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Phytoplankton standing stock and primary production in the Western Baltic

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Abstract

The main studies on phytoplankton ecology carried out in Kiel Bight during the last decades are briefly reviewed. Special emphasis is laid on the hydrographical structure of this transitional area between the Baltic Sea and the North Sea, as it strongly affects the seasonal cycle of phytoplankton standing stock and species succession through vertical stratification and advection processes. Both these hydrographical features prevail during the growth period of phytoplankton and are responsible for large variations in population density and nutrient supply. The seasonal species succession is also influenced by advection. The annual primary production figure of about 150 g $C \cdot m^{-2}$ approaches the upper limit of values recorded for other parts of the western and southern Baltic. Total irradiation appears to exert the strongest influence on the seasonal cycle of primary production as long as water temperatures are low, giving way in summer to temperature as the determining factor for the production rate.

Introduction

Planktological studies in the western Baltic Sea possess a long history, dating back to the latter decades of the last century and calling to mind many famous names such as Victor HENSEN, Carl APSTEIN and Karl BRANDT. This first period of intensive study, which was put to an end by World War I, was crowned by the work of LOHMANN (1908). He succeeded in recording an entire seasonal cycle of phyto- and zooplankton together with the relevant hydrographical and chemical data at a station situated at the outer entrance to Kiel Fjord in 1905/06. To this day, LOHMANN's work remains unique in its thoroughness and the consistency with which a detailed weekly sampling programme was adhered to.

The founding of the Institut für Meereskunde in Kiel-Kitzeberg in 1937 ushered in a new era of plankton research in Kiel. Johannes KREY (1912 – 1975) became the founder of a new school of planktologists after World War II. Without neglecting the traditional microscopic analysis of species composition and abundance, he introduced modern biochemical methods in order to measure seasonal changes in the main constituents of seston – autotrophic phytoplankton, heterotrophic bacterio- and zooplankton and detritus – in a quick and reliable way and to correlate them with prevailing environmental factors. For this purpose, long-term observation series were initiated at several stations in Kiel Bight (KREY 1961, KREY et al. 1978).

It is the intention of this paper to give a brief review of the work on phytoplankton standing stock and primary production carried out by Kiel planktologists at the permanent station Boknis Eck in the western Kiel Bight during the last two and a half decades. For this it is necessary to first describe the hydrographical regime of the area in some detail, as it exercises a strong influence on ecological processes governing the seasonal cycle of phytoplankton.

Prevailing hydrographic conditions

The shallow and narrow Belt Sea in the western Baltic acts as a connecting pipe between two reservoirs, the Baltic Sea and the North Sea (Fig. 1). The basic pattern of the current system, which is determined by a water surplus originating from the large catchment area of the Baltic, consists of an outflow of low-salinity water at the surface and a compensatory current in the opposite direction in the deep. This inflow of more saline water from the North Sea causes the water column to be strongly stratified during most of the year, with a characteristic tilt of the isopycnics in the Belt Sea area. This basic pattern, however, is often disturbed by the action of winds and differences in air pressure over both reservoirs. These disturbances may cause short-term reversals in the prevailing currents at surface or bottom. Strong oscillations are thus a characteristic feature of the hydrographic regime in this transitional area.

The daily records of light vessels give a good impression of the amplitude and time scale of such hydrographic oscillations. It is regrettable that two of the former three light vessels positioned in Kiel Bight (Fig. 2), namely "Kiel" and "Flensburg", have been replaced by automatic light-houses, thus terminating long-term hydrographic data series from these locations. To demonstrate the seasonal range and regional differences of the oscillations in water movement by means of daily salinity records we must therefore go back to the year 1961 (Fig. 3 and 4).

