Temporal variability of micro- and nanoplankton in the German Bight in relation to hydrographic structure and nutrient changes

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Variability in micro- and nanoplankton biomass in the German Bight is described based on 34 annual cycles measured five times week \(^{-1}\) near the island of Helgoland. Sources of variability include not only succession of plankton populations within the seasonal cycle but also changes in the hydrographic structure of the nearby stratified water masses of the outer German Bight. The expected effect of increasing inorganic nutrient concentrations (eutrophication) on long-term changes of phytoplankton stocks could not be determined definitively, because of the overriding effect of hydrographic changes. Indications for eutrophication effects – frequent plankton blooms and oxygen depletion in the bottom water due to accumulated organic particles – are restricted to the outer German Bight. Diatoms and flagellates exhibit different seasonal cycles, with particularly large inter-annual fluctuations in the summer dinoflagellate stocks. Nanoplankton populations appear to have increased sharply at the end of the 1970s. As other plankton and abiotic factors have changed in the southern North Sea at the same time, possible larger-scale events must be considered as well as regional causes.

Key words: Eutrophication effects, German Bight, nanoplankton, North Sea, phytoplankton.

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Introduction

Magnitude and type of temporal variability in plankton populations determine whether cause-effect relationships can be detected in natural or anthropogenic changes. Long-term time-series measurements with high temporal resolution are required to separate man-made from natural sources of variability. This is particularly true in areas of large hydrographic variability such as the German Bight. Therefore, the Biologische Anstalt Helgoland started measuring plankton, inorganic nutrients, and hydrographic parameters as early as 1962 and these are continuing to this day. The data and their significance to understanding the eutrophication problem of the German Bight have been described by Gillbricht (1988, 1994), Radach et al. (1990), and Hickel et al. (1995).

Based on the Helgoland time series, the anthropogenic impact in the German Bight with respect to nutrient enrichment has been clearly documented (Hickel et al. 1993, 1995). However, the expected increasing long-term trends in phytoplankton in response to the eutrophication process are not always clearly represented by the data. This is in contrast to the enhancement of phytoplankton stocks observed for instance in Dutch coastal waters influenced by the River Rhine (Schaub and Gieskes, 1991). Schaub and Gieskes showed that increased nutrient discharges from the river Rhine during the growing season (April–September) resulted in an increased plankton algae biomass.

A similar response might have been expected in the German Bight, because its position within the residual current system along the continental coast and its relatively small water volume compared to the amount of inflowing river water make the German Bight one of the most extended areas within the North Sea that is exposed to eutrophication. This paper describes some difficulties in proving the response of phytoplankton growth to eutrophication in the area in relation to hydrographic variability.

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Data and methods

The Helgoland monitoring station is situated at 5 m water depth in a narrow channel ("Helgoland Roads") between the two islands. Sampling started in 1962, thrice weekly until 1974 and five times per week (Monday through Friday) thereafter. The surface water samples are taken as representative of the entire water column, which is always well-mixed as a result of strong tidal currents. Of the many parameters measured, quantitative phytoplankton data, nitrate and phosphate concentrations and salinity are considered here. Inorganic nutrients were measured immediately after sampling using standard methods (Grasshoff et al., 1983). Salinity was determined with an inductive salinometer.

Plankton counts were carried out with an inverted microscope under three magnifications. In accordance with size and taxonomic unit, counted units were converted to biomass (Hagmeier, 1961; Strathmann, 1967) in terms of organic carbon, so that they could be compared and summed. The resulting time series (Fig. 1) is one of the longest and among those with the highest temporal resolution available for the North Sea. While continuity has been good, with little change of personnel involved in counting, information on species identification has been moderate. Priority was set to the continuity of counting frequent species, genera, or at least size groups of nano- and microplankton organisms.

Data for Elbe river discharge were taken from ARGE Elbe (1990, 1995).

