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The spring bloom in the German Bight:

Effects of high inorganic N:P ratios on the phytoplankton development

by

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Glossary

A1 - A3	KUSTOS working group "Atmosphere"
ANOVA	Analysis of variance
ARGE	Arbeitsgemeinschaft Elbe
B1 - B4	KUSTOS working group "Biosphere"
BOD	Biological oxygen consumption
CDT	Consumption doubling time
Chl	Chlorophyll a
DIN	Dissolved inorganic nitrogen (NO_3 + NO_2 + NH_4)
DOM	Dissolved organic matter
DON	Dissolved organic nitrogen
DOP	Dissolved organic phosphorus
Drift investigation	Field investigation tracking a drifting buoy from 04/28/ - 05/08/1995
G1 - G3	KUSTOS working group "Geosphere"
Grid	For convenience term used for sampled grid of stations
Grid 0	04/22/ - 04/24/1995
Grid 1	04/24/ - 04/27/1995
Grid 5	05/02/ - 05/04/1995
Grid 8	05/08/ - 05/11/1995
H1 - H3	KUSTOS working group "Hydrosphere"
KUSTOS	Coastal Fluxes of matter and energy: the transition land-ocean in the south-eastern North Sea
NH_4	Ammonia
n.m.	Nautical miles
NO_2	Nitrite
NO_3	Nitrate
NP	Treatment in the enclosures
NP8	Enclosure with initial nitrate : phosphate ratio of 8
NP20	Enclosure with initial nitrate : phosphate ratio of 20
NP60	Enclosure with initial nitrate : phosphate ratio of 60
NP110	Enclosure with initial nitrate : phosphate ratio of 110
PAR	Photosynthetically available radiation
pC	Particulate carbon
PDT	Production doubling times
PE-PA	Polyethylen-polyamide
pN	Particulate nitrogen
PO_4	Phosphate
POM	Particulate organic matter
pP	Particulate phosphorus
PSU	Practical salinity units
RV	Research vessel
SEM	Standard error of means
Si	Silicate
TCA	Trichloroacetic acid
TdR	[methyl-^{3}H] thymidine
TN	Total nitrogen (DIN+DON+pN)
µM	µmol l^{-1}
w/v	Weight per volume
ZISCH	Zirkulation und Schadstoffumsatz in der Nordsee

1. General introduction

Nutrient and contaminant inputs to estuaries and coastal seas are globally ubiquitous problems that have caused, and are continuing to cause, fundamental changes in the structure and function of coastal ecosystems. Cultural eutrophication has been associated with low dissolved oxygen concentrations, declining fish and shellfish stocks, increased frequency of novel and toxic algal blooms and other ecosystem level alterations (Conley et al., 1993). Human activities have increased the input nitrogen and phosphorus to aquatic ecosystems, while silicate is not added to any significant extent with nutrient enrichment (Officer & Ryther, 1980). This resulted in changes in the Si:N and Si:P ratios. Additionally, enhanced growth of diatoms due to phosphorus enrichment of the freshwater may have caused increased deposition and preservation of diatom silica in freshwater sediments, reducing the silicate input into the estuaries and adjacent waters (Conley et al., 1993). Many investigations already have shown that ratios of nutrients and availability of dissolved silicate can regulate the species composition of phytoplankton assemblages (Kilham, 1971; Tilman et al, 1982; Egge & Aksnes, 1992; Sommer, 1994).
The nutrient concentrations in the inner German Bight are mainly influenced by the Elbe river (Lucht & Gillbricht, 1973; ARGE Elbe 1977-1998). Successfull management efforts reduced especially the phosphorus input into coastal waters, thus changing the ratios of dissolved inorganic nitrogen to phosphate loads (Appendix Fig. A, Fig. B) in the river over the past years (Hamm, 1996). The reaction of the spring diatom bloom in the German Bight to high N:P and N:Si ratios was one of the questions addressed in the project KUSTOS (Coastal Fluxes of Matter and Energy). The spring bloom is the dominant feature in the annual cycle of phytoplankton biomass development (Hickel et al., 1997). Enhanced eutrophication is believed to result in increased biomass production of the phytoplankton as well as in modifications of the phytoplankton assemblage (Officer & Ryther, 1980; Ryther & Officer, 1981). Particulate organic matter produced by the bloom may be transported over long distances. Its remineralization may consume oxygen in the bottom water and enhance eutrophication in regions which may be far away from the original source of input (Hickel, 1997).
Biogeochemical changes caused by the spring bloom 1995 in the inner German Bight were investigated by quasi-synoptical sampling of eight successive grids of stations. Additionally a drifting buoy investigation was conducted, in which a developing bloom was monitored for 10 days. The reaction of the dominant phytoplankton species to increasing NO_3:PO_4 ratios, based on rising nitrate concentrations, was evaluated in an additionall enclosure experiment. Results of these combined field and enclosure studies help to increase our knowledge about the biological variablity of coastal ecosystems and may serve as a database for new management strategies to predict environmental changes and their ecological consequences.

2. Introduction to the German Bight

a) Hydrography

The southern and central North Sea is characterized by a strong interaction of the water with the seafloor which is at a depth of less than 100 m (Pingree et al., 1978). Water properties throughout the area are more or less influenced by drainage from the coast (Becker et al., 1990). The general decrease of depth from north to south is interrupted by the rather shallow Dogger Bank. Channel-like features like the postglacial Elbe valley in the German Bight may act as pathways for bottom water (Becker et al., 1990). Main inflow paths are the southward inflow along the British coast and the inflow through the Dover Strait (Lee, 1980). The Jutland Current transports the water to the Skagerrak. This circulation pattern results from the tidal residual current and the net effects of winds over the North Sea. Along the coast, this pattern is reinforced by the effects from the low - salinity river admixtures (Becker et al.,1990).

Long-duration offshore winds, however, can cause a pycnocline. With rising water temperatures and increasing river flow towards spring the so-called convergence zone of the German Bight (Goedecke, 1955) can develop with a thermo-haline stratification of variable duration and locality, generally being strongest between April and June. The discontinuity layer is generally found between 5 - 15 m in shallow regions and 15 - 20 m in deeper regions of the German Bight. Stratification loses intensity with falling temperatures during autumn until the water body is well mixed again in winter (Becker et al.,1990). Low exchange rates, strong frontal dynamics and a large freshwater inflow from the rivers Elbe, Weser, Ems, and Rhine are characteristic for the German Bight. More detailed information on the hydrography of the North Sea and German Bight is given e.g. by Hill (1973), Lee (1980), and Otto (1983).

River plume fronts can be expected near the mouths of most major rivers, but their position may vary depending on wind, tide and runoff. River discharges are only slowly diluted compared to other coastal areas around the North Sea (Brockmann et al., submitted). Therefore nutrient-rich plumes of the rivers Elbe and Weser may cover large areas (Brockmann & Eberlein, 1986). Atmospheric deposition (Schulz et al., submitted) and input from the Rhine as well as waters transported over long distances coming into the Bight through the Channel and along the British south coast (Brockmann & Kattner, 1998) further contribute to the nutrient input into the German Bight. Fronts may have a significant ecological impact with regard to the spreading and mixing of water masses. Increasing stratification enhances biological productivity by retaining phytoplankton in the photic layer. Seasonal warming, enhanced by freshwater influx, may produce a discontinuity layer, which separates the upper surface layer from the bottom water. In the upper layer nutrients may be depleted by biological activity, while the deeper layer may be enriched with nutrients due to lower photosynthetic activity and remineralisation of sedimented biomass (Brockmann & Eberlein, 1986).

b) Trends in Elbe river discharge and nutrient load

The Elbe river with its tributary area of about 150000 km² has a long year average of surface runoff of about 722 $m^3 s^{-1}$ (ARGE Elbe 1990) with strong variations. The average discharge volume of the river tends to be highest in the months March and April with 1040 and 1120 $m^3 s^{-1}$, respectively (analysis of data from 1926 to 1975; ARGE Elbe, 1977). The runoff of 1000 - 1700 $m^3 s^{-1}$ encountered during the spring 1995 investigations was a typical average for spring, while the yearly average discharge of 908 $m^3 s^{-1}$ for 1995 may be considered as high. 1987 was the last time that a higher value than this was measured with 1130 $m^3 s^{-1}$.The yearly discharge amounted to only 510 $m^3 s^{-1}$ in 1993 and to 861 $m^3 s^{-1}$ in 1994.
A clearly defined plume and stratified zone (Fig. 7, 8) developed 1995 for grid 1 due to the freshwater influence. The progressing of higher haline water towards the coast in the less shallow regions of the German Bight is a typical feature. Steadily decreasing runoff resulted in a less intense, nevertheless detectable freshwater influence for surface and bottom waters during the grid investigations 5 and 8 (Fig. 9-12).
The TN and nitrate load of the Elbe river displayed an oscillating pattern with most recent maxima in 1988 and 1994. The phosphate load was decreasing from the early eighties to early nineties and then remained on the same level until 1997 (Appendix Fig. A, data measured at Cuxhaven/Brunsbüttel by ARGE Elbe 1977 - 1997).
A load of 130000 t a^{-1} TN (90000 t a^{-1} nitrate), 11000 t a^{-1} TP (2000 t a^{-1} phosphate) and 63000 t a^{-1} silicate was estimated for the Elbe in 1993. In 1994 200000 t a^{-1} TN (150000 t a^{-1} nitrate), 8000 t a^{-1} TP (2000 t a^{-1} phosphate) and 111000 t a^{-1} silicate were discharged (ARGE Elbe, 1995). For 1995 the discharge resulted in an input of 190000 t a^{-1} TN (150000 t a^{-1} nitrate), 7000 t a^{-1} TP (2000 t a^{-1} phosphate) and 120000 t a^{-1} silicate into the German Bight (ARGE Elbe, 1996). Estimates of yearly averages should be evaluated with care, since they are based on data with an extremely high seasonal variability.
In calculations based on the yearly averages of nutrient inputs and average runoff volumes, TN concentrations decreased slightly since the early eighties. Nitrate concentrations, though, rose to a peak value in 1988, compared to 1980 and decreased only since 1992 (ARGE Elbe, 1977 to 1997). Concentrations of TP per volume oscillated. Highest concentrations were related to years with low runoff, reflecting the higher contribution of point source input to total input for phosphorus compared to nitrogen.
Discharge during winter has a high potential to influence the extent and intensity of the spring diatom bloom. The monthly average of DIN to phosphate concentration at the river kilometre 693, near to the Elbe river mouth, showed a trend of increasing molar DIN:PO_4 ratios for January to April (Appendix Fig. B). Ratios rose to above 200 for the Elbe in recent years.
No trends became obvious for the ratio between DIN and silicate, especially as silicate measurements are available only since 1989. The monthly averages of DIN and silicate concentrations (at 693 km) resulted in an average ratio of about 2.4 for January to April (1989 - 1996).
An average concentration (weekly measurements in week 1 to 17) of almost 200 µM nitrate, 3.3 µM phosphate (NO_3:PO_4 molar ratio 61) and 125 µM silicate (NO_3:Si molar ratio: 1.6) was measured in the Elbe water for 1995 (ARGE Elbe, 1996). In 1994 the average concentrations, especially for nitrate (250 µM) were higher (ARGE Elbe, 1997), resulting in a NO_3:PO_4 ratio of 81.

Diatoms use silicate in about the same ratio as nitrogen. Ratios of nitrate to silicate larger than 1 thus may indicate a silicate limitation of the diatoms (Levasseur & Therriault, 1987). Nitrate to silicate ratios started out only slightly elevated for phytoplankton use in January with around 1.35 in 1994 and 1995. They then rose towards the end of May to maximum ratios higher than 10 for 1994, while they remained around 5 for 1995. A shift in silicate concentrations is often related to human influences. Eutrophication of rivers, sometimes in combination with man-made lakes, which enhance the residence time of the water, favour phytoplankton blooms and reduce the input of silicate into the sea (van Bennekom & Salomons, 1980). Diatoms probably consume significant amounts of nutrients in the tidal region of the Elbe during the summer despite its suboptimal light conditions, since each year a distinct valley of silicate concentrations was observed for the months of June to August (ARGE Elbe, 1989 - 1997).

c) Long-term trends in nutrients, oxygen and phytoplankton

Nutrients

Different authors came to different results concerning the degree of increase of eutrophication for the German Bight in the last decades, depending on the original dataset used, the method of analysis as well as the time period and region considered. Radach et al. (1990) detected a winterly increase in nitrate, nitrite, and phosphate and a decrease in silicate concentration in an analysis of Helgoland Roads data (1962 to 1984, time period of January to April). They revealed rather unchanged annual cycles of meteorological and oceanographic parameters with a high natural variability. Additionally, they estimated an increase of sea surface and air temperature by about 1 °C (Radach et al., 1990).
From Helgoland Roads data of 1962 until recently a doubling of phosphate concentrations was extracted for the years 1962 to 1972 by Hickel et al. (1997). Phosphate concentrations then remained on a level of about 0.9 µM for the ten following years and a slight decrease was then monitored since 1985 (e.g. 1994: 0.6 µM phosphate). Nitrate increased steeply since 1980/81 and values rose to 3-4 fold concentrations in 1987/88. After 1991 concentrations dropped during some dry years but then rose to a record high in 1993/94 with concentrations above 40 µM nitrate at Helgoland. Overall the nitrate values reaching Helgoland Road rose since 1980, while elevated phosphate concentrations above 2 µM did not reach Helgoland Road any more since 1985 (Hickel et al., 1997).

Originally the German Bight displayed a strong seasonal cycle with a nitrate surplus in winter and spring and a phosphate surplus in summer. Since 1980 rising N:P ratios were monitored with the onset of strong nitrate eutrophication (Lucht & Gillbricht, 1979, Hickel et al., 1997). Values above 100 became typical for winter and since 1988 ratios around 16 were not even reached during summer anymore, but may remain above 50 (Hickel et al., 1997). For only a few months in late summer, nitrate limitation of algal growth after Redfield et al. (1963) remains possible and the area may even develop towards a surplus supply of nitrogen over the entire year (Hickel et al., 1997).

Oxygen

The biological oxygen demand can be considered as indirect indicator of eutrophication. Settling particles increase the organic content of the sediment and enhance the eutrophication effects in these regions, possibly producing zones of high oxygen demand. Another possible fate of increased phytoplankton production is its ultimate use as food by zooplankton or benthic suspension feeders, which could result in an increased production of these groups (Gerlach, 1990).
Gerlach (1990) states that "before 1981 marine biologists believed the waters of the German Bight to be well mixed by tidal currents and deep water never to stagnate". A lowering of the oxygen content by 20 - 30 % below saturation was known only from above the mud bottoms off the mouth of the river Elbe, where sewage sludge had been dumped. Gehrke (1916) nevertheless stated a reduction of oxygen down to 48 - 60% in the bottom water of the central North Sea for investigations in the years 1902 - 1908 already. Low values occurred after the establishment of the summer stagnation and depended on its persistence.

In regions where the productive coastal water overlies the heavier North Sea water during certain hydrographic conditions, oxygen deficiencies are more likely to occur than elsewhere, especially if the North Sea water is oxygen deficient due to prolonged stagnation already (e.g. Hickel, 1989). Wide regions of the German Bight and the waters west of Denmark became oxygen deficient in 1981 to 1983. North-west of Helgoland oxygen levels lower than 4 ml l^{-1} or 50 % saturation were recorded. In some places values were even lower than 2 ml l^{-1} (Gerlach, 1990). Oxygen-deficient areas were thus found mainly in the direction of the average residual current. They were located quite far away from the zones of nutrient input (Hickel et al., 1989), in regions which rarely display a stable stratification, but rather commonly encounter wind induced mixing. The transport of organic particles and algal blooms may have contributed to the accumulation of organic substance to the regions, where oxygen deficiencies had developed (Hickel et al., 1997). Hickel et al. (1997) also considered an indirect eutrophication by the transport of nutrients in organic matter also as a trigger for blooms around Fano and in the northern German Bight. A transport of nutrients bound in organic matter to regions distant from the origin is supported by our drift data (see chapter 5). The monitored bloom only started to grow intensively at the outer margins of the turbidity zone and then needed some time to deplete key nutrients. When the algae reached stationary state, sedimentation may have occurred in the main transportation direction of the current. The following remineralization can feed, after a mixing of nutrients in the upper layer, new blooms in quite a distance from the original nutrient source.
The oxygen situation in the German Bight improved in the years following the strong deficiencies in 1981 to 1983. Oxygen values above 5 mg l^{-1} were measured in August 1984. For June 1985 they remained above 8 mg l^{-1} and for August 1986 oxygen concentrations of 7 mg l^{-1} could be found in most parts of the inner German Bight. Only offshore, northwest of Horns Reef, values were lower than 2 mg l^{-1} (Gerlach, 1990). Estimates from Gerlach (1990) showed however, that organic particles may nevertheless reduce the oxygen content of the deep water in the Helgoland Bight to critical concentrations within a month during summer. He concluded that, even in years without any exceptionally large phytoplankton production, oxygen stress must be expected in the bottom layer when the water is stratified.

Phytoplankton

Several investigators have demonstrated considerable changes in phytoplankton and zooplankton abundance and composition occurring during the last 40 years in the North Atlantic and the North Sea (e.g. Colebrook, 1982, Gillbricht, 1988, Gerlach, 1990, Hickel et al., 1997) and tried to correlate changes of phytoplankton biomass to ambient nutrient levels, river discharge and climate (e.g. Gieskes & Kraay, 1977, Gillbricht, 1983, Hickel, 1990, Gieskes & Schaub, 1990, Cadee & Hegeman, 1993).
An increase in bloom events was found for example for the Skagerrak/Kattegat. Dinoflagellates such as the toxic *Gyrodinium aureolum*, *Prorocentrum minimum* and *Lepidodinium viride* have formed prominent blooms since 1980 (Gerlach, 1990). *Coscinodiscus wailesii*, an introduced species from the American Pacific Coast, occurs massively in the German Bight since 1984 (Hickel et al., 1997, Rick & Dürselen, 1995). *Dinophysis acumunata* caused diarrhoeic shellfish poisoning in 1976, 1979, 1981 and later years (Gerlach, 1990). *Biddulphia (Odontella) sinensis* showed a first mass occurence 1903 in the German Bight and the Skagerrak (Gerlach, 1990) after it was introduced with ballast water from the Red Sea and Japan and has been present since then.
The spring bloom in the German Bight is generally dominated by diatoms. Blooms of *Phaeocystis* may follow, accompanied by another increase in diatoms. Flagellates form major blooms during summer. Large dinoflagellates like *Ceratium* species dominate the biomass from mid June to mid September (Hickel et al., 1997). Total phytoplankton biomass amounted to as much as 100 µg l^{-1} in 1996 as a yearly average (Hickel, pers. Comm., Appendix Fig.C) and was generally close to 75 µg l^{-1} or slightly above in the years 1987 to 1994.
The diatoms should profit most from an increase in nutrient concentrations due to their high uptake and consumption rates, but the eutrophication of the German Bight did not result in a strong increase in biomass of diatoms at Helgoland Road. Depending on the statistical method employed, different values were obtained for phytoplankton increase (Gerlach, 1990). Radach & Berg (1986) stated that there was a strong increase in flagellate biomass by a factor of 10 - 15 at Helgoland Road, while the total phytoplanton biomass increased by a factor of 2 - 3 only. A trend of rising flagellate biomass is based mainly on the rapid increase of nanoflagellate (< 20 µm) biomass towards the end of the seventies. Small heterotrophic and autotrophic flagellates species were not differenciated for samples from Helgoland Road. Hickel et al. (1997) therefore calculated the relation between species carbon excluding the flagellates < 20µm. Phases of increasing dinoflagellate numbers were revealed, which extended over several years, but did not form a continuous trend (Hickel et al., 1997). Nanoflagellate biomass indicated a positive correlation with winter data of nitrate concentrations (Hickel et al., 1997). The significant correlation between flagellates and nitrate was lost though, when salinity effects were excluded from the calculation. Flagellates < 10µm increased slightly in less haline water (Hickel et al., 1997) and additional growth promoting substances (organic substances for heterotrophs, chelating agents) in the river water were discussed as a possible reason for increasing flagellate numbers (Hickel et al.,1997).
The relative availability of nitrogen and phosphorus may strongly affect the species composition of the phytoplankton, too (e.g. Kilham & Hecky, 1988). Radach et al. (1990) suggested silicate as a limiting factor for diatoms. As the diatoms make only limited use of the plentiful nitrogen nutrients, flagellates may take over a leading role. Since the ratio between nitrate and phosphate shifted over the years, it may well be possible that the surplus nitrate caused changes in the species composition (Hickel

et al., 1997). Smayda (1990) discussed that N:Si and P:Si river discharge ratios may affect flagellate dominance relative to diatoms and Sommer (1994) could show in competition experiments that marine diatoms became dominant at high Si:N ratios, while flagellates were the superior competitors at lower ratios.
Other investigations revealed an overall increase in flagellates during the last decades, also. A development from diatom to dinoflagellate dominance was already mentioned by v. Bennekom et al. (1975). Fransz (1986) found indications that the increased nutrient discharge in the Dutch Wadden area multiplied the summer flagellate biomass 2 - 4 fold since 1930, resulting in a shift from diatom dominance towards other algae. Cadée (1986 a,b) mentioned increased flagellate numbers in the Dutch Wadden Sea between 1973 -1985 and found an increasing dominance of *Phaeocystis* in the western Dutch Wadden Sea (Cadée, 1992).

3. Materials and Methods

3.1. Project "KUSTOS": Research goals

The important role of the shelf waters and their coasts as an essential line of intersection for fluxes of matter and energy resulted in the establishment of the International Geosphere-Biosphere programme (IGBP). Land Ocean Interaction in the Coastal Zone (LOICZ) is a core project of the IGBP. The interdisciplinary project KUSTOS (Coastal fluxes of matter and energy: the transition land-ocean in the south-eastern North Sea) was the German contribution to LOICZ. It was funded by the German Federal Ministry of Education, Science, Research and Technology (BMBF, number 03F011A) with a budget of about 12.173.000 DM from January 1994 to December 1997.
The goal of KUSTOS was to analyze and quantify fluxes of matter and energy from the land to the ocean throughout the coastal region of the German Bight. The main focus was on the interaction between the Elbe estuary, the Wadden Sea (up to the 10 m depth line) and the open German Bight. The project TRANSWATT (Transport, transfer and transformation of biomass elements in wadden regions), which was funded by the BMBF during the same time period as KUSTOS, concentrated on the shallow Wadden Sea region, thereby forming a conceptual unit with KUSTOS.
Main activities during KUSTOS included three seasonal field investigations covering winter, spring and summer. Grids of stations were sampled several times, combined with drifting buoy and enclosure or laboratory experiments. Meteorological, hydrographical, chemical and biological data were collected by 13 groups working on up to four research vessels.

3.2. Strategy of the field investigations in spring 1995

The KUSTOS drift investigation of 1995 focused on the study of turnover processes in the river Elbe plume front to characterize changes, at least for a water mass at one particular depth, which was continuously tracked by a drifting buoy. Additionally, grids of stations were sampled repeatedly on a short time scale. Some grids of stations were sampled before the drift investigation and other grids were sampled during or after the drift investigation. These data permit a rough estimation of net conversion processes within a larger region by comparing consecutive grids. A simple comparison of grid data, however, does not take the water movement during the sampling period into account. Hydrodynamic models can be applied to improve the estimate of biologically induced changes compared to advective processes. An exact quantification of turnover processes based on grid samplings within the German Bight remains difficult, though. Data collected during the drift investigation can improve estimates of changes for a certain region and enclosure experiments were applied to further quantify single processes.

The distance between stations of the grid was 10 n.m. (Fig.1). The grid displayed in Fig. 1 was sampled twice by 2 vessels (Grid 0: 4/22-4/24/95; Grid 1: 4/24 - 4/27/95) quasisynoptically to gather information about the current situation of the system with regard to hydrography and biology. A drifting buoy with an underwater sail was released

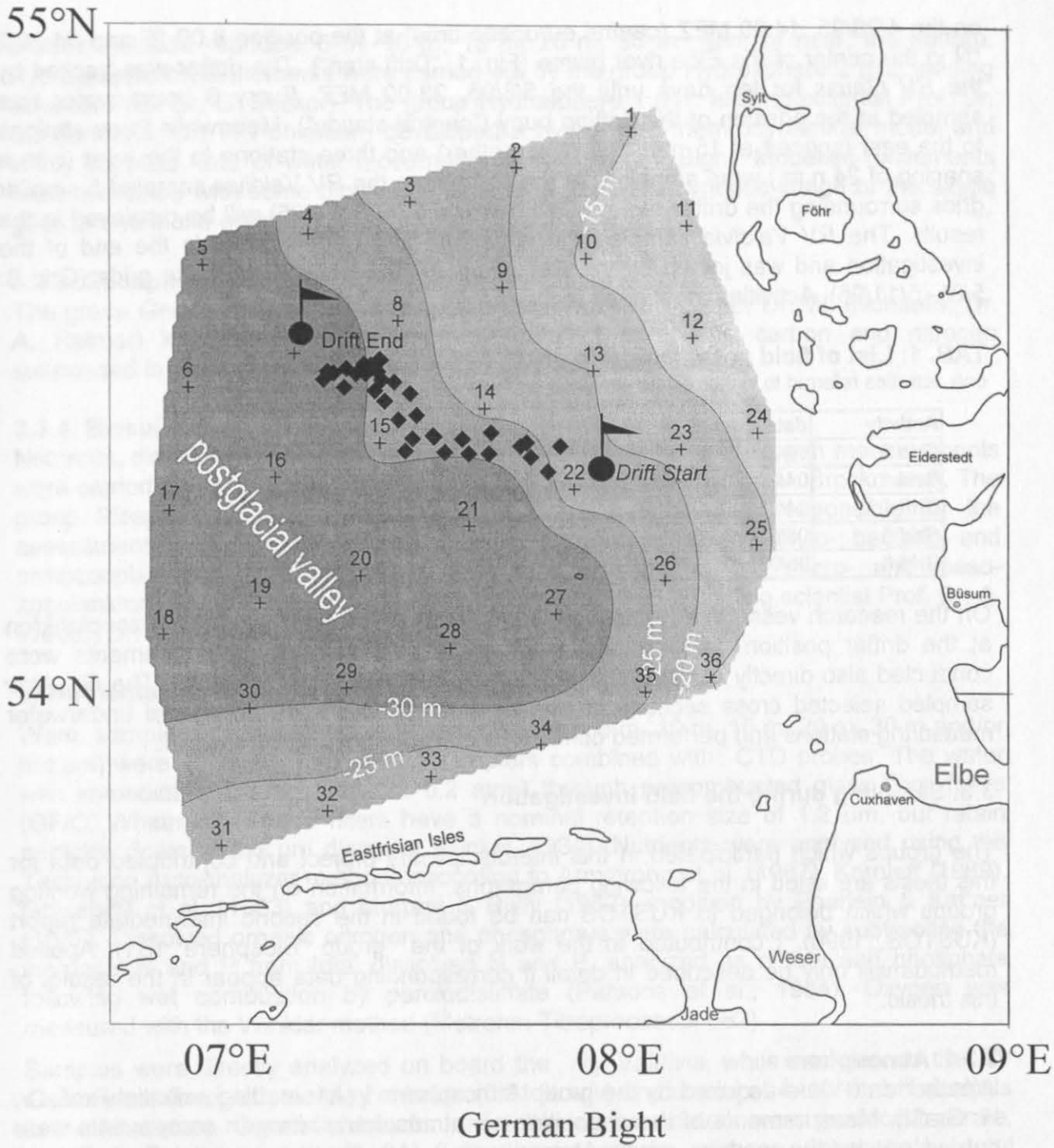


Fig. 1 KUSTOS spring 1995

- depth profile of the German Bight
- position of grid stations 1 to 36
- track of drifting buoy

on the 4/28/95, 14:00 MEZ (central european time) at the position 8.00 °E and 54:20,2 °N in the center of the Elbe river plume (Fig. 1, "Drift start"). The drifter was tracked by the *RV Gauss* for ten days until the 5/8/95, 23:00 MEZ. Every 6 hours water was sampled at the position of the drifting buoy ("central station"). Meanwhile three stations to the east (spaced at 15 n.m. from each other) and three stations to the west (with a spacing of 24 n.m.) were sampled. At the same time the *RV Valdivia* sampled 5 smaller grids surrounding the drifter region. Grid number 5 (5/2/-5/4/95) will be displayed in the results. The *RV Valdivia* sampled the large grid twice again towards the end of the investigation and was joined by the *RV Gauss* for the last one of these grids (Grid 8: 5/8/ - 5/11/95). Activities mentioned in the results are listed in Tab. Xxx.

TAB. 1: List of field activities during KUSTOS:
only activities referred to in the results are listed

Activity	date
Grid 0	04/22/ - 04/24/95
Grid 1	04/24/ - 04/27/95
Drift	04/28/ - 05/08/95
Grid 5	05/02/ - 05/04/95
Grid 8	05/08/ - 05/11/95

On the research vessel *RV Heincke* different studies were carried out with zooplankton at the drifter position. Meteorological as well as air chemistry measurements were conducted also directly at the drifter position by staff on the *RV Heincke*. The *RV Atair* sampled selected cross sections in the region, was in charge of several underwater measuring stations and performed continuous surface light measurements.

3.3. Sampling during the field investigation

The groups which participated in this interdisciplinary project and contributed data for this thesis are listed in the following paragraphs. Information on the remaining working groups which belonged to KUSTOS can be found in the second intermediate report (KUSTOS, 1996). I contributed to the work of the group "Biosphere" (B1). Applied methods will only be described in detail if corresponding data appear in the results of this thesis.

3.3.1. Atmosphere

Weather data were acquired by the group Atmosphere 1 (A1: leading scientist Prof. Dr. H. Graßl). Measurements of the deposition of atmospheric nitrogen components were carried out by the working group Atmosphere 3 (A3: leading scientist Prof. Dr. W. Dannecker). Some data of the group A1 were used for the modelling of small-scale meteorological phenomena in the coastal region (A2: leading scientists Prof. Dr. Schatzmann. Dr. H. Schlünzen). The meteorological data were used as input for the hydrodynamic models.

3.3.2. Hydrosphere

The vessels *RV Valdivia* and *RV Gauss* were each equipped with a CTD (Conductivity - Temperature-Density) system with mounted sampling bottles, which could be used for depth-dependent water sampling. Standardized sampling depths during KUSTOS

cruises included surface, 5 m, 10 m, 15 m, 20 m, 30 m and, or near, the bottom. Hydrographic measurements were carried out by the group Hydrosphere 2 (H2: leading scientist Prof. Dr. G. Becker). The group Hydrosphere 1 (H1: leading scientist Prof. Dr. Sündermann, Dr. T. Pohlmann) developed a hydro- and thermodynamical model and kindly supplied data of water movements in the German Bight. Modelled movements were combined with some biogeochemical data to gain a synoptic image of the single grids and to make different grids synoptic to each other.

3.3.3. Geosphere

The group Geosphere 3 (G3: leading scientists Prof. Dr. Kempe, Dr. W. Michaelis, Dr. A. Reimer) kindly supplied geochemical data of particulate carbon and nitrogen suspended in the water column for the grid and drift investigations.

3.3.4. Biosphere

Nutrients, dissolved organic components, pH, fluorescence and oxygen measurements were carried out by the group Biosphere 1 (B1: leading scientist Dr. U. Brockmann). The group Biosphere 2 (B2: leading scientist Dr. H.J. Rick) was responsible for the assessment of standing stocks and production parameters of the phyto-, bacterio- and protozooplankton. Investigations of the standing stock of the micro- and meso-zooplankton were carried out by the group Biosphere 3 (B3: leading scientist Prof. Dr. A. Weber, Dr. M. Krause).

a) Nutrients, dissolved organic substances and oxygen

Water samples from standardized depths (surface, 5 m, 10 m, 15 m, 20 m, 30 m and/or bottom) were obtained from rosette samplers combined with CTD probes. The water was immediately filtered (vacuum 0.2 atm.) through precombusted glass fibre filters (GF/C, Whatman). These filters have a nominal retention size of 1.2 µm, but retain particles down to 0.4 µm diameter (Hickel, 1984). Nutrients were analysed using the Technicon AutoAnalyzer methods according to Armstrong et al. (1967), Koroleff (1969), Grasshoff et al. (1983) and Murphy & Riley (1962), modified by Eberlein & Kattner (1987). Dissolved organic nitrogen and phosphorus were calculated by subtracting the inorganic N and P from total dissolved N and P, analyzed as nitrate and phosphate following wet combustion by peroxidisulfate (Parsons et al., 1984). Oxygen was measured with the Winkler method (Metrohm Titroprocessor 682).

Samples were directly analyzed on board the *RV Valdivia*, while samples on the *RV Gauss* were fixed with mercury chloride (0.01 % w/v) and stored at 4 -10°C until analysis in the laboratory. Generally data for the following parameters were produced: nitrate, nitrite, ammonia, total nitrogen, dissolved organic nitrogen, phosphate, total phosphorus, dissolved organic phosphorus, particulate phosphorus, carbohydrates and amino acids.

b) Phytoplankton (group B1 and B2):

Species, cell number and carbon content:
Phytoplankton samples were taken from the CTD-bottles and preserved with 0.5 ml formaline (16%) on 100 ml sample for species determination and cell counting in the lab with an inverted microscope (Utermöhl, 1958). If enough individuals were present at least 400 cells were counted for each sample, resulting in an accuracy of about 10% as percentage of count (Lund et al.,1958). An entire sedimentation chamber (Hydrobios) was counted for large organisms, while at least four cross sections were counted for organisms <20 µm. Size parameters such as height and length were measured to calculate biovolumes based on specific geometric bodies for different phytoplankton species (Kellar et al.,1980;Rick,1991). *Thalassiosira* species were estimated as being cylinders for example. The size of at least 20 cells per species and sample was measured. An estimate of organic carbon content of the algae was determined by applying the ratio of cellular carbon to cell volume given in Strickland & Parson (1972).

Chlorophyll: Chlorophyll was analyzed immediately in vivo by means of a fluorometer (Turner) after the addition of 100 µl DCMU (1g l^{-1}) to 100 ml sample volume and an incubation in the dark for ten minutes. In addition, the 5m depth samples were filtered (47 mm Whatman GF/F), stored deep-frozen and later determined spectrophotometrically after extraction in acetone (Jeffrey & Humphrey, 1975; Sterman, 1988).

Primary production: Laboratory incubators (e.g. Rick, 1990) were used to determine primary production with the ^{14}C-technique (Steemann-Nielsen,1952; acidification and bubbling technique described in Schindler et al., 1972; Becker, 1987). Alkalinity and dissolved inorganic carbon were measured according to Strickland & Parsons (1972). Primary production samples were drawn 3 times a day, from 4 depths (1m, 5m, 10m, 20 m), at the central station during the drift investigation. The easterly and westerly stations were not sampled. Handling generally followed the recommendations of UNESCO (1994). Triplicate samples were stored in a laboratory incubator under appropriate in-situ temperature and 4 different light conditions (200, 90, 30 and 25 µmol m^{-2} s^{-1} PAR) for 4 hours after addition of 0,1 ml ^{14}C-$NaHCO_3$ (2-5 µCi 100 ml^{-1}; Amersham) per 100 ml. Scintillation counts were measured with a liquid scintillation counter (Beckman LS 6000).
Average attenuation coefficients for three depth intervals (1-5 m; 5-10 m, 10-15 m) were calculated from vertical light profiles, which had been evaluated with a LiCor 193SB for morning, noon and evening situations for several of the grid stations and all central stations of the drift. Surface radiation (PAR) measurements were carried out continuously on the RV Atair with a QSR-240 (FA. LICOR). The PAR values for standard depths of grid stations without direct depth dependent measurements were estimated from the surface PAR data and calculated average attenuation coefficients. Primary production values from the laboratory incubator were then adapted to the natural light conditions in the water column.
The number of samples for primary production measurements had to be reduced for the quasisynoptical grid sampling campaigns due to short station distances (1hour). Several P/I curve measurements were carried out in the incubator to gain information on the light dependence of chlorophyll-specific assimilation rates of different phytoplankton communities. This information was used to produce an estimate of primary production

for the whole grid. Our estimates do not account for daily variations in the chlorophyll-specific assimilation rate. A simple 1-D model (Smith, 1936) was used to calculate the primary production for those stations and/or depths without direct primary production measurements. Chlorophyll content, the light-dependent curve of chlorophyll specific assimilation rates and the light conditions were used as input data for each sampling depth, station and daytime interval. Production for 24 hours was estimated considering a daytime interval dependent production (5.00 - 8.30, 8.30 - 14.00, 14.00 - 19.00 UTC). Setchell & Packard (1979) investigated phytoplankton respiration in the Peruvian upwelling and estimated that phytoplankton respiration averaged 14 % of gross fixed carbon. Riemann et al. (1993) estimated a respiratory loss of 12 % for algal cultures. A loss of 15 % of the total primary production due to algae respiration was assumed for the KUSTOS grid estimates, which also fits well into the range of 10 - 35% stated by Keller & Riebesell (1989). Production values were then depth integrated for the scaling-up approach (Rick et al., submitted).

c) Bacterial production

Bacterial activity was determined using the [methyl-^{3}H] thymidine method (Fuhrmann & Azam, 1980). Subsamples (10 ml, triplicates, 1 control) from standard depths (0, 5, 10, 20, and bottom) were supplemented with [methyl-^{3}H]thymidine (TdR, NEN Dupont, specific activity: 80 mCi μmol^{-1}) to a final concentration of 6 nmol l^{-1} (the pre-checked saturation level) and incubated in the dark at an in-situ temperature for 2 h (termination by adding 200 µl 35% formaldehyde). The samples were filtered on 0.2 µm Poretics filter, washed once with 10 ml ice-cold prefiltered sea water and 5 times with 2 ml of 5% ice-cold trichloroacetic acid (TCA). Scintillation cocktail (5 ml, Filtercount, Packard) was added to the filters and the counts were measured in a liquid scintillation counter (Packard Tri-Carb 1900 TR).
The TdR-uptake rates were converted into production rates using the factor 1.5 x 1018 cells per mol TdR (Admiraal et al., 1985) and 20 fg C per cell (JGOFS, 1990). The bacterial production rate was assumed to be equal to bacterial respiration, supposing a growth efficiency of 50% (Jahnke & Craven,1995).

3.4. Strategy of the enclosure experiment (groups B1 and B2)

The biological groups of KUSTOS (B1 for nutrients and B2 for phytoplankton) conducted enclosure experiments on the island of Helgoland in August 1995 (Fig. 2). Additionally, groups B3 (mesozooplankton) and B4 (meroplankton) conducted grazing experiments based on supply of algae from the different enclosures. I belonged to group B1 and was in charge of planning and organizing the experimental setup in cooperation with group B2. I isolated the algal clones, cultivated them for inocculation and contributed to general sampling and analysis (nutrients, particulate carbon and nitrogen, chlorophyll). I counted the phytoplankton in the enclosures and analyzed the enclosure data shown in this thesis.

The main purpose of the experiment was to gain insight into the factors controlling daily production along a nutrient and salinity gradient in eutrophic estuarine waters, undisturbed by processes such as advection and grazing. We wanted to find out, if inorganic N:P ratios above 16, frequently found in the Elbe River plume, can cause

enhanced assimilation of nitrogen and/or carbon in the phytoplankton. Other questions were if rising N:P ratios could promote a change in phytoplankton community structure and if a minor shift in salinity (such as in a frontal zone) could also cause a change in phytoplankton nutrient assimilation and/or community structure.
The chemical and biological situation observed in the German Bight during the spring drift investigation 1995 was reconstructed. A 2x4 factorial batch culture design was used to study the reaction of the phytoplankton on a range of inorganic N:P ratios (Fig. 3). Algal species that dominated in spring 1995 were inocculated. Four interconnected outdoor pools were filled with freshwater and kept at a constant temperature of 15 °C by a heat exchanger. 24 plastic barrels (with an additional PE-PA inner plastic lining), filled with 300 l of 5 µm filtered seawater, were placed in these pools. Half of the seawater was diluted with small amounts of suprapure water in order to obtain the salinity of 26 PSU from 32 PSU. A ratio of N:P 8 was present in the unenriched controls. The other enclosures were enriched once with nitrate-nitrogen to molar N:P ratios of 20, 60 and 110. Ambient concentrations of silicate and phosphate were around 15 µM and 0.9 µM, respectively. Each treatment was replicated three times. All enclosures were inocculated with the same mixture and amount of algae. The clones of the different species had been isolated during a previous cruise, kept as unialgal cultures and prepared for the experiment as large-volume monospecies cultures. They were raised in media after v. Stosch & Drebes (1964), modified to 1/10 of their suggested nutrient concentration for nitrate, phosphate and manganese. Mixing of the different species took place shortly before inoculation of the enclosures. The mixture included the diatom *Ditylum brigthwellii*, which was the dominating species during the drift investigation. Furthermore *Thalassiosira rotula, T. punctigera* and *T. weisflogii* were added as important diatom representatives of different size. A *Rhodomonas* species was chosen as a representative for flagellates. Flagellates smaller than 5 µm were included in the enclosures, because they were not removed by filtering. The inner plastic liner of each enclosure was closed on top and only a sampling hose reached out. Each enclosure was mixed constantly by soft air bubbles, which evolved from a pressure hose fixed at the bottom of each enclosure.

3.5. Sampling during the enclosure experiments

During the enclosure experiment, ambient light intensities were monitored continuously and the pH of the water was measured daily. The light:dark cycle was 13:11 hours with maximum daytime light of about 2450 - 3050 µmol s^{-1} m^{-2}. Samples were drawn from the different enclosures each morning by opening the sampling tube. All 24 treatments were sampled for nutrients, dissolved organic components, particulate carbon and nitrogen, chlorophyll (fluorometric) as well as phytoplankton biomass and species counts. One enclosure of the three replicate treatments was randomly assigned to be the "main enclosure" for a more intensive sampling, e.g. primary production, bacterial production and additional spectrophotometric chlorophyll measurements. The applied methods resemble those applied in the field investigations (3.3.4.), but GF/F filters (Whatman) were always used for filtering. In the following only treatments will be listed that differ from the procedures described under 3.3.4..

Fig. 2: Enclosure setup behind the "ecolab" of the Biologische Anstalt Helgoland

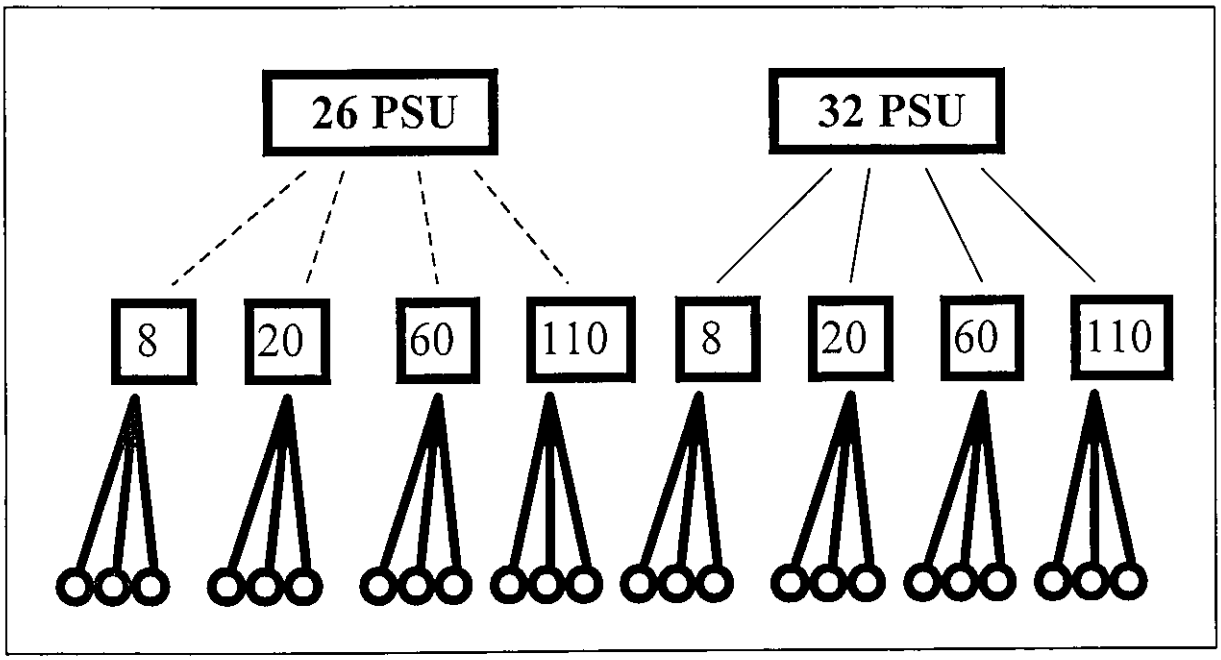


Fig. 3: Experimental setup of the enclosures 1995 with 2 applied salinities (26 and 32 PSU) and 4 different inorganic N:P treatments with three replicates each

a) Nutrients, dissolved and particulate organic substances and oxygen

For nutrients, dissolved organics and oxygen see 3.3.4. a).

Particulate carbon and nitrogen: Samples were filtered through precombusted GF/F filters (Whatman, 25 mm) and frozen at -20° C. Later the dried filters were wrapped into tin foil and flash combusted in a Heraeus CHN-O Rapid analyser.

b) Phytoplankton

Biomass and species: I analysed the formaline-fixed phytoplankton with an inverted microscope and calculated biomass from representative size measurements of the different species as described under 3.4.4.b). Generally at least 200 - 400 cells were counted per species in sedimentation chambers (Hydrobios). However, for the first day of the experiment cell counts were generally below 100.
Chlorophyll: Chlorophyll was analysed in vivo with a Shimadzu Fluorimeter. Additionally samples from the "main" enclosures were filtered (GF/F Whatman), frozen and analysed spectrophotometrically after acetone extraction (Jeffrey & Humphrey,1975; Sterman,1988) within two months. These data were applied to calibrate the fluorescence units measured with the fluorometer to actual chlorophyll concentrations for all enclosures.

Primary production: Each day the nine so-called "main" enclosures were sampled and incubated in.situ for 24 h. Thus real net-productivity of the phytoplankton community was measured, including the effects of both light and dark respiration of the samples.

c) Bacterial production
An in-situ incubation was carried out for 2 hours prior to scintillation counting.

d) Carbon balance
Carbon balances were calculated for the different enclosures. Mean carbon flash-combustion values of all three replicates were compared to carbon values of the algae converted from their biovolume. Biomass was calculated from cell volume twice. One calculation represented all three replicate treatments and another calculation referred to only the "main" enclosure of each treatment, since primary production and bacterial production measurements were conducted in only these "main" enclosures.
Two different approaches, described in the equations I) and II), were applied for carbon estimations based on rates. Since the bacterial production is probably mainly fed by exudates of the phytoplankton the bacteria live on carbon which was previously measured as primary production. I accounted for this by substracting the bacterial respiration from the primary production value, assuming a 50% carbon production efficiency of the bacteria (Ducklow, 1983, Biddanda et al., 1993). Respiratory losses of the phytoplankton were included in the measurement of primary production, since the incubation lasted 24 h. The first measurement of particulate carbon (flash combustion) was used as initial start value in both estimate approaches.

Parameters in the calculations are:
f_n = particulate carbon value measured by flash combustion on day n
P_n = particulate carbon value of daily primary production on day n
R_n = bacterial carbon respiration on day n
C_n = estimated particulate carbon in the enclosure on day n

I.) $C_1=f_1+(P_1-R_1)$; $C_2=f_2+(P_2-R_2)$, ... $C_n=f_n+(P_n-R_n)$

II.) $C_1=f_1+(P_1-R_1)$, $C_2=C_1+(P_2-R_2)$, $C_3=C_1+C_2+(P_3-R_3)$,
$C_n=C_1+...+C_{n-1}+(P_n-R_n)$

The estimates in Fig. 154 - 161 marked *"C rates (daily initi)"* were calculated with equation I). The estimates marked *"C rates"* were based on equation II).

3.6. Statistical analysis of the data

The different treatments were initiated to be very similar at the beginning with a continuous development towards a difference in the stationary phase. One way or two way ANOVAs (ANOVA=Analysis of Variance) were used to test for significant differences in the stationary phase of the dominating phytoplankton species (163 - 211 h). Repeated measurement ANOVAs were applied on the data of biological oxygen demand. All ANOVAs were performed on log transformed data to obtain homogenity of variances (Sokal and Rohlf, 1995), using the program SigmaStat. If in some rare cases the distribution deviated from normality, this is indicated in the summary tables of the respective ANOVA results.

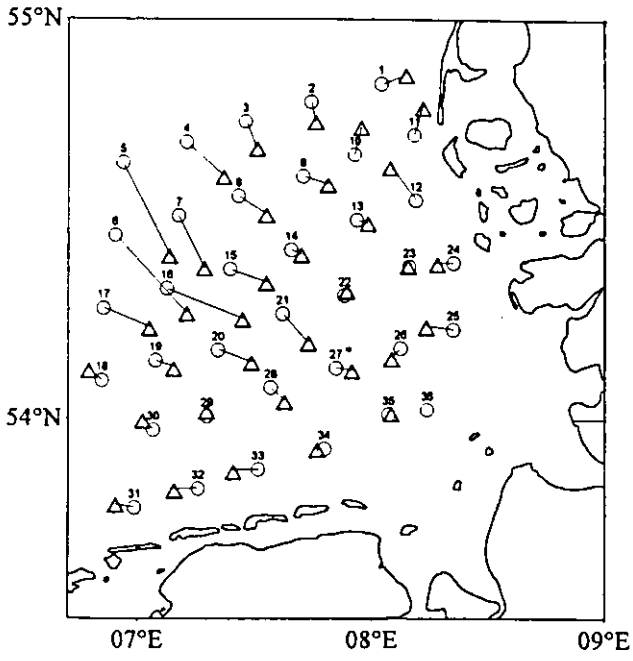
4. Grid investigation spring 1995: results and discussion

Many investigations covering the region of the German Bight focused on the question of wether the ecosystem of the German Bight has changed during the last decades and if this change can be related to human activity or natural causes (Radach et al., 1990; Hickel et al., 1997). Long term monitoring programmes indicated an increase in the nutrient discharge via rivers into the North Sea (Radach et al., 1990). In 1985, up to 80% of the total nutrient pool (N and P) in the continental coastal zone was estimated to be of anthropogenic origin (Nelissen & Stefels, 1988, in Riegman et al., 1992). To define a rising anthropogenic impact on the plankton system of the German Bight, an increased nutrient input by the rivers and/or the atmosphere into the system has to be matched by net advective processes that transport less nutrients out of the system than the input amounts to. Additionally, as a consequence, an increase in nutrients would have to result in an increase of phytoplankton production and biomass.

Hickel et al. (1997) discussed that a growth promoting effect of eutrophication in the German Bight can develop only when a suitable hydrographic structure is present. A sufficient freshwater runoff and low winds are necessary for the buildup of a strong stratification which faciliates phytoplankton growth due to an improved light climate. Thus the amount of phytoplankton production strongly depends on hydrographic conditions, both with respect to the beginning of the spring bloom and the intensity of the summer production. Atmospheric processes, influencing water turbidity and precipitation, are superimposed on nutrient influences (Gerlach, 1990).

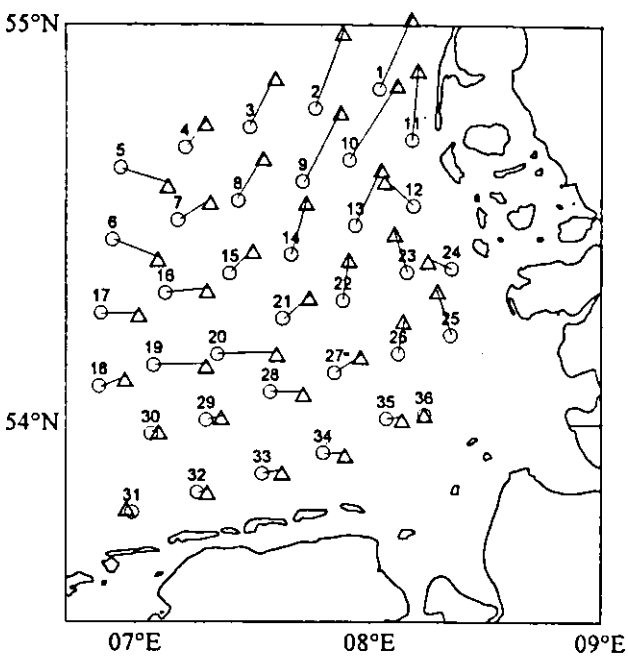
Riverine nutrient loads follow the seasonal pattern of freshwater discharge into the North Sea. In dry years nitrogen compounds tend to accumulate on land. During heavy rainfall these are washed into the rivers. Most of the nitrogen reaches the North Sea during winter and variation is large among years (Gerlach, 1990). The Elbe river has an unfavourable light climate for the growth of algae due to a high content of suspended particulate matter. Therefore eutrophication did not cause extreme reactions considering e.g. nuisance blooms, in the past decades. The yearly discharge of 90000 - 280000 t TN and 7000 - 13000 t TP may, however, cause strong eutrophication reactions in the system of the German Bight (ARGE Elbe, 1995), since residence times of the water are long enough to channel an essential amount of nutrients into phytoplankton production. Turnover times of water in the ICES box 5A, which includes the area of the German Bight, were estimated to range between 27 - 36 days (Lenhart, 1990; in Damm et al., 1994).

Elbe nutrient loads vary greatly from year to year and it was not possible to establish a simple correlation between high annual loads of nutrients and high phytoplankton biomass at Helgoland (Gerlach,1990, see also chapter 2c). Several investigations demonstrated the influence of the rivers on the nutrient regime of the inner German Bight, but additional investigations were recommended to follow their influence further into the open German Bight (Hickel et al., 1997). Currents entering the German Bight from different directions can transport nutrients into the German Bight in addition to the load of the Elbe. Gerlach (1990) for example stated an input of 767000 t N/a and 112000 t P entering from the north into the region of the German Bight (south of 56° N) and an additional input of 705000 t N and 82000 t P by the Channel water.



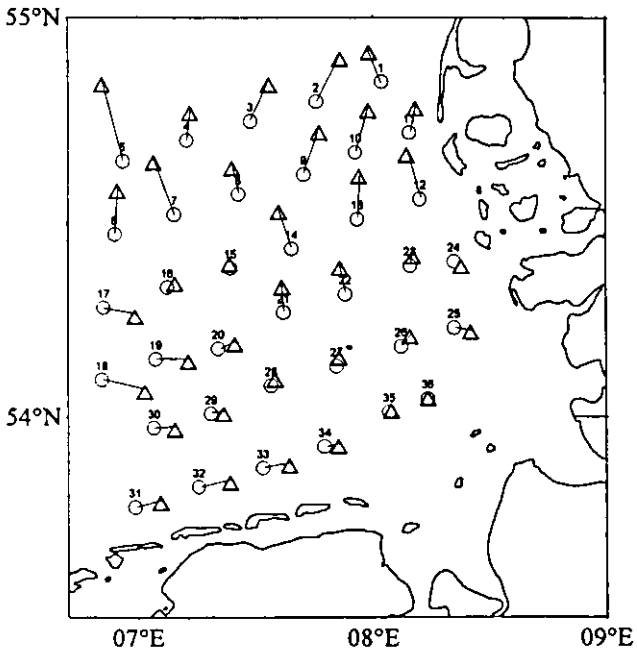
Grid 1 on 1: model data for upper layer

Fig. 4



Grid 5 on 5 : model data for upper layer

Fig. 5



Grid 8 on 8 : model data for upper layer

Fig. 6

Fig. 4-6: Synoptic grid station positions

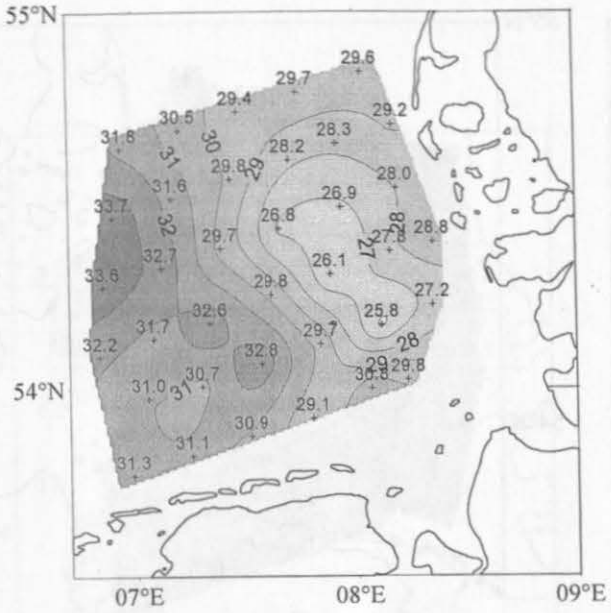
Synoptic positions of grid 1 to grid 8 are connected by a line with the original geographical position of the respective stations. Circles mark the original station at which the water was sampled. A triangle indicates the modelled location of this same water mass at the time of sampling the last station number 36 as reference point. Movements were calculated for a start of water particles in a depth of 7.5 m.

Data supplied by group Hydrosphere I (Prof. Sündermann, Dr. T. Pohlmann).

Chapter 4 focuses on the grid 1 (04/24 - 04/27/95), grid 5 (05/02 - 05/04) and grid 8 (05/09 - 05/11/95) surveys of KUSTOS in 1995. Grid 1 was sampled before the start of the drift investigation (which is described in detail in chapter 5). Grid 5 represented the situation in the German Bight during the drift, while grid 8 was the final grid following the drift investigation. Each grid was sampled quasisynoptically in 2.5 days, beginning with station 1 and ending with station 36 (Fig. 1). The possible movement of water masses in the area of the German Bight during the investigated spring season is given in Fig. 4 to 6. These figures are based on model results supplied by the „Hydrosphere I" group (Dr. T. Pohlmann, Prof. Dr. Sündermann). Further details about their lagrangian model are described in Pohlmann et al. (submitted) and Mayer (1995).
A shift of positions due to water movement was calculated for a start of model water particles at a depth of 7.5 m. Movements were related to the time of sampling the last station with number 36. Thus no transport can be found for station 36, since this was the reference point. The synoptic positions of grid 1 were plotted together with their original geographical position in Fig. 4. Water movements during grid 5 and grid 8 were modelled and displayed in the same way. Greatest transport distances were found in the north eastern region for grid 5 (Fig. 5). During grid 8 (Fig. 6) modelled transports were low and resulted in hardly any movement in the grid itself.
Since the model application may, to a certain extent, also be a source of error, the data in Fig. 7 - 64 were plotted at their original geographic positions at which the respective samples were drawn. Only for figures 66 -71 the model was applied.

