

# Phytoplankton and fronts in the German Bight

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**SUMMARY:** There are two distinct frontal systems in the German Bight: a tidal mixing front north of the East Frisian Islands and a river plume front deriving mainly from the Elbe river in the East. Phytoplankton species composition revealed significant differences between these two types of fronts. The distribution of chlorophyll *a* and phytoplankton carbon showed maxima at both fronts in spring; however, the standing crop at the tidal mixing front was dominated to more than 90 % by autotrophic nanoflagellates with low photosynthetic rate ( $0.72 \mu\text{g C } \mu\text{g Chl } a^{-1} \text{ l}^{-1}$ ), whereas neritic diatoms with relatively high photosynthetic activity ( $4.1 \mu\text{g C } \mu\text{g Chl } a^{-1} \text{ l}^{-1}$ ) formed more than 90 % of the peak at the river plume front. It is supposed that the diatom peak at the Elbe river plume front was generated and maintained there by increased water column stability in conjunction with an improved nutrient supply, whereas the nanoflagellate maximum at the tidal mixing front is traced back to convergent accumulation. In summer, during periods of calm weather, even small frontal gradients may lead to high biomass accumulations of particularly the dinoflagellates *Ceratium fusus* and *Noctiluca scintillans*. Both species are typical for the summer plankton in this area. The *Ceratium fusus* biomass reached values of more than  $1 \text{ mg C l}^{-1}$  in the surface waters adjacent to the front, whereas the *Noctiluca* concentration amounted to as much as  $4 \text{ mg C l}^{-1}$ . The former showed an unusually high percentage of aberrant forms in the frontal peak, which may be a result of chemical interference.

**Key words:** phytoplankton, fronts, German Bight, pollution, cell anomalies.

## INTRODUCTION

The spatial and temporal distribution of phytoplankton in the German Bight has been subject to many investigations (WULFF, 1935; DREBES & ELBRÄCHTER, 1976; HAGMEIER, 1978; CADÉE, 1986). Most of these studies were carried out on rigid sampling grids or at drogue-stations and detailed observations related to the major physical features in this region are scarce. Two distinct frontal systems are known from the German Bight (BECKER & PRAHM-RODEWALD, 1980; KRAUSE *et al.*, 1986). One of these is of the river plume type deriving mainly from the fresh water outflow of the Elbe river in the eastern part of the German Bight; the other is a tidal mixing front, separating off-shore summer stratified water from a tidally mixed water mass along the East-Frisian Islands.

The biological significance of fronts has been documented in a variety of papers. Fronts may act as population barriers (BRANDT & WADLEY, 1981; HOLLIGAN, 1981) and have often been noted as areas

of increased phytoplankton standing stock (SAVIDGE, 1976; SIMPSON *et al.*, 1979; PINGREE *et al.*, 1978; SELIGER *et al.*, 1981; BEARDALL *et al.*, 1982). These could be accompanied by intense biological activity at various trophic levels (DUFOUR & STRETTA, 1973; FLOODGATE *et al.*, 1981).

There is much evidence that the phytoplankton maximum associated with many fronts is a result of passive convergent accumulation (SELIGER *et al.*, 1981; LE FÈVRE, 1986) but some workers found indices for enhanced *in situ* growth, which was explained in terms of favourable light and nutrient conditions at the front (PINGREE *et al.*, 1978; HOLLIGAN, 1981). The relative importance of these two different mechanisms, however, is still an open question (LODER & PLATT, 1985; LE FÈVRE, 1986).

In 1984, an interdisciplinary research group was formed in order to elucidate the role of fronts in the German Bight with respect to mixing processes, nutrient distribution and biological implications. The objective of the present study is to evaluate the effects of both types of fronts on phytoplankton and pro-

to zooplankton distribution, with emphasis on the community structure. Detailed information on the hydrographical structures is given by KRAUSE *et al.* (1986), and BUDÉUS (1989).

## MATERIALS AND METHODS

Observations were made from R.V. «Victor Hensen» on transects perpendicular to the general orientation of the front. Position of stations referred to in this study are shown in figure 1. Density profiles and data of the stratification parameter  $\bar{V}$  were kindly provided by G. BUDÉUS (BUDÉUS, 1989). Vertical chlorophyll *a*-profiling was done with a Variosens fluorometer, which was calibrated against discrete samples. In addition, horizontal chlorophyll *a*-profiles were recorded continuously between stations on water pumped through a Turner fluorometer from 2.50 m depth and adjusted by multiple calibration (PARSONS *et al.*, 1984).

Discrete water samples were collected with a 10 l-Niskin bottle-rosette fitted with CTD probe and fluorometer. Photosynthetic activity was measured by the  $^{14}\text{C}$  technique. After addition of  $4\ \mu\text{Ci}$  of  $\text{NaH}^{14}\text{CO}_3$ , subsamples were incubated for 6 hours in 100 ml Duran glass bottles in a flowing seawater tank under artificial illumination. PAR-light intensity was  $250\ \mu\text{E m}^{-2}\text{ sec}^{-1}$ . After filtration and fuming of the filters over concentrated HCl, radioactivity was assayed in a Packard scintillation counter using Lumagel as scintillation cocktail. Quench correction was made using the internal standard method. Rates of carbon fixation were corrected at each depth by subtraction of a separate dark bottle value.