Results

Short-term variation

Among the possible sources of variability in plankton populations in the inshore coastal water, the main problem seems to be the separation of effects resulting from the sequence of different water masses from those due to succession within the same water mass. This can be deduced from the short-term (day-to-day) variation of salinity and nitrate concentrations, which often change too quickly for being attributable to changes within a water mass (Fig. 2). Sudden peaks and troughs indicate the arrival of a different water mass which probably represents the edge of the Elbe river plume. While this plume passes east of Helgoland to the northwest during periods of westerly winds, as is generally the case, it might be driven to Helgoland under easterly wind conditions. This causes a sharp fall in salinity and a sharp rise in the nitrate, at least after Elbe river floods.

The direct influence of the Elbe river, which is by far the most important freshwater source in the German Bight, can be deduced from the relation between discharge volume and time-delayed salinity decreases at Helgoland (Fig. 3). The measuring gauge for the run-off at Neu Darchau is situated 150 km upstream from the river mouth and out of reach of the tidal influence that dominates the lower Elbe estuary. The average discharge volume is 750 m$^3$ s$^{-1}$. Only when discharge volumes
reach about 1000 m³ s⁻¹ does the correlation between the two increase. Also, the cross-correlation coefficient is greatest at a time-lag of 24 days. Therefore, this period is taken as the average time needed for the Elbe river floods to flow from the measuring gauge to the monitoring station. The scatter of the cross-correlation coefficients is not surprising, since the delay time will also depend on wind direction and speed.
Seasonal cycles

The largest regular source of phytoplankton variability is caused by the seasonal cycle of the two main components: diatoms representing non-motile cells, and flagellates representing kinetic forms whose swimming ability may be advantageous in stratified water columns (Fig. 4). Overall, phytoplankton biomass may range from about 20 to 800 µg C dm⁻³ with occasionally even higher values during bloom peaks. While short-term wax and wane of the populations influence each specific annual cycle, comparison of many such cycles exhibits regular features. Diatoms show a marked spring bloom, followed by further blooms during summer, while flagellates produce pronounced summer blooms, dominated mainly by large dinoflagellates. Furthermore, a “baseline” flagellate biomass of 10–20 µg C dm⁻³ is present throughout the year.

Inter-annual variation

Superimposed upon the regular patterns, irregular components appear to cause considerable inter-annual variation (Fig. 1). The inter-annual fluctuations in the seasonal cycles of plankton biomass vary within about one order of magnitude. These differences are more likely due to weather and hydrographic conditions than to changes in nutrients or light conditions per se. However, the inter-annual variations are not completely irregular. Regular cycles in diatom and flagellate biomass of about 3 to 5 years emerge (Fig. 5) when seasonal effects are excluded by Fourier analysis and partial Fourier synthesis (Radach and Berg, 1986; Eickhoff, 1992). These might be related to cycles in river run-off, Atlantic inflow and/or changes in hydrographic patterns such as the extent of vertically stratified areas in the southern North Sea. A conspicuous result is that diatom and flagellate cycles mostly alternate, indicating that favourable growth conditions for these main groups may be mutually exclusive. In addition, there is a sudden and pronounced increase in flagellate biomass at the end of the 1970s, after which the regular cycles continue at a higher level.

Long-term trends

Long-term trends in nutrients (Fig. 6) have been well established (Hickel et al., 1993, 1995). Phosphate showed a twofold increase within one decade from 1962 onwards, followed by a stable high level for another decade and a decrease from the mid-1980s onwards as a result of measures taken to reduce phosphate loads of rivers. Nitrate concentrations, in contrast, did not rise before the end of the 1970s, but increased then dramatically, particularly during wet winters with large Elbe river floods. Such years of almost doubling of nitrate concentrations were 1981/82, 1986/87, and 1994/95. The decoupling of phosphate and nitrate loads has resulted in a marked increase of the N/P ratio in the inner German Bight waters, a potential source of altered living conditions for phytoplankton populations.

According to Fig. 6, also total phytoplankton biomass has increased by about threefold. However, the trend appears to be largely due to flagellates only (Fig. 7). When these data are split in a winter and summer period, a sudden and consistent increase in biomass during winter is observed at the end of the 1970s (Hickel et al., 1994). The summer values are much more variable.