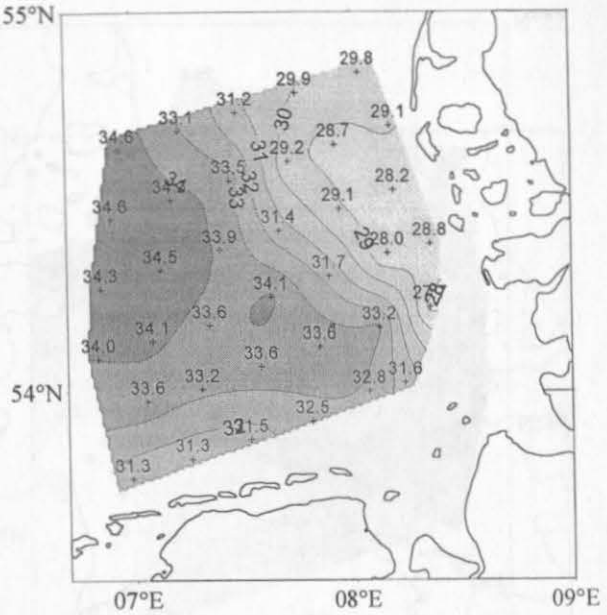
4.1. Stocks

Our data indicate that regional spring blooms started in the shallower regions off the North and East Frisian Isles prior to our investigation. The spring bloom set in during our investigation in the outer region of the turbidity zone and the north-western part of the Bight. Hickel et al. (1997) mentioned the start of the spring bloom of the phytoplankton in the freshwater influenced coastal area as a typical pattern. The shallowness of the coastal regions prevents the phytoplankton from being permanently mixed below the photic zone. In situations when the entire German Bight is well mixed, these regions may offer a better light climate for the onset of the spring bloom, despite their generally higher turbidity compared to the open sea.
Salinity data for surface and bottom layer are given in Fig. 7 - 12 for the grid sampling campaigns 1, 5 and 8. The salinity distribution is strongly influenced by the discharge of the Elbe river. Strong changes in nutrient concentrations were observed for the central German Bight between grid 1 and grid 8 (Fig. 13 -18, 22 - 30) in spring 1995, while the coastal current, entering the German Bight from the south-west, had a low loading of inorganic nutrients over the entire time of investigation.



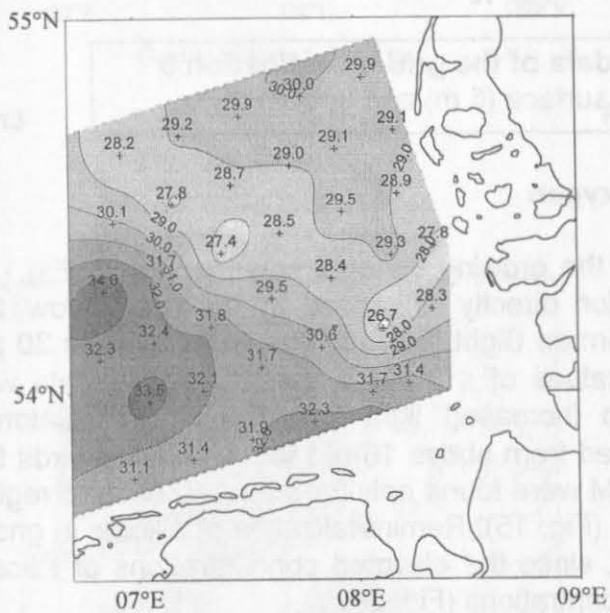
Grid 1: Salinity (PSU) 5 m

Fig. 7



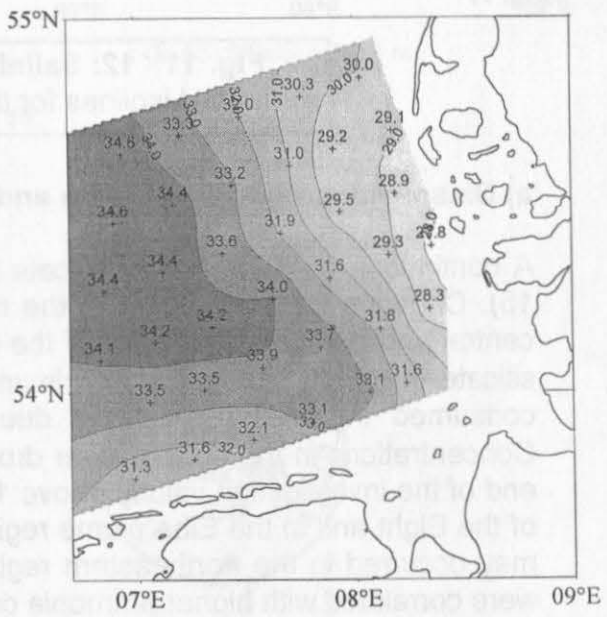
Grid 1: Salinity (PSU) bottom

Fig. 8



Grid 5: Salinity (PSU) 5 m

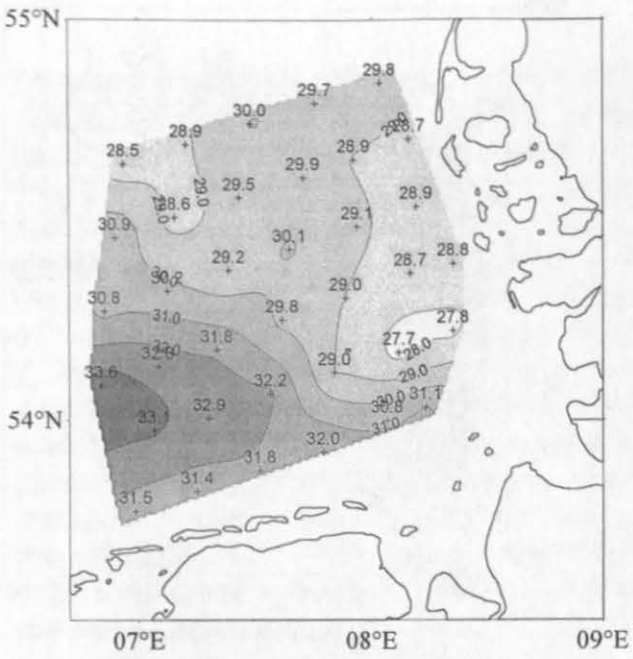
Fig. 9



Grid 5: Salinity (PSU) bottom

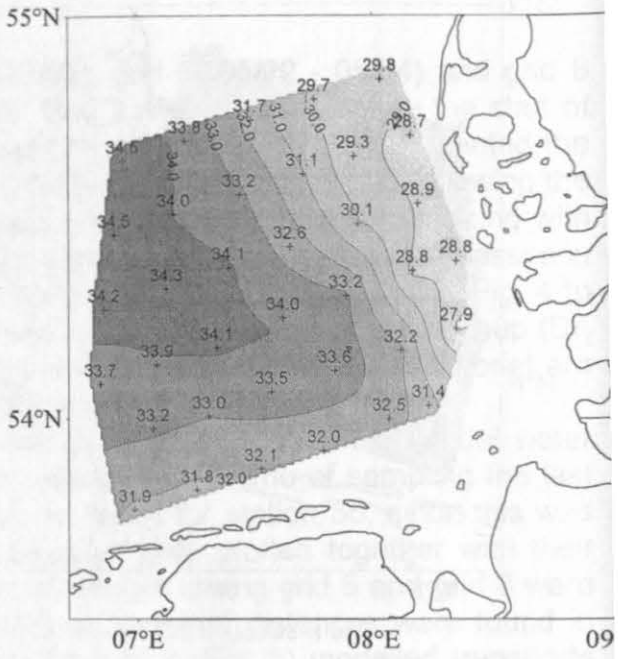
Fig. 10

Fig. 7 - 10: Salinity data of the grid investigations 1 and 5
PSU isolines for the surface (5 m) and bottom layer



Grid 8: Salinity (PSU) 5m

Fig. 11



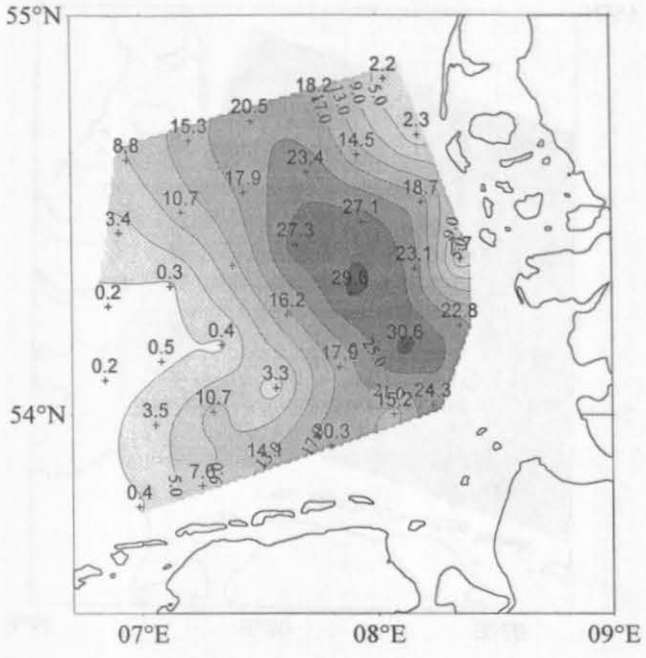
Grid 8: Salinity (PSU) bottom

Fig. 12

Fig. 11 - 12: Salinity data of the grid investigation 8
PSU isolines for the surface (5 m) and bottom layer

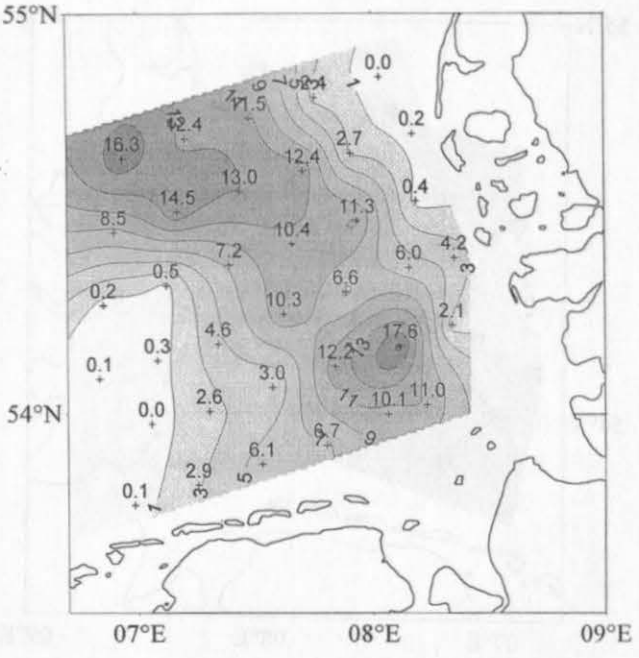
a) Dissolved inorganic nutrients and oxygen

A continuous consumption of silicate by the growing diatoms was monitored (Fig.13 - 15). Changes were strongest in the region directly influenced by the river inflow, the central and north western area of the German Bight. Surface values as high as 30 µM silicate in grid 1 dropped to maximum values of ≤ 3 µM in grid 8. Less silicate was consumed in the bottom layer due to increased light limitation of the diatoms. Concentrations in the bottom layer dropped from above 15 µM to ≤ 4 µM. Towards the end of the investigation values above 1 µM were found only for the north eastern region of the Bight and in the Elbe plume region (Fig. 15). Remineralization of silicate in grid 8 may occurred in the northeastern region, since the elevated concentrations of silicate were correlated with higher ammonia concentrations (Fig. 26).
Initial nitrate values at the surface were very high. They reached maximum concentrations between 90 and ≥110 µM in grid 0 (from 04/22 - 04/24/95). Nitrate values (Fig. 16 -18) around 87 µM at the surface in grid 1 were reduced to values of 60 - 40 µM in the plume region by the time of sampling grid 8. The high nitrate load of the lighter Elbe river water resulted in generally elevated nitrate concentrations for the upper layer compared to the bottom. Other components than nitrate were negligible in their percentual contribution to DIN for this spring season. Likewise more than 75% of TN in the estuaries and off the North Frisian Isles was contributed by dissolved inorganic nitrogen (Brockmann et al., submitted) at that time. In many rivers nitrate is the most important reservoir of inorganic nitrogen during spring. In the Rhône concentrations



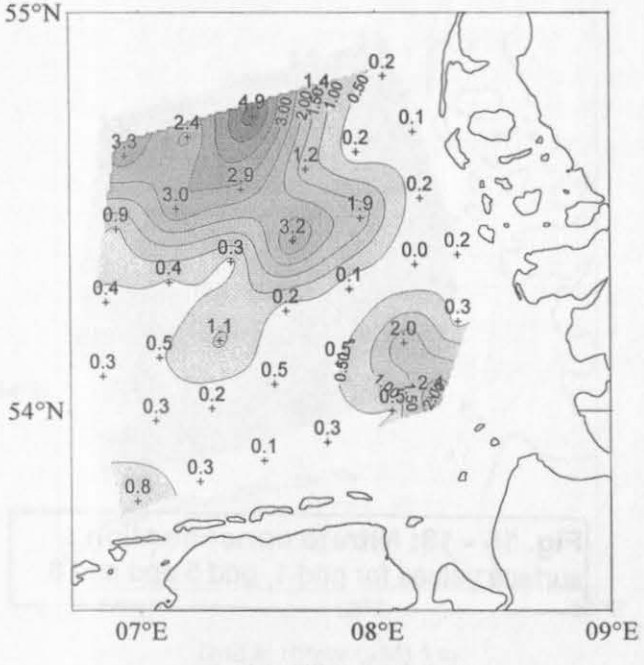
Grid 1: Silicate (µM) 5 m

Fig. 13



Grid 5: Silicate (µM) 5 m

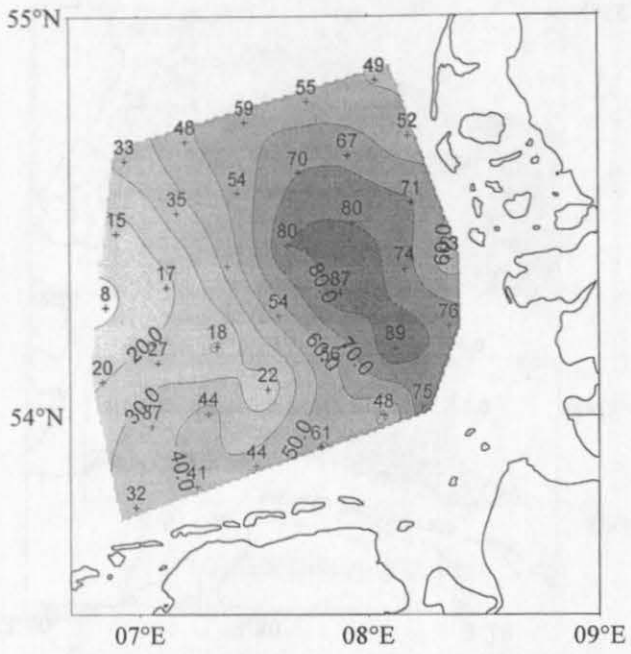
Fig. 14



Grid 8: Silicate (µM) 5m

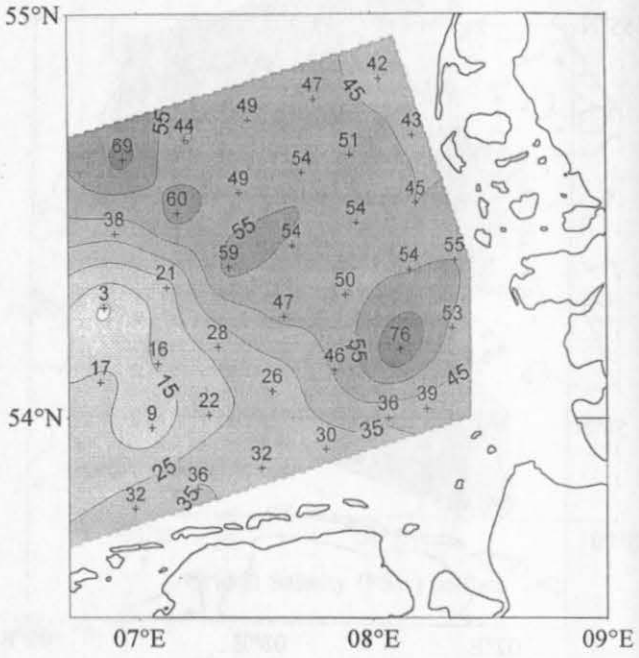
Fig. 15

Fig. 13 - 15: Silicate concentration
surface values for grid 1, grid 5 and grid 8



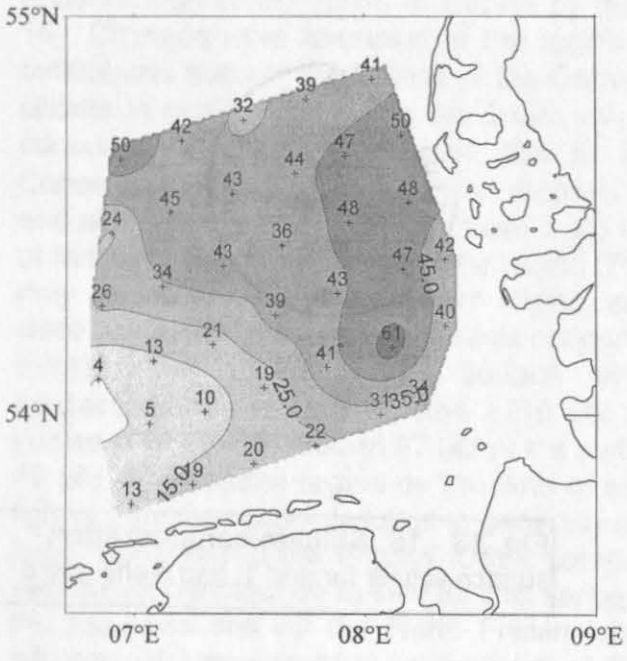
Grid 1: Nitrate (µM) 5 m

Fig. 16



Grid 5: Nitrate (µM) 5 m

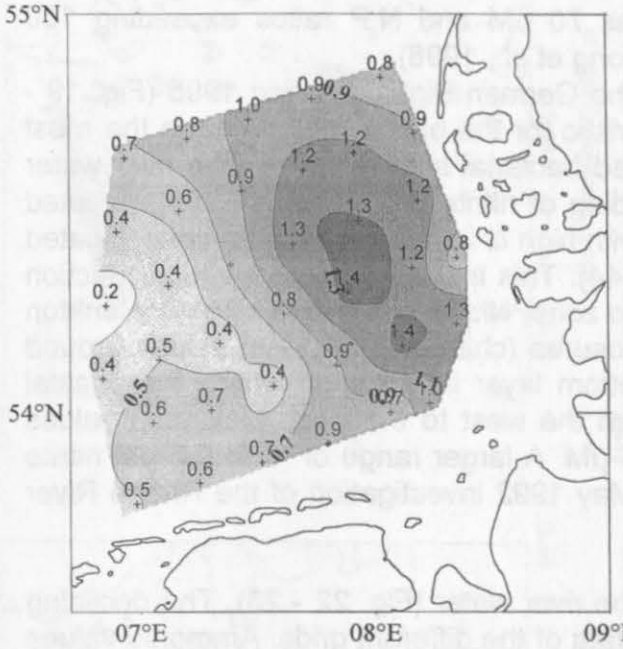
Fig. 17



Grid 8: Nitrate (µM) 5 m

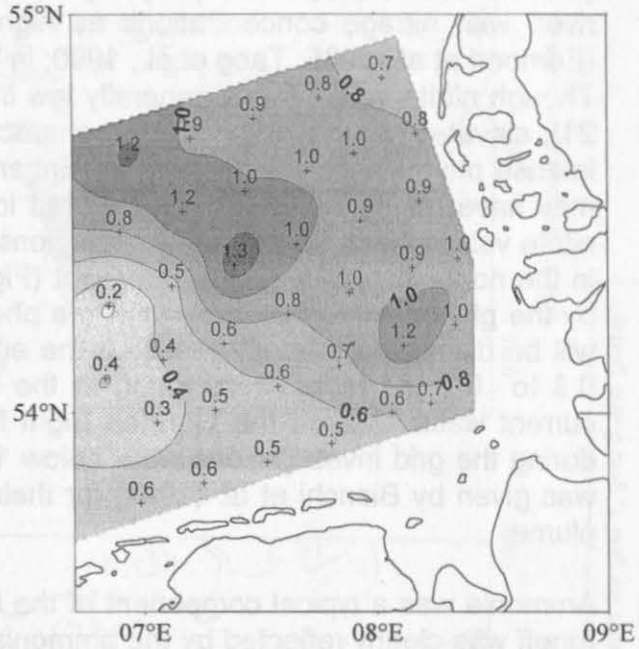
Fig. 18

Fig. 16 - 18: Nitrate concentration surface values for grid 1, grid 5 and grid 8



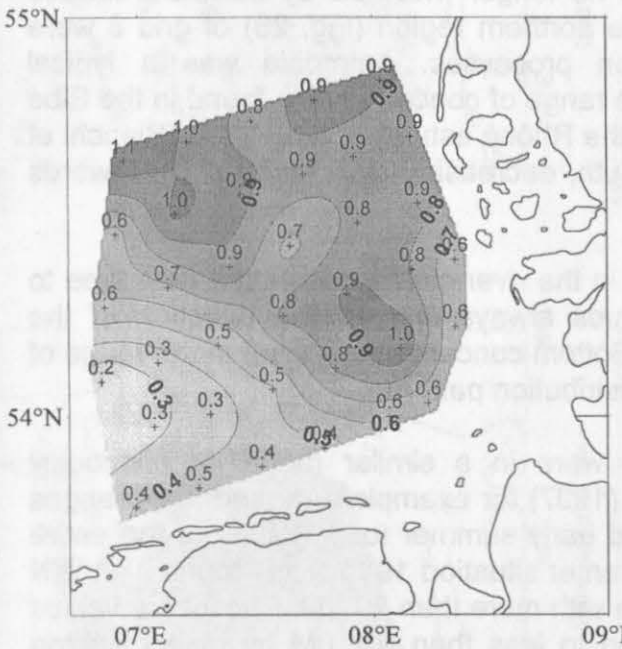
Grid 1: Nitrite (µM) 5m

Fig. 19



Grid 5: Nitrite (µM) 5 m

Fig. 20



Grid 8: Nitrite (µM) 5 m

Fig. 21

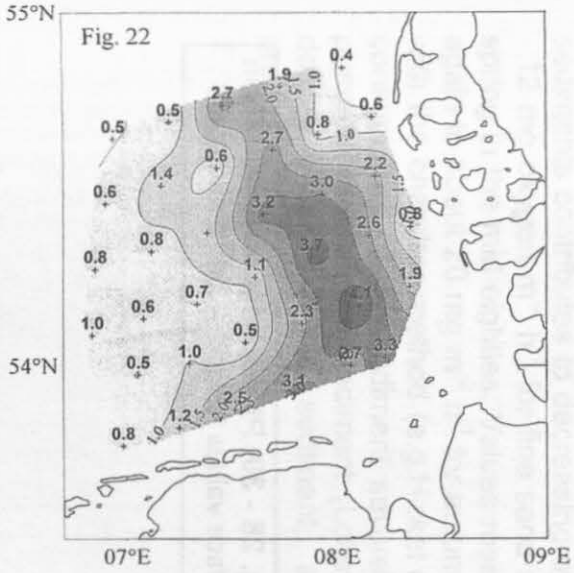
Fig. 19 - 21: Nitrite concentration
surface values for grid 1, grid 5 and grid 8

ranged from 110 µM at the river mouth down to 2 µM in the seawater in May 1992 (Bianchi et al., 1994). The Chanjiang is also considered to be an unusually nitrogen-rich river, with nitrage concentrations as high as 70 µM and N:P ratios exceeding 100 (Edmond et al., 1985; Tang et al., 1990; in Wong et al., 1998)
Though nitrite values were generally low in the German Bight in spring 1995 (Fig. 19 - 21), elevated values seemed to be characteristic for the plume region before the most intense phytoplankton bloom set in. Enhanced bacterial activity in the Elbe river water may have resulted in a slightly elevated loading of nitrite. In grid 8 however, elevated nitrite values were mostly related to regions with high chlorophyll concentrations, located in the northwestern region of the Bight (Fig. 44). This indicated some nitrite production by the phytoplankton or bacteria in the photic zone. Nitrite production of phytoplankton will be discussed in more detail for the enclosures (chapter 6). Lowest values around 0.3 to 0.1 µM nitrite were found at the bottom layer in a region where the coastal current water entered the German Bight from the west to the east. Maximum values during the grid investigations were below 1.5 µM. A larger range of 3 to 0.5 µM nitrite was given by Bianchi et al. (1994) for their May 1992 investigation of the Rhône River plume.

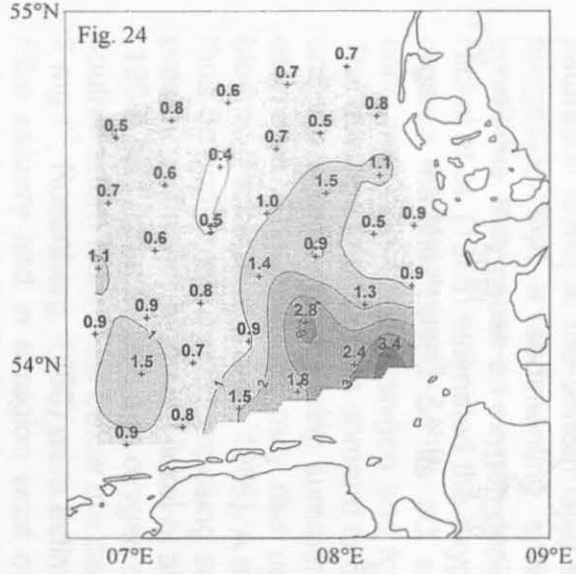
Ammonia was a typical component of the Elbe river water (Fig. 22 - 26). The declining runoff was clearly reflected by the ammonia data of the different grids. Ammonia values ranged from above 4 µM to below 0.5 µM in grid 1 and decreased over time, probably due to consumption by phototrophs (Fig. 22, 24, 26). Remineralization processes in the bottom layer (Fig. 23 - 25) may have caused the generally wider area of elevated concentrations in north westerly plume orientation in the bottom water compared to the surface. This became especially evident for grid 8 (Fig. 27), where the band of high ammonia concentrations at the bottom was no longer matched by elevated surface values (Fig. 26). Higher surface values in the northern region (Fig. 26) of grid 8 were also possibly the result of remineralization processes. Ammonia was a typical component of the Rhône river plume, too. The range of concentrations found in the Elbe plume are comparable to values reported for the Rhône estuary in May 1992 (Bianchi et al., 1994) with around 10 µM at the river mouth, decreasing by a factor of 10 towards the sea.

Surface phosphate concentrations of 0.9 µM in the river plume decreased over time to values below 0.1 µM. Slightly elevated values always marked the direction of the northwest pointing river plume (Fig. 28 - 30). Bottom concentrations were in the range of surface values and displayed a comparable distribution pattern.

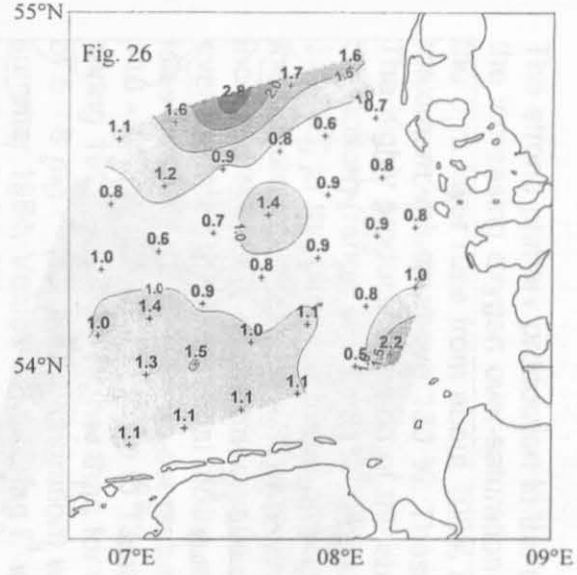
Nutrient concentrations during spring 1995 were in a similar range as previously measured in this area. Brockmann & Kattner (1997) for example analysed the changes in nutrient concentrations between winter and early summer for a survey of the entire North Sea and published data for an early summer situation 1986. They found high DIN concentrations for instance in front of the Elbe with more than 20 µM. Phosphate values were reduced to less than 0.2 µM and often to less than 0.1 µM by phytoplankton utilization.



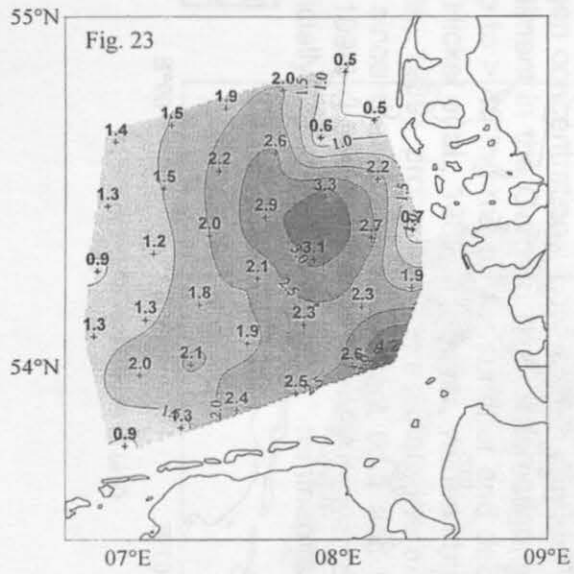
Grid 1: Ammonia (µM) 5 m



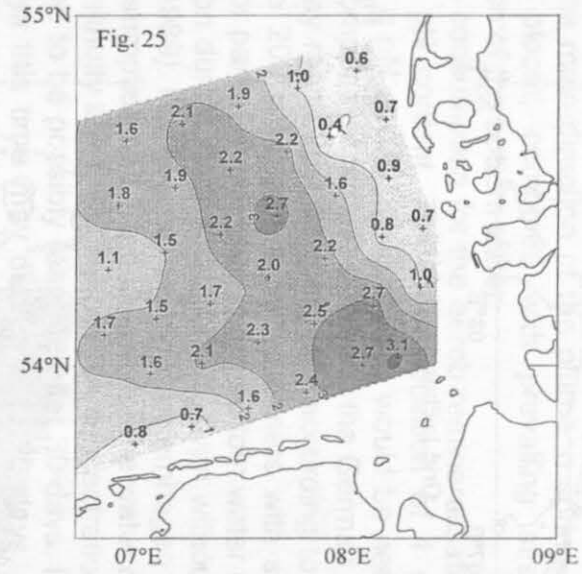
Grid 5: Ammonia (µM) 5m



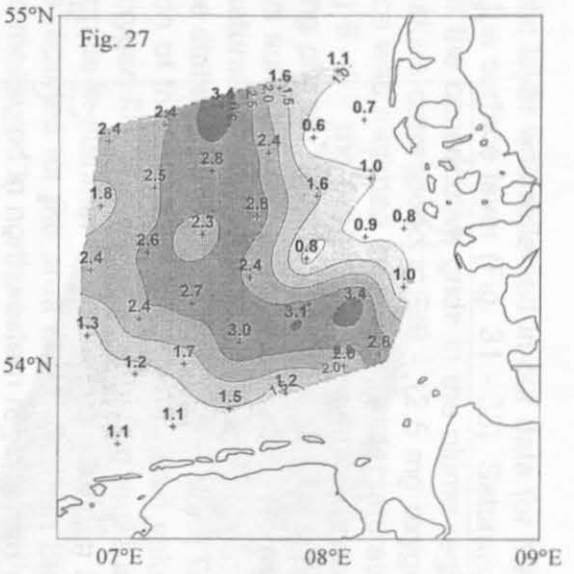
Grid 8: Ammonia (µM) 5 m



Grid 1: Ammonia (µM) bottom layer

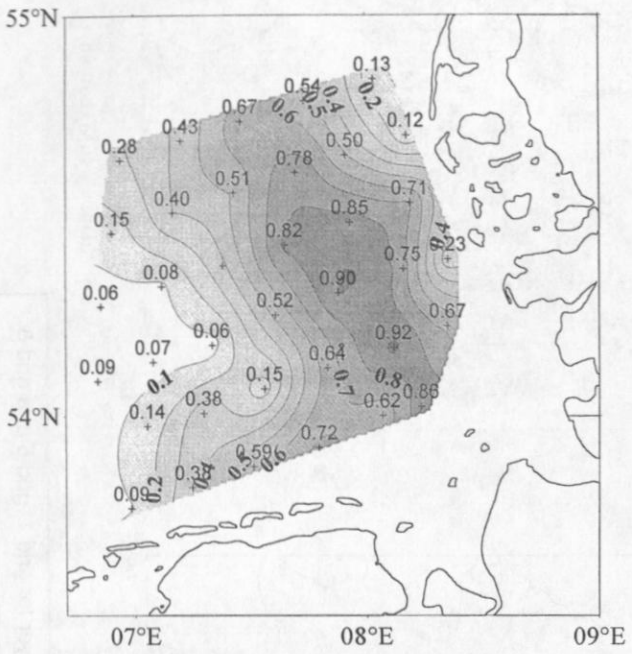


Grid 5: Ammonia (µM) bottom



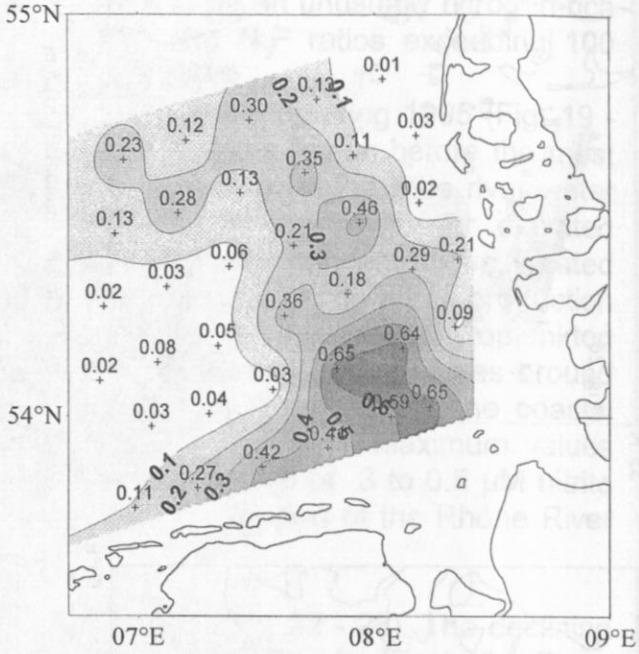
Grid 8: Ammonia (µM) bottom

Fig. 22 - 27: Ammonia concentrations surface and bottom layer for grid 1, grid 5 and grid 8



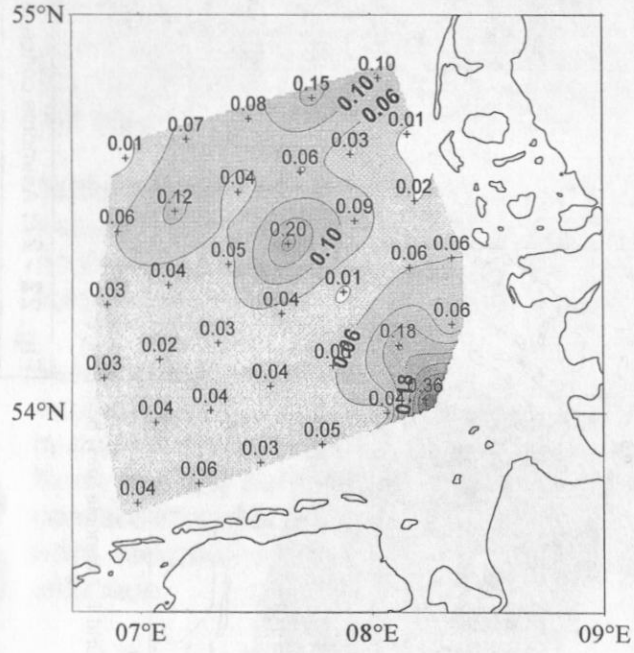
Grid 1: Phosphate (µM) 5 m

Fig. 28



Grid 5 : Phosphate (µM) 5 m

Fig. 29



Grid 8: Phosphate (µM) 5 m

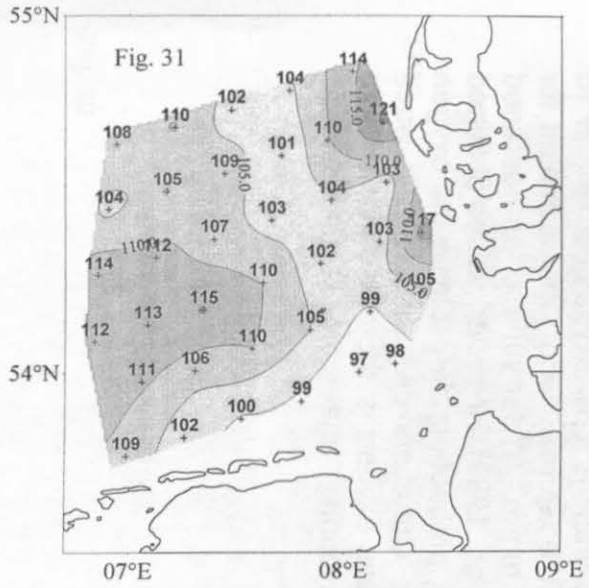
Fig. 30

Fig. 28 - 30: Phosphate concentration surface values for grid 1, grid 5 and grid 8

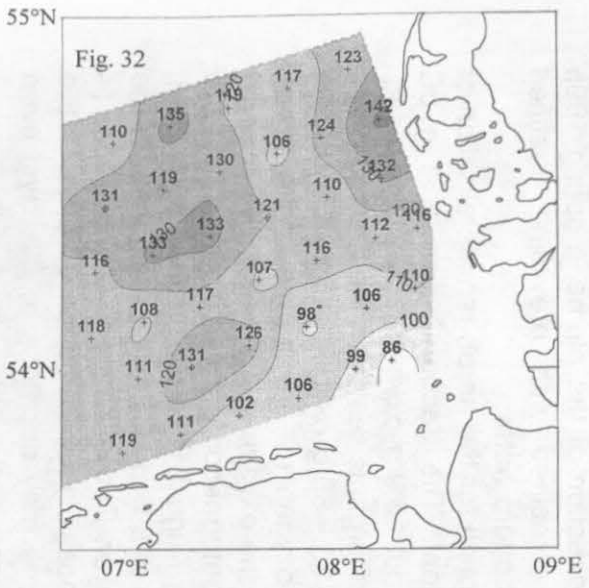
The strong primary production in the photic layer was reflected in our data for 1995 by the increasing oxygen over-saturation of the surface layer (Fig. 31 - 33). Saturation for the 5 m layer rose from about 100% over the consecutive grids in the plume region to maximum values above 130 %. These values correspond to 9.9 - 12.5 mg oxygen l^{-1}. The highly productive region of the surface was matched by a slight undersaturation at the bottom (range of 98 - 81% , equalling 8 - 9.7 mg oxygen l^{-1}) for all three grids (Fig. 34 - 36) in the direction of the propagating plume. Nevertheless, the oxygen supply at the bottom layer (Fig. 34 - 36) was always sufficient and far from depleted. No marked increase or clearly defined decrease of saturation level was found for the bottom layer over the three grids. The tidal mixing at the stations in front of the East and North Frisian Isles possibly resulted in an oversaturation of the bottom layer (Fig. 36) with values of 110 - 140 % (equivalent to up to 13 mg oxygen l^{-1}). The oxygen saturation measured in spring 1995 was a lot higher than for example in summer 1984. Ambient oxygen levels of 5 - 8 mg l^{-1} (50 - 80% saturation) were reported for the area of the German Bight in summer 1984. Values below 5 mg l^{-1} were measured in northwestern regions and at the mouth of the Weser river (Hickel et al.,1989). Nevertheless, the lowered oxygen saturation levels at the bottom layer in the main direction of the plume in spring 1995 suggested that a sedimenting spring bloom, combined with prevailing stratified conditions, may cause an oxygen depletion of the bottom water.

Hickel et al. (1986) estimated the oxygen consumption for the aerob remineralisation of organic material based on its pC and pN content. The decomposition of 1 g pC consumes about 3.5 g oxygen and for 1 g pN about 18.9 g oxygen would be needed. The average total oxygen demand to decompose all organic seston in the German Bight under a square meter during summer may reach 20 - 80 g oxygen, according to their estimates. These values may rise up to 200 g oxygen m^{-2} in summers with strong blooms (Hickel et al., 1986, 1989). A major part of the oxygen in the bottom water could thus be consumed by decomposing seston during stagnation periods, even without the presence of major blooms (Hickel et al., 1989). For August 1984 v. Westernhagen et al. (1986) calculated an average oxygen consumption of 8.7 mg O_2 m^{-3} for the water of the south-eastern North Sea below the discontinuity layer. Critical oxygen concentrations (< 2 mg l^{-1}, Rosenberg, 1980) were estimated to be possibly reached after 30 days. In the Elbe estuary and in a region west of Sylt this time may decrease to 20 days, even without strong phytoplankton blooms (v. Westernhagen et al., 1986).

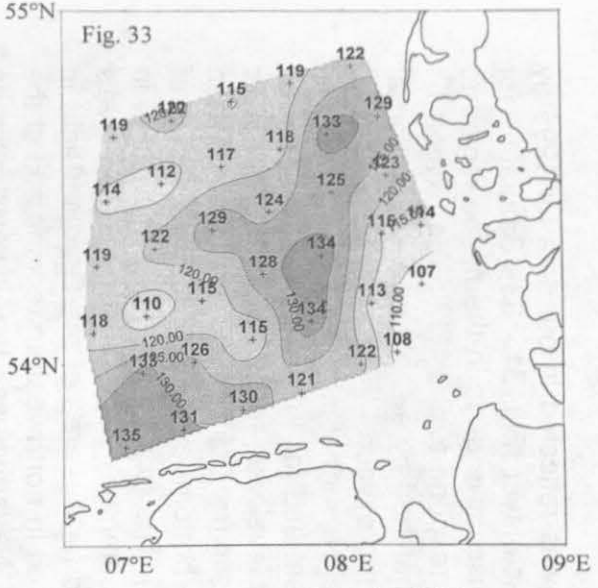
In addition to the oxygen consumption in the water column the oxygen demand of the sediments contributes to decreasing oxygen concentrations. Low oxygen demand of 10 - 12 mg oxygen m^{-2} h^{-1} for fine sand sediment in the German Bight was estimated for spring in the mid eighties. Values rose up to > 40 mg m^{-2} h^{-1} for summer and declined again to about 20 mg m^{-2} h^{-1} for autumn (Hickel et al., 1989). However, values obtained with the chamber method (e.g.Hickel et al., 1989), probably underestimate the oxygen consumption of the sediment severely, since the chambers prevent tidal and wave pumping through the sediment (Lohse, 1998). Less oxygen is thereby delivered into deeper zones of the sediment, artificially favouring anaerobic remineralisation processes in the samples.



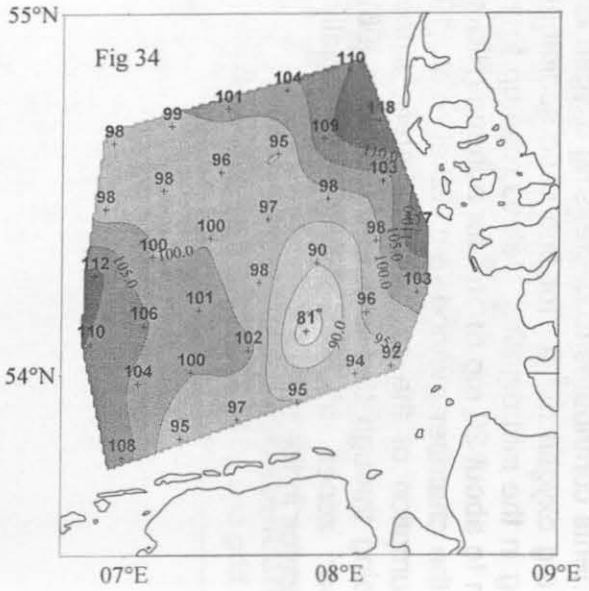
Grid 1: Oxygen Sat. (%) 5 m



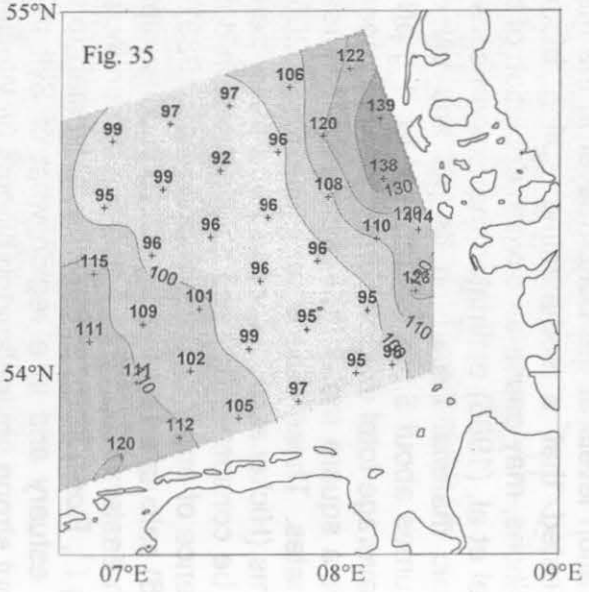
Grid 5: Oxygen Saturation (%) 5 m



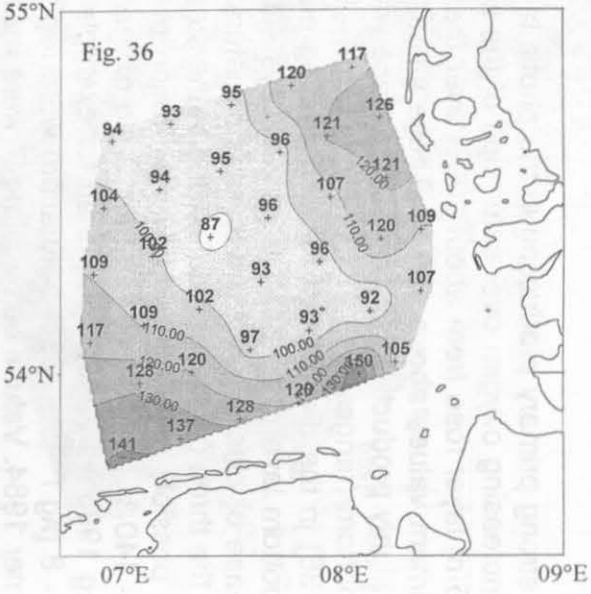
Grid 8 : Oxygen Saturation (%) 5 m



Grid 1: Oxygen saturation (%) bottom



Grid 5: Oxygen Saturation (%) bottom



Grid 8: Oxygen Saturation (%) bottom

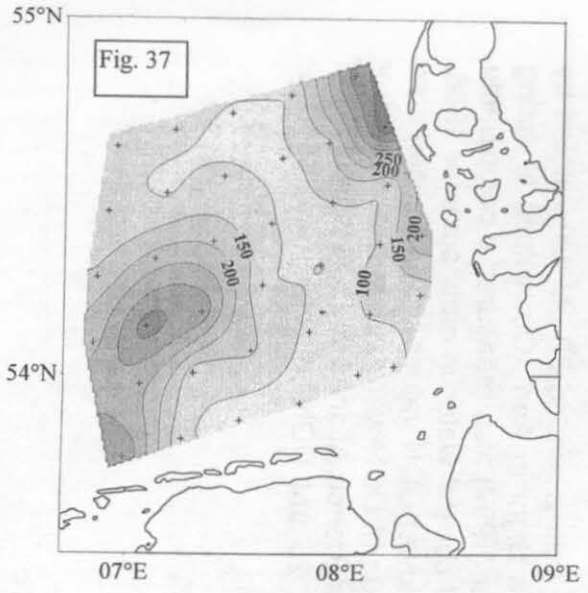
Fig. 31 - 36: Oxygen saturation (%) surface and bottom layer grid 1, grid 5 and grid 8

b) Ratio of dissolved inorganic nitrogen to phosphate ($DIN:PO_4$)

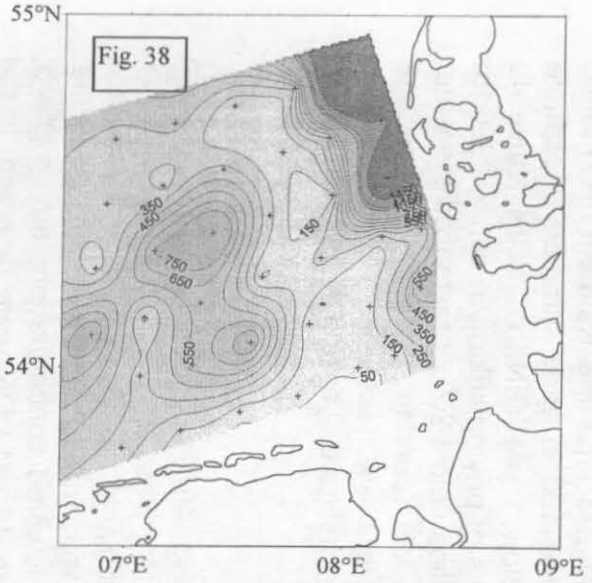
$DIN:PO_4$ ratios above 50 indicate a phosphorus limitation, while ratios below 15 are believed to signal potential nitrogen limitation of the phytoplankton (e.g. Goldmann et al., 1979). The increasing phosphate limitation during spring 1995 was reflected in the development of $DIN:PO_4$ ratios (Fig. 37 - 39). Previous phytoplankton growth may have caused the high ratios in the shallow coastal region off the East Frisian Isles and off the northernmost North Frisian Isles during grid 1 in spring 1995. The phosphate input by the Elbe combined with only little phytoplankton growth in the turbidity zone resulted in lower ratios in the frontal region during the first grid (around 100; Fig. 37), compared to the rest of the grid area. Ratios rose to above 150 (Fig. 38) and well above 600 for the last grid (Fig 39), even exceeding 1000 in some regions due to almost complete phosphate consumption by the phytoplankton (Fig. 38, 39). The frontal region displayed the steepest increase in ratios over the time of the 3 grids because of the onset of a strong spring diatom bloom in this area.
With regard to the previously described historical development in the German Bight the observed ratios can be considered as being typical. Brockmann & Kattner (1997) found $DIN:PO_4$ ratios in the German Bight that exceeded 100 in early summer. Phosphate concentrations during their investigation were below 1 µM. $DIN:PO_4$ ratios above 40 were observed combined with high standing stocks of phytoplankton in spring 1986 for the German Bight by Hickel et al. (1989), too. Ratios below 20 characterized the water from the open North Sea. Highest ratios were generally found in springtime with average ratios around 90 (April 1985) and 114 (April 1986) for the surface layer. Ratios tended to be below "Redfield" in September/October of the investigated years (Hickel et al., 1989).

c) Dissolved organic nitrogen (DON)

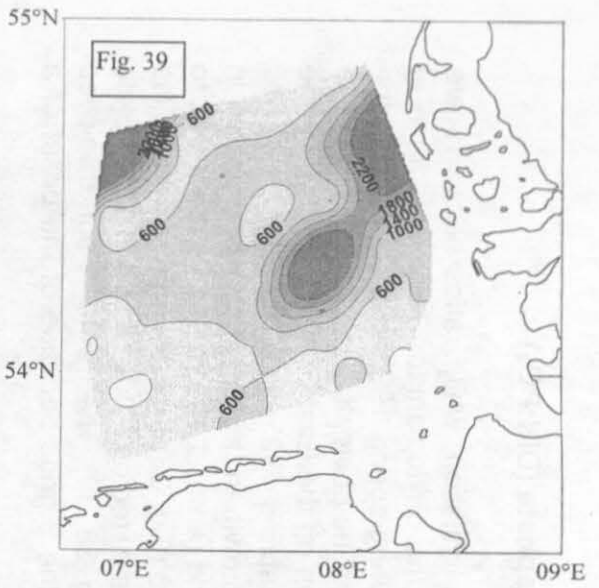
Our data suggest an input of DON by the river (Fig. 40), a consumption (northeastern region Fig. 41) and possibly some excretion (Fig. 41, western region and Fig. 42 north-northeastern region) of DON by the phytoplankton. DON reached average concentrations around 10 - 15 µM (Fig. 40 - 42) without any distinct pattern over time. The northern half of the investigated region had lowered concentrations during grid 5, except for one western „hot spot" (Fig. 29), where 40 µM DON were detected. In the same region elevated ammonia concentrations were found at the surface (Fig. 26), suggesting remineralization processes.
DON concentrations of 7 - 13 µM with maximum values around 20 µM were stated by Hickel et al. (1989) for the region of the German Bight in April. Our values of spring 1995 are in the same range. Brockmann & Kattner (1997) also measured a comparable range of about 8 - 16 µM DON in the continental coastal water in early summer 1986. Studies of seasonal variations indicate generally lower DON values in winter compared to summer. Less than 5 µM in winter and up to 10 µM DON were measured in summer in the English Channel (Butler et al., 1979). At the French Atlantic coast less than 6 µM DON were found in winter, compared to about 25 µM DON in spring and summer (Feuillet-Girard et al., 1988).



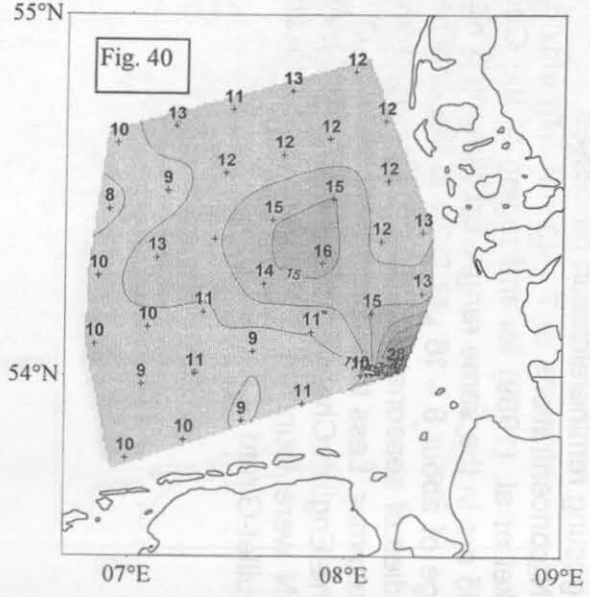
Grid 1: DIN/PO4 Ratio 5 m



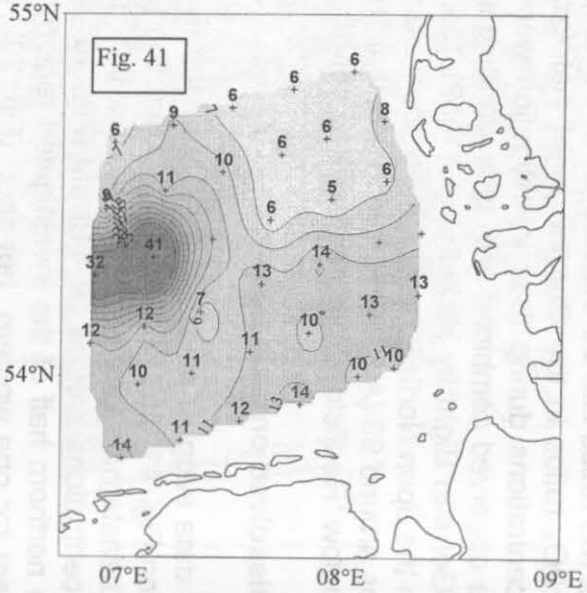
Grid 5: DIN/PO4 Ratio 5 m



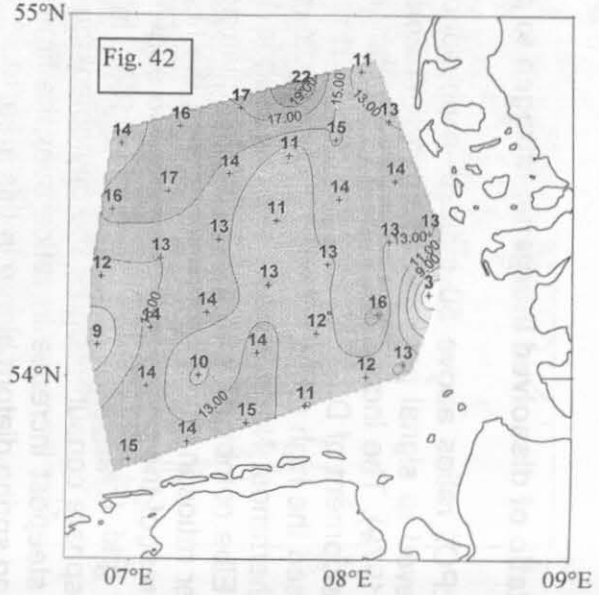
Grid 8: DIN/PO4 ratio 5 m



Grid 1: DON (µM) 5 m



Grid 5: DON (µM) 5 m



Grid 8: DON (µM) 5 m

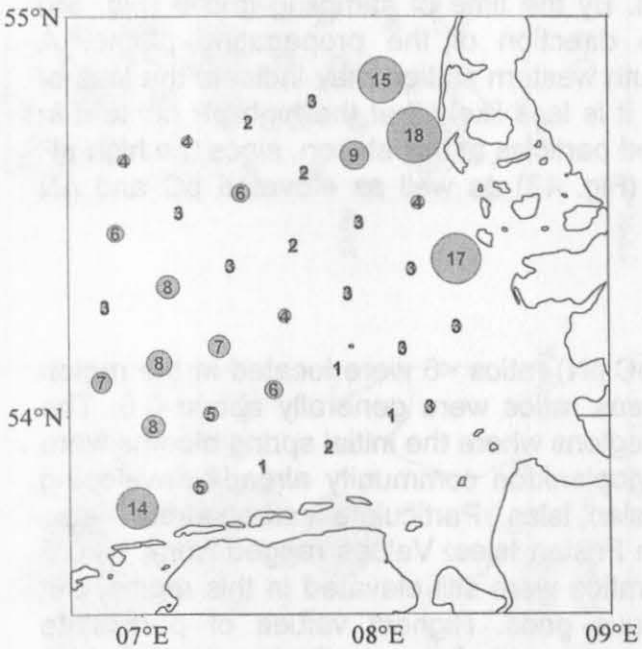
Fig. 37- 42: DIN:PO_4 ratios and DON concentration surface layer for grid 1, grid 5 and grid 8

d) Particulate organic matter (POM)

The distribution of POM is shown by proportional scaling of a circle as a symbol for data values, in order to indicate that POM may show a less predictable distribution over geographic range compared to dissolved inorganic nutrients. POM has a rather increased patchiness compared to dissolved components, since it is affected in different scales by local processes like grazing or sedimentation in addition to general advection and transport processes.

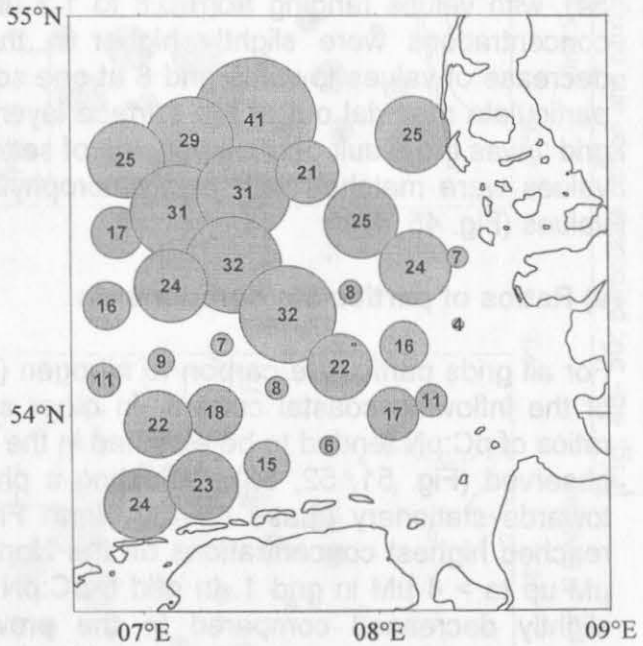
Chlorophyll

The chlorophyll distribution marked the regions of the preceeding blooms in grid 1 with elevated concentrations above 14 µM (Fig. 43) off the North Frisian Isles and less pronounced off the East Frisian Isles. In the central region only small amounts of 2 to 6 µg Chl a l^{-1} were initially present, but values strongly increased towards grid 8 to 25 - 40 µg l^{-1}(Fig. 44) due to favourable bloom conditions. Maximum values were located in the north western region of grid 8. Concentrations also continued to increase off the North and East Frisian Isles, but they only reached maximum values around 25 µg Chl a l^{-1}. A transgression of the phytoplankton population into stationary state may have been induced by the strong phosphate depletion in this area. Comparable ranges of surface values of chlorophyll were observed by Hickel et al. (1989). They measured about 5 - 10 µg Chl l^{-1} in the Elbe plume region in spring 1986, while values rose up to 40 µg l^{-1} Chl further north (Hickel et al., 1989).



