

# Phytoplankton dynamics affected by the coastal upwelling events in the Gulf of Finland in July–August 2006

INGA LIPS\* AND URMAS LIPS

MARINE SYSTEMS INSTITUTE, TALLINN UNIVERSITY OF TECHNOLOGY, AKADEEMIA RD. 21B, 12618 TALLINN, ESTONIA

\*CORRESPONDING AUTHOR: inga@sea.ee

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The response of phytoplankton to the observed coastal upwelling events in the central Gulf of Finland in July–August 2006 is described on the basis of chlorophyll *a* and phytoplankton community/biomass data. Due to the nutrient supply, advection, replacement/mixing of water masses and changes in water temperature, not only single phytoplankton species were affected but the entire phytoplankton community changed several times during a 2-month period. A faster response of nanoplanktonic species to the upwelled nutrients and high biomass of photosynthetic ciliate *Myrionecta rubra* were observed in the upwelling waters. The highest phytoplankton biomass was observed in the area of domed isopycnals in the context of developing downwelling 3 weeks after a relatively weak upwelling near the northern coast of the Gulf of Finland. An increase of biomass was observed also after the relaxation of a major upwelling event near the southern coast. Multi-dimensional scaling analysis matches this relatively high biomass community with the communities observed outside the area of upwelling influence 2 weeks earlier. We suggest that the observed biomass increase could be connected to the relaxation of upwelling and subsequent reversal of surface water mass movement together with the utilization of mostly regenerated but also stored nutrients.

**KEYWORDS:** coastal upwelling; nutrients; phytoplankton; Gulf of Finland; Baltic Sea

## INTRODUCTION

Phytoplankton growth in the sea is primarily controlled by nutrient availability and solar radiation. The generation time of phytoplankton is mostly one to a few days during nonsexual reproduction, which could result in a time scale of a day to a few weeks for a noticeable change in phytoplankton biomass. Species-specific nutrient requirements are important factors in regulating the phytoplankton community and will lead to modifications in the community structure when nutrient availability changes (Sommer, 1989). Phytoplankton distribution in coastal waters, e.g. Baltic Sea, varies over small distances

(less than 10 km) and short time scales (few days). Such changes are strongly associated with local changes in nutrient concentrations in the euphotic zone. The key to understand local changes observed in phytoplankton dynamics in coastal waters lies in explaining the possible mechanisms of nutrient supply to the euphotic zone.

The summer period in the Baltic Sea area is characterized by the development of a strong seasonal thermocline. This strong stratification prevents mixing between the nutrient depleted upper layer and the nutrient-rich lower layers. Wind-induced vertical mixing (Lilover *et al.*, 2003) and upwelling (Zhurbas *et al.*, 2008) are the important processes in bringing nutrient-rich waters from

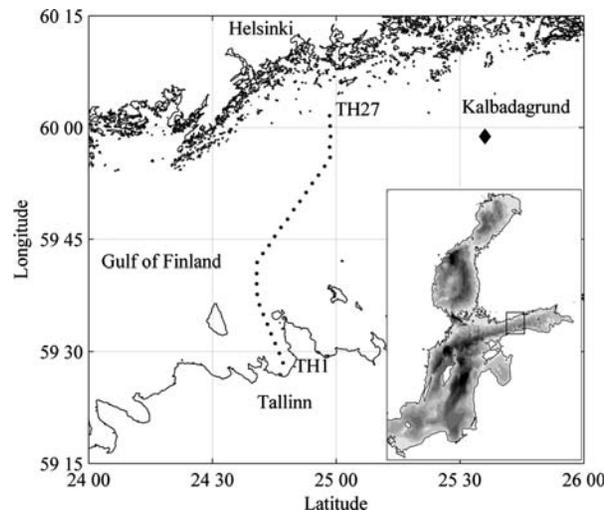
deeper layers to the surface at this time of year. The speed of biological response to high nutrients and light is taxon-specific and may also be influenced by initial macro-nutrient concentrations/ratio (i.e. “shift-up” dynamics described by Dugdale *et al.*, 1990) and the presence of micronutrients (Hutchins *et al.*, 1998). While the nutrient ratios in oceanic water are close to Redfield (Tyrell, 1999), adjacent seas like the Baltic Sea deviate strongly from this ratio showing large regional and seasonal differences (Danielsson *et al.*, 2008). Baltic Sea deep water and summer sub-thermocline water have characteristically low dissolved inorganic nitrogen to dissolved inorganic phosphorus (DIN:DIP) ratios due to the widespread internal loading of phosphate (Pitkänen *et al.*, 2001; Carstensen *et al.*, 2006). Based on a low DIN:DIP ratio in the upwelling water, the filamentous nitrogen-fixing cyanobacteria would be expected to out-compete other phytoplankton species but as shown in previous studies (Kanoshina *et al.*, 2003; Vahtera *et al.*, 2005) upwelled waters have too low temperatures for cyanobacteria to benefit from the upward transported nutrients and due to the wind-forced Ekman transport the cyanobacteria filaments in the upper layer will be advected away from the upwelling region. At the same time, coastal upwelling in the Baltic Sea has been shown to stimulate the growth of other phytoplankton and also phototrophic ciliate species during upwelling events (Heiskanen, 1995; Kanoshina *et al.*, 2003; Kononen *et al.*, 2003; Krężel *et al.*, 2005; Vahtera *et al.*, 2005).

The typical lifespan of upwelling ranges from 0.5 to 10 days in the Baltic Sea (Bychkova and Viktorov, 1987). Nutrient concentration may be changed on a time scale for a few days and could result in transient consequences for growth, fluctuations in biomass and competition between phytoplankton species. The objective of this paper is to describe phytoplankton distribution and analyse changes in community structure influenced by several consecutive coastal upwelling events in the Gulf of Finland in July–August 2006. Such extensive hydrophysical, chemical and biological (including phytoplankton community data) data collected before, during and after several coastal upwelling events has seldom been analysed previously in order to link changes in phytoplankton community with changes in hydrophysical and the chemical environment in the Baltic Sea.

## METHOD

### Study area and sampling

Mapping of hydrographic, chemical and biological fields was carried out in the central part of the Gulf of



**Fig. 1.** Map of the study area and location of measurements/sampling stations TH1–TH27.

Finland (Fig. 1) in July–August 2006 (11 July, 19–20 July, 25 July, 8 August, 15–16 August, 22 August and 29 August). The southernmost sampling station TH1 was located <2 km off the coast in the Tallinn Bay and the northernmost station TH27 ~5 km from the archipelago area off Helsinki. The width of the gulf in the study area is <80 km. The water depths are 25–40 m in the inner Tallinn Bay followed by a steep bottom sloping to ~90 m in the southern part of the open gulf and a general northward shallowing with remarkable irregularities of the sea bed. Vertical profiles of temperature, salinity and chlorophyll *a* fluorescence were recorded at 27 stations (distance between stations 2.6 km) and water samples for inorganic nutrient ( $\text{PO}_4^{3-}$ ,  $\text{NO}_2^- + \text{NO}_3^-$ ), chlorophyll *a* and phytoplankton analyses were collected at 14 stations (except on 19–20 July when sampling was made only at the northernmost stations TH19–27; distance between stations 5.2 km) from the upper mixed layer (UML). Water samples for nutrient analyses were collected also from the seasonal thermocline with a vertical resolution of 2.5–5.0 m.

