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DYNAMICS OF COASTAL EUTROPHICATED SYSTEMS

1992-1996

FINAL SYNTHESIS REPORT

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INTRODUCTION

COASTAL EUTROPHICATION

The coastal zone, at the interface between land, ocean and atmosphere, plays a major role as recipient of large amounts of nutrients from human activities, including industrial effluents, agricultural runoff, and municipal sewage. Manifest effects of man-induced coastal eutrophication usually appear as qualitative changes of the structure and functioning of the pelagic and benthic food-web with resulting undesirable effects (e. g. invasions of undesirable or toxic phytoplankton species, extinction of key species on higher trophic levels, reduced yields of harvestable fish or invertebrate populations...). This alteration of the ecosystem structure and functioning is primarily driven by changes in nutrient ratios available to coastal phytoplankton with respect to silicon availability.- severely deficient compared to nitrogen and phosphorus - and to nitrogen forms (oxidized versus reduced nitrogen), resulting from the interplay of several factors as anthropogenic activities (land use modification, waste water purification treatments, hydraulic managements, farming practices,...), biogeochemical transformations occuring in the river systems (Billen *et al.*, 1991) and meteorological conditions. Contrasting with seasonal upwelling of deep-waters at the shelf break supplying well-balanced N:P:Si new sources of nutrients to coastal phytoplankton and stimulating the development of diatoms, and hence the linear food-web 'diatom-mesozooplankton-fish' (Claustre *et al.*, 1992), anthropogenic nutrient sources are stimulating the explosive development of opportunistic large non-siliceous phytoplankton, notable for their high resistance to direct grazing pressure and fast biodegradation. Man-induced coastal eutrophication is then accompanied by major changes in the flows of energy and material within the system, affecting the global significance of coastal seas in terms of natural resources (water quality and harvestable biological resources), carbon exportation and sequestration and of greenhouse gazes emitters (Lancelot, Granada Euroconference, avril 1995).
Since the biological structure of the coastal system may strongly affect the fate of the nutrients and hence the eutrophication process, the extent to which a certain nutrient load results in undesirable effects will not only be determined by nutrients, hydrodynamical and geomorphological conditions. Natural coastal systems, due to their high dynamical, flexible and versatile properties with respect to nutrient enrichment are able to handle inputs of nutrients of continental source below a certain limit, or critical load, without manifestation of undesirable effects. The implicated role of biotic processes means that the critical nutrient load may change with both nutrient composition (N, P, Si) and food web structure, and that different community structures thus may show different susceptibilities to destabilization when subjected to increased nutrient supply.

Management of coastal resources needs then to develop mechanistic biogeochemical models that describe ecosystem changes in response to nutrient changes caused by either human activities and/or natural conditions. Such models have to be based on the best available understanding of mechanisms controlling food-web structure and functioning.

COASTAL NORTH SEA EUTROPHICATION

The continental coastal zone of the North Sea is receiving the discharge of 7 major west-European rivers draining regions characterized by high population densities and industrial activity and intensive agricultural practices. It constitutes one example of man-induced eutrophicated coastal ecosystem displaying versatile and flexible food-chain structural and functioning properties in response to nutrient change driven either naturally or anthropogenically (Hansen *et al.*, 1992) with however visible resulting harmful environmental effects (Lancelot, 1995). Clearly, transient foam accumulations observed every spring at sea surface and on the beaches are resulting from food chain disruption due to the proliferation of one single non-siliceous species, the gelatinous colony-forming *Phaeocystis*, largely unpalatable for mesozooplankton and refractory to microbial degradation (Billen and Thingstad, 1994; Lancelot and Rousseau, 1994; Lancelot, 1995). The explosive development of *Phaeocystis* colonies succeeding to the early spring development of silicate-controlled diatoms is sustained by freshwater sources of nutrients, severely deficient in silicon compared to nitrogen and phosphorus with respect to coastal diatom silicon requirements and phytoplankton phosphorus needs (Billen *et al.*, 1991). To which extent this relative change in phytoplankton community structure is affecting the structure and functioning of the pelagic and benthic food-web and hence the overall yield of harvestable biological resources and the water quality is not known. Observational evidence of complex changing planktonic food-webs however exists (Hansen *et al.*, 1992; Rousseau *et al.*, in preparation) For instance, the dominance of mesozooplankton-unpalatable *Phaeocystis* colonies has been deviating the classical planktonic food web - diatom-mesozooplankton - towards a complex microbial food-web initiated by microprotozoa actively grazing on *Phaeocystis* cells originated from disrupted colonies (Weisse and Scheffell-Möser, 1990). Part of the *Phaeocystis*-derived production is however resuming the classical food-web through mesozooplankton feeding activity on protozoa (Hansen *et al.*, 1992). Little is known about efficiency of mesozooplankton grazing on protozoa. However the positive link observed between copepod abundance and *Phaeocystis* blooms (Franz *et al.*, 1992) strongly suggests that protozooplankton occupies a strategic position as a link between *Phaeocystis* and mesozooplankton.

SCIENTIFIC OBJECTIVES AND PROJECT METHODOLOGY

Even if no toxicity is attributable to *Phaeocystis* to date, its dramatic invasion is being seriously considered regarding the nuisances it causes to the coastal ecosystem and to recreative and aquaculture activities and the uncertainty surrounding its impact on higher trophic levels and related biological harvestable resources. Reduction of harmful *Phaeocystis* blooms in the continental coastal waters of the North Sea through the formulation of national and international regulations on sewage treatment facilities and farming practices aiming at the reduction of riverine nutrient delivery to the coastal sea is nowadays a main concern of public authorities. However the basic scientific knowledge required to properly assess the extent of nutrient reduction as well as its priority target (ammonium, nitrate, phosphorus) is up to now insufficient.

As a first step in this direction, the overall objective of this five-year project was to increase our understanding of mechanisms governing eutrophication in the coastal North Sea and develop an integrated land-coastal sea system approach that combines field (monitoring and process-level) and numerical experimentation to set up a scientific computer tool that could provide guidance for making selection among the control actions available for counteracting eutrophication in the Belgian coastal zone of the North Sea.

Specific objectives were:

- To conduct annually a high-resolution seasonal survey of key chemical and biological components at the station 330 - a reference station of the Belgian coastal waters, intensively sampled since 1988 - for (I) monitoring the impact of natural versus anthropogenic changes on coastal North Sea eutrophication and its related biogeochemical cycles; (ii) implementing a long-term data base in the coastal North Sea for monitoring changes in *Phaeocystis* colony blooms proliferation; and (iii) providing time-serie data for the calibration and validation of the mathematical model.
- To conduct process-level studies to improve our understanding of mechanisms determining the successful development of *Phaeocystis* colony blooms in the coastal North Sea and the associated changes in the microbial food-web.
- To synthesize process results in the existing mechanistic biogeochemical MIRO model describing C, N, P, Si cycling through key chemical and biological compartments of the *Phaeocystis*-dominated ecosystem of the North Sea;
- To couple the revised MIRO model to the RIVERSTRAHLER model (Garnier *et al.*, 1995) describing riverine nutrient delivery to the coastal sea and use the resulting computer tool for predicting *Phaeocystis* colony blooms changes in response to different scenarios of nutrient reduction in North Sea watershed.

RESULTS

1. TIME-SERIE OBSERVATIONS AT STATION 330

1.1 MONITORING DESCRIPTION

The reference station 330 (51°26.05N 02°48.50E; Fig.1) has been intensively monitored since 1988 in the scope of the previous national programme *Action de Recherche Concertée en Océanographie* (SPPS 1988-1992) and the E.C. projects *Dynamics of Phaeocystis blooms in nutrient enriched coastal zones* (Environment 1988-1992) and *Modelling Phaeocystis blooms, their causes and consequences* (STEP 1990-1993).

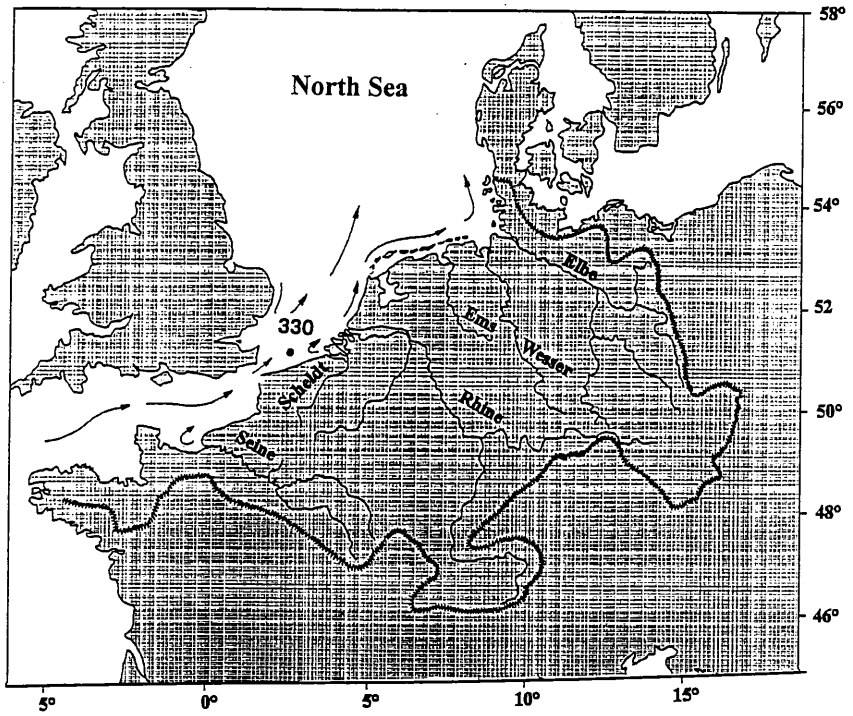


Figure 1 : map of the studied area

This data base was continued in the scope of the present project and of the EC project "*Biogeochemistry of Phaeocystis colonies and their derived aggregates*" (Environment 1994-1996). The monitoring work was extended in terms of time resolution and monitored parameters. More explicitly, the monitoring program included the weekly (vegetative season) to monthly (winter months) sampling of surface waters at station 330.

From 1993 to 1996, the following physico-chemical and biological variables were measured: salinity, temperature, suspended matter, major inorganic nutrients (NO_3+NO_2, NH_4, $Si(OH)_4$, PO_4) and chlorophyll a concentrations, phytoplankton (diatoms, *Phaeocystis* free-living cells and colonies, autotrophic nanoflagellates), bacteria, nano- and microzooplankton abundance and carbon biomass.

During 1993 and 1994, dissolved and particulate manganese and iron concentrations were also determined in order to assess the impact of *Phaeocystis* colony blooms on the biogeochemical cycle of Mn and Fe. It has been recently shown that physico-chemical conditions for Mn/Fe precipitation can be reached inside actively photosynthesizing colonies (e.g. Lancelot and Rousseau, 1994).

Available data since 1988 are gathered in the annex of the present report. This section includes also a short description of methods.

1.2. INTERANNUAL VARIATIONS OF DIATOMS-*PHAEOCYSTIS* COLONY BLOOMS IN THE BELGIAN COASTAL WATERS : NATURAL VERSUS HUMAN-INDUCED FORCING

Massive blooms of *Phaeocystis* colonies succeeding to a moderate early spring development of silicate-controlled diatoms is a recurrent phenomenon in the eutrophicated coastal waters of the North sea (Fig.2). The further analysis of mean nutrient and phytoplankton data gained since 1988 in relation with information on nutrient riverine sources (Table 1), gives strong evidence that the observed explosive development of *Phaeocystis* colonies has been stimulated by changes in the nutrient coastal environment driven by riverine nutrient loads. Freshwater sources of nutrients, indeed severely deficient in silicon compared to nitrogen and phosphorus (Table 1), have been shown to strongly modify, quantitatively but also qualitatively, the nutrient environment of the coastal phytoplankton with a large nitrate excess over silicate and phosphorus with respect to coastal diatom silicon requirements (Brzezinsky, 1985) and phytoplankton phosphorus needs (Redfield, 1963).

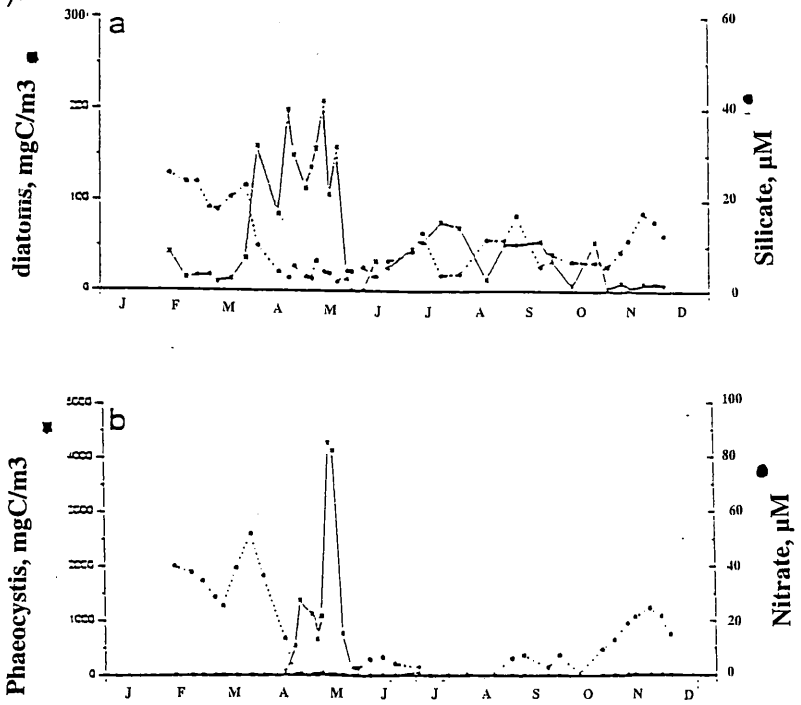


Figure 2: Typical spring phytoplankton succession and nutrients cycle in the Belgian coastal waters

TABLE 1. Nutrient discharge and winter concentration in the Belgian coastal waters

River inputs :	
nitrogen : 10^3 T y^{-1} (% nitrate)	58 (44)
phosphorus :10^3 T y^{-1}(% phosphate)	7.3 (45)
silicate : 10^3 T y^{-1}	27
molar N:P - N:Si - P:Si	29 - 3.4 - 0.11
Average winter concentrations	
nitrate : µM	35
phosphate : µM	1.2
silicate : µM	12
molar N:P - N:Si - P:Si	30 - 3 - 0.11
Coastal phytoplankton	
molar N:P - N:Si - P:Si	16 - 1.2 - 0.07

Supporting this, high-resolution time-series of nitrate and phytoplankton data collected in 1993, 1994 and 1995 when combined to existing data recorded in the whole Southern Bight of the North Sea show a strong positive correlation between the magnitude of *Phaeocystis* colony blooms in the continental coastal waters of the North Sea and the stock of nitrate left over after the early spring diatom community decline (Fig.3) (see also in **Rousseau *et al.*, submitted; manuscript #1**);

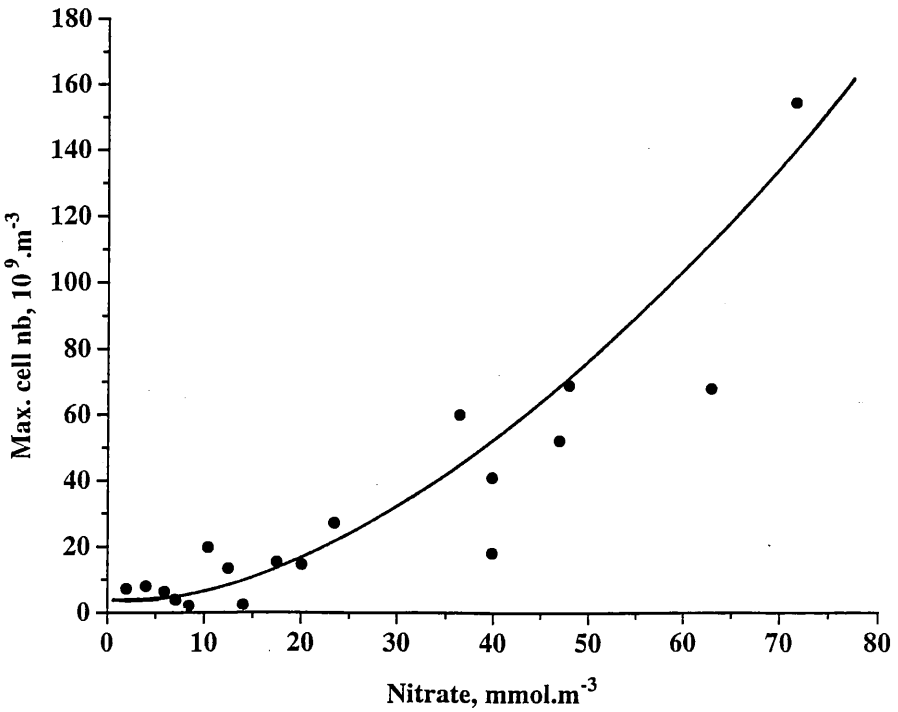


Figure 3 Relationship between *Phaeocystis* colony bloom magnitude and nitrate concentration at *Phaeocystis* onset. Data set: 1988-1995

A further comprehensive analysis of inorganic nutrients and phytoplankton data collected at station 330 in spring 1993, 1994 and 1995 (Fig.4) reveals that the observed large interannual fluctuations of nitrate concentrations left over at diatom decline are resulting from large fluctuations in the magnitude of the spring diatom bloom suggesting that factors controlling silicate and nitrate availability in spring are those determining the amplitude of *Phaeocystis* colony blooms.

