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**PHYTOPLANKTON DYNAMICS AFFECTED BY THE COASTAL
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AUGUST 2006**

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Review

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2 **PHYTOPLANKTON DYNAMICS AFFECTED BY THE COASTAL UPWELLING EVENTS**
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4 **IN THE GULF OF FINLAND IN JULY-AUGUST 2006**
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52 Keywords: Coastal upwelling, nutrients, phytoplankton, Gulf of Finland, Baltic Sea.
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ABSTRACT

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 two 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 three 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. MDS analysis matches this relatively high biomass community with the communities observed outside the area of upwelling influence two 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.

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 outcompete 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).

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

22 **Study area and sampling**

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24 Mapping of hydrographic, chemical and biological fields was carried out in the central part of the Gulf
25 of Finland (Fig. 1) in July–August 2006 (11 July, 19–20 July, 25 July, 8 August, 15–16 August, 22
26 August and 29 August). The southernmost sampling station TH1 was located < 2 km off the coast in
27 the Tallinn Bay and the northernmost station TH27 about 5 km from the archipelago area off Helsinki.
28 The width of the gulf in the study area is < 80 km. The water depths are 25–40 m in the inner Tallinn
29 Bay followed by a steep bottom sloping to about 90 m in the southern part of the open gulf and a
30 general northward shallowing with remarkable irregularities of the sea bed. Vertical profiles of
31 temperature, salinity and chlorophyll *a* fluorescence were recorded at 27 stations (distance between
32 stations 2.6 km) and water samples for inorganic nutrient (PO_4^{3-} , $\text{NO}_2^- + \text{NO}_3^-$), chlorophyll *a* and
33 phytoplankton analyses were collected at 14 stations (except on 19–20 July when sampling was made
34 only at the northernmost stations TH19–27; distance between stations 5.2 km) from the upper mixed
35 layer. Water samples for nutrient analyses were collected also from the seasonal thermocline with a
36 vertical resolution of 2.5–5.0 metres.
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52 **Chemical and biological analyses**

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54 Measurements were carried out using a NBIS Mark III CTD (conductivity, temperature, depth) probe
55 and an SBE 19 CTD probe (Sea-Bird) equipped with a WETStar fluorimeter (WET Labs). The salinity
56 values were calculated using algorithms from Fofonoff and Millard Jr. (1983) and are presented
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2 without units. Salinity data were quality checked against the water sample analyses by a high precise
3 salinometer AUTOSAL (Guildline). A rosette sampler with 8 Niskin water samplers (volume 1.7 l) was
4 used for sampling. To represent the upper mixed layer (UML), the samples were prepared by pooling
5 three (in case of a shallow UML – two) samples taken from the surface layer from the 1-m depth down
6 to the seasonal thermocline, the depth of which was determined from the CTD casts.
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13 Nutrient analyses were carried out according to the guidelines of the American Public Health
14 Association (APHA, 1992; methods 4500-NO₃ F and 4500-P F) and analysed using an automatic
15 nutrient analyzer μ Mac 1000 (Systea S.r.l.). The lower detection range for phosphate-phosphorus and
16 nitrate+nitrite-nitrogen was 1 ppb (parts per billion; 0.03 μ M and 0.07 μ M, respectively; with a
17 measurement uncertainty of 20% near the detection limit). Samples for phosphates (PO₄³⁻) were mostly
18 analysed immediately onboard after sampling and samples for dissolved inorganic nitrogen compounds
19 (NO₃⁻+NO₂⁻) determination were deep-frozen after collection and analysed later in the on-shore
20 laboratory.
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29 The chlorophyll *a* (Chl *a*) content from UML (pooled sample prepared as described above) was
30 determined on Millipore APFF glass-fibre filters following the extraction at room temperature in the
31 dark with 96% ethanol for 24 hours. Chlorophyll *a* content from the extract was measured
32 spectrophotometrically (Thermo Helios γ ; photometric accuracy: $\pm 0.005A$ at 1A) in the laboratory
33 (HELCOM, 1988).
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40 Phytoplankton sub-samples (100 ml) were preserved with acid Lugol solution and analysed using the
41 Utermöhl (1958) technique and PhytoWin software by Kahma Ky. Cyanobacterial filaments were
42 counted as 100- μ m segments and other phytoplankton species as single cells or colonies. All biomass
43 data are given as wet weight.
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49 **Data analysis**

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51 Statistical analysis was performed using the PRIMER 6.0 software (PRIMER-E Ltd) with user
52 guidelines (Clarke and Warwick, 2001). To compare the community structure at different sampling
53 stations on different sampling days the ordination of samples by multi-dimensional scaling (MDS) was
54 performed. Biomass of all species at all stations was used for Bray-Curtis similarity coefficient
55 (transformed by square root) calculations.
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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,b). On the basis of water sample analyses, only PO_4^{3-} 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,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 μM of $\text{NO}_3^- + \text{NO}_2^-$ and 0.79 μM of PO_4^{3-} 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_4^{3-} concentrations in the upwelling water within a week between surveys on 8 and 15–16 August (Fig. 3c,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

