No. 25

Studies on planktonic brackish water microprotozoans with special emphasis on the role of ciliates as grazers

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Academic dissertation in Hydrobiology, to be presented, with the permission of the Faculty of Biosciences of the University of Helsinki, for public criticism in the Lecture Room XII, University Main Building, Aleksanterinkatu 5, Helsinki, on December 3rd 2004, at 12 noon.

HELSINKI 2004

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

I Setälä, O. & Kivi, K. 2003: Planktonic ciliates in the Baltic Sea in summer: distribution, species association and estimated grazing impact. – Aquat. Microb. Ecol. 32: 287-298.

II Setälä, O. 1991: Ciliates in the deep water layer of the Baltic. – Arch. Hydrobiol. 122: 483-492.

III Setälä, O., Autio, R., Kuosa, H., Rintala, J. & Ylöstalo, P.: Survival and photosynthetic activity of *Dinophysis acuminata* populations in the Baltic Sea. – Harmful Algae (in press).

IV Kivi, K. & Setälä, O. 1995: Simultaneous measurement of food particle selection and clearance rates of planktonic oligotrich ciliates (Ciliophora: Oligotrichina). – Mar. Ecol. Prog. Ser. 119: 125-137.

V Setälä, O., Autio, R. & Kuosa, H. 2004: Predator-prey interactions between a planktonic ciliate *Strombidium* sp. (Ciliophora, Oligotrichida) and the dinoflagellate *Pfiesteria piscicida* (Dinamoebiales, Pyrrophyta). – Harmful Algae (in press).

To the Beatles

CONTRIBUTIONS

	I	II	III	IV	V
Original idea	OS, KK	OS	OS, RA	KK	OS, RA, DKS
Study design and methods	OS, KK	OS	OS, RA, HK	KK	OS, RA, HK
Data gathering	OS	OS	OS, RA, HK, JR, PY	OS, KK	OS, RA
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GLOSSARY

Autotrophy, heterotrophy and mixotrophy in planktonic environments

In plankton ecology, autotrophy means carbon photoautotrophy, i.e. the ability to assimilate dissolved CO_2 from the water. Therefore, planktonic bacteria, for example, are categorized as heterotrophs, even though they are able to take up inorganic nutrients, and compete with algae for nutrient reserves. Autotrophs by definition are self-sustaining and able to obtain nutrition from inorganic compounds. A heterotroph, however, is able to use only carbon from organic sources for biosynthesis. Energy for this process is provided by sunlight (photoheterotrophs – mainly some bacteria) or by chemical processes (chemoheterotrophs – all animals, fungi, most bacteria, some parasitic plants). Osmotrophy is a mode of heterotrophy in which an organism takes up organic substances in solution, i.e. dissolved organic compounds.

The majority of organisms can be classified into two groups: those relying solely on photosynthesis and those relying solely on the assimilation of organic substances to meet their nutritional requirements. Some organisms, however, are able to combine phototrophy and heterotrophy. Such mixotrophy is a widespread phenomenon in aquatic habitats, especially in unicellular organisms. Many primarily phototrophic "algae" can take up dissolved organic matter or ingest bacteria or other organisms and use them as a heterotrophic, alternative source of carbon or nitrogen. Similarly, phagotrophic "protozoa" are photosynthetic due to the presence of algal endosymbionts. Mixotrophy requires investment in both photosynthetic and heterotrophic cellular apparatus, and the benefits must outweigh the costs involved.

Cilia and ciliates

Ciliates are unicellular organisms that have hair- or whip-like organelles, cilia, projecting from the surface of the cell. Although there are exceptions, cilia are normally numerous in ciliates and occur on the cell in longitudinal rows. Cilia are made up of microtubules and are covered by an extension of the plasma membrane. They are motile and designed either to move the cell itself or to move substances over and around the cell.

Endosymbiosis

The endosymbiotic theory of eukaryote evolution (symbiotic theory) was introduced by Lynn Margulis in 1975. This theory is now considered to explain the single most important event of the organic world, the relationship between organisms that live within another organism in a mutually beneficial relationship, whereby one cell serves as the host and the other as the symbiont. It is proposed that the ancestors of eukaryotic cells were symbiotic consortiums of prokaryote cells with one or more species as endosymbionts. This concept attributes the origin of chloroplasts and mitochondria to endosymbiotic events between a heterotrophic host prokaryote and a photosynthetic prokaryote (cyanobacteria) and an aerobic heterotroph. These endosymbionts would have gained entry to the host cell as undigested prey or as internal parasites, after which the relationship between the cells became mutually beneficial for both partners. The present understanding is that eukaryotic cells originated in a symbiosis between several prokaryotes that continued to live on as organelles within the new type of cell.

Guild

The term "guild" describes groups of functionally similar species in a community, i.e. species with similar requirements and foraging habits, and, consequently, similar roles in the community. In competitive communities, guilds would represent "arenas" having the potential for intense interspecific competition, with strong interactions within guilds but weaker interactions with the remainder of their community.

Meroplankton

Meroplanktonic organisms spend a part of their life floating freely in the water column and hence are planktonic, but they also live in the benthos (e.g. eggs and planktonic larvae of benthic invertebrates).

Metazooplankton

Metazooplankton constitute a category not based on size and include pelagic multicellular organisms. In the Baltic Sea, metazooplankton consist mostly of copepods, cladocerans, rotifers and meroplanktonic larvae.

Pallium

The pallium, previously termed the feeding veil, is a feeding apparatus found in some thecate dinoflagellate species (species that possess a cellulose skeleton made up of the thecal plates). This plastic structure emerges from a certain area of a feeding dinoflagellate cell surrounding the prey and thus enables external feeding.

Phagotrophy

Phagotrophy is a type of nutrition by heterotrophy. Phagotrophic organisms are able to ingest and utilize particulate food.

Plastid

Plastid is the general name for a cell organelle of plants and algae that is enclosed by two or more membranes. Pigments are synthesized and stored in chromoplasts. Chloroplasts are the main type of chromoplast. They contain chlorophyll, are responsible for the green coloration of most plants, and perform photosynthesis. Kleptoplastids are plastids stolen from their algal prey by a phagotrophic cell, such as a ciliate or a dinoflagellate, and later used for photosynthesis in the predator (= host) cell itself.

Protozoa

Protozoa is a collective term for the members name of the subkingdom (formerly a phylum) that includes the simplest organisms of the animal kingdom. They consist of phagotrophic unicellular organisms ranging in size from microscopic to macroscopic (Fenchel 1987). The smallest protozoans are flagellates about 3 µm in diameter; the largest, now extinct, were foraminiferans up to 10 cm in diameter. Most protozoans are free-living animals, but some are commensalistic, mutualistic or parasitic.

Pseudopod

A pseudopod is a protrusion of cytoplasm put out by a cell. Pseudopods occur predominantly among amoeboid protozoa, in which they serve for locomotion and feeding. The pallium of thecate dinoflagellates is also a pseudopod.

Taxis

Almost every “animal” is able to move at some point of its life. For lower animals such as protozoans the movement is often undirected and random, and is called kinesis. Taxis involves more complex behaviour than kinesis as it means oriented movement in response to an external stimulus. Different taxes are the result of various kinds of stimuli, and are described by adding a prefix to the word taxis. The most common forms of taxis are phototaxis – movement in response to light; chemotaxis – movement in response to a chemical; and geotaxis – movement in response to gravity. Movements towards a stimulus are positive taxes, and movements away from a stimulus are negative taxes.

Threshold feeding

In plankton ecology, the term threshold feeding refers to a situation in which, at low (species-specific) prey concentrations, the feeding efficiency of grazers is reduced. This type of feeding behaviour may occur when both the prey handling time and the search rate for prey are dependent on the density of the prey. It has been thought that threshold feeding is especially beneficial in providing a refuge for prey (Chow-Fraser & Sprules 1992).

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Setälä, O. 2004: Studies on planktonic brackish water microprotozoans with special emphasis on the role of ciliates as grazers.. – W. & A. de Nottbeck Foundation Sci. Rep. 25: 1-48. ISBN 951-98521-5-8; ISBN 952-10-0267-0 PDF.

The ecology of brackish water planktonic microprotozoans was studied between 1989 and 2002 in the south-west coastal waters of the northern Baltic Sea, in the open waters of the Baltic Proper and in the Choptank River, a tributary of Chesapeake Bay, USA. The studies combined monitoring data on the vertical distribution of various ciliate species and experimentally derived species-specific information on their role as grazers in planktonic food webs. The vertical distribution of the mixotrophic dinoflagellate *Dinophysis acuminata* and its photosynthetic efficiency at different depths were examined during a two-year study.

In the course of three research cruises, in 1998, 1999 and 2001, it was found that the deep-water basins of the Baltic Proper were inhabited by distinct microprotozoan communities. In 1998 and 1990, large unidentified ciliates were detected under low oxygen conditions at the Bornholm and Gotland Deep stations, where traces of H_2S were also found. These deep water communities are presumably connected to the upper pelagic system by one-way transport only, that is, by receiving settling organic matter from surface layers.

In 2001, a dense community of phototrophic dinoflagellates, mostly *Dinophysis acuminata*, was recorded at 77m depth in the Gotland Deep. During the following summer, the photosynthetic efficiency of *D. acuminata* was studied from the coastal thermocline layer and from the nitracline (75-80 m) in the Gotland Sea. These measurements showed photosynthetic activity in all the populations studied, with differences in their photosynthetic carbon uptake rates. Overall, photosynthesis of the *D. acuminata* populations was saturated at light levels between 250 and 500 $\mu E\ m^{-2}s^{-1}$. The maximum photosynthetic activity in the populations originating below the thermocline, and also in one artificially darkened population, was markedly lower than that in the populations originating from the upper water layers, possibly reflecting their history, e.g. the time spent in different light environments.

Species-specific clearance rates and the prey size selectivity of natural ciliate communities were experimentally studied by using a suspension of different sized wheat starch particles as food. The experiments revealed two different feeding strategies, specialistic and generalistic, in the nine oligotrich ciliates studied. The clearance rates for the most common particle sizes ranged from 1.9 to 11.4 µl $cell^{-1}\ h^{-1}$.

The functional response of a planktonic ciliate, *Strombidium* sp., feeding on a non-toxic strain of the dinoflagellate *Pfiesteria piscicida* was experimentally studied with four different prey concentrations of stained live prey, non-toxic zoospores (NTZ). The data gathered were used to calculate predator-prey specific ingestion and clearance rates. The ingestion rates ranged from 0.68 to 14.26 NTZ $ind^{-1}h^{-1}$, and with a predator-prey specific handling time of 2.83 min the maximum particle uptake rate, U_{max} was 21.18 NTZ $ind^{-1}h^{-1}$. At the lowest *Pfiesteria* NTZ concentrations, the feeding efficiency of *Strombidium* sp. was reduced, possibly indicating threshold feeding. It was concluded that the formation of non-toxic *Pfiesteria piscicida* blooms requires periods of low grazing pressure or a means to escape grazing.

Samples for studying the ciliate communities of the open Baltic Sea were taken in 1998 and 1990 from two transects extending from the Kattegat to the entrance of the Gulf of Finland. The abundance of ciliates (the photoautotrophic ciliate *Mesodinium rubrum* excluded) was highest close to the surface, where maximum values ranged from approx. 7 000 to 20 000 cells l^{-1} in different areas. The dominant groups of heter-

otrophic ciliates were small strobilidiids, strombidiids and prostomatiids. *Mesodinium rubrum* was most abundant in the surface water, but during both cruises concentrations of this ciliate were also found in deeper layers in the daytime (down to 80 m). Community grazing was estimated by a size-dependent, mostly experimentally derived, exponential function. It was estimated that in 1988, the ciliate community cleared close to 50 % of the water volume daily, whereas in 1990, the highest values were up to 125 % cleared daily. In both years, the communities were dominated by small (≤30 mm) ciliates, which were also responsible for most of the grazing.

Correlation analysis revealed three distinct ciliate associations in the data of both years. Some of these groups may represent true feeding guilds bound together by utilization of the same resources, whereas others may be kept together by abiotic factors or the internal dynamics (e.g. predator-prey relationships) of the association.

The northern Baltic Sea microprotozoan communities show fluctuations in abundance and species composition not only seasonally but also spatially. Different ciliate species may be held together by utilization of the same food resources or by predator-prey relationships, and may form associations in different parts of the water column. Communities in the deep water layers may be overlooked when biological sampling is targeted at the upper part of the water column. The study showed that, due to their species-specific feeding characteristics, suspension-feeding ciliates may not always form a single functional group in terms of their role as grazers in the planktonic food web. However, owing to the generally high cell-specific clearance efficiencies of planktonic suspension-feeding ciliates, they can at times be significant grazers in planktonic communities.

