

Nutrient dynamics in European water systems

(A digest from the Eloise results)

CONTENT

1	ELOISE FROM START TO PRESENT	3
1.1	ELOISE Science plan.....	3
1.2	Synthesis of the ELOISE results, realizing the ELOISE’s added value.....	4
2	DEFINITION OF THE DOCUMENTED TOPICS.....	6
2.1	Definition of the documented topics.....	6
3	CHARACTERISATION OF THE NUTRIENT SOURCES	8
3.1	Atmospheric nutrient inputs.....	9
3.1.1	Improved spatio-temporal resolution for the assessment of atmospheric deposition.....	9
3.1.2	Atmospheric deposition on the watersheds	12
3.1.3	Short and local but significant effects on coastal productivity	12
3.1.4	Phosphorus, a neglected aspect of the atmospheric deposition	13
3.1.5	Modelling advances towards an improved assessment of the atmospheric deposition.....	13
3.1.6	Implications for management activities.....	14
3.2	Riverine and groundwater inputs	15
3.2.1	Integrated Nitrogen model for multiple source assessment in Catchments (INCA).....	15
3.2.2	The RIVERSTRAHLER model, from the river source to deep-sea.....	17
3.2.3	Groundwater, the hidden giant	19
4	NUTRIENT PROCESSING IN ESTUARIES AND COASTAL AREAS – WHAT PROCESSES GOVERN THE FATE?	21
4.1	Sediment biogeochemistry.....	22
4.1.1	The importance of benthic nutrient pools in eutrophic systems	22
4.1.2	Mechanisms behind the sediment buffering capacity	23
4.1.3	The share of controlling factors in denitrification rates	24
4.1.4	Denitrification is not the obligate route for nitrogen to escape	25
4.1.5	New developments at the frontline of process modelling.....	26
4.2	Role of vegetation in nutrient cycling (PROJECTS: ECOFLAT, NICE,	28
4.2.1	Microalgal mats versus denitrification	28
4.2.2	N-sequestration in macrophyte biomass.....	30
4.2.3	Rooted macrophytes and sediment buffering capacity	32
4.3	Modelling at scale of basins.....	33
4.3.1	Simple models for simple questions	33
4.3.2	Requirements for an assessment of fluxes within the coastal system.....	34
4.3.3	When biology has to be coupled with physics	35
4.3.4	Complexity increase is challenging our computing capacity.....	37
4.3.5	Including dynamic sediment modelling should be the next challenge	39
5	EFFECTS OF ALTERED NUTRIENT DISCHARGES ON THE FUNCTIONING OF COASTAL AND ESTUARINE FOOD WEBS.	42
5.1	Eutrophication, definition(s).....	42
5.2	Different perception of eutrophication	44

5.3	Nutrient loading and the response in coastal pelagic communities.....	46
5.3.1	Analysis of effects on food webs based on flow networks.....	46
5.3.2	Regional specificities in nutrient effects	48
5.3.3	Effects of perturbation/observation scales on the nutrient effects	50
5.3.4	Effect of altered nutrient discharge on the <i>Phaeocystis</i> bloom in the North Sea.....	51
5.3.5	Effects of altered nutrient discharges on diatoms	52
5.3.6	Propagation of the nutrient signal through the pelagic food web	54
5.4	Nutrient fluxes in coastal benthic communities.....	57
5.4.1	Food sources for meiobenthos and macrobenthos	59
5.4.2	What controls the nutritive flux to macrobenthos.....	61
5.5	References	64

1 Eloise from start to present

1.1 ELOISE SCIENCE PLAN

ELOISE – how the land-ocean interaction operates, and how this is influenced by human activities.

ELOISE is the European Union's thematic network where coastal zone research is combined to focus on the important questions of how the land-ocean interaction operates, and of how this is influenced by human activities. Operating since 1996 there have been 59 ELOISE projects, rendering it the world's largest coastal research initiative. Throughout the period it has been intended that ELOISE contribute directly to activities within integrated coastal zone management and spatial planning, and thus to European coastal policy.

After the publication of its science plan as a result of a workshop of European coastal scientists (1994), the ELOISE cluster of projects was set up as the European contribution to the IGBP program LOICZ. The aim was to bundle efforts of the European scientific community in elucidating some of the outstanding scientific problems in the study of the role of coastal systems in the interaction between the terrestrial and the oceanic realms.

The science plan highlighted the following objectives:

1. **Significance of coastal seas in global change.** *Emphasis in this section was on origin and fate of organic matter, nutrients, trace elements, sediments and biogases. The approach stressed the biogeochemical functioning of coastal ecosystems, and its interaction with the structure (biological structure, e.g. species composition, but also geomorphological structure) of coastal ecosystems.*
2. **Human impact on coastal seas.** *The approach emphasized the regional and global consequences of human impact through pollution, eutrophication and physical disturbance.*
3. **Socio-economic development and coastal seas.** *The focus was on a strategic approach to the management of sustainable coastal zone resource use and development. Much emphasis was placed on multidisciplinary approaches of natural and socio-economic sciences, and on the analysis of management failures as a basis for better management in the future.*
4. **Methodology and Implementation of ELOISE.** *The science plan pleaded for the development of a European scientific infrastructure for coastal zone research tools and data management.*

Proposals for European R&D projects in the fourth and fifth frameworks were invited (amongst others) for the topics proposed in the ELOISE science plan. These proposals were evaluated on the basis of their scientific excellence and their contribution to European scale economic and social development. Acknowledged projects matching topics from the ELOISE science plan were clustered within the ELOISE cluster. Co-ordination between the projects in the cluster was achieved primarily through the ELOISE Open Science Meetings organized by the European Commission. These meetings were also a means to stimulate discussions and generate joint activities between projects.

After ten years of implementation, more than fifty projects have been clustered as ELOISE projects. About half of them are still running and have not yet published many results. Most of the scientific results from the projects that have been completed are available in the form of publications (<http://www.nilu.no/projects/eloise/>).

1.2 SYNTHESIS OF THE ELOISE RESULTS, REALIZING THE ELOISE'S ADDED VALUE

Since July 2002 the Secretariat for the Eloise cluster is hosted by a Consortium whose members are:

- National Institute of Ecology, Centre for Estuarine and Coastal Ecology (NIOO), Yerseke (NL)
- Free University of Amsterdam, Institute for Environmental Studies (IVM), Amsterdam (NL)
- University of East Anglia, CSERGE, Norwich (GB)
- Centre for Ecological Economics (CEE), Kjeller, (N).

The main tasks of the Secretariat are:

1) Technical and administrative management of ELOISE

Aiming at supporting the application of ELOISE research in European coastal policy, in coastal management, and in future research both within and beyond Europe:

- organizing the annual Conference
- documenting and promoting project results
- link with related research programmes such as LOICZ
- liaison between ELOISE and European coastal management stakeholders (HELCOM, OSPAR, Mediterranean and Black Sea Conventions ...)
- maintenance of web site resources and newsletter publication
- compilation of the most important results from ELOISE in a meta database aggregated to coastal management level.

2) Scientific coordination of current and past ELOISE findings

Aiming at the dissemination of the ELOISE findings, the implementation of recommendations, and the realization of the ELOISE added value for coastal management.

- developing and applying a framework for integrated assessment of environmental and socio-economic aspects of changes caused by major anthropogenic and natural drivers.
- documenting, and refining tools for application of our understanding of land-ocean interactions generated within ELOISE.
- organizing workshops targeted specifically at the realisation of the added value of ELOISE for coastal management.

Three workshops were organized in 2003:

- **Demands at the European and Global level, (upscaling). [NIOO-CEME]**
upscaling of ELOISE results to European and Global scale issues.
- **Integration into European Policy: Environmental Impact Assessment. [IVM-VU]**
integration of ELOISE results into European policy.
- **Developing coastal futures for Europe. [CSERGE-UEA]**
looking ahead to the coastal future and its associated needs for science, policy and management tools.

The initial step for the ELOISE year 2 (2004) project is the assembly of ELOISE information into digests on four selected themes:

- a) Habitat dynamics at the coast-catchment interface, including ecosystem change, landuse, and responses
- b) Climate change, including coastal change, erosion, policy response, management
- c) Nutrient dynamics, including eutrophication, stoichiometry, habitat consequences, climate change, policy and economic angles
- d) Contaminant budgets, behaviour, habitat and ecological consequences, policy and socio-economic angles

The present document, contribution by the NIOO-CEME to the assembly of ELOISE results into digests, is dealing with the third theme (nutrient dynamics). Aiming at an improved representativeness only peer-reviewed published (or in press) papers are taken into consideration.

2 Definition of the documented topics

2.1 DEFINITION OF THE DOCUMENTED TOPICS

The European coastal zones are areas of great concern because of growing problems associated with increasing inputs of nutrients. These have resulted in a higher incidence of harmful algal blooms and other eutrophication phenomena and caused deleterious impacts on fisheries and tourism (Lancelot et al. 1989). To understand the impacts of increased nutrient additions to the coastal area, the full magnitude and seasonality of nutrient inputs must be described (de Leeuw et al. 2001)= first workshop

2d workshop

3rd workshop

Table 1

Matching list of the ELOISE projects (C for completed projects) with the three selected topics (See list in text below)

Project Acronyme		Project Title (URL)	1	2	3
ANICE		Atmospheric Nitrogen Inputs into the Coastal Ecosystem C (http://www.tno.nl/instit/fel/anice/)	x		
BASIC		Baltic Sea cyanobacteria C (?)		x	
BIOGEST		Biogases Transfers in Estuaries. C (http://www.ulg.ac.be/oceanbio/biogest/biogest.htm)		x	
COMWEB		Comparative analysis of food webs based on flow networks: Effects of nutrient supply on structure and function of coastal plankton communities. C (?)		x	x
COSA	x	Costal Sands as Biocatalytical Filters (http://eu-cosa.org/en/index.html)	X	x	
DANLIM	x	Detection and Analysis of Nutrient Limitation in Coastal Plankton Communities across a Hierarchy of Temporal and Physiological-Systemic Scales (http://www2.fimr.fi/en/tutkimus/tutkimusalueet/uuututkimus/danlim.html)		x	x
DANUBS		Nutrient Management in the Danube Basin and its impact on the Black Sea (http://danubs.tuwien.ac.at/)	X	x	
DOMAINE	x	Dissolved organic matter (DOM) in coastal ecosystems: transport, dynamics and environmental impacts (http://www.domaine.ku.dk/)	X	x	
ECOFLAT		The eco-metabolism of estuarine intertidal flat. C (http://www.nioo.knaw.nl/CEMO/ECOFLAT/ecoflat.htm)		X	X
EROS-21		Biogeochemical Interactions between the Danube River and the North-Western Black Sea. C (?)	X	X	x
ESCAPE		Entangled sulfur and carbon cycles in Phaeocystis dominated ecosystems. C (http://www.biol.rug.nl/escape/)		X	
EULIT		Effects of Eutrophicated seawater on rocky shore ecosystems studied in large littoral mesocosms. C (?)		X	
EUROTROPH	x	Nutrients Cycling and the Trophic Status of Coastal Ecosystems (http://www.ulg.ac.be/oceanbio/eurotroph/)	X	X	
BIOGEST		Biogases Transfers in Estuaries. C (http://www.ulg.ac.be/oceanbio/biogest/biogest.htm)		X	
INCA		Integrated Nitrogen Model for European Catchments (http://www.rdg.ac.uk/INCA/)	X	X	
ISLED		Influence of rising sea level on ecosystem dynamics of salt marshes. C (?)		X	
KEYCOP		Key coastal processes in the mesotrophic Skagerrak and the oligotrophic Northern Aegean: A comparative study. C (http://biologi.uio.no/mzk/keycop/home.htm)			X
MEAD		Marine Effects of Atmospheric Deposition (http://www.uea.ac.uk/env/mead)	X		
METROMED		Dynamic of Matter Transfer and Biogeochemical Cycles: Their Modelling in Coastal Systems of the Mediterranean Sea. C (?)			X
NAME	x	Nitrate in Aquifers and influences on carbon cycling in Marine Ecosystems. (www.natur.ribeamt.dk/name)	X		
NICE		Nitrogen Cycling in Estuaries. C (http://www.dmu.dk/LakeandEstuarineEcology/NICE)		X	
NTAP	x	Nutrient dynamics mediated through turbulence and plankton interactions (www.icm.csic.es/bio/projects/ntap/)		X	
PHASE		Physical Forcing and Biogeochemical Fluxes in Shallow Coastal Ecosystems-PHASE. C (http://www.nioo.knaw.nl/cemo/phase/main.htm)		X	x
RANR		Regional analysis of subsurface retention of nitrogen and the impact of such retention on the export of nitrogen from land to sea. C (http://www.mai.liu.se/ranr/index.html)	X	X	
ROBUST		The role of buffering capacities in stabilising coastal lagoon ecosystems. C (http://www.epoc.u-bordeaux.fr/fr/Robust/default.html)		X	
SUB-GATE	x	Submarine groundwater-fluxes and transport-processes from methane-rich coastal sedimentary environments. C4 (http://www.geomar.de/projekte/Sub-GATE/)	X	x	

We will document the new insights gained from the ELOISE research on topics related with the role of coastal systems in land-ocean interaction. Most of it will be on biogeochemical cycles of carbon and nutrients with a focus on the eutrophication problematic.

Three mainstream topics were identified based on the up to date list of publications from the ELOISE projects:

1. Relating nutrient fluxes to land-based activities, atmospheric and river processes
2. Nutrient processing in estuaries and coastal areas – what processes govern the fate?
3. Effects of altered nutrient discharges on the functioning of coastal and estuarine foodwebs

3 Characterisation of the nutrient sources

The European coastal zones are areas of great concern because of growing problems associated with increasing inputs of nutrients since the late 1960s. These have resulted in a higher incidence of harmful algal blooms and other eutrophication phenomena and caused deleterious impacts on fisheries and tourism (Lancelot et al. 1989). Since the late 1980s agreements have been made at national and international levels to substantially reduce the nutrient emissions to the aquatic environments. For example, dramatic changes in the discharge of phosphorus to the North-Sea have already been observed, whereas nitrogen emissions did not change much over the same period (de Jonge et al. 2002). The implementation of these measures represents a high cost for the community (Conley et al. 2002) and this demands an efficient assessment of their effects on the environment with respect to their objectives. Comprehensive monitoring programs are required to determine if reductions in nutrients are achieved by the measures taken and should help decision makers to choose appropriate additional measures to fulfil the objectives.

At world scale, efficient assessment tools for nutrient management are also urgently needed for the developing countries where explosive industrialisation, urbanisation and demography heavily impact on the environment (eutrophication, drinking water resources).

3.1 ATMOSPHERIC NUTRIENT INPUTS

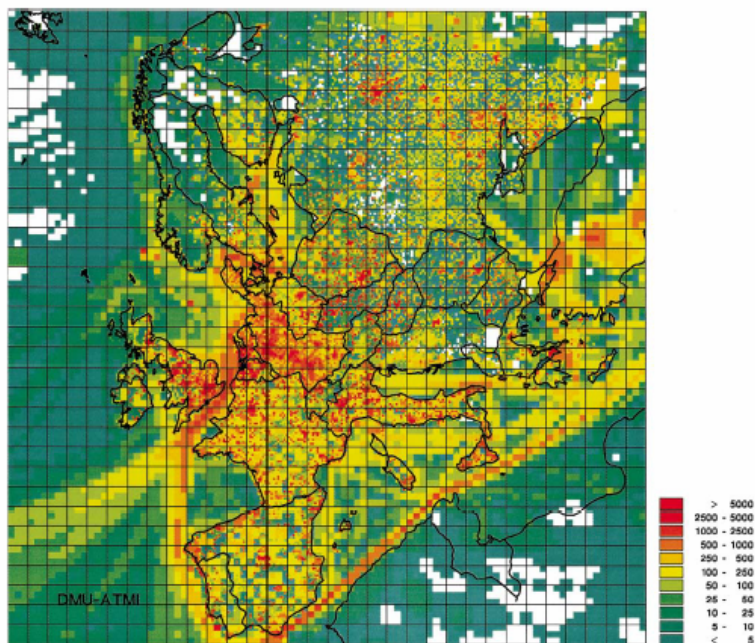
3.1.1 Improved spatio-temporal resolution for the assessment of atmospheric deposition

A significant fraction of the nutrients entering the coastal system consist of nitrogen compounds which are introduced both as inorganic species and as dissolved organic nitrogen (DON). Terrestrial inputs of nitrogen are often dominated by riverine transport, especially in the winter. However, atmospheric deposition of nitrogen compounds has been shown to be a significant terrestrial input to the coastal seas, especially in summer and fall. As an example, the atmospheric contribution to the total land based nitrogen input has been reported to be on the order of 30% for the total North Sea (North-Sea-Task-Force 1993).

As for the origin of the nitrogen that leads to atmospheric N deposition, two important sources are recognized (Hertel et al., 2002). For the North Sea it is estimated that 38% of the total deposition originates from emissions related to agricultural activity (NH₃ and NH₄⁺) and 72% due to emissions from combustion sources (mainly traffic, industry and power production) (aerosol phase NO₃- and gas phase NO_y compounds). A remarkable finding of this study is that ship traffic is a very significant source of marine-deposited N (Figure 1).

Figure 1

Total annual NO_x emissions in 1998 for the model domain given in ton NO₂ per 16:67 km x 16:67 km grid. The shipping routes are clearly identified by their emissions on this map.



The experimental and modelling results support the hypothesis on the importance of coastal effects on nitrogen inputs to the regional seas.

Model calculations in (Hertel et al. 2002) show that the wet deposition dominates strongly the nitrogen deposition to the North Sea with an average contribution of 81% (Table 2). Only at the coastline close to the agricultural emissions is dry deposition more significant, and even here the contribution is only about 25–30%. This is also seen in the contribution from NH_x of more than 50% at the coastline whereas the general picture is a contribution of 30–40%. This again means that nitrogen oxides from combustion processes

dominates the nitrogen deposition and mainly in the form of wet deposition of nitrate from atmospheric particles.

Table 2

Estimation of the different chemical forms and deposition modes of atmospheric nitrogen into the North Sea. From Hertel et al. (2002)

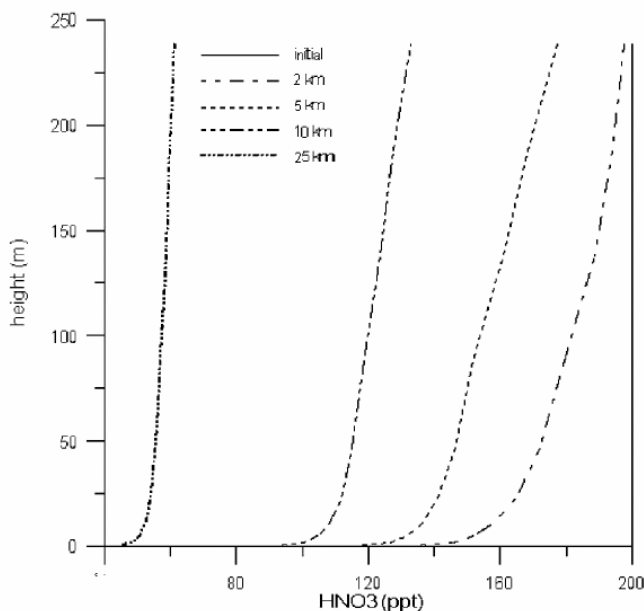
	Wet deposition (kt N)	Dry deposition (kt N)	Total deposition (kt N)
NH ₃	24	19	43
NH ₄ ⁺	191	36	227
NO _y gas	151	43	194
NO ₃ ⁻	210	35	245
N total	577	132	709

In ANICE project (de Leeuw et al. 2001) focus is on quantifying the deposition of atmospheric inputs of nitrogen compounds (HNO₃, NO₃, NH₃ and NH₄⁺) into the sea, both near the coast and in open water, and the governing processes. Of particular emphasis within ANICE are the relevant spatio-temporal scales for the deposition processes in the coastal zone:

Due to their reactivity and due to scavenging by sea salt aerosol, a significant fraction of the gaseous species such as NH₃ and HNO₃ may be removed from the atmosphere in the first 10–20 km across the coastline (de Leeuw et al. 2001). As a result, the magnitude of the inputs drastically decreases with the distance from the coast (Figure 2).

Figure 2

Modelled concentration profiles of nitric acid for various distances from the coast (from de Leeuw et al., 2001)



In particular HNO₃ reacts directly with sea spray aerosol and evidence of the sea spray replacement reaction is presented. Current atmospheric chemistry transport models do not include such reactions. Work is underway in several groups to implement heterogeneous chemistry involving HNO₃.

Large deposition of nitrogen may occur during short periods (de Leeuw et al. 2003). This is illustrated with an example for the ANICE experiment in August 1999, when the southern North Sea experienced a

short period of strong south-easterly flow. Mass concentrations of ammonium and nitrate aerosol in the fine and coarse fractions measured at WAO during this period are presented in Figure 3. During during the period centred on 26 August 1999, the atmosphere provided enough nitrogen to fix $5.3 \text{ mmolCm}^{-2} \text{ day}^{-1}$.

