Spatial and temporal distribution of two new phytoplankton diatom species in the German Bight in the period 1988 and 1996

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Several samplings in the German Bight between 1988 and 1996 showed that during this time two phytoplankton diatom species which had not previously been present established themselves in the phytoplankton communities of this area. The species are *Coscinodiscus wailesii* Gran & Angst and *Thalassiosira punctigera* (Castracane) Hasle. Both species can be found during each season in special regions or in the whole area. Especially *C. wailesii*, the largest diatom in the German Bight with a diameter up to 500 µm, is able to dominate phytoplankton standing stocks in respect to carbon biomass. During winter this species is present in low abundance but during spring and summer it is able to produce blooms. The highest biomass during the sampling period was determined to be 360 µg C l^{-1} (corresponding to 2000 cells per litre). The success of *C. wailesii* is due first of all to its wide tolerance to different temperatures and salinities and its big size, unsuitable for planktonic herbivores. *T punctigera* showed a maximum biomass of 150 µg C l^{-1} during the cruises. This species also has a wide temperature and salinity tolerance.

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INTRODUCTION

The qualitative and quantitative composition of the phytoplankton has been examined intensively for special regions of the North Sea especially since the 1970s (e.g. Dodge 1977; Gieskes & Kraay 1975; Tangen 1979; Wandschneider 1980; Hagmeier 1984; Cadée 1986; Veldhuis & al. 1986; Hesse 1988; Colijn & al. 1990). In the German Bight a continuous long-term observation of the biological, chemical and physical parameters has been carried out at a fixed point at Helgoland Roads since 1962 with samplings on each working day (e.g. Hagmeier 1978; Gillbricht 1983; Radach & Berg 1986; Hickel & al. 1992; Hickel & al. 1993). The analysis of these data till 1984 showed a clear increase of phytoplankton biomass (Hagmeier 1978; Gillbricht 1983; Radach & Berg 1986) since then no obvious trend could be observed (Hickel & al. 1992). The increase was characterized by flagellates while the biomass of diatoms even showed a slight significant decrease (Radach & Berg 1986). In addition to the quantitative change of phytoplankton biomass and the shift in the importance of indigenous species from different taxonomical groups during the last decades there is another important observation. At present, several species in the North Sea phytoplankton which originally are not indigenous in this area can be found: e.g. *Odontella* (*Biddulphia*) *sinensis* (Greville) Grunow (Ostenfeld 1908), *Corethron criophilum* Castracane and *Stephanopyxis palmeriana* (Greve) Grunow (Drebes 1991), *Gyrodinium aureolum* Hulburt (Tangen 1977), *Pleurosigma planktonicum* Simonsen (Boalch & Harbour 1977 a), *Thalassiosira punctigera* (Castracane) Hasle (Kat 1982) as well as *Coscinodiscus wailesii* Gran & Angst (Boalch & Harbour 1977 b; Rincé & Plaumier 1986). Although the natural transport by ocean currents is responsible for the appearance of foreign phytoplankton species, the main cause is the spreading with ballast water of ships (Gerlach 1992) and the settling of marine fauna cultures (e.g. mussels) from foreign sea areas (Rincé & Plaumier 1986). Especially the species *C. wailesii* and *T. punctigera* both appeared in the German Bight at the beginning of the 1980s. This paper will show data on spatial and temporal distribution of these two species during the last decade. Some of the distribution data of *C. wailesii* already were shown earlier in Rick & Dürselen (1995). However, at that time the biomass of the species was far overestimated. The corrected values by using a new conversion factor (see *Material and methods* below) are now shown in this text. In addition it seems desirable to show the complete time series for the last decade.

MATERIAL AND METHODS

The distribution and abundance of the two diatoms *Coscinodiscus wailesii* and *Thalassiosira punctigera* were examined in the German Bight between 1988 and 1996 during four interdisciplinary projects: ZISCH (Circulation and contaminant fluxes in the North Sea, 1985-1989), PRISMA (Processes in the contaminant cycle between sea and atmosphere, 1990-1993), TUVAS (Transport, conversion and variability of pollutants and nutrients in the North Sea, 1991-1992) and KUSTOS (Fluxes of matter and energy in coastal waters of the German Bight, 1994-1997). The exact periods of time of all cruises, number of stations, depths of sampling and the location of the research area are shown in Table 1.

Water samples for determination of phytoplankton biomass were taken with Niskin bottles from different depths and each time 100 to 250 ml were fixed with Formol for later analysis.

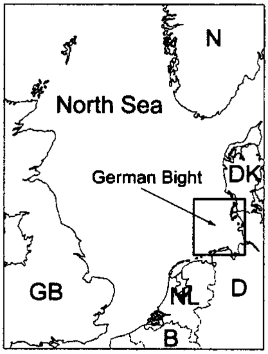
Counting of *T. punctigera* and most of the other phytoplankton species was carried out using an inverted microscope (Utermöhl 1958) and a 10 ml sedimentation chamber after adding a drop of Lugol. In contrast the large cells of *C. wailesii* as well as those of *Coscinodiscus granii* Gough and *Coscinodiscus concinnus* W.Smith cannot be counted correctly by using this method because of their relatively low abundance in contrast to other species. During the first three projects, cells of these species were counted in the whole fixed water samples in a petri dish using a stereo microscope. During the KUSTOS cruises *C. wailesii* and the two sister species were quantified immediately on board after rinsing a defined volume (0.5 or 1 litre) of the unfixed water sample through a 5 cm glass fibre filter. The easily recognizable cells were then counted using a stereo microscope.