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CONTENTS

INTRODUCTION

The structure and function of planktonic microbial food webs

The open waters of the oceans and their enclosed seas – the pelagial – cover 70 % of the earth's surface and are inhabited by a wide spectrum of organisms. At the smaller end of the spectrum are minuscule algal cells, phytoplankton, that grow suspended in the sunlit surface layer. Their photosynthesis produces organic matter that sustains bacteria, unicellular protozoa and small zooplankton. These, in turn, serve as food for the higher levels of the marine food web (fish and whales). The pelagic organisms are, with some revisions, categorized according to the size-based exponential classification proposed by Sieburth et al. (1978), which also takes the functional role of an organism in the food web into account. In this categorization, planktonic organisms span a size range extending from 0.02-0.2 µm (femtoplankton) to 20-200 cm (megaplankton). Each size group may comprise one or more trophic levels.

Textbooks of the 1970s describing the pelagial food chain assumed that the bulk of pelagic primary production is channelled through herbivorous zooplankton to fish and other pelagic carnivorous organisms (e.g. Steele 1974). In the late 1970s and early 1980s, however, the premises of the structure and function of the planktonic food webs were thoroughly re-evaluated by several authors (e.g. Pomeroy 1974, Sorokin 1977, Williams 1981, Azam et al.1983, Sherr et al. 1986, Sherr & Sherr 1987). The paradigm of the microbial loop (Azam et al. 1983) presented the role of pelagic microbes in a completely new light. Studies on the functional diversity of these organisms were expanded with the development of techniques such as the use of electron microscopy for viral counts in aquatic environments (Bratbak & Heldal 1993), radio labelling (Fuhrman & Azam 1980, 1982) and epifluorescence microscopy (Hobbie et al. 1977, Porter & Feig 1980, Haas 1982). The basic concept of the microbial loop considers free planktonic bacteria not only as decomposers but also as producers of organic particulate matter, which, most importantly, are able to incorporate dissolved organic matter into particulate form (Azam et al. 1983). Bacterioplankton actually competes with phytoplankton for mineral nutrients and is grazed by nano- and micro-sized protists. The model of the microbial loop as it was first presented is today further supported by additional information on trophic interactions and the routes of energy and matter within pelagic food webs, such as the importance of small ciliates in the pelagial environment (Sherr et al. 1986), phagotrophic protists as links between fixed carbon (from bacteria and algal cells) and higher trophic levels (e.g. Sherr et al. 1986, Stoecker & Capuzzo 1990), and mixotrophy among ciliates (e.g. Blackbourn et al. 1973, Jonsson 1987, Stoecker et al. 1987) and phototrophic algae (e.g. Bird & Kalff 1987, Bockstahler & Coats 1993, Jones 1994, Stoecker et al. 1997).

Microprotozoans

The focus of the studies presented in this thesis is on microzooplankton, i.e. heterotrophic planktonic organisms in the size range 20-200 µm (Sieburth et al. 1978). The term mi-

crozooplankton includes protozoans such as ciliates and heterotrophic dinoflagellates, but it also refers to rotifers, meroplanktonic organisms such as the larvae of cirripeds, and juvenile stages of copepods. For practical reasons and in order to define the functional role of the organisms in question more accurately, Kivi (1996) proposed the term microprotozoan instead of microzooplankton for micro-sized unicellular planktonic phagotrophs. Microprotozoan is the term applied in this thesis. Of the heterotrophic flagellates, only euglenoids, dinoflagellates and the siliceous flagellate *Ebria tripartita* were included in the original definition by Kivi.

The abundance and role of microprotozoans in the planktonic food web were long underestimated, mainly because of the inadequate methods applied for collecting and preserving samples. When nets are used in sampling, only a small fraction of micro- or nano-sized cells tend to be captured. Small species, which actually are the most abundant, pass through the nets, and naked species are often ruptured (e.g. Johannes 1965, Smetacek 1981). However, already Lohmann (1911) used centrifugation to concentrate small planktonic organisms, and was thus able to distinguish nanoplanktonic flagellates in his water samples. The fixatives also destroy fragile cells such as naked ciliates or dinoflagellates (Putt & Stoecker 1989, Stoecker et al. 1994). Due to these shortcomings in sampling techniques, the less frail components of microprotozoan communities, e.g. the tintinnids, have been more intensively studied than, say, aloricate ciliate species (e.g. Jørgensen 1927, Kofoid & Campbell 1929, Verity 1985, 1987, Heinbokel 1978a,b, Heinbokel & Beers 1979).

The abundance and diversity of microprotozoan communities vary both spatially and seasonally. Microprotozoan communities are regulated by environmental resources such as light (Song et al. 1980, Jonsson 1994, Figueroa et al. 1998), temperature, (Rassoulzadegan 1982, Verity 1985), prey abundance and size (e.g. Heinbokel & Beers 1979, Fenchel 1980b, Verity 1985, Jonsson 1986, Rassoulzadegan et al. 1988, Hansen 1991, Hansen et al. 1994) and grazing pressure from higher trophic levels, crustacean zooplankton in particular (e.g. Stoecker & Egloff 1987, Stoecker & Capuzzo 1990, Gifford 1991, Kivi et al. 1996). Due to the higher primary productivity in coastal areas, the biomass of microprotozoans in marine coastal and estuarine environments is generally higher than in open ocean areas (e.g Beers et al. 1980, Boikova 1985, Gast 1985). Microprotozoans, notably ciliates and phagotrophic dinoflagellates, are considered key grazers of especially nanoplankton in marine environments, which transfer their production to metazoans (e.g. Stoecker & Capuzzo 1990, Dolan 1991b, Kivi et al. 1996, Merrel & Stoecker 1998).

Planktonic food web in the Baltic Sea

Phytoplankton

In the northern Baltic Sea, photosynthesis is light-limited during the winter, and inorganic nutrients tend to accumulate in the water column. The spring bloom of planktonic algae begins at the break up of the ice cover or often even below the ice cover, usually in March - April. The spring bloom phytoplankton community, which is dominated by

chain forming diatoms and dinoflagellates (Kononen & Niemi 1986, Niemi & Åström 1987, Heiskanen & Kononen 1994), is responsible for a major part of the annual planktonic primary production (up to 60 %; Kuparinen 1984, Kuosa & Kivi 1989). When the surface waters warm up, the seasonal thermocline is formed (usually at 10-15 m depth), and vertical mixing between the surface and lower water layers is reduced. Consequently, the inorganic nutrient pool in the euphotic layer is reduced or depleted. A proportion of the springtime production (11 %; Lignell et al. 1993) is grazed by metazooplankton, and most of the primary production from the pelagic system is lost by sedimentation (72 %; Lignell et al. 1993). The primary production and biomass of phytoplankton communities are low in summer, and communities are characterized by small nanoflagellates and picoplanktonic algae (Niemi 1975, Huttunen & Kuparinen 1986), the latter sometimes accounting for up to 50 % of the primary production (Kuosa 1990a). Because the productive water column is more or less depleted in inorganic nutrients at that time, production is based on nutrients regenerated within the microbial loop and on incidental upwelling events (Niemi 1975, 1982, Haapala 1994). In July and August, the abundance of dinoflagellates such as *Heterocapsa triquetra* and *Dinophysis* spp. (Kononen & Niemi 1986, Kononen et al. 2003) may increase, and outbreaks of cyanobacterial blooms may occur, depending on the prevailing nutrient and weather conditions (e.g. Kononen 1992).

Annual succession of microprotozoans

In the northern Baltic Sea, the annual succession in the microprotozoan community involves a biomass peak in spring and another, smaller, peak in late-summer. The increase in the biomass of heterotrophic microprotozoans is associated with the onset of the phytoplankton spring bloom, and maximum abundances and biomass values (up to 6.2×10^4 cells l^{-1} and 90 µg C l^{-1}; Kivi 1986) generally occur soon after the peak in the phytoplankton bloom. Marked changes in species composition take place during the annual cycle (Kivi 1986). During the spring, at a time when abundances of metazooplankton communities are still fairly low (Viitasalo 1992, Johansson et al. 1993, Viitasalo et al. 1995, Johansson et al. 2004), ciliate communities are characterized by relatively large species, such as tintinnids, large *Strombidium* species, *Euplotes* spp., *Bursaria* spp., *Didinium gargantua*, *Lacrymaria rostrata* and *Askenasia* cf. *stellaris* (Smetacek 1981, Kivi 1986, Johansson et al. 2004). The peak abundances of heterotrophic dinoflagellate species of the genus *Protoperidinium* occur during the spring bloom, when the siliceous flagellate *Ebria tripartita* also increases in abundance (Kivi 1986). During early and mid-summer, the ciliate community consists mostly of naked oligotrichs, which are known to be effective grazers of pico- and nano-sized phytoplankton (e.g. Gast 1985, Rassoulzadegan et al. 1988, Bernard & Rassoulzadegan 1990, Kuosa 1990a, Dolan 1991b). The summertime microprotozoan communities are subject to efficient grazing by metazooplankton species that have increased in abundance after the spring bloom (Viitasalo 1992, Johansson et al. 1993, Viitasalo et al. 1995).

Suspension-feeding ciliates and phagotrophic dinoflagellates

Ciliates

Planktonic ciliates are unicellular organisms that, in the Baltic Sea, generally span a size range of approx. 10-100 µm in their largest diameter. Although the smallest ciliate species are <20 µm, or even <10 µm, in their largest diameter, and do not actually fit the definition of micro-sized protists, they have been included in this thesis because of their functional role in the food web (and also because they can be counted with the same methods as larger cells). The abundance of marine ciliates varies, depending on the season and environment. Thus, for example, in temperate coastal environments cell numbers generally fluctuate between <100 and 10^5 cells l^{-1} (Table 1.), but occasionally ten times higher abundances may be found (e.g. 162 × 10^3 cells l^{-1}; Andersen & Sørensen 1986; 140 × 10^3 cells l^{-1}; own unpublished observations).

Ciliates are active swimmers and use their cilia both for filtering and for propelling themselves through the water column. Ciliates are able to orient and relocate themselves between various patches in the water column. Different stimuli may induce kinetic or tactic responses in ciliates (Fenchel & Jonsson 1988, Fenchel & Blackburn 1999). They may respond, for instance, to changes in light (Song et al. 1980, Finlay & Fenchel 1986), to chemicals (Naem & Fenchel 1994), to mechanical stimuli (Naitoh & Eckert 1974, Jonsson & Johansson 1997) and to gravity (Fenchel & Finlay 1984). Ciliates have been shown to remain in patches where food is available by altering their swimming behaviour (e.g. Fenchel & Jonsson 1988, Naem & Fenchel 1994, Jonsson & Johansson 1997). They are also able to sense chemical gradients from point sources of food within a distance of few centimetres (Fenchel & Blackburn 1999); for a cell 50 µm in diameter this means a distance over 2000 times its own size. Such chemosensory mechanisms create small-scale patchiness of

Table 1. Ciliate abundance and biomass in temperate marine environments.

Location	**Abundance** 10^3 cells l^{-1}	**Biomass** µg C l^{-1}	**Reference**
Southern California	5-23	<1-9	Beers et al. 1980
Kiel Bight	2 – 92	1-56	Smetacek 1981
Limfjorden	1-162		Andersen & Sorensen 1986
coastal northern Baltic Sea	62	1-90	Kivi 1986
Baltic Sea proper	7-20	8	Paper I
Chesapeake Bay	2-85	2-205	Coats & Revelante 1999
Baltic Sea proper	9	20	Johansson et al. 2004
Baltic Sea proper	104	69	Setälä unpublished

these organisms within the water mass but may also result in ciliate movements across longer distances. For example, benthic, microaerophilic species, i.e. species that thrive in reduced oxygen tension, may escape temporary anoxic conditions by moving to the overlying water column (Finlay et al. 1986, Fenchel et al. 1990, paper II). Another example of targeted movement across longer distances is found in the phototrophic ciliate *Mesodinium rubrum*, which is thought to have the potential to sequester nutrients from deeper water layers and return to the euphothic layer to photosynthesize (Heiskanen 1995, Crawford & Lindholm 1997, Olli 1999).

Microprotozoans, in general, display considerable variation in metabolic rates per unit weight (Fenchel & Finlay 1983), which is linked to the physiological state of the cells. Growth rates of over 1 d^{-1} have commonly been found in ciliates (Verity 1985, Jonsson 1986, Dolan 1991b, Strom & Morello 1998). The high growth potential of planktonic ciliates permits a rapid increase in the abundance of ciliate communities under favourable conditions. The growth rates are subject to environmental conditions such as prey concentration and temperature. Growth is enhanced at elevated temperatures, but it also increases with increasing food concentrations up to species-specific saturation food levels (Verity 1985).

Ciliate feeding and food selection

A number of studies have focused on the important role played by filter-feeding ciliates, i.e. species that feed by sieving smaller particles with their cilia, in planktonic food webs (e.g. Heinbokel 1978a,b, Capriulo & Carpenter 1980, Fenchel 1980 a,b,c,d, Jonsson 1986, Andersen & Sørensen 1986, Sherr & Sherr 1987, Bernard & Rassoulzadegan 1990, papers IV and V). Less is known about the feeding of predaceous ciliates in marine environments (e.g. Stoecker et al. 1986, Hewett 1988, Jakobsen & Hansen 1997).

