Vol. 186: 43–57, 1999 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published September 17

Spatial and temporal variability of a dinoflagellate-cyanobacterium community under a complex hydrodynamical influence: a case study at the entrance to the Gulf of Finland

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ABSTRACT: Variability of nutrients and pelagic biological parameters (primary production and chlorophyll *a* [chl *a*] in flagellate and cyanobacterial size fractions, nitrogen fixation, phytoplankton species abundance) was followed for 12 d in July 1996 at an anchor station at the entrance to the Gulf of Finland. Simultaneously, meso-scale physical fields and plankton distribution were mapped over the surrounding 15 × 30 km area. The study period coincided with the intense blooming of a dinoflagellate *Heterocapsa triquetra* Ehrenberg and cyanobacterium *Aphanizomenon flos-aquae* (Linné) Ralfs community. A complex background of hydrodynamical processes was observed in the study area, including downwelling, formation and development of an anticyclonic eddy and jet currents. Our hypothesis was that the horizontal scale of patches decreases and the variation of biological parameters increases when moving from the overall community level (chl *a*) to the size class level and further to the species level. The horizontal distribution of chl *a* was closely related to the different water masses, but the distribution of the 2 dominant species differed and showed high variability even within water masses. The temporal variability of the pelagic biological parameters at the anchor station (estimated by the coefficient of variation) was between 25 and 95% and it may be explained by horizontal patchiness. The results confirmed our hypothesis by showing that the coefficient of variation of summational parameters (total chl *a*, total primary production) was always lower than that of parameters specific to plankton size (chl *a* and primary production in <20 and >20 µm size classes), functional group (diazotrophs) or species. Phytoplankton in the size range equal to or greater than 20 µm exhibited particularly pronounced variability, while the smaller size fractions were less affected.

KEY WORDS: Hydrophysical control · Baltic Sea · Plankton patchiness · *Aphanizomenon flos-aquae* · *Heterocapsa triquetra*

INTRODUCTION

During the last few decades, convincing evidence of the strong physical impact on plankton dynamics has emerged in the marine and freshwater ecological literature. Plankton communities are, by definition, continuously and passively transported by moving fluid. Successional changes are repeatedly interrupted by dynamical processes at the frontal or upwelling/downwelling jets and eddies, as well as by wind-induced turbulence. The structure of the plankton community is thus highly modulated by the growth stimulating and inhibiting effects of physical processes through nutrient transport and changing illumination conditions, and by the mixing of water masses from different origins having different species composition.

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The relationship between plankton growth and the horizontal scale of patchiness was theoretically derived by Kierstead & Slobodkin (1953). On the assumption of a growth rate of 1 division d^{-1}, the minimum scale of horizontal patchiness was estimated to be 1 km. However, different taxonomical, functional and size groups of plankton exhibit different growth rates and susceptibilities to loss factors (e.g. grazing and sedimentation), and on that basis it can be presumed that the horizontal scales differ as well (Kononen & Leppänen 1997). Studies on the horizontal distribution of plankton have revealed that the composition of an individual community is much more unpredictable than that of the overall plankton community, and it tends to be mosaical rather than a smoothly varying continuum (e.g. Mackas et al. 1985). This encourages the hypothesis that, at a fixed position, through which water masses with different scale horizontal patches are continuously moving, plankton organisms with different growth rates show different levels of temporal variability.

Because of the scarcity of methodologies for studying plankton dynamics over a wide range of spatio-temporal scales, plankton ecologists are confronted with the problem of sampling. The time scales of principal pelagic biological processes, such as growth and grazing, are short, which imposes practical difficulties in synoptic field measuring campaigns. Furthermore, in coastal areas wind forcing induces a variety of physical processes which may alter within a few days. As a result, it is difficult to carry out sampling with the temporal and spatial coverage and resolution needed to link phenomena of pelagic biology to hydrophysical phenomena. As a matter of practical necessity, sampling at a fixed station is a widely used strategy in plankton ecology. This strategy has proven to be satisfactory for following the succession in seasonal scale, as shown by several yearly and longer-term investigations on plankton dynamics (e.g. Kononen & Niemi 1984), but only with qualifications is it suitable for studies on a shorter time scale.

Typical to brackish water bodies like the Baltic Sea is the existence and interplay of water masses of different properties. Satellite images and several ship-borne investigations have shown that meso-scale patchiness of the surface layer of the Baltic Sea is pronounced both in physical (Kahru et al. 1995, Pavelson et al. 1997) and in biological (Kononen et al. 1992, 1996, Moisander et al. 1997) fields. Several studies carried out during phytoplankton blooms have revealed a typical patch size of phytoplankton ca 10 to 40 km (Kahru et al. 1991, Kononen et al. 1992, 1996, Moisander et al. 1997), a size that corresponds well with meso-scale hydrophysical structures. In these studies, a good correlation was observed between the spatial distribution of microphytoplankton species and water masses. Very few studies of horizontal patchiness in other groups of organisms have been carried out in the Baltic Sea. As one example, Heinänen & Kuparinen (1991) found the level of variability of pelagic bacteria to be constant in late summer at scales of 0.1 and 1000 km.

In this paper we present the results of a 12 d multidisciplinary field study carried out in late July 1996 at the entrance to the Gulf of Finland. By daylight, nutrients and pelagic biology (primary production in flagellate and cyanobacterial size fractions, nitrogen fixation, phytoplankton species) were measured at an anchor station, and at night the meso-scale physical fields, nutrients and plankton distribution were mapped over an area of 15 × 30 km. Our aims were to evaluate the variability of the pelagic biological parameters at a fixed station during a time period of 10 d, when there were no nutrient inputs from the layer below the thermocline, and to estimate the extent to which the variability could be explained by the succession of meso-scale hydrodynamical processes. Our hypothesis was that the variation of biological parameters increases and the horizontal scale of patches decreases when moving from the overall community level (chl *a*) to the size class level and further to the species level.

MATERIAL AND METHODS

The entrance to the Gulf of Finland is characterized by marked hydrodynamic activity. The salinity distribution in the area is influenced by water exchange between the northern Baltic Proper and the Gulf. In general, the saltier water of the Baltic Proper flows into the Gulf along the southern coast, while the less saline water of the Gulf flows in the opposite direction along the northern coast (Alenius et al. 1998). Studies by Kahru et al. (1986), Kononen & Nõmmann (1992) and Pavelson et al. (1997) have revealed the existence of an east-west oriented quasi-permanent salinity front between these water masses. Wind forcing over the coastal area of the Gulf with its irregular bottom topography causes marked short-time-scale deviations from the general circulation scheme, resulting in a dynamic system characterized by weaker and stronger fronts, upwelling and downwelling, and jets and eddies (e.g. Kononen & Nõmmann 1992, Haapala 1994, Talpsepp et al. 1994).

Measurements were carried out on-board RV 'Aranda' (Finnish Institute of Marine Research) from 15 to 26 July 1996 at the entrance to the Gulf of Finland (Fig. 1). For definition of the observation window and selection of the sampling depths and phytoplankton species to be counted, a large-scale pilot survey was

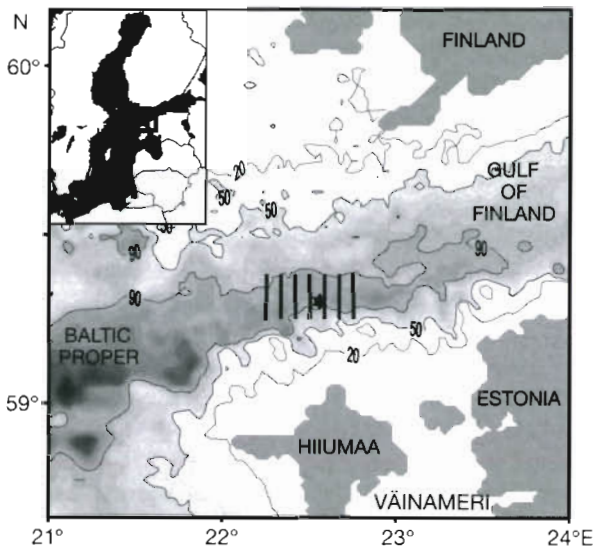

Fig. 1 The study area in the Gulf of Finland. The lines show the idealized ship route during the meso-scale surveys. In reality, the surveys consisted of 3 to 6 successive transects of different length. (*) Anchor station. Depth contours are given in metres

carried out on 15-16 July. This consisted of CTD casts, nutrient sampling and a semi-quantitative analysis of phytoplankton species composition at 12 stations covering an area of ca 45 × 25 km. During 16 to 26 July an intensive study was carried out, involving daytime CTD casts and water samplings at the anchor station (AN; 59° 17' N, 22° 33' E), nighttime towed CTD/chl *a* fluorescence mapping and ship-mounted acoustic Doppler current profiler (ADCP) velocity mapping (except night of 19-20 July) and simultaneous phytoplankton, chl *a* and nutrient sampling with a flow-through (FT) system. The methods and results of the ADCP and towed chl *a* fluorescence mapping are presented in detail by Pavelson et al. (1999).

