Importance and abundance of the recently established species *Coscinodiscus wailesii* Gran & Angst in the German Bight

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ABSTRACT: Grids of 17 to 50 stations in the German Bight were sampled 18 times within the framework of the multidisciplinary programmes ZISCH and PRISMA in winter and spring of 1988/89 and from April 1991–April 1992. The frequent abundance of *Coscinodiscus wailesii* Gran & Angst, a recently established large diatom, was noteworthy, as it dominated the phytoplankton biomass over long periods (e.g. 12/88–3/89 and 8/91–11/91). The bulk of the phytoplankton carbon during these periods (up to 90 %) could be attributed to this species. Blooms of *Coscinodiscus wailesii* producing up to 1400 µg carbon l^{-1}, were recorded in early spring of 1989 and autumn of 1991. The potential consequences for the whole ecosystem refer to the huge size of this organism, which may cause reduced exploitation of its primary production by native consumers. Furthermore, sedimentation and remineralisation processes may be affected. For *C. wailesii*, a doubling of biomass in 70 h could be estimated on the basis of data from four successive surveys in 1991. Results from laboratory cultures under comparable conditions confirm this rate. In the survey area, no increase in biomass was recorded for the related *Coscinodiscus granii* Gough, although there was sufficient silicate supply for growth. Field data showed 8–10 times lower copper and 10–20 times lower cadmium and zinc accumulation in *C. wailesii*, compared to concentrations found in native phytoplankton species. Subsequent laboratory tests suggested that one reason for the remarkable success of *C. wailesii*, mainly in inshore regions, may be derived from its tolerance of higher doses of heavy metals due to very low sorption.

INTRODUCTION

The spreading of plankton species in different parts of the world oceans is not a new phenomenon. Spreading may be caused by ocean currents transporting drifting organisms, by merchant ships transferring ballast water (Gerlach, 1992) or by stocking the seas with living organisms native to other countries (Rince & Plaumier, 1986).

For the North Sea, a number of examples of new arrivals in the phytoplankton are known, e.g. *Odontella (Biddulphia) sinensis* Grev. (Ostenfeld, 1908, 1909); *Thalassiosira punctigera* Castr. (Kat, 1982); *Thalassiosira hendeyi* Hasle & Fryxell (Rick, 1990) *Corethron criophilum, Stephanopyxis palmeriana* (Drebes, 1991); *Gyrodinium aureolum*

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Hulburt (Tangen, 1977); *Pleurosigma planktonicum* Simonsen (Boalch & Harbour, 1977a); *Coscinodiscus wailesii* Gran & Angst (Boalch & Harbour, 1977b; Robinson et al., 1980; Rince & Plaumier, 1986). In most cases these new arrivals are not stock-forming in their new distribution areas, with the exception of the mentioned dinoflagellate, and the large centric diatoms *Odontella sinensis* and *Coscinodiscus wailesii*. They may have a strong impact on the structure of the pelagic ecosystem by partly replacing native populations during certain seasons.

Coscinodiscus wailesii shows a worldwide distribution. A review is given in Rince & Plaumier (1986). It is found both in the Pacific (Gran & Angst, 1931; Cupp, 1943; Gotelli, 1971; Guo Yujie, 1981; Manabe & Ishio, 1991) and in the Atlantic Ocean (Patten et al., 1963; Mahoney & Steimle, 1980; Marshall, 1984). In 1977 the species was first recognized in waters off the southern coast of England waters (Boalch & Harbour, 1977a). Since then it has spread through the whole North Sea.

MATERIAL AND METHODS

Distribution and abundance of *Coscinodiscus wailesii* Gran & Angst was analyzed in the North Sea within the project studies ZISCH I (1986/87: circulation and Transfer of Pollutants in the North Sea), ZISCH II (1988/89: Circulation and Transfer of Pollutants in the German Bight), PRISMA (1991/92: Transport, Transfer and Transformation Processes in the German Bight), TUVAS (1991/92: Transport, Conversion and Variability of Pollutants and Nutrients in the German Bight), and OPTINOM (1991/92: Improvement of the North Sea Monitoring). Additional data were obtained during a ten year period of studies (1982–1992) in the outer Scheldt estuary near Breskens (The Netherlands).

During the ZISCH I programme, the phytoplankton was analyzed in the entire North Sea at 131 stations. In the following 3 years (11/88–4/92) the German Bight was sampled with 18 grids of 17–51 stations. These studies concentrated on the measurement of the heavy metal content in the phytoplankton and on the recording of the species composition of the primary producers.

Samples for phytoplankton analysis were collected at 2 to 4 different depths with rosette samplers (CTD), fixed with buffered formol and processed by the technique of the inverted microscope within 3 months after sampling. Cell volume and carbon content of the cells were calculated, based on quantitative data of plankton analysis according to Rick (1990) and Strickland & Parsons (1972).

To avoid metal contamination from the research vessel, samples for heavy metal determination of the plankton were taken by rubber dinghy in the surface layer by using a modified (no metal parts) plankton net (55 μm mesh size). Direct microscopic control of these samples followed, in order to estimate the percentage of phytoplankton content. An aliquot of each net sample was fixed with buffered formol for subsequent quantitative plankton analysis.

The cells were concentrated on Sartorius cellulose nitrate filters (pore size 0.2 μm) for trace metal analysis, if the phytoplankton content consisted of over 90 % of the entire seston. For purification procedure of filters see Mart (1979a).

Heavy metal analysis was carried out using the Differential Pulse Anodic Stripping Voltammetry method (DPASV; Metrohm VA Processor 646 and VA Elektrode 647) after

conditioning the filter samples in an oxygen plasma processor (Plasma Technics model 200G). For prevention of contamination and other risks in accuracy in voltametric trace metal analysis see Mart (1979a, b, c, 1982) and Mart et al. (1980).

Additional laboratory data were obtained using batch and semicontinuous cultures of *Coscinodiscus wailesii*. The clone used was isolated from a net plankton sample taken from the outer Scheldt estuary near Breskens (The Netherlands) in February 1991. The non-axenic unialgal stock cultures were kept both in 20-ml Scinti-Vials and 1-l Duran-bottles at 12 °C and a quantum scalar irradiance of 18 μE m^{-2} s^{-1} (cool white fluorescent tubes, Phillips TLM 33 RS/65) in a 12 : 12 h light/dark cycle. Experiments were carried out in Celstir bottles (Zinsser) at the same light/dark cycle and a light level of 50 μE m^{-2} s^{-1} (LI-COR LI-185B Quantummeter with LI-190SB Quantum sensor). The cultures were stirred using a Wheaton-Biostir-6 system (Zinsser). Dilution rates varied from 0.2 to 0.5 day^{-1}.

Media were prepared using 0.2-μm membrane-filtered North Sea water from the German Bight (4/91). The salinity ranged from 31 to 32 ‰. The media were enriched with nutrients according to Von Stosch & Drebes (1964). N and P were added at 0.1, Si at 1.0 strength, specified in μmol dm^{-3}: N: 56, P: 30, Si: 35, Fe: 1.0, Mn: 0.1. The vitamins B$_{12}$, biotine, and thiamine were added to final concentrations of 50 μg dm^{-3}. In order not to change the complexing capacity of the seawater, there was no addition of chelating agents. Relative complexing capacity (RCC) was measured by a voltamperometric method using lead as indicator metal (complexing time 10 min; 0.5 μg Pb dm^{-3} 10 min $\triangleq$ RCC = 1; Rick, 1990).

The treatment of samples for heavy metal analysis of the cultured algae was the same as in field samples. Heavy metal contents of the media were analyzed using the DPASV method after UV photolysis according to Mart (1979c). Bioconcentration factors (BCF) were calculated based on the metal concentration both in the medium and the algae.

