Bivalve grazing, nutrient cycling and phytoplankton dynamics in an estuarine ecosystem

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BIVALVE GRAZING, NUTRIENT CYCLING AND PHYTOPLANKTON DYNAMICS IN AN ESTUARINE ECOSYSTEM

T.C. Prins

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Stellingen

1. Grazers vergroten de hoeveelheid anorganische nutriënten in de waterkolom zowel door regeneratie, als door vermindering van de hoeveelheid nutriënten opgeslagen in fytoplanktonbiomassa.
Sterner, 1989. In: Plankton ecology: succession in plankton communities, Sommer (ed.), Springer Verlag, Berlin, 107-170.
Dit proefschrift

2. De hypothese van Sterner dat nutriëntenregeneratie door zoöplankton de P-limitatie van het fytoplankton kan versterken, als gevolg van het feit dat de P-excretie door het zoöplankton dan relatief laag is ten opzichte van andere nutriënten, berust op de onjuiste veronderstelling dat de nutriënten ratio bepalend is voor de mate van limitatie van het fytoplankton.
Sterner, 1989. In: Plankton ecology: succession in plankton communities, Sommer (ed.), Springer Verlag, Berlin, 107-170.

3. De biodepositie door mossels in de Oosterschelde is door Ten Brinke & Dronkers sterk onderschat als gevolg van de aanname dat mossels in de winter een lage filtratie-activiteit hebben.
Ten Brinke & Dronkers, 1993. Neth. J. Sea Res. 31: 19-36.
Dit proefschrift

4. Verhoging van de nutriëntenbelasting van de Oosterschelde zal, bij gelijkblijvende schelpdierbiomassa, niet leiden tot een aanzienlijke toename in fytoplanktonproduktie.

5. Uit het belang van hoge lichtinstraling voor de vorming van *Phaeocystis sp.* kolonies kan worden afgeleid dat slecht weer in het late voorjaar gunstig is voor de mosselgroei.
Peperzak, 1993. J. Plankton Res. 15: 809-821
Dit proefschrift

6. De Nederlandse natuur wordt vaak met een park vergeleken; vanwege de vele vogel-, egel- en zeehondenopvangcentra is de analogie met een verzorgingstehuis toepasselijker.

7. Het verdient aanbeveling politici eerst met de modellen van het Centraal Plan Bureau te laten werken voordat ze hun beleid op de resultaten baseren.

8. De term 'flexibilisering van de arbeidsmarkt' wekt ten onrechte de suggestie dat er ook voor werknemers iets te kiezen valt.

9. Een weg is bergopwaarts langer dan bergafwaarts.

Stellingen behorend bij het proefschrift *Bivalve grazing, nutrient cycling and phytoplankton dynamics in an estuarine ecosystem* van Theo Prins
Wageningen, 7 februari 1996

VOORWOORD

Dit proefschrift is het resultaat van onderzoek dat ik de afgelopen jaren heb uitgevoerd in opdracht van het Rijksinstituut voor Kust en Zee. Tijdens dit onderzoek en het schrijven van mijn proefschrift heb ik ondersteuning gehad van vele mensen en instanties, die ik graag op deze plaats wil bedanken:
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Richard Dame participated in some of our field experiments. I would like to thank him for the many stimulating discussions and his comments on manuscripts. I am very pleased that he wanted to be a member of the committee.
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With Harald and Ragnhild Asmus of the Biologische Anstalt Helgoland we carried out an intercalibration experiment between the tunnel and the 'Sylt flume' in Königshafen at the Island of Sylt. I would like to thank them for the pleasant collaboration, the animated discussions and their hospitality.
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Gerhard Cadée heeft fytoplankton gegevens van het Marsdiep beschikbaar gesteld.
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Tot slot wil ik het Rijksinstituut voor Kust en Zee bedanken voor de financiële ondersteuning.

CONTENTS

INTRODUCTION

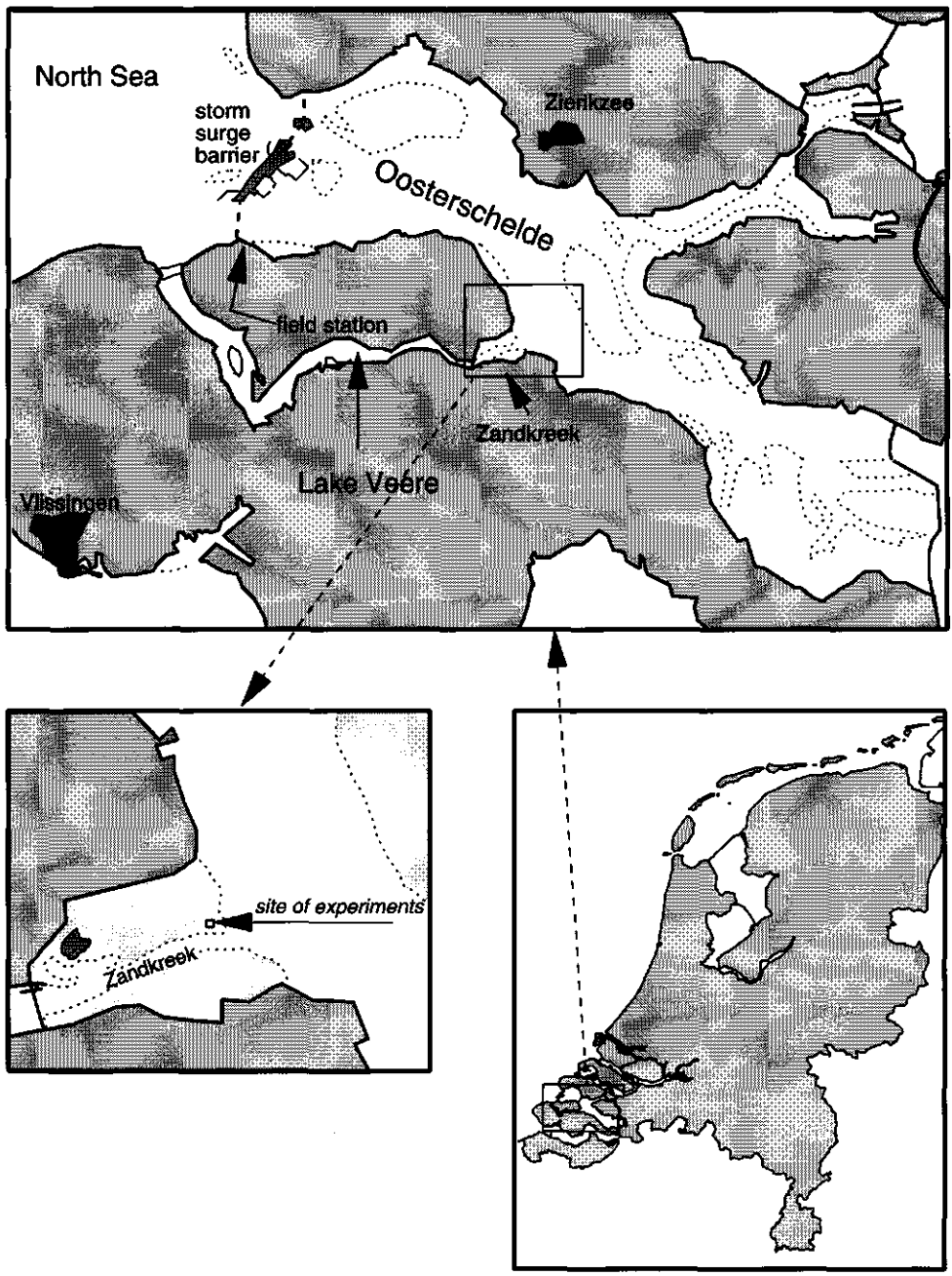

Figure 1.1. Map of the Oosterschelde estuary. Dotted lines indicate intertidal flats.
At the detailed map of the Zandkreek the site of the experiments is indicated. Light shaded areas are intertidal flats.

It is commonly accepted in ecology that plant biomass and production can be controlled by the availability of limiting resources (nutrients, light). In the last decade, there has been growing attention for the effect of trophic interactions with herbivores on composition, biomass and production of the producers. The relative contribution of bottom-up (resource limitation) and top-down (consumer control) forces is still a subject of much debate (Hunter & Price, 1992; Power, 1992). Top-down effects of herbivores on plants have been observed in terrestrial systems, but the most striking examples stem from studies of aquatic algal communities (Strong, 1992).

Grazing may quantitatively affect the plant community by decreasing plant biomass. In addition, there are many qualitative effects of grazing on plants. Field and laboratory observations indicate that grazing may stimulate plant growth rates (a.o. McNaughton, 1979; Sterner, 1986). The main factor enhancing algal growth rates in aquatic systems seems to be the effect of grazers on nutrient availability (Sterner, 1986; Bianchi & Jones, 1991). Grazing can increase the availability of nutrients directly through excretion by the animals or mineralization of waste products, or indirectly by reducing the biomass of primary producers resulting in a reduced storage of nutrients in plant biomass (Sterner, 1989). Consequently, an increase in grazing pressure may lead to a stimulation of plant growth rates, which under certain conditions may even lead to an optimization of primary production under moderate grazing levels (McNaughton, 1979; Hilbert et al., 1981).

In natural planktonic systems with a multi-species algal community, indirect effects of grazing may result in more complex responses. The composition of the phytoplankton is the net result of specific growth rates, and mortality rates due to grazing or other factors (e.g. sedimentation). Species differ in the response of their growth rates to nutrient supply, and the combined effect of grazing losses, changes in nutrient availability and competition for limiting resources can lead to shifts in the phytoplankton community. In its turn, this shift in composition may affect the level of primary production (Carpenter & Kitchell, 1984; Bergquist et al., 1985). Moreover, the stoichiometry of nutrients regenerated by the grazers, may deviate from the nutrient ratios of their food source. This may affect the stoichiometry of the algal nutrient resource and influence algal succession (Sterner, 1989). Summarizing, there are a number of direct and indirect mechanisms related to grazing, that affect the response of planktonic communities to grazing and modulate the top-down control of herbivores on their food source.

In many temperate shallow coastal systems bivalve suspension feeders are dominant components of the ecosystem, and are often the most important consumers of phytoplankton (Wolff, 1983). The abundance of bivalve suspension feeders in estuaries has led to early recognition of the potential effect of suspension feeding bivalves on

sedimentation of particulate matter. Verwey (1952) suggested that the filtering activity of the cockle *Cerastoderma edule* and the mussel *Mytilus edulis* in the Dutch Wadden Sea enhanced the deposition of locally produced organic material as well as of allochtonous organic material, imported from the North Sea. From his estimates he inferred that the activity of the bivalves played an important role in the sedimentation processes in the Wadden Sea. Similar early statements about the impact of bivalves on estuarine sedimentation were made by Haven & Morales-Alamo (1966, 1972).

From field observations of low phytoplankton concentrations in an area of extensive mussel culture Cadée & Hegeman (1974) suggested that mussel grazing had severely reduced phytoplankton biomass in this part of the Wadden Sea. Direct observations of phytoplankton concentrations in water flowing across bivalve beds showed that the bivalves can deplete water of phytoplankton in shallow coastal areas (Wright et al., 1982; Carlson et al., 1984). Observations in San Francisco Bay led to the hypothesis that bivalve grazing kept phytoplankton biomass at a low level (Cloern, 1982; Nichols, 1985), and could act as a eutrophication control, maintaining phytoplankton biomass in estuarine systems low in spite of high nutrient supply (Officer et al., 1982).

For a long time, the effect of bivalve suspension feeders on nutrients has merely been considered as a process removing nutrients from the water column (e.g. Kuenzler, 1961; Jordan & Valiela, 1982). It was hypothesized by Dame et al. (1980) that bivalve communities may form a major coupling between the water column and the benthic system, by translocating particulate material from the water column to the sediments, and by forming a key link in estuarine biogeochemical cycles. Observations showed that high amounts of nutrients were regenerated by oyster reefs, and it was suggested that the bivalves may form a major feedback loop between the benthic and the pelagic system (Dame et al., 1984). Estimates of the amounts of nutrients regenerated through excretion by mussel populations and through mineralization of biodeposits led to the suggestion that this regeneration might have a positive feedback on phytoplankton primary production in parts of the Baltic Sea (Kautsky & Wallentinus, 1980; Kautsky & Evans, 1987). In an extensive study of Lake Grevelingen, a stagnant, saline lake, it was shown that benthic suspension feeders (mainly *Mytilus edulis*) were the main consumers of phytoplankton (De Vries, 1984). The bivalves also had a major influence on nutrient cycling by increasing storage of nutrients in the benthic system and accelerating regeneration of nutrients through excretion and mineralization of biodeposits. It was suggested that this stimulation of nutrient regeneration promotes phytoplankton growth (De Vries & Hopstaken, 1984).

From the above it can be inferred that bivalves are dominant consumers in many shallow coastal ecosystems, and can be considered key-stone herbivores (Strong, 1992). However, most statements about the effects of bivalve grazing on the pelagic system are based on extrapolations of laboratory measurements with individual animals to the scale

of an entire estuary (e.g. Cloern, 1982; Officer et al., 1982). These estimates may represent a severe overestimation of *in situ* feeding rates (Doering & Oviatt, 1986). At the time the present study was initiated, only limited information was available on the quantitative importance of the feedback loop from bivalves to the pelagic system by nutrient recycling, as hypothesized by Dame et al (1980, 1984). Studies had shown that oyster reefs release significant amounts of inorganic nutrients (Dame et al., 1984, 1985). Mussel beds in the Dutch Wadden Sea had also shown high rates of nutrient release to the water column (Dame & Dankers, 1988).

In this thesis, we have tested the hypothesis that the population of the blue mussel *Mytilus edulis* exerts a top-down control of phytoplankton biomass by grazing, and has a major impact on nutrient cycling in an estuarine system like the Oosterschelde. The combination of grazing control and nutrient regeneration may promote phytoplankton growth rates and can induce functional and structural changes in the planktonic community. Part of this hypothesis has been tested by evaluating the results of *in situ* observations of material exchange between mussel beds and the pelagic system. The effect of bivalve grazing on functioning and structure of the phytoplankton has been studied in a mesocosm experiment.

The effect of bivalves on nutrient cycling, and the quantitative significance on ecosystem level, has become the subject of a number of studies in recent years. Some of these studies have attempted to quantify the exchange of material between the pelagic system and a bivalve community by the use of *in situ* methods (Dame et al., 1984, 1985, 1989; Dame & Dankers, 1988; Asmus et al., 1990; Asmus & Asmus, 1991). Mesocosm studies established the impact of bivalves on nutrient cycling and production (Doering & Oviatt, 1986; Doering et al., 1986, 1987) and the effect of grazing on the pelagic community (Horsted et al., 1988; Riemann et al., 1988, 1990; Olsson et al., 1992; Granéli et al., 1993). In the present study, research was focused on the Oosterschelde estuary and the effect of the blue mussel *Mytilus edulis* on the cycling of particulate and dissolved nutrients.

The Oosterschelde estuary as a case study

The Oosterschelde is an estuary with a high biomass of benthic suspension feeders. The most important species are the cockle *Cerastoderma edule* (average annual biomass 5.0 g C m^{-2}) and the blue mussel *Mytilus edulis* (5.6 g C m^{-2}), and the biomass of these species exceeds the biomass of other benthic suspension feeders (tunicates, sponges, hydroids, oysters; 2.7 g C m^{-2}) or zooplankton (0.5 g C m^{-2}). First estimates of the filtration activity of mussels and cockles showed that the bivalves can potentially filter the entire volume of the estuary within 4-5 days (Smaal et al., 1986). The animals consume a major part of the phytoplankton primary production (Scholten et al., 1990),

while microphytobenthos is assumed to be unimportant as a food source (Smaal & Van Stralen, 1990). Consequently, the Oosterschelde estuary is a typical example of a system where bivalve suspension feeders can have a strong impact on the pelagic system through filtration of material. Model simulations indicate that phytoplankton biomass is likely to be subject to severe top-down control by the population of bivalve suspension feeders (Herman & Scholten, 1990).

The Oosterschelde estuary has shown some drastic changes in the hydrography in the 1980's, as a consequence of the construction of a storm-surge barrier in the mouth of the estuary and a number of auxiliary dams at the landward ends of the estuary (Fig. 1.1). Before the construction of the storm-surge barrier, the residence time of the water in the estuary was 5-50 days, the tidal volume was $1230 \cdot 10^6$ m^3 and the freshwater load was low (70 m^3 s^{-1}). After the construction of the barrier and auxiliary dams in 1987 the tidal volume had decreased to $880 \cdot 10^6$ m^3, the residence time had increased to 10-150 days and the freshwater load had been reduced to 25 m^3 s^{-1}. As a result of the reductions in freshwater load the system may nowadays be characterized as a tidal bay with a low external nutrient loading (Smaal & Nienhuis, 1992). Production by phytoplankton contributes for *ca* 85% to overall primary production (Scholten et al., 1990). As a consequence of the limited exchange with the North Sea, import of allochtonous organic matter was relatively unimportant in both the pre- and the post-barrier situation: the Oosterschelde functions as a self-sustaining ecosystem (Scholten et al., 1990). Phytoplankton primary production was nutrient limited during most of the spring-summer season in the pre-barrier situation. Mainly as a result of the reduced fresh water loads after the construction of the auxiliary dams inorganic nutrient concentrations have decreased and the period of nutrient-limitation of the phytoplankton (predominantly N and Si) has extended (Wetsteyn & Kromkamp, 1994). Regeneration of nutrients within the estuary is assumed to be an important nutrient source for primary production during spring and summer, and this process has gained relative importance after 1987 due to reduced external loading. Nutrient regeneration by the bivalve suspension feeders in the estuary could potentially be an important factor influencing nutrient cycling and promoting phytoplankton growth rates.

Outline of this thesis

In this study, *in situ* measurements of the fluxes of particulate and dissolved material between a mussel bed and the water column were carried out. This was done by using a Benthic Ecosystem Tunnel, a flow-through tunnel that can be set up on an intertidal bivalve community. The use of the Benthic Ecosystem Tunnel as a device to measure *in situ* exchange of material between a mussel bed and the water column is evaluated in Chapter 2. To gain a better insight in the processing of particulate material

by bivalves under natural conditions, the uptake of particulate matter by an intertidal mussel bed was quantified. Chapter 3 presents results of *in situ* measurements carried out in the years 1987-1989. The effect of weather conditions on food supply to the mussel bed and on local resuspension processes are discussed. Observed *in situ* filtration is compared to results of laboratory measurements on individual filtration rates. Fluxes of inorganic nutrients from the mussel bed to the water column have also been measured during these *in situ* experiments. Results are presented in Chapter 4. In Chapter 5, the composition of the fluxes of particulate and dissolved material is compared and used to determine the proportion of nutrients stored in the mussel bed. The relative contribution of excretion and mineralization to the regeneration of nutrients is estimated. The observed *in situ* release of inorganic nutrients by the mussel beds is used to assess the quantitative significance of nutrient regeneration by the mussels for the phytoplankton in the Oosterschelde. Chapter 6 presents the results of a year-round study of particulate matter filtration by the mussel bed, and the effects of seasonal variation in abiotic and biotic factors on filtration activity and the strength of top-down control of phytoplankton by mussel grazing. In a mesocosm study, the interactions between mussels and phytoplankton were studied. The effects of the mussels on nutrients, phytoplankton composition and production in the mesocosms are presented in Chapter 7. Finally, in Chapter 8 results are summarized and discussed.

CHAPTER TWO

IN SITU MEASUREMENT OF FLUXES OF PARTICULATE AND DISSOLVED MATTER BETWEEN A MUSSEL BED AND THE WATER COLUMN WITH A BENTHIC ECOSYSTEM TUNNEL; METHODOLOGICAL CONSIDERATIONS

ABSTRACT

The exchange of material between the water column and a mussel bed has been measured *in situ* with a Benthic Ecosystem Tunnel. Several experiments have been carried out to test the suitability of this technique for measurements at a mussel lot in the Oosterschelde estuary. Observations on the vertical concentration gradients of particulate matter in the field, and on the vertical distribution of fluorescence in the tunnel, showed that it was sufficient to measure the inflow and outflow of the tunnel at one sampling height for an accurate determination of inflow and outflow concentrations. The current speeds in the tunnel were reduced, compared to the current speeds outside the tunnel. This reduction caused a sedimentation of suspended particulate matter and particulate organic carbon in the tunnel in a control experiment. In a replication experiment two tunnels were employed simultaneously. Generally similar fluxes were observed with both tunnels.

INTRODUCTION

Several *in situ* methods are applied to quantify the exchange of material between the water column and the benthic system. One of the most commonly used methods is the application of bell jars. Although this method has been applied successfully at sediments with a relatively low biomass of benthic animals, it cannot be used when large suspension feeding bivalves are present because of the rapid depletion of oxygen and particulate matter, and the accumulation of ammonium. Another drawback of the method is the fact that the relatively limited water circulation in these devices may affect metabolic rates of the benthic system (Boynton et al., 1981).

First attempts to quantify material exchange between bivalve communities and the water column were made by sampling water upstream and downstream of a bivalve bed. This method has been used to measure respiration and phytoplankton uptake by bivalve suspension feeders. The method proved successful in small inlets or creeks, where the bivalves cover a large part of the area, lateral transport is impossible, and consequently a well-defined water mass flows across the bivalve bed (e.g. Nixon et al., 1971; Wright et al., 1982; Carlson et al., 1984). However, in many cases tidal flow patterns are more complex and special measures have to be taken to enclose a known volume of water during its passage across the bivalve population. In areas with relatively shallow water depths prevention of lateral transport will be sufficient, and this has been achieved by the construction of an open-channel flume on a mussel bed (e.g. Asmus et al., 1990). However, when the water column above the bivalve population is large or when current speeds are high, the flux of water across the bivalve bed has to be limited even more in order to be able to detect material exchange between the water column and the bivalves. A method developed especially for measurements on bivalve beds under the latter conditions is the Benthic Ecosystem Tunnel (BEST), a flow-through tunnel that covers part of a bivalve bed (Dame et al., 1984).

In this thesis, results are shown of measurements to quantify uptake and release of particulate and dissolved material by mussel beds in the Oosterschelde estuary. In June 1983 a first attempt was made to measure uptake of material by mussels in the Oosterschelde estuary. This was done by sampling the water column at two depths, 0.5 metre above the bottom and at mid depth, both upstream and downstream of a mussel lot. Sampling was carried out from two ships anchored at approximately 600 metres from each other. The results showed that concentrations of suspended particulate matter and chlorophyll-*a* were higher close to the bottom, compared to mid depth, and the measurements failed to show a decrease in concentrations after passage of the mussel lot (Steijaert, 1986). These results indicated that it was not possible to quantify fluxes between mussels and the water column in the Oosterschelde by the relatively simple method of sampling upstream and downstream of the mussel bed. In the Wadden Sea the Benthic Ecosystem Tunnel had successfully been employed on a mussel bed by Dame & Dankers (1988), and therefore this method was used to measure material exchange between the water column and mussel beds in the Zandkreek, an inlet that forms part of the Oosterschelde estuary.

In flux measurements with a Benthic Ecosystem Tunnel, certain requirements have to be met to get reliable results. A description of the current speed distribution in the tunnel is necessary for the calculation of the water flow through the tunnel. An analysis of vertical particle concentration gradients has to be made, as field and flume studies have shown that depletion of particulate material within the benthic boundary layer above a mussel bed may occur (Fréchette et al., 1989; Butman et al., 1994. This may lead to strong vertical gradients in particle concentrations, both at the inflow and at the outflow of the tunnel. If such vertical concentration gradients exist, the quantification of particle concentrations at the inflow and the outflow of the tunnel may not be accurate when only one sampling height is used, and this may result in serious biases in the estimated particulate matter uptake by the mussel bed (Fréchette et al., 1993). Finally, effects of the tunnel itself on fluxes between the water column and the sediment (e.g. enhancement of sedimentation or resuspension) have to be established.

Several experiments were carried out to study the methodological aspects of the Benthic Ecosystem Tunnel technique. A study was made of the vertical gradients in particle concentrations above the mussel lot in the Zandkreek. In addition, some experiments were carried out under controlled conditions to determine the patterns of current flow and particle distribution in the tunnel. The effect of the tunnel itself on fluxes of particulate and dissolved matter was determined in a control experiment, where all mussels had been replaced by empty shells. The accuracy of the estimated fluxes of particulate and dissolved matter between a mussel bed and the water column was evaluated based on the results of an *in situ* replication experiment, when two tunnels were employed simultaneously.

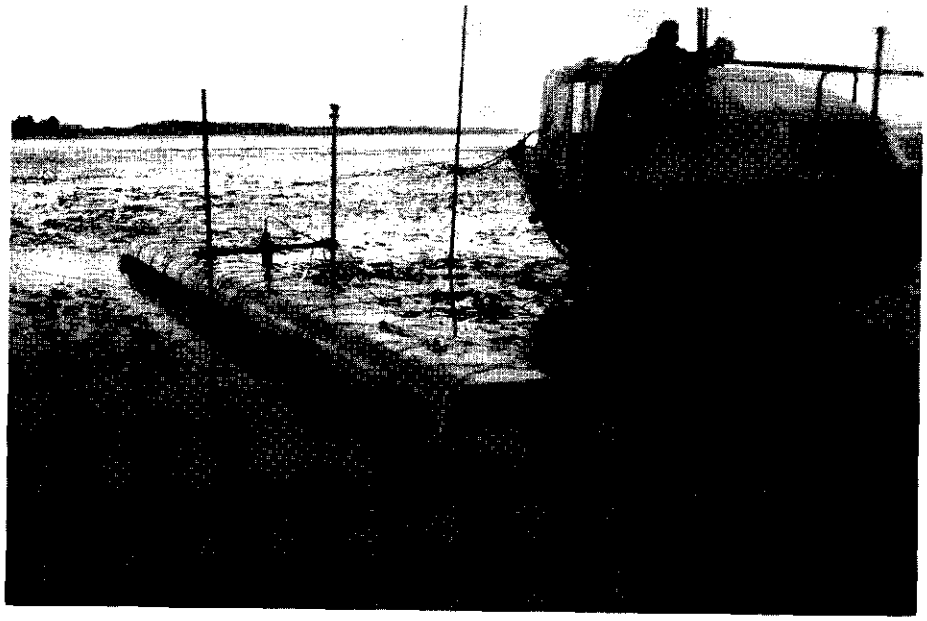

Figure 2.1. Photograph of a Benthic Ecosystem Tunnel.

MATERIAL AND METHODS

Description of the Benthic Ecosystem Tunnel

The benthic ecosystem tunnel technique was originally developed by Dame et al. (1984) for flux measurements on intertidal oyster reefs. The tunnel used in this study was a modified version of the tunnel used by Dame & Dankers (1988) for experiments on mussel beds in the Wadden Sea, with similar dimensions as the latter one. The tunnel (Fig. 2.1) consisted of 12 long plexiglass parts, joined by bolts. The plexiglass top of the tunnel was fixed on a frame of stainless steel plates, that were pushed into the sediment 15 cm deep, and were attached on 1 m long poles. This design ensured a firm and stable placement of the tunnel on the relatively soft sediment of the mussel bed. Neoprene gaskets prevented leakage at the connections between the plexiglass parts and between the top of the tunnel and the steel frame. The tunnel had a total length of 12 metre, and a width of 0.8 metre. The top of the tunnel was 40-45 cm above the sediment. Water was sampled at either end of the tunnel. The sampling height was 5 cm above the mussel bed. The length of the tunnel between sampling points was 9.6 metre and the cross-sectional area was 0.225 m^2. The bottom surface between the sampling points was 7.7 m^2. A NSW Meerestechnik current speed meter was mounted at the centre of the tunnel, with the

sensor at 20 cm above the bottom. During experiments current speeds were continuously measured with this current meter and data were stored on a datalogger.

In the field, the tunnel was set up during low water, with its longitudinal axis parallel to the observed main current direction. Care was taken not to disturb the part of the sediment or mussel bed within the tunnel or in front of both ends of the tunnel. Sampling of the inflow and outflow of the tunnel started as soon as the tunnel was entirely covered by water, and lasted until the tunnel started to fall dry. Water samples were collected with battery-driven pumps, from a ship anchored alongside the tunnel. Water in the tunnel is turbulently mixed at current speeds above 1 cm s^{-1} (Dame & Dankers, 1988). When current speeds were below 1 cm s^{-1}, no sampling was carried out.

Particle concentration profiles in the field

All BEST experiments have been carried out at an intertidal mussel lot, in the northeastern part of the Zandkreek, an inlet in the central part of the Oosterschelde estuary. The mussel lot was situated close to the tidal channel through the inlet, and lies at the edge of a deep channel in the main estuary (Fig. 1.1). The depth of the site is approximately 1.3 m below N.A.P. (Dutch Ordnance Level), and the inundation time is *ca* 9 hours. To determine the vertical distribution of seston and phytoplankton in the water column above a mussel lot at this site, samples were collected from three depths (5 cm above the bottom, 40 cm above the bottom, surface) on 22 January 1986 (Willemse, pers. comm.). Measurements were carried out from 1.5 hour before high water slack to 3 hours after high water slack. Maximum current speed during flood tide, measured at 40 cm above the bottom, was 18 cm s^{-1}. During ebb tide, maximum current speed was 30 cm s^{-1}. At a second sampling point at the mussel lot, approximately 50 m downstream from the first point, water samples were collected at 1 m above the bottom and at the surface. The concentrations of SPM, POC, and chlorophyll-*a* measured at the various sampling depths were compared with a two-way ANOVA, followed by a multiple comparisons test (Tukey-Kramer method, Sokal & Rohlf, 1981).

Velocity and particle concentration profiles in the Benthic Ecosystem Tunnel

In order to determine the distribution of current speed and particles in the tunnel, experiments were carried out under controlled conditions. The tunnel was set up in an open channel flume at the facilities of the Institute for Forestry and Nature Research (I.B.N.-D.L.O.) at Texel. Sea water was pumped through this flume tank and vertical velocity profiles in the tunnel were measured at two current speeds with the tunnel placed on a mussel bed. Concentration profiles in the tunnel at low current speeds were studied with the tunnel set up on bare sediment in this open channel flume, and with the tunnel set up on a mussel bed in the flume. Duplicate water samples were taken at the entrance and at the outflow of the tunnel at 5 heights (2, 4, 8, 16 and 32 cm above the bottom).

The concentration of fluorescent material was measured immediately after sampling with a Turner fluorometer.

Particulate and dissolved matter fluxes in an *in situ* control experiment

An *in situ* experiment was carried out in July 1988, with the objective to determine if the Benthic Ecosystem Tunnel enhanced exchange between the water column and the mussel bed. One day before the experiment started, all mussels were removed from an area of 12 by 1 metre, and replaced by empty mussel shells. The tunnel was set up on this bed of empty shells, and measurements were carried out with all mussels removed from the tunnel site and replaced by empty mussel shells. During two tidal cycles the water at the inflow and the outflow of the tunnel was sampled each half hour. Samples were collected in polythene bottles, and transported to the laboratory where they were processed. Inflow and outflow concentrations were compared with a Wilcoxon signed-ranks test (Sokal & Rohlf, 1981).

Experiment with replicate tunnels

On 29 June 1988 an experiment was carried out on a mussel lot in the Zandkreek with two tunnels, set up on mussel beds within 10 metres distance from each other. During two tidal cycles the water at the inflow and the outflow of both tunnels was sampled each half hour. Samples were collected in polythene bottles, and transported to the laboratory. Inflow concentrations of particulate and dissolved matter, and fluxes of particulate matter measured with both tunnels were compared with a Wilcoxon signed-ranks test. Fluxes of inorganic nutrients were compared with a Mann-Whitney U-test (Sokal & Rohlf, 1981).

Analytical procedures

Suspended particulate matter dry weight (SPM) was analysed after filtration of a 1 litre sample on pre-weighed Whatman GF/C filters, careful rinsing with distilled water and drying for 48 hours at 70 °C. To analyse particulate organic carbon (POC), a part of this filter was taken, treated with HCl gas to remove inorganic carbon, put into a tin cup and burned at 1380 °C in a Carlo-Erba Elementary Analyser. The CO_2 formed was detected by a Katarometer. Particulate nitrogen (PN) was determined by filtration of a subsample of 0.5 litre on a Whatman GF/C filter, followed by an alkaline persulphate destruction and detection of the nitrogen as nitrate with a Technicon Autoanalyser. Particulate phosphorus (PP) was determined by filtration of 0.5 litre on a Whatman GF/C filter, an acid persulphate destruction and determination of the phosphorus as phosphate on a Technikon autoanalyser. Chlorophyll-*a* and phaeophytin-*a* were determined after filtration of a 1 litre subsample on Whatman GF/C filters. Chlorophyll-*a* and phaeophytin-*a* were extracted according to Gieskes & Kraay (1984) and analysed by

HPLC method with a 85-100% acetone/water-water gradient, using a reversed phase RP18 Novopack column (Waters) in a Spectra Physics Chromatography station. Chlorophyll-*a* was detected with a Perkin Elmer LS-2B fluorometer (excitation: 410-430 nm; emission: >530 nm). A standard chlorophyll-*a* solution was used for calibration. Dissolved inorganic nutrients (PO_4^{3-}, NO_3^-, NO_2^-, NH_4^+, H_4SiO_4) were analysed with a Technikon autoanalyser, in the filtrate after filtration of 0.25 litre through a Whatman GF/C filter.

The observed current velocities in the tunnel were used to calculate water fluxes through the tunnel. Fluxes of particulate organic and dissolved inorganic matter were calculated from the difference between inflow and outflow concentrations times the water flux. After the experiment the mussel bed was sampled by taking six 0.0177 m^2 core samples from the area that had been covered by the tunnel. The samples were sieved through a 1 mm sieve. Shell length of the mussels was measured to the nearest millimetre. Mussel dry weights (excluding the shell) were measured after drying at 70 °C for 48 hours, ash-free dry weights (AFDW) were determined as weight loss after incineration in a muffle furnace at 520 °C for 4 hours. All other macro-organisms were enumerated, dried and burned as above. From these data the ash-free dry weight of other macrobenthos species was calculated.

RESULTS

Vertical profiles of SPM, POC and chlorophyll-*a* in the field

Concentrations of SPM and POC measured at three different depths above a mussel lot in the Zandkreek at 22 January 1986 (5 cm and 40 cm above the bottom, surface) showed no significant differences ($p>0.05$) between depths. Chlorophyll-*a* concentrations, sampled at 5 cm above the bottom were on average 14% lower than chlorophyll-*a* concentrations at the surface (Fig. 2.2). The difference in chlorophyll-*a* concentrations at the two depths was significant ($p<0.05$). Differences between chlorophyll-*a* concentrations at 5 and 40 cm above the bottom, and between chlorophyll-*a* levels at 40 cm and at the surface were not significant.

At the second, downstream, sampling point SPM and POC concentrations were significantly higher near the bottom compared to concentrations near the water surface. No significant differences in chlorophyll-*a* concentrations were observed.

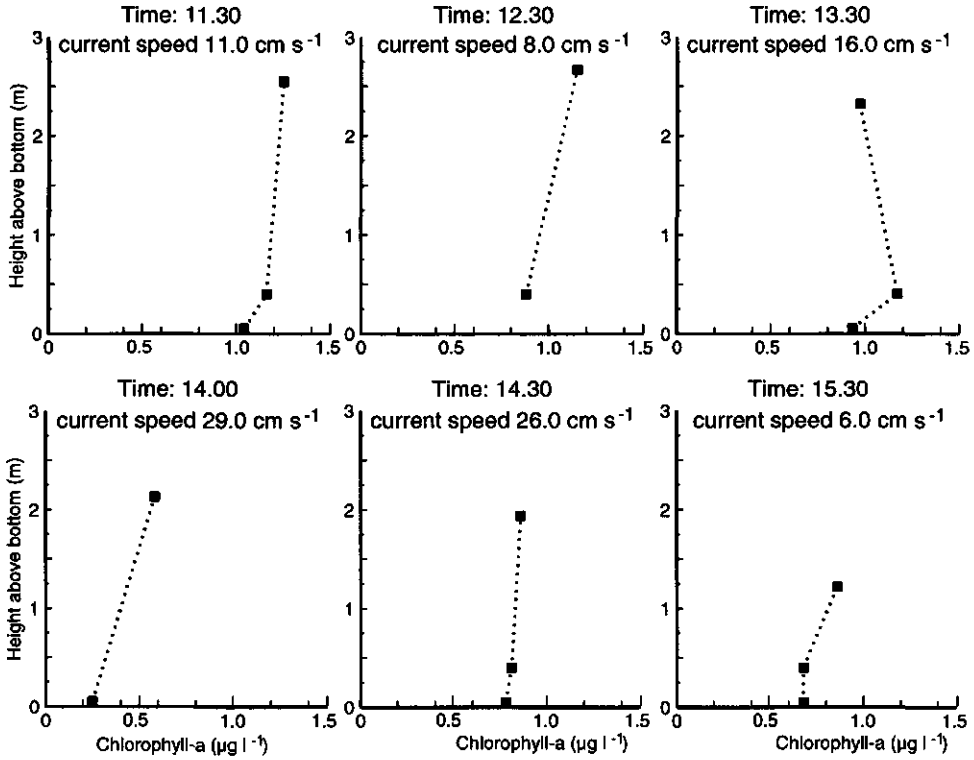

Figure 2.2. Vertical distribution of chlorophyll-*a* at a mussel lot in the Zandkreek, during a tidal cycle on 22 January 1986.

Current speed profiles in the Benthic Ecosystem Tunnel

The vertical current speed distribution above the mussel bed in the Benthic Ecosystem Tunnel is shown in Figure 2.3-a. Current speed distributions were measured at two current speeds. Measured current speeds fitted well to the general 'law of the wall' (e.g. Nowell & Jumars, 1987):

$$U = \frac{U_*}{\kappa} \ln\left(\frac{z}{z_0}\right) \qquad (2.1)$$

where U is current velocity, U_* is friction velocity, κ is Von Karman's constant, z is height above the bottom and z_0 is the bottom roughness parameter. At low current speed the correlation coefficient r was 0.85 (n=9), at high current speeds r=0.98 (n=9). The walls of the tunnel caused a much weaker inhibition of the current speeds (Fig. 2.3-b).

The observed relations between current speed and distance to the bottom or distance to the tunnel wall were used to calculate a distribution pattern of current speeds across the cross-sectional area. From this distribution an average current speed through the tunnel could be estimated, and compared to the current speeds in the tunnel at 20 cm above the bottom and outside the tunnel at 20 cm above the bottom (Table 2.1). The average current speed in the tunnel was 84% of the current speed at 20 cm above the bottom, which is the height at which current speeds were measured during the *in situ* experiments on mussel beds. Current speed in the tunnel was reduced with 40-50% compared to the current speed outside the tunnel.

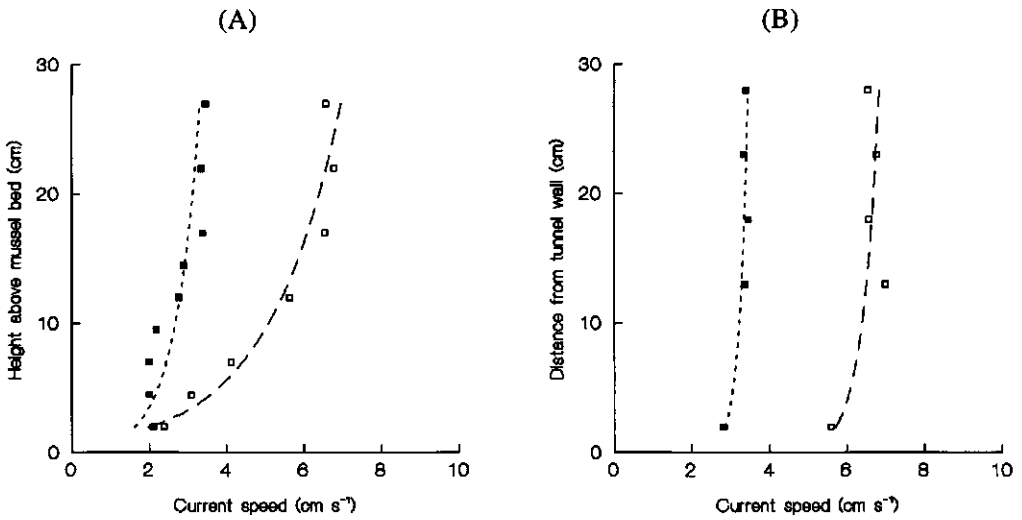

Figure 2.3. Current speed distribution within the Benthic Ecosystem Tunnel at two current speeds, with mussels on the sediment.