Since the flagellate stock in winter consisted mainly of nanoflagellates, this group had to be inspected separately in order to evaluate their significance not only in winter but also in summer. While the larger dinoflagellates and smaller nanoflagellates were treated together as a mixed group in earlier publications (Radach et al., 1990), the entire data set has been re-examined using the original counting sheets, in order to separate nanoplanckton (<20 µm) from microplankton (>20 µm), and to recalculate the biomass values.

When searching for potential causes of the sudden rise in nanoplanckton, the nearby main source of freshwater input must be considered first, because the Elbe river mouth lies only at 60 km distance from the monitoring station. A significant positive correlation between nanoplanckton and the discharge volumes has been found, but also with nitrate concentrations. These two are clearly interdependent, but by taking salinity as a tracer for the relative amount of river water reaching Helgoland the potential influence of nitrate can be differentiated from other, not measured, riverine components (e.g. yellow substance or organic matter of potential food value for bacteria). The relation between nanoplanckton and salinity as well as nitrate concentrations was tested by multiple and partial correlation analysis (Table 1). While a significant negative correlation was found between nanoplanckton and salinity and a positive one with nitrate concentrations, the partial correlation with nitrate, after elimination of salinity, was no longer significant. Hence, we may conclude that the positive influence of river water was not caused by nitrate, but probably by some other organic component of river water.

A parallel increase of nanoplanckton and nitrate concentrations was also found during winter when all samples characterized by salinities below the monthly median value were excluded (Fig. 8). This restriction ensures that the data used only reflect conditions at the station when the water mass was outside the direct influence of the Elbe river plume.
Figure 4. Seasonal cycles of biomass (µg C l⁻¹) of diatoms (a) and dinoflagellates (b), Helgoland Roads, 1978–1990. Monthly median values over the entire period (---); 25% and 75% quartiles (— —) are also given.
Discussion

The sudden increase in plankton biomass can now be attributed to the nanoplankton only, of which by far the largest portion consisted of naked flagellates. The nanoplankton stock did not vary much over the annual cycle (Hickel et al., 1997). This observation, in combination with the consideration that growth conditions in the turbulent waters around Helgoland for autotrophic plankton are very poor during winter, suggests that the nanoplankton counted consisted mainly of hetero- or mixotrophic species. The high proportions of heterotrophs in nanoflagellate abundance, particularly in the smallest size class (<5 μm), as found by van Duyl et al. (1990) in southern North Sea coastal waters support this view. Unfortunately, the auto- or heterotrophic nature of the nanoplankton from Helgoland could not be differentiated during the rapid routine counting procedure, nor could potential losses caused by the preservation method be quantified.

Heterotrophic nanoflagellates are part of the “microbial loop” in which bacteria act as food source (Fenchel, 1990). The microbial loop would profit from enrichment with inorganic nutrients only indirectly, if this were to lead to a higher primary production rate (or if inorganic nutrient enrichment is correlated with organic matter enrichment, such as in river or waste waters).

After separating from the nanoplankton stock, the autotrophic microplankton no longer shows a clear positive correlation with the increasing eutrophication of the German Bight. It became apparent that neither diatom biomass, nor dinoflagellate biomass without the

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Figure 5. Diatom (a) and flagellate (b) biomass values showing cycles >2 years after Fourier analysis and partial Fourier synthesis, Helgoland Roads, 1962–1993. The dashed line indicates the overall mean value of all data.
Figure 6. Annual median values of phosphate (a) and nitrate (b) concentrations (µmol l⁻¹), and median values of phytoplankton biomass (c) (µg C l⁻¹) (——) during the vegetation period (March through September) with values for nanoplanckton (---) inserted, Helgoland Roads, 1962–1995.
The nanoplankton component showed a clear long-term upward trend, possibly due to the enormous inter-annual variations which might have masked minor trends. Explanations for the large inter-annual changes of phytoplankton stocks, and the apparently missing response of the phytoplankton stocks to increasing nutrient levels might be found in the hydrographic patterns of this area. These are dominated by a convergence zone between the continental coastal water and the North Sea water, which is characterized by intense vertical density stratification and which extends northwest of Helgoland (Goedecke, 1968). In summer, this stratified water is the site of large dinoflagellate blooms which might or might not reach Helgoland, depending on the proximity of the frontal systems.

