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Vertical distribution and settling of spring phytoplankton in the offshore NW Baltic Sea proper

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ABSTRACT: We studied the vertical distribution and settling of dominant diatoms and dinoflagellates during the 1996 spring phytoplankton bloom in the offshore NW Baltic Sea proper. We sampled phytoplankton at 11 depths (to 80 m) and collected settling cells in sediment traps at 25, 50 and 100 m depth, every week from March 26 to May 7. Phytoplankton were counted and sized from both water and trap samples, to estimate the share of phytoplankton in bulk settling carbon. Diatoms, mainly *Chaetoceros* spp. and *Achnanthes taeniata*, dominated the early bloom, but were replaced by the dinoflagellates cf. *Scrippsiella hangoei* and *Peridiniella catenata* when inorganic nitrogen was depleted above the seasonal pycnocline at ca. 10 m depth. By late April, vertically migrating dinoflagellates had depleted inorganic nitrogen down to 30 m, well below the seasonal pycnocline. We found clear species-specific sedimentation patterns. *Scrippsiella hangoei* and *Chaetoceros* spp., which dominated in the water column, were clearly underrepresented in the traps, while *Thalassiosira baltica* and *T. levanderi*, which were sparse in the water column, were overrepresented in sediment traps. Only 4, 3 and 0.5 g C m^{-2} (or 16, 12 and 2% of phytoplankton primary production) settled as intact phytoplankton cells at 25, 50 and 100 m, respectively, although these numbers may be overestimated due to migrating *P. catenata*. The settling bulk carbon was ~3 g C m^{-2} or 12% of the primary production at all depths. This is low compared to other estimates from coastal waters and suggests additional loss mechanisms, e.g. disintegration in the water column and grazing by zooplankton overwintering in the permanent halocline area.

KEY WORDS: Phytoplankton · Spring bloom · Sedimentation · Diatoms · Dinoflagellates · Vertical distribution · Baltic Sea

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INTRODUCTION

Spring blooms are conspicuous events in temperate waters. In a few weeks, most of the easily available inorganic nutrients in the upper water column are consumed and the phytoplankton biomass produced disappears almost as quickly as it appeared. Due to the low biomass of zooplankton in spring and, therefore, low grazing pressure (von Bodungen et al. 1981, Kuparinen et al. 1984, Larsson et al. 1986b), sedimentation is thought to be the predominant loss process of spring blooms (Reynolds & Wiseman 1982, Riebesell 1989). This flux of newly produced phytoplankton cells to the sediments is considered the main supply of food to the benthic system in the Baltic Sea (Elmgren 1978). Due to species-specific sedimentation (Passow 1991a, Heiskanen 1998, Tallberg & Heiskanen 1998), the species composition of the spring phytoplankton bloom influences both the quantity and quality of material settling to the benthos (Passow 1991a, Heiskanen & Kononen 1994, Olli & Heiskanen 1999). Rapidly settling diatoms can reach the sediment relatively intact (Davies & Payne 1984) and are, therefore, high quality food for benthic deposit feeders (Òlafsson & Elmgren 1997, Lehtonen & Andersin 1998). With the exception of settling resting cysts (Heiskanen 1993), dinoflagel-

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lates seem instead to disintegrate in the water column and settle as unidentifiable detritus (Heiskanen & Kononen 1994, Olli & Heiskanen 1999), or be retained as suspended particles or dissolved organic matter in the water column (Heiskanen 1998). Whether diatoms or dinoflagellates dominate the spring bloom may thus greately influence the input of carbon to the deep water.

In the Baltic Sea, most studies of particle settling are from coastal areas (e.g. Smetacek et al. 1978, Smetacek 1980, Forsskåhl et al. 1982, Larsson et al. 1986b, Heiskanen & Kononen 1994), where resuspended particulate material may bias estimates of flux as well as of composition of settled material (Blomqvist & Larsson 1994). In the offshore Baltic Sea, flux estimates are less likely to be influenced by resuspension, but since few studies are available (Leppänen 1988, Leppänen & Kononen 1988, Passow 1991a, Struck et al. 2004), our understanding of the settling dynamics is limited (Blomqvist & Heiskanen 2001).

Use of particulate organic carbon (POC) and nitrogen (PON) for measurements of bulk settling material (e.g. Leppänen 1988) mean that both detritus and resuspended material will be included in the flux estimates (Horn & Horn 1993). By combining these measurements with microscope identification, and counting of phytoplankton cells in water column samples and sediment trap material, it is possible to estimate the amount of settled newly produced material (Horn & Horn 1993). It is also possible to identify whether carbon fluxes are severely biased by migrating species entering the traps (Heiskanen 1995, 1998).

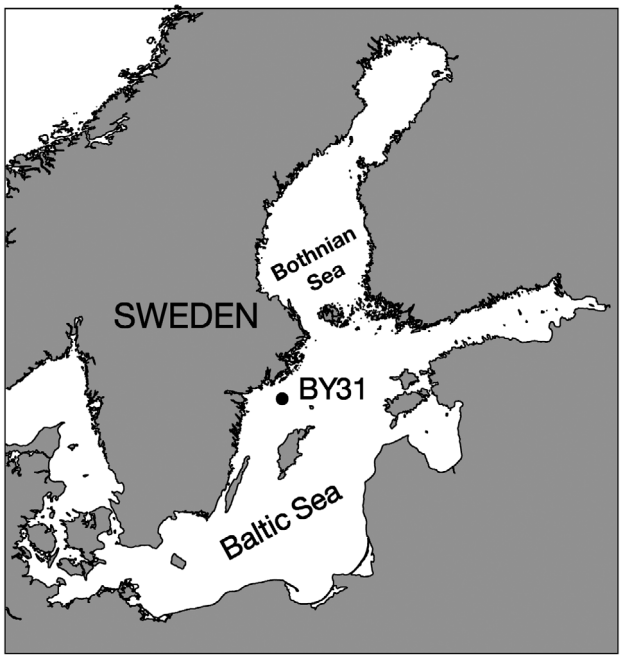

Fig. 1. Location of the sampling station BY31 (Landsort Deep), NW Baltic Sea proper

This study of the spring phytoplankton bloom in the offshore Baltic Sea proper aimed to quantify the settling flux of carbon and how it was influenced by the species composition of the bloom. The study site, the Landsort Deep, is the deepest in the Baltic Sea (459 m) and has a well-studied phytoplankton species composition (Larsson & Hajdu 1997, Hajdu 2002). We quantified the contribution of different species to the spring vertical carbon flux using microscopical analysis of phytoplankton in the water column and in settled material as well as carbon analysis of settled particulate organic carbon (POC). We focused on the diatoms and dinoflagellates, which dominate the spring phytoplankton biomass and are easily recognisable in microscopic analysis.