Doubling times were calculated from changes in cell number during exponential growth.

RESULTS

North Sea

Figure 1 displays the distribution of *Coscinodiscus wailesii* during the ZISCH summer cruise in May–June 1986, as well as the observations of some other authors. Only 10 of the 131 stations sampled showed an occurrence of this species. It was found mainly in the northern parts of the sampling area near the Orkney, Shetland, and Faroe islands. *C. wailesii* occurred in the southern part of the North Sea only at two stations in the most outer part of the German Bight. During the ZISCH summer campaign, the species was not stock-forming. It was found in a salinity and temperature range from 34.41–35.28 ‰ S and 6.84–8.92 °C, respectively.

Scheldt estuary

Since the early 'eighties, the species composition of the phytoplankton in the outer Scheldt estuary was analyzed 50 times in 10 years. There, *Coscinodiscus wailesii* was first
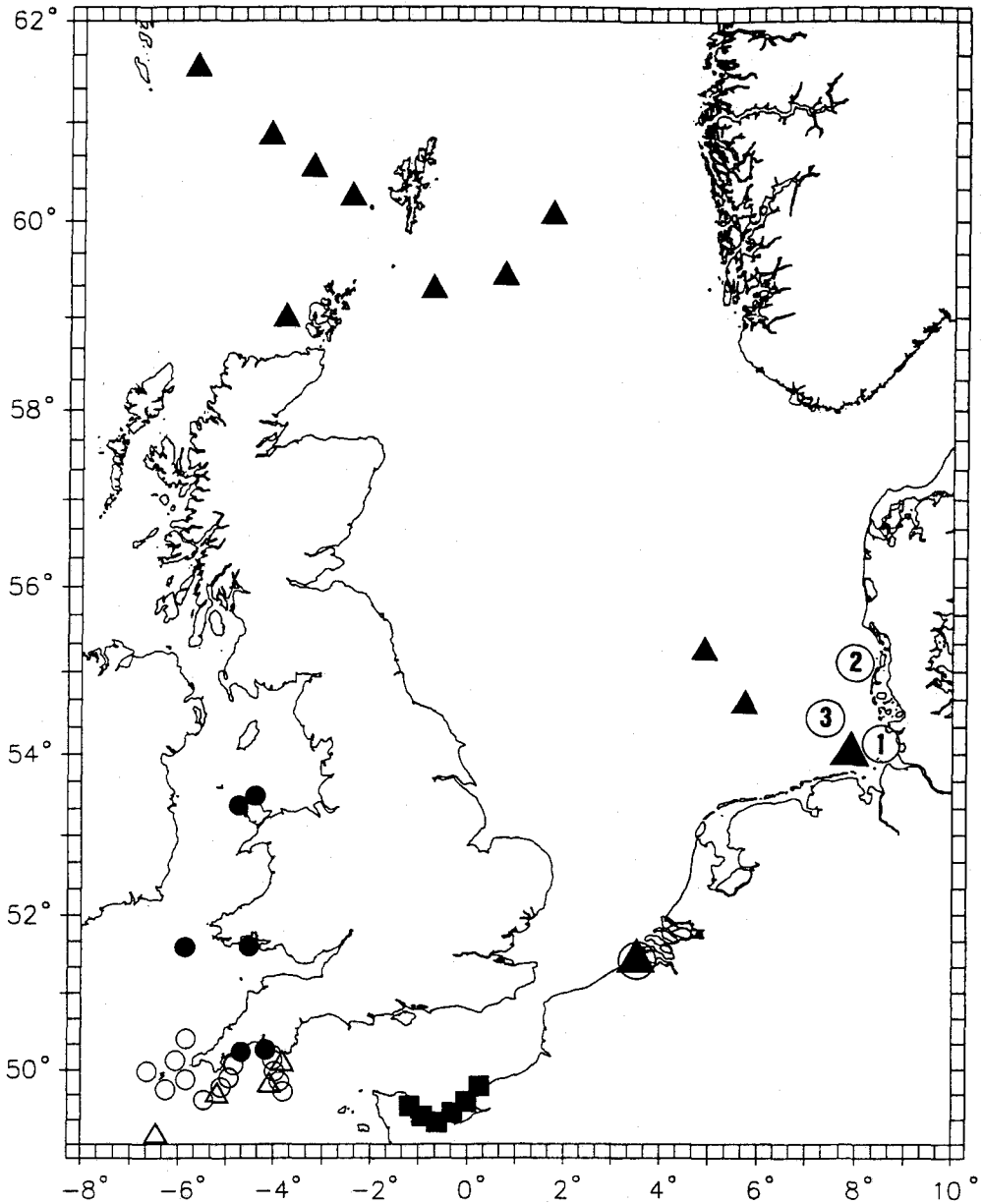
Fig. 1. Distribution pattern of *Coscinodiscus wailesii* Gran & Angst in the North Sea and adjacent waters. This study's data and the data of other authors are given in one general map. Small filled triangles: ZISCH campaign May–June 1986, Rick (1990); large filled triangle: this study; circled triangle: 10 year period (1982–1992), Scheldt estuary; filled squares: Rince & Plaumier (1986); small open circles: Robinson et al. (1980); open triangles: Boalch & Harbour (1977a); open circle 1: Gillbricht in Rince & Plaumier (1986); open circle 2: Drebes in Rince & Plaumier (1986); open circle 3: Hesse (1988)

recognized in 1982. More than 50 % of the samples contained *C. wailesii*. It was most abundant from September to March in salinity and temperature ranges of 24–32 ‰ S and 0–20 °C. No proof exists of its occurrence in early summer (June/July). In most cases, we found *C. wailesii* accompanied by *Thalassiosira punctigera* Castr. and *Thalassiosira hendeyi* Hasle & Fryxell, two other introduced species.

German Bight

Table 1 shows the abundance and biomass development of *C. wailesii* during two campaigns (18 cruises) of investigation (1: 11/88–5/89; 2: 4/91–4/92) in the German Bight. Figures 2–7 describe the accompanying spatial distributions. The data point out that *Coscinodiscus wailesii* has established itself in the German Bight area during the last decade. In some periods (11/88–3/89 and 8/91–10/91) more than 90 % of the phytoplank-

Table 1. Abundance and biomass of *Coscinodiscus wailesii* in the German Bight during the programs ZISCH II, PRISMA, TUVAS and OPTINOM. The campaign period, the number of the sampled stations, the percentage of stations in which *C. wailesii* was stock-forming and mean/ maximum biomass levels in carbon units for the whole water column are given

Cruise	Sampled stations	Percent- age[*]	Biomass (mg C m^{-3})	
			Max.[**]	Mean[***]
ZISCH II				
11/88	23	39	314	175.9
12/88	23	22	142	69.1
01/89	17	71	170	45.9
02/89	17	41	382	141.0
03/89	8	63	1270	475.3
04/89	17	29	178	92.7
05/89	20	20	357	113.6
PRISMA				
04/91	50	0	0	0
08/91-1	51	52	1004	142.3
08/91-2	33	48	550	212.3
08/91-3	44	34	812	179.2
08/91-4	42	47	1705	348.4
08/91-5	51	41	1325	482.6
TUVAS-OPTINOM				
09/91	20	85	421	220.0
10/91	20	80	445	131.1
01/92	18	44	29	14.0
03/92	18	83	210	80.2
PRISMA				
04/92	42	59	551	96.4

