ensis spp.*	SF
Eteo long	*Eteone longa*	P
Eury pulc	*Eurydice pulchra*	P
Gamm sali	*Gammarus salinus*	O
Gast spin	*Gastrosaccus spinifer*	O
Haus aren	*Haustorius arenarius*	SF
Hete fili	*Heteromastus filiformis*	SSDF
Hydr ulva	*Hydrobia ulvae*	SDF
Maco balt	*Macoma balthica*	SDF
Mana aest	*Manayunkia aestuarina*	SF
Meso slab	*Mesopodopsis slabberi*	SDF
Mya aren	*Mya arenaria*	SF
Myse bide	*Mysella bidentata*	SDF
Myti edul	*Mytilus edulis*	SF
Nemertinae	*Nemertinae*	P
Neom inte	*Neomysis integer*	O
Neph cirr	*Nephtys cirrosa*	O
Neph homb	*Nepthys hombergii*	O
Nere dive	*Nereis diversicolor*	O
Nere succ	*Nereis succinea*	O
Oligo	*Oligochaeta*	SSDF
Ophe spp.	*Ophelia spp.*	SDF
Petr phol	*Petricola pholadiformis*	SF
Pleu glab	*Pleusymtes glaber*	O
Pygo eleg	*Pygospio elegans*	SDF
Poly spp.	*Polydora spp.*	SF
Retu obtu	*Retusa obtusata*	P
Scol armi	*Scoloplos armiger*	SSDF
Scro plan	*Scrobicularia plana*	SDF
Spio bomb	*Spiophanes bombyx*	SDF
Spio spp.	*Spio spp.*	SDF
Spis spp.	*Spisula spp.*	SF
Thar mari	*Tharyx marioni*	SDF

Chapter four

Spatio-temporal patterns of intertidal macrobenthic communities in the Schelde estuary, NW-Europe

T. Ysebaert, P. Meire, and N. De Regge

Abstract

The Schelde estuary (NW-Europe) was investigated for spatial and temporal variation of macrobenthos community structure and function. Five locations were sampled monthly during two years to investigate changes in macroinfaunal species assemblages.

Spatial variation among the five locations was larger than seasonal variation and was on a regional scale strongly influenced by salinity and on a local scale by sediment characteristics. Abundance and biomass were highest at the polyhaline location, and decreased towards the meso-/oligohaline locations. The Abundance Biomass Comparison-curves indicated that the structural complexity level decreased from the polyhaline zone towards the mesohaline zone. Here only one to two species dominated the community. Trophic diversity was highest at Paulina, where the biomass was, to a great extent, dominated by suspension feeders (*C. edule*). In the mesohaline locations deposit feeders dominated the biomass, whereas omnivores (*N. diversicolor*) mainly dominated in the low salinity locations.

Seasonality was evident for all diversity measures, total abundance and biomass at all five locations. All commonly observed macrobenthic species showed distinct seasonal patterns. The general pattern was that of an increase in abundance during late spring and early summer, coinciding with an increase in temperature, followed by a decrease towards winter. This decrease could be very sharp in time, or slowly decreasing towards winter, depending on the species and/or location considered. Lowest abundances were observed in late winter and early spring. Seasonal variation in biomass followed abundance patterns, especially at the low salinity locations.

Community variation was higher during periods of peak recruitment (spring-early summer) than during non-recruitment periods. Variability in environmental variables (mainly salinity) was highest at the low salinity locations, and this coincided with highest variability in macrobenthic communities. It is argued that in the meso-/oligohaline transition zone, where salinity conditions show large, seasonal fluctuations, benthic communities change frequently, resulting in communities that seldom progress beyond early benthic-community succession. On the other hand, macrobenthic communities in the polyhaline zone appeared to be dominated more by long living species.

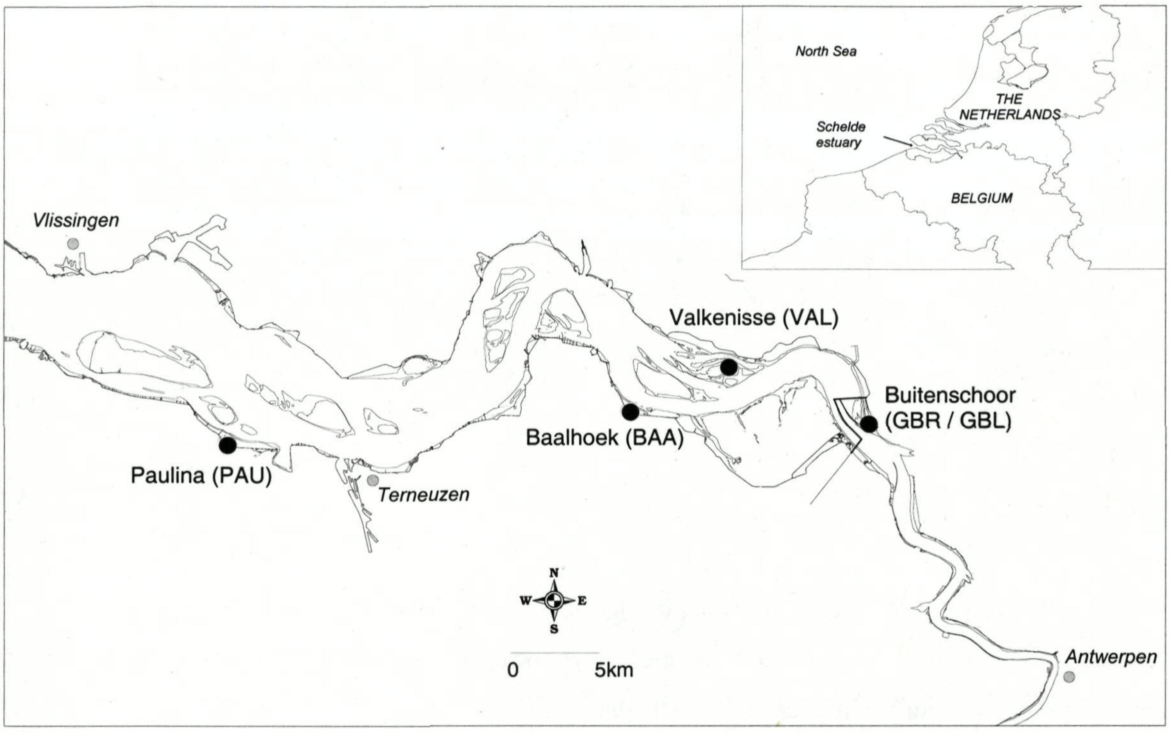


Figure 4.1. Map of the Schelde estuary with the position of the four intertidal mudflats and the five sampling locations respectively.

Introduction

Estuaries, in general, are shallow, open and dynamic systems, that are characterised by widely varying and often unpredictable hydrological, morphological and chemical conditions (DAY et al. 1989). In the estuarine ecosystem, macrobenthos is one of the important structuring elements of the food web and plays an important role in the system dynamics of estuaries (HERMAN et al. 1999). Several studies indicate that macrozoobenthic populations show large variations both in space and time (DÖRJES et al. 1986; HEIP et al. 1987; HOLLAND et al. 1987; BEUKEMA 1989; WARWICK et al. 1991; YSEBAERT et al. 1993; DAUER 1996). However, short- and mid-term seasonal variations of the quantitative composition of estuarine soft-bottom macrobenthic populations and assemblages along the estuarine salinity gradient are not well documented. Knowledge of the environmental variability and related population effects on a wide range of spatio-temporal scales is fundamental to better understand the functioning, stability and resilience of estuarine ecosystems and how humans influence them (WIENS 1989; LEVIN 1992; THRUSH et al. 1999).

For the Schelde estuary, one of the most extensively studied European estuaries (MEIRE & VINCX 1993; HEIP & HERMAN 1995; HERMAN & HEIP 1999; VAN DAMME et al. subm.), large scale spatial patterns of the macrobenthos are well known (e.g. YSEBAERT et al. 1993, 1998a) and long-term monitoring programmes are being conducted (CRAEYMEERSCH, 1999), but information on the short-term seasonal variation is lacking.

The purpose of the present work is to quantitfy the spatial and temporal (seasonal) variability in macrobenthic species composition, species assemblages and functional diversity (trophic structure) along the salinity gradient in the Schelde estuary. The analysis includes the identification of the environmental factors controlling the observed spatial and temporal patterns of variability in the macrobenthic communities for a two year study period. Spatial analysis includes regional (among salinity zones) and local (muddy versus sandy sampling location) patterns.

Materials and methods

Study area

The Schelde estuary, a macrotidal, turbid, nutrient-rich, heterotrophic coastal plain estuary, is situated in NW Europe, near the border between the Netherlands and Belgium (Figure 4.1). It measures 160 km with a surface area of approx. 350 km^2. Mean tidal amplitude increases from 3.8 m at Vlissingen to 4.94 m near the Dutch-Belgian border. The river discharge varies from 20 m^{3}s^{-1} during summer to 600 m^{3}s^{-1} during winter, with a mean yearly average of 105 m^{3}s^{-1} (BAEYENS et al. 1998). The residence time of the water in the estuary is rather high, ranging from one to three months, depending on the river discharge (SOETAERT & HERMAN 1995b). The most seaward region has a residence time of about 10-15 days. A maximum turbidity zone is found near the Dutch-Belgian border, but this zone moves over a large distance, up to the freshwater tidal zone, depending among others on the freshwater runoff (BAEYENS et al. 1998; HERMAN & HEIP 1999). Also in this zone of the estuary oxygen concentration decreases rapidly, mainly due to the heavy loading with nutrients and organic material, causing high microbial activity (e.g. GOOSEN et al. 1995, 1999). The estuary is subjected to extensive dredging and dumping, being 10–15 10^6 m^3 per year at present, to maintain the shipping channel to the port of Antwerpen.

Sampling locations were situated in the downstream part of the estuary between the Dutch-Belgian border and Vlissingen (Figure 4.1). This part of the estuary is well mixed, and characterized by a complex network of flood and ebb channels surrounded by several large intertidal flats and marshes (35% of the area). The water column is moderately to well oxygenated, with oxygen saturation increasing from 20-60 % at the border to 90-100 % at the mouth of the estuary.

The study was carried out on five sampling loations situated on four intertidal mudflats (Figure 4.1):

- Location Paulinaschor (approx. 200 m from the shore, height: +0.35 m NAP (NAP= Dutch Ordnance Level, similar to Mean Sea Level)) in the lower part of the esutary. The mudflat is a relatively sheltered area along the south bank, protected from the main channel by a sand flat.

- Location Baalhoek (approx. 175 m from the shore, +0.6 m NAP) in the middle part of the estuary. The mudflat is relatively broad (500m), with a shallow slope with small drainage channels. Only slight changes in elevation were observed since 1990, but a drainage channel disturbed the site.
- Location Valkenisse, on the east side of a large sand flat in the middle part of the estuary (+0.7 m NAP). The location is situated in a sedimentary environment; it raised by 0.3-1.0 m since 1990.
- GBL and GBR, two locations on the Buitenschoor mudflat, in the inner part of the estuary. This mudflat has a very shallow slope and is protected by a sand flat and a dam. The 'muddy' location GBR is situated northwards from the dam (150 m from the shore, +1.5 m NAP), and the 'sandy' location GBL southwards from the dam (75 m from the shore, +1.6 m NAP).

Macrobenthic sampling and laboratory analysis

The macrozoobenthos was sampled monthly between March 1993 and August 1994. At each location 15 samples were taken with a small core (∅ 4.5 cm) to a depth of 20 cm. Additionally five samples were taken with a core of 15 cm diameter to a depth of 40 cm. The large cores were sieved in the field through a 3 mm mesh. All benthic samples were preserved in buffered formaline (see also YSEBAERT et al. 1993). In the laboratory the 15 small core samples were sieved through a 1 mm mesh and sorted after staining with 0.02 % Rose Bengal. Organisms were counted and identified to species level, except *Nemertea* and *Oligochaeta.* Since Annelids were often broken due to handling, only parts with a head structure were counted. The large cores were used to estimate the abundance of the larger individuals of bivalves and *Arenicola marina.* Ash-free dry weight (AFDW) biomass was measured by drying all specimens at 105 °C for 12 h and ashing at 550 °C. Population parameters were estimated for the dominant macrobenthic species.

Environmental variables

Also monthly, five sediment cores (∅ 2.5 cm) were taken to a depth of 10 cm at each location for the analysis of sediment granulometry (laser diffraction method with a Coulter Particle Size Analyser). Organic matter (OM) in the sediment was estimated by percentage ignition loss. TOC was measured by 'non-dispersive infrared measurement' with Dohrman-DC 180 Carbon Analyser. Water quality parameters were derived from monthly monitoring campaigns at the following monitoring points: Vlissingen, Terneuzen, Zuidergat, Lamswaarde and Doel, representing the seaward conditions of the estuary and the conditions at Paulina, Baalhoek, Valkenisse and GBR-GBL, respectively.

Data analysis

Species richness, Shannon Wiener diversity index (H'), Pielou's evenness index (J'), abundance and biomass were computed for each sampling month. Patterns on relative species abundance and biomass were produced by *k*-dominance curves that plot cumulative ranked abundances or biomasses against (log) species rank (LAMBSHEAD et al. 1983). Curves for species abundance and biomass were compared with the Abundance Biomass Comparison method (ABC-method, WARWICK 1986), giving an indication of the 'stress' condition of the location (unstressed, moderately stressed, heavily stressed patterns, see MEIRE & DEREU 1990).

Species were classified into feeding groups based on information of the food source from literature (e.g. FAUCHALD & JUMARS 1979; BARNES 1982). Species that feed on more than one food source were classified by their most common feeding mechanism.

Numerical classification and ordination (based on log transformed abundance data) were used to analyze community structure and its relationship to matching environmental data for the five locations together and for each location separately (FIELD et al. 1982). Classification was applied by an agglomerative clustering method (Group Average Sorting (GAS) of Bray-Curtis dissimilarities, CLIFFORD & STEPHENSON 1975) and a hybrid technique (Two-Way Indicator Species Analysis – TWINSPAN, HILL 1979). Several multivariate ordination techniques were used to investigate the maximum (unconstrained) amount of variation in the species data set (indirect techniques: PCA, CA) and the relationship between species composition and the measured environmental variables (direct techniques: RDA, CCA). A preliminary detrended correspondence analysis (DCA; with detrending by segments) was performed to determine the gradient length in standard deviation (SD) units, on which it was decided whether linear (PCA, RDA) or unimodal (CA, CCA) response models had to be applied (JONGMAN et al. 1987; TER BRAAK 1994; TER BRAAK & SMILAUER 1998). Correspondence analysis (CA) and Canonical Correspondence Analysis (CCA) were used for the analysis of all five locations together, Principal Component Analysis (PCA) and Redundancy analysis (RDA) for each location separately. Forward selection of environmental variables was used to identify a subset of factors that significantly and independently explained the variation in the dataset. The significance of the addition of single variables, as well as the significance of the first ordination canonical eigenvalue and the sum of all canonical eigenvalues were tested with Monte Carlo permutation tests (10^3 permutations) (TER BRAAK & VERDONSCHOT 1995; TER BRAAK & SMILAUER 1998).

Alternatively, for the temporal variation in the structure of macrobenthic communities at each location, similarity among the monthly samplings was also evaluated using the Bray-Curtis index on abundance data, and further summarized by Multidimensional Scaling (MDS ordinations in two dimensions) (KRUSKAL & WISH 1978; CLARKE 1993).

Table 4.1. Abiotic characterisation of the five sampling locations (corresponding water quality monitoring point). Distance from the mouth of the estuary and sampling period for each location is given. Mean values and min.-max. are given for observed water quality (temperature, salinity, oxygen concentration, pH, suspended matter SPM, and Chlorophyll *a* (Chl *a*) concentration) and sediment variables (median grain size, mud content and TOC).

Location	CODE	Distance (km)	Sampling period	Temp. °c	Salinity psu	Oxygen mg.l^{-1}	PH	SPM mg.l^{-1}	Chla µg.l^{-1}	Median µm	Mud vol. %	TOC mg.kg^{-1}
Paulina	PAU	15	Mar93-Aug94[1]	12.8	24.2	9.1	8.0	36	10	70	45	20
(Terneuzen)			16 months	3.2-22.3	16.0-27.9	6.8-11.3	7.8-8.2	8-117	2-49	59-82	36-54	7-35
Baalhoek	BH	40	Mar93-May94[2]	12.3	16.4	8.9	7.8	62	12	75	43	17
(Zuidergat)			14 months	4.9-18.9	4.2-22.3	7.1-11.0	7.6-8.1	20-183	2-52	39-100	25-62	8-32
Valkenisse	PVV	43	Apr93-Aug94[3]	13.3	13.3	8.0	7.8	58	12	168	8	1.3
(Lamswaarde)			16 months	5.1-19.4	2.2-19.9	6.3-10.7	7.6-8.1	14-160	3-41	148-181	2-16	0.7-3.7
Buitenschoor R	GBR	60	Mar93-Aug94[4]	14.6	7.8	4.5	7.5	78	8	47	58	37
(Doel)			17 months	6.0-24.3	0.7-13.0	1.3-10.9	7.3-7.7	20-230	1-18	37-63	50-64	31-49
Buitenschoor L	GBL	60	Mar93-Aug94[4]	14.6	7.8	4.5	7.5	78	8	128	25	5.2
(Doel)			17 months	6.0-24.3	0.7-13.0	1.3-10.9	7.3-7.7	20-230	1-18	120-136	19-29	1.0-9.3

Missing sampling months: [1]Apr94,Jul94 [2]Apr94 [3]Jul94 [4]Apr94

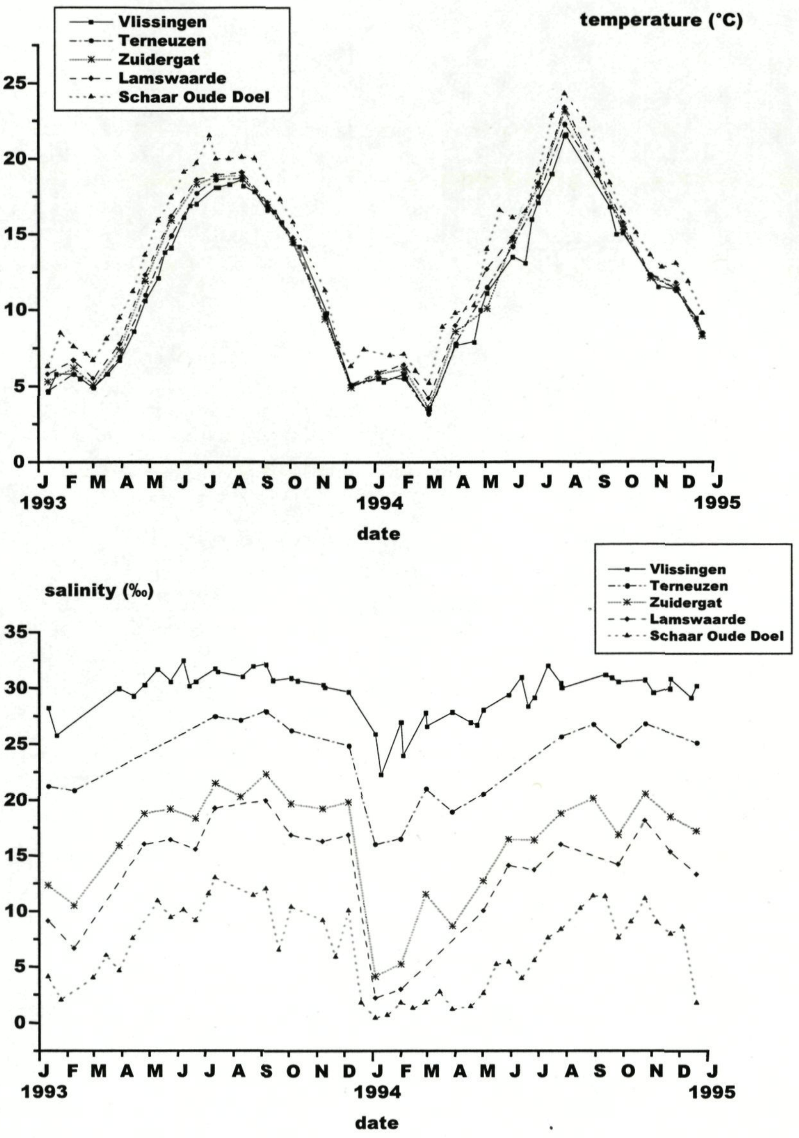


Figure 4.2. Monthly measurements of temperature (°C) and salinity at five monitoring stations along the Schelde estuary (for geographic positions of the stations, see text) for the period January 1993 – December 1994.

Results

Abiotic characteristics

Water quality parameters and sediment characteristics of each sampling location are summarised in Table 4.1. All locations showed a similar seasonal pattern for temperature temperature (Figure 4.2) and the study period was characterized by mild winters and normal summers. Based on the mean salinity conditions, Paulinaschor was situated in the polyhaline zone (salinity 18-30), Baalhoek and Valkenisse in the α-mesohaline zone (10-18) and GBR and GBL in the β-mesohaline zone (5-10). A seasonal pattern was observed at all locations with high salinities in summer and lower salinities in

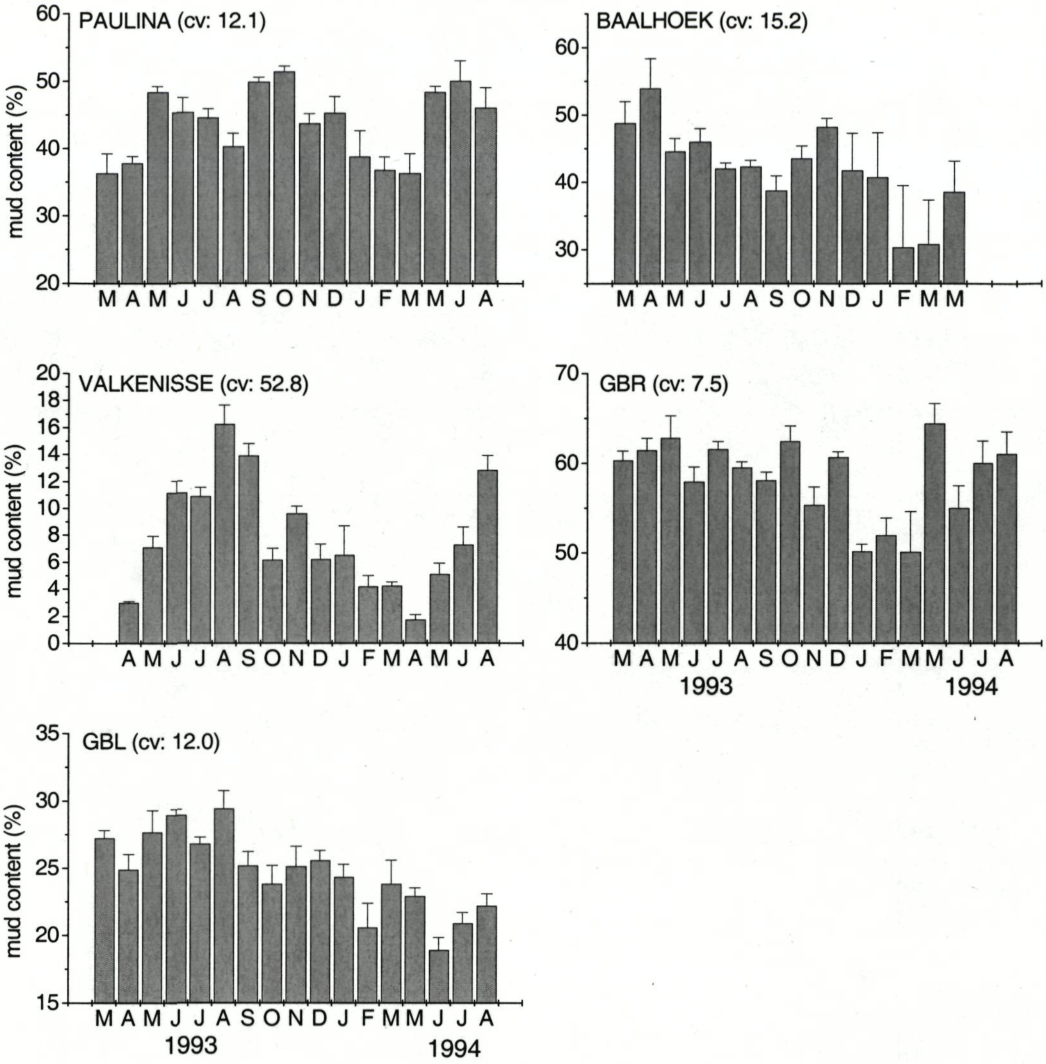


Figure 4.3. Monthly variation in mean (± SE) mud content (volume% < 63 μm) at the five intertidal locations Paulina, Baalhoek, Valkenisse, GBR and GBL. (cv = coefficient of variation) for the period March 1993 – August 1994.

winter and spring (Figure 4.2), which was largely due to varying freshwater runoff from the Schelde basin. These variations were much more pronounced in the mesohaline locations and diminished towards the mouth of the estuary (coefficient of variation decreased from 50% at GBR and GBL to 13% at Paulina). Between December 1993 and February-March 1994, extremely low salinities were observed due to a very high river runoff in that period. At 'Doel', salinities then dropped to 0.5-2.5, turning the conditions to almost freshwater. At 'Lamswaarde' and 'Zuidergat' salinity dropped from respectively 17 and 20 in December 1993 to 2.5 and 4 in January 1994.

Mean dissolved oxygen concentrations in the water column were lowest at 'Doel' and increased with increasing salinity. At 'Doel' the water column was highly undersaturated for dissolved oxygen during late spring and most of the summer period. Mean suspended matter concentrations in the water column were highest at 'Doel' (high turbidity zone) and diminished with increasing salinity. Chlorophyll *a* concentrations were lowest at 'Doel' but showed distinct and short peaks in time,

Table 4.2. List of species observed in Paulina (PAU), Baalhoek (BAA), Valkenisse (VAL), Buitenschoor Right (GBR) and Buitenschoor Left (GBL). Feeding guilds are indicated between brackets: sdf=surface deposit feeder; ssdf=sub-surface deposit feeder; sf=suspension feeder; o=omnivore; p=predator. x = species observed. Rare species observed only 1 to 3 times are indicated with resp. 1, 2 and 3.

	Pau	Baa	Val	GBR	GBL		Pau	Baa	Val	GBR	GBL
Crustacea						**Annelida**					
Bathyporeia pilosa/sarsi (sdf)		1	x		3	*Anaitides mucosa* (p)	x				
Haustorius arenarius (sf)			1			*Arenicola marina* (ssdf)	x		x		
Corophium arenarium (sdf)			x			*Capitella capitata* (ssdf)	x	1			
Corophium volutator (sdf)	1	x	x	x	x	*Etone longa* (p)		x	x	x	1
Crangon crangon (p)	3	1	3	2		*Heteromastus filiformis* (ssdf)	x	x	x	x	
Carcinus maenas (o)	x	1	3			*Manayunkia aestuarina* (sf)				x	
Eurydice pulchra (p)			1			*Nephtys* spp. (o)			2		
Cyathura carinata (o)	x	1				*Nephtys hombergii* (o)	x		2		
Mollusca						*Nereis diversicolor* (o)	x	x	x	x	x
Cerastoderma edule (sf)	x	x	x			*Nereis succinea* (ssdf)	1		x		
Macoma balthica (sdf)	x	x	x	x	x	*Polydora ligni* (sdf)	x	x	x		2
Mya arenaria (sf)	3	x	x	1		*Pygospio elegans* (sdf)	x	x	x	2	x
Scrobicularia plana (sdf)	x	x	x			*Spio* spp. (sdf)	x				
Abra tenuis (sdf)	x					*Tharyx marioni* (sdf)	x	1			
Mysella bidentata (sf)	x					*Oligochaeta* (ssdf)	x	1		x	x
Petricola pholadiformes (sf)		1									
Ensis spp. (sf)		2				**Nemertea** (p)	1	x	x	1	2
Bivalve spp. (-)		1	1								
Hydrobia ulvae (sdf)	x	x	x	2	2	**Total number of species**	26	21	24	10	11
Retusa obtusata (sdf)	x					(°without rare species)	20°	13°	16°	5°	6°

coinciding with phytoplankton production (blooms).

The sediment at Paulina consisted of very fine sand (moderately oxidised), at Baalhoek it varied between mud and very fine sand (reduced), at Valkenisse it consisted of fine sand (very well oxidised), at GBR it was muddy, black and highly sulfidic (extremely reduced), and at GBL it consisted of fine sand (moderately oxidised). At Valkenisse, and to a lesser extent also at Paulina, a seasonal variation in mud content was observed in both years, with low values in winter and spring and increasing values during summer (Figure 4.3). At GBR seasonal variability was lowest, with lower mud contents only observed during the period January-March 1994, coinciding with the high river runoff. At Baalhoek and GBL mud content decreased slightly during the study period.

Diversity, abundance and biomass of the benthic macrofauna

A total of 35 macrobenthic species were recorded at the five locations (Table 4.2). Mean diversity decreased from the polyhaline zone towards the mesohaline zone (Table 4.3). On a temporal scale the number of species was higher in summer and autumn as compared to winter and spring in all locations, except at Baalhoek were only little variation was observed (Figure 4.4). The Shannon-Wiener

Table 4.3. Mean (± SE) and min.-max. values observed for the diversity measures (number of species, Shannon-Wiener H' and evenness J'), total abundance in ind m^{-2} and total biomass in g AFDW m^{-2} for the considered study period. cv = coefficient of variation (%).

Location	Number of species	Shannon-Wiener H'	Evenness J'	Abundance ind m^{-2}	Biomass g AFDW m^{-2}
Paulina	16.5 ± 0.6	1.91 ± 0.04	0.68 ± 0.01	24134 ± 1590	67.6 ± 7.1
	12-19 (cv: 14.2)	*1.62-2.25 (cv: 8.5)*	*0.61-0.77 (cv: 6.1)*	*12282-33473 (cv: 26.6)*	*42.4-158.0 (cv: 41.7)*
Baalhoek	11.2 ± 0.4	1.51 ± 0.03	0.64 ± 0.03	16573 ± 1083	28.4 ± 2.5
	8-13 (cv: 17.8)	*1.28-1.70 (cv: 8.2)*	*0.53-0.82 (cv: 15.1)*	*10372-27000 (cv: 24.5)*	*17.6-51.8 (cv: 33.2)*
Valkenisse	13.1 ± 0.9	1.57 ± 0.10	0.61 ± 0.04	32139 ± 7918	18.4 ± 3.1
	8-20 (cv: 27.8)	*0.52-2.10 (cv: 26.5)*	*0.20-0.79 (cv: 25.1)*	*3335-91297 (cv: 98.6)*	*3.8-44.9 (cv: 67.9)*
GBR	4.4 ± 0.4	0.86 ± 0.09	0.62 ± 0.05	7063 ± 912	3.4 ± 0.4
	2-8 (cv: 38.0)	*0.43-1.50 (cv: 43.0)*	*0.27-0.97 (cv: 32.2)*	*1928-14504 (cv: 53.2)*	*0.9-5.9 (cv: 44.7)*
GBL	5.1 ± 0.4	0.83 ± 0.05	0.55 ± 0.04	14257 ± 2234	10.1 ± 1.0
	3-8 (cv: 29.0)	*0.51-1.20 (cv: 22.5)*	*0.28-0.94 (cv: 30.8)*	*4653-31396 (cv: 64.6)*	*4.6-18.6 (cv: 39.7)*

diversity showed a different temporal pattern among locations. Maximum diversity values were reached during summer and autumn at Paulina, Valkenisse and GBR, indicating that in this period more species contributed to the total abundance than in winter and spring. The opposite pattern was observed at Baalhoek and GBL, indicating that here numerical dominance of only a few species was more pronounced in summer and autumn as compared to the spring and winter situation. The relative variation of the different diversity measures was highest at GBR, GBL and Valkenisse.

Mean total abundance was highest in Valkenisse, followed by Paulina, Baalhoek, GBL and GBR (Table 4.3). Mean total biomass decreased from the polyhaline zone towards the mesohaline zone. Both abundance and biomass showed large seasonal variations at all locations, with lower values in

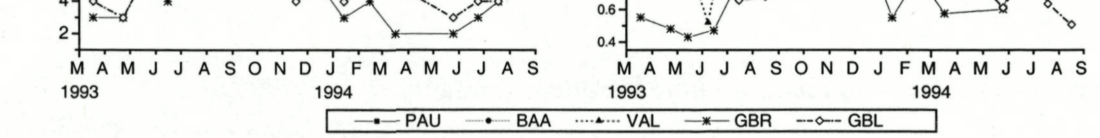


Figure 4.4. Monthly variation in diversity measures (Number of species N_0 and Shannon-Wiener diversity index H') at the five sampling locations for the period March 1993 – August 1994.

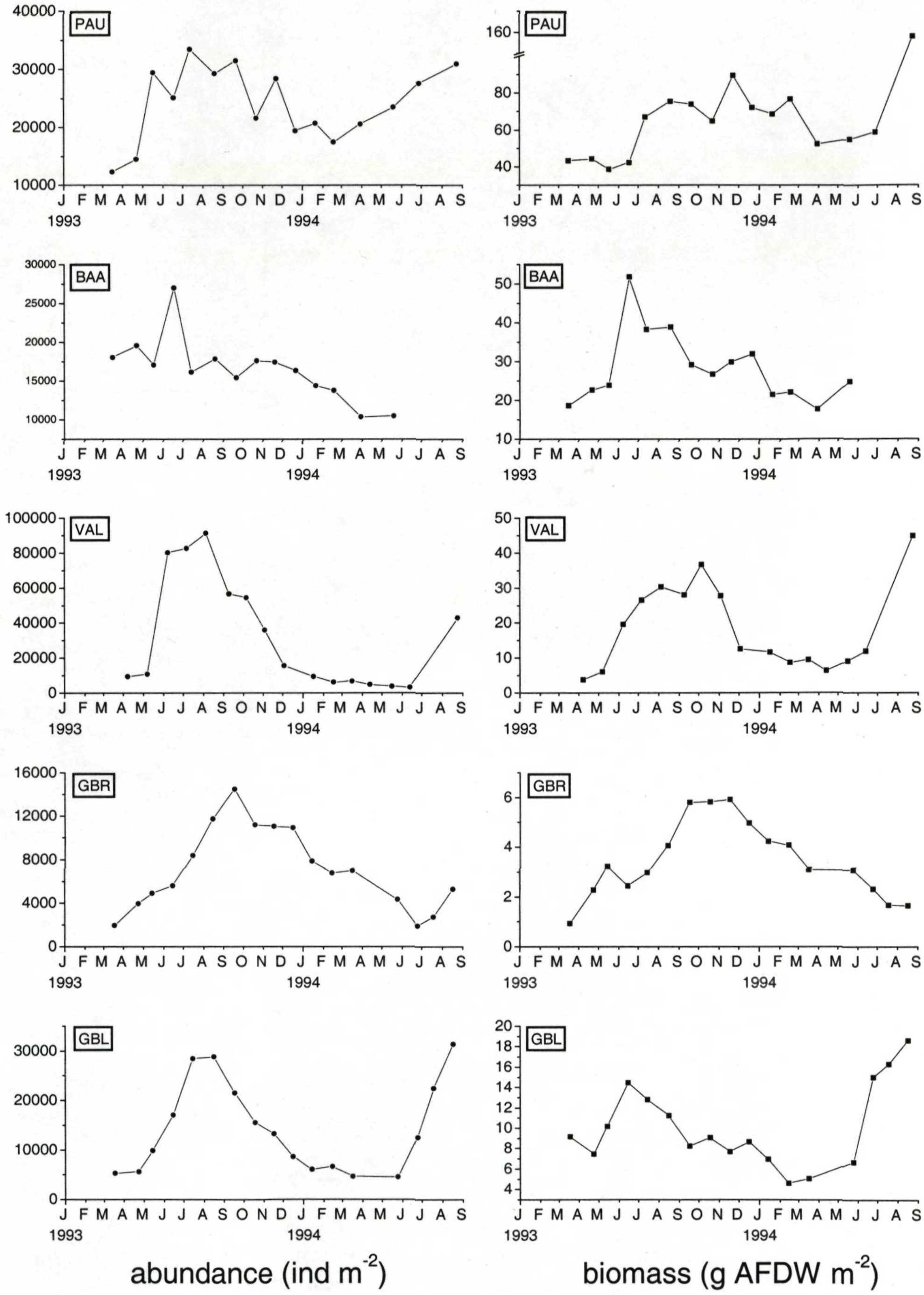


Figure 4.5. Monthly variation in total abundance (ind m^{-2} ± SE) and total biomass (g AFDW m^{-2}) at the five sampling locations for the period March 1993 – August 1994.

winter and early spring, and an increase in late spring and summer (Figure 4.5). These variations in abundance were most pronounced at Valkenisse, GBR and GBL, where the increase during late spring and summer time amounted to 20, 8 and 7 times respectively. At Paulina this increase in abundance was much less pronounced. At Baalhoek only a slight increase during June was observed, whereas the rest of the year abundance showed a slightly decreasing trend. The month of increase and of peak

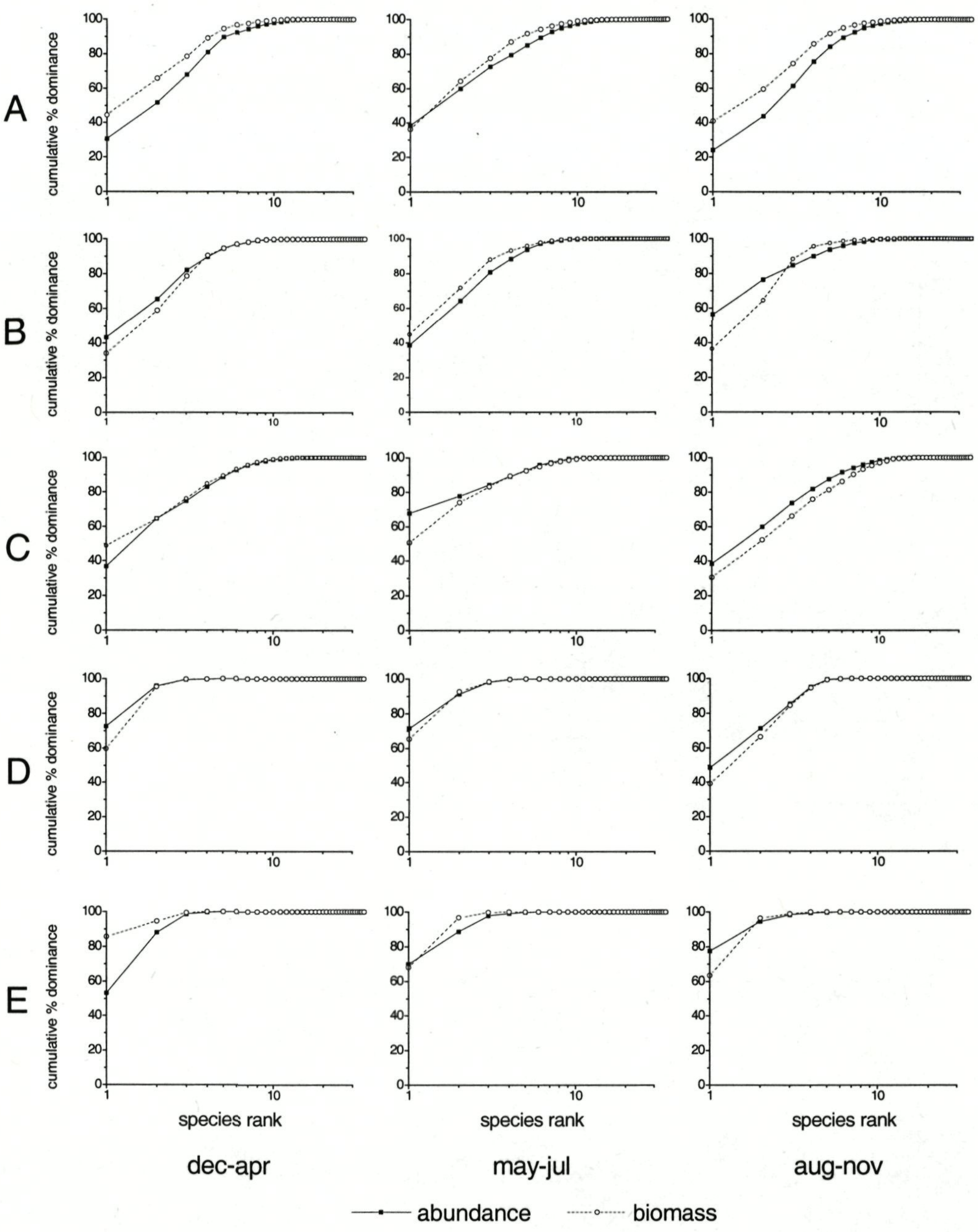


Figure 4.6. Abundance Biomass Comparison curves (ABC-curves) for the different sampling locations, showing the winter – early spring situation (December - April), the spring – early summer (recruitment) situation (May - July), and the late summer – autumn situation (Jul-Oct). A = Paulinaschor; B = Baalhoek; C = Valkenisse; D = GBR; E = GBL.

abundance differed among locations, with a shift in the month of increase from May to June/July from the polyhaline towards the mesohaline zone. A similar seasonal trend was observed for biomass. Peak biomass occurred later in the season as compared to peak abundance.

The ABC-curves indicated that the structural complexity level decreased from the polyhaline zone towards the mesohaline zone (Figure 4:6). At GBR and GBL only one to two species dominated the community. The evaluation of the curves according to Warwick's model showed an 'unstressed' pattern for Paulina, and an 'unstressed to moderately stressed' pattern for the other locations. As to

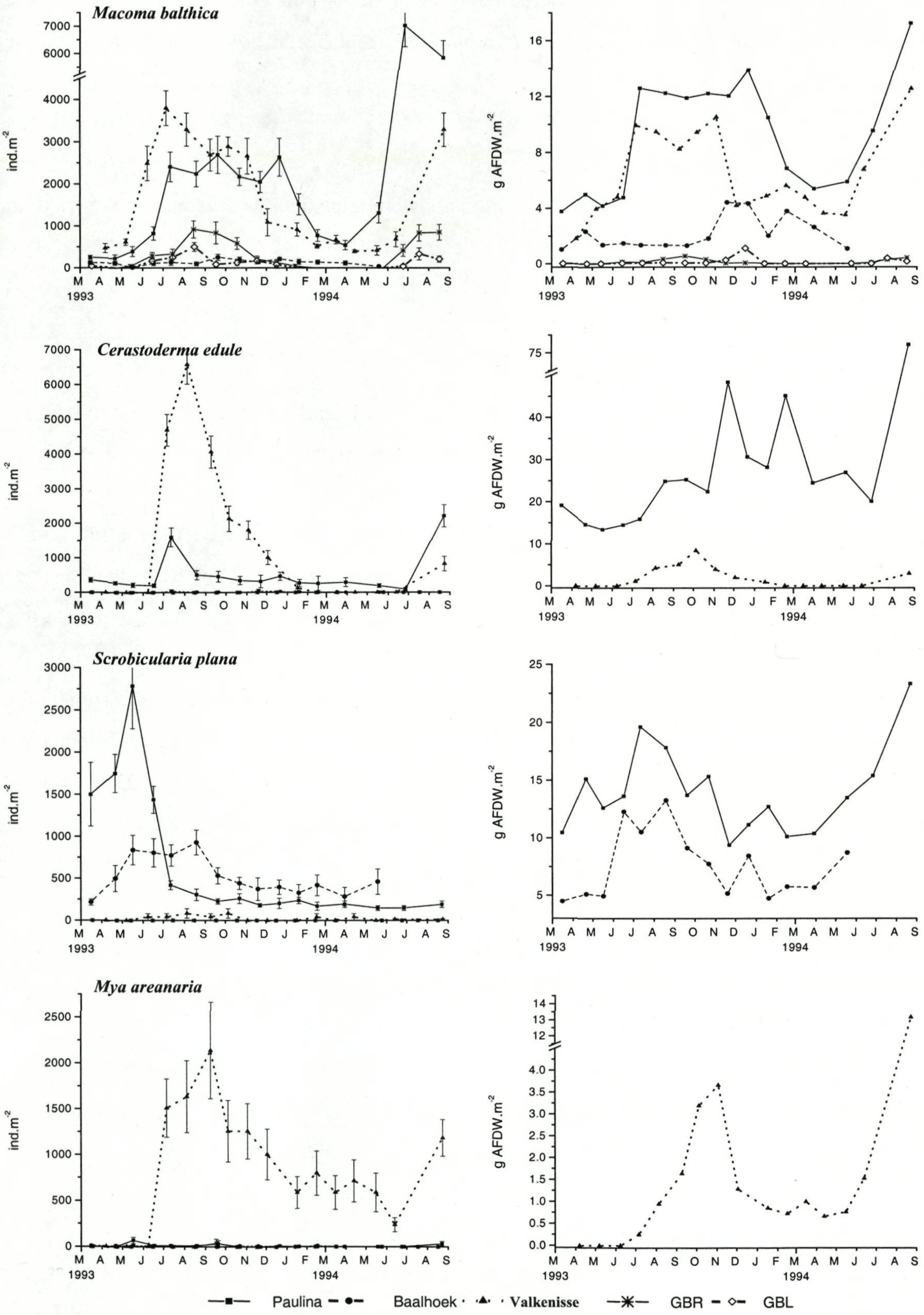


Figure 4.7. Temporal changes in abundance (left) and biomass (right) of the molluscs *Macoma balthica* (surface deposit feeder), *Cerastoderma edule* (suspension feeder), *Scrobicularia plana* (surface deposit feeder) and *Mya arenaria* (suspension feeder).

temporal variation, numerical dominance increased in spring/early summer (May-July), especially at Valkenisse, and decreased in summer/autumn, except at GBL and Baalhoek where a further increase was observed.

Seasonal dynamics of key species

Temporal trends in total abundance and total biomass were related to the seasonal dynamics of the most important species of the related macrobenthic communities.

Molluscs

The dominant bivalve species showed clear seasonal patterns and recruitment (spatfall) at one or more locations (Figure 4.7). *M. balthica* was observed at all locations. Spatfall appeared in both years in May-June and peak densities were reached in July or August, being highest at Paulina and Valkenisse. Densities decreased rapidly at GBR and GBL, where *M. balthica* totally disappeared during winter. At Paulina and Valkenisse densities remained relatively high after the spatfall, and decreased only in late autumn (Valkenisse) or winter (Paulina). Biomass was highest at Paulina and Valkenisse and also showed a clear seasonal pattern. However, biomass changes were more due to the growth of the adult individuals, rather than to the arrival of spatfall.

C. edule was only common at Paulina and Valkenisse. In Paulina numbers increased from 250-375 ind m^{-2} in the period March-June 1993 up to 1550 ind m^{-2} in July (spatfall). Abundance dropped in August and declined further after December up to approximately 100 ind.m^{-2} in spring 1994. Biomass increased towards autumn, but was highly variable thereafter. The distinct increase in August 1994 was related to growth of newly arrived spatfall. In Valkenisse, *C. edule* was absent until June 1993, after which an explosive increase was noticed in July and August, due to new spatfall, up to a maximum of 6550 ind m^{-2}. From September numbers decreased rapidly to zero in February 1994. In August 1994 new spatfall was observed, but at much lower densities. Biomass values at Valkenisse reflected the growth of the spatfall.

S. plana was only common at Paulina and Baalhoek. Spatfall was observed in the period March-April 1993, after which numbers decreased rapidly at Paulina. From November 1993 on, a steady level in abundance was reached at both locations, being highest at Baalhoek. In 1994 no spatfall of this species was observed. Biomass increased towards summer, and decreased towards winter. Subsequent growth in spring-summer 1994 caused a clear increase in biomass.

M. arenaria was only common at Valkenisse, whereas at Paulina and Baalhoek the species was irregularly observed in very low densities. As for *C. edule*, *M. arenaria* was also absent until June 1993, after which spatfall was observed in July. Numbers decreased towards winter and in 1994 new spatfall was observed. Biomass increased towards November, reflecting growth of the spatfall, after which biomass decreased in winter and spring due to mortality. In June-August biomass increased again, due to the new arrived spatfall and subsequent growth.

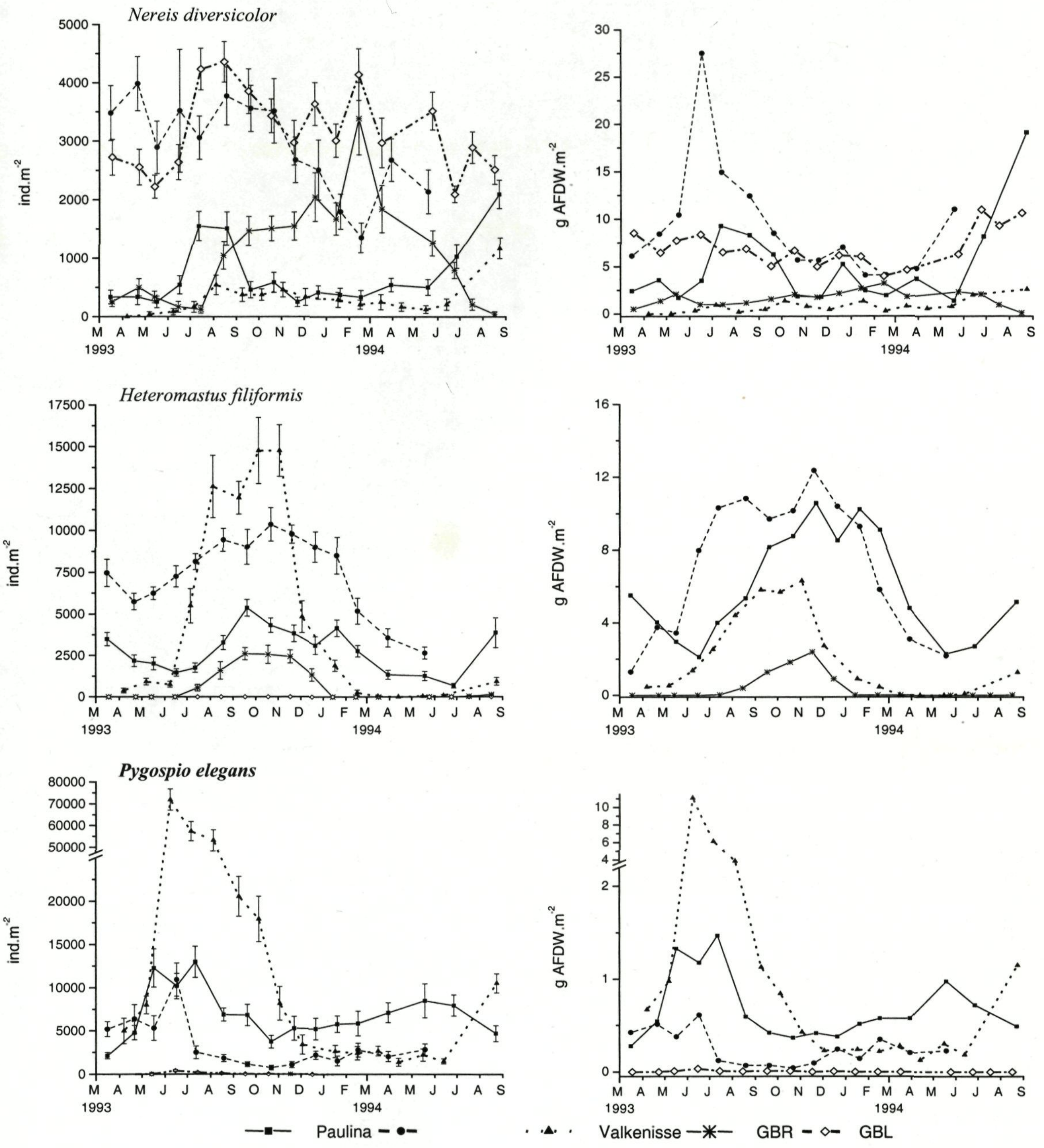


Figure 4.8. Temporal changes in abundance (left) and biomass (right) of the annelids *Nereis diversicolor* (omnivore), *Heteromastus filiformis* (subsurface deposit feeder) and *Pygospio elegans* (surface deposit feeder).

Hydrobia ulvae was the only gastropod observed at all locations (at GBR and GBL only two observations of a few individuals). Densities fluctuated strongly. At Paulina abundances were below 250 ind m^{-2} throughout the year, with a peak in May-June 1993 (max.. 1250 ind m^{-2}), but no peak in 1994. At Baalhoek no clear seasonal trend was observed. At Valkenisse clear seasonal trends were observed with an increase in abundance in spring and a peak in August, being much higher in 1994 (8500 ind m^{-2}) as compared to 1993 (1200 ind m^{-2}).