MATERIALS AND METHODS

Phytoplankton and sedimentation. We sampled the Landsort Deep station (BY31, 58° 35′ N, 18° 14′ E, depth 459 m, Fig. 1) weekly during the 1996 spring bloom (March 26 to May 7). Phytoplankton samples were taken at 0, 2.5, 5, 10, 20, 30, 40, 50, 60 and 80 m with serial 5 l water samplers (Hydrobios). Subsamples of 200 ml were immediately preserved with acetic Lugol's solution (0.75 ml Lugol 200 ml^{-1} seawater). Settling material was collected in gimbal suspended cylindrical sediment traps (dual cylinders with inner diameter of 10.5 cm, height 50 cm, Larsson et al. 1986a) from March 26 to May 21. Before deployment, 2 ml of chloroform was added as preservative. The traps were moored at 25, 50 and 100 m depth, 5 n miles east of BY31 (58° 36′ N, 18° 23′ E, depth 180 m) to reduce the impact of long anchor lines on the vertical position of traps exposed to currents. We have no indication of systematic differences between the 2 locations that would jeopardize comparison of water column and sediment trap data.

One set of traps was emptied weekly from March 26 to May 7, and finally on May 21 for counts and identification of settling cells. The April 23 to 30 sample from 25 m depth was lost. Upon retrieval, water was siphoned from the trap cylinders and the remaining sediment with some water was allowed to settle overnight in Imhoff funnels in darkness at 5°C. The clear supernatant was siphoned off and the remaining aliquot diluted to 199 ml with (filtered) seawater and 1 ml acetic Lugol's solution. Two more sets of traps were used to collect material for carbon analysis and were emptied every second week (March 26 to May 21). Settling material from the 2 trap cylinders per set was pooled to obtain enough material for analysis.

Zooplankters were removed with a 250 µm net and the remaining sample treated as described in Blomqvist & Larsson (1994). Carbon content was determined with a LECO CHN-analyser (CHN-900, 600-800-300, EDTA as standard).

Dominating phytoplankton species (diatoms and dinoflagellates) in the water column and sediment trap samples were counted after sedimentation in settling-chambers (10 to 50 ml), using an inverted microscope (Leica DM IRB and Wild M-40). Before enumeration, sediment trap samples were diluted with 7 ppt NaCl solution to obtain a suitable cell density. A magnification of 100 to 300× was used for cell counts and 200 to 600× for size measurements. A minimum of 50 units (cells or colonies) of the dominating species were counted and measured per sample, giving a maximum counting error of ±28% (corresponding to a 95% confidence limit for the counts) (Lund et al. 1958, HELCOM 1988). We used linear interpolation to calculate cell densities in the depth intervals 0–25, 25–50 and 50–100 m (as cells m^{-2}). Cell densities at 25 m depth were calculated as the mean of densities at 20 and 30 m, and cell densities at 100 m were assumed to be the same as at 80 m depth. Phytoplankton cell volumes were calculated from size measurements according to Edler (1979), with modifications given in HELCOM (1988). Mean cell volumes were calculated for every species for each sampling date, depth and depth-interval based on cell size measurements. Cell volumes were converted to carbon according to Menden-Deuer & Lessard (2000). Compared to carbon calculations according to Edler (1979), commonly used in publications from the Baltic Sea region, Menden-Deuer & Lessard (2000) gives 15 to 30% higher carbon content for diatoms encountered in this study, while the carbon content of dinoflagellates are about the same (±4% compared to Edler 1979).

Daily sedimentation loss rates for the phytoplankton species were calculated as the proportion (%) of the average cell concentration (cells m^{-2}) in the 0–25 m water column (standing stock) that was recovered per day in the 25 m sediment trap.

Hydrography. Salinity (PSU) and water temperature were measured with a CTD-probe (Meerestechnik Elektronik) and water density calculated as sigma-t (σ_t). We assumed that the mixed layer extended down to the top of the seasonal pycnocline (the depth where σ_t changed more than ~0.03 m^{-1}). Water for inorganic nutrient analysis was taken from 0, 5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80 and 100 m depth with serial 5 l water samplers (Hydrobios). Standard flow injection analysis (QuikChem® 8000 Method 31-115-01-3-A, 31-107-04-1-A, 31-107-06-1-A and 31-115-01-3-B Lachat Instruments) was used to measure dissolved inorganic phosphorus (DIP), nitrogen (DIN) ($NO_2^- + NO_3^- + NH_4^+$) and silica (DSi). A nutrient was considered depleted when its concentration was close to the detection-limit (DIP; 0.015 µM, DIN; 0.05 µM, DSi 0.1 µM).

Phytoplankton primary production. Rates of ^{14}C-uptake were determined in 80 ml polycarbonate bottles at 0, 1, 2, 4, 6, 8, 10, 12.5, 15, 20, 25 and 30 m depth (production below 20 m low, <0.6 µg C l^{-1}), with dark bottles at 0, 4 and 25 m. Each bottle received 4 µCi of carrier-free $NaH^{14}CO_3$. After *in situ* incubation for ca. 4 h around noon, 10 ml sub-samples of unfiltered seawater were transferred to glass scintillation vials, 2 drops of 1 M HCl added and bubbled with air for at least 30 min before adding 10 ml of Lumagel Safe (Lumac LSC B.V.) and counting in a Tri-Carb 1600 TR (Packard).

Total carbon dioxide concentration and carbon uptake was calculated according to Öström (1974). Dark uptake was calculated by linear interpolation between the incubation depths and subtracted from the light uptake. Daily primary production was calculated by multiplying by total daily insolation and dividing by insolation during the incubation period. Integrated ^{14}C uptake rates were linearly interpolated over depth.

Chlorophyll *a*. Chlorophyll *a* samples (2 l) from 0, 5, 10, 15, 20, 30, 40, 50, 60 and 80 m, (3 ml magnesium hydroxide carbonate, 10 g l^{-1} added per sample) were collected on Whatman GF/F filters (47 mm Ø), which were wrapped in aluminium foil and stored frozen (–20°C). Filters were homogenised in 90% acetone with a piston grinder, centrifuged and the clear supernatant analysed in a Hitachi U2000 spectrophotometer. Calculations followed Jeffrey & Humphrey (1975).

Contour plots. Contour plots of the vertical distribution patterns of environmental variables and phytoplankton species were generated in Surfer® 8.0 using triangulation with linear interpolation.

Statistics. ***Approximation of coefficient of variation for the phytoplankton biomass:*** Biomass of individual phytoplankton species was calculated as the product of cell abundance and the estimated mean cell volume for each sample depth. Since time restrictions prevented replication and it was assumed that the 2 measurements were independent, we used the propagation of error formula (Rice 1993) to estimate variation of the biomass estimates:

$$C_b \approx \sqrt{C_a^2 + C_v^2 / n} \quad (1)$$

where C_b, C_a and C_v are the coefficients of variation for biomass, cell abundance and cell volume, respectively and n is the number of counted cells.

If we assume that the cell abundance is Poisson-distributed, then $C_a = \sqrt{1/n}$ (Lund et al. 1958, Venrick 1978). For each sample, a minimum of 50 units were counted and measured, resulting in a C_a of maximum 14%.

The coefficient of variation for the cell volume (C_v) was estimated from cell volume measurements for all species and equalled 45%. Insertion in Eq. (1) gives a maximum coefficient of variation for the biomass (C_b) of 15.5%. The addition of the volume measurement error only increased the biomass coefficient of variation from 14 to 15.5%, i.e. the main contribution to the biomass error is from the number of counted cells per sample.

