The uptake and release of material by the cockle *Cerastoderma edule* L. in the Western Scheldt Estuary, SW Netherlands

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Contents

Abstract

In situ experiments were carried out on natural cockle beds in the Western
Scheldt in autumn, spring and summer, using a Benthic Ecosystem Tunnel. From
this tunnel, inflowing and outflowing water was sampled at regular intervals
and analyzed for seston, POC, PON, POP, chlorophyll-*a*, phaeophytin-*a* and dis-
solved inorganic nutrients. In two cases, significant uptake of chlorophyll-*a*
and release of ammonium and phosphate have been observed in tunnel experi-
ments, but in general differences between inflow and outflow were not signifi-
cant and uptake and release alternated. Filtration rates were comparable under
field and laboratory conditions. However, improvements are required on the
measuring devices to achieve more accurate flux measurements. Preliminary
budget calculations of benthic-pelagic coupling for cockles in relation to
benthic and pelagic algae were done with literature data. It is shown that in
spring, cockles may have a limited impact on phytoplankton in the Western
Scheldt, but that in autumn this impact may be large due to lower primary
production and increased cockle biomass. Cockles may ingest a substantial por-
tion of benthic diatom daily production, when benthic diatoms are suspended
and available for filtration.

1 Introduction

Bivalve filter feeders are dominant organisms in many estuaries, and can
have a profound influence on biological processes (e.g. Cloern 1982). Bivalve
species occurring in high densities have the potential to filter the total
water volume of an estuary at a rate comparable to the water residence time
(Smaal and Prins 1993). Already in 1952, Verwey pointed at the important role
of cockles and mussels in organic matter transport in the Wadden Sea. Since
then, a growing number of experiments has been carried out which show substan-
tial rates of uptake and release of material on beds of bivalve filter fee-
ders. Experiments were done in mesocosms (e.g. Doering and Oviatt 1986), by
taking water samples over a bivalve bed (Fréchette and Bourget 1985a, 1985b,
Fréchette et al. 1989, Smaal et al. 1986, Peterson and Black 1991, Muschenheim
and Newell 1992) or with various kinds of flumes placed on bivalve beds (Dame
et al. 1984, Dame and Dankers 1988, Dame et al. 1991, Prins and Smaal 1990,
Prins and Smaal in press, Asmus and Asmus 1991, Zurburg 1993). Postma (1954)
was the first to indicate the importance of phosphate excretion by bivalves.
Release of other nutrients from bivalve beds, notably ammonium and silicate,
has been reported later (e.g. Dame et al. 1984, Prins and Smaal 1990). When
these nutrients are released through direct bivalve excretion or bacterial
mineralization of faeces and pseudofaeces, they can be recycled by phytoplank-
ton in the water column. This process is an aspect of benthic-pelagic coupling
(Dame et al. 1980, Prins and Smaal 1990, for a review of benthic-pelagic cou-
pling in general, see Graf (1992)). Some model calculations show that, in some
estuaries, bivalve filter feeders can act as a euthrophication control via
benthic-pelagic coupling (Officer et al. 1982, Loo and Rosenberg 1989, Herman
and Scholten 1990). In this view, filter feeders increase the turnover of
phytoplankton by excreting nutrients, but keep phytoplankton at a low level
even in bloom situations by high feeding rates.

In this study the focus is on the common cockle *Cerastoderma edule* L., a
bivalve filter feeder. In the Western Scheldt Estuary, cockles occur in densi-
ties of up to $7400/m^2$ with biomass maxima of 340 g AFDW/m^2 on intertidal mud-
flats, and dominate the macrobenthos biomass in the marine part of the estuary
(Ysebaert and Meire, 1991). Commercial fishery on cockles is extensive in the
area. The Western Scheldt is the estuary of the River Scheldt, and has a total
surface of ca 300 km^2, of which tidal flats comprise 80 km^2. The estuary has a

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tidal discharge of 44,000 m³/s at Vlissingen, while the river input is only 100 m³/s. Nutrient levels, especially of N and P, are high, due to waste water discharge along the River Scheldt. Phytoplankton is dominated by diatoms, although in spring, a bloom of the flagellate *Phaeocystis* sp. may occur (Koeman et al. 1992). On the surface of intertidal mudflats, benthic diatoms grow abundantly (Sabbe and Vyverman 1991, D. de Jong, unpubl. data, and own obs.) For other estuaries it has been reported that benthic diatoms can be suspended in the water column and thus become available as food for filter feeders (de Jonge 1992, de Jonge and van Beusekom 1992, Muschenheim and Newell 1992).

The aim of this study was to test the suitability of a flume method, the Benthic Ecosystem Tunnel (see section 2.1), for measuring uptake and release of material by a natural cockle bed in the Western Scheldt. For comparison, clearance rates of individual cockles taken from the tunnel were determined in the laboratory. The results of the first three experiments were used (1) to compare clearance rates of cockles in the field and individual cockles held in the laboratory, (2) to compare nutrient release from a natural cockle bed and rates extrapolated from individual excretion rate measured in the laboratory, and (3) to estimate the influence of cockles on material fluxes in the Western Scheldt estuary. Some preliminary results of diatom composition of near-bottom water and stomach contents of cockles will also be presented. The research fits into a framework of studies by the National Institute of Coastal and Marine Management into carrying capacity and sustainable use of water systems. Ultimate goal of the experiments on cockle beds is to quantify the influence of the cockle population of the Western Scheldt on C and N cycles in the estuarine ecosystem. For this purpose some budget calculations were done with literature data.
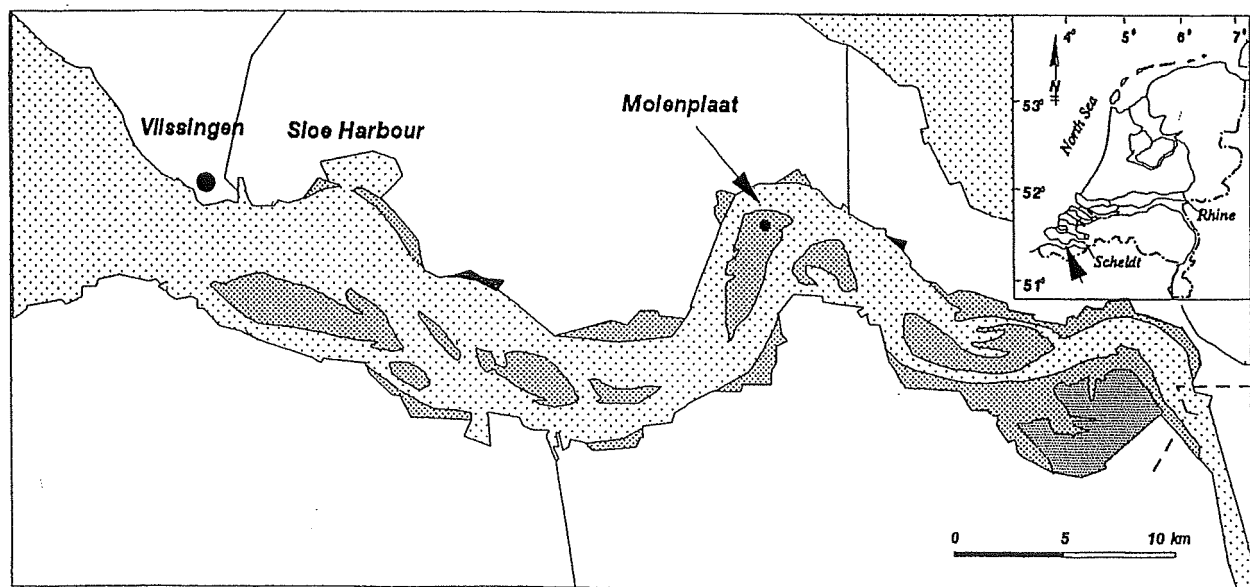

Figure 1 Map of the Western Scheldt. The experimental site is designated by a black dot.

2 Material and Methods

2.1 Benthic Ecosystem Tunnel experiments

Three experiments were carried out on Molenplaat, an intertidal mudflat in the Western Scheldt (see fig. 1), where cockles occur in fairly high densities (up to $1384/m^2$, Ysebaert and Meire 1991). In September 1992 a site alongside a tidal channel was used, lying 75 cm below mean water level, emerged for about 4.5 h per tide. In April and June/July 1993 experiments were carried out on a higher part in the middle of the mudflat, at 24 cm below NAP, emerged for about 6 h per tide. Dates of experiments were within a few days of neap tide. Experiments were done with a Benthic Ecosystem Tunnel (BEST), a device for measuring *in situ* uptake and release of material on a bivalve bed by sampling water flowing in and out of the tunnel. The tunnel is aligned to the mean current direction. For all three experiments, a BEST of 12 x 0.8 m was used (fig. 2), with 10 m between the two sampling points. It consists of 25 cm high stainless steel side plates, pushed about 5 cm into the sediment, and covered by perspex U-shaped segments. The side plates are fastened with bolts to iron poles, driven ca. 60 cm deep into the sediment. Height of the perspex roof above the bottom was ca. 40 cm, cross-sectional area was about $0.308 m^2$, and $7.5 m^2$ of cockle bed was covered between sampling points. For the June 1993 experiment, the BEST of the IBN-DLO served as a control. This tunnel has a cross-sectional area of about $0.225 m^2$, and covers a surface of $8.3 m^2$ between sampling points. Samples of in- and outflowing water were taken with battery-driven pumps. Current velocity in the tunnels was measured with electro-magnetic induction current meters (Marsh-McBirney and NSW Meerestechnik) mounted inside the tunnel halfway between sampling points. Current velocity outside the tunnel was measured in 1993 with a meter mounted outside the tunnel. These devices were operated from a small boat anchored alongside the tunnel. Because of low natural densities, cockles from the surrounding area were added on the experimental site, two weeks in advance of an experiment. In April, several thousands of cockles from the Sloe harbour area were bought from a cockle fisher and also added to the natural population, two weeks in advance of the experiment. In the control tunnel, in June/July 1993, cockles were removed from the sediment. In April and June/July 1993, current velocity in the tunnels was reduced by placing five iron rods of 1 cm diameter into the sediment at the entrance of the tunnel, at equal distances. Reduced water flux through the tunnel enhanced the possibility of detection of material fluxes.
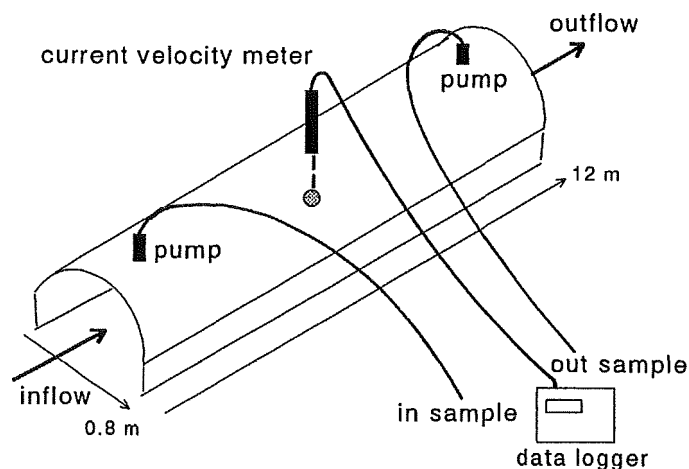

Figure 2 Schematic representation of Benthic EcoSystem Tunnel

Experiments lasted two subsequent tidal cycles. Sampling started when water level above the mudflat reached ca. 1 m. Samples of in- and outflowing water were taken at 30 min (1992) or 20 min (1993) intervals and sampling stopped when water level dropped below 1 m with the receding tide. Samples were transported in 1 l polythene bottles to the laboratory and filtered within a few hours, and stored before further analysis took place. After each experiment, cockle density and frequency distribution in the tunnel were determined by taking 10 bottom cores of 1/16 m^2. Samples were stored at -20°C. Shell length was measured to the nearest 0.1 mm with callipers, along the longest axis of the shell. The soft parts were excised from the shell, and DW and AFDW were determined by respectively drying for 48 h at 70°C, and combusting for 2 h at 450°C.

2.2 Sample analysis

Number of particles with equivalent spherical diameter > 3 μm in each sample was determined with a Coulter counter. Seston was determined by filtering 500 ml of sampled water over a pre-weighed, ashed Whatman GF/C glass fiber filter, rinsing with about 100 ml distilled water, drying the filter for 24h at 60°C, and weighing. Particulate organic carbon (POC) was determined as weight loss after ashing of the seston filter. Particulate organic nitrogen (PON) and phosphorus (POP) were determined by filtering 500 ml of sampled water over a Whatman GF/C filter, rinsing with sea-water isotonic salt solution (30 g $NaCl.l^{-1}$) and combusting the filter in a Carlo Erba analyser. Chlorophyll-*a* and phaeophytin-*a* were determined by HPLC after filtering 1 l (September 1992 and April 1993) or 500 ml (June/July 1993) of sampled water over a Whatman GF/C filter, adding some $MgCO_3$ solution, and rinsing with sea-water isotonic salt solution. Dissolved inorganic nutrients were determined by autoanalyzer in the filtrate obtained after filtering over a Whatman GF/C filter.

2.3 Calculation of mass fluxes

Mass fluxes of material were calculated by multiplying the difference in concentration between inflow and outflow by the water flux through the tunnel at sampling time. Figure 3 illustrates this procedure. Water flux was calculated from current velocity measurements multiplied by 0.85 to correct for shear on the bottom and at the tunnel sides. Only samples at current velocities > 2 cm/s were used for analysis, we assumed water in the tunnel to be well mixed at these speeds (Prins et al., in prep.). A positive sign is used for influx, and a negative sign for flux out of the sediment.

2.4 Calculation of clearance rate in the tunnel

Clearance rate of a standard cockle of 1 g DW in the tunnel can be calculated from chlorophyll-*a* concentrations in the following way (after Coughlan, 1969):

$$CR_{bed} = \frac{Q \ln (C_{in} / C_{out})}{A} \quad \text{in } m^3/m^2.h$$

where CR_{bed} is clearance rate of the cockle bed, Q is water flux (m^3/h) through the tunnel, C_{in} is chlorophyll-*a* concentration (μg/l) in the inflowing water, C_{out} is chlorophyll-*a* concentration (μg/l) in the outflowing water, and A is

the surface (m^2) of the cockle bed between sampling points. Clearance rate is then converted to rate per standard animal of 1 g DW by dividing CR_{bed} by the metabolic biomass in the tunnel, B_m:

$$B_m \quad = \quad \Sigma \, (\, n_i \, W_i^{\,b}) \qquad\qquad in \; g/m^2$$

where n_i is the number of cockles of size class i, W_i is DW of a cockle of size class i, and b is the weight exponent of the allometric function $CR = aW^b$. A value of 0.556 was chosen for b in this study (Newell and Bayne 1980).