Phyto- and protozooplankton samples preserved

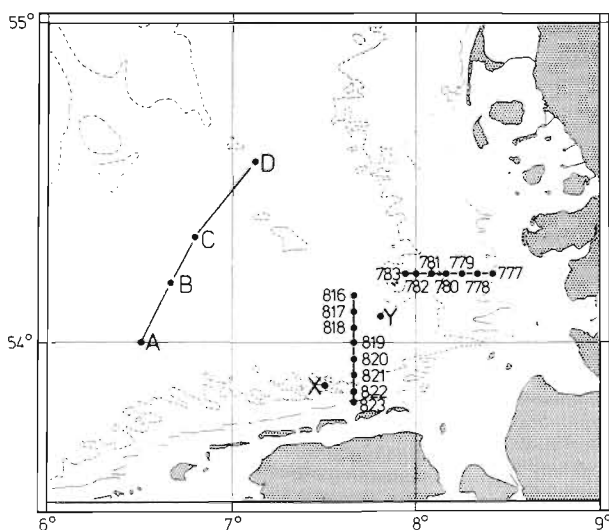


FIG. 1. — Study area showing frontal transects chosen for detailed observation with location of sampling stations referred to in text.

with lugol iodine solution were evaluated under an inverted microscope equipped with phase contrast. Conversions into carbon values were made following the recommendations of the Baltic Marine Biologists working group 9 (EDLER, 1979).

## RESULTS

In May 1986, the two frontal types in the German Bight were subjected to an intensive, quasi-synoptic study. Several transects were occupied across the fronts with stations approximately 3 nautical miles apart. For each frontal type, a distinctive transect exhibiting marked frontal characteristics was chosen for detailed biological analysis.

### River plume front

The river plume front was marked by a sharp foamline indicating a convergent flow regime (LE FÈVRE, 1986). Figure 2 shows the corresponding density distribution. The strong frontal gradients were caused by both temperature as well as salinity. A cold ( $< 6.0\ ^\circ\text{C}$ ) and saline ( $> 32.5$ ) off-shore water mass was separated by the front from a warmer ( $> 9.0\ ^\circ\text{C}$ ) and less saline ( $> 28.0$ ) coastal water body, which was mainly affected by the fresh-water input of the Elbe river. Due to the density-forced inclination of the isopycnals a strong stratification is established, which is reflected by stratification

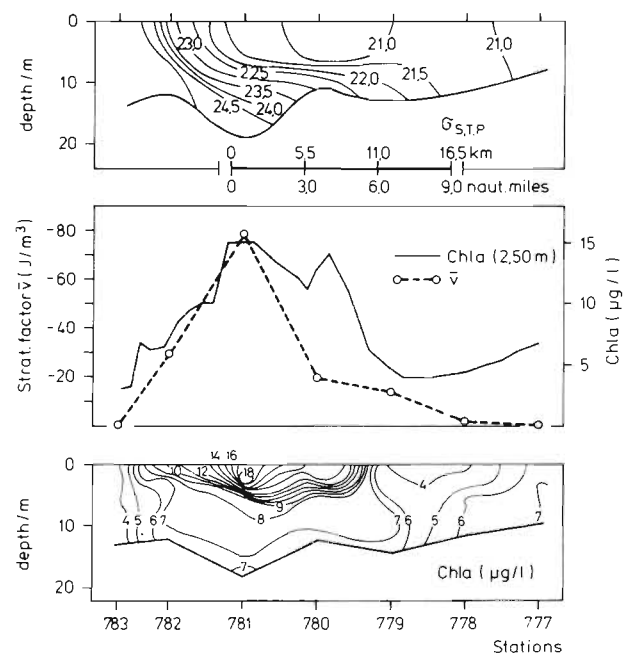


FIG. 2. — Elbe river plume front characteristics in May 1986. Top: Density section across the front. Middle: Variation of the stratification factor  $\bar{V}$  and of surface chlorophyll *a*. Bottom: Chlorophyll *a* isopleths.

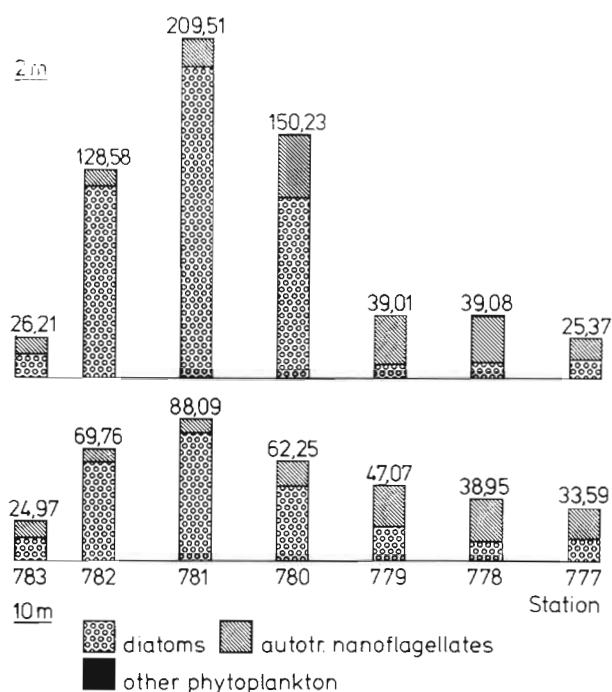


FIG. 3. — Phytoplankton biomass ( $\mu\text{g C l}^{-1}$ ) and composition at two depths along the transect across the Elbe river plume front, showing frontal diatom peak at the surface of St. 781.

parameter  $\bar{V}$  (Fig. 2; SIMPSON *et al.*, 1979). Maximum stability ( $-80 \text{ J m}^{-3}$ ) was found at station 781.

