Study and modeling of eutrophication-related changes in coastal planktonic food-webs

A contribution of the AMORE (Advanced MOdeling and Research on Eutrophication) consortium

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Introduction

The AMORE (Advanced Modeling and Research on Eutrophication) is an interdisciplinary consortium composed of biologists and physical and ecological modelers focusing research activities on coastal eutrophication with special interest in harmful algal blooms. The long-term objective of AMORE is to develop an integrated environmental research methodology for managing water quality and resources of the eutrophicated *Phaeocystis*-dominated coastal North Sea ecosystem, focusing on the Belgian continental shelf. The questions addressed by AMORE are: (i) the natural capacity of coastal ecosystems to assimilate nutrients originating from land-based sources; (ii) the level of nutrient reduction required to protect living resources from the harmful effects of nutrient enrichment; (iii) the monitoring of positive/negative effects of current nutrient reduction programs. Between 1997 and 2001 AMORE investigations especially focused on mechanisms through which a change in nutrient loads induces modification in the phytoplankton community structure and how this change affects in turn the structure and functioning of the planktonic food-web and the related biogeochemical cycles. The chosen research methodology included and combined observation, experimentation and numerical work as follows:

- continuation of the high time-resolution monitoring of nutrients and algal blooms at station 330 of the Belgian monitoring network chosen as reference station since 1988 for its average properties with respect to Belgian coastal waters (Ruddick et al., 1999);

- conduction under field and laboratory-controlled conditions of process-level studies on key phyto-, zoo- and bacterio-plankton communities;

- implementation of the three-dimensional ecological model 3D-MIRO based on the online coupling between the COHERENS 3D hydrodynamic model set up for the region between 51°N and 52.5°N using a horizontal grid of ~ 2.5km and an improved version of the MIRO ecological model based on new knowledge gained and making use of new data assimilation technics;

This paper summarizes main results obtained pointing out success, deficiencies and further research needs.

Eutrophication Status Of Belgian Coastal Waters

Nutrient enrichment and algal blooms

The Belgian Coastal Zone (BCZ) is part of the nutrient-enriched eastern Southern Bight of the North Sea invaded every spring by undesirable algal blooms reaching biomass higher than 30 mg Chl *a* m^{-3}. BCZ is a high dynamical system with waters resulting of the mixing between the in-flowing Atlantic waters and freshwater inputs from the Ijzer, Scheldt and Rhine rivers. Numerical simulations with the COHERENS three-dimensional hydrodynamic model forced with *in situ* meteorological conditions clearly showed that the geographical extend of the river plumes is driven by wind speed and direction under control of the North Atlantic Oscillation (NAO) index (Ruddick et al., in prep.). Overall the nutrient enrichment in BCZ reflects the cumulative inputs of nutrients from atmospheric and direct sources, Scheldt, Ijzer and Rhine rivers, local benthic remineralization and the in-flowing Atlantic waters themselves enriched by nutrient loads by the river Seine and Somme. The relative importance of these different nutrient sources in BCZ is not known yet and varies locally. Analysis of historical winter nutrient data from the Belgian monitoring network revealed a 50% reduction of PO_4 enrichment between 1972 and 1999 with no discernible change in dissolved inorganic nitrogen and silicate. Altogether these trends induced also significant qualitative (N:P:Si) changes in the nutrient coastal environment with however no observable impact on the magnitude of spring algal blooms regularly monitored at station 330 between 1988 and 2000. These blooms were recurrently characterised by the succession of three communities: the high-silicified early spring diatoms, the low-silica demanding *Chaetoceros* and *Rhizosolenia*, and *Phaeocystis* colonies. The latter two communities were blooming together but their relative abundance displayed interannual variation which was not directly related to nutrient trends. Two approaches were conducted to understand mechanisms controlling phytoplankton successions at station 330:

Observational and experimental study of bottom-up controls of diatom/Phaeocystis successions: current knowledge