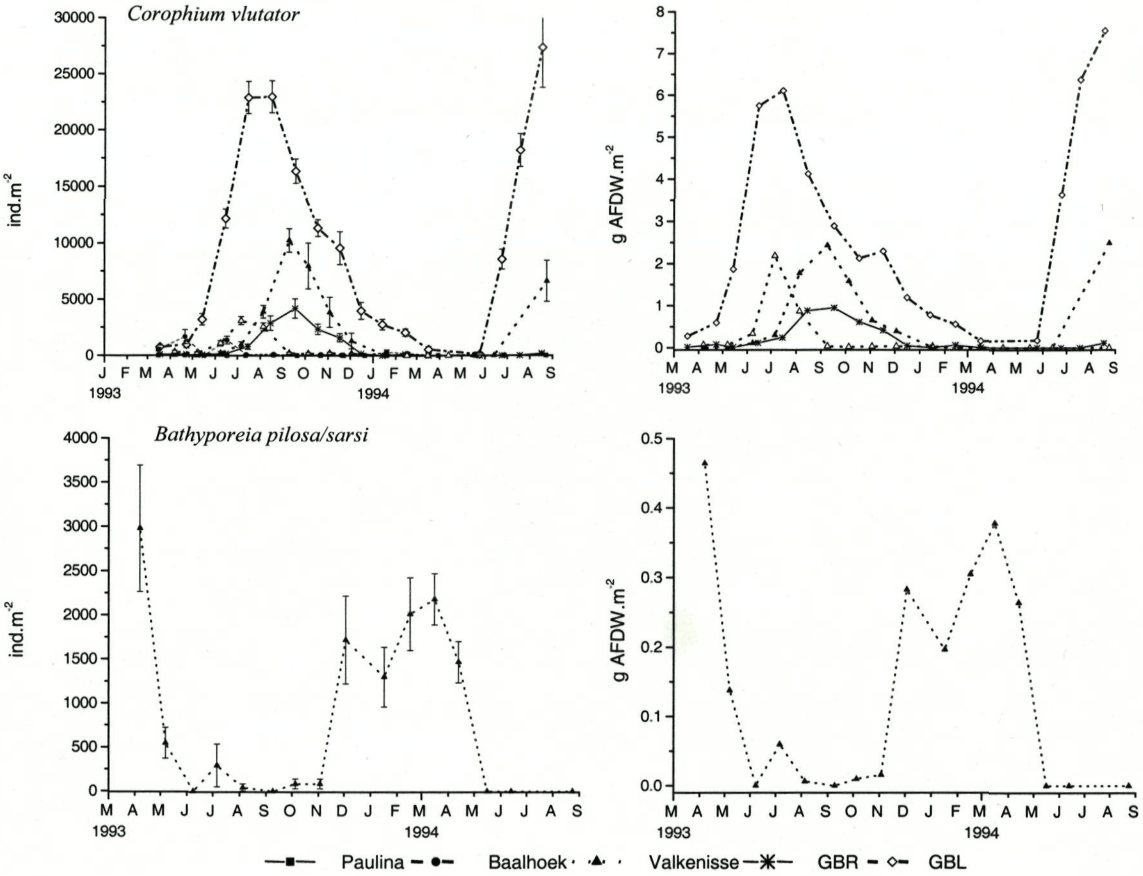


Figure 4.9. Temporal changes in abundance (left) and biomass (right) of the amphipods *Corophium voluator/arenarium* and *Bathyporeia pilosa*. *C. arenarium* was only observed at Valkenisse and is indicated by open up triangles.

Annelids

The most dominant polychaetes were *N. diversicolor*, *H. filiformis* and *P. elegans* (Figure 4.8). *N. diversicolor* was observed year round at all locations but seasonal patterns differed. Abundance increased in July 1993 at Paulina and GBL, and in August 1993 at Valkenisse and GBR. In Paulina abundance declined rapidly in September, whereas at the other locations abundance only slightly declined towards winter. In the period June-August 1994 an increase was only observed at Paulina and Valkenisse. At Baalhoek no clear seasonal trend was observed, except for a decrease during winter. Biomass values did not show clear seasonal patterns, except at Paulina, and were highest at Baalhoek, with a peak biomass of 27 g AFDW.m^{-2} in June 1993.

The capitellid *H. filiformis* showed clear seasonal patterns in abundance, especially at Valkenisse and GBR. Here, peak abundance was reached in August-September 1993, but dropped in December to zero during winter. In the period June-August 1994, none of the locations showed a distinct increase in abundance. The biomass pattern was similar to the changes in abundance.

The spionid *P. elegans* occurred in high numbers at Paulina, Baalhoek, and Valkenisse, in low numbers at GBL. The seasonal pattern was similar among locations. Abundance increased very rapidly in May-June to peak densities. At GBL, and especially at Baalhoek, peaks were very short. Numbers decreased at all locations to a relatively steady level in winter and spring, being highest at Paulina (5500 ind m^{-2}), and lower at Baalhoek and Valkenisse (2000 ind m^{-2}), but zero at GBL. Abundance observed in 1994 was much lower as compared to 1993, especially in Valkenisse. Biomass values followed the same trend as abundance. Other spionid species, like *Polydora ligni* and *T. marioni*, showed similar seasonal patterns.

Crustaceans

The amphipod *Corophium volutator* was a common species at Valkenisse, GBL and GBR, especially at GBL where it dominated the community in summer (Figure 4.9). Increase in abundance was earlier in GBL (May-June) as compared to GBR and Valkenisse (July-August). Peak densities were highest in GBL (25000 ind.m^{-2}). Biomass more or less followed the trend in abundance, but e.g. in GBL also growth of the different cohorts influenced biomass trends (pers. observ.).

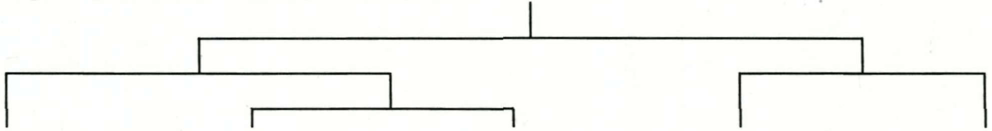
Corophium arenarium was only observed at Valkenisse in 1993, showing a different seasonal pattern as compared to *C. volutator*. Numbers of *C. arenarium* increased already in June to reach a peak in July and August. In August, when numbers of *C. volutator* started to increase, numbers of *C. arenarium* decreased to almost zero in September-October.

Another amphipod, *Bathyporeia pilosa/sarsi*, was also common at Valkenisse. It was the only macrobenthic species with a completely inverted seasonal pattern, showing highest densities during winter, and nearly disappearing in summer.

Trophic structure

Surface deposit (SDF) and subsurface deposit feeders (SSDF) numerically dominated at all locations (Table 4.4), but at different ratios: SDF at Valkenisse (71%), GBL (69%) and Paulina (58%), and SSDF at GBR (69%) and Baalhoek (50%). Omnivores were only important at Baalhoek, GBR and GBL with resp. 18, 15 and 22 % of the total abundance observed. At these three locations, almost no suspension feeders (SF) were observed, whereas at Paulina and Valkenisse respectively 3 and 12 % SF were observed. Based on biomass values, an increasing importance of SF was observed at Paulina and Valkenisse (respectively 42 and 21 %), whereas at the other three locations Baalhoek, GBR and GBL an increasing importance of omnivores was observed (respectively 33, 47 and 69 %). On a seasonal scale, the relative proportion of the different feeding types was in general consistent through the year at Paulina and Baalhoek, whereas at Valkenisse, GBR and GBL clear seasonal shifts were observed, as demonstrated by the biomass (Figure 4.10). At Valkenisse the spring and winter periods were characterized by a dominance of SDF, but in summer other feeding guilds were also observed in the community. At GBR and GBL the community was dominated by omnivores and SSDF (only GBR) in winter, whereas towards summer also SDF appeared in the community.

Table 4.4. Mean abundance (A: ind m $^{-2}$), mean biomass (B: g AFDW m $^{-2}$) and number of observations (N) for the macrobenthic species observed at the five sampling locations. Boldfaced numbers represent the three most dominant species (abundance and biomass) for each location.



	Paulina N=16 months			Baalhoek N=14 months			Valkenisse N=16 months			GBR N=17 months			GBL N=17 months		
Species	A	B	N	A	B	N	A	B	N	A	B	N	A	B	N
Tharyx marioni	**4031**	1.04	16	3	0.004	-	-	-	-	-	-	-	-	-	-
Retusa obtusata	202	0.09	12	-	-	-	-	-	-	-	-	-	-	-	-
Abra tenuis	68	0.13	11	-	-	-	-	-	-	-	-	-	-	-	-
Spio sp.	97	0.02	11	-	-	-	-	-	-	-	-	-	-	-	-
Cerastoderma edule	520	**28.1**	16	10	0.02	6	1353	1.78	8	-	-		-	-	-
Eteone longa	874	0.42	16	51	0.06	7	359	0.23	12	1	0.001	2	-	-	-
Scrobicularia plana	642	**14.0**	16	521	**7.58**	14	21	1.25	15	1	0.0001	1	-	-	-
Mya arenaria	7	0.04	11	8	0.70	6	921	**1.86**	14	2	0.0001	1	-	-	-
Heteromastus filiformis	2800	5.89	16	**7307**	**7.18**	14	**4354**	**2.03**	15	661	**0.40**	8	-	-	-
Nereis succinea	3	0.004	1	-	-	-	196	0.19	14	-	-	-	-	-	-
Cyathura carinata	-	-	-	931	0.61	14	8	0.01	3	-	-	-	-	-	-
Corophium arenarium	-	-	-	-	-	-	506	0.23	10	-	-	-	-	-	-
Bathyporeia sp.	-	-	-	6	0.003	1	794	0.13	11	-	-	-	7	0.001	3
Pygospio elegans	**7080**	0.68	16	**3332**	0.25	14	**16806**	1.74	16	5	0.001	2	54	0.004	7
Hydrobia ulvae	234	0.10	14	601	0.22	14	935	0.27	16	7	0.003	2	10	0.001	2
Polydora ligni	204	0.07	7	308	0.06	11	1457	0.24	8	-	-	-	5	0.001	2
Macoma balthica	2060	**9.24**	16	135	2.15	14	1683	**6.49**	16	324	0.14	12	118	0.13	11
Nereis diversicolor	696	5.03	16	**2926**	**9.33**	14	301	0.81	15	**1073**	**1.63**	17	**3166**	**7.00**	17
Oligochaeta	**4393**	0.52	16	6	0.0015	1	-	-	-	**4235**	**1.06**	17	**1179**	**0.27**	17
Corophium volutator	3	0.002	1	328	0.15	12	**2195**	0.61	9	**748**	0.21	12	**9639**	**2.73**	17
Manayunkia aestuarina	-	-	-	-	-	-	-	-	-	-	-	-	67	0.001	6
Suspension feeders	765	28.24		331	0.79		3737	3.87		2.5	0.0003		72	0.002	
Surface deposit feeders	14037	25.20		4927	10.40		22941	10.66		1084	0.35		9828	2.86	
Sub-surface deposit feeders	7288	8.25		8247	7.80		4575	2.57		4896	1.46		1179	0.27	
Omnivores	836	5.33		2929	9.34		327	0.91		1072	1.63		3166	7.00	

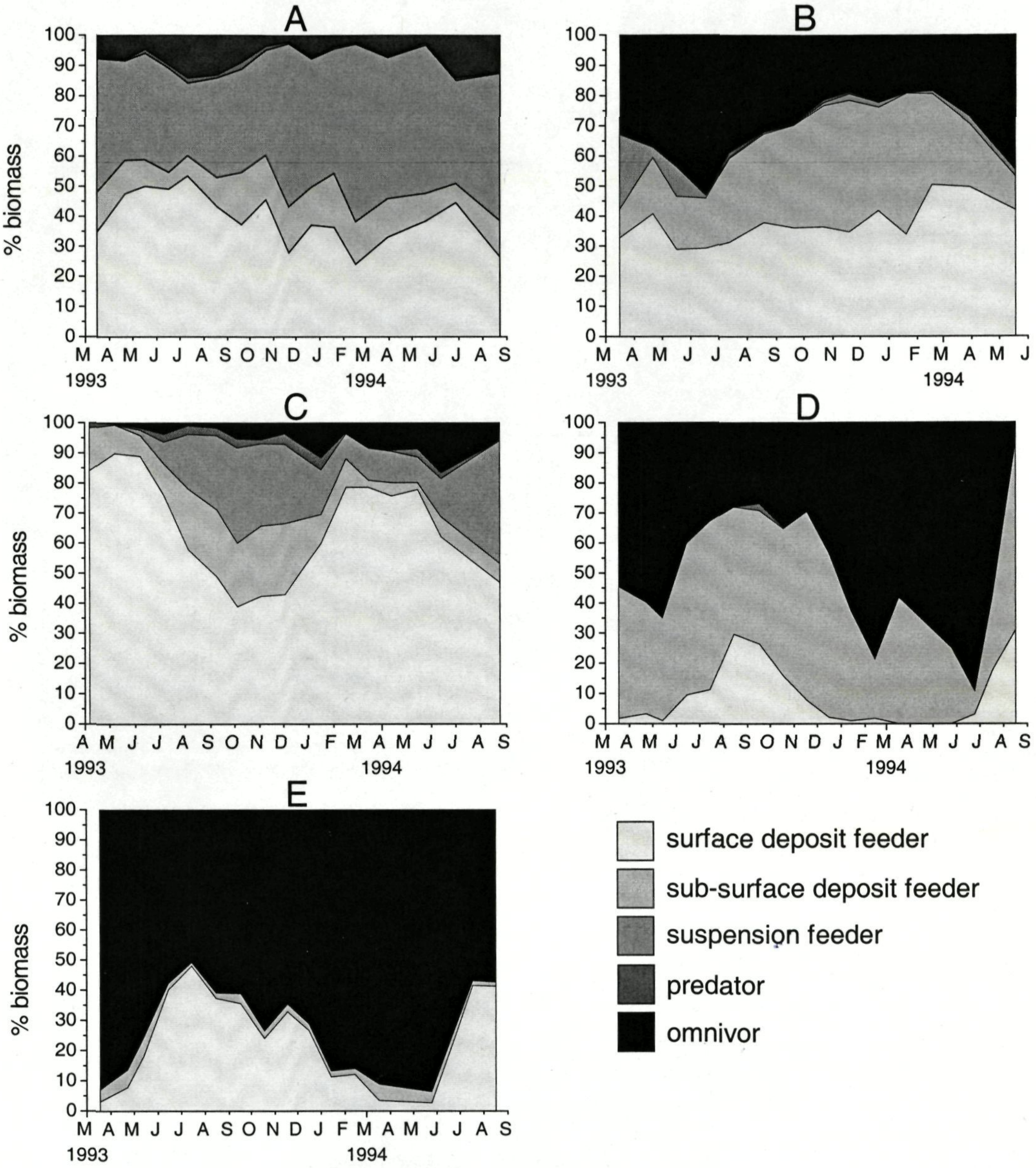


Figure 4.10. Temporal variation in the trophic structure of macrobenthic assemblages (in terms of biomass) at the five sampling locations. A = Paulinaschor; B = Baalhoek; C = Valkenisse; D = GBR; E = GBL.

Classification and indicator species

The cluster analysis based on monthly density samples of all locations, showed a distinct separation among the five locations (Figure 4.11). In a first division, the low salinity locations GBL and GBR were separated. In a next division, all GBL sampling months were separated from the GBR sampling months, except for the three spring months March-May 1993. For the other three locations, all sampling months of Paulina were first separated from Baalhoek and Valkenisse. In the latter cluster, first the spring sampling months of Valkenisse were separated, followed by a further division of all Baalhoek sampling months and the remaining Valkenisse sampling months. It was clear from the cluster analysis that spatial segregation dominated upon seasonal variation among the five locations.

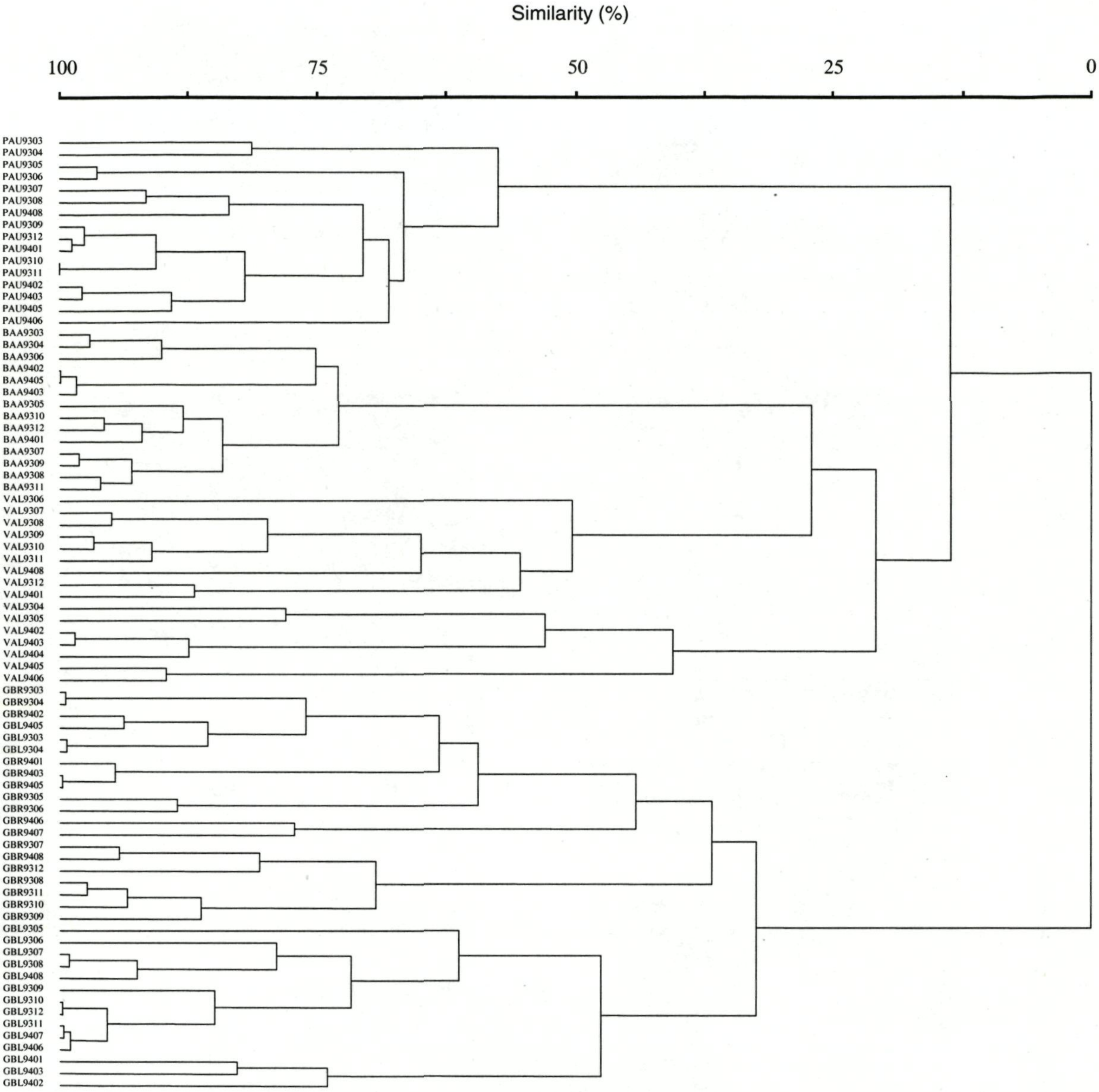


Figure 4.11. Group average sorting of all sampling months of the five locations based on abundance data using Bray-Curtis similarities. Locations are Paulina (PAU), Baalhoek (BAA), Valkenisse (VAL), GBR and GBL. Months are abbreviated as follows: 9303 = March 1993; 9304 = April 1993; …

The dissimilarity among sampling months within one location was most pronounced at Valkenisse, GBR and GBL, and was lowest at Baalhoek.

Table 4.4 summarizes the main species composition and community structure at each location. The macrobenthic community at Paulina was characterized by some typical polyhaline species, such as *Abra tenuis* and *Tharyx marioni*. *T. marioni*, together with *Pygospio elegans* and Oligochaeta were numerically dominant, whereas biomass was dominated by the bivalves *Cerastoderma edule*, *Scrobicularia plana* and *Macoma bathica*. The macrobenthic community at Baalhoek was numerically dominated by *Heteromastus filiformis*, and to a lesser extent by *P. elegans* and *Nereis*

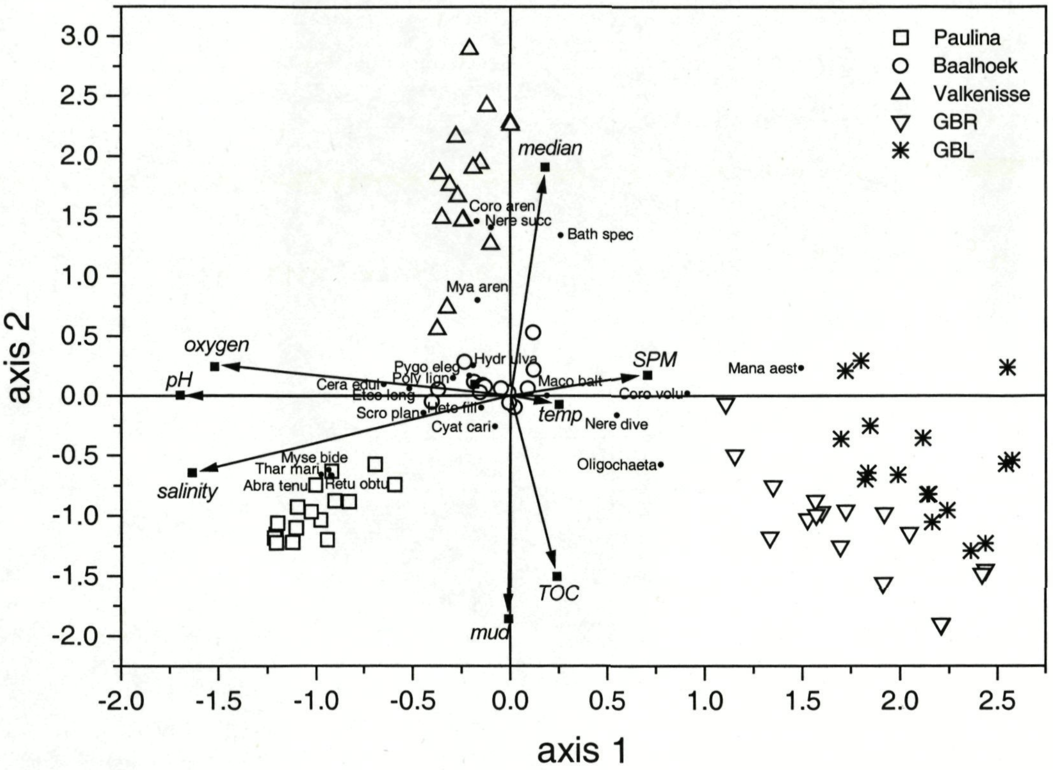


Figure 4.12. CCA ordination diagram on the monthly abundance data of all five locations together. Only most important species are presented. Environmental variables are presented as arrows. Environmental variables are the surface water quality parameters salinity, temperature (temp), oxygen concentration (oxygen), suspended matter (SPM) and pH, and the sediment characteristics mud content (mud), median (median grain size) and TOC. The orthogonal projection of a species point onto an environmental arrow represents the approximate center of the species distribution along that particular environmental gradient. Species names are represented by the first four letters of the genus and species name respectively.

diversicolor. *Cyathura carinata* was the most common crustacean at Baalhoek and was absent at the other locations. Biomass was dominated by *N. diversicolor*, *H. filiformis* and *S. plana*. The macrobenthic community at Valkenisse was numerically dominated *by P. elegans*, whereas biomass was mainly determined by *M. balthica*. Several crustaceans, such as *Bathyporeia spec.* and *Corophium arenarium* were only observed at Valkenisse. At GBR Oligochaeta and at GBL *C. volutator* were numerically dominant. *N. diversicolor*, also appearing in relatively high numbers, especially contributed to the total biomass in these communities, at GBL 70% and at GBR 50% on a yearly average, respectively. .*Manayunkia aestuarina*, a typical brackish water species, was only observed at GBL in very low densities.

Species-environment associations

The first two axes of the CCA (Figure 4.12) had eigenvalues of 0.30 and 0.20 and explained 37.7% of the species variation. They were significant by Monte Carlo statistics and represented 80.8% of the species-environment relation. On the correlation biplot of the CCA the five locations have different positions, which was in general agreement with the cluster analysis. The first axis was strongly correlated with salinity (r = -0.75), with the polyhaline location Paulina situated at the left side of the

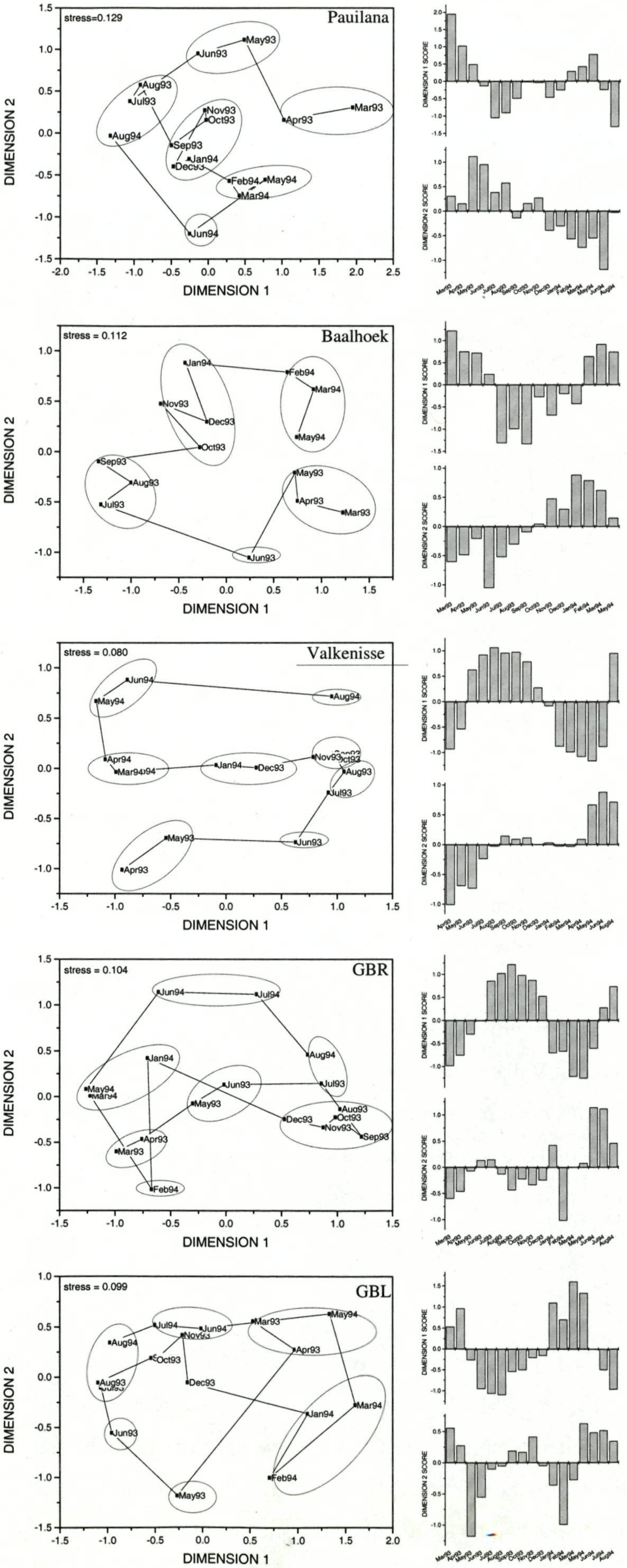


Figure 4.13. Temporal variability in macrobenthic community structure at each location. Left-hand column: ordination diagram by multidimensional scaling (MDS). Lines connect successive sampling months and circles indicate clusters obtained by Group Average Sorting of Bray-Curtis dissimilarities. Right-hand column: scores of the first and second ordination axes as a function of time. A = Paulinaschor; B = Baalhoek; C = Valkenisse; D = GBR; E = GBL.

diagram and the β-mesohaline locations GBR and GBL at the right side. Besides salinity, also oxygen concentration and pH correlated strongly with the first axis. The sediment characteristics correlated strongly with the second axis (median grain size: r= 0.82; mud content: r= -0.80), along which axis especially Valkenisse was differentiated. Also GBL and GBR were mainly differentiated along the second axis. Forward selection and Monte Carlo permutation tests of environmental variables also showed that salinity and median grain size, and to a lesser extent also oxygen concentration, contributed significantly and independently to explaining the variation in the CCA.

The position of the different species in the diagram reflected their spatial distribution. Species observed at only one location were situated near the corresponding location (e.g. *A. tenuis* and *T. marioni* at Paulina, *C. arenarium* and *Bathyporeia pilosa/sarsi* at Valkenisse, *C. carinata* at Baalhoek and *M. aestuarina* at GBL). Other species, like *M. balthica* and *H. filiformis*, which were observed at all locations, were situated in the centre of the diagram.

Although spatial segregation dominated upon seasonal variation, it was observed from the CCA diagram that sampling months from Paulina and Baalhoek were more lumped, whereas sampling months from Valkenisse, GBR and GBL were more spread in the ordination space, indicating larger temporal changes in community structure here.

Temporal variability in macrobenthic community structure

Seasonal variability was analyzed for each location separately by MDS ordinations that provided good representations with stress values between 0.08 and 0.13 (Figure 4.13). The first MDS axis showed strong correlation with salinity, especially at GBL (r= -0.85, $p<0.001$) and GBR (r=0.80, $p<0.001$), and to a lesser extent also at Valkenisse (r=0.66, p=0.005) and Baalhoek (r=0.64, p=0.01), whereas at Paulina salinity was more correlated with the second MDS axis (r=0.52, $p<0.05$). Temperature was strongly correlated with the first axis at GBL (r=-0.68, $p<0.005$) and to a lesser extent also at Paulina (r=-0.53, $p<0.05$), and with the second axis at GBR (r=0.69, $p<0.01$). Mud content strongly correlated with the first MDS axis at Valkenisse (r=0.82, $p<0.0001$).

In general, the sampling months seemed to move through ordination space in a more or less cyclic pattern, but spring sampling months did not necessarily return to the same position from year to year. This more or less cyclic movement through the ordination space was clearly demonstrated by the changes of the scores along the first ordination axis. The distance between late summer – early autumn sampling months was smaller in comparison with spring months, indicating more distinct community changes during spring months. The August sampling month of both years was found more or less at the same position, indicating a similar benthic community structure in summer in both years.

At Paulina all sampling months showed a relatively high similarity (Figure 4.11). Months were more or less clustered in a successive way, with clusters being March-April 1993, May-June 1993, July-August 1993/1994, October 1993 – January 1994, February-May 1994 and June 1994. Baalhoek was characterized by the highest similiarities among sampling months, indicating relatively small

Table 4.5. Results of the PCA and RDA ordinations on the monthly sampling occasions of each location separately. Given are the eigenvalues of the first and second axis for both ordination methods. For the RDA also the percentage variance of the species data and the percentage variance of the species-environment relation explained by the axes is given cumulatively. Both the first canonical eigenvalue as the sum of all canonical eigenvalues were statistically significant by Monte Carlo permutation test ($p<0.01$), except for Paulina (not signifiant). Correlations (*$p<0.05$; **$p<0.01$; ***$p<0.001$) of environmental variables with the axes are given only for those environmental variables that contributed significantly and independently to explaining the variation in the RDA (forward selection with Monte Carlo permutation tests; °:$p<0.05$; °°$p<0.01$; °°°:$p<0.001$).

	Axis 1	Axis 2		Axis 1	Axis 2
Paulina			**Valkenisse**		
Eigenvalue PCA	0.30	0.23	Eigenvalue PCA	0.58	0.13
Eigenvalue RDA	0.194	0.094	Eigenvalue RDA	0.50	0.10
% variance of species data	19.4	28.8	% variance of species data	49.9	59.4
Species – environment relation	43.1	64.1	Species – environment relation	74.4	88.6
Temperature°	-0.72**	0.17	Mud content°°°	-0.79***	-0.33
			Temperature°	-0.39	-0.77***
Baalhoek			**GBR**		
Eigenvalue PCA	0.34	0.25	Eigenvalue PCA	0.61	0.15
Eigenvalue RDA	0.314	0.214	Eigenvalue RDA	0.49	0.12
% variance of species data	31.4	52.8	% variance of species data	48.9	61.0
Species – environment relation	43.4	72.9	Species – environment relation	70.3	87.8
Salinity°°	-0.71**	0.08	Salinity°°°	-0.79***	0.08
Mud content°	-0.36	0.68**	Temperature°	-0.35	0.59*
			Median grain size°	0.27	-0.12
GBL					
Eigenvalue PCA	0.48	0.23			
Eigenvalue RDA	0.414	0.114			
% variance of species data	41.4	52.8			
Species – environment relation	66.2	84.5			
Salinity°°	0.83***	0.27			

changes in the macrobenthic community from month to month. However, spring, summer and winter months were clearly segregated in the MDS ordination. In Valkenisse a relatively large dissimilarity was observed among certain groups of months. Based on the cluster analysis, spring months (Feb-June) of both 1993 and 1994 were separated from all other months. Other months were clustered in a successive way, which was clearly demonstrated in the MDS ordination. Large changes were observed from month to month, except for the late summer – autumn (Jul-Nov) period. In GBR and GBL basically the same pattern was observed as for Valkenisse, with large changes in ordination space during winter and spring months, and smaller changes during late summer - autumn.

The results of the PCA and RDA ordinations are summarized in Table 4.5. Eigenvalues of the first axis were strong at GBR, Valkenisse and GBL and suggest the gradient that it represented is highly significant and by far the most important. Eigenvalues of the second axis were low. Only at Paulina both axes of the RDA had low eigenvalues, which were not statistically significant. Temperature or salinity were most important in determining the first RDA ordination axis for all locations, both parameters also covarying to some extent (range of $r = 0.55\text{-}0.67$; $p<0.03$). At Valkenisse mud content (strongly correlated with salinity and temperature: $r = 0.73$; $p<0.001$) was highly correlated with the first ordination axis, reflecting the high seasonal variation in mud content at this location. The graphical biplot diagrams of the PCA and RDA yielded similar projections of the sampling months as those observed in the MDS ordinations, and are therefore not presented.

Discussion

Spatial variability in macrobenthic species distributions

The data from this study confirm the previously observed pattern of both species distribution and relative dominance (abundance and biomass) along the estuarine salinity gradient of the Schelde estuary (WOLFF 1973; MEIRE et al. 1991; YSEBAERT et al. 1993, 1998a, this thesis). The spatial variation between the five locations was larger than the seasonal variation and was on a regional scale strongly influenced by salinity and on a local scale by sediment characteristics (see also e.g. FLINT & KALKE 1985).

The pattern of species richness and diversity declining with decreasing salinity is observed in most estuaries (e.g. BOESCH 1977; WOLFF 1983; MICHAELIS 1983; YSEBAERT et al. 1998a), as well as the trend from lower biomass in the low salinity zones to higher biomass in the polyhaline zone (MEIRE et al. 1991; HEIP et al. 1995; YSEBAERT et al. 1998). No clear trend in abundance was observed, similar to other observations in the Schelde estuary (YSEBAERT et al. 1993, 1998a, this thesis).

On a more local scale (within the same salinity zone), sediment type clearly influenced the observed macrobentic communities. In the α-mesohaline, as well as in the β-mesohaline zone, the macrobenthic community structure differed between the 'muddy' location and the 'sandy' location. Several studies indeed have indicated sediment characteristics (e.g. mud content) being important factors influencing the distribution of benthic populations (e.g. GRAY 1974; BEUKEMA 1976; ZAJAC & WHITLATCH 1982a,b; MEIRE et al. 1994; MANNINO & MONTAGNA 1997). However, as the range of sediment parameters in our study is relatively small, relative to the tolerance of the different species, most species were observed both in the sandy as in the muddy locations, but differing in relative dominance.

Temporal variability in macrobenthic species distributions

In this study seasonality was evident for all diversity measures, total abundance and biomass at all five locations. All commonly observed macrobenthic species showed distinct seasonal patterns. The general pattern was that of an increase in abundance during late spring and early summer, coinciding with an increase in temperature, followed by a decrease towards winter. This decrease could be very sharp in time, or slowly decreasing towards winter, depending on the species and/or location considered. Lowest abundances were observed in late winter and early spring. Seasonal variation in biomass followed abundance patterns, especially at GBR, GBL and Valkenisse, indicating that biomass is mainly determined by the recruitment (and successive disappearance) of newly settled individuals. At Paulina the temporal pattern in biomass was more due to the summer growth in established populations of the larger species, mainly the bivalves *C. edule* and *S. plana*., although the sharp biomass increase in August 1994 was due to newly settled *C. edule* spatfall.

A sampling interval of one month is probably too long to detect the exact time of settlement. However, both the month when the population abundance of a species increased as the magnitude of this increase varied among species, among the five locations and between both years.

For bivalves spatfall was observed for all species. For each species the observed period of spatfall was similar among locations, but differed among species: earliest for *S. plana* (March-April), followed by *M. balthica* (May-June), *C. edule* and *M. arenaria* (both July). An extensive literature exists on the reproduction and recruitment of bivalves. In general, duration, timing and number of spawning periods vary from year to year, differ from place to place and depends on water temperature and age (e.g. MÖLLER & ROSENBERG 1983; BACHELET 1986; HARVEY & VINCENT 1989; DUCROTOY et al. 1991; ESSINK et al. 1991; HONKOOP & VAN DER MEER 1997). In this study recruitment of *M. balthica*, *C. edule* and *M. arenaria* spatfall was observed in both years, for *S. plana* only in 1993. *S. plana* is known to have very irregular spat fall (ESSINK et al. 1991). Enhanced recruitment success is often noticed for intertidal bivalve species after severe winters (e.g. BEUKEMA 1979, 1982). As in this study both winters were normal to mild, without severe frost periods, the effect of severe winters could not be investigated, but successful reproduction was apparent for all species.

Polychaetes, especially the spionid (e.g. *P. elegans*) and capitellid (*H. filiformis*) species showed a distinct recruitment success. The period of observed recruitment was similar among locations, but differed among species, being in general earlier (May-June) for the spionid species as compared to *H. filiformis* (July-August).

For the dominant amphipod *C. volutator* the increase in abundance was observed earlier at GBL (May-June) as compared to GBR and Valkenisse (July-August). This can probably be explained by the fact that in GBL a population of *C. volutator* remained present in the preceding winter, reproducing in May-June, whereas at the other two locations no *C. volutator* were observed in the preceding winter, making the settlement of new recruits depending on an influx from other places. Indeed, the overwintering generation breeds from May to June, which gives rise to a subsequent summer-breeding generation which reproduces between the beginning of July and September (e.g. MÖLLER & ROSENBERG 1982; PEER et al. 1986; pers. observ.). At Valkenisse also a remarkable temporal segregation in the occurrence of amphipods was observed, with in winter and early spring *Bathyporeia* spp. being present, in early summer

C. arenarium and in late summer – autumn *C. volutator*. This segregation in time could be attributed to the seasonal variation in mud content, being low in winter and increasing towards summer and autumn. Normally, these amphipod species are expected to be spatially segregated, as *Bathyporeia*, like most Haustoriidae, is a typical, well adapted inhabitant of unstable, sandy sediments (BOUSFIELD 1970; KHAYRALLAH & JONES 1980), whereas a spatial segregation was observed for *C. arenarirum* and *C. volutator*, preferring sandy (% silt < 10%) and muddy (% silt > 10%) respectively (FLACH 1993, 1996). At Valkenisse this temporal succession in amphipod species might be related to the clear seasonal variation in mud content.

Spatio-temporal variability in environment and macrobenthic community structure

Greatest temporal variability in water quality parameters was observed at the low salinity locations GBL and GBR and variability was lowest at the polyhaline location Paulina. Not only variability in salinity was greatest, also oxygen concentration showed highest variability at GBL and GBR. Variability in sediment characteristics was similar among locations, except for Valkenisse where a distinct seasonal pattern was observed in mud content . This clear seasonal variation in mud content was also observed on another sand flat in the Westerschelde (Molenplaat), and WIDDOWS et al. (subm.) attributed this variation to a complex interaction between biological (bio-stabilisation through microphytobenthos, most pronounced in spring and summer) and physical processes (storm conditions and wave action, most pronounced in winter). The other locations were located on mudflats, situated along the banks of the estuary, and are thus more sheltered. Although variability in mud content was low at these locations, sedimentation or erosion could have appeared, as was also demonstrated on another intertidal mudflat (DE BROUWER et al. 2000). In summary, therefore, highest environmental variability was observed at GBL and GBR (highest physicochemical variability) and at Valkenisse (highest physical variability), and was lowest at the polyhaline location Paulina.

Greatest temporal variability in the general macrobenthic characteristics (number of species, total abundance and total biomass) was observed at the locations Valkenisse, GBR and GBL and variability was lowest at Paulina and Baalhoek. Therefore, it is concluded that, due to a more varying environment, temporal (short-term seasonal) variations in macrobenthic communities are much more distinct at these locations.

Both regional as local processes will determine the observed variability in the different macrobenthic communities. Reproductive activity is obviously related to water temperature, as temperature induce gamete production and release of larvae into the water column. As a result, recruitment was observed at all intertidal locations and changes in the communities were higher during periods of peak recruitment (spring-early summer) than during non-recruitment periods at all locations. The magnitude of recruitment differed among locations and is dependent on a complex interaction of different physical and biological processes. Initial settlement (and secondary dispersal) will be mainly determined by hydrodynamics, active substrate selection and inter- and intraspecific competition (e.g. BUTMAN 1987; SNELGROVE & BUTMAN 1994). For instance, at Valkenisse, situated in a sedimentary environment as indicated by the slow but continuous raise of the site, hydrodynamic conditions are probably favourable for settlement of larvae and food, as here very high and distinct peaks in recruitment were observed (e.g. *P. elegans*, *H. filiformis*).

The remaining spatio-temporal variability in macrobenthic community structure is probably more related with stress and disturbance events. Stress and disturbances emerge as important structuring forces in soft-sediment systems, stress being associated with events over broader scales in space and time, and disturbance associated with discrete events (such as storms, severe winters) (e.g. ZAJAC & WHITLATCH 1985; HALL et al. 1994). The salinity gradient acts as a physiological stress for stenohaline marine and freshwater species and places environmental stress on euryhaline species. In our study, the wider fluctuations in salinity in the mesohaline zone of the estuary, especially at GBL and GBR, resulted in a reduction of the number of species, a low biomass and a high variability. At GBL and GBR salinity conditions may change from mesohaline to almost freshwater in a one month period, as was observed in January 1994. In spring and summer salinity conditions were more favourable, allowing species like *M. balthica*, to settle down in low densities. However, *M. balthica* hardly showed any growth during summer (pers. observ.) and completely disappeared during winter. Besides *M. balthica*, also other species settled down in summer in the mesohaline zone and completely disappeared in winter (e.g. *P. elegans* at GBL, *H. filiformis* at GBR and *C. edule* at Valkenisse). This clearly coincided with the dramatic decline in salinity at that time. Therefore, spatial distribution of several macrobenthic species shifted geographically on seasonal time scales.

Additional stress in GBL and GBR might arise from the low dissolved oxygen concentrations during several months a year, especially in summer, and the high SPM concentrations. At GBR the very reduced sediment could be an additional stress factor. At Valkenisse additional stress of increased wave action during winter, as could be deduced from the decreasing mud content in winter, causing instability of the bed, might also result in a more pronounced change in macrobenthic community here.

In summary, community changes appeared much more pronounced in winter period at GBL and GBR, and to a lesser extent also at Valkenisse. At Paulina in winter only minor changes in community structure were observed.

We suggest that at the meso-/oligohaline transition zone, where salinity conditions show large, seasonal fluctuations, benthic communities change frequently, resulting in communities that seldom progress beyond early benthic-community succession. Dominance by small, newly settled benthos that feed at or near the sediment-water interface is characteristic of such disturbance (GASTON et al. 1998). The macrobenthic species observed in this zone of the estuary are typically very mobile (e.g. the amphipod *C. volutator*), opportunistic (tubificid Oligochaeta, capitellid *H. filiformis*) or omnivorous (the nereid *N. diversicolor*), strategies which resemble the early response to 'succession after disturbance series' (RHOADS et al. 1978) or 'distance to pollution source series' (PEARSON &

ROSENBERG 1978). In this zone of the estuary probably physical and physiological stress coincides with 'high loading' stress. On top of that, sediment contamination with metals and organic micropollutants is rather high in sediments in the meso/oligohaline zone of the Schelde estuary (e.g. SRINETR 1997, ZWOLSMAN 1999), provoking additional stress (e.g. RAKOCINSKI et al. 1997).

On the other hand, in the polyhaline zone environmental variability was less, resulting in a community that did not show drastic changes, although also here seasonal patterns were obvious. The dominant species of this community were in general more long-living species, such as *C. edule* and *S. plana*.

The above described relation between community patterns and stress/disturbance was also obvious from the ABC-curves curves, indicating that the structural complexity level decreased from the polyhaline zone towards the mesohaline zone.

Spatio-temporal variation in trophic and functional structure

The regional and local patterns observed in macrobenthic community structure are also reflected in clear differences in trophic structure among the five locations. Generally, trophic diversity increased with salinity (GASTON et al. 1998) and showed highest temporal variability at the locations GBL, GBR and Valkenisse. Especially at GBL trophic structure changed from a co-dominance of omnivores and surface deposit feeders in summer to an almost exclusive dominance of omnivores in winter.

The general observation of suspension feeders being associated with sandy substrates and (surface) deposit feeders with muddy sediments, as well as both groups being spatially separated (trophic-group amensalism of RHOADS & YOUNG 1970) is not supported by this study (see also HERMAN et al. 1999).

Suspension feeders (*C. edule*) constituted an important part of the macrobenthic biomass at the polyhaline location Paulina, and their biomass diminished with increasing salinity, being almost absent at the low salinity locations GBL and GBR. This is in accordance with several other studies in the Schelde estuary (e.g. YSEBAERT et al. 1993, 1998a, in prep.), and is most likely linked with primary productivity of the phytoplankton in the system (HEIP et al. 1995; HERMAN et al. 1999), as suspension feeders were shown to depend mainly on pelagic food sources (HERMAN et al. in press).

In comparison with suspension feeders, deposit feeders depend more on local food conditions, such as the availability and quality of the organic matter, and the biomass and productivity of microphytobenthos (HERMAN et al. 1999, in press). Deposit feeders appeared in high densities at all five locations. The occurrence of sub-surface deposit feeders seemed to be related with mud content (and TOC). Within the same salinity zone, it was indeed observed that abundance and biomass of sub-surface deposit feeders was much higher at the 'muddy' locations as compared to the 'sandy locations'.

Mean total biomass of deposit feeders decreased considerably with decreasing salinity, especially for surface deposit feeders. A similar phenomenon was also observed by YSEBAERT et al. (in prep.) on a much larger data set on the Schelde estuary. Several factors could explain this decrease, such as facultative suspension feeding by several polychaete and bivalve species (e.g. *M. balthica* (OLAFFSON 1986; KAMERMANS 1994) and 'interface' feeding spionid polychaetes (DAUER et al. 1981; TAGHON & GREENE 1992)). Therefore, surface deposit feeders in the polyhaline zone might profit from the higher phytoplankton primary production (high quality food source) in this part of the estuary, resulting in a higher biomass. This might explain the higher biomass values observed for SDF at Paulina. Indirectly, this was observed by a clear difference in growth rate for *S. plana* and *M. balthica* at Paulina and Baalhoek (pers. observ.). For instance, newly settled *S. plana* grew between March/April and August/September from 2 to 20 mm at Paulina and from 2 to 12 mm at Baalhoek, both sites having similar mud and TOC contents, and salinity conditions within the tolerance of the species. Unfortunately, no data on microphytobenthos were available for the sampling locations.

For the low salinity locations GBL and GBR, also salinity stress could explain the lower SDF biomass here. Especially the larger bivalve species experience here lethal (e.g. for *S. plana*) or suboptimal salinity conditions (e.g. for *M. balthica*), and SDF is dominated here by the small amphipod *C. volutator*. Additionally, the nearly absence of SDF at GBR might be explained by the fact that SDF, which mainly live in tubes or burrows (e.g. *C. volutator*, *P. elegans*), were not capable of maintaining there burrows in the very soft sediment present, characterized by a very fluffy top layer.

Omnivores, mainly the nereid *N. diversicolor*, did not show a clear trend in absolute biomass values along the salinity gradient, but their high relative dominance in the lower salinity zones was apparent, and also observed by (YSEBAERT et al. 1993,1998a, in prep.).

Spatiotemporal patterns and estuarine management

Many monitoring programmes are being conducted to study the effect of man-induced changes of the environment (e.g. pollution, coastal engineering works, dredging/dumping activities, etc.) on the occurrence of macrobenthic populations. These programmes are mostly designed as large scale (spatial variation) and/or long-term (temporal variation) surveys. However, often because of financial and/or logistic limitations, both the small-scale spatial variation as the short-term temporal variation is often neglected in these studies. E.g., in the Schelde estuary a large scale/long-term macrobenthic monitoring programme is running based on a spring and autumn sampling. However, seasonal patterns are a major source of variation for many estuarine systems and organisms, as was demonstrated for the macrobenthos in this study. Therefore, long-term study designs must consider carefully the frequency of sample collection or most of the observed variation will be due to inadequate sampling (HOLLAND et al., 1987). Also the incorporation of these short-term seasonal variations (especially the large seasonal variations in biomass) into ecosystem models should be considered, in order to improve the predictability of these models. Thus, in assessing the overall role of macrobenthos to the entire ecosystem, the variability associated with estuarine environmental changes, as was observed in this study, must be integrated. Sampling in only one of the 'biotic zones' will not provide adequate characterization of the benthos' importance throughout the estuary. Evenmore it is crucial to collect the necessary environmental parameters such as sediment characteristics, food related parameters (e.g. microphytobenthos), waterquality etc. to be able to interpret changes in benthic communities. Especially, more knowledge is needed on the contribution and interaction of multiple stressors in estuarine ecosystems in order to determine natural versus human induced disturbances.

Acknowledgements

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Chapter five

A comparison of the macrobenthic distribution and community structure between two estuaries in SW Netherlands

P.M. Meire, J. Seys, T. Ysebaert and J. Coosen

Abstract

The Wester- and Oosterschelde are the only two remaining estuaries in the Delta area of SW Netherlands. In the Westerschelde the normal estuarine gradient from a brackish to a marine tidal system is found, whereas in the Oosterschelde major coastal engineering works have profoundly changed the character of the area. There is now no salinity gradient, and turbidity and pollution are very low.

The intertidal macrofauna of both estuaries was studied intensively in 1987 and found to be similar in species composition. However, more species occurred in the Oosterschelde mainly because of the presence of extensive mussel beds. The average density was greater in the Westerschelde, but biomass was much greater in the Oosterschelde.

Multivariate statistical analyses (TWINSPAN and DECORANA) were used to determine similarities between stations and almost no overlap occurred between stations from the Ooster- and Westerschelde. Water parameters (salinity, turbidity etc.) correlated with the first ordination axis and sediment parameters (median grain size, mud content) were correlated with the second axis. A gradient from a suspension feeder community in the Oosterschelde and polyhaline zone of the Westerschelde to a deposit feeder dominated community in the brackish zone of the Westerschelde was found. These correspond to coastal and detritus food chains. It is concluded that the absence of filter feeders in the brackish part of the Westerschelde is caused by the highly dynamic character of the estuary rather than by pollution or lack of food. Increased dredging activities could further impoverish the fauna.