Figure 3

Variations in nitrogen deposition on the Norfolk coast (Weybourne) as a result of changes in wind regime (de Leeuw et al. 2003)

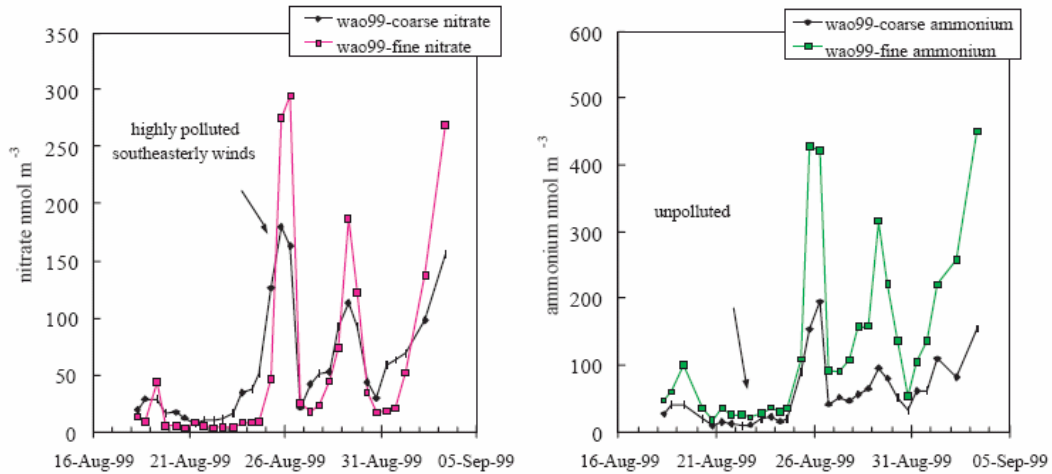
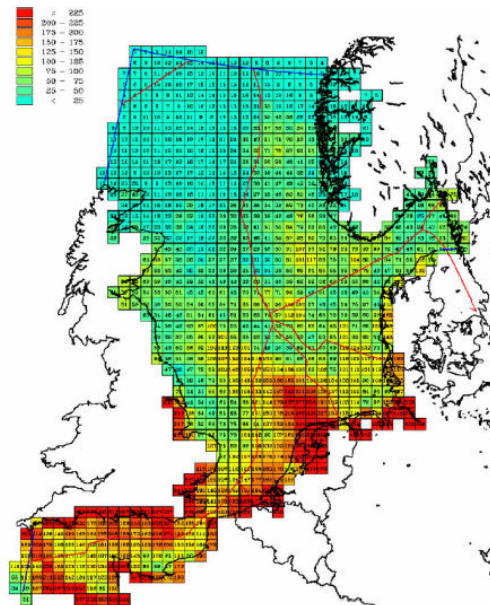


Fig. 1. Temporal variation of the concentrations of nitrate and ammonium in the fine and coarse fractions measured at Weybourne during the ANICE experiments in August/September 1999.

The spatial distribution of nitrogen deposition to the North Sea (de Leeuw et al. 2003) shows strong gradients near the source areas that result from the processes described above. They have the effect of focusing atmospheric deposition into coastal areas (Figure 4).

Figure 4

Total atmospheric nitrogen deposition to the North Sea in August 1999. Deposition values are given in kgNkm^{-2} (de Leeuw et al. 2003)



3.1.2 Atmospheric deposition on the watersheds

Spatially, two ways of atmospheric inputs are important: direct deposition onto the water surface of estuaries and coastal seas, and atmospheric deposition in the watersheds. The latter source, as it operates over large surfaces with often elevated atmospheric concentrations of nitrogen (because they are close to emission sources), is quantitatively important, even though a relatively small fraction of the deposited N eventually reaches the rivers.

Nitrogen inputs from atmospheric deposition over the Tweed catchment was estimated by Jarvie et al. (2002) as $3 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for both $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$, based on 1994 meteorological and emission data. The contribution of atmospheric deposition to nitrate concentrations in the Tweed river was estimated as between 5 and 10%. In North-American estuaries, Castro & Driscoll (2002) calculated that between 15 and 42 % of the N input into the estuary was derived from atmospheric deposition on watershed and river. This suggests that (direct and indirect) atmospheric input of N might be responsible for a significant proportion (one-third to one-half) of the total (non oceanic) N input into a coastal system as the North Sea. More research is needed at smaller scales, with particular emphasis on the non-linear interaction with biology. Moreover, the atmospheric chemistry needs further process study and development of models. As atmospheric input of nitrogen is dependent on human-influenced sources, a continuous monitoring seems to be essential at the European scale.

3.1.3 Short and local but significant effects on coastal productivity

Assessment of the impact of atmospheric nitrogen on coastal ecosystems will be based on comparisons of phytoplankton nitrogen requirements, other external nitrogen inputs to the ANICE area of interest and the direct nitrogen fluxes provided by ANICE.

During spring and summer, the water column is stratified, the mixed layer is shallow and water column nutrient levels are depleted. Therefore, during this period, the atmosphere may represent the dominant source of new nitrogen to surface waters (e.g., Galloway et al., 1994; Spokes et al., 2000; Plate, 2000). The impact of atmospheric inputs on surface water biogeochemistry may be enhanced if deposition occurs in short, high concentration, pulses.

The largest contributions to nitrogen atmospheric deposition come from wet deposition of aerosol phase nitrogen compounds (NH_4 and NO_3). These components are tightly coupled to the distribution and amount of precipitation. Therefore it can be expected that the amount of deposition of these components can change significantly from year to year. This again suggests that long-term studies are needed when the magnitude and seasonality of atmospheric nitrogen load to the North Sea has to be explored (Hertel et al. 2002).

In the Kattegat Strait, the events of high atmospheric wet deposition could increase the growth of chlorophyll around 20% or more (Hasager et al. 2003). Similarly, results by Spokes et al. (2000) suggest that about 30% of the new production in eastern Atlantic surface waters off Ireland can be supported by atmospheric inputs in May 1997 and that most of the input occurs during short lived, high-concentration, south-easterly transport events.

The local nature of high nitrogen wet deposition events makes it a challenge to infer the cause-effect relationship at daily time scale between atmospheric deposition and algal blooms.

3.1.4 Phosphorus, a neglected aspect of the atmospheric deposition

Nixon (1997) states: “*The atmosphere is not a significant source of P under modern conditions*”. However in a review by de Jonge et al. (2002), HPO_4 deposition is accounted for 1.4, 4.8 and 7.2 % of the total phosphorus input to the Ems estuary, the Chesapeake Bay and the Baltic Sea. It is also true is that Aerosol N:P ratio is universally very high (Baker et al. 2003), so that aerosol is always deficient in P relative to phytoplankton requirements. Phytoplankton utilisation of atmospheric nutrient inputs will therefore tend to drive the ecosystem towards P limitation. According to the principle that the first limiting factor is the one that controls the process, the quantity of deposited phosphorus may control the intensity of primary production. In the Mediterranean where abundant cyanophyceae are actively fixing the atmospheric N_2 , N is not considered as a limiting factor and a lot of effort is put on the assessment of phosphorus deposition. Migon et al. (2001) noted that a rain event is likely to input within a single day up to 17 mmol m^{-2} of reactive P to surface waters at a northwestern Mediterranean coastal site, which may theoretically induce a biological production of $20 \text{ mg C m}^{-2} \text{ day}^{-1}$.

Markaki et al. (2003) estimated the effect of the phosphorus deposition by 38% of the new production observed in Creta during the summer and autumn period (i.e., when water stratification is at its maximum).

3.1.5 Modelling advances towards an improved assessment of the atmospheric deposition

The aim of the atmospheric nitrogen inputs into the coastal ecosystem (ANICE) project is to improve transport–chemistry models that estimate nitrogen deposition to the sea.

An interesting feature of the ANICE project is the use of two atmospheric chemistry transport models, ACDEP and METRAS, both with their respective aerosol modules (de Leeuw et al. 2001).

ACDEP is used to estimate atmospheric inputs of nitrogen to the whole North Sea, integrated over periods varying from 6 h to a year.

METRAS in turn, is used for studying scenarios for specific days, to calculate the atmospheric nitrogen input to coastal waters with a high resolution in space (some 100 m) and time (minutes). The combined modelling effort is expected to lead to a major improvement in the estimate of atmospheric inputs into the North Sea, which can subsequently be used in effect studies.

The strong spatial variations in atmospheric composition imply that a coarse grid model will not be able to correctly predict the effect of coastal processes at very short fetches on the nitrogen input, unless these processes are included through a coastal sub-grid or a proper parameterisation. Current models use grids that are too coarse to describe the governing processes with sufficient accuracy, particularly in coastal regions (de Leeuw et al. 2001).

From the available ELOISE results and closely related research activities in Europe, we can conclude that state-of-the-art analytical tools and models are available, and that these are able to supply good estimates of atmospheric N input, as well as of the responsible sources, at a relatively coarse temporal and spatial scale. Application to other areas than the North Sea might be wanting, but the models should be generic enough to extrapolate easily.

3.1.6 Implications for management activities

ANICE evaluates the effect of short episodes with very high atmospheric nitrogen concentrations. One such episode resulted in an average deposition of $0.8 \text{ mmol N m}^{-2} \text{ day}^{-1}$, which has the potential to promote primary productivity of $5.3 \text{ mmol C m}^{-2} \text{ day}^{-1}$. Most of the deposition occurs during short periods with high atmospheric concentrations. This atmospheric nitrogen is almost entirely anthropogenic in origin and thus represents a human-induced perturbation of the ecosystem.

Hence, the episodic fluxes largely determine the total primary productivity due to atmospheric N deposition in the area. For the southern North Sea, the atmospheric contribution is estimated at ca 5.5% of the total required new nitrogen, for the entire North Sea the atmospheric contribution is ca 3.2%. Although these numbers may not seem impressive, presented results show that most of the nitrogen is delivered during short episodes.

As atmospheric input of nitrogen is dependent on human-influenced sources, a continuous monitoring seems to be essential at the European scale.

3.2 RIVERINE AND GROUNDWATER INPUTS

The ELOISE projects INCA, RANR, EROS2000/EROS21 have focused on the modelling of nutrient transformation processes in the watershed and the river network. The main aim was to relate statistics of land use and human (agricultural, domestic) practices of nutrient input into the system, to the load of rivers.

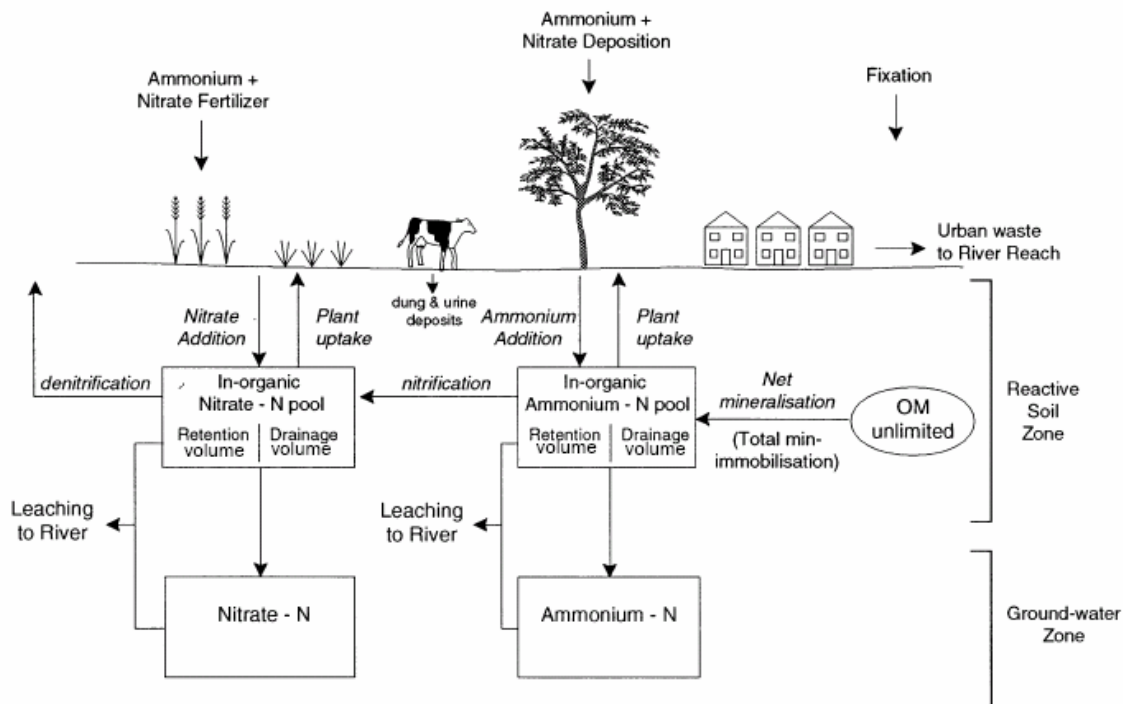
3.2.1 Integrated Nitrogen model for multiple source assessment in Catchments (INCA)

The INCA project, see overview in (Neal et al. 2002), has developed a generic deterministic model for application across Europe. A primary task of the EU-INCA project has been the development of a generic model applicable to the wide range of climatic regimes across Europe with process equations that will work from dry land Mediterranean environments through temperate Atlantic systems to Arctic Northern Scandinavian conditions.

INCA is a deterministic model that includes land and river processes, and is driven by spatially explicit input data. The model accounts for stocks of ammonium and nitrate in the soil and ground water pools, and in the stream reaches. The model also simulates the flow of water through the plant/soil system from different land use types to deliver the N load to the river system, which is then routed downstream after accounting for direct effluent discharges, and in-stream nitrification and de-nitrification. Figure 5 illustrates the land and river processes in the INCA model.

Figure 5

Overview of land (upper panel) and instream (lower panel) processes in the INCA model from Wade et al (2002)



The ability of the INCA model to reproduce broad-scale spatial patterns and seasonal dynamics in river flows and nitrate concentrations as observed by Jarvie et al. (2002) for the Tweed, suggests that the processes controlling first order variability in river water nitrate concentrations are represented successfully within the model.

INCA was successful in simulating downstream average spatial variations in flow and nitrate concentrations, including the effects of flow and nitrate inputs from major tributaries (Jarvie et al. 2002). The model simulations provide valuable clues about key sources of nitrogen within the catchment and their variability in time and space. The simulations demonstrated the importance of leaching from arable land to the loads of nitrate draining from the Tweed catchment (up to approximately 70% of monthly nitrate loads in 1995).

One of the valuable functions of INCA is its ability to be used as a management tool, allowing an analysis of strategies which might be adopted to improve water quality. The model now provides a valuable tool by which to assess contributions of different catchment sources of nitrogen and the possible effects of future changes in catchment land use and management. Some examples of the scenarii calculated with INCA for the Tweed river (Jarvie et al. 2002):

- ✓ -a 20% reduction in fertiliser inputs is predicted to result in average reductions of 12% in-stream nitrate concentration
- ✓ -by allowing all arable land to revert to its semi-natural state (ungrazed, unfertilized grassland), INCA predicts an average nitrate reduction at Norham of 57%.
- ✓ -by allowing all grazing land to revert to its semi-natural state (ungrazed, unfertilised grassland), INCA predicts an average reduction in nitrate concentrations of 20%.

However, the variability in model fit along the river reaches and through time highlights considerable local variability in processes controlling the leaching and transport of nitrogen along the catchment-river continuum (Jarvie et al. 2002).

One problem seems to be an over-estimation of NO₃ concentrations during the summer low-flow periods and the subsequent period of wetting up and catchment nitrate delivery during the subsequent winters. This may reflect the inability of INCA to model in-stream uptake of nitrogen by aquatic plants, which are an important feature of the tributaries in the lower agricultural parts of the basin. For applications of INCA to slow-flowing lowland eutrophic rivers, the possibility of incorporating a plant uptake component needs to be investigated.

While seasonal variability in nitrate concentrations was well represented by model simulations, extremely high flows and associated intermittent high nitrate concentrations were often poorly simulated. This problem is likely to remain for a deterministic model as INCA.

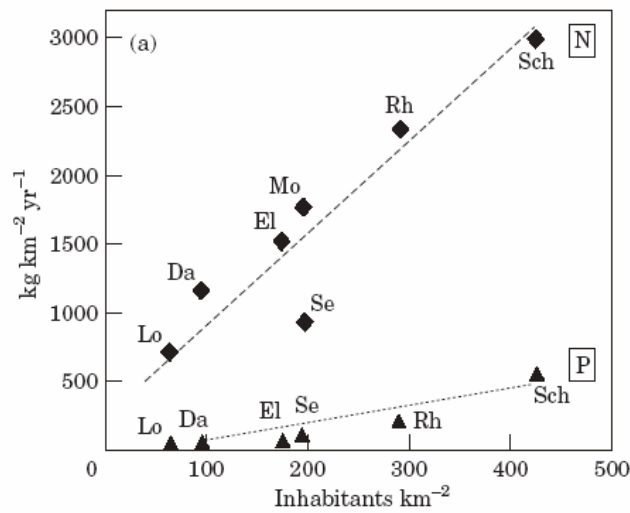
Wade et al (2002b) have developed INCA-P, a version of the model for phosphorus. Linking INCA-P with INCA could provide a more complete assessment of the combined impacts of N and P in river systems, especially in situations where a system is alternately N and P limited. This development is important in that the impacts of the nutrients on the aquatic environment are linked to biological functioning in a connected fashion and there is a major need for an integrated nitrogen and phosphorus model to examine their relative importance and potential nutrient limitation.

3.2.2 The RIVERSTRAHLER model, from the river source to deep-sea

A full coupling of models was established from the watershed, over the river, to the coastal area and the deep sea for the EROS2000/EROS21 projects. The study case was the Danube as it influences the north-western shelf of the Black Sea and the whole of the Black Sea proper. The RIVERSTRAHLER model (Billen & Garnier 2000, Garnier et al. 2002), which was first applied to the Seine (Billen et al. 2001), was used to describe nutrient and ecological dynamics in the Danube watershed and river. This model synthesises the hydrological network of a river basin by stream order (HYDROSTRAHLER module), which reduces the computational load to a reasonable level. For different sub-basins, nutrient and organic inputs are derived from gross statistics (population density, type and intensity of industrial activity, fertiliser application, land use) (Figure 6).

Figure 6

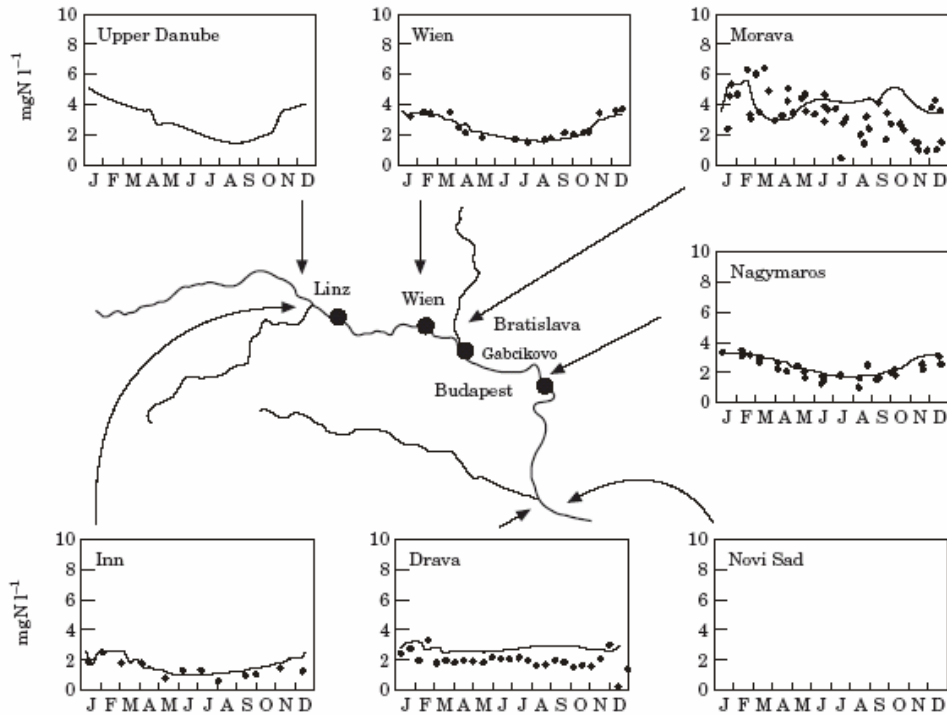
Relationship between specific fluxes of nitrogen and phosphorus (kg N or P km^{-2}) and population density ($\text{inhabitants km}^{-2}$), Da: Danube River; El: Elbe River; Lo: Loire River; Mo: Mosel River; Rh: Rhine River; Sch: Scheldt River; Se: Seine River. From Garnier et al.(2002).



The river model for the different stream orders of several sub-basins represent full ecological dynamics, including transformations of nutrients in the ecosystem (biogeochemical RIVE module). A reasonable agreement was found between the simulations of the model and the observations (Figure 7). The sharp drop in N and P delivery to the Black Sea, observed since 1991, was simulated with a scenario constructed to reproduce new constraints based on documented modifications of human activity in the watershed.

Figure 7

Upper course of the Danube River, simulation by the RIVERSTRAHLER model of the seasonal nitrate variations for the period 1988–1990. Experimental data for the same period are given for comparison. From Garnier et al.(2002).



Application of the RIVERSTRAHLER model to the Seine river system did allow to establish a comprehensive budget of nitrogen transfers through the whole drainage network and to quantify the overall retention by riparian wetlands (Billen & Garnier 2000). It was shown that 25 – 55% of the nitrogen coming from below the root-zone of agricultural land or from the aquifers was retained or eliminated before reaching surface water. The lower retention was found in areas where dense agricultural draining had been installed, thus by-passing riparian wetlands. At the scale of the Seine catchment, riparian retention represents 70–110 ton N y⁻¹, while in-stream retention accounts for only 24–32 tonN y⁻¹.

