DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
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EVOLUTIONARY LIFE-STRATEGIES OF AUTOTROPHIC PLANKTONIC MICRO-ORGANISMS IN THE BALTIC SEA

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PRESS

By studying individual species in greater detail, we will be able to understand the shaping forces of the abiotic environment on the one hand, and biotic interactions, including competition and predation, on the other.

(Verity & Smetacek 1996)

CONTENTS

ORIGINAL PUBLICATIONS

This thesis is based on the following original papers, which are referred to by their Roman numerals

I Olli, K., Heiskanen, A.-S. & Seppälä J. 1996. Development and fate of *Eutreptiella gymnastica* bloom in nutrient enriched enclosures in the coastal Baltic Sea. *Journal of Plankton Research*. 18: 1587–1604.

II Olli, K. 1996. Resting cyst formation of *Eutreptiella gymnastica* (Euglenophyceae) in the northern coastal Baltic Sea. *Journal of Phycology*. 32: 535–542.

III Heiskanen, A.-S. & Olli, K. 1996. Sedimentation and buoyancy control of *Aphanizomenon flos-aquae* (Nostocales, Cyanophyta) in nutrient replete and nutrient deplete coastal area of the Baltic Sea. *Phycologia*. 35 (6 Supplement): 94–101.

IV Olli, K., Heiskanen, A.-S., Lohikari, K. 1997. Vertical migration of autotrophic micro-organisms during a vernal bloom at the coastal Baltic Sea — coexistence through niche separation. *Hydrobiologia*. Submitted.

V Olli, K., Heiskanen, A.-S. 1997. Seasonal stages of phytoplankton community structure and sinking loss in the Gulf of Riga. *Journal of Marine Systems*. Submitted.

VI Olli, K. 1997. Diel vertical migration of phytoplankton and heterotrophic flagellates in the Gulf of Riga. *Journal of Marine Systems*. Submitted.

ABSTRACT

During the years 1993–1995 several research projects were carried out at the Tvärminne Zoological Station, SW Gulf of Finland, and at the southern part of the Gulf of Riga to study the structure and functioning of the pelagic ecosystem. These studies revealed several important aspects of the life-strategies of dominant species exemplified by the formation of deep resting populations and differential vertical migration of the micro-organisms in the water column.

A mesocosm experiment at the SW coast of Finland unveiled a high potential of *Eutreptiella gymnastica* (Euglenophyceae) to utilise pulsed nutrient inputs (e.g. through upwellings) and gain dominance in the phytoplankton community in the coastal waters. The success of the species was supported by high growth rate (1.03 divisions day^{-1}) and vertical migration to deeper nutrient rich layers. However, the duration of *Eutreptiella* blooms is controlled by the high grazing losses (exponential grazing loss rate –0.60 day^{-1}) by the ambient zooplankton populations, stressing the importance of the species in the food-chain.

The potential for subsequent blooms of *Eutreptiella gymnastica* is apparently granted by the deposition of resting cysts to the benthic seed bank. It is hypothesised that blooms of *E. gymnastica* can have an impact on the vertical flux of particulate organic carbon (POC) through sedimentation of polysaccharide rich resting cysts and zooplankton fecal pellets packed with indigestible polysaccharide (paramylon) particles.

Vertical migration of autotrophic micro-organisms was investigated on a diel basis in field conditions during two spring bloom periods (1994 at the SW coast of Finland; 1995 at the southern Gulf of Riga) and one midsummer period (1994 at the southern Gulf of Riga). The results indicate a significant vertical niche separation among the dominant species of vernal bloom dinoflagellates (*Peridiniella catenata* and *Scrippsiella hangoei*) in the Gulf of Finland. The temporal dynamics of vertical distribution of dominant species in the Gulf of Riga revealed a species specific pattern which was modified by the environmental factors and a potential of several species to benefit from deep nutrient pools. The seasonal pattern in the vertical distribution of *Mesodinium rubrum* (an autotrophic ciliate) revealed strong surface accumulations during the peak of the vernal bloom, as opposed to nearly uniform occurrence down to 30 m depth during the post-bloom period. This seasonal pattern was evident at both of the investigated areas.

In 1993–1995 the phytoplankton community structure and sedimentation was studied on a seasonal basis in the southern part of the Gulf of Riga. The results indicate that phytoplankton sedimentation was low in midsummer and early autumn periods. In spring the sedimentation was dominated by the vertical flux of the dominant diatom species *Thalassiosira baltica*, which formed a deep resting population. The sedimentation of *T. baltica* was apparently not induced by nutrient depletion but rather by vertical stabilisation of the water column. It also demonstrated the different scenarios in the sedimentation of phytoplankton, depending on whether the spring community is dominated by diatoms (high sedimentation) or dinoflagellates (low sedimentation).

INTRODUCTION

Life cycles and behavioural adaptations of pelagic micro-organisms

The pelagic realm hosts a large number of autotrophic micro-organisms (Hutchinson 1961; Sournia *et al.* 1991). Yet a relatively limited number of species are dominating with respect to biomass build up, production, or energy and matter transfer. The last decades have revolutionised our knowledge about the structure and functioning of the pelagic food-webs by erecting a new paradigm of microbial loop (Pomeroy 1974; Williams 1981; Azam *et al.* 1983). This paradigm implies that parallel to the relatively short grazing food chain (phytoplankton—mesozooplankton—fish) also a less efficient route exists: dissolved organic matter (DOM; largely algal exudates, spills of zooplankton sloppy feeding, DOM released by viral lysis) — bacteria — heterotrophic nanoflagellates as main consumers of planktonic bacteria and pico-algae—ciliates—mesozooplankton—fish. The many steps sum up to a considerable dissipation energy loss, which according to the laws of thermodynamics is needed to keep the route in action. However, in spite of the relative inefficiency, this pathway enables the channelling of a part of the primary production, which otherwise remains inaccessible for higher trophic levels, back to the grazing food chain. Thus the microbial loop acts both as a sink and link in the pelagic food web.

Evidence is accumulating on the abundance and potential impact of viruses in marine environments (Proctor & Fuhrman 1990; Suttle *et al.* 1990; Heldal & Bratbak 1991; Bratbak *et al.* 1993; Suttle *et al.* 1994; Emiliani 1993; Hara *et al.* 1996), which has led to the formulation of initial conceptual frameworks (Bratbak *et al.* 1992). Estimations of bacterial (Steward *et al.* 1992; Fuhrman & Noble 1995) or eucaryotic pico-phytoplankton (Cottrell & Suttle 1995) mortality due to viral lysis challenge the idea that grazing by nano-sized heterotrophic flagellates is the main route by which pico-sized algae and bacteria are lost in most marine and brackish environments (Fenchel 1984; Wikner & Hagström 1988; Kuuppo-Leinikki 1990; Kuosa 1991; Sanders *et al.* 1992; Gonzáles 1996).

While these findings have extended our knowledge of the biological components of the upper water column and their relationships to fluxes of materials and energy, they have not advanced our understanding why specific pelagic forms occur in time and space, and why only some attain dominant status and contribute the bulk of biogenic fluxes emanating from the mixed layer (Verity & Smetacek 1996). Survival and persistence are the virtues that define successful species, whether or not they dominate community biomass and material flux. In this respect all the modern species of today's world are evolutionarily advanced and successful, irrespective of the possible morphological or cytological simplicity. However, the bulk of large-scale biogenic cycling and pro-

duction is dependent on relatively few key taxa. The question stands: what makes these organisms so fit with the environment, what are the properties of the key taxa that lead to their dominant role in the pelagic ecosystem structure to such an extent that they shape the trophic pathways, and drive the biogeochemical fluxes. Regardless of their phylogenetic descent, the organisms face common basic challenges to survive (Fig. 1). They have to acquire resources, evade or frustrate predators, and propagate viable descendants. Predation or predator avoidance and resource acquisition act through morphologies, behavioural adaptations and life history strategies of pelagic organisms. What often remains unnoticed, is that the quantities that are of ecological interest in terms of their survival value are not the absolute magnitude of individual rates but, rather, the difference between rates.

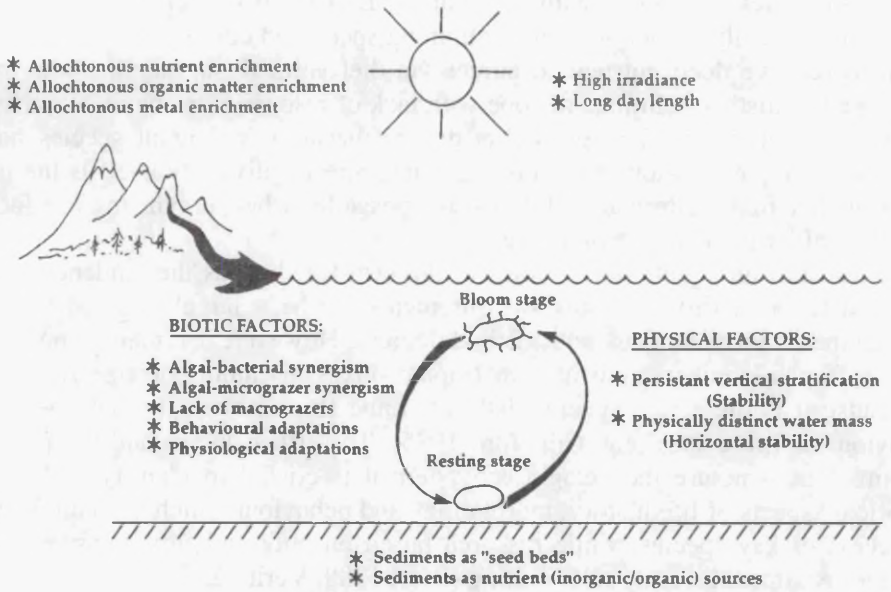

Figure 1. Relevant physical, chemical, and biotic factors that synergetically act as environmental variables mediating bloom potentials and magnitudes (modified from Paerl 1988).

The investigations of planktonic systems have evolved by using two principal approaches: 1) estimation of flows of mass and energy across trophic levels; 2) study of mechanisms by which individual populations maintain their existence. Both of these views have broad applicability to aquatic environments. Mass flux and energy flow based studies require basic input-output analysis balanced on carbon or nutrients or else accounting for the fluxes of chemically bound potential energy between subsets of the system. Community and population studies are tied ultimately to the natural selection theory, where energy flux is of lesser interest than individual fitness. Both above approaches are

based on fundamental and sound principles, but do not derive from each other. Neither approach surpasses or encompasses the other. The evolutionary life-strategies is broadly defined as the collective term for the myriad of processes by which autotrophic micro-organisms sustain and propagate themselves. However, a focus solely on physiological growth lends well to energetic and mass flux approaches, but poorly to population dynamic studies.

In the past years special attention has been paid to allometric relationships in cell size and individual processes, which hold the promise of predicting metabolic rates and production from simple measurements (e.g. Moloney & Field 1989). However, some of these allometries can conflict. In phytoplankton there is a surface-to-volume dilemma: small cell size grants better nutrient acquisition, photosynthetic efficiency, and growth rate, but leaves the organisms more conspicuous to grazers (Kiørboe 1993). Survival of larger cells depends on their strategies for coping with deprivation. Large cell size enables storage of nutrients, usually higher absolute swimming speed and consequently the potential to retrieve deep nutrient resources via diel vertical migration. Some may invoke life history solutions to cope with lack of resources or abundant grazers. The array of potential responses is diverse because individual species have evolved unique solutions for their problems. Species diversity itself is the evidence that many alternate solutions are possible, when organisms are faced with conflicting demands in nature.

Research on aquatic ecosystems in the last decades has the tendency to be biased towards flux and bulk measurements (perhaps largely due to the advancements in techniques and methodologies). However, it remains one-sided to stuff planktonic organisms into trophic boxes, pyramids or size fractions, because it is the actual species that determine fluxes, often through their behaviour or life cycles (e.g. Crawford 1995). To further understand the mechanisms that structure the pelagic ecosystem it is crucial to identify and study critical aspects of life history, morphology and behaviour which account for the success of key species, while research based on bulk and flux measurements alone remains inherently self-limiting (Paerl 1988; Verity & Smetacek 1996).

The case of the Baltic Sea

In the Baltic Sea a large part of the annual new production falls to the period of phytoplankton spring bloom. While in many boreal coastal areas the spring bloom is dominated by diatoms, in the northern Baltic Sea dinoflagellates appear to be equally important (Kononen & Niemi 1984; Heiskanen & Kononen 1994; Andersson *et al.* 1996; Olli 1997; paper V; Fig. 2). There has been considerable discussion on what determines the outcome of the vernal diatom-dinoflagellate competition. While the role of physical auxiliary energy is indisputable (e.g. Margalef 1978; Levasseur *et al.* 1984), Granéli *et al.* (1989) suggested the stimulating role of river-borne humic substances to the growth of dinoflagellates. The outcome of the vernal diatom — dinoflagellate competition

has considerable impact on the fate of the freshly produced organic matter. While the diatom dominated blooms are subjected to rapid sedimentation to the benthos (Bodungen *et al.* 1981; Christensen & Kanneworff 1986; Passow 1991a; Waite *et al.* 1992a, 1992b; Olesen 1993), the fate of the dinoflagellate bloom is more obscure, probably disintegration in the water column and subsequent sedimentation as slowly falling phytodetritus (Noji *et al.* 1986; Sellner *et al.* 1993; Heiskanen & Kononen 1994).

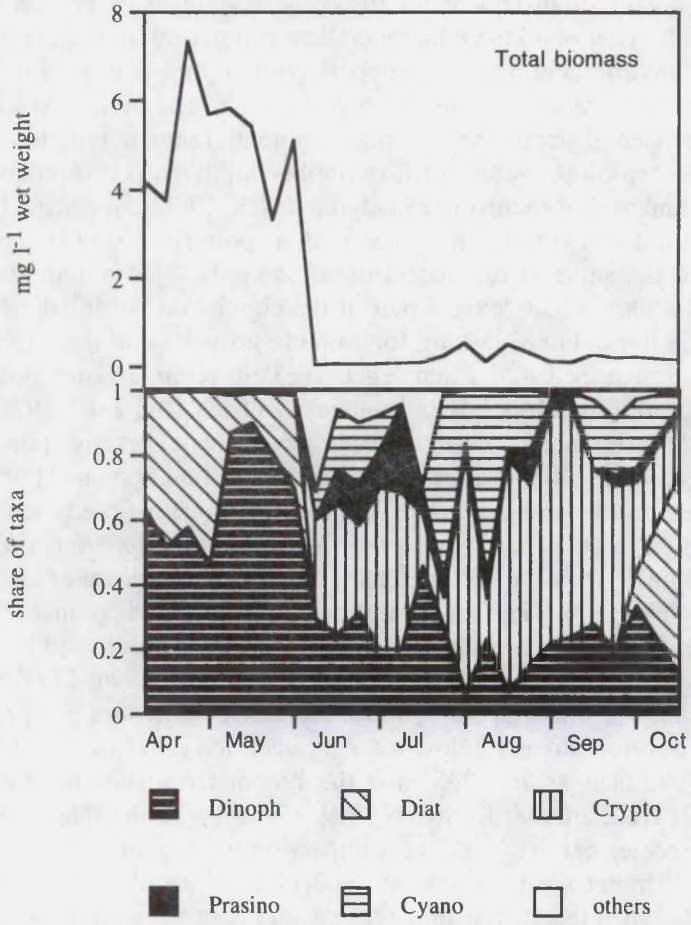

Figure 2. Dynamics of phytoplankton development in the surface layer (integrated from 0–5 m) of the western Gulf of Finland (P1 in Fig. 3) during the growth season in 1994 (excl. picoplankton). Upper panel depicts the total biomass (µg l^{-1} wet weight), and the lower panel the relative share of different groups. Note that the spring bloom was largely dominated by dinoflagellates. (unpublished data).

The diatom blooms are known to be terminated by nutrient depletion and/or vertical stabilisation of the water column (Davis *et al.* 1980; Bienfang 1981; Bienfang *et al.* 1982; Bienfang & Harrison 1984). Nutrient starvation leads to increased density of the diatom cells and consequently sedimentation from the

water column (Wiseman *et al.* 1983; Davey 1988). Nutrient depletion can lead to increased stickiness of diatom cells which, when accompanied with sufficient density of the populations, leads to aggregate formation, which further enhances the sedimentation rate (Alldredge & Gotschalk 1989; Kiørboe *et al.* 1990; Riebesell 1991a, 1991b; Kiørboe & Hansen 1993; Olesen 1993). However, this sedimentation could apparently have a survival value for the coastal bloom diatom species by providing a quick refugee in times when the surface layer turns to a hostile environment for the cells (Hargraves & French 1983; Smetacek 1985). In most planktonic habitats there is a period during the annual cycle where the environment does not support growth, thus a way to overlive hostile periods is of a survival value for a population. The ability to survive periods of environmental stress and to maintain potential seed population in the benthos poised to exploit the return of favourable conditions is of fundamental importance to planktonic organisms (Sandgren 1983, 1988; Smetacek 1985). On the other hand, it is a well-known paradox that spore formation is certainly not necessary for the survival or success of some neritic bloom diatoms (e.g. *Sceletonema costatum*), which leave a part of the population unsettled, as fugitive cells in the water column, lurking for suitable growth conditions (Kilham & Kilham 1980; Smetacek 1985). Such vegetative cells retain division potential during winter but are limited by low light intensity (Takahashi *et al.* 1978) and there may be little difference between the ecological roles of resting spores and resting cells. In general resting stages are considered to function as (1) defence against adverse environmental conditions, (2) a defence against predation, (3) a means of dispersion in areas having adverse environmental conditions (Wall & Dale 1968; Sarjeant 1974; Dale 1983; Heaney *et al.* 1983; Sarjeant *et al.* 1987; Hallegraeff & Bolch 1992). The first is most generally accepted (Blanco 1995).

In the western Gulf of Finland the vernal bloom is often dominated by dinoflagellates (Kononen & Niemi 1984; Heiskanen & Kononen 1994; Fig. 2). The two prominent dinoflagellate species, *Peridiniella catenata* and *Scrippsiella hangoei* start to develop already below the ice (when ice cover occurs) (Niemi & Åström 1987; Larsen *et al.* 1995) and the bloom terminates in late May (Heiskanen 1993; Heiskanen & Kononen 1994; Fig. 2). Yet, the relative dominance of either species can have different impact on the fate of the production and is linked to different life-histories. At the decline of the bloom the population of *S. hangoei* goes through sexual process and forms resting cysts which sediment out of the water column (Heiskanen 1993), while the fate of *P. catenata* is more obscure.

At the summer period a conspicuous feature of the phytoplankton in the Baltic Sea is the mass occurrence of cyanobacterial blooms (Kahru *et al.* 1994; Rantajärvi 1995). Apart from the more fresh-water eastern Gulf of Finland, the responsible species are *Aphanizomenon flos-aquae* and *Nodularia spumigena*. Both species can produce toxins (Sivonen *et al.* 1989; Carmichael 1992), and pose a health hazard to humans and terrestrial fauna (Nehring 1993; Olli 1996). Being able to fix atmospheric N_2, these species possess a degree of autonomy over the ambient nitrogen resources. It has been suggested that in the Baltic Sea

these species benefit from low N/P ratios which gives them an advantage over other species (e.g. Niemi 1979), however, on global scale this hypothesis is not strongly supported (see Smith 1990; Howarth & Marino 1990). The appearance of the blooms is largely linked to local upwelling and the delivery of recycled phosphate from the deep waters (Kononen & Nõmmann 1992; Kononen *et al.* 1996). Although in the Baltic Sea N_2 fixation by planktonic cyanobacteria is relatively important compared to other parts of the world (for a review see Howarth *et al.* 1988), Lindahl & Wallström (1985) found that nitrogen fixation by *A. flos-aquae* accounted only 1% of the nitrogen requirement of the species in the SW Bothnian Sea. Even more, there is evidence that nutrient limitation can cause loss of buoyancy and sedimentation of *A. flos-aquae* (paper III).

Buoyancy regulation and the ability to perform diel vertical migration (DVM) through the water column appears to be a major strategy responsible for the ecological success, and particularly the notorious surface scums of gas vacuolated cyanobacteria (Oliver 1994). Apart from cyanobacteria, also a number of micro-flagellates are capable of DVM. The main advantage of this behavioural adaptation appears to be sequestration of vertically separated light and nutrients, but also avoidance of over-illuminated surface layers. Differential requirements of the species with respect to light and nutrients can lead to differences in the vertical distribution. This demonstrates that individual species exploit different parts of the water column which can lead to coexistence of closely related species (Sommer 1982) and apparently increases species diversity. This is exemplified by the extremely stable conditions under the permanent ice of Antarctic lakes, where the algal species or assemblages of associated species distribute vertically because they have sufficient time to exploit the attenuated light at their preferred depth (Viner 1985). This somewhat contrasts to Connel's (Connell 1978) intermediate disturbance hypothesis with respect to maximal species richness and diversity (Sommer 1995).

Mesozooplankton is known to perform flexible DVM, still this is commonly aimed to predator avoidance (Hays *et al.* 1995; Nesbitt *et al.* 1996), rather than food acquisition (however, see Williamson *et al.* 1996), and commonly occurs in opposite phase to that of phytoplankton (yet, see Ohman *et al.* 1983; Hays *et al.* 1996). Predator avoidance appears to be one of the key strategies which accounts for the success of many dominant aquatic organisms and has received relatively little attention compared to resource acquisition strategies (Verity & Smetacek 1996). Predator avoidance among phytoplankton is largely based on cell or colony size and morphology (Kiørboe 1993) or chemical defence (Forsyth *et al.* 1990; Larsson & Dodson 1993; Gilbert 1996). Indeed, the bloom forming filamentous cyanobacteria have developed effective protection against herbivores (Holm *et al.* 1983; Fulton 1988; DeMott & Moxter 1991; DeMott *et al.* 1991; Haney *et al.* 1995; Epp 1996). In the Baltic Sea they are almost not grazed by the ambient zooplankton populations (Sellner *et al.* 1994, 1996).

As the vertical movements within the water column, the possibility of life-form shift between the sediment and the water column is another intriguing aspect of algal migration (Hansson 1993). Lately Hansson (1996) and Hansson &

Tranvik (1997) have argued that estimations of benthic recruitment rates can improve the predictable value of conventional models of algal population size fluctuations, comprising classically of growth, sinking and grazing rates. Resting stage formation is a common feature in the life history of many algal groups, including diatoms (Davis *et al.* 1980; Smetacek 1985; McQuoid & Hobson 1995), chrysophytes (Agbeti & Smol 1995), green algae (Cain & Trainor 1976; O'Kelly 1983) and dinoflagellates (Blanco 1995; Chapman & Pfiester 1995). Resting cyst formation among euglenoids in laboratory cultures (Triemer 1980) and natural environments (paper II) has been reported infrequently. As algae are able to detect optimal nutrient concentrations (Klemer 1976; Cullen & Horrigan 1981), they may also be able to detect concentrations of zooplankton exudates, and it may be adaptive to stay on the sediment surface during periods of high grazing pressure from zooplankton (Hansson 1993). Resting cysts may determine, to a great extent, both the survival strategy and population dynamics of the species, which imply that they are a very important phase in the life cycle (Blanco 1995).

STUDY AREA

The studies in this thesis were carried out at the Tvärminne Zoological station (University of Helsinki), situated on the Hanko Peninsula, on the SW coast of Finland (papers I, II, III, IV) and in the southern Gulf of Riga (papers III, V, VI), the Baltic Sea (Fig. 3).

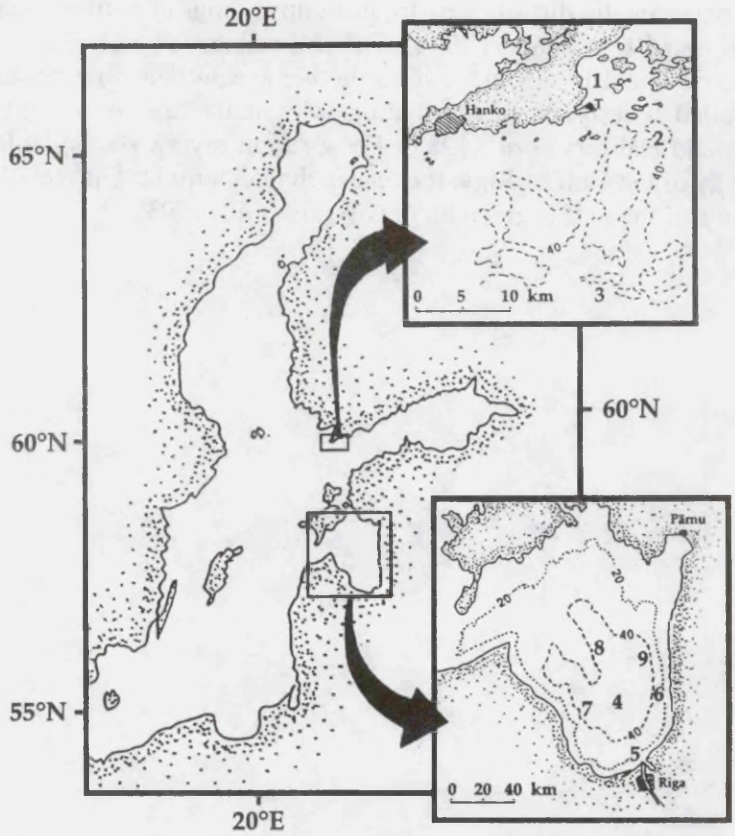

Figure 3. The study area. Sampling sites in the Gulf of Finland: 1 — Tvärminne Storfjärden, papers I and II; 2 — Storgadden, paper IV; 3 — P1, paper III. Sampling sites in the Gulf of Riga: 4 — Stn. 119, papers III, V and VI; 5–9 — Stns. 101A, 137, 135, 121 and 121A, paper V. T — Tvärminne Zoological Station.

Baltic Sea is the largest brackish water area in the world. It is non tidal, shallow (mean depth 60 m), and it's water balance comprises of freshwater supply from river runoff, and the water exchange through the Danish straits. Due to the large salinity difference between these waters, a perennial halocline (at ca 60–80 m) separates the surface layer from the subhalocline deep layer. The salinity of the deep water ranges 14–18 PSU in the Arkona basin to 7–9 PSU at the entrance to the Gulf of Finland. The surface salinity range from 12–15 PSU at the Belt

Sea to 1 PSU in the innermost gulf areas. A seasonal thermocline usually develops at a depth of 10–30 m in April–May.

The Gulf of Finland is directly connected to the main basin of Baltic Sea without notable sills, while the Gulf of Riga forms a relatively closed subsystem and the water exchange is restricted by shallow sounds (max. depth 30 m). In the SW coast of Finland thermal stability develops in the water column in May and prevails throughout the summer. The thermocline lies at ca 10 m depth, and is occasionally disturbed by frequent upwellings of nutrient rich cold deep water (Niemi 1973; Haapala 1994). Thermal stability is broken in autumn when the water column in mixed down to the permanent halocline at ca 60 m depth. A detailed description of the hydrography of the area is presented by Niemi (1975) and Hällfors *et al.* (1983). For a recent review on the hydrography and biology of the Gulf of Riga, the reader should consider Ojaveer (1990), nutrient balance of the gulf is given in Yurkovskis *et al.* (1993)

METHODS

Sampling and sample fixation

Water column samples were collected from nutrient enriched enclosures (papers I, II) or coastal and open sea areas (papers III, IV, V, VI). For sedimentation measurements (papers III, V) simple cylindrical sediment traps were used with an aspect ratio of ca 6. The deployment times were short (*ca* 24 h) and thus no preservatives were used to prevent microbial degradation in the sediment traps. The pros and cons of preservatives in sediment traps has attained much attention (Taylor *et al.* 1986; Gundersen & Wassmann 1990; Gundersen 1991; Lee 1991; Heiskanen 1995), however, for short term moorings unpoisoned traps are suggested (Lee *et al.* 1992; Hedges *et al.* 1993).

The mesocosms (papers I, II) were designed to act as big sediment traps and the settled material was pumped out from the conical bottom of the enclosures every second day by a hose and a hand pump.

In the Gulf of Riga undisturbed bottom nepheloid layer was sampled with BioProbe bottom water sampler (from GEOMAR, Kiel; Thomsen 1995) with water intakes at 5, 10, 20 and 45 cm above the sediment surface.

The net phytoplankton samples were fixed with acid Lugol's solution. Samples for heterotrophic flagellates and autotrophic picoplankton were preserved with unbuffered glutaraldehyde (Bloem *et al.* 1989) up to a final concentration of 2.5%. For electron microscopical analysis the samples stayed Lugol fixed for several months, and only then the routine procedure starting with glutaraldehyde fixation was proceeded (paper II). Lugol fixation is not quite appropriate for this purpose, and was done only because the unawareness of the need for EM. However, the results appeared satisfactory.

Sample preparation and microscopy

Net phytoplankton was counted by using Leica DM IL inverted microscope (phase contrast optics) and the classical method of sedimentation chambers (Lund *et al.* 1958; Utermöhl 1958).

Filtration and staining of heterotrophic flagellates and autotrophic picoplankton was done as soon as possible after the sampling, usually within a couple of days. Before that samples were kept in glass scintillation vials in dark at approximately 6°C. According to Gundersen *et al.* (1996) 2.5% glutaraldehyde fixation will not stop proteolytic enzyme activity of micro-organisms and thus quick slide preparation is advocated. The slides were prepared by filtering 1–5 ml of the sample onto black Nuclepore polycarbonate filters (pore size 0.2 μm) and supported by Sartorius cellulose nitrate membrane filters (pore size 0.2 μm). Staining was done with DAPI (Porter & Feig 1980). A vacuum of < 10kPa was used. After air-drying the filters were mounted into paraffin or immersion oil and covered with a cover slip. The slides were kept deep-frozen

and dark until examination. According to Kuuppo (1994) frozen slides will retain the micro-organisms unchanged for months.

Microscopical examination was done with an epifluorescence microscope (Leica DM RB or Leitz Dialux) by using 100* oil immersion objective. For the pico-cyanobacteria a green excitation light was used, while for the heterotrophic nanoflagellates and eucaryotic autotrophs UV-violet and blue excitation lights were used.

More specific methodological details could be found in the material and methods chapter of each paper.

RESTING STAGES

It could be postulated that all phytoplankton species growing in habitats with fluctuating environmental conditions over the annual cycle must have a resting stage to overlive hostile periods. Clearly, these stages are not known for all the described species. One reason for this could be the morphological similarity of vegetative and resting stage. Resting stages of diatoms could be morphologically distinct spores or just physiologically resting cells (Hargraves & French 1983; Sicko-Goad *et al.* 1989). Hallegraeff & Bolch (1992) cultured small pennate diatoms (*Navicula*, *Nitzschia*, *Neodelphineis*), which they consider as not having resting stages, and non-cyst forming species of dinoflagellates (*Gymnodinium simplex*, *Katodinium rotundatum*), from sediments being stored in the dark at 4°C for 6 months. This apparent contradiction suggests that some type of dormant stage occurs, probably overlooked in previous studies. Absence of evidence is not evidence of absence. Even more, in laboratory conditions initiation of resting cysts formation of dinoflagellates may be hampered by lack of self-compatible clones, or heterotallic clones of identical mating type (Jensen & Moestrup 1997). Apart from laboratory observations of heterotrophically grown *Euglena gracilis* (Triemer 1980), resting cyst formation of euglenoids was not known previously. In this respect the description of resting cyst of *Eutreptiella gymnastica* in field conditions (paper II) provides a novel information for the whole group of autotrophic euglenoids and helps to explain the frequent occurrence of the species in the coastal areas.

Resting stage formation

In many algal groups resting cyst formation is preceded by sexual reproduction (e.g. dinoflagellates), while in others sexuality is not known (e.g. euglenoids).

There is an extensive literature on factors causing cyst formation, dinoflagellates probably being the best studied. In many dinoflagellates, sexuality and subsequent cyst formation has often been reported as a response to stress (Anderson & Lindquist 1985). In most studies, nutrient depletion has been pointed out as a direct cause of life-form shift (Anderson *et al.* 1984, 1985 Coats *et al.* 1984; Anderson & Lindquist 1985; Anderson & Stolzenbach 1985; Binder & Anderson 1987; Blackburn *et al.* 1989; Doucette *et al.* 1989; Park & Hayashi 1993) and the physical factors are considered to be less important. Above all, shortage of nitrogen has been underlined as inducer of sexual production in dinoflagellates (Pfiester 1976, 1977; Pfiester & Skvarla 1979; Pfiester *et al.* 1984; Sako *et al.* 1984; Hickel 1988; Chapman & Pfiester 1995). In cultures experiments nutrient starvation has been used to induce sexuality and encystment by resuspending actively growing cells into culture medium lacking one essential nutrient, usually nitrogen (Pfiester 1975; Turpin *et al.* 1978; Walker & Steidinger 1979). In the mesocosm experiment described in papers I and II the enclosures were manipulated with weekly pulses of nutrients (N and

P) in a ratio similar to that below the permanent halocline in the Baltic Sea (*ca* 4:1), intended to simulate coastal upwellings. This implies that phosphorus was added in excess to what phytoplankton would normally take up and suggests a potential nitrogen limitation. Nitrogen limitation was also confirmed by the relative depletion rates of the nutrients, particularly after the last addition (see Fig. 2 in paper I) suggesting that this factor might have induced the cyst formation of *Eutreptiella gymnastica*. The sole study on euglenoid encystment by Triemer (1980) points out nitrogen starvation as a causal factor. Phosphorus starvation as a trigger of sexual production has been shown on several dinoflagellates (Stosch 1973; Anderson *et al.* 1985; Hickel 1988). This suggests that metabolic pathways of these two nutrients may each induce a mechanism for initiating the shift to sexual production. Cells initiate sexuality as intracellular pools of limiting nutrients reach minimum or subsistence levels, which may happen several days after extracellular nutrients have been exhausted (Anderson *et al.* 1985; Anderson & Stolzenbach 1985).

In a few cases a change in temperature (Eren 1969; Stosch 1973; Hickel 1988), irradiance (Stosch 1973) or iron deficiency (Doucette *et al.* 1989; Blanco 1995) have been found to induce encystment of dinoflagellates. Stosch & Drebes (1964) found that decreasing light intensity, photoperiod and temperature enhanced cyst production.

Spore formation of marine diatoms is usually associated with limiting nutrients, particularly nitrate (Durbin 1978; Davis *et al.* 1980; Hollibaugh *et al.* 1981; Kuwata & Takahashi 1990; Oku & Katamani 1997). Resting cells are formed by freshwater and some marine diatoms under conditions of low light and decreasing temperature (Hargraves & French 1975; Durbin 1978; Gibson & Fitzsimons 1990). Indeed, in the Gulf of Riga (paper V) low light and decreasing temperature were evidently encountered by the settling cells of *Thalassiosira baltica*, while the nutrients were still plenty in the surface layer. It is likely that decreasing turbulence and increasing vertical stability were the cause of *T. baltica* sedimentation, as is common with diatom blooms (Margalef 1978; Levasseur *et al.* 1984). Lack of nutrient starvation was supported by the findings of Lundsgaard *et al.* (1998) that *T. baltica* sedimented as single cells, not in aggregates as is common to decline phase of diatom blooms in nutrient deplete conditions (Kiørboe & Hansen 1993; Olesen 1993). The resting cells of *T. baltica* were morphologically similar to growing population, revealed a bright red autofluorescence under green excitation light in epifluorescence microscopy and were abundantly found in the bottom nepheloid layer throughout all the studied seasons.

Some studies on dinoflagellate sexuality and cyst formation have indicated that it does not occur under nutrient replete conditions, even when growth rate was reduced by non-optimal temperatures or due to high batch culture densities (Anderson *et al.* 1984, 1985; Chapman & Pfiester 1995). This is different from encystment of chrysophytes which is believed to be dependent on a combination of endogenous factors, primarily cell density of compatible mating clones, end exogenous (environmental) factors (Sandgren & Flanagin 1986; Sandgren

1988). However, there are reports of dinoflagellate sexuality under seemingly favourable culture and field conditions (Wall *et al.* 1970; Zingmark 1970; Beam & Himes 1974; Morey-Gaines & Ruse 1980; Anderson *et al.* 1983). This controversy might be due do difficulties in identifying favourable conditions. Species nutrient requirements differ, and even during the growth phase nutrients might be limiting to an extent which triggers cyst formation. Intermediate rounded cells of *Eutreptiella gymnastica* were found in the bottom water already in the beginning of the mesocosm experiment when nutrients were plentiful (papers I and II). The role of nutrient limitation is supported by the findings that more significant encystment took place after the first nutrient pulse was exhausted, cell numbers had declined and migration to deeper layers clearly pointed to inadequate nutrient supply of the cells.

However, once sexuality has been initiated, several factors can mediate the process. Anderson *et al.* (1984) found that low light decreased cyst yield in dinoflagellates, probably due to small motile cell yield and not due to specific inhibition of encystment. In contrast, encystment was more sensitive to temperature than was growth rate: optimal cyst production occurred over a relatively narrow temperature range and no cysts were formed at some temperatures that permitted growth (Anderson *et al.* 1984). Once encystment has been initiated, nutrient enrichment causes a low response, which can be explained by relative irreversibility of sexual production in some dinoflagellates (Pfiester 1976; Pfiester & Skvarla 1979; Pfiester & Anderson 1987), i.e. if sexual production has started before nutrient additions, a relatively large proportion of cells will not be affected and still produce cysts. This is in accord with our findings (papers I and II) with cyst formation of *E. gymnastica*: once initiated supposedly due to nutrient limitation, the process proceeds also after new nutrient pulse. However, lack of clear response to nutrient depletion could also be due to delay in the sedimentation of the cysts (or cells undergoing encystment) and the time lag after the trigger: 48–72 h in the case of *Euglena gracilis* according to Triemer (1980).

Park & Hayashi (1993) found that cyst formation of *Peridinium bipes* f. *occulatum* from Lake Kizaki (Japan) was observed in continuous darkness, however, the rates increased with irradiance (36% at 105 $\mu Em^{-2}s^{-1}$ and ca 1% in darkness, at 15°C). Once the cyst formation is triggered by lowered nitrogen levels, irradiance could affect the number of cysts produced (Anderson *et al.* 1984, 1985; Sako *et al.* 1984, 1987), which is however, different from the results of Chapman & Pfiester (1995). We have no direct evidence on the effect of light on the encystment of *Eutreptiella gymnastica*. However, it is unreasonable to imagine that the large amounts of polysaccharide in the intermediate forms of *E. gymnastica* cysts (paper II) could be accumulated without photosynthesis in the light. Thus it is suggested that at least the early phase of cyst formation can not take place in darkness.

Encystment efficiency

The reported encystment efficiency among dinoflagellates varies considerably. Most often an encystment efficiency of 0.1–0.2 cysts cell^{-1} (indicating that 20–40% of the cells encysted successfully, as two mating cells are needed to produce one cyst) has been reported. Anderson *et al.* (1984) noted a large range in cyst yield at different temperatures, but relatively constant motile cell yield which resulted in a substantial change in encystment efficiency (varying from 0.01–0.13 cysts cell^{-1}). However, over a wide range of light intensities a tight coupling between the cell yield was found which reflected in a relatively constant cyst/cell ratio of 0.11–0.17.

A mesocosm experiment is a good opportunity to estimate encystment efficiency, because advective losses can be eliminated. Nevertheless, the <0.5% of the total population of *E. gymnastica* encysted (papers I and II). As there is no reason to assume sexual reproduction in the case of euglenoids (which implies that one cell can produce one cyst), this leaves the encystment efficiency as low as <0.005 cysts cell^{-1}. The fate of the rest of the population was probably grazing and other losses (paper II).

Timing of encystment

Wall & Dale (1968) observed that cysts of the marine dinoflagellate *Peridinium* were formed at the end or just after the exponential growth phase. This is in agreement with the encystment of *Scrippsiella hangoei* in the western Gulf of Finland (Heiskanen 1993; Olli, unpublished data). Pollingher & Serruya (1976) observed that massive encystment of *Peridinium cinctum* in Lake Kinnereth (Israel) was never observed at the end of the bloom. This agrees with Park & Hayashi (1993) who found that in Lake Kizaki (Japan) cysts of *Peridinium bipes* were formed throughout the bloom from early summer to late fall and massive encystment was never observed at the end of the bloom.

These and many other examples suggest a general pattern that in marine environments cyst formation of dinoflagellates takes place during a short period after the culmination of the bloom, while in lacustrine habitats the process is more extended. However, this may be due to the usually more eutrophic conditions in lakes. In more oligotrophic marine systems the exponentially growing population is likely to meet nutrient depletion during one generation time after the ambient and intracellular reserves are exhausted. This makes the nutrient limitation more severe and causes also irreversible induction of sexual reproduction. In more eutrophic lakes nutrient regeneration could blur the initiation of sexuality in temporal scale. This might have been also the case with *E. gymnastica* (papers I and II) as the already eutrophic coastal water was even more eutrophied by manipulations and nutrient regeneration was likely to occur at significant rates. A recent support to such mechanism was provided by the study and argumentation of Ishikawa & Taniguchi (1996) on the annual study

of encystment and excystment of *Scrippsiella* spp. in natural conditions (Onagawa Bay, NE Japan). In this eutrophic bay cyst formation and recruitment proceeds throughout the year, although with considerable seasonal fluctuations, which coincide with short-term depletions of nutrients.

Dormancy period

Newly formed cysts of *Gymnodinium catenatum* required only a few days for maturation (Bravo & Anderson 1994; Blackburn *et al.* 1989). This indicates that in the absence of regulatory factors newly formed cysts should germinate and resume motile existence soon after every bloom, providing the inocula for a nearly continuous motile population throughout the year and leaving a few ungerminated cysts in the sediments at any time (Bravo & Anderson 1994), which evidently is not the case. Maturation or mandatory dormancy interval has been found not to be effected by low storage temperature in species like *G. catenatum* (Bravo & Anderson 1994) and *Scrippsiella trochoidea* (Binder & Anderson 1986), but opposite is the case of *Alexandrium tamarense* cysts (Anderson 1980). Mandatory dormancy of *Peridinium bipes* was 16 weeks under dark cold conditions (Park & Hayashi 1993). However, as shown recently by Montresor & Marino (1996) the length of mandatory dormancy period can strongly depend on environmental conditions. They found that cysts of *Alexandrium pseudogonyaulax* that were not exposed to cold-dark conditions showed a long dormancy period and low germination success.

The maximum time span of cyst viability is much more difficult to estimate. In the case of diatoms resting stages can remain viable in sediments for decades (Sicko-Goad *et al.* 1986). There is no data on the mandatory dormancy of euglenoid cysts, however, the large amount of reserve products (paper II) suggest that the cysts of *Eutreptiella gymnastica* were able to preserve viability for prolonged periods.

Excystment

Life form shift (recruitment) can be a passive process induced by turbulence (Lund 1954), a seasonal, or a directed behavioural phenomenon which is mainly triggered by environmental variables. Different algae respond to different environmental variables. Hansson (1993) showed that life-form shift was triggered by light (*Gymnodinium*, *Synura*), depth of oxycline (*Synura*, *Cryptomonas*), nutrients (*Cryptomonas*), and possibly also grazer abundance. In an experimental study 41% of the variation in recruitment of *Gymnodinium* was explained by the depth of the euphotic zone, 64% of the recruitment of *Cryptomonas* was explained by the depth of the oxycline, 52% of the variation in recruitment of *Synura* was explained by the depth of the euphotic zone and the oxycline. *Peridinium pusillum* and *P. wisconsiense* showed low recruitment at high zooplankton abundance and high recruitment at low zooplankton abun-

dance, indicating that the presence of grazers can induce shifts in life-form of some algal groups (Hansson 1993). Thus different parts of the algal "seed bank" are activated under different conditions.