Grid 1: Chl a (µg/l) 5 m

Fig. 43



Grid 8: Chl a (µg/l) 5 m

Fig. 44

Particulate carbon (pC), nitrogen (pN) and phosphorus (pP)

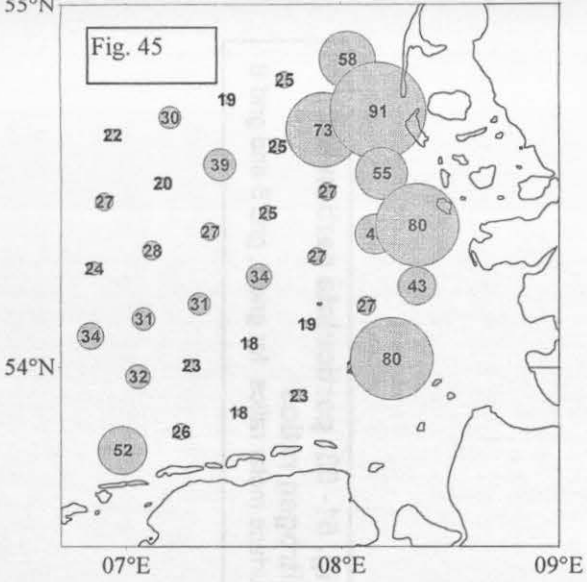
The geographical distribution of particulate carbon (Fig. 45) reflected the elevated chlorophyll values off the North and East Frisian Isles for grid 1 with a standing stock of 55 to 90 µM pC. Other stations had lower concentrations with about 20 - 30 µM pC. The stations off the North and East Frisian Isles continued to dominate the distribution pattern in grid 5. Highest values observed there ranged from about 50 to 90 µM pC (Fig. 46). In grid 8 (Fig. 47) highest standing stocks of pC (more than 80 - 110 µM) were finally found at the north-westernmost stations. The pC in the south-central area of grid 8 remained lower and reached maximum values of only 50 to 60 µM pC. The distribution patternmatches the higher haline region of grid 8 at the surface (Fig. 11).
Values off the North Frisian Isles in spring 1995 were generally above those reported for spring 1985 by Hickel et al., (1989). They measured concentrations of about 200 - 600 µg pC l^{-1} (16 - 50 µM, about 14.5 g m^{-2}) in the unstratified region off the North Frisian Isles.

The distribution pattern for pN was comparable to pC (Fig. 48-50). High values above 10 µM were initially found only at the North Frisian coast. Values then rose to ≥10 µM at the north western stations and stocks > 20 µM pN were reached locally. The pN concentrations measured during spring 1995 are in the same range as reported by Brockmann & Kattner (1997) for this region. They found pN concentrations of around 1-3 µM in the central North Sea while elevated values of > 10 µM pN were measured off the East Frisian Isles during early summer 1986.

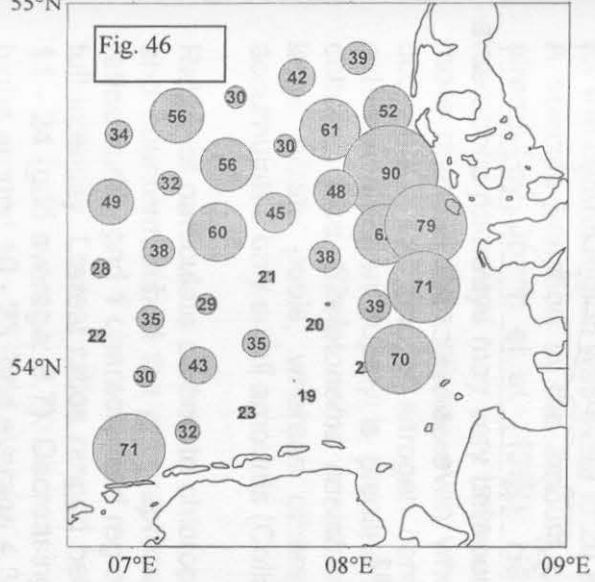
Particulate phosphorus (pP) was also elevated off the North Frisian coast in grid 1 (Fig. 54), with values ranging from 0.8 to 1.3 µM. By the time of sampling grid 8 (Fig. 55) concentrations were slightly higher in the direction of the propagating plume. A decrease of values towards grid 8 at one south western station may indicate the loss of particulate material out of the surface layer. It is less likely that the high pP content in grid 1 was the result of resuspension of settled particles at this station, since the high pP values were matched with high chlorophyll (Fig. 43) as well as elevated pC and pN values (Fig. 45, 48).

e) Ratios of particulate components

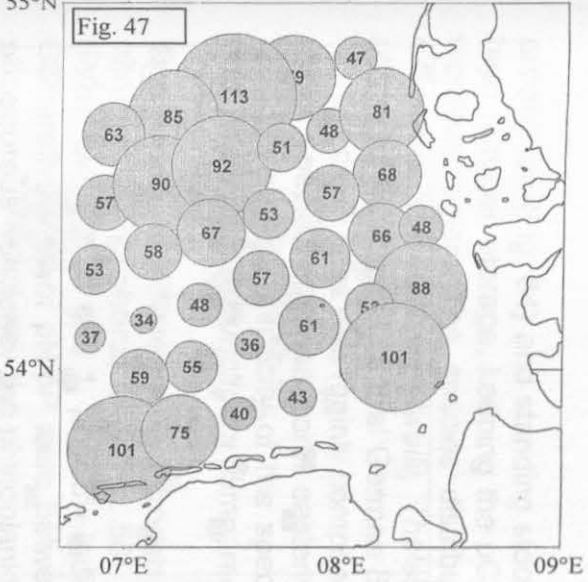
For all grids particulate carbon to nitrogen (pC:pN) ratios <6 were located in the region of the inflowing coastal current. In other areas ratios were generally above 6.6. The ratios of pC:pN tended to be elevated in the regions where the initial spring blooms were observed (Fig. 51, 52, 53), indicating a phytoplankton community already developing towards stationary phase off the North Frisian Isles. Particulate carbohydrates also reached highest concentrations off the North Frisian Isles. Values ranged from < 0.5 µM up to > 4 µM in grid 1. In grid 8 pC:pN ratios were still elevated in this region, but slightly decreased compared to the previous grids. Highest values of particulate carbohydrates did not match the distribution pattern of elevated pC:pN ratios in grid 8 anymore. Concentrations by then were elevated in the central and north western region in grid 8 (up to 10 µM). The accumulation of carbohydrates in this region of high primary



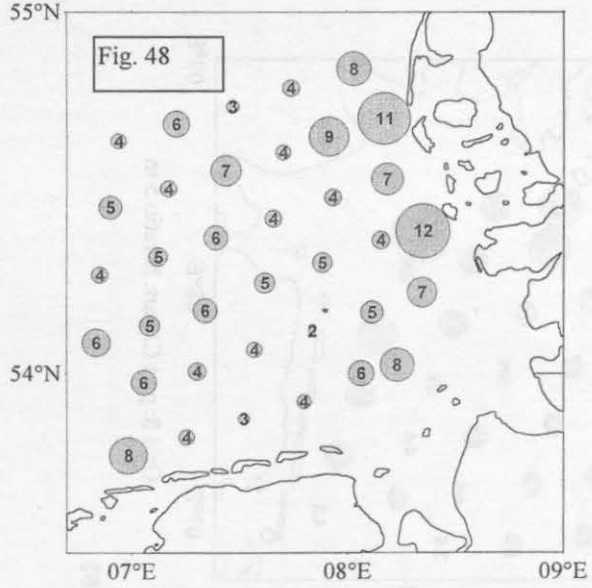
Grid 1: part. C (µM) 5 m



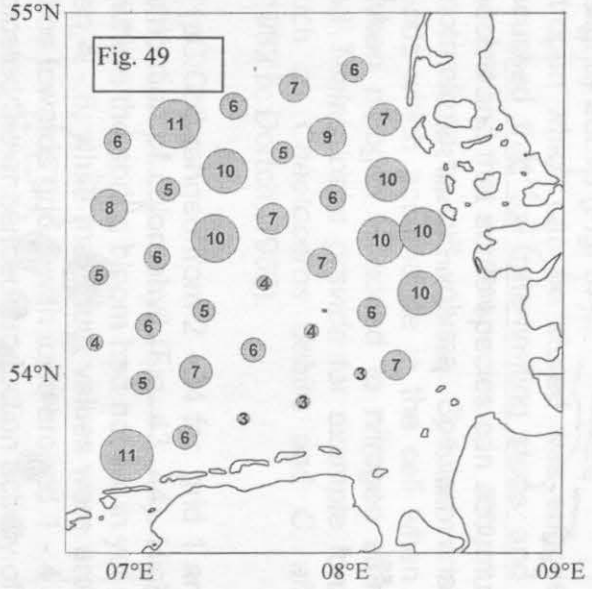
Grid 5: part. C (µM) 5 m



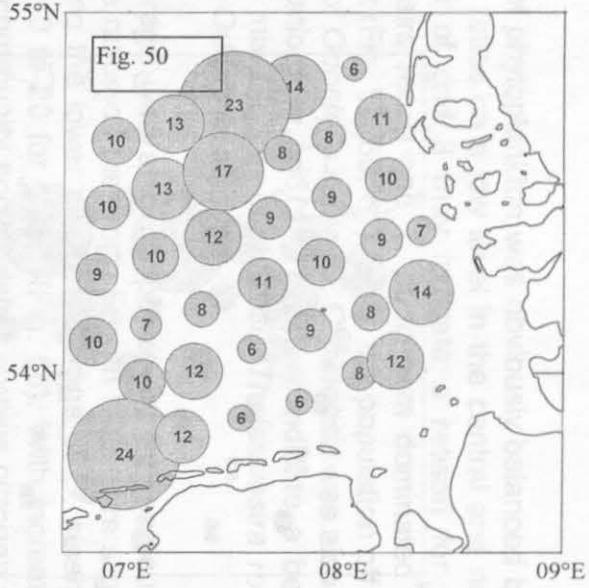
Grid 8: part. C (µM) 5 m



Grid 1: part. N (µM) 5m

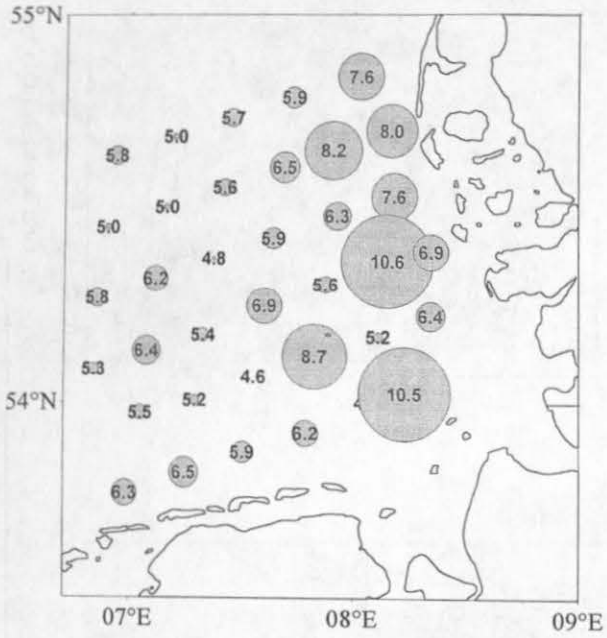


Grid 5: part. N (µM) 5 m



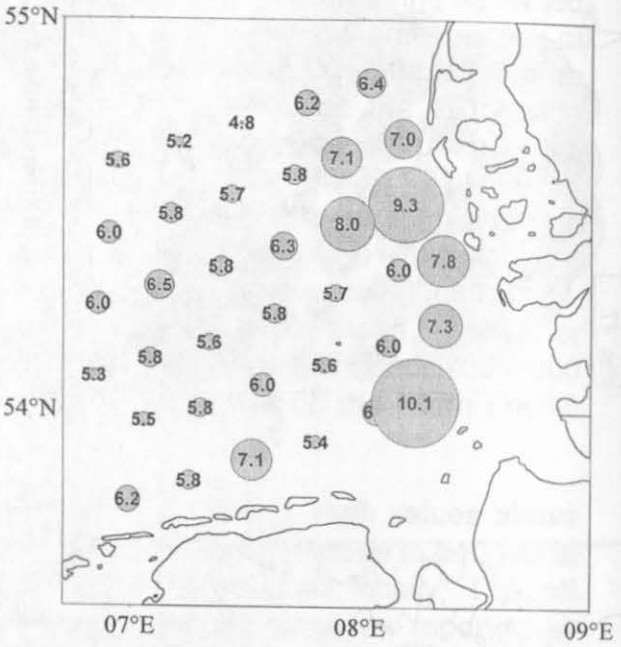
Grid 8: part. N (µM) 5 m

Fig. 45- 50: particulate carbon and nitrogen (µM) surface layer grid 1, grid 5 and grid 8



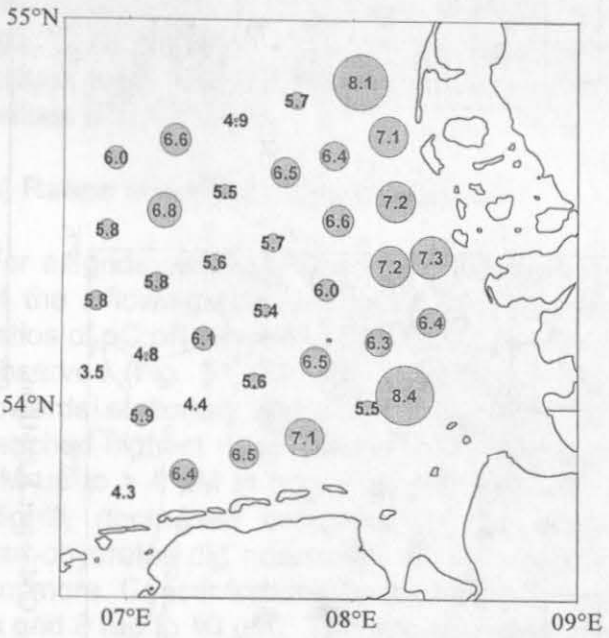
Grid 1: part. C/ part. N ratio 5 m

Fig. 51



Grid 5: part. C/part N ratio 5 m

Fig. 52



Grid 8: part C/ part. N ratio 5 m

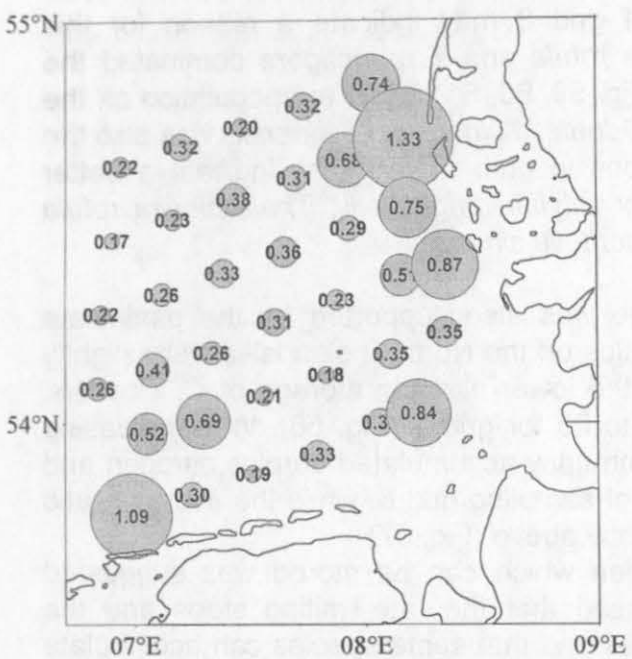
Fig. 53

Fig. 51- 53: particulate carbon to nitrogen ratios
surface molar ratios for grid 1, grid 5 and grid 8

production (Fig. 64) and standing stocks of phytoplankton was obviously balanced by a high nitrogen storage, keeping the pC:pN ratios on a low level in the central and north western region. The species distribution of grid 8 may indicate a reason for this difference. *Ditylum brightwellii, Thalassiosira rotula* and *T. punctigera* dominated the phytoplankton in the central German Bight (Fig. 59, 60, 61), while the population off the North Frisian Isles was mainly composed of *Odontella sinensis*. *O. sinensis* was also the major species at those north easterly stations in grid 1. This may indicate a better nitrogen storage capacity of the species mix *Ditylum brightwellii, Thalassiosira rotula* and *Thalassiosira punctigera* compared to *Odontella sinensis*.

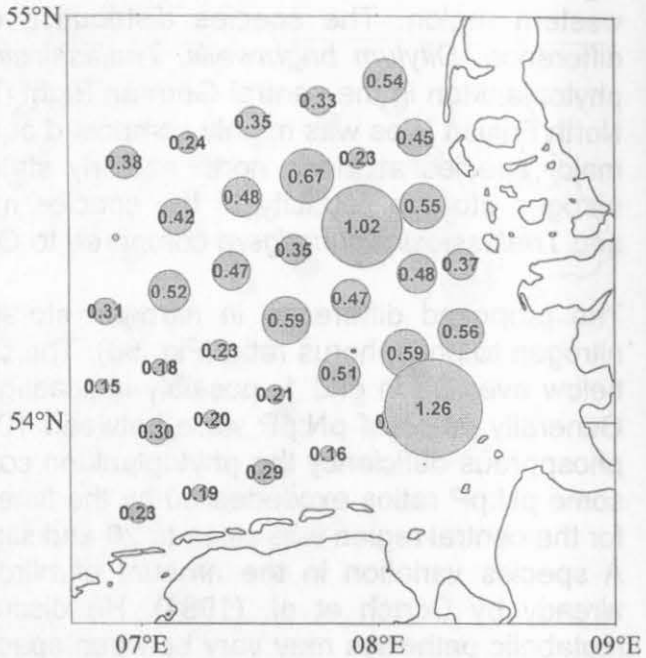
The proposed difference in nitrogen storage was also supported by the particulate nitrogen to phosphorus ratio (Fig. 56). The ratios off the North Frisian Isles were slightly below average in grid 1, possibly indicating the lower nitrogen storage of *O. sinensis*. Generally ratios of pN:pP were between 10 to 20 for grid 1 (Fig. 56). With increasing phosporous deficiency the phytoplankton community accumulated surplus nitrogen and some pN:pP ratios exceeded 60 by the time of sampling grid 8, while the average ratio for the central region was close to 20 and slightly above (Fig. 57).
A species variation in the amount of nitrogen which can be stored was suggested already by Dortch et al. (1984). He discussed that the rate-limiting steps and the metabolic pathways may vary between species and that some species can accumulate more nitrogen than others, even when normalized to cell volume. Species variation occurred in the kind of nitrogen compounds which accumulate in the cell when the external nitrogen supply is plentiful or when nitrogen is added to nitrogen starved cultures, also. *Skeletonema costatum* and *Thalassiosira gravida* for example formed large nitrate pools, whereas others, such as *Chaetoceros debilis* and *C. affinis* accumulated only small amounts (Collos, 1982 b; Dortch, 1982).

Ratios of particulate carbon to chlorophyll (pC:Chl) ranged from 2 - 24 for grid 1 and 8 and countermatched the geographical distribution of chlorophyll (Fig. 43, 44). Highest ratios during grid 1 characterized regions, where the spring bloom had not set in yet with full intensity. Lowest ratios ranged between 4 - 8, while maximum values were around 11 - 24 (grid average: 8.7). Decreasing ratios towards grid 8 with lows around 1 - 4 and highs around 10 - 23 (grid average 4.3) indicated the enhanced production activity of the phytoplankton.



Grid 1: part. P (µM) 5 m

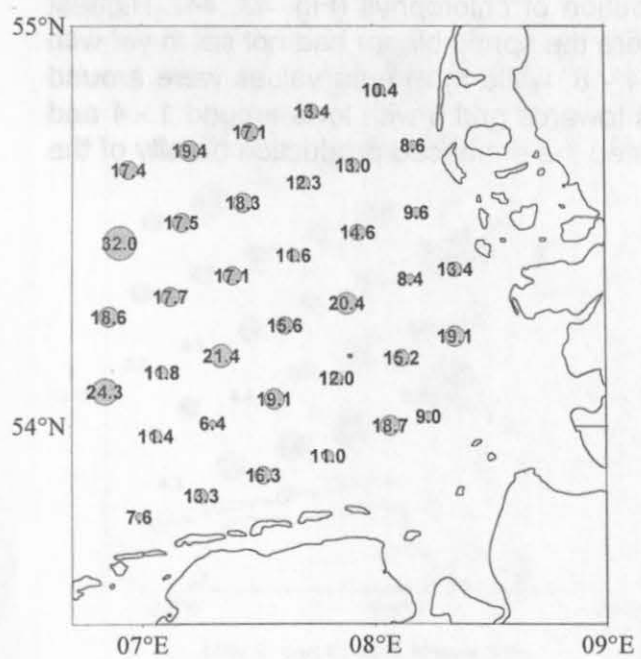
Fig. 54



Grid 8: part. P (µM) 5 m

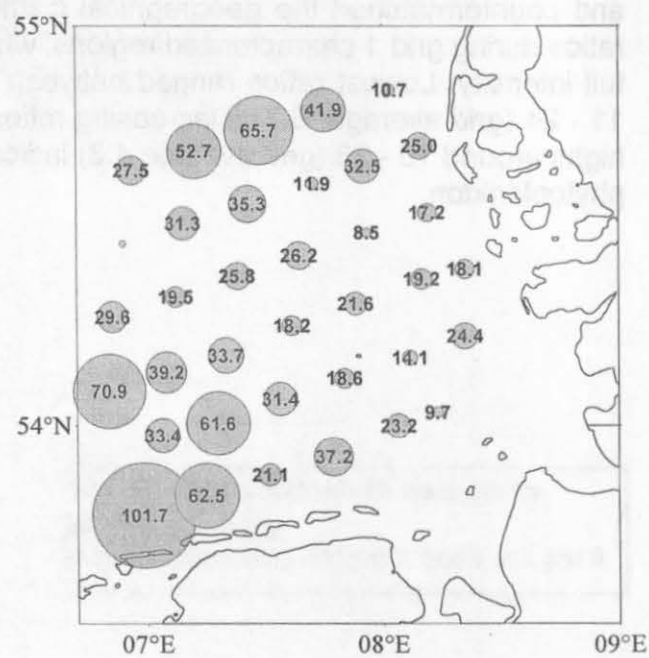
Fig. 55

Fig. 54- 57: particulate phosphorus concentration and particulate nitrogen to phosphorus ratios surface grid 1 and grid 8



Grid 1: molar part N/part P ratio 5 m

Fig. 56



Grid 8: molar part N/ part P ratio 5 m

Fig. 57

f) Phytoplankton

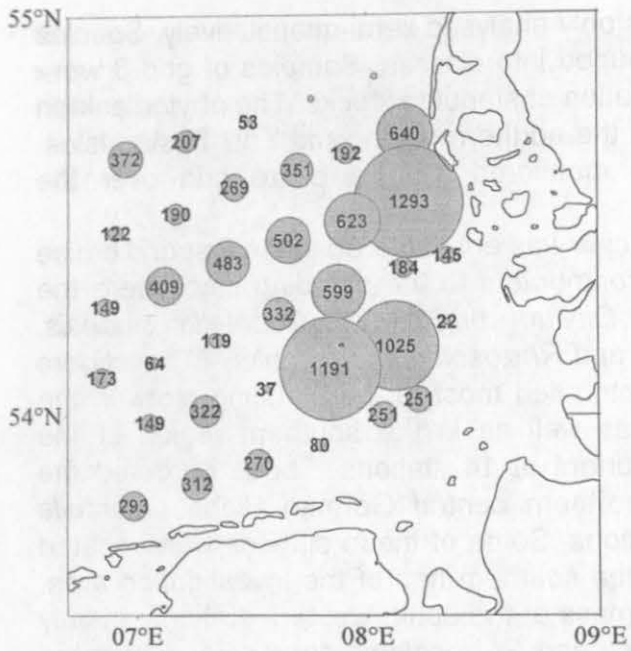
On the first grid phytoplankton samples were only analysed semi-quantitatively. Species occurrence and their cell densities were grouped into classes. Samples of grid 8 were analysed in detail by cell counting and calculation of standing stocks. The phytoplankton analysis confirmed blooms prior to grid 1 off the northern North and East Frisian Isles. An increase of standing stock was then monitored for the entire grid over the investigated period of 18 days.

A typical mixture of spring phytoplankton species was encountered in the first grid cruise (grid 1: 04/25 - 04/27/95). Most important contributors to the standing stock were the diatom species *Thalassiosira punctigera, Ditylum brightwellii, Odontella sinensis, Coscinodiscus wailesii, Cerataulina pelagica* and *Rhizosolenia shrubsolei. T. punctigera* was important at almost all stations and contributed most to the standing stock in the eastern region off the North Frisian Isles as well as in the southern region of the German Bight. *Ditylum brightwellii* was important at 14 stations. These bordered the North Frisian coast and spread into the northern central German Bight. *Odontella sinensis* was an important species at 13 stations. Some of these stations were located north easterly, while others were located in the southern half of the investigation area. *Coscinodiscus wailesii* contributed to the biomass at the south western stations, mainly off the East Frisian Isles. *Cerataulina pelagica* and *Rhizosolenia shrubsolei* dominated the westernmost to central stations and marked the region of the inflowing coastal current.

The phytoplankton distribution pattern of grid 1 is coherent with the quantitative analysis of the drift, which is described and discussed in chapter 5. Results of the quantitative phytoplankton analysis of grid 8 (05/08 - 05/11/95), sampled after the drift investigation, are shown for the surface layer in figures 58 - 62. For each figure the size of the circle is proportional to the calculated carbon values. For readability reason the scaling could not remain proportional between the graphs for the different species.

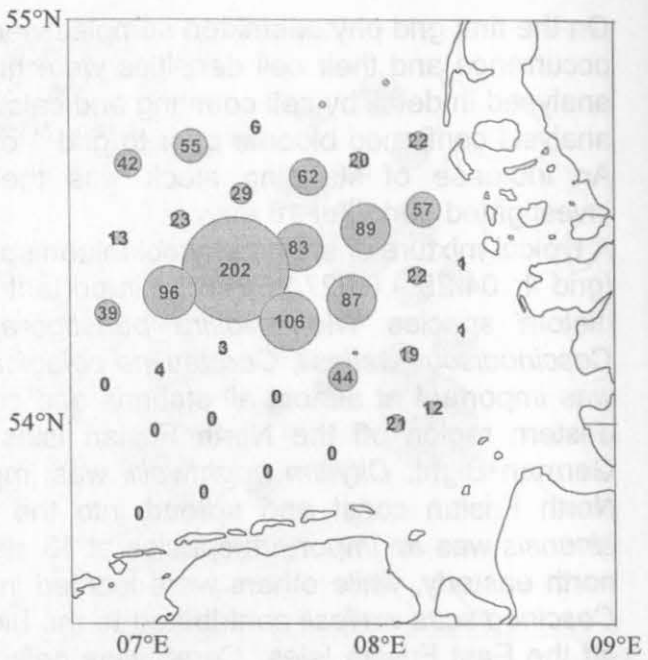
Thalassiosira punctigera (Fig. 61) still contributed an important proportion to the standing stock on almost all stations in grid 8 (10 - 64 µg C l^{-1}). *Ditylum brightwellii* (Fig. 59) dominated the phytoplankton in the central German Bight (maximum values above 200 µg C l^{-1}), accompanied by *T. rotula* (Fig. 60, maximum values of 300 - 550 µg C l^{-1}). *Odontella sinensis* (Fig. 62) was dominant off the North Frisian Isles (500 - 900 µg C l^{-1}). Maximum values of calculated total phytoplankton biomass (600 to 1200 µg C l^{-1}) were located in the eastern half of the German Bight (Fig. 58) due to the regional distribution of *Odontella sinensis.*

The general importance of *Thalassiosira* species for the spring bloom in the German Bight is supported by other spring data. The species *Thalassiosira nordenskiöldii* in addition to *T. rotula* and *Coscinodiscus concinnus* were dominant for example in spring 1985 (Hickel, et al., 1989). In spring 1986 *Thalassiosira nordenskiöldii* became important again, sometimes contributing more than 700 µg C l^{-1} to the standing stock. It was accompanied by *Skeletonema costatum* (< 200 µg l^{-1}) and *Porosira glacialis. T. rotula* was also present, but not considered as dominant compartment of the bloom. Carbon contribution by the *Thalassiosira* species in the spring bloom 1995 did not reach the maximum given by Hickel et al. (1989) for *T. nordenskiöldii* (700 µg C l^{-1}), while total calculated phytoplankton biomass exceeded this value at several stations. A major



Grid 8: total phytoplankton (µg C/l) 5 m

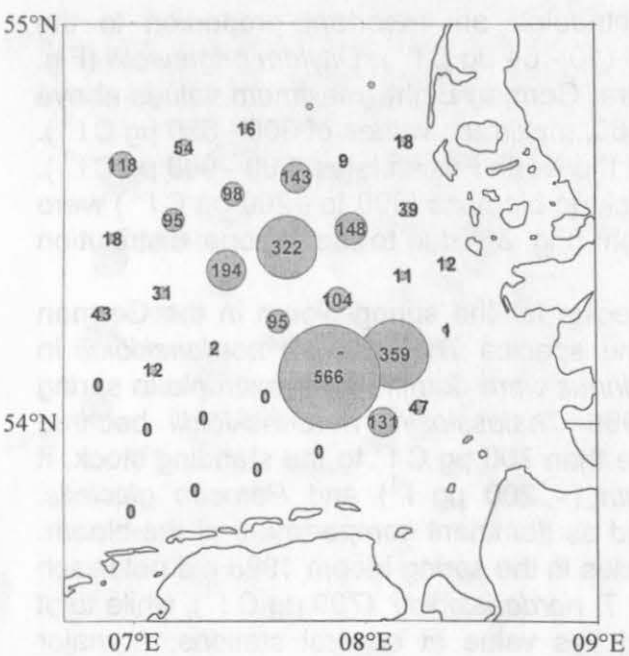
Fig. 58



Grid 8: Ditylum brightwellii (µg C/l) 5 m

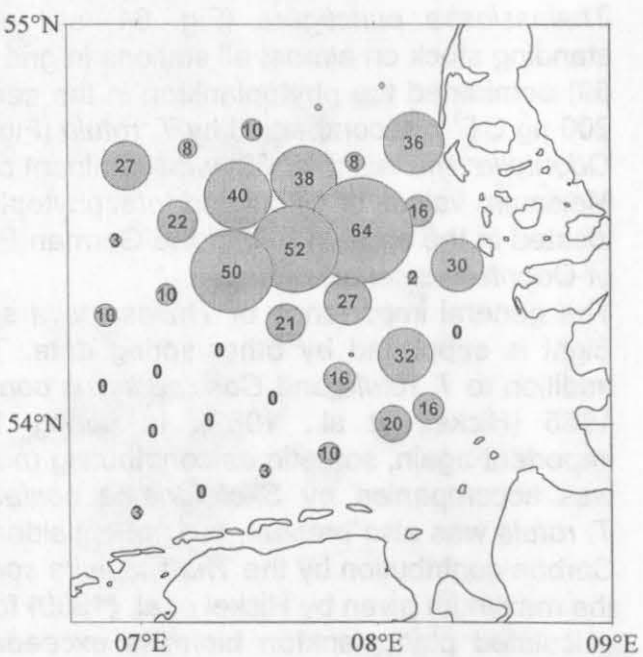
Fig. 59

Fig. 58- 61: Particulate carbon : total phytoplankton, *D. brightwellii*, *T. rotula* , *T. punctigera*; surface grid 8; calculated from biovolume; scaling of circle proportional to stated value



Grid 8: Thalassiosira rotula (µg C/l) 5 m

Fig. 60



Grid 8: Thalassiosira punctigera (µg C/l) 5 m

Fig. 61

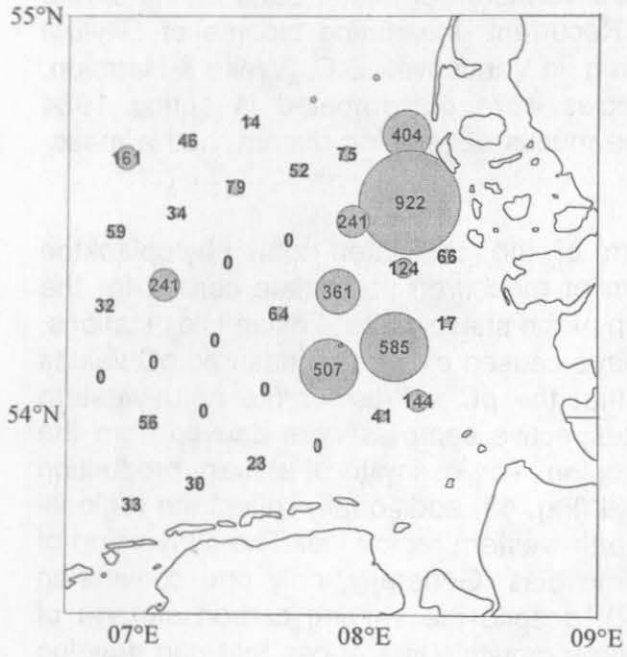
contribution of *Ditylum brightwellii* to the spring bloom was not revealed in the years investigated by Hickel et al. (1989) and a massive bloom of this species during spring may be considered as somewhat atypical. Recurrent dominating blooms of *Ditylum brightwellii* were monitored rather in autumn, e.g. in Vancouver, B.C. (Waite & Harrsion, 1992). The main spring phytoplankton species were outcompeted in spring 1984 likewise, when *Coscinodiscus wailesii*, a large mucus developing diatom, had a mass-occurence (Hickel et al., 1989).

Differences between the distribution pattern of the calculated total phytoplankton biomass (Fig. 58) and the distribution pattern of measured particulate carbon for the same grid (Fig. 47) are obvious. Resuspension at the shallow East Frisian Isles stations, which are strongly influenced by tides, may have caused elevated measured pC values in that region. It is not very likely though, that the pC values for the north-western stations were influenced by resuspension. Respective samples were derived from the surface layer in a deeper, strongly stratified region. The estimate of primary production rate (Fig. 64) and standing stock of chlorophyll (Fig. 43) additionally reflect the regional distribution of high particulate carbon in the north-western region well.The conversion of the cell counts to pC may have caused some bias. Generally, only one conversion factor is applied (Strickland & Parson, 1972), despite the varying carbon storage of phytoplankton cells in exponential and stationary growth. Differences that can develop between calculated and measured carbon are discussed in more detail for the enclosure experiment (chapter 6).

4.2. Rates

a) Primary production

Results for the primary production are shown as depth integral for a square meter per day (Fig. 63, 64). Light-saturated production was reached with 135 µmol m^{-2} s^{-1} during grid 1 and 8. Light-saturated chlorophyll-specific assimilation rates (P^B_{max}) in the first grid (04/25-04/27/95) averaged to 6.5 mg C mg Chl a $^{-1}$ h^{-1} (variation 12%, n= 12) for all depths. In grid 8 (5/9 - 5/11/95) values for the surface layer were clearly lower (2.5 mg C mg Chl_a^{-1} h^{-1}, variation 24%) than for the 10 and 20 m samples (6.9 mgC mgChl $_a$ $^{-1}$ h^{-1}; variation 22%). The nutrient data indicate that a silicate depletion in the upper water column caused this depression in assimilation rate. An increase of primary production between grid 1 and 8 was most obvious for the central and northwestern region of the German Bight (Fig. 63, 64). Stations with high production rates during grid 1 indicated a transition towards a more stationary state towards grid 8. Estimated primary production rates ranged from 1 to 10 g C m^{-2} d^{-1} in the first grid and from 1 to 16 g C m^{-2} d^{-1} in grid 8.
These values were high even for spring. An overview of primary production measurements conducted in the German Bight is given in Rick et al. (submitted). While the spring 1995 data amounted to about 120 g C m^{-2} $month^{-1}$ in grid 1 and 189 g C m^{-2} $month^{-1}$ in grid 8, estimates by Rick (1990) for spring 1986 reached only 18 - 36 g C m^{-2} $month^{-1}$. Estimates by Joint & Pomroy (1993) for May 1989 likewise reached only 47 g C m^{-2} $month^{-1}$. On the other hand, investigations by Aletsee et al. (1991) during the



Grid 8 : Odontella sinensis (µg C/l) 5 m

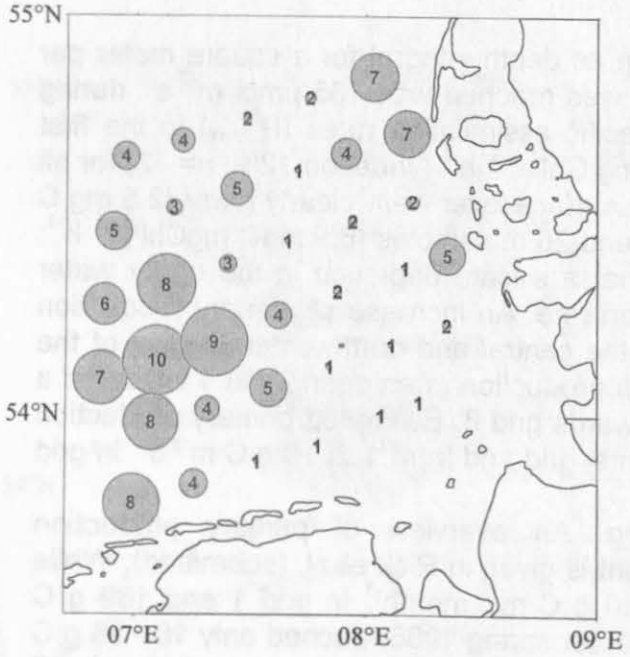
Fig. 62

Fig. 62: Particulate carbon

O. sinensis; surface grid 8; calculated from biovolume; scaling of circle proportional to value

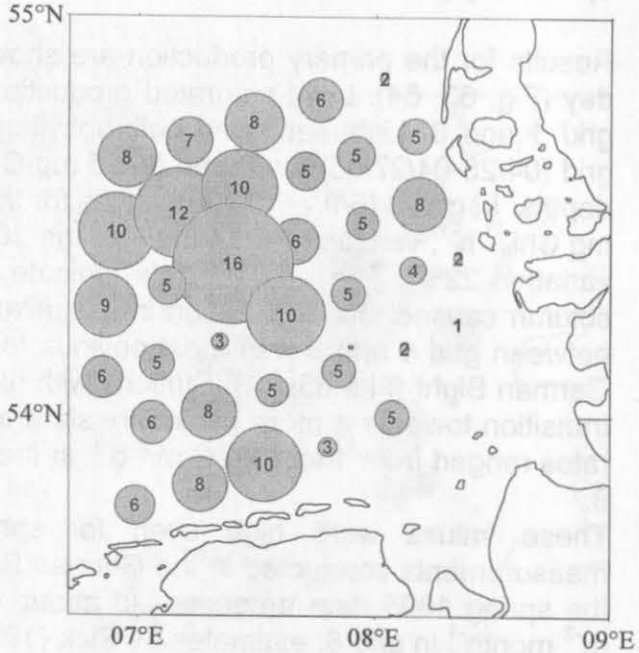
Fig. 63 and 64: Estimated primary production

for surface grid 1 and grid 8, scaling of circle proportional to value, for more information refer to chapter 3.



Grid 1: estimated primary prod. (gC/m2*d)

Fig. 63



Grid 8 : estimated primary prod. (g C/m²*d)

Fig. 64

same month resulted in values as high as 145 g C m^{-2} $month^{-1}$ in the region overlapping the area investigated by Joint & Pomroy (1993). These differences clearly reflect the variability of the system. The investigations by Joint & Pomroy (1993) were later in the month than the investigation by Aletsee et al. (1991), so possibly Joint & Pomroy (1993) were sampling the post-spring bloom situation by that time.

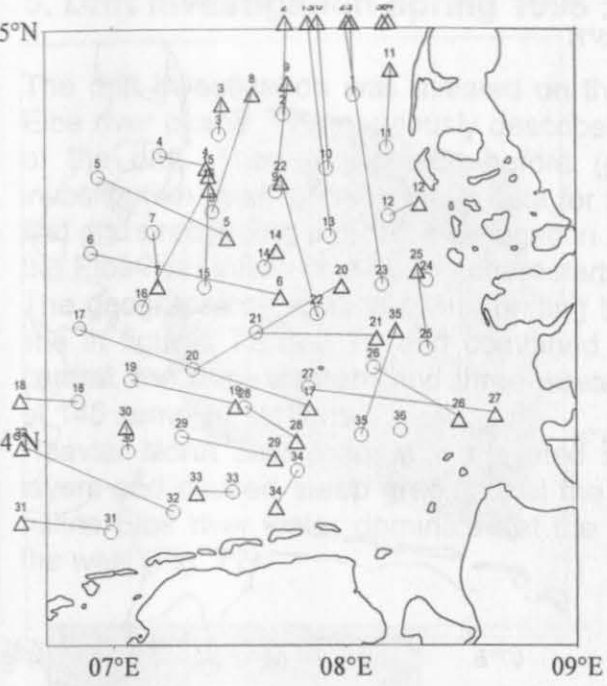
4.3. Estimates of nutrient consumption and POM production in the German Bight

Imports and exports of nutrients can be calculated using actual nutrient gradients and translocation of water masses estimated by hydrodynamic models. It is more difficult to quantify the turnover of nutrients and organic compounds upon which the hydrodynamic regime is superimposed. Approaches to estimate nutrient consumption and POM production in a highly variable system as the German Bight are based on some more or less severe simplifications. For an estimate of biologically induced changes in between different grids during the spring investigation 1995, Brockmann et al. (submitted) calculated vertically integrated means of concentrations of one grid and compared these with means of depth-integrated data from grids sampled later in time. The differences were expressed as change per day, so they could additionally be used for a comparison of changes during different seasons. This integrating approach results in gradients that reflect neither the mixed nor the bottom layer of a stratified water mass. It does not account for any transport process either. A further problem in a seasonal comparison is caused by the seasonally differing relationship between the biological turnover and the transport of water masses. Both factors have a major impact on the rate of change in the system. To partly overcome these problems, Brockmann et al. (submitted) included an estimate of the transport processes in the seasonal budget. They correlated the integrated nitrate data with salinity data. For winter 1996 and spring 1995 the two parameters showed a linear relationship. No acceptable relationship between nitrate and salinity could be established for summer, since biological processes dominated. Nitrate gradients, resulting solely from shifts of salinity between the grid samplings, were calculated for the last grid to reflect approximate advective processes. These results were then compared to the nutrient gradients produced by a simple grid to grid difference of the depth-integrated data. A comparison of both produced an estimate of the proportion of change caused by biological activity. Advective processes proved to be relevant for spring 1995. They may have been responsible for a change in nitrate concentration that was comparable to the decrease caused by the activity of the phytoplankton. The integration of the highly active suface layer with the biologically less active layers resulted in lower consumption and production estimates compared to the approach described below, which only considered the surface layer.

A lagrangian model, developed by the group „Hydrosphere I" (Dr. T. Pohlmann, Prof. Dr. Sündermann), was combined with the biological and biochemical data of the grids to estimate biologically induced changes in the surface layer in between grid 1 and grid 8. Modelled movements of the water mass within the single grids are shown in Fig. 4 - 6. The transport of water at all stations was referenced by the model to station 36 as the last station of the single grid.

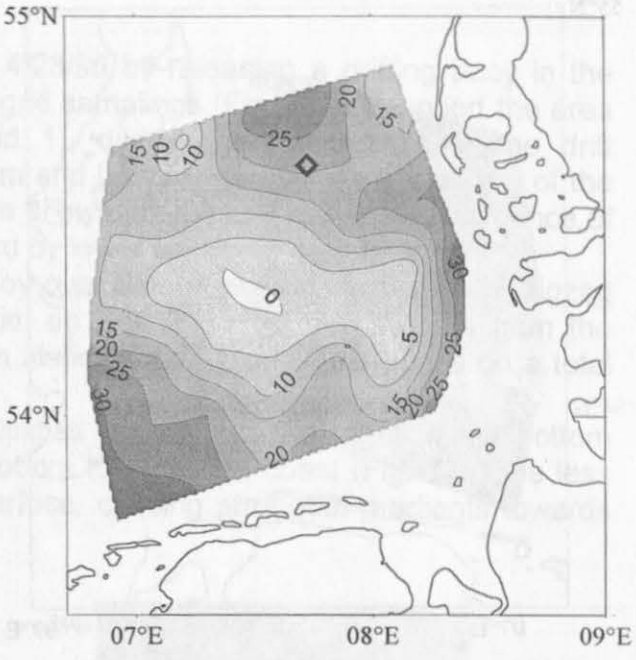
With the same procedure it is possible to model the water movement between the single grids. Grid data of the different stations can be moved in a way that makes a grid synoptic to another grid that follows in time. Suggested water translocation for the time in between grid 1 and grid 8 is shown in Fig. 65. Circles mark the starting point of a model water particle in 7.5 m depth on the 04/24/95 (grid 1). A triangle marks its modelled final position on the 05/11/95 (end of grid 8). Water was transported over relevant distances. Movements followed the general current system through the German Bight and water of several stations left the area of investigation, especially northbound in front of the North Frisian Isles.
The model was applied to our biochemical data with the assumption that any vertical movement of particles was negligible during the investigated period. First the data of grid 8 were moved to make the grid synoptic in itself (see movements in Fig. 6). The modelled transports displayed in Fig. 65 were applied for grid 1, followed by a comparison between the adapted data for grid 1 and 8. Model water particles of grid 1 did not necessarily move onto some point of measured data in grid 8 over time. Estimates of nutrient loss and particulate matter gain were thus based on a comparison of values that were regionally close to each other. This procedure remains subjective to a certain extend. One has also to keep in mind, that the estimates shown in Fig. 66- 71 can only be as reliable as the model is considered to be reliable in reflecting the true hydrological situation in the field. Moreover, grazing, particle sedimentation and other processes in the water column are not included in the model. Especially for the shallower coastal stations there may have been some vertical movement, too, which was not considered in this application of the model. Thus the results can by no means reflect processes taking place in the field with a high degree of accuracy. Results may, however, give a rough idea of the net change over the investigated period of time.
The regional distribution of elevated consumption or loss of silicate (Fig. 67), nitrate (Fig. 66) and phosphate (Fig. 68) overlapped with areas of enhanced theoretical production of particulate carbon (Fig. 69), particulate nitrogen (Fig. 70) and produced chlorophyll a (Fig. 71). The region of the inflow of the more haline, nutrient poor coastal current (Fig. 9, 13,16, 28) was characterized by low consumption and a minor increase of biomass for the investigated time. Nitrate consumption ranged from zero to 33 µM (Fig. 66). On average 16 µM nitrate was lost in the surface layer. Silicate (Fig. 67) was lost in the range of 2 to 25 µM (average 11 µM). For phosphate (Fig. 68) estimated consumption was between zero and 0.75 µM (average 0.4 µM). Particulate carbon was assimilated with maximum values of up to 75 µM at the surface (average 31 µM). The gained particulate nitrogen ranged from of zero up to 20 µM (average 5.1 µM). A range between almost none to 38 µg l^{-1} (average 13 µg l^{-1}) chlorophyll was produced.

Estimates of biologically induced changes in highly variable systems may be improved by hydrodynamic models with high resolution. The diversity of organisms, their regional abundance and their possibly patchy distribution may cause variations, however, which are not attributed for in such a model. The drift investigation 1995 was initiated to improve the estimates of biological conversion during spring by tracking a water mass for several days. Results of the drift are shown and discussed in chapter 5.



Grid 1 to 8 (04/24-05/11/95): model data upper layer

Fig. 65

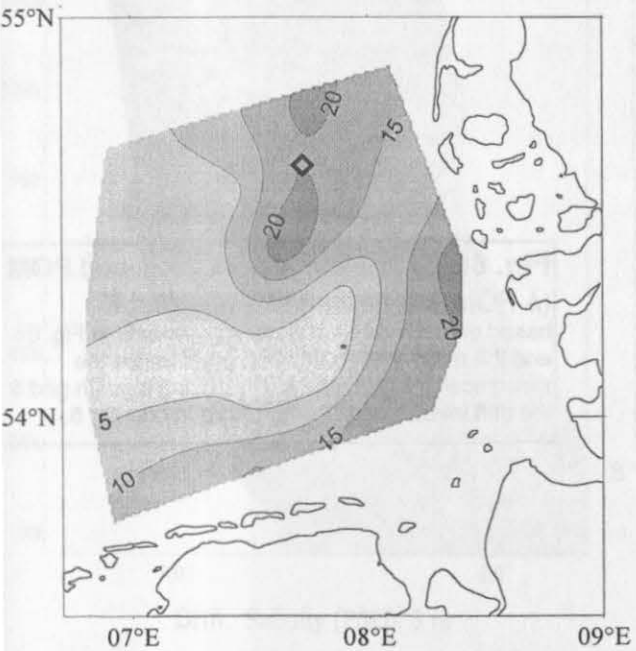


Grid 1 to 8: theoretical nitrate (µM) consumption 5 m

Fig. 66

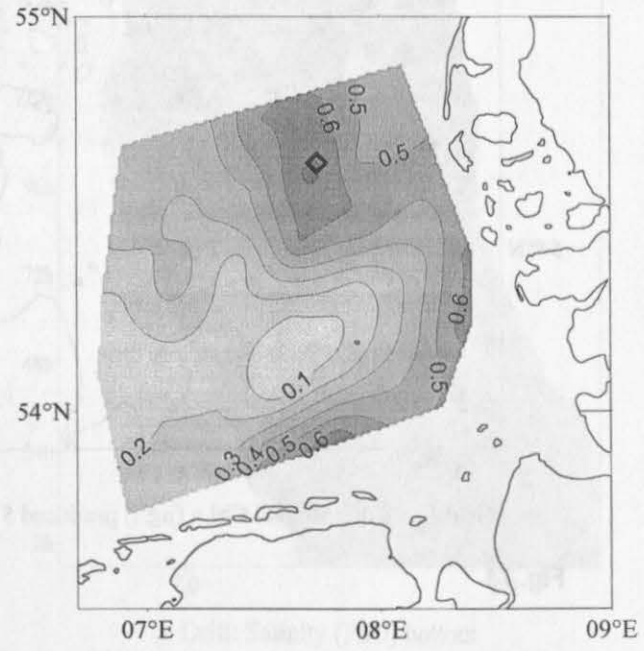
Fig. 65: Modelled movement of water between grid 1 and grid 8
start of water particles at 7.5 m, circles=position in grid 1; triangle= modelled position in grid 8 (see chapter 4.3); data provided by Hydrosphere 1 (Prof. Dr. Sündermann, Dr. T. Pohlmann)

Fig. 66 - 68: Estimates of consumed nutrients (Δ nutrient µM) between grid 1 and grid 8
based on the modelled water movements in Fig. 65 and the measured dissolved nutrients; diamond locates the theoretical final position of the drifting buoy in grid 8 ; the drift investigation is described in chapter 5.



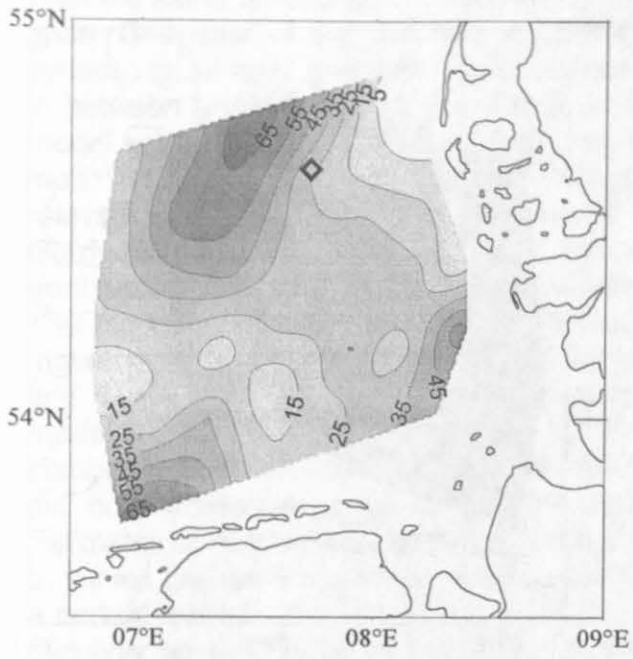
Grid 1 to 8 : theoretical silicate (µM) consumption 5 m

Fig. 67



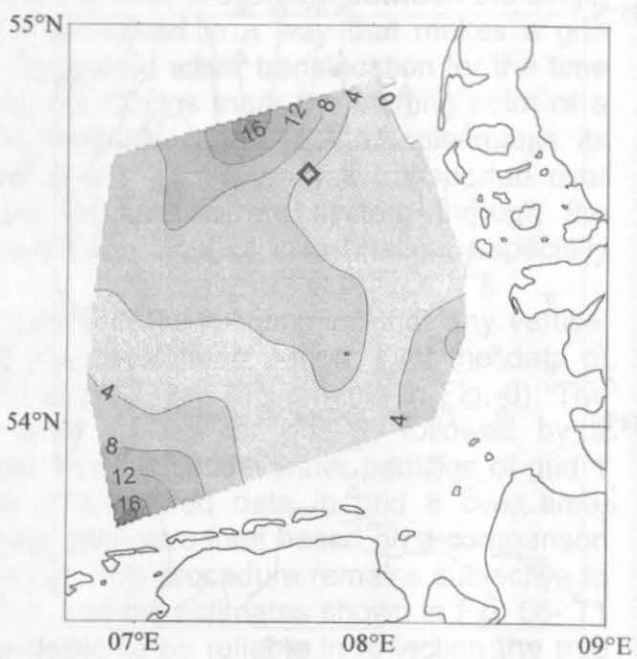
Grid 1 to 8: theoretical phosphate (µM) consumption 5 m

Fig. 68



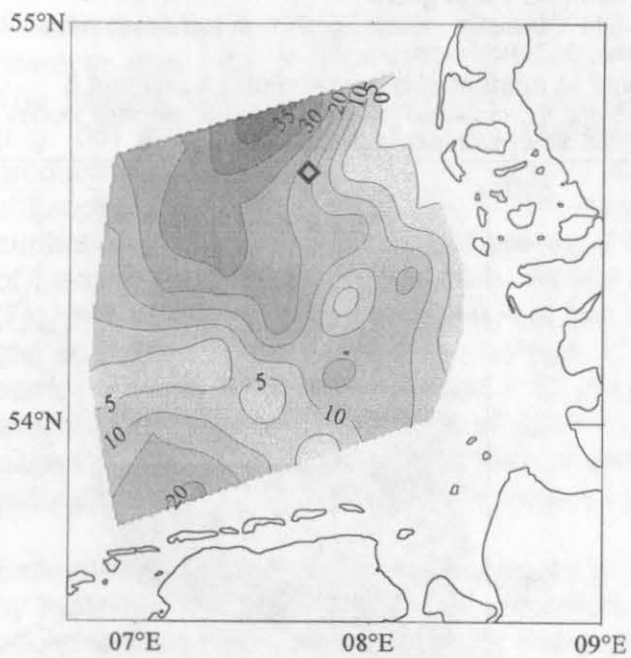
Grid 1 to 8: theoretical part. carbon (µM) bound 5 m

Fig. 69



Grid 1 to 8: theoretical part. nitrogen (µM) bound 5 m

Fig. 70



Grid 1 to 8: theoretical Chl a (µg/l) produced 5 m

Fig. 71

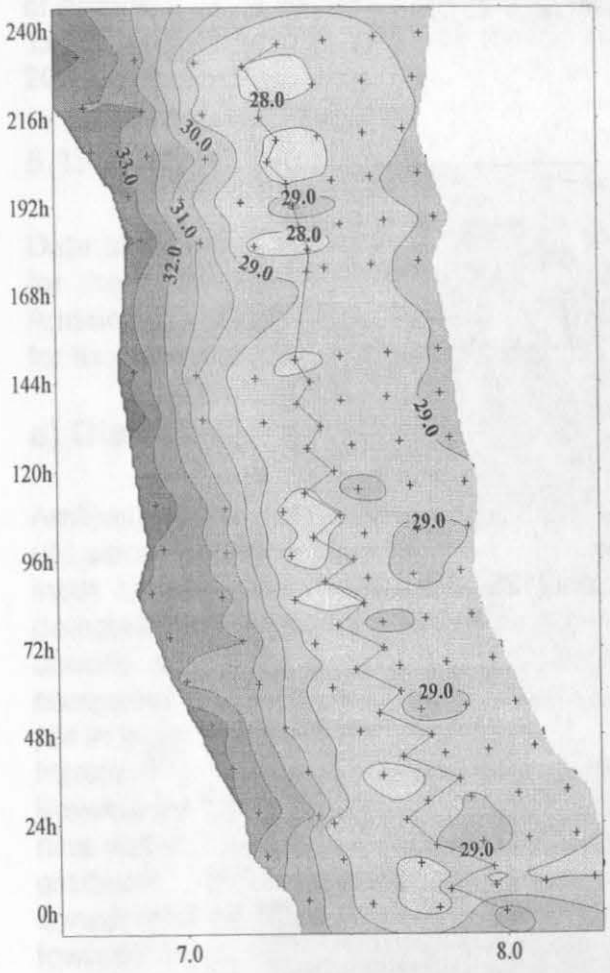
Fig. 69 - 71: Estimates of produced POM (Δ POM) between grid 1 and grid 8
based on the modelled water movements in Fig. 65 and the measured POM; diamond locates the theoretical final position of the drifting buoy in grid 8 ; the drift investigation is described in chapter 5.

5. Drift investigation spring 1995 : Results and discussion

The drift investigation was initiated on the 4/28/95 by releasing a drifting buoy in the Elbe river plume. The previously described grid samplings (Fig. 1) surrounded the area of the drift. They took place before (grid 1), during (grid 5) and after the drift investigation (grid 8).The salinity data for 5 m and bottom layer (close to bottom) of the first grid preceeding the drift investigation are shown in figures 7 and 8. The influence of the Elbe river inflow was clearly characterized by lower salinity in both layers.