[*] percentage of the sampled stations where *Coscinodiscus wailesii* was stock-forming.
[**] maximum carbon content of *Coscinodiscus wailesii* (mg C m^{-3}) for this particular cruise.
[***] mean carbon content of *Coscinodiscus wailesii* (mg C m^{-3}) at each station where this species was stock-forming.
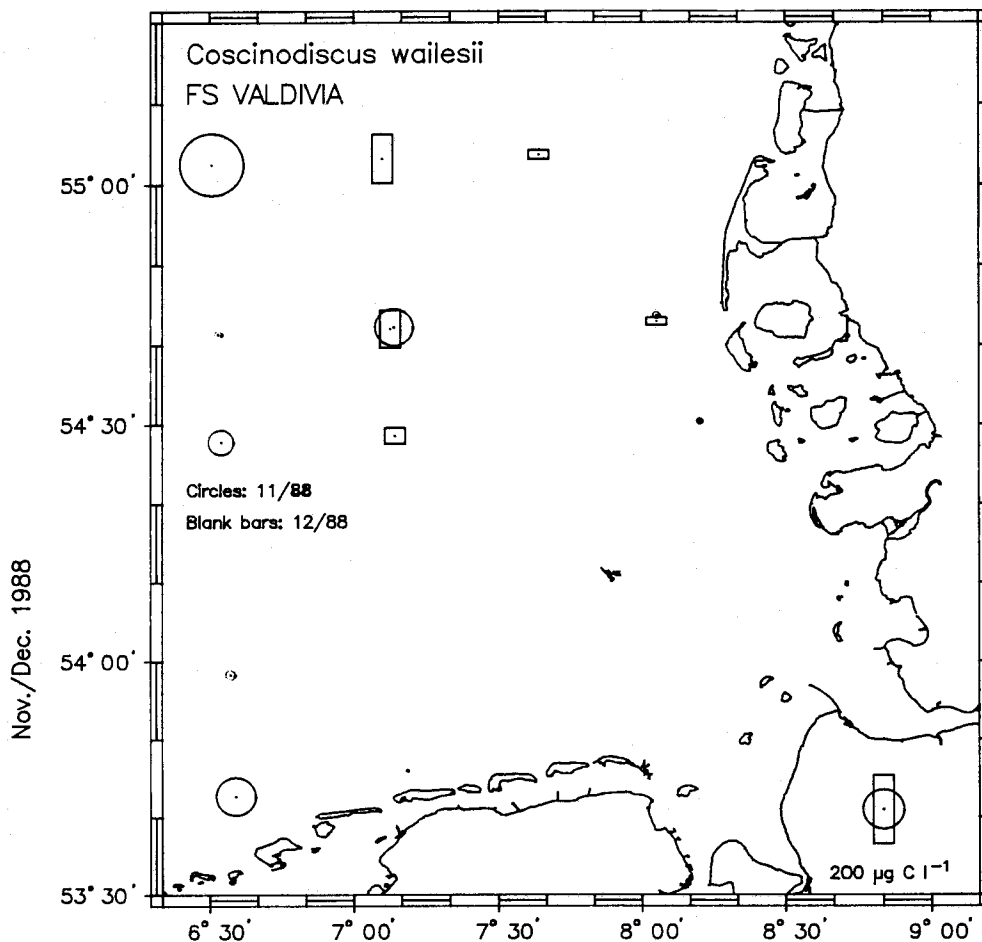
Fig. 2. Spatial distribution and biomass of *Coscinodiscus wailesii* in the German Bight. Results of two winter cruises in November and December 1988. The biomass data are given as mean carbon values (μg C dm⁻³) for the upper layer (0–20m) of the water column. Symbol size compares to the biomass value (see legend lower right)

ton biomass was bound in this species. We found *C. wailesii* in a temperature and salinity range from 2.0–17.0 °C and 27–34 ‰ S, respectively.

In winter, the species was merely present near the outer borders of the German Bight with low biomass levels (Figs 2, 5, 7). Spring showed a richer abundance in the western region; the species was absent in the area of the Elbe River plume (Figs 4, 6, 7). In summer and early autumn, there were records of *C. wailesii* in the coastal and eastern part of the German Bight (Fig. 5), while it was more abundant at the western and northern borders of the survey region in late autumn (Fig. 5).

During the PRISMA programme in August 1991, four successive grids of 40 to 50 stations were sampled in the German Bight. Each station was resampled in a time course of 72 h. The data of this survey are shown as mean values in Table 1. *C. wailesii* was most
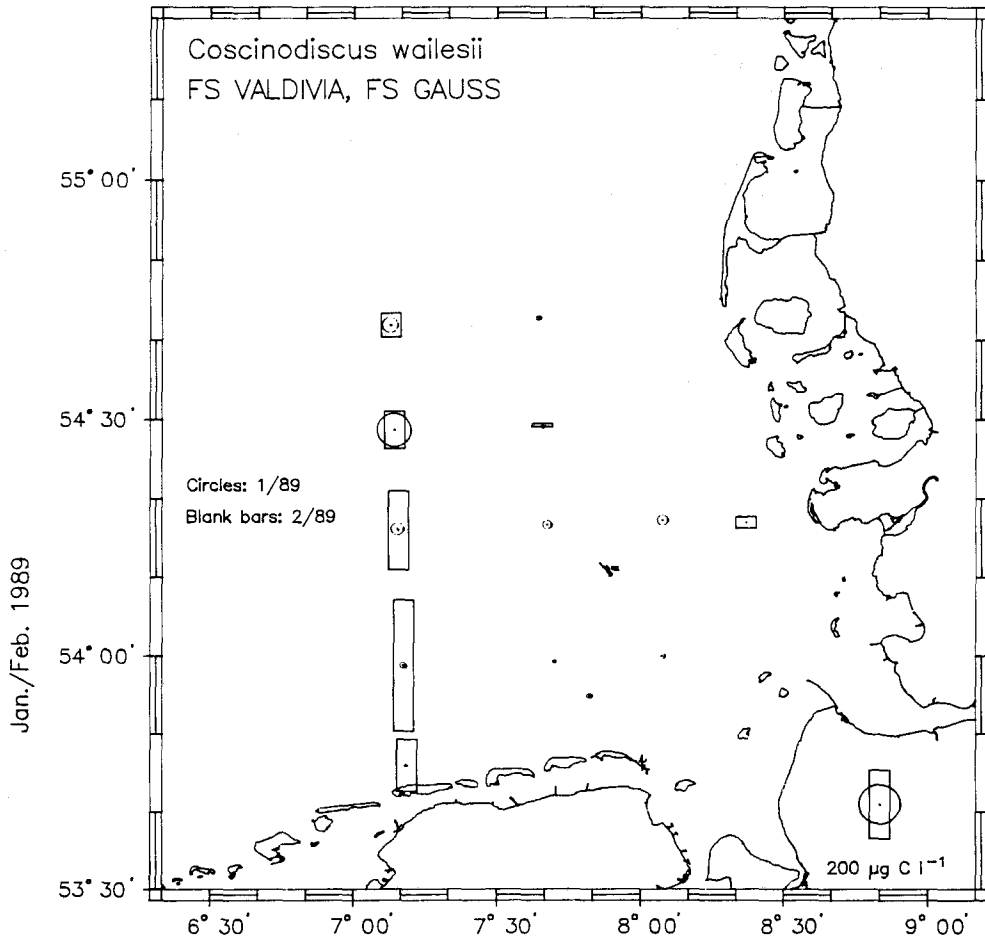
Fig. 3. Spatial distribution and biomass of *Coscinodiscus wailesii* in the German Bight. Results of two winter cruises in January and February 1989. The biomass data are given as mean carbon values (µg C dm^{-3}) for the upper layer (0–20m) of the water column. Symbol size compares to the biomass value (see legend lower right)

abundant in the coastal area of the German Bight (8.10°–7.5°E, 54.13°–54.43°N, 9 stations) with increasing biomass during the survey period (15th–29th August). It was accompanied by the native species *Coscinodiscus granii* Gough. For the area mentioned, mean biomass doubling-times for both species were calculated on the basis of the integrated biomass values from the upper layer of the water column (0–20 m). No significant growth of *C. granii* was determined while *C. wailesii* showed doubling-times of 70 h.

