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Description of the long-term (1991–2005) temporal and spatial distribution of phytoplankton carbon biomass in the Dutch North Sea

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A B S T R A C T

Since the beginning of the 1990s phytoplankton species composition and abundance have been monitored at a high frequency (bi-weekly in the growing season and monthly in winter) at a number of fixed stations on the Dutch Continental Shelf, of which 18 are used in this study. Phytoplankton carbon biomass has been calculated from species-specific biovolume/cell data and summed over all species per functional group enumerated in the samples. The species are divided into four functional groups *i.e.* diatoms, flagellates, autotrophic and mixotrophic dinoflagellates and *Phaeocystis* spp. The total number of phytoplankton samples analysed up to and including 2005 is almost 4000. The annual mean phytoplankton biomass over all stations remained stable at around 145 mg C m^{-3}. However, the phytoplankton composition has changed significantly, with increases in diatoms and dinoflagellates and compensating decreases in flagellates and *Phaeocystis*. With increasing distance from the shore, coinciding with a decrease in nutrient availability and increasing water depth, total phytoplankton biomass as well as the biomass of diatoms, flagellates and *Phaeocystis* spp. decreased. This pattern was not true for the dinoflagellates, which occurred at more or less the same biomass throughout the region. Stations near river mouths and in the Wadden Sea outlets had much higher phytoplankton biomass than stations further from freshwater discharges. The data, split in two periods (1991–1998) and (1999–2005) and averaged over the whole Dutch Continental Shelf, had been aggregated into seasonal biomass distributions. The seasonal phytoplankton biomass distribution was unimodal in both periods, with similar spring maxima of around 300 mg C m^{-3}. The spring maximum occurred one month earlier, in April, in the second period. *Phaeocystis* over the whole study period remained the dominant near-shore species as it has been since the first phytoplankton observations at the end of the 19th century.

1. Introduction

The area under study in this paper is the Dutch Continental Shelf (DCS), a relatively small part (56,785 km^2) of the greater North Sea (572,000 km^2). In the larger scheme of primary production as defined by Longhurst et al. (1995) the North Sea belongs to the coastal boundary domain, with classical nutrient-limited spring and (sometimes) fall blooms on the continental shelves. This classical seasonal phytoplankton pattern on the DCS is often obscured by the highly variable freshwater runoff from the rivers Rhine, Meuse and Scheldt, especially in the so-called "coastal river", a Region of Freshwater Influence (ROFI), driven by Coriolis turning (*cf.* Mann and Lazier, 1996), in a relatively narrow band of approximately 20–40 km wide, usually distinguishable from the clearer North Sea water because of its higher suspended matter content. Marine systems such as the North Sea and certainly the coastal areas that are strongly affected by anthropogenic pressures are highly variable both in terms of biotic and abiotic properties. Until the early 1970s the Dutch part of the North Sea was not systematically monitored. However, research cruises did provide incidental information on various aspects of phytoplankton dynamics (Gieskes and Kraay, 1980; Gieskes and Kraay, 1984; Colijn et al., 1990; Bakker et al., 1990; Riegman and Colijn, 1991; Zevenboom et al., 1991; Joint and Pomroy, 1993; Richardson et al., 1998). Also Reid et al. (1990) in their phytoplankton review note that all cruises and projects were focused on different aspects of phytoplankton dynamics, and most were severely limited in their spatial and temporal coverage. One of the recommendations for future work in this review was "a return to the microscope", a recommendation which has been followed up in the Dutch monitoring program since 1990. Another recommendation was to secure the future of the few long time-series of phytoplankton observations made in the North Sea, to wit the CPR for the whole North Sea, and on a local scale the German Helgoländer Reede data from 1962 on (Wiltshire and Dürselen, 2004) and the Dutch Marsdiep data from the early 1970s on (Cadée and Hegeman, 2002; Philippart et al., 2000, 2007). To these older datasets now also the

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phytoplankton dataset assembled since 1990 as part of the Dutch marine monitoring program should be added, as this is the only one that covers the whole DCS. The Dutch marine monitoring programme, which was begun in 1973, in the first decades primarily provided information on the variability of abiotic variables, such as nutrients, salinity, temperature and oxygen. The only biotic variable systematically observed was chlorophyll-*a* as a proxy for phytoplankton biomass, albeit not a very reliable proxy (Kruskopf and Flynn, 2006), because the Chl:C ratio may vary by an order of magnitude. An additional problem is that chl-*a* tells us nothing about phytoplankton community composition, but just provides a rough estimate of total phytoplankton (carbon) biomass.

Fortunately, from 1990 on much more detailed information on phytoplankton community composition was obtained by quantitative microscopical analysis of the phytoplankton samples in order to detect long-term trends in phytoplankton composition (Koeman et al., 2006). The identification was in most cases down to species, but in some cases only to genus, family name or an even higher taxonomic level. The unit of the results of the cell counts is cells/l per taxon. Although lots of information may be hidden in the community structure of any sample, the analysis of these data is complicated. Even with sophisticated statistical analysis no clear relation between abundance and environmental variables such as nutrients, temperature, etc. could be found (Zuur et al., in press), and as a consequence, this extensive dataset up to now has only been used to extract the abundance of certain nuisance and potentially toxic species for use in the first and second Comprehensive Procedure of OSPAR (Baretta-Bekker et al., 2008). Also for the Water Framework Directive (WFD) which applies in the 1-nautical-mile coastal zone, the abundance data were used as part of the assessment. However, the cell-count numbers (abundances), combined with the carbon biomass per cell data (Menden-Deuer and Lessard, 2000) proved to be much more informative as they allowed us to condense indirect (biomass) information into one value: the phytoplankton carbon biomass in mg C m^{-3} per taxon.

