On the distribution and importance of picocyanobacteria in a boreal inshore area (Kiel Bight, Western Baltic)

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Abstract. From April to October 1986 abundance and vertical distribution of picocyanobacteria were studied at four stations in Kiel Fjord and Kiel Bight. Both picocyanobacteria and autotrophic, eukaryotic picoplankton cell numbers were estimated by epifluorescence microscopy whereas larger phytoplankton (>3 μm) was enumerated by the Utermöhl settling technique. Picocyanobacteria cell numbers peaked in July and August near the water surface (1.4–2.6 × 10^8 cells l^{-1}). Although picocyanobacteria abundance increased from the outer Kiel Bight to the more eutrophic inner stations of Kiel Fjord, their contribution to total phytoplankton biomass decreased. During summer up to 52% of phytoplankton carbon and up to 97% of autotrophic picoplankton carbon were contributed by picocyanobacteria. Therefore picocyanobacteria are an important component of the summer phytoplankton community in boreal inshore waters, too.

Introduction

Since their recent discovery by Johnson and Sieburth (1979) and Waterbury *et al.* (1979) it has become obvious that marine coccoid cyanobacteria are widely distributed and highly abundant, so playing an important role as primary producers. There have been numerous reports of picocyanobacteria from the open ocean but only a few examinations of coastal waters are documented (Krempin and Sullivan, 1981; Joint and Pipe, 1984; Glover *et al.*, 1985a; Takahashi *et al.*, 1985; El Hag and Fogg, 1986; Joint *et al.*, 1986; Waterbury *et al.*, 1986). Since the importance of picocyanobacteria in both oceanic and neritic waters is now widely accepted, it has become desirable to know what contribution they can make in a boreal inshore area and whether their vertical and seasonal distribution is similar to those in neritic and oceanic offshore waters.

The plankton of Kiel Bight is typically marine and similar to that characteristic for boreal coastal waters (Smetacek, 1981), and the seasonal distribution pattern of larger phytoplankton is well documented. It is characterized by a diatom spring bloom and a dinoflagellate autumn bloom [For a summary of Kiel Bight plankton ecology see Smetacek *et al.* (1984)]. Smaller phytoplankton in the nano- and picoplankton range and especially picocyanobacteria, however, were not considered in previous investigations in Kiel Bight.

This study reports on the seasonal and spatial distribution of picocyanobacteria in Kiel Bight and the more eutrophic Kiel Fjord and reveals their high contribution to the phytoplankton community in this boreal inshore area.

Materials and methods

The four sampling stations are placed on a transect through Kiel Fjord and Kiel Bight (Figure 1) and were chosen to be representative of both the eutrophic