Water temperature is usually considered to be the major environmental factor regulating the germination of dinoflagellate cysts (Wall & Dale 1968; Anderson & Morel 1979; Endo & Nagata 1984; Ishikawa & Taniguchi 1996) and diatom resting stages (McQuoid & Hobson 1995). However, other factors can override favourable or permissive temperatures and prevent germination (Anderson & Morel 1979; Anderson *et al.* 1983; Heaney *et al.* 1983; Lewis *et al.* 1985). E.g. low light or low oxygen conditions can retard or inhibit excystment (Anderson *et al.* 1987), and an endogenous annual clock has even been described as a regulatory factor (Anderson & Keafer 1987).

Bravo & Anderson (1994) found a similar temperature optimum for excystment and growth of motile cells of *Gymnodinium catenatum*, while Binder & Anderson (1987) found in the case of *Scrippsiella trochoidea* the optimal temperature for excystment was higher than that of growth. In one of the few (perhaps only) quantitative annual investigations of cyst production and recruitment in natural conditions Ishikawa & Taniguchi (1996) found that temperature was the dominating factor controlling *in situ* germination of *Scrippsiella* spp. cysts, however, it was modified by other factors, presumably oxygen saturation and endogenous rhythm. Interestingly, this led to maximal recruitment in late autumn when the growth conditions were unfavourable, although the authors argued this strategy to be highly advantageous for building large population and allowing the species to dominate over others in northern temperate coastal waters (Ishikawa & Taniguchi 1996).

Light conditions have been found to have no effect on encystment of some species of dinoflagellates (Endo & Nagata 1984; Sako *et al.* 1984). However, Binder & Anderson (1986) and Anderson *et al.* (1987) demonstrated that light does effect germination. In four out of five dinoflagellates studied by Anderson *et al.* (1987) darkness delayed germination, but did not prevent it. Binder & Anderson (1986) found no excystment of *Peridinium bipes* f. *occulatum* under continuous darkness, while 81% of cysts excysted after 3 days in 15°C at 105 $\mu Em^{-2}s^{-1}$. Bravo & Anderson (1994) found that excystment rates of *Gymnodinium catenatum* were retarded significantly (but not prevented) in darkness. Anderson & Wall (1978) found that germination was not appreciably different in dark and light. Yet this controversy can depend on the experimental methods. Binder & Anderson (1986) demonstrated that brief exposure to low-intensity light before and during the experiment may be sufficient to act as a photomorphogenetic trigger to initiate dinoflagellate cyst germination and light requirements for excystment may differ among species. Since brief exposure to light is almost unavoidable in experimental cyst studies, it is difficult to say with absolute certainty that germination will not occur in complete darkness.

From theoretical considerations light does not need to be an obligatory component for germination of cysts in case reserve products have not been exhausted during prolonged dormancy. E.g. the cysts of *Eutreptiella gymnastica*

were rich in storage carbohydrates (*ca* 2/3 of the cyst volume when calculated from the 3 fold volume increase during encystment; paper II) which could provide energy for upwards migration in darkness. If nutrient depletion appears to be the chief cause of cyst formation in dinoflagellates (and probably other groups), it would be natural to expect the nutrient requirements met for excystment. Hollibaugh *et al.* (1981) have found that unlike resting stage formation, recruitment of diatoms is not influenced by nutrient concentrations because cells do not begin uptake until after germination. However, recent evidence indicates that dinoflagellate cysts can actually take up phosphorus, and possible also nitrogen, from the rich reserves in the porous sediment water; enough for several cell doublings (Rengefors *et al.* 1996).

The survival value of life-form shift of planktonic micro-organisms does not depend only on the success of resting stage formation and recruitment. The dormant populations can be jeopardised by redistribution from coastal regions to deep areas where recruitment is unlikely, grazing by benthic meiofauna or planktonic organisms. Although resting forms are known to be more resistant to zooplankton grazing than actively growing populations, the depth distribution of *Protoperidinium brevipes* in the Gulf of Riga (paper VI) suggests that grazing on dormant *Thalassiosira baltica* population could be significant. However, for bloom initiation only a small inoculum is needed (Stedinger & Haddad 1981) and thus the role of grazing on dormant population has probably negligible effect on the annual succession. Even more, according to Ishikawa & Taniguchi (1996), cyst deposition on an annual scale exceeded recruitment approximately an order of magnitude in Onagawa Bay (NE Japan), leaving a large residual seed bank in the sediments.

VERTICAL MIGRATION OF AUTOTROPHIC MICRO-ORGANISMS

With the word plankton we are used to designate organisms which are passively drifting in the water column and are unable to thrive against water motion. As with many other definitions, also this is not absolutely true. Regulated by a variety of endogenous and exogenous factors, many autotrophic micro-organisms possess a degree of control over their vertical position in the water column, resulting in depth distribution patterns not explained by physiological growth, sinking or herbivorous grazing (Hasle 1950). Such patterns include thin surface accumulations and vertical movements of peak cell concentrations, which are often observed on a diel scale (papers III, IV, VI), but could also involve more stable subsurface maxima (Reid *et al.* 1978; Rasmussen & Richardson 1989; Kuosa 1990; Lindholm 1992; Bjørnsen *et al.* 1993; paper I) at depths where light and nutrient conditions might be favourable. The principal mechanisms to move vertically are by active swimming with the help of flagella (e.g. Kamykowski *et al.* 1992) and change of cell density by means of gas vacuolation or changes in cell sap ion concentrations.

The best investigated groups of phytoplankton with respect to vertical migration are probably dinoflagellates and cyanobacteria. However, the phenomenon is known also on cryptomonads (Arvola 1984; Pick & Lean 1984; Salonen *et al.* 1984; Jones 1991; Gasol *et al.* 1992, 1993) and a variety of other micro-flagellates (Happey-Wood 1976, 1988; Yamochi & Abe 1984; Watanabe *et al.* 1988; MacKenzie 1991; Griffin & Aken 1993). Some large diatoms (Villareal 1992; Waite & Harrison 1992; Villareal & Carpenter 1994; Moore & Villareal 1996a, 1996b) and non-motile dinoflagellates (Anderson & Sweeney 1978; Kahn & Swift 1978; Ballek & Swift 1986) are able to control their buoyancy by means of regulating the ion concentrations in the cells sap.

The adaptive significance of diel vertical migration (DVM) of autotrophic micro-organisms could be summed as diurnal exploitation of the high levels of irradiance near the surface, where low concentrations of inorganic nutrients would normally limit growth, and a nocturnal descent to a layer where readily available nutrients are utilised to fulfil metabolic requirements. The net result is optimisation of growth rate within the constraints of the environmental limitations and ecological strategy of the species, and is suggested to grant the species an advantage over non-motile ones (e.g. diatoms and coccoid chlorophytes), which can lead to nuisance blooms such as the red tides (Raven & Richardson 1984; Lieberman & Shilo 1994) and cyanobacterial scums (Paerl & Ustach 1982; Ganf & Oliver 1982). Sibley *et al.* (1974) found that migration of *Peridinium pienardii* f. *californicum* revealed more pronounced surface accumulations as the density of the bloom increased and interpreted this as being the result of a shelf-shading effect. This suggests that the competitional advantage can take the form of monopolising the available light, also known in the case of cyanobacterial scums (Paerl & Ustach 1982).

In spite of the general consensus on the adaptive significance, the actual triggers and mechanisms why the bulk of cells appears where it does and what are the ecological consequences of such behaviour, are still a matter of dispute.

Dark nutrient assimilation

Dark nutrient assimilation is probably a prerequisite for any nutritional benefit for autotrophic micro-organisms performing vertical migration on a diel scale, and consequently has received considerable attention.

Eppley *et al.* (1968) calculated that the size of the phytoplankton stock produced during a bloom required the nutrients, especially nitrogen, be utilised from the entire water column (0–10 m), not just from the upper meters or so where the bulk of cells resided during daytime. Thus they concluded that a combination of vertical migration and dark assimilation of nitrogen are responsible for the high cell concentrations and act as the survival factors of the blooms.

Nocturnal uptake of the limiting nutrient has been suggested by Lieberman & Shilo (1994), Harrison (1976) and Olsson & Granéli (1991). However, Blasco (1978) investigated an upwelling area off the Baja California coast, and concluded quite the opposite: nitrate assimilation in darkness was not required for the growth and migration of dinoflagellates.

Field studies performed on populations dominated by *Gonyaulax polyedra* found little diel variation in nitrate reductase activity of the species, while in the case of diatoms a clear drop was noticed (Packard & Blasco 1974), suggesting a special ability of dinoflagellates to assimilate nitrate in the dark. However, MacIsaac (1978) measured rates of nutrient uptake using the stable isotope ^{15}N as a tracer and found it clearly insufficient to support active growth of the population. Dortch & Maske (1982) studied a bloom of *Gymnodinium sanguineum*, a motile naked dinoflagellate, with enzyme activity assays and concluded that the rates in the dark were significant and that the development of the population could probably be attributed to vertical migration and nocturnal uptake of nutrients.

Unlike experiments on natural populations, laboratory studies on cultures of dinoflagellates have produced more clear-cut results. *Gonyaulax polyedra*, a thecate red-tide dinoflagellate could indeed fulfil its requirements for growth with nitrate taken up during the dark period of the light-dark cycle (Harrison 1976). Evidence for nocturnal nitrogen assimilation include also disappearance of nitrate from the medium during the dark period (Cullen & Horrigan 1981) and a rapid increase in cellular N and subsequent continuation of growth after nocturnal exposure to nitrate (Heaney & Eppley 1981). Yet, the migratory dinoflagellate *Heterocapsa* (*Cachonina*) *niei* has been characterised as having a limited ability to take up and reduce nitrate at night (Hersey & Swift 1976).

Cullen (1985) provided an explanation to this apparent conflict in the dark nitrogen assimilation ability. He found that modification of culture conditions

can elicit a pronounced change in the magnitude of nocturnal nitrate assimilation. A culture of *Heterocapsa niei*, grown with sufficient nitrate in the media, takes up about 60% less nitrate nocturnally as compared to during the day, while after a short period of nitrate depletion the cells readily take up and reduce added nitrate either during the light or dark period (Cullen 1985). Even more, this response seems to be more general and has been found also on a diatom *Sceletonema costatum* (Cullen 1985) and the chlorophytes *Clamydomonas* and *Dunaliella* (Syrett 1981).

If the dark nitrogen assimilation capacity is associated to the nutritional status of the cells, then it can also explain the controversy in the field studies, because accurate description of the nutritional patterns of natural populations are difficult to obtain. Cullen (1985) has explained the above controversy in field results in the context of environment and the types of measurements made. He pointed out that the field measurements of MacIsaac (1978) on nitrogen uptake utilised relatively large inoculations of the tracer (10 μg-at N l^{-1}), which might not fulfil the requirement of the absence of external nutrients in the surface water during the day. Consequently, the hypothesis concerning the relative importance of nocturnal nitrate uptake was not tested in an entirely appropriate way (Cullen 1985).

Energy regulation of dark nitrate uptake

Most algae and higher plants are adapted to spend about half their live in the dark by maintaining metabolic processes in the absence of light at the expense of photosynthetic products accumulated during the day. This is also relevant to the DVM because assimilation of nitrate represents a large energetic demand on the cells (Syrett 1981). Accordingly nocturnal nitrate assimilation depends on the sufficiency of carbohydrates. Carbohydrates are accumulated in response to nutrient depletion or to increments of supersaturating light intensity, and are degraded in darkness, in the absence of CO_2, or when adequate nutrients are restored after nitrogen depletion.

If the utilisation of photosynthetic intermediates for metabolic processes is less than the production by photosynthesis, the storage of starch is stimulated; if the demand for intermediates exceeds the supply, starch will be degraded and utilised (Cullen 1985). According to Cullen (1985) this biochemical mechanism supports the storage of carbohydrate during the day and assimilation of nitrate at night at the expense of the energy stored in the carbohydrate. When migration through a subsurface nutricline forces a diel cycle on the availability of nitrogen, nitrogen deficiency during the day should stimulate the accumulation of carbohydrate (Mykelstad 1974; Haug *et al.* 1979), concurrently enhancing the capacity for sustained uptake and reduction of nitrate in the dark. If inorganic nitrogen is depleted throughout the whole water column, accumulated carbohydrate is not mobilised at night and the carbohydrate content and C/N of the population will rise in response to nutrient depletion (Eppley *et al.* 1968;

Cullen & Horrigan 1981; Heaney & Eppley 1981). However, when nitrogen is still available within the reach of vertical migration, the cell carbon increases linearly during the light period and decreases during the dark period (Weiler & Karl 1979).

Photosynthesis and carbohydrate accumulation in the upper layer, followed by utilisation during the descend to the lower layer where nitrogen assimilation takes place, has been noted by many authors (MacIsaac 1978; Cullen & Horrigan 1981; Dortch & Maske 1982). Consequently there is a downwards transport of carbon in the form of carbohydrates and an equivalent upward transport of nitrogen as cellular proteins. Fraga *et al.* (1992) found that 65% of the stored carbon is used for synthesis of proteins and nucleic acids and 35% are used for respiration in this process. However, in spite of having sufficient light, some species have a limited carbohydrate storage capacity and for cellular division need two journeys of ascent and descent (Fraga *et al.* 1992). It is possible that the carbon storage capacity is the regulatory factor in the out of phase timing of ascent and descent, which is often observed empirically (Weiler & Karl 1979; Heaney & Furnass 1980; Olsson & Granéli 1991).

Nutrient status

If changes in behavioural patterns are directly associated with changes in chemical composition or physiological state (i.e. carbohydrate metabolism; Cullen 1985), this explains evidence from several empirical end experimental studies in vertical migration pattern. Laboratory experiments have shown that when nutrients are replete throughout the water column, the cells tend to maximise the time spent near the surface, within the constraint of completing nocturnal descent. When nitrate is depleted in the surface layer, behaviour is modified to provide more exposure to deep nutrients while still maintaining a high rate of photosynthesis during the day. *Gonyaulax polyedra* increases its exposure to nutrients by beginning its nocturnal decent earlier (Eppley *et al.* 1968; Heaney & Eppley 1981), whereas other species [*Gymnodinium sanguineum* (syn. *splendens*), *Gyrodinium aureolum*] restrict their diurnal ascent to a subsurface layer, often close to nitricline, in which light intensity is approximately saturating for photosynthesis (Cullen & Horrigan 1981; Dahl & Brockmann 1989). When nitrogen is not available within the range of vertical migration, *Gonyaulax polyedra* no longer migrates to the surface during the day, yet resumes normal migration pattern after addition of nitrogen (Eppley *et al.* 1968). However, other species (e.g. *Heterocapsa niei*) do proceed with the migration for several days (Eppley *et al.* 1968). In the Gulf of Riga the vertical distribution of flagellates in nutrient replete spring season was restricted to mid-day surface avoidance (paper VI) while during the more nutrient deplete summer situation a nocturnal deep distribution was evident (papers III and IV). The differences between spring and summer distribution were particularly pronounced in the case of the fast swimming autotrophic ciliate *Mesodinium rubrum*

(papers IV and VI). The intraspecific migratory patterns can thus be linked to relative fluxes of light and nutrients.

Species specific vertical distribution

There seem to be also interspecific differences. Blasco (1978) studied several species of dinoflagellates and ranked them according to their maximum distribution with respect to light penetration. *Gonyaulax polyedra* tolerated high irradiance and low nitrate during the day as long as a source of adequate nutrients was encountered at night to support growth and to utilise stores of carbohydrate, which is in agreement with the findings of (Eppley *et al.* 1968; Heaney & Eppley 1981). Other species (*Ceratium furca*, *Gymnodinium* sp., *Ceratium dens*, *Gonyaulax digitata* and *Prorocentrum micans*) displaced their maxima at 50 and 25% light levels. Frempong (1984) showed that *Ceratium hirundinella* did accumulate to the surface at noon when the irradiance was 300 $\mu E\ m^{-2}d^{-1}$, but at full sun (ca 1700 $\mu E\ m^{-2}d^{-1}$) formed a subsurface peak at the level of ca 150 $\mu E\ m^{-2}d^{-1}$. This is in accord with the results of Heaney & Talling (1980), Cullen & Horrigan (1981) and Heaney & Eppley (1981). Clement *et al.* (1988) found that *Dinophysis* sp. from a French coast accumulated to the surface at sunrise and in the afternoon, while the cells descended before midday, probably due to saturating light intensity. This type of mid-day surface avoidance appears to be common among autotrophic micro-organisms (papers III, IV and VI).

Finally there is evidently a group of algae that do not perform diurnal vertical migration (e.g. *Scrippsiella hangoei*; paper IV) or have a negative phototactic response (e.g. *Peridinium depressum*; Blasco 1978). Assimilation of nutrients will thus be in large part light-driven and nocturnal assimilation of nitrate would be relatively unimportant. According to Blasco (1978) this supports the hypothesis that migration is of phototactic nature and demonstrates the different specific light preferences which can lead to vertical niche separation (Sommer 1982, Sommer 1982, 1985; papers IV and VI). Vertical niche partitioning is also known among coexisting different sized cyclopoid copepods in lakes, as discussed by Maier (1993).

Physical barriers

Heaney & Eppley (1981) found that a 4°C m^{-1} temperature gradient (22.2–26.2°C) did not prevent rapid migration of *Ceratium furca*, yet when lower temperature was 16,5°C decent of cells was appreciably restricted and cells concentrated to the thermocline at night. Blasco (1978) found that even weak density discontinuities acted as barriers for downwards migration for dinoflagellates. Cullen & Horrigan (1981) found that *Gymnodinium sanguineum* (syn. *splendens*) migrated through a temperature gradient of as large as 8.5°C over 1 m under N sufficiency. Frempong (1984) concluded that thermocline was not

a barrier for downwards migration of *Ceratium hirundinella*, but the cells avoided oxycline. Yet Kamykowski & Zentara (1976), Blasco (1978), Tyler & Seliger (1978), Heaney & Eppley (1981) and Kamykowski (1981) have shown that thermal/density gradients retard the downwards migration of dinoflagellates. E.g. *Heterocapsa niei* crossed a 10°C gradient in a 1,7 m deep tank but did not cross a 15°C gradient (Kamykowski 1981). Kamykowski & Zentara (1976) demonstrated that dinoflagellates are able to cross a considerable temperature gradient, however, when below optimal temperatures are reached, swimming speed decreases or can stop, thus reducing the vertical range of migration. The extremes of species capabilities probably vary, depending on integrated environmental stress imposed by light intensity, salinity and nutrient availability (Kamykowski 1981, 1985; Kamykowski *et al.* 1988, 1989). Thus, absolute temperatures near the extremes of the species capabilities rather than temperature gradients *per se* apparently determine organism behaviour (Kamykowski 1981). The above evidence thus indicate that temperature discontinuities do restrict migration, but this depends on the nutritional status of the cells. During nutrient replete spring period (paper VI) the vertical distribution of motile cells in the Gulf of Riga was restricted to the isothermal upper mixed layer. Even more, newly created shallow thermocline during a calm and sunny day caused a considerable accumulation of cells to the temperature discontinuity. This demonstrates the importance of temperature gradients in concentrating the cells in nutrient replete conditions.

The effect of salinity gradients is much less studied. Rasmussen & Richardson (1989) demonstrated that the cells of *Alexandrium tamarense* (syn. *Gonyaulax tamarensis)* were able to penetrate (cells were introduced to the bottom of the experimental column and migrated upwards) an artificial halocline of 7 PSU (occurring over a few centimetres), however a 10 PSU gradient was penetrated only when the light climate at the halocline was considerably reduced.

Turbulence avoidance — a hypothetical benefit

It has been shown that turbulence inhibits the growth of dinoflagellates by preventing nuclear division (Berdalet 1992) or cause loss of longitudinal flagellum (Thomas & Gibson 1990). Pollingher & Zemel (1981) showed that intermitting shaking of 2 h day^{-1} during dark phase inhibited nuclear division of *Peridinium cinctum* f. *westii* while the same procedure in light time had no such effect. From long term time series they demonstrated that a wind of 6–8 m s^{-1}, particularly during the dark period, efficiently prevented bloom formation (Pollingher & Zemel 1981). Estrada *et al.* (1987, 1988) showed that turbulence had strongest effect on dinoflagellates from all the groups of phytoplankton. There is also evidence that dinoflagellate cell division takes place during the dark phase of the diel cycle (Weiler & Karl 1979; Pollingher & Zemel 1981; Olsson & Granéli 1991). Also a toxic red tide raphidiophycean *Heterosigma*

akashiwo has been observed to divide during dark period when the bulk of cells resides in deeper layers (Takahashi & Hara 1989). As wind induced turbulence decays with increasing depth, the diel vertical migration can be an adaptation to maximise cell division success by migrating to layers of lesser interference. This might be an additional adaptational advantage of flagellate diel vertical migration, which has not received much attention. Crawford & Purdie (1992) have shown that *Mesodinium rubrum* actively avoids layers with elevated small-scale turbulence.

Triggers: phototaxis or gyrotaxis?

The actual triggering mechanisms of vertical movements is of utmost importance in understanding the phenomenon. Blasco (1978) found that except *Gonyaulax polyedra*, all species considered by her reacted negatively to high light intensities at noon and accumulated to subsurface depths, which she interpreted as a phototactic response. Eppley *et al.* (1968) found that *Heterocapsa niei* migrated even in continuous darkness and continuous illumination for at least 24 hours, which they interpreted as a geotactic response. This is in accord with Weiler & Karl (1979) who found that the vertical migration of *Ceratium furca* in laboratory conditions continued for even 6 days in continuous darkness, although there was a tendency for the aggregation to become less pronounced with time. They concluded that migration was independent of phototactic response and probably governed by endogenous rhythm.

According to Weiler & Karl (1979) diel rhythms may be divided into two major categories: those that are a passive response to environmental fluctuations during a 24 h cycle and cease when the organism is transported to a constant environment (exogenous diel rhythms), and those that are entrained by environmental variations, but that ultimately result from physiological processes and persist under constant conditions with a freerunning period which is different from 24 h (endogenous or circadian rhythms).

The vertical migration pattern of *Ceratium furca* was not only a passive response to diel changes in illumination and phototaxis, because with lateral illumination on 12:12 light-dark cycle, cells concentrated at the side of the tube closest to the light source (Weiler & Karl 1979). Direct experimental evidence on phototaxis and gravitaxis in the marine dinoflagellate *Prorocentrum micans* was demonstrated by Eggersdorfer & Häder (1991) who concluded that high irradiance caused the cells to exhibit negative phototaxis (maximum in early afternoon) and low irradiance caused positive phototaxis (maximum in the morning and night), and the precision of negative gravitactic orientation was in maximum in early afternoon. The significance of light on vertical migration is underlined by field studies, where cloudy weather lessens the intensity of migration (Hasle 1954; Eppley *et al.* 1968; Staker & Bruno 1980). The vertical migrational behaviour of *Heterosigma akashiwo* was controlled by light/dark cycle as was elegantly demonstrated by Takahashi & Hara (1989) — switching

from a normal 14:10 light-dark cycle to 3:3 LD cycle changed also the migration frequency to a 3:3 hour cycle. When the test tubes were illuminated from below during the light cycle, the cells still migrated up, not towards the light source, indicating that the dark/light cycle triggered the migrational behaviour while the orientation of swimming was regulated by other factors (gravitaxis) (Takahashi & Hara 1989).

Uncertainties in vertical migration studies in field conditions

The study of vertical migration in field conditions poses a number of ambiguities which can be controlled to some extent, but not eliminated. In most cases the sampling scheme includes vertical profiling of the water column over a certain time intervals from a fixed station (as in papers III, IV and VI). Thus, when horizontal advection occurs (and it usually does), the subsequent profiles represent different water masses. Advection in combination with horizontal patchiness in cell abundance (Kuosa 1988; Kahru *et al.* 1990) inevitably causes variability in the cell numbers in the time series. However, Passow (1991b), during an extensive patchiness study in the southern Baltic Sea, concluded that patchiness in the migratory behaviour was small and that the patchy distribution of cell concentrations is unimportant in the investigations of migration pattern as long as the migratory behaviour is horizontally homogeneous. Yet Passow did not consider (or did not encounter) the possible vertical heterogenity in horizontal advection. E.g. Frempong (1984) noted that a 4-fold increase of *Ceratium hirundinella*, similar to those associated to vertical migration, in a surface layer of a hydrodynamically well studied Esthwaite Water (UK), which was attributed to advection. Species may exhibit spatial and temporal patchiness in response to countercurrent flow (Kamykowski & Zentara 1976). Eppley *et al.* (1984) showed that mixed populations of *Ceratium tripos* and *Gonyaulax polyedra* got separated due to countercurrent flows at different depths and different vertical migration patterns. Even more, differential movements of water layers in combination with particular vertical distribution patterns of the cells has been shown to selectively keep the populations in bloom areas and avoid flushing losses in estuarine environments (Tyler & Seliger 1978, 1981; Horstmann 1980; Anderson & Stolzenbach 1985).

Besides horizontal advective transport also wind induced turbulence (Yamazaki & Kamykowski 1991), internal waves (Kamykowski 1974), Langmuir circulation (Ledbetter 1979; Evans & Taylor 1980), and upwelling can redistribute the cells in the water column and thus blur the inherent vertical distribution patterns of the organisms. Frempong (1984) has studied the seasonal variation in the vertical distribution of *Ceratium hirundinella* in Esthwaite Water (UK), found that wind > 4 m s^{-1} led to a fairly even distribution of cells in the mixed layer. Thus the actual vertical distribution in an natural water body is a combination of the physical water movements and the active

thrive of the cells against it. However, even in field situations with average weather conditions different species exhibit significantly different vertical distribution patterns (papers III, IV and VI), although changes on a diel scale are not necessarily as clear as the classical vertical migration patterns in the textbooks.

A way around to avoid the advective transport and exclude most of the turbulent mixing is to enclose a part of the water column into artificial mesocosms (Watanabe *et al.* 1995; paper I). Although providing a good amount of control on the environment and an insight to the intrinsic behavioural adaptations of the species, it does not confirm that these potentials are met in fully natural conditions.

BUOYANCY CONTROL OF CYANOBACTERIA

A variety of cyanobacteria are able to control their buoyancy, and hence the vertical position in the water column by means of gas vesicle production. The ecological success of many gas-vacuolated cyanobacteria in a wide range of aquatic ecosystems has been attributed to buoyancy regulation and the ability of vertical migration in the water column (Reynolds & Walsby 1975; Walsby & Reynolds 1980; Ganf & Oliver 1982; Reynolds 1984; Rijn & Shilo 1985; Reynolds *et al.* 1987; Konopka 1989). Gas vesicles are hollow, elongated cellular inclusions with conical ends. The balance between the mass of other cell constituents (usually exceeding the density of water) and the degree of gas vacuolation per unit cell volume determines whether the organisms will sink or float. The proteinaceous wall of gas vesicles is permeable to gases, but impermeable to water (Walsby 1969; Falkenberg *et al.* 1972). Major cell components of buoyancy regulation are gas vacuoles, but also polysaccharides, which function as cellular ballast as many other storage polymers such as polyphosphate and cyanophycine granules (Klemer 1991). One or more of the three mechanisms can be involved: regulation of gas vesicle synthesis, gas vesicle collapse and change in other cell constituents, particularly carbohydrates (Oliver & Walsby 1988). However, accumulating evidence during the last decades indicate that the buoyancy regulation is a complex process where temperature, availability of inorganic carbon, mineral nutrients and light play an interacting role, superimposed by a degree of species specific responses.

The buoyancy regulating function of gas vesicles

Walsby (1969) was the first who associated low light intensities with gas vesicle accumulation and buoyancy increase in *Anabaena flos-aquae*, and he suggested two means by which gas vesicle content might decrease with increases in light intensity: (1) more rapid growth might dilute cellular concentrations of gas vesicles and/or (2) turgor pressure increases resulting form "excess" photosynthesis which might collapse turgor sensitive gas vesicles. The first mechanism results from an unmatch in the rates of gas-vesicle formation and cell growth. Reynolds & Walsby (1975) found that gas vacuolation in natural populations is inversely related to growth rate. In light limited cultures of *Aphanizomenon flos-aquae* gas vesicle content per unit of protein decreased and cells were non-buoyant at all growth rates exceeding 20% of the maximum growth rate (Kromkamp *et al.* 1986, 1988; Konopka *et al.* 1987a), which was interpreted as a result of dilution of relative gas vesicle content. However, gas vacuole production was proportional to cell growth in light-limited cultures of *Microcystis*, and cells were buoyant in light limited cultures (Thomas & Walsby 1985; Kromkamp *et al.* 1988). Additional increase of light caused carbohydrate accumulation in 3–4 h and subsequent loss of buoyancy (Kromkamp *et al.* 1988). In the latter process turgor pressure increases with light, as low

molecular weight photosynthate (Reynolds & Walsby 1975; Grant & Walsby 1977), and potassium ions transported by light dependent pumps (Allison & Walsby 1981), accumulate in the cells.

The role of ballast polysaccharide

Since the first works of Walsby (1969, 1970) decreased buoyancy has extensively been studied and frequently attributed to gas vesicle collapse (Reynolds & Walsby 1975; Walsby & Reynolds 1980; Utkilen *et al.* 1985; Rijn & Shilo 1985). The general coincidence of turgor pressure rise and buoyancy loss has in many experiments been interpreted as a casual relationship, however, not always correctly (Oliver 1994). Gibson (1978a, 1978b) was the first to suggest the role of polysaccharide in cyanobacterial buoyancy regulation. Cell components such as high molecular weight carbohydrate (1600 kg m^{-3}), protein (1300 kg m^{-3}) and lipid can account for 90% of the cell dry weight (Oliver & Walsby 1984; Oliver *et al.* 1985; Thomas & Walsby 1985; Utkilen *et al.* 1985) and changes in their amount can alter the cell buoyancy.

Kromkamp *et al.* (1986), Kromkamp & Mur (1984) and Utkilen *et al.* (1985) have pointed out that changes in polysaccharide content is much more important in short term buoyancy changes (< generation time) than the effect of changes in gas-vesicle content. Buoyancy changes through synthesis and utilisation of carbohydrate applies particularly to species with less turgor sensitive gas vesicles, e.g. *Microcystis aeruginosa*, *Oscillatoria agardhii* (Kromkamp & Mur 1984; Oliver *et al.* 1985; Thomas & Walsby 1985; Utkilen *et al.* 1985) and the oceanic genus *Trichodesmium* (Walsby 1978; Villareal & Carpenter 1990; Romans & Carpenter 1994). In such species, diel changes in buoyancy are largely attributable to light effects on polysaccharide synthesis, i.e. increase in polysaccharide and specific gravity at higher light intensities or during a photoperiod and decrease in those variables at lower light intensities or during a dark period.

However, when it comes to diel vertical migration the time scales of response mechanism is decisive. While turgor pressure collapse of gas vesicles may result in rapid buoyancy loss (approximately 20–180 min), the gas vesicle synthesis required to restore buoyancy is a slow process and scales to cell generation time (>1 d) (Hayes & Walsby 1984; Konopka *et al.* 1987a; Reynolds *et al.* 1987). In contrast, buoyancy regulation through carbohydrate ballast content occur rapidly and at rates determined by the photosynthesis and respiration (Reynolds *et al.* 1987; Ibelings *et al.* 1991). Consequently, variations in the vertical distribution of *Aphanizomenon flos-aquae* in the time scale of 24 h can be attributed to ballast polysaccharide accumulation and utilisation (paper III). This is supported by the study of Walsby *et al.* (1995) in the southern Baltic Sea, who found that the gas vesicles of *Aphanizomenon flos-aquae* and *Nodularia* sp. were strong enough to support vertical excursion down to the perennial halocline (60–90 m).

Polysaccharide accumulation capacity

Kromkamp *et al.* (1986) transferred a low light (10 μE m^{-2} d^{-1}; light-dark cycle) adapted culture of *Aphanizomenon flos-aquae* to high light (50 μE m^{-2} d^{-1}) and observed a buoyancy loss in 2 h. Yet, gas vesicle collapse occurred only after 5 h at irradiance >100 μE m^{-2} d^{-1}, thus the buoyancy change was apparently due to an increase in the cellular carbohydrate (Kromkamp *et al.* 1986). However, cultures acclimated to continuous light showed increased turgor pressure rise and gas vesicle collapse after 2 h, when shifted to 200 μE m^{-2} d^{-1} (Kromkamp *et al.* 1986). Thus the relative importance of gas vesicle collapse and carbohydrate accumulation depends on the physiological state of the cells. Foy & Smith (1980) have shown that *Oscillatoria*, acclimated to shorter light periods, store carbohydrate more effectively. Under continuous light cells have a low carbohydrate storage capacity and increase in irradiance will lead to increase in low molecular intermediates of photosynthesis resulting in large turgor pressure rise (Kromkamp *et al.* 1986). It is interesting to note that this partly parallels to the carbohydrate balance in dinoflagellates (Cullen 1985), and implies that polysaccharide accumulation is an adaption to the light-dark cycle.

Macronutrients and carbon limitation

Reynolds (1972, 1973), Reynolds & Walsby (1975) and Lewis (1983) have associated cyanobacterial blooms with low concentrations of nitrogen and (or) phosphorus. Parallel to Walsby's (Walsby 1970) interpretation on the effect of light on buoyancy (i.e. light limited growth permits gas vesicle accumulation in cells at low intensities and dilutes cellular gas vesicle content at high intensities), Reynolds (1972, 1973) related buoyancy increase of *Anabaena* and *Microcystis* to phosphorus and nitrogen limited growth, respectively and a consequent accumulation of gas vesicles. Lewis (1983) associated surface scums of *Microcystis aeruginosa* with N limitation and viewed surface accumulation as an adaptation to gain access to fixed nitrogen as well as CO_2. However, Konopka *et al.* (1993) found that addition of phosphate decreased rapidly the buoyancy of metalimnic *Oscillatoria agardhii*, and the suggested mechanism implied accumulation of yet unidentified P rich ballast polymer.

However, contrary evidence was provided by Klemer (1976) who showed that metalimnic populations of *Oscillatoria agardhii* moved toward the surface in response to relaxation of N and P limitation. Klemer (1978) used chemostat cultures to show that the relative gas-vesicle content of the cells of nitrogen limited *Oscillatoria rubescens* vary directly with the available nitrogen, probably because N is needed for gas vesicle protein synthesis.

According to a general consensus based on field and laboratory studies, buoyancy decreases when macronutrients (N and P) are limiting and increases when inorganic carbon is limiting (Walsby & Klemer 1974; Klemer 1978, 1991; Booker & Walsby 1981; Klemer *et al.* 1982; Paerl & Ustach 1982; Spencer & King 1985, 1989; Rijn & Shilo 1985; paper III; Fig. 4). Booker &

Walsby (1981) found that carbon dioxide limitation accompanied a surface accumulation of *Anabaena flos-aquae* in a lab tank, whereas enrichment with dissolved carbon reduced the intensity of such blooms. Klemer *et al.* (1982) showed experimentally that transitions from nitrogen limitation to carbon limitation permitted increase in the gas-vesicle content of *Oscillatoria rubescens*, while transition from carbon limitation to nitrogen limitation had the opposite effect. These findings were verified by Paerl & Ustach (1982) with pH adjusted samples from natural blooms. They interpreted intense surface accumulations of cyanobacteria at high pH and low CO_2 concentration as evidence of their preference for CO_2 over bicarbonate.

The negative role of carbon results from the energy capture through photosynthesis and the fate of the fixed carbon in the cells. When macronutrients are readily available, the captured energy is used for cell growth and carbohydrates do not accumulate. However, when growth is restricted by mineral nutrients, the energy capture exceeds that utilised in growth, and carbohydrates start to accumulate. If the fixed carbon is directed into soluble photosynthetic intermediates, the turgor pressure rises causing collapse of gas vesicles and buoyancy loss (Dinsdale & Walsby 1972), whereas insoluble forms of carbohydrate contribute to ballast (Gibson 1978a). As a result of either of these mechanisms, carbon limitation is expected to promote buoyancy and has been implicated in surface bloom formation, whereas carbon enrichment of carbon-limited cells can decrease buoyancy and has been shown to cause bloom dispersal (Reynolds & Walsby 1975; Booker & Walsby 1981; Paerl & Ustach 1982; Klemer *et al.* 1988). The balance between the accumulation and incorporation of carbon is altered by irradiance and nutrient deficiency (Haug *et al.* 1979).

Excess production of carbohydrates could lead to exudation out of the cells, as is known in the case of diatoms (Kiørboe & Hansen 1993), and increase the stickiness of the cells leading to entanglement to sinking detrital aggregates (paper III). In this case the sinking aggregate could overweight the regain of buoyancy of the cyanobacterium, and result in sedimentation loss.

Polysaccharide stores represent a source of both energy and structural components that can support continued cell growth under poor irradiance conditions (e.g. during DVM to deeper nutrient replete layers). Konopka *et al.* (1987b) and Kromkamp *et al.* (1989) found that buoyancy changes of *Microcystis* in the light corresponded to an increase in gas vesicle content while in the dark there was no increased protein synthesis, although carbohydrate reserves were utilised, probably for respiration. However, the results of Deacon & Walsby (1990) indicate that gas vesicle production can occur in the dark in case of sufficient energy reserves in the form of carbohydrates. Dark gas vesicle protein synthesis, however, is important for buoyancy regain for cells settled out of the photic layer due to gas vacuole collapse. Yet, dark utilisation of carbohydrates is temperature dependent (Foy 1983; Thomas & Walsby 1986). At low temperatures growth rate, gas vesicle synthesis and carbohydrate utilisation are reduced which prevent regaining buoyancy, which can account for the disappearance of blooms at the end of the growth season (Thomas & Walsby 1986).

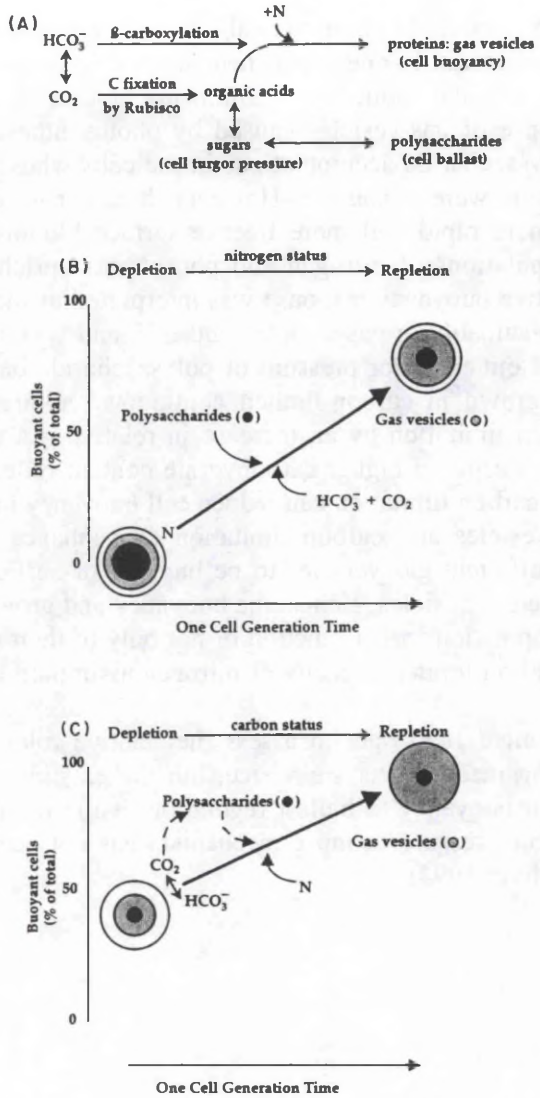

Figure 4. Buoyancy effects of carbon and nitrogen flows in cyanobacteria (modified from Klemer 1990). (A) Carbon accumulation as osmotically active photosynthate (organic acids, sugars, etc.) or as polysaccharide can reduce buoyancy within a single photoperiod via turgor increases that collapse gas vesicels or via the ballast effect of polysaccharide. Carbon accumulation in gas vesicles increases buoyancy, but response times are on the order of generation time. Note also the possibly different pathways of carbon source. The form of inorganic carbon depends on the pH of the medium, and the uptake preferences can be species specific. (B) Recovery from nitrogen limitation involves rapid consumption of polysaccharides and synthesis of gas vesicles (C) During recovery from carbon limitation, the negative buoyancy effect of polysaccharide synthesis may initially outweight the positive effect of gas vesicle synthesis, but the latter prevails within a generation time.

Carbon paradox

Klemer *et al.* (1988) reported a controversial effect of carbon enrichment on the buoyancy of cyanobacteria. In one experiment surface additions of bicarbonate to natural (*Anabaena*) and induced (*Oscillatoria*) blooms in softwater lakes hastened the collapse of gas-vesicles caused by photosynthesis driven turgor increase or by polysaccharide accumulations in the cells whose reserves of nitrogen of phosphorus were exhausted. However, bicarbonate enrichment was found to induce more rapid and more intense surface blooms by subsurface (metalimnetic) populations of nitrogen and phosphorus enriched *Oscillatoria* (Fig. 4). This positive buoyancy response was interpreted as increases in nitrogen uptake and presumably in gas-vesicle synthesis, and was apparently unrelated to changes in either turgor pressure of polysaccharide ballast. Similarly, *Microcystis* cells grown in carbon-limited continuous cultures responded to relaxation of carbon limitation by an increase in relative gas vacuolation and buoyancy increase, despite a higher carbohydrate content (Klemer 1991). Apparently sustained carbon limitation can reduce cell buoyancy by restricting the synthesis of gas vesicles and carbon limitation can enhance buoyancy only when cells have sufficient gas vesicles to be buoyant or sufficient energy reserves to synthesise gas vesicles. Hence, the buoyancy and growth responses of nitrogen limited populations are a function of not only of their nitrogen supply but also of their carbon-limited capacity of nitrogen assimilation (Klemer *et al.* 1988; 1991).

Sufficiently detailed field data to assess the relative roles of the various buoyancy regulating mechanisms are scarce, but the existing ones invariably attribute changes in buoyancy to ballast regulation, while the prominence initially given to turgor pressure collapse mechanism has not been supported by recent evidence (Oliver 1994).

CONCLUDING REMARKS

In the following summary, the main findings of the studies in these thesis are presented.

1) The frequent upwellings in the coastal areas of the northern Baltic Sea can lead to occasional blooms of opportunistic phytoplankton species, as exemplified by *Eutreptiella gymnastica*. The ecological success is due to high growth potential, but also due to behavioural adaptations like vertical migration and selection for optimal depth strata, and life-cycle strategies like resting cyst formation. However, after using their chance, persistent blooms of such species are unlikely in more stable conditions where the ambient zooplankton has an efficient top-down control on them.

2) Autotrophic euglenoids do produce resting cysts in natural environments. Judging on the amount of storage carbohydrates, these resting stages are adapted for prolonged dormancy. However, as the storage polysaccharide of euglenoids is not digestible by the majority of the zooplankton, such mass occurrences of euglenoids can be an intriguing uncovered pathway of high quality (for benthic bacteria) particulate organic carbon.

3) In the Gulf of Riga (probably the most eutrophied part of the Baltic Sea), a large part of the primary production is recycled in the upper water column and direct sedimentation of phytoplankton cells in low. Sedimentation of fresh phytoplankton material is largest during the vernal bloom, when the dominant diatom species fall out of the stratified water column and form resting stages in the bottom nepheloid layer. When the nutrients are still not depleted from the upper layer, this leads to dominance of spring dinoflagellates.

4) The autotrophic micro-organisms in the Baltic Sea reveal distinct patterns of vertical depth distribution. Partly these distributions are driven by diel vertical migration and possess a great deal of species specificity. The vertical separation of specific niches can support co-existence of closely related and/or dominating species and suggest that each exploit a different part of the spatio-temporally fluctuating spectrum of resources.

5) Both, vertical migration, either on diel basis or longer, and formation of benthic resting stages, can be seen as means of displacing the population in relation to the vertical gradients of environmental (e.g. nutrients, light, temperature) and biological (e.g. predator abundance) factors. These evolutionary life-strategies differ only in the temporal scale of the vertical displacement, however, the ultimate aim is to cope with the occasionally hostile environment, maximise the population growth rate and minimise the sum of loss rates on a long run.