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2 At the beginning of study on 11 July 2006, phytoplankton Chl *a* and biomass distribution (Fig. 3e,f) in
3 the UML were patchy along the cross-section between Tallinn and Helsinki in the Gulf of Finland. The
4 Chl *a* concentrations varied between 3.4 and 7.1 mg m⁻³ and the total wet weight phytoplankton
5 biomass ranged between 580 and 2050 mg m⁻³. A comparison of Chl *a* and biomass values revealed
6 some discrepancies in their horizontal distributions on 11 July, especially at station TH17 where a local
7 minimum of Chl *a* (4.8 mg m⁻³) coincided with a local maximum of total biomass (1920 mg m⁻³). On
8 19 July, an upwelling event, which developed in the northern part of the cross-section, influenced Chl *a*
9 and phytoplankton biomass values in the UML. Against a background of a relatively low
10 phytoplankton Chl *a* and biomass level in the northern part of the study area, higher values were
11 measured at station TH25, which could be regarded as the upwelling front (see Fig. 3a). However, a
12 significant maximum of total biomass (1820 mg m⁻³) was associated with a relatively moderate
13 maximum of Chl *a* (5.1 mg m⁻³). A more uniform distribution of phytoplankton Chl *a* and biomass with
14 lower values in the southern part and higher values in the central and northern part of the study transect
15 was observed on 25 July. The Chl *a* and biomass distributions were well correlated, the values varied
16 between 3.9 and 6.4 mg m⁻³, and 480 and 1380 mg m⁻³, respectively.
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30 A clear decline in Chl *a* concentration and phytoplankton biomass in the Tallinn Bay and a sharp
31 increase in the northern part of the cross-section were observed on 8 August. The decrease of Chl *a*
32 from 4.2 to 1.8 mg m⁻³ and total biomass from 950 to 290 mg m⁻³ at the southern end of the study
33 transect was related to the low phytoplankton biomass in the cold upwelled water. The highest Chl *a*
34 (14.3 mg m⁻³) and biomass (2320 mg m⁻³) values were measured at stations TH23 and TH25 in the
35 area, which could be regarded as an area of the horizontal convergence of surface waters due to the
36 northward Ekman drift in the UML.
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45 The decrease in inorganic nutrient concentrations coincided with an increase in Chl *a* and
46 phytoplankton biomass values during the stabilization and relaxation phases of the observed upwelling
47 (Fig. 3e,f; 15–16 and 22 August respectively). The average phytoplankton Chl *a* and biomass values at
48 the four southernmost sampling stations (TH1, TH3, TH5, TH7) occupied by the upwelling event on 8
49 August increased from 1.8 mg m⁻³ and 290 mg m⁻³ to 3.8 mg m⁻³ and 600 mg m⁻³ by 15–16 August and
50 to 5.0 mg m⁻³ and 800 mg m⁻³ by 22 August. At the same time the phytoplankton Chl *a* and biomass
51 decreased at the northernmost part of the study transect from the observed maximum values on 8
52 August to 6.6 mg m⁻³ and 750 mg m⁻³ by 15–16 August and to 5.4 mg m⁻³ and 720 mg m⁻³ by 22
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2 August. At the sampling stations in the open gulf (TH9–TH21) the temporal variability of Chl *a* and
3 phytoplankton biomass in the period from 8 August to 22 August was not as high as that described
4 above in relation to the southernmost and northernmost parts of the study transect. However, a local
5 maximum of phytoplankton biomass of 820 mg m⁻³ at station TH13 on 15 August and a local minimum
6 of biomass of 470 mg m⁻³ at station TH11 on 22 August was noted. The maximum was related to the
7 upwelling front (see Fig. 3a,b; 15–16 August) and the minimum to a slightly colder and saltier surface
8 water patch (Fig. 3a,b; 22 August).

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16 The last upwelling event at the end of August also had a significant impact on the Chl *a* (decrease from
17 5.0 to 2.7 mg m⁻³) and the total phytoplankton biomass (decrease from 800 mg m⁻³ to 480 mg m⁻³) and
18 distribution in the upwelling area in the Tallinn Bay. At the same time both the Chl *a* and biomass
19 decreased also on the rest of the study transect (but the decrease was less pronounced), where, on
20 average, the Chl *a* concentration decreased from 4.7 to 3.6 mg m⁻³ and total biomass from 620 to 450
21 mg m⁻³.

22 23 24 25 26 27 28 29 **Dynamics of phytoplankton species and community structure**

30 31 *July*

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33 The dynamics of horizontal distribution of some phytoplankton key species are shown in Figure 4. At
34 the beginning of the study (11 July) the distribution of phytoplankton species in the UML did not show
35 any distinguishable pattern. Phytoplankton wet weight biomass (Fig. 3f) was patchy along the sampled
36 cross-section and filamentous cyanobacteria species/groups were dominating in the community
37 (*Aphanizomenon* sp. (L.) Ralfs, *Prochlorothrix* Burger-Wiersma, Stall et Mur, 1989/*Pseudanabaena*
38 Lauterborn group and *Anabaena* (Bory) spp.), except at station TH17 where the dinoflagellate
39 *Heterocapsa triquetra* (Ehrenberg) Stein was dominant (1039 mg m⁻³; 54% of total wet weight
40 biomass). Very high abundances of *Chrysochromulina* spp. Lackey were recorded on 11 July when
41 maximum biomass values of these species were measured at stations TH7, TH13 and TH15 (Fig. 4;
42 78–83 mg m⁻³ corresponding to over 2.4 × 10⁶ cells L⁻¹). Among nanoflagellates high biomass values
43 were also contributed by prasinophytes, *Pyramimonas* spp. Schmarida, especially at stations TH7,
44 TH11, TH23 and TH25 (>100 mg m⁻³; >12% of total wet weight biomass).

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56 The development of an upwelling event near the Finnish coast on 19 July caused changes in the
57 species distribution and community structure in the northernmost part of the study transect. At station
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2 TH27 biomass was mostly formed by *H. triquetra* (36% of total wet weight biomass), *Myrionecta*
3 *rubra* (Lohmann 1908) Jankowski 1976 (26%), *Dinophysis acuminata* Claparède and Lachmann (11%)
4 and *Aphanizomenon* sp. (11%). In comparison with the biomass values measured a week before, the
5 following changes were observed: *H. triquetra* biomass increased from 169 mg m⁻³ to 368 mg m⁻³, *M.*
6 *rubra* from 6 mg m⁻³ to 265 mg m⁻³, *D. acuminata* from 0 mg m⁻³ to 111 mg m⁻³ and *Aphanizomenon*
7 sp. biomass decreased from 157 mg m⁻³ to 110 mg m⁻³. At station TH25 the biomass of *H. triquetra*
8 was about three times higher than that at station TH27 and more than a half of total wet weight biomass
9 was formed by this species (1013 mg m⁻³; 56%). The second dominant species at station TH25 was
10 *Aphanizomenon* sp. (368 mg m⁻³; 22%). Among small flagellates *Eutreptiella* spp. de Cunha dominated
11 but the biomass was low (22–24 mg m⁻³; 25–35% of total nanoplankton wet weight biomass).
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21 On 25 July phytoplankton biomass was gradually increasing towards the north along the cross-section.
22 Higher biomass values at stations TH25–TH27 (1284–1381 mg m⁻³) were dominated by *H. triquetra*,
23 *Aphanizomenon* sp. and *Nodularia spumigena* Mertens (324–542 mg m⁻³, 25–39 %; 292–339 mg m⁻³,
24 21–26 % and 130–211 mg m⁻³, 9–16 % respectively). At the other stations *N. spumigena* was detected
25 in significant amounts only at station TH3 (~300 mg m⁻³; 31%) and *H. triquetra* had higher biomass
26 also at stations TH11–TH23 (260–440 mg m⁻³; 24–41%). Among nanoflagellates *Chrysochromulina*
27 spp. had higher biomass at stations TH17–TH21 (36–43 mg m⁻³; 3.4–4 % of total wet weight biomass)
28 and *Pyramimonas* spp. in a wider open gulf area at stations TH15–TH23 (64–137 mg m⁻³; 6–13 %)
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37 August