During the daytime study at the AN, water samples for measurement of phytoplankton, *in situ* primary production and nitrogen fixation were taken daily between 08:00 and 10:00 h local time, at 2.5 m intervals from the surface to a depth of 17.5 m. Sampling was done with a 1.6 m long, 50 l water sampler. Each sample was poured into a 100 l container and mixed continuously until the subsamples for analysis were removed. Chl *a* concentration was measured as fluorescence with a Sea Tech, Inc., fluorometer mounted on a SeaBird 911Plus CTD profiler. The conversion of *in situ* fluorescence to chl *a* was done by applying a relationship derived by linear regression from simultaneous *in situ* measurements of fluorescence and sampling of chlorophyll at different depths. Additionally, a pooled sample representing the upper layer (from the sea surface down to the seasonal thermocline) was prepared for the determination of primary production and chl *a* content in different size fractions. Nutrient samples were taken with a Hydro-Bios 1.5 l sampler from depths of 5, 10, 15, 20, 22.5, 25, 27.5, 30, 32.5, 35, 37.5, 40 and 60 m and near the bottom. During the nighttime surveys, nutrient and phytoplankton samples were taken from an FT system pumping water from a depth of 5 m. The use of a 20 or 30 min sampling interval gave a horizontal resolution of ca 4 or 6 km, respectively.

Dissolved inorganic nutrients (PO_4, NO_3, NO_2 and SiO_4) were determined according to the guidelines for the second stage of the Baltic monitoring programme (BMEPC 1983).

Samples for quantifying phytoplankton species (500 ml) were preserved with Lugol's solution and species were counted with the Utermöhl (1958) technique. Samples taken at the AN were examined superficially for species composition and homogeneous distribution before the counting. Only species appearing in abundance greater that 50 counting units were included in the analysis proper. The 2 most abundant species, *Aphanizomenon flos-aquae* (Linné) Ralfs[1] and *Heterocapsa triquetra* Ehrenberg, which according to the coefficient of variation (CV) also showed the highest temporal variability at the AN, were counted in the samples taken by the FT system. Cyanobacterial filaments were counted as 100 µm segments and other phytoplankton as single cells or colonies. The carbon biomass for species was calculated according to Edler (1979).

Primary production *in situ* was measured by adding 3.7 µCi as $NH_4{}^{14}CO_3$ to 60 ml samples. Duplicate samples and a dark sample were incubated for 24 h *in situ*. For the determination of assimilation number, primary production was also measured in the pooled sample by adding 1.8 µCi to three 30 ml samples and incubating the samples for 2 h at various light levels (12, 25, 50, 70, 100 and 110% of daylight). After incubation, radioactivity in the total sample (particulate production and exudates) was measured in a sample poured through a 20 µm mesh (<20 µm particulate production and exudates) and in a sample collected onto a Whatman GF/F filter (<20 µm particulate production).

Size fractionation for chl *a* was achieved by pouring the pooled sample through a 20 µm mesh. The chl *a* concentration was determined on Whatman GF/F filters after extraction at room temperature in the dark with 96% ethanol for 24 h. The concentration was measured with a Perkin Elmer LS-2B fluorometer (BMEPC 1988).

Nitrogen fixation was measured by acetylene reduction method (Burris 1972). Ninety ml subsamples were

[1]Taxonomy under revision

taken from the 100 l containers (see above) into 118 ml serum vials. After 21 July nitrogen fixation was also measured from 20 µm net samples representing the upper layer. Vials were sealed with crimp seals, 10 ml of acetylene was added and the vials were incubated for 3 h *in situ*. At the end of incubation, 5 ml of gas was withdrawn from each vial and stored in gas-tight evacuated tubes (Exetainers, Labco). Ethylene was measured within a month with a Shimadzu GC 9A gas chromatograph equipped with a flame ionization detector and a Porapak T column with ovenheat of 80°C, and N_2 as carrier gas. Nitrogen fixation was additionally measured in water or net samples taken from the surface layer by $^{15}N_2$ method (Flett et al. 1980, Moisander et al. 1996). Five ml of 98% $^{15}N_2$ was added to 118 ml serum vials filled with water or net samples. After 3 h of incubation *in situ*, the samples were filtered on precombusted GF/F filters and the filters were stored in the freezer. The mass spectrometric analysis for ^{15}N content was performed from freeze-dried samples by Dr Martti Esala (Agricultural Research Centre of Finland, Jokioinen). All nitrogen fixation measurements were made in triplicate or quadruplicate.

RESULTS

Hydrophysical background and nutrient conditions at the anchor station

The temperature of the upper layer increased during the study period from 13.6 ± 0.2 to 15.5 ± 0.2°C. The relatively strong westerly winds (8 to 13 m s^{-1}) which blew from 15 to 17 July caused an intensive downwelling north of Hiiumaa Island. In the offshore direction the downwelling zone with lowered thermocline extended to the northern part of the study area (data

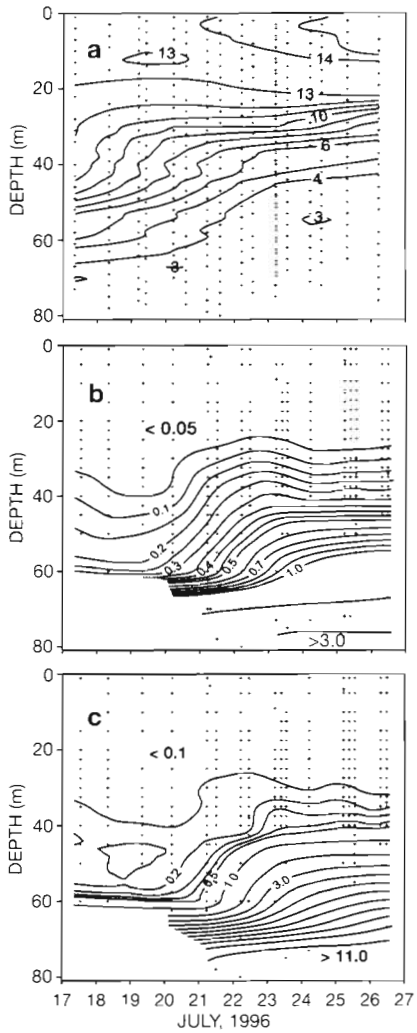

Fig. 2. Temporal vertical distribution of (a) temperature (°C), (b) phosphate and (c) nitrate (µM) at the anchor station. (•) Positions of sampling. Note that contour interval in (b) and (c) is not constant

Table 1. Characteristics of the upper layer at the anchor station for 3 successive periods of differing in hydrophysical conditions. bd: below detection

	Period I 17–19 July	Period II 20–21 July	Period III 22–26 July
Hydrophysical conditions	Downwelling	Periphery of anticyclonic eddy	Cyclonic side of jet
Salinity (psu)	6.65–6.70	6.32–6.37	6.36–6.49
Mean current velocity (cm s^{-1}) and direction	5.9 W	16.5 NW	17.0 NW
Beginning of the thermocline (m)	35	20	26
Upper mixed layer depth (m)	12	9	18
SiO_4 (µM)	5.4–6.8	4.6–4.7	4.7–5.5
Chlorophyll in 0–20 m (mg chl *a* m^{-2})	52–79	47–52	63–69
Total primary production (g C m^{-2} d^{-1})	1.3–2.0	0.8–1.1	1.1–2.1
Primary production >20 µm (% of total)	9–10	23–24	23–29
chl *a* >20 µm (% of total)	14–20	32–33	22–39
Assimilation number <20 µm (mg C m^{-3} h^{-1}/mg chl *a* m^{-3})	0.9–1.7	1.1–1.7	1.0–1.6
Assimilation number >20 µm (mg C m^{-3} h^{-1}/mg chl *a* m^{-3})	0.8–0.9	0.5–1.2	0.5–1.5
Nitrogen fixation (µmol C_2H_2 m^{-2} h^{-1})	bd	bd	21.6–67.4

not shown) and covered the position of the AN, where the thermocline was lowered down to 45 m (Fig. 2a). The downwelling event lasted until 19 July and thereafter the thermocline was found, just as before the downwelling, at about 30 m depth.