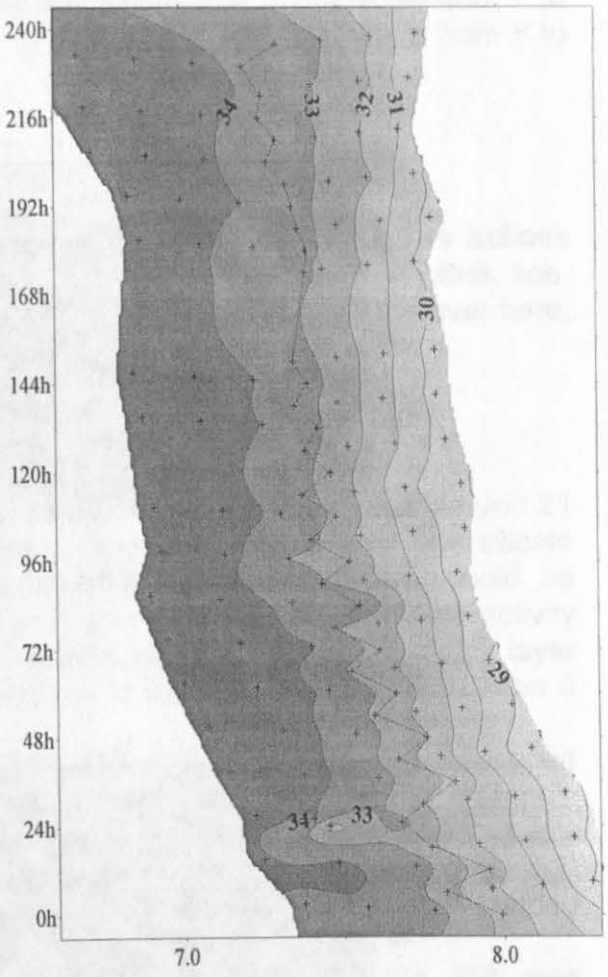
The geographical position of the drifting buoy over time is marked with a black zigzag line in figures 72 and 73 and combined with an isoline plot of salinity data from the central, the three eastern and three western stations. This type of plot relies on a total of 145 sampled stations.

Heavier North Sea water with elevated salinities flowed into the Bight in the bottom layers and caused steep gradients at the bottom towards the coast (Fig. 73). The less haline Elbe river water dominated at the surface, causing strongest gradients towards the west (Fig. 72).



Drift: Salinity (PSU) 5 m

Fig. 72



Drift: Salinity (PSU) bottom

Fig. 73

Fig. 74 - 76 Salinity: depth-dependent distribution at all drift stations (Central, three easterly and westerly stations); Fig. 74: Start of the drift (0-9 h), Fig. 75: middle of the drift (125-133 h) and Fig. 76: end of drift (Fig. 76; time 229-237 h).

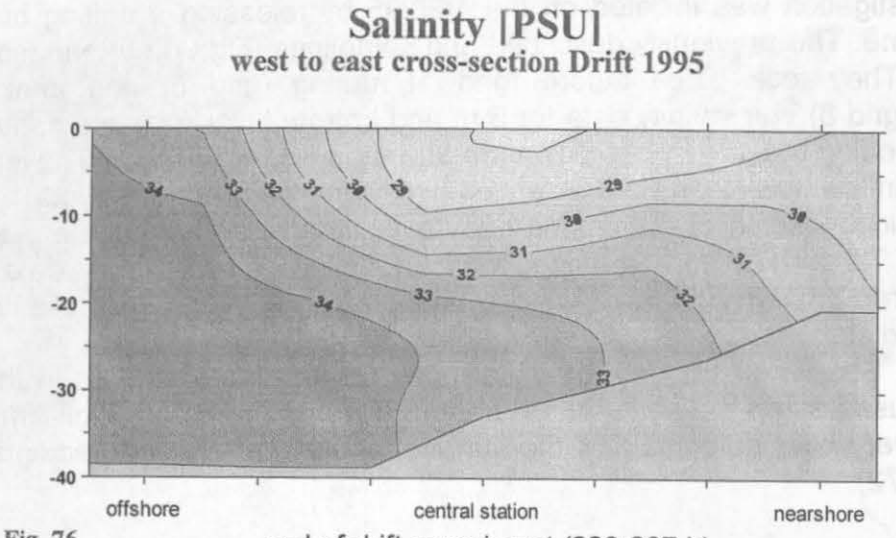
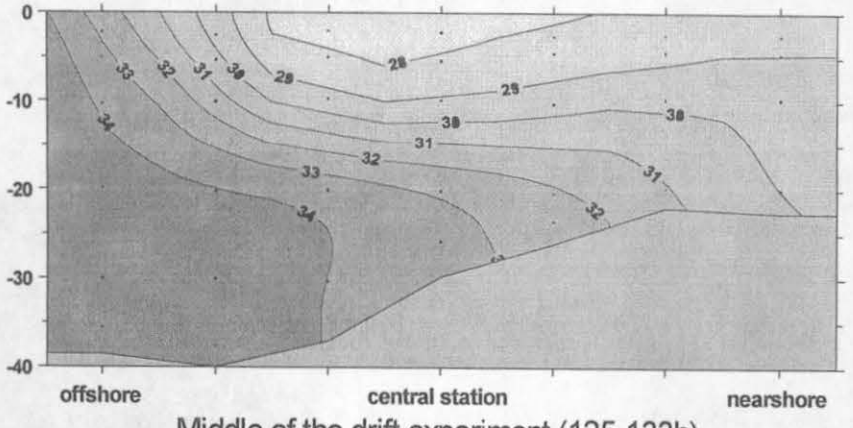
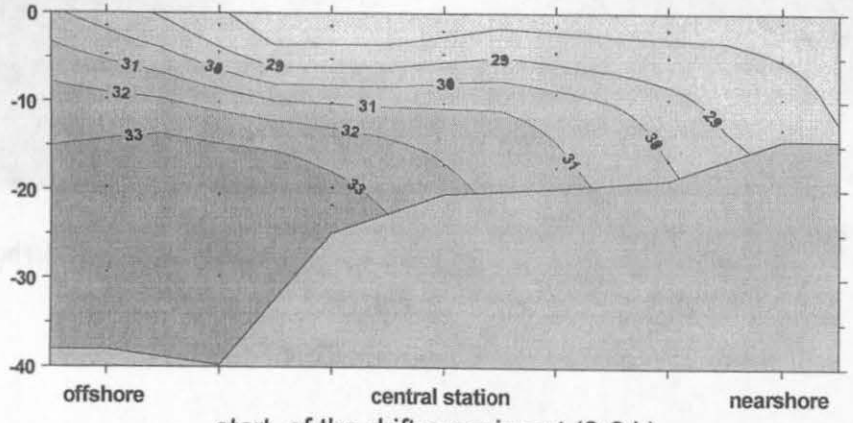


Fig. 76 end of drift experiment (229-237 h)



Middle of the drift experiment (125-133h)

Fig. 75



start of the drift experiment (0-9 h)

Fig. 74

The drifting buoy was less successful in tracking the same water mass below the discontinuity layer compared to the surface layer as a result of this hydrological feature. This suggestion is supported by the depth-dependent salinity distribution (Fig. 74 to 76). Data of the central drifter position as well as the three easterly and westerly stations are plotted for the start of the drift (Fig. 74; time 0-9 h), the middle (Fig.75; time 125-133 h) and the end of the drift (Fig. 76; time 229-237 h). The discharge from the river flowed over more haline waters and remained a discrete lens at a considerable distance from the river mouth, while slight changes in the deeper layers occurred due to the coastal current inflow. Thus the buoy mainly followed the same type of water for 10 consecutive days in the surface layer. A combination of low advective processes (low wind around 1-2 Beaufort, towards the end 5), low wave action, low residual current and a strong freshwater impact (1700 - 1000 $m^3 s^{-1}$ runoff from the Elbe) as well as a stable discontinuity layer around 7-12 m were the overall reasons for the successful drift investigation. In many drift investigations the initial water body was typically lost after a few days due to unfavourable weather and hydrographic conditions. In the course of the drift investigation 1995 we followed the start and beginning decrease of a spring diatom bloom. The bloom was initiated by high inorganic nutrient levels and high solar radiation of around 750 - 800 $W m^{-2}$, which caused a rise of surface water temperature from 7 to 12 °C (end of the Grid 1 to end of Grid 8) and an increase in air temperature from 8 to 20 °C.

5.1. Stocks

Data at the central, the three easterly, and three westerly stations are given as isolines for the surface layer over time.The track of the drifter is marked with a black line. Additional plots from the central station display data from surface to bottom over time, for the evaluation of depth-dependent processes.

a) Dissolved inorganic nutrients

Ambient silicate was rapidly consumed by the diatoms (Fig.78). Initial values around 21 µM silicate dropped to values <1 µM towards the end of the investigation. The silicate input by the river water, overlying higher haline water with less silicate, could be detected at the start of the drift (Fig. 77). The higher intensity of biological activity caused a steeper gradient of silicate concentrations over time in the surface layer compared to the deeper layers. Final concentrations of silicate remained as high as 5 µM in layers below 5 m.

Nitrate (Fig. 79, 80) and phosphate (Fig. 85, 86) distribution patterns were influenced likewise by depth dependent phototrophic biological activity and the inflow of eutrophic river water (Fig. 79, 80, 85, 86). Gradients at the surface reflected the observed salinity gradients. Steep gradients of dissolved nitrate (Fig. 80) and nitrite (Fig. 82) concentrations were identified towards the west, while no clear gradient developed towards the east.

The initial concentration of nitrate, originating from the river plume (Fig. 79), was extremely high. Surface values above 60 - 70 µM (Fig. 80) were reduced to about 45 µM in the course of the drift. Other nitrogen components like nitrite (Fig. 81, 82) and ammonia (Fig. 83, 84) did not show a clear development over time.

Fig. 77

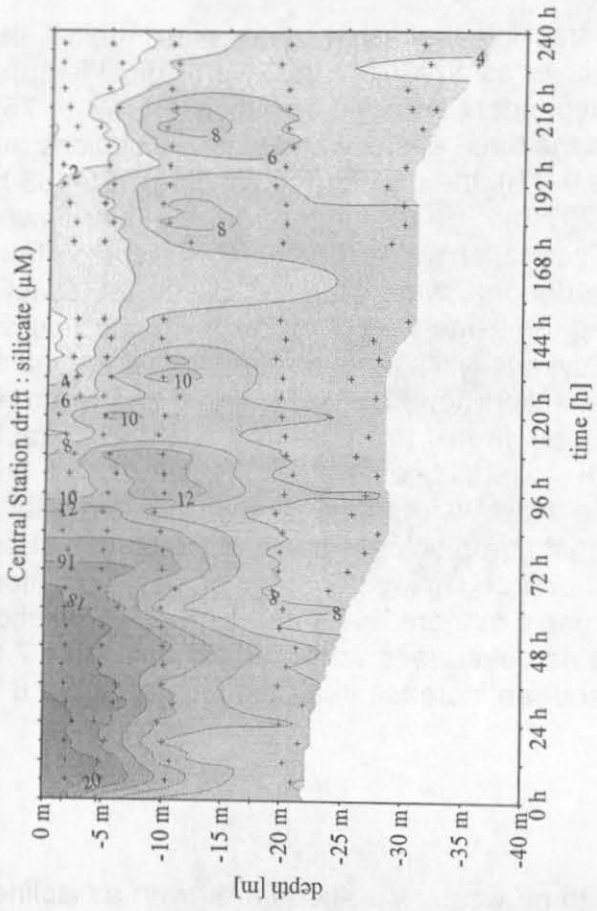
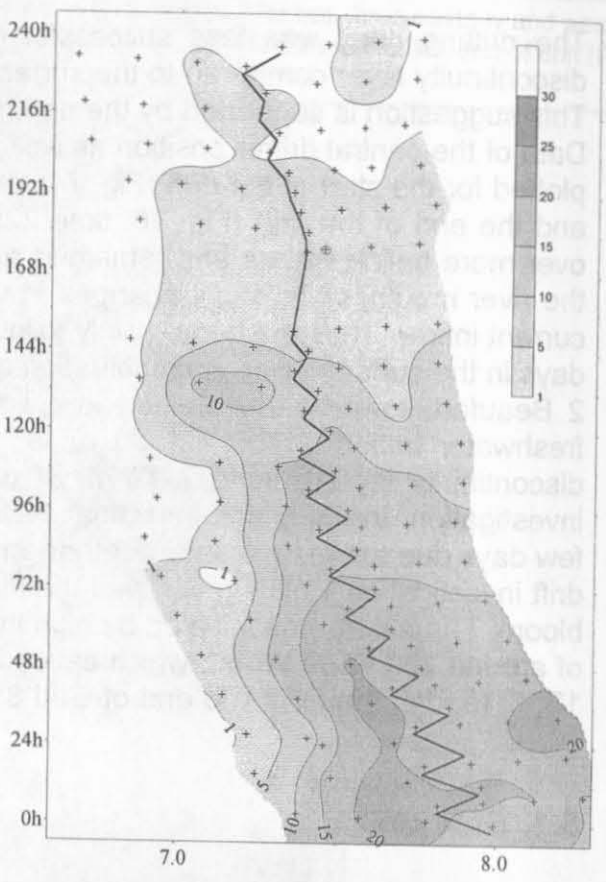


Fig. 78



Drift: Silicate [µM] 5 m

Fig. 79

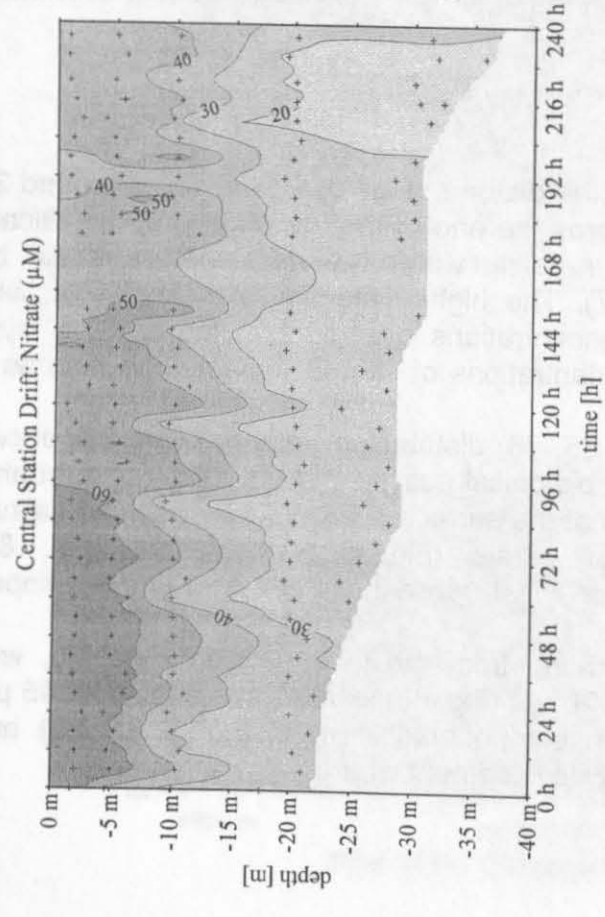
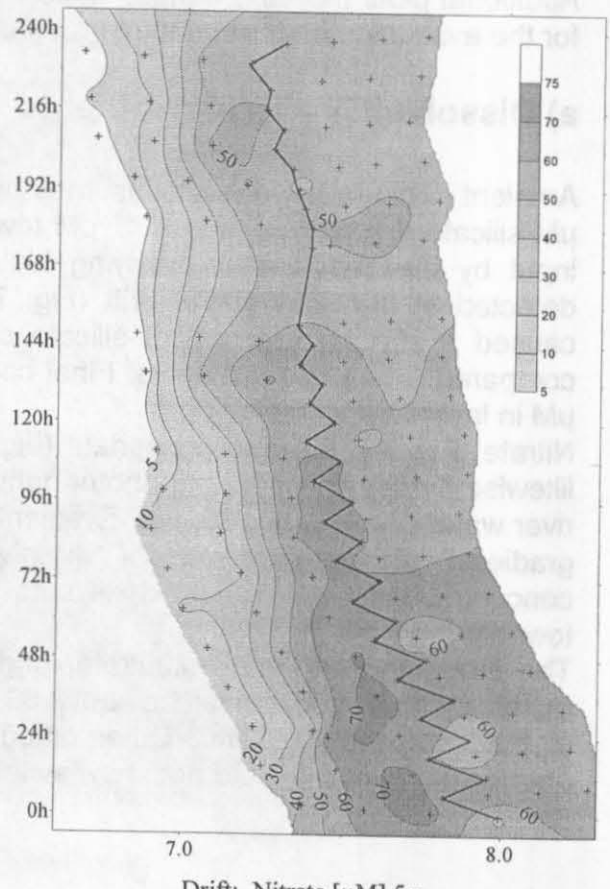


Fig. 80



Drift: Nitrate [µM] 5m

Nitrite concentrations at the central station were higher than at the westerly stations (Fig. 82). Values remained slightly higher at the central station in the surface layer than below (Fig. 81). Nitrite may have been excreted by phytoplankton growing well in surplus nitrate supply, since the phytoplankton was more productive at the central station than at the western station (see e.g. pC:Chl ratios). It was also more productive in the upper layer compared to the bottom layer. The excretion of nitrite by phytoplankton is discussed in more detail in chapter 6.
Ammonia displayed a heterogenous pattern (Fig. 83, 84). Values in the bottom layer were higher (2-3 µM) than at the surface (below 1 µM). High surface values above 2 µM were measured at the easterly stations for the start of the drift (Fig 84). Surface concentrations remained around 0.8 - 2.2 µM even towards the end of the drift.
The uptake of phosphate by the phytoplankton reduced concentrations in the upper layer over time (Fig. 86). No clear trend developed for the deeper layers (Fig. 85). Elevated bottom values compared to the surface may have been the result of local phosphate remineralisation.

b) Ratio of dissolved inorganic nitrogen to phosphate

As discussed for the grid, observed ratios indicated a strong phosphorus limitation. The ratio of inorganic nitrogen to phosphate rose from ratios of around 100 to extremely high values above 1000 over time (Fig. 88) due to phosphate depletion of the surface water. Ratios above 100 were typically found in the upper 15 m, while they remained lower at the bottom (Fig. 87). This may have been caused by remineralization processes and/or a slower phosphate consumption by phototrophic organisms close to the bottom. Only towards the end of the drift ratios also rose in the deeper layers.

c) Dissolved organic nitrogen (DON)

Dissolved organic nitrogen components displayed no clear trend over time (Fig. 89, 90). As much as 16 µM DON was measured in the region of the central station at 5 m. Generally the concentration was lower in layers below 10 m (6 - 10 µM), indicating an enhanced production of DON by phytoplankton in the surface layer.

d) Particulate organic matter (POM)

Chlorophyll

The chlorophyll data strongly reflected the growth of biomass during the course of the drift (Fig. 91,92). Surface values rose from around 4 µg Chl l^{-1} to above 80 µg Chl l^{-1} at 192 h. After 192 h concentrations dropped to about 50 µg Chl a l^{-1}. Concentrations closer to the bottom increased only towards the end of the drift (Fig. 91) due to less favourable light conditions for the growth of phytoplankton. Increasing values below 20 m after 192 h were probably also caused by sedimenting nutrient stressed phytoplankton cells. The suggestion of increased sedimentation of cells towards the end of the investigation is supported by a high percentage of *Ditylum brightwellii* spermatogonia in the phytoplankton counts. The ability of of *D. brightwellii* to sink and ascent will be discussed in the subchapter phytoplankton.

Fig. 81

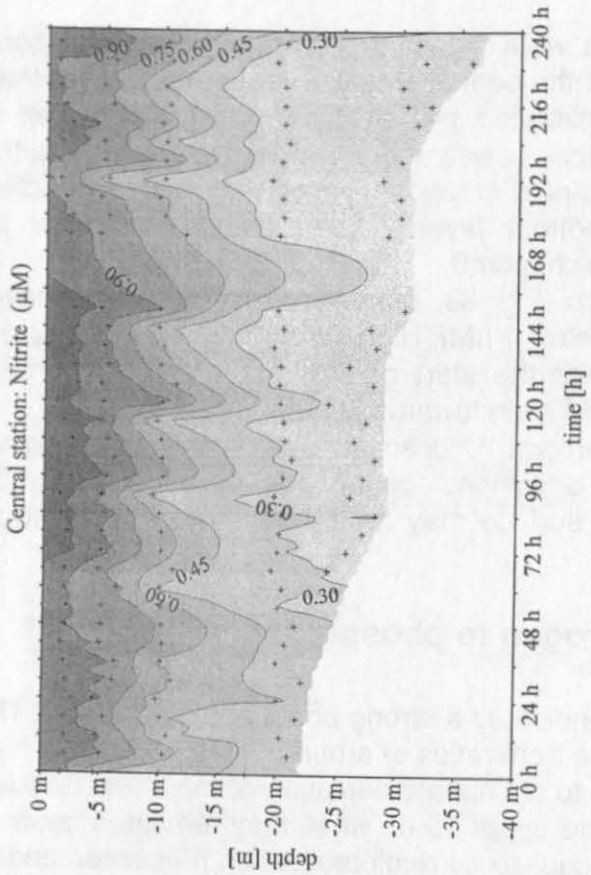


Fig. 82

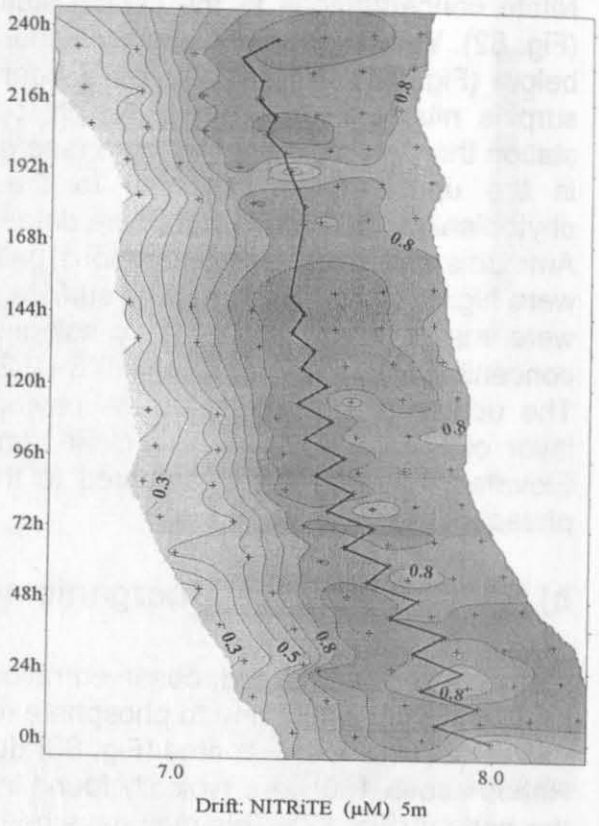


Fig. 83

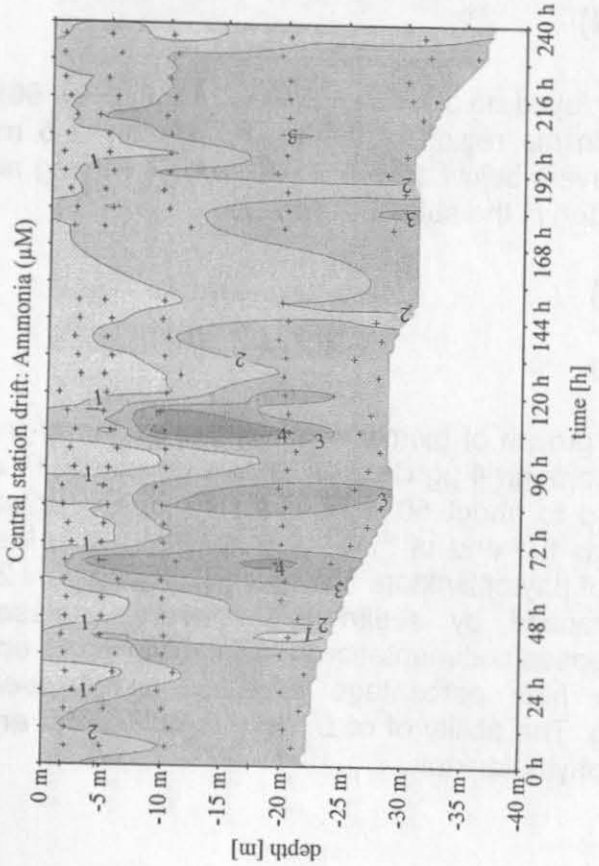


Fig. 84

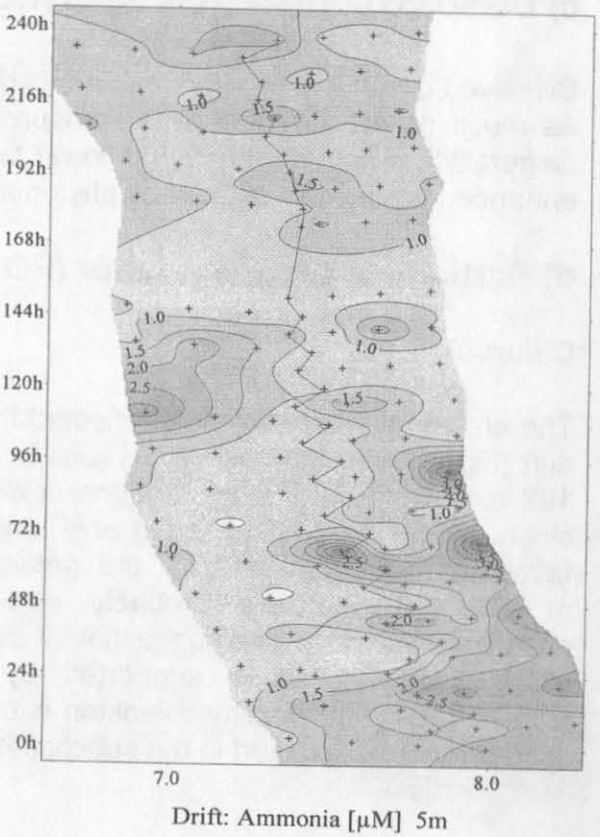


Fig. 85

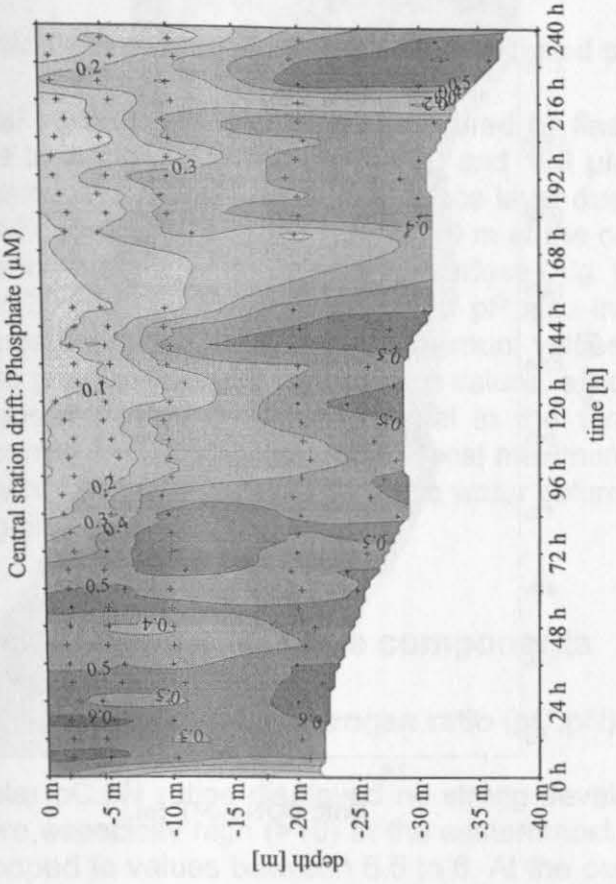


Fig. 86

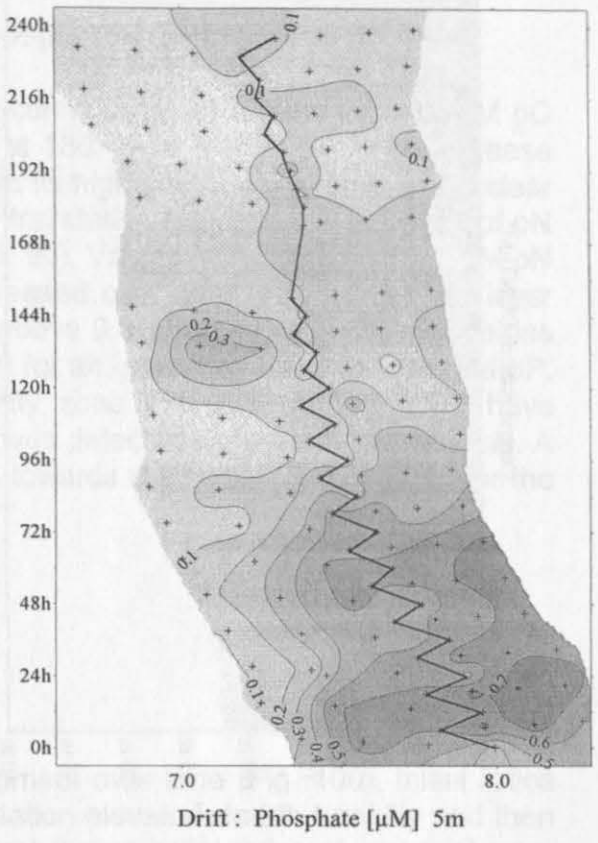


Fig. 87

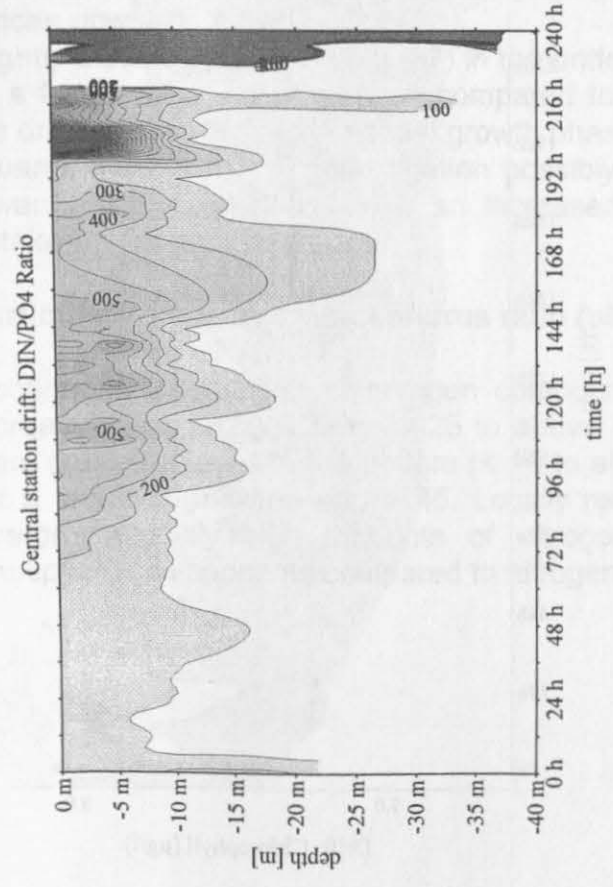


Fig. 88

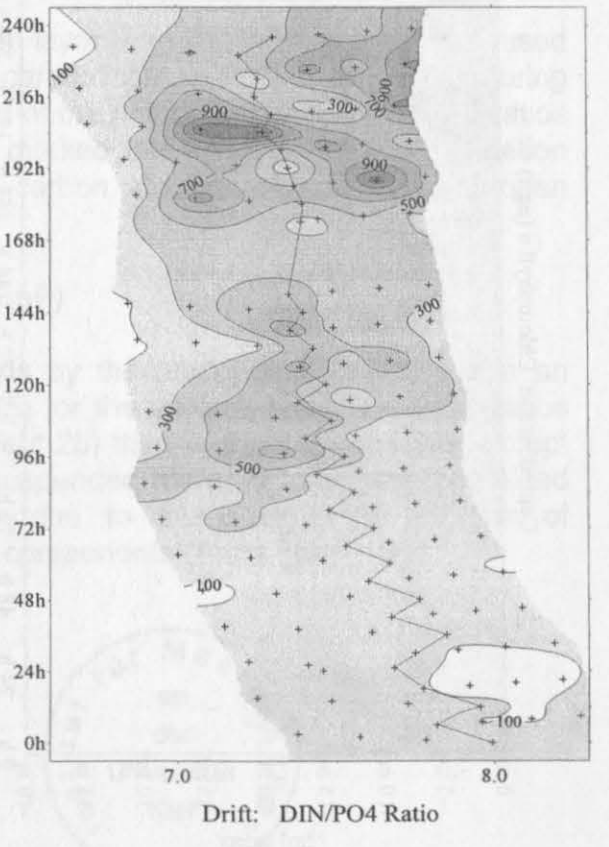


Fig. 89

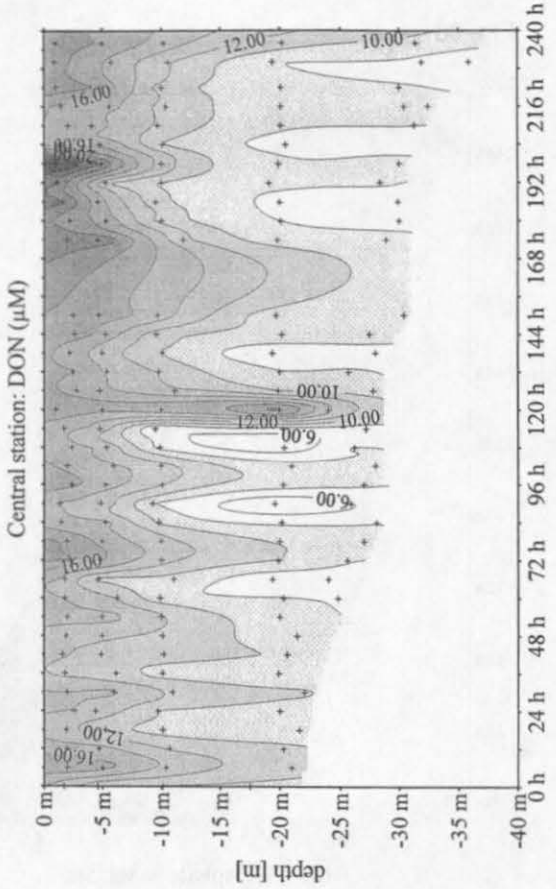


Fig. 90

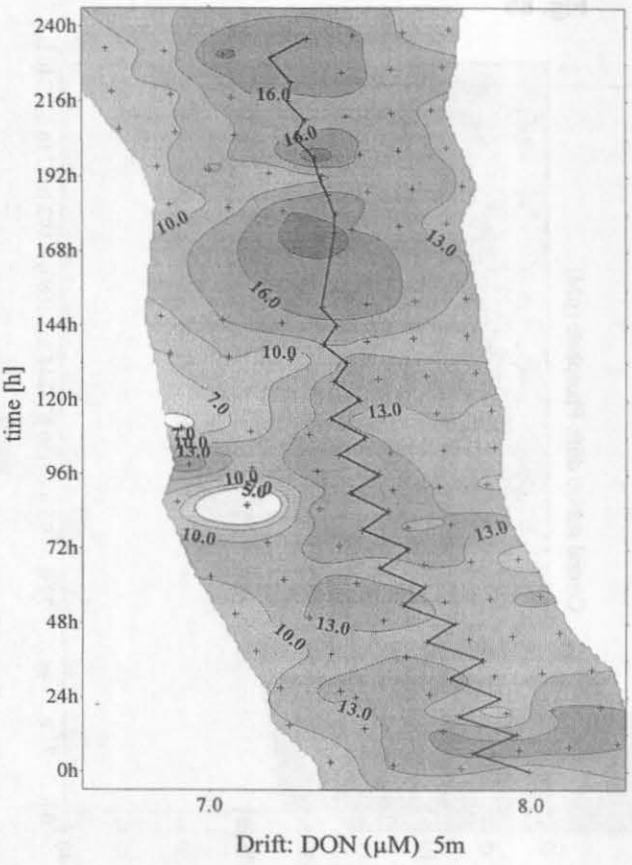


Fig. 91

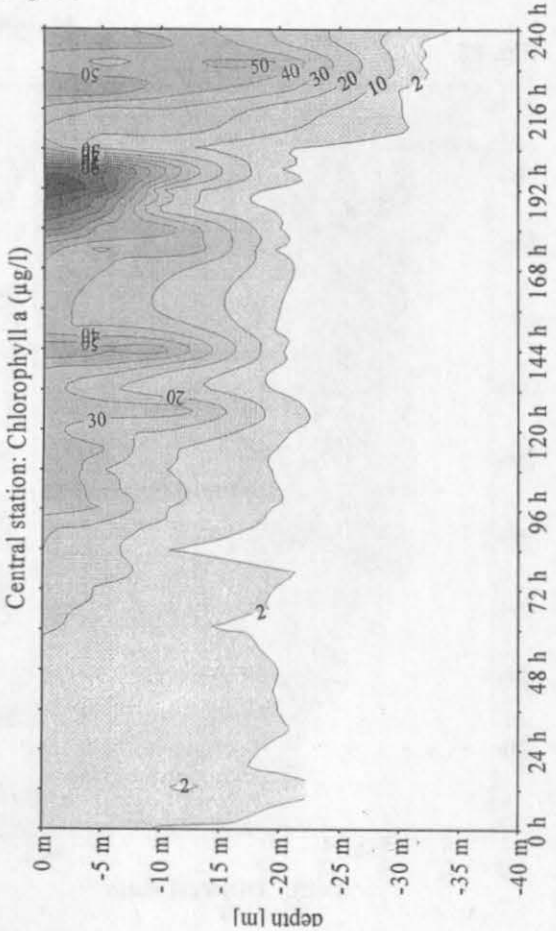
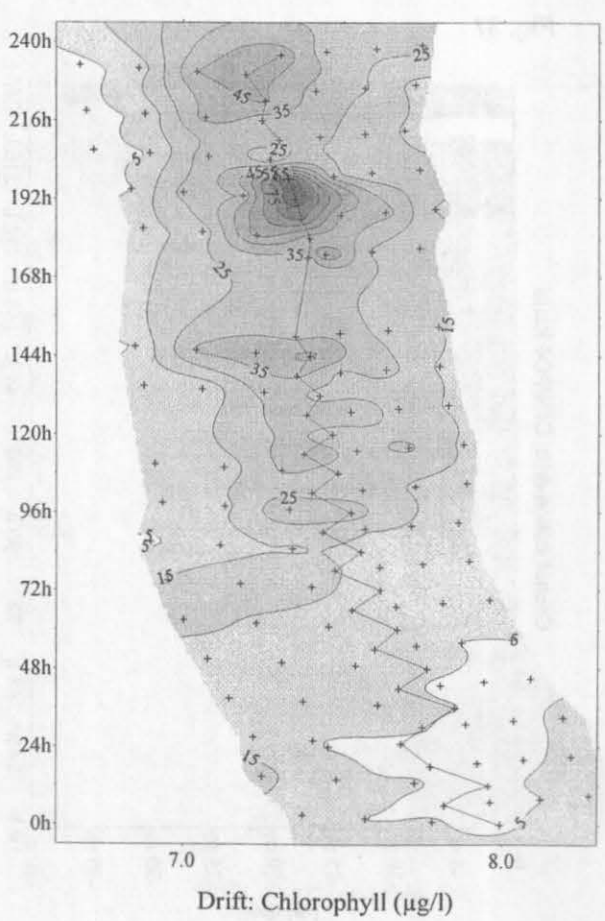


Fig. 92



Particulate carbon (pC), nitrogen (pN) and phosphorus (pP)

Initial surface values of pC (measured by flash-combustion) of around 25 - 30 µM pC rose to a maximum between 120 and 180 µM at 180 - 216 h (Fig. 94). This increase became most evident for the surface layer due to its high phototrophic activity. No clear trend developed in layers below 10 m at the central station (Fig. 93). An increase of pN was monitored (especially at the surface (Fig. 95, 96). Values increased from < 5 µM pN to > 20 µM pN. Concentrations of pP also increased over time (Fig. 97). Upper layer values below 0.3 µM rose to maximum values above 0.8 µM over time. Bottom values were generally lower than surface values, except for an initital maximum of 0.65 µM pP. Resuspension of settled material in the turbitity zone of the Elbe river may have occurred in this area, since this local maximum was detected likewise for pC and pN. A loss of organic material out of the water column towards the bottom is less likely for the beginning bloom situation.

e) Ratios of particulate components

Particulate carbon to nitrogen ratio (pC:pN)

Molar pC:pN ratios displayed no strong development over time (Fig. 100). Initial ratios were especially high (>10) at the easternmost station elevated due to turbidity and then dropped to values between 5.5 to 6. At the central station initial ratios of around 7 were observed, which decreased to ratios of about 6. Ratios < 6 were found for the time in between the start and end of the drift. A similar range of pC:pN ratios in the euphotic zone was observed by Slawyk et al. (1978) with ratios of 5.4 - 9.1 in the northwest African upwelling area.
Slightly elevated pC:pN (11 to < 7) in the bottom layer (Fig. 99) may have been caused by a faster recycling of nitrogen compared to carbon compounds. Lower ratios during the drift indicated the exponential growth phase of the phytoplankton, while rising ratios towards the end of the investigation possibly marked the transition of the population towards stationary phase with an increased carbon storage compared to nitrogen uptake.

Particulate nitrogen to phosphorus ratio (pN:pP)

Continuous assimilation of nitrogen compounds by the phytoplankton resulted in an increase of pN:pP over time (< 25 to above 45) for the surface layer (Fig 98). Ratios were generally lower in the bottom (< 15 to about 25) than in the surface layer, except for a few local maxima above 45. Locally resuspended material may have contained overproportionally high amounts of nitrogen due to a faster remineralization of phosphorus components compared to nitrogen components (Antia et al., 1963).

Fig. 93

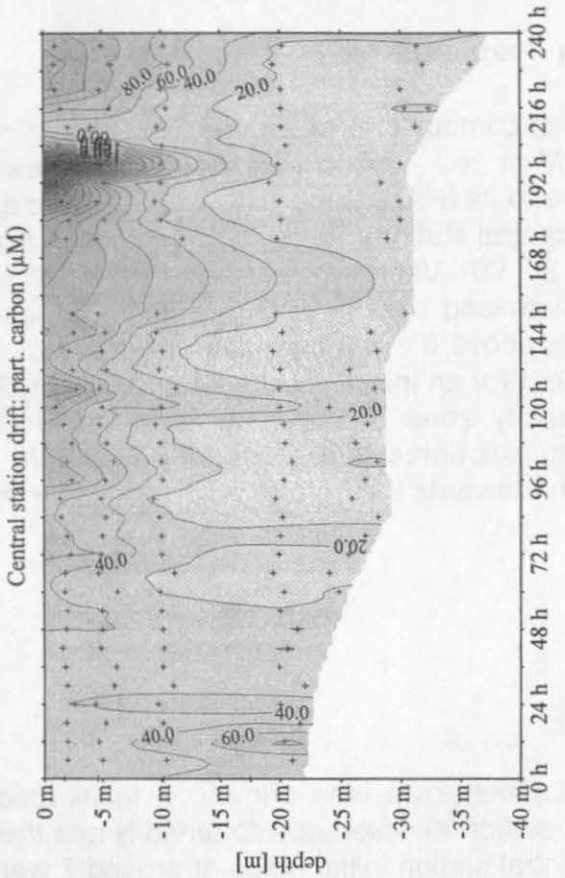
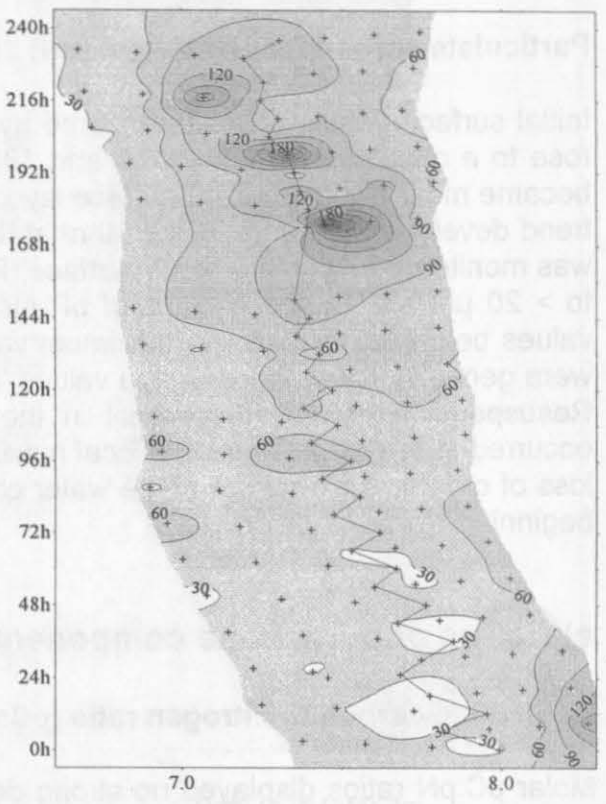


Fig. 94



Drift: part. carbon (µM) 5 m

Fig. 95

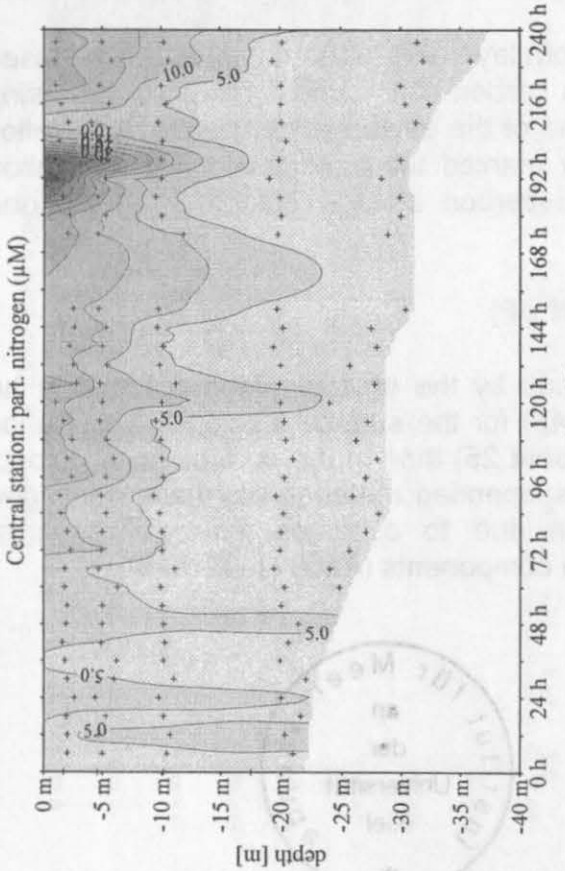
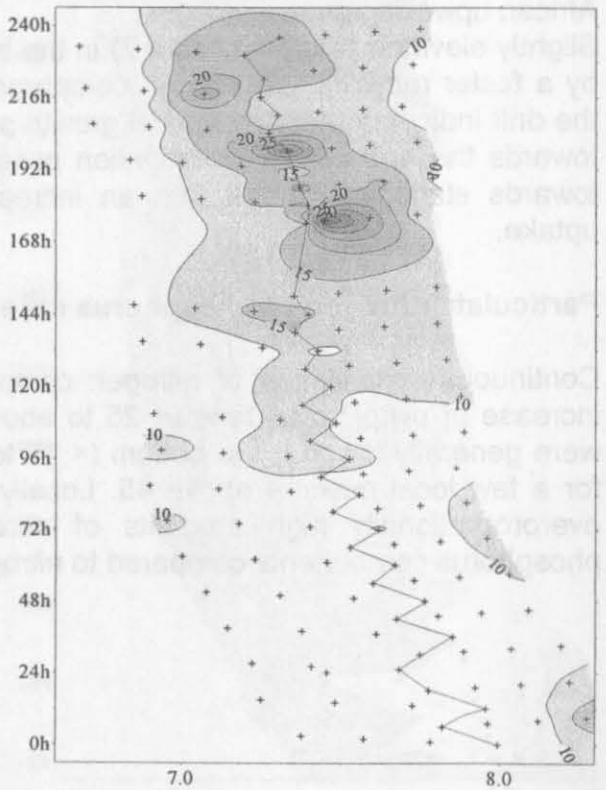


Fig. 96



Drift: part. nitrogen (µM) 5 m

Fig. 97

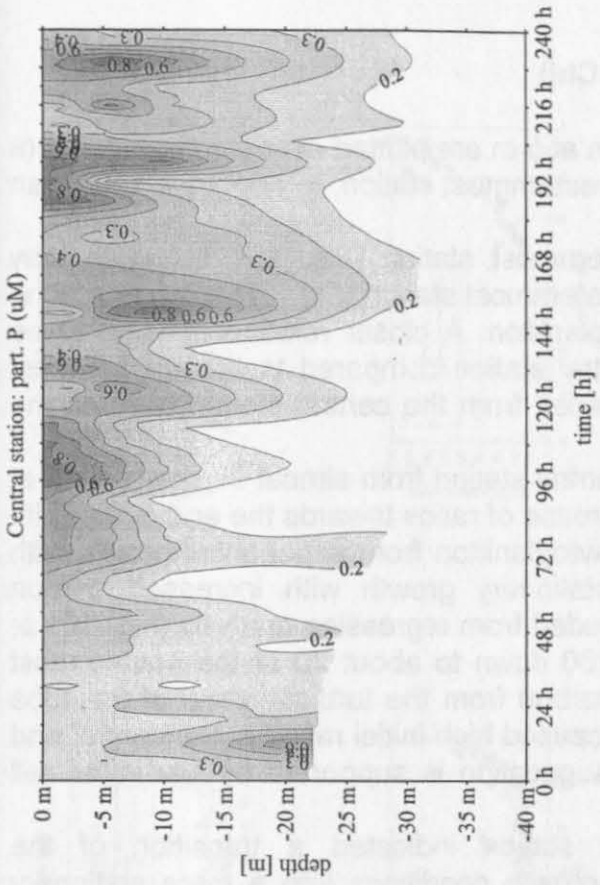


Fig. 98

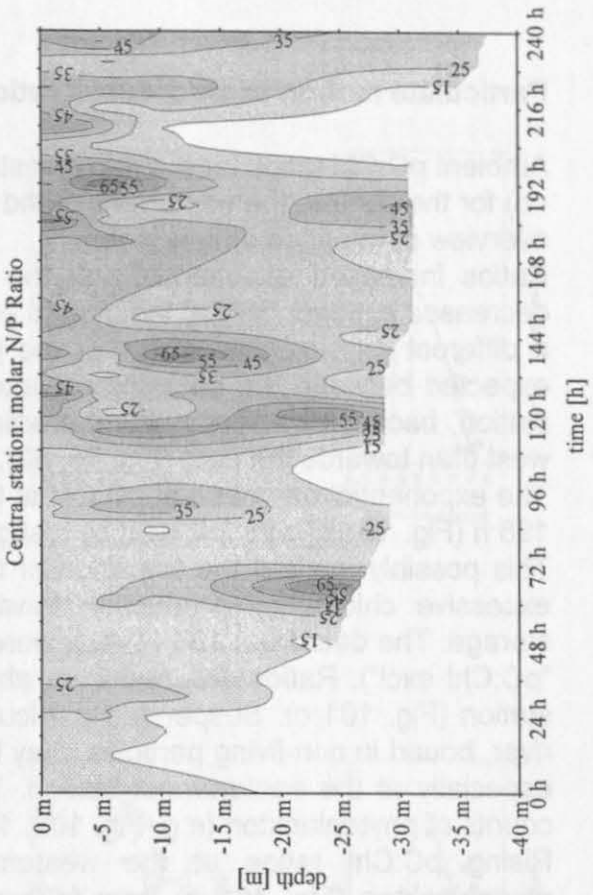


Fig. 99

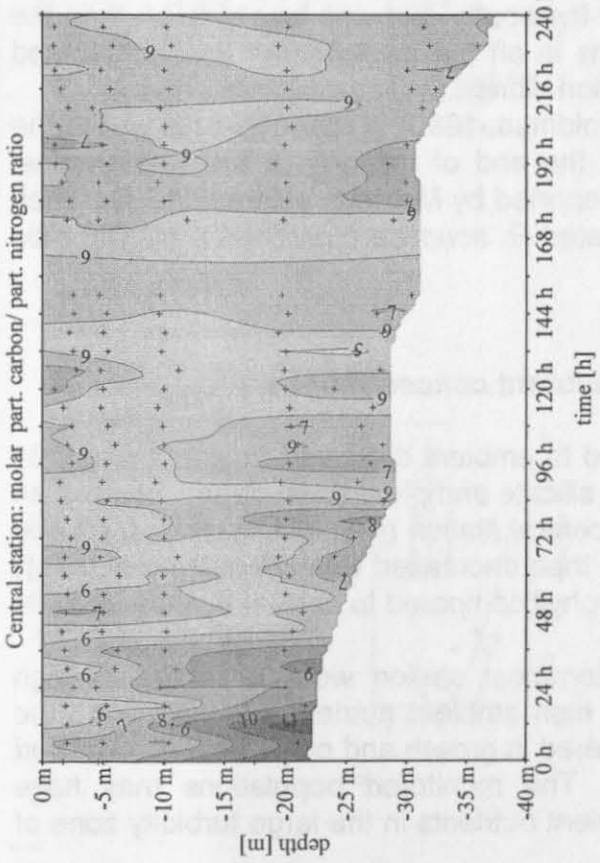
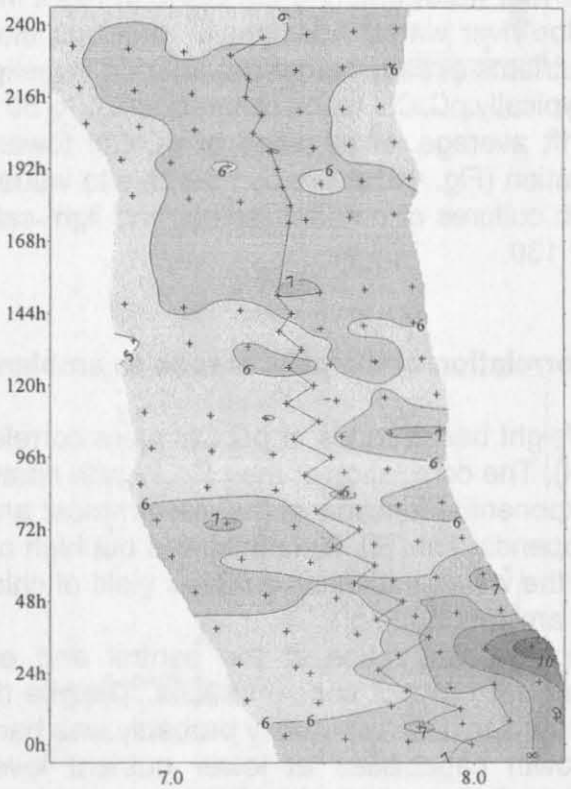


Fig. 100



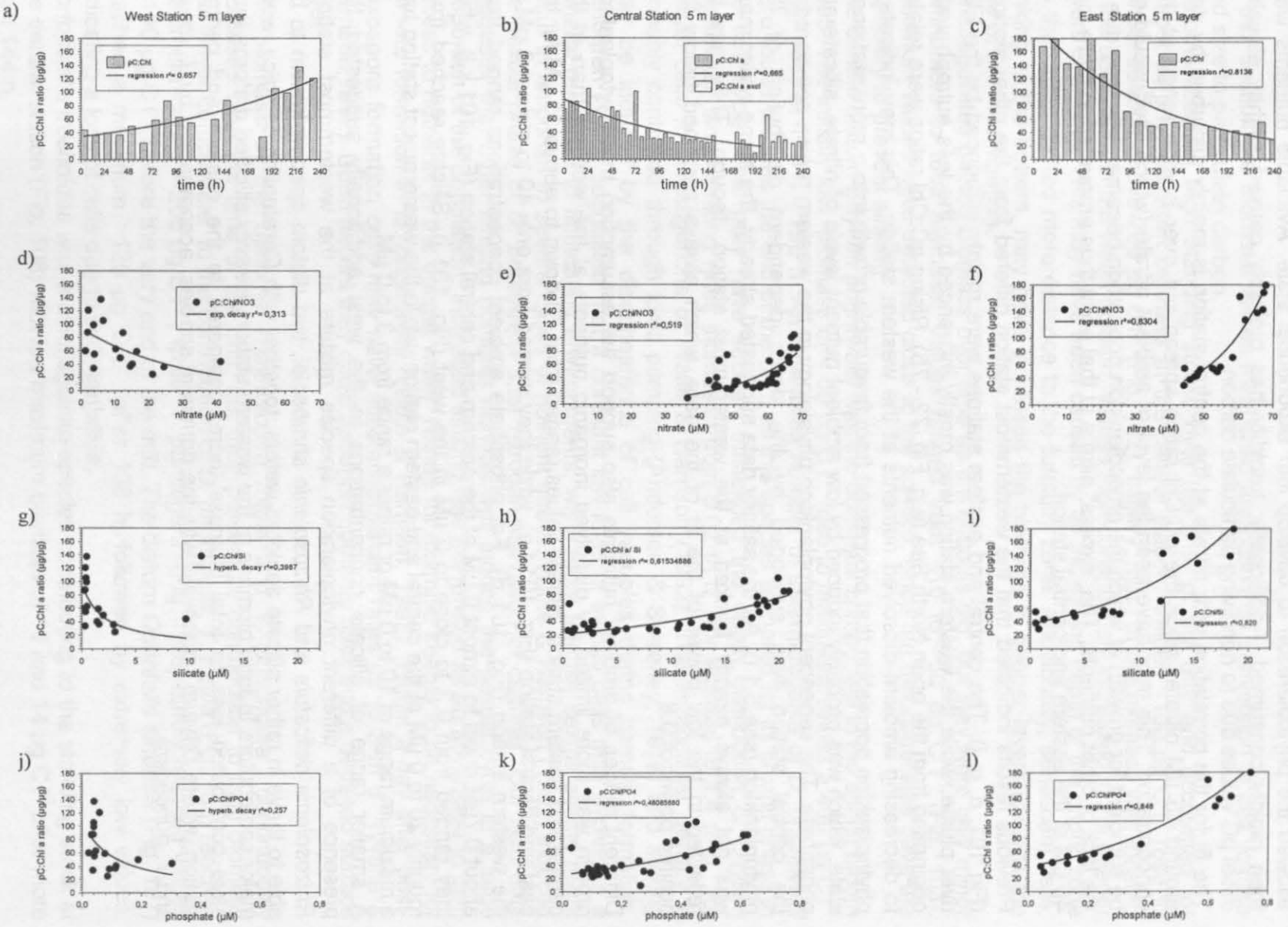
Particulate carbon to chlorophyll ratio (pC:Chl)

Ambient pC:Chl ratios for the drift investigation at 5 m are plotted over time in Fig. 101(a - c) for the central, the easternmost and the westernmost station. In appendix Tab. D an overview of the fitted data is given.
Ratios increased exponentially at the westernmost station (Fig. 101 a), while they decreased exponentially at the central and easternmost station (Fig. 101 b, c), indicating a different physiological status of the phytoplankton. A closer relationship had to be expected between the easternmost and central station compared to the westernmost station, because steeper nutrient gradients faced from the central station towards the west than towards the east (Fig. 78, 80).
The exponential decrease of pC:Chl at the central station from almost 90 down to 25 at 198 h (Fig. 101 b) was followed by a slight increase of ratios towards the end of the drift. This possibly marked the transition of the phytoplankton from exponential growth with excessive chlorophyll production towards stationary growth with increased carbon storage. The data from 198 - 240 h were excluded from regression analysis (Fig. 101 b; "pC:Chl excl"). Ratios dropped from above 180 down to about 30 at the easternmost station (Fig. 101 c). Suspended particulate carbon from the turbidity zone of the Elbe river, bound in non-living particles, may have caused high initial ratios at the central and especially at the easternmost station. This suggestion is supported by low initial cell counts of phytoplankton (e.g. Fig. 102, 103).
Rising pC:Chl ratios at the westernmost station indicated a transition of the phytoplankton (Fig. 101 a) from favourable growth conditions into a more stationary state. Increased carbon storage may have been induced by strong nutrient limitation at the start of the drift already. Less nutrients may have been available, since the coastal current water entering the German Bight from the south-west was less eutroph than the Elbe river water. Additionally, previous blooms in off the East Frisian Isles consumed nutrients already before the the drift investigation started.
Typically pC:Chl ratios range from 25 to 50 (Goldman, 1980), a range that fits well to the drift average. High ratios of pC:Chl towards the end of the drift at the westernmost station (Fig. 101a) are comparable to values reported by Moore & Villareal (1996). Their lab cultures of nutrient replete and light-saturated *R. acuminata* reached a pC:Chl ratio of 130.

