

Microalgal plankton composition in shallow coastal inlets in contrasting trophic and alternative community states

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Abstract As the trophic state of the environment changes, communities develop into divergent states. These community states are conventionally reflected through primary producers, because they are directly affected by nutrient availability. Studies of submerged macrophytes often focus on community composition to decipher the vegetative (community) state of the environment, while planktic microalgae are usually viewed more cursorily. Although microalgal plankton composition has been related to the trophic state of shallow temperate lakes, corresponding qualitative knowledge is lacking for shallow inlets in the sea. We assessed the composition of microalgal plankton in relation to that of submerged macrophytes in shallow

inlets in the northern Baltic Sea during one ice-free season. Microalgal plankton composition varied distinctively among inlets in different trophic and vegetative states especially during early and mid-season, before becoming comparably uniform. These patterns were consisted both inside and outside of macrophyte beds and during day and night. Local and diurnal variation was comparably high in eutrophic and charophyte-dominated inlets, but only during early season. Microalgal plankton composition not only reflects the state of littoral communities in varying trophic conditions, but it may also be important for the whole trophic structure of those communities.

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Introduction

Shallow inlets in the sea and shallow lakes resemble each other. In both systems, the trophic state of the environment shapes community structure and function in a comparable way (Scheffer, 1998). The associated alterations in community state are reflected mainly through primary producers (e.g., McGlathery et al., 2007; Scheffer & van Nes, 2007). Submerged macrophytes, i.e., vascular plants and macroalgae, are often approached by studies focusing on their community

composition and thus expressing the vegetative (community) state of the environment. By contrast, phytoplankton and other planktic microalgae are usually viewed as one or a few functional entities (e.g., Jeppesen et al., 1998; van Donk & van de Bund, 2002). Often, only the total biomass of phytoplankton or that of some larger taxonomical groupings is used to reflect the state of the community (Dahlgren & Kautsky, 2004). Although changes in microalgal plankton composition along trophic gradients have been described for shallow temperate lakes (Duarte et al., 1992; Jensen et al., 1994; Scheffer et al., 1997; Jeppesen et al., 2000), corresponding knowledge is lacking for shallow inlets in the sea. In this paper, we assess the variation in the structure of planktic microalgae in shallow inlets in the northern Baltic Sea. These lagoon-like inlets represent a landscape-level gradient of trophic and vegetative states. More extensive information on primary producers is needed for understanding how littoral systems generally function and what impact they may have on the surrounding coastal ecosystem. Such knowledge is especially important for the northern Baltic, where the composition of littoral, microalgal plankton is virtually (Kuosa, 1988) unstudied.

As primary producers interchange along trophic gradients, gradual replacement of species can get interrupted by more dramatic shifts into contrasting and more stable community states (Scheffer & van Nes, 2007). By identifying and investigating communities in such states should encapsulate much of the variation in community composition in the hypothetical gradient of change between them (sensu Patton, 1990). The hypothesis that systems can have two (or several) alternative stable states, i.e., different sets of abiotic and biotic conditions relatively resistant to change (May, 1977), was first empirically attested in shallow lakes. The dramatic switch between a submerged plant-dominated state with clear water and a phytoplankton-dominated one with turbid water filled the criteria (Phillips et al., 1978) for a regime shift (Scheffer et al., 1993). Alternative stable states may also be formed when submerged plants give way to stoneworts, i.e., charophytes (Hargeby et al., 1994) or floating plants (Scheffer et al., 2003). Also in shallow inlets in the sea, primary producers shift from submerged plants toward phytoplankton (Viarioli et al., 2008). This happens often through phases involving opportunistic and usually epiphytic macroalgae

(Dahlgren & Kautsky, 2004). Although less abrupt than in lakes, these transitions are often considered as switches into alternative states (Sand-Jensen & Borum, 1991; Dahlgren & Kautsky, 2004; Viarioli et al., 2008).

Lagoon-like inlets in the northern Baltic, i.e., flads (Ingmar, 1975) are convenient study systems. Their trophic state is coupled to post-glacial rebound (Lambeck et al., 1998). As the Earth's crust rises and flads get more isolated from the surrounding sea, their trophic state tends to increase (Munsterhjelm, 2005). Associated changes in the vegetative state of the flads have been thoroughly characterized (Munsterhjelm, 2005; Rosqvist, 2010) and classified into three distinctive regimes (a–c below) (Rosqvist et al., 2010). Flads in the lower end of the natural trophic gradient¹ are typified by diverse ($S > 15$) macrophyte communities (a) taking up a relatively low share of the flad volume. In the opposite end, one or two species of either vascular plants (b) or stoneworts (c) dominate the community of submerged macrophytes (Appelgren & Mattila, 2005). Especially stoneworts tend to occupy a large part of the flad volume. In addition, local anthropogenic disturbance (eutrophication and dredging) has in many cases led to a phytoplankton-dominated, turbid state (e.g., Rosqvist, 2010). Flads representing entire gradients of trophic and/or vegetative states can easily be found within a landscape providing a given pool of potential inhabitants. The numerous flads of the northern Baltic are also regionally important ecological units. Like other shallow inlets in the sea, they function as coastal filters for nutrient run-off and are thus highly important for the biological productivity of the surrounding landscape (McGlathery et al., 2007). Consequently, flads are also important targets for conservation measures (Wallström et al., 2000).

This study has several practical aims. To cover maximum variation in the structure of microalgal plankton at a landscape level, flads typifying respective end of the natural trophic gradient (Scheinin & Mattila, 2010) and representing the three contrasting vegetative states (Rosqvist et al., 2010) were chosen

¹ The term “natural trophic gradient” means that local anthropogenic impact on the flads along the gradient is as small as possible. The term is thus relative to the general trophic state of the Baltic Sea.

for the survey. The flads were surveyed over an ice-free season to consider seasonal succession. Finally, to cover local and diurnal variation, samples were taken in two habitat types, in open water and macrophyte beds, at both day and night within each flad and phase of the season.

We expected microalgal plankton structure to vary primarily among the flads and along the season and secondarily within the flads and the different phases of the season. That is, we presumed local and diurnal variation to depend on the flad and on seasonal succession. This main assumption was split up into four hypotheses. (1) Variation among the flads is related primarily to their trophic state and secondarily to their vegetative state. (2) Differences among the trophic and vegetative states depend on the phase of the season. (3) The broad-scale spatio-temporal variation does not depend on the habitat type and/or the

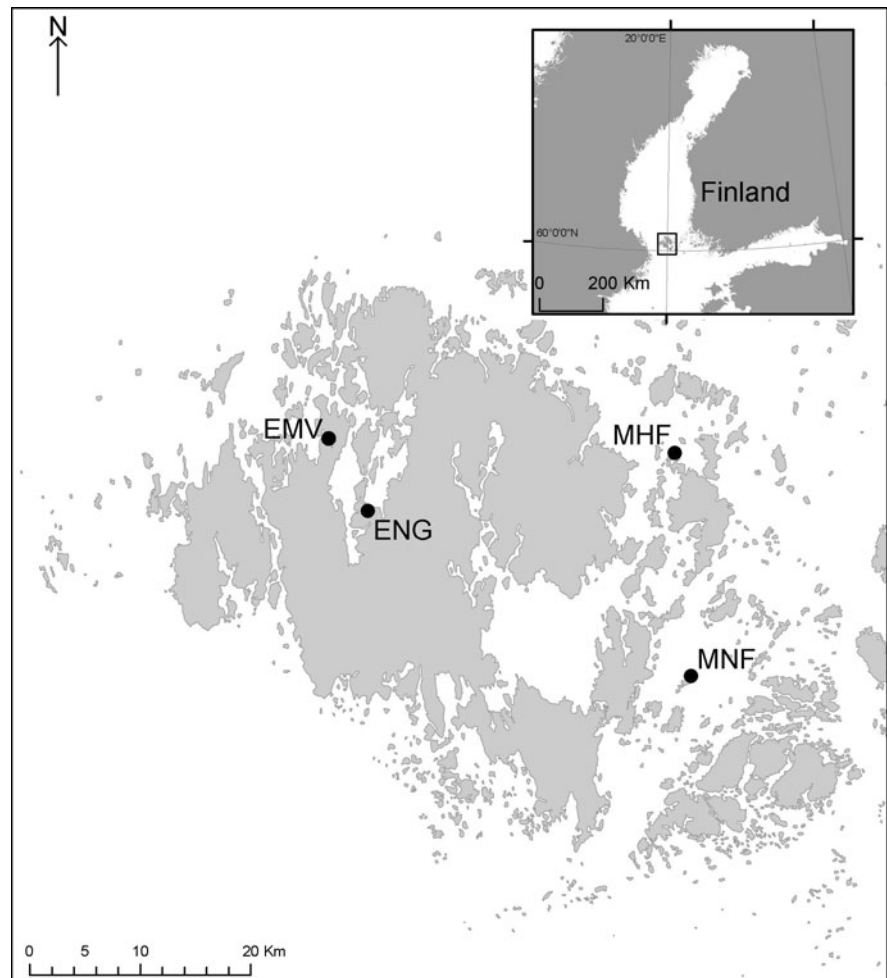
time of day. (4) By contrast, the small-scale spatio-temporal (i.e., diurnal and local) variation depends on the trophic and vegetative states of the flad as well as the phase of the season.