Cockle Tunnel   Control Tunnel
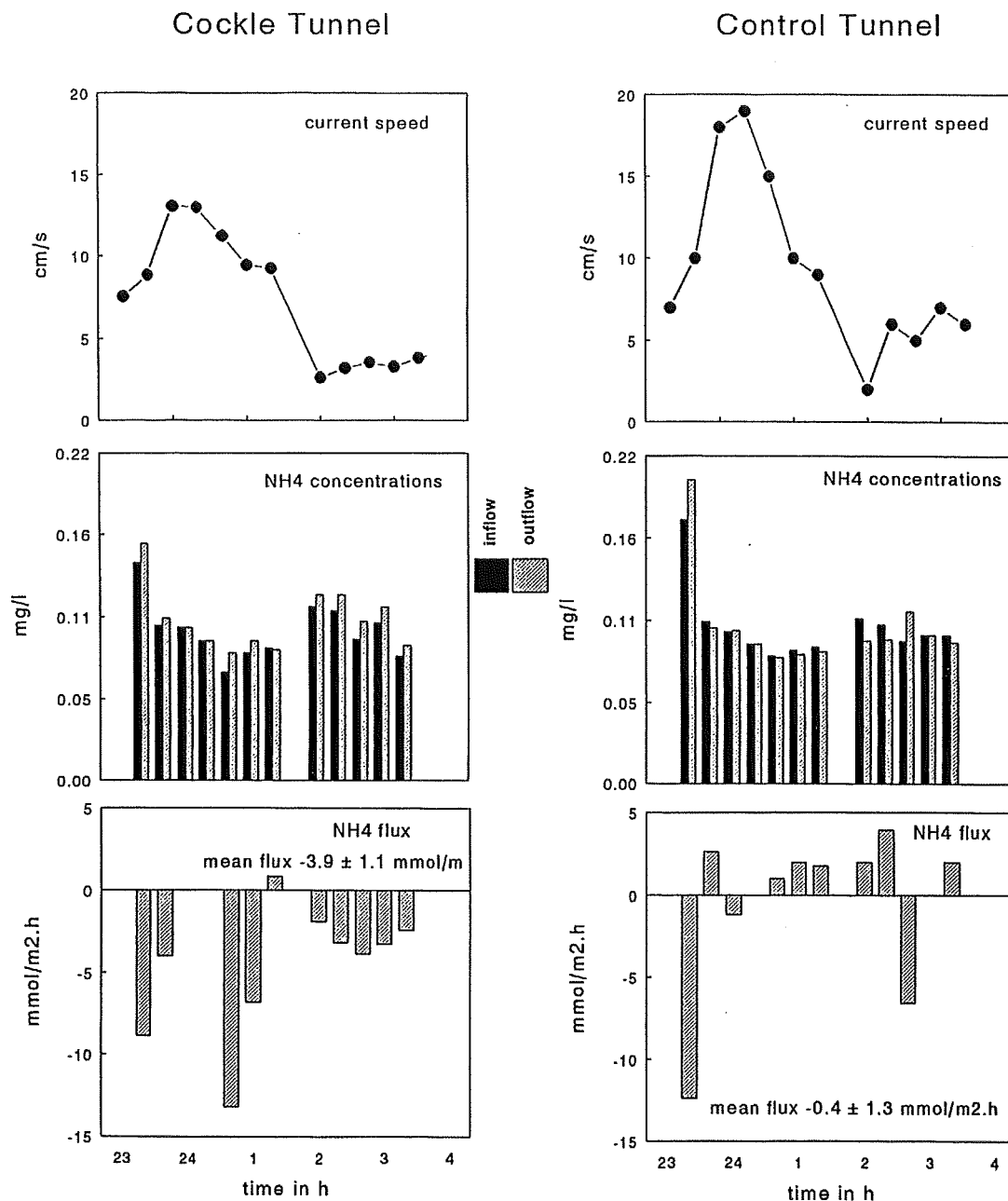
Figure 3 Example of procedure for computation of mass fluxes from current velocity measurements and concentrations of, in this case, ammonia in inflow and outflow of the tunnel. The three graphs in the left column are for tunnel with cockles, right three graphs are for control tunnel. The graphs in the top row give current velocity at each water sampling time, while graphs in the middle row give ammonia concentrations for inflow and outflow of the tunnels at each sampling time. The lower row of graphs shows the fluxes of ammonia at each sampling time, calculated from concentration differences between inflow and outflow (middle row) and current velocity (top row) converted to water flux through the tunnel. Example for June/July 1993 experiment, second tidal cycle.

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2.5 Laboratory measurements of clearance rate

A subsample of cockles was taken from the tunnel immediately after a BEST experiment. The animals were transported to the laboratory and placed in a raceway onto sediment taken from the tunnel, and provided with running sea water from the Eastern Scheldt. Measurements were done within a week after the BEST experiment. Clearance rate was measured with natural Eastern Scheldt water. 14 Cockles were put into small cups with silicious sand (median grain size of 210 μm) and placed in individual flow-through chambers of ca. 600 ml. Two control chambers contained a cup of sand without a cockle. A water flow of ca. 4 1/h was maintained trough the chambers with a Watson-Marlow 503s or 504s peristaltic pump. Water in the chambers was mixed gently with magnetic stirrers. Samples of outflowing water were taken after a 16 h acclimatizing period, and analyzed with a Coulter counter. Particles with equivalent spherical diameter > 3 μm were counted. Clearance rate for each individual cockle was calculated with the following formula, using the outflow of the control chamber as the inflow value, to correct for sedimentation in chambers or tubing:

$$CR = Q * (C_{in} - C_{out}) / C_{in},$$

where CR = clearance rate in 1/h, Q is flow through the chamber in 1/h, C_{in} = number of particles > 3 μm per ml in outflow of control chamber, and C_{out} = number of particles > 3 μm per ml in outflow of chamber with cockle. After the experiment, cockle length, DW and AFDW were determined as described in 2.1.

2.6 Diatom composition of cockle stomachs and near-bottom water

To obtain stomach contents, cockles were stored on ice after sampling. Dissection took place within 2 hours after sampling, using a stereo microscope, cold light source, small scissors and a 1 ml syringe. Stomach contents were stored in 10 ml of Lugol's solution. Near-bottom water was collected with the normal sampling tubes from the tunnel, taking 1 l and storing it with 4 ml concentrated Lugol's solution. To determine diatom composition, 5 ml of sample was taken and put into a 10 ml cuvette. 200 Diatom cells were counted at 400x magnification under an inverted microscope (Zeiss) after at least 24 h settling time. Distinction was made between pennate (mostly benthic, Hummel 1985, p.61), and centric (unicellular or chain-forming, mostly pelagic in origin, Hummel 1985, p.61) diatoms.

2.7 Statistical analysis

Statistical analysis of the data was done using Statistix 4.0 and Systat 5.0 statistical packages. Significance of a mass flux was determined over one tidal cycle at a time, comparing pairs of inflow and outflow data by a Wilcoxon signed ranks test. For the June/July 1993 experiments, fluxes in the control and cockle tunnel were compared per tidal cycle using a Mann-Whitney U-test.

3 Results

Cockle density and biomass in the tunnel are given in table 1 for each experiment. Density and biomass were higher in 1993 than in 1992 because more cockles were added to the tunnel site. Other macrobenthos species were scarcely observed in cores from the tunnel in all experiments, and biomass is supposed to have been negligible as compared to cockle biomass. This has been quantified in June/July 1993 (Table 1). Length distributions of cockles in the tunnel are shown in figure 4. The large cockles present in September had presumably been fished after the experiment, and in April only small animals of around 10 mm were left over. In April we added a large amount of 30 - 40mm cockles originating from a mudflat in the mouth of the Western Scheldt on the site, while in June/July somewhat smaller cockles from the surrounding mudflat area were added.

Table 1 Cockle densities and AFDW per m^2 in the tunnel for three BEST experiments. Means ± s.e., 10 cores in September 1992 and April 1993, 5 cores in June/July 1993

experiment	$\#/m^2$	g AFDW/m^2	other benthos AFDW/m^2
23/24 September 1992	232 ± 69	85 ± 14	not determined
14/15 April 1993	1133 ± 120	194	not determined
30 June / 1 July 1993:			
Cockle tunnel	1680 ± 130	200 ± 16	4 ± 1
Control tunnel	64 ± 11	5 ± 1	not found
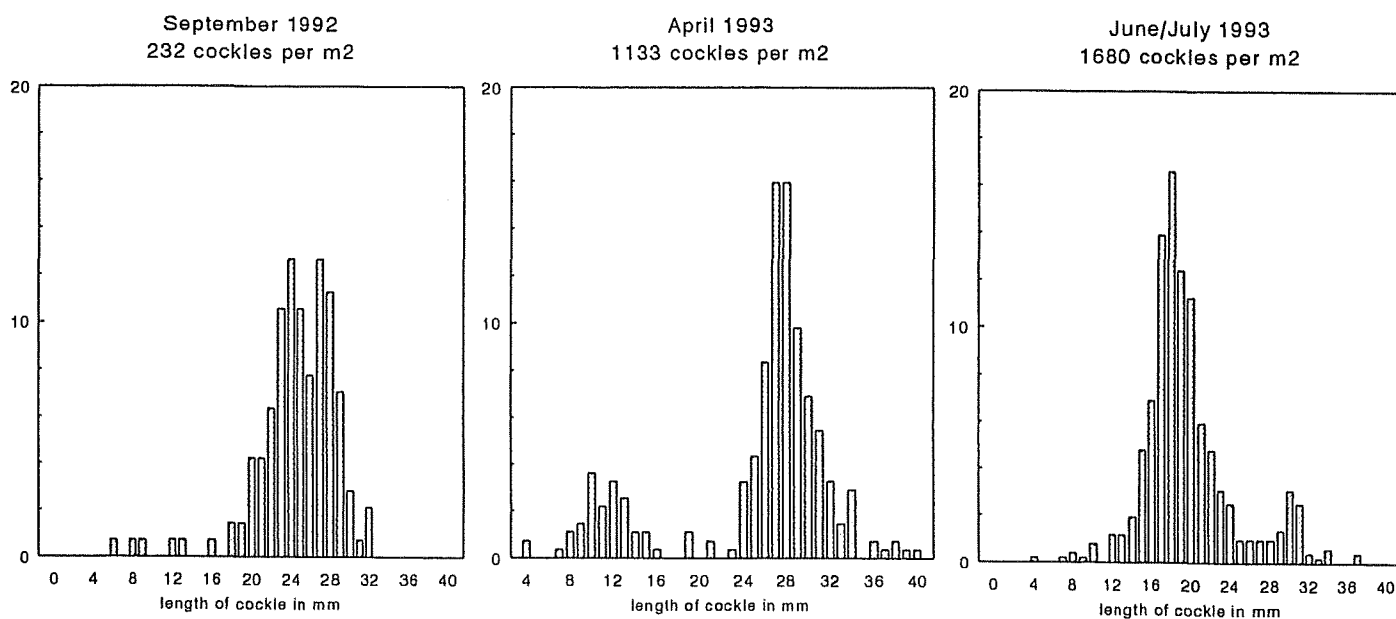
Figure 4 Length distribution of cockles in the tunnel for the three experiments. One class per mm length. Mean frequency in percent of mean total per core of 1/16 m^2.

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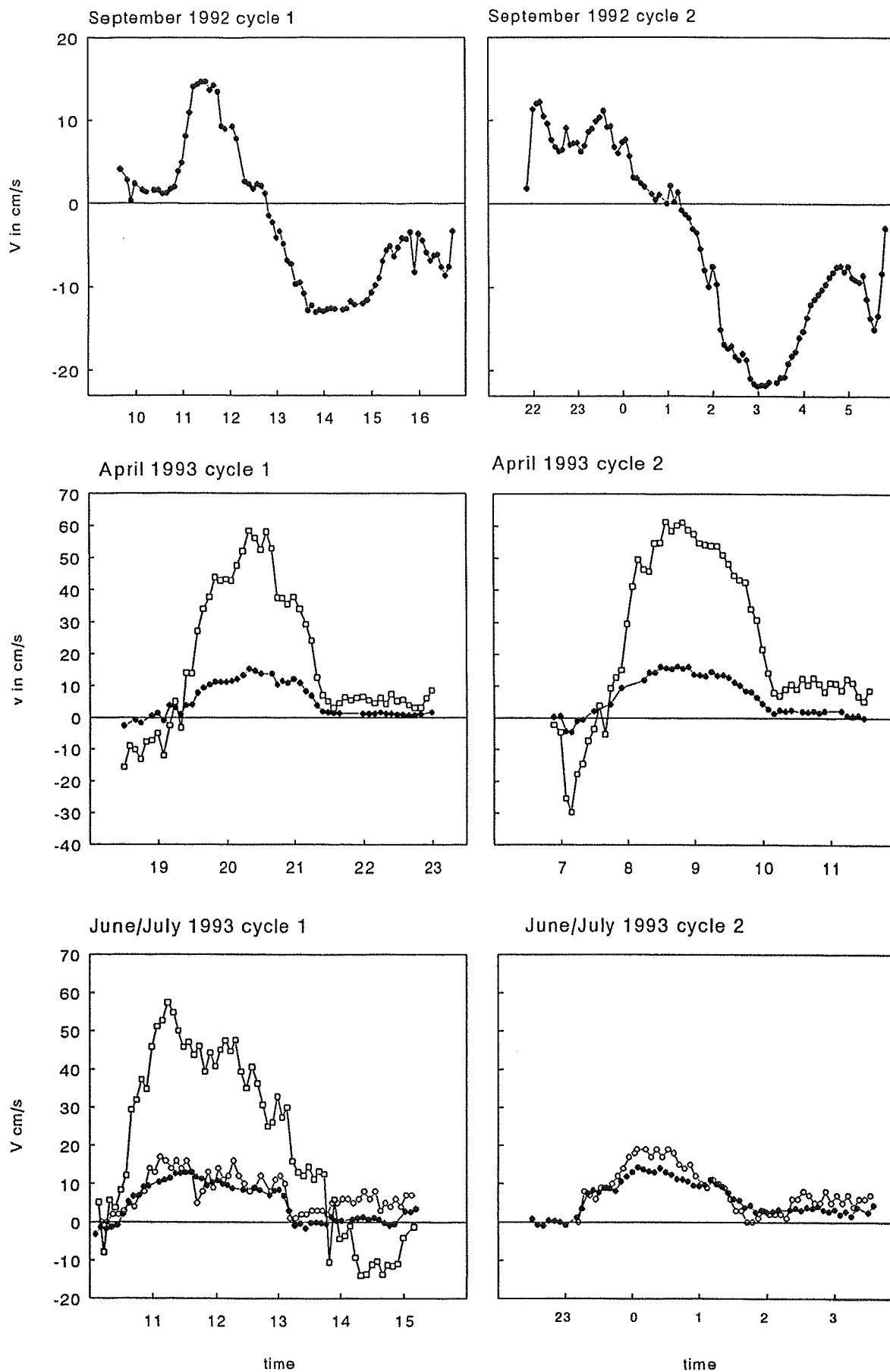
Figure 5 Current velocity measurements for the three experiments, plotted per tidal cycle. Closed dots for tunnel with cockles, open dots for control tunnel (June/July experiment only), open squares for velocity measured outside tunnel.

Current velocity profiles measured in and outside the tunnels are presented in figure 5. On the experimental site in September 1992 a clear reversal of current direction occurred at the turn of the tide. This was not observed on the site used in 1993 experiments. The effect of current velocity reductions (carried out on purpose, see section 2.1) in 1993 experiments was clearly visible. In the control tunnel in June/July 1993, velocity was higher than in the tunnel with cockles (Mann-Whitney U-test, p<0.0001). This could be caused by tunnel design differences and effects resulting from the position of the tunnels on the mudflat. However, current velocities at water sampling times did not differ significantly between cockle and control tunnel (Mann-Whitney U-test, p > 0.05). Since fluxes were calculated using only the velocities at water sampling times, there is no effect on further results.