6) It appears that the common nominator in the behavioural adaptations and life cycle strategies studied in these thesis is the balance between carbon and mineral nutrient metabolism. Accumulation of organic carbon in the cells is largely the result of excess photosynthesis, which remains uncoupled with cell growth due to lack of mineral nutrients. Although the consequent mechanisms

differ considerably, polysaccharide accumulation and consumption seems to be a key factor in the vertical distribution of both, the cyanobacteria and dinoflagellates, and possibly also in the formation of benthic resting stages. If the balance between photosynthesis and nutrient availability is biased towards the former, the cells tend to displace themselves vertically in the water column to reduce irradiance and/or increase nutrient availability. When the uncoupling exceeds a threshold level, resting stage formation may follow as a solution for longer scale survival.

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LÄÄNEMERE AUTOTROOPSETE PLANKTILISTE MIKROORGANISMIDE EVOLUTSIOONILSED ELUSTRATEEGIAD

Kokkuvõte

Aastail 1993–1995 uuriti Tvärminne Zooloogiajaamas (Helsingi Ülikool; Soome edelarannik) ja Liivi lahe lõunaosas pelaagilise ökosüsteemi toimimist ja struktuuri. Uuringutes ilmnesid mitme domineeriva planktonorganismi olulised kohastumused eluks antud keskkonnas. Lähemalt uuriti puhkevormide moodustamist ja fütoplanktoni vertikaalset migratsiooni.

Aastal 1993 korraldati Tvärminne Zooloogiajaamas kolm nädalat kestnud eksperiment mille jooksul manipuleeriti umbes 50 m^3 mahuga kilekottidesse suletud planktonikooslust. Eksperimendi käigus ilmnes domineeriva liigi, *Eutreptiella gymnastica* (Euglenophyceae), võime omastada kiiresti kord nädalas lisatud toitaineid, mille tulemusena moodustus peaaegu üheliigiline kooslus. Liigi edukuse antud tingimustes tagasid suur kasvukiirus (1,03 jagunemist päevas) ja vertikaalne migratsioon sügavamatesse toitaineterikastesse kihtidesse. Samas kontrollib *E. gymnastica* populatsiooni zooplankton (eksponentsiaalne ärasöömisest tingitud kadu –0.60 päevas), mis vähendab selle liigi suuremate õitsengute tõenäosust rannikuvetes, aga rõhutab liigi tähtsust planktilises toiduahelas.

Järgnevate õitsengute potentsiaali tagavad setetesse ladestatavad tsüstid, mis moodustab omalaadse seemnepanga. Eugleniidide põhilist varuainet paramüülon-tärklist suurem osa zooplankton ei seedi. Sellest tulenevalt võib oletada, et ulatuslikumad eugleniidide õitsengud mõjutavad otseselt settiva orgaanilise aine kvaliteeti, mis mõjutab omakorda bentose kooslusi. Hüpoteetiliselt võib oletada, et varuainerikkad tsüstid ja paramüülonirikkad zooplanktoni väljaheited tagavad tunduvalt rikkama partikulaarse orgaanilise süsiniku sadenemise just eugleniidide õitsengute puhul.

Autotroofsete mikroorganismide ööpäevast vertikaalset migratsiooni uuriti kahel kevadperioodil (1994 Soome lahe loodeosas; 1995 Liivi lahe lõunaosas) ja kesksuvisel perioodil (1994 Liivi lahe lõunaosas). Tulemused näitavad olulist vertikaalse jaotuvuse erinevust domineerivate kevadõitsengu liikide vahel (*Peridiniella catenata* ja *Scrippsiella hangoei*). Põhiliste fütoplankterite vertikaalse jaotuvuse ajaline dünaamika Liivi lahes näitas olulist liigispetsiifilisust, mida omakorda mõjutasid keskkonnategurid. Samas ilmnes liikide potentsiaal kasutada sügavamates kihtides olevaid toitaineid. Autotroofse ripslooma, *Mesodinium rubrum*, vertikaalses jaotuvuses ilmnesid olulised aastaajalised erinevused: kevadperioodil kogunesid organismid pinnakihtidesse, vastandina suvisele, suhteliselt ühtlasele jaotuvusele kogu veesamba ulatuses (0–30 m).

Aastail 1993–1995 uuriti fütoplanktoni koosluse struktuuri ja settimist Liivi lahe lõunaosas erinevatel aastaaegadel. Settimine oli suhteliselt tühine kesk- ja hilissuvel, mis näitab koosluse võimet kinni hoida toitaineid ja tagada kõrge

produktiivsus. Kevadel põhjustas ränivetika *Thalassiosira baltica* vajumine küllalt kõrge vertikaalse orgaanilise aine voo. *T. baltica* moodustas allpool termokliini puhkepopulatsiooni, mis oli küllalt arvukas kogu vegetatsiooniperioodi vältel. Kuna pinnakihi toitainesisaldus oli kevadperioodil suur, tingis *T. baltica* settimise ilmselt veekihi vertikaalne (termiline) stabiliseerumine. See demonstreerib ühelt poolt keskkonnategurite mõju ränivetikate ja dinoflagellaatide omavahelisele konkurentsile kevadperioodil (stabiilne veesammas on soodus dinoflagellaatidele), teiselt poolt erinevaid stsenaariume orgaanilise aine voogude kanaliseerumisel, sõltuvalt kumb vetikarühm domineerib.

PUBLICATIONS

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Development and fate of *Eutreptiella gymnastica* bloom in nutrient-enriched enclosures in the coastal Baltic Sea

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Abstract. Response of the phytoplankton community to bottom-up (nutrients, organic carbon source) and top-down (fish) manipulations, both singly and together, were studied daily during a 3 week period in July 1993 by using eight 50 m^3 mesocosms in the coastal northern Baltic Sea. Nutrient additions (once per week) invoked a series of blooms of *Eutreptiella gymnastica* Throndsen (Euglenophyceae) (up to 13 × 10^3 cells ml^{-1}) which formed the major part (60–90%) of the total autotrophic biomass. After rapid depletion of nutrients (2–3 days) from the surface layer (0–6 m) downwards migration and a subsequent peak of *E.gymnastica* in the lower part of the water columns (6–12 m) followed. Settled material collected from the bottom of the enclosures contained a considerable amount of *E.gymnastica* cells and resting cysts. Nevertheless, sinking loss rates of *E.gymnastica* were estimated to be less than 1% day^{-1} of the suspended cell numbers. The fate of *E.gymnastica* blooms was estimated to be grazing through mesozooplankton. However, provided the nutrients are plentiful in the water column, the growth potential of *E.gymnastica* appears to exceed the ambient grazing pressure. If the nutrients become depleted, it seems to be effectively controlled by mesozooplankton grazing, which is probably limiting the likelihood of massive *E.gymnastica* blooms in the coastal Baltic Sea. Our study suggests that *E.gymnastica* appears to be a fast-growing fugitive (bloom) species with flexible behavioural (vertical migration) and life history (cyst formation) adaptations which is able to exert dominant role and direct trophic relations similar to other bloom species adapted for decaying turbulence and high nutrient environments.

Introduction

Massive blooms of algae are often reported as a result of increased eutrophication of the marine environment. In the Baltic Sea several phytoplankton species are capable of producing noxious and sometimes also toxic blooms (Sivonen *et al.*, 1989; Kononen, 1992; Leppänen *et al.*, 1995). In the open sea, extensive blooms of cyanobacteria are observed regularly (Kahru *et al.*, 1994), while in the coastal embayments, blooms of phytoflagellates are occasionally recorded (Lindholm and Virtanen, 1992). Unexpected and hazardous phytoplankton blooms have been claimed to be a sign of ecosystem disturbance caused by increased nutrient availability combined with favourable hydrographical conditions and inefficient (or selective) top-down control of the algal community (Pearl, 1988; Verity and Smetacek, 1996).

Euglenoid flagellates are common members of the phytoplankton of the Baltic coastal waters. The species belonging to the marine or brackish water genus *Eutreptiella* are present in the spring and occasionally in the summer phytoplankton assemblage, but rarely in high numbers (Niemi, 1975; Edler *et al.*, 1984;

Niemi and Åström, 1987). Occasionally they may contribute significantly to the phytoplankton biomass after the decline of the spring bloom (Piirsoo and Porgasaar, 1985), after upwelling events in summer (Heiskanen, 1995), or form conspicuous subsurface blooms near anoxic boundary layers in the stratified coastal embayments (Lindholm, 1994). Extensive blooms of *Eutreptiella* spp. have been reported in the coastal waters of Japan (Okaichi, 1969; Iwasaki, 1971; Yamochi, 1984a,b). These blooms have been suggested to be favoured by heavy nutrient enrichments and by the availability of micro-elements or mud extracts (Okaichi, 1980; Takahashi and Fukazawa, 1982; Yamochi, 1984a), which characterize other bloom-forming key species (e.g. red-tide dinoflagellates) from the area. However, the ecology and environmental adaptations of the bloom forming euglenoids in marine and coastal habitats are poorly known.

Responses of the planktonic community to the episodic (pulsed) or continuous nutrient additions can be studied by using large scale ecosystem enclosures (Grice and Reeve, 1982; Lalli, 1990). In such systems the uncertainties caused by advective transport and patchiness are minimized, and the responses of the whole planktonic community to the bottom-up (nutrients) or top-down (predation) manipulations can be studied (Gamble and Davies, 1982; Steele and Gamble, 1982; Takahashi *et al.*, 1982). However, it is quite unpredictable which phytoplankton species may benefit from the improved nutrient availability or enforced top-down control. Moreover, enclosing part of the pelagic system within a mesocosm reduces the vertical mixing and thus reshapes the structure of the community and outcome of the competitive selection (Harrison and Turpin, 1982; Cushing, 1989). In such situations, fugitive phytoplankton species which have a high growth potential and flexible behavioural, morphological, physiological or life history adaptations may gain competitive advantage and form dense, almost unialgal blooms.

The present experiment was designed to study the ecosystem responses on the bottom-up (inorganic nutrients and organic carbon substrate enrichments) and top-down (addition of fish fry) manipulations in the coastal northern Baltic during the summer minimum of phytoplankton production and biomass. The physical scale of the mesocosms was sufficiently large to include the whole euphotic layer above the thermocline and also to allow diurnal vertical movements of micro- and meso-sized planktonic organisms. Nutrient enrichments were adjusted to be equal with the surface layer nutrient attainment during upwellings, which are frequent phenomena in the study area (Haapala, 1994). Sticklebacks are common visually feeding pelagic fish forming dense schools in the shallow littoral waters of the northern Baltic, thus suitable as top predators in mesocosm experiments. The density of fish fry was adjusted to ensure effective predation on mesozooplankton within the time scale of the experiment. Organic carbon substrate (sucrose) was added in order to stimulate productivity of heterotrophic bacteria and to invoke competition for inorganic nutrients between autotrophic phytoplankton and bacteria. The single and combined effects of the manipulations were studied in eight large-scale enclosures in the archipelago region of south-west Finland, Baltic Sea, during 3 weeks in July 1993.

In this paper, we focus on the responses of the dominant phytoplankton species,

Eutreptiella gymnastica, to the bottom-up and top-down manipulations during the experiment. We present and discuss the impact of growth, behavioural and life history adaptations of *E.gymnastica* on the overall channelling of the external nutrient input in the experimental enclosures and in the coastal planktonic ecosystem.

Method

The mesocosm experiment was carried out between 8 and 28 July in the outer archipelago zone nearby the Tvärminne Zoological station, south-west coast of Finland (Station XII of Niemi, 1975). The study site is relatively sheltered from wave action and the water depth varies between 20 and 36 m. It is influenced by surface water from the open Gulf of Finland with salinity 5–6 PSS (practical salinity scale) and oligohaline surface water from the inner archipelago (3–5 PSS) (Niemi, 1975).

The plastic enclosures had a total volume of ~50 m^3 (diameter 2.3 m) and a total depth of 14 m, which was below the typical euphotic surface layer depth in the study area (Niemi, 1975). During the installation, the enclosures were first lowered below the thermocline (~15 m depth), then filled with ~14 m surface water column water by lifting the collar up. The enclosures were fastened to wooden platforms which were moored ~30 m away from a central buoy, and arranged in a circular manner in order to avoid any uneven shading. The enclosures were loosely covered with plastic sheets which allowed air exchange but prevented contamination by sea birds.

The experiment was carried on for 21 days. Nutrients (N + P) and sucrose (S) were added in the beginning and during days 7 and 14, while fish (F) (stickleback fry, *Gasterosteus aculeatus* L.) were added in the start of the experiment to the enclosures 5 and 6 (400 individuals $enclosure^{-1}$, Table I). The combined nitrogen and phosphorus enrichments (final concentrations: 15 µg PO_4-P l^{-1}, 30 µg NH_4-N l^{-1} and 30 µg NO_3-N l^{-1}) were adjusted to correspond to the average nutrient concentrations below the seasonal thermocline in the study region (Niemi, 1975; Haapala, 1994; Heiskanen and Leppänen, 1995). Sucrose addition (400 µg C l^{-1}) was roughly equal to the total amount of carbon exuded by phytoplankton during

Table I. Experimental design

Enclosure	Treatment		
	Nutrients (N + P)	Sucrose (S)	Fish (F)
1	–	–	–
2	+	–	–
3	+	–	–
4	+	–	–
5	–	–	+
6	+	–	+
7	–	+	–
8	+	+	–

+ = addition; – = no addition

a 3-week period in summer (Lignell, 1990). Stickleback fry were added to accent the control of top trophic level by predation on the mesozooplankton populations and thus advocate net phytoplankton growth by decreasing their grazing loss rates. Based on previous experience, the amount of fish was considered to provide an explicit effect during the time range of the experiment. The enclosures were subjected to three treatments arranged in two 2^2 factorial designs (N + P and F; N + P and S). Single nutrient addition (N + P) was replicated in three enclosures to assess the between-unit variability (Table I). Nutrients and sucrose were added after the water column sampling in the morning by lowering a 12 m long tubing into the enclosures and gently rotating and lifting it up while the nutrient and sucrose solution was poured into a funnel at the top of the tubing. This ensured a homogeneous distribution of nutrients and sucrose in the enclosures from the beginning of the manipulation period.

Water column samples were taken daily between 7 and 11 a.m. Discrete samples were taken at 1-m intervals and pooled for two integrated samples which represented the water column layers of 0–6 m and 6–12 m. Dissolved inorganic nutrients (PO_4-P, NH_4-N and NO_3-N) were analysed immediately from the upper water layer (0–6 m) according to Grasshoff *et al.* (1983). Total chlorophyll *a* (Chl) concentrations were analysed daily from the upper and lower water column, while the samples for size fractionation of Chl (fractions >2 μm and <20 μm) were measured every other day from the upper water column samples only. Samples for the total Chl and the Chl fraction <20 μm (pre-filtered through 20 μm mesh) were filtered on Whatman (GF/F) glass-fibre filters, while the fraction >2 μm was filtered on Nuclepore filters. The filters were immediately placed in vials containing 96% ethanol, sonicated and extracted for 24 h in total darkness. The Chl concentration was measured using a spectrofluorometer (Shimadzu RF 5001), which had been pre-calibrated with pure chlorophyll *a* (Sigma).

Subsamples for phytoplankton counts were taken every other day (i.e. days 0, 2, 4, etc.) both from the upper and lower water column samples and fixed with acid Lugol solution. Aliquots of 50 ml were counted by using LEICA DM IL inverted microscope with phase contrast optics. Roughly 100–1000 cells of *E.gymnastica* were counted per sample, depending on the cell concentrations.

Settled material from the lowest conical part of the enclosures was collected by using a hand pump connected to the bottom of the enclosures with a 14 m long tubing. Every second day (days 1, 3, 5, etc., i.e. with 1 day shift compared to the phytoplankton samples from the water column) 5 l of bottom water were pumped out which, on visual inspection, were judged to contain most of the settled material. The first 3 l were always dark and murky, while the last 2 l were almost clear water. Subsamples of settled material were preserved with acid Lugol solution. Due to high content of detritus only 2 ml of bottom water samples were counted by using the inverted microscope method and dilution was used when necessary.

Daily settling rates of *E.gymnastica* cells were calculated by using their concentrations in the bottom water according to the following equation:

$$f = c \times v/(t/24) \times s \quad (1)$$

where f = flux of cells (cells m^{-2} day^{-1}), c = concentration of *E.gymnastica* cells in the bottom water material (cells ml^{-1}), t = time between subsequent sediment samplings (h), s = enclosure surface area (m^2), v = volume of the bottom water sample (ml).

The loss rates were calculated according to the formula:

$$l = f/b \tag{2}$$

where l = loss rate (day^{-1}), b = *E.gymnastica* cell numbers in water column (cells m^{-2}).

As the water-column samples and the bottom-water settled material were not taken on the same day, the vertical flux rate was divided by the standing stock of the previous day (i.e. a 1 day shift).

For hypothesis testing on the significance of the manipulations, differences between means of depth integrated cell concentrations in the enclosures were analysed using ANOVA with succeeding days as replicates. The variances of cell abundances in the eight enclosures were plotted against the mean values and from the slope of the least-square line a power transformation coefficient calculated (power = 1 – slope) to correct the data for heteroscedasticity (Norusis, 1994a). After the power transformation (0.75) the hypothesis of homoscedasticity could not be rejected (Levene test, $P = 0.83$). General significance of manipulation effects were assessed by one-way ANOVA (different enclosures as treatments), separate main effects by one-way ANOVA with covariation.

Results

In the beginning of July an upwelling caused an inflow of cold water from the sea zone, resulting in a decrease of water temperature from 16 to 10°C and increase of surface water salinity from 5.3 PSS to 5.6 PSS on the evening of 6 July. When the enclosures were filled, the surface layer temperature was 11°C and salinity 5.7 PSS, while at 12 m depth they were 5°C and 5.9 PSS, respectively. Water temperatures in the enclosures (Figure 1) followed closely temperatures outside (Pearson's $r = 0.99$, $P < 0.0001$).

The initial nutrient concentrations were low in the enclosures. After the additions, NO_3-N and NH_4-N were depleted from the surface layer within 2 days, while PO_4-P was consumed more slowly (Figure 2). Chl values in the upper layer varied between 2 and 6 μg l^{-1} in the non-enriched and between 5 and 40 μg l^{-1} in the nutrient enriched enclosures (Figure 3). Nutrient enrichments invoked a series of Chl peaks (days 2, 10 and 16), caused by the growth of the nano-size fraction (2–20 μm) and only minor increase in the pico- (<2 μm) and micro- (>20 μm) fractions (Figure 3).

The phytoplankton at the start of the experiment were dominated by *E.gymnastica*. The cell numbers at the start were 800–1000 ml^{-1} in the upper (SD = 223; CV = 22%; $n = 8$) and 500–900 ml^{-1} (SD = 140; CV = 19%; $n = 8$) in the lower water columns, respectively. The mean cell abundances, when averaged over the whole water column (0–12 m) had a lower variability (SD = 115; CV = 13%; $n = 8$). The

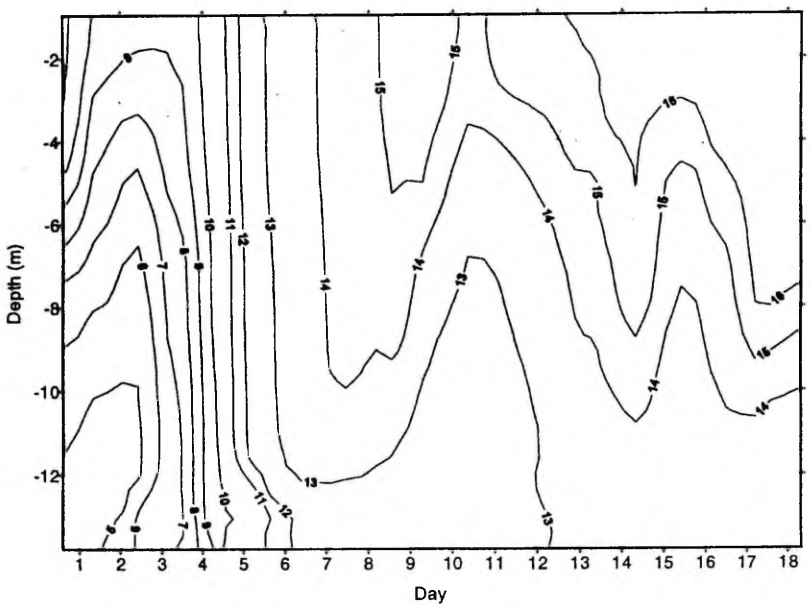

Fig. 1. Fluctuations of water column temperatures (°C) in enclosure 1 (control) during the experimental period.

response of *E.gymnastica* to the nutrient additions can be clearly seen as a sharp increase of the standing stock, and a decrease thereafter (Figure 4). The increase was most pronounced after the third addition in enclosure 6 (N + P + F). The variability (CV%) of *E.gymnastica* abundance among all the enclosures caused by different treatments was between 13 and 230%, while the variability between replicate enclosures was much less (CV = 3–43%). The major variation occurred at the end of the experiment when *E.gymnastica* populations collapsed.

The initial cell numbers of *E.gymnastica* were quite similar in the upper and lower water layers (Figure 4). Soon after nutrient addition most of the cells appeared in the upper water column and their concentrations in the lower layer were minimal. After a couple of days, during which the mineral nutrients were used up from the upper layer (Figure 2), the surface cell numbers had declined and those in the lower layer had increased. The same pattern was repeated after the second and third nutrient additions on days 7 and 14, respectively (Figure 4). The usual peak values were 3–6 $\times$ 10^3 and 2–5 $\times$ 10^3 cells ml^{-1} in the upper and lower layers, respectively. The corresponding minimal values were 3–4 times less. During day 16, the maximum cell numbers of 13 $\times$ 10^3 cells ml^{-1} were observed in the upper water column of unit 6 (N + P + F). After the last nutrient additions, the numbers of *E.gymnastica* collapsed in all units except in unit 6. Other species took over the dominance of phytoplankton biomass (mainly small cryptomonads and *Aphanizomenon flos-aquae*). The cell numbers of *E.gymnastica* in the upper layer of the enclosures without nutrient manipulation decreased continuously, while in the lower layer their numbers increased until days 2 or 4, but decreased

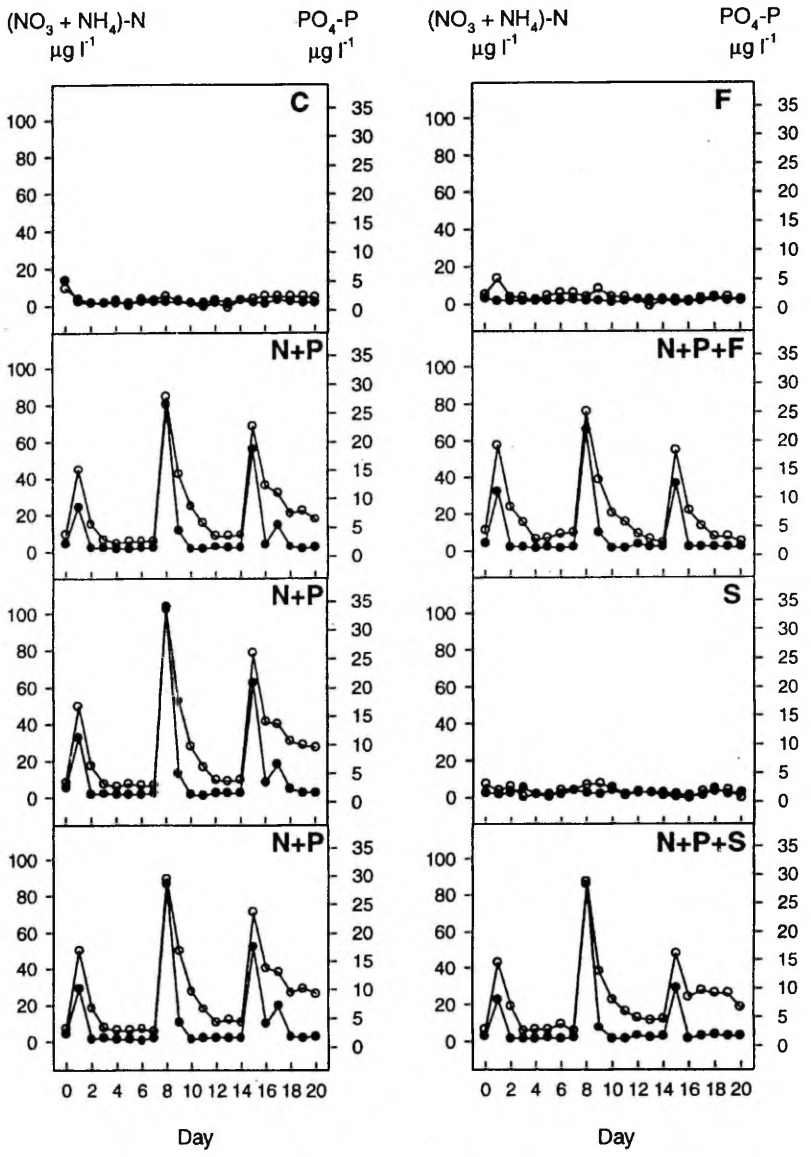

Fig. 2. Nutrient concentrations (µg l^{-1}) in the upper layer (0–6 m) of the enclosures. $(NO_3 + NH_4)$-N: filled circles, (PO_4)-P: open circles. C = control; N + P = nutrient (N, P) additions; F = fish addition; N + P + F = nutrient (N, P) and fish addition; S = sucrose addition; N + P + S = nutrient (N, P) and sucrose addition.

continuously thereafter, and reached the initial low values on days 8 or 10 (Figure 4).

In the nutrient-enriched enclosures, *E.gymnastica* was the dominant phytoplankton species almost throughout the whole experiment, while in the enclosures without nutrient additions, it was dominant only during the first half of the

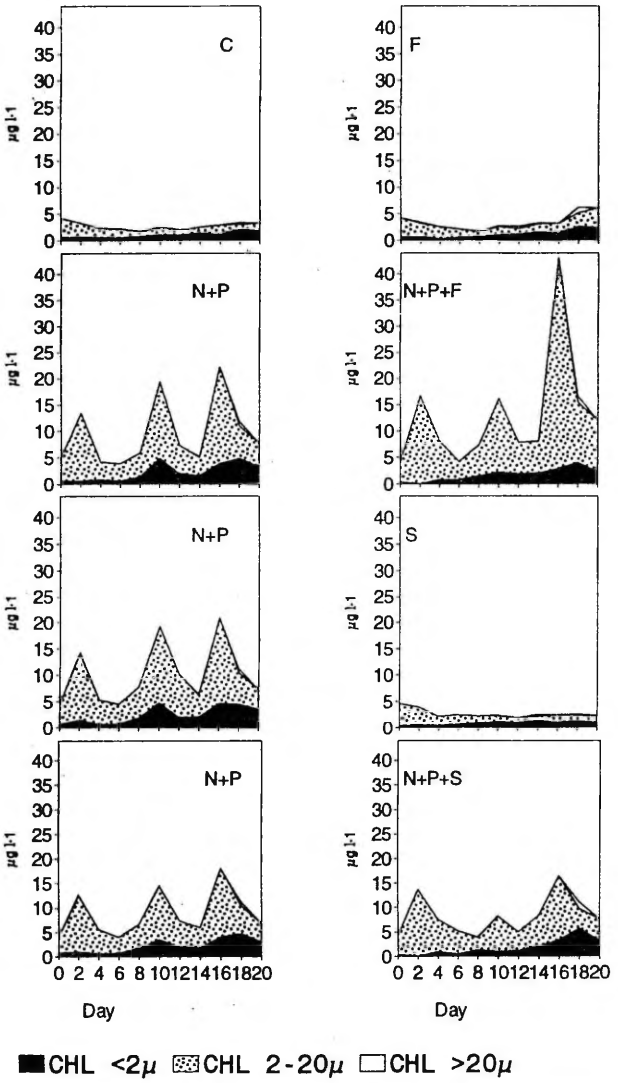

Fig. 3. Fractionated Chl in the upper layer (0–6 m) of the enclosures. Abbreviations as in Figure 2.

experiment (Figure 5). We found a highly significant correlation between total Chl and the cell numbers of *E.gymnastica* almost in all enclosures in the upper layer ($r = 0.69 - 0.96$; $P < 0.005$–0.001) except units 1 and 5 which received no nutrient additions (Table II). Elimination of the picoplanktonic fraction (i.e. using Chl fraction >2 µm) resulted in even higher correlation coefficients ($r = 0.92$–0.98; $P < 0.001$) in all enclosures except unit 5. Total Chl from the upper layer in unit 5 had a significant correlation ($r = 0.87$; $P < 0.001$) with the total biomass of other micro- and nanophytoplankton species. In the lower layer, high significant correlation ($r = 0.90$–0.98; $P < 0.001$) between *E.gymnastica* numbers and total Chl was found in

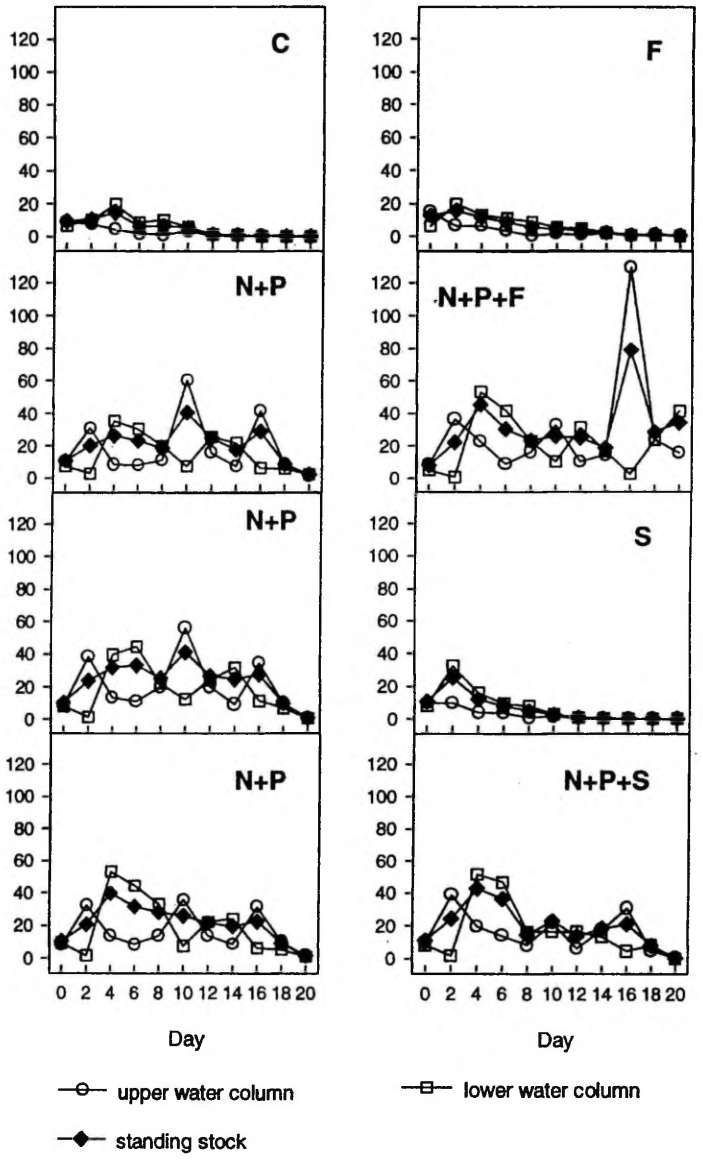

Fig. 4. Abundance of *E.gymnastica* (cells × 10^2 ml^{-1}) in the upper (open circles), lower (open squares) layers of the enclosures and the total standing stock (cells × 10^9 m^{-2}) (filled diamonds). Abbreviations as in Figure 2.

all units (Table II). The average Chl content of the cells was calculated using weighted least-square regression (Norusis, 1994b) between Chl and cell numbers, where the data points were weighted by the reciprocal of *E.gymnastica* counting precision (95% CL). Although the Chl content tended to be larger in nutrient manipulated enclosures and in the upper layer, the differences were not

Table II. Correlation between *Eutreptiella gymnastica* abundance and chlorophyll *a*

	Enclosures							
	1	2	3	4	5	6	7	8
Total chl *a* versus *E.gymnastica* (upper water column)	NS	0.88**	0.85**	0.84**	NS	0.96**	0.84**	0.69*
Chl *a* (>2 μm) versus *E.gymnastica* (upper water column)	0.93**	0.92**	0.92**	0.94**	NS	0.98**	0.96**	0.94**
Total chl *a* versus *E.gymnastica* (lower water column)	0.96**	0.91**	0.89**	0.95**	0.94**	0.95**	0.98**	0.94**

NS, not significant, * $P < 0.005$, ** $P < 0.0001$.

statistically significant and the mean value was 2.78 ± 0.17 (95% CL; $n = 176$) μg Chl (cells × 10^6)$^{-1}$.

The settled detrital material in the bottom water of the enclosures also contained high numbers of *E.gymnastica* cells. Part of the cells were healthy looking while others were senescent or dead in various phases of degradation. After the first experimental week, high numbers of resting cysts and rounded cells undergoing encystment were also found. The absolute concentration of the cells and cysts was an order of magnitude higher in the 5 l of bottom water than in the water column, reaching values above 10^5 ml^{-1}.

Sedimentation rates of *E.gymnastica* did not vary significantly (one-way ANOVA, $P < 0.6$) between the enclosures (Figure 6). Neither was the variability in the sedimentation pattern of *E.gymnastica* explained by the variability of cell numbers in the water column during the previous day (linear regression, $r^2 < 0.2$). Thus, the manipulations had no significant effect on the sedimentation rates of *E.gymnastica*. However, compared to the suspended cell numbers in the water column, the daily loss rates of *E.gymnastica* were low (0.05–0.6% day^{-1}).

Discussion

Nutrient enrichments had a highly significant effect on *E.gymnastica* numbers (ANOVA, $P < 0.001$) and evoked a quick biomass increase. The fractionated Chl values from the upper layer indicated that the corresponding Chl peaks were mainly due to increase in the nano-size (2–20 μm) fraction. From the nano-fraction 60–90% of the biomass was made up by *E.gymnastica*.

Nutrient addition and subsequent depletion of the upper water column induced a vertical migration of *E.gymnastica*, reflected in the oscillating vertical distribution pattern of the cells in the nutrient-enriched enclosures. The swimming speed of *E.gymnastica* has been measured to be more than 10 m 12 h^{-1} (Throndsen, 1973a), which is quite sufficient to explain the observed migration pattern in the enclosures. Quick downwards migration indicated that the cells may have become nutrient limited in the upper water column. The surface avoidance was probably caused by high respiration costs in the warmer, highly illuminated and nutrient-depleted environment, which could not be compensated by the production rates due to nutrient limitation. Our estimate of the Chl content of

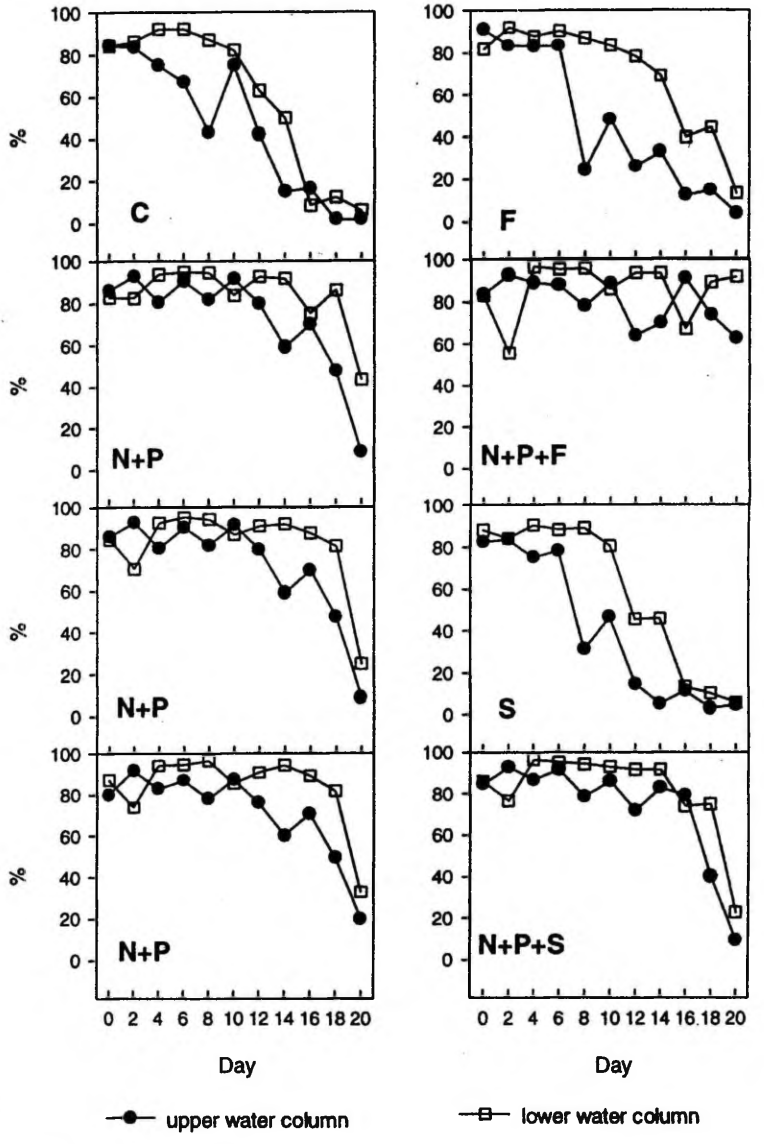

Fig. 5. The share of *E.gymnastica* (%) from the total micro- and nanophytoplankton biomass in the upper and lower layers of the experimental enclosures. Abbreviations as in Figure 2.

E.gymnastica [2.78 μg (cells × 10^6)$^{-1}$] was much higher than that reported by Thomas *et al.* (1984) for *E.gymnastica* in laboratory conditions [0.490 – 0.510 μg (cells × 10^6)$^{-1}$]. Even higher values can be calculated from the data of Lindholm (1994) [~6 μg (cells × 10^6)$^{-1}$] for a distinct subsurface maximum in the Åland archipelago, northern Baltic Sea. This suggests that the vertically migrating populations in our experiment were not particularly adapted to either light-saturated or low-light environments. However, as the maximum in the total standing stock

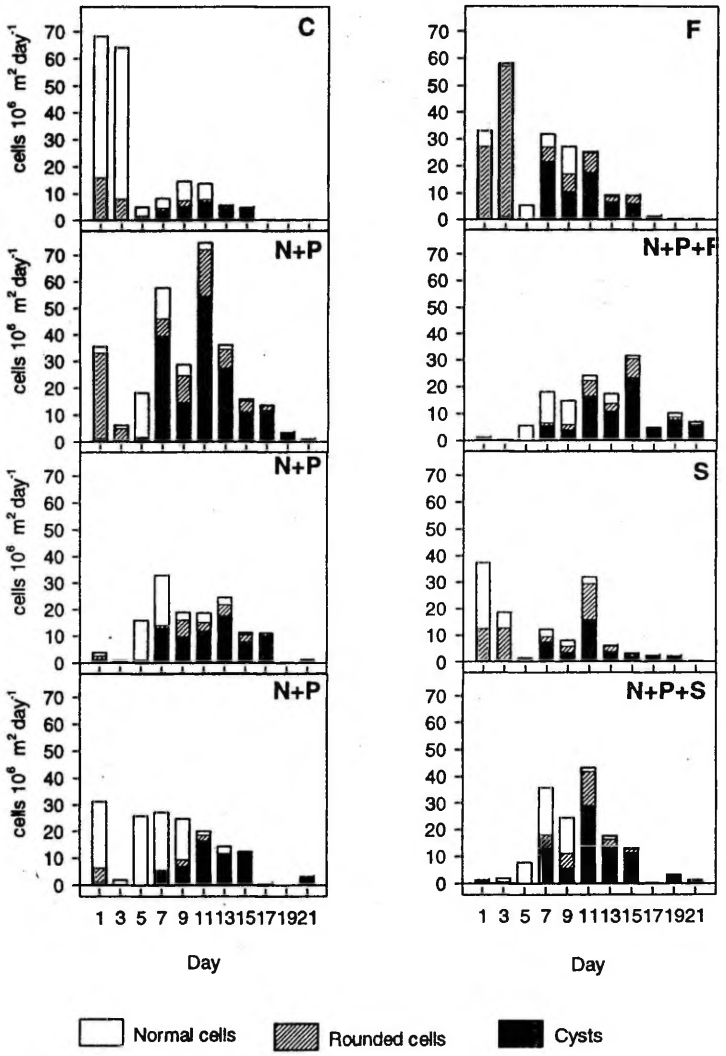

Fig. 6. Sedimentation of *E.gymnastica*, calculated as daily vertical flux (cells m^{-2} day^{-1}) of normal cells, rounded cells undergoing encystment and cysts, to the bottom of the enclosures. Abbreviations as in Figure 2.

was achieved when the bulk of cells had already descended to the lower layer, they were obviously able to exploit nutrients and maintain high growth rates in low light. In the lower part of the enclosures the cells apparently gained at least two advantages: lower respiration losses due to lower temperature and higher nutrient concentrations.

Flagellated forms are known to benefit from reduced turbulence in enclosure experiments (Davis, 1982) and migratory behaviour enables the cells to sequester the optimal light and nutrient environment, resulting in a competitional

advantage over the non-flagellated species (Olsson and Graneli, 1991). It should be kept in mind that prior to the experiment the plankton community was in a post-upwelling condition and a natural nutrient enrichment had occurred about a week before. Thus, species favoured by occasional pulses of cold nutrient rich water had established vital populations already. Firm starting position and abrupt response caused the dominance of *E.gymnastica* over other species during the experiment. However, on a longer time scale the adaptive strategies of *E.gymnastica* were of limited value, which could be seen from the collapse of the populations (excluding enclosure 6) on the last experimental day.

The addition of stickleback fry caused a notable increase of the *E.gymnastica* populations, by reducing the mesozooplankton abundance (K.Kivi, personal communication) with subsequent relaxation of the grazing rates (one-way ANOVA, covariate (N + P), main effect (F) $P = 0.040$). Generally it takes longer time for the manipulations to take effect on higher trophic levels (Gamble and Davies, 1982) suggesting the effect on *E.gymnastica* being more clear towards the end of our experiment. In our study the statistical significance of F manipulation increased when subsequent data points from the beginning of the experiment were excluded from the analysis [e.g. one-way ANOVA, covariate (N + P), main effect (F), days 8–20, $P = 0.013$; days 14–20, $P = 0.006$]. Relaxation of mesozooplankton grazing was evidently reflected in the much higher biomass increase in enclosure 6 (with nutrient and fish additions) compared to enclosures 2–4 (nutrient additions alone) during nutrient sufficient growth between days 14 and 16 (Figure 4). Using the cell counts on subsequent days we can calculate the net exponential growth rate (k) of *E.gymnastica*, according to equation (3):

$$N_t = N_0^{ekt} \tag{3}$$

where N_0 and N_t are the standing populations on day 0 and t, respectively.

From equation (3) the growth rate follows as:

$$k = (\ln N_t - \ln N_0)/t \tag{4}$$

To distinguish the observed net growth rate (k) from other exponential rates, let us identify it as k_n, the gross growth rate as k' and the loss rates as k_l (Reynolds, 1984). Thus:

$$k_n = k' - k_l \tag{5}$$

The highest net increase of *E.gymnastica* population was observed in unit 6 after the third nutrient addition (Figure 4). As the loss rates by sedimentation were negligible, mesozooplankton grazing was apparently of minor importance (i.e. k_l considered insignificant) and nutrients were non-limiting, it could be assumed that the net population increase of *E.gymnastica* between days 14 and 16 was close to the gross growth rate under the given environmental conditions (i.e. k_n approached k'). Calculating the exponential growth rate of *E.gymnastica* standing stock (between days 14 and 16) according to equation (4) we obtain 0.72 day^{-1}

(equivalent to ~1.03 divisions day^{-1}). This value is close to the maximum growth rates obtained for the same species in laboratory conditions at the optimal salinity (25 PSS) but considerably higher than the growth rate at 5 PSS salinity obtained in the same investigation (Throndsen, 1973b). However, we have reasons to consider our result conservative, as it was unlikely that all the loss rates were completely eliminated (e.g. parasites, viral attacks). Moreover, the abundances during days 14 and 16 were used, which probably included a lag period as the nutrients were also added on day 14. This is supported by the exponential growth rate based on total Chl concentrations (0–12 m) between days 15 and 16 which was even higher (0.84 day^{-1}).