Materials and methods

Sites and schedule

Sampling took place in four flads in the archipelago of Åland Islands (Fig. 1). Hamnflada (MHF) and Norrflada (MNF) represent flads with comparably low and Mjärdvik (EMV) and Notgrund (ENG) with comparably high-trophic state (as defined in Wallström et al. (2000) and Scheinin & Mattila (2010)). The first letter in each abbreviation refers to the trophic state of the flads, mesotrophic (M) and eutrophic (E), and the

Fig. 1 The surveyed flads belong to the Åland Islands. Hamnflada (MHF) and Norrflada (MNF) are in comparably low and Mjärdvik (EMV) and Notgrund (ENG) in comparably high trophic states



following two letters to the names of the flads. Both MHF and MNF have been inhabited by a relatively even mixture of several different macroalgae and vascular plants, sago pondweed (*Potamogeton pectinatus*) being barely the most common of them. In EMV, the macrophyte community has been dominated by the vascular plant sago pondweed and in ENG by a stonewort (coral stonewort (*Chara tomentosa*)) (Appelgren & Mattila, 2005; Rosqvist et al., 2010). The mesotrophic flads are generally characterized by shorter macrophytes (Appelgren & Mattila, 2005; Snickars et al., 2009) and an order of magnitude lower biomass of both zooplankton (Scheinin & Mattila, 2010) and zooplanktivorous fish (Järvinen, 2005; Snickars et al., 2009) than the eutrophic ones. However, macrophytes tend to occupy roughly the same percentage of water volume in the mesotrophic flads and in EMV.

Phytoplankton and other planktic microalgae with partly similar roles in the food web (Cercozoans, Ciliophores and Cyanophytes) were surveyed in the four flads at six occasions, in the middle of each month during the ice-free season from May to October in 2007. The season was divided into three main phases according to the main seasonal succession patterns of macrophyte communities in northern Baltic flads (Rosqvist, 2010). May and June are regarded as early season, July and August as mid-season, and September and October as late season. Samples were taken in two types of contiguous habitats, one in open water and another in a dense stand of macrophytes, in the middle of each flad. This was done at midday at every sampling occasion. At every other occasion, the two habitat types were sampled also at midnight. Data from the three occasions with both day- and nighttime sampling could be used for assessing variation in microalgal plankton composition within each flad. The whole dataset, grouped according to the three seasonal phases, was used for assessing variation among the flads and over the season.

Field procedures

A suite of abiotic water characteristics was measured and the species assemblage and (horizontal and vertical) coverage of submerged macrophytes was assessed each month in each flad. Samples (1.9 l Limnos-sampler) for the analysis of salinity, temperature, turbidity, and concentrations of total phosphorus

and total nitrogen were taken at 0.5 m depth in the middle of the flad late in the forenoon. After this, macrophytes were mapped by visual observations while diving (Jensén & van der Maarel, 1980 and references therein) along three transects. One transect split the flad longitudinally, from the bottom to the mouth. The two other transects were transversal and divided the flad into three equally long zones. Macrophyte composition (cover percentage) was mapped within 1 m² squares at eight equidistant spots along the longitudinal transect and at seven equidistant spots along each of the transversal transects. The height of the macrophytes was measured at each corner and in the middle of the mapping frame. The average of the five values was used for expressing the general height of the macrophyte cover within each frame. In addition, the coverage of epiphytic filamentous algae was estimated between 0 and 100% at 25% steps.

The area for sampling planktic microalgae consisted of a habitat with (for each flad) maximally dense monoculture of a characteristic macrophyte species bordered by an equally large (*ca* 2 m²) habitat with bare bottom. The area was to be located within 50 m from the middle of the flad, where all flads were almost equally deep (*ca* 2.0 m). The mid-points of the habitats were marked out with buoys.

Microalgal plankton was sampled by the marker buoys in a randomized order. Sampling exactly the same spots at both day and night was avoided. The samples were taken with a tube ($\varnothing = 12$ cm, $l = 3.6$ m, $V_{\max} = 38$ l) covering the whole water column apart from the 20 cm closest to the bottom. The tube was slid down along a rail from a rack on a boat, and valves at both ends of the tube were closed. Sample volume was 20–24 l depending on the water level. After homogenizing the contents of the sampler by see-sawing it on its hinged rack, a 100 ml subsample for microalgal plankton was run from a tap on the side of the tube and preserved in 1% Lugol solution.

Laboratory analysis

The water characteristics were measured as described in Scheinin and Mattila (Scheinin & Mattila, 2010). Microalgal plankton was identified to species level according to the HELCOM checklist for species designations (Hällfors, 2004). However, cases where

the exact identity of the species was uncertain (indicated by “sp.”) may include more than one species. The organisms were counted either as individual cells or as filaments depending on the species. Analyses were conducted with a Nikon TE 200 inverted microscope according to the Utermöhl method (Utermöhl, 1958) using 10 ml sedimentation chambers. Appropriate sedimentation times for various species were tested prior to analysis. In general, the whole bottom area was analyzed using 10-, 20- and 40-times magnifications. Two to four diagonal transects were used to enumerate especially abundant species. The size of approximately 10–20 cells or filaments of each species was recorded with a Nikon DS L2 (DS-2Mv camera).

Assessment of microalgal plankton structure

The abundances of the planktic microalgae were converted to biomasses according to HELCOM (Olenina et al., 2006). All further data analyses are based on the biomass data. Variation in microalgal plankton structure was assessed from five aspects: (1) species assemblage, (2) species abundance-environment relations, (3) group abundances, (4) community-level composition, and (5) community-level metrics.

Species assemblage describes which species occur in a given sample. Species biomass data were transformed to binary (0/1) values to indicate the presence or absence of species (Online Appendix 1—Supplementary material) associated with each flad, sampling occasion, habitat type and time of day.

Species abundance-environment relations, i.e., relationships among the abundance of each species of microalgal plankton and its environment were investigated by Canonical correspondence analysis (CCA) (Ter Braak & Šmilauer, 2002), as the method suits well for data with unimodal species responses and quantitative measurements for the underlying environmental variables (McCune, 1997). In addition to all the encountered species, seven environmental variables were included in the analysis. The trophic state of the flads was quantified by the concentrations of total phosphorus ($\mu\text{g l}^{-1}$) and total nitrogen ($\mu\text{g l}^{-1}$), and the state of the macrophyte communities by the proportion of flad volume covered by macrophytes (%). Similarly, habitat type was expressed as the proportion of its volume covered by macrophytes (%). Light intensity at the different times of day was

quantified in relation to annual variation by calculating the solar elevation angle ($^{\circ}$) (e.g., Briggs & Smithson, 1986). Finally, seasonal succession (i.e., sampling occasion) was expressed directly by day length (h) and indirectly by water temperature ($^{\circ}\text{C}$). A Monte Carlo test with 499 permutations was used to evaluate the significance of the analysis. The centroid of the CCA plot represents average environmental conditions. The abundances of species with scores differing only little from the centroid correlate with average environmental conditions or with a wide range of them. The larger the difference, the more the abundance of the species is associated with specific environmental conditions. The length and orientation of an environmental vector represents its magnitude and direction of maximum change in the ordination space. The proximity and alignment of a species with a particular vector shows how closely the variation in the abundance of the species is related to the environmental variable in question (Ter Braak & Šmilauer, 2002).

Group abundance means the abundance of individuals representing respective main taxonomical group found in the study. Phytoplankton species were grouped into their taxonomic divisions: Bacillariophyta, Chlorophyta, Cryptophyta, Dinophyta, Euglenophyta and Prasinophyceae, and the other planktic microalgae into Cercozoa, Ciliophora, and Cyanophyta. The grouping was applied principally to allow for comparisons across systems (Gasiūnaitė et al., 2005) and time periods (Sommer et al., 1986) with different species assemblages (Online Appendix 1—Supplementary material).