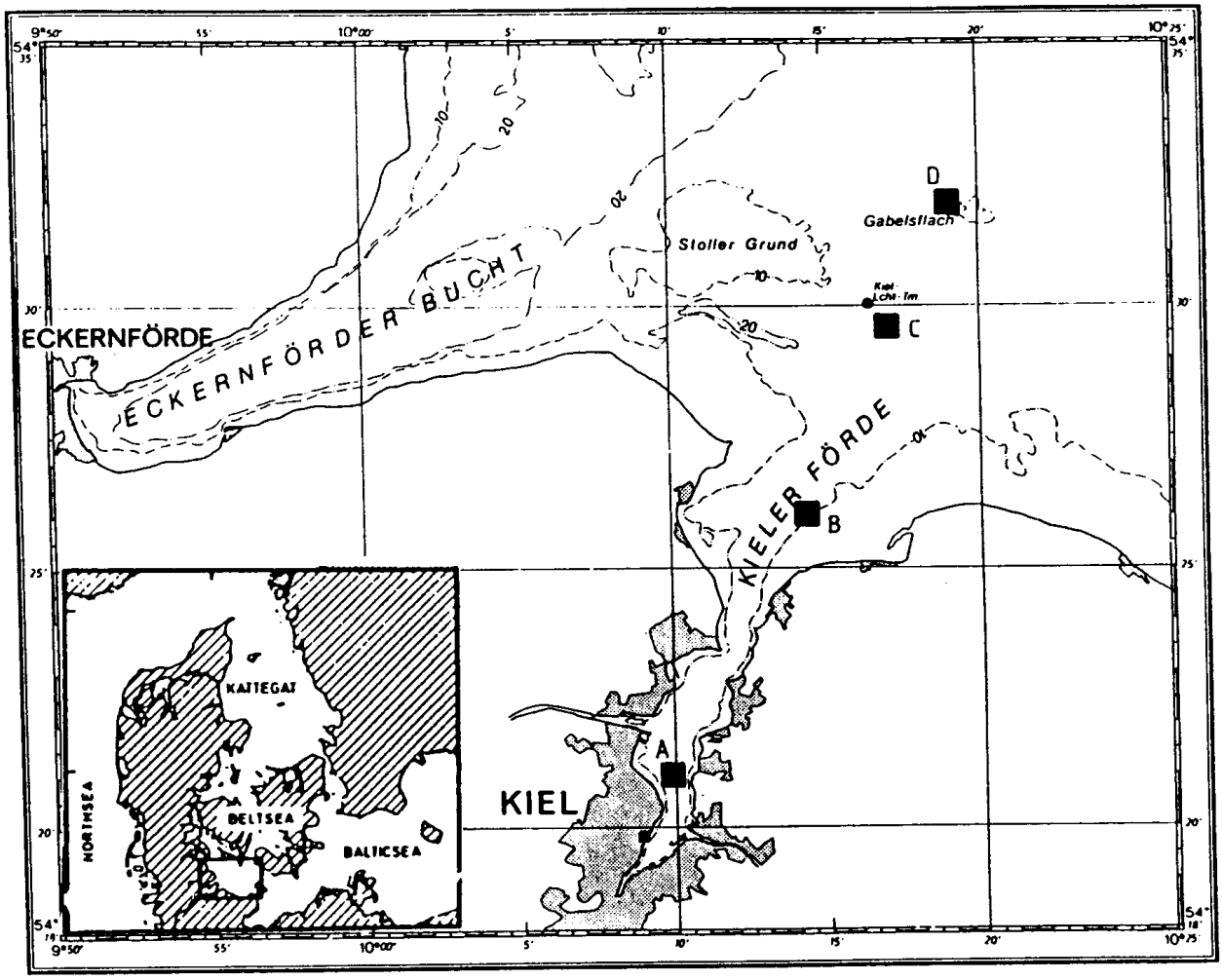

Fig. 1. Location of sampling stations in the southwestern part of Kiel Bight.

fjord and the open bight. Kiel Bight is enclosed to the west and south but open to influx of higher salinity Kattegat water from the northwest and lower salinity water from the Baltic proper from the east. Water in Kiel Bight is mesohaline and the density structure of the water column is salinity- rather than temperature-dependent. The average water depth is 17 m; the depth of the euphotic zone in Kiel Bight during summer is about 14 m.

Samples were taken from April to October 1986, one to two times per month. On June 12 and July 1 stations of greater depths (17 m resp. 28 m) in the vicinity of station D were examined instead of the 12 m standard station.

Temperature and salinity were recorded every 1 m with a WTW Conductometer LF 191. Samples for cell counts and nutrient analyses were taken from three or four depths at each station. At least one of them was situated above, within and beneath the pycnocline. During vertically mixed conditions, sampling depths were distributed evenly throughout the water column. Nitrate, nitrite and ammonia were measured in samples frozen on collection (Grasshoff *et al.*, 1983).

For picocyanobacteria and eukaryotic picoplankton, known volumes of living samples were filtered onto 0.2 μm membrane filters and counted under a Zeiss epifluorescence-microscope. Cyanobacteria could be separated from eukaryotic picoplankton by their different autofluorescence (Davis and Sieburth, 1982;

Takahashi *et al.*, 1985). Cell numbers of both picocyanobacteria and eukaryotic picoplankters were converted into carbon-biomass assuming 0.7 pg C $cell^{-1}$, which seemed to be an appropriate mean for these organisms. This conversion factor will be discussed later in more detail.

Surface samples for Utermöhl counts (Utermöhl, 1958; Hasle, 1978) were taken once each month at each station and fixed by adding formaldehyde (buffered with hexamethylenetetramine) to a final concentration of 0.4%. For October no such samples were available. Cell numbers of autotrophic phytoplankton were converted into biomass using the conversion factors given by Smetacek (1975). Organisms ≤3 μm were not considered in Utermöhl-counts as they cannot be reliably quantified with this method (Davis and Sieburth, 1982; Furuya and Marumo, 1983; Reid, 1983). As the presence of chlorophyll in flagellates 3–15 μm in size was difficult to judge in preserved material generally, 50% of them were considered as autotrophs.

Results

Vertical temperature and salinity profiles were very similar at all stations so their seasonal variation is only shown for station C (Figures 2 and 3).

Surface temperatures ranged from 0.7 to 21.6°C. In the inner fjord, at station A, they were generally 0.5–1°C higher than in open Kiel Bight. In May, June and the beginning of September they were 1°C lower due to upwelling events in the inner fjord.

At the beginning of this study the water column was totally mixed. In May a thermocline built up at the outer three stations at the depth of 7–9 m. At station A a thermocline did not develop until mid-June. It remained until July and deepened to ~10 m. During the same period strong heating occurred, achieving the year's highest recorded temperatures on July 1. Mid-July was characterized by a continuous vertical temperature gradient with a weak thermocline very near the bottom at the deeper stations B and C. From August to the end of this study temperature was almost homogeneous down to a depth of 12 m, falling down to 12–13°C in October.

Like temperature, salinity was vertically homogeneous in April. Thereafter it decreased near the surface and increased near the bottom. In May and June a clear halocline at 8 m depth separated bottom- from surface-water. During July the salinity gradient became weaker but strengthened again at the end of August. This halocline became separated by an upwelling event in the inner fjord during early September. On August 26 the halocline centred at 13‰ was found at 6 m depth, whereas it increased in September to 16‰ and 12 m depth. Because of its greater depth in September, it could not be recorded at the shallower stations A and D.