The size range of particles that can be ingested by a planktonic grazer depends on the feeding mode (e.g. filter feeding or raptorial) and specific feeding mechanisms of the cell (Fig. 1). For filter feeders, limits on the size of ingested prey may be set by the free space between adjoining cilia of the membranelles surrounding the oral area and the velocity of the water current generated by the feeding organelles (Fenchel 1986), by the width of the cell mouth, the cytostome (Fenchel 1986, Jonsson 1986) or, as in tintinnids, by the diameter of the lorica oral opening (Heinbokel 1978b, Dolan et al. 2002). Filter feeding is an adaptation to the exploitation of small particles by a larger organism. The optimum predator to prey size ratio for planktonic filter-feeding ciliates has been proposed to range from 1:1 to 1:30, with an average of 1:8 (Hansen et al. 1994 and references therein). Predatory ciliates, in contrast, feed by direct interception of the prey, and the prey size may well approximate, or even exceed, the size of the predator (Fenchel 1987, Hewett 1988).

Planktonic filter-feeding ciliates use their cilia both for movement and for filtering their prey objects from the water. The outcome of this manner of feeding depends on the amount of water that is filtered while the ciliate is swimming and on the number of suitable particles that are brought to the

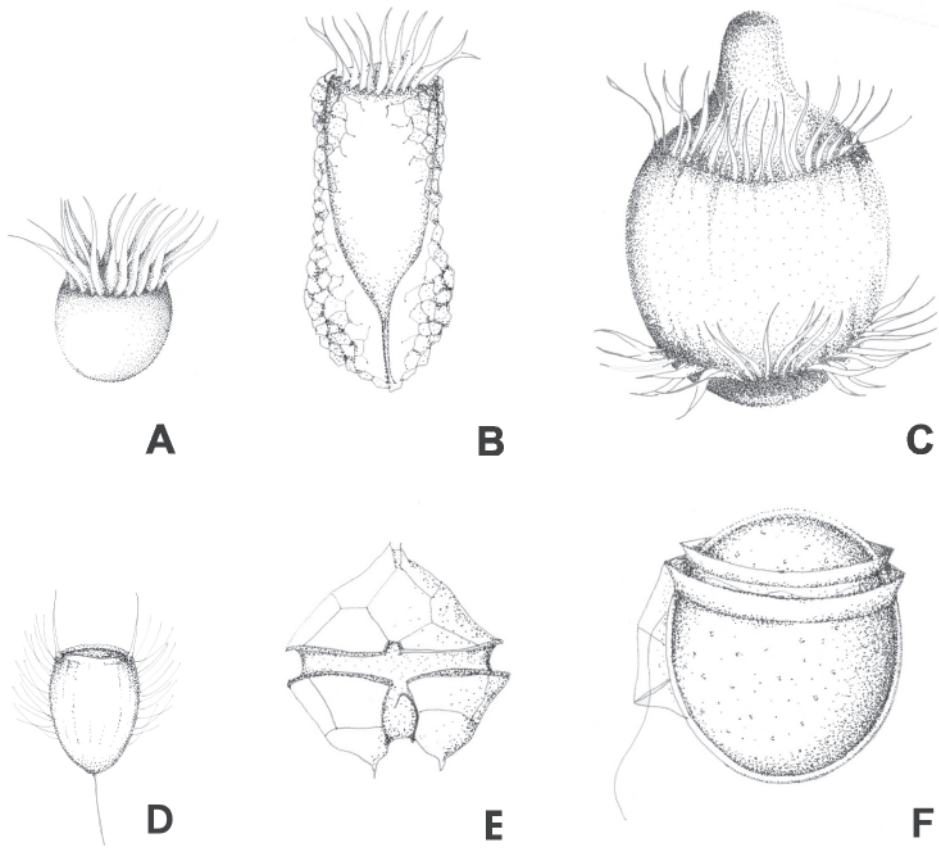


Figure 1. Common Baltic microprotozoans and their approximate sizes (ESD, estimated spherical diameter). Suspension feeding ciliates: A) *Lohmanniella oviformis* (15-25 µm), B) *Tintinnopsis lobiancoi* (cell 40-60 µm, lorica 50-300 µm). Predatory ciliates: C) *Didinium gargantua* (50-70 µm), D) *Balanion comatum* (10-30 µm). Dinoflagellates: E) *Protoperidinium brevipes* (30-40 µm), F) *Dinophysis rotundata* (30-50 µm).

cytostome. If ciliates did not choose between different types of prey, the only discriminating factor would be prey size, which would be determined by the structure of the sieving apparatus. In that case, species-specific feeding efficiency would depend only on the volume of water filtered and the concentration of suitably sized prey in the water. This concept of ciliates as solely mechanical filterers, a view supported by the extensive works of certain authors, e.g. Fenchel (1980 a,b,c,d) and Jonsson (1986), may not entirely hold in the light of present knowledge. While the concentration of suitable prey is no doubt the main factor affecting feeding efficiency in suspension-feeding ciliates, the mode of feeding of planktonic ciliates has been found to vary from species to species

(e.g. paper IV) and to be subject to environmental dynamics. Experimental studies have shown that phagotrophic ciliates may be selective predators (Stoecker et al. 1981, 1986, 1988, Verity 1991a,b, paper IV) and that prey size is a key factor affecting prey selectivity in ciliates (e.g. Fenchel 1980b, Fenchel 1986, Rassoulzadegan et al. 1988, paper IV, Dolan et al. 2002). Prey selection may, however, also be affected by other factors, such as temperature and chemical stimuli (Rassoulzadegan 1982, Verity 1988, Fenchel & Blackburn 1999). Ciliates may be prefer nutritious prey over "poor quality" food (Verity 1991b) or they can be specialized in feeding on a certain type of prey, as in the case of the tintinnid *Favella ehrenbergii* or the prostomatid *Balanion* sp., both of which have been found to prefer dinoflagellates to other phytoplankton prey available (Stoecker et al. 1981, 1986).

Estimating ciliate feeding

Estimates of the grazing impact of planktonic ciliates have been given in a number of studies (e.g. Heinbokel & Beers 1979, Verity 1986, Gifford 1988, Rassoulzadegan et al. 1988, Paranjape 1990, Hall et al. 1993, Stoecker et al. 2000, paper I). Owing to their generally high growth efficiencies and clearance rates, ciliate communities can have a significant impact on the phytoplankton standing stock, with grazing rates typically exceeding 50 % of primary production in marine environments (Capriulo & Carpenter 1980, Andersen & Sørensen 1986, Verity 1986, Paranjape 1987).

To evaluate the impact of a planktonic grazer on the prey community, certain feeding-related variables must be determined. These variables are species-specific, yet they permit generalizations to be made to some extent to other species, e.g. those of the same size or with a similar feeding mode. The uptake of particulate prey by ciliates has been evaluated with experimental techniques based on the use of live or dead cultured or natural prey labelled with different methods (e.g. Sherr & Sherr 1987, Rublee & Gallegos 1989, Dolan & Coats 1991, Sherr et al. 1991, Li et al. 1996) or inert particles (Borsheim 1984, Jonsson 1986). The following sections present measurements of the basic parameters – ingestion and clearance.

Ingestion

Ingestion rate (I) denotes the number of prey particles ingested per predator cell in a time unit ($cell_{prey}\ cell_{ciliate}^{-1}\ h^{-1}$). The ingestion rate can be experimentally estimated directly, by observations of ingested prey particles inside a ciliate cell, or indirectly, as the disappearance of prey from the experimental water over time. It might be useful to use both methods, although the results ought to be the same for both. Sometimes direct observations are not reliable or cannot be made, for instance, in work with species that have opaque loricas or shells. Furthermore, if the predator has high ingestion rates and/or the prey density is very high, it is difficult to count the precise number of ingested prey. With very small prey, the number and volume of food vacuoles, rather than the number of individual ingested prey objects, have to be estimated (Fenchel 1980b). For calculations and comparisons of species-specific growth rates with different foods, the inges-

tion rate may be expressed as ingested carbon (usually pg or µg C cell^{-1} h^{-1}).

Clearance

Clearance rate (C) is a derivative of ingestion rate and is calculated by dividing the latter by prey concentration. The clearance rate denotes the water volume that an individual grazer can clear of food particles in a time unit (with microprotozoans, usually µl cell^{-1} h^{-1}). The maximum ingestion rate for a ciliate and its prey is determined by combining the prey concentration and the rate at which food vacuoles are formed. According to Fenchel (1980d), the maximum particle uptake rate (U_{max}) in ciliates is actually a measure of the maximum rate at which food vacuoles are formed. During the ingestion of a particle, the cytostome is blocked and a ciliate cannot take up new particles (Fenchel 1980a, Jonsson 1986). Larger prey particles induce a larger number of vacuoles, causing the ingestion rate to decrease, whereas several small particles are packed in a smaller number of vacuoles. Thus, the larger the prey, the longer is the handling time spent by the predator.

The term clearance itself does not distinguish between the time spent searching for prey and that spent handling the prey, from successful capture of the particle to the formation of a food vacuole. When plenty of suitable prey are available, the ciliate does not have to allocate time to searching for prey, and spends it mostly in handling. Thus, the higher the prey concentration, the less time the ciliate allocates to filtering and the more time to handling, so the actual filtering rate decreases. In contrast, at a low prey concentration the grazer has to sweep greater water volumes to find prey, and the clearance rate increases (Fig. 2). High prey concentrations may interfere with the filtering of prey particles by clogging the feeding apparatus (Jonsson 1986). It has also been discussed whether low prey concentrations might change ciliate feeding behaviour (i.e. threshold feeding), but examples of such behaviour are rare (Verity 2000, paper V). Nevertheless, the existence of a feeding threshold would be beneficial, especially in patchy environments, as the grazer could cease feeding and concentrate on the search for new food patches instead of continuously filtering in a place where no or little food is available.

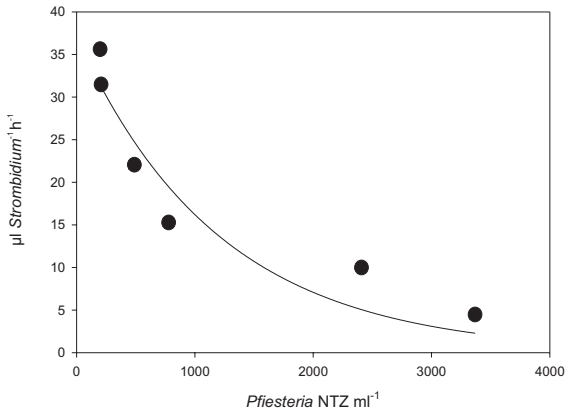


Figure 2. The clearance rate of the ciliate *Strobilidium* sp. in different prey concentrations. NTZ = nontoxic zoospores of *Pfiesteria piscicida* (data from paper V).

Functional response

According to Holling (1959, 1965), predation rates increase with increasing prey population density. This is due to two effects: 1) each predator increases its consumption rate when exposed to higher prey densities, and 2) predator density increases with increasing prey densities. These effects are considered as two different responses to prey density: 1) the functional response and 2) the numerical response. The models created by Holling describe three different functional response types (Fig. 3). All three have a phase of increasing consumption rate with increasing prey concentration below an incipient limiting prey concentration (ILC), a food concentration above which predators are assumed to ingest at maximum rates (Chow-Fraser & Sprules 1992 and references therein). It is important to distinguish between different types of functional response because different assumptions are made of the feeding components (search, feeding duration and handling time) in each type of response (Chow-Fraser & Sprules 1992). In the type-I response, the search rate is constant but handling time negligible, and thus the ingestion rate increases linearly below ILC. In the type-II response, the search rate is constant and handling time is neither negligible nor dependent on prey density. The shape of the curve (Fig. 3 B) of ingestion is determined by the maximum number of prey that can be ingested in a certain time period. When the predator spends more time handling the prey with increasing prey density, the filtering rate decreases continuously. In the type-III response, both handling time and search rate vary with prey concentration. The type-III functional response will arise whenever an increase in food density leads to an increase in the consumer's searching efficiency or to a decrease in its prey handling time. The ingestion rate is initially depressed at low prey densities, after which an increase in density leads to a more than linear increase in ingestion rate (Fig. 3 C). In both type-I and -II responses, a suspension feeder is assumed to graze at maximum rates until its food supply is depleted. In the type-III response, a refugium is provided for the prey, since ingestion is reduced at low prey concentrations, allowing co-existence between phytoplankton and its grazer (Chow-Fraser & Sprules 1992).

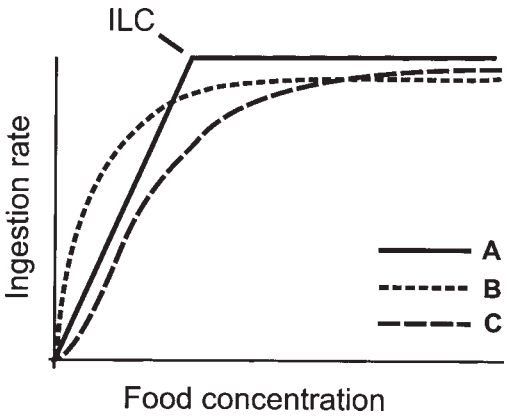


Figure 3. Idealized models of filter feeder's ingestion rate as a function of food concentration (after Holling 1959, 1965 and Chow-Fraser & Sprules 1992), also named Holling type I, II and III functional responses. ILC = incipient limiting food concentration, below which the ingestion rates increase. A = type I, B = type II, C = type III.