Figure 7 shows the spatial distribution and biomass of the related species *Coscinodiscus wailesii* and *Coscinodiscus concinnus* W. Smith during the PRISMA spring campaign in April 1992. Both species have identical distribution patterns, but the areas of maximum
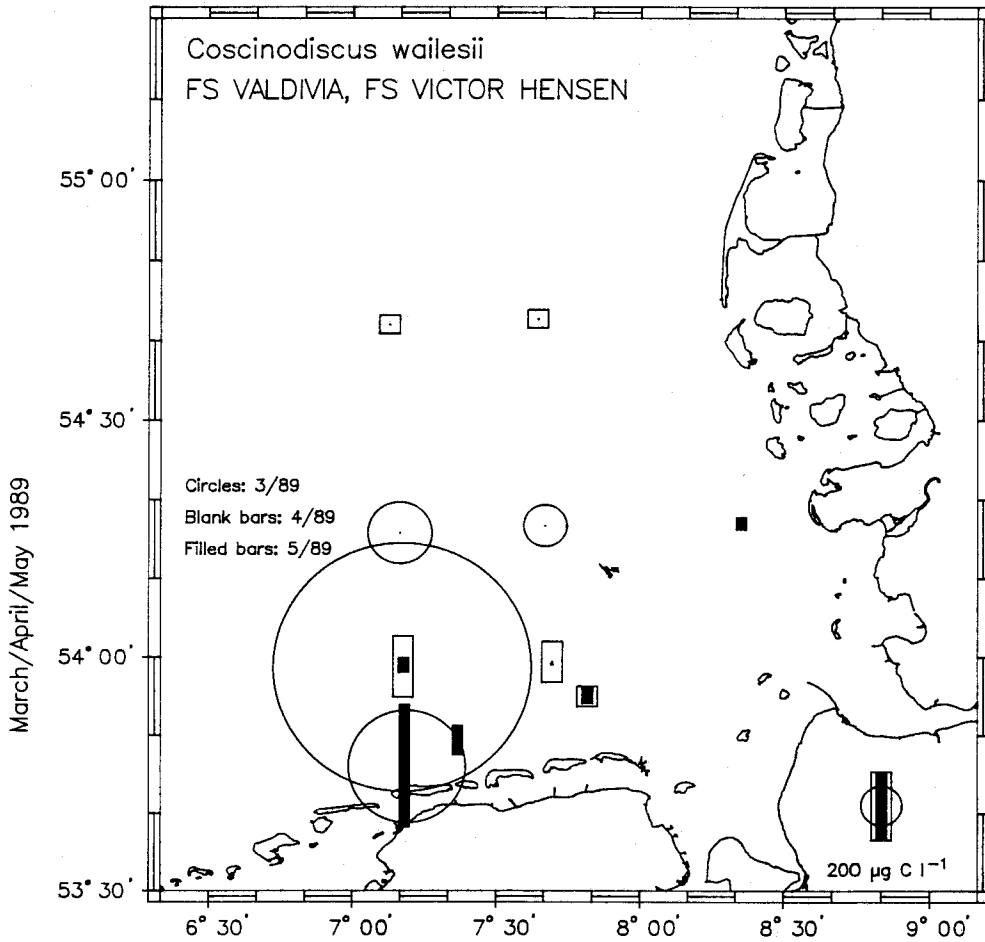
Fig. 4. Spatial distribution and biomass of *Coscinodiscus wailesii* in the German Bight. Results of three spring cruises in March, April and May 1989. The biomass data are given as mean carbon values (µg C dm^{-3}) for the upper layer (0–20m) of the water column. Symbol size compares to the biomass value (see legend lower right)

cell numbers differ. *C. concinnus* exceeds *C. wailesii* in the outer bight, while *C. wailesii* is dominant in the East Frisian coastal waters.

Bioconcentration of trace metals

Field data concerning bioconcentration factors of trace metals in natural phytoplankton assemblages in the German Bight suggest that communities dominated by *Coscinodiscus wailesii* show less accumulation of zinc and copper than communities dominated by other species (Table 2; Figs 8, 9). The same can be found for the accumulation for lead and cadmium (Figs 10, 11). Only at three stations (19, 31, 40 – compare Figs 8–11)
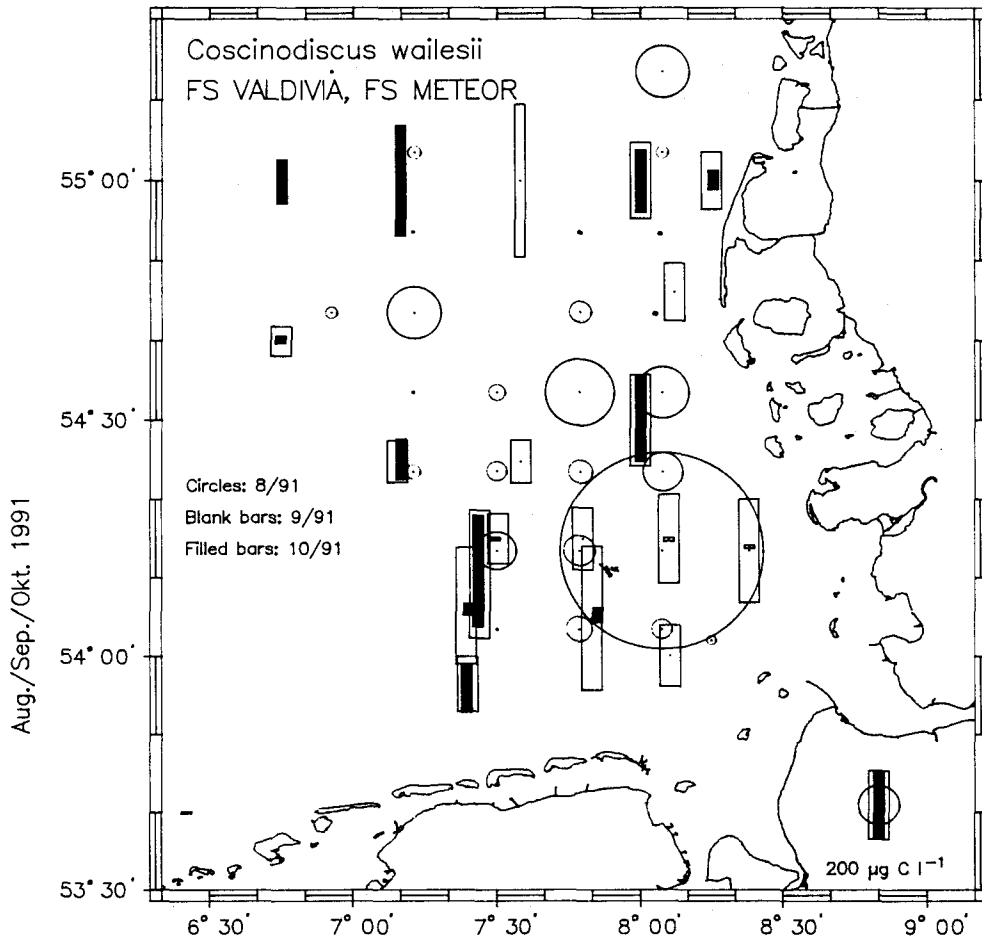
Fig. 5. Spatial distribution and biomass of *Coscinodiscus wailesii* in the German Bight. Results of three cruises in summer and autumn (August 1991, September 1991, October 1991). The biomass data are given as mean carbon values (μg C dm^{-3}) for the upper layer (0–20m) of the water column. Symbol size compares to the biomass value (see legend lower right)

where *C. wailesii* was abundant, were relatively high metal contents (Zn, Cu, Cd) in the plankton found. They were located at the outer distribution border of *C. wailesii*, where this species was mainly accompanied by the centric diatom *Rhizosolenia shrubsolei* Cleve.