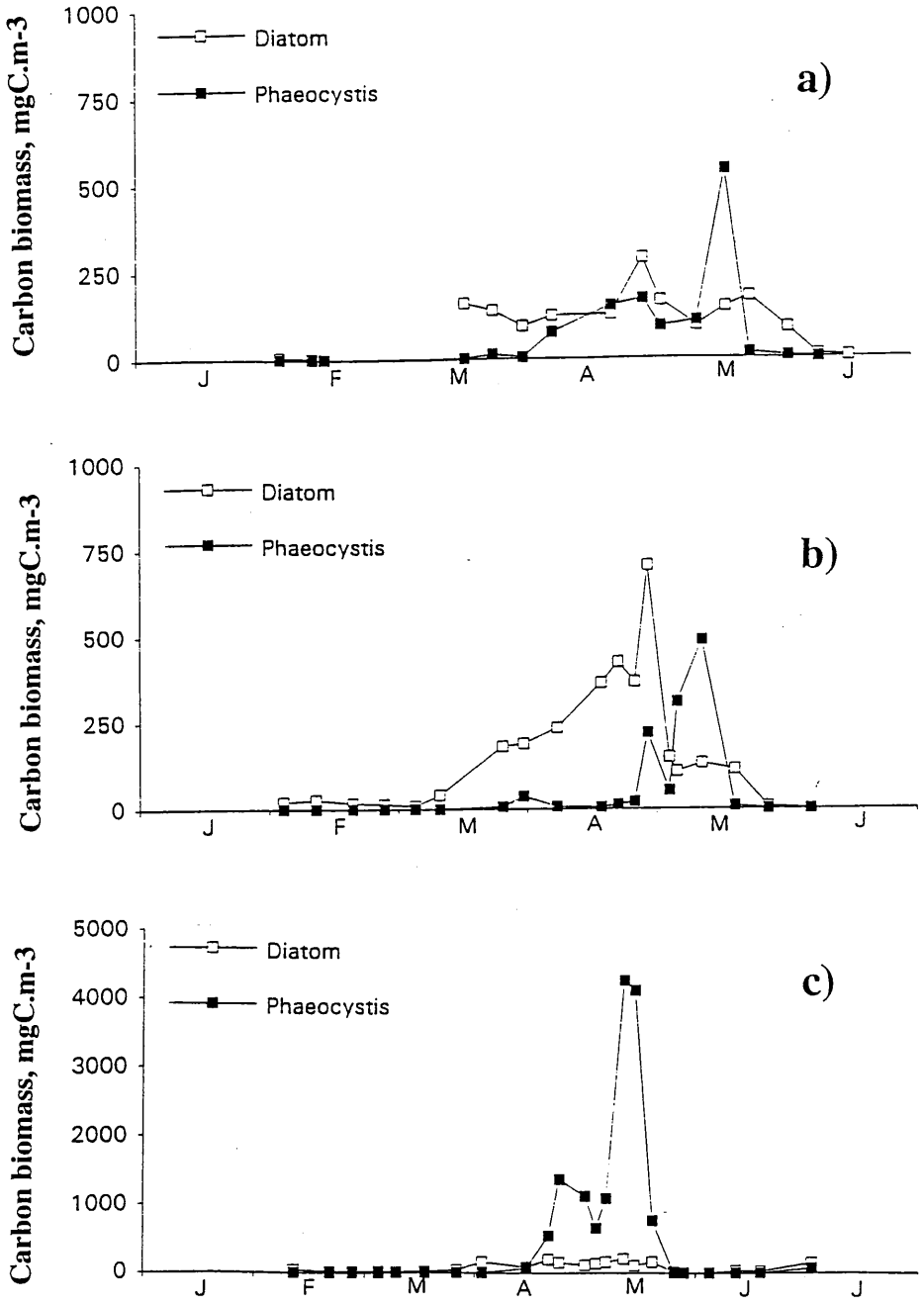
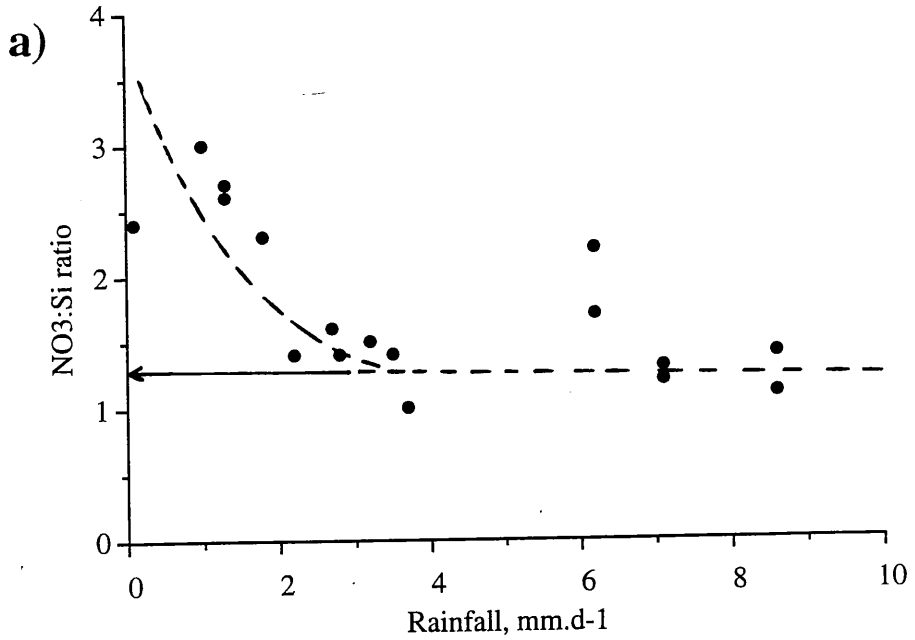


Figure 4 Interannual variations of diatom-*Phaeocystis* colony blooms in 1995(a), 1994 (b), 1993 (c) at station 330 (Belgian coastal waters)

Comparison of time-series data recorded in two contrasting years - 1993 (Fig.4c) and 1994 (Fig.4b) - suggests that the unusual spectacular diatom event of 1994 (Fig.4b) could be attributed to the exceptional meteorological rainy conditions having prevailed on the NW-Europe watershed during late winter-early spring (from December 1993 to April 1994). Contrasting, 1993 was characterized by a cold and dry winter-spring period and the magnitude of *Phaeocystis* colonies reached was the maximum ever recorded for station 330.

The impact of winter rainfall on the nitrate and silicate availability in the Belgian coastal waters and subsequently on the magnitude and extent of diatoms and *Phaeocystis* colony blooms is analyzed *in extenso* in **Rousseau *et al.* (manuscript #1)**. Main conclusions are illustrated by the empirical relationships linking the variations of respectively the winter NO_3:Si ratio (Fig.5a) and the ratio between diatom and *Phaeocystis* colony carbon biomass integrated over the whole spring period (Fig.5b) with winter rainfall conditions on the Scheldt watershed. Interestingly enough the winter NO_3:Si ratio is negatively correlated to rainfall conditions, reaching values close to the diatom NO_3:Si at high rainfall (Fig. 5a). The decrease of the NO_3:Si ratio at high rainfall can be explained by the increase of the relative contribution of diffuse (soil leaching) as compared to point (industrial and urban waste water) sources of nutrients. Contrary to point sources releasing anthropogenic N and P, high rainfall increases the contribution of diffuse sources by increasing Si leaching from rock minerals and NO_3 used as fertilizers.

Summarizing, persistent low winter rainfall are disadvantaging diatoms, due to reduced Si availability but are sustaining important *Phaeocystis* colonies development through the low consumption of NO_3 by the silicate-controlled diatoms. Reversely, persistent rainfall higher than 200 mm seems to be necessary to allow diatoms to dominate the spring phytoplankton bloom in the Belgian coastal waters (Fig.5b) under the present-day conditions of anthropogenic pressure.



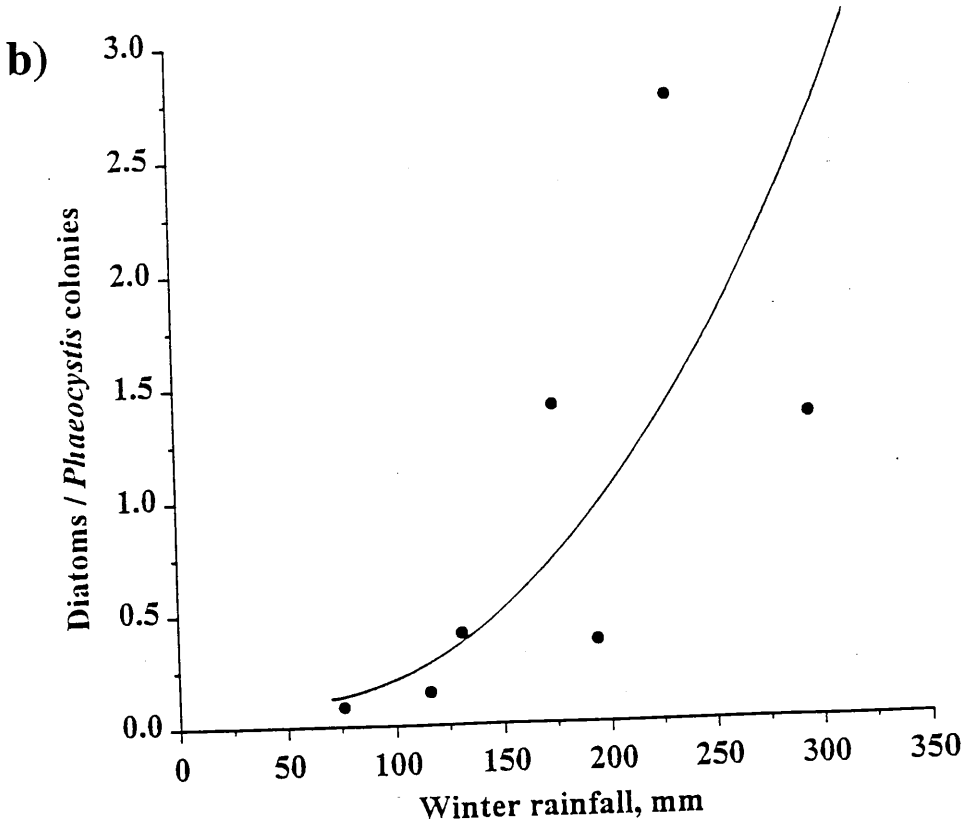


Figure 5 Relationship between winter NO_3:Si ratio (a), spring diatom:*Phaeocystis* colony bloom ratio (b) and winter rainfall

1.3. INTERANNUAL VARIATIONS OF DIATOM SPRING SUCCESSIONS

Natural and human-induced variability in the coastal nutrient environment, although strongly modifying the relative abundance of spring diatoms and *Phaeocystis* colonies (Fig.5), has no impact on either the temporal diatom-*Phaeocystis* colony succession or the intrinsic diatom succession in the Belgian coastal waters. The same seasonal species succession is repeating every year with the onset staggering however between mid-February and mid-March. Basically three diatom communities are succeeding. The late winter-early-spring diatom community is composed of small, neritic species including *Thalassiosira nordenskoldii*, *T. rotula*, *Asterionella glacialis*, *Thalassionema nitzschoïdes*, *Plagiogramma brockmanii*, and *Skeletonema costatum*. The growth of this diatom community, typical of the Southern Bight of the North Sea, is controlled by the winter concentration of silicate (**Rousseau *et al.* submitted; manuscript #1**). *Phaeocystis* colonies appear as the early spring diatom community declines. The later diatom community composed of *Chaetoceros* spp. and *Schroederella* sp., both of which require relatively low levels of silicate, appear at the same time. As the *Phaeocystis* bloom develops, additional diatoms, *Cerataulina* sp. and *Rhizosolenia* spp., mainly *R. delicatula,* become abundant as well. The fluctuations in this community of larger diatoms and *Phaeocystis* colonies (Fig.2; Fig.4) appear to result from the competition for nitrate, suggesting that both occupy the same ecological niche.

1.4. INTERANNUAL VARIATIONS OF MICROHETEROTROPH SPRING SUCCESSIONS

Spring phytoplankton developments at station 330 are recurrently accompanied by the development of various heterotrophic microorganisms : bacteria (free-living and attached to phytoplankton-derived aggregates), nanoprotozooplankton, microprotozooplankton and the giant dinoflagellate *Noctiluca* (Fig.6). Together with autotrophic nanoflagellates, these different microorganisms are composing the so-called *microbial food-web* and display complex trophic interactions: nanoprotozooplankton is feeding on bacteria, microprotozooplankton are ingesting bacteria and nanoflagellates; *Noctiluca* is an opportunistic omnivorous feeder on all kind of living and dead particles.

Mechanisms regulating these trophic interactions and the related efficiency of the microbial food-web were appraised throughout the comparison of time-serie data collected at station 330 along the two contrasting spring phytoplankton successions of 1993 and 1994 (Fig.6). Such comparison provides information on the impact of a change in phytoplankton species dominance on the structure and functioning of the planktonic food-web. This analysis shows that major differences were to be observed in microzooplankton successions. Details are as follows:

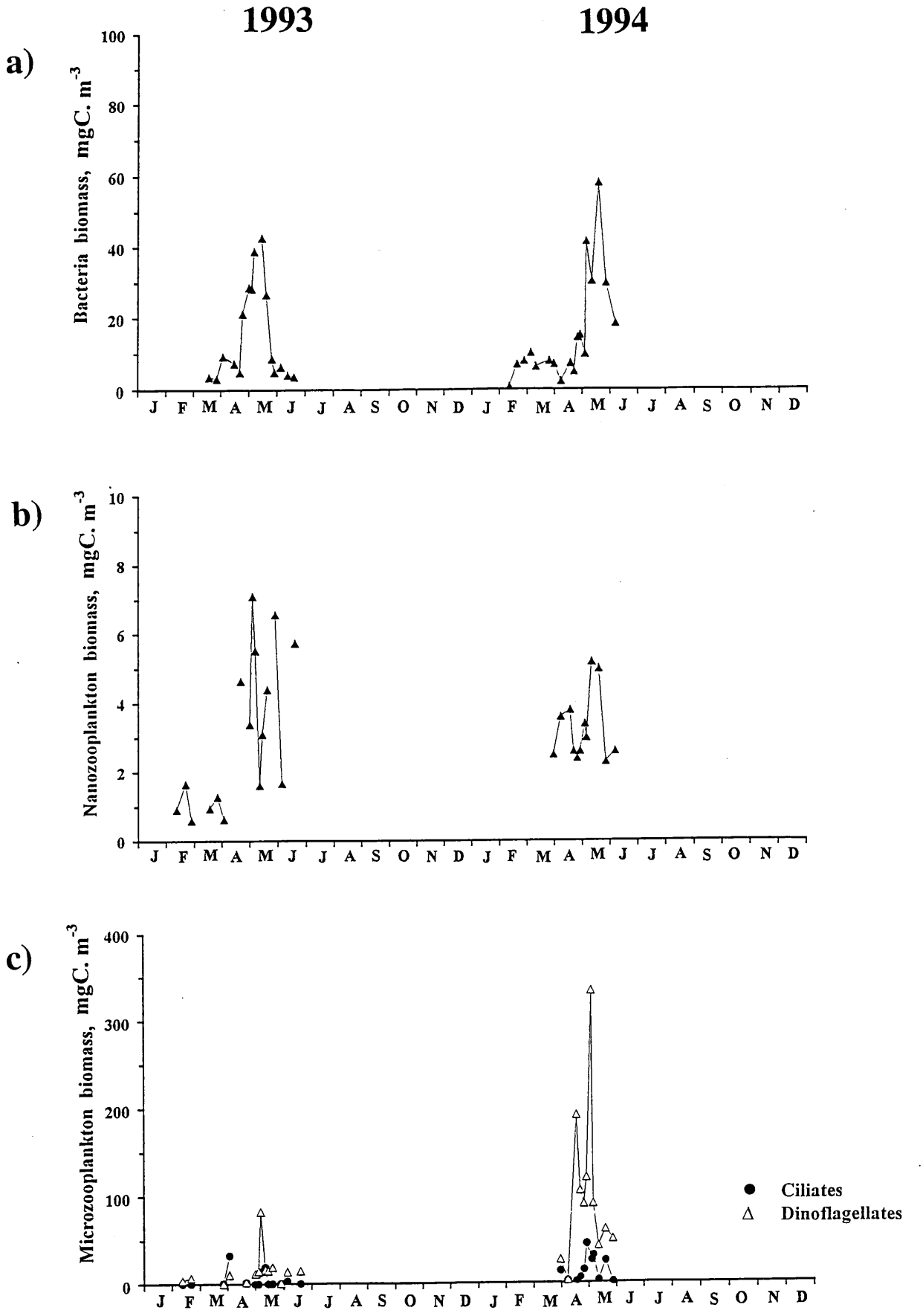


Figure 6 Spring succession of bacteria (a), nanoprotozooplankton (b) and microzooplankton (c) at station 330 in 1993 and 1994

The biomass reached by free-living bacteria was similar in 1993 and 1994 (respectively 40 and 60 mgC.m^{-3}) and correlated to the diatom and *Phaeocystis* spring developments with a delay of 8 to 10 days. At its maximum, bacterial biomass was composed at 58 % of attached bacteria to *Phaeocystis*-derived aggregates (Fig.7). These attached bacteria distinguish from free-living bacteria by their important cellular biomass (Fig.7; **Becquevort *et al.*, in press; manuscript #2**). Budget calculation estimated to 55% the contribution of *Phaeocystis*-attached bacteria to the mineralisation of *Phaeocystis* colony production (Fig.8) demonstrating the importance of *Phaeocystis* colonisation by bacteria at the stationary and senescent phase of the bloom, an often observed phenomenon but never quantified.