For the estimation of biomass parameters a geometrical form was assigned to each species (a cylinder for *C. wailesii* and *T. punctigera*) and all necessary dimensions for the determination of the volume were measured (Hillebrand & al. 1999). For *T. punctigera* the measurement of diameter and height was done simultaneously during the counting in the sedimentation chambers but for *C. wailesii* after counting with fixed net samples (sampled with a 55 µm phytoplankton net). To convert to carbon biomass for *T. punctigera* and nearly

Table 1. Some details about each sampling presented in this paper.

Grid no.	Period of time	Project	Number of sampled stations	Sampled depths
1	29 Nov - 4 Dec 1988	ZISCH II [1]	23	5,10,15,20 m
2	6 Dec - 8 Dec 1988	ZISCH II [1]	21	5,10,15,20 m
3	20 Jan - 23 Jan 1989	ZISCH II [1]	17	5,10,20 m
4	27 Feb - 3 Mar 1989	ZISCH II [2]	17	5,10,15,20 m
5	21 Mar - 22 Mar 1989	ZISCH II [1]	8	5,10,20 m
6	10 Apr - 13 Apr 1989	ZISCH II [3]	17	0,10,15,20 m
7	2 May - 6 May 1989	ZISCH II [1]	20	0,5,10,15,20 m
8	13 Apr - 18 Apr 1991	PRISMA [1]	41	0,5,10,20 m
9	12 Aug - 17 Aug 1991	PRISMA [1]	51	5,10,20 m
10	15 Aug - 18 Aug 1991	PRISMA [2]	32	5,10,20 m
11	19 Aug - 21 Aug 1991	PRISMA [2]	43	5,10,20 m
12	22 Aug - 25 Aug 1991	PRISMA [2]	41	5,10,20 m
13	26 Aug - 29 Aug 1991	PRISMA [2]	51	5,10,20 m
14	6 Sep - 11 Sep 1991	TUVAS [1]	21	5 m
15	1 Oct - 11 Oct 1991	TUVAS [4]	19	5 m
16	6 Jan - 11 Jan 1992	TUVAS [2]	18	5 m
17	6 Mar - 11 Mar 1992	TUVAS [5]	18	5 m
18	7 Apr - 11 Apr 1992	PRISMA [1]	42	0,5,10,20 m
19	8 Aug - 11 Aug 1994	KUSTOS [2]	28	0,5,10,20 m
20	25 Apr - 27 Apr 1995	KUSTOS [2]	35	0,5,10,15,20m
21	9 May - 11 May 1995	KUSTOS [2]	36	0,5,10,20 m
22	22 Feb - 26 Feb 1996	KUSTOS [1]	31	5,10,20 m
23	1 Mar - 3 Mar 1996	KUSTOS [1]	33	5 m

Location of research area



Research vessels

[1]R/V *Valdivia*
[2]R/V *Gauss*
[3]R/V *Victor Hensen*
[4]R/V *Meteor*
[5]R/V *Alkor*

all other diatom species (except those described below) the factor according to Strickland & Parsons (1972) was used: 0.0875 pg C μm^{-3}. The factor used for non-diatoms is: 0.14 pg C μm^{-3}. Because of its size (diameter up to 500 µm) and a thickness of the cytoplasmatic layer of about 6 µm *C. wailesii* has a relation between plasma volume and total cell volume which is about five times smaller compared with a mean diatom for which the conversion factor of Strickland & Parsons (1972) is valid. So we used for this species as well as for *C. granii* and *C. concinnus* a correspondingly adapted conversion factor: 0.0175 pg C μm^{-3}.

Both biomass (µg C l^{-1}) and abundance (cells per litre) were integrated to a maximum water depth of 20 m at all stations and afterwards averaged for one litre.

Water temperature and salinity were measured by a working group of the Bundesamt für Seeschiffahrt und Hydrographie (BSH, Hamburg) with a CTD system.

RESULTS AND DISCUSSION

Coscinodiscus wailesii is distributed world-wide. The species occurs both in the Pacific (Gran & Angst 1931; Cupp 1943; Yuchien 1981; Manabe & Ishio 1991) and the Atlantic Oceans (Mahoney & Steimle 1980; Marshall 1984). In 1977, *C. wailesii*, at that time called *Coscinodiscus nobilis* (Grunow), was observed for the first time in the Celtic Sea (Boalch & Harbour 1977b), in the English Channel (Rincé & Plaumier 1986) and in the southern Irish Sea (Robinson & al. 1980). It pre-

Table 2. Details about the population of *C. wailesii* and *T. punctigera* for each sampling period.