Correlation of the pC:Chl ratio to ambient nutrient concentrations

Weight based ratios of pC:Chl were correlated to ambient dissolved nutrients (Fig. 101 d-l). The correlation of the pC:Chl with nitrate, silicate and phosphate clearly followed an exponential function at the easternmost and central station (Fig. 101, e, h, k, f, i, l and appendix Tab. E). Ratios started out high and then decreased with decreasing nutrients in the water, indicating a higher yield of chlorophyll compared to carbon by consumption of ambient nutrients.
High pC:Chl ratios at the central and easternmost station were observed at high ambient nutrient concentrations. Despite the high ambient nutrient concentrations the phytoplankton community probably was hampered in growth and only reached improved growth capabilities at lower nutrient levels. The monitored populations may have originally been limited by light and not by ambient nutrients in the large turbidity zone of

Fig. 101


a)
West Station 5 m layer
pC:Chl
regression r²= 0.657
pC:Chl a ratio (µg/µg)
time (h)
b)
Central Station 5 m layer
pC:Chl a
regression r²=0,665
pC:Chl a excl
pC:Chl a ratio (µg/µg)
time (h)
c)
East Station 5 m layer
pC:Chl
regression r²=0,8136
pC:Chl a ratio (µg/µg)
time (h)
d)
pC:Chl/NO3
exp. decay r²= 0,313
pC:Chl a ratio (µg/µg)
nitrate (µM)
e)
pC:Chl/NO3
regression r²=0,519
pC:Chl a ratio (µg/µg)
nitrate (µM)
f)
pC:Chl/NO3
regression r²=0,8304
pC:Chl a ratio (µg/µg)
nitrate (µM)
g)
pC:Chl/Si
hyperb. decay r²=0,3987
pC:Chl a ratio (µg/µg)
silicate (µM)
h)
pC:Chl a/ Si
regression r²= 0,61534686
pC:Chl a ratio (µg/µg)
silicate (µM)
i)
pC:Chl/Si
regression r²=0,820
pC:Chl a ratio (µg/µg)
silicate (µM)
j)
pC:Chl/PO4
hyperb. decay r²=0,257
pC:Chl a ratio (µg/µg)
phosphate (µM)
k)
pC:Chl/PO4
regression r²=0,48085680
pC:Chl a ratio (µg/µg)
phosphate (µM)
l)
pC:Chl/PO4
regression r²=0,848
pC:Chl a ratio (µg/µg)
phosphate (µM)

the Elbe river. With increasing distance to the river mouth light conditions improved and allowed the phytoplankton to develop into exponential state. Available nutrients were then rapidly consumed. Additionally, turbidity has probably caused slightly elevated initial pC values due to non-living particulate carbon.
The fit for the correlation with nitrate at the central station is mainly disturbed by data around 45 µM nitrate, since the pC:Chl ratios spread out over a wide range at that concentration. This may have been the level of ambient nitrate (which itself would still be sufficient for growth) at which the phytoplankton population became stationary due to the lack of other nutrients. The "excess" nitrate at that point thus amounted to more than 40 µM at the eastern and central station.

Previous results indicated that the westernmost station differed from the other stations (Fig 101, d, g, j). The central and eastern stations were mainly influenced by the Elbe river plume, while the western station was mostly influenced by the less eutroph water originating from the open North Sea (e.g. Fig. 72 - 76). Rising pC:Chl ratios were related to decreasing ambient dissolved nutrients at the western station. This may indicate a phytoplankton population that progressed from favourable growth into a more stationary state, which was probably induced by low ambient nutrient levels of nitrate, silicate and phosphate. The senescent phytoplankton physiology in the western region compared to the central station was supported by the depth dependent distribution of the phytoplankton (see 5.1.f). As the salinity data suggested already, the same water mass was not always exactly tracked at the westernmost station, though. This may be reflected in the low power of the fit of the data, which always remained below the desired power of 0.8.

Different ranges of ambient nutrients also support the assumption that phytoplankton growth was more limited by dissolved inorganic nutrients at the western than at the central and eastern station. Nitrate values ranged from 70 down to above 35 µM for the east and central station (Fig. 101 f,e), while they ranged from only 40 to almost 0 µM at the western station (Fig. 101 d). For phosphate ambient concentrations ranged from about 0.7µM down to almost 0 µM at the eastern and central station (Fig. 101 k,l), while they ranged from 0.3 to close to 0 µM in the west (Fig. 101 j). Silicate reached from roughly 20 to 0 µM at the central and eastern station, while the westernmost station had a maximum range of 10 to 0 µM or rather a range from 3 to 0 µM.
A smaller range of silicate concentrations in the west additionally suggested the presence of a different phytoplankton species mixture at the westernmost station. *Rhizosolenia delicatula* and *Rhizosolenia shrubsolei*, two diatom species known to be able to thrive in rather silicate depleted waters, together with *Cerataulina pelagica*, were major contributors to total biomass at the western station. Heavily silicified diatoms thus have contributed less to total biomass there, compared to the eastern and central station, where *Ditylum brightwellii* was the dominant species, accompanied by *T. rotula* and *T. punctigera*.

f) Phytoplankton

In this section the biomass values mentioned are based on conversion of cell volume and size to particulate carbon.
Diatoms reached high standing stocks over the time of the drift and accounted for almost all phytoplankton biomass at the central station. Values <100 µg C l^{-1} rose to concentrations above 700 µg C l^{-1} (Fig. 102). Initially, most of the biomass was located in the upper 5 m of the water column. Values then continuously increased in the deeper layers over time. This may have been caused by an increasing depth of the photic zone as the drifter gained more distance to the turbidity zone. Additionally, senescent cells, sinking to the bottom, may have increased the biomass in deeper layers towards the end of the investigation.
Dinoflagellates gained biomass over time as the diatoms did, but they were only minor contributors to total biomass. Values ranged from <10 to >50 µg C l^{-1} (Fig. 103). Maximum values were detected close to the surface, since the dinoflagellates have the capability to prevent sinking.
The centric diatom *Ditylum brightwellii* was the dominant component in the spring bloom 1995. The initially low biomass of < 50 µg C l^{-1} rose to maximum values > 400 µg C l^{-1} (Fig. 104) at 174 h - 198 h. An increasing number of spermatogonia of *D. brightwellii* were found towards the end of the drift, as this species prepared for its sexual phase in the cell cycle. This may have strongly influenced the depth distribution of *Ditylum brightwellii*, since sinking rates increased from 0.02 m d^{-1} for asexual to 1.4 m d^{-1} for sexual cells in investigations of Waite & Harrison (1992). The intracellular density is probably controlled through ionic pumping (Anderson & Sweeney, 1978) and sinking may be induced by the disappearance of cell vacuoles during gamete formation. Sandgren (1981) suggested that a constant low level of sexual cells may evolve as a general response to fluctuating environments, while more intense sexual events might occur in response to severe cases of nutrient stress. Waite & Harrison (1992) induced the sexual phase of *D. brightwellii* after nitrogen starvation of cultures. Our field data suggests, that other limiting nutrients may as well induce the sexual cycle in a large proportion of the population. Increased sinking was interpreted as an advantage to gain access to nutrients in the deeper water. Nitrate for example seems to be necessary for gamete formation in *D. brightwellii* (Waite & Harrison, 1992). Within a day after post-auxospore formation cells may have substantial ascent rates up to 3 m d^{-1} (Waite & Harrison,1992). Upon ascent they could transport nutrients back into a depleted surface layer.

The biomass of the diatoms *Thalassiosira rotula* and *T. punctigera* continuously increased over the time of the drift, but their percentual contribution to total biomass was never comparable to the contribution of *D. brightwellii*. *T. rotula* (Fig. 105) reached maximum values > 200 µg C l^{-1}, while *T. punctigera* (Fig. 106) hardly reached values > 100 µg C l^{-1} before the very end of the drift. The diatom *Odontella sinensis* (Fig. 107) reached a maximum >120 µg C l^{-1} after 198 h, followed by extremely low values, indicating a loss of cells due to sedimentation.
Scrippsiella trochoidea was a dinoflagellate species contributing to the standing stock at the central station (Fig. 108) with low maximum biomass of 11 and 14 µg C l^{-1} after more than 144 h.

Fig. 102

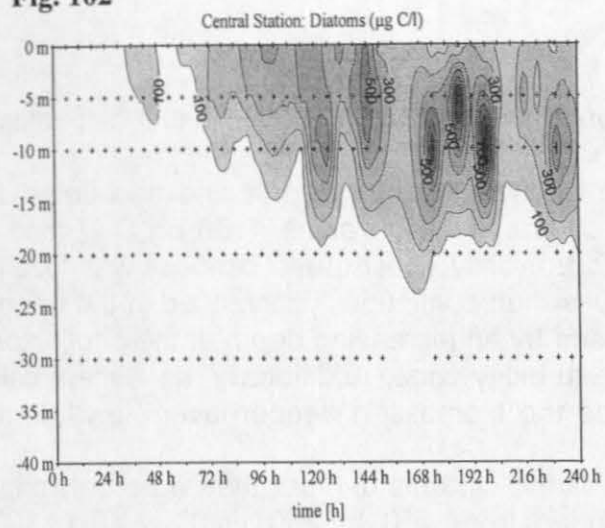


Fig. 103

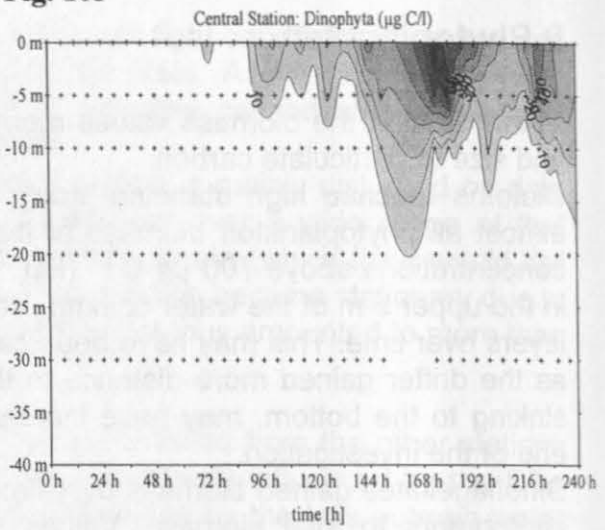


Fig. 104

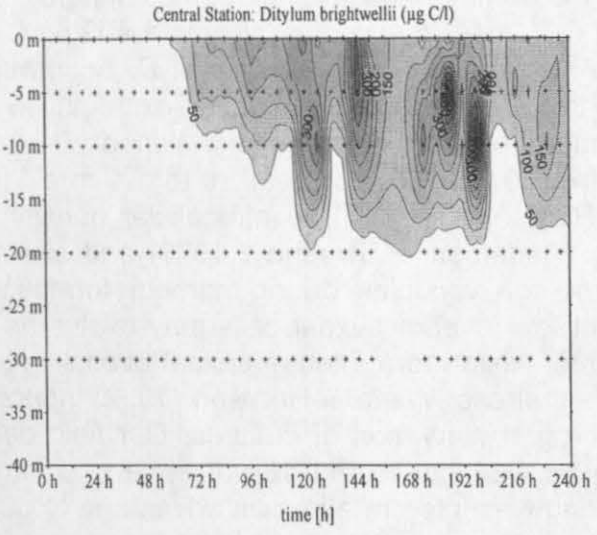


Fig. 105

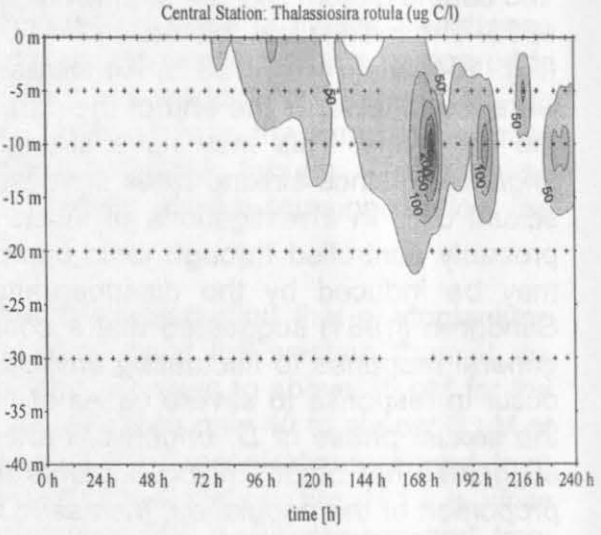


Fig. 106

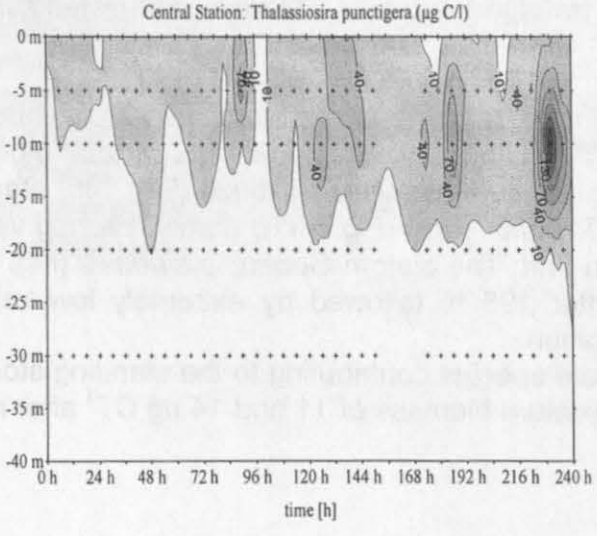


Fig. 107

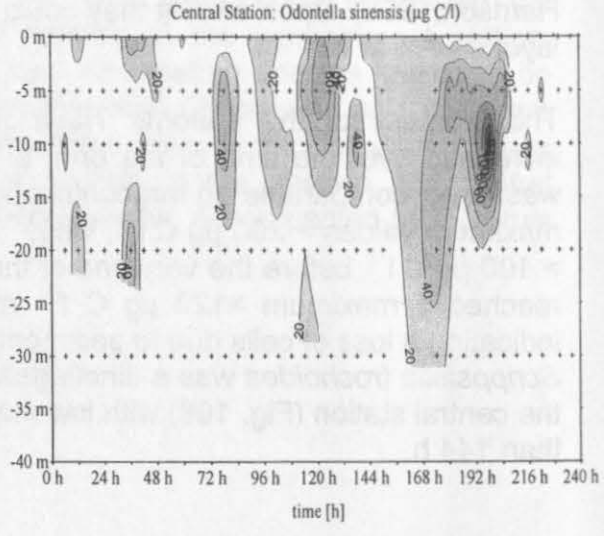
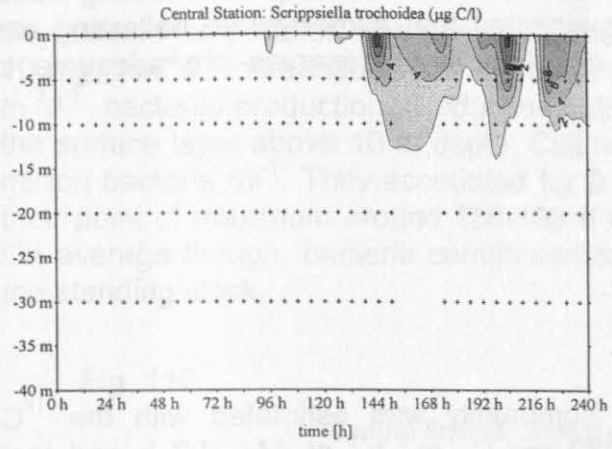


Fig. 108



Diatoms dominated the total phytoplankton biomass also at the westernmost station. Values of about 80 µg C l^{-1} at the surface rose to > 300 µg C l^{-1} at 121 h. A continuous decrease to values around 35 µg C l^{-1} followed until the end of the drift. Biomass tended to be elevated below the surface layer. This suggests that a large proportion of senescent and sinking cells was lost from the upper layer over the time.

Dinoflagellates, ranging from 4 to 11 µg C l^{-1}, were not important for the total standing stock, but they shared their time of maximum biomass and the subsequent overall decrease after 121h with the diatoms. Contrasting to the diatoms, though, they clearly displayed highest stock in the upper layer and decreasing values towards the bottom, due to their swimming capability.

Ditylum brightwellii, the most important species of the central station, lost significance at the westernmost station. Biomass values were mostly < 5 µg C l^{-1} with a maximum around 35 µg C l^{-1} at 154 h, and a subsequent decrease. Most important diatoms at the western station were the weakly silicified species *Rhizosolenia delicatula* and *Rhizosolenia shrubsolei*. *R. delicatula* reached a surface maximum of about 220 µg C l^{-1} at 121h and decreased thereafter, while *R. shrubsolei* reached a surface maximum of 130 µg C l^{-1} already at 97 h and decreased to 2 µg C l^{-1}over time. Especially *R. delicatula* displayed a depth-dependent distribution with elevated values >300 µg C l^{-1} in the deeper water column compared to the surface, causing the overall depth-distribution of diatom biomass mentioned before. Maximum values were reached below 10 m at 97 h already, decreasing continuously thereafter. *Cerataulina pelagica*, another diatom, reached a maximum of 140 µg C l^{-1} at the surface and decreased to about 15 µg C l^{-1} afterwards. *Thalassiosira punctigera* reached values between 8 and 17 µg C l^{-1} and decreased towards 0 µg C l^{-1}. *Thalassiosira rotula* did not display any consecutive trend and contributed extremely low biomass varying between 1 - 6 µg C l^{-1} at the surface. The contribution of both *Thalassiosira* species to total biomass thus lost importance at the westernmost station compared to the central station.

Rhizosolenia species may indicate an increased recycling of nutrients at the westerly station. Cells possibly accumulate nutrients in the deeper layers and return to the surface via buoyancy reversal. Recent evidence supports the hypothesis that at least mat forming oceanic *Rhizosolenia* species use buoyancy reversals to undergo vertical migrations, allowing them to exploit sources of nutrients in deeper water (Villareal et al., 1993). Solitary *Rhizosolenia* chains may also transport new nitrogen to the euphotic zone in oligotrophic seas (Moore & Villareal, 1996). Retention of *R. debyana* in the surface layer is dependent upon several physiological properties of the cells, such as silification, size, and cell sap density (Villareal, 1988). Comparable to the discussed ascent of *D. brightwellii* post-auxospore cells (Waite & Harrison,1992), an ascension by post-auxospore cells of *Rhizosolenia setigera* was observed (Smayda & Boleyn,1966). Rhizosolenia mats observed by Villareal et al. (1993) had ascent rates of up to

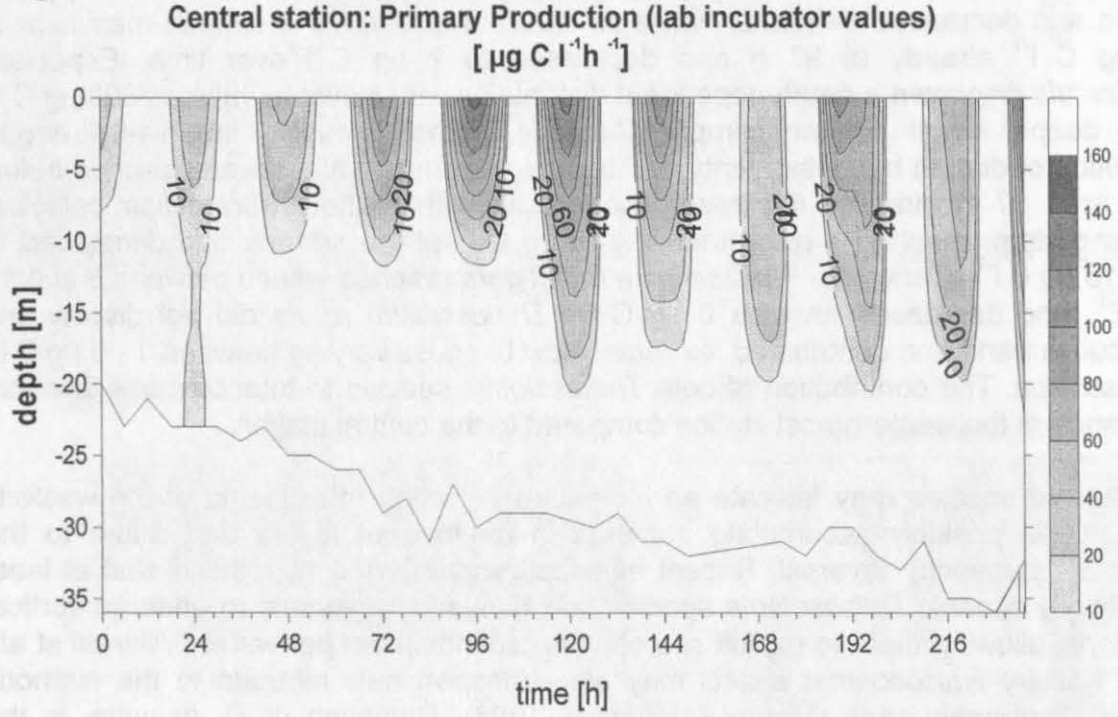
6.4 m h^{-1}. Villareal et al.(1993) suggested that nitrogen stress is related to buoyancy. Ascending mats had higher nitrate concentrations in their cell sap than sinking mats. Calculations of Moore & Villareal (1996) suggested that carbohydrate ballasting can account for sufficient buoyancy changes and that these reserves are adequate to support nitrate uptake in the dark.

5.2. Rates

a) Primary production

Primary production of the phytoplankton community was estimated with the ^{14}C-technique. It reached a maximum with >130 mg C m^{-3} h^{-1} at 144-192 h and then dropped to values between 70 - 90 mg C m^{-3} h^{-1} towards the end of the drift (Fig. 109). Production rates > 10 mg C m^{-3} h^{-1} were observed in a depth of 10 - 15 m most of the time. The fraction of phytoplankton <20 µm accounted for less than 40% (standarddeviation 27%) on overall average to total primary production during the drift investigation.

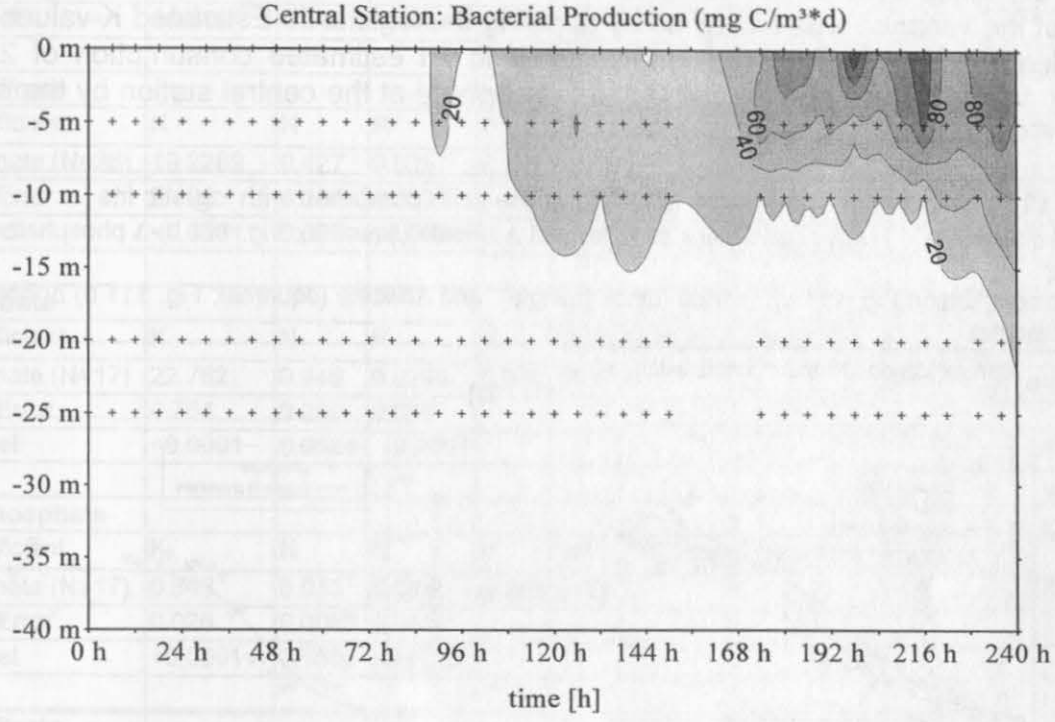
Fig. 109



b) Bacterial production

Thymidine incorporation was used as a measure of bacterial production. Values below 10 mg C $m^{-3}d^{-1}$ increased over the time of the drift to maximum values of > 100 mg C $m^{-3}d^{-1}$ bacterial production. Production values above 20 mg C $m^{-3}d^{-1}$ were confined to the surface layer above 10 m depth. Cell numbers ranged from 0.5 to maxima with 3.5 million bacteria ml^{-1}. They accounted for 0 to > 50 µg C l^{-1} standing stock and shared their point of maximum around 186-198 h with the highest stock of diatoms (Fig. 102). On average though, bacteria contributed to less than 10% (standarddeviation 11%) of the standing stock.

Fig. 110



5.3. Estimates of nutrient consumption and POM production

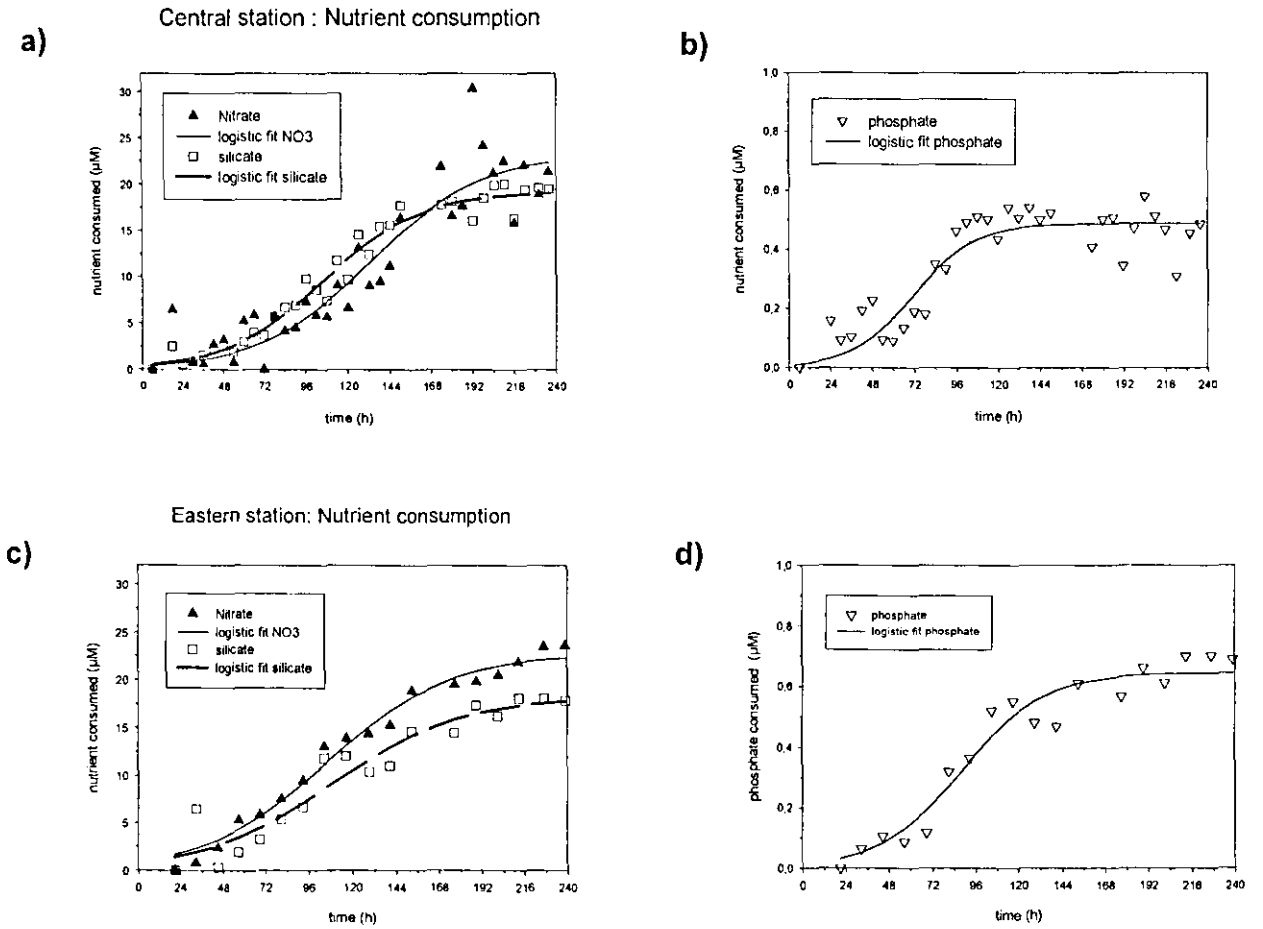
Successful drift investigations allow for the calculation of local net turnover in a defined water mass at a certain depth. The results for the drift investigation 1995 were conclusive for the surface layer and demonstrated that this layer was successfully tracked for the central station. The development of a phytoplankton community from exponential growth to increasing senescence state was observed for the upper layer.
Biological status of the western station differed from the central and eastern station, due to the prominent frontal structuring in this region. Nutrient consumption and gain in POM over ten days was calculated, resulting in an optimized evaluation of processes taking place in the field during spring season, compared to the broad estimates of the grid surveys. However, the results need to be evaluated and applied carefully, too, since again grazing and sedimentation losses of POM were not considered. The consumption of inorganic nutrients at the central station was comparable to the consumption at the

easternmost station. Larger differences were found for the produced POM. Factors other than the pure phytoplankton bloom had sufficient strength to disturb the pattern of POM measured at the easternmost station. Increased mixing and turbidity for instance, may have had a strong influence at the shallower easternmost station.

Dissolved inorganic nutrients

The depletion of dissolved nutrients (concentration difference) over time was calculated by defining 6 hours runtime of the drift as zero consumption. Values at 236 hours were defined as final depletion. Consumption of nitrate at the central station was plotted over time and calculated with a logistic fit (Fig. 111 a), which explained 88% of the variance. In the same graph the consumption of silicate over time was combined with a logistic fit, which explained 97% of the variance. For the consumption of phosphate (Fig. 111 b) 85 % of the variance was explained by applying the logistic fit. Estimated K-values were considered as being significant and resulted in an estimated consumption of 23 µM nitrate, 19 µM silicate and around 0,5 µM phosphate at the central station by the end of the drift (Tab. 2).

Fig. 111: Nutrients consumed over the time of the drift combined with logistic fits
Central station Fig. 111a)Δ nitrate(black triangle) and Δ silicate (squares); Fig. 111 b) Δ phosphate (open triangle)
Easternmost station Fig. 111 c) Δnitrate (black triangle) and Δsilicate (squares); Fig. 111 d) Δphosphate (open triangle)



Tab. 2: **Logistic fit of the consumption of dissolved inorganic nutrients at the central and eastern station for the surface layer :** central station (C), easternmost station (E), calculated consumption doubling times (CDT) based on R- estimates; listed R values are based on hours.
Model: $f=K/(1+((K-N)/N)*euler^{(-R*x)})$; software applied SigmaPlot

C: nitrate								
Coefficient	K	N	R	r^2	Std E Estimate	Power (0.05)	$F_{0.05\,(2,33)}$	CDT
Estimate (N=36)	23.238	0.356	0.0315	0.883	3.083	1	125	22 h
Std. Error	2.057	0.268	0.0067					
p-level	<0.0001	0.193	<0.0001					
C: phosphate								
Coefficient	K	N	R	r^2	Std E Estimate	Power (0.05)	$F_{0.05\,(2,33)}$	CDT
Estimate (N=36)	0.489	0.009	0.0562	0.864	0.075	1	105	12.3 h
Std. Error	0.020	0.007	0.0121					
p-level	<0.0001	0.242	<0.0001					
C: silicate								
Coefficient	K	N	R	r^2	Std E Estimate	Power (0.05)	$F_{0.05\,(2,33)}$	CDT
Estimate (N=36)	19.2289	0.427	0.0357	0.973	11.985	1	614	19.4 h
Std. Error	0.490	0.126	0.0031					
p-level	<0.0001	0.002	<0.0001					
E: nitrate								
Coefficient	K	N	R	r^2	Std E Estimate	Power (0.05)	$F_{0.05\,(2,15)}$	CDT
Estimate (N=17)	22.762	0.946	0.0296	0.980	11.519	1	376	23.4 h
Std. Error	0.754	0.259	0.003					
p-level	<0.0001	0.0024	<0.0001					
E: phosphate								
Coefficient	K	N	R	r^2	Std E Estimate	Power (0.05)	$F_{0.05(2,15)}$	CDT
Estimate (N=17)	0.646	0.013	0.044	0.945	0.0603	1	129	15.8
Std. Error	0.026	0.0086	0.0077					
p-level	<0.0001	0.1507	<0.0001					
E: silicate								
Coefficient	K	N	R	r^2	Std E Estimate	Power (0.05)	$F_{0.05(2,15)}$	CDT
Estimate (N=17)	18.220	0.798	0.0283	0.918	19.238	1	84	24.5
Std. Error	13.625	0.448	0.006					
p-level	<0.0001	0.096	0.0003					

Even though we believe to have followed exactly the same water mass only for the central station, data at the easternmost station produced comparably good results for the consumption of dissolved nutrients in the 5 m layer. The logistic fit explained more than 90% of the variance for all parameters (Fig. 111 c,111 d). Estimated K values for the easternmost station were comparable to the ones at the central station. A consumption of almost 23 µM nitrate, 18 µM silicate and 0,65 µM phosphate was estimated.

The fit of phosphate consumption over time indicates a long plateau phase for both stations (Fig. 111 b, d), which was reached at about 132 h. At that time neither the data for silicate nor nitrate reach a plateau at those stations (Fig. 111 a, c). Therefore phosphate was assumed to be the strongest limiting factor for the situation monitored during the drift 1995. This assumption is supported by high particulate nitrogen to phosphorus ratios exceeding >45 towards the end of the drift for the surface (Fig. 98).

No proper fit for dissolved inorganic nutrient consumption could be achieved for the westernmost station, but an overall consumption was also monitored there. Samples were probably sometimes drawn from different water masses due to the steep gradients towards the west (see salinity Fig. 72, e.g.). Thus the data did not represent a continuous biological development.

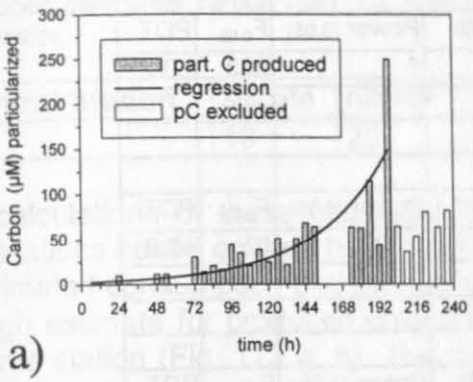
The estimated R values of consumption of dissolved inorganic nutrients were applied to calculate consumption doubling times (comparable to the calculation of generation times, but based on data of consumed nutrients). Note that R values in Tab. 2 are based on an hour. The consumption doubling times (CDT) of 22 and 19.4 hours were comparable for nitrate and silicate at the central station. Phosphate was consumed faster with a CTD of 12.3 hours. Slower CDT of 23.4 and 24.5 h were estimated for nitrate and silicate at the eastern station. Phosphate was consumed faster again with 15.8 h. Fastest uptake of phosphate is probably the result of the well known luxury consumption of this nutrient by phytoplankton. Enhanced turbidity and mixing of the shallow eastern station may have caused slower growth and thus slower CDT for all dissolved nutrients.

b) Particulate organic matter

The continuous reduction of dissolved nutrients in an exponential bloom situation was well described by the applied model functions. It is more difficult to follow the production of POM with models because additional factors like grazing and sinking may have a strong influence on the distribution pattern of POM.
A drop in produced pC, pN and Chl a at 204 h and a consecutive slow rise again (Fig 112 a-d) made a proper fit for produced POM at the central station impossible. Only after exclusion of all data later than 198 h, a good exponential growth fit became possible for all POM data, except for phosphorus. No good fit was achieved for pN and pC data at the easternmost station (Fig. 112 e, f), while a linear regression may be suggested for chlorophyll (Fig. 112 g). Production doubling times were calculated from the estimated coefficients for pN, pC and chlorophyll. The estimated PDT (Tab. 3) were slower than the CDT of the dissolved nutrients. Community growth rate estimates based on biochemical data create a fictitious average. Especially the growth rates estimated from PDT result in net rates, integrating growth and an unknown degree of grazing and/or sedimentation. Additionally, dissolved inorganic nutrients may have been consumed by components other than the phytoplankton, for example bacteria, which were not included in the measurements.

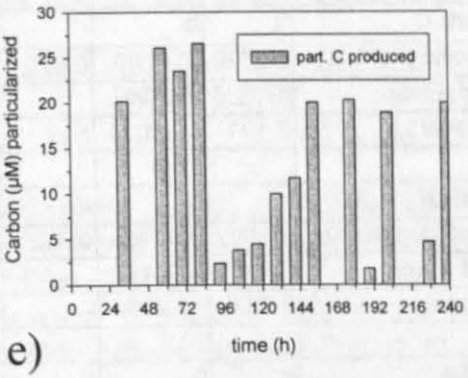
Fig 112: Production of POM during the drift (6 - 198 h)
a) - d) Central Station ; e) - g) Eastern Station
Calculation of newly produced POM with values at 6 hours defined as zero production

Central Station

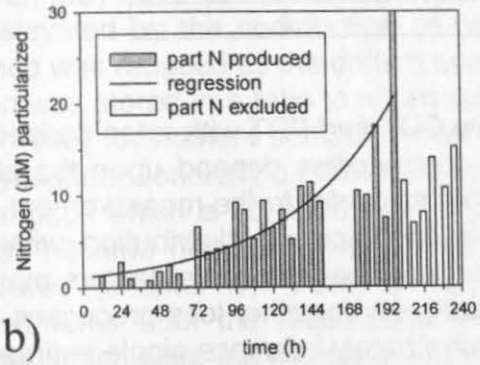


a)

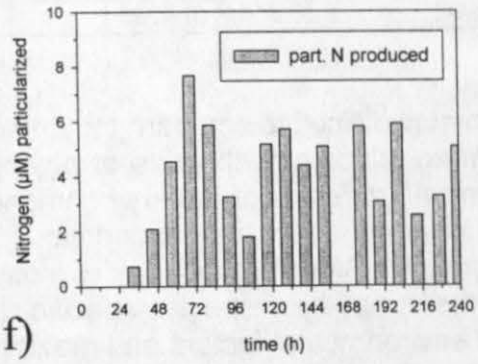
Eastern Station



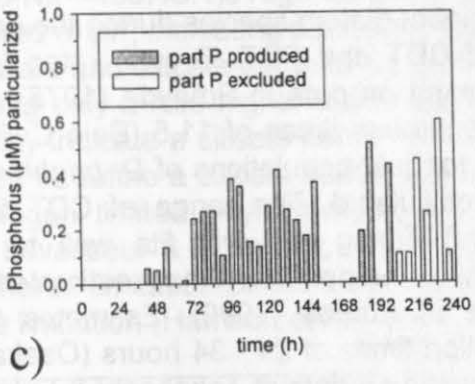
e)



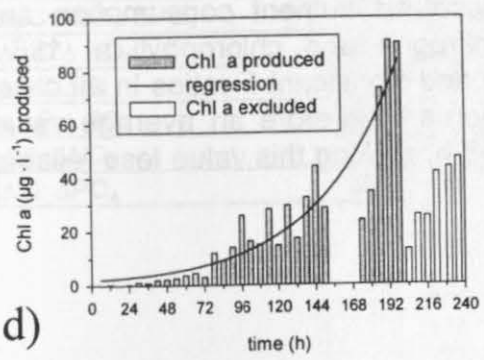
b)



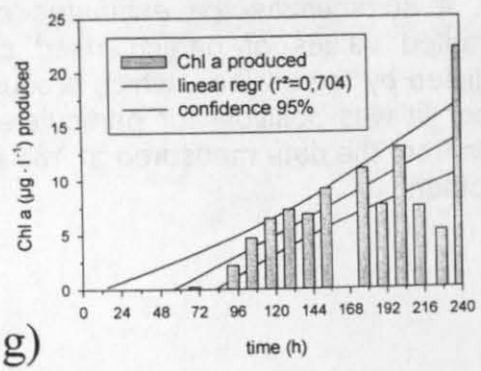
f)



c)



d)



g)

Tab. 3: **Results of fitting POM data for the surface at the central station**
Standard error of the estimate (StdEstimate); standard error of coefficient (Std. Error); F-ratio for alpha = 0.05; model f=a*exp(b*x); PDT = production doubling time in hours; applied software SigmaPlot

part. C	a	b	r^2	StdEstimate	Power (0.05)	$F_{0.05}$	PDT
Coefficient(N=30)	23.639	0.0209	0.675	28.99	1	583	33.2
Std. Error	17.625	0.0040					
p-level	0.191	<0.0001					
part. N	a	b	r^2	Std Estimate	Power (0.05)	$F_{0.05}$	PDT
Coefficient(N=30)	1,1582	0,0145	0,652	4.173	0.999	52	47.8
Std. Error	0,4971	0,0025					
p-level	0,0272	<0,0001					
Chl a	a	b	r^2	Std Estimate	Power (0.05)	$F_{0.05}$	PDT
Coefficient(N=30)	1,8117	0,0194	0,856	9.734	1	166	35.7
Std. Error	0,6921	0,0021					
p-level	0,0141	<0,0001					

It remains difficult to compare the drift community CDT and PDT with rates derived from literature, since growth rates of phytoplankton communities depend upon the physio-chemical properties of the environment at the time and prior to the measurement. They also depend upon the taxonomic composition and biomass distribution within the community. Growth responses of individual species to environmental factors may vary and there may be a species-specific rate of grazing and/or other loss processes. Thus local environmental factors and grazing stress will strongly influence single estimates of community growth rate (Furnas, 1990). Considerable variability exists in the in-situ growth rates reported for phytoplankton species and defined groups, as reviewed in Furnas (1990). *Ditylum brightwellii* was the dominant diatom species during the drift and thus had a major influence on the calculated CDT and PDT. Growth rates for this species are listed in Furnas (1990) and are based on data in Smayda (1975), Rivkin (1986), Paasche (1968), and Baars (1981). Generation times of 11,5 (Baja California) to 26 hours (Chesapeake Bay) were estimated for field populations of *D. brightwellii*. In cultures generation times of 16 hours were calculated. The range of CDT for the dissolved inorganic nutrients (22 -12.3 hours) during the drift fits well to these estimates, while the PDT were generally slower. Generation times estimated from chlorophyll production are given for example in Furnas (1990). Estimates for *D. brightwellii* displayed a large variability. Generation times of 24 - 34 hours (Osaka Bay) and 22 - 240 hours (North Pacific) were listed, based on data of Takahashi & Fukazawa (1982) and Martin et al. (1989).

Tab. 4 summarizes the estimates of the dissolved nutrient consumption and the estimated values of particularised carbon, nitrogen and chlorophyll at 198 h as predicted by regressions, which produced high and significant F-ratios in all cases. No proper fit was possible for particulate phosphorus. Therefore an average value was taken from the data measured at 186 h and 198 h, making this value less reliable than the others.

Tab. 4: Consumed dissolved nutrients and accumulated POM at the central Station for the surface layer

Values in µg l^{-1} for Chl a and in µM for all others; dissolved silicate, nitrate and phosphate values as well as produced particulate carbon (part. C), particulate nitrogen (part. N) and chlorophyll (Chl a) for the central station.

Central Station	silicate	nitrate	phosphate	pC	pN	pP	Chl a
	19	23	0.67	148	21	0.48	84

Ratio calculations of these estimated changes are given in Tab. 5. These and the interpretations based on their height can of course only be as reliable as one considers the estimated consumption and production values to be reliable.

The high estimate for produced chlorophyll is supported by high pC and pN values at the same station (Fig. 112 a, b). The resulting pC:Chl (weight:weight) ratio of 21 may indicate that the phytoplankton has had favourable growth conditions and did not yet accumulate an excessive amount of carbon in the stationary phase. The pC yield, however, may have been underestimated to some extent, since initial values may have been elevated by the contribution of non-living particles from the turbitity zone. This influence was reduced as the drifting buoy gained distance from the Elbe mouth.

Carbon was stored in a ratio to nitrate consumed ($pC:NO_3$=6,4) expected after Redfield et al. (1963) for nutrient sufficient phytoplankton. The ratio for pC:pN with 7 was only slightly higher. Generally a lower ratio of $pC:NO_3$ than pC:pN may indicate some nitrate consumption which is not channeled into particulate nitrogen of the phytoplankton. This process became more evident for nitrate consumption and carbon production in the enclosures (chapter 6). Some phosphate may also be routed into some other compartments than the measured POM ($pP:PO_4$ = 0.7), for example DOP and/or bacteria, which were not completely held back by the filters used for pP analysis.

The ratio of pN:pP of 44 was elevated in favor for nitrogen, compared to the Redfield ratio (C:N:P=106:16:1). High amounts of nitrogen and carbon (308:44:1) were stored compared to pP, indicating a phosphorus limited population towards the end of the drift.

The nitrate and silicate demand for carbon assimilation were comparable with pC:Si of 7.8 being only a little higher than the $pC:NO_3$ of 6.4. The ratio of consumed $Si:NO_3$ of 0.83 may indicate a silicate deficit towards the end of the drift, since ratios below 1 are believed to define a silicate deficit, while ratios above 1 are considered as being typical for nitrogen limited phytoplankton (Parsons et al., 1961; Furnas, 1978; Brzezinski, 1985, Levasseur & Therriault, 1987). The high ratio of $Si:PO_4$ may again indicate the phosphorus limitation of the community, since ratios of $Si:PO_4$ below 3 are given for silicate limitation (Harrison et al.,1977).

Central station surface	Ratio
ΔpC:ΔpN	7:1
ΔpC:ΔpN:ΔpP	308:44:1
$\Delta pC:\Delta NO_3$: ΔPO_4	221:34:1
Δ pC:Δ NO_3	6.4:1
Δ pC:Δ Si	7.8:1
Δ pP:Δ PO_4	0.7:1
$\Delta Si:\Delta NO_3$	0,83:1
$\Delta SI:\Delta PO_4$	28:1

Tab. 5: Ratios of produced POM and consumed nutrient
molar ratios; only for comparison with chlorophyll a weight/weight ratio

Drift estimates and grid estimates can not be compared directly. The grid estimates o depletion of dissolved nutrients in chapter 4 are based on almost 18 days, while the drif took place during only 10 of those days. The system thus had time to develop further ir between the grid samplings number 1 and 8. The water of the starting position of the drifting buoy cannot be tracked directly to its approximate final geographical setting ir the modelled figures of estimated consumption and production (Fig. 66 to 71) since this movement was modelled. Grid 1 was sampled before the drift investigation started and grid 8 was sampled after the drift investigation ended. To be able to compare the range of change estimated with both investigations, the time difference between the end of the drift investigation and the sampling of the same region in grid 8 had to be ignored. The time difference between the start of sampling grid 1 and the start of the drift investigation (5 days) had to be ignored, also (Tab. 1).

Even for simple transport several simplifications have to be accepted. Movements for station 22, being fairly close to the starting position of the drifting buoy (see Fig. 1), were modelled for the time of grid 1 onto grid 8 (Fig. 65). Since the drift was started after sampling grid 1 and not at the same time, you have to postulate zero water transport for the hours between sampling station 22 on grid 1 and the start of the drift investigation. Hardly any transportation within the grid 1 can be seen for station 22, in Fig. 47, which may justify this simplification. Secondly you have to assume no water movement at station 22 in between the end of the drift and sampling station 22 on the following grid 8. Again this assumption is supported by data of the modelled transports within grid 8, where only short transport distances occurred (Fig. 6). Only by making these simplifications may you pinpoint the region, where the water mass sampled at the start of the drift would be located at in grid 8 by simply following the transport of station 22 in between grid 1 and grid 8 (Fig. 65) from its starting position (circle) to its end position (triangle). The approximate region is marked with a diamond square (Fig. 66 - 71). The water of the drift station would be found in a region of of 15-20 µM silicate, 20-25 µM nitrate and more than 0,6 µM phosphate consumption (Tab. 6, Drifting buoy).

Tab. 6: Comparison of different estimates for production of POM and nutrient loss: range of values for grid with average (av.) for 36 stations (based on a model over 18 days); values for drift (based on continuously tracking and sampling of water for 10 days) and range of values for simplified placement of drifter endposition into regional grid model estimate.

Parameter estimated	Grid (Model)	Drift (Datafit)	Drifting buoy (simplified model) final position in grid 8 marked with diamond in Fig. 66-71
Δ silicate (µM)	2-25, av. 11	19	15-20
Δ nitrate (µM)	0-23, av. 16	23	20-25
Δ phosphate (µM)	0-0.75, av. 0,4	0.67	> 0,6
Δ part. C (µM)	0-75, av. 31	148	25-35
Δ part. N (µM)	0-20, av. 5	21	4-8
Δ Chl a (µg l^{-1})	0-38, av. 13	84	10-20

Despite the simplifying assumptions stated above these values for the dissolved inorganic nutrients fit very well to measured data for the drift investigation (Tab 6). In the particulate phase though, values were lower than the drift data would suggest. The assimilated carbon would amount to only 25 - 35 µM and 4 - 8 µM nitrogen as well as 10 - 20 µg l^{-1} chlorophyll would have been produced.
Ambient dissolved inorganic nutrient levels were low already by the end of the drift. No major shifts in consumption of these had to be expected for the time after the drift. This resulted in a good comparability of the estimates described above. Lower estimates of POM for the grids and the theoretical geographical position of the drifting buoy in grid 8, compared to the calculated production during the drift though, indicate a grazing or sedimentation loss of POM over the additional time.
The data of the drift allowed for fairly reliable calculations of loss and gain over the investigated period of ten days, while the grid data displayed broad ranges of possible change in a larger region. Especially the values for POM were influenced by processes though that could not be accounted for in the field. The enclosure investigations were conducted to improve estimates of POM production under varying nutrient regimes (chapter 6).

6. Enclosure experiment spring 1995: Results and discussion

A nutrient ratio of N:P around 16 was stated by Redfield et al. (1963) as the optimum supply for phytoplankton, resulting in non limited growth. This ratio was generally accepted for phytoplankton in exponential growth (e.g. Takahashi et al, 1985). Inorganic N:P ratios above 16 are frequently found in the Elbe river plume (see grid and drift 1995). High ratios are caused by high nitrate loads of the river runoff. Ratios much higher than N:P 16, based on very high nitrate and low phosphate concentrations, may have detrimentral effects on the system, if they would still promote the growth of the phytoplankton. For coastal management it is an important question, whether there is a necessity to further reduce the load of nitrogen in addition to phosphorus or if the reduction of phosphorus input into the marine system is sufficient.
The enclosure experiment was conducted to study the processes observed in the field in more detail and to measure the production of POM and consumption of dissolved inorganic nutrients undisturbed by advection and grazing. The chemical and biological situation observed during the spring drift 1995 in the German Bight was reconstructed. We wanted to investigate whether elevated N:P ratios, produced by the addition of nitrate, may result in an enhanced assimilation of particulate nitrogen and/or carbon in a phytoplankton population encountered during the a spring bloom. Two slightly different salinities were applied to find out if a shift in salinity, typically encountered in a frontal zone, can additionally cause a change of the phytoplankton nutrient assimilation and/or community structure. For further details of the setup refer to chapter 3.4..
The different salinity treatments are marked with symbols filled in black for the salinity of 32 PSU and unfilled for the salinity of 26 PSU in all following graphs. The different treatments of nitrate to phosphate ratio (in the following "NP") are marked with an upside down triangle for NP 8, a circle for NP 20, a triangle for NP 60 and a square for NP 110. The legends of the different graphs show the nitrate to phosphate treatment level as first number combined with the respective salinity treatment as second number. Thus the code "8-32" for example refers to the nitrate to phosphate ratio of 8 in the salinity treatment of 32 PSU.

6.1. Stocks

The development of dissolved inorganic and organic matter in the different enclosures is displayed over time in Fig. 113 to 134 and 137 to 156. The average of the three replicates is given with standard deviations. Very small deviations between the replicates indicate a successful and parallel initiation of all 24 enclosures. No reaction to the difference of 6 PSU became obvious for the dissolved components (Fig. 113 to 128).

a) Dissolved inorganic nutrients

Silicate (Fig. 113, 114) was consumed rapidly in all enclosures and concentrations had already reached a minimum after 144 h.
Nitrate (Fig. 115 and 116) was depleted at about the same time in the treatments NP 8 and NP 20, while the offered nitrate was consumed in the treatment of NP 60 only at the end of the experiment. A surplus amount of around 50 µM remained in the treatments of

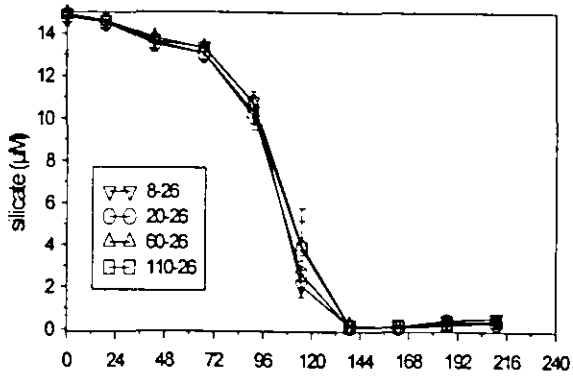


Fig. 113

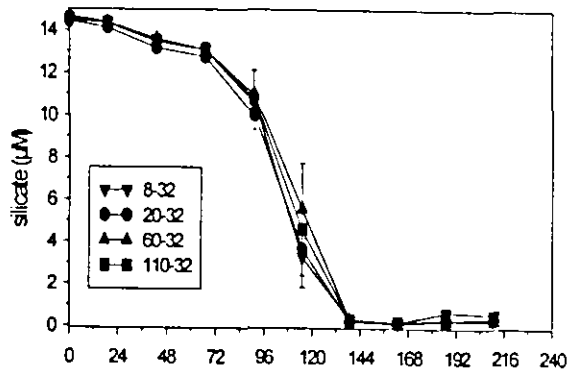


Fig. 114

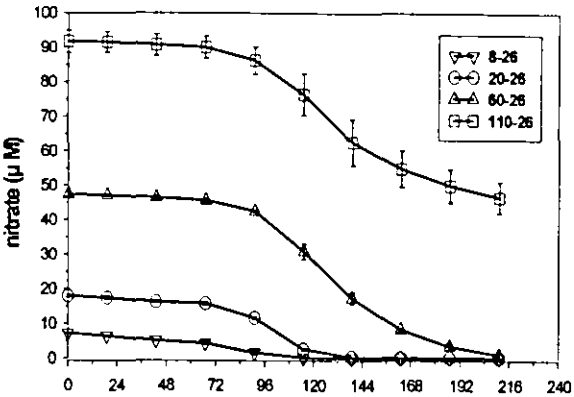


Fig. 115

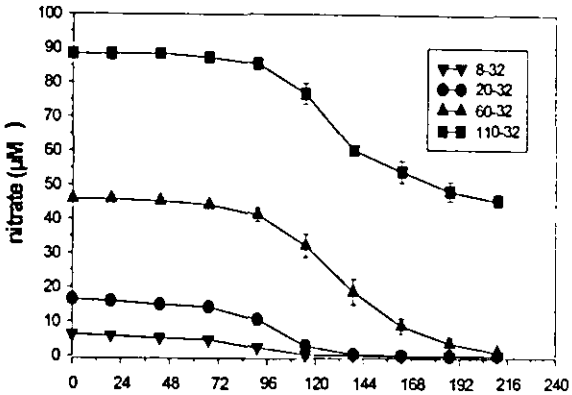


Fig. 116

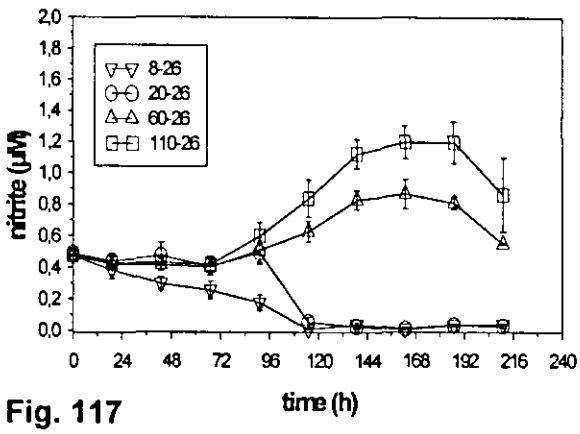


Fig. 117

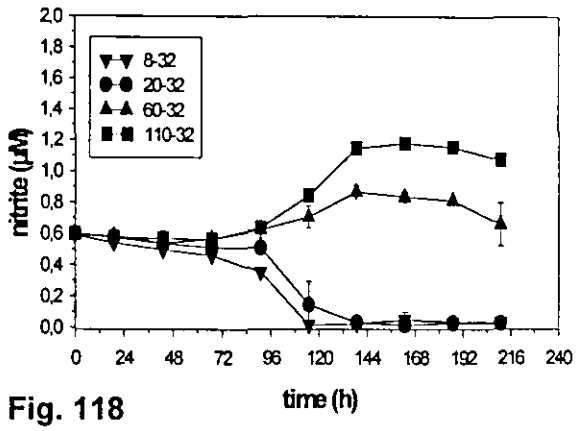


Fig. 118

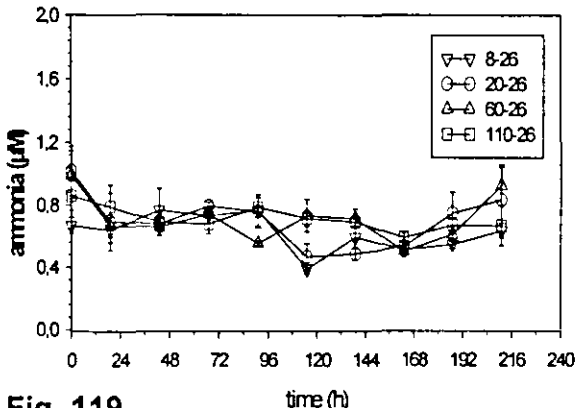


Fig. 119

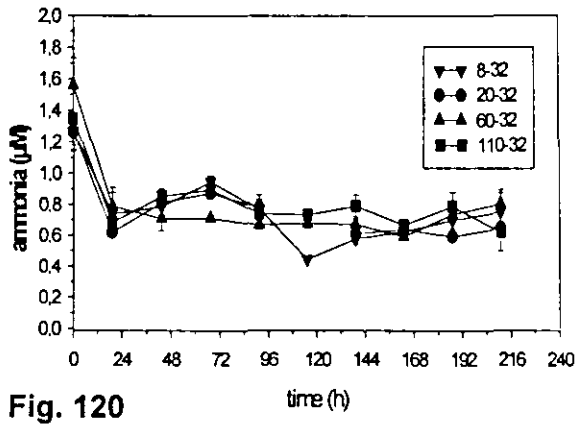


Fig. 120

NP 110. This amount resembled the surplus found after the bloom in the drift investigation (chapter 5).
The high and the low NP treatments developed an obvious difference in their nitrite content (Fig. 117, 118). Nitrite increased in NP 60 and NP 110 after 120 h, while concentrations fell towards detection limit at about the same time in NP8 and NP20. Nitrite loss was measured at the time of nitrate depletion in the respective enclosures (Fig. 115,116,117,118). An uptake of nitrite is often measured, when nitrate is close to exhaustion in phytoplankton cultures (Collos, 1998). Elevated levels of nitrite in the enclosures NP60 and NP110 may have been caused by an algal excretion of surplus nitrite in the process of nitrate assimilation. Several intermediate compounds are accumulated in the reduction pathway during assimilation of nitrate, which ultimately leads to protein synthesis. The established concentration gradient may cause diffusion or leakage of material to the outside (Collos, 1998). Kiefer (1976) developed a model of algal nitrite excretion. He expected maximum production of nitrite in the cell, when it was supplied with sufficient light to achieve the enzyme dependent transport and transfer of nitrate to nitrite. Nitrite excretion is exhibited by a wide variety of phytoplankton species in culture (Collos,1998). It may represent between zero and 50% of the nitrate uptake in the light (25% for *T. pseudonana* e.g.) and between zero and 96% in the dark. A higher excretion during the dark was attributed to the light requirements of the nitrite reductase, since ferredoxin, the electron acceptor for this enzyme, is synthesized during photosynthesis only (Losada et al., 1981). Maximum levels of nitrite concentrations in the NP60 and NP110 treatments of the enclosures remained below 1 µM (Fig. 117, 118). Meanwhile a lot of nitrate was taken up (Fig. 115, 116). If excreted nitrite was not taken up immediately again, its excretion thus remained fairly low compared to the possible amount suggested by Collos (1998). Collos (1998) also tried to assess the relative importance of active excretion versus passive diffusion and concluded that nitrite release is mainly an active process which depends on nitrate uptake.
Some authors (e.g. Bianchi et al., 1992) proposed the existence of anaerobic microniches around particulate aggregates in oxygenated waters. The abundance of particles combined with high nitrate concentration may favour nitrate reduction and denitrification. Nitrate ammonification and denitrification as a source for nitrite in the enclosures are very unlikely, though. The enclosures were mixed by airbubbles and did not display extremely dense cell numbers nor strong formation of aggregates.
Bacterial nitrification may have contributed to elevated nitrite levels to some extend. Bacterial production (Fig. 167,168) rose at the same time the elevated nitrite concentrations were measured. Elevated production rates of the bacteria at higher NP ratios were found for the 32 PSU treatments, while the pattern was less clear for the 26 PSU treatments. These enclosures, however, also displayed a nitrite production in the highest NP treatments. A loss of ammonia due to bacterial nitrification was not detectable either (Fig. 119, 120). Concentrations of ammonia remained around 0.8 µM after initially elevated values at the first day. Thus it is very likely that the elevated nitrite levels measured in the enclosures were caused by the activity of the phytoplankton.