Community-level composition describes the species assemblage and the relative abundance of those species in an association of planktic microalgae as a whole. Detrended correspondence analysis (DCA) (Ter Braak & Šmilauer, 2002) was applied to study variation in the composition of microalgal plankton and macrophytes, respectively. As opposed to the CCA, each DCA is unconstrained by any environmental variables and thus shows only how closely the included sampling units resemble each other.

Community-level metrics describe the composition of microalgal plankton from a functional perspective. Seven community-level metrics: total density ($n l^{-1}$), total biomass ($\mu\text{g l}^{-1}$), mean biomass ($\mu\text{g n}^{-1}$), mean cell diameter (μm), species richness (S), group richness (F) and Shannon's diversity index value (H') (Shannon, 1948) were applied to compare the microalgal associations. This was done in two steps. First, 3-way

ANOVAs using data from the three occasions (June, August, and September) with both day- and nighttime samples were used to evaluate whether any of the community-level metrics would vary significantly with habitat type (flad \times occasion \times habitat type) or the time of day (flad \times occasion \times time of day). Both types of 3-way ANOVAs were followed by respective 2-way ANOVAs and independent samples *t* tests. The data were ranked in percentiles (Crocker & Algina, 1986) within each sampling occasion to make them homoscedastic (according to Levene's tests) while retaining their normality (according to Kolmogorov–Smirnov tests). Second, after demonstrating that habitat type and the time of day did not alone or as a part of any interaction vary significantly with any of the community-level metrics, 2-way ANOVAs (flad \times phase of the season) on all data were performed. The data were transformed and validated as described above. Student–Newman–Keuls (SNK) tests were applied for pairwise comparisons among the flads within each phase of the season when the two factors interacted significantly. When they did not, the procedure was continued with 1-way ANOVAs with flad and phase of the season as factors. Post hoc tests were carried out as described above.

The ordination analyses were done in Canoco 4.5, while CanoDraw was used to produce the associated plots. The other statistical analyses were carried out in SPSS 18. GraphPad Prism 5 was used to visualize the results from those analyses.

Results

Environmental variables

Apart from nutrient levels, the investigated abiotic conditions were quite similar among the flads regardless of their trophic and vegetative states (Fig. 2). Salinity stayed between 4 psu and 6 psu in all the flads throughout the season (Fig. 2a). Temperature varied characteristically along the season, while differences among the flads stayed small (Fig. 2b). In the very beginning of the season, turbidity was considerably higher in the eutrophic flads, especially in ENG, than in the mesotrophic flads. During the rest of the season, differences between the meso- and eutrophic flad types were much smaller (Fig. 2c). The meso- and eutrophic flad types differed from each other most with respect to total phosphorus and especially

nitrogen concentrations (Fig. 2d, e). Although total phosphorus concentrations and their dynamics were highly similar in both eutrophic flads, ENG had higher concentrations of total nitrogen during the beginning of the season. In general, variation in nutrient concentrations among the flads was most pronounced until the middle of the season. Differences in N:P-ratios were generally small (Fig. 2f). Similarly, differences in pH among the flads were small and moreover unsystematic. The values decreased subtly along the season regardless of the flad (Fig. 2g).

Macrophytes were generally shorter (Fig. 2h) in the meso- than in the eutrophic flads. The area covered by macrophytes was larger in MNF and ENG than in MHF and EMV throughout the season (Fig. 2i). By contrast, the water volume occupied by macrophytes was considerably higher in ENG than in any other flad and slightly higher in EMV and MNF than in MHF. Also these differences persisted throughout the season (Fig. 2j). The number of macrophyte species was considerably higher in the mesotrophic than in the eutrophic flads (Fig. 2k). In the beginning of the season, macrophytes were more infested with epiphytes in the mesotrophic than in the eutrophic flads. Differences among the flads faded by mid-season, and the epiphyte cover stayed at a generally high level (Fig. 2l).

Macrophyte composition varied distinctively among the flads representing different vegetative states (Fig. 3). Eigenvalues for the plotted first and second DCA-axes were 0.84 and 0.24 of a total of 2.50. Although the macrophyte communities in the mesotrophic flads differed from each other, they formed a cluster that clearly stands out from a corresponding eutrophic cluster, further divided into two distinctive subclusters for each flad. The macrophyte communities in both mesotrophic flads were characterized by cyclic seasonal variation, beginning and ending with rather similar communities. In comparison, seasonal variation in the eutrophic flads is comparably small. The mesotrophic flads were extensively covered by short and/or flat species such as autumnal starwort (*Callitriche hermaphroditica*) and slender sea lettuce (*Monostroma balticum*). The sago pondweed dominating the macrophyte community in EMV formed tall and dense occurrences, while large parts of the bottom were completely unvegetated. In EMV, the dominating coral stonewort grew tall and occupied the majority of the available bottom area. Each habitat type where microalgal plankton was sampled was structurally quite uniform regardless of the flad and the

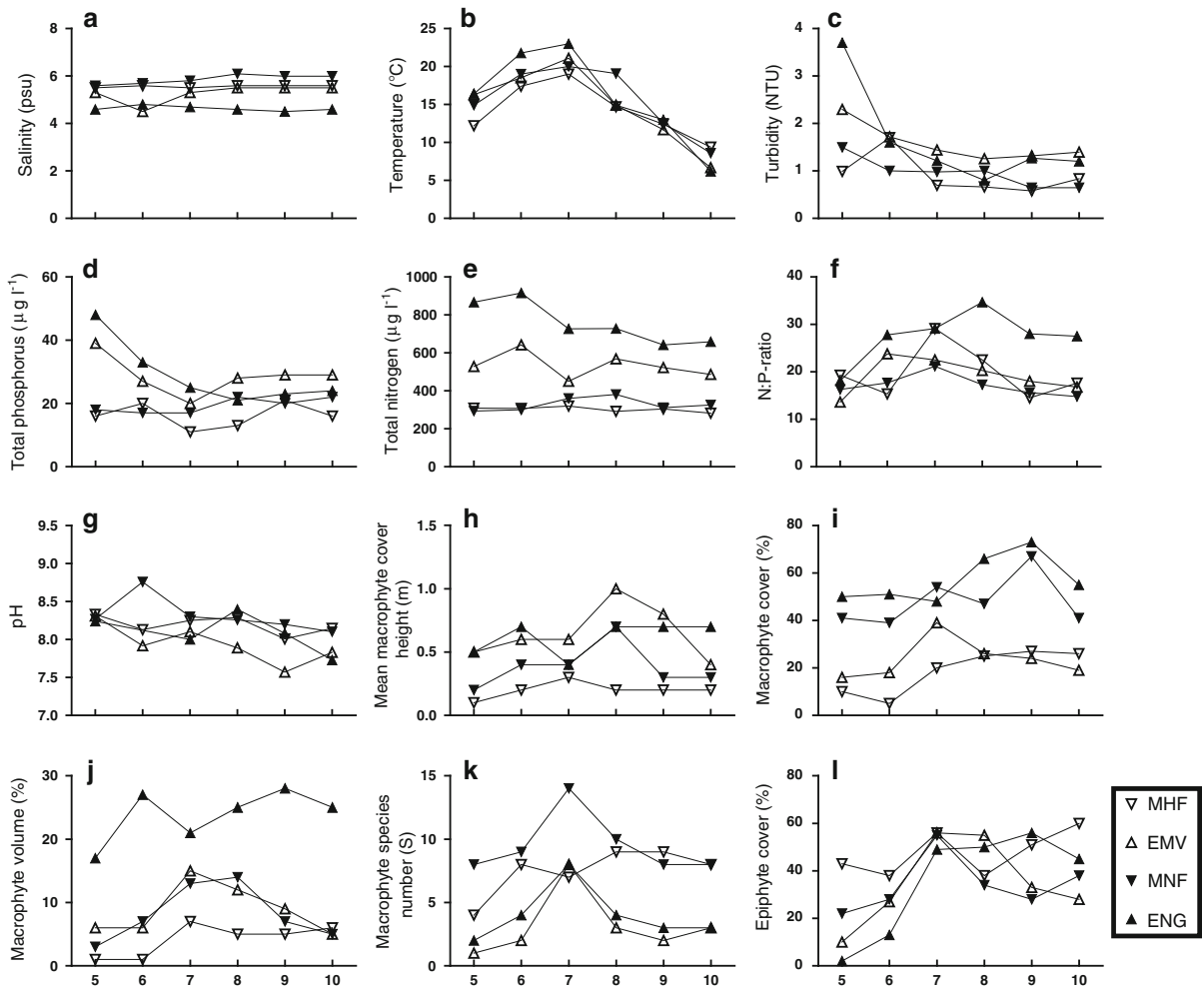


Fig. 2 a–l The abiotic characteristics **a** salinity, **b** temperature (°C), **c** turbidity (NTU), **d** total phosphorus concentration (µg l⁻¹), **e** total nitrogen concentration (µg l⁻¹), **f** N:P-ratio, **g** pH, and macrophyte community characteristics **h** mean macrophyte cover height (m), **i** macrophyte cover (%),

j macrophyte volume (%), and **k** macrophyte species number (S) and **l** epiphyte cover (%) were assessed in each of the four flads (MHF, EMV, MNF and ENG) once a month, from May (5) to October (10)

sampling occasion. The open water habitats were always clear of macrophytes, while the water volume covered by macrophytes in the macrophyte-covered habitat varied between 20% and 40%, varying mainly with the sampling occasions.