During the downwelling a related eastward jet above the lowered thermocline (Fig. 3a–c) passed the AN mainly from the north. The jet carried Baltic Proper water with approximately the same salinity (6.7 psu) as the waters with the same origin to the south of it. Because of the along-shore flow instability induced by the irregular bottom relief (see Fig. 1), a branching of the jet occurred, and by 20 July the southern branch had transformed into a nearly barotropic anticyclonic eddy (Fig. 3d). The fixed limits of the study area enabled only partial mapping of the eddy, i.e. up to the termination of observations only the western part had been covered (Fig. 3d–h). The eddy was about 20 km in diameter and had maximal velocities up to 25 cm s^{-1} and a relatively steady upper layer salinity of ~6.7 psu. On 20 July, fresher open Gulf of Finland water with a salinity of 6.3 to 6.4 psu appeared in the AN area from the south-east, transported in the periphery of the anticyclonic eddy (Fig. 3d,e).

Starting from 22 July until the last mapping, a strong north-west directed jet (to the south of the anticyclonic eddy) flowed through the study area (Fig. 3f,g). The jet was narrow, with a width of 4 to 6 km and a core velocity of about 35 cm s^{-1}. The AN was located on the cyclonic side of the jet, i.e. to the left of the jet looking downstream. The cyclonic side of the jet appeared as a zone of downwelling (e.g. Claustre et al. 1994). In our case the upper isolines were lowered by 6 to 8 m (Fig. 2). Less saline water (6.4 to 6.5 psu), probably caught by the jet in the coastal sea from the shallow Väinameri (see Fig. 1), dominated in the upper layer (0 to 15 m).

A schematic presentation of the hydrodynamical phenomena prevailing during the cruise can be seen in Fig. 4. Table 1 presents the ranges of selected parameters characterising the upper layer at the AN during 3 periods of differing physical processes.

The nutrient concentrations were typical of late summer conditions, with inorganic phosphorus and nitro-

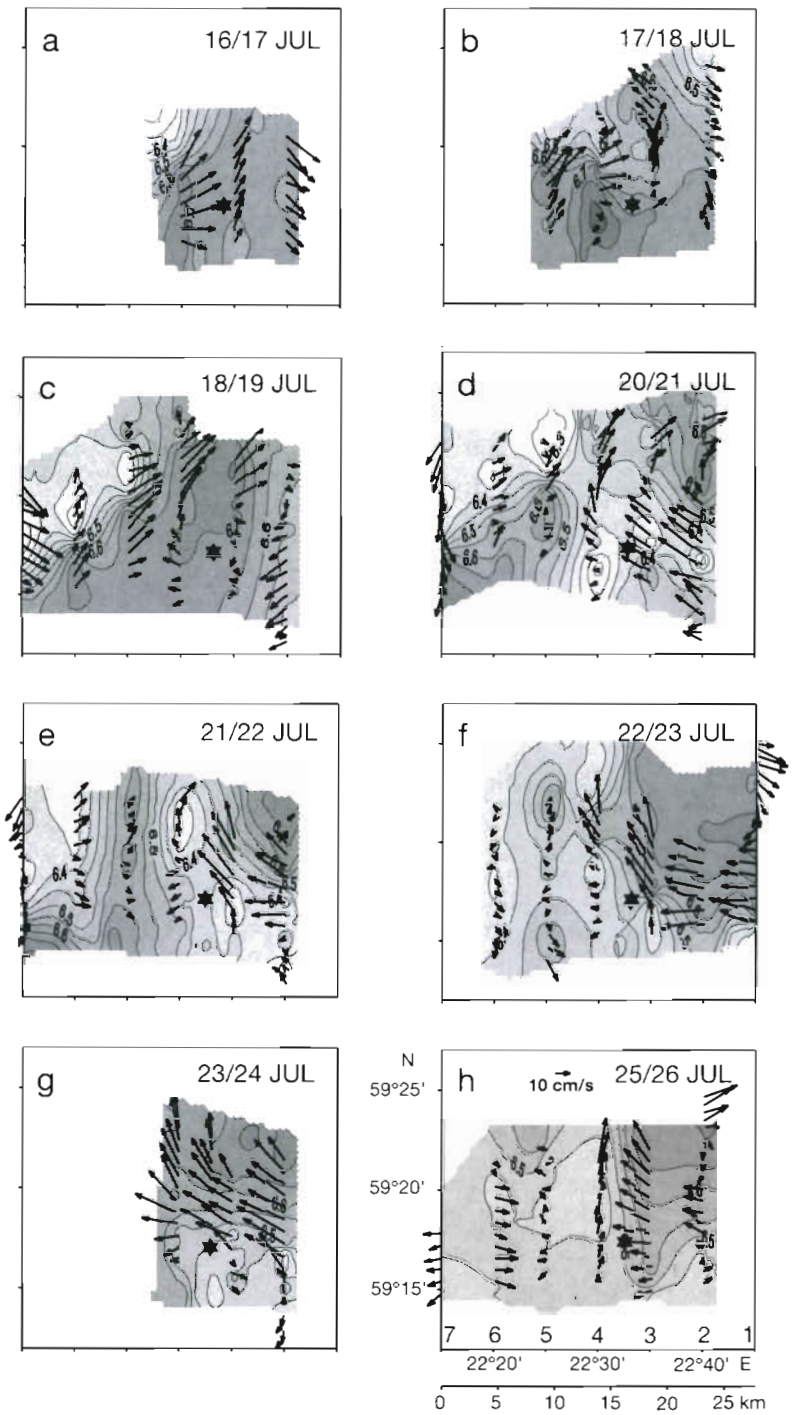

Fig. 3. Horizontal distributions of salinity at a depth of 5 m overlaid with the current vectors from the shipboard ADCP at a depth of 12 m on successive dates. The scale of current vectors is presented in (h) (figure redrawn from Pavelson et al. 1999)

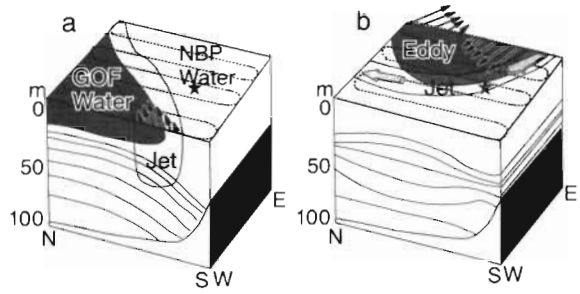

Fig. 4. A schematic presentation of the main hydrodynamical processes and phenomena during the study period: (a) downwelling and related jet, and (b) anticyclonic eddy and jet in its periphery. Parallel dotted lines on the upper faces: transects followed by the towed CTD/fluorometer; (★) position of the anchor station. Lines on the front faces indicate the isopycnals (though in b they actually belong to the back face). The thin arrows show the flow pattern in the downwelling related jet (a) and the anticyclonic eddy (b), and the thick arrows in (b) show the flow in the jet in the eddy periphery. In (a) GOF is the Gulf of Finland and NBP the northern Baltic Proper

gen below the detection level in the near-surface layer. Owing to scarcity of diatoms in the plankton community, there was a relatively high concentration, 4.6 to 6.8 µM, of silicate in the surface layer (Table 1). The vertical nutrient distribution reflected the hydrodynamical forcing during the study period. The temporal course of the vertical distributions of phosphate and nitrate is presented in Fig. 2b,c. Owing to the downwelling at the beginning of the study, the layer exhausted of PO_4 and NO_3 (<0.1 µM) extended down to 40 m, but after the relaxation of the downwelling it extended only to 25–30 m. The SiO_4 concentrations observed in the upper layer at the AN (except on 17 July) were within the range of the mean ± standard deviation (SD) estimated from the preceding or following meso-scale survey data (Fig. 5a). The horizontal distribution of the SiO_4 concentrations at 5 m depth (Fig. 6) was significantly correlated with the salinity distribution ($r^2 = 0.38$, $p < 0.0001$), indicating a clear relationship with the water masses.

Variability of pelagic biology at the anchor station and in the surrounding area

The temporal development of the vertical distributions of primary production and chl *a* at the AN are presented in Figs. 7 & 8, respectively. Total primary production *in situ* at the AN varied 2.5-fold (0.8 to 2.1 g C m^{-2} d^{-1}, Table 1), and total chl *a* integrated from surface to 20 m depth 1.5-fold (47 to 79 mg chl *a* m^{-2}, Table 1). Lowest values for both were observed on 20-21 July in the flow in the periphery of the anticyclonic eddy. During the downwelling on 17 to 19 July the portion of the <20 µm size fraction was about 90% of the total primary production and 80 to 86% of the total chl *a*, but afterwards only 71 to 77% of the primary production and 61 to 78% of the chl *a* (Table 1). Over the whole study period the variability estimated by CV of both chl *a* and primary production was lower in the smaller size fraction (Table 2). The vertical distribution of chl *a* followed the density stratification. In the downwelling situation the layer containing chl *a* extended down to 50 m depth, whereas after the relaxation of downwelling it occupied only the upper approximately 30 m layer (Fig. 8).