Comparisons of phytoplankton carbon (PC) and total particulate organic carbon (POC) in sediment traps: Estimates of phytoplankton carbon were assumed to have the same maximum coefficient of variation (C_{PC}) as biomass (C_b 15.5%) since it was calculated by multiplying biomass with a fixed factor.

The total particulate organic carbon was estimated from duplicate samples and we used all samples to estimate the coefficient of variation to C_{POC} = 9.1%.

Approximate 95% confidence intervals for PC and POC were calculated using the estimated coefficients of variation and assuming normally distributed data.

For each depth, the ratio PC/POC was calculated and a test was made of the hypothesis that all particulate organic carbon found in a sediment trap is phytoplankton carbon, i.e. H_0: PC/POC = 1. The coefficient of variation for this ratio ($C_{PC/POC}$) was calculated according to Eq. (1) and gave:

$$C_{PC/POC} \approx \sqrt{C_{PC}^2 + C_{POC}^2} = \sqrt{0.155^2 + 0.091^2} \approx 0.18$$

The test was done assuming normally distributed data and the test score used was:

$$z = [(PC/POC) - 1]/(C_{PC/POC} \cdot PC/POC)$$

p-values < 0.05 were regarded as significant.

RESULTS

Hydrography and nutrients

The water temperature in the top 30 m of the water column was near 0°C in March (Fig. 2a), gradually increasing to about 3.5°C in mid-May. A seasonal pycnocline gradually formed due to salinity stratification of the surface water, with mixed layer depth decreasing from 30 to about 15 m by mid to late March, and then varying between 5 and 20 m (Fig. 2b, c). Mixed layer salinity varied from 6.2 to 6.8 (Fig. 2b) with occa-

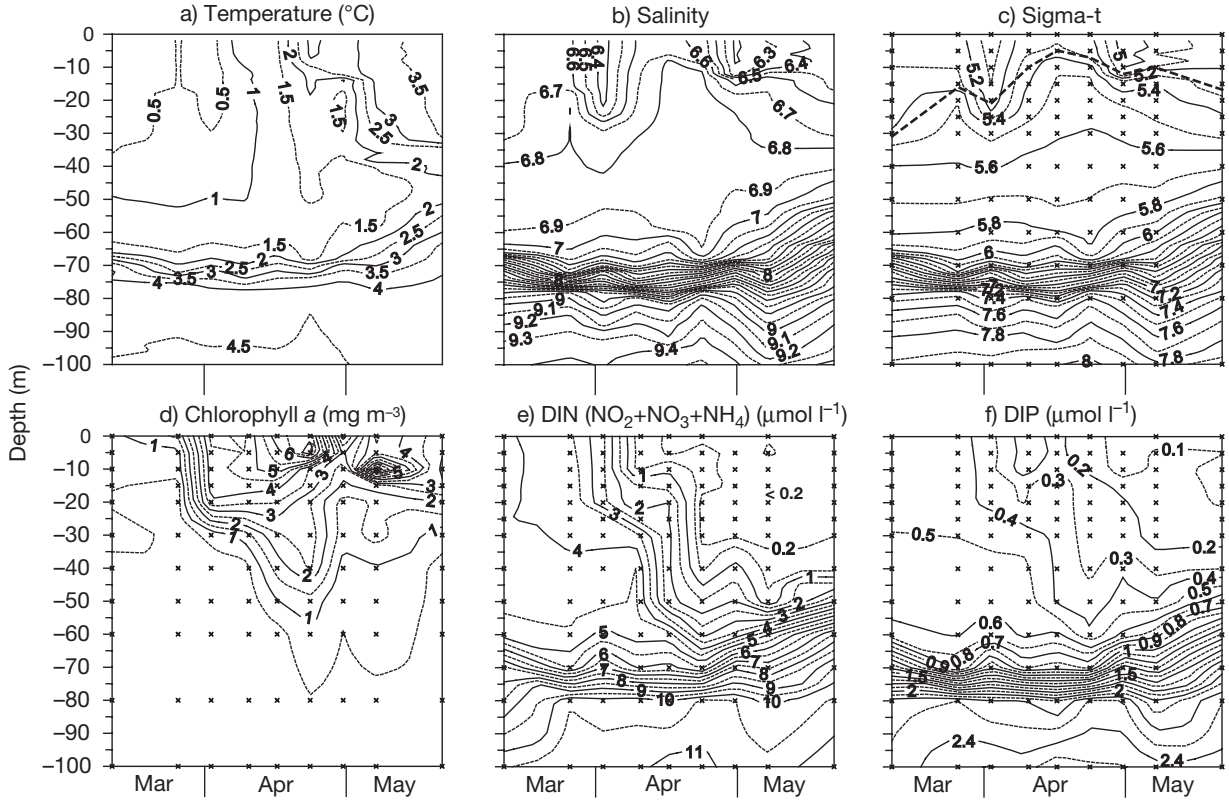

Fig. 2. Hydrography and dissolved inorganic nutrients at the sampling station March to May 1996. (a) Temperature (°C), (b) salinity, (c) sigma-t with mixed layer depth indicated by a broken bold line, (d) chlorophyll *a* (mg m^{-3}), (e) nitrogen (DIN = NO_2 + NO_3 + NH_4) (µmol l^{-1}) and (f) phosphate (DIP = PO_4) (µmol l^{-1}). Sampling depths indicated by × in c–f

sional drops indicating spring flood influence from coastal sources or low salinity water from the Bothnian Sea to the north. Water temperature and salinity remained relatively stable below the mixed layer, and down to the permanent halocline at 60 to 80 m depth (Fig. 2a, b).

The spring phytoplankton bloom commenced in early April, when chl *a* increased 4-fold from 1 to 4 mg m^{-3} (Fig. 2d). By mid April, the dissolved inorganic nitrogen (DIN) was depleted in the mixed layer and 2 wk later to 30 m depth (Fig. 2e). Nitrogen controlled the spring bloom since neither DIP (Fig. 2f) nor silica were depleted (silica decreased from 14 to 9 µM, data not shown).

Vertical distribution of common diatoms and dinoflagellates

Initially, the diatoms *Chaetoceros* spp. (mainly *C. wighamii* Brightwell, some *C. holsaticus* Schütt) and *Achnanthes taeniata* Grunow (syn. with *Pauliella taeniata* [Grunow] Round & Basson) dominated in the surface layer (0 to 20 m), while *Thalassiosira levanderi* van Goor, *Thalassiosira baltica* (Grunow) Ostenfeld and *Skeletonema costatum* (Greville) Cleve were sparse (Table 1). Early in the bloom, *A. taeniata* was restricted to the top 30 m, but 3 wk later, a considerable biomass was found below the seasonal pycnocline, down to 50 m depth (Fig. 3a). *Chaetoceros* spp. settled from the mixed surface layer within a week of its peak biomass, with a tendency to biomass accumulation at the top of the permanent halocline and very few cells below (Fig. 3b). Virtually no *S. costatum* (Fig. 3c) or *T. levanderi* (Fig. 3d) were found below 30 m depth, in contrast to *T. baltica*, which was found down to 80 m depth especially at the end of the period (Fig. 3e).