Introduction

The benthic macrofauna of the whole Delta area in the south-western part of the Netherlands was studied intensively by WOLFF (1973). However, since then the area has been changed profoundly by

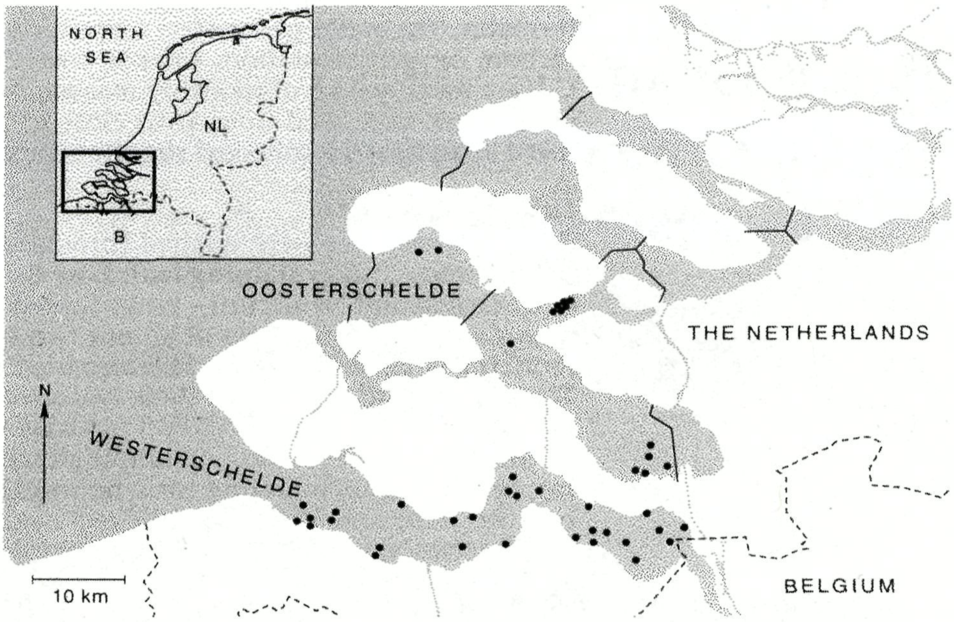

Figure 5.1. Location of the sampling stations in the Oosterschelde and the Westerschelde.

major coastal engineering projects. Several estuaries have been dammed and in the Oosterschelde a storm-surge barrier has been built. This has strongly influenced the hydrodynamic properties of the estuary and stimulated much research (see also SMAAL et al. 1991). The Westerschelde has remained the only natural estuary in the whole Delta area, showing a clear gradient in salinity, turbidity, nutrient load etc., although it is severely polluted. Surprisingly little is known about the ecological value of the Westerschelde.

In the present study, the distribution of the macrobenthos in both estuaries is described and compared in relation to the prevailing environmental factors.

Materials and methods

Study area

The Westerschelde is the estuarine part of the River Schelde, bordered at the east by the Dutch-Belgian border and at the west by the line Breskens-Vlissingen (Figure 5.1). The freshwater input, mainly through the River Schelde, is small (on average 105 $m^3.s^{-1}$, CLAESSENS 1988) compared to a tidal volume of 10^9 m^3. The mean tidal range is 3.85 m at the mouth and 4.58 m at the Belgian border. Typical estuarine gradients in the abiotic factors are present from the mouth to the river, such as a decrease of chlorinity and oxygen content and an increase in turbidity, particulate organic matter and nutrients (Table 5.1). There is a high anthropogenic stress due to dredging activities and from large

Table 5.1. Abiotic characteristics of the Oosterschelde (OS) and the Westerschelde (between the Dutch-Belgian border and the mouth) (WS) estuary (data from Rijkswaterstaat).

	Tidal range, m	Chloride content, g Cl·l^{-1}	Sus-pended matter, mg·l^{-1}	Secchi disc trans-parency, m	Mean N content, mg·l^{-1}	Mean P content, mg P·l^{-1}	Mean mud content, bottom, %	Mean Cd content, dissolved, µg·l^{-1}
OS	2.8-3.8	14-18	4- 9	2.1-2.3	0.9-1.2	0.09-0.14	2.6	0.03-0.05
WS	3.8-4.5	4-17	27-66	0.2-0.8	1.6-8.1	0.18-0.86	3.3	0.13-0.22

amounts of inorganic and organic contaminants from various effluents, especially in the brackish part and the River Schelde (MOERLAND 1987; DUURSMA et al. 1988).

Since the closure of the Volkerak Dam in 1969, the freshwater input in the Oosterschelde (through Volkerak sluices, a few small rivers, and some polderwater discharge) has been strongly reduced and regulated at about 50 $m^3.s^{-1}$ (SMAAL et al. 1991). This has resulted in a stable high chlorinity in the whole area and small nutrient and pollutant loads with very low concentrations of suspended matter (Table 5.1). The exchange with water from the North Sea was reduced after the construction of the storm-surge barrier in 1987. The mean tidal amplitude is lower than in the Westerschelde (3.5 m near Yerseke). The creek flow-rates are low and vary between 0.5 $m^3.s^{-1}$ and 1.2 $m^3.s^{-1}$ (see also SMAAL et al. 1991).

The sampling programme

The survey was carried out in September–October 1987. In the Westerschelde (Figure 5.1), 28 sampling stations were placed in different habitat types along the whole gradient. Within each station 2-4 sites were chosen, and at each site 10 cores, 4.5 cm diameter (15.9 cm^2), and 3 cores, 15 cm diameter (176.6 cm^2), were taken to a depth of 30 cm. The larger cores were washed in the field through a 3-mm-mesh sieve, whereas the smaller ones were fixed in the field with 35 % neutral formalin, brought to the laboratory and washed through a 1-mm-mesh sieve. The data from the Oosterschelde are from two different sampling programmes. The first programme was carried out at the Slikken van Vianen, an intertidal area in the central part of the estuary, where the interaction between waders and macrozoobenthos has been investigated since 1979 (MEIRE 1987; MEIRE & KUIJKEN 1984; MEIRE & COOSEN 1985; MEIRE & ERVYNCK 1986). In each of the six permanent study plots situated in the different habitat types (defined according to inundation time and sediment type), 30 cores, 4.5 cm in diameter (15.9 cm^2), and 5 cores, 15 cm in diameter (176.6 cm^2), were taken to a depth of 30 cm. The treatment of these samples was as described for the Westerschelde.

The second programme was started in 1983 to investigate the effects of the construction of the storm-surge barrier on the macrozoobenthos. Eight permanent stations were chosen in the intertidal

Table 5.2. Mean density, biomass and species composition of the locations sampled in the Oosterschelde and the Westerschelde.

	Oosterschelde	Westerschelde
Mean total density, N · m^{-2}	16501	24042
Mean total biomass, g AFDW · m^{-2}	111.5	14.6
Species richness	43	36

Species composition:

Species found in both estuaries
- *Cerastoderma edule* (Linnaeus)
- *Hydrobia ulvae* (Pennant)
- *Macoma balthica* (Linnaeus)
- *Mya arenaria* (Linnaeus)
- *Mysella bidentata* (Montagu)
- *Retusa obtusa* (Montagu)
- *Anthozoa* sp.
- *Bathyporeia* sp.
- *Carcinus maenas* (Linnaeus)
- *Corophium* sp.
- *Crangon crangon* (Linnaeus)
- *Gammarus* sp.
- *Anaitides* sp.
- *Antinoella sarsi* (Kinberg)
- *Arenicola marina* (Linnaeus)
- *Capitella capitata* (Fabricius)
- *Eteone* sp.
- *Heteromastus filiformis* (Claparède)
- *Magelona papillicornis* (Müller)
- *Nemertea* indet.
- *Nephtys hombergii* (Savigny)
- *Nereis diversicolor* (Müller)
- *Nereis succinea* (Leuckart)
- Oligochaeta indet.
- *Polydora* sp.
- *Pygospio elegans* (Claparède)
- *Scoloplos armiger* (Müller)
- *Spio filicornis* (Müller)
- *Tharyx marioni* (Saint Joseph)

Species in Westerschelde only
- *Manayunkia aestuarina* (Bourne)
- *Ophelia rathkei* (McIntosh)
- *Scolelepis squamata* (Müller)
- *Spiophanes bombyx* (Claparède)

Species in Oosterschelde only
- *Crassostrea angulata* (Lamarck)
- *Crepidula fornicata* (Philibert)
- *Lepidochitona cinerea* (Linnaeus)
- *Littorina littorea* (Linnaeus)
- *Mytilus edulis* (Linnaeus)
- *Scrobicularia plana* (da Costa)
- *Jaera albifrons* (Leach)
- *Melita palmata* (Montagu)
- *Pagurus bernhardi* (Linnaeus)
- *Urothoe poseidonis* (Reibisch)
- *Lanice conchilega* (Pallas)
- *Microphthalmus aberrans* (Webster & Benedict)
- *Pholoe minuta* (Fabricius)
- *Scolelepis foliosa* (Audouin & Milne Edwards)

area, taking account of the west-east gradient, and sampled twice a year (March–April, August–September). At each station, three sets of 5 core samples, 10.3 cm in diameter (83 cm^2), were taken to a depth of 30 cm. They were sieved in the field on a 1-mm-mesh sieve and fixed with 7 % neutral formalin. The water parameters (chlorinity, suspended matter, particulate organic carbon, oxygen saturation, total-N, total-P, dissolved Si, chlorophyll-*a*, dissolved Cd) are mean values of monthly measurements for 1987 (Rijkswaterstaat, unpublished data). Data were used from areas close to the sampling station. Samples for sediment analysis were collected simultaneously with the macrofaunal samples.

Laboratory methods

The small samples were washed through a 1-mm-mesh sieve and all organisms were extracted, after staining with Rose Bengal, identified to species level – except Oligochaeta and Nemertini – and counted. Bivalves were measured to the nearest mm. Density and biomass of all but two species are based on the small samples. From the large samples only *Mya arenaria* L. and *Arenicola marina* L. were extracted. The density and biomass of these two species is entirely based on the large samples. Ash-free dry weight (AFDW) biomass was obtained by weighing (± 0.0001 g) all individuals per species per sample after drying for 12 hours (110°C), and weighing again after incinerating for 2 hours (550°C). All bivalves were weighed without the shell and length-weight regressions were calculated. The resulting station/species abundance matrix data were analysed using the multivariate techniques TWINSPAN and DECORANA (GAUCH 1982). For the analysis the following congeneric species pairs were combined because of identification problems: *Corophium arenarium* Crawford/*C. volutator* Pallas, *Anaitides mucosa* Orsted/*A. maculata* L., *Eteone longa* Fabricius/*E. flava* Fabricius, *Bathyporeia pilosa* Lindstrom/*B. sarsi* Watkin and *Gammarus* sp. The cut-levels used in the TWINSPAN analysis were: 0, 1, 4, 16, 64, 256, 1024, 4096, 9999. No data transformation nor down-weighting of rare species was used.

Results

The total number of species was lower in the Westerschelde (36) than in the Oosterschelde (43) (Table 5.2) although the species composition was comparable and there were 29 species in common. The latter are all typical estuarine organisms such as *Cerastoderma edule, Hydrobia ulvae, Macoma balthica, Nereis diversicolor, Nephtys hombergii and Arenicola marina.* Fourteen species were found only in the Oosterschelde, although some of them *(Mytilus edulis, Scrobicularia plana)* are known to be present in limited numbers in the Westerschelde (pers. obs.). Seven species were restricted to the Westerschelde samples.

The mean total density was higher in the Westerschelde than the Oosterschelde, respectively 24042 (SE: 4244) and 16501 (SE: 3343) individuals.m^{-2}. However, mean total biomass was much higher in the Oosterschelde (11-1-.5 g AFDW.m^{-2}; SE: 36.3 g) than in the Westerschelde (14.6 g AFDW.m^{-2}; SE: 3.3 g).

Based on the densities of each species per station, seven station groupings can be separated using

Figure 5.2. TWINSPAN based on the densities of macrobenthic organisms in Oosterschelde and Westerschelde in 1987. Seven groeps were separated and within each group the mean densities of the species are represented with dots.

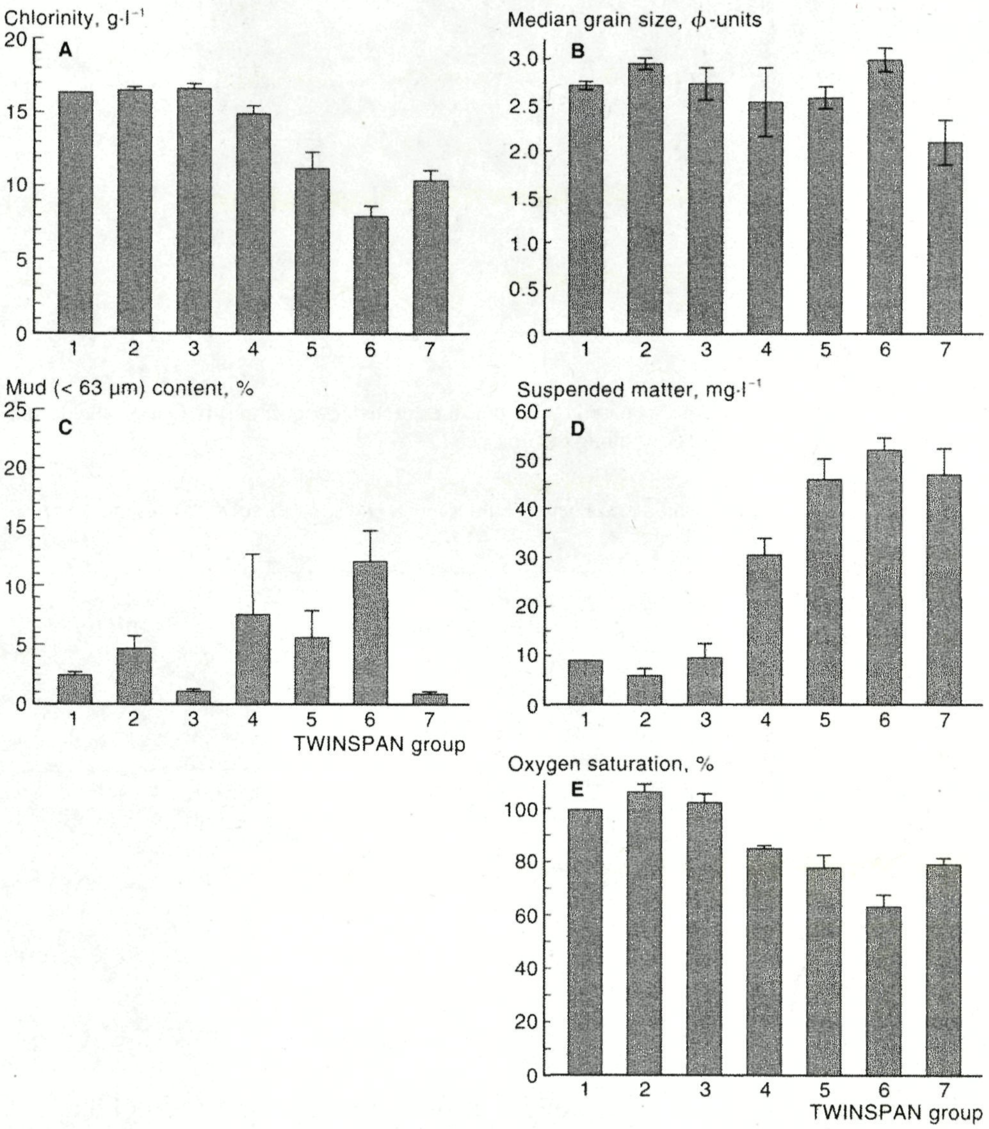

Figure 5.3. Abiotic factors (mean values ± SE) per TWINSPAN-group: chlorinity, median grain size, mud content, suspended matter, oxygen saturation.

TWINSPAN (Figure 5.2). Group 1 stations are in the Oosterschelde and are characterised by the presence of *M. edulis* and a series of species such as *Crepidula fornicata and Littorina littorea* which are associated with the mussel beds. Group 7 consists of two stations with an impoverished benthic fauna whereas the remaining five groups have a rather similar species composition although the relative abundance of species differs between groups. After the second division in the analysis, all samples from the Oosterschelde are separated from those in the Westerschelde. When performing TWINSPAN on the biomass data all samples from both estuaries were separated after the first division (unpublished data). However, groups identified were very similar, therefore further analysis here is restricted to the analysis based on the density of the macrofauna.

In order to characterise the seven TWINSPAN-groups (Figure 5.2), average values of some important abiotic factors are given in Figure 5.3 A- E. With the exception of group 7 – which consists of two impoverished stations – a clear gradient in salinity between the groups is observed. Groups 1 –

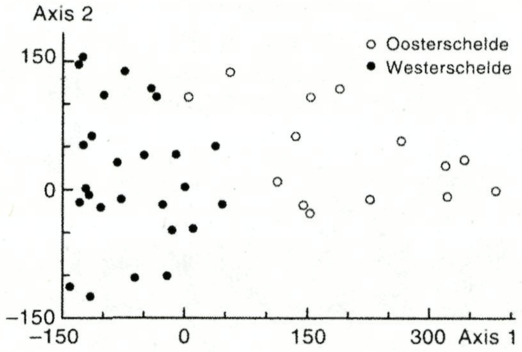

Figure 5.4. Detrended Correspondance Analysis based on the densities of macrozoobenthos in Oosterschelde and Westerschelde: position of the sampling stations along the first two DCA-axes.

Table 5.3. Correlation coefficients (Spearman's rank) between the scores on the two first DCA-axes and some environmental factors.

	Axis 1		Axis 2	
Factor	r_s	Significance	r_s	Significance
Chlorinity	0.70839	***	0.42963	**
O_2-saturation	0.75881	***	0.39758	*
Particulate organic carbon	−0.76803	***	−0.26775	n.s.
Suspended matter	−0.81476	***	−0.32976	*
Total-P content	−0.63559	***	−0.45601	**
Total-N content	−0.69314	***	−0.47044	**
Dissolved Si	−0.70235	***	−0.45474	**
Dissolved Cd	−0.81719	***	−0.07609	n.s.
Median grain size	0.19376	n.s.	−0.51253	***
Mud content	−0.22151	n.s.	−0.61466	***
Inundation time	−0.11953	n.s.	−0.24170	n.s.

* $p \leq 0.05$; ** $p \leq 0.005$; *** $p \leq 0.001$; $n = 40$.

3 (all stations from the Oosterschelde) and group 4 (stations from the marine part of the Westerschelde) have high mean chlorinities (14.9-16.6 g $Cl^-.l^{-1}$). Group 6 consists of stations in the brackish part of the Westerschelde, group 5 (11.2 g $Cl^-.l^{-1}$) and group 7 (10.3 g $Cl^-.l^{-1}$) are intermediate. Oxygen saturation follows a similar gradient, with more than 100% saturation on a yearly base in the Oosterschelde, only 84 % in the marine part of the Westerschelde decreasing to 63% in the brackish part. Suspended matter, nutrients etc, follow an opposite gradient with low values in the Oosterschelde and increasing values towards the brackish part of the Westerschelde. Sediment parameters also differ between groups: groups 1 – 3 consist of fine sand (median grain size: 134-154 µm) with a low mud content (1.0-4.6 %), whereas the Westerschelde groups (4 – 7) consist of fine to medium sand (125-233 µm) and higher mud contents (0.8-12.0 %).

A Detrended Correspondance Analysis (DECORANA) based on the species abundance matrix reveals the same gradients (Figure 5.4). Stations from the Oosterschelde and Westerschelde are clearly separated along the first axis (eigenvalue: 0.696) which is related to the water chlorinity, suspended matter, nutrient content and pollution stress (Cd content) (Table 5.3). The second axis (eigenvalue: 0.290) is correlated with sediment characteristics (median grain size, mud content) (Table

Table 5.4. Mean biomass (g AFDW.m^{-2}), number of species and density (N.m^{-2}) and biomass (g AFDW.m^{-2}) of some species in the different TWINSPAN-groups.

TWINSPAN-group	1	2	3	4	5	6	7
Mean biomass	300.7	64.6	48.8	36.5	6.9	16.2	0.5
Number of species	25.3	17.4	17.3	17.8	12.2	11.3	6.5
Density							
Heteromastus filiformis	2704	405	67	1004	2745	5342	32
Polydora ligni/ciliata	294	4	2	334	118	3615	0
Pygospio elegans	112	129	996	7228	6026	9872	24
Hydrobia ulvae	42	10675	1849	8	65	17	0
Scoloplos armiger	196	439	1166	51	0	0	0
Macoma balthica	363	617	446	2846	851	1625	0
Cerastoderma edule	3207	2417	520	4249	333	461	0
Biomass							
Macoma balthica	3.4	3.3	1.7	4.4	1.8	1.4	0
Cerastoderma edule	179.6	49.4	34.3	17.1	1.0	1.0	0

5.3). Axes 3 and 4 (eigenvalues: 0.156 and 0.063, respectively) are unimportant and not considered further. The biomass data gave similar results.

The abiotic gradients are reflected in the faunal parameters. Total biomass and species richness were highest in the mussel beds (group 1) and in the Oosterschelde as a whole in comparison to the Westerschelde (Table 5.4). Within the Westerschelde, the lowest values were found in the brackish part (group 6). Species were not distributed uniformly over the different groups. Some species *(Heteromastus filiformis, Polydora ligni-ciliata* and *Pygospio elegans)* were much more abundant in the Westerschelde. Other species *(Hydrobia ulvae* and *Scoloplos armiger)* had higher densities in the Oosterschelde. The density of *Macoma balthica* and *Cerastoderma edule* was highest in group 4 stations but their biomass was higher in the Oosterschelde (Table 5.4). This can be attributed to the differences in length – frequency distributions, since larger individuals were almost absent in the Westerschelde (Figures 5.5 and 5.6), particularly in the brackish part. This feature also applies to *Mya arenaria* whose largest individuals measured only between 6 and 7 mm, although densities varied between a few and 4350. m^{-2}.

The difference between the TWINSPAN-groups is not only reflected in the species composition but also in the distribution of trophic and major taxonomic groups (Figures 5.7 and 5.8). A gradual decrease in the proportion of the biomass of filter feeders and a gradual increase in that of deposit feeders occurred from the Oosterschelde to the brackish part of the Westerschelde (Figure 5.7). A similar gradient can be found for taxonomic groups where it seem that polychaetes replaced molluscs in the brackish, more turbid zone of the Westerschelde (Figure 5.8).

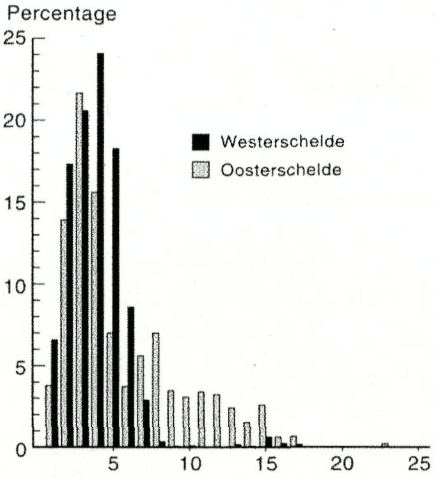

Figure 5.5. Length-frequency distributions of *Macoma balthica*, as found in the Oosterschelde (n = 514) and Westerschelde (n = 2249) in 1987.

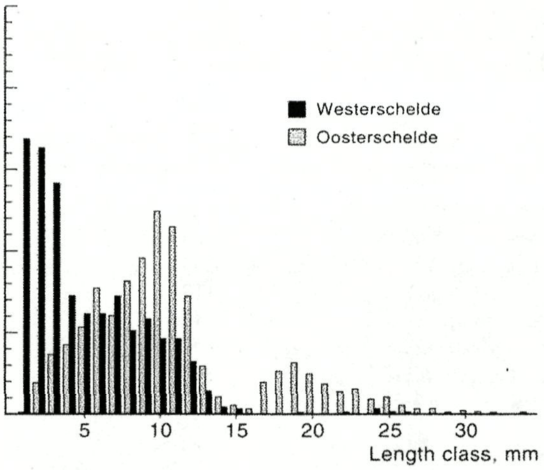

Figure 5.6. Length-frequency distributions of *Cerastoderma edule*, as found in the Oosterschelde (n = 1745) and Westerschelde (n = 1481) in 1987.

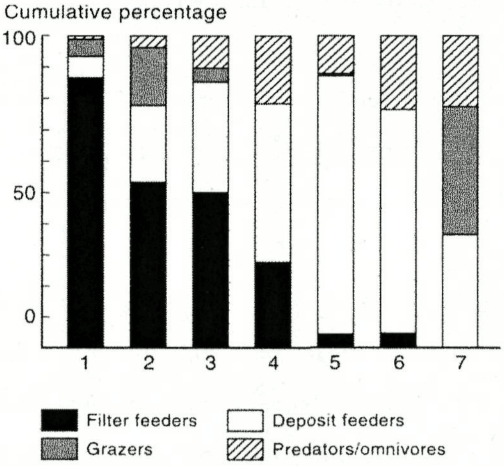

Figure 5.7. Relative biomass proportions of the different trophic groups over the seven TWINSPAN-groups.

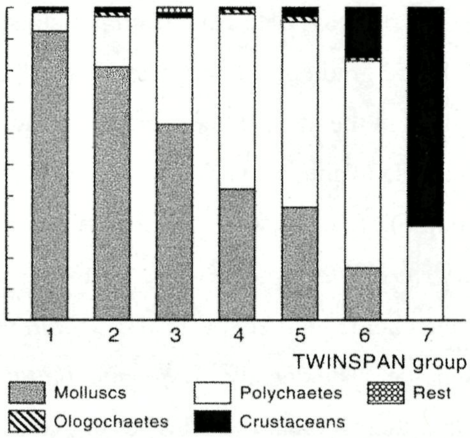

Figure 5.8. Relative biomass proportions of the different systematic groups over the seven TWINSPAN-groups.

Discussion

The species composition was similar between both estuaries and is typical for Northwest European estuaries (WOLFF 1973). Although the area sampled in the Oosterschelde is about 20% less than in the Westerschelde, seven more species were found, indicating the higher diversity. However, most species found in only one estuary are known also to occur in the other (unpublished data), although in low numbers or in small patches. Some differences exist however. *Manayunkia aestuarina* is a typical brackish water species and is only found in the Westerschelde at chlorinities of 5-8 g $Cl^-.l^{-1}$. *Crassostrea angulata* on the other hand occurs only in the Oosterschelde. This species has been

Table 5.5. Comparison of the macrobenthic fauna in the Ems, Weser and Westerschelde. The data for Ems and Weser are extracted from MICHAELIS (1983).

	Ems	Weser	Westerschelde
Zone 1:			
Chlorinity, g Cl$\cdot$l^{-1}	2.5-6.5	3.5-5	4.5-6.5
Total number of species	8	17	13
Mean biomass (g AFDW$\cdot$m^{-2})	2.5		9
Numerical dominant species in common:	Oligochaeta/*Nereis diversicolor*/*Corophium volutator*		
Zone 2:			
Chlorinity, g Cl$\cdot$l^{-1}	6.5-9	5-8	6.5-9
Total number of species	35	20	17
Mean biomass (g AFDW$\cdot$m^{-2})	8.8		15
Numerical dominant species in common:	*Nereis diversicolor*/*Corophiumvolutator*/Oligochaeta/ *Macoma balthica*/*Heteromastus filiformis*		
Zone 3:			
Chlorinity, g Cl$\cdot$l^{-1}	9-13	8-13	9-13
Total number of species	34	28	28
Mean biomass (g AFDW$\cdot$m^{-2})	13.6		8.4
Numerical dominant species in common:	*Macoma balthica*/*Heteromastus filiformis*/*Arenicola marina*		
Zone 4:			
Chlorinity, g Cl$\cdot$l^{-1}	13-17	13-17	13-17
Total number of species	80-140*	120*	34
Mean biomass (g AFDW$\cdot$m^{-2})	22		33
Numerical dominant species in common:	*Heteromastus filiformis*/*Pygospio elegans*		

*Based on more surveys than has been used for the Westerschelde.

Table 5.6. Comparison of some general characteristics of the Ems, Weser, Elbe, Eider, Westerschelde and Oosterschelde. Data from KÜHL & MANN (1983), CLAESSENS (1988) and Anon. (1986.)

	Mean flood volume, 10^6 m^3	Mean tidal amplitude, cm
Eider	40	273
Elbe	650	297
Ems	780	311
Weser	155	364
Westerschelde	1100	382-490
Oosterschelde	850*	308

*This is the value predicted for the period after the construction of the storm surge barrier. In the pre-barrier period a value of 1220 10^6 m^3 was measured.

cultivated for some years by oyster farms and is now spreading gradually throughout the estuary.

The gradient in the fauna of the Westerschelde is similar to that found by VERMEULEN & GOVAERE (1983) and can also be compared with those of the Ems and the Weser (MICHAELIS 1983). In the upper and middle parts of these estuaries, the same species are dominant (zones 1, 2 and 3 in Table 5.5) although some differences exist. Species such as *Macoma balthica, Heteromastus filiformis and Pygospio elegans* are much more abundant in the Westerschelde-mouth compared to the other estuaries. For *H. filiformis,* mean biomass values of 7.1 g AFDW.m^{-2} were found compared to less than 1 g AFDW.m^{-2} in Ems- and Weser-mouth. In contrast, a typical brackish water species such as *Streblospio shrubsolii* is common in the brackish part of the Weser, much rarer in the Ems and lacking in the Westerschelde. The polychaete *Manayunkia aestuarina* follows the opposite trend.

Compared to the Loire (ROBINEAU 1987), more species have been found in the Westerschelde.

The biomasses found on the mussel beds in the Oosterschelde were lower than those recorded by ASMUS (1987) for the Danish Wadden Sea. However, the overall biomass of macrobenthos in the Oosterschelde is high in comparison to the Westerschelde and other estuarine areas such as the Dutch Wadden Sea, which has an average value of 27 g AFDW.m^{-2} (BEUKEMA 1983). However, the average value of over 110 g AFDW.m^{-2} for the Oosterschelde is too large because mussel beds were overrepresented in the samples compared with their actual distribution. VAN DER MEER et al. (1989) estimated the average biomass for the whole Oosterschelde at nearly 50 g AFDW.m^{-2}. In the Westerschelde a gradient from lower biomass values in the brackish (9 g AFDW.m^{-2}) to higher biomass in the marine zone (33 g AFDW.m^{-2}) was found, a trend which is found in other estuaries such as the Ems (Table 5.5). The biomass in the Westerschelde on average was higher than in the Ems.

In the present study, the water parameters (salinity, turbidity etc.) and sediment characteristics (median grain size and mud content) were found to be the most important factors influencing the estuaries' macrozoobenthos. This agrees with VERMEULEN & GOVAERE (1983) who analysed the benthic fauna along four transects in the Westerschelde. The importance of these factors is very well documented (e.g. GRAY 1974, MICHAELIS 1983). Compared to the Oosterschelde, Ems, Weser, Elbe and Elder, the Westerschelde had the largest tidal amplitude and flood volume (Table 5.6), both indicating the highly dynamic character of the system. However, this factor is difficult to measure but is considered here to have a very important influence on the fauna. The greater dynamics of the Westerschelde compared to the Oosterschelde is partly reflected in the greater variability of the sediment types (median grain size varied between 123 and 176 µm in the Oosterschelde and between 71 and 292 µm in the Westerschelde; mud content varied between 0.4 and 7.7 % in the Oosterschelde and between 0.7 and 36.3 % in the Westerschelde).

The trophic structure of the benthic communities differed strongly between the Ooster- and Westerschelde and also within the Westerschelde a clear gradient was found. This corresponds with different types of food chains within the estuaries as suggested by HUMMEL et al. (1988). The brackish part of the Westerschelde is characterised by a detritus-based food chain, the mouth of the estuary by a coastal phytoplankton-based food chain. The large input of organic matter from the river and the flocculation of organic material in the brackish zone results in high concentrations of organic matter. The corresponding low transparency inhibits primary production although concentrations of nutrients are high. Organic detritus is an important link between primary and secondary production, bacteria being essential for the transfer of energy through this food chain. In the marine tidal zone, the importance of suspended organic matter is less and the primary production is higher. Therefore the energy flow from nutrients through phytoplankton to zooplankton and zoobenthos is more important than the flow from detritus to zooplankton and zoobenthos. The high proportion of filter feeders in the Oosterschelde and in the marine part of the Westerschelde and the predominance of deposit feeders in the brackish part are consistent with these food chains. Some problems exist however. First of all, although the proportion of deposit feeders in the brackish part was much higher, their actual biomass was not. Highest values were found on the mussel beds (24 g AFDW.m^{-2}) where the input of pseudofaeces probably is a very important food source for the deposit feeders, but in groups 2 and 3 their biomass was at least similar to the values found in the Westerschelde (1 3, 17, 20, 7 and 12 g AFDW.m^{-2} in TWINSPAN-groups 2 – 6, respectively). This is despite the much lower values of suspended matter or detritus in the Oosterschelde. The absence of filter feeders in the brackish part of the Westerschelde, and hence the predominance of deposit feeders warrants further consideration. A poor food supply for filter feeders should explain their absence. Indeed, primary production is lower in the Westerschelde (100 g C. m^{-2} in the brackish part and 200 g C. m^{-2}.y^{-1}in the marine part) compared to the Oosterschelde (300 g C. m^{-2}.y^{-1}, unpubl. results Rijkswaterstaat). The differences in primary production are however much smaller than the differences in the biomass of filter feeders (255, 31 and 25 g AFDW.m^{-2} in TWINSPAN-groups 1 – 3 compared with 11, 0.5 and 0.75 g AFDW.m^{-2} in TWINSPAN-groups 4 – 6, respectively). Therefore it is likely that several other factors, such as turbidity, salinity, exposure time, pollution, oxygen saturation, sediment dynamics etc., contribute to the difference in trophic structure. Analysis of the distribution of individual bivalve species, such as *Mya arenaria,* suggests that the master-factor causing the absence of this and other filter feeders from the Westerschelde, is its highly dynamic nature, corresponding to the 'Umlagerung' (mobility of the sediment) as described by JEPSEN (1965).

The differences in basal food sources (detritus versus phytoplankton) between the brackish and marine part of the Westerschelde and the Oosterschelde have certainly an impact on the composition of the macrobenthic populations. However, it also seems probable that hydrodynamic factors to a large extent determine the benthos. The dynamic nature of the Westerschelde is presently influenced by dredging. About 15 million cubic metres are removed yearly from the channels, of which a large part is dumped again in the river in the flood channels (BELMANS 1988). The deepening of the channels causes a greater volume of water entering the estuary and hence an increase of current velocities. This has also caused an increase in tidal amplitude during the last decades (DOEKES 1986). These processes may strongly influence macrobenthic populations in the Westerschelde in future years.

Acknowledgements

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Chapter six

Zonation of intertidal macrobenthos in estuaries of Schelde and Ems

T. Ysebaert, P. Meire, J. Coosen and K. Essink

Abstract

Based on data, collected in 1980-1990, the intertidal benthic macrofauna of the Schelde and Ems estuaries was compared. The spatial occurrence of the benthic macrofauna along the salinity gradient, including the freshwater tidal area was emphasized. Both estuaries appeared to have a very similar species composition, especially at genus level. The higher number of species observed in the Schelde estuary was probably due to a greater habitat diversity. In both estuaries species diversity decreased with distance upstream. The total density did not vary along the estuarine gradient, whereas biomass is highest in the polyhaline zone.

In both estuaries distinct intertidal benthic communities were observed along the salinity gradient: a marine community in the polyhaline zone, a brackish community in the mesohaline zone, and a third community in the oligohaline and freshwater tidal zones of the estuary. These three communities were very similar between both estuaries. Their main characteristics were discussed together with the occurrence and distribution of the dominant species.

For the Schelde estuary and to a lesser extent also for the Ems estuary, there was evidence that antropogenic stress had a negative effect on the intertidal macrobenthic communities of the oligohaline/freshwater tidal zone. Only Oligochaeta were dominating, whereas the very euryhaline and/or true limnetic species were missing. In the mesohaline zone, the Schelde estuary was dominated by large numbers of short-living, opportunistic species, whereas in the Ems estuary relatively more stable macrobenthic communities were observed. A comparison with some other European estuaries showed in general similar trends as those observed for the Schelde and Ems estuaries.

Introduction

Estuaries are transitional environments between rivers and the sea, and are characterized by largely varying and often unpredictable hydrological, morphological and chemical conditions (DAY et al. 1989; MCLUSKY 1989, 1993; COSTANZA et al. 1993). In most of the world's estuaries, this natural

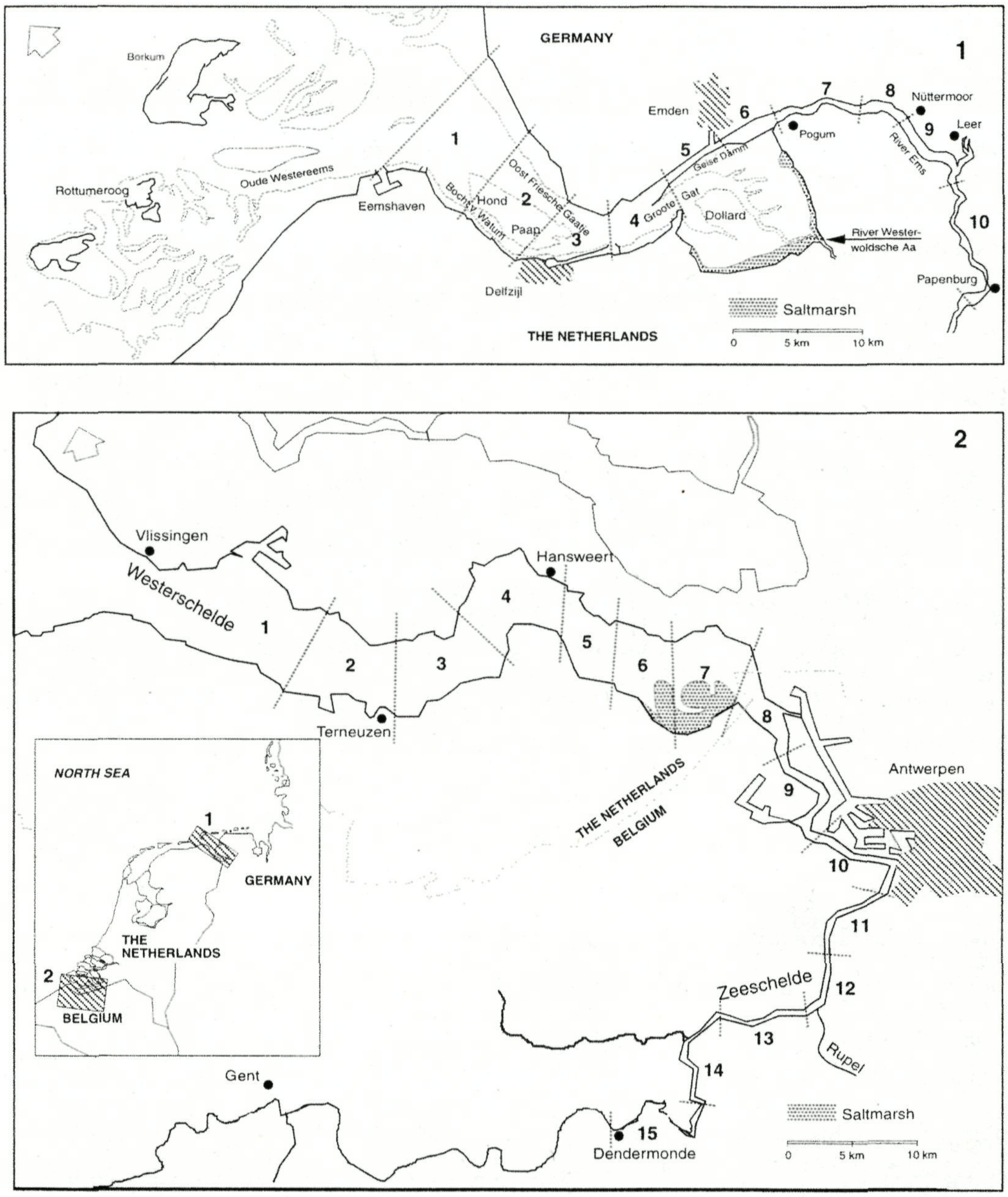

Figure 6.1. The Ems (1) and Schelde (2) estuary subdivided into 10 and 15 sub-areas respectively.

stress is intensified by human activities. Land reclamation, drainage of waste from domestic, industrial and agricultural activities, shipping and dredging are mainly responsible for the direct and indirect loss of the estuarine environment (DAVIDSON et al. 1991; GRAY, 1997). This may have important negative effects on the biota and thus on the ecological structure of the system. Estuarine ecosystems are not only ecosystems with unique biodiversity characteristics, but they are also highly productive systems. They perform several vital functions, e.g. as nursery areas for fish and shrimp, feeding areas for migrating and wintering waterbirds, migration routes for anadromous and catadromous fish, etc. (ODUM 1983; DAY et al. 1989; MCLUSKY 1989).

Until recently, estuarine management strategies did not take into account these important ecosystem functions, but were mainly based on purely economical interests. Nowadays, estuarine management often tries to incorporate the functioning of the ecosystem. This, however, requires knowledge of the functional processes and structure of communities and foodwebs in estuaries.

Within the estuarine foodweb, benthos takes a central role, being one of the most important primary consumers. Macrobenthos, in its turn, is the main food item of many estuarine fish and bird species, and may also be consumed by man. Besides its central role within the estuarine foodweb, benthos is also relatively sensitive to antropogenic influences, on species, population as well as on community level (e.g. PEARSON & ROSENBERG 1978; BAYNE et al. 1988; DAY et al. 1989). Macrobenthic communities of severely impacted estuaries (e.g. Schelde estuary) are therefore expected to be affected in a certain way. The degree of human impact can be estimated by comparing the present situation with historical or geographical (e.g. a relatively pristine estuary) references. In the absence of quantitative historical data to show when the estuary was unaffected by human impact, as for the Schelde estuary, a comparison with another estuary can be considered.

The purpose of this paper is to examine the intertidal benthic macrofauna of two estuaries of more or less the same latitude but with a different degree of anthropogenic stress: the heavily polluted and highly stressed Schelde estuary and the relatively moderately stressed Ems estuary. The spatial occurrence of the macrobenthos along the complete salinity gradient is emphasized. The study is based on a compilation of datasets, collected from 1980 to 1990.

Materials and methods

Study area

The tidal limit was used as the upstream boundary of an estuary. The classification of the estuarine divisions by MCLUSKY (1993) was followed:

- Freshwater tidal part or limnetic zone (salinity < 0.5 p.s.u.);
- Upper part or oligohaline zone (salinity 0.5 - 5 p.s.u.);
- Inner part or mesohaline zone (salinity 5 - 18 p.s.u.);
- Middle/lower part or polyhaline zone (salinity 18 - 30 p.s.u.).

Schelde estuary

The Schelde estuary measures 160 km between the mouth at Vlissingen (The Netherlands) and Gent (Belgium), where it is artificially stemmed (Figure 6.1). The mean tidal amplitude varies from 3.8 m at Vlissingen to a max. of 5.2 m near the tributary Rupel, and diminishes upstream to 2 m near Gent. The river discharge varies from 20 m^3s^{-1} during summer to 400 m^3s^{-1} during winter, with a yearly average of 105 m^3s^{-1}. The total volume of the estuary ($2.5*10^9$ m^3) is large in comparison with the volume of fresh water that enters each day from the river ($9*10^6$ m^3). The mean annual chlorinity decreases from ± 16.6 g Cl^- l^{-1} (salinity 30 p.s.u.) near Vlissingen to ± 4.5 g Cl^- l^{-1} (salinity 8.1 p.s.u.) at the Belgian-Dutch border. From the tributary Rupel onwards the water becomes fresh. The lower and middle estuary, the Westerschelde, between the Dutch-Belgian border and Vlissingen (55 km), is a well mixed region characterized by a complex morphology with flood and ebb channels surrounding several large intertidal mud- and sandflats. The surface of the Westerschelde is 310 km², of which tidal flats and marshes cover 34 %. The average depth is around 10 m. The water column is moderately to well oxygenated, with oxygen saturation increasing from 20-60 % at the Dutch-Belgian border to 90-100 % at the mouth of the estuary. The middle estuary is especially subject to extensive dredging and dumping. The inner and upper estuary, together with the freshwater tidal part, the Zeeschelde, between the Dutch-Belgian border and Gent (105 km), is characterized by a single channel, bordered with relatively small mudflats and marshes (28 % of total surface). On an European scale, however, these freshwater tidal mudflats and marshes are a very rare habitat. The Zeeschelde is heavily polluted by domestic, industrial and agricultural waste loads. The presence of a nearly anoxic water column during most of the year is one of the striking features of this area. The chemical, physical and biological properties of the Schelde estuary have been documented in detail by HEIP (1988, 1989), MEIRE et al. (1992), and in several papers in MEIRE & VINCX (1993) and HEIP & HERMAN (1995).

Ems estuary

The Ems estuary is situated in the northeast of The Netherlands on the border with Germany. The total length between Papenburg and Eemshaven amounts to 80 km (Figure 6.1). Mean tidal amplitude amounts to 2.2 m near Delfzijl and reaches a maximum of 3.2 m near Emden. It diminishes upstream to about 1.8 m where tidal propagation is stopped by a weir. On a yearly basis, the average freshwater input amounts to 115 m^3s^{-1}. The major source of freshwater inflow is the river Ems, with a mean discharge of ± 100 m^3 s^{-1}, ranging from 25 to 390 m^3 s^{-1}. The Westerwoldsche Aa, a small canalized river discharging into the Dollard, has a mean river runoff of 12.5 m^3 s^{-1}. The mean annual chlorinity decreases from ± 16 g Cl^- l^{-1} (salinity 28.5 p.s.u.) near Eemshaven to ± 8 g Cl^- l^{-1} (salinity 14.5 p.s.u.) at the mouth of the Dollard, and near Nüttermoor the water becomes fresh. The lower estuary downstream of the Dollard has a funnel shape. This region extends to Eemshaven where the estuary joins the Wadden Sea. Most flats lie along the shore, but a large tidal flat (the Hondpaap) divides the estuary into two parts creating two channels. The total surface of the lower estuary is 155 km^2 of which 36 % comprises tidal flats. The average water depth is 3.5 m, the channel being 9-10 m deep. The inner part of the estuary consists of a shallow bay, the Dollard (100 km^2). Tidal flats cover 85 % and the mean water depth in the Dollard is shallow (1.2 m). The upper estuary is characterized by a single channel, bordered with very small mudflats. The Ems estuary suffers less from pollution

Table 6.1. Mean salinity (yearly average), number of locations and number of samplings (sampling times) per sub-area in the Schelde and Ems estuary. For the position of the sub-areas: see Figure 6.1.

	Sub-areas														
Schelde estuary	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Polyhaline				Mesohaline				Oligohaline				| Limnetic		
Salinity p.s.u.	28	25	22	20	17	13	12	9	5	2.4	1.6	0.7	0.5	<0.5	<0.5
No. locations	23	31	13	18	27	39	16	21	2	1	2	2	2	4	3
No. samplings	27	31	13	18	47	78	16	21	2	1	2	2	2	4	3

	Sub-areas									
Ems estuary	1	2	3	4	5	6	7	8	9	10
	Polyhaline				Mesohaline			Oligohaline/limnetic		
Salinity p.s.u.	28	25	22	20	17	14	9	5	1.8	<0.5
No. locations	33	51	25	10	23	96	52	10	15	22
No. samplings	104	62	42	21	26	97	52	10	15	22

compared with the Schelde estuary. Nutrient concentrations in the water are dominated by discharges from the river Ems and the small river Westerwoldsche Aa. In the early 1980s conditions improved, especially in the Dollard, due to a reduction of waste discharge by a developing sanitation scheme (ESSELINK et al. 1989). Dissolved oxygen concentrations rarely drop below 70 % of the saturation value, even in the maximum turbidity zone. The chemical, physical and biological properties of the Ems estuary have been documented by ANONYMOUS (1985), BARETTA & RUARDIJ (1988), DE JONGE (1992), DE JONGE & ESSINK (1992).

Sampling methods and laboratory procedures

Most of the faunistic data were derived from earlier reports of our own institutes (Ems estuary: EPPINGA 1991; EPPINGA & ESSINK 1990; KLEEF 1991; VISSER et al. 1987; Schelde estuary: e.g. MEIRE et al. 1991; YSEBAERT & MEIRE 1991; YSEBAERT et al. 1993) or from reports of other Institutes (Ems estuary: RHODE 1982; STEUWER & KÖRITZ 1986; BÖHME 1989; Schelde estuary: HEIP et al. 1986; JANSSEN et al. 1988). Although RHODE (1982) provided data older than 1980, it was also used because it is the only one available on the freshwater tidal part of the Ems estuary.

Most of the studies except for RHODE (1982) sampled macrobenthos quantitatively, using a corer (several diameters) and sieving with a 1.0 mm mesh aperture, except for BÖHME (1989) who used 0.6 mm and RHODE (1982) who used 0.125 mm. However, the laboratory procedures differed substantially among different studies, especially among those of the Ems estuary. Often not all species were quantified (e.g. Spionids, *Heteromastus filiformis*, *Hydrobia ulvae*, *Marenzelleria viridis*), and biomass was not always determined to species level. In most studies Oligochaeta were either not

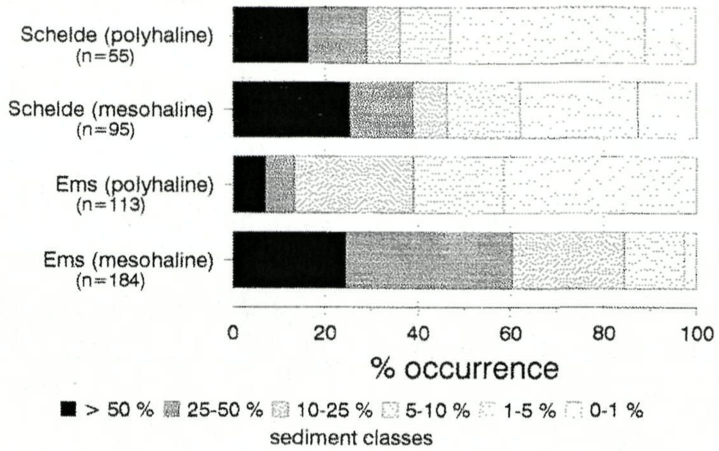

Figure 6.2. Frequency of occurrence (%) of different sediment types in the polyhaline and mesohaline zone of the Schelde and Ems estuaries respectively. Sediments were divided in six classes based on the mud content (< 53 μm) of the sampling locations.

considered or considered as one group. Only a few studies included sediment characteristics (e.g. grain size distribution, median grain size, mud content). So the observed range in mud content (fraction < 53 μm) was not considered in detail. For more details on the sampling methods and laboratory procedures see YSEBAERT & MEIRE (1993).

Data analysis

Based on salinity gradient and morphological characteristics (e.g. occurrence of tidal flats) the Ems and Schelde estuaries were divided into 10 and 15 sub-areas, respectively (Figure 6.1, Table 6.1).

Because sampling methods and laboratory procedures differed, analysis had to be limited to 65 taxa (or less) from the 84 taxa recorded. Epibenthic species like Mysids, *Crangon crangon*, *Carcinus maenas* and *Gammarus* spp., that were not always identified, were excluded from the analyses. Species that could not be identified to species level, or species with difficult identification keys, were considered as genus: *Corophium* spp., *Bathyporeia* spp., *Hydrobia* spp., *Tellina* spp., *Harmothoe* spp., *Urothoe* spp. Oligochaeta were considered as one group. Analysis was performed on presence/absence and % occurrence (65 species; all samples), and on density and biomass (35 and 24 species respectively; no Oligochaeta; polyhaline and mesohaline zone only; only autumn samples to reduce seasonal variability).

The faunal change along the estuarine gradient was analysed by means of the coenocline similarity projection (CSP) (after BOESCH 1977), using the qualitative Sørensen similarity coefficient. The similarity indices between the different sub-areas were then projected along the salinity gradient, the so-called coenocline similarity projections (BOESCH 1977). This simple graphical technique projects a between-site similarity matrix as a series of curves plotted for sites/areas ordered along an environmental gradient. The average slopes of all projected similarity curves were computed for each between-site interval to get a better presentation of the rate of coenocline change. The derived index,

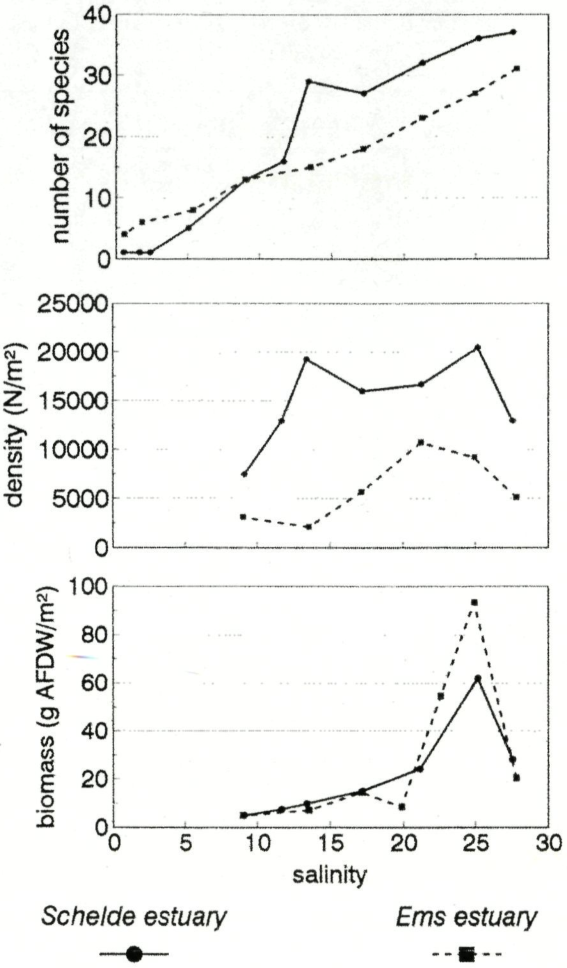

Figure 6.3. Total number of species (Oligochaeta considered as one group) and total density (Nm^{-2}) and total biomass (g $AFDWm^{-2}$, Oligochaeta and *M. viridis* not included) observed along the salinity gradient of the Schelde and Ems estuaries.

called index of faunal change, indicates in which zone large or small faunal changes occurred. The following multivariate analyses were applied: classification by TWINSPAN cluster analysis (HILL 1979) and by an agglomerative clustering method (group average sorting (GAS) of Bray-Curtis dissimilarities) and ordination by non-metric multi-dimensional scaling (MDS), using the Bray-Curtis similarity measure. MDS stress values < 0.05 means excellent presentation (CLARKE 1993). Plotting of the TWINSPAN/GAS clusters on 2-D ordination planes aided in evaluating the divisions imposed. GAS and MDS were performed using the statistical package PRIMER (CARR et al. 1993; CLARKE 1993). Density and biomass data were subjected to $\sqrt{}\sqrt{}$ transformation prior to analysis. Mean values are presented with standard errors.