A: Vertical profiles of mean horizontal current speed in relation to the distance from the mussel bed.

B: Vertical profiles of mean horizontal current speed in relation to the distance from the tunnel wall.

Table 2.1.
Current speeds at 20 cm above the bottom in the tunnel, at a reference site outside the tunnel, and average current speed in the tunnel.

Current speed outside tunnel at 20 cm above bottom ($cm\ s^{-1}$)	Current speed in tunnel at 20 cm above bottom ($cm\ s^{-1}$)	Average current speed in tunnel ($cm\ s^{-1}$)
6.2	3.0	2.6
10.7	6.2	5.1

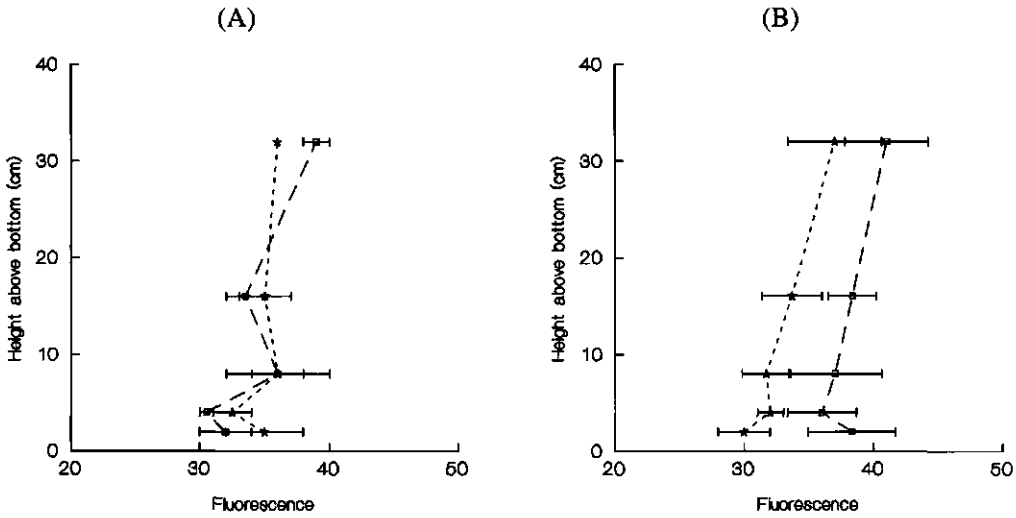

Figure 2.4. Vertical distribution of fluorescence at the inflow (dashed line, squares) and outflow (dotted line, stars) of the Benthic Ecosystem Tunnel.
A: with a low current speed and bare sediment.
B: with a low current speed and mussels present.

Particle concentration profiles in the Benthic Ecosystem Tunnel

Measurements of the vertical distribution of phytoplankton in the tunnel were carried out under controlled conditions, with the tunnel set up in an open channel flume. Figure 2.4-a shows the fluorescence at the inflow and outflow of the tunnel, with the tunnel set up on bare, sandy sediment and with a current speed of *ca* 1.5 cm s^{-1} at the centre of the tunnel. Vertical fluorescence profiles at the inflow and outflow of the tunnel did not show a significant correlation with height above the bottom (Spearman rank correlation, $p>0.05$). No difference in fluorescence between inflow and outflow of the tunnel was observed either, showing that the concentration and the vertical distribution pattern of fluorescence were not affected by passage through the tunnel.

In the experiment with the tunnel set up on a mussel bed, current speed in the tunnel was *ca* 2.5 cm s^{-1}. The vertical distribution of fluorescence at the inflow of the tunnel did not show a significant correlation with height above the bottom. At the outflow of the tunnel, fluorescence showed a significant increase with height above the bottom (Spearman rank correlation = 0.517, $n=15$, $p<0.05$). Fluorescence close to the bottom was 19% lower than at the highest sampling point. At all sampling heights, fluorescence at the outflow of the tunnel was lower than at the inflow (Figure 2.4-b). The observed decrease in fluorescence was 10-20 %. The results showed that filtration by the mussels had an effect on total fluorescence and on the vertical distribution of fluorescence.

The total flux of fluorescent material from the water column to the mussel bed was calculated by two methods. The first method used the observed profiles of current speed and fluorescence at the inflow and the outflow of the tunnel, which probably gives the best estimate of the flux to the mussel bed (Fréchette et al., 1993). The total flux of material according to this method was 44120 fluorescence units s^{-1}. The second method was similar to the method used in the *in situ* experiments in the Oosterschelde. In this calculation, only the fluorescence concentration at *ca* 5 cm above the bottom was used, and combined with the average current speed in the tunnel. The latter method gave an estimated flux of 41230 units s^{-1}. The comparison of these two methods indicated that the 'simpler' method of estimating particle flux by sampling at one height gave a value that was 7% lower than the more detailed method with 5 sampling heights, under the present conditions of current speed and mussel activity.

Control experiment

In the *in situ* experiment with a mussel bed made of empty mussel shells, concentrations of particulate and dissolved material at the inflow and the outflow of the tunnel were measured during two tidal cycles. SPM concentrations showed a significant decrease in the water passing through the tunnel ($p<0.05$) during both tidal cycles. In one tidal cycle, POC concentrations at the outflow of the tunnel were significantly lower than at the inflow of the tunnel. None of the other measured variables (PN, PP, chlorophyll-*a*,

phaeophytin-*a*, dissolved inorganic nutrients) showed significant differences between inflow and outflow concentrations.

Flux estimates using replicate tunnels

At 29/30 June 1988 *in situ* measurements were carried out simultaneously with two tunnels. The two tunnels were at different mussel beds, within *ca* 10 metre distance. The composition of the mussel bed showed distinct differences (Fig. 2.5). Tunnel 1 was set up on a mussel bed with an average density of 2852 ± 825 (mean ± s.d., n=3), and a biomass of 1448 g ash-free dry weight m^{-2}. Tunnel 2 was placed on a mussel bed with more, and larger mussels (density 3396 ± 608; biomass 2147 g m^{-2}). The concentrations of particulate matter and dissolved inorganic nutrients at the inflow of both tunnels were comparable. Chlorophyll-*a* inflow concentrations and fluxes are shown in Figure 2.6. Fluxes of SPM, POC, PN and chlorophyll-*a* did not differ between the two tunnels. With one exception for silicate, fluxes of inorganic nutrients measured with the two tunnels, were not significantly different. Fluxes of chlorophyll-*a* and inorganic nutrients are shown in Table 2.2.

Table 2.2.

Inflow concentrations of chlorophyll-*a*, and fluxes of chlorophyll-*a* and dissolved inorganic nutrients (average per tidal cycle ± s.d.) during a simulatneous experiment with two tunnels. Significant differences between tunnels are indicated: $^{*}p \leq 0.05$. Negative fluxes indicate release by the mussel bed.

		Inflow concentrations	Fluxes			
		chl-*a* $\mu g\ l^{-1}$	chl-*a* $mg\ m^{-2}h^{-1}$	PO_4^{3-} $mmol\ m^{-2}h^{-1}$	NH_4^{+} $mmol\ m^{-2}h^{-1}$	H_4SiO_4 $mmol\ m^{-2}h^{-1}$
1st tidal cycle (n=16)	tunnel 1	0.65 ±0.28	2.1 ±2.2	-0.44 ±2.05	356 ±1844	59 ±84
	tunnel 2	0.57 ±0.29	1.2 ±2.4	-0.11 ±0.77	-678 ±1157	30 ±51
2nd tidal cycle (n=12)	tunnel 1	0.56 ±0.23	2.5 ±2.6	-0.30 ±1.64	213 ±1144	131* ±131
	tunnel 2	0.57 ±0.22	2.1 ±2.1	-0.07 ±0.78	251 ±639	46* ±46

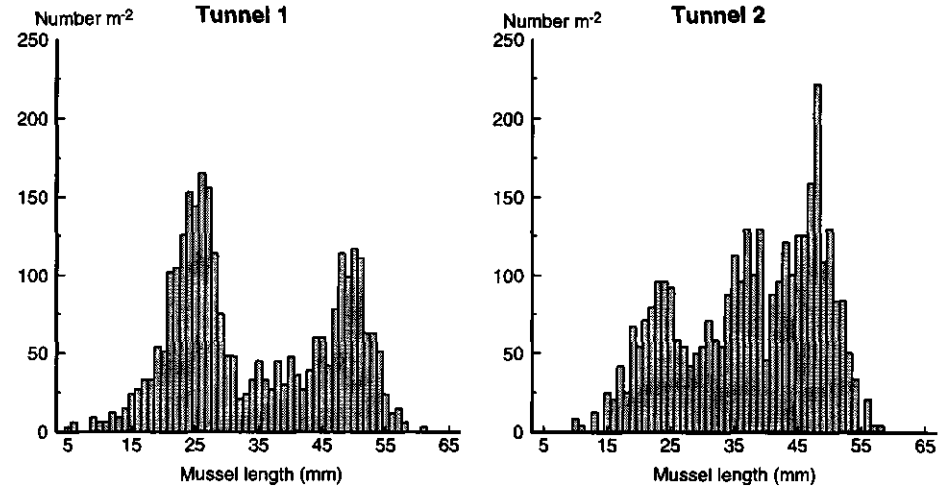

Figure 2.5. Length-frequency distribution of both mussel beds used in the replication experiment.

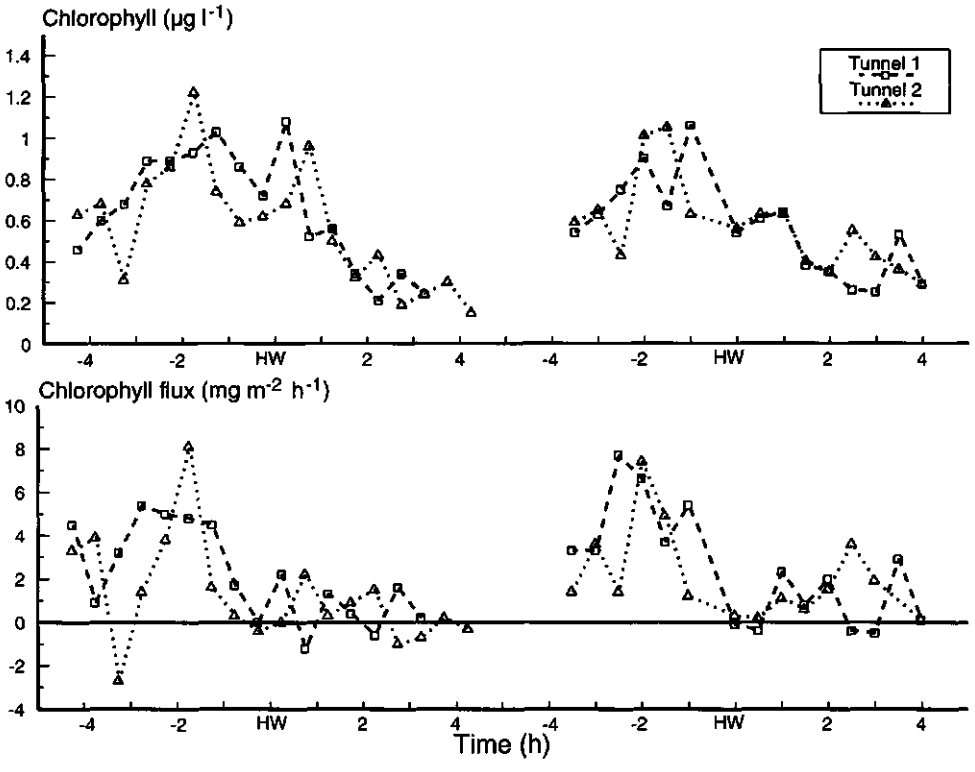

Figure 2.6. Chlorophyll-*a* inflow concentrations and fluxes of two tunnels operating simultaneously. Positive fluxes indicate uptake by the mussel bed, negative fluxes indicate release.

DISCUSSION

Vertical concentration gradients in the field

Field observations of the vertical distribution of SPM, POC and chlorophyll-*a* during a tidal cycle in the Zandkreek did not unequivocally indicate that particulate matter or phytoplankton showed a vertical concentration gradient in the boundary layer close to the mussel bed. Although chlorophyll-*a* concentrations at 5 cm above the bottom were significantly lower than concentrations near the surface at the first sampling point, no concentration differences were observed within the first 40 cm above the bottom. At the second, downstream point SPM and POC concentrations showed an increase near the bottom, and no gradient in chlorophyll-*a* was observed. These observations corresponded with results from a more extensive study of vertical SPM and chlorophyll-*a* profiles above mussel beds at 3 other sites in the Oosterschelde (Haas, 1987). In that study, only in one out of a total of twelve tidal cycles, lower chlorophyll-*a* concentrations were observed at 5 cm above the bottom compared to surface chlorophyll-*a* concentrations. More often, highest concentrations of SPM and chlorophyll-*a* were observed at the sampling point close to the bottom, which probably was caused by resuspension (Haas, 1987). Other observations on mussel beds in the Oosterschelde also showed an increase in SPM and chlorophyll-*a* concentrations close to the bottom (Smaal et al., 1986; Steijaert, 1986).

In an experiment in a 17-metre, circulating, flume at Woods Hole Oceanographic Institution it was shown that depletion of phytoplankton above a mussel bed leads to vertical gradients in phytoplankton concentrations, with lower concentrations close to the mussel bed (Butman et al., 1994). The flume experiment showed that a more uniform vertical distribution of phytoplankton occurs when current speed is high or mussel filtration rates are low. In a comparable study in the field, strong vertical gradients in phytoplankton concentrations and depletion of material close to the bottom have been observed on an intertidal mussel bed in a small tidal inlet (Fréchette et al., 1989). The vertical gradient of phytoplankton concentration above a mussel bed is the combined result of horizontal advection, mussel grazing and vertical mixing. When advective transport and vertical mixing are not high enough, the high filtration activity of the mussels will lead to depletion of phytoplankton in the benthic boundary layer and this will create a vertical gradient in phytoplankton concentration. This may be observed *in situ* in systems like small tidal inlets, where the bivalves occupy a relatively large area and lateral transport is prevented by the shores. Mussel beds in the Oosterschelde estuary are mainly found on intertidal flats and on the slopes of the tidal channels (Van Stralen & Dijkema, 1994). Generally, tidal currents on the mussel lots are strong, and resuspension of sedimented material in combination with advective transport probably prevents the development of food-depleted benthic boundary layers in the Oosterschelde.

At our study site, water during flood tide originated from a deep tidal channel and was not affected much by mussel beds. During ebb tide, water came from the Zandkreek bay, which is an area with a small tidal channel and extensive tidal flats that are used as mussel lots. The results of the experiment on 22 January 1986 did not show a clear depletion of particulate organic matter or phytoplankton in the water layer close to the bottom, in the period just before and after high water slack when current speeds are low and the probability of the development of a benthic boundary layer is highest. It is not likely that this was due to a low filtration activity of the mussels, as mussels do not reduce their filtration rates at low temperatures (Widdows & Bayne, 1971; Widdows, 1978; Loo, 1992; Chapter 6). From the fact that no depletion close to the bottom was observed it can be concluded that vertical mixing and horizontal advection at this site was high enough to supply particulate organic matter to the benthic boundary layer, which is probably due to the strong tidal currents, and this prevented the development of strong vertical gradients in particle concentration. In the absence of a vertical concentration gradient sampling at one point at the inflow of the tunnel was sufficiently accurate to determine the flux of particulate matter through the tunnel.

Current speed and fluorescence profiles in the tunnel

The observed current speed distribution in the tunnel showed that the current velocity was reduced close to the mussel bed and along the walls of the tunnel. The mussel bed had a stronger effect on current speeds than the tunnel walls, as a consequence of the larger shear stress induced by mussel bed roughness. The conversion factor of 0.84 to recalculate current speeds at 20 cm above the bottom to average current speeds in the tunnel was the same as measured earlier in experiments on oyster reefs and mussel beds with a Benthic Ecosystem Tunnel of the same dimensions as our tunnel (Dame et al., 1984; Jongsma, 1987). The reduction of current speed in the tunnel, compared to the current speeds outside the tunnel, was larger than the values of 20% reported by Dame et al. (1989) and 33% observed by Jongsma (1987). The observed reduction in current speed, compared to the flow outside the tunnel, may lead to enhanced sedimentation of particles in the the tunnel. This would result in an overestimation of particulate matter filtration by the mussels in the *in situ* experiments. In the control experiment carried out in July 1988, all mussels had been replaced by empty mussel shells. This made it possible to establish the physical effect of mussel bed roughness and current speed reduction in the tunnel, on the changes in material concentrations in the water flowing through the tunnel. Indeed, results from the control experiment showed some sedimentation of SPM and POC in the tunnel. No sedimentation of chlorophyll-*a* was observed in this *in situ* experiment (also see Chapter 3). From the latter observations it can be concluded that the employment of a Benthic Ecosystem Tunnel reduced current speeds over the mussel bed, which led to enhanced sedimentation of particulate matter,

but not of chlorophyll-*a*. It should be realized however, that part of the material deposited in the tunnel by physical sedimentation in the control experiment, would have been filtered by mussels, if the animals had been present. Consequently, at least part of the physical deposition was replaced by biological deposition in the experiments with living mussels in the tunnel. The rate of physical sedimentation in the control experiment, therefore, was an overestimation of the sedimentation rates in the experiments with mussels in the tunnel. As chlorophyll-*a* concentrations in the tunnel outflow were not lower than inflow concentrations in the *in situ* control experiment, it can be concluded that estimates of material fluxes and mussel filtration rates based on chlorophyll-*a* were not biased by additional sedimentation. The difference in behaviour between SPM and POC on the one hand, and chlorophyll-*a* on the other hand, suggested that mainly silt or detritus settled in the tunnel in the control experiment. This can be explained by the lower settling velocities of living phytoplankton cells compared to suspended particulate matter in the Oosterschelde (Ten Brinke, 1993).

When the tunnel was placed on a bare sediment in an open channel flume, the concentration and distribution of fluorescent particles remained unchanged during passage through the tunnel. This is consistent with the observation that no sedimentation of chlorophyll-*a* in the tunnel was observed in the *in situ* control experiment. In the experiment with the tunnel placed on a mussel bed, fluorescence at the outflow of the tunnel showed a positive correlation with height above the mussel bed. The uptake of fluorescent material by the mussel bed caused a decrease in the concentration of fluorescent particles, and a vertical gradient in fluorescence. These results agreed with the flume observations by Butman et al. (1994), as discussed above. It was argued by Fréchette et al. (1993) that the development of vertical gradients in phytoplankton concentration in the tunnel may lead to errors in the estimate of the phytoplankton fluxes to the mussel bed. In our experiment the fluorescence flux to the mussel bed was estimated by using the observed fluorescence values at *ca* 5 cm above the bottom and the average current speed through the tunnel. This estimate was only 7% lower than the flux calculated by a more elaborate method, using the observed vertical current speed and fluorescence distributions. The difference in fluorescence between inflow and outflow was 10-20 % at a current speed of 2.5 cm s^{-1}. We assume that under these conditions (decrease in fluorescence < 20%, current speed > 2.5 cm s^{-1}) the bias in the estimated flux of phytoplankton is small, when only one sampling height at the inflow and the outflow of the tunnel is used. During the *in situ* measurements in the Oosterschelde, less than 7% of the observations showed a decrease of more than 20% in chlorophyll-*a* concentrations at current speeds below 3 cm s^{-1}. Chlorophyll-*a* fluxes in this group of observations (also see Chapter 3) were not significantly different from the fluxes in the remaining observations, taking into account the chlorophyll-*a* concentrations at the inflow of the tunnel and mussel biomass (ANCOVA, $p>0.05$). We conclude that the estimates of

particulate matter fluxes in the tunnel experiments carried out in the Zandkreek were not seriously affected by a bias in the estimates of outflow concentrations. This disagreed with model results of Fréchette et al. (1993). As was recognized by Frechette et al., their model was developed for a free-flow situation, and did not consider wall effects of the tunnel. The development of a boundary layer along the walls of the tunnel will lead to enhanced mixing, and increased turbulent mixing in the tunnel may have been responsible for the relatively weak development of vertical concentration gradients. Earlier observations have shown that water in the tunnel is turbulently mixed at current speeds above 1 cm s^{-1}. From this we suggest that the model of Fréchette et al. (1993) was not valid for the Benthic Ecosystem Tunnel, and that the drawbacks of the tunnel method were less important than suggested by those authors.

Accuracy of flux estimates

Measurements of sediment-water exchange often show a substantial variability, even on a relatively small spatial scale (e.g. Boynton et al., 1980; Blackburn & Henriksen, 1983; Boynton & Kemp, 1985; Hammond et al., 1985; Hopkinson, 1987). In general, this variability is assumed to be related to spatial variability in macrofauna abundance, that influences sediment irrigation and bioturbation (Hammond et al., 1985; Hopkinson, 1987). In our replication experiment, fluxes of inorganic nutrients were relatively low. This was ascribed to the fact that this experiment was carried out during a period of several weeks with low food concentrations (also see Chapter 4). In one tidal cycle silicate fluxes measured with the two tunnels showed a significant difference, all other fluxes were comparable. The size-distribution and biomass of the mussels in the two tunnels showed considerable differences. Despite that difference, the fluxes of chlorophyll-*a* were not significantly different. Unfortunately, the concentration of chlorophyll-*a* was quite low during this experiment, and sometimes close to the detection limit (0.10 µg l^{-1}). This means that the detection of differences between inflow and outflow was less precise, and that made it more difficult to detect differences between the fluxes measured with the two tunnels. Consequently, it can be concluded from this experiment that the two tunnels generally showed comparable flux estimates, but the fluxes of chlorophyll-*a* and inorganic nutrients were low, and this affected the reliability of the comparison.

The tunnel method has also been evaluated by an intercalibration between the Benthic Ecosystem Tunnel and an open channel flume, that has been used to study exchange between the water column and mussel beds in the German Wadden Sea near the island of Sylt (e.g. Asmus et al., 1990; Asmus & Asmus, 1991). This intercalibration was carried out in June 1989 in the Wadden Sea near Sylt. Two tunnels were used, with one tunnel placed on a mussel bed, and the second tunnel placed on bare sand. At the same site, an open channel flume with two channels of 20 m length, a width of 4 m and

a height of 2 m was used. One channel of the flume enclosed an intertidal mussel bed, the second channel of the flume served as a control and enclosed a bare sandy sediment where all mussels had been removed. An extensive description of the experimental results is given in Asmus et al. (1992).

Fluxes of dissolved inorganic nutrients were measured during two consecutive tidal cycles. No release of inorganic nutrients was observed in the control (bare sediment) tunnel and flume. A significant release of ammonium and phosphate was observed in both the mussel tunnel and the mussel flume. A summary of the results is shown in Table 2.3. When comparing the fluxes estimated with the two different methods, it should be kept in mind that the ratio between water volume and sediment surface in the tunnel was much smaller (*ca* 0.3 m^3 m^{-2}) than in the flume (*ca* 0.6-1.5 m^3 m^{-2}). Due to this difference, the sensitivity of the tunnel method for detecting small sediment-water fluxes is higher at comparable current speeds. Moreover, water column processes may have a larger influence on the net fluxes observed with the flume. Consequently, the larger variation observed in the flume results could have been caused by water column processes interfering with sediment-water fluxes, and by the lower sensitivity of the method. The fluxes of ammonium, which are often the most distinct fluxes of dissolved matter from a bivalve bed (e.g. Dame et al., 1984, 1989; Dame & Dankers, 1988, Asmus & Asmus, 1991, Chapter 4), showed similar values for both methods. Fluxes estimated for phosphate showed larger differences, but the difference between the two methods was not statistically significant (Mann-Whitney U-test, $p>0.05$).

Table 2.3.

Fluxes of ammonium, phosphate and phytoplankton carbon (mean ± s.e.) observed during a simultaneous experiment with an open-channel flume and with the Benthic Ecosystem Tunnel. Negative fluxes indicate release by the mussel bed. Summary of results from Asmus et al. (1992).

	NH_4^+ mmol m^{-2} h^{-1}	PO_4^{3-} mmol m^{-2} h^{-1}	phytoplankton-C mg m^{-2} h^{-1}
Tunnel, mussels	-4.0 ± 0.69 (n=9)	-0.4 ± 0.11 (n=9)	74 ± 26 (n=4)
Flume, mussels	-6.5 ± 1.82 (n=9)	-1.6 ± 0.77 (n=9)	328 ± 114 (n=4)

Uptake of phytoplankton carbon was estimated for one tidal cycle in this experiment. The uptake of phytoplankton carbon was not significant in the control tunnel

and flume. In the mussel tunnel a significantly lower uptake of phytoplankton carbon was measured than in the mussel flume (Table 2.3). This difference in results illustrated the basic difference between the two methods. In the tunnel the supply of food particles to the boundary layer by vertical mixing is interrupted, whereas a continuous supply of new material from higher water layers is still possible in the flume. As a consequence of the low current speeds in this experiment (<4 cm s^{-1} in the mussel tunnel) the horizontal flux of material was relatively low and the supply of material by vertical mixing was more important than at high current speeds. This led to major differences between the tunnel and the flume in the supply of material to the mussel bed, and a much stronger depletion of phytoplankton in the tunnel (mean: 42%) than in the flume (27%). Consequently, a significantly lower amount of material was filtered by the mussels in the tunnel.

The phytoplankton counts were used to calculate clearance rates as well. Clearance rates (the volume of water filtered by the mussels) are probably not affected by the small differences in food concentration between the tunnel and the flume, and thus are a better indication of mussel activity than material fluxes. The clearance rate of the mussels in the tunnel was 2.1 ± 1.0 m^3 m^{-2} h^{-1} (mean ± s.e., n=4), the clearance rate in the flume was 2.9 ± 1.1 m^3 m^{-2} h^{-1}. This difference between tunnel and flume was not significant ($p>0.05$).

From the comparison between flume and tunnel technique it can be concluded that both methods gave similar estimates of sediment-water fluxes of inorganic nutrients. In the flume the precision of the method may be smaller due to a larger water-volume:sediment-surface ratio, and water column processes may affect the observed fluxes which could complicate interpretation of the results. This makes the tunnel a more appropriate method for measuring sediment-water fluxes of dissolved materials. The flux of particulate matter between the water column and a mussel bed is determined by mussel filtration, horizontal advection and vertical mixing. At low current speeds vertical mixing is relatively important. As this vertical flux is prevented by the tunnel, significant depletion of material in the tunnel may occur and the observed flux of material will be an underestimation of the flux under natural conditions. In the flume only lateral transport is interrupted by the system, and the underestimation will be much smaller. At higher current speeds however, vertical mixing is less important, depletion of particulate material will be much smaller, and consequently the underestimation of the particulate flux by the tunnel method is much smaller. Concluding, the flume method is suited for conditions with low current speeds, and the tunnel method is more suited for systems with high current speeds. Current speeds observed in the *in situ* tunnel experiments carried out in the Zandkreek ranged up to 31 cm s^{-1}, with an average of 9.1 cm s^{-1}. As was already discussed above, the decrease in chlorophyll-*a* concentration in the tunnel experiments was less than 20% in the majority of observations, which means that the measured fluxes only slightly underestimated the flux of chlorophyll-*a* under natural conditions.

CHAPTER THREE

FILTRATION AND RESUSPENSION OF PARTICULATE MATTER AND PHYTOPLANKTON ON AN INTERTIDAL MUSSEL BED IN THE OOSTERSCHELDE ESTUARY

Based on: T.C. Prins, A.C. Smaal, N. Dankers & A.J. Pouwer. Filtration and resuspension of particulate matter and phytoplankton on an intertidal mussel bed in the Oosterschelde estuary Mar. Ecol. Prog. Ser., submitted.

ABSTRACT

In situ measurements were carried out on an intertidal mussel bed in the Oosterschelde estuary. Exchange of suspended particulate matter and phytoplankton between the water column and the mussel bed was measured with a Benthic Ecosystem Tunnel. *In situ* clearance rates of the mussel bed were compared to clearance rates of individual mussels measured in a field station under ambient conditions.

Concentrations of suspended particulate matter and POC in the water column above the tidal flat were affected by wind-induced resuspension. Resuspension of chlorophyll-*a* was small. Uptake of SPM and POC by the mussel bed was highly variable. Under calm weather conditions, uptake rates were correlated with inflow concentrations. Net uptake of phytoplankton was relatively higher than the uptake of POC, indicating that a major part of the POC was resuspended and exported from the mussel bed after filtration. In addition, wind stress induced considerable resuspension and export of SPM and POC from the mussel bed. Chlorophyll-*a* uptake was less influenced by wind, and high rates of uptake, caused by mussel filtration, were observed. The result of filtration and resuspension processes was a net uptake by the mussel bed of particulate matter containing a relatively high proportion of phytoplankton.

Clearance rates of the mussel bed ranged from 1.3 to 7.1 $m^3\ m^{-2}\ h^{-1}$. *In situ* measured clearance rates were slightly lower than rates observed in measurements with individual animals in a field station.

INTRODUCTION

Bivalve suspension feeders may have a considerable impact on benthic-pelagic coupling in estuarine and coastal ecosystems (Dame, 1993). In estuaries with high densities of bivalves, these suspension feeders have the potential to filter the entire volume in a few days (see Smaal & Prins, 1993 for review), and control of phytoplankton biomass by grazing is likely. Many observations of low phytoplankton concentrations have been related to high bivalve grazing pressure (e.g. Cadée & Hegeman, 1974; Cloern, 1982; Carlson et al., 1984; Nichols, 1985; Smaal et al., 1986; Hily, 1991). The activity of the bivalves may significantly increase the sedimentation of particulate organic material (Verwey, 1952; Haven & Morales-Alamo, 1972).

Most of the hypotheses concerning the impact of bivalves on the pelagic system are based on the extrapolation of individual rates of filtration of bivalves to the scale of an estuary. However, scaled-up bivalve grazing rates, estimated from laboratory measurements with algal diets, may severely overestimate *in situ* filtration rates (Doering & Oviatt, 1986). Moreover, data on seston concentration and composition in the feeding zone of the bivalve population are often lacking, and therefore observations of bivalve feeding rates should best be done under natural conditions. Several studies have been carried out *in situ* on oyster reefs and mussel beds using tunnels or flumes. This method enables the study of bivalve activity under ambient conditions of food supply, animal density and abiotic factors like current speed. These *in situ* studies have shown that fluxes of suspended particulate matter often display an erratic pattern of uptake and release, whereas a consistent uptake of phytoplankton by the mussel bed is observed (Dame et al., 1984, 1989, 1991; Dame, 1987; Dame & Dankers, 1988; Asmus et al., 1990; Asmus &

Asmus, 1991). Release of particulate matter by the bivalve bed has been related to resuspension caused by high current velocities or wind-induced turbulence (Dame et al., 1989; Asmus et al., 1990). From these *in situ* observations it can be inferred that laboratory data on clearance rates of bivalves may be of limited value for the estimate of particulate matter fluxes from the water column to the benthic system. Scaled-up values of bivalve grazing rates only represent a potential impact on the water column, as resuspension and interactions between the animals are not taken into account.

As part of an ecosystem study (Nienhuis & Smaal, 1994), *in situ* measurements of material exchange between the water column and an intertidal bed of the blue mussel *Mytilus edulis* were carried out in the Oosterschelde estuary. In this estuary the blue mussel is very abundant and may greatly affect phytoplankton concentrations (Smaal et al., 1986; Herman & Scholten, 1990). It has been shown that the mussel beds process large amounts of particulate matter and are significant sources of inorganic nutrients (Dame et al., 1991; Chapters 4 and 5). In this study, we present the results of *in situ* measurements of the exchange of particulate material between the water column and an intertidal mussel bed. We will test the hypothesis that the net flux of material is determined by mussel filtration and abiotic conditions, and cannot be predicted from data on individual grazing rates only. Net fluxes of material between the water column and the bivalves will be related to abiotic factors, and filtration rates of the mussel bed will be compared to rates determined with individual animals under semi-natural conditions.

MATERIAL AND METHODS

In situ experiments

Material exchange between a mussel bed and the water column was measured with a Benthic Ecosystem Tunnel (Fig. 2.1). Experiments were carried out in 1987 (June and September), 1988 (June and September) and 1989 (April). All measurements were carried out at the same site, near the low tide level at an intertidal mussel bed in the Zandkreek, in the central part of the Oosterschelde estuary (Fig. 1.1). On 29/30 June 1988 measurements were carried out with two tunnels used simultaneously on two mussel bed within a distance of 10 m from each other. On 6/7 July 1988 a control experiment was carried out with one tunnel, to distinguish between effects of mussel bed morphology and effects of mussel activity. One day before the experiment started, all mussels from an area of 12 by 1 metre were removed and replaced by empty mussel shells.

All experiments lasted two tidal cycles, and water samples were taken every 30 min. during the period of submersion (8-9 h) of the tunnel. Due to rough weather conditions, the experiment on 28/29 September 1988 had to be ended after one tidal cycle. Samples were collected in polythene bottles, and transported to the laboratory where they were processed. SPM, POC, chlorophyll-*a* and phaeophytin-*a* were

determined as described in Chapter 2. Chlorophyll-*a* data were converted to phytoplankton carbon using carbon:chlorophyll ratios determined from routine microscopical observations on phytoplankton (Bakker, pers. comm.). These ratios varied between 17 and 110. After each experiment mussel biomass was determined (see Chapter 2).

Fluxes of particulate material between the mussel bed and the water column were calculated from the difference between inflow and outflow concentrations and the flux of water through the tunnel (Chapter 2). For each tidal cycle, inflow and outflow particle concentrations were compared with a Wilcoxon signed-ranks test. Fluxes were denoted as significant when the difference between inflow and outflow concentrations was significant. Clearance rates (volume of water swept clear of particles) were estimated from the difference between inflow and outflow concentrations of chlorophyll. Assuming an equal distribution of the mussels in the tunnel and a constant filtering rate during the sampling period (*ca* 5 minutes), the concentration of particulate matter in the water flowing through the tunnel will decrease exponentially. The clearance rate of the mussel bed (CR_{bed}) could be calculated from the inflow and outflow concentrations (C_{in} and C_{out}), the water flow through the tunnel (Q), and the surface of the mussel bed between the sampling points (A) with the following formula:

$$CR_{bed} = \ln\left(\frac{C_{in}}{C_{out}}\right) \cdot \frac{Q}{A} \qquad (in\ m^3 m^{-2} h^{-1}) \qquad \textbf{(3.1)}$$

In order to enable a comparison between the observed *in situ* clearance rates and laboratory data on mussel clearance rates, the *in situ* rates were standardized to rates for an animal of 1 g ash-free dry weight (ADW). Clearance rate is an allometric function of body weight ($CR = a \cdot W^b$, Bayne et al., 1976). As the mussel population consisted of a range of size-classes, clearance rates were standardized by dividing the observed rates by the metabolic mussel biomass. The metabolic biomass B_m was calculated from the numbers (n_i) and individual weights (W_i) of the mussels of each size class *i*:

$$B_m = \sum (n_i \cdot W_i^b) \qquad (in\ gram\ m^{-2}) \qquad \textbf{(3.2)}$$

The value of the weight-exponent b is 0.67 (Jones et al., 1992).

In some observations chlorophyll-*a* concentrations were close to or below the detection limit (<0.20 µg l^{-1}), and these data were not included.

Laboratory experiments

After each field experiment a random sample of 14-25 mussels from the mussel bed was transported to the R.I.K.Z. field station (Fig. 1.1). After acclimatization in running seawater for 24 hours, individual mussels were put into flow-through chambers (0.3 l) with natural seawater pumped through the chambers at a rate of 5-6 $l \cdot h^{-1}$. In- and outflows of the chambers were sampled after another 24 hours, and particle concentrations were measured with a Coulter Counter Model Industrial D. Clearance rates of the mussels were calculated from the following formula (Hildreth & Crisp, 1976):

$$CR = F \cdot \frac{(C_1 - C_2)}{C_2} \qquad (in\ l\ h^{-1}) \qquad \textbf{(3.3)}$$

with C_1 = outflow concentration of a control chamber (without mussels)

C_2 = outflow concentration of the mussel chamber

F = flow rate through the chamber

After clearance rates were measured, individual ash-free dry weights were assessed, and individual clearance rates were recalculated to rates per unit body weight by dividing the individual clearance rates by the metabolic weight (ADW^b) of the animal, using the weight exponent b=0.67.

Assessment of wind influence on sediment resuspension

Two methods were used to analyse the effect of wind on sediment resuspension and on the suspended particulate matter composition. First, we looked at correlations between the concentrations of seston components (SPM, POC and chlorophyll-*a*) and seston composition (expressed as POC/SPM, chlorophyll-*a*/SPM and phaeophytin-*a*/chlorophyll-*a* ratios) on the one hand, and wind speed on the other hand. To account for the differences in seston concentration and composition between the experiments, we standardized the values of the parameters by calculating the deviation from the median value, for each tidal cycle. At the site of our experiments, fetch length was long (>6500 m) for wind directions between 30° and 110°. All other wind directions had smaller fetch lengths (<2500 m). Therefore, we did the correlation analysis separately for winds with a long, and winds with a short fetch.

The second method determined a threshold value for the wind speed, above which resuspension might occur. It was shown by Carper & Bachmann (1984) that sediment resuspension may occur when the base of a wave extends to the bottom of a water column. The wave base is assumed to be one-half of the wavelength, and when wavelength L is more than twice the water depth h the wave is said to 'feel the bottom'. The wavelength of a wave is related to its period, and wave period T can be estimated from wind velocity U and fetch F by the following empirical relation (CERC, 1977):

$$\frac{g \cdot T}{2 \cdot \pi \cdot U} = 1.20 \cdot \tanh[0.077 \cdot (\frac{g \cdot F}{U^2})^{0.25}] \qquad \textbf{(3.4)}$$

with g is the gravitational constant (9.8 m s^{-2}).
Wavelength can be calculated from:

$$L = \frac{g \cdot T^2}{2 \cdot \pi} \qquad (in\ m) \qquad \textbf{(3.5)}$$

The wind speed threshold above which wind-waves may induce resuspension is the wind speed where L/h>2. Formulas 4 and 5 indicate that wavelength is a function of wind speed and fetch length. Water depth varies during the tidal cycle, leading to a changing wind speed threshold during the tidal cycle.

Data on wind speed and wind direction during our *in situ* experiments were supplied by the Royal Netherlands Institute of Meteorology (K.N.M.I.), and had been collected by the meteorological station at Vlissingen, which is at *ca* 20 km from the experimental site. Wind speed was assumed constant for one hour. Wind velocities below 4 m s^{-1} were assumed to have no effect on mixing in the surface water layer (Therriault & Platt, 1981; Demers et al., 1987). Fetch lengths were estimated from navigation charts. Actual water depths at the site of experiments were calculated from water levels measured at a continuous monitoring station in the Oosterschelde estuary near Zierikzee (Fig. 1.1).

Table 3.1.
Abundance, median length and ash-free dry weight (ADW) of the mussels in the mussel bed, and total macrobenthos biomass.

date	numbers m^{-2} mean ± s.d.	median length mm	ADW mussels g m^{-2}	Total ADW macrobenthos g m^{-2}
10/11 June 1987	1458 ± 269	42	891	1009
16/17 Sept 1987	1779 ± 284	43	1273	1382
8/9 June 1988	3349 ± 933	42	2187	2315
29/30 June 1988 (A)	2852 ± 825	29	1448	1534
29/30 June 1988 (B)	3396 ± 608	39	2147	2270
28/29 Sept 1988	2599 ± 1205	37	1721	1815
12/13 April 1989	6497 ± 1004	32	1206	1217
26/27 April 1989	4680 ± 1178	32	1569	1659

RESULTS

Mussel bed

The median length of the mussels in the mussel bed varied between 29 and 43 mm. Mussel biomass in the experiments ranged from 891 to 2187 g ash-free dry weight m^{-2} (Table 3.1).

Concentration and composition of particulate matter

Quantitative (SPM, POC, chlorophyll-*a*) and qualitative (chlorophyll/SPM) seston parameters showed changes with a factor 2-20 during a tidal cycle. Box-and-whisker plots (Wilkinson, 1992) of SPM, POC, chlorophyll-*a* and the proportion of chlorophyll-*a* in the seston are shown in Figure 3.1. POC concentrations showed a stronger correlation with SPM (partial r=0.711, n=215) than with chlorophyll-*a* (partial r=0.533). In most observations POC concentrations were between 5-20% of SPM. High chlorophyll-*a* concentrations were observed on 10/11 June 1987 and in April 1989, very low chlorophyll-*a* concentrations occurred in June 1988. In most observations phaeophytin-*a* concentrations were below the detection limit.