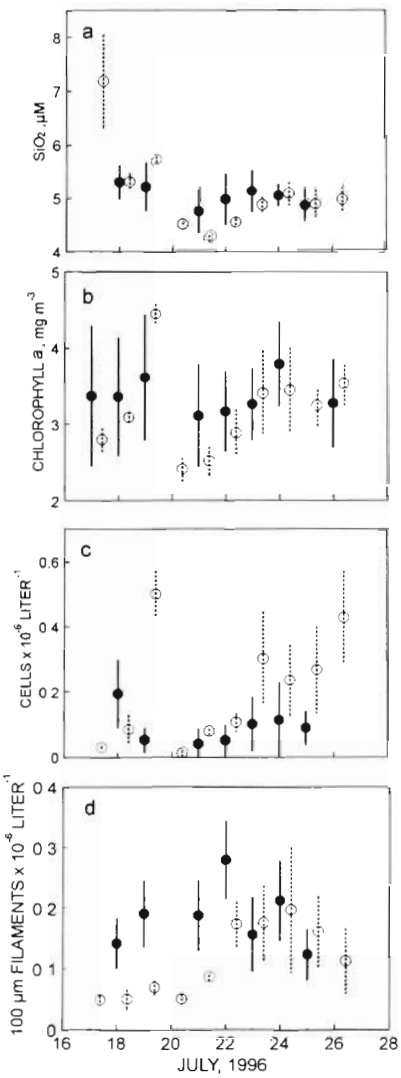

Fig. 5. (a) Concentration of silicate, (b) concentration of chl *a*, (c) abundance of *Heterocapsa triquetra* and (d) abundance of *Aphanizomenon flos-aquae* in the study area. Means and standard deviations in the upper layer at the anchor station (⊕) and at 5 m depth estimated from the meso-scale survey data (♦) are shown. Note that at the anchor station the standard deviation indicates the daytime vertical variability, and in the meso-scale survey it indicates the nighttime horizontal variability

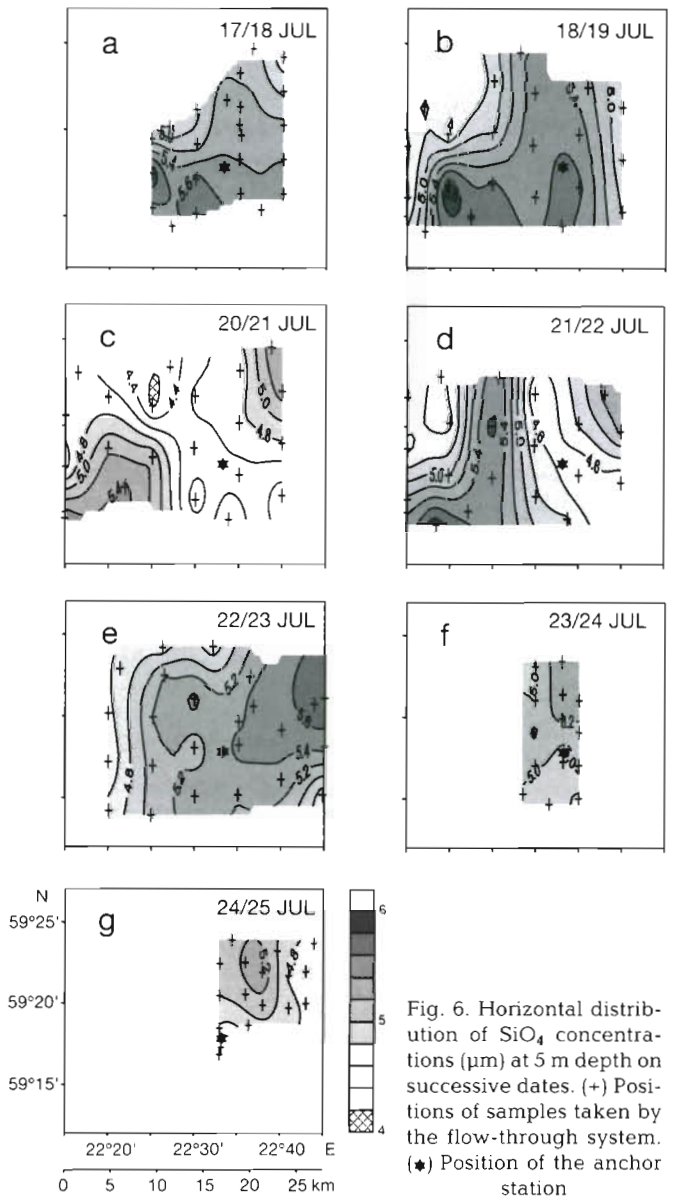

Fig. 6. Horizontal distribution of SiO_4 concentrations (µm) at 5 m depth on successive dates. (+) Positions of samples taken by the flow-through system. (*) Position of the anchor station

The total chl *a* concentrations at the AN were always within the range of the mean ± SD observed during the meso-scale survey (Fig. 5b). The horizontal distribution of chl *a* in the surface layer is presented in Fig. 9. During the downwelling, higher chl *a* concentrations were observed in the southern part of the study area (Fig. 9a,b). The distribution of chl *a* concentrations in the anticyclonic eddy was variable, but the chl *a* concentration was clearly lower in the less saline water from the open Gulf of Finland advecting into the area in the periphery of the eddy on 20-21 July than in the surrounding saltier water masses (Figs. 8 & 9c,d). From 22 July onward the area was affected by the strong north-west directed jet carrying chlorophyll-rich water from the shallow coastal sea (Figs. 8 & 9e–g).

Detectable nitrogen fixation in water samples was found only on 22 to 25 July (not measured on 26 July), when the strong jet passed through the AN (Fig. 7). Nitrogen fixation, integrated over the upper layer, varied between 21.6 and 67.4 µmol C_2H_2 m^{-2} h^{-1} (Table 1). The conversion factor between acetylene reduction and ^{15}N incorporation was 2.5 to 2.9. Acetylene reduction generally decreased as a function of depth. Even at the lowest incubation depths, which were in the dark, nitrogen fixation continued, although at decreased rates.

The dominant phytoplankton species in the study area were *Heterocapsa triquetra* (an average of 25% of the total biomass at the AN), *Aphanizomenon flos-aquae* (16%), *Dinophysis norvegica* Claperede & Lachmann (14%) and *Chrysochromulina* spp. 6 × 8 µm Lackey (12%) (Table 2). The cells of *H. triquetra* were ca 20 to 30 µm long and 15 to 20 µm wide. The 20 µm plankton net used for size fractionation of primary production and chl *a* probably allowed part of the cells of *H. triquetra* to pass through with the smaller flagellates, but retained *A. flos-aquae* filaments. The good and significant correlations of *A. flos-aquae* abundance with chl *a* ($r^2 = 0.79$, $p < 0.001$) and primary production ($r^2 = 0.72$, $p < 0.01$) in the >20 µm size fraction and the weaker correlation of *H. triquetra* with chl *a* ($r^2 = 0.38$, $p < 0.08$) in the <20 µm size fraction support this. Using a carbon to chl *a* ratio of 64, determined in our earlier study in the same area (Kononen et al. 1998), we calculate that *H. triquetra* contributed an average of 19% (range 3 to 55%) of chl *a* in the <20 µm size fraction, and *A. flos-aquae* 24% (range 17 to 33%) of chl *a* in the >20 µm size fraction.

The abundance of *Aphanizomenon flos-aquae*, both at the AN and in the meso-scale survey, increased from 17 to 22–24 July and thereafter decreased (Fig. 5d). Apart from the high abundances at the AN on July 19 and in the FT system on 17-18 July, the abundance of *Heterocapsa triquetra* increased towards the end of the study period (Fig. 5c). With some deviations (21 to 23 July), the vertical distribution of the 2 dominating species coincided with that of chl *a* (Fig. 8). For both *H. triquetra* and *A. flos-aquae*, several mean abundances in the vertical profile measured at the AN deviated sharply from the meso-scale survey mean ± SD (Fig. 5c,d). A marked maximum of *H. triquetra* was observed at the AN on 19 July, whereas the highest abundances in the meso-scale survey were detected on 17-18 July (Fig. 5c) in the downwelling region in the southern part of the study area (Fig. 10a). The regression analysis against latitude on 17-18 July revealed a significant ($p < 0.005$) offshore decrease for both species, with the decrease of *H. triquetra* 3 times that of *A. flos-aquae*.