Table 6.2. Species observed in the Schelde and Ems estuaries (presence indicated by x; rare species (= < 10 times observed) indicated with number of observations). Feeding types: DF, Deposit Feeder; FF, Filter/suspension feeder; O, Omnivor; P, Predator.

Species	Feeding type	Schelde	Ems	Species	Feeding type	Schelde	Ems
Annelida, Polychaeta				**Mollusca, Bivalva**			
Alkmaria romijni	DF	1		Abra alba	FF	1	
Anaitides mucosa	P	x	X	Cerastoderma edule	FF	x	x
Arenicola marina	DF	x	X	Ensis directus	FF		1
Atylus swammerdami	P	1		Ensis sp.	FF	6	
Autolytus prolifer	P	1		Macoma balthica	DF	x	x
Boccardia redeki	FF	1		Mya arenaria	FF	x	x
Capitella capitata	DF	x	X	Mysella bidentata	FF	x	2
Eteone longa	P	x	X	Mytilus edulis	FF	x	x
Eumida sanguinea	P	2		Scrobicularia plana	DF	x	x
Harmothoe spec.	DF		X	Spisula sp.	FF	x	
Harmothoe sarsi	DF	2		Tellina fabula	DF	2	
Heteromastus filiformis	DF	x	X	Tellina sp.	DF	1	
Lanice conchilega	DF	6		Tellina tenuis	DF	1	
Lepidonotus squamatus	P		1	**Mollusca, Gastropoda**			
Magelona papillicornis	DF	4	X	Assiminea grayana	DF	4	
Manayunkia aestuarina	FF	x		Gastropod fresh water	DF		x
Marenzelleria viridis	P		X	Hydrobia ulvae	DF	x	x
Nephtys caeca	P	1		Hydrobia ventrosa	DF		3
Nephtys hombergii	P	x	X	Littorina littorea	DF	2	3
Nereis diversicolor	O	x	x	Potamopyrgus jenkinsi	DF		4
Nereis succinea	DF	x	x	Retusa obtusa	P	x	x
Nereis spec.	DF	x	x	**Crustacea, Amphipoda**			
Ophelia limacina	DF	2		Bathyporeia pelagica	DF	x	
Ophelia rathkei	DF	3		Bathyporeia pilosa/sarsi	DF	x	x
Polydora spec.	DF	x	1	Bathyporeia sp.	DF	x	x
Pygospio elegans	DF	x	x	Corophium arenarium	DF	x	x
Scoloplos armiger	DF	x	x	Corophium volutator	DF	x	x
Scolelepis foliosa	P/DF		9	Corophium sp.	DF	x	x
Scolelepis squamata	DF	x		Gammarus locusta	O		3
Spiophanes bombyx	DF	x		Gammarus salinus	O	x	
Spio spec.	DF	2	5	Gammarus sp.	O	x	5
Streblospio shrubsolii	DF		8	Gammarus fresh water	O		2
Tharyx marioni	DF	x	x	Haustorius arenarius	FF	x	
Annelida, Oligochaeta				Urothoe poseidonis	DF	3	
Oligochaeta	DF	x	x	Urothoe sp.	DF		1
Limnodrilus hoffmeisteri	DF	x	x	**Crustacea, Isopoda**			
Monopylephorus irroratus	DF		x	Eurydice pulchra	P	x	
Paranais litoralis	DF		x	Idotea chelipes	-		1
Paranais spec.	DF		2	Cyathura carinata	-	x	
Tubificoides benedeni	DF	x	x	Sphaeroma rugicauda	-	1	1
Tubifex costatus	DF	x	x	**Crustacea, Decapoda**			
Tubifex tubifex	DF		1	Carcinus maenas	O	x	x
Hirudinea				Crangon crangon	P	x	x
Theromyzon tessulatum	P		1	**Crustacea, Mysidacea**			
Nemertinae				Mysidacea	O	x	x
Nemertini	P	x	x	**Insecta**			
				Ceratopogonidae larvae	-		x

Results

Sediment characteristics

A wide variety of sediment types was observed in both the poly- and mesohaline zones of the

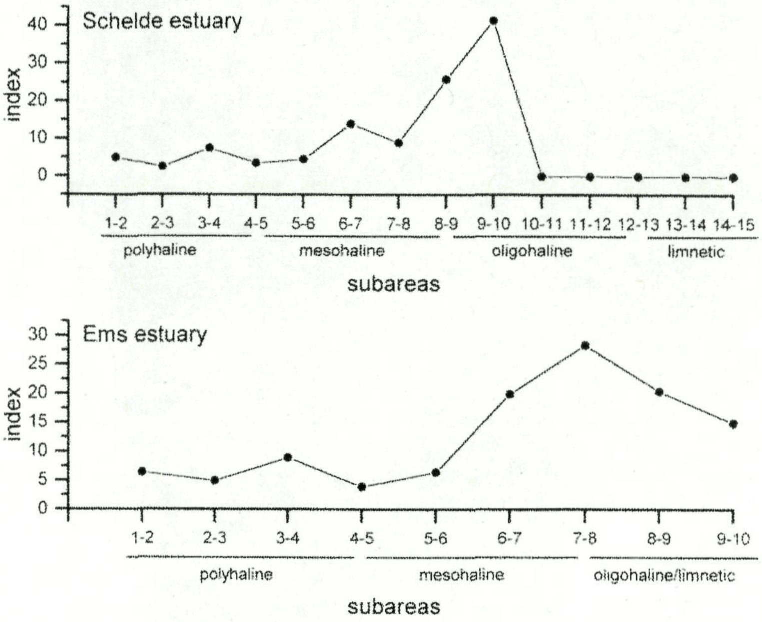

Figure 6.4. Index of faunal change based on coenocline similarity projections (qualitative data). For explanation: see text.

Schelde and Ems estuaries (Figure 6.2). In the Schelde estuary ± 10 % of the locations had a mud content < 1%. These very coarse sediments were not observed in the Ems estuary. In general, the polyhaline zones of both estuaries were characterized by relatively coarser sediments than the mesohaline zones. The mesohaline zone of the Ems estuary was dominated by very fine sediments, in the Schelde estuary a wide range of sediment types was observed within this zone. For the freshwater tidal part the few data generally revealed very fine sediments with a mud content >25 %.

General trends in diversity, density, and biomass

In general, the total number of species was higher in the Schelde than in the Ems estuary (Table 6.2). In the Schelde estuary lot of species were, however, observed only a few times. In both estuaries the common species and genera occurred. A gradual decrease in the total number of species in each sub-area was observed from the mouth towards the freshwater tidal part (Figure 6.3); more species disappeared than were replaced by new species upstream. This is most pronounced in the Schelde estuary, where in the oligohaline and freshwater tidal parts no new species were observed. Only Oligochaeta were found (YSEBAERT et al. 1993) and no freshwater organims. On the other hand, in the Ems estuary freshwater species like freshwater gastropods and gammarids and insect larvae were observed (RHODE 1982). The mean number of species of the sampling locations per zone also decreased upstream with high numbers in the polyhaline zone and lower numbers towards the mesohaline and oligohaline zone. In the Schelde estuary, 12.8 ± 0.5 and 7.2 ± 0.3 species were observed in the polyhaline and mesohaline zone, respectively. In the Ems estuary the same trend was observed with 10.4 ± 0.2 species in the polyhaline zone and 5.5 ± 0.2 species in the mesohaline zone. In the oligohaline and freshwater tidal zone of the Ems estuary, the mean number of species decreased

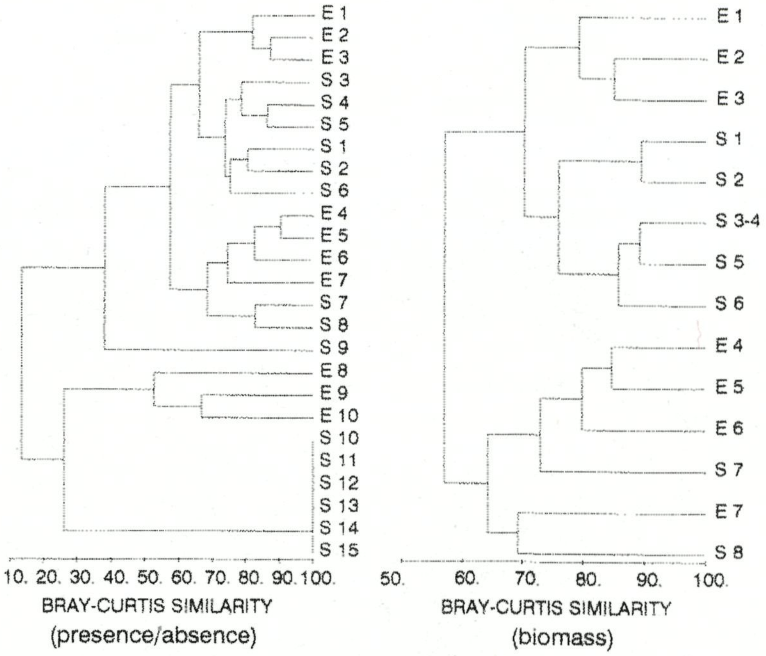

Figure 6.5. Hierarchical agglomerative clustering of macrobenthic communities based on presence/absence data of 65 species (all sub-areas) and on fourth root transformed biomass data of 24 species (poly-and mesohaline zone only) respectively, using group-average linking on Bray-Curtis similarities (Schelde: 15 sub-areas S1-S15 and Ems: 10 sub-areas E1-E10).

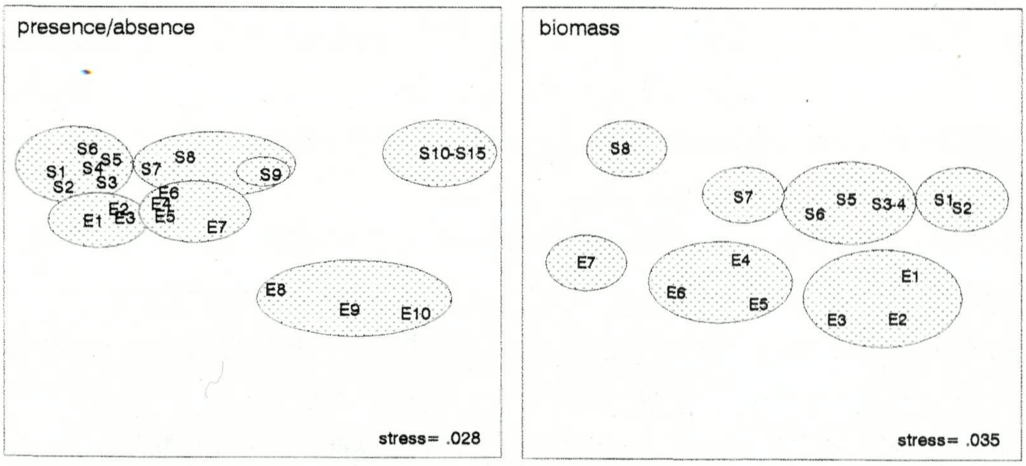

Figure 6.6. MDS ordination based on presence/absence data of 65 species (all sub-areas) and on fourth root transformed biomass data of 24 species (poly-and mesohaline zone only) respectively. Communities as identified by GAS and TWINSPAN are circled.

further to 3.6 or less. In both estuaries, total density (without Oligochaeta) did not show a clear trend along the salinity gradient except for a slight decrease towards the mesohaline zone and towards the mouth (Figure 6.3). Density was significantly higher in the Schelde estuary than in the Ems estuary. Oligochaeta were more abundant in the mesohaline zone than in the polyhaline zone. Biomass was highest in the polyhaline zone, and decreased towards the mesohaline and freshwater tidal part (Figure 6.3). In the polyhaline zone, the outermost area (mouth) had a lower biomass than the inner areas. The scarce information on the oligohaline and freshwater tidal parts indicated a relatively low biomass

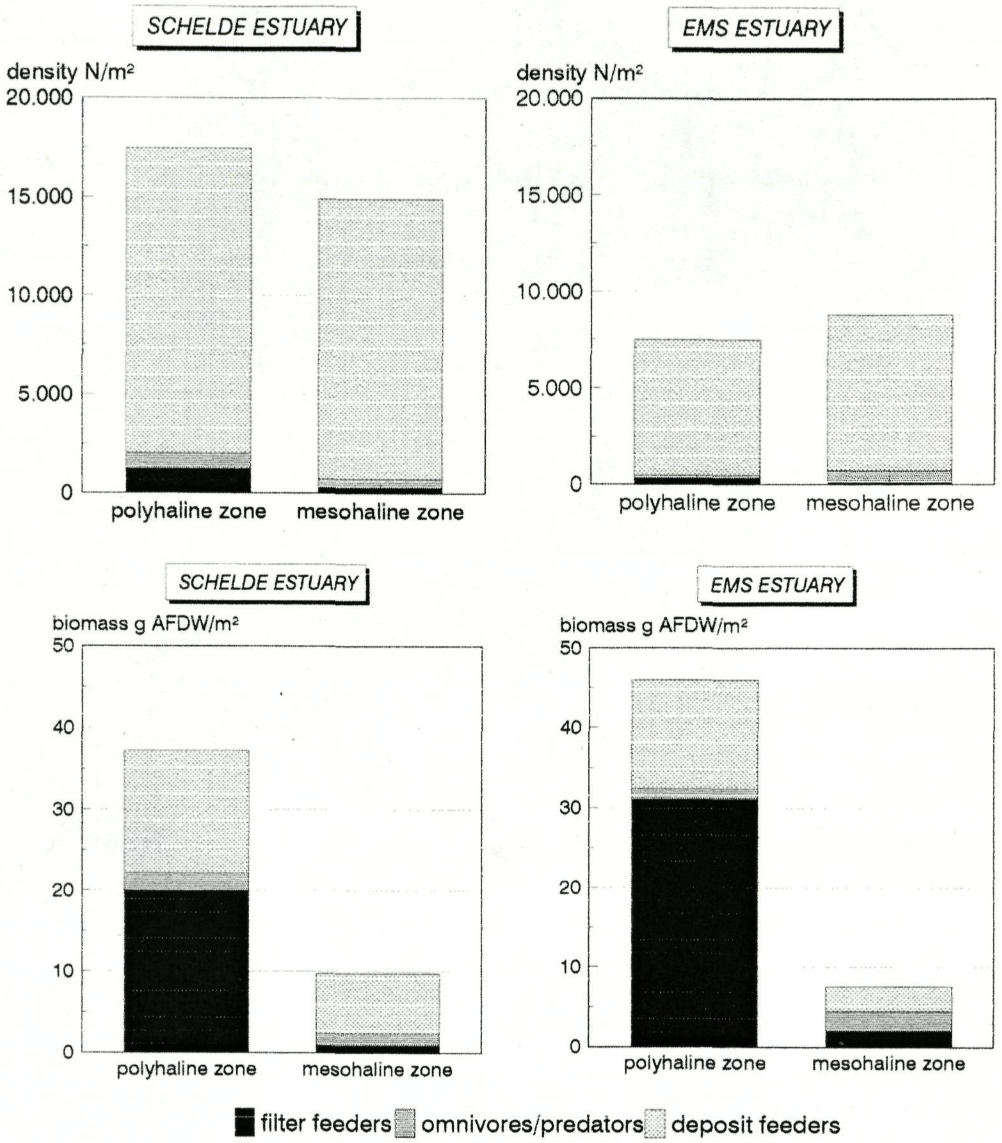

Figure 6.7. Feeding strategies -based on density and biomass respectively- of the intertidal macrobenthos in the polyhaline and mesohaline zone of the Schelde and Ems estuary.

in these regions. RHODE (1982) gave biomass values of 0.6-3.1 g AFDWm^{-2} for this section of the Ems. Similar data were found in the Schelde estuary, except for one location in the freshwater tidal zone where a biomass of 45 g AFDWm^{-2} was observed.

In the polyhaline zone, many species were present with no one species really dominating. In the mesohaline zone, fewer species occurred, but in relatively higher numbers, indicating only a few really dominant species occurred here. This was even more pronounced in the oligohaline and freshwater tidal part of both estuaries where Oligochaeta dominated.

Estuarine zonation and characterisation of benthic communities

The index of faunal change, based on the coenocline similarity projections, did not change

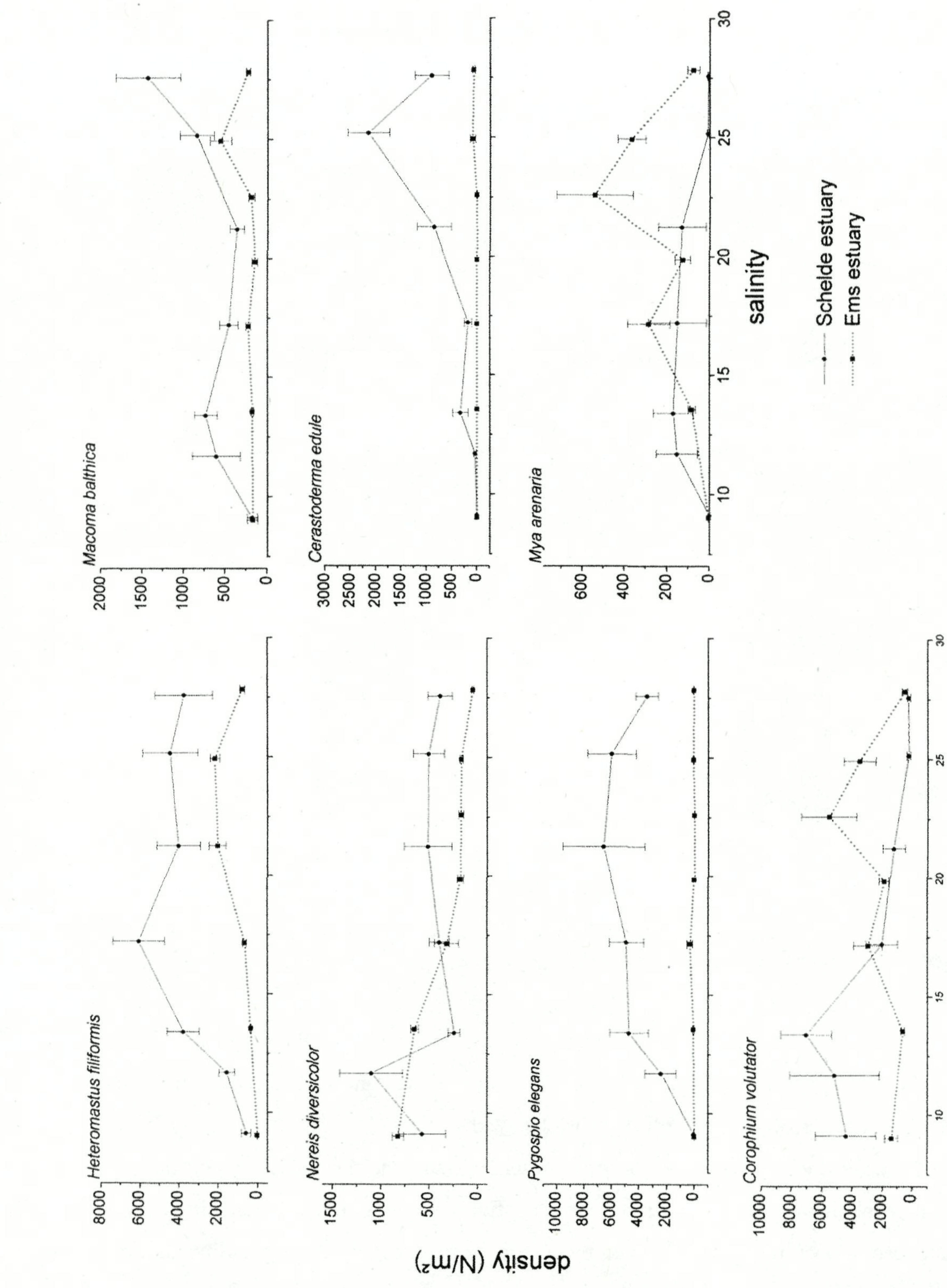

Figure 6.8. Density (Nm^{-2} ± SE) of some important macrobenthic species along the salinity gradient of the Schelde and Ems estuary (full line: Schelde estuary; dotted line: Ems estuary).

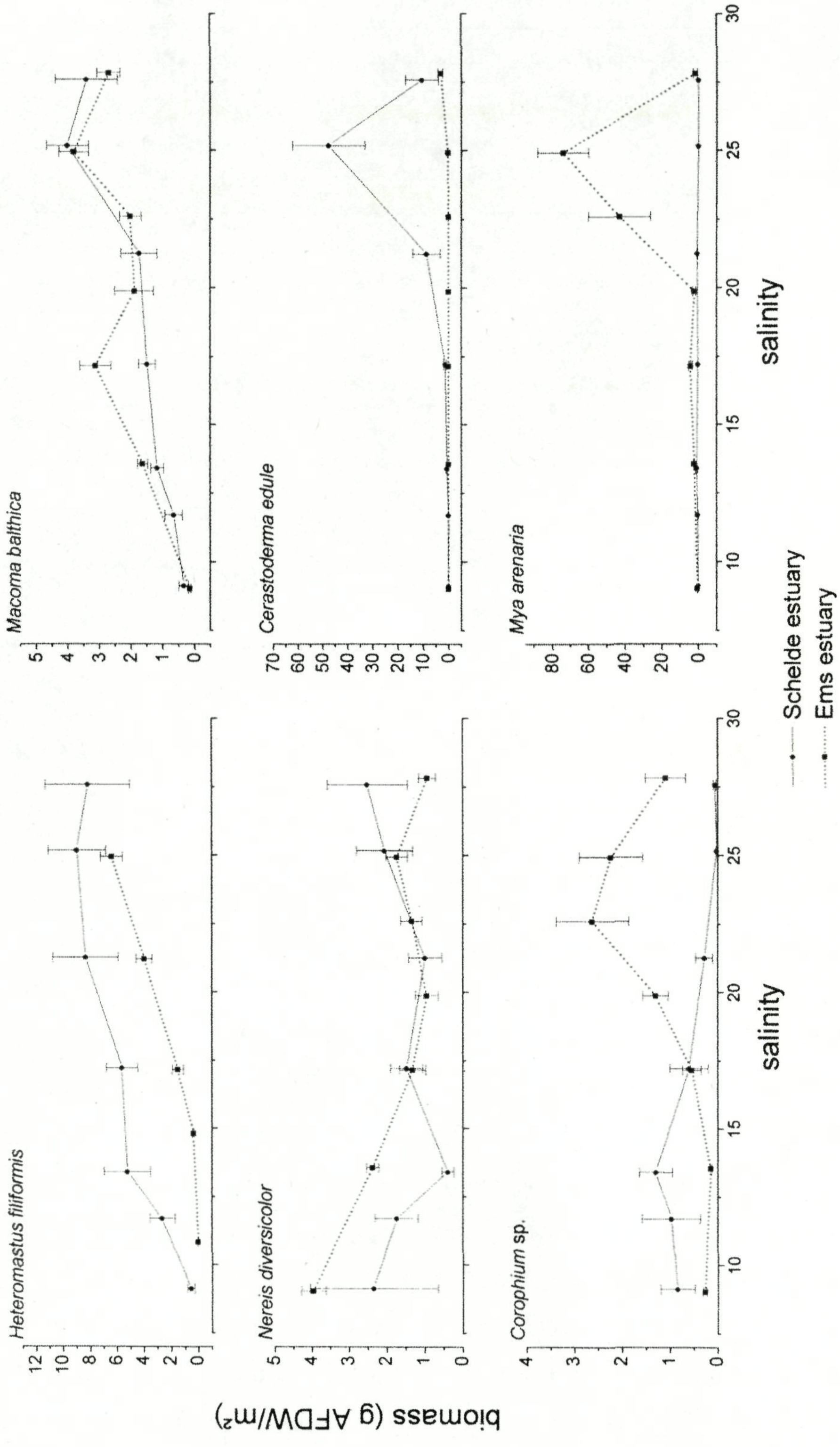

Figure 6.9. Biomass (g AFDWm^{-2} ± SE) of some important macrobenthic species along the salinity gradient of the Schelde and Ems estuary (full line: Schelde estuary; dotted line: Ems estuary).

Table 6.3. Mean occurrence (O, %), density (D, Nm^{-2} ± SE, (maximum density)), and biomass (B, g $AFDWm^{-2}$ ± SE, (maximum biomass)) of the most dominant species in the polyhaline and mesohaline zone of Schelde and Ems estuaries (D and B, autumn samples only). ? = insufficient data.

Species		Schelde polyhaline Subarea 1-4 O: n=89 D: n=58 B: n=50	Schelde mesohaline Subarea 5-8 O: n=162 D: n=123 B: n=89	Ems polyhaline Subarea 1-4 O: n=229 D: n=199 B: n=141	Ems mesohaline Subarea 5-7 O: n=175 D: n=172 B: n=158
Macoma balthica	O	87	81	98	94
	D	855 ± 151 (5217)	578 ± 82 (5869)	332 ± 49 (7048)	177 ± 20 (3332)
	B	2.9 ± 0.4 (15.9)	1.0 ± 0.1 (4.22)	2.5 ± 0.2 (13.9)	± 0.1 (8.8)
Nereis diversicolor	O	69	60	86	97
	D	466 ± 107 (3928)	447 ± 89 (6983)	117 ± 10 (838)	607 ± 33 (2719)
	B	1.7 ± 0.4 (13.7)	1.5 ± 0.6 (49.6)	1.0 ± 0.1 (8.2)	2.5 ± 0.2 (10.7)
Heteromastus filiformis	O	83	81	78	62
	D	4072 ± 758 (21668)	3816 ± 588 (32570)	1700 ± 165 (9000)	355 ± 62 (10057)
	B	8.0 ± 1.4 (43.3)	3.6 ± 0.7 (26.5)	5.2 ± 0.6 (15.9)	0.5 ± 0.1 (6.1)
Corophium sp.	O	58	70	76	97
	D	590 ± 272 (13026)	5561 ± 1082 (51350)	2734 ± 583 (45126)	1278 ± 189 (18066)
	B	0.13 ± 0.07 (2.9)	1.0 ± 0.2 (9.1)	2.0 ± 0.4 (16.7)	0.4 ± 0.1 (3.1)
Cerastoderma edule	O	65	19	51	0
	D	1311 ± 221 (7448)	211 ± 75 (5240)	65 ± 22 (3507)	0
	B	19.7 ± 5.2 (199.9)	0.6 ± 0.2 (9.1)	1.5 ± 0.4 (30.3)	0
Mya arenaria	O	14	22	77	59
	D	50 ± 39 (2247)	142 ± 61 (4352)	286 ± 51 (5345)	89 ± 16 (2098)
	B	0.2 ± 0.1 (5.0)	0.3 ± 0.2 (12.7)	29.6 ± 5.9 (457.0)	1.9 ± 0.2 (15.2)
Pygospio elegans	O	89	78	18	6
	D	5374 ± 1220 (56630)	3953 ± 774 (52564)	?	69 ± 36 (4879)
	B	0.4 ± 0.1 (5.0)	0.3 ± 0.2 (2.6)	?	?

significantly within the polyhaline zone of both estuaries (Figure 6.4), but became more pronounced in the mesohaline zone; the largest faunal change was observed in the transition between the mesohaline and oligohaline zone. In the Schelde estuary, from sub-area 10 on the index became zero, implying no further changes in faunal composition (only Oligochaeta). On the other hand, in the upstream areas of the Ems estuary the index remained relatively high implying a further faunal change in the freshwater tidal part of this estuary, as indicated by the appearance of some freshwater species.

Multivariate analyses with presence/absence, % occurrence and density and biomass data all gave similar results. The general pattern was illustrated with the group average sorting of Bray-Curtis similarities and the MDS (Figures 6.5 and 6.6) on presence/absence data and biomass data respectively. The analyses on presence/absence data, which included the freshwater tidal and oligohaline zones, resulted in three geographically separated communities in each estuary. The first division separated the oligohaline and freshwater zones of both estuaries from the higher salinity zones. In a further division the high salinity zones were divided into a polyhaline and a mesohaline zone. In the Schelde, some of the mesohaline sub-areas (5-6) grouped together with the polyhaline sub-areas. Within each zone, the Schelde sub-areas were clearly separated from the Ems sub-areas. The biomass, excluding the freshwater and oligohaline zones, was similar. Within the high salinity zones, the mouth of both estuaries was separated from the more upstream situated sub-areas. In the mesohaline zone, the upper sub-areas were clearly separated.

In each estuary three communities could be distinguished: a marine community in the polyhaline zone, a brackish community in the mesohaline zone and a third community in the oligohaline and freshwater tidal zones. The community in the polyhaline zone of both estuaries was characterized by a relatively high diversity due to the occurrence of several species that were restricted to this zone (e.g. *Magelona papillicornis*, *Scoloplos armiger*, *Mysella bidentata*, *Anaitides mucosa*) or species that rarely penetrated the estuary up to the middle reaches (e.g. *Nephthys hombergii*, *A. marina*). The most common species (both in terms of occurrence and density) within the polyhaline community were however typically euryhaline species like *H. filiformis*, *N. diversicolor*, *M. balthica*, *Hydrobia ulvae*, *Eteone longa*, *Corophium* sp. (Ems estuary only), *P. elegans* (Schelde estuary only). In the Schelde estuary *Cerastoderma edule, Tharyx marioni and C. capitata* were also common. The polyhaline communities were dominated numerically by deposit feeders (Figure 6.7). In terms of biomass a filter feeder dominated: *C. edule* in the Schelde estuary and *M. arenaria* in the Ems estuary, respectively (Figure 6.7).

The mesohaline community of both estuaries was characterized by a low diversity. The most common species were *C. volutator*, *H. filiformis*, *N. diversicolor*, and *Macoma balthica.* Towards the oligohaline zone, only *C. volutator* and *N. diversicolor* appeared, together with Oligochaeta. In terms of feeding strategies, the mesohaline community was numerically dominated by deposit feeders in both estuaries (Figure 6.7). The biomass of the mesohaline community of the Schelde estuary was dominated mainly by deposit feeders (*M. balthica*, *P. elegans*, *H. filiformis*, *Corophium* sp.), while in the Ems estuary a more diverse community with equal numbers of deposit feeders, omnivores (*N. diversicolor*) and filter feeders (*M. arenaria*) was found (Figure 6.7).

The freshwater tidal and oligohaline zones of both estuaries were characterized by an impoverished benthic community, dominated by Oligochaeta. In the Ems estuary some typical freshwater organisms (e.g. insect larvae (Ceratopogonidae), freshwater gastropods), and some euryhaline species, penetrating the estuary up to the oligohaline (e.g. *Corophium volutator*) or up to the freshwater tidal zone (e.g. *Nereis diversicolor*) were also observed. Deposit feeders dominated the oligohaline and freshwater tidal zones of both estuaries.

The dominant species

Annelids dominated the intertidal macrobenthos of the Ems and Schelde estuaries and by molluscs (bivalves) and crustaceans (amphipods) to a lesser extent. Information on the occurrence, density and biomass is summarized in Table 6.3 and Figures 6.8 and 6.9.

Annelids

H. filiformis was the most common polychaete in the Schelde estuary, but the second most common in the Ems estuary. In both estuaries *H. filiformis* became less common below a salinity of ± 12 p.s.u. In the Schelde estuary, high densities occurred both in the polyhaline and mesohaline zone, whereas in the Ems estuary much lower densities were observed in the mesohaline zone. Total densities were much higher in the Schelde estuary as compared to the Ems estuary. In the Schelde and to a lesser extent also in the Ems estuary, this species represented an important part of the total biomass. It was the most important deposit feeding polychaete. *N. diversicolor* was another very common species, and the most common omnivore, up to the very low salinity zones in both estuaries. It penetrated more upstream in the Ems estuary (up to the limnetic region) than observed in the Schelde estuary, where the species was absent in the oligohaline zone. *N. diversicolor* had a relatively large contribution to the total biomass, especially in the mesohaline zone of both estuaries. The spionid *P. elegans* was a very common polychaete in the Schelde estuary, reaching very high densities in both the poly- and mesohaline zone, but only occurred occasionally in the Ems estuary in very low densities. This difference could partly be attributed to methodological differences (see above), but later studies also observed low densities of *P. elegans* in three stations in the Dollard region (DEKKER 1992, 1993). The contribution of *P. elegans* to the total biomass was minimal. *E. longa* was a common species in both estuaries, especially in the polyhaline zone, but its contribution to the total density and biomass was low. *Marenzelleria viridis*, a North American brackish water spionid, was observed in the Ems estuary first in 1983, but had not been observed in the Schelde estuary. Since then, this species has become more and more dominant, especially in the Dollard region of the Ems estuary (ESSINK & KLEEF 1988; 1993). Due to the lack of quantitative data the contribution of *M. viridis* to the total density and biomass was not considered in this study. To date, this species however makes up to 50-75 % of the total biomass of the intertidal mudflats of the Dollard (DE JONGE & ESSINK 1992; ESSINK & KLEEF 1993; ESSINK et al. 1998).

Molluscs

M. balthica was the most common mollusc species in both estuaries, occurring in decreasing density and biomass from the marine reaches up to the oligohaline zone. Total density was higher in the Schelde estuary than in the Ems estuary, but biomass was similar, implying smaller individuals (spat) in the Schelde estuary. Indeed, in the Dollard region populations consisted of different year classes, whereas in the Schelde estuary only spat was found in areas with similar salinities. Probably additional stress factors such as pollution or increased hydrodynamics caused decreased survival of these animals in the Schelde estuary. *M. balthica* had a large contribution to the total biomass. *C. edule* was a very common species in the polyhaline part of the Schelde estuary, contributing > 50 % to the total biomass. In the mesohaline part of this estuary, *C. edule* was much less common and most of the individuals found were young spat. On the other hand, in the Ems estuary *C. edule* was observed only occasionally in low densities and biomasses. In the mesohaline part the species was absent. *M. arenaria* showed a reverse pattern, being common in the Ems estuary and rather rare in the Schelde estuary. In the polyhaline zone of the Ems estuary *M. arenaria* contributed for ± 65 % to the total biomass, in the mesohaline zone for 26 %. Other bivalves were much less common and included *Scrobicularia plana* and *Mytilus edulis*. No intertidal mussel beds were observed in either estuaries, except for a few small areas on the German side of the Ems estuary (BÖHME 1989). The only common gastropod of both estuaries was *H. ulvae*, being most common in the polyhaline zone. Mean densities were comparable with locally very high peak densities.

Crustaceans

By far the most important crustaceans in both estuaries were amphipods of which *Corophium* is the most common. *Corophium* sp. was observed along the whole estuarine gradient. In the Schelde estuary density was much higher in the mesohaline zone, whereas in the Ems estuary the reverse was observed. In the mesohaline part of the Schelde estuary *Corophium* sp. was one of the most dominating species. The amphipods *Bathyporeia* sp. and *H. arenarius*, and the isopod *E. pulchra* were regularly observed in the Schelde estuary, especially in the mesohaline zone. In the Ems estuary, *Bathyporeia* sp. was much less common, and *H. arenarius* and *E. pulchra* were totally absent. In the Schelde estuary, these species were typically found in relatively coarse sediments, situated in highly dynamic areas (e.g. megaripples) (see also YSEBAERT et al. 1993).

Discussion

Species composition and distribution

The Schelde and Ems estuaries show a very similar species composition, especially at the genus level. Most of the common species are the same in both estuaries. More species are however observed in the Schelde estuary. The observed difference in number of species is most likely related with the different available habitat (sediment) types in both estuaries. Very coarse sediments rarely occur along the Ems estuary, whereas in the Schelde estuary both the polyhaline and mesohaline zones contain areas with coarse sediment. Beside the low dynamic habitats (e.g. mudflats) typical for both estuaries, the intertidal zone of the Schelde estuary is therefore also characterized by the occurrence of high dynamic habitats (e.g. 2D- and 3D- megaripples). The associated typical mobile benthic infauna (e.g. amphipods (*Bathyporeia* spp., *H. arenarius*) and isopods (*E. pulchra*)) is regularly observed in the intertidal zone of the Schelde estuary (see also YSEBAERT et al. 1993). In the intertidal zone of the Ems estuary mainly uniform low dynamic areas are observed, especially in the mesohaline zone (Dollard region). The common species *M. balthica*, *C. volutator* and *N. diversicolor* are observed in >

90% of all locations considered, indicating a relatively uniform occurrence along the whole estuary (polyhaline and mesohaline zone).

Since more sampling locations are considered in the Ems estuary than in the Schelde estuary, the observed difference in number of species cannot be due to sampling intensity. To some extent this difference can however be explained by methodological differences in both field and laboratory techniques used (see Material & Methods). E.g., species like *Manayunkia aestuarina*, *Spiophanes bombyx*, *Polydora* sp. are observed regularly in the Schelde estuary, and not in the Ems estuary. Studies like STEUWER & KÖRITZ (1986) and BÖHME (1989) which determine Spionids up to species level, however, also do not mention the presence of *Polydora* sp..

A compilation of the large amount of historical data of the intertidal macrofauna of the Ems estuary from 1950 to 1980 is discussed in MICHAELIS (1983). In general, the species commonly observed in our study are similar to those also observed earlier. *M. aestuarina* and *Polydora* sp., mentioned by MICHAELIS (1983) as less common, are not observed in this study. The absence of *H. arenarius* and *E. pulchra* (MICHAELIS 1983) is consistent with our findings.

For the Schelde estuary, less historical data are available. Data of the Westerschelde from 1965 to 1973 (WOLFF 1973) indicate a similar distribution and similar dominant species. *N. diversicolor* no longer appears up to the freshwater tidal zone, as compared to earlier in the Schelde estuary and to the present situation in the Ems estuary.

The macrobenthic fauna observed in the Schelde and Ems estuaries is very similar with observations from other European estuaries. DAVIDSON et al. (1991) classifies British aquatic estuarine communities into seventeen hard shore communities and 16 soft shore communities. Within the soft shore communities five communities are found on more than 20 % of 102 estuaries. The most common of these are a muddy sand community in areas of variable or normal salinity, and a mud community in more sheltered areas of variable and reduced salinity. These two communities also dominate in the Schelde and Ems estuaries, with the same dominating species, being in the muddy sand community the polychaetes *A. marina*, *P. elegans*, *N. hombergii*, *S. armiger* and *S. bombyx* and the molluscs *M.*, *C. edule* and *H. ulvae*, and in the variable/reduced salinity mud community the polychaetes *N. diversicolor* and *Ampharete grubei* and the bivalves *S. plana* and *M. arenaria,* in addition to those of the normal/variable salinity muddy sand community. The exposed sand community (DAVIDSON et al. 1991) is also found in the Schelde estuary, being dominated by crustaceans, mainly small amphipod species such as *H. arenarius*, and polychaete worm species such as *N. cirrosa*. Two soft shore communities, mussel beds and beds of marine grasses (DAVIDSON et al. 1991), are not found in the Schelde and Ems estuaries.

Several studies describe the distribution and abundance of macrofauna along an estuarine salinity gradient. In the Forth estuary (Scotland) MCLUSKY (1987) observes in the upper estuary a Oligochaeta population to dominate. In the inner/middle estuary the number of species increases with typical representatives being *N. diversicolor*, *M. balthica*, *C. volutator* and *H. ulvae*. The absence of the last three species further upstream is attributed to the high organic enrichment and severe oxygen depletion in that upper part of the Forth estuary (MCLUSKY 1987). At some places of the middle Forth estuary, also *C. edule* and *M. arenaria* appear. In the lower Forth estuary diversity increases further and typical representatives are the molluscs *M. balthica*, *C. edule*, *M. arenaria* and *H. ulvae* and the annelids *Nephtys hombergii* and *Arenicola marina*. In the Shannon estuary, Ireland's largest estuary and one of the very few major European estuaries with little antropogenic influence, the few available data indicate that the main macrofaunal species found in the inner/middle estuary appear to be *M. balthica*, *N. diversicolor*, *N. hombergii* and *C. volutator* (WILSON et al. 1993), and also *H. ulvae* and *S. plana*. (MERNE 1985). The most upstream sites appear to contain only *N. diversicolor*. The low diversity in the Shannon estuary is probably explained by the very high mud and silt content of the sediments. A more detailed investigation of one intertidal mudflat in the poly/mesohaline zone of the Shannon estuary shows 26 species of which oligochaetes, the polychaetes *T. marioni*, *P. elegans*, *N. diversicolor* and *C. capitata*, the bivalves *M. balthica* and *S. plana*, and the amphipod *C. volutator* are the most abundant (O'SULLIVAN 1980). In the Loire estuary (France) diversity is decreasing upstream (ROBINEAU 1987). The polyhaline zone is characterized by *C. edule*, *M. arenaria*, and *N. caeca*, the mesohaline zone by oligochaetes, *C. volutator*, *M. balthica*, *H. ulvae* and *N. diversicolor*. In the Weser estuary (Germany), the middle and upper reaches are characterized by oligochaetes, *C. volutator*, *N. diversicolor*, *H. filiformis*, *M. balthica*, *S. shrubsolii* (KOLBE 1992). From 1986, *M. viridis* invades the Weser estuary and becomes one of the dominating species here. This successful invasion is very similar to that observed in the Ems estuary (ESSINK & KLEEF 1988).

Community structure

Both estuaries are characterized by the occurrence of three benthic communities along the salinity gradient: a marine community in the polyhaline zone, a brackish community in the mesohaline zone, and a third community in the oligohaline and freshwater tidal zones. These three communities are very similar in both estuaries, but differ within each estuary.

Most of the dominating species of the marine community are typically euryhaline species, that also dominate in the brackish community. The marine community in the Schelde estuary tends to penetrate further into the estuary as compared to the Ems. In the Schelde, several 'marine' species are indeed observed in the mesohaline zone as well. Often these species only occur there temporarily, not being able to reproduce (e.g. successfull spatfall of *C. edule* not surviving the winter because of lower salinities; pers. observ.). This confirms earlier findings that macrobenthic communities are not static, but that the boundaries of the estuarine zones are continuously fluctuating in space and time, especially in the mesohaline and oligohaline zones (REMANE 1958; DEN HARTOG 1964, 1971; WOLFF 1973; MCLUSKY 1989; RIEDEL-LORJE et al. 1995).

Our findings that in both estuaries the macrobenthic trophic structure is dominated to a large extent by suspension feeders in the polyhaline zone and by deposit feeders in the mesohaline zone is supported by the general findings of HUMMEL et al. (1988) and HAMERLYNCK et al. (1993). These authors describe two separate food chains in the Westerschelde: a photo-autotrophic coastal food chain in the polyhaline zone and a heterotrophic chain in the mesohaline zone. Thus, in the Schelde and Ems estuaries, the high biomass values of suspension feeders (*C. edule* and *M. arenaria*) can be explained by a high primary production in the polyhaline zone (e.g. KROMKAMP et al. 1995). In the mesohaline zone deposit feeders are favoured by the riverine input of large amounts of suspended matter (detritus). In the Schelde estuary this is reflected in the presence of mainly opportunistic, short-living, smaller species, occurring in very high densities (e.g. *P. elegans*, *C. volutator*, *H. filiformis*). Besides food availability, also the dynamic environment probably favours these opportunistic species and inhibits the presence of stable populations of longer living animals. The macrobenthic trophic structure in the meso- and oligohaline zones of the Ems estuary (Dollard region) appears, however, more diverse than in the Schelde estuary, also containing a substantial portion of suspension feeders (*M. arenaria*). Besides the less dynamic environment, large amounts of microphytobenthos, which are resuspended in the watercolumn by wind or tidal driven fluxes, may here provide a source of primary production to be consumed by suspension feeders (DE JONGE 1992). The contribution of resuspended microphytobenthos to the total primary production in the Schelde estuary is as yet unknown, but it may be significant (DE JONG & DE JONGE 1995). In addition, high concentrations of suspended matter, may hamper the occurrence of suspension feeders in the mesohaline zone of the Schelde estuary.

Data on European freshwater tidal habitats are very scarce, not only for the benthic compartment, but for the whole ecosystem (ODUM 1988). Based on CASPERS (1948) and WOLFF (1973) for the Elbe estuary (Germany) and the former Biesbosch (The Netherlands), respectively, the benthic community of the freshwater tidal area is expected to contain more than 30 species, eight of which belong to Oligochaeta, ten to Chironomidae, eight to molluscs and four to crustaceans. The benthic community of the oligohaline and freshwater tidal zones of both Schelde and Ems estuaries can therefore be characterized as impoverished communities dominated by Oligochaeta, which are more pronounced in the Schelde estuary. Elevated concentrations of pollutants observed in the Schelde estuary (VAN ECK et al. 1991, VAN ZOEST & VAN ECK 1993; ZWOLSMAN & VAN ECK 1993), and the fact that large parts of the system are often completely anoxic, especially during summer time (VAN DAMME et al. 1995), may account for this. The almost exclusive dominance of Oligochaeta often observed in the upper parts of other estuaries can also be attributed mostly to organic enrichment associated with severe oxygen depletion (MCLUSKY et al. 1980; MCLUSKY 1987; SHILLABEER & TAPP 1989).

MEES et al. (1995), who report on the hyperbenthos in the Schelde, Ems and Gironde estuaries, find that the low salinity hyperbenthic community is completely absent in the Schelde estuary, but present in the other two estuaries. These authors attribute this absence in the Schelde estuary to oxygen deficiency. They also mention a shift towards higher salinity zones for several brackish species like *Neomysis integer*, *Mesopodopsis slabberi*, *Pomatoschistus microps* and *Gammarus salinus*.

An improvement in water and sediment quality in the Schelde estuary will re-establish a more diverse freshwater community and will allow euryhaline species to penetrate further upstream in the estuary. This is already observed in the upper Forth estuary (Scotland) where a reduction in the organic inflow has resulted in a reduction in oligochaete numbers and a further penetration intertidally of some euryhaline and brackish water species like *N. diversicolor*, *C. volutator* and *M. aestuarina* (MCLUSKY et al. 1993). Also in the Tees estuary (north east England) an increase in diversity and abundance with a penetration of marine fauna into the estuary is observed after water quality improvements (SHILLABEER & TAPP 1989). It must be stressed that a recovery of benthic and fish communities in these reaches of the estuary not only depends on a good water quality but also on the presence of sufficient natural habitats. Due to the direct loss of habitats by channelization and reclamation, this is hampered in several estuaries (e.g. Weser estuary, SCHUCHARDT et al. 1993).

Conclusions

Both in the Schelde estuary and to a lesser extent also in the Ems estuary, antropogenic stress appears to affect the intertidal macrobenthic communities in a negative way in the oligohaline/freshwater tidal zone. In the mesohaline zone, the Schelde estuary is dominated by high numbers of short-living, opportunistic species, whereas in the Ems estuary relatively more stable macrobenthic communities are observed. This is probably more related with higher physical stress (both natural and antropogenic) in this zone of the Schelde estuary than with pollution effects. Genuine brackish water species are not common in both estuaries, which can also be attributed to the environmental deterioration due to human impacts (MICHAELIS et al. 1992).

In comparison with other European estuaries, diversity, density and biomass are often higher in the poly- and mesohaline reaches of the Schelde and Ems estuary. The dominating macrobenthic species in most of the European estuaries are very similar and all showed a high tolerance towards the high-frequency/high-amplitude variations of the estuarine environment, inhabited a wide range of habitats and showed, in certain life stages, a high degree of mobility (dispersion). These possible 'keystone' organisms can contribute to the estuarine ecosystem resilience by modifying the impact on the ecosystem structure resulting from environmental changes (COSTANZA et al. 1993) and their role in the functioning of the estuarine ecosystem should be studied in more detail in the future. The limited amount of present data on the oligohaline and freshwater tidal zones of European estuaries, show in most cases an impoverished fauna, suffering mainly from a high organic enrichment in this part of the estuary. Pollution effects are however not always directly visible. More research should be undertaken on chronic effects (e.g. hampered reproduction or decreased growth rate) of pollution. Estuarine management should also pay special attention to the morphological structure of the estuarine system. Changes in the physical nature of the estuary (e.g. reclamation, canalization, dredging) will certainly affect the survival of the estuarine ecosystem, directly and indirectly. A thorough understanding of both the natural and antropogenic stress acting on macrobenthic communities in estuaries is therefore necessary.

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Chapter seven

The subtidal macrobenthos in the mesohaline part of the Schelde estuary (Belgium): influenced by man?

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Abstract

The macrobenthos of the subtidal, mesohaline zone of the Schelde estuary (Belgium) was sampled in October 1996 and 1997 at 54 and 73 sampling locations respectively. Sediments ranged from silty to very coarse, with the dominant sediment type being silt (33% of all locations). Of the 35 macrobenthic species observed, only seven species occurred in more than 20% of the samples. The polychaete *Heteromastus filiformis* and Oligochaeta were most common. Multivariate techniques revealed three distinct communities, linked mainly with sedimentological factors: (1) a species-poor (9 species) comunity with a dominance of the amphipod *Bathyporeia pilosa*, a low mean abundance and biomass (86 ind m^{-2}, 0.0189 g AFDW m^{-2}), and a mean median grain size of 215 ±19 µm (fine sand); (2) a species-rich (22) community, with the small polychaete *Polydora ligerica* as indicator species, a relatively high mean abundance and biomass (2298 ind m^{-2}, 1.395 g AFDW m^{-2}, oysters excluded), a mean median grain size of 133 ±41 µm, and also the occurrence of sediments with hard substrates being characteristic for this community; (3) a community with an intermediate species richness (12), abundance and biomass (248 ind m^{-2}; 0.249 g AFDW m^{-2}), with *H. filiformis* and Oligochaeta as indicator species, and a median grain size of 76 ±9 µm. In the study area several typical brackish water species were observed (e.g. *Polydora ligerica*, *Corophium lacustre*, *Gammarus salinus*).

Mean total abundance and biomass were very low, and the benthic communities appeared to be under stress, with a dominance of mainly small, sub-surface deposit and surface deposit feeding opportunistic species. This is probably a combined effect of both natural physical and human-induced disturbance. Only sediments with hard substrates (e.g. rocks) seems to favour species richness, providing a shelter against physical disturbance.

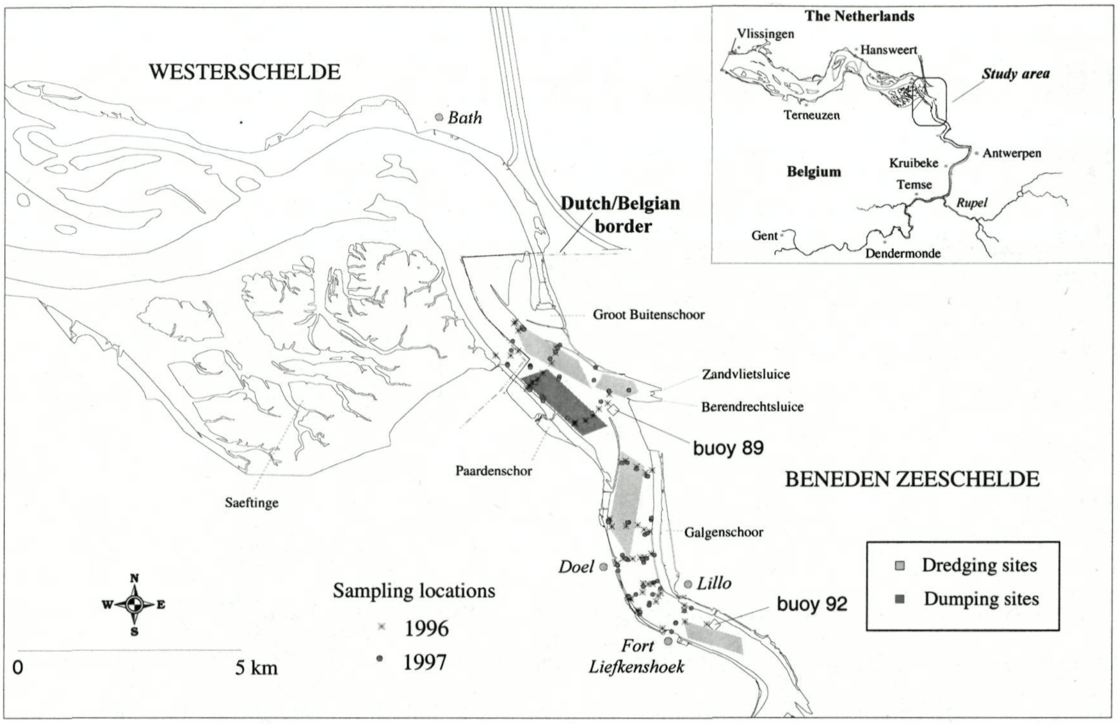

Figure 7.1. Geographical view of the Beneden Zeeschelde area with indication of the 54 and 73 sampling locations in 1996 and 1997, and with the main dredging and dumping sites in this part of the estuary.