Nitrate was found in concentrations >10 μmol l^{-1} in April and became depleted during May. During summer nitrate was very near or even below the limit of detection and ammonia, which averaged ~0.75 μmol l^{-1}, with some temporal maxima of up to 8 μmol l^{-1}, became the main nitrogen source for primary production. From late September on, nitrate concentrations recovered

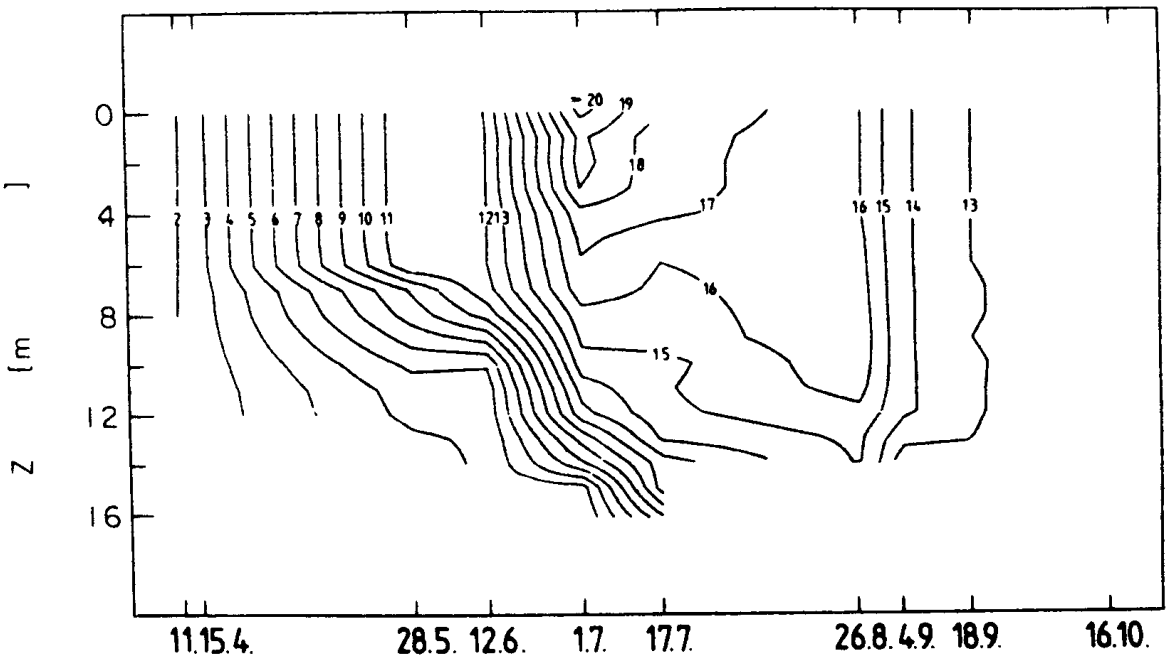

Fig. 2. Seasonal temperature distribution (°C) at station C.

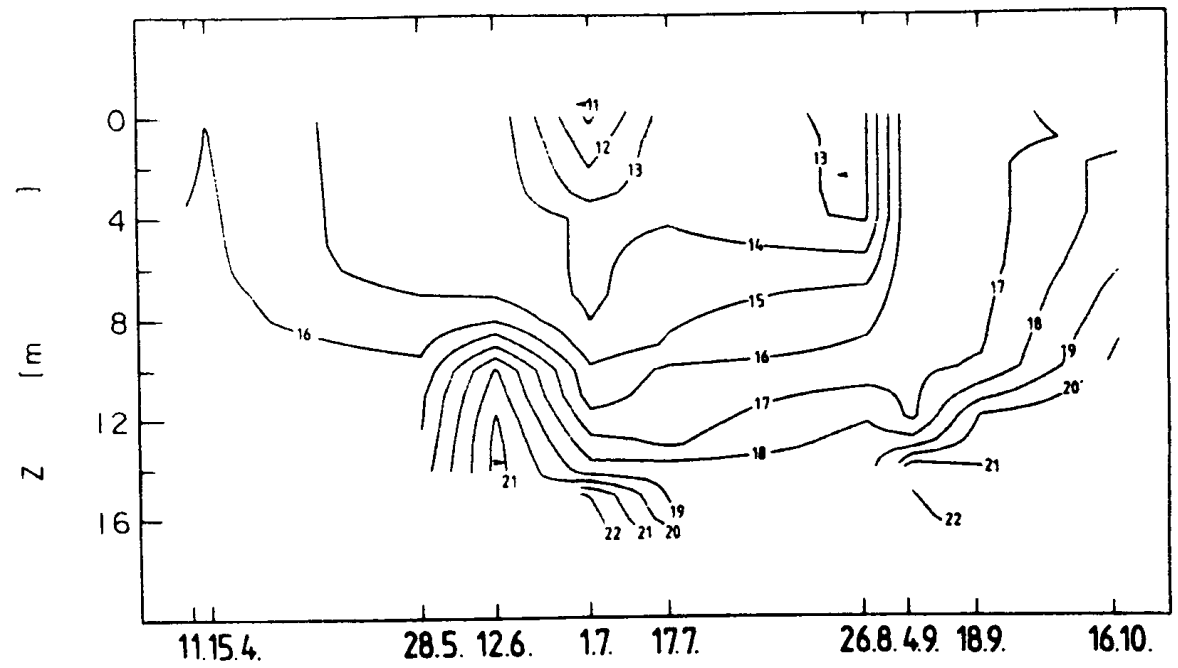

Fig. 3. Seasonal salinity distribution (‰) at station C.

1–2 μmol l^{-1}. Nitrite ranged over 0.2–0.3 μmol l^{-1}, never attaining major importance as a nitrogen source for phytoplankton growth. In early September it peaked up to 1.2 μmol l^{-1}, presumably because of oxygen depletion in bottom water of Kiel Bight. As ammonia had reached up to 6 μmol l^{-1} at this time and levels of nitrate had recovered, nitrite might still have played only a minor role in phytoplankton nutrition.