Around April 10, the spring bloom dinoflagellate cf. *Scrippsiella hangoei* (Schiller) Larsen increased in biomass (Fig. 3f). Two weeks later, diatoms were virtually absent while another dinoflagellate, *Peridiniella catenata* (Levander) Balech (Fig. 3g), was co-dominant with *S. hangoei* and later, totally dominated the final bloom phase (Fig. 4a). Neither dinoflagellate species was found below 50 m depth, except for a low biomass (3 to 10 mg C m^{-3}) of *S. hangoei* at 60 and 80 m depth in early May (Fig. 4a), but both species had considerable biomass below the upper mixed layer late in the bloom (Fig. 3f, g).

According to data from the regular phytoplankton monitoring at this station, the aforementioned diatom and dinoflagellate species made up 80 to 90% of the total phytoplankton biomass >2 µm during the 1996 spring bloom (Larsson & Hajdu 1997).

Species-specific settling

Sedimentation patterns were species-specific and the proportion of each species in the sediment traps differed from those in the water column (Table 1 & Fig. 4b). *Thalassiosira levanderi* and *T. baltica* were proportionally more, and *Scrippsiella hangoei* and *Chaetoceros* spp. less common in the sediment trap material, than in the water column samples (Table 1 & Fig. 4). Consequently, the first 2 species had comparatively higher sedimentation loss rates than the latter 2 species (Table 2 & Fig. 4b). Of the dinoflagellates, *S. hangoei* was particularly scarce in the sediment trap material (Table 1 & Fig. 4b), while *Peridiniella catenata* dominated in the 0 to 50 m water column late in the bloom as well as in the 25 and 50 m sediment traps, but was virtually absent below 50 m and in the 100 m trap (Fig. 4b).

Early in the bloom, settling was low and the few cells found in the traps were mostly *Achnanthes taeniata* and *T. levanderi* (Fig. 4b). *A. taeniata* biomass peaked in the water column already 1 wk after the bloom start, but occurred in low biomass throughout the bloom (Fig. 4a) and was a substantial part of cells found in traps at all depths (Fig. 4b & Table 1). *T. levanderi* dominated the shallow trap already in the second week and with time, made up a considerable part of the cells in the intermediate and deep traps. *T. baltica* showed a similar settling pattern (Fig. 4b).

Settled phytoplankton carbon and total particulate organic carbon

Sedimentation of phytoplankton carbon as intact cells (PC) and total particulate organic carbon (POC) was low early in the bloom (March 26 to April 10) (Table 3). While POC and PC was similar at 25 m (19 to 24 mg C m^{-2} d^{-1}), the amount of PC decreased with depth and was significantly lower ($p < 0.001$) than POC at 50 and 100 m (Table 3). Following the decline of the diatom bloom in mid-April, sedimentation of both POC and PC increased at all depths. From April 10 to May 7, all the settled POC was equal to PC at 25 and 50 m (Table 3), while less than 25% of the POC could be identified as phytoplankton carbon at 100 m. In May (May 7 to 21), when the diatoms were gone from the water column (Figs. 3 & 4a), POC remained high (>100 mg C m^{-2} d^{-1}), but only 24% of it could be identified as PC at 25 and 50 m, and even less, 10%, at 100 m (Table 3).

Primary production versus phytoplankton sedimentation

During the initial phase of the bloom (March 26 to April 16), little (2 to 7%) of the daily primary produc-

Table 1. Average phytoplankton carbon biomass (mg C m^{-2}) in different depth intervals during the deployment of the sediment traps and phytoplankton biomass in sediment traps (mg C m^{-2} d^{-1}) (March 26–May 21). Percent (%) of total phytoplankton biomass per depth interval or depth in brackets. nd = no data

Species	Date	Water column (mg C m^{-2})			Sediment trap (mg C m^{-2} d^{-1})		
	dd/mm	0–25 m	25–50 m	50–100 m	25 m	50 m	100 m
Achnanthes taeniata	26/03–02/04	573 (53)	25 (34)	0 (–)	5 (54)	1 (58)	0.7 (78)
	02/04–10/04	683 (18)	30 (12)	0 (–)	2 (8)	0.4 (11)	0.6 (31)
	10/04–16/04	190 (5)	53 (8)	13 (10)	20 (35)	33 (52)	0.5 (21)
	16/04–23/04	155 (4)	268 (13)	102 (22)	24 (15)	19 (20)	3 (24)
	23/04–30/04	131 (5)	349 (17)	157 (29)	nd	20 (16)	9 (26)
	30/04–07/05	63 (3)	137 (13)	97 (20)	4 (2)	13 (9)	9 (40)
	07/05–21/05	21 (<1)	17 (2)	56 (11)	0.6 (2)	2 (4)	2 (11)
Chaetoceros spp.	26/03–02/04	274 (25)	34 (46)	0.2 (81)	0.7 (8)	0.2 (7)	0 (–)
	02/04–10/04	1389 (37)	71 (29)	2 (81)	2 (7)	1 (24)	0.5 (28)
	10/04–16/04	1717 (42)	398 (59)	97 (71)	10 (18)	5 (8)	0.3 (14)
	16/04–23/04	615 (17)	399 (19)	266 (58)	4 (3)	12 (13)	3 (23)
	23/04–30/04	87 (3)	75 (4)	231 (42)	nd	3 (2)	15 (43)
	30/04–07/05	52 (2)	34 (3)	65 (13)	0.2 (<1)	2 (2)	4 (17)
	07/05–21/05	7 (<1)	2 (<1)	8 (2)	0.2 (1)	0.3 (<1)	1 (6)
Skeletonema costatum	26/03–02/04	10 (1)	1 (2)	<0.1 (19)	<0.1 (<1)	<0.1 (<1)	0 (–)
	02/04–10/04	23 (1)	2 (1)	0 (–)	0.1 (<1)	<0.1 (<1)	<0.1 (<1)
	10/04–16/04	17 (<1)	1 (<1)	0.1 (<1)	0.3 (<1)	0.2 (<1)	<0.1 (<1)
	16/04–23/04	4 (<1)	0.6 (<1)	0.4 (<1)	0.3 (<1)	0.6 (<1)	0.2 (2)
	23/04–30/04	1 (<1)	1 (<1)	1 (<1)	nd	0.1 (<1)	0.6 (2)
	30/04–07/05	1 (<1)	0.8 (<1)	1 (<1)	<0.1 (<1)	0.1 (<1)	0.3 (1)
	07/05–21/05	0 (–)	0 (–)	0 (<1)	<0.1 (<1)	<0.1 (<1)	<0.1 (<1)
Thalassiosira baltica	26/03–02/04	62 (6)	4 (5)	0 (–)	1 (12)	0.4 (16)	0.2 (22)
	02/04–10/04	95 (3)	13 (5)	0 (–)	3 (10)	0.2 (6)	0.2 (9)
	10/04–16/04	83 (2)	44 (7)	8 (6)	10 (17)	6 (10)	0.3 (11)
	16/04–23/04	86 (2)	88 (4)	50 (11)	16 (10)	7 (7)	0.7 (5)
	23/04–30/04	96 (3)	98 (5)	98 (18)	nd	21 (17)	3 (7)
	30/04–07/05	62 (3)	81 (8)	108 (22)	3 (2)	16 (10)	3 (12)
	07/05–21/05	5 (<1)	69 (6)	106 (20)	3 (11)	4 (9)	3 (18)
Thalassiosira levanderi	26/03–02/04	51 (5)	7 (9)	0 (–)	2 (24)	0.4 (16)	0 (–)
	02/04–10/04	98 (3)	27 (11)	0.4 (19)	20 (74)	2 (58)	0.2 (12)
	10/04–16/04	63 (2)	29 (4)	5 (4)	9 (16)	16 (26)	1 (43)
	16/04–23/04	15 (<1)	10 (<1)	9 (2)	8 (5)	26 (28)	5 (37)
	23/04–30/04	0.6 (<1)	2 (<1)	4 (1)	nd	2 (2)	6 (17)
	30/04–07/05	0.2 (<1)	0 (–)	0 (–)	0 (–)	0 (–)	0.5 (2)
	07/05–21/05	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0.1 (1)
Peridiniella catenata	26/03–02/04	66 (6)	2 (3)	0 (–)	<0.1 (<1)	0.1 (4)	0 (–)
	02/04–10/04	195 (5)	7 (3)	0 (–)	0 (–)	<0.1 (<1)	0.4 (20)
	10/04–16/04	272 (7)	17 (3)	0 (–)	8 (13)	3 (5)	0.3 (11)
	16/04–23/04	704 (20)	487 (24)	18 (4)	110 (67)	29 (31)	1 (9)
	23/04–30/04	1041 (36)	624 (31)	18 (3)	nd	75 (59)	0.6 (2)
	30/04–07/05	1759 (84)	594 (57)	41 (8)	144 (93)	105 (68)	0.2 (<1)
	07/05–21/05	2560 (94)	887 (76)	81 (15)	19 (71)	33 (73)	0.2 (1)
Scrippsiella hangoei	26/03–02/04	45 (4)	1 (1)	0 (–)	0.1 (1)	<0.1 (<1)	0 (–)
	02/04–10/04	1277 (34)	98 (39)	0 (–)	0.2 (<1)	<0.1 (<1)	0 (–)
	10/04–16/04	1774 (43)	128 (19)	14 (10)	0.1 (<1)	0.1 (<1)	<0.1 (<1)
	16/04–23/04	1953 (55)	818 (40)	18 (4)	0.5 (<1)	<0.1 (<1)	<0.1 (<1)
	23/04–30/04	1522 (53)	885 (44)	42 (8)	nd	5 (4)	1 (3)
	30/04–07/05	162 (8)	192 (19)	178 (36)	3 (2)	17 (11)	6 (27)
	07/05–21/05	145 (5)	186 (16)	280 (53)	4 (14)	6 (14)	10 (63)