### Chemical and biological analyses

Measurements were carried out using a NBIS Mark III CTD (conductivity, temperature and depth) probe and an SBE 19 CTD probe (Sea-Bird) equipped with a WETStar fluorimeter (WET Labs). The salinity values were calculated using algorithms from Fofonoff and Millard Jr (Fofonoff and Millard Jr, 1983) and are presented without units. Salinity data were quality checked against the water sample analyses by a high precise salinometer AUTOSAL (Guildline). A rosette sampler with

8 Niskin water samplers (volume 1.7 l) was used for sampling. To represent the UML, the samples were prepared by pooling three (in case of a shallow UML—two) samples taken from the surface layer from the 1-m depth down to the seasonal thermocline, the depth of which was determined from the CTD casts.

Nutrient analyses were carried out according to the guidelines of the American Public Health Association (APHA, 1992; methods 4500-NO<sub>3</sub> F and 4500-P F) and analysed using an automatic nutrient analyzer  $\mu$ Mac 1000 (Systea S.r.l.). The lower detection range for phosphate-phosphorus and nitrate + nitrite-nitrogen was 1 ppb (parts per billion; 0.03 and 0.07  $\mu$ M, respectively; with a measurement uncertainty of 20% near the detection limit). Samples for phosphates (PO<sub>4</sub><sup>3-</sup>) were mostly analysed immediately onboard after sampling and samples for dissolved inorganic nitrogen compounds (NO<sub>3</sub><sup>-</sup> + NO<sub>2</sub><sup>-</sup>) determination were deep-frozen after collection and analysed later in the on-shore laboratory.

The chlorophyll *a* (Chl *a*) content from UML (pooled sample prepared as described earlier) was determined on Millipore APFF glass-fibre filters following the extraction at room temperature in the dark with 96% ethanol for 24 h. Chl *a* content from the extract was measured spectrophotometrically (Thermo Helios  $\gamma$ ; photometric accuracy:  $\pm 0.005$  A at 1 A) in the laboratory (HELCOM, 1988).

Phytoplankton sub-samples (100 mL) were preserved with acid Lugol solution and analysed using the Utermöhl (Utermöhl, 1958) technique and PhytoWin software by Kahma Ky. Cyanobacterial filaments were counted as 100- $\mu$ m segments and other phytoplankton species as single cells or colonies. All biomass data are given as wet weight.

## Data analysis

Statistical analysis was performed using the PRIMER 6.0 software (PRIMER-E Ltd) with user guidelines (Clarke and Warwick, 2001). To compare the community structure at different sampling stations on different sampling days, the ordination of samples by multi-dimensional scaling (MDS) was performed. Biomass of all species at all stations was used for Bray–Curtis similarity coefficient (transformed by square root) calculations.

## RESULTS

### Upwelling events and related temperature, salinity and nutrient dynamics

According to the wind stress estimates, southward cross-gulf Ekman drift prevailed in July and northward cross-

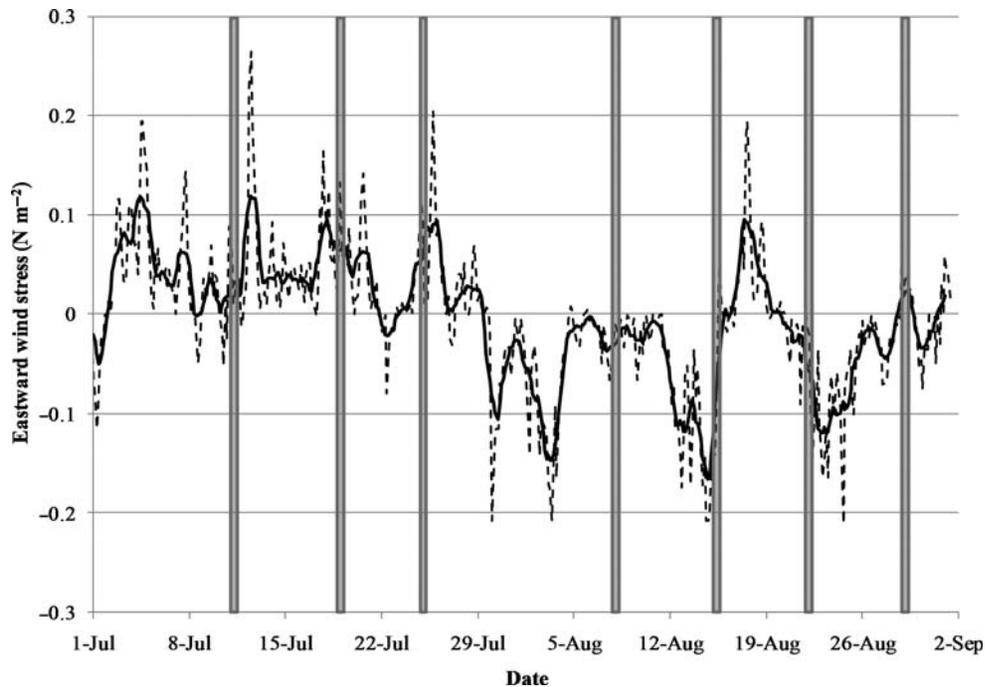
gulf Ekman drift prevailed in August 2006 (with an exception from 15 to 20 August) in the surface layer of the Gulf of Finland (Fig. 2). Three upwelling events occurred and were mapped during the study period. A relatively weak upwelling was present near the northern coast on 19–20 July. A major upwelling event developed near the southern coast in the first half of August and was mapped on 8 August and 15–16 August. The next upwelling event near the southern coast, which appeared in late August, was sampled on 29 August.

The upwelling event near the northern coast caused a drop in temperature in the UML at the two northernmost stations from 19–20°C to 14–17°C on 19 July, but no changes in the UML salinity were observed (Fig. 3A and B). On the basis of water sample analyses, only PO<sub>4</sub><sup>3-</sup>-Concentrations in the UML slightly exceeded the lower detection range at some stations on 19 July, but it is not clear whether this could be attributed to the upwelling event or not (Fig. 3C and D).

Wind-induced northward drift of surface waters and development of an upwelling in the beginning of August along the southern coast brought cold and saltier waters with high amounts of inorganic nutrients into the surface layer (Fig. 3A–D; 8 August). The concentrations as high as 0.48  $\mu$ M of NO<sub>3</sub><sup>-</sup> + NO<sub>2</sub><sup>-</sup> and 0.79  $\mu$ M of PO<sub>4</sub><sup>3-</sup> were measured in the upwelling area. A widening of the upwelling area and a drop of nitrates + nitrites concentrations below the lower detection range and a decrease of PO<sub>4</sub><sup>3-</sup> concentrations in the upwelling water within a week between surveys on 8 and 15–16 August (Fig. 3C and D) was observed. After the relaxation of the upwelling, an increase of sea surface temperature was observed and the UML water was depleted of inorganic nutrients (22 August). The formation of next upwelling, which was sampled on 29 August, caused a drop of sea surface temperature from 15–16°C to 10–12°C and an increase in salinity from 4.8 to 5.6, although it did not bring detectable amounts of nitrates + nitrites into the UML but only amounts of phosphates compared with the previous upwelling event.