Period of time	Found at ... stations	Percentage of total phytoplankton carbon biomass minimum/maximum	Mean cell size diameter/height (µm)	Maximum cell number integrated (N l^{-1})
Coscinodiscus wailesii				
29 Nov - 4 Dec 1988	10	6 / 99	339 / 226	140
6 Dec - 8 Dec 1988	5	42 / 96	329 / 242	80
20 Jan - 23 Jan 1989	12	27 / 98	361 / 231	70
27 Feb - 3 Mar 1989	7	49 / 97	316 / 211	295
21 Mar - 22 Mar 1989	5	59 / 99	313 / 209	910
10 Apr - 13 Apr 1989	5	10 / 36	323 / 161	128
2 May - 6 May 1989	5	1 / 4	321 / 232	228
12 Aug - 17 Aug 1991	26	12 / 63	350 / 235	746
15 Aug - 18 Aug 1991	16		359 / 216	285
19 Aug - 21 Aug 1991	15		350 / 264	535
22 Aug - 25 Aug 1991	20		358 / 225	840
26 Aug - 29 Aug 1991	20		349 / 234	710
6 Sep - 11 Sep 1991	16		343 / 203	280
1 Oct - 11 Oct 1991	16		314 / 206	225
6 Jan - 11 Jan 1992	5		345 / 283	6
6 Mar - 11 Mar 1992	11		333 / 269	124
7 Apr - 11 Apr 1992	28		322 / 249	517
8 Aug - 11 Aug 1994	25	0.1 / 97	266 / 175	2067
25 Apr - 27 Apr 1995	35		327 / 252	34
22 Feb - 26 Feb 1996	31		357 / 246	104
1 Mar - 3 Mar 1996	33		344 / 227	60
Thalassiosira punctigera				
29 Nov - 4 Dec 1988	11	0.3 / 56	68 / 34	160
6 Dec - 8 Dec 1988	13	1 / 76	80 / 40	80
20 Jan - 23 Jan 1989	15	0.5 / 42	85 / 42	60
27 Feb - 3 Mar 1989	16	0.5 / 71	81 / 40	149
21 Mar - 22 Mar 1989	8	0.4 / 52	82 / 38	140
10 Apr - 13 Apr 1989	15	2 / 13	77 / 39	1021
2 May - 6 May 1989	19	0.3 / 21	86 / 42	5554
13 Apr - 18 Apr 1991	15	0.1 / 12	78 / 35	763
8 Aug - 11 Aug 1994	11	0.1 / 6	58 / 39	500
9 May - 11 May 1995	32	0.3 / 22	89 / 27	4088