Phagotrophic dinoflagellates

Dinoflagellates constitute a heterogeneous group of organisms, with more than 2 000 living species described. Approximately 90 % of these species are marine; moreover, 50 % of free-living species lack chloroplasts and rely on the ingestion of particulate food (Gaines & Elbrächter 1987). There are also species that can combine phototrophy and heterotrophy. These species usually have permanent chloroplasts and are primarily photosynthetic, but there are also "colourless" species that use chloroplasts robbed from their algal prey for photosynthesis (Stoecker 1999) (see section Mixotrophy among ciliates).

A dinoflagellate cell normally has two flagella, which enable active movement of the cell. The swimming speed of a phagotrophic dinoflagellate is commonly greater than that of its prey. Dinoflagellates that swim faster than their prey can be referred as the "searching type", whereas those able to catch prey that swim faster than themselves are the "trapping type" (Hansen & Calado 1999). Phagotrophic dinoflagellates incorporate three different types of feeding mechanism: direct engulfment, pallium feeding with a pseudopodium that envelopes the prey outside the predator cell, and tube feeding, i.e. sucking out the prey contents with a feeding tube (Hansen & Calado 1999).

Direct engulfment occurs mainly among naked species and pallium feeding among heterotrophic thecate species. Tube feeding has been described for both heterotrophic and mixotrophic thecate and athecate species. The heterotrophic thecate species *Dinophysis rotundata* feeds on ciliates with a feeding tube (Hansen 1991), and a similar feeding mechanism has been proposed for photosynthetic *Dinophysis* species (Jacobson & Andersen 1994). Since the feeding mechanisms permit the intake of comparatively large particles, dinoflagellates are considered raptorial feeders.

The genus *Protoperidinium,* which is abundant during the spring bloom in the Baltic Sea (Kivi 1986), is able to feed on large chain-forming diatoms by means of a pallium. The content of the prey is liquefied and taken up by the pallium. As a consequence, only an empty frustule of the prey remains, and no food vacuoles are formed inside the predator (Hansen & Calado 1999).

The proposed optimum predator to prey size ratio for heterotrophic dinoflagellates is about 3:1 (range 7:1 to 1:0.4) (Hansen et al. 1994 and references therein). Heterotrophic dinoflagellates differ from ciliates in their higher relative optimum prey size. Since the prey preferences of similar-sized ciliates and heterotrophic dinoflagellates do not necessarily overlap, a ciliate feeding on a phagotrophic dinoflagellate smaller than itself may derive "double benefit" by eating its competitor. Species-specific clearance rates of heterotrophic dinoflagellates have been found to range from <1 to 28.3 µl $cell^{-1}$ h^{-1} (Lessard & Swift 1985, Hansen 1992, Jeong & Latz 1994).

The growth rates of heterotrophic dinoflagellates are approximately one-third of those of ciliates, ranging from about 0.3 to 1.1 d^{-1} (Hansen 1992, Nakamura et al. 1995, Strom & Morello1998). These low growth rates may be due to low growth efficiency (Hansen 1992 and references therein). As in ciliates, growth rates increase with increasing food concentration until a satiation level is reached, and decrease with increasing cell

size owing to the increase in respiratory losses (Fenchel & Finlay 1983, Hansen 1992).

Mixotrophy in planktonic microprotozoans

All living organisms have a limited number of strategies to obtain energy and matter for growth and sustenance. The ecological literature refers to organisms that are able to use alternative nutritional modes as mixotrophs. Mixotrophy is defined as the capability of an organism to act as an autotroph and a heterotroph, and is primarily applied to organisms that are both phototrophic and phagotrophic. Mixotrophy is prevalent in planktonic unicellular organisms, such as chrysophytes, prymnesiophytes, dinoflagellates and ciliates, and among the sarcodines (Stoecker 1998 and references therein). The term mixotroph commonly refers primarily to phototrophic algae capable of phagotrophy or osmotrophy, and to phagotrophic protozoa able to photosynthesize. Mixotrophy may be used to renew cellular reserves of carbon, macronutrients, amino acids (Stoecker & Gustafson 2003) and trace elements such as iron or phospholipids (Raven 1997, Stoecker 1998).

The role of mixotrophy in different environments is difficult to quantify, since there is probably a continuum between strictly autotrophic and heterotrophic organisms in general, and available data suggest that there is a gradient among mixotrophs, some species being more autotrophic and some more heterotrophic (Jones 1994). Mixotrophy is presumably regulated by environmental factors, such as the availability of light, nutrients and prey, all of which have an influence on cell physiology. Thus, mixotrophy is regulated in different ways in different species.

The functional role of an organism in the food web is determined by its trophic status. Classic trophodynamic food web models rely on the dichotomy between plants and animals that separates primary producers from consumers by their trophic level. Autotrophic organisms are responsible for primary production, which heterotrophs at different trophic levels use to satisfy their nutritional demands. Food web models incorporating mixotrophy have been presented by e.g. Thingstad et al. (1996) and Stoecker (1998). When mixotrophy is added to the trophodynamic models, no segregation can be made by trophic level, and questions arise as to the effects of mixotrophy on the functioning of the food web. Determining the transfer of matter and energy then becomes more complex.

Mixotrophy among ciliates

The first functional chloroplasts inside a planktonic ciliate, *Laboea strobila* (Lohmann), were discovered in the early 1970s (Blackbourn et al. 1973). Mixotrophic ciliates photosynthesize by using endosymbiotic algae or chloroplasts robbed from their algal prey (kleptochloroplasts). Among the ciliates, photosynthesis with algal endosymbionts is especially common in freshwater environments (Hecky & Kling 1981, Lee et al. 1985), where the biomass of these species may be equal to or higher than that of the phytoplankton (Hecky & Kling 1981). Chloroplast enslavement in planktonic ciliates is confined mainly to the oligotrichs, to the family *Strombidiidae* in particular (Jons-

son 1987, Stoecker et al. 1987, Laval-Peuto & Rassoulzadegan 1988, Lindholm & Mörk 1989, Stoecker & Silver 1990). Plastids from different algal groups may be used in this sense. Whereas in some taxa mixotrophy seems to be associated with oligotrophic environments, mixotrophic protists may be abundant in eutrophic and mesotrophic environments as well (Stoecker 1998 and references therein). According to Stoecker et al. (1987, 1989), in temperate coastal surface waters about 20-70 % of all ciliate communities were mixotrophic. Corresponding values for coastal Antarctic water range from 25 % to 47 % during the spring bloom and from 40 % to 52 % in the Nordic Seas in summer (Putt 1990).

Mixotrophy among flagellates

The idea that photosynthetic organisms are able to utilize organic material is not new. Phototrophic flagellates can be able to utilize organic particles (phagotrophy) or dissolved organic substances (osmotrophy) (Granéli et al. 1999). Observations based on conventional light microscopy revealed phagotrophy among certain phytoflagellates back in the early 1900s (Hofender 1930). Later, novel methods involving the use of fluorescently or radioactively labelled particles (Lessard & Swift 1985, Rublee & Gallegos 1989, Sherr et al. 1991, Li et al. 1996) or latex beads (Bird & Kalff 1987, Jones & Rees 1994) as particulate prey revealed phagotrophy in phototrophic cells. Phototrophic flagellates are important grazers of bacteria, picoplanktonic algae and micro-sized planktonic organisms, and in some environments, e.g. estuarine and coastal waters, phytoflagellates may account for >50 % of the flagellate bacterivory in summer (Stoecker 1998 and references therein).

The relative commonness of mixotrophy (e.g. Jacobson & Anderson 1996) is not surprising, since phagotrophy has been a crucial element in the evolution of all photosynthetic organisms. According to current theories, photosynthesis in eukaryotic cells is the outcome of one or more endosymbiotic events involving ingestion of photosynthetic organisms: at first, photosynthetic cyanobacteria. In the evolution of photosynthetic organisms, phagotrophy is thus considered a primitive character; its absence only developed later. Worth mentioning is that mixotrophy appears to be common among harmful marine algae species (e.g. Jones et al. 1993, Nygaard & Tobiesen 1993, Jacobson & Andersen 1994, Lewitus 1999). Studies on the role of mixotrophy in the Baltic Sea area are still sparse. This thesis, too, looks only briefly at the subject of mixotrophy, in papers III and V, with reference to the special characters of the dinoflagellates *Dinophysis acuminata* (Baltic Sea) and *Pfiesteria piscicida* (Choptank River, USA).

The mixotrophic dinoflagellate *Pfiesteria piscicida* is a potentially toxic species that has been extensively studied due to its links to fish kills off the east coast of the USA (e.g. Burkholder et al. 1995, Steidinger et al. 1996, Burkholder & Glasgow 1997a,b, Stoecker et al. 2000, 2002). *P. piscicida* has a complex life cycle that includes amoeboid and flagellate forms, temporary cysts and several nutritional modes, such as the utilization of fish tissues, phagotrophy and photosynthesis with kleptochloroplasts (Burkholder & Glasgow 1997b).

Mixotrophy is often difficult to detect. Among the genus *Dinophysis* its importance has been a subject of controversy. Studies on the physiology and ecology of *Dinophysis* species are difficult to perform, as all attempts to establish a true culture of *Dinophysis* spp. have so far failed (Sampayo 1993, Maestrini et al. 1995, Granéli et al. 1997, Nishitani et al. 2003). Therefore experimental work has to be carried out on recently isolated cells of unknown nutritional history. However, the lack of true cultures corroborates the idea of photosynthetic *Dinophysis* species being mixotrophs that need an additional compound lacking in the culture media used.

OUTLINE OF THE THESIS

This thesis presents an effort to fuse information on the function of different microprotozoan compartments in planktonic food webs into a broader picture. Except for paper V, the studies describe the role of Baltic Sea microprotozoan communities in food webs and concentrate on the interactions between trophic levels. The studies on the abundance and occurrence of microprotozoans in different parts of the Baltic Sea (papers I, II and III) make use of experimental information at species level (papers III and IV).

Papers II and III examine communities in extreme environments, i.e. in the cold, saline, nutrient-rich and poorly oxygenated deep-water layers of the Baltic Proper. Paper III deals with experiments on the photosynthetic activity of different *Dinophysis acuminata* populations and describes the first observations of deep water communities. The observations of deep-water ciliates, which were first reported in paper II, are also included in paper I.

The feeding of natural communities of oligotrichous ciliates was experimentally studied in the coastal area of the Baltic Sea (paper IV) and, for comparison, also in the Choptank River, a tributary of Chesapeake Bay, USA (paper V). The method described in paper IV permits simultaneous measurements of ciliate clearance rates and of food particle selection by size. In paper V the functional response of one ciliate species feeding on living, fluorescently labelled (= vital-stained) prey was studied with different prey concentrations.

Paper I combines monitoring data gathered in two years from two transects extending from the southern Baltic Sea (Kattegat) to the entrance of the Gulf of Finland, and gives estimates of the grazing impact on ciliate communities, and the structure of different ciliate assemblages.

MATERIAL AND METHODS

Study area

Material for the studies presented in this thesis was collected near the Tvärminne Zoological Station (papers III and IV), on the southwest coast of Finland, and during research cruises from open sea stations between the Kattegat and the entrance to the Gulf of Finland (papers I and II), from deep water stations in the Gotland Sea (paper III), and from Chesapeake Bay, USA (Paper V). The laboratory work was carried out at the Tvärminne Zoological Station and at Horn Point Environmental Laboratory, Maryland, USA. The Baltic Sea study sites are shown in Fig. 4.