Continuous surface-profiling of chlorophyll *a* showed a broad maximum situated in the stratified part of the transect and centred around the most stable station 781 adjacent to the front (Fig. 2). The ver-

tical chlorophyll *a*-profile (Fig. 2) revealed that this maximum was restricted to the surface only. Highest values were about  $18 \mu\text{g Chl } a \text{ l}^{-1}$ , whereas in the surrounding water chlorophyll *a* concentrations were about 3 to 4 times lower.

Total phytoplankton carbon (PPC) correlated well with discrete Chl *a*-values ( $r = 0.889$ ;  $P < 0.01$ ). PPC-concentrations in the frontal peak reached  $210 \mu\text{g C l}^{-1}$  (Fig. 3). The bulk of this phytoplankton consisted of diatoms and some autotrophic nanoflagellates (Fig. 3). The latter dominated the turbulent coastal water, whereas the phytoplankton in the stratified water adjacent to the front was nearly exclusively made up by diatoms. A small neritic form, *Thalassiosira nordenskiöldii* Cleve, accounted for 83 % of total phytoplankton biomass within the peak. There were, however, a variety of other diatom species being concentrated at the same time. Table I presents enumerations of predominant species in the surface water of this transect.

Measurements of photosynthetic rate, which were performed under identical light and temperature conditions for all samples, showed a pronounced productivity maximum within the phytoplankton patch adjacent to the front. Surface values were about 3 times higher than in the mixed saline offshore water or the vertically mixed brackish coastal watermass (Table II). Silicate and phosphate concentrations were very low, ranging from  $0.5 \mu\text{M}$  to  $1.0 \mu\text{M}$  Si and  $< 0.03$  to  $0.1 \mu\text{M}$  P, respectively (BROCKMANN, pers. comm.), which is, according to BENNEKOM *et al.* (1975) and RHEE (1982), in the range of diatom growth limita-

TABLE I. — Enumerations of predominant phytoplankton species along a transect across the Elbe river plume front in May 1986. Values are given as  $\mu\text{g cell-carbon l}^{-1}$ . Species which exhibit a frontal maximum are starred.

Species	Station-No.						
	783	782	781	780	779	778	777
<i>Asterionella glacialis</i> *	0.02	1.34	3.21*	1.15	0.10	0.06	1.29
<i>Chaetoceros spec.</i> *	0.13	0.55	1.40*	1.20	0.25	0.01	0.01
<i>Leptocylindrus minimus</i>	—	0.01	0.19	0.46	1.02	3.79	6.19
<i>Plagiogramma brockmanni</i>	0.03	0.10	0.16	0.07	0.05	1.30	1.04
<i>Raphoneis surirella</i>	—	0.05	0.09	0.19	0.17	0.68	1.33
<i>Rhizosolenia setigera</i>	0.65	2.59	1.88	2.37	0.43	0.80	0.38
<i>Thalassionema nitzschioides</i> *	0.28	2.26	5.90*	3.23	0.39	0.11	0.34
<i>Thalassiosira nordenskiöldii</i> *	11.99	107.74	173.62*	98.13	3.13	1.39	0.11
<i>Thalassiosira punctigera</i> *	0.62	1.06	2.30*	1.11	0.17	—	—
<i>Thalassiosira spec.</i>	0.05	0.95	1.83	2.64	2.13	1.17	0.16

TABLE II. — Photosynthetic rate at two depths along a transect across the Elbe river plume front in May 1986.

Stations		783	782	781	780	779	778	777
Photosynth. rate [ $\mu\text{g C } \mu\text{g Chl } a^{-1} \text{ h}^{-1}$ ]	2 m	1.40	3.46	4.10	2.49	1.49	1.48	1.16
	10 m	1.29	2.66	2.54	2.06	1.55	1.16	1.53

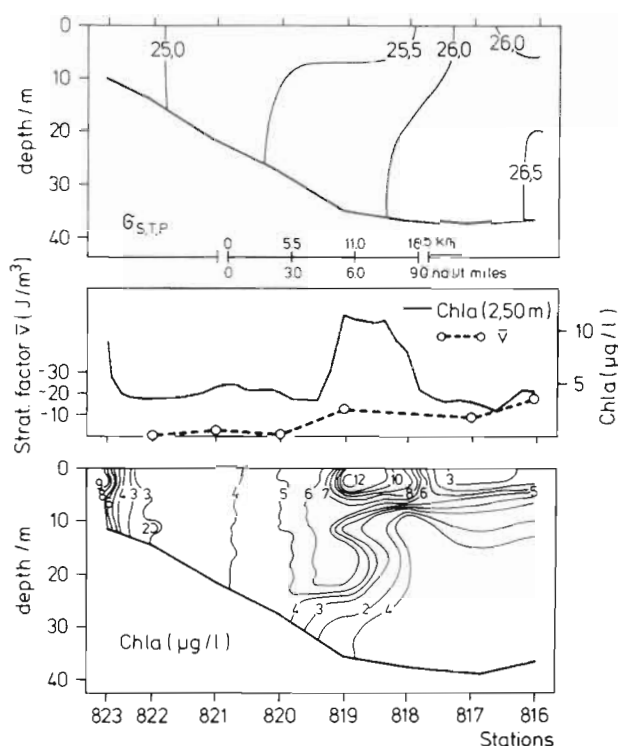


FIG. 4. — East Frisian tidal mixing front characteristics in May 1986. Details as in figure 2 legend.

tion. Total inorganic nitrogen, however, was present in sufficient quantities ( $> 15 \mu\text{M N}$ ). There was a weak correlation ( $r = 0.497$ ;  $P < 0.05$ ) between silicate concentrations and photosynthetic rate.