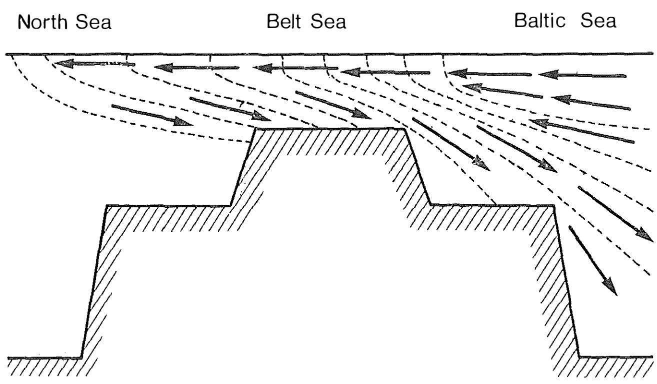

Figure 1

Schematic diagram of the basic current regime between North Sea and Baltic Sea. The dashed lines symbolize the isopycnics

By far the strongest variations are found in the upper water layer in the Fehmarn Belt, which is the main pathway for water exchange via the Great Belt. The main halocline tends to lie above the 15 m depth in spring and early summer and then below for the rest of the year. The very strong vertical stratificiation caused by the in- and outflowing water masses manifests itself in a salinity difference of as much as 20 ‰. An almost complete vertical mixing of the water column was observed only twice during the year, in spring and in late autumn.

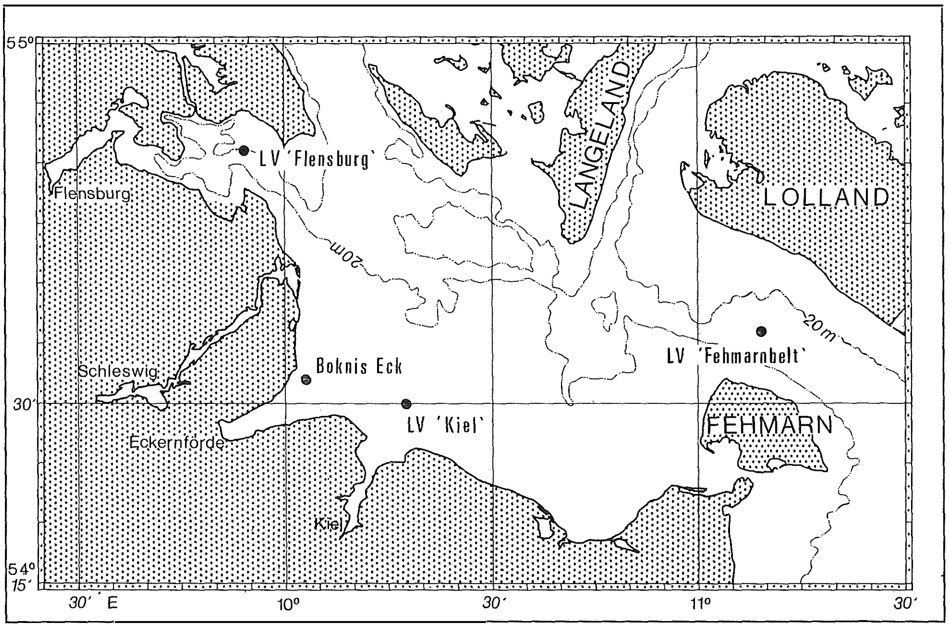

Figure 2

Map of Kiel Bight with the position of three light vessels and the permanent station "Boknis Eck". The dashed line follows the 20 m depth contour

The oscillations are far less pronounced in the western part of Kiel Bight, where our permanent station Boknis Eck is situated. They are, however, still strong enough to demonstrate the dominating role of advection in this area. A characteristic feature is the outflow of low-salinity water in spring as a result of snow and ice melting in the northern Baltic and its adjacent catchment area. Judging by the records for 1961, this outflow is indicated by a sudden drop in salinity which we observe in Fehmarn Belt at the beginning of April and a few days later in the western Kiel Bight. This is precisely the time when the phytoplankton spring bloom has passed its peak in our area. The sudden arrival and overlaying of the original water by these outflowing water masses with their low salinity and sparse plankton content may lead the observer to believe that the aged phytoplankton bloom, having entered the death phase, has sedimented from one day to the next.

The average seasonal salinity stratification between surface and bottom water at Boknis Eck, based on monthly observations over a 19 year period, as shown in Fig. 5, reflects the strong outflow of surface waters from April to June and the compensating inflow of more saline bottom water, the peak being reached in August. This summer stratification of the water column alternates with a practically complete vertical mixing in winter. Fig. 5 further shows how great the amplitude of annual variation of this characteristic seasonal pattern is, although it must be borne in mind that a number of the deviations observed reflect only short-term oscillations, as documented by the daily records maintained by the light vessels.