Phosphate (Fig. 121, 122) was reduced to very low concentrations after 120 hours runtime of the experiment, remaining around zero then for most enclosures. A slightly slower consumption became evident for the nitrogen deficient treatment NP8.

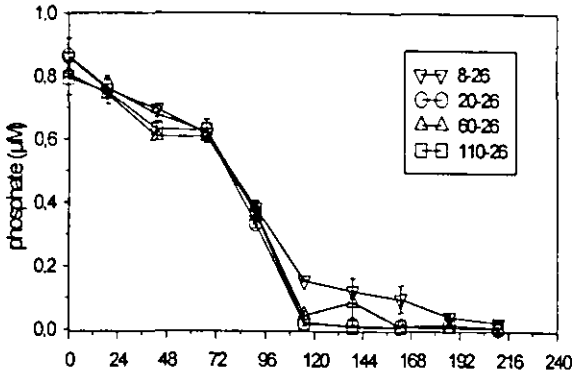


Fig. 121

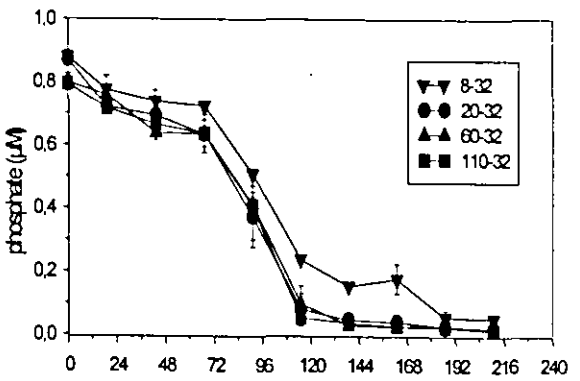


Fig. 122

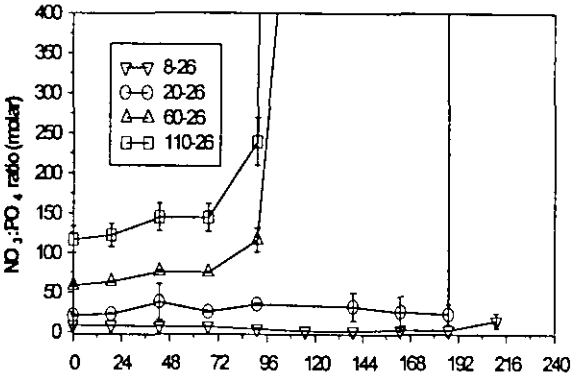


Fig. 123

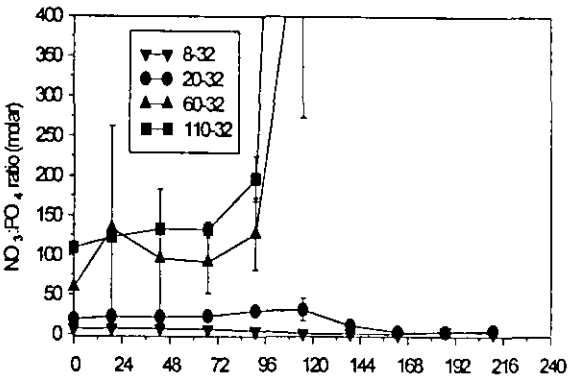


Fig. 124

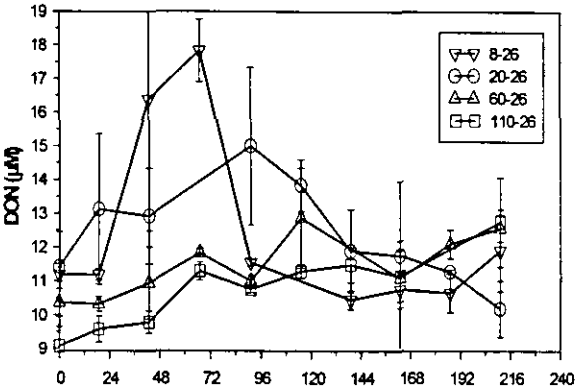


Fig. 125

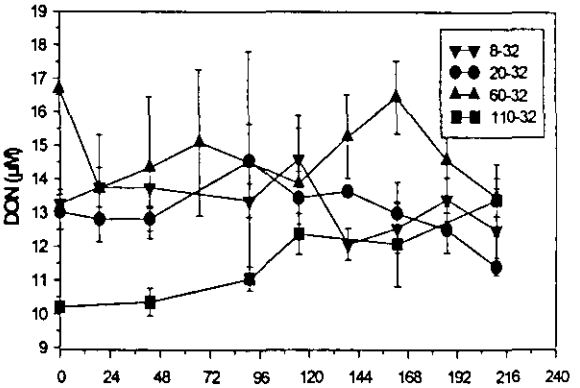


Fig. 126

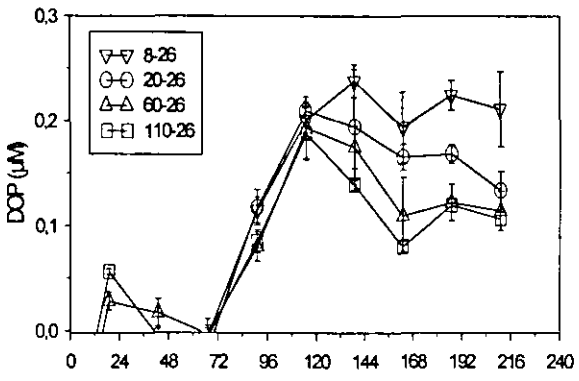


Fig. 127

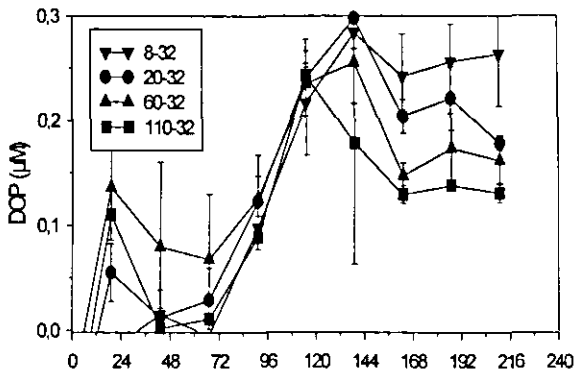


Fig. 128

In order to determine which nutrient was probably limiting first in the enclosures ambient concentrations were compared to values considered as limiting for phytoplankton. Fisher et al. (1988) assumed that the phytoplankton is limited by a certain nutrient, if the ambient concentration of it is below the k_s value for uptake. Their suggested limiting concentrations with DIN $\leq$ 1 µM, PO_4 $\leq$0.5 µM and silicate $\leq$ 5 µM were high. Dortch & Whitledge (1992) discussed lower k_s values from literature and based their criteria for nutrient limitation on DIN $\leq$ 1 µM, PO_4 $\leq$0.2 and silicate $\leq$2. The NP8 enclosures were already limited by nitrogen after 91 hours runtime, if their criteria are applied. All other enclosures were phosphorus limited at 91 h, while silicate was depleted only below 2 µM after 115 hours. A discussion of limitation based on the ambient dissolved nutrient concentration only may be erraneous, since phosphate can be stored to a certain extend in the cells, while such a possibility is not known for silicate. A co-limitation of phosphate and silicate seems rather likely for the enclosure treatments NP20 to NP110 around 115 h, if the phosphate storage is taken into account.

b) Dissolved inorganic nitrogen to phosphate ratio

The ratio of nitrate to phosphate (Fig. 123,124) in the water rose to extremely high values after 96 hours as a consequence of the high nitrate concentrations in the NP treatments 60 and 110. The treatments NP20 and NP8 remained around their initial ratios of 20 or 8 respectively, except for the final value in NP 20 at 26 PSU, which is caused by an extremely low phosphate value.

c) Dissolved organic nitrogen (DON) and phosphorus (DOP)

A detailed interpretation of the development of the dissolved organic nitrogen (DON) remains difficult (Fig. 125, 126) due to large deviations. After an initial rise in the low NP8 and NP20 at 26 PSU an overall loss of around 1 µM was observed compared to the starting values. No inital rise of DON in NP8 and 20 became evident at 32 PSU, but again an overall loss of around 1 µM may be calculated from start to end of the experiment. In NP110 the DON increased by about 3 µM over time in both salinities. For NP60 the reaction seemed to differ with salinity. An overall increase of around 2 µM was measured at 26 PSU, while the DON first increased, but then fell again during the last days of the experiment at 32 PSU.
Studies of Bronk & Glibert (1993) showed that generally DON can be released and taken up during incubations. In Chesapeake Bay they observed surface water concentrations of DON with maxima around noon (about 25 µM) and minima at night (about 20 µM). They suggested that phytoplankton must have been responsible for at least some fraction of the DON uptake.
DON consumption by the phytoplankton (and bacteria) rather than an excretion was likely in the nitrogen-limited situation of NP8. The initial release of DON in the enclosures NP8 and 20 at 26 PSU may have been a stress reaction of the phytoplankton, which did not become obvious at the higher salinity treatments, though. Cellular products containing high amounts of nitrogen may have been excreted continuously in a surplus nitrogen environment like NP60 and NP110. A higher sampling frequency (shorter than every 24 h) is needed to link any variation in the DON concentrations to excretion or consumption processes. Collos et al. (1996) for example

evidenced large diel variations in DON in a coastal pond. Nitrate assimilation resulted in an extensive release of DON, while ammonium assimilation did not or to a much smaller extent (Collos et al.,1996). For their experimental system they proposed that nitrate was taken up and released mostly as DON as no nitrite accumulated. DON was taken up directly again or broken down to ammonium, which was then used to produce particulate nitrogen. All these processes were closely coupled over 24 hour periods.

The development of dissolved organic phosphorus (DOP) was more consistent than the pattern of DON. Values steeply increased after about 72 hours in all treatments (Fig. 127, 128). The rise in DOP concentrations was monitored (Fig. 127,128) at the time of the fastest consumption of phosphate, the steepest increase in primary production rate, and highest assimilation numbers. Possibly there was a leakage of DOP products out of the cells in this highly productive phase. A maximum of 25% of the lost phosphate was found in the DOP phase. Final DOP concentration depended on the initial NP treatment. Highest concentrations were found in the nitrate limited enclosures of NP8. Lowest values were measured in the treatments with surplus nitrate (NP110). Increasing phosphate limitation may stimulate the production of DOP degrading enzymes. Phosphate can be regenerated from organic compounds by free and cell bound enzymes of phytoplankton and bacteria (hydrolytic degradation by alkaline phosphatase and 5` nucleotidase; Tamminen, 1989, Chróst, 1991). A threshold level of 1 µM phosphate was defined for the regulatory function of phosphate on alkaline phosphatase activity in investigations by Nausch (1998). A further stimulation of alkaline phosphatase production in algal and bacterial cells may be induced below 0.2 µM phosphate (Nausch, 1998). For a summer investigation Nausch (1998) estimated that the organic phosphorus pool may be converted within 3 to 10 hours, when phosphate concentrations are at the detection limit and hydrolysis rates are around 10 - 30% h^{-1}.

d) Particulate organic matter

Initially the phytoplankton encountered nutrient conditions sufficient for growth in all enclosures. The difference in starting NP ratios had an impact on the assimilation of particulate organic matter only after a certain time.
Log-tranformed data of the stationary phase of the dominant phytoplankton species were used to analyze the differences between the treatments. Stationary state was reached by 163 hours and ANOVA results are based on the analysis of data from 163 to 211 hours. Results of simple one way ANOVA tests are given in the following. No significant effect of salinity and no significant interaction between salinity and NP treatment could be proven by two way ANOVA runs on the data for particulate matter. Effects of different NP treatments were significant for particulate carbon, nitrogen and chlorophyll with p-levels <0.0001 (Tab. 7 and Appendix Table F for details).

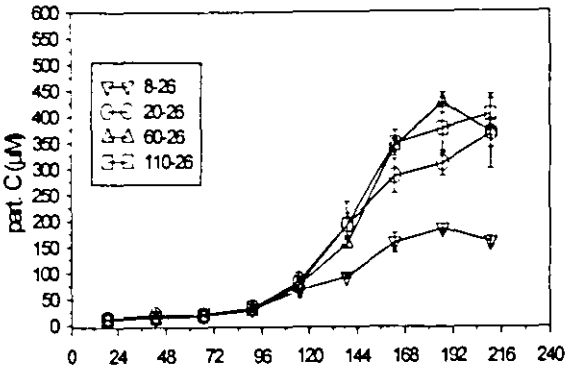


Fig. 129

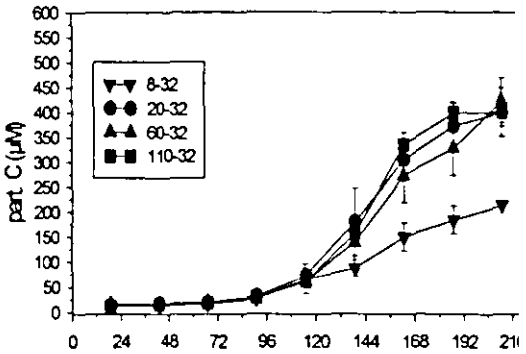


Fig. 130

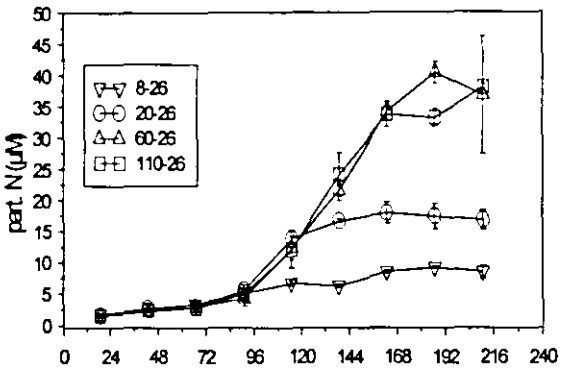


Fig. 131

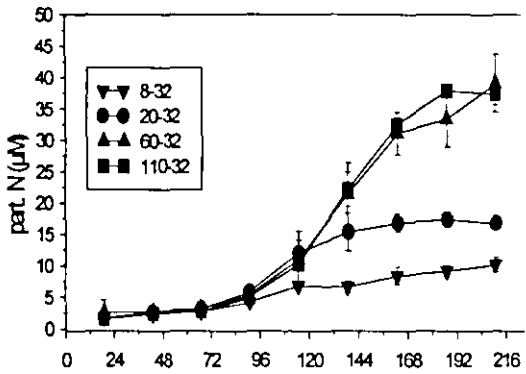


Fig. 132

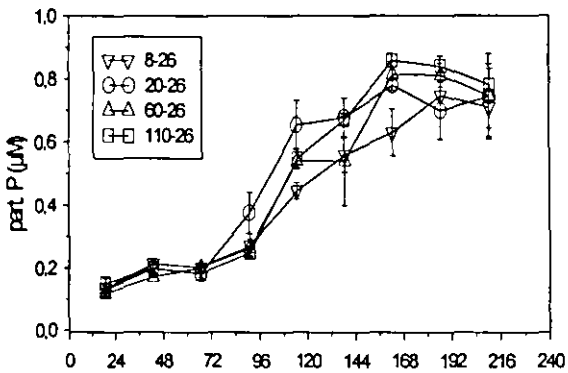


Fig. 133

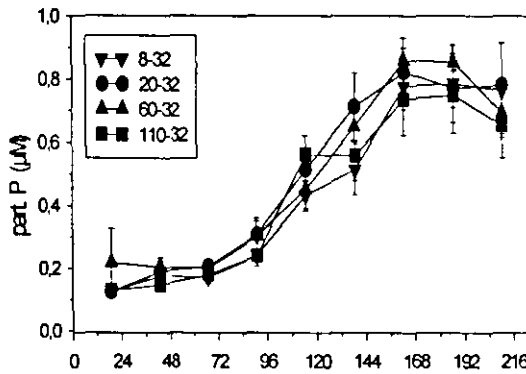


Fig. 134

Carbon assimilation was significantly impaired in the nitrogen deficient treatments N compared to all other treatments (Fig. 129, 130, Tab. 7 and Appendix Tab. F) significant increase of particulate carbon could be proven between the treatment NP20 to NP110 at 26 PSU (Tab. 7). No significantly increased carbon particularisat could be proven in between NP20 and NP110 at 32 PSU, though. The calcula means of the log-transformed data and standard errors of the mean for particul carbon are shown for the different treatments in Fig. 135.

Tab. 7: Significant multiple comparison (Tukey test) results (p=<0.05) fo particulate components

Component tested ("component"), salinity treatment applied ("salinity") and the comparison of groups wi the respective NP treatment ("group") are listed with the calculation of the difference of the means of thes groups (diff. means). For the complete table of the ANOVA results see appendix Tab. F.

component	salinity	group	diff. means
pC	26 PSU	8 vs 20	0.267
		8 vs 60	0.337
		8 vs 110	0.345
		20 vs 110	0.0785
	32 PSU	8 vs 20	0.287
		8 vs 60	0.276
		8 vs 110	0.317
pN	26 PSU	8 vs 20	0.299
		8 vs 60	0.616
		8 vs 110	0.602
		20 vs 60	0.317
		20 vs 110	0.303
	32 PSU	8 vs 20	0.271
		8 vs 60	0.575
		8 vs 110	0.596
		20 vs 60	0.305
		20 vs 110	0.325
Chl a	26 PSU	8 vs 20	0.376
		8 vs 60	0.551
		8 vs 110	0.492
		20 vs 60	0.175
	32 PSU	8 vs 20	0.305
		8 vs 60	0.481
		8 vs 110	0.464
		20 vs 60	0.176
		20 vs 110	0.159

The treatment NP8 had significantly lower amounts of particulate nitrogen compared to all other treatments (Fig. 131, 132) at both salinities. With rising NP treatment a significant increase in particulate nitrogen was calculated up to the treatment NP60. No further gain was induced in between NP60 and 110. The pattern of particulate nitrogen was very similar for both salinities. Calculated means and SEM of the particulate nitrogen in the enclosures are shown in Fig. 136.

Eppley et al. (1968) already provided evidence for an internal reservoir of nitrate-nitrogen after rapid uptake in light. In nitrogen-sufficient phytoplankton internally accumulated nitrate is reduced by nitrate reductase and further assimilated to a variety of intermediate compounds, such as ammonium and free amino acids before it is incorporated into protein and chlorophyll (e.g. Dortch et al., 1982). In the enclosures some additional nitrogen assimilated was used for chlorophyll production (Fig. 141,142). Significantly less chlorophyll was produced in NP8 compared to all higher NP treatments. A further significant increase of chlorophyll was proven in between NP20 and NP60. The difference between NP20 and NP110 was significant for the 32 PSU enclosures only, since mean Chl a concentrations were slightly reduced in the NP110 treatment at 26 PSU (Fig. 136).

Phytoplankton growing on excess nitrogen increased the intracellular concentrations of amino acids in investigations of Dortch (1982). Amino acids and other nitrogen containing compounds may be used for growth, when external nitrogen is not available any more (Dortch, 1982, Dortch et al., 1984). In the enclosures the storage capacity of the phytoplankton for excess nitrogen was possibly reached with the NP60 treatment, limiting any further increase in particulate nitrogen at higher ambient nitrate levels. Dortch (1982) discussed the nitrogen storage in persistent and transient pools as a means of the phytoplankton to buffer its growth from the effects of a changing nitrogen

supply in the natural environment. Based on own data and on investigations by Collos (1982 a,b) he also suggested, that the rate-limiting steps and the metabolic pathways may vary between species and that some species can accumulate more stored nitrogen than others, even when the concentrations are normalized to cell volume. Thus the results found in the enclosures are probably very well applicable to the situation in the field in spring 1995, since in both situations *D. brightwellii* was the dominant species. Reactions would have possibly varied, if a different species assemblage would have been inocculated. Different nitrogen storage capabilities of phytoplankton communities composed of different species were also indicated by data from the the grid investigation (chapter 4).

Fig. 135: Means and SEM pC
log transformed data (163-211h) for all NP treatments and 26 and 32 PSU

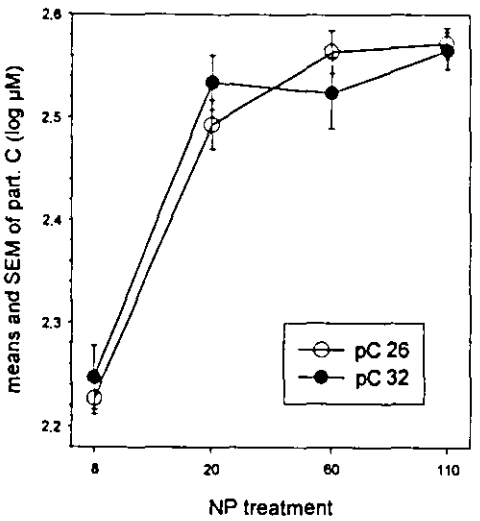
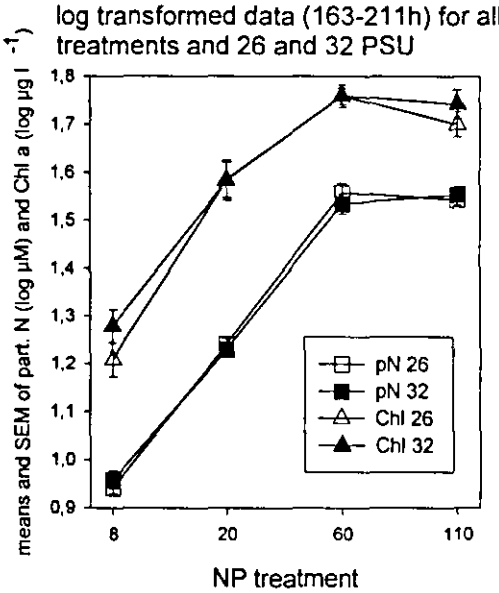


Fig. 136: Means and SEM pN and Chl
log transformed data (163-211h) for all NP treatments and 26 and 32 PSU



No significant differences were observed for the formation of part. phosphorus (Fig. 133, 134).

Major differences between the treatments NP8 and 20 versus NP60 and 110 became obvious for the particulate C to N ratios (Fig. 137, 138). The ratio of pC:pN rose in all treatments well above the value suggested by Redfield et al. (1963). The nitrogen sufficient treatment of NP20 and also the nitrogen deficient treatment NP8 had final values above 20. Values remained around 10 due to the storage of excess nitrogen by the phytoplankton in the surplus treatments NP60 and 110. The difference between the treatments developed at a time when phosphate and silicate were reduced to low concentrations, while ratios during exponential growth were close to "Redfield" in all treatments.

Ratios of pC:pN given by Laws & Bannister (1980) for phosphate limited cultures of *T. fluviatilis* cover the same range as found in the enclosures. They calculated ratios rising from 8.5 at fast growth rate to about 20 at slow growth rate. Nitrate limitation resulted in very similar pC:pN ratios with 8.7 at fast and 16.5 at slow continuous growth (Laws & Bannister, 1980). Slawyk et al. (1978) also related fast growth rates to a rapid decrease

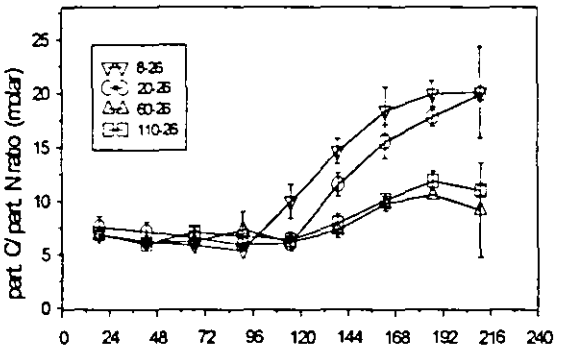


Fig. 137

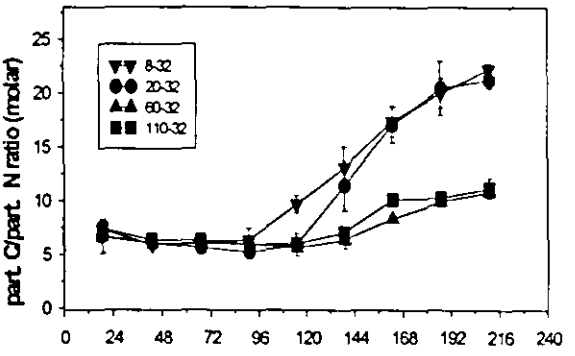


Fig. 138

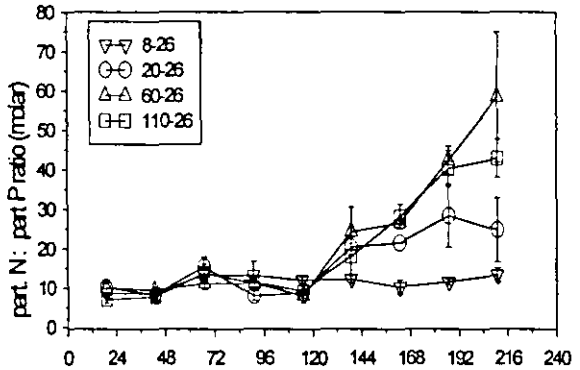


Fig. 139

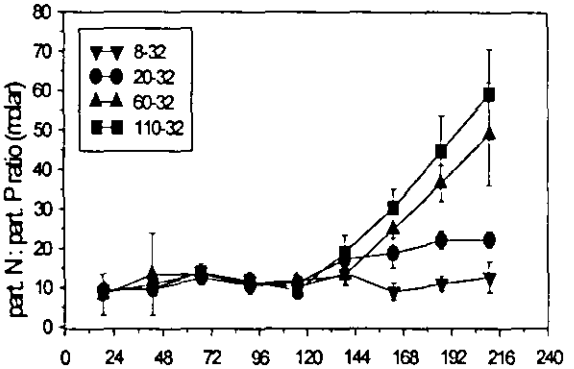


Fig. 140

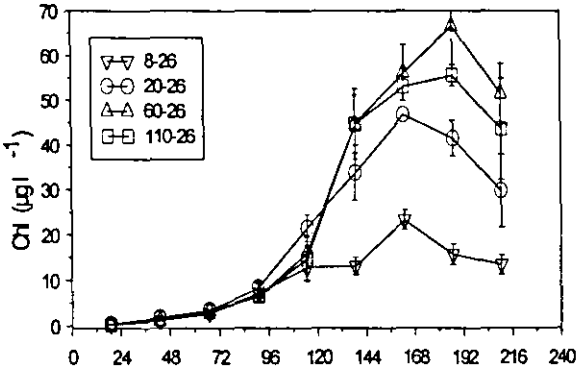


Fig. 141

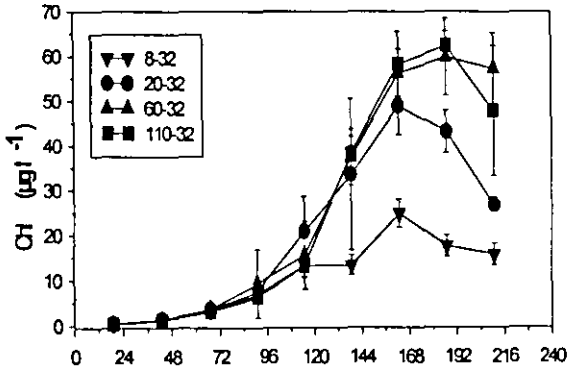


Fig. 142

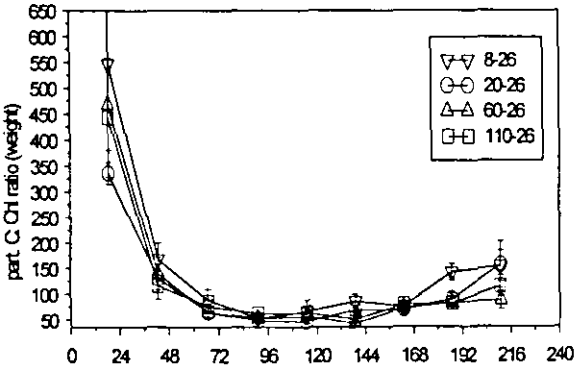


Fig. 143

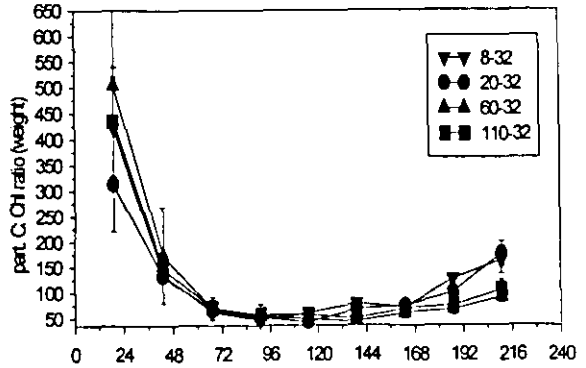


Fig. 144

in pC:pN ratios in the field. Applicability of the Redfield ratio of 6.6 for pC:pN thus seems to be restricted to phytoplankton in exponential growth phase.
Many investigators referred to the Redfield ratio to estimate the standing stock of carbon in the field (e.g. Takahashi et al., 1985). It is probably not possible to do so in field situations when stationary phytoplankton may be monitored. Sambrotto et al. (1993) demonstrated, that net organic carbon production greatly exceeded that predicted from nitrate consumption and the Redfield pC:pN ratio for coastal waters and open ocean sites.

Particulate nitrogen to phosphorus ratios in the enclosures (Fig. 139, 140) displayed a pattern comparable to the pC:pN ratios. Values remained below 25 for the nitrate deficient and sufficient treatments NP8 and NP20. Excess nitrogen storage of the surplus treatments NP60 and NP110 was reflected in rising ratios from around 10 up to 60. As Dortch & Whitledge (1992) summarized, ratios above 30 may indicate phosphorus limitation, whereas ratios below 10 indicate nitrogen limitation. Final pN:pP ratios in the enclosures were thus in the expected range for the respective NP treatments.

Initially high particulate carbon to chlorophyll ratios (pC:Chl) around 450 indicated that the algae were inocculated out of stationary cultures into the enclosures. Ratios fell to below 100 during exponential growth of the phytoplankton in the enclosures (Fig. 143, 144). When stationary phase was reached, values increased again.
Rising values with decreasing growth rates are a common feature, shown e.g. by Laws & Wong (1978) and Eppley & Renger (1974) for diatoms and flagellates. NP8 and 20 reached final ratios around 150 to 160, while NP60 and 110 remained around 90 -115 due to their increased chlorophyll production. Davidson et al. (1991) calculated ratios of 25 for cells of *Isochrysis galbana* before the nitrogen in the medium had been exhausted, while ratios rose up to 100 towards the end of their batch culture experiment. Falkowski et al. (1985) calculated a ratio of 64 for cultures of *T. weisflogii* grown under sufficient light. In a phosphate limited culture of *T. fluviatilis*, Laws & Bannister (1980) observed a range of pC:Chl ratios of 223 - 63 depending on growth rate of the algae (slow to fast). Likewise Laws et al. (1983) described the pC:Chl ratios of *T. weisflogii* as a function of relative growth rate and found ratios above 150 for slow growth and a ratio of about 100 at μ_{max} for phosphate limited cultures. Nitrate limited cultures had a ratio of above 300 at slow growth and dropped to ratios of about also at μ_{max}. Only ligh limited cultures exhibited ratios below 100 in their experiments.

e) Phytoplankton

The enclosures were inocculated with a mixture of phytoplankton species containing *Ditylum brightwellii, Thalassiosira weisflogii, T. rotula, T. punctigera* and a *Rhodomonas* flagellate. Flagellates smaller < 5µm were included in the media because of the 5 µm filtration of the seawater used in the enclosures. The development of the species cell number in absolute numbers with standard deviations for the three replicate treatments is plotted over time on a linear scale in Fig. 145 - 156. Calculated generation times refer to the exponential phase of growth.

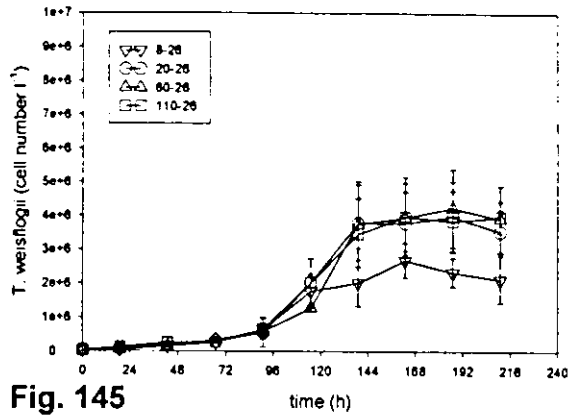


Fig. 145

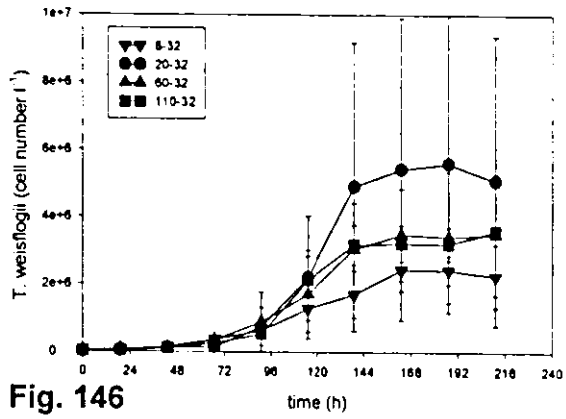


Fig. 146

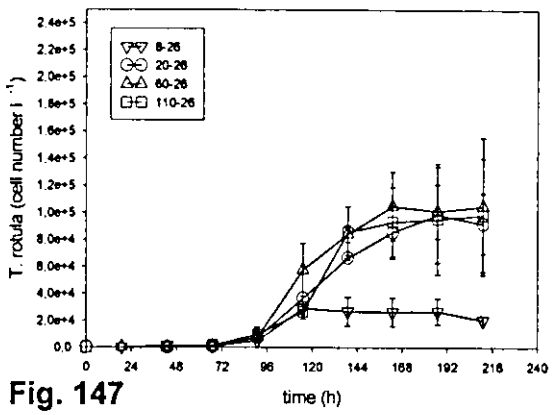


Fig. 147

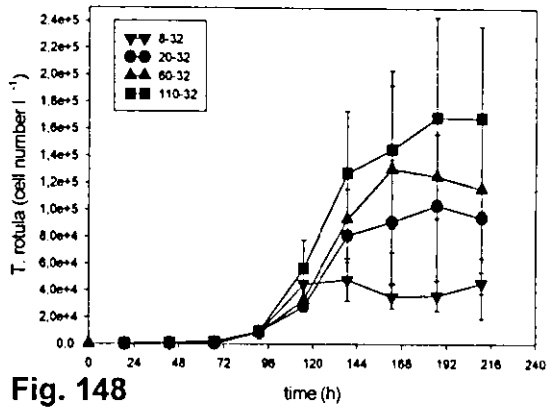


Fig. 148

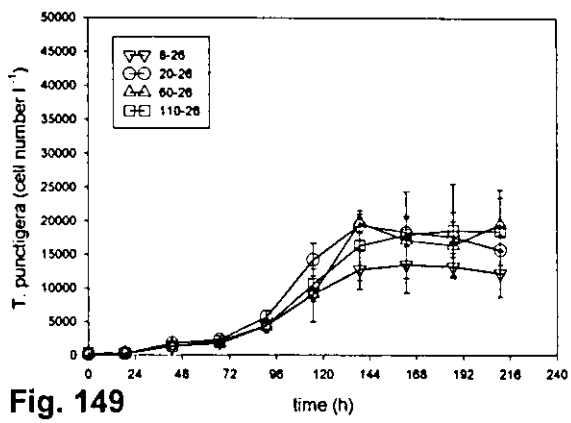


Fig. 149

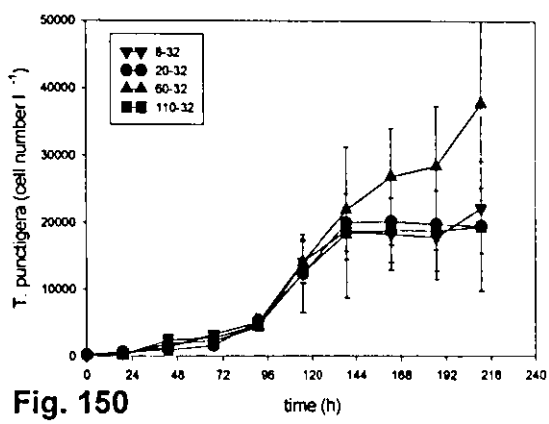


Fig. 150

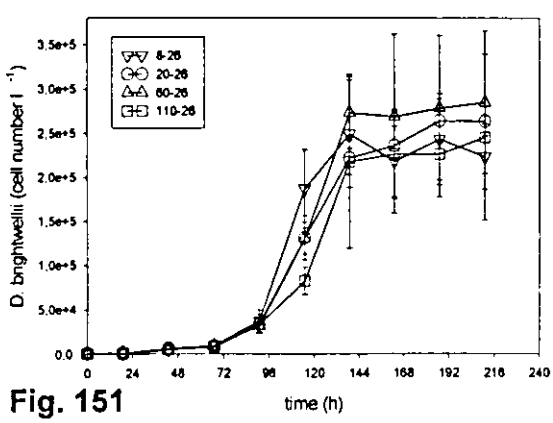


Fig. 151

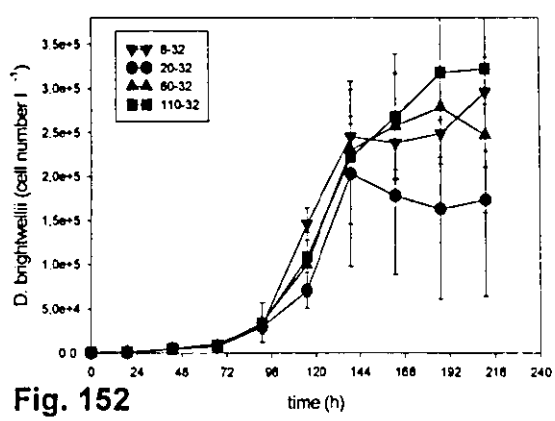


Fig. 152

Tab. 8: Significant multiple comparison (Tukey test) results (p=<0.05) for species cell number
Species cell numbers tested ("Species") for stationary phase, salinity applied and the comparison of groups with the respective NP treatment (group) are listed with the calculation of the difference of the means of these groups (diff of means) and their q statistic (q). For the complete table of the ANOVA results see appendix Tab. H.

species	salinity	group	diff of Means	q
T. weisflogii	26 PSU	8 vs 20	0.200	6.190
		8 vs 60	0.227	7.047
		8 vs 110	0.220	6.818
T. rotula	32 PSU	8 vs 20	0.292	3.930
		8 vs 60	0.488	6.559
		8 vs 110	0.597	8.026
		20 vs 110	0.305	4.096
	26 PSU	8 vs 20	0.578	13.234
		8 vs 60	0.627	14.354
		8 vs 110	0.581	13.312
T. punctigera	32 PSU	20 vs 60	0.188	3.905
	26 PSU	8 vs 20	0.128	3.917
		8 vs 60	0.128	3.917
		8 vs 110	0.138	4.200
D. brightwellii	32 PSU	8 vs 20	0.231	4.390
		20 vs 60	0.218	4.141
		20 vs 110	0.290	5.510
Rhodomonas	32 PSU	8 vs 60	0.457	10.573
		8 vs 110	0.367	8.474
		20 vs 60	0.342	7.914
		20 vs 110	0.252	5.814
	26 PSU	8 vs 20	0.216	5.467
		8 vs 60	0.427	10.812
		8 vs 110	0.484	12.265
		20 vs 60	0.211	5.345
		20 vs 110	0.268	6.798

Standard deviations of cell numbers very often overlapped for the different treatments. Therefore ANOVAs were calculated for the cell numbers during stationary phase of the diatom species to test for significant differences on species level. Significant Tukey test comparison results are listed in Tab. 8. The calculated means for each species and treatment are shown in addition to the respective standard error of the mean in Fig. 157-160. For further details of the ANOVA results on species level see Appendix Tab. H.

Significant increases in cell numbers were proven for some but not all species between the nitrogen deficient conditions and sufficient nitrogen supply.

T. weisflogii did not display very pronounced differences of the means (Fig. 159, squares, "Tw") and the increase of cell number in between NP 8 and the other treatments was significant at 26 PSU only. All treatments above NP8 reacted very parallel (Fig. 145). An increase in nitrate above NP20 did not result in higher cell numbers at 26 PSU. All treatments at 32 PSU reached higher cell numbers than in NP8 and NP 20 reached highest numbers (Fig. 146). An average generation time of 22.5 hours was calculated for the exponential phase. Growth was slowest in the NP 110 and fastes in NP 60 at both salinities. The observed generation times were slow compared to cultures, which doubled cell numbers in 9.2 hours (Falkowski et al. ,1985) or 10.5 hours (Post et al., 1985) at high irradiance. In Furnas (1990) also fast generation times below 5 hours were listed for small *Thalassiosira* species. Only low irradiance caused slow generation times of 26.8 hours (Falkowski et al.,1985) and 34 hours (Post et al.,1985) in cultures.

Cell numbers of *T. rotula* continuously increased with rising NP treatment at 32 PSU (Fig. 148). Differences were significant for NP 8 versus all others and NP20 versus NP110 (Fig. 157, "Tr 32"). At 26 PSU the reaction of *T. rotula* (Fig. 147) to the NP

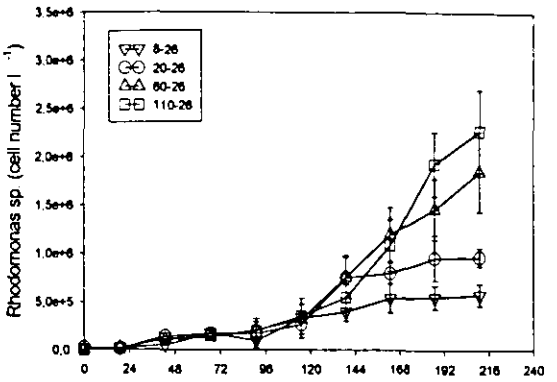


Fig. 153

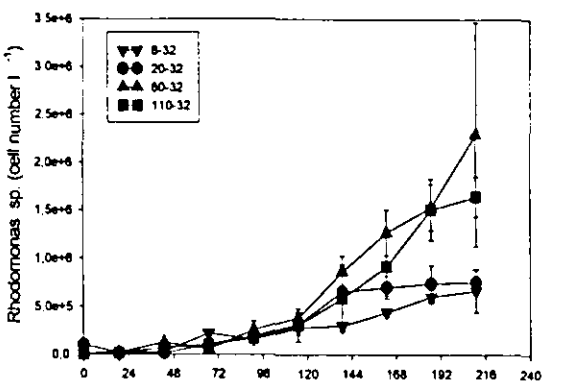


Fig. 154

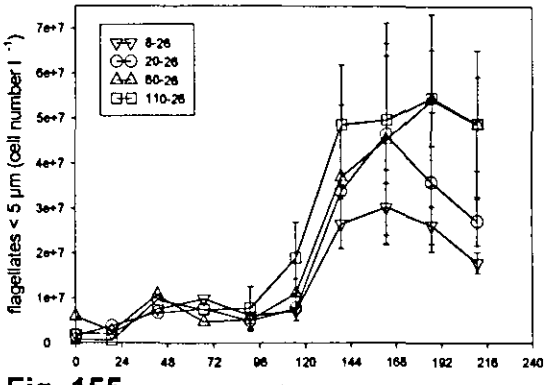


Fig. 155

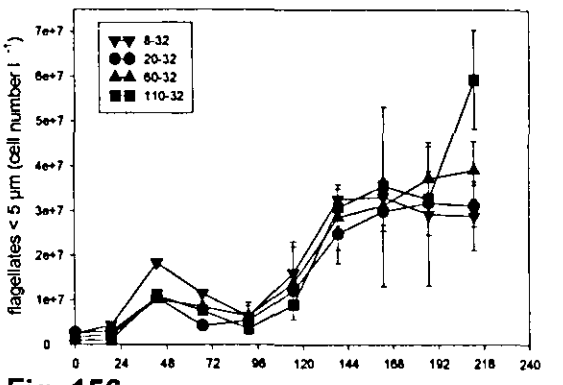


Fig. 156

treatments was similar to the reaction of *T. weisflogii*. Cell numbers significantly increased from NP8 towards all others treatments (Fig. 157, circle symbol, "Tr 26"), but no further increase of cell numbers could be proven for any treatment above NP20. The effect of salinity resulted in significantly higher means of the cell number of *T. rotula* in 32 PSU compared to 26 PSU treatments (Fig. 158, "Tr"). Schöne (1974) showed that a change in salinity affected rather the yield of *T. rotula* than the growth rate. A yield increase of 25 % may be reached by increasing the salinity from 26 to 32 PSU. This is supported by our results. The optimum range of salinity is supposed to range between 20 - 33 PSU (Schöne, 1974) and 25 - 30 PSU (Krawiec, 1982). Compared to *D. brightwellii*, *T. rotula* may be less tolerant for low salinities (Rijstenbil et a., 1989).
T. rotula reached generation times of on average 13 hours. It grew fastest in NP 8 (8 hours and 10.3 hours respectively) and slowest in NP 20 (19.5 hours) at 26 PSU, while at 32 PSU the treatment of 110 was slowest (16.9 hours). Comparable generation times of this species are mentioned for Narragansett Bay with 12 hours (Furnas,1990). Generation times of 16.4 to 21 hours (Rick,1993) and 13-15 hours (Rick,1984) were observed for unialgal laboratory cultures. In multispecies mesocosms this species grew very fast with a doubling in 9.3 - 12.4 hours (Rick, 1993).

Significantly reduced cell numbers were counted for *T. punctigera* in the NP 8 treatments at 26 PSU (Fig.149 and Fig. 157, hexagon, "Tp26"). No further increase of cell yield was observed above NP20. Almost no reaction occurred from deficient conditions towards NP20 and NP110 at 32 PSU (Fig. 150). A higher mean of cell numbers was only reached in NP60 (Fig. 157, hexagon, "Tp32"). The differences between the two applied salinities resulted in a significant decrease in mean cell number at 26 PSU (Fig. 158, „Tp"). Further investigations would be necessary to find out if this reaction is based on a preference to higher salinities or other causes. With an average of 23 hours the generation times of *T. punctigera* were comparable to those of *T. weisflogii*. At 26 PSU generation time was slowest in NP8 (34 hours) and fastest in NP 20 (19 hours), while at 32 PSU NP 60 was fastest (15 hours) and NP 110 slowest (23 hours). Generation times were comparable to the time of 24 hours (Rick,1990) and 22.7 - 26.3 hours (Rick, 1993) calculated for unialgal cultures.

Fig. 157: Means and SEM *T. rotula* (Tr) and *T. punctigera* (Tp)
log transformed data (163-211h) for all NP treatments and 26 and 32 PSU

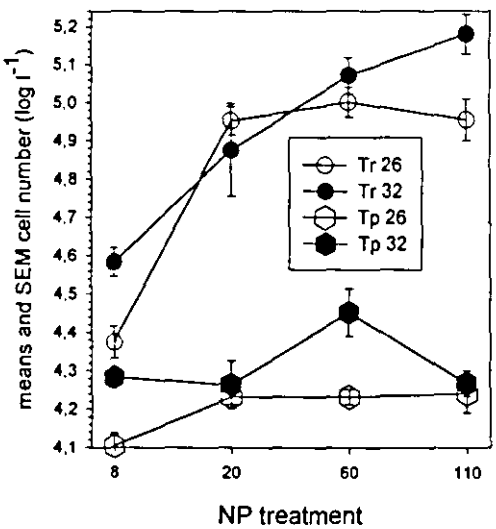
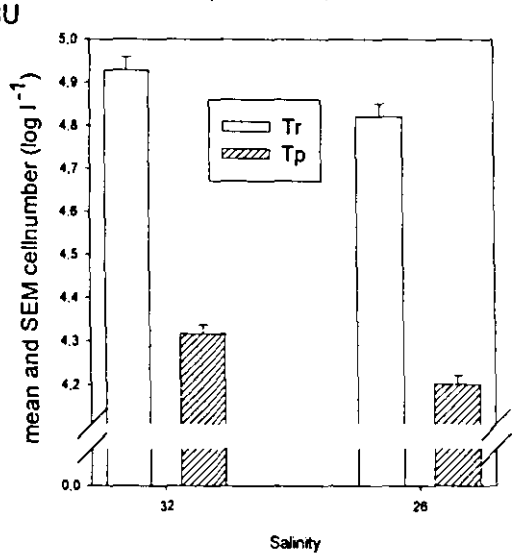


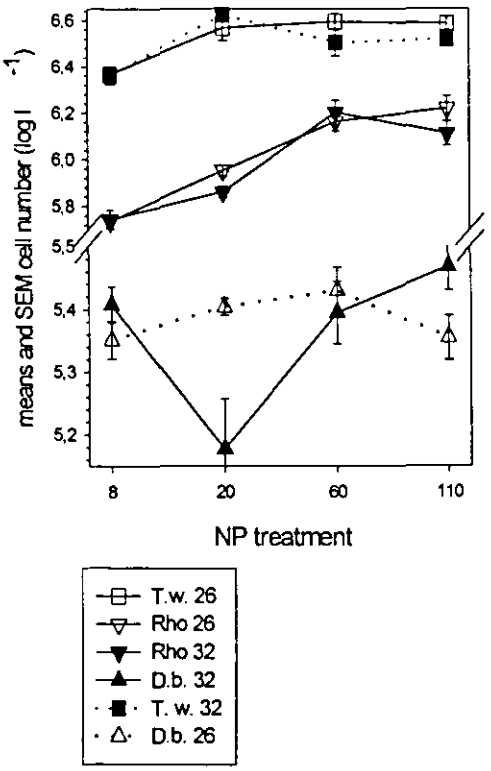
Fig. 158: Means and SEM T. rotula (Tr) and T. punctigera (Tp)
log transformed data (163-211h) at 26 and 32 PSU



No distinct pattern developed for the dominant species *Ditylum brightwellii* at 26 PSU (Fig. 151). A slight increase of the mean was calculated with rising NP ratios up to NP60 (Fig. 159, symbol triangle up, "D.b. 26"). Mean cell numbers were reduced thereafter towards NP110. Further laboratory experiments would be needed to find out if the mean cell numbers were possibly reduced due to a slightly negative effect of high nitrate concentrations in NP110 compared to NP60. Other data of the enclosures may support this hypothesis, since the respective treatment had a less steep increase in primary production (Fig. 163), less maximum chlorophyll yield (Fig. 141), and only the same BOD (Fig. 169) as the NP60 treatment. Burkholder et al. (1992) already discussed direct negative effects of nitrate on eelgras survival that were unmediated by epiphytes or other community components. Carbon is needed to convert nitrate via ammonia immediately into amino acids. In media with high nitrate concentrations, plants

may not have been able to fix enough carbon to support their total carbon demand and despite non-limiting light conditions an insufficient amount of carbon may be available for structural growth (Burkholder et al., 1992). Elevated nitrate concentrations could thus have caused direct physiological effects in the eelgras by forcing the plants into carbon limitation or other severe internal nutrient imbalance. Phosphorus limitation for example may be caused by consumption in active nitrate transport, amino acid synthesis and other energy-requiring processes associated with elevated nitrate uptake (Turpin, 1991). At 32 PSU the average cell yield of *D. brightwellii* strongly decreased in NP20 compared to all other treatments (Fig. 152) and NP110 reached highest mean cell numbers (Fig. 159, "D.b. 32"). No other species reacted with a strong increase in cell number at that NP level to compensate for the lowered cell number at NP20, but a decrease in the mean content of particulate carbon was not observed (Fig. 135). Since *D. brightwellii* was dominating the total biomass (80-50%, Fig. 161,162) it would have been difficult for other species anyway to buffer a major decrease in cell numbers of *D. brightwellii.* Possibly the fewer cells of *D. brightwellii* had an elevated carbon content per cell compared to cells in other treatments and thus prevented a reduction in measured particulate carbon. The interaction between salinity and NP treatment became significant (see Appendix Tab. H) due to the reaction of this species in the NP20 treatment at 32 PSU. Further laboratory experiments would have to be conducted to find a plausible explanation for this reaction. Rijstenbil et al. (1989) studied the effect of the large salinity range of 13.6 to 4.8 on the nitrogen metabolism of *D. brightwellii.* Low salinities inhibited photosynthesis and growth, deformed cells and stimulated respiration. Additionally the cellular levels of carbohydrates decreased and the uptake capacity as well as the affinity to ammonium was severely altered. The species is described as euryhaline by Brand (1984), despite the findings of Rijstenbil et al. (1989).

Fig. 159: Means and SEM *T. weisflogii (T.w.), Rhodomonas (Rho), D. brightwellii (D.b.);* log transformed cell numbers (163-211h) all NP treatments and 26 and 32 PSU

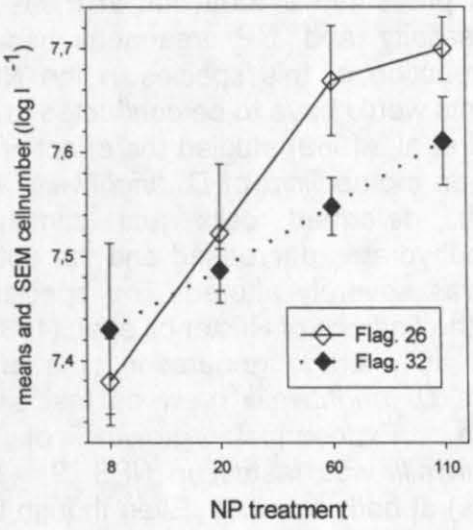


With an average generation time of 14 hours *D. brightwellii* grew as fast as *T. rotula.* Exponential growth of *D. brightwellii* was fastest in NP8 (9 - 11.4 hours) at both salinities. Even though final cell numbers differed at 26 PSU and 32 PSU for NP20 the generations times remained very comparable with 15 and 15.3 hours. Overall the estimated generation times were slightly slower for the 32 PSU than for the 26 PSU treatments. Comparable generation times of this species were listed with 11.5 - 26 hours for field populations and about 16 hours for lab cultures in a review of Furnas (1990).

The *Rhodomonas* flagellates reacted strongly to the different NP treatments (Fig. 153, 154), but the species never accounted for much of the total biomass. Mean cell numbers increased continuously with rising NP ratio up to

NP60 (Fig. 159, symbol triangle down, "Rho26" and "Rho32"). A significant gain in cell numbers was calculated for NP 8 towards the other treatments as well as for NP 20 towards all higher treatments. Only at 32 PSU the increase between NP8 and NP20 was not significant. With rising NP treatment the respective Si:N ratio dropped, since all enclosures had the same initial silicate concentration. Thus the increase of *Rhodomonas* cell counts with increasing NP level is comparable to results of competitive exclusion experiments between diatoms and flagellates conducted by Sommer (1994). *Rhodomonas* gained maximum relative importance at low Si:N ratios in his experiments, combined though with low irradiance levels. Generation times of *Rhodomonas* around 30 hours in the enclosures remained slow compared to *D. brightwellii.*

Fig. 160: Means and SEM
flagellates <5µm; log transformed cell numbers (163-211h) for all NP treatments and 26 and 32 PSU



The small flagellates displayed a swinging pattern over time (Fig. 155, 156). Like *Rhodomonas,* they continuously increased their mean cell numbers with rising NP ratios (Fig. 160). Significant increases of flagellate numbers could be proven though only for NP8 versus NP60 and 110 at 26 PSU. Average cell numbers were generally lower in the 32 PSU treatments. The increase with rising NP treatments fits well to the observed increase of flagellates at Helgoland Roads (Hickel et al., 1997). Hickel et al. (1997) also calculated a slight increase of flagellates <10 µm in less haline water, which may be reflected in the 26 PSU treatment. Large and small microflagellates tend to exhibit a wide possible range of generation times, collected for example in Furnas (1990). Generation times for the flagellates in the enclosures averaged to about 17.5 hours with strong deviations.