tion settled as intact identifiable cells (Table 4). After the diatom peak in mid April, this fraction increased to 40% (Table 4). The total amount of carbon, estimated from cell counts, that settled into the 25 m trap during the whole spring period (26 March to 7 May) was 4 g C m^{-2} or 16% of the primary production (24.9 g C m^{-2}, Table 5). A similar amount, 3 g C m^{-2} or 12% of the primary production, was estimated for the sediment trap at 50 m, while only 0.5 g C m^{-2} or 2% of the primary production reached the 100 m sediment trap below the halocline in the form of intact cells (Table 5). The settled total particulate organic carbon (POC) (Table 5)

was 3.0 to 3.1 g C m^{-2} for the same period at all 3 depths, i.e. only 12% of the primary production settled as POC.

DISCUSSION

Settling of spring bloom primary production

Temperate spring phytoplankton blooms are considered to export a considerable fraction of the primary production (PP) to deeper waters, but reported variability is large. Wassmann (1991), when compiling data from the Baltic Sea, Norwegian fjords and the Atlantic Ocean, found that between 14 and 85% (average 46%) of the spring bloom primary production settled out. Most of the data were of coastal origin and potentially biased by resuspension (Blomqvist & Larsson 1994). Methodological differences (trap designs, preservatives, exposure time etc.) further complicate comparison of different studies (Hargrave & Burns 1979, Bloesch & Burns 1980, Gardner 1980, Blomqvist & Håkansson 1981). Much variability may also stem from differences in food-web structure affecting sedimentation loss (Peinert et al. 1989, Wassmann 1998). Our results indicate a mixed layer spring settling loss at the lower end (4 g C m^{-2} or ~15% of PP) given by Wassmann (1991). Stigebrandt (1991) used 25 yr of oxygen measurements and calculated oxygen fluxes through the sea surface to estimate net production of organic matter in the top 15 m of 2 Baltic Sea proper sub-areas to 38 and 49 g C m^{-2} yr^{-1}. Earlier, Rahm (1987) arrived at a similar export production estimate of 50 g C m^{-2} yr^{-1}, from calculations of below halocline oxygen consumption. Our carbon settling of 3 to 4 g C m^{-2} in spring is less than 10% of the above yearly estimates and may seem low in comparison, and recent calibration of similar traps as used in this study against ^{234}Th flux suggested under trapping in spring by a factor of about 2 (Gustafsson et al. 2004). Struck et al. (2004) arrived at similar new production estimates (28 to 66 g C m^{-2} yr^{-1}, calculated assuming C/N = 8) as above but measured a very low flux of 1 g C m^{-2} (March–May, average 1995–1998) in traps moored at 140 m in the Eastern Gotland Basin. They concluded water column remineralisation to be very effective, particularly below the halocline. In addition to under-trapping, several factors may have added to a low carbon settling in 1996. Available time series suggest a between year variability in primary production of a factor of 2 and PP in 1996 was in the lower end of that range (U. Larsson pers. comm.). This, combined with an early shift from diatoms to dinoflagellates, likely resulted in a low settling loss.