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39 The development of upwelling near the southern coast of the gulf in the beginning of August had a
40 dramatic influence not only on the distribution pattern of temperature, salinity and nutrients (Fig. 3 a-d;
41 8 August) but also on the phytoplankton Chl *a* and total biomass distribution (Fig. 3e,f) and community
42 structure (Fig. 4) along the entire cross-section. On 8 August the surface waters at stations TH1–TH7,
43 previously dominated by filamentous cyanobacteria and the dinoflagellate *H. triquetra* (54–78 % and
44 8–20 % of total wet weight biomass respectively), were dominated by the photosynthetic ciliate *M.*
45 *rubra* (23–42 %) and small-sized flagellates *Pyramimonas* spp. and *Pseudopedinella* spp. N. Carter
46 1937 (19–30 % and 8–17 % respectively). The decrease in filamentous cyanobacteria biomass at
47 stations TH1–TH7 in comparison with that measured before the development of upwelling was, on
48 average, from 76 mg m⁻³ to 5 mg m⁻³ and in dinoflagellate *H. triquetra* biomass from 101 mg m⁻³ to 8
49 mg m⁻³. The increase in *Pyramimonas* spp. biomass was, on average, from 47 mg m⁻³ to 64 mg m⁻³ and
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2 in *Pseudopedinella* spp. biomass from 10 mg m⁻³ to 33 mg m⁻³ in the same area. *M. rubra* increased in
3 biomass from 2 mg m⁻³ to 97 mg m⁻³. Very high biomass communities in the northern part of the cross-
4 section at stations TH23–TH25 were dominated by filamentous cyanobacteria *Aphanizomenon* sp. (23–
5 26 %), *Anabaena* spp. (15–22 %) and *Prochlorothrix/Pseudanabaena* group (9–18 %). The increase in
6 biomass, if compared with that measured on 25 July in the same area, was as it follows: from 250 mg
7 m⁻³ to 566 mg m⁻³ in *Aphanizomenon* sp., from 48 mg m⁻³ to 384 mg m⁻³ in *Anabaena* spp. and from
8 102 mg m⁻³ to 401 mg m⁻³ in *Prochlorothrix/Pseudanabaena* group biomass. Dinoflagellate *H.*
9 *triquetra* had high (yet lower than that observed in July) biomass value only at station TH25
10 contributing with 18 % to the total wet weight biomass. Among small flagellates very high biomass
11 was formed by *Pyramimonas* spp. at stations TH23 and TH25 (230–480 mg m⁻³; 10–20 % of total wet
12 weight biomass; Fig. 4). The biomass of the latter species increased between the two surveys from 56
13 mg m⁻³ to 356 mg m⁻³.
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25 By 15–16 August the upwelling area had widened off shore (Fig. 3a–d) and at the same time an
26 increase in Chl *a* and phytoplankton biomass were detected (Fig. 3e–f). Even the total biomass values
27 in the area affected by upwelling (stations TH1–TH11) had increased, the community was still
28 dominated by *M. rubra* (25–47 %) and small-sized flagellates *Pyramimonas* spp. and *Pseudopedinella*
29 spp. (11–23 % and 11–26 % respectively). *M. rubra* biomass increased in comparison with the previous
30 week, on average, from 97 mg m⁻³ to 168 mg m⁻³, and *Pyramimonas* spp. and *Pseudopedinella* spp.
31 biomass from 64 mg m⁻³ to 98 mg m⁻³ and from 33 mg m⁻³ to 90 mg m⁻³ respectively. Additionally,
32 small flagellates *Chrysochromulina* spp. (1.4–11 % of total wet weight biomass) and cryptomonads
33 (3.7–7 %) appeared in the community in a considerable amount. The increase in biomass, on average,
34 from 6 mg m⁻³ to 22 mg m⁻³ and from 16 mg m⁻³ to 26 mg m⁻³ respectively, was measured. The highest
35 biomass of *M. rubra* (446 mg m⁻³, 55 %) was measured at station TH13 in the upwelling front. In less
36 saline waters, which appeared at the northern end of the study transect (stations TH21–TH27, Fig. 3b),
37 the communities were dominated by filamentous and colonial cyanobacteria species (72–88 %).
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50 After the change in wind direction from mainly easterly winds to south-westerly winds in the period
51 from 16–20 August, the relaxation of upwelling occurred by 22 August and the phytoplankton
52 community structure in the sea area previously affected by upwelling changed. *M. rubra* was still one
53 of the dominants (12–28%) in this region but the other dominants were N₂-fixing filamentous
54 cyanobacteria *Aphanizomenon* sp. (14–43 %) and *Anabaena* spp. (6–16 %). In comparison with the
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2 sampling on 15–16 August, the increase, on average, from 7 mg m⁻³ to 205 mg m⁻³ in *Aphanizomenon*
3 sp. and from 4 mg m⁻³ to 59 mg m⁻³ in *Anabaena* spp. biomass was measured at stations TH1–TH11. At
4 the southernmost station TH1 10 % of total wet weight biomass was formed by *H. triquetra*. Small
5 flagellates dominating during the upwelling event had decreased in biomass. Chrysophytes
6 *Pseudopedinella* spp. had almost disappeared from the community. Prasinophytes *Pyramimonas* spp.
7 contributed 3–10 % to the total wet weight biomass (decrease from 90 mg m⁻³ to 6 mg m⁻³ on average).
8 Prymnesiophytes *Chrysochromulina* spp. and cryptomonads had slightly decreased in biomass
9 (contributing 3–7.5 % and 2–4 % of total wet weight biomass respectively).
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18 The development of the next upwelling event along the southern coast of Gulf of Finland, which was
19 sampled on 29 August, changed the phytoplankton community structure in the area affected by the
20 upwelling again. The ciliate *M. rubra* slightly increased in biomass compared with the previous week
21 (Fig. 4) and contributed 18–53 % of total wet weight biomass. Similarly to the previous upwelling
22 event *Pyramimonas* spp. had a considerable share in the total wet weight biomass (12–26 %) at stations
23 TH1–TH5. At the same time *Pseudopedinella* spp. did not show any increase in biomass during this
24 upwelling event (Fig. 4). Instead, the contribution of *H. triquetra* and heterotrophic naked
25 dinoflagellates to the total wet weight biomass slightly increased (5–21 % and 3–19 % respectively at
26 stations TH1–TH7), although the biomass of *H. triquetra* stayed relatively low (110 mg m⁻³). The
27 contribution of *Aphanizomenon* sp. to the total wet weight biomass was very small at the near shore
28 station but gradually increased off shore (Fig. 4). The biomass of cryptophytes and *Chrysochromulina*
29 spp. (Fig. 4) was low in the area affected by the upwelling on 29 August.
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41 MDS analysis