D. brightwellii was the major contributor to the standing stock in all treatments (Fig. 161 a), 162 a)), followed by *T. weisflogii.* All differences in between treatments for sum parameters like chlorophyll values or particulate organic matter must have been mainly influenced by the reaction of these two species, since *T. punctigera, T. rotula, Rhodomonas* and the flagellates < 5µm did not contribute a large percentage to the standing stock in the enclosures.

Fig. 161 and 162: Contribution (%), of the different species to the total biomass
All NP treatments with standard deviations of the three replicates. Fig. 161a) and 162 a) display species exceeding 10% contribution (Tw= *T. weisflogii*, Tp = *T. punctigera*, Db= *D. brightwellii*) at 26 and 32 PSU; Fig. 161 b) and 162 b) display species contributing less than 10% (Tr = *T. rotula*, Rho= *Rhodomonas*, Mni= small flagellates (<5µm).

Fig. 161 a)

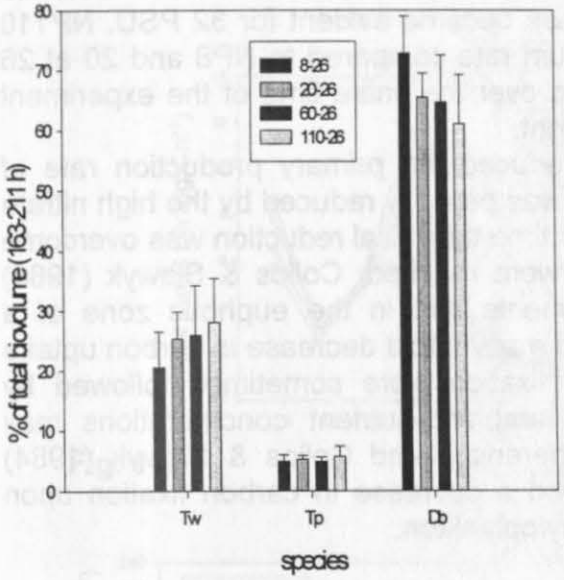


Fig. 161 b)

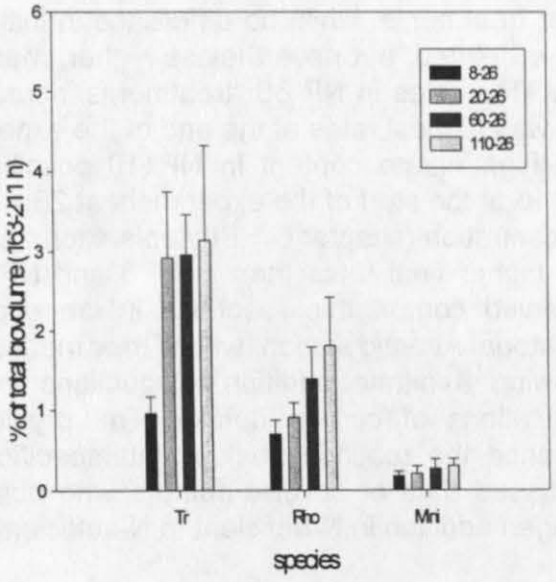


Fig. 162 a)

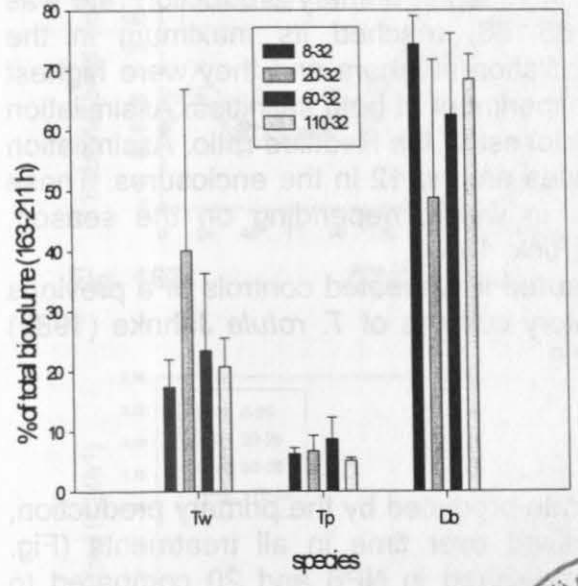
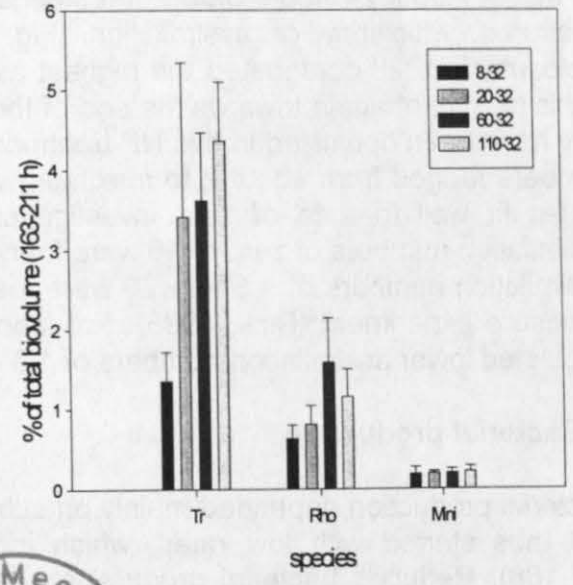


Fig. 162 b)



6.2. Rates

a) Primary production

A prolonged increase in primary production activity was observed with rising NP treatment (Fig. 163, 164) and maximum production rates above 1500 mg C m^{-3} d^{-1} were reached in some treatments. Rates for the last days of the enclosures were highest for NP60 and 110, followed by NP20 and NP8. The strongest difference developed between the nitrogen deficient treatments NP8 and all others.
At 26 PSU the initial increase in production rate was less steep for NP110 than for the other treatments, while no difference in initial rise became evident for 32 PSU. NP110 had a belated, but nevertheless higher, maximum rate compared to NP8 and 20 at 26 PSU. The rates in NP 60 treatments increased over the entire time of the experiment and was highest rates at the end of the experiment.
The high nitrate content in NP110 possibly reduced the primary production rate of NP110 at the start of the experiment at 26 PSU was possibly reduced by the high nitrate concentration (chapter 6.1 Phytoplankton). Over time this initial reduction was overcome and higher final rates than in NP8 and NP20 were reached. Collos & Slawyk (1984) observed comparable reactions in lab experiments and in the euphotic zone of a Equatorial Atlantic station, where they measured a sevenfold decrease in carbon uptake following a nitrate addition. Reductions in C fixation were sometimes followed by stimulations of carbon uptake. The previous ambient nutrient concentrations may influence the reaction besides interspecific differences and Collos & Slawyk (1984) discussed data of several authors who observed a decrease in carbon fixation upon nitrogen addition in N-deficient to N-sufficient phytoplankton.

Calculated assimilation numbers offer a better way of comparison with literature data, since absolute primary production rates are very dependent on the ambient biomass of the algae. About 24 hours before the steepest increase in primary production rate was measured, efficiency of assimilation (Fig. 165,166) reached its maximum in the enclosures. NP20 contributed the highest assimilation numbers and they were highest in this treatment again towards the end of the experiment at both salinities. Assimilation may have been optimized in this NP treatment closest to the Redflied ratio. Assimilation numbers ranged from about 2 to maximum values around 12 in the enclosures. These values fit well to data of field investigations, in which, depending on the season, assimilation numbers of zero to 10 were found (Rick, 1990).
Assimilation numbers of < 5 to > 20 were measured in untreated controls of a previous enclosure experiment (Rick, 1993). For laboratory cultures of *T. rotula* Jahnke (1982) calculated lower assimilation numbers of 1.3 - 2.9.

b) Bacterial production

Bacterial production depended mainly on substrate produced by the primary production, and thus started with low rates, which increased over time in all treatments (Fig. 167,168). Reduced bacterial production was measured in NP8 and 20 compared to NP60 and 110 at 32 PSU, indicating less substrate for the bacteria to grow on. In the 26

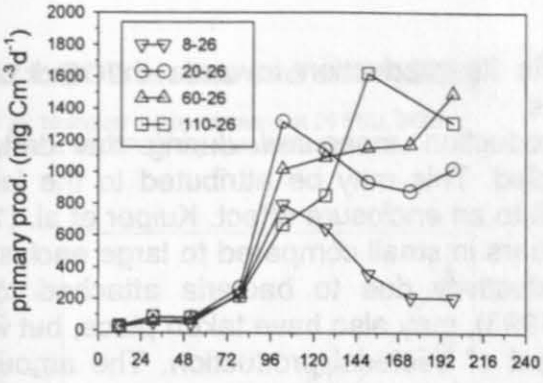


Fig. 163

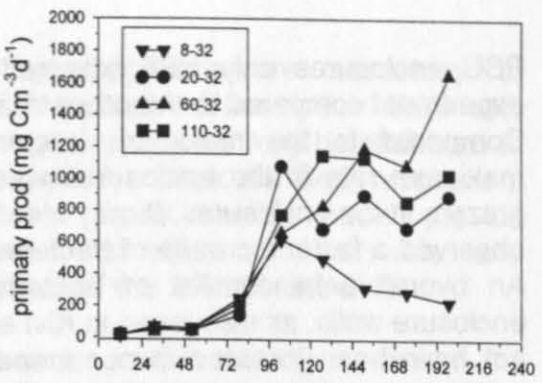


Fig. 164

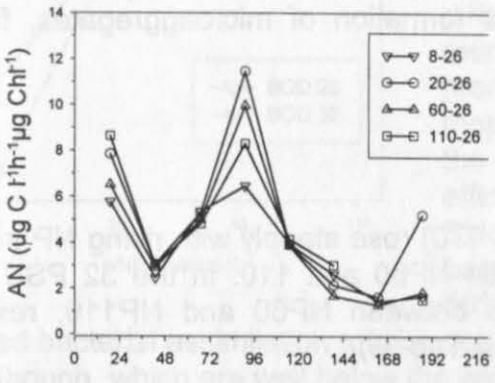


Fig. 165

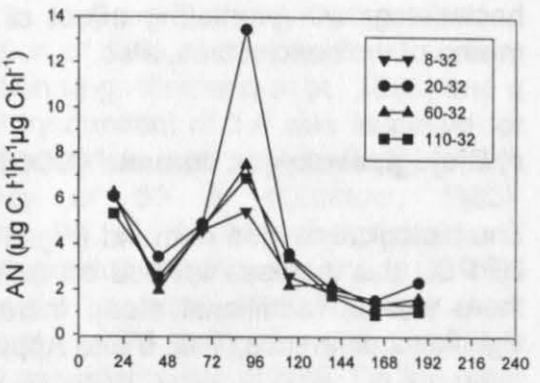


Fig. 166

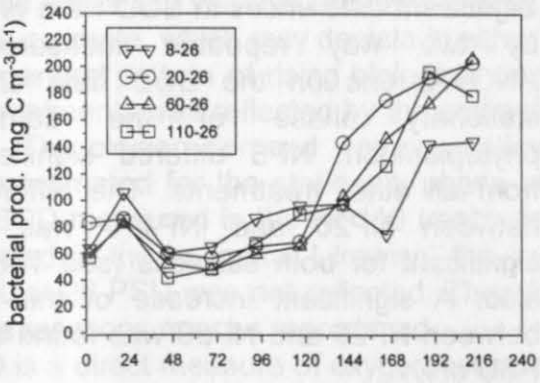


Fig. 167

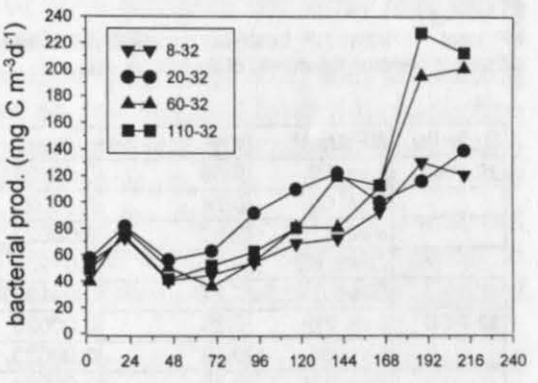


Fig. 168

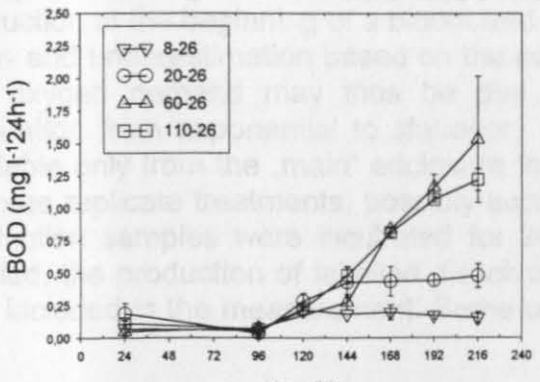


Fig. 169

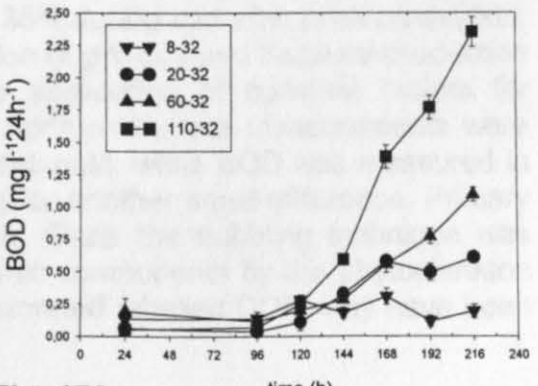


Fig. 170

PSU enclosures only NP8 was reduced in its production towards the end of the experiment compared to the other treatments.
Compared to the maximum bacterial production measured during the drift, the maximum rate in the enclosures was doubled. This may be attributed to the lack of grazers in the enclosures. It may also be due to an enclosure effect. Kuiper et al. (1983) observed a faster increase of bacterial numbers in small compared to large enclosures. An overall enhancement of bacterial productivity due to bacteria attached to the enclosure walls, as discussed in Kivi et al. (1993), may also have taken place, but would not have been included in our measurement of bacterial production. The amount of particulate carbon produced during the runtime of the enclosures was generally higher though, than the standing stock found towards the end of the drift, thus a higher particle density in the water was offered for attached bacteria. Kivi et al. (1993) discussed the bacterial growth promoting effect of the formation of microaggregates, favoured by mixing of their enclosures, also.

c) Biological oxygen demand (BOD)

The biological oxygen demand (Fig. 169, 170) rose steeply with rising NP treatment. At 26 PSU this increase leveled off between NP60 and 110. In the 32 PSU treatments there was an additional steep increase between NP60 and NP110, resulting in a significant difference (Tab. 9 and Appendix Tab. G).

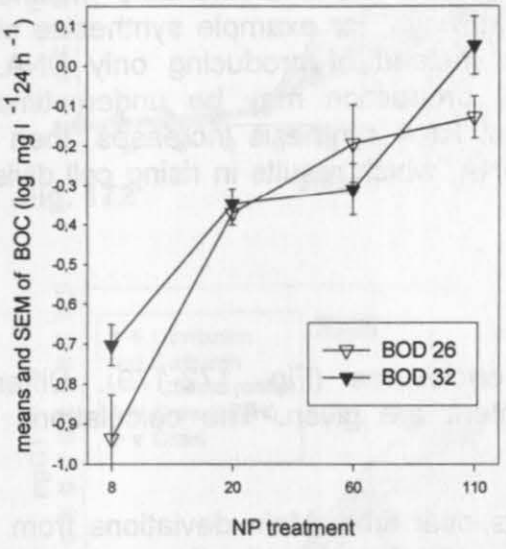
Tab. 9: Signficant differences in BOD (Tukey)
NP treat = initial NP treatment number; diff. Means= difference between the means of the treatments.

Salinity	NP treat	diff. means	p-level
26 PSU	8 vs. 20	0.56	0.000231
	8 vs. 60	0.74	0.00023
	8 vs. 110	0.81	0.00023
	20 vs. 60	0.18	0.01255
	20 vs. 110	0.24	0.001987
32 PSU	8 vs. 20	0.35	0.00023
	8 vs. 60	0.39	0.00023
	8 vs. 110	0.75	0.00023
	20 vs. 110	0.4	0.00023
	60 vs. 110	0.36	0.00023

Significant differences in BOD were proven by two way repeated measurement ANOVA runs on the BOD data of the stationary phase of the dominant phytoplankton. NP8 differed significantly from all other treatments. The difference between NP20 and NP110 was also significant for both salinities (see Tab. 9), also. A significant increase of the BOD between NP20 and NP60 was found at 26 PSU only.
The calculated means of BOD (Fig. 171) displayed a continuous rise with increasing NP treatment.

Fig. 171: BOD means and error (SEM)

BOD 26: biological oxygen demand at 26 PSU, BOD 32: demand at 32 PSU; log transformed data 163 - 211h



Further investigations are necessary to reveal, how much of the rise in BOD with increasing nitrate levels may be attributed to bacterial and/or phytoplankton respiration. Results of these studies could provide important information on the role and significance of this effect in the field.

The measured BOD was compared to the oxygen demand estimated from the bacterial and primary production in the enclosures to gain information on the relation of these different approaches. A phytoplankton respiration of 15% of the measured primary production (e.g. Riemann et al., 1993) and a respiratory quotient of 1.4 was assumed for the estimation as well as a bacterial growth efficiency of 50 % (Ducklow, 1983). Biddanda et al. (1994) also determined bacterioplankton growth efficiencies of 26 - 50% on the Louisiana shelf. Pomeroy et al. (1995) stated bacterial assimilation efficiencies of only 1-28% during summer in the Gulf of Mexico, though, which are well below the widely assumed value of 50%. On the other hand efficiencies above 80% were reached in laboratory cultures supplied with an optimal mixture of substrates (Payne & Wiebe, 1978). Obviously the growth efficiencies can be extremely variable and the applied factor of 50% bacterial efficiency remains a rough estimate, which may deviate in either direction in reality.

The general pattern of rising biological oxygen demand (Fig. 169, 170) with increasing NP treatments was reflected by the estimate based on primary and bacterial production data. The oxygen demand was overestimated though for the exponential phase and underestimated for the stationary phase of the phytoplankton. The strong increase of the BOD measured in the NP110 treatment compared to the NP60 at 32 PSU was not reflected in the estimate. Likewise, the lower BOD of NP60 at 32 PSU compared to NP60 at 26 PSU was not reflected. Therefore, further experiments should investigate if these reactions may be reproduced.

BOD is a direct measure of oxygen consumption, while primary production rates as well as bacterial thymidine uptake may only be tranferred into estimated oxygen demand. Respiration may also differ with physiological status. Keller & Riebesell (1989) for example found nighttime respiration of phytoplankton to be about 10% of the daytime production at the beginning of a bloom and about 35% during and after peak production. Over- and underestimation based on the conversion of primary and bacterial production into oxygen demand may thus be due to the application of constant factors for respiration from exponential to stationary state. Additionally rate measurements were available only from the „main" enclosure for this estimate, while BOD was measured in all three replicate treatments, possibly accounting for another small difference. Primary production samples were incubated for 24 hours. Since the bubbling technique was applied, the production of labelled dissolved organic components by the phytoplankton was included in the measurement. Some of the excreted labelled DOM may have been

consumed by bacteria and possibly lost again through respiratory processes prior to the measurement. Primary production may thus have been underestimated especially during times of high production of DOM by the phytoplankton and strong bacterial consumption. Bacterial production may also be underestimated by the applied measurement of thymidine uptake. Bacteria possibly do not take external thymidine for DNA synthesis or they assimilate it on other pathways, for example synthesize other macromolecules to build up RNA or proteins instead of producing only DNA. In conditions of unbalanced growth the biomass production may be underestimated additionally by the thymidine method, since first RNA synthesis increases, then the production of proteins and only finally of new DNA, which results in rising cell division rates (Chin-Leo & Kirchman, 1988).

d) Carbon balance

Carbon balances were calculated for the enclosures (Fig. 172-179). Different approximations for the particulate carbon content are given. The calculations are described in chapter 3.5 d).

All approaches yielded fairly comparable results over time. Main deviations from the particulate carbon measured by flash-combustion were found for the the content based on cell size (Fig. 172-179). In the exponential growth phase the carbon content was overestimated by conversion of cell volume into pC, especially for NP8. During the development of the phytoplankton community towards stationary state, the carbon content per cell increased and was underestimated by the constant factor. Calculations ended up close to the values given by flash-combustion during stationary state only in the nitrogen deficient treatments NP8.

Fig. 163 - 170: Carbon balance in the enclosures

Mean particulate carbon data of all 3 replicate treatments produced by flash-combustion ***("C combustion", symbol: filled circles)*** are plotted together with the mean carbon content based on calculation from size measurements of the phytoplankton ***("C cells all parallels", symbol: cross).*** Furthermore two different estimates of the carbon content based on the rate measurements of primary production and bacterial production are given.

"C rates" (symbol: filled upside down triangle) is based only on the initial value of particulate carbon measurement by flash-combustion. The increase of pC over time was calculated by adding the amount of C produced by primary production and subtracting bacterial respiratory losses. Consecutive estimates were based on the estimate of the respective previous day.

„C rates (daily init)" (triangle) is based again on the initial value of pC measurement by flash-combustion. The carbon change between the first and second day based on primary and bacterial production was added to that initial value and plotted for the second day. This estimate for the second day was not used in the further calculation. The carbon change between second and third day based on production rates was added again to the flash-combustion carbon value of the second day and plotted for the third day. Following days were estimated in the same manner. By doing so, this estimate "readjusted" each day to the measured particulate carbon value and thus did not accumulate the differences between flash-combustion and production measurements over time.

"C cells main" (symbol: open circle) refers to the carbon content based on cell volume of the "main" enclosure, since rate measurements (primary production, bacterial production) were also conducted only in the "main" enclosure of the three replicates.

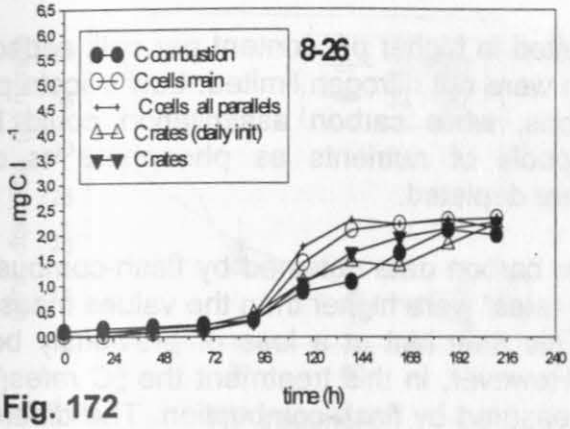


Fig. 172

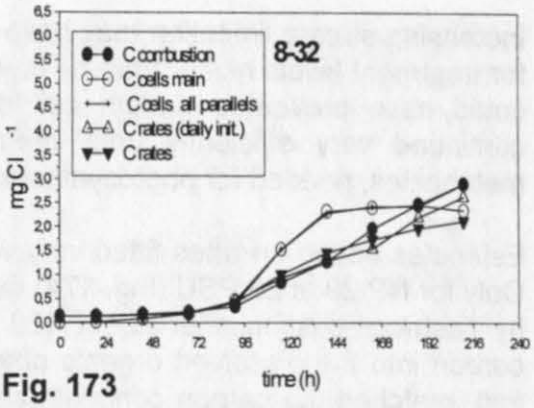


Fig. 173

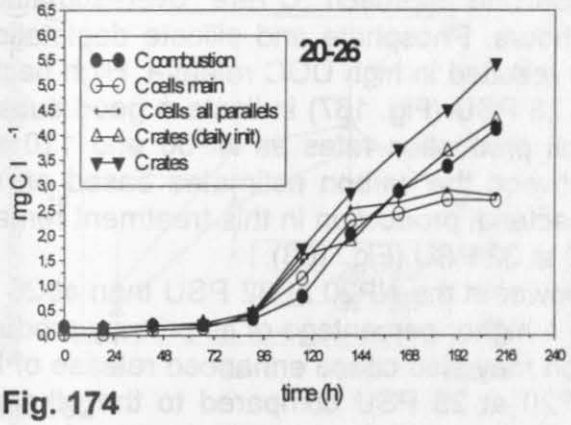


Fig. 174

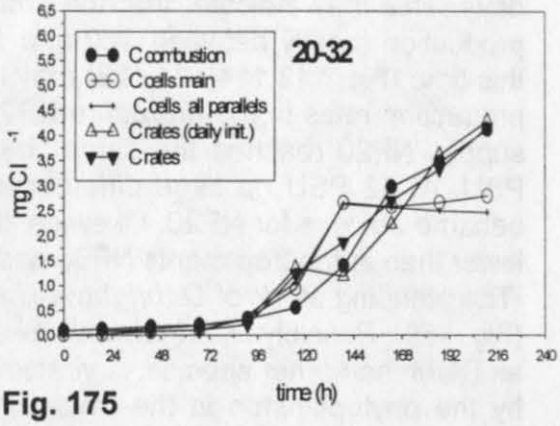


Fig. 175

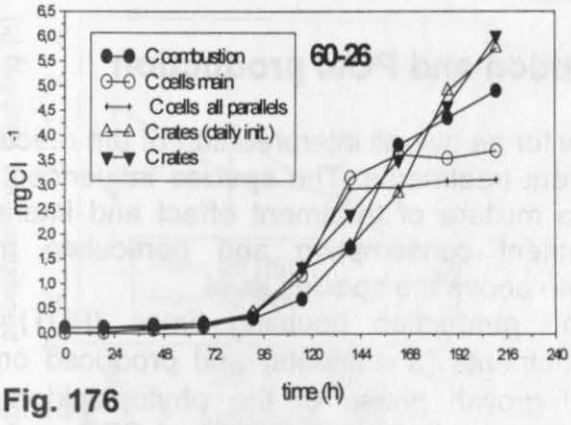


Fig. 176

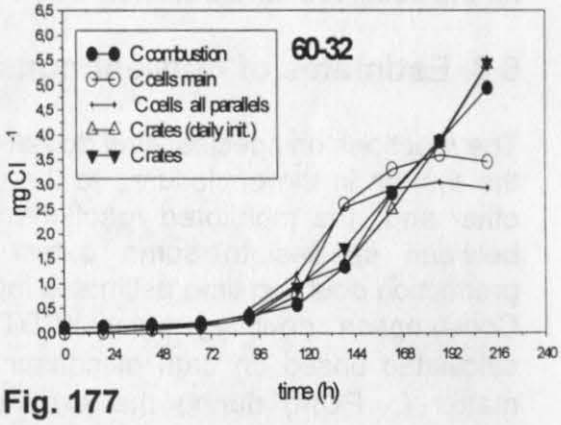


Fig. 177

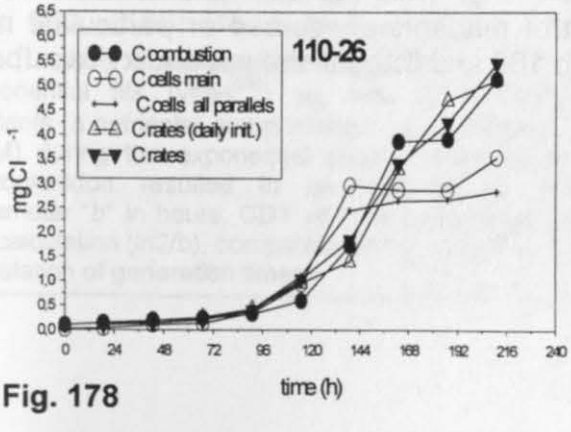


Fig. 178

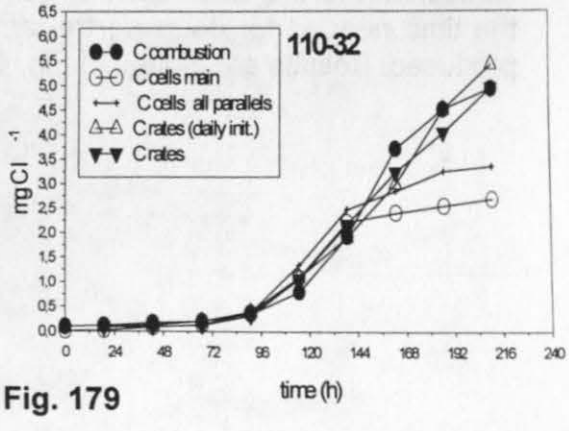


Fig. 179

Increasing silicate limitation may have resulted in higher pC content per cell, especially for treatment levels higher than NP8, which were not nitrogen limited. Low silicate pools could have prevented diatom cell divisions, while carbon assimilation could have continued very efficiently until internal pools of nutrients as phosphate or other metabolites, needed for photosynthesis, were depleted.

Estimates based on rates fitted very well to carbon data obtained by flash-combustion. Only for NP 20 at 26 PSU (Fig. 174) the „C rates" were higher than the values measured by flash-combustion after about 120 h. This may hint at a loss of previously bound carbon into the dissolved organic phase. However, in this treatment the *„C rates(daily init)"* matched the carbon concentration measured by flash-combustion. The difference between this *„C rates(daily init)"* and the *„C rate"* remained about equal for the last 4 days. This may indicate, that the production rate approach *„C rate"* overestimated pC production mostly between 120 and 144 hours. Phosphate and silicate depletetion at this time (Fig. 113,114,121,122) may have resulted in high DOC release. High bacterial production rates in the enclosure NP20 at 26 PSU (Fig. 167) indicate a good substrate supply. NP20 reached the same bacterial production rates as NP60 and 110 at 26 PSU. At 32 PSU no large differences between the carbon estimates based on rates became obvious for NP20. Likewise, the bacterial production in this treatment remained lower than in the treatments NP60 and 110 at 32 PSU (Fig. 168).
The standing stock of *D. brightwellii* was lower in the NP20 at 32 PSU than at 26 PSU (Fig. 159). Possibly *D. brightwellii* released a higher percentage of its primary production as DOM than other species. A viral infection may also cause enhanced release of DOM by the phytoplankton in the treatment NP20 at 26 PSU compared to the others. No deteriorating cells became obvious though during microscopic analysis, thus the reason for the observed difference remains uncertain.

6.3. Estimates of nutrient consumption and POM production

The reactions on species level do not allow for an overall interpretation of the reaction of the system in the enclosures to the different treatments. The species influenced each other and the monitored reactions are a mixture of treatment effect and interaction between species to some extent. Nutrient consumption and particulate matter production doubling time estimates integrate above the species level.
Consumption doubling times (CDT) and production doubling times (PDT) were calculated based on data of consumed nutrients (Δ nutrients) and produced organic matter (Δ POM) during the exponential growth phase of the phytoplankton. The exponential fit parameter "b" ($y=ae^{(bx)}$) was used in the calculation of CDT and PDT, comparable to the calculation of generation time. Thus the CDT and the PDT indicate the time needed for doubling the amount of nutrients consumed or particulate matter produced. Results are plotted in Fig. 180 to 186 and listed in the appendix (Tab. I, J).

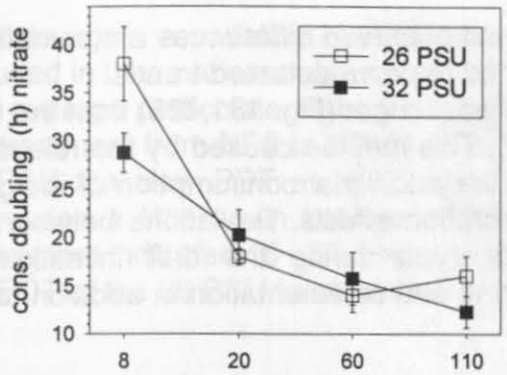


Fig. 180

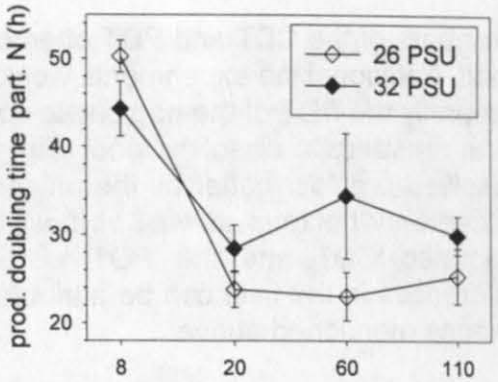


Fig. 181

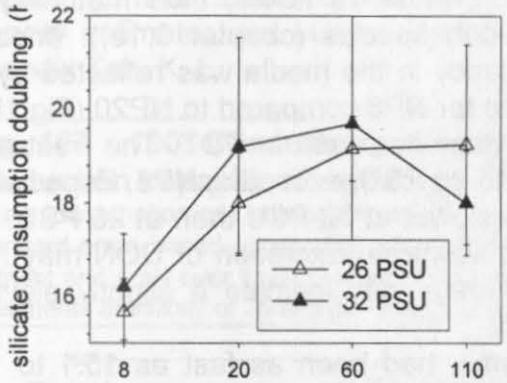


Fig. 182

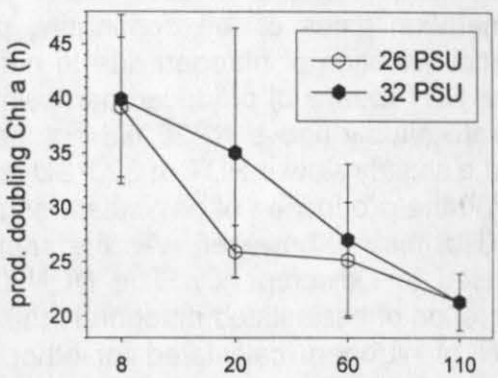


Fig. 183

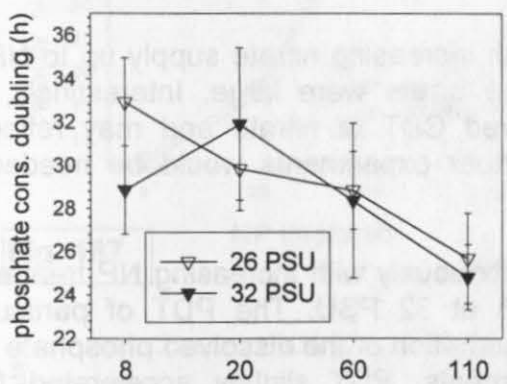


Fig. 184

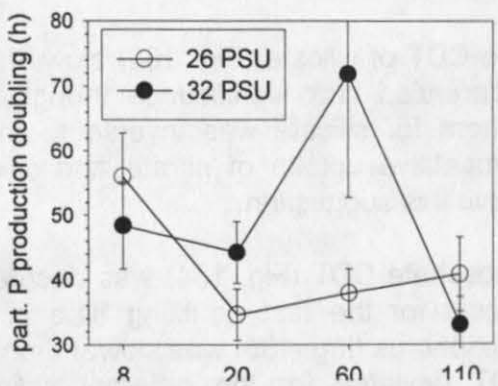


Fig. 185

Fig. 180 - 186: Consumption (CDT) and production doubling times (PDT)

Exponential fits ($y=ae^{(bx)}$) on data of consumed nutrients (Δ nutrients) and produced organic matter (Δ POM) during the exponential growth phase of the phytoplankton resulted in an estimate for the parameter "b" in hours. CDT and PDT are based on the calculation (ln2/b), comparable to the approach for calculation of generation times.

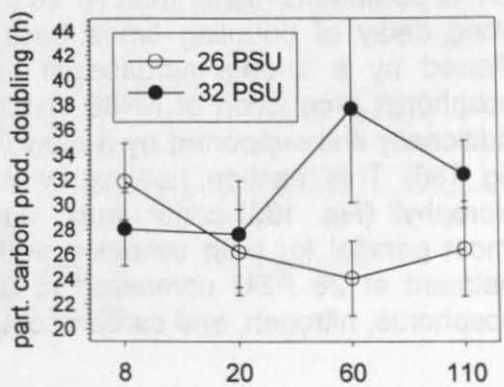


Fig. 186

Error bars of the CDT and PDT often overlapp and observed differences are sometimes small. Additional lab experiments would be needed to prove detected trends.
Generally the PDT of the particulate component was longer (Fig. 181,185) than the CDT for the respective dissolved pool (Fig. 180, 184). This may be caused by the release of dissolved organic matter by the phytoplankton, the additional consumption of inorganic nutrients by bacteria as well as possible wall sorption effects. Deviations between the estimated CDT and the PDT were also observed during the drift investigation. Differences in the field can be attributed to grazing and sedimentation in addition to the reasons mentioned above.

The consumption doubling time of nitrate (Fig. 180) was slow in nitrogen deficient conditions compared to surplus situations. An increasing speed was observed even between NP20 and NP60. Fastest CDT were around 15 hours, thus matching the generation times of the dominating phytoplankton species (chapter 6.1e)). Impaired particularisation of nitrogen due to nitrate deficiency in the media was reflected by the slow PDT means of produced particulate nitrogen for NP8 compared to NP20 (Fig.181). Nitrate supply above NP20 did not induce a further decrease in PDT. The treatments had a slightly slower PDT at 32 PSU compared to 26 PSU, excepting NP8. Especially in NP60 the production of particulate nitrogen was slower at 32 PSU than at 26 PSU. The CDT of nitrate, however, was the same at both salinities. Excretion of DON may have caused this discrepancy. The DON (Fig. 126) data may indicate a slightly elevated excretion of assimilated nitrogen in this treatment.
PDT of nitrogen, calculated for other mesocosms, had been as fast as 15.1 to 17.2 hours, depending on the silicate supply (Rick, 1993). PDT of 22 - 50 hours for the different NP treatments in the enclosures may thus be considered as being slow compared to these results.

The CDT of silicate (Fig. 182) slowed down with increasing nitrate supply up to NP60. Differences lack significance though, since the errors were large. Interestingly, the pattern for silicate was inverse to the observed CDT of nitrate and may reflect a competitive uptake of nitrate and silicate. Further experiments would be needed to prove this suggestion.

Phosphate CDT (Fig. 184) was decreasing continuously with increasing NP treatment, except for the fast doubling time in the NP8 at 32 PSU. The PDT of particulate phosphorus (Fig. 185) was slower than the consumption of the dissolved phosphate and PDT deviated for the different salinity treatments. PDT slightly accelerated from deficient (NP8) to sufficient nitrate conditions (NP20) at both salinities.
PDT of treatments higher than NP20 then slightly slowed down at 26 PSU. At 32 PSU a strong delay of doubling times became obvious between NP20 and NP60. It was followed by a strong increase in speed of PDT. The "peak" of slow particulate phosphorus production of NP60 at 32 PSU is supported by 15 single measurements. Additionally it is supported by a slow PDT of particulate nitrogen (Fig. 181) and carbon (Fig. 186). This reaction, however, was not reflected in the chlorophyll PDT. The PDT of chlorophyll (Fig. 183) continuously decreased with increasing NP treatment and were almost parallel for both salinities, with the exception of the faster PDT in the NP20 treatment at 26 PSU compared to 32 PSU. The different reaction of of particulate phosphorus, nitrogen, and carbon compared to chlorophyll PDT in NP60 at 32 PSU may

indicate again a variation in PDT due to the loss of DOM, while chlorophyll was not included in these release processes.
The average particulate carbon (Fig. 186) PDT was slightly decreasing with increasing NP treatment from NP8 to NP 20 at 26 PSU and remained about leveled thereafter. At 32 PSU the slow PDT at NP60 reflected the reaction of pP and pN. Average PDT decreased a little again between NP60 to NP110. Estimates for another mesocosm experiment indicated 15 - 27.3 hours PDT for pC (Rick, 1993), which was in the range of the PDT of the 26 PSU treatments.

Logistic fits were applied to estimate consumption capacities (nitrate, silicate, phosphate) and production capacities (particular nitrogen). These may be used to compare the final nutrient consumption and POM prduction in the different enclosures. Capacity estimates are summarized in Tab. 10 and further details may be found in Appendix Tab. K, L.

Fig. 187 - 190: Consumption capacities of dissolved inorganic nutrients and production capacity of particulate nitrogen
Mean consumption and produciton capacity estimates (µM) of the triplicate treatments with respective standard error; based on significant logistic fits ($y= a/(1+((a-b)/b)\cdot euler^{(-cx)})$) applied on the data of Δ nutrient and Δ pN over time. Treatment number = code for respective NP treatment; 26 and 32 PSU= treatments at salinity of 26 and 32 PSU; part.N= particulate nitrogen

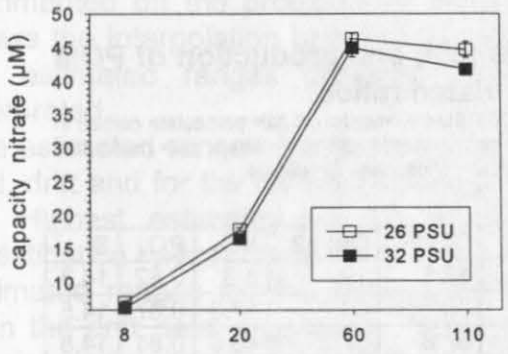


Fig. 187

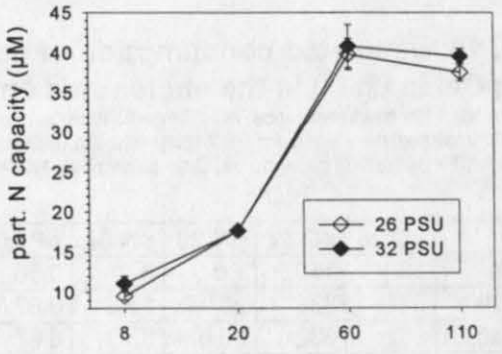


Fig. 188

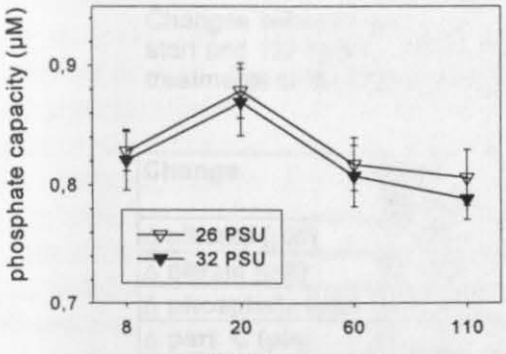


Fig. 189

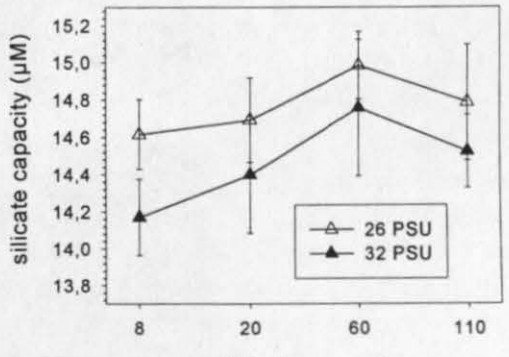


Fig. 190

Average nitrate consumption and particulate nitrogen production capacities were very comparable and parallel for both salinity treatments (Fig. 187, 188). A steep increase in capacity from deficient to sufficient and surplus nitrate treatments was followed by a leveling or slightly decreasing capacity at NP110.
Since silicate levels were not changed in the treatments capacity variations (Fig. 189) were small and standard errors overlap. The average indicated a slight increase in capacity with improved nitrate supply, reaching a maximum at NP60. At 32 PSU an overall lowered silicate capacity compared to 26 PSU became obvious, again lacking significance though. Phosphate capacity (Fig. 190) was highest at NP20, followed by almost leveled capacities in NP8, NP60 and NP110. Values were very similar at both salinities over all NP treatments.

Average capacities for the stationary phase were calculated for pC and pP, since the logistic function, though being overall significant for these parameters, fitted to capacities that were higher than the measured data suggested. For chlorophyll average values had to be used, since a logistic fit became impossible due to decreasing concentrations towards the last day of the experiment. The consumption and production capacity values (Tab 10) as well as their ratios will be discussed in detail in the following chapter and compared to the results of the drift experiment.

Tab. 10: Estimated consumption of nutrients (µM) and production of POM (µM; Chl in $\mu g \cdot l^{-1}$) in the enclosures and calculated ratios
NP 8 to NP 110= treatment ratios; pC 26= particulate carbon gain in 26 PSU treatments; pC 32= particulate carbon in 32 PSU treatments; numbers for PSU treatment are applied in the same manner for the other labels; pN= particulate nitrogen, pP= particulate phosphorus, Chl= chlorophyll, NO_3= nitrate, PO_4 = phosphate, Si=silicate.

	pC 26	pC 32	pN 26	pN 32	pP 26	pP32	Chl 26	Chl 32	NO_3	PO_4	Si
NP 8	160	170	7.6	8	0.56	0.65	19,5	19	6.8	0.82	14.3
NP 20	311	339	16	15.8	0.67	0.61	39	39.2	17.3	0.87	14.5
NP 60	362	332	35.6	33.1	0.67	0.58	57.8	57.3	45.6	0.81	14.8
NP 110	360	367	34.8	34	0.68	0.59	50.5	55.8	43.2	0.80	14.7

7. General discussion

Results of the grid samplings, the drift investigation and the enclosures are discussed in the first part of the general discussion with respect to reliablility, differences in overall carbon production and ratios. The Elbe - German Bight system is compared to the Mississippi - Louisiana shelf system and possible management approaches are discussed in the second part.

1. Comparison between grid, drift investigation and enclosure experiment

The estimation of biologically induced turnover of nutrients and organic matter from consecutive grid samplings remains difficult, even when a hydrodynamic model is applied to account for advective processes. The lagrangian model water particles of grid 1 for example, did not necessarily move onto some point of measured data in grid 8 (see chapter 4.3). Estimates of changes in nutrients and particulate matter were based on a comparison of values that were only regionally close to each other and the procedure remained subjective to a certain extent. Though large-scale monitoring studies have provided valuable insight into plankton ecology they have their limitations, including the very different spatial and temporal scales on which different planktonic phenomena may take place. Bohle-Carbonell (1994) critically commented on the problems of defining a suitable measurement strategy, which allows the interpolation between two sampling sites. With these drawbacks in mind the estimated ranges obtained from the grid samplings should be carefully interpreted.
The estimated range of nutrient consumption and POM production are listed for the grid, drift and for the different treatments in the enclosures in the summarizing table 11. Highest estimates for the consumption of dissolved nutrients in the grid investigation were close to the estimated consumption in the drift. However, estimated ranges for the produced particulate carbon and chlorophyll were lower than the drift data suggested. This indicated that strong additional processes, like grazing and sedimentation, were superimposed on pure advective transport.

Tab. 11: Comparison of estimated changes
Changes between grid 1 and grid 8 ("Grid"), between the start and 192 hours of the drift ("Drift") and in the different treatments of the enclosures ("Enclosures")

Change	Grid (model)	Drift (datafit)	Enclosures (datafit)
Δ silicate (µM)	2 - 25	19	14.5
Δ nitrate (µM)	0 - 23	23	6.8 - 45.6
Δ phosphate (µM)	0 - 0.75	0.67	0.80 - 0.87
Δ part. C (µM)	0 - 75	148	160 - 367
Δ part. N (µM)	0 - 20	21	7.6 - 34.8
Δ Chl a (µg l^{-1})	0 - 38	84	19 - 55.8

The successful drift investigation produced more reliable estimates for net nutrient consumption and production of POM for the tracked surface layer, but again the effects of grazing and sedimentation on the overall change were not quantified. This insufficiency may have been the major reason for the observed differences in the particulate carbon and nitrogen estimates compared to the enclosure experiment. Especially the amount of produced carbon estimated for the drift was low (Tab. 11), considering that initial nutrient conditions of the drift closest resembled those in the highest NP treatments in the enclosures. These reached a production of more than 300 µM carbon (Tab. 12). Carbon loss due to sedimentation may have been enhanced towards the end of the drift, when the bloom began to stagnate. Senescence was induced by an increasing depletion of phosphate and silicate in the water (Fig. 77, 78, 85, 86). The assumption of a more stationary bloom after 198 h was supported by reduced primary production rates (Fig. 109), a loss of particulate organic matter (Fig. 112 a, b) and rising particulate carbon to chlorophyll ratios (Fig. 101 a) at the central station. Grazing pressure by a growing standing stock of grazers probably increased over time. The biomass of small zooplankton was included in the POM measurements. Respiratory carbon losses though, a possible sloppy feeding and the excretion of carbon-rich fecal pellets may account for additional reductions of POM. A rising mesozooplankton respiration was estimated over the time of the drift. It accounted for an average of 1.4 g C $m^{-2}d^{-1}$ or 16,5% respiration of the daily primary production at the central station. Highest values exceeded 2 g C $m^{-2}d^{-1}$ (Rick et al., submitted). An increasing proportion of total respiration was attributed to bacteria and heterotrophic nanoflagellates towards the end of the drift, indicating further senescence of the system. The turbidity in the river plume may have caused an additional underestimation of Δ pC, as initially non-living particles from the turbidity zone may have contributed to the measured particulate carbon values. As the drifter gained distance to the Elbe estuary some of these particles sedimented from the surface layer and reduced the measured gain of carbon to some extent. A Δ pC/Δ Chl ratio (weight/weight) of 21 for the drift (Tab. 11) possibly supports the suggestion of an underestimated carbon production, as this ratio seems to be a little too low for a phytoplankton community transgressing towards a stagnant growth.

Experimental approaches overcome many of the problems encountered in the field, but they also create new ones. The enclosures excluded processes like advection and grazing as well as resuspension of sediment. A contribution of non-living particles to the particulate carbon in the water column was likewise prevented. Wall sorption effects were added due to the experimental setup, compared to field investigations. Losses due to wall adsorption were small because the water for the enclosures was filtered and no organisms were inocculated that tend to attach to surfaces. In addition the short runtime of the experiments prevented strong periphyton growth on the enclosure walls. Some species may also selectively profit from the removal of grazers. When the grazing pressure artificially is reduced, small fast growing species may outcompete others. The agreement of enclosure results with processes in the field may thus vary depending on the experimental design and setup. Despite their drawbacks meso- and microcosms often are the only method available to study processes in a system (Pomeroy & Wiebe, 1988 in Kivi et al., 1993). They offered the best approach to measure the maximum amount of carbon possibly produced by algae and bacteria with a given amount of nutrients. The observed reaction of the plankton on rising N:P ratios may be well applicable to the field in situations of negligible grazer influence on nutrient recycling and POM consumption. The maximum amount of possibly bound particulate carbon may be an

important information for coastal management, because oxygen deficiencies could be caused during its remineralisation. Maximum carbon storage may vary with species, as the nitrogen storage capacitiy does (Dortch, 1982; see also chapter 4.1 e), and further investigations would have to test, if these differences are large enough to have an effect in the field.

Limiting nutrients for phytoplankton growth are often evaluated by enrichment experiments or by calculating ratios between inorganic nutrients in the water samples and comparing them to estimates of corresponding ratios in phytoplankton biomass (Redfield et al. 1963; Beers & Herman, 1969). These calculations need to be applied carefully, since they neglect the dynamic trophic relationships within the planktonic community. As Banse (1974 a) already warned, the ratio of removal of inorganic nitrogen and phosphate from the photic layer of the sea should not be interpreted as the elemental ratio in newly formed phytoplankton or POM. Especially the production of dissolved organic components results in higher consumption of nutrients compared to the amount measured in the algae. In addition to ambient nutrient concentrations the availability of nutrients for primary producers may also depend on the intensity of DOM excretion, the regeneration rate of nutrients and in some systems on nutrient competition between algae and bacteria. In situations of high standing stocks of zooplankton the algal carbon may be overestimated in the field, because small zooplankton is generally included in the carbon analysis (Banse, 1974 b). Sedimentation and grazing may reduce the absolute carbon amount, but also may change the C:N:P ratio of particulate matter. Fecal pellets for example tend to be a lot poorer in nitrogen than the food source of the grazer (Anderson, 1994) and grazers enhance the recycling of nutrients by their excretion of nitrogen compounds. Non-living particles may contribute to an unknown extent to the measured carbon, phosphorus or nitrogen content. Banse (1977) suggested, that the dissolved organic phase itself may even be responsible for the formation of non-living particles in the sea. More recent investigations on "mucilagine" in the Adria (Stachowitsch et al., 1990) and on transparent exopolymeric particles (TEP) off the californian coast (Passow & Alldredge, 1994) support this hypothesis. The amount of carbon bound in these particles is probably of minor importance though, compared to other particular carbon sources (Passow, pers. comm.).

Estimated changes in dissolved inorganic nutrients and POM for the drift and the different enclosure treatments were converted to ratios (Tab. 12) and compared to the Redfield ratios. In the enclosure treatments NP20, NP60 and NP110 as well as in the drift less particulate nitrogen production was measured than nitrate consumption, supporting the criticism of Banse (1974 a). Deviations were strongest for the highest treatments in the enclosures. This may be attributed to enhanced excretion of DON with rising or excess nitrate supply. Slightly more particulate nitrogen was measured in the NP8 treatment compared to the consumption of nitrate. Nitrogen deficient enclosures may have assimilated dissolved organic nitrogen in addition to a lesser extent of DOM excretion. Deviations can also be found for particulate phosphorus to phosphate (Tab. 12).
The Δ pC:Δ pN ratios were elevated (21 - 10) in the enclosures, whereas they resulted in a ratio expected after Redfield et al. (1963) for the drift. The carbon storage in the stationary phase of the highest NP treatments in the enclosures was more balanced with additional nitrate uptake than in the lower NP treatments, resulting in lower Δ pC: Δ pN ratios. The Δ pC:Δ pP were likewise above the Redfield ratio.

Tab. 12: Estimated consumption of nutrients (µM) and production of organic matter (µM; Chl a in µg l^{-1}) in the drift and enclosures with calculated ratios of the changes

NP 8 to NP 110 = treatment ratios; C = particulate carbon, C 26= C gain in 26 PSU treatments; C 32= C gain in 32 PSU treatments; numbers for PSU treatment are applied in the same manner for the other labels; N= particulate nitrogen, P= particulate phosphorus, Chl a = chlorophyll a, NO_3 = nitrate, PO_4 = phosphate, Si = silicate. Ratios for C:N and C:N:P molar, ratios for C:Chl weight based (g:g); consumption of dissolved nutrients in the enclosures is given as mean value for both salinity treatments since deviations were negligible.

	ΔC		ΔN		ΔP		ΔChl a		ΔNO_3	ΔPO_4	ΔSi
Redfield											
C:N:P	106		16		1						
C:N	6.6		1								
Drift change (µM)	***148***		***21***		***0,48***		***84***		***23***	***0.67***	***19***
C:N:P	308		43,8		1						
C:N	7		1								
C:N:PO_4	221		31.3		0.72					1	
C:Chl (g:g)	21.2						1				
C:Si	7.8										1
Enclosures (PSU)	**ΔC 26**	**ΔC 32**	**ΔN 26**	**ΔN 32**	**ΔP 26**	**ΔP 32**	**ΔChl 26**	**ΔChl 32**	**ΔNO_3**	**ΔPO_4**	**ΔSi**
NP 8 change (µM)	***160***	***170***	***7.6***	***8***	***0.56***	***0.65***	***19.5***	***19***	***6.8***	***0.82***	***14.3***
C:N:P	286	262	13.6	12.3	1	1					
C:N	21.1	21.3	1	1							
C:N:PO_4	195	207	9.3	9.8	0.68	0.79				1	
C:Chl (g:g)	98.6	107.5					1	1			
C:Si	11.2	11.9									1
NP 20 change (µM)	***311***	***339***	***16***	***15.8***	***0.67***	***0.61***	***39***	***39.2***	***17.3***	***0.87***	***14.5***
C:N:P	464	556	23.9	25.9	1	1					
C:N	19.4	21.5	1	1							
C:N:PO_4	358	390	18.4	18.2	0.78	0.7				1	
C:Chl (g:g)	95.8	103.9					1	1			
C:Si	21.4	23.4									1
NP 60 change (µM)	***362***	***332***	***39.8***	***40.8***	***0.67***	***0.58***	***57.8***	***57.3***	***45.6***	***0.81***	***14.8***
C:N:P	540	572	59.4	70.3	1	1					
C:N	9.1	8.1	1	1							
C:N:PO_4	447	410	49.1	50.4	0.83	0.71				1	
C:Chl (g:g)	75.2	69.6					1	1			
C:Si	24.5	22.4									1
NP 110 change (µM)	***360***	***367***	***37.5***	***39.5***	***0.68***	***0.9***	***50.5***	***55.8***	***43.2***	***0.80***	***14.7***
C:N:P	529	622	55.1	43.9	1	1					
C:N	9.6	9.3	1	1							
C:N:PO_4	450	459	46.9	49.4	0.85	0.74				1	
C:Chl (g:g)	85.6	79					1	1			
C:Si	24.5	25									1

The Δ pN : Δ pP ratio of almost 44 for the drift compared well to the range given for the NP60 and NP110 treatments (average of 55). Less nitrogen was stored in the lower NP treatments (ratios below 26). N:P ratios above 30 may indicate phosphorus limitation in the system, while ratios below 10 are supposed to characterize nitrogen limitation (Healey & Hendzel, 1979, Goldman et al., 1979, Suttle & Harrison, 1988). The NP8 treatment thus was close to nitrogen limitation, while NP20 moved close to phosphorus limitation. Ratios in NP60 and NP110 as well as the drift indicated strong phosphorus limitation.

The final ratios ΔpC:ΔpN:ΔpP always were strongly elevated in favour for particulate carbon, compared to the Redfield et al. (1963) ratio. Other publications, which described phytoplankton in limiting situations, supported the observed high ratios. Goldmann et al. (1979) measured cell ratios of 63:5:1 for nitrogen limited cultures of *T. pseudonana* and even 1300:115:1 for phosphorus limited *Monochrysis lutheri*. In times of maximum biomass, C:N ratios up to 25 and C:P ratios up to 750 may be observed in eutrophic lakes (Sommer, 1994).

The concept of Redfield was developed for open oceanic systems and reflects the ratio of the maximum cell quota for nitrogen and phosphorus. Phytoplankton characterized by maximum cell quotas grows at least close to μ_{max}. Maximum growth rates may be reached in oceanic systems, though ambient nutrients are hardly measurable, as they resemble a steady state chemostat culture with zooplankton and bacteria as inflow and overflow mechanisms (Goldman et al., 1979). The low biomass and residual nutrient levels do not preclude the possiblility of high growth rates, because zooplankton grazing and nutrient regeneration within the euphotic zone may keep this highly dynamic system in a balanced state. Goldman et al. (1979) insisted on a clear distinction of coastal and upwelling systems from those oceanic systems. Ratios above Redfield were thus expectable for the nutrient limited systems drift and enclosures (Tab. 12), because the application of Redfield ratios is restricted to situations of maximum growth or when factors other than N or P are limiting (Sommer, 1994). Likewise, ratios close to Redfield were found in the enclosures during the exponential growth phase of the algae.

High Δ pC:Δ Si in the NP20, 60 and 110 treatments of the enclosures reflect the increasing carbon storage in the stationary state. Diatoms still may have sufficient amounts of metabolites to conduct photosynthesis, while the cell division is already inhibited due to silicate deficiency. The pC:Si ratio displays a high variability and strongly depends on the physiological state of the diatoms. Ratios above 20 were reported by Wassmann et al. (1996) for mesocosms dominated by *Skeletonema costatum*, while this species is listed with a twofold lower ratio of 14.3 in data summarized by Brzezinski (1985). Ratios mostly between 2 to 10 are given by Brzezinski (1985), but high ratios were observed in cultures of less silicified species like *Chaetoceros* sp. (25) or *Thalassiosira pseudonana* (20).