Beginning on 20 July the spatial distributions of the 2 species differed markedly. The development of patches of

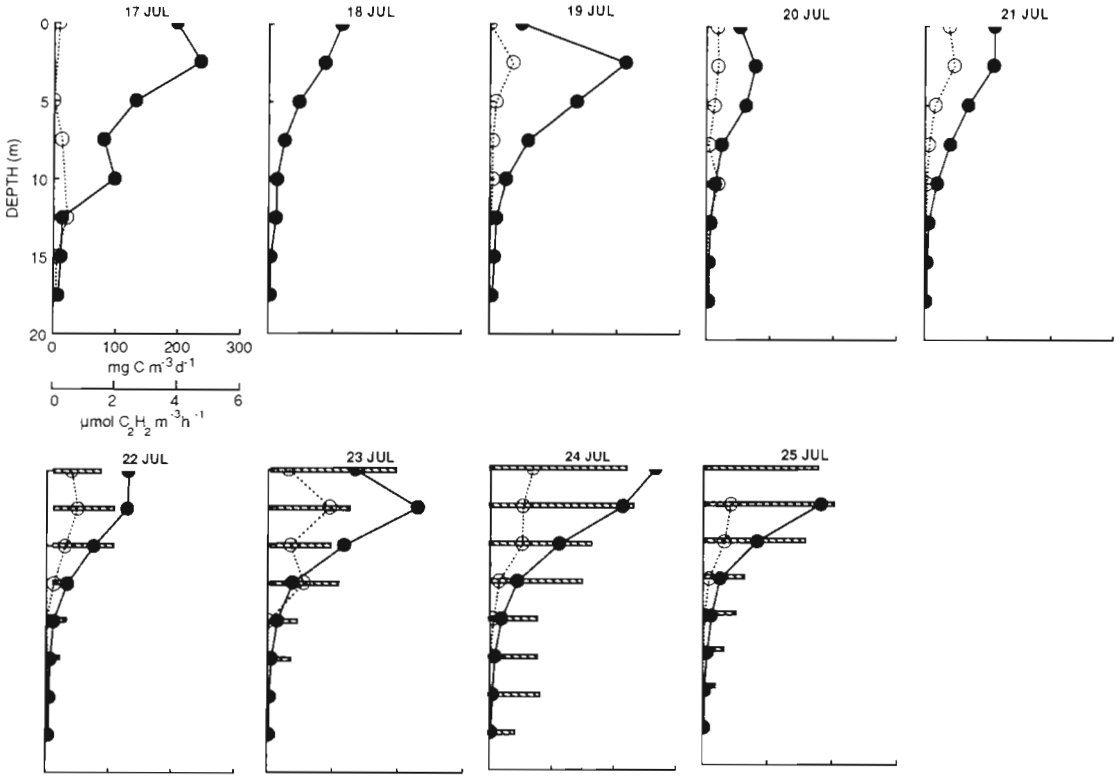

Fig. 7. Particulate primary production (lines) and nitrogen fixation (bars) at the anchor station. (●) Primary production in the <20 µm size fraction; (○) primary production in the >20 µm size fraction. Scale of nitrogen fixation is given above the lower left panel

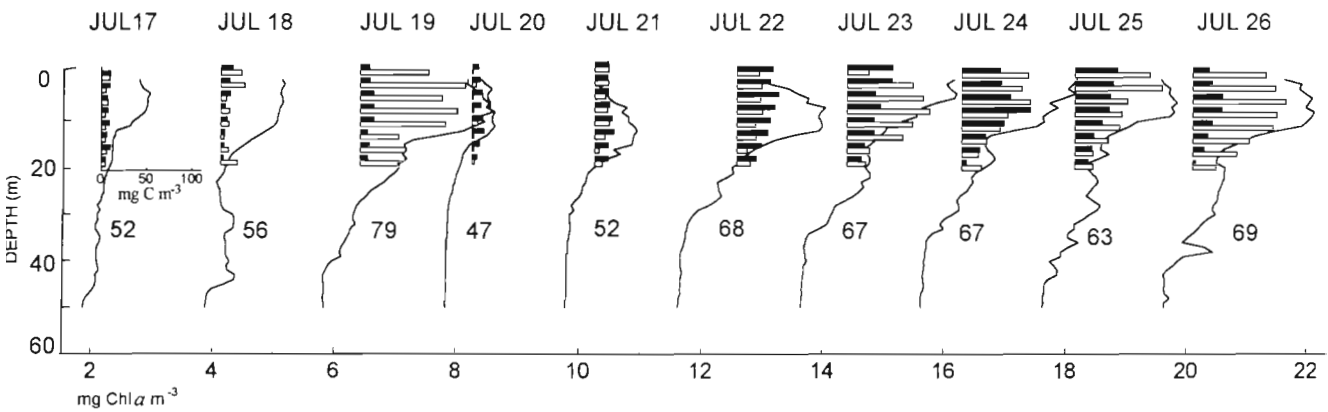

Fig. 8. Vertical distribution of chl *a* concentration (lines) and abundances of *Aphanizomenon flos-aquae* (filled bars) and *Heterocapsa triquetra* (open bars) at the anchor station. Chl *a* profiles are cumulatively offset by 2 mg chl *a* m^{-3}. The numbers adjacent to each profile indicate the values of integrated chlorophyll over the 0 to 20 m layer in mg chl *a* m^{-2}. The scaling of the abundances of the species is given at the leftmost profile

Heterocapsa triquetra was more or less in accordance with the main hydrodynamical events. The abundances were highest within the anticyclonic eddy and lowest in its periphery (Fig. 10c–g). During the first part of the study period the distribution of *Aphanizomenon flos-aquae* was more random than that of *H. triquetra* and barely related to the eddy (Fig. 11c,d). Moreover, the low saline waters advecting in the periphery of the north-westward directed jet were rich in *A. flos-aquae* (Fig. 11d–f), while abundances of *H. triquetra* were relatively low.

Table 2. Carbon values of the dominating phytoplankton species, average, standard deviation and coefficient of variation (CV) of the biomass of phytoplankton species, chl *a*, primary production and nitrogen fixation in the upper layer at the anchor station during the whole study period

	Carbon value (pg cell^{-1})	Average	SD	CV (%)
Phytoplankton species (mg C m^{-3})				
Aphanizomenon flos-aquae	175	19.7	10.2	52
Microcystis spp.	17	3.6	1.0	29
Dinophysis norvegica	1330	13.9	5.0	36
Gymnodinium spp. 8 × 10 µm	45	4.8	1.8	37
Heterocapsa triquetra	175	34.1	25.5	75
Heterocapsa rotundata	35	5.1	1.3	26
Chrysochromulina spp. 3 × 5 µm	3	8.8	3.5	40
Chrysochromulina spp. 6 × 8 µm	20	11.1	6.4	58
Cryptophyceae spp.	1–40	4.5	4.2	94
Other species	3–5000	10.8	4.5	42
Chlorophyll (mg chl *a* m^{-3})				
Total		3.8	0.9	23
<20 µm		2.6	0.8	30
>20 µm		1.3	0.8	59
Primary production (g C m^{-2} d^{-1})				
Total		1.4	0.4	31
<20 µm		1.1	0.4	36
>20 µm		0.3	0.1	44
Nitrogen fixation (µmol C_2H_2 m^{-2} h^{-1})		33.7	22.0	65

DISCUSSION

The weather in Northern Europe and the Baltic Sea was exceptionally cold and stormy in June-July 1996 (Finnish Meteorological Institute), and the annual late summer cyanobacterial bloom was delayed by ca 2 wk relative to previous years (see Heinänen et al. 1995, Kononen et al. 1996, 1998). Nutrients were exhausted much deeper in the water mass during our study than in late July 1994, when calm weather prevailed in the northern Baltic Sea for several weeks. For example, the mean NO_3 concentration at 40 m was 0.3 ± 0.3 µM in 1996 compared with 1.7 ± 1.1 µM in 1994 (Laanemets et al. 1997, Kononen et al. 1998). This suggests that in 1996 a considerably larger amount of nutrients had been transferred into the plankton ecosystem due to the extreme hydrometeorological conditions. Furthermore, precipitation in the several weeks before our study was much greater than the long-term average, so that the atmospheric input of inorganic nitrogen by rainfall may have had an additional impact on the nutrient budget of the Baltic Sea ecosystem.