Microalgal plankton structure

Species assemblage

Most of the 100 species of planktic microalgae that were encountered (Online Appendix 1) were seen only

sporadically. Only the Ciliophore *Mesodinium rubrum* was present in all the samples. The Bacillariophytes *Meridion circulare* and *Navicula vanhoeffeni*, and the Dinophytes *Heterocapsa triquetra* and *Katodinium* sp. occurred often in the mesotrophic flads, while the eutrophic flads were characterized by the Chlorophytes *Monoraphidium contortum*, *M. komarkovae*, *Oocystis* sp., *Scenedesmus acuminatus*, and *S. verrucosus*, the Cyanophytes *Merismopedia glauca*, *M. tenuissima*, *Microcystis* sp. and *Planktolyngbya limnetica*, the Dinophyte *Protoperidinium brevipes*, and the Euglenophyte *Lepocincilis ovum*. Few corresponding character species were found in any

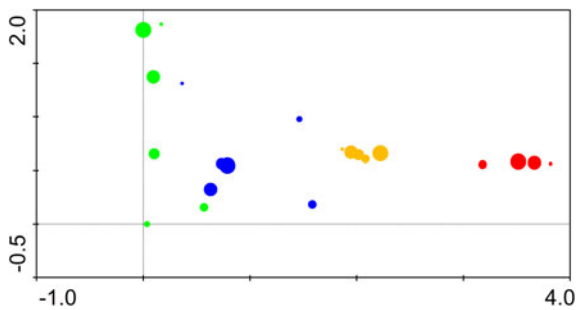


Fig. 3 The DCA ordination shows the similarity in macrophyte composition among the four flads and each month of the growing season. The cold colors represent the mesotrophic (blue for MHF and green for MNF) and the warm ones the eutrophic (orange for EMV and red for ENG) flads. The size of the circles grows along with time. The smallest circles stand for May and the largest ones for October. Eigenvalues for the plotted first and second DCA-axes were 0.84 and 0.24 of a total of 2.50

particular flad. The Bacillariophytes *Amphora veneta* and *Navicula capitata* occurred frequently only in MHF, and the Dinophyte *Protoperidinium granii* was often present only in ENG. Only a few species were generally associated with particular sampling occasions. The Bacillariophytes *Navicula vanhoeffeni* and *Nitzschia* sp. and the Dinophyte *Heterocapsa triquetra* occurred commonly in both ends of the season and scarcely in the middle, while the Bacillariophyte *Navicula longissima* and the Cyanophyte *Pseudanabaena* sp. exhibited opposite patterns. Further, the Cryptophyte *Cryptomonas* sp. and the Dinophyte *Katodinium* sp. occurred more and more commonly toward the end of the season, while another Dinophyte, *Gymnodinium* sp., had reversed patterns of occurrence. None of the microalgal plankton species seemed generally, within the trophic states, or at given times of day characteristic for either habitat type.

Species abundance-environment relations

The relative abundances of the microalgal plankton species were clearly related to the studied environmental factors. The first CCA axis ($\lambda_1 = 0.52$, $r = 0.94$) explained 36.5% and the second one ($\lambda_2 = 0.35$, $r = 0.79$) 24.2% of the total 85.6% of species-environment variation captured by the analysis (Fig. 4). The Monte Carlo test with 499 permutations showed that both the first canonical axis ($\lambda_1 = 0.94$, $F = 7.20$) and the sum of all canonical axes (trace = 1.42, $F = 3.50$) were highly significant

($P < 0.01$). The first ordination axis was strongly negatively correlated with flad temperature (TempL) ($r = -0.74$), flad total nitrogen concentration (TotNL) ($r = -0.66$), day length (DLL) ($r = -0.57$), and flad volume covered with macrophytes (3DL) ($r = -0.47$). The second CCA axis was strongly negatively correlated with flad volume covered with macrophytes (3DL) ($r = -0.60$). Light intensity (LIL) and sampling habitat volume covered with macrophytes (3DS) and flad total phosphorus concentration (TotPL) had only a minor impact on any of the ordination axes. Flad temperature (TempL) and day length (DLL) co-varied strongly ($r = 0.87$) with each other just like mean flad nitrogen concentration (TotNL) and flad volume covered with macrophytes ($r = 0.75$) did with each other.

The results of the CCA indicate that variation in microalgal plankton structure (i.e., the assemblage of species and their relative abundances) was primarily attributable to large-scale environmental patterns: the trophic state of the environment, flad volume covered by macrophytes and seasonal succession. The smaller-scale environmental conditions were less and/or less consistently related to microalgal plankton composition. That is, habitat type and the time of day could just be weakly associated with the plankton composition. Alternatively or simultaneously, the magnitude and direction of the association could depend on the large-scale environmental patterns and thus fade in the analysis.

Group abundances

During early and mid-season, the total biomass of planktic microalgae was on average an order of magnitude as high in the eutrophic as in the mesotrophic flads (Fig. 5). In both mesotrophic flads, the bulk of the total biomass consisted of Ciliophores (i.e., *Mesodinium rubrum*). In MHF, also Cyanophytes and Bacillariophytes contributed considerably. *M. rubrum* constituted a large part of the microalgal plankton biomass also in both eutrophic flads. However, the bulk in EMV consisted of Cyanophytes. In ENG, Dinophytes was the most abundant group, while the contribution of Cryptophytes was almost equal with that of *M. rubrum*. During late season, differences in group abundances among the flads became small mainly because microalgal plankton biomass peaked

