CHAPTER 1

• Introduction and thesis outline •

1.1. Introduction

Benthic-pelagic coupling can be summarised as the quantitative relationship between biological processes occurring in the water layer (pelagos) and in the seabed (benthos). (Grebmeier & McRoy 1989, Gooday & Turley 1990, Graf 1992). From the perspective of benthic ecology, this coupling consists of the delivery of algal organic matter being the ultimate food source for shelf and deep sea organisms and the return of the end products of benthic metabolism (nutrients, CO₂, metabolites) to the water column. The return of nutrients is of vital importance for the growth of algal communities in the upper water layer. The response of the benthic organisms timed with this phytodetrital input indicates food limitation and suggests adapted behaviour of the community to their food supply. To understand how and to which extent the benthos depends its food, it is essential to study the timing, the amount and the quality of the incoming phytodetritus on the one hand, and the timing and the degree of the benthic response on the other hand.

This thesis describes various aspects of the benthic-pelagic coupling in the southern and eastern part of the North Sea. Spatial and temporal (seasonal and tidal) variations in the composition and flux of phytodetritus were measured conjointly with the metabolic processes occurring in the sediment. So-called biomarkers, phytopigments and fatty acids were used to indicate for the amount, quality and origin of particulate organic matter in water and sediments. The benthic metabolism was assessed by determining oxygen demand and bulk RNA and DNA concentrations in the sediment.

1.2. Benthic ecology

Until the early seventies, the accepted view was that benthic organisms were sustained by a steady vertical rain of particles to the seabed (Steele 1974). The finding that this supply was pulsed and depended on the seasonal succession of algal communities in the upper photic water layers, in both deepsea and shelf seas, profoundly changed the view on benthic ecology (Smetacek & Hensrikson 1979, Billett et al. 1983, Baker et al. 1985). Since then, many aspects of benthic ecosystem functioning and of the ecology of individual benthic organisms have been addressed in the context of the seasonal or otherwise pulsed input of benthic food. Sediment oxygen uptake, nutrient fluxes, growth and metabolism of organisms, hatching and spawning of e.g. bivalves, all these aspects have demonstrated to be importantly governed by the intra-annual variation in detritus sedimentation (De Wilde et al. 1984, Christensen & Kanneworff 1985, Rowe & Phoel 1992, Campos-Creasey et al. 1994, Lozano et al. 1995).

The insight into the temporal variation of benthic processes developed parallel with growing knowledge about the seasonal processes in the water column. The algal community displays an annually recurrent succession, both in primary production and in species composition. This succession depends on light, and properties of water bodies like temperature and nutrient concentrations, wind (water turbulence) and grazing by zooplankton (e.g. Bauerfeind et al. 1990, Kierboe et al. 1990, Tett et al. 1993, Van der Wal et al. 1993). In temperate shelf seas, like the North Sea, springtime normally displays an algal bloom mostly of diatoms. However, in coastal areas increasingly often a bloom is formed by Phaeocystis sp., thought
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to be related to increased eutrophication (Bätje & Michaelis 1986). Depleting concentrations or changing ratios of nutrients, water temperature and wind often invoke a change in the algal production and species composition. The amount and composition of sedimenting phytodetritus (Billett et al. 1983, Olesen & Lundsgaard 1985) usually reflect such changes, whether or not mediated by zooplankton grazing (Welschmeyer & Lorenzen 1985, Kiørboe et al. 1990, Brussaard et al. 1995).

The availability of fresh organic particles for benthic organisms is not only governed by the production and subsequent export from the productive photic zone but also by the water depth and the hydrography. Depth is a critical factor determining the quality and quantity of detrital particles reaching the sea floor. With increasing depth, the residence time of particles in the water column is longer, which leads to more intensive grazing on and degradation of particles. Hence, in deeper waters the sea floor receives lower amounts of particles of lower quality (Salén et al. 1982, Hedges et al. 1988, Lee & Wakeham 1988). Near-bottom currents, next to being indispensable for the oxygen supply to benthic organisms, largely determine which particles stay in suspension or settle on the seafloor, thereby setting the limits for sediment morphology (Eisma & Kalf 1987a). High (tidal) current velocities can cause resuspension of settled detritus which brings particles temporarily out of reach of the benthic organisms. Further, alternate sedimentation and resuspension is accompanied by the process of aggregation and disintegration. This causes a change in the physical properties of particles (Allèredge & Gotschalk 1989, Turley et al. 1995, Kiørboe et al. 1996), which itself influences the sedimentation and resuspension of particulate material (Chen et al. 1994, 1995). Ongoing resuspension might eventually transport detritus from the area of production (Van Haren & Joordens 1990). Furthermore, currents do not only influence the supply but also the intake of particles by organisms feeding in the near-bottom water layer. High near-bottom current speeds may limit the feeding capacities of suspension-feeding organisms (LaBarbara 1984, Fréchette et al. 1989, Miller et al. 1992). Next to its importance for the functioning of the benthic ecosystem, the near-bottom current regime also facilitates the dispersion and settlement of planktonic larvae of benthic organisms (Roegner et al. 1995) and hence the structure of benthic communities (see reviews by Osman & Whitlatch 1996, Eckman 1996, Hadfield & Strathmann 1997).