Hetrocapsa triquetra bloom

Heterocapsa triquetra is a common species in the area, but it normally appears in much lower abundances (Kononen & Niemi 1984) than were observed during our study. Exceptionally high abundances of this species were observed throughout the northern Baltic Proper and the western Gulf of Finland in 1996 (Tore Lindholm pers. comm., Finnish Institute of Marine Research unpubl. material). Since the bloom was detected at several sites, we conclude that its horizontal extent was on the order of hundreds of kilometres. From the vertical distribution of nutrient reserves and the possible input of nitrogen by preceding heavy rainfall, it would seem that nutrient replenishment sufficient for bloom formation had taken place before our study began. Furthermore, the renewal process of the Baltic deep water may have stimulated the *H. triquetra* bloom. A long stagnation (1976 to 1993) in the deep water of the central Baltic Sea had led to oxygen-depleted conditions, which in turn via vertical exchange caused a low ratio of dissolved inorganic nitrogen to phosphorus in the northern Baltic Proper (Wulff & Rahm 1988), favouring nitrogen-fixing cyanobacteria (Kononen et al. 1996). The last major inflow of saline and oxygenated water from the North Sea in 1993 and 2 smaller inflows during winter 1993-1994 made the central Baltic deep water oxic (Matthäus & Lass 1995). We can hypothesize that the renewal of the deep water may have caused changes in the nitrogen to phosphorus ratio in the upper layers of the northern Baltic Proper, shifting the nutrient conditions towards conditions more favourable for dinoflagellates than diazotrophic cyanobacteria.

High abundance of *Heterocapsa triquetra* is an indication that grazing was not efficient enough to sup-

press the biomass formation. This species is favoured food for copepods (Turner & Anderson 1983, Sellner & Olson 1985, Stoecker & Sanders 1985), tintinnids (Aelion & Chisholm 1985) and heterotrophic dinoflagellates (Nakamura et al. 1995). Wide evidence has shown that growth and grazing efficiency of crustacean and ciliate grazers is highly temperature dependent (Huntley & Lopez 1992, Peters 1994). In embayments of Cape Cod, on the east coast of the United States, Aelion & Chisholm (1985) showed a temperature-dependent switching of the growth and ingestion rates of a tintinnid on *H. triquetra* at temperatures of 11 to 16°C. Below these temperatures the tintinnid predator grows and ingests too slowly to efficiently control the dinoflagellate growth. During the first days of our study the average surface water temperature was 13.5°C, which was ca 2 to 3°C below the average of the previous 22 yr (Haapala & Alenius 1994). We conclude that, before the study period, grazing by copepods and tintinnids was insufficient to suppress the bloom development of *H. triquetra*.

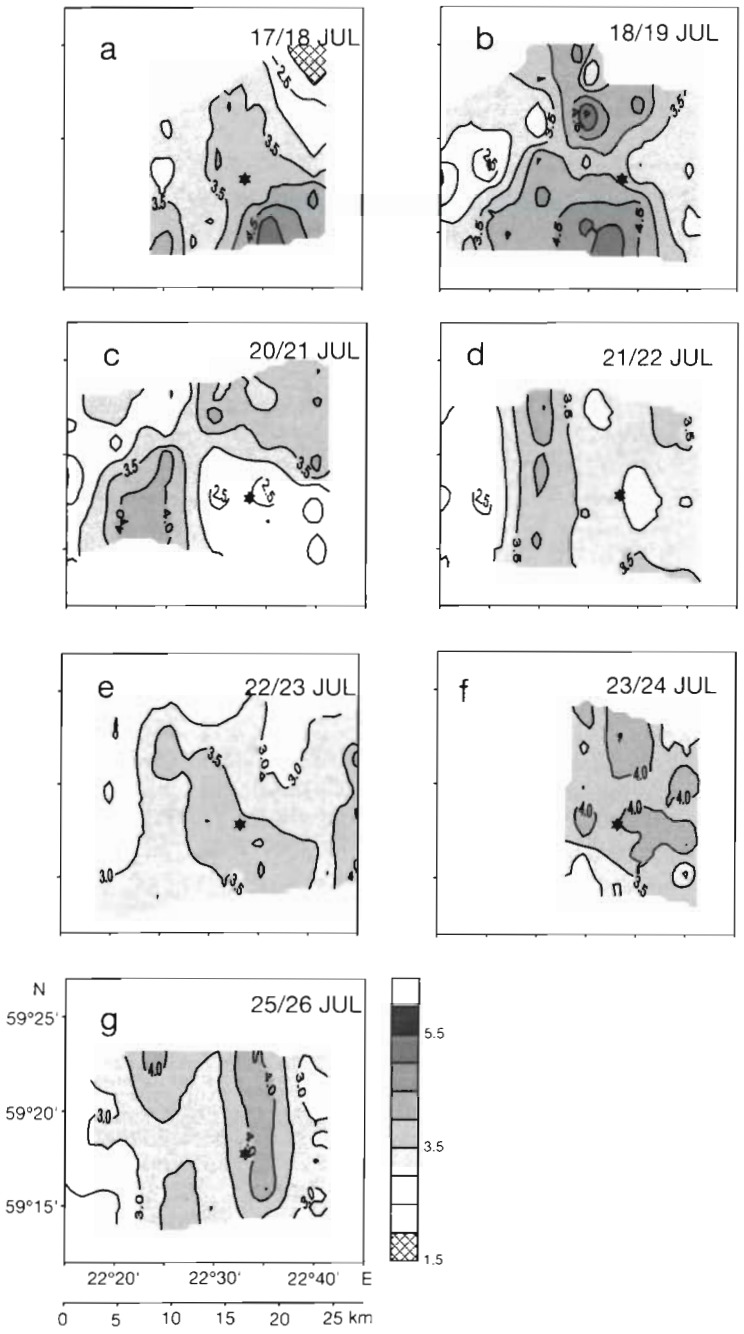

Fig. 9. Horizontal distribution of chl *a* concentrations at 5 m depth on successive dates (figure redrawn from Pavelson et al. 1999). (*) Location of the anchor station

Meso-scale patchiness and temporal variability of phytoplankton species

Earlier studies carried out in the Baltic Sea during the phytoplankton spring bloom (Kahru et al. 1991, Kononen et al. 1992) and late summer bloom (Kononen et al. 1996, Moisander et al. 1997) have revealed a good correlation between species abundance and water masses. The results were based on measurements at sparse stations on the transects so that the horizontal patchiness was poorly resolved. In the present study, repeated FT synoptic snapshots enabled us to estimate the range of abundance meso-scale variability of 2 dominant species at the entrance to the Gulf of Finland, where water masses from the open Gulf and the northern Baltic Proper mix with coastal waters.

During the downwelling period, waters with high chl *a* concentrations originating from the northern Baltic Proper were observed in the southern part of the study area (Fig. 9a,b). On the species level, extremely high abundance of *Heterocapsa triquetra* (Fig. 10a) and relatively low abundance and more uniform spatial distribution of *Aphanizomenon flos-aquae* (Fig. 11a) were observed. This would suggest that nutrient conditions had become more favourable for *H. triquetra* in the northern Baltic Proper. Species-specific motility may have an additional impact on patch formation in the downwelling zone. Using a modelling approach, Franks (1992) showed that strong swimmers tend to concentrate in convergent zones, whereas weaker swimmers are more evenly distributed. The regression slope of motile *H. triquetra* versus latitude on 17-18 July was ca 3 times as steep as that of non-motile *A. flos-aquae*, which suggests that the tendency for accumula-

tion in the downwelling zone might have been stronger for *H. triquetra*. It is notable that the presence of the 2 water masses of different origin (Gulf and northern Baltic Proper) was reflected in more than 10-fold variation in the *H. triquetra* abundance in a relatively small area. Marked difference sometimes showed up even in neighbouring samplings, i.e. within distances of about 5 km (Fig. 10a).

On 19 July, in the surface layer at the AN, the abundance of *Heterocapsa triquetra* was about 8 times as high (Fig. 5c), and the chl *a* (Fig. 5b) and primary production (Fig. 7) were about twice as high as on the previous or the following day. From 18 to 19 July integrated chl *a* in the 0 to 20 m layer increased by ca 40%, which suggests that the increase was caused by horizontal rather than vertical processes. However, the meso-scale mapping of *H. triquetra* by FT on 18-19 July (Fig. 10b) before sampling at the AN did not reveal patches with extremely high abundance of *H. triquetra*. Hence the only explanation can be the existence of *H. triquetra*-rich patches with sizes evidently smaller than the horizontal resolution of phytoplankton sampling by the FT system, i.e. <5 km.

After the formation of the anticyclonic eddy, on 20–22 July, the highest abundances of *Heterocapsa triquetra* were observed inside the eddy, and the lowest in the periphery (Fig. 10c, d). We suggest that the eddy formed from the northern Baltic Proper water (saline and rich in chl *a*) which was carried to the area by a downwelling jet (see also Pavelson et al. 1999). The cells of *H. triquetra* that were trapped in the eddy did not mix with the surrounding low abundance waters from the open Gulf, and therefore the species abundance remained relatively high for several days.