Figure 4 gives a general view of the development of phytoplankton biomass as the sum of Utermöhl- (>3 μm) and epifluorescence cell counts (≤3 μm) of surface samples. There was a very similar development at the two fjord stations

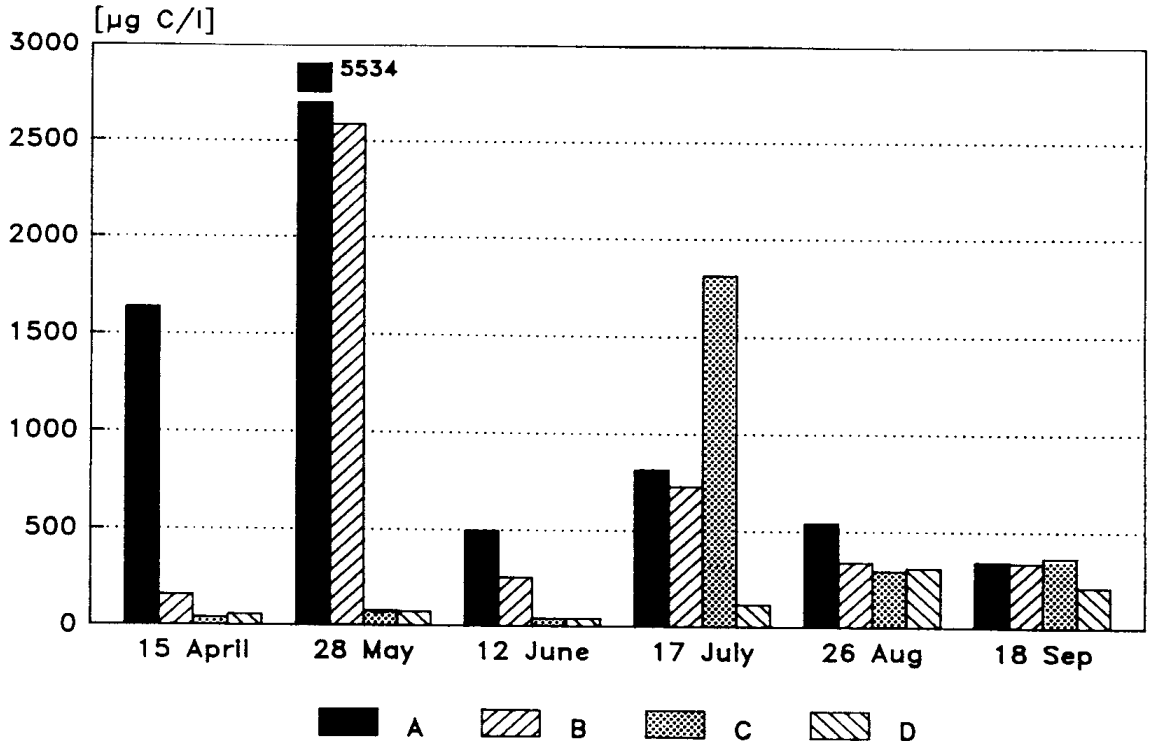

Fig. 4. Total phytoplankton carbon (µg C l^{-1}), Utermöhl and epifluorescence cell counts combined, of surface samples at the four stations.

(A and B) on the one hand and at the two bight stations (C and D) on the other. In general, biomass decreased towards the open Kiel Bight.

The diatom spring bloom had ceased by April 15 except at station A. The two fjord stations were characterized by a bloom in late May consisting of the silicoflagellate *Dictyocha fibula* (syn. *Distephanus speculum*). Most of these specimens represented the non-skeletal 'flagellate X' (Dunne, 1984; Neuer, 1986). At station C this species was found in greater depths (10 m) but not at station D; phytoplankton biomass was much lower in the surface samples of these stations. Biomass in June was the lowest in the study but recovered in July, mainly due to the occurrence of *Ceratium* spp. Additionally, high cell numbers of *Mesodinium rubrum* contributed to the high biomass at station C. In August and September the biomass was intermediate and mainly comprised *Prorocentrum minimum* and some *Ceratium tripos*. At station A *P.mininum* remained growing until the end of October, so forming a 'red tide' in Kiel Fjord. A detailed description of species succession is given in Jochem (1987).

Fluorescence counts of picocyanobacteria were obtained from May 28 on. Before this date only eukaryotic cells were enumerated but the occurrence of cyanobacteria was noted to be very low.