3.2.3 Groundwater, the hidden giant

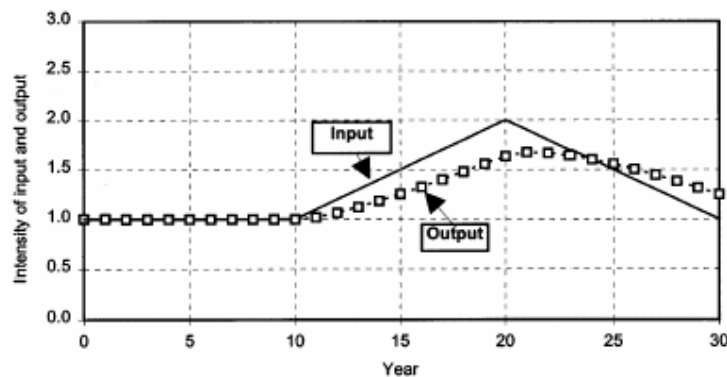
The modelling activities within RANR project has concentrated on the role of groundwater in the coupling between watersheds and rivers. One of the basic problems attacked was the delay in response of German major rivers (case study was the Elbe) after the considerable reductions of N input in arable land in former East Germany from 1990 onwards. In the same vein, several major Eastern European rivers have shown a lack of response to the dramatic decrease in the use of commercial fertilisers that started in the late 1980s. Hypothesis was made that the delay in response was explained by the long residence times of groundwater reservoirs and by the large amounts of organic nitrogen that have accumulated in soil during periods of higher application rates.

In the project the groundwater residence times were calculated for some East-German watersheds by using WECU, a supra-regional GIS-supported stochastic model (Kunkel & Wendland 1997). It was shown that the groundwater residence times in the upper aquifer vary regionally, differentiated between less than 1 year and more than 2000 years.

Grimvall et al (2000) presented a purely theoretical analysis of pools and fluxes explaining why the response to increased input of fertilizers in the 1950s and 1960s appears to have been more rapid than the response to decreased input in the 1990s. This conceptual model has two reservoirs, one fast-responding and one with a long response time. It shows a dual response to changes in nutrient loadings, (1) reacts rapidly to increased input from point and diffuse sources and (2) has a very long lag time after a reduction of the input (Figure 8).

Figure 8

Impact of changed input on the output of a model comprising two parallel compartments with different residence times (1 and 10 years, respectively). From Grimvall et al (2000).



The core of the model system RANR that was developed consists of:

- (i) a nitrogen leaching model that extracts the essence of a process-oriented soil nitrogen model (SOILN) and specifies the minimum information needed to compute the total amount of nitrogen leached from the root-zone of a given area
- (ii) a runoff separation model that divides the total runoff into surface runoff and groundwater runoff.
- (iii) a two-dimensional groundwater residence time model (WEKU) equipped with a denitrification routine
- (iv) a GIS-procedure for extrapolating nitrogen fluxes from monitored catchments to entire regions.

- ✓ In contrast to the INCA project, the RANR project has not embarked on the construction of fully deterministic models for nutrient dynamics in watersheds. Instead it applied a combination of deterministic models, statistical models and a meta-modelling based upscaling from one-dimensional vertical process models.
- ✓ The moderate demands on the spatial resolution of input data by RANR implies that the system is operational for large areas and shows potential for studies on a European scale.
- ✓ The RANR concept can be applied in any area where agriculture is a major source of nitrogen deliveries to surface water and groundwater residence times may be significant. Such areas are prevalent in the European pleistocene lowland, which ranges from the Netherlands in the west to the Baltic republics and Ukraine in the east.

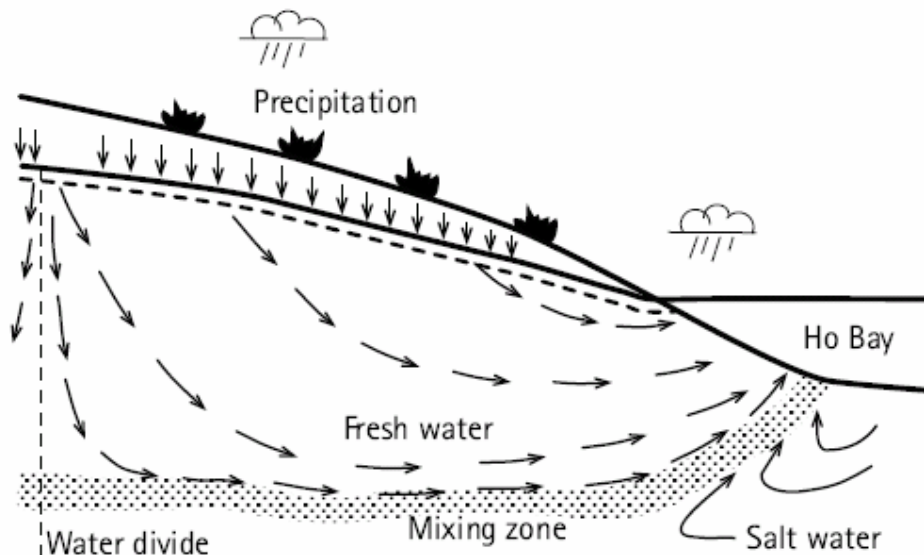
Groundwater dynamics are not only important within watersheds discharging in a river. Direct submarine groundwater discharge can be a very important route of nutrient transport to the sea. Water fluxes up to 40 % of the river water flow have been reported by Moore (1996) for the ca 400 km US coastline between the mouth of the Savannah river and Cape Fear.

The project SUBGATE studied the direct submarine groundwater discharge (SGWD) to the sea in a Baltic area (Kaleris et al. 2002). At the SUBGATE study site, the discharge rate is approximately $0.05 \text{ m}^3 \cdot \text{s}^{-1}$ per km of land-sea interface. Modelling showed that the pattern of discharge is spatially very variable, and that the process is very difficult to measure from field data alone.

The importance of groundwater discharge for nutrient fluxes to the sea is currently investigated in the NAME project (Gregersen 2002). NAME follows the route of nitrate all the way through the groundwater aquifer, passing the shoreface and into the marine environment at the Danish Ho Bay site (Figure 9) and detailed studies document the processes involved (Gregersen 2003). The groundwater at the NAME study site is draining agricultural fields and has nitrate concentrations normally ranging from 50-75 mg/l.

Figure 9

Nitrate-bearing groundwater infiltrates from areas with intense agriculture and discharges through the shoreface and seabed at the Ho Bay site (NAME project). From Gregersen (2003)



The geographical setting of an aquifer that discharges nitrate-containing groundwater directly into the marine environment is found at many places along the European coastline. The results obtained at this locality may therefore serve as a benchmark for assessing the problem at other localities in Europe.

4 Nutrient processing in estuaries and coastal areas – what processes govern the fate?

The European coastal zones are areas of great concern because of growing problems associated with increasing inputs of nutrients since the late 1960s. These have resulted in a higher incidence of harmful algal blooms and other eutrophication phenomena and caused deleterious impacts on fisheries and tourism (Lancelot et al. 1989).

Nutrients brought to the coastal areas through rivers, groundwater and atmosphere (Section 3) are made available to a large scale of transforming processes that will eventually determine the fate of these nutrients:

- Export to the open sea
- Cycling in pelagic and/or benthic production and mineralization processes
- Burial in sediment.

Beside investigations at the scale of processes, a huge effort has been put on the modelling of these transformation cycles in models at different levels of integration.

Significant progresses have been achieved in our understanding of these processes and in our capacity to predict their control on the nutrient fate in coast ecosystems.

4.1 SEDIMENT BIOGEOCHEMISTRY

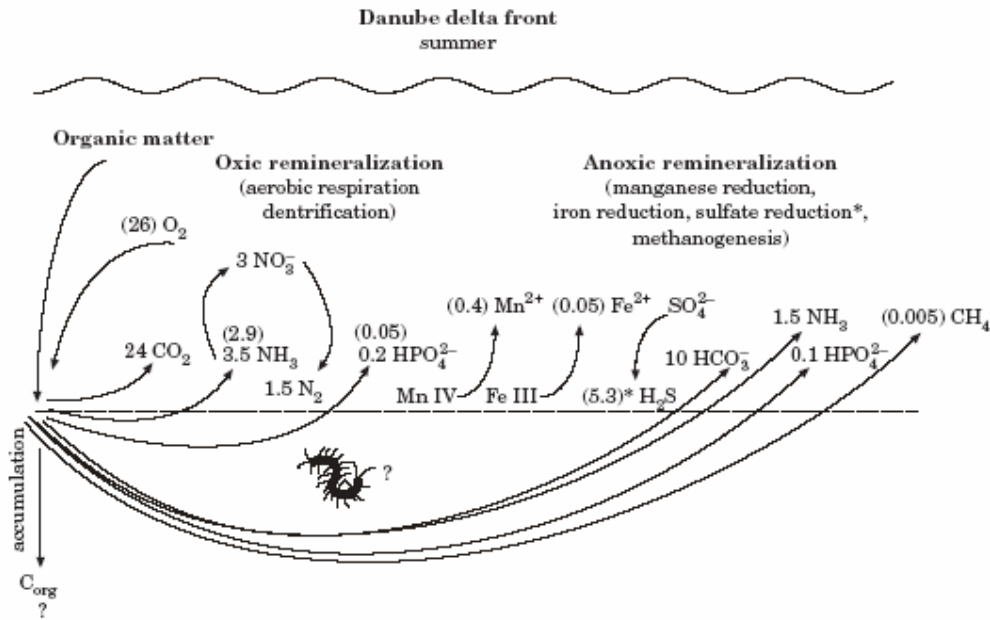
4.1.1 The importance of benthic nutrient pools in eutrophic systems

Within the EROS-2000 and EROS-21 projects, sediment biogeochemistry was studied as an important part of the whole ecosystem response of the north-western Black Sea shelf to variations in nutrient and organic input from the Danube and other major rivers.

Friedl et al. (1998) present results of benthic lander incubations at Black Sea stations influenced by the Danube or Dniester inputs. Sediment-water fluxes of oxygen, ammonium, silicate, orthophosphate, iron, manganese and sulphide were simultaneously measured at sites along an onshore-offshore transect. In general, a decrease of all benthic fluxes with distance from the coast was observed. Benthic regeneration of phosphate and silicate was very important. The estimate shows that benthic recycling of phosphorus and silica may be of the same order of magnitude as the input by the Danube river. Since the nutrient loads of the Danube are strongly phosphorus deficient $N:P=25$, the sediments are an important source to sustain high productivity. The $N:P$ ratio of estimated benthic fluxes 1.8–7.4 is far lower than the Redfield ratio 16 and the ratio of the Danube. 25, indicating intense denitrification in this system.

Figure 10

Rough estimate of diagenetic processes due to oxygen consumption and flux of reduced components at the Danube delta front in summer. Values in parentheses represent measured fluxes. Fluxes expressed in $\text{mmol m}^{-2} \text{day}^{-1}$. From Friedrich et al. (2002)



Friedrich et al. (2002) present similar results, but add seasonal dynamics. They show that oxygen depletion in summer leads to enhanced iron and manganese outfluxes from the sediments. Mass balance calculations of the nitrogen fluxes indicate that denitrification is an important remineralization pathway in the summer, with denitrification rates in the range of a few $\text{mmol NO}_3 \text{ m}^{-2} \text{ day}^{-1}$ (Figure 10). During spring, oxic remineralization and denitrification are important for the decomposition of organic matter. Therefore, the Black Sea shelf acts as a strong sink for the riverine nitrate load. As a result, the N/P ratios of benthic fluxes in summer are as low as 4:1 and 1.5:1 in the high and low flux areas, respectively. A rough comparison of

the river's nutrient load and the benthic recycling over a certain area showed that the near-shore benthic phosphate and silica recycling account for 50% and 35% of the Danube input in summer, respectively. Since the river input is phosphate deficient, this strong benthic nutrient recycling is an important factor sustaining high productivity in the coastal zone area of the Black Sea.

4.1.2 Mechanisms behind the sediment buffering capacity

Wijsman et al.(2002) provided a coupled diagenetic model for the shelf sediments of the Black Sea exposed to the Danube runoff. They predict from model runs that there are critical organic loading levels of sediments, where the sediment chemistry suddenly switches from oxic mineralisation to iron/manganese dominated mineralisation, and from these to sulphate reduction dominated mineralisation. The responses are highly non-linear due to the dynamics of re-oxidation of the reduced reaction products, which decrease redox potential and push the system further into the more reduced state. These sudden changes have also consequences for the buffer capacity of these sediments towards sulphide and phosphorus release.

Figure 11

Effect of the organic matter flux to the sediment on the relative importance (%) of the various mineralization pathways. The Mn-Fe and Fe-S swaps are indicated. From (Wijsman et al. 2002)

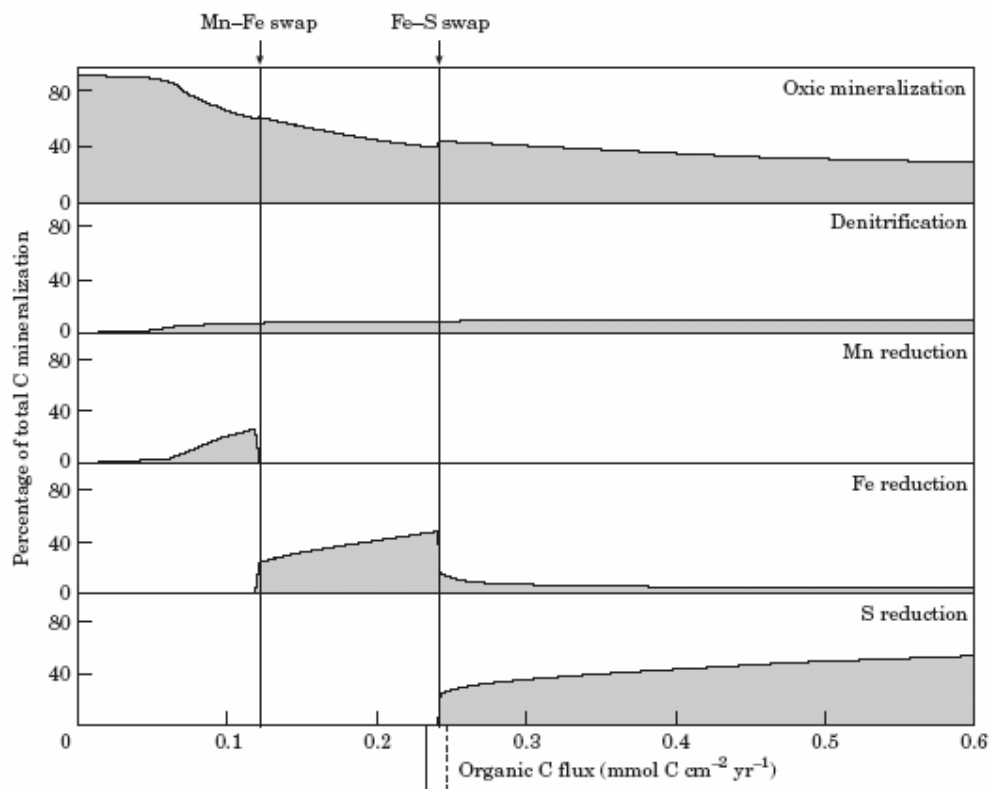
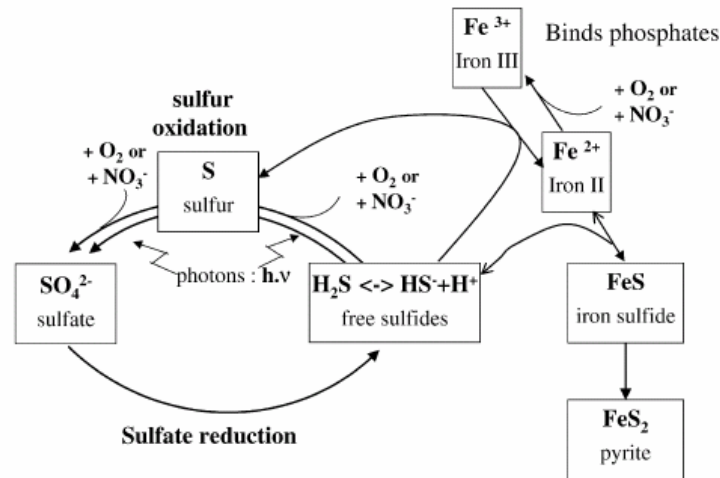


Figure 12

Interactions between sulfur cycling and iron chemistry in the sediment. Note that amorphous Fe_3^+ has as strong capacity to bind phosphates. From De Wit et al. (2001).



In the same vein, De Wit et al. (2001), in an overview of the ROBUST project, discuss the link between Fe, Ca, sulphide and phosphorus dynamics in sediments. They identify different benthic 'buffers' that can gradually be filled. As an example, Fe can react with free sulphide and thereby detoxify the sulphide. Fe and Ca sequester phosphorus in the sediment (Figure 12), preventing its release and re-use for further primary production.

Limitations of the sediment buffering capacities towards free sulphide were described by Heijs et al. (2000) in a hypertrophic coastal lagoon (Valle Smarlacca, Italy). In this hypertrophic environment where the 2 cm water layer overlying the organic rich sediment was permanently anoxic, sulphide was always present. A slurry experiment showed that Ca bound phosphorus was released after the addition of sulphide whereas it is generally acknowledged that sulphide releases phosphate from the Fe-bound pool only. In eutrophic coastal lagoons this process acts as a positive feedback on eutrophication, resulting in increased sulfide production in the sediment. As oxygen becomes the limiting factor the sulphide cannot be removed and toxic concentrations are reached.

Several pieces of evidence for the benthic buffering capacities have been brought forward, but a further working out of this model of alternative stable states, as well as a direct experimental test, would be very worthwhile.

4.1.3 The share of controlling factors in denitrification rates

Denitrification is a major sink in the nitrogen cycle with fixed-N eliminated as gaseous product. In sediments, denitrification can be sustained by nitrate diffusing from the overlying water column or generated in the sediment by nitrification. In recent years, there has been increasing interest in denitrification processes in the coastal zone, due to the capacity of denitrification to reduce the impacts of anthropogenic nitrogen loads. Several factors are known to influence denitrification, such as temperature, the concentration of nitrate in the water column, organic input to the sediment, benthic algae, bottom fauna activity, salinity and water residence time.

Intense but local denitrification rates were linked with massive deposition of SPM in the Gironde estuary by Abril et al. (2000) for the BIOGEST project. Fluid mud layers (so called "Crème de vase") that form at every slack tide around neap tides, include every time a quantity of nitrate which is very effectively denitrified as the fluid mud rapidly becomes anoxic. The process is probably not extremely important for the estuary-wide nitrogen budget, but demonstrates very nicely how denitrification depends on spatially and temporally variable oxic-anoxic interfaces.

High nitrogen concentrations in the water column, high organic loading, abundant bottom fauna and the rapid exchange of oxic water contributed to very high denitrification rates (average $140 \text{ kg N ha}^{-1}\text{yr}^{-1}$) in the Danish Randers fjord (Nielsen et al. 2001). In this case denitrification rates could not be explained solely by NO_3^- concentrations in the water column and O_2 uptake by sediment as suggested from other studies. The authors ascribed this to a system specific matrix of interactions between the denitrification process, algae and animal activity.

A unique feature of intertidal flats is the periodic exposure and inundation of the sediments. These create large temporal variation in physical and chemical conditions at the sediment surface. Rates of denitrification can reasonably be expected to be radically different during periods of inundation or exposure: accumulation of NH_4^+ and NO_3^- in the sediment could stimulate coupled nitrification/denitrification during exposure, while exclusion of the NO_3^- supply from overlying water could simultaneously have the opposite effect. Despite these potential effects of exposure, most measurements of denitrification in intertidal sediments have however for practical reason been conducted during the periods of inundation.

As first, Ottosen et al. (2001) presented measurements of denitrification rates from intertidal mudflats (Tagus Estuary, Portugal) through the tidal cycle. Denitrification rates ranged from 8.5 to $11.5 \mu\text{mol N m}^{-2} \text{ h}^{-1}$ at night to below $2 \mu\text{mol N m}^{-2} \text{ h}^{-1}$ during the day. Salt stress, light inhibition and depletion of NH_4^+ by benthic diatoms could contribute to the low daytime activity. Coupled nitrification-denitrification activity at night during exposure was not significantly different from the activity measured when the sediment was inundated, but was 3 times lower than rates measured at a subtidal station in the estuary.

4.1.4 Denitrification is not the obligate route for nitrogen to escape

Until recently, denitrification was recognized as the only important process removing nitrogen from the fixed pool in natural environments. Recently, however, it was discovered that ammonium is oxidized anaerobically in sediments in the presence of nitrate and that this alternative pathway contributes significantly to benthic N_2 production (Dalsgaard & Thamdrup 2002, Thamdrup & Dalsgaard 2002).

Incubations with ^{15}N -labeled nitrate or ammonium demonstrated that during this process, N_2 is formed through one-to-one pairing of nitrogen from nitrate and ammonium, which clearly separates the process from denitrification. Nitrite, which accumulated transiently, was likely the oxidant for ammonium, and the process is thus similar to the ANAMMOX process known from wastewater bioreactors ($\text{NH}_4^+ + \text{NO}_2^- \Rightarrow \text{N}_2 + 2\text{H}_2\text{O}$). Anaerobic ammonium oxidation accounted for 24 and 67% of the total N_2 production at two typical continental shelf sites, whereas it was detectable but insignificant relative to denitrification in a eutrophic coastal bay.

In current models of benthic nitrogen transformations, the ammonification-nitrification-denitrification pathway from organic nitrogen to N_2 involves the production of both ammonium and nitrate, either of which may

escape the sediment. With the coupled ammonium oxidation-nitrate reduction, ammonium may be consumed in the anoxic zone of the sediment, thus reducing its chance of escape. Furthermore, the process produces twice as much N_2 as does denitrification per molecule of nitrate or nitrite consumed, which augments N_2 production in sediments in which nitrification rates limit the supply of nitrate and nitrite. Thus, the process may help explain the very efficient conversion of ammonium to N_2 , which is typically inferred for shelf sediments, and which has hitherto been attributed solely to tight coupling of nitrification and denitrification.

The anammox process has two characteristic intermediates, hydroxylamine and hydrazine, and identification of these compounds would further verify that the biochemistry of the anammox process is also responsible for the anaerobic oxidation of NH_4^+ in marine and estuarine sediments (Dalsgaard & Thamdrup 2002). Depending on its (unknown) importance for estuarine systems, it may require a thorough revision of our views on coastal N cycles. This discovery illustrates extremely well the importance of continued fundamental research, even on relatively well studied problems as the environmental nitrogen cycle. Current concepts and models may have to be adjusted to incorporate new discoveries.