Beside nutrients, temperature and light are important " bottom-up " factors controlling bloom onset and species succession. Considerable progress based on observation and experimentation has been achieved in understanding their relative role in the control of phytoplankton successions in Belgian coastal waters. Evidence now exists that a light threshold of 12 µmole m^{2} s^{-1} in the water column is required for the onset of the spring succession. This threshold is reached between mid-February and mid-March and relies on physical processes determining the load of suspended matter. This light level corresponds to the light required by early spring diatoms for an optimised cell division rate (Meyer *et al.,* 2000). These early spring diatoms are also more competitive compared to *Phaeocystis* at the low temperature of late February-early March (5-6°C, Rousseau, 2000). On the contrary, *Phaeocystis* colonies optimize their growth at higher temperature and light but are better flexible to light change (Meyer *et al*., 2000). It is therefore concluded that, in the absence of any other limitation, *Phaeocystis* colonies are able to outcompete early spring diatoms at the higher light intensity of April. On the other hand, difference in temperature adaptation could not be evidenced for *Phaeocystis* and *Rhizosolenia*. A possible difference in light adaptation has still to be investigated. Seasonal changes of nutrients suggest that the magnitude of the early spring diatom bloom is controlled by the availability of both PO_4 and $Si(OH)_4$ and that the silicification level is related to ambient silicic acid (Rousseau et al., submitted). This observation, also supported by 0D-MIRO model runs, suggests that "excess new nitrates" (i.e. left over after early spring diatom growth) but regenerated PO_4 and Si (for diatoms only) sustain the growth of *Phaeocystis* and *Rhizosolenia*. For the first time, phosphate limitation was demonstrated in the Belgian coastal waters via the measurement of phosphatase activity (Becquevort et al., in prep). One major result is that this enzymatic activity is associated to mainly large particles including phytoplankton cells and their attached bacteria. The highly significant correlation between phosphatase activity and *Phaeocystis* suggests that the colonies play a major role in phosphate regeneration and are cleaving organically-bound phosphorus for their own utilisation, hence competing with bacteria for phosphate uptake during this period of low ambient phosphate. Further investigations making use of specific probes for locating phosphatases on cell membrane are required for stating on the mixotrophy ability of *Phaeocystis*.

Interannual variability of diatom-Phaeocystis blooms at station 330: synergy between climate and human activity

A sophisticated statistical analysis was conducted on the 10-year time serie data set of nutrients and diatom-*Phaeocystis* successions at station 330 and relevant data on nutrients loads by the river Seine, Scheldt and Rhine and meteorological conditions. This analysis (Breton et al., in prep.) revealed a complex interaction between the climate (NAO) and anthropogenic (land-based nutrients) forcing which has a strong impact on the hydrological features and related nutrient signature of the Belgian coastal waters. Years with a strong positive NAO index were showing a higher influence of nutrient-enriched in-flowing Atlantic waters in the Belgian coastal zone and at station 330 in particular. Subsequent statistical correlation's not only corroborated the key role of phosphate but suggest that, between 1992 and 2000, the magnitude of *Phaeocystis* blooms was controlled by P loads discharged by the river Seine.

From this comprehensive and statistical analysis it is concluded that appropriate identification of *Phaeocystis* P uptake mechanisms, their competitiveness with bacteria for P acquisition, and pathways and turnover rate of phosphate is of prime importance for assessment of impacts on the coastal ecosystem of future reductions of land-based P and N inputs. Although it seems obvious from these observations that no reduction of undesirable *Phaeocystis* blooms would be achieved without decreasing land-based nitrates, model simulations with 90% reduction of solely phosphorus also predict significant reduction of *Phaeocystis* blooms explained by the phosphate limitation of the early spring diatom bloom. Clearly more knowledge is needed on how nutrient inputs are used and recycled before leaving the area of concern before being able to predict the response of the coastal ecosystem to change in nutrient inputs.