The growth rate calculated from the average values of the three replicate enclosures (units 2–4) within the same time interval was 0.12 day^{-1}. As the presence of mesozooplankton grazers in the replicate nutrient enriched enclosures was the only difference from enclosure 6, accepting the conservative growth rate (0.72 day^{-1}) as an approximation of the gross growth rate (k') and assuming equal gross growth potentials (because all other conditions were equal), the difference in the growth rates between enclosure 6 and those of enclosures 2–4 during days 14–16 can be attributed to mesozooplankton grazing. Thus the loss rate due to grazing during the last week of the experiment in nutrient-manipulated enclosures (except unit 6) was ~0.12 day^{-1} – 0.72 day^{-1} = –0.60 day^{-1}. Based on this reasoning, we consider grazing by mesozooplankton to be the main loss factor of *E.gymnastica*, which, combined with nutrient limitation, caused the decline in cell numbers in between the nutrient additions. Euglenoids are generally considered to be poor food items for zooplankton because their reserve product, paramylon, is rarely digestible for the grazers (Hirayama *et al.*, 1979; Walne and Kivic, 1990). Although the cells may have been grazed by zooplankton, the paramylon grains passed undigested through the gut, thus diminishing the nutritional gain. This is supported by the electron microscopic examinations of the faecal pellets from the settled material, which were all filled with intact paramylon grains (K.Olli, in preparation).

In enclosures without nutrient manipulation the initial peak on day 2 was probably caused by mixing of deep layer nutrients to the euphotic layer during enclosure installations. In enclosure 7, which had only sucrose addition, we could expect the most severe nutrient limitation after the peak on day 2, as heterotrophic bacteria are able to outstrip phytoplankton in uptake of mineral nutrients in the Baltic if sufficient carbon source is provided (Smetacek *et al.*, 1980, 1982). Calculating the net decrease rate for *E.gymnastica* according to equation (4) for the period between days 2 and 16 in enclosure 7 (by visual judgement the period from the start of the decline until near zero concentrations) we obtain –0.319 day^{-1} (ranging from –0.21 to –0.55 day^{-1}). Assuming negligible (zero) growth rate due to nutrient limitation, we can consider this as the sum of all loss rates (k_l) for the non-nutrient manipulated enclosures. In the control enclosure the exponential decrease lasted until day 18 and the average loss rate was even slightly higher (mean –0.367 day^{-1}, range from +0.045 to –0.755 day^{-1}) than in enclosure 7. In enclosure 5, with fish addition, the decline clearly lasted for the longest period of time (from day 2 to 20) resulting in the lowest loss rate (mean –0.198 day^{-1}, range

from –0.078 to –0.533 day^{-1}). Thus, also in non-nutrient enriched enclosures, *E.gymnastica* had lower average loss in the units manipulated with top predator than in those without fish.

In the nutrient-manipulated enclosures, the sucrose addition did not cause significant difference from the three replicate enclosures, and in the non-nutrient manipulated enclosures sucrose addition resulted in lower loss rates (and higher average cell numbers) compared to the control, although not statistically significant. It can be suspected that the stronger nutrient limitation was compensated by benefit from sucrose, high bacterial abundance or both. Walne and Kivic (1990) have mentioned the dependence of euglenoid nutrition on bacteria in connection with the need for (bacterially produced) vitamins B_1 and B_{12}. Lindholm (1994) has discussed the possibility that substances from bacteria-rich anoxic boundary layers could have stimulated the sub-surface population maximum of *E.gymnastica* in the Åland archipelago. Lewitus and Kana (1994) have shown that in some flagellates light limitation of photosynthesis can be partially offset by respiration of exogenous organic substrates, which could have provided enhanced survival of the *E.gymnastica* population in unit 5 (S) compared to the control (C).

The role of Eutreptiella gymnastica in the coastal waters of the northern Baltic Sea

Eutreptiella gymnastica is a species which tolerates a wide range of temperatures and salinities (Throndsen, 1973b). Moreover, it appears to be an extreme r-strategist with high growth potential in environments of elevated nutrient levels and decreasing turbulence. The ability to migrate vertically provides it with the flexibility to sequester the vertical gradients of nutrients and light in the water column. Maintenance of deep living refuge populations through resting cyst formation is analogous to the life cycle strategies of diatoms (Smetacek, 1985), dinoflagellates (Margalef *et al.*, 1979) and some cyanobacteria (Pearl, 1988), and may serve as an adaptation to survive over hostile environmental conditions or periods of excessive grazing providing a seed bank for later recruitment. Accordingly *E.gymnastica* shares many evolutionary adaptations characteristic of opportunistic bloom species, which exert a dominant role in the pelagic ecosystem structure to such an extent that they shape the trophic pathways, and hence drive the biogeochemical cycles (Verity and Smetacek, 1996). It seems that *E.gymnastica* is a species with a particular combination of environmental adaptations, which contributes to the bulk of biogenic fluxes in certain environmental conditions. As such it fits to the rationale originally presented by Margalef (1978) and further elaborated by Smetacek (1985), Pearl (1988) and others (e.g. Verity and Smetacek, 1996), which addresses the evolutionary adaptations of individual key species in combination of the physical environment as the shaping forces of the biotic and abiotic interactions.

Our results suggest that the growth potential of *E.gymnastica* exceeds the ambient grazing pressure in the Baltic in nutrient rich low turbulence conditions, like pulsed nutrient discharges in the coastal areas or periods of decaying turbulence after upwelling. Zooplankton are probably able to control their numbers

after the external nutrient supply has been consumed. Thus, it seems possible that during summer a substantial fraction of the episodic new production pulses (based on external nutrient input) could be channelled through *E.gymnastica* to the grazing food chain. However, since the reserve product of *Eutreptiella* (paramylon) does not seem to be digestible for the majority of zooplankton, a respectable part of the biomass (especially carbon) is transformed to zooplankton faeces.

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RESTING CYST FORMATION OF *EUTREPTIELLA GYMNASTICA* (EUGLENOPHYCEAE) IN THE NORTHERN COASTAL BALTIC SEA[1]

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ABSTRACT

Resting cyst formation of Eutreptiella gymnastica *Throndsen was observed during a mesocosm experiment, where nutrient enrichment had induced almost a unialgal bloom. Cells and resting cysts of* E. gymnastica *were examined in scanning (SEM) and transmission electron microscopy (TEM) and light microscopy. Mature cysts were spherical, with a smooth thick mucilaginous cover that appeared layered when observed with the TEM. Intermediate forms were spherical and lacking flagella and a mucilaginous cover; the euglenoid pellicular striation and canal opening were easily visible. The volume of these intermediate spherical cells and mature cysts was estimated to have increased threefold compared to flagellated cells and contained many paramylon grains. When the cells were grazed by zooplankton, the paramylon grains passed the gut intact and were packed into fecal pellets. Intact undigested paramylon grains were observed in SEM after the breaking up of the pellets.*

Key index words: Baltic Sea; Euglenophyta; Eutreptiella gymnastica; *mesocosm; mucus; paramylon; resting cyst*

Resting stage formation is a common feature in the life history of many algal groups, including diatoms (Smetacek 1985, McQuoid and Hobson 1995), chrysophytes (Agbeti and Smol 1995), green algae (Cain and Trainor 1976, O'Kelly 1983), and dino-

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flagellates (Pfiester and Anderson 1987, Blanco 1995). Cyst formation among euglenoids has been reported infrequently (Leedale 1967, Rosowski 1977, Triemer 1980), although several works deal with mucus structure and production in detail (Rosowski and Kugrens 1973, Rosowski 1977, Rosowski and Willey 1977, Triemer 1980, Willey 1984). Most of this work has been done with laboratory cultures, and the ecological significance of cyst formation in nature is not known. There is a consensus that mucilage secretion occurs, at least to some extent, in all euglenoid species (Leedale 1967), although flagellated cells may lack a permanent coating (Rosowski 1977). Different kinds of mucus are produced and released by muciferous bodies and mucocysts (Willey 1984), although according to Triemer (1980) cyst formation involves secretion of mucilage produced in the Golgi apparatus into the reservoir and subsequent deposition of a thick-layered cover over the cell surface. Triemer (1980) demonstrated that nitrogen limitation induced encystment on heterotrophically grown *Euglena gracilis* Klebs (strain Z Pringsheim). The ecological significance of encystment is poorly known because studies from natural communities are lacking.

The present study was performed in connection with a mesocosm experiment, designed to assess community level responses to the bottom-up (mineral nutrient enrichments, organic carbon source) and top-down (fish) manipulations during the summer in the coastal Baltic Sea. Extensive, almost unialgal blooms of *Eutreptiella gymnastica* were induced by nutrient enrichments in large-scale enclosures, and resting cysts of the species formed in both nutrient-enriched and nonenriched enclosures. *Eutreptiella gymnastica* is a common species in the Baltic (Edler et al. 1984, Piirsoo and Porgasaar 1985, Lindholm 1994, Heiskanen 1995) as well as in the coastal areas of the North Sea (Throndsen 1973). It seems to be favored by elevated nutrient concentrations (Okaichi 1980, Takahashi and Fukazawa 1982) and is more abundantly found in the coastal waters than in offshore areas (Throndsen 1973). Under certain circumstances, it forms almost unialgal blooms (present study) and distinct subsurface maxima near anoxic layers (Lindholm 1994). Cyst formation of the brackish water and marine genus *Eutreptiella* has not been reported earlier. Transmission and scanning electron microscopic as well as light microscopic examinations of the cells and cysts were made, and the quantitative and ecological aspects of encystment are discussed.

MATERIALS AND METHODS

The mesocosm experiment was conducted in the outer archipelago zone of the southwestern coast of Finland, at the entrance of the Gulf of Finland. The study site (st. XII, 59°51'30"N, 23°16'E; cf. Niemi 1975) has a depth of 20–36 m and is relatively sheltered and influenced by oligohaline surface water (salinity 3–5 PSS) inflow from the inner archipelago during the spring and by Baltic surface water (salinity 6–7 PSS) during frequent upwelling events (Niemi 1975, Haapala 1994).

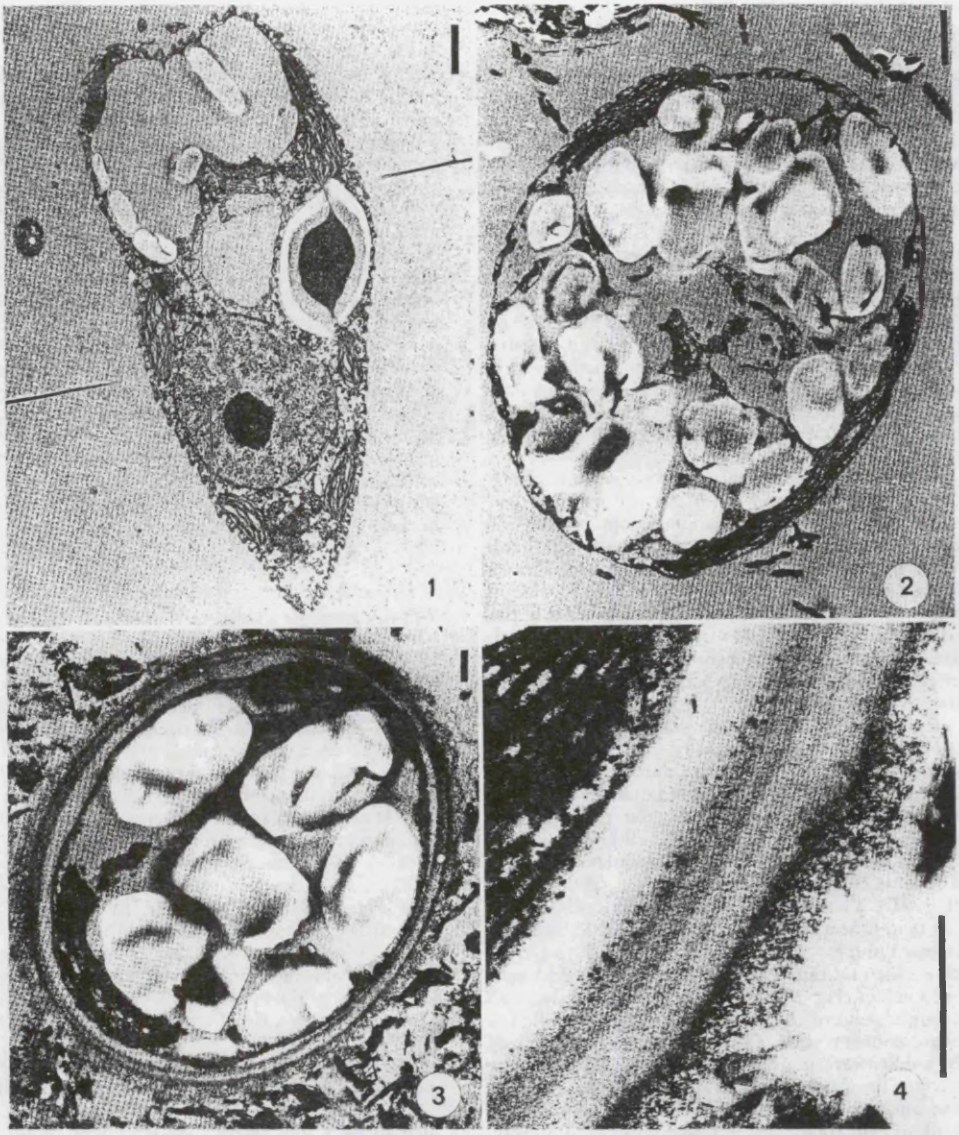
Eight plastic enclosures (total depth 14 m, volume 50 m^3 each) were manipulated with single and combined additions of nutrients (15 μg PO_4-P·L^{-1}, 30 μg NH_4-N·L^{-1}, and 30 μg NO_3-N·L^{-1}), organic carbon source (sucrose, 400 μg C·L^{-1}), and fish (stickleback fry, 400 individuals·enclosure^{-1}) during a 3-week period from 8 to 28 July 1993. The mineral nutrients, added at the beginning of each week to promote phytoplankton development, were adjusted to correspond to the average nutrient levels below the seasonal thermocline in the study area (Niemi 1975), hence simulating upwelling events. Fish were added to predate on mesozooplankton and thus relax the grazing pressure on phytoplankton. Every other day (beginning from day 0), discrete water samples were taken at 1-m intervals and pooled for two integrated samples representing the upper (0–6 m) and lower (6–12 m) layers, respectively. Sedimented material (5 L of bottom water) was removed every second day (beginning from day 1), by using a hand pump connected to the lower conical part of the enclosures. Subsamples for phytoplankton quantification from the upper and lower water column samples and the sedimented material were preserved immediately with acid Lugol solution. Biomass (wet weight) estimates were based on cell counts (approximately 100–1000 cells per sample, Leica DM IL inverted microscope with phase-contrast optics) and cell volume estimates, assuming a density of 1. Dissolved inorganic nutrients were analyzed immediately from the upper water layer according to Grasshoff et al. (1983).

For scanning electron microscopy (SEM) analysis, 1–5-mL aliquots of bottom water sample were fixed with glutaraldehyde (final concentration 2.5%) for 2 h, filtered on a 0.2-μm Nucleopore membrane filter, and rinsed several times with 0.1 M phosphate buffer at pH 7.3. Dehydration was done in an ethanol series (10%, 30%, for 10 min, 50%, 75%, 94%, for 30 min, stored overnight in absolute ethanol) and finally in a Balzer CPD 020 critical-point drier followed by coating with gold/palladium in a JEOL Fine Coat JFC 1100CX sputtering device. Samples were examined in a JEOL JSEM 820 scanning electron microscope at 10 kV.

Transmission electron microscopy (TEM) samples were prepared by concentrating the Lugol-fixed sample suspension by centrifugation and fixing with glutaraldehyde overnight (final concentration 2.5%). Fixative was removed by washing several times with phosphate buffer (pH 7.3, 0.1 M), followed by postfixation with OsO_4 (1% solution in phosphate buffer) for 1 h. Cells were dehydrated in ethanol series (50%, 70%, 94% and absolute for 5, 10, 20, and 45 min, respectively) and embedded in Epon LX 112. Thin sections were stained in uranyl acetate (30 min) followed by lead citrate (2 min). TEM preparations were examined in a JEOL JEM-100CX transmission electron microscope at 60 kV. The electron microscopic work was carried out at the Department of Electron Microscopy, University of Helsinki.

RESULTS

Under the light microscope, living flagellated cells of *Eutreptiella gymnastica* were of variable shape, from oval to elongate. Cell length varied between 15 and 20 μm, and cell volume was estimated to be 525 μm^3 (equivalent spherical diameter 10 μm). The cells swam vigorously, but after some time under the coverslip they dropped their flagella and started to engage in a pronounced euglenoid motion. Metabolic cells changed their shape from spherical to T-shaped and needle-like. The length of these cells varied from 10 to 25 μm. Cysts were spherical or slightly elongated in the light microscope, surrounded by a



FIGS. 1–4. TEM sections of *Eutreptiella gymnastica*. FIG. 1. Longitudinal section of a flagellated cell. FIG. 2. Intermediate rounded cell. FIG. 3. Mature cyst. FIG. 4. Cyst wall with typical layered structure. Scale bars = 1 μm.

thick cover. Intermediate forms between mature cysts and flagellated cells were spherical, with cell contents and size similar to those of cysts, but lacked the thick cover. The diameter of the cysts and intermediate forms were approximately 15 μm, and the estimated volume was 1770 μm^3.

In TEM, the cells had a single large parietal pyrenoid surrounded by two opposite cup-shaped par-

amylon shields (Fig. 1), which is characteristic of the species (Throndsen 1973, Walne et al. 1986). Compared to the flagellated cells, there were many more paramylon grains in the intermediate spherical forms (Fig. 2) and mature cysts (Fig. 3), covering most of the cross-section area of the TEM micrographs. The flagellated cells and intermediate forms had no sign of a polysaccharide layer outside the pellicula, in contrast to the thick and layered mucilaginous cover of mature cysts (Fig. 4).

The pellicular striation of the cells, not visible in the light microscope, was easily seen in SEM (Fig. 5). The intermediate forms lacked flagella, but the canal opening and pellicular striations were present (Fig. 6). A mucilage coating on the cell surface of these intermediate forms could not be seen. Mature cysts were covered with a layer of mucus, which looked smooth or slightly wavy and without any protrusions in SEM (Fig. 7). Pellicular striations and the canal opening were not visible through the mucilage cover.

In SEM, the individual intact paramylon grains were scattered around in the detrital material and were especially abundant around zooplankton fecal pellets, which seemed to be filled with them (Fig. 8). With higher magnification, the paramylon grains looked elliptical, closed or with cavities inside, forming rings. The borders between the segments of the paramylon crystals could be seen, as well as the striated surface, which agrees with the study of Kiss et al. (1988) on paramylon structure of *Euglena gracilis* (strain Z Pringsheim).

Eutreptiella gymnastica dominated the initial phytoplankton community enclosed into the mesocosms (about 10^6 cells·L^{-1}, forming about 80% of the total biomass). The species responded quickly to the nutrient additions, which was reflected in a rapid biomass increase within 2–3 days (Fig. 9A, B), followed by a subsequent decline of the populations as the nutrients become depleted from the surface layer (Fig. 9D). The depth-integrated mean cell numbers fluctuated according to the nutrient additions between 1 and 8×10^6 cells·L^{-1} (Fig. 9A, B), whereas those without nutrient additions decreased to near zero values (Fig. 9C). Nutrient additions caused an accumulation of the cells to the upper layer (maximum concentration 13×10^6 cells·L^{-1}), followed by a downward migration after the depletion of the surface layer nutrient concentrations (Fig. 10A). In the enclosures without nutrient manipulation, the bulk of cells stayed in the lower water column (Fig. 10B).

The mineral nutrient concentrations in the enclosures were low, and the added nitrogen was depleted in 2 days, while phosphate was consumed more slowly (Fig. 9D). The nutrient ratio stayed low during the whole experimental period, with only temporary elevations just after the additions in the nutrient-manipulated enclosures (Fig. 9D). In the enclosures without nutrient manipulations, the concentrations of phosphate and mineral nitrogen were in the range of 0.5–3 $\mu g \cdot L^{-1}$ and the ratio fluctuated in the range of 1–3.

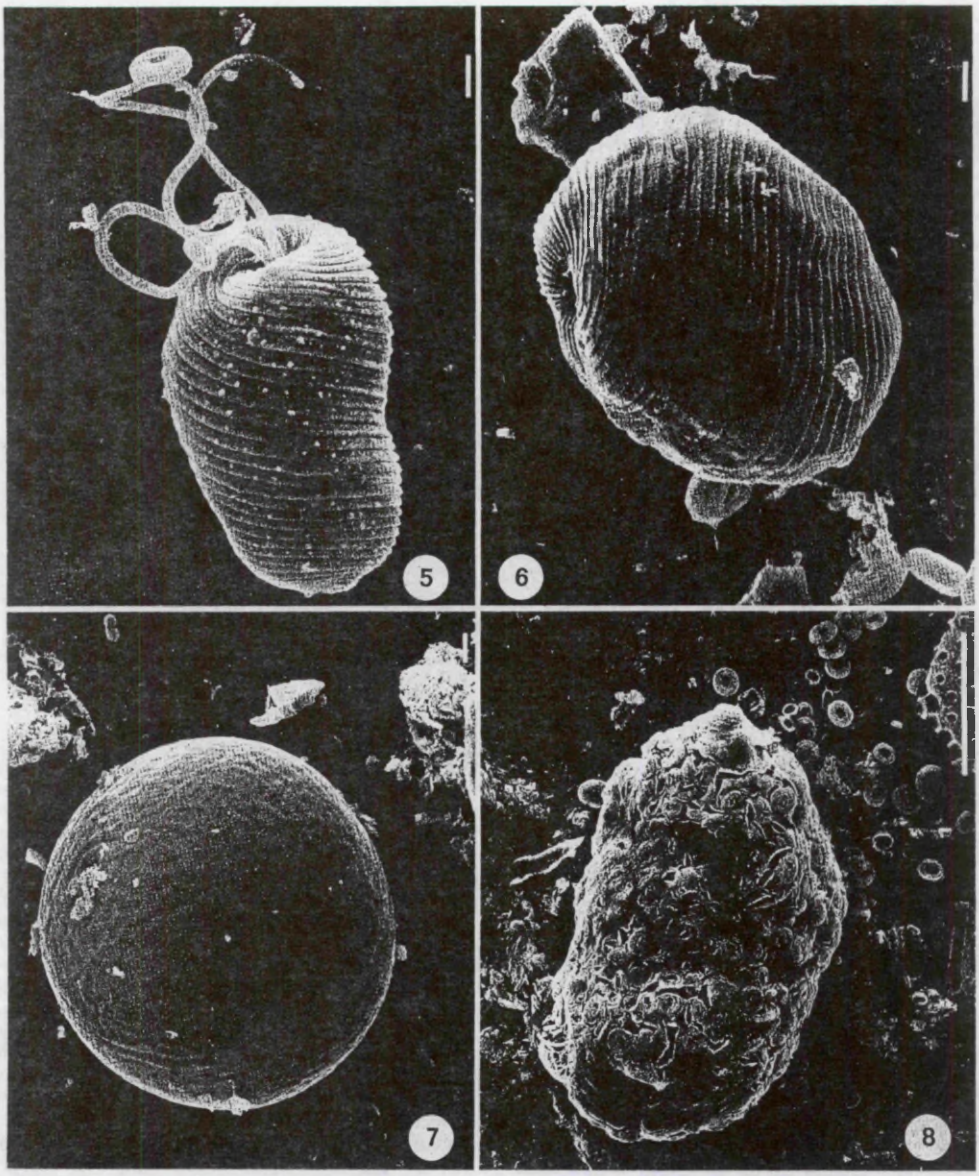
The cysts and intermediate forms were found among the detrital material from the bottom water of the enclosures. The concentration of cells in the 5 L bottom water was an order of magnitude higher compared to the water column, reaching values above 10^8 cells·L^{-1}. However, compared to the total number of *Eutreptiella gymnastica* in the water column, only a small fraction of the population was estimated to form cysts or to sink as vegetative or spherical cells to the bottom of the enclosures. The maximum number of cysts was observed during the second week of the experiment; thereafter, their numbers declined (Fig. 9A–C). However, the abundance of cysts and intermediate forms did not show any high correlation with the measured environmental parameters (temperature in the bottom layer, nutrient concentrations and ratios in the upper layer) or abundance of flagellated cells in the water column. Also, cross-correlations with a range of time lags could not be interpreted in a meaningful manner.

DISCUSSION

The morphology and ultrastructure of the *Eutreptiella gymnastica* cells were in accord with previous descriptions of the species (Throndsen 1973, 1993, Walne et al. 1986). The first phase of encystment consisted of a loss of flagella, formation of a large number of paramylon grains, and a subsequent rounding up and swelling of the cells. The final phase of encystment apparently consisted of the formation of the mucilaginous cover, because the spherical intermediate cells had no sign of mucus cover visible in SEM and TEM, although they were already filled with paramylon grains. In the light microscope, the thickness of the mucilage cover of the cysts was variable, probably due to different stages of maturity. The layered cyst wall structure observed in TEM (Fig. 4) is in accord with the findings of Triemer (1980). Euglenoid mucus has been reported to consist of glycoproteins and polysaccharides (Cogburn and Schiff 1984) or of macromolecular carbohydrates with very little, if any, proteins (Willey et al. 1977).

The increase of the cell volume during encystment could partly be explained by the extensive formation of paramylon granules. The spherical intermediate cells and mature cysts contained numerous paramylon grains, which agrees with earlier findings by Triemer (1980) concerning mature cysts of heterotrophically grown *Euglena gracilis*.

The euglenoid reserve product, paramylon (β-1,3-glucan), is not digestible by the majority of zooplankton grazers (Hirayama et al. 1979, Walne and Kivic 1990), thus diminishing their potential nutritional gain. The mesozooplankton fecal pellets examined during this study (Fig. 8) were packed with para-



FIGS. 5–8. Scanning electron micrographs of *Eutreptiella gymnastica*. Scale bars in Figures 5–7 = 1 μm. FIG. 5. Flagellated cell. FIG. 6. Intermediate rounded cell. FIG. 7. Mature cyst. FIG. 8. Zooplankton fecal pellet that is filled with paramyon grains. Several elliptical ring-shaped paramylon grains are scattered around the pellet. Scale bar = 10 μm.

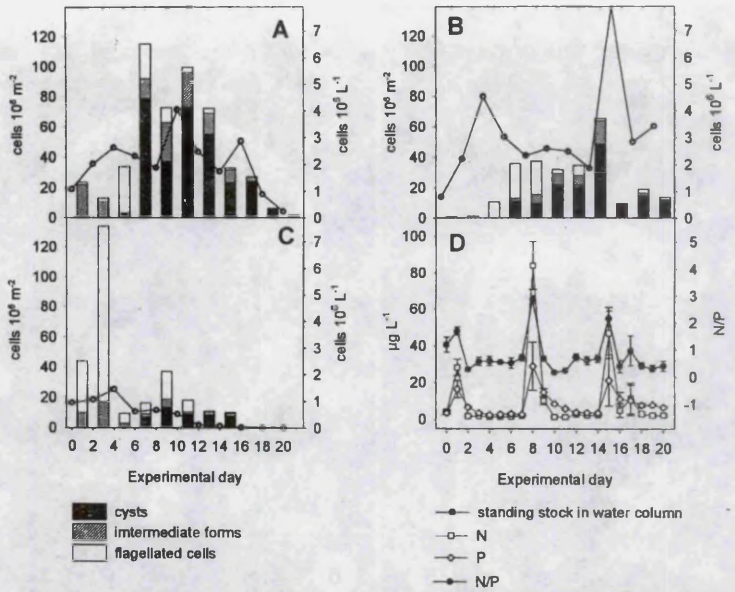


FIG. 9 A) and B). The abundance of cells, intermediate forms, and mature cysts in the bottom water of the enclosures (bars) and mean concentration of flagellated cells in the water column (points). A) Enclosure 2, with mineral nutrient addition; B) enclosure 6, with mineral nutrient and fish addition; C) enclosure 1, control (no manipulations); D) mineral nutrient concentrations and nutrient ratios in the upper water column (mean values of nutrient manipulated enclosures; N = nitrate + ammonium; P = phosphate). Error bars = ±SD between the enclosures; n = 5.

mylon grains, indicating that the reserve product had passed through the guts mostly intact, and supports the idea that *Eutreptiella gymnastica* was grazed by the mesozooplankton.

Encystment of *Eutreptiella gymnastica* may take place on the sediment surface, supported by the high numbers of intermediate rounded cells found there, while none were found from the water column. Alternatively, the first phase of encystment could take place in the water column followed by rapid sedimentation due to absence of flagella and excess density caused by carbohydrate ballast. Accumulation of polysaccharides is known to increase the density of phytoplankton cells (Klemer 1991, Oliver 1994, Romans and Carpenter 1994). Encystment in the water column is typical for the vernal bloom dinoflagellates from the area (Heiskanen 1993).

However, the actual triggering factor of the encystment remains obscure, because cyst formation occurred in both the nutrient-enriched and nonenriched enclosures. The added nutrients were depleted from the upper water column within 2 days (Fig. 9D). The subsequent downward migration (Fig. 10A) and decreased cell density of *Eutreptiella gymnastica* suggested that cells in the surface layer might have become nutrient-limited. Triemer (1980) reported that mineral nutrient limitation led to encystment of a heterotrophically grown *Euglena gracilis* culture. Encystment may have been triggered in the upper water column by nutrient depletion. The process of encystment could probably take a couple of days, as significant numbers of mature cysts did not appear before the beginning of the second week of the experiment in the bottom water of the enclosures (Fig. 9A–C). According to Triemer (1980), cells of *E. gracilis* encysted within 48–72 h after nutrient depletion under laboratory conditions. Cyst formation within a 2–3-day delay relative to the triggering factor could mask any clear response of encystment to measured environmental parameters in our experiment. The mineral nutrient ratios in the enclosures were below the Redfield ratio, and also the added nutrient ratio was relatively low (1:4, as typical of the water masses below the seasonal thermocline in the area). As nitrogen was always depleted more quickly than phosphorus, it seems likely that *E. gymnastica* might have been potentially nitrogen-limited. A low N:P ratio was typical of the whole experimental period and of all the enclosures (with slight increases just after the nutrient additions). Thus, it is possible that the low nutrient ratio, rather than nitrogen limitation, was responsible for triggering the encystment.

Nevertheless, the quantitative role of *Eutreptiella*

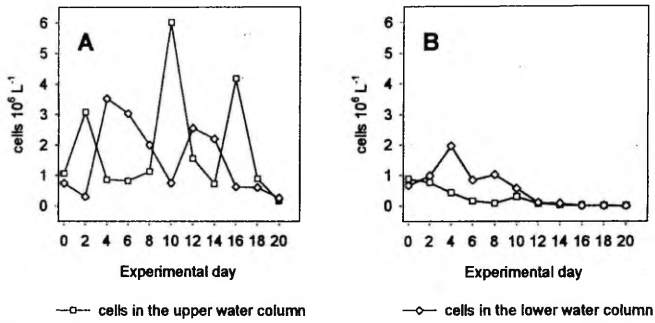


FIG. 10. The abundance of flagellated cells in the upper and lower water columns of enclosures A) 1 and B) 2. Manipulations as in Figure 9.

gymnastica cyst formation was negligible because the numbers of settled cysts never exceeded 0.5% of the cell numbers in the water column. However, accumulation of reserve product into the cells suggests that the cysts could survive prolonged dormancy and have food reserves sufficient for the germination of new vegetative cells. Thus, even a small fraction of the population could survive over adverse periods of time.

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III

Heiskanen, A.-S. & Olli, K. 1996. Sedimentation and buoyancy control of *Aphanizomenon flos-aquae* (Nostocales, Cyanophyta) in nutrient replete and nutrient deplete coastal area of the Baltic Sea. *Phycologia*. 35 (6 Supplement): 94–101.

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Sedimentation and buoyancy of *Aphanizomenon* cf. *flos-aquae* (Nostocales, Cyanophyta) in a nutrient-replete and nutrient-depleted coastal area of the Baltic Sea

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ANNA-STIINA HEISKANEN AND KALLE OLLI. 1996. Sedimentation and buoyancy of *Aphanizomenon* cf. *flos-aquae* (Nostocales, Cyanophyta) in a nutrient-replete and nutrient-depleted coastal area of the Baltic Sea. *Phycologia* **35** (Supplement): 94–101.

Daily variation of *Aphanizomenon* cf. *flos-aquae* Ralfs *ex* Bornet *et* Flahaut (Nostocales, Cyanophyta) biomass and sedimentation was studied in the southern Gulf of Riga (GoR) and in the coastal area of the Gulf of Finland (GoF), Baltic Sea, during July and August 1994. In the GoR, variation in the vertical distribution of *Aphanizomenon* biomass was investigated during two diurnal cycles. In both regions, net phytoplankton biomass was dominated by *Aphanizomenon*, although no massive surface blooms were observed. Nutrient-replete conditions in the GoR resulted from deep mixing as well as remineralization in midwater. The subsequent increase in nutrients in the euphotic zone (mainly ammonium) and decrease of the mixed layer depth was favourable for *Aphanizomenon*, which was able to maintain positive buoyancy in the upper water column and increase its biomass. The biomass and sedimentation rates of *Aphanizomenon* were *c.* four times higher in the GoR than in the GoF. However, the daily loss rates related to the surface layer biomass were much lower in the GoR (1–12% d^{-1}) than in the GoF (10–40% d^{-1}). In the GoF, nutrient concentrations were lower and the high light intensities reached deeper than in the GoR. Moreover, the supply of deep water nutrients (mainly nitrogen) was restricted due to the shallow stratified surface layer in the GoF. This indicated that in nitrogen-deficient and high irradiance conditions *Aphanizomenon* could not maintain positive buoyancy and a considerable part of the population was lost by sinking. Vertical flux of *Aphanizomenon* bundles was partly mediated by physical entanglement and transport with other detrital aggregates. It is suggested that the surface accumulation and bloom formation of *Aphanizomenon* in the GoF was mainly restricted by the supply of deep water nitrogen.

INTRODUCTION

During summer, cyanobacterial blooms occur regularly in the Baltic Sea. At times they cover huge areas (Kahru *et al.* 1994) and form conspicuous surface blooms that may be toxic (Sivonen *et al.* 1989). The fate of the blooms has been a matter of speculation, because it is unknown whether the cyanobacterial biomass is grazed by zooplankton, lost by sedimentation or decomposed by microbial action in the surface layer (Sellner 1992).

Cyanobacteria are able to control their buoyancy by varying their gas vacuole or carbohydrate content. The physiological and structural mechanisms and environmental constraints controlling buoyancy have been studied intensively during the last decades and are described in several reviews (Walsby & Reynolds 1980; Klemer 1985; Reynolds *et al.* 1987; Walsby 1987; Humphries & Lyne 1988; Klemer 1991; Oliver 1994). Due to their ability to control their position in the water column, sedimentation losses of cyanobacteria have been generally considered to be negligible (Reynolds & Walsby 1975). Indeed, the average sinking losses from the summer-time phytoplankton in the Baltic Sea, mainly dominated by cyanobacteria, have appeared to be small (Heiskanen & Kononen 1994). However, due to the highly episodic and patchy occurrence of cyanobacteria, it is often difficult to obtain sufficiently high frequency measurements combined with adequate hydrographical observations to assess the fate of the blooms.

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The present study aims to estimate the short-term loss rates of the common chain-forming cyanobacteria species, *Aphanizomenon* cf. *flos-aquae* Ralfs *ex* Bornet *et* Flahaut, based on intensive daily sampling in two coastal areas representing different trophic environments by using combined water column and sediment trap sampling during late summer 1994.

MATERIAL AND METHODS

The Gulf of Riga (GoR; Fig. 1A) is a semi-enclosed shallow coastal area (maximum depth 62 m), connected to the Baltic proper by shallow straits. Salinity varies between 4 and 7 practical salinity units (PSU). The Gulf of Riga is one of the most eutrophic areas of the Baltic, receiving substantial fresh water and untreated waste water and nutrient supply from its drainage area. A general description of its hydrography and nutrient balance of the Gulf of Riga is presented by Yurkovskis *et al.* (1994).

The second study area, at the entrance to the Gulf of Finland (GoF; Fig. 1B), is directly connected to the open Baltic and to the eastern part of the GoF without any sills or thresholds. It is influenced by several water masses including surface water from the eastern GoF (salinity between 5 and 6 PSU) and the Baltic winter water, frequently upwelling from the deeper areas of the GoF (salinity between 7 and 8 PSU). For a detailed description of the study area, see Niemi (1975), Haapala (1994), and Heiskanen & Kononen (1994).

Hydrography, nutrients, suspended biomass and sedimen-

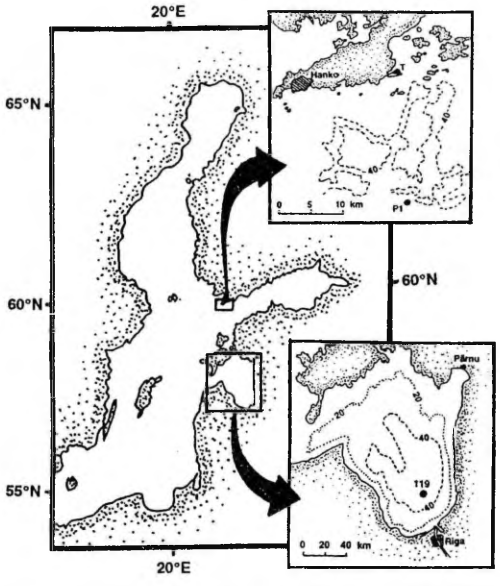

Fig. 1. Map of the two study areas in the Baltic Sea. A. Gulf of Riga. The schematic isobaths of 20 and 40 m are shown with stippled and broken lines, respectively. 119, sampling station. B. Coastal area at the entrance to the Gulf of Finland. The schematic isobath of 40 m is shown with a broken line. P1, sampling station; T, Tvärminne Zoological Station.

tation of algae were studied in the GoR 26 June to 7 July 1994 on board the R/V *Marina*. Sampling station 119 (total depth 42 m), located in the southern part of the GoR (Fig. 1A), was visited five times. During each visit, sediment traps were deployed at 10, 15, 20 and 35 m depth for 21–23 h. Water samples were taken and CTD casts were made at the start and end of each sediment trap collection period. Five-liter water samples for algal counts were taken at the start of each visit (five times) according to the stratification revealed by CTD and mixed to a pooled sample, which represented the integrated mixed-layer sample. The samples were preserved with Lugol's acid solution. Discrete water column samples were taken at the start and end of each visit to station 119 (10 times) from fixed depths (0, 2.5, 5, 10, 15, 20, 30 and 40 m) for determination of dissolved inorganic nutrients. Vertical distribution of *Aphanizomenon* was studied during two diurnal cycles: 26–27 June and 6–7 July. Water samples were taken with a Ruttner water sampler at 3-m intervals from the surface to 30 m depth every 4 h and immediately fixed with Lugol.

In the GoF, sampling station P1 (Fig. 1B; total depth 60 m) was visited daily between 8 and 10 from the land-based laboratory (Tvärminne Zoological Station, University of Helsinki) 2–9 August. CTD profiles were made, and discrete and pooled water column samples were taken (down to 50 m depth) as in the GoR. The downwelling irradiance photosynthetically active radiation was measured with a submersible quanta meter (Li-Cor). Two replicate series of sediment trap arrays were emptied and reinstalled daily at 10, 20, 30 and 40 m.

The sediment traps were cylindrical with an inner diameter of 52 mm and total height of 330 mm. There were two replicate cylinders at each depth. In the GoF, two sediment trap arrays were deployed, and the contents of three replicate cylinders were combined. The fourth sediment trap cylinder had a Petri dish at the bottom, containing a highly viscous fluid made of polymers of acrylic amide, in which setting aggregates remained intact (Lundsgaard 1995). The sample volumes were adjusted to a total volume of 1 l with filtered sea water (Whatman GF/F). Subsamples for phytoplankton counts were taken from a homogeneous suspension and preserved with Lugol.

Dissolved inorganic phosphate was determined in duplicate by the molybdate method and analyzed manually with a spectrophotometer according to Grasshoff *et al.* (1983). The lowest detection limit of the phosphate analysis was 0.01 μM PO_4-P, and the mean difference between the two replicates was 0.01 μM. Ammonium was determined in duplicate by the indophenol blue method and analyzed manually with a spectrophotometer according to Grasshoff *et al.* (1983). The detection limit of the ammonium analysis was 0.05 μM NH_4-N, and the mean difference between two replicates was 0.03 μM. Nitrate was first reduced in a copperized cadmium reductor to nitrite (NO_2), and the sum of nitrate and nitrite concentrations was then analyzed in a spectrophotometer as azo dye formation (Grasshoff *et al.* 1983). The detection limit of the nitrate analysis was 0.02 μM NO_3-N, and the mean difference between the two replicates was 0.01 μM for concentrations below 2 μM NO_3-N.

Phytoplankton counts were made from single samples using an inverted microscope fitted with phase-contrast optics. A minimum of 100 filaments was measured and enumerated by counting at least two transects or 20 equally distributed fields from each sample. The species-specific 95% confidence limits of the counts (as a percentage of the units counted; CL%) were calculated as

$$CL\% = 200/\sqrt{n} \quad (1)$$

where n is the number of counting units enumerated per sample (Lund *et al.* 1958).

Counts were converted to biomass (mg m^{-3}) and presented as wet weight (ww) by calculating the algal volumes according to Sicko-Goad *et al.* (1977) and Edler (1979) and assuming a density of 1 g cm^{-3} for algal cells. For *Aphanizomenon*, a mean volume of 1600 μm^3 was used for a filament length of 100 μm. The samples were counted 1 month after fixation, which we have observed to be sufficient time for total disintegration of *Aphanizomenon* bundles to single filaments.

The error caused by the potential positive buoyancy of *Aphanizomenon* was estimated to be minor. It was observed that 3–11% (n = 8) of the total biomass remained buoyant in the upper part of the settling column during a routine sedimentation procedure of Lugol-fixed samples from the Baltic (V. Gran, personal communication). In our material, only *c.* 5% of the *Aphanizomenon* filaments remained buoyant beneath the coverslip when a Lugol-fixed sample was dispensed directly to the Utermöhl chamber. Compared to the estimated counting error of 10–20%, the error due to positive buoyancy was small and therefore neglected.

Sedimentation rates (S; mg m^{-2} d^{-1}) of *Aphanizomenon* biomass were calculated according to the following equation:

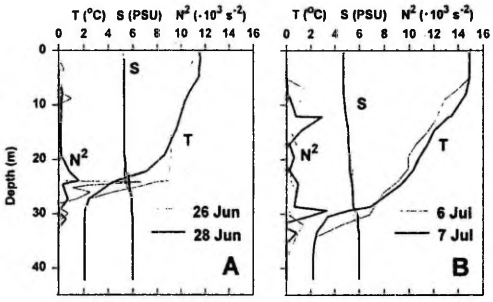

Fig. 2. Gulf of Riga. Temperature (T), salinity (S; PSU), and stratification (square of the Brunt-Väisälä frequency: N^2) at the beginning of the study period (A) (26 and 28 June 1994) and at the end of the study period (B) (6 and 7 July 1994).

$$S = c \cdot V/A \cdot t \quad (2)$$

where c is biomass (ww; mg ml^{-1}), V the total volume (ml) of the sediment trap sample, A the collection area of the sediment traps (m^2), and t the collection time (d). The sinking loss rates (L, % d^{-1}) were calculated as

$$L = 100 \cdot S/C \quad (3)$$

where C is biomass (mg m^{-2}) integrated for the surface layer of 0–10 m.