After detritus is deposited on the seafloor, it becomes buried by the mediation of physical and biological processes. Its subsequent mineralisation is in most cases largely performed by bacteria. Both aerobic and anaerobic bacteria dominate the degradation processes in marine sediments (Henrichs & Doyle 1986, Mackin & Swider 1988, Jørgensen & Revsbech 1989). Although the direct contribution of the larger infaunal organisms (meiobenthos and macrobenthos) to detritus mineralisation usually is minor, they exert an important indirect influence through bioturbation and bio-irrigation. Mobile deposit-feeding meiofauna and macrofauna are responsible for horizontal and vertical mixing the organic matter in the sediments, thus bringing bacteria and organic matter with each other in contact. Through mixing and bio-irrigation, i.e. creating water flows through sediment burrows, they stimulate the exchange of nutrients, oxygen and breakdown products between the sediment and the water. In this manner, they enhance bacterial metabolism and organic matter degradation (Bianchi et al. 1988, Yingst & Rhoads 1980, Webb & Montagna 1993, Osinga et al. 1997, Diaz et al. 1994, Van Duyl & Kop 1994).

The majority of the non-predatory metazoans thrive either on the phytodetritus, the bacteria, or on a combination of both. Especially some benthic protozoa, like nanoflagellates (Hondeveld et al. 1994), and meiofauna, such as certain nematode species (Moens & Vincx 1997), have specialised in feeding on bacteria. On the other hand, other
protozoa (foraminifera) and most macrobenthos seem to rely more on phytodetritus for growth and metabolism (Christensen & Kanneworff 1985, Gooday & Turley 1990, Campos-Creasey et al. 1994), although various species seem to be able to adapt their ingestion to the prevailing food source (Pearson & Gage 1984).

Knowledge on primary production, and the factors influencing its spatial and temporal succession, has advanced far enough to be able to create quantitative models. However, many questions still remain unanswered concerning the relation between pelagic physical and biological processes and the structure and functioning of benthic ecosystems. What proportion of the primary production arrives when at the seafloor, and what is its composition? If it is resuspended and transported by currents, what is the contribution of advection to benthic organic matter supply? Does the nature of the organic matter change as a result of these processes? How much and which quality of particles is available to benthic organisms? Furthermore, the food web structure of benthic ecosystems is largely unknown. Studies on the gut contents of macrobenthic species have revealed their ingestion preferences. However, the feeding habits of smaller organisms remain unclear for many species, as do the variability of feeding, the metabolic and life-history adaptations to changing food supply and quality, the competition for food sources and the partitioning of the available food, etc. As yet, models regarding organic matter processing in and the ecology of benthic systems are still in their infancy. The large spatial heterogeneity in organic matter concentrations and faunal distributions in the sediments, the low accessibility of the seafloor, the high diversity in habitats and a lack of laboratory experiments and quantitative field studies can be considered as the main reasons why marine benthic ecology in subtidal habitats lags behind in comparison to other study areas.

This thesis contains studies on North Sea benthic ecology pertaining to the amount and composition of particulate organic matter near and in the seabed, its temporal and spatial variation, and the concurrent metabolic response of the benthic community. Both qualitative and quantitative queries are treated, directed at a better description of the labile organic matter present in the benthic realm, and at the balance between supply of detritus to and its mineralisation in sediments.

1.3. Biomarkers

Novel developments in analytical chemistry, especially chromatography, have enabled researchers to unravel the chemical composition of labile organic material and tissues of organisms to a high degree. However, as Blumer (1975) already stated, we cannot analyse all of those thousands, if not millions, of organic molecules that make up the organic matrix in natural systems. Therefore, we have to select certain individual compounds that tell us a specific story. Such compounds or groups of compounds are called biomarkers. Thus, the following definition is used here: biomarkers are those organic molecular compounds that uniquely indicate for specific organism groups, or specific (bio)chemical and ecological processes.