### Tidal mixing front

The density profile of the tidal mixing front in May 1986 is shown in figure 4. Gradients were mainly determined by temperature. Stratification was not yet very strong, maximal  $\bar{V}$ -values were about  $18 \text{ J m}^{-3}$  (fig. 4). More detailed hydrographical information is given by BUDÉUS (1989).

As in the case of the river plume front, there was a distinct chlorophyll *a*-maximum on the stratified side adjacent to the front (Fig. 4). Chlorophyll *a*-concentrations within the peak were about  $12 \mu\text{g Chl } a \text{ l}^{-1}$ , which accounted for more than twice the concentration in the surrounding water. This patch was restricted to the surface layer only (Fig. 4). Corresponding PPC-values in the peak were  $253 \mu\text{g C l}^{-1}$ , which, in spite of the comparably lower Chl *a*-concentration, was somewhat higher than at the river plume front. This indicates a lower Chl *a*/PPC ratio of the patch-forming organisms at the tidal mixing front. Microscopic analysis revealed a phytoplankton composition, which was very contrary to the situation at the river plume front: the frontal biomass peak was made up to more than 90 % by an unidentified nano-

flagellate species (Fig. 5), which was similar to flagellate «X» described by DUNNE (1984), although smaller in diameter ( $11 \mu\text{m}$ ). Maximum cell concentration of this form was almost  $10^7 \text{ cells l}^{-1}$ . Diatoms (*Thalassiosira nordenskiöldii* Cleve, *Asterionella glacialis* Castracane, *Rhizosolenia delicatula* Cleve a.o.), on the other hand, were the most important members in the shallowest nearshore water (St. 823), and their abundance was at minimum in the flagellate-dominated frontal peak. Detailed information about the distribution of predominant species is given in table III.

The photosynthetic rate of the nanoflagellate population which formed the frontal phytoplankton peak was extremely low (Table IV). Higher photosynthetic activity was found in the nearshore diatom assemblage (St. 823).

Silicate concentrations were at minimum ( $< 0.8 \mu\text{M Si}$ ) in the deep mixed water and in the surface layer on the stratified side (BROCKMANN, pers. comm.) suggesting silicate limitation for diatom growth. The stock of inorganic nitrogen and phosphate, however, was far from exhaustion ( $> 15 \mu\text{M N}$  and  $> 0.30 \mu\text{M P}$ , respectively). There was no significant correlation between photosynthetic rate and nutrient concentrations.

A striking feature at the investigated tidal mixing front was a pronounced accumulation of heterotrophic dinoflagellates which accompanied the phytoplankton maximum (Fig. 6). Their biomass ( $320 \mu\text{g}$

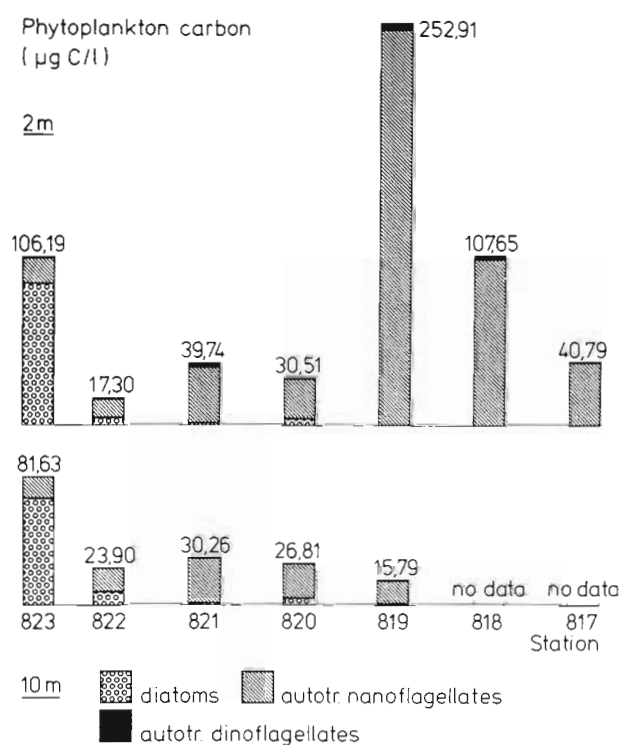


FIG. 5. — Phytoplankton biomass ( $\mu\text{g C l}^{-1}$ ) and composition at two depths along the transect across the East Frisian tidal mixing front, showing frontal nanoflagellate peak at the surface of St. 819.

TABLE III. — Enumerations of predominant phyto- and protozooplankton species along a transect across the East-Frisian tidal mixing front in May 1986. Values are given as  $\mu\text{g cell-carbon l}^{-1}$ . Species which exhibit a frontal maximum are starred.

Species	Station-No.						
	823	822	821	820	819	818	817
Phytoplankton:							
<i>Asterionella glacialis</i>	19.34	0.01	—	—	—	—	—
<i>Platogramma brockmanni</i>	1.30	0.02	—	—	—	—	—
<i>Rhizosolenia delicatula</i>	15.22	3.60	1.17	4.28	0.20	0.15	0.59
<i>Rhizosolenia shrubsolei</i>	1.67	0.48	0.03	0.08	—	0.23	0.20
<i>Thalassiosira nordenskiöldii</i>	50.32	0.86	—	—	0.01	0.01	0.02
<i>Gonyaulax grindleyi</i> *	—	0.20	1.76	0.39	2.35*	—	—
<i>Peridinium trochoideum</i>	—	0.02	0.15	0.05	0.98	1.02	0.09
Cryptomonads spp.	11.21	6.92	13.48	10.48	7.29	11.21	4.49
Nanoflagellate spec.*	1.96	3.08	20.18	12.05	236.31*	90.26	32.80
Protozooplankton:							
<i>Cochlodinium helix</i> *	—	0.04	0.48	0.35	19.16*	2.98	1.04
<i>Gymnodinium spec.*</i>	0.84	1.99	3.02	5.08	19.02*	—	—
<i>Gyrodinium spec.*</i>	3.60	2.91	7.97	9.94	245.89*	23.48	15.42
<i>Peridinium quarnerense</i> *	—	0.04	1.38	1.72	10.22*	1.91	0.21
Ciliates spp.	16.35	14.84	10.10	23.45	4.25	12.02	7.66

TABLE IV. — Photosynthetic rate at two depths along a transect across the East-Frisian tidal mixing front in May 1986.