The results of subsequent laboratory experiments concerning the bioconcentration of zinc and copper in *C. wailesii* are shown in Table 4.

DISCUSSION

Figure 1 shows the distribution of *C. wailesii* Gran & Angst in the North Sea and adjacent waters. Our own results and the data of other authors are shown in one general

Table 2. Bioconcentration factors (BCF) of zinc and copper in natural phytoplankton populations (August 1991, German Bight). The relative complexing capacity (RCC) of the seawater varied from 0.8 to 1.5 during the cruise. BCF, zinc and copper content of the seawater, standard deviations, minimum and maximum value are given

Mean Zn content, water:	472 ± 237	ng Zn kg^{-1}
Minimum value:	232	ng Zn kg^{-1}
Maximum value:	1025	ng Zn kg^{-1}

Phytoplankton	BCF zinc	Standard deviation	Min. value	Max. value	n
C. wailesii abundant	29300	25000	7300	62200	12
Other species abundant	189900	160300	18000	562100	9

Mean Cu content, water:	390 ± 74	ng Cu kg^{-1}
Minimum value:	306	ng Cu kg^{-1}
Maximum value:	624	ng Cu kg^{-1}

Phytoplankton	BCF copper	Standard deviation	Min. value	Max. value	n
C. wailesii abundant	4430	3790	980	11460	12
Other species abundant	15610	11340	2050	29940	9

map. *C. wailesii* was discovered in 1977 by Boalch & Harbour (1977a) in the Celtic Sea, the English Channel (Rince & Plaumier, 1986) and the southern part of the Irish Sea (Robinson et al., 1980). Simonsen (in Rince & Plaumier, 1986) stated that the species occurs at nearly all North Sea coastlines.

The data of Boalch & Harbour (1977a) and Robinson et al. (1980), who recorded high biomasses of *C. wailesii* in winter and spring in inshore waters, while cell numbers declined towards May, correspond well with our findings in the Scheldt area and the German Bight.

The observed wide range of salinity and temperature for species occurrence confirms the reports from Rince & Plaumier (1986), who stated that *C. wailesii* occurred in open ocean, as well as in estuary and inshore, regions.

During the 'eighties, *C. wailesii* became an important member of the phytoplankton in the German Bight (Gillbricht and Drebes in Rince & Plaumier 1986; Hesse, 1988;

Table 3. Bioconcentration factors (BCF) for the trace metals copper and zinc. *Coscinodiscus wailesii* in semicontinuous cultures (dilution rate 0.5–0.2 d^{-1}, 12 °C, light dark cycle: 12:12 h; 50 $\mu E\ m^{-2}\ s^{-1}$). Mean biomass doubling-times, ranges of the zinc, copper content, and RCC (relative complexing capacity) of the media are given. n = number of data points

Range of Cu content (medium):	1–8	$\mu g\ Cu\ kg^{-1}$
Range of Zn content (medium):	3–5	$\mu g\ Zn\ kg^{-1}$
RCC:	0.8 ≙ 0.4	$\mu g\ Pb\ kg^{-1}$ 10 min
Doubling-time:	107.9 ± 37.2	

Trace metals	BCF	Standard deviation	Min. value	Max. value	n
Copper	2700	910	1000	4790	65
Zinc	5890	1660	2200	9710	67

Table 4. Bioconcentration factors (BCF) and volume-related metal content of various North Sea phytoplankton species in semicontinuous cultures with literature references

Species	COPPER Content medium (ng kg^{-1})	Content cells (10^{-10} ng μm^{-3})	BCF	ZINC Content medium (ng kg^{-1})	Content cells (10^{-10} ng μm^{-3})	BCF	Author
Scrippsiella trochoidea	450	50 ±14	11200 ± 3100	6300	450 ± 80	7070 ±1260	Corves (1992)
Gyrodinium aureolum	620	120 ± 10	19350 ± 1600	5800	460	8000	Rick (1990)
Phaeocystis globosa	1130	185	16390	9500	1300 ± 20	13700	Rick (1990)
Micromonas pusilla	3800	830 ±195	21800 ± 5100	14600	325 ±180	2200 ±1200	Rick (1990)
Thalassiosira rotula	480	66 ± 4	13700 ± 830	2800	134 ± 28	4820 ±1030	Corves (1992)
Thalassiosira punctigera	780	60 ± 6	7400 ± 900	8840	370 ± 75	4180 ± 840	Kleinert (1987)

Dürselen, 1990; Hagmeier, 1991; Aletsee & Rick, 1990; Aletsee et al., 1992), but there are still periods when this species cannot be found: Hesse (1988) reports high biomasses of *C. wailesii* in spring 1984 in the outer German Bight, while in 1985 only the related native species *Coscinodiscus concinnus* W. Smith was present. Bauerfeind et al. (1990) observed only *Coscinodiscus concinnus* in spring 1985 and 1986; *C. wailesii* is not mentioned. Our
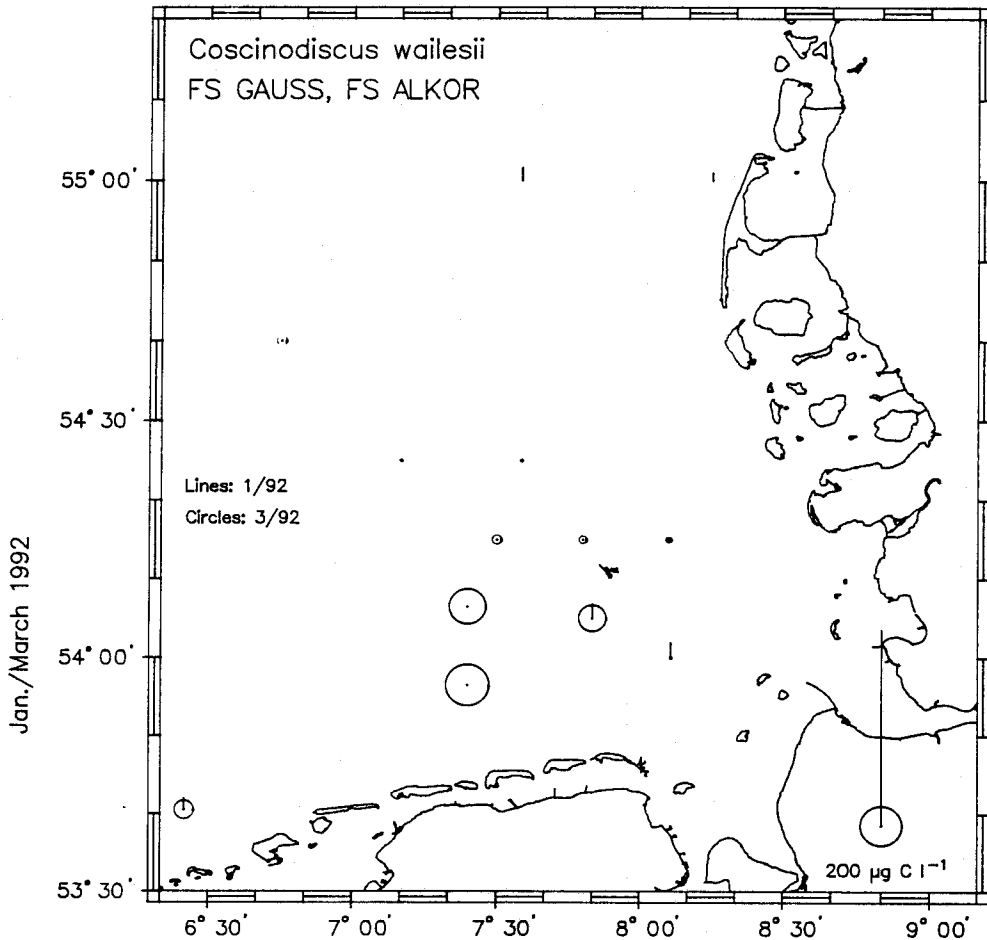
Fig. 6. Spatial distribution and biomass of *Coscinodiscus wailesii* in the German Bight. Results of two cruises in winter and early spring 1992. The biomass data are given as mean carbon values (µg C dm^{-3}) for the upper layer (0–20m) of the water column. Symbol size compares to the biomass value (see legend lower right)