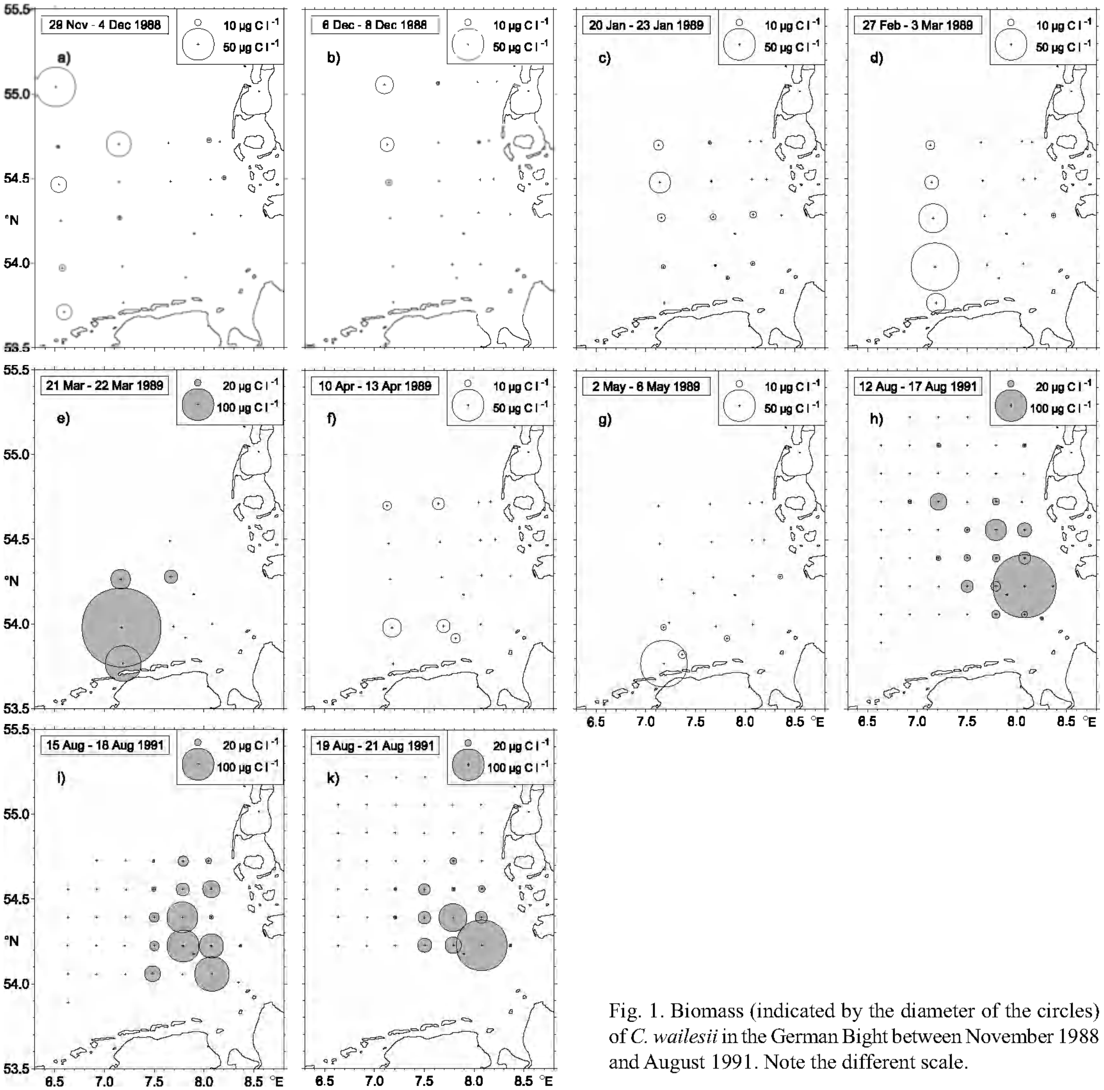


Fig. 1. Biomass (indicated by the diameter of the circles) of *C. wailesii* in the German Bight between November 1988 and August 1991. Note the different scale.

sumably reached these areas by the rearrangement of the French oyster cultures to a species more resistant against infections from the Indopacific Ocean during the 1970s (Rincé & Plaumier 1986). Conspicuous was the strong production of mucilage of the species which is not known from the pacific forms (Rincé & Plaumier 1986).

From this time on *C. wailesii* spread around the whole North Sea during the following years. In 1982 it was observed for the first time in the outer Scheldt Estuary (Rick & Dürselen 1995). In this area it mainly turned out with an important share of biomass especially between September and March. Also Boalch & Harbour (1977b) and Robinson & al. (1980) determined the highest share of biomass of *C. wailesii* for winter and spring. In May and June 1986 the species also appeared in the north-west of the North Sea around the Faeroe, Orkney and Shetland Islands as well as in the central North Sea (Rick & Dürselen 1995).

During the 1980s, *C. wailesii* attained, especially for the phytoplankton communities of the German Bight, an increasing importance (Rincé & Plaumier 1986; Hesse 1988). However, there were also periods when the species was not found or played a secondary role. For example Hesse (1988) found high biomasses of *C. wailesii* in spring 1984 in the outer German Bight

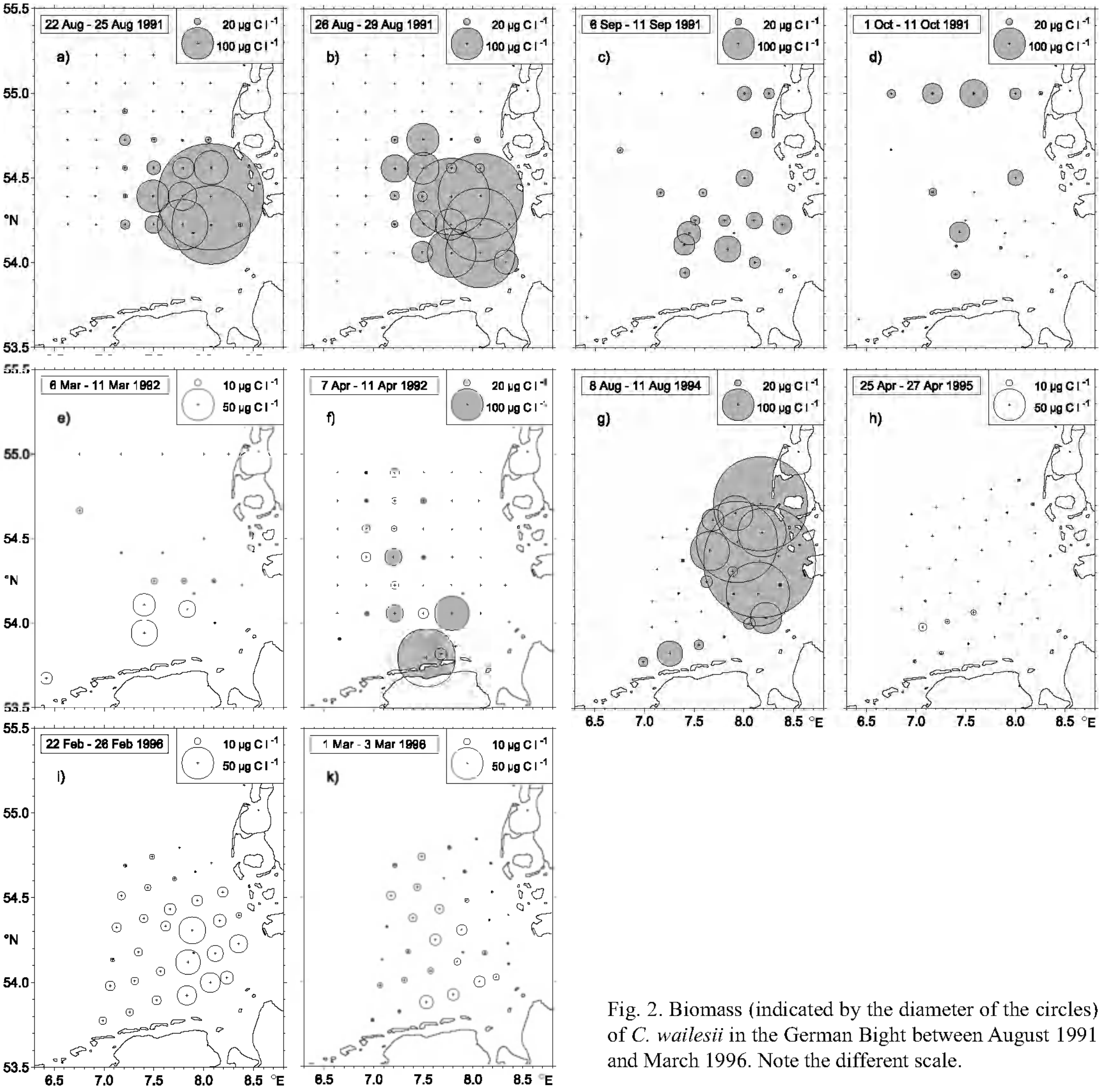


Fig. 2. Biomass (indicated by the diameter of the circles) of *C. wailesii* in the German Bight between August 1991 and March 1996. Note the different scale.