An extended description of the most frequently used biomarkers in marine ecology is outside the scope of this chapter. It suffices to say that the major compound groups such as proteins, sugars and lipids all contain individual compounds, rather simple as well as complex molecules, which can be used as indicators for certain ecological processes. In the studies described in this thesis, attention is given to two special groups of (lipid) biomarkers, viz. phytoglobins and fatty acids. These compounds are called lipid biomarkers, because they are extracted with, relatively apolar, organic solvents.

Especially on phytoglobins there exists a considerable body of knowledge concerning the chemotaxonomy of these components.
Reviews on phytopigments and their physiological functions are given by Jeffrey (1980), Rowan (1989) and Jeffrey and Vesk (1997). Phytopigments in the marine environment occur in all phototrophic organisms, which are mainly algae but also some species of bacteria (cyanobacteria, purple and green bacteria) belong to this group. The phytopigments themselves can be discriminated into two functional groups, viz. the chloropigments and the carotenoids. Chloropigments consist of all chlorophylls, viz. chlorophyll $a$, $b$, $d$, divinyl-chlorophylls and chlorophyll $c_1$, $c_2$ and $c_3$. Carotenoids are the main accessory pigments, of which fucoxanthin is one of the most widespread among the various algal groups. Furthermore, and this is crucial in the use of phytopigments as biomarkers, up to a certain extent phytopigments or a combination of them are specific for the group to which an algal species belongs. High concentrations of fucoxanthin and chlorophylls $c_1$ and $c_2$, in combination with diadinoxanthin are characteristic for bacillariophyceae (diatoms), alloxanthin is specific for cryptophyceae, peridinin is typical for (autotrophic) dinoflagellates, etc. Therefore, in pelagic ecology the phytopigment composition in the water column is often used to follow algal species succession (e.g. Gieskes & Kraay 1983, Van der Wal et al. 1993) or to distinguish different water masses (Claustre et al. 1994). Hence, since detritus supply in most subtidal habitats predominantly originates from the algal production in the photic zone, the chlorophyll $a$ concentration in sedimentary organic matter reveals the input of recently deposited phytodetritus. Algal matter is a high-quality food source for most heterotrophic organisms; it contains high concentrations of proteins, lipids, sugars and other essential compounds (e.g. Navarro et al. 1996). As will be explained further on, algae also contain high amounts of essential lipids, the polyunsaturated fatty acids (e.g. Skerratt et al. 1995). Because of the high correlation between chlorophyll $a$ and essential polyunsaturated fatty acids, chlorophyll $a$ can also be called a quality marker for organic matter as a food source for benthic invertebrates. A further insight into the quality of algal detritus is given by the principal degradation products of chlorophyll $a$, the phaeopigments. These pigments, mainly consisting of phaeophorbides $a$ and phaeophytins $a$, are normally absent from living algal material. However, when algal matter is senescent or decaying, enzymatic activity from the algal cell itself (autolysis) or from bacteria and metazoons can produce these molecules. The proportion of phaeopigments to chlorophyll $a$ can therefore act as an additional quality marker. Modern reversed-phase high-performance liquid chromatography (HPLC) can detect the whole set of phytopigments in one analysis, chloropigments, phaeopigments and the carotenoids (Gieskes & Kraay 1983, Mantoura & Llewellyn 1983).

The next group of biomarkers used in the studies described in this thesis concerns the fatty acids. Fatty acids are found in the cell membranes of all living organisms and in energy reserves of all metazoons. They are mostly part of a larger complex of molecules, phospholipids in the case of membranes, and triglycerides or wax esters in the case of energy reserves (Gurr & James 1980). Important is to note that at certain points the biosynthetic pathways of fatty acids diverge between bacteria, algae, vascular plants and animals. Saturated, odd-numbered, branched fatty acids, especially iso and ante-iso C15 and C17 (with 15 and 17 carbon atoms, respectively), are specifically produced by bacteria (Haack et al. 1994, Rajendran et al. 1994). On the other hand, algae and vascular plants have the unique ability to create straight, long-chain polyunsaturated fatty acids (pufas), especially C20:5 and C22:6 (respectively, with 20 carbon atoms and 5 unsaturated bonds, and with 22 carbon atoms and 6 unsaturated bonds) (DeMort et al. 1972, Volkman et al. 1989). Furthermore, terrestrial (vascular) plants produce waxes in the epi-cuticular layer on their leaves. These waxes contain even-numbered, saturated straight long-chain fatty acids with more
than 22 carbon atoms. River input into coastal seas can often be traced in this manner (Salot et al. 1988). Animals do not possess the biosynthetic pathways to produce the above mentioned branched and polyunsaturated fatty acids. Their lipid composition with respect to these fatty acids depends on what they feed. Among other things, pufas perform an important role in maintaining the fluidity of cell membranes under low temperatures and are thus essential fatty acids for most animals (Langdon & Waldock 1981, Marsh et al. 1989, Delaunay et al. 1993).