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43 Multi-dimensional scaling (MDS) analysis of similarities in the community structure at all stations
44 during the entire study period clearly categorized the phytoplankton composition into several
45 distinguishable clusters. Area 1 in Figure 5 includes stations before the upwelling event on 11 and 25
46 July and those which were not affected by the major upwelling on 8 August (23c–27c in Fig. 5). The
47 same community structure was revealed on 19–20 July, except that at station TH27 (marked as 27x in
48 Fig. 5). Thus, the phytoplankton community was relatively stable in the area in July and the high
49 biomass community observed on 8 August in the northern part of the study transect matches with the
50 July community.
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2 The stations sampled during the major upwelling event in the southern part of the study transect were
3 grouped in area 2 (1c–7c and 1d–11d). Station TH1 was not placed at the same point in different weeks
4 as the bigger share of *Chrysochromulina* spp. and cryptomonads was found in the southernmost part of
5 the upwelling area on 15–16 August compared with the communities on 8 August. Area 3 includes the
6 stations from the central part of the study area (9c–21c) sampled on 8 August where the phytoplankton
7 community clearly differed from both the July community and the upwelling water community.
8 Dissimilar communities to all those described above were observed on 15–16 August in the areas
9 outside the upwelling waters whereas the community in the upwelling front (13d) was closer to the
10 upwelling community than to the communities outside the upwelling area.
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20 MDS analysis shows strong similarity in the community structure at stations TH1–TH9 (1e–9e) on 22
21 August with the community structure sampled on 8 August at stations TH9–TH21 (9c–21c; area 3 in
22 Fig. 5). The phytoplankton community at station TH13 (13e) on 22 August matches the same group
23 while the community in a colder water patch at station TH11 (11e) was slightly different. The
24 communities at the rest of stations on 22 August were close to the community observed at stations
25 TH21–TH27 (21d–27d) a week earlier. Area 4 includes the stations sampled in the upwelling area on
26 29 August. Those communities differed from the ones observed during the previous upwelling event in
27 the same area. The communities in the northern half of the study transect, which stayed outside the
28 upwelling influence on 29 August, diverged from the previously observed communities as well.
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37 DISCUSSION