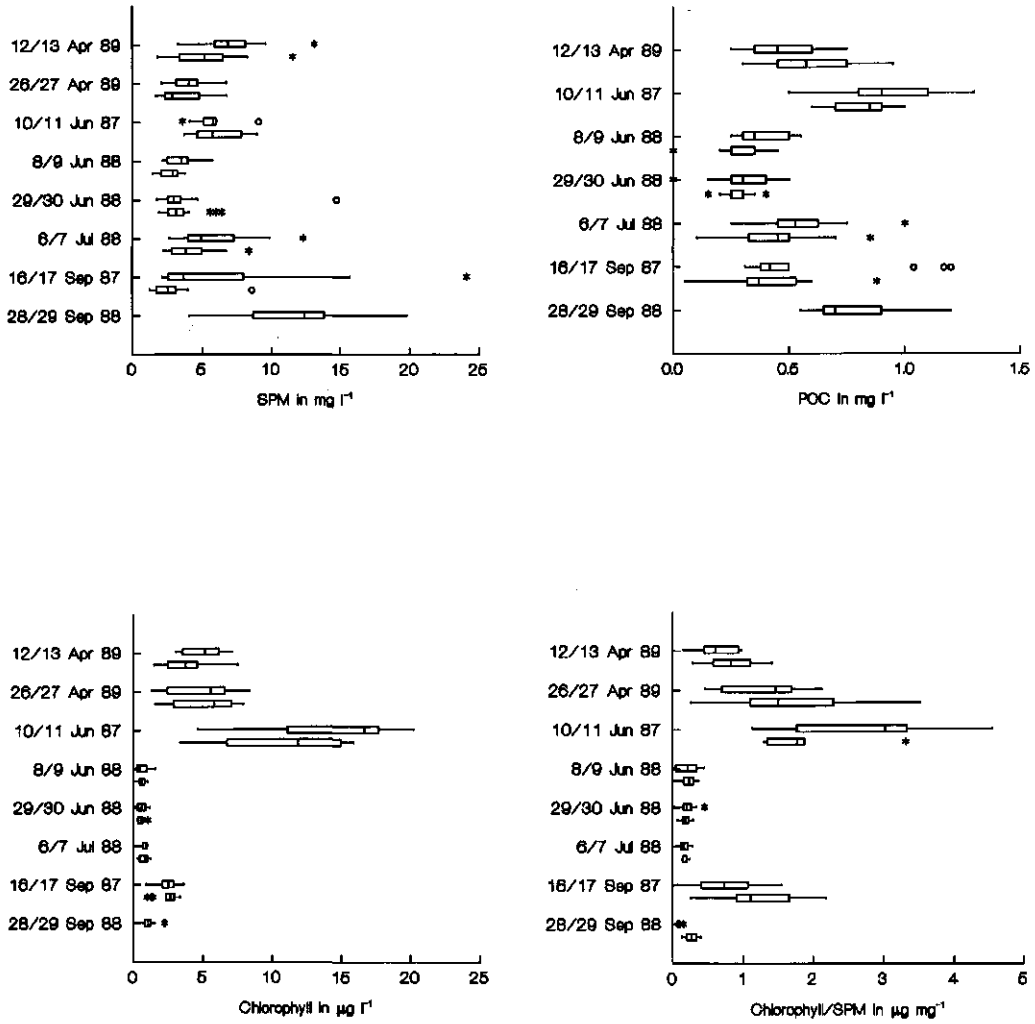

Figure 3.1. Box-and-whisker plots of SPM, POC and chlorophyll-*a* concentrations, and chlorophyll/SPM ratio at the inflow of the tunnel. Each data set represents one tidal cycle. At 28/29 September 1988 only one tidal cycle was sampled.

Table 3.2.
Water temperature, maximum wind velocities, median wind direction, and average current velocities in the tunnel during first/second tidal cycle of each experiment.

	Temperature (°C)	Wind velocity ($m\ s^{-1}$)	Wind direction (°)	current velocity ($cm\ s^{-1}$)
10/11 June 1987	14.3	6.7/ 7.2	180/160	9.5/ 9.2
16/17 September 1987	17.9	5.7/ 8.7	80/210	5.1/ 4.3
8/9 June 1988	15.4	4.6/ 4.1	270/350	10.2/10.8
29/30 June 1988	16.6	3.6/ 4.1	290/100	9.4/10.9
6/7 July 1988	16.9	10.3/ 8.2	190/240	10.9/10.2
28/29 September 1988	15.2	14.9/ -	230/ -	9.8/ -
12/13 April 1989	8.2	3.6/ 3.6	70/200	10.7/ 8.2
26/27 April 1989	10.2	7.7/ 8.2	340/160	9.4/11.2

Abiotic conditions during the experiments are summarized in Table 3.2. Long periods (> 1 hour) with wind speeds exceeding the threshold for wind-induced resuspension were observed during the measurements made on 10/11 June 1987, 16/17 September 1987, 6/7 July 1988, 28/29 September 1988 and 26/27 April 1989.
For wind directions with a long fetch, a significant correlation was observed between wind speed and standardized SPM and POC concentrations, POC/SPM, chlorophyll-*a*/SPM and phaeophytin-*a*/chlorophyll-*a* ratios during ebb tide (Table 3.3). SPM, POC and the phaeophytin-*a*/chlorophyll-*a* ratio increased at high wind speeds, whereas the POC/SPM and chlorophyll-*a*/SPM ratios showed a decrease. During flood tides no significant correlations were observed. For wind directions with a short fetch, the only significant relation was a positive correlation between wind speed and the phaeophytin-*a*/chlorophyll-*a* ratio during ebb tide.

Table 3.3.

Spearman rank correlation coefficients of relation between wind speed and seston concentration and composition during ebb tides. $^{*}p<0.05$; $^{**}p<0.010$; ^{NS} not significant.

	Long fetch (wind direction 30°-110°)	Short fetch (all other wind directions
SPM	0.319^{*} (n=34)	0.114^{NS} (n=92)
POC	0.307^{*} (n=34)	-0.013^{NS} (n=77)
chlorophyll-*a*	-0.151^{NS} (n=33)	-0.005^{NS} (n=91)
POC/SPM	-0.401^{*} (n=34)	0.069^{NS} (n=74)
chlorophyll-*a*/SPM	-0.544^{**} (n=33)	-0.040^{NS} (n=90)
phaeophytin-*a*/chlorophyll-*a*	0.520^{**} (n=33)	0.282^{**} (n=88)

The results showed that chlorophyll-*a* concentrations were generally higher during flood tide than during ebb tide. Significantly higher flood concentrations of chlorophyll-*a* were observed in 10 of the 15 tidal cycles (Mann-Whitney U-test, $p<0.05$). This pattern was less evident for SPM and POC, with respectively 3 and 4 tidal cycles showing significantly higher flood concentrations. SPM, POC and pigment inflow concentrations during 3 experiments with high wind speeds are shown in Figure 3.2. With some exceptions, wind velocities above the wind speed threshold for resuspension coincided with increases in SPM, POC and the phaeophytin/chlorophyll ratio during ebb tides. Slight increases in chlorophyll-*a* concentrations at high wind speeds were observed at 16/17 September 1987 and 6/7 July 1988. In contrast, no increases in SPM, POC and pigment ratio were observed in the second tidal cycle on 17 September 1987 when westerly winds (with a short fetch) dominated, and during the second tidal cycle on 6/7 July 1988, when wind speed exceeded the threshold during a short period at the end of the tidal cycle only. Effect of the wind on SPM, POC and pigment ratio was not observed during flood tides.

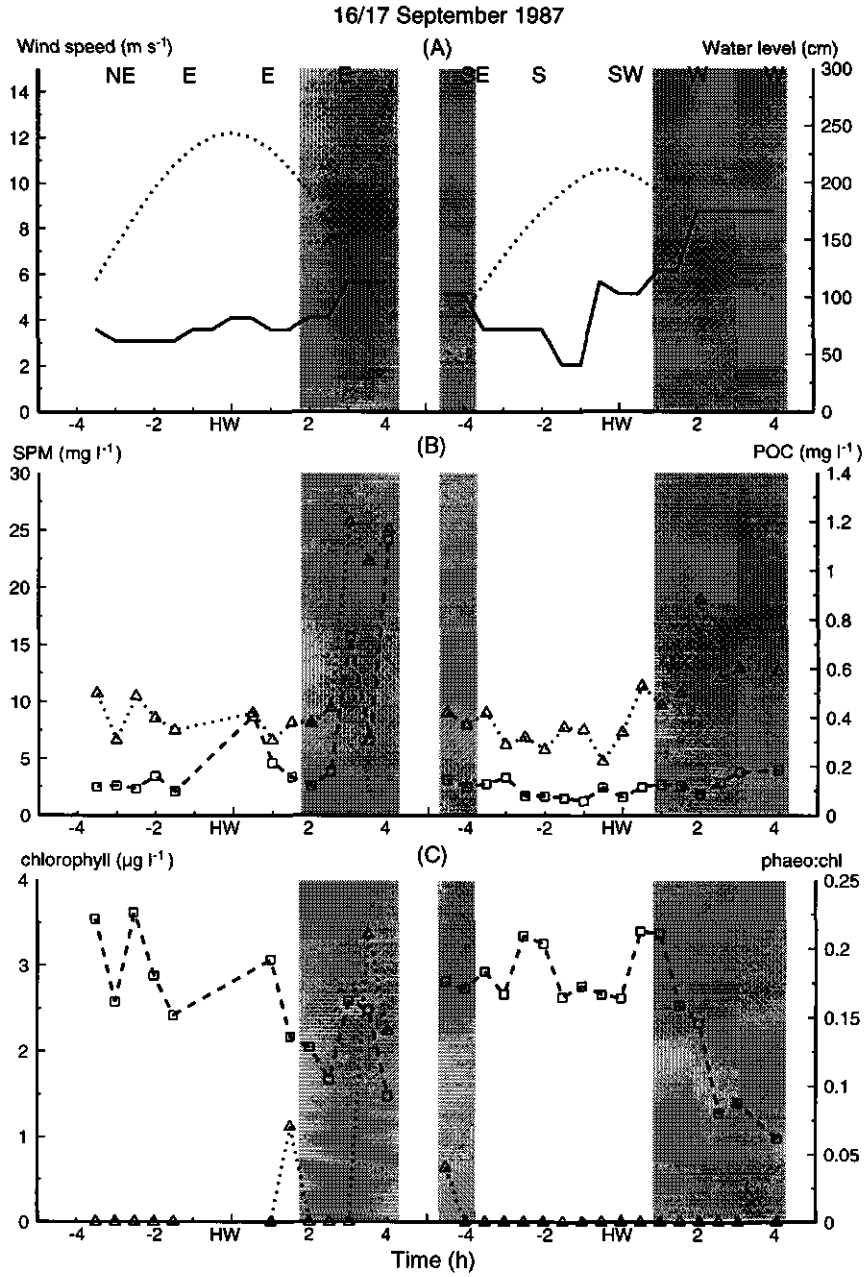

Figure 3.2. Water depth (dotted line), wind velocity (line) and wind direction [upper chart], concentrations of SPM (squares), POC (triangles) [middle chart], and chlorophyll-*a* (squares) and phaeophytin-*a*/chlorophyll-*a* ratio (triangles) [lower chart] during 2 consecutive tidal cycles. The horizontal axis gives time in hours before or after highwater slack (HW). The shaded area indicates periods with wind speeds above the wind speed threshold for resuspension (see text).

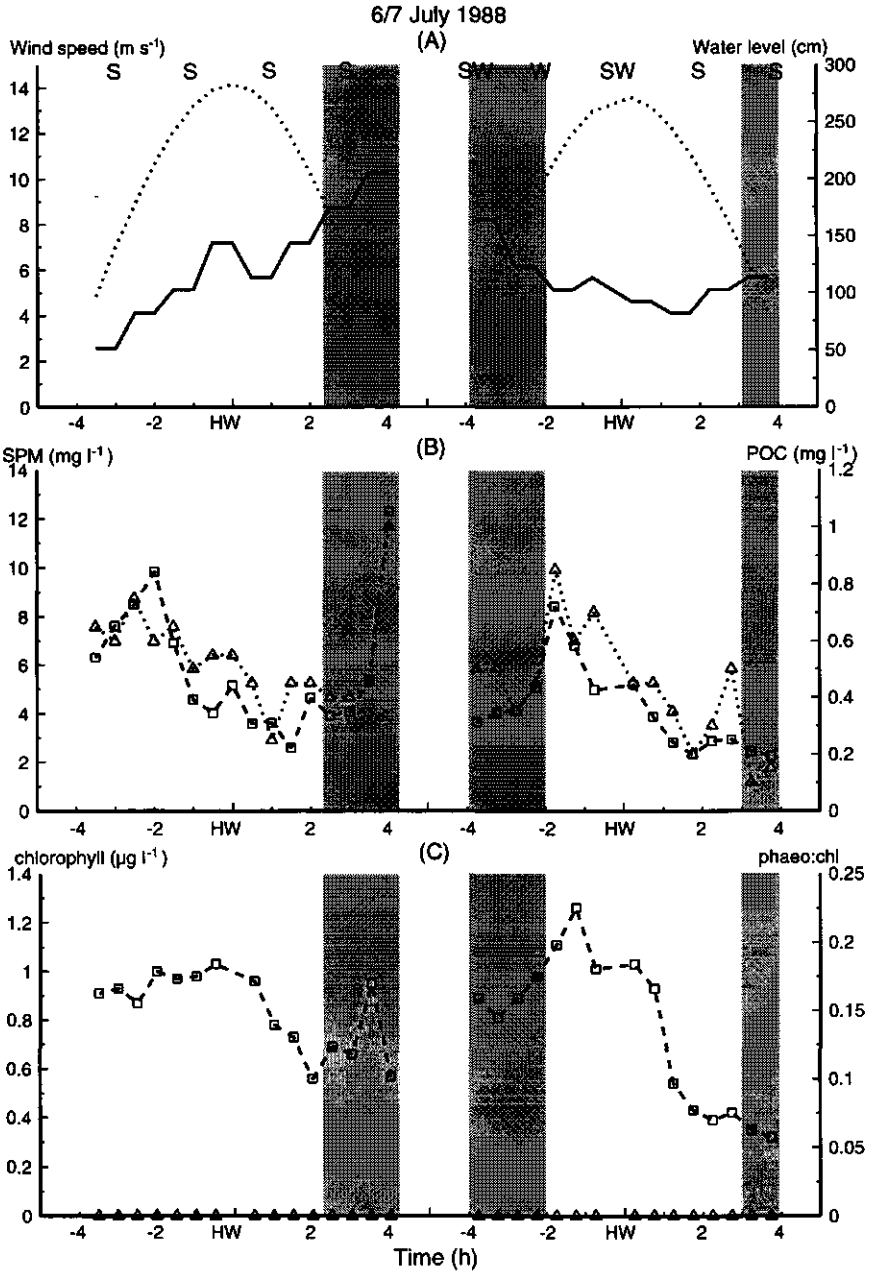

Figure 3.2. *continued*

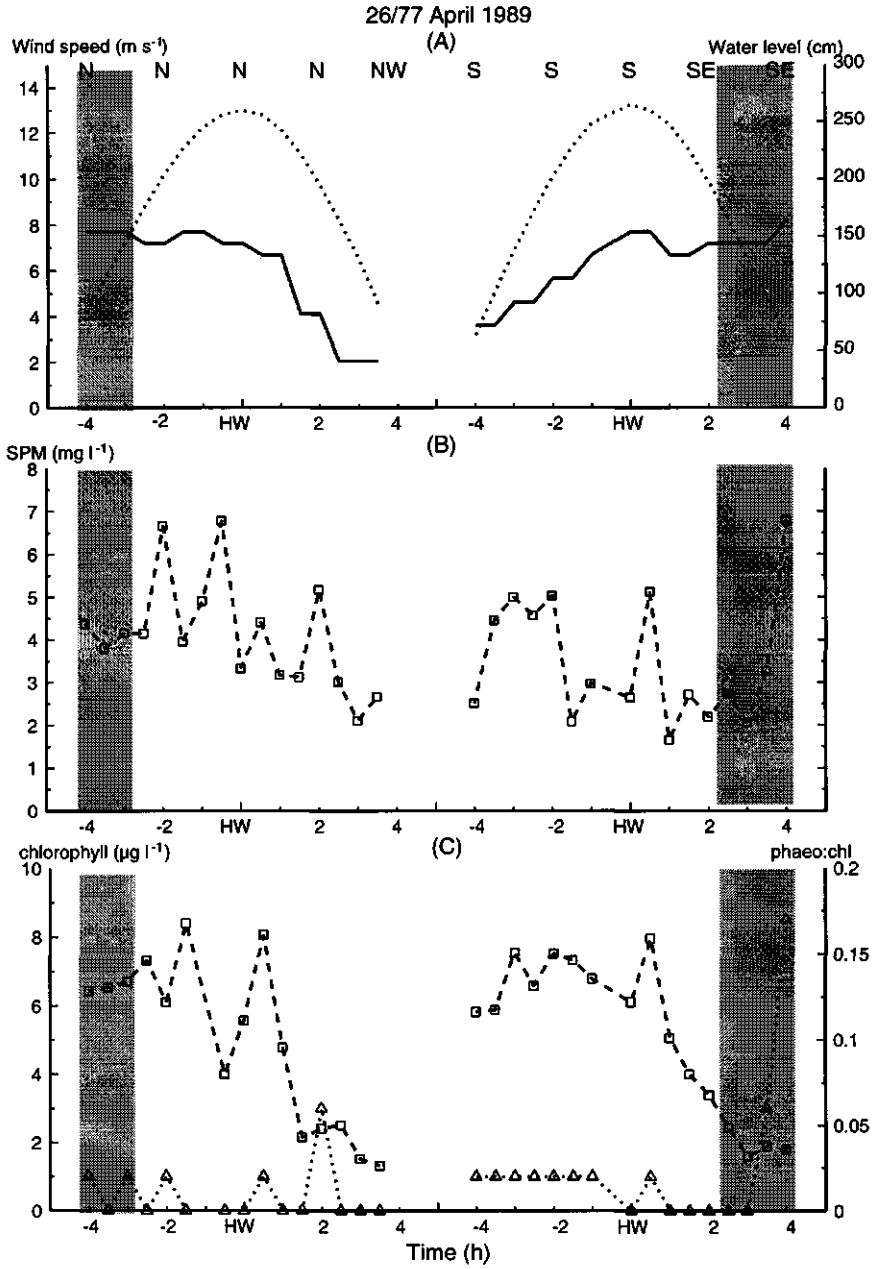

Figure 3.2. *continued*

Table 3.4.

Fluxes of suspended particulate matter (SPM), particulate organic carbon (POC) and phytoplankton carbon (Phyto-C). Values are average fluxes per tidal cycle ± standard error. Positive values indicate uptake by the mussel bed, negative values indicate release. (A) and (B) are values for two replicate tunnels. On 28/29 September 1988 only one tidal cycle was sampled.

n.d. = not determined; *=p<0.050 **=p<0.010 ***=p<0.001 (Wilcoxon test)

	SPM		POC		Phyto-C	
	g m^{-2} h^{-1}	n	g m^{-2} h^{-1}	n	g m^{-2} h^{-1}	n
10/11 June 1987	5.5 ± 8.5	9	2.73** ± 0.74	10	0.991** ± 0.168	12
	-44.5 ±32.7	8	-0.65 ± 1.66	8	0.654 ± 0.306	7
16/17 September 1987	-25.4 ±13.7	12	-0.94 ± 0.54	12	0.063* ± 0.028	12
	-1.74 ± 2.09	17	0.24 ± 0.28	17	0.093*** ± 0.017	17
8/9 June 1988	8.0 ± 5.9	13	0.17 ± 0.30	13	0.105 ± 0.059	13
	5.5* ± 2.2	15	0.48 ± 0.38	13	0.090 ± 0.043	15
29/30 June 1988 (A)	4.8* ± 2.0	16	0.36 ± 0.46	16	0.040** ± 0.010	16
	12.9 ± 7.5	15	0.21 ± 0.32	13	0.047** ± 0.013	15
29/30 June 1988 (B)	3.0 ± 5.3	18	-0.68* ± 0.29	16	0.024 ± 0.011	18
	6.2*** ± 1.4	14	0.25 ± 0.19	11	0.040*** ± 0.011	14
28/29 September 1988	1.0 ± 14.2	17	0.84 ± 0.64	16	0.051* ± 0.019	17
12/13 April 1989	30.4 ± 15.3	17	0.71 ± 0.96	16	0.203*** ± 0.035	17
	19.0*** ± 4.9	18	1.49 ±0.36	17	0.141*** ± 0.021	18

Table 3.4.
Continued

	SPM		POC		Phyto-C	
	g m^{-2} h^{-1}	n	g m^{-2} h^{-1}	n	g m^{-2} h^{-1}	n
26/27 April 1989	17.6 ± 12.4	15	n.d.		0.330*** ± 0.073	15
	22.2* ± 9.0	16	n.d.		0.430*** ± 0.096	15
6/7 July 1988 (control)	8.9** ± 5.5	16	1.10* ± 0.58	16	-0.001 ± 0.018	15
	11.5* ± 4.3	15	0.97 ± 0.73	13	0.017 ± 0.009	15

Fluxes of particulate matter

Wilcoxons test comparing inflow and outflow concentrations showed that in most tidal cycles a significant decrease in phytoplankton concentrations occurred as the water flowed through the tunnel. No significant difference between inflow and outflow chlorophyll-*a* concentration was observed in the control experiment. Only few tidal cycles showed significant changes in SPM or POC. The control experiment showed a decrease of SPM and POC concentrations (Table 3.4).

Calculated fluxes of SPM and POC showed that uptake dominated in most tidal cycles (Table 3.4). Material fluxes were significantly correlated with inflow concentrations in the observations with wind speeds below the wind speed threshold (SPM: $r=0.412$, $p<0.001$, $n=176$; POC: $r=0.595$, $p<0.001$, $n=143$). A number of observations at higher wind speeds clearly deviated from this pattern, with often large quantities of material resuspended and exported from the mussel bed, and a lack of correlation between inflow concentration and flux (Fig. 3.3-a, b). Chlorophyll-*a* fluxes showed a high correlation with inflow concentrations ($r=0.872$, $p<0.001$, $n=175$) at wind speeds below the wind speed threshold. Wind speeds above the wind speed threshold only occasionally caused resuspension of chlorophyll-*a* on the mussel bed (Fig. 3.3-c). In the experiment on 29 June 1988 small differences were observed between the fluxes measured with the two tunnels, but these differences were not significant (ANCOVA, $p>0.05$).

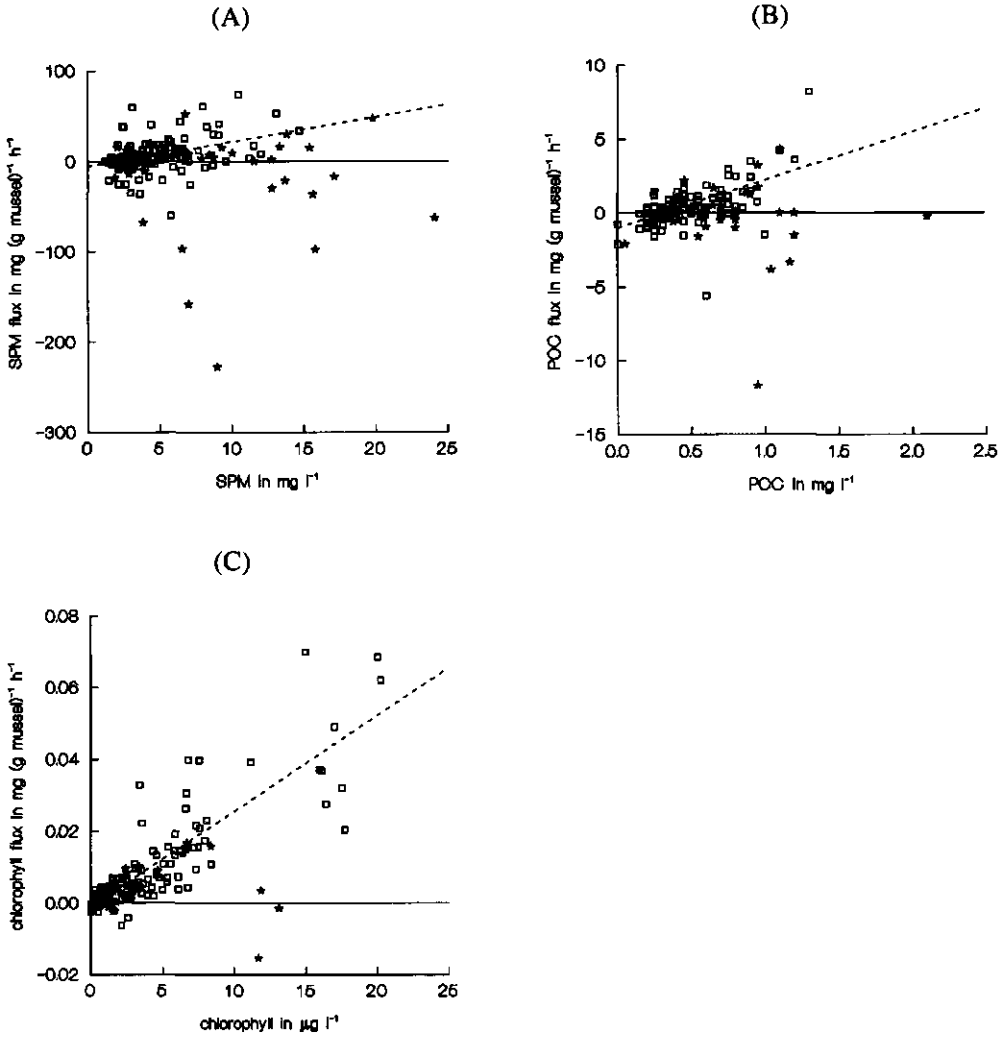

Figure 3.3. Weight-specific fluxes of suspended particulate matter (A), particulate organic carbon (B) and chlorophyll-*a* (C) in relation to the inflow concentrations. Open squares and regression line give results with wind speeds below the resuspension threshold, stars give results with wind speeds above the threshold. Positive values indicate uptake by the mussel bed, negative values indicate export from the mussel bed.

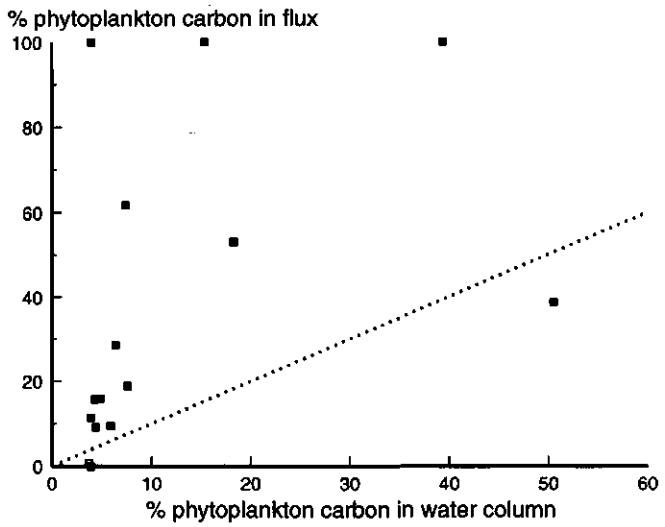

Figure 3.4. Proportion of phytoplankton carbon in POC-flux to the mussel bed compared to the contribution of phytoplankton to POC in the water column. Each data point gives the average composition during one tidal cycle, with exclusion of observations with wind speeds above the resuspension threshold. The open squares show the results of the control experiment.

Composition of fluxes

The contribution of phytoplankton to the total amount of POC in the water column was below 10% in most of our experiments. In June 1987, during a diatom bloom, phytoplankton contributed for *ca* 40% to POC. The proportion of phytoplankton carbon in the carbon flux to the mussel bed was higher than the phytoplankton fraction in water column POC in all tidal cycles, with the exception of one tidal cycle in June 1987 when phytoplankton concentrations in the water column were very high (Fig. 3.4). In these data, observations done at wind speeds above the wind speed threshold were not included, so the proportionally higher uptake of phytoplankton was not due to wind-induced export of POC. In three tidal cycles even a net release of POC was observed, simultaneously with an uptake of phytoplankton C.

Clearance rates

Clearance rates were calculated from the difference between inflow and outflow concentrations of chlorophyll-*a*. As high wind velocities could induce resuspension and mask the effects of mussel filtration, observations made at wind speeds above the wind speed threshold were not included in the calculation of clearance rates. In several observations in June 1988 chlorophyll-*a* inflow or outflow concentrations were close to or

below the detection limit, and clearance rates could not be determined accurately from these data sets. *In situ* measured clearance rates of the mussel bed varied between 1.3 and 7.1 $m^3\ m^{-2}\ h^{-1}$ (Table 3.5).

Within a tidal cycle, no consistent differences in clearance rates were observed between flood and ebb tide, or in relation to changes in seston quantity or quality. Mussel bed clearance rates measured with the two tunnels on 29 June 1988 were similar, in spite of marked differences in mussel biomass.

Mussel bed clearance rates were recalculated to an individual rate per unit body weight, and compared to the results of clearance rate measurements with individual animals under semi-natural conditions. In most cases, the differences between *in situ* measured clearance rates and rates from the laboratory experiments were not significant. One tunnel on 29/30 June 1988 gave a significantly lower estimate of *in situ* clearance rate. Results from the June 1987 experiment showed significantly higher *in situ* clearance rates (Table 3.5).

Table 3.5.

Clearance rates, measured *in situ* from chlorophyll-*a* concentrations, and clearance rates measured in the laboratory. Individual rates were standardized to rates for a mussel of 1 g ash-free dry weight. Values are means ± standard error.

* significantly different from lab results (t-test, $p<0.05$).

	in situ clearance rates			laboratory clearance rates	
	n	$m^3\ m^{-2}\ h^{-1}$	$l\ h^{-1}\ g\ ADW^{-1}$	n	$l\ h^{-1}\ g\ ADW^{-1}$
10/11 June 1987	12	5.2 ± 1.35	5.3*	14	3.2 ± 0.40
15/16 September 1987	16	1.6 ± 0.31	1.3		
8/9 June 1988	20	5.8 ± 1.83	2.4	14	2.7 ± 0.40
29/30 June 1988 (A)	29	4.0 ± 0.76	2.6		
				14	3.7 ± 0.36
29/30 June 1988 (B)	20	3.2 ± 0.70	1.3*		
28/29 September 1988	2	1.3 ± 0.70	0.7	14	1.6 ± 0.24
12/13 April 1989	35	7.1 ± 0.60	3.4		
				22	4.3 ± 0.87
26/27 April 1989	23	5.0 ± 0.93	2.3		

DISCUSSION

Supply of particulate matter and phytoplankton to the mussel bed

Mussels live in a highly dynamic environment with respect to the quantity of the particulate matter in the water column and the quality of the seston as a food source. Our results showed that both the quantity and the quality of the suspended particulate matter could vary considerably within one tidal cycle, with changes within a tidal cycle being as large as (seasonal) differences between experiments. The large, short-term, variability in both quantity and quality of the food for bivalve suspension feeders is typical of estuarine environments (a.o. Cadée, 1982; Berg & Newell, 1986; Smaal et al., 1986; Fréchette et al., 1989; Asmus et al., 1990; Fegley et al., 1992). Wind-induced resuspension has been shown to increase SPM concentrations on a short time scale in shallow coastal waters (Shideler, 1984; Gabrielson & Lukatelich, 1985; Demers et al., 1987; Asmus et al., 1990; De Jonge, 1992; Arfi et al., 1993). Depletion of food from the water column by the zoobenthos on a tidal flat is a regularly occurring phenomenon (Carlson et al., 1984; Kamermans, 1994), leading to lower concentrations during ebb. In our experiments, the tidal variation in seston concentrations and composition was related to abiotic factors.

As a consequence of local hydrodynamics, water from deep tidal channels flowed across the intertidal area during flood tide. After high water slack, the current direction was reversed and water flowing across the intertidal mussel bed drained from an extensive area of intertidal flats (mainly mussel lots). Consequently, during ebb tide chlorophyll-*a* concentrations were generally lower than during flood, and lowest concentrations were observed at the end of the ebb tide.

Although our observations were limited to periods with relatively low wind speeds (maximum wind speed 14.9 m s^{-1}), the results suggested that wave action caused by high wind speeds had a considerable impact on the food supply to the mussel bed during ebb tides. High SPM and POC concentrations and increased phaeophytin-*a*/chlorophyll-*a* ratios coincided with high wind speeds, and were observed mainly at the end of the ebb tides when the wind speeds were above the calculated threshold for wind-wave resuspension. High phaeophytin-*a*/chlorophyll-*a* ratios are often observed in estuarine sediments, and are an indication for the presence of high amounts of algal detritus (Cadée & Hegeman, 1977; Colijn & Dijkema, 1981). The increased phaeophytin-*a*/chlorophyll-*a* ratios in our observations showed that significant resuspension of algal detrital matter occurred. This was presumably due to resuspension of mussel biodeposits (cf. Fréchette & Bourget, 1985). During flood tides, wind influence on the composition of the seston was less clear. As discussed above, water came from deep tidal channels during flood, and was probably less affected on a short time scale by wind-induced resuspension than the water during ebb, which drained from a shallow, intertidal area.

Due to resuspension, microphytobenthos may form a major contribution to pelagic algal biomass (Baillie & Welsh, 1980; Grant et al., 1990; De Jonge & Van Beusekom,

1992; Kamermans, 1994) but this is not a general phenomenon (Fréchette & Bourget, 1985; Fréchette & Grant, 1991; Asmus & Asmus, 1993). The limited resuspension of chlorophyll-*a*, observed in our experiments, indicated that microphytobenthos was a minor food source for the mussels at our study site. In general, microphytobenthos is assumed to be quantitatively unimportant as a food source for mussels in the Oosterschelde (Smaal & Van Stralen, 1990).

The potential effect of wind on resuspension of sediments was determined from empirical formulas on the relation between wind speed, fetch and wave characteristics. The formulas used (CERC, 1977) have been shown to adequately describe the minimum wind speeds at which resuspension of bottom material may occur in lakes and in shallow estuarine environments (Carper & Bachmann, 1984; Shideler, 1984; Demers et al., 1987; Simon, 1989; Arfi et al., 1993). For winds with a long fetch length, highly significant correlations between wind speed and SPM or POC concentrations or the phaeophytin-*a*/chlorophyll-*a* ratio were observed. These three parameters showed strong increases when wind speeds had exceeded the wind speed threshold calculated according to Carper & Bachmann (1984). There was a time lag between the moment wind speeds exceeded the threshold and the moment resuspension actually occurred (Fig. 3.2). This may have been due to the high cohesiveness of the sediment at the mussel lots (Nowell et al., 1981) or may point at an overestimation of wind-induced wave action at our study site. For winds with a short fetch, the only significant correlation was the correlation between wind speed and the phaeophytin-*a*/chlorophyll-*a* ratio. Although wind speeds exceeded the calculated threshold in the second tidal cycle of September 1987, no resuspension was observed (Fig. 3.2-a). It should be taken into consideration that we used wind data obtained from a weather station at 20 km from our study site. Especially for the wind directions with a short fetch, actual wind speeds at the study site may have been reduced due to the proximity of land. This may have resulted in an overestimation of actual wavelengths. Moreover, the empirical formulas to calculate wind-waves do not consider the complex relations between factors like wind, fetch length, changing water depths during the tidal cycle and local geomorphology, which all affect wave development. Nevertheless, the observed correlations between high wind speeds and increases in SPM, POC and phaeophytin-*a*/chlorophyll-*a* ratio indicate that wind action may significantly affect food conditions for bivalve suspension feeders in the intertidal on a short time scale.

Material exchange between the water column and the mussel bed

The net fluxes of SPM, POC and phytoplankton carbon observed in our experiments were in the same range as *in situ* measured fluxes on mussel beds in the Wadden Sea (Dame & Dankers, 1988; Asmus et al., 1990; Dame et al., 1991). Mean SPM uptake in our experiments was equivalent to 118 g m^{-2} day^{-1}, assuming an

inundation time of 18 hours. This value agreed quite well with estimates of net sedimentation rates on mussel beds in the Oosterschelde (97-194 g m^{-2} day^{-1}; Ten Brinke, 1993). We observed a consistent uptake of chlorophyll-*a* and a highly significant correlation between water column concentrations of chlorophyll-*a* and fluxes from the water column to the mussel bed, at wind speeds below the threshold for resuspension. The fluxes of SPM and POC showed more variability than the chlorophyll-*a* fluxes, but still showed a significant correlation with the respective inflow concentrations under calm weather conditions.

In the control experiment, an uptake of SPM and POC was observed. This indicated that some sedimentation of seston particles occurred in the tunnel, probably due to a reduction of the current velocity in the tunnel compared to the water flow outside the tunnel (Chapter 2). No uptake of chlorophyll-*a* was observed in the control experiment. The difference in behaviour between SPM and POC on the one hand, and chlorophyll-*a* on the other hand, suggested that mainly silt or detritus settled in the tunnel in the control experiment. This can be explained by the lower settling velocities of living phytoplankton cells compared to suspended particulate matter in the Oosterschelde (Ten Brinke, 1993). The observed sedimentation in the control tunnel implied that some part of the SPM and POC fluxes, observed in the mussel experiments, may have been due to sedimentation.

Wind-induced turbulence affected the fluxes of particulate material measured with the Benthic Ecosystem Tunnel. Occasionally, we observed high rates of export of SPM and POC from the mussel bed, coinciding with high wind velocities. The tunnel probably diminished the effects of waves on the sediment of the mussel bed, although the tunnel is made of flexible material. Moreover, our observations were limited to the period when the tunnel was entirely submerged, which means that water depth was more than 0.40-0.45 m. At lower water depths, it has been shown that small wavelets near the flood front may cause significant resuspension (Anderson, 1980). A flume study on an intertidal mussel bed in the Wadden Sea also showed a predominant export of particulate matter during a moderate gale (maximum wind velocity 10.5 m s^{-1}; Asmus et al., 1990). The latter observations and the results from our study show that wind action may be an important factor determining the net flux of particulate matter to and from a mussel bed. High rates of biodeposition during periods of calm weather may alternate with periods when export dominates. It was technically not possible to carry out experiments during gales, so our observations were limited to relatively low wind speeds and water depths of more than 40 cm, and should therefore be considered as a minimum estimate of the exchange processes caused by wind influence.

The consistent uptake of phytoplankton carbon, along with a more erratic pattern of POC uptake, resulted in net carbon fluxes with a much higher proportion of phytoplankton carbon than was to be expected from the seston composition. This was not due to wind-induced resuspension of carbon-rich sediment material, as results presented

in figure 3.4 include observations at low wind velocities only. Preferential ingestion of algal material by bivalves will lead to production of pseudofaeces with a relatively low proportion of algae compared to the seston (Kiørboe & Møhlenberg, 1981; Newell & Jordan, 1983; Prins et al., 1991),. Pseudofaeces have a very loose structure and a low settling velocity (0.5-1.0 cm s^{-1}; Oenema, 1988), are ejected into the water current by the mussels, and are probably easily resuspended (Risk & Moffat, 1977; Nowell et al., 1981) and exported from the mussel bed.

In addition to the export from the mussel bed of pseudofaeces, some resuspension of faeces may have occurred in our experiments. There are no literature data on the erodibility of mussel faeces, but freshly egested faecal pellets of deposit feeders are more easily transported than the surrounding sediment (Risk & Moffat, 1977; Taghon et al., 1984). Observations on mussel beds have shown that only 15-40 % of the upper layer of the sediment consisted of identifiable faecal pellets, and this was assumed to be due either to resuspension of part of the faeces, or to a rapid degradation of the faeces in the sediment (Ten Brinke et al., 1995). Assuming that the mussels filtered POC at the same rates as chlorophyll, it could be calculated from our observations at low wind speeds that approximately 50% of the POC filtered by the mussels, was resuspended and exported from the mussel bed. Therefore, tidal currents play an essential role not only in the supply of food to the mussel beds, but also in the transport of waste products. Wind-induced resuspension will occur more randomly, but the quantitative effects may be much larger.

As a net result of filtration by the mussels and resuspension of biodeposits, only a fraction of the suspended particulate matter filtered by the mussel population was stored as biodeposits in the sediment. Moreover, the proportionally higher net uptake of phytoplankton indicated that the mussels had far more impact on phytoplankton standing stock than on the concentration of suspended particulate matter in the water column.