### Horizontal distribution of phytoplankton Chl *a* and biomass

At the beginning of study on 11 July 2006, phytoplankton Chl *a* and biomass distribution (Fig. 3E and F) in the UML were patchy along the cross-section between Tallinn and Helsinki in the Gulf of Finland. The Chl *a* concentrations varied between 3.4 and 7.1 mg m<sup>-3</sup> and the total wet weight phytoplankton biomass ranged between 580 and 2050 mg m<sup>-3</sup>. A comparison of Chl *a* and biomass values revealed some discrepancies in their



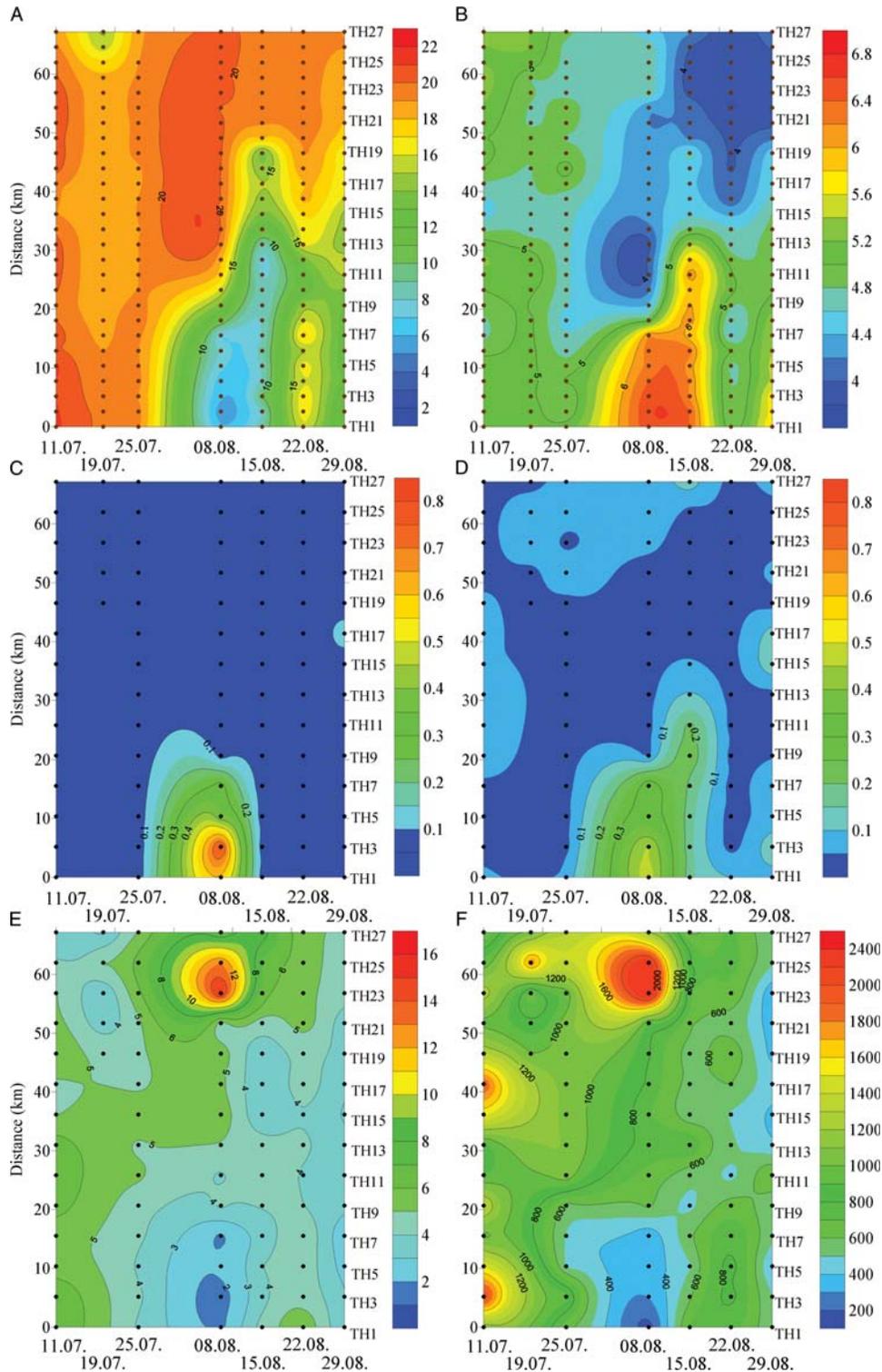
**Fig. 2.** Eastward wind stress (dashed line) in July–August 2006 estimated using wind data from Kalbådagrund meteorological station. Daily average wind stress is shown as the solid line and vertical grey areas indicate the periods of sampling.

horizontal distributions on 11 July, especially at station TH17 where a local minimum of Chl *a* ( $4.8 \text{ mg m}^{-3}$ ) coincided with a local maximum of total biomass ( $1920 \text{ mg m}^{-3}$ ). On 19 July, an upwelling event, which developed in the northern part of the cross-section, influenced Chl *a* and phytoplankton biomass values in the UML. Against a background of a relatively low phytoplankton Chl *a* and biomass level in the northern part of the study area, higher values were measured at station TH25, which could be regarded as the upwelling front (Fig. 3A). However, a significant maximum of total biomass ( $1820 \text{ mg m}^{-3}$ ) was associated with a relatively moderate maximum of Chl *a* ( $5.1 \text{ mg m}^{-3}$ ). A more uniform distribution of phytoplankton Chl *a* and biomass with lower values in the southern part and higher values in the central and northern part of the study transect was observed on 25 July. The Chl *a* and biomass distributions were well correlated, the values varied between  $3.9$  and  $6.4 \text{ mg m}^{-3}$ , and  $480$  and  $1380 \text{ mg m}^{-3}$ , respectively.

A clear decline in Chl *a* concentration and phytoplankton biomass in the Tallinn Bay and a sharp increase in the northern part of the cross-section were observed on 8 August. The decrease of Chl *a* from  $4.2$  to  $1.8 \text{ mg m}^{-3}$  and total biomass from  $950$  to  $290 \text{ mg m}^{-3}$  at the southern end of the study transect was related to the low phytoplankton biomass in the cold upwelled water. The highest Chl *a* ( $14.3 \text{ mg m}^{-3}$ )

and biomass ( $2320 \text{ mg m}^{-3}$ ) values were measured at stations TH23 and TH25 in the area, which could be regarded as an area of the horizontal convergence of surface waters due to the northward Ekman drift in the UML.