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41 Patti et al. (2008) have suggested that in the major coastal ocean upwelling regions several driving
42 factors, such as nutrient concentration, light availability, shelf extension and a surface turbulence proxy
43 must be taken into account when investigating the phytoplankton biomass distribution. Wind-driven
44 transport and mixing play three key roles in shelf productivity: nutrient supply to the euphotic zone,
45 light control through vertical mixing of primary producers, and offshore export of near surface
46 plankton. However, while the first process yields a strong positive biological response to upwelling
47 winds, the other two influences lead to negative productivity responses to increased wind (Largier et
48 al., 2006). During the coastal upwelling events in the Baltic Sea, the distribution of phytoplankton
49 biomass and production have been found to be strongly influenced by the combined effects of physico-
50 chemical processes and to be related to the strength of wind and hence upwelling events (Kononen and
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2 Niemi, 1986; Vahtera et al., 2005; Zalewski et al., 2005; Nausch et al., 2009). In the Gulf of Finland
3 there is a strong upwelling-downwelling coupling because of the elongated shape and relatively short
4 distance (48–135 km) between northern and southern coasts. The development of upwelling along the
5 southern coast of Gulf of Finland in the first half of August 2006 had a strong influence on the spatial
6 distribution of phytoplankton biomass/species (Fig. 3f and 4) and community structure (Fig. 5) along
7 the entire cross-section between Tallinn and Helsinki. In general, a strong biomass decrease in the area
8 affected by the major upwelling event and an increase of biomass near the opposite coast was observed,
9 and there was strong evidence of negative and positive effects of this event on different phytoplankton
10 species.
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20 In plankton community studies very often phytoplankton are divided into several size-classes. At low
21 nutrient levels phytoplankton species succession usually proceeds towards small and motile species
22 with high surface to volume ratios, which give an advantage in nutrient uptake (e.g. Kiørboe, 1993). In
23 ocean upwelling systems larger and especially diatom species are considered to dominate the
24 phytoplankton community (e.g. Lassiter et al., 2006; Anabalón et al., 2007). In contrast to the general
25 understanding and expectations, in our observations the smaller phytoplankton size fraction showed a
26 faster response to the upwelled nutrients compared with the larger size fraction. It was shown by
27 Kuvaldina et al. (2010) that a clear increase in Chl *a* mostly in <20 µm size class occurred during the
28 stabilisation phase of the upwelling (sampled on 15–16 August 2006) while an increase of Chl *a* in
29 larger size fraction was observed after the upwelling relaxation on 22 August. Stolte et al. (1994)
30 described how larger phytoplankton cells can only become dominant when NO₃⁻ is the major nitrogen
31 source available and NH₄⁺ is low or at detection levels, as is typically seen in oceanic coastal upwelling
32 ecosystems. Koike et al. (1986) found that on average only 50% of the NO₃⁻ uptake is by organisms in
33 the <20µm size fraction, while all the NH₄⁺ uptake occurred the same fraction. According to the Finnish
34 marine monitoring data (http://www.itameriportaali.fi/en/tietoa/helcom_seuranta/en_GB/bmp_data)
35 the NH₄⁺ concentrations in the lower layers of the Gulf of Finland where the upwelling water originates
36 were comparable to the nitrates+nitrites concentrations in July-August 2006. The median and mean
37 values being 1.6 and 1.8 µM, respectively, between the 30 metres depth and the sea bed. High NH₄⁺
38 concentrations in the upwelling waters have been also measured earlier in the Gulf of Finland, e.g. up
39 to 1.43 µM by Haapala (1994) in summer and up to 3.2 µM by Lignell et al. (2003) in autumn whereas
40 in the later case the nitrate concentrations up to 2.2 µM were observed. Thus, we suggest that the
41 phytoplankton growth observed in the upwelling area, initially mostly in the smaller size fraction
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2 (*Pyramimonas* spp. and *Pseudopedinella* spp.), could be related to the possible higher proportion of
3 ammonium in the upwelled dissolved inorganic nitrogen pool.
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7 As shown by the previous studies in the Gulf of Finland (Kanoshina et al., 2003; Vahtera et al., 2005)
8 the growth of *Eutreptiella gymnastica* Thronsen, *Chrysochromulina* spp. and cryptophyceans has
9 been influenced by the coastal upwelling events. During our study *Eutreptiella* spp. dominated among
10 nanoflagellates (25–35% of total nanoplankton wet weight biomass) only on 19 July in the upwelling
11 area at the northernmost part (stations TH25–TH27) of the cross-section but the biomass values were
12 very low. There was no biomass increase observed in connection to the major upwelling event along
13 the southern coast in August. Chrysophytes *Pseudopedinella* spp. were abundant only during the major
14 upwelling event near the southern coast and their increased biomass values were limited with the
15 upwelling time and area except for slightly increased biomass near the northern coast on 8 August (Fig.
16 4). *Pyramimonas* spp. were also positively influenced by the major upwelling event in August near the
17 southern coast of the Gulf of Finland although the highest biomass was observed on 8 August in the
18 northern part of the study transect. *Chrysochromulina* spp. had highest biomass on 11 July and a
19 decrease in biomass was observed during the initiation phase of the upwelling while a consecutive
20 increase in biomass followed during the stabilisation phase and the biomass stayed relatively high also
21 after the relaxation of upwelling.
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36 Mesocosm studies (Uitto and Hällfors, 1997; Lagus et al., 2004; Kangro et al., 2007) have shown that
37 *Pseudopedinella* spp. have high growth rates in high nutrient enrichment conditions and the other
38 experiments (Kononen et al., 1993; Andersson et al., 2006) have also revealed the positive response of
39 *Pyramimonas* spp. to nutrient enrichment following the sharp decline caused by predation of increased
40 microzooplankton community. Thus, these species have a high requirement for nutrients, and hence
41 might have a competitive advantage during upwelling events which explains the increase in their
42 biomass in the major upwelling area in our study. As shown by studies of Hajdu et al. (1996) stronger
43 stratification may be one of the factors influencing *Chrysochromulina* spp. abundance positively during
44 summer to early autumn in the Baltic Sea. New input of limiting nutrients during the upwelling event at
45 the beginning of August together with the stabilisation of upwelling and rise of the UML temperature
46 (leading to development of stratification) might have caused the *Chrysochromulina* spp. biomass
47 increase in the Estonian coastal waters observed on 15–16 August. Also phosphorus deficiency in the
48 UML gives a competitive advantage through toxin production (Estep and MacIntyre, 1989) and hence
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2 helps to explain the high abundances at periods with low phosphate concentrations (e.g. along our
3 study transect in July 2006, Fig. 4).
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7 Among larger size fraction the biomass of the photosynthetic ciliate *M. rubra* increased remarkably
8 during the upwelling event and remained at high values till the end of August almost along the entire
9 cross-section. The biomass increase of latter species during the upwelling event was first connected
10 with the vertical transport of seed population from lower layers followed by growth in the nitrate rich
11 upwelled waters in the euphotic layer. The former conclusion is supported by sampling on 11 July at
12 stations TH1–TH3 where in the lower part of thermocline (17.5–20 m) biomass of this species of up to
13 246 mg m⁻³ was measured. High biomass values and even blooms of *M. rubra* have been observed in
14 upwelling areas (e.g. review by Crawford, 1989). The species has been shown to have a high demand
15 for inorganic nitrogen, but also one to four times higher uptake rate for nitrate than e.g. diatoms or