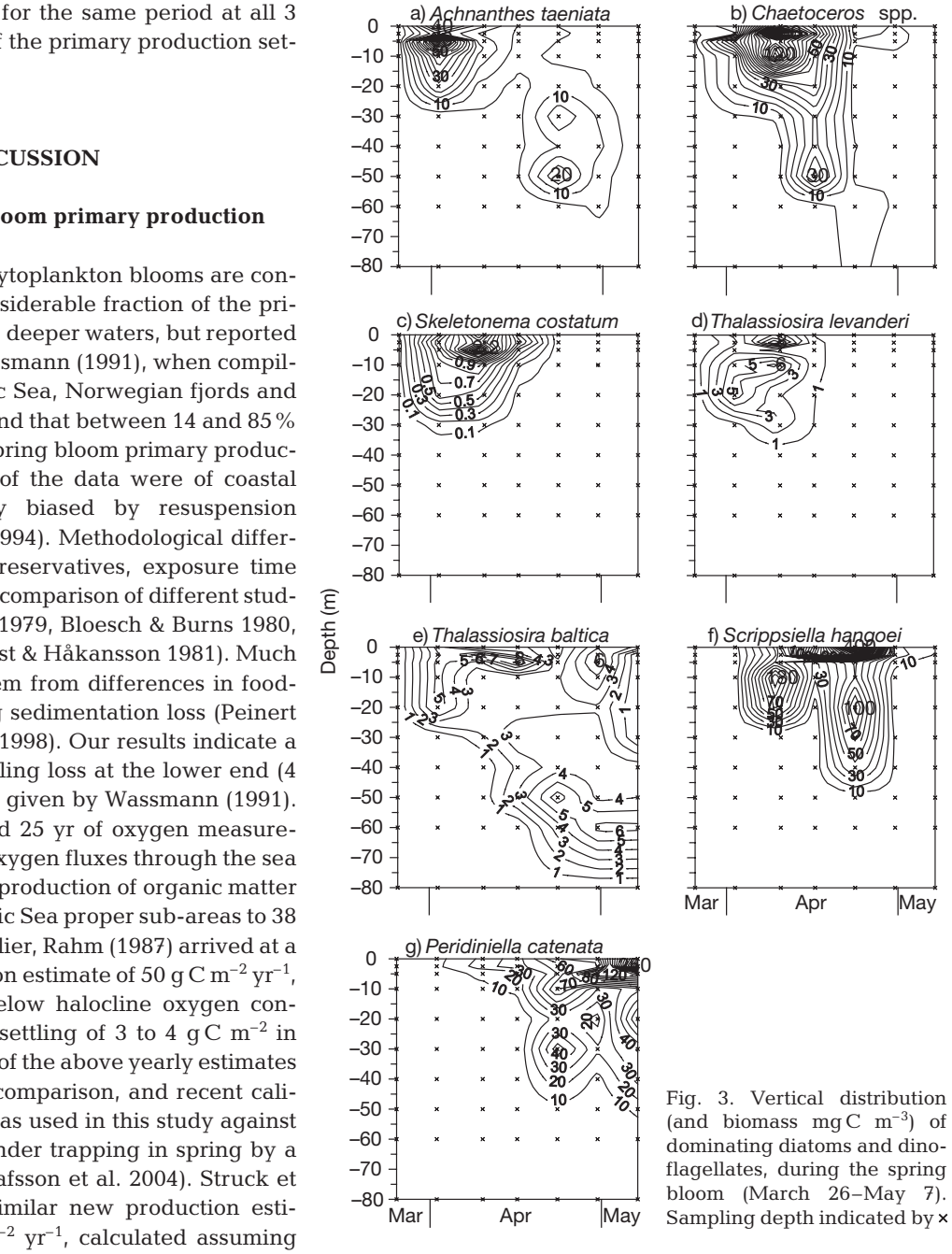

Fig. 3. Vertical distribution (and biomass mg C m^{-3}) of dominating diatoms and dinoflagellates, during the spring bloom (March 26–May 7). Sampling depth indicated by ×

Water column

Kahru & Nômmann (1990) concluded that the spring bloom in the Baltic Sea proper was initiated by salinity stratification and light since the bloom starts before the maximum density temperature (about 2.5°C, Stigebrandt 2001) was reached in the surface water. They found spring blooms in the northern Baltic Sea proper to progress from the coast to the open sea and from north to south, with the central Baltic as the last area to bloom. The salinity stratification is provided by horizon-

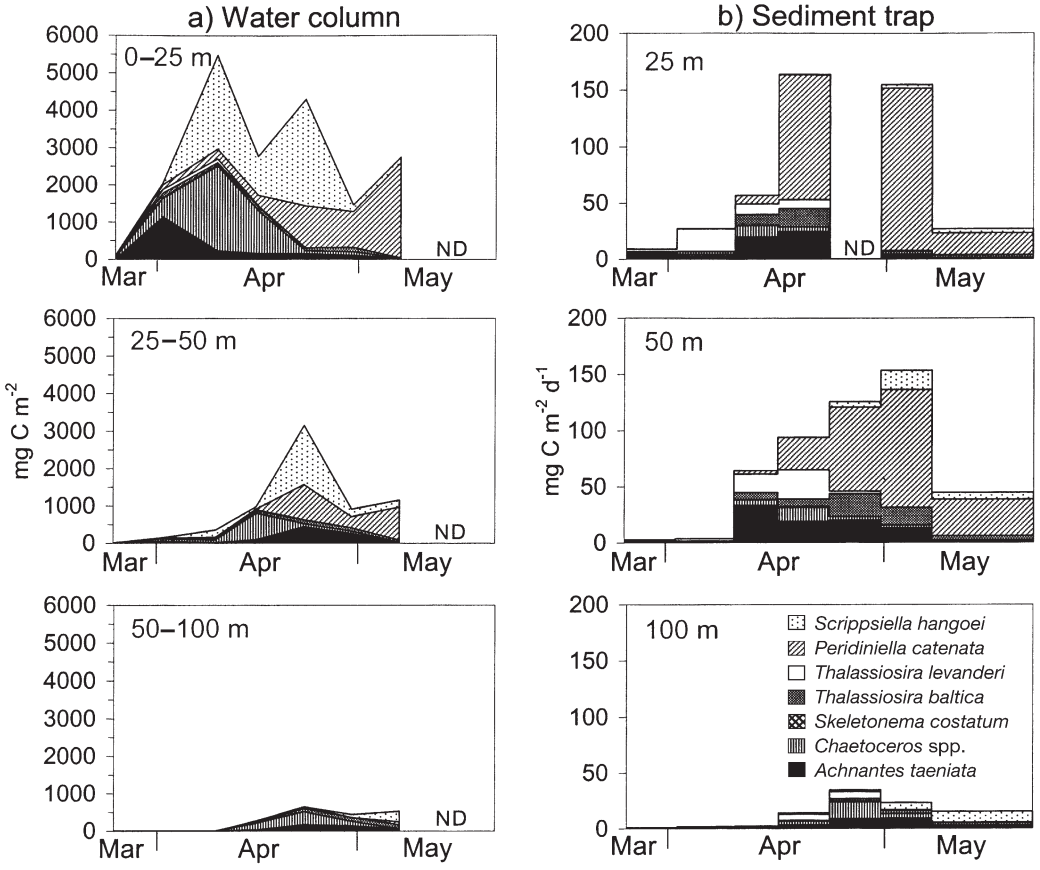

Fig. 4. Species composition in (a) integrated water column samples 0–25, 25–50 and 50–100 m (mg C m^{-2}), and (b) sediment trap samples from 25, 50 and 100 m depth (mg C m^{-2} d^{-1}) during the spring bloom in 1996 at the Landsort Deep station (BY31). (ND = no data)

Table 2. Settling ratio: Percentage (%) of the average cell concentrations in the 0–25 m water column which settles daily at 25 m depth during the studied periods (March 26–May 7). nd = no data

Date	*Achnanthes taeniata*	*Chaetoceros* spp.	*Skeletonema costatum*	*Thalassiosira baltica*	*Thalassiosira levanderi*	*Peridiniella catenata*	*Scrippsiella hangoei*
26/03–02/04	1	<1	<1	2	5	<0.1	<1
02/04–10/04	<1	<1	<1	3	16	≪0.1	<0.1
10/04–16/04	11	<1	2	13	8	2	<0.1
16/04–23/04	17	1	9	22	44	6	<0.1
23/04–30/04	nd	nd	nd	nd	nd	nd	nd
30/05–07/05	6	<1	1	5	≪0.1	7	2

tal advection of lower salinity water (Eilola 1997). This seems to be particularly important in the NW part of the Baltic Sea proper where juvenile freshwater from the Gulf of Bothnia spreads along the Swedish coast, probably in narrow coastal currents (Eilola & Stigebrandt 1998). Such currents may well be responsible for the observed variability in surface salinity with time in the study area, if they change in direction and in salt content. They can also supply the surface water with the buoyancy needed to initiate the spring bloom (Kaiser & Schulz 1978, Smetacek & Passow 1990).