Several published ELOISE studies document the occurrence and rate of Dissimilatory Nitrate Reduction to Ammonia (DNRA), a process consuming nitrate and reducing it to ammonium.

Welsh et al. (2001) documented the DNRA from a seagrass meadow, and stressed the importance of the process as a possible source of N_2O to the atmosphere. The process was also measured by Christensen et al. (2000) under trout cages in a Danish fjord. The authors show that significant DNRA only occurs under the heavy organic loading of the sediment, occurring right underneath the cages. Little is known about the factors determining the occurrence and rate of the DNRA process. This point needs further study.

N_2O is released as a by-product of several transformations in the nitrogen cycle, including nitrification, denitrification and dissimilatory nitrate reduction. Its release is thus closely linked to the intensity of these processes. It is, however, also under environmental control.

In the Scheldt, de Bie et al. (2002) demonstrated that in particular nitrification under suboxic conditions leads to enhanced N_2O production. Such conditions can easily be met around the Maximum Turbidity Zone in estuaries. There appear to be multiple controlling factors: nitrate availability for benthic N_2O production during denitrification and oxygen (and ammonium and nitrate) for pelagic N_2O production during nitrification and denitrification, respectively. These processes are not exclusive but rather additive and may alternate in their relative importance depending on the system, the season and tidal cycle.

4.1.5 New developments at the frontline of process modelling

Beside the empirical and budget methods, mechanistic tools have been developed to simulate the main benthic nutrient processes. Current modelling approaches have however become increasingly inaccessible to the experimental geochemist, since they often require an in-depth understanding of the underlying numerics and programming language (Meysman et al. 2003a). A very generic non-linear coupled diagenetic model was developed within the ECOFLAT project (Meysman et al. 2003a, b). The authors propose a new modelling approach implementing the object-oriented technology and the concept of problem-solving environment to increase the popularity, the productivity and the possibilities of modelling

applications. They were successfully implemented in the object-oriented problem-solving environment MEDIA (Modelling Early DIAgenesis), which enables the design of costumer-tailored diagenetic models and provides an efficient numerical solution for these models (Meysman et al. 2003b). Application of this modelling tool to some of the datasets produced within this and other ELOISE projects would be a most meaningful exercise.

4.2 ROLE OF VEGETATION IN NUTRIENT CYCLING (PROJECTS: ECOFLAT, NICE,

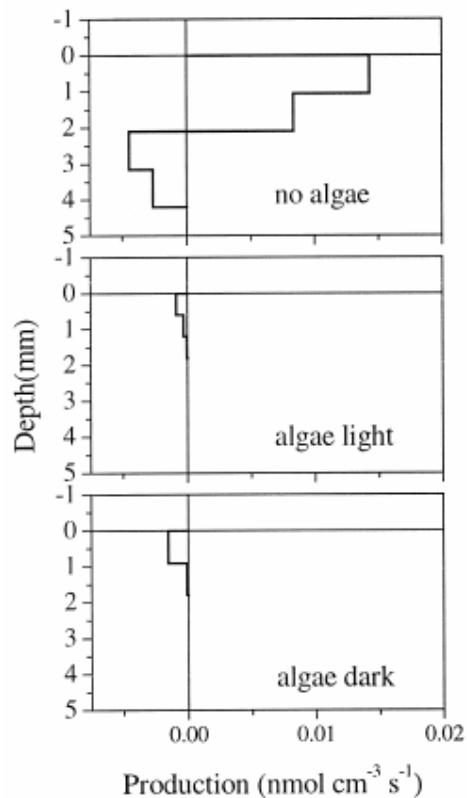
4.2.1 Microalgal mats versus denitrification

Until recently and mostly based on theoretical considerations, it was assumed that the oxygen release into the sediments by benthic plants (directly by benthic algae, *via* aeration of the rhizosphere by macrophytes) created favourable conditions for coupled nitrification-denitrification. Ammonia produced by ammonification in the sediment can be oxidised to nitrate in oxic sediment layers and can diffuse into the anoxic zone and be denitrified. In principle, the extension of oxic-anoxic interfaces in sediment therefore increases the probability of coupled nitrification-denitrification.

Risgaard-Petersen (2003) convincingly showed for studies of sediments inhabited by microalgae (Thornton et al. 1999, Sundback et al. 2000, Ottosen et al. 2001) supported with experimental evidences that this anticipated effect is overruled by ammonium (and nitrate) uptake by the algae. The diurnal integrated coupled nitrification–denitrification rates in alga-colonized sediments were between 4 and 51% of the activity measured in heterotrophic sediment. Competition for the nitrogen substrate decreases the amount of inorganic nitrogen available to nitrifying bacteria for coupled nitrification-denitrification. The consumption of DIN is direct by the algae, but also indirect by bacteria that quickly incorporate extracellular polysaccharides produced by the algae (Middelburg et al. 2000).

Figure 13

Production profile of NO_3^- in the alga-free sediment and 23 in the alga-inoculated sediment, from Risgaard-Petersen (2003)



At a community level, the autotrophy-heterotrophy status of sediment communities will determine whether the sediment as a whole acts as a sink or source of nutrients. When the sediment is net

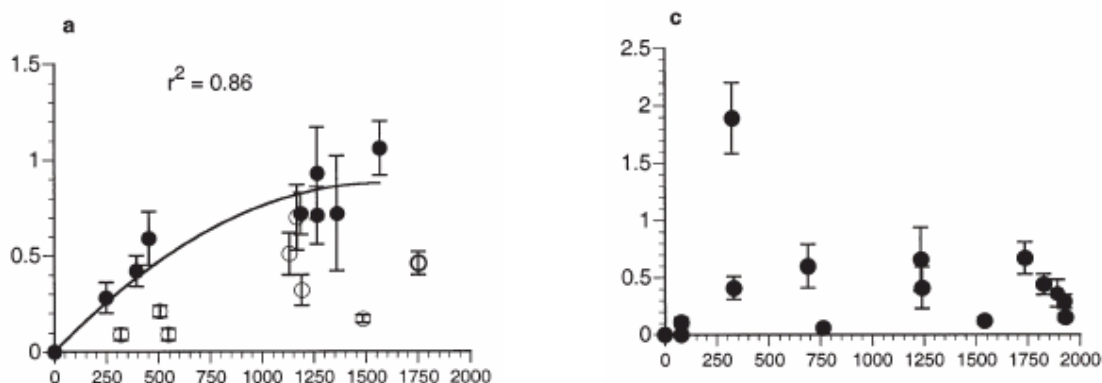
heterotrophic a fraction of the dissolved inorganic nitrogen released by diagenetic processes may become available for denitrification. In autotrophic sediments, the released nitrogen is efficiently incorporated by primary producers (Risgaard-Petersen 2003); the nitrogen cycle is closed.

Sundback et al. (2000) show that cold-climate microtidal (NE Kattegat) sandy sediments function as a N-sink during winter and early spring, while no clear seasonal pattern is found for silty sediment. Calculated N demand of the microphytobenthos far exceeded the measured sediment net uptake of N, supporting the idea that sandy systems in low-nitrogen areas can be highly productive through a closed recycling of N. The ratio between calculated microphytobenthic N demand and measured denitrification rates suggests that denitrification play a role of minor importance in these sandy, cold-climate microtidal sediments.

An active *in situ* recycling of biomass was also observed by Barranguet et al. (1997) on a tidal flat (Westererschelde) where the fate of the microphytobenthic biomass on a tidal flat by the use of pigment biomarkers. The fate of microphytobenthos appears to include rapid bacterial degradation in spring, episodic grazing by benthic animals in surface layers of sediments in the centre of the flat, and export by resuspension in sediments more exposed to currents. Benthic-pelagic exchange of microphytobenthos was further discussed by Lucas & Holligan (1999), (Lucas et al. 2000) and Middelburg et al. (2000). In general, export of microphytobenthic biomass was very limited at muddy sites, but even in sandy sites the major part of the production is consumed *in situ*.

Due to the coupling between the microphytobenthic (production) and bacterial (nitri/denitri-fication) activities, factors controlling microphytobenthos will also modulate the benthic potential of denitrification. Miles & Sundback (2000) measured microphytobenthic production at three sites across Europe with different tidal regimes. Production at the subtidal sites was mostly controlled by the light availability, a function of diel variation and variable turbidity in the water column. Daily productivity at the intertidal site was controlled mainly by the tidal exposure patterns. Variations in productivity during the emersion period suggested the influence of other factors than light, e. g. nutrient limitation.

Figure 14
Biomass Specific Productivity ($\text{mgC mgChl}_a^{-1} \text{h}^{-1}$) as function of the Irradiance $\mu\text{mol Photons m}^{-2}\text{s}^{-1}$ at (a) a subtidal site by clear (full circles) and turbid (empty circles) water and at (c) an intertidal site.



Despite of the different sediment type, tidal amplitude and species composition, the biomass and yearly integrated productivity at the sites was of the same order of magnitude. The main difference between the sites was in the degree of intra-site variation, being greatest for the intertidal site.

Serodio et al. (2001) identifies active migratory rhythms as the main cause for short-term variability in intertidal benthic primary productivity. The results of this study indicate that the effects of migratory rhythms in regulating the community photosynthetic response are actually more important than those resulting from photophysiological adaptation, therefore identifying microalgal migratory behaviour as the main factor controlling short-term variability in the community light utilisation efficiency.

4.2.2 N-sequestration in macrophyte biomass

Studies on sediments dominated by seagrass confirm the trend that 'vegetated' sites are autotrophic or only slightly heterotrophic, and that N uptake and storage in biomass is a dominant factor in the sediment N cycle.

Welsh et al. (2000) drew up a N budget of a *Zostera noltii* system (Arcachon Bay). DIN fluxes towards the plants and sediments were entirely dominated by the plants. Surprisingly, the plant community showed a high dark assimilation activity for inorganic-N, and differences in light and dark fluxes of DIN, nitrate and ammonium were never significant. In general, denitrification was very low. Similarly, rates of denitrification coupled to nitrification were consistently low, probably due to the competition between nitrifying bacteria and the *Zostera* roots for ammonium.

Overall, data demonstrated that the *Zostera* meadows represent a highly conservative environment for nitrogen, where the N-cycle is dominated by the primary productivity of the plant community and the associated assimilatory demand for fixed-N to support this productivity. Conversely, N-losses via denitrification are extremely low and are more than balanced by N-inputs from N-fixation.

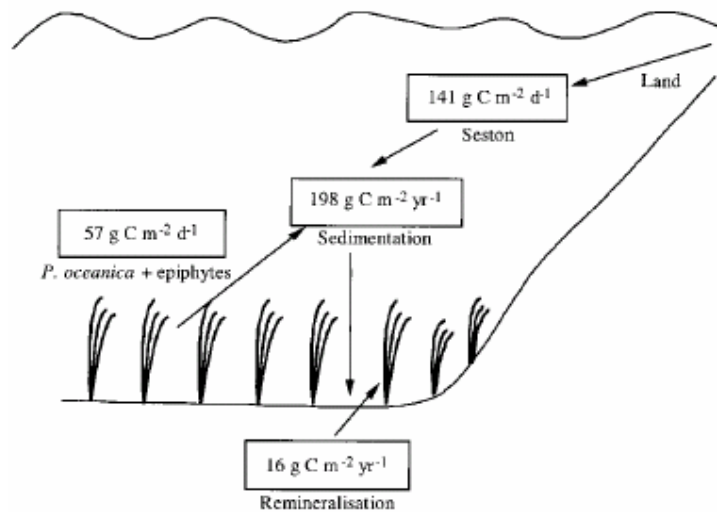
Thus, in this macro-tidal lagoon, export of nitrogen as plant biomass and/or N-burial in the sediments are probably the major loss mechanisms for anthropogenic N-inputs.

The function of seagrass beds as sinks for nitrogen (// places where minor denitrification occurs) is furthermore supported by many other studies within ELOISE. Risgaard-Petersen & Ottosen (2000) showed in eelgrass beds, N sequestration in spring and summer, N-release during autumn and very low denitrification rates throughout the year. De Wit et al. (2001) also concluded that plant biomass and detritus is a major temporary sink for nutrients (N and P) at vegetated sites. Boschker et al. (2000) showed in samples from *Zostera* beds across North-western Europe that there was no significant biomass transfer from the seagrass to the local bacteria, the *Zostera* detritus appeared to be either buried or exported from the beds.

Similar findings have been reported by Gacia et al. (2002) who documented the importance of burial of organic matter in *Possidonia* seagrass meadows with a tentative carbon budget (Figure 15). Detritus from the *Possidonia*–epiphyte complex ($57 \text{ g C m}^{-2}\text{yr}^{-1}$) contributed 29% of the 198 g C m^{-2} deposited annually. This is about half of the calculated *Possidonia* production ($110 \text{ g C m}^{-2} \text{ yr}^{-1}$). The remaining of production must be exported or respired during decay. Deposition of seston material should provide an input of $141 \text{ g C m}^{-2} \text{ yr}^{-1}$ to the seagrass sediments. Only a small fraction (10%) of the organic carbon entering the sediments is respired, so that most of these inputs contribute to a net accumulation of organic carbon, estimated at about $182 \text{ g C m}^{-2} \text{ yr}^{-1}$. These results show that *Possidonia* meadows are important sites of net organic carbon burial, derived from both sedimented sestonic particles and seagrass detritus. The incomplete mineralisation of the deposited detritus suggest that significant N and P burial may also occur under the *possidonia* meadows.

Figure 15

Tentative carbon budget in a *Possidonia oceanica* meadow (northeast Spain) from Gacia et al. (2002).



Hansen et al. (2000) made a carbon and nitrogen balance for a *Zostera* community, including the plants, sediments and microalgae. The eelgrass community acted as a sink for dissolved inorganic nitrogen. In April, the community nitrogen uptake was dominated by the sediment-microalgae compartment, as the nitrogen uptake by the eelgrass leaves was insignificant due to the low biomass of the eelgrass leaves. In August, the uptake of nitrogen by sediment-microalgae was about half the uptake in April and comparable to the uptake by eelgrass leaves. The sediment system as a whole acted as a sink for N. Important amounts of nitrogen were stored in plant tissue. A substantial amount (80 to 90%) of the nitrogen demand for eelgrass production in August was supplied from the sediment. This is in agreement with the observation of roots being of major importance for the nitrogen uptake in eelgrass. The seagrass community as a whole as well as the sediment-microalgae compartment changed from net carbon production in April to net carbon consumption in August.

The dynamic of nitrogen uptake and release by macroalgae (e.g. *Ulva lactuca*) is clearly distinct than what has been described for sea grasses.

Naldi & Viaroli (2002) and Naldi & Wheeler (2002) showed much faster rates of uptake, storage and release of nitrogen by *Ulva* and other macroalgae than by seagrass. The fast turnover of nitrogen, with considerable release at relatively short time scales, as well as the major and fast release upon decomposition of the algae, may lead to very strong fluctuations in nutrient concentrations within a growing season. These dynamics are faster than those in eelgrass-dominated systems, and probably provide a habitat for much 'faster', opportunistic species and occasionally for intense phytoplankton blooms.

4.2.3 Rooted macrophytes and sediment buffering capacity

Beside their active role with respect to the N-sequestration, macrophytes also greatly modify the characteristics and functioning of the benthic microbial ecosystem.

Ottosen et al. (1999) measured the coupled nitrification-denitrification rates in the rhizosphere of four different aquatic macrophytes including *Zostera marina*. The variability in denitrification activity was mainly due to differences in the ability of the plants to oxidize the rhizosphere. Denitrification in the rhizosphere of *Zostera* was lower than in that of other rooted macrophytes, correlating with the higher oxygenation of the rhizosphere by *Zostera*. The high oxygenation potential by *Zostera* was further confirmed by Heijs et al. (2000) and Azzoni et al. (2001).

Conversely Welsh et al. (2001) observed low densities of nitrifying (nitrate and ammonium oxidising) bacteria within the rhizosphere by *Zostera noltii* mostly inhabited by large populations of sulphur-oxidising bacteria. Hypothesis was made that the nitrifying bacteria (with a relative low affinity for Oxygen) may be out-competed by both heterotrophs and chemolithotrophs. Furthermore DNRA (Dissimilatory Nitrate Reduction to Ammonium) was observed as the dominant sink for nitrate rather than denitrification in these sediments. Conclusively, due to the combination of small populations of nitrifiers and the dominance of DNRA as a sink for nitrate, coupled nitrification-denitrification is unlikely to be a quantitatively significant process within the seagrass rhizosphere. Direct evidences of denitrification were found to be restricted to the surficial sediments.

Higher plants play the role of buffer against the released of sulphide in areas of high organic deposition. This mechanism is mainly supported by the plant capacity to inject oxygen into the sediment and stimulate the populations of sulphur-oxidising bacteria (de Wit et al. 2001, Gribsholt & Kristensen 2002, Holmer et al. 2002).

4.3 MODELLING AT SCALE OF BASINS

The coastal area forms a complex system where very different bodies of water enter in contact. This discontinuity provides a boundary layer for physical, chemical and biological processes in the water column, the sediment and their interactions. These three gradients and their possible interactions form a highly intricate system whose fully assessment would require yet non-existing highly sophisticated modelling tools. There is a whole family of models to describe the processes occurring in coastal areas from 0-D simple box to complex 3-D coupled models. The most complex model is not always the best choice: complexity is an expensive matter that demands a lot of input data and has the tendency to produce emerging patterns that may be not representative for the real world. Corrections for these artefacts require investments in additional research for the proper fine tuning. As a consequence it should be, for each question addressing the functioning of a given ecosystem, an optimal level of modelling complexity sufficient to get the required information. Beneath this level, the model predictions will not get the focus adapted to the question and beyond, they will become dependent on properties that exceed the scope of the original issue. Examples of questions addressed on coastal nutrient processes and the hereto applied model by the ELOISE projects is given below.

4.3.1 Simple models for simple questions

Nielsen et al. (2001), employing both flux measurements and hydrodynamic models, compared the 2 estimates for nutrient retention in estuaries and discussed whether complex models or direct measurements may be substituted by simple models. Application of simple models would indeed dramatically reduce the investigation efforts and increase their implementation in actual management. They concluded that whereas empirical models were valuable for quantification of nutrient retention in general, more information than input of nutrients and water residence time was needed if they were to be applied on an individual estuary basis. Nielsen et al. (2001) suggest that retention should be estimated by either mass balance or direct measurements in each individual estuary. The 2 methods gave different estimates of especially phosphorus, since phosphorus sedimentation can be high in estuaries with freshwater input of organic matter. Mass balance provides an overall estimate of the 'filter effect' in the estuary, while information about nutrient sink-sources in the sediment is obtained by flux measurements. They especially recommended direct measurements to elucidate the response of nutrient loading or shifts in biological structure in estuaries.

When the main objective is to determine whether continental margins export or import nutrients with the open sea and what is their effect on the carbon cycle in terms of a source or sink of CO₂, a LOICZ-type box model appears to be a suitable tool.

Durrieu de Madron et al. (2003) calculated for METRO-MED the Shelf-slope exchanges and budgets of organic and inorganic nutrients for the continental margin of the Gulf of Lions in the North-western Mediterranean.

A LOICZ-type box model was used to estimate the exchange patterns at the boundaries of the coastal system. This box-modeling approach considers that the system over the period of interest is at steady state. Given that the inputs of water and dissolved material to the system are known, the model uses the water volume and salt conservation within the system to infer the exchanges with the adjacent open ocean. The

conservative water budget is build upon, river and sewage discharges, precipitation, evaporation, and mixing and residual flows at the boundary with the open ocean.

The classical LOICZ single box system was used to describe the unstratified water column during wintertime (Nov.- May), from November to early May, and a modified version of the model with two-layers system as the water-column became stratified (June-Oct.).

The exchange fluxes predicted by the box model (despite large uncertainty values) generally indicate that the shelf area acts as a sink for dissolved inorganic nutrients (Tusseau-Vuillemin et al. 1998), and as a source to the offshore waters for most of the organic matter.

During the winter however, the DOP flux showed an opposite trend to those of other organic matter and the Gulf of Lion acts then as a net sink for both DOP and DIP. This is in accordance with previous results (Diaz et al. 2001) as a severe phosphorus depletion was systematically detected in the shelf waters relative to those of the slope during the winter-early spring.

The margin occasionally acts as a source of nitrate and particulate matter to the open sea mainly in winter, during events of dense shelf water cascading that washes out towards the intermediate or deep slope waters (Bethoux et al. 2002).

The DIP budgets suggest that the biological system on the shelf is autotrophic and thus acts as a sink of CO₂. In addition, the DIN budgets suggest that denitrification predominates over nitrogen fixation, and that the system is net denitrifying and thus acts as a source of N₂.

4.3.2 Requirements for an assessment of fluxes within the coastal system

The first step in the assessment of the nutrient fluxes at the scale of a coastal area consists in the understanding of the physical issues.