Characteristics of the northern Baltic Sea

The Baltic Sea is one of the world's largest brackish water basins. The brackish character is maintained by incidental inflows of high salinity North Sea water through the Danish Straits in the southern part of the basin, and by riverine freshwater inflow from catchment areas. The surface water salinity ranges from 1 psu in the northernmost part of the Baltic (Bothnian Bay) and the inner parts of the Gulf of Finland to approximately 9 psu in the southernmost part of the basin (Voipio 1981). The Baltic Sea is relatively shallow, its average depth being 55 m. Nevertheless, the geomorphology is characterized by deep basins. The water balance of the Baltic Sea is positive, i.e. river run-off and precipitation together exceed evaporation. This, together with the narrow and shallow entrance at the Danish Straits, creates the permanent salinity stratification, the halocline (at 60-80 m in the Bal-

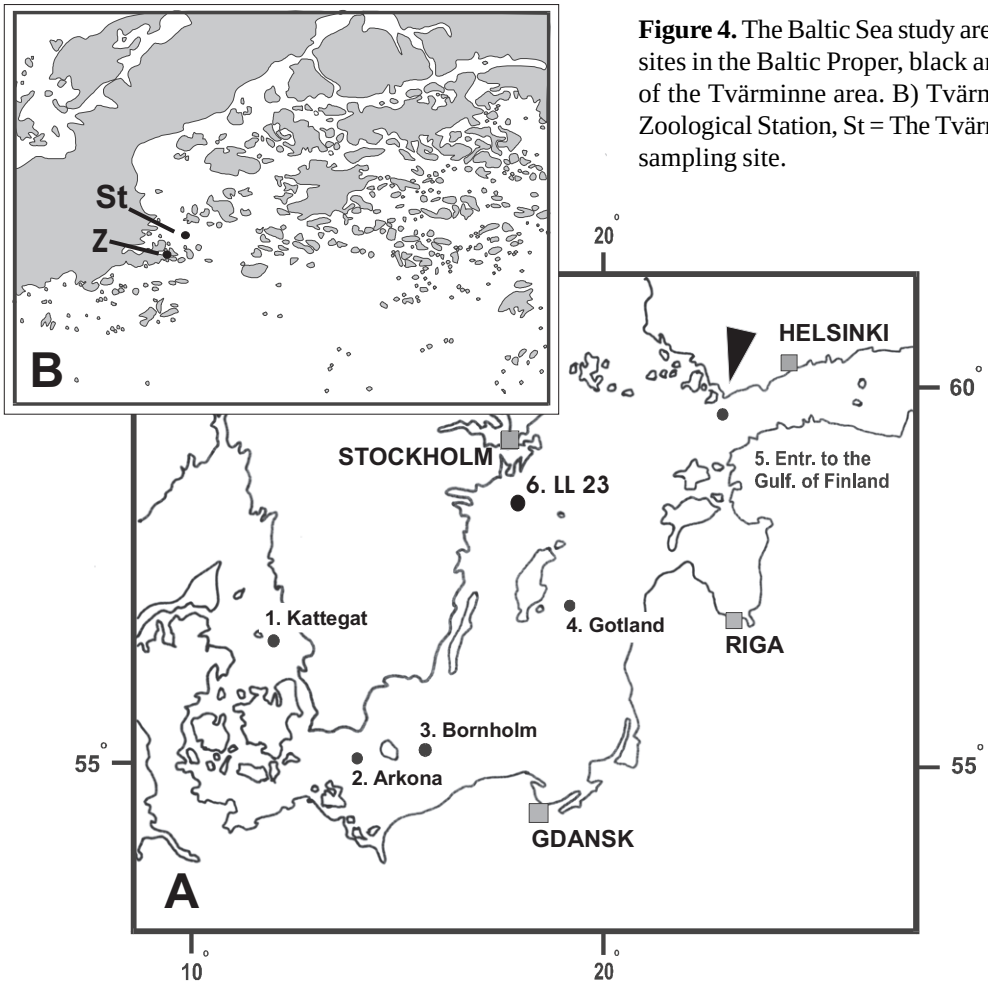


Figure 4. The Baltic Sea study area. A) Sampling sites in the Baltic Proper, black arrow = location of the Tvärminne area. B) Tvärminne area, Z = Zoological Station, St = The Tvärminne Storfjärd sampling site.

tic Proper), that separates the more saline deep water from the surface waters (Voipio 1981). Regional differences in the extent of the productive period in the Baltic are due to differences in the duration of the ice cover and to the high irradiance values during the summer. The seasonal variation in water temperature ranges from below +0 °C to over +20 °C at the time of the summer temperature maximum.

Chesapeake Bay and Choptank River

Chesapeake Bay is the largest estuary in the United States. A comparatively shallow temperate estuary situated within Virginia and Maryland, it has a drainage basin of 165 760 km^2, a mean depth of 8.4 m and a surface area of 6.5×10^3 km^2 (Smodlanka et al.1999). The Bay is a partially mixed estuary in which the primary mechanism of transport is unidirectional, gravitational circulation due to freshwater discharge. Chesapeake Bay has a net surface flow seawards and a net bottom flow of higher saline water landwards. It is characterized by rapid changes in stratification and vertical homogeneity that are influenced by flow rates, temperatures, tides and storms. Nutrient concentrations and phytoplankton biomass vary in response to seasonal patterns of riverine nutrient inputs, and phytoplankton blooms often lead to bottom water hypoxia (Malej et al. 1999). Microprotozoans in Chesapeake Bay exhibit seasonal oscillations reflecting changes in temperature, riverine inputs of dissolved and particulate substances, stratification and chlorophyll *a*. Numerically, ciliates dominate the microprotozoan assemblages in the Bay (approx. 95 %; Coats & Revelante 1999), and have their maximum abundances and biomass in spring and early summer, with minima in mid- to late summer. The highest values of planktonic ciliates in the central region of the Bay approximate 35-40 $\times 10^3$ cells l^{-1}.

The Choptank River is a tidal tributary on the eastern shore of Chesapeake Bay. The longest river on the eastern shore of Maryland, it flows 120 km from western Delaware to Chesapeake Bay. It is tidal fresh for most of those miles, but turns brackish as it nears the Bay.

Sampling

No nets or pumps were used to collect live field material for any of these studies. Water samples were taken with tube samplers of various design and volume. In paper III, large volumes of water were collected and subsequently concentrated with two plankton nets of different size embedded in water (Maestrini et al. 1995). This was done to get concentrated samples containing the dinoflagellate *Dinophysis acuminata* for experimental purposes.

Fixatives

Of the fixatives available, acid Lugol's iodine (Hällfors et al. 1979) is most commonly used to fix microprotozoan samples. The concentration ranges from <1 % to 10 %, depending on the purpose of fixation. The higher the Lugol concentration, the more the cells tend to shrink. Severe shrinkage (in Lugol concentrations of approx. 5 % or higher) may render discrimination between certain species unreliable. Species are easier to identify when

fixed with low Lugol concentrations, but Putt & Stoecker (1989) point out that the cells then tend to rupture or burst more readily than when fixed with high Lugol concentrations, at least in fully marine environments. However, observations made on fixation effects on Baltic Sea ciliates are not fully compatible with the aforementioned findings (own unpublished observations). The low concentrations (<1 %) of acid Lugol's solution (used in all studies presented in this thesis) do not cause severe shrinkage in ciliate cells, and therefore no serious underestimation of cell biovolumes is assumed to have occurred.

The use of formaldehyde water solutions (formaline) to fix microprotozoans is not encouraged, since cell loss is then higher than with acid Lugol's solution (Putt & Stoecker 1989). Further, cells fixed with formaline are transparent and may be difficult to spot in the samples; Lugol-fixed cells are brownish and therefore easier to find. Formaldehyde has, however, one advantage: it preserves the autofluorescence of chloroplasts, at least for a short period.

Glutaraldehyde has routinely been used to fix nanoflagellates and bacterioplankton, and nowadays is also applied to ciliates, at least in studies of ciliate mixotrophy. In general, samples for epifluorescence microscopy and electron microscopy are fixed with glutaraldehyde. The autofluorescence of glutaraldehyde-fixed photosynthetic cells and also fluorescent stains (e.g. Hobbie et al. 1977, Li et al. 1996) are visible in epifluorescence microscopy, and the samples remain well preserved for several years if they are stored in dark and cold. Glutaraldehyde was used as fixative in the grazing study discussed in paper V, and to preserve the cellular contents of *Dinophysis acuminata* reported in paper III.

Microscopy

Cells were counted according to Utermöhl (1958) on fixed samples. A method of concentrating larger volumes (usually 1:8 or 1:10) of fixed samples with a 10 µm polycarbonate filter before the sample settled in 50 ml tubes (Kivi 1986) was applied in papers I and II. This procedure allowed the larger cells that often occur only in very low numbers in samples from open sea areas to be included in the counts. The smallest cells (ESD, estimated spherical diameter, <10 µm) were, however, excluded from the counts. This does not usually seriously affect estimates of ciliate community biomasses, since the contribution of cells <10 µm to total biomass estimates is not significant. The cell counts of Lugol-fixed samples were done under inverted microscopes with bright field and phase contrast illuminations, using magnifications of between 125 and 500 ×. A 50-ml sample usually settled 24 h before counting. Glutaraldehyde-fixed samples (papers III and V) were studied by epifluorescence microscopy to count the ingested, fluorescently labelled *Pfiesteria* zoospores inside the ciliate *Strombidium* sp. (paper V) or to study the cellular contents of *Dinophysis acuminata* (paper III), as described in the relevant papers.

Carbon content estimates

Biovolume

Carbon content estimates of planktonic microprotozoans are based on cell volume conversion factors. The estimated cell biovolume is usually derived from microscopic measurements of the length and width of the

cell in question. These measurements are then fitted to the geometric formula that best fits the shape of the cell. Living cells are difficult to measure, since many species, ciliates at least, do not stay long in one spot. For convenience, the measurements are usually made on fixed samples. In work on monocultures, more precise cell size measurements of fixed or living cells can be made with electronic particle counters.

Fixatives and conversion factors as sources of error

Microprotozoans are fragile organisms, and the use of fixatives invariably causes some loss in cell numbers. It may also lead to underestimates (or sometimes overestimates) of cell biovolume and its derivative: estimated organic carbon content (Choi & Stoecker 1989, Putt & Stoecker 1989, Stoecker et al. 1994). To convert biovolumes to carbon, a carbon:volume factor of 0.11 pg μm^{-3} (Edler 1979) has been widely employed for Lugol-fixed microprotozoans in the Baltic Sea (excluding dinoflagellates, for which 0.13 pg μm^{-3} is recommended; Edler 1979), and was also used in papers I and II. This conversion factor probably underestimates ciliate carbon content, at least when high concentrations of Lugol's solution are used (Putt & Stoecker 1989). Therefore the use of an experimentally determined carbon:volume ratio that takes cell shrinkage into account is recommended for Lugol-fixed marine ciliates (Putt & Stoecker 1989). Their conversion factor of 0.19 pg μm^{-3} for oligotrichous ciliates fixed with 2 % acid Lugol's iodine was employed in paper V for *Strombidium* sp. Menden-Deuer & Lessard (2000) presented different volume-dependent equations for dinoflagellates, diatoms and assemblages of taxonomically diverse protist plankton. The carbon contents of *Dinophysis acuminata* and *Pfiesteria piscicida* in papers III and V were estimated by applying the equation of Menden-Deuer & Lessard (2000) for dinoflagellates (pg C $cell^{-1} = 0.760 \times volume^{0.819}$). This equation takes into account the relative decrease in carbon content of both thecate and athecate dinoflagellates with increasing cell volume. Clearly, then, the use of fixatives and conversion factors should be given careful consideration. For example, comparisons of growth and grazing rates depend on reliable carbon density estimates. If both cell volume and carbon content are underestimated, which may be the case when a fixative that shrinks cell volumes and a low carbon conversion factor are used simultaneously, the biomass will be underestimated.

Measurements of photosynthetic activity (P - E measurements)

The photosynthetic activity of different *Dinophysis acuminata* populations was measured in August 2002 (paper III). These measurements were triggered by the discovery in August 2001 of a dense *Dinophysis* spp. community in unlit deep water, where photosynthesis cannot occur. The measurements were conducted to establish whether the photosynthetic rates of *D. acuminata* cells originating from different depths (i.e. different light environments) varied. Cells for these measurements were collected at one open-ocean station in the northern Baltic Sea and at one station on the southwest coast of Finland. Photosynthetic carbon uptake was

measured with a *P – E* incubator supplying 16 light levels. The protocol of these studies is presented in paper III.

Grazing experiments

The studies on planktonic ciliates feeding on particulate prey (papers IV and V) were based on direct particle uptake counts, i.e. the calculations of ingested particles inside individual grazer cells. The wheat starch suspension used as artificial food for natural ciliate assemblages (paper IV) contained particles ranging in size from 1.4 to 40 µm. Thus not only the overall uptake rates, but also preferences for certain sized prey could be investigated.

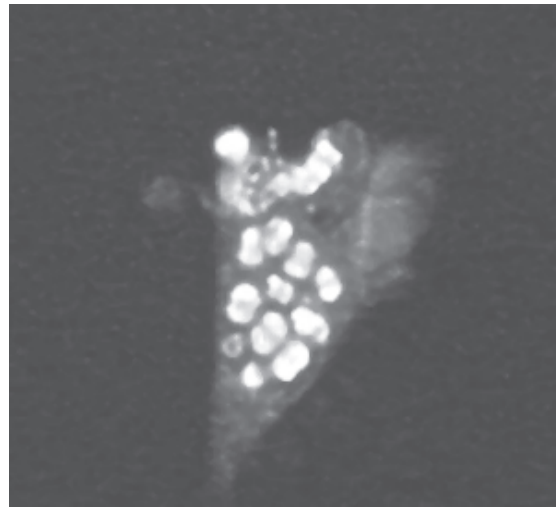
Comparative data on ciliate feeding efficiency were obtained from another brackish environment, Chesapeake Bay, in a grazing experiment conducted in June 2000. These experiments were performed using live prey in a case study with a planktonic ciliate species, *Strombidium* sp., feeding on the dinoflagellate *Pfiesteria piscicida* (paper V). Before the experiment, a dense culture of *P. piscicida* was stained with the vital fluorescent stain CMFDA (5-chloromethyl-fluorescein diacetate) according to Li et al. (1996). Live prey serves as a good alternative to inert particles in feeding experiments measuring ingestion rates. Fluorescently labelled prey cells were viable (swimming and able to divide) after staining, and the ingested prey were easy to count inside the ciliate cells (Fig. 5). To compare different methods in evaluating grazers' impact on prey, feeding was also indirectly evaluated by monitoring the disappearance of prey from the experimental water.