In the GoF, the Petri dishes containing viscous acrylic amide fluid were carefully lifted from the sediment trap cylinders and photographed using a stereomicroscope (Wild M8) combined with an automated camera system (Wild MPS 45/51). The number of *Aphanizomenon* bundles in each Petri dish were counted from the photographs (magnification 1 : 10), and the fraction of bundles attached to detrital aggregates was enumerated. The 95% confidence limits (as a percentage of the counts) were calculated as in eq. (1).

The vertical density differences and the degree of stratification in the water column were described by the buoyancy term (square of the Brunt-Väisälä frequency: N^2; s^{-2}), calculated over 0.5-m depth intervals for the whole water column (e.g. Harris 1986, p. 45):

$$N^2 = (g/p) \cdot (d\rho/dz) \quad (4)$$

where g is the acceleration due to gravity (9.81 m s^{-2}) and p is the density at depth z.

RESULTS

Hydrography and nutrients

At the beginning of the study period in the GoR, the surface layer was relatively homogeneous due to strong winds prior to our arrival. The thermocline was situated between 20 and 25 m, and the surface layer temperature was 9–11°C (Fig. 2A). The depth of the euphotic layer decreased from 5.5 to 4.0 m during the experiment (M. Olesen, personal communication). At the end of the study period, the surface water had warmed to 15°C, and a secondary thermocline had formed

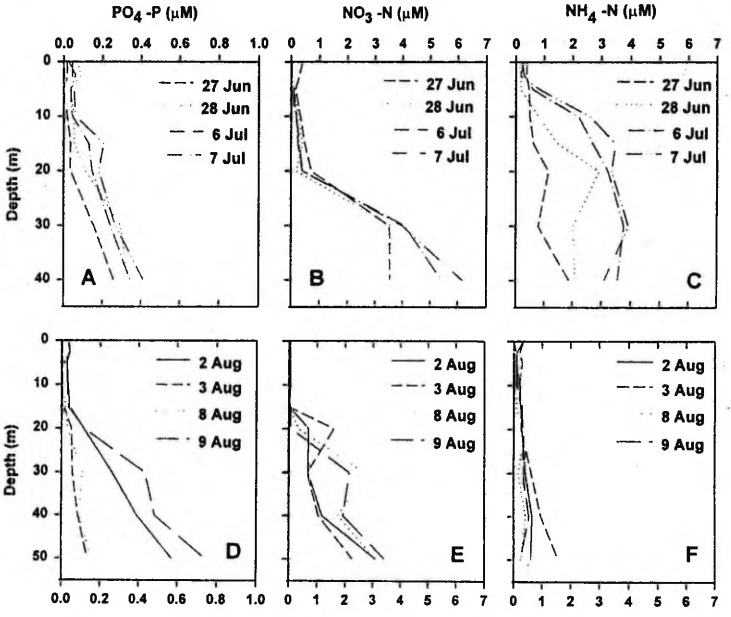

Fig. 3. Vertical distributions of phosphate (PO_4-P), nitrate (NO_3-N) and ammonium (NH_4-N) concentrations (A–C) in the Gulf of Riga and (D–F) in the Gulf of Finland.

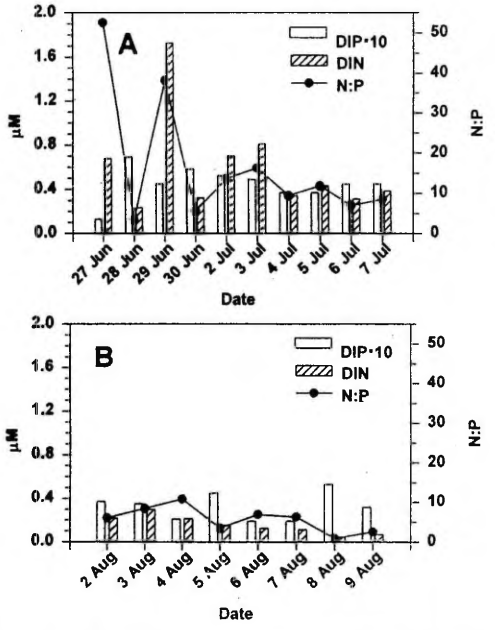

Fig. 4. Daily fluctuations in concentrations of dissolved inorganic phosphorus (DIP × 10) and nitrogen (DIN = NO_3 + NO_2 + NH_4) (columns) and the molar N:P ratio (lines) in the surface layer of 0–5 m (A) in the Gulf of Riga and (B) in the Gulf of Finland.

between 5 and 15 m, while the primary thermocline had descended to 30 m depth (Fig. 2B). The mixed layer depth (depth of the maximum N^2) ascended from 30 to 7 m during the study period (Fig. 2). The value of the maximum Brunt-Väisälä buoyancy (N^2) varied between 0.002 and 0.010 s^{-2}.

Phosphate [dissolved inorganic phosphate (DIP)] concentrations were low to a 20-m depth (< 0.1 µM PO_4-P) at the start of study period but increased slightly at a 15-m depth (up to 0.2 µM PO_4-P) after formation of the secondary thermocline (Fig. 3A). The nitrate concentrations were also low in the mixed surface layer (< 0.5 µM NO_3-N; Fig 3B), while ammonium was abundant, especially at the thermocline (Fig. 3C). At the end of the study period, > 3 µM NH_4-N at 15 m depth indicates effective mineralization below the secondary thermocline. The molar DIN:DIP ratio (DIN = NO_3 + NO_2 + NH_4) was 3.4–52.6 in the surface layer and followed the fluctuations of DIN (values integrated for the upper 5 m; Fig. 4A), while it was more stable in deeper water (range 20.5–31.2, mean 27.0). During the first 4 days of the study, the DIN concentrations increased *c.* 1.5 µM in the surface layer and decreased thereafter. Also, the increase (+ 0.056 µM) and decrease (−0.024 µM) of DIP was significant during the first 3 d (Fig. 4A). Thereafter, only the fluctuations of DIN were significant and the DIN:DIP ratio was more stable, varying between 5.9. and 16.4.

In the GoF, the surface water temperature was high (> 20°C), and the water column was homogeneous to 10 m depth at the start of the study (Fig. 5A). There was a secondary thermocline between 10 and 16 m and a primary thermocline between 20 and 25 m (Fig. 5A). By the end of study the depth of the mixed surface layer had decreased and the salinity of the surface water had increased (Fig. 5A, B). The euphotic surface layer varied between 12.5 and 13.5 m, and the high photon fluxes > 50 µmol m^{-2} s^{-1} reached to *c.* 7–8 m depth (Fig. 5A). The depth of the maximum N^2 varied between 10 and 6 m, rising towards the surface at the end of the study period (Fig. 5C). The values of N^2 were similar to those in the GoR (Fig. 3).

Nutrient concentrations were low down to 15 m (Fig. 3D–F). Phosphate concentrations were generally < 0.05 µM PO_4-P in the surface layer but increased strongly in deeper water (Fig. 3D). Nitrate concentrations were generally below the detection limit (< 0.07 µM NO_3-N) in the surface layer but increased to 1.6 µM below the thermocline (at a 20-m depth) on 3 August (Fig. 3E). In contrast to the GoR, ammonium concentrations were low throughout the upper water column but slightly elevated below 30 m (Fig. 3F). The DIN:DIP ratio was relatively stable, varying between 0.9 and 10.7 (mean 5.7) at the surface 0–5 m (Fig. 4B) and between 4.2

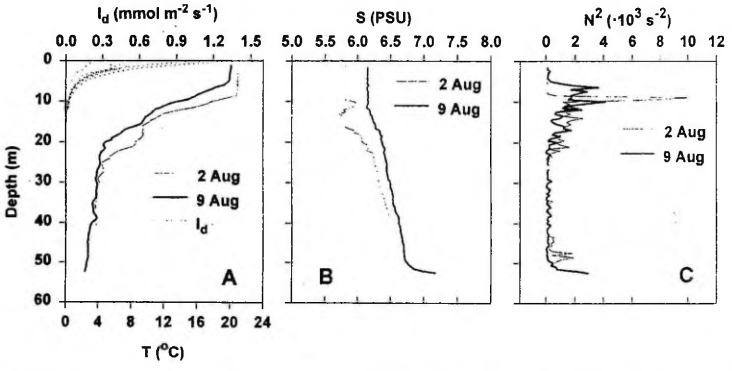

Fig. 5. Gulf of Finland. A. Downwelling irradiance (I_0) and water column temperature (T). B. Salinity (S). C. Stratification (square of the Brunt-Väisälä frequency: N^2) at 2–9 August 1994.

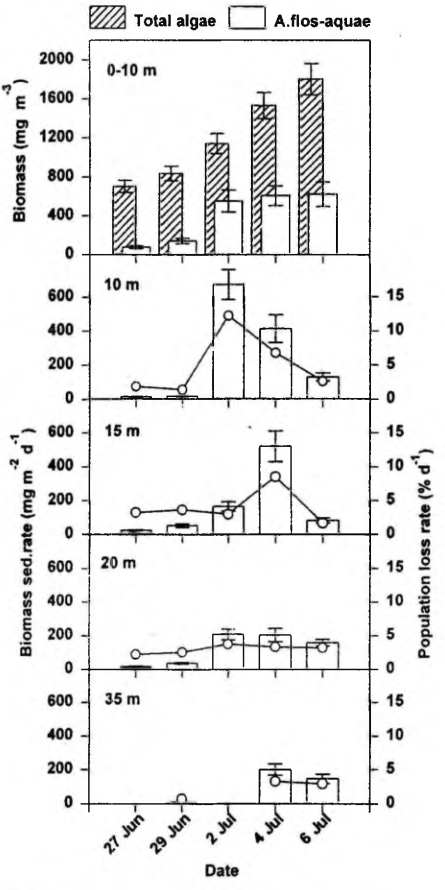

Fig. 6. Gulf of Riga. Biomass concentration (ww) of *Aphanizomenon* and total phytoplankton (excluding picoplankton) in the upper water column (0–10 m) and sedimentation rates of *Aphanizomenon* at 10, 15, 20 and 35 m depths. Daily population loss rates (lines) are calculated as percentage of the suspended biomass in the surface layer. Vertical bars represent the calculated 95% CLs of the counts.

and 8.3 (mean 5.9) below the surface. The daily variations of DIN were generally small, while the fluctuations of DIP were higher than ± 0.01 μM in five times out of seven (Fig. 4B).

Phytoplankton biomass and sedimentation

In the GoR, the total algal biomass (excluding picoplankton) above 10 m increased from 600 to 1800 mg m^{-3} (ww) during the study period (Fig. 6). *Aphanizomenon* was the most dominant species, contributing up to 50% of the total micro- and nanophytoplankton biomass, with a maximum biomass of *c.* 500 mg m^{-3}. Sedimentation rates of *Aphanizomenon* varied from *c.* 650 mg m^{-2} d^{-1} at 10 m to almost zero at 35 m (Fig. 6). The daily loss by sedimentation was generally < 4%, being slightly elevated at 10 and 15 m in early July (7–12% d^{-1}; Fig. 6).

In the GoF, the total algal biomass (excluding picoplankton) varied between 200 and 450 mg m^{-3} (Fig. 7). The biomass of *Aphanizomenon* was 30–100 mg m^{-3} and contributed up to 40% to the total micro- and nanoalgal biomass in the surface layer. Sedimentation rates of *Aphanizomenon* were highest at a 10-m depth, varying between 150 and 300 mg m^{-2} d^{-1} (Fig. 7). In the lower part of the water column, sedimentation rates of *Aphanizomenon* were generally < 150 mg m^{-2} d^{-1}. The daily loss rates were high, between 20 and 45% of the surface layer biomass at 10 m, between 7 and 20% at 20 m, and between 3 and 25% at 30 m (Fig. 7).

Vertical distribution of *Aphanizomenon* in the GoR

During the first diurnal cycle of the study (26–27 June), the biomass peak of *Aphanizomenon* varied between 0 and 12 m (Fig. 8). In the evening, at 20:00 hours, 45% of the total integrated biomass was in the surface layer between 0 and 3 m and *c.* 32% between 9 and 15 m. At midnight the *Aphanizomenon* population had two peaks: 24% of the biomass was in the surface layer and 67% between 9 and 15 m. At 8:00 hours, 90% of the biomass had accumulated above 9 m (Fig. 8). The total integrated biomass in the water column was relatively constant during the first five sampling occasions, indicating that horizontal transport was negligible. However, between 8:00 and 12:00 hours, the total integrated *Aphanizomenon* biomass decreased significantly (Fig. 8), suggesting that advective transport occurred.

During the second diurnal cycle (6–7 July), most of the *Aphanizomenon* population was constantly above 9 m depth (Fig. 9). The peak of the biomass varied between 0 and 6 m, being at the surface in the morning (8:00) and at midnight (24:00), and at 6 m depth in the afternoon (16:00) (Fig. 9). The fluctuations of the total integrated biomass were significant in the afternoon (between 12:00 and 16:00) and in the morning between 4:00 and 8:00 (Fig. 9). Nevertheless, the vertical distribution remained relatively constant, although the population may have been advected horizontally. This suggested spatial homogeneity in the vertical distribution of *Aphanizomenon*, although there may have been patchiness in the total biomass concentrations.

Sedimentation of *Aphanizomenon* bundles in the GoF

In the GoF, the total number of settled *Aphanizomenon* bundles was 0.5–16.6 cm^{-2} d^{-1} between 3 and 8 August (Fig. 10). There was no significant difference among the four depths (Kruskal-Wallis one-way ANOVA, $p = 0.93$); neither were daily differences significant. The fraction of bundles attached to aggregates was generally higher in traps deeper than 10 m (Fig. 10), the mean percentages 51, 69, 77 and 85% at 10, 20, 30 and 40 m depths. There was a positive correlation between the fraction of bundles entangled with aggregates (%) and depth ($r = 0.59$, $p = 0.006$), which suggested that bundles may have settled together with detrital aggregates into the deeper sediment traps.

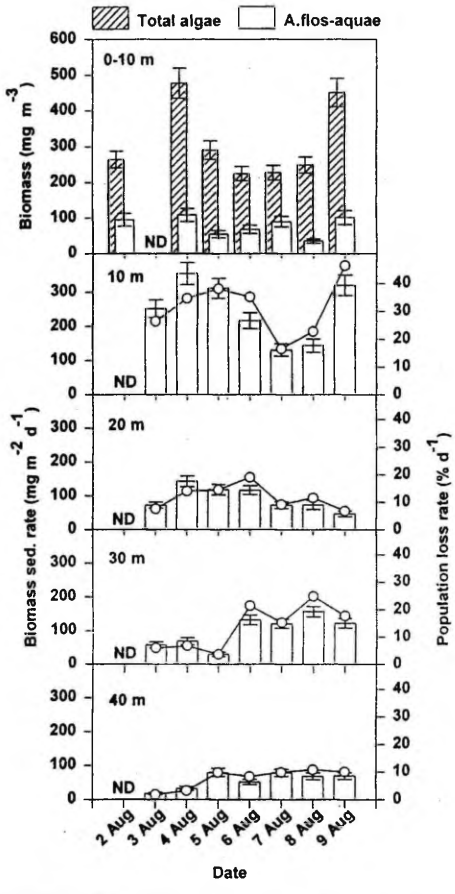

Fig. 7. Gulf of Finland. Biomass concentration of *Aphanizomenon* and total algae as in Fig. 6, and sedimentation rates of *Aphanizomenon* at 10, 20, 30 and 40 m depths. Daily population loss rates (lines) and vertical bars as in Fig. 6. ND, no data.

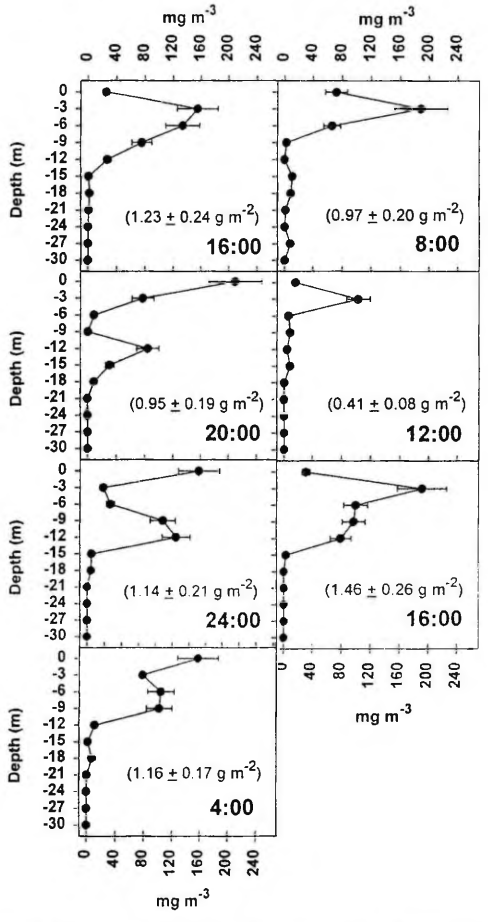

Fig. 8. Gulf of Riga. Diurnal vertical distribution of *Aphanizomenon* biomass sampled at 4-h intervals from 16:00 on 26 June 1994. Error bars represent the 95% CLs of the counts. The numbers in parentheses are total biomass of *Aphanizomenon* integrated for the whole water column ± the 95% CLs at each sampling time.

DISCUSSION

There was a clear difference in biomass and sinking loss of *Aphanizomenon* between the two investigation sites. In the GoR, a major part of the *Aphanizomenon* population was able to remain buoyant and to control its vertical position in the surface layer. This was independent of mixing depth, which was relatively deep and reached well below the euphotic layer. The deep mixing as well as effective remineralization in mid-water resulted in nutrient-replete conditions in the GoR. The initial deep water nutrient supply invoked biomass increase and promoted the buoyancy control of *Aphanizomenon*.

At the beginning of the study, *Aphanizomenon* began moving downwards during midday when high irradiances prevailed. High light intensities have been shown to decrease the buoyancy by increasing the photosynthetate accumulation and resulting in increased turgor pressure and subsequent collapse of gas vacuoles (Grant & Walsby 1977) regardless of the availability of nutrients or inorganic carbon (Spencer & King 1989). The maximum midday surface irradiance was 1600–1800 μmol m^{-2} s^{-1} during the study period (M. Olesen, personal communication), which indicated that a photon flux higher than 50 μmol m^{-2} s^{-1} reached down to *c.* 4 m at the start when the euphotic layer was *c.* 5.5 m deep. Accumulation of carbohydrates has been shown to increase the density of *Aphanizomenon* and result in buoyancy loss if cells are exposed to photon fluxes rates > 50 μmol m^{-2} s^{-1} for more than 2 h (Kromkamp *et al.* 1986).

After residing in the deeper strata of low irradiance and high nutrient concentrations, *Aphanizomenon* regained positive buoy-

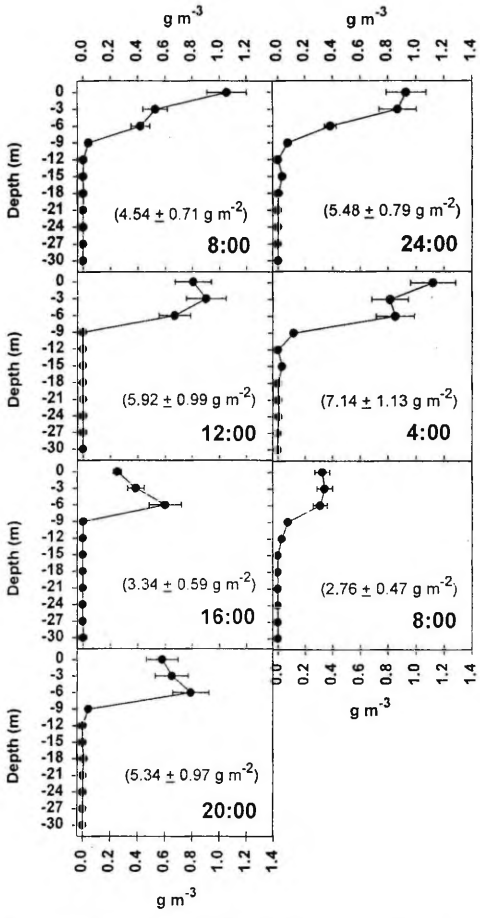

Fig. 9. Gulf of Riga. Diurnal vertical distribution of *Aphanizomenon* biomass sampled at 4-h intervals from 8:00 on 6 July. Error bars and the values in parentheses as in Fig. 8.

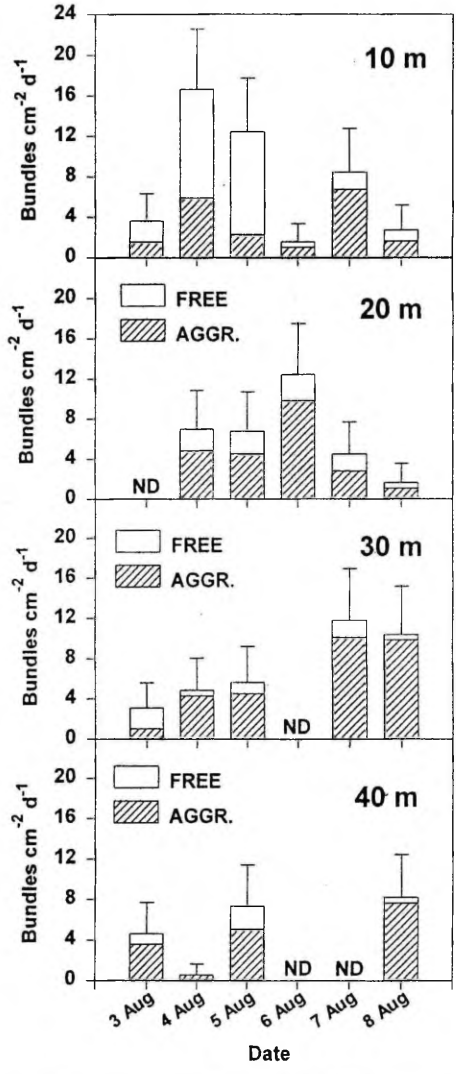

Fig. 10. Gulf of Finland. Sedimentation rates of free *Aphanizomenon* bundles and bundles attached to detrital aggregates at 10, 20, 30 and 40 m depths. Vertical bars show the upper 95% CLs of the total numbers of bundles settled. ND, no data.

ancy and started to ascend towards the surface during the early morning hours (Fig. 8). Availability of nutrients (especially nitrogen) promotes synthesis of gas vacuoles and increases the consumption of polysaccharides, leading to reduction of the carbohydrate ballast (e.g. Oliver 1994). The vertical range of *Aphanizomenon* decreased along with shallowing of the euphotic surface layer and mixed layer depth (Figs 2, 9) and with the increase of nutrients in the upper part of the water column at the end of the study period (Fig. 3). The vertical movements of *Aphanizomenon* were therefore probably controlled by decreasing penetration of light and by increasing availability of nitrogen in the surface layer, which both promoted buoyancy and resulted in surface accumulation and subsequent low daily sinking loss rates of *Aphanizomenon*.

In the GoF, DIN concentrations and the DIN:DIP ratio were low throughout the water column. There was little fluctuation in nutrient concentrations in the surface layer suggesting that the supply of nutrients from below the mixed surface layer was small. Moreover, the euphotic layer was deeper than the mixed surface layer depth (Fig. 5) and high midday light intensities (> 50 μmol m^{-2} s^{-1}) reached deeper in the GoF than in the GoR. In such a nitrogen-deficient and high irradiance environment, sinking losses of *Aphanizome-*

non were high, indicating that the population was mostly negatively buoyant, preventing biomass increase. Deprivation of nitrogen decreases the cell buoyancy by preventing synthesis of the protein-rich gas vacuoles (Klemer *et al.* 1982). In addition, photosynthetically fixed carbohydrates are not used in protein synthesis and polysaccharides accumulate, thus increasing the density of cells and resulting in buoyancy loss (Spencer & King 1989; Klemer 1991). Combined with aggregation to other detrital material, this promoted rapid transport to greater depths. However, the high loss rates do not necessarily imply that the population is permanently lost from the surface layer. The ability of the gas vesicles to withstand the pressure down to the depth of the permanent halocline of the Baltic (60–90 m) and regain positive buoyancy with an average floating velocity of 22 m d^{-1} (Walsby *et al.* 1995) allow the cells to rapidly ascend to the surface layer. The results of this study implicate that, although *Aphanizomenon* is capable of fixing molecular nitrogen, successful buoyancy control, growth and establishment of a bloom depend on the supply of deep water nutrients, particularly nitrogen.

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IV

Olli, K., Heiskanen, A.-S., Lohikari, K. 1997. Vertical migration of autotrophic micro-organisms during a vernal bloom at the coastal Baltic Sea — coexistence through niche separation. *Hydrobiologia*. Submitted.

VERTICAL MIGRATION OF AUTOTROPHIC MICRO-ORGANISMS DURING A VERNAL BLOOM AT THE COASTAL BALTIC SEA — COEXISTENCE THROUGH NICHE SEPARATION

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Key words: Baltic Sea, *Mesodinium rubrum*, *Peridiniella catenata*, *Scrippsiella hangoei*, spring bloom, vertical migration

Abstract

Vertical migration of two dinoflagellate species (*Peridiniella catenata* and *Scrippsiella hangoei*) and a phototrophic ciliate (*Mesodinium rubrum*) were studied during the peak and decline of a vernal bloom at the SW coast of Finland. During the diel cycle part of the populations of *P. catenata* and *M. rubrum* were observed in the deeper layers with elevated nutrient concentrations, while *S. hangoei* remained in the upper nutrient depleted mixed layer. Using a correspondence analysis the vertical distribution patterns of the species and chlorophyll *a* were examined over a temporal scale of hours and weeks. The vertical migration was reflected in much higher variability in the depth distribution of *P. catenata* and *M. rubrum* over a diel scale, compared to *S. hangoei*. The analysis revealed also significant differences in species specific depth distribution patterns over both time scales. It is discussed that the co-existence of the two dominant dinoflagellate species during the vernal bloom is due to niche separation through behavioural adaptations.

Introduction

In coastal temperate areas stratification of the water column during spring is commonly accompanied by outburst of phytoplankton development and consequent nutrient depletion from the illuminated layer. This results in an unfavourable situation for the primary producers where light and nutrients are spatially separated, and together with decaying turbulence is commonly considered to trigger the mass sedimentation of vernal bloom diatoms (Heiskanen & Kononen, 1994; Olesen, 1993; Waite *et al.*, 1992a, 1992b). Several autotrophic micro-organisms are capable of sustained directed swimming, covering a considerable vertical distance during a diel cycle (Kamykowski, 1995; Throndsen, 1973). A common consensus on the competitional advantage of the diel vertical migration (DVM) is that during the day time it enables the micro-organisms to exploit high light levels near the surface where low concentrations of inorganic nutrients would normally limit growth; during night the cells descend to deeper layers where nutrient demands are fulfilled (Cullen, 1985; Eppley *et al.*, 1968; Lieberman & Shilo, 1994). Thus it results in optimised specific growth rate of the cells within the constraints of the ecological limits and can influence the production rates, both seasonally and annually (Heaney & Butterwick, 1985).

The pattern of vertical migration is a result of the physiological and behavioural adaptations of the micro-organisms interacting with a complex of environmental factors. A physiological prerequisite to the nutritional advantage of DVM seems to be the ability of

dark nutrient assimilation (Cullen & Horrigan, 1981; Heaney & Eppley, 1981; Olsson & Granéli, 1991), which is an energy demanding process (Cullen, 1985). The triggers for directed swimming could be phototaxis or gravitaxis interacting with the inner rhythm of the cells (Cullen & Horrigan, 1981; Eppley *et al.*, 1968) and modified by the physical environment (Kamykowski & McCollum, 1986). However, when a certain threshold or dose of photons have been absorbed, the upward migration ceases at optimal optical depth (Blasco, 1978; Passow, 1991), which is also dependent on the nutritional status of the cells (Anderson & Stolzenbach, 1985; Cullen & Horrigan, 1981; Heaney & Eppley, 1981). Distinct depth maxima have been noted in many species of marine autotrophic micro-organisms (Lindholm, 1995; Lindholm & Mörk, 1990; Owen *et al.*, 1992; Viner, 1985). In these cases the cells evidently take advantage of the elevated nutrient levels, but to sustain viable populations for longer periods have to return to the upper layers later. Another type of advantages is to reduce loss rates, either through sinking, predation or physical transport to regions unfavourable for growth (Cullen, 1985). Zooplankton is known to perform diel vertical migration and spend the light time in the deep layers to reduce grazing by visual feeding fish (Iwasa, 1982). Resistance to predation is clearly an adaptive advantage to enhance persistence of population (Fielder 1982). Nutrient starvation has been shown to suppress the vertical migration of dinoflagellates in tank experiments (Eppley *et al.*, 1968). Numerous studies have dealt with the effects of temperature (Kamykowski & McCollum, 1986) the steepness of thermocline (Kamykowski, 1981; Kamykowski & Zentara, 1976), halocline (Olsson & Granéli, 1991; Rasmussen & Richardson, 1989; Tyler & Seliger, 1981) and turbulent mixing of the water column (Blasco, 1978) on the vertical migration of micro-organisms. In estuarine and tidal environments migratory behaviour enables the cells to be carried with subsurface currents to annual bloom areas (Tyler & Seliger, 1978, 1981) or avoid flushing losses from estuary (Crawford & Purdie, 1992). Small scale turbulence is proposed to have greater inhibitory effect of dinoflagellate motility compared to other algal classes (Kamykowski, 1995; Thomas & Gibson, 1990) and also *M. rubrum* has been shown to actively avoid turbulent water layers (Crawford & Purdie, 1992).

It is likely that the complex of environmental triggers determining the vertical distribution patterns in nature are much more complex than the scare experimental data can explain (Passow, 1991). Majority of the experiments with laboratory cultures have attempted to model the effect of single physical or chemical factors, and the interactions have remained largely uncovered (Heaney & Eppley, 1981), leading to difficulties in interpretation of field data.

In the present study we investigated the vertical profiles and migration of the vernal key species (*Peridiniella catenata* and *Scrippsiella hangoei*) and an autotrophic ciliate (*Mesodinium rubrum*) during two diel cycles of an annual spring bloom event in the SW coast of Finland, the northern Baltic Sea. These species were chosen on the basis of adequate abundance, previous knowledge of migratory behaviour (Heiskanen, 1995; Lindholm & Mörk, 1990; Passow, 1991) and the theoretical size considerations (Sommer, 1988). The focus is on the ability of the species to migrate down to nutrient rich layers during a vernal bloom when light and nutrient availability is vertically separated. The results indicate a considerable difference between the species to vary the vertical distribution as well as species specific vertical distribution patterns over the observed time scales.

Material and methods

The sampling was carried out at the Storgadden station, outer archipelago region, about 6 km off the SW coast of Finland (59° 47' N, 23° 20' E) near the entrance to the Gulf of Finland, the Baltic Sea. The salinity in the study area is generally 5–7 PSU. Salinity and temperature variability can be induced by upwellings, as well as by lateral surface water transport from the inner archipelago sea (Haapala, 1994; Niemi, 1975). The sampling site was approximately 50 m deep, relatively large basin surrounded by shallower areas and small rocky islets.

Two 24 hour sampling periods (first period: May 5–6 starting at 20.00; second period: May 27–28 starting at 8.00) were chosen, to coincide the peak and fall of the vernal phytoplankton bloom in 1994. During both sampling periods the station was visited seven times in 4 hour intervals. Upon arrival vertical profiles of temperature, salinity and density were measured (CTDplus 100). The under water light attenuation was measured with LiCor light meter. Once during both periods a mineral nutrient (NO_3-N, NH_4-N, PO_4-P) profile was taken at vertical intervals of 6 meters. Samples for CHL and mineral nutrients were taken to the shore in plastic bottles placed in a cool box. Nutrients were analysed immediately according to (Grasshoff *et al.*, 1983), CHL samples were filtered on Whatman (GF/F) glass-fibre filters, sonicated and extracted in 94% ethanol for 24 h in total darkness. CHL concentration of the extract was measured with a spectrofluorometer (Shimadzu RF 5001), which was calibrated with pure chlorophyll *a* (Sigma).

Phytoplankton and chlorophyll *a* (CHL) was sampled with a 7 L Limnos water sampler with 3 m vertical intervals, from surface to 36 m depth. Sub-samples (300 ml) for phytoplankton were fixed immediately with Lugol solution. The phytoplankton samples were counted with the inverted microscope technique (Lund *et al.*, 1958); at least 200 cells (or chains of *Peridiniella catenata*) were attempted to count depending on the density of the samples. Biomass was estimated from algorithms between cell volume and wet weight. To evaluate the variability caused by sampling and subsequent sub-sampling four replicate samples were taken from 6 m layer on two occasions during the second period, and four replicate sub-samples form one of the replicate samples.

Wind and radiation data were obtained from Längden stationary weather station, approximately 5 km SW from the sampling station. Current velocity was measured continuously by an Aanderaa RCM 4 current meter, moored at the depth of 20 m at the sampling station.

We analysed the depth profiles of the species and CHL by correspondence analysis (ADE-4 software; http://biomserv.univ-lyon1.fr). The data was arranged in a matrix with 13 columns (corresponding to the 13 discrete depths) and 28 rows consisting of 4 blocks (the three species and CHL), each consisting of 7 rows (corresponding to the sampling time). Correspondence analysis was used to project 7 profiles of each species and CHL with 13 depth variables to a few ordination axis which describe most of the variability in the data set. These projections preserve the original Euclidean distances and enables simultaneous visualisation of the differences of depth profiles on two dimensional space. The profiles were grouped according to species (4 groups) or sampling time (7 groups) and the statistical significance of the between-groups difference tested with a random permutation test.

Results

Weather

During both periods a clear and calm weather prevailed. The maximum midday light intensities at the surface were up to 1400 μE m^{-2} s^{-1}. The 1% light level, equal to approximately 10 μE m^{-2} s^{-1}, during midday was measured at the depths of 7 m and 12 m during the first and second period, respectively (Fig. 1). According to the Längden weather station the wind magnitude at the area varied between 2–9 m s^{-1}, blowing from N–NE and from N–NW during the first and second period, respectively. Due to the distance between the sampling site and the weather station, these measurements are likely to differ somewhat from the local wind at the sampling station, where on many occasions windless weather with no waves prevailed.

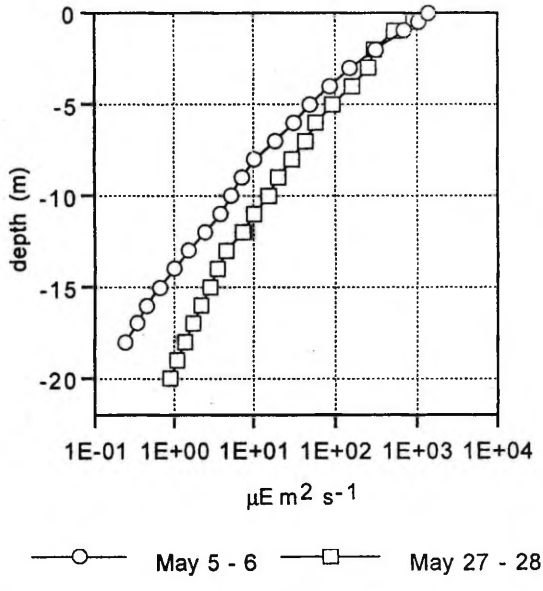

Figure 1. Under water light attenuation during the first (May 5–6) and second (May 27–28) period. Note the log scale of X-axis.

Hydrography

The surface water temperature on May 5–6 increased from 3,4 to 4,8°C during the 24 hours, creating a shallow thermocline and weak water column stability (Fig. 2A). The intermediate layer between 3 and 20 m had a temperature of 3°C, and layer below that 1°C. During May 27–28 a surface mixed layer down to 15 m with a temperature of 7,5°C had developed, below that the temperature decreased gradually to 1°C at 40–50 m depth (Fig. 2B). The halocline had descended from 18 m on May 5–6 to 22 m on May 27–28, which was also reflected in the Brunt-Väisälä buoyancy term (N^2) (Fig. 2A, B).

The current velocities at 20 m depth were low during the first period (0–2.5 m s^{-1}) and somewhat higher during the second period (1.5–5 cm s^{-1}). These can be considered as rela-

tively low values, since velocities as high as 35 cm s^{-1} were measured during the other periods of the spring bloom.

On May 5–6 the mineral nutrients had been utilized from the upper 12 m. Elevated levels of phosphate were measured at 18 m depth and nitrate at 24 m (Fig. 2A). On May 27–28 elevated levels of phosphate and nitrate were found at 30 m depth, however ammonium had increased in the surface layer (0–12 m) (Fig. 2B).

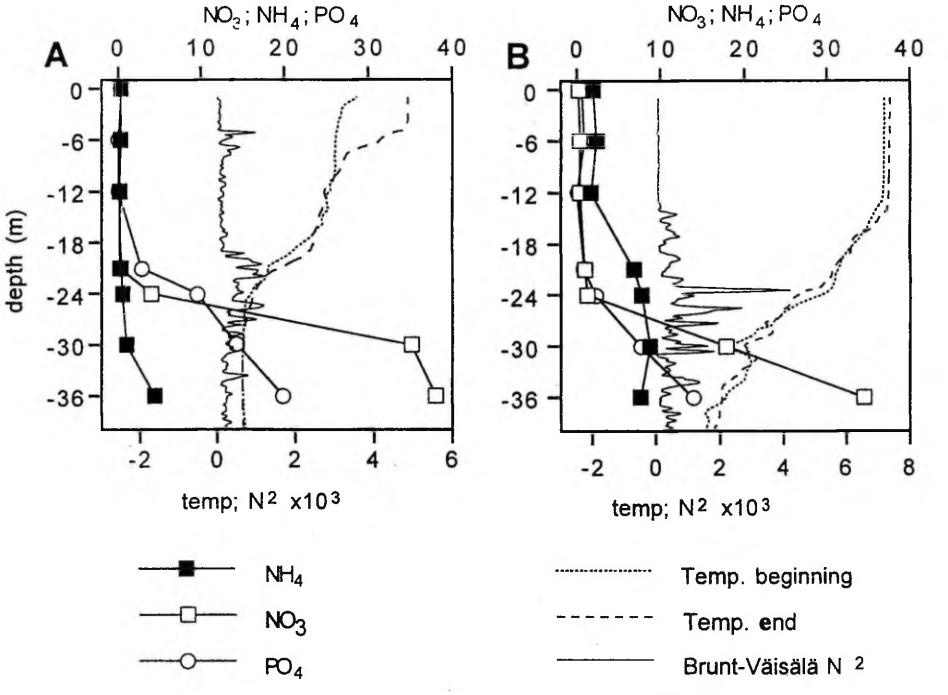

Figure 2. Profiles of mineral nutrient concentrations (µg l^{-1}; scale on the upper X-axis), Brunt-Väisälä buoyancy term (s^{-1}), and water temperature (°C) in the beginning and end of the first (A) and second (B) period (scale on the lower X-axis).

Phytoplankton abundance

In 1994 the phytoplankton vernal bloom at the western Gulf of Finland was dominated by dinoflagellates and diatoms. According to the data obtained from a weekly monitoring station (59° 40.3' N, 23° 14.5' E), the total phytoplankton biomass in the upper mixed layer (0–10 m) was 5,7 mg l^{-1} on May 3 and 3,2 mg l^{-1} on may 24 (Olli, unpublished data). On May 3 approximately half of the total biomass was formed by the dominant dinoflagellate species *Scrippsiella hangoei* and *Peridiniella catenata* (33% and 12%, respectively), while on May 24 their share was even larger (60% and 15% for *S. hangoei* and *P. catenata*, respectively), mainly due to the decline of the diatom populations. The abundance of *Mesodinium rubrum* was much lower and the species did not contribute significantly to the total autotrophic biomass. According to subjective estimations these proportions were approximately the same at our study site. The decline of the bloom was reflected in considerable

decrease (84%) of CHL concentration and the abundances of *Mesodinium rubrum* (36%), *Peridiniella catenata* (20%) and *Scrippsiella hangoei* (83%), compared to the first period. The variability of species abundances between replicate samples (estimated as coefficient of variation; n=4) was between 5–8% and somewhat higher in the case of *P. catenata* (15%). The variability in the abundance of *M. rubrum* between replicate sub-samples was 7%. The change in the standing stock of the species and CHL (0–36 m) is presented in Figures 3 and 4; the variability of the standing stock of species and CHL within both sampling periods is presented in Table 1.

Table 1

Variability (% coefficient of variation) of the standing stock of the species and CHL concentration

Species and CHL	I period	II period
Mesodinium rubrum	27	14
Peridiniella catenata	14	19
Scrippsiella hangoei	24	24
CHL	15	20

Vertical distribution of CHL and phytoplankton

On May 5 the bulk of *Mesodinium rubrum* cells was concentrated to the upper 0–3 (6) m layer (30–170 cells ml^{-1}), with a less pronounced peak (5–15 cells ml^{-1}) at about 30 m depth (Fig. 3A). Also on May 27 a vertical distribution with two depth maxima were observed, upper one (0–12 m) 8–18 cells ml^{-1}, and a lower one (25–33 m) 6–10 (14) cells ml^{-1} (Fig. 4A). On May 5 the dinoflagellate *Peridiniella catenata* had a depth distribution characterised by 2 maxima, a pronounced surface peak (100–300 cells ml^{-1}) at 0–6 m and a smaller one at 21–27 m (Fig. 3B). On May 27 most of the cells were concentrated above the 21 m depth (10–25 cells ml^{-1}), with peak abundances often at 21 m depth (Fig. 4B). *Scrippsiella hangoei* was concentrated to the upper 10 m layer (600–1200 cells ml^{-1}) during the first period, while below that depth the cell concentrations decreased to 0–200 cells ml^{-1} (Fig. 3C). During the second period the cells were more evenly distributed in the surface water, concentrations of 50–100 cells ml^{-1} reaching down to 18 m depth, and less than 20 cells ml^{-1} below that (Fig. 4C). The distribution of the principal phytoplankton species was also reflected in the CHL concentrations. On May 5 CHL concentration in the upper 0–3 m was an average 20 $\mu g\ l^{-1}$ (Fig. 3D). Below the 10 m depth a sharp decrease in the CHL values down to 5–7 $\mu g\ l^{-1}$ was observed. The depth maximum (260 cells ml^{-1}, 24 m layer) of *Peridiniella catenata* is well reflected in the CHL profile on the first sampling occasion (16.00; 13.4 $\mu g\ l^{-1}$). On May 27 the surface values of CHL had dropped to 2–3 $\mu g\ l^{-1}$, decreasing almost constantly to 0.5 $\mu g\ l^{-1}$ at 36 m depth (Fig. 4D).