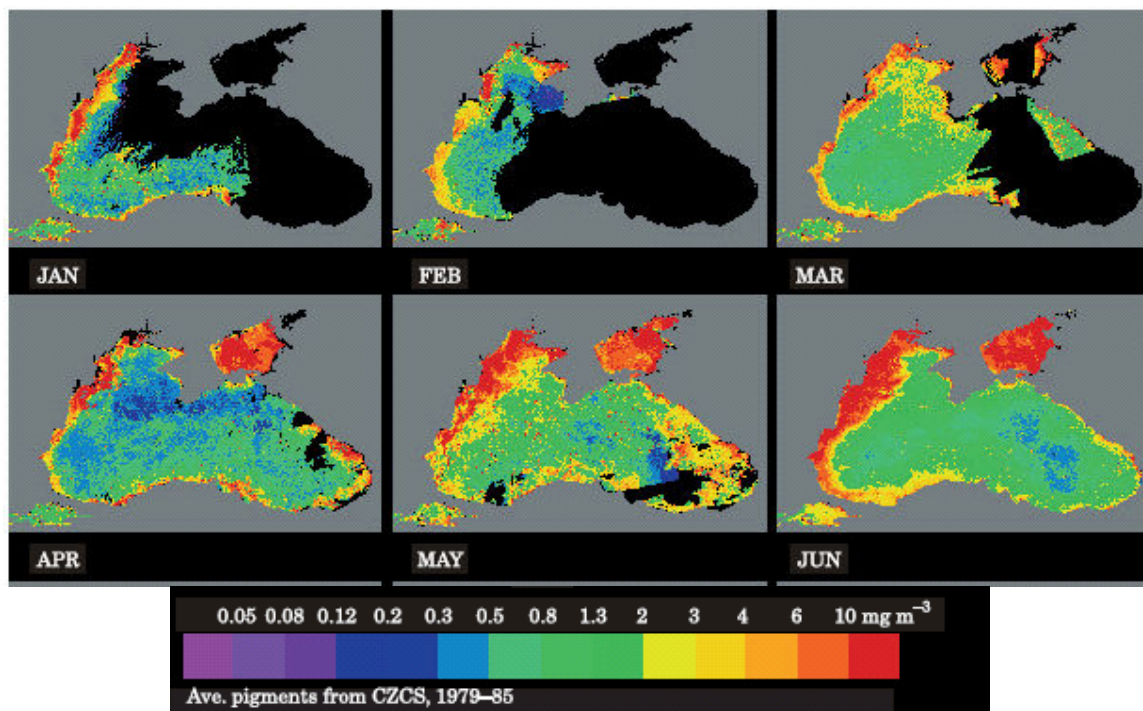
A comparative analysis of two 3D hydrodynamic models (DMG-MOM, GHER) for the water circulation in the Black Sea was given by Stanev et al. (2002) and provided a solid basis for further studies on the interactions between physical and biological processes (Beckers et al. 2002, Lancelot et al. 2002). The circulation models (DMG-MOM, GHER) applied to the Black Sea were shown to adequately reproduce physical processes with different time- and space-scales such as coastal waves, internal waves, baroclinic Rossby and topographic waves (Stanev et al. 2002). The authors recognized however that new parameterizations for mixing were required to reach a better consistency between the models and the real mixing processes.

Beckers et al. (2002) illustrated the performance of a coarse- (15 km) and a high- resolution (5 km) 3-D model (GHER-3D) by simulating the general circulation of the Black Sea. The results by the 3D model were further used to produce information for a 0-D coupled model.

Both coarse and high resolution models give a general circulation pattern compatible with classical views of circulation in the Black Sea (e.g. reversal of the current during the summer season). Of these two models, only the high resolution model adequately resolves the frontal dynamics (eddies and coastal upwellings, see on Figure 18). The high spatial resolution in the model is furthermore needed to reproduce the observed distribution of chlorophyll as observed by Barale et al. (2002) (Figure 16).

Figure 16

Average pigments concentrations from the CZCS over the periode 1979-1985 From (Barale et al. 2002).



4.3.3 When biology has to be coupled with physics

Since it is difficult to calibrate and validate a fully coupled 3-D biological–hydrodynamical model capable of dealing with changes in the ecosystem structure, first a 3-D hydrodynamical model is implemented and validated to be latter on, coupled with biological models (Gregoire et al. 1998, Lancelot et al. 2002).

As a promising exploratory step Gregoire et al. (1998) attempted the on-line embedding of a biological model into the 3D hydrodynamical model with a superimposed cycle for the light intensity. The ecosystem model with 13 state variables was defined by a nitrogen cycle considering several phytoplankton and zooplankton sizes and including the microbial loop (Figure 17). No vertical flux is allowed in this model since a zero flux is imposed at the sea surface considered as a rigid boundary, while the bottom is supposed to permit only sinking fluxes towards sediments. The model ran for six months, from the beginning of January until the end of June, this takes a computation time of about 4 days on a power parallel system!

A rather realistic scenario for the phytoplankton development was simulated with a succession of blooms:

- 1.- Diatom bloom (the strongest) in winter in the Danube plume area.
- 2.- Weaker and shorter bloom of nanoflagellates in May fuelled with the ammonium generated from the winter bloom.
- 3.-bloom of dinoflagellates at the end of June, supported with newly discharged and regenerated nutrients.

Nitrogen, and phosphate limit the phytoplankton growth at the end of spring, whereas silicate does not seem to be limiting.

Figure 17

Schematic representation of the ecosystem model. The model is defined by a nitrogen cycle which is described by 13 state variables. The food-web is composed of two branches: the linear food-chain and the microbial food-chain. Copepods feed on the three phytoplankton species and on the microzooplankton, with a large size prey preference, initiating the linear food-chain. Ciliates are grazing on bacteria and nanoflagellates linking the microbial and the linear food-chain. The N:P ratio of the phytoplankton, the zooplankton and of bacteria, as the diatoms N:Si ratio, are assumed constant.

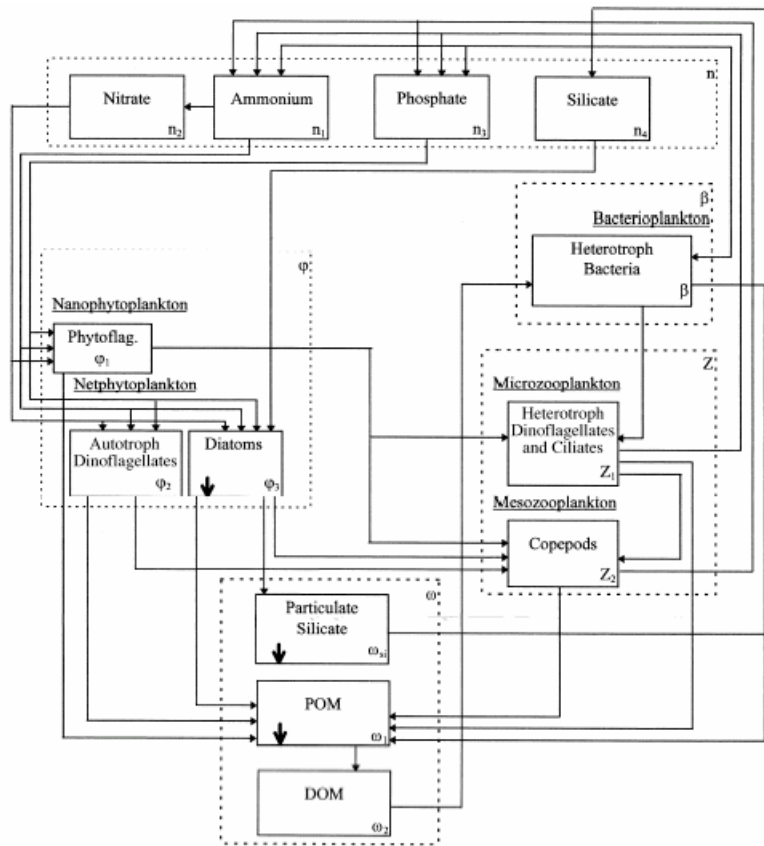


Figure 18

Salinity fields from the GHER 3-D model with a fine (5km) resolution (left panel) and contemporary (May) phytoplankton concentrations from the coupled biological model (right panel). The 17 ppt isohaline, extern boundary for the Danube inputs, is coloured in dark green From (Beckers et al. 2002).

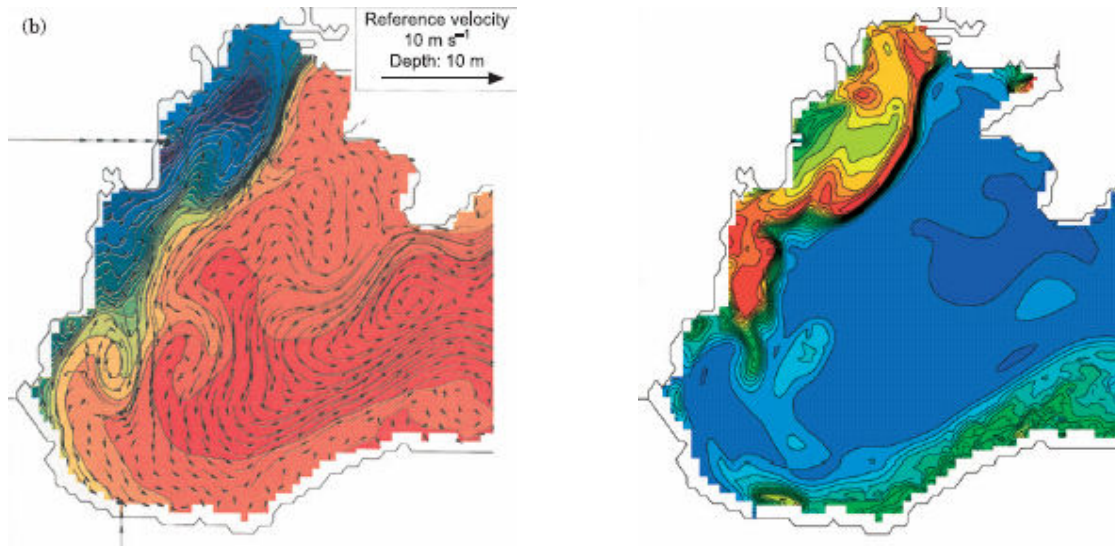
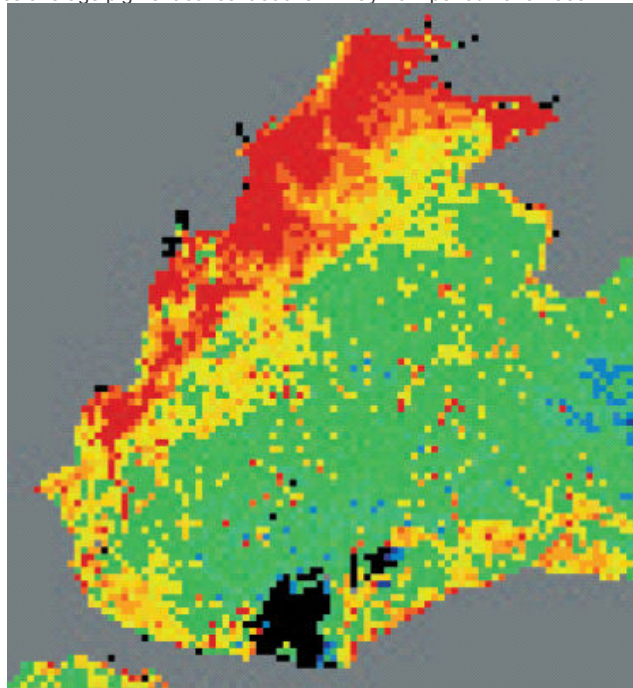


Figure 19

CZCS estimate of the sea surface average pigment concentrations in May from period 1979-1985.



The dependency of phytoplankton on the Danube freshwater input was clearly stressed by the correlation between the plume of the Danube and the phytoplankton concentrations on the shelf (Figure 18). The accumulation of phytoplankton biomass in this area is further exacerbated due to the fact that the water mass discharged by the Danube river is eventually trapped in an anticyclonic gyre. This pattern was furthermore well in accordance with the field observation as shown by the satellite photography in Figure 19. The salinity in the gyre remains at values below 17 ppt (dark green isohaline on Figure 18) and can be easily used to trace this water mass that is enriched by nutrients from the river discharge. Ecosystem processes in these waters that are fuelled with river-borne nutrients are expected to be different compared to open sea waters which gain their nutrients from upwellings and entrainments.

The model used by Gregoire et al. (1998) was a prototype due to be improved on many crucial aspects:

- Explicit modelling of other macronutrients (C at least) than N alone
- Incorporation of important species to the Black Sea such as *Noctiluca*, *Aurelia*, *Mnemiopsis*
- Incorporation of biogeochemical processes in the water column and in the sediment and atmospheric deposition.

4.3.4 Complexity increase is challenging our computing capacity

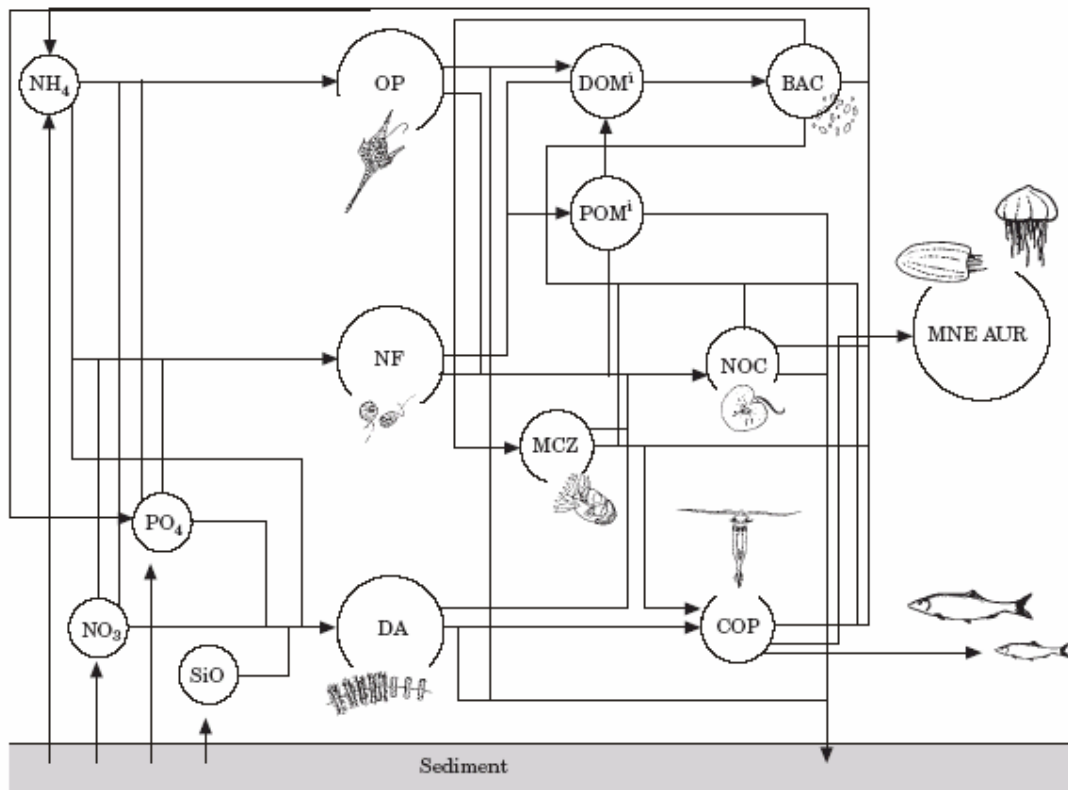
Lancelot et al. (2002) implemented the ecological model BIOGEN, describing the carbon, nitrogen, phosphorus and silicon cycling throughout aggregated chemical and biological compartments of the planktonic and benthic marine systems, in the north-western Black Sea.

Particular attention was paid to establishing the link between quantitative and qualitative changes in nutrients, phytoplankton composition and food-web structures. The BIOGEN numerical code structure includes 34 state variables (Figure 20) assembled in five interactive modules describing the dynamics of:

- (1) phytoplankton, three groups diatoms, nanophytoplankton, non-silicified opportunistic species.
- (2) meso- and microzooplankton with high food selectivity.
- (3) gelatinous organisms (omnivorous Noctiluca, carnivores Aurelia and Mnemiopsis) as trophic dead-end.
- (4) planktonic and (5) benthic bacteria both responsible for organic matter degradation and associated nutrient regeneration processes.

Figure 20

Diagrammatic representation of the structure of the BIOGEN model. Inorganic nutrients include ammonium (NH₄), nitrate (NO₃), phosphate (PO₄) and silicic acid (SiO). Organic matter is composed of dissolved (DOM_{1,2}) and particulate (POM_{1,2}) matter each with two different biodegradability classes. Phytoplankton is composed of three groups: diatoms (DA), autotrophic nanoflagellates (NF) and opportunists (OP). Bacterioplankton is represented by BAC. Zooplankton includes microzooplankton (MCZ) and copepods (COP). The gelatinous food-chain is composed of Noctiluca (NOC), Aurelia (AUR) and Mnemiopsis (MNE).



The complexity of the physical features in the Danube-influenced Black Sea continental shelf would ideally require the implementation of BIOGEN in a 3-D frame of high spatio-temporal resolution (Beckers et al. 2002). The complexity of the BIOGEN model (Figure 20) makes its direct coupling with the required 3-D physical model technically unworkable.

Lancelot et al. (Lancelot et al. 2002) present the first steps preliminary to the implementation of the 3-D BIOGEN:

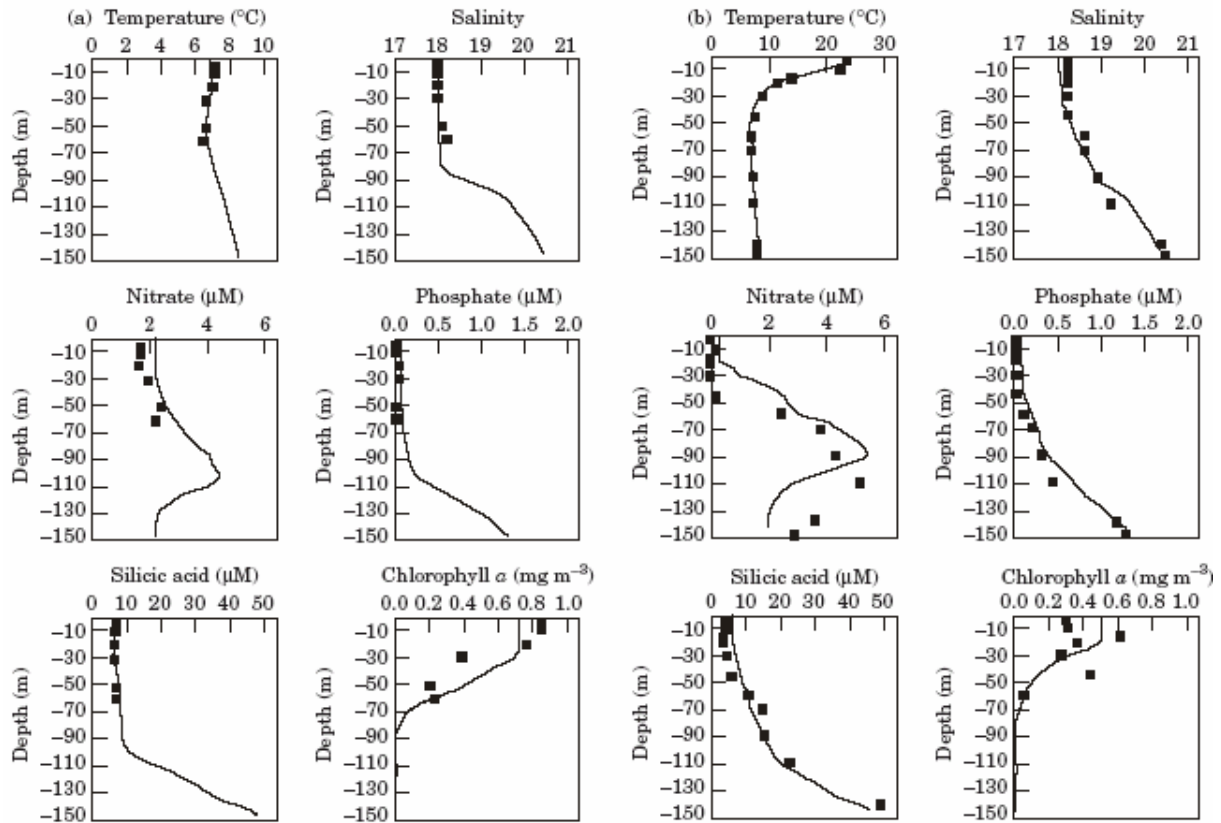
- 1.- BIOGEN model coupled with a 1-D vertically resolved physical model
- 2.- BIOGEN model implemented as a two-box model resulting from the coupling between the 1-D vertically resolved open-area model and a volume-variable 0-D box model of the coastal area submitted to Danube inputs and bordered with the 17ppt isohaline (Figure 18).

The capability of the BIOGEN model to simulate the recent ecosystem changes reported for the Black Sea was demonstrated by running the model for the period 1985–1995. Reasonable agreement is

observed between model predictions and data available for the central basin, both seasonally and in magnitude. As an example, Figure 5 compares selected vertical profiles of BIOGEN simulations and nutrients and chlorophyll a observations for spring and summer periods (Figure 21a-b).

Figure 21

1-D BIOGEN simulations in the open Black Sea water column. Observations recorded in (a) April 1997 and (b) July 1995. data (squares), model (line).