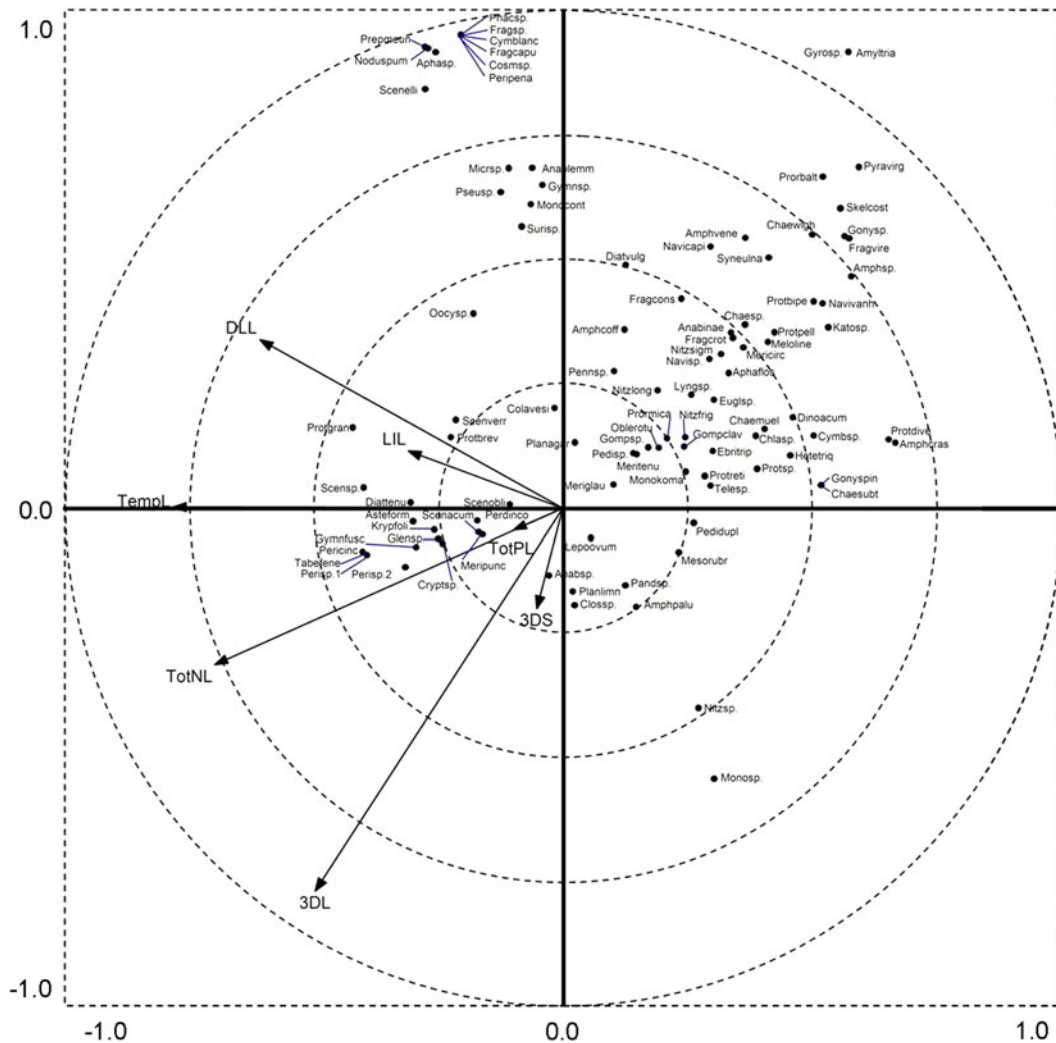


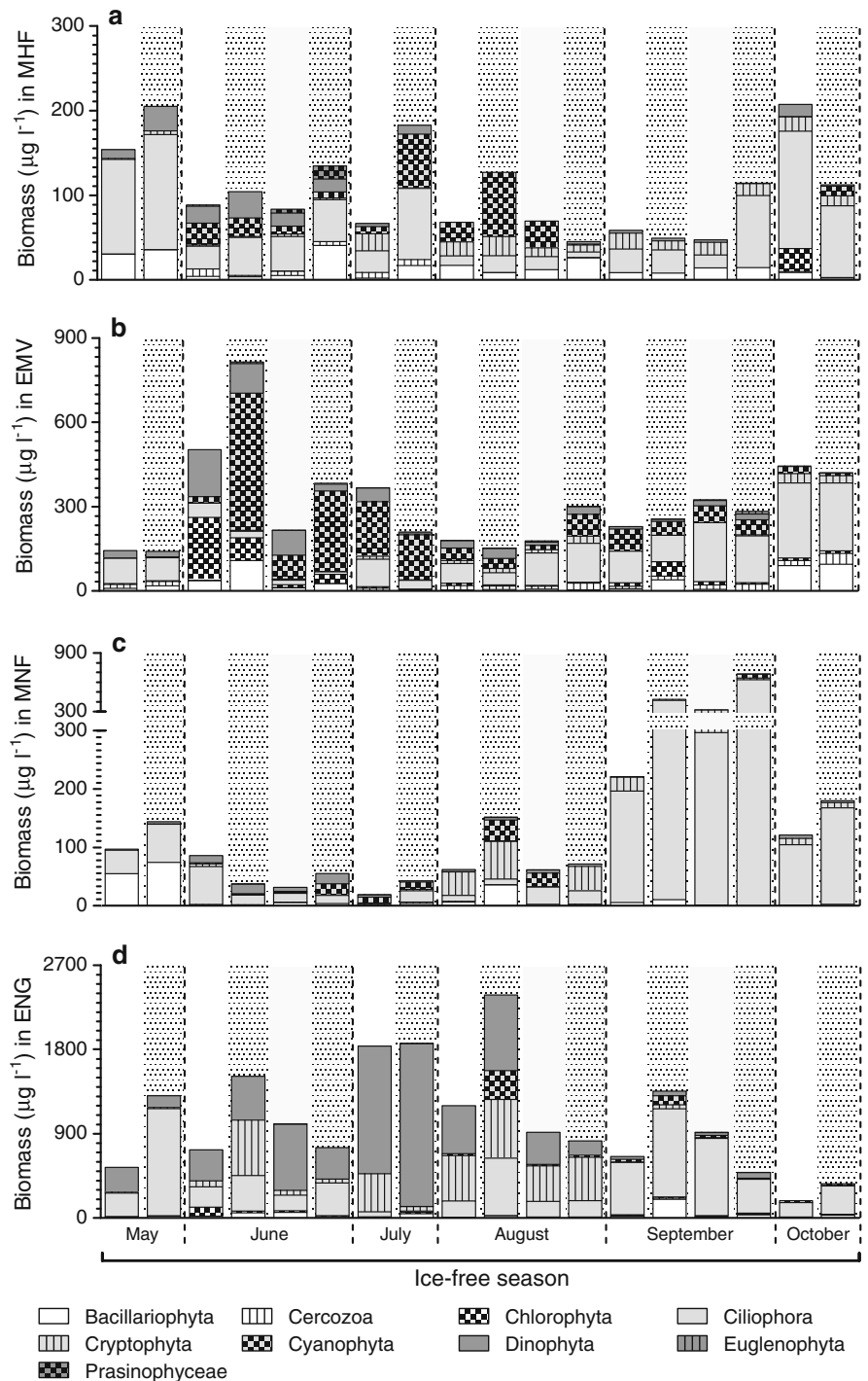
Fig. 4 The first CCA axis ($\lambda_1 = 0.94$) explained 36.5% and the second one ($\lambda_2 = 0.79$) 24.2% of the total 85.6% of species-environment variation captured by the analysis (Monte Carlo permutation test ($n = 499$): trace = 1.42, $F = 3.50$, $P = 0.002$). The first ordination axis was strongly negatively correlated with flad temperature (TempL) ($r = -0.736$), flad nitrogen concentration (TotNL) ($r = -0.657$), day length (DLL) ($r = -0.572$) and flad volume covered with macrophytes (3DL) ($r = -0.467$). The second CCA axis was strongly negatively correlated with flad volume covered with macrophytes (3DL) ($r = -0.604$). Light intensity (LIL) and sampling habitat volume covered with macrophytes (3DS) and flad phosphorus concentration (TotPL) had only a minor impact on any of the ordination axes. Flad temperature (TempL) and day length (DLL) co-varied strongly

($r = 0.867$) with each other just like mean flad nitrogen concentration (TotNL) and flad volume covered with macrophytes ($r = 0.748$) did with each other. The centroid of the CCA plot represents average environmental conditions. The abundances of species with scores differing only little from the centroid correlate with average environmental conditions or with a wide range of them. The larger the difference, the more the abundance of the species is associated with specific environmental conditions. The length and orientation of an environmental vector represents its magnitude and direction of maximum change in the ordination space. The proximity and alignment of a species with a particular vector shows how closely variation in its abundance is related to the vector

in the mesotrophic flads but not in the eutrophic ones and *M. rubrum* became explicitly dominant in all the flads. Differences among the habitat types and times of day were often considerable throughout the season but

specific for each flad and sampling occasion. None of the microalgal plankton groups could thus be associated specifically with either of the habitat types in general or at any particular time of day.

Fig. 5 The stacked bars illustrate the biomasses ($\mu\text{g l}^{-1}$) of the nine microalgal plankton groups in **a** MHF, **b** EMV, **c** MNF, and **d** ENG in the middle of each month (*x*-axis in **d** during the ice-free period. The *shadings and patterns* behind the bars indicate the times of day and the habitat types the plankton communities represent. *White background color* stands for the middle of the day and *gray* for the middle of the night. *Clear background pattern* displays open habitats, while habitats covered by macrophytes are indicated by the *dotted pattern*. Note that the scales on the *y*-axes differ among the flats and that the *y*-axis in **c** is divided into two segments with different scales



Community-level composition

The composition of the studied associations of planktic microalgae varied distinctively. The results of the DCA were highly meaningful and fulfilled the criteria

for statistical validity. The first ($\lambda_1 = 0.68$) and second ($\lambda_2 = 0.47$) DCA-axes had clearly higher eigenvalues than the following two axes ($\lambda_3 = 0.24$ and $\lambda_4 = 0.15$) and explained together more (22.4% vs. 16.8%) of the cumulative percentage variance of

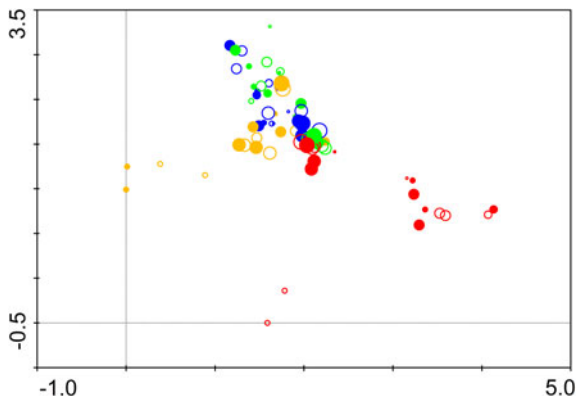


Fig. 6 The DCA ordination shows the similarity in microalgal plankton composition among all the 72 samples. The cold colors represent the mesotrophic (blue for MHF and green for MNF) and the warm ones the eutrophic (orange for EMV and red for ENG) flads. The size of the circles grows along with time. The smallest circles stand for samples taken in May and the largest ones for samples taken in October. Further, the open circles represent samples taken in open water and the filled ones samples from dense macrophyte beds. Since different symbols are not used to distinguish between samples taken at day and night, samples from June, August, and September are represented in double. Eigenvalues for the plotted first and second DCA-axes were 0.68 and 0.47 of a total of 4.60

species data than the corresponding axes in the CCA carried out using the same data (Fig. 6).