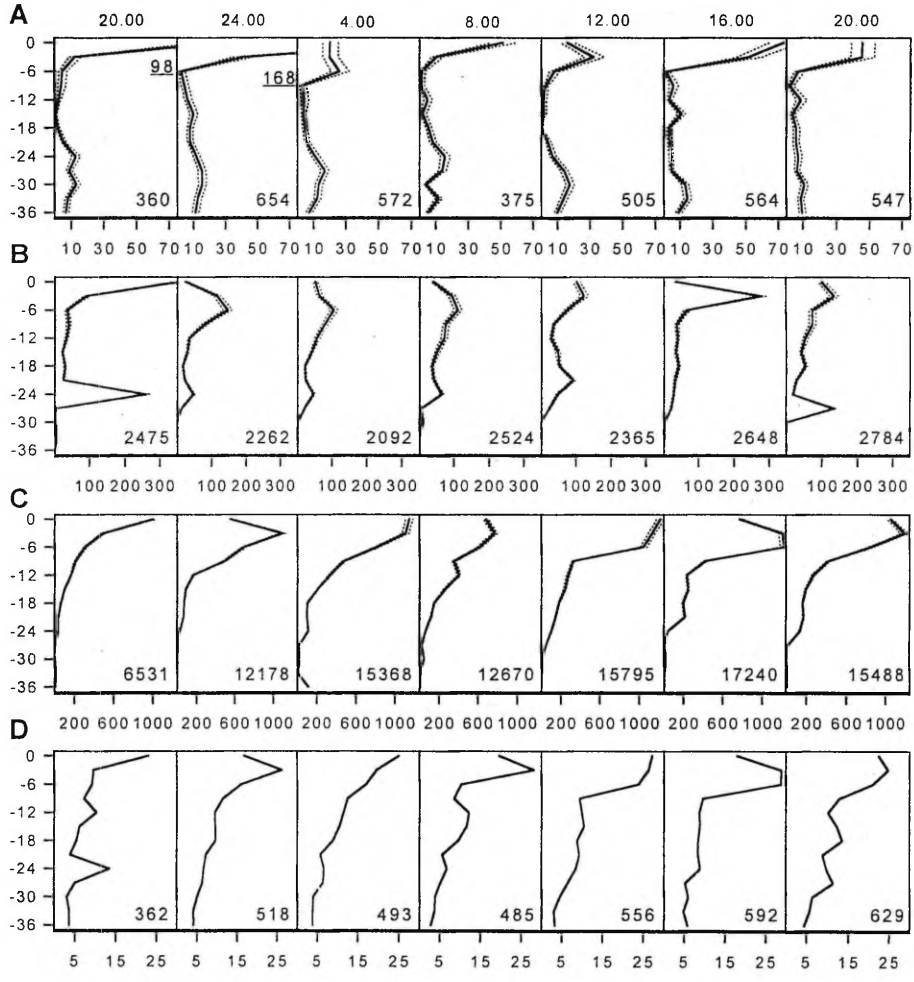

Figure 3. Vertical abundance (cells ml^{-1}) profiles of *Mesodinium rubrum* (A), *Peridiniella catenata* (B), *Scrippsiella hangoei* (C) and CHL concentration ($\mu g\ l^{-1}$) (D) during the first period. Respective sampling times are on A panel. Numbers in the lower right part of graphs depict the standing stock (0–36 m) of phytoplankton (cells x 10^6 m^{-2}) (A–C) and CHL (mg m^{-2}) (D). Numbers in the upper right part of panel A represent out of scale surface values. Dashed lines show the 95% confidence limits of cell counts.

Correspondence analysis on the data set from the first period reveals that if the profiles are grouped according to the species (connected to their respective centres of gravity), there is very little overlap between the groups, indicating much more similarity of the depth profiles within the same species than between different species. A reasonably good separation of species groups is achieved with the first two ordination axes (Fig. 5A). However, the second axis is highly influenced by the pronounced depth maxima of *Peridiniella catenata* on the first and last profile. The best separation of species groups is achieved on an ordination plane defined by the first and third axes (Fig. 5B). This between-species difference was statistically tested by randomly exchanging the data points (depth profiles) between groups (corresponding to species and CHL) and comparing the new between-group variability (i.e.

the spread of the centres of gravity) with the original one. Out of the 1000 permutations none resulted in a higher between-group inertia (i.e. that with every random exchange the new groups were closer to each other compared to the original one), indicating highly significant differences in the vertical distribution patterns between the species. Symmetrically the groups were defined by the sampling time and the permutation test revealed no significant difference between groups. The same applies also to the data set from the second sampling period (27–28 May). The difference between groups defined by species was statistically highly significant, but not when defined by sampling time. Another effect which is easily seen from Figure 5 is the different degree of spread between the species. The depth profiles of *M. rubrum* and even more those of *P. catenata* are much more different compared to those of *S. hangoei* and CHL which are quite similar during the diel cycle.

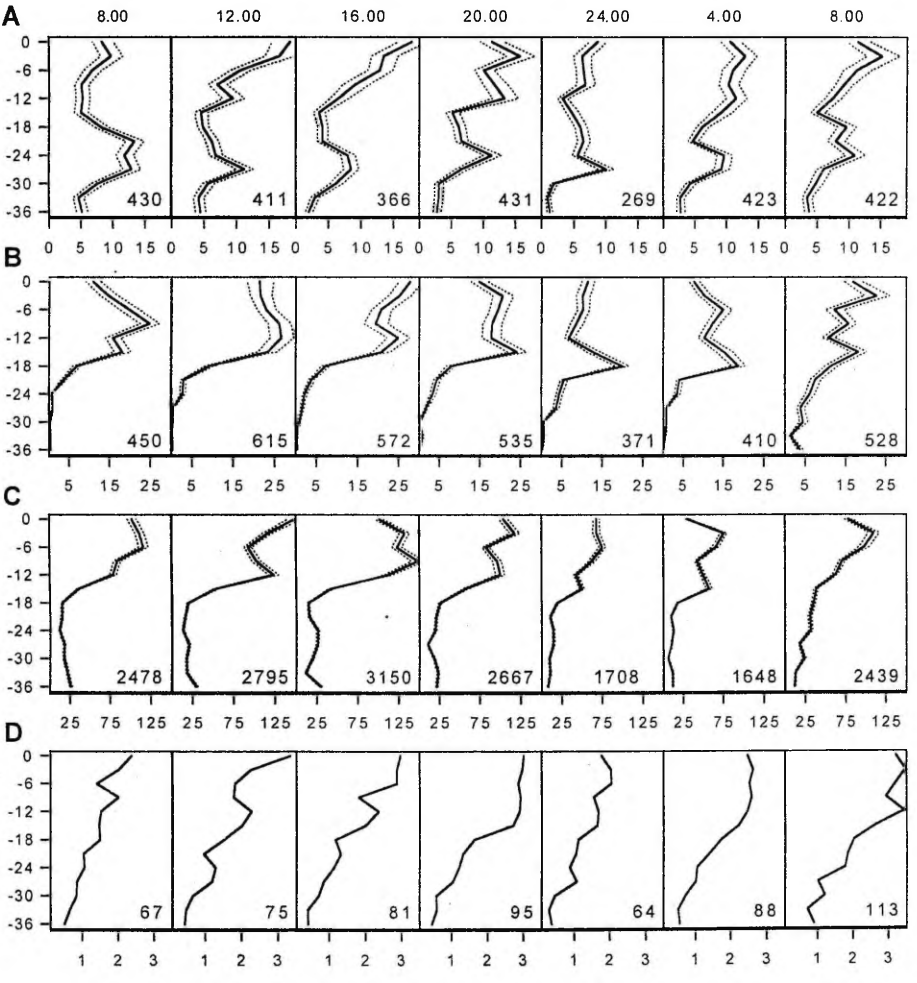

Figure 4. Vertical profiles of the species and CHL during the second period. Notations as in Fig. 3.

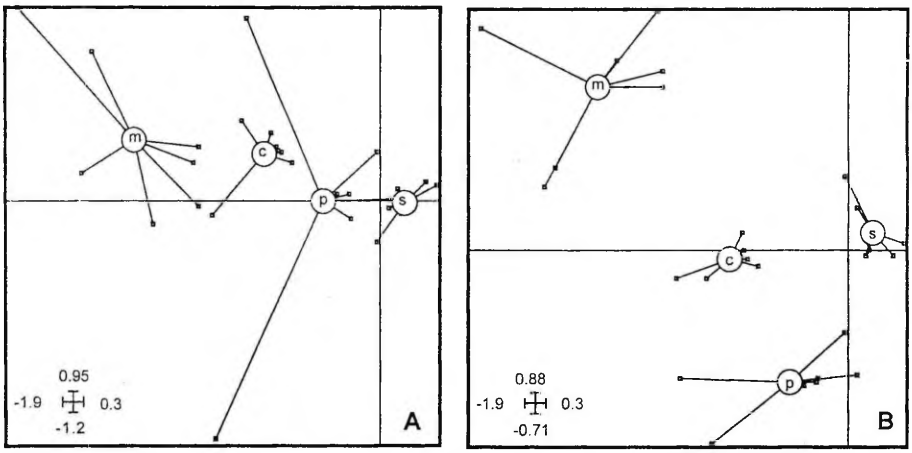

Figure 5. Projection of the vertical distributions of *Mesodinium rubrum* (m), *Peridiniella catenata* (p), *Scrippsiella hangoei* (s) and CHL (c) during the first period onto two-dimensional plane. Groups, defined by the species and CHL are connected to their respective centres of gravity. Axes are defined to maximize the variability between all data points. A —first (X) and second (Y) axis. Note the large spread of *P. catenata.* B — first (X) and third (Y) axis. Numbers in lower left corner delineate the range of the axes.

To test whether the species specific nature of the depth profiles applies over a temporal scale of 3 weeks (with considerable change in species abundances and hydrography in between), we performed a correspondence analysis on the pooled data of both periods. Between-group (4 groups corresponding to species and CHL, each with 14 depth distribution profiles) analysis resulted in remarkably good separation of the species on the two first ordination axes (Fig. 6), which was also statistically highly significant (permutation test). The spread of the data points within species reflects now a change in the depth distribution pattern in the time scale of hours (within period) and weeks (over the two periods). The spread in *Mesodinium rubrum* is clearly largest, which actually is caused by a considerable shift in depth profile patterns between the periods. The spread of *Peridiniella catenata*, which was clearly largest when the two periods were considered separately, is now comparable to that of *Scrippsiella hangoei* — characterised by relatively uniform depth distribution within periods. This is due to relatively larger shift of the depth distributions of *S. hangoei* compared to *P. catenata*. The spread of CHL is clearly smallest, resulting from relatively uniform depth distributions within periods and smallest shift in between periods. Based on row weighted correspondence analysis (the second ordination axis agrees considerably well with the depth gradient), the general direction of the shift if the depth distributions between the two periods appeared to be directed towards greater depths, except in the case of *P. catenata*. The significance of the shift between two periods was tested with a between-group permutation test, the groups defined by the periods. Out of 10000 random permutations only 78 resulted in larger distance between the centres of gravity of the groups.

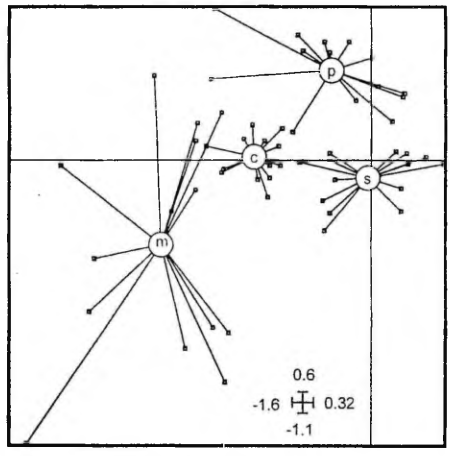

Figure 6. Projection of the pooled data from both periods onto between-group ordination plane. Axes are defined to maximize the variability between centres of gravity. Notations as in Fig. 5.

Discussion

The peak and decline phases of the vernal bloom were dominated by dinoflagellates with a potential to perform vertical migration. During both periods the illuminated layer was nutrient depleted. The vertical profiles of the species studied revealed that over the diel cycle part of the populations of *Mesodinium rubrum* and *Peridiniella catenata* were able to reside deep enough to take advantage of the nutrients below the pycnocline, while *Scrippsiella hangoei* seemed to be concentrated to the upper nutrient depleted layer. The depth profiles of *M. rubrum* and especially that of *P. catenata* changed much more during the diel cycle compared to *S. hangoei* and CHL, which was probably caused by the migratory behaviour of the former. The depth profile patterns were significantly different between the species, over a temporal scale of hours as well as weeks. This indicates the importance of species specific behavioural adaptations in the vertical distribution. However, these conclusion could have been emphasized by artifacts like inaccuracy in sampling, turbulent mixing and horizontal advection of water mass, which will be discussed below.

Sampling and counting errors

The populations of the micro-organisms were assumed to have a random Poisson distribution. The relative precision of the estimated abundance is related to the number of cells counted. In figures 3 and 4 the estimated mean abundances of the organisms are shown with 95% confidence limits of the direct counts. Additional variation is introduced with the procedure of sampling and sub-sampling (Vernick, 1972). However, the replicability of the counts from parallel samples and sub-samples was relatively good, thus giving a reliable estimate of the population abundance. Yet another aspect of the sampling error is related to the vertical resolution of the discrete samples. The accumulation of autotrophic microorganisms to depth maxima could occur in relatively thin layers (Lindholm, 1992), making it difficult to uncover the real maxima with routine sampling from too few discrete depths. *Mesodinium rubrum* is known to accumulate on very thin layers (Cloern *et al.*, 1994; Craw-

ford, 1989; Lindholm & Mörk, 1990; Owen *et. al.*, 1992). A very pronounced surface accumulation to the thermally stratified surface water was unveiled during the first period in our study (Fig. 3A). It can not be ruled out that the high variability of the standing stock of *M. rubrum* during the first period was caused by missing some thin accumulation layers. This problem can be avoided by using *in situ* continuous fluorescence profile measurements (Cloern *et al.* , 1994). The interpretation however, requires highly monospecific blooms and would have been less valuable in our case, where CHL profiles are clearly a synthesis of the abundance of all the species. However, the accumulation layers are probably thinner in strongly stratified environments like wind-sheltered small lakes, saline lakes and sheltered and coastal lagoons (Lindholm, 1992), compared to open coastal areas.

Another likely source of error is turbulent mixing and horizontal patchiness. It is well known that Langmuir rotation can cause horizontal patchiness of micro-swimmers (Reynolds, 1984; Smayda, 1970). Planktonic micro-organisms at the study area are known to have patchy mesoscale horizontal distribution in summer (Kuosa, 1988), yet in the scale of 100–200 m errors caused by sample preparation seem to be more crucial (Kuuppo-Leinikki, 1993). During our study period the horizontal mesoscale variability of CHL surface concentrations (1.5 m depth), measured with *in situ* flow-through fluorometer (Turner design) was approximately 20% (Jukka Seppälä, personal communication). The current velocities at 20 m depth were low and during the course of four hours could cause a water mass transport of less than 300 m and 300–600 m during the first and second period, respectively. Yet, as the physical forcing acts on motile cells and prevents them reaching optimal depth, the actual vertical distribution of the population is a combination of water movements counteracted by the active response of cells to fulfil their physiological requirements (Kuosa, 1988; Sommer, 1985). If the physical forcing overwhelms the ability of the cells to control their vertical position, we would not expect to see significantly different depth distribution patterns between species, which is the case in our study and applies also to time scale of three weeks. The physical mixing in open coastal areas is rather a rule than exception, which might be the reason why classical theoretical day time surface accumulation and night time dispersal or downwards migration is rarely encountered in field studies. Yet it is also likely that the actual triggers and physiological requirements of the cells are more complex than the classical migration theory explains. In our study a depth accumulation of a small proportion of *Mesodinium rubrum* was found during the first period. The ability for diel vertical migration is widely known in *M. rubrum* (Crawford, 1989; Passow, 1991; Williams, 1996), but it is also known that in low temperatures the species can tolerate darkness for several days or weeks (Lindholm, 1985). Vertical migration studies in the Baltic Sea reveal that part of the population remains in deep layers and is not migrating, at least in the diel scale (Lindholm & Mörk, 1990; Passow, 1991). However, the ecology of *M. rubrum* is quite different from the two dinoflagellates studied. In the study area *M. rubrum* does not form annual blooms, but is still quite abundant throughout the summer. In our study the relative decrease of the abundance was lowest in *M. rubrum*. However, it revealed the greatest change of depth distribution between the two periods. The depth distribution was much more uniform on the second period compared to the sharp surface peaks on the first period. Relatively uniform depth distribution (0–30 m) of *M. rubrum* in summer has been also noticed from the Gulf of Riga, the Baltic Sea (Olli, unpublished data).

The vertical migration of the chain forming dinoflagellate *Peridiniella catenata* is also known from previous studies in the Baltic Sea (Heiskanen, 1995; Passow, 1991). In our study *P. catenata* exhibited pronounced depth maxima during the first period and also accumulated in nutrient rich layers below the pycnocline during the second period. It is possi-

ble that chain formation has been selected in the evolution as adaptation to migration, since according to hydrodynamical considerations increased cell number in chain increases the swimming speed (Fraga *et al.*, 1989). This would enable long duration of blooms of *P. catenata* based on deep nutrient supply. It is in contrast to the behaviour of *Scrippsiella hangoei*, which in our study did not show migrational behaviour and remained in the upper nutrient depleted layer. In our study area *S. hangoei* is known to form bloom densities in thin layers under the ice in early spring (Larsen *et al.*, 1995). The nutrient supply of *S. hangoei* in the upper water layer during the spring bloom is not clear. High affinity to low nutrient concentrations could explain the competitional success of this species, although no data is available. Dinoflagellate cells are known to accumulate and store excess nutrients which are used when ambient nutrients decrease (Bhovichitra & Swift, 1977; Chapman & Pfiester, 1995; Dortch *et al.*, 1984). Mixotrophy can be an additional way of nutrition, common in many dinoflagellates. Although it has not been proved with *S. hangoei*, it has been noted that pure cultures of the species get axenic over time (Guy Hällfors, personal communication), suggesting that the species can feed on bacteria. If this is true it might be that *S. hangoei* does not need to migrate to fulfil its nutrient requirements. It is hypothesized here that the co-existence of the two dominant dinoflagellate species during the vernal bloom is due to niche separation, a hypothesis which is supported by the behavioural difference found during this study. Sommer (1982, 1985) has interpreted variations in vertical migration as differential light requirements leading to niche separation and coexistence of closely related cryptomonads in Lake Constance. However, it is necessary to extend this to nutrition strategies, as light preferences are closely related to nutritional status. It has been suggested that vertically migrating dinoflagellates (Fraga *et al.*, 1992) and *Mesodinium rubrum* (Lindholm & Mörk, 1990) can act as nutrient pumps to transport nutrients from deep layers to the euphotic zone, which through regeneration get available to non-migrating species (Prego, 1992). In our study regenerated nitrogen was accumulating during the second period in the surface layer, however, the phosphate depleted layer was even deeper compared to the first period. Generally the vernal bloom phytoplankton in the area does not discriminate between ammonium and nitrate (Tamminen, 1995), although species specific differences can exist. If deep phosphorus taken up by vertically migrating *M. rubrum* and *P. catenata* could be channelled to *S. hangoei* it implicates that the vernal bloom, dominated by dinoflagellates in the area is not terminated by nutrient depletion after the formation of thermal stratification, as is generally assumed in diatom dominated blooms, but rather due to internal species specific life cycle events. The *S. hangoei* bloom in the area terminates in late May by massive cyst formation followed by rapid sedimentation (Heiskanen, 1993); the fate of *P. catenata* bloom is unknown as cyst formation and large scale sedimentation has not been observed. Further lab experiments on the nutrient uptake kinetics and mixotrophy of *S. hangoei* could clarify the niche separation mechanisms. Unfortunately lab experiments with *M. rubrum* and *P. catenata* are hampered by difficulties in culturing (Crawford, 1989; Lindholm, 1985, Guy Hällfors, personal communication).

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SEASONAL STAGES OF PHYTOPLANKTON COMMUNITY STRUCTURE AND SINKING LOSS IN THE GULF OF RIGA

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Abstract

In this paper we present the biomass, species composition and sinking losses of phytoplankton and heterotrophic flagellates obtained during three seasonal stages (May 1995; June–July 1994; August 1993) from the Gulf of Riga — an eutrophied, semi-enclosed area in the Baltic Sea. The Gulf was characterised by intensive dinoflagellate (mainly *Peridiniella catenata*) dominated spring bloom (2700–7600 $\mu g\ l^{-1}$ wet weight) while the diatom *Thalassiosira baltica* contributed most (80–90%) to the settling phytoplankton biomass (up to 6.5 $g\ m^{-2}\ d^{-1}$). The mineral nutrients were abundant during the bloom and it is suggested that the differential sedimentation of species was caused by physical factors (thermal stratification of the water column). The phytoplankton biomass in summer (780–2600 $\mu g\ l^{-1}$) was dominated by high abundance of a filamentous cyanobacterium *Aphanizomenon flos-aquae*, autotrophic nanoflagellates and pico-plankton. The primary vertical flux of phytoplankton (<1 $g\ m^{-2}\ d^{-1}$) was mainly due to non-motile species and aggregate-bound picoplankton and *A. flos-aquae*. Below the pycnocline resuspended dormant diatom populations caused a significant (up to 1 $g\ m^{-2}\ d^{-1}$) secondary flux. Large heterotrophic dinoflagellates (*Gyrodinium/Gymnodinium*) were abundant (up to 500 $\mu g\ l^{-1}$) in the middle layers and associated to ammonium regeneration. The early autumn stage was a post cyanobacterial bloom situation with relatively low phytoplankton abundance (330–860 $\mu g\ l^{-1}$) dominated by *A. flos-aquae* and nanoflagellates. Also the sedimentation of phytoplankton was lowest (up to 340 $mg\ m^{-2}\ d^{-1}$).

Our results indicate high seasonal differences in the phytoplankton community structure and sedimentation. However, the high within season temporal variability overrules the variability between different areas of the southern part of the Gulf.

Introduction

The Gulf of Riga is an eutrophic semi-enclosed basin in the eastern part of the Baltic Proper. Due to considerable industrial and agricultural activities in the drainage area the nutrient load has been high during several last decades (Laznik *et al.*, 1988). This has resulted in increased eutrophication, characterised by high values of chlorophyll *a* and phytoplankton biomass. In spite of the long history of investigations, specific studies of the phytoplankton dynamics and the fate of the primary production are rare. There are numerous studies on the general patterns of the phytoplankton spring bloom and annual dynamics in the Baltic Sea (Niemi, 1973; Alasaarela, 1979a; 1979b; Edler, 1979a; Hobro, 1979a; 1979b), while only a few deal simultaneously with sedimentation losses of phytoplankton from the euphotic layer (Heiskanen and Kononen, 1994).

According to these and other studies the break-out of phytoplankton vernal bloom ranges from February-March in the south (Kattegat; Olesen, 1993) to June in the north (Bothnian Bay; Alasaarela, 1979a; 1979b). The principal group of phytoplankton has been reported to be diatoms, although in many cases dinoflagellates dominate. In spite of substantial research and conceptual frameworks (Margalef, 1978; Granéli *et al.*, 1989) the factors determining the outcome of the vernal diatom — dinoflagellate competition have remained obscure. However, these two scenarios can have a quite different effect on the fate of the organic material produced during the bloom period. In the Baltic Sea a diatom dominated bloom is largely subjected to rapid sedimentation out of the water column (Bodungen *et al.*, 1981; Passow, 1991; Olesen, 1993). This pulse of fresh organic material can account for the majority of annual organic matter input to the benthic community (Bodungen *et al.*, 1981; Smetacek, 1984). Smetacek (1985) argues that this sedimentation "loss" is closely coupled with the life cycle strategies of diatoms by providing a quick refugee in times when the surface layers turn to a hostile environment for the cells. The fate of vernal dinoflagellate blooms can vary and seems to be species-specific. In the western Gulf of Finland, the dominant vernal dinoflagellate *Scrippsiella hangoei* goes through sexual process, cyst formation and ultimately a quick sedimentation (Heiskanen, 1993), while the fate of another dominant dinoflagellate, *Peridiniella catenata* seems to be mainly disintegration in the water column (Heiskanen and Kononen, 1994).

There are considerable annual fluctuations in the magnitude, duration and species composition during the vernal bloom developments in particular areas (Hobro, 1979a). However, above these there seems to be also distinct differences between neighbouring regions. The dominant dinoflagellate species in the western Gulf of Finland, *Scrippsiella hangoei* has not been frequently reported from other areas, possibly due to taxonomic confusion (Larsen *et al.*, 1995). However, according to our study it does not seem to belong to the vernal plankton community in the Gulf of Riga.

During summer large areas of the Baltic Sea suffer from major cyanobacterial blooms. Although a natural phenomenon which has been recorded over a century in the Gulf of Riga (Olli, 1996), the blooms seem to have extended spatially and temporarily due to anthropogenic eutrophication (Kahru *et al.*, 1994). The fate of these blooms remains largely unknown as the bulk of the biomass does not sediment (Heiskanen and Kononen, 1994; Heiskanen and Olli, 1996) and is not grazed by the ambient zooplankton populations (Sellner *et al.*, 1996).

In this paper we give an overview of the taxonomic composition, abundance, distribution and sedimentation losses of the major phytoplankton species and groups in the southern

part of the Gulf of Riga. The general approach of the project was to obtain "temporal snapshots" of the structure and function of the planktonic food web and sinking losses from various trophic compartments during different stages of the productive season. The aim of this study was also to quantify sinking loss from the seasonal phytoplankton community and to estimate the impact of heterotrophic micro-organisms to the mineralisation and the fate of sinking organic matter in the water column. We summarise the results from three years of field studies, covering two weeks during the vernal (3–12 May 1995), midsummer (28 June – 7 July 1994), and early autumn (26 August – 3 September 1993) stages of the annual production cycle. The organisms under study include the whole range from picoplanktonic cyanobacteria, pico-sized eucaryotic autotrophs to net phytoplankton, but also heterotrophic nanoflagellates and heterotrophic dinoflagellates.

Material and methods

The basic sampling programme was repeated over several diurnal cycles during every cruise at the central station (Stn. 119; visited every second time) and at the spatial stations (Stn. 101A, 135, 137A, 121 and 121A; visited once during a season) located in the different hydrographical regions of the Gulf of Riga (Fig. 1). During the 24 h sojourn at each station, the following basic sampling schedule was completed

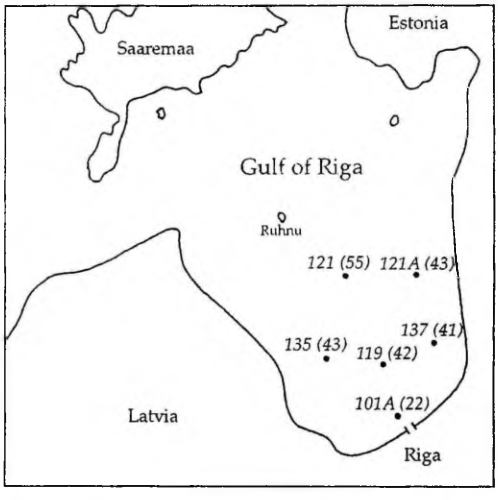

Figure 1. A scheme of the sampling stations in the southern part of the Gulf of Riga. Numbers in parenthesis depict the depth of the station.

Water column measurements

Hydrographic water column properties were measured upon arrival, and before the departure from each sampling station. These measurements included CTD-casts for salinity and temperature, conductivity, turbidity, fluorescence, oxygen, and pH profiles (for details see Olesen *et al.*, 1998). The depths for the pooled samples were decided separately at each station according to the stratification revealed by the CTD-cast. The water column was di-

vided into 2 or 3 layers: 1) upper mixed layer above the thermocline/pycnocline, and 2) deep water layer below the thermocline/pycnocline. At stations where a third layer was observed (e.g. three layer structure caused by thermal or density stratification) samples were taken and pooled from each of the 3 layers separately. Analyses from the pooled water samples included determinations for chlorophyll *a* (CHL) and phaeopigments, dissolved inorganic nutrients (NO_3-N, PO_4-P, NH_4-N) and abundance and biomass of planktonic micro-organisms. Pooled samples for cell number and biomass determinations of planktonic micro-organisms were taken only once per station (e.g. upon arrival).

Sedimentation measurements

Sediment traps were deployed immediately after arrival and retrieved approximately 24 h later, before the departure from the station. Mooring depths were 8, 12, and 16 m at the Stn. 101A, and 11, 21, and 35 m at all other stations during the cruise in 1993. In 1994 and 1995, the mooring depths were 10, 15, 20 and 35 m at all stations, except at the Stn. 101A where the depths were 10, 15 and 20 m. The sediment traps had duplicate cylinders with a HD-ratio > 6 (height: 45 or 33 cm, and diameter: 7.2 or 5.2 cm). No preservatives were used inside the cylinders. After retrieval, the content of the trap cylinders was mixed thoroughly, poured into plastic jars and filled to a fixed volume with filtered sea water. Settled material was splitted for bulk measurements (total particulate material, CHL and phaeopigments, particulate organic carbon, nitrogen and phosphorus analyses (see Reigstadt *et al.*, 1998). Also the cell numbers and biomass of picoplankton, autotrophic and heterotrophic nanoflagellates, and phytoplankton were enumerated from the sediment trap samples.

Sample analysis

Subsamples (100–300 ml) for net phytoplankton counts were taken from the pooled water column and sediment trap samples and fixed immediately with acid Lugol solution. Within six months the samples were counted with inverted microscope (Leica DM IL, 125 and 500* magnification, phase contrast optics), by using aliquots of 10–50 ml. For larger species the whole chamber bottom or up to 6 cross transects over the chamber bottom were counted with a 10* objective, for smaller species 2–6 cross transects were counted with a 40* objective. In general over 100 counting units of the principal species were counted. In the case of *Aphanizomenon flos-aquae* the length of each counted filament was measured, the samples were not counted before all the filament bundles were disintegrated. Biomass was estimated from cell volumes (Edler, 1979b), assuming a density of 1 g ml^{-1} for the micro-organisms; in the following biomass is expressed as wet weight.

Subsamples (20 ml) for pico-cyanobacteria, a variety of miscellaneous autotrophic pico- and nano-sized flagellated and coccoid eucaryotes (ANANO), and heterotrophic nanoflagellates (HNANO) were also taken from the pooled water column and sediment trap samples, fixed immediately with pre-filtered (0.2 µm) glutaraldehyde up to a final concentration of 2.5%. Within 2–3 days 5 ml of the sub-samples was filtered onto black Nuclepore (0.2 µm pore size) filters, stained with DAPI, air dried, mounted into paraffin or immersion oil and covered with a cover slip. The slides were kept deep-frozen and dark until counting. The counting was done within a six months period using a Leica DM RB epifluorescence microscope. A green excitation light for pico-cyanobacteria and UV-violet excitation light for the

rest of the organisms was used. Depending on the cell density 60 to 100 fields were counted for the eucaryotes and above 20 for the pico-cyanobacteria. Subsamples (100–250 ml) for CHL measurements were filtered onto Whatman (GF/F) glass-fibre filters and kept deep-frozen and dark until analysing. The filters were sonicated in 96% ethanol, and extracted for 24 hours in darkness. The CHL concentration was measured using a spectrofluorometer (Shimadzu RF 5001), which had been pre-calibrated with pure chlorophyll *a* (Sigma).

To calculate the net vertical flux of the organisms the abundance of the species in the sediment traps was corrected by subtracting the abundance in the surrounding water column. The vertical flux for each species was calculated according to the formula:

$$f = (b1 - b2) \times t \times \frac{v}{24} \times a$$

where:
f — net vertical flux of the biomass of the species (mg m^{-2} d^{-1}); b1 — biomass of the species in the sediment trap sample (mg l^{-1}); b2 — biomass of the species in the pooled water sample surrounding the sediment trap (mg l^{-1}); v — volume of the sediment trap (l); a — surface area of the sediment trap (m^2); t — duration of the mooring (h). For the total vertical flux of phytoplankton or heterotrophic flagellates the positive specific fluxes were summed.

The daily loss rates of the species were calculated according to the formula:

$$l = \frac{f}{s}$$

where:
l — daily loss rates (d^{-1}); s — standing stock of the organisms above the sediment trap (mg m^{-2})

Results

Inorganic nutrients (pooled samples)

In spring 1995 nitrate concentrations in the upper mixed layer decreased from 116 to 20 µg l^{-1} in the upper mixed layer in Stn. 119 (Fig. 2A). In the spatial stations the nitrate concentrations varied from 6 (Stn. 135) to 196 µg l^{-1} (Stn. 101A). Phosphate and ammonium were relatively low (1.3–10.6 µg l^{-1} and 1–7 µg l^{-1}, respectively) (Fig. 2A). In the deep layers nitrate was 90–120 µg l^{-1}, phosphate was 21–30 µg l^{-1} and ammonium 3–23 µg l^{-1}. In midsummer 1994, nutrient concentrations were low (generally <30 µg l^{-1} NO_3–N, <130 µg l^{-1}, NH_4–N, and <4 µg l^{-1} PO_4–P) in the surface layer (Fig. 2B). Nitrate and phosphate concentrations were elevated below 20 m depth and ammonium concentrations were high in the intermediate and in the deep water layers (up to 200 µg l^{-1}). In late August 1993, ammonium concentrations were high in the surface layer (130–240 µg l^{-1}) (Fig. 2C), while the concentrations of phosphate were higher in the deep layer (130–270 µg l^{-1}) than in the surface layer (10–30 µg l^{-1}). The concentrations of nitrate varied normally 20–50 µg l^{-1} in the surface layer and 540–620 µg l^{-1} in the deep layer indicating effective nitrification.

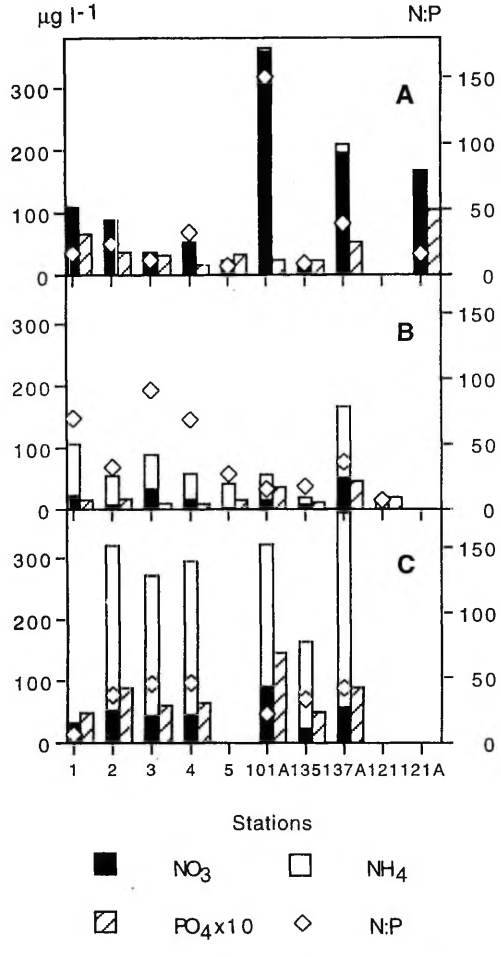

Figure 2. Daily fluctuations in concentrations of nitrate (NO_3), ammonium (NH_4) and phosphate (PO_4×10) (columns) and N:P weight ratio (diamonds) in the upper mixed layer in the Gulf of Riga during the spring (A), midsummer (B) and early autumn (C). When water column stratification was comparable in the beginning and end of the sojourn, a mean value of the nutrient concentration between the two samplings was taken. The time series form Stn. 119 is numbered as 1–5. From the spatial stations 121 was not visited in 1995 and 1993, Stn. 121A not in 1994 and 1993, and in 1993 there were four sojourns to Stn. 119.

Chlorophyll *a*

During the spring cruise in 1995, CHL concentrations in the surface water layer varied between 8–38 µg l^{-1} with an increasing trend in time, and in the deep water layer between 2–8 µg l^{-1} (Fig. 3). The highest CHL concentration was measured on the last day in Stn. 119 (92 µg l^{-1} at 2 m depth in a narrow chlorophyll maximum). In mid-summer 1994 there was a gradual increase of CHL from ca 5 to 9 µg l^{-1} at the surface layer in Stn. 119 (Fig. 4). In the spatial stations CHL concentrations varied between 4–12 µg l^{-1}, being the highest at

Stn. 101A (outside the Daugava river mouth) and lowest in the northernmost Stn. 121. The ratio of fluorescence before and after acidification (R/Ra) indicated that the phytoplankton in the surface and middle layers was healthy (R/Ra close to pure CHL), while in the deeper water layers it was more degraded. During the late summer cruise in 1993 the concentrations of CHL in the surface mixed layer were clearly the lowest and varied between 1–2 $\mu g\ l^{-1}$, without any clear spatial or temporal trend (Fig. 5). In deeper layers the values were 0.5–1 $\mu g\ l^{-1}$.

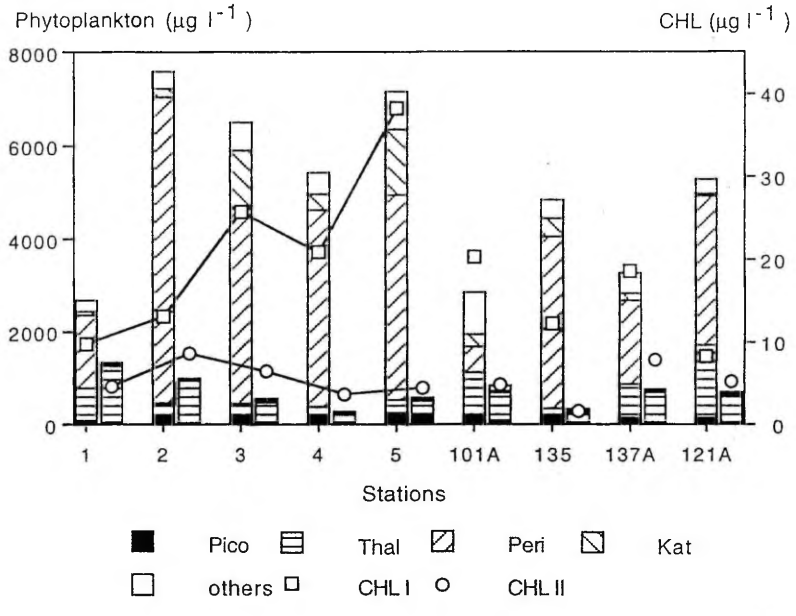

Figure 3. Biomass concentrations (wet weight) of main groups of phytoplankton (columns) and CHL (lines and symbols) in the Gulf of Riga during spring 1995. Left column of the group and CHL I represent surface mixed layer, right column and CHL II represent deep layer. Pico — pico cyanobacteria and ANANO; Peri cat — *Peridiniella catenata*; Kato rot — *Katodinium rotundatum*; Thal bal — *Thalassiosira baltica*. Stations as in Fig. 2.

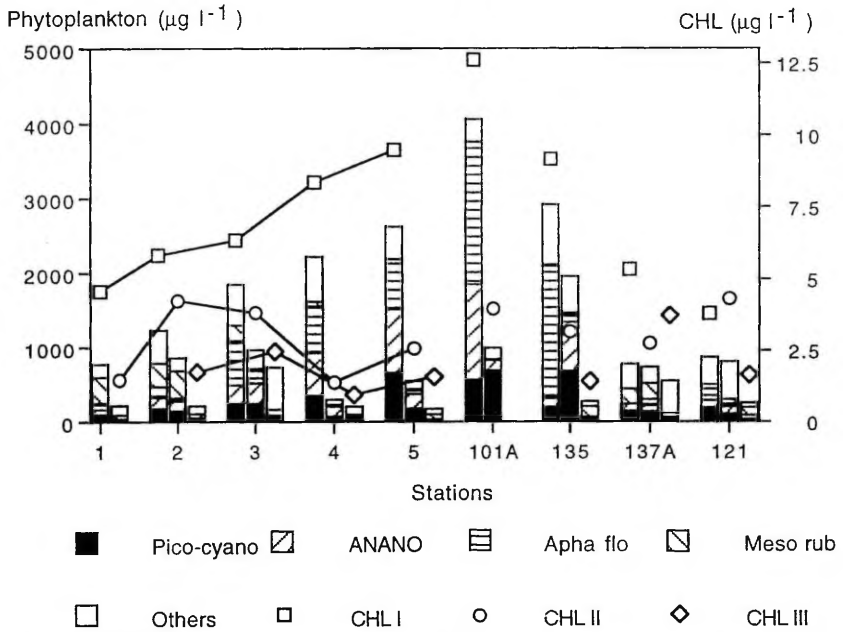

Fig. 4. Biomass concentrations (wet weight) of main groups of phytoplankton (columns) and CHL (lines and symbols) in the Gulf of Riga during midsummer 1994. Columns in groups represent the mixed layers from surface (left) to bottom (right). CHL values in different layers are marked with I–III (surface to bottom). Pico-cyano — pico-cyanobacteria; Apha flo — *Aphanizomenon flos-aquae*; Meso rub — *Mesodinium rubrum*. Stations as in Fig. 2.

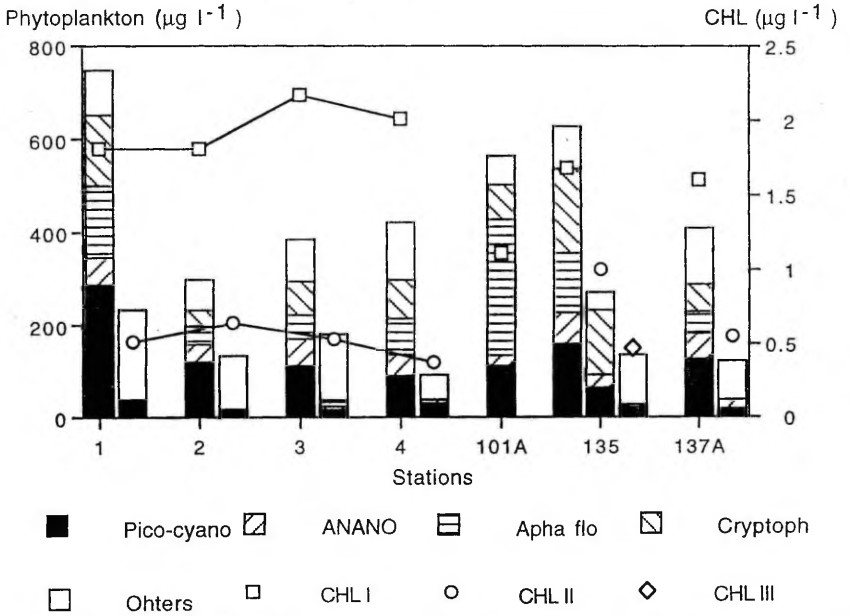

Fig. 5. Biomass concentrations (wet weight) of main groups of phytoplankton (columns) and CHL (lines and symbols) in the Gulf of Riga during early autumn 1993. Columns and lines as in Fig. 4. Cypto — cryptophytes *Teleaulax* spp. and *Plagioselmis prolonga*; other groups as in figure 4. Stations as in Fig. 2.

Phytoplankton species composition and biomass

In spring 1995 the total autotrophic biomass ranged from 2700–7600 μg l^{-1} in the upper layer and 300–1300 μg l^{-1} in the deeper layer (Fig. 3). The dominant species were the dinoflagellates *Peridiniella catenata* (1600–6600 μg l^{-1}) and *Katodinium rotundatum* (150–1500 μg l^{-1}), and a diatom *Thalassiosira baltica* (150–1600 μg l^{-1}) (Fig. 3). Highest biomass in a discrete fluorescence maximum (2 m depth; Stn. 119) was 27.2 mg l^{-1} (*P. catenata* 17.1 mg l^{-1}; *K. rotundatum* 7.6 mg l^{-1}). The biomass of subdominant species is given in Table 1. The total standing stock of autotrophic compartment (integrated over the whole water column) was in the range of 70–140 g m^{-2} (33 g m^{-2} in Stn. 101A). The standing stock of heterotrophic flagellates is given is Table 2.