Mean mass fluxes of material for all three experiments are given in tables 2, 3 and 4. Statistical comparison of fluxes in the cockle tunnel and the control tunnel is also listed in table 4. On the whole, ranges of fluxes were large and few fluxes were computed from significant differences in concentration of inflowing and outflowing water. In September, significant outfluxes of seston, POC, POP and phaeophytin-a occurred, no doubt due to the strong SW wind of 6 to 7 Beaufort during the experiment. Under such turbulent conditions it was impossible to measure any influence of cockles on the water flowing through the tunnel. The results of this experiment are therefore not discussed further.

In 1993 weather conditions were more favourable, and chlorophyll-a uptake could be detected, although uptake was only significant in the second tidal cycle of the April experiment (table 3). In June/July, chlorophyll-a uptake was observed in both cockle and control tunnel in the first tidal cycle. In the second tidal cycle, chlorophyll-a uptake occurred in the cockle tunnel, while in the control tunnel an outflux of chlorophyll-a occurred, possibly due to suspension of benthic diatoms. The difference in mean chlorophyll-a fluxes between the tunnels was not significant (Table 4). Phaeophytin-a fluxes showed no clear pattern. In the second tidal cycle in June/July a significant uptake of phaeophytin-a occurred, while release occurred in the control tunnel. The difference in fluxes between the tunnels was not significant (Table 4). No significant differences were found between inflow concentrations of all parameters and between water fluxes for cockle and control tunnel in June/July 1993 (Mann-Whitney U test).

Large variations in seston flux were found in both 1993 experiments. In April and in June/July in the first tidal cycle, seston was transported out of the tunnel. Only during the second cycle in June/July seston uptake occurred, twice as much in the cockle tunnel relative to the control tunnel. But the difference between the tunnels was not significant (Table 4). We never observed significant differences in particulate C, N and P between inflow and outflow of the tunnel.

For dissolved inorganic nutrients, flux data do not show a clear pattern. In April, trends for uptake of all nutrients (except for nitrate) occurred, but only for phosphate this uptake was significant. In June/July, release of nutrients nearly allways occurred in the control tunnel, sometimes being significant. In the cockle tunnel, uptake seemed to occur during the day in the first tidal cycle, while release was found at night during the second tidal cycle. This trend was reversed for nitrate. Significant differences between fluxes in cockle and control tunnel were found for ammonium (release in cockle tunnel relative to control tunnel), phosphate (at day more uptake, at night more release from cockle tunnel relative to control tunnel) and silicate (uptake in cockle tunnel at day relative to control tunnel).

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Table 2 BEST September 23 and 24, 1992 Molenplaat Western Scheldt. Mean fluxes ± s.e., range in parentheses. Particulate fluxes in $g/m^2.h$, chlorophyll-*a* and phaeophytin-*a* fluxes in $mg/m^2.h$, dissolved material fluxes in $mmol/m^2.h$. Positive flux means uptake in the tunnel, negative flux means release from the tunnel. Differences between inflow and outflow concentrations tested with Wilcoxon signed ranks test, significance denoted by asterisks: * p< .05, ** p< .01

	cycle 1 (day, n=12)		cycle 2 (night, n=12)	
seston	-1 ± 100	(-680/870)	-240 ± 95**	(-990/65)
POC	2.3 ± 1.6	(-5.9/13)	-2.0 ± 0.9*	(-11/0.3)
PON	0.1 ± 0.11	(-0.48/1.3)	0.07 ± 0.04*	(-0.11/0.41)
POP	0.02 ± 0.07	(-0.41/0.65)	-0.14 ± 0.09*	(-1.2/0.08)
chlorophyll-a	0.5 ± 0.9	(-7.8/5.2)	-2.2 ± 2.2	(-27/6.0)
phaeophytin-a	0.21 ± 0.12	(-0.15/1.2)	-0.51 ± 0.40*	(-3.7/3.4)
ammonia	3.6 ± 1.8	(-4.5/15)	1.7 ± 2.6	(-11/23)
nitrite	3.4 ± 2.1	(-5.6/20)	1.4 ± 2.3	(-15/14)
nitrate	82 ± 50	(-140/460)	42 ± 57	(-300/350)
phosphate	3.4 ± 2.9	(-11/25)	4.2 ± 1.9*	(-4.5/15)
silicate	20 ± 12	(-250/110)	8.6 ± 12	(-80/70)

Table 3 BEST April 14 & 15, 1993 Molenplaat Western Scheldt. Mean fluxes ± s.e., range in parentheses. Particulate fluxes in $g/m^2.h$, chlorophyll-*a* and phaeophytin-*a* fluxes in $mg/m^2.h$, dissolved material fluxes in $mmol/m^2.h$. Positive flux means uptake in the tunnel, negative flux means release from the tunnel. Differences between inflow and outflow concentrations tested with Wilcoxon signed ranks test, significance denoted by asterisks: * p< .05, ** p< .01

	cycle 1 (night, n=6)		cycle 2 (day, n=11)	
seston	-63 ± 53	(-328/57)	-27 ± 23	(-146/141)
POC	-1.5 ± 1.1	(-4.8/2.8)	0.1 ± 0.8	(-5.7/4.9)
PON	-0.22 ± 0.13	(-0.59/0.14)	0.18 ± 0.10	(-0.08/1.2)
POP	-0.02 ± 0.03	(-0.15/0.06)	0.02 ± 0.02	(-0.04/0.18)
chlorophyll-a	5.0 ± 4.3	(-13/20)	3.1 ± 1.8*	(-6.6/17)
phaeophytin-a	-0.06 ± 0.44	(-2.2/1.2)	-0.19 ± 0.30	(-3.2/0.61)
ammonia	3.0 ± 1.6	(-2.5/9.6)	1.2 ± 0.8	(-2.0/5.1)
nitrite	0.3 ± 0.5	(-1.0/2.2)	0.7 ± 1.0	(-5.0/7.0)
nitrate	-20 ± 25	(-140/69)	130 ± 86	(-290/680)
phosphate	1.1 ± 0.3*	(-0.2/1.9)	3.0 ± 0.8*	(0.1/7.7)
silicate	13 ± 7	(-15/34)	8 ± 16	(-73/120)

Table 4 BEST June 30 & July 1, 1993 Molenplaat Western Scheldt. Mean fluxes ± s.e., range in parentheses. Particulate fluxes in $g/m^2.h$, chlorophyll-*a* and phaeophytin-*a* fluxes in $mg/m^2.h$, dissolved material fluxes in $mmol/m^2.h$. Positive flux means uptake in the tunnel, negative flux means release from the tunnel. Differences between inflow and outflow concentrations tested with Wilcoxon signed ranks test. Mann-Whitney U-test for comparing fluxes from cockle and control tunnel. Significance denoted by asterisks: * $p<.05$, ** $p<.01$

| | tidal cycle 1 (day, n=8) | | | | tunnels |
	cockle tunnel		control tunnel		compared
seston	-23 ± 46	(-270/240)	-140 ± 120	(-910/340)	n.s.
POC	1.0 ± 2.6	(-7.0/19)	-0.1 ± 2.6	(-14/11)	n.s.
PON	0.1 ± 0.2	(-0.6/1.7)	-1.0 ± 0.8	(-6.2/1.6)	n.s.
POP	0.14 ± 0.10	(-0.12/0.84)	0.03 ± 0.06	(-0.21/0.41)	n.s.
chlorophyll-a	12 ± 11	(-24/76)	16 ± 14	(-17/110)	n.s.
phaeophytin-a	0.7 ± 0.9	(-2.4/6.2)	1.8 ± 1.7	(-3.2/14)	n.s.
ammonia	3.9 ± 3.3	(-3.8/27)	-1.0 ± 1.7	(-7.3/7.3)	n.s.
nitrite	1.0 ± 1.3	(-3.4/7.4)	-1.9 ± 1.1*	(-8.4/0.8)	n.s.
nitrate	-7 ± 15	(-72/73)	-38 ± 18*	(-140/2.5)	n.s.
phosphate	0.5 ± 0.4	(-1.4/2.8)	-1.4 ± 0.5**	(-4.7/0.0)	*
silicate	7.9 ± 2.6**	(0.0/23)	-2.8 ± 1.2	(-8.1/2.3)	**

| | tidal cycle 2 (night, n=12) | | | | tunnels |
	cockle tunnel		control tunnel		compared
seston	27 ± 51	(-460/340)	14 ± 36	(-210/330)	n.s.
POC	0 ± 3	(-22/15)	0.2 ± 0.7	(-3.8/5.3)	n.s.
PON	0.2 ± 0.4	(-2.6/3.1)	-0.0 ± 0.2	(-1.7/1.0)	n.s.
POP	no data				
chlorophyll-a	32 ± 30	(-68/350)	-10 ± 20	(-230/57)	n.s.
phaeophytin-a	1.2 ± 0.7*	(-0.4/7.8)	-0.2 ± 1.0	(-10/4.1)	n.s.
ammonia	-3.9 ± 1.1**	(-13/0.8)	-0.4 ± 1.3	(-12/3.9)	**
nitrite	-0.1 ± 0.2	(-2.0/1.2)	-1.4 ± 1.8	(-21/4.1)	n.s.
nitrate	4.8 ± 2.2	(-9.5/15)	-8.3 ± 19	(-210/79)	n.s.
phosphate	-1.3 ± 0.3**	(-3.4/0.0)	0.2 ± 0.3	(-1.9/2.2)	**
silicate	-1.1 ± 0.6**	(-6.4/1.2)	-3.3 ± 1.9*	(-22/1.6)	n.s.
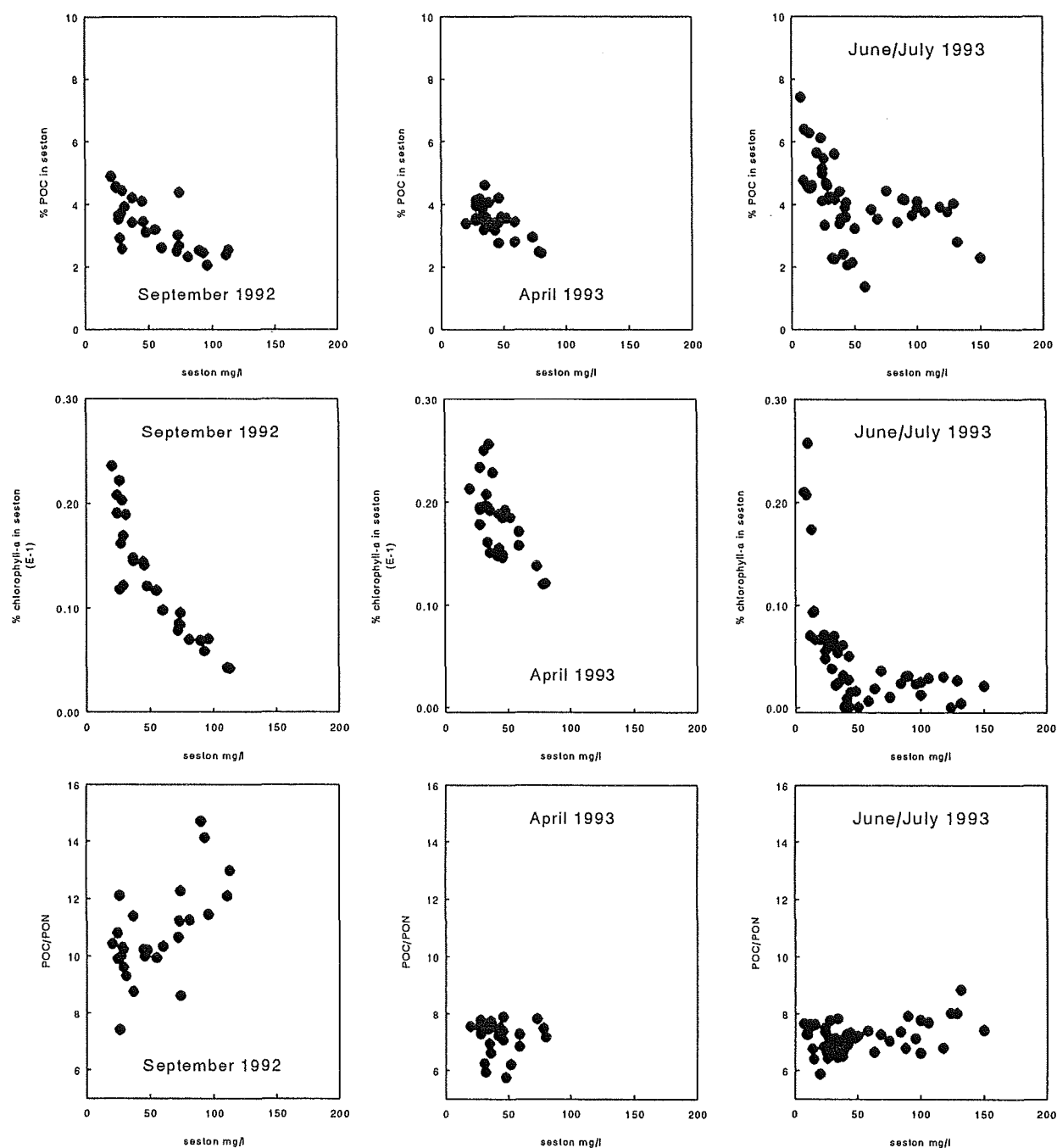
Figure 6 Seston composition of inflowing water in all three experiments. Upper row, percentage of POC, middle row, percentage of chlorophyll-a, and lower row, POC/PON ratio versus seston concentration. Note that in the middle row, printed scales on the Y-axis for September 1992 and April 1993 are 10 times smaller than the scales for June/July 1993.

Seston concentrations in inflowing water were high in all experiments (fig. 6) (September 60 ± 10 mg/l; range 20 - 304 mg/l, April 43 ± 3 mg/l; range 20 - 80 mg/l, June/July 51 ± 5 mg/l; range 7 - 150 mg/l), while chlorophyll-a and POC content (in percent of total seston) decreased with increasing seston concentration. However, C/N ratio (as POC/PON) showed no relation with seston concentration in 1993 experiments, but a positive relation in September 1992. Still, mean C/N ratio remained low (September; 11 ± 0.37, April; POC/PON = 7.08 ± 0.16, June/July; POC/PON = 7.19 ± 0.07), indicating food of high quality for filter feeders (Navarro et al. 1993). Organic material in the water will have consisted mainly of algae with typical C/N ratios of 5 to 8 (Fenchel and Jørgensen 1976), while detritus, with higher C/N ratios of 10 to 35 (Russel-Hunter 1970), made up only a minor part.

Clearance rates measured from chlorophyll-a uptake in the tunnels, recalculated per g AFDW, were similar to values found in the laboratory with cockles taken from the tunnel after a field experiment. Clearance rates for laboratory and tunnel respectively, in l/g DW.h, for April were 1.28 ± 0.32 (n=6) and 1.68, and for June/July 2.70 ± 0.46 (n=7) and 2.98. Clearance rate measured in the laboratory was significantly lower in April than in June/July (Mann-Whitney U-test, p = 0.0321).