Introduction

The inner and upper parts of estuaries are often severely impacted by man. Land reclamation results in a high degree of estuarine habitat loss. Drainage of wastewater, dredging for shipping, safety constructions (e.g. dykes, storm surge barriers), fixation of banks, etc. change the chemical and physical properties of these estuarine habitats (COSTANZA et al. 1993; GRAY, 1997).

The Schelde estuary is one of the larger NW-European estuaries with a complete salinity gradient, including a large freshwater tidal area. Especially the part between the Dutch-Belgian border and the Rupel is severely impacted and heavily polluted by domestic, industrial and agricultural waste loads and the concentrations of micropollutants are high (VAN ECK & DE ROOIJ 1993; SOETAERT & HERMAN 1995a,b; ZWOLSMAN 1999). From the 1980's on water quality has started to improve slowly, and this improvement continues in the 1990's (VAN DAMME et al. 1995; VAN ECK et al. 1998). Near the Dutch-Belgian border, the large industrialized area of the harbour of Antwerpen is situated. Being a major sedimentation area, this zone is dredged intensively in order te keep it accessible for navigation (CLAESSENS et al. 1991). The last decade several harbour infrastructures (e.g. container terminals) have been constructed in the area, and a further deepening of the shipping channel has been undertaken.

Although the intertidal macrobenthic communities along the Schelde estuary are well known (e.g. YSEBAERT et al. 1993, 1998a), recent data about the spatial distribution of macrobenthos in the mesohaline subtidal part of the Zeeschelde were lacking almost completely thus far. However, knowledge of the present status of the macrobenthos in this part of the estuary could give an indication of the present ecosystem health, since benthos is recognized as a suitable ecological group for monitoring and detecting effects of stress and pollution (e.g. PEARSON & ROSENBERG 1978; BOESCH & ROSENBERG 1981; WARWICK & CLARK 1993; DIAZ & ROSENBERG 1995; GASTON et al. 1998).

In this study the spatial distribution of macrobenthic communities in the mesohaline subtidal part of the Zeeschelde is described based on data collected in 1996 and 1997. The results are compared with the species diversity along the complete Schelde salinity gradient and with data from 1952 (LELOUP & KONIETZKO 1956). Possible effects on benthic communities of dredging operations and other anthropogenic influences, like the occurrence of hard substrates within the sediment are discussed.

Materials and methods

Study area

The Schelde estuary, a macrotidal coastal plain estuary, is situated near the border between The Netherlands and Belgium. It measures 160 km with a surface area of approximately 350 km^2. The Westerschelde (55 km) represents the downstream Dutch part with the poly-/mesohaline zone of the estuary; the Zeeschelde (105 km), the Belgian part of the Schelde estuary, represents the meso-/oligohaline and freshwater tidal zones (Figure 7.1). The mean tidal range is 3.8 m in Vlissingen, 5.2 m in Antwerpen and 2.0 m in Gent.

The study area is situated in the maximum turbidity and mesohaline zone of the Zeeschelde (BAEYENS et al. 1998; FETTWEIS et al. 1998), between the Dutch-Belgian border and Fort Liefkenshoek (Figure 7.1). In this part of the estuary mean tidal range is about 4.94 m.

Sampling and laboratory analysis

Temperature, salinity and oxygen concentrations were measured monthly at two buoys in the study area (Figure 7.1). The macrobenthos was sampled in October 1996 and October 1997 in respectively 9 and 10 transects (Figure 7.1). In every transect about 6–7 locations were sampled, divided over three depth strata (<2.95 m; 2.95–7.95 m; >7.95 m below MLLWS). In total 54 and 73 locations were sampled in 1996 and 1997. On each location one Van Veen grab (0.105 m^2) was taken, from which one small core (∅ 2 cm) for sediment analysis was taken. The benthic samples were sieved through a

1 mm mesh in the field and preserved in neutralized formaline. Position and water depth of the grab sample were noted.

In the laboratory samples were sorted after staining with 0.02% Rose Bengal. All organisms were identified to species level, except for the genus Ostrea, the Oligochaeta and one Spionid specimen, and counted. The ash-free dry weight (AFDW) biomass was obtained by drying all specimens at 105°C for 12 h and ashing them at 550 °C.

Sediment characteristics (median grain size, mud content (volume% <63 μm) were determined by laser diffraction with a Malvern Mastersizer S. Six sediment types were distinguished, according to KRAMER et al. (1994). Sediment samples containing hard substrates (e.g. stones) were all classified as type 7. Maximum ebb and flood current velocities were estimated for an average tide with the hydrodynamical model SCALDIS (VAN DER MEULEN & SILEON 1997), having a spatial resolution of 100 m.

Data analysis

Macrobenthic species were classified into trophic groups based on the food source: sub-surface deposit feeders (SSDF), surface deposit feeders (SDF), suspension feeders (SF), omnivores (O) and predators (P). Spionid species and *Macoma balthica* (Linnaeus) were classified as SDF–SF, as these species may switch between both feeding types.

The abundance/biomass comparison method – ABC (*k*-dominance curves for species abundance and biomass (LAMBSHEAD et al. 1983) was used to detect environmental stress (WARWICK 1986; MEIRE & DEREU 1990).

To identify groups of similar locations the following analyses were performed on the density datasets of 1996, 1997 and 1996–1997 together (fourth root transformed): a classification (clustering based on the Bray-Curtis similarity index and Group Average Sorting – GAS) (CLIFFORD & STEPHENSON 1975), an ordination (Multi Dimensional Scaling – MDS) (KRUSKAL & WISH 1978), and a hybrid technique (Two-Way Indicator Species Analysis – TWINSPAN) (HILL 1979). Cut-levels used were 0, 2.0, 2.3, 2.7, 3.5, 4.5. Rare species (single observation), the epibenthic shrimps *Crangon crangon* (Linnaeus) and *Palaemon longirostris* (Milne Edwards), empty samples (3 in 1996, 5 in 1997) and samples with only one individual were excluded from the analyses. The relationship between the spatial distribution of the locations in the MDS ordination and the environmental variables was indicated by a Spearman Rank Order Correlation between the axes from the ordination and the environmental variables. The clusters, resulting from the multivariate analyses, were characterized by their typical species composition, diversity (Shannon Wiener diversity index H') and the environmental variables. Statistical differences for biotic and abiotic variables among groups were analysed by Kruskal-Wallis test. Mean values are given with standard error (SE).

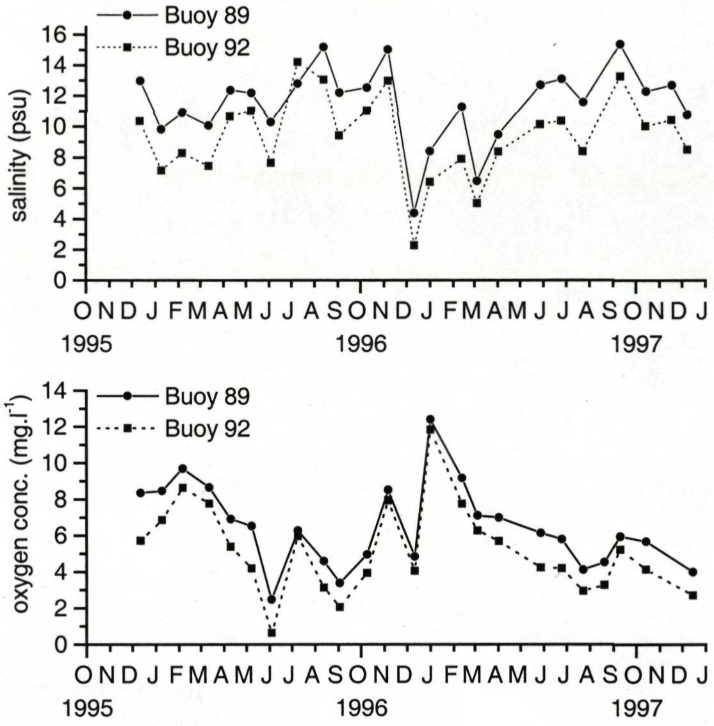

Figure 7.2. Monthly measurements of salinity and oxygen concentrations at buoy 89 and 92 whithin the study area (for geographic positions of the buoys, see Figure 7.1).

Results

Abiotic characterisation of the sampling locations

Water quality measurements at the two buoys in the study area (Figure 7.1) showed a strong seasonal pattern in water temperature and smaller seasonal fluctuations in salinity and oxygen concentrations, which were related to the river runoff, being higher in winter (Figure 7.2). The area was mesohaline (yearly average 1996: 10.5 psu; 1997: 10.1 psu) throughout the year (one exception in December 1996). Oxygen concentrations were often less than 5 mg O_2 l^{-1}, especially in summer.

Mean median grain size and mean mud content were 141 ± 19 µm and 38 ± 4% respectively, both showing a large variation. In both years the dominant sediment type was silt (Table 7.1). 5.5% in 1996 and 12% in 1997 belonged to the sediment types medium sand (250–500 µm) and coarse sand (500–1000 µm), hereafter considered together as the sediment type medium-coarse sand. 13% in 1996 and 20.5% in 1997 of the samples were of sediments with hard substrates. Mud fraction slightly decreased and median grain size slightly increased with depth, but there was no significant correlation with depth (median grain size: Spearman R=0.18; *P*=0.06 and mud fraction: Spearman R=-0.17; *P*=0.08; N=86).

Based on model calculations, mean maximum ebb and flood current velocities were 0.886 ± 0.06 m.s^{-1} and 0.786 ± 0.020 m.s^{-1} (N=127) respectively. Only at three locations the model calculated current velocities lower then 0.20 m.s^{-1}. Highest current velocities observed were 1.23 and 1.16 m.s^{-1} under ebb and flood condititions respectively. No correlation was found between current velocities

Table 7.1. Sediment types, based on median grain size, of the subtidal sampling locations in 1996 (N=54) and 1997 (N=73) respectively.

Sediment type		Range (µm)	1996		1997	
			# samples	%	# samples	%
type 1	clay	< 2	0	0,0	0	0,0
type 2	silt	2 - 63	18	33,3	24	32,9
type 3	very fine sand	63 - 125	9	16,7	9	12,3
type4	fine sand	125 - 250	17	31,5	16	21,9
type 5	medium sand	250 - 500	3	5,5	7	9,6
type 6	coarse sand	500 - 1000	0	0,0	2	2,7
type 7	hard substrate	--	7	13,0	15	20,5

and depth (N=127; Spearman R=0.13; *P*=0.16), nor between current velocities and median grain size (N=106; Spearman R=0.13; *P*=0.20) or mud content (N=106; Spearman R=-0.12; *P*=0.22).

General characteristics of the macrobenthic fauna

Of the 35 species observed (28 in 1996; 24 in 1997), 31% were annelids, 26% molluscs and 43% arthropods (Table 7.2). Only seven species occurred in more than 20% of the samples. The polychaete *Heteromastus filiformis* (Claparède) (65% of the samples in 1996, 33% in 1997) and Oligochaeta (61.5% in 1996, 50.7% in 1997) were most common. Six species were observed only once. The number of species per location was low (Figure 7.3); locations with one or two species were most common (44%).

The mean total density of all locations was 681 ± 171 ind m^{-2}; the mean density in 1996 (861 ± 341 ind m^{-2}) was noticeable higher than in 1997 (549 ± 158 ind m^{-2}), although not significantly (Mann-Whitney U-test: N(1996)=54; N(1997)=73; *U*=1720; *P*=0.2227). Densities were dominated by annelids (87% of the total density; 89% in 1996; 84% in 1997) (Table 7.2). Arthropods occurred to a lesser extent and molluscs occurred only in very low densities (Figure 7.4). Most locations had a total density between 100–1000 ind.m^{-2} in 1996 (42%) and between 10–100 ind m^{-2} in 1997 (44%) (Figure 7.3). Highest densities observed were 17352 and 9286 ind m^{-2} in 1996 and 1997 respectively.

The mean total biomass of all locations was 0.94 ± 0.35 g AFDW m^{-2}. In 1996 mean biomass (1.26 ± 0.75 g AFDW m^{-2}) was higher than in 1997 (0.68 ± 0.24 g AFDW m^{-2}), although not significantly (Mann-Whitney U; N(1996)=54; N(1997)=73; *U*=1911.5; *P*=0.77). The difference in biomass was caused by the high biomass of a few oysters (*Crassostrea angulata* (Lamarck) and *Ostrea* spp. found at 3 and 2 sampling locations in 1996 and 1997 respectively, and making 67% of total biomass in 1996 and only 20% of total biomass in 1997. If oysters were removed from the dataset, mean biomass of both years was more comparable (1996: 0.41 ± 0.13 g AFDW m^{-2}; 1997: 0.55 ± 0.16 g AFDW m^{-2}). Contrary to density, biomass was not only dominated by annelids (1996: 50%; 1997: 30%), but also by arthropods (1996: 42%; 1997: 66%) (Figure 7.4). The dominant annelids were *Polydora ligerica* (Ferronière) and *H. filiformis*; the dominant arthropods were *Crangon crangon* and *Palaemon*

Table 7.2. Number of observations (%), mean density (ind m^{-2}) and mean biomass (g AFDW m^{-2}) of all macrobenthic species observed in the subtidal, mesohaline zone of the Zeeschelde estuary in 1996 (N=54) and 1997 (N=73) respectively.

	1996			1997		
	# observations %	Density ind m^{-2}	Biomass g AFDW m^{-2}	# observations %	Density Ind m^{-2}	Biomass g AFDW m^{-2}
Annelida						
Eteone longa (P)	5,5	0,9	0,0004	*	*	*
Harmothoe impar (P)	3,6	0,4	0,0004	1,4	0,1	0,0001
Heteromastus filiformis (DF)	65,5	143,4	0,0575	32,9	74,4	0,0642
Marenzellaria spp. (P)	1,8	0,4	-	1,4	0,3	*
Nereis diversicolor (O)	*	*	*	1,4	0,1	0,0001
Nereis succinea (DF)	25,5	23,0	0,0492	26,0	22,2	0,0403
Oligochaeta (DF)	61,5	58,2	0,0015	50,7	72,3	0,0014
Polydora ligerica (SDF-SF)	34,5	479,6	0,0908	27,4	232,0	0,0501
Polydora ligni (SDF-SF)	23,6	47,0	0,0085	27,4	55,3	0,0077
Pygospio elegans (SDF-SF)	16,4	4,2	0,0002	15,0	6,0	0,0016
Spionidae spp. (SDF-SF)	1,8	0,2	-	*	*	*
Molllusca						
Barnea candida (SF)	1,8	0,4	0,0040	*	*	*
Cerastoderma edule (SF)	1,8	0,2	0,0004	*	*	*
Crassostrea angulata (SF)	5,5	2,4	0,8432	*	*	*
Hydrobia ulvae (SDF)	3,6	0,4	0,0001	*	*	*
Macoma balthica (SDF-SF)	16,4	2,9	0,0267	16,4	3,3	0,0206
Mya arenaria (SF)	9,1	2,1	0,0037	4,1	1,2	0,0004
Mytilus edulis (SF)	7,3	1,0	0,0002	2,7	0,4	0,0006
Ostrea spp. (SF)	*	*	*	2,7	0,4	0,1337
Petricola pholadiformis. (SF)	*	*	0,0004	1,4	0,4	-
Arthropoda						
Bathyporeia elegans (SDF)	7,3	0,9	0,0002	1,4	0,1	0,0000
Bathyporeia pilosa (SDF)	31,0	23,4	0,0023	22,0	5,9	0,0004
Corophium insidiosum (SDF)	11,0	8,3	0,0005	13,7	5,7	0,0002
Corophium lacustre (SDF)	14,5	15,2	0,0019	13,7	16,2	0,0016
Corophium volutator (SDF)	23,6	23,7	0,0049	32,9	38,4	0,0055
Crangon crangon (P)	14,5	1,4	0,0517	15,1	1,8	0,1755
Eurydice pulchra (P)	9,1	1,9	0,0015	9,6	1,0	0,0022
Gammarus salinus (O)	1,8	0,2	0,0003	4,1	1,3	0,0011
Melita palmata (SDF)	1,8	0,2	0,0004	1,4	0,3	0,0006
Mesopodopsis slabberii (O)	3,6	0,4	0,0001	5,5	0,7	0,0000
Neomysis integer (O)	1,8	0,2	-	*	*	*
Palaemon longirostris (P)	3,6	0,5	0,0845	9,6	1,0	0,1241
Pleusymtes glaber (SDF)	12,7	4,8	0,0008	15,1	8,7	0,0011
Rhithropanopeus harrisii (P)	3,6	0,5	0,0186	9,6	1,3	0,0481
Balanus spp. (SF)	Present			present		

*, not found; -, not determined

longirostris (Table 7.2). It should be emphasized that these arthropods were all epibenthic species, and therefore do not belong to the sedentary infauna. Most locations (55%) had a total biomass between 0.01–1 g AFDW m^{-2} (Figure 7.3), with a maximum of 40 g AFDW m^{-2} (a location with 12 oysters) in 1996 and 15 g AFDW m^{-2} in 1997.

The macrobenthic community was numerically dominated by SDF–SF species (59%), which were

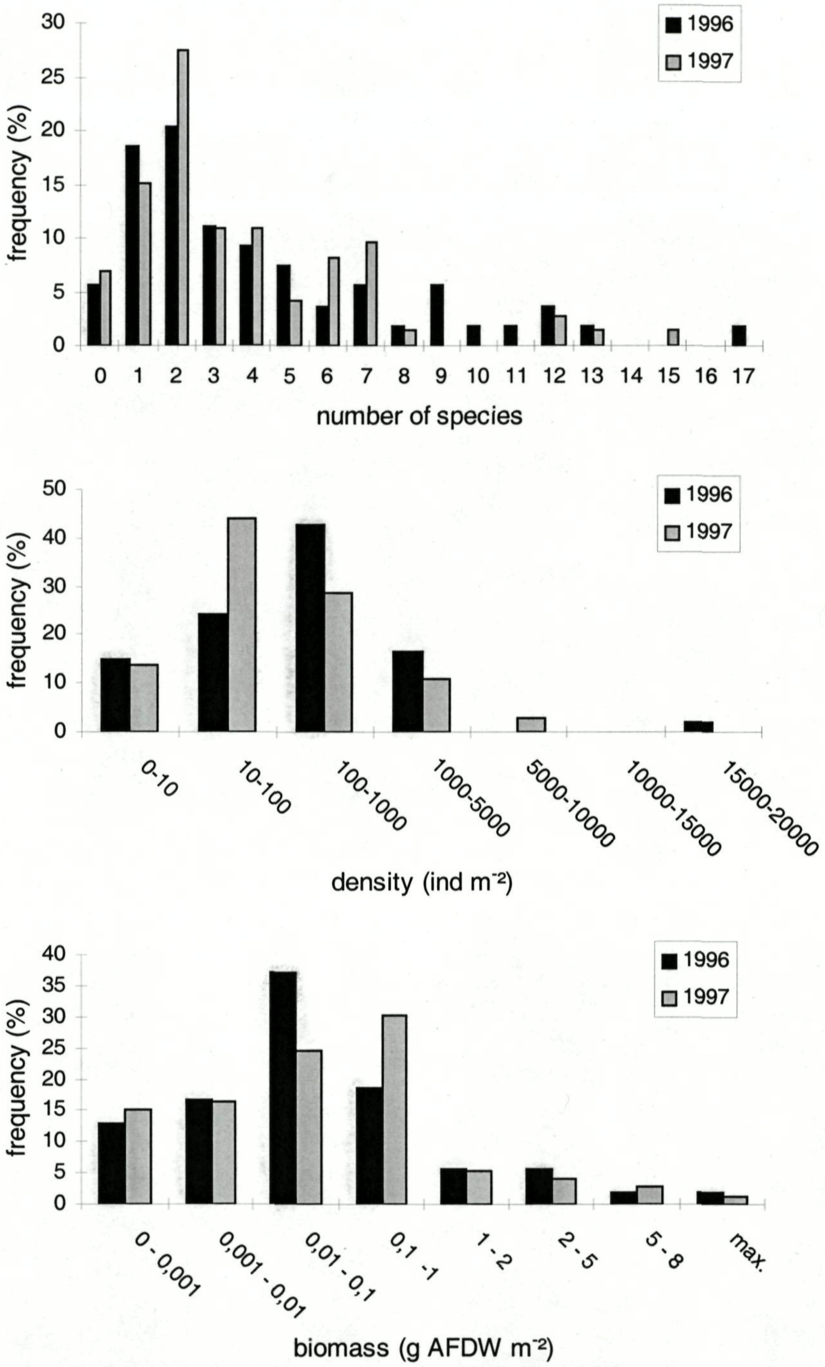

Figure 7.3. Species distribution (%), density distribution (%) and biomass distribution (%) of the 54 and 73 sampling locations in 1996 and 1997 respectively.

mainly the spionids *Polydora ligerica* and *Polydora ligni* (Webster). The other important group were SSDF with 29%, being represented by *H. filiformis* and Oligochaeta. Suspension feeders (oysters) dominated the biomass (47%), but when these few oysters were excluded predators dominated (55%), followed by SDF–SF (spionids) with 20%. The predators were mainly the epibenthic shrimps *C. crangon and P. longirostris*, not being a permanent part of the benthic infauna.

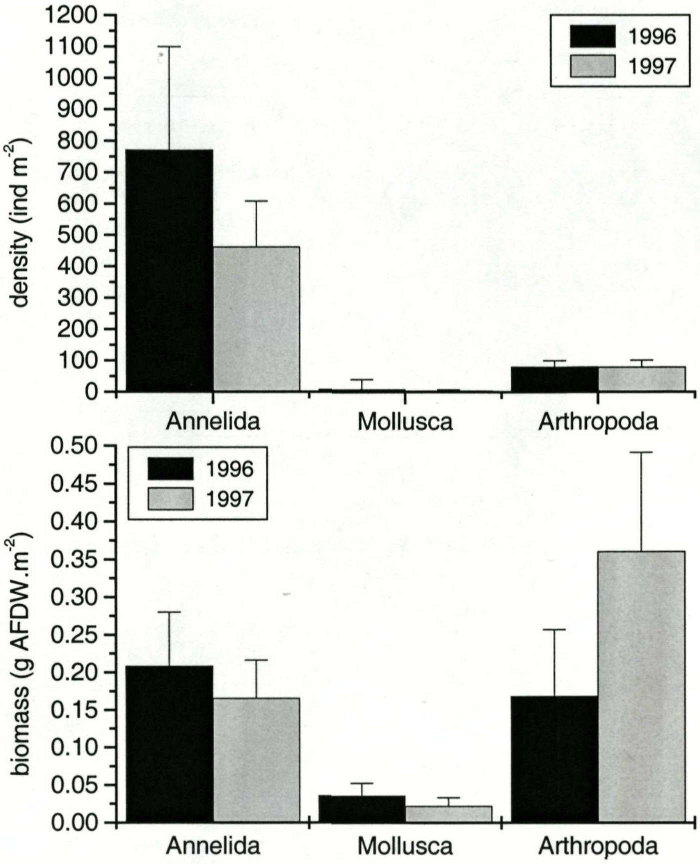

Figure 7.4. Mean density (ind m^{-2}) and mean biomass (g AFDW m^{-2}) of Annelida, Mollusca and Arthropoda in 1996 and 1997. The biomass of oysters is not included in the mean total biomass of the Mollusca.

The *k*-dominance curves for species abundance and biomass (besides oysters) (ABC-curves) showed a stressed pattern, as indicated by the abundance curve falling above the biomass curve (Figure 7.5). This means that the benthic community was dominated by one or a few very small species and only a few larger species were present.

Community structure and environmental variables

The multivariate analyses did not produce a distinction between the datasets of 1996 and 1997. Therefore the further analysis and discussion of community structure is based on the data of both years together. Both Twinspan and Cluster analyses produced three clusters, which also returned in the MDS ordination (Figure 7.6A). In the GAS-classification the first cluster (cluster 1) was separated at a 15% similarity, the two remaining at a 35% similarity. 16 locations mutually showed very little similarity and did not form a cluster. These locations were considered as group 4 (restgroup).

Neither macrobenthos species richness, density, biomass, nor one of the MDS-axes were significantly correlated with depth (Table 7.3). On the other hand, mud content was significantly correlated with macrobenthos species richness and density, being highest for the silt type sediment. Both axes of the MDS ordination were significantly correlated with mud content and median grain

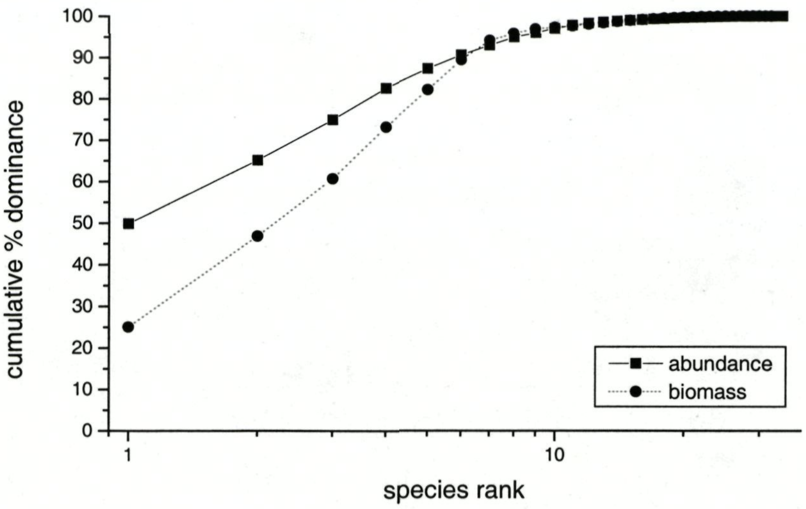

Figure 7.5. Combined k-dominance curves for species abundance and biomass (ABC-curve), based on all sampling locations (1996 and 1997 together).

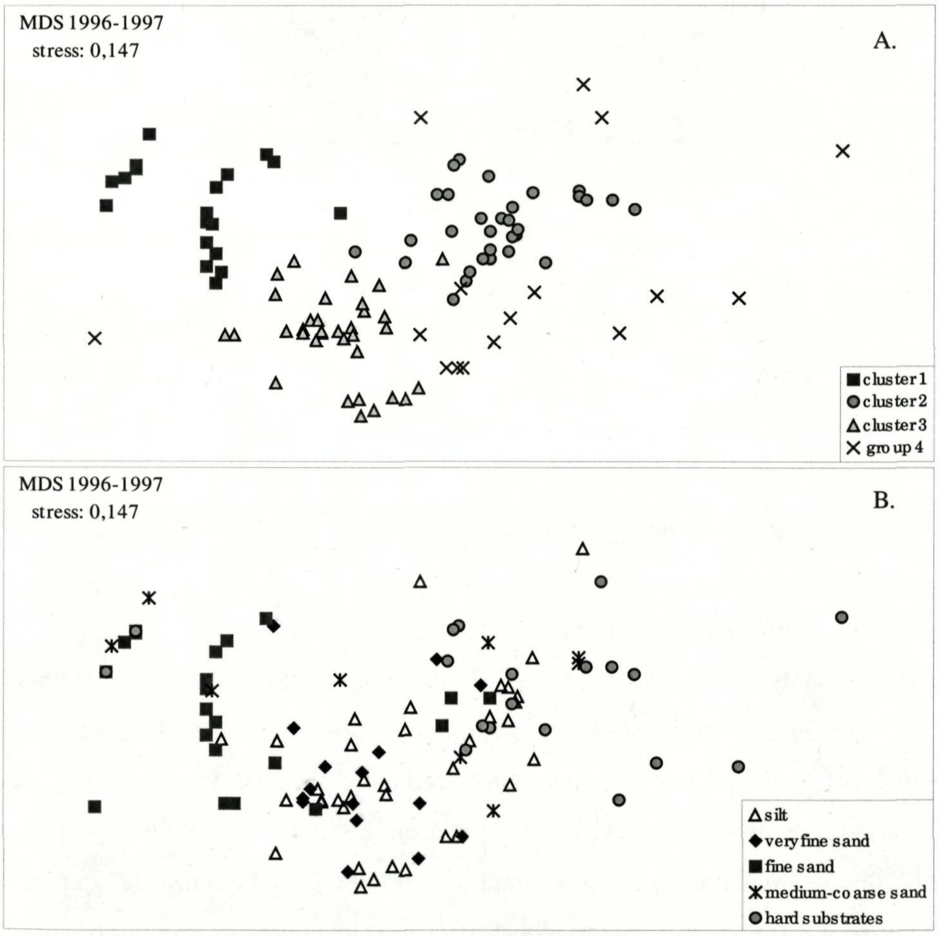

Figure 7.6. MDS ordination of species density data from 1996 and 1997 together. A. Clusters superimposed on the ordination. B. Sediment types superimposed on the ordination.

Table 7.3. Spearman Rank Order Correlations between environmental factors (depth, mud content, median grain size) and the number of species, biomass, density, and MDS X- and Y- co-ordinates. The Spearman R and the P-value are given. Significant correlations at the level $P<0,05$ are in bold.

	Depth (N=105)		mud fraction (N=86)		median grain size (N=86)	
	R	*P*	R	*P*	R	*P*
Number of species	-0,052	0,60	0,24	**0,03**	-0,14	0,20
Biomass	-0,108	0,27	0,05	0,63	0,001	0,99
Density	0,04	0,67	0,30	**0,005**	-0,20	**0,05**
MDS X co-ordinates	0,15	0,12	0,57	**<0,0001**	-0,41	**<0,0001**
MDS Y co-ordinates	0,10	0,31	-0,42	**<0,0001**	0,39	**0,0002**

size, indicating that the distribution of the samples in the MDS ordination was mainly determined by the sediment parameters. The superimposed sediment types on the ordination (Figure 7.6B) showed a clear tendency of grouping. Cluster 1 mostly occurred on fine sand sediment (70%), cluster 2 on silt (34%) and hard substrate (34%) sediments, and cluster 3 mainly on silt (58%) – very fine sand (39%) sediments.

The ABC-curves for each cluster separately showed a similar stressed pattern as observed for all sampling locations together (see Figure 7.5). The abiotic and biotic characteristics of the three clusters and the statistical difference among the clusters are summarized in Table 7.4. Cluster 1 was characterized by a species-poor benthic fauna with a typical dominance of the amphipod *Bathyporeia pilosa* (Lindström) (Figure 7.7A, 7.8A). Cluster 2 consisted of locations with a relatively species-rich benthic fauna with a high mean density and biomass. The small polychaete *Polydora ligerica* was the

Table 7.4. Biotic and abiotic characterization of the three clusters (mean ±SE), with indication of the test statistic (H) of the Kruskal-Wallis test together with the P-level for differences among the three clusters.

	Cluster 1 (n=23)	Cluster 2 (n=35)	Cluster 3 (n=31)	H	*P*-level
Total number of species	9	22	12		
Mean number of species	2.3 ±0.25	8.8 ±0.56	2.9 ±0.22	71.245	<0.0001
Shannon-Wiener diversity H'	0.53 ±0.079	1.20 ±0.097	0.69 ±0.069	16.037	0.0003
Mean density (ind m^{-2})	86 ±18	2298 ±613	248 ±76	40.513	<0.0001
Mean biomass (g AFDW m^{-2})	0.02 ±0.004	3.07 ±1.343	0.25 ±0.087	44.397	<0.0001
Indicator species					
Bathyporeia pilosa	65±13	0.6±0.43	2.7±1.81	68.873	<0.0001
Polydora ligerica	5.2 ±4.36	1379 ±571	0	58.779	<0.0001
Heteromastus filiformis	2.4 ±0.86	234 ±143	170 ±70	20.876	<0.0001
Oligochaeta	6.3 ±4.75	168 ±56	54 ±11	22.275	<0.0001
Mud content (%)	7.5 ±3.38	48 ±5.9	48 ±4.1	22.509	<0.0001
Median grain size (μm)	215 ±19	133 ±41	76 ±9	22.776	<0.0001
Depth	6.2 ±1.1	6.3 ±0.8	5.1 ±0.8	0.827	0.661

Mean biomass of cluster 2 with oysters included, without oysters mean biomass amounted to 1.40 ±0.372 g AFDW m^{-2}.

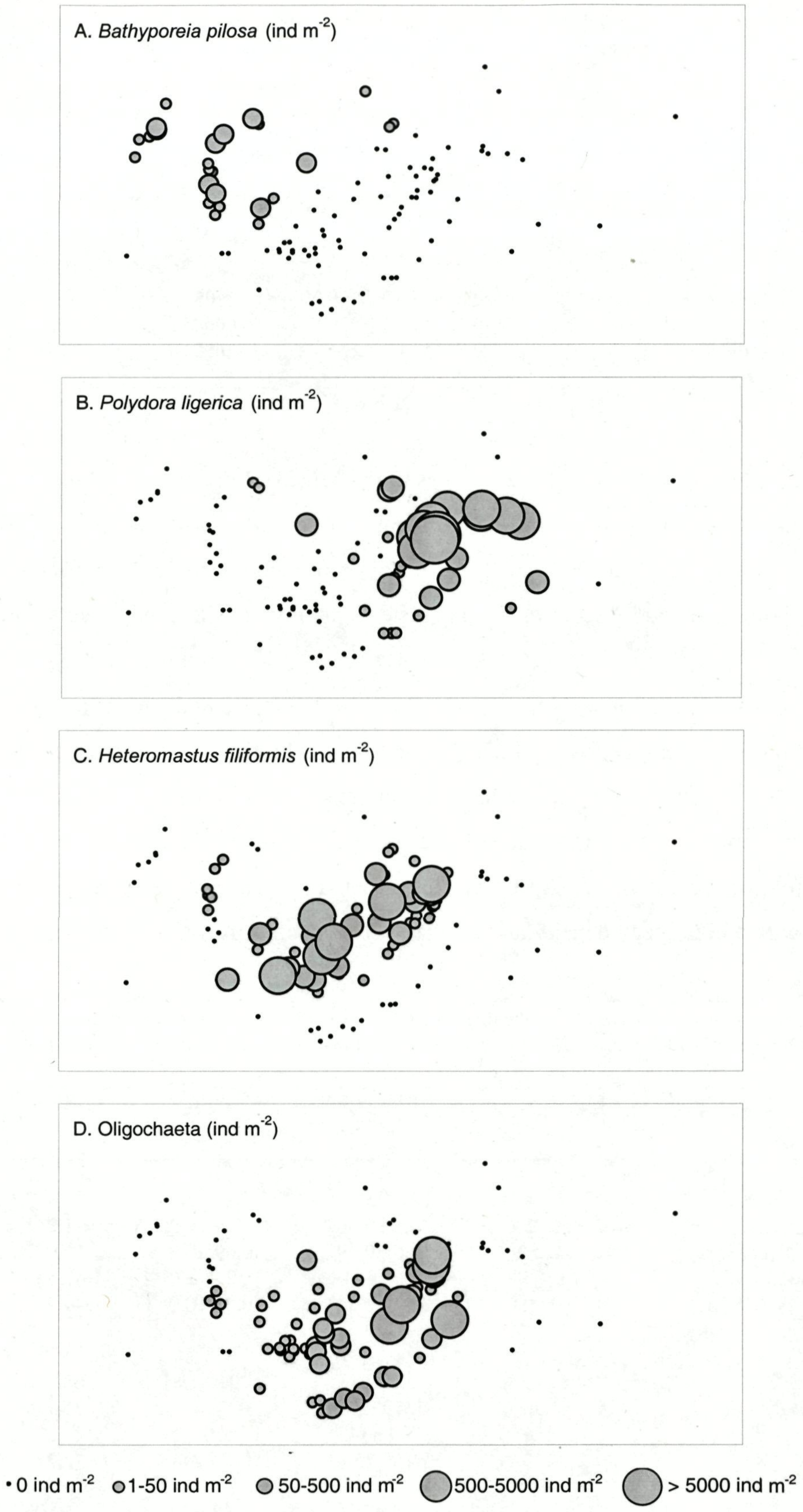

Figure 7.7. MDS configuration from Figure 6 with circles scaled in size to represent individual species density of A. *Bathyporeia pilosa*, B. *Polydora ligerica*, C. *Heteromastus filiformis* and D. Oligochaeta.

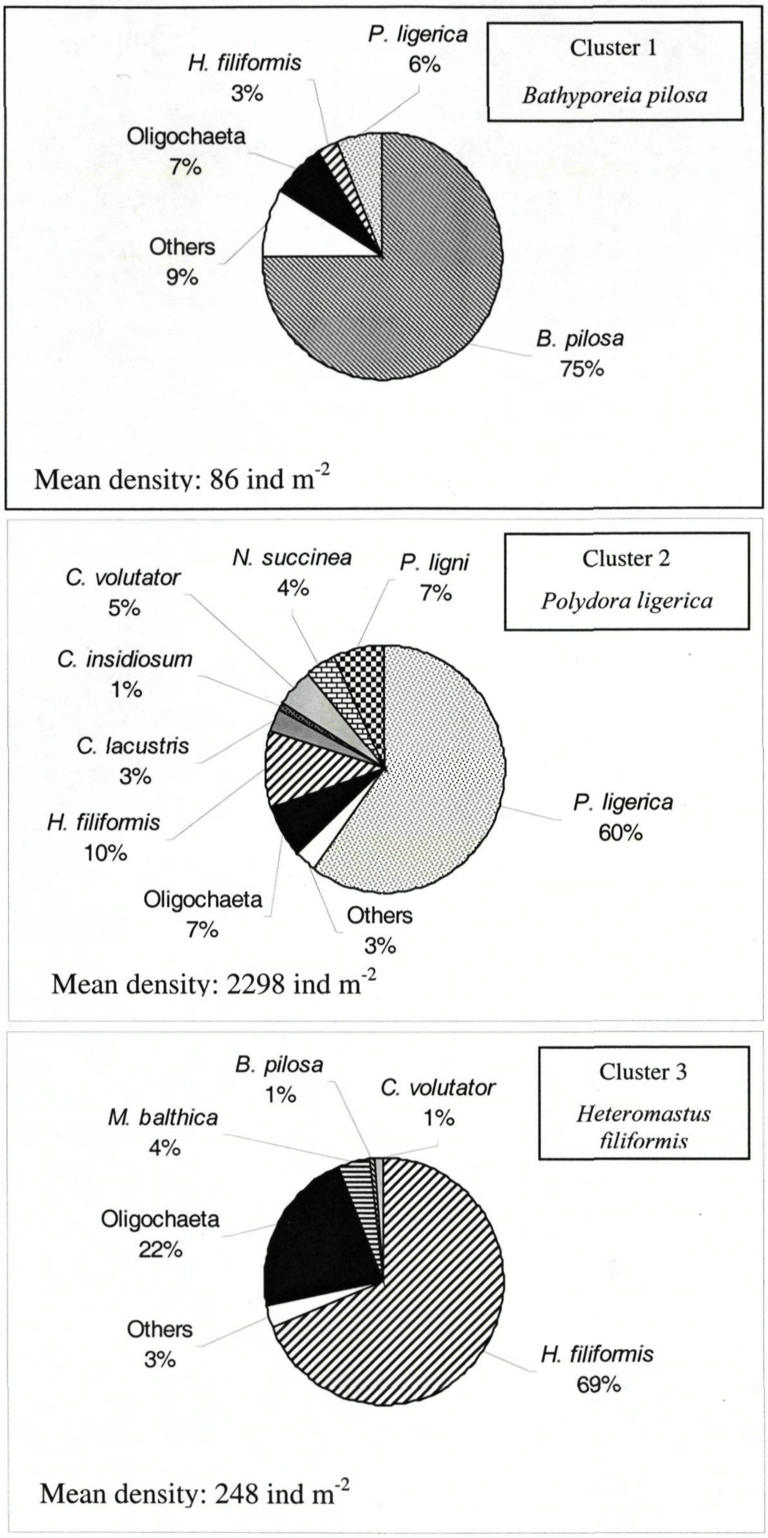

Figure 7.8. Mean species density per cluster based on density data 1996 and 1997 together. For full species names: see Table 7.2.

indicator species (Figure 7.7B, 7.8B). Oysters occurred exclusively in this cluster, explaining the relatively high biomass. Cluster 3 was characterized by intermediate species richness, density and biomass. The indicator species of this cluster were *Heteromastus filiformis* and Oligochaeta (Figure

7.7C,D and 7.8C). *Macoma balthica,* only present in low densities, appeared almost exclusively in cluster 3. Sediment characteristics were significantly different among the three clusters, depth was not significantly different.

Of group 4, 37% of the locations were situated in the silt sediment type, 30% on hard substrates, and the remaining locations in the other sediment types. Generally the samples contained few species in low densities. Characteristically 57% of the locations of group 4 were found in the depth stratum >7.5 m, with a mean depth of 9.5 ±1.4 m, which was noticeably deeper than the mean depth of the three clusters.

Discussion

Species diversity along the salinity gradient in the Schelde estuary

The most important variables controlling the occurrence of benthic organisms on an estuarine scale are salinity and sediment characteristics (e.g. WOLFF 1973; BOESCH 1977; HOLLAND et al. 1987; RAKOCINSKI et al. 1997; YSEBAERT et al. 1998a), which are in turn determined largely by hydrodynamic conditions (e.g. WILDISH & KRISTMANSON 1979; WARWICK & UNCLES 1980; WARWICK et al. 1991; HALL 1994). It is assumed that the environmental stress, due to salinity and hydrodynamic conditions, is greatest in the subtidal part of the middle and upper regions of estuaries, resulting in a lower diversity of benthic invertebrates predicted in these areas. The aim of this study was to investigate the macrobenthic community of the subtidal mesohaline part of the Zeeschelde estuary.

SEYS et al. (1999b) recently investigated the benthos of the Zeeschelde, but this study concentrated on Oligochaeta, and therefore was based on only one small sediment core per sampling location (diameter 3.5 cm). Only a few locations were situated within the subtidal mesohaline part of the Zeeschelde estuary. Apart from two Oligochaeta species found (*Heterochaeta costata* (Claparède) and *Tubificoides heterochaetus* (Michaelsen)), only four macrobenthic species were determined in these locations: *Polydora ligerica*, *Heteromastus filiformis*, *Nereis succinea* (Frey & Leuckart) and *Macoma balthica.* The different sampling method and the small amount of locations may explain the large difference in species number as compared to this study.

The subtidal part of the Westerschelde was recently studied as part of a monitoring programme (e.g. BRUMMELHUIS et al. 1997; CRAEYMEERSCH 1999). For the same period (autumn 1996–1997), 55 macrobenthic species were observed. Species diversity decreased from the polyhaline zone (40 species, 30 sampling locations each year), over the poly-/mesohaline transition zone (31 species, idem) to the α-mesohaline zone (27 species, idem). In this study no further decrease in the number of species was observed in the β-mesohaline part of the estuary. Instead, species diversity slightly increased (35 species). The presence of sediments with hard substrates, often having a high macrobenthic species richness, may account for this. Also, the sampling effort in this study was larger as compared to the sampling effort in the monitoring programme of the Westerschelde. When considering the available data from this study for all sampling years (1990–1997), to increase the sampling effort, about 100 taxa were found in the subtidal part of the Westerschelde. The number of species also decreased from the polyhaline (70 species) towards the mesohaline zone (50 species). Therefore, the observed species diversity was also a function of sampling effort. Many species were reported to occur irregularly and rather accidentally, with in general very few species per sampling location, and this was also observed in this study. On the other hand, species diversity 'hot spots' were sometimes observed. In this study one sampling location represented 17 macrobenthic species, half of the total number of species observed.

Species diversity was reported to be much lower in the oligohaline zone of the Zeeschelde, characterised by an impoverished benthic fauna, with a few Oligochaeta species and very few macrobenthic species, such as *P. ligerica* and *Corophium volutator* (Pallas) (YSEBAERT et al. 1993; SEYS et al. 1999b). In the subtidal freshwater tidal zone the community was almost completely composed of a few Oligochaeta species (SEYS et al. 1999b). This very low species diversity was explained by the heavy pollution in the oligohaline and freshwater tidal zones of the Zeeschelde.

The subtidal mesohaline part of the Zeeschelde was characterized by some typical 'genuine brackish-water' species, species which according to REMANE (1969) showed a distribution strictly limited to the mixohaline zones without expansion into the marine or freshwater regions (WOLFF 1973 ; MICHAELIS et al. 1992). In our study the observed 'brackish-water' species are the polychaete *Polydora ligerica*, the amphipods *Gammarus salinus* (Spooner), *Corophium insidiosum* (Crawford) and *Corophium lacustre* (Vanhöffen), the shrimp *Palaemon longirostris* and the crab *Rhitropanopeus harrisii* (Gould). The remaining species were euryhaline and also occurred in the whole Westerschelde. The observation of *Marenzelleria* spp., an immigrant from North-American shores (BASTROP et al. 1997; ESSINK & SCHÖTTLER 1997), and for the first time reported to occur in Europe in 1982 (MCLUSKY et al. 1993), is the most southern observation of *Marenzelleria* to date (YSEBAERT et al. 1996; ESSINK 1999).

Subtidal versus intertidal macrobenthos

The observed species richness of the subtidal zone of the Zeeschelde was higher than that of the intertidal zone, the densities and biomass however were lower. In a study from 1990–1996 on 24 intertidal locations within the study area, 24 species were found, five of which (*Corophium volutator*, *Heteromastus filiformis*, *Nereis diversicolor* (Müller), *Macoma balthica* and Oligochaeta) contributed to 96% of mean densities and 99,3% of mean biomass (pers. observ.). The same five species were also found subtidally, but generally at much lower densities. *Polydora ligerica*, the most abundant species of the subtidal zone of the Zeeschelde, was not found intertidally. Total mean intertidal densities were

7000 ±1060 ind m^{-2}, being dominated by *C. volutator* (37%) and total intertidal mean biomass was 4.79 ±0.34 g AFDW m^{-2}, being dominated by *N. diversicolor* (40%).

Historical comparison with LELOUP & KONIETZKO (1956)

The macrobenthos of the β-mesohaline part of the Zeeschelde has been studied in 1952 on 21 subtidal locations in the same area of the Zeeschelde (LELOUP & KONIETZKO 1956). At that time anthropogenic pressure was lower but but water quality was already bad. The number of species in 1952 (15 species) was lower as compared to this study (35 species), but sampling effort was also lower. Eleven of the taxa were found in both studies. Some recently very abundant species, like *Polydora ligerica* and *Heteromastus filiformis*, were totally absent in 1952. The subtidal macrobenthic community in 1952 resembled cluster 1 of this study, being dominated by *Bathyporeia pilosa*, and showing low mean densities (85 ±24 ind m^{-2}). Communities of cluster 2 and 3 were nearly absent. As shown in this study, the occurrence of the community of cluster 1 is related to the presence of relatively coarse, sandy sediments. In 1952, the sediment was indeed coarser as compared with this study, as 70% of the sampling locations contained less than 5% of mud (fraction <50 µm, determined by sieving).

Human impacts

The mesohaline subtidal zone of the Zeeschelde is by nature characterized by a high degree of 'unstability', caused by large fluctuations in salinity, high current velocities and high turbidity, making an assessment of human impacts on the benthic communities difficult. Human activities, such as the discharge of waste and dredging of sludge, are superimposed on these natural processes and, moreover, interfere with them. The combination of favourable hydrodynamic conditions, several fine suspended matter sources (including a large antropogenic part), and the flocculation process, leads in salinity zone 2–10 psu to bottom sediments that locally contain high percentages of fine material (BAEYENS et al. 1998). Being a major sedimentary environment, the shipping channel is extensively dredged. The processes of sedimentation and resuspension, at least locally, are probably enhanced by these dredging operations, that increased from 11 million m^3 dredged and 4 million m^3 dumped in the period 1951–1960 to 20 million m^3 dredged and 11 million m^3 dumped in 1981–1990 (CLAESSENS pers. com.).

The fact that the subtidal zone of the Zeeschelde is a highly stressed environment was in this study confirmed by the very low density and biomass of the macrobenthos, and the most common occurrence of *Heteromastus filiformis* and tubificid Oligochaeta, small, sub-surface deposit-feeding, opportunistic species. It was also clear from the ABC-curves that the communities considered were under stress. This provides strong evidence that the communities remain in early succession, and indicates stress or disturbance (e.g. WARWICK 1986; GASTON et al. 1998). The occurrence of three different macrobenthic communities in 1996–1997, two of which are typical for muddy sediments (clusters 2 and 3), might be explained by a difference in origin and magnitude of disturbance. A less common, typically low-diversity community (cluster 1) was found on more sandy sediments, being dominated by the amphipod *Bathyporeia pilosa*, a well adapted inhabitant of unstable, sandy sediments (KHAYRALLAH & JONES 1980). This community is characteristic for the mesohaline, subtidal part of the Schelde estuary, at places where by nature tidal current speeds and instability of the (sandy) sediment become the limiting factors (CRAEYMEERSCH 1999). It was also the only dominant community in 1952.

The dredging and dumping activities might have direct effects (being washed out, being buried) on the occurrence of macrobenthos. 70% of the samples taken at locations where intensive dredging took place (Figure 7.1) belonged to cluster 3, dominated by the capitellid *H. filiformis* and tubificid Oligochaeta, which are known to be very tolerant to both physcial and chemical (organic enrichment, anoxia) disturbance factors (RAKOCINSKI et al. 1997; GASTON et al. 1998). Although most of the locations from cluster 2 and 3 occurred in silty sediments, species characteristics for cluster 2 (e.g. *Polydora ligerica*) were almost completely absent at dredging and dumping sites.

In the study area also several 'hard substrates' were constructed (e.g. dams, dykes, rubbles) to suppress erosion, to conduct the streamflow and for safety reasons. In many places these constructions subsided, causing the occurrence of stones and other similar hard substrates in the river, next to natural substrates like peat and shells. Most of the sediments with hard substrates were characterised by a high number of species and a relatively high density (cluster 2), although a lot of the samples taken were incomplete. Hard substrates can form a suitable habitat for several soft bottom species, as these substrates might provide shelter and prohibit species being washed out from the sediment. *Balanus* spp., often found in several layers on these hard substrates, might provide shelter for other animals, or create a multitude of habitats for other species, even for soft bottom ones, when silt is deposited in between (DITTMER 1983). The hard substrates also allowed the settlement of bivalves, like oysters. These suspension feeders could be considered an indication of improving water quality.

Acknowledgements

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Chapter eight

Biological and physical characteristics of intertidal, cohesive sediments in the mesohaline part of the Schelde estuary (Belgium)

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Abstract

The biological (zoobenthos and microphytobenthos) and physical characteristics of intertidal, cohesive sediments were studied in April and September 1997 on ten locations, situated on three mudflats in the mesohaline part of the Schelde estuary. The sediment at the sites was muddy (< 63µm) or consisted of very fine sand (<125 µm). Sediment characteristics of the top 0-0.5 cm layer (median grain size, mud content, organic matter and bulk density) were strongly correlated and did not differ significantly between April and September. Chlorophyll *a* and fucoxanthin contents in the top layer (0-0.5 cm) of the sediment were about 7 times higher in April than in September, but a large spatial variation was observed, especially in April, which was mainly attributed to a difference in elevation of the mudflats. The high pigment contents in April were accompanied by a relative low abundance of the zoobenthos. In April Oligochaeta were numerically most important in the 1000 µm and 500 µm fraction of the zoobenthos, and Nematodes in the 250 µm fraction. The critical shear stress for erosion, measured *in situ* with the SedErode device, varied between 0.26 and 0.43 N.m^{-2} in April. The critical shear stress for erosion was significantly lower in September when pigment contents were low and zoobenthos abundance was high. In September *Corophium volutator* and *Heteromastus filiformis* dominated the 1000 µm fraction, Oligochaeta and *C. volutator* the 500 µm fraction, and Nematodes, *Manayunkia aestuarina*, Oligochaeta and Copepoda the 250 µm fraction. Zoobenthos species showed a different vertical distribution pattern in the sediment, mainly reflecting their difference in feeding habits.