Filtration activity of the mussel bed

The changes in chlorophyll-*a* concentrations observed *in situ* with a tunnel, are the net result of mussel grazing, sedimentation and resuspension. The control experiment showed that sedimentation of chlorophyll-*a* was negligible in the tunnel. Resuspension mainly occurred in relation to wind-induced turbulence. Calculated *in situ* clearance rates were based on observations at low wind velocities only, and we assumed that wind-induced resuspension of chlorophyll-*a* was negligible in these observations. Observed clearance rates of the mussel bed varied between 1.3 and 7.1 m^3 m^{-2} h^{-1}, depending on biomass and activity of the mussels. Earlier estimates of mussel bed grazing rates based on extrapolation of individual measurements ranged from 3.5 to 5.9 m^3 m^{-2} h^{-1} (Jørgensen, 1980; Fréchette et al., 1989). In a 12-month experiment on a semi-natural mussel bed

with a biomass between 600 and 1200 g ADW, clearance rates up to 2.7 m^3 m^{-2} h^{-1} were observed (Chapter 6).

With the exception of June 1987, *in situ* clearance rates were slightly lower than rates estimated in experiments with individual mussels under semi-natural conditions. However, the variation in the estimates of weight-standardized clearance rates was quite large and only the rates observed with tunnel B on 29/30 June 1988 were significantly lower than the rates determined in the field station. On this date *in situ* chlorophyll-*a* concentrations were very low and this reduced the accuracy of the determined clearance rates. Therefore, the low clearance rates observed in tunnel B may be considered an artefact due to the low chlorophyll-*a* concentrations.

A number of factors may influence *in situ* mussel clearance rates. Current velocities above 25 cm s^{-1} have been shown to reduce clearance rates (Wildish & Miyares, 1990). This was probably a minor factor in our experiments, as in less than 3% of our observations current velocities were higher than 20 cm s^{-1}. In our *in situ* experiments, the mussels were exposed to large, short-term changes in food quantity and quality. Mussels mainly respond to short-term changes in the food supply by varying pseudofaeces production coupled with selection processes, but may also change clearance rates (Bayne, 1993; Bayne et al., 1993). Although this adds to the variability observed in the field, it does not necessarily imply lower *in situ* clearance rates. A physical hindrance of feeding of the mussels at the inner side of mussel patches may cause a reduced overall clearance rate. External pressure on the shells of mussels will impair shell opening, which is a critical factor in controlling pumping rates (Fréchette et al., 1992). Finally, we cannot exclude that some chlorophyll-*a*, filtered by the mussels, was resuspended again by the tidal currents. This would lead to an underestimation of *in situ* clearance rates. Still, our data showed that clearance rates, measured in experiments with individual animals fed with natural seawater, generally agreed with clearance rates observed by *in situ* measurements, and may be used to estimate grazing by mussel beds in the field.

Conclusions

Our observations support the view that mussel beds process large amounts of particulate material. *In situ* clearance rates were comparable to values used by Smaal et al. (1986) and Van Stralen & Dijkema (1994), who estimated that the mussel population in the Oosterschelde filters the entire volume of the estuary in less than 10 days and this corroborates the hypothesis that the mussel population in the Oosterschelde has a major effect on phytoplankton biomass (Smaal et al., 1986; Herman & Scholten, 1990). A major part of the faeces and pseudofaeces produced by the bivalves was transported from the mussel bed by tidal currents. Wind related turbulence affected the composition of the seston supply to the mussel beds, and induced a significant export of particulate material. The net result of biofiltration, biodeposition and resuspension processes was a high

uptake of phytoplankton, and a relatively reduced uptake of SPM and POC. Consequently, the mussel bed acted as a selective filter for high quality food material.

CHAPTER FOUR

THE RELEASE OF INORGANIC NUTRIENTS BY AN INTERTIDAL BED OF THE BLUE MUSSEL *MYTILUS EDULIS* L.

Based on: T.C. Prins & A.C. Smaal, 1990. Benthic-pelagic coupling: the release of inorganic nutrients by an intertidal bed of Mytilus edulis. In: Trophic relationships in the marine environment, M. Barnes & R.N. Gibson (eds.), Aberdeen University Press, Aberdeen, pp.89-103.

ABSTRACT

In situ measurements of the fluxes of chlorophyll-*a* and inorganic nutrients on an intertidal mussel bed showed a significant uptake of chlorophyll-a and a significant release of inorganic nutrients. The measurements were done by sampling the in- and outflow of a benthic ecosystem tunnel for a number of tidal cycles during 1987-1989 on a mussel culture lot in the Oosterschelde estuary, the Netherlands. A control experiment with empty mussel shells showed no uptake of chlorophyll-*a* and no significant release of nutrients.

Chlorophyll-*a* fluxes showed a linear relation with inflow concentrations. Nutrient release rates were highest in periods of phytoplankton blooms. Daytime release rates of Si and N were lower than rates during night time, probably as a consequence of algal uptake of nutrients within the tunnel.

Compared with other sources of inorganic nutrients, nutrient regeneration by mussel beds may be important in increasing the nutrient availability for phytoplankton and in stimulating the primary production in parts of the Oosterschelde estuary.

INTRODUCTION

Suspension feeding bivalves occur in high densities in many estuaries. In these systems the bivalves have a large influence on the pelagic system through filtration of particles and release of dissolved material (Dame et al., 1980). A reduction in phytoplankton concentrations due to the filtration activity of benthic animals has been reported several times, both in the benthic boundary layer (Wildish & Kristmanson, 1984; Fréchette & Bourget, 1985b) and in the entire water column (Cadée & Hegeman, 1974; Wright et al., 1982; Carlson et al., 1984; Nichols, 1985; Peterson & Black, 1987).

The sediment under suspension feeding populations is an important site of mineralization (Kautsky & Wallentinus, 1980; Dame et al., 1984; Kaspar et al., 1985; Boucher & Boucher-Rodoni, 1988). Dame et al. (1984, 1985) showed that oyster beds release high amounts of inorganic nutrients. However, with regard to the fluxes of material between the pelagic system and a mussel bed few data from *in situ* measurements are available yet (Dame & Dankers, 1988).

The Oosterschelde estuary, The Netherlands, is characterized by a high biomass of the bivalves *Mytilus edulis* (average annual biomass 5.0 g $C \cdot m^2$) and *Cerastoderma edule* (5.0 g $C \cdot m^{-2}$) (Smaal et al., 1986). Other suspension feeders have a lower biomass: zooplankton about 0.5 g $C \cdot m^{-2}$ (Tackx et al., 1990) and tunicates, sponges and hydroids about 2.7 g $C \cdot m^{-2}$ (Leewis & Waardenburg, 1990). The bivalve populations may play an important role in the cycling of material. Based on laboratory measurements of individual clearance rates, Smaal et al. (1986) estimated that once in about 4 days the volume of the western and central part of the Oosterschelde estuary can be filtered by the animals. Smaal & Van Stralen (1990) have shown a good correlation between primary production and mussel growth, which suggests a high turnover of the phytoplankton.

In 1986 the construction of a storm-surge barrier in the mouth of the Oosterschelde was completed, and in 1987 compartment dams on the eastern and northern boundaries were closed (Fig. 1.1). Due to the barrier the tidal exchange between the estuary and the North Sea decreased to 70 % of the former tidal volume; the mean residence times of the water increased from 5 days in the mouth and 50 days in the eastern part to 10 and 150 days, respectively; due to the compartment dams the freshwater inflow has been reduced to 35 % of the pre-barrier values and consequently the nutrient loads are reduced (Smaal et al., 1991).

In the pre-barrier situation, nutrient concentrations were high in winter, with a rapid decrease of P, N and Si in spring. From the molar ratios between N, P and Si, and the half-saturation constants for nutrient uptake by the phytoplankton, Wetsteyn et al. (1990) concluded that diatom growth was limited by the low silicate concentrations in summer. N:P ratios in summer are below 16, suggesting that non-diatom growth is potentially N-limited.

It is expected that in the post-barrier situation the regeneration of nutrients within the estuary has become more important for the primary production, due to the reduced import of nutrients. As the estuary is well mixed (Dronkers & Zimmerman, 1982), and the suspension feeders have a considerable impact on the pelagic system (Smaal et al., 1986), benthic-pelagic coupling may have become a more dominant phenomenon in nutrient cycling in the Oosterschelde estuary.

In this paper results of *in situ* measurements of chlorophyll-*a* uptake and nutrient release on an intertidal mussel bed are presented, and the effects on the nutrient availability for phytoplankton are discussed.

MATERIAL AND METHODS

Fluxes of chlorophyll-*a* and inorganic nutrients between the mussel bed and the water column were measured with a Benthic Ecosystem Tunnel. Water samples were taken from the inflow and outflow of the tunnel every 30 min during the period of submersion. Samples were collected in 1 litre polythene bottles, and transported to the laboratory where they were processed. Inflow and outflow concentrations were compared statistically with the Wilcoxon matched-pairs test (Sokal & Rohlf, 1981). Fluxes were calculated from the difference between inflow and outflow concentrations multiplied by the water flow through the tunnel.

Experiments were carried out in April (1989), June (1987, 1988) and September (1987, 1988). All measurements were carried out on an intertidal mussel culture lot in the Zandkreek (Fig. 1.1). A control experiment, with all live mussels removed and replaced by empty mussel shells was carried out in July 1988. An extensive description of the methods used is given in chapters 2 and 3.

RESULTS

Chlorophyll

As an example, Figure 4.1 shows the results of the measurement on 12/13 April 1989. In all experiments the mussel bed caused a significant decrease in chlorophyll-*a* concentrations in the water passing through the tunnel. The results of the measurements, including a statistical comparison of inflow and outflow concentrations, are summarized in Table 4.1. In the control experiment on a bed of empty mussel shells, no significant decrease in chlorophyll-*a* concentrations was observed.

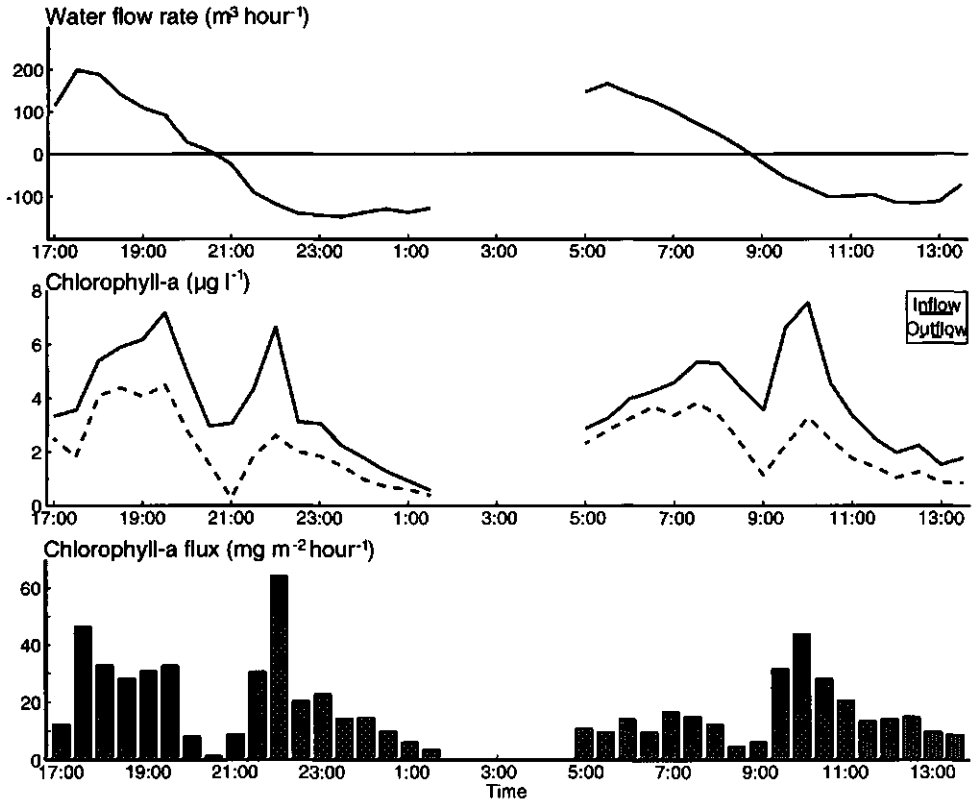

Figure 4.1. Water flux through tunnel (upper chart), chlorophyll-*a* inflow (———) and outflow (— — —) concentrations (middle chart), and chlorophyll-*a* fluxes (lower chart) measured in two tidal cycles on 12 April 1989.

Table 4.1.

Observed *in situ* fluxes of chlorophyll-*a* and dissolved inorganic nutrients. Values are means ± standard error. Positive fluxes indicate uptake by the mussel bed, negative fluxes indicate release. On 29/30 June 1988 two tunnels were used simultaneously.

* = p<0.050; ** = p<0.010; *** = p<0.001 (Wilcoxon-test)

	Chlorophyll-*a* in mg m^{-2} h^{-1}		Dissolved inorganic nutrients in mmol m^{-2} $hour^{-1}$					
Date	n		n	PO_4^{3-}	H_4SiO_4	NH_4^+	NO_3^-	NO_2^-
12/13 April 1989	35	19.2*** ±2.3	35	-0.99*** ±0.18	-2.19*** ±0.38	-10.54*** ±0.85	-2.59** ±0.82	-0.20 ±0.14
26/27 April 1989	30	23.0*** ±3.6	31	-0.43** ±0.15	-0.46 ±0.47	- 6.70*** ±0.69	-1.74*** ±0.45	-0.17 ±0.14
11/12 June 1987	17	30.8*** ±5.8	20	-0.58** ±0.17	-3.19** ±1.21	-17.07*** ±4.89	-6.53** ±2.42	-0.16 ±0.15
8/9 June 1988	28	2.4* ±0.9	28	-0.26*** ±0.09	-1.85** ±0.72	- 4.30*** ±1.70	0.04 ±0.43	0.00 ±0.00
29/30 June 1988 (1)	31	2.3*** ±0.4	20	-0.21 ±0.40	1.47 ±1.49	- 3.54** ±2.44	1.12 ±3.19	0.16 ±0.65
29/30 June 1988 (2)	32	1.6*** ±0.4	25	-0.09 ±0.15	-0.88* ±0.70	- 1.53 ±1.20	-0.80 ±1.06	-0.25 ±0.28
16/17 September 1987	29	3.9*** ±0.7	25	0.04 ±0.21	-2.41** ±1.57	- 1.38 ±1.30	-0.29 ±0.34	0.11 ±0.20
28/29 September 1988	19	1.5* ±0.6	15	-0.57 ±0.63	-3.69 ±3.09	- 6.87* ±2.98	-3.85 ±3.09	-1.58* ±0.89
6/7 July 1988 (control)	30	0.4^{ns} ±0.5	28	-0.21 ±0.50	0.87 ±1.72	0.93 ±3.28	-2.19 ±3.30	-0.24 ±0.83

Inorganic nutrients

The inflow and outflow concentrations of phosphate and ammonium, and calculated fluxes, during the experiment on 12/13 April 1989 are shown in Figures 4.2 and 4.3. Significant differences between inflow and outflow concentrations were observed in a number of experiments, and all significant changes were caused by releases of nutrients. Table 4.1 gives the mean fluxes and the results of Wilcoxon's test, comparing in- and outflow concentrations. The control experiment showed no significant uptake or release of nutrients.

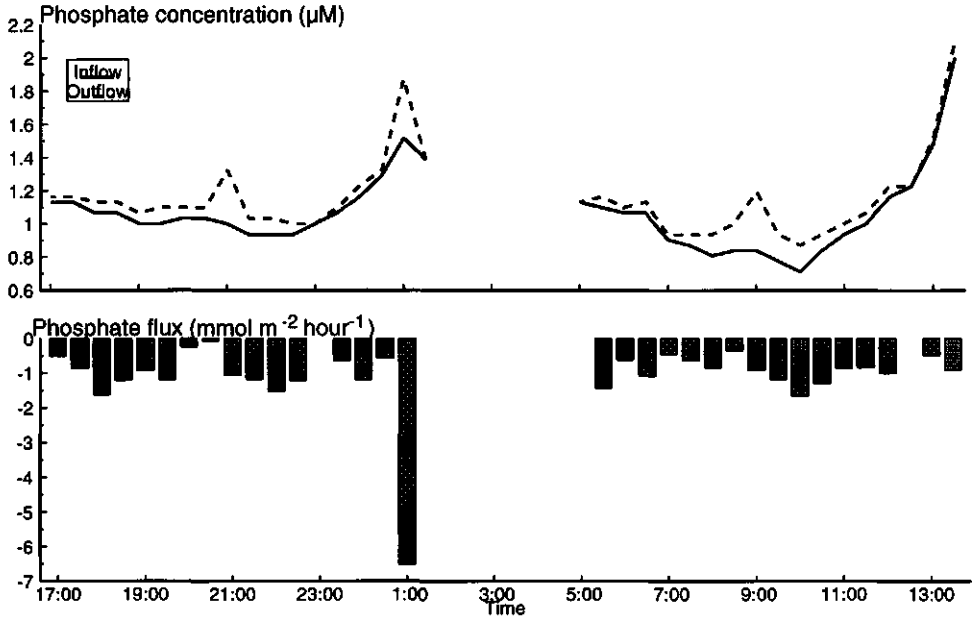

Figure 4.2. Phosphate *inflow* (———) and outflow (– – –) concentrations and calculated *fluxes* measured in two tidal cycles on 12 April 1989.

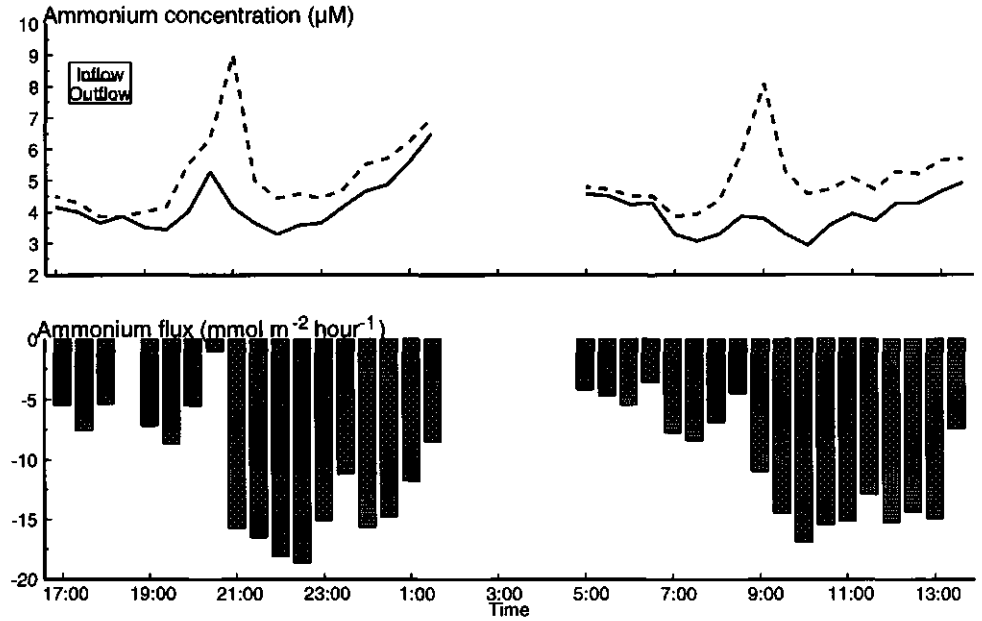

Figure 4.3. Ammonium inflow (———) and outflow (– – –) concentrations and calculated fluxes measured in two tidal cycles on 12 April 1989.

Effect of light on nutrient release

The experiment carried out in June 1987 fell in a period of high phytoplankton concentrations. The average concentration over the two weeks preceding the experiment was 10.8 μg l^{-1} (Wetsteyn & Bakker, 1991). The measurements carried out in June 1988 fell in a long period of low chlorophyll-*a* concentrations (average over preceding two weeks 1.5 μg l^{-1}). In April 1989 no differences in average chlorophyll-*a* concentrations in the period prior to the experiments in the same month occurred (mean concentration: 7.5 μg l^{-1}). As measured fluxes may be influenced by direct uptake of the nutrients by algae, a distinction was made between data collected during daytime, and the results of the night measurements. No significant day/night differences between the release rates of nutrients from the mussel bed were observed in the experiments carried out in April 1989, June 1988 and September 1987 and 1988. In June 1987 a significant difference between day and night fluxes of silicate, ammonium and total dissolved inorganic N (DIN) was observed. Moreover, fluxes of ammonium and silicate observed in June 1987 were much higher than fluxes observed in the experiments in June 1988 (Table 4.1). Average day and night fluxes observed in June 1987 are shown in Table 4.2.

Table 4.2.

Day and night fluxes of phosphate, silicate, ammonium, and nitrate (means ± s.e.) in June 1987. + = uptake ; - = release

	phosphate	silicate	ammonium	nitrate
day (n=14)	0.64 ±0.14	1.1 ±1.07	6.2 ± 0.91	-8.3 ±3.1
night (n=6)	0.43 ±0.48	8.1 ±2.13	37.3 ±10.37	-2.9 ±3.8

DISCUSSION

Chlorophyll-*a*

The results of the tunnel measurements showed significant decreases of the chlorophyll-*a* concentrations in the water passing the mussel bed. As has been discussed in Chapter 3, the control experiment showed no significant decrease in chlorophyll-*a* concentrations. The tunnel did not enhance sedimentation of chlorophyll-*a*, and this indicated that the observed fluxes of chlorophyll-*a* to the mussel bed were caused by filtration activity of the mussels. The flux of phytoplankton to the mussel bed correlated well with the concentration of phytoplankton chlorophyll-*a* concentration (Chapter 3), showing that the uptake of phytoplankton by the mussel bed mainly depended on the concentrations in the water column. Consequently, the experiments carried out in June 1987 and April 1989, when phytoplankton concentrations were high, also showed the highest uptake of phytoplankton by the mussel bed.

Inorganic nutrients

The ammonium release rates by the mussel bed (1.5-17.1 mmol m^{-2} h^{-1}) belong to the upper range of reported rates. Nowicki & Nixon (1985) measured ammonium fluxes from muddy sediments of 0.02 - 0.44 mmol m^{-2} h^{-1}. Dame et al. (1984, 1985) measured ammonium release rates in the range 0.1-16.9 mmol m^{-2} h^{-1} on an oyster bed. Other authors report release rates on oyster beds up to 0.38 mmol m^{-2} h^{-1} (Boucher & Boucher-Rodoni, 1988; Lerat et al., 1990). Few data exist on the release of ammonium on mussel beds. Nixon et al. (1976) measured a maximum flux of 5 mmol m^{-2} h^{-1}, which is low compared with the rates in this study. Dame & Dankers (1988) measured an average release at night of 7.9 mmol N m^{-2} h^{-1} on a Wadden Sea mussel bed in summer, which is well in the range of the rates reported in this study.

Phosphate was also released on the mussel beds. The pattern was less consistent than with ammonium; only in four experiments concentration differences between in- and outflow were significant. The rates measured were lower than rates measured on a mussel bed in the Wadden Sea (1.6 mmol P m^{-2} h^{-1}; Dame & Dankers, 1988). The rates were higher than rates measured on muddy sediments (0.05 mmol m^{-2} h^{-1}; Nowicki & Nixon, 1985) and rates measured on oyster beds (yearly mean: 0.03 mmol m^{-2} h^{-1}; Dame et al., 1989).

A significant release of silicate was observed several times. There are relatively few data on release of silicon by the benthic system. Aller & Benninger (1981) measured maximum release rates of 0.8 mmol Si m^{-2} h^{-1} in estuarine sediments. No silicate release rates from oyster reefs or mussel beds were mentioned by Dame et al. (1984) and Dame & Dankers (1988). Still, silicate must be considered of major importance with respect to the phytoplankton community. Low levels of silicate may lead to a shift in the phytoplankton composition from diatoms to flagellates, and may increase the chance of

nuisance blooms of algae (Officer & Ryther, 1980). Moreover, silicate is probably limiting the primary production in the Oosterschelde estuary (Wetsteyn et al., 1990).

Few significant differences of in- and outflow concentrations of nitrate and nitrite were observed, but in general there was a release of nitrate. Uptake of nitrate has been described, both on oyster beds (Boucher & Boucher-Rodoni, 1988) and on mussel beds (Dame & Dankers, 1988). The uptake or release of nitrate probably reflects the rate of denitrification in the sediment of bivalve communities (Boucher & Boucher-Rodoni, 1988). Excretion of ammonium and phosphate by the mussels may have been responsible for part of the fluxes observed in this study. As will be discussed more extensively in Chapter 5, excretion by the mussels was not high enough to account for the observed fluxes of inorganic nutrients. Mineralization processes in the sediment of the mussel bed must have been an important source of inorganic nutrients.

Effect of light and organic matter supply on nutrient release

In June 1988 very low rates of nutrient release were measured. The experiments in that month were all carried out during a long period of low chlorophyll-*a* concentrations. As a consequence of low concentrations of chlorophyll-*a* in the water column, the flux to the mussel bed must have been low. The low supply of substratum to the mineralization process in the mussel bed probably was the explanation for a reduced regeneration rate of nutrients, and lower release rates from the mussel bed. In June 1987 the experiment was carried out during a phytoplankton bloom. The much higher supply of material to the mussel bed probably caused the much higher ammonium and silicate release rates in comparison to June 1988.

A significant difference between day and night fluxes was observed in the measurements in June 1987. The release rates of ammonium and silicate were lower during the day. This may be explained by immediate uptake of a large part of the released nutrients by primary producers within the tunnel. There were no dense mats of macroalgae or benthic diatoms covering the mussel bed. Moreover, in all other observations day/night differences were not observed. The coincidence of lower night fluxes and high phytoplankton concentrations in June 1987 suggest that part of the inorganic nutrients released from the mussel bed, were taken up by phytoplankton. Nowicki & Nixon (1985) and Dame & Dankers (1988) also reported lower daytime fluxes of nutrients from the sediment, probably due to uptake by benthic or pelagic primary producers. Day and night differences of ammonium concentrations in a shallow estuary, with high concentrations at dawn, were observed by Litaker et al. (1988) and ascribed to nutrient regeneration by microzooplankton in combination with uptake by phytoplankton during the day. No differences between day and night fluxes were observed in April 1989, despite relatively high phytoplankton concentrations, which may have been due to lower rates of primary production as a consequence of lower irradiance.

Table 4.3.

Mean concentrations, fluxes and turnover times due to nutrient regeneration on mussel beds of P, Si and N in the central part of the Oosterschelde. Mean fluxes measured in April and September, and mean night fluxes observed in June 1987 were used in the calculations.

The turnover time T is calculated from:

$$T(days) = \frac{concentration \cdot volume_{basin}}{release\ rate\ per\ day}$$

Volume of compartment = $996 \cdot 10^6$ m^3 ; surface area = $89.62 \cdot 10^6$ m^2; surface mussel lots = $9.2 \cdot 10^6$ m^2; residence time water = 35 days; biomass mussels = 1458 tons ash-free dry weight

	P			Si			N		
	April	June	Sept	April	June	Sept	April	June	Sept
mean conc. (μM)	0.77	1.6	2.8	4.9	5.5	6.8	53	23	15
Total flux mussel beds (10^3 mol day^{-1})[1]	14	13	4	28	239	53	215	1013	104
Turnover time (days)	55	126	699	176	23	127	244	23	139
Total flux Lake Veere (10^3 mol day^{-1})[2]	?	?	?	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
Total flux other sediments (10^3 mol day^{-1})[3]	74	74	74	?	?	?	537	537	537

[1]this study; [2]Coosen, pers.comm.; [3]mean rates from Oenema, 1988

Mussel beds as a source of inorganic nutrients

Using the measured release rates of nutrients on mussel beds and the monthly average values of the nutrient concentrations in the period 1987-1989 (Wetsteyn et al., 1990; Wetsteyn & Kromkamp, 1994), and the estimated biomass of mussels in the central part of the Oosterschelde (Smaal et al., 1986), the turnover times of the nutrients in April, June and September have been calculated (Table 4.3). In June, turnover times of nitrogen and silicate due to the regeneration on mussel beds (e.g. 15 and 19 days) are lower than the residence time of the water in the central part of the Oosterschelde (about 55 days).

Relative to other sources, the mussel beds seem to be a major source of nutrients. Nutrient load from the brackish Lake Veere into this part of the Oosterschelde is several orders of magnitude smaller than the estimated fluxes from the mussel beds.

Other biota may add to nutrient regeneration. Zooplankton biomass is, however, small (Tackx et al., 1990) and consequently of minor influence. No data are available on nutrient fluxes from beds of *Cerastoderma edule*. Oenema (1988) estimated the regeneration of nutrients by anaerobic mineralization in silty sediments with the exception of mussel lots; his estimate for nitrogen is about as large as the regeneration on mussel beds. The mussel beds are, however, concentrated on only 10 % of the area in the central part of the Oosterschelde (Smaal et al., 1986).

These calculations stress the importance of mussel beds as a site of nutrient regeneration. The release of nutrients by the mussel beds is potentially important to phytoplankton, as the primary production in the Oosterschelde in summer is nutrient-limited (Wetsteyn et al., 1990).

In estuaries with a high biomass of bivalve suspension feeders, the grazing pressure reduces the phytoplankton biomass (Cloern, 1982; Officer et al., 1982). On the other hand, the recycling of inorganic nutrients may stimulate the primary production (Rosenberg & Loo, 1983; Bertness, 1984; Doering et al., 1986, 1987; Sterner, 1986) and it may be concluded that these suspension feeders act as a driving force in the turnover of phytoplankton and nutrients in estuaries.

CHAPTER FIVE

THE ROLE OF THE BLUE MUSSEL *MYTILUS EDULIS* L. IN THE CYCLING OF NUTRIENTS IN THE OOSTERSCHELDE ESTUARY

Based on: T.C. Prins & A.C. Smaal, 1994. The role of the blue mussel Mytilus edulis in the cycling of nutrients in the Oosterschelde estuary (The Netherlands). Hydrobiologia 282/283: 413-429

ABSTRACT

The fluxes of particulate and dissolved material between mussel beds and the water column in the Oosterschelde estuary have been measured *in situ* with a Benthic Ecosystem Tunnel. An uptake of POC, PN and PP was observed. POC and PN fluxes showed a significant positive correlation, and the average C:N ratio of the fluxes was 9.4. There was a high release of phosphate, nitrate, ammonium and silicate from the mussel bed into the water column. The effluxes of dissolved inorganic nitrogen and phosphate showed a significant correlation, with an average N:P ratio of 16.5. A comparison of the *in situ* measurements with individual nutrient excretion rates showed that excretion by the mussels contributed only partly to the total ammonium flux from the mussel bed. Phosphate excretion by the mussels accounted for a larger part of the phosphate flux from the mussel bed. The mussels did not excrete silicate or nitrate. Mineralization of biodeposition on the mussel bed was probably the main source of the regenerated nutrients.

From the *in situ* observations net budgets of N, P and Si for the mussel bed were calculated. A comparison between the uptake of particulate organic N and the release of dissolved inorganic N (ammonium + nitrate) showed that little N is retained by the mussel bed, and suggested that denitrification is a minor process in the mussel bed sediment. On average, only 2/3 of the particulate organic P, taken up by the mussel bed, was recycled as phosphate. A net Si uptake was observed during phytoplankton blooms, and a net release dominated during autumn. It is concluded that mussel beds increase the mineralization rate of phytoplankton and affect nutrient ratios in the water column. A comparison of N regeneration by mussels in the central part of the Oosterschelde estuary with model estimates of total N remineralization showed that mussels play a major role in the recycling of nitrogen.

INTRODUCTION

A dominant feature of estuaries and shallow coastal areas is the interaction between the water column and the benthic system (Zeitzschel, 1979). This benthic-pelagic coupling affects many of the physical, chemical and biological processes in shallow marine systems. Populations of suspension feeding bivalves can attain high densities (Bahr, 1976; Wolff, 1983; Asmus, 1987; Jørgensen, 1990) and often dominate the estuarine fauna (Wolff, 1983). Dame et al. (1980) suggested that bivalve populations play a significant role in the coupling between the water column and the benthic system in an estuary. The bivalves increase the sedimentation of particulate material in estuaries (Verwey, 1952; Haven & Morales-Alamo, 1972; Sornin et al., 1983, 1986; Dame et al., 1984; Smaal et al., 1986; Kautsky & Evans, 1987) and may even cause a depletion of plankton biomass (Wright et al., 1982; Carlson et al., 1984; Wildish & Kristmanson, 1984; Fréchette & Bourget, 1985b; Nichols, 1985). Indeed, *in situ* observations on reefs of the American oyster *Crassostrea virginica* (Dame et al., 1985, 1989) and on beds of the blue mussel *Mytilus edulis* (Dame & Dankers, 1988; Asmus & Asmus, 1991; Dame et al., 1991; this thesis) have shown that a high uptake of particulate matter occurs.

The presence of large numbers of bivalves does not merely lead to a removal of material from the water column. *In situ* measurements have shown that high amounts of

inorganic nutrients (N, P, Si) are released from oyster reefs (Dame et al., 1984, 1985, 1989) and mussel beds (Dame & Dankers, 1988; Asmus et al., 1990; Asmus & Asmus, 1991; Dame et al., 1991; this thesis). The large fluxes of inorganic nutrients from these bivalve communities into the water column are due to direct excretion by the bivalves and to mineralization processes in the sediment. The production of biodeposits by the bivalves enriches the sediment with organic material and stimulates mineralization processes (Dahlbäck & Gunnarson, 1981; Kautsky & Evans, 1987; Dame et al., 1991).

The availability of nutrients in coastal marine systems is largely dependent on benthic nutrient regeneration processes (Zeitzschel, 1979; Nixon, 1981). The regeneration of nutrients by bivalves possibly plays an important role in the cycling of nutrients in coastal systems and may influence pelagic production (Dame et al., 1985, 1991; Doering et al., 1986; Kautsky & Evans, 1987). In addition to an overall increase in nutrient regeneration rates, the benthos may affect nutrient ratios as a consequence of differences in the regeneration rates of N, P and Si (Doering et al., 1987; Dame et al., 1991).

Bivalve suspension feeders are very abundant in the Oosterschelde estuary. The biomass of the blue mussel *Mytilus edulis* (5.6 g C m^{-2}, Smaal et al., 1986) is controlled by mussel culture, whereas wild stocks of the cockle *Cerastoderma edule* (5.0 g C m^{-2}, Smaal et al., 1986) are present. As a consequence of the construction of a storm surge barrier in the mouth of the estuary and the construction of dams on the eastern and northern boundaries of the estuary, a number of abiotic changes have taken place. Among others, the water exchange with the North Sea and the freshwater discharge have decreased (Smaal et al., 1991). Due to the longer residence time of the water in the estuary benthic-pelagic exchange processes will get more dominant in the ecosystem. The decreased freshwater discharge led to a significant reduction in nutrient load (Wetsteyn & Bakker, 1991). It is to be expected that the tendency to 'oligotrophication' will extend the period of nutrient limitation of primary production, and will lead to an increased dependence of phytoplankton primary production on nutrient regeneration processes.

From laboratory estimates of filtration rates it was calculated that the bivalve population in the Oosterschelde may filter the entire volume of the basin in 4-5 days (Smaal et al., 1986). This is further supported by the results of *in situ* observations of chlorophyll uptake by mussel beds, from which a turnover time of phytoplankton of 5 days was calculated (Dame et al., 1991). High rates of inorganic nutrient release from mussel beds in the Oosterschelde have been reported earlier. A comparison of nutrient turnover time as a consequence of nutrient release from mussel beds, and the residence time of the water in the Oosterschelde estuary suggests that the mussel beds may be a major source of regenerated nutrients, particularly nitrogen (Dame et al., 1991; this thesis).

We hypothesize that nutrient regeneration by mussel beds plays a significant role in the cycling of nutrients in the Oosterschelde estuary. In the present study we present

results of *in situ* observations on the uptake and release of particulate organic nutrients and dissolved inorganic nutrients by intertidal beds of *Mytilus edulis* in the Oosterschelde estuary. We will compare the size and composition of the particulate and the dissolved material fluxes between the water column and the mussel bed, and will discuss the contribution of the bivalves to the regeneration of nutrients in the estuary.

MATERIAL AND METHODS

In situ measurements

In this chapter results are used from the experiments described in chapters 3 and 4. The methods to determine the exchange of POC and inorganic nutrients between the mussel bed and the water column have been described extensively in the previous chapters. In addition, samples were collected during these experiments to determine fluxes of particulate nitrogen and phosphorus. The analytical methods have been described in chapter 2.

Particulate silicon was not measured in our experiments. The amount of biogenic silicon taken up from phytoplankton by the bivalves was calculated by combining carbon:chlorophyll ratios measured by Bakker (pers. comm.) with the chlorophyll-*a* fluxes. The phytoplankton uptake was recalculated to carbon units, and from the observed diatom fraction in the phytoplankton biomass (Bakker, pers. comm.) and a C:Si ratio of 106:16 (Day et al., 1989) the flux of diatom-bound silicon was calculated.

Laboratory experiments

After each field experiment a random sample of 14-25 individuals from the mussel population were transported to the R.I.K.Z. field station at Jacobahaven (Fig. 1.1), where they were kept in running seawater, pumped directly from the Oosterschelde, for 24 hours. After this acclimation period the animals were placed in small flow-through chambers with a volume of 0.3 l, and incubated for 24 hours for the determination of individual clearance rates (see chapter 3). After this measurement the animals were incubated for 1-2 hours in closed chambers. The water was sampled before and after incubation and the inorganic nutrient concentrations (phosphate, silicate, ammonium, nitrate, nitrite) were determined. The individual rates of nutrient excretion (U) were calculated from the following formula :

$$U = \frac{C_t - C_0}{t} \cdot V \qquad (in\ \mu mol\ h^{-1}) \qquad \textbf{(5.1)}$$

where C_0 is the nutrient concentration at t=0, C_t is the concentration at the end of the experiment, t is the incubation time and V is the volume of the chamber. After the

experiment the ash-free dry weight (ADW) of the animals was determined, as described in chapter 3.

Comparison of *in situ* fluxes with individual excretion rates

The amounts of nutrients excreted by the bivalves depend on the biomass and the size of the animals. The individual excretion rates are an allometric function of body weight (Bayne & Widdows, 1978). In order to enable a comparison between the *in situ* rates of nutrient release from the bivalve community and the laboratory observations of individual nutrient excretion rates, the *in situ* fluxes were recalculated to rates per unit body weight:

$$a = \frac{F}{\sum n_i \cdot W_i^{0.68}} \qquad (in\ \mu mol\ gADW^{-1}\ h^{-1}) \qquad (5.2)$$

where F is the observed *in situ* flux, n_i is the number of mussels from sizeclass i, with an individual ash-free dry weight W_i, and 0.68 is the weight-exponent for nutrient excretion (Bayne & Widdows, 1978). The nutrient excretion rates of the individual animals, measured in the field station, were also recalculated to rates per unit body weight by dividing the excretion rate by the metabolic weight ($W^{0.68}$) of the animal.

Pooling of results

Experiments in June 1987 were carried out during a phytoplankton bloom, whereas all observations in June 1988 fell within a long period of very low phytoplankton concentrations. The inorganic nutrient fluxes observed in these two periods differed significantly (Chapter 4). In the comparison of uptake and release rates of particulate and dissolved nutrients the results of these two periods have been treated separately. The results of the two series of observations in April 1989 have been pooled.