The seasonal changes in salinity clearly indicate how greatly the prevailing current system influences the structure of the water masses in our area. To sum up, we have a

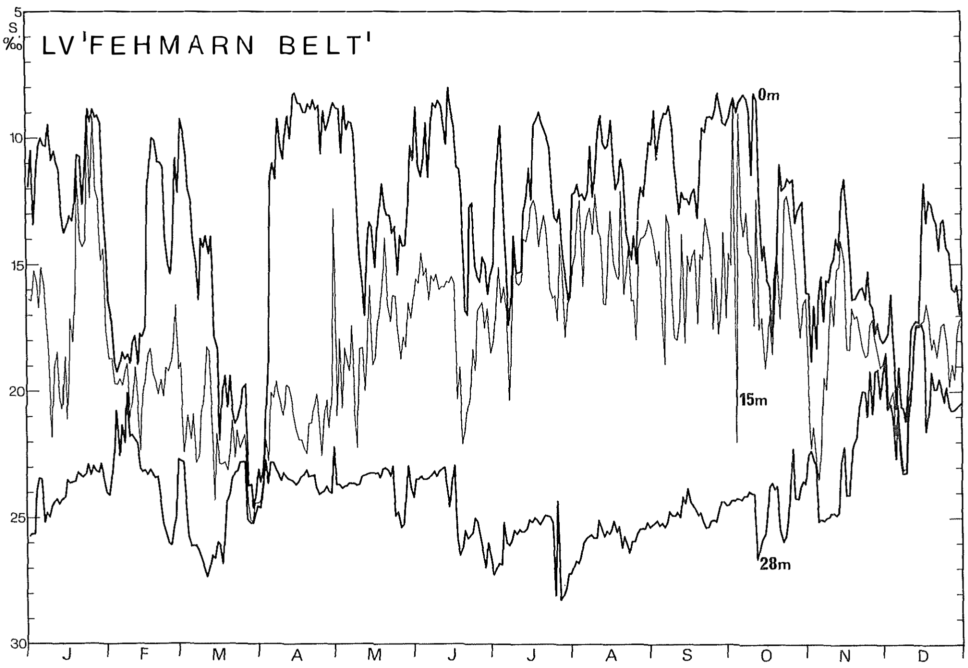

Figure 3
Daily salinity records (0,15 and 28 m) from LV "Fehmarn Belt" in 1961

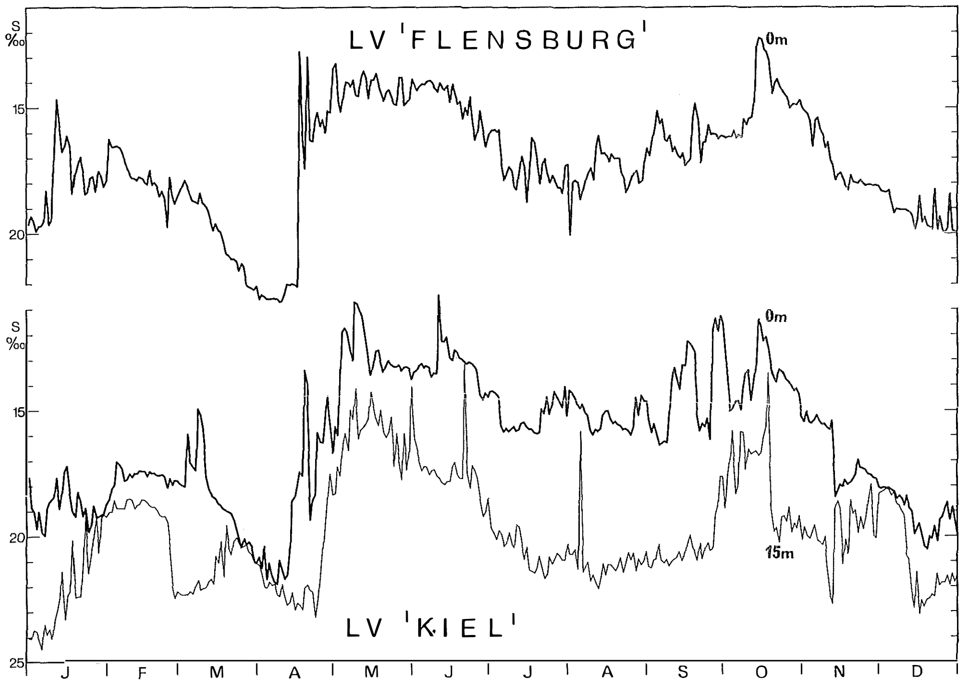

Figure 4
Corresponding salinity records from LV "Flensburg" (0 m) and "Kiel" (0 and 15 m)