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In general, the results from this field study indicate that physical and biological processes interact in a complex manner, and that their contribution to sedimentological processes appears to differ spatially and temporally.

Introduction

Estuaries are transitional environments between rivers and the sea and are characterised by largely varying and often unpredictable hydrological, morphological and chemical conditions (DAY et al. 1989). Knowledge of the environmental variability and related population effects on a wide range of spatio-temporal scales is fundamental to better understand the functioning, stability and resilience of these ecosystems and the antropogenic influence on them.

The physicochemical characteristics of estuaries vary strongly with season, especially in the oligo- and mesohaline parts. As a consequence, seasonal fluctuations in the occurrence of benthic invertebrates are often very large in these parts of an estuary (HOLLAND et al. 1987). For the Schelde, one of the larger NW-European estuaries with a complete salinity gradient, the intertidal macrobenthic communities along the estuarine salinity gradient are well described (e.g. MEIRE et al. 1991; YSEBAERT et al. 1993, 1998a). These studies, based on autumn samples only, demonstrated a clear decrease in macrobenthic species diversity and biomass from the polyhaline zone towards the meso-/oligohaline zone. However, within the mesohaline zone more detailed information on the spatio-temporal variation of the zoobenthos, in relation to the abiotic environment, is lacking.

Benthos in general plays an important role in the system dynamics of estuaries (e.g. HERMAN et al. 1999). Besides its central role in the benthic and pelagic food chains, various biological factors resulting from the presence itself of benthic organisms may affect sediment transport processes by influencing the physical stability and erodability of the natural cohesive sediments in complex ways (UNDERWOOD & PATERSON 1993; GERDOL & HUGHES 1994a; GRANT & DABORN 1994; YALLOP et al. 1994; PATERSON 1997). Especially the stabilising or destabilising role of the macrofauna is not clear (LUCKENBACK 1986; GERDOL & HUGHES 1994a; MOURITSEN et al. 1998; DE DECKERE et al. subm.), whereas the stabilising effects of benthic microalgae are well accepted (HOLLAND et al. 1974; PATERSON 1997).

The aim of this study is to investigate the variations in zoobenthos and microphytobenthos (algal biomass) occurrence between spring (April) and autumn (September) in relation to environmental characteristics of cohesive sediments, based on a sampling of ten locations on three mudflats in the intertidal mesohaline part of the Schelde estuary. Not only macrobenthos (> 1000 µm), but also the smaller fraction of the zoobenthos (sieved through 500 and 250 µm mesh size), as well as the vertical distribution of the benthos in the sediment are considered.

Materials and Methods

The Schelde estuary

The Schelde estuary is situated in the NW of Belgium and the SW of The Netherlands. This macrotidal estuary is a heterotrophic ecosystem (HEIP et al. 1995; SOETAERT & HERMAN 1995a), which is under permanent stress caused by a high load of waste water and by extensive dredging activities for the maintenance of shipping traffic to the harbour of Antwerpen.

The study area, situated near the Dutch/Belgian border, about 55-60 km upstream of the mouth, experiences mesohaline salinity conditions (5-18) most of the time (BAEYENS et al. 1998; FETTWEIS et al. 1998). Surface water salinity was 9.5 in April 1997 and 15.4 in September 1997. Prior to both sampling events salinity was on average 7.25 and 10.50 during the periods January-March and June-August 1997 respectively. The mean tidal range is about 4.94 m, ranging from 5.64 m during spring tide to 4.02 m during neap tide.

The turbidity maximum is situated at about 110 km from the mouth during dry periods and at about 50 km during wet periods (WOLLAST & MARIJNS 1981). Periods with high rainfall are more concentrated during winter. This explains to a major part the observed coupling of suspended mud concentration with seasons in the study area, where the high suspended mud concentrations are generally occurring during winter and the low ones during summer (FETTWEIS et al. 1998). The combination of favourable hydrodynamic conditions, several fine suspended matter sources, and the flocculation process, leads in salinity zone 2-10 to bottom sediments that contain locally high percentages of fine material (BAEYENS et al. 1998).

Description of the study sites

The field measurements were carried out on ten intertidal locations (Figure 8.1). The ten locations were sampled in April (8-9-10) and September (2-3-4) 1997 under dry weather conditions. Mean temperature of the surface sediment was 14.3 °C (range 8.6-18.0 °C) in April and 21.3 °C (range 18.7-26.3 °C) in September. The locations were situated on three mudflats that differ in exposure to tidal currents (Figure 8.1). The Galgenschoor (GS) mudflat has a relatively steep slope and is directly connected to the main channel. The Paardenschor (PS) mudflat has a less steep slope and is protected by a submerged dam near the navigation channel. The Buitenschoor (GB) mudflat has a shallow slope and is protected by a sandflat and a dam. 3D hydrodynamic model simulations (FETTWEIS & SAS 1999) showed that maximum flood currents during spring tide differ substantially in magnitude among the three mudflats, respectively 0.7-0.9 $m.s^{-1}$ on the Galgenschoor, 0.5-0.6 $m.s^{-1}$ on the Buitenschoor and 0.25-0.45 $m.s^{-1}$ on the Paardenschor. Maximum ebb currents during spring tide are substantially lower on the Galgenschoor (± 0.4 $m.s^{-1}$) and the Paardenschor (0.1-0.2 $m.s^{-1}$), but have the same magnitude as the maximum flood currents on the Buitenschoor. Maximum currents during neap tides

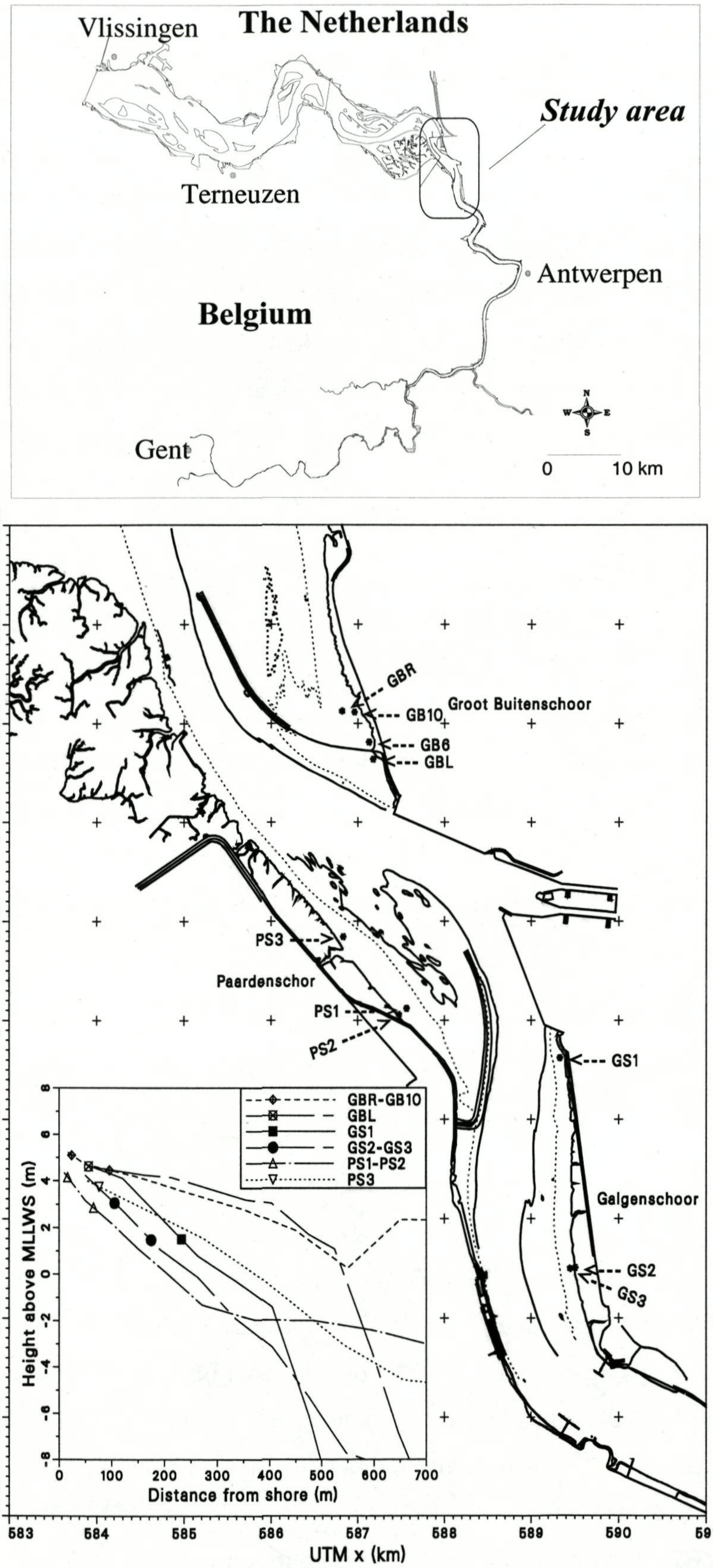

Figure 8.1. Map of the Schelde estuary with a detailed map of the mesohaline part showing the three mudflats (Buitenschoor (GB), Galgenschoor (GS) and Paardenschor (PS)) and the ten sampling locations. For each mudflat the slope and the height above Mean low low water spring (MLLWS, m) of each sampling location are given.

Table 8.1. Sediment characteristics of the ten sampling locations in April and September (average per location). Height = height of each location in +m MLLWS; D50 = median grain size; Mud = volume % < 63 µm; Org. = organic content in weight %; ρ = bulk density of the sediment; τ_{cr} = critical shear stress for erosion. (GB = Buitenschoor, GS = Galgenschoor, PS = Paardenschor).

Sampling location	*Height M*	*D50 µm*		*Mud %*		*Org. %*	ρ $kg.m^{-3}$	τ_{cr} $N.m^{-2}$
Depth range (cm)		*0-0.5*	*0-10*	*0-0.5*	*0-10*	*0-0.5*	*0-0.3*	
APRIL								
GBR	4.91	27	41	74	62	12	1315	0.43 (0.42-0.43)
GB10	5.55	43	63	62	50	9	1256	0.42 (0.39-0.45)
GB6	5.61	27	61	72	51	12	1332	0.26 (0.25-0.26)
GBL	5.07	68	136	48	23	5	1493	0.33 (0.27-0.37)
GS1	1.96	43	59	63	52	7	1563	0.26 (0.25-0.29)
GS2	3.50	118	60	29	52	3	1811	0.30 (0.30-0.31)
GS3	1.92	31	34	72	66	10	1546	0.30 (0.27-0.36)
PS1	3.30	52	35	58	69	6	1507	0.35 (0.29-0.38)
PS2	4.61	30	28	76	75	8	1306	0.30 (0.26-0.35)
PS3	4.20	61	76	52	41	3	1642	0.32 (0.29-0.39)
SEPTEMBER								
GBR	4.91	33	28	73	75	7	1477	0.25 (0.22-0.27)
GB10	5.55	37	48	71	59	5	1589	0.29 (0.26-0.33)
GB6	5.61	37	37	70	67	7	1559	0.27 (0.26-0.28)
GBL	5.07	124	131	27	23	3	1783	0.29 (0.27-0.30)
GS1	1.96	41	75	63	44	5	1445	0.24 (0.23-0.26)
GS2	3.50	36	50	72	60	7	1402	0.29 (0.29-0.30)
GS3	1.92	45	34	62	68	7	1432	0.25 (0.27-0.36)
PS1	3.30	27	40	77	66	7	1464	0.23 (0.22-0.25)
PS2	4.61	35	42	71	64	6	1566	0.26 (0.26-0.27)
PS3	4.20	37	64	71	49	5	1531	0.26 (0.24-0.28)

are about 15-40% lower than during spring tides.

The height of the sampling locations differed considerably, ranging from +1.92 m MLLWS to +5.61 m MLLWS (Table 8.1, Figure 8.1), resulting in a different period of flooding between approximately 9.30 h and 1.40 h during a mean tidal cycle.

The sampling locations are situated in a sedimentary environment. Mean accumulation rates based on ^{210}Pb profiles were respectively 4.5 mm.yr^{-1} for the Buitenschoor inside the submerged dam (GBR, GB6, GB10), 2.4-3.9 mm.yr^{-1} for the Paardenschor (PS1) and the Galgenschoor (GS1, GS3) and zero for the Buitenschoor outside the dam (GBL) (WARTEL et al. 1998).

Field sampling

At each location 15 macrobenthic samples were taken with a corer (∅ 4.5 cm) to a depth of 10 cm. Nine samples were sectioned into following intervals: 0-1 cm; 1-3 cm; 3-5 cm; 5-10 cm. Nine additional cores (∅ 2.0 cm) were sampled in September and sectioned in the same way. All samples were fixed with buffered formaline.

For pigment analysis three random sediment samples of the top 1 cm were taken at each location with a corer (∅ 2.0 cm) and immediately frozen. Each sample, consisting of two subsamples, was sectioned in two parts: a surface sample (0-0.5 cm) and the layer of 0.5-1.0 cm. For sediment granulometry the surface layer (0-0.5 cm) and the layer 0-10 cm were collected in the same way as for the sampling for pigments. One sample (0-0.3 cm) was taken for determination of the sediment bulk density and related sediment characteristics.

The critical shear stress for erosion, defined as the minimum applied bed shear stress required to initiate erosion and to remove sediment from the bed surface, was measured *in situ* at each location using the instrument SedErode. SedErode is a portable, fully contained instrument (MITCHENER et al. 1996). The basic principle of SedErode is that known shear stresses are applied to a mud surface and the bed response (suspended sediment concentration) is monitored. From this the critical shear stress is derived. Three erosion tests were performed at each location. The accuracy of SedErode measurements depends on several factors: the basic accuracy of the applied shear stress, which is 20% based on calibration against hot film shear stress probes, the size of the shear stress increments used during the test, and the microtopography of the sediment. For the April survey, the increment was approximately 0.2 $N.m^{-2}$, which corresponded to the relatively hard sediments during this time. However, the sediments were considerably softer during the September survey, and it was decided to lower the increment to 0.1 $N.m^{-2}$ in order to obtain a higher accuracy at the low range of the SedErode instrument. This resulted in an error due to the chosen shear stress increment of respectively ± 0.1 $N.m^{-2}$ and ± 0.05 $N.m^{-2}$.

Laboratory measurements

All zoobenthic samples were sieved through a 1000 μm mesh and sorted after staining with 0.02 % Rose Bengal. In April, three of the vertically sectioned samples were further sieved through a 500 μm and a 250 μm mesh, whereas in September the nine small cores were used for this. These smaller zoobenthic fractions were only analysed to a depth of 5 cm. Organisms were counted and identified to species level, except Nemertini, Oligochaeta, Nematoda and Copepoda. For Annelids, often broken due to handling, only parts with a head structure were counted. Ash-free dry weight (AFDW) of the 1000 μm fraction was measured by drying at 105 °C for 12h and ashing at 550 °C.

The occurrence of algal biomass (microphytobenthos) was based on the observed content of chlorophyll *a*. The accessory pigment fucoxanthin was used as an indicator of diatom (Bacillariophyceae) biomass (BROTAS & PLANTE-CUNY 1998; PATERSON et al. 1998). Pigments were analysed by High-performance liquid chromatographic analysis (HPLC), using a modified method of MANTOURA & LLEWELLYN (1983).

Sediment granulometry was measured by laser diffraction method (Malvern Mastersizer). Total organic content was determined by ignition loss.

Statistical analyses

For each location averages for both biological and environmental variables were calculated. The vertical distribution of the zoobenthos was expressed as the mean percentage of the abundance observed in each depth range at each location. Locations with less than five individuals of a certain species were omitted.

The relationships between biotic and environmental parameters were determined using Spearman rank correlation (SOKAL & ROHLF 1981). Since the same locations were sampled in each season, the general trend in seasonal variation of biotic and environmental variables was analysed using the Wilcoxon matched-pairs Signed rank test (SOKAL & ROHLF 1981).

Multivariate ordination techniques were used to investigate the relationship between zoobenthic species composition and pigments and environmental variables respectively. A preliminary Detrended Correspondence Analysis on all 20 sampling locations yielded axes of short length (below 2 SD), so a linear ordination method, Redundancy Analysis (RDA) (JONGMAN et al. 1987; TER BRAAK 1994) was applied further, using the computer programme CANOCO 4.0 (TER BRAAK & SMILAUER 1998). Zoobenthos densities were log(x+1) transformed prior to analysis and were represented as the sum of the three fractions (1000, 500 and 250 μm).

Results

Sediment characterisation

Based on the median grain size (D50) most locations were classified as mud (< 63 μm) or very fine sand (63 - 125 μm) in April and September, only location GBL had a median grain size > 125 μm (Table 8.1). Generally a significantly higher mud content and a lower median grain size was found in the top layer (0-0.5 cm) than in the 0-10 cm layer (Wilcoxon matched-pairs Signed-rank test Z= 2.538, p=0.01 and Z=2.165, p=0.03 respectively, n=20), except for station GS2, where a more sandy top layer was observed in April.

The organic content of the sediment varied between 3 and 12 %, and was significantly correlated with the mud content of the top layer(r=0.68, p=0.001, n=20). The bulk density of the sediment varied between 1256 and 1811 kg.m^{-3} and was significantly correlated with the mud content of the top layer (r= -0.64, p=0.002, n=20) and organic content (r= -0.71, p=0.0004, n=20). None of the sediment characteristics was correlated with the height of the sampling locations.

The critical shear stress for erosion was the only sediment characteristic that significantly differed between April and September (Table 8.2). The critical shear stress for erosion per location varied

Table 8.2. Comparison of sediment characteristics, pigment contents (chlorophyll *a* and fucoxanthin), and zoobenthos characteristics (diversity, density, biomass) between spring (April) and autumn (September). Mean and Standard Deviation of the parameters in both months with the Z-value and associated probability of the Wilcoxon matched pairs signed rank test are given. NS= not significant, *p<0.05, **p<0.01.

: 0-3 cm ?
ccumulation
mud in ?
t on
mudflat

	April (n=10)	September (n=10)	Z-value	p-value
Sediment characteristics				
Density of the sediment ($kg.m^{-3}$)	1477 ± 176	1525 ± 110	0.7645	NS
Median grainsize 0-10 cm (μm)	59.3 ± 31.1	54.9 ± 30.3	0.7644	NS
Mud content 0-10 cm (%)	54.1 ± 15.1	57.4 ± 15.2	1.0783	NS
Median grainsize 0-0.5 cm (μm)	49.9 ± 27.9	45.0 ± 28.0	0.2548	NS
Mud content 0-0.5 cm (%)	60.5 ± 14.7	65.9 ± 14.4	0.3567	NS
Organic matter (%)	7.4 ± 3.1	5.9 ± 1.5	1.7838	NS
Critical erosion shear stress ($N.m^{-2}$)	0.33 ± 0.06	0.27 ± 0.02	2.6500	**
Pigment contents				
Chlorophyll *a* 0-0.5 cm ($\mu g.g^{-1}$)	34.5 ± 31.0	4.27 ± 1.34	2.5992	**
Chlorophyll *a* 0.5-1.0 cm ($\mu g.g^{-1}$)	8.13 ± 6.12	4.06 ± 1.80	1.8857	NS
Fucoxanthin 0-0.5 cm ($\mu g.g^{-1}$)	12.5 ± 10.9	1.70 ± 0.53	2.4286	**
Fucoxanthin 0.5-1.0 cm ($\mu g.g^{-1}$)	2.74 ± 2.41	1.54 ± 0.57	1.7838	NS
Zoobenthos 1000 μm				
Diversity (N_0)	3.8 ± 2.6	6.7 ± 2.2	2.3102	*
Total density ($ind.m^{-2}$)	3311 ± 3383	16675 ± 12431	2.7011	**
Total biomass ($g\ AFDW.m^{-2}$)	1.307 ± 1.606	6.689 ± 5.447	2.7011	**
Zoobenthos 500 μm				
Diversity (N_0)	3.6 ±1.0	4.8 ± 1.8	1.6103	NS
Total density ($ind.m^{-2}$)	35567 ± 25391	64405 ± 45028	1.9876	*
Zoobenthos 250 μm				
Diversity (N_0)	4.1 ± 1.2	6.8 ± 1.8	2.5205	*
Total density ($ind.m^{-2}$)	162493 ± 151782	339460 ± 228706	2.1915	*

between 0.26 and 0.43 $N.m^{-2}$ in April and between 0.24 and 0.29 $N.m^{-2}$ in September. Especially at Buitenschoor and Paardenschor the mean values of the critical shear stress for erosion were higher in April than in September, whereas at Galgenschoor the values were similar during both surveys.

Pigment contents

Mean chlorophyll *a* and fucoxanthin contents of the top layer (0-0.5 cm) were about seven times higher in April than in September (Table 8.2). Pigment contents were significantly higher in the surface layer (0-0.5 cm) in April (Wilcoxon matched-pairs Signed-rank test Z= 2.8, p=0.005, n=10), whereas in September contents were similar in both layers.

The spatial variation in pigment contents among the three mudflats was similar in April. The highest contents were 3-4 times bigger than the lowest measured values. The highest pigment contents (surface layer) occurred on the Buitenschoor (26-86 $\mu g\ g^{-1}$ chlorophyll *a* and 10-31 $\mu g\ g^{-1}$

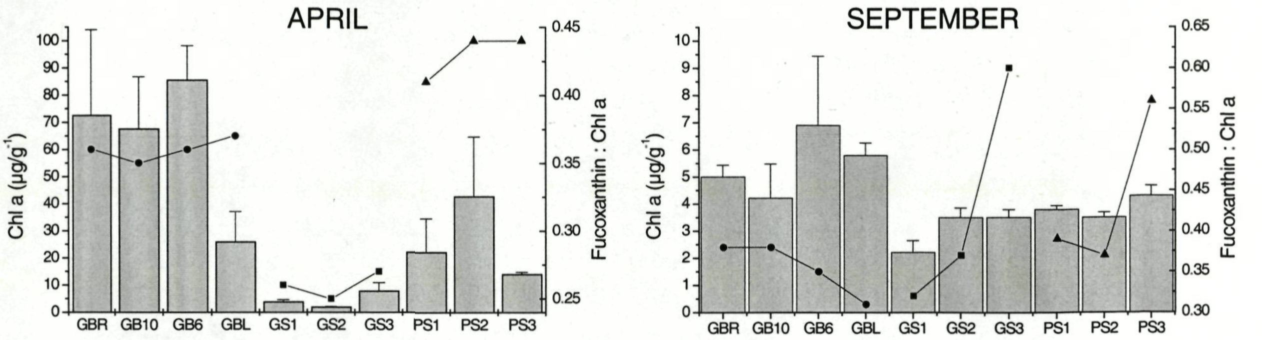

Figure 8.2. Chlorophyll *a* contents (µg.g^{-1}, bars) and ratio of Fucoxanthin to Chl *a* (lines, presented for each mudflat separately) in the top sediment layer (0-0.5 cm) at the ten sampling locations in April and September, respectively. (GB = Buitenschoor, GS = Galgenschoor, PS = Paardenschor). Note the difference in scale between April and September.

fucoxanthin), intermediate ones on the Paardenschor (14-43 µg.g^{-1} and 6-19 µg g^{-1}) and lowest ones on the Galgenschoor (1.8-7.8 µg g^{-1} and 0.5-2.1 µg.g^{-1}) (Figure 8.2). This high spatial variation in pigment contents in April could be linked to the heterogeneity in algae layers observed on the mudflats during the measurements. In September the spatial variation and the pigment contents were much lower. The total range of chlorophyll *a* and fucoxanthin contents on all mudflats was 2.2-6.9 µg g^{-1} and 0.7-2.4 µg g^{-1} respectively. The highest values were found also on the Buitenschoor in September.

The ratio of fucoxanthin to chlorophyll *a* in the 0-0.5 cm layer was different among the mudflats in April, but was relatively constant within each mudflat. The highest ratios were measured on the Paardenschor, indicating the highest diatom dominance. In September the ratios were more comparable among the mudflats, with extreme values at the locations GS3 and PS3 respectively. The ratio of fucoxanthin to chlorophyll *a* in the deeper layer (0.5-1.0 cm) was similar as the one for the top layer.

Characterisation of the zoobenthos

In the 1000 µm fraction of the zoobenthos a total of 13 species were found. *Eteone longa*, *Corophium lacustre*, *Mya arenaria* and *Crangon crangon* were only observed once and at very low densities. Total density and total biomass of the 1000 µm fraction largely varied among the ten locations in both April and September, being highest in both months on Paardenschor, and lowest on Galgenschoor (Figure 8.3a and 8.4). Oligochaeta represented 81 % of the total density observed in April. However, in terms of biomass Oligochaeta were less dominant (Figure 8.4). Mean total diversity (N_0) was significantly higher in September. Density and biomass showed also a significant (5fold) increase. Species dominance then clearly differed among mudflats (Figure 8.3a and 8.4). *Corophium volutator* dominated the community at Buitenschoor (70% and 51% of the total density and biomass, respectively). *Heteromastus filiformis* was more dominant at Paardenschor (60% and 66% of the total density and biomass, respectively). On both mudflats, *M. balthica* and *N. diversicolor* contributed substantially to the total biomass. Lowest densities and biomasses were observed at

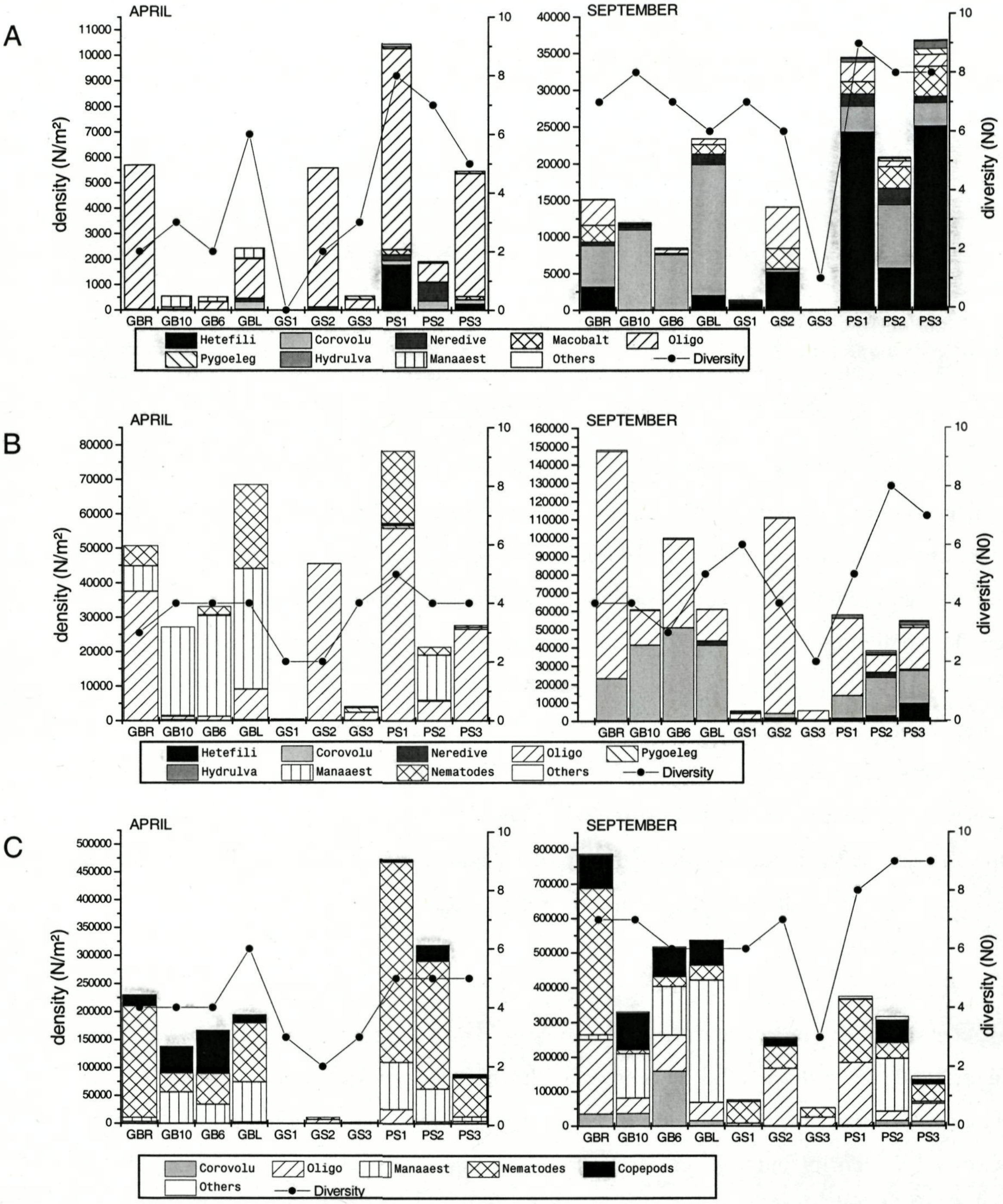

Figure 8.3. Density (N.m^{-2}, bars) and diversity (N_0, line) of the most important zoobenthic species for the 1000 µm (A), 500 µm (B) and 250 µm (C) fractions at the ten sampling locations in April and September, respectively. Note the differences in scale between April and September.

Galgenschoor; only at GS2 values comparable to the other two mudflats were found.

Total density of the 500 µm fraction of the benthos was lowest for Galgenschoor (Figure 8.3b). This fraction of the benthos was mainly dominated by Oligochaeta in April (52% of the total density). *Manayunkia aestuarina* was also a dominant species of the benthic community at Buitenschoor (54%

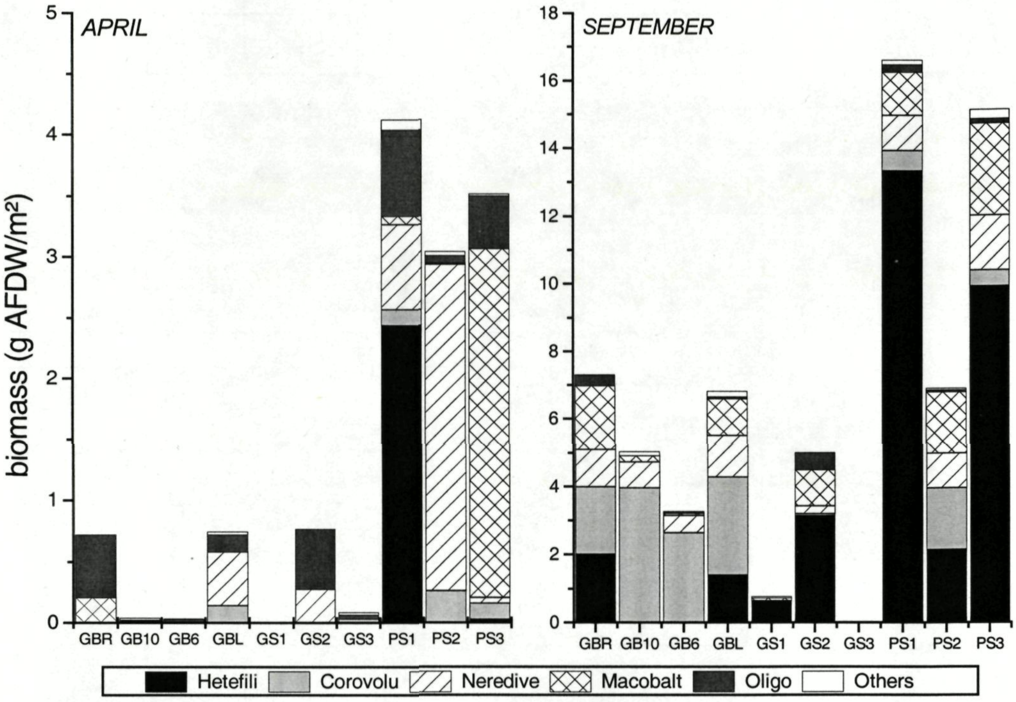

Figure 8.4. Biomass (g AFDW.m^{-2}) of the five most important macrobenthic species for the 1000 μm fraction at the ten sampling locations in April and September, respectively. Note the difference in scale between April and September.

of the total density). At some locations Nematoda appeared in this fraction of the benthos. Mean total density doubled significantly in September as compared to April. Oligochaeta still dominated (62% of the total density), but also other macrobenthic species appeared more frequently, such as *C. volutator*, especially predominantly present at Buitenschoor, *H. filiformis*, *N. diversicolor* and *Hydrobia ulvae*. Hardly any macrobenthic species were found in the 500 μm fraction at the Galgenschoor site. Both *M. aestuarina* and Nematoda were not found in the 500 μm fraction in September.

Total density of the zoobenthos was also lowest for Galgenschoor in the 250 μm fraction (Figure 8.3c). The fraction was dominated by Nematoda in April (65% of the total density), and to a lesser extent by Copepoda and *M. aestuarina*. At Galgenschoor, the 250 μm fraction was nearly devoid of benthos. Mean total density doubled significantly in September, especially at Buitenschoor. This was mainly due to an increase of Oligochaeta and *M. aestuarina*, and also *C. volutator* was observed in this fraction. Copepoda densities increased in September whereas Nematoda densities in general decreased.

Vertical distribution of the zoobenthos

The common species in both seasons mostly belonged to smaller taxa and showed a change in distribution from a higher abundance in the upper layer of the sediment in April towards a deeper distribution in September (Figure 8.5). In April, Oligochaeta from the 250 μm and 500 μm fractions were most abundant in the top 0-1 cm layer of the sediment (about 70%), whereas Oligochaeta from

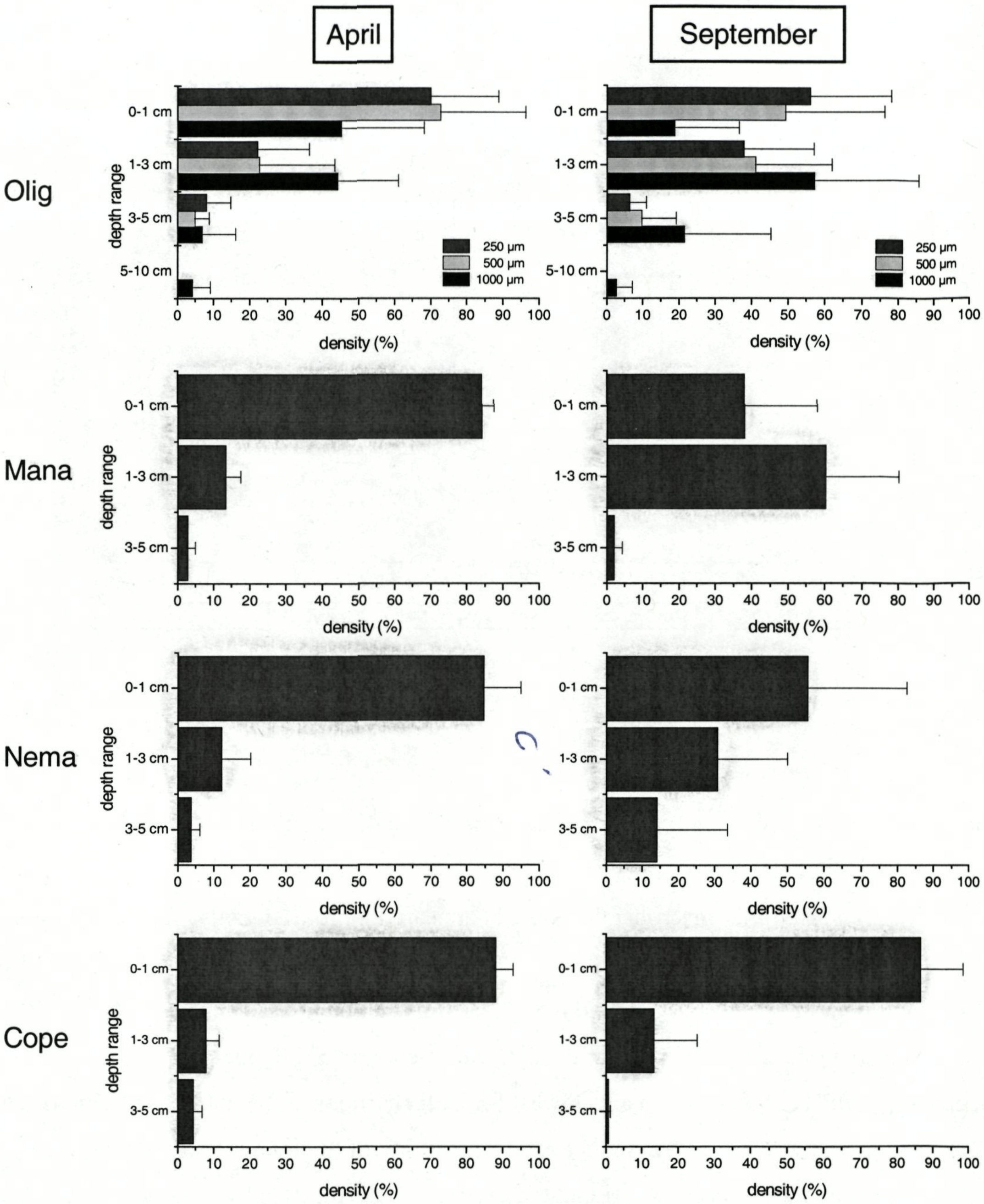

Figure 8.5. Vertical depth frequency distributions (± SD) of Oligochaeta (Olig), *Manayunkia aestuarina* (Mana), Nematodes (Nema) and Copepoda (Cope) in April and September. For Oligochaeta each fraction (250, 500 and 1000 µm) is given, other species based on the 250 µm fraction.

the 1000 µm fraction were equally present in the top 0-1 cm and the 1-3 cm layers (about 45 %). In September, the 1-3 cm layer became relatively more important for all fractions of Oligochaeta. *M. aestuarina* shifted from a 85% occurrence in the top 0-1 cm layer in April towards a 60% occurrence in the 1-3 cm layer in September. Most Nematodes occurred in the top 0-1 cm layer in both months, but in September relatively more individuals also occurred in the deeper layers. Copepoda were found almost exclusively in the upper layer of the sediment in both seasons. The macrobenthic species, that

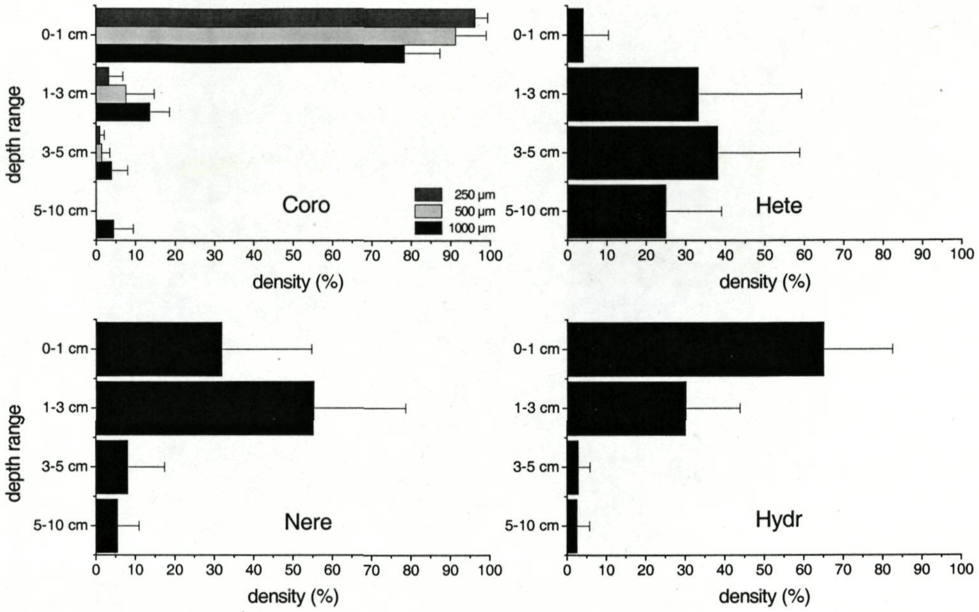

Figure 8.6. Vertical depth frequency distributions (± SD) of the dominant macrobenthic species in September: *Corophium volutator* (Coro), *Nereis diversicolor* (Nere), *Heteromastus filiformis* (Hete), and *Hydrobia ulvae* (Hydr). For *C. volutator* each fraction (250, 500 and 1000 µm) is iven, other species based on the 1000 µm fraction.

Table 8.3. Significant Spearman correlations between biotic and environmental parameters (top 0-0.5 cm sediment layer only) for April (n=10) and September (n=10) means. ***=p<0.005 **=p<0.01 *=p<0.05. Zoobenthic species abundance represents the sum of the three fractions (1000, 500 and 250 µm). (Bulk dens = bulk density of the sediment; Median = median grain size).

	April (n=10)	September (n=10)
Chlorophyll *a*	Fucoxanthin: .99*** Height: .85*** Bulk dens: -.88***	Fucoxanthin: .73* Height: .79**
Fucoxanthin	Chl *a*: .99*** Height: .85*** Bulk dens: -.88***	Chl *a*: .73*
Zoobenthos density 1000 µm	-	-
Zoobenthos biomass 1000 µm	-	Median: -.71* Mud: .62*
Zoobenthos density 500 µm	-	Height: .62*
Zoobenthos density 250 µm	Chl *a*: .66*	Height: .73*
Corophium volutator density	Species nearly absent	Height: .99*** Bulk dens: .83** Chl *a*: .82**
Heteromastus filiformis density	Species nearly absent (except PS1)	Median: -.62*
Oligochaeta density	-	Mud: .66*
Manayunkia aestuarina density	Bulk dens: -.65* Chl *a*: .64* Fucoxanthin: .64*	Height: .86** Bulk dens: .87** Chl *a*: .71*
Copepoda density	Height: .94*** Bulk dens: -.79** Chl *a*: .94*** Fucoxanthin: .94***	Height: .92*** Chl *a*: .62*
Nematodes density		Median: -.67* Mud: .65*

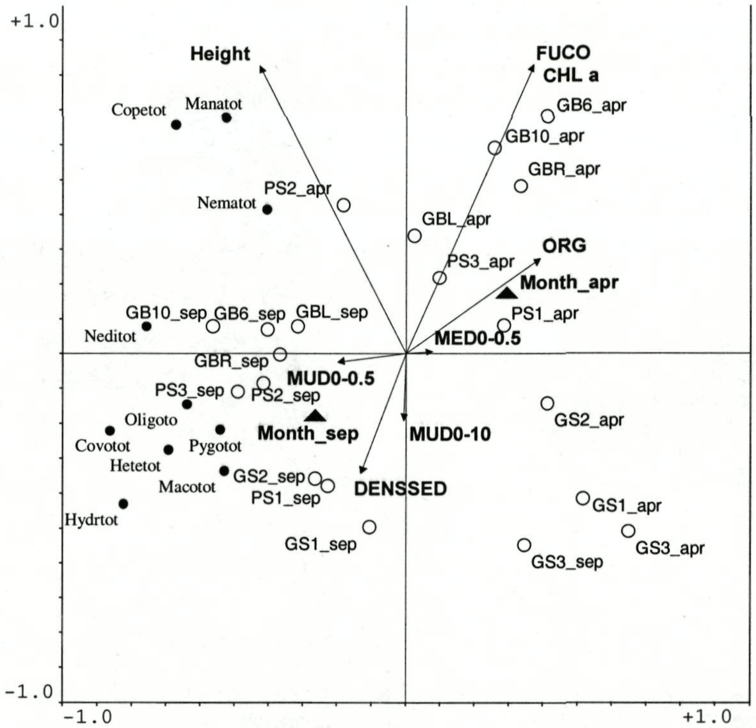

Figure 8.7. RDA ordination diagram showing the spatial and temporal variation of the 20 sampling locations. The first four eigenvalues are 0.49, 0.19, 0.06 and 0.03. Shown are centroids of month (April = Month_apr and September = Month_sep) and environmental variables as arrows. Environmental variables are: height, chlorophyll a and fucoxanthin contents of the 0-0.5 cm layer (CHL *a* and FUCO) mudcontent of the 0-0.5 cm and the 0-10 cm layers (MUD0-0.5 and MUD0-10), median grain size of the 0-0.5 cm layer (MED0-0.5), organic matter (ORG), and bulk density of the sediment (DENSSED). Benthic species are represented by circles and should be interpreted as arrows. Benthic species represents the sum of density of the three fractions (1000, 500 and 250 μm) together. (Copetot = Copepoda; Covotot = *Corophium volutator*; Hetetot = *Heteromastus filiformis*, Hydrtot = *Hydrobia ulvae*; Macotot = *Macoma balthica*; Manatot = *Manayunkia aestuarina*; Nematot = Nematoda; Neditot = *Nereis diversicolor*; Oligotot = Oligochaeta; Pygotot = *Pygospio elegans*).

were only dominant in September, showed a different vertical distribution pattern (Figure 8.6). All fractions of *C. volutator* occurred almost exclusively in the top 0-1 cm layer of the sediment. *H. filiformis* showed a clearly different pattern with higher densities occurring in the deeper layers of the sediment. *N. diversicolor* was mainly present in the top 3 cm of the sediment, especially in the 1-3 cm layer. *H. ulvae* clearly preferred the top layer of the sediment, and was nearly absent deeper than 3 cm.

Relationships between biotic and environmental parameters

In April, both chlorophyll *a* and fucoxanthin contents were strongly positively correlated with each other and with height of the location, and negatively correlated with the bulk density of the sediment (Table 8.3). In September only chlorophyll *a* was positively correlated with height, whereas the correlation between both pigments was less significant.

Some typical benthic species of the top layer of the sediment (Figure 8.5, 8.6) were positively correlated with pigment contents. *C. volutator*, nearly absent in April, showed a very high correlation with height and a high correlation with chlorophyll *a* contents in September. The observed *Corophium* densities were significantly correlated with the decrease in chlorophyll *a* contents between April and

September (Chl a_{apr} - Chl a_{sep}) (r = 0.90, p=0.0003). *M. aestuarina* and Copepod densities were positively correlated with height and pigment contents both in April and September, and also with the chlorophyll *a* decrease (r = 0.68, p=0.03 and r = 0.77, p=0.01 respectively).

The biomass of the macrobenthos was significantly correlated with mud content in September (Table 8.3). *H. filiformis*, Oligochaeta, and Nematoda were significantly more abundant in more muddy sediments in September.

Based on both months together, a significantly positive correlation was observed between critical shear stress for erosion and chlorophyll *a* and fucoxanthin contents (r= 0.61, p=0.004 and r= 0.53, p=0.017 respectively, n=20). Only the GB6 location had deviating results with high pigment contents but relatively low critical shear stresses for erosion.

Our results indicated that sediments with lower bulk density, i.e. a higher mud fraction, generally had a lower critical shear stress for erosion. However, it should be emphasised that the data show considerable scatter within each location, which is related to the measurement procedure itself, to the heterogeneity of the sediments on the mudflats and to the occurrence of organic matter of diverse origin.

Figure 8.7 displays the RDA ordination diagram (triplot) with the major variation in the twenty sampling occasions across space and time. The first two axes of the RDA had eigenvalues of 0.49 and 0.19, respectively, and explained 68% of the species variation. They were both significant by Monte Carlo statistics and represented 85% of the species-environment relation. The positions of the centroids in the diagram for April and September showed that the first axis mainly represented the change with time: all April stations, except PS2, were situated on the right-side, and all September stations, except GS3, on the left-side of the diagram. The second axis mainly represented the change with height and with correlated pigment contents. Since pigment contents clearly had a seasonal variation, the second axis also partly explained the difference between April and September. Benthic species situated in the upper left quadrant were species which were abundant during both months (e.g. *M. aestuarina*, Copepoda, Nematoda), whereas benthic species situated in the lower left quadrant were species which were typically abundant in September.

Discussion

The sediment characteristics (median grain size, mud content and organic matter) of the sampling locations were not significantly different between April and September. Although our observations are limited in time (2 observations), long-term monthly observations at the GBL and GBR locations confirm that no clear seasonal variation of mud content occurs (pers. observ.). This is in contrast to the observed seasonal variation of mud content and fixation of mud during summer on the sand flats in the downstream, polyhaline zone of the Schelde estuary (HERMAN et al. 1999, pers. observ.). The processes involved in the sediment dynamics on the sandflats in the polyhaline zone and the investigated mudflats in the mesohaline zone are equal (i.c. hydrodynamics and biological processes). The clear seasonal differences in mud dynamics found on sandflats and mudflats is thought to be mainly the result of differences in the relative importance of the involved processes. The observation that the mud content is not declining on the investigated mudflats during winter can be explained by the facts that (1) these areas are closer situated to the turbidity maximum zone during winter and thus are flooded by water with a higher averaged suspended sediment concentration, (2) that the suspended sediment concentration is always higher in the mesohaline zone of the Schelde estuary, and (3) that the hydrodynamic conditions are favourable for deposition and formation of mudflats. Another important difference between both intertidal areas is that sand flats are more exposed as they form the transition between ebb- and flood-channels, whereas mudflats are situated along the banks of the estuary and are thus more sheltered. Although no difference in mud content was oberseved between the two sampling months, sedimentation or erosion could have appeared, as was also demonstrated on another intertidal mudflat (DE BROUWER et al. 2000).

Despite the fact that the sediment characteristics were spatially and temporally relatively homogenous among the ten sampling locations, the biological variables (micropythobenthos and zoobenthos) showed substantial spatial and temporal (seasonal) variability.

In April, much higher chlorophyll *a* and fucoxanthin contents were observed as compared to September, which can be attributed to the spring bloom of diatoms on the intertidal mudflats, resulting in a visible microalgal mat, as also observed in the polyhaline zone of the Schelde estuary (DE JONG & DE JONGE 1995; BARRANGUET et al. 1997). The lower pigment contents in September may be ascribed to grazing by benthic invertebrates, as indicated by the relation between the density of some typically surface feeding species (e.g. *C. volutator*) and a decrease in microphytobenthos biomass. Increased grazing by zoobenthos might indeed decrease microalgae populations (MORRISEY 1988; GERDOL & HUGHES 1994a). Chlorophyll levels in intertidal sediments at the Bay of Fundy declined as population size *of C. volutator* increased through summer (HARGRAVE et al. 1983). Besides grazing by macro- and meiofauna, other factors might have caused the lower pigment contents in September, being nutrient limitation, desiccation, or resuspension in the water column (DE BROUWER et al. 2000).

A clear relation with height (exposure time) was observed with highest pigment contents in the upper shore sediments (Buitenschoor mudflat), intermediate contents in the middle shore sediments (Paardenschor mudflat) and lowest contents at the lower shore sediments (Galgenschoor mudflat). This is in accordance with several other observations on intertidal mudflats (e.g. UNDERWOOD & PATERSON 1993; DE JONG & DE JONGE 1995; BARRANGUET et al. 1997). The locations on the Galgenschoor were situated very low in the intertidal zone and therefore flooded most of the time. These sites will experience the stress of light limitation, especially being situated in a high turbidity zone of the estuary (MACINTYRE & CULLEN 1996).

Normally siltier and finer sediments contain more microphytobenthos than sandy sediments (DE JONG & DE JONGE 1995; LUCAS & HOLLIGAN 1999). The more sandy GBL location in April had indeed lower pigment contents as compared to the more muddy locations on the Buitenschoor mudflat (same height). This positive correlation between mud and chlorophyll *a* content is however not necessarily the result of a negative correlation between hydrodynamic energy and chlorophyll *a* as suggested by DE JONG & DE JONGE (1995). The occurrence of certain morphological features like mudflats or sand flats is related to the domination of a group of processes (tidal asymmetry between ebb and flood currents, cohesive sediment transport and characteristics, availability of mud).

The zoobenthos clearly undergoes seasonal variations with low diversity, density and biomass in April (spring) and significantly higher densitiy and biomass in September (autumn). In April the macrobenthic community is mainly dominated by Oligochaeta, whereas in September *C. volutator* and *H. filiformis* dominate. Also in September *N. diversicolor* and *M. balthica* are observed at most locations. The lack of or the very low densities of several macrobenthic species in April can be attributed to the lower salinity conditions in winter and spring in this zone of the estuary, as was also demonstrated by long-term monthly observations at the GBL location (1990-1999, pers. observ.). In estuarine systems with high seasonal variability in river flow rate, the upper estuarine fauna may switch each year between an oligohaline and a mesohaline fauna, with high mortalities in between (e.g. MARCHAND & GASCUEL 1988), which result in communities that seldom progress beyond early benthic-community succession.

In this study sediment characteristics, being similar for most locations, do not explain for the large difference observed in zoobenthic species occurrence. It is argued that the hydrodynamical conditions and the elevation of the sample location can give an explanation for the macrobenthic species occurrence. The higher tidal currents observed at the Galgenschoor sampling locations can result in a higher mud dynamic and thus a less favourable environment for benthos. On the other hand, the elevation of the sampling locations was the main factor controlling the occurrence of microphytobenthos, which is a high-quality food source for several zoobenthic species. Indeed, the presence and quality of food, together with the feeding habits of a benthic species, seems to be a very important factor which determines the occurrence of a benthic species (DAUWE et al. 1998; HERMAN et al. 1999).