The abundance of picocyanobacteria (Figure 5) was quite similar at each station. During summer it was greater towards the inner fjord. Until June, $<1.3 \times 10^7$ cells l^{-1} were observed at all stations. Biomass was slightly higher in late May (4–7 µg C l^{-1}) than in mid-June (2 µg C l^{-1}), but increased rapidly thereafter. The first population maximum was reached on July 1. Cell numbers amounted to $1.4–1.9 \times 10^8$ cells l^{-1} in Kiel Fjord but only to 8.0×10^7 cells l^{-1} at station D, so contributing up to 130 µg C l^{-1} in Kiel Fjord and 56 µg C l^{-1} in

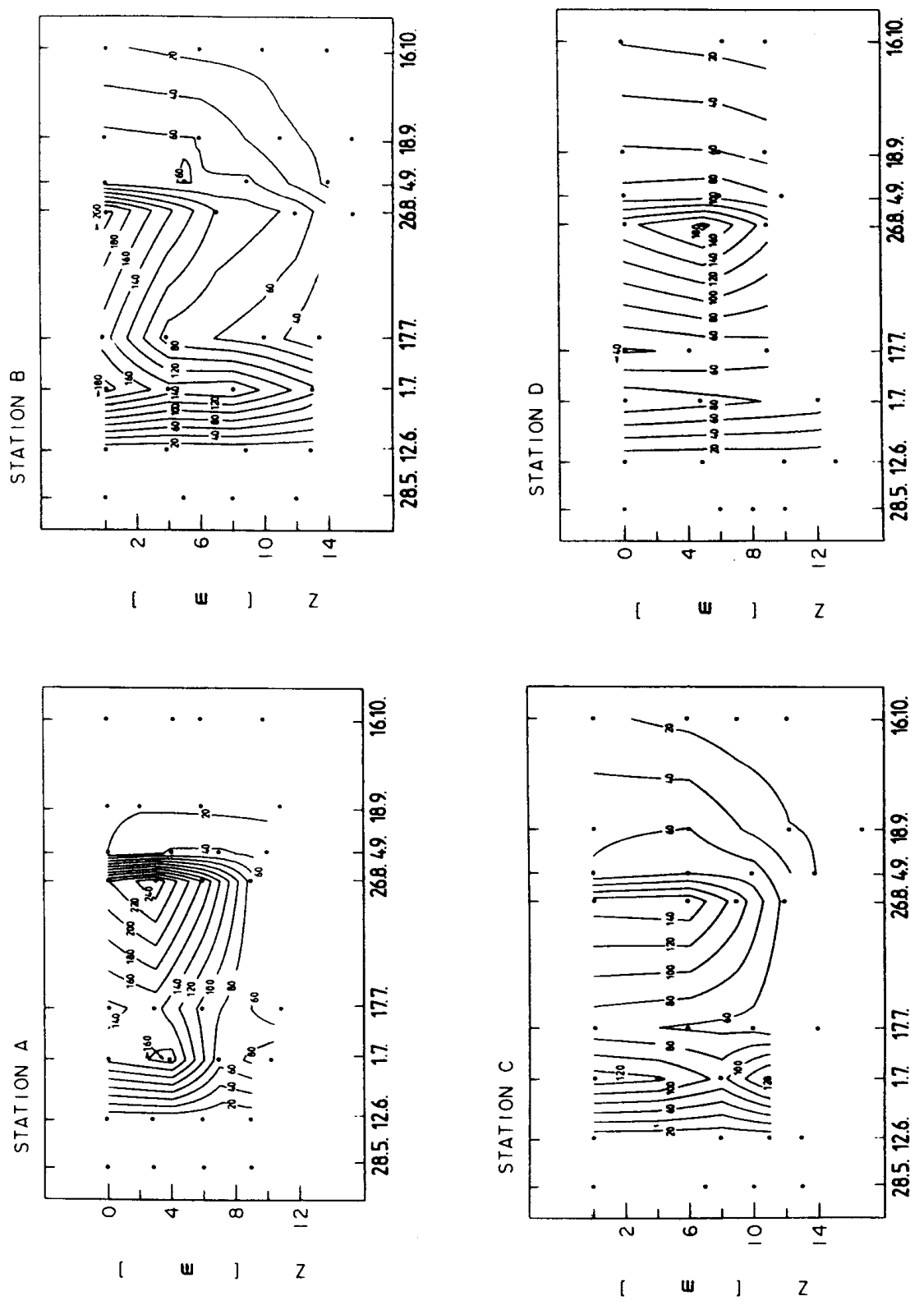

Fig. 5. Abundance of picocyanobacteria (10^6 cells l^{-1}) at the four stations.

Kiel Bight. In mid-July cell numbers were significantly lower. Another population maximum was found in late August, ranging from 1.5×10^8 cells l^{-1} at the Kiel Bight stations to 2.6×10^8 cells l^{-1} in the inner fjord. Thereafter, picocyanobacteria cell numbers decreased rapidly, dropping to $<2 \times 10^7$ cells l^{-1} and <14 μg C l^{-1} in October. This decrease was found more pronounced at the fjord stations.

Generally, highest population densities were found in the upper 5 m. Only at station D, where the density gradient was very weak during summer, was no clear vertical distribution structure apparent.

The contribution of picocyanobacteria to total phytoplankton biomass, calculated from the addition of Utermöhl- and fluorescence counts, is depicted in Figure 6. All stations tended to show the same high cyanobacterial contribution during the summer months July–September. During their second population maximum in late August picocyanobacteria made up 30–52% of phytoplankton biomass. Unfortunately, there are no Utermöhl data available for July 1, the date of the first cyanobacteria maximum. A similarly high contribution might have been expected for this date. A greater contribution by picocyanobacteria was found at the outer stations than in the inner fjord (station A).

Figure 7 shows the contribution of picocyanobacteria to picoplankton biomass, the sum of cyanobacterial and eukaryotic autotrophs ≤3 μm, as obtained by fluorescence counts. In May and June only ≤25% of picoplankton biomass was contributed by coccoid blue-greens but ~75–97% during summer.