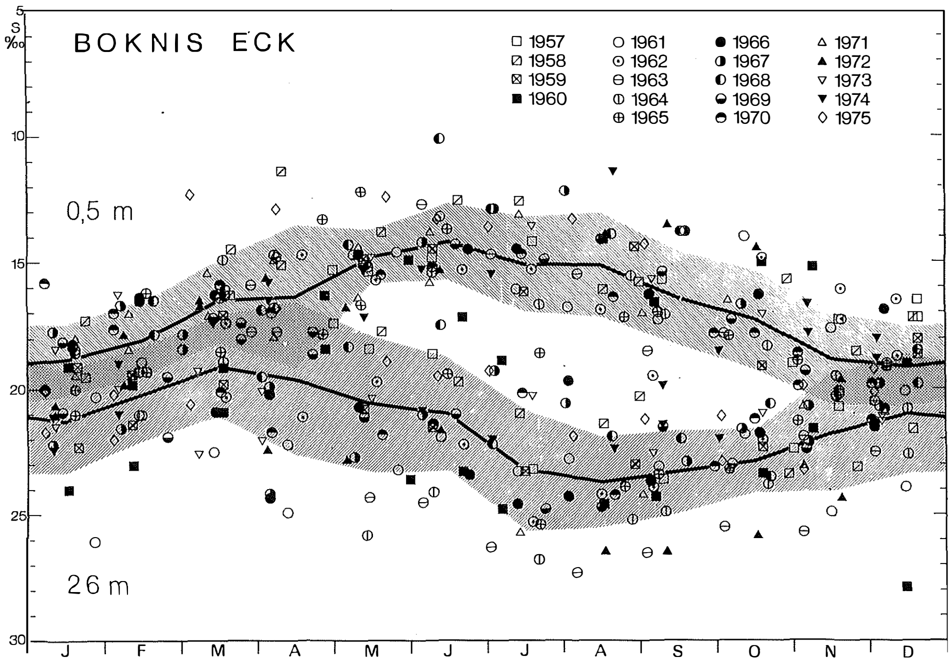

Figure 5

Mean annual cycle of salinity at 0.5 m (above) and 26 m depth (below) at the permanent station "Boknis Eck", based on monthly observations from 1957–1975 (KREY et al. 1978). The measurements for each year are individually marked. Shaded areas indicate the standard deviation for the monthly means

mixing of the water masses in winter, after which they separate into two main layers moving in opposite directions until the next mixing in the following winter. Obviously, this is a greatly simplified picture of a complex reality. Yet it serves to stress the fact that advection processes affecting plankton studies at a fixed station such as ours in the western Kiel Bight are most pronounced from spring to autumn, coinciding with the main growth period of phytoplankton.

Phytoplankton standing stock

The seasonal fluctuations in the phytoplankton standing stock measured as chlorophyll a concentration at the permanent station Boknis Eck (KREY et al. 1978) are on a comparable scale with the hydrographic variations. The values plotted in Fig. 6 are monthly measurements at 5 m depth, which is taken as representative for the euphotic zone. Despite the wide annual variation, which extends to at least one order of magnitude at all seasons, the classical pattern for higher latitudes, i.e., a pronounced spring bloom and a lesser autumn bloom, is still clearly discernible. The lowest values, found from April to June, are probably ascribable to outflowing surface waters from the Baltic proper.