The decrease in inorganic nutrient concentrations coincided with an increase in Chl *a* and phytoplankton biomass values during the stabilization and relaxation phases of the observed upwelling (Fig. 3E and F; 15–16 and 22 August, respectively). The average phytoplankton Chl *a* and biomass values at the four southernmost sampling stations (TH1, TH3, TH5 and TH7) occupied by the upwelling event on 8 August increased from  $1.8$  and  $290 \text{ mg m}^{-3}$  to  $3.8$  and  $600 \text{ mg m}^{-3}$  by 15–16 August and to  $5.0$  and  $800 \text{ mg m}^{-3}$  by 22 August. At the same time, the phytoplankton Chl *a* and biomass decreased at the northernmost part of the study transect from the observed maximum values on 8 August to  $6.6$  and  $750 \text{ mg m}^{-3}$  by 15–16 August and to  $5.4$  and  $720 \text{ mg m}^{-3}$  by 22 August. At the sampling stations in the open gulf (TH9–TH21), the temporal variability of Chl *a* and phytoplankton biomass in the period from 8 August to 22 August was not as high as that described above in relation to the southernmost and northernmost parts of the study transect. However, a local maximum of phytoplankton biomass of  $820 \text{ mg m}^{-3}$  at station TH13 on 15 August and a local minimum of biomass of  $470 \text{ mg m}^{-3}$  at station TH11 on 22 August was



**Fig. 3.** Temporal changes of temperature (**A**, °C), salinity (**B**), nitrate + nitrite–nitrogen (**C**,  $\mu\text{M}$ ), phosphate–phosphorus (**D**,  $\mu\text{M}$ ), chlorophyll *a* concentration (**E**,  $\text{mg m}^{-3}$ ) and phytoplankton biomass (**F**,  $\text{mg m}^{-3}$ ) in the UML along the study transect from 11 July to 29 August 2006. Dots indicate measurements (A and B) or sampling (C–E) points; sampling dates are shown on the *x*-axis; distance in kilometres from station TH1 and sampling stations are shown on the *y*-axes.

noted. The maximum was related to the upwelling front (Fig. 3A and B; 15–16 August) and the minimum to a slightly colder and saltier surface water patch (Fig. 3A and B; 22 August).

The last upwelling event at the end of August also had a significant impact on the Chl *a* (decrease from 5.0 to 2.7 mg m<sup>-3</sup>) and the total phytoplankton biomass (decrease from 800 to 480 mg m<sup>-3</sup>) and distribution in the upwelling area in the Tallinn Bay. At the same time, both the Chl *a* and biomass decreased also on the rest of the study transect (but the decrease was less pronounced), where, on average, the Chl *a* concentration decreased from 4.7 to 3.6 mg m<sup>-3</sup> and total biomass from 620 to 450 mg m<sup>-3</sup>.

## Dynamics of phytoplankton species and community structure

### July

The dynamics of horizontal distribution of some phytoplankton key species are shown in Fig. 4. At the beginning of the study (11 July), the distribution of phytoplankton species in the UML did not show any distinguishable pattern. Phytoplankton wet weight biomass (Fig. 3F) was patchy along the sampled cross-section and filamentous cyanobacteria species/groups were dominating in the community (*Aphanizomenon* sp. (L.) Ralfs, *Prochlorothrix* Burger-Wiersma, Stall et Mur, 1989/*Pseudanabaena* Lauterborn group and *Anabaena* (Bory) spp.), except at station TH17 where the dinoflagellate *Heterocapsa triquetra* (Ehrenberg) Stein was dominant (1039 mg m<sup>-3</sup>; 54% of total wet weight biomass). Very high abundances of *Chrysochromulina* spp. Lackey were recorded on 11 July when maximum biomass values of these species were measured at stations TH7, TH13 and TH15 (Fig. 4; 78–83 mg m<sup>-3</sup> corresponding to over  $2.4 \times 10^6$  cells L<sup>-1</sup>). Among nanoflagellates, high biomass values were also contributed by prasino-phytes, *Pyramimonas* spp. Schmarida, especially at stations TH7, TH11, TH23 and TH25 (>100 mg m<sup>-3</sup>; >12% of total wet weight biomass).

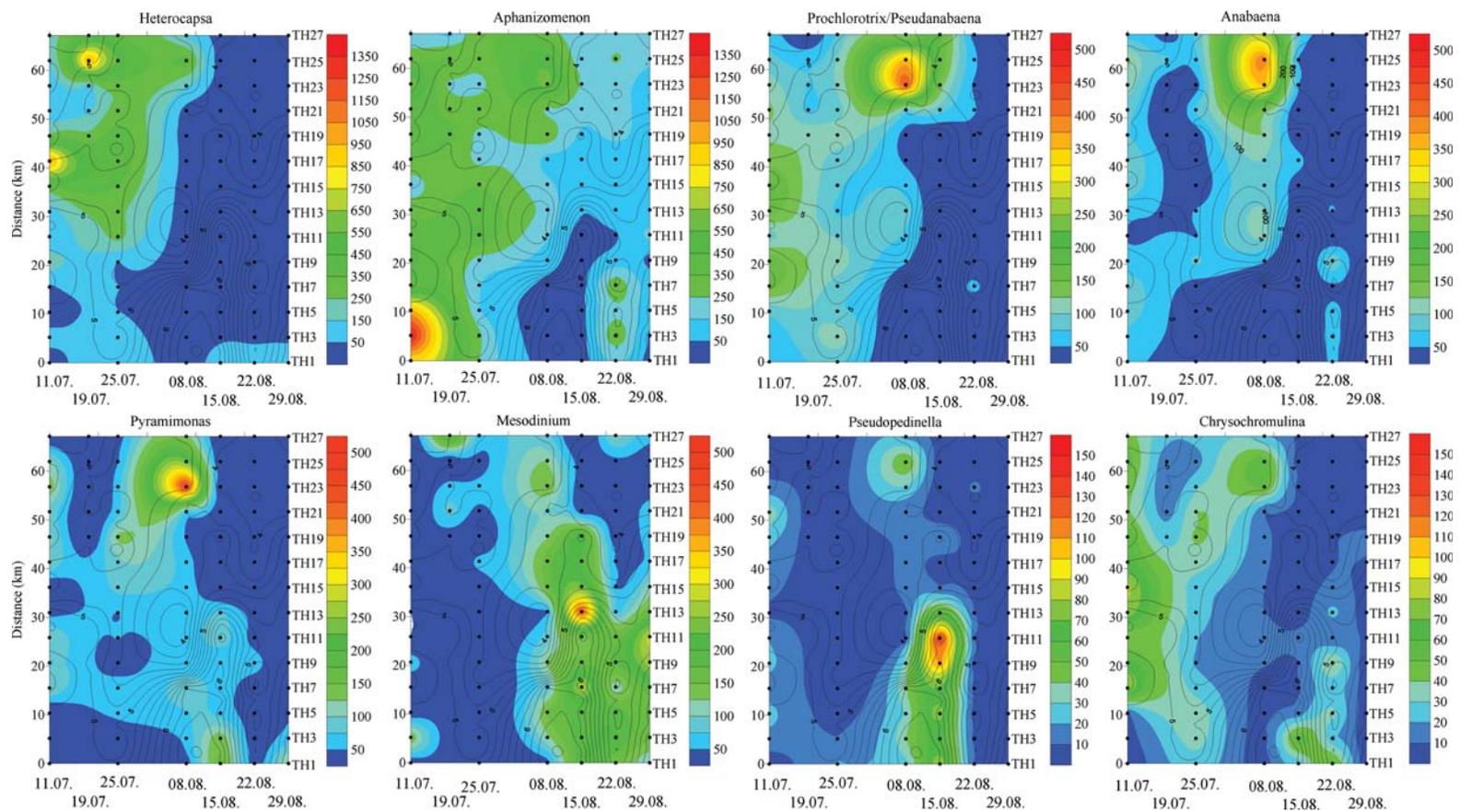
The development of an upwelling event near the Finnish coast on 19 July caused changes in the species distribution and community structure in the northernmost part of the study transect. At station TH27, biomass was mostly formed by *H. triquetra* (36% of total wet weight biomass), *Myrionecta rubra* (Lohmann 1908) Jankowski 1976 (26%), *Dinophysis acuminata* Claparède and Lachmann (11%) and *Aphanizomenon* sp. (11%). In comparison with the biomass values measured a week before, the following changes were observed: *H. triquetra* biomass increased from 169 to 368 mg m<sup>-3</sup>, *M. rubra*