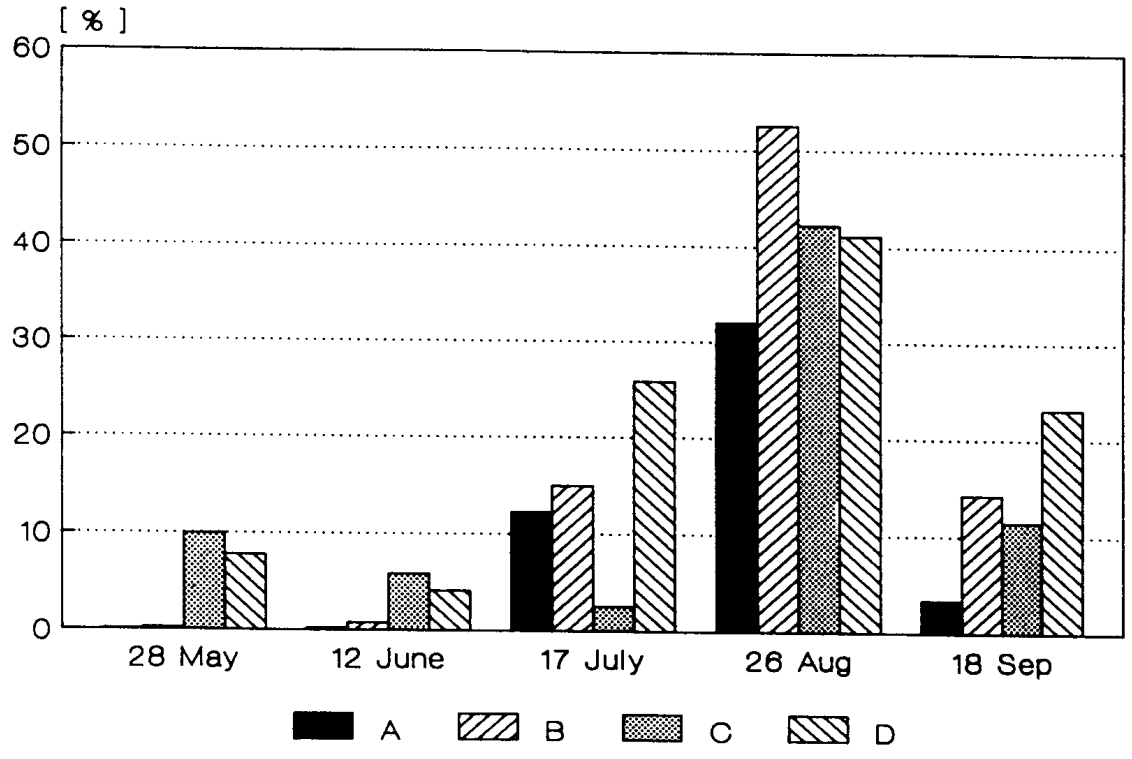

Fig. 6. Contribution of picocyanobacteria to total phytoplankton carbon as shown in Figure 4 at the four stations.

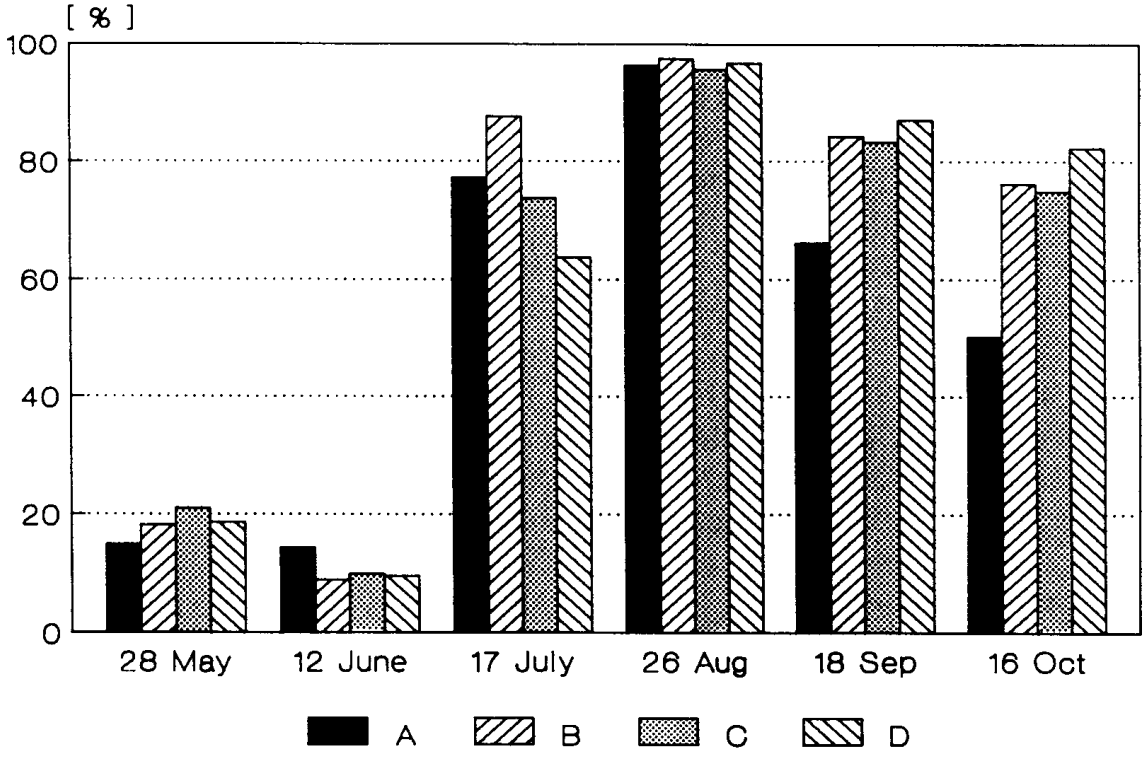

Fig. 7. Contribution of picocyanobacteria to autotrophic picoplankton carbon (surface samples).