The wide scattering seen in the data mirrors not only seasonal changes in phytoplankton standing stock but also differences in density of the populations borne by the varying water masses encountered at our station. Since the standard methods for chlorophyll a measurement yield fairly accurate results, the scattering cannot be

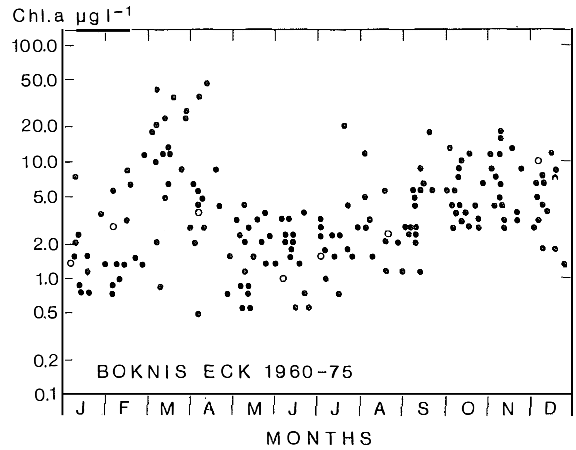

Figure 6

Monthly records of chlorophyll a at 5 m depth at "Boknis Eck" from 1960–1975 (o two or more coinciding values) according to KREY et al. 1978

ascribed to methodological errors. These strong variations observed in month to month measurements presage the problems to be faced at least in our area by the recently launched international monitoring programme for the Baltic Sea.

The monthly sampling programme initiated by J. KREY at Boknis Eck in 1957 was intensified by a team of young planktologists under the leadership of B. ZEITZSCHEL and V. SMETACEK within the framework of the Joint Research Programme (SFB) 95 in the early seventies. A 2-year study period with a detailed sampling programme during spring and summer brought to light the occurrence of several smaller phytoplankton blooms in summer. Though their number varies from year to year, they nevertheless form a characteristic feature of the seasonal cycle of phytoplankton standing stock between the two major peaks in spring and autumn (SMETACEK 1975, 1978). These summer blooms are evidenced less by the chlorophyll a recordings than by the carbon values calculated for the phytoplankton biomass, since the appearance of dinoflagellates after the diatom spring bloom leads to a considerable increase in the ratio of carbon to chlorophyll. This is due to the dinoflagellates possessing a higher carbon content than diatoms on account of their organic cell walls and the absence of large vacuoles.

Primary production

Irradiation, temperature and nutrient supply are usually considered the chief environmental factors governing the growth of phytoplankton. The influence of the first two factors on primary production is illustrated in Fig. 7. This diagram, taken from v. BODUNGEN (1975), shows a section of the detailed studies carried out by the SFB 95 team at Boknis Eck. Primary production and chlorophyll a, which can be taken as an index for the standing stock of phytoplankton, have been integrated for the upper 20 m of the water column. We can therefore expect a close relationship between both curves. This, however, is evident only at the beginning and end of the growth season. Later in the year, the production rate seems to be independent of standing stock and mainly governed by irradiation and temperature.

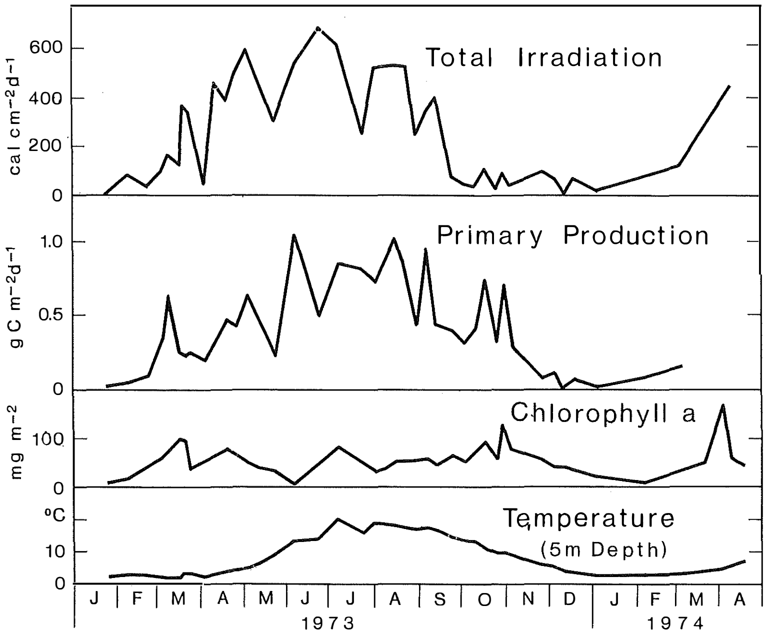

Figure 7

Annual cycle of total irradiation, primary production, chlorophyll a content and water temperature at "Boknis Eck" after v. BODUNGEN (1975)

To better analyse this relationship we have plotted primary production against total irradiation in Fig.8 and subdivided the values into 4 categories according to the average temperature of the euphotic zone. In order to assess the influence of temperature, we have calculated two separate regression lines for cold water ($<$ 10°C) and warm water ($>$ 10°C); the equations are given in Table 1.