4.3.5 Including dynamic sediment modelling should be the next challenge

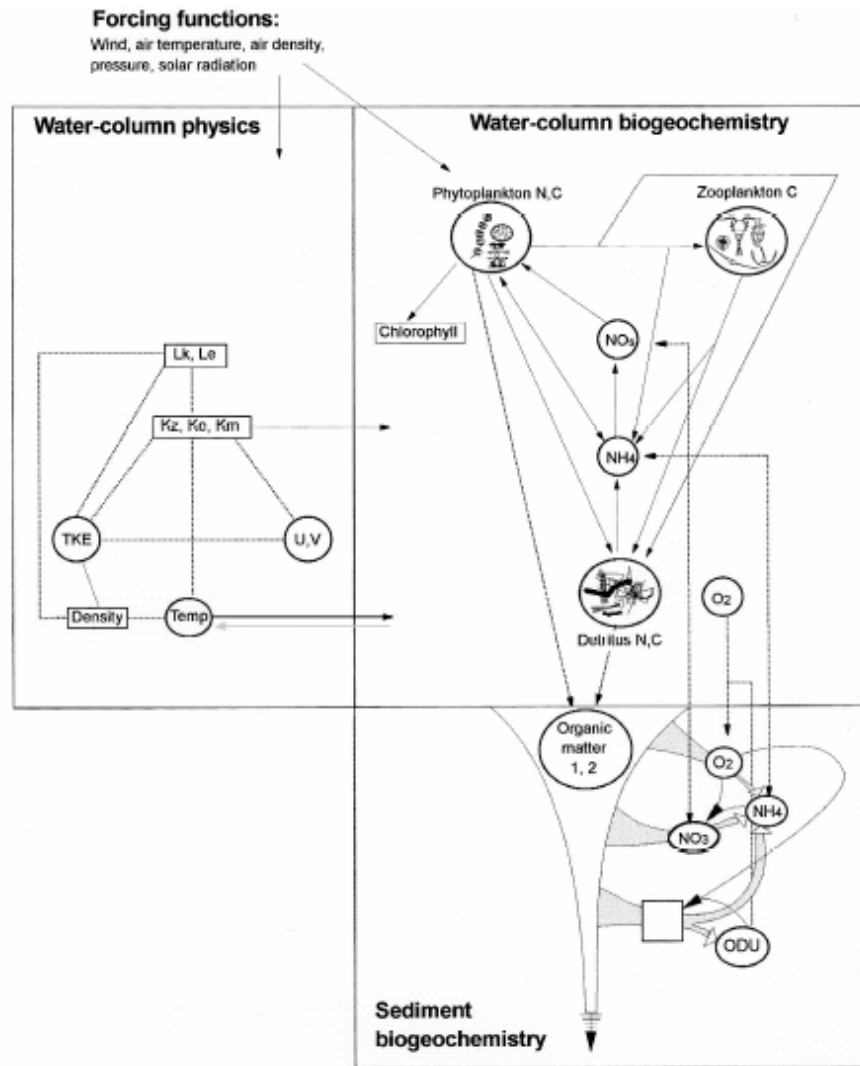
Ocean modelling is now at a stage where increasingly complex hydrodynamical models are coupled to increasingly complex biological descriptions (See work by Lancelot et al. (2002)). Compared to the effort spent in this area, the linking between sediment and water column processes is still in its infancy. In coastal environments, benthic primary production, groundwater input, extensive resuspension–deposition cycles and advective flows may strongly affect sediment–water exchange and should therefore be included in coupled benthic–pelagic models.

The crucial problem of coupling sediment diagenetic models to ecological models for the water column was stressed by Soetaert et al. (2000). As the full dynamic calculation of diagenesis for every cell of the water model is too costly, they propose a number of alternative efficient schemes that allow for a very reasonable representation of benthic processes in coupled ecosystem models (Figure 22) at a relatively low computation cost (

Table 3).

Figure 22

Schematic representation of the fully coupled model; encircled are the prognostically modeled components, enclosed by rectangles are derived components from Soetaert et al. (2000).



Soetaert et al. (2000) conclude their paper with the following recommendations:

Increases in computing capabilities may soon offer the ability to describe sediment–water dynamics with much more detail, but because of the problems associated with parameter estimation and proper initialisation, the most complex models may not always be the most suitable. We recommend that for each problem, the choice of a lower boundary type should be carefully considered and the pros and cons of each boundary level evaluated (See Table 3). It is our hope that current work may facilitate reaching the ultimate decision.

Table 3

Summary of model characteristics for the various levels of sediment–water exchange parameterisation. + Accounted for; - not accounted for or not appropriate; ± partially accounted for, depending on the exact formulation From Soetaert et al. (2000).

Level	Mass conservation	Retention capacity	Speciation characteristics of efflux	Short- and medium-term response	Long-term effects	Initialisation of sediment	Parameter requirements	Calibration and validation data	Computational demand
4 — Fully coupled diagenetic model	+	+	+	+	+	Special attention for slow-reacting components	Bioturbation, irrigation, advection rate	Vertical profiles; in situ fluxes	High
3 — Vertically integrated model	+	+	±	±	+	Special attention for slow-reacting components	Speciation characteristics of return flux	In situ fluxes	Low
2 — Reflective boundary	+	+	±	–	–	–	Speciation characteristics of return flux	Long-term averaged fluxes	Insignificant
1 — Solute flux or BW concentration imposed	–	+	–	–	–	–	Bottom water concentrations or sediment fluxes	–	Insignificant
0 — Sediment ignored	+	–	–	–	–	–	None	–	None

5 Effects of altered nutrient discharges on the functioning of coastal and estuarine food webs.

Man-made alteration in the emission of nutrients to a water body mainly consists in the increase of the loading for one or more chemical species. Ecosystems respond to these changes by developing characteristic structural and functional patterns. Both the change in nutrient supply and the related symptoms are usually described under the term of eutrophication.

5.1 EUTROPHICATION, DEFINITION(S)

The concept of eutrophication has been originally defined by northern European limnologists early in the 20th century, when distinction was made between oligotrophic and eutrophic lakes. It was hypothesised that lakes evolved from oligotrophic (nutrient-poor) to eutrophic (nutrient rich) as a result of human activity (cultural eutrophication).

Eutrophication was defined by the European Commission (in the Urban Waste Water Treatment Directive of 1991) as:

"the enrichment of water by nutrients especially compounds of nitrogen and phosphorus, causing an accelerated growth of algae and higher forms of plant life to produce an undesirable disturbance to the balance of organisms and the quality of the water concerned."

Eutrophic freshwaters have consistently higher biomass of (usually) phytoplankton than is found in oligotrophic lakes, and eutrophication is generally the result of addition of phosphate. This is due to the capacity of the, common in freshwaters, cyanobacteria to fix N₂. Therefore, their growth is not limited by the availability in inorganic nitrogen.

Marine eutrophication slightly differs from its freshwater counterpart. Estuarine and coastal waters are mostly better flushed than lakes and this dilution counteracts the accumulation of phytoplankton biomass (one of the most obvious eutrophication symptom). Furthermore, marine eutrophication typically involves sporadic increases in phytoplankton biomass - more, or bigger blooms, rather than consistently high levels of phytoplankton. Marine phytoplankters are most often limited in their growth by a shortage of nitrogen (as nitrate or ammonium) rather than of phosphate; N-fixing cyanobacteria generally do not dominate phytoplankton in eutrophied coastal seas.

However it is a fact that nutrients are naturally present in the environment and needed to sustain the ecosystem productivity. Eutrophication should then be clearly defined as a situation when the quantity of nutrients brought to a system exceeds its capacity to process it within its present structures. Elliott & de Jonge (2002) mention the definition by Schramm & Nienhuis (1996):

"the process of natural or man-made enrichment with nutrient elements, mainly of nitrogen and phosphorus, beyond the maximum critical level of the self-regulatory capacity of a given system for a balanced flow and cycling of nutrients"

This definition refers to the assimilative capacity of the aquatic systems, i.e. the ability to absorb change or inputs before that the undesirable disturbance develops or environmental homeostasis (Elliott & de Jonge 2002). According to this definition, critical levels for nutrient supply may vary from one system to another and

uniform policy for nutrient sanitation may be either too restrictive or too permissive with respect to their objectives (avoidance of undesirable disturbance).

Colijn et al. (2002) propose a review on the effects of eutrophication in selected compartments of the North Sea ecosystem. On the basis of a selected number of papers they discuss the extent to which this fertilisation has been effective on different levels of the trophic foodweb, both qualitatively and quantitatively. The unorthodox goal for this review was to document, within the framework of the Norwegian Maricult programme (The Possibilities and Constraints for Increased Sustainable Harvest and Use of Marine Resources www.maricult.org), on the positive effects of eutrophication. Positive effects encompass a stimulation of biomass of certain trophic levels, of enhanced productivity or a change in the food web structure, which might positively influence food conversion in the trophic web.

This idea finds its roots in the concept of the assimilative capacity or environmental homeostasis of aquatic systems, a domain of nutrient enrichments for which no undesirable effects are observed (see definition by Schramm & Nienhuis (1996) on page 42).

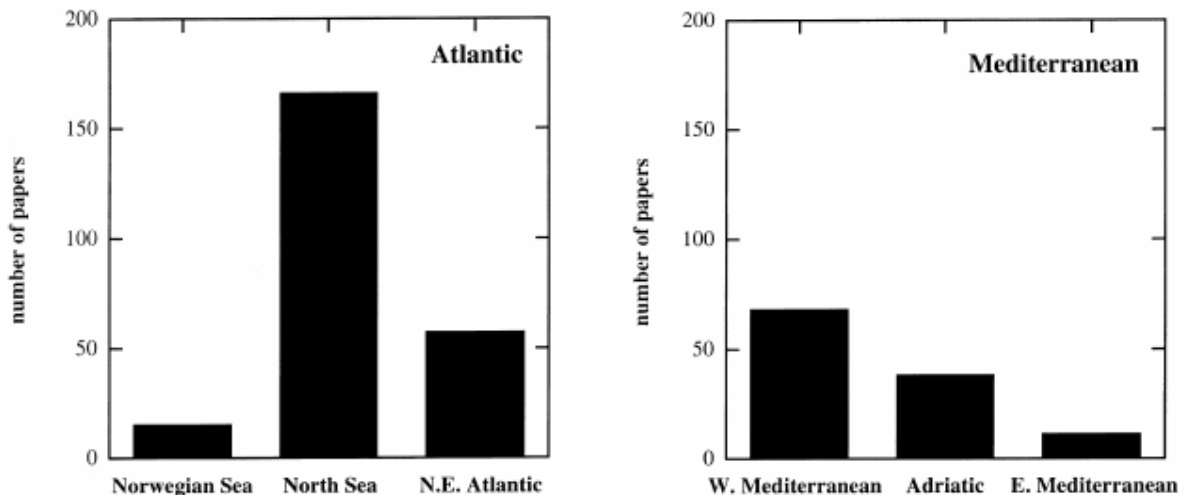
(Colijn et al. 2002) conclude that answering to what extent increased nutrient loadings can be claimed as being harmless, positive or negative from the anthropogenic point of view, is hampered by the lack of good assessment criteria for marine ecosystems: a thorough analysis of all compartments involved by means of long-term-series long enough to discriminate between man-made and natural variability is required.

This seems however not to be a practical option for: i.-causal relationships that are needed for the definition of sounded policies are hard (and expensive) to get from field data and ii.-existing data are concentrated to restricted areas in Europe whereas large domains have not been investigated (see below).

The effects of altered (increased/unbalanced) nutrient emissions in coastal ecosystems have been extensively described in the literature during the last decades whereas the research effort was not homogenously distributed geographically across Europe (Figure 23 and Vidal et al. (1999)).

Figure 23

The distribution of the number of papers on coastal eutrophication published in different regions of the Atlantic coast of Europe and the Mediterranean Sea between 1988 and 1997 From (Vidal et al. 1999)



The present imbalance of the data set between the Atlantic (mostly North Sea) and the Mediterranean coast is a matter of serious concern, for models successful for the Atlantic may not necessarily apply to the Mediterranean coastal region. For example, Atlantic coastal waters are mostly nitrogen-limited, whereas available information for the Mediterranean suggests phosphorus limitation (Vidal et al. 1999). Beside the necessary progress in knowledges at the process level, the second challenge will be to customize the management policies to the specificity of the different European coastal systems.

5.2 DIFFERENT PERCEPTION OF EUTROPHICATION

There is a large and continuously increasing amount of publications dealing with the effects of eutrophication on coastal ecosystems (Vidal et al. 1999). Elliott & de Jonge (2002) indicate that whereas many scientific studies research in detail the causes and initial effects of the eutrophication, public and nature conservation concerns relate rather to high profile events. The latter include fish kills, closed fisheries, the reduced biodiversity of habitats, seabed de-oxygenation, reduced aesthetic quality of the coastal environment and even complete ecosystem collapse over extensive fjords and seas. Because of these events and public perceptions, scientists, policy makers and regulators are required to take a holistic view towards understanding the problems and producing remedial actions.

Elliott & de Jonge (2002) define for the EUROTROPH project the actual and potential problems of nutrients and eutrophication with reference to 'symptoms of ecosystem pathology' divided in primary and secondary symptoms of change (Table 4).

Table 4

Primary and secondary effects of eutrophication (developed extensively after an original format by Schramm & Nienhuis, 1996) from (Elliott & de Jonge 2002)

Causes	increased nutrient inputs; high residence time/slow flushing rate.
Primary effects	occurrence of blooms of toxic or tainting phytoplankton forms; increasing plant/algal biomass production; occurrence of blooms of micro-algae which may be a nuisance (and cause aesthetic pollution) through foaming (e.g. <i>Phaeocystis</i> , <i>Chaetoceros socialis</i>); decline or disappearance of certain perennial plants, often replaced by annual, fast growing opportunistic species such as foliose or filamentous green algae (e.g. <i>Ulva</i> , <i>Enteromorpha</i>); reduced diversity of the flora (and associated fauna); changes to photic regime through shading.
Secondary effects	increased particulate and dissolved organic matter in seawater and sediments; nuisance mat formation to hinder fishing and navigation; nuisance mat formation producing anoxic conditions; increase in microbial community and thus oxygen depletion, leading to hypoxic processes such as H ₂ S and CH ₄ production; development of opportunistic macrobenthic populations and thus changes along the Pearson-Rosenberg continuum; poor water quality, especially water column oxygen depletion, thus affecting fishes and zooplankton; mortalities of higher organisms through effects of neuro-toxins; hindrance to intertidal feeding by wading birds and ducks.

The symptoms listed in Table 4 are used by Elliott & de Jonge (2002) to produce a conceptual model that integrates empirical observations on the main effects of eutrophication on ecosystem structure and functioning (Figure 24). This conceptual model makes the link between bottom-up causes versus top-down consequences. The former includes the physical nature of the system, the input levels and the initial

5.3 NUTRIENT LOADING AND THE RESPONSE IN COASTAL PELAGIC COMMUNITIES

Models integrating the nutrient driven processes in coastal ecosystems are a promising alternative for the empirical linking between nutrient loadings and effects on ecosystems in (too scarce) long-term series as suggested by Colijn et al. (2002).

Predicting the fate of nutrients added to an ecosystem implies a representative assessment of the pathways among the ecosystem components. Over the past decades, the scientific view on the pelagic food-web has changed from a linear food-chain model to a food-web model, in which the microbial food-web plays an essential role. This paradigm change has important consequences for modelling the effects of eutrophication on coastal ecosystems.

5.3.1 Analysis of effects on food webs based on flow networks.

This was the main objective of the COMWEB project to develop efficient analytical, numerical and experimental methods for assessing and predicting the effects of nutrient (N, P, Si) supply on the stability and persistence of pelagic food web structure and function in coastal waters (Olsen et al. 2001).

The field experiments were performed at different regional locations in order to cover the diversity of European coastal waters (Baltic, Mediterranean, North Sea, and the Norwegian coastal currents).

Reconstruction of flow network was done by inverse mathematical methods partly developed in the COMWEB project. Inverse modelling require time courses of biotic and abiotic components, trophic structure with all fluxes to be estimated and general physiological information used to constrain the flux calculations. The output is the average fluxes between components during the experimental period.

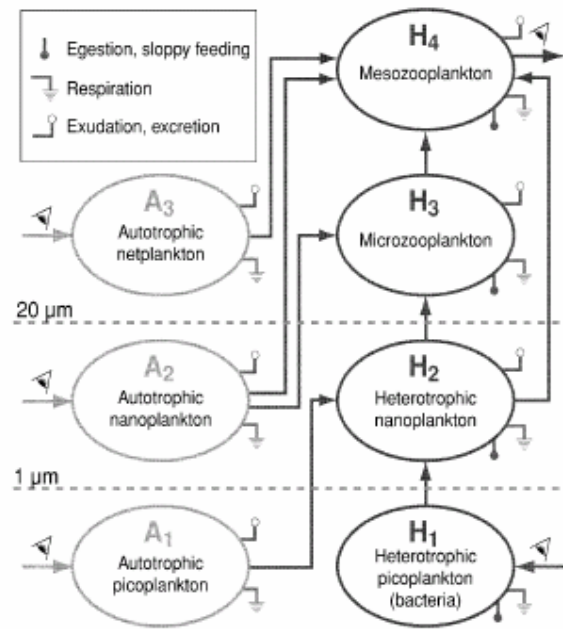
The COMWEB project was characterized by a common platform of conceptual and experimental approaches that was applied at all sites. It may be argued that individual case solutions could have been further optimized with more customized food web structures but this would have been to the detriment of the capacity of comparisons and generalisations of the outcomes for regional waters. The chosen scheme, with slight regional modifications was sufficient for the general objective of comparing coastal, pelagic food web structure and function during nutrient enrichment.

The generalised trophic structure used in the flow network construction included 3 or 4 functional autotrophic (denoted A1–4) and 4 heterotrophic (H1–4) compartments (Figure 25). The indices 1 to 4 correspond to the size class to which these organisms belong and/or to their relative position along trophic chains (Figure 25).

The resulting network is obviously a simplified scheme; which should be critically examined for the necessity of additional fluxes or components. For example; micro-algae (A4) was only present in low numbers in Baltic waters (zero in Mediterranean and NE Atlantic) and no mixotrophic fluxes were included. Viral degradation of bacteria was introduced in Baltic and NE-Atlantic waters (but not North Sea), because it improved substantially the inverse solutions. Moreover, the activity of H4-predators (e.g. jellyfish; H5) was omitted, although this most likely constrained the dynamical resolution of the mesozooplankton (H4) activities in the output of the inverse model.

Figure 25

Generic food web structure used during flow network construction of C, N and P for the COMWEB project. From (Olsen et al. 2001)



5.3.2 Regional specificities in nutrient effects

Short-term (<1 month in mesocosms) and medium term (Summer-Autumn in lagoons) effects of nutrient perturbations were examined by Olsen et al. (2001) along a trans-european gradient (See previous section). Oligotrophic Mediterranean waters showed generally lower biomasses of all functional planktonic groups and a stronger relative contribution of heterotrophic nano-plankton than both Baltic and NE Atlantic waters, which showed more comparable concentrations of functional plankton groups.

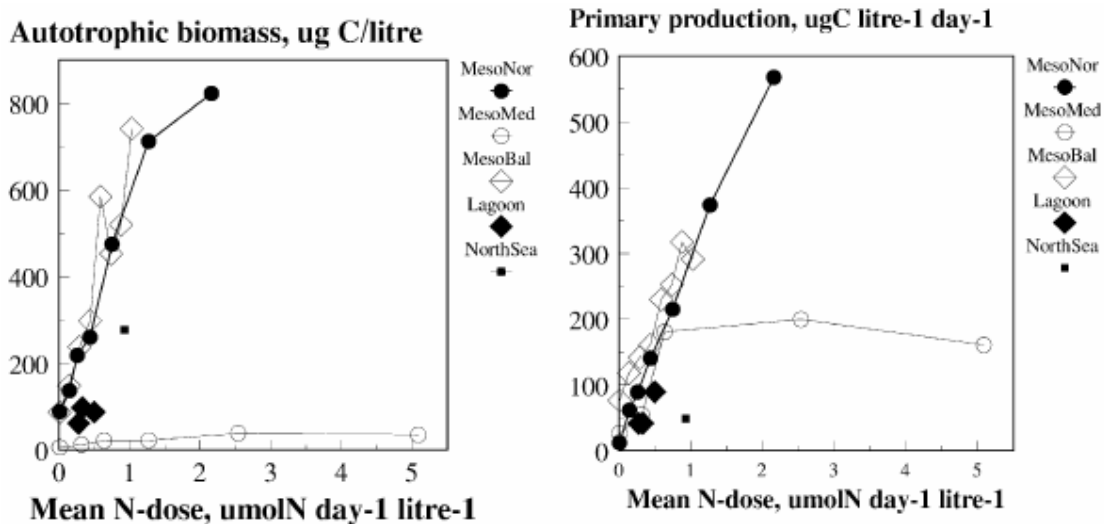
High, balanced nutrient addition to NE Atlantic waters in the short-term mesocosm experiments resulted in severe blooms of diatoms within 9–14 days, even though the initial diatom density was very low (Figure 26). Conversely, Mediterranean waters were characterised by very low accumulation of phytoplankton biomass as long as nutrients (N, P, Si) were added in Redfield proportion (Figure 26). Medium-term responses in the lagoon were qualitatively similar, but lower in magnitude, since larger grazers had been able to adapt to the new situation.

The constructed flow networks indicated that the microbial pathway from nano-phytoplankton (A1) and bacteria (H1) through nano-zooplankton (H2) ending in ciliates (H3) (Figure 26) was only moderately affected by the nutrient loading rate. This supports the view of a dynamic microbial food web showing growth and feeding rates that were well balanced and close to their maxima already in the initial plankton community. This is a reasonable assumption, since the incubations were started with summer communities.

The added nutrients were mostly transferred through nano and net phytoplankton (A2, A3) to mesozooplankton (H4) whereas ciliates (H3) mainly feeding on phytoplankton, and heterotrophs were minor components of the food for meso-zooplankton. The lower food web could therefore rather be described as one respiratory microbial food chain and two parallel food chains to higher levels with relatively limited interaction.

Figure 26

Comparison of dose response along the geographic gradient in the COMWEB projects. Left panel: Autotrophic biomass as a function of nitrogen dose, Right panel: Primary production as a function of nitrogen dose. From (Olsen et al. 2001).