from 6 to 265 mg m<sup>-3</sup>, *D. acuminata* from 0 to 111 mg m<sup>-3</sup> and *Aphanizomenon* sp. biomass decreased from 157 to 110 mg m<sup>-3</sup>. At station TH25, the biomass of *H. triquetra* was about three times higher than that at station TH27 and more than a half of total wet weight biomass was formed by this species (1013 mg m<sup>-3</sup>; 56%). The second dominant species at station TH25 was *Aphanizomenon* sp. (368 mg m<sup>-3</sup>; 22%). Among small flagellates, *Eutreptiella* spp. de Cunha dominated but the biomass was low (22–24 mg m<sup>-3</sup>; 25–35% of total nanoplankton wet weight biomass).

On 25 July, phytoplankton biomass was gradually increasing towards the north along the cross-section. Higher biomass values at stations TH25–TH27 (1284–1381 mg m<sup>-3</sup>) were dominated by *H. triquetra*, *Aphanizomenon* sp. and *Nodularia spumigena* Mertens (324–542 mg m<sup>-3</sup>, 25–39%; 292–339 mg m<sup>-3</sup>, 21–26% and 130–211 mg m<sup>-3</sup>, 9–16%, respectively). At the other stations, *N. spumigena* was detected in significant amounts only at station TH3 (~300 mg m<sup>-3</sup>; 31%) and *H. triquetra* had higher biomass also at stations TH11–TH23 (260–440 mg m<sup>-3</sup>; 24–41%). Among nanoflagellates, *Chrysochromulina* spp. had higher biomass at stations TH17–TH21 (36–43 mg m<sup>-3</sup>; 3.4–4% of total wet weight biomass) and *Pyramimonas* spp. in a wider open gulf area at stations TH15–TH23 (64–137 mg m<sup>-3</sup>; 6–13%).

### August

The development of upwelling near the southern coast of the gulf in the beginning of August had a dramatic influence not only on the distribution pattern of temperature, salinity and nutrients (Fig. 3A–D; 8 August), but also on the phytoplankton Chl *a* and total biomass distribution (Fig. 3E and F) and community structure (Fig. 4) along the entire cross-section. On 8 August, the surface waters at stations TH1–TH7, previously dominated by filamentous cyanobacteria and the dinoflagellate *H. triquetra* (54–78 and 8–20% of total wet weight biomass, respectively), were dominated by the photosynthetic ciliate *M. rubra* (23–42%) and small-sized flagellates *Pyramimonas* spp. and *Pseudopedinella* spp. N. Carter 1937 (19–30 and 8–17%, respectively). The decrease in filamentous cyanobacteria biomass at stations TH1–TH7 in comparison with that measured before the development of upwelling was, on average, from 101 mg m<sup>-3</sup> to 8 mg m<sup>-3</sup> and in dinoflagellate *H. triquetra* biomass from 76 mg m<sup>-3</sup> to 5 mg m<sup>-3</sup>. The increase in *Pyramimonas* spp. biomass was, on average, from 47 to 64 mg m<sup>-3</sup> and in *Pseudopedinella* spp. biomass from 10 to 33 mg m<sup>-3</sup> in the same area. *Myrionecta rubra* increased in biomass from 2 to 97 mg m<sup>-3</sup>. Very high biomass communities in the northern part of the



**Fig. 4.** Temporal change of biomass of different phytoplankton species in the UML along the study transect from 11 July to 29 August 2006. Dots indicate sampling points; sampling dates are shown on the x-axis; distance in kilometres from station TH1 and sampling stations are shown on the y-axes. Corresponding salinity distribution is shown by black contour lines.

cross-section at stations TH23–TH25 were dominated by filamentous cyanobacteria *Aphanizomenon* sp. (23–26%), *Anabaena* spp. (15–22%) and *Prochlorothrix/Pseudanabaena* group (9–18%). The increase in biomass, if compared with that measured on 25 July in the same area, was as follows: from 250 to 566 mg m<sup>-3</sup> in *Aphanizomenon* sp., from 48 to 384 mg m<sup>-3</sup> in *Anabaena* spp. and from 102 to 401 mg m<sup>-3</sup> in *Prochlorothrix/Pseudanabaena* group biomass. Dinoflagellate *H. triquetra* had high (yet lower than that observed in July) biomass value only at station TH25 contributing with 18% to the total wet weight biomass. Among small flagellates, very high biomass was formed by *Pyramimonas* spp. at stations TH23 and TH25 (230–480 mg m<sup>-3</sup>; 10–20% of total wet weight biomass; Fig. 4). The biomass of the latter species increased between the two surveys from 56 to 356 mg m<sup>-3</sup>.

By 15–16 August, the upwelling area had widened off shore (Fig. 3A–D) and at the same time an increase in Chl *a* and phytoplankton biomass were detected (Fig. 3E and F). Even the total biomass values in the area affected by upwelling (stations TH1–TH11) had increased, the community was still dominated by *M. rubra* (25–47%) and small-sized flagellates *Pyramimonas* spp. and *Pseudopedinella* spp. (11–23 and 11–26%, respectively). *Myrionecta rubra* biomass increased in comparison with the previous week, on average, from 97 to 168 mg m<sup>-3</sup>, and *Pyramimonas* spp. and *Pseudopedinella* spp. biomass from 64 to 98 mg m<sup>-3</sup> and from 33 to 90 mg m<sup>-3</sup>, respectively. Additionally, small flagellates *Chrysochromulina* spp. (1.4–11% of total wet weight biomass) and cryptomonads (3.7–7%) appeared in the community in a considerable amount. The increase in biomass, on average, from 6 to 22 mg m<sup>-3</sup> and from 16 to 26 mg m<sup>-3</sup>, respectively, was measured. The highest biomass of *M. rubra* (446 mg m<sup>-3</sup>, 55%) was measured at station TH13 in the upwelling front. In less saline waters, which appeared at the northern end of the study transect (stations TH21–TH27, Fig. 3B), the communities were dominated by filamentous and colonial cyanobacteria species (72–88%).