whereas one year later only the indigenous sister species *Coscinodiscus concinnus* turned out. This species was also observed by Bauerfeind & al. (1990) during spring 1985 and 1986. They didn't find *C. wailesii*.

Between November 1988 and May 1989 for the first time the possibility was given to follow the development of the phytoplankton in the German Bight for the transition between late autumn and late spring with monthly samplings. Between late November 1988 and early March 1989 (Fig. 1a-d) *C. wailesii* frequently appeared at some stations in the west of the German Bight. At the beginning of March cell numbers already were up to 300 per litre (77 µg C l^{-1}) in the south-western area (Table 2). In addition, during January and February there was another large diatom present, *Coscinodiscus granii*, which could only be found at stations at which *C. wailesii* also occurred. But *C. granii* never reached the abundance of *C. wailesii*. During March 1989 (Fig. 1e) biomass of *C. wailesii* increased to 254 µg C l^{-1} in the south-west. This already corresponded to cell numbers of above 900 per litre (Table 2). *C. granii* was again observed as an accompanying species. Finally during April (Fig. 1f) and May 1989 (Fig. 1g) only isolated living cells of *C. wailesii* could be found. During all ZISCH cruises *C. wailesii* was dominant especially in the south-west, offshore close to the East Friesian Islands as well as in the outer German Bight, in water with higher salinity. The total phytoplankton biomass at these stations was almost exclusively formed by this species (Table 2). In the eastern area influenced by the river Elbe, it only could be found occasionally.

For the sampling of a grid of 51 stations in April 1991 during the PRISMA project unfortunately no biomass values are available for *C. wailesii*. The species was found at most of the stations of the middle and inner German Bight. But it was proportionally not so important as described below for the summer of the same year. The main distribution was in an area which reached from the middle of the German Bight north-west of Helgoland to the north-east close to Sylt.

During August 1991, the grid was sampled five times for a brief time (Fig. 1h-2b). The main distribution of *C. wailesii* at this time was in the south-east close to the North Friesian Islands and in the middle of the German Bight. For two and a half weeks the biomass clearly increased in these areas, from a mean biomass for all stations of about 30 µg C l^{-1} at the beginning of the examination time to nearly 100 µg C l^{-1} per station at the end. The estimated growth rate of the species during this time was between 0.24 and 0.21 d^{-1} which corresponds well with the determined growth rates from laboratory cultures under similar conditions (Dürselen 1995). The maximum biomass was 341 µg C l^{-1} which corresponded to an integrated cell number of 840 per litre (Table 2). At this station the highest abundance was 1120 cells per litre at a depth of 5 m.

A little more than a week later the abundance had clearly decreased (Fig. 2c). Only in the south-east of the German Bight could maximum biomasses of the species up to 84 µg C l^{-1} be determined. Again a month later, the main distribution area now was in the north of the German Bight (Fig. 2d) with a maximum biomass of 89 µg C l^{-1}. *C. wailesii* in the south-east was almost absent. During January of the following year no great biomasses could be found. Nevertheless the species could be detected at some stations. During March the development began again, now south and south-west of Helgoland (Fig. 2e). From this area *C. wailesii* spread towards the north-west till April (Fig. 2f). The highest biomass during this time was 185 µg C l^{-1} in the south of the German Bight close to the Island of Langeoog.

Also during the PRISMA and TUVAS samplings *C. granii* nearly always appeared as accompanying species to *C. wailesii*. The distribution areas of both species in the German Bight are nearly identical, very rarely could one of both species be found on its own. However, *C. granii* never reached the biomasses of its sister species (maximum 30 %, mostly much less). During the cruise in August 1991 a maximum biomass of 40 µg C l^{-1} was measured; at the same station *C. wailesii* reached 200 µg C l^{-1}.

In April 1992 the third large *Coscinodiscus* species *C. concinnus* which occurred in the German Bight was found in great amounts. In this case the distribution areas of *C. wailesii* and *C. concinnus* overlapped. The first-named species formed larger biomasses in the south, *C. concinnus* mainly appeared in the north. Maximum values for both species showed the same range (circa 180 µg C l^{-1}).

In August and September 1993 *C. wailesii* turned out mainly in the south-east of the German Bight between Helgoland and the Elbe estuary (Hagmeier pers. commn). In August 1994, very high biomasses of *C. wailesii* occurred for a short time (Fig. 2g) as already observed for the same period of time in 1991. The species was found at nearly all stations. But the main distribution area was in the east of the German Bight. In this area the highest biomass was 361 µg C l^{-1} which corresponded to a cell number of more than 2000 per litre (Table 2). At this station 2800 cells per litre were counted at a depth of 5 m and still 2000 at a depth of 20 m. This was the highest abundance of this species ever found during the shown cruises. But the cells of the whole population in the German Bight at this time in mean were the smallest of all samplings (Table 2). Close to the East Friesian Islands in the south of the German Bight cell numbers above 500 per litre were still found.