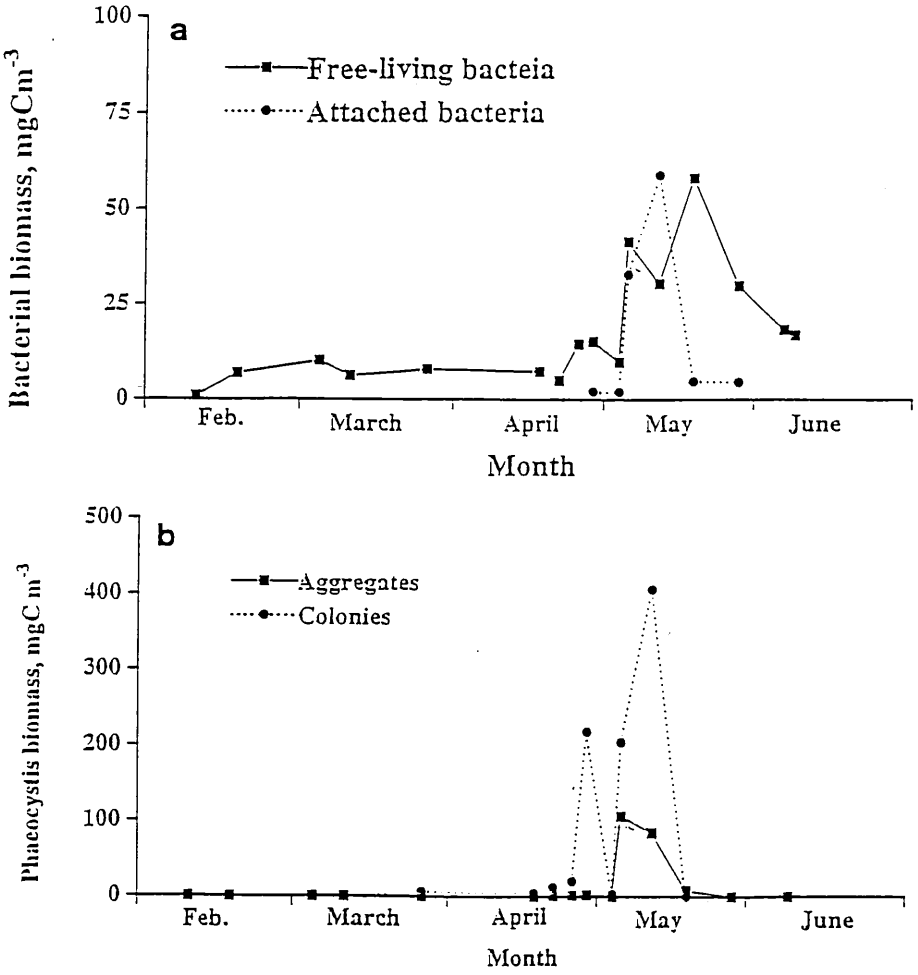


Figure 7 Free-living and particle attached bacteria (a) in relationship with potential attachment substrates - *Phaeocystis* colonies and their derived aggregates (b). Spring 1994, Station 330

During both years, nanoprotozooplankton biomass was kept at a low level (5 $mgC.m^{-3}$; Fig.6), along the whole spring period suggesting that their growth is actively controlled by microprotozooplankton grazing pressure (Fig.6).

Contrary to bacteria and nanoprotozooplankton, microprotozooplankton successions, composed in majority of dinoflagellates and few ciliates, were apparently high sensitive to the changes in diatom-*Phaeocystis* colony blooms observed in 1993 and 1994 (Fig.4). An unusual tremendous development of heterotrophic dinoflagellates was indeed observed in 1994 at diatom decline (Fig.6c) possibly in response to phytoplankton dominance change (Fig.4b). Dinoflagellates are indeed known to actively ingest diatoms. The early presence of dinoflagellates at the time of *Phaeocystis* colony inception could have in turn repress the development of *Phaeocystis* colonies by grazing efficiently on free-living cells, so preventing them to initiate colony formation. The *Phaeocystis* bloom reduction observed in 1994 could then be partly explained by a top-down control through the unusual development of dinoflagellates observed in 1994. These microorganisms have indeed been shown (Hansen *et al.*, 1993) to indirectly control *Phaeocystis* flowering by grazing on the free-living cell stage initiating new colonies. Fig.8 gives a diagrammatic representation of microbial food-web changes in response to changes in spring diatom-*Phaeocystis* colonies dominance. The important question on how this change is affecting the structure and overall functioning of the pelagic food chain is still to be investigated.

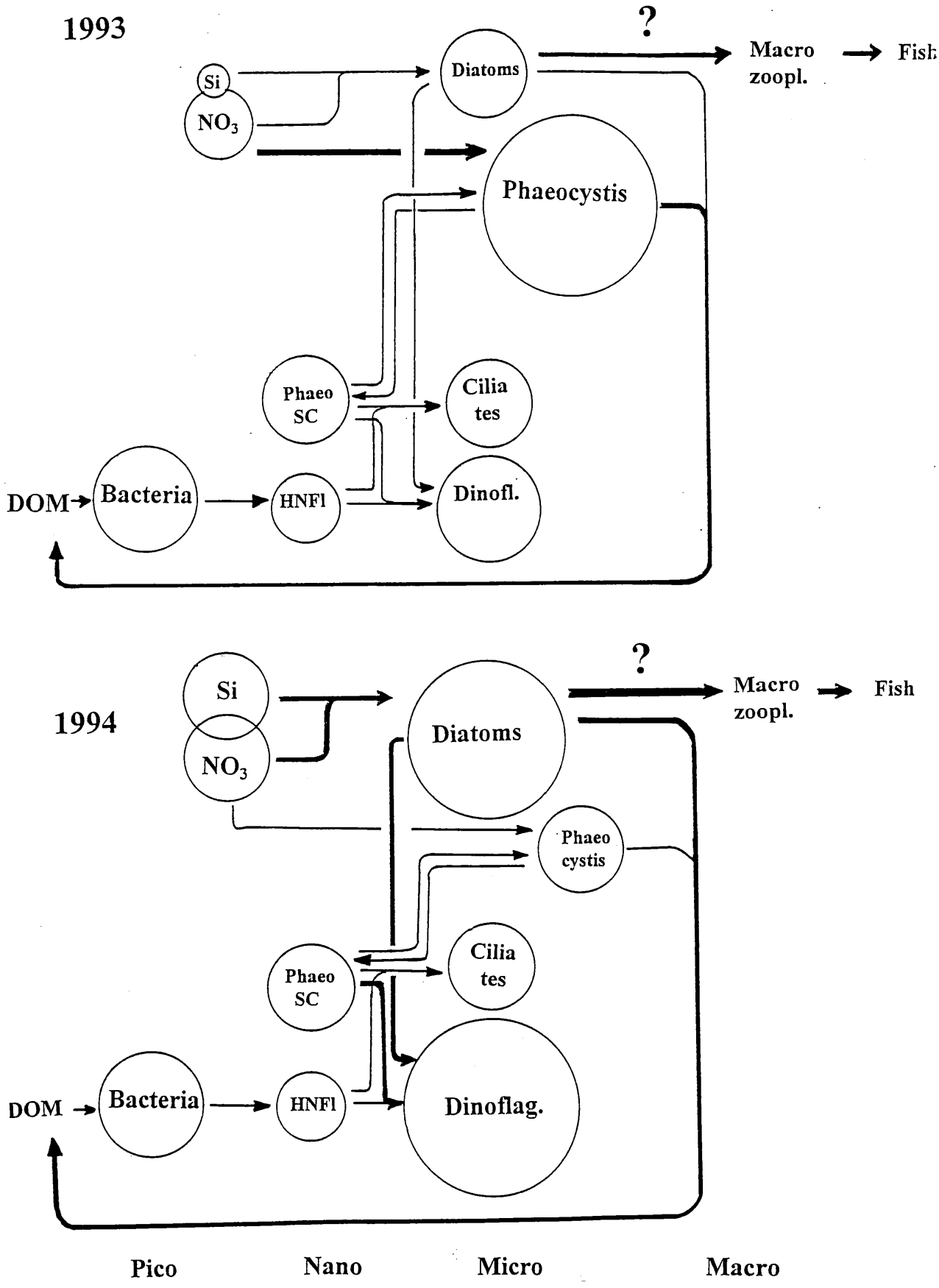


Figure 8 Alternated pattern of the microbial food-web structure in 1993 and 1994

Recurrent blooms of *Noctiluca* are developing massively in June, at the end of the spring succession of auto- and heterotrophic microorganisms reaching about 100 mgC m^{-3} . The maximum biomasses reached in early June coincided with a huge accumulation of NH_4 and PO_4 concentrations, evidencing the significant role played by this dinoflagellate in nutrient regeneration (Fig. 9).

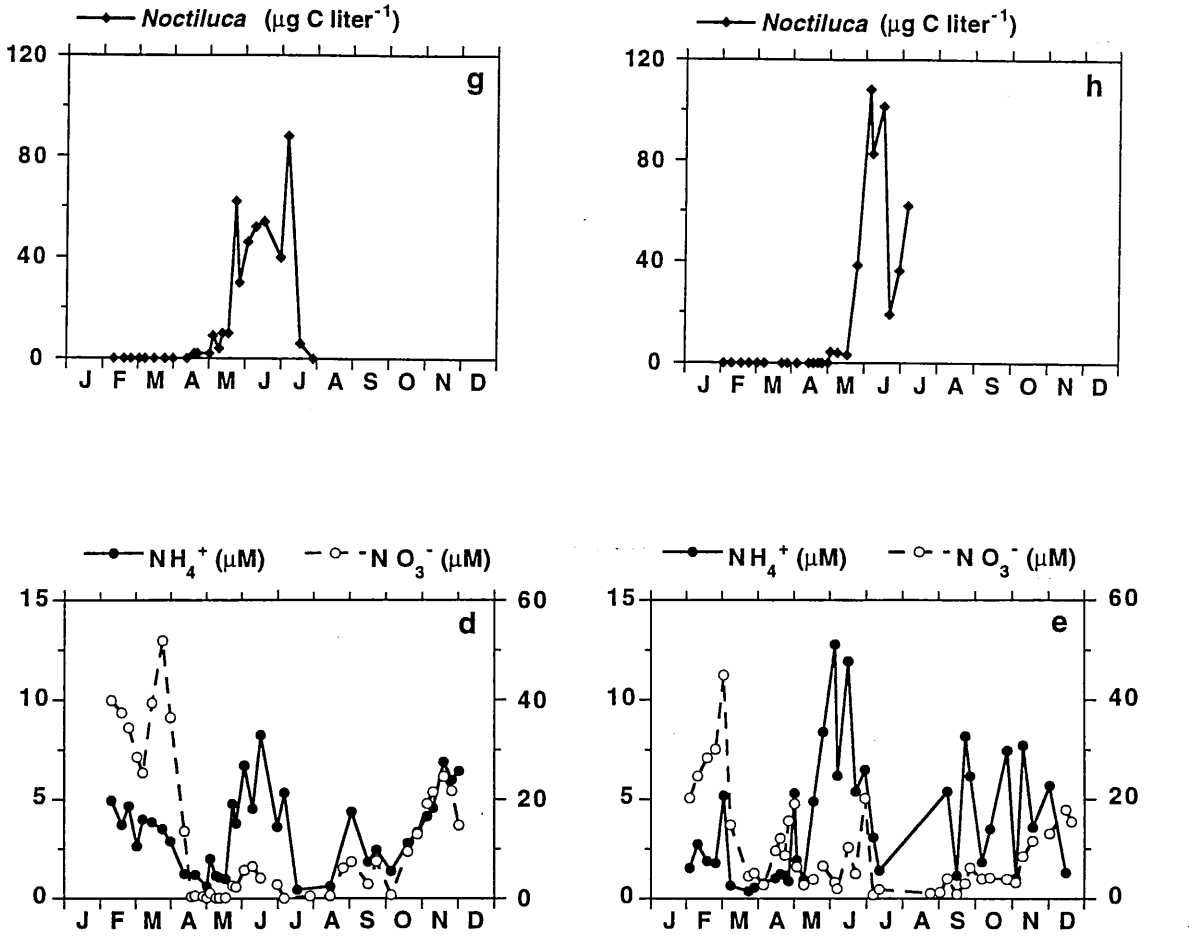


Figure 9 Seasonal evolution of *Noctiluca* and ammonium concentrations at station 330 in 1993 and 1994.

1.5 Mn and Fe cycling in the Belgian coastal waters

Laboratory work on cultures of *Phaeocystis* colonies gives evidence that high pH and O_2 concentrations reached within the mucilaginous matrix of highly-photosynthesizing *Phaeocystis* colonies give conditions for precipitation of ferromanganese oxy-hydroxides within the colony (Lubbers *et al.*, 1990; section 2. , this report). When important, this biologically-driven chemical reaction would greatly affect the geochemical cycle of these trace elements.

The physico-chemical and biological processes controlling Fe/Mn precipitation/solubility were therefore investigated in the Belgian coastal waters in 1993 and 1994. Great difference was expected due to the occurrence of contrasting diatom-*Phaeocystis* colonies abundance. These data were complemented in 1994 by identical time-serie measurements at the Marsdiep station (Dutch coastal waters) under higher influence of continental inputs of nutrients and trace metals.

In both areas, the seasonal variations of dissolved Fe and Mn were consistent with the wax and wane of phytoplankton spring blooms (Fig.10; **Schoemann *et al.*, submitted; manuscript #3**) although the role of *Phaeocystis* colonies as precipitating agent of ferromanganese oxy-hydroxides could not be evidenced. Rather the most important feature was the transient accumulation of dissolved Mn/Fe after spring bloom termination and coinciding with *Noctiluca* maximal development. Combining these observations allows to savely conclude that the biogeochemical cycle of Fe and Mn in the eutrophicated shallow coastal waters of the North Sea is driven by the magnitude of phytoplankton-derived material reaching the sediment and by the importance of the heterotrophic activity that install in the water column after the spring bloom. In this eutrophicated area, the biogeochemical role of *Noctiluca* in installing redox conditions to maintain trace metals diffusing from the sediment under their dissolved form is exemplar. Due to their voracious feeding behavior, this organism litteraly cleans the water column of all living and dead particles installing heterotrophic conditions in the water column. This event is however highly transient, *Noctiluca* disappearing due to food shortage. This analysis is described *in extenso* in **Schoemann *et al.*, submitted (Manuscript #3)**.