Table 1

Regression equations for the dependence of primary production (mg C $\cdot$ m^{-2} $\cdot$ d^{-1}) on total irradiation (cal $\cdot$ cm^{-2} $\cdot$ d^{-1}) at Boknis Eck (see Fig. 8)

Average temperature of the euphotic zone	2°–10°C	10°–20°C
Number of observations	24	15
In log-transformation	$y = 0.604\ x + 0.988$	$y = 0.277\ x + 2.144$
Without log transformation	$y = 9.7\ x^{0.604}$	$y = 139.6\ x^{0.277}$
Correlation coefficient (r)	0.758	0.766
Confidence level	$>$ 99.9%	$>$ 99.9%

The influence of irradiation on the rate of primary production is apparently greater during the low temperature period from November to the end of May than during the warmer months. In the summer season, light plays a subordinate role to temperature, which then appears to be the main factor promoting the production rate.

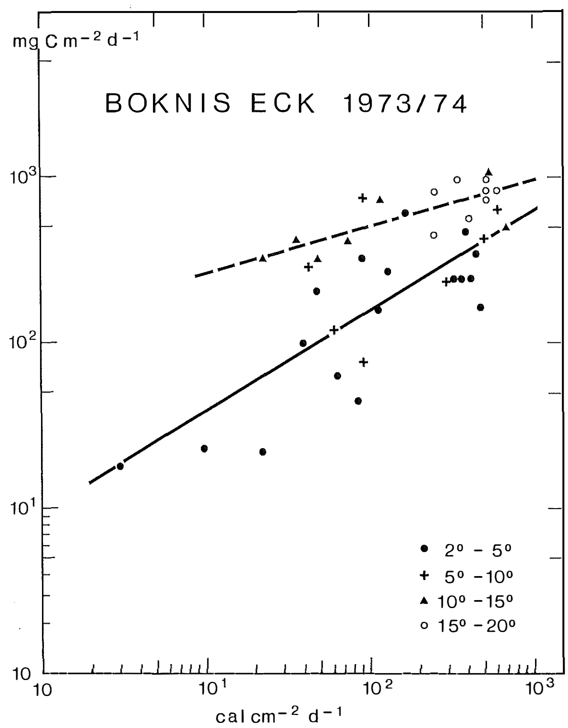

Figure 8

Relationship between primary production and total irradiation based on data recorded at "Boknis Eck" in 1973/74 by v. BODUNGEN (1975) with regression lines for lower (< 10°C) and higher temperatures (> 10°C). The temperature at 5 m depth is taken as representative of the euphotic zone

In a statistical analysis of the seasonal variation observed in the assimilation number of phytoplankton in Bedford Basin, Nova Scotia, Canada, HARRISON and PLATT (1980) found temperature to be the most significant co-variate for the observed variation. Similar results stressing the importance of temperature were obtained by LASTEIN and GARGAS (1978), who studied the dependence of phytoplankton photosynthesis on environmental factors in shallow lakes of Denmark. Both these studies, however, are based on incubator measurements where light and temperature effects are much easier to demarcate than in our *in situ* experiments.

The annual primary production measured at Boknis Eck in 1973 amounted to 158 g $C \cdot m^{-2}$ (v. BODUNGEN 1975). Though the author regards this value as exceptionally high, comparably high values are reported from the eastern Gotland Sea, the Hanö Bight and the Sound. A compilation of the amount of primary production in different areas of the Baltic is found in LENZ (1981).

Grazing and nutrients

We shall now consider grazing pressure and nutrient depletion as responsible for keeping the summer stock of phytoplankton at a comparatively low level in our area, despite the irregular number of smaller peaks produced by the so-called summer blooms already mentioned (SMETACEK 1975, 1978).

The abundance of herbivorous and omnivorous copepods in Kiel Bight may be taken as an index for the grazing pressure exercised on phytoplankton. The copepod abundance reaches its maximum in May and June and remains elevated until September when it drops drastically to a very low winter level followed by a slight increase towards spring (SCHNACK 1978). The copepod occurrence correlates inversely with the standing stock of phytoplankton, as when the latter is high in spring and autumn the grazing pressure by copepods is low and vice versa.