Diatom counts of water samples from the tunnel show that up to 50 % of the diatoms can be of benthic origin (fig. 7), showing that resuspension of surface sediment was important during those experiments. No clear change in diatom composition seems to take place in the course of a tidal cycle. Diatom counts of cockle stomach contents showed the same distribution (fig. 8) as found for the water in April. In June/July 1993, Phaeocystis sp. colonies were also present in the water. No stomach samples were taken in June/July.
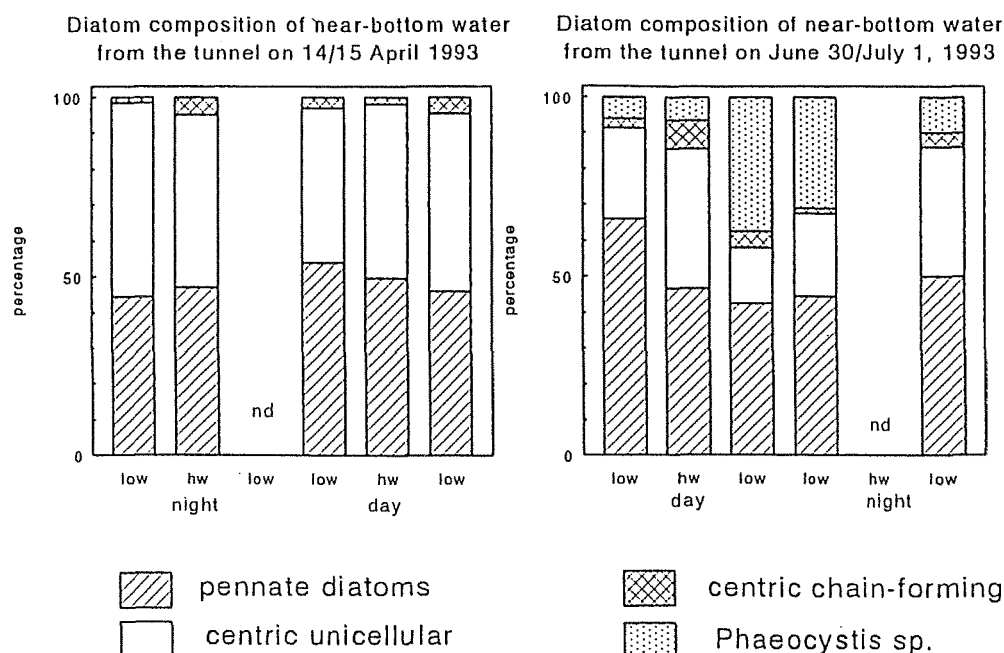
Figure 7 Diatom composition of water samples from the tunnel from April and June/July 1993 experiments. Relative abundance of diatom groups (pennate, unicellular centric and chain-forming centric diatoms, and Phaeocystis) in percentage of 200 cells counted per sample at start of experiment, high water and end of experiment, for day and night cycles.

diatom composition in stomachs of eight
cockles from the tunnel, April 1993
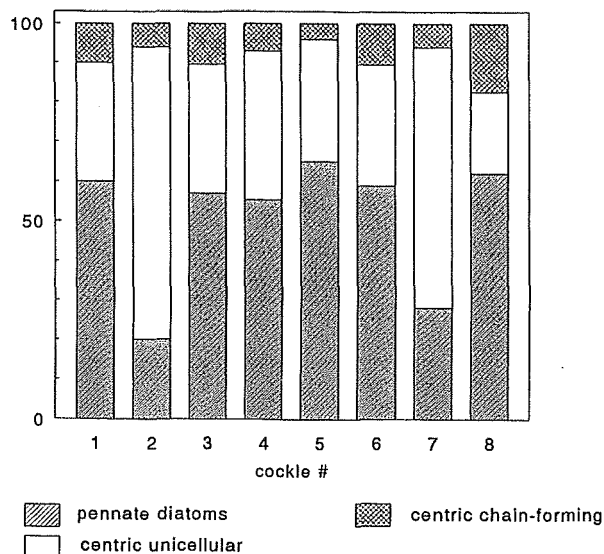
Figure 8 Diatom composition in stomachs of cockles sampled during the April 1993 tunnel experiment. Relative abundance of diatom groups (pennate, unicellular centric and chain-forming centric diatoms) in percentage of 200 cells counted per stomach sample.

4 Discussion

Large variations were found in mass fluxes in tunnels with cockles in all three experiments, and also in the control tunnel. It is difficult to draw conclusions from these results. We will discuss results for cockle and control tunnel in the June/July 1993 experiment, the only experiment in which a control tunnel was used. Notwithstanding the current velocity reduction measures taken, a trend for net export of particular and dissolved material - significant in only one case - took place in the control tunnel (table 4). When fluxes in the cockle tunnel are corrected for flux occurring in the control tunnel, a trend for net import of particulate material emerges. For dissolved inorganic nutrients, a trend for uptake prevailed during the day, while release occurred at night. This pattern could be caused by benthic diatoms growing in the cockle tunnel, utilizing nutrients released by the cockles at day. At night no benthic diatom primary production takes place, and cockle release products leave the tunnel. But then uptake of dissolved inorganic nutrients should have taken place during the day by benthic diatoms in the control tunnel too, which we did not find. The chlorophyll-a concentrations of the sediment in cockle and control tunnel were 13.36 ± 2.68 μg/g and 16.20 ± 2.55 μg/g respectively, indicating that benthic diatoms were present indeed. These chlorophyll-a concentrations are in the range normally found on the Molenplaat in June and July (D. de Jong, unpubl. data). Concentrations did not differ significantly between cockle and control tunnel (Mann-Whitney U-test, p=0.43). Suspension of these benthic diatoms could also have caused some of the variation in chlorophyll-a fluxes measured in the tunnels.

Cockle clearance rates measured in the laboratory did not differ from those measured for cockles in the tunnel, and were comparable to a literature value of Prins and Smaal (1989) (fig. 9). Ammonium and phosphate releases are compared to literature data in table 5, since excretion was not measured in the laboratory for individual Western Scheldt cockles in this study. Contrary to expectation, releases we found are high in relation to values found in a BEST experiment in the Eastern Scheldt (Prins and Pouwer 1990) and in a

14
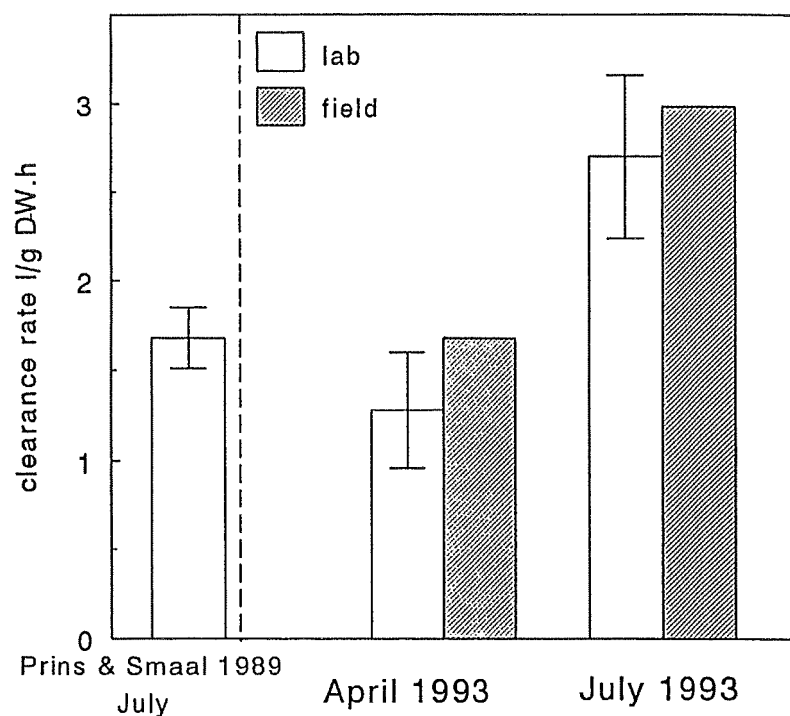
Figure 9 Cockle clearance rates compared for laboratory and field. Values measured in same month are comparable. Laboratory clearance rates with s.e., tunnel clearance rates calculated (see material and methods section).

Table 5 Ammonium and phosphorus releases of the experiment in June/July 1993, second tidal cycle (Table 4 lower panel) compared to other experimental data on cockles. A BEST experiment on a mussel bed is selected for comparison.

study	biomass g AFDW/m^2	ammonia flux μmol/m^2.h	phosphate flux μmol/m^2.h
BEST, Cockle bed, Eastern Scheldt[a]	6.3	580	90
Cockles in aquarium[b]	130 - 170 g DW	84	2.3
BEST, Cockle bed, Western Scheldt[c]	200	3400	1100
BEST, Mussel bed, Eastern Scheldt[d]	1448	6700	709

[a] Prins and Pouwer (1990); July, [b] Lindström Swanberg 1991; laboratory in March, [c] this study; June/July 1993, [d] Prins and Smaal 1990; June 29, 1988.

laboratory study where cockles were kept in aquaria (Lindström Swanberg 1991). Ammonium release on the cockle bed is half of ammonium release on a mussel bed in the Eastern Scheldt in the same month, while phosphate release is in the same order of magnitude in both experiments. But the validity of releases on the cockle bed is highly questionable since they were only observed during one out of four tidal cycles. For ammonium, the quantitatively most important nutrient excreted (Prins and Smaal 1990), out of four tidal cycles, significant efflux was measured only one time, while mean influx occurred in the other three cycles. It is difficult to find feasible explanations for the alternations of influx and outflux also found for other dissolved inorganic nutrients in the 1993 experiments. In addition, the range in magnitude of fluxes during one tidal cycle is large for all parameters measured, so few fluxes were significantly different from zero flux.

An evaluation of field conditions during the experiments could help in understanding these results. Weather conditions were bright with low wind speeds for both 1993 experiments. Still, current velocity reduction was needed to enhance the possibility of detecting the influence of the cockles on the water flowing through the tunnel (fig. 5). In April, sediment was eroded alongside the tunnel, leaving holes under the side plates, so that water could enter the tunnel halfway between the sampling points. Effects of water processing by cockles are possibly masked by such an influx of water into the tunnel. It could also explain release of seston, POC, POP and phaeophytin-*a* in the second cycle of the April experiment. In the June/July experiment we prevented erosion almost completely by protecting both sides of the two tunnels with sand bags.

Mean seston concentrations of 40 - 60 mg/l we found in inflowing water were high as compared to mean values for other systems (e.g. Western Wadden Sea 5 - 20 mg/l (Prins et al. in press), Eastern Scheldt 20 - 30 mg/l (Smaal et al. 1986)). Clearance rate is negatively correlated with seston concentration in the cockle (Foster-Smith 1975, Prins et al. 1991), and cockles in the tunnel will have pumped with reduced clearance rates at the high seston concentrations prevailing. This also reduced their impact on water flowing through the tunnel, and thus detection of that impact will be even more difficult. Another possible problem lies in cockle biomass attained in the tunnel, which was low when compared to experiments with mussels *Mytilus edulis* where biomasses of > 1000 g AFDW/m^2 can be attained. It will be difficult to get a higher cockle biomass in the tunnel, since cockles are infaunal bivalves and cannot be piled on top of each other like (epifaunal) mussels. Densities reached in the tunnel in our experiments are near the maximum possible. Summarizing we can say that the BEST method, that yielded good results with mussels (Dame and Dankers 1988, Prins and Smaal 1990, Prins and Smaal in press) and oysters *Crassostrea virginica* (Dame et al. 1984, 1992) in low seston, low current velocity environments, meets serious problems when applied on cockle beds in the Western Scheldt. Zurburg (1993) met similar problems when operating the tunnel with oysters *Crassostrea gigas* in the Bay of Marennes-Oléron (France). It may be possible that improvements on the tunnel equipment solve these problems, but other field methods need also be considered.

The results of diatom composition in cockle stomachs and near-bottom water (fig. 7, 8) indicate that cockles ingest all kinds of diatoms present in the water. These results are supported by work of Kamermans (1992), who studied algal composition of water and stomach contents of the bivalve filter feeders *Cerastoderma edule, Mya arenaria* and *Mytilus edulis* in the Western Wadden Sea. For all species, algal composition of stomach contents and overlying water showed high correlations. She also found suspended benthic diatoms in near-bottom water, to a percentage of around 30% of all algae present.

To evaluate the influence of cockles on material fluxes in the Western Scheldt estuary, simple budget calculations were done using clearance rate values and literature data (see Appendix for details on calculations). Cockle biomass of the May 1992 census was used, including the estimation of September 1992 biomass (Kesteloo - Hendrikse and van Stralen 1992). Benthic diatom data for 1989 - 1992 were taken from Frandzel (1993), while for other factors averaged monthly values over 1980 - 1985 were used from MOSES, a model of the Scheldt Estuary (Soetaert et al. 1992). Benthic diatom primary production can occur year-round (Cadée and Hegeman 1974), and for calculations we used the same average yearly level for July and September. In the Wadden Sea, Cadée and Hegeman (1974) found production to be in the same order of magnitude in July and September. Results are presented in diagram form for 'July 1992' and 'September 1992' in figure 10. The term 'available algae' is used to describe the mixture of pelagic and suspended benthic algae that is available to cockles in near-bottom water on the mudflats. Since data for the Western Scheldt are still poor, no benthic/pelagic ratio of some sort was used in the budget calculations. In July (fig. 9, left) phytoplankton primary production is high, and cockles could filter less than 10% of daily production. Filtration capacity would be nearly 50% of benthic diatom daily production, and could be limiting benthic diatom stock, if substantial suspension occurs. In September (fig. 9, right), phytoplankton primary production is much lower than in July, and now the cockles, which have grown in summer, and thus have higher clearance rates, could ingest the entire daily production. Absolute ingestion is lower than in July, because algal concentration in the water is lower and clearance rate remained the same in the calculations (although it varies seasonally, Newell and Bayne 1980). Effect on benthic diatoms could be more important than in July, because autumn storms can intensify wind-driven suspension. Ammonium excretion by cockles is insignificant to the N pool in both July and September, as is the need of N for primary production. From these calculations, it is not probable that cockle excretion is important to phytoplankton in the Western Scheldt. Also, it seems that cockles could not act as

Western Scheldt, July   Western Scheldt, September
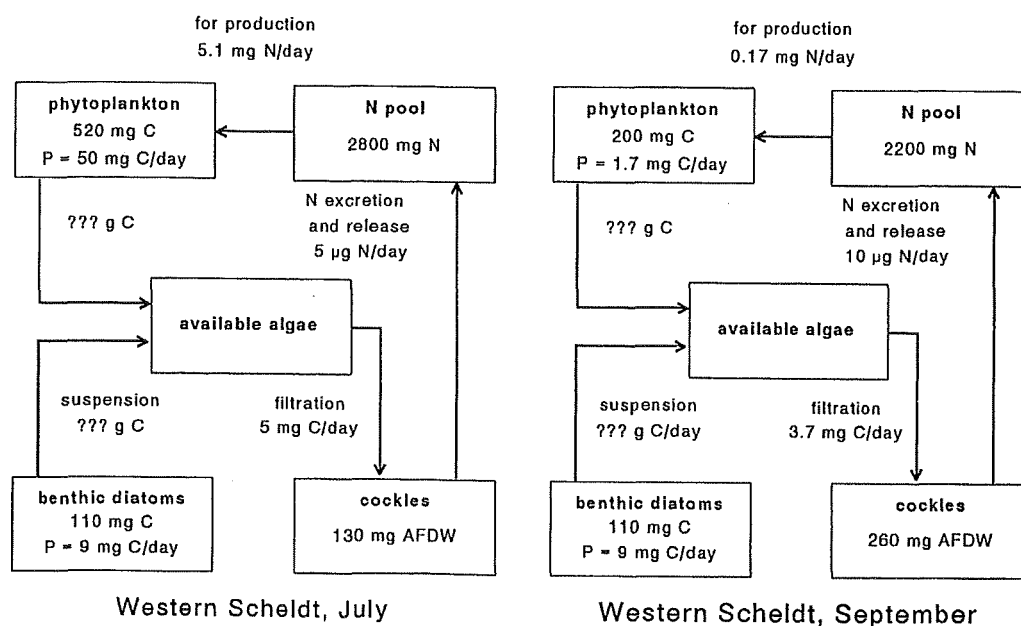
Figure 10 Budget calculations for the marine part of the Western Scheldt for July (left) and September (right). All values are in mg per m³, except for N excretion, µg/m³. Average biomass for cockles was 3.9 g AFDW/m² in July and 7.7 g AFDW/m² in September. For benthic diatoms, yearly averaged biomass was 4.36 g C/m², production was 0.37 g C/m². See Appendix for calculations.

a eutrophication control, able to control algal blooms, as suggested in calculations for other systems (Officer et al. 1982, Loo and Rosenberg 1989, Herman and Scholten 1990, Smaal and Prins 1993). But in autumn and winter, periods with low and even negative net phytoplankton primary production (Soetaert et al. 1992), cockles could have an important effect on phytoplankton, as long as temperatures are high enough for filtration activity to take place (Newell and Bayne 1980). Ingestion of benthic diatoms by cockles could be important in all seasons, depending on the amount of suspension taking place. Investigations on the diatom composition of near-bottom water will have to be done to elucidate the importance of this process.