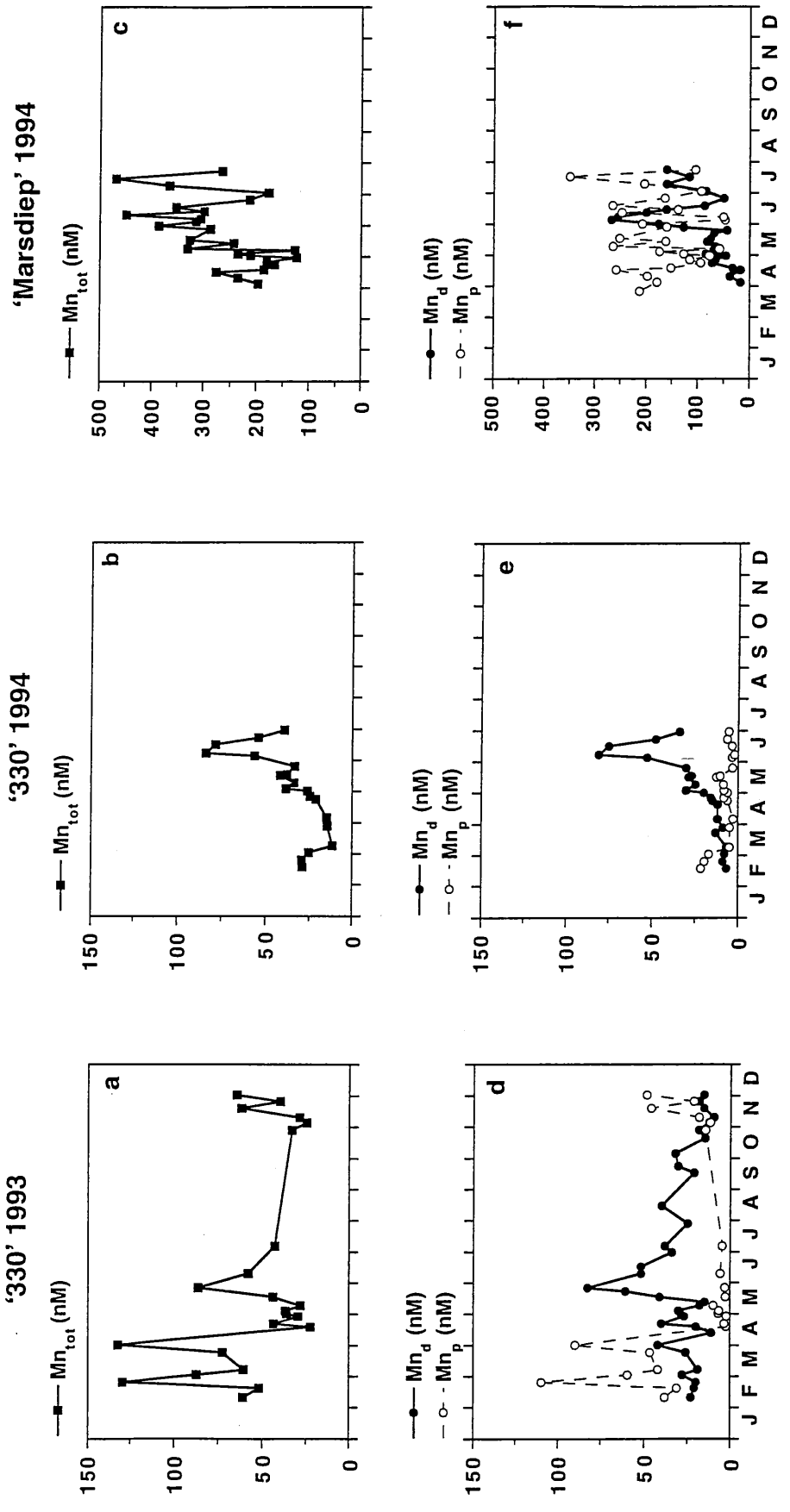


Figure 10 Seasonal evolution of Mn in the Belgian (1993 & 1994) and Dutch (1994) coastal waters

2. PROCESS-LEVEL STUDIES

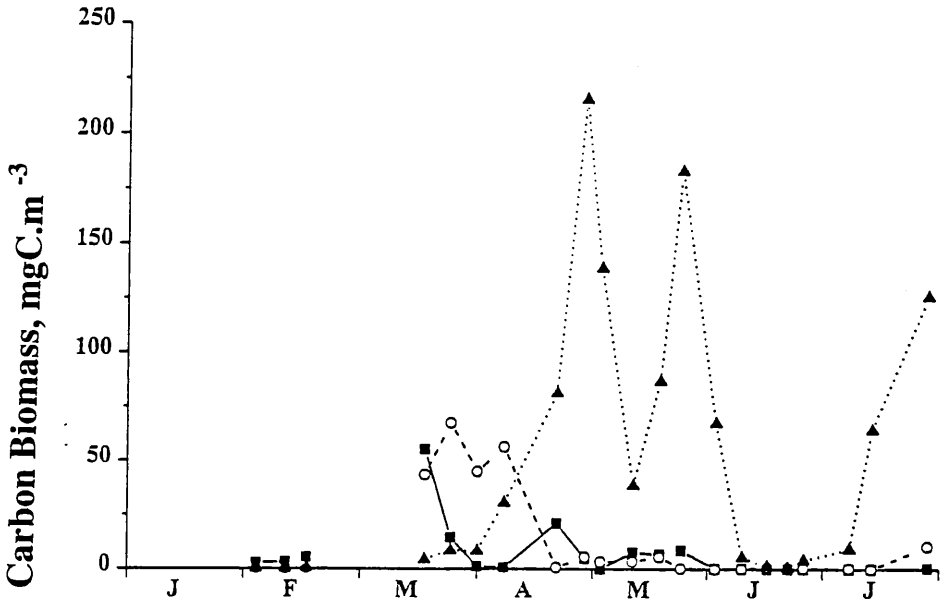
2.1. MECHANISMS REGULATING SPRING PHYTOPLANKTON SUCCESSIONS

2.1.1 Diatom-*Phaeocystis* colony successions

Diatom dynamics was investigated in spring 1995 in the Belgian coastal waters based on the measurement of the silica metabolism. Methods were developed for estimating the silica content of diatom communities succeeding during the spring bloom as well as their silicate assimilation rate (N. Daoud, 1995). The new radio-tracer ^{32}Si method of Tréguer *et al.* (1993) was applied in combination with ^{14}C-protein synthesis measurement as an index of phytoplankton growth (Lancelot *et al.*, 1986). Important mechanisms regulating the intrinsic diatom and diatoms - *Phaeocystis* colonies successions in the coastal North Sea were evidenced .

Silicate concentration and the intrinsic diatom succession:

The frustules of the three diatom communities, currently succeeding in spring (section 1.3.; this report), were shown to be characterized by different silicate content which positively relates to ambient silicate (Fig.11);



	Diatom community	Molar Si/C
—■—	Early spring	0.35
-- o--	*Chaetoceros* spp. *Schroederella* sp.	0.15
····▲····	*Rhizosolenia* spp. *Guinardia flaccida*	0.04

Figure 11 Spring diatom succession at station 330 in 1995 and their silica content

Silicate availability, temperature and the diatoms/*Phaeocystis* succession

The comprehensive analysis of time-serie data (section 1, this report) shows that under non-limiting concentrations of silicate and nitrate, diatoms outcompete *Phaeocystis* colonies in the coastal North Sea. Temperature-dependent growth experiments performed on diatom and *Phaeocystis* communities sampled throughout the winter-spring in the coastal North Sea (Fig.12; **Lancelot *et al.*, manuscript #4**) demonstrate that the only early spring diatom community grows better than *Phaeocystis* at temperatures typical of early spring (5-8°C). Conditions which lead to the successful development of the *Rhizosolenia* spp. community in spring 1994 are not understood yet although a better resistance to grazing pressure has been suggested elsewhere.

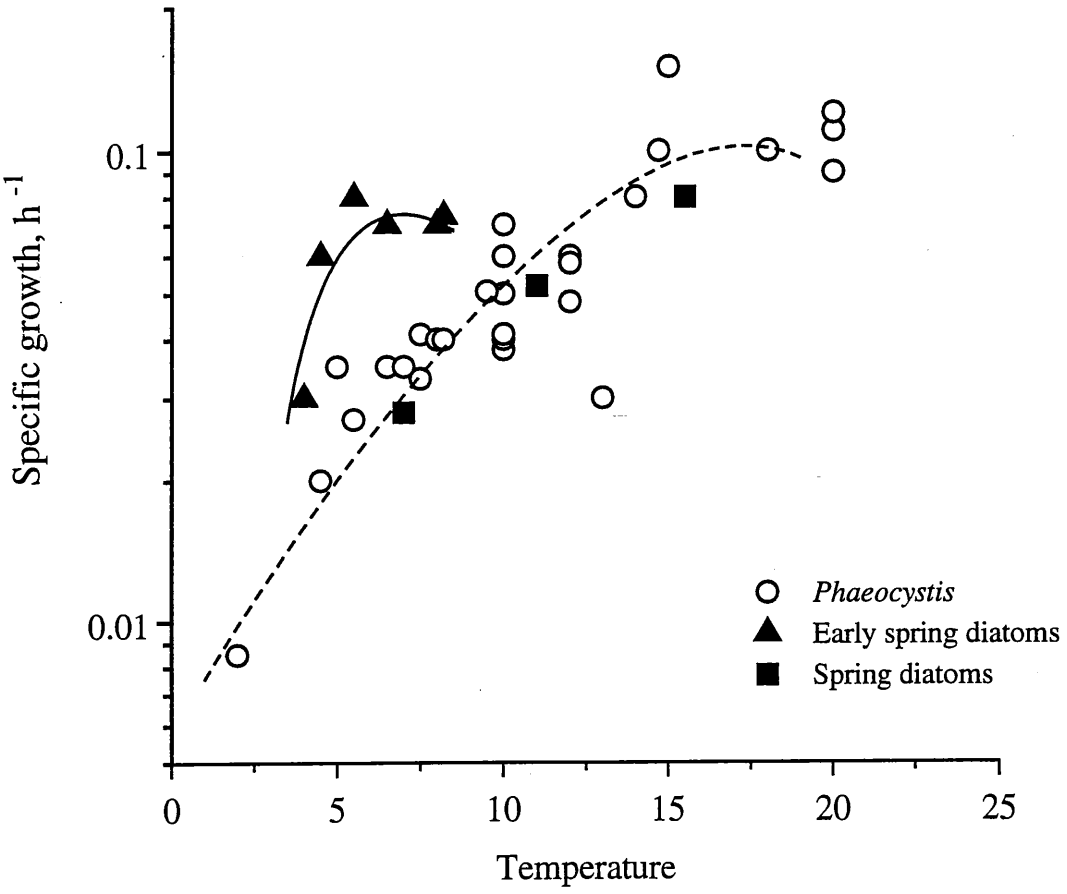


Figure 12 Temperature-dependent growth of coastal North Sea dominant spring phytoplankton groups

2.1.2 *Phaeocystis* life forms

Phaeocystis is characterized by an unusual heteromorphic life cycle (Fig.13), which alternates between gelatinous colonies and different type of free-living cells, and sets it apart from other members of the haptophyte class (**Lancelot *et al.*, in press; manuscript #4**).

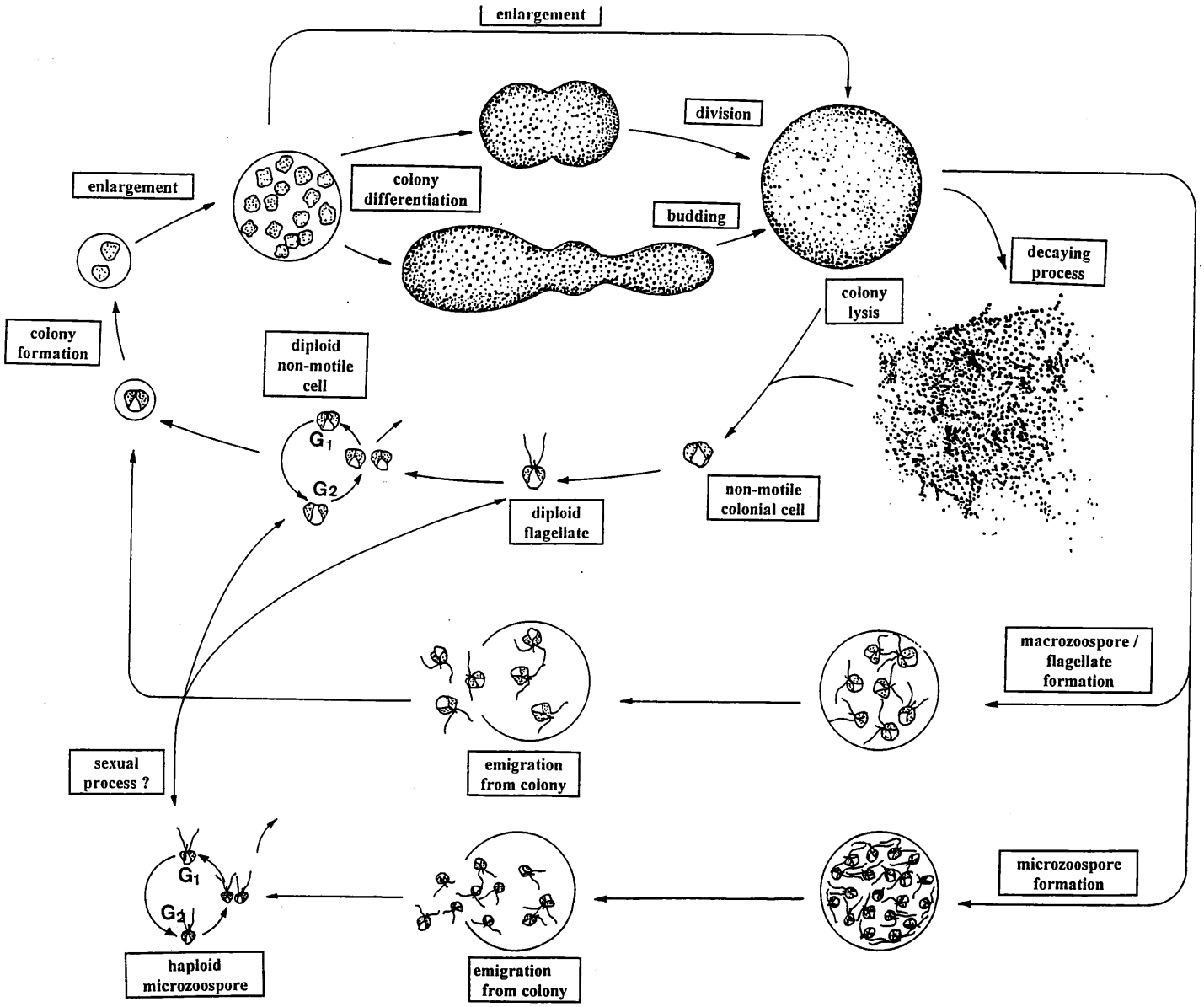


Figure 13 Current status of *P. globosa* life cycle as compiled from culture and field observations

The dominance of one form over the other in natural environments has dramatic consequences for planktonic and benthic ecosystem structure and functioning and can have severe environmental and biogeochemical consequences (**Lancelot and Rousseau, 1994; manuscript #5**). *Phaeocystis* life forms and the mechanisms determining their occurrence were investigated, based on microscopical observations and physiological experimentation.