After the change in wind direction from mainly easterly winds to south-westerly winds in the period from 16 to 20 August, the relaxation of upwelling occurred by 22 August and the phytoplankton community structure in the sea area previously affected by upwelling changed. *Myrionecta rubra* was still one of the dominants (12–28%) in this region, but the other dominants were N<sub>2</sub>-fixing filamentous cyanobacteria *Aphanizomenon* sp. (14–43%) and *Anabaena* spp. (6–16%). In comparison with the sampling on 15–16 August, the increase, on average, from 7 to 205 mg m<sup>-3</sup> in *Aphanizomenon* sp. and from 4 to 59 mg m<sup>-3</sup> in *Anabaena* spp. biomass was

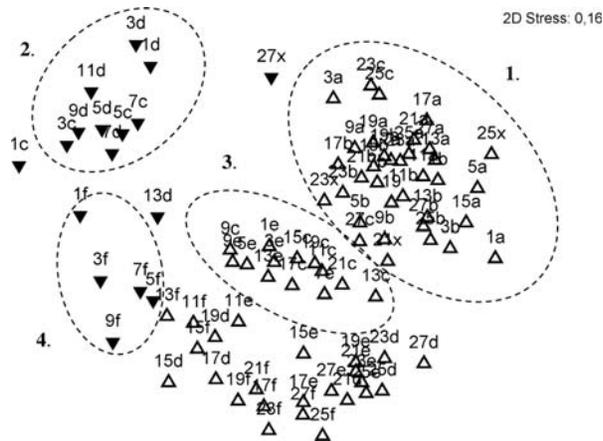
measured at stations TH1–TH11. At the southernmost station TH1, 10% of total wet weight biomass was formed by *H. triquetra*. Small flagellates dominating during the upwelling event had decreased in biomass. Chrysophytes *Pseudopedinella* spp. had almost disappeared from the community. Prasinophytes *Pyramimonas* spp. contributed 3–10% to the total wet weight biomass (decrease from 90 to 6 mg m<sup>-3</sup> on average). Prymnesiophytes *Chrysochromulina* spp. and cryptomonads had slightly decreased in biomass (contributing 3–7.5 and 2–4% of total wet weight biomass, respectively).

The development of the next upwelling event along the southern coast of Gulf of Finland, which was sampled on 29 August, changed the phytoplankton community structure in the area affected by the upwelling again. The ciliate *M. rubra* slightly increased in biomass compared with the previous week (Fig. 4) and contributed 18–53% of total wet weight biomass. Similarly to the previous upwelling event, *Pyramimonas* spp. had a considerable share in the total wet weight biomass (12–26%) at stations TH1–TH5. At the same time, *Pseudopedinella* spp. did not show any increase in biomass during this upwelling event (Fig. 4). Instead, the contribution of *H. triquetra* and heterotrophic naked dinoflagellates to the total wet weight biomass slightly increased (5–21 and 3–19%, respectively, at stations TH1–TH7), although the biomass of *H. triquetra* stayed relatively low (110 mg m<sup>-3</sup>). The contribution of *Aphanizomenon* sp. to the total wet weight biomass was very small at the near shore station but gradually increased off shore (Fig. 4). The biomass of cryptophytes and *Chrysochromulina* spp. (Fig. 4) was low in the area affected by the upwelling on 29 August.

## MDS analysis

MDS analysis of similarities in the community structure at all stations during the entire study period clearly categorized the phytoplankton composition into several distinguishable clusters. Area 1 in Fig. 5 includes stations before the upwelling event on 11 and 25 July and those which were not affected by the major upwelling on 8 August (23c–27c in Fig. 5). The same community structure was revealed on 19–20 July, except that at station TH27 (marked as 27x in Fig. 5). Thus, the phytoplankton community was relatively stable in the area in July and the high biomass community observed on 8 August in the northern part of the study transect matches with the July community.

The stations sampled during the major upwelling event in the southern part of the study transect were



**Fig. 5.** MDS plot for all sampled stations based on Bray–Curtis similarity distances of phytoplankton composition. Stations are indicated as numbers TH1–TH27 = 1–27 and sampling dates as letters: a—11 July, b—25 July, c—8 August, d—15 August, e—22 August, f—29 August and x—19 July. Filled triangles mark the stations sampled in the upwelling areas.

grouped in area 2 (1c–7c and 1d–11d). Station TH1 was not placed at the same point in different weeks as the bigger share of *Chrysochromulina* spp. and cryptomonads was found in the southernmost part of the upwelling area on 15–16 August compared with the communities on 8 August. Area 3 includes the stations from the central part of the study area (9c–21c) sampled on 8 August where the phytoplankton community clearly differed from both the July community and the upwelling water community. Dissimilar communities to all those described above were observed on 15–16 August in the areas outside the upwelling waters, whereas the community in the upwelling front (13d) was closer to the upwelling community than to the communities outside the upwelling area.

MDS analysis shows strong similarity in the community structure at stations TH1–TH9 (1e–9e) on 22 August with the community structure sampled on 8 August at stations TH9–TH21 (9c–21c; area 3 in Fig. 5). The phytoplankton community at station TH13 (13e) on 22 August matches the same group, while the community in a colder water patch at station TH11 (11e) was slightly different. The communities at the rest of stations on 22 August were close to the community observed at stations TH21–TH27 (21d–27d) a week earlier. Area 4 includes the stations sampled in the upwelling area on 29 August. Those communities differed from the ones observed during the previous upwelling event in the same area. The communities in the northern half of the study transect, which stayed outside the upwelling influence on 29 August, diverged from the previously observed communities as well.

## DISCUSSION

Patti *et al.* (Patti *et al.*, 2008) have suggested that in the major coastal ocean upwelling regions several driving factors, such as nutrient concentration, light availability, shelf extension and a surface turbulence proxy must be taken into account when investigating the phytoplankton biomass distribution. Wind-driven transport and mixing play three key roles in shelf productivity: nutrient supply to the euphotic zone, light control through vertical mixing of primary producers and offshore export of near surface plankton. However, while the first process yields a strong positive biological response to upwelling winds, the other two influences lead to negative productivity responses to increased wind (Largier *et al.*, 2006). During the coastal upwelling events in the Baltic Sea, the distribution of phytoplankton biomass and production have been found to be strongly influenced by the combined effects of physico-chemical processes and to be related to the strength of wind and hence upwelling events (Kononen and Niemi, 1986; Vahtera *et al.*, 2005; Zalewski *et al.*, 2005; Nausch *et al.*, 2009). In the Gulf of Finland, there is a strong upwelling–downwelling coupling because of the elongated shape and relatively short distance (48–135 km) between northern and southern coasts. The development of upwelling along the southern coast of Gulf of Finland in the first half of August 2006 had a strong influence on the spatial distribution of phytoplankton biomass/species (Figs 3F and 4) and community structure (Fig. 5) along the entire cross-section between Tallinn and Helsinki. In general, a strong biomass decrease in the area affected by the major upwelling event and an increase of biomass near the opposite coast was observed, and there was strong evidence of negative and positive effects of this event on different phytoplankton species.