MAIN RESULTS AND DISCUSSION

The open Baltic Sea summer pelagial system contains diverse ciliate associations (paper I)

Paper I presents information on the distribution of ciliate species at various depths at five open sea stations in the Baltic Sea. The information, which was collected during two years, 1988 and 1990, was used to analyse the prevalence of ciliate associations. The dataset, in general, was typical of the mid-summer season, with its dominance of small cells (ESD <30; especially strombidiids, strobilidiids and prostromatids). To study the likelihood of inter-specific ciliate associations and their connections with abiotic and biotic factors, Pearson's correlation coefficients were calculated between all ciliate species, temperature and chl-*a* concentrations. Associations between ciliate species

Figure 5. *Strombidium* sp. with ingested, fluorescently labelled *Pfiesteria piscicida* zoospores (paper V).



were determined by the significance of the correlation factors between cell numbers of the different species from the whole data. The associations were based on "head" species, i.e. the species with the highest number of statistically significant correlations with other species. This method revealed three different species associations in the two-year data (Fig. 6). The tightest bond between species was that between *Coleps* spp., large unidentified ciliates, and *Metopus* sp., which were restricted to cold, saline and poorly oxygenated water (association 1 in both years). All the other associations were formed by a diverse selection of species (strombidiids and prostomatiids in particular) from the upper water layers. The "head" species in association 2 in both years was *Strobilidium spiralis*, which is common in summer in the northern Baltic Sea (Kivi 1986, Johansson et al. 2004). The "head" species of association 3 was *Lohmanniella oviformis* in 1988 and *Mesodinium pulex* in 1990.

The co-existence of different suspension-feeding ciliates cannot just be explained as the outcome of competition for resources between species, simply because the history of the species is unknown. The associations could have been formed due to utilization of the same food resources or preference for similar environmental features, or even due to the inner dynamics of an association such as predator-prey relationships. The term guild was not used in this study, although it is possible that some of these associations do in fact represent true feeding guilds, in which the largest member of a group may be feeding on the smaller species (Dolan 1991a). More probable, however, is that several factors are responsible for keeping the associations together. The strong correlations calculated between the species and the spatial co-occurrence of the members of an association suggest true connections between the species.

It is possible that the occurrence of certain species in deep water was due merely to abiotic environmental factors such as low oxygen concentrations, whereas the communities in the euphotic layer were affected by biotic resources, e.g. the abundance of a certain type of prey. There are species-specific physical controls on the range of the particle size spectrum of any filter feeder. This has ecological consequences for niche separation in the food web. Ecological theories state that competing species may co-exist in a resource continuum if their niche positions are displaced (Begon et al. 1996). Suspended food particles for ciliate filter feeders, including both prokaryotes and eukaryotes, form a continuous size spectrum from <1 to >10 µm, and thus offer a wide range of prey varying in size and type. The smallest diameter of the largest cells that can be used by protozoan filter feeders is roughly 20-30 µm (Fenchel 1986). Summer communities in the Baltic Sea are often dominated by naked oligotrichs (Gast 1985, Kivi 1986, Witek 1998, Johansson et al. 2004, paper I). These species, which are especially abundant in the upper euphotic zone, feed mainly on prey <10 µm in diameter, nanoplanktonic algae in particular (Jonsson 1986, Rassoulzadegan et al. 1988, Bernard & Rassoulzadegan 1990). One factor that affects the use of common resources by different species in a food web is the prevalence of mixotrophy. The role of mixotrophy has not, however, been evaluated in the discussion on ciliate assemblages, mainly because of the lack of quan-

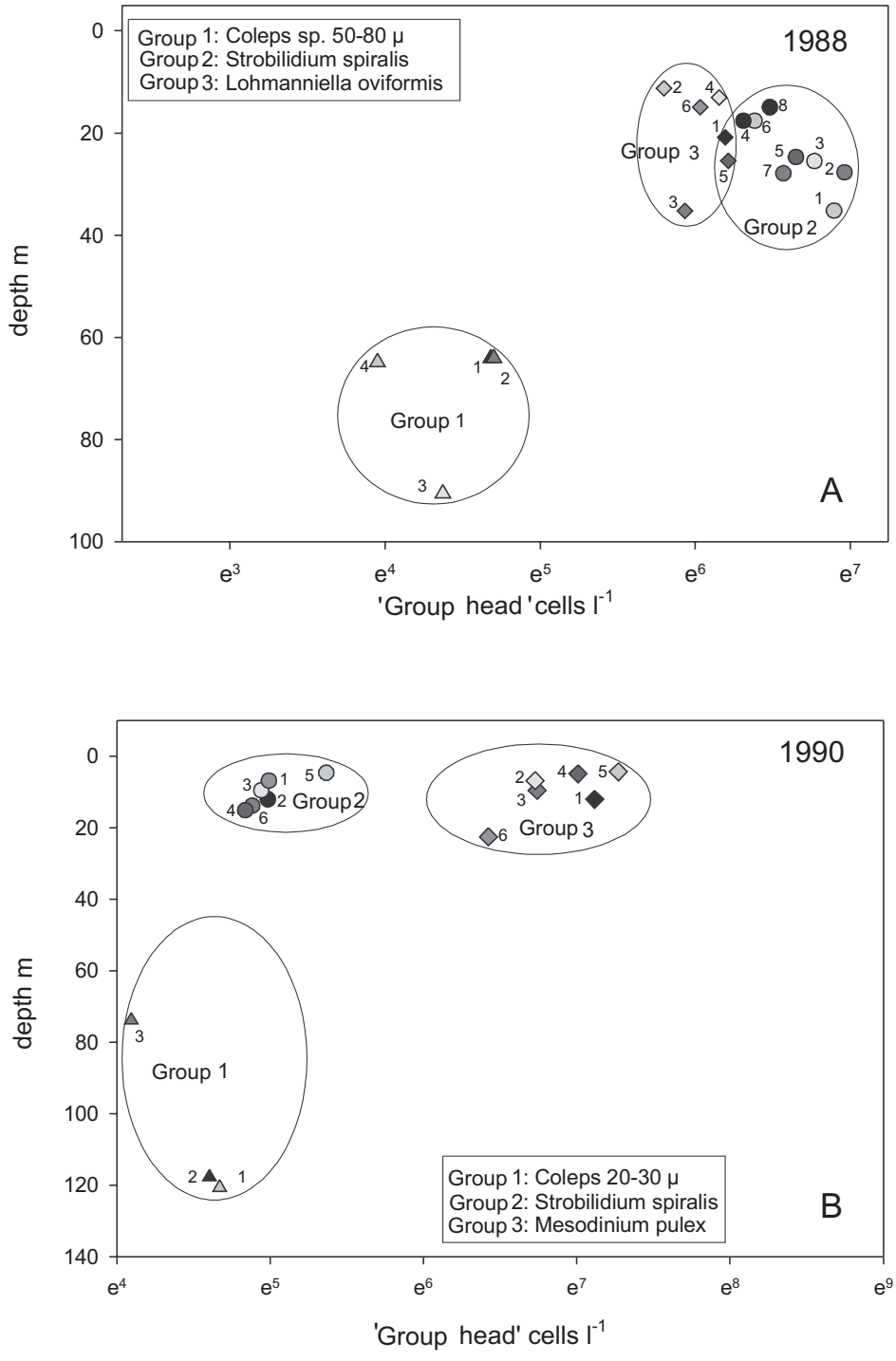


Figure 6. Three different ciliate associations found in 1988 and 1990 at five stations in the Baltic Proper that were distinguished by correlation analysis (paper I).

titative information on the occurrence of mixotrophy among Baltic Sea ciliates. However, some species have been observed to retain chloroplasts (Kuosa 1990c, own observations), and some (*Laboea strobila* and *Strombidium conicum;* Stoecker & Michaels 1991) are known to be mixotrophs in other sea areas. Clearly, then, the ability of a species to use alternative nutritional sources is beneficial in the competition with other, co-existing species, a factor that should be kept in mind when evaluating interactions between species.

The grazing experiments presented in paper IV showed that ciliate species have different prey preferences, a finding that may explain the typical co-existence of *Strobilidium spiralis* and the somewhat smaller *Strobilidium* sp. (ESD 40 µm) in summer. The larger *S. spiralis* has a strong preference for prey of a certain size and also has somewhat higher clearance rates; the smaller *Strobilidium* sp., in contrast, is able to extend its feeding to larger prey. Such feeding behaviour may explain the co-existence of different species in assemblages. Associations 2 and 3, described in paper I during both years, included species with a different optimum prey size and (what may be even more important in these associations) prey size ranges, especially at the higher end of the prey size continuum. The largest species are able to extend their feeding to larger prey items, but may also feed on the smallest ciliates. The abundance of tintinnids in this dataset was low, as is the case in general in the open sea areas of the Baltic in summer (Kivi 1986, Johansson et al. 2004, paper I and own unpublished observations). It would be of interest to perform a similar analysis in coastal waters, where the abundance and diversity of tintinnid species, which also feed on small nanoplanktonic organisms (paper IV), is usually higher, and to study any assemblages found.

The discussion on the interactions between the various feeding modes of microprotozoans and the availability of different prey types, and also the top-down control of metazooplankton, can be broadened to cover species succession. The seasonal succession of planktonic microprotozoans in the northern Baltic Sea has been described by Kivi (1986). Microprotozoan communities show seasonal fluctuations that reflect annual cycles in water temperature, stratification and other hydrodynamic events and chl-*a* concentrations. Similarly, the total biomass of ciliate communities shows considerable fluctuations during the growth season, and the species composition of these communities undergoes seasonal changes. Some species are abundant throughout the growth season, with maximum abundances at certain times, whereas other species occur only during certain periods. Clearly, the distribution and abundance of a species depend, among other things, on the stage of its life cycle, its nutritional status, its life history and resource requirements, its interactions with other species and environmental conditions. In an environment as patchy and changing as the pelagial, such information is hard to obtain and, further, to use as a tool to explain different characters in planktonic communities. For example, correlation analyses between existing communities and environmental factors (e.g. chl-*a* vs. ciliate abundance in paper I) should be interpreted with caution, since they are based not on information on the available resources (planktonic algae) that allowed the grazers (ciliates) to grow,

but merely on knowledge of what remained of the resources after the grazers had found their way to that particular spot. In this discussion, the role of environmental factors in the formation of microprotozoan communities is restricted to the role of prey and predators.

In the northern Baltic Sea, abundances of predaceous species such as *Didinium gargantua* and of large suspension feeding ciliates (e.g. large *Strombidium* spp. and *Bursaria* spp.) are higher during the spring bloom than during the summer. Heterotrophic dinoflagellates of the genus *Protoperidinium* and also the siliceous flagellate *Ebria tripartita* are usually most abundant in spring, when the bulk of the phytoplankton biomass consists of large filamentous diatoms and also of thecate dinoflagellates (especially *Peridiniella catenata* and *Scrippsiella hangoei*). The abundance of these species declines as summer approaches, possibly due to a shift in the phytoplankton community structure towards dominance of small flagellated species and to the increasing grazing pressure from metazooplankton, notably the copepods. No quantitative information is available on the grazing impact of the microprotozoan communities in spring (of special interest would be to monitor the grazing of *Protoperidinium* spp. on diatoms). In summer, the phytoplankton communities, which are characterized by pico- and nanoplanktonic flagellates, are suitable prey for suspension feeding ciliates and also for small heterotrophic and mixotrophic dinoflagellates. These, again, are the preferred prey for metazooplankton (e.g. Stoecker & Capuzzo 1990, Kivi et al. 1996, Merrel & Stoecker 1998), which, through their feeding impact, shape the structure of the microprotozoan communities. Small cells tend to dominate summer ciliate communities, although, typically, a continuum of different size groups still exists, the cell numbers decreasing with increasing size. This finding, too, is in accordance with the general view that the number of organisms in planktonic ecosystems is highest in the smallest size groups, and decreases with increasing size (Sieburth et al. 1978). Any "gaps" in the size continuum may well reflect metazoan grazing pressure, which is targeted at prey of a certain size. In paper I, metazoan grazing was thought to be the reason for the low number of medium-sized ciliates (Fig. 7).

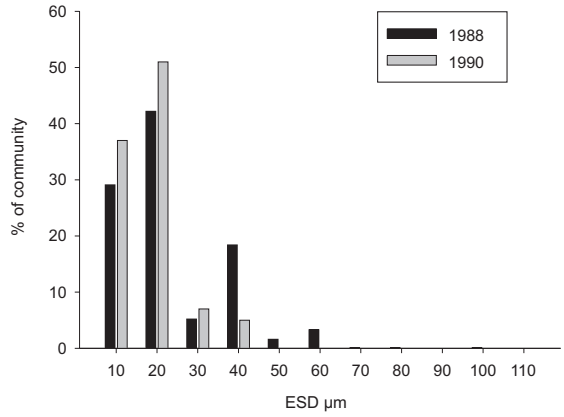


Figure 7. Average size distributions (ESD µm) of planktonic ciliates (*Mesodinium rubrum* excluded) at five stations in the Baltic Proper in 1988 and 1990. For example, the size class 30 µm includes species with the largest measured diameter (D) exceeding 30 µm, up to 40 µm (30 <D≤40) (paper I).