Phaeocystis life forms : description

The life cycle of *Phaeocystis globosa* (the *Phaeocystis* species growing in the Belgian coastal waters) and the mechanisms determining the occurrence of the different life forms have been studied based on microscopy observations and flow-cytofluorimetry analyses conducted on natural populations, mainly during the monitoring at station 330, and *Phaeocystis* cultures. The latter strain was isolated from the Belgian coastal waters and was maintained in laboratory-controlled conditions of temperature, light and nutrients. Flowcytometry analysis was carried out by Dr D. Vaulot at the Roscoff Biological Station (CNRS et Université Pierre et Marie Curie, Paris 6). This study is described *in extenso* in **manuscript #6 (Rousseau *et al.*,1994)**. Present knowledge on the *Phaeocystis* life cycle is summarized on Fig.13. It shows complex alternations between three types of cells (vegetative non-motile, vegetative flagellate and microzoospore) and various types of gelatinous colonies. The latter - composed of thousands of cells embedded in a mucilaginous matrix - occasionally reach several mm in diameter. Individual cells, 3-10 µm in diameter, are distributed within the gel matrix of the colonies, which vary in form from little (20 µm) to large homogeneous spheres and to large ill-formed colonies invaded by bacteria and protists. This variety in colony form appears to be largely a function of life stage although controlling factors are not well known (**Rousseau *et al.*, 1994; manuscript #6**). Interestingly enough, the haploidy of microzoospores, revealed by flow-cytometry analysis, suggests that these cells are involved in sexual process such as meiosis and conjugation. To which extent this process is determinant for spreading of *Phaeocystis* colonies is not known.

Phaeocystis life forms : environmental control

Despite intensive research efforts, factors controlling the occurrence and dominance of *Phaeocystis* life forms in natural environments, and in particular the transition from the free-living to the colonial stage are not fully understood (**Rousseau *et al.*, 1994; manuscript #6**). The nutrient status, in particular phosphate limitation, is now believed to be a major factor driving colony formation from free-living cells (Veldhuis and Admiraal 1987). Furthermore, the dominant form of inorganic nitrogen is likely an important clue for understanding the dominance and the biogeographical distribution of the colonial stage. Experiments performed with cultures of *Phaeocystis* (Riegman *et al.* 1992) demonstrate that free-living cells outcompete colonial forms in ammonium- and phosphate-limited conditions whereas colonies dominate in nitrate-replete cultures. This suggests that free-living *Phaeocystis* cells would be prevalent in environments which rely on regenerated nitrogen and that colonial forms would rely on nitrate supply and thus would be associated with new production. Accordingly elevated f_{NO3} ratios (the ratio of nitrate uptake to

the total inorganic nitrogen uptake rate) have been measured in the Belgian coastal waters of the North Sea (mean: 0.62, range: 0.5 -0.8; Lancelot *et al.* 1986). Along spring, f_{NO3} decreased from 0.8-0.9 at the beginning of the *Phaeocystis* bloom to 0.4-0.5 at its decline. Interestingly enough the worldwide distribution of free-living cells and colonies supports this hypothesis (**Lancelot *et al.*, in press; manuscript #4**). Solitary cells are cosmopolitan in distribution, and are an important component of the haptophycean assemblage which dominates oceanic nanophytoplankton in many areas. On the other hand, massive blooms of *Phaeocystis* colonies have been observed in turbulent, nutrient-rich environments at all latitudes. In all areas, the colonial form largely dominates. Its rapid development is sustained by new sources of nitrate of natural (winter deep convection) or anthropogenic (coastal areas under the influence of river discharge) origin as showed by the positive relationship between the maximum Chl.*a* concentration reached by colonies in each *Phaeocystis*-dominated environment and the nitrate reduction observed during the bloom (Fig.14).

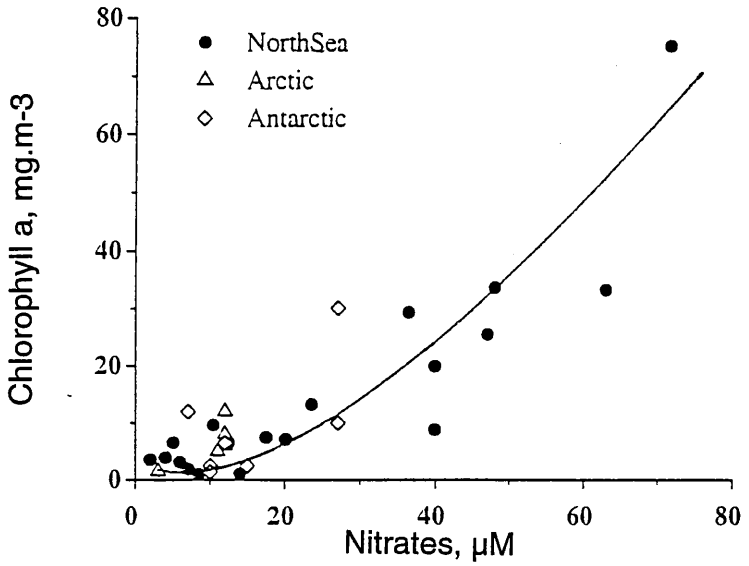


Figure 14 Empirical relationship between maximum *Phaeocystis*-Chl.*a* and nitrate reduction in *Phaeocystis* colony-dominated ecosystems

The unique ability of *Phaeocystis* to form colonies and in particular to synthesize the mucilaginous matrix embedding the cells has been often suggested to explain their successful development in many environments (**Lancelot and Rousseau, 1994; manuscript #5**). The gel-forming exopolysaccharides of the colonial matrix, may enable *Phaeocystis* colonies to outcompete other phytoplankters in turbulent waters by increasing buoyancy and retention in surface waters and by avoiding consumption by indigenous mesozooplankton due to their large size. Also, the demonstrated energy and phosphate storage capacity of the colonial matrix resulting from the physico-chemical properties of the gel and of the physiological properties of the colonial cells (**Lancelot and Rousseau, 1994; manuscript #5**) may also impart a competitive advantage to *Phaeocystis* colonies over diatoms when energy-costly nitrate is the dominant nitrogen source. A similar storage capacity of trace metals by actively photosynthesizing colony cells was suggested but never demonstrated. The mechanisms of Mn/Fe assimilation,

sorption and precipitation by *Phaeocystis* colonies were studied by using specific radiotracers (^{54}Mn, ^{59}Fe, ^{14}C) in combination with different chemical treatments. For instance, pre-incubation treatment of *Phaeocystis* colonies with DCMU (dichloromethylurea), a photosynthesis inhibitor allowed to distinguish between active photosynthetic uptake of Mn/Fe and passive sorption of trace metals on surfaces. Furthermore the post-incubation washing of radioactive *Phaeocystis* colonies with the reductive solution of Ti-complexed by citrate and EDTA was used to specifically isolate dissolved Mn/Fe actually assimilated by the cells through elimination of amorphous Mn/Fe oxyhydroxides and extracellular Fe/Mn. Results obtained conclude that the mechanisms regulating tracer element transfers by *Phaeocystis* colonies are not equivalent for Mn and Fe. Passive transfers, independent of photosynthetic activity, represent the largest part of total Fe uptake by *Phaeocystis* colonies. Contrasting, active photosynthetic Mn precipitation and accumulation are the most important Mn uptake processes by *Phaeocystis* colonies. Furthermore, Mn uptake by *Phaeocystis* colonies is strongly regulated by ambient light (Fig.15) and available dissolved Mn (Fig.16).

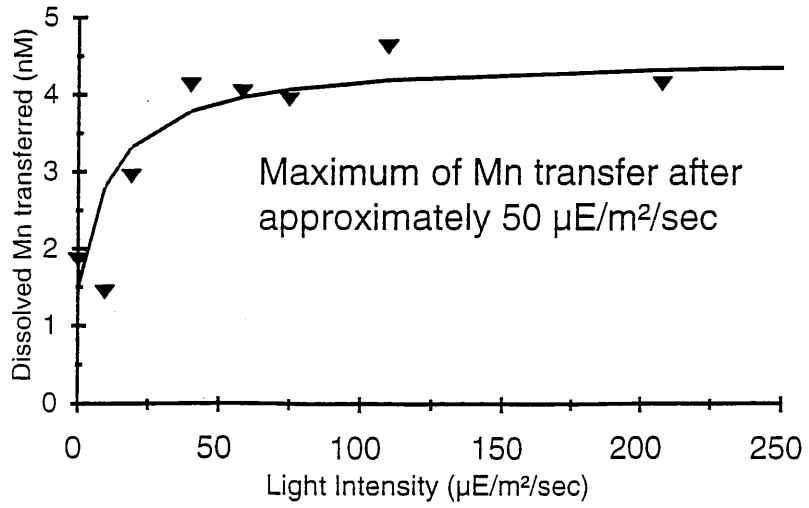


Figure 15: Relationship between Mn uptake by *Phaeocystis* colonies and light intensity. (V. Schoemann unpublished data)

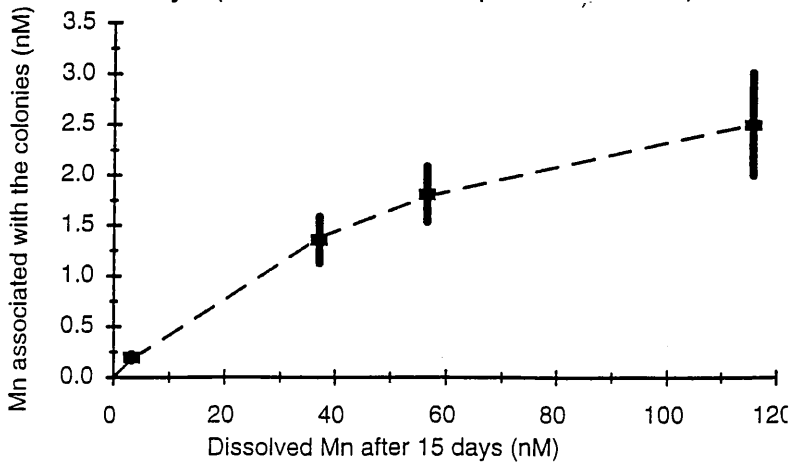


Figure 16: Relationship between Mn accumulation by *Phaeocystis* colonies and ambient dissolved Mn. (V. Schoemann, unpublished data)

2.2. MICROBIAL DEGRADATION OF *PHAEOCYSTIS*-DERIVED ORGANIC MATTER

Phaeocystis-derived organic matter - composed at about 80 % of polysaccharides due to the colonial matrix - has long been considered as refractory material owing to the presence of foam accumulation on the beaches bordering the North sea, at the time of *Phaeocystis* bloom maximum development and decline. Contrasting, the very transient nature of this spectacular event on the one hand and the very simple sugar composition of the colony matrix (70 % glucose, 15 % xylose, 15 acidic sugar) (**Thingstad and Billen, 1994; manuscript #7**) on the other hand would suggest that *Phaeocystis*-derived organic matter is readily biodegradable. Other controlling factors such as an inadequate constitutive enzymatic equipment of ambient bacteria for the hydrolyze of released *Phaeocystis*-derived polymers and/or a shortage of nutrients to fulfill the nitrogen and phosphorus needs of bacteria growing on this nutrient-deprived organic matter source have been investigated. Both these hypotheses were investigated.

Enzymatic activity measurements

β-glucosidase is needed to hydrolyze *Phaeocystis* colony-derived organic matter composed of β-linked monosaccharides (**Thingstad and Billen, 1994; manuscript #7**). β-glucosidasic activity was then measured along the spring phytoplankton bloom of 1994 and compared with simultaneous measurements of ecto-proteolytic activity, a constitutive enzyme of bacteria. The observed concomitant evolution of both ecto-enzymatic activities with respect to phytoplankton development suggests that bacterial β-glucosidase is either constitutive like ecto-protease or is induced beforehand by the presence of dissolved polysaccharides actively produced mucilaginous diatoms as *Chaetoceros socialis* which regularly bloom before *Phaeocystis* **(Becquevort *et al.*, in press; manuscript #2)**.

Microbiological assays

Classical microbiological assays using different kind of *Phaeocystis*-derived material were run under laboratory-controlled conditions to determine the biodegradability of *Phaeocystis*-derived organic matter. The different *Phaeocystis*-derived substrates - *Phaeocystis* colonies; *Phaeocystis* cells, *Phaeocystis* mucilage - were isolated from pure cultures of *Phaeocystis* colonies, making use of a combination of techniques (reverse filtration, high-vacuum pressure filtration, ultra-sonication) and were seeded with *in situ* bacteria. These bioassays were kinetically analysed during 30 days for organic matter (DOC) utilization and bacterial development. The biodegradable fraction of the DOC pool is defined by the difference between initial DOC_0 and $DOC_{-30\ days}$ concentrations. An additional bioassay composed of *Phaeocystis* mucilage amended with inorganic nutrients was conducted to test the nutrient limitation hypothesis. A control-bioassay was run with the culture medium (aged seawater sampled at station 330). Results are illustrated by Fig.17.

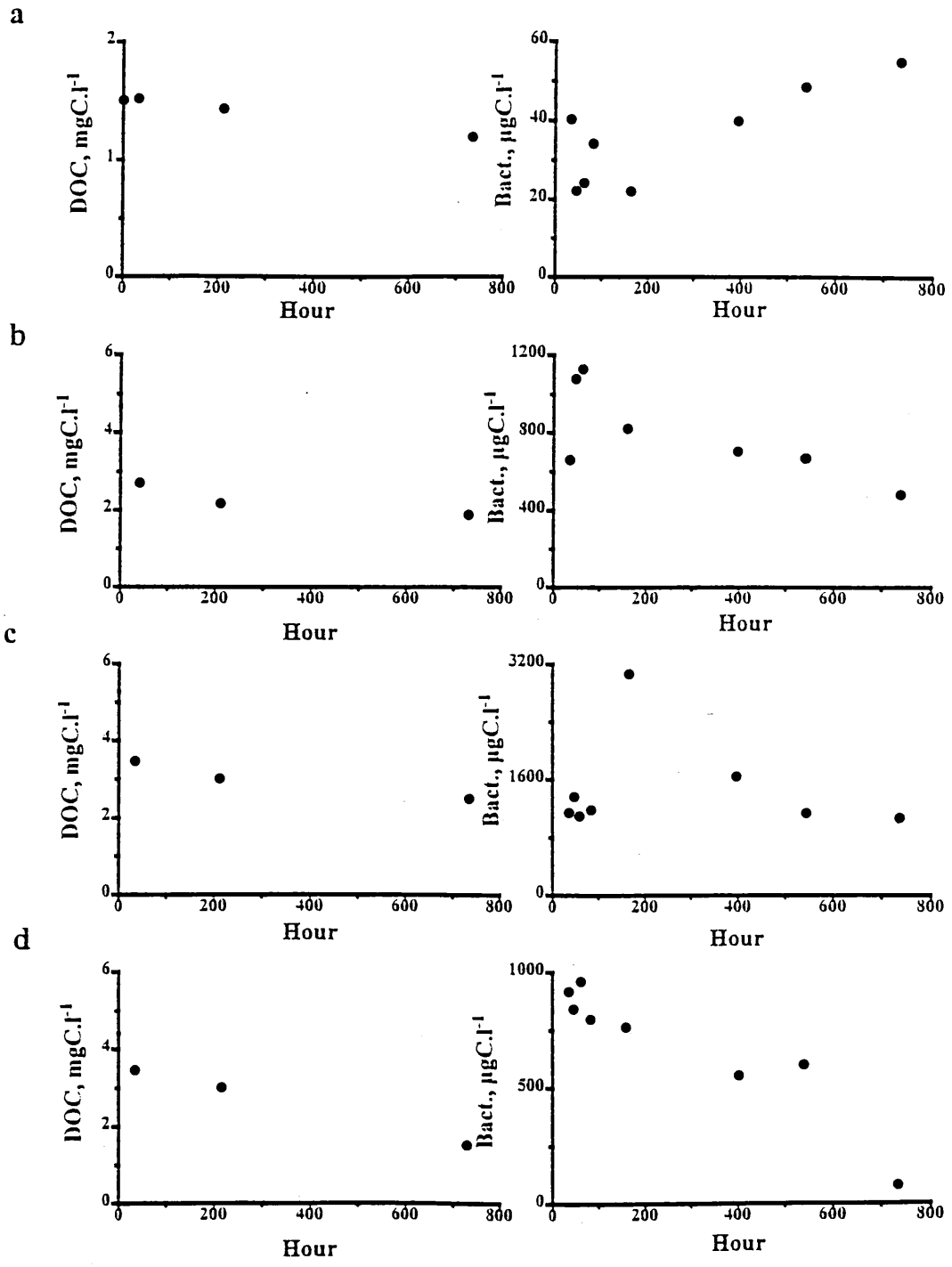


Figure 17 Kinetics of dissolved organic matter (DOC) consumption and of bacterial biomass in microbial bioassays composed of culture medium (a), *Phaeocystis* cells-derived DOC (b), *Phaeocystis* colony-derived DOC (c), *Phaeocystis* colonial matrix-derived DOC (d)

The similar $DOC_{-30\ days}$ of 1.5 gC m^{-3} determined in each bioassay indicates that a refractory DOC of 1.5 gC m^{-3} is characteristic of the coastal North Sea ecosystem. Accordingly this DOC concentration is typical of Belgian coastal waters in winter (Rousseau *et al.,* 1990). In term of biodegradability, no difference was observed between the different bioassays (Fig.17, left panel) suggesting that all *Phaeocystis*-derived organic substances are readily biodegradable. Unfortunately none of the bioassays was nutrient-limited and the hypothesis of nutrient shortage could not be tested.