Several taxa, common in April and September (mainly smaller species like Oligochaeta, Nematodes and *Manayunkia aestuarina*), showed a shift from a dominant position in the upper layer of the sediment in April towards a more dominant distribution deeper in the sediment in September. This shift could possibly be explained by a shift in feeding habits of these taxa, as is supported by a population study on Oligochaeta at the GBR station in the same period (SEYS et al. 1999a). The latter observed a shift in species composition from a dominance of the Naididae *Paranais litoralis* and *Amphichaeta sannio*, two small, typically surface diatom feeding oligochaete species, in April, to a dominance of the larger tubificids *Heterochaeta costata* and *Tubificoides heterochaetus*, two typically sub-surface 'head-down' deposit feeders in September. Besides feeding habits other factors may have influenced the deeper distribution in September, e.g. the higher surface sediment temperatures in September.

In September the difference in occurrence and vertical distribution of the macrobenthic species reflected the different feeding guilds of the species. *C. volutator* is a typical surface deposit feeder that consumes large numbers of diatoms and bacteria, together with organic material and sediment particles (NIELSEN & KOFOED 1982; MURDOCH et al. 1986; GERDOL & HUGHES 1994b). *C. volutator* almost exclusively occurred in this study in the upper layer of the sediment, where highest chlorophyll *a* contents were present. On the other hand, the polychaete *H. filiformis* occurred deeper in the sediment. *H. filiformis* is known as a typical sub-surface deposit feeder, deriving all its food from sediment ingested in the anaerobic layer below the surface, depositing its faecal pellets at the surface (CADÉE 1979). *M. balthica*, mainly juveniles having a mean length of 3,45 mm (n=367), was situated in the top layer of the sediment. This is in accordance with several studies in which it was demonstrated that small *Macoma* lives at the top layer of the sediment with an increasing depth occurrence with size of the animal (ZWARTS & WANINK 1989; DAVEY & PARTRIDGE 1998). The gastropod *H. ulvae* is a typical grazer, feeding mainly on benthic diatoms (JENSEN & SIEGISMUND 1980) and therefore found in the top layer of the sediment, as also demonstrated by this study. Like *C. volutator*, this species was significantly correlated with chlorophyll *a* contents.

Most studies on macrobenthic communities do not include the fractions smaller than 1000 µm. This study indicated that both 500 and 250 µm fractions where characterised by a high abundance of both meiobenthic and macrobenthic (mainly in September) species. Especially in this zone of the estuary, characterised by meso-/oligohaline salinity conditions, it is important to include these smaller fractions, as the benthic community is often populated here by very small species (e.g. *M. aestuarina*) or immature stages of larger species (e.g. *C. volutator*). It has been shown that for the study of estuarine Oligochaeta, these fractions are essential, since only a small part of the Oligochaeta occur in the 1000µm fraction (SEYS et al. 1999b).

The critical shear stress for erosion of the upper layer of the sediments in this study showed a difference between both surveys and a positive correlation with pigment contents. This is in accordance with a number of field and laboratory studies demonstrating that sediment-inhabiting algae, particularly epipelic diatoms and cyanobacteria, can protect sediment from erosion and stabilise cohesive sediments (HOLLAND et al. 1974; YALLOP et al. 1994) through production of extracellular polymeric substances (GRANT et al. 1986; UNDERWOOD et al. 1995; SMITH & UNDERWOOD 1998). The lower values for critical shear stress for erosion in September might be the result of lower pigment contents (no algal mat present) or of a higher macrofauna activity (LUCKENBACK 1986; DE DECKERE et al. subm.) at that time. In the literature both stabilising as well as destabilising forces are ascribed to macrofauna, in some cases by a single species. For instance, *Corophium volutator* may increase directly sediment stability by binding particles with the secretions used to construct their tubes or burrow walls (MEADOWS & TAIT, 1989; MEADOWS et al. 1990; MOURITSEN et al. 1998). In contrast, GERDOL & HUGHES (1994a) found that *C. volutator* caused destabilisation of the sediment bed due to grazing on microphytobenthos and reworking of the sediment by burrowing and tube formation.

However, in our study the data on the critical shear stress for erosion showed considerable variability within each sampling location, and the relatively low resolution of the SedErode instrument call for a careful interpretation of the results.

Acknowledgements

This study is part of the hydraulic and morphological study of the Deurganck tidal dock, which has been carried out for the Ministry of the Flemish Community, Waterways and Marine Administration. We are grateful for the logistic assistance provided by the Maritime Scheldt division and for the bulk density analyses, which were carried out at Flanders Hydraulics. Thanks to Nico De Regge and Jan Soors for their assistance in the field and the laboratory. We are also grateful to Prof. Dr. M. Vincx and Dirk Van Gansbeke of the University of Ghent, Zoology Institute, Marine Biology Section for the analysis of the pigment contents. We thank Eric de Deckere and Greet De Gueldre for their comments on the manuscript. This study was partly supported by the FWO project G.0104.99.

Chapter nine

Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression

T. Ysebaert, P. Meire, P.M.J. Herman and H. Verbeek

Abstract

The aim of this study is to contribute to the development of statistical models to predict macrobenthic species response to (changes in) environmental conditions in estuarine ecosystems. Ecological response surfaces are derived for ten estuarine macrobenthic species. Logistic regression is applied on a large data set, predicting the probability of occurrence of macrobenthic species in the Schelde estuary as a response to the predictor variables salinity, depth, current velocity and sediment characteristics. Single logistic regression provides good descriptions of the occurrence along one environmental variable. The response surfaces obtained by multiple logistic regression provide estimates of the probability of species occurrence across the spatial extent of the Schelde estuary with a relatively high degree of success. Results from subsampling 50% of the original data ten times indicate final models were stable. A visual, geographical comparison is presented between the mapped probability surfaces to the species occurrence maps.

We conclude that where patterns of distribution are strongly and directly coupled to physicochemical processes, as is the case at the estuarine macro- and meso-scale, our modelling approach was capable of predicting macrobenthic species distributions with a relatively high degree of success, although processes controlling estuarine macrobenthic distribution cannot be determined using this method. The models and predictions might be used for evaluation of the effects of different management schemes within the Schelde estuary.

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what do you need for this?

Introduction

Estuaries are transitional environments between rivers and the sea and are characterised by widely varying and often unpredictable hydrological, morphological and chemical conditions (DAY et al. 1989). For benthic animals with limited mobility (after settlement) this variability represents a

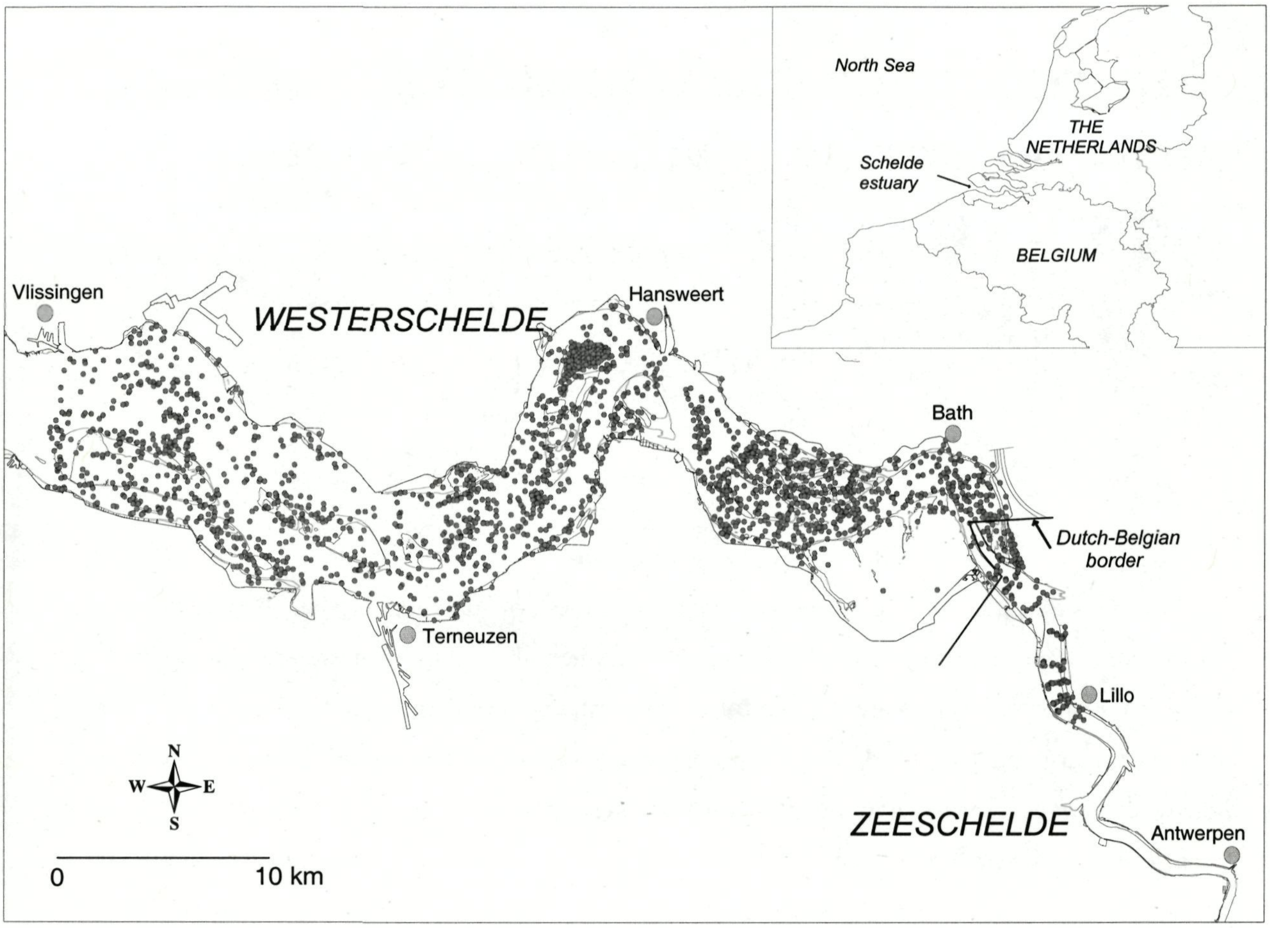

Figure 9.1. Map of the Schelde estuary with sampling locations.

problem with which they have to cope. During their lifetime and at different temporal scales varying from hours (tidal influence) to years, they have to cope with very different conditions of salinity, currents, drying and flooding, temperature, food availability, suspended sediment etc. As a consequence, estuarine benthos can be expected to be composed of eurytope species, for which it is not easy to establish how their occurrence, density or biomass relates to the features of their environment.

A quantitative prediction of the patterns of occurrence of macrobenthic animals in estuaries is a desirable goal for several reasons. Benthic-pelagic links in estuaries are in general very important (HERMAN et al. 1999). Understanding the dynamics of the system requires a quantitative insight in benthic processes, which may be responsible for up to half of the total system mineralisation. Macrobenthos is important in benthic remineralisation processes, both directly as an important component of the system, and indirectly through its structuring effect on the sediment community. Macrofauna is also an important food resource for epibenthic crustaceans, fish and birds. Humans harvest many species of shellfish and crustaceans. Rational management of these resources requires predictive capabilities of the dynamics of the populations.

Evaluation of the consequences of human induced impacts or changes in an estuarine system will likely include the possible responses of the benthos. Nowadays, macrobenthos is often used in monitoring programmes as bioindicator for possible changes in the system. Within this ecological indicator system approach, a lot of studies have investigated the structure of macrobenthic communities in relation to the abiotic environment, coupling the dominance patterns (e.g. ABC method, WARWICK 1986) or functional life-history characteristics (trophic structure) (PEARSON & ROSENBERG 1978; BOESCH & ROSENBERG 1981; GASTON et al. 1998) of the macrobenthos to human impacts. But within coastal marine and estuarine ecosystems little attempts have been made to statistically model the responses of individual macrobenthic species to environmental variables on a large, e.g. estuarine scale and use these models to predict the distribution and occurrence of macrobenthos (CONSTABLE 1999). However, there are increasing demands for reliable and quantitative predictive tools. On the one hand, these are required to interpret *post-hoc* any changes that have been observed in the benthic community. A quantification of species preferences and tolerances to environmental conditions may help to understand and establish system properties. On the other hand, they are needed to predict future species response to anticipated changes in environmental conditions.

The aim of this study is to contribute to the development of statistical models to predict macrobenthic species response to (changes in) environmental conditions in estuarine ecosystems. In this paper so-called response curves and surfaces are fitted through mathematical relations (SWAN 1970; AUSTIN 1987) obtained by logistic regression. The advantage of logistic regression is that the probability of occurrence of an event can be predicted as a function of one or more independent variables (HOSMER & LEMESHOW 1989; TREXLER & TRAVIS 1993). Logistic regression has been applied in many ecological studies, e.g. in vegetation analysis (HUISMAN et al. 1993; LENIHAN 1993; VAN DE RIJT et al. 1996) and bird and wildlife species distributions (OSBORNE & TIGAR 1992; BUCKLAND & ELSTON 1993; VENIER et al. 1999). In the field of marine and estuarine animal ecology this technique has hardly been used.

In our approach physicochemical factors, acting at different spatial scales, are used as predictors for the occurrence of several macrobenthic species. The realised environmental niches of estuarine macrobenthic species are thus defined and validated. The next step will be to investigate the possibility of using the models for evaluation of the effects of different management schemes and to investigate the applicability of the models in other estuarine systems.

Materials and methods

Study area

The Schelde estuary, a turbid, nutrient-rich, heterotrophic system, measures 160 km from the mouth near Vlissingen (The Netherlands) to Gent (Belgium) and is one of the longest estuaries in NW-Europe with still a complete salinity gradient. The study area is limited to the Westerschelde (Dutch part) and a small part of the Zeeschelde (Belgian part) near the Dutch-Belgian border (Figure 9.1), comprising the complete polyhaline and mesohaline zone of the estuary. The mean tidal range increases from 3.8 m at Vlissingen to 5.0 m near the border. The river discharge varies from 20 m^3s^{-1} during summer to 600 m^3s^{-1} during winter, with a mean yearly average of 105 m^3s^{-1} (BAEYENS et al. 1998). The residence time of the water in the estuary is rather high, ranging from one to three months, depending on the river discharge (SOETAERT & HERMAN 1995b). The most seaward region has a residence time of about 10-15 days.

The lower and middle estuary, called the Westerschelde (55 km), is a well mixed region characterised by a complex morphology with flood and ebb channels surrounding several large intertidal flats and salt marshes. The surface of the Westerschelde amounts to 310 km^2, with the intertidal area covering 35%. The average channel depth is approximately 15-20 m. In the lower and middle estuary a multiple channel equilibrium exist and upstream of the Dutch/Belgian border, the estuary is characterised by a single channel. The turbidity maximum is situated in this region of the estuary but moves over a quite large distance, depending among others on the tidal action and river run off (BAEYENS et al. 1998). Nowadays, dredging activities for shipping and pollution are the major anthropogenic stressors. About 8-12 million m^3 of sediment is dredged yearly to keep the port of Antwerpen accessible. For more details on the ecological and physicochemical properties of the estuary see MEIRE & VINCX (1993), HEIP & HERMAN (1995), BAEYENS et al. (1998), HERMAN & HEIP (1999) and VAN DAMME et al. (subm.).

Macrobenthos data

An extensive data set on macrobenthos is available for the Schelde estuary. A total of 3112 macrobenthos samples, mainly within the framework of monitoring programmes, were collected in the study area by different institutes in the period 1978-1997. By far most data were collected and analysed by two institutes, namely the Centre for Estuarine and Coastal Ecology NIOO-CEMO (e.g. CRAEYMEERSCH et al. 1996; BRUMMELHUIS et al. 1997; CRAEYMEERSCH 1999) and the Institute of Nature Conservation (before that at the University of Gent) (e.g. YSEBAERT & MEIRE 1991, 1998; DE NEVE et al. 1998), mainly in co-operation with the National Institute for Marine and Coastal Management (RWS-RIKZ). 90% of the samples were collected from 1990 onwards. 54% were taken in autumn (September-October), 32% in spring (March-April-May). Most sampling locations (68%) were sampled only once, but several locations were sampled two to five times in the sampling period considered, and a few were sampled more frequently within a long term programme.

In general multiple sediment cores were used for sampling the intertidal zone, and either a Van Veen grab or a Reineck box corer for the subtidal zone. All samples were sieved on a 1 mm mesh. For more details on the sampling methods and the design of the monitoring programmes we refer to MEIRE et al. (1991), YSEBAERT et al. (1993) and CRAEYMEERSCH (1999).

Abiotic variables

For each sample the following abiotic environmental variables were added to the macrobenthos database: depth/elevation, salinity, current velocities (maximum ebb and flood current velocities), sediment characteristics (median grain size and mud content). At subtidal stations depth was recorded at the time of sampling. The elevation of the intertidal stations was measured directly in the field or from a Geographical Information System, storing all bathymetric data in the area. For 2874 samples (92%) depth was added in the database. Depth is expressed in m NAP (NAP, Dutch Ordnance level, similar to Mean Sea Level).

Salinity was estimated for each sampling location using a 2Dh-hydrodynamic model SCALDIS400 (LIEVENSE 1994) with a spatial resolution of 400 meter. The model calculations are based on values for mean tidal conditions with a yearly averaged discharge, giving an average salinity value. The advantage of using the SCALDIS400 model is that a high spatial resolution is obtained but the estimates are not seasonally defined. Therefore also monthly to fortnightly measurements at nine stations along the Westerschelde were used to represent the temporal variation in salinity, but at a much coarser spatial resolution than model salinity. For each sample the temporal salinity was determined as the average salinity of the three months previous to the date of sampling. Estimates obtained from model simulations are called 'model salinities', whereas the values derived from field observations are called 'temporal salinities'.

Current velocities (maximum ebb and flood current velocities in $m.s^{-1}$) for each sampling location were estimated with the SCALDIS100 model (DEKKER et al. 1994) for mean tidal conditions, with a spatial resolution of 100 meter. For 3037 samples (98 %) current velocity estimates were added to the database.

Samples for sediment grain size analysis (by laser diffraction technique) were collected during several campaigns. For 1502 and 1386 samples (48 % and 45%) median grain size and mud content (volume % < 63 μm) values were added to the database respectively.

Statistical analysis

Logistic regression (COX 1970; HOSMER & LEMESHOW 1989; TREXLER & TRAVIS 1993; JONGMAN et al. 1995) falls within the general framework of Generalized Linear Models (GLM) (NELDER & WEDDERBURN 1972; MCCULLAGH & NELDER 1989) and can be used to analyse the relationship between a binary response variable and one or more explanatory variables. Logistic regression is used here to model the response of twenty macrobenthic species occurrence to the abiotic environmental predictors. The choice of using binary (presence/absence) data was inspired by the fact that the data could not be considered as homogeneously collected. Different sampling methods, different sampling months (seasonality) and years (long-term fluctuations) certainly affected the observed variation in density and biomass data. To minimise this variation presence-absence data were used. Indeed, the presence-absence of most macrobenthic species appeared to be much less seasonally differentiated as compared to density and biomass (YSEBAERT et al. in prep.). As many species were often found accidentally, we decided to treat densities < 50 N.m^{-2} as absences (0) for most species (except for *Arenicola marina* and *Nephtys cirrosa*).

In the logistic regression model, a binary response variable is related to one or more predictor variables through the logistic link function:

$$\text{logit}\ \{p(x)\} = \log\ \{p(x)\ /\ 1-p(x)\} = b_0 + b_1x + b_2x^2 \qquad (1)$$

e

where $p(x)$ is the probability that the species occurs as a function of an environmental variable x and b_0, b_1, b_2 are the regression parameters. Equation (1) can be rewritten to define the estimated probability $p(x)$ as

$$p(x) = \{e^{(b0 + b1x + b2x^2)}\}\ /\ \{1 + e^{(b0 + b1x + b2x^2)}\} \qquad (2)$$

which is bound between 0 and 1.

The logistic link means that the probability of a species occurring is a logistic, s-shaped function when the linear predictor is a first-order polynomial, but for higher polynomials the predicted probability function will be more complex. For second-order polynomials it will approximate a bell-shaped function (Gaussian logit curve), which is an ecologically realistic response (TER BRAAK & LOONMAN 1986). Although skewed and more complex response curves can theoretically occur, they cannot be fitted with the GLM approach. Generalized additive models were developed for this purpose but were not used in this study (e.g. BIO et al. 1998). In this study, a response surface for each macrobenthic species on each of the independent variables was generated by logistic regression with the statistical package SAS (SAS Inst. Inc. 1985). The regression parameters were estimated using the maximum likelihood method, assuming binomially distributed errors. The global model significance, as well as the significance of the different regression parameters, was tested using the –2lnL statistic based on the χ^2-test ($p<0.05$), where L is the maximized likelihood. Besides response curves for each single abiotic variable separately, also all variables were simultaneously used in a stepwise multiple logistic regression analysis to derive a multivariate model that would predict the presence or absence of macrobenthic species. Negative depth values, ranging from –56.4 to +2.2 m, were replaced by positive values by changing sign (value*-1) and adding 2.5 m. Since sediment characteristics were only available for a limited set of data, the analyses were run separately without (n=2827) and with (n=1423) sediment data, hereafter called data set A and data set B respectively. The significance of the independent variables was tested using the χ^2-test ($p<0.05$) on the Wald statistic.

The resulting set of regression equations was validated internally. As a measure of classification accuracy the percentage of concordant pairs was used (a pair is concordant if the observation with larger ordered value of the response has a higher predicted event probability than does the observation with the smaller ordered value of the response). The predictive success of the response surfaces was further evaluated by cross tabulating observed and predicted responses (2x2 contingency table). The threshold at which this evaluation was made was determined by choosing that p-level which corresponded with the actually observed ratio between absences and presences. At p-values below that threshold the species was predicted to be absent, whereas at p-values above that threshold the species was predicted to be present. Besides the overall percentage correctly predicted, we examined also the *sensitivity* (the proportion of presences that were predicted to be presences) and *specificity* (the proportion of absences that were predicted to be absences). The probability of the observed contingency table occurring by random chance, given the row and column totals, was calculated with the Fisher's Exact Test. The Fisher's exact test consists of calculating the actual probability of the observed 2x2 contingency table with respect to all other possible 2x2 contingency tables with the same column and row totals. The hypothesis was tested if the proportion of presences predicted as present was greater than the proportion of absences predicted as present.

The ability of the final models to predict the probability of occurrence was evaluated by randomly splitting the data (from data set A) into two equal groups, building the model with the chosen variables using half of the data. We conducted ten such runs with ten different splits of the data on each species. Firstly, we tested these ten model runs, based on the random selections of 50 % of the data, for consistency of their prediction. For each species model we generated random sets of abiotic conditions, by generating 1000 uniformly distributed random numbers. For each species, ranges for the environmental variables were chosen relative to their observed distribution. For example, for the cockle *Cerastoderma edule* numbers varied in the ranges 10-30, 7-33, 0-20, 0-1 and 0-1.1 for model salinity, temporal salinity, depth, maximum ebb and maximum flood current velocity respectively. Temporal salinity was forced to be in a range of +/- 3 of model salinity, and maximum flood current velocity likewise was selected in the range of +/- 0.1 $m.s^{-1}$ of maximum ebb current velocity. We then generated predicted p-values for the 10 models, which were compared mutually. Secondly, we tested the predictions with the other half of the data sets by examining the overall percentage correctly predicted, the sensitivity and specificity for each of the ten data sets. This procedure examines the ability of the model to predict the occurrence of the species for locations that are not included in the model and is therefore a more rigorous test of classification accuracy.

Table 9.1. Environmental variables with numbers of observations, median, minimum and maximum values.

Variable		Observations	Median	Minimum	Maximum
Model salinity	psu	3112	22.3	5.69	31.61
Temporal salinity	psu	3112	19.1	1.15	32.39
Depth	NAP	2874	-2.9	-56.4	+2.2
Maximum ebb current velocity	$m\ s^{-1}$	3037	0.60	0.01	1.64
Maximum flood current velocity	$m\ s^{-1}$	3037	0.64	0.01	1.61
Median grain size	µm	1502	162	16	664
Mud content (< 63 µm)	%	1386	7.0	0	95.45

For ten contrasting macrobenthic species results are presented in detail: the polychaetes *Heteromastus filiformis, Pygospio elegans, Nereis diversicolor, Nephtys cirrosa, Spio spec.* and *Arenicola marina*, the molluscs (bivalves) *Macoma balthica* and *Cerastoderma edule,* and the crustaceans (amphipods) *Bathyporeia spec.*and *Corophium volutator.* These species represent different types of distribution and are indicator species for the macrobenthic assemblages found in the Schelde estuary, contributing substantially to the total density and biomass observed (YSEBAERT & MEIRE 1999; YSEBAERT et al. 1993, 1998a, in prep.).

For *M. balthica*, *C. edule*, *C. volutator* and *N. cirrosa* also a visual, geographical comparison is presented between the mapped probability surfaces to the species occurrence maps.

Results

Characterisation of the abiotic environment

Average model salinity, based on model calculations, varied between 5.7 and 31.6 for the whole study area (Table 9.1). Most samples (60%) were situated in the polyhaline zone (salinity >18), 31% in the α-mesohaline zone (salinity 10-18) and 15% in the β-mesohaline zone (salinity 5-10). The depth ranged between –56.4 m NAP and +2.2 m NAP. About 50% of the sampling occasions were situated in the intertidal zone (> -2 m NAP). Most of the subtidal samples (68%) were situated above –10 m NAP. Maximum ebb and flood current velocities varied between 0.01 and 1.64 $m.s^{-1}$, with a mean of 0.64 $m.s^{-1}$. 11 % of the samples had current velocities <0.25 $m.s^{-1}$, 27 % between 0.25-0.5 $m.s^{-1}$, 24 % between 0.50-0.75 $m.s^{-1}$, 22 % between 0.75-1.00 $m.s^{-1}$ and 16 % >1.00 $m.s^{-1}$. Median grain size varied between 16 and 664 µm, with a mean of 165 µm. Mud content varied between 0 and 95 %, with a mean of 19%. 13 % of the samples were characterised as muddy (median grain size in range 2 - 63 µm), 19 % as very fine sand (63-125 µm), 54% as fine sand (125-250 µm) and 15% as medium sand (250-500 µm). More details on the abiotic environment of the same data set as used in

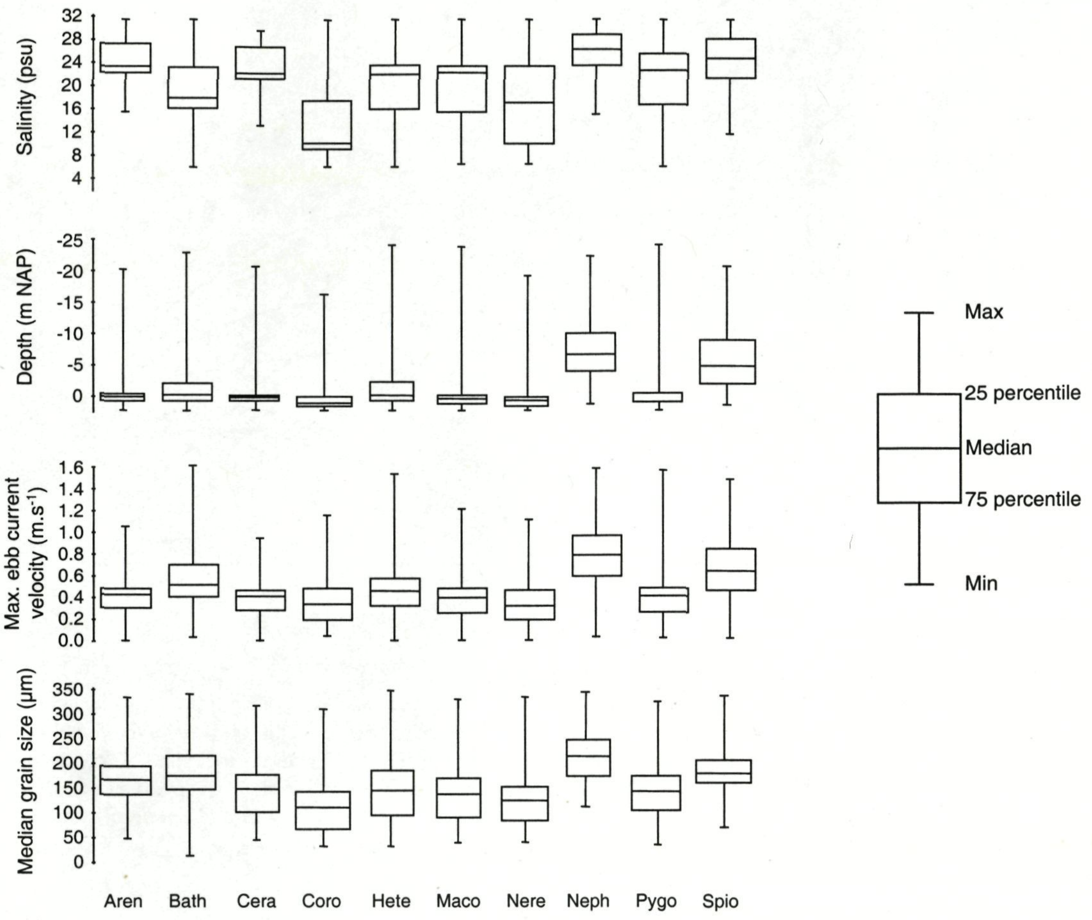

Figure 9.2. Boxes and Whisker plots for ten macrobenthic species with respect to (model) salinity, depth, maximum ebb current velocity and median grain size in the Schelde estuary. Species are ordered alphabetically: *Aren = Arenicola marina, Bath = Bathyporeia spec., Cera = Cerastoderma edule, Coro = Corophium volutator, Hete = Heteromastus filiformis, Maco = Macoma balthica, Nere = Nereis diversicolor, Neph = Nephtys cirrosa, Pygo = Pygospio elegans, Spio = Spio spec.*

this paper can be found in YSEBAERT & MEIRE (1999) and YSEBAERT et al. (in prep.).

Observed distributions of macrobenthic species along environmental variables

In Figure 9.2 the observed distribution of ten macrobenthic species along the environmental variables salinity, depth, maximum ebb current velocity and median grain size is presented by means of box and whisker plots. Characteristic polyhaline species, such as *A. marina*, *C. edule*, *N. cirrosa* and *Spio spec.* clearly distinguished from mesohaline species such as *C. volutator and N. diversicolor*, although the latter had a very wide range of occurrence. Species like *Bathyporeia spec.*, *H. filiformis*, *M. balthica* and *P. elegans* take intermediate positions. With respect to depth, most species were observed mainly in the intertidal zone. Only *N. cirrosa* and *Spio spec.* were typically subtidal species, and *Bathyporeia spec.* and *H. filiformis* appeared to be present both in the intertidal and the subtidal zone.

Most species had a median occurrence between 0.3 and 0.5 m.s^{-1} for maximum ebb current

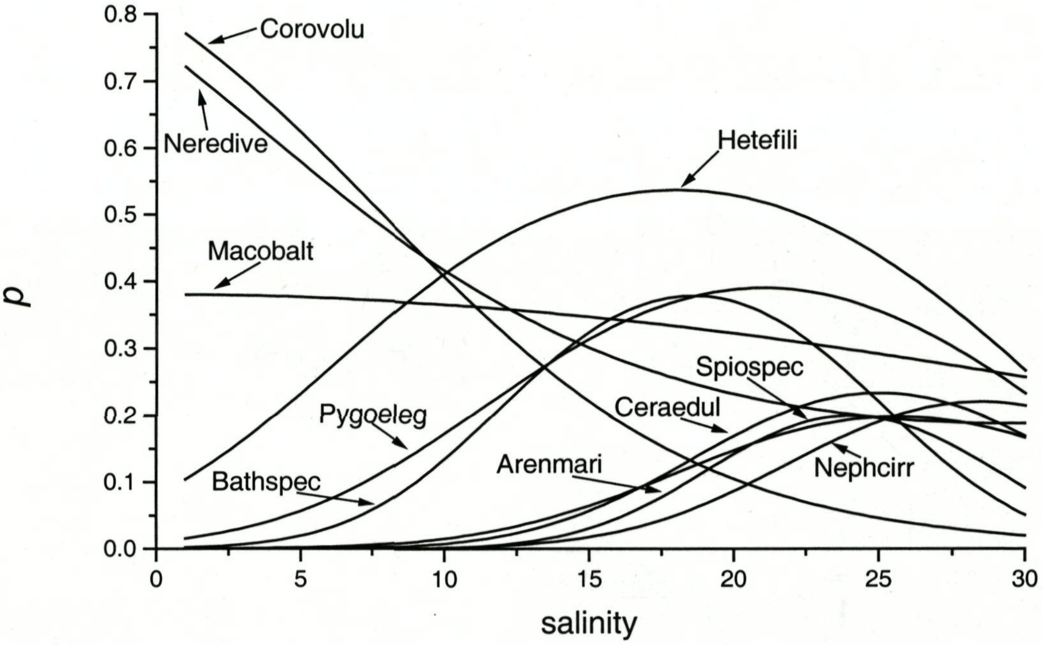

Figure 9.3. Probability of occurrence of ten macrobenthic species in relation to (model) salinity (psu) in the Schelde estuary, as fitted with logistic regression (p= species probability of occurrence). Species abbreviations are: Hete fili = *Heteromastus filiformis*; Maco balt = *Macoma balthica*; Pygo eleg = *Pygospio elegans*; Bath spec = *Bathyporeia* spp.; Cera edul = *Cerastoderma edule*; Neph cirr = *Nephtys cirrosa*; Nere dive = *Nereis diversicolor*; Coro volu = *Corophium volutator*; Spio spp.; Aren mari = *Arenicola marina*.

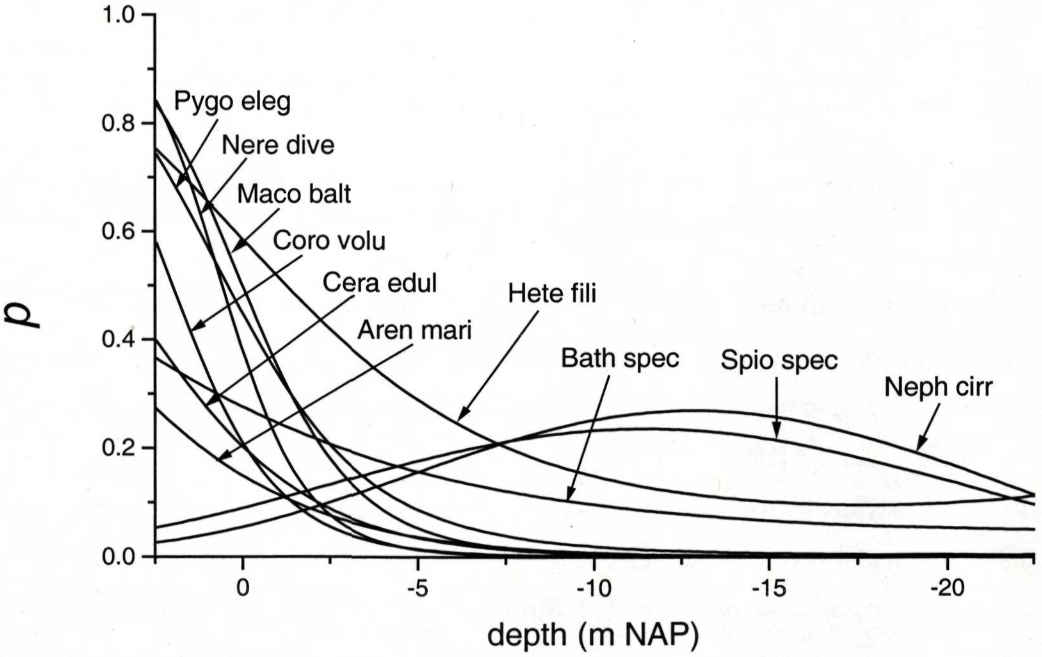

Figure 9.4. Probability of occurrence of ten macrobenthic species in relation to depth (m NAP) in the Schelde estuary, as fitted with logistic regression (p= species probability of occurrence). For species abbreviations: see Figure 9.3.

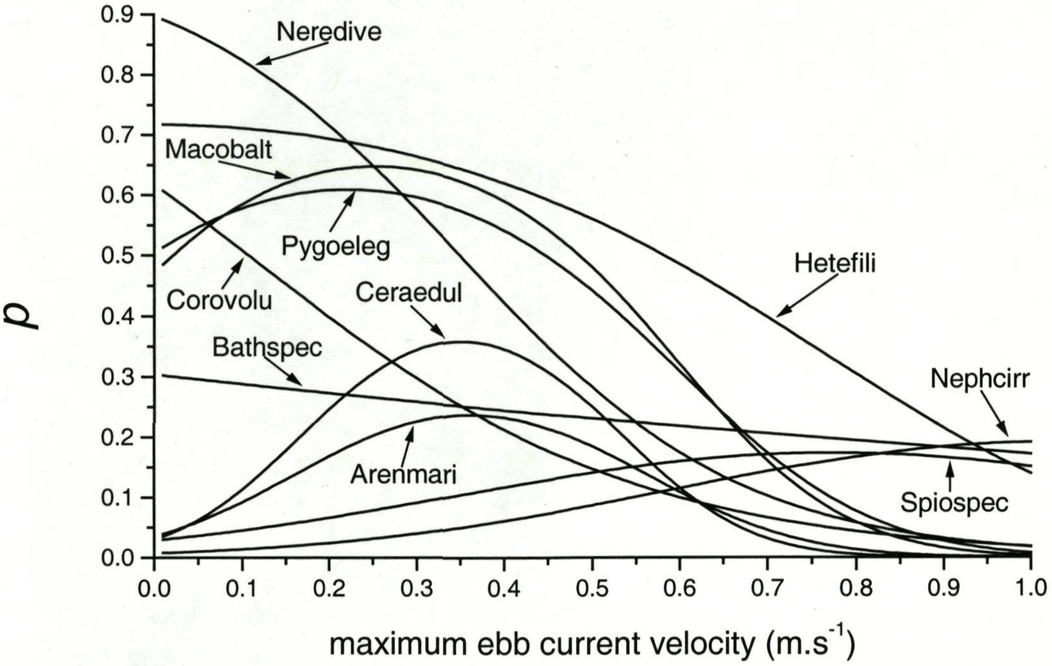

Figure 9.5. Probability of occurrence of ten macrobenthic species in relation to maximum ebb current velocity (m.s^{-1}) in the Schelde estuary, as fitted with logistic regression (p= species probability of occurrence). For species abbreviations: see Figure 9.3.

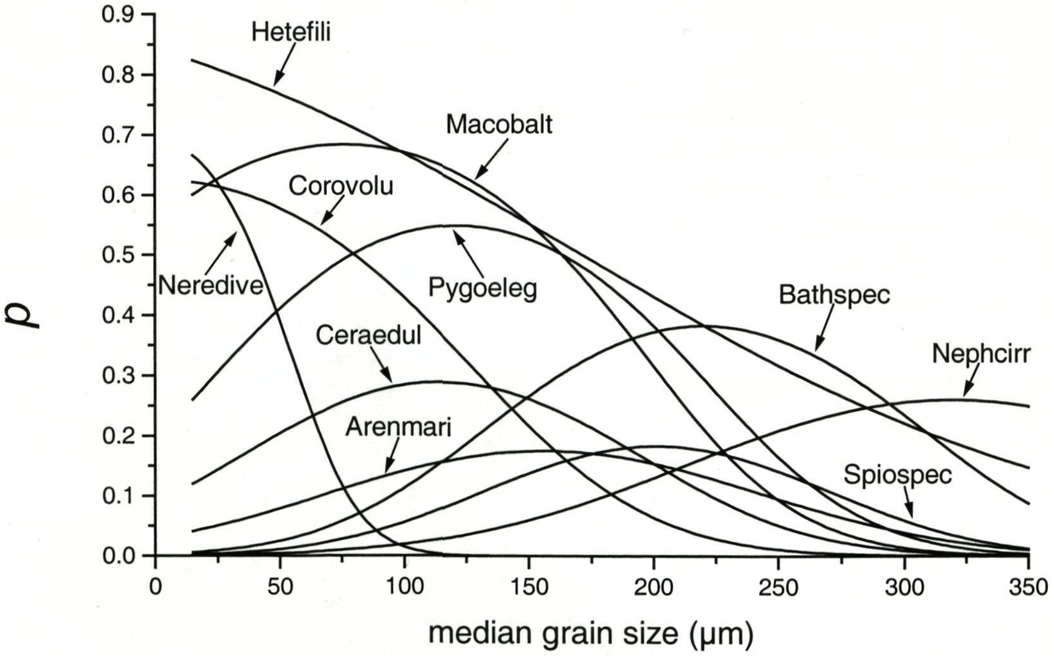

Figure 9.6. Probability of occurrence of ten macrobenthic species in relation to median grain size (μm) in the Schelde estuary, as fitted with logistic regression (p= species probability of occurrence). For species abbreviations: see Figure 9.3.

Table 9.2. Diagnostics for final multiple logistic regression models for each of ten macrobenthic species for the data set without sediment data (data set A) and the data set with sediment data (data set B). See Appendix 9.1 for the variables included in each model. Species abbreviations are: Hete fili = *Heteromastus filiformis*; Maco balt = *Macoma balthica*; Pygo eleg = *Pygospio elegans*; Bath spec = *Bathyporeia* spp.; Cera edul = *Cerastoderma edule*; Neph cirr = *Nephtys cirrosa*; Nere dive = *Nereis diversicolor*; Coro volu = *Corophium volutator*; Spio spp.; Aren mari = *Arenicola marina*.

[illegible]

1 − B×100 / A

Diagnostics

Data set A	*Hete fili*	*Maco balt*	*Pygo eleg*	*Bath* spp.	*Cera edul*	*Neph cirr*	*Nere dive*	*Coro volu*	*Spio* spp.	*Aren mari*
# Present	1164	820	773	583	352	339	660	394	304	269
# Absent	1663	2007	2054	2244	2475	2488	2167	2433	2523	2558
A Intercept only (-2 Log L)	3831	3405	3317	2877	2125	2074	3072	2283	1930	1777
B Intercept + covariates (-2 Log L)	2897	1915	1965	2356	1176	1623	1581	1210	1485	1214
Chi-square	952	1490	1352	521	949	451	1491	1074	445	563
DF	8	6	7	7	9	6	6	5	6	8
Probability	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Concordant pairs	92.9 %	91.1 %	90.3 %	79.1 %	93.0 %	82.2 %	82.3 %	92.5 %	83.6 %	88.8 %
p-treshold	0.51	0.61	0.50	0.38	0.42	0.32	0.47	0.33	0.29	0.35
% correctly predicted	75.2 %	85.5 %	85.6 %	78.1 %	90.0 %	84.0 %	88.3 %	90.2 %	87.8 %	89.5 %
Sensitivity	69.9 %	75.0 %	75.7 %	46.8 %	59.9 %	33.3 %	75.0 %	64.7 %	43.1 %	44.6 %
Specificity	80.0 %	89.8 %	90.8 %	86.2 %	94.3 %	90.9 %	92.4 %	94.3 %	93.1 %	94.2 %
Fisher exact-test: 1-tailed p	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

Diagonstics

Data set B	*Hete fili*	*Maco balt*	*Pygo eleg*	*Bath* spp.	*Cera edul*	*Neph cirr*	*Nere dive*	*Coro volu*	*Spio* spp.	*Aren mari*
# Present	686	562	492	331	232	102	454	313	169	172
# Absent	607	731	910	962	1061	1191	839	1089	1124	1121
Intercept only (-2 Log L)	1788	1770	1817	1471	1217	714	1676	1489	1003	1014
Intercept + covariates (-2 Log L)	1091	770	990	1044	679	449	896	750	604	620
Chi-square	696	1000	827	427	538	264	780	739	399	394
DF	12	8	7	7	7	6	8	5	8	8
Probability	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Concordant pairs	89.2 %	91.7 %	91.5 %	85.3 %	92.0 %	91.1 %	94.0 %	92.7 %	91.0 %	90.8 %
p-treshold	0.56	0.61	0.35	0.46	0.42	0.19	0.50	0.36	0.42	0.36
% correctly predicted	81.4 %	87.3 %	79.7 %	80.8 %	87.5 %	91.8 %	75.9 %	88.9 %	89.8 %	86.9 %
Sensitivity	82.5 %	85.4 %	71.1 %	62.5 %	65.1 %	48.0 %	65.6 %	75.1 %	60.9 %	50.6 %
Specificity	80.2 %	88.8 %	84.4 %	87.1 %	92.4 %	95.6 %	81.4 %	92.8 %	94.1 %	92.4 %
Fisher exact-test: 1-tailed p	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

velocity, with lowest values observed for *C. volutator* and *N. diversicolor*. Only *N. cirrosa* and *Spio spec.* had a median occurrence at much higher current velocities. For maximum flood current velocity similar results were obtained. *C. volutator* and *N. diversicolor* were observed mainly in very fine sand sediments, whereas *Spio spec.* and especially *N. cirrosa* were observed in coarser sediments.

Response curves for a single environmental (explanatory) variable

As an example of the obtained response curves for a single abiotic variable, Figures 9.3-9.6 show the fitted Gaussian logit curves for the ten macrobenthic species in relation to model salinity, depth, maximum ebb current velocity and median grain size. For all species at least one regression parameter was significantly entered in the different models by forward selection. The obtained response curves were in general agreement with the observed distributions from Figure 9.2.

Species like *C. volutator* and to a lesser extent also *N. diversicolor* showed a high probability of occurrence at low salinity (Figure 9.3). For *C. volutator* a steep decrease of the curve was observed with increasing salinity, whereas for *N. diversicolor* the decrease in the curve was much smoother, indicating that the species could also be observed at higher salinity. *Bathyporeia spec.* showed a bell-shaped curve with an optimum at intermediate salinities. Both at the lower end and at the upper end of the salinity range the probability of occurrence of this species decreased. Several species, like e.g. *C. edule, Arenicola marina, Spio spec.* and *N. cirrosa*, showed a clear optimum towards the higher end of the salinity range. These species differed in the position of their optimum, and in their tolerance towards the lower end of the salinity range. *M. balthica* showed an almost horizontal curve, indicating a very broad tolerance for salinity. Another species showing a broad tolerance for salinity was *H. filiformis*. In general 'temporal salinity' gave similar results as 'spatial salinity'.

The response curves in relation to depth showed for most macrobenthic species (e.g. *N. diversicolor, C. volutator, P.elegans, C. edule*) similar curves, with high probabilities of occurrence above NAP, and decreasing probabilities of occurrence with increasing depth (Figure 9.4). These species differed in their tolerance towards the deeper end of the depth range. *H. filiformis*, for instance, showed a relatively high tolerance with still a relatively high probability of occurrence in the subtidal zone. *Bathyporeia spec.* showed only a slightly higher probability of occurrence in the intertidal zone, indicating a very broad depth tolerance. Species showing an optimum in the subtidal zone of the estuary were *N. cirrosa* and *Spio spec.*

Species like *C. volutator* and *N. diversicolor* showed the highest probability of occurrence at the lowest ebb current velocities (Figure 9.5). Other species like *M. balthica* and *P. elegans* showed a broad tolerance in the range 0-0,5 m.s^{-1}, after which a steep decline was observed in the probability of occurrence with increasing current velocities. This broad tolerance was even more pronounced for *H. filiformis*, which only showed a decrease of the probability of occurrence at the highest current velocities. *Bathyporeia spec.* on the other hand showed an almost horizontal curve, indicating that current velocity did not discriminate well for this species. Several species showed a unimodal, bell-

Table 9.3. Summary of classification diagnostics for 50% of data (based on data set A, n=2827) used to build models. 50% of data was resampled ten times to create ten sets of data to build models (a) and ten sets of data to test models (b). Standard deviation is in brackets. Consistency of the ten model runs (a) for each species was tested on random sets of abiotic conditions, by generating 1000 uniformly distributed random numbers. The generated predicted p-values for the ten model runs were compared mutually and the range of the linear correlation coefficients between all pairs is presented.

Species	Correlation between 10 model runs	Mean concordance	Threshold p	% correctly predicted	Sensitivity	Specificity
(a) Model fitting data						
Heteromastus filiformis	0.976-0.999	82.4 (0.75)	0.50 (0.015)	75.5 (0.69)	70.0 (1.28)	79.3 (0.68)
Macoma balthica	0.968-0.998	91.2 (0.56)	0.59 (0.014)	85.9 (0.54)	75.4 (1.55)	90.1 (0.42)
Pygospio elegans	0.889-0.998	90.5 (0.78)	0.50 (0.010)	86.3 (0.76)	74.9 (1.77)	90.6 (0.56)
Bathyporeia spec.	0.979-0.999	79.2 (0.91)	0.38 (0.011)	77.7 (0.97)	47.2 (2.53)	85.9 (0.66)
Cerastoderma edule	0.895-0.991	92.8 (0.41)	0.41 (0.020)	89.9 (0.90)	59.1 (2.73)	94.2 (0.54)
Nephtys cirrosa	0.889-0.996	82.4 (0.70)	0.32 (0.018)	84.1 (0.80)	34.3 (2.11)	91.0 (0.51)
Nereis diversicolor	0.958-0.998	93.0 (0.43)	0.43 (0.012)	87.7 (0.88)	66.0 (4.63)	92.7 (0.49)
Corophium volutator	0.963-0.999	92.3 (0.76)	0.33 (0.012)	90.3 (1.18)	64.5 (2.08)	94.2 (1.32)
Spio spec.	0.973-0.999	83.5 (1.08)	0.29 (0.015)	87.4 (0.90)	42.1 (3.10)	93.0 (0.53)
Arenicola marina	0.889-0.994	88.6 (0.35)	0.35 (0.017)	89.2 (0.77)	43.1 (3.91)	94.1 (0.49)
(b) Model testing data						
Heteromastus filiformis			0.50 (0.022)	75.3 (1.48)	70.2 (1.86)	78.9 (1.38)
Macoma balthica			0.61 (0.022)	95.0 (0.41)	74.4 (1.15)	89.4 (0.42)
Pygospio elegans			0.52 (0.024)	86.4 (0.64)	74.9 (1.69)	90.6 (0.45)
Bathyporeia spec.			0.39 (0.020)	78.6 (0.83)	46.8 (2.58)	86.6 (0.56)
Cerastoderma edule			0.41 (0.020)	89.9 (0.87)	59.7 (2.74)	94.3 (0.53)
Nephtys cirrosa			0.33 (0.026)	85.1 (0.73)	30.2 (2.02)	91.6 (0.46)
Nereis diversicolor			0.42 (0.024)	87.9 (0.86)	69.6 (2.01)	92.5 (0.72)
Corophium volutator			0.34 (0.032)	90.4 (0.57)	67.2 (2.43)	94.4 (0.34)
Spio spec.			0.29 (0.024)	88.7 (0.69)	42.3 (2.44)	93.7 (0.41)
Arenicola marina			0.35 (0.030)	89.1 (0.78)	42.4 (4.84)	94.0 (0.45)

shaped curve with a clear optimum (e.g. *C. edule, A. marina*). *N. cirrosa* was the only species showing an optimum towards the higher end of the current velocity range. Similar results were obtained for maximum flood current velocity.

The response curves in relation to median grain size clearly showed different responses for the different macrobenthic species (Figure 9.6). *N. diversicolor* showed the highest probability of occurrence in very muddy sediments with a low median grain size, with a steep decrease in the probability of occurrence with increasing median grain size. The same pattern was observed for *C. volutator*, but showing a broader tolerance. This tolerance was even more pronounced for *M. balthica* and *H. filiformis*. *C. edule* and *P. elegans* showed a bell-shaped curve with an optimum between 100-150 μm. This optimum shifted more towards a higher median grain size for *A. marina* (approx. 155 μm), *Spio spec.* (approx. 200 μm) and *Bathyporeia spec.* (approx. 225 μm). *N. cirrosa* showed an optimum towards the higher end of the median grain size range.

Multiple logistic regression

For each macrobenthic species a multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run separately with and without sediment data.

Appendix 9.1 indicates the order in which the environmental variables were entered into the stepwise selection models. In all models, salinity (either model salinity, temporal salinity or both), depth, current velocity and sediment characteristics (for the models based on data set B) were entered into the models. Only for *M. balthica* salinity was not entered in the model based on data set A, which corresponds with the univariate model for salinity in which *M. balthica* showed a large tolerance.

The final model for each species contained between five and nine variables with concordant pairs of 79.1% to 93% for data set A, and between five and twelve variables with concordant pairs of 85.3% to 94.0% for data set B (Table 9.2). The explained deviance between the intercept only model and the intercept+covariates model varied between 18.2 and 48.5 % and between 29.0 and 52.5 % for data set A and B respectively. All final models were highly significant with *P*-values at 0.0001 for both data sets. The sensitivity and specificity were moderate to high for most species, the sensitivity being higher in most cases for the data set with sediment characteristics.