Less saline water originating from the Gulf of Bothnia is expected to carry other phytoplankton species, particularly after a winter with ice cover, as in 1996. The peak of the 'ice-alga' *Achnanthes taeniata* (Heacky et al. 1998) early in the bloom coincided with a marked drop in salinity. After salinity increased again, this species was only present in low abundance, indicating a replacement of the surface water. Although *A. taeniata* was also common in the ice-covered coastal area NW of station BY31 (H. Höglander unpubl. data), the comparatively low freshwater out-

Table 3. Comparison of total settling particulate organic carbon (POC) and settling phytoplankton carbon (PC, estimated from cell counts) from March 26 to May 21. Biomass values in mg C m^{-2} d^{-1} with estimated 95% confidence limits (see 'Materials and methods'). Also given is phytoplankton carbon as % of total settling particulate organic carbon, with estimated 95% confidence limits (see 'Materials and methods'). Hypothesis testing of H_0: POC = PC, i.e. PC/POC-ratio = 1 with standardized normal distribution. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, nd = no data

Date dd/mm	Depth (m)	Total particulate organic carbon (POC) mg C m^{-2} d^{-1}	Phytoplankton carbon (PC) mg C m^{-2} d^{-1}	Phytoplankton carbon as % of POC
26/03–10/04	25	24 ± 4	19 ± 6	79 ± 29
(15 d)	50	24 ± 4	3 ± 1	13 ± 5***
	100	39 ± 7	1 ± 0.4	4 ± 1***
10/04–23/04	25	100 ± 18	114 ± 35	114 ± 41
(13 d)	50	101 ± 18	80 ± 25	80 ± 29
	100	61 ± 11	9 ± 3	14 ± 5***
23/04–07/05	25	99 ± 18	nd	nd
(14 d)	50	95 ± 17	140 ± 43	147 ± 53
	100	123 ± 22	29 ± 9	24 ± 9***
07/05–21/05	25	112 ± 20	27 ± 8	24 ± 9***
(14 d)	50	198 ± 36	45 ± 14	23 ± 8***
	100	154 ± 28	15 ± 5	10 ± 4***
Total	25	82 ± 15	77 ± 24[a]	94 ± 34[a]
26/03–21/05	50	103 ± 19	66 ± 20	64 ± 23**
(56 d)	100	92 ± 17	13 ± 4	15 ± 5***

[a]To estimate total sedimentation at 25 m, we used the averages of April 16–23 and April 30–May 7 to estimate the sedimentation for April 23–30 (where data was missing)

flow to this area and the general circulation in the Baltic makes an influence of this coastal water at the open sea station BY31 less likely.

The decrease in the surface layer diatom biomass (the dominant *Chaetoceros* spp. and the sub-dominant *Achnanthes taeniata*, *Skeletonema costatum*, *Thalassiosira levanderi*), coincided with a decrease in the mixed layer depth during the first 2 wk of April, and depletion of mixed-layer dissolved inorganic nitrogen (DIN) to 10 m depth. Nitrogen depletion is a common cause of diatom bloom collapse in the Baltic Sea (e.g. von

Table 4. Average daily primary production, daily phytoplankton carbon sedimentation (based on cell counts, mg C m^{-2} d^{-1}) and percentage of daily settled primary production (% d^{-1}). (nd = no data)

Date	Primary production (mg C m^{-2} d^{-1})	Sedimentation of phytoplankton carbon (mg C m^{-2} d^{-1})			Percentage of primary production settling as phytoplankton carbon (% d^{-1})		
	0–25 m	25 m	50 m	100 m	25 m	50 m	100 m
26/03–02/04	445	9	2	0.9	2	0.6	0.2
02/04–10/04	756	27	4	2	4	0.5	0.2
10/04–16/04	949	57	64	2	6	7	0.3
16/04–23/04	680	164	94	14	24	14	2
23/04–30/04	315	nd	126	35	nd	40	11
30/04–07/05	441	155	154	23	35	35	5

Table 5. Total primary production, sedimentation of phytoplankton carbon (PC, estimated from cell counts and cell volumes) and total settling particulate organic carbon (POC) for the period March 26 to May 7 (in g C m^{-2} $period^{-1}$) ± 2SD. Percent (%) of the primary production that settled at different depths is in brackets

Date	Primary production (g C m^{-2} $period^{-1}$)	Sedimentation 25 m (g C m^{-2} $period^{-1}$)		Sedimentation 50 m (g C m^{-2} $period^{-1}$)		Sedimentation 100 m (g C m^{-2} $period^{-1}$)	
		PC	POC	PC	POC	PC	POC
26/03–07/05	24.9	4.0 ± 1.2[a] (16)	3.0 ± 0.6 (12)	3.0 ± 0.9 (12)	3.0 ± 0.5 (12)	0.5 ± 0.2 (2)	3.1 ± 0.6 (12)

[a]To estimate total sedimentation for 25 m for the whole spring period, we used averages of April 16–23 and April 30–May 7 to estimate sedimentation for April 23–30 (where data was missing)

Bodungen et al. 1981, Larsson et al. 1986b, Kuuppo et al. 1998). Silica deficiency can also cause the decline of diatom blooms (Bienfang et al. 1982), but was obviously not the cause here, since there was still plenty of silica left in the water column. In contrast to other diatoms, the large-celled *T. baltica* persisted in low abundance throughout the study despite continuous settling losses, suggesting a slow, steady growth in the nitrogen- deficient mixed layer possibly sustained by internally stored nutrients.

A shift from a dominance of diatoms to dinoflagellates during the spring bloom is commonly seen in the investigated area (Larsson & Hajdu 1997, Hajdu 2002), as well as in other parts of the Baltic Sea proper (e.g. Niemi 1973, Kononen & Niemi 1984, Niemi & Åström 1987, Heiskanen & Kononen 1994, Wasmund et al. 1998). Our data indicate that the early shift from non-swimming diatoms to swimming dinoflagellates resulted from the establishment of a shallow mixed layer that limited the fraction of the winter-storage of inorganic nitrogen available to the diatoms and enhanced their sedimentation out of the photic zone. This suggests that the dominance of diatoms in spring is climatically controlled and determined by the balance between the spreading of juvenile freshwater (Eilola & Stigebrandt 1998), which stabilise the water column, and wind-forced mixing.