RESULTS

Fluxes of particulate material

The average flux of particulate material between the water column and the mussel bed was calculated for each tidal cycle. The fluxes showed a large variation between measurements: POC fluxes had a range between a release from the mussel bed of 40 mmol m^{-2} h^{-1} and an uptake by the mussel bed of 227 mmol m^{-2} h^{-1}, PN fluxes varied between 1.27 (release) and 23.14 (uptake) mmol m^{-2} h^{-1}, and PP fluxes between 1.17 (release) and 1.23 (uptake) mmol m^{-2} h^{-1}. In the control experiment with empty mussel shells a minor uptake of POC was observed, whereas PN uptake was not significant ($p>0.05$). Average fluxes per tidal cycle in all experiments are shown in Figure 5.1. POC and PN fluxes showed a significant correlation ($r^2=0.75$, $p<0.001$). The dashed line

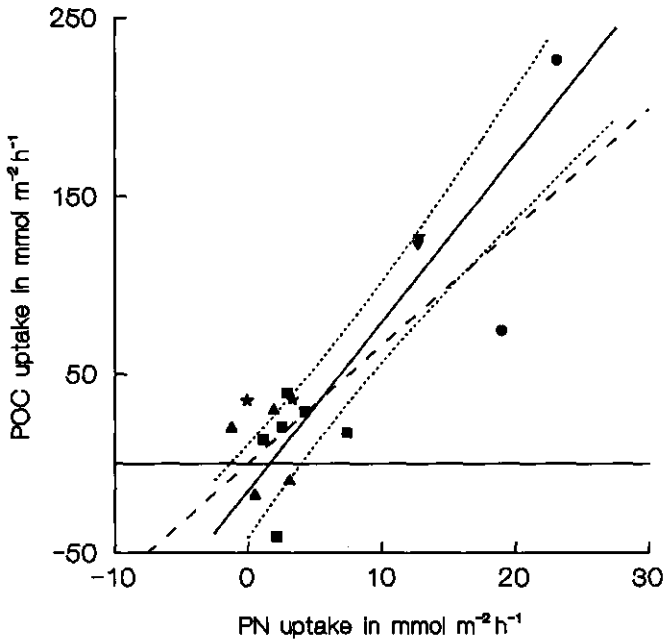

Figure 5.1. The uptake of particulate organic carbon (POC) and particulate organic nitrogen (PN) by mussel beds (average per tidal cycle). Negative values indicate release of material from the mussel bed into the water column. The solid line is the geometric mean regression line between POC and PN fluxes with 95% confidence interval. The dashed line represents the Redfield ratio C:N = 6.6:1.

● = June 1987; ▲= September 1987, 1988; ■= June 1988;
▼ = April 1989; ★= control mussel bed.

represents the C:N ratio (by atoms) of living phytoplankton (6.6; Redfield et al., 1963). From the geometric mean regression (Ricker, 1973) a molar C:N ratio of the fluxes to the mussel bed (excluding the control measurement) of 9.4 ± 1.4 (mean ± standard error, n=14) was estimated. In general, the fluxes were composed of material with a low C:N ratio compared to the seston at the inflow of the tunnel; the C:N ratios in the seston varied between experiments from 7.7 (June 1987) to 21.3 (September 1988). The C:N ratio of the suspended particulate material was higher at the outflow of the tunnel than at the inflow (Wilcoxon matched pairs-test, $p<0.010$, n=164).

Fluxes of dissolved material

There was a predominant release of dissolved inorganic nutrients from the mussel bed. The tidal averages of DIN fluxes (ammonium+nitrite+nitrate) varied between an uptake by the mussel bed of 3.8 mmol m^{-2} h^{-1} and a release of 33.7 mmol m^{-2} h^{-1} (average per tidal cycle). Orthophosphate fluxes ranged from 0.08 mmol m^{-2} h^{-1} (uptake) to 0.86 mmol m^{-2} h^{-1} (release). The fluxes of DIN and phosphate are shown in Figure 5.2. No significant fluxes were observed in the control experiment with empty mussel shells. One observation (night tidal cycle in June 1987) showed a very high release of DIN, and a much higher (86:1) N:P ratio than the other observations. With exclusion of this observation and the control, the fluxes showed a significant positive correlation ($r^2 = 0.69$, $p<0.001$) and the geometric mean regression estimate of the N:P ratio of the dissolved inorganic fluxes was 16.5 ± 2.7 (n=15), which was not significantly different from the Redfield ratio.

Silicate fluxes ranged from 2.8 mmol m^{-2} h^{-1} (uptake) to 6.1 mmol m^{-2} h^{-1} (release) (Fig. 5.3). Silicate fluxes in the control experiment were not significant. Due to the high DIN release in the night tidal cycle of June 1987, this observation showed a very high N:Si ratio. When this observation was excluded, DIN and silicate fluxes were not significantly correlated. In general, the N:Si ratio of the fluxes was higher than the Redfield ratio.

Contribution of excretion by the bivalves to nutrient release

In the laboratory experiments excretion of ammonium and phosphate by the mussels was observed. No significant excretion of silicate or nitrate occurred. The excretion rates of ammonium and phosphate were correlated ($r^2=0.61$, $p<0.001$), and the average N:P ratio of the excretion was 7.7. The N:P ratio of the excretion was not significantly different between experiments (ANOVA, $p>0.05$). The observed *in situ* release rates by the mussel bed of ammonium, nitrate and phosphate were recalculated to rates per unit body weight, and were compared to the individual excretion rates per unit body weight. The estimated ammonium excretion by the mussels generally was much smaller than the observed *in situ* flux (Fig. 5.4). Excretion of ammonium was equal to 13-80 % of the *in situ* ammonium release by the mussel bed. The phosphate excretion by the mussels corresponded for a larger part with the *in situ* release, and estimated excretion rates were even equal to the observed *in situ* fluxes in June 1988 (Fig. 5.5).

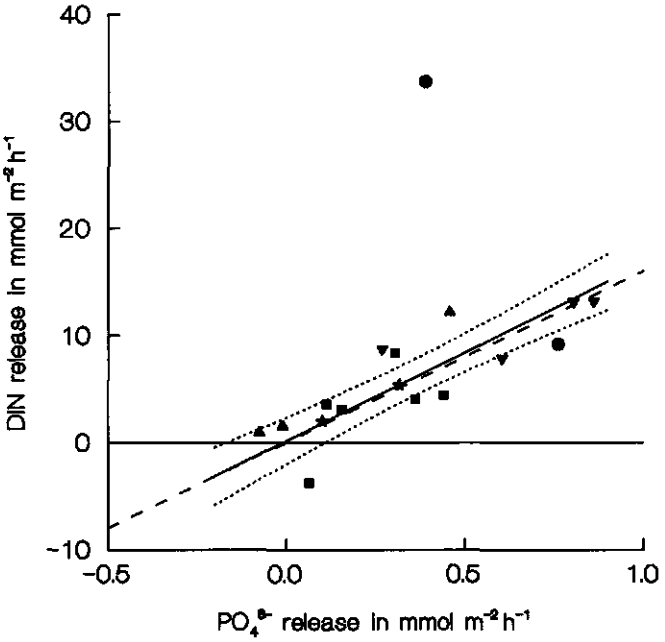

Figure 5.2. The release of dissolved inorganic nitrogen (DIN, $NO_2^-+NO_3^-+NH_4^+$) and PO_4^{3-} by mussel beds (average per tidal cycle). Negative values indicate uptake of nutrients by the mussel bed. The solid line is the geometric mean regression line between DIN and phosphate fluxes with 95% confidence interval. The dashed line represents the Redfield ratio N:P = 16:1. Symbols as in Fig. 5.1.

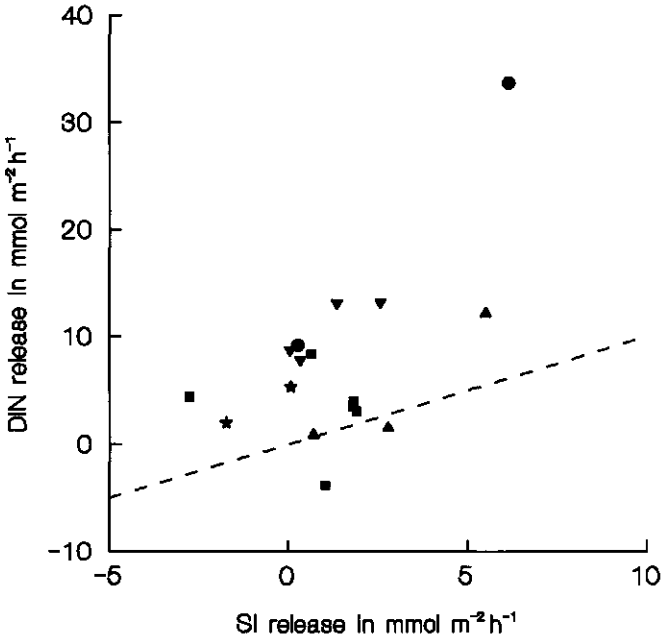

Figure 5.3. The release of dissolved inorganic nitrogen (DIN, $NO_2^-+NO_3^-+NH_4^+$) and silicate by mussel beds (average per tidal cycle). The dashed line represents the ratio N:Si = 1:1. Symbols used as in Fig. 5.1.

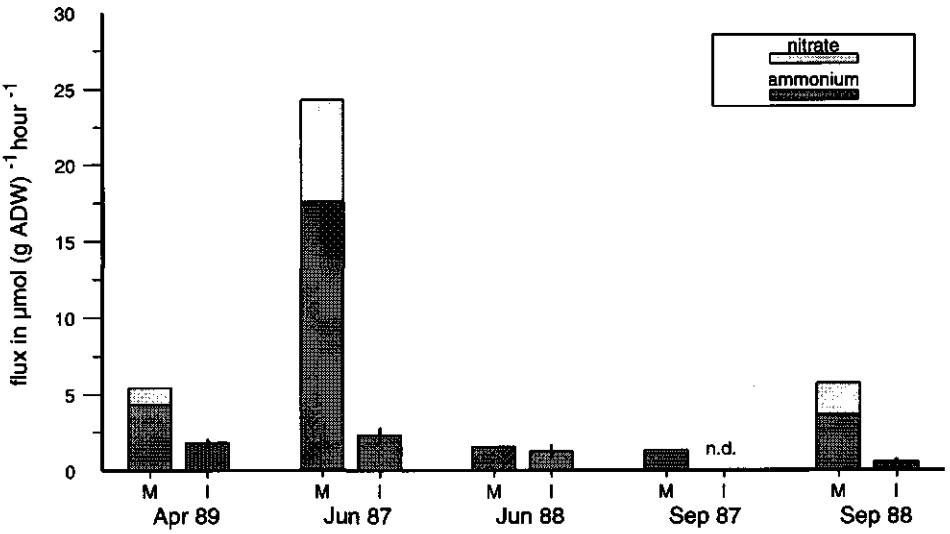

Figure 5.4. The *in situ* flux of dissolved inorganic nitrogen from the mussel bed, recalculated to a rate per unit body weight (M), and the individual NH_4^+ excretion rate per unit body weight (I). The error bars indicate the 95% confidence limits. n.d. = not determined

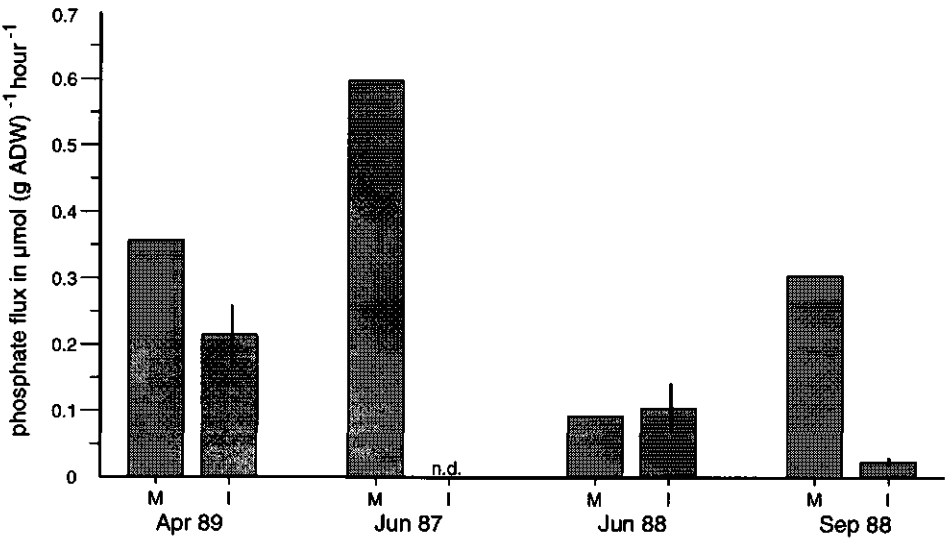

Figure 5.5. The *in situ* flux of PO_4^{3-} from the mussel bed, recalculated to a rate per unit body weight (M), and the individual PO_4^{3-} excretion rate per unit body weight (I). The error bars indicate the 95% confidence limits.

Table 5.1.
Uptake of particulate nitrogen (PN) and release of NH_4^+ and dissolved inorganic nitrogen (DIN; NO_2^- $+NO_3^-+NH_4^+$) (mean ± s.e.) by an intertidal mussel bed.

month	PN uptake mmol m^{-2} h^{-1}	n	NH_4^+ release mmol m^{-2} h^{-1}	n	DIN release mmol m^{-2} h^{-1}	n
April	12.8 ± 1.68	33	8.7 ± 0.60	67	10.9 ± 0.74	65
June 1987	21.7 ± 6.35	17	17.1 ± 4.89	20	24.0 ± 5.66	20
June 1988	3.3 ± 0.89	75	3.2 ± 4.02	73	3.4 ± 1.93	70
September 1987	-0.5 ± 0.90	29	1.4 ± 1.30	25	1.2 ± 1.42	23
September 1988	2.0 ± 2.16	47	6.9 ± 2.98	15	12.0 ± 6.48	14

Table 5.2.
Uptake of particulate phosphorus (PP) and release of PO_4^{3-} (mean ± s.e.) by an intertidal mussel bed.

month	PP uptake mmol m^{-2} h^{-1}	n	PO_4^{3-} release mmol m^{-2} h^{-1}	n
April	0.9 ± 0.25	33	0.7 ± 0.12	66
June 1987	0.2 ± 0.66	17	0.6 ± 0.17	20
June 1988	0.6 ± 0.33	27	0.2 ± 0.12	70
September 1987	-0.2 ± 1.63	3	0.0 ± 0.21	25
September 1988	0.9 ± 0.30	17	0.6 ± 0.63	15

Table 5.3.
Uptake of biogenic silicon (POSi) and release of silicate (mean ± s.e.) by an intertidal mussel bed.

month	POSi uptake mmol m^{-2} h^{-1}	n	H_4SiO_4 release mmol m^{-2} h^{-1}	n
April	2.32 ± 0.23	63	1.63 ± 0.32	67
June 1987	3.63 ± 0.68	17	3.20 ± 1.21	20
June 1988	0.56 ± 0.12	88	0.58 ± 0.57	74
September 1987	0.15 ± 0.03	29	2.41 ± 1.57	25
September 1988	0.17 ± 0.04	18	3.69 ± 3.09	15

N, P, and Si budgets of the mussel bed

From the observed uptake of PN and PP and the release of DIN and phosphate by the mussel bed an estimate was made of the net budgets of nitrogen and phosphorus. Results were averaged for April 1989, June 1987, June 1988, September 1987 and September 1988. In Table 5.1 the resulting nitrogen budget of the mussel bed is shown. The highest uptake of PN and the highest release of DIN was observed in April 1989 and in June 1987. With the exception of September 1988, the budgets showed a DIN release that was approximately equal to the uptake of PN.

Table 5.2 shows the mean uptake of particulate phosphorus (PP) and the mean release of phosphate. The results showed that in most observations uptake of PP was higher than the release of phosphate, although the differences were not significant. The release of phosphate was higher than the PP uptake in June 1987, when observed PP uptake rates were low. On average, the phosphate release from the mussel bed was equal to 64 % of the PP uptake by the mussel bed.

The uptake of biogenic silicon was calculated from the amount of diatoms taken up by the mussel bed. The estimated silicon budget (Table 5.3) showed that uptake of silicon was significantly higher than release in April 1989 (Mann-Whitney test, $p<0.010$). Silicate release in June 1988 was low. Regeneration of silicate was significantly higher than the estimated uptake of silicon by the mussel bed in September 1987 (Mann-Whitney test, $p<0.050$).

DISCUSSION

Uptake of particulate matter

The *in situ* observations on exchange of material between mussel beds and the water column in the Oosterschelde estuary showed that the mussel beds process high amounts of particulate material. Earlier published estimates of the amount of particulate C, N and P filtered and biodeposited by bivalves in estuaries show a large range (e.g.Kuenzler, 1961; Sornin et al., 1986; Kautsky & Evans, 1987; Dame & Dankers, 1988; Asmus et al., 1990; Dame et al., 1991), which is a consequence of differences in filter feeder biomass, concentrations of particulate material in the water column, resuspension due to turbulence etc. Our observations fall within the range of published fluxes. The net flux of particulate matter to the mussel bed consisted of material with a low C:N ratio (9.4) compared to the composition of the seston. This low C:N ratio can be explained by resuspension and export of a carbon-rich component of the filtered material. This is supported by the fact that the C:N ratio of the seston was higher at the outflow than at the inflow of the tunnel. As a result of this process the net flux of particulate matter from the water column to the mussel bed consisted of material with a relatively high food quality, as was discussed already in chapter 3.

Contribution of excretion to nutrient release

As the density of the mussels was high, it is obvious that excretion by the bivalves might contribute significantly to the nutrient release into the water column. In order to assess the contribution of excretion by mussels to the observed nutrient release we compared the *in situ* fluxes from the mussel bed to direct excretion rates by the animals.

Estimates of the contribution of ammonium excretion by bivalves to the sediment-water fluxes vary between 5-90% (Kaspar et al., 1985; Murphy & Kremer, 1985; Doering et al., 1986, 1987; Dame et al., 1989; Asmus et al., 1990). In our experiments the excretion by the mussels accounted for 13-80% of the total ammonium flux from the mussel bed. The ammonium excretion rates in our experiments corresponded with published values (Bayne & Scullard, 1977; Bayne & Widdows, 1978; Hawkins et al., 1985). We did not measure any nitrate excretion by the mussels although Boucher & Boucher-Rodoni (1988) have observed a small rate of nitrate excretion by the oyster *Crassostrea gigas*. Our results showed that in most observations direct excretion by the mussels could only partly explain the amount of inorganic nitrogen released by the mussel bed. More than 50 % of the ammonium and all of the nitrate released by the mussel bed came from another source.

The excretion rates of phosphate by the mussels in our experiments were comparable to rates observed by Kautsky & Wallentinus (1980) (0.01-0.61 µmol g ADW^{-1} h^{-1}) and Asmus et al. (1990) (0-0.73 µmol g ADW^{-1} h^{-1}). The results suggested that phosphate excretion by the mussels accounted for a major part of the observed phosphate flux from the mussel bed.

Mussels can excrete silicate (Asmus et al., 1990). Silicate excretion is related to the feeding activity and depends on the amount of diatoms in the food ingested by the mussels (Asmus et al., 1990). In our experiments silicate excretion rates were below the detection limit, and we conclude that the contribution of direct excretion by the mussels to the silicate flux from the mussel bed in our measurements was insignificant.

Our results show that the direct excretion of inorganic nutrients by the mussels contributed only partly to the release of DIN and phosphate by the mussel beds, while silicate excretion was unimportant. Other benthic fauna was a small (< 10 %) fraction of the total biomass in the mussel bed, and we assume that the contribution of excretion by other organisms in the mussel bed was insignificant. We therefore conclude that mineralization of organic matter deposited on the mussel bed (biodeposition) must be an important source of inorganic nutrients in the sediment of a mussel bed.

Size and composition of dissolved inorganic nutrient flux

Our observations of nutrient release rates show agreement with published data on nutrient regeneration by bivalve communities. The fluxes of dissolved inorganic nutrients from beds of bivalve suspension feeders into the water column are significantly higher than sediment-water fluxes from other benthic habitats (Table 5.4). Total fluxes of ammonium, nitrate and phosphate, as well as fluxes per unit biomass, are highest from bivalve communities that attain high densities, and accumulate high amounts of biodeposition, like beds of *Mytilus edulis*, *Crassostrea virginica* and *Crassostrea gigas*. This reflects the dependence of the mineralization process in the sediment on the supply of organic matter by biodeposition. The production of biodeposits is determined by the concentration of particulate matter in the water column, the clearance rate of the bivalves, and the density of the bivalves. The accumulation of biodeposition on the bivalve bed is dependent on local physical conditions (current speed, turbulence etc.). Infaunal species like the cockle *Cerastoderma edule* or the carpet clam *Ruditapes decussatus* do not accumulate large amounts of biodeposition on the sediment. Consequently, the nutrient efflux from these communities is much smaller.

When compared to the biomass of the macrobenthos, relatively high silicate fluxes have been observed in experiments with *Cerastoderma edule*, *Mercenaria mercenaria* and *Arenicola marina*. This may have been caused by higher rates of bioturbation (Asmus, 1986; Helder & Andersen, 1987) or higher temperatures (Helder et al., 1983; Doering et al., 1987) in these experiments.

Nitrogen regeneration

Ammonium was the main component of the released inorganic nitrogen, while nitrate comprised ca 20 % of the total DIN flux. In general, nitrite fluxes were negligible. Only in one series of measurements a significant release of nitrite was observed, which accounted for 8 % of the DIN flux (Chapter 4). Our results are in accordance with most observations on benthic nitrogen regeneration that show ammonium to be the main constituent of the DIN flux (Nixon, 1981; Nixon & Pilson, 1983).

Nitrate was predominantly released from the mussel bed in our experiments, which is unlike most observations of sediment-water fluxes, where nitrate fluxes between the water column and bivalve communities are usually small and erratic, and are often directed into the sediment (e.g. Murphy & Kremer, 1985; Doering et al., 1987; Boucher & Boucher-Rodoni, 1988; Dame & Dankers, 1988; Dame et al., 1989; Asmus et al., 1990). A large uptake of nitrate from the water was observed on mussel beds by Dame & Dankers (1988), which was ascribed to uptake by microphytobenthos. Our results agree with the significant release of nitrate from the sediment observed in spring and summer in oyster cultivation areas (Feuillet-Girard et al., 1988; Lerat et al., 1990), and the increased nitrification observed in the presence of oysters (Boucher & Boucher-Rodoni, 1988;

Table 5.4.

Minimum and maximum nutrient fluxes between bivalve beds and the water column. The period of observations and the biomass of the dominating bivalve species are included. For comparative purposes results obtained on *Arenicola marina* flats and on sediments without dense bivalve communities are included. Positive fluxes indicate a release into the water column.

NH_4^+ mmol m^{-2} h^{-1}	NO_3^- mmol m^{-2} h^{-1}	PO_4^{3-} mmol m^{-2} h^{-1}	H_4SiO_4 mmol m^{-2} h^{-1}	period	biomass g ADW m^{-2}	species
-0.020/29.52	-5.46/6.37	-0.43/0.85	-1.66/8.16	Apr-Sep	890-2190	*Mytilus edulis*, Oosterschelde[1]
0.71/15.71	-5.71/-1.43*	-1.94/2.90	-0.36/2.14	Jun-Aug	820-940	*Mytilus edulis*, Wadden Sea (west)[2]
0.60/5.52	-0.06/1.07	-0.21/0.85	-0.49/2.66	Jul-Sep	1560	*Mytilus edulis*, Wadden Sea (east)[3]
4/5	-	-	-			*Mytilus edulis*, laboratory[4]
0.00/0.37	-0.02/0.01	-0.00/0.12	0.02/1.21	May-Nov	-**	*Mytilus edulis*, Mediterranean Sea[5]
-0.16/0.81	-0.20/0.34	0.06/0.22	0.04/0.98	June	20-100	*Cerastoderma edule*, Oosterschelde[6]
0.12/16.9	-1.2/0.10*	-	-	Jun-Aug	200	*Crassostrea virginica*, South Carolina[7]
1.00	0.00*	0.03	-	year	200	*Crassostrea virginica*, South Carolina[8]
0.05/0.38	-0.11/0.05*	-	-	year	100-200	*Crassostrea gigas*, France[9]
0.02/0.40	-0.15/0.03	-0.00/0.05	-	year	20-140	*Mercenaria mercenaria*, California[10]
0.23	0.02*	-	0.10/0.70	Apr-Aug	16 ind.m^{-2}	*Mercenaria mercenaria*, mesocosm[11]
0.02/0.04	-0.01/-0.00	0.00/0.01	0.00/0.03	Nov-Mar	90 ind.m^{-2}	*Ruditapes decussatus*, Portugal[12]
-0.30/0.40	-0.25/0.00	-	-2.50/1.00	Feb-Nov	-	*Arenicola marina*, Wadden Sea (east)[13]
-0.13/1.02	-1.15/1.10	-0.02/0.05	-0.46/0.50	-	-	other estuarine / marine sediments[14]

1=this study; 2=Dame & Dankers, 1988; Dame et al., 1991 ; 3=Asmus et al., 1990; Asmus & Asmus, 1991 ; 4=Nixon et al., 1976a ; 5=Baudinet et al., 1990 ; 6=Prins & Smaal, unpublished results; 7=Dame et al., 1984, 1985 ; 8=Dame et al., 1989 ; 9=Boucher & Boucher-Rodoni, 1988 ; 10=Murphy & Kremer, 1985 ; 11=Doering et al., 1987 ; 12=Falcao & Vale, 1990 ; 13=Asmus, 1986 ; 14=reviews in Nixon, 1981; Lerat et al., 1990 .

* $NO_2^- + NO_3^-$ ** sediment under rope culture

Boucher-Rodoni & Boucher, 1990). The observed nitrate release (Boucher & Boucher-Rodoni, 1988; Feuillet-Girard et al., 1988; Boucher-Rodoni & Boucher, 1990; Lerat et al., 1990; this study) seems to indicate that, in addition to ammonification, nitrification is an important process at the sediment-water interface of bivalve beds. This may be related to the high nitrification potential of bivalve faecal pellets (Henriksen et al., 1984), and an increased nitrification due to resuspension of biodeposition (Owens, 1986).

Many publications on benthic nutrient regeneration mention sediment-water fluxes with anomalously low N:P ratios (<10). The main cause for this phenomenon is assumed to be a loss of nitrogen from the sediment due to denitrification (Boynton et al., 1980; Nixon, 1981; Seitzinger, 1988). Denitrification has been observed in areas with rope cultures of mussels (Kaspar et al., 1985; Baudinet et al., 1990). Denitrification can also occur in anaerobic microniches within faecal pellets (Jørgensen, 1977; Sayama & Kurihari, 1983), but a rapid breakdown of the faecal pellets, as was observed by Oenema (1988), would prevent the development of anoxic microsites and inhibit denitrification within the pellets. In many sediments nitrification in the aerobic layer and denitrification in the anaerobic sediment layer are tightly coupled processes (Jenkins & Kemp, 1984; Kemp et al., 1990). It was hypothesized by De Vries & Hopstaken (1984) that the presence of benthic epifauna may cause a spatial separation of nitrification and denitrification. A mussel bed is characterized by an impoverished infauna, due to oxygen deficiency and H_2S production (Asmus, 1987). This may result in a reduced bioturbation and hence a decreased transport of nitrate to the deeper sediment layers. Experimental results with oysters showing high rates of nitrification without immediate denitrification (Boucher & Boucher-Rodoni, 1988) support this hypothesis. Our observations show fluxes with N:P ratios close to the Redfield ratio, and our estimates of the nitrogen budget of the mussel bed (Table 5.1) indicate that little nitrogen was retained by the mussel bed. From this we conclude that denitrification in the sediment of the mussel bed must have been a minor process compared to the total fluxes of nitrogen between the water column and the mussel bed.

The highest release of DIN was observed in the night tidal cycle in June 1987. Nutrient fluxes during the day period were significantly lower, probably as a consequence of uptake by microalgae (Chapter 4). The high nitrogen release coincided with high phytoplankton concentrations, leading to a high supply of organic matter to the mussel bed. The initial degradation of mussel biodeposits concerns the mineralization of the labile fraction, and this seems to occur on a very short time scale (3-10 days) (Stuart et al., 1984; Grenz et al., 1990). Grenz et al. (1990) suggest that intestinal bacteria, deposited with the faeces, are responsible for the rapid initial phase of mineralization. The fast initial degradation of biodeposits may explain the high release of DIN in a period (June 1987) with a high supply of organic matter.

Phosphorus release

The highest phosphate release rates have been observed on mussel beds in the western Dutch Wadden Sea (Dame & Dankers, 1988; Dame et al., 1991). Phosphate fluxes from mussel beds in the German Wadden Sea (Asmus et al., 1990) and the Oosterschelde (this study) were lower. The difference is probably caused by the relatively high discharge of phosphorus into the western Dutch Wadden Sea (Van der Veer et al., 1989; Van Raaphorst & Van der Veer, 1990), compared to the German Wadden Sea (Hickel, 1989) and the Oosterschelde estuary (Wetsteyn & Bakker, 1991).

Whereas the mussel bed seemed very efficient in recycling N, the estimated P budget suggested that P may partly be retained (Table 5.2). Dame et al. (1989) also observed a retention of P by an oyster reef, and estimated that on an annual basis only 11 % of the particulate P flux was recycled as phosphate. Our results showed a higher recycling of P (64 %), but relative to N a larger amount of P was stored in the mussel bed. Our results from June 1987 deviated from this pattern, with a low uptake of PP and a higher phosphate release than PP uptake. The observations in June 1987 were done during a phytoplankton bloom (13.1 μg chlorophyll a l^{-1}) and a high uptake of PN and chlorophyll a (Chapter 3) was observed. The low uptake of PP does not fit with this, and may have been due to analytical or sampling errors. Often, phosphate fluxes from the sediment seem unaffected by the presence of macrofauna or are even lower than macrofaunal phosphate excretion (Nixon et al., 1980; Murphy & Kremer, 1985; Doering et al., 1987), which is probably due to adsorption of phosphate on sediment particles under aerobic conditions (Balzer et al., 1983). The retention of phosphorus on the mussel bed in our experiments may have been caused by adsorption of phosphate on sediment particles in the aerobic sediment layer (Balzer et al., 1983) and on resuspended biodeposition (Oenema, 1988).

Silicate release

Few data are available on the release of silicate from sediments. The highest release of silicate has been observed on mussel beds (Asmus et al., 1990; Dame et al., 1991: this study). Compared to other estuarine sediments *Arenicola marina* flats and sediments under mussel rope cultures show relatively high release rates of silicate, too (Aller, 1979; Asmus, 1986; Helder & Andersen, 1987), probably as a consequence of bioturbation and ventilation of burrows (Aller, 1979; Asmus, 1986; Helder & Andersen, 1987).

The uptake of silicon by the mussel bed was estimated from the observed chlorophyll fluxes and from observations on the phytoplankton composition in the Oosterschelde estuary. It is clear that this conversion adds considerably to the uncertainty in the estimated particulate silicon flux. In addition, our estimates of silicon uptake by the mussel bed were probably an underestimate as we have only estimated the particulate

silicon supply from diatoms, and did not take into account possible other sources, e.g. clay particles.

The silicate release rates were lower than the estimated uptake of biogenic silicon in April, and in June 1987 when a high phytoplankton concentration caused a high uptake of biogenic silicon (Table 5.3). Our results showed a silicon accumulation in the mussel bed during spring, probably connected to the spring phytoplankton bloom (Wetsteyn & Bakker, 1991). High silicate release was observed in the night tidal cycle of June 1987. The lower silicate fluxes during the day observations were probably due to uptake of silicate by diatoms during the day (Chapter 4). A rapid remineralization of silicate has been suggested by several authors (Callender & Hammond, 1982; Baudinet et al., 1990) and may explain the high silicate effluxes in the June 1987 measurement. The high silicate release in fall probably reflected the increased rate of dissolution of silicate at higher water temperatures (Helder et al., 1983).

Nutrient budget of the mussel bed

An estimate was made of the amount of nitrogen and phosphorus that the mussels need to maintain a positive growth rate. In the calculations we used the biomasses of the mussel beds in our experiments, and we assumed a constant C:N:P ratio for mussel flesh (225:58:1; Vink & Atkinson, 1985). Growth rates were used that are typical for mussels of this size in the central part of the Oosterschelde estuary (0.3-1.0 % day^{-1}; Van Stralen, 1988; Smaal & Van Stralen, 1990). Although this calculation can only give an approximation of the assimilation of N and P by the mussels, the estimates (Table 5.5) show that the amounts of N and P assimilated by the mussels were relatively small compared to the observed PN and PP fluxes. This estimate makes it probable that a substantial fraction of the particulate N and P flux to the mussel bed was not assimilated by the mussels and was deposited on the sediment as faeces or pseudofaeces. This corresponded with earlier estimates showing that 85-93 % of the filtered nutrients are biodeposited by bivalves (Kuenzler, 1961; Sornin et al., 1986; Feuillet-Girard et al., 1988). Silicon is not assimilated by the animals, although a small fraction may be excreted by the mussels after digestion of diatoms (Asmus et al., 1990). Consequently, practically all biogenic silicon filtered will be biodeposited. Due to mineralization of the biodeposition most of the N and Si is recycled, whereas P is partly retained by the mussel bed, probably through sediment adsorption. Therefore, it can be concluded that the mussel population may be an important agent in the nutrient cycling in an estuary, as the mussels transform particulate organic nutrients into inorganic nutrients which are recycled to the pelagic system, while only a small fraction of the nutrients is stored in biomass or biodeposition.

Table 5.5.
Estimated assimilation of PN and PP by the mussels, necessary to enable observed growth rates.

month	N uptake by mussels mmol m^{-2} h^{-1}	P uptake by mussels mmol m^{-2} h^{-1}
April	3.43	0.059
June 1987	1.32	0.023
June 1988	2.14	0.037
September	1.53	0.026

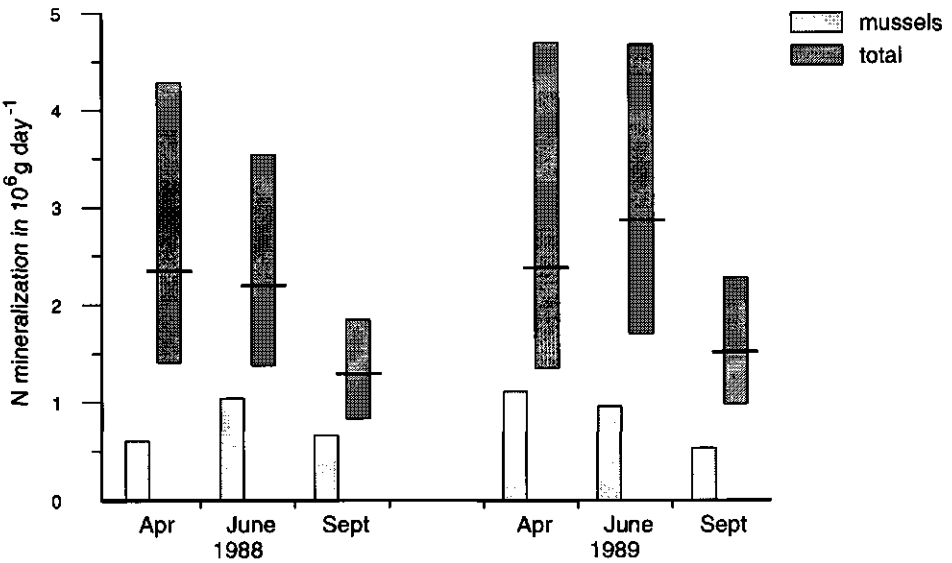

Figure 5.6. The amount of nitrogen mineralized by mussel beds in the central part of the Oosterschelde estuary, compared to estimates of total nitrogen mineralization (benthic + pelagic) from the Oosterschelde ecosystem model SMOES. The bar represents the 10-90% range of model estimates, the line shows the median.

Significance on system level

The density of mussels in the Oosterschelde estuary is high, and the grazing pressure probably keeps phytoplankton biomass low (Smaal et al., 1986; Herman & Scholten, 1990). Nevertheless, the mussel population not only acts as a sink for nutrients. Net storage of nutrients in biomass or biodeposition seems relatively small. The main effect of the mussel population is to increase the mineralization rate of nutrients that were stored in phytoplankton biomass. Nutrient turnover rates as a consequence of regeneration on mussel beds are much higher than the rates of water renewal in the central part of the Oosterschelde, and it was proposed earlier that the regeneration of DIN and Si by mussel beds may be an important source of nutrients for the phytoplankton in summer (Dame et al., 1991; Chapter 4), when primary production is nutrient-limited (Wetsteyn & Bakker, 1991).

In order to establish the role of the mussels in the cycling of nutrients in the Oosterschelde estuary, the exchange of material between the water column and the mussels should be compared with the fluxes between the other components in the ecosystem. The nitrogen regeneration on the mussel beds was estimated from the observed *in situ* DIN release (this study) and total mussel biomass in the area (Van Stralen & Dijkema, 1994). These rates were compared to estimates of the total nitrogen mineralization (pelagic + benthic) calculated with the model SMOES (Simulation Model Oosterschelde EcoSystem). This model describes the carbon and nutrient fluxes between the main functional groups in four spatial compartments of the Oosterschelde estuary and was calibrated with an extensive data set of field observations (Klepper, 1989; Scholten & Van der Tol, 1994). An uncertainty analysis with the model eventually gives a range of values for the model variables. A comparison was made for the years 1988-1989, for the central part of the Oosterschelde area. The results (Fig. 5.6) show that the estimated nitrogen regeneration by the mussels is equal to about 50 % of the median value of the model result for total nitrogen mineralization. Of course, the error in these estimates is quite large as a consequence of the variability in the *in situ* observations and the uncertainty in the estimates of mussel biomass. Moreover, the range of values for the nitrogen mineralization calculated by the ecosystem model is large. Nevertheless, this comparison supports the hypothesis that the mussel population plays a major role in the recycling of nitrogen in the central part of the Oosterschelde ecosystem.

The suggestion has been made that mussels may even increase eutrophication, due to the high regeneration of nutrients by mussel populations (Baudinet et al., 1990). As was suggested by Herman & Scholten (1990) however, an effective 'top-down' control by grazing can keep phytoplankton biomass low, even when nutrient loading to an ecosystem is high. The presence of high amounts of filter feeders merely leads to a higher turnover of phytoplankton (Doering et al., 1986; Sterner, 1986; Doering, 1989; Asmus & Asmus, 1991). The control on phytoplankton biomass stabilizes the ecosystem (Herman &

Scholten, 1990), as long as the primary producers do not escape filter feeder control by shifts to species that are not or less efficiently filtered, like macrophytes, small cells (Riemann et al., 1988) or *Phaeocystis pouchetii* (Wolters, 1988; Chapter 6).

CHAPTER SIX

SEASONAL VARIATION IN THE FILTRATION RATES OF A SEMI-NATURAL MUSSEL BED IN RELATION TO SESTON COMPOSITION

Based on: T.C. Prins, N. Dankers & A.C. Smaal, 1994. Seasonal variation in the filtration rates of a semi-natural mussel bed in relation to seston composition. J. Exp. Mar. Biol. Ecol. 176: 69-86

ABSTRACT

In September 1988 a mussel bed, with a biomass of 1362 g ash-free dry weight m^{-2}, was created in a concrete tank with a continuous supply of natural seawater. Measurements of particulate matter uptake by the mussel bed were carried out monthly from December 1988 till December 1989. Fluxes of suspended particulate matter, POC, PN, PP and chlorophyll-*a* were significantly correlated with water column concentrations. A control experiment showed that sedimentation did not affect observed fluxes. Clearance rates of the mussel bed varied between 0.4 and 2.7 m^3 m^{-2} h^{-1}. Seasonal variation in the filtration activity of the mussel bed could be attributed to changes in the composition of the suspended particulate matter: individual clearance rates of the mussels were reduced in the period April-June, which coincided with a bloom of *Phaeocystis* sp. Moreover, clearance rates decreased with increasing SPM concentrations, and showed a positive correlation with chlorophyll-*a*.

INTRODUCTION

Bivalve suspension feeders occur in high densities in many estuarine systems (Wolff, 1983). Depletion of phytoplankton biomass as a consequence of bivalve filtration has been observed on a local scale (Wright et al., 1982; Carlson et al., 1984; Nichols, 1985; Navarro et al., 1991). On the scale of entire estuaries, estimates have shown that populations of bivalve suspension feeders may filter the entire water column in *ca* 2 to 10 days (Smaal et al., 1986; Hily, 1991; Smaal & Prins, 1993), and model simulations suggest that grazing by bivalves may lead to an effective control of phytoplankton biomass (Cloern, 1982; Officer et al., 1982; Herman & Scholten, 1990).

Most of these estimates were made by extrapolating laboratory observations of clearance rates to an entire estuary. As was shown by Doering & Oviatt (1986) these extrapolations may severely overestimate the *in situ* filtration rates. Clearance rates, measured in the laboratory, may not represent the natural rates as environmental conditions, affecting the pumping activity of bivalves, may differ between the laboratory and the field situation. A number of factors have been observed to be important in determining clearance rates, like body size and physiological state of the mussels, oxygen concentration, concentration and composition of the suspended particulate matter, and current speed (a.o. Bayne et al., 1976; Winter, 1978; Bayne & Newell, 1983; Jørgensen, 1990; Wildish & Miyares, 1990). *In situ* measurements of filtration rates of individual mussels were carried out by Fréchette et al. (1989). Although these experiments give some information on clearance rates of individual bivalves under natural conditions, it remains unclear whether *in situ* filtration rates of bivalve populations can be extrapolated from the individual rates, as manipulation of mussels shortly before measurements may affect filtration rates (Vismann, 1990).