Discussion

The concentrations of picocyanobacterial cells found in the study area were one to two orders of magnitude greater than those reported for tropical oceans (Johnson and Sieburth, 1979; Waterbury *et al.*, 1979; Glover *et al.*, 1986) but were of the same order as in other coastal waters (Takahashi *et al.*, 1985; El Hag and Fogg, 1986; Waterbury *et al.*, 1986). During summer, from July to beginning of September, cyanobacteria were one order of magnitude more abundant than eukaryotic picoplankters. Similar concentrations have been reported from the North Atlantic (Murphy and Haugen, 1985), the Gulf of Maine (Glover *et al.*, 1985a) and the Gulf of Finland (Kuosa, 1988).

Picocyanobacteria in Kiel Bight were spherical and ellipsoid cells of 1.0–2.5 μm in size. From Kattegat and Central Baltic waters Schmaljohann (1984) reported rod-shaped *Synechococcus*-type cyanobacteria of 0.6–0.8 × 0.9–1.5 μm, with larger cells of up to 1.5 × 2.0–3.0 μm occurring especially at lower salinity. Kuosa (1988) reported spherical 0.5–1.5 μm and rod-shaped 0.5–1.5 × 0.7–2.5 μm *Synechococcus*-type cells in the Gulf of Finland. Picocyanobacteria in Kiel Bight and other parts of the Baltic Sea seem to be larger than reported for the open oceans and shelf seas (Johnson and Sieburth, 1979; Krempin and Sullivan, 1981; Joint and Pipe, 1984; Takahashi *et al.*, 1985; El Hag and Fogg, 1986; Glover *et al.*, 1986; Waterbury *et al.*, 1986). El Hag and Fogg (1986) reported an increasing size towards the coast, which is also known for pelagic bacteria (Floodgate *et al.*, 1981).

Since the conclusions on the importance of picocyanobacteria in Kiel Bight presented here all rely upon cell counts, the conversion of picocyanobacterial

cell numbers into organic carbon is crucial and must be discussed in some detail. Assuming a cell density of 1.1 g ml^{-1}, dry wt 30% of wet wt and carbon content of 50% dry wt, the conversion would be of $C = 0.165V$. Other conversion equations found in the literature are:

$$\log C = 0.866 \log V - 0.46 \quad \text{(Strathmann, 1967)}$$
$$\log C = 0.94 \log V - 0.60 \quad \text{(Eppley } et\ al.\text{, 1970)}$$
$$C = 0.11\ V \quad \text{(Edler, 1979)}$$

The different carbon contents of differently sized cells as resulted from each of these equations are given in Table I. They also show the range of carbon content of picocyanobacteria in Kiel Bight. The size distribution of picocyanobacteria was not recorded on each sampling occasion but seemed to be fairly constant throughout the year. The most abundant cell types were spheres of ~2 μm in diameter and ellipsoids of 2 × 2.5 μm. In regard to the variations shown in Table I and the fact that the conversion factors of larger phytoplankton in use here (Smetacek, 1975) at least partly rely upon the formula given by Strathmann (1967), a mean of 0.7 pg C $cell^{-1}$ seemed most appropriate for picocyanobacteria in Kiel Bight and was used in this study. Waterbury *et al.* (1986) reported a mean of 0.21 pg C $cell^{-1}$ for picocyanobacteria and Cuhel and Waterbury (1984) 0.29 pg C $cell^{-1}$, but their cells were significantly smaller than in Kiel Bight.

On the basis of Utermöhl and fluorescence counts of surface samples, picocyanobacteria contributed 8–52% of phytoplankton carbon and 75–97% of picoplankton carbon during summer. Although picocyanobacteria cell numbers decreased towards the open Kiel Bight, their relative importance increased in this direction. Similarly, Glover *et al.* (1985a) reported a *Synechococcus* contribution of 50–99% to picoplankton, decreasing towards more productive stations, and Takahashi *et al.* (1985) found them to make up ≤79% of picoplankton carbon in coastal waters off Japan.

Despite the high contribution of picocyanobacteria to picoplankton biomass in Kiel Bight, there was no correlation between picoplankton chlorophyll or picoplankton primary production and cyanobacteria biomass (Jochem, 1987). This may involve low assimilation numbers and high C/Chl *a* ratios of picocyanobacteria in Kiel Bight. Also, Glover *et al.* (1985b) found a low productivity/cell. Takahashi *et al.* (1985) gave C/Chl *a* ratios of up to 79 for *in situ* populations off Japan and Cuhel and Waterbury (1984) reported a ratio of 133 for Sargasso Sea *Synechococcus* WH7803 (= DC-2). The high contribution of picocyanobacteria to picoplankton biomass and a low productivity/cell may explain why picoplankton assimilation numbers in the study area were not higher than those of other size fractions.