The lacking response in biomass accumulation in the Mediterranean water mesocosms was shown to be a result of high phytoplankton lysis rate (Agusti et al. 1998). This was most likely due to the tight feeding control of pico-phytoplankton (A1) by nano zooplankton (H2) (Figure 26)

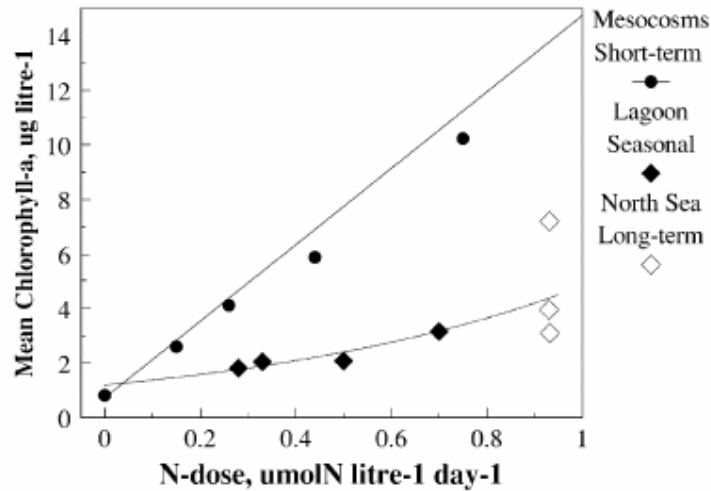
The experimental time scale in the mesocosm experiments was too short for the grazers (ciliates and copepods) to take control over the diatom populations developing in the Atlantic water mesocosms after the nutrient addition. It is furthermore suggested that adjustment of the benthic compartment could further reduce the response at longer scales.

5.3.3 Effects of perturbation/observation scales on the nutrient effects

A comparison of short-term (weeks) and intermediate-term responses (seasonal) of variable nutrient supply rates to open and closed NE Atlantic waters showed that the temporal scale of nutrient enrichment and observation affected the quantitative ecological responses (Olsen et al. 2001).

Figure 27

Short-term, seasonal, and long-term response in summer averages of chlorophyll a as a function of nutrient dose supplied to NE Atlantic waters. From (Olsen et al. 2001).



The response of chlorophyll-a to the N dose, was higher in the closed mesocosms exposed to short-term perturbation of the nutrient supply, than in open systems exposed for >4 summer/autumn months (Figure 27). The Atlantic lagoon developed from the natural relatively oligotrophic situation towards a situation comparable to the eutrophicated North Sea. This suggests that responses on seasonal and long-term scale may be relatively equal.

The differences between short-term responses in mesocosms and seasonal responses is most likely a result of the different time scales of perturbation and observation, as well as the variable exchange rates with surrounding waters (water dilution rate).

The short-term response of autotrophic biomass with increasing nutrient supply rate was immediate and almost linear in all types of coastal waters. The larger grazers were not able to show a numerical response within the period of the mesocosm experiment.

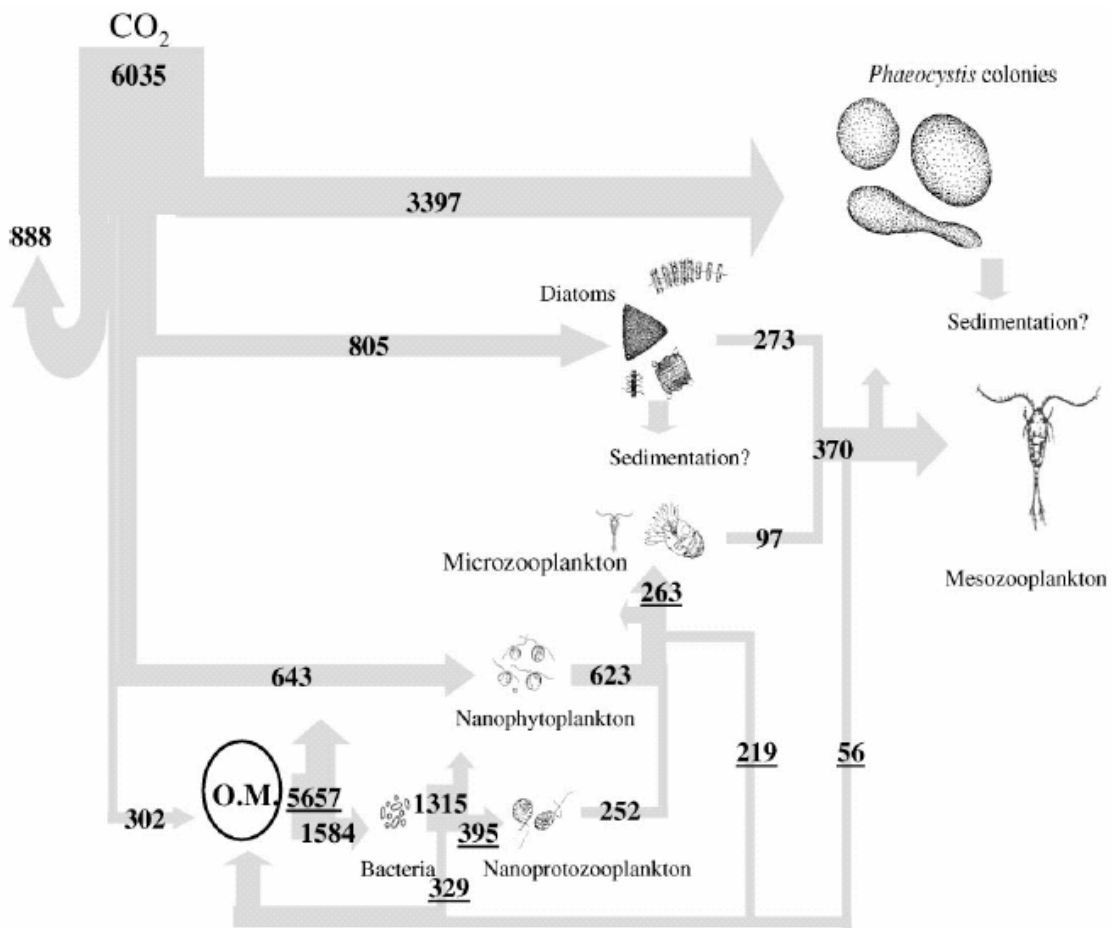
The effect of water dilution rate and exposure time in the open systems has to be considered beside the level of the nutrient dose. It follows that experimental mesocosm systems can only predict short-term effects of nutrient perturbations, which may be relevant for natural upwelling events and other extreme episodes.

5.3.4 Effect of altered nutrient discharge on the *Phaeocystis* bloom in the North Sea

One of the common pattern highlighted by Olsen et al. (2001) was that primary production, mesozooplankton grazing and growth, fraction of primary production consumed by grazers, and bacterial production relative to primary production were all well related to the nutrient loading rate. However, closer examination of the North Sea coastal system (Gasparini et al. 2000, Rousseau et al. 2000) shows that the major response to nutrient additions in disequilibrium (much higher N additions than P and Si) is translated into a bloom of *Phaeocystis globosa*, a species that is not grazed by copepods and actually inhibits copepod grazing on diatoms. This is consistent with mesocosm experiments (PHASE projects) where tanks enriched with nitrogen or phosphorus showed large development of *Phaeocystis* that were not consumed by the copepods in the mesocosms (Escaravage & Prins 2002).

Phaeocystis production is mainly processed by the microbial foodweb, and transfer of this production (via microzooplankton) to mesozooplankton is particularly poor: only 1.6 %, compared to 34% transfer efficiency from diatom production to mesozooplankton grazing. A scheme for the foodweb structure and flows in spring is given in Figure 28 (From Rousseau et al., 2000).

Figure 28
Carbon budget established on basis of integrated flows for the spring period (26 February–6 June). Flows are expressed in $\text{mgC m}^{-3} \text{ period}^{-1}$. Underlined figures are not directly measured but estimated. O.M. represents the pool of organic matter. From (Rousseau et al. 2000).

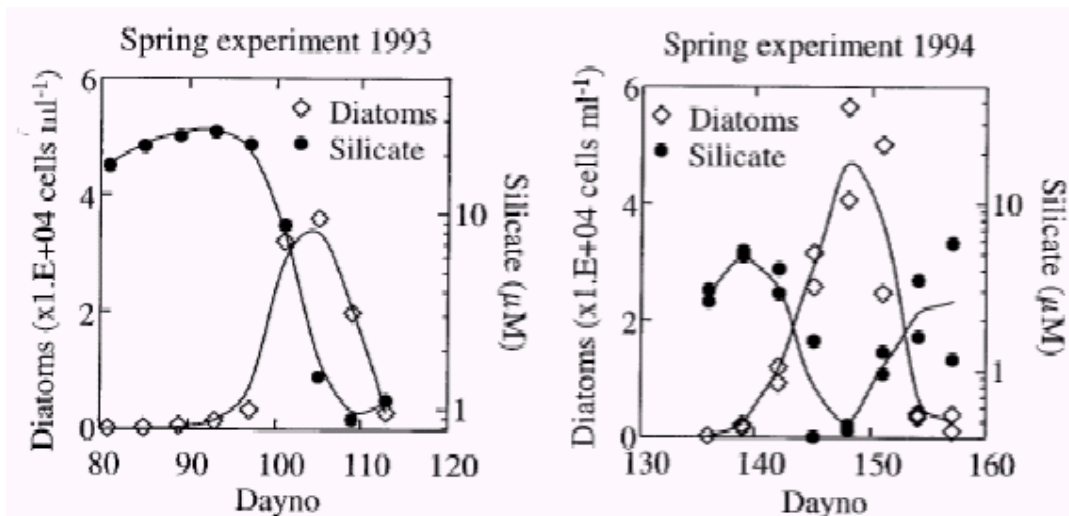


5.3.5 Effects of altered nutrient discharges on diatoms

Silicate availability has been abundantly described in the literature as a crucial factor in determining whether flagellates or diatoms will dominate phytoplankton assemblages. It has also been discussed that anthropogenic eutrophication and the associated high N/Si ratio, could be the cause of the increase in toxic phytoplankton blooms observed in marine coastal waters during recent decades (Smayda 1990, Egge & Asknes 1992, Schöllhorn & Granéli 1993, Sommer 1994, Schöllhorn & Granéli 1996). An important notion brought up by these studies is that the development of non-diatom phytoplankton depends on the quantity of nitrogen and phosphorus left over by diatoms after the spring bloom becomes Si limited. In the same vein, Egge & Asknes (1992) observed in mesocosm experiments that diatoms needed at least 2 μM to successfully develop; at lower Si concentrations, non-diatom species developed and numerically dominated phytoplankton (at least temporarily). The dependency of the diatom spring bloom on silicate was also clearly demonstrated in mesocosm experiments by Escaravage & Prins (2002) where diatom populations systematically collapsed by silicate concentration between 2 and 1 (Figure 29).

Figure 29

Time series for silicate concentrations and diatom abundances in mesocosm spring experiments. From (Escaravage & Prins 2002).



Other mesocosm experiments (NTAP project, Isefjord DK) by Havskum et al. (2003) described the competition for nutrients between diatoms and bacteria in mesocosms where different amounts of nutrients (N, P, Si) and glucose were added. In the mesocosm set where no silicate was added, enrichment with phytoplankton nutrients and glucose led to a replacement of diatoms by heterotrophic bacteria ($> 2 \mu\text{m}$). In the mesocosm set where silicate was kept replete, diatoms competed successfully with bacteria for the uptake of mineral nutrients.

The altered nutrient inputs (through the Danube) to the Black Sea (Si:N ratio from 42 to 2.8 and mean NO_3 concentrations from 1.3 to 7.9 μM between 1960 and 1992) have resulted in distinct shifts in phytoplankton blooms (Humborg et al. 1997). While diatom blooms increased by a factor of 2.5, blooms of non diatoms such as dinoflagellates and prymnesiophytes increased by a factor 6.

The previous observations from mesocosm experiments or from the field (Black Sea) are consistent with the traditional concept of eutrophication where diatom are mostly limited by silicate and other phytoplankton either by N or P.

However a closer look to the biogeochemical transformations of inorganic nutrients in the mixing zone between the Danube and the north-western Black Sea by Ragueneau et al. (2002) suggests a different scenario: This study reveals an efficient biotic (freshwater phytoplankton) and abiotic (adsorption) removal of phosphorus from the inflowing river water, strong benthic denitrification and high benthic dissolved silicate regeneration. Nutrient concentrations decrease consequently extremely rapidly across the salinity gradient, especially PO_4 , which reaches depletion levels at a salinity of 10 ppt in spring and summer.

Both Si/P and Si/N ratios significantly increase across the salinity gradient, rapidly relieving the Silicate limitation potentially present in the river end-member ($\text{Si/N} < 1$). The combination of PO_4 removal processes and nitrification of regenerated NH_4 contribute in spring to increase the N/P molar ratio from c. 50 in the river end-member to about 150 at a salinity of 10. Together, the elevated Si/P and N/P ratios at a salinity of greater than 3 induce a potential limitation of the brackish spring diatom activity by ambient PO_4 .

Between spring and summer, the system loses inorganic nitrogen through denitrification and NO_3 is almost depleted at a salinity of as low as 12. Nitrogen limitation and/of colimitation with P-availability of phytoplankton growth can thus be suggested for this period of the year.

In contrast to spring and summer depletion levels of NO_3 and PO_4 at a relatively low salinity, DSi never reaches concentrations lower than 3–5 μM , well above the threshold of 2 μM defined by Egge & Asknes (1992).

The results by Ragueneau et al. (2002) suggest that despite the potentially Si-limiting signature of the Danube waters, DSi does not limit diatom growth in the Danube estuary and north-western Black Sea. Rather, PO_4 depletion in spring 1997 and NO_3 and PO_4 depletion in summer 1995 could be responsible for the negligible diatom growth in the lower Danube estuary and Black Sea waters.

5.3.6 Propagation of the nutrient signal through the pelagic food web

In the model by Rousseau et al. (2000), there are almost no trophic interactions between the *Phaeocystis* bloom and zooplankton, the fate of the bloom is rather to be exported to the benthos via sedimentation (Figure 28). However, observations from other ELOISE studies suggest possible trophic links between zooplankton and *Phaeocystis*, either at the onset or decay of the bloom:

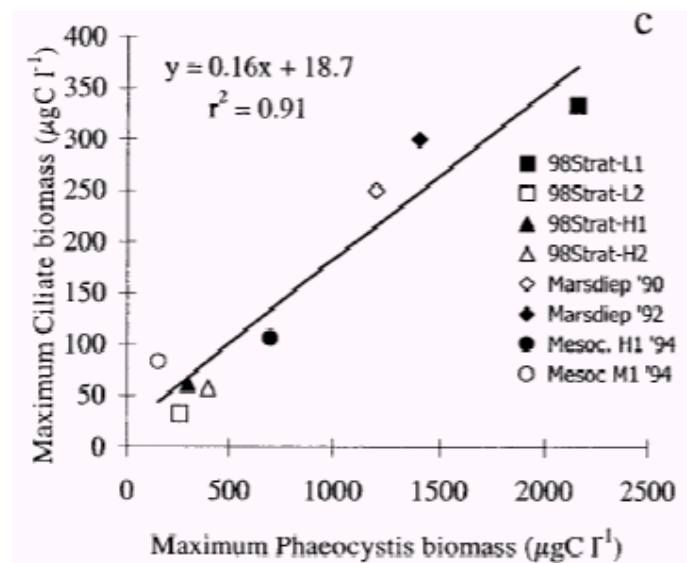
Gasparini et al. (2000) stressed the role of copepod in stimulating the *P. globosa* bloom in the Southern Bight of the North Sea. Firstly, the low grazing pressure exerted on this colonial alga may contribute to its prodigious development. Moreover, preferential grazing on diatoms may result in a reduction of inter-specific competition for nitrate and phosphate among alga. Lastly, the selective removal of microzooplankton organisms by the copepods may limit their development and may subsequently reduce the microzooplankton grazing pressure on *Phaeocystis* cells.

Monitoring on the progression and fate of phytoplankton blooms in fjords of Northern Norway by Archer et al. (2000) suggested that the microzooplankton grazing on single cells and small colonies of *Phaeocystis* was high enough to decrease the rate of formation of larger colonial phases.

Escaravage & Prins (2002) shown from both mesocosm experiments (PHASE project, Oosterschelde) and field observations from the literature (Marsdiep) that there is a rather constant ratio between the heights of consecutive *Phaeocystis* and ciliates peaks (Figure 30). Systematic observations of ciliates grazing cells from (within) disrupted colonies of decaying *Phaeocystis* blooms supported the assumption that a significant fraction of the bloom may be used within the water column.

Figure 30

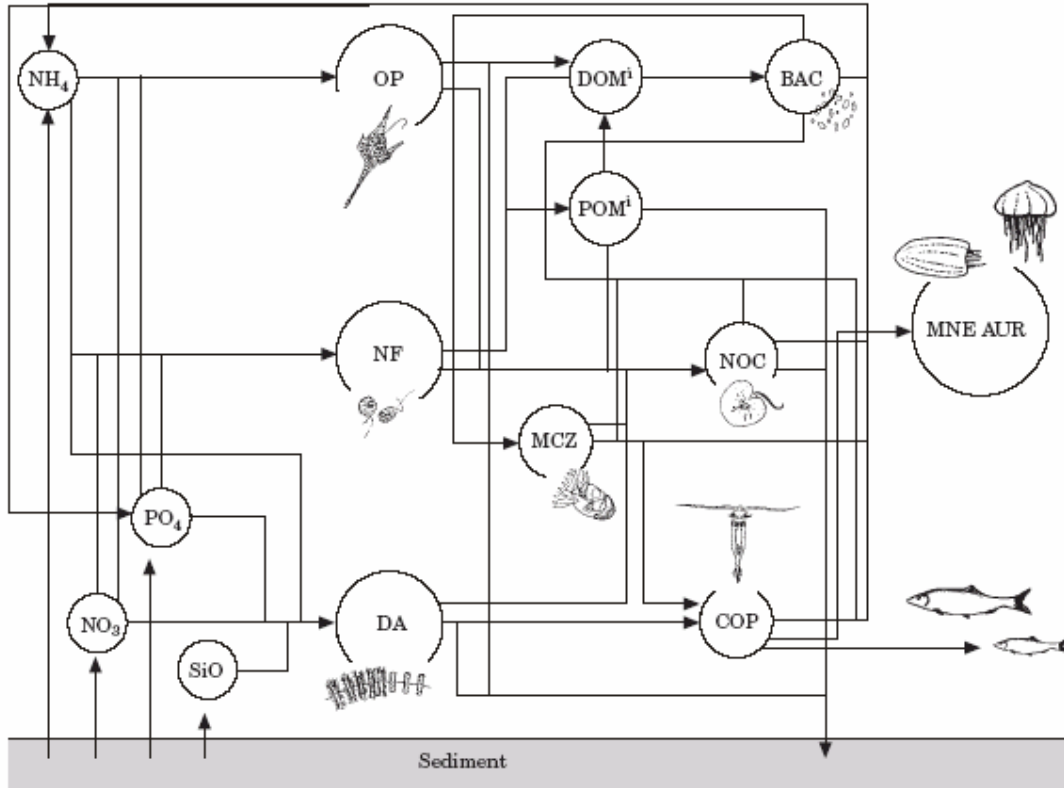
Maximum ciliate biomass as function of the preceding *Phaeocystis* bloom (all in $\mu\text{g C l}^{-1}$) in the mesocosm experiment from 1998, the Marsdiep (1990, 1992) (van Boeckel et al., 1992; Brussart et al., 1995) and previous mesocosm experiments (Mesocosm M1, H1 in 1994 in Wetsteyn & Vink-Lievaart, 1995; Escaravage et al., 1999). From (Escaravage & Prins 2002).



These examples stress the need of ecological models that explicitly describe the bottom-up and top-down controls of the pelagic food chain for an adequate representation of the fate of the nutrients brought into the water column. This was attempted by Lancelot et al. (2002) for the EROS project with BIOGEN, a high trophic-resolution ecological model that was applied to the Black Sea system (Figure 31).

Figure 31

Diagrammatic representation of the structure of the BIOGEN model. Inorganic nutrients include ammonium (NH_4), nitrate (NO_3), phosphate (PO_4) and silicic acid (SiO). Organic matter is composed of dissolved ($\text{DOM}_{1,2}$) and particulate ($\text{POM}_{1,2}$) matter each with two different biodegradability classes. Phytoplankton is composed of three groups: diatoms (DA), autotrophic nanoflagellates (NF) and opportunists (OP). Bacterioplankton is represented by BAC . Zooplankton includes microzooplankton (MCZ) and copepods (COP). The gelatinous food-chain is composed of Noctiluca (NOC), Aurelia (AUR) and Mnemiopsis (MNE). From (Lancelot et al. 2002).



The model was used to hindcast the changes in the Black Sea shelf ecosystem over the past decades. It demonstrates in a dramatic way the importance of nutrient ratios in the input waters for the functioning and structure of the ecosystem:

The BIOGEN simulations in the open Black Sea in agreement with the results by Ragueneau et al. (2002), indicate that the surface layer planktonic system is driven by winter phosphate availability, which determines the magnitude and extent of the early spring diatom bloom.

BIOGEN predictions clearly demonstrate that limiting nutrients determines the structure of the phytoplankton community, which in turn constrains the structure and functioning of the planktonic food-web:

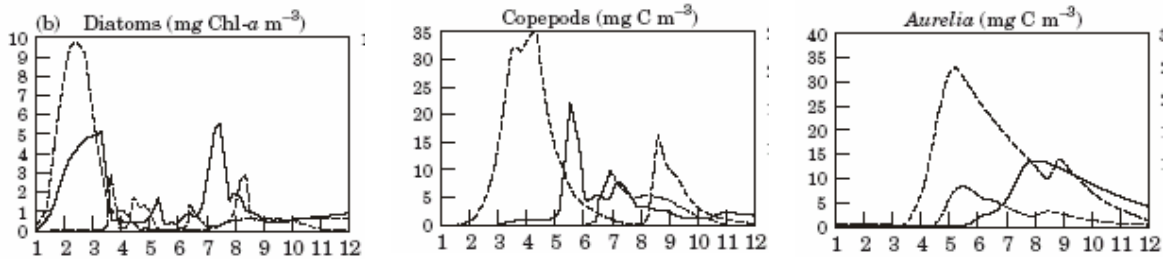
Well-balanced N:P:Si nutrient enrichment, as observed, for example, in 1991, has a positive effect on the diatom–copepod linear food-chain, while the regenerated-based microbial food-chain remains at its basic level. When present in the system, gelatinous carnivores also benefit from this enrichment through their feeding on the increased copepod biomass.