Microalgal plankton composition and its dynamics were largely similar between both mesotrophic flads. Plankton composition diverged gradually from May until August, to return close to its original state by the end of the season. The microalgal plankton associations in EMV and in the mesotrophic flads were similar in May. In June, the association in EMV had diverged considerably to its own compositional direction, to develop (in the long term more and in the short term less consistently) back toward its original state and thus also toward the mesotrophic compositional types for the rest of the season. The composition of microalgal plankton in ENG differed clearly from that in all the other flads during early and mid-season, before becoming similar with the composition in the other flads, especially the mesotrophic ones. During early season, considerable compositional differences were found between the different habitat types in ENG. These were the only habitat-level differences large enough to clearly disrupt the principal compositional clustering after flads and seasonal succession. Notable habitat-level differences were detected also in EMV during June and August.

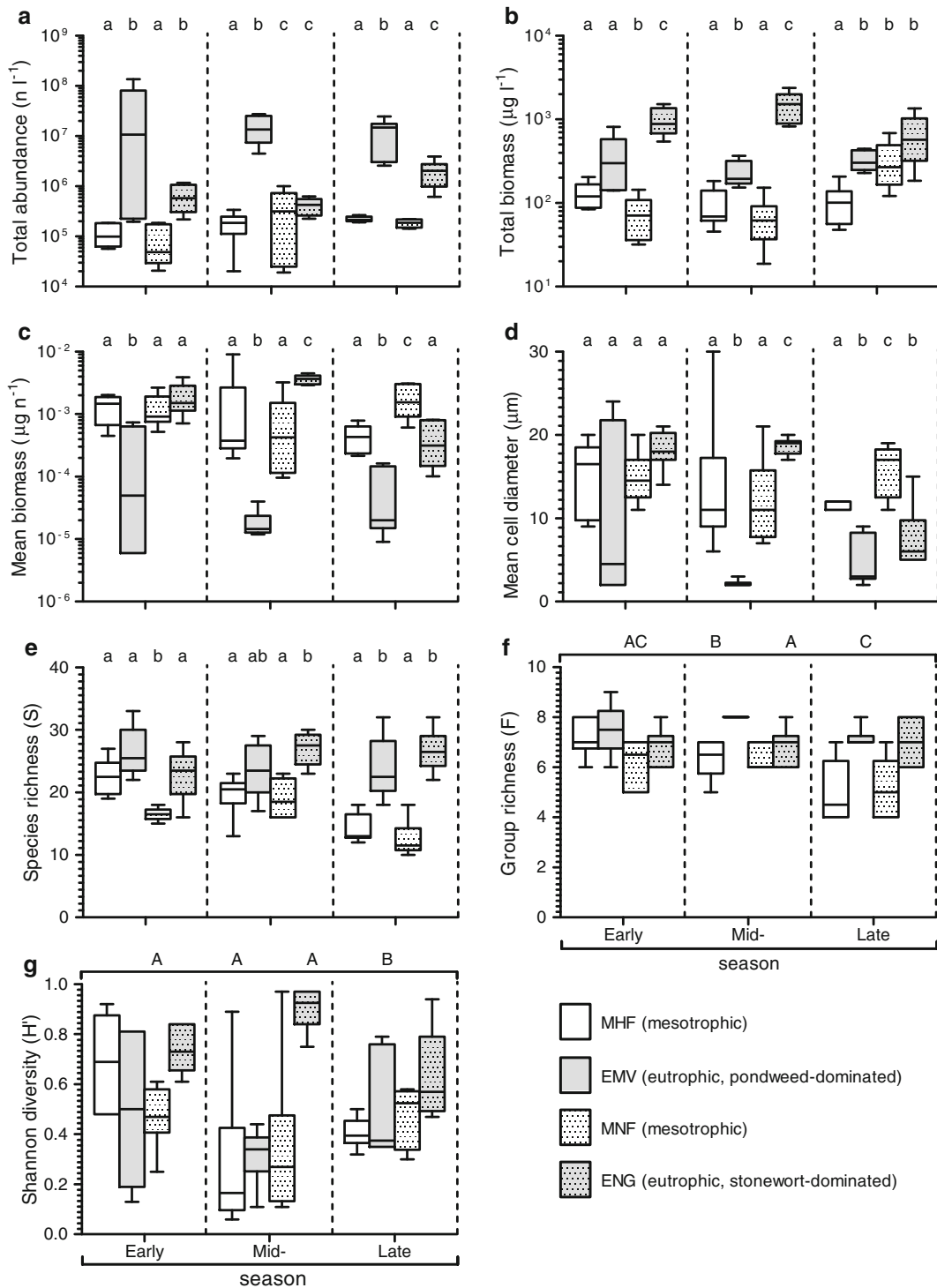
Further, corresponding differences that were dependent on the time of day were found in MHF in August and in MNF in June and August. In general, microalgal plankton composition changed very little between day and night.

Community-level metrics

Habitat type and the time of day did not vary significantly with any of the community-level metrics either as a part of any interaction with the other environmental factors (3- and 2-way ANOVAs) or as individual factors (independent samples *t* tests). Thus, it was appropriate to analyze the data by 2-way ANOVAs (flad \times phase of the season) and subsequent 1-way ANOVAs and SNK post hoc tests to demonstrate possible differences in the community-level metrics among the flads.

The total density of microalgal plankton ranged from around $20\,000\text{ n l}^{-1}$ to almost $150,000,000\text{ n l}^{-1}$ (Fig. 7a) and varied significantly among the flads depending on the phase of the season (2-way ANOVA: $F = 2.641$; $df = 6,60$; $P = 0.024$). Variation among the flads was significant during early (1-way ANOVA: $F = 24.774$; $df = 3,20$; $P < 0.001$), mid- (1-way ANOVA: $F = 15.673$; $df = 3,20$; $P < 0.001$) and late season (1-way ANOVA: $F = 42.544$; $df = 3,20$; $P < 0.001$). During early season, total density was significantly higher in the eutrophic than in the mesotrophic flads (SNK: $P < 0.05$). During mid-season, total density was significantly higher in EMV than in any of the other flads and significantly higher in MNF and ENG than in MHF (SNK: $P < 0.05$). During late season, total density was significantly higher in EMV than in any of the other flads and significantly higher in ENG than in the mesotrophic flads (SNK: $P < 0.05$).

The total biomass of microalgal plankton varied between about $20\ \mu\text{g l}^{-1}$ and $2,400\ \mu\text{g l}^{-1}$ (Fig. 7b). Variation among the flads depended significantly on the phase of the season (2-way ANOVA: $F = 3.214$; $df = 6,60$; $P = 0.008$) and was significant during early (1-way ANOVA: $F = 15.722$; $df = 3,20$; $P < 0.001$), mid- (1-way ANOVA: $F = 39.013$; $df = 3,20$; $P < 0.001$) and late season (1-way ANOVA: $F = 7.007$; $df = 3,20$; $P < 0.001$). During early season, total biomass was significantly higher in ENG than in any of the other flads and significantly higher in MHF and EMV than in MNF (SNK: $P < 0.05$). During mid-



season, total biomass was significantly higher in ENG than in any of the other flads and significantly higher in EMV than in the mesotrophic flads (SNK: $P < 0.05$).

During late season, total biomass was significantly lower in MHF than in all the other flads (SNK: $P < 0.05$).