5 Conclusions

In two cases, significant uptake of chlorophyll-*a* and release of ammonium and phosphate have been observed in tunnel experiments, but in general fluxes were not significant and varied between influx and outflux. Filtration rates though are comparable under field and laboratory conditions. However, improvements are required on the tunnel equipment to achieve more accurate flux measurements. Preliminary budget calculations show that cockles may have a limited impact on phytoplankton in the Western Scheldt in July, but that in September this impact may be large due to lower primary production and increased cockle biomass through growth. Depending on the amount of resuspended benthic diatoms available for filtration, cockles may ingest a substantial portion of benthic diatom daily production. The availability of benthic versus pelagic algae to cockles in different seasons is subject of further research.

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Appendix 1 - Calculation of budgets for the Western Scheldt

Basic data for MOSES compartments nrs 7 - 13 (Soetaert et al. 1992), where cockles occur according to Kesteloo-Hendrikse and van Stralen (1992).

total water volume at mid-tide

= 1/2*(mean HW volume + mean LW volume)

= $2.545*10^9$ m^3

total surface of tidal flats

= $8.433*10^7$ m^2 (Kesteloo-Hendrikse and van Stralen 1992)

mean water depth = volume at mid-tide / surface at HW (MOSES)

= 10 m

Cockle biomass in Western Scheldt in 1992 (Kesteloo-Hendrikse and van Straalen 1992):

May 1992	September 1992 (estimate)
7834 ton fresh + shell	15437 fresh + shell
410 ton DW (5.2% of fresh)	800 ton DW
330 ton AFDW (4.2% of fresh)	650 ton AFDW
4.9 g DW or 3.9 g AFDW per m^2	9.5 g DW or 7.7 g AFDW per m^2
0.16 g DW or 0.13 g AFDW per m^3	0.31 g DW or 0.26 g AFDW per m^3

Phytoplankton monthly average for 1980 - 85 period (MOSES)

July	September
phytoplankton biomass	
0.519 g Phytoplankton-C/m^3	0.201 g Phytoplankton-C/m^3
5.2 g phyto-C/m^2	2.0 g phyto-C/m^2

netto primary production (corrected for phytoplankton respiration)

0.0489 g C/m^3.day	0.00169 g C/m^3.day

Nitrogen pool in monthly averages for 1980 - 85 period (MOSES)

	July	September
N as NH_4	0.264 g N/m^3	0.165 g N/m^3
N as NO_3 or NO_2	2.547 g N/m^3	2.012 g N/m^3
total N	2.8 g N/m^3	2.2 g N/m^3

Nitrogen demand for phytoplankton primary production (N/C = 0.104, MOSES)

July
0.0489 g C/m^3.day * 0.104 = 0.0051 g N/m^3.day
September
0.00169 g C/m^3.day * 0.104 = 0.00017 g N/m^3.day

Benthic diatoms (Frandzel 1993), average 1989 - 1993 over all tidal flats

Biomass (yearly average)
109 mg chlorophyll-a/m^2 and C/chlorophyll-a ratio of 40
4.36 g C/m^2
Area with benthic diatoms is 6.33 * 10^7 m^2 (Frandzel 1993), 280 ton C for total Western Scheldt, 110 mg C/m^3

Gross production (de Jong et al. in press, after Cadée and Hegeman 1977)
Production = 1.22 * Biomass + 1.77 in g C/m^2.year
           = 1.22 * 109 mg chlorophyll-a/m^2 + 1.77
           = 135 g C/m^2.year
           = 0.37 g C/m^2.day
23 ton C/day for total Western Scheldt, 9 mg C/m^3.day

Cockles filter at 0.003 m^3/g DW.h in both months (assumption)

July
0.003 m^3/g DW.h * 4.9 g DW/m^2 * 20 hours/day * 0.519 g phyto-C/m^3
= 0.15 g phyto-C/m^2.day (0.29 m^3/m^2.day)
or per m^3: 0.003 * 0.16 * 20 * 0.519 = 0.0050 g C/m^3.day
this is 10 % of phytoplankton daily production in July

September
0.003 m^3/g DW.h * 9.5 g DW/m^2 * 20 hours/day * 0.201 g phyto-C/m^3
= 0.11 g phyto-C/m^2.day (0.57 m^3/m^2.day)
or per m^3: 0.003 * 0.31 * 20 * 0.201 = 0.0037 g C/m^3.day
this is 220 % of daily phytoplankton production in September

Excretion of ammonia by cockles
1.6 μg NH$_4$/g AFDW.h (Prins and Smaal, 1989) used in both months.

July
1.6 μg NH$_4$/g AFDW.h * 24 h * 3.9 g AFDW/m^2 = 150 μg NH$_4$/m^2.day
or per m^3: 1.6 * 24 * 0.13 g AFDW/m^3 = 5.0 μg NH$_4$/m^3.day

September
1.6 μg NH$_4$/g AFDW.h * 24 h * 7.7 g AFDW/m^2 = 300 μg NH$_4$/m^2.day
or per m^3: 1.6 * 24 * 0.26 = 10 μg NH$_4$/m^3.day

BEST September 23 & 24, 1992, Molenplaat Western Scheldt

sample number	chla in ug/l	chla out ug/l	feoa in ug/l	feoa out ug/l	dn in mg/l	dn uit mg/l	nh4 in mg/l	nh4 out mg/l	no2 in mg/l	no2 out mg/l	no3 in mg/l	no3 out mg/l	no3no2 in mg/l	no3no2out mg/l
1	4.58	5.18	0.21	0.3	2.199	2.131	0.053	0.065	0.049	0.065	1.423	1.878	1.472	1.943
2	4.72	5.27	0.22	0.29	1.879	2.221	0.054	0.066	0.057	0.069	1.66	1.966	1.717	2.035
3	3.83	3.4	0.73	0.53	1.622	2.212	0.12	0.095	0.053	0.056	1.387	1.487	1.44	1.543
4	4.8	4.77	0.1	0.1	2.007	2.018	0.069	0.071	0.057	0.057	1.458	1.452	1.515	1.509
5	5.47	5.12	0.46	0.38	1.853	1.857	0.079	0.067	0.066	0.053	1.542	1.248	1.608	1.301
6	4.73	5.57	0.33	0.1	1.951	1.841	0.078	0.072	0.063	0.065	1.424	1.506	1.487	1.571
7	4.8	5.66	0.37	0.41	1.926	1.446	0.064	0.068	0.054	0.057	1.244	1.282	1.298	1.339
8	5.8	6.24	0.39	0.43	1.902	1.788	0.06	0.069	0.044	0.056	0.984	1.33	1.028	1.386
9	6.2	6.21	0.38	0.4	1.988	2.015	0.059	0.07	0.05	0.067	1.218	1.62	1.268	1.687
10	5.71	5.89	0.36	0.36	1.997	1.985	0.071	0.071	0.063	0.061	1.488	1.456	1.551	1.517
11	6	5.81	0.38	0.4	1.843	1.724	0.045	0.061	0.035	0.051	0.832	1.17	0.867	1.221
12	5.3	5.48	0.36	0.34	1.934	1.857	0.068	0.06	0.061	0.051	1.498	1.255	1.559	1.306
13	6.14	5.77	0.39	0.36	1.939	2.032	0.07	0.071	0.064	0.059	1.537	1.423	1.601	1.482
14	6.69	5.87	0.37	0.37	1.954	1.919	0.069	0.071	0.055	0.062	1.227	1.462	1.282	1.524
20	3.53	4.12	0.12	0.27	2.317	2.46	0.064	0.063	0.064	0.064	1.935	2	1.999	2.064
21	4.37	4.21	0.17	0.27	2.362	2.04	0.062	0.059	0.062	0.05	1.838	1.463	1.9	1.513
22	3.07	3.1	0.27	0.26	2.226	1.946	0.086	0.071	0.066	0.058	1.785	1.593	1.851	1.651
23	6.24	6.2	0.54	0.58	1.934	1.799	0.075	0.048	0.062	0.06	1.556	1.631	1.618	1.691
24	5.66	5.93	0.14	0.47	1.906	nd	0.083	0.08	0.064	0.062	1.486	1.471	1.55	1.533
25	5.39	4.91	0.1	0.1	1.811	1.815	0.072	0.062	0.059	0.044	1.353	1.026	1.412	1.07
26	5.05	5.69	0.1	0.1	nd	1.599	0.077	0.064	0.062	0.053	1.457	1.246	1.519	1.299
27	8.25	7.07	0.61	0.57	1.818	1.735	0.072	0.07	0.062	0.062	1.409	1.407	1.471	1.469
28	6.29	6.49	0.36	0.35	1.724	1.757	0.065	0.077	0.058	0.063	1.337	1.475	1.395	1.538
29	5.34	5.37	0.13	0.26	1.907	1.902	0.07	0.064	0.062	0.054	1.465	1.304	1.527	1.358
30	5.31	4.99	0.23	0.11	1.988	1.855	0.046	0.052	0.039	0.049	0.963	1.222	1.002	1.271
31	6.66	6.77	0.41	0.1	1.98	1.845	0.051	0.062	0.045	0.059	1.138	1.476	1.183	1.535
32	6.68	6.43	0.35	0.36	2.057	1.769	0.057	0.049	0.053	0.045	1.367	1.143	1.42	1.188
33	6.83	6.5	0.39	0.35	1.752	1.53	0.062	0.056	0.058	0.053	1.447	1.327	1.505	1.38

BEST September 23 & 24, 1992, Molenplaat Western Scheldt

sample number	dp in mg/l	dp out mg/l	po4 in mg/l	po4 out mg/l	poc in mg/l	poc out mg/l	pon in mg/l	pon out mg/l	pop in mg/l	pop out mg/l	si in mg/l	si out mg/l	seston in mg/l	seston out mg/l
1	0.269	0.271	0.182	0.245	1.1	0.8	0.111	0.126	0.064	0.078	0.633	0.851	24	17
2	0.255	0.271	0.226	0.254	0.98	1.68	0.094	0.139	0.054	0.092	0.848	0.98	20	49
3	0.248	0.295	0.226	0.238	7.61	5.57	0.44	0.386	0.365	0.29	0.932	0.897	304	163
4	0.25	0.26	0.193	0.211	2.88	2.1	0.222	0.154	0.137	0.102	0.662	0.655	113	111
5	0.246	0.239	0.221	0.187	2.29	1.93	0.162	0.155	0.109	0.113	0.661	0.544	93	89
6	0.278	0.229	0.239	0.21	2.66	2.52	0.22	0.21	0.154	0.157	0.665	0.65	111	105
7	0.233	0.198	0.183	0.178	2.96	1.81	0.239	0.17	0.188	0.107	0.618	0.581	205	72
8	0.237	0.23	0.152	0.198	1.91	2.21	0.171	0.197	0.11	0.112	0.438	0.605	73	73
9	0.25	0.248	0.172	0.221	1.73	2.28	0.185	0.155	0.1	0.106	0.548	0.749	62	90
10	0.249	0.247	0.215	0.204	1.67	1.57	0.152	0.152	0.085	0.068	0.698	0.645	89	60
11	0.242	0.231	0.141	0.17	1.65	1.5	0.15	0.147	0.076	0.068	0.419	0.57	59	48
12	0.241	0.237	0.206	0.198	1.5	1.27	0.147	0.145	0.078	0.067	0.674	0.587	49	37
13	0.245	0.244	0.214	0.2	1.3	0.95	0.133	0.128	0.063	0.06	0.733	0.662	38	26
14	0.246	0.238	0.18	0.211	1.21	1.22	0.139	0.131	0.062	0.057	0.577	0.75	32	31
20	0.273	0.283	0.249	0.25	0.75	0.74	0.078	0.06	0.048	0.039	0.89	0.923	29	24
21	0.281	0.255	0.235	0.2	0.79	0.8	0.079	0.08	0.034	0.035	0.836	0.677	27	22
22	0.266	0.24	0.239	0.222	0.92	0.89	0.076	0.079	0.04	0.041	0.848	0.739	26	26
23	0.24	0.206	0.216	0.202	1.99	3	0.231	0.199	0.128	0.128	0.702	0.777	74	110
24	0.233	0.207	0.209	0.189	1.89	2.05	0.168	0.182	0.114	0.148	0.687	0.643	81	90
25	0.227	0.23	0.192	0.156	1.39	1.29	0.136	0.126	0.061	0.047	0.551	0.424	54	29
26	0.211	0.211	0.197	0.182	1.17	1.04	0.099	0.101	0.056	0.046	0.592	0.507	44	28
27	0.235	0.223	0.204	0.218	3.75	3.25	0.27	0.265	0.16	0.108	0.577	0.579	112	74
28	0.221	0.227	0.211	0.226	1.84	1.85	0.166	0.181	0.08	0.072	0.552	0.6	67	45
29	0.234	0.24	0.228	0.223	1.65	1.56	0.131	0.137	0.057	0.053	0.603	0.521	49	37
30	0.242	0.232	0.175	0.194	1.12	1.09	0.102	0.101	0.039	0.034	0.386	0.493	25	24
31	0.245	0.232	0.2	0.231	2.53	1.98	0.171	0.173	0.072	0.076	0.459	0.608	178	96
32	0.248	0.232	0.201	0.192	1.76	1.76	0.157	0.177	0.083	0.066	0.563	0.473	74	55
33	0.229	0.223	0.213	0.216	1.84	1.59	0.155	0.159	0.074	0.058	0.593	0.556	65	46