During 17 to 21 July the abundances of *Aphanizomenon flos-aquae* at the AN were considerably lower than the mean abundance values of the FT survey (Fig. 5d), but were nevertheless close to the minimal values measured for FT samples. The FT chl *a* and phytoplankton mapping on 18-19 July revealed water with lower chlorophyll concentrations (Fig. 9b) and poor in *A. flos-aquae* (Fig. 11b) on the eastern side of the study area. Probably this water was the same water sampled at the AN on 19, 20 and 21 July. By the night of 20-21 July, the 'hole' of low abundance of the species was found at AN and about 5 to 6 km northwards (Figs. 9c & 11c). This corresponds to an advection speed of 6 cm s^{-1} towards the NW, which is close to the measured current speed (Fig. 3c).

The north-westward jet observed from 22 July onward carried water with low salinity (Fig. 3f,g), but higher chl *a* than in the open Gulf of Finland water (Fig. 9f,g). A corresponding tongue-like intrusion of *Aphanizomenon flos-aquae*, with noticeable inner structure, was observed in the middle of the southern part of the study area (Fig. 11e). *Heterocapsa triquetra* was present only in low abundances (Fig. 10d,e). The jet had originated from the coastal region, most probably from the shallow Väinameri (Fig. 1). Low conversion factor values between C_2H_2 reduction and $^{15}N_2$ uptake, measured in this water mass at the AN, support the idea that the *A. flos-aquae* cells were not phosphorus limited (de Nobel 1998). Also, very low conversion factors had a negative relationship with

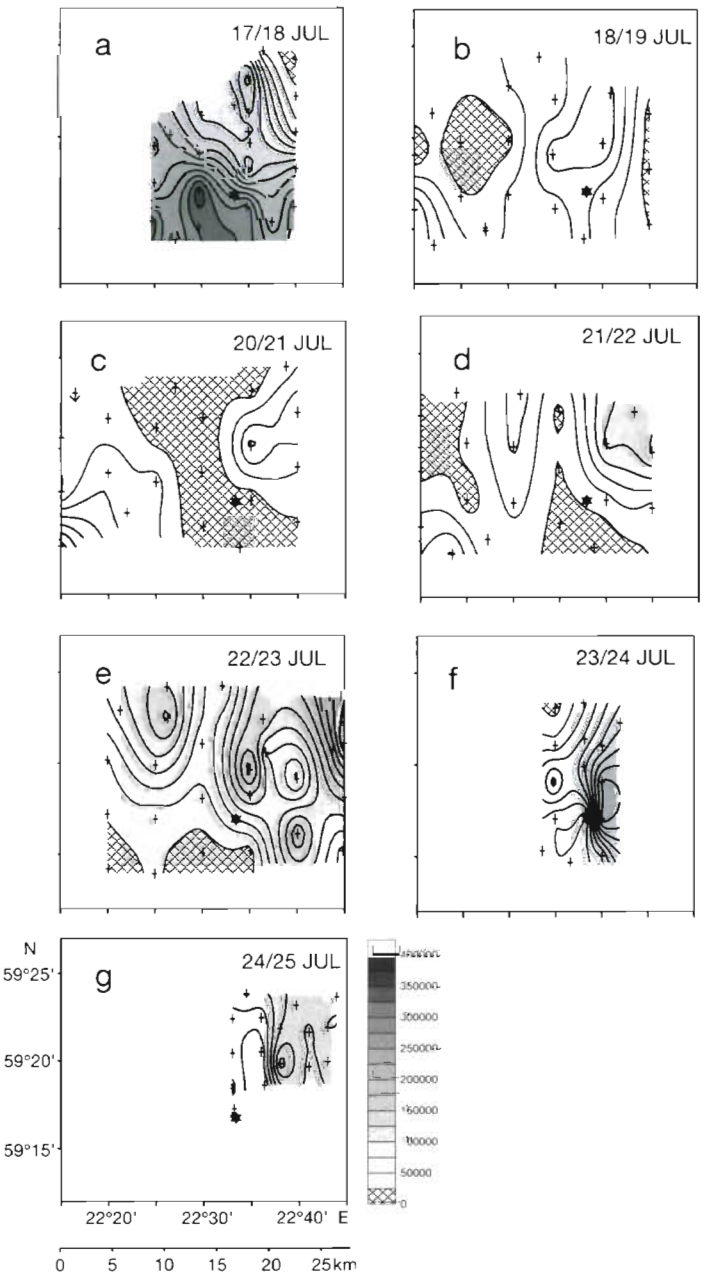

Fig. 10. *Heterocapsa triquetra*. Horizontal distribution of abundance (cells l^{-1}) at 5 m depth on successive dates. (+) Positions of samples taken by the flow-through system. (✱) Position of the anchor station

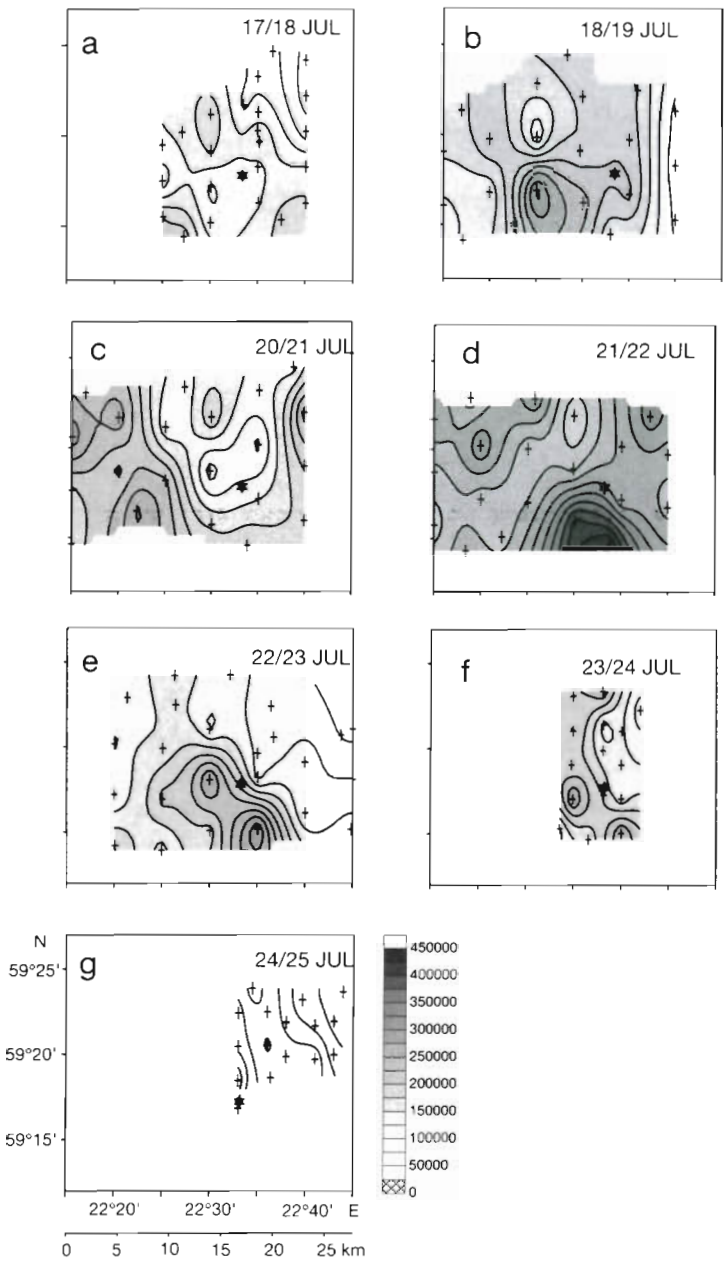

Fig. 11 *Aphanizomenon flos-aquae*. Horizontal distribution of abundance (100 µm filaments l^{-1}) at 5 m depth on successive dates. (+) Positions of samples taken by the flow-through system. (✱) Position of the anchor station

biomass-normalized nitrogen fixation activity in a previous study (Moisander et al. 1996). Thus, the low conversion factors may indicate high nitrogen fixation activity per cell. This in turn suggests that the fresher water mass may have been exposed to higher phosphorus concentrations in the coastal waters, with consequent stimulation of the growth of *A. flos-aquae*.