The seasonal availability of essential nutrients is demonstrated by the example of inorganic phosphorus in Fig. 9 (according to v. BODUNGEN 1975). The marked depletion within the upper layer during summer also holds true for inorganic nitrogen compounds with the exception of ammonia as an excretory product of heterotrophic organisms, which along with organic excretion products maintains phytoplankton growth.

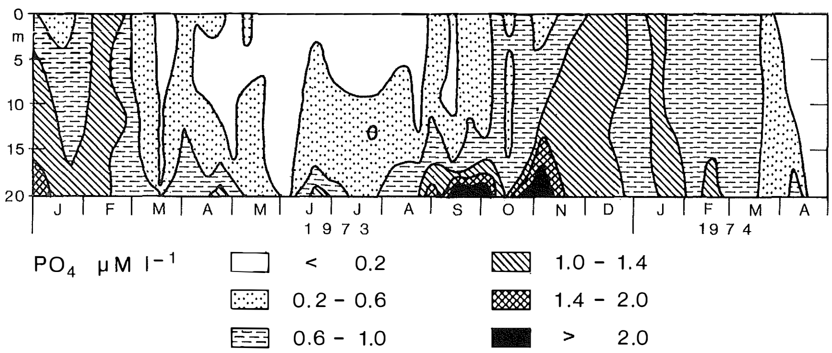

Figure 9
Annual cycle of inorganic phosphorus at "Boknis Eck" in 1973/74 after v. BODUNGEN (1975)

Fig. 9 gives an impression of the occasional intrusions of nutrient-rich waters from the bottom into the euphotic zone. These nutrient inputs are thought to be the cause of the summer blooms of phytoplankton (SMETACEK 1975, 1978). Here we can plainly trace the influence of advection processes causing the nutrient pulses.

Much work has been devoted by the SFB 95 to investigating processes of nutrient release from the sea bottom. One possible mechanism found to generate such nutrient pulses from the bottom is the displacement of interstitial pore water through the inflow of water with higher salinity and density (SMETACEK et al. 1976). We have seen in Fig. 5 that, as a rule, salinity of the bottom water at Boknis Eck tends to increase from March to August. The importance of interactions between sediment and water for nutrient dynamics in shallow water ecosystems like the Belt Sea area has been stressed by ZEITZSCHEL (1980).

Species succession

The seasonal species succession of phytoplankton was recently studied in details by SMETACEK (1975, 1978). A shorter account is given by LENZ (1977). The contributions of the main systematic groups to the standing stock of phytoplankton, expressed as carbon biomass for the upper 20 m of the water column – this approximates the average depth of the euphotic zone – are shown in Fig. 10.

The dominance of dinoflagellates after the diatom spring bloom is a typical feature of the phytoplankton cycle in higher latitudes. The decline of the diatoms after the spring bloom is often explained by the exhaustion of the available silica in the stratified water column. Though the problem of Si-limited growth of diatoms has been intensively studied in laboratory experiments, no definite solution has yet been found (PAASCHE and ØSTERGREN 1980). In late autumn, the diatoms are believed to take advantage firstly of the nutrients brought up into the euphotic zone through increased mixing of the water column, secondly of the irradiation still available and thirdly of the absence of grazers to build up a second peak of standing stock (Fig. 10).

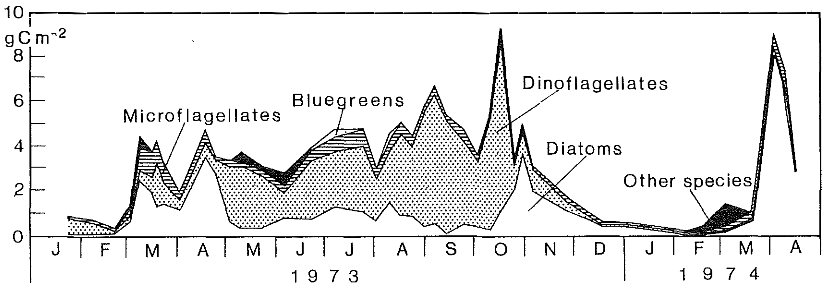

Figure 10

Seasonal cycle of main phytoplankton groups at "Boknis Eck" in 1973/74 after SMETACEK (1975)

The first dominant dinoflagellate species in the course of the year is the small *Prorocentrum balticum*, forming a regular bloom in May. Later on, various *Ceratium* species usually take over the leading role in regard to phytoplankton biomass (SMETACEK 1975, 1978).