The development of the pC:Chl ratio may serve as an indicator for the physiological status of the phytoplankton community in field investigations, as a linear relationship between the ratio and growth rate is predicted (Chalup & Laws, 1990). However, the pC/Chl ratio is not uniquely related to relative growth rate, but strongly influenced by for example illumination conditions (Laws & Bannister, 1980, Chalup & Laws, 1990), so its application as indicator for relative growth rate is limited (Goldman, 1980). Most datasets on the relationship between pigments and other population properties have been derived from steady state in continuous culture (Laws & Wong, 1978, Herzig & Falkowski, 1989, in Davidson et al., 1991). It is unlikely though, that natural populations experience steady-state growth, as nutrient availability is often discontinuous and irradiance varies on a diurnal or even hourly basis. A varying

contamination of phytoplankton samples with nonliving particles (Banse, 1977), as mentioned before and discussed in chapter 5.1.e), also remains a general problem for the interpretation of field data. A typical range of pC:Chl ratios of 25 - 50 was given by Goldman (1980). The ΔpC:ΔChl ratio of the drift were in a comparable range, while ratios were strongly elevated in favour for carbon in the enclosures.

The enclosures indicate that the nutrient supply in the German Bight is still sufficient to induce high carbon fixation by the spring bloom. Increasing N:P ratios above the Redfield ratio may enhance the amount of carbon stored. Phytoplankton, growing on an excess of nitrogen, also accumulates high intracellular concentrations of nitrogen. These may be used for growth, when external nitrogen is not available (Dortch, 1982, Dortch et al., 1984). The accumulated nitrogen may be transported with the particles to regions far away from their origin. Excess nitrate, not consumed by the phytoplankton, may likewise be transported to other regions. A transport of nitrate rich water from the Elbe far to the north was monitored for example in the high runoff years 1987/88 (Hickel et al.,1997). The northwesterly propagation of the eutrophic river water towards the North Sea was probably blocked by frontal systems. *Chrysochromulina polylepis*, a toxic flagellate, also bloomed massively in the Skagerrak/Kattegat region in the year 1988 (Maestrini & Graneli, 1991). It could have been favoured by the high nitrate concentrations in combination with special statification conditions (Gerlach,1990) and its toxicity may have been induced by phosphate deficiency (CEC, 1989; in Hickel et al., 1997).
Nutrients that may have been limiting before, are replenished during remineralization of transported particles, possibly resulting in enhanced production in the respective area. Particle sedimentation and following remineralization may cause oxygen deficits in the bottom water in stagnating conditions. Discussion about the true detrimental effects of eutrophication was provoced by Boddeke & Hagel (1991). They called the eutrophication of the North Sea continental zone during the last decades a "blessing in disguise" and related a decrease of livestock in the Dutch coastal zone to a lowered input of phosphate to the system. Eutrophication of the coastal zones may of course enhance productivity and hence the important fishery yield. However, Cadée & Hegeman (1993) linked the lower secondary production in the respective area rather to overfishing and other causes than to phosphate reduction and stressed the necessity to continue to reduce eutrophication with all efforts. Eutrophication may possibly cause a quantitative change in primary production and a shift in species, which may be detrimental from the human viewpoint (Gerlach, 1990) and the negative effects of an increased primary production probably outweigh the positive effects.

2. Comparison of the Elbe-German Bight and the Mississippi-Louisiana shelf system - implication for management and some research needs

The influence of the Elbe on the German Bight system may be compared to various other systems, like Rhône, Rhine or Po and their adjacent seas. The Mississippi - Louisiana shelf system was chosen because of an excellent available database and certain similarities to the German Bight. Management strategies and some further research needs are discussed for the German Bight.

The NECOP program (Nutrient Enhanced Coastal Ocean Productivity) was initiated in 1989 by the NOAA (National Oceanic and Atmospheric Administration) to investigate the effects of nutrient discharge into the coastal waters of the United States (Wenzel & Scavia, 1993). The Mississippi river - Louisiana shelf sytem was chosen as the initial study site for NECOP, since a significant impact of increased anthropogenic eutrophication on productivity and water quality was observed in this system (Atwood et al., 1994). A close coupling between nutrient discharge of the river, net productivity and hypoxia were revealed and their extent indicated the detrimental effects of eutrophication on the entire coastal environmental quality (Rabalais et al., 1996). The Mississippi as well as the Elbe main river channel were morphologically altered in history, combined with widespread landscape alterations in the respective watersheds (Kausch, 1996 a, b; Nachtnebel, 1996; Rabalais et al. 1996). Anthropogenous additions of nitrogen and phosphorus resulted in dramatic changes of water quality in both rivers during the last century (ARGE Elbe, 1977-98; Turner & Rabalais, 1991). The respective rivers are the main sources of freshwater inflow to the adjacent marine systems (ARGE Elbe, 1977-98; Dinnel & Wiseman, 1986) and highest runoff occurs in spring (ARGE Elbe, 1977-98; Rabalais et al., 1996). Both rivers discharge into tidally influenced, open shelf sytems. Circulation patterns retain the freshwater in the vicinity of the river mouths for extended periods (Becker et al., 1990; Rabalais et al., 1996) and a haline stratification due to the freshwater discharge is a common feature in both systems. Tidal and wind induced mixing is nevertheless frequently observed and may result in totally homogenous water bodies (Becker et al., 1990; Wiseman et al., 1982, 1986). The intensity of the high annual production of about 320 g C m^{-2} yr^{-1} for the Mississippi plume (Lohrenz et al., 1990) and about 420 g C m^{-2} yr^{-1} for the German Bight (Rick et al., submitted) depends on the ambient nutrient input, nutrient regeneration, light intensity and hydrographic conditions. Light limitation is the major feature in the direct plume regions. Particulate carbon flux to the sea bed was quantified in the Mississippi plume region (0.18 - 1.8 mg C m^{-2} d^{-1}) for different seasons (Redalje et al.,1994; Qureshi, 1995; in Rabalais et al., 1996). High sedimentation rates have to be expected especially after the spring bloom (Jensen et al., 1990). The Mississippi ranks among the world top ten rivers with a discharge volume of 580 km^3 a^{-1}, while the Elbe releases only about 22.8 km^3 a^{-1}. Its watershed of 150000 km^2 is more than an order of magnitude smaller than the Mississippi shed (Kausch, 1996 a; Milliman & Meade, 1983). Higher average light intensities in the subtropical region result in higher temperatures, which in turn will cause more stable thermic stratification (e.g. Lampert & Sommer, 1993) in the Mississippi delta than in the German Bight. The spring discharge of the Mississippi river rapidly forms the Louisiana coastal current. It is highly stratified and flows, on average, westward along the Louisiana coast and then southward along the Texas coast, driven by winds from the southeast (Rabalais et al., 1996). The main current flow of the Mississippi plume may be reversed and turn to the north and east when coastal upwelling is favoured by winds along the

coast of southern Texas towards late spring. Combined effects of the initial spring flood discharge, the vernal warming and the return flow along the shelf break may cause a secondary pycnocline (Cochrane & Kelly, 1986). Especially during spring and early summer a large amount of particulate organic carbon, originating from high phytoplankton production, is sedimenting through both pycnoclines on the Louisiana shelf. The frequency and severeness of hypoxia in the bottom water is strongly influenced by the occurrence of the secondary pycnocline (Rabalais et al.,1992 a,b, 1994; 1996; Justic et al., 1993; Malakoff, 1998). Winds have to be strong to break up both pycnoclines in the Mississippi plume region, whereas even moderate winds may be able to induce a total mixing of the water column in the German Bight. Therefore oxygen deficiencies in the German Bight may generally be less severe than in the Gulf of Mexico. Another difference between the two systems may be detected in the development of the the nutrient supply ratios. With eutrophication the nutrient ratios in the Mississippi shifted towards the "optimum" Redfield ratio of N:Si:P = 16:16:1 (Justic et al., 1995). The Elbe is characterized by high N:P ratios above 100 due to the efficient phosphate reduction (Hamm, 1996). The Si:N ratio in the Elbe indicates a silicate limitation (Conley et al., 1993), despite a recent rise of ratios from 0.25 to 0.4 due to a reduction in nitrate (ARGE Elbe, 1990-1998). This may favour a more frequent occurrence of nuisance blooms in the German Bight (Smayda, 1990; Hickel et al., 1997) compared to the Louisiana shelf. However, Rabalais et al. (1996) observed a restructuring of the phytoplankton community from strongly silicified diatoms towards less heavily silicified species in the Mississippi region, but the effects of eutrophication on the ratio between flagellate and diatom abundance probably still play a minor role. All three macronutrients may be limiting in the Missisippi region, depending on region and season (Rabalais et al., 1996; Dortch & Whitledge, 1992; Smith & Hitchcock, 1994), whereas a deficiency of nitrate probably can be excluded for most of the year in the German Bight (this study; Rick et al., submitted.; Hickel et al., 1997).

Even though the nutrient load of the Elbe was reduced over the past decades the conditions in the German Bight are far from pristine (ARGE Elbe, 1977 - 1998; Müller, 1996; Adams et al., 1996). The Elbe likely had a higher silicate and lower P and N load before the anthropogenic eutrophication set in. Diatoms may have dominated the phytoplankton and nuisance blooms probably were rare. Limited carbon assimilation prevented the occurrence of hypoxia in the bottom water.
Constantly increasing eutrophication caused rising DIN and DIP input, while no comparable anthropogenic input of silicate occurred. The nutrient-rich spring discharge of the Elbe river, in combination with vernal warming, produces a strong thermo-haline stratification and favours bloom conditions at the outer margins of the plume. Increased carbon assimilation caused events of oxygen depletion in the bottom water (Rachor & Albrecht, 1983; Gerlach, 1984, Hickel et al., 1989; Niermann & Bauerfeind, 1990;). The improved phosphate supply to the freshwater may have enhanced the growth of diatoms and the subsequent burial of biogenic silicate in the freshwater sediments (Conley et al., 1993), thus reducing the dissolved silicate input into the adjacent coastal system. The change in the availability of the nutrients as well as their changing ratios influenced the population structure of the plankton system.
Finally, the DIP load was successfully reduced by improved management of the point sources, while the load of DIN remained rather unchanged (Hamm, 1996). Possibly the input of silicate into the coastal waters increased again, as diatom blooms in the freshwater were less favoured due to the reduction of phosphate. Trends for silicate

are difficult to evaluate though, since the inputs into the German Bight, like for nitrate, strongly depend on the respective runoff of the Elbe (Appendix Fig. A). The ratio of Si:N is nervertheless far away from the desirable ratio of 1 and thus may still favor nuisance blooms. The phosphate input remained on a constant niveau of around 2000 t a^{-1} and detrimental effects of eutrophication may still be expected.
Different scenarios may be imaginable for the future development of the German Bight. Without any further reduction of nutrient inputs the German Bight would remain at its present state, but the situation may get worse, if accumuative effects of constantly high eutrophication develop.
Initiatives to reduce the nitrogen input up to now only had slight effects. At present state ground water contributes to about 42 % of the total nitrogen input into surface waters. The pool of nitrogen in the ground water is so large, that at first it will buffer any positive effect of nitrogen reduction (Hamm, 1996). Another 40% of the recent nitrogen input is emitted by point sources. This level may be strongly reduced over the next years, because the communal sewage treatment plants, at present being responsible for about 30% of the input, are increasingly equipted with denitrification techniques (Hamm, 1996). The over-fertilization of the freshwater sources though, can not be significantly reduced without reduction of the diffuse nitrogen sources. Increased efforts should be undertaken for example to optimize fertilization in agriculture. As Meissner et al. (1993) discussed, the relative rise in agricultural yield due to fertilization may level off or even drop with a rising application of agro-chemicals. The environment and especially the ground water as a first step, could also profit from an extensivation of agriculture areas. Studies in the eastern part of Germany, where about 10% of all acres were suddenly turned into fallows, however, have shown, that an abrupt introduction of a fallow first increases problems of nitrogen runoff to almost double amount in the first year. Extensivation has to be a planned process, in which a sufficient plant cover is to be preferred to rotating fallows to stepwise deaccumulate the substances in the soil (Meissner et al., 1993).
Atmospheric nitrogen input needs to be considered as an additional diffuse source of nitrogen. Mean annual nitrogen deposition was estimated to be as high as 68000 t per year for the region of the German Bight (Beddig et al., 1995). A reduction of nitrogen input into the German Bight would have no immediate effect on the spring bloom size (Gerlach, 1990), since at present nitrogen is available in surplus for phytoplankton at the end of the winter and towards summer. Only when nitrate is reduced to limiting levels, a significant decrease in biomass production may be expected. Nitrate reductions remaining above the limiting level may nevertheless positively influence the system. The export of nitrogen compounds by the currents to other regions would be reduced. Additionally the biological oxygen demand of plankton communities may decrease, if the respective observations in the enclosures are valid for the field.
Most investigations describe phosphate as the limiting nutrient for the German Bight at its present state. The phosphorus input by point sources was efficiently reduced by about 60% from 1975 to 1995 (estimated from data in Hamm, 1996). The introduction of phosphate free washing powders as well as phosphate precipitation in the sewage treatment plants were most efficient measures. Point sources still contribute about 30000 t P a^{-1} to the phosphorus load in Germany and diffuse sources are estimated with a contribution of about 24000 P a^{-1}. These values indicate the strong eutrophication with phosphorus (Hamm, 1996) compared to the estimated natural background of 2400 t a^{-1}. Further reductions of phosphate input could indirectly again influence the silicate availability. The burial of biogenic silicate in freshwater sediment may decrease due to decreasing diatom production, thus

resulting in an increase in dissolved silicate within the Elbe and the adjacent coastal waters. Besides the lowered biomass production due to phosphate limitation the rising Si:N ratio in the coastal water would further reduce the danger of nuisance blooms (Smayda, 1990; Riegman et al., 1991; Sommer, 1994). Increasing Si:N ratios would additionally be produced by a further reduction of nitrate. The simultaneous reduction of nitrate and phosphate thus may be the most efficient approach to improve the environmental conditions in the German Bight.
An addition of silicate would be a theoretical approach to increase the Si:N ratios without further N and P reduction. However, this would be a tremendous effort, since a rough estimation reveals that at least 190000 t silicon a^{-1} would be necessary to supplement the Elbe with sufficient silicate (based on Elbe input data 1994; ARGE Elbe, 1996). The consequences of artificial silicate enrichment of marine waters is investigated in the european project MARICULT (Sommer, 1998). High Si:N:P ratios may favour short food chains (diatoms - copepods - fish) and increase the fish yield (Sakshaug, 1995). This marine agricultural approach, which conflicts the recent politics of environmental protection, provoced intense discussion. Setbacks as well as possible advantages need to be critically evaluated (Sommer, 1998). Problems resulting from high biomass production by diatoms would remain and are indicated for example in studies of the Mississippi. Extremely high silicate concentrations were historically present in this river and nitrate was probably limiting. With rising eutrophication nitrogen levels increased and the formerly high Si:N ratio shifted towards the optimum Redfield ratio (Justic et al., 1995). This resulted in an enhanced diatom production. As a consequence, an elevated sedimentation of biogenic silicate was observed by Rabalais et al. (1996) and the organic material favoured the occurrence of oxygen deficits in the bottom water.

Investigations on the effect of eutrophication on processes closely above and in the sediment are missing for the German Bight, as proposals to study the coupling between benthos and pelagial were not funded in KUSTOS. Compared to the structure and results of the NECOP program in the Gulf of Mexico, following investigations are necessary to close some research gaps for the German Bight:

- Investigations on the coupling between pelagial and benthos should quantify the primary production, sedimentation and fate of the particulate matter in the sediment regionally and seasonally combined with a detailed study of the fluxes of matter in the water-sediment interface (e.g. Miller-Way et al., 1994; Josefson & Conley, 1997).
- Core analyses of the sediment could give indications for the historical development of eutrophication and the occurrence of oxygen deficits as well as the historical development of biologically available silicate (Rabalais et al., 1996, Turner & Rabalais, 1994; Sen Gupta et al., 1996; Nelsen et al., 1994; Eadie et al., 1994).
- Biological and hydrodynamic models are needed, which include phosphate, nitrate and silicate as potentially limiting nutrients, the first trophic levels and the sediment. The produced models should have predictive power to aid in the evaluation of different coastal managegment strategies (Bierman et al., 1994).

8. Summary

The aim of the project KUSTOS was to analyze and quantify fluxes of matter and energy from the land to the ocean throughout the coastal region of the German Bight. The KUSTOS drift investigation of spring 1995 focused on the study of turnover processes in the front of the river Elbe plume to characterize changes in a water mass, which continuously was tracked by a drifting buoy. Additionally, grids of stations were sampled repeatedly on a short time scale. Some grids of stations were sampled before and others during or after the drift investigation. The chemical and biological situation observed in the German Bight during the spring drift investigation 1995 was then reconstructed in an enclosure experiment to study processes undisturbed by advection, grazing or sedimentation.

- Chlorophyll data of the KUSTOS spring 1995 investigation in the German Bight indicated blooms off the North Frisian Isles and the western East Frisian Isles previous to our investigation. In other regions the spring bloom started during the grid investigations and a strong consumption of nutrients and an increase in particulate matter was observed. Phosphate concentrations were reduced to < 0.1 µM and silicate concentrations dropped to ☼ 1 µM for most parts of the inner German Bight, while nitrate remained in surplus concentrations of > 40 µM in the central region. Initial DIN/PO_4 ratios generally were above 100 and rose to ratios above 600 for the central region, indicating a phosphorus limited system. A large area of the German Bight was dominated by the diatoms *D. brightwellii*, *T. rotula* and *T. punctigera*, while *O. sinensis* was very important off the North Frisian Isles. Spring blooms dominated by *Thalassiosira* species can be expected, while a dominant contribution of *D. brightwellii* to the standing stock is rather uncommon. Ratios of particulate carbon to nitrogen and particulate carbohydrate data indicated that a phytoplankton community dominated by *D. brightwellii*, *T. rotula* and *T. punctigera* may have an improved nitrogen storage capability compared to a community dominated by *O. sinensis*. *Cerataulina pelagica* and *Rhizosolenia shrubsolei* characterized the region of the less eutrophic coastal current entering the German Bight from the west. Primary production rates at the surface were high and caused an oxygen oversaturation of the surface layer. Oxygen did not become depleted in the bottom water during the time of the spring investigations, but slight undersaturations were detected, mainly in the direction of the propagating river plume. A hydrodynamic model was applied to the biological and biochemical data of the grid samplings to account for advective processes in the estimation of biologically induced changes in between two grids.

- The drift investigation 1995 was initiated to improve the estimates of biological conversion during spring. Water was sampled at the position of the drifting buoy, the central station, every 6 hours. Meanwhile, a transect was sampled with 3 stations to the east and three stations to the west. The initial surface water was successfully tracked for 10 days at the central station, while the hydrographic conditions were less favourable for tracking the initial water mass at the eastern and western stations. At the easternmost and central station phytoplankton growth was initially reduced due to the turbidity in the Elbe river plume. As the drifter gained distance to the plume decreasing particulate carbon to chlorophyll ratios as well as rising cell numbers marked the exponential growth of the community. The phytoplankton then transgressed towards stationary state, induced by depletion of phosphate and silicate, causing rising ratios in the last days of the investigation.

Phytoplankton at the westernmost station was progressing from a situation initially favourable for growth towards a more stationary state. This was indicated by exponentially rising pC/Chl ratios over the entire investigated period. Towards the end of the drift investigation the phytoplankton community reached a more stationary state and biomass was probably lost from the surface layer at all stations. *Ditylum brightwellii* became the dominant phytoplankton species at the central and easternmost stations, while *Rhizosolenia* species and *Cerataulina pelagica* were major contributors to the standing stock at the less eutrophic westernmost station. Consumption doubling times (CDT) of silicate may roughly indicate the net generation time of the observed diatom community in the field. Estimated CDT of silicate (24.5 hours) were slower at the eastern station than at the central station (19.4 hours), possibly due to stronger turbidity and some mixing in this nearshore region. Production doubling times (PDT) of particulate organic matter were generally slower than the estimates for the CDT of the nutrients, because some of the nutrients lost from the dissolved phase were routed into other compartments than the phytoplankton cells, for example by processes like DOM production, bacterial consumption, grazing and sedimentation. A high net consumption of inorganic nutrients (23 µM NO_3, 0.67 µM PO_4, 19 µM Si) and maximum net production of particulate matter (148 µM pC, 21 µM pN, 0.48 µM pP, 84 µg Chl l^{-1}) was estimated for the surface layer at the central station. Estimates of the produced POM for the drift were higher than the range of values suggested by the grid samplings.

- Enclosure experiments were conducted to improve the estimates of possible POM production by excluding losses due to sedimentation, grazing, advection or vertical diffusion. In the setup of constantly mixed small enclosures grazing heterotrophs larger than 5 µm were excluded by filtering. A 2x4 factorial batch-culture design with triplicate treatments was chosen. The dominant phytoplankton community, observed in spring 1995, was inocculated into media with slightly varying salinity (26 and 32 PSU) and four increasing inorganic N:P ratios (variation of nitrate). The assimilation capacity of the cells for nitrate was probably reached with the highest nitrate additions to the media (NP60, NP110). A surplus of around 50 µM nitrate remained in the highest treatment level (NP110). No strong reaction on the slight change of salinity became evident while significant reactions of increased nitrate supply could be proven for the production of particulate organic matter. Ratios above N:P 20 significantly increased the particulate nitrogen and chlorophyll content of the phytoplankton at both salinities, while a significant increase in particulate carbon above the NP20 treatment could be proven only for 26 PSU. The biological oxygen demand of the community significantly increased towards stationary phase with rising NP treatment. Further investigations are necessary to prove the indications of a slightly negative effect of nitrate concentrations above the NP60 treatment at 26 PSU. Likewise, observed reactions on species level need to be further investigated for their relevance. Treatment ratios above NP20 caused a significant increase in cell numbers of *T. rotula* and *T. punctigera* at 32 PSU as well as *Rhodomonas* at both salinities. *D. brightwellii* always dominated the total biovolume with a contribution of at least 60-80 %. Only small changes were observed in the average percentual contribution by the different other species. Trends indicated a decreasing contribution of *D. brightwellii* with rising NP treatment and an increased contribution of *T. weisflogii*, *T. rotula* and *Rhodomonas*. The rising N:P ratio in the treatments resulted also in an increasing

N:Si ratio, which possibly gave smaller diatoms and non-silicified species an advantage over larger diatoms.

The amount of consumed inorganic nutrients in the different enclosure treatments covered a range that was comparable to the consumption estimated for the drift investigation. Variations between the different approaches were a lot larger for the estimated produced POM. Processes like particle sedimentation and grazing were not considered in the field and observed changes during the drift and grid samplings only reflect net changes in the system.
Carbon and nitrogen were produced in a ratio of 7 in the drift, whereas ratios were elevated in the enclosures (21 - 9). Lowest ratios were observed in the highest NP ratio treatments, as the carbon storage in the stationary phase was more balanced with additional nitrate uptake than in the lower NP treatments. The ratio of produced nitrogen to phosphorus of almost 44 in the drift fitted well to the observed ratios in the excess nitrate treatments (average 57). The ratios in the other NP treatments remained lower (< 26), as their nitrogen storage was limited. The ratios of the highest NP treatments as well as the ratio calculated for the drift investigation indicate phosphorus limited systems. High amounts of carbon were stored in the phytoplankton compared to phosphorus, resulting in ratios which were always higher than the 106:16:1 ratio suggested by Redfield. The particulate carbon assimilation can be strongly underestimated by applying this ratio to a situation in which phytoplankton growth may become stationary. As already suggested by several authors, the Redfield ratio is be restricted to situations of maximum growth or when factors other than nitrogen or phosphorus are limiting.

The results of the spring investigations show possible reactions of the plankton community in the German Bight to high N:P ratios. The introduced estimation approaches are, despite their respective insufficiencies and uncertainties, an important piece in the puzzle of predicting environmental changes due to anthropogenic eutrophication. Quasi-synoptic grid samplings combined with high-resolution hydrographic models allow a broad estimation of the range of biologically induced changes in a larger region. Drift investigations in combination with enclosure experiments may be preferrable approaches to estimate production capacities of the phytoplankton in a defined environment. The estimates clearly show that the Redfield ratio should not be used in coastal-estuarine management to answer the question, if a further reduction of nitrogen input into the system is necessary as long as the N:P ratio remains above 16. For further investigations intensive approaches to estimate the effects of increasing eutrophication on the sediment should be mandatory. In addition, the effects of grazing on the loss of POM from the water column and on the recycling of nutrients need to be quantified with more detail in future experiments.

9. Literature

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10. Appendix

Grid investigation

Fig. A: Yearly average run-off and nutrient load of the Elbe
(extracted from ARGE Elbe Zahlentafeln Be11/98, 1980 - 1997, kindly supplied by M. Bergemann)

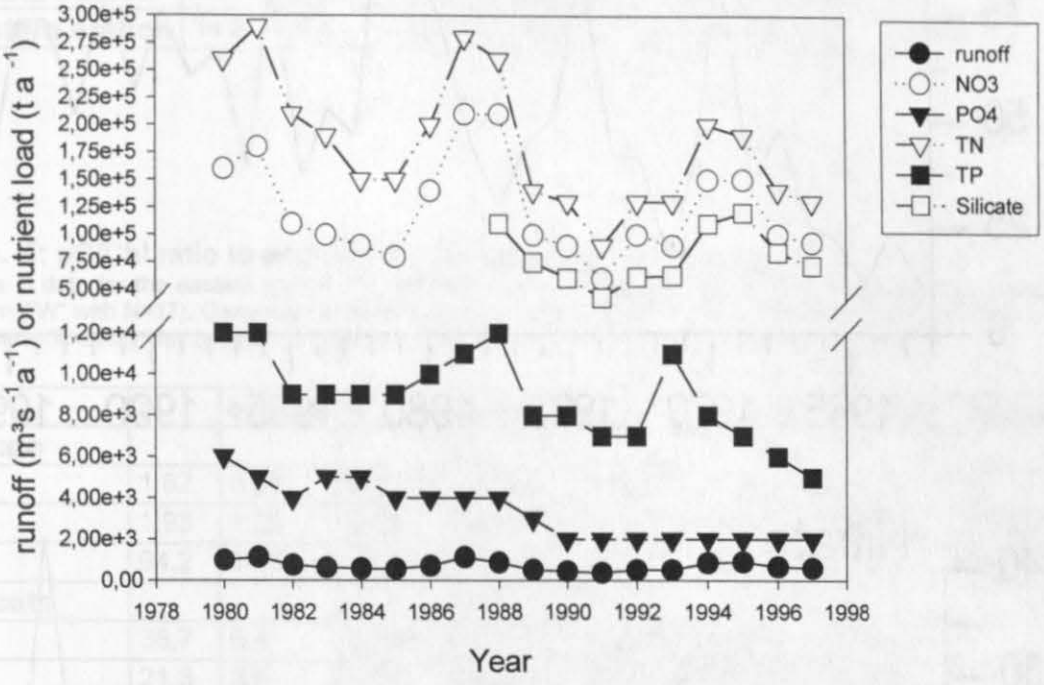


Fig. B : Development of monthly average discharge ratio of DIN/PO_4 (molar) at the Elbe 693 km (extracted from ARGE Elbe Reports 1977 - 1997, mostly bi-weekly measurements)

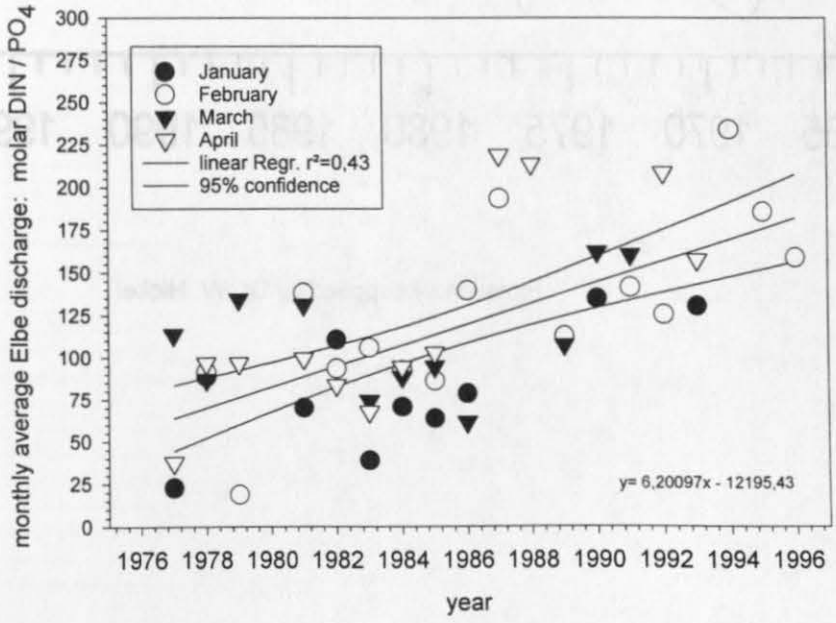
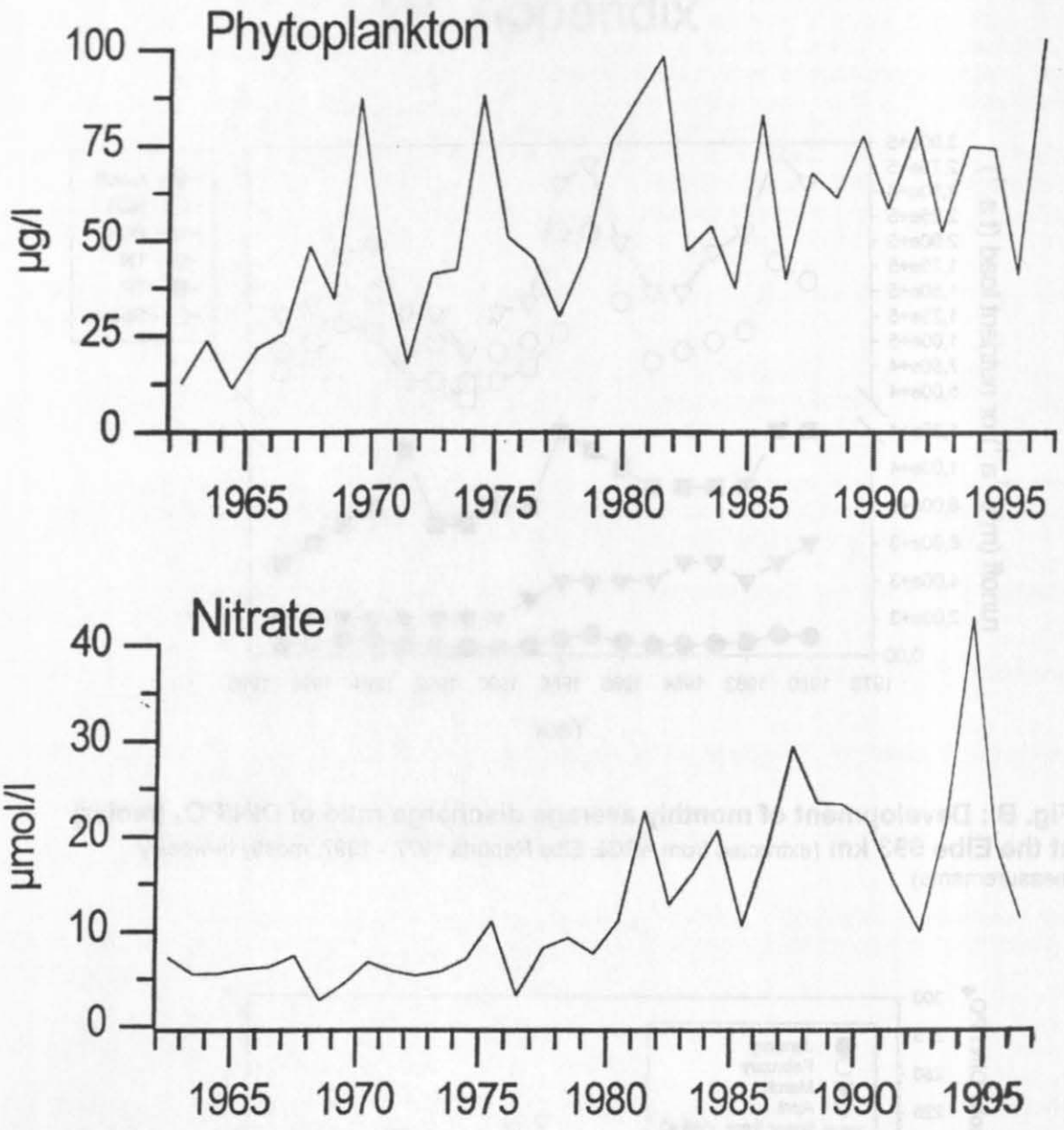


Fig. C: Phytoplankton and nitrate Helgoland Roads 1962 - 1996



Plots kindly supplied by Dr. W. Hickel

Drift investigation

Tab. D: Exponential fit parameters for pC/Chl ratios of the drift

fitted function $y=a\ e^{(b*x)}$; for easternmost and westernmost station data from 0 - 240 h are included, for central station the data was fitted up to 198 h.

	a	error a	b	error b	r^2	p-level	Power
eastern station	204	17.6	-0.008	0.001	0.814	<0.0001	1
central station	88.7	6.8	-0.007	0.001	0.665	<0.0001	1
western station	34.2	6.5	0.005	0.001	0.657	0.0001	0.988

Tab. E: pC/Chl ratio to ambient dissolved nutrients curve fit

Curve fit data for the eastern station ("E" with N=19), the central station ("C" with N=37) and the westernmost station ("W" with N=17). Generally an exponential curve fit ($y=a\ e^{(b*x)}$) was applied, but for the western station a hyperbolic decay was applied ($y=(a\ b)/b+x$)) for silicate and phosphate; Power for alpha=0.05.

	a	error a	b	error b	r^2	p-level a	p-level b	Power
Nitrate								
E	1.82	0.68	0.0678	0.006	0.83	0.0109	<0.0001	1
C	1.93	1.29	0.05	0.01	0.52	0.145	<0.0001	0.999
W	94.2	14.4	-0.03	0.016	0.31	0.0001	0.0494	0.66
Silicate								
E	36.7	6.4	0.086	0.012	0.82	<0.0001	<0.0001	1
C	21.3	3.5	0.06	0.009	0.62	<0.0001	<0.0001	1
W	98.8	18.4	1.86	1.34	0.4	<0.0001	0.185	0.795
Phosphate								
E	37.7	5.9	2.17	0.26	0.84	<0.0001	<0.0001	1
C	26.1	3.8	1.83	0.33	0.48	<0.0001	<0.0001	0.998
W	109.4	36.1	0.101	0.098	0.26	0.008	0.318	0.551

Enclosures

Tab. F: Results of significant ANOVA calculations for POM

One way ANOVAs (32 PSU; 26 PSU) are based on the 4 NP-treatment groups with three replicates each at one respective salinity (PSU). Log - transformed data of the particulate components for the stationary phase (163 - 211 h) of the dominating phytoplankton species were analysed. Two way ANOVAs testing the effect of salinity and the interaction with the NP treatment showed no significant differences and are not shown. (Norm.=Normality test, CV= constant variance).

component	PSU	Source	DF	SS	MS	F	p-level	Power	Norm	CV
part. carbon	26	NP	3	0.709	0.236	72.486	<0.001	1	0.334	0.474
		Residual	32	0.104	0.00326					
		Total	35	0.814						
	32	NP	3	0.590	0.197	27.563	<0.001	1	0.633	0.193
		Residual	32	0.228	0.00713					
		Total	35	0.818						
part. nitrogen	26	NP	3	2.303	0.768	408.424	<0.001	1	0.418	0.446
		residual	32	0.0601	0.00188					
		total	35	2.363						
	32	NP	3	2.155	0.718	316.481	<0.001	1	0.255	0.209
		residual	32	0.0726	0.00227					
		total	35	2.228						
Chl a	26	NP	3	1.652	0.551	64.386	<0.001	1	0.237	0.947
		Residual	32	0.274	0.00855					
		Total	35	1.925						
	32	NP	3	1.342	0.447	48.349	<0.001	1	0.058	0.722
		Residual	32	0.296	0.00925					
		Total	35	1.638						

Tab. G: Biological Oxygen Demand

The effect of salinity was not significant in a three way repeated measurement ANOVA. Therefore the different salinity treatments were tested in a two way repeated measurement ANOVA with 3 repeated measurements for 168 h, 192 h and 216 h. (Norm.=Normality test, CV= constant variance).

PSU	Source	DF Effect	MS Effect	DF Error	MS Error	F-value	p-level	Power	Norm.	CV
26	NP	3	1.212243	8	0.007913	153.206	2.1E-07	1	0.011	0.715
	time	2	0.105386	16	0.008738	12.0611	0.00064	0.981		
	NP*time	6	0.231063	16	0.008738	26.4445	1.9E-07	1		
32	NP	3	0.856614	8	0.001124	762.253	3.6E-10	1	0.002	0.143
	time	2	0.297818	16	0.003394	87.7554	2.4E-09	1		
	NP*time	6	0.054938	16	0.003394	16.188	5.5E-06	1		

Tab. H: Species cell numbers ANOVA

One way ANOVAs (32 PSU; 26 PSU) are based on the 4 NP-treatment groups with three replicates each at the one respective salinity. Log - transformed cell numbers of *T. weisflogii, T. rotula, D. brightwellii* were analysed for the stationary phase (163 - 211 h). For *Rhodomonas* and the small flagellates the same time frame was chosen for comparability, though they didn't reach stationary phase during the experiment. In two way ANOVAs (32*26 PSU) the effect of salinity and the interaction with the NP treatment was tested for the stationary phase.

Species	PSU	Source	DF	SS	MS	F ratio	p-level	Power
T. weisflogii	32	NP ratio	3	0.313	0.104	2.687	0.063	0.39
		Residual	32	1.241	0.0388			
		Total	35	1.553				
	26	NP ratio	3	0.318	0.106	11.303	<0.001	0.998
		Residual	32	0.300	0.00938			
		Total	35	0.618				
T. rotula	32	NP ratio	3	1.852	0.617	12.394	<0.001	0.999
		Residual	32	1.594	0.0498			
		Total	35	3.446				
	26	NP ratio	3	2.404	0.801	46.726	<0.001	1
		Residual	32	0.549	0.0171			
		Total	35	2.953				
	26*32	NP ratio	3	3.989	1.330	39.719	**<0.001**	1
		Sal	1	0.207	0.207	6.171	**0.016**	0.608
		NP x Sal	3	0.267	0.0889	2.656	0.056	0.405
		Residual	64	2.143	0.0335			
		Total	71	6.605	0.0930			
T. punctigera	32	NP ratio	3	0.220	0.0735	3.534	0.026	0.566
		Residual	32	0.666	0.0208			
		Total	35	0.886				
		NP ratio	3	0.117	0.0390	4.041	0.015	0.657
		Residual	32	0.309	0.00965			
		Total	35	0.426				
	26*32	NP ratio	3	0.203	0.0677	4.446	**0.007**	0.751
		Salinity	1	0.235	0.235	15.444	**<0.001**	0.976
		NPx Sal	3	0.134	0.0448	2.943	**0.040**	0.47
		Residual	64	0.974	0.0152			
		Total	71	1.547	0.0218			
D. brightwellii	32	NP ratio	3	0.437	0.146	5.831	0.003	0.874
		Residual	32	0.800	0.0250			
		Total	35	1.238				
	26	NP ratio	3	0.0402	0.0134	1.592	0.211	0.155
		Residual	32	0.269	0.00841			
		Total	35	0.309				
	26*32	NP ratio	3	0.178	0.0592	3.545	**0.019**	0.597
		Salinity	1	0.0095	0.00956	0.572	0.452	0.05
		NPx Sal	3	0.300	0.1000	5.983	**0.001**	0.907
		Residual	64	1.069	0.0167			
		Total	71	1.556	0.0219			
Rhodomonas	32	NP ratio	3	1.228	0.409	24.293	<0.001	1
		Residual	32	0.539	0.0168			
		Total	35	1.767				
	26	NP ratio	3	1.313	0.438	31.175	<0.001	1
		Residual	32	0.449	0.0140			
		Total	35	1.762				
Flag. < 5µm	32	NP ratio	3	0.164	0.0546	2.496	0.077	0.348
		Residual	32	0.700	0.0219			
		Total	35	0.864				
	26	NP ratio	3	0.589	0.196	8.806	<0.001	0.984
		Residual	32	0.714	0.0223			
		Total	35	1.303				

Tab. I: Consumption and production doubling times in the enclosures

Parameter estimates were won by applying an exponential fit to the data of respective consumption or production during the exponential phase.

Component for which consumption or production estimates were calculated (comp), applied salinity (PSU) and nitrate:phosphate treatment (group) of the respective enclosures.

Each estimate is based on measurements of three replicate enclosures over the time of exponential growth. The average consumption doubling times in hours (av. CDT) were calculated from the growth rate per hour estimates (Appendix Tab. J) and a standard deviation from the average is given (dev.).

pN= particulate nitrogen, pC = particulate carbon, pP= particulate phosphorus and Chl = chlorophyll a

comp	PSU	group	av. CDT	dev.	comp	PSU	group	av. CDT	dev.
nitrate	26	8	37.7	3.90	**pN**	26	8	50.27	1.82
		20	18.5	0.84			20	23.85	2.05
		60	14.5	1.75			60	23.02	2.74
		110	16.3	2.05			110	25.37	3.15
	32	8	28.7	2.02		32	8	44.29	3.11
		20	20.3	2.60			20	28.46	2.68
		60	15.7	2.74			60	34.44	7.13
		110	12.3	1.65			110	29.98	2.20
silicate	26	8	15.7	0.71	**pC**	26	8	31.84	3.07
		20	18	1.07			20	26.16	3.45
		60	19.2	0.69			60	24.06	3.00
		110	19.3	2.13			110	26.42	3.81
	32	8	16.2	1.14		32	8	28.04	2.94
		20	19.2	2.33			20	27.61	4.27
		60	19.7	3.12			60	37.65	7.51
		110	18	1.12			110	32.39	2.72
phosphate	26	8	32.9	2.03	**pP**	26	8	55.99	6.77
		20	29.8	1.92			20	34.61	3.97
		60	28.8	1.80			60	37.91	3.73
		110	25.7	2.09			110	40.83	5.75
	32	8	28.9	2.04		32	8	48.42	6.74
		20	31.9	3.52			20	44.21	4.78
		60	28.4	3.59			60	71.87	19.13
		110	24.8	1.51			110	33.05	4.24
					Chl a	26	8	39.19	6.40
							20	25.92	2.42
							60	25.14	5.34
							110	21.28	2.61
						32	8	39.92	7.77
							20	35.03	11.45
							60	27.01	6.97
							110	21.28	2.61

Tab. J: Parameter estimates for consumption doubling and production doubling times during exponential growth phase of the phytoplankton in the enclosures Model: $y = ae^{(bx)}$, applied software Sigma Plot; listed are the component for which consumption or production estimates were calculated (comp), the applied salinity (PSU) and nitrate:phosphate treatment (group) of the respective enclosures. Each estimate is based on measurements of three replicate enclosures over the time of exponential rise. Co = estimated coefficient, estimate= estimate for coefficient, Std.error = standard error of coefficient estimate, SEEstim= Standard error of exponential fit, p.N= particulate nitrogen, pC = particulate carbon, pP= particulate phosphorus and Chl = chlorophyll a, F-ratio= F ratio of ANOVA (all significant)

comp	PSU	group	Co	estimate	Std. error	P	Power	SEEstim	r^2	F-ratio
nitrate	26	8	a	0.8837	0.1722	0.0001	1	0.7571	0.91	151.02
			b	0.0185	0.0019	<0.0001				
		20	a	0.2026	0.0378	0.0001	1	0.5539	0.99	1569.78
			b	0.0376	0.0017	<0.0001				
		60	a	0.0631	0.0416	0.1499	1	1.4611	0.95	280.98
			b	0.0484	0.0058	<0.0001				
		110	a	0.1072	0.0657	0.1235	1	1.5018	0.94	223.16
			b	0.0431	0.0054	<0.0001				
	32	8	a	0.3859	0.0679	<0.0001	1	0.4076	0.97	424.52
			b	0.0242	0.0017	<0.0001				
		20	a	0.2557	0.1253	0.0593	1	1.5002	0.92	171.25
			b	0.0346	0.0044	<0.0001				
		60	a	0.0783	0.0675	0.2647	1	1.7929	0.89	126.28
			b	0.0449	0.0077	<0.0001				
		110	a	0.0165	0.0143	0.2682	1	1.0388	0.95	285.05
			b	0.0571	0.0076	<0.0001				
silicate	26	8	a	0.0779	0.0174	0.0004	1	0.4393	0.99	182.58
			b	0.0443	0.002	<0.0001				
		20	a	0.1423	0.0362	0.0013	1	0.5838	0.98	911.68
			b	0.0386	0.0023	<0.0001				
		60	a	0.1572	0.0231	<0.0001	1	0.3128	0.99	2201.99
			b	0.0362	0.0013	<0.0001				
		110	a	0.168	0.0747	0.0399	1	1.0086	0.94	246.07
			b	0.0363	0.004	<0.0001				
	32	8	a	0.0816	0.0277	0.0101	1	0.615	0.98	712.10
			b	0.0428	0.003	<0.0001				
		20	a	0.1615	0.0791	0.0592	1	1.0902	0.93	202.74
			b	0.0365	0.0044	<0.0001				
		60	a	0.1476	0.0917	0.1284	1	1.1904	0.89	120.43
			b	0.0358	0.0056	<0.0001				
		110	a	0.1153	0.0309	0.002	1	0.5023	0.98	829.69
			b	0.0387	0.0024	<0.0001				
phosphate	26	8	a	0.0637	0.0085	<0.0001	1	0.0428	0.97	488.28
			b	0.0211	0.0013	<0.0001				
		20	a	0.059	0.0095	<0.0001	1	0.0541	0.97	452.87
			b	0.0233	0.0015	<0.0001				
		60	a	0.0481	0.0075	<0.0001	1	0.0449	0.97	529.62
			b	0.0241	0.0015	<0.0001				
		110	a	0.0347	0.0081	0.0006		0.0581	0.96	343.79
			b	0.0271	0.0022	<0.0001				
	32	8	a	0.04	0.0074	<0.0001	1	0.0441	0.96	387.60
			b	0.0241	0.0017	<0.0001				
		20	a	0.0645	0.0162	0.0012	1	0.0853	0.91	152.13
			b	0.0219	0.0024	<0.0001				
		60	a	0.0429	0.0139	0.0073		0.0862	0.90	134.95
			b	0.0247	0.0031	<0.0001				
		110	a	0.0296	0.0055	<0.0001		0.0418	0.98	607.25
			b	0.028	0.0017	<0.0001				

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comp	PSU	group	Co	estimate	Std. error	P	Power	SEEstim	r^2	F-ratio
pC	26	8	a	5.1033	1.1421	0.0005	1	6.0045	0.93	194.65
			b	0.0219	0.0021	<0.0001				
		20	a	3.6688	1.3689	0.0171	1	9.6328	0.90	131.66
			b	0.0268	0.0035	<0.0001				
		60	a	2.565	1.0155	0.0233	1	8.3064	0.91	152.54
			b	0.0291	0.0036	<0.0001				
		110	a	3.495	1.4481	0.029	1	10.0425	0.87	104.47
			b	0.0266	0.0038	<0.0001				
	32	8	a	3.5237	0.9664	0.0024	1	6.0638	0.93	194.76
			b	0.0249	0.0026	<0.0001				
		20	a	3.6969	1.568	0.0324	1	10.1516	0.85	87.86
			b	0.0255	0.0039	<0.0001				
		60	a	6.5953	2.4845	0.018	0.998	11.1517	0.75	43.84
			b	0.0189	0.0037	0.0001				
		110	a	4.9324	0.953	0.0001	1	4.897	0.94	246.20
			b	0.0215	0.0018	<0.0001				
pN	26	8	a	1.3986	0.0715	<0.0001	1	0.2508	0.98	902.69
			b	0.0138	0.0005	<0.0001				
		20	a	0.464	0.1248	0.0021	1	1.0304	0.96	332.85
			b	0.0292	0.0025	<0.0001				
		60	a	0.3576	0.1395	0.0216	1	1.2474	0.92	181.40
			b	0.0304	0.0036	<0.0001				
		110	a	0.4836	0.1801	0.0169	1	1.3312	0.91	146.02
			b	0.0276	0.0034	<0.0001				
	32	8	a	1.0773	0.1186	<0.0001	1	0.4562	0.95	293.75
			b	0.0157	0.0011	<0.0001				
		20	a	0.7011	0.1689	0.0009	1	1.0318	0.94	236.70
			b	0.0245	0.0023	<0.0001				
		60	a	0.963	0.4217	0.0374	0.998	2.0765	0.74	42.71
			b	0.0207	0.0042	0.0002				
		110	a	0.685	0.123	<0.0001	1	0.6974	0.96	360.81
			b	0.0232	0.0017	<0.0001				
p P	26	8	a	0.0995	0.0143	<0.0001	1	0.0434	0.87	
			b	0.0125	0.0015	<0.0001				86.70
		20	a	0.0626	0.0149	0.001	1	0.068	0.91	
			b	0.0202	0.0023	<0.0001				124.34
		60	a	0.0617	0.0113	0.0001		0.0466	0.92	158.48
			b	0.0184	0.0018	<0.0001				
		110	a	0.0693	0.017	0.0013	1	0.0657	0.85	73.59
			b	0.0172	0.0024	<0.0001				
	32	8	a	0.0763	0.0148	0.0002	1	0.0494	0.85	72.41
			b	0.0145	0.002	<0.0001				
		20	a	0.0803	0.0135	<0.0001	1	0.0485	0.90	121.71
			b	0.0158	0.0017	<0.0001				
		60	a	0.1315	0.0315	0.0011	0.931	0.085	0.58	17.71
			b	0.0101	0.0026	0.0018				
		110	a	0.0459	0.0131	0.0038	1	0.0634	0.89	101.77
			b	0.0212	0.0027	<0.0001				
Chl a	26	8	a	1.2207	0.4384	0.0133	1	2.4227	0.80	63.67
			b	0.018	0.0029	<0.0001				
		20	a	0.8257	0.2731	0.0081	1	3.0566	0.94	263.97
			b	0.0269	0.0025	<0.0001				
		60	a	0.9038	0.7035	0.2172	1	8.9812	0.78	56.43
			b	0.0284	0.0059	0.0002				
		110	a	0.4553	0.241	0.0771	1	4.6437	0.92	190.81
			b	0.0329	0.004	<0.0001				
	32	8	a	1.5132	0.6485	0.033	0.999	3.4998	0.74	44.57
			b	0.0178	0.0034	<0.0001				
		20	a	1.9736	1.6872	0.2592	0.955	11.6475	0.54	19.01
			b	0.0212	0.0066	0.0057				
		60	a	1.023	0.8923	0.2685	0.997	9.8996	0.70	37.16
			b	0.0268	0.0067	0.001				
		110	a	0.4553	0.241	0.0771	1	4.6437	0.92	190.81
			b	0.0329	0.004	<0.0001				

Tab. K: Consumption and production capacities

Parameter estimates were won by applying a logistic fit to the data of respective consumption or production. For a detailed list of results see Appendix Tab. L. Listed are the component for which capacities were estimated (comp), the applied salinity (PSU) and nitrate:phosphate treatment (group) of the respective enclosures. Each estimate is based on measurements of three replicate enclosures over time and the standard error of the estimate is given (std. Error). pN= particulate nitrogen, estimate = consumed or produced amount in µM.

component	PSU	group	estimate	std. error
nitrate	26	8	7.1911	0.1556
		20	17.9288	0.2375
		60	46.3086	0.7988
		110	44.7153	1.1725
	32	8	6.3142	0.1124
		20	16.5627	0.4004
		60	44.9593	1.3461
		110	41.781	0.8597
phosphate	26	8	0.8283	0.0163
		20	0.8788	0.023
		60	0.8173	0.0221
		110	0.806	0.0235
	32	8	0.821	0.0253
		20	0.8692	0.0281
		60	0.8074	0.0257
		110	0.7881	0.0172
silicate	26	8	14.6152	0.186
		20	14.6917	0.2268
		60	14.9839	0.1824
		110	14.7845	0.3109
	32	8	14.1708	0.206
		20	14.3986	0.3148
		60	14.7568	0.3671
		110	14.5211	0.196
p N	26	8	9.5419	0.4657
		20	17.7044	0.5557
		60	39.8023	1.9573
		110	37.5352	1.1094
	32	8	11.1123	0.9068
		20	17.6719	0.6389
		60	40.8063	2.6759
		110	39.538	0.9523

Tab. L: Parameter estimates for calculation of consumption and production capacities of the phytoplankton in the enclosures

logistic fit (Model: $y = a/(1+((a-b)/b)\cdot euler^{(-cx)})$) to the data of respective consumption or production; component for which capacities were estimated (comp), applied salinity (PSU) and nitrate:phosphate treatment (group) of the respective enclosures. Each estimate is based on measurements of three replicate enclosures over time and the standard error of the coefficient estimate is given (std. Error) as well as the significant ($p<0.0001$ in all cases) F-ratio of the ANOVA and the standard error of the logistic fit (SEEstimation).
pN= particulate nitrogen.

comp	PSU	treat	Co	estimate	std. Error	P	Power	SEEstimation	r^2	$F_{(2,27)}$-ratio
nitrate	26	8	a	7.1911	0.1556	<0.0001	1	0.4979	0.97	451.26
			b	0.25	0.0837	0.0059				
			c	0.0493	0.0052	<0.0001				
		20	a	17.9288	0.2375	<0.0001	1	0.7588	0.99	1596.58
			b	0.0053	0.0035	0.1434				
			c	0.0841	0.0069	<0.0001				
		60	a	46.3086	0.7988	<0.0001	1	1.5165	0.99	2228.35
			b	0.0635	0.0234	0.0115				
			c	0.0516	0.003	<0.0001				
		110	a	44.7153	1.1725	<0.0001	1	2.1292	0.99	1029.36
			b	0.0774	0.0398	0.0623				
			c	0.0495	0.0042	<0.0001				
	32	8	a	6.3142	0.1124	<0.0001	1	0.3599	0.98	793.40
			b	0.05	0.0226	0.0355				
			c	0.0602	0.0057	<0.0001				
		20	a	16.5627	0.4004	<0.0001	1	1.2258	0.97	523.11
			b	0.017	0.0157	0.289				
			c	0.0715	0.0095	<0.0001				
		60	a	44.9593	1.3461	<0.0001	1	2.3875	0.98	823.60
			b	0.0559	0.0343	0.1148				
			c	0.0509	0.0049	<0.0001				
		110	a	41.781	0.8597	<0.0001	1	1.7618	0.99	1413.70
			b	0.0184	0.0109	0.1025				
			c	0.0594	0.0046	<0.0001				
phosphate	26	8	a	0.8283	0.0163	<0.0001	1	0.0423	0.98	821.21
			b	0.0269	0.0066	0.0004				
			c	0.0412	0.0032	<0.0001				
		20	a	0.8788	0.023	<0.0001	1	0.0698	0.97	384.02
			b	0.0132	0.0068	0.0625				
			c	0.0525	0.0066	<0.0001				
		60	a	0.8173	0.0221	<0.0001	1	0.0617	0.97	405.60
			b	0.0167	0.0072	0.0287				
			c	0.0465	0.0054	<0.0001				
		110	a	0.806	0.0235	<0.0001	1	0.0736	0.96	318.38
			b	0.0042	0.0034	0.2225				
			c	0.0616	0.0095	<0.0001				
	32	8	a	0.821	0.0253	<0.0001	1	0.0597	0.97	419.04
			b	0.0181	0.0072	0.0188				
			c	0.0409	0.0046	<0.0001				
		20	a	0.8692	0.0281	<0.0001	1	0.0783	0.95	277.94
			b	0.0215	0.0105	0.0506				
			c	0.0453	0.0062	<0.0001				
		60	a	0.8074	0.0257	<0.0001	1	0.0755	0.95	282.02
			b	0.0096	0.0062	0.1321				
			c	0.0522	0.0078	<0.0001				
		110	a	0.7881	0.0172	<0.0001	1	0.0534	0.98	585.71
			b	0.0034	0.0021	0.1203				
			c	0.0623	0.0072	<0.0001				

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comp	PSU	group	co	estimate	std. error	p-level	Power	SEEstimate	r^2	$F_{(2,27)}$
silicate	26	8	a	14.6152	0.186	<0.0001	1	0.6172	0.99	1782.6
			b	0.0003	0.0003	0.2819				
			c	0.1089	0.0096	<0.0001				
		20	a	14.6917	0.2268	<0.0001	1	0.7205	0.99	1250.9
			b	0.0036	0.0028	0.2				
			c	0.0846	0.0079	<0.0001				
		60	a	14.9839	0.1824	<0.0001	1	0.5311	0.99	2275.4
			b	0.0109	0.0049	0.0345				
			c	0.07	0.0044	<0.0001				
		110	a	14.7845	0.3109	<0.0001	1	0.9345	0.98	724.30
			b	0.0096	0.0079	0.2356				
			c	0.073	0.0083	<0.0001				
	32	8	a	14.1708	0.206	<0.0001	1	0.656	0.99	1427.0
			b	0.0016	0.0013	0.2113				
			c	0.09	0.0078	<0.0001				
		20	a	14.3986	0.3148	<0.0001	1	0.9472	0.98	668.92
			b	0.0094	0.0081	0.2546				
			c	0.0731	0.0086	<0.0001				
		60	a	14.7568	0.3671	<0.0001	1	1.0389	0.98	573.74
			b	0.0097	0.0089	0.2863				
			c	0.069	0.0086	<0.0001				
		110	a	14.5211	0.196	<0.0001	1	0.5823	0.99	1812.1
			b	0.0063	0.0035	0.0809				
			c	0.0746	0.0054	<0.0001				

comp	PSU	group	Co	Estimate	Std. Error	P	Power	SEEstim	r^2	F-ratio
part. N	26	8	a	9.5419	0.4657	<0.0001	1	0.6051	0.96	316.81
			b	1.1729	0.1796	<0.0001				
			c	0.0226	0.0025	<0.0001				
		20	a	17.7044	0.5557	<0.0001	1	1.4896	0.97	361.45
			b	0.0635	0.0508	0.2225				
			c	0.0575	0.0081	<0.0001				
		60	a	39.8023	1.9573	<0.0001	1	3.2525	0.96	319.40
			b	0.0551	0.0517	0.2966				
			c	0.0498	0.0074	<0.0001				
		110	a	37.5352	1.1094	<0.0001	1	2.033	0.98	800.95
			b	0.0645	0.0384	0.105				
			c	0.0498	0.0048	<0.0001				
	32	8	a	11.1123	0.9068	<0.0001	1	0.7694	0.95	240.96
			b	1.0711	0.2098	<0.0001				
			c	0.0204	0.0028	<0.0001				
		20	a	17.6719	0.6389	<0.0001	1	1.453	0.96	340.71
			b	0.2371	0.1235	0.0654				
			c	0.0428	0.0056	<0.0001				
		60	a	40.8063	2.6759	<0.0001	1	3.1166	0.96	318.66
			b	0.2315	0.152	0.1393				
			c	0.0375	0.0055	<0.0001				
		110	a	39.538	0.9523	<0.0001	1	1.5578	0.99	1442.15
			b	0.0605	0.027	0.0336				
			c	0.0485	0.0035	<0.0001				

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