BEST September 23 & 24, 1992, Molenplaat Western Scheldt

sample number	current cm/s	flow Q m3/m2.h	chl flux mg/m2.h	feo flux mg/m2.h	nrf flux mmol/m2.h	din flux mmol/m2.h	nh4 flux mmol/m2.h	no2 flux mmol/m2.h	no3 flux mmol/m2.h	don flux mmol/m2.h	poc flux g/m2.h	pon flux g/m2.h	pop flux g/m2.h	pnf flux mmol/m2.h	po4 flux mmol/m2.h	dop flux mmol/m2.h	si flux mmol/m2.h	zs flux g/m2.h
1	2.369	22.32735	-1.78618	-0.26792	0.014459	-0.10270	-0.00255	-0.00340	-0.09675	0.117165	0.893094	-0.04465	-0.04167	-0.00019	-0.00604	0.005857	-0.02317	20.83886
2	1.652	15.56976	-1.14178	-0.14531	-0.05071	-0.04893	-0.00177	-0.00177	-0.04537	-0.00177	-1.45317	-0.09341	-0.07888	-0.00107	-0.00187	0.000803	-0.00978	-60.2031
3	4.931	46.47368	2.664491	1.239298	-0.26113	-0.03452	0.011065	-0.00132	-0.04426	-0.22661	12.64084	0.334610	0.464736	-0.00939	-0.00239	-0.00699	0.007745	873.7053
4	14.69	138.4503	0.553801	0.930918	-0.01450	0.005274	-0.00263	0	0.007911	-0.01977	14.39883	1.255282	0.646101	-0.00595	-0.01071	0.004763	0.004615	36.92008
5	9.26	87.27364	4.072770	0.526896	-0.00332	0.265145	0.009974	0.010805	0.244366	-0.26847	4.189135	0.081455	-0.04654	0.002627	0.012762	-0.01013	0.048623	46.54594
6	1.823	17.18141	-1.92431	0.203827	0.017999	-0.01276	0.000981	-0.00032	-0.01341	0.030762	0.320719	0.022908	-0.00687	0.003621	0.002143	0.001477	0.001227	13.74512
7	-4.055	38.21756	4.382280	0.474004	-0.17470	0.016378	0.001455	0.001091	0.013831	-0.19108	-5.86002	-0.35160	-0.41274	-0.00575	-0.00082	-0.00673	-0.00493	-677.724
8	-9.43	88.87586	5.214050	0.322956	-0.09649	0.310642	0.007617	0.010157	0.292867	-0.40713	3.555034	0.308102	0.023700	-0.00267	0.017584	-0.02025	0.070677	0
9	-12.85	121.1086	0.161478	0	0.031142	0.495968	0.012687	0.019608	0.463673	-0.46482	8.881303	-0.48443	0.096886	-0.00104	0.025523	-0.02656	0.115918	452.1390
10	-12.54	118.1869	2.836487	0.266659	-0.01350	-0.03827	0	-0.00225	-0.03601	0.024762	-1.57582	0	-0.26789	-0.00101	-0.00559	0.004574	-0.02982	-456.989
11	-10.61	99.99712	-2.53326	-0.15800	-0.11333	0.352370	0.015237	0.015237	0.321895	-0.46570	-1.99994	-0.03999	-0.10666	-0.00473	0.012472	-0.01720	0.071902	-146.662
12	-6.287	59.25371	1.422089	-0.13488	-0.04345	-0.14728	-0.00451	-0.00564	-0.13713	0.103835	-1.81711	-0.01580	-0.08690	-0.00101	-0.00203	0.001019	-0.02454	-94.8059
13	-3.578	33.72193	-1.66361	0	0.029867	-0.03789	0.000321	-0.00160	-0.03661	0.067765	-1.57765	-0.02248	-0.01348	-0.00014	0.001885	0.001885	-0.01140	-53.9550
14	-7.59	71.53423	-7.82107		-0.02384	0.166231	0.001362	0.004768	0.160100	-0.19007	0.095378	-0.07630	-0.04768	-0.00246	0.009537	-0.01199	0.058930	-9.53789
20	7.34	69.17803	-5.44200	-1.38356	-0.09421	-0.04216	0.000658	0	-0.04282	-0.05204	0.092237	0.166027	0.083013	-0.00297	-0.00029	-0.00267	-0.01087	46.11868
21	10.37	97.73517	2.085017	-1.30313	0.299721	0.363016	0.002792	0.011169	0.349054	-0.06329	-0.13031	-0.01303	-0.01303	0.010929	0.014712	-0.00378	0.073999	65.15678
22	7.38	69.55502	-0.27822	0.092740	0.185480	0.142422	0.009936	0.005299	0.127186	0.043057	0.278220	-0.02782	-0.00927	0.007778	0.005085	0.002692	0.036102	0
23	2.088	19.67898	0.104954	-0.10495	0.025301	-0.00862	0.005060	0.000374	-0.01405	0.033922	-2.65010	0.083963	0	0	0.001184	0.001692	-0.00702	-94.4591
24	0.076	0.716284	-0.02578	-0.03151	nd	0.000136	0.000020	0.000013	0.000102	nd	-0.01528	-0.00133	-0.00324	0.000080	0.000061	0.000018	0.000150	-0.85954
25	-1.633	15.39069	-0.98500	0	0.000586	-0.05159	-0.00146	-0.00219	-0.04793	0.052181	-0.20520	-0.02052	-0.02872	0.000198	-0.00238	0.002581	-0.00930	-51.3023
26	-7.48	70.49750	6.015787	0	nd	-0.15643	-0.00872	-0.00604	-0.14166	nd	-1.22195	0.018799	-0.09399	0	-0.00454	0.004548	-0.02853	-150.394
27	-18.25	172.0026	-27.0617	-0.91734	-0.13596	-0.00655	-0.00327	0	-0.00327	-0.12941	-11.4668	-0.11466	-1.19255	-0.00887	0.010357	-0.01923	0.001638	-871.479
28	-21.79	205.3663	5.476437	-0.27382	0.064543	0.303159	0.023470	0.009779	0.269910	-0.23861	0.273821	0.410732	-0.21905	0.005299	0.013249	-0.00794	0.046940	-602.408
29	-20.79	195.9415	0.783766	3.396320	-0.00933	-0.32656	-0.01119	-0.01492	-0.30044	0.317238	-2.35129	0.156753	-0.10450	0.005056	-0.00421	0.009270	-0.07651	-313.506
30	-15.22	143.4454	-6.12033	-2.29512	-0.18169	0.375690	0.008196	0.013661	0.353832	-0.55738	-0.57378	-0.01912	-0.09563	-0.00616	0.011722	-0.01789	0.073088	-19.1260
31	-9.57	90.19533	1.322864	0.093242	-0.11596	0.311818	0.009449	0.012026	0.290343	-0.42778	-6.61432	0.024052	0.048104	-0.00504	0.012026	-0.01706	0.063995	-986.135
32	-7.42	69.93201	-2.33106		-0.19181	-0.15984	-0.00532	-0.00532	-0.14918	-0.03196	0	0.186485	-0.15851	-0.00481	-0.00270	-0.00210	-0.02997	-177.161
33	-13.6	128.1772	-5.63980	-0.68361	-0.27100	-0.15991	-0.00732	-0.00610	-0.14648	-0.11108	-4.27257	0.068361	-0.27344	-0.00330	0.001653	-0.00496	-0.02258	-324.715
average cycle 1	-2.30107	68.44087	0.316943	0.232744	-0.05011	0.084973	0.003515	0.003238	0.078219	-0.13508	2.192468	0.062404	0.008718	-0.00208	0.003464	-0.00555	0.019583	-3.99889
s.e.	2.159039	10.63366	0.896772	0.112925	0.021846	0.050643	0.001663	0.001981	0.047344	0.053944	1.529485	0.103816	0.068362	0.000891	0.002679	0.002659	0.011617	92.49916
cycle 2	-6.32135	96.27231	-2.29250	-0.50991	-0.03031	0.041752	0.001590	0.001265	0.038896	-0.08322	-2.06124	0.065619	-0.14720	0.000073	0.003993	-0.00391	0.007936	-248.590
s.e.	2.787331	16.78164	2.066529	0.404606	0.039144	0.057354	0.002370	0.002127	0.053336	0.055182	0.870739	0.033720	0.081625	0.001476	0.001806	0.002262	0.011489	87.64772

BEST April 14 & 15, 1993, Molenplaat Western Scheldt

sample number	chla in ug/l	chla out ug/l	feoa in ug/l	feoa out ug/l	dn in mg/l	dn out mg/l	nh4 in mg/l	nh4 out mg/l	no2 in mg/l	no2 out mg/l	no3 in mg/l	no3 out mg/l	no2no3 in mg/l	no2no3 out mg/l
1	5	4.77	0.2	0.15	4.489	4.512	0.049	0.027	0.046	0.046	3.875	4.053	3.921	4.099
2	5.48	6.42	0.19	0.22	4.479	4.472	0.031	0.03	0.047	0.046	3.932	4.086	3.979	4.132
3	4.26	2.61	0.13	0.14	4.069	4.001	0.03	0.033	0.043	0.044	3.716	3.635	3.759	3.679
4	6.55	5.8	0.17	0.14	4.026	4.022	0.027	0.022	0.044	0.045	3.623	3.631	3.667	3.676
5	6.91	6.28	0.18	0.16	3.966	3.927	0.028	0.021	0.043	0.043	3.563	3.559	3.606	3.602
6	5.41	6.16	0.14	0.27	3.019	3.866	0.031	0.028	0.044	0.043	3.384	3.422	3.428	3.465
7	5.46	5.63	0.24	0.16	3.83	3.902	0.024	0.022	0.043	0.041	3.394	3.519	3.437	3.56
8	6.29	5.67	0.19	0.2	2.901	3.691	0.024	0.024	0.041	0.041	3.601	3.604	3.642	3.645
9	9.63	8.8	0.33	0.35	4.159	3.696	0.022	0.023	0.041	0.041	3.761	3.77	3.802	3.811
10	6.21	6.85	0.21	0.2	3.975	3.988	0.025	0.025	0.041	0.038	3.589	3.39	3.63	3.428
11	8.11	6.01	0.3	0.34	3.848	3.942	0.028	0.044	0.04	0.04	3.473	3.526	3.514	3.566
12	6.87	5.76	0.35	0.28	3.56	3.52	0.026	0.024	0.042	0.041	3.452	3.454	3.492	3.495
13	7.76	7.4	0.2	0.2	3.197	3.808	0.036	0.027	0.043	0.043	3.064	3.121	3.106	3.164
21	6.74	6.79	0.19	0.19	3.212	3.385	0.027	0.022	0.043	0.043	3.991	3.979	4.034	4.022
22	6.68	6.96	0.19	0.22	3.204	4.049	0.024	0.023	0.043	0.036	3.961	3.242	4.004	3.278
23	5.44	5.44	< 0.10	0.27			0.028	0.022	0.044	0.043	3.583	3.924	3.627	3.967
24	6.85	7.29	0.16	0.15	4.004		0.028	0.024	0.042	0.04	3.352	3.59	3.394	3.63
25	6.67	6.26	0.26	0.25	4.003		0.026	0.027	0.036	0.039	3.557	3.266	3.593	3.305
26	10.12	9.29	0.35	0.32	3.672		0.031	0.029	0.041	0.04	3.261	3.078	3.302	3.118
27	9.23	9.08	0.32	0.3	3.541		0.028	0.027	0.039	0.039	3.239	3.321	3.278	3.36
28	8.51	8.69	0.24	0.26	3.416		0.029	0.031	0.039	0.044	3.325	3.169	3.364	3.213
29	8.97	7.98	0.2	0.18	3.271		0.029	0.021	0.04	0.04	3.437	2.273	3.477	2.301
30	8.69	8.05	0.25	0.24	3.675		0.021	0.02	0.04	0.04	3.691	1.9	3.731	1.922
31	9.32	8.48	0.27	0.27	3.874		0.022	0.026	0.039	0.039	3.484	3.544	3.523	3.584
32	10.08	8.81	0.33	0.35	2.474		0.023	0.028	0.04	0.04	3.403	3.376	3.443	3.416
33	9.69	9.61	0.34	0.24										
34	9.38	10.19	0.19	0.25										

BEST April 14 & 15, 1993, Molenplaat Western Scheldt

sample number	dp in mg/l	dp out mg/l	po4 in mg/l	po4 out mg/l	poc in mg/l	poc out mg/l	pon in mg/l	pon out mg/l	pop in mg/l	pop out mg/l	si in mg/l	si out mg/l	seston in mg/l	seston out mg/l
1	0.276	0.177	0.249	0.16	0.98	0.82	0.126	0.108	0.042	0.042	2.529	2.498	28	17
2	0.175	0.167	0.157	0.152	1.09	1.45	0.143	0.21	0.052	0.039	2.548	2.474	34	37
3	0.157	0.16	0.145	0.143	0.68	0.65	0.09	0.083	0.032	0.032	2.279	2.216	20	16
4	0.16	0.154	0.145	0.141	1.16	0.96	0.152	0.142	0.046	0.042	2.232	2.217	28	24
5	0.184	0.181	0.167	0.164	1.22	1.44	0.184	0.208	0.052	0.053	2.2	2.168	36	38
6	0.143	0.152	0.141	0.138	1.11	1.39	0.152	0.186	0.049	0.058	2.13	2.075	28	47
7	0.153	0.151	0.14	0.139	1	1.14	0.134	0.171	0.044	0.043	2.095	2.123	28	35
8	0.128	0.145	0.137	0.138	1.16	1.38	0.195	0.181	0.051	0.053	2.167	2.149	32	34
9	0.156	0.149	0.142	0.143	1.86	2.11	0.299	0.293	0.08	0.099	2.264	2.274	52	94
10	0.148	0.154	0.138	0.135	1.36	1.24	0.188	0.174	0.062	0.056	2.148	2.13	42	38
11	0.155	0.161	0.139	0.144	1.48	1.5	0.198	0.191	0.064	0.064	2.103	2.076	43	41
12	0.143	0.152	0.139	0.14	1.58	1.5	0.223	0.2	0.073	0.079	2.072	2.063	46	46
13	0.175	0.136	0.168	0.137	1.3	1.31	0.208	0.174	0.059	0.055	2.06	2.062	31	38
21	0.151	0.146	0.154	0.154	1.28	1.16	0.162	0.14	0.053	0.055	2.483	2.474	46	41
22	0.141	0.161	0.152	0.142	1.37	1.27	0.182	0.153	0.051	0.044	2.462	2.172	43	38
23	0.15	0.152	0.152	0.147	1.3	1.09	0.168	0.17	0.052	0.049	2.271	2.443	36	33
24	0.167	0.157	0.151	0.137	1.28	1.39	0.328	0.249	0.056	0.057	2.199	2.203	33	37
25	0.17	0.148	0.133	0.132	1.39	1.41	0.186	0.178	0.063	0.064	2	2.072	34	36
26	0.157	0.143	0.144	0.137	2.04	1.99	0.28	0.282	0.104	0.095	2.031	1.997	59	52
27	0.148	0.14	0.138	0.135	1.73	2.04	0.3	0.295	0.104	0.103	1.957	1.961	48	56
28	0.14	0.145	0.136	0.132	1.94	1.59	0.262	0.239	0.073	0.071	1.95	2.021	46	45
29	0.139	0.124	0.139	0.11	1.62	1.41	0.233	0.193	0.062	0.059	2.033	1.61	35	36
30	0.15	0.147	0.144	0.075	1.55	1.72	0.205	0.22	0.065	0.074	2.212	1.52	38	52
31	0.147	0.151	0.139	0.137	1.66	1.95	0.242	0.24	0.09	0.077	2.046	2.104	59	95
32	0.12	0.148	0.139	0.138	2.16	2.43	0.276	0.305	0.105	0.119	2.026	2.05	73	115
33					1.96	2.08	0.273	0.328	0.103	0.099			80	88
34					1.94	1.93	0.259	0.256	0.091	0.087			78	78