The cause of the observed increase in nanoplankton is a complex one. It is partly explained by Elbe river run-off, but a positive relation between nanoplankton and nitrate remains, when only open sea conditions of relatively high salinity are considered. This does not necessarily mean that there is a direct influence of the suddenly increased nitrate levels on heterotrophic nanoplankton. The true cause of the sudden increase in the latter in the German Bight coastal waters remains unexplained. It is of note, however, that also other abiotic and biotic parameters in the marine environment of the North Sea and even beyond changed at approximately the same time, which suggests potential large-scale effects of climatic sources (Lindeboom et al., 1994).

Based on research cruises covering the whole German Bight, Hickel et al. (1986) investigated the horizontal

Table 1. Correlation coefficients (r) between nanoflagellate biomass (F) and salinity (S), and nitrate (N), corresponding p-values and number of observations (n), Helgoland Roads, January through March, 1978-94.

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<th>Type</th>
<th>Correlation</th>
<th>r</th>
<th>p</th>
<th>n</th>
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<td>n.s.</td>
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Figure 7. Median values of flagellate biomass (µg C l⁻¹) during winter (January–March) (—), summer (June–August) (—), and the entire year (—), Helgoland Roads, 1962–1994.
distribution of dinoflagellate densities. They observed very similar patterns with steep horizontal gradients in August 1979 and 1982, during maximum extension of the vertically stratified water column. Apparently, dinoflagellates normally bloom in the surface water of the vertically stratified water column in the convergence zone, and not in the adjacent highly turbulent coastal water itself.

The suspicion that the variable hydrographic structure, such as the extension of the vertically stratified water column, may override biological succession in the German Bight has been tested by comparing years of distinctly different hydrographic conditions (Hickel et al., 1992, 1993). In order to test how direct eutrophication by Elbe river water inflow might be reflected in phytoplankton biomass, they compared 1981/82 and 1987/88, when particularly large Elbe river floods were recorded. In 1981/82, a calm weather situation prevailed with widespread vertical stratification and the largest plankton blooms ever were recorded, whereas 1987/88, exhibiting even higher nutrient inputs from rivers, was characterized by stormy weather which prevented stratification and no conspicuous plankton blooms occurred. Apparently, eutrophication of the inner German Bight could enhance phytoplankton stocks only if stratified water masses with their clearer surface layer, and therefore better illumination conditions, cover large parts of the area. The conclusion can only be that potential eutrophication effects may be completely overridden by hydrographic events.

Given this conclusion, Helgoland might not be the best place to prove eutrophication effects on phytoplankton growth. Its position at the boundary between continental coastal and North Sea waters is characterized by large and unpredictable variations in stratification patterns, caused by adjacent oscillating frontal systems of the convergence zone between marine waters from the north and estuarine waters fed by nearby rivers from the south.

There is, however, indirect evidence for eutrophication effects in the German Bight. Oxygen deficiency in the bottom water of the outer German Bight has been observed only since 1980 (von Westernhagen et al., 1986, Hickel et al., 1989). These events were associated with extended extinction of bottom fauna. It is unlikely that such phenomena would have been overlooked in this well-investigated and heavily fished area during earlier years. Furthermore, large phytoplankton blooms have been found frequently in the outer German Bight and Jutland waters (Bauerfeind et al. 1990), which might be the result of eutrophication in these clearer waters, where the light climate for phytoplankton is better than in the coastal zone.

The consequences for long-term monitoring of plankton in the German Bight are obvious. The time series must be complemented by extending the monitoring to
the north-west into the convergence zone and the edge of the North Sea water, where the plankton populations of stratified waters can be recorded. Therefore, additional monthly transects from Helgoland towards the north-west have been carried out since 1994, in addition to existing transects to the Elbe and Eider river estuaries sampled on a routine basis.

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