Easily overlooked patches for planktonic microprotozoans exist in the deep-water layers of the Baltic Sea (papers I, II and III)

Distinct microprotozoan communities were found in deep water (77-136 m) during three research cruises, in 1988, 1990 and 2001 (Fig. 4). The ciliate communities described in papers I and II were detected when biological water sampling was extended to include the deep water layers below the halocline (down to 90 and 140 m, Bornholm and Gotland Basins) in 1988. Ciliates occurred in these basins in low densities (16-130 cells l^{-1}) in a water layer approximately 15 m thick (75-90 m and 120-136 m). The ciliates were found as a result of intensive sampling in the oxic-anoxic boundary layer but also due to concentration of the samples before microscopy. During the second cruise, in 1990, the oxic-anoxic water interface was sampled once again to see whether these ciliates were present.

During the research cruise in 2001 (paper III) a search was made for fluorescence signals below the thermocline at several open sea stations in the Baltic Proper. The aim was to find thin layers of the dinoflagellates *Dinophysis acuminata* and *Dinophysis norvegica*, species that in the Baltic are typically concentrated in the thermocline region, at 15-25 m (Kuosa 1990b, Carpenter et al. 1995). Although this cruise was dedicated partly to the search for *Dinophysis* communities, the discovery that a fluorescence peak at a depth of 77 m in the Gotland Deep was due to a dense community (approx. 18 000 cells l^{-1}) of phototrophic dinoflagellates came as a surprise.

Crucial for a successful description of the distribution and diversity of planktonic communities is the creation of a plausible sampling strategy. Planktonic organisms are not distributed homogeneously in the water column (e.g. Cushing 1962, Wiebe & Holland 1968) but vary in abundance both horizontally and vertically on different scales in space and time. In general, however, the biomass of planktonic algae (primary producers) and protists (grazers of primary producers) is concentrated more or less in the euphotic zone. As a consequence of the overall high light attenuation, the euphotic zone in the northern Baltic Sea is relatively shallow, not exceeding 20-30 m (e.g. Aarup 2002). The regular sampling of planktonic organisms and other biological variables usually covers the water column well down to the thermocline; below that, however, the interval between water samples may be 10-20 m or more. Conventional vertical sampling may often miss or underestimate small-scale patches (Donaghay et al. 1992). Thin layers of phytoplankton at different depths range in thickness from centimetres to a few metres, and may extend horizontally for kilometres and exist for days (Kononen et al. 1999, McManus et al. 2003). The occurrence of certain species within a patch is a result of hydrodynamic effects and the swimming capabilities of the species (Kononen et al. 2003). In a study on a small fjord in East Sound, Canada, 80 % of phytoplankton layers were found to be <2 m thick (Dekshenieks et al. 2001). In such layers the abundance of organisms may be several times as high as in the water column above or below.

The “large” ciliates found at the Bornholm and Gotland Deep stations in 1988 and 1990 (paper II) occurred in deep water under low oxygen conditions with some traces of H_2S. The species were not identified, but

on the basis of their size and shape they were judged to be of benthic origin and to have migrated upwards due to the anoxic conditions prevailing in deeper water layers. It was further thought that since these cells were found only in poorly oxygenated waters, they presumably had low tolerance for high oxygen concentrations. Planktonic bacteria, which increased in both size and abundance with depth, could possibly serve as prey for ciliates at those depths. These deep-water communities are presumably connected to the upper pelagic system through one-way transport only, i.e. they receive settling organic matter from the surface layers. Owing to the size of the ciliates, and their high organic carbon contents, they have a substantial effect on estimates of ciliate carbon for the whole water column.

The use of submersible sensors, such as CTD (conductivity-temperature-density) probes, which collect information on hydrographical parameters from the water column, are useful tools in oceanographic studies. Conducting such measurements before the collection of biological water samples enables sampling to be targeted at layers of interest such as density and temperature gradients. Without the use of a CTD probe equipped with a fluorescence sensor, the deep-water *Dinophysis* spp. community detected in 2001 (paper III) would have been overlooked. The occurrence of these species in deep water raises interesting questions about their ecology. Were the cells there driven incidentally by hydrodynamic events? Or had they migrated downwards actively and, if so, what were the triggering factors? Did mixotrophy play a role? In the following year no such dense deep-water communities were observed; nevertheless, *D. acuminata* was found in lower concentrations at all the deep-water stations visited.

For the present, we can only speculate on the reasons for the occurrence of these deep water *Dinophysis* spp. communities. One might be active migration in search of higher nutrient concentrations. On the other hand, mixotrophy would be useful for survival in darkness for longer periods. Phototrophic dinoflagellate species have been found to undertake vertical migrations (e.g. Cullen & Horrigan 1981, Cullen 1985, Cullen & MacIntyre 1998, Kononen et al. 2003). The migrational patterns of dinoflagellates are related to various environmental factors, such as light and nutrients, of which daily irradiance (migration to optimal light conditions) is of major importance (e.g. Hasle 1950). The absolute swimming speeds of dinoflagellate cells range from <0.1 mm s^{-1} to >6 mm s^{-1} and thus permit daily migrations over a distance exceeding several meters (Kamykowski & McCollum 1986, Levandowsky & Kaneta 1987). Cell size and swimming speed are generally related, i.e. larger cells are faster than smaller ones. Small-scale phototactic (Lassus et al. 1990, Figueroa et al. 1998) migration has been recorded in *Dinophysis* spp., but there is no evidence of migration triggered by other factors. Kononen et al. (2003) recently reported that a deep-water chlorophyll maximum in the northern Baltic was due to vertical migration of the bloom-forming, mixotrophic (Legrand et al. 1998, Litaker et al. 2002) dinoflagellate *Heterocapsa triquetra*. They assumed that the *H. triquetra* population at the surface had experienced a situation in which an unbalanced N:P ratio after an upwelling event had provided the productive water column with phosphate. Consequent-

ly, the nitrogen-depleted *H. triquetra* population migrated from the euphotic zone down to the top of a nitracline at a depth of 30-35 m, where only <0.1% of the surface illumination was available, and stayed there for 3-6 days. The reason for such a prolonged migration was thought to be renewal of nitrogen reserves.

Mixotrophy in the genus *Dinophysis* has been a subject of controversy. Evidence for mixotrophy in photosynthetic *Dinophysis* spp. includes findings of food vacuoles (Jacobson & Andersen 1994) and high carbon uptake rates in the dark (Granéli et al. 1997). Mixotrophy has also been used to explain the inconsistency between the measured photosynthetic efficiency and growth rates (Gisselson et al. 2002). Further, the failure to establish true cultures of *Dinophysis* species supports the idea that photosynthetic *Dinophysis* species are obligate mixotrophs, which need some additional compound lacking in the culture media so far used.

During the summer of 2002, studies were conducted on the photosynthetic activ-

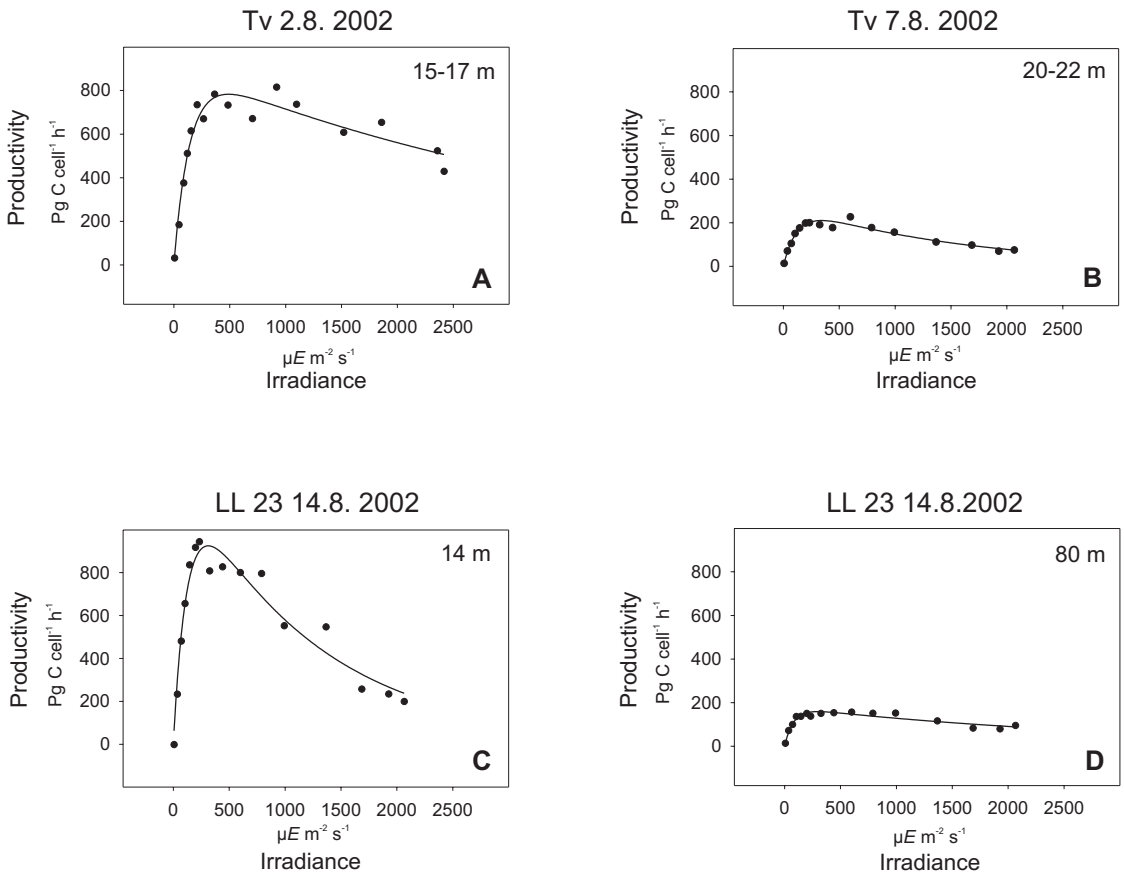


Figure 8. Photosynthetic carbon uptake rate of different Baltic Sea *Dinophysis acuminata* populations in August 2002. A and B = Tvärminne Storfjärd C and D = LL 27 (paper III).

ities of *D. acuminata* populations from the thermocline layer at various localities and from the nitracline (75-80 m) at one station in the Gotland Sea (paper III). These measurements showed photosynthetic activity in all the populations studied, but with differences in their photosynthetic carbon uptake rates. Photosynthesis of the *D. acuminata* populations was saturated at light levels between 250 and 500 μE m^{-2} s^{-1}, resulting in maximum cell-specific carbon uptake rates (P_m) between 160 and 925 pg C $cell^{-1}$ h^{-1} (Fig. 8). The maximum photosynthetic rates of the cells originating from below the thermocline, and of one artificially darkened population from the thermocline, were markedly lower than those of the populations originating from upper water layers. This discrepancy in maximum photosynthetic rates was most likely due to the cells' recent history, e.g. the time spent in different light environments.

On the basis of the information available on dinoflagellate swimming speeds in general and the results of the photosynthetic efficiency of *D. acuminata* populations, it was estimated that the *Dinophysis* spp. communities of the thermocline region would be able to migrate upwards to photosynthesize on a diurnal basis (paper III). However, no such pattern has been observed in the Baltic Sea *Dinophysis* spp. (studies on *Dinophysis norvegica*; Carpenter et al. 1995, Gisselson et al. 2002). If the photosynthetic *Dinophysis* spp. in the Baltic Sea were able to perform prolonged migrations such as those noted in *Heterocapsa triquetra* (Kononen et al. 2003), the reason for their "visit" to deep water layers might also be the renewal of nutrient reserves.

The grazing impact of planktonic ciliates in the open sea areas of the northern Baltic may at times be of major importance, but it shows marked variations both spatially and seasonally (paper I)

The results presented in paper IV demonstrated that different ciliate species had different feeding strategies, and suggested that generalizations about ciliate feeding should be treated with caution. Further, evidence exists that variation in growth and grazing parameters among populations or clones of the same species can be of the same magnitude as the variation between different, closely related ciliate species (Weisse & Montagnes 1998, Weisse 2002). However, in order to estimate the impact of diverse ciliate communities, some generalizations have to be made, as was done in paper I, in which the dataset was used to estimate the clearance efficiencies of these communities. The size-specific clearance rates given in paper IV were combined with additional published data, and a size-dependent equation of ciliate clearance was produced (Fig. 9; present-

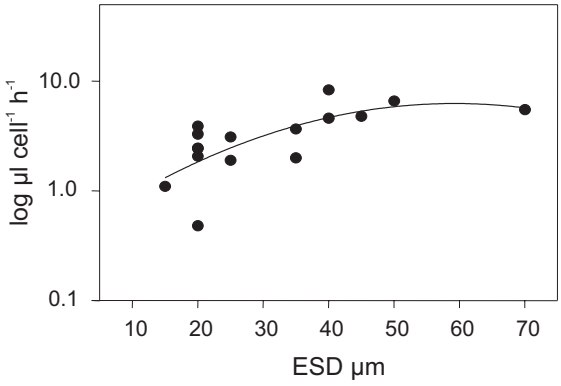


Figure 9. Experimentally obtained ciliate clearance rates (log µl $cell^{-1}$ h^{-1}) vs. ciliate ESD (estimated spherical diameter) (paper I).

ed in Kivi 1996). Application of this equation to the dataset given in paper I provided estimates of the total community clearance.