investigations in May 1986 and April 1991 also provided no evidence for the occurrence of *C. wailesii* in the German Bight. These results may lead to the assumption that the appearance of one species may inhibit the occurrence of the other. No evidence for an excluding mechanism can be revealed, on the basis of the data of the PRISMA spring cruise in 1992 (Fig. 7). In this period, both species had identical distribution patterns; only the areas of maximum cell numbers differed. The greater offshore abundance of *C. concinnus* is in accordance to the prediction of Baars (1988), who mentioned deeper water columns and high light regime as growth conditions favoured by *C. concinnus*.

The available 3-year data set shows the distribution features for *C. wailesii* in the area of the German Bight (Figs 2–7). It remains to be seen whether these results describe
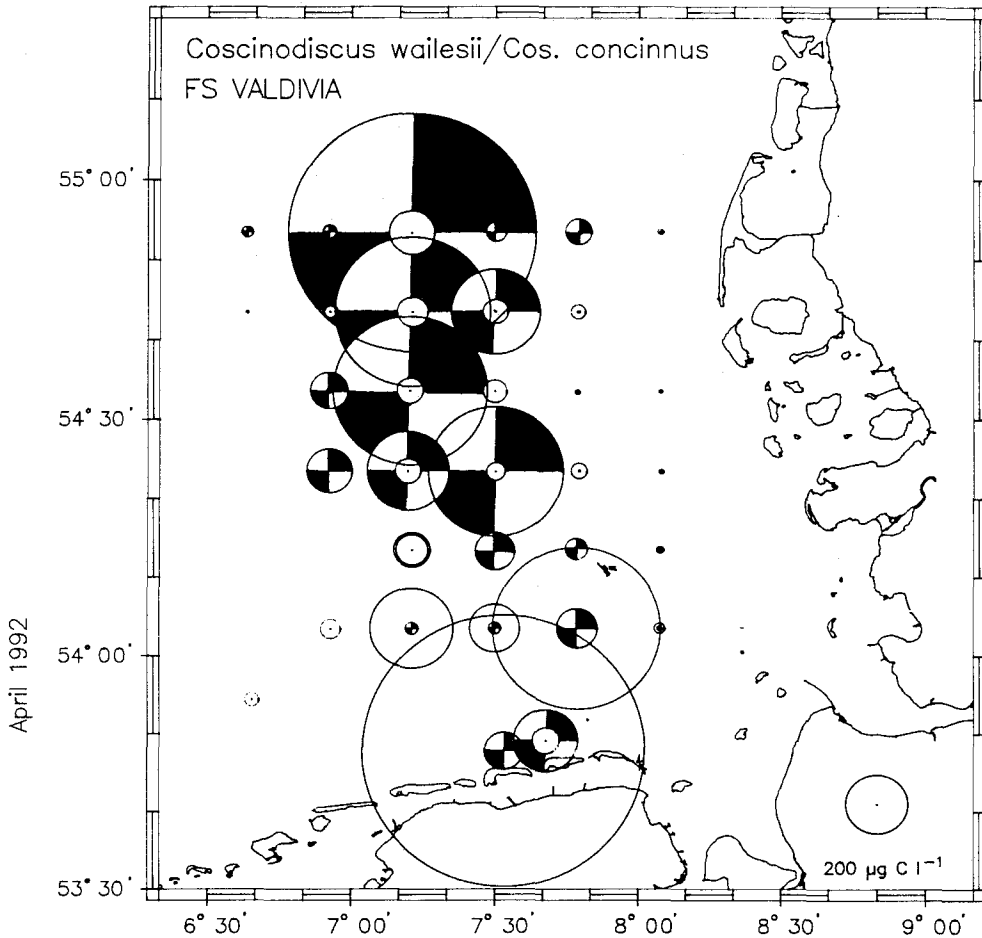
Fig. 7. Spatial distribution and biomass of the introduced *Coscinodiscus wailesii* and the native *Coscinodiscus concinnus* in the German Bight during the PRISMA spring cruise in April 1992. The biomass data are given as mean carbon values (μg C dm^{-3}) for the upper layer (0–20m) of the water column. Symbol size compares to the biomass value (see legend lower right). *C. wailesii* is displayed by the unfilled circles, *C. concinnus* by the crossed circles

a regular seasonal distribution pattern of the species, since any variability in circulation, light and nutrient regime may have a strong impact on the species' annual development.

Some questions remain to be answered: (1) What are the reasons for the success of *Coscinodiscus wailesii* in the North Sea area? (2) What is the effect of the spreading of *Coscinodiscus wailesii* on the ecosystem of the German Bight?