Nitrogen or phosphate limitation, on the other hand, directs the structure of the planktonic food-web towards the dominance of an active microbial foodweb in which bacteria and microzooplankton play a key role; the former as nutrient regenerator, the latter as a trophic path to the copepods and hence to the linear food-chain.

Furthermore, model simulations suggests, under conditions of well-balanced nutrient enrichment, a positive link between fishing pressure and gelatinous carnivores: overfishing, in addition to eutrophication, could have played a role in the destabilization of the Black Sea ecosystem reported for the years 1989–1991 (Gucu 2002).

Figure 32

BIOGEN predictions of Diatoms, Copepods and Jellyfish *Aurelia* biomass in the Danube–Black Sea mixing zone. (—), 1985; (---), 1991; (· · ·), 1995.



Model scenarios of changing Danube nutrient inputs to the north-western Black Sea observed over the 1985–1995 period show that the mechanistic BIOGEN model, based on food-chain structure and physiological concepts, has the required trophic resolution to address the ecological changes evident in the Black Sea since the 1960s.

Model result analyses indicate that coastal eutrophicated-related problems are not only driven by the quantity of nutrients discharged into the coastal system, but that the balance between them is just as important.

5.4 NUTRIENT FLUXES IN COASTAL BENTHIC COMMUNITIES

Increased nutrient discharges are expected to increase primary production in the water column and secondary the vertical flux of organic matter to the sediment. The basic features of the response of benthic deposit-feeding communities to organic enrichment are (Pearson & Rosenberg 1978):

- 1.-Large species are replaced by smaller species
- 2.-Deep-dwelling bioturbating species are replaced by surface or sub-surface deposit-feeding species.
- 3.-K-strategists (long life-span, few offspring's) replaced by the more opportunistic R-strategists (short life-span, intense reproduction)
- 4.-Density decreases to collapses by free sulphide release.
- 5.-Decrease in species diversity

At the scale of entire estuaries, a literature review has revealed a tight correlation between macrobenthic biomass and primary production in the system (Herman et al. 1999). This relation suggests a bottom-up control on macrobenthos and has consequences for possible effect of eutrophication – in particular it also predicts a decrease of (harvestable) benthic populations upon eutrophication abatement).

These features clearly point out that tight relations exist between the flux of nutrients from the water column and the macrobenthic community below it. These relations may be described symptomatically as by Pearson & Rosenberg (1978) or analytically:

The former approach supports a large amount of details (about 100 species are described by Pearson & Rosenberg (1978)) but has a low predictive value since the environmental gradient along which the changes take place is a proxy for the actual controlling factors. The absence of explicitly defined controlling factors in the typology by Pearson & Rosenberg (1978) makes its exportation to other ecosystems difficult. For example it has been pointed out by Beukema (1988) and Craeymeersch (1991) that many estuarine samples exhibit abundance biomass curves typical for disturbed sites after Pearson & Rosenberg (1978) without other obvious signs of eutrophication or human disturbance.

In the analytical approach, the controlling factors are explicitly defined (measurable) and the relations with the ecological (taxonomic, functional) groups are valid in any given system. The analytical approach cannot support the amount of details of its empirical counterpart, but it allows predictions that are within the domains of definition for the processes that are taken into account. This approach still requires an extensive effort for the quantification of the interactions between the different components of the benthos to reach the state of the art achieved in the representation of pelagic systems.

Numerous studies, also in the ELOISE context, have addressed the rates and regulations of biogeochemical processes, such as denitrification, sulphate reduction etc. (see above: sections 4.1, 4.2). Focus was on the sediment biochemistry pathways involved in the nutrient flux at the water-sediment interface and within the sediment. From these studies predictions can be made on the effect of increased

nutrient flux (eutrophication) on the quality of habitat for the benthic fauna (e.g. Figure 11 on page 23 by Wijsman et al. (2002) and also Friedl et al. (1998), de Wit et al. (2001) and Friedrich et al. (2002)).

A second aspect for the effect of nutrients penetrating sediment concerns their implication in the benthic food web. In contrast to pelagic food web where the resource pools and potential fluxes to consumers are rather well identified, benthic food-webs (especially in soft-sediment) are still badly understood:

The importance of the (bacterial) biomass as food for benthic heterotrophic microeukaryotes in comparison with detrital organic matter deposited onto the sediment and/of with the microphytobenthos, remains largely unresolved.

For the macrofauna, there are clear evidences that the feeding interactions between deposit-feeders and bacteria are weak and that non living detrital matter should be regarded as the prime energy source of subsurface deposit-feeders (Heip et al. 1995). It remains however unclear which fraction of the total organic matter in sediments can be considered as food resources (Heip et al. 1995, Herman et al. 1999).

These issues were tackled in ELOISE projects as ECOFLAT, ISLED, EUROSAM, KEYCOP...). The ECOFLAT project studied processes of benthic–pelagic exchange and of benthic interactions on the Molenplaat, an intertidal flat (1.5km²) in the Westerschelde, SW Netherlands. The locations studied on the flat showed a diversity in physical forcing and biological and chemical characteristics that spans almost the range observed in the whole estuary.

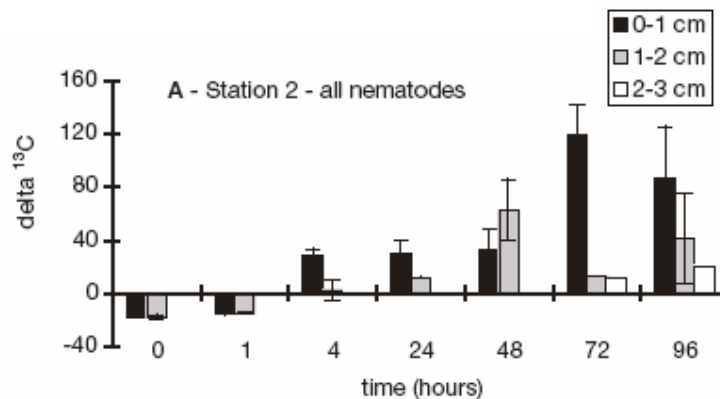
5.4.1 Food sources for meiobenthos and macrobenthos

Study on distributions of nematodes and microphytobenthos op de Molenplaat by Moens et al. (1999) suggest that nematodes (>90% of meiofauna) actively migrate towards specific optimal food patches and that this dynamic aspect requires the use of a centimetre spatial resolution to be highlighted. Inconsistent observations in this study are ascribed to the inability for correlation techniques to adequately infer relations between candidate grazers and their food in an heterogeneous and non-steady state system.

Tracer experiments (stable isotope) on the Molenplaat by Middelburg et al. (2000) and Moens et al. (2002) showed that tidal flat nematodes preferentially utilize labile, locally produced organic matter (microphytobenthos or deposited phytoplankton). This holds for surface- as well as subsurface-dwelling nematodes, time-lags between deposition/production on the sediment surface and assimilation of organic matter by subsurface individuals probably being determined by sediment mixing rates (Figure 33). There was no indication that organic matter from terrestrial or riverine origin contributes significantly to the benthic food web in this study.

Figure 33

$H^{13}CO_3^-$ pulse-chase experiment: stable carbon isotope ratios of the nematode fauna at MP 2, From (Moens et al. 2002)



Experimental results (cultures) by (Hamels et al. 2001) provide the first quantitative data on predation of benthic ciliates by predatory nematodes (*Enoploides longispiculosus*). These ciliates belonged to different taxonomic groups, were of different sizes, and included swimming as well as creeping, and bacterivorous as well as a strictly herbivorous species. The grazing pressure of the nematodes on the ciliates was estimated by a daily removal of 18 to 40% (conservative estimate) of the ciliate field production. These results implies that carbon transfer from primary producers and bacteria to predatory nematodes may be mediated largely by the microbial food web. This is consistent with the incorporation of microalgal carbon (^{13}C) by the predatory nematod *E. longispiculosus* that was observed by Moens et al. (2002) and attributed to the grazing on herbivory ciliates acting as an intermediary trophic step.

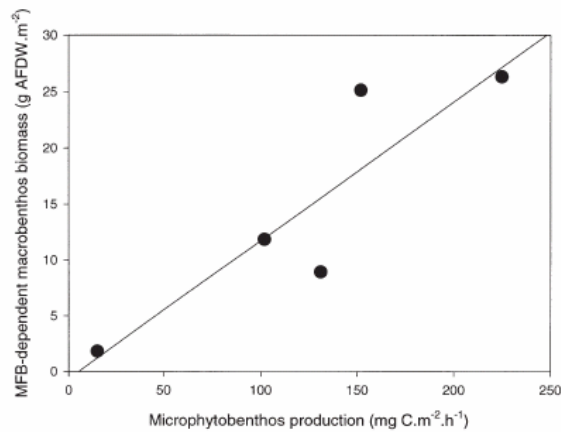
The importance of microphytobenthos as food source for macrofauna deposit feeder was clearly stressed in a study (stable isotope) by Herman et al. (2000). Conversely, macrofauna filter-feeders were shown to strongly depends on phytoplankton food-source. For examples, the cockles were labelled almost exclusively by the pelagic algae, in marked contrast to the benthic grazers. Intermediate isotope ratios (between phytoplankton and microphytobenthos) were measured by *M. balthica* and *P. elegans*, feeding on both types of algal material (pelagic algae within faecal biodeposits of suspension feeders). Also deep

dwelling worm species as *Heteromastus filliformis* show a natural stable isotope ratio very near to that of microphytobenthos and very different to the ratio of the bulk of sediment organic matter. This suggests a strong selectivity by macrofauna in uptake for algal detritus.

A field confirmation for the trophic link between deposit feeding macrofauna and microphytobenthos was produced by Herman et al. (2000). First a degree of dependence on microphytobenthos is approximated for the macrofauna species isotope signature and used to weigh the corresponding biomass. Second the macrofauna biomass at 5 study locations is plotted against the microphytobenthos production. The clear relation between the microphytobenthos production and the macrofauna biomass (Figure 34) illustrates the tight trophic link between both compartments as was suggested by their isotopic ratios.

Figure 34

Relation between microphytobenthic primary production (Hamels et al. 1998, C. Barranguet unpubl. data) and macrobenthic biomass that is calculated to be directly dependent on microphytobenthos (MFB) (see Table 2 for parameters and 'Discussion' for calculation). Linear correlation coefficient is 0.91 ($n = 5$, $p = 0.034$). AFDW: ash-free dry wt. From (Herman et al. 2000).



Stable isotope techniques (natural ratios or pulse-chase) have shown here their ability to identify trophic pathways in benthos. Further progress and application of these techniques should greatly contribute to a better representation of the trophic fluxes between the benthos components.

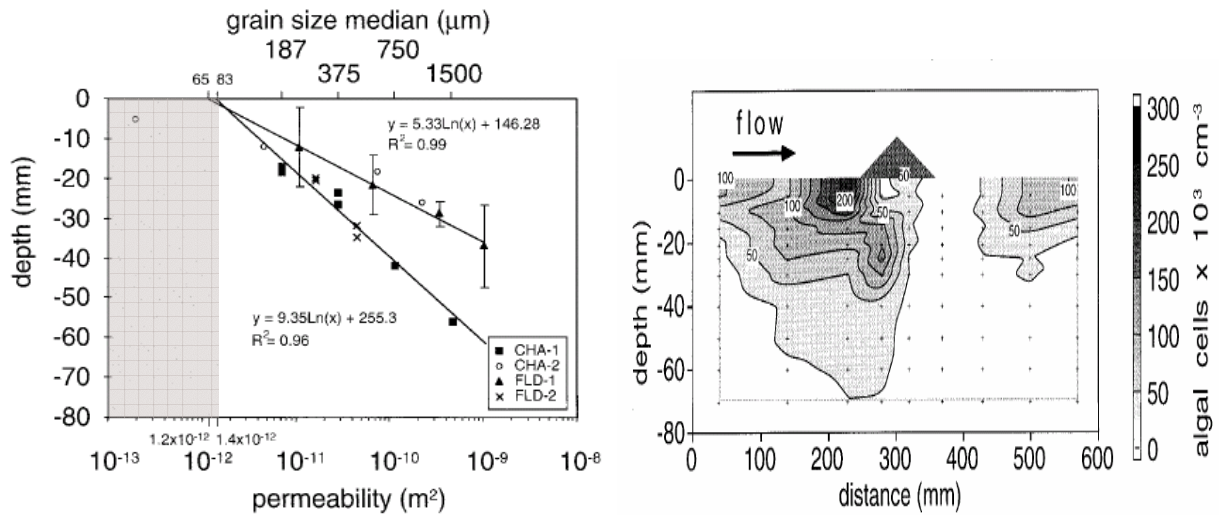
Results on both meiofauna and macrofauna (Herman et al. 2000, Moens et al. 2002) highlights the tight link between these benthic organism and sources of fresh produced organic matter either phytoplankton or microphytobenthos. These results jointly indicate that organic matter quality is very important, and that there is a large difference, for benthic animals, between 'organic matter' and 'food' (Dauwe et al. 1999).

5.4.2 What controls the nutritive flux to macrobenthos

It has been shown in the previous section that benthic organisms strongly depend for their food requirements on fresh organic matter either produced by the phytoplankton and microphytobenthos rather than on the bulk of benthic organic matter. To become available to macrofauna, the organic matter has to be deposited and/or buried on/in the sediment. The processes governing these fluxes are yet not completely understood.

Turbulence of the water column has a profound influence on vertical mixing, and thus on the benthic-pelagic coupling. Reduced vertical mixing rates leading to stratification effectively cut phytoplankton blooms from benthic grazing. Conversely, experiments within the PHASE project demonstrated that benthic beds of filter feeding mussels can themselves enhance turbulent mixing of the water column, and therefore increase the fluxes of food towards the bed (Herman et al., 1999).

Figure 35
 Left: Algal penetration depth vs. permeability for chamber and in situ experiments (No advective particle transport is possible in the gray zone). Right: Isoline diagrams generated from algal cell counts in a Flume ripple experiment. From (Huettel & Rusch 2000).



Deposition of phytoplankton blooms on the sediment surface theoretically requires low current velocities. High permeable rippled sediments (median > 100 μm) that are common in area with high hydrodynamics, have however been shown (Huettel & Rusch 2000) to act as an efficient trap for phytoplankton (Figure 35). Cycling of the POM through the sands accelerates the decomposition of this organic matter. With efficient particle trapping, acceleration of degradation, and fast nutrient release, the nonaccumulating permeable sediments become important sites of POM decomposition, tightening the cycling of matter in the coastal shelf.

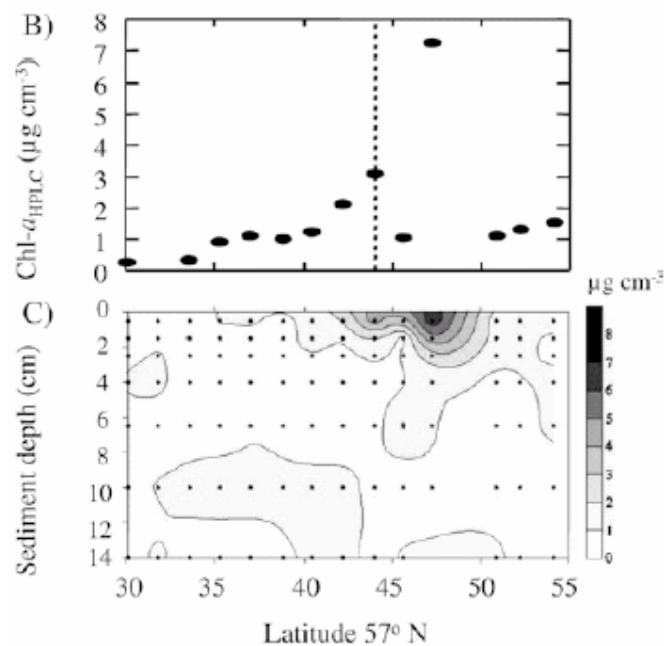
A rapid burial of organic matter was observed by Josefson et al. (2002) in the KEYCOP project after labelled phytodetritus was added as one pulse on the surface of an intact sediment core (Swedish west coast) in still water. The burial mainly occurred from both passive transportation through irrigation of borrows or active dragging of the material into the sediment by ophiuroids. Over the 2 months of the incubation period, about 90% of the added label was buried into the sediment but not directly respired. The weight

specific incorporation of the ^{14}C labelled algal was at the end of the experiment one order of magnitude higher by the surface deposit feeders compared with the subsurface deposit feeders. This is in accordance with the view that surface deposit feeders mainly feed on fresh matter, whereas subsurface deposit feeders utilise older food resources.

The extensive burial of phytoplankton cells in sediment was furthermore evidenced in the KEYCOP project by Josefson & Hansen (2003) who observed increased values of Chlorophyll a and fucoxanthin and a deeper distribution in the sediment in a frontal area (Baltic Sea), which is the area of expected high sedimentation of phytoplankton material. An innovative result was that these pigments was bound inside living cells that represented nearly the same biomass as the entire population in the overlying water column under bloom conditions. This forwards our understanding of how, for instance, the spring bloom input can serve as food for benthic organisms many months after its deposition (Hansen & Josefson 2001, 2003).

Figure 36

Distributions of pigments in the sediment across the Kattegat–Skagerrak front (vertical broken lines at position of the 29 ppt surface isohaline): **Top:** Chl a measured by HPLC in the top centimetre of the sediment. **Bottom:** fucoxanthin concentrations against latitude and sediment depth



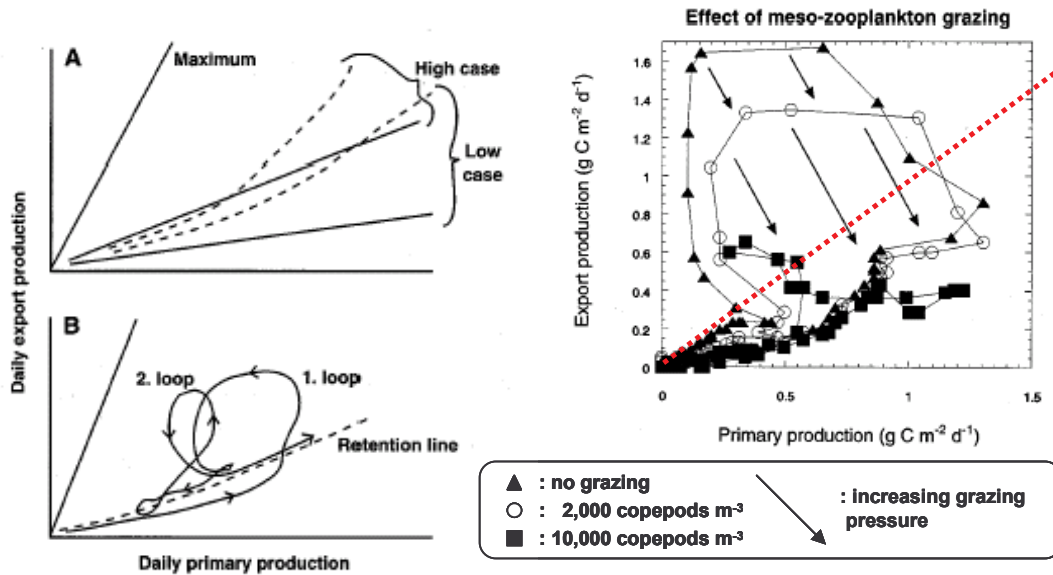
The transport of particulate organic matter to depth not only depends on bottom-up regulation as determined by physical forcing, but also on the structure and function of the prevailing planktonic food web. Wassmann (1998). Based on field observations and model exercises (Wassmann 1998) studied the relation between the daily total primary production (PT) and the export production (PE) directed towards the sediment. The form of this relation is given on PE vs PT diagrams (Figure 37). Each major 'disturbance' (e.g. light, stratification, nutrients advection, upwelling) gives rise to 1–2 retention lines (below the 1:1 line) and one loop. The size and form of the loop is dependent on the type of phytoplankton present, the types of grazers and grazing efficiency. Zooplankton grazing will lower the angle of the retention line and lower the excursion of the export loop (Figure 37). Model predictions by Wassmann (1998) showed a potential tremendous decrease of the flux towards the sediment due to copepod grazing (Figure 37). This stress the

pivotal role played by the top-down regulation (i.e. grazing) for the regulation of vertical flux towards the sediment

The processes highlighted by Wassmann (1998) were clearly exemplified in an ESCAPE field study (Norwegian fjords) by Reigstad et al. (2000) where the match (and occasional mismatch) between the timing of the copepod advection (from the adjacent shelf) into the fjord determined whether the spring bloom reaches the bottom as ungrazed phytoplankton cells (mismatch) or as faecal pellets. In the case of trophic mismatch the total input to the sediment is about $390 \text{ mg C m}^{-2}\text{d}^{-1}$ against about $190 \text{ mg C m}^{-2}\text{d}^{-1}$ when trophic matching is prevailing (copepods advected to the fjords).

Figure 37

Left.-Schematic representation of the relationship between daily total primary (PT) and export production (PE). (A) when sinking rate and grazing are assumed as fixed function of PT. (B) the stochastic (more probable) case when the relationship between PT and PE is not proportional, but greatly variable in time A 'retention line' (stippled) may appear and 'loops' (full line) of variable size depending on the closeness of the coupling between PT and PE over time may take place. **Right.**- The seasonal (March to September) PT vs. PE relationship (March at the origin, points chronologically connected with a line) as a function of variable grazing pressure based on a model presented by Wassmann & Slagstad (1993). From (Wassmann 1998). The 1:1 (red) retention line has been plotted on the graph.



5.5 REFERENCES

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