16 dinoflagellates (Wilkerson and Grunseich, 1990). The latter helps also explain the rapid exhaustion of
17 inorganic nitrogen compounds in *M. rubra* dominated upwelling areas. The competitive advantage
18 during nutrient limitation is retained probably by changing the trophic status from phototrophy to
19 phagotrophy (e.g. Yih et al., 2004) and by the species' very high swimming speed (e.g. Lindholm,
20 1985; Villarino et al., 1995), which allows it to exploit resources from deeper water layers as well as
21 from nutrient patches.
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36 A *H. triquetra* bloom has been detected in the upwelling area in the Gulf of Finland in 1998
37 (Kanoshina et al., 2003) when the biomass values reached as high as 4 500 mg m⁻³. During our study
38 in 2006 the biomass of this species was high (up to 1 040 mg m⁻³) mostly only in July in the northern
39 part of the Gulf of Finland. High biomass values did not extend to the Tallinn Bay and no remarkable
40 biomass increase was found during and after the major upwelling event near the southern coast where
41 biomass only up to 100 mg m⁻³ was measured. We noticed that the highest *H. triquetra* biomass values
42 observed at station TH17 on 11 July and at station TH25 on 19 July were associated with relatively low
43 Chl *a* concentrations. Kononen et al. (1999) have shown that at low irradiances Chl *a* concentration in a
44 pure culture of *H. triquetra* decreased rapidly while the cells could maintain their in vivo fluorescence
45 for a week. Since the Chl *a* fluorescence in the UML at these stations was remarkably high (data not
46 shown here), we suggest that *H. triquetra* was transported there from the seasonal thermocline. This
47 suggestion is supported by the CTD data from 19 July showing that the isopycnal, which surfaced in
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2 the upwelling front (station TH25), was located at 12 m depth at a distance of 5 km towards the open
3 gulf (station TH23).
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7 Vahtera et al. (2005) found relatively high biomass of *Aphanizomenon* sp. in the upwelling front in the
8 northern part of the Gulf of Finland in 1998 and they explained this by the displacement of populations
9 of *Aphanizomenon* sp., which before the upwelling event resided in the thermocline. We observed
10 similarly relatively high biomass of *Aphanizomenon* sp. biomass in the upwelling front on 19 July in
11 the northern part of the gulf. However, the biomass of *Aphanizomenon* sp. was negligible during the
12 major upwelling event sampled on 8 and 15–16 August near the southern coast also on 11 July the
13 biomass of this species up to 1300 mg m^{-3} was measured at stations TH1–TH3 at 12.5 m depth (upper
14 part of the thermocline; at the same time its biomass did not exceed 150 mg m^{-3} at 15 m depth and
15 below). It could be explained by the fact that the upwelled water during the major event near the
16 southern coast had its origin from much deeper layers than that during the earlier upwelling in the
17 northern part. It was estimated by Lips et al. (2009) that the upwelling water on 8 August consisted of a
18 mixture of waters from below the thermocline and from the UML with a share of 85 % and 15 % while
19 the higher temperatures observed in the upwelling water on 19 July indicate that this water mass had its
20 origin mainly from the seasonal thermocline.
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34 There was a clear increase in phytoplankton Chl *a* and biomass after the relaxation of the major
35 upwelling sampled on 22 August (Fig. 3e,f). However, the highest total phytoplankton biomass was
36 observed on 8 August in the northern part of the study transect. Even the observed major upwelling
37 event brought large amount of inorganic nutrients to the nutrient depleted UML it can be seen from the
38 nutrient analyses that nitrates+nitrites were below the lower detection range already by 15–16 August
39 and phosphates by 22 August (Fig. 3c,d). In contrast, the phosphate concentrations exceeding the lower
40 detection range were observed in the UML in the northern part of the study transect on 25 July and 8
41 August. Due to our sampling strategy we could not point to a direct link between the upwelling
42 observed on 19–20 July and the slightly elevated phosphate content observed in the northern gulf on 25
43 July and 8 August. We rather relate the elevated phosphate content and high phytoplankton biomass to
44 the meso-scale features observed at the mentioned sampling days. Especially, a clear relationship was
45 evident on 8 August, when according to the vertical distributions of temperature, salinity and density
46 (Lips et al. 2009), anti-cyclonic like vertical distribution of isopycnals was observed in the
47 downwelling area coupled with the major upwelling. The highest biomass values at stations TH23 and
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2 TH25 coincided with this meso-scale feature where domed isopycnals caused shallowing of the UML
3 to only 5 metres against the background of relatively deep UML in the rest of the downwelling area.
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7 Earlier modelling and field experiments have shown that regardless of how much nutrient is upwelled
8 during the upwelling phase, if a suitable period of relaxation follows, all is taken up within 72 h = 3
9 days (Zimmerman et al., 1987; Dugdale et al., 1990) and high levels of primary productivity are found
10 in 3 to 7 day old upwelled waters after the relaxation following the upwelling impulse (Botsford et al.,
11 2006; Wilkerson et al., 2006) in the ocean upwelling systems. When upwelling relaxes and the supply
12 of new nutrients decreases/disappears, phytoplankton populations may survive by using intracellular
13 storages or regenerated forms of nutrients such as ammonium and urea (e.g. Bode et al., 1997). As the
14 nitrates+nitrites were exhausted rapidly and there was still plenty of phosphates in the UML on 15–16
15 August (Fig. 3d) one could hypothesize that the depletion of the latter nutrient and the increase of
16 biomass of filamentous N₂-fixing cyanobacteria *Aphanizomenon* sp. and *Anabaena* sp. (Fig. 4)
17 observed on 22 August could be due to the growth induced by upwelled excess dissolved inorganic
18 phosphorus (DIP). However, the results of MDS analysis indicated very high similarity of
19 phytoplankton community in the area previously affected by the upwelling (stations TH1–TH13,
20 except station TH11) on 22 August to the community found in the central part of our cross-section
21 during the intensive upwelling event on 8 August (Fig. 5). Thus, the phytoplankton biomass increase
22 could be connected to the relaxation of upwelling and subsequent reversal movement of surface water
23 masses together with the utilization of mostly regenerated but also stored nutrients. While, because of a
24 long time for bloom development, the phytoplankton community may be lost from the system and
25 moved quite far in oceanic upwelling areas (e.g. Botsford et al., 2006), in the case of variable wind-
26 induced upwelling in the elongated Gulf of Finland, plankton community may not move far before
27 being brought back again. The absence of cyanobacteria dominated community described on our study
28 transect on 15–16 August and possibly some other changes observed in the community structure could
29 be related to the along-shore (along the gulf axis) advection, which has been shown to be very
30 important in coastal upwelling systems, e.g. in the California Current System (Botsford et al., 2006).
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51 The development of a next upwelling event by 29 August caused a decrease in phytoplankton biomass
52 and the observed changes in the community composition support the above described importance of
53 wind-induced Ekman transport in shaping the overall response of phytoplankton to the coastal
54 upwelling events in the Gulf of Finland ecosystem. The response of the phytoplankton community to
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2 several consecutive upwelling events in the same area is not similar and is most probably influenced by
3 the amount and ratio of upwelled nutrients, but also by the strength of the upwelling that determines
4 from which layers the upwelled water originates from and consequently what is the initial community
5 structure in the upwelling area.
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10 **Conclusions**