As this still results in numerous biomass values per sample, we have further aggregated the phytoplankton species into four functional groups (diatoms, flagellates, autotrophic dinoflagellates and *Phaeocystis* spp.), following the approach taken in the European Regional Seas Ecosystem Model (ERSEM) modelling projects (Baretta et al., 1995; Baretta-Bekker and Baretta, 1997). The small portion of undefined cells, typically <3%, has been ignored. Each sample is thus reduced to four carbon biomass values, one for each functional group. Seasonal changes in species composition within any one functional group thus only can express themselves in the carbon biomass.

Aggregating our phytoplankton data into functional groups had the added advantage of providing an extensive carbon biomass dataset which may be used directly for the validation of the simulated biomass of the corresponding functional groups in coupled hydrodynamical-ecological models of the North Sea and to test whether these models indeed do reproduce the observed seasonal and spatial distribution and composition of the phytoplankton community.

This ataxonomical approach probably will be anathema to taxonomically interested specialists, but presenting the data disaggregated to species would have made it impossible to see the forest for the trees. However, to address autecological questions, it obviously will be necessary to go to the species level of detail.

The objective of this paper thus is a first description of the spatial and temporal distribution of carbon biomass of the major phytoplankton functional groups, calculated from cell counts per species and their biovolume, on the Dutch Continental Shelf (DCS). The phytoplankton monitoring data from 1991 up to and including 2005 have been used.

2. Materials and methods

2.1. Description of the study area

The North Sea is a shallow shelf sea on the European continental shelf, situated between the United Kingdom in the west and Belgium, The Netherlands, Germany, Denmark and Norway in the east. It is part of the NE Atlantic Ocean. The whole Dutch Continental Shelf lies in the North Sea.

The general circulation in the North Sea is basically tidally driven, but with a strong temporal variability induced by wind. The circulation is weak and variable, but generally counterclockwise. Water from the North Atlantic enters the North Sea in the north-west, flowing southward in the direction of the English channel, on its way southward mixing with the freshwater discharges of the British rivers to flow from there together with Channel water along the Belgian and Dutch coast northward, leaving the North Sea with the Norwegian coastal current. Additionally there is a tidally-driven exchange with Atlantic waters through the Channel with a net (in)flow northward (*cf.* Otto et al., 1990).

The depth on the Dutch Continental Shelf increases from the Dutch coast to the central North Sea and from south to north from less than 10 m to around 50 m in the Oyster Grounds. The tidal range varies from 1 m to 3.5 m along the Dutch coast. In the southern part the water column is generally well mixed by tidal currents throughout the year, but in regions of freshwater influence, near river outflows, short-term haline stratification does occur. In the deeper parts thermal stratification occurs during summer.

The two most striking anomalies on the DCS are the Dogger Bank, which is very shallow indeed (18 m) and the Oyster Grounds (Fig. 1). The Dogger Bank has a sandy bottom and the Oyster Grounds have a muddy bottom (www.noordzeeatlas.nl), as a consequence of being a (temporary) deposition area (Van Raaphorst et al., 1998).

2.2. Monitoring programme

Since the 1970s an extensive national monitoring programme has been run in The Netherlands, monitoring the environmental variables

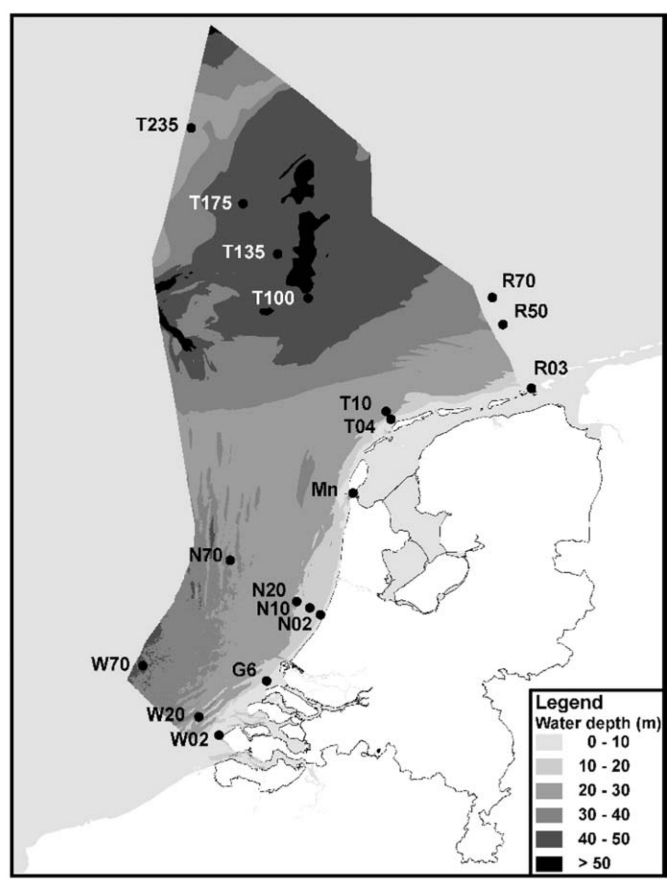

Fig. 1. Map of Dutch Continental shelf with bathymetry and the marine monitoring stations used in this study.