BEST April 14 & 15, 1993, Molenplaat Western Scheldt

sample number	current cm/s	flow m3/m2.h	zsflux g/m2.h	pocflux g/m2.h	ponflux g/m2.h	no2flux mmol/m2.h	nh4flux mmol/m2.h	po4flux mmol/m2.h	sio4flux mmol/m2.h	no3flux mmol/m2.h	popflux g/m2.h	dn flux mmol/m2.h	dp flux mmol/m2.h	chlaflux mg/m2.h	feoaflux mg/m2.h
3	9.43	11.85011	47.40046	0.355503	0.082950	-0.84643	-2.53931	0.764523	26.66275	68.56138	0	57.55770	-1.14678	19.55269	-0.11850
4	11.25	14.1372	56.5488	2.82744	0.141372	-1.0098	5.049	1.824154	7.5735	-8.0784	0.056548	4.0392	2.736232	10.6029	0.424116
5	15.33	19.26429	-38.5285	-4.23814	-0.46234	0	9.632145	1.864286	22.01633	5.504083	-0.01926	53.66481	1.864286	12.13650	0.385285
6	13.76	17.29136	-328.535	-4.84158	-0.58790	1.235097	3.705292	1.673358	33.96518	-46.9337	-0.15562	-1046.12	-5.02007	-12.9685	-2.24787
7	12.08	15.18021	-106.261	-2.12522	-0.56166	2.168601	2.168601	0.489684	-15.1802	-135.537	0.015180	-78.0696	0.979368	-2.58063	1.214416
8	3.896	4.895869	-9.79173	-1.07709	0.068542	0	0	-0.15793	3.147344	-1.04911	-0.00979	-276.266	-2.68483	3.035439	-0.04895
22	2.155	2.708059	13.54029	0.270805	0.078533	1.354029	0.193432	0.873567	28.04775	139.0781	0.018956	-163.450	-1.74713	-0.75825	-0.08124
23	9.53	11.97577	35.92733	2.514913	-0.02395	0.855412	5.132476	1.931577	-73.5655	-291.695	0.035927	0	-0.77263	0	-3.23346
24	11.89	14.94144	-59.7657	-1.64355	1.180374	2.134492	4.268985	6.747751	-2.13449	-254.004	-0.01494	4273.254	4.819822	-6.57423	0.149414
25	15.72	19.75438	-39.5087	-0.39508	0.158035	-4.23308	-1.41102	0.637238	-50.7969	410.6089	-0.01975	5648.341	14.01923	8.099296	0.197543
26	16.09	20.21933	141.5353	1.010966	-0.04043	1.444238	2.888476	4.565656	24.55205	264.2956	0.181974	5303.243	9.131313	16.78205	0.606580
27	14.53	18.25897	-146.071	-5.66028	0.091294	0	1.304212	1.766997	-2.60842	-106.945	0.018258	4618.217	4.711994	2.738846	0.365179
28	11.25	14.1372	14.1372	4.94802	0.325155	-5.049	-2.0196	1.824154	-35.8479	157.5288	0.028274	3449.476	-2.28019	-2.54469	-0.28274
29	6.543	8.222195	-8.22219	1.726661	0.328887	7.047596	4.698397	7.691731	124.2138	683.6168	0.024666	1921.057	3.978481	8.139973	0.164443
30	2.527	3.175529	-44.4574	-0.53983	-0.04763	4.082823	0.226823	7.068113	78.48093	406.2409	-0.02857	833.5764	0.307309	2.032338	0.031755
31	2.024	2.543439	-91.5638	-0.73759	0.005086	-0.18167	-0.72669	0.164092	-5.26855	-10.9004	0.033064	703.8060	-0.32818	2.136489	0
32	2.231	2.803563	-117.749	-0.75696	-0.08130	0	-1.00127	0.090437	-2.40305	5.406873	-0.03924	495.4297	-2.53225	3.560526	-0.05607
average cycle 1	10.95766	13.76984	-63.1947	-1.51651	-0.21984	0.257910	3.002621	1.076345	13.03081	-19.5888	-0.01882	-214.200	-0.54530	4.963061	-0.06525
s.e.	1.495515	1.879324	53.30489	1.072398	0.130856	0.458419	1.572827	0.311864	6.725045	25.31369	0.026867	158.7905	1.103808	4.340661	0.436112
cycle 2	8.59	10.79453	-27.4726	0.067094	0.179458	0.677712	1.232200	3.032847	7.515429	127.5663	0.021690	2462.086	2.664342	3.055666	-0.19441
s.e.	1.644244	2.066223	23.02834	0.766766	0.103792	0.970376	0.747853	0.841602	16.18046	86.10769	0.017103	642.7467	1.517280	1.795153	0.297647

BEST June 30 & July 1, 1993, Molenplaat Western Scheldt
DGW tunnel (with cockles) concentrations

sample number	seston in mg/l	seston out mg/l	poc in mg/l	poc out mg/l	pon in mg/l	pon out mg/l	no2 in mg/l	no2 out mg/l	nh4 in mg/l	nh4 out mg/l	po4 in mg/l	po4 out mg/l	si in mg/l	si out mg/l
1	12	16	0.55	0.56	0.072	0.076	0.134	0.143	0.253	0.106	0.202	0.169	0.651	0.404
2	7	8	0.52	0.35	0.068	0.072	0.129	0.12	0.101	0.101	0.16	0.157	0.339	0.298
3	13	13	0.59	0.68	0.078	0.079	0.12	0.12	0.083	0.082	0.154	0.153	0.266	0.252
4	90	75	3.75	2.57	0.473	0.369	0.113	0.113	0.077	0.071	0.145	0.144	0.21	0.198
5	118	140	4.63	5.21	0.68	0.701	0.102	0.106	0.078	0.078	0.135	0.138	0.212	0.203
6	68	72	2.41	2.87	0.331	0.382	0.104	0.097	0.079	0.076	0.135	0.133	0.179	0.17
7	34	40	1.42	1.32	0.2	0.19	0.101	0.102	0.078	0.081	0.132	0.134	0.164	0.159
8	24	27	0.99	1.01	0.134	0.138	0.1	0.1	0.077	0.083	0.132	0.132	0.158	0.158
9	100	38	3.9	1.63	0.501	0.255	0.103	0.102	0.077	0.075	0.135	0.136	0.148	0.173
10 nd														
11 nd														
12 nd														
13 nd														
14 nd														
15	29	43	1.23	1.21	0.185	0.17	0.107	0.107	0.081	0.08	0.137	0.137	0.137	0.165
21 nd														
22	58	60	0.8	0.8	0.108	0.104	0.123	0.122	0.146	0.159	0.186	0.197	0.467	0.486
23	32	31	0.73	0.91	0.102	0.107	0.122	0.123	0.104	0.109	0.157	0.163	0.253	0.254
24	48	36	1.03	0.56	0.144	0.081	0.119	0.118	0.103	0.103	0.149	0.153	0.198	0.196
25	96	124	3.52	4.91	0.493	0.655	0.11	0.11	0.094	0.094	0.14	0.142	0.15	0.15
26	100	76	4.1	2.98	0.618	0.401	0.105	0.107	0.073	0.086	0.128	0.133	0.137	0.14
27	34	26	1.91	1.44	0.244	0.202	0.103	0.103	0.086	0.094	0.127	0.132	0.134	0.134
28	25	24	1.37	1.45	0.206	0.207	0.104	0.103	0.089	0.088	0.127	0.127	0.148	0.159
29	27	23	1.27	1.09	0.177	0.151	0.104	0.106	0.085	0.091	0.13	0.134	0.158	0.158
30	39	28	1.39	1.18	0.206	0.168	0.118	0.119	0.117	0.125	0.142	0.145	0.158	0.162
31	43	20	1.55	1.17	0.215	0.18	0.113	0.113	0.114	0.125	0.136	0.136	0.14	0.143
32	26	15	0.87	0.85	0.135	0.131	0.11	0.113	0.095	0.107	0.133	0.138	0.132	0.134
33	15	12	0.68	0.63	0.106	0.114	0.107	0.109	0.106	0.117	0.131	0.137	0.129	0.132
34	38	48	1.29	1.86	0.185	0.233	0.111	0.11	0.084	0.091	0.13	0.134	0.156	0.156
35	24	32	1.24	1.15	0.165	0.157	0.108	0.111	0.1	0.101	0.128	0.146	0.131	0.164

BEST June 30 & July 1, 1993, Molenplaat Western Scheldt
DGW tunnel (with cockles) concentrations

sample number	no3 in mg/l	no3 out mg/l	pop in mg/l	pop out mg/l	dn in mg/l	dn out mg/l	dp in mg/l	dp out mg/l	chla in ug/l	chla out ug/l	feoa in ug/l	feoa out ug/l
1	1.954	2.267	0.028	0.024	2.714	2.435	0.241	0.188	8.43	10.77	0.41	0.34
2	2.003	1.958	0.017	0.018	2.785	2.507	0.191	0.189	14.7	16.81	0.33	0.54
3	1.919	1.926	0.022	0.023	2.493	2.521	0.18	0.18	22.59	20.85	0.58	0.58
4	1.783	1.796	0.153	0.101	2.177	2.338	0.169	0.17	28.19	23.53	2.22	1.84
5	1.617	1.7	0.184	0.156	1.654	2.267	0.125	0.166	35.61	33.87	3.24	3.01
6	1.641	1.557	0.106	0.116	2.102	2.163	0.156	0.16	24.48	25.32	1.51	1.56
7	1.598	1.614	0.061	0.058					20.61	18.28	0.66	0.63
8	1.587	1.588	0.051	0.045					16.43	17.62	0.45	0.52
9	1.673	1.67							12.67	3	0.31	0.11
10 nd												
11 nd												
12 nd												
13 nd												
14 nd												
15	1.718	1.702							11.1	10.46	0.18	0.2
21 nd												
22	2.009	1.99							3.8	3.65	0.17	0.17
23	2.007	2							7.12	7.05	0.19	0.17
24	1.923	1.91							7.72	8.72	0.2	0.21
25	1.746	1.739							22.44	15.14	1.11	0.63
26	1.645	1.645							25.08	0.46	1.25	0.91
27	1.577	1.56							18.29	16.6	0.57	0.49
28	1.566	1.554							16.2	16.74	0.45	0.4
29	1.615	1.624							16.81	14.95	0.46	0.41
30	1.855	1.871							0.36	12.91	0.31	0.42
31	1.759	1.733							0.37	17.33	0.55	0.5
32	1.706	1.704							15.21	13.21	0.37	0.32
33	1.632	1.664							14.12	12.12	0.3	0.26
34	1.609	1.621							12	9.6	0.35	0.32
35	1.628	1.689							11.47	10.34	0.32	0.33

BEST June 30 & July 1, 1993, Molenplaat Western Scheldt
IBN tunnel (control) concentrations

sample number	seston in mg/l	seston out mg/l	poc in mg/l	poc out mg/l	pon in mg/l	pon out mg/l	no2 in mg/l	no2 out mg/l	nh4 in mg/l	nh4 out mg/l	po4 in mg/l	po4 out mg/l	si in mg/l	si out mg/l
1	16	21	0.74	0.67	0.097	0.082	0.133	0.136	0.106	0.104	0.171	0.172	0.36	0.337
2	9	9	0.43	0.44	0.059	0.059	0.113	0.124	0.1	0.112	0.153	0.162	0.222	0.253
3	10	20	0.64	0.76	0.088	0.102	0.114	0.115	0.098	0.105	0.145	0.15	0.18	0.193
4	106	83	4	3.23	0.519	0.941	0.111	0.111	0.094	0.087	0.145	0.146	0.156	0.159
5	129	205	5.21	6.41	0.649	0.869	0.106	0.106	0.086	0.086	0.138	0.14	0.141	0.146
6	88	90	3.68	2.91	0.541	0.394	0.105	0.104	0.09	0.091	0.137	0.137	0.131	0.132
7	43	89	1.75	2.27	0.246	0.318	0.086	0.102	0.08	0.089	0.115	0.135	0.102	0.121
8	23	32	1.41	1.47	0.206	0.209	0.099	0.1	0.094	0.087	0.133	0.134	0.125	0.129
9 nd														
10	84	73	2.89	2.25	0.392	0.277	0.111	0.115	0.088	0.081	0.144	0.148	0.147	0.157
11	75	74	3.33	2.66	0.472	0.425	0.112	0.109	0.075	0.076	0.142	0.141	0.11	0.116
12	63	66	2.42	2.17	0.363	0.3	0.107	0.11	0.077	0.076	0.138	0.141	0.121	0.129
13	42	59	1.64	1.58	0.237	0.233	0.109	0.112	0.087	0.087	0.145	0.146	0.136	0.135
14	29	51	1.21	1.25	0.171	0.181	0.115	0.114	0.087	0.08	0.149	0.144	0.143	0.132
15 nd														
21	132	118	3.72	2.62	0.42	0.315	0.141	0.141	0.105	0.098	0.18	0.179	0.31	0.306
22	41	53	0.99	1.19	0.136	0.151	0.126	0.125	0.177	0.204	0.21	0.219	0.507	0.564
23	34	31	0.77	0.77	0.119	0.104	0.127	0.127	0.109	0.105	0.17	0.17	0.234	0.243
24	44	38	0.91	0.92	0.124	0.124	0.124	0.125	0.102	0.103	0.162	0.162	0.188	0.187
25	124	136	4.69	4.91	0.584	0.683	0.097	0.114	0.094	0.094	0.144	0.14	0.121	0.156
26	150	126	3.45	3.06	0.464	0.389	0.111	0.108	0.086	0.085	0.131	0.132	0.139	0.137
27	38	41	1.68	1.44	0.258	0.223	0.104	0.103	0.09	0.087	0.132	0.129	0.137	0.145
28	28	19	1.29	1.19	0.166	0.165	0.103	0.096	0.092	0.089	0.13	0.125	0.136	0.132
29 nd														
30	50	10	1.62	0.81	0.224	0.122	0.114	0.118	0.111	0.096	0.142	0.148	0.156	0.171
31	31	34	1.32	1.5	0.195	0.203	0.113	0.111	0.107	0.097	0.142	0.141	0.132	0.134
32	20	16	1.13	0.96	0.192	0.132	0.106	0.111	0.096	0.116	0.139	0.142	0.122	0.129
33	14	16	0.88	0.75	0.13	0.11	0.106	0.109	0.1	0.1	0.145	0.14	0.131	0.124
34	24	44	1.2	1.67	0.163	0.224	0.111	0.112	0.1	0.095	0.141	0.141	0.13	0.138
35 nd														