In spring 1995 *C. wailesii* could be found at nearly all stations in the whole German Bight but never in considerable numbers (Fig. 2h). The maximum biomass was 12 µg C l^{-1}.

Remarkable were the relatively high biomasses of *C. wailesii* at the end of February 1996 (Fig. 2i) at water temperatures between –1.5 and +1.5 °C (Fig. 3b) which were caused by a continual long cold spell. During this period, offshore wind (and because of this little vertical mixing) and a high solar radiation were predominant. Due to these factors there was a sufficient nutrient supply so that the whole phytoplankton could grow to unusual high biomasses very early (own unpublished data). *C. wailesii* was found in the whole German Bight; the highest biomass was 42 µg C l^{-1} corresponding to an abundance of more than 100 relatively large cells per litre (Table 2). Already during the weeks before the cruise high abundances of the species not typical for this season were observed in the German Bight (Hagmeier pers. commn). Also *C. concinnus* occurred in high numbers. This species caused a large bloom during the following weeks, one of the reasons which led to unusual consequences for the ecosystem of the German Wadden Sea (Höpner & Oelschläger 1997). On

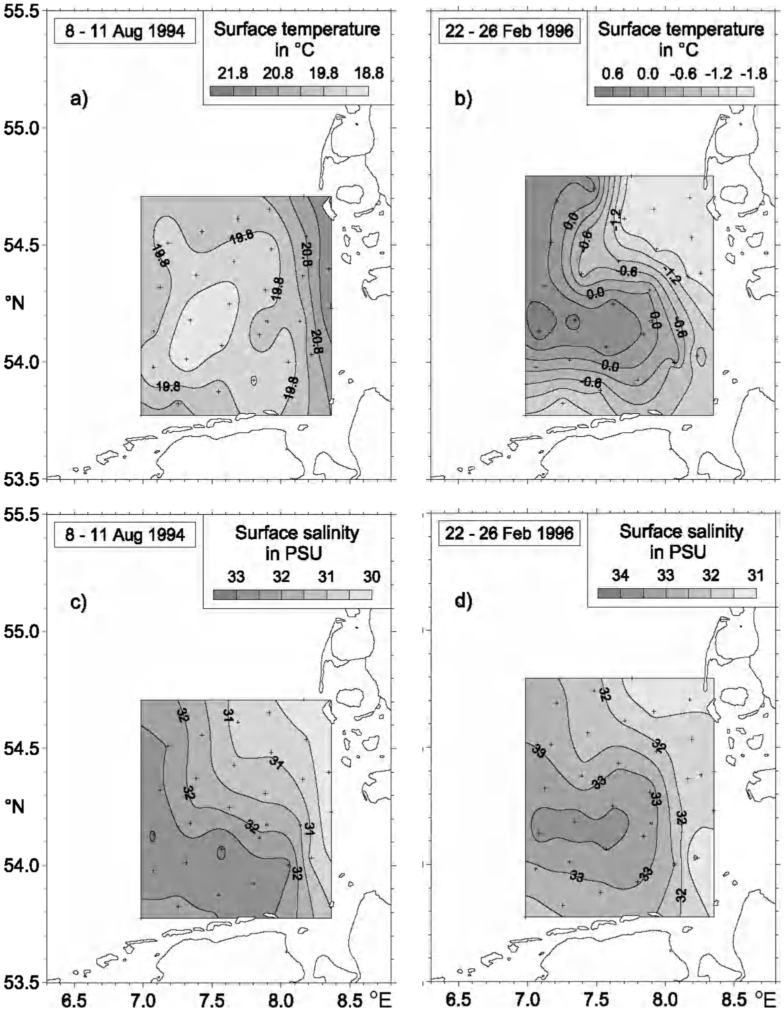


Fig. 3. Surface temperature and surface salinity in the German Bight during the sampling in August 1994 and February 1996 (data from BSH, Hamburg).

the other hand the biomasses of *C. wailesii* decreased but the species could still be found in the whole area at the beginning of March (Fig. 2k).

All these observations clearly show that *C. wailesii* has established itself in the German Bight during the last decade and it is very important for the pelagic ecosystem. Often it comprises more than 90 % of the whole phytoplankton biomass in some areas (Table 2).

The data seem to indicate a regular seasonal distribution pattern of *C. wailesii* in the German Bight. During winter, the species occurs in the north and the west of the area in low biomasses but is often dominant (Fig. 1a-d). In the inner German Bight the species is absent. An exception was the unusual winter in 1996 (Fig. 2i-k). During spring high biomasses occurred in the west and especially in the south-west close to the East Friesian Islands (Figs 1e, 2e-f). During summer very high biomasses could be found in the south-east and close to the North Friesian Islands (Figs 1h-2b, 2g). During autumn the distribution moved to the north and the outer German Bight (Fig. 2d). In between there also were periods when *C. wailesii* only could be found occasionally or even not at all. But these periods seem to dwindle during the last years. Especially samplings during the KUSTOS project show that meanwhile the species can be found in the whole area at each time.