As mentioned before, the species is able to cope with considerable fluctuations of temperature and salinity (Aletsee & Rick, 1990; Dürselen, 1990) and it also seems to have the ability to handle a wide range of nutrient concentrations (Rince & Plaumier, 1986). In addition, *C. wailesii* proved to be very tolerant of metals. Field data (Figs 8–11, Table 2)
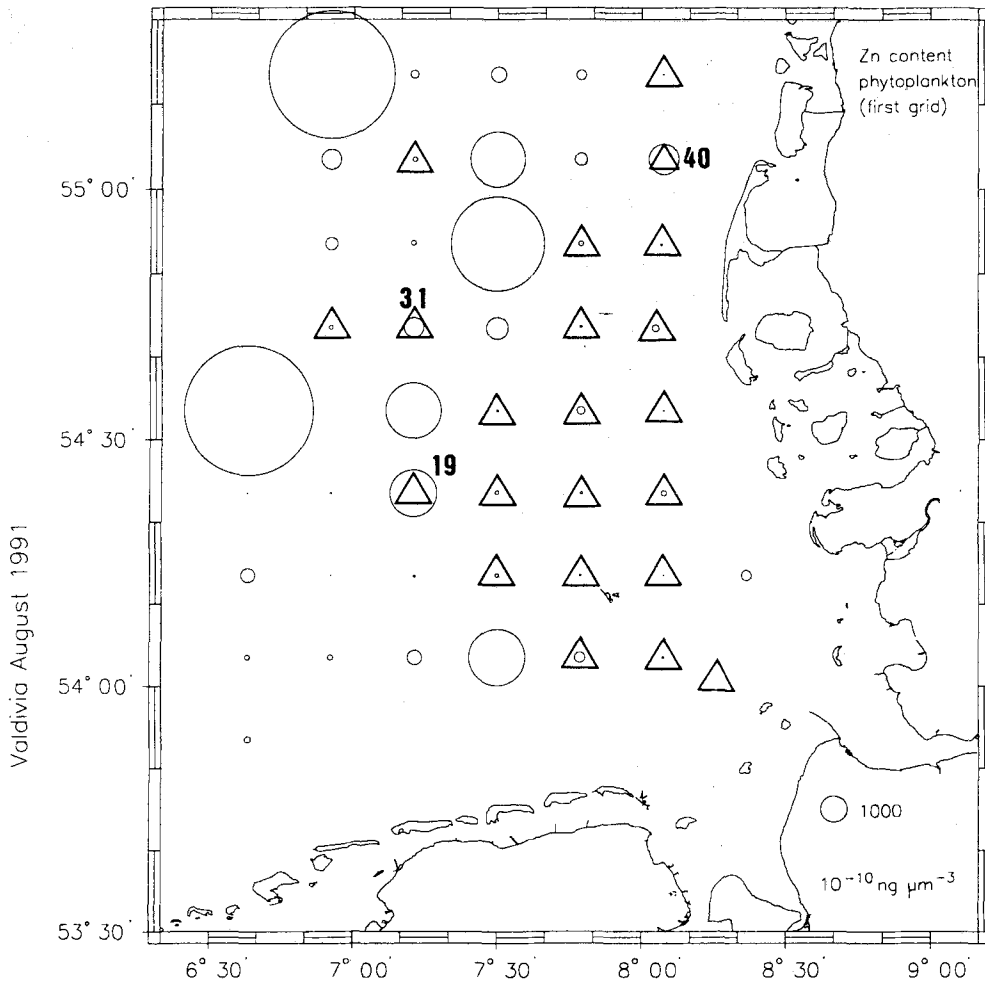
Fig. 8. Spatial distribution of the volume-related zinc content of 50 μm net plankton in the German Bight during the PRISMA summer cruise in August 1991. Symbol size compares to the value of the zinc content (see legend lower right). Stations with stock-forming occurrence of *C. wailesii* are marked by unfilled triangles. For numbered stations compare text

and results of laboratory experiments (Table 3) show that, in comparison to native phytoplankton organisms (Table 4), the species bioconcentration of trace metals is low. The bioconcentration factors for zinc measured in field experiments were higher than factors determined in laboratory experiments. This was caused by different concentrations of this metal in the water during field (0.2–0.7 μg Zn kg^{-1}) and laboratory experiments (3.0–5.0 μg Zn kg^{-1}). The concentration-dependent metal sorption of the phytoplankton follows the Langmuir isotherm (e.g. Simonis, 1988), a hyperbolic saturation curve. After reaching the curves saturation point, the bioaccumulation declines with rising metal concentration in the water.
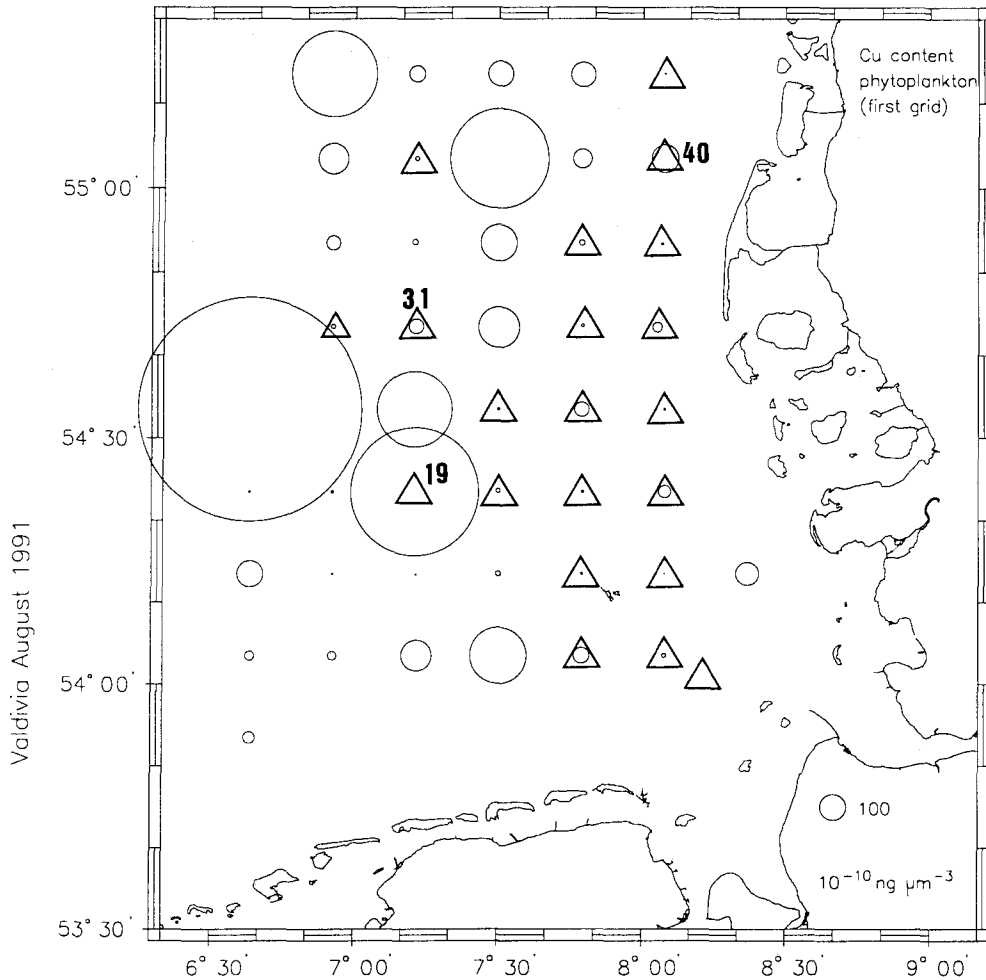
Fig. 9. Spatial distribution of the volume-related copper content of 50 µm net plankton in the German Bight during the PRISMA summer cruise in August 1991. Symbol size compares to the value of the copper content (see legend lower right). Stations with stock-forming occurrence of *C. wailesii* are marked by unfilled triangles. For numbered stations compare text

It is unlikely, however, that the high biomass densities of *C. wailesii* during the PRISMA summer cruise (August 1991) were triggered by heavy metal effects, since the measured copper and zinc concentrations in the surrounding water were low (Table 2).