The first *in situ* observations of rates of chlorophyll-*a* uptake by an undisturbed mussel bed were made by Wright et al. (1982). More extensive results of particulate matter uptake by bivalves were obtained in experiments on oyster reefs, using a Benthic

Ecosystem Tunnel (Dame et al., 1984, 1985, 1989; Dame, 1987). Similar types of experiments with tunnels or flumes have been carried out on mussel beds in various estuaries (Dame & Dankers, 1988; Asmus et al., 1990; Asmus & Asmus, 1991; Dame et al., 1991; this thesis). Results from these studies can be used to estimate the rates of water processing by mussel beds. However, the interpretation of field results is rather complicated as the fluxes of particulate matter between the water column and the bivalve community are not only related to filtration by the mussels, but may also be influenced by sedimentation and resuspension processes. Moreover, differences have been observed in the behaviour of the different components of the suspended particulate matter: phytoplankton or chlorophyll-*a* fluxes are correlated with the concentrations in the water column, and show a consistent pattern of uptake (Dame & Dankers, 1988; Asmus et al., 1990; Asmus & Asmus, 1991; Dame et al., 1991; this thesis). Fluxes of total seston show no correlation with water column concentrations, and vary between uptake and release, indicating that resuspension of faeces and pseudofaeces and/or erosion of the mussel bed affects the net fluxes of particulate material (Asmus et al., 1990; Dame et al., 1991; chapter 3).

In order to assess the seasonal variation in clearance rates of a mussel bed under natural conditions with respect to food supply and temperature, but with exclusion of sedimentation and resuspension, we have carried out an experiment with a semi-natural mussel bed in a continuous flow tank supplied with natural sea water. During one year monthly observations were made of biomass and density of the mussel bed, and particulate matter uptake by the mussels.

MATERIAL AND METHODS

Mussel bed

A concrete tank of 5 m width, 40 m length and 1 m depth at the Institute for Forestry and Nature Research (I.B.N.-D.L.O.) at Texel was used. On the bottom of this tank a sand layer of 5 cm thickness was spread out. In September 1988 a mussel bed was created on top of this sediment by spreading 120 kg (wet weight including empty shells etc.) of mussels in a row of 12 m long and 0.8 m wide. The mussels were collected from an intertidal flat in the western Wadden Sea, near the island of Texel. The mussel population consisted mainly of mussels from the 1986 spatfall, with an initial mean length of 39 mm (range 9-57 mm), and a mean ash-free dry weight of 586 mg (Table 6.1). Natural seawater, pumped directly from the Wadden Sea, flowed through the tank and over the mussel bed in a lengthwise direction. The water flow through the tank varied between 100 - 200 m^3 h^{-1}. The water supply was interrupted and the tank was drained for 3 hours during each 12 hour period, in order to simulate a tidal cycle. This

Table 6.1.
Number of mussels, average individual length and ash-free dry weight (ADW), and total mussel biomass (ash-free dry weight) of the experimental mussel bed.

date	length (mm) mean ± s.d.	ADW (mg)	total biomass (g m^{-2})
22-9-1988	38.9 ±13.1	586	1362.0
1-12-1988	43.0 ± 8.6	568	913.2
26-1-1989	41.5 ±10.5	482	910.7
22-2-1989	43.3 ± 8.7	466	833.9
30-3-1989	43.4 ± 8.8	429	825.7
20-4-1989	42.8 ±10.0	430	764.3
18-5-1989	42.4 ±10.6	585	1188.6
19-6-1989	45.3 ± 7.2	512	1071.4
11-8-1989	47.3 ± 6.1	664	637.3
11-9-1989	46.9 ± 6.7	782	659.0
9-10-1989	49.5 ± 4.8	825	693.8
6-11-1989	49.4 ± 5.7	789	654.3
11-12-1989	50.0 ± 5.5	719	595.2

low water period was alternately in the morning during one week, and in the afternoon during the next week.

Sampling procedure

Fluxes of particulate matter on the mussel bed were measured with a Benthic Ecosystem Tunnel placed on the mussel bed. The method used was similar to the method in the *in situ* experiments in the Oosterschelde, as described in the previous chapters. The tunnel was placed on the mussel bed one day before measurements were carried out, and was removed again the day after the measurements.

From December 1988 till December 1989 measurements were carried out monthly (with the exception of July 1989). In addition, a control experiment was carried out in May 1989. A control mussel bed was made of empty mussel shells, and one day after the measurements on the mussel bed identical measurements were carried out on the control bed.

For each measurement the inflow and outflow of the tunnel were sampled four times a day. Two sets of samples were collected during day time, and two sets of samples were collected during the night (between sunset and sunrise). All samples were collected in duplicate. Samples were collected in 1 litre glass bottles, and immediately processed at the laboratory. Subsamples were taken for the determination of suspended particulate matter (SPM), particulate organic carbon (POC), particulate nitrogen (PN), particulate phosphorus (PP), chlorophyll-*a* and phaeophytin-*a*. All chemical analyses were done at the laboratory of R.I.K.Z. in Middelburg. Analytical methods were described in chapters 2, 3, and 4.

After each measurement the mussel bed was sampled at 5 different sites. From a surface of 0.25 m^2 all mussels were collected, and fresh weight and shell length were measured. From the samples 32 mussels were chosen at random, and these mussels were used to establish the relation between shell length and ash-free dry weight. The other mussels were put back on the mussel bed.

Calculation of fluxes and clearance rates

The effect of the mussel bed on the concentrations of the various particulate parameters (SPM, POC, PN, PP, and chlorophyll-*a*) in the water flowing through the tunnel was tested for each month with a two-way ANOVA, by comparing inflow and outflow concentrations (duplicates) of each sampling time (Sokal & Rohlf, 1981). The same procedure was used to test the changes in the control experiment.

The measured current velocities were used to calculate water flow through the tunnel (Dame & Dankers, 1988). Material fluxes were calculated from the difference between inflow and outflow concentrations multiplied by the water flow. Clearance rates (volume of water swept clear of particles) were also estimated from the differences between inflow and outflow concentrations. The clearance rate of the mussel bed (CR_{bed}) was calculated from the inflow and outflow concentrations (C_{in} and C_{out}), the water flow through the tunnel (Q), and the surface of the mussel bed between the sampling points (A) with the following formula:

$$CR_{bed} = \ln\left(\frac{C_{in}}{C_{out}}\right) \cdot \frac{Q}{A} \qquad (in\ m^3\ m^{-2}\ h^{-1}) \qquad (6.1)$$

The amount of water filtered by a mussel bed depends on the individual clearance rates and the density of the mussels. Clearance rate is an allometric function of body weight ($CR = a \cdot W^b$, Bayne et al., 1976). As the mussel population consisted of a range of size-classes, the number of mussels on the bed decreased and the mussels increased in size during the year the experiment was carried out, the observed clearance rates had to be adjusted. Clearance rates were standardized to rates per 1 gram ash-free dry weight by

dividing the observed rates by the metabolic mussel biomass, as described in chapter 3. The metabolic biomass B_m was calculated from the numbers (n_i) and individual weights (W_i) of the mussels of each size class *i*:

$$B_m = \sum (n_i \cdot W_i^b) \qquad (in\ gram\ m^{-2}) \qquad (6.2)$$

Clearance rates were calculated from the concentrations of each of the particulate parameters (SPM, POC, PN, PP, and chlorophyll-*a*). An analysis of variance was carried out to test whether significant differences occurred between the clearance rates calculated from each of these five parameters, and between the different sampling times within a month or between months. Significant treatment effects were analyzed with a multiple comparisons test (Tukey-Kramer method; Sokal & Rohlf, 1981). All statistical tests were done with the Systat Inc. statistical software package.

RESULTS

Biomass of the mussel bed

The average length and ash-free dry weight of the mussels and total mussel biomass are shown in Table 6.1. Weight loss of the mussels occurred during the winter period (December 1988 - April 1989). Weight loss also occurred between May and June 1989. The fastest growth rate was observed between April and May 1989 (5.5 mg day^{-1}). Growth rates in the period June-September were 2.8 mg day^{-1}. Predation by oystercatchers caused a strong reduction in density (from ca. 2000 to ca. 960 mussels m^{-2}) and biomass of the mussel bed in the period between June and August 1989.

Seasonal change in temperature and particulate matter concentrations

The water temperature at the time of experiments is shown in Fig. 6.1. Lowest temperatures were observed in December 1988 (4.4 °C), highest temperatures in June 1989 (21.5 °C). Suspended particulate matter (SPM) concentrations showed the highest values in winter (24.6 mg l^{-1}), and lowest in summer (Fig. 6.2). POC concentrations (Fig. 6.3) varied between 0.2 and 1.4 mg l^{-1} during most of the year. Very high POC concentrations (up to 3.4 mg l^{-1}) were observed in May. A clear seasonal trend in chlorophyll-*a* concentrations was observed, with high values in spring (April-May) and late summer (August-September) (Fig. 6.4). POC, PN and PP were all significantly correlated with chlorophyll-*a*.

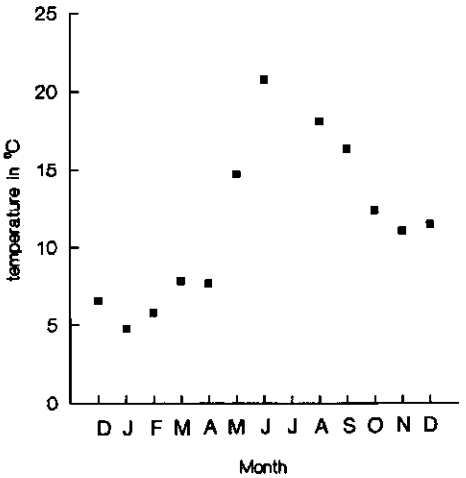

Figure 6.1. Water temperatures (average of 4 observations) during the experiments.

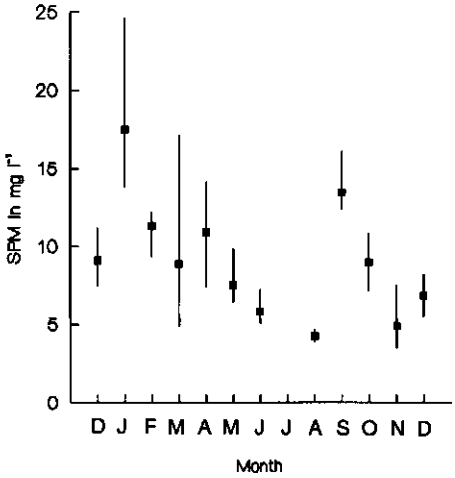

Figure 6.2. Average suspended particulate matter concentrations in the inflow of the tunnel. Bars indicate range (n=4).

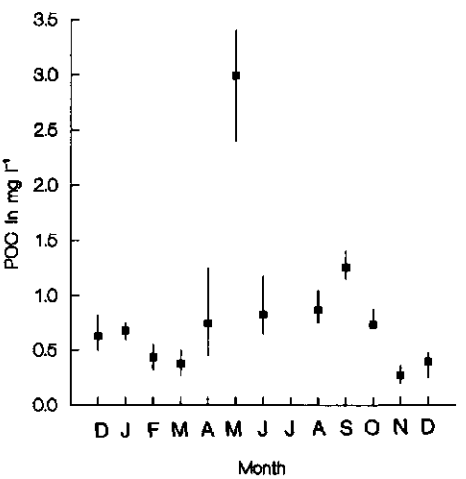

Figure 6.3. Average particulate organic carbon concentrations in the inflow of the tunnel. Bars indicate range (n=4).

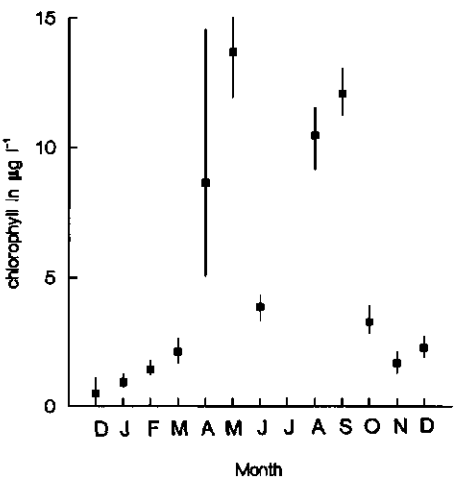

Figure 6.4. Average chlorophyll-*a* concentrations in the inflow of the tunnel. Bars indicate range (n=4).

Particulate matter fluxes

The current speeds observed in the tunnel varied between 2.5 and 6.5 cm s^{-1}. Outflow concentrations of SPM, POC, PN, PP and chlorophyll-*a* were significantly lower than inflow concentrations in nearly all mussel bed observations (Table 6.2). The average concentration decrease during the passage of water through the tunnel was 20-30 % for all seston parameters. No significant differences between inflow and outflow concentrations were observed in the control experiment. Average fluxes of material are shown in Table 6.2. A highly significant correlation was observed between the water column concentrations of the seston components and the fluxes in the mussel bed experiments (Table 6.3), but not in the control experiment ($p>0.05$).

Table 6.2.

Fluxes of suspended particulate matter (SPM), particulate organic carbon (POC), particulate nitrogen (PN), particulate phosphorus (PP), and chlorophyll-*a* (CHL). Positive fluxes indicate uptake by the mussel bed. All values are means of 4 observations. A 2-way ANOVA was used to test whether concentration differences between inflow and outflow were significant.
(* $p<0.050$; ** $p<0.010$; *** $p<0.001$).

Month	SPM g m^{-2} h^{-1}	POC mg m^{-2} h^{-1}	PN mg m^{-2} h^{-1}	PP mg m^{-2} h^{-1}	CHL mg m^{-2} h^{-1}
December 1988	8^{***}	775^{**}	92^{***}	-	0.7
January	25^{**}	608^{***}	66^{***}	26^{***}	0.9^{***}
February	12^{**}	285^{*}	90^{***}	24	2.4^{***}
March	13	581^{***}	72^{***}	17^{***}	3.7^{***}
April	7	877^{***}	73^{***}	20^{**}	5.5^{*}
May	9^{*}	3163^{***}	188^{***}	16^{*}	15.4^{***}
June	6^{***}	1159^{*}	121^{**}	3	4.9^{***}
August	3^{**}	1033^{***}	131^{***}	24^{***}	14.7^{***}
September	15^{***}	1375^{***}	152^{***}	48^{***}	14.6^{***}
October	8^{**}	775^{***}	75^{***}	17^{*}	2.7^{***}
November	7^{***}	287^{*}	38^{**}	10^{***}	2.2^{***}
December 1989	9^{***}	323	38	12^{*}	3.1^{***}
control (May)	2	441	3	-12	-3.1

Table 6.3.
Product-moment correlation coefficients (r) between inflow concentrations and observed fluxes in the mussel experiments.

parameter	r	n	P
SPM	0.72	47	<0.001
POC	0.88	48	<0.001
PN	0.60	48	<0.001
PP	0.61	44	<0.001
chlorophyll-*a*	0.91	48	<0.001

Clearance rates

Clearance rates calculated from the water flow rates and inflow and outflow concentrations of each of the particulate parameters (SPM, POC, PN, PP, and chlorophyll-*a*) were not significantly different. Clearance rates at the different sampling times within a month did not significantly differ from each other either. Between months, there was a highly significant difference in clearance rates (Table 6.4). Standardized clearance rates (average of all observations in a month) with their 95 % comparison intervals are shown in Fig. 6.5. Clearance rates were reduced in January, and April-June. Highest clearance rates were observed in August.

Table 6.4.
Summary of ANOVA of standardized clearance rates. Factors are month, samples within one month, and seston parameter.

Source of variation	df	Mean square	F	p
Months	11	3.466	4.76	<0.001
Samples within months	36	0.919	1.26	ns
Seston parameters	4	1.724	2.37	ns
Error	181	0.728		

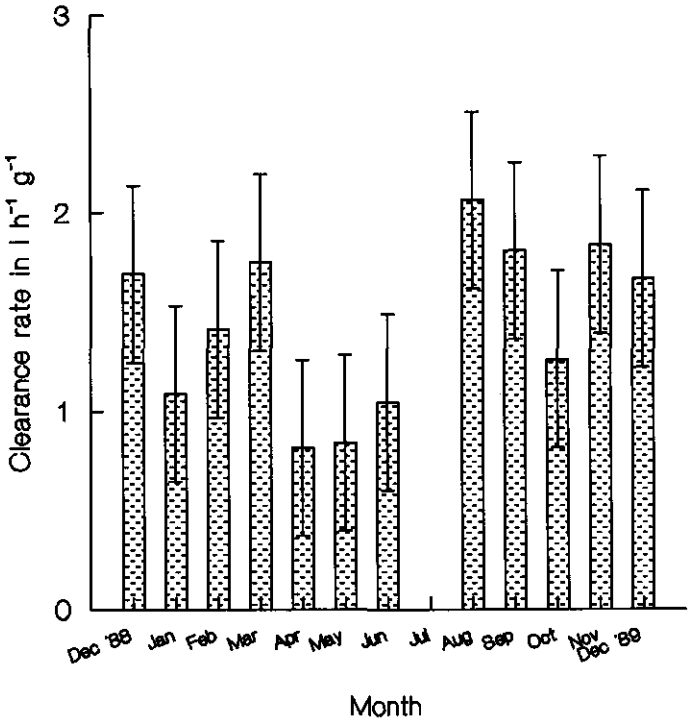

Figure 6.5. Monthly averages of the standardized clearance rates (± 95% comparison intervals) of the mussels (n=4).

DISCUSSION

Experimental conditions

The *in situ* fluxes of particulate matter between water column and bivalve beds, as observed with tunnels or flumes (Dame et al., 1985, 1989, 1991; Dame, 1987; Dame & Dankers, 1988; Asmus et al., 1990; Asmus & Asmus, 1991; this thesis) depend on a number of abiotic and biotic variables. The processes involved are filtration by the bivalves, sedimentation and resuspension. In our control experiment in May 1989 changes in the concentrations of particulate matter were not significant, indicating that settling of particles in the tunnel did not occur, even at the relatively low current velocities in our experiments. We assumed that the behaviour of seston particles in the tunnel was not significantly different in the other months, and that sedimentation was negligible in all observations.

The results of various *in situ* experiments on bivalve beds with tunnels or flumes show a consistent uptake of chlorophyll-*a*, and chlorophyll-*a* fluxes are correlated with

the water column concentrations (Asmus & Asmus, 1991; Dame et al., 1991; Chapter 3). Other seston parameters like SPM and POC show a more erratic behaviour, and the relation between the fluxes and the water column concentrations is generally much less clear (Asmus & Asmus, 1991; Dame et al., 1991; Chapter 3). The different behaviour of SPM and POC, compared to chlorophyll-*a*, is presumably due to resuspension of biodeposits as a consequence of high current speeds (Dame et al., 1989) or wind- and wave-induced turbulence (Fréchette & Bourget, 1985a; Asmus et al., 1990; Dame et al., 1991; Chapter 3). In periods of high turbulence therefore mussel beds can act as sources of POC or phaeopigments (Fréchette & Bourget, 1985a; Asmus et al., 1990; Chapter 3). In our experiments the tunnel was set up in a tank and sheltered against wind influence. Wave action was negligible and current velocities were low, so turbulence was small in comparison to the field conditions on a mussel bed. The agreement between the clearance rates calculated from each of the seston parameters indicated that resuspension of POC or phaeopigments did not occur. The highly significant correlations between on the one hand the fluxes of SPM, POC, PN, PP and chlorophyll-*a* and, on the other hand, the respective inflow concentrations (Table 6.3) also supported the view that resuspension of biodeposits has been negligible in our experiments.

The concentrations of SPM observed in our experiments were lower than in the Western Wadden Sea, where SPM winter concentrations vary between 20-140 mg l^{-1} (Cadée, 1982). POC concentrations were comparable to the minimum values observed in the Wadden Sea (0.5-1.0 mg l^{-1}), and peak values of chlorophyll-*a* in the Wadden Sea are also higher (>20 µg l^{-1}) than in our experiments (Cadée, 1982; Cadée & Hegeman, 1991). The daily variation in SPM concentrations in our experiments (average coefficient of variation: 18%) was smaller than the tidal variation observed in the Western Wadden Sea (cv: 47%; Cadée, 1982), but the daily variation in chlorophyll-*a* concentrations showed a better resemblance to the tidal variation (cv: 17%; Wadden Sea: 23%). This suggested that there may have been some settling of inorganic seston particles in the supply-pipes of the tank. Nevertheless, the seasonal variation closely resembled observations in the Western Wadden Sea (Cadée, 1982; Cadée & Hegeman, 1991). The quality of the suspended particulate matter in our experiments, expressed as the percentage of POC in the suspended matter, was slightly higher (October-April: 2-12 %; April-September: 8-48 %) than in the Wadden Sea (October-April: 2-4 %; April-September: 8-20 %; Cadée, 1982).

The biomass of the mussel bed varied from 1362 g ADW m^{-2}, immediately after the installation of the mussel bed, to 595 g ADW m^{-2} at the end of the experiment. These biomass values were similar to densities on mussel beds in the Wadden Sea and the Oosterschelde estuary (Dame & Dankers, 1988; this thesis). The main growth of the mussels took place from April-September. This agreed with the growth pattern of mussels on intertidal beds and culture lots in the Wadden Sea. Shell length growth rates in this

period (1.2 mm $month^{-1}$) and the increase in body weight (2.3 mg day^{-1}) were comparable to growth rates of similar-sized mussels in the Western Wadden Sea (Dankers et al., 1989) and the Oosterschelde estuary (Van Stralen, 1988).

From the results of the control experiment and the calculated clearance rates, as discussed above, we concluded that sedimentation and resuspension of particulate matter in the tunnel were not important in our experiments. Therefore, the concentration changes observed in the water flowing through the tunnel were due solely to the filtration activity by the mussels. The quantity and composition of the suspended particulate matter in our experiments reflected the conditions in the Wadden Sea. The calculated fluxes and clearance rates in our experiments were the result of the filtration activity by the mussel bed, under natural conditions with regard to temperature, seston concentration and composition, mussel condition and density of the mussel bed.

Filtration of particulate matter

The observed particulate matter fluxes were mainly determined by the water column concentrations (Table 6.3). Accordingly, a comparison of our results to material fluxes observed in other estuaries or coastal areas is of limited value as long as particle concentrations and mussel bed density are not taken into account. The fluxes observed in our study agree with fluxes of particulate matter observed in tunnel experiments in the Western Wadden Sea (Dame & Dankers, 1988; Dame et al., 1991) and the Oosterschelde estuary (Dame et al., 1991; this thesis).

The clearance rates of the mussel bed in our experiments correspond to a total clearance of 0.4 to 2.7 $m^3\ m^{-2}\ h^{-1}$. Similar values (1.4 to 3.1 $m^3\ m^{-2}\ h^{-1}$) can be calculated from the results of Wright et al. (1982) (his Table 2), where mussel densities were higher (3840 m^{-2}) but total mussel biomass was comparable (ca. 900 g DW m^{-2}). Other estimates, based on the extrapolation of laboratory observations of clearance rates, range from 3.5 to 5.9 $m^3\ m^{-2}\ h^{-1}$ (Jørgensen, 1980; Fréchette et al., 1989). Results from tunnel measurements on mussel beds in the Oosterschelde estuary showed clearance rates between 1.3 and 7.1 $m^3\ m^{-2}\ h^{-1}$, but mussel biomass in these experiments was higher (Chapter 3).

In order to relate our results to published values of clearance rates of individual mussels, we standardized clearance rates to rates for an animal of 1 g ash-free dry weight. The standardized clearance rates varied between 1.0-2.0 $l\ g^{-1}\ h^{-1}$ in most months. In laboratory experiments, with algal cultures as food, very high clearance rates have been observed sometimes (e.g. Møhlenberg & Riisgård, 1979). These laboratory values may seriously overestimate the filtration activity of bivalves under more natural conditions (Doering & Oviatt, 1986). Our results are in the lower range of published data on clearance rates in laboratory experiments (a.o. Winter, 1978; Møhlenberg & Riisgård, 1979; Bernard & Noakes, 1990), but corroborate results obtained in experiments with

natural particle suspensions (Bayne & Widdows, 1978; Widdows et al., 1979a, 1984; Smaal et al., 1986; Bayne et al., 1987; Navarro et al., 1991). In contrast to the opinion of Jørgensen (1990) that clearance rates lower than maximal pump capacities are an indication of adverse conditions, our results show that clearance rates of undisturbed mussels under natural conditions may be much lower than the maximum capacity.

Seasonal variation in filtration activity

Reduced clearance rates were observed in January, and in the period April-June. The highest clearance rates were observed in August. A fast growth in body weight without a concomitant increment in gill size (for example due to growth of gonads) may result in a reduction in weight-standardized clearance rates. Therefore clearance rates were examined after standardization to the square of shell length (Jones et al., 1992), which resulted in a seasonal pattern for clearance rates that was similar to that observed in weight-standardized clearance rates. This indicated that the decreases in clearance rates in January and April-June were not due to weight-standardization, and that clearance rates were probably affected by other factors like temperature, current speeds, physiological condition, seston quantity or seston quality.

Owing to the ability of mussels to adapt to low temperatures, clearance rates have been shown to be independent of temperature after acclimatization (Widdows & Bayne, 1971; Widdows, 1978; Loo, 1992). The lack of correlation between the standardized clearance rates and water temperatures in our experiments agreed with this. Current speeds in our experiments were low and below the threshold at which clearance rates may be inhibited by water flow (Wildish & Miyares, 1990).

During spawning the gills of mussels seem to become leaky, as a consequence of which reduced clearance rates have been observed (Newell & Thompson, 1984; Famme et al., 1986; Jørgensen et al., 1988). The reduction in clearance rates may last for a period of 5-10 days after the onset of spawning (Newell & Thompson, 1984). Mussels in the Western Wadden Sea generally spawn in March-April (Pieters et al., 1980). Observations on the gonad development of mussels sampled from the mussel bed in April and May 1989 showed that the mussels had spawned before 19 April (date of sampling) (A. Wagenvoort, pers. comm.). This indicated that the low clearance rates in April-June were not due to spawning.

Mussels regulate their clearance rates in response to the concentration of particles and the quality of the SPM. Clearance rates decrease as the concentration of particles increases (Widdows et al., 1979a; Kiørboe et al., 1980; Bayne & Newell, 1983). A higher quality of the SPM (in terms of organic content by weight or by volume) has been shown to lead to an increase in clearance rates (Bayne et al., 1984, 1987). A similar adaptation of clearance rates to food quality is suggested from *in situ* observations by Navarro et al. (1991).

It was not possible to find a straightforward relation between the individual clearance rates in our study and parameters describing quantity or quality of the particulate matter (SPM, POC, PN, PP, chlorophyll-*a* concentrations, POC/SPM, PN/SPM, chlorophyll-*a*/SPM, C:N ratio). Rather, both the low clearance rates in April-May and the high clearance rates in August-September coincided with high chlorophyll-*a* concentrations, which suggested that the phytoplankton composition might have affected clearance rates. Routine phytoplankton observations on field samples collected close to the sea water inlet of our experimental tank, showed that the haptophycean *Phaeocystis* sp. dominated the phytoplankton from the end of April till June (Cadée, pers. comm.; Cadée, 1992). In April and May *Phaeocystis* sp. accounted for more than 60% of total cell counts, in June it was still the most dominant species. The high peak in POC concentrations observed in May is a typical phenomenon during *Phaeocystis* blooms (Cadée & Hegeman, 1991). The high chlorophyll-*a* concentrations in August-September were caused by a bloom of the diatom *Leptocylindrus minimus* (Cadée, 1992). Reduced feeding of mussels with *Phaeocystis* sp. as food has been observed in laboratory experiments by Wolters (1988).

We decided to test the hypothesis that the variation in clearance rates could be attributed to an inhibitory effect of *Phaeocystis* sp., in combination with an adaptation to changes in the quantity or quality of the seston. Several statistical models were tested in an analysis of covariance, with phytoplankton composition (*Phaeocystis* sp. bloom in April-June versus remaining months) as treatment, and with different subsets of parameters describing seston quantity (SPM, POC, PN, PP, chlorophyll-*a* concentrations) and seston quality (POC/SPM, PN/SPM, chlorophyll-*a*/SPM, C:N ratio) as covariates. The best fitting models showed a significant effect of *Phaeocystis* sp. on mussel clearance, and a significant correlation of clearance rates with SPM and chlorophyll-*a* concentrations, or with the amount of chlorophyll-*a* per mg SPM (Table 6.5).

The results of this analysis of covariance agreed with observed relationships between filtration rates and seston composition. Clearance rates have been shown to decrease in response to increasing particle concentrations (Widdows et al., 1979a; Kiørboe et al., 1980; Bayne & Newell, 1983). The positive correlation between chlorophyll-*a* concentrations and clearance rates in our results corresponded with observations showing an adaptation of clearance rates by mussels in response to changes in seston quality (Bayne et al., 1984, 1987; Navarro et al., 1991).

Furthermore, our results strongly suggest an inhibitory effect of *Phaeocystis* sp. on the filtration activity of the mussels. *In situ* observations with tunnels and flumes in the German Wadden Sea also show reduced feeding rates of mussels during a *Phaeocystis* sp. bloom (Asmus et al., 1992). Rejection of *Phaeocystis* sp. colonies immediately after

Table 6.5.

Summary of results of covariance analysis, relating standardized clearance rates (CR) to algal composition (presence/absence of *Phaeocystis* bloom) and to SPM (mg l^{-1}) and chlorophyll-*a* (CHL, µg l^{-1}) concentrations (Table 6.5-a), or to chlorophyll-*a*/SPM (µg mg^{-1}; Table 6.5-b) as covariates.

Table 6.5-a.

Source of variation	df	Mean square	F	p
Algal composition	1	5.917	30.66	<0.001
SPM	1	0.904	4.68	<0.050
CHL	1	0.797	4.13	<0.050
Error	44	0.193		

covariate	regression coefficient	s.e.
SPM	-0.033	0.015
CHL	0.031	0.013

Table 6.5-b.

Source of variation	df	Mean square	F	p
Algal composition	1	5.742	28.63	<0.001
CHL/SPM	1	1.163	5.80	<0.050
Error	45	0.201		

covariate	regression coefficient	s.e.
CHL/SPM	0.226	0.088

entering the inhalant siphon of *Macoma balthica* was observed by Kamermans (1992). Adverse effects of algae on the filtration activity of mussels have also been demonstrated for the dinoflagelate *Gyrodinium aureolum* (Widdows et al., 1979b), and for the chrysophycean *Aureococcus anophagefferens* (Tracey, 1988). The inhibitory effects of

Aureococcus anophagefferens and *Phaeocystis* sp. have been attributed to clogging of the gills of the mussels by a polysacharide mucus (Pieters et al., 1980; Tracey, 1988). Experiments with cultured *Phaeocystis* sp. have shown that a reduction in clearance rates of mussels also occurred when the *Phaeocystis* sp. culture consisted mainly of single cells (Wolters, 1988). This suggests that the negative effect on clearance rates is not only related to clogging of the gills. Indeed, inhibition of copepod grazing due to anti-predation compounds produced by *Phaeocystis* sp. was observed by Estep et al. (1990).

The reduced feeding rates of the bivalves have been shown to cause starvation and mortality (Pieters et al., 1980; Tracey, 1988; Beukema & Cadée, 1991). In spite of the low clearance rates in our experiments, fluxes of POC and PN were high in May and June. The weight loss of the mussels that occurred between May and June suggested that either ingestion (cf. Kamermans, 1992) or digestibility of the food was too low to prevent starvation.

The intensity of *Phaeocystis* sp. blooms in the Dutch coastal waters shows a rising trend during the last decades (Cadée & Hegeman, 1991) probably related to increased nutrient loadings (Cadée & Hegeman, 1986). This shift in phytoplankton composition towards a dominance of *Phaeocystis* sp. during a major part of the growing season may have serious implications for mussel culture. The Western Wadden Sea and Oosterschelde estuary are extensively used for mussel culture in the Netherlands. Blooms of *Phaeocystis* sp. are most dominant in the period of April to June in these areas (Cadée & Hegeman, 1986, 1991; Bakker et al., 1990) which coincides with the period right after spawning (Pieters et al., 1980), when mussels have low carbohydrate reserves (Bayne et al., 1976) and are more sensitive to starvation (Gabbott, 1976). At the ecosystem level, the shift in the phytoplankton community to a less edible species reduces the 'top-down' control of phytoplankton biomass by bivalve grazing in these estuaries.

CHAPTER SEVEN

NUTRIENT CYCLING AND PHYTOPLANKTON DYNAMICS IN RELATION TO MUSSEL GRAZING IN A MESOCOSM EXPERIMENT

Based on: T.C. Prins, V. Escaravage, A.C. Smaal & J.C.H. Peeters, 1995. Nutrient cycling and phytoplankton dynamics in relation to mussel grazing in a mesocosm experiment. Ophelia 41: 289-315

ABSTRACT

An experiment was carried out with four 3 m^3 land-based mesocosms in May/June 1993. The mesocosms were supplied with a high nutrient loading, and 4 different amounts (20, 40, 80 and 160) of 17-19 mm mussels. Phytoplankton development, concentrations of nutrients, and primary production, bacterial production and mussel growth were followed during four weeks.

Phytoplankton biomass was significantly reduced in the mesocosms with the highest mussel biomass. The phytoplankton in the mesocosm with the highest mussel biomass had a higher proportion of diatoms than the other mesocosms. Phytoplankton growth rates were highest in the mesocosms with high mussel biomass, which was explained as the result of a shift towards faster growing algae (diatoms) and increased nutrient availability due to nutrient regeneration. The reduction in phytoplankton biomass by grazing was higher than the increase of phytoplankton growth rates. As a consequence, total primary production was lowest in the mesocosm with high mussel biomass.

Mussel growth rates were reduced in the mesocosm with the highest mussel biomass, due to intraspecific food competition. Mussel growth in the mesocosm with the lowest mussel biomass was reduced also, which could not be explained from phytoplankton biomass or production, and suggested that food quality was reduced.

INTRODUCTION

The interactions between herbivores and primary producers are characterized by a combination of negative and positive feedbacks. Plant biomass may be severely reduced as a consequence of 'top-down' control caused by grazing. On the other hand, grazing may have a positive feedback on plant productivity by stimulating growth rates. It has been shown both experimentally and by using simulation models, that an increase in plant growth rates as a consequence of grazing may lead to a maximization of net primary production under moderate grazing levels (a.o. McNaughton, 1979; Hilbert et al., 1981; Sterner, 1986; Bianchi & Jones, 1991; DeAngelis, 1992). The main factor responsible for this increase in primary production is probably enhanced nutrient recycling by the grazers (Bianchi & Jones, 1991).

In many coastal ecosystems bivalve suspension feeders are the most dominant primary consumers (Wolff, 1983). Field observations of low phytoplankton biomass have been attributed to high grazing rates by bivalves in systems like San Francisco Bay (Cloern, 1982; Nichols, 1985; Alpine & Cloern, 1992), Oosterschelde (Smaal et al., 1986; Herman & Scholten, 1990), Wadden Sea (Cadée & Hegeman, 1974) and Bay of Brest (Hily, 1991). A simulation model by Officer et al. (1982) suggested that bivalves may exert an effective phytoplankton control. Bivalve communities have also been shown to be important sources of inorganic nutrients (Kautsky & Wallentinus, 1980; Dame et al., 1985; Dame & Dankers, 1988; Asmus & Asmus, 1991; this thesis), and thus may form a major feedback loop between the pelagic and the benthic system (Dame, 1993; Smaal & Prins, 1993). Extrapolations of *in situ* measured values of nutrient release by oyster reefs

and mussel beds suggest that bivalves may significantly affect nutrient cycling at the scale of entire estuaries (Dame et al., 1989, 1991; chapter 6).

The impact of grazing and nutrient regeneration by bivalves on the phytoplankton has been studied mainly in experimental systems. Mesocosm or enclosure studies on the interactions between bivalves and phytoplankton have supplied contradictory results, however. Enclosure experiments with high densities of the blue mussel *Mytilus edulis* showed that the biomass of larger phytoplankton was effectively controlled, but picoplankton became dominant in the phytoplankton (Riemann et al., 1988; Olsson et al., 1992; Granéli et al., 1993). Experiments carried out with the MERL mesocosms showed that in the presence of the clam *Mercenaria mercenaria* nutrient mineralization and phytoplankton production increased, but pelagic biomass was not affected by bivalve grazing (Doering et al., 1986, 1987). Finally, manipulation of oyster density in a field experiment showed that the presence of oysters resulted in elevated concentrations of inorganic nutrients, whereas phytoplankton concentrations were not affected (Dame & Libes, 1993).

We have carried out a 4-week experiment in May/June 1993 with 4 land-based mesocosms. All mesocosms were exposed to a continuous external nutrient supply. Four different mussel densities were used in the mesocosms; 20 (mesocosm ***n*=20**), 40 (mesocosm ***n*=40**), 80 (mesocosm ***n*=80**) and 160 mussels (mesocosm ***n*=160**). The objective of the experiment was to explore the relationships between mussel grazing and phytoplankton biomass, and to study the effects of nutrient recycling by the bivalves on primary and secondary production.

MATERIAL AND METHODS

Mesocosm description

The experiment was carried out with 4 land-based mesocosms at the field station of the National Institute for Coastal and Marine Management/R.I.K.Z. near the mouth of the Oosterschelde estuary (SW Netherlands). The mesocosms consisted of black solid polyethylene tanks (height 3 m, ϕ 1.2 m, volume 3000 l). A sediment container of 150 l was placed on the bottom of this tank. Azoic sand with a median grain size of 210 µm and an initial organic matter content of 0.16 % was used as a sediment. The water was continuously mixed with a rotating mixer. Mixing time of the water column was *ca* 10 minutes. A scraper, made of a blade of solid polyethylene, was used to prevent the development of fouling organisms on the walls of the tanks. Above the mesocosms an optical diffusor of structured plexiglass (Groenendijk, Pl 20070 TK) was installed to ensure a homogeneous light climate in the water column.

Each of the 'pelagic' tanks was connected to two 16 l benthos chambers (Perspex). The benthos chambers were designed especially to contain filter-feeders like the mussel,

and to enable the quantification of fluxes of particulate and dissolved material between the bivalve community and the water column. The chambers were shielded from light. A 5 cm sand layer was added to each chamber. Water was pumped from an outlet at 2.6 m depth in the pelagic tank with a 701 VB/R Whatson-Marlow tubing pump at a rate of 70 l h^{-1} per chamber. The water re-entered the pelagic tank again just below the water surface, after passing through the benthos chambers. With the use of an automated system in- and outflow of the benthos chambers were alternately pumped through a bypass containing a Turner fluorometer and a Stork-Servex Datasonde 3 with multiparameter water quality data logger for the registration of fluorescence, oxygen, temperature, conductivity and pH. Data were stored on a personal computer. Heating of the mesocosms by solar radiation was diminished by spraying sea water on the outer wall of the tanks and by shielding the tanks from direct sunlight. An extensive description of the mesocosm design is given in Peeters et al. (1993a).

Mesocosm manipulations

In this experiment, all mesocosms were filled simultaneously on the evening of 16 May 1993 with water pumped directly from the Oosterschelde estuary. On the morning of 17 May 1993 (= Day 1) the water column was sampled to determine the initial concentrations of particulate and dissolved substances and phytoplankton. A continuous addition of inorganic nutrients was started, with a relatively low P loading (4.9 µmol $NaNO_3$ l^{-1} day^{-1}; 0.15 µmol NaH_2PO_4 l^{-1} day^{-1}; N:P=33; 1.4 µmol Na_2SiO_3 l^{-1} day^{-1}). This rate of nutrient loading was typical for the spring conditions of the Dutch coastal zone (Smaal et al., 1994). The mesocosms were continuously flushed with seawater at a rate of 100 l day^{-1}, resulting in a residence time of the water of 30 days.

Four different densities of mussels (length: 18.0 ± 0.8 (mean ± s.d., n=30); ash-free dry weight including shell: 71 ± 14 mg) were used in the experiment: 160 mussels (Mesocosm ***n*=160**), 80 mussels (Mesocosm ***n*=80**), 40 mussels (Mesocosm ***n*=4**), 20 mussels (Mesocosm ***n*=20**). The mussels had been collected in the week before the experiment, from the low water tidal level at a site near the field station. The mussels were added to one of the benthos chambers of each mesocosm, the second benthos chamber of each mesocosm served as a control.