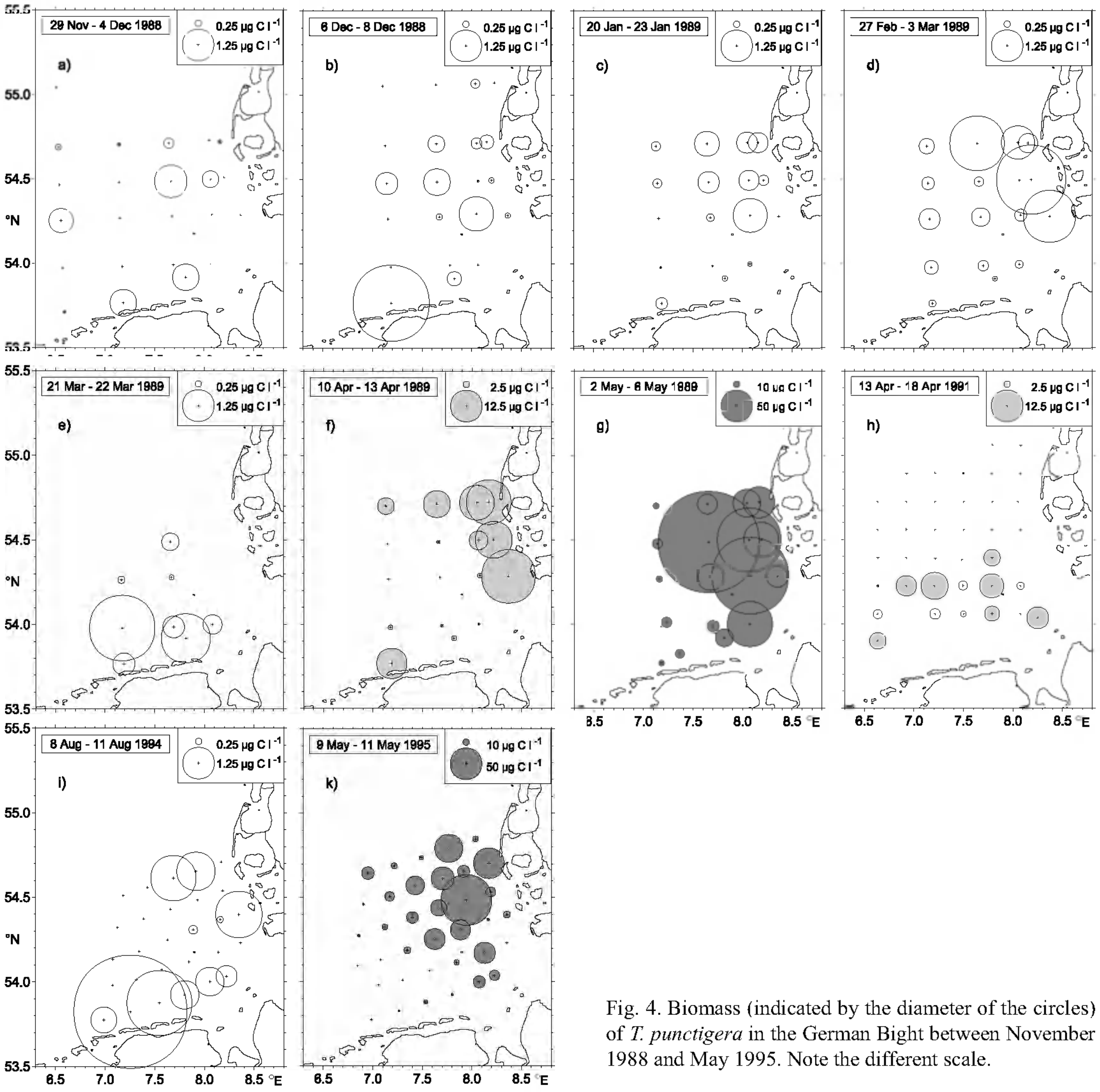


Fig. 4. Biomass (indicated by the diameter of the circles) of *T. punctigera* in the German Bight between November 1988 and May 1995. Note the different scale.

The reasons for the success of *C. wailesii* in the North Sea are that apart from other factors the species is able to grow over a wide range of temperature (< 0 °C to > 20 °C) and salinity (24-35 psu) (Rincé & Plaumier 1986; Rick & Dürselen 1995). As an example for this tolerance Fig. 3 shows the surface temperature and salinity measured during the samplings in August 1994 and in February 1996, both periods *C. wailesii* appeared in great amounts (Fig. 2g, i). The species occurs in the open ocean, in coastal areas and also in estuaries where both parameters can greatly vary. In addition *C. wailesii* can also cope with a large range of nutrient concentrations (Rincé & Plaumier 1986).

A further factor in this connection is certainly also the high tolerance of *C. wailesii* to heavy metals. Data from cruises in the German Bight as well as laboratory experiments show that the species accumulates the heavy metals zinc, copper and cadmium less than other diatoms, even if there are high concentrations in the water (Dürselen 1995; Rick & Dürselen 1995).