Final models for each species appeared quite stable, as ten model runs (based on the random selections of 50 % of the data) on randomly generated sets of abiotic conditions generated highly correlated predictions (Table 9.3). All linear correlation coefficients between pairs of models were in the range of 0.89 to 0.99 for each species. Also the % of concordant pairs, % correctly predicted, sensitivity and specificity did not change much as a function of which random set of 50% of the data is used to build the model (Table 9.3a) and test the model (Table 9.3b). The standard deviations of these diagnostics were low which suggested that the models were not very dependent on any particular set of observations.

Maps of the probability of occurrence of the macrobenthic species appeared to be fairly consistent with the observations of presence and absence in the Schelde estuary, as shown in Figures 9.7 to 9.10 for *M. balthica*, *C. edule*, *C. volutator* and *N. cirrosa* respectively. *M. balthica* was observed along the complete salinity gradient, mainly in the intertidal zone, and the highest probabilities of occurrence coincided with this distribution. This was also observed for *C. edule* and *C. volutator*, two species with respectively a mainly polyhaline, intertidal distribution and a mainly mesohaline, intertidal distribution. *C. edule* showed a low probability of occurrence in the α-mesohaline zone, whereas *C. volutator* showed a low probability of occurrence in the polyhaline zone of the estuary. *N. cirrosa* was a relatively common species in the subtidal, polyhaline zone of the Schelde estuary, penetrating the estuary up to the α-mesohaline zone. The model predicted a much broader distribution for this species, as was observed from the high probabilities of occurrence at almost all sampling locations in

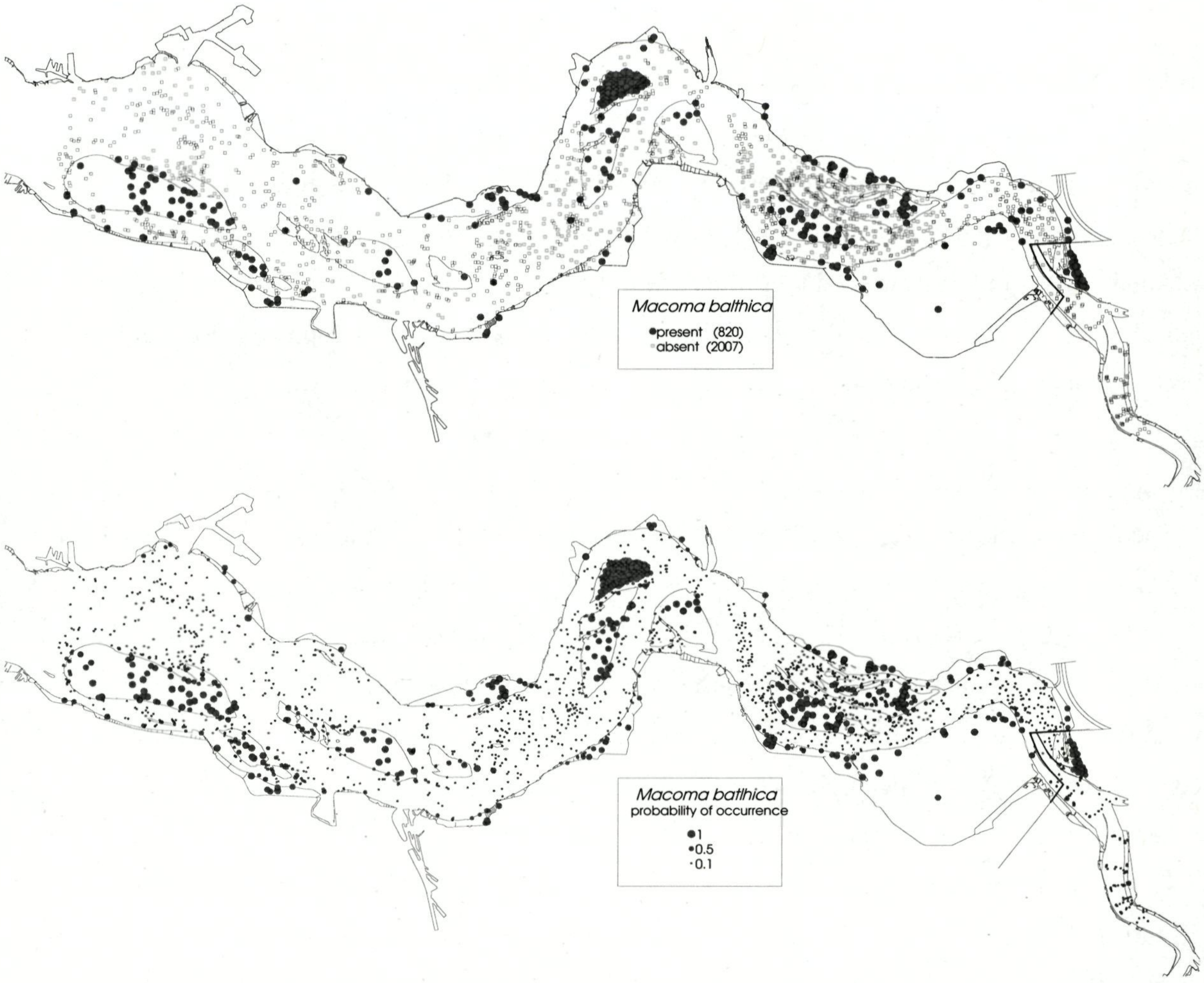

Figure 9.7. The observed distribution (presence/absence) of *Macoma balthcia* (top panel) and the distribution of the determined probabilities of species occurrence based on the multiple logistic regression model without sediment data (bottom panel). Probabilities of occurrence (p) are shown on a graduated scale.

the subtidal, polyhaline zone. Upstream of the polyhaline zone the model showed a decreasing probability of occurrence.

Discussion

In his review on ‘ecology of benthic macro-invertebrates in soft-sediment environment: progress towards quantitative models and predictions’, CONSTABLE (1999) stated that the established need for developing statistical models and rigorous experimental designs has not penetrated far into the soft-substratum ecological literature. In this study we statistically modelled and predicted the distribution (presence/absence) of individual macrobenthic species at scales relevant to management, based on small-scale core-sample information and environmental habitat variables including salinity, depth,

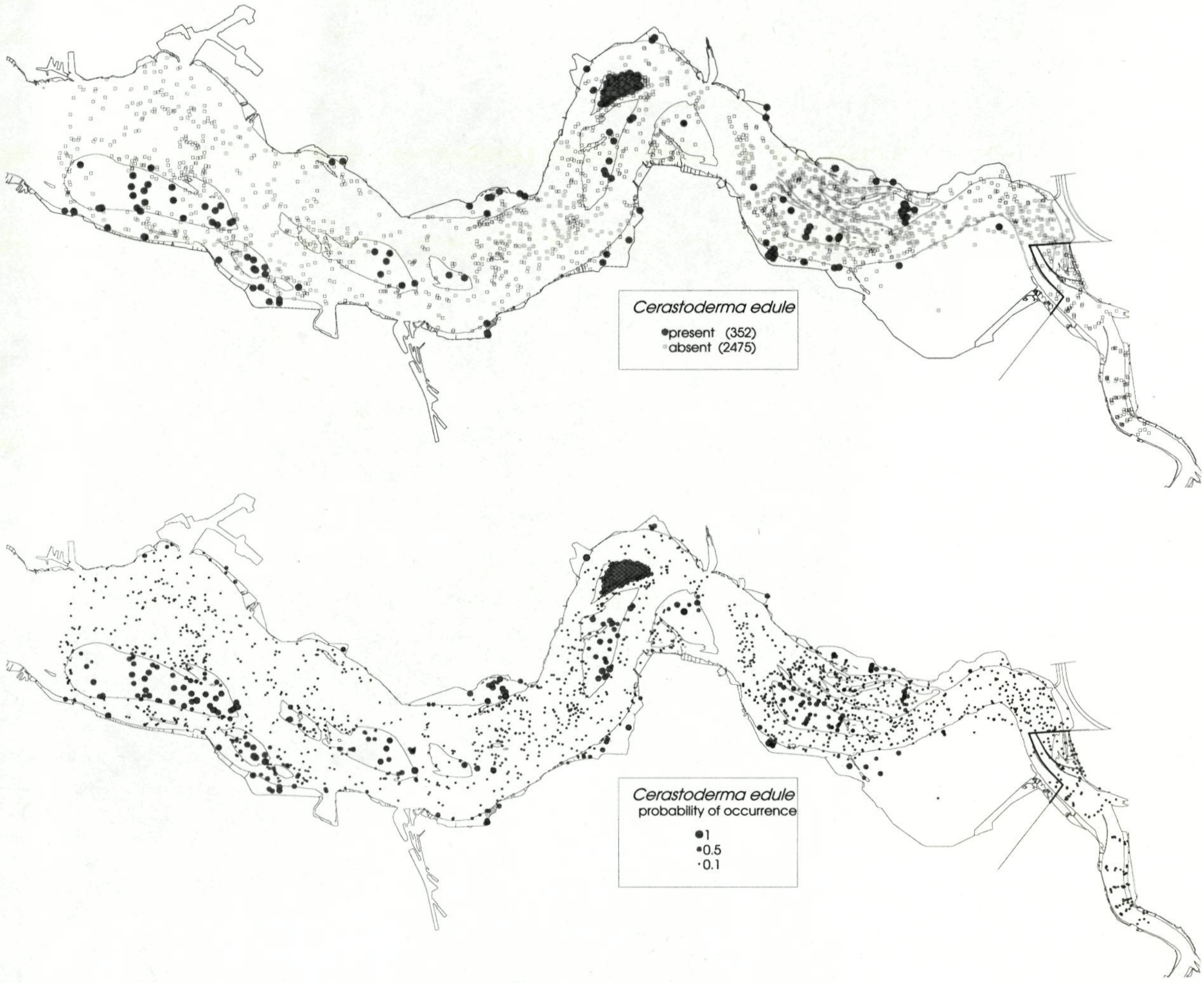

Figure 9.8. The observed distribution (presence/absence) of *Cerastoderma edule* (top panel) and the distribution of the determined probabilities of species occurrence based on the multiple logistic regression model without sediment data (bottom panel). Probabilities of occurrence (p) are shown on a graduated scale.

currents (flow) and sediment composition.

Our model approach gave environmental response surfaces for individual macrobenthic species based on several known deterministic abiotic environmental variables, being salinity, depth/elevation, tidal currents and sediment characteristics, which act at different spatial scales. Salinity obviously is a major determining factor for species distributions in estuaries (BOESCH 1977; WOLFF 1983; DITTMER 1983; MICHAELIS 1983; MANNINO & MONTAGNA 1997; YSEBAERT et al. 1998a) and will determine the large-scale, longitudinal distributions. By including ‘temporal salinity’, we also built in the possible role of seasonal variation in salinity in explaining species distribution (e.g. HOLLAND et al. 1987). Depth/elevation, especially when considering the full range from the deep subtidal zone to the high intertidal zone, has a pronounced effect on the macrofauna species distribution along the vertical gradient within estuaries (CRAEYMEERSCH 1999; YSEBAERT & MEIRE 1999). Related to depth are the tidal currents, which are generally stronger in the subtidal than

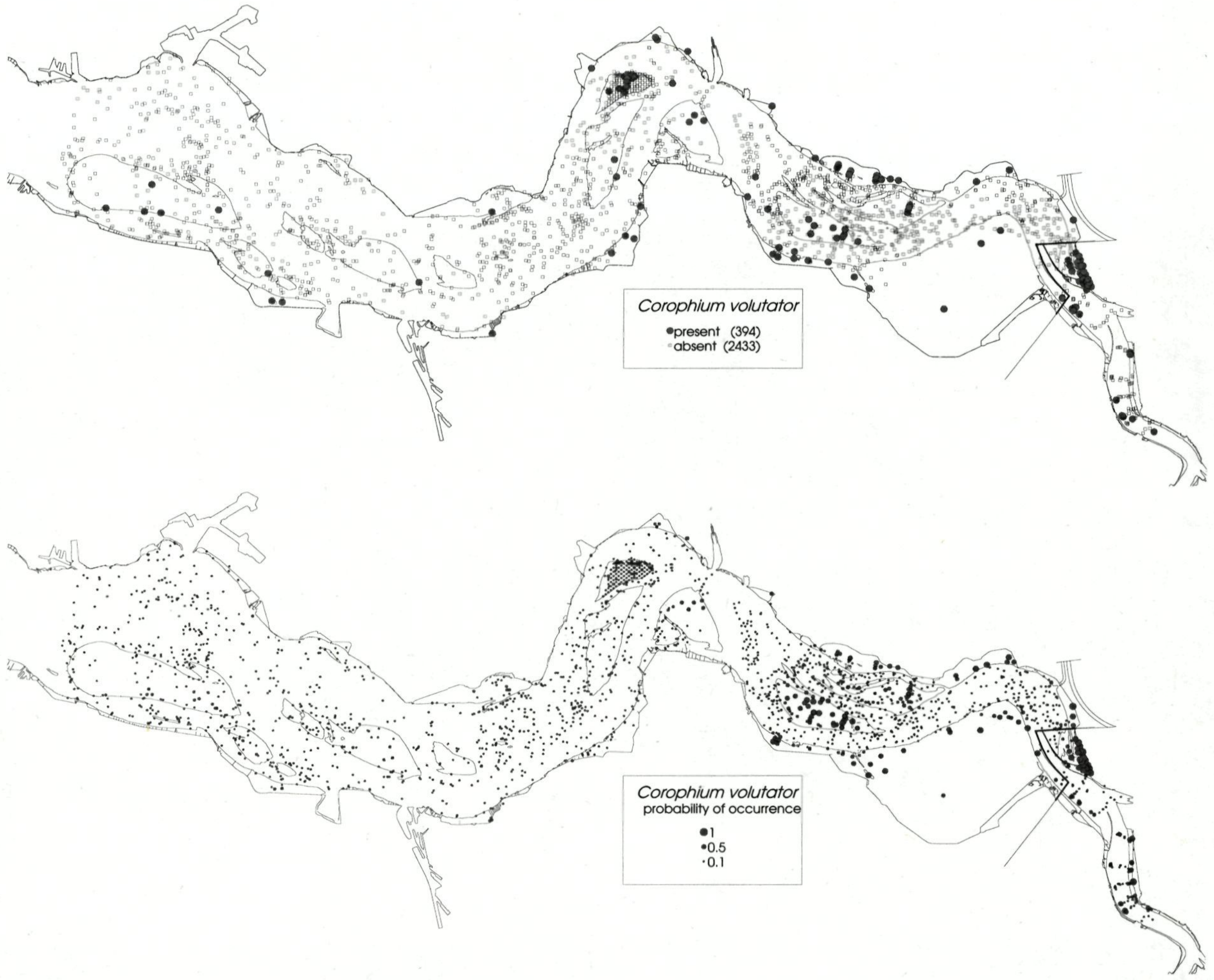

Figure 9.9. The observed distribution (presence/absence) of *Corophium volutator* (top panel) and the distribution of the determined probabilities of species occurrence based on the multiple logistic regression model without sediment data (bottom panel). Probabilities of occurrence (p) are shown on a graduated scale.

in the intertidal zone. WARWICK & UNCLES (1980) related the subtidal distribution of macrobenthic species to the tidal stress which is most pronounced in the channels. Interactions of macrobenthic communities with their environment have traditionally been considered in the context of “static” physical factors such as sediment characteristics and tidal inundation or exposure time, which are in turn determined largely by hydrodynamic processes (NOWELL & JUMARS 1984; WARWICK et al. 1991; HALL 1994). The importance of hydrodynamic variables such as current velocity, bed shear stress and wind-wave activity have also been recognised as influencing larval settlement and post-settlement transport (GRANT 1983; BUTMAN 1987; COMMITO et al. 1995), availability of particulate food resources (MILLER et al. 1992; WILDISH & KRISTMANSON 1997) and the stability of the substratum (WARWICK et al. 1991; BELL et al. 1997; GRANT et al. 1997). At the local (smaller) spatial scale sediment composition has been shown to influence estuarine benthic assemblage structure and species distribution (GRAY 1974; BEUKEMA 1976; JUNOY & VIÉTEZ

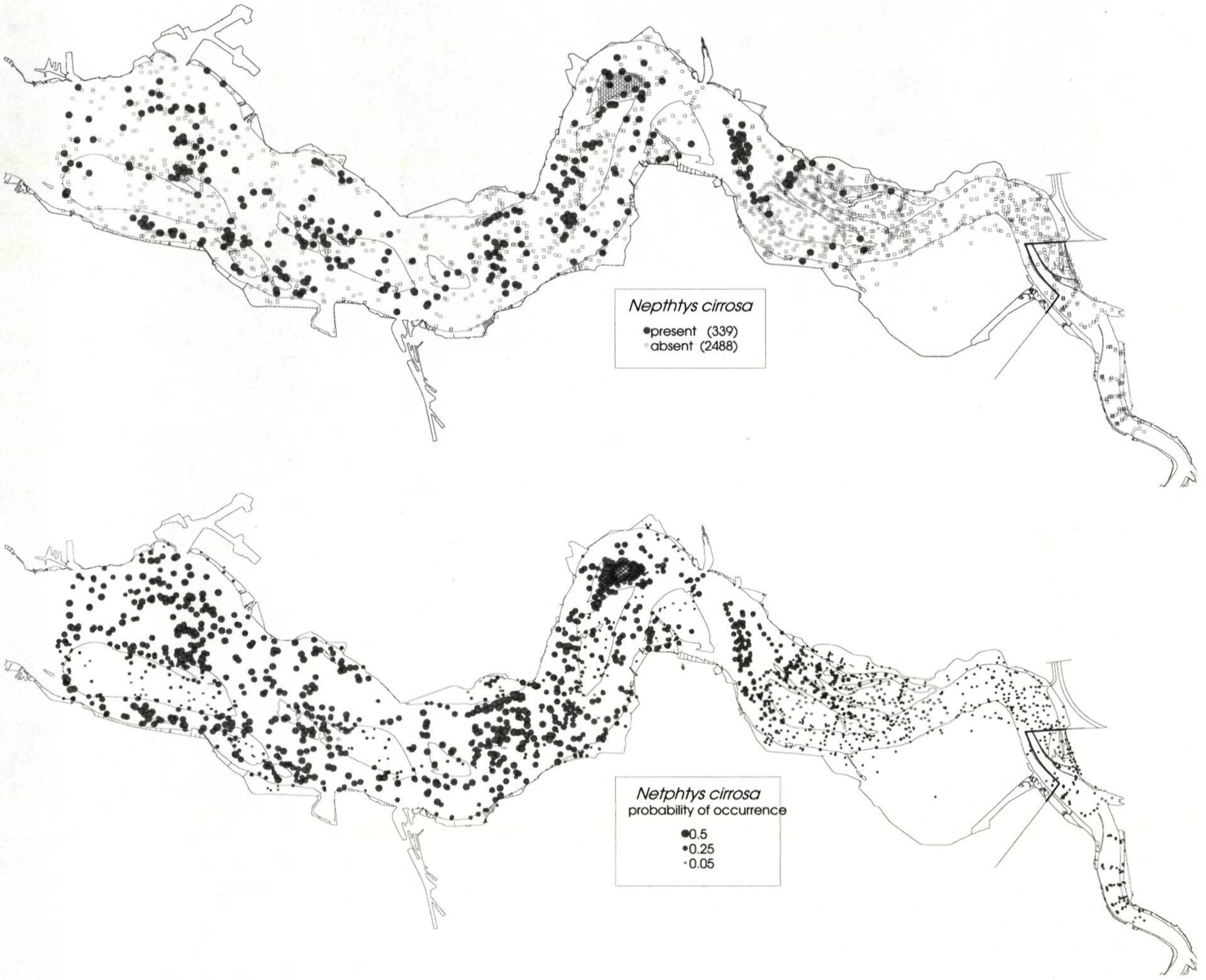

Figure 9.10. The observed distribution (presence/absence) of *Nephtys cirrosa* (top panel) and the distribution of the determined probabilities of species occurrence based on the multiple logistic regression model without sediment data (bottom panel). Probabilities of occurrence (p) are shown on a graduated scale.

1990; WARWICK et al. 1991; MEIRE et al. 1994).

These abiotic environmental variables (salinity, depth, maximum ebb and flood current velocities, median grain size and mud content) were used to statistically model and predict, through logistic regression, the distribution (presence/absence) of individual estuarine macrobenthic species at the estuarine macro- and meso-scale. Logistic regression has been applied in many ecological studies but in the field of marine and estuarine animal ecology this technique has hardly been used. On a univariate level, the obtained response curves in function of the different abiotic environmental variables were in general agreement with the descriptive statistics on the occurrence of the different species along these gradients and are in general agreement with findings of the literature (see also YSEBAERT & MEIRE 1999).

In most of our multivariate models, one or more estimates of salinity, depth, current velocity and sediment characteristics (for the models with sediment data) are entered into the models. This multivariate modelling approach allowed incorporation of heterogeneity both within and across scales. Several of the environmental variables included in this analysis are correlated (see also YSEBAERT et al. in prep.). As an example, depth is highly correlated with current velocities and to a lesser extent with sediment characteristics. Many pairs of mutually correlated variables were nevertheless included in the stepwise procedure in the same model. This is likely caused by the fact that these correlations were not spatially consistent. When examined at different scales, the correlation between two variables may change. Therefore, when one variable is entered into the model, a second variable that is on average correlated with the first may still explain variation in the probability of occurrence.

In our model approach we used environmental variables as predictors for the distribution of macrobenthic species. An alternative, but not mutually exclusive viewpoint is that distributions are controlled more directly by biotic interactions, such as predation and inter- and intraspecific competition (WILSON 1991; OLAFSSON et al. 1994). The relative importance of processes determining the spatial distribution of macrofaunal species may depend on the scale considered. Biologically generated patterns tend to be more important at micro-scale (< 1m) but are less likely to appear at a macro- or meso-scale (LEGENDRE et al. 1997; THRUSH et al. 1997). However, relatively large-scale patterns generated by biological interactions have also been described. The lugworm *Arenicola marina* influences the distribution of many other species by its bioturbating activities, e.g. the polychaete *Pygospio elegans* (REISE 1985), the amphipod *Corophium volutator* (FLACH 1992), the seagrass *Zoltera noltii* (PHILIPPART 1994). It is likely, in such cases, that the environmental factors determining the distribution of the superior competitor will be indirectly reflected in the response functions for the expelled species, falsely suggesting a direct dependence on abiotic factors where in fact a biologically mediated dependence may be the case. Similar arguments may be valid with respect to the possibilities for settlement of some species. If the abiotic conditions at a particular place are within the tolerance limits of the adults, but conditions are adverse for settlement of juveniles, this may lead to absence of the species. In summary, therefore, the patterns described by the response curves should not be interpreted as descriptions of the physiological limits of the species or of the adults in the species, but as descriptions of actual distribution patterns as a function of abiotic variables, whatever the direct or indirect dependence on these variables may be.

Quantifying the associations between the probability of occurrence of estuarine macrobenthic species and abiotic environmental variables allows us to generate predictions of distribution, which may be robust even if the mechanisms or processes are not known. Indeed, the type of pattern analysis conducted in this study does not allow to draw any direct conclusions on the processes that determine macrobenthic species distribution. Nevertheless, pattern analysis and modelling are critical steps in ecological research and resource management (THRUSH et al. 1999). Where patterns of distribution are strongly and directly coupled to physicochemical processes, as is the case at the estuarine macro- and meso-scale, our modelling approach was capable of predicting macrobenthic species distributions with a relatively high degree of success.

We are able to predict the probability of occurrence for some species better than for others. This variability in success may have different causes. It is difficult to ascertain that all (or most) of the relevant factors for the distribution of a species have been taken into account. Statistical approaches such as the one followed here depend on the ability to assemble sufficient environmental information at all sampling points. Potentially important factors related to food availability (e.g. biomass and productivity of microphytobenthos - HERMAN et al., in press; productivity of the phytoplankton - HERMAN et al., 1999) have not been taken into account. Likewise, we have restricted our analyses here to single species, excluding possible strong interactions between different macrobenthic populations. The spatial resolution for most abiotic variables used was very high, but may still have been insufficient, especially at the edges of the intertidal flats. Strong gradients in height, current velocities and sediment composition may occur at these edges, and this may be a reason for the relatively high percentage of prediction failures at these edges. Moreover, intertidal flats are mobile over time, and we have imposed a fixed bathymetry and current patterns onto a biological data set gathered over a ten year period. From the sampling practice we know that some edges of tidal flats may move tens or even hundreds of meters in a few years time. Although preliminary trend analyses did not reveal strong evolutions of the biological communities over the past ten years, some trends could also have gone unnoticed and caused additional unexplained variation. Finally, our analysis has not taken into account the small-scale spatial structure of macrobenthic populations. Due to patchiness of the populations, and the size of the sampling units, a zero observation (species is absent) can have quite different meanings: either the species is really absent from the zone sampled, or it is present very nearby but missed by the sampling. It can be expected that such effects are variable between species. Rare, large or very clumped populations are expected to have more 'false zeros' then abundant, small and homogeneously distributed populations. Correction of the estimation methods for these effects would require a thorough investigation of small-scale distributions of the different species, which could potentially lead to an improvement of the prediction success. Identifying patterns at various spatial scales may also provide a clue as to the kinds of processes that operate at that particular scale (THRUSH et al. 1999).

The next step will be to investigate the possibility of using the models and predictions for evaluation of the effects of different management schemes (e.g. a further deepening of the shipping channel) within the Schelde estuary. This requires an evaluation of the robustness of the models to different states of the system. The most appropriate test for this robustness is to investigate the applicability of the models in other estuarine systems. Including process information, especially on the feeding habits of the macrobenthic species, and natural history information will certainly improve the quality and generality of the models by making the predictions more robust to changes in physico-chemical forcing of the system and in the long-term will allow the development of models of the action and interaction of processes operating at different scales (ALLEN & STAR 1982; WIENS 1989; THRUSH 1991; SCHNEIDER 1994; THRUSH et al. 1999).

Acknowledgements

We thank all the people involved in taking and sorting the samples that made up our database. In particular we thank Johan Craeymeersch and John Buijs who were responsible for much of the sampling and for setting up large parts of the database. The help of Marijn van Helvert was needed for the hydrodynamical simulations. We thank Greet De Gueldre for comments on the manuscript. This study was part of the ECOFLAT project, a research project funded by the European Commission in the framework of ENVIRONMENT & CLIMATE Programme (contract number ENV4-CT96-0216), being part of ELOISE (European Land Ocean Interactions Studies). This is contribution no. xxx to the EU programme ELOISE and contribution no. Xxx of the Netherlands Institute of Ecology.

Appendix 9.1. The maximum-likelihood estimates of the logistic regression parameters for the species response surfaces. The probability of occurrence is calculated as $p = e^{-x} / (1 + e^{-x})$, where x is the solution to the regression function. Parameters derived both from the model without sediment data (n=2827 samples) and the model with sediment data (n= 1293 samples) are presented. Negative depth values, ranging from –56.4 to +2.2 m, were replaced by positive values by changing sign (value*-1) and adding 2.5 m.

Without sediment data		With sediment data	
Heteromastus filiformis			
Intercept	-2.2298	Intercept	-7.5618
Max. flood	removed	Max. flood	-2.9286
Max. ebb^2	-0.7335	Depth	-0.2340
Temporal sal.^{2}	-0.00426	Median	-0.00552
Temporal sal.	0.1147	Model sal.	0.4851
Model sal.	0.3433	Model sal.^{2}	-0.00845
Model sal.^{2}	-0.00845	Mud	0.1073
Max. flood^2	-1.7250	Mud^2	-0.00114
Depth^2	0.00448	Max. flood^2	removed
Depth	-0.1261	Temp. sal^2	-0.0129
		Temp. sal.	0.3599
		Depth^2	0.00732
		Max. ebb	7.7127
		Max. ebb^2	-4.9373
Nereis diversicolor			
Intercept	7.3822	Intercept	-9.0758
Max. flood	-1.1788	Max. ebb	-3.8073
Depth	-0.6146	Median	-0.00954
Depth^2	0.0106	Depth	-0.6606
Model sal.	-0.4199	Depth^2	0.0197
Max. ebb	-2.8955	Model sal.	-0.0878
Model sal.^{2}	0.00871	Model sal.^{2}	removed
		Mud^2	-0.00024
		Temp. sal.	-0.3703
		Temp. sal^2	0.0105
Corophium volutator			
Intercept	6.6438	Intercept	6.2743
Model sal.	-0.4245	Median	-0.0111
Max. ebb	-3.2311	Max. ebb	-3.3653
Depth	-0.4134	Model sal.	-0.1884
Depth^2	0.00755	Depth	-0.4738
Model sal.^{2}	0.00582	Depth^2	0.0145
Nephtys cirrosa			
Intercept	-19.6625	Intercept	-13.8353
Temp. sal.	0.7573	Depth	0.5568
Max. ebb	7.4088	Temp. sal	0.8223
Temp. sal^2	-0.0151	Depth^2	-0.0181
Max. ebb^2	-3.6803	Temp. sal^2	-0.0154
Model sal.	0.4195	Mud	-0.1074
Model sal.^{2}	-0.00728	Max. ebb^2	-0.8913
Cerastoderma edule			
Intercept	-13.2667	Intercept	-11.5229
Max. flood	removed	Max. flood	-4.0737
Model sal.	0.6427	Model. sal.	0.6943
Depth	-0.3871	Median^2	-0.00004
Model sal.^{2}	-0.0129	Model sal.^{2}	-0.0114
Temp. sal.	0.2972	Temp. sal.	0.4338
Max. flood^2	-4.0479	Depth	-0.1868
Depth^2	0.00696	Temp. sal^2	-0.0103
Max. ebb^2	-18.4287		
Max. ebb	14.7480		
Temp. sal.^{2}	-0.00503		

Without sediment data		With sediment data	
Macoma batlhica			
Intercept	0.4229	Intercept	0.6798
Max. flood	3.5401	Median^2	-0.00006
Depth	-0.4422	Depth	removed
Depth^2	0.00823	Model. sal.	-0.3009
Max. flood^2	-5.8467	Max. flood^2	-10.5546
Max. ebb^2	-4.7585	Temp. sal^2	0.3963
Max. ebb	3.6948	Temp. sal.	0.3963
		Model sal.^{2}	0.0140
		Depth^2	-0.0980
Pygospio elegans			
Intercept	-5.2640	Intercept	-7.5609
Max. flood	removed	Max. flood	-3.1578
Depth	-0.3914	Model sal.	0.9682
Depth^2	0.0103	Model sal.^{2}	-0.0213
Model sal.	0.6872	Median^2	-0.00006
Model sal.^{2}	-0.0156	Depth	-0.4163
Max. ebb^2	-1.0291	Depth^2	0.0125
Max. flood^2	-2.3810	Median	0.0102
Bathyporeia spec.			
Intercept	-7.2309	Intercept	-2.6535
Depth	-0.2882	Mud	-0.0978
Temp. sal^2	-0.00626	Depth	-0.4620
Temp. sal.	0.1585	Depth^2	0.0126
Max. ebb^2	1.1721	Max. ebb	4.1235
Depth^2	0.00571	Temp. sal.^{2}	-0.0125
Model sal.	0.6689	Temp. sal.	0.3857
Model sal.^{2}	-0.0169	Max. ebb^2	-1.7495
Spio spec.			
Intercept	-16.9542	Intercept	-17.1183
Temp. sal.^{2}	removed	Temp. sal.	1.1932
Temp sal.	0.3402	Model sal.^{2}	-0.00635
Model sal.^{2}	-0.0204	Max. flood	6.0268
Model sal.	0.7173	Max. flood^2	-2.7218
Max. ebb^2	-0.5283	Model sal.^{2}	-0.0151
Max. ebb	removed	Median^2	-0.00003
Max. flood	8.0842	Mud	-0.1292
Max. flood^2	-5.1461	Mud^2	0.00146
Arenicola marina			
Intercept	-13.4934	Intercept	-9.3460
Max. flood	-1.9627	Model sal.	0.2921
Model sal.	1.0284	Max. flood	-3.3583
Model. sal^2	-0.0194	Temp. sal^2	-0.00260
Depth	-0.2633	Depth	1.4338
Max. ebb^2	-6.6295	Depth^2	-0.3155
Max. ebb	5.4847	Max. ebb	3.0047
Depth^2	0.00438	Median^2	-0.00007
Temp. sal^2	-0.00099		

Chapter ten

Waterbird communities along the estuarine salinity gradient of the Schelde estuary, NW-Europe

T. Ysebaert, P.L. Meininger, P. Meire, K. Devos, C.M. Berrevoets, R.C.W. Strucker and E. Kuijken

Abstract

The zonation of non-breeding waterbirds along the Schelde estuary (The Netherlands-Belgium), one of the longest estuaries in NW-Europe with still a complete salinity gradient, including a large freshwater tidal area, was described. Numbers of birds were counted monthly over the period October 1991 to June 1997. Highest numbers of waterbirds were observed in late autumn and winter, with annual peak numbers ranging between 150,000 and 235,000 individuals for the whole estuary. Based on a multivariate analysis different waterbird communities were observed along the salinity gradient. The polyhaline areas of the estuary were numerically dominated by the waders Oystercatcher and Dunlin. Due to the presence of a large brackish marsh in the mesohaline zone, the waterbird community in this area was dominated by the herbivores Wigeon and Greylag Goose. In the oligohaline and freshwater tidal areas, the waterbird community was dominated by duck species, with Teal and Mallard being the most important. The international importance of the Schelde estuary for waterbirds was evidenced by the fact that for 21 waterbird species the 1% level criterion, according to the Ramsar convention, was exceeded. The relation of the observed diversity and commnity patterns with the functional and habitat diversity of the Schelde estuary as well as the effect of recent conservation measures to preserve this habitat were discussed.

Introduction

Estuaries are defined as inlets of the sea reaching into a river valley as far as the upper limit of tidal rise (FAIRBRIDGE 1980). Estuaries are cited among the most productive biomes of the world (ODUM 1983; DAY et al. 1989; COSTANZA et al. 1993) and support important biogeochemical processes that are central to the planet's functioning, e.g. nutrient cycling (BILLEN et al. 1991; COSTANZA et al. 1997). Birds benefit from this high level of productivity, and for many waterbird

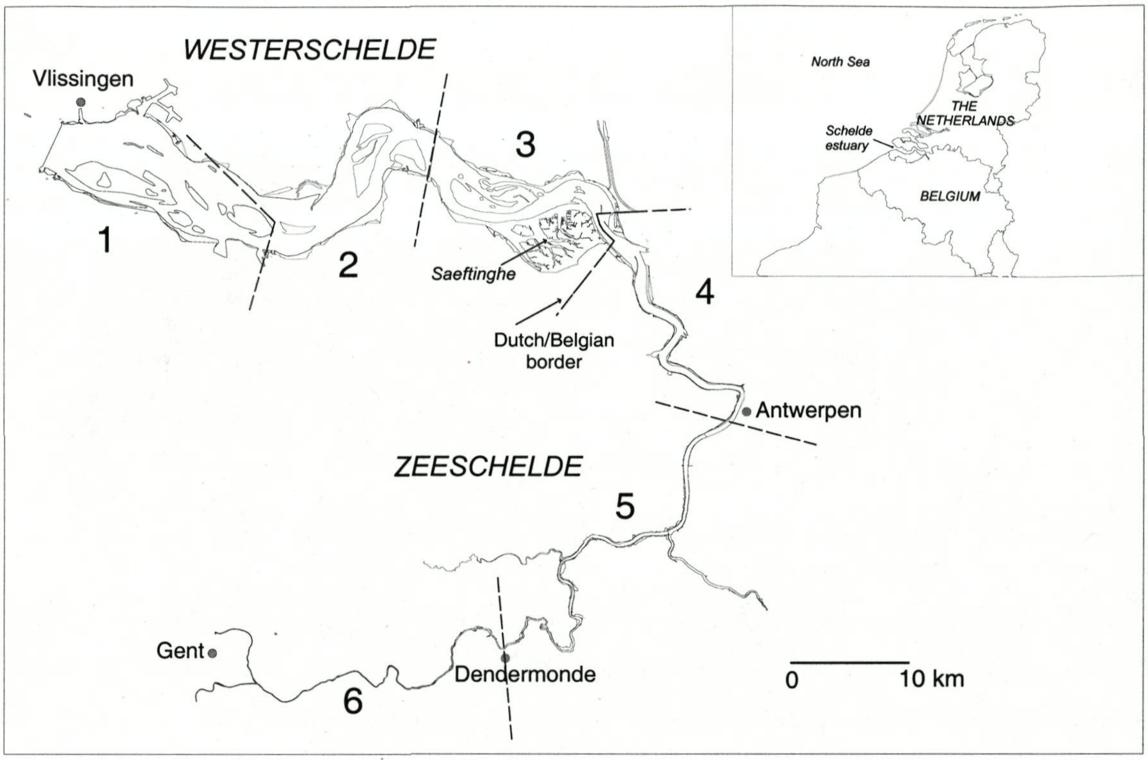

Figure 10.1. Map of the Schelde estuary situated between Vlissingen (The Netherlands) and Gent (Belgium), with its division in Westerschelde (areas 1-3), and Zeeschelde (areas 4-6).

species estuaries are of vital importance for one or more stages of their life cycle (e.g. PIENKOWSKI & EVANS 1984; SMIT & PIERSMA 1989; DAVIDSON et al. 1991; ENS et al. 1994). However, most of the threats to biodiversity are precisely in the estuarine zone and are a direct result of human population and demographic trends (PRATER 1981; SMIT et al. 1987; DAVIDSON et al. 1991; SUCHANEK 1994; GRAY 1997; MCLUSKY 1999).

Because of their position at the top of the food web birds are good indicators of environmental changes (FURNESS & GREENWOOD 1993). Waterbirds are widely used in monitoring programmes as an indicator of the value of wetland habitats (MOSER et al. 1993; SCOTT & ROSE 1996). Within the Ramsar Convention (Convention of Wetlands of International Importance Especially as Waterfowl Habitat, Ramsar 1971, and 1982 Protocol) the 1% criterion states that a wetland should be considered internationally important if it regularly supports 1% of the individuals of a population of one species of waterfowl (ATKINSON-WILLES 1976; BOYD & PIROT 1989; SCOTT & ROSE 1996).

Several papers demonstrate the importance of coastal and estuarine areas for waterbirds (e.g. MEIRE et al. 1989; DAVIDSON et al. 1991; SCHEKKERMAN et al. 1994; MELTOFTE et al. 1994). However, very few papers deal with the zonation of waterbird communities along a complete salinity gradient, including poly- and mesohaline as well as freshwater tidal areas. Especially freshwater tidal areas are nowadays very rare habitats, and knowledge on these areas is poor (ODUM 1988).

The Schelde estuary is one of the longest estuaries in NW-Europe with still a complete salinity gradient according to the classification of estuarine divisions of MCLUSKY (1993, 1999). In this paper the zonation of non-breeding waterbird communities along the salinity gradient of the Schelde estuary is described. Emphasis is given to the spatial and seasonal distribution. Annual trends will be discussed elsewhere. The importance of the Schelde estuary as a wetland for waterbirds according to the Ramsar convention is determined. The possible relation of the observed diversity and commnity patterns with the functional and habitat diversity of the Schelde estuary as well as the effect of recent conservation measures to preserve this habitat are discussed.

Materials and methods

Study area

The Schelde estuary measures 160 km from Vlissingen (The Netherlands) upstream to Gent (Belgium) (Figure 10.1). The width is about 100 m at Dendermonde, 500 m at Antwerpen, 1500 m near the Dutch-Belgian border, and 4500 m at Vlissingen with a maximum of 7800 m. The mean tidal range increases from 3.8 m at Vlissingen to 5.3 m at Antwerpen. At Gent the tidal range is still 2 m. The Westerschelde (55 km) represents the downstream Dutch part of the estuary. It is a well mixed region, characterized by a complex morphology with flood and ebb channels surrounding several large intertidal flats. The surface of the Westerschelde amounts to 310 km², with the intertidal area covering 35%. The Zeeschelde (105 km), the Belgian part of the estuary, is characterized by a single channel, bordered by relatively small mudflats and marshes (28% of total surface). The surface of the Zeeschelde amounts to only 44 km². Human activities are mainly concentrated in the Zeeschelde, where agglomerations and industries are located close to the river banks. The intertidal zone is often absent (e.g. quays, wharfs) or very narrow, consisting only of dikes with a steep hard substrate of rubble. Upstream of Dendermonde, the estuary is almost completely canalized.

Bird counts

In the Westerschelde, waterbird censuses were organised by the National Institute for Coastal and Marine Management (RIKZ) (e.g. MEININGER et al. 1997, 1998). Every month counts were performed during high tide, when birds concentrated on roosts. In the Zeeschelde, a waterbird monitoring programme was carried out by the Institute of Nature Conservation (e.g. YSEBAERT et al. 1998b, 1999). Here, monthly censuses were done at low tide from boats, when birds were present in the intertidal zone. In both Westerschelde and Zeeschelde count dates were set close to mid-month.

Neighbouring areas, between which bird movements were frequent, were counted on the same day. For the Westerschelde missing counts were covered by the method of imputing (UNDERHILL & PRŸS-JONES 1994). The results presented in this study deal with counts over the period October

Table 10.1. Surface area (ha) of the intertidal zone (tidal flats and marshes) and subtidal zone in the different areas along the Schelde estuary. Areas 1-3: Westerschelde. Areas 4-6: Zeeschelde.

Area	Classification	Tidal flats	Marsh	Subtidal	TOTAL
1	lower/middle (polyhaline)	2898	51	10195	13144
2	middle/inner (poly/mesohaline)	2456	76	6564	9069
3	inner (α-mesohaline)	3020	2383	3342	8745
4	inner/upper (β-meso/oligohaline)	514	181	2005	2700
5	upper/tidal fresh (oligohaline/limnetic)	196	297	948	1441
6	tidal fresh (limnetic)	9,5	30,5	250	290
TOTAL	whole estuary	9093,5	3018,5	23304	35389

1991 to June 1997, representing 69 observation months. For the Zeeschelde no counts were available for the period May-August 1992. During the six-year observation period, only two winters (1995/96 and 1996/97) were really cold with respectively 14 and 18 days showing freezing temperatures all day. The other winters ranged from mild to normal with on average 4 days with freezing temperatures all day.

Data analysis

Numbers of divers, grebes, cormorants, herons, geese, swans, ducks, coots, and waders were dealt with. Exotic waterbird species (8 species) and species which were only observed once (9 species) were excluded from all further analyses. Gulls and terns were not considered.

Based on the classification of MCLUSKY (1993,1999) six areas were recognized along the estuarine salinity gradient (Figure 10.1, Table 10.1). In the Westerschelde the boundaries of the areas were defined so that birds roosted and feeded in the same area (MOSTERT et al. 1990). Surfaces of the intertidal (tidal flats and marshes) and of the subtidal zone were obtained from non-published reports (Table 10.1). Area 3 was characterized by the presence of the marsh of Saeftinghe, one of the largest brackish marshes in NW-Europe. For the Zeeschelde the long stretches of only hard substrate with rubble (man-made constructions) were also considered as part of the intertidal surface. The surface of these constructions was estimated from aerial photographs, being 26, 54, and 52 ha respectively for area 4, 5 and 6.

Vegetation structure of the marshes changed along the salinity gradient, from a relatively low vegetation in the saltmarshes of areas 1-2 to a more pronounced vertical structure with reed beds and willow scrubs in the freshwater tidal marhses of areas 5-6.

Monthly mean numbers of waterbirds for the whole study period were calculated for each waterbird species and for each area over the six observation years. Also means were calculated for four periods, that were distinguished by season-related functions of the estuary for waterbirds: 1) summer (moulting and breeding): June, July; 2) autumn (staging): August, September, October, November; 3) winter (wintering): December, January, February; 4) spring (staging): March, April, May. Year-to-year fluctuations in waterbird numbers were not considered, only the impact of severe versus mild winters on the estuarine zonation of waterbirds.

Waterbird species were divided into functional (trophic) guilds based on feeding type. All waders and the Shelduck were considered as carnivores, here called benthivores as they feed on benthos on the tidal flats, diving ducks and scoters as diving benthivores, grebes, divers, cormorants, herons and sawbills as piscivores. Several duck species (Teal, Mallard, Pintail) mainly foraged on the mudflats along the low water edge, probably feeding on small macrofauna (e.g. Oligochaeta) and organic material (pers. observ.), and were considered as omnivores. The remaining duck species (mainly Wigeon), geese, swans and coots were considered as herbivores.

As a measure of species diversity, the dominance pattern (numerical diversity) within areas and seasons was determined from *k*-dominance curves, that plot cumulative ranked abundances against (log) species rank (LAMBSHEAD et al. 1983). The zonation of waterbird communities along the salinity gradient was analysed by multivariate statistics based on annual means per season. The methods of classification and ordination (GAUCH 1982) were used to indicate the degree of (dis)similarity in waterbird species composition (community structure) among areas for each season. The agglomerative clustering method (Group Average Sorting GAS of Bray-Curtis dissimilarities) (CLIFFORD & STEPHENSON 1975) and ordination by non-metric multi-dimensional scaling (MDS) (KRUSKAL & WISH 1978) were applied. Data were fourth root transformed prior to analysis. The results for the winter season were representative for the other seasons, so only these results are discussed in detail. Dominance curves, GAS and MDS were performed with the statistical package PRIMER (CARR et al. 1993; CLARKE 1993).

Finally, the mean of the annual peak numbers for the whole study period was determined for each waterbird species and compared with the 1% criterion of the Ramsar Convention to evaluate the international importance of each of the six areas and of the Schelde estuary as a whole (PERENNOU et al., 1994; SCOTT & ROSE, 1996). The population estimates were based on MEININGER et al. (1995), SCOTT & ROSE (1996) and ROSE & SCOTT (1997).

Results

Species composition and total numbers of waterbirds

A total of 80 waterbird species were observed in the Schelde estuary, with respectively 69, 61 and 68 species in the Westerschelde areas 1, 2 and 3, and 56, 47 and 37 species in the Zeeschelde areas 4, 5 and 6. Scientific names for species mentioned in the text are given in Table 10.2.

The monthly mean numbers of waterbirds showed clear seasonality (Figure 10.2), with lowest

Het macrobenthos van het Schelde- en Eems-estuarium was zeer gelijkend in soortensamenstelling (hoofdstuk 6). In beide estuaria werd een duidelijke afname in soortenaantal waargenomen met dalend zoutgehalte. De densiteit vertoonde geen duidelijke trend langsheen de zoutgradiënt, de biomassa daarentegen was duidelijk hoger in de mariene zone. Beide estuaria werden gekenmerkt door drie gemeenschappen: een mariene gemeenschap, een brakke gemeenschap en een zoetwatergemeenschap. In het Schelde-estuarium, en in mindere mate ook in het Eems-estuarium, kon de zeer arme bodemfauna in het zoetwatergetijdengebied toegeschreven worden aan vervuiling. Enkel weinig gevoelige Oligochaeta werden hier in grote aantallen aangetroffen. De brakke zone van het Schelde-estuarium werd gekenmerkt door grote aantallen kleine, vaak opportunistische soorten, dit in tegenstelling tot het Eems-estuarium waar een meer stabiele macrobenthos gemeenschap werd waargenomen.

De brakwaterzone van de Zeeschelde werd meer in detail onderzocht (hoofdstukken 7, 8). De bodem van de subtidale zone werd hier gekenmerkt door verschillende sedimenten, gaande van zeer slibrijke tot zeer zandige (hoofdstuk 7). De wormen *Heteromastus filiformis* ~~and~~ en Oligochaeta waren het meest algemeen. Ook enkele zeer typische brakwatersoorten werden aangetroffen (bv. *Polydora ligerica*, *Corophium lacustre*, *Gammarus salinus*). Aantallen en biomassa's waren gemiddeld zeer laag, en de waargenomen gemeenschappen werden voornamelijk gedomineerd door zeer kleine, opportunistische soorten, indicatief voor systemen onder stress. Op basis van multivariate analyses werden drie gemeenschappen onderscheiden, welke duidelijk gerelateerd waren aan de sedimentsamenstelling van de bodem. x

In het intergetijdengebied werd onderzoek verricht naar de biologische (zowel zoobenthos als microphytobenthos) en fysische karakteristieken van cohesieve sedimenten en hun mogelijke interacties (hoofdstuk 8). Hiertoe werd een voorjaarssituatie vergeleken met een najaarssituatie op drie slikgebieden in de Zeeschelde. Het sediment op deze slikken bestond uit zeer fijn zand tot slibrijk. ? [De verschillende fysische sediment karakteristieken waren onderling sterk gecorreleerd, en vertoonden geen significante verschillen tussen de twee onderzoeksperiodes (April en September). Het p160 + [illegible]? microphytobenthos en het zoobenthos daarentegen vertoonden wel duidelijke verschillen tussen beide // seizoenen. Microphytobenthos biomassa was vele malen hoger in april, en vertoonde een grote ruimtelijke variatie, gerelateerd aan de hoogteligging van de bemonsteringslokaties. De densiteit en biomassa van het zoobenthos was in april laag, voornamelijk gedomineerd door Oligochaeta en Nematoda. In september waren diversiteit, densiteit en biomassa van het zoobenthos sterk toegenomen. De resultaten toonden aan dat fysische en biologische processen op een complexe manier op elkaar inwerken, en dat hun effect op sedimentologische processen ruimtelijk en temporeel verschilden.

Het ontwikkelen van ecologische voorspellingsmodellen is noodzakelijk wil men menselijke ingrepen in ecosystemen gaan evalueren en voorspellen. De zeer grote macrobenthos dataset liet toe om een statistisch model te ontwikkelen voor het voorspellen van de aanwezigheid van macrobenthos (hoofdstuk 9). Logistische regressie werd toegepast om de probabiliteit van voorkomen van macrobenthos soorten te voorspellen in functie van de omgevingsfactoren zoutgehalte, diepte, stroomsnelheden en sediment karakteristieken. Univariate en multivariate logistische regressie konden het voorkomen van de verschillende soorten met relatief grote zekerheid voorspellen. Gemodelleerde verspreidingskaarten vertoonden grote overeenkomst met de werkelijk waargenomen verspreiding. In situaties waar verspreidingspatronen duidelijk gekoppeld zijn aan fysicochemische omgevingsfactoren, zoals in estuariene ecosystemen, blijkt de toegepaste modelering een relatief betrouwbare voorspellingsmethode, alhoewel de onderliggende processen hiermee niet kunnen bepaald worden. De bruikbaarheid van dergelijke modellen voor het voorspellen van effecten van beheer voor het Schelde-estuarium worden momenteel onderzocht.

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Het belang van he Schelde-estuarium voor watervogels werd onderzocht aan de hand van maandelijkse monitoringsgegevens verzameld in de periode 1991-1997 (hoofdstuk 10). De hoogste aantallen aan watervogels werden waargenomen in de herfst en de winter, met jaarmaxima van 150,000 tot 235,000 watervogels. Op basis van multivariate verwerkingstechnieken werden verschillende watervogelgemeenschappen waargenomen langsheen de zoutgradiënt. De mariene zone van het estuarium werd gekenmerkt door hoge aantallen steltlopers, voornamelijk Scholeksters (*Haematopus ostralegus*) en Bonte Strandlopers (*Calidris alpina*). De aanwezigheid van Saeftinghe, een zeer groot brakwaterschor, verklaart de grote aantallen herbivoren in dit deel van het estuarium, zoals de Smient (*Anas penelope*) en de Grauwe Gans (*Anser anser*). Langsheen de Zeeschelde neemt het aandeel van eenden in de watervogelgemeenschap toe, met als typische vertegenwoordigers in het zoetwatergetijdengebied de Wintertaling (*Anas crecca*) en de Wilde Eend (*Anas platyrhynchos*). Het Schelde-estuarium is van internationaal belang voor 21 soorten watervogels (meer dan 1% van de volledige NW-Europese populatie). De waargenomen patronen in diversiteit en gemeenschapsstructuren waren duidelijk gerelateerd met de functionele en habitat diversiteit, waarbij voedselbeschikbaarheid een belangrijke rol speelt.

ABITAT !! ?

Dit proefschrift heeft aangetoond dat het voorkomen van macrobenthos in belangrijke mate bepaald wordt door de dynamiek, typisch voor een estuarien ecosysteem. Macrobenthosgemeenschappen mogen dan ook niet beschouwd worden als statische entiteiten. Het belang van de sturende omgevingsvariabelen verschilt evenwel tussen estuaria en tussen verschillende zones binnen één estuarium, afhankelijk van regionale en lokale fysische en fysicochemische condities. Ook de beschouwde schaalgrootte van een studie, zowel in ruimte als in tijd, speelt hierbij een rol. ?

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Appendix. List of reports of Tom Ysebaert related to the different topics of this thesis.

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