Stations		823	822	821	820	819	818	817
Photosynth. rate	2m	2.21	1.36	1.37	0.96	0.72	—	0.66
	[ $\mu\text{g C } \mu\text{g Chl } a^{-1} \text{ h}^{-1}$ ]	2.18	1.58	1.34	0.86	0.69	—	1.04

$\text{Cl}^{-1}$ ) was even higher than the high biomass levels of the phytoplankton in the peak. This protozooplankton mass occurrence was mainly due to a *Gyrodinium spec.* (Table III), which was very similar to *G. fusiforme* Kofoid & Sweezy, but had a phagotrophic mode of nutrition. Microscopic analysis suggested that its preferred diet were diatoms. It seems likely that it also fed on nanoflagellates which would undergo rapid disintegration within the cell body of the predator and hence escape recognition.

#### Weak frontal structures

During calm summer periods very high biomass accumulations were found even at relatively small density gradients. In August 1984, during a standard survey along a fixed sample grid, a red tide phenomenon caused by the phagotrophic dinoflagellate *Noctiluca scintillans* (Macartney) Kofoid, was observed in the southwestern part of the German Bight at such a weak frontal structure (fig. 7), which obviously belonged to the northwestern area of the tidal mixing front (KRAUSE *et al.*, 1986). The red tide patch was restricted to the uppermost 2 metres only and gave the water an intensive orange colour and a jelly-like

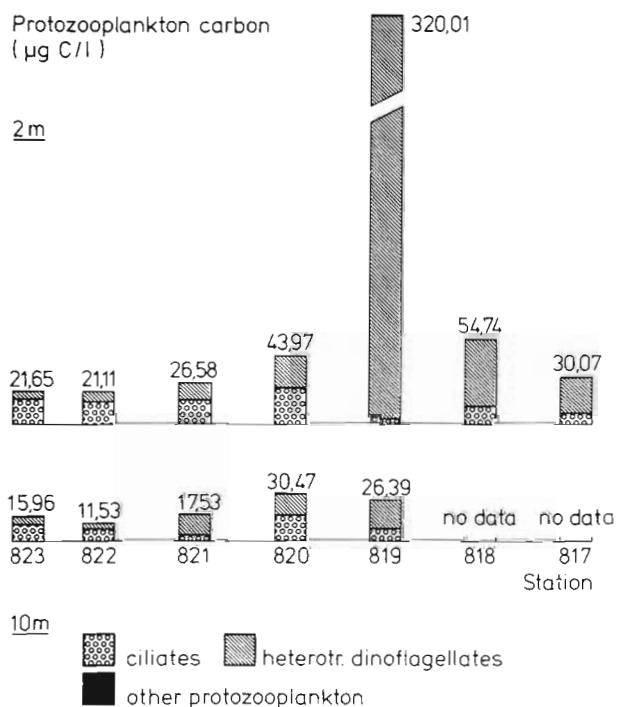


FIG. 6. — Protozooplankton biomass ( $\mu\text{g C l}^{-1}$ ) and composition at two depths along the transect across the East-Frisian tidal mixing front, showing frontal dinoflagellate peak at St. 819.

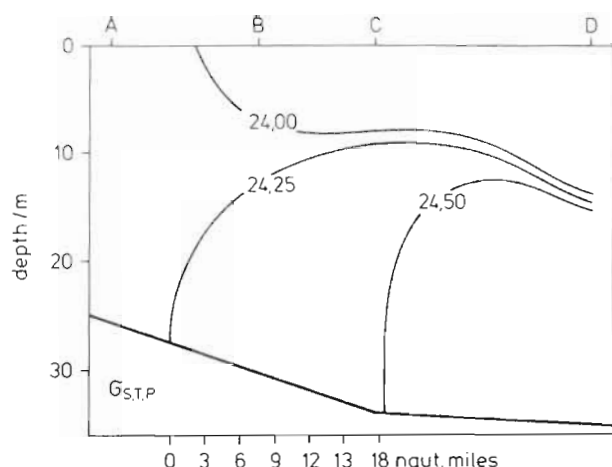


FIG. 7. — Density section showing a weak frontal structure in the southwestern part of the German Bight in August 1984.

consistence. Figure 8 illustrates the protozooplankton biomass distribution along a transect across the front, which comprised 4 stations only. For more complete information, 2 further stations (X, Y), lying apart from the transect in the surrounding water, were included. In the frontal patch (St. B), the *Noctiluca* concentration amounted to as much as  $4 \text{ mg C l}^{-1}$ , which corresponds to a cell concentration of about  $22 \times 10^3 \text{ cells l}^{-1}$  and accounted for more than 99 % of the total protozooplankton carbon. *Noctiluca* red tides associated with fronts have been mentioned previously and are considered as evidence for passive, convergent accumulation (LE FÈVRE, 1986). More details on the observed red tide, its implications for the pelagic foodweb structure and aspects of its temporal evolution are given by SCHAUMANN *et al.* (1988).