Food-web structure and trophic efficiency

Specific grazing experiments conducted during AMORE (Gasparini et al., 2000) clearly demonstrated that Phaeocystis colonies are not grazed by indigenous zooplankton (Temora longicornis) but the reason was not identified. Process-level studies conducted in spring 1998 allowed calculating the budget of carbon transfer through the planktonic network (Rousseau *et al.,* 2000). This calculation indicates that most of *Phaeocystis* production escapes direct grazing and flows through the microbial network where *Phaeocystis* cells are grazed by microzooplankton and *Phaeocystis*-derived DOC is rapidly recycled. This suggests that Phaeocystis-derived organic matter is biodegradable and that insignificant carbon is transferred to mesozooplankton and exported to the sediment. Fieldwork conducted in spring 1999 and 2000 concluded indeed that most of organic matter synthesised during the spring bloom is biodegradable *per se* (Déliat et al., in prep.). The very low bacterial growth yield of 0.1 (Déliat et al., in prep.) indicates that most organic carbon taken up is mineralised rather than building biomass. This result agrees very well with the low trophic efficiency of the microbial food web estimated by Rousseau *et al.* (2000), based on independent budget calculations. Also in agreement with budget calculation, sedimentation rates measured at station 330 were negligible (0-3 m d^{-1}). On this basis, it was further hypothesized that adult copepods would be in food shortage during *Phaeocystis* blooms which could impact negatively not only on the next generation of copepods but also on fish recruitment by starvation of fish larvae. This hypothesis was however challenged by additional field data on egg production by copepods suggesting alternate sources of good quality food for copepods. Yet the picture is even more complicated due to the presence between April and June of a huge mass of gelatinous zooplankton. Main species are the appendicularian *Oïkopleura dioica* occurring at high density (~ 4500 ind m-3) before and after *Phaeocystis*, the ctnephores *Pleurobrachia* at the decline of *Phaeocystis* and the dinoflagellate *Noctiluca scintillans* forming often red tides in June. Little is known about the trophic status of these gelatinous organisms due to their extreme fragility and the difficulty of sampling undamaged organisms. Current knowledge reports these gelatinous as opportunistic and voracious and it might be that *O. dioica* and *N. scintillans* are those who benefit from *Phaeocystis* matter and associated bacteria. The presence of *Pleurobrachia* is more worrying as ctnephores are generally reported as carnivorous, feeding on fish larvae and competing with them for copepods. Gelatinous zooplankton are on the other hand considered as trophic dead-ends and large amounts of NH_4 and PO_4 are released as catabolic products or after their death. In agreement, huge accumulations of NH_4 and to a lesser extent PO_4 have been recorded in the BCZ *at N. scintillans* bloom decline. However some other observations reporting *O. dioica* as preferred food of flatfish larvae suggest that carbon and nutrient recycling might not be the unique role of gelatinous in the Southern Bight of the North Sea. Clearly additional ecological studies involving copepods, gelatinous zooplankton, bacteria and fish larvae have to be conducted at the time of *Phaeocystis* blooms and decline to better assess the impact of *Phaeocystis* blooms on higher trophic levels and the resulting effect on nutrient retention in BCZ.

Assessment and Mitigation Tools

Due to the complexity of bottom-up and top-down controls of marine food webs and the NA0 driven hydrodynamic features, the link between human activity and the response of the coastal ecosystem cannot be fully understood by simple correlation between events. Coupled physical-biological models which are based on physical, chemical and biological principles and describe ecosystem carbon and nutrient cycles as a function of environmental pressure are ideal tools to handle this complexity. When validated these models can be used to assess the magnitude and extent of algal blooms and related damage in response to changes in land-based nutrients and climate. A 3D-ecological model (3D-MIRO) of high spatial and trophic resolution to resolve the changing nutrients loads, the complex biology and hydrodynamics and the tight coupling between the benthic and pelagic realm that characterizes BCZ was implemented in AMORE. The model results of the online coupling of the COHERENS 3D hydrodynamic model and an upgraded version of the ecological model MIRO based on new knowledge gained (Lancelot et al., in prep.) and making use of new data assimilation technics for estimating model parameter errors (Spitz et al., in prep.). The 3D-MIRO model was run to simulate the annual cycle of inorganic and organic nutrients, phytoplankton (diatoms & *Phaeocytis*), bacteria and zooplankton (microzooplankton & copepods) in the Southern Bight of the North Sea for the period 1995-1999. These model runs gave a first view of spatial variability within the domain (Ruddick et al., in prep). The results demonstrated a number of observed processes such as the diatom-*Phaeocystis* succession and the related depletion of silicates and nitrates; the seasonal evolution and magnitude of bacteria, micro- and meso-zooplankton. Less simulated were the seasonal evolution of phosphate, the transient accumulation of ammonium in June and the summer and fall diatoms. This was attributed to the absence of parameterization for regeneration processes associated to gelatinous organisms (not considered as state variable of the model) and the low description of processes involved in P benthic diagenesis. Clearly these parameterizations have to be improved before using 3D-

MIRO as a tool for predicting the response of *Phaeocystis* blooms to future reduction of land-based P and N to BCZ.

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