Contrasting, calculation of bacterial growth efficiency - the ratio between DOC initial consumption and bacterial biomass initial growth (Fig.17) - indicates that *Phaeocystis* mucilage-derived DOC is a less interesting substrate for bacterial growth (bacterial growth efficiency of 0.3) compared to *Phaeocystis* cell-derived DOC (bacterial growth efficiency of 0.45).

Combining these results, demonstrates that the transient foam accumulation observed at the time of *Phaeocystis* blooms are not reflecting a lag phase required for the induction of β-glucosidasic activity but rather a transient shortage of inorganic nutrients needed for bacterial utilization of the large carbon source provided after *Phaeocystis* colonies disruption.

2.3. PROTOZOAN GRAZING ON *PHAEOCYSTIS* FREE-LIVING CELLS AND BACTERIA

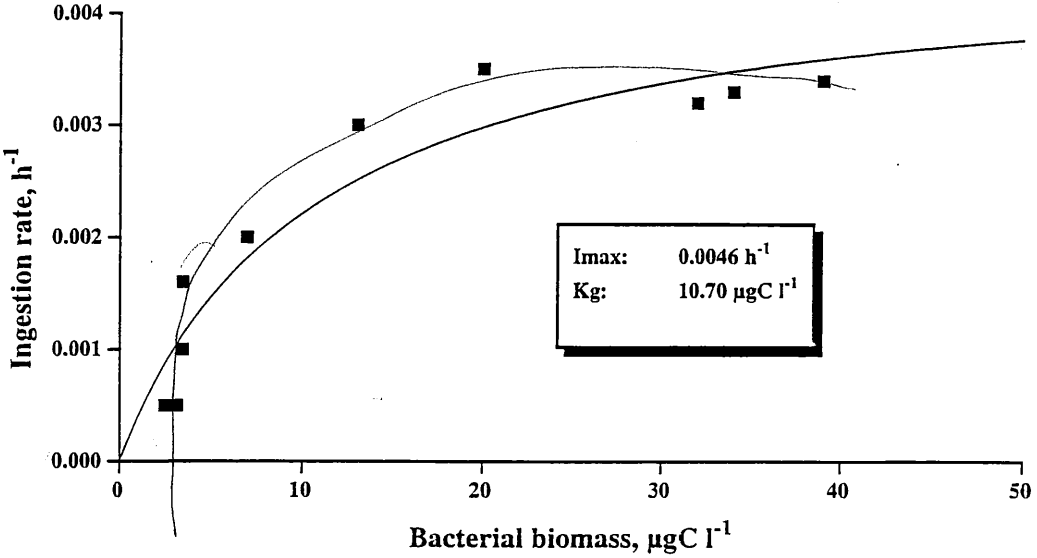
Protozooplankton has a key trophic position linking the microbial to the mesozooplankton-based food-web. The knowledge of mechanisms regulating protozooplankton feeding rate is particularly important In *Phaeocystis*-dominated ecosystem due to their demonstrated ability to efficiently ingest *Phaeocystis* free-living cells. Colony disruption indeed provides at the time of *Phaeocystis* decline a huge amount of *Phaeocystis* free-living cells directly available for protozooplankton. On the other hand, some experimental evidence exists that protozoa might efficiently control *Phaeocystis* blooms during their initial phases when the share of solitary cells relative to total *Phaeocystis* colony biomass is higher than during later stages of the bloom (Weisse *et al.* 1994).

Feeding activity of the protozoan community developing during *Phaeocystis* blooms has been investigated in the Belgian coastal waters on natural populations. Sampled communities were dominated by oligotrich ciliates which were using both bacteria and *Phaeocystis* solitary cells as preys. The parameters characterizing the protozoan feeding activity on bacteria and *Phaeocystis* solitary cells were determined making use of the method based on the uptake of fluorescent-labeled preys (**Becquevort and Menon, in prep., manuscript#8**). In parallel, food selectivity, *i.e.* the influence of food concentration and quality on the protozoan feeding behavior, was investigated using a novel method (**Menon *et al.*, 1995 (manuscript #9)**. Shortly the methodology consisted in measuring the kinetic parameters describing the ingestion rate of natural assemblages of protozoa in the presence of various concentrations of competitive preys: bacteria and flagellates.

Results of these experiments are described *in extenso* in **Becquevort and Menon, in prep., (manuscript#8)** and can be summarized as follows:

Ciliate ingestion of both bacteria (Fig.18a) and *Phaeocystis* cells (Fig.18b) is described by an hyperbolic function analogous to the Michaelis-Menten kinetics. The maximum ingestion rate (Imax) of *Phaeocystis* cells is three times higher than that of bacteria (Fig.18) although both ingestion rates are saturating at the same food concentration (similar half-saturation constants Kg of 10 mg C m^{-3}).

a)



b)

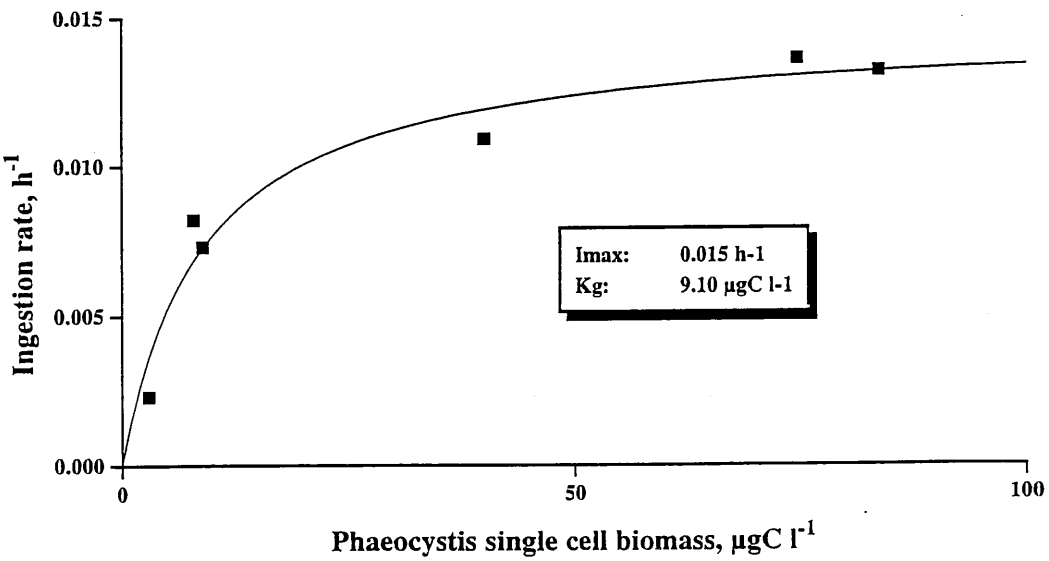


Figure 18 Michaelis-Menten kinetics describing the functional response of ciliate ingestion on bacteria (a) and on *Phaeocystis* cells (b).

Food selectivity experiments show that the presence of bacteria didn't affect the maximum ingestion rate of ciliates on *Phaeocystis* cells (Fig.19a). However a significant competitivity between bacteria and *Phaeocystis* solitary cells preys was evidenced by the observed decrease of the protozoan affinity for *Phaeocystis* solitary cells at increasing concentration of bacteria (Fig.19b).

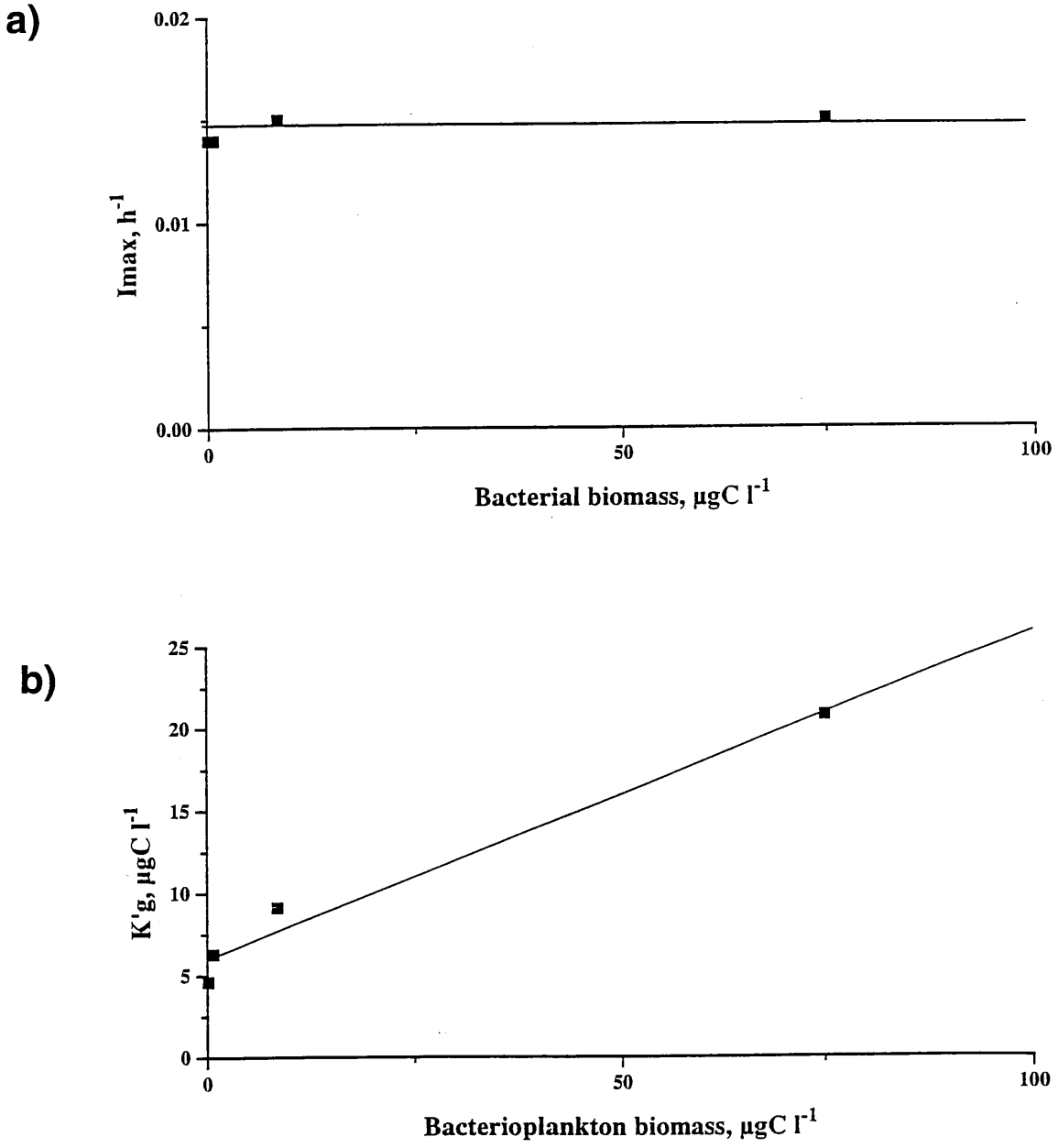


Figure 19 Relationship between ciliate maximum ingestion rate (Imax) of *Phaeocystis* cells (a) and apparent half-saturation constant (Kg') (b) and bacterial biomass.

3. MODELING WORK

3.1. METHODOLOGY

An integrated network of mechanistic biogeochemical models (**Lancelot *et al.*, 1996; manuscript#10**), consisting of the off-line coupling of a biogeochemical model of *Phaeocystis* blooms development in the coastal North Sea - the MIRO model - with a river system model calculating riverine nutrient delivery to the coastal zone, as a function of hydrology, land use and waste water purification policies - the RIVERSTRAHLER model (**Garnier *et al.*, 1995; manuscript#11**) - has been developed for predicting the response of the *Phaeocystis*-dominated coastal ecosystem to changes in riverine nutrient loads resulting from changes occurring in the watershed. Basically these mechanistic models are describing and predicting the cycling of carbon, nitrogen, phosphorus and silicon through aggregated key components of the freshwater and coastal ecosystems over seasons and years in response to the physical and nutrient forcing. Such mathematical models, therefore, are based on physiological and geochemical principles. The numerical code synthesizes knowledge on the kinetics and the factors controlling the main auto- and heterotrophic processes involved in the functioning of the river and marine coastal ecosystem. The code is continuously in development relying on progress in experimental aquatic ecology. Current development of the MIRO model, in particular its ability to reproduce the present-day eutrophication in the continental coastal waters of the North Sea, especially the magnitude and extent of *Phaeocystis* blooms, and explore the coastal ecosystem response to nutrient reduction scenarios scheduled for the next 25 years is shortly presented below.

3.2. THE MIRO MODEL : MODELING PRESENT-DAY *PHAEOCYSTIS* BLOOMS IN THE BELGIAN COASTAL WATERS

3.2.1. Description of the MIRO model

The MIRO ecological model describes the cycling of carbon, nitrogen, phosphorus and silicon through aggregated chemical and biological compartments of the planktonic and benthic components of the coastal area (Fig.20). Thirty-two state variables and twenty-six processes linking them were identified as important from the knowledge of the structure and functioning of *Phaeocystis*-dominated ecosystems. The model results of the assemblage of 4 modules describing the dynamics of phytoplankon, zooplankton, organic matter degradation and nutrient regeneration in the water column and the sediment. Mathematical formulation of kinetics, parameters and forcing functions were determined from process-level studies and are described in (Tables 2-5).

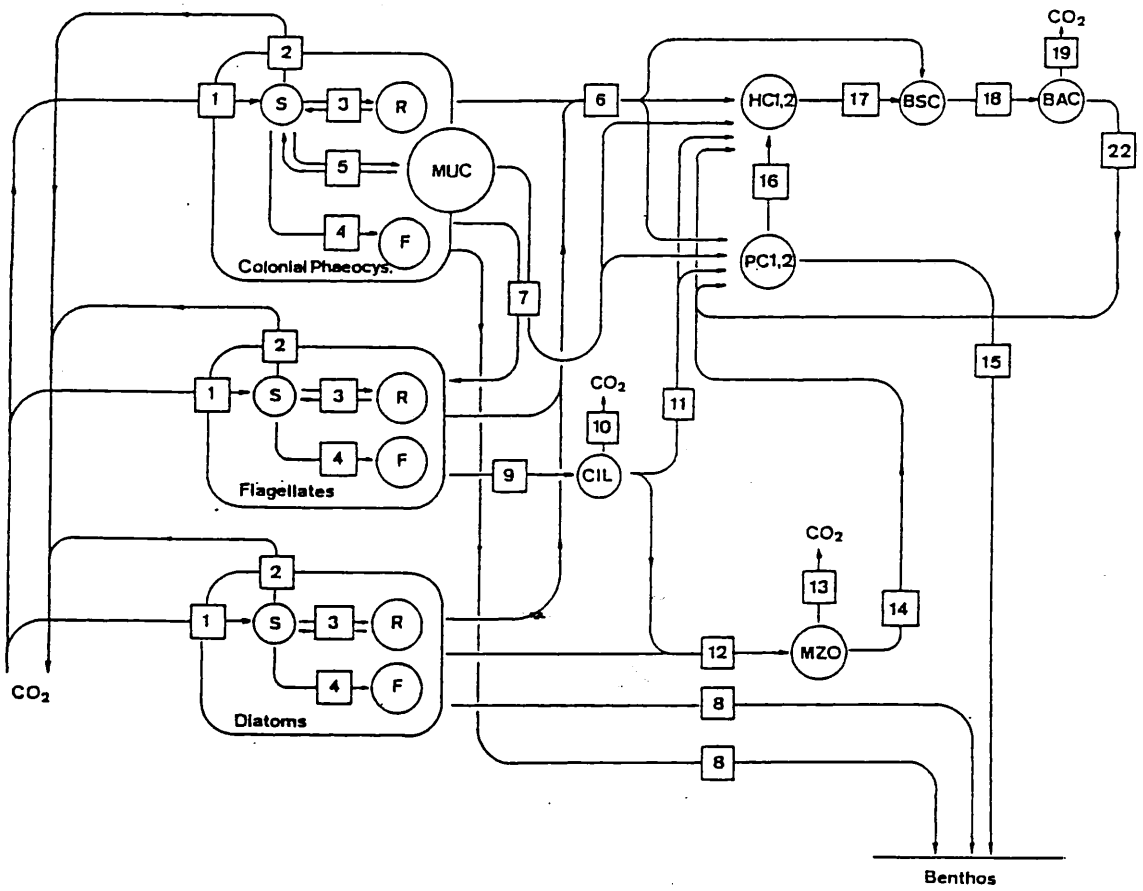


Figure 20 Structure of the MIRO model : carbon cycling. Legend for state variables (circles) and processes linking them (numbers) in text.