During a 4-week experiment samples of the water column were collected regularly, to follow the development of water column concentrations of particulate (2 times $week^{-1}$) and dissolved (3 times $week^{-1}$) matter, phytoplankton composition (2 times $week^{-1}$), primary productivity (2 times $week^{-1}$) and bacterial production (2 times $week^{-1}$). Exchange of dissolved materials between the water column and the benthos chambers was measured by sampling the in- and outflow of the benthos chambers (3 times $week^{-1}$).

At the end of the experiment, samples were collected of the particulate material sedimented at the bottom of the pelagic tank, and of the particulate material accumulated

in the benthos chambers. The samples were subsampled for the analysis of POC, PN and PP.

Particulate and dissolved nutrients

Particulate organic carbon (POC), particulate nitrogen (PN) and particulate phosphorus (PP) were determined with the analytical methods described in chapter 2. Dissolved substances were analyzed in the filtrate after filtration of 0.25 litre through a Whatman GF/C filter. DOC was determined by a colorimetric method (Schreurs, 1978). Dissolved inorganic nutrients (DIN:NH_4^++NO_3^-+NO_2^-), PO_4^{3-} and H_4SiO_4 were determined with an Autoanalyzer. Total dissolved nitrogen (TDN) was determined as nitrate after an alkaline persulphate destruction. Total dissolved phosphorus (TDP) was determined as inorganic phosphate after an acid persulphate destruction (Grasshoff et al., 1983). Dissolved organic nitrogen (DON) was calculated from the difference between DIN and TDN, dissolved organic phosphorus (DOP) from the difference between TDP and PO_4^{3-}.

Phytoplankton biomass, composition and production

Chlorophyll-*a* and phaeophytin-*a* were analyzed according to methods described in chapter 2. The observed chlorophyll-*a* values were used to convert the continuously measured fluorescence data to chlorophyll-*a*. Phytoplankton samples were fixed with acid Lugol's iodine solution. Phytoplankton cell numbers and species composition were determined as described by Escaravage et al. (1995).

The daily integral irradiance (PAR in kJ cm^{-2}) was recorded directly under the optical diffusor with a LiCor Quantum SR sensor (Peeters et al., 1993b). Light measurements were combined with *in situ* observations of light attenuation to estimate mean daily irradiance integrated over the entire water column. Primary production was determined by ^{14}C-incubations twice a week. Water samples were incubated for 2 hours with 185 Bq ^{14}C-bicarbonate (Amersham) at 8 different light intensities in a thermostated incubator. The observed photosynthesis-irradiance (P-I) relationship was fitted to a nonlinear model (Eilers & Peeters, 1988). Curve parameters for intermediate days were estimated by trapezoidal interpolation. Daily primary production values were calculated by combining daily measured values of irradiance and chlorophyll-*a* with P-I curve characteristics, according to Eilers & Peeters (1988).

Potential nutrient limitation of the phytoplankton was indicated by ratios of inorganic nutrients in the water column that deviated from N:P:Si=16:1:16 (Gillbricht, 1988). To determine whether phytoplankton was actually nutrient limited, we compared inorganic nutrient concentrations in the water column to half-saturation constants for nutrient uptake K_s (N=2 µM; P=0.5 µM; Si=2 µM; Peeters & Peperzak, 1990)) according to Zevenboom (1986).

Bacterial production

Pelagic bacterial production was estimated by measuring the incorporation of methyl-^{3}H-thymidine (2.92-3.18 TBq mmol^{-1}, Amersham Ltd.) into DNA (Fuhrman & Azam, 1982). Samples of 5 ml were placed in glass vials. A diluted solution of tritiated thymidine was added to a final concentration of 19 nM. Control incubations were fixed with 1.5% formaldehyde (final concentration) before the addition of tritiated thymidine. After an incubation in the dark for 45-60 minutes the experimental vials were fixed with formaldehyde. The samples were filtered on cellulose nitrate filters (0.2 µm pore size) and rinsed with 5% trichloroacetic acid (Ellenbroek & Cappenberg, 1991). Radioactivity on the filters was determined by liquid scintillation counting using external standardization. Bacterial production was calculated from the following conversion factors: $11 \cdot 10^{-15}$ g C cell^{-1}, $2 \cdot 10^{18}$ cells produced per mole of thymidine incorporated (Ducklow & Carlson, 1992).

Bivalve filtration rates

Clearance rates of the mussels were calculated from the fluorescence recordings of inflow and outflow of the benthos chambers, after a correction for background fluorescence when necessary. The population clearance rate (CR_{pop}), i.e. the total volume of mesocosm water cleared free of particles by the mussels, was calculated from:

$$CR_{pop} = Q \cdot \frac{(C_i - C_{o,mussels})}{C_i} \qquad (l \cdot h^{-1}) \qquad \textbf{(7.1)}$$

with Q = water flow through chamber (l h^{-1})
C_i = inflow fluorescence
$C_{o,mussels}$ = outflow fluorescence mussel chamber

As a consequence of the fact that some refiltration of the water occurred in the benthos chambers, population clearance rates were lower than the sum of the clearance rates of the individual mussels. Individual clearance rates (CRind) were calculated, assuming an exponential decrease of the particle concentration in the water flowing through the chamber and after correction for sedimentation measured in the control chamber:

$$CR_{ind} = \frac{Q}{n} \cdot \left[\ln\left(\frac{C_i}{C_{o,mussels}}\right) - \ln\left(\frac{C_i}{C_{o,control}}\right)\right] \qquad (l \cdot h^{-1} \cdot mussel^{-1}) \qquad \textbf{(7.2)}$$

with n = number of mussels
$C_{o,control}$ = outflow fluorescence control chamber

Mussel biomass and growth

A group of 30 mussels was chosen at random from the mussels collected in the field to determine initial dry weights and ash-free dry weights. Dry weights DW (including shell) were measured after drying the mussels for 48 hours at 70 °C. Ash-free dry weights ADW (including shell) were measured from weight loss after incineration for 4 hours at 540 °C in a muffle furnace. At the end of the experiment shell lengths of all mussels were measured again to the nearest mm. Subsamples of 30 mussels (20 in Tank 4) were taken to measure DW and ADW. Growth was determined as increase in shell length, and weight-specific growth rates were calculated from the increase in DW or ADW:

$$\mu = \ln\left(\frac{W_t}{W_0}\right)\Delta t^{-1} \quad (day^{-1}) \qquad (7.3)$$

with W_0, W_t = DW or ADW at begin and end of the experiment

RESULTS

General experimental conditions

Daily values of surface irradiance varied from 8.0 to 10.0 kJ cm^{-2}. Water temperatures were the same in all mesocosms, and varied between 12-21 °C during the experiment. Average temperature change in the mesocosms during a day was *ca* 1.5 °C. In general mesocosm temperatures followed water temperatures in the Oosterschelde estuary within 2 °C.

The net input of N and P, calculated as the sum of inorganic nutrients added, and import and export of inorganic nutrients, organic dissolved matter and particulate matter, showed only slight differences between mesocosms. The net addition was 4.86 µmol N l^{-1} day^{-1}, and 0.184 µmol P l^{-1} day^{-1}.

Mussel filtration

The clearance rates of the mussel populations in the four mesocosms reflected the differences in mussel biomass between the mesocosms (Fig. 7.1). The mean clearance rate of the mussel population in mesocosm ***n*=160** was 969 l day^{-1}, which was equal to 32% of the volume of the mesocosm per day. In the other mesocosms mean rates of grazing by the mussels were equal to resp. 17% day^{-1} (***n*=80**), 15% day^{-1} (***n*=40**) and 5% day^{-1} (***n*=20**). Clearance rates showed considerable day-to-day variation during the experiment. In all mesocosms maximum clearance rates were observed round day 20. In the last 4-5 days of the experiment clearance rates decreased, especially in mesocosm ***n*=160**, ***n*=80** and ***n*=40**. The changes in clearance rates showed no statistically significant relation with either changes in numbers of the most abundant phytoplankton species, or

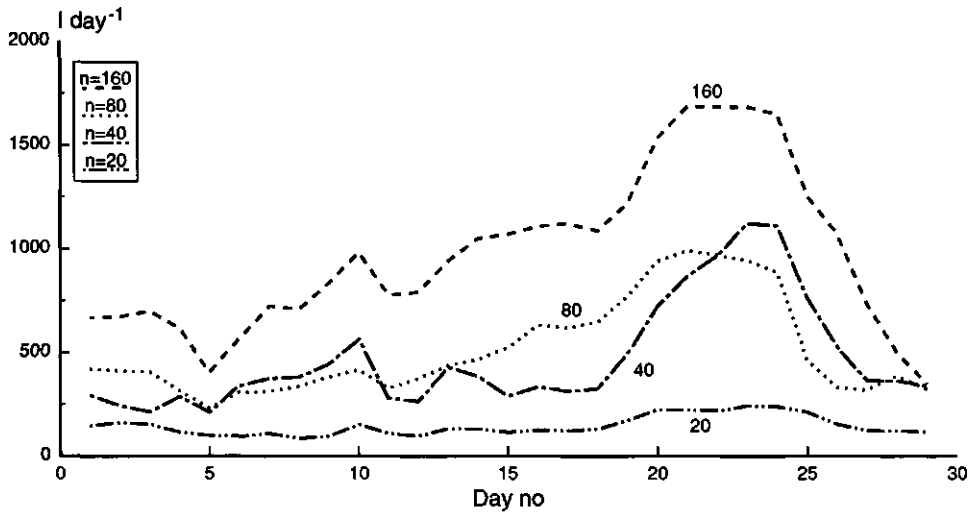

Figure 7.1. Clearance rates of mussel populations in the four mesocosms (total volume of water cleared free of particles).

with bulk parameters describing particle concentrations (SPM, POC, chlorophyll-*a*, total cell numbers).

Individual clearance rates were lower in mesocosm ***n*=20** than in the other mesocosms. Clearance rates, averaged over the entire experiment, were 0.41 ± 0.44 l mussel^{-1} hour^{-1} (mean ± s.d.; *n*=29) in mesocosm ***n*=160**, 0.28 ± 0.18 l h^{-1} (***n*=80**), 0.37 ± 0.37 l h^{-1} (***n*=40**) and 0.19 ± 0.08 (***n*=20**).

Regeneration of dissolved nutrients in the benthos chambers

Changes in the concentrations of inorganic nutrients in the water flowing through the mussel chambers were statistically tested by comparing inflow and outflow concentrations using Wilcoxons test (Sokal & Rohlf, 1981). A significant increase in NH_4^+ and PO_4^{3-} was observed in the mussel chambers with high mussel densities. In some of the control chambers significant changes in NH_4^+ or NO_3^- were observed too (Table 7.1). Sediment-water fluxes of NH_4^+ and PO_4^{3-} were higher in the mussel chamber than in the control chamber in mesocosms ***n*=160**, ***n*=80** and ***n*=40**. NO_3^- fluxes were generally directed into the sediment, as a consequence of which sediment-water fluxes of DIN were smaller than NH_4^+ fluxes. Recalculated to rates of nutrient release per unit body weight, nutrient fluxes in the mussel chambers were equal to 2.3-4.0 µmol NH_4^+ (g ADW)$^{-1}$, and

Table 7.1.

Fluxes of NH_4^+, NO_3^- and PO_4^{3-} between the water column and the benthos chambers in µmol $hour^{-1}$ (mean ± s.d., n=12). Positive values indicate release into the water column, negative values indicate uptake from the water column.

	Mesocosm ***n*=160**	Mesocosm ***n*=80**	Mesocosm ***n*=40**	Mesocosm ***n*=20**
Mussels				
NH_4^+	81.8 ±33.0**	55.0 ±24.6**	40.8 ±34.5**	17.5 ±29.0
NO_3^-	-14.4 ±32.3	-5.2 ±54.2	-10.2 ±30.5	27.9 ±56.9
PO_4^{3-}	9.1 ± 5.6**	4.8 ± 5.7*	4.0 ±10.1	-0.9 ± 9.1
Control				
NH_4^+	11.5 ±20.9	21.2 ±26.4**	15.8 ±22.4*	22.1 ±23.0**
NO_3^-	-20.2 ±43.3	-25.6 ±39.0*	10.2 ±26.6	-25.8 ±59.3
PO_4^{3-}	2.2 ± 8.1	1.0 ± 7.7	0.9 ± 8.0	0.3 ±10.0

0.23-0.25 µmol PO_4^{3-} (g ADW)$^{-1}$. No significant release of silicate or dissolved organic nutrients was observed in the benthos chambers.

The amount of NH_4^+ released by the mussels was equal to *ca* 12-18% of the amount of PN filtered by the mussels. PO_4^{3-} released by the mussels was, on average, equal to 30% of the amount of PP filtered by the mussels in the ***n*=160** mesocosm, 24% of PP filtration in mesocosm ***n*=80**, and 20% in mesocosm ***n*=40**.

Inorganic nutrient concentrations and light conditions

Water column concentrations of DIN at the onset of the experiment were *ca* 23 µM. DIN concentrations decreased only slightly to 17-20 µM in the third week, and even increased in the last week to values between 20 and 40 µM. Silicate concentrations started at 2.5-3.0 µM at Day 1 and dropped to values between 0.5-1.0 µM after Day 10, coinciding with the first peak in chlorophyll-*a*. Silicate concentrations increased again towards the end of the experiment to 3-4 µM in mesocosms ***n*=160** and ***n*=80** and *ca* 1 µM in mesocosms ***n*=40** and ***n*=20**. PO_4^{3-} concentrations were below 0.25 µM during the entire experiment, and were often below the detection limit (0.06 µM). N:P ratios and PO43- concentrations in the mesocosms indicated that P was the limiting nutrient during the entire experiment, for both diatoms and other algae.

Light extinction in the water column of the mesocosms was mainly determined by a combined effect of chlorophyll-*a* and total particle concentration, and was lowest in

mesocosm ***n*=160** and highest in mesocosm ***n*=20**. Mean water column daily irradiance varied due to changes in surface irradiance and particle concentrations. Mesocosm ***n*=160** had the highest values, mesocosm ***n*=20** had the lowest values (Table 7.2).

Plankton biomass and species composition

After an initial increase in all mesocosms due to phytoplankton growth, chlorophyll-*a* concentrations reached a maximum between day 10 an day 15. A decrease occurred in all mesocosms, but after day 22 concentrations started to increase again in the two mesocosms with lowest mussel density (Fig. 7.2). Average concentrations as well as maximum values of chlorophyll-*a* showed a negative correlation with mussel biomass.

A high concentration of solitary motile cells of *Phaeocystis sp.* (*ca* $20 \cdot 10^3$ cells ml^{-1}) was present in the mesocosms at the start of the experiment (Fig. 7.3). The number of *Phaeocystis sp.* cells decreased sharply in the first week in all mesocosms. In mesocosm ***n*=160** *Phaeocystis sp.* concentrations remained lower than in the other meosocosms until the last week. The increase in cell numbers in the mesocosms after Day 10 consisted of a mixture of solitary and colonial cells. The concentration increase in mesocosm ***n*=40** from Day 20 on was exclusively due to colonial cells.

Table 7.2.

Mean water column irradiance, P_{max} values and specific production rates observed in the four mesocosms. Means are based on all observations over the 4 week period of the experiment (n=29). Between parentheses minimum and maximum values are shown.

	water column irradiance (kJ cm^{-2} day^{-1})	P_{max} (mg C (mg chlorophyll)$^{-1}$)	specific production (mg C (mg chl)$^{-1}$ day^{-1})
Mesocosm ***n*=160**	1.76 (1.27-2.12)	7.9 (6.1-12.9)	21.5 (12.8-36.5)
Mesocosm ***n*=80**	1.69 (1.32-2.07)	6.1 (3.5-8.4)	18.6 (10.7-27.6)
Mesocosm ***n*=40**	1.63 (1.22-1.98)	5.2 (2.6-7.8)	15.1 (10.7-15.1)
Mesocosm ***n*=20**	1.57 (1.24-2.12)	5.1 (3.1-6.5)	15.2 (10.3-24.2)

Microflagellates increased considerably in all mesocosms in the first days of the experiment with highest numbers observed in mesocosm ***n*=20**, and slowly decreased after Day 10. On most days, µ-flagellate concentrations remained lower in mesocosm ***n*=160** than in the other mesocosms. Concentrations in mesocosm ***n*=80** were generally lower than in mesocosm ***n*=40** and ***n*=20** (Fig. 7.4).

Diatom species were generally much lower in numbers than *Phaeocystis sp.* or µ-flagellates (Fig. 7.5). In the first 2 weeks of the experiment the diatom populations of the mesocosms were dominated by *Rhizosolenia delicatula.* After Day 14, *R. delicatula* had disappeared and the diatom populations of the mesocosms were dominated by different mixtures of *Asterionella glacialis*, small (<10 µm) *Chaetoceros* species, *Nitzschia delicatissima* and *Cerataulina bergonii.*

The fraction of diatoms in the phytoplankton differed substantially between mesocosms (Fig. 7.6). The proportion of diatoms in mesocosm ***n*=160** was higher than in the other mesocosms in nearly all observations. This was mainly due to lower numbers of µ-flagellates in this mesocosm. The high diatom fraction in mesocosm ***n*=80** at Day 22 was caused by the bloom of *A. glacialis.* Diatoms became more dominant in mesocosms ***n*=40** and ***n*=20** at the end of the experiment.

Heterotrophic dinoflagellates reached relatively high densities in mesocosm ***n*=40** and ***n*=20** (average concentrations 98, 131 cells ml^{-1}) with maximum numbers observed in the second and third week of the experiment. Numbers of dinoflagellates were lower in mesocosm ***n*=160** (24 cells ml^{-1}) and ***n*=80** (35 cells ml^{-1}) and showed less fluctuations.

Water column processes

Only small differences in primary production were observed between the mesocosms in the first 2 weeks of the experiment. In the last 2 weeks, higher primary production was observed in mesocosms ***n*=40** and ***n*=20** (Fig. 7.7). Averaged over the entire experiment, primary production showed a negative correlation with mussel density. The specific production rates (production per unit chlorophyll-*a*) showed large variation during the experiment. Highest rates of specific production were observed in mesocosm ***n*=160**, with maximum values at the end of the first week of the experiment (Fig. 7.8). This peak in growth rates coincided with an increase in the fraction of diatoms in the phytoplankton. In mesocosm ***n*=80** high growth rates were observed between Day 20 and Day 25, coinciding with a high fraction of diatoms in the phytoplankton due to a bloom of *A. glacialis.* A slight increase in specific production rates was observed in mesocosms ***n*=40** and ***n*=20** on Days 24-26. Almost during the entire experiment, growth rates in mesocosm ***n*=160** and ***n*=80** were higher than in the other two mesocosms. With the exception of day 1, P_{max} values in mesocosm ***n*=160** were also higher than in the other mesocosms. Results are summarized in Table 7.2.

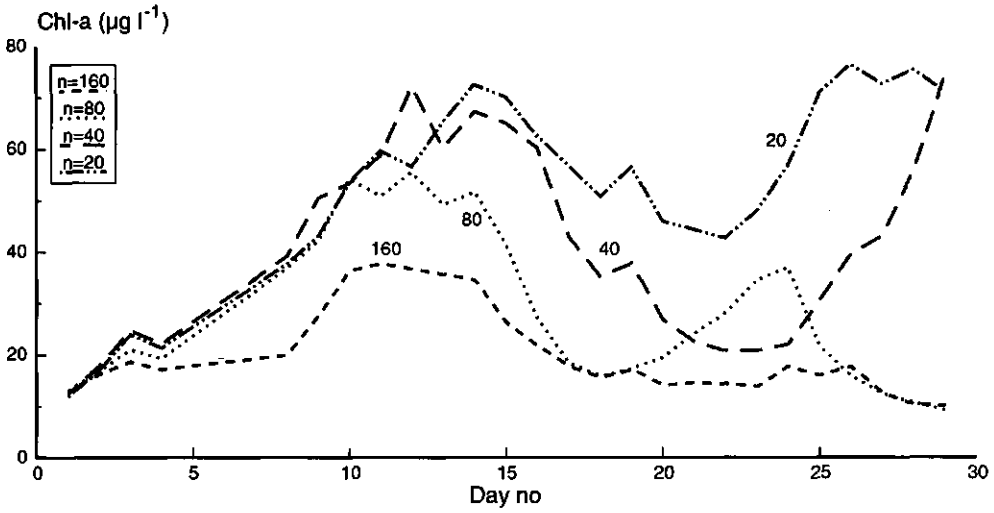

Figure 7.2. Changes in chlorophyll-*a* concentrations in the four mesocosms.

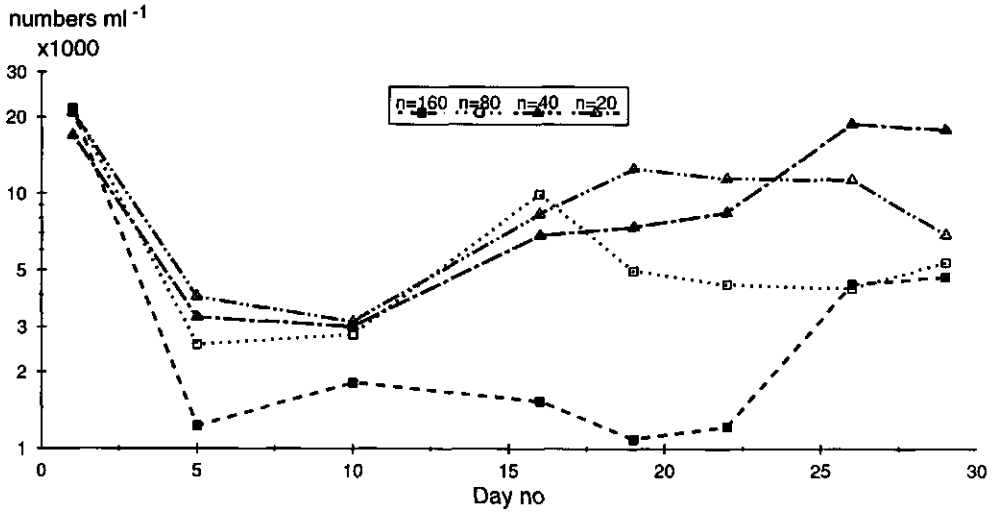

Figure 7.3. Concentration of *Phaeocystis sp.* cells.

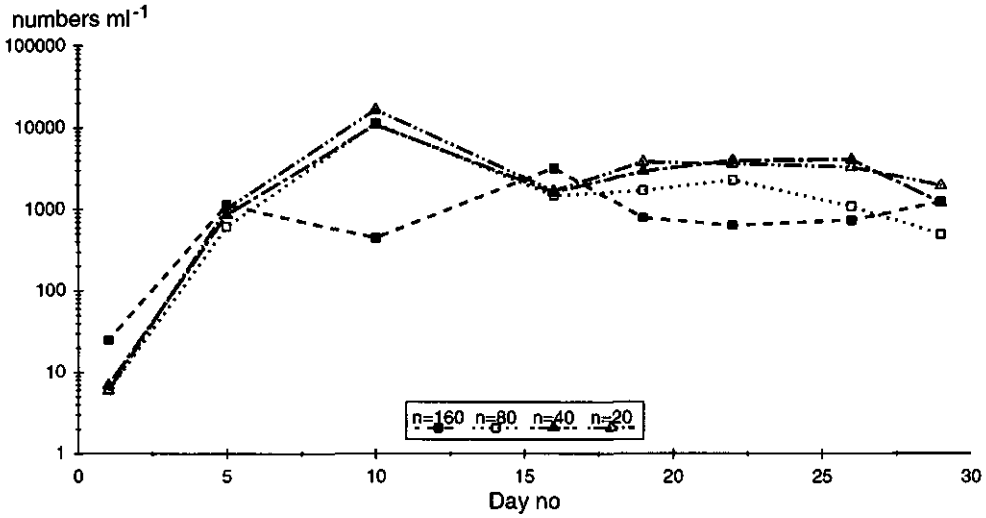

Figure 7.4. Concentrations of μ-flagellates.

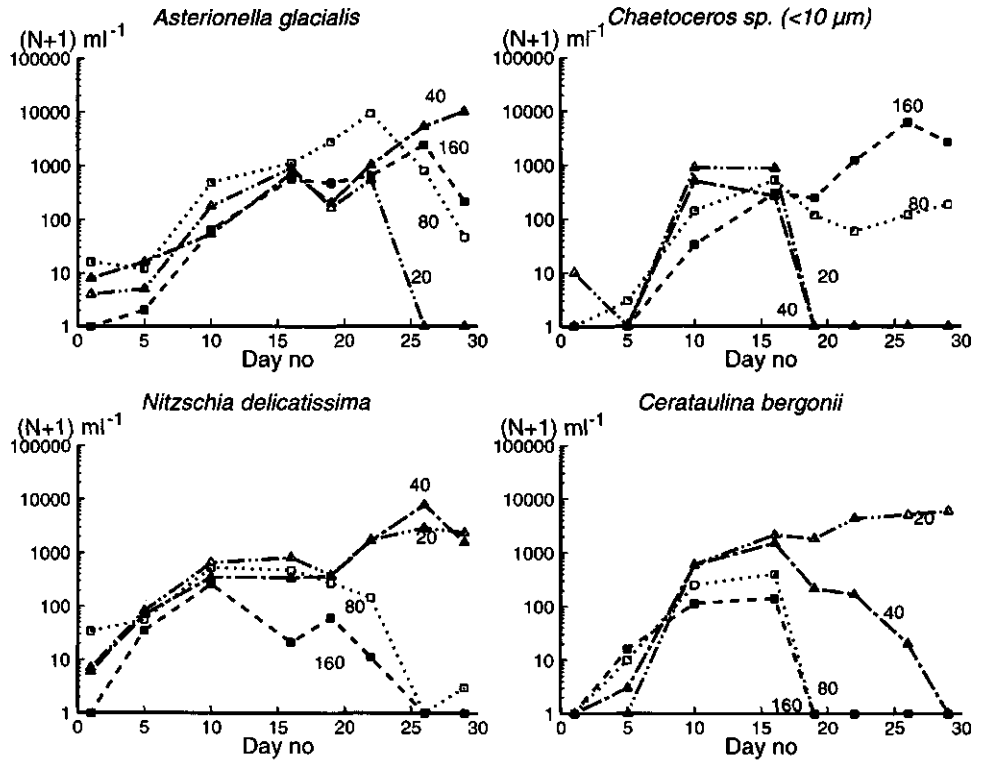

Figure 7.5. Numbers of 4 of the most abundant diatom species.

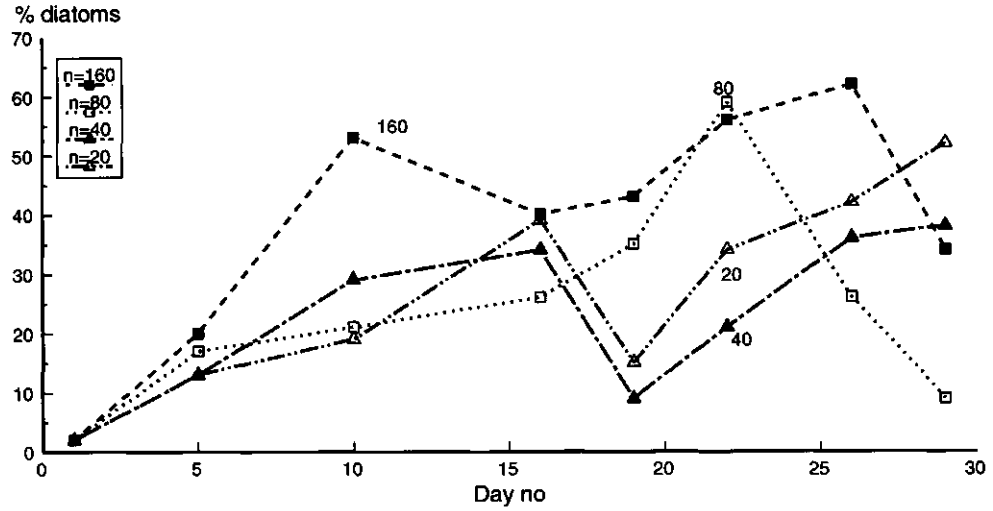

Figure 7.6. The percentage of diatoms (by numbers) in total phytoplankton cell counts.

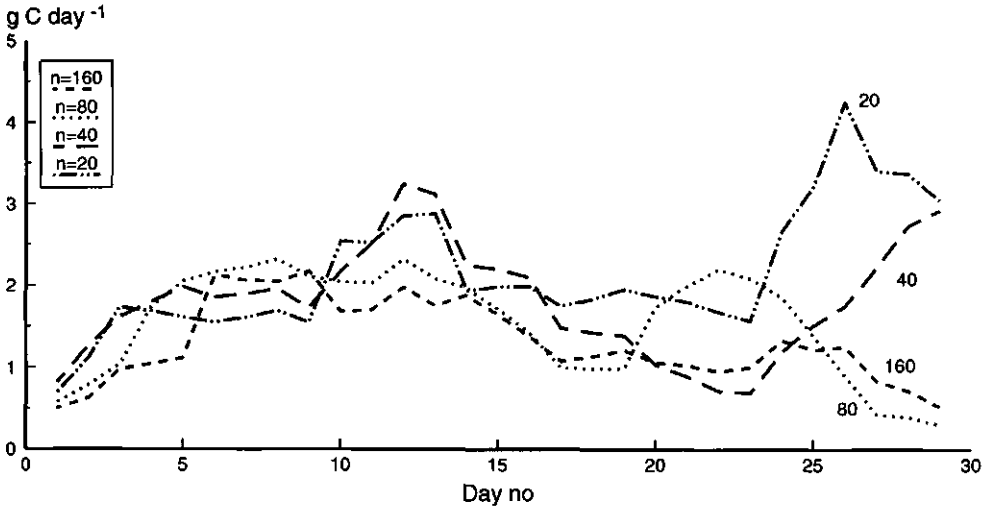

Figure 7.7. Daily values of phytoplankton primary production (as estimated from ^{14}C incubations) in the four mesocosms.

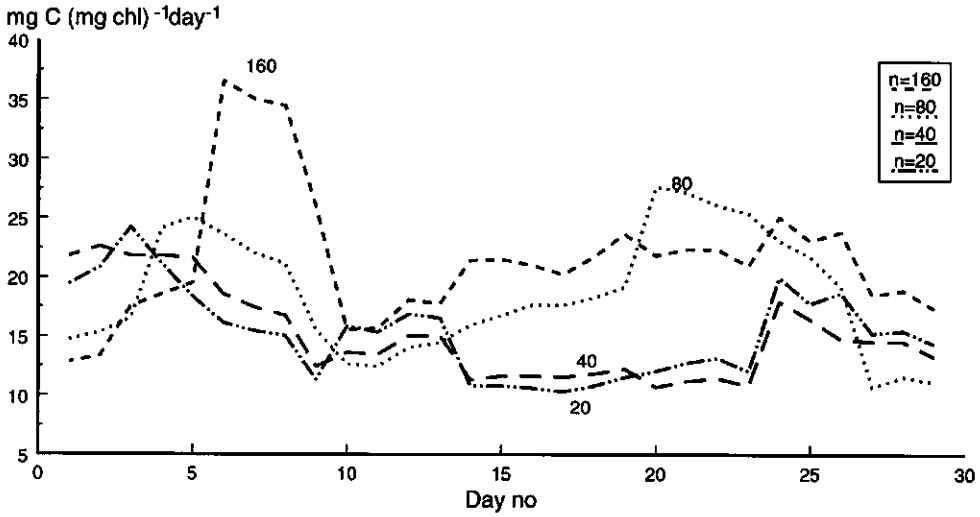

Figure 7.8. Daily values of specific production of the phytoplankton population.

Bacterial production showed an irregular pattern with values between 0.04 and 0.26 g C day^{-1} in mesocosms ***n*=160** and ***n*=80**. In mesocosms ***n*=40** and ***n*=20** bacterial production was higher, and reached a maximum at Day 21 (mesocosm ***n*=40**: 0.40 g C day^{-1}, mesocosm ***n*=20**: 0.48 g C day^{-1}). Bacterial production increased from mesocosm ***n*=160** to mesocosm ***n*=20**, and was equal to 8-12% of primary production (Table 7.3).

A comparison of the rates of primary production and mussel filtration and growth (Table 7.3) showed that in mesocosm ***n*=160** on average 56% of the primary production was filtered by the mussels, and the increase in mussel biomass was equal to 53% of C filtration. In mesocosm ***n*=80** and ***n*=40** mussel filtration was 34% and 33% of primary production, respectively. The increase in mussel biomass in mesocosm ***n*=80** was equal to 58% of C filtration.

The phosphorus demand of the phytoplankton exceeded the external PO_4^{3-} supply with a factor 2-3 in all mesocosms. Regeneration of PO_4^{3-}, due to mussel activity alone, was not high enough to sustain primary production, and the gap between phytoplankton P demand on the one hand and P supply from nutrient additions and regeneration in the benthos chambers on the other hand, increased from mesocosm ***n*=160** to mesocosm ***n*=20**. It should be noted that PO_4^{3-} regeneration, due to mineralization in the water column or the sediment of the pelagic system, was not measured.

Filtration and regeneration by the mussels affected the distribution of P (Fig. 7.9). With an increase in mussel biomass, an increasing part of the available phosphorus was

stored in mussel biomass, and storage in pelagic biomass decreased. The amount of P present in the inorganic nutrient pool in the water column was highest in mesocosm ***n*=160** and lowest in mesocosm ***n*=20**. Part of the phosphorus was stored in detritus on the sediment of the pelagic system or in the benthos chambers. The amounts of PP sedimented in the pelagic tanks of the four mesocosms at Day 29, ranged from 13-38 mg P, and were approximately equal to the amounts of PP accumulated in the control benthos

Table 7.3.

Mean phytoplankton standing stock, and phytoplankton primary production, pelagic bacterial production, mussel filtration and increase in mussel biomass. Values are averaged over the entire duration of the experiment.

Tentative P budget, with P demand of the phytoplankton estimated from primary production results with Redfield ratio C:P=106:1.

	Mesocosm			
	***n*=160**	***n*=80**	***n*=40**	***n*=20**
Mean chlorophyll-*a* ($\mu g\ l^{-1}$)	19.4	27.2	39.0	48.6
Primary production (g C day^{-1})	1.31	1.55	1.81	2.15
Bacterial production (g C day^{-1})	0.11	0.16	0.22	0.23
Export (g C day^{-1})	0.01	0.03	0.07	0.09
Mussel filtration (g C day^{-1})	0.74	0.53	0.60	0.22
Increase in mussel biomass (g C day^{-1})	0.39	0.31	0.13	0.04
P demand phytoplankton (mmol day^{-1})	1.03	1.21	1.42	1.69
PO_4^{3-} regeneration in benthos chambers (mmol day^{-1})	0.27	0.14	0.12	-0.01
PO_4^{3-} input (mmol day^{-1})	0.45	0.45	0.45	0.45

chambers (17-31 mg P). The amounts of P accumulated in the mussel chambers were resp. 100 mg (mesocosm ***n*=160**), 96 mg P (***n*=80**), 65 mg (***n*=40**) and 43 mg (***n*=20**). The remainder of P, present in the mesocosms, was assumed to be DIP in the interstitial water of the sediment or DIP adsorped to sediment particles (Prins et al., 1994).

Mussel growth rates

Significant differences between the growth rates of the mussels in the four mesocosms occurred. High growth rates were observed in mesocosms ***n*=80** and ***n*=40**, and significantly lower growth rates (Tukey HSD-test, $p<0.05$) in mesocosms ***n*=160** and ***n*=20** (Table 7.4).

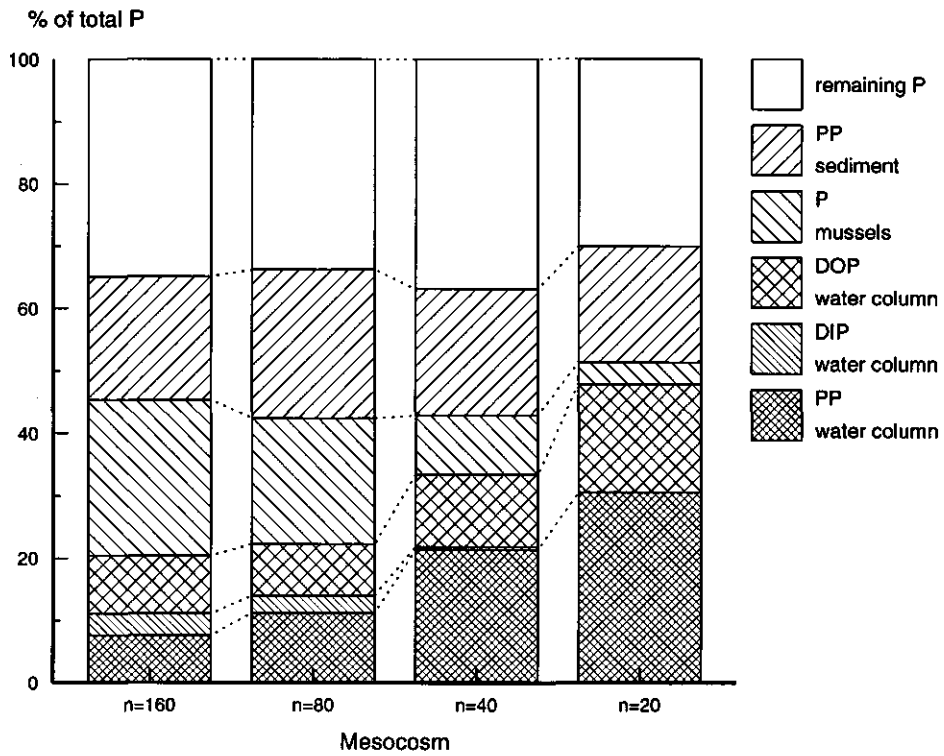

Figure 7.9. Accumulation of phosphorus in the various nutrient pools in the mesocosms at the end of the experiment. The total amount of P present in the mesocosms was estimated from the initial concentrations in water column and sediment and mussel biomass at Day 1, and the net import of P. The amount of P in the mussels was estimated from the increase in mussel biomass, using a C:P ratio of 225 (Vink & Atkinson, 1985).

Table 7.4. Shell lengths at Day 29, and weight-specific growth rates based on dry weights (DW) and ash-free dry weights (ADW) of the mussels between Day 1 and Day 29 (mean ± s.d.)

	Shell length (mm)	μ_{DW} (day^{-1})	μ_{ADW} (day^{-1})
mesocosm ***n*=160**	23.58 ± 2.08 (n=160)	0.024 ± 0.0015 (n=30)	0.036 ± 0.0023 (n=30)
mesocosm ***n*=80**	24.96 ± 1.51 (n=80)	0.032 ± 0.0008 (n=30)	0.049 ± 0.0008 (n=30)
mesocosm ***n*=40**	24.82 ± 1.76 (n=40)	0.028 ± 0.0010 (n=30)	0.045 ± 0.0011 (n=30)
mesocosm ***n*=20**	22.75 ± 2.20 (n=20)	0.022 ± 0.0020 (n=20)	0.031 ± 0.0030 (n=20)

DISCUSSION

Mesocosm conditions

In our mesocosm experiment we have tried to simulate the development of a phytoplankton bloom and the interactions with bivalve grazing under environmentally realistic conditions with respect to light, turbulence and nutrient loading. Light and hydrodynamic conditions in the mesocosm were similar to the conditions in the Dutch coastal zone of the North Sea (Peeters et al., 1993b). External nutrient loading was relatively high, but comparable to nutrient inputs to the Dutch coastal zone or other eutrophic marine coastal waters ((Nixon & Pilson, 1983; Nienhuis, 1993). The phytoplankton community that developed consisted mainly of species that are common to Dutch coastal waters in spring and early summer (Bakker et al., 1990). Chlorophyll-*a* concentrations were rather high, but still comparable to values observed during phytoplankton blooms in systems like the Oosterschelde estuary or the Dutch Wadden Sea (Cadée, 1982; Wetsteyn & Kromkamp, 1994). The range in mussel densities in the mesocosms represented a range in bivalve grazing pressure, from very low (*ca* 5% of the mesocosm volume day^{-1}) to high (*ca* 32% of the volume day^{-1}). The low mussel grazing rate in mesocosm ***n*=20** was of the same magnitude as the flushing rate of the mesocosm, and thus can be assumed to have had minor effects on the pelagic system. The highest grazing pressure employed in our experiment was typical for estuaries with a high bivalve biomass (Smaal & Prins, 1993).