Apart from the protozooplankton *Noctiluca scintillans* the predominant phytoplankton species during the time of investigation was *Ceratium fusus* Dujardin, which is, like *Noctiluca*, a very common species of the summer plankton of the German Bight. As it could be traced from the standard survey, *Ceratium fusus* showed a widespread distribution all over the area of investigation, but exhibited, just like *Noctiluca*, a prominent peak in the water adjacent to the front (Fig. 8). The *Ceratium* concentration in this peak amounted to more than  $1 \text{ mg C l}^{-1}$ , representing  $6 \times 10^5 \text{ cells l}^{-1}$ .

The most striking feature of this *Ceratium fusus* accumulation, however, was the large amount of aberrant forms found within the patch (Fig. 9). Major form variations were cells with supernumerary antapical horns and very short forms (Fig. 10), which may be precursors of microgametes (ELBRÄCHTER, pers. comm.). These abnormal individuals accounted for as much as 12 % of the total *Ceratium* population in the frontal patch, whereas their occurrence in the surrounding waters was less than 0.5 %.

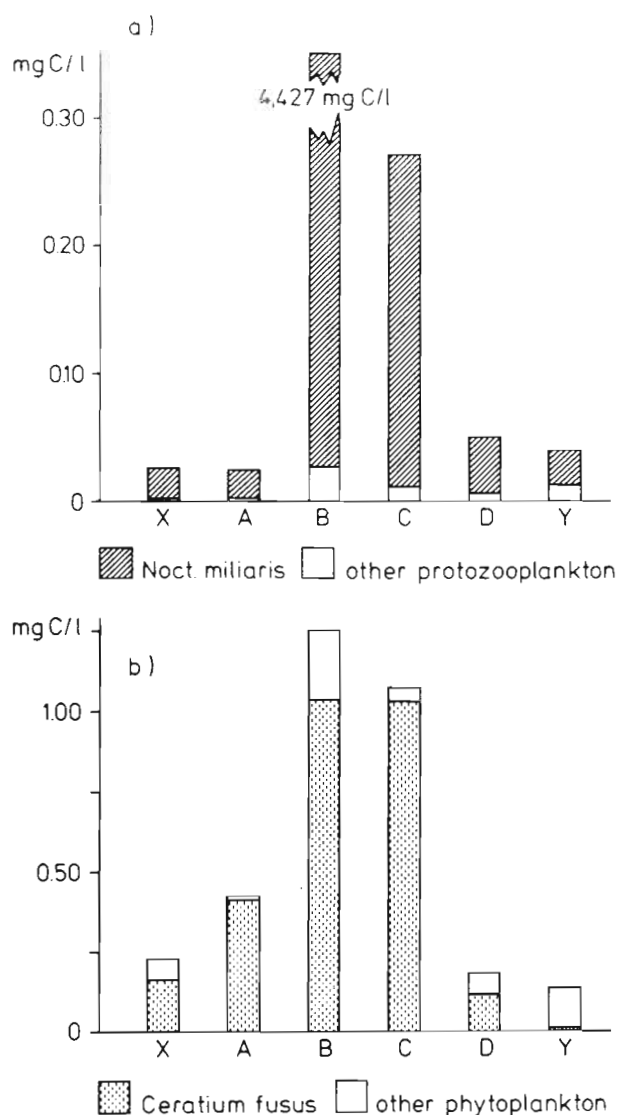


FIG. 8. — Biomass ( $\mu\text{g C l}^{-1}$ ) and composition of: a) protozooplankton, and b) phytoplankton, in the surface water (1m) along a transect (A-D) across the front in August 1984. Two further stations (X, Y) lying outside the transect (fig. 1) are included. Note the frontal peak of *Noctiluca miliaris* and *Ceratium fusus* at St. B.

## DISCUSSION

The results clearly demonstrate that fronts in the German Bight may be sites of high phytoplankton standing crops similar to those observed at other fronts in European waters. The following discussion will mainly deal with the mechanisms which might be responsible for the observed high frontal biomass concentrations. At first sight, it seems evident that the diatom peak adjacent to the Elbe river plume front has to be traced back to increased water column stability, according to SVERDRUP's (1953) critical depth model. A significant correlation between PPC-surface-values and the stratification factor  $\bar{V}$  ( $r = 0.898$ ;  $P < 0.01$ ), which became even more significant when

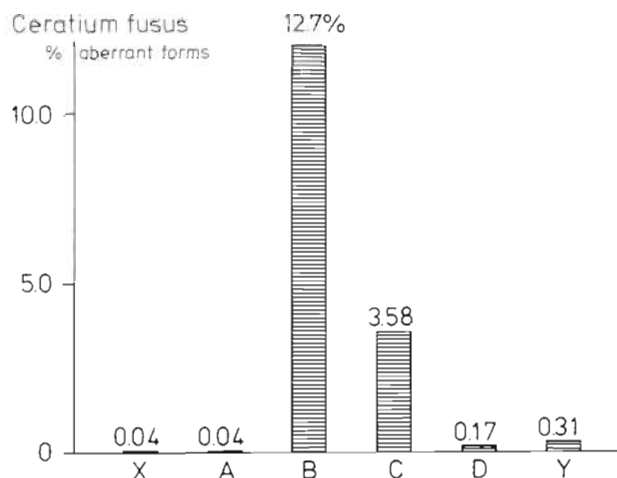


FIG. 9. — Percentage of aberrant forms of *Ceratium fusus* at stations corresponding to figure 8. Note the high percentage of form variations in the frontal peak at St. B.

only diatom carbon was considered ( $r = 0.916$ ;  $P < 0.01$ ), supports this view.