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14 During the upwelling events in the Baltic Sea transport of large amounts of inorganic nutrients from the
15 lower layers to the surface layer may occur. Due to the nutrient intrusion, changes in temperature,
16 advection and replacement/mixing of water masses not only single phytoplankton species are affected
17 but also the entire phytoplankton communities are changed in a short time period. The response of
18 different phytoplankton species/size classes tends to be very much influenced by the concentration/ratio
19 of upwelled nutrients also by the strength of the upwelling events that determines the water layers
20 where the upwelling water originates from. In general we found that the increase of biomass takes
21 much longer time than the observed abrupt changes in the phytoplankton community caused by
22 upwelling or horizontal advection (convergence/divergence) of water masses. Thus, one should be
23 careful in using the collected and analysed chemical and phytoplankton data for assessing the status of
24 the Gulf of Finland ecosystem due to the very dynamic nature of this estuary and the background
25 information (climatic conditions, prevailing hydrophysical processes) have to be considered for this
26 purpose.
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45 Institute of Marine Research) for access to their marine monitoring data.
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Figure legends

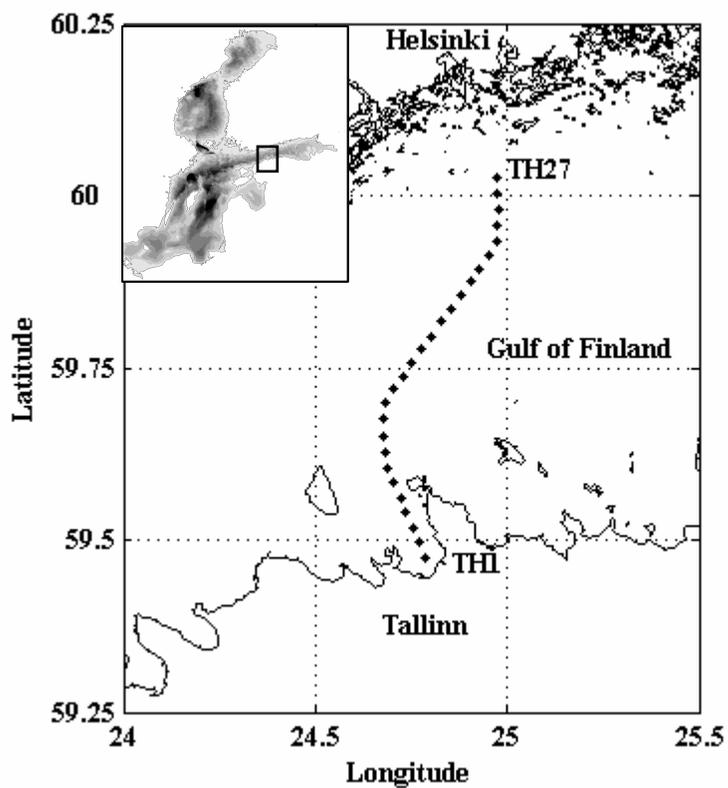
Figure 1. Map of the study area and location of measurements/sampling stations TH1–TH27.

Figure 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.

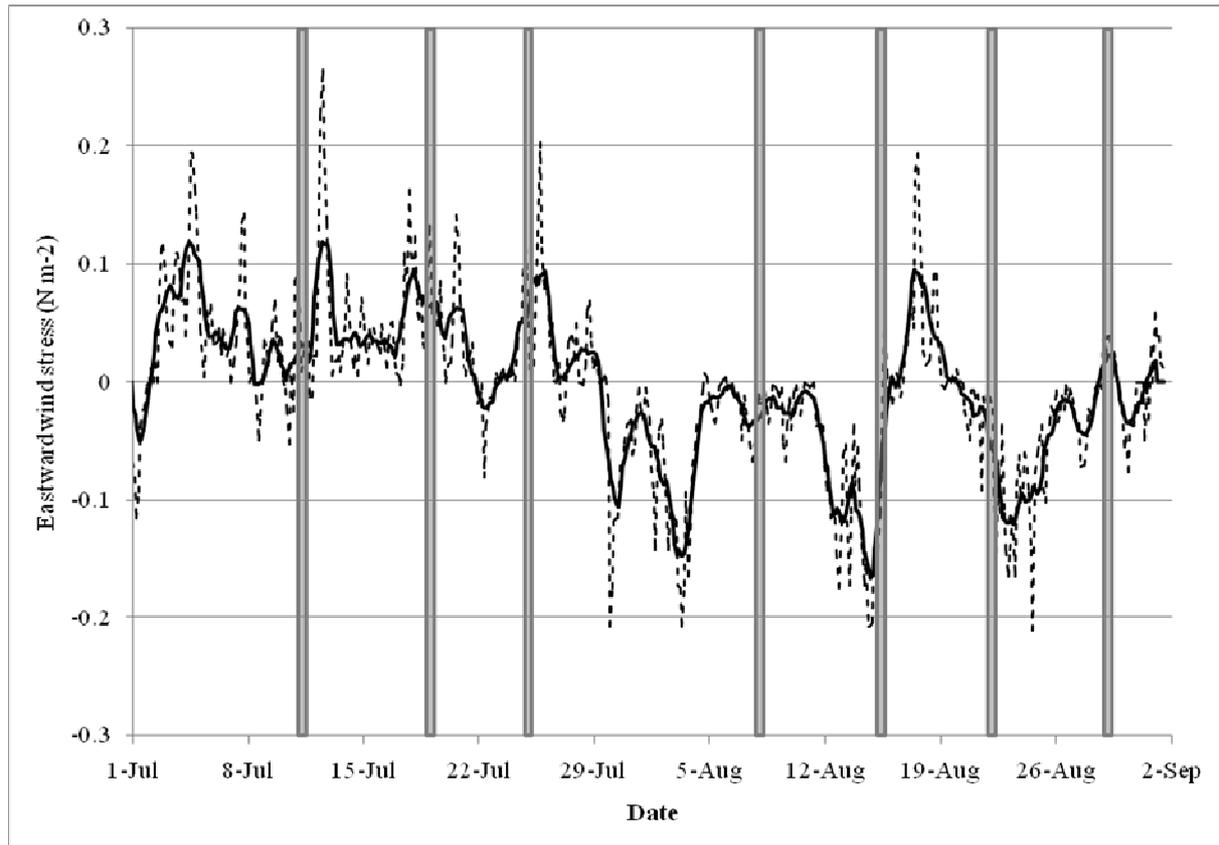
Figure 3. Temporal changes of temperature (a, °C), salinity (b), nitrate+nitrite-nitrogen (c, μM), phosphate-phosphorus (d, μM), chlorophyll *a* concentration (e, mg m^{-3}) and phytoplankton biomass (f, mg m^{-3}) in the UML along the study transect from 11 July to 29 August 2006. Dots indicate measurements (a–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.

Figure 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.