Scrippsiella hangoei became abundant when DIN was depleted in the surface mixed layer and then continued to increase its biomass and vertical distribution concomitant to an extension of the nitrogen-depleted layer to 30 m depth. Olli et al. (1998) considered *S. hangoei* to be non-migratory and a resident of the nutrient-depleted mixed layer. Our data, however, suggest migration for nutrients to sub-pycnocline waters to sustain the observed increase in biomass. It is not possible to determine to what extent actively migrating cells were responsible for the observed distribution to 40 m depth in late April, but estimates of potential migration amplitudes for similar sized dinoflagellates (Sommer 1988) suggest a substantial contribution from settling cells. A substantial settling is also indicated by the drastic decline of *S. hangoei* a week after the peak. Nutrients at below 30 m decreased further when *Peridiniella catenata*, known to migrate vertically (Passow 1991b, Heiskanen 1995), also built up a substantial biomass and helped to consume most of the DIN down to 40 m depth. The dominance of *P. catenata* late in the bloom suggests they out-compete *S. hangoei* by migrating deeper, since DIN was depleted almost down to 50 m depth. This is consistent with the observation that species (e.g. *P. catenata*) that form cell chains swim faster than single-celled species (Fraga et al. 1989).

Selective sedimentation

Differences in species composition between the water column and the sediment traps indicate large between-species variability in settling. Waite et al. (1992b) found similar differences in settling of the genera *Thalassiosira* and *Chaetoceros* in Auke Bay (Alaska), with higher sedimentation loss rates of *Thalassiosira* than of *Chaetoceros* species. *Thalassiosira* species are nutrient-sensitive (Waite et al. 1992a) and seem to need high nutrient concentrations to sustain rapid growth, to compensate for their high settling rate. *T. levanderi*, with a high growth rate at the beginning of the bloom as well as a high sedimentation rate, disappeared quickly from the water column once nitrogen was depleted in the mixed layer, as has regularly been observed in the area (S. Hajdu, unpubl. data) and also reported by Passow (1991a). Mucus produced by senescent cells (e.g. *T. levanderi*), can induce aggregate formation and greatly increase the settling rate of diatoms (Smetacek 1985). To the extent that aggregate formation occurred, in this case it seemed to be a selective process which did not remove species from the water column. Much of the large-celled *T. baltica* population was found at deeper depths late in the bloom, indicating settlement as intact cells. Thick cells walls and rapid settling presumably prevented this species from disintegrating in the water column while settling. The slow settling of delicate *Chaetoceros* cells may be due to their long hair-like spines, which increase friction and lower sinking rates (Smayda & Boleyn 1966, Brönmark & Hansson 1998). Disintegration of the delicate cells might be another explanation for their low recovery in the sediment traps.

Dinoflagellates have also been found to disintegrate in the water column (Heiskanen & Kononen 1994) and hence, their vegetative cells are seldom found in sediment traps. The colony forming *Peridiniella catenata* was, however, found in the 25 and 50 m sediment traps in about the same proportions as in the water column (Table 1). *P. catenata* is a vertically migrating species (Passow 1991b, Olli et al. 1998) and has been found to actively swim into sediment traps, which may bias the measurements, especially when preservatives are used (Heiskanen 1995). Passow (1991b) found *P. catenata* to migrate to at least 30 m depth, but our water column data indicate they may actually migrate to 50 m depth. We used a preservative (chloroform) and our settling rates of *P. catenata* may be biased by vertically migrating cells. Since *P. catenata* constituted the bulk of settling cells above the halocline, PC and POC settling rates also may therefore be overestimated. Below 50 m and in the 100 m trap we found very few *P. catenata* indicating a very low settling rate or high loss through disintegration or grazing in the halocline layer.

The other dominant dinoflagellate, *Scrippsiella hangoei*, was very abundant in the surface layer, but rare in the sediment traps. *S. hangoei* has very thin and delicate plates (Larsen et al. 1995) and is sensitive to preservatives such as formaldehyde, which cause deformation and dissolution of the cells (Heiskanen 1995). If chloroform has a similar effect, this could explain a low recovery in the traps. *S. hangoei* is reported to form resting cysts that settle rapidly (Heiskanen 1993), but we found no cysts in the sediment traps or in the water column. Cyst formation can be preceded by planozygotes, large cells with a diameter >22 µm according to Kremp & Heiskanen (1999). We found these larger cells throughout the bloom, but they were scarce (<10% of total abundance) and we found no mass production of planozygotes. Cell size remained at a mean diameter of 18 to 19 µm throughout the bloom.

Phytoplankton carbon and total particulate organic carbon (POC) in settling material

Early in the bloom, particulate organic carbon (POC) and phytoplankton carbon (PC) were not statistically different in shallow traps indicating almost all carbon settled as intact cells. On 1 occasion, estimated PC clearly exceeded POC in material collected at 50 m depth. Differences in exposure time and losses due to the preservative used (cf. Kähler & Bauerfeind 2001) may have reduced the carbon content of the settled POC due to longer exposure time (2 wk compared to 1 wk). Over-estimation of PC when converting cell volumes to carbon might be another explanation for the discrepancies between PC and POC.

POC settling rates were very similar at all trap depths when summed over the bloom period (3.0 to 3.1 g C m^{-2}, March 26 to May 7, Table 5) and were only 12% of measured phytoplankton primary production (24.9 g C m^{-2}). Contrary to POC, the fraction of recognisable cells decreased with depth, particularly from 50 to 100 m, as did the number of cells in the water mass. This suggests that diatoms as well as dinoflagellates are rapidly degraded and will settle as unrecognisable detritus or not at all. This is well known for dinoflagellates (Heiskanen & Kononen 1994), but diatoms are generally considered to settle as intact cells (Davies & Payne 1984). During the bloom (March 26 to May 7), only 18% of the POC settled in the 100 m trap could be attributed to recognisable phytoplankton, of which 87% was diatoms.

Predation by mesozooplankton is commonly considered of minor importance in spring due to the low zooplankton abundance (Larsson et al. 1986b), although migrating zooplankton may alter the collected material in the trap, if no preservative is used (Lee et al. 1992). The open Baltic Sea proper has an over-wintering population of *Pseudocalanus* in the deep water, if the water carries sufficient oxygen, even below the permanent halocline (E. Gorokhova pers. comm.) (Ackefors 1969). They start to reproduce in spring and their grazing might explain some of the loss of cells from 50 to 100 m depth. Microzooplankton may also consume a significant fraction of spring phytoplankton in the Baltic proper (Johansson et al. 2004).

Concluding remarks

Our estimated export production is lower than generally reported from coastal waters (e.g. Larsson et al. 1986b, Wassmann 1991, Heiskanen & Leppänen 1995) and suggests that extrapolation from coastal studies may overestimate offshore settling rates. Furthermore, our estimates of settling rates at 25 and 50 m depth were likely biased by trapped vertically migrating dinoflagellates. This bias is counteracted by a likely under-trapping (Gustafsson et al. 2004) and consequently, the absolute magnitude of export production is uncertain.

It is not clear why settling of recognisable cells decreased sharply below 50 m depth, as indicated by cell numbers in the water mass and in traps, but disintegration due to lowered settling rates in the pycnoline and grazing from deep over-wintering zooplankton populations likely contributed.

The low sedimentation of identifiable cells below the halocline and the species-specific sedimentation patterns may complicate the interpretation of paleoecological studies of sedimentary records since settling species composition at depth will not accurately mirror the true surface phytoplankton community.

It is commonly assumed that silica availability determines the dominance of diatoms in spring, but our data indicate that climate factors determining the mixed layer depth, and consequently the amount of nutrients available to non-swimming diatoms, may initiate a decline in diatoms and succession to dinoflagellates even while significant amounts of silica are still present.

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