Table 1

Ranges of biomass (μg l^{-1}) of the main speceis of phytoplankton in the pooled water samples. When the surface and second layer had significantly different cell abundances (marked with *; Wilcoxon paired signed-rank test, p<0.05), the range accounts only the surface layer

Taxon or group	1993	1994	1995
Aphanizomenon flos-aquae	47–665*	40–1900*	<23*
Chaetoceros danicus	<6	—	<14
Dictyosphaerium subsolitarum	—	14–136	—
Dinophysis acuminata	7–53	32–206*	1.3–9.5*
Eutreptiella sp.	—	<20	10–310*
Katodinium rotundatum	4–18*	<15	37–1415*
Mesodinium rubrum	—	6–360	37–192*
Monoraphidum sp.	<1.3	6–41*	14–40*
Oocystis spp.	4–40	4–50	—
Peridiniella catenata	—	—	554–6580*
Plagioselmis prolonga	8–20*	2–23*	3–17*
Pyramimonas spp.	1–5*	<4*	37–156*
Teleaulax spp.	26–161*	12–223*	50–117*
Thalassiosira baltica	<101	<115	143–1571
Woronichinia compacta	1–21	3–23	6–20
ANANO	39–68*	68–1281*	20–79*

Table 2

Standing stock of main groups of heterotrophic flagellates (g m^{-2}). DINO — heterotrophic dinoflagellates (incl. *Gymnodinium/Gyrodinium*); HNANO — nanoflagellates

	119/1	119/2	119/3	119/4	119/5	101A	135	137A	121	121A
1995										
DINO	1.78	1.34	1.43	1.87	1.56	0.02	4.05	1.38		5.44
HNANO	1.42	3.67	2.81	2.58	3.30	1.89	2.17	2.76		3.01
1994										
DINO		8.00	12.34	12.09	16.43	6.77	1.23	14.67	8.19	10.89
HNANO	3.75	3.36	4.71	5.81	4.19	2.05	4.32	2.90	4.07	
1993										
DINO		0.44	0.19	0.47	0.53		0.05	0.11	0.37	
HNANO	0.73	1.52	1.65	1.16		0.60	1.00	1.17		

During the midsummer period in 1994 the total biomass in the surface layer of Stn. 119 increased from 770 to 2600 μg l^{-1}, and was highest in Stn. 101A (4000 μg l^{-1}) (Fig. 4). The most abundant phytoplankton species in the upper layer was *Aphanizomenon flos-aquae* (90–680 μg l^{-1}; but 1900 and 1800 μg l^{-1} in Stn. 101A and 135, respectively) (Fig. 4). However, the main biomass increase in Stn. 119 was due to the growth of pico-cyanobacteria (from 100 to 660 μg l^{-1}) and ANANO (from 70 to 850 μg l^{-1}; mainly a pico-sized diatom *Thalassiosira pseudonana* and a small cryptophyte *Hemiselmis virescens*). In the spatial stations these figures were similar, somewhat higher in Stn. 101A (560 μg l^{-1} and 1280 μg l^{-1} for pico-cyanobacteria and ANANO, respectively). A resuspended dormant population of *Thalassiosira baltica* was abundant (up to 560 μg l^{-1}) below the pycnocline, particularly in the bottom nepheloid layer sampled with BioProbe bottom water sampler (Thomsen, 1995) (data not shown). The abundance of heterotrophic flagellates was generally higher compared to the spring situation in 1995 (Table 2). Large (40–60 μm) naked dinoflagellates of the *Gymnodinium/Gyrodinium* group were particularly abundant (150–530 μg l^{-1}) in the middle and deep layers, yet, almost absent in Stn. 101A.

In early autumn 1993, the total phytoplankton biomass in the surface layer (330–860 μg l^{-1}) was dominated by *Aphanizomenon flos-aquae* (40–200 μg l^{-1}; but as high as 670 μg l^{-1} in Stn. 101A during an additional sampling). However, a major bloom of filamentous cyanobacteria had taken place in the Gulf which disappeared prior to our cruise (Maija Balode, pers. commun., see also Kahru *et al.*, 1994). Other more important groups were the cryptophytes and pico-cyanobacteria (Table 1). The total autotrophic standing stock was in the range of 10–24 g m^{-1}.

Sedimentation and loss rates of CHL and phytoplankton

The total vertical flux of phytoplankton biomass (wet weight) is given in Table 3, and the species with consistent net flux pattern (net flux in >70% of the cases) and their median loss rates and share from the total phytoplankton flux is given in Table 4. The principal constituting species in spring 1995 was *Thalassiosira baltica* (flux 0.2–6 g m^{-2} d^{-1}; loss rates 3–75% d^{-1}), contributing generally 90% of the total phytoplankton vertical flux (Table 4). The dominant species in the water column, *Peridiniella catenata* and *Katodinium rotundatum*, usually had a flux <100 mg m^{-2} d^{-1} and loss rates <3% d^{-1}, yet, higher in Stn. 101A (flux < 500 mg m^{-2} d^{-1} and < 300 mg m^{-2} d^{-1}, respectively; loss rates 9–15% d^{-1}). Several other diatom and nanoflagellate species had loss rates >10% d^{-1} in Stn. 101A, while usual loss rates remained <4% d^{-1} in other stations. The sedimentation of CHL varied between 0.5–14 mg m^{-2} d^{-1} and the flux of heterotrophic flagellates remained generally <100 mg m^{-2} d^{-1} (loss rates <5% d^{-1}).

In midsummer 1994 the total vertical flux of phytoplankton was 0.05–1.4 g m^{-2} d^{-1} (Table 3). From the dominant species in the water column, *Aphanizomenon flos-aquae* had a very uneven sedimentation pattern, from no net sedimentation to 500 mg m^{-2} d^{-1} (loss rates <7% d^{-1}). A consistent net flux was revealed by pico-cyanobacteria (<180 mg m^{-2} d^{-1}) and ANANO (<200 mg m^{-2} d^{-1}; 200–940 mg m^{-2} d^{-1} in Stn. 101A), however, the loss rates were seldom >5% d^{-1}. In many cases an elevated vertical flux in the deepest sediment trap (35 m depth; i.e. below the pycnocline) was caused by the resuspension of the dormant population of *Thalassiosira baltica* (70–80% of the total phytoplankton flux in these cases; Table 3). The sedimentation of CHL above the pycnocline was <2.5 mg m^{-2} d^{-1} and increased in the lowest sediment trap up to 3.6 mg m^{-2} d^{-1} due to resuspension of *T. baltica*.

The sedimentation of HNANO was <30 mg m^{-2} d^{-1} and loss rates were usually <5% d^{-1}. However, the vertical flux of the *Gymnodinium/Gyrodinium* type heterotrophic dinoflagellates was commonly 100–500 mg m^{-2} d^{-1} (except in Stn. 101A where these organisms were absent) and the loss rates were very high (up to 77% d^{-1}; as an extreme 175% d^{-1}) suggesting vertical migration and subsequent entrapment into the sediment traps (see also Olli, 1998).

Table 3

Sedimentation (mg m^{-2} d^{-1}) of phytoplankton biomass. Depth values in paranthesis in 1993 denote sediment trap depths in Stn. 101A. In 1994 sedimentation in the lower trap is given also after correction for the resuspended *Thalassiosira baltica* (35*)

Depth(m)	119/1	119/2	119/3	119/4	119/5	101A	135	137A	121	121A
1995										
10	3308	1697	280	226	1026	1980	481	1624		858
15	1691	2263	511	236	1079	3401	770	2543		1587
20	4242	2102	1644	3285	2076	5094	1116	5070		1184
35	6120	6362	2200	804	4209		1773	6549		5671
1994										
10	61	237	620	250	304	567	193	211	89	
15	47	237	370	994	308	1372	191	198	64	
20	67	229	301	542	426	1212	162	168	142	
35	704	744	1282	669	586		576	389	392	
35*	118	217	273	532	536			179	352	
1993										
11(8)		102	34	82		34	37	181		
21(12)		149	33	40		338	82	85		
35(16)		138	73	70		41	142	196		

In early autumn 1993 the phytoplankton sedimentation was mainly <150 mg m^{-2} d^{-1}. The sedimentation pattern of *Aphanizomenon flos-aquae* was variable, from no net sedimentation to 150 mg m^{-2} d^{-1} (loss rates <33% d^{-1}; median 0.2% d^{-1}). A consistent flux pattern and higher loss rates were revealed by several non-motile species (*Oocystis* spp., *Woronichinia compacta*, *Sphaerocystis* sp, also *Thalassiosira baltica*; Table 4). Sedimentation of CHL was <1 mg m^{-2} d^{-1} and heterotrophic flagellates <10 mg m^{-2} d^{-1}.

Discussion

The three studied seasonal stages (spring, middle of summer and early autumn) differed substantially with respect to total biomass of phytoplankton. The phytoplankton biomass was highest in spring (2700–7600 µg l^{-1}) dominated by dinoflagellates, lower in midsummer (779–2600 µg l^{-1}) characterised by high abundance of *Aphanizomenon flos-aquae* and increasing amount of picoplankton, and lowest in early autumn (330–860 µg l^{-1}) dominated by *A. flos-aquae* and nanoflagellates. Compared to the western Gulf of Finland (Niemi, 1975; Niemi and Åström, 1987; Lignell *et al.* 1993; Heiskanen and Kononen, 1994; Olli, unpublished data) the average and maximum biomass during the spring bloom and summer periods were alike or somewhat higher in the Gulf of Riga. However, due to the high within season variability of the phytoplankton biomass in the Gulf of Riga we can not conclude it to be on average higher than in adjacent areas. The high variability was probably due to

patchy distribution, but also due to increase (growth) within a time scale of 2 weeks (e.g. midsummer 1994). The relatively low early autumn phytoplankton biomass values agree with those reported by Heiskanen and Kononen (1994) from the Gulf of Finland.

Table 4

Concistency of vertical flux and median loss rates of individual taxa. Only species with net vertical flux in >70% of the observed cases in each year are included (1993 n=18; 1994 — 1995 n=35)

Year	Taxon	Consistency (%)	loss	% of total flux
1995	*Thalassiosira baltica*	100	21.2	88.4
	Melosira arctica	86	4.0	1.2
	Chaetoceros wighamii	83	2.4	<0.1
	Woronichinia compacta	83	1.3	0.2
	*Gymnodinium/Gyrodinium**	80	1.7	60.5
	Monoraphidium sp.	74	0.8	0.2
	Plagioselmis prolonga	74	1.1	<0.1
	Chaetoceros danicus	71	0.5	<0.1
	Katodinium rotundatum	71	0.4	3.6
1994	*pico-cyanobacteria*	100	1.5	16.6
	ANANO	94	1.3	19.6
	Oocystis spp.	91	1.7	1.7
	Woronichinia compacta	91	1.6	1.3
	Thalassiosira baltica	86	9.9	3.0
	*Gymnodinium/Gyrodinium**	86	9.5	61.6
	Aphanizomenon flos-aquae	74	1.2	24.2
1993	*Oocystis* spp.	100	4.7	32.1
	Woronichinia compacta	89	2.6	2.0
	Thalassiosira baltica	83	24.7	11.8
	Sphaerocystis sp.	78	3.4	0.7
	Pyramimonas spp.	78	0.9	0.5
	*Dinophysis rotundata**	78	0.9	6.5
	Chaetoceros danicus	72	0.7	0.1

During the spring cruise in 1995 the phytoplankton was dominated by the dinoflagellates *Peridiniella catenata* and *Katodinium rotundatum*. Dinoflagellates are commonly reported as a (sub)dominant group during the vernal bloom in the Baltic Sea (Edler, 1979a; Hobro, 1979b; Niemi and Åström, 1987; Heiskanen and Kononen, 1994). However, a common dominant winter and spring dinoflagellate in the coastal areas of the Baltic Proper, *Scrippsiella hangoei* was not present in the Gulf of Riga. The only notably abundant diatom species during the 1995 spring bloom was *Thalassiosira baltica*, while the other typical spring species from the area (Olli, 1993) and from the Gulf of Finland (Niemi and Åström, 1987; Heiskanen and Kononen, 1984) *Sceletonema costatum*, *Achnanthes taeniata*, *Melosira arctica*, *Chaetoceros holsaticus*, *C. wighamii*, *C. danicus*, *Diatoma elongatum* were of low abundance.

The abundance of HNANO was comparable or slightly higher than reported from the coastal areas of the western Gulf of Finland (Kuuppo, 1994; Olli, unpublished data).

Sources of uncertainty

The calculation of vertical flux involves cell abundance estimates in the sediment trap and in the surrounding water column. Both estimates are subjected to errors of sampling, subsampling and counting (see Vernick, 1971; Duarte *et al.*, 1990) which can propagate to the final sedimentation estimate. Even more, the sediment traps integrates over the whole exposure time, while water column samples used for the phytoplankton vertical flux and loss rate calculations were taken only in the beginning of the sediment trap deployment. Thus care must be taken in interpreting occasional high fluxes and loss rates of individual species. As extremes tend to influence mean values, median was used to describe loss rates and relative importance of the sedimentation of species on a seasonal scale (Table 4). Total sedimentation of phytoplankton biomass represents an upper value as it has been obtained by summing only the positive fluxes. A more significant indication of true sedimentation is a consistent positive flux values, displayed by several non-motile forms (e.g. *Oocystis* spp., *Woronichinia compacta*).

The fate of the vernal bloom phytoplankton biomass

In the coastal Baltic Sea the fate of the newly produced organic matter during spring is largely determined by the species composition, specific life cycles and evolutionary adaptations of the dominant phytoplankton groups. When the bloom is dominated by diatoms, the bulk of the new production sediments out of the productive layer as resting cells, cysts or vegetative cells (Olesen, 1993; Heiskanen and Kononen, 1994). During a dinoflagellate dominated bloom the cells can pass sexual reproduction and encystment followed by rapid sedimentation (e.g. *Scrippsiella hangoei*; Heiskanen, 1993) or disintegrate in the water column and thus contribute to the slowly sinking phytodetrital pool (Sellner *et al.*, 1993; Heiskanen and Kononen, 1994).

During the present study the dominant vernal bloom species (the dinoflagellates *Peridiniella catenata* and *Katodinium rotundatum*) had only a minor impact on the total phytoplankton sedimentation, while the diatom *Thalassiosira baltica* formed 90% of the settled phytoplankton biomass. This is in accord with the findings of Heiskanen and Kononen (1994) from the Gulf of Finland and Passow (1991) from the central Baltic Sea, where the number of diatoms settled in comparison to the average suspended cell concentration in the surface layer, were considerably higher compared to the other phytoplankton species.

Depletion of nutrients usually leads to ceased growth and accelerated sinking of diatoms (Bienfang and Harrison, 1984; Harrison *et al.*, 1986; Davey, 1988; Waite *et al.*, 1992). However, during the spring cruise nutrients were not depleted from the surface mixed layer. The water column stabilisation due to thermal stratification is another major factor leading enhanced sedimentation of diatoms (Bodungen *et al.*, 1981; Smetacek *et al.*, 1984; Ruiz *et al.*, 1996). High turbidity caused by high phytoplankton biomass decreases the depth of euphotic layer, giving even more advantages to motile species capable of controlling their vertical position in the water column. Light limitation is known to increase the sedimentation rates of diatoms (Culver and Smith, 1989; Riebesell, 1989).

It is proposed here that the decline of the diatom populations in the Gulf of Riga was controlled by water column stability caused by thermal stratification, leading to the inability of the heavy *Thalassiosira baltica* cells to compete with the flagellates in maintaining buoyancy. The relatively high abundance of cells in the lower water column, high sedimentation

rates (up to 5400 mg m^{-2} d^{-1}) and loss rates suggest that the share of diatoms in the water column might have been larger during the earlier stage of the bloom. The fate of the *Thalassiosira* population is thus sedimentation to the bottom. Generally, the life cycle of several vernal diatoms in coastal areas involves the formation of resting cells and quick sedimentation to dark and cold bottom layers (Smetacek, 1985; McQuoid and Hobson, 1995) where the dormant population can survive for prolonged periods (Anita, 1976). Indeed, during our study this population of *T. baltica* resting cells was found in the water column below the pycnocline and particularly abundantly in the bottom nepheloid layer during the summer cruises.

The sedimentation of other spring bloom species, however was insignificant. Even the high absolute values obtained for the dominant species (up to 300 µg m^{-2} d^{-1} in the case of *Peridiniella catenata*) were usually only a fraction of percentage from the total population. There is no information on the life cycle, possible sexual process or cyst formation of this species in the Baltic Sea. Due to the low abundance and longer generation times the zooplankton is usually not able to control the phytoplankton spring bloom in the Baltic Sea (Forsskåhl *et al.*, 1982; Peinert *et al.*, 1982). It is assumed that the bulk of the biomass disintegrates in the water column and contributes to the slowly sinking phytodetrital pool. Similar scenarios have been suggested for the dinoflagellate blooms in the Cheasapeake Bay, where direct sedimentation of vegetative cell account only for a fraction of the populations while the settling detrital materiel is rich in dinoflagellate pigments and their degradation products (Sellner *et al.*, 1993). Also in the southern Baltic Sea (Kiel Bight), the fate of the autumnal *Ceratium* blooms was mainly dissolution and decomposition in the water column, while sedimentation was negligible (Noji *et al.*, 1986).

The role of pico-nano fraction and filamentous cyanobacteria in midsummer

The midsummer stage in 1994 was characterised by increasing abundance of pico-sized autotrophs, mainly *Thalassiosira pseudonana* (Bacillariophyceae) and *Hemiselmis virescens* (Cryptophyceae) and pico-cyanobacteria. It is known that smaller species gain dominance in nutrient enriched environments due to their high growth rates and nutrient uptake potential (r-selected species *sensu* Margalef, 1978). Prior to the cruise in 1994 strong winds had mixed the water column down to 25–30 m, which followed by a consistent stabilisation period during the cruise, created a nutrient enriched stratified environment favourable to opportunistic, fast growing species. This explains the increase of pico-cyanobacteria and ANANO fraction in the surface layer and parallels to the stage I of Margalef's successional model (Margalef, 1958).

It is interesting to note the consistent net vertical flux and significant contribution to the total phytoplankton sedimentation of these smallest planktonic autotrophs, although the loss rates remained low (Table 4). From the theoretical size considerations it is clear that these organisms do not sink as single individual cells. However, when forming aggregates, or after entanglement to sinking detrital particles, such pathway is likely. This is supported by the direct evidence from epifluorescence microscopy, where detrital aggregates were heavily colonised by pico-cyanobacteria. It is also likely that the ANANO compartments in the sediment traps were bound to sinking aggregates which disintegrated later during sample processing (the samples were gently, but thoroughly shaken before sub-sampling and filtration). It has been shown that the stickiness of *Thalassiosira pseudonana* increases by more

than two orders of magnitude as the cells become nutrient limited and growth ceases (Kiørboe *et al.*, 1990).

In addition to high abundance of ANANO in summer 1994 the summer stage was also characterised by high abundance of nano-sized cryptomonads, *Teleaulax acuta*, *T. amphioxeia* and *Plagioselmis prolonga*. *Teleaulax* was also abundant in other seasons, but contributed significantly to the total biomass only in early autumn 1993. However, the significance of small species can not be assessed through biomass because of the general size dependence of vital physiological processes like production and respiration (Joint, 1991; Tang, 1995), indicating that relatively more energy and matter is channelled through an equivalent biomass of smaller species. This is particularly true in the case of cryptomonads, which are generally considered as a preferred and good quality food for the zooplankton (Burkill *et al.*, 1987; Skogstad *et al.*, 1987; Ahlgren *et al.*, 1990; Burns and Xu, 1990).

The role of filamentous cyanobacteria in the elemental cycles of the Baltic Sea is still unclear. They can form dense blooms and surface scums, which often coincides with calm weather and elevated surface temperature in the Baltic Sea (Niemi, 1979; Kahru *et al.*, 1994). Surface accumulation are regulated by buoyancy control through gas vacuole synthesis and production and utilisation of condensed carbohydrates (Reynolds *et al.*, 1987; Oliver, 1994). It is suggested that the potential to fix atmospheric nitrogen (Elder and Parker, 1984; Lindahl and Wallström, 1985) provides an advantage over other algal groups and that the heterocystous cyanobacteria are generally favoured by low N/P ratios (Niemi, 1979) in the Baltic Sea. However, depletion of macro-nutrients, particularly nitrogen causes loss of buoyancy (Klemer *et al.*, 1982; Spencer and King, 1989; Klemer, 1991), probably because relatively much N is needed for the synthesis of the proteineous walls of the gas vesicles and/or accumulation of high molecular carbohydrate ballast unmatched by cell tissue build up (Klemer, 1978; Kromkamp *et al.*, 1986).

During the midsummer stage in 1994 *Aphanizomenon flos-aquae* increased in abundance, while another important species, *Nodularia spumigena* was only rarely encountered. Although *A. flos-aquae* contributed significantly to the total vertical flux of phytoplankton biomass (Table 4) the population remained well buoyant and the sedimentation loss rates were low. This contrast with the findings of Heiskanen and Olli (1996) from a nutrient deplete situation in the Gulf of Finland, where *A. flos-aquae* had loss rates up to 40% d^{-1}. However, the filaments can recover buoyancy in the deep nutrient replete layers through synthesis of new gas vesicles by using energy accumulated in the carbohydrates (Kromkamp *et al.*, 1986). As the filamentous cyanobacteria are only poorly grazed in the Baltic Sea (Sellner *et al.*, 1994; 1996), their biomass probably disintegrates largely in the water column and channels to the microbial food-web.

A major factor influencing the sedimentation pattern in 1994 was the high amount of resuspended *Thalassiosira baltica* cells in the lower sediment trap (35 m) below the pycnocline, causing a significant signal also in the CHL sedimentation. It is assumed that the specific sedimentation speed of this dormant population was quite high and the resuspension is rather a function of turbulent energy in the deep layers, which was quite variable (see Floderus *et al.*, 1998) and explains the variability of the secondary flux. It is suggested here that the primary vertical flux values of particulate matter should be corrected for the secondary sedimentation of *T. baltica* dormant population.

Post-bloom stage in early autumn 1993

The early autumn stage was characterised by low abundance of phytoplankton and heterotrophic flagellates and low sedimentation. High abundance of tintinnid ciliates (from the genus *Heliocostomella*) was observed in 1993 (data not shown) which, according to visual estimates, overwhelmed the total micro-phytoplankton biomass and the whole system was probably net heterotrophic. *Heliocostomella* is known to appear as short "blooms" in connection with high numbers of the filamentous cyanobacterium *Aphanizomenon flos-aquae* (Kivi, 1996). The diet of tintinnids is known to be nano-plankton and also pico-cyanobacteria (Verity and Villareal, 1986; Bernard and Rassoulzadegan, 1993). Thus it could be speculated that in connection with the decline of the *Aphanizomenon* bloom the biomass of the cyanobacterium disintegrated in the water column, introducing large amounts of dissolved organic carbon to the system. This fuelled the microbial loop carbon pathway which cascaded to ciliates. The high abundance of tintinnid ciliates could have controlled the populations of heterotrophic nanoflagellates and bacteria during the 1993 late summer period.

A characteristic feature seemed to be a consistent flux of several non-motile species (e.g. *Oocystis* spp., *Woronichinia compacta*, *Thalassiosira baltica*, *Sphaerocystis* sp.). Although these species were of moderate abundance and as such did not contribute much to the total sedimentation, the generally consistent net flux and loss rates of approximately 5% d^{-1} suggest a real sedimentation process. It is also supported by the finding that these species were found in measurable quantities in the middle and deep layers of the water column, in contrast to the nano-flagellated species (e.g. *Pyramimonas* spp., *Plagioselmis prolonga*, *Teleaulax* spp.; Table 1). It is likely that a 5% daily loss rate of non-motile species has no significant impact on population dynamics and is probably compensated by other processes, e.g. higher resistance to grazing due to mucilage envelopes (Porter, 1976). Yet it points out the adaptional advantage of flagellated forms in stagnant water columns (Viner, 1985).

The role of heterotrophic dinoflagellates

The role of heterotrophic dinoflagellates in the mineralisation processes was particularly pronounced in mid summer 1994. The understanding of the ecological role of heterotrophic dinoflagellates in the food-web has been hampered by lack of experimental and observational data, largely due to difficulties in recognising and handling the delicate organisms (Lessard and Swift, 1985; Hansen, 1991a). The maximum biomass of heterotrophic dinoflagellates can exceed that of phytoplankton and other zooplankton groups (Hansen, 1991b), growth rates can be up to 1.7 divisions day^{-1} (Jacobson and Anderson, 1993), grazing rates are comparable to ciliates (Lessard and Swift, 1985), and the range of prey items include heterotrophic bacteria, flagellates, diatoms, other heterotrophic dinoflagellates, ciliates and mesozooplankton eggs (Kimor, 1981; Lessard and Swift, 1985; Jacobson and Anderson, 1986; Hansen, 1991a; Bockstahler and Coats, 1993; Jacobson and Anderson, 1993;). Many studies stress the co-occurrences of heterotrophic dinoflagellate maxima with blooms of diatoms or other large phytoplankton (Hansen, 1991b; Lessard, 1991), providing clues to food preferences, and demonstrating a departure from the currently believed more or less fixed size relationship between prey and predator of 1:10 (Azam *et al.*, 1983), however, see also Hansen *et al.*, (1994).

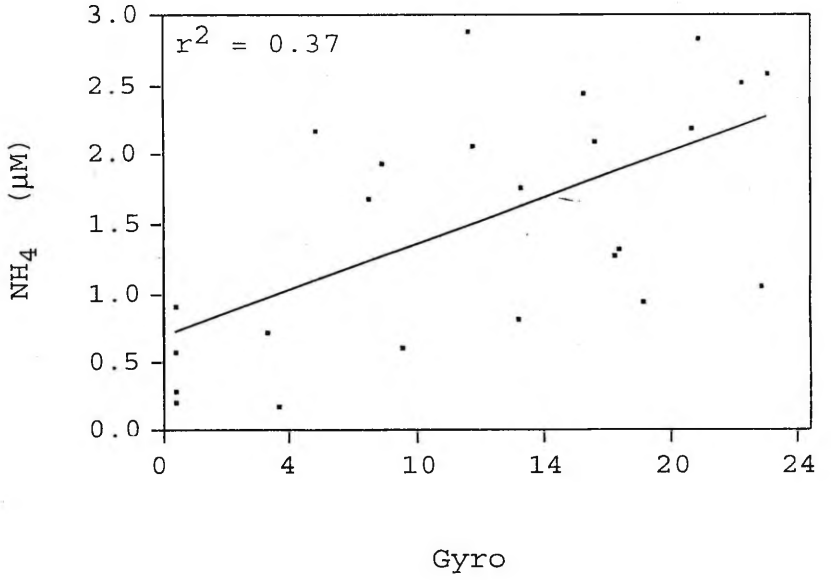

Fig. 6. Linear best fit of ammonium concentration (NH_4 µM) and square root transformed abundance of the naked dinoflagellates (Gyro).

During the present study, large (40–60 µm) naked heterotrophic dinoflagellates of the *Gymnodinium/Gyrodinium* type were particularly abundant during the summer cruise in 1994. The depth profiles of cell abundance in our study revealed maxima at about 20 m Olli, 1998) layer which coincides with the maxima of vertical ammonium profiles. The linear fit between the abundance of these organisms (square root transformed) and the concentration of ammonium had a slope of 0.067 ($p = 0.0017$) and a coefficient of determination (r^2) 0.37 (Fig. 6). It is suggested that these heterotrophic dinoflagellates were responsible for the ammonium regeneration during the summer cruise which also underlines their role in mineralisation of organic matter. Heterotrophic dinoflagellates have been implicated as important contributors to ammonium regeneration also in the Oslofjord (Paasche and Kristiansen, 1982). The measured high vertical flux values for the heterotrophic dinoflagellates in the depth of 20 meters were probably not real values, but rather artefacts due to vertical migration and subsequent entrapment into the cylinders. Contamination of sediment trap fluxes by vertically migrating autotrophic dinoflagellates is known from the Gulf of Finland (Heiskanen, 1995). It is possible that the dinoflagellates were attracted to the sediment traps by higher concentration of prey organisms or settling attached to detrital aggregates. The dinoflagellates from sediment traps were more often observed to have ingested food particles than those from the water column samples. Common prey items were *Thalassiosira baltica* cells, ciliates, rotifers (*Keratella* sp.) and spermatophores of copepods, the later exceeded the size of the dinoflagellate up to an order of magnitude. Large naked dinoflagellates were much less abundant in spring 1995, which is surprising in the light of the occurrence patterns reported in literature (Hansen, 1991b; Lessard, 1991).

There was also an abundant population of thecate heterotrophic dinoflagellates (e.g. *Protoperidinium bipes*, *P. brevipes*, several unidentified species) during all the periods studied, although in times of high phytoplankton biomass (i.e. spring 1995) they remained

relatively unnoticed. The vertical distribution profiles of *P. brevipes* was studied in summer 1994 (Olli, 1998) and revealed significant abundance peaks just below the pycnocline (25–30 m). As diatoms are believed to be the sole prey items for the genus *Protoperidinium* (Jacobson and Anderson, 1986), it is hypothesised here that the *P. brevipes* population was preying on the abundant (up to 560 $\mu g\ l^{-1}$) resuspended population of *Thalassiosira baltica* resting cells. The feeding mechanism of *Protoperidinium* involves engulfment of the prey within a pseudopod, transportation of the prey cell content through the pseudopod, and leaving the empty but intact frustule behind (Jacobson and Anderson, 1986). This could have been the reason for numerous empty frustules in the bottom layer, although we can not rule out other death causes. Following the hypothesis of Smetacek (1985), it appears that indeed, the vernal diatoms benefit from a life strategy which involves sedimentation of the populations after the spring bloom to avoid grazing and respiration losses in the nutrient depleted and warm surface mixed layer which
no more supports growth. However, even in bottom layers the dormant populations can be subjected to grazing. In our study the abundance of *T. baltica* cells in the deep resuspension water was less in 1993 compared to 1994, which might have been due to grazing, although we can not rule out the impact of horizontal sediment transportation to deep accumulation areas (Floderus *et al.*, 1998). Growth and grazing rate estimates of *Protoperidinium* on diatoms indicate that a significant proportion of diatom standing crop may be grazed (Jacobson and Anderson, 1993). Thus in the Gulf of Riga the fate of the settled diatoms is at least partly grazing by planktonic heterotrophic dinoflagellates.

Concluding remarks

We found a clear seasonal difference in the species composition and biomass of phytoplankton and heterotrophic nanoflagellates in the Gulf of Riga. The total autotrophic biomass was in the same range or slightly higher compared to available data from adjacent areas. However, the temporal variability (in the time scale of days) of phytoplankton biomass and sedimentation in Stn. 119 was greater than the spatial variability, and thus we conclude that there were no significant differences in the phytoplankton species composition, biomass and sedimentation between the distinct areas of the southern part of the Gulf of Riga (with a possible exception of Stn. 101A).

The fate of the dinoflagellate dominated spring bloom was probably disintegration in the water column and sedimentation in the form of slowly sinking phytodetritus. The relative abundances of species in the water column were not proportionally reflected in the sedimented material. The species contributing most to the settling phytoplankton biomass was the diatom *Thalassiosira baltica*. *T. baltica* formed a dormant population in the bottom nepheloyd layer which was often resuspended in the water column below the pycnocline.

The stabilisation period in midsummer 1994 was characterised by increase of picoplankton and *Aphanizomenon flos-aquae*. The species contributed also most to the total phytoplankton vertical flux, although the loss rates were low. large heterotrophic dinoflagellates were associated with the accumulation of ammonium in the sub-surface depth in midsummer 1994, which underlines their role as demineralisers. The grazing potential and place in the food-web structure of these organisms needs further research.

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VI

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DIEL VERTICAL MIGRATION OF PHYTOPLANKTON AND HETEROTROPHIC FLAGELLATES IN THE GULF OF RIGA

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Abstract

Vertical distribution of a phototrophic ciliate (*Mesodinium rubrum*), autotrophic dinoflagellates (*Peridiniella catenata*, *Katodinium rotundatum*, *Dinophysis acuminata*), a cryptomonad (*Teleaulax* sp.), a filamentous cyanobacterium (*Aphanizomenon flos-aquae*), a non-motile chlorophyte (*Monoraphidium* sp.) and two heterotrophic dinoflagellates were studied during two diel periods in spring (May 1–2 and 27–28; 1995) and summer (June 26–27 and July 6–7; 1994) in the southern part of the Gulf of Riga, the Baltic Sea. The two seasons, corresponding to the vernal bloom and summer stage, differed considerably with respect to phytoplankton community, hydrography and vertical distribution of the species. In spring the cells stayed in the upper mixed layer above a strong thermocline at 12–15 m depth, and changes in the vertical distribution were related to surface avoidance in the middle of the day. By using correspondence analysis the vertical distribution of all the motile species were shown to differ significantly from the non-motile *Monoraphidium*, but not from each other. The vertical migration was reflected in a higher variability in the depth distribution patterns of the motile species, compared to *Monoraphidium*. In summer 1994, *Aphanizomenon*, *Dinophysis* and *Teleaulax* showed similar depth distribution patterns during the first period, but different from *Mesodinium* and the heterotrophic dinoflagellates, while during the second period all the autotrophic species had a specific depth distribution pattern. *Mesodinium rubrum* revealed a considerably different depth distribution between the two seasons, characterised by surface accumulation in spring and relatively uniform depth distribution over the whole sampling range (0–30 m) in summer. The results demonstrate different vertical niche separation strategies between species depending on resource availability.

Introduction

The well known concepts of phytoplankton life strategies from fresh waters (Reynolds, 1988) and marine environments (Margalef, 1978) emphasise scarcity of ecological space where all the environmental factors are optimal for growth; a common case is that light (also due to strong vertical mixing) or nutrients are limiting. In temperate boreal regions reduced vertical mixing (e.g. due to thermal or salinity stratification) in spring prolongs the residence time of cells in the illuminated layer, leading to increase of production and ultimately to the outbreak of the vernal bloom (Kahru and Nõmmann, 1990; Sverdrup, 1953). In the absence of additional resources (e.g. through advection or upwelling) the stratified illuminated layer fails to meet the nutrient demands of the exponentially growing populations for prolonged periods, leading to a vertical separation of light and nutrients — clearly an unfavourable condition for primary producers. Alone or together with increasing water column stability, this leads to sedimentation of vernal bloom diatoms (Bienfang *et al.*, 1982; Bienfang and Harrison, 1984; Davey, 1988; Waite *et al.*, 1992; Heiskanen and Kononen, 1994). In nutrient deplete and stratified conditions the ability to use deep nutrient resources

provides an advantage over non-motile species (e.g. diatoms) and might prolong the vernal bloom.

It is commonly agreed that the potential to perform diurnal vertical migration (DVM) grants the micro-organisms with competitional advantage to exploit high light levels near the surface where low concentrations of inorganic nutrients would normally limit growth, while during night the cells descend to deeper layers where nutrient demands are fulfilled and intercellular reserves recharged (Eppley *et al.*, 1968; Cullen, 1985; Lieberman and Shilo, 1994). Apart from deep nutrient retrieval the control on vertical position enables the cells to exploit micro-scale pachiness in the water column (Hamner, 1988; Owen, 1989). Yet another aspect has been pointed out by Sommer (1982), involving variation in migration as a consequence of differential light requirements leading to ecological niche separation and relaxation of interspecific competition. Indeed, in field conditions redispersal by turbulent motion counteracts the behavioural adaptations of vertical migration. Thus the actual vertical profiles of cell abundance are a consequence of both, the behavioural life strategies of the species to optimise the growth conditions and the external physical forcing.

The range of autotrophic organisms capable of prolonged directed vertical movements involves besides the flagellated phytoplankton also the gas-vacuolated cyanobacteria and the autotrophic ciliate *Mesodinium rubrum*. The species for the present study were selected on the basis of previous knowledge of migration potential (Lindholm, 1985; Passow, 1991; Heiskanen, 1995), theoretical size considerations (Sommer, 1988) and sufficient abundance. We investigate the vertical profiles and migrational behaviour of several dominant species of phytoflagellates (*Peridiniella catenata*, *Katodinium rotundatum*, *Dinophysis acuminata*, *Teleaulax* spp.), a filamentous cyanobacterium (*Aphanizomenon flos-aquae*) and a phototrophic ciliate (*Mesodinium rubrum*) during the vernal bloom and summer periods in the southern part of the Gulf of Riga. Two heterotrophic dinoflagellates (*Protoperidinium brevipes* and a large naked dinoflagellate of the *Gymnodinium/Gyrodinium* type were included in the study due to their high abundance and potential impact to the planktonic system. As a reference point a coccoid chlorophyte *Monoraphidium mirabile* was included as a passive, non-motile autotroph in spring 1995.

Material and methods

The sampling was carried out at station 119 (57° 18' N; 23° 51' E; depth 42 m) in the southern part of the Gulf of Riga, the Baltic Sea. In 1994 two 24 hour sampling periods (June 26–27 starting at 16.00 and July 6–7 starting at 8.00) were chosen which were the first and last full 24 h sojourns to the station. In May 1995 the same sampling procedure was repeated during one 28 hour period (May 1–2 starting at 20.00) while due to weather constraints the second period (May 7–8 starting at 1.00) was reduced to 20 h. During each period vertical profiles of phytoplankton were taken at 4 hour intervals using a 3 l Ruttner water sampler (1994) or an array of 5 l Niskin water samplers (1995). The vertical range was from the surface to 30 m layer (which was below the primary pycnocline) with 3 m vertical intervals. Sub-samples (100 ml) for phytoplankton were retrieved within a couple of minutes and fixed immediately with acid Lugol solution. The cell concentrations were determined with inverted microscope (Leica DM IL, phase contrast optics, 125* and 500* magnification); at least 200 counting units were attempted to count depending on the density of the sample; in the case of *Aphanizomenon flos-aquae* the length of the counted filaments was measured.

CTD profiles of salinity, temperature and *in situ* fluorescence (Q Instruments, DK) were taken at least twice during each diurnal cycle to assess the water column stability and vertical distribution of chlorophyll *a*. Photosynthetically active radiation (PAR) reaching the sea surface was measured continuously using a Li-Cor 190-SA sensor and a Grant (UK) logger as integrator. A wind-meter was fixed at the uppermost top of the vessel (ca 10 m from the sea surface) and connected to the Grant data logger (wind speed was averaged for every 10 minutes) during the whole cruise in 1995. Mineral nutrients were determined from discrete profiles taken from 0 m, 2.5 m, 5 m, 10 m, 15 m, 20 m, 30 m and 40 m depths at the beginning and end of the stay at the station. Mineral nutrients (NO_3-N, NH_4-N, PO_4-P) were analysed immediately on board the vessel applying standard colorimetric methods (Grasshoff *et al.*, 1983).

The depth profiles of the species were analysed by correspondence analysis (ADE-4 software; anonymous ftp: biom3.univ-lyon1.fr). The cell abundance data were arranged in a matrix with 11 columns (corresponding to the 11 discrete depths) and rows corresponding to sampling times, arranged in blocks corresponding to the species (thus each row corresponds to a depth profile of a particular species on a given time). With correspondence analysis the 11 discrete depths were reduced to a few ordination axes, enabling a simultaneous visualisation of the depth profiles of the species on a two dimensional space (usually the first two axes encountered for >85% of the information). It is possible to group the profiles defined by species (profiles of one species belonging to one group) or symmetrically by sampling time. Further, the total variation in the data set can be partitioned into within-groups and between-groups variability. The significance of the between groups variability can be tested statistically with a random permutation test. This involves a random exchange of data points (corresponding to the vertical profiles of the micro-organisms) between the defined groups and comparing the original variability between the group centres (i.e. respective centres of gravity) with the newly recalculated variability. If the original between group variability exceeds significantly the simulated variability (at least 1000 permutations were performed), the original groups were considered to be statistically different.

Results

Weather, hydrography, nutrients

During both cruises the average wind speed was relatively moderate (generally 3–6 m s^{-1}). On May 2, 1995, a cloudless and calm weather prevailed (maximum mid-day radiation 1700 µE m^{-2} s^{-1}; wind below 1 m s^{-1}), which resulted in an increase of the surface layer temperature from 4.5°C to 6.7°C during the day and a formation of a sharp secondary thermocline at 3 m depth (Fig. 1A). The primary thermocline and main density discontinuity (measured as Brunt-Väisälä buoyancy; N^2) were at the depth of 15 m (Fig. 1A). Mineral nutrients were plenty in the surface layer. During May 2 NO_3-N increased from ca 80 µg l^{-1} to 105 µg l^{-1} in the upper 10 m layer; PO_4-P remained 5–6 µg l^{-1} and NH_4-N decreased from 2.4 to 1.2 µg l^{-1} . Below the pycnocline phosphate values were 20–30 µg l^{-1} and nitrate was 90–130 µg l^{-1} (Fig. 2A). During the second period a calm weather turned windy (up to 8 m s^{-1}) towards the evening of May 7. This caused a decay of the initially pronounced pycnocline at 15 m (May 7, 8:00) by the evening (May 7; 20:00, see Fig. 1B beginning and end temperature profiles), resulting in a significant increase of nutrients in the surface layer (Fig. 2B) (NO_3-N increase from 8 µg l^{-1} to 58 µg l^{-1}; PO_4-P from 0.5 µg l^{-1} to 1.5 µg l^{-1} and NH_4-N from 0.8 to 3.1 µg l^{-1} at 2.5 m depth). However, the main density dis-

continuity remained at 15 m (Fig. 1B). There was a dense fog on May 7 and the maximum radiation did not exceed 500 μE m^{-2} s^{-1}.

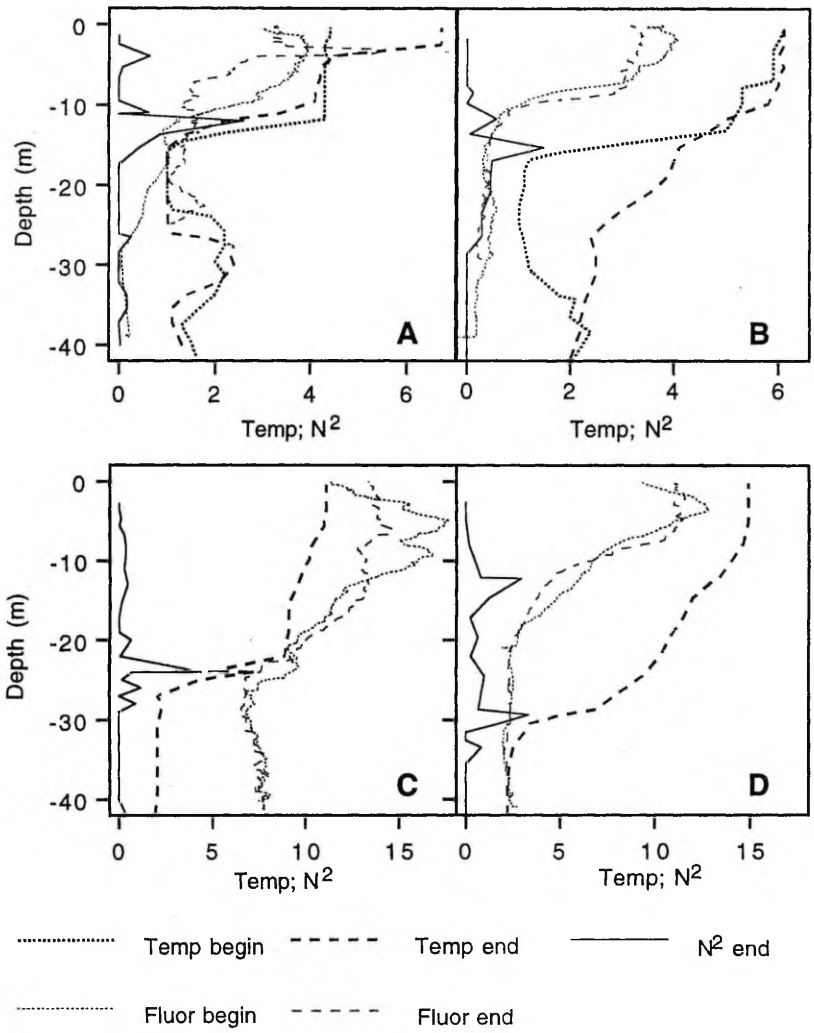

Fig. 1. Temperature (°C), *in situ* fluorescence (relative units), and stratification (square of the Brunt-Väisälä frequency: N^2, s^{-1}) in May 2, 1995 (A; Temp begin 7.30; N^2 and Temp end 20.50; Fluor begin 9.30; Fluor end 22.30), May 7, 1995 (B; Temp begin 8.15; N^2 and Temp end 19.50; Fluor begin 8.30; Fluor end 20.30), June 27, 1994 (C; Temp and N^2, 7.45; Fluor begin — June 26, 18.30; Fluor end — June 27, 19.30) and June 7, 1994 (D; Temp and N^2, 00.20; Fluor begin — July 6, 8.00; Fluor end — July 7, 4.15). Measurements taken at the beginning and end are given separately only in case of substantial difference.