BEST June 30 & July 1, 1993, Molenplaat Western Scheldt
IBN tunnel (control) concentrations

sample number	no3 in mg/l	no3 out mg/l	pop in mg/l	pop out mg/l	dn in mg/l	dn out mg/l	dp in mg/l	dp out mg/l	chla in ug/l	chla out ug/l	feoa in ug/l	feoa out ug/l
1	2.215	2.255	0.022	0.026	2.863	2.819	0.204	0.202	10.69	11.88	0.33	0.33
2	1.806	2.022	0.021	0.015	2.423	2.654	0.185	0.186	18.69	16.89	0.46	0.42
3	1.833	1.85	0.024	0.025	2.525	2.573	0.181	0.181	25.76	23.35	0.76	0.65
4	1.761	1.795	0.166	0.138	2.267	1.671	0.166	0.156	30.57	23.05	2.39	1.43
5	1.694	1.691	0.208	0.226	2.352	2.374	0.162	0.161	34.32	35.16	3.01	3.28
6	1.637	1.638	0.129	0.123	1.954	2.214	0.152	0.167	27.17	26.99	1.93	1.72
7	1.331	1.591	0.072	0.08					21.66	22.05	0.75	0.7
8	1.553	1.551	0.054	0.056					16.4	18.72	0.38	0.52
9 nd												
10	1.785	1.81							20.17	18.87	0.86	0.73
11	1.761	1.729							7.79	10.06	0.19	0.23
12	1.672	1.733							11.71	12.76	< 0.10	0.25
13	1.692	1.72							11.5	13.27	0.22	0.23
14	1.727	1.717							18.72	11.51	0.39	0.19
15 nd												
21	2.312	2.314							5.94	7.36	0.31	0.33
22	1.918	1.907							3.64	3.5	0.16	0.21
23	1.981	1.975							8.23	7.14	0.21	0.17
24	1.911	1.926							6.81	6.07	0.19	0.18
25	1.553	1.718							0.4	13.52	< 0.10	0.62
26	1.628	1.624							32.22	28.03	1.79	1.49
27	1.571	1.557							23.17	21.07	0.94	0.69
28	1.546	1.478							17.14	16.68	0.57	0.47
29 nd												
30	1.779	1.856							0.34	0.25	0.55	0.44
31	1.741	1.728							21.66	20.56	0.71	0.59
32	1.643	1.705							13.31	13.76	0.35	0.34
33	1.835	1.662							13.05	11.56	0.3	0.26
34	1.687	1.669							13.31	14.28	0.41	0.55
35 nd												

BEST June 30 & July 1, 1993, Molenplaat Western Scheldt

sample number	Q dgw	Q ibn	seston dgw	seston ibn	poc dgw	poc ibn	pon dgw	pon ibn	no2 dgw	no2 ibn	nh4 dgw	nh4 ibn	po4 dgw	po4 ibn
	m3/m2.h	m3/m2.h	g/m2.h	g/m2.h	g/m2.h	g/m2.h	g/m2.h	g/m2.h	mmol/m2.h	mmol/m2.h	mmol/m2.h	mmol/m2.h	mmol/m2.h	mmol/m2.h
1	2.588678	2.754	-10.3547	-13.77	-0.02588	0.19278	-0.01035	0.04131	-1.66415	-0.59014	27.18112	0.393428	2.755689	-0.08883
2	11.54852	7.344	-11.5485	0	1.963248	-0.07344	-0.04619	0	7.424049	-5.77028	0	-6.29485	1.117598	-2.13212
3	13.87330	14.688	0	-146.88	-1.24859	-1.76256	-0.01387	-0.20563	0	-1.04914	0.990950	-7.344	0.447525	-2.36903
4	16.28605	14.688	244.2908	337.824	19.21754	11.30976	1.693749	-6.19833	0	0	6.979737	7.344	0.525356	-0.47380
5	12.08887	11.934	-265.955	-906.984	-7.01154	-14.3208	-0.25386	-2.62548	-3.45396	0	0	0	-1.16989	-0.76993
6	12.16427	11.016	-48.6571	-22.032	-5.59556	8.48232	-0.62037	1.619352	6.082137	0.786857	2.606630	-0.78685	0.784791	0
7	11.22179	7.344	-67.3307	-337.824	1.122179	-3.81888	0.112217	-0.52876	-0.80155	-8.39314	-2.40467	-4.72114	-0.72398	-4.73806
8	8.809046	7.344	-26.4271	-66.096	-0.17618	-0.44064	-0.03523	-0.02203	0	-0.52457	-3.77530	3.672	0	-0.23690
22	9.512764	6.426	-19.0255	-77.112	-2.00635	-1.2852	0.038051	-0.09639	0.679483	0.459	-8.83328	-12.393	-3.37549	-1.86561
23	11.14639	9.18	11.14639	27.54	7.725320	0	-0.05573	0.1377	-0.79617	0	-3.98085	2.622857	-2.15736	0
24	16.43685	16.524	197.2422	99.144	-22.7424	-0.16524	1.035521	-1.72675	1.174060	-1.18028	0	-1.18028	-2.12088	2.250580
25	16.36145	17.442	-458.120	-209.304	15.86181	-3.83724	-2.65055	1.03275	-2.02319	-21.1795	-13.1507	0	-1.05557	-0.44419
26	14.16233	13.77	339.8959	330.48	5.604991	5.3703	3.073226			2.950714	-6.81457	0.983571	-2.28424	0.888387
27	11.92551	9.18	95.40410	-27.54	-0.93393	2.2032	0.500871	0.3213		0.655714	0.833870	1.967142	-1.92346	1.332580
28	11.67418	8.262	11.67418	73.44	0.692722	0.8262	-0.01167	0.008262	0.833870	4.131	-1.88496	1.770428	-0.31922	-0.35535
30	3.29868	1.836	36.28548	-16.524	1.529029	1.48716	0.125349	0.187272	-0.23562	-0.52457	-3.16152	1.967142	-0.35535	0.177677
31	4.023761	5.508	92.54650	18.36	0.089321	-0.99144	0.140831	-0.04406	0	0.786857	-3.82808	3.934285	0.177677	-0.44419
32	4.466098	4.59	49.12708	-12.852	0.207219	0.7803	0.017864	0.2754	-0.95702	-1.63928	-3.25631	-6.55714	-0.72033	1.036451
33	4.144398	6.426	12.43319		-2.75554	0.83538	-0.03315	0.12852	-0.59205	-1.377	-2.41714	0	-0.80214	0
34	4.834294	5.508	-48.3429	-110.16		-2.58876	-0.23204	-0.33598	0.345306	-0.39342		1.967142	-0.62377	
average cycle 1			-23.2478	-144.470	1.030649	-0.05393	0.103258	-0.98994	0.948314	-1.94255	3.947308	-0.96717	0.467135	-1.35108
s.e.			45.74495	119.2760	2.645729	2.570413	0.225314	0.794698	1.251600	1.088980	3.285127	1.660935	0.396904	0.543215
cycle 2			26.68883	14.1525	0.272680	0.219555	0.162379	-0.00933	-0.13094	-1.44257	-3.87446	-0.40982	-1.28187	0.214693
s.e.			51.38848	36.49081	2.464157	0.653010	0.349329	0.175218	0.242928	1.781541	1.113242	1.274833	0.294780	0.290882

BEST June 30 & July 1, 1993, Molenplaat Western Scheldt

sample number	si dgw mmol/m2.h	si ibn mmol/m2.h	no3 dgw mmol/m2.h	no3 ibn mmol/m2.h	pop dgw g/m2.h	pop ibn g/m2.h	dn dgw mmol/m2.h	dn ibn mmol/m2.h	dp dgw mmol/m2.h	dp ibn mmol/m2.h	chla dgw mg/m2.h	chla ibn mg/m2.h	feo dgw mg/m2.h	feo ibn mg/m2.h
1	22.83584	2.262214	-57.8754	-7.86857	0.010354	-0.01101	0.051588	0.008655	0.004425	0.000177	-6.05750	-3.27726	0.181207	0
2	16.91033	-8.13085	37.12024	-113.307	-0.01154	0.044064	0.229320	-0.12117	0.000745	-0.00023	-24.3673	13.2192	-2.42518	0.29376
3	6.936652	-6.81942	-6.93665	-17.8354	-0.01387	-0.01468	-0.02774	-0.05035	0	0	24.13955	35.39808	0	1.61568
4	6.979737	-1.57371	-15.1227	-35.6708	0.846874	0.411264	-0.18728	0.625289	-0.00052	0.004738	75.89301	110.4537	6.188700	14.10048
5	3.885710	-2.13107	-71.6697	2.557285	0.338488	-0.21481	-0.52932	-0.01875	-0.01598	0.000384	21.03464	-10.0245	2.780441	-3.22218
6	3.909945	-0.39342	72.98565	-0.78685	-0.12164	0.066096	-0.05300	-0.20458	-0.00156	-0.00533	-10.2179	1.98288	-0.60821	2.31336
7	2.003892	-4.98342	-12.8249	-136.388	0.033665	-0.05875					26.14678	-2.86416	0.336653	0.3672
8	0	-1.04914	-0.62921	1.049142	0.052854	-0.01468					-10.4827	-17.0380	-0.61663	-1.02816
22	-6.45509	-13.0815	12.91018	5.049							1.426914	0.89964	0	-0.3213
23	-0.39808	-2.95071	5.573198	3.934285							0.780247	10.0062	0.222927	0.3672
24	1.174060	0.590142	15.26279	-17.7042							-16.4368	12.22776	-0.16436	0.16524
25	0	-21.8025	8.180726	-205.566							119.4386	-228.839	7.853497	-10.8140
26	-1.51739	0.983571	0	3.934285							348.6766	57.6963	4.815193	4.131
27	0	-2.62285	14.48098	9.18							20.15411	19.278	0.954041	2.295
28	-4.58628	1.180285	10.00644	40.12971							-6.30406	3.80052	0.583709	0.8262
30	-0.47124	-0.98357	-3.76992	-10.098							-41.3984	0.16524	-0.36285	0.20196
31	-0.43111	-0.39342	7.472699	5.114571							-68.2429	6.0588	0.201188	0.66096
32	-0.31900	-1.1475	0.638014	-20.3271							8.932197	-2.0655	0.223304	0.0459
33	-0.44404	1.6065	-9.47291	79.407							8.288797	9.57474	0.165775	0.25704
34	0	-1.57371	-4.14368	7.081714							11.60230	-5.34276	0.145028	-0.77112
average														
cycle 1	7.932764	-2.85235	-6.86910	-38.5314	0.141896	0.025933					12.01104	15.98123	0.729620	1.805017
s.e.	2.607803	1.157540	15.43896	18.21046	0.103821	0.058659					10.57651	13.69207	0.870972	1.733771
cycle 2	-1.12068	-3.34960	4.761543	-8.32210							32.24312	-9.71167	1.219786	-0.24633
s.e.	0.601948	1.932232	2.224761	18.70605							30.13146	19.60763	0.690244	0.988250

BEST April 14 & 15, 1993, Molenplaat Western Scheldt

sample number	chla in ug/l	chla out ug/l	feoa in ug/l	feoa out ug/l	dn in mg/l	dn out mg/l	nh4 in mg/l	nh4 out mg/l	no2 in mg/l	no2 out mg/l	no3 in mg/l	no3 out mg/l	no2no3 in mg/l	no2no3 out mg/l
1	5	4.77	0.2	0.15	4.489	4.512	0.049	0.027	0.046	0.046	3.875	4.053	3.921	4.099
2	5.48	6.42	0.19	0.22	4.479	4.472	0.031	0.03	0.047	0.046	3.932	4.086	3.979	4.132
3	4.26	2.61	0.13	0.14	4.069	4.001	0.03	0.033	0.043	0.044	3.716	3.635	3.759	3.679
4	6.55	5.8	0.17	0.14	4.026	4.022	0.027	0.022	0.044	0.045	3.623	3.631	3.667	3.676
5	6.91	6.28	0.18	0.16	3.966	3.927	0.028	0.021	0.043	0.043	3.563	3.559	3.606	3.602
6	5.41	6.16	0.14	0.27	3.019	3.866	0.031	0.028	0.044	0.043	3.384	3.422	3.428	3.465
7	5.46	5.63	0.24	0.16	3.83	3.902	0.024	0.022	0.043	0.041	3.394	3.519	3.437	3.56
8	6.29	5.67	0.19	0.2	2.901	3.691	0.024	0.024	0.041	0.041	3.601	3.604	3.642	3.645
9	9.63	8.8	0.33	0.35	4.159	3.696	0.022	0.023	0.041	0.041	3.761	3.77	3.802	3.811
10	6.21	6.85	0.21	0.2	3.975	3.988	0.025	0.025	0.041	0.038	3.589	3.39	3.63	3.428
11	8.11	6.01	0.3	0.34	3.848	3.942	0.028	0.044	0.041	0.04	3.473	3.526	3.514	3.566
12	6.87	5.76	0.35	0.28	3.56	3.52	0.026	0.024	0.04	0.041	3.452	3.454	3.492	3.495
13	7.76	7.4	0.2	0.2	3.197	3.808	0.036	0.027	0.042	0.043	3.064	3.121	3.106	3.164
21	6.74	6.79	0.19	0.19	3.212	3.385	0.027	0.022	0.043	0.043	3.991	3.979	4.034	4.022
22	6.68	6.96	0.19	0.22	3.204	4.049	0.024	0.023	0.043	0.036	3.961	3.242	4.004	3.278
23	5.44	5.44	< 0.10	0.27			0.028	0.022	0.044	0.043	3.583	3.924	3.627	3.967
24	6.85	7.29	0.16	0.15	4.004		0.028	0.024	0.042	0.04	3.352	3.59	3.394	3.63
25	6.67	6.26	0.26	0.25	4.003		0.026	0.027	0.036	0.039	3.557	3.266	3.593	3.305
26	10.12	9.29	0.35	0.32	3.672		0.031	0.029	0.041	0.04	3.261	3.078	3.302	3.118
27	9.23	9.08	0.32	0.3	3.541		0.028	0.027	0.039	0.039	3.239	3.321	3.278	3.36
28	8.51	8.69	0.24	0.26	3.416		0.029	0.031	0.039	0.044	3.325	3.169	3.364	3.213
29	8.97	7.98	0.2	0.18	3.271		0.029	0.021	0.04	0.028	3.437	2.273	3.477	2.301
30	8.69	8.05	0.25	0.24	3.675		0.021	0.02	0.04	0.022	3.691	1.9	3.731	1.922
31	9.32	8.48	0.27	0.27	3.874		0.022	0.026	0.039	0.04	3.484	3.544	3.523	3.584
32	10.08	8.81	0.33	0.35	2.474		0.023	0.028	0.04	0.04	3.403	3.376	3.443	3.416
33	9.69	9.61	0.34	0.24										