The phytoplankton module considers 3 phytoplankton groups: diatoms (DIA), free-living nanoflagellates (PHS) and *Phaeocystis* colonies (PHC). Due to their trophic fate, *Phaeocystis* free-living cells and colonies are considered as separate state variables, even though they constitute two different stages of the life cycle of the same phytoplankter (*e.g.* Rousseau *et al.*, 1994). The kinetics of phytoplankton activities is described according to the AQUAPHY model of Lancelot *et al.* (1991). It considers 3 intracellular pools - monomers (S); reserve material (R); functional and structural metabolites (F) - and

distinguishes the processes of photosynthesis (1) directly dependent on light availability, from the process of growth (4) controlled by the availability of intracellular monomers and ambient nutrients. One single nutrient is limiting phytoplankton growth, according to the Liebig law of minimum. With respect to *Phaeocystis* colonies, an additional pool of extrapolymers (MUC) has been added to consider the mucilaginous matrix in which the cells are embedded and which serves as reserve of energetic material (5). Beside respiration (3), loss processes include excretion, cellular lysis (6), under control of nutrient stress; sedimentation (diatoms and *Phaeocystis* colonies) (8); zooplankton grazing (12).

The zooplankton module of the MIRO model considers two groups of zooplankton : the microzooplankton (CIL) feeding on free-living flagellates (9) and the mesozooplankton (MZO) grazing (12) on diatoms and microzooplankton according to a preference for the latter (F. Hansen, pers. comm.). *Phaeocystis* colonies escape grazing. Colonies are however submitted to a nutrient stress-dependent process of colonial disruption (7) which releases in the water column free-living cells and dissolved organic polymers. A simplified description of zooplankton dynamics has been chosen, considering grazing as an hyperbolic Michaelis-Menten function of food items with however a threshold value below which no grazing is possible. Zooplankton growth and excretion (14) are calculated from grazing rates based on growth efficiency, zooplankton stoechiometry and the calculated nutrient composition of food. First-order mortality is considered.

Organic matter degradation by planktonic bacteria is described according to the HSB model of Billen (1989), considering two classes of biodegradability for both dissolved (HC1 and HC2) and particulate (PC1 and PC2) organic matter. Ectoenzymatic hydrolysis of these polymers (17) produces monomers (BS) that can be taken up by bacteria (18). These processes are described by standard Michaelis-Menten kinetics. According to their origin, carbon and nitrogen contribute in variable proportions to the pools of organic matter. This proportion, compared to the bacterial C:N ratio determines whether net ammonification or ammonium uptake accompanies bacterial activity. All organic phosphorus is assumed to be released directly as ortho-phosphate during hydrolysis of polymeric organic matter and phosphorus is taken up by bacteria in its inorganic form only.

Benthic organic matter degradation and nutrient (N, P, Si) recycling is calculated making use of the algorithms developed by Lancelot and Billen (1985) and Billen *et al.*, (1989). These algorithms, by solving steady-state diagenetic equations expressing the mass balance of organic carbon, oxygen, inorganic forms of nitrogen and phosphorus in the sedimentary column, calculate the fluxes of nitrate, ammonium and phosphate across the sediment-water interface resulting from a given sedimentation flux of particulate organic matter. Furthermore, a first-order kinetics describes benthic silicon redissolution and release of silicic acid to the water column.
from the Channel to the German Bight.

Table 2 : The MIRO Model : equations and parameters. Phytoplankton module.

Process	Equation	Parameters					
		Symbol	Signification	DIA	PHS	PHC	Unit
Photosynthesis	$k_{max}\ (1\text{-}exp\text{-}(\alpha\ I/k_{max})\ F$	k_{max}*	Maximal photosynthesis	0.12	0.1	0.28	h^{-1}
		α	Photosynthetic efficiency	0.0024	0.002	0.0056	$h^{-1}\ (\mu Em^{-2}s^{-1})^{-1}$
Reserve synthesis	$sr_{max}\ \frac{S/F}{Ks+S/F}\ F$	sr_{max}*	Maximal storage rate	0.1	0.1	0.1	h^{-1}
		Ks	Half-saturation constant	0.06	0.06	0.06	dimensionless
Mucus synthesis	$smuc_{max}\ \frac{S/F}{Ks+S/F}\ F$	$smuc_{max}$*	Maximal mucus synthesis	-	-	0.18	h^{-1}
Reserve catabolism	$K_r R$	K_r*	Catabolism rate	0.06	0.06	0.06	h^{-1}
Growth	$\mu_{max}\ \frac{S/F}{Ks+S/F}\ lnut\ F$	μ_{max}*	Maximal growth	0.05	0.09	0.09	h^{-1}
	with lnut = $\frac{(NO3+NH4)}{KN+NO3+NH4}$	K_N	Half-saturation ct for nitrogen uptake	0.8	0.5	0.2	µM
	or $\frac{PO4}{KP+PO4}$	K_P	Half-saturation ct for PO_4	0.2	0.1	0.1	µM
	or $\frac{Si(OH)_4}{K_{Si}+Si(OH)_4}$	K_{Si}	Half-saturation ct for $Si(OH)_4$ uptake	0.4	-	-	µM

Table 2 (follow) : The MIRO Model : equations and parameters. Phytoplankton module.

Respiration	maint F + CES growth	maint CES***	Basal metabolism ct Biosynthesis cost	0.0004 0.4-0.8	0.0008 0.4-0.8	0.0008 0.4-0.8	h^{-1} dimensionless
Excretion	K_{exc} photosynthesis	K_{exc}	Excretion ct	0.05	0.05.	0.05	h^{-1}
Cellular lysis (PHYlys)	K_{lys} (F+R+S)	K_{lys}**	Autolysis ct	0.001	0.0025	0.002	h^{-1}
Colony lysis	K_{lyscol} (R+S+F+MUC)	K_{lyscol}***	Colony lysis ct			0.002	h^{-1}
Sedimentation	K_{sed} (F+R+S)	K_{sed}**	Sedimentation ct	0.0005	0.0005	0.0005	h^{-1}
N uptake	Growth / CN	CN	Phytoplankton-F C/N	4	4	4	µM/µM
Ammonium preference (rpi)	$(\frac{NH_4}{NH_4+NO_3})\,\alpha_{rpi}$	α_{rpi}	Relative preference index	0.1	0.1	0.75	dimensionless
PO_4 uptake	Growth / CP	CP	Phytoplankton-F C/P	80	80	80	µM/µM
$Si(OH)_4$ uptake	Growth/CS_i	CS_i	Phytoplankton-F C/$_{Si}$	2			µM/µM

Forcing temperature dependence : parameters with *

p(T)	p*exp (- (T-Topt)²/dti²)	Topt dti	Optimal temperature Temperature interval	5.5 1.6	15 8	15 8	°C °C

Limiting dependence : parameters with **

p(lnut)	p**(1+5) (1-lnut)						

Inorganic nitrogen source - dependence : CES ***

CES (N)	0.4 rpi + 0.8 (1-rpi)						
Klyscol (N)	3 K_{lyscol} *** if $NO_3 < NH_4$ or $NO_3 = 0$						

Table 3 : The Miro Model : Equations and parameters. Zooplankton module.

Process	Equation	Parameters			
		Symbol	Signification	Value	Unit
Ciliates : CIL : 1 prey = PHS					
Grazing (CILgraz)	$gCIL_{max} \frac{PHS - THS_{CIL}}{KgPHS + (PHS - THS_{CIL})} \cdot CIL$	$gCIL_{max}$*	max. grazing rate	0.15	h^{-1}
		THS_{CIL}	Food threshold of CIL	2	$mgCm^{-3}$
		KgPHS	Half-saturation ct on PHS	15	$mgCm^{-3}$
Growth (CILgwth)	Y_{CIL}CILgraz	Y_{CIL}	Growth yield	0.5	dimensionless
Cellular lysis (CILlysis)	K_{dCIL} CIL	K_{dCIL}	Mortality constant	0.002	h^{-1}
NH_4 regeneration	CILgraz CN_{PHS}^{-1} - CILgwth CN_{CIL}^{-1}	CN_{CIL}	Ciliate C/N ratio	4	µM/µM
Mesozooplankton MZO : 2 preys : Prey 1 = DIA and prey 2 = CIL					
Grazing (MZOgraz)	$gMZO_{max} \Sigma(Prey_{1,2}\text{-}THS_{MZO})/Kg_{app1,2}+(Prey_{1,2,}\text{-}THS_{MZO})$	gMZO*$_{max}$	Max. grazing rate	0.05	h^{-1}
		THS_{MZO}	Food threshold	5	$mgCm^{-3}$
	with : $Kg_{app1} = Kg_{DIA}(1 + CIL)/K_{gCIL}$	Kg_{DIA}	Half-saturation ct for DIA grazing	50	$mgCm^{-3}$
	$Kg_{app2} = Kg_{CIL}(1 + DIA)/K_{gDIA}$	Kg_{CIL}	Half-saturation ct for CIL grazing	25	$mgCm^{-3}$

Table 3 (follow) : Zooplankton module.

Growth (MZOgwth)	Y_{MZO} MZOgraz	Y_{MZO}	Growth yield	0.25	dimensionless
Egestion	E_Z MZOgraz	E_Z	Egested fraction of ingestion	0.25	"
Mortality (MZO lysis)	K_{dMZO} MZO	K_{dMZO}*	Total mortality	0.002	h^{-1}
NH_4 regeneration	$MZOgraz_{DIA}.CN_{DIA}^{-1}+MZOgraz_{CIL}CN_{CIL}^{-1}-MZOgwth\ CN_{MZO}^{-1}$	CN_{MZO}	Mesozooplankton C/N ratio	4.5	dimensionless

Temperature control : parameters with *

p(T)	$p*exp - (T-Topt)^2/dti^2)$	Topt dti	Optimal temperature Temperature interval	16 8	°C °C

Table 4 : Planktonic organic matter degradation module.

Process	Equation	Parameters			
		Symbol	Signification	Value	Unit
$PC_{1,2}$ production by organism lysis	$\varepsilon p_{1,2}(PHYlys+BAClys+CILlys+MZOlys)+\varepsilon p_3 MUC$	εp_1 εp_2 εp_3	PC_1 fraction in lysis pducts PC_2 fraction in lysis pducts PC_2 fraction in colony lysis	0.1 0.4 0.5	dimensionless dimensionless dimensionless
Ectoenzymatic hydrolysis	$k_{1,2}b.PC_{1,2}$	k_1b* k_2b	PC_1 hydrolysis rate PC_2 hydrolysis rate	0.005 0.00025	h^{-1} h^{-1}
$PC_{1,2}$ sedimentation	(vsm/depth)	Vsm	$PC_{1,2}$ sinking rate	0.01	m h^{-1}
$HC_{1,2}$ production by lysis	$\varepsilon d_{1,2}(PHYlys+BAClys+CILlys+MZOlys)+$ εd_3 MUC	εd_1 εd_2 εd_3	HC_1 fraction in lysis pdcts HC_2 fraction in lysis pdcts HC_2 fraction in colony lysis	0.3 0.2 0.5	dimensionless dimensionless dimensionless
Exoenzymatic $HC_{1,2}$ hydrolysis	$e_{1,2_{max}} \frac{HC_{1,2}}{KH_{1,2}+HC_{1,2}} BAC$	e_{1max}* e_{2max}* KH_1 KH_2	Max. rate of HC_1 hydrolysis Max. rate of HC_2 hydrolysis Half sat cst for HC_1 hydrolysis Half sat cst for HC_2 hydrolysis	0.75 0.25 250 2500	h^{-1} h^{-1} $mgCm^{-3}$ $mgCm^{-3}$
Monomers uptake (Bupt)	$b_{max} \frac{BS}{K_{BS}+BS} BAC$	b_{max}* K_{BS}	Max BS uptake rate Half sat cst for uptake	6 25	h^{-1} $mgCm^{-3}$
Bact. growth (Bgwth)	Y.Bupt	Y	Growth yield	0.3	dimensionless

Table 4 (follow) : Planktonic organic matter degradation module.

Bact.mortality (BAClys)	kdb.BAC	kdb*	Bact. lysis rate	0.03	h^{-1}
Ammonification	(1-Y)/Y.Bgwth/CN_{BAC}	CN_{BAC}	Bact. C:N ratio	4	µM/µM

Temperature forcing : parameters with

p(T)	p*exp (- (T-Topt)²/dti²)	Topt dti	Optimal temperature Temperature interval	30 18	°C °C

$18^2 = 324$

Table 5 : Benthic nutrient regeneration module.

Process	Equation	Parameters			
		Symbol	Signification	Value	Unit
Diffusion (interst.phase)	Fick law	Di	App.diffusion coefficient	$5\ 10^{-5}$	cm^2/s
Mixing (solid phase)	Fick law	Ds	Mixing coefficient	$5\ 10^{-6}$	cm^2/s
orgN mineralisation	$k_{1,2}b.PC_{1,2}/CN$	k_1b* k_2b	orgN hydrolysis rate of PC_1 orgN hydrolysis rate of PC_2	0.005 0.00025	h^{-1} h^{-1}
orgP mineralisation	$k_{1,2}b.PC_{1,2}/CP$	k_1p* k_2p	orgP hydrolysis rate of PC_1 orgP hydrolysis rate of PC_2	0.05 0.0025	h^{-1} h^{-1}
Benthic nitrification	$KH_{1,2}$ NH_4 (in oxic layer)	$KH_{1,2}$	1st order nitrification cst	1	h^{-1}
NH_4 adsorpt/desorpt	1st order equilibrium	Kam	1st order adsorpt cst for NH_4	6	dimensionless
PO_4 adsorpt/desorpt (in benthos)	1st order equilibrium	Kpa Kpe	PO_4 adsorpt. (oxic layer) PO_4 adsorpt. (anoxic layer)	35 1.7	dimensionless dimensionless
SiO_2 redissolution	Kdb.Si.SIB	KdbSi	Silica redissolution rate	0.000075	h^{-1}

Temperature control : parameters with *

p(T)	p*exp (-(T-Topt)²/dti²)	Topt dti	Optimal temperature Temperature interval	30 18	°C °C

3.2.2. Model application

For a first application of the MIRO model to the continental coastal waters of the North Sea, a multi-box model has been considered on the basis of the hydrological regime. Such a low resolution of the hydrodynamics is reasonable in this tidally well-mixed area. In order to take into account the cumulated nutrient enrichment of Atlantic waters by the Seine and Scheldt rivers, three successive boxes , assumed to be homogeneous, have been chosen from the Baie de Seine to the Wadden Sea area of the Dutch coastal zone, on the basis of the hydrological regime. The offshore limit of the boxes is taken along a residual streamline so that inshore-offshore exchanges can be neglected. Each successive box is treated as an open system, receiving waters from the upwards adjacent box and exporting water to the downwards box. The seasonal variation of the state variables are calculated by solving the different equations expressing mass conservation in the system according to the Euler procedure.

The boundary conditions are provided by the results of the calculations performed for the conditions existing in the western Channel area, considered as a quasi oceanic closed system. Forcing functions are observed seasonal irradiance and seawater temperature and monthly riverine nutrient discharges of 1985 (source : North Sea Task Force, 1992).

The prediction capability of the MIRO model can be appraised from Fig. 21 and 22 which compare respectively predicted chlorophyll a concentrations and *Phaeocystis* cellular density and nutrient concentrations in the 3 sub-areas of the continental coastal waters of the North Sea with observations at the respective reference stations of the observational network, from 1988 to 1993. In spite of a reasonable general agreement between predictions and observations, in particular in the timing and magnitude of *Phaeocystis* blooms, the model does not predict properly the fast decline of *Phaeocystis* blooms, especially in the northern part of the simulated area where non-observed elevated biomass is predicted along the summer season. This discrepancy between predictions and measured data could originate either from the oversimplification of the hydrological regime, neglecting for instances the influence of the Wadden Sea in the Dutch coastal area or from a low description of mechanisms prevailing for *Phaeocystis* blooms termination and degradation.