In plankton community studies very often phytoplankton are divided into several size classes. At low nutrient levels, phytoplankton species succession usually proceeds towards small and motile species with high surface to volume ratios, which give an advantage in nutrient uptake (e.g. Kjørboe, 1993). In ocean upwelling systems, larger and especially diatom species are considered to dominate the phytoplankton community (e.g. Lassiter *et al.*, 2006; Anabalón *et al.*, 2007). In contrast to the general understanding and expectations, in our observations the smaller phytoplankton size fraction showed a faster response to the upwelled nutrients compared with the larger size fraction. It was shown by Kuvaldina *et al.* (Kuvaldina *et al.*, 2010) that a clear increase in Chl *a* mostly in <20  $\mu\text{m}$  size class occurred during the stabilization phase of the upwelling (sampled

on 15–16 August 2006), while an increase of Chl *a* in larger size fraction was observed after the upwelling relaxation on 22 August. Stolte *et al.* (Stolte *et al.*, 1994) described how larger phytoplankton cells can only become dominant when  $\text{NO}_3^-$  is the major nitrogen source available and  $\text{NH}_4^+$  is low or at detection levels, as is typically seen in oceanic coastal upwelling ecosystems. Koike *et al.* (Koike *et al.*, 1986) found that on average only 50% of the  $\text{NO}_3^-$  uptake is by organisms in the  $<20\ \mu\text{m}$  size fraction, while all the  $\text{NH}_4^+$  uptake occurred the same fraction. According to the Finnish marine monitoring data ([http://www.itameriportaali.fi/en/tietoa/helcom\\_seuranta/en\\_GB/bmp\\_data](http://www.itameriportaali.fi/en/tietoa/helcom_seuranta/en_GB/bmp_data)), the  $\text{NH}_4^+$  concentrations in the lower layers of the Gulf of Finland where the upwelling water originates were comparable to the nitrates + nitrites concentrations in July–August 2006. The median and mean values were 1.6 and 1.8  $\mu\text{M}$ , respectively, between the 30 m depth and the sea bed. High  $\text{NH}_4^+$  concentrations in the upwelling waters have been also measured earlier in the Gulf of Finland, e.g. up to 1.43  $\mu\text{M}$  by Haapala (Haapala, 1994) in summer and up to 3.2  $\mu\text{M}$  by Lignell *et al.* (Lignell *et al.*, 2003) in autumn, whereas in the later case the nitrate concentrations up to 2.2  $\mu\text{M}$  were observed. Thus, we suggest that the phytoplankton growth observed in the upwelling area, initially mostly in the smaller size fraction (*Pyramimonas* spp. and *Pseudopedinella* spp.), could be related to the possible higher proportion of ammonium in the upwelled dissolved inorganic nitrogen pool.

As shown by the previous studies in the Gulf of Finland (Kanoshina *et al.*, 2003; Vahtera *et al.*, 2005), the growth of *Eutreptiella gymnastica* Thronsdén, *Chrysochromulina* spp. and cryptophytes has been influenced by the coastal upwelling events. During our study, *Eutreptiella* spp. dominated among nanoflagellates (25–35% of total nanoplankton wet weight biomass) only on 19 July in the upwelling area at the northernmost part (stations TH25–TH27) of the cross-section, but the biomass values were very low. There was no biomass increase observed in connection to the major upwelling event along the southern coast in August. Chrysophytes *Pseudopedinella* spp. were abundant only during the major upwelling event near the southern coast and their increased biomass values were limited with the upwelling time and area except for slightly increased biomass near the northern coast on 8 August (Fig. 4). *Pyramimonas* spp. were also positively influenced by the major upwelling event in August near the southern coast of the Gulf of Finland, although the highest biomass was observed on 8 August in the northern part of the study transect. *Chrysochromulina* spp. had highest biomass on 11 July and a decrease in biomass was

observed during the initiation phase of the upwelling while a consecutive increase in biomass followed during the stabilization phase and the biomass stayed relatively high also after the relaxation of upwelling.

Mesocosm studies (Uitto and Hällfors, 1997; Lagus *et al.*, 2004; Kangro *et al.*, 2007) have shown that *Pseudopedinella* spp. have high growth rates in high nutrient enrichment conditions and the other experiments (Kononen *et al.*, 1993; Andersson *et al.*, 2006) have also revealed the positive response of *Pyramimonas* spp. to nutrient enrichment following the sharp decline caused by predation of increased microzooplankton community. Thus, these species have a high requirement for nutrients, and hence might have a competitive advantage during upwelling events which explain the increase in their biomass in the major upwelling area in our study. As shown by studies of Hajdu *et al.* (Hajdu *et al.*, 1996), stronger stratification may be one of the factors influencing *Chrysochromulina* spp. abundance positively during summer to early autumn in the Baltic Sea. New input of limiting nutrients during the upwelling event at the beginning of August together with the stabilization of upwelling and rise of the UML temperature (leading to development of stratification) might have caused the *Chrysochromulina* spp. biomass increase in the Estonian coastal waters observed on 15–16 August. Also phosphorus deficiency in the UML gives a competitive advantage through toxin production (Estep and MacIntyre, 1989) and hence helps to explain the high abundances at periods with low phosphate concentrations (e.g. along our study transect in July 2006, Fig. 4).

Among larger size fraction, the biomass of the photosynthetic ciliate *M. rubra* increased remarkably during the upwelling event and remained at high values till the end of August almost along the entire cross-section. The biomass increase of latter species during the upwelling event was first connected with the vertical transport of seed population from lower layers followed by growth in the nitrate-rich upwelled waters in the euphotic layer. The former conclusion is supported by sampling on 11 July at stations TH1–TH3 where in the lower part of thermocline (17.5–20 m), biomass of this species of up to 246  $\text{mg m}^{-3}$  was measured. High biomass values and even blooms of *M. rubra* have been observed in upwelling areas (e.g. reviewed by Crawford, 1989). The species has been shown to have a high demand for inorganic nitrogen, but also one to four times higher uptake rate for nitrate than e.g. diatoms or dinoflagellates (Wilkerson and Grunseich, 1990). The latter helps also explain the rapid exhaustion of inorganic nitrogen compounds in *M. rubra* dominated upwelling areas. The competitive advantage during nutrient limitation is

retained probably by changing the trophic status from phototrophy to phagotrophy (e.g. Yih *et al.*, 2004) and by the species' very high swimming speed (e.g. Lindholm, 1985; Villarino *et al.*, 1995), which allows it to exploit resources from deeper water layers as well as from nutrient patches.