Thus, the fatty acid composition of organic matter in water and sediments gives important clues about the origin and quality of the organic matter. Since unsaturated fatty acids are faster degraded than saturated fatty acids, the proportion of these components in the total fatty acid pool can act as a marker for the state of degradation of the labile organic matter.

Gas chromatography in combination with mass spectrometry (GC-MS) is a suitable method for identification and quantification of the fatty acids present in organic matter. (Kennicutt & Jeffrey 1981).

1.4. Research area: the North Sea

The North Sea is a semi-enclosed coastal shelf sea in the north-west of Europe (see Fig. 1.1). Following a counter-clockwise net water circulation, with an additional input of water from the English Channel (Otto et al. 1990), suspended matter is transported likewise (see arrows in Fig. 1.1). Ultimately, it is deposited in the Wadden Sea, the German Bight and especially the Skagerrak (Eisma & Kalf 1987a).

The southernmost part of the North Sea, between the Netherlands and the United Kingdom is characterised by strong tidal near-bottom water currents, up to 100 cm.s\(^{-1}\) near the English Channel (Jago et al. 1993). The sediment consists mostly of medium coarse to fine sand with areas of gravel near the English coast. This area is characterised by a lack of sedimentation. More likely, it is an area of net-erosion from the seafloor and the coastal areas (Eisma & Kalf 1987a).

There is a considerable input of suspended matter from the continental rivers (Eisma 1981). Around the north of the Netherlands, currents follow the coastline and bend towards the German Bight, an area at the outlet of the German river Elbe. Despite relatively high tidal current velocities, a substantial deposition of suspended matter is found here (Eisma & Kalf 1987a, Puls et al. 1997). The southern North Sea, especially along the Dutch coast and in the German Bight, demonstrates a high phytoplankton production partially caused by high nutrient levels as a result of eutrophication (Bauerfeind et al. 1990, Reid et al. 1990).

About 40 nautical miles north of the Dutch Wadden islands, roughly at the 40-m isobath and at the transition zone from the Southern Bight to the Oyster Ground, the Frisian Front is situated. It is characterised by lower current velocities than in the southern Bight (\(< 25 \text{ cm.s}\(^{-1}\)). Temporarily, suspended matter settles, but no net deposition occurs (De Haas et al. 1997). Important to note is that this tidal front demonstrates an increased primary production, benthic biomass and macrobenthic abundance, compared to areas north and south of it. This is most likely the result of the enhanced settlement of phytodetritus, in combination with the reflux of nutrients to the photic zone, stimulating primary production (Baars et al. 1991, Creutzberg 1985). North of this zone, the sea floor levels off at ca. 50-m depth, until it rises again to about 20 m in the north where the Dogger Bank is situated. This area is called the Oyster Ground, a basin-shaped area with a depth of \(~50\) m, characterised by moderate current velocities (max. 15 cm.s\(^{-1}\). Van Raaphorst et al. 1998), a lack of net-deposition and sediments consisting of fine sand with silt. The North Sea north of the Oyster Ground has not been a study area and will not be treated further.

The Skagerrak, in the north-eastern North Sea, is a hydrographical complex area (Svansson 1975). Its relatively large depth (max. 760 m) is an extraordinary feature in
the bottom topography of the North Sea. Annually, $46 \times 10^6$ tons of sediment accumulate in this area (De Haas & Van Weering 1997). Although near-bottom currents are usually relatively weak (5 - 10 cm.s$^{-1}$, Svansson 1975), they can periodically become stronger, thereby transporting material in pulses into the area. The sediments here contain high concentrations of clay and silt.

1.5. Research rationale and thesis outline

The studies described in this thesis are part of a research programme jointly acquired by and carried out at the Netherlands Institute for Sea Research (NIOZ) at Texel, the Netherlands, and the Centre for Estuarine and Marine Ecology (NIOO-CEMO) in Yerseke, the Netherlands. The project has been funded by the Netherlands Organisation for Scientific Research (NWO) in The Hague, as a part of the Dutch Global Change Programme (Verstoring van Aardsystemen, VvA). Part of the programme was called Carbon sinks in the North Sea (VvA, theme 4), and was directed at studying the geological, chemical and biological mechanisms relating to the deposition of organic matter to the bottom in the southern and eastern part of the North Sea. The idea behind the VvA programme was to study the possible negative and positive feed-back mechanisms for the so-called intensified greenhouse effect as a result of carbon dioxide emissions by man, which would give a better insight in the marine carbon cycle.