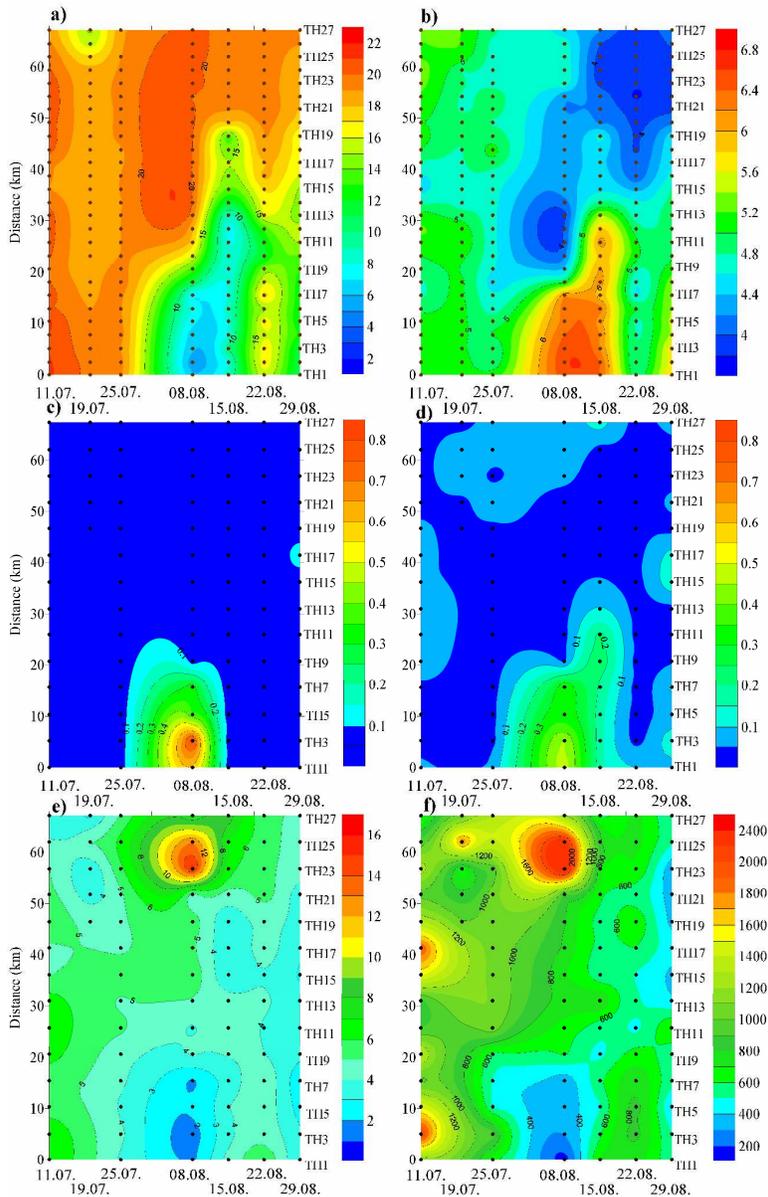
Figure 5. MDS plot for all sampled stations based on Bray-Curtis similarity distances of phytoplankton composition. Stations are indicated as numbers TH1–TH27 = 1–27 and sampling dates as letters: a – 11 July, b – 25 July, c – 8 August, d – 15 August, e – 22 August, f – 29 August and x – 19 July. Filled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



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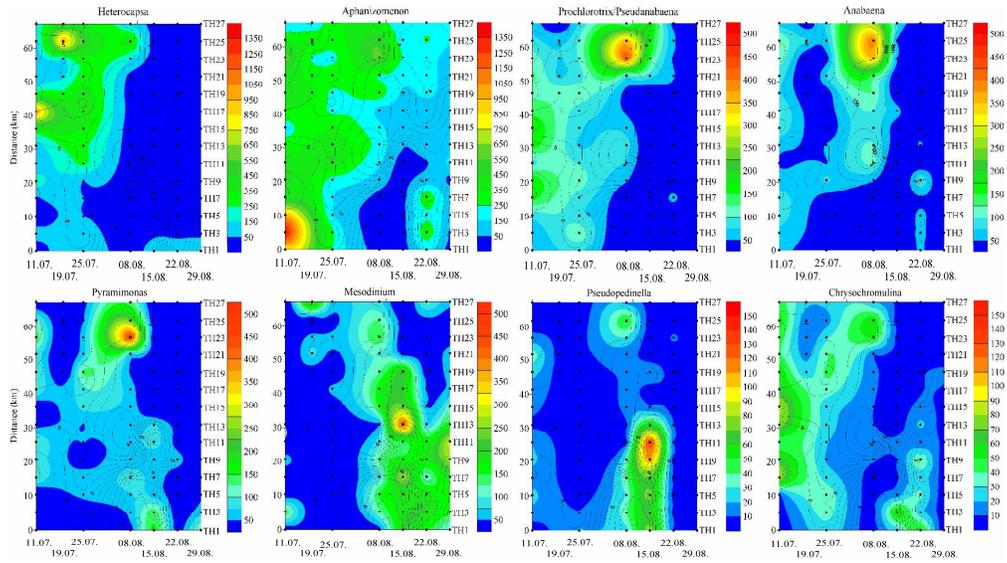


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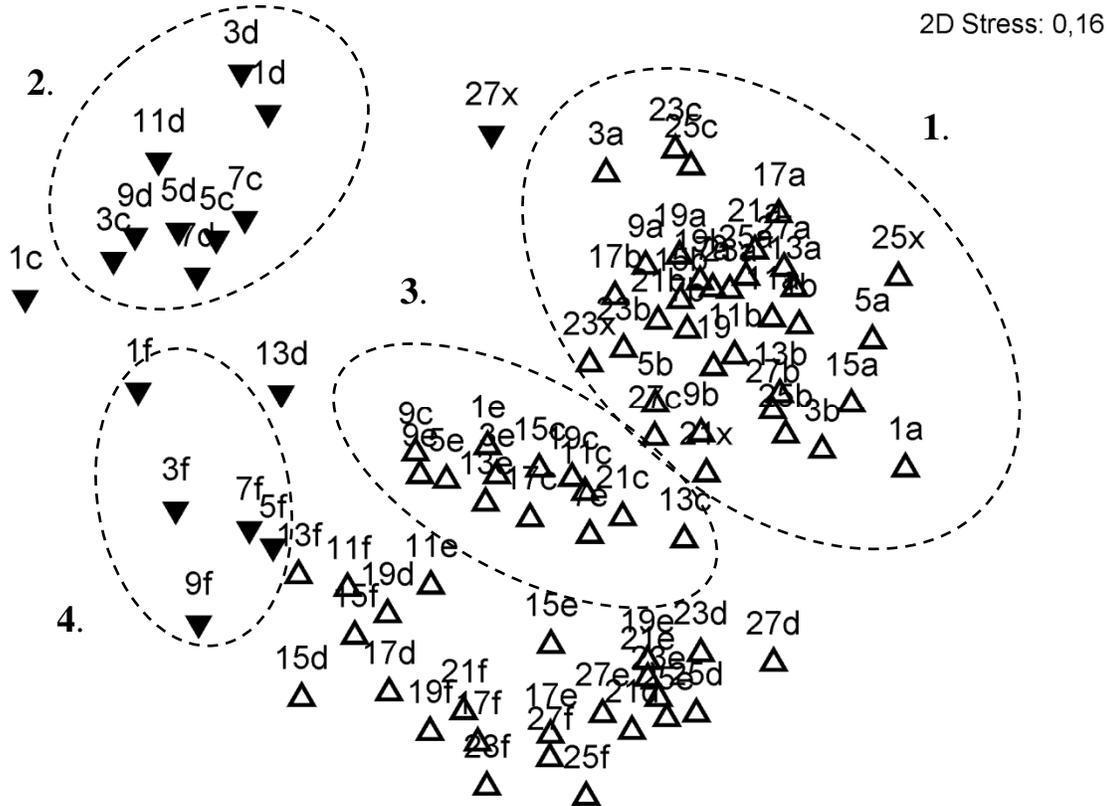
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