A *H. triquetra* bloom has been detected in the upwelling area in the Gulf of Finland in 1998 (Kanoschina *et al.*, 2003) when the biomass values reached as high as  $4500 \text{ mg m}^{-3}$ . During our study in 2006, the biomass of this species was high (up to  $1040 \text{ mg m}^{-3}$ ) mostly only in July in the northern part of the Gulf of Finland. High biomass values did not extend to the Tallinn Bay and no remarkable biomass increase was found during and after the major upwelling event near the southern coast where biomass only up to  $100 \text{ mg m}^{-3}$  was measured. We noticed that the highest *H. triquetra* biomass values observed at station TH17 on 11 July and at station TH25 on 19 July were associated with relatively low Chl *a* concentrations. Kononen *et al.* (Kononen *et al.*, 1993) have shown that at low irradiances Chl *a* concentration in a pure culture of *H. triquetra* decreased rapidly while the cells could maintain their *in vivo* fluorescence for a week. Since the Chl *a* fluorescence in the UML at these stations was remarkably high (data not shown here), we suggest that *H. triquetra* was transported there from the seasonal thermocline. This suggestion is supported by the CTD data from 19 July showing that the isopycnal, which surfaced in the upwelling front (station TH25), was located at 12 m depth at a distance of 5 km towards the open gulf (station TH23).

Vahtera *et al.* (Vahtera *et al.*, 2005) found relatively high biomass of *Aphanizomenon* sp. in the upwelling front in the northern part of the Gulf of Finland in 1998 and they explained this by the displacement of populations of *Aphanizomenon* sp., which before the upwelling event resided in the thermocline. We observed similarly relatively high biomass of *Aphanizomenon* sp. biomass in the upwelling front on 19 July in the northern part of the gulf. However, the biomass of *Aphanizomenon* sp. was negligible during the major upwelling event sampled on 8 and 15–16 August near the southern coast; also on 11 July, the biomass of this species up to  $1300 \text{ mg m}^{-3}$  was measured at stations TH1–TH3 at 12.5 m depth (upper part of the thermocline; at the same time its biomass did not exceed  $150 \text{ mg m}^{-3}$  at 15 m depth and below). It could be explained by the fact that the upwelled water during the major event near the southern coast had its origin from much deeper layers than that during the earlier upwelling in the northern part. It was estimated by Lips *et al.* (Lips *et al.*, 2009) that the upwelling water on 8 August consisted of a

mixture of waters from below the thermocline and from the UML with a share of 85 and 15%, whereas the higher temperatures observed in the upwelling water on 19 July indicate that this water mass had its origin mainly from the seasonal thermocline.

There was a clear increase in phytoplankton Chl *a* and biomass after the relaxation of the major upwelling sampled on 22 August (Fig. 3E and F). However, the highest total phytoplankton biomass was observed on 8 August in the northern part of the study transect. Even the observed major upwelling event brought large amount of inorganic nutrients to the nutrient depleted UML, it can be seen from the nutrient analyses that nitrates + nitrites were below the lower detection range already by 15–16 August and phosphates by 22 August (Fig. 3C and D). In contrast, the phosphate concentrations exceeding the lower detection range were observed in the UML in the northern part of the study transect on 25 July and 8 August. Due to our sampling strategy, we could not point to a direct link between the upwelling observed on 19–20 July and the slightly elevated phosphate content observed in the northern gulf on 25 July and 8 August. We rather relate the elevated phosphate content and high phytoplankton biomass to the meso-scale features observed at the mentioned sampling days. Especially, a clear relationship was evident on 8 August, when according to the vertical distributions of temperature, salinity and density (Lips *et al.*, 2009), anti-cyclonic like vertical distribution of isopycnals was observed in the downwelling area coupled with the major upwelling. The highest biomass values at stations TH23 and TH25 coincided with this meso-scale feature where domed isopycnals caused shallowing of the UML to only 5 m against the background of relatively deep UML in the rest of the downwelling area.

Earlier modelling and field experiments have shown that regardless of how much nutrient is upwelled during the upwelling phase, if a suitable period of relaxation follows, all is taken up within  $72 \text{ h} = 3 \text{ days}$  (Zimmerman *et al.*, 1987; Dugdale *et al.*, 1990) and high levels of primary productivity are found in 3- to 7-day-old upwelled waters after the relaxation following the upwelling impulse (Botsford *et al.*, 2006; Wilkerson *et al.*, 2006) in the ocean upwelling systems. When upwelling relaxes and the supply of new nutrients decreases/disappears, phytoplankton populations may survive by using intracellular storages or regenerated forms of nutrients such as ammonium and urea (e.g. Bode *et al.*, 1997). As the nitrates + nitrites were exhausted rapidly and there was still plenty of phosphates in the UML on 15–16 August (Fig. 3D), one could hypothesize that the depletion of the latter

nutrient and the increase of biomass of filamentous  $N_2$ -fixing cyanobacteria *Aphanizomenon* sp. and *Anabaena* sp. (Fig. 4) observed on 22 August could be due to the growth induced by upwelled excess dissolved inorganic phosphorus (DIP). However, the results of MDS analysis indicated very high similarity of phytoplankton community in the area previously affected by the upwelling (stations TH1–TH13, except station TH11) on 22 August to the community found in the central part of our cross-section during the intensive upwelling event on 8 August (Fig. 5). Thus, the phytoplankton biomass increase could be connected to the relaxation of upwelling and subsequent reversal movement of surface water masses together with the utilization of mostly regenerated but also stored nutrients. While, because of a long time for bloom development, the phytoplankton community may be lost from the system and moved quite far in oceanic upwelling areas (e.g. Botsford *et al.*, 2006), in the case of variable wind-induced upwelling in the elongated Gulf of Finland, plankton community may not move far before being brought back again. The absence of cyanobacteria dominated community described on our study transect on 15–16 August and possibly some other changes observed in the community structure could be related to the along-shore (along the gulf axis) advection, which has been shown to be very important in coastal upwelling systems, e.g. in the California Current System (Botsford *et al.*, 2006).

The development of a next upwelling event by 29 August caused a decrease in phytoplankton biomass and the observed changes in the community composition support the above-described importance of wind-induced Ekman transport in shaping the overall response of phytoplankton to the coastal upwelling events in the Gulf of Finland ecosystem. The response of the phytoplankton community to several consecutive upwelling events in the same area is not similar and is most probably influenced by the amount and ratio of upwelled nutrients, and also by the strength of the upwelling that determines from which layers the upwelled water originates from and consequently what is the initial community structure in the upwelling area.

## CONCLUSIONS

During the upwelling events in the Baltic Sea, transport of large amounts of inorganic nutrients from the lower layers to the surface layer may occur. Due to the nutrient intrusion, changes in temperature, advection and replacement/mixing of water masses, not only single phytoplankton species are affected but also the entire phytoplankton communities are changed in a short time

period. The response of different phytoplankton species/size classes tends to be very much influenced by the concentration/ratio of upwelled nutrients also by the strength of the upwelling events that determines the water layers where the upwelling water originates from. In general, we found that the increase of biomass takes much longer time than the observed abrupt changes in the phytoplankton community caused by upwelling or horizontal advection (convergence/divergence) of water masses. Thus, one should be careful in using the collected and analysed chemical and phytoplankton data for assessing the status of the Gulf of Finland ecosystem due to the very dynamic nature of this estuary and the background information (climatic conditions and prevailing hydro-physical processes) have to be considered for this purpose.

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