There was an obvious parallel development of cyanobacterial abundance with temperature increase. The population maximum in early July coincided with the temperature maximum of the year (>20°C); the August-maximum occurred at 16–17°C. In the Irish Sea El Hag and Fogg (1986) found the population

Table I. Carbon content of differently sized picocyanobacterial cells according to equations given by different authors

Cell type and size (μm)	Cell volume (μm^3)	Cellular organic carbon content (pg C $cell^{-1}$)			
		Assumption	Edler (1979)	Strathmann (1967)	Eppley *et al.* (1970)
Ellipsoid 2.2 × 2.5	6.34	1.04	0.70	1.72	1.43
Ellipsoid 2 × 2.5	5.23	0.86	0.58	1.44	1.19
Sphere dia. 2	4.20	0.70	0.46	1.20	0.97
Sphere dia. 1.5	1.77	0.29	0.19	0.57	0.43
Ellipsoid 1.0 × 1.5	0.79	0.13	0.08	0.28	0.20

maximum at 17.5°C, as did Krempin and Sullivan (1981) off California and Waterbury *et al.* (1986) in Woods Hole Harbor. El Hag and Fogg (1986) and Murphy and Haugen (1985) quote a significant correlation between picocyanobacteria biomass and temperature, which can be confirmed for Kiel Bight, too. The second maximum in August seems to have been influenced by factors other than temperature. Furthermore, high abundance of picocyanobacteria fell within the period of nitrate depletion and low concentrations of inorganic nitrogen (<2.5 μmol l^{-1} in Kiel Fjord and <1.5 μmol l^{-1} in Kiel Bight).

Picocyanobacteria showed a distinct relation to the surface that might depend on a significant decrease of temperature with depth during stratified conditions in summer. In mid-July at Station D, where a clear temperature gradient was missing, their vertical distribution was homogeneous. Other results from coastal waters show population maxima at the surface, too (Krempin and Sullivan, 1981; El Hag and Fogg, 1986; Kuosa, 1988). In the open ocean, however, population maxima are often found at greater depths, mostly near the 1% light level (Glover and Morris, 1981; Morris and Glover, 1981; Li *et al.*, 1983; Glover *et al.*, 1985a,b; Murphy and Haugen, 1985; Iturriaga and Mitchell, 1986). This observation may depend upon the low light-saturation requirement of photosynthesis in picocyanobacteria (Glover and Morris, 1981; Morris and Glover, 1981; Li *et al.*, 1983; Platt *et al.*, 1983; Glover *et al.*, 1985a,b). Moreover, Glover and Morris (1981) and Morris and Glover (1981) report a high oxygen sensitivity of picocyanobacteria and Glover *et al.* (1985a) point to a more efficient utilization of the blue and green portion of the light. Because of small temperature differences between the surface and the 1% light depth in tropical oceans these physiological features of cyanobacteria may influence their vertical distribution. In view of the different vertical distribution pattern of picocyanobacteria in Kiel Bight, it seems unlikely that they have the same physiological characteristics as *Synechococcus* in the open tropical ocean studied hitherto. Furthermore, the positive correlation with water temperature may overcome the possible physiological advantage to deeper populations where strong vertical temperature gradients and much higher turbidity exists, as in many boreal coastal waters. Physiological studies on coastal *Synechococcus* are now required. Different physiological characteristics combined with larger cell size may lead to the identification of other species, or at least, races of '*Synechococcus*'.

In the central Baltic the well-documented occurrence of summer blooms of filamentous blue-greens during nitrogen limitation has been explained in terms of their N_2-fixation capability (Lindahl *et al.*, 1978; Lindahl and Wallström, 1980). These blooms of filamentous blue-greens are visible with the naked eye and generally remain restricted to the surface layer. In Kiel Bight filamentous cyanobacteria are of minor importance and usually contribute <10% of total phytoplankton biomass, in most cases <1%, as in 1983 and 1984 (Stienen, 1986). In the summer of 1985 Neuer (1986) observed only 0.2–1.2 μg C l^{-1} with a maximum of 4.5 μg C l^{-1} of filamentous blue-greens. On the other hand, data presented here indicate a much higher biomass of coccoid picocyanobacteria throughout the whole euphotic zone, which may have a much greater impact on the pelagic ecosystem if capable of N_2-fixation, too. Rippka and Waterbury

(1977) were not able to detect any nitrogenase activity in non-heterocystous cyanobacteria, but other investigators proved its occurrence (McCarthy, 1980; Bold and Wynne, 1985). Mitsui *et al.* (1986) report N_2-fixation by marine *Synechococcus*.

This study clearly reveals marine picocyanobacteria to be a significant component of the phytoplankton community in a boreal inshore area and further supports the reported trend toward higher cyanobacteria populations in eutrophic waters reported in the literature (Waterbury *et al.*, 1979; Glover *et al.*, 1985a; El Hag and Fogg, 1986). Therefore coccoid cyanobacteria might be similarly important in other eutrophic coastal waters and fjords. Picocyanobacteria cannot be neglected in phytoplankton research in such ecosystems any longer. In view of their potential ecological importance in boreal coastal waters as presented here, a further investigation on their actual physiological performance would be highly desirable. Such investigations are planned by the newly established working group on ultraplankton at the Institut für Meereskunde Kiel.

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