The application of the Sverdrup model assumes that light and not nutrients or other growth parameters are limiting photosynthesis. Very low silicate and phosphate concentrations, however, suggest that the diatom population was seriously nutrient limited during the present investigation. This implies that a stimulation of growth due to increased water stability may only account for the period before nutrient depletion was established.

The pronounced maximum of photosynthetic activity within the frontal diatom peak cannot be explained either in terms of light or temperature, as these conditions were identical for all activity measurements conducted. Because of the similarity in species composition at adjacent stations of the profile it is also very unlikely that changes in the phytoplankton species assemblages were responsible for the ob-

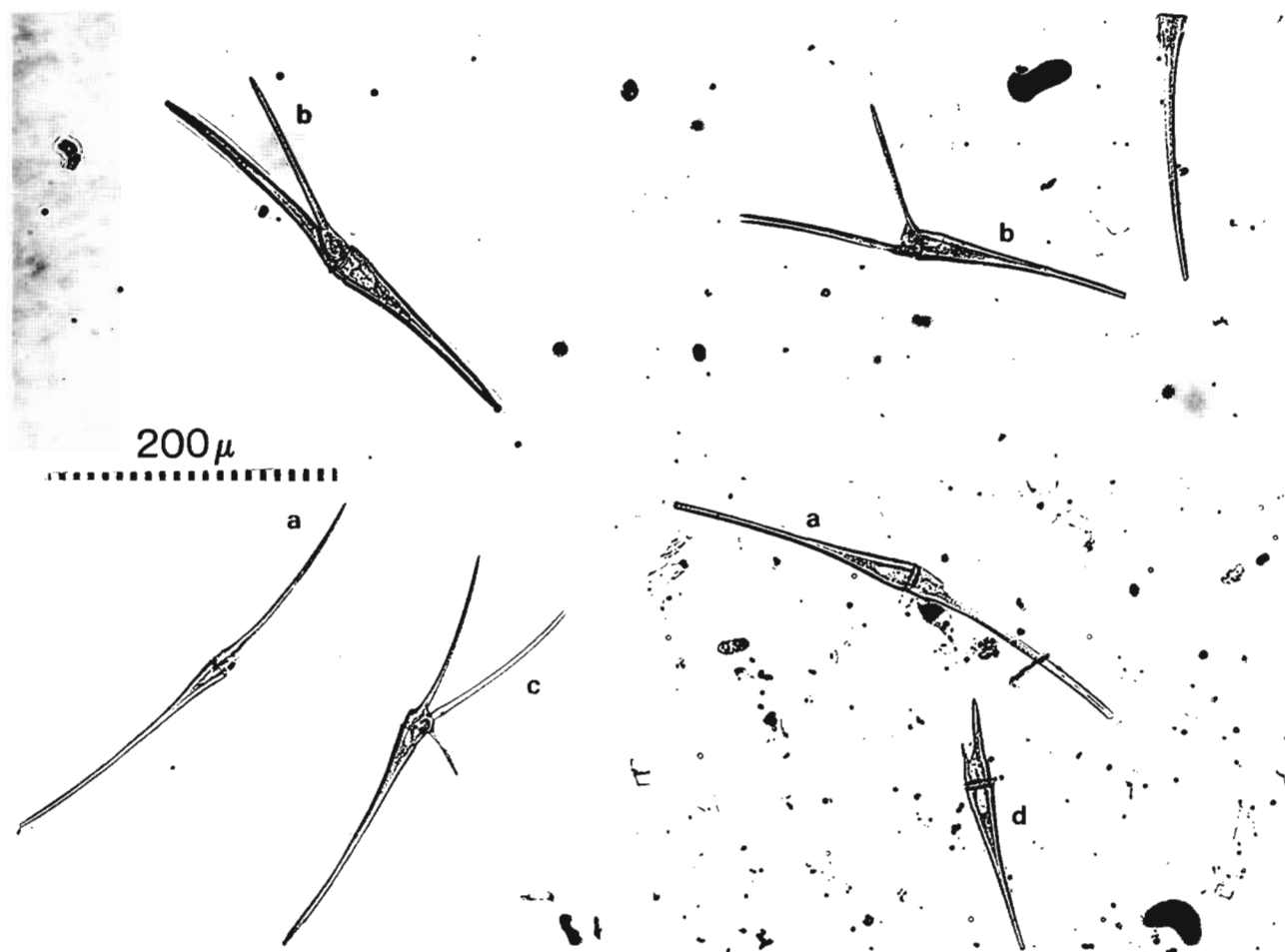


FIG. 10. — Aberrant forms of *Ceratium fusus* observed in the dense frontal phytoplankton patch in August 1984. a) usual habitus; b) forms with one supernumerary antapical horn; c) forms with two supernumerary horns; d) forms with shortened horns (probably precursors of microgametes).

served differences in photosynthetic rate. Similarly, salinity differences cannot account for the productivity variations, because in the critical range from St. 777 to St. 781  $\Delta S < 0.5$ .