According to these estimates, the ciliate communities may be significant grazers of pico- and nanoplanktonic communities. Ciliate abundances at five open-sea stations were found to range from about 7 to 10 × 10^3. The communities were dominated by small (ESD £30 µm) species, which were thus also responsible for most of the grazing. The daily community clearance rate varied considerably between stations and depths, being in general higher in 1990 than in 1988. It was further estimated that in 1988 the ciliate community was able to clear close to 50 % of the water volume daily, whereas in 1990 the highest clearance rate amounted to 125 % daily. The grazing control of ciliate communities on lower trophic levels was thus different in these two years. In 1988, ciliates were probably not controlling the pico- and nanoplankton communities with their low (average 21 %) community clearance percentage. In 1990, however, the control was tighter (average community clearance 52 %). The estimates of community clearance efficiency are consistent with data collected from other marine temperate waters, where ciliates are estimated to consume from 20 % to >100 % of daily primary production (Heinbokel & Beers 1979, Capriulo & Carpenter 1980, Andersen & Sørensen 1986, Paranjape 1987).

Oligotrich suspension-feeding ciliates exhibit a variety of species-specific feeding patterns and thus constitute a diverse functional group in terms of grazing characteristics (papers IV and V)

Species-specific differences in clearance efficiency and the prey size selectivity of natural ciliate communities were studied in paper IV. The use of wheat starch particles in grazing experiments permitted simultaneous measurements of these parameters to be made in nine oligotrich ciliate species that play a key role in the summer microprotozoan communities of the northern Baltic Sea. The clearance rates of all the oligotrichs studied in paper IV ranged from 1.1 to 6.6 µl $cell^{-1}$ h^{-1}. The corresponding clearance rates of the most popular particle size were higher (1.9-11.4, Table 2). With the exception of one species (*Strobilidium* sp. 40 µm), the largest species (*Strombidium spiralis*, *Strombidium conicum* and *Tintinnopsis lobiancoi*) also had the highest clearance rates.

Table 2. Clearance rates of different ciliate species (µl $cell^{-1}$ h^{-1}). C_t average clearance rate on the whole species-specific particle spectrum; C_p average clearance rate on the most popular particle size (paper IV).

Species	C_t	C_p
Lohmanniella oviformis	3.3	5.3
Strobilidium sp. 40 µm	4.6	10.1
Strobilidium spiralis	6.6	11.4
Strobilidium sp. 20 µm	3.9	7.5
Strobilidium spp. 25 µm	3.1	5.5
Strombidium conicum	3.7	8.1
Tintinnidium fluviatile	1.1	1.9
Tintinnopsis beroidea	1.9	8.4
Tintinnopsis lobiancoi	4.8	5.8

The volume-specific clearance rate of a filter feeder measures its ability to compete for food resources. This ability, however, varies among ciliates, depending on their feeding mechanisms. In general, it can be expected (at least when comparing ciliates with similar feeding modes) that the larger the cell, the higher is the clearance rate (Bernard & Rassoulzadegan 1990). Such was the case in the grazing study on starch particles (paper IV), in which a statistically significant correlation ($p < 0.01$) was found between ciliate biomass and clearance rate in the whole particle range. The biovolume of a ciliate affects not only the volume of water it is able to filter but also the size of the prey it selects (see ciliate feeding and food selection from page 9 onwards). However, paper IV showed that the preference for prey of a certain size did not depend directly on the size of the grazers. Two different feeding strategies were noted: specialistic, in which the ciliates fed on a narrow particle size spectrum, and generalistic, in which the particles used covered a wider size range. Of interest is that the aforementioned *Strobilidium* sp. (40 µm) ingested particles up to 26.6 µm in diameter, and that the preferred prey size was 9.8 µm, whereas the larger *Strobilidium spiralis* (cell size 40-60 µm) had the highest observed preference for particles of a certain size (5.6 µm) and did not ingest particles >16.8 µm. Of the tintinnids, the smaller species, *Tintinnopsis beroidea* and *Tintinnidium fluviatile,* preferred small prey, whereas the larger *Tintinnopsis lobiancoi* was able to ingest a wider particle size spectrum (Table 3).

Table 3. Ingested particle size ranges (R) for different ciliate species and the most popular particle sizes (P) (paper IV).

Species	R (µm)	P (µm)
Lohmanniella oviformis	1.4 – 11.2	5.6
Strobilidium sp. 40 µm	1.4 – 26.6	9.8
Strobilidium spiralis	1.4 – 16.8	5.6
Strobilidium sp. 20 µm	1.4 – 5.6	2.8
Strobilidium spp. 25 µm	1.4 – 9.8	5.6
Strombidium conicum	2.8 – 25.2	4.2
Tintinnidium fluviatile	1.4 – 8.4	4.2
Tintinnopsis beroidea	1.4 – 8.4	4.2
Tintinnopsis lobiancoi	2.8 – 23.8	5.6

The case study on the feeding of one *Strombidium* species on the dinoflagellate *Pfiesteria piscicida* raised interesting questions about interactions between these two species (paper V). First, the clearance rates as a function of prey density did not follow the type-II response (see section Functional response and Fig. 3, p. 18), according to which the clearance rate decreases continuously as prey abundance increases. The measured clearance rates of *Strombidium* sp. were lower at the lower end of the range of *Pfiesteria* concentrations than at higher prey concentrations, indicating a feeding threshold. The interactions between these two species were also interesting in that they indicate that the presence of a predator may affect prey density through some other mechanism than feeding. This was found when data from direct observations of ingested *Pfiesteria* NTZ were compared with values of total NTZ loss from the experimental water, and ingestion was found to represent only a fraction of the total NTZ loss in the presence of ciliates. It was concluded that there must have been other, grazer-related factors affecting the disappearance of *Pfies-*

teria. The loss of *Pfiesteria* cells might possibly be attributed to disturbance in the water caused by the actively swimming (and filtering) ciliates. It is also possible that *Pfiesteria* zoospores were able to sense the ciliates, and rapidly encysted to escape predation. Flagellated stages of *P. piscicida* are known to be very sensitive to physical disturbance (Burkholder & Glasgow 1997b), which induces encystment of the zoospores within a short period.

In general, estimates of the clearance rates of planktonic suspension-feeding ciliates range from <1 (e.g. Lessard & Swift 1985, Jonsson 1986) to 84.7 µl $cell^{-1}$ h^{-1} (Capriulo & Carpenter 1980). The clearance rates from the two grazing studies presented in papers IV and V fit well within this range, yet clearly demonstrate that the estimates are species-specific.

Concluding words

Micro-sized phagotrophic protozoans are an essential component of planktonic ecosystems. As is evident from the studies presented in this thesis, their functional role in food webs varies in time and space in many ways. Nevertheless, these miniscule organisms all share certain basic characteristics that clarify their significant role as part of the pelagic ecosystem. Microprotozoans are unicellular. They generally have higher metabolic rates than multicellular organisms, and can thus go through rapid changes in abundance (i.e. under optimal conditions they grow fast). They have a wide variety of feeding mechanisms, which enable them to use very small and/or very large prey (compared with their own size). In addition, mixotrophic microprotozoans are able to use alternative nutritional sources, a characteristic that helps them to survive under unpredictable conditions or to manage in “bad times”. Microprotozoans are efficient grazers and at times able to clear over 100 % of the water column daily. They also serve as good-quality food for metazooplankton, and thus constitute an important pathway of energy and matter from pico- and nanoplanktonic organisms to higher trophic levels.

ACKNOWLEDGEMENTS

This thesis is based on studies conducted at the Tvärminne Zoological station, the Finnish Institute of Marine Research and Horn Point Environmental Laboratory (Maryland, USA) during 1988-2001. For this work I received financial support from the Academy of Finland, the Walter and Andrée de Nottbeck Foundation and the Finnish Environment Institute (FIMR). The English of this thesis was checked by Gillian Häkli.

With a good conscious I put the blame for all this on Professor Emeritus Åke Niemi, who with deceptive innocence suggested that I should take part in a research cruise on the Baltic Sea. That cruise turned out to be a month-long adventure onboard the Soviet R/V Viktor Bugaev. With Seppo Kaitala as our innovative boss, I and my companions, Riitta Autio and Sanna Tanskanen, learned not only a few words of Russian but also many items of practical use, such as how to buy enough supplies for a voyage that long. The memory of that cruise is something I shall cherish as long as I live. Thank you Åke…

The first years of my career as a hydrobiologist I spent at the Institute of Zoology, where endless days went by peering through a microscope trying to figure out what those weird hairballs in my samples were. I was given guidance on that topic by Kai Kivi, who really must have had fun with the surrealistic drawings I kept placing on his desk, desperately hoping that he'd give me a clue. Even though neither of us was often much the wiser, the basis of our fruitful collaboration was created. After moving my desk (it really was small but even so there was actually no room for it) to the Laboratory of Hydrobiology in Fabari I enjoyed coffee table discussions with Riitta Autio, Jan Ekebom, Maria Ekman-Ekebom, Riggert Munsterhjelm, Pimma Åhman and Jouko Rissanen. With particular fondness, I remember the bizarre discussions that were held in the room of Heikki Salemaa, our warm-hearted teacher.

I first made contact with the biology department of FIMR in the late 1980s. All that I know about identifying planktonic creatures that have more than one cell but still fit nicely onto a teaspoon has been learned from Kalle Purasjoki, Soili Saesmaa and Ilppo Vuorinen. Thanks to Anne Heinänen I had the opportunity to study ciliate samples from the Baltic Proper in 1988, including the deep ones. I am grateful to Maija Huttunen and Seija Hällfors, both of whom showed great forbearance in helping me with phytoplankton problems. Likewise Jukka Seppälä and Pasi Ylöstalo gave their helping hand to me on several occasions. Thank you all in the department of biology for making me feel welcome when I came up to the fifth floor.

During the five years I spent with the research project SILMU, I enjoyed working with Harri Kuosa and the rest of our group, a.k.a. Harri's Angels. I still don't think that HK blue is at its best fried in deep fat but, thanks to Harri, I've seen practically every single James Bond and Arnold Schwarzenegger movie available on VHS at that time in the course of our winter research field sessions... Harri Kuosa became my supervisor when SILMU got under way, and ever since has backed me up in all my endeavours in the field of plankton ecology. Without his patient, sometimes rather sarcastic, support, this adventure would surely have ended much earlier and not so happily. Our meandering discussions on protist ecology and rock were a rewarding and enjoyable experience.

During the years I worked with them, the magnificent staff of the Tvärminne Zoological Station made every effort to ensure that things ran smoothly. The laboratory technicians Elina Salminen, Mervi Sjöblom, Ulla Sjölund and Bebbe Åström patiently helped me in every possible way. Without them, many obstacles would have been that much harder to overcome! My special thanks go to Lallu Keynäs, whose nerves at times must have been made of rubber. I am deeply grateful for the assistance she gave me with microscopes and, indeed, equipment in general.

Since transferring to SYKE, I have had the pleasure to work with a bunch of people from the PELAG project: Timo Tamminen, Purjo Kuuppo, Ripsu Lignell, Pirjo Tuomi, Kai Kivi and Sanna Sopanen. Working with them and later, after moving downstairs, with the rest of the gang at the East End of the second floor has been a lot of fun. I thank everyone in the ITO group for creating such a good spirit, and especially I thank Saara Bäck, Pekka Kotilainen, Heikki Peltonen, Pekka Punttila (a hang-around member) and Antti Räike for their support and "inspiring company", which is demonstrated in the number of solved crosswords (not quite entirely by me).

The four months I spent at Diane Stoecker's Lab at Horn Point in 2000 were essential in pointing the direction in which I should continue my work. A big hug to Diane for being such a wonderful herself! Working with Diane, Dan Gustafson and Matt Johnson was of course great fun but it also gave Riitta and me insight into a different way of doing experimental work and set the MIXO project in motion. I would like to say a big thank you to Janne Rintala and Jonna Piiparinen for keeping everyone's spirits up during fieldwork sessions onboard R/V Aranda and at Tvärminne.

During the last few years I have managed to struggle with my work with the caring support of my friends Riitta and Pimma. You both know what your role in this venture has been. I also thank Sanna, who has shared a room with me and put up with my mumblings and need to listen to music while trying desperately to work herself, and Purjo who helped me put this whole package together.

I also thank the Setälä family (especially the rap granny of my two boys) for their help on many occasions and for not questioning whether or not this whole thing really made any sense.

Real life at home is my power generator. With the love of Jakke, Niko and Pohti, my dear mental backbone, I was able to keep my feet on the ground and gain a wider perspective on an undertaking that at times threatened to turn into a monster.

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