At this point, we must again turn our attention to the influence of advection processes on the occurrence of phytoplankton species in our area in summer. A clear indication of advection is the observation of blue-green algae in July and August. These are transported into the Kiel Bight with outflowing water originating in the Arkona Sea or further north in the Baltic proper, where these species thrive in water of low salinity throughout the summer and often accumulate at the sea surface (HORSTMANN 1975). They can be traced in outflowing water as far as the Skagerrak.

On the other hand, we suspect that inflowing water from the Kattegat is the main source of dinoflagellates, especially *Ceratium* species, which become abundant in our area in summer and autumn. From their depth distribution, shown in Fig. 11 after SMETACEK (1975), it appears that they predominate first in the deeper layers, from where they subsequently spread upwards into the entire water column.

Concluding remarks

Other aspects of phytoplankton ecology have also been thoroughly investigated in Kiel Bight during recent years. The relationship between phytoplankton succession and the composition of particulate matter was studied by SMETACEK and HENDRIKSON (1979) and the sedimentation of phytoplankton and other seston components by ZEITZSCHEL (1965), v. BRÖCKEL (1975) and SAURE (1981).

In an attempt to quantify the energy flow through the pelagic part of the shallow water ecosystem in Kiel Bight, v. BRÖCKEL (1978) has elucidated the role of phytoplankton

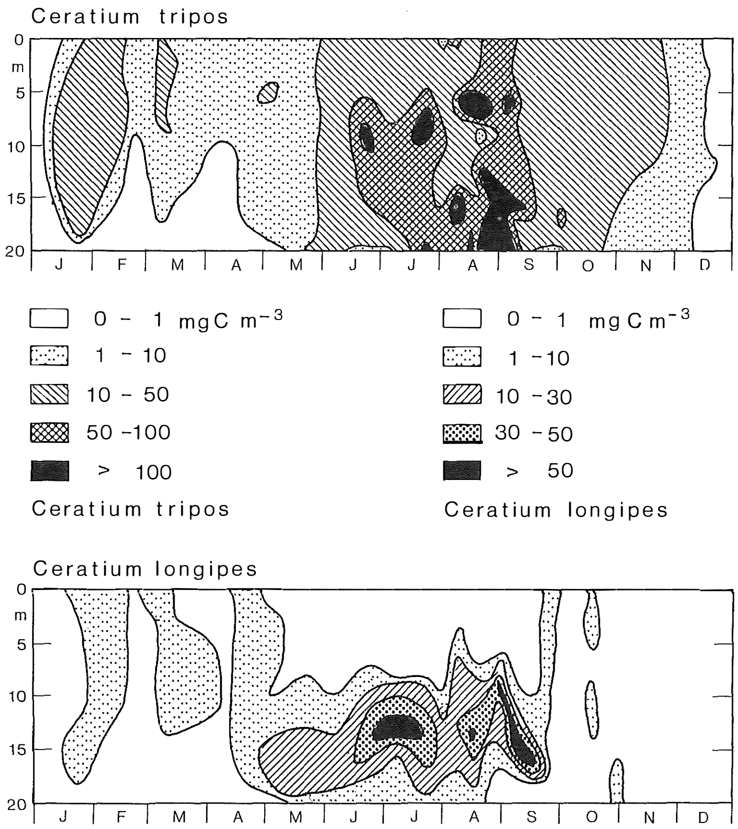

Figure 11

Seasonal occurrence of two *Ceratium* species at "Boknis Eck" in 1973/74 according to SMETACEK (1975)

as primary producer. The average transfer efficiency from photosynthetic active radiation (PAR) – 45 % of total irradiation was taken as mean value – to phytoplankton was found to amount to 0.77 %. It was estimated that about 40 % of the phytoplankton net production was taken up by zooplankton; about 25 % was directly remineralized by bacterioplankton and the remainder of 35 % sedimented to the sea bottom to benefit the benthos fauna.

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