Mussel filtration rates

Filtration rates of the mussel populations were correlated with mussel density. However, there was a considerable variation in the clearance rates during the course of the experiment in all mesocosms. When exposed to uni-algal diets, mussels have been shown to reduce their clearance rates in response to high algal concentrations (>10^4 cells ml^{-1}; Riisgård, 1991). In our experiment maximum cell concentrations exceeded this threshold, although concentrations were below 10^4 cells ml^{-1} during part of the experiment in mesocosm ***n*=160**. However, the variation in clearance rates could not be related to changes in phytoplankton cell numbers. Phytoplankton formed the main fraction of the particulate organic matter in the water column of the mesocosms, but still *ca* 40-60% of the seston consisted of particulate inorganic matter, and the functional response of filtration rates on particle concentration is more complex with diets comprising mixtures of algae, detritus and inorganic particles. When mussels are exposed to a broad spectrum of particles of varying quality, which we believe was the case in the mesocosms, mussels may vary filtration rates to optimize net energy gain (Willows, 1992; Bayne, 1993). Moreover, acclimation has been shown to affect clearance rates (Bayne et al., 1993). Therefore, we suggest that the variation in clearance rates during the experiments was the result of acclimation and of responses to changes in food concentration and quality. Mussels from the size class used in our experiment show clearance rates of 0.4-0.7 l ind^{-1} h^{-1} when fed with natural sea water (Smaal et al., 1986). This indicates that individual clearance rates in the mesocosm were reduced. This reduction, as well as the differences in individual clearance rates between mesocosms, may reflect time-averaged adaptation to the conditions in the mesocosms (Bayne, 1993).

Grazing control of phytoplankton biomass and composition

The mesocosms had similar initial chlorophyll-*a* concentrations, but the systems began to diverge in the second week. Marked effects of mussel grazing on phytoplankton biomass were observed in mesocosms ***n*=160** and ***n*=80**. Mesocosm ***n*=40** showed only small differences with mesocosm ***n*=20**. Average biomass as well as maximum biomass levels attained showed a negative relation with grazing intensity. From the observed specific production rates and an average C:chlorophyll ratio of 35 (Haas, pers. comm.), it was estimated that phytoplankton growth rates ranged from 0.4-1.0 day^{-1} in mesocosm ***n*=160**, and from 0.4-0.8 day^{-1} in mesocosm ***n*=80**. Mussel grazing rates were, on average, equal to *ca* 32% of the volume of the mesocosm per day in mesocosm ***n*=160**, and 17% in mesocosm ***n*=80**. This implied that phytoplankton mortality rates due to mussel grazing in these mesocosms were 0.32 day^{-1} and 0.17 day^{-1}. It was argued by Officer et al. (1982) that, in the theoretical situation when bivalve grazing is the only control of phytoplankton biomass, grazer-induced mortality rates should be of the same magnitude as phytoplankton growth rates to effectively control phytoplankton biomass. Similarly, Ott &

Fedra (1977) showed that benthic consumers can regulate phytoplankton biomass, when they constitute a significant nutrient storage pool, with relatively low maintenance costs. In our mesocosms there must have been additional loss factors (e.g. pelagic grazing, sedimentation, flushing) affecting phytoplankton biomass. Thus, the grazing rates in the mesocosms with high mussel density were high enough to reduce pelagic biomass. Bivalve biomass formed a major nutrient storage compartment in mesocosms ***n*=160** and ***n*=80** (Fig. 7.9). Thus, the reduction in total biomass and the lower oscillations in phytoplankton biomass with increasing mussel biomass in our mesocosms, corroborate the hypothesis of Officer et al. (1982) and Ott & Fedra (1977) on phytoplankton regulation by benthic suspension feeders.

Whereas total phytoplankton biomass (expressed as chlorophyll-*a*) showed a negative relation with mussel density, the development of various phytoplankton species could not be related to grazing by the mussels. At the start of the experiment, the phytoplankton was dominated by *Phaeocystis sp.* flagellates, which were present in high numbers in the seawater that was added to the mesocosms. The decrease in *Phaeocystis sp.* cell numbers could be interpreted as a reaction to the changes in environmental conditions following the incubation in the mesocosms. The small differences in cell concentrations between mesocosms ***n*=80**, ***n*=40** and ***n*=20** suggested that grazing was of minor importance in the regulation of *Phaeocystis sp.*, and we assume that P-limitation was the main regulating factor (Escaravage et al., in prep.). Numbers of µ-flagellates showed a strong increase after the start of the experiment, and maximum numbers were observed on Day 10. The concentration differences between mesocosms were relatively small, but still lower concentrations were observed in mesocosm ***n*=160**, and highest concentrations in mesocosms ***n*=40** and ***n*=20**.

Diatom composition showed clear differences between mesocosms. Whereas the abundance of some species showed a negative relation with grazing rate, other species (e.g. *Chaetoceros*) seemed to benefit from grazing. The phytoplankton community of mesocosm ***n*=160** had a much higher dominance of diatoms than the other mesocosms. Diatoms tend to have higher growth rates than non-diatom species (Furnas, 1990), and may outcompete flagellates when silicate concentration is not limiting growth (Egge & Aksnes, 1992). High loss rates by grazing will lead to a shift in the phytoplankton community towards fast-growing species (Furnas, 1990). Silicate concentrations in the mesocosms were below 2 µM during part of the experiment, which was in the range of limiting concentrations (Officer & Ryther, 1980; Egge & Aksnes, 1992) but nutrient ratios and a comparison of PO_4^{3-} concentrations to half-saturation constants for nutrient uptake (cf. Zevenboom, 1986) indicated that P was the limiting nutrient. We hypothesize that the high grazing pressure by the mussels in mesocosm ***n*=160** favoured the dominance of faster-growing diatoms over non-diatom species. In mesocosm ***n*=80** grazing losses were lower, and hence the shift in phytoplankton composition was less

conspicuous. The increased dominance of diatoms at the end of the experiment in mesocosms ***n*=40** and ***n*=20** could be ascribed to the diatoms gradually outcompeting non-diatoms. Likewise, the decreasing dominance of diatom species in mesocosm ***n*=160** at the end of the experiment coincided with a decreasing grazing activity of the mussels in this mesocosm.

Impact of mussels on pelagic production

Growth rates of the phytoplankton were lower than 1 doubling day^{-1}, which is much smaller than maximal growth rates (Furnas, 1990). This agrees with our observation that phytoplankton production was light- and P-limited. Phytoplankton growth rates showed substantial differences between mesocosms. Highest growth rates were observed between Day 5 and 10 in mesocosm ***n*=160**, coinciding with an increasing proportion of diatoms in the phytoplankton. From Day 5 onwards growth rates in mesocosm ***n*=160** were higher than in mesocosms ***n*=40** and ***n*=20**. In mesocosm ***n*=80**, high growth rates were observed around Day 20 coinciding with a dominance of diatoms (mainly *A. glacialis*). The results pointed at a relation between diatom abundance and specific production, and we suggest that the high phytoplankton growth rates observed in mesocosms ***n*=160** and ***n*=80** were due to a predominance of diatoms, which have higher growth rates than flagellates (Furnas, 1990). As was discussed above, this predominance of diatoms was probably a direct effect of grazing. Particle concentrations were lowest in mesocosms ***n*=160** and ***n*=80** and light conditions were better (Table 7.2), but light limitation showed only small differences between mesocosms. P_{max}- values of the algae in mesocosm ***n*=160** and ***n*=80** were higher than in mesocosm ***n*=40** and ***n*=20** too, indicating that the increased algal growth rates in ***n*=160** and ***n*=80** were not due to different light conditions, but reflected physiological differences between the algal communities.

Concentrations of PO_4^{3-} were below 0.25 µM during the entire experiment in all mesocosms and indicated that P was limiting algal production. The estimated uptake of P by the algae varied from 1.0 mmol P day^{-1} in mesocosm ***n*=160** to 1.7 mmol P day^{-1} in mesocosm ***n*=20** (Table 7.3). The external load of PO_4^{3-} was only 0.45 mmol P day^{-1}. Therefore, primary production mainly depended on recycling of nutrients. Regeneration of NH_4^+ and PO_4^{3-} in the benthos chambers was related to mussel biomass. The nutrient fluxes observed in the mussel chambers , expressed as rates per mussel, were approximately equal to the (broad) range of published excretion rates of mussels (Bayne & Scullard, 1977; Bayne & Widdows, 1978; Kautsky & Wallentinus, 1980). A comparison with *in situ* observations of nutrient fluxes from mussel beds (chapter 6) showed that NH_4^+ and PO_4^{3-} fluxes were smaller than maximum *in situ* fluxes. Silicate effluxes were not significant in this study, in contrast to *in situ* observations of high rates of silicate release. This indicated, that direct excretion of NH_4^+ and PO_4^{3-} by the mussels

was probably the main source of inorganic nutrients, and mineralization of biodeposits was of minor importance. This is different from the situation on mussel beds in the field (Chapter 5), and probably a consequence of the short duration of the experiment leading to a relatively low accumulation of biodeposits.

Although nutrient regeneration by the benthos was highest in mesocosm ***n*=160**, and may have supplied *ca* 25% of phytoplankton P demand, total primary production was highest in mesocosm ***n*=20**. The difference between phytoplankton P demand on the one hand, and supply of PO_4^{3-} by external loading and benthic regeneration on the other hand, increased from mesocosm ***n*=160** to mesocosm ***n*=20**. This indicated that an increasing amount of the primary production was sustained by nutrient regeneration through other pathways. The ammounts of sedimented particulate organic matter on the bottom of the pelagic systems were comparable to the amounts accumulated by sedimentation in the control benthos chambers. These amounts were lower than the amounts in the mussel chambers. Considering the fact that PO_4^{3-} effluxes from the control chambers were not significantly different from zero, we assumed that regeneration of PO_4^{3-} by the benthic system in the pelagic tanks was not important either. Bacterial production increased from mesocosm ***n*=160** to mesocosm ***n*=20**, as did the number of heterotrophic dinoflagellates. These data suggest that mussel grazing caused structural changes in the heterotrophic plankton community, leading to a relatively high contribution of nutrient regeneration by the bivalves in the mesocosms with high mussel biomass, whereas pelagic P regeneration dominated in the mesocosms with high phytoplankton biomass (and low mussel biomass). This agrees with conclusions drawn from enclosure studies showing that mussels exerted a strong regulation of heterotrophic consumption, as a consequence of grazing control of microzooplankton ((Horsted et al., 1988; Riemann et al., 1988, 1990).

The accumulation of P in the various nutrient pools showed that, due to grazing and nutrient regeneration, availability of phosphate was increased in the mesocosms with high mussel densities, as a smaller proportion of nutrients was stored in phytoplankton biomass and a larger part in the inorganic nutrient pool. Concluding, grazing by the mussels caused a shift in the composition of the phytoplankton community, favouring faster-growing diatoms. In addition, the reallocation of nutrients from the phytoplankton to the dissolved nutrient pool stimulated phytoplankton growth rates.

In experiments in the MERL mesocosms higher phytoplankton production was observed in mesocosms with the bivalve *Mercenaria mercenaria*, compared to mesocosms without bivalves (Doering et al., 1986). In these experiments benthic nutrient regeneration increased in the presence of bivalves. It was suggested by Doering et al. (1986) that the higher phytoplankton production was sustained by faster recycling through both the pelagic and the benthic subsystem. The stimulation of phytoplankton growth rates in the presence of bivalve suspension feeders agrees with our results. Contrary to our results, Doering et al. (1986) did not observe a control of pelagic biomass by bivalve

grazing, possibly due to changes in phytoplankton structure. In enclosure experiments a strong impact of mussel grazing on phytoplankton biomass and structure has been observed. Whereas larger phytoplankton was severely reduced as a result of mussel grazing, control of cells in the picoplankton size range (<3 μm) appeared less efficient, leading to a dominance of small flagellates or cyanobacteria (Horsted et al., 1988; Olsson et al., 1992; Granéli et al., 1993). The water column in these enclosure experiments was not artificially mixed. Moreover, water column turnover due to mussel grazing rates was *ca* 1 day^{-1}. The lack of control of phytoplankton biomass in the latter experiments indicates that, under certain conditions, phytoplankton may escape from grazing control through changes in community structure.

Mussel growth

Mussels consumed the major part of primary production in mesocosm ***n*=160**, and approximately 30% of this primary production was converted into mussel biomass. Mussel growth was equal to 53% and 58% of the estimated filtration of C in mesocosms ***n*=160** and ***n*=80** respectively. Assuming that no pseudofaeces were produced and that the absorption efficiency was 85% (Hawkins et al., 1986; Prins et al., 1991), this would mean that net growth efficiencies (growth/absorption) were equal to 62% and 69% respectively. These efficiencies are high, but within the range of observed values. Net growth efficiencies have maximum values of *ca* 75% (Jørgensen, 1990). The fraction of phytoplankton primary production converted into mussel biomass was very high in mesocosms ***n*=160** and ***n*=80** (30 and 20%, resp.). In an experimental system Rodhouse et al. (1981) observed a food chain efficiency (bivalve production : net primary production) of 27%, which is close to our values. This suggests that systems with high mussel biomass may be very efficient in converting algal production into secondary production.

Mussel growth rates showed marked differences between mesocosms. Highest growth rates were observed in mesocosms ***n*=80** and ***n*=40**. These rates were comparable to maximum growth rates of 0.24 mm day^{-1} observed with similar sized mussels under eutrophic conditions (Riisgård & Poulsen, 1981). The large decrease in fluorescence (45%) in the water flowing through the mussel chamber of mesocosm ***n*=160** suggested that food competition between the mussels caused the reduction in growth rates in this mesocosm. Mussels in mesocosm ***n*=20** showed lower growth rates too, although phytoplankton biomass and production were highest in this mesocosm. As phytoplankton concentrations were high, the reduction of mussel growth in mesocosm ***n*=20** was probably not due to food competition with pelagic consumers. A possible explanation may be that food quality in mesocosm ***n*=20** was lower than in the other mesocosms. The quality of algae as food for bivalves differs widely between species, even between related species, although in general diatoms are assumed to be better food (De Pauw, 1981). Food quality of algae also depends on factors like growth conditions, physiological state

and biochemical composition of the algae (e.g. Wikfors et al., 1984; Enright et al., 1986; Sterner et al., 1993; Van Donk & Hessen, 1993), but no general statements on the suitability of algal species can be made.

Conclusions

Our experiment showed, that even under conditions with a high external nutrient load, mussel grazing may exert an effective control on phytoplankton biomass. Grazing induced a shift in the composition of the phytoplankton population, leading to a higher proportion of diatoms in the mesocosms with high mussel density. As a consequence of this change in phytoplankton structure, and as a result of increased nutrient availability due to grazing and nutrient regeneration, phytoplankton growth rates were highest in the mesocosms with high mussel density. This shows that mussel grazing may significantly alter process rates and structure of the pelagic system.

CHAPTER EIGHT

CONCLUDING REMARKS

CONCLUDING REMARKS

This thesis has considered the impact of the suspension feeding bivalve *Mytilus edulis* on nutrient cycling and phytoplankton in an estuarine ecosystem. The research was started within the framework of an extensive research project with the objective to evaluate the changes in the Oosterschelde ecosystem as an effect of a coastal engineering project (Nienhuis & Smaal, 1994). The Oosterschelde estuary is a system where mussels are dominant consumers, which is at least partly due to the strong regulation of mussel biomass by fisheries. As a consequence, the Oosterschelde estuary is a typical example of an ecosystem where herbivores have a strong impact on the entire pelagic system.

The main emphasis in this study has been on the impact of the mussels on the exchange of material between the water column and the benthic system. This exchange has been studied with an *in situ* method designed to measure exchange of particulate and dissolved material between an undisturbed bivalve community and the water column, under natural conditions with respect to food supply, current speed, temperature etc. The method was evaluated in chapter 2. It was concluded that the method was suitable for *in situ* measurements of the fluxes of particulate and dissolved matter between the mussel bed and the water column.

Mussel beds filter considerable amounts of material. The amount of material filtered is determined by mussel biomass, mussel activity and the supply of particulate material to the mussel bed. The *in situ* experiments, carried out in the years 1987-1989, showed that the quantity and quality of the suspended particulate matter varied considerably at a short time scale. A tidal variation was observed, with the supply of relatively phytoplankton-rich water to the intertidal flats during flood tide. During ebb, phytoplankton concentrations in the water were generally reduced, probably as a consequence of depletion by suspension feeders. Superimposed on this tidal variation changes in seston quantity and quality at the time scale of hours were observed. This short-term variation was related to wind-induced resuspension of bottom material. The observed increases in SPM, POC and phaeophytin-*a* levels during these resuspension events indicated that resuspension of algal detrital material, probably biodeposits, occurred.

It was shown in Chapter 3 that under calm weather conditions a good correlation between the concentrations of SPM, POC and chlorophyll-*a* in the water column and the size of the respective fluxes to the mussel bed was observed. From a comparison of the composition of the fluxes with the composition of the seston it became clear that the fluxes contained a relatively high proportion of phytoplankton. After filtration, mussels

are able to selectively ingest phytoplankton, while other particles are rejected through the pseudofaeces. As a result, the pseudofaeces have a reduced chlorophyll-*a* content (Kiørboe & Møhlenberg, 1981; Prins et al., 1991). Mussels eject the pseudofaeces into the water column. Pseudofaeces have a low settling velocity and are easily resuspended (Risk & Moffat, 1977; Nowell et al., 1981). This makes it probable that in the sequence of filtration, selection, ingestion and pseudofaeces formation, a fraction of the non-algal material that was filtered by the mussels and then rejected as pseudofaeces, was exported from the mussel bed. Consequently, the net flux of material to the mussel bed had a high proportion of chlorophyll-*a*, whereas part of the POC and of the particulate inorganic matter, filtered by the mussels, was exported immediately. Under rougher weather conditions sometimes a significant net export of SPM and POC from the mussel bed was observed as a result of wind-induced resuspension. The results indicated that only a part of the material that was filtered by the mussels, was stored in the mussel bed, due to immediate export of pseudofaeces by tidal currents or to more occasional wind-wave resuspension.

Previous estimates indicated that the mussel population in the Oosterschelde may filter the entire volume of the Oosterschelde in approximately 10 days (Smaal et al., 1986; Van Stralen & Dijkema, 1994). The generally low phytoplankton concentrations in the Oosterschelde have been attributed to the severe 'top-down' control exerted by the mussel, together with the other dominant bivalve suspension feeder *Cerastoderma edule* (Smaal et al., 1986; Herman & Scholten, 1990). The observed *in situ* filtration activity of the mussel beds, presented in chapter 3, agrees with the values used in earlier published estimates of mussel grazing pressure.

Recent ecophysiological studies have shown that bivalves respond to short-term changes in the quantity and quality of the seston by regulating ingestion rates. This regulation may be achieved by changes in clearance rates, or by rejection of variable amounts of filtered material as pseudofaeces in combination with pre-ingestive selection. The nature of this physiological response depends on both quality and quantity of the seston, and on acclimation (Bayne, 1993; Navarro & Iglesias, 1993). When exposed to diets with a low organic content, mussels mainly respond to these short-term changes by modifying the rate of pseudofaeces production (Bayne, 1993; Navarro & Iglesias, 1993). Our *in situ* experiments carried out in the Oosterschelde, showed no effect of the changes in seston concentration and composition during a tidal cycle on clearance rates (Chapter 3); this is consistent with the hypothesis that ingestion is regulated by pseudofaeces production when seston quality is low. The seasonal variation in clearance rates of a mussel bed was studied by monthly measurements on a semi-natural mussel bed (Chapter 6). Clearance rates showed a positive response to chlorophyll-*a* concentrations and were negatively affected by SPM concentrations. The relations observed in the latter experiment were probably the result of adaptation on a longer time scale (Bayne, 1993).

In the mesocosm experiments presented in Chapter 7, mussel clearance rates were generally lower than rates observed in experiments with natural seawater, and showed considerable temporal variation. In the mesocosms the mussels were exposed to seston with a much higher proportion of algae than is commonly observed *in situ*. The reduced and variable clearance rates in the mesocosm experiment agree with the current idea that it is more optimal for bivalves to regulate ingestion by changes in clearance rates, when the animals are exposed to diets with a high organic content (Iglesias et al., 1992; Bayne, 1993; Navarro & Iglesias, 1993).

In addition to the effects of seston quantity and quality on the seasonal variation of clearance rates, a strong inhibitory effect of the presence of the alga *Phaeocystis sp.* on mussel clearance rates was observed. This inhibition of mussel clearance rates may lead to a breakdown of the top-down control of phytoplankton biomass and may increase the risk of massive algal blooms.

In general, a release by the mussel bed of ammonium, phosphate and silicate was observed during the *in situ* measurements. In June 1987 an experiment was carried out during a long period of high phytoplankton concentrations, resulting in a large flux of organic matter from the water column to the mussel bed. A high release of inorganic nutrients was observed during that experiment. In June 1988 chlorophyll-*a* concentrations in this part of the Oosterschelde estuary were low for a number of consecutive weeks. In that period a number of *in situ* measurements were carried out, all showing low uptake rates of chlorophyll-*a*, and a small release of inorganic nutrients. It was inferred from these results, that the difference in organic matter supply to the mussel bed was the cause for the difference in nutrient release between the observations from June 1987 and the results from June 1988. Moreover, it was shown that considerable day/night differences in fluxes occurred in June 1987. During daytime, much lower release of inorganic nutrients by the mussel bed was measured, which was attributed to immediate uptake of the nutrients by algae.

Budgets presented in Chapter 5, suggested that only a small proportion of the nutrient fluxes to the mussel bed were stored in mussel biomass. The remainder was stored in the sediment as biodeposits. Mineralization of the biodeposition and excretion by the mussels resulted in a release of inorganic nutrients. In the case of nitrogen, there was an approximate equilibrium between the net uptake of particulate N by the mussel bed and the release of dissolved inorganic N by the mussel bed, indicating that storage of N by the mussel bed was of minor importance. The contribution of direct excretion by the mussels to the DIN flux from the mussel bed was relatively small. Silicon fluxes showed some retention in spring, and predominantly a release in autumn. The uptake of particulate P by the mussel bed was somewhat higher than the release of phosphate. On

average approximately 35% of the P uptake was retained by the mussel bed. In addition to storage in mussel biomass, which was estimated to be small in relation to the total flux of particulate P, sorption of phosphate on sediment particles might be responsible for some of the P retention.

The relatively low retention of nutrients by the mussel bed may seem surprising, and contradictory to the observed growth of mussels and accumulation of biodeposits. However, the observed mussel production at the mussel lots in the Oosterschelde is close to or lower than the biomass seeded at the lots on an annual basis (Van Stralen & Dijkema, 1994), as the growth of individual mussels is balanced by mortality. This means that net storage of nutrients in mussel biomass is of minor importance. The accumulation of nutrients in biodeposits was more or less balanced by mineralization and resuspension. It should be realized, however, that as a consequence of the large fluxes of material towards and from the mussel bed it was not possible to detect small differences between uptake and release. Retention by the mussel bed of a relatively small fraction of the filtered material could still result in the accumulation of a considerable amount of organic matter in the sediment of the mussel bed.

The net result of uptake and release processes is a rapid cycling of organic matter, with a conversion of particulate organic matter into dissolved inorganic nutrients. It was estimated in Chapter 4 that the amount of nitrogen, regenerated by the mussel beds in the central part of the Oosterschelde, was of the same order of magnitude as regeneration due to mineralization in all other sediments, that cover a much larger area. A comparison of the rates of nitrogen regeneration by mussel beds to estimates of total mineralization (benthic + pelagic) in the central part of the Oosterschelde was presented in Chapter 5, and indicated that the mussels contributed significantly to the nitrogen mineralization. The rapid recycling of nutrients by the mussels may stimulate phytoplankton growth rates in summer, when primary production is limited by low levels of N and Si (Wetsteyn & Kromkamp, 1994).

A mesocosm experiment was carried out to explore the relations between mussel grazing, nutrient cycling and phytoplankton development under more controlled conditions. Four mesocosms were used with different densities of mussels to establish a gradient in grazing pressure. The development of phytoplankton biomass was inversely related to mussel biomass, showing the strong effect of mussel grazing on phytoplankton standing stock. In all mesocosms phytoplankton growth was P-limited.

In spite of a significant contribution to P-regeneration by the bivalves in the mesocosms with high mussel density, estimates indicated that nutrient regeneration by the mussels was not the most important source of regenerated P. A tentative P balance suggested that external loading and pelagic mineralization contributed significantly to the

regeneration of nutrients, and overall nutrient regeneration was higher in the low mussel biomass mesocosms. Still, the availability of phosphate was highest in the mesocosms with the highest mussel density. The experiment demonstrated the major impact that grazing may have on the various nutrient pools. In the mesocosms with low mussel density a major fraction of P was stored in phytoplankton biomass. In the mesocosms with high mussel density, grazing resulted in a reduction of phytoplankton biomass, a consequently lower storage of P in phytoplankton biomass and an increase of the dissolved inorganic nutrient pool. As a consequence of the increased availability of phosphate in the latter mesocosms the phytoplankton community showed increased growth rates. As was shown by Sterner (1989), even without regeneration of nutrients by the grazers, grazing will increase nutrient availability, simply by preventing the monopolization of this resource by the algal community. The increased phytoplankton growth rates in the high mussel biomass mesocosms coincided with a shift in the composition of the phytoplankton community towards a dominance of diatoms. The results showed that grazing resulted in a transfer of nutrients from the phytoplankton pool to the pools of dissolved inorganic nutrients and grazer biomass, a change in phytoplankton composition, and a change in phytoplankton growth rates.

Many temperate coastal ecosystems have large populations of bivalve suspension feeders. Densities of bivalve suspension feeders, typical for bivalve dominated systems, are in the range of 2-8 g ADW m^{-3}. This includes systems like San Francisco Bay, Bay of Marennes-Oléron, Western Wadden Sea and Oosterschelde estuary (Smaal & Prins, 1993). The initial mussel biomass in the mesocosm experiment ranged from 0.5 to 3.8 g ADW m^{-3}, and the treatments with the highest mussel biomass were comparable to the above-mentioned systems with respect to bivalve density.

Results presented in this thesis demonstrated that bivalves affect the pelagic system in various ways. Our mesocosm experiment showed that grazing may induce shifts in phytoplankton species composition towards faster growing species. Moreover, grazing has an effect on the relation between nutrient supply and phytoplankton production. Under nutrient-limiting conditions, bivalve grazing has been shown to have a positive effect on phytoplankton growth rates. This is caused by an increase in nutrient availability. As our observations in the Oosterschelde showed, the mussel population in that estuary filters particulate nutrients, and recycles dissolved inorganic nutrients. The contribution of nitrogen mineralization on mussel beds to total mineralization may be significant, even on the scale of an estuary like the Oosterschelde. The mesocosm experiment demonstrated that regeneration of nutrients by the grazers is not the only factor leading to an increase of the dissolved inorganic nutrient pool. Cropping of the algal community by grazing

reduces the accumulation of nutrients in the phytoplankton, and this alone may be sufficient to enlarge the pool of dissolved nutrients (cf. Sterner, 1989).

Our *in situ* observations of grazing rates of the mussels confirmed the hypothesis on top-down control of phytoplankton by bivalve grazing in the Oosterschelde (e.g. Smaal et al., 1986; Herman & Scholten, 1990). Our mesocosm experiment showed a strong regulation of phytoplankton biomass by bivalve grazing. From this it can be inferred that in bivalve dominated systems phytoplankton biomass is determined by grazing, even when nutrients are not limiting. This leads to the conclusion that the response of phytoplankton to changes in external nutrient load will be limited. Similar phenomena have been observed in freshwater systems with dominating large herbivores (e.g. Mazumder, 1994; Mazumder & Lean, 1994). As was argued by Herman & Scholten (1990), top-down control of phytoplankton biomass by bivalve grazing makes a system more resilient to increases in the external nutrient loading, and in this sense the bivalve population acts as a eutrophication control. Eutrophication control by using bivalve suspension feeders has been suggested as a means to combat algal blooms, both in marine and freshwater systems (Takeda & Kurihara, 1994; Ogilvie & Mitchell, 1995). However, it should be realized that grazing will also enlarge the pool of inorganic nutrients. As was pointed out by Herman & Scholten (1990), this large pool of unused nutrients may be profitable to any primary producer that is less susceptible to grazing by the bivalve, for example macro-algae like *Ulva sp.* or the colony-forming *Phaeocystis sp.*. Eutrophication control by bivalves involves the risk of a sudden shift in an ecosystem towards another, equally undesirable state, and should therefore be accompanied by nutrient input reduction.

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SAMENVATTING

Schelpdieren zijn belangrijke consumenten van plantaardig materiaal in veel ondiepe kustsystemen. De Oosterschelde is een typisch voorbeeld van zo'n systeem, met een hoge biomassa van de mossel *Mytilus edulis* en de kokkel *Cerastoderma edule*. Deze twee schelpdiersoorten verzamelen hun voedsel door eencellige algen uit het water te filtreren. In dit proefschrift is de invloed van mossels op de kringloop van anorganische voedingsstoffen en op de ontwikkeling en produktie van het fytoplankton (in het water zwevende eencellige algen) bestudeerd. Het onderzoek is deels uitgevoerd door veldexperimenten en deels door mesokosmos-experimenten.

De uitwisseling van deeltjes en opgeloste stoffen tussen een mosselbank en de waterkolom is gemeten met behulp van een verplaatsbare tunnel, die op een mosselbank in het intergetijdegebied geplaatst kon worden. De tunnel werd evenwijdig aan de stroomrichting geplaatst, zodat tijdens de periode van hoogwater het water door de tunnel stroomde. Door gelijktijdig het instromende en uitstromende water te bemonsteren en de stroomsnelheid in de tunnel te meten, kon berekend worden hoe groot de uitwisseling van materiaal tussen de mosselbank en de waterkolom was. Deze metingen zijn uitgevoerd op een mosselperceel in de Zandkreek, in het centrale deel van de Oosterschelde. Met behulp van deze zogenaamde 'Benthic Ecosystem Tunnel' kan de opname en afgifte van materiaal door een mosselbank gemeten worden onder natuurlijke omstandigheden, voor wat betreft factoren als o.a. stroomsnelheid, voedselaanbod en temperatuur. De bruikbaarheid van deze methode is geëvalueerd in hoofdstuk 2. In een controle-experiment, waar de mossels waren vervangen door lege schelpen, vond enige bezinking van slib plaats in de tunnel. Dit was het gevolg van een verlaging van de stroomsnelheid van het water tijdens passage door de tunnel. Er trad geen sedimentatie van fytoplankton op. Een evaluatie van de resultaten leidde tot de conclusie dat het mogelijk was een accurate schatting van de opname en afgifte van materiaal door de mosselbank te maken met behulp van deze tunnelmethode.

Mossels leven in een omgeving met een grote fysische dynamiek, als gevolg van getij- en weersinvloeden. De veldwaarnemingen, uitgevoerd in de jaren 1987 tot 1989, lieten zien dat het voedselaanbod van de mossels grote variatie vertoont over de periode van een getij. Voor een deel werd dit veroorzaakt doordat, op de plaats waar de veldmetingen zijn verricht, tijdens vloed het water direct uit een diepe geul kwam en relatief veel eencellige algen bevatte. Het water tijdens de ebfase stroomde weg van een groot intergetijdegebied. Als gevolg van voedselopname door organismen in dat intergetijdegebied waren de algenconcentraties tijdens de ebfase verlaagd. Naast deze variatie over een getijcyclus trad er opwerveling van sediment op onder invloed van de wind. Het effect van de wind was het sterkst bij windrichtingen met een lange strijklengte

en in het deel van de getijcyclus met een geringe waterhoogte boven het mosselperceel. Deze opwerveling leidde tot grote variatie over korte tijd in de kwaliteit en de hoeveelheid van het zwevende materiaal dat als voedselbron voor de mossels dient.
Metingen van de opname van deeltjes door een mosselbank, gepresenteerd in hoofdstuk 3, lieten zien dat mosselbanken grote hoeveelheden deeltjes uit het water filtreren. Onder rustige weersomstandigheden was er een duidelijk verband tussen de concentratie van deeltjes in het water en de hoeveelheid materiaal die door de mossels gefiltreerd werd. Uit een vergelijking tussen de samenstelling van het seston (het zwevende materiaal in het water) en de hoeveelheid van de verschillende bestanddelen van het seston die door de mosselbank werden opgenomen bleek dat er netto relatief veel fytoplankton werd opgenomen door de mosselbank. Hieruit kon worden afgeleid dat een deel van het, door de mossels gefiltreerde, materiaal weer wordt geëxporteerd van de mosselbank. Vermoedelijk gaat het hier vooral om opgewervelde faeces en pseudofaeces. Deze opwerveling vindt onder alle omstandigheden plaats, maar uit metingen bij hogere windsnelheden bleek dat de opwerveling wordt versterkt door golfwerking bij hoge windsnelheden. De filtratie-activiteit van de mossels gemeten in het veld is vergeleken met de resultaten van activiteitsmetingen aan individuele dieren, onder meer gecontroleerde omstandigheden in het veldstation van het RIKZ, met natuurlijk zeewater als voedsel. De activiteitsschattingen uit de veldmetingen op de mosselbank kwamen in grote lijnen overeen met de resultaten van de metingen aan individuele dieren. Deze gegevens vormden een onderbouwing voor eerder gepubliceerde schattingen over de graasdruk van mossels in de Oosterschelde. Uit de gegevens kan worden afgeleid dat de mossels in de Oosterschelde in ongeveer 10 dagen tijd het gehele volume van de Oosterschelde kunnen filtreren.

Mosselbanken vormen een bron van anorganische nutriënten (voedingsstoffen), die worden afgegeven aan de waterkolom. Het gaat hierbij vooral om ammonium, fosfaat en silicaat (hoofdstuk 4). Hoge afgifte van deze voedingsstoffen werd waargenomen bij metingen in juni 1987. De metingen vielen in een periode met een fytoplanktonbloei in dit deel van de Oosterschelde en de hoge afgifte van voedingsstoffen werd verklaard uit een hoge aanvoer van organisch materiaal. Dag-nacht verschillen in de afgifte van nutriënten door de mosselbank werden verklaard uit directe opname van de vrijgekomen stoffen door algen gedurende de dag. Een vergelijking van de gemeten nutriëntenfluxen met directe uitscheiding van nutriënten door de mossels, gaf aan dat excretie door de mossels slechts een deel van de waargenomen flux kan verklaren. Geconcludeerd werd in hoofdstuk 5 dat mineralisatie van faeces en pseudofaeces in het sediment van de mosselbank een belangrijke bron van anorganische nutriënten vormt. Een vergelijking van de hoeveelheid voedingsstoffen die door de mosselbank wordt opgenomen door filtratie van zwevende stof met de afgifte van anorganische voedingsstoffen wees uit dat een mosselbank slechts een klein deel van de opgenomen nutriënten opslaat, terwijl het

grootste deel wordt weer afgegeven aan het water. Een schatting van de bijdrage van mossels aan de totale mineralisatie van stikstof in het centrale deel van de Oosterschelde werd gemaakt door een vergelijking van de veldwaarnemingen met de resultaten van een simulatiemodel voor het Oosterschelde ecosysteem. Uit deze vergelijking bleek dat de mosselpopulatie potentieel een grote rol speelt bij de regeneratie van stikstof in dit deel van de Oosterschelde.

De seizoensvariatie in filtratie-activiteit van een mosselbank is gemeten onder gecontroleerde omstandigheden in een doorstroomsysteem bij IBN-DLO op Texel (hoofdstuk 6). De resultaten toonden aan dat mossels verlaagde filtratie-activiteit hadden in januari, als reactie op hoge concentraties van zwevende stof. Een sterk verlaagde filtratie-activiteit werd waargenomen in de periode april-juni. Dit viel samen met een bloei van de alg *Phaeocystis sp.*. De verlaagde pompsnelheden worden geweten aan een negatief effect van deze alg, mogelijk doordat het slijmkapsel van de *Phaeocystis*-kolonies de kieuwen verstopt. Een andere mogelijke verklaring is dat de alg stoffen uitscheidt die de pompsnelheid van de mossels beïnvloeden. Het negatieve effect van *Phaeocystis sp.* op de filtratie-activiteit van de mossels kan tot gevolg hebben dat de begrazing van het fytoplankton door de schelpdieren sterk vermindert, wat de kans op massale algenbloeien vergroot.

In hoofdstuk 7 worden de resultaten van een mesokosmos-experiment besproken. In dit experiment zijn 4 mesokosmos-eenheden gebruikt. Deze eenheden zijn te beschouwen als levende modellen, die de omstandigheden in de Nederlandse kustwateren met de bijbehorende biologische processen deels nabootsen. In dit experiment hadden de vier mesokosmos-eenheden ieder een andere hoeveelheid mossels. De hoeveelheden varieerden van een hoge dichtheid aan mossels, vergelijkbaar met onder meer de Oosterschelde, tot een acht maal lagere. De fytoplankton biomassa toonde een sterk negatief verband met de mosseldichtheid, als gevolg van de grote invloed van begrazing door de mossels op de algenontwikkeling. In de systemen met hoge mosseldichtheid bleek het fytoplankton voor een groter deel uit diatomeeën (eencellige kiezelwieren) te bestaan, wat waarschijnlijk een gevolg was van de in het algemeen grotere groeisnelheid van diatomeeën ten opzichte van flagellaten (eencellige algen met een zweepstaart). De fytoplanktongroei in alle mesokosmos-eenheden was fosfaat-gelimiteerd. Er was een positief effect van de mossels op de hoeveelheid fosfaat in de waterkolom. Dit werd veroorzaakt doordat begrazing de fytoplankton biomassa beperkte en daardoor de opslag van fosfaat in algenbiomassa beperkte, in combinatie met teruglevering van fosfaat via uitscheiding door de mossels en mineralisatie. Als gevolg van de verhoogde fosfaatbeschikbaarheid, waren de groeisnelheden van het fytoplankton in de mesokosmos-eenheden met hoge mosselbiomassa hoger dan in de systemen met lage mosselbiomassa.

In hoofdstuk 8 worden de resultaten uit de voorgaande hoofdstukken besproken en met elkaar in verband gebracht. Geconcludeerd wordt dat in systemen met een hoge

biomassa van filtrerende schelpdieren, het pelagisch systeem sterk kan worden beïnvloed door de graasactiviteit van deze dieren. Begrazing van het fytoplankton kan leiden tot een verschuiving in de soortensamenstelling naar snelgroeiende soorten. In periodes waarin het fytoplankton nutriënten-gelimiteerd is, kan begrazing leiden tot een hogere nutriëntenbeschikbaarheid en verhoging van de groeisnelheid van het fytoplankton. Onder omstandigheden waar de fytoplankton groei niet door nutriënten gelimiteerd is, kan de sterke begrazing toch de fytoplanktonbiomassa laag houden, wat betekent dat ecosystemen met grote schelpdierbestanden relatief ongevoelig zijn voor hoge nutriëntentoevoer. Een hogere nutriëntenbelasting verhoogt echter wel het risico op het ontstaan van bloeien van algensoorten, die niet door de schelpdieren begraasd worden.

CURRICULUM VITAE

Theo Prins werd geboren op 11 maart 1958 te Den Haag. In 1976 haalde hij het Atheneum-B diploma aan het Thomas More College te Den Haag. In hetzelfde jaar werd begonnen met de studie Biologie aan de Rijksuniversiteit Leiden. Tijdens de doctoraalfase werd voor het hoofdvak Aquatische Oecologie onderzoek verricht bij het Delta Instituut voor Hydrobiologisch Onderzoek te Yerseke. Tevens is voor de nevenrichtingen onderzoek uitgevoerd bij de vakgroep Ethologie, en bij de vakgroep Natuurbeheer aan de Landbouwuniversiteit Wageningen. De studie werd afgerond in mei 1983.
Van augustus 1983 tot februari 1985 werd de vervangende dienstplicht vervuld bij het Delta Instituut voor Hydrobiologisch Onderzoek. Vanaf maart 1985 is hij werkzaam als projectmedewerker bij het Centrum voor Estuariene en Mariene Oecologie van het Nederlands Instituut voor Oecologisch Onderzoek te Yerseke. Er is onderzoek verricht op een aantal verschillende projecten in opdracht van Rijkswaterstaat, Rijksinstituut voor Kust en Zee. Een deel van de resultaten van dit onderzoek zijn beschreven in dit proefschrift.