In comparison to native species of similar size, *C. wailesii* displays differing environmental demands. Data won by sampling a grid of 40–50 stations in the German Bight in short time intervals (August 1991) showed no biomass increase for the native *Coscinodiscus granii* Gough, while *C. wailesii* reached biomass doubling-times comparable to those in laboratory cultures under similar conditions. Simultaneously-monitored nutrient and trace metal levels gave no evidence for nutrient depletion or toxic effects of metals
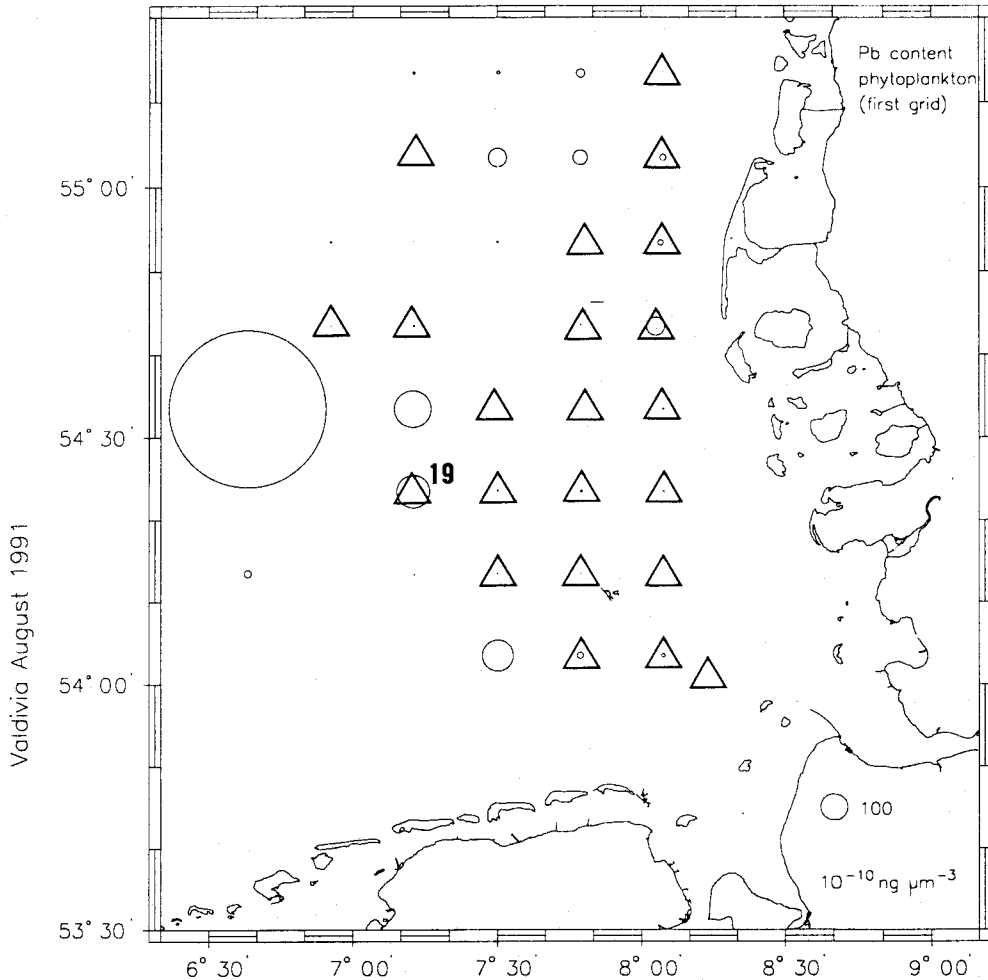
Fig. 10. Spatial distribution of the volume-related lead content of 50 μm net plankton in the German Bight during the PRISMA summer cruise in August 1991. Symbol size compares to the value of the lead content (see legend lower right). Stations with stock-forming occurrence of *C. wailesii* are marked by unfilled triangles. For numbered stations compare text

(compare Rabsch & Elbrächter, 1980) for this campaign period. Maybe a micronutrient that is of lesser importance for the growth of *C. wailesii* than that of *C. granii* was the determining factor.

Experiments conducted by Roy et al. (1989) give another hint for possible reasons for the success of *C. wailesii*. The copepods *Temora longicornis* O.F.R. Müller and *Calanus helgolandicus* Claus, both native to the North Sea, showed inefficient or "sloppy" grazing behaviour when raised on *C. wailesii*. Possibly, the primary consumers in the German Bight avoid the ingestion of *C. wailesii*, and the species derives its dominance from this.
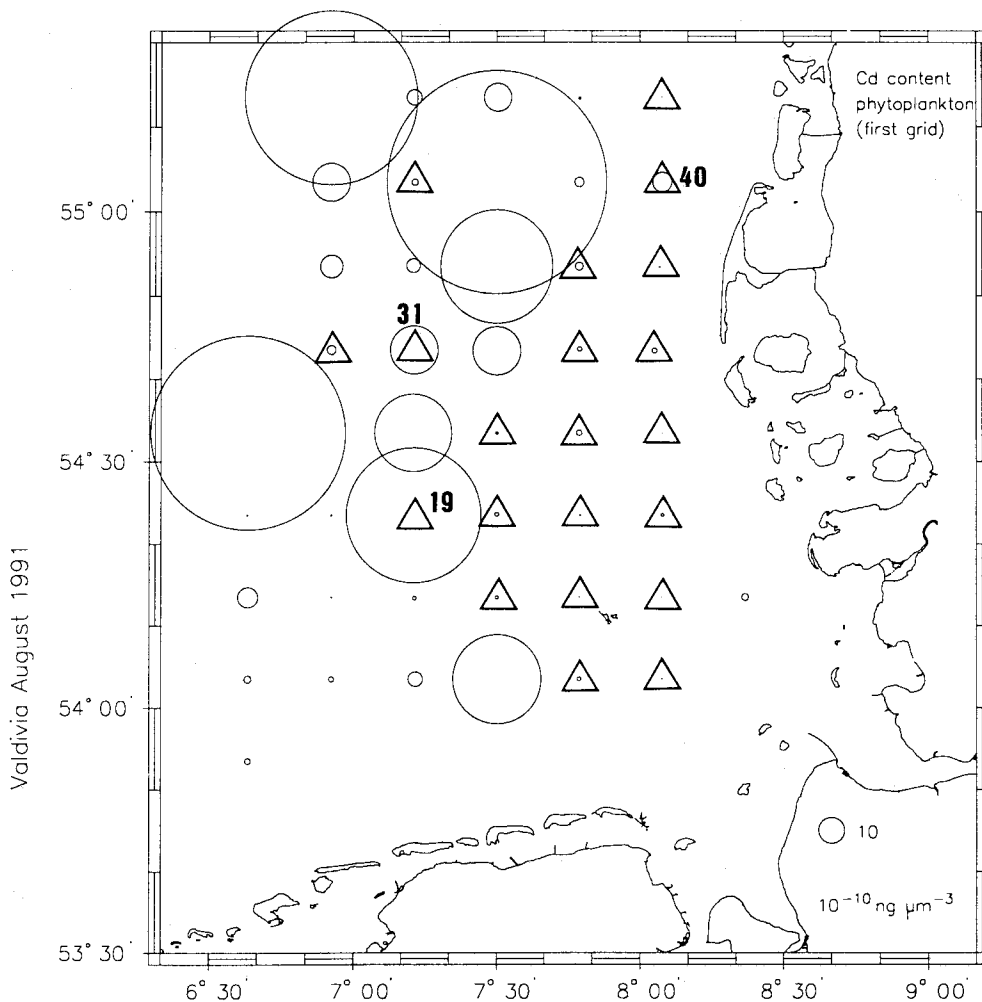
Fig. 11. Spatial distribution of the volume-related cadmium content of 50 μm net plankton in the German Bight during the PRISMA summer cruise in August 1991. Symbol size compares to the value of the cadmium content (see legend lower right). Stations with stock-forming occurrence of *C. wailesii* are marked by unfilled triangles. For numbered stations compare text

The results of three years of research in the German Bight illustrate that *C. wailesii* can supersede native species at times or at least decrease their biomass development. Grazing by copepods may be reduced, and mass development of *C. wailesii* may then have consequences for the following trophic levels.

Prompt sedimentaion of *C. wailesii* resulting from silicate depletion of the water (Manabe & Ishio, 1991) contributes only a limited amount of carbon remineralisation in the water column. Manabe & Ishio (1991) studied an autumn bloom of the species in Inland Seto Sea. After sedimentation, the cells were conserved in the bottom mud due to

low temperatures in winter. In spring, decomposition of the organic components caused oxygen deficits in the bottom water. Consequences of oxygen depletion for benthic organisms are widely known, even for the area of the outer German Bight (v. Westernhagen & Dethlefsen, 1983; Rachor & Albrecht, 1983; Rachor, 1985). For the inner German Bight, such eminent outcome is rather unlikely since vertical circulation is initiated frequently by tidal mixing processes.

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