The frontal maximum in photosynthetic rate rather indicates a local stimulation by nutrients or other, more subtle chemical growth factors. Enhanced nutrient regeneration due to intense remineralisation of accumulated organic substances (FLOODGATE *et al.*, 1981; JACOBSON *et al.*, 1983) or nutrient complementation by admixture of the water masses adjacent to the front (DUFOR & STRETTA, 1973; SAVIDGE, 1976; BEARDALL *et al.*, 1982) as well as accumulation of trace metals or organic growth factors may have accounted for the observed productivity maximum at the front. Convergent flow, indicated by the foam line, may have contributed to accumulation and prevented diffusion of this dense phytoplankton bloom (OKUBO, 1978).

In contrast to the situation at the Elbe river plume front, the mass occurrence of the unidentified, athecate nanoflagellate at the tidal mixing front north of the East Frisian Islands can hardly be explained in terms of nutrient stimulation, since nitrogen and phosphate concentrations were well above half saturation levels known from culture experiments in the literature (EPPELEY & THOMAS, 1969; RHEE, 1982). The absence of a significant frontal maximum in photosynthetic rate and the lack of any significant correlation between nutrient concentrations and productivity confirm this conjecture.

In this case, convergent accumulation is most likely to play a major role in patch formation, flocking together positively phototactic flagellates at the surface adjacent to the front. In a numerical model JAMES (1984) demonstrated the possibility of convergent flow at shelf sea fronts. SELIGER *et al.* (1981) found a convergent accumulation of positively phototactic dinoflagellates at a front in Chesapeake Bay and LE FÈVRE (1986), too, emphasizing the importance of convergence as an accumulation mechanism at the Ushant front.

In the same manner, phagotrophic dinoflagellates seemed to be concentrated at the tidal mixing front. In addition, a better food supply offered by the mass occurrence of the small autotrophic nanoflagellates may account for the observed protozooplankton peak.

Very low silicate concentrations in the absence of a significant amount of diatoms on the stratified side suggest that a diatom bloom preceded the flagellate population at the tidal mixing front. BAUERFEIND (pers. comm.) observed a widespread diatom spring bloom a few weeks prior to the present investigation all over the German Bight, dominated by *Thalassiosira nordenskiöldii*. Moreover, KUIPER (1977) found, in enclosure experiments with natural North Sea

coastal plankton, a succession of a *T. nordenskiöldii* dominated diatom bloom and unidentified nanoflagellates.

It thus appears that the phytoplankton community at the tidal mixing front, which was dominated by nanoflagellates, actually exhibits a more advanced stage of succession than the one at the river plume front, where *T. nordenskiöldii* prevailed. Obviously, the improved nutrient supply prolonged the maintenance of the diatom bloom at the river plume front.

The high population density at fronts, whether it is caused by enhanced production or passive convergent accumulation or both, may have a considerable impact on the community structure of other trophic levels in the German Bight.

As was shown by SCHAUMANN *et al.* (1988), the *Noctiluca* red tide resulted in an explosive development of smaller protozooplankters and fungi, whereas copepods were excluded. A large number of phagotrophic dinoflagellates was associated with the nanoflagellate mass occurrence at the tidal mixing front, and it seems very likely that they also fed on the small nanoplankters.

In the aftermath of dense *Ceratium* «blooms» at the edge of the Elbe river plume serious oxygen deficiency accompanied by fish mortality was observed in summer 1981 and 1982 (DETHLEFSEN & WESTERHAGEN, 1983; RACHOR & ALBRECHT, 1983).

The frontal effect, however, may not be restricted to trophic aspects only, but may be of significance in the life strategies of many phytoplankters. TYLER & SELIGER (1981) and TYLER *et al.* (1982) demonstrated that fronts may act as retention barriers for distinct phytoplankton populations, ensuring maintenance of these populations in their habitat. There are some indications that under certain conditions, which still have to be investigated in more detail, this is the case at the Elbe river plume front, as well.

The enhanced occurrence of aberrant individuals is an interesting phenomenon in dense frontal phytoplankton patches. In *Ceratium* cultures, form variations have occasionally been observed. The very high population density was proposed to be the direct cause of the observed anomaly by means of mechanical interference (HASLE & NORDLI, 1951). However, for natural populations such a theory seems less probable.

During a *Ceratium fusus* bloom in Oslofjorden (Norway), HASLE & NORDLI (1951) recorded some aberrant individuals very similar to those observed in the present study, however in a much lower percentage ( $< 1\%$ ). The authors put forward a hypothesis which stresses the importance of chemical influence on form variations with special emphasis on nutrients. Our detailed study on the *Noctiluca* red tide patch revealed high inorganic phosphate and ammonium concentrations, which were probably due to en-



hanced cell lysis of the organisms in the patch. These and other metabolites may have affected *Ceratium* cell growth. Pollutants, too, have to be considered as possible factors for the observed cell anomalies. There are reports on trace metal accumulations in frontal foam (SZEKIELDA, 1972) and particulate matter (SICK *et al.*, 1978). In addition, KLEMAS & POLIS (1977) reported high concentrations of hydrocarbons at frontal zones, deriving from oil spills.

The increased occurrence of forms with shortened horns in the *Ceratium* patch, which are considered to be precursors of microgametes, suggests that dense frontal phytoplankton accumulations are likely to provide favourable sites for high sexual reproduction. A similar conclusion was drawn by TYLER *et al.* (1982), who found sexual stages and fusing gametes of another dinoflagellate, *Gyrodinium aureolum*, at a frontal convergence in the Potomac River (Chesapeake Bay).

The present case studies reveal some interesting aspects of the biological impact of German Bight fronts; however, no conclusion can be drawn with regard to the general importance of such structures for the ecosystem of the area. For this purpose, sampling of high spatio-temporal resolution supported by remote sensing techniques is required to study the highly variable frontal systems in this shallow part of the North Sea.

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