There was a clear relationship between the FT maps of silicate (considered as a passive tracer in the absence of diatoms), chl *a* and the alteration of water masses of different origin due to meso-scale physical processes. Furthermore, the correlations between FT and AN silicate and chl *a* support the assumption that variations in these fields are related to water masses. The assumption is further supported by the high correlations of these parameters in the FT and AN samples when taking into account advection (see 'Representativeness of the flow-through data'). The FT maps of the 2 dominant species showed a more than 10-fold variation in abundance over the survey area, reflecting a marked variability in the water masses of different origin. The mean coefficients of variation over all surveys confirmed the observed peculiarities in the distributions of parameters, and were 7% for silicate, 18% for total chl *a*, 30% for *Aphanizomenon flos-aquae* and 77% for *Heterocapsa triquetra*. Thus we reiterate that the distribution and variability of silicate and total chl *a* were closely related to the different water masses, while on species level there were additional features of decreased horizontal scale of abundance variability and high temporal variations.

The relatively high current speeds of 6 to 17 cm s^{-1} measured at the AN correspond to the 5 to 15 km distance traversed by the water parcel in a day, i.e. the water sampled on one day was sometimes outside of the observation area on the following day. Thus it was not possible by use of the property conservation equation to separate quantitatively the variability due to biological factors (growth, sinking, grazing) from the variability due to pure advective transport (e.g. Kononen et al. 1998). The hydrodynamical background at the AN (downwelling, periphery of anticyclonic eddy, cyclonic side of the jet) suggests that vertical downward motion prevailed throughout the study period. The observed low and invariable assimilation numbers in both flagellate and cyanobacterial size fractions (Table 1) reveal that the activity of phytoplankton remained at a constant level. We conclude that nutrient replenishment by vertical transport was unlikely at the AN site, as well as in water masses carried through, and therefore enhancement due to growth was minor. Thus the observed temporal variability of measured biological parameters at the AN must have been caused by

spatial patchiness carried by the current through the site. The coefficient of variation for phytoplankton species fluctuated in a wide range, from 26 to 94%, while for *Heterocapsa triquetra* and *Aphanizomenon flos-aquae* it was 75 and 52%, respectively (Table 2). The much lower coefficients of variation for total chl *a* (23%) and primary production (31%) support our hypothesis.

Representativeness of the flow-through data

We now attempt to evaluate the consistency of the data collected by the conventional sampling at the AN and by sampling from the moving ship during the FT meso-scale survey. Our evaluation is undertaken for the sake of the latter sampling, where the quality of the output may be considered questionable for several reasons (e.g. representativeness of the uptake of seawater when the ship is moving, flow of water through the long tubes of the sampling system). To test the level of representativeness of the FT data we compared them with temporally shifted AN data at the same depth by taking advection into account. For this purpose, from every mapping 2 to 3 samples located upstream from the AN were chosen and the measurements were averaged to give the FT sampling with reduced variations. The correlations were calculated between the FT mapping and the samples at the AN ~8 h after and ~16 h before the FT survey. We included in the analysis the samples of silicate, chl *a* and the 2 dominant species, *Heterocapsa triquetra* and *Aphanizomenon flos-aquae*. All calculations are presented in Table 3.

There was good correlation ($r^2 \approx 0.7$, $p < 0.03$, $n = 7$) between the FT and subsequent (8 h) AN sampled silicate and chl *a* over the whole period. As we expected, the correlations for these same parameters were considerably weaker and non-significant when the FT data with the AN data taken 16 h before were compared. The small number of observations may explain the lack of significance. When the outlier FT and AN (21 July) data pair of chl *a* was removed from the analysis the correlation became almost perfect ($p < 0.0001$, $n = 6$). Together these estimates show that the use of silicate and chl *a* data obtained from the FT samples is justified in the present study. It is fair to assume, moreover, that the FT sampling of other chemical and biological parameters was also representative.

No correlation was found between the abundance of *Aphanizomenon flos-aquae* in samples taken at the AN and by FT. This lack of correlation may be explained by the small number of observations ($n = 7$); counting errors (theoretically in our data <13%) are accentuated by the aggregation of cyanobacterial filaments as well as by the small-scale patchiness.

Table 3. Correlations of chemical and biological parameters between the anchor station (AN) samples (5 to 6.6 m) and flow-through (FT) samples (5 m) taking into account advection between the sampling sites. The calculations were made for the FT samples against 2 different samples at the AN (16 h before and 8 h after the FT samples). All FT and AN data pairs ($n = 7$), except for any outliers when such existed ($n = 6$), were used in the calculation. The values in parentheses show the correlation when the average abundances over the 2.5 to 4.1 and 5 to 6.6 m depth intervals at the AN were used instead. $^{*}p < 0.03$; $^{**}p < 0.0001$

Parameter	n	AN before FT (16 h)	AN after FT (8 h)
SiO_4	7	0.49	0.65*
	6	0.27	
Chl *a*	7	0.29	0.72*
	6	0.28	0.98**
Aphanizomenon flos-aquae	7	0.16	0.11
Heterocapsa triquetra	7	0.00 (0.00)	0.04 (−0.04)
	6	0.45 (0.46)	0.44 (0.23)

To our surprise, there was a considerable, though non-significant correlation for *Heterocapsa triquetra* ($r^2 \approx 0.4$, $n = 6$), which was masked by the very high abundance in the FT samples on 17-18 July. The mapping on this date as a whole was very high, revealing abundance levels about 2-fold greater than other mappings (see Fig. 5c). Most problematic for the *H. triquetra* data, however, was the systematic difference in abundances in the FT and AN samples over the whole period. The linear regression line fitted to the data (taking advection into account) indicated, as a mean, abundances 2.5 times as high in the AN samples as in the FT samples.

The discrepancy in the abundances of *Heterocapsa triquetra* in the FT and AN samplings is hard to explain because the most suspect aspects could easily be excluded. First, a casual coincidence in a small ensemble was excluded because the mean abundance over the whole area was almost always markedly lower than the nearest (in time) abundance at the AN (see Fig. 5c). Second, a check of the species counting was carried out for both sample sets, and no significant deviations from the first counting were found. Third, the effect of possible differences in sampling depths of the FT (5 m) and at the AN (5 to 6.6 m) was excluded by consideration of the vertical profiles of abundance of the species (Fig. 8). When average abundances over 2.5 to 4.1 and 5 to 6.6 m depth intervals at the AN were used in the calculations, the correlation between the AN and FT samples was weaker but there was no significant shift in the ratio of the 2 data sets.

Behavioural adaptations of motile dinoflagellates in regard to light (phototaxis) and gravity (geotaxis), as documented in both laboratory experiments and field studies (review by Levandowsky & Kaneta 1987), might conceivably be reflected as discrepancies in the abundances of time-lagged data. It is known that surface aggregation of dinoflagellates occurs during the day, and subsurface dispersal at night, but the taxis combinations behind the vertical motility behaviour may be species specific (Kamykowski et al. 1998). The phototactic behaviour of *Heterocapsa triquetra* was demonstrated in laboratory conditions by Braarud & Pappas (1951) and in the field in a well-mixed estuarine embayment on the east coast of the United States by Anderson & Stolzenbach (1985). In our case the possible phasing of sampling times (08:00 to 10:00 h at the AN and about midnight during the FT) with the cycles of vertical motility cannot be excluded, but there is no experimental information on the combined phototactic/geotactic behaviour of *H. triquetra* available for the latitude at which this study was performed; speculations can therefore not be made. To summarize, the low abundance of *H. triquetra* in the FT samples seems to be a non-trivial problem and for the present we leave the discussion open. We would argue that the discrepancy was not, however, related to the FT system since for the other parameters it performed reasonably well (silicate and chl *a*) or a logical consistency was found (*Aphanizomenon flos-aquae*) between the AN and FT samples.

CONCLUSIONS

This case study, carried out in a coastal region under changing wind forcing, shows that the temporal variability of pelagic biological parameters at a fixed position may be explained by horizontal patchiness related to meso-scale hydrodynamical processes. The observed abundance distribution of functionally different phytoplankton species could be explained by the inflow of waters of different origin to the study area, and by species-specific characteristics affecting their vertical distribution. In conformation of the initial assumption we made, the scale of the patches decreased and the magnitude of the variability increased when moving from overall community level (chl *a*) to the species level. Phytoplankton in the size fraction equal to or greater than 20 µm exhibited the most pronounced variability, whereas the distributions of species in the smaller size fraction were more uniform.

Acknowledgements. Our thanks are due to the crew of RV 'Aranda' for cooperation and flexibility during the cruise. Likewise, we thank Ms Pirjo Tikkanen and Mr Hannu Haahti for performing the nutrient analyses, Ms Tuovi Vartio for primary production measurements, Mr Tero Purokoski for ADCP measurements, Dr Martti Esala for ^{15}N determinations, Ms Riitta Olsonen for statistical advice and Ms Kathleen Ahonen for language revisions. The comments of 3 anonymous referees helped us to improve our paper. Financial support was provided by the Maj and Tor Nessling Foundation.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: September 11, 1998; Accepted: March 19, 1999
Proofs received from author(s): August 13, 1999