In 1994 windless weather with no or little waves prevailed during the both periods. The maximum mid-day radiation levels were 2000 μE m^{-2} s^{-1} and 1800 μE m^{-2} s^{-1} during the first and second periods in 1994, respectively. On June 27 the water temperature decreased

from 12°C at the surface to 8°C at the pycnocline (25 m depth), and dropped to 1°C below the pycnocline (Fig. 1C). Mineral nutrients were still quite high, NO_3-N was 10–28 μg l^{-1} on June 26 and 5–7 μg l^{-1} on June 27 in the upper 10 m layer and 250 μg l^{-1} below the pycnocline at 22 m depth. Phosphate was 0.6 μg l^{-1} on June 26 and up to 2.8 μg l^{-1} on June 27 in the upper 10 m layer and 5–11 μg l^{-1} below the pycnocline. There was a notable accumulation of NH_4-N from 83 μg l^{-1} on June 26 to 209 μg l^{-1} (at 20 m depth) on June 27 (Fig. 2C). On July 7 the pycnocline was less pronounced and the water column temperature decreased gradually from 15° at the surface to 7° at 30 m depth, while the main density discontinuities were at 12 m and 30 m (Fig. 1D). On July 6 phosphate and nitrate were quite low (0.8–1.9 μg l^{-1} and 2.7–5.9 μg l^{-1}, respectively in the upper 10 m layer; Fig. 2D), but there was a pronounced accumulation of ammonium already below 5 m and particularly in the middle layers (157–269 μg l^{-1} in 15–30 m depth; Fig. 1D).

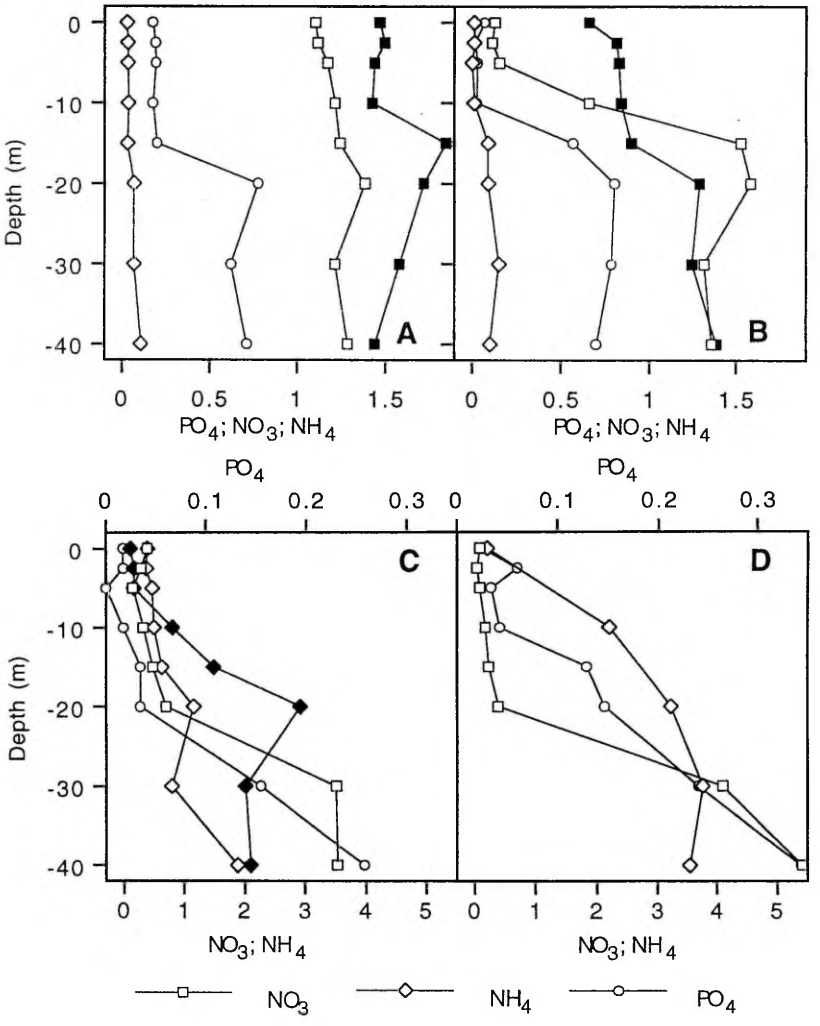

Fig. 2. Vertical distribution of phosphate (PO_4-P), nitrate (NO_3-N) and ammonium (NH_4-N) concentrations (μg l^{-1}) during May 2–3, 1995 (A), May 7–8, 1995 (B), June 27–28, 1994 (C) and July 6, 1994 (D). Filled symbols denote measurements taken at the end of the sojourn.

Vertical distribution of the phytoplankton

For the general description of the phytoplankton species composition and abundance see Olli & Heiskanen (1998).

In spring 1995 the population of the dominant species, *Peridiniella catenata*, was above the pycnocline (Figs. 3A; 4A). The depth profiles were quite similar during both periods in 1995, although cell abundance had increased by a factor of three. On several cases distinct concentration maxima were observed either on the surface (e.g. during daytime on May 7) or at 3–6 m depth (e.g. 16.00 on May 2; 1.00 and 18.00 on May 7). Also *Katodinium rotundatum* was concentrated to the upper 12 m layer. The main variation of cell abundance appeared just in the upper 6 m layer (Figs. 3B; 4B). There was a notable concentration of cells in the 3 m layer in the end of the first period, which coincides with the development of secondary thermocline. On average the abundance of cells had increased an order of magnitude by the second period. During the first period in 1995 the population of *Mesodinium rubrum* was in the upper 15 m layer, concentrated to the 3 m layer during mid-day and to the surface in the end of the period (Fig. 3C). During the second period most of the cells were in the upper 9–12 m layer, without any sharp depth stratification peaks (Fig. 4C). The cell abundances had increased by a factor of 4 compared to the first period. *Teleaulax* sp. also stayed in the upper 12 m with mid-day peaks at 3–6 m during the first period, and there were no pronounced surface accumulations. There was also no major difference in the cell abundance between the two periods (Figs. 3D; 4D). The non-motile *Monoraphidium* was relatively evenly distributed in the upper 6–9 m throughout the two periods; below the concentrations decreased gradually, but substantial amount of cells were found in the deeper layers also (Figs 3E; 4E).

The *in situ* fluorescence profile taken in the morning (9.30) of May 2 revealed a smooth distribution of CHL down to 10 m and a decrease at the very surface layer (Fig. 1A; Fluor begin). This agreed well with the temperature gradient (Fig. 1A). The evening profile (22.00) showed a strong and narrow CHL peak at the depth of 3 m, which coincided with the depth of the newly formed thermocline (Fig. 1A). During the second period the fluorescence profile was again fairly even in the upper 0–9 m layer (Fig. 1B).

In 1994 the dominant phytoplankton species *Aphanizomenon flos-aquae* had a clear bimodal distribution during the dark time with one maximum at about 9–12 m and another at the surface (0 m) (Fig. 5A). During the light time maximum cell concentrations were at the 3 m depth. During the second period such bimodal distribution was not noticed and the bulk of cells was in the upper 9 m with peak abundances varying between 6 m and the surface (Fig. 6A). *Dinophysis acuminata* was in the upper 0–3 m during the light period while during the dark period high cell concentrations were found down to 15 m (Fig. 5B). During the second period the bulk of cells was in the upper 9 m with main variation just in the upper surface layer (Fig. 6B). During light time cells seemed to avoid the surface and were concentrated to the 3 m layer, while during the dark time the population was more evenly distributed in the upper 6–9 m. In 1994 *Mesodinium rubrum* had a somewhat uniform depth distribution over the whole sampling range with some maxima at 30 m depth even (Figs. 5C; 6C). On several occasions the species showed distinct accumulations at narrow depths (e.g. 12.00 on second period; 20.00 on first period). However, the uniform depth distribution over the whole sampling range was in sharp contrast to the distribution in spring, when most of the cells were in the upper 12 m layer. *Teleaulax* sp. was likewise concentrated to the upper 6 m during the light time while during the dark time peak cell concentrations were at 12–18 m depth (Figs. 5D; 6D).

The *in situ* fluorescence revealed a bimodal distribution in the evening (18.30) of June 26, having peaks at 4.4 and 9 m (Fig. 1C; Fluor begin). On the evening of June 27 (19.30) the fluorescence was more uniform down to the pycnocline (Fig. 1C; Fluor end). On both cases a decrease of fluorescence was notable at the pycnocline (25 m) (Fig. 1C). During the second period the main decrease of fluorescence was at 10 m depth, which coincides with the upper density discontinuity (Fig. 1D).

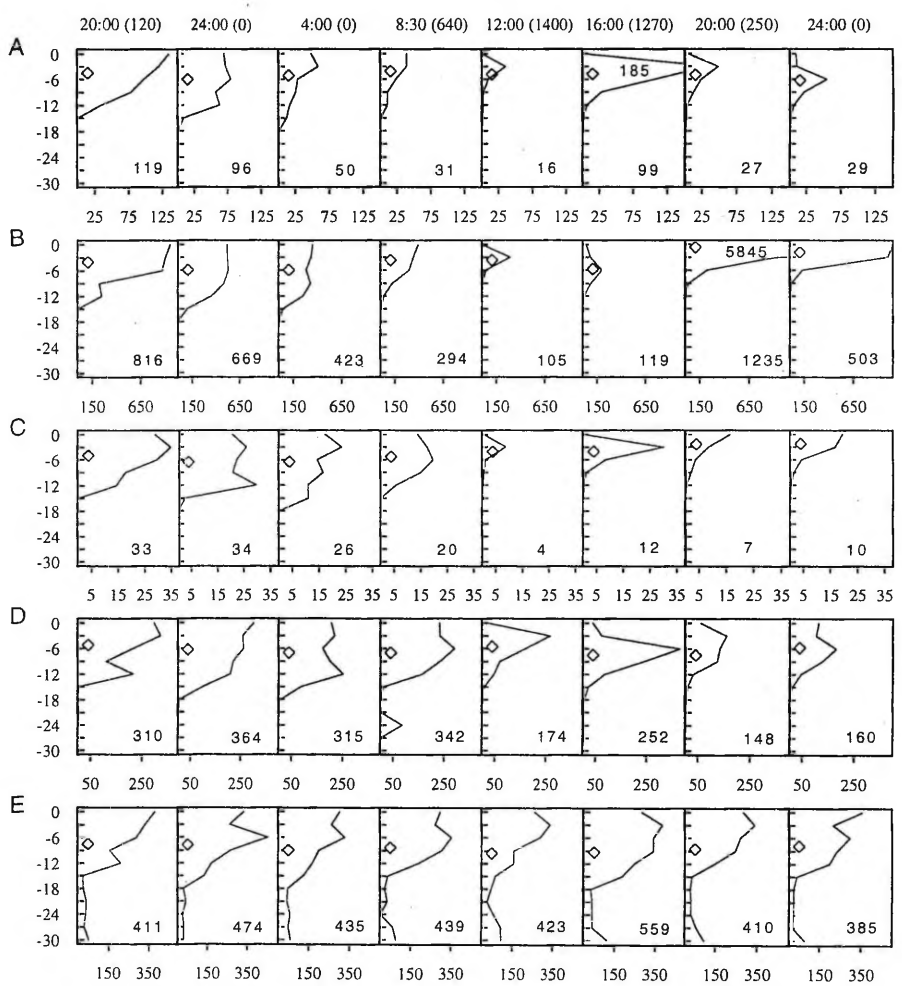

Fig. 3. Diurnal vertical distribution of *Peridiniella catenata* (A), *Katodinium rotundatum* (B), *Mesodinium rubrum* (C), *Teleaulax* spp. (D) and *Monoraphidium mirabile* (E) cell concentrations (cells ml^{-1}) on May 1–2, 1995. Respective sampling times are on A panel, surface radiation ($\mu E\ m^{-2}\ s^{-1}$) in parenthesis. Numbers in lower parts of the graphs depict the standing stock (0–30 m) of phytoplankton (cells x $10^7\ m^2$). Numbers in the upper part represent out of scale values. Diamonds show the weighted average depth of the population (i.e. the centre of gravity on the vertical axis).

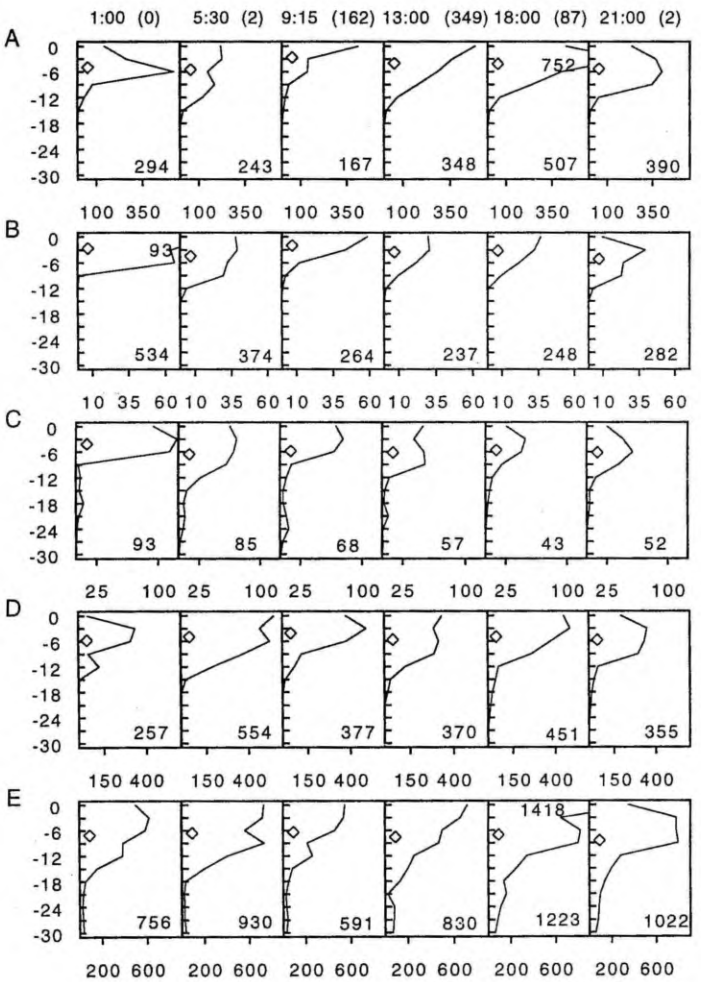

Fig. 4. Diurnal vertical distribution of phytoplankton on May 7, 1995. Notation as in Fig. 3, except concentration of *Katodinium rotundatum* (B) is in cells x 10^2 ml^{-1}, and standing stock in cells x 10^8 m^2.

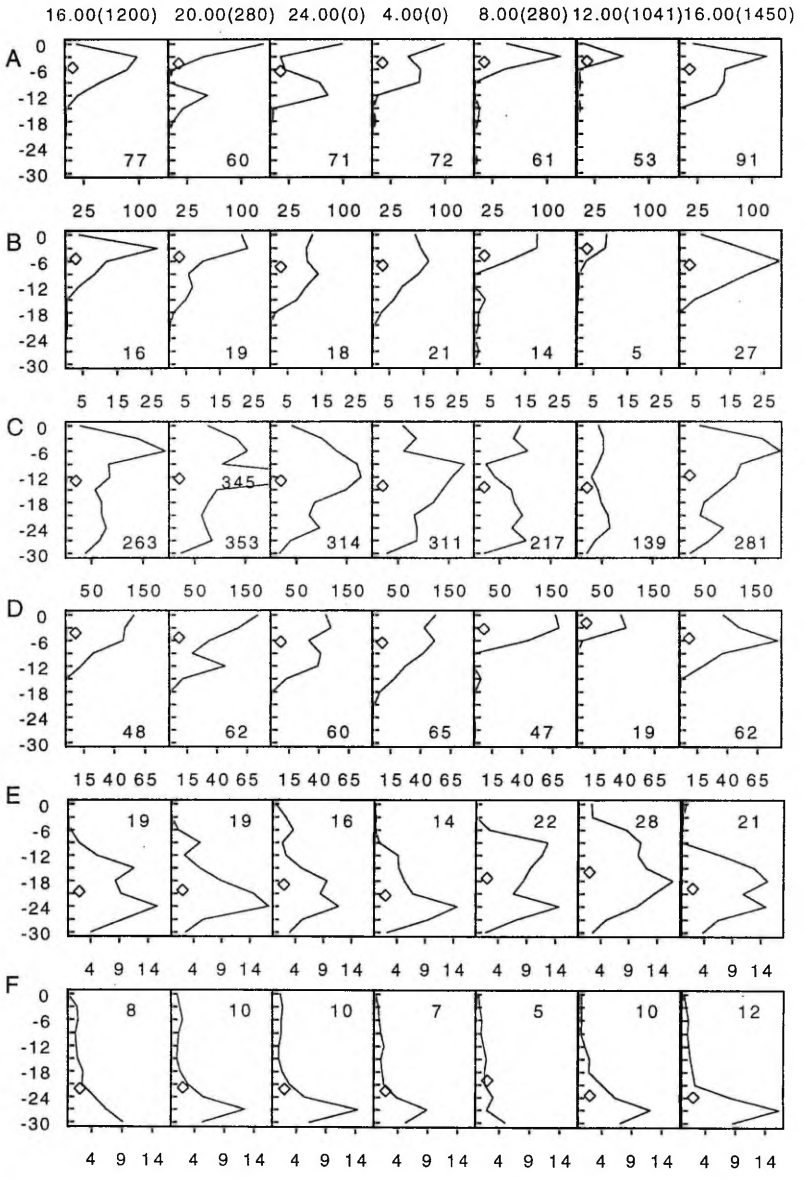

Fig. 5. Diurnal vertical distribution of *Aphanizomenon flos-aquae* (A), *Dinophysis acuminata* (B), *Mesodinium rubrum* (C), *Teleaulax* spp. (D), naked heterotrophic dinoflagellates (E) and *Protoperidinium brevipes* (F) on June 26–27, 1994. Cell concentrations in cells ml^{-1}, *Aphanizomenon flos-aquae* is in 100 µm filaments ml^{-1}. Other notations as in Fig 3.

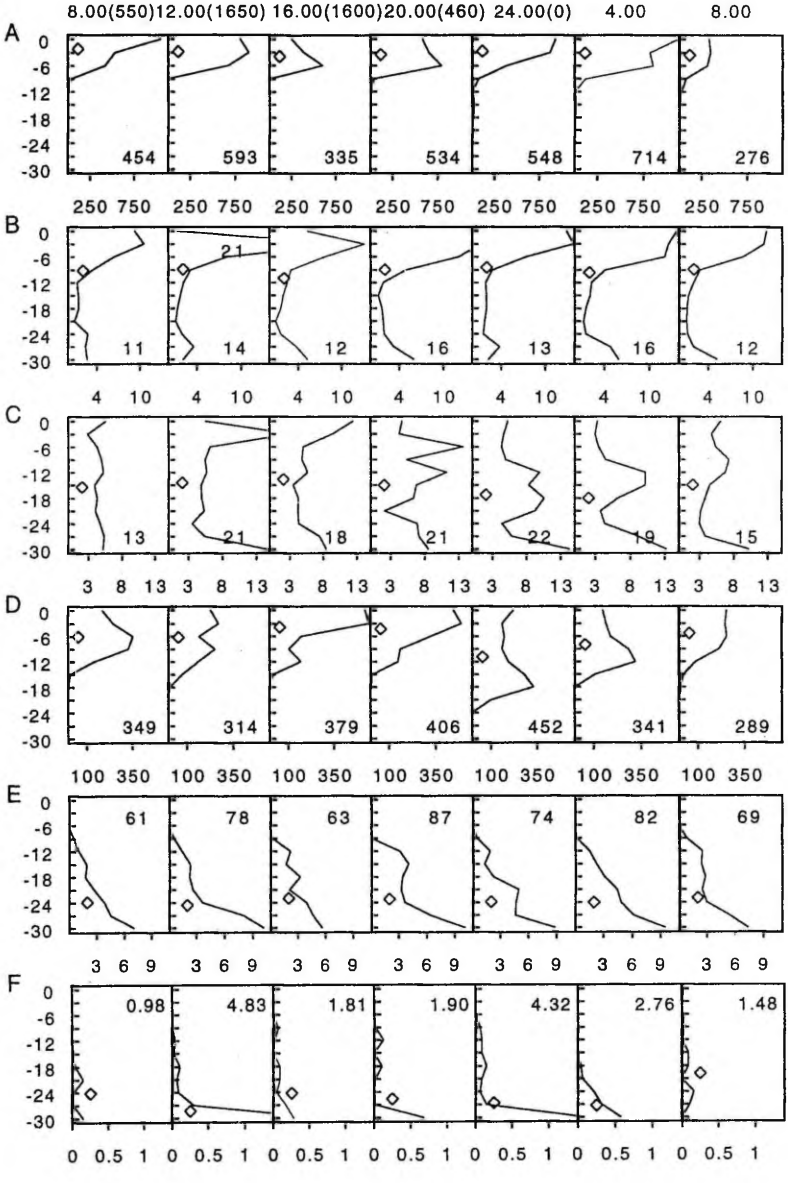

Fig. 6. Diurnal vertical distribution of phytoplankton in July 6–7, 1994. Notations as in Fig. 5, except naked heterotrophic dinoflagellates and *Protoperidinium brevipes*, standing stock in cells x 10^6 m^2.

Vertical distribution of heterotrophic flagellates

The naked dinoflagellates of the *Gymnodinium/Gyrodinium* type were rare in the surface layers from 0–3 m. The peaks occurred in the deep waters at 24 m or in the middle layers up to 9 m. During the first period the abundance of the organisms decreased explicitly below the 24 m layer (Fig. 5E). In contrast, during the second period the cell abundances increased from 9 to 30 m, where also the maxima were found (Fig. 6E). Indeed, possibly even higher abundances could have been found below 30 m depth. During the first period *Protoperidinium brevipes* had obvious abundance peaks at 27 m depth mainly, below the numbers decreased (Fig. 5F). During the second period the species was much less abundant and the cell maxima were often found at the 30 m depth (Fig. 6F).

Data analysis

Correspondence analysis on the data set from the first period in spring 1995 reveals that if the profiles are grouped by species (connected to their respective centres of gravity), there is no overlap between *Monoraphidium* and the rest of the species, capable of active movements (Fig. 7A). This indicates that the depth distribution of the motile species were different from the profiles of the non-motile *Monoraphidium*. When all the species were regarded as separate groups, the between groups difference was significant at 0.052 level (i.e. 52 random simulations out of 1000 resulted in higher between-groups variability). However, when comparing *Monoraphidium* against the motile species the difference was highly significant (i.e. none of the random permutations resulted in between-groups variability exceeding the original one). From Fig. 7A it could also be seen that the spread of data points corresponding to the motile species is much larger compared to the non-motile *Monoraphidium*, which had a relatively uniform distribution during all the eight sampling times.

As a next step the significance of differences between the motile species were questioned and the between-groups analysis was repeated with *Monoraphidium* excluded from the data matrix. No difference was found between the species, the within-groups variability contributed 75% of the total variability.

When the groups were defined by the sampling times (8 groups) a significant difference was found (0.008), which was not the case when *Monoraphidium* was included in the data matrix. This shows that much of the variability in the data matrix is due to differences in distribution patterns between different sampling times, while *Monoraphidium* does not fit to the scheme. This can be interpreted as synchronous vertical movements of the motile species in time, which can be seen as a relatively uniform distribution in the upper 12 m layer at the beginning of the period and subsequent surface avoidance during the day time, a similar behaviour of all the motile species. Projection of the data on the first factorial plane reveals that the vertical profiles taken at 12.00 and 16.00 locate relatively close to each other and separately from the rest of the groups. Additionally the profile of *Peridiniella catenata* from 20.00 locates near this group. All these profiles were characterised by pronounced sub-surface peaks at 3–6 layer.

Basically the same applies also to the data set from the second spring period. The difference between groups defined by the five species was significant (0.012), but not when the groups were defined by sampling time. After excluding *Monoraphidium* from the data matrix there were no significant differences between the species, but a significant difference between sampling times (0.008). The first sampling time (1.00) was separated from the rest

by the third factorial axis and the last group (21.00) was with relatively less scatter, indicating relatively uniform distribution of all the species, which was probably due to the wind mixing.

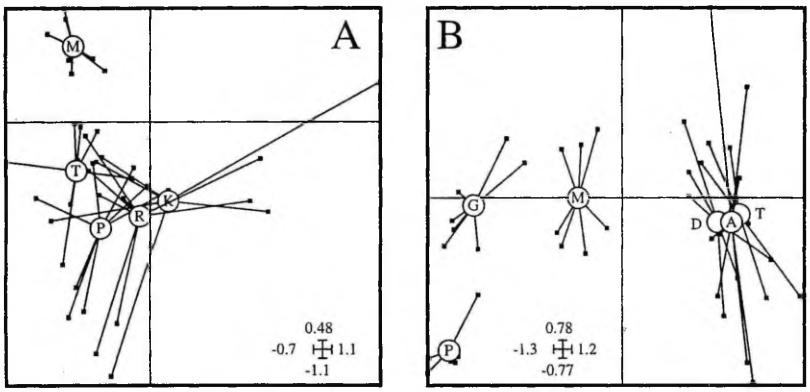

Fig. 7. A. Projections of the vertical distributions of *Peridiniella catenata* (P), *Katodinium rotundatum* (K), *Mesodinium rubrum* (R), *Teleaulax* spp. (T) and *Monoraphidium mirabile* (M) in May 1–2, 1995, onto the first factorial plane. B. Projection of *Aphanizomenon flos-aquae* (A), *Dinophysis acuminata* (D), *Mesodinium rubrum* (M), *Teleaulax* spp. (T), naked heterotrophic dinoflagellates (G) and *Protoperidinium brevipes* (P) in June 26–27, 1994, onto the first factorial plane. Groups defined by the species are connected to their respective centres of gravity. Axes are defined to maximise the variability of all data points. Numbers depict the range of the axes.

In further analysis the data matrixes from the both spring periods were pooled. The analysis of pooled data showed clearly the separation of *Monoraphidium* from the motile species, which on their own did not show significant between species differences.

The first factorial plane for the data set from the first period in 1994 (Fig. 7B) indicates a clear separation of both heterotrophic dinoflagellates and *Mesodinium rubrum* as groups by themselves and also from the rest of the species. Relatively small spread of the group defined by *Protoperidinium* corresponds well with the quite similar profiles in Fig. 6F, with the profile lacking pronounced deep accumulation (8.00) extending from the rest on the factorial plane also. The reasonably uniform depth distribution of *Mesodinium rubrum* also stands separately on the factorial plane and are almost closer to the naked dinoflagellates than to the rest of the autotrophic species. There is no significant difference between the depth profiles of *Aphanizomenon flos-aquae*, *Dinophysis acuminata* and *Teleaulax* sp. during the first period.

Further analysis of the sampling times involving these three species revealed that profiles taken at 20.00, 24.00 and 4.00 are relatively similar, also the first and last profiles (both taken at 16.00) and the profiles taken at 8.00 and 12.00. These more or less homogenous groups differ statistically significantly. The dark time profiles were characterised by bimodal depth distribution (e.g. *Aphanizomenon* and *Teleaulax*).

The second period in 1994 was characterised by a relatively small within species variability (35% of the total is attributed to within-groups variability) and a separation of all the species on the first factorial plane, except for the heterotrophs. The variability of *Protoperidinium brevipes* is much larger compared to the others (partly due to the inaccuracy of the cell counts due to very low cell abundances) and overlaps with the naked dinoflagellates (both have increased cell abundances towards deeper depths with maxima at the 30 m layer

on this period; Fig. 6EF). The autotrophic species have all relatively low within-group variability, compared to the between-groups variability.

As a next step the data matrixes from both periods of the summer period were pooled. The resulting first factorial plane showed clearly that the heterotrophic species formed groups by themselves, so did *Mesodinium* and also *Dinophysis* from the second period. The rest of the groups formed one homogenous cluster.

Two species, *Teleaulax* and *Mesodinium* were studied on both years, and thus the patterns of vertical distribution could be compared over a time scale of year, involving two different annual stages. The pooled analysis on *Teleaulax* showed that 87% of the variability was due to within-groups differences and the remaining 13% of between-groups variability was not statistically significant, i.e. the depth profile patterns in spring were not different from those in summer. Similar analysis on the *Mesodinium* data gave opposite results, the depth profile pattern in spring was significantly different from the summer profiles. This is clearly evident also from Fig. 8, where in spring the cells are in the upper 12 m layer, while in summer they are distributed relatively evenly over the sampling range.

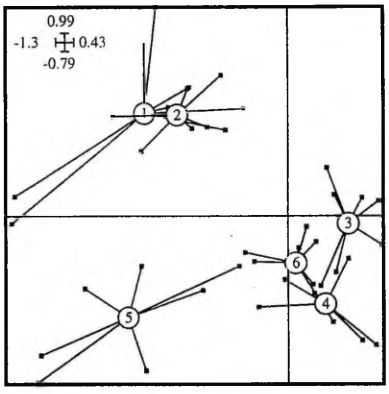

Fig. 8. Projections of the vertical distribution of *Mesodinium rubrum* onto the first factorial plane. Groups are defined according to periods and areas: 1 — GOR, May 1–2, 1995; 2 — GOR, May 7, 1995; 3 — GOR, June 26–27, 1994; 4 — GOR, July 6–7, 1994; 5 — GOF, May 5–6, 1994, 6 — GOF, May 27–28, 1994. Note the similarity of the vertical profiles during summer in GOR and late spring in GOF. Axes are defined to maximise the variability of all data points. Numbers depict the range of the axes.

A similar change in the depth distribution of *Mesodinium rubrum* was observed during a study in the NW Gulf of Finland (GOF) (Olli *et al.*, 1997), where the cells were concentrated to the top layer during the peak of the spring bloom (May 5 –6), but had rather continuous depth distribution during the decline phase of the bloom (May 27–28). This similarity between the two areas advocated to analyse the joint data set of *M. rubrum* involving six groups. The first factorial plane (Fig. 8) shows that the profiles from the decline period in GOF group together with the profiles from the summer period in the Gulf of Riga (GOR), profiles from the spring period in GOR group together and the profiles from the peak of the spring bloom in GOF stand somewhat separately. The actual difference between the bloom peak profiles from GOF compared to those from GOR was that in GOF the cells were concentrated to the upper 0–6 m layer while in GOR the surface accumulation was not so sharp.

Discussion

The present study revealed species specific changes in the vertical distribution of different micro-organisms in environmental conditions differing with respect to nutrients, light and hydrography.

During the spring bloom period a strong thermocline set a boundary to the depth distribution of the micro-organisms. However, the mineral nutrients were plentiful in the upper water column, eliminating thus any need for deep nutrient retrieval. Yet the analysis revealed a significant difference in the depth distribution profiles of the motile species and the non-motile *Monoraphidium*. The vertical movements of the motile species were demonstrated by the higher spread of the data points on the factorial plane (indicating larger change in the vertical profile pattern in time) compared to the rather uniform profiles (corresponding to smaller spread of points on the factorial plane) of *Monoraphidium*. The main variation was just in the upper layers (0–6 m). As nutrients were plentiful in the water column, it is hypothesised here that the observed vertical movements were thrived by search for optimal optical depth, and demonstrate thus the advantage of motile species over the non-motile ones.

The vertical profiles indicate a surface avoidance of all the motile species during the light time in the first period, not matched with similar behaviour on the second period. This coincides with the differences in the radiation between the two periods. During the first period the radiation levels were 3–4 times higher than during the second period. It is possible that the radiation levels during the calm and cloudless day exceeded the optimal for these micro-organisms and downwards migration avoided photoinhibition.

Photoinhibition is a function of radiation levels combined with the light history of the cells and has frequently been reported in connection with weak vertical mixing of the water column (Vincent *et al.*, 1984; Elser, 1985). Heaney and Eppley (1981) have found that dinoflagellates tolerate radiation levels of 1000 $\mu E\ m^{-2}\ s^{-1}$ in nutrient replete conditions, above that level subsurface accumulation was observed, while in nutrient deplete conditions the preferred light level was 150 $\mu E\ m^{-2}\ s^{-1}$.

The *in situ* fluorescence profiles from the spring period showed a quite uniform distribution of the chlorophyll *a* in the upper 10 m in the beginning of the first period (coinciding well with the abundance of dominant species in this layer), while in the evening a sharp chlorophyll *a* peak appeared just at the border of the newly created thermocline at 3 m depth (Fig. 1A). The reason why such peaks appear remains unclear. As photosynthesis is temperature dependent (Davison, 1991), it is possible that the thin warmed layer combined with optimal light appeared the most suitable environment for growth, resulting in a considerable accumulation of cells. Alternatively the downwards migrating cells might have stopped at a sharp temperature gradient. It has been shown experimentally that sharp temperature changes can decrease the swimming speed of dinoflagellates and act as effective barriers for vertical migration (Heaney and Eppley, 1981), although opposite results are also known (Kamykowski, 1981). The actual outcome depends also on the nutritional status of the cells (Heaney and Eppley, 1981).

In the nutrient replete conditions in spring 1995 there was no difference in the depth distribution patterns of the motile species, suggesting that all the species occupied the same vertical niche. In summer 1994 the situation was different. Apart from *Mesodinium rubrum* the other autotrophic species revealed an overlapping vertical distribution during the first period in 1994, while there was a significant difference during the second period. The different behavioural responses to the changing environmental conditions can be seen as

strategies for optimal resource exploitation through vertical niche separation leading to co-existence of different species (Sommer, 1982; 1984). The results indicate the importance of species specific behavioural adaptations in the vertical niche separation exemplified by accumulations to optimal optical depth and retrieval of deep nutrients. The vertical separation of the heterotrophic dinoflagellates is not surprising as they do not need light as energy source.

Indeed, the nutritional benefits of these movements can be questioned due to the relatively high concentrations of nitrogen in the upper layer. Generally the area is regarded as phosphorus limited (Yurkovskis *et al.*, 1993) and phosphate was quite low during our study also, thus it can be possible that the species got nutritional benefits by migrating below the surface mixed layer during the dark time.

Vertical distribution of *Mesodinium rubrum*

The distribution of *Mesodinium rubrum* was considerably different from the rest of the autotrophic species. Indeed, *M. rubrum* is a cosmopolitan species with unusual physiological and behavioural properties (Lindholm, 1985). Perhaps the most remarkable is the swimming speed which can exceed 5 mm s^{-1} (Lindholm, 1981). This is roughly an order of magnitude more than reported for the dinoflagellates (Throndsen, 1973; Kamykowski, 1995; Kamykowski and McCollum, 1986). Thus from the point of the swimming capacity it is realistic to cover a range of 30 m during one diurnal cycle.

The ability for diurnal vertical migration of *M. rubrum* is widely known (Crawford, 1989; Passow, 1991; Williams, 1996). However, previous migration studies from the Baltic Sea indicate that part of the population remains in deep layers and does not migrate, at least not on the diurnal scale (Lindholm and Mörk, 1990; Passow, 1991). It is known that at low temperatures the species can tolerate darkness for several days or weeks (Lindholm, 1985). This is in accord with the present findings in the vertical distribution of the species in summer 1994. The reasons of the remarkable difference in the vertical distribution of *M. rubrum* in spring and summer remain unclear. However, these results are in good agreement with those obtained from a comparable coastal area in the Gulf of Finland (Olli *et al.*, 1997) where the vertical distribution of *Mesodinium rubrum* revealed a clear accumulation to the upper 9 m during the peak of the vernal bloom, while during the late decline phase the cells were distributed fairly evenly over the range of 0–36 m with some maxima at 24–27 m depth. The similarity of the summer profiles from the Gulf of Riga and the profiles from the decline phase of the vernal bloom from the Gulf of Finland was apparent also from the factorial plane. Further investigations are needed to verify if this is a general rule in the Baltic and in other areas, and also to clarify the reasons and mechanisms of such behaviour.

Vertical distribution of *Aphanizomenon flos-aquae*

During the present study the vertical distribution of *A. flos-aquae* revealed a bimodal distribution during the first period in 1994, where at least part of the population was found below the secondary thermocline (9 m), while during the light time the whole population was concentrated to a subsurface layer with a peak at 3 m. During the second period a significant biomass of *Aphanizomenon flos-aquae* had been formed, yet no major bloom was observed and the whole population remained buoyant.

The gas-vacuolated filamentous cyanobacteria are known to perform DVM by controlling the buoyancy (Klemer, 1985; Villareal and Carpenter, 1990; Oliver, 1994) which appears a major strategy in bloom formation and in competition for light and nutrients (Booker and Walsby, 1981; Reynolds *et al.*, 1987). There are several mechanisms for buoyancy control, involving formation and collapse of gas vacuoles, accumulation and utilisation of carbohydrates (Walsby, 1978; Klemer *et al.*, 1982; Konopka *et al.*, 1987). *A. flos-aquae* is able to fix gaseous nitrogen (Lindahl and Wallström, 1985), thus it is suggested that it is not limited by lack of mineral nitrogen in the water column, while low nitrogen to phosphorus ratio provide an advantage over other species and favour bloom formations (Niemi, 1979).

However, the results of Lindahl and Wallström (1985) from SW Bothnian Sea indicate, that nitrogene fixation of *A. flos-aquae* corresponded to only 1% of the nitrogen requirement for the primary production during the summer. Nitrogen limitation has been often reported to cause buoyancy loss of gas vacuolated cyanobacteria (Klemer *et al.* 1982; Spencer and King, 1985), primary because the energy captured in photosynthesis could not be channelled to cell growth, but rather accumulates in the form of high-molecular carbohydrates which acts as ballast (Konopka *et al.* 1987). In the present study it is thus possible that the population of *A. flos-aquae* remained more buoyant during the second period due to higher NH_4-N concentrations in the upper water column.

Vertical distribution of autotrophic flagellates

The vertical migration of cryptomonads has not received much attention in the marine environments, although even small species can have high swimming speed (Throndsen, 1973). In lakes the vertical migration of cryptomonads is well known (Pick and Lean, 1984; Jones, 1988; 1991; Smolander and Arvola, 1988) and has been shown to be important in hypolimnetic phosphorus retrieval (Salonen *et al.*, 1984). During the present study the vertical distribution of *Teleaulax* sp. was investigated during the spring bloom and summer stage. The comparison of the profiles from the two seasons revealed no significant differences. However, the depth profiles from the summer period reveal a deeper distribution during the dark time (24.00, a maximum at 18 m during the second period) suggesting a deep nutrient retrieval.

The vertical distribution of *Dinophysis acuminata* unveiled some deep accumulation at the lower depths of the sampling range during the second period. These deep residing cells were found in all the occasions during the second period and according to the poor appearance, were not probably part of the active population, but rather sinking or dead cells which had accumulated to the density gradient. These deep residing cells, however, influenced the statistical analysis and positioned the whole group separately from the others, and also from the profiles of *D. acuminata* from the first period. Yet a closely related species, *D. norvegica* has been found to form healthy deep maxima at the depth of thermocline in the Baltic Sea (Carpenter *et al.*, 1995). The low light level at the depth of the maximum cell densities (12–15 m) suggested mixotrophic nutrition (Carpenter *et al.*, 1995). *D. acuminata* is a common species in the Baltic Sea, but has not been reported to be dominant, form blooms or cause any toxic problems. However, it has been hazardous in the coastal areas of France, where the DVM has been observed and accounts probably to it's ecological success (Clement *et al.*, 1988). Also other species of the genus are reported to cause toxic red tides (Subba Rao and Pan, 1993; Reguera *et al.*, 1995).

Vertical distribution of heterotrophic dinoflagellates

There was also a considerable variation in the depth distribution of an abundant population of naked heterotrophic dinoflagellates between the depths of 9 and 24 m during the first period in 1994. The distribution was less variable during the second period, increasing possibly below the sampling range. The thecate heterotrophic dinoflagellate *Protoperidinium brevipes* had distribution maxima in the cold water below the pycnocline.

Little is known about the ecology and trophic role of planktonic heterotrophic dinoflagellates in marine coastal ecosystems. Few data exist on what could guide the vertical population distribution of these organisms. Often the maxima of heterotrophic dinoflagellates are associated to blooms of their prey organisms (Hansen, 1991; Lessard, 1991) giving thus clues to diet preferences. The organisms are known to form subsurface maxima at or below the pycnocline, associated with sinking diatoms (Lessard, 1991). During summer 1994 there were not many diatoms in the middle layers of the water column, clearly insufficient to support the abundant population of the naked heterotrophic dinoflagellates. The ingested prey items (Olli and Heiskanen, 1998) suggested that the population was not specialised to one prey type.

It has been claimed that species from the heterotrophic genus *Protoperidinium* feed exclusively on diatoms (Jacobson and Anderson, 1986). There were always large numbers of *Thalassiosira baltica* cells below the pycnocline in 1994 (Olli and Heiskanen, 1998). *T. baltica* is an abundant vernal bloom species in the area, and after sedimentation maintains a large dormant population in the bottom nepheloid layer (pers. obs.) where it is resuspended to the whole water column below the primary pycnocline. These resuspended cells were also found in large quantities below the pycnocline. However, the dormant cells were never found in the water column and sediment traps above the pycnocline, indicating that the water column was efficiently separated into two distinct water bodies. Thus it appears that separation of the water column by a strong pycnocline indirectly determined the vertical distribution of *Protoperidinium brevipes*, and supports the view that the genus feeds only on diatoms.

Sources of uncertainity

Indeed, the above conclusions can be sensitive to several limitations in the used methods and errors like inaccuracy in sampling, turbulent mixing and vertical redistribution of the cells and horizontal advection of the water mass.

The relative precision of cell abundance estimates is related to the number of cells counted (Duarte *et al.*, 1990). In all but the case of *Protoperidinium brevipes* during the second period in 1994, the cell counts were sufficiently high not to cause significant alterations in the shape of the depth distributions. Additional variation is introduced with the procedures of sampling and subsampling (Vernick, 1971). A comparable investigation during a vernal bloom period from the Gulf of Finland (Olli *et al.*, 1997) revealed that counts from replicate samples and sub-samples had a coefficient of variation between 5–8%, which gives a relatively good estimate of the cell abundance.

An additional aspect of the sampling error is related to the vertical and temporal resolution of the discrete samples. It is usual that autotrophic micro-organisms accumulate in relatively thin layers (Lindholm, 1985), making it difficult to reveal the actual maxima with pre-set sampling schedule. Indeed, during the present study the narrow fluorescence peak at

the secondary thermocline suggests that the 3 m vertical resolution might miss some important features in the vertical distribution, which may also change significantly the shape of the depth profiles. Moreover, it was observed that such distinct peaks were relatively short lived and disappeared within a hour. However, the narrow temporal peaks are unlikely to change the main conclusions based on larger scale and more general depth distribution patterns.

Another likely source of inconstancy is turbulent mixing and horizontal pachiness. Wind induced turbulent mixing causes vertical redistribution of cells in the water column. Even more, Langmuir rotation causes both, horizontal and vertical pachiness of motile cells in the scale of the rotation cells (Smayda, 1970; Reynolds, 1984). Nevertheless, during the present study the weather was windless during most of the time, except the end of the second period in 1995 when the original sampling schedule was not fulfilled. The last profile from that sampling series revealed relatively uniform vertical distribution of cells in the mixed layer and relatively high similarity between the species. The horizontal mesoscale distribution of phytoplankton is patchy in the Baltic (Kuosa, 1988; Kuuppo-Leinikki, 1993), but in the scale of 100–200 m errors caused by sampling procedures have shown to override this (Kuuppo-Leinikki, 1993).

Acknowledging these possible ambiguities, it is still obvious that if the physical forcing overrules the adaptational behaviour of the motile micro-organisms, we would not expect to see significant differences in the vertical distribution patterns between the species, particularly when compared to a non-motile one as was the case in the 1995. Indeed, the results would be different in the case of controlled laboratory experiments, yet in nature the actual vertical distribution of micro-organisms is a combination of water movements counteracted by the active response of the cells to fulfil their physiological requirements (Sommer, 1985).

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