The shelf seas are responsible for a fifth to a third of the global marine primary production, while they make up less than a tenth of the Earth’s surface. It has been postulated that the carbon which is not recycled within the marine biological system, is either buried on the shelf itself, or transported to and deposited on the continental slopes (Walsh et al. 1991, Hedges & Keil 1995). Concerning the role of continental slopes as depo-centres, other programmes have been initiated, such as the Ocean-Margin Exchange (OMEX) projects.

The studies described in this thesis have focused at the nature and fate of biogenic carbon in the benthic realm of the North Sea. More specifically, the objectives of this project were to:

- describe and quantify the particulate organic matter sedimenting to the seabed;
- assess the concentration and nature of the recently buried organic matter in the sediment;
- monitor the metabolic reaction of the benthic ecosystem;
- acquire insight in the temporal and spatial variation in the above mentioned processes, especially regarding locations in the North Sea considered as depositional and non-depositional areas.

From previous studies on sediment communities (Duineveld et al. 1991), and nutrient fluxes at the sediment-water interface in the North Sea (e.g. Lohse et al. 1995), it was expected that notable differences would be found in the amount and type of detrital material supplied to and present in these sediments and the concurrent benthic metabolism in various areas in the North Sea. To highlight these differences, stations were chosen on basis of their differences in depth, sediment type and hydrography, thus representing certain benthic habitats within the North Sea. Another criterion for the selection was the knowledge already present on other ecosystem aspects (pelagic, sediment communities, nutrient fluxes at the sediment-water interface, bacterial production). A total of 5 stations were selected, one at the Broad Fourteens (in the Southern Bight), one at the Frisian Front, one at the Oyster Grounds, one in the German Bight, and one in the Skagerrak. A detailed description of these stations is given in the chapters in question.

In chapter 2, the origin and quality of particulate organic matter in the near-bottom water at four selected locations in the
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North Sea are described. Samples were taken during winter, spring and late summer 1994. Organic carbon, total nitrogen, chlorophyll $a$ and fatty acids were analysed on samples obtained with three sampling techniques, from the lowest 3 meters of the water column. Spatial and seasonal variations in particle concentrations and composition are discussed within the context of local hydrography and as a food source for benthic invertebrates.

Chapter 3 goes into more detail on the short-term (tidal) variations of the amount and composition of particles in the near-bottom water. Two locations in the southern North Sea were sampled during 12 consecutive hours in fall 1995 and spring 1996. Changes in the amount and composition (total suspended matter, organic matter and chlorophyll $a$ concentration) of samples from 3 meter above bottom and from the bed load are given. They are evaluated in the light of differences in local hydrography and their relevance as a food source for benthic animals.

Chapter 4 describes the annual cycle of phytodetrital input to the sediments and the benthic oxygen consumption at three locations, south of, at and north of a frontal zone, in the southern North Sea in 1993. Furthermore, the growth of a deposit-feeding bivalve was monitored. The seasonal variations of the amount and (algal group) composition of the phytodetritus are discussed, and compared with the variations in benthic oxygen demand and bivalve growth.

In Chapter 5, the down-core concentrations of chlorophyll $a$ in the sediments at the three above mentioned stations across the Frisian Front are modelled. Fluxes of chlorophyll $a$-related carbon to the sediment are calculated and compared with the carbon mineralisation, which was deduced from the sediment oxygen consumption. The seasonal differences between supply and degradation of carbon at the three sites are discussed, and an annual carbon budget is estimated.

Chapter 6 contains a study on the amount and quality of labile organic matter in the sediment at 4 stations in the North Sea, and the concurrent benthic metabolic reaction measured during winter, spring and late summer 1994. The difference with the two former chapters is that in this study two depositional and non-depositional areas were visited (the same as in chapter 2). Further, next to chlorophyll $a$, also fatty acids have been analysed, giving additional information on the nature of sedimentary organic matter. The benthic response to the mainly phytodetrital input has been assesses not only with oxygen consumption measurements, but also with RNA and DNA concentrations in the sediment. Results are discussed within the context of the balance between supply and mineralisation, and of the origin and fate of labile organic matter. Striking discrepancies between the supply and mineralisation of organic matter at station Skagerrak are highlighted.

Lastly, in chapter 7 the results of the studies in chapter 2 to 6 are summarised. Further, the studies in this thesis are shortly reflected, and an outline for future research in this field is given.