Another indication for the success of *C. wailesii* is the following observation. The species nearly always occurs together with the similarly large indigenous sister species *C. granii*. But this species never reached the biomasses of *C. wailesii*. *C. granii* also occurred as accompanying species of *C. wailesii* during the five samplings of the grid in August 1991. Whereas the biomass of the latter species increased immensely with a growth rate between 0.24 and 0.21 d^{-1} during the recorded period of time, as previously described, there was no increase for *C. granii*. A possible explanation could be the different tolerance to heavy metals, because *C. granii* is known to be extremely sensitive (Rabsch & Elbrächter 1980). The measured heavy metal concentrations in water (Schmidt unpublished data) during the examination period, however, exclude a toxic effect for *C. granii*. And also the macronutrient data (Brockmann unpublished data) do not indicate a deficient situation. Possibly a micronutrient plays a decisive role which is of less importance for *C. wailesii* than for the sister species *C. granii*.

Experiments from Roy & al. (1989) showed another advantage for *C. wailesii* which obviously is relevant for the natural environment, too. The two copepod species *Temora longicornis* O.F.Müller and *Calanus helgolandicus* Claus both indigenous in the North Sea showed an inefficient grazing if *C. wailesii* was offered as food. Also other examinations (e.g. Harris 1982; Berggreen & al. 1988) verify that copepods prefer phytoplankton cells smaller than 100 µm. Cells of *C. wailesii* nearly always have a diameter above 350 µm. Possibly these consumers avoid the uptake of *C. wailesii* cells in the natural environment as long as other smaller primary producers are present. This is again an advantage for *C. wailesii* in contrast to other species. If *C. wailesii* is despised as food by copepods this can also have consequences for the following trophic levels by development of a bloom of this diatom. In contrast *Crangon crangon* Linné feeds and digests the cells of *C. wailesii* in a sufficient amount (Buchholz pers. commn). The frequent occurrence of the diatom could have a positive effect for the population of decapods.

Thalassiosira punctigera is a diatom of medium size with a thick cell wall. In contrast to the other species of this genus in the natural environment it normally occurs as individual cells and does not build chains (the species is able to build chains in laboratory cultures under special conditions). Today the species is distributed world-wide. Until a few years ago it could still be found only rarely in the eastern North Atlantic (Hasle 1983) while it was frequent in the North Pacific (Makarova 1970). In the English Channel the species, at that time called *Thalassiosira angstii* (Gran) Makarova, appeared in 1978 (Kat 1982). In 1979 *T. punctigera* was observed in the Skagerrak for the first time (Hasle 1983). In March 1981, it could be detected in the Dutch offshore plankton for the first time. In the same year the spreading of the species along the Dutch coast into the German Bight could be followed. By April it had spread along the whole Dutch coast (Kat 1982). Conspicuous were the high cell numbers in the estuaries of the rivers Rhine and Meuse, that is in water with low salinity. Towards the open sea the abundance decreased clearly. Kat (1982) inferred that the preferred distribution of *T. punctigera* is in water with lower salinity (estuarine form). Today the species is permanently present in the German Bight.

T. punctigera was found in low abundances during the winter of 1988/89 (Fig. 4a-e). Between November and April the main occurrence of *T. punctigera* was mostly in coastal areas sometimes also in the middle of the German Bight. The biomass increased rapidly during April (Fig. 4f) and May (Fig. 4g). In April the main distribution area was in the east of the German Bight close to the North Friesian Islands with biomasses up to 18 µg C l^{-1}. This corresponded to cell numbers of above 1000 per litre (Table 2). In May there was a strong development of the species in the east and the middle of the German Bight with a maximum biomass of 163 µg C l^{-1}.

In spring 1991, *T. punctigera* was exclusively distributed in the south of the German Bight (Fig. 4h) with a maximum biomass of about 11 µg C l^{-1}. In summer 1991 as well as in spring 1992, the species could only be found occasionally at some stations.

In summer 1994 *T. punctigera* occurred in the extreme south and at some places in the north-east of the German Bight (Fig. 4i). The maximum biomass was 4.5 µg C l^{-1} which corresponded to a cell number of about 500 per litre (Table 2). In spring 1995 *T. punctigera* was found almost in the whole of the German Bight (Fig. 4k) and reached, especially in the north-east, similar high abundances of more than 4000 cells per litre (82 µg C l^{-1}) which was also observed in May 1989 in this area. All in all the impression of Kat (1982) is confirmed that maximum biomasses of the species occur in water with lower salinity.

Although the seasonal distribution maximum of *T. punctigera* is in spring, it seems to be able to cover a larger ecological range than other diatoms with regard to physical and chemical environmental parameters as the measured biomasses show during other seasons. However, the ranges are not so extremely large as described for *C. wailesii* above.

On the other hand the tolerance of *T. punctigera* to heavy metals is similar to *C. wailesii*. The uptake rates for copper and cadmium were significantly lower in laboratory cultures as for example for the indigenous species *Thalassiosira rotula* Meunier (Rick 1990). *T. punctigera* even survived a copper pollution of 5000 ng l^{-1} for more than four weeks with a reduced photosynthesis and growth performance of about 50 %. After returning to a medium of more natural copper concentration the species reached its normal growth rate again. This fact certainly also contributes to the species establishing itself in the German Bight.

Which consequences especially the spreading of *C. wailesii* has for the whole ecosystem of the German Bight on a medium- and long-term have to be shown by future observations during the next years. Examinations up to now point out that *C. wailesii* is able to supersede indigenous species or at least to hinder their development during special periods.

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