◀ **Fig. 7** The box-and-whiskers (min/max) plots ($n = 6$) for the seven community-level metrics **a** total density ($n\ l^{-1}$), **b** total biomass ($\mu\text{g}\ l^{-1}$), **c** mean biomass ($\mu\text{g}\ n^{-1}$), **d** mean cell diameter (μm), **e** species richness (S), **f** group richness (F), and **g** Shannon's diversity index value (H') describe microalgal plankton communities in MHF (white boxes), EMV (gray boxes), MNF (white dotted boxes), and ENG (gray dotted boxes) during early (May and June), mid- (July and August) and late (September and October) season. The values of the variables **a–e** depended simultaneously on the flad and the phase of the season, while those of the variables **f** and **g** depended only on the flad. Thus, the five first variables were compared among the flads separately within each phase of the season and the two last variables within the whole season. Homogeneous subsets (SNK: $P < 0.05$) are marked by lower cases in the comparisons within the phases and by upper cases in the comparisons within the season

The mean biomass of microalgal plankton ranged from $ca\ 6 \times 10^{-6}\ \mu\text{g}\ n^{-1}$ to $9 \times 10^{-3}\ \mu\text{g}\ n^{-1}$ (Fig. 7b) and varied significantly among the flads depending on the phase of the season (2-way ANOVA: $F = 4.398$; $df = 6,60$; $P = 0.001$). Variation among the flads was significant during early (1-way ANOVA: $F = 6.212$; $df = 3,20$; $P = 0.004$), mid- (1-way ANOVA: $F = 21.396$; $df = 3,20$; $P < 0.001$), and late season (1-way ANOVA: $F = 16.859$; $df = 3,20$; $P < 0.001$). During early season, mean biomass was significantly lower in EMV than in any of the other flads (SNK: $P < 0.05$). During mid-season, mean biomass was significantly higher in ENG than in any of the other flads and significantly higher in the mesotrophic flads than in EMV (SNK: $P < 0.05$). During late season, mean biomass was significantly higher in MNF than in any of the other flads and significantly higher in MHF and ENG than in EMV (SNK: $P < 0.05$).

The mean diameter of the microalgal plankton cells varied between about $2\ \mu\text{m}$ and $30\ \mu\text{m}$ (Fig. 7d). Variation among the flads depended significantly on the phase of the season (2-way ANOVA: $F = 5.463$; $df = 6,60$; $P < 0.001$). Differences among the flads were significant only during mid- (1-way ANOVA: $F = 15.673$; $df = 3,20$; $P < 0.001$) and late season (1-way ANOVA: $F = 20.140$; $df = 3,20$; $P < 0.001$). During mid-season, mean cell diameter was significantly higher in ENG than in any of the other flads and significantly higher in the mesotrophic flads than in EMV (SNK: $P < 0.05$). During late season, mean cell diameter was significantly higher in MNF than in any of the other flads and significantly higher in MHF than in the eutrophic flads (SNK: $P < 0.05$).

The number of microalgal plankton species ranged from about 10–30 per sample (Fig. 7e). Mean species richness varied significantly among the flads depending on the phase of the season (2-way ANOVA: $F = 2.826$; $df = 6,60$; $P = 0.017$). Variation among the flads was significant during early (1-way ANOVA: $F = 10.184$; $df = 3,20$; $P < 0.001$), mid- (1-way ANOVA: $F = 6.314$; $df = 3,20$; $P = 0.003$), and late season (1-way ANOVA: $F = 23.000$; $df = 3,20$; $P < 0.001$). During early season, species richness was significantly lower in MNF than in any of the other flads (SNK: $P < 0.05$). During mid-season, species richness was significantly higher in ENG than in the mesotrophic flads (SNK: $P < 0.05$). During late season, species richness was significantly higher in the eutrophic than in the mesotrophic flads (SNK: $P < 0.05$).

The number of microalgal plankton groups varied from four to nine per sample (Fig. 7f). Average group richness varied significantly among the flads regardless of the phase of the season (1-way ANOVA: $F = 13.685$; $df = 3,68$; $P < 0.001$). Group richness was significantly higher in EMV than in any of the other flads and significantly higher in ENG than in MNF (SNK: $P < 0.05$).

Shannon's diversity index values on microalgal plankton species diversity varied from 0.06 to 0.97 per sample (Fig. 7g). The average values were significantly higher in ENG than in any of the other flads regardless of the phase of the season (1-way ANOVA: $F = 7.724$; $df = 3,68$; $P < 0.001$ /SNK: $P < 0.05$).

Discussion

Microalgal plankton structure

Environmental conditions conformed to the premises, and the four main hypotheses of the study were mostly supported. Microalgal plankton structure varied characteristically with the trophic and the vegetative states of the flads. The relative strength of respective correlation depended on which variables were used to assess the structure. In any case, differences among the trophic and vegetative states depended on the phase of the season. Structural variation was largest during early and mid-season. During late season, the plankton structure became comparably uniform in all flads regardless of how the structure was assessed.

None of this broad-scale spatio-temporal variation depended on the habitat type or on the time of day. Conversely, this small-scale (i.e., local and diurnal) variation depended on the trophic and vegetative states of the flads as well as on the phase of the season.

Based on their occurrence frequency, several plankton species could be distinguished as generally characteristic for either trophic state regardless of any other environmental conditions. By contrast, the vegetative state of the eutrophic flads was not indicated by corresponding character species except for the Dinophyte *Protoperidinium granii*, which occurred frequently in the stonewort-dominated ENG. A purely qualitative assessment of microalgal plankton structure may thus reflect the position of a flad on a trophic gradient but not necessarily its vegetative state. Because the seasonal variation of microalgal plankton assemblages is so high at high latitudes (e.g., Gasiūnaitė et al., 2005), the frequently occurring species may be considered as true character species. The relative abundances of the different species were attributable to both the trophic and the vegetative states of the flads and nearly as prominently to seasonal succession. Owing to the co-variation among the variables reflecting the trophic and vegetative states it would not, however, be valid to rank their potential impacts on microalgal plankton abundances only based on the available data. The abundances of each microalgal plankton group seemed equally strongly related to the trophic and vegetative states of the flads. Even if many microalgal plankton groups differed in their abundance among the habitat types and times of day within some flads and occasions, none of the groups could be generally associated with either habitat type. The overall composition of the microalgal plankton associations appeared more attributable to the vegetative than to the trophic state of the flads. In this respect, the most prominent differences between the habitat types were found in the eutrophic flads, especially in the stonewort-dominated ENG. However, those differences were limited to early season. In contrast to the compositional patterns, the community-level metrics or the functional properties of the studied microalgal assemblages were generally more related to the trophic than to the vegetative state of the flads. Although variation among the flads representing different trophic and vegetative states depended strongly on the phase of the season, three general patterns can be highlighted. First, several species co-exist in respective eutrophic than in respective mesotrophic flad. Second,

microalgal plankton is more abundant in the eutrophic than in the mesotrophic flads. Third, microalgal plankton in EMV is characterized by very small-sized species compared with the rest of the flads.

Comparisons with other systems

The biota of the brackish (4 psu–7 psu) northern Baltic is composed of a mixture of freshwater and marine organisms (Bonsdorff & Blomqvist, 1993). Although salinity levels in the investigated flads do not differ from those in the open northern Baltic, several of the microalgal plankton groups in the littoral are characterized by freshwater-associated species. For instance, typically freshwater-associated Dinophytes like *Gymnodinium fuscum*, *Peridinium cinctum*, and *P. inconspicuum* and the Bacillariophyte *Asterionella formosa* occur together with marine Dinophytes such as *Heterocapsa triquetra* and *Dinophysis acuminata* and the Bacillariophyte *Skeletonema marinoi*, species common for the open Baltic Sea (HELCOM (Olenina et al., 2006)). This unique mixture of, on one hand, freshwater and marine, and on the other, littoral and pelagial microalgal plankton species emphasizes that microalgal plankton groups are not fully comparable across systems.

The mesotrophic flads were dominated by Bacillariophytes, the photosynthetic Ciliophore *Mesodinium rubrum*, Cryptophytes, and Cyanophytes. Such large contributions by Bacillariophytes and Cyanophytes are characteristic for mesotrophic conditions also in shallow lakes (Duarte et al., 1992; Jeppesen et al., 2000). Ciliophores are often neglected in phytoplankton studies. However, *Mesodinium rubrum* is likely to be one of the most important planktic primary producers in many littoral systems (Lindholm, 1985; Crawford, 1989). This seems particularly true for the mesotrophic flads. The Ciliophore may also have an important role as a secondary producer in these environments, as it may feed upon the relatively abundant Cryptophytes (Lindholm, 1985). Apart from the relatively high abundance of Cyanophytes, the relative quantities of the groups did not resemble those in other coastal waters of the northern Baltic (Niemi, 1973; Thamm et al., 2004; Gasiūnaitė et al., 2005).