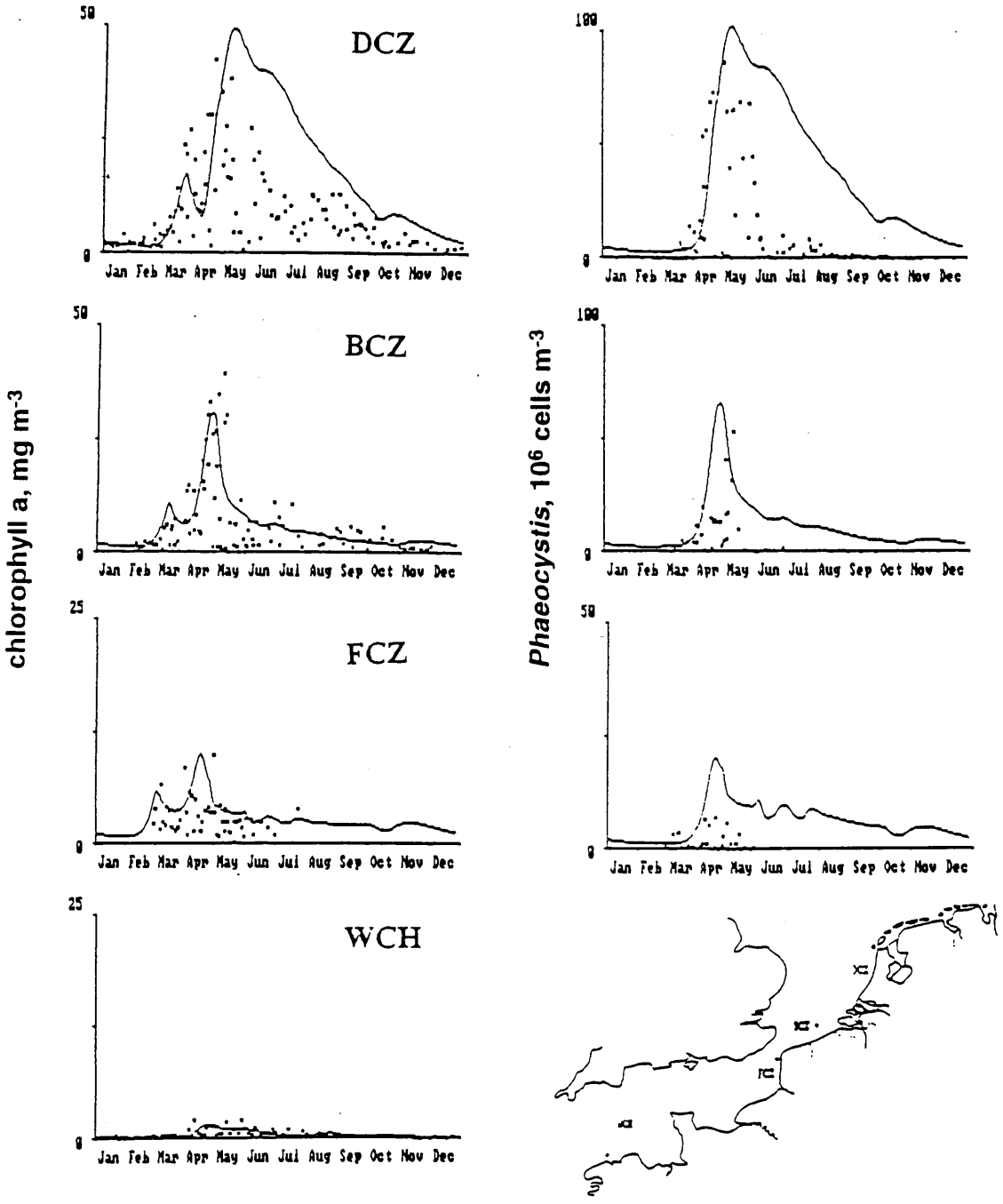


Figure 21 Observed (dots) and predicted (line) phytoplankton development in the coastal North Sea. Total chlorophyll a concentrations (a) and *Phaeocystis* cell density (b)

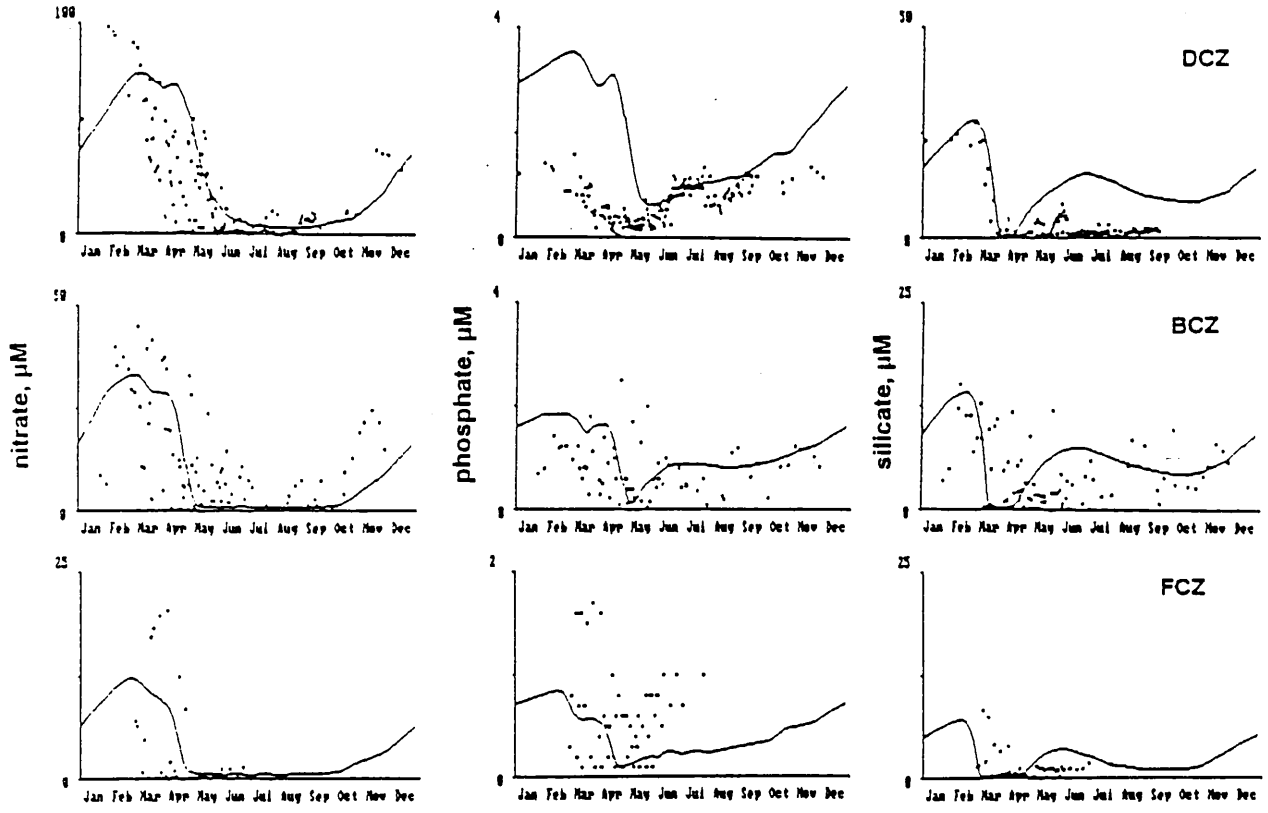


Figure 22 Observed (dots) and predicted (line) nutrient concentrations in the coastal North Sea.

3.3. MODELING *PHAEOCYSTIS* BLOOMS IN RESPONSE TO NUTRIENT REDUCTION SCENARIOS

The appropriateness of the integrated modeling approach for coastal management purpose is shown by exploring the response of the MIRO model to reduction scenarios of riverine nutrient delivery of the coastal zone consequent to the application of the Ministerial Declaration at the second International Conference of the North sea of November 1997 (50% reduction of P and/or N & P reaching the North Sea) on the one hand and on the other hand the EC guideline of May 1991 on urban waste water treatment for sensitive areas, *i.e.* 90 % phosphate removal and/or 75 % denitrification.

3.3.1. Application of the North Sea Conference decision

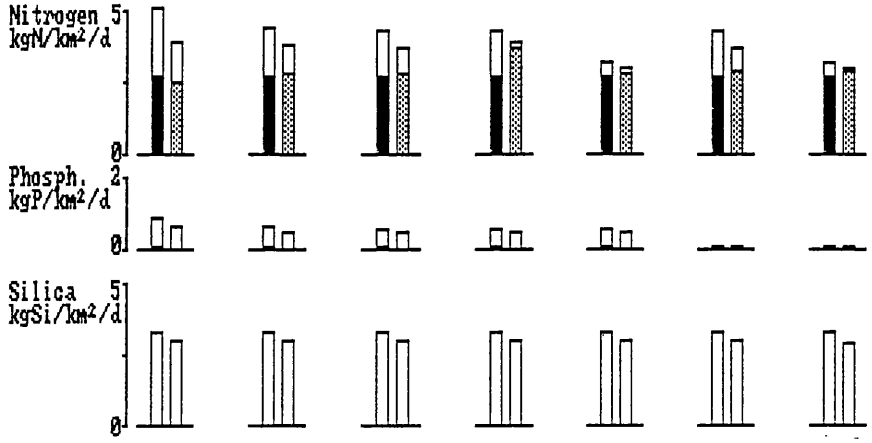
Nutrient reduction scenarios were established by modifying nutrient riverine inputs of 1985, according to the North Sea Conference Ministerial Declaration of 1987 *i.e.* 50% of P load on the one hand and 50% reduction of N **&** P discharge to the coastal sea on the other hand. MIRO model runs (Table 6) show that significant reduction of *Phaeocystis* blooms are reached when both N and P loads to the Southern Bight of the North Sea are reduced by 50%. Interestingly enough, 50% reduction of both N and N & P loads to the coastal sea are primarily affecting diatom spring development reducing their bloom magnitude by more than 30%. Consequence for biological harvestable resources are not predicted by MIRO but should be considered.

Table 6 MIRO model scenarios: application of North Conference decision of 1987

Scenarios	**Diatoms %reduction**	***Phaeocystis* %reduction**
French coastal waters		
50% P removal	42	7
50% N & P removal	42	**35**
Belgian coastal waters		
50% P removal	47	0
50% N & P removal	47	**41**
Dutch coastal waters		
50% P removal	33	30
50% N & P removal	33	**56**

3.3.2 Application of EC guideline of May 1991 on urban waste water treatment

Nutrient reduction scenarios were established by modifying nutrient riverine inputs of 1985, according to the results generated by application of the RIVERSTRAHLER model to watersheds similar to those of the rivers Seine, Scheldt and Rhine and for various scenarios of urban waste water treatment. (Fig.23) These calculations were based on published level of urban waste water treatment reached in the different watersheds. Due to the marked seasonality of both river flow discharge and nutrient transformation within the river system, a summer (April-September) and a winter (October-March) nutrient reduction factors were considered.



0: no treatment
1: 85% 2nd treatment
2: 100% 2nd treatment
3: 100% 2nd treatment & nitrification
4: 75% denitrification
5: 90% P removal
6: 75% denitrification & 90% P removal

legend

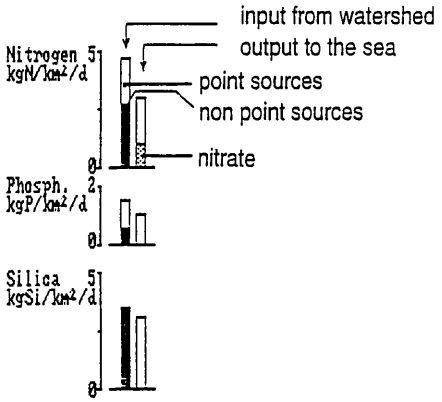


Figure 23 Example of nutrient reduction scenarios applied on the Seine river (240 inhabitants per km^2)

The extent of *Phaeocystis* colony blooms reduction expected from the application of the EC guideline of May 1991 can be appraised on Fig.25 which compares predicted *Phaeocystis* blooms after nutrient abatement scenarios with present-day predictions. Slight differences in the response of the coastal ecosystem are to be observed between sub-areas. Severe reductions of *Phaeocystis* blooms colonies are predicted after 90 % P removal. By contrast, very little bloom reduction is achieved in the scenario involving the denitrification treatment of waste waters. This is explained by the importance of diffuse sources of nitrogen. Interestingly enough, the simultaneous application of phosphorus removal and denitrification treatment of urban waste waters is not required for obtaining the largest reduction of *Phaeocystis* blooms in the coastal North Sea.

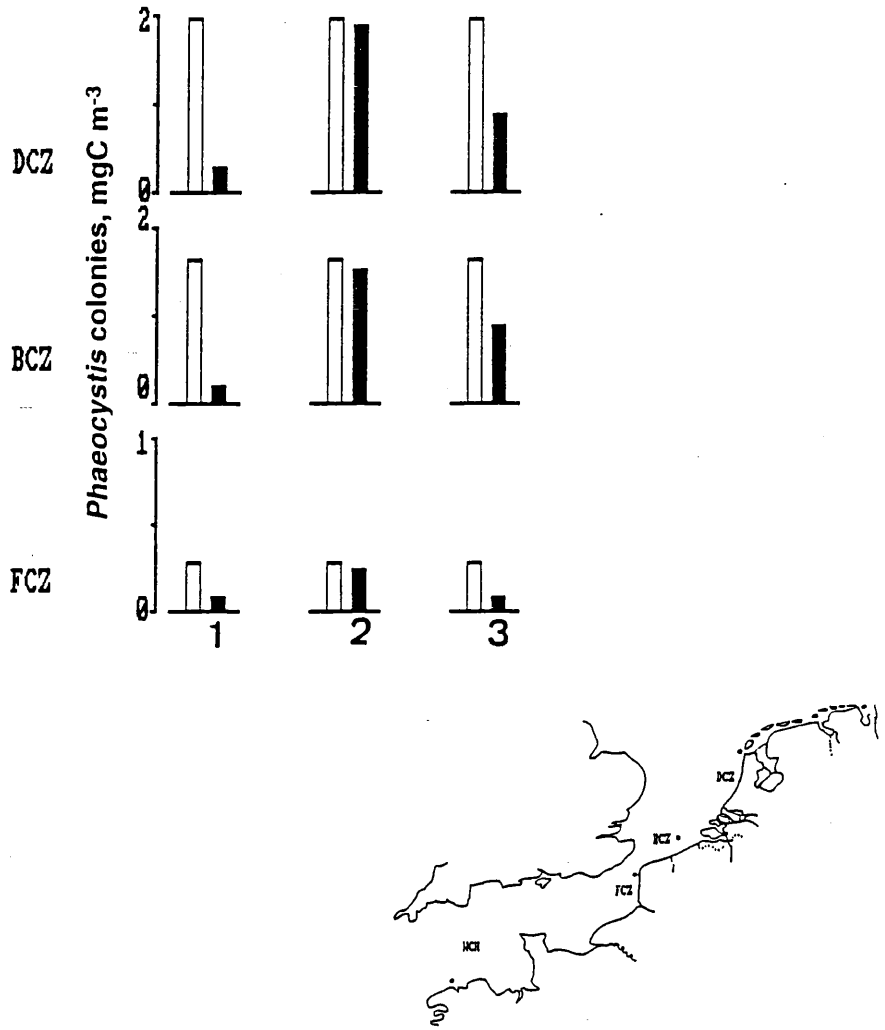


Figure 25 Predicted present-day magnitude of *Phaeocystis* blooms (white block) and after nutrient reduction scenarios (black block) : 1 = 90% P removal; 2 = 75% denitrification; 3 = 90% P removal and 75% denitrification

Conclusion

These exploratory nutrient reduction scenarios clearly show that the proposed measures by the European Commission don't achieve the 50% reduction of N and P load to the coastal North Sea needed to substantially reduce *Phaeocystis* blooms in the eutrophicated Southern Bight of the North Sea. This is due to the complex interactions between the continental and coastal marine system. Only the integrated land-coastal sea modeling approach developed during this project is able to provide guidance to better select the available control actions on the watershed in order to reduce the development of *Phaeocystis* colony blooms. Further numerical work has to be done in this direction and should be supported by infrastructure development *i.e.* the setting up of permanent monitoring stations of *Phaeocystis* colony bloom development in the key sites of the coastal North Sea for assessing long-term changes of the ecosystem functioning resulting of waste water purification policies and climate change and verify model predictions.

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