The eutrophic EMV was dominated by Cyanophytes. Also Chlorophytes and *M. rubrum* contributed substantially to the total biomass. High relative biomasses of Cyanophytes (Duarte et al., 1992;

Scheffer et al., 1997; Jeppesen et al., 2000) and Chlorophytes (Jensen et al., 1994; Jeppesen et al., 2000) are typical even for shallow eutrophic lakes and for the coastal and open waters of the northern Baltic (Niemi, 1973; Gasiūnaitė et al., 2005). The microalgal plankton association in ENG, in turn, was characterized by a high share of Dinophytes. In shallow temperate lakes, members of this group are associated rather with oligotrophic conditions (Jeppesen et al., 2000). By contrast, Dinophytes comprise a high proportion of planktic microalgal biomass in the eastern and northern coasts of the Baltic, within a broad range of nutrient and salinity levels (Gasiūnaitė et al., 2005). Also Cryptophytes and *M. rubrum* contributed notably to the total biomass in ENG. In both eutrophic flads, Bacillariophytes were absent in May, increased in abundance in June, vanished for the rest of the summer and had a moderate autumnal peak in September/October, thus resembling near-shore patterns in nearby freshwater (Tallberg et al., 1999) and brackish water environments (Niemi, 1973). The summer bloom in ENG was otherwise similar to that in EMV, except for the dominating status of Dinophytes instead of Cyanophytes, which tend to dominate the summer bloom also in eutrophic temperate lakes (Watson et al., 1997; Jeppesen et al., 2000). It is possible that ENG is intrinsically more prone to exert blooms of Dinophytes than EMV because of accumulation of dinoflagellate resting cysts. Once such cyst beds are established, especially in physically restricted shallow environments, they may cause dominant blooms reinforcing the population (Cembella et al., 2005).

Also the insignificance of Diatoms (Bacillariophyta) distinguished microalgal plankton in flads from that in the northern Baltic pelagial. Diatoms tend to dominate the microalgal plankton of the coastal northern Baltic, especially in the spring (Gasiūnaitė et al., 2005). In the flads, however, they were generally represented by few species and appeared in low abundances. Diatoms are generally adapted to turbulent conditions and high nutrient levels (Margalef, 1978). Flads may thus be too sheltered environments for diatoms. Alternatively, diatoms may have been abundant in some flads for a short time right after the ice break and thus not included in the samples. By dominating the spring bloom (Niemi, 1975), diatoms often exhaust the pool of silicon and thus limit their own abundance later on in the season. The small

autumnal peaks of diatoms seen in the eutrophic flads are presumably caused by cold water favoring certain diatom species (Wasmund et al., 2008).

In summary, what is known about changes in the relative quantity of the main microalgal plankton groups from trophic gradients in shallow lakes seems in general terms applicable to the studied flads, except for ENG. In this respect, its microalgal plankton community is a bit of an oddity, although patterns within the flad were somewhat coherent with observations in shallow lakes. When nutrient levels range from intermediate to high, patches of macrophytes tend to be inhabited by Cryptophytes and other small and motile organisms. Fast-sinking species such as many Bacillariophytes and Chlorophytes are more confined to open water (Balls et al., 1989; van Donk et al., 1990).

Maintenance and stability of the community states

The structural patterning of microalgal plankton among the flads supports their classification into ones in three alternative states. Nevertheless, the stability of the chosen, “stable” community states (i.e., the hypothetical extremes) need to be evaluated to assess how well the study sites can be considered to encapsulate landscape-level variation in microalgal plankton structure in the study system. Out of the studied flads, EMV appears to have the highest potential to be in a transitional state. On one hand, its microalgal plankton community is dominated by Cyanophytes. They are unmatched competitors in low light. Cyanophytes also facilitate such conditions, because they can inflict exceptionally high turbidity per unit phosphorus (Scheffer et al., 1997). If these conditions occurred a bit earlier in the spring, the growth of pondweed sprouts could be hampered. Such an event would cause a threshold for the re-establishment of any submerged macrophytes in the flad and thus promote a new, Cyanophyte-dominated and macrophyte-poor state. The potential release of the high phosphorus reserves (Appelgren & Mattila, 2005) from the sediment into the water column would further stabilize such a new state. On the other hand, a reduction of nutrient concentrations in the water column especially in the beginning of the season could drastically promote pondweed and impede Cyanophyte growth through competition with phytoplankton causing less turbidity.

The consequent conditions of high light availability could allow the establishment of other submerged macrophytes in the phosphorus-rich sediment further restraining internal load into the water column. Stoneworts could be potential colonizers of such fertile bottoms, especially since they already girdle the flad. Stoneworts could outcompete other macrophytes and Cyanophytes through allelopathy and by impacting nutrient availability, consumer composition, sedimentation, resuspension and light availability (reviewed in van Donk & van de Bund, 2002). Accordingly, the community in ENG can be in a stable state. According to the earlier reasoning, even the mesotrophic communities should be stable due to the small internal nutrient reserve in those flads (Appelgren & Mattila, 2005). Transient increases in water column nutrient concentrations would thus not easily inflict any self-maintaining processes promoting the growth of Cyanophytes and other planktic microalgae. However, the ample occurrence of filamentous macroalgae in all the flads calls into question the stability of their communities. In other shallow bays of the northern Baltic, such conditions have been related to transient or intermediate community states (Dahlgren & Kautsky, 2004). This association is only hypothetical, since no mechanistic studies back up the hypothesis.

Potential processes behind the observed patterns of microalgal plankton structure

Although the trophic state of the environment is a central determinant for microalgal plankton structure (Watson et al., 1997; Jeppesen et al., 2000), inorganic nutrient levels can not be used as unambiguous predictors (Kalff & Knoechl, 1978). Microplankton structuring is always more intricate and context-dependent than what such proxies could indicate. Based on our results, the direct and indirect interdependence between microalgal plankton and macrophytes seems fundamentally important. Basically, microalgal composition may co-vary with that of macrophytes because (1) both types of primary producers are shaped by common factors such as the trophic state of the environment and/or (2) the primary producers regulate each others' composition.

In general, macrophytes and planktic microalgae affect each other in many ways by competing for and modifying the availability of light and nutrients (Barko & James, 1998; Mulderij et al., 2007). In

addition, macrophytes can increase the sinking loss of phytoplankters (van de Bund et al., 2004) and produce allelopathic compounds against them (Wium-Anderesen et al., 1982). However, sago pondweed is not known to produce allelopathic substances (Körner & Nicklisch, 2002), and the allelopathic potential of Charophytes is thought to be low (Mulderij et al., 2007). Effects between microalgal plankton and macrophytes can also be indirect. Both plankton and macrophytes can modify trophic interactions at several trophic levels physically and chemically (Timms & Moss, 1984; Burks et al., 2000; Scheinin et al., 2012). Such effects on different consumer levels can cascade down to either group of primary producers (Carpenter et al., 1985; Scheffer et al., 1993).

The explicit differences in microalgal plankton structure between patches of open water and dense macrophytes being distinctive for ENG can tempt one to regard the structuring role of macrophytes less important in the other flads. However, this is likely to be a matter of scales. The processes macrophytes are involved in operate at different scales of space and time. That is, different processes may be responsible for shaping microalgal plankton communities at habitat and landscape-levels. Accordingly, this study does suggest, that habitat-level processes can be more important in ENG than in the other flads. The spectrum of such processes can be wide.

Future perspectives

The structure and seasonal dynamics of microalgal plankton vary considerably and distinctively with the trophic and vegetative states of the flads. The observed patterns seem to follow those observed in shallow temperate lakes rather than those observed in the pelagial of the northern Baltic. The role of planktic primary production in the littoral zones of the northern Baltic and other coastal areas should receive more emphasis. Gradients in trophic and vegetative states should be studied in greater detail and include even heavily eutrophied environments. Even other gradients such as those of salinity should be incorporated in the studies. In order to understand how the observed patterns come about, especially processes through which microalgal plankton and macrophytes regulate each other need further study, at several spatial and temporal scales. Finally, microalgal plankton

composition reflects the state of the studied littoral communities most distinctively during early and mid-season, before macrophyte composition has reached its annual climax and tends to be applied as an environmental indicator. Thus, microalgal plankton composition may have